

Chapter 2

Evolutionary History of the Large Herbivores of South and Southeast Asia (Indomalayan Realm)

Faysal Bibi and Grégoire Métais

Abstract Modern day South and Southeast Asia falls almost entirely within a single biogeographic region, the Indomalayan Realm. Here, we review the Cenozoic geological and environmental history of the Indomalayan Realm, and the evolutionary history of the large herbivorous mammals that have inhabited it. For the most part bounded by major physical features, the cohesiveness of the Indomalayan Realm in its mammalian faunas can be recognized as far back as the middle Miocene or even earlier. Many of the extant large herbivores of the Indomalayan Realm have a diverse fossil record in this part of the world, though a few, such as cervids, are relative newcomers. Many extant clades that are not currently present in the Indomalayan Realm had records in the region up to the Pleistocene, including giraffids, hippopotamids, and reductant antelopes. The island archipelago of Southeast Asia in particular witnessed radiative speciation of numerous clades including proboscideans and ruminants, at least through the climatic cycles of the Pleistocene, if not earlier. If there is a single common thread to the evolutionary history of Indomalaya's large herbivores, it may be the loss of taxonomic diversity, with much greater taxonomic representation recorded at numerous times in the past in almost all large herbivore clades. Today, diversity loss continues at the hands of anthropogenic, rather than natural, environmental causes, which threaten to violently curtail millions of years of evolutionary heritage.

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2.1 Introduction

The region is of comparatively small extent, but it has a very diversified surface, and is proportionately very rich.

So begins Wallace's (1876) chapter on the Oriental Region, a geographic area characterized by a cohesive assemblage of birds, mammals, reptiles, and insects that differentiates it from the rest of Asia to the north, Australasia to the southeast, and Africa and Arabia to the west. As the smallest of the world's six main continental biogeographic regions, the Indomalayan Realm (as it is now better known, Udvardy 1975) is not to be underestimated as a center of global biodiversity, both present and past. In terms of large herbivores, the Indomalayan Realm is three times as rich in species as the Neotropics, which is twice as large in area, and almost as rich in species as the Afrotropics, which is three times as large in area. Its smaller size is also no indication of its animal diversity—three of the world's most recently discovered large mammals, the kouprey, the saola, and the large antlered muntjac have come from the Indomalayan area. The saola was only described in 1992 (Dung et al. 1993), indicating that even in the late twentieth century, large animals entirely unknown to the outside world were still to be found in little explored stretches of Southeast Asian forests. More recent but no less spectacular, the discovery of the living Laotian rodent *Laonastes aenigmamus*, nowadays restricted to the rugged Annamite Mountains (Lao People's Democratic Republic) that turns out to be a surviving member of a clade (Diatomyidae) that was formerly believed to have been extinct for more than 11 million years (Dawson et al. 2006).

Though names have changed, Wallace's faunal regions have remained much the same as when he defined them over 100 years ago (though see Holt et al. 2013, for a recent update, including newly defined Saharo-Arabian and Sino-Japanese realms, and an Oriental-Oceanian boundary east of Sulawesi). With the notable exception of Afghanistan, modern South and Southeast Asia (SSEA) falls almost entirely within the Indomalayan Realm (Fig. 2.1). In discussing the late Cenozoic evolution of this region's large herbivores, the distinctiveness of the Indomalayan faunas is a principal theme, namely because the physical and climatic barriers to dispersal that account for this region's cohesive character appear to have been in place since at least the middle Miocene, if not even earlier (e.g., Wang et al. 2013).

The fossil record of the Indomalayan region is as impressive as its living faunas. A large number of fossil sites are known from throughout SSEA that record the Eocene to Holocene evolution of the modern physical, vegetational, and faunal characteristics of the region. Many of the extant large herbivores in SSEA have fossil records indicating a long period of presence and evolution in the region (e.g., bovids, tragulids). Others, though well established in SSEA today, are relative newcomers to the region (e.g., cervids). Yet other clades have far more complex histories than indicated

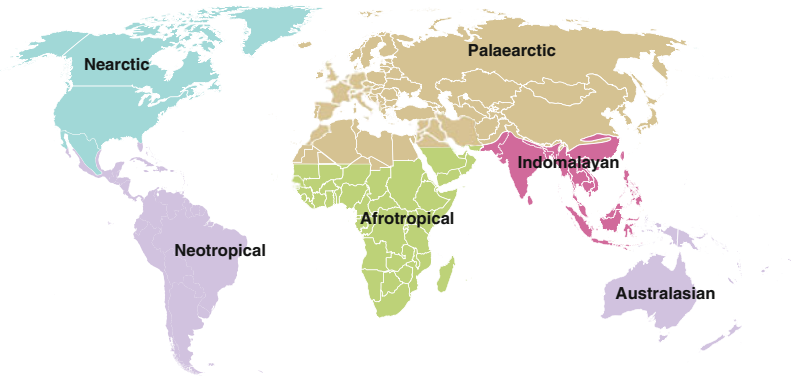


Fig. 2.1 Terrestrial Realms of the world. SSEA falls almost entirely within the Indomalayan Realm. Exact realm boundaries differ among different sources (modified from Wikimedia Commons, user *Lokal_Profil*, CC-BY-SA-2.5)

by their living representatives (e.g., proboscideans), and there are fossil taxa that are entirely absent from the region today (e.g., giraffids, hippopotamids).

The evolutionary history of the large herbivores of SSEA is a large topic, and no single paper can do justice to the immense wealth of geological, paleontological, archaeological, zoological, and genomic information on the subject. In what follows, we present some basic geological background to the development of the modern SSEA landscape (Sect. 2.2); followed by some of the broader scenarios of large herbivore evolution (Sect. 2.3), particularly regarding the emergence of present day climatic and geological configurations and the continuous interplay of environmental change and faunal evolution in the region (Sect. 2.4); an introduction to some of the main fossil deposits of the region yielding large herbivores (Sect. 2.5); and summaries of the main evolutionary features of the large herbivore clades of the Indomalayan Realm, both living and extinct (Sect. 2.6). We end with a brief consideration of SSEA's past, present, and future biodiversity (Sects. 2.7–2.8).

2.2 Geological Background

2.2.1 Physical Boundaries

The Indomalayan Realm is bounded by prominent physical barriers, topographical features resulting from the collision of the Indian Subcontinent with Eurasia during the early Cenozoic and the subsequent uplift of the Tibetan Plateau. The Indomalayan and Palearctic Realms are separated by the Himalayan mountain chain, its tectonic tributaries to the west, and a complex transitional zone around the Yangtze River (Xie et al. 2002), that was established synchronously with the uplift of the eastern Tibetan Plateau (Zheng et al. 2013). The main geographical,

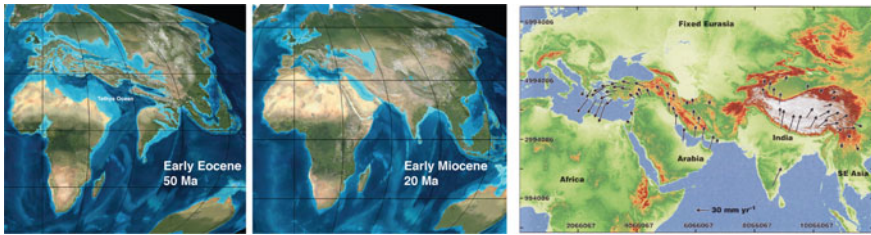


Fig. 2.2 Collision of Afro-Arabia and India with Laurasia during the Cenozoic, with closure of the Tethys Ocean and the formation of stable land bridges between southern and northern continents by 20 Ma, and the continuing development of the Himalayan-Alpine mountain belt thereafter (paleomaps from Blakey 2008, tectonic map from Edwards and Grasemann 2009)

topographical, and structural feature of SSEA is the Himalayan mountain chain, being the largest and highest mountainous zone on the planet, the Cenozoic history of which has greatly influenced the landscapes, climate, and evolutionary history of mammalian communities of the region. The Himalayas form part of the 10,000 km-long Alpine-Himalayan belt, which includes the European Alps, the Zagros Mountains of Iran, and the Indo-Burmese mountains, stretching from Spain to Indonesia, and that formed as a result of the closure of the Neotethys Ocean over the past 180 million years (Fig. 2.2).

2.2.2 *Closure of the Neotethys Sea and the Formation of the Mountain Chains of Southern Asia*

The closure of the Neotethys is the result of the breakup of the supercontinent of Gondwana from the early Jurassic onwards, and the associated northward movement of the Indian and Afro-Arabian plates, which began to collide with Eurasia by the middle Paleogene, or around 35 Ma (Allen and Armstrong 2008). The Alpine-Himalayan collision system, resulting from the closure of the Neotethys (its western part represented by the closed residual Mediterranean Sea) consists of high mountain chains and great plateaus that were formed during the Cenozoic. The Turkish–Iranian and Tibetan are the two great plateaus that were uplifted as a result of the closure of the Neotethys and subsequent continental collision (Şengör and Kidd 1979). The final closure of the Neotethys Ocean during the early Neogene triggered intense crustal deformation, with faulting and folding to accommodate major compressional forces that resulted in the high elevations and sharp topographic relief of much of southern and central Asia.

While the Alps, Zagros, Himalaya, and Indo-Burmese mountain chains are products of the same broad geodynamic process (i.e., closure of the Neotethys), the mode and timing of this process vary along the wide belt. Here, we focus on the two main areas where the disappearance of the Neotethys Ocean and the subsequent intercontinental collision have greatly shaped the topography and climate of southern and southeastern Asia (Popov et al. 2004).

2.2.3 *Collision of the Afro-Arabian Continent with Eurasia*

The collision of the Afro-Arabia plate with Eurasia has shaped the Western border of the Indomalayan Province and conditioned the land connection with Eurasia. The Indo-Pakistan plate is bounded by the Chaman-Ornach-Nal left lateral transform fault system and the Makran accretionary prism related to the northward subduction of the Arabian Sea lithosphere (Bender and Raza 1995). This collision brought about the gradual closure of the Neotethys Ocean through northward subduction of oceanic lithosphere, producing the Urumieh-Dokhtar volcanic arc in Iran (Dewey et al. 1973) and the Chagai volcanic arc along the Pakistan and Afghanistan borders (Nicholson et al. 2010). Around the same time, at about 25 Ma, a new oceanic basin, the Red Sea, was formed as Arabia began to separate from Africa, and seismically.

Reconstructing the history of the closure of the Neotethys requires various sources of data that sometimes lead to contradictory conclusions, and geological structures such as the Zagros orogen or Anatolian crustal faults can be variously interpreted. Consequently, controversy surrounds the exact sequence of events and the timing of continental collision. Plate kinematic reconstruction (Van Hinsbergen et al. 2009) shows that during the early Cenozoic (ca. 56 Ma) the Tethyan oceanic basin was ca. 1300 km wide, while the Tethys Ocean itself was wider still as it covered much of the Arabian carbonate platform (Fig. 2.2). The Tethyan oceanic basin gradually narrowed through the Cenozoic, eventually closing and disconnecting the Indian and Atlantic Oceans from each other. The exact timing of this disconnection, however, is controversial. Oceanographic, plate tectonic, and climatic modeling studies as well as stable neodymium isotope data indicate the persistence of a marine connection between the Indian and Atlantic oceans through a residual Tethyan seaway well into the middle Miocene (Stille et al. 1996; McQuarrie et al. 2003). Geological evidence, however, indicates an initial collision of the submerged Arabian and Eurasian plate margins during the Late Eocene (ca. 35 Ma, Allen and Armstrong 2008), and marine faunal evidence indicates the progressive creation of separate Mediterranean and Indian Ocean marine realms shortly thereafter (Harzhauser et al. 2002, 2007). Both bivalve and gastropod assemblages show biogeographical divergence and two separate Tethyan sub-provinces during the Oligocene, with a greatly increased endemism during the early Miocene (Harzhauser et al. 2002, 2007). The collision of submerged continental margins did not immediately result in the formation of continental land bridges between Arabia and Asia. Late Oligocene mammals from Ethiopia indicate the seaway was still a barrier to terrestrial mammals at 27 Ma (Kappelman et al. 2003), but a major influx of Eurasian mammals into Africa around the Oligocene–Miocene boundary (23 Ma) indicates that a secure land connection between Afro-Arabia and Eurasia had developed by this time (Bernor et al. 1987).

The closure of the Neotethys resulted in the disruption and reorganization of global oceanic current systems, and this certainly contributed to the elevated global temperatures that characterized the Middle Miocene Climatic Optimum (MMCO) event at 17–15 Ma (Flower and Kennett 1994). This interval of global warming,

detected in both marine and continental sediments, was marked by a 3–4 °C increase in global temperature (You et al. 2009).

2.2.4 Collision of the Indian Subcontinent with Eurasia

The Himalayas provides a classic example of the collision of two continental plates (e.g., Molnar and Tapponnier 1977; Yin 2010). The northward movement of the Indian plate can be reconstructed through magnetic anomalies on the Indian Ocean floor (Patriat and Achache 1984). Continental collision of India into Asia from the Eocene to the present day has resulted in major crustal shortening and thickening that has produced the Himalayan and Tibetan Plateau.

The tectonic evolution of the Indian plate, which traveled around 9000 km in 160 million years, is largely the story of its separation from Gondwana and its subsequent collision with the Kohistan-Ladakh Arc and Asia. By the start of the Cenozoic (65 Ma), the Indian Subcontinent had become an island continent entirely separated from Africa and Antarctica. Blazing northwards at a geologically rapid rate of ca. 20 cm/year, the Indian plate began its collision with Asia during the Early Eocene (ca. 50 Ma), slowing its rate down to 5 cm/year thereafter (Copley et al. 2010; Chatterjee et al. 2013). Most data suggest that the India-Eurasia continental collision began near the Paleocene-Eocene transition (ca. 55 Ma, Beck et al. 1995), and sedimentary deposits eroded from the rising Himalayas date back to the Middle–Late Eocene epoch (49–34 Ma), providing evidence for early mountain building (Najman et al. 2001; Zhuang et al. 2015). With the continuing convergence of India with Asia through the Paleogene, the northern edge of the Indian plate was fractured, thrust, and uplifted, resulting in the formation of the Himalayas. The Higher, Lesser, and Sub-Himalayas are thus slices of the old Indian shield that have been stacked over each other along a series of southward verging thrusts. Fully, one third of the original Indian plate was subducted beneath Asia during the initial phases of collision and now lies buried beneath the Tibetan Plateau (Guillot et al. 2003). For roughly a million square kilometers beneath the Tibetan Plateau, the crust is about twice as thick as the average continental crust (Mattaueer et al. 1999; Van der Voo et al. 1999).

2.2.5 Climatic Implications of Himalayan Uplift

Over long time scales, geography and topography and atmospheric circulation interact to produce major climatic patterns (Ruddiman 1997, e.g. Molnar et al. 2010), and the Indomalayan region is one in which the interactions between physical processes and biotic feedbacks are plain to see. The South and East Asian monsoon systems are major climatic features of the Indomalayan region that have shaped vegetation and biodiversity over many millions of years. Monsoons are

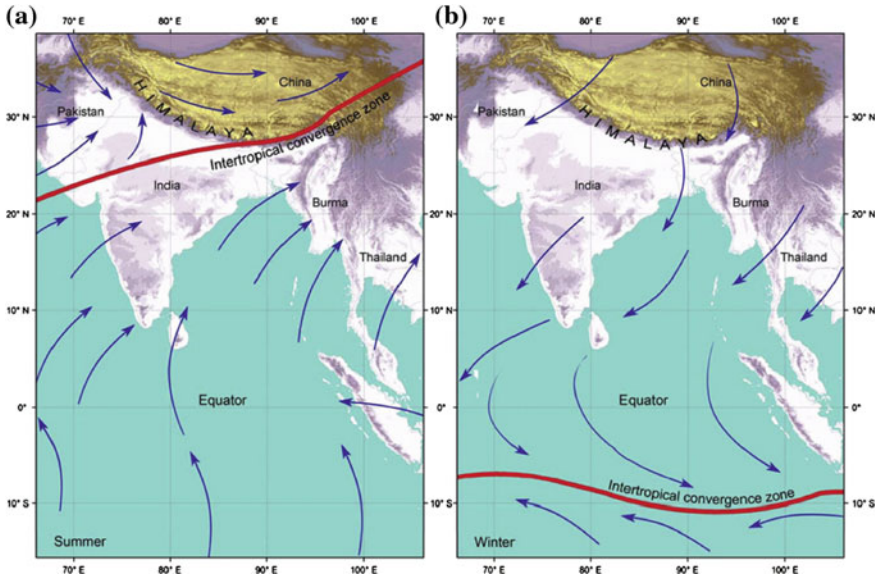


Fig. 2.3 The climate of southern and SE Asia is dominated by monsoon winds, which are related to the uplift of the Himalaya-Tibetan Plateau. **a** Summer winds from the southwest carry moisture from the Indian Ocean and bring heavy rains from June to September. **b** Winter winds blow from the northeast and carry little moisture. Temperatures remain high as the Himalayan mountains prevent cold air from passing southwards into the Indian Subcontinent (from Chatterjee et al. 2013)

strong onshore and offshore winds that are produced by differences in heat capacity between land and water (Fig. 2.3). In winter, the Himalayas and the Tibetan Plateau become cold, which cools the air above them. This cool, dense air descends and flows toward the Indian Ocean and displaces the warmer air there. In summer, the mountains and plateaus heat up, causing the air above them to rise and draw strong winds, the summer monsoons, in from the Indian Ocean. Sweeping northward from the Bay of Bengal, the Indian summer monsoon strikes the eastern Himalayas with great force, producing a tropical depression and torrential rain. This seasonal climatic pattern has profoundly shaped landscape and vegetation, and therefore the habitats of animals in the region.

When this monsoonal regime got started, and how it varied through the Cenozoic remain open questions. The age of inception of the South and East Asian monsoons remains controversial but a variety of environmental indicators suggest that the East Asian monsoon, at least, was established during the late Eocene (Licht et al. 2014) with an intensification by the start of the Miocene (ca. 24 Ma, Sun and Wang 2005), probably correlated with a period of major uplift. Interestingly, the marine climatic record suggests a breakdown of Indian monsoonal seasonality over the Himalayas and southern China between 17 and 15 Ma ago during the Mid-Miocene Climatic Optimum (MMCO) (You et al. 2009). However, this temporary disruption of Indian monsoonal intensity is not reflected in palynological

data from southern India, which instead indicates modern-like temperature and precipitation cyclicality with only slightly reduced rainfall seasonality during the MMCO (Reuter et al. 2013). Palynological assemblages from different late Oligocene to Miocene localities of northern Thailand (Sepulchre et al. 2010) reveal a major climatic reorganization occurring near the Oligocene–Miocene transition, and significant vegetational variability during the Miocene, suggesting further parameters controlling climate and paleo-environments there. This Oligocene–Miocene climatic transition is also documented in loess sequences, fossil leaves and pollen records from China that show that the transition from a mainly zonal to a monsoon climate system occurred in the latest Oligocene in East Asia (Sun and Wang 2005; Guo et al. 2008). Moreover, fossil floras from southern China suggest a climatic differentiation of southern China (warm and humid) versus the rest of China (greater seasonality) during the Miocene (Yao et al. 2011). This may indicate the early differentiation of the northeastern limit of the Indomalayan Realm as directly related to the strengthening of the monsoonal system.

At an average elevation of 5000 m, the Tibetan Plateau, bounded to the north by the Kunlun Shan, Altyn, and Qilian mountains, and to the south by the Himalayas, forms a major topographic barrier to atmospheric flow between southern and Central Asia. The mountains and highlands forming the Tibetan Plateau dramatically affect continental albedo and atmospheric energy balance, stimulate intense seasonality on their southern slopes, and produce a massive rain shadow on their leeward (northern) slopes. The Tibetan Plateau has been an important contributor to long-term Cenozoic cooling, at both local and global scales, as well as to Northern Hemispheric glaciation (Hay et al. 2002). Rapid uplift of the surface topography of the Higher Himalaya by 8 Ma coincides with a substantial increase in precipitation and erosion of rising mountains as revealed from deep-sea sediments in the Bay of Bengal (Ganges-Brahmaputra drainage) and the Arabian Sea (Indus drainage) (Prell and Kutzbach 1992). According to Clift (2008), the intensification of monsoons 8 Ma ago (producing increasing erosion) may have been triggered when the Tibetan Plateau reached a threshold height of 2000 m. This period also records enhanced aridity in the Asian interior, and the onset of Indian and East Asian monsoons (An et al. 2001; Patnaik et al. 2012). Further uplift of the Himalayas and the Tibetan Plateau in the Pliocene also resulted in enhanced aridity in the Asian interior (Gobi and Mongolian deserts) (Ramstein et al. 1997; An et al. 2001), as evidenced by the deposition of extensive eolian (loess) deposits in central and eastern China at about 2.5 million years ago (An et al. 2001).

Though the inception and strengthening of the Indian-Asian monsoon system is classically linked to the uplift of the Tibetan Plateau during the Neogene (Prell and Kutzbach 1992; Clift and Plumb 2008), simulations show that a monsoon-like climatic regime existed during the Eocene regardless of the exhumation of the Tibetan Plateau (Huber and Goldner 2012). Models of early monsoonal dynamics have highlighted the role of several parameters that are often neglected in previous reconstructions of the monsoon's history, such as sea-surface temperature and greenhouse gas concentration (Huber and Goldner 2012; Licht et al. 2014).

Likewise, the opening and closure of oceanic gateways as a result of continental plate motions and related changes of ocean-atmosphere circulation probably had a major effect on global climate. For example Ramstein et al. (1997) and Fluteau et al. (1999) stressed the combined role of the closure of the Tethys and the retreat of the Paratethyan epicontinental sea (both occurring around the time of the Eocene–Oligocene transition) in the formation of large-scale patterns of monsoonal climate, at least as much as the influence of the uplift of the Tibetan Plateau (see also Zhang et al. 2007). Further complicating the picture is the fact that the early (Paleogene) history of the Asian monsoon is relatively poorly documented and additional data are needed to test large-scale paleoclimatic interpretations based on model simulations. It remains clear, however, that atmospheric circulation in the absence of the Himalayas and Tibetan Plateau would have been very different from what it is today.

2.3 Environment and Evolution

2.3.1 *Modern Climates and Herbivore Habitats*

The relationships of temperature, precipitation, and seasonality go a long way toward explaining the vegetational characteristics of any region on earth. Except at high altitudes, modern SSEA is characterized by the presence of a warm climate year-round. Precipitation in its northern areas from (Pakistan to Bangladesh and Myanmar) is monsoonal and markedly seasonal, with rains falling mainly in summer (June–September) and much of the rest of the year remaining relatively dry. The southern (equatorial) portions of SSEA (mainly Sri Lanka and SE Asia) have less strongly seasonal rainfall patterns, with some places receiving more rainfall during the northern winter (November–February). Much of the vegetational and faunal characteristics of southern Asia from Pakistan to Bangladesh are in turn a product of the monsoonal climate regime, resulting especially in a dominance of drier, more xeric habitats (deciduous forests, woodlands, grasslands) and a much lower proportion of humid forests than in equatorial and southeastern Asia.

Some of the large herbivore species of SSEA can be found living in a wide range of habitats, perhaps most tolerant among these being sambar deer (*Rusa unicolor*) and elephant (*Elephas maximus*). Many species, however, are restricted to humid forested habitats such as the tapir (*Tapirus indicus*), bovids like serows (*Capricornis* spp.) and the saola (*Pseudoryx nghetinhensis*), and cervids such as muntjacs (*Muntiacus* spp.), hog deer (*Axis porcinus*), and tufted deer (*Elaphodus*). The grasslands and dry forests of the Indian Peninsula are home to a range of species more tolerant of drier, more open habitats. Among these are axis deer (*Axis axis*), nilgai (*Boselaphus tragocamelus*), blackbuck (*Antilope cervicapra*), and chinkara (*Gazella bennettii*), the last being particularly well adapted to semi-arid and arid habitats.

2.3.2 The Late Miocene Reduction of Forested Habitats

The fossil record indicates that for much of the Cenozoic, humid forest habitats, today restricted to equatorial regions, covered much of the subtropical and temperate regions of the world. Global temperature reconstructions based on the oxygen isotopic composition of benthic foraminifera retrieved from oceanic drill cores indicate that global temperatures have been gradually decreasing since about 15 Ma (Zachos et al. 2001), or just after an especially warm period known as the Mid-Miocene Climatic Optimum. In SSEA, as in much of the world, the early and middle Miocene fossil record indicates that environments were much more humid and forested than today. The switch to drier, more open habitats is particularly well recorded in the Siwaliks of northern Pakistan, where the fossil ape *Sivapithecus* and other forest taxa had gone extinct by 8.1 Ma (e.g. Nelson 2007) as humid forest habitats fairly rapidly gave way to drier, deciduous forests and grasslands.

Through their finely resolved sedimentary and fossil sequences, the Siwalik deposits of the Potwar Plateau provide one of the world's best records of increasing aridity and increasing seasonality of terrestrial environments since 10 Ma. In particular, the Siwalik geochemical and faunal evidence indicates a transition from wet monsoonal forests before 8.5 Ma, to dry monsoonal forests at 7.0 Ma, to savannah habitats at 6.0 Ma (Badgley et al. 2008), with increasing proportions of grassland species into the Pliocene and Pleistocene (Patnaik 2015). The Siwaliks provided the first paleosol carbon isotopic data indicating a major vegetational replacement of C_3 vegetation habitats by C_4 vegetation in the late Miocene between about 8 and 6 Ma (Quade et al. 1989, 1992; Quade and Cerling 1995), a phenomenon that was later demonstrated to have occurred at many low-latitude locations around the world (Cerling et al. 1997). Barry et al. (2002) found elevated levels of speciation and extinction during this period of major vegetational change (Fig. 2.4). Badgley et al.

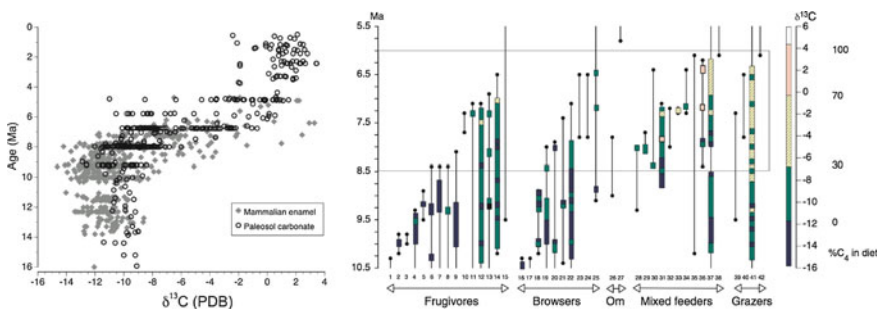


Fig. 2.4 At left, the carbon isotopic shift indicating rapid expansion of C_4 (tropical grass) habitats in northern Pakistan between 8 and 6 Ma as recorded in herbivore tooth enamel and in paleosol carbonates. At right, coincident with C_4 vegetation expansion, Siwalik faunas record a loss of many frugivorous and browsing lineages, and an increase in mixed feeders and grazers. Both panels from Badgley et al. (2008)

(2008) determined that the expansion of grassland habitats negatively impacted forest herbivores the most, with 15 out of 17 browsing and frugivorous lineages going extinct during this time, and while grazing and mixed feeding herbivores also suffered extinctions, these were balanced by an almost equal number of immigrants that preserved this dietary niche. Palynological data from the sub-Himalayan region in Nepal similarly provides evidence for the replacement of forests by grasslands between 8 and 6.5 Ma (Hoorn et al. 2000). A similar loss of humid forest habitats, termed as the ‘mid-Vallesian crisis,’ is recorded slightly earlier in southern Europe (e.g., Agustí et al. 1997, 2003), implicating global-scale climatic changes in the loss of forest habitats through the late Miocene.

2.3.3 *The Pleistocene and Holocene: Extinctions and Insularity*

Another time of great extinction among SSEA large herbivores is the late Pleistocene. The late Pleistocene to early Holocene transition (about 14–10,000 years BP) witnessed the extinction of many species of large herbivores across the globe. In the Americas and Australasia the extinctions were particularly severe, and in these regions and northern Eurasia all species of 1000 kg or greater were lost (Stuart 1999). In contrast, SSEA and sub-Saharan Africa appear to have been less affected, with elephants and rhinoceroses surviving (though just barely) in both regions. Though debate continually rages, the main causes of the late Pleistocene megaherbivore extinctions were probably a combination of human overkill and climate change, but the evidence surrounding extinction events, as well as their timing, varies from continent to continent. In general, there is a good correspondence between the first appearance of humans and the onset of mega herbivore extinctions in North America (11.5–11 ka), South America (15–10 ka), and Australasia (72–44 ka) (Martin 1967; Alroy 2001; Barnosky et al. 2004; Sandom et al. 2014). In contrast, humans or their tool making ancestors (e.g., *Homo erectus*) evolved in Africa, and have also lived in Europe and Asia, including SSEA, since the early Pleistocene, or around 1.8 Ma (Swisher et al. 1994). A popular view holds that the extinctions in sub-Saharan Africa and SSEA were less severe on account of a much older coevolution of humans and fauna (Martin 1966), but human overkill does not explain all the observed extinction patterns (MacPhee 1999; Barnosky et al. 2004; Louys et al. 2007; Campos et al. 2010). Factors such as disease might also have played a role (MacPhee and Marx 1997).

Detailed assessment of extinction severity in the late Pleistocene of SSEA is complicated by a relatively low number of late Pleistocene sites, and poor chronological control at most of these. However, Louys et al.’s (2007) faunal lists show that, though many large herbivore species did disappear, extinctions in the late Pleistocene of Southeast Asia may not necessarily have been more severe than

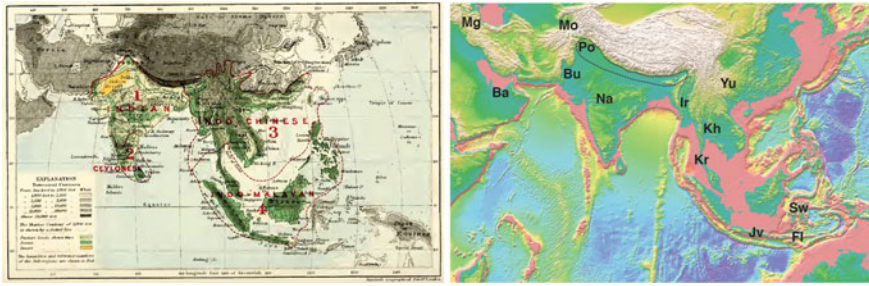


Fig. 2.5 *Left*, the Indomalayan (Oriental) Realm and its provinces, as described by Wallace (1876). *Right*, digital elevation map of SSEA showing the shallowness of the seaway around the Indonesian islands, and the locations of some of the fossil sites mentioned in the text. *Ba* Baynunah, United Arab Emirates; *Bu* Bugti Hills, Pakistan; *Fl* Flores, Indonesia; *Ir* Irrawady Basin, Myanmar; *Jv* Java, Indonesia; *Kh* Khorat, Thailand; *Kr* Krabi Basin, Thailand; *Mg* Maragheh, Iran; *Mo* Molayan and Taghar, Afghanistan; *Na* Narbada Valley, India ; *Sw* Sulawesi, Indonesia; *Po* Potwar Plateau, Pakistan, and encircled in *dotted line* is the extent of the Siwalik deposits of the Indian Subcontinent; *Yu* Yunnan Province, China

during preceding intervals of time. This brings up the question of whether SSEA, like sub-Saharan Africa, experienced a pronounced late Pleistocene extinction pulse at all or whether it was all just ‘evolution as usual.’ If anything, as Louys et al. point out (also Woodruff 2010), fluctuating sea levels throughout the Pleistocene (especially over the last 800 kyr) probably had a much stronger influence in shaping the extant faunas (herbivores included) of southeastern Asia than the last glacial to interglacial transition at the Pleistocene-Holocene boundary (or even a massive volcanic eruption for that matter, Louys 2007, 2012a, b).

Today, the Malaysian Peninsula, Sumatra, Java, and Bali are not separated by any significant stretch of ocean. The great distances between Borneo and the Philippines are deceptive because the ocean separating these islands from each other and from the Asian mainland is shallow, and is in fact an inundated continental shelf rather than a true oceanic basin (Fig. 2.5). With a sea level drop of just 40–50 m the Sunda shelf would be joined such that one could walk from the Malaysian Peninsula to Java and Borneo, and a drop of 120 m would extend an almost continuous dry land connection to parts of the Philippines (Voris 2000; Tougaard 2001; Woodruff 2010), thereby providing regular and easy access for the dispersal of large mammals into the Southeast Asian island archipelago at numerous times during the Pleistocene.

Global sea level rises and falls cyclically (mainly tracking astronomical cycles), but the intensity (amplitude) of these cycles has changed through time. Today, sea levels are at a maximum level that has not changed significantly over the past 4 myr (Fig. 2.2 in Woodruff 2010). However, minimum sea levels have over time become progressively lower, especially with increases in astronomic cyclic variability (causing global cooling and increases in polar ice volume). Cyclical drops of 50 m

or more probably began to take place around 2.7 Ma, reaching 100 m or more on several occasions since *ca* 0.8 Ma (Woodruff 2010). Regardless of tectonic uplift, much of the Southeast Asian archipelago was repeatedly connected to the Asian mainland throughout the Pleistocene, providing an easy route for colonization of these islands. Van den Bergh (1999) and van den Bergh et al. (2001a, b) review the routes and timing of mammalian dispersal between mainland SE Asia and the island archipelago, specifically in the direction of Java. These authors state that, in accordance with the sea level record, early dispersals took place during the Early Pleistocene (after 2.5 Ma), and increased with the formation of land bridges at 0.8 Ma, which was also a time of a major faunal turnover between Early Pleistocene and Middle Pleistocene island faunas.

Indeed, many of the large herbivore species that are restricted to islands appear to have originated from a mainland ancestor during the Pleistocene. Among these are the ‘dwarf’ buffaloes, namely the tamaraw of Mindoro Island (*Bubalus mindorensis*), the mountain and lowland anoa of Sulawesi and Butung islands (*B. quarlesi* and *B. depressicornis*), and the extinct *Bubalus cebuensis* of Cebu (Croft et al. 2006) among other fossil species. Genomic age estimates (Tanaka et al. 1996; Bibi 2013; Hassanin et al. 2013) suggest that the divergence date of the water buffalo (*Bubalus bubalis*) and the lowland anoa was probably between 2 and 1 Ma, implying an early Pleistocene age for the first colonization of these islands by the mainland buffalo. This is in agreement with the fossil record, the oldest indications of buffalo from the modern SE Asian archipelago being *Bubalus palaeokerabau* at 1.2 Ma from Ci Saat in Java (Louys et al. 2007). The Javan Rusa deer (*Rusa timorensis*) of Java and Bali is estimated to have diverged from the sambar (*R. unicolor*) during the middle Pleistocene, or less than 1 Ma (Pitra et al. 2004; Gilbert et al. 2006; Hassanin et al. 2012), suggesting a younger and separate dispersal event than that of the dwarf buffaloes.

Van den Bergh (1999) and van den Bergh et al. (2001a, b), following Thenius (1970), point out one seeming exception to the mainly Pleistocene timing of large mammal dispersal into the Southeast Asian archipelago. The *Babyrousa* lineage, they suggest, may have crossed to Sulawesi and nearby islands from the mainland Sunda Shelf as early as the mid-Oligocene, when a land bridge connection with the mainland may have last existed before the Pleistocene. This would make the babirusa the oldest continuous inhabitant among the large mammals of the Southeast Asian islands. Unfortunately, nothing at all is known of the fossil record of the babirusa prior to the Pleistocene (Hooijer 1948a, b; Hardjasasmita 1987; Groves 2001a, b). Molecular estimates suggesting that *Babyrousa* diverged from Suinae between 18 and 9 Ma (Gongora et al. 2011) might support Miocene colonization of SE Asian islands. The evolutionary and geographic origins of the babirusa lineage, whether on the Asian mainland, on Sulawesi, or on other islands, will have to await further fossil discoveries.

2.4 Paleobiogeography

2.4.1 *Boundaries and Cohesiveness of the Indomalayan Realm*

Much of the evolutionary history of mammals in SSEA reflects a basic biogeographic similarity to the geographic limits of modern Realms dating back to at least the late Miocene. Sclater (1858) and Wallace (1876) classified the world's terrestrial animal faunas into six major zoogeographic regions, with SSEA united as a single Oriental Region (Fig. 2.5), today more commonly known as the Indomalayan Realm (Udvardy 1975). Through several name changes, the basic boundaries of Wallace's biogeographic divisions have remained relatively unchanged in over 100 years (Fig. 2.1). The northwestern and northern limits of the Indomalayan Realm are bounded by the Sulaiman, Hindu Kush, and Himalayan mountain ranges. Comparison of late Miocene faunas from the Kabul basin in Afghanistan indicates almost no similarity to contemporaneous faunas from the Siwaliks only ~300 km to the southeast in northern Pakistan (Brunet et al. 1984; Beden and Brunet 1986; Sen et al. 1997). In contrast, Miocene faunas from Pakistan to Thailand and southern China all share many taxa in common, documenting the coherency of the Indomalayan Realm and its isolation from Central Asia to the north for at least the majority of the Neogene. The reasons for biogeographic differentiation in the Miocene may be similar to those today, namely elevated mountain chains and associated latitudinal climatic and environmental differences. Environmental conditions in the Molayan fauna (ca. 8–7 Ma) of the Kabul Basin indicate the presence there of a relatively open and dry sclerophyllous shrubland, but one that was composed entirely of C₃ vegetation (Zazzo et al. 2002; Merceron et al. 2004), in stark contrast to the C₄ grasses that had begun to take hold at this time in northern Pakistan and SSEA. Today, C₄ grasses are widespread in areas that are hot and receive a summer rainy season, such as tropical seasonal and monsoonal environments. In contrast, C₃ grasses dominate in areas receiving winter rains (e.g., Mediterranean biomes), and at higher latitudes and elevations.

To the northeast, the boundaries of the Indomalayan Realm do not overlap cleanly with major physical or political boundaries. While China for the most part harbors vegetation and animal assemblages different than those in SSEA, biogeographic zonation distinguishes southern China (i.e., south of about 29° N) as part of the Indomalayan Realm rather than the Palaearctic Realm to the north. A similar configuration is known at least as far back as the late Miocene, when faunas from sites in Yunnan Province are unlike contemporaneous sites from central and northern China, and are instead similar to those from the Siwaliks and Myanmar (Flynn and Qi 1982; Wei 1987; Qiu and Qiu 1995; Ni and Qiu 2002; Dong and Qi 2013). Climatic reconstructions for the Xiaolongtan fossil flora (Xia et al. 2009) indicate that temperatures in southern China were about the same in that part of the late Miocene as today, though precipitation may have been quite a bit higher.

The southern boundaries of the Indomalayan Realm are delimited by the Indian and Pacific Oceans. Perhaps the most significant changes along this front have taken place on the Sunda Shelf (Malaysia, Indonesia, Philippines), as its low-lying crust has been variably exposed or submerged, and its islands and archipelagos connected or isolated, by global sea level drops or rises. SSEA is connected to the Australian continent through a porous network of islands that make up the Southeast Asian archipelago but the faunas of these continental regions are starkly different. The transitional nature of the mammals and birds across this island archipelago has historically not been so clean-cut, and ‘too many lines’ have been proposed in attempts to categorize it (Simpson 1977). Many authorities have put the boundary between the Indomalayan and Australian Realms along what is termed Wallace’s Line, a division that passes most famously between the islands of Bali and Lombok which are less than 40 km apart, while others have preferred a demarcation to the east of Sulawesi (Udvardy 1975; Holt et al. 2013).

2.4.2 Late Paleogene and Neogene Relationships with Africa

The Indomalayan Realm’s closest modern comparison lies with Africa and specifically with the Afrotropical Realm, which covers sub-Saharan Africa and the southern portion of the Arabian Peninsula. Today, these two regions share obvious similarities in their large herbivore faunas, such as the presence of rhinocerotids, tragulids, elephants, as well as a high diversity of bovids. These similarities extend back in time into the Miocene, having been greater in the late Miocene than they are today (Thomas 1984; Bibi 2011). However, prior to the Miocene, Africa and Eurasia were separated by the Tethys Ocean throughout the entire Cenozoic. Rare occurrences of Oligocene and earliest Miocene assemblages in SSEA and Africa provide a picture of the past years of isolation, and the first instances of faunal exchange between these two landmasses.

For a long time, most of our knowledge of Afro-Arabian mammalian communities in the earliest Tertiary has come from the Fayum depression of northwestern Egypt. Vertebrate paleontological research in the Fayum Depression began in 1879, with Georg Schweinfurth’s recovery of whale and fish fossils on the island of Geziret el-Qarn in Birket Qarun (Schweinfurth 1886). Since then, the marine Eocene formations underlying the famous continental series have yielded additional cetacean remains (Gingerich 2008). The age of the Fayum fossil fauna has been a matter of some controversy (Kappelman et al. 1992; Seiffert 2006), but it seems that the terrestrial deposits of the Fayum Depression include the Eocene–Oligocene transition. The mammal fauna from the Fayum Depression has been intensively studied since the early twentieth century, and it shows a dominance of African endemics (e.g., afrotheres), as might be expected at this early age. A few Asian elements are present, however, and include primates (Seiffert 2012), marsupials (Hooker et al. 2008), and anthracotheriid artiodactyls (Ducrocq 1997).

Another important late Paleogene African fauna is that from the late Oligocene of Chilga, Ethiopia (Kappelman et al. 2003). This fauna documents a time interval poorly represented in Afro-Arabia between archaic, endemic Afro-Arabian faunas of the late Eocene and early Oligocene as known from the Fayum Depression, and early Miocene replacement faunas, principally documented in eastern Africa, containing Eurasian ungulate migrants such as ruminants, suids, and rhinos. The Chilga fauna includes taxa belonging predominantly to the paenungulate orders (Hyracoidea, Embrithopoda, and Proboscidea) and is globally comparable to the Fayum fauna (Kappelman et al. 2003). Most notably, and together with the late Oligocene elephantimorphs of Eritrea (Shoshani et al. 2006), the Chilga fauna includes the oldest known deinotheres and elephantoids, whose prior fossil records did not extend before the early Miocene (Sanders et al. 2004). The Chilga fauna indicates the continuing biogeographic separation of Afro-Arabia from Eurasia into the latest Paleogene as a result of the Neotethys Sea between these landmasses, and the lack of formation of stable land bridges between the regions at this time. However, while exhibiting a high degree of endemism, Paleogene African faunas do record episodic trans-Tethyan faunal exchanges between Eurasia and Afro-Arabia during the Paleogene and even earlier, during the Mesozoic (see Gheerbrant and Rage 2006).

A great faunal exchange took place between Eurasia and Afro-Arabia in the early Miocene, much as would take place between North and South Americas during the late Pliocene (e.g., MacFadden 2006). In this scenario, the Oligocene to Miocene fossil sequences of Pakistan (see below) plays a critical role in understanding the timing and nature of faunal exchanges. In southern Asia, early Palaeogene vertebrate faunas were for a long time only documented by a few localities in northern Pakistan that yielded fragmentary fossils (Zu Dehm and Oettingen-Spielberg 1958). Until the reassessment of the age of the Chitarwata Formation (Welcomme et al. 2001), the Oligocene was considered as lacking in the entire Indian continent. As such, the Bugti fauna provides a unique window for documenting the transition between the early middle Eocene faunas from the Indo-Pakistani region (e.g., Thewissen et al. 2001a, b), and the Neogene Siwaliks faunas of the Potwar Plateau.

The Proboscidean Datum Event (PDE), supposedly recording the first appearance of proboscideans in Eurasia and the establishment of terrestrial land connections between Afro-Arabia and Eurasia, was long considered as a reliable biochronologic marker dated at 17.5 Ma. Introduced by Madden and Van Couvering (1976), the PDE became less a datum than an interval when the fossil record of Eurasian proboscideans became better known. Tassy (1990) cast serious doubt on the consistency of such a datum, and suggests a diachrony between the first appearance of elephants in Europe (where the PDE is around 18 Ma) and the rest of Asia. Beyond the PDE, the introduction of African large mammals into Eurasian faunas was certainly multi-phased, and depended on both biotic (e.g., dispersal abilities) and abiotic (e.g., sea-level lowering) factors. A thorough analysis of the Oligocene–Miocene sequence exposed in the Sulaiman Range of Pakistan reveals first

occurrences of African migrants much earlier than expected by previous ideas, namely during the late Oligocene (Antoine et al. 2003a, b; Barry et al. 2005).

Faunal interchanges between Africa and Eurasia were therefore diachronous, occurring over an interval of time rather than as a single event, and were probably determined by many different biological and physical parameters. The exchange of faunas between Africa and Eurasia in the late Paleogene and early Neogene was a critical event in the evolutionary history of the ungulate faunas of both continental areas, though it appears to have impacted African faunas more severely than the Eurasian ones. Indeed, many endemic African mammal clades were reduced or even totally gone by the middle Miocene, replaced by incoming Eurasian taxa such as rhinos, bovids, and suids (e.g., Ungar et al. 2012 and therein).

Though similarities can always be found at higher (family) taxonomic levels, it is interesting that the Afrotropical and Indomalayan Realm rarely shared the same species among them. Among fossil bovids, which are very abundant and diverse, only a small handful of occurrences of the same or similar species can be counted in the late Miocene, though this itself is still significantly more than could be counted for the Pliocene or Pleistocene (Bibi 2011). Perhaps the clearest example of a fauna that combined both African and Indomalayan species is that of the late Miocene Baynunah Formation in the United Arab Emirates (Whybrow and Hill 1999). This fauna is mainly African in composition, but interestingly includes Indomalayan species that are never recorded in Africa such as the bovid *Pachyportax latidens* and the suid *Propotamochoerus hysudricus* (Bishop and Hill 1999; Gentry 1999; Hill et al. 2012; Bibi et al. 2013). The Baynunah fauna therefore offers a glimpse into late Miocene biogeographic configurations that reflect a greater overlap of biogeographic boundaries between the Indomalayan and Afrotropical realms at this time.

The Pliocene and Pleistocene probably saw more dispersal of large herbivores into SSEA from Africa than in the opposite direction. This includes the Asian elephant, *Elephas maximus*, the lineage of which (*Elephas* spp.) first evolved in Africa in the early Pliocene and dispersed into SSEA by the late Pliocene. This and other examples of late Neogene continental dispersal are discussed below.

2.5 The Major Fossiliferous Deposits of SSEA

2.5.1 The Bugti Hills, Pakistan

The succession of fossiliferous Tertiary units exposed in Pakistan makes this area one of the most critical for the study of mammalian evolution on the western border of the Indomalayan Realm. The Sulaiman and Kirthar Ranges are north–south mountains resulting from Plio-Pleistocene deformation of Mesozoic and Cenozoic sedimentary rocks. These Mesozoic units had accumulated on the Indian platform of the eastern Tethys Ocean prior to Indian collision. The early Cenozoic sequences record the onset of continental collision, and the thick late Paleogene and Neogene sequences record the emergence of the area and the establishment of the Himalayan

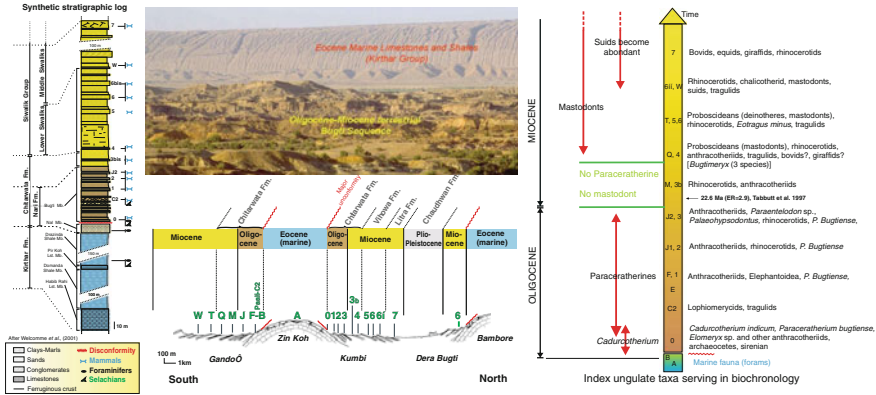


Fig. 2.6 Biostratigraphic framework of the Bugti Hills, which documents about 30 million years of terrestrial ecosystem evolution in the Indian Subcontinent. The photo is taken facing north and captures the Gandoi area with the Zin Koh Anticline in the background. The biostratigraphic chart on the left shows the distribution of fossiliferous horizons in the sequence (letters for the Gandoi Syncline, numbers for the Dera Bugti Syncline), and proposed biochronologic correlations with the Siwaliks and the Zinda Pir area. At right, large herbivore fossil taxa indicative of biochronology (adapted from Welcomme et al. 2001; Métails et al. 2009b; Antoine et al. 2013)

foreland and the Indus drainage. The fossiliferous sequence recording the transition from marine to terrestrial deposition is exposed on the eastern side of the Sulaiman Range, and is best exposed in the Bugti Hills, a region ruled by the Baloch Bugti tribe (Fig. 2.6). The Bugti Hills have been known for their fossil discoveries since 1846 when Vickary, a soldier in the British Army, first reported ‘large bones,’ which were subsequently identified and described by Blanford (1883). The conglomerates and sandstones yielding fossil vertebrates were then ascribed to the ‘Upper Nari Formation,’ and soon became famous for their ‘large fossil mammals’ described in several reports (Pilgrim 1907, 1908, 1910a, b, 1912; Forster-Cooper 1913, 1915, 1924). These fluvial deposits and their fossil content, including the giant rhino *Paraceratherium* (= *Indricotherium*, *Baluchitherium*) were then considered to be pre-Siwalik in placement and early Miocene in age (Pilgrim 1912). The stratigraphy and the time slices represented in the Bugti Series, however, turned out to be more complex than previously evaluated, with the sedimentary sequence there documenting an interval (with numerous gaps) ranging from the middle Oligocene to the Pleistocene. The classical early Miocene ‘Bugti fauna’ is actually made up of different fossiliferous horizons yielding distinct mammal assemblages that were erroneously considered as a single unit (Welcomme et al. 2001). No magnetostratigraphic study has yet been undertaken in the Bugti Hills and relative ages continue to be provided only by mammalian biochronology. The only radiometric date available is a fission track date of 22.6 ± 2.9 Ma from a tuffaceous horizon in the vicinity of Lundo (Tabbutt et al. 1997), a locality situated stratigraphically at the top of the Bugti Member of the Oligocene to Miocene Chitrawata Formation (Welcomme et al. 2001; Métails et al. 2009; Antoine et al.

2013). The biostratigraphic (Downing et al. 1993; Lindsay et al. 2005) and magnetostratigraphic (Friedman et al. 1992) work carried out in the nearby Zinda Pir Dome (150 km NE of the Bugti region) has also helped provide important age correlations. The Bugti sequence is divided into formations that can be recognized across the Sulaiman foothills (Fig. 2.6). These include the Chitarwata Formation (Oligocene-early Miocene), Vihowa (early middle Miocene, and correlative with the Kamlial Formation, the lowermost unit of the Siwaliks in the Potwar Plateau), Litra (late Miocene, roughly Chinji-Nagri equivalent), and Chaudhwan (Plio-Pleistocene). Ungulate mammals are particularly well represented in these successive faunas and most of them serve as key index taxa for establishing biochronological correlations. For example among ruminants, tragulids and lophiomerycids are common in the Chitarwata Formation, while bovids and giraffids become more common in the Vihowa Formation (Ginsburg et al. 2001; Métais et al. 2003; Barry et al. 2005; Métais et al. 2009b).

2.5.2 *The Siwalik Hills of Pakistan and India*

Located in northeastern Pakistan and northwestern India, along the southern flanks of the Himalayas, the Siwalik Hills present one of the largest, most complete, and richest sequences of Neogene fossil mammals anywhere in the world. These foothills of the Himalayan Range essentially consist of Miocene to Pleistocene molassic deposits derived from the erosion of the rising Himalaya, and preserve a fairly continuous record of deposition by drainages ancestral to the modern Indus, Ganges, and Brahmaputra (Friend et al. 2001). Siwalik sediments consist of conglomerates, sandstones, and shales with a thickness of around 5000 m, with vertebrate fossils occurring as dense aggregates of disarticulated elements, hundreds or even thousands in number, filling small channels within braided river systems.

Lyell (1830, pp. 7–8) relates that the fourteenth century Persian historian Ferishta noted the discovery of ‘bones of elephants and men, some of them petrified’ in the Siwaliks area in the process of waterway excavations ordered by the emperor Feroz Shah the Third (also in Murchison 1868, p. 4). Siwalik fossils may have also provided inspiration for some of the stories in the Mahabharata, the Indian literary epic assembled in the first millennium B.C.E. (van der Geer et al. 2008).

Siwalik fossils are among the oldest studied fossils, with scientific descriptions of these appearing before the mid-nineteenth century by the naturalist Hugh Falconer and his colleague, the engineer Proby T. Cautley. The Siwaliks have since then been the target of numerous local and international scientific expeditions and continue to produce what is certainly the best representation of Miocene terrestrial biotic evolution for the entire SSEA region. The Siwaliks sequence has been divided into several geological formations (Fig. 2.7). These include the Kamlial (18.3–14.2 Ma), Chinji (14.2–11.2 Ma), Nagri (11.2–9.0 Ma), Dhok Pathan (10.1–ca. 3.5 Ma), Tatrot (3.5–3.3 Ma), and Pinjor (2.5–0.6 Ma) formations (Barry et al. 2002; Nanda 2002). Formational boundaries, however, appear to be time

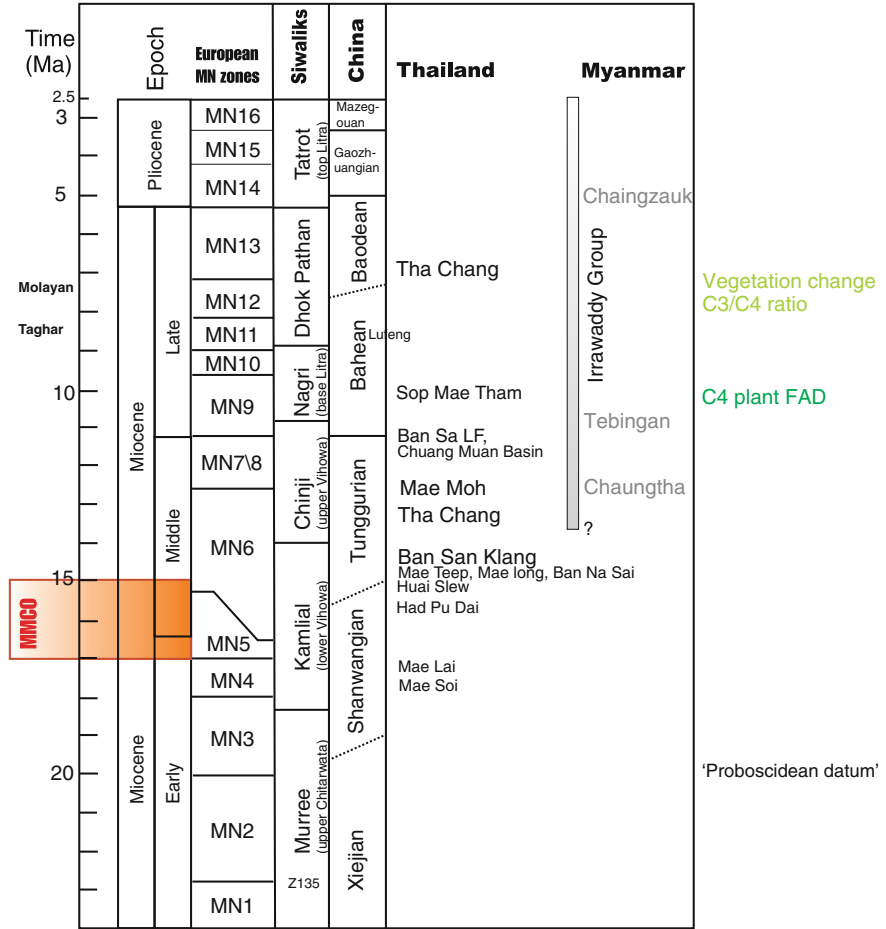


Fig. 2.7 Chronology and correlation of key SSEA Neogene localities with large herbivores. Tentative correlation with the European MN zones is also provided. MMCO designates the Middle Micoene Climatic Optimum, which marks an attenuation of the Asian Monsoon regime for about 2 Ma (based on Barry et al. 2002; Sen 1998; Kunimatsu et al. 2004; Chavasseau et al. 2006; Ogino et al. 2011; Antoine et al. 2013; Qiu et al. 2013)

transgressive in places, and many other formations are named from overlapping time intervals. Oftentimes fossils are referred to similarly named ‘faunas’ (e.g., Chinji fauna, Tatrot fauna), regardless of the actual formation of origin.

Tripathi (1986) reviewed the history of geological study up to that time, but the most synthetic recent summaries of the geology, chronology, and faunal composition of the Miocene Siwaliks are provided by Barry et al. (2002, 2013), Flynn et al. (2013), and Patnaik (2013). Barry et al. (2002) presented precise ages for a large sequence of sites spanning from 10.7 to 5.8 Ma using magnetostratigraphy, which then allowed for large-scale analyses of faunal diversity and ecological

dynamics (Barry et al. 2002; Badgley et al. 2008). A very large number of publications describe Siwalik fossils, and many of these have been cited here in sections below summarizing the history of different clades of fossil herbivores.

Among the many fossil taxa recovered there, the Siwaliks have received attention for the occurrence of a hominoid, *Sivapithecus*. Much of the recent work from the Siwaliks has gone into understanding the habitat preferences of *Sivapithecus*, and the reasons for its extinction there by 8.1 Ma, which appear to be a result of climatic changes and a major loss of forest habitats at that time (Nelson 2007; Badgley et al. 2008).

2.5.3 Paleogene and Neogene Fossil Deposits of Myanmar

The present drainage of the Irrawaddy River and its tributaries forms a large basin extending from north to south through central Myanmar (Fig. 2.8). The formation and sedimentary infilling of the Irrawaddy Basin is closely related to the collision of India with the southern margin of Asia, and the erosion of the resulting uplifted terrain (Bender 1983). From the late middle Eocene, the Irrawaddy Basin has been intermittently flooded by the sea, but the large majority of its deposits are fluvial in origin (Bender 1983). Neogene continental deposits are well exposed in the Irrawaddy basin, and late Paleogene deposits in the Chindwin basin (a tributary of the Irrawaddy). Climatically, the north–south extending Indo-Burmese Ranges (1500–4000 m) impede the passage of humid summer monsoonal winds from the southwest into central Myanmar, producing arid conditions in this area. At present, central Myanmar is a semi-arid zone with an annual precipitation of 600–1000 mm and a mean annual temperature of around 30 °C (Bender 1983). In contrast, the western and southern parts of Myanmar receive 3000–4000 mm of rainfall annually and are covered with tropical rainforests. At their northern extent, the Indo-Burman Ranges are continuous with the Himalayan-Tibetan Plateau.

The late Middle Eocene Pondaung Formation is about 2000 m thick, and the lower part of the upper member yielding fossil vertebrates is comprised of fluvio-deltaic deposits (Soe et al. 2002). The Pondaung fossil fauna is one of the richest Paleogene mammalian faunas in SSEA. Mammalian fossils from this formation were first described by Pilgrim and Cotter (1916). Among the Pondaung mammals, artiodactyls and perissodactyls dominate, with anthracotheres, small ruminant-like artiodactyls, and primitive rhinos and tapiromorphs, along with carnivores, primates, and rodents (Colbert 1938; Ducrocq et al. 2000; Tsubamoto et al. 2002, 2005; Métais 2006; Métais et al. 2007). Interestingly, the Pondaung Formation has yielded a diacodexeid-like artiodactyl (Ducrocq et al. 2015), thus shifting up the youngest occurrence of these basal artiodactyls fairly common from the early Eocene deposits of Holarctic areas and India, and suggesting that Southeast Asia may have played as early as Eocene the role of refuge pretty much as it does now. The paleoenvironment of the Pondaung fauna is reconstructed as mangroves and dry dipterocarp forest (Licht et al. 2015) under a with monsoonal regime, supplied by large rivers that were located not far from

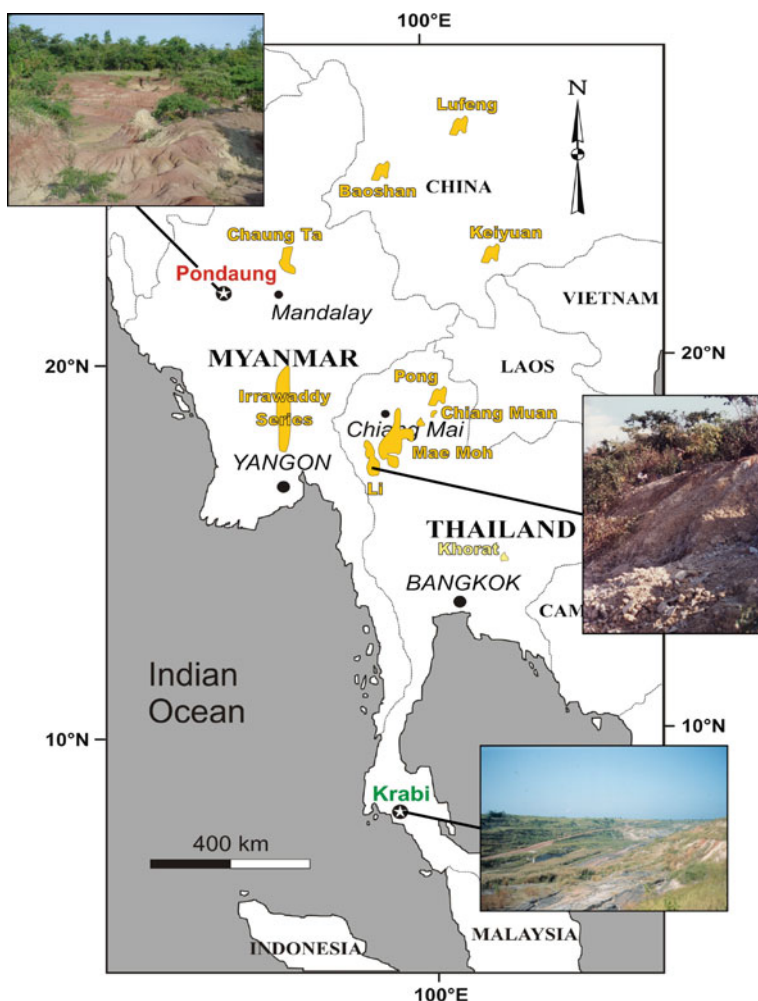


Fig. 2.8 Tertiary basins in Myanmar, Thailand, and southern China. Photos of Saba Pondaung, Pondaung Formation (G. Métais), an outcrop in the Li Basin (L. Ginsburg), and the Krabi Coal Seam (S. Ducrocq)

the coast of the eastern Tethyan Sea. At this time there are no herbivorous species with truly hypsodont cheek teeth (as in living horses), also reflecting a general absence of dry and open habitats.

The Neogene and Quaternary fluvial deposits of the Irrawaddy Formation are well exposed along the banks of the modern Irrawaddy River, can reach thickness of 2000 m, and span the Middle Miocene to the Pleistocene (Fig. 2.7) (Bender 1983). Mammalian fossils from these sediments have been documented since the late nineteenth century (e.g., Lydekker 1876a, b) and were loosely correlated with those of the Siwaliks of the Indian subcontinent through biostratigraphy (Colbert 1938, 1943).

The lithology of the Irrawaddy series is quite homogeneous, and fossil vertebrates are to be found scattered in thick repeating sandy units. Biochronological correlations with Neogene faunas of Thailand and the Siwaliks of Pakistan sometimes provide the only age indication. For example, several taxa described from the locality of Chaungtha also occur in the Chinji Formation (14–11 Ma, Barry et al. 2002) of the Siwaliks and the Mae Moh Formation of northern Thailand (Chavasseau et al. 2006). This suggests that, like today, SE Asia and Pakistan during the middle Miocene belonged to the same biogeographical region and perhaps shared a similar forested environment under a monsoon-like climate regime (Ducrocq 1994). The abundance of silicified fossil wood of Dipterocarpaceae (Bande and Prakash 1986) in the ‘Lower Irrawaddy’ series suggests the existence of tropical rainforests during the early Neogene.

Late Miocene faunas of the Irrawaddy Formation are dated to between 10.4 and 8.8 Ma on the basis of biochronology and magnetostratigraphy (Jaeger et al. 2012). Stable isotope data on the fossil equid *Hipparion* indicate an evergreen forest in a C₃-vegetation environment, suggesting humid conditions there, prior to the replacement of C₃ forested habitats by C₄ grasslands between 8 and 6 Ma (discussed above).

Several ‘Irrawaddy faunas’ have been reported from the Chaingzauk area, and correlations with the Plio-Pleistocene Tatrot-Pinjor faunas or with the latest Miocene (ca. 6–5 Ma) upper Dhok Pathan faunas of the Siwaliks have been proposed (Fig. 2.7) (Colbert 1938). The Chaingzauk faunas are abundant in ungulates, with rhinocerotids, bovids, hippopotamids, tragulids, anthracotheres, monkeys, suids, and proboscideans. Carbon and oxygen isotopic investigation indicates that mammals inhabited a transitional environment between woodland and grassland (Zin-Maung-Maung-Thein et al. 2011) and that C₄ grassland habitat expansion had taken place by the latest Miocene in Myanmar, as it did in the Siwaliks of Pakistan. The present day arid environment of central Myanmar (the driest region in SE Asia) must have developed gradually during the late Miocene to early Pliocene, and is probably related to the continuing uplift of the Indo-Burmese Ranges and the Himalaya-Tibetan Plateau.

2.5.4 *Paleogene and Neogene of Thailand*

The Cenozoic mammal localities of Thailand range chronologically from late Eocene to Pleistocene, and geographically from the peninsular region to the north of the country (Figs. 2.7 and 2.8). A number of small basins form part of a NW–SE rift zone that crosses Myanmar and Laos and ends in the gulf of Thailand. The Tertiary rift basins of central Thailand are delimited to the west by the Sagaing fault zone and to the east by the Red River fault zone (Morley 2002). These major strike-slip faults resulted from tectonic activity associated with the Himalayan orogeny that forced the area of Indochina to move to the southeast relative to the remainder of Asia (Tapponnier et al. 1986). During the Cenozoic, the subsidence of these small pull-apart basins and subsequent infilling with fluvio-lacustrine

sediments resulted in the deposition of thick sedimentary sequences that are accessible largely due to mining activities.

The coalmine of Krabi (Fig. 2.8) has yielded one of the most diverse assemblage of fossil mammals from Southeast Asia. Mammalian biostratigraphy indicates a late Eocene age (Ducrocq et al. 1995), while magnetostratigraphic work suggests the Krabi section is earliest Oligocene, between 34 and 31 Ma in age (Benammi et al. 2001). The Krabi fauna, comprising over 30 species (Ducrocq et al. 2006) is generally considered as a reference fauna in South Asia. The main coal seam, which has yielded most of the fossil mammals, is sandwiched between overlying lacustrine sediments and underlying fluvial sediments. The abundant unionid shells, crocodiles remains, and freshwater turtles suggest fluvio-lacustrine and wetland environments for the Krabi fauna. Despite the high diversity of the large mammal fauna, micromammal remains are very scarce, and most vertebrate remains belong to medium and large herbivorous mammals typical of swampy environments. Ungulate mammals, especially artiodactyls, are fairly well represented at Krabi, with anthracotheriids (five species in three genera) forming the majority of the fossil mammals collected there. Perissodactyls are usually an important component of Asian Paleogene mammal faunas (Russell and Zhai 1987), but the Krabi fauna is dominated by artiodactyls (about 15 different species), with only two rhinocerotoid perissodactyls (Ducrocq et al. 2006). The low diversity of perissodactyls in Krabi could either reflect an incompleteness of the Paleogene fossil record in southern Asia, or a greater diversity of artiodactyls in lower latitudes relative to a greater diversity of perissodactyls in higher latitudes in Central Asia at this time. The greater diversity of dental patterns for artiodactyls in Krabi (ruminants, anthracotheres, suoids) seems to be analogous to that of perissodactyls from most other Paleogene Asian localities. Beyond anthracotheres, artiodactyls are represented by tragulid and lophiomerycid ruminants (Métais et al. 2001), a suid (Ducrocq et al. 1998), and a tayasuid (Ducrocq 1994). The body mass cenogram of the Krabi fauna (Ducrocq et al. 1995) is quite similar to that of extant faunas living in humid tropical forests (Legendre 1989), suggesting a closed canopy forest habitat.

The middle Miocene localities of Thailand are situated in the northwestern part of the country. These basins are filled mainly by fluvio-lacustrine Neogene deposits, and intercalated lignite seams are commercially exploited. Different basins have been investigated and it seems that most mammal localities from northern Thailand occur in a time span ranging from about late early to early late Miocene (Von Koenigswald 1959; Ginsburg 1984; Ducrocq et al. 1994), overlapping with the Kamlial and Chinji faunal zones of the Siwaliks in Pakistan. About 45 species of mammals (from chiropterans to proboscideans) are reported from the different basins of northern Thailand (Ducrocq et al. 1995).

The principal fossiliferous localities are situated in the basins of Li, Mae Moh, Chiang Muan, and Pong (Fig. 2.8). Magnetostratigraphic studies have been carried out on different sequences of the Mae Moh and Chiang Muan Basins and provide further constraint for dating mammal localities (Benammi et al. 2002; Coster et al. 2010). The Mae Moh coal mine has produced a diversified late middle Miocene fauna (Suraprasit et al. 2015), including the early bovid *Eotragus*, and lagomerycids *Lagomeryx* and *Stephanocemas* (Suraprasit et al. 2014). The Li Mae Long fauna in

the Li Basin is the most diversified fauna, the early middle Miocene age of which is constrained by micromammals (Mein and Ginsburg 1997). Large mammals are represented by the proboscidean *Stegolophodon*, the rhinocerotid *Gaindatherium*, the lagomerycid *Stephanocemas rucha*, the tragulid *Siamotragulus haripounchai*, the anthracothere *Brachyodus* cf. *onoideus*, and the suid *Conohyus sindiensis* (Mein and Ginsburg 1997; Ducrocq et al. 2003). This fauna has been correlated with the European Mammal Zone MN4 (late early Miocene), making this the oldest Neogene fauna from northern Thailand.

The Chiang Muan Basin has yielded a younger fauna which is supposedly late middle Miocene in age (Chaimanee et al. 2003; Pickford et al. 2004; Sukanuma et al. 2006) and probably correlative with the upper Chinji-lower Nagri faunas of the Siwaliks. The fauna from the Ban Sa locality in the Chiang Muan basin includes a tetralophodont mastodon, rhinocerotids, tragulids, bovids, suids, and hominoid primates. The Neogene Vietnamese site of Hangmon (Ginsburg et al. 1992; Covert et al. 2001) and the presumed contemporaneous Chinese faunas, such as at Lengshuigou, Tunggur, Tsaidam or Lufeng, do not provide meaningful comparisons with the Thai locality because of their distinctly different mammalian assemblages, suggesting a degree of provincialism in the Chinese ruminant faunas of this time.

Several fossil vertebrate localities of late Miocene to Pliocene age have also been reported in Nakhon Ratchasima Province (Khorat), northeastern Thailand (Chaimanee et al. 2004; Hanta et al. 2008; Claude et al. 2011). The ungulate mammal fauna includes proboscideans (*Deinotherium indicum*, *Gomphotherium* sp., *Stegolophodon* sp.), an anthracotheriid, a suid (*Hippopotamodon sivalensis*), rhinocerotids (*Chilotherium palaeosinense*, *Brachypotherium perimense*, *Alicornops complanatum*), bovids, giraffids (*Sivatherium* sp.) and some hipparionine equids. This assemblage seems to correlate to the upper Nagri and lower Dhok Pathan Formations of the Siwaliks and indicates a late Miocene age, or between about 9 and 7 Ma (Barry et al. 2002).

2.5.5 Afghanistan

Though part of SSEA as defined politically, Afghanistan's faunas resemble those of Central Asia, eastern Europe, and the Middle East more so than those of the Indomalayan Realm. Afghanistan is accordingly classified within the Palearctic (or Saharo-Arabian) Realm (Holt et al. 2013), and the distinction between its faunas and those of the Indomalayan Region (even nearby Pakistan) is visible at least as far back as the late Miocene (Brunet et al. 1984).

The known fossil record of Cenozoic mammals in Afghanistan is limited to a handful of Miocene-Pliocene localities in intramontane basins. A few small mammal remains were first reported by Lang and Lavocat (1968) from the Bamian Basin (150 km west-northwest of Kabul), and revised by Flynn (1983). Raufi and Sickenberg (1973) reported on mammal remains from the Sarobi and Jalalabad Basins, about 60 km East of Kabul. Between 1976 and 1979, French paleontological expeditions prospected different basins southeast of Kabul where the late Neogene

Lataband series (Mennessier 1961) was exposed, and several fossil mammal localities of late Miocene to Pliocene age were discovered (Heintz et al. 1978a, b). Among these, the site of Molayan bears the richest assemblage so far recovered from Afghanistan, both in terms of taxonomic diversity and number of specimens (Heintz et al. 1978a, b; Brunet et al. 1984; Sen 2001). Faunal studies suggest a Middle Turolian (ca. 8–6.5 Ma) age for Molayan (Sen 1998) while Taghar, another locality stratigraphically lower than Molayan, has yielded large mammals that all indicate an early Turolian age (ca. 9–8 Ma) (Sen et al. 1997). Geographically, Molayan and Taghar are situated close to the border between two paleobiogeographical provinces, the Greco-Iranian and the Siwalik provinces (de Bonis et al. 1992). However, the mammalian faunas from these two Afghan localities are firmly Greco-Iranian in composition, with hardly a species in common with the Potwar Plateau only some 300 km to the southeast (Brunet et al. 1984). Both Molayan and Taghar have yielded diverse ungulate faunas including Bovidae, Giraffidae, Equidae, Chalicotheriidae, Rhinocerotidae, Gomphoteriidae, Deinotheriidae, and Suidae. Cervid remains are also known from Taghar, which is interesting since cervids have not been recorded from the late Miocene and early Pliocene faunas south of the Himalayas (Heintz and Brunet 1982, and see below). Studies of microwear and stable isotopes of fossil bovids from Molayan indicate an open and partly forested alluvial plain forming hilly landscapes, where evergreen sclerophyllous shrubs and C₃ grasses constituted the majority of the vegetation (Zazzo et al. 2002; Merceron et al. 2004).

2.5.6 *Southern China and Northern Vietnam*

While not within the boundaries of political SSEA, southern China and northern Vietnam forms the north-easternmost part of the Indomalayan Realm. Fossil sites at least as old as the late Eocene record the evolution of Indomalayan mammals here since at least that time, indicating similarities to contemporaneous SSEA faunal assemblages to the south, and differences from Chinese and Central Asian assemblages to the north. During the late Eocene up to the Miocene, numerous pull-apart basins formed on the southern Chinese microplate and northern Vietnam along the strike-slip Red River faults system (Pubellier et al. 2008). It resulted thick sequences of terrestrial (often coal bearing) sediments that have produced faunas mostly documented by large mammals. The Naduo and Gongkang Formations in the Bose Basin of southern China probably straddle the Eocene-Oligocene transition, and their faunas is dominated by anthracotheres, tapiroids, earliest suoids (Liu 2001), and at a lesser extent ruminants (Wang et al. 2007 and reference therein). The Naduong Basin of northern Vietnam has also yielded a rich fauna and flora reported by Böhme et al. (2011, 2013). The large mammals includes anthracotheriids (Böhme et al. 2013; Ducrocq et al. 2015), the rhinocerotid *Epiaceratherium naduongense*, and traguloids. The fossil mammals from Na Duong show unexpected similarities with European (Böhme et al. 2013) and to some extent to African faunas (Ducrocq et al. 2015). The Na Duong Formation probably deposited within a swamp ecosystem with both aquatic and non-aquatic environments. Fossil

plants suggest a forest of Dipterocarpaceae, and the sedimentary sequence exposed in the Na Duong basin pleads for tropical humid condition without a dry season (Böhme et al. 2013). During the Neogene, the main fossil sites of southern China are those of Yunnan Province, mainly in the Xiaolongtan, Lufeng, Yuanmou, and Zhaotong Basins (Dong and Qi 2013; Wang et al. 2013), while the Early Miocene Hang Mon fauna represent the only and still poorly documented record of Miocene mammals in Vietnam (Ginsburg et al. 1992). Numerous localities of Pleistocene are also known in southern China (Li 1981; Ji 1982; Huang and Zhang 2006).

2.5.7 *Southeast Asian Islands*

The fossil record of the Southeast Asian archipelago is primarily Pleistocene in age. Fossil sites are known from the islands of Java, Sumatra, Flores, Borneo, Sulawesi, and several of the Philippine islands, among others (e.g., Croft et al. 2006; Louys and Meijaard 2010). The fossil record of these islands tells a story of insular evolution of mainland mammal lineages, with waves of dispersal into the islands associated with the major and cyclical sea level drops characteristic of the Pleistocene (discussed above).

2.6 Evolutionary History of the Large Herbivores of SSEA

2.6.1 *Artiodactyla*

Artiodactyls (or cetartiodactyls) are the most diverse clade of extant large mammals, occurring in continental areas from the equator to high latitudes, as well as both marine and freshwater habitats around the world. Artiodactyls such as oxen, goat, sheep, pigs, and camels played a pivotal role in the Neolithic development of human settlements and agricultural and cultural practices, and are to this day a critical source of productivity and food for humanity.

This clade has been the focus of much scientific attention over the past few decades, particularly as genomic sequencing techniques came to be applied to phylogenetic reconstruction. The classical concept of Artiodactyla as proposed by Richard Owen in 1848 for terrestrial, even toed ('cloven hoofed') ungulates (i.e., pigs, hippos, camels, and ruminants) was challenged by molecular phylogenies based on RNA, cytochrome *b*, or other molecular markers (Fig. 2.9). These phylogenies offered numerous hypotheses of relationships within Artiodactyla that were all distinct from those classically admitted by comparative anatomical approaches since the mid nineteenth century. Most surprisingly, molecular phylogenies suggested that cetaceans (whales and dolphins) were closely related to extant hippos, and thus nested deep within Artiodactyla (e.g. Montgelard et al. 1997).

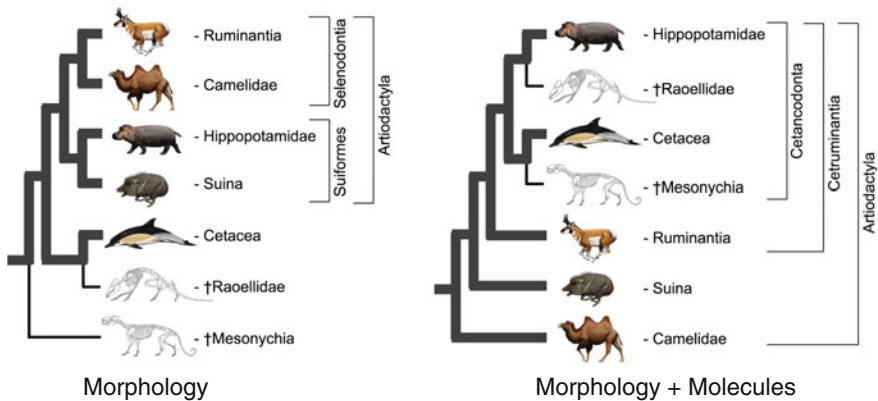


Fig. 2.9 The phylogenetic tree of artiodactyls produced by morphological characters versus a tree obtained from analysis of morphological and molecular characters combined. Both approaches recognize the relationship of whales to artiodactyls, but are conflicted on relationships among the artiodactyl clades (modified from Spaulding et al. 2009)

These provocative topologies in support of a ‘whippo’ clade were vindicated by the paleontological discovery of a primitive fossil whale ankle bone with a double-trochlea astragalus, a definitive anatomical feature of artiodactyls (Gingerich et al. 2001; Thewissen et al. 2001a, b). The exact evolutionary origins of Cetacea within Artiodactyla, however, remain uncertain, particularly relative to numerous poorly understood early fossil artiodactyls. Raoellids, a small group of early to middle Eocene amphibious artiodactyls endemic to India and Pakistan, display morphological and histological features suggestive of a degree of adaptation to aquatic life (Thewissen et al. 2007), making them possibly ancestral to Cetacea (Geisler and Uhen 2005). Several inconsistencies remain between molecular and morphological phylogenies, especially regarding the relationships of tylopods and ruminants within Artiodactyla. Molecular analyses also support a closer relationship of ‘whippos’ to ruminants than to pigs or camels (Fig. 2.9), a clade named Cetruminantia (e.g., Hassanin et al. 2012). Further paleontological work is needed to better illuminate the early history of these groups, using multidisciplinary approaches to decode the evolutionary history of morphological changes and their potential functional and phylogenetic significance.

The relationships of artiodactyls among placental mammals are also a matter of debate, often accentuated by this clade’s scanty early Paleogene fossil record, and the difficulty in securely determining the position of extinct basal groups to extant crown clades. Molecular (Madsen et al. 2001; Meredith et al. 2011) as well as combined morphological-molecular phylogenies (O’Leary et al. 2013) suggest that artiodactyls are part of the clade Laurasiatheria that also includes carnivores, bats, pangolins, and perissodactyls. Laurasiatheres and archontes (rodents and primates) are thought to originate in the Holarctic area sometime between the early Cretaceous and the Paleocene. Beyond topologies of phylogenetic trees, divergence time (i.e.,

inter- or intra-ordinal diversification) is often a matter of controversy between paleontologists and molecular biologists. Molecular biologists use many different approaches and inevitably rely on the fossil record to calibrate molecular evolutionary rates and derive molecular age estimates, often with contradictory results.

The fossil record provides slightly less room for chronological ambiguity. Artiodactyls first appear in the fossil record in the earliest Eocene (ca. 55 Ma) of Eurasia, India, and North America (Rose 2006). They are mostly documented by the genus *Diacodexis*, although several enigmatic and poorly documented forms from the late Paleocene to the early Eocene of China may indicate higher taxonomic diversity in Asia near the Paleocene–Eocene boundary (Tong and Wang 2006). During the Middle Eocene, several groups of basal artiodactyls (usually named dichobunoids) diversified concurrently in the three main Holarctic areas. However, with the exception of tylopods (including camelids), which first appeared and diversified in North America (Honey et al. 1998), the earliest representatives of the lineages leading to the crown artiodactyl clades are to be found in Southeast Asia (Webb and Taylor 1980; Ducrocq 1994, 1997; Métais et al. 2001, 2007).

The modern dominance of artiodactyls among Asian herbivore faunas was not always as such in the past. The prevalence of perissodactyls over artiodactyls in the Eocene faunas of Asia is clearly perceptible, both in terms of taxonomic diversity and demographic abundance. The average size of artiodactyls (most of which were ecologically similar to extant rabbits) was much smaller than that of perissodactyls, suggesting that these early ungulates were ecologically divergent and not sharing the same food resources. During the Oligocene and Neogene, however, artiodactyls became larger and more diverse while the diversity of perissodactyls decreased. This reverse, continental scale trend between the two main groups of Asian ungulates appears to have been the result of vegetational changes that favored the digestive efficiency of ruminants (foregut fermenters) relative to perissodactyls (hindgut fermenters) (Janis 1989).

Suidae

SSEA has the highest diversity of suid species in the world today, represented by several species of *Sus*, *Porcula salvanus*, and the peculiar babirusa (*Babyrusa* spp.) recently divided among three species. It is interesting that most babirusa species are restricted to particular islands of Southeast Asia, suggesting that their differentiation must have been related to processes of island formation (tectonic motions and sea level changes).

Suids are omnivores that rely on plant-based diets, but opportunistically incorporate a large range of small animals. Unlike most herbivores that possess teeth with long enamel ridges (lophodont, selenodont), suids tend to have teeth with rounded cusps (bunodont). Humans and bears are two other taxa with similarly bunodont teeth, a functional similarity that gives away the omnivorous diets of these three otherwise distantly related taxa. Suioidea (alternately Suina or Suiformes) is the clade uniting pigs (Suidae), peccaries (Tayassuidae), and extinct fossil taxa that are closely related to these living groups. The earliest fossil suoids are known from the late middle or late Eocene of SSEA, suggesting that the origins

of both suids and tayassuids are to be found in the Eocene of SSEA (Rose 2006; Harris and Liu 2007; Orliac et al. 2010a, b). Basal suoids have been described from the Eocene Krabi Basin of Thailand (Ducrocq 1994; Ducrocq et al. 1998; Orliac et al. 2011). One of these, *Egatochoerus*, was initially described as a tayassuid, but later reassigned to the base of Suiodea (Orliac et al. 2010a, b).

The earliest suids may be early Miocene Eurasian hyotheriines (Orliac et al. 2010a, b) though the taxonomy of Suidae below the family level has a complicated and unsettled history (Harris and Liu 2007). Other extinct fossil suid clades from the Neogene include the Tetraconodontinae and Listriodontinae. Living suids, however, may all be assigned to a single subfamily, Suinae, with the exception of the babirusa (Gongora et al. 2011). The earliest fossils of Suinae appear in the middle Miocene of both SSEA (Chinji) and Europe (at about 13 Ma or younger) (Harris and Liu 2007). A notable fossil suine from the late Miocene of SSEA is *Propotamochoerus hysudricus*, which is recorded in the Siwaliks of northern Pakistan from 10.2 to 6.8 Ma (Badgley et al. 2008). This long-lived species is known only from SSEA with the notable exception of an occurrence in the late Miocene Baynunah fauna of the United Arab Emirates (Bishop and Hill 1999; Bibi et al. 2013). The earliest fossils attributed to *Sus* are from the earliest Pliocene of SSEA and Europe (Harris and Liu 2007).

Molecular phylogenies estimate the divergence of Suidae and Tayassuidae at 47–23 Ma, Suinae and *Babyroussa* at 18–9 Ma, and the origin of crown Suinae at 15–7 Ma (Gongora et al. 2011). These ranges appear broadly compatible with the fossil record (Orliac et al. 2010a, b), though Thenius (1970) proposed an Oligocene or older split of the babirusa from other pigs. The babirusa, with its bizarre horn-like canines, has an enigmatic evolutionary history. Besides a few Pleistocene occurrences, the babirusa has no fossil record, and it has been proposed that its colonization of Southeast Asian islands may have been as old as the Oligocene, in contrast to the other mammalian lineages inhabiting the Southeast Asian archipelago, most of which are believed to have dispersed there in the Pleistocene (van den Bergh et al. 2001a, b).

Schizochocerus gandakasensis, recorded from 10.1 to 8.7 Ma in the Siwaliks (Badgley et al. 2008) is a member of an enigmatic group of pig and peccary-like species generally referred to as palaeochoerids (Boisserie et al. 2010; Orliac et al. 2010a, b). There is no consensus as to the position of the different ‘palaeochoerid’ taxa, but a recent analysis suggests *Schizochocerus* may be an early suid, with other ‘palaeochoerids’ lying closer to peccaries (Orliac et al. 2010a, b). *Pecarichoerus* from the early and middle Miocene Siwaliks (Colbert 1933) was first thought to be a peccary but was later placed among the ‘palaeochoerids’ (Orliac et al. 2010a, b).

Hippopotamidae

Though today restricted to Africa, hippopotamids were previously more widely distributed across Eurasia, with a presence in SSEA from the late Miocene to the late Pleistocene. Until recently, many Asian and African fossil hippopotamids, as well as the living west African pygmy hippo, were classified in the genus *Hexaprotodon*. A recent review (Boisserie 2005) determined that *Hexaprotodon*, first named on the basis of fossil material from the Siwaliks by Falconer and

Cautley (1836a, b, c), is in fact a restricted clade of extinct SSEA hippopotamids. The earliest SSEA hippo is *Hexaprotodon sivalensis* (Fig. 2.10), which is recorded at 5.9–3.5 Ma in the Siwaliks (Badgley et al. 2008). The lineage survives into the

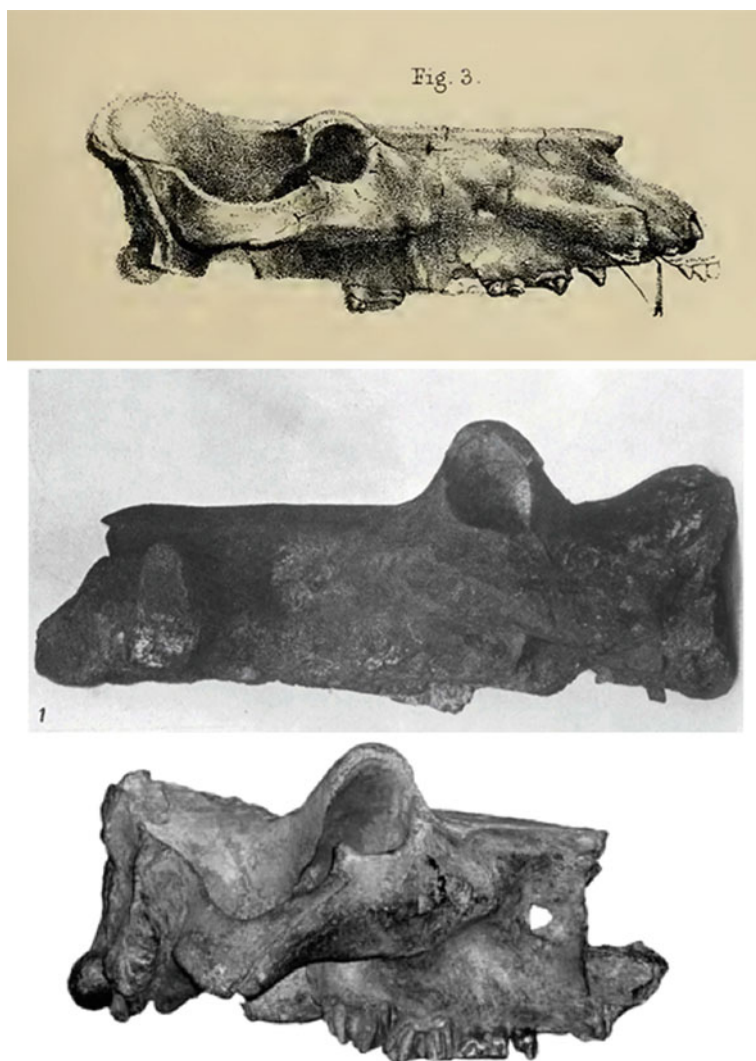


Fig. 2.10 Fossil hippopotamids from southern Asia. From top: *Hexaprotodon sivalensis* from the latest Miocene to Pliocene of India and Pakistan (from Falconer in Murchison 1868, p. 2), *Hex. palaeindicus* from Pleistocene India (from Boissarie 2005 Fig. 2.8), and *Hexaprotodon* sp. from Pleistocene Indonesia (from Hooijer 1950, p. 2). Note the evolution of elevated orbits in the younger specimens, a feature indicative of a semi-aquatic lifestyle as in modern hippos, evolved in parallel in Asian *Hexaprotodon* and African *Hippopotamus* clades (Boissarie 2005). Crania are not to scale

late Pleistocene of Central India as *Hex. palaeindicus*, and possibly as a different species in Indonesia (Colbert 1935a, b; Hooijer 1950; Boissérie 2005; Chauhan 2008; Patnaik et al. 2009). While the living African pygmy hippo has often been classified as *Hexaprotodon liberiensis*, numerous morphological differences indicate it is better assigned to a separate genus, *Choeropsis liberiensis* (Boissérie 2005). All members of *Hexaprotodon* are therefore extinct, and the only occurrence of this clade outside SSEA is in the form of *Hex. bruneti* from Ethiopia at 2.5 Ma, and which appears to have been an immigrant into eastern Africa from SSEA (Boissérie and White 2004).

Hexaprotodon sivalensis possessed relatively low orbits that indicate more terrestrial habitats than in living hippos. By Pleistocene times, the orbits had become highly elevated above the skull profile, as seen in *Hex. palaeindicus* (Fig. 2.10). High orbits are found in living *Hippopotamus amphibius*, and indicate that the Pleistocene SSEA hippo was also well adapted to a semi-aquatic lifestyle (Boissérie 2005).

Anthracotheriidae

Anthracotheres are an extinct group of artiodactyls that were diverse and widespread from the Eocene to the Miocene of Eurasia, Africa, and North and Central America. The earliest fossil anthracotheres are recorded from the middle Eocene of southeast Asia (Myanmar, Vietnam, and southern China) and North America, though the family's origins are certainly older and probably in southern Asia (Pilgrim 1928; Tsubamoto et al. 2002; Ducrocq and Lihoreau 2006a, b; Lihoreau et al. 2007; Tsubamoto 2010; Böhme et al. 2013). A fossil anthracothere has been reported from the Eocene of Timor Island (Von Koenigswald 1967), but it is a somewhat anomalous occurrence and its original provenience has been put to question (Ducrocq 1996; Lihoreau et al. 2007a, b). The last worldwide occurrence of anthracotheres is also in southern Asia, with *Merycopotamus dissimilis* (Fig. 2.11) recorded from Pakistan, India, Myanmar, and Java, with its youngest records in Pakistan at around 2.5 Ma (Steensma and Hussain 1992; Dennell et al. 2006; Lihoreau et al. 2007a, b; Badgley et al. 2008) and possibly as young as 1.7 Ma (Dennell et al. 2006). Certain anthracotheres achieved very large sizes and a semi-aquatic lifestyle, and this group may have given rise to the Hippopotamidae (Boissérie et al. 2005 and references therein).

The main records of SSEA anthracotheres come from two lineages from the Siwaliks of northern Pakistan. There, the *Microbunodon* lineage is recorded from 13.8 to 9.2 Ma, while the long-lived *Merycopotamus* lineage is recorded from 13.9 to 2.5 Ma (Badgley et al. 2008). The *Merycopotamus* lineage is well studied, and apart from a single occurrence in the late Miocene of Iraq, is known only from SSEA (Lihoreau et al. 2007a, b; Hanta et al. 2008). During the late Miocene, this lineage exhibited increased adaptation to aquatic habitats, including the evolution of elevated orbits (as in Hippopotamidae), increased body mass, and development of less cursorial limbs; its presence in the Tigris-Euphrates basin of Iraq suggests dispersal there from southern Asia during a sea level regression at about 10 Ma (Lihoreau et al. 2007a, b).

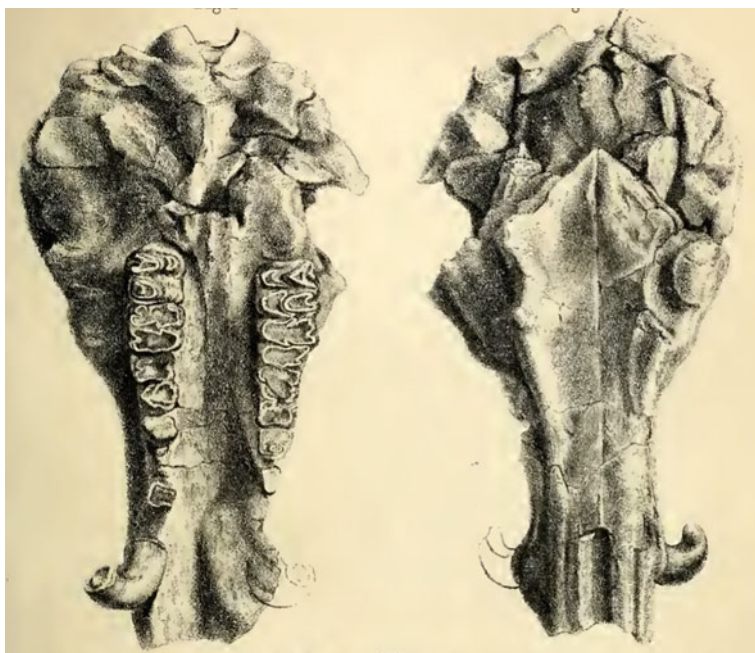


Fig. 2.11 Skull of the hippopotamus-like anthracothere, *Merycopotamus dissimilis*, recorded from the late Miocene to the terminal Pliocene in Pakistan, Nepal, Myanmar, and Indonesia (from Murchison 1868, p. 13)

Tragulidae

Tragulids comprise a clade of ruminants that is today relict in terms of its diversity and distribution, and that in morphology bears resemblances to early Paleogene artiodactyls, including primitive ruminants. Tragulids are the only extant survivors of an earliest Eocene diversification of hornless ruminants but their Paleogene fossil record is scanty. Interestingly, tragulids are physiologically conservative in that they only have a three-chambered stomach, rather than the more derived four-chambered stomach of most other ruminants. Today, tragulids are represented by several species of chevrotain or mouse deer (*Tragulus* spp.) from SE Asia including the Philippines, *Moschiola* spp. from India and Sri Lanka, and the larger water chevrotain *Hyemoschus aquaticus* from central Africa. The earliest fossil tragulid is *Aracheotragulus krabiensis* from the late Eocene of Thailand (Métais et al. 2001), and another enigmatic bunodont form (Métais et al. 2007), and they are otherwise documented in Europe, Turkey, and Pakistan. Early tragulids seem to have been restricted to densely forested and humid environments where they probably fed on fruits, seeds, soft leaves, and occasionally on invertebrates, as living tragulids do (Dubost 1978). There is evidence of varied mixed feeding strategies along a graze-browse spectrum among several species of *Dorcatherium* from the early Miocene of Kenya, suggesting that tragulids partitioned dietary niche

space much as some bovids do today (Ungar et al. 2012). *Siamotragulus* is known from the middle Miocene of Thailand (Thomas et al. 1990), Myanmar (Chevasseau et al. 2006), and Pakistan (Ginsburg et al. 2001), and *Yunnanotherium* from the late Miocene of Lufeng, southern China (Han 1986). Another genus, *Afrotragulus*, has been recently described from the early Miocene of Africa (Sánchez et al. 2010). The size of these fossil tragulids did not exceed that of the extant *Hyemoschus*, and tragulids of size equal to or smaller than *Tragulus javanicus* (i.e., <2 kg) are reported from the middle Miocene of the Siwaliks (West 1980) and Kenya (Pickford 2001). Almost nothing is known of the evolution of tragulids since the end of the Miocene (Rössner 2007), and their fate today is probably tied to the shrinking forest habitats of tropical Asia and Africa.

Moschidae

With only a single genus and six species, Moschidae is among the least diverse ruminant families. Five of the six living species of musk deer, all belonging to the genus *Moschus* (Groves et al. 1995), occur along the northern edges of southern Asia, mainly in and around the Himalayas and into southern China. Moschids are small, deer-like ungulates that lack horns or cranial appendages of any kind, with males possessing prominent dagger-like upper canines. Nowadays, *Moschus* species inhabit the mountainous forests of central and eastern Asia, with some species living at high altitudes (≥ 4000 m, Groves et al. 1995). Musk deer are extremely territorial and feed on leaves, flowers, and various other soft items. Males are known to mark their territory with musk secretions (hence their name), and though endangered, their scent glands are still in high demand in China for medicinal or aromatic purposes.

Evolutionarily, moschids have long posed a problem because, unlike other advanced (pecoran) ruminants, they lack cranial appendages and possess large upper canines. These are primitive morphological features, similar to the condition in tragulids. Although lacking the double lacrimal orifice characteristic of cervids, morphological analyses have supported relationships to cervids and antilocaprids (e.g., Janis and Scott 1987). A supertree analysis combining behavioral, molecular, and morphological data also supported affinities with cervids (Hernández Fernández and Vrba 2005). In total contradiction, however, molecular analyses have consistently indicated that moschids are more closely related to bovids (Hassanin and Douzery 2003; Meredith et al. 2011; Hassanin et al. 2012).

Several putative moschids first appeared in the late Oligocene of Europe and Asia with late Oligocene and early Miocene taxa such as *Dremotherium* and *Amphitragulus*, and the enigmatic *Prodremotherium* from the Oligocene of Asia (Métais and Vislobokova 2007 and references therein). These potential stem moschids went extinct by the end of Agenian European Land Mammal Age (ca. 20 Ma), at the same time as the first appearance of cervids in Europe. From the middle Miocene, the moschids *Micromeryx* and *Hispanomeryx* are known from Europe and China (Sánchez et al. 2011). These two genera extended into the late Miocene (and probably into the mid-Pliocene for *Micromeryx*) and are thought to be closely related to the genus *Moschus*, which first appeared during the late

Miocene in China and eastern Europe (Vislobokova and Lavrov 2009). During the early Miocene, moschids also spread to North America, where they experienced an endemic radiation with six genera in the subfamily Blastomerycinae, all of which went extinct near the end of the Miocene (Prothero 2007).

Lophiomerycidae

This extinct family, probably closely related to tragulids, is known from Eocene to Oligocene fossil sites across Eurasia. The oldest lophiomerycids come from the middle Eocene of China (Guo et al. 2000) and are found in western Europe shortly after the Eocene–Oligocene transition (Stehlin 1909; Brunet and Sudre 1987a, b). Asian lophiomerycids diversified in the Oligocene with *Lophiomerx*, reported from China, Pakistan, Central Asia, the Caucasus, and western Europe. In *Lophiomerx*, the central metacarpals and metatarsals are unfused, while the lateral metatarsals are reduced (at least in western European species) (Fig. 2.12). These characters indicate that *Lophiomerx* may have inhabited forested or swampy habitats, as in the living tragulid *Hyemoschus aquaticus*.

Bovidae

With over 130 living species, Bovidae is the most diverse family of extant large mammals. Thirty species are found in SSEA, most of these endemic to the region. Among these is the saola, *Pseudoryx nghetinhensis*, endemic to the forests of Laos and Vietnam, and which was only scientifically discovered in 1992 (Dung et al. 1993). Although somewhat goat-like in appearance, the saola is in fact the closest living relative of the clade comprising buffaloes and oxen (Bovini). The discovery of the saola was totally unexpected, since more than 50 years had passed since the last scientific discovery of a new living large mammal (the kouprey, from Cambodia) (Urbain 1937). This offered a reminder of the sheer richness of Southeast Asia's biodiversity, and of the potential for future discoveries to be made there.

Diets of bovid species may generally be characterized as relying either on browse (leaves) or graze (grass), or a combination of both. They inhabit a wide range of habitats from humid rainforests to semi-arid plains and deserts, and from coastal areas to the high altitudes of the Himalayas. The earliest fossil bovids are recorded at around 18 Ma from both SSEA (Pakistan) and Europe (France)

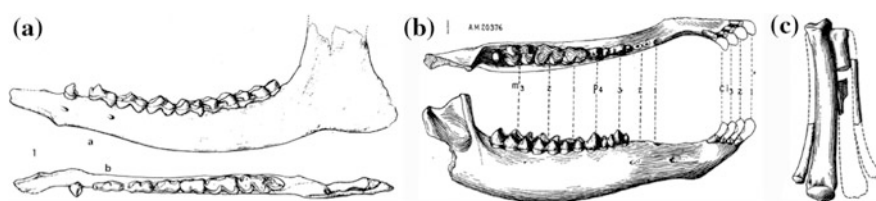


Fig. 2.12 **a** Lower jaw (holotype) of *Lophiomerx mouchelini* from the early Oligocene of Villebramar (SW France), MP 22. (from Brunet and Sudre 1987a, b). Notice the retention of a p1 in this species, which is significantly smaller than in *L. chalaniati*, the type species of the genus. **b** Lower jaw (holotype) and **c** partial metacarpals of *Lophiomerx angarae* from the late Eocene of Ardyn Obo, Mongolia (from Matthew and Granger 1925). Specimens not to scale

(Ginsburg and Heintz 1968; Solounias et al. 1995; Ginsburg et al. 2001; Antoine et al. 2013) and the crown clade probably originated around this time or shortly thereafter (Bibi 2013). SSEA has been an important arena of bovid evolution, especially since this region's faunas were partly isolated from those of Central Asia and Africa throughout much of the Neogene (Brunet et al. 1984; Bibi 2007; Lihoreau et al. 2007a, b).

Most extant SSEA bovids can be classified among four subclades (tribes): Bovini, comprising buffaloes and oxen; Antilopini, gazelles and relatives; Caprini, wild goats, sheep, and relatives; and Boselaphini, represented only by the nilgai and chousingha. With the exception of Boselaphini, which are today endemic to the Indian Subcontinent, these tribes are all widespread. Bovini today range across Eurasia, Africa, and North America, but both the fossil record and phylogenetic reconstructions indicate the origins of the Bovini are probably in the Middle Miocene of SSEA (Pilgrim 1939; Hassanin and Ropiquet 2004; Bibi 2007; Hassanin et al. 2013). Bovini developed many of their characteristic dental features in the late Miocene (around 9 Ma), and may have first spread out of SSEA and into Africa coincident with major environmental changes and the spread of tropical (C₄) grassland habitats (Bibi 2007). The lineage leading to the Asian buffalo (*Bubalus* spp.) is first recognized in the late Pliocene *Proamphibos* in the Siwaliks (Tatrot Formation) (Pilgrim 1939; Bibi 2009), and continues with *Hemibos* in the late Pliocene and Pleistocene (Pilgrim 1939; Gentry 1978; Barry et al. 1982; Bibi 2009). *Bubalus* populated Southeast Asian islands and differentiated into several 'dwarfed' species. These are represented today by the tamaraw (*Bubalus mindorensis*) of Mindoro Island, and the mountain and lowland anoas (*B. quarlesi* and *B. depressicornis*) of Sulawesi and Buton (Groves 1969). Records of fossil buffalo from the modern SE Asian archipelago include *Bubalus cebuensis* of Cebu (Croft et al. 2006), and the oldest records may be of *Bubalus palaeokerabau* at 1.2 Ma at Ci Saat in Java (Louys et al. 2007). This latter date matches the early Pleistocene age estimates for the dispersal of *Bubalus* from the mainland onto the islands (Tanaka et al. 1996; Bibi 2013; Hassanin et al. 2013).

Little is known about the evolution of wild oxen (*Bos* spp.), but their present ranges along with molecular phylogenies also suggest an SSEA origin for this clade, which includes the progenitor of domesticated cows (*Bos primigenius*) and the cold-adapted yak and bison clade (Hassanin and Ropiquet 2004; Hassanin et al. 2013). *Bison sivalensis* from the Pliocene or Pleistocene Siwaliks has been proposed as closely related to both bison and yak (Lydekker 1878; Pilgrim 1939; Olsen 1990), and its oldest records may come from the Tatrot formation at around 3 Ma (Khan et al. 2010). *Bos namadicus* and *Bos acutifrons* are two other SSEA fossil bovines that may be related to other living species of *Bos*. *Bos namadicus*, also referred to as the 'Narbada Ox' or Indian aurochs (Fig. 2.13) (Lydekker 1898; Gentry et al. 2004), had a horn span of about 1.25 m (as estimated from Lydekker 1878, p. 11) and was probably conspecific with the aurochs of Europe, *Bos primigenius* (Rütimeyer 1878; Lydekker 1898, p. 19; Gentry 1967). Molecular evidence suggests two or three separate domestication events for cattle around

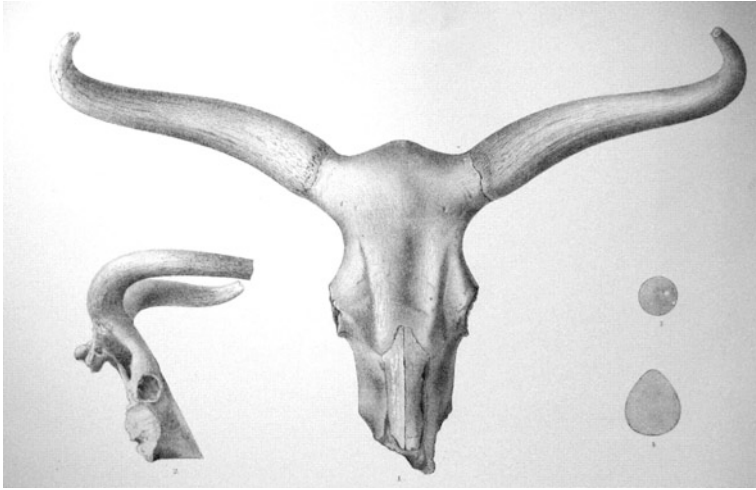


Fig. 2.13 The Narbada Ox or Indian aurochs, *Bos namadicus* or *B. primigenius namadicus*, may be the Pleistocene progenitor of domesticated cattle, and perhaps specifically of the zebu (*Bos taurus indicus*) (Gentry et al. 2004) (figure from Lydekker 1878, p. 11)

10,000 years ago, one of which occurred in the vicinity of northern India or Pakistan (Loftus et al. 1994; McTavish et al. 2013).

Gaur (*Bos gaurus*), banteng (*Bos javanicus*), and kouprey (*Bos sauveli*) are SSEA's wild oxen. Gaur and banteng have both been domesticated, but little is known about the kouprey. First described in 1937, the kouprey was only rarely sighted up through the 1960s, and a lack of convincing evidence of any viable populations since that time suggests that the kouprey may be extinct (MacKinnon and Stuart 1988; www.iucnredlist.org). Suggestions that the kouprey may be a feral hybrid of banteng and zebu cattle (Galbreath et al. 2006) have been refuted (Hassanin and Ropiquet 2004, 2007), and molecular age estimates suggest a divergence from the gaur and banteng in the late Pliocene or early Pleistocene (Hassanin and Ropiquet 2004).

Molecular evidence has shown the saola (*Pseudoryx nghetinhensis*) to be the living sister taxon to Bovini (Hassanin and Douzery 1999; Gatesy and Arctander 2000; Hassanin et al. 2013), and its geographic range and morphologically conserved features provide further support for a SSEA origin of Bovini. No fossils of the saola are known, but presumably its lineage has inhabited the forests of southeast Asia at least since its divergence from the Bovini, which molecular estimates place at between about 14 and 10 Ma (Hassanin et al. 2012; Bibi 2013).

While totally restricted to Africa today, Reduncini (e.g., waterbuck, reedbuck, lechwe) have an ancient fossil record in SSEA. Reduncins are documented in the late Miocene Siwaliks as early as 9.3 Ma (Pilgrim 1939; Barry et al. 2002; Badgley et al. 2008). Reduncin species are also recorded in the younger (late Pliocene–Pleistocene) formations of the Siwaliks (Pilgrim 1939; Khan et al. 2008), up into the Late Pleistocene (Vrba et al. 2015).

Alcelaphini (e.g., wildebeest, hartebeest) and Hippotragini (e.g., roan, oryx) are also today restricted to Africa (and Arabia), but show up as fossils in the younger levels of the Siwaliks. Pilgrim (1939) described *Sivatragus brevicornis* and *Sivatragus bohlini* from the Tatrot and Pinjor formations, respectively, and *Sivoryx sivalensis* and *Sivoryx cautleyi*, from the Pinjor and an unknown horizon, respectively. Vrba and Gatesy (1994) demonstrated the affinities of *Sivatragus* with *Hippotragus*, and *Sivoryx* with *Oryx*, and argued for a migration event of these hippotragins out of Africa and into SSEA at around 3–2.5 Ma, coincident with global cooling and sea level lowering (Vrba 1995).

Antilopini (e.g., gazelles) and Caprini (e.g., goats, sheep) have a large fossil record, but most of this is not resolved phylogenetically. Caprini are represented by eastern Asian and island dwelling serows (*Capricornis* spp.) and by essentially central Asian montane species (*Capra*, *Ovis*, *Hemitragus*, *Budorcas*, *Naemorhedus*), the fossil record for all of these species being poor. Antilopini are far less diverse elements of the SSEA fauna, and the three living species (*Gazella bennetti*, *G. subgutturosa*, *Antilope cervicapra*) are found in relatively dry habitats of the Indian Subcontinent. The blackbuck (*A. cervicapra*) is the only living antilopin with spiraling horns and may be the sole survivor of a late Miocene radiation of diverse spiral-horned antilopins (e.g., *Prostrepsiceros* spp.) that ranged from Greece through to Afghanistan (Gentry 2003, 2010).

Giraffidae

Living giraffes (*Giraffa*, *Okapia*) are also restricted to Africa, but the family has a fossil record spanning much of southern Europe and southern Asia. Early Miocene giraffids or giraffid-like taxa appear about the same time in Africa, the Mediterranean, and Pakistan (Solounias 2007). They persist in all these regions into the Pleistocene, and attain a peak diversity in the late Miocene and Pliocene, when it is not uncommon to find several species at a single locality (Solounias 2007). Across this geographic range, and since the late Miocene, giraffids have been represented by different forms including some similar to *Giraffa* (with a long neck and long limbs), others more like *Okapia* in form, and the extinct sivatheres (Sivatheriini) which reached large sizes and had short necks and short stocky limbs (Fig. 2.14).

SSEA fossil giraffes are known mainly from the Siwaliks and were described by Falconer and Cautley (1844), Lydekker (1882a, b), Pilgrim (1911), and Colbert (1935a, b) the latter author recognizing no less than 13 different species in the Siwaliks sequence. More recent accounts of Siwalik faunas (Barry et al. 2002; Badgley et al. 2008) recognize less diversity. *Giraffa punjabiensis* is recorded as ranging from 8.9 to 7.2 Ma (Badgley et al. 2008), followed by *Giraffa sivalensis* in the upper Siwaliks (late Pliocene to Pleistocene). Falconer and Cautley (1844, reprinted in Murchison 1868, p. 16), illustrate an elongated neck vertebra of *G. sivalensis*, demonstrating it had a long neck as in modern *Giraffa camelopardalis*.

Sivatheres are known from the Miocene to Pleistocene, from SSEA to Greece and into Arabia and across Africa. In the Siwaliks, they are represented by at least a single long-lived lineage comprising *Giraffokeryx punjabiensis* (13.6–10.3 Ma) and

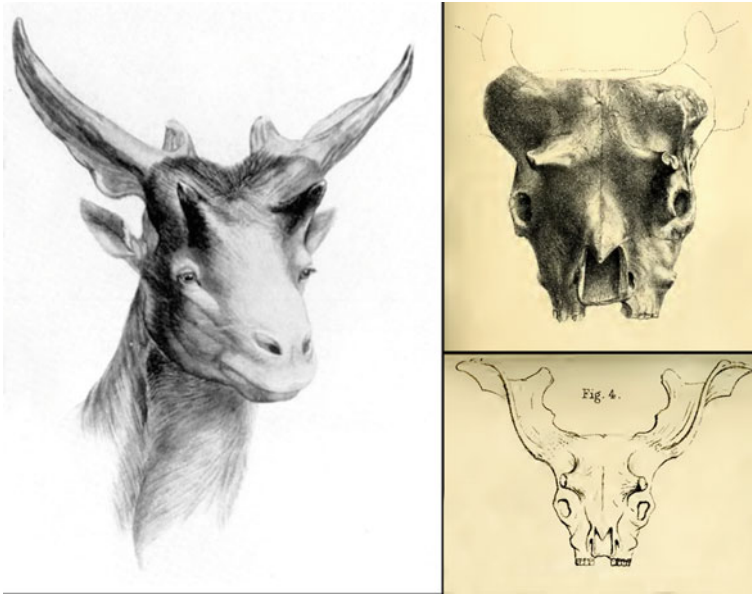


Fig. 2.14 The head of *Sivatherium giganteum*, a massive giraffid with palmate antler-like ossicones that inhabited SSEA in the late Pliocene and Pleistocene. *Left* sketch from Colbert (1936), *right* sketches from Falconer (in Murchison 1868, p. 19 and 21)

Bramatherium megacephalum (10.3–7.1 Ma) (Barry et al. 2002; Badgley et al. 2008). Pliocene and Pleistocene sivatheres were massive, and are typified by *Sivatherium giganteum*, which had palmate branching ossicones (Fig. 2.14) (Falconer and Cautley 1836a, b, c). With a lower molar row length of around 170 mm (metrics in Khan et al. 2011), *S. giganteum* would have weighed around 3,000 kg (our estimate using the prediction equations in Janis 1990). *Sivatherium giganteum* persists in the Indian Subcontinent up to about 1.7 Ma (Dennell et al. 2006, 2008), or perhaps as late as 0.6 Ma (Rao et al. 1995; Nanda 2002).

Cervidae

The cervid (deer) family today spans arctic to tropical latitudes, and tundra to rainforest habitats in both the new and old worlds. They reach very high diversity in SSEA, with some 20 species (genera *Cervus*, *Axis*, *Muntjacus*, *Rucervus*, *Rusa*). Cervids are divided into two subclades, the Cervinae, including most Eurasian deer species (=Plesiometacarpalia), and the Capreolinae (or Odocoileinae), comprising primarily American deer (=Telemetacarpalia) (Groves 2007; Hassanin et al. 2012). All SSEA deer belong to Cervinae, which is distinguished by the retention of the proximal ends of the lateral metacarpals (distal in Capreolinae).

The earliest stem cervids are known from the early Miocene of Europe (Germany, France, Spain) (Azanza 1993; Gentry et al. 1999). The middle Miocene *Euprox*, also from Europe, may be close to the origin of the crown clade (Gentry 1994; Gentry et al. 1999). A mid-Miocene or earliest late Miocene origin for the

crown clade is also supported by molecular age estimates (Gilbert et al. 2006; Hassanin et al. 2012; Bibi 2013).

If there is a single main ecological difference between deer (cervids) and antelopes (bovids) it is the fact that deer never truly adapted to and diversified in xeric habitats. Compared to bovids, which have evolved numerous independent radiations into a diversity of open habitats (in Bovini, Alcelaphini, Hippotragini, Caprini, Antilopini), cervids are by contrast still strongly tied to the presence of water and tree cover. One of the main features distinguishing the modern large mammal fauna of southern Asia from that of Africa is the presence of deer in southern Asia, but this may be the result of a relatively recent (late Pliocene) immigration southwards from Central Asia. Cervids are known in Asia from the middle Miocene (*Dicrocerus*, *Lagomeryx*, *Stephanocemas*), but, with the exception of a middle Miocene occurrence in northern Thailand (Ginsburg and Ukkakimapan 1983; Suraprasit et al. 2014), Miocene cervids are documented only from areas situated north of the Alpine-Himalayan Range. There are no fossil cervids from the rich Neogene sedimentary record of Pakistan (Sulaiman Range and Potwar Plateau) older than the first appearance of *Cervus* in the Pliocene and Pleistocene Tatrot and Pinjor beds (Fig. 2.15) (Barry et al. 1982, 2002). (Reported cervids from Miocene and Pliocene Siwaliks [Ghaffar et al. 2006, 2010, 2011a, b; Samiullah and Akhtar 2007] are fragmentary and appear to be bovids). Upper Siwaliks cervids were described by Lydekker (1876a, b) and Brown (1926), and revised by Azzaroli (1954).

Late Miocene to late Pliocene mammal localities in Iraq (Thomas et al. 1980), United Arab Emirates (Bibi et al. 2013), and Saudi Arabia (Thomas et al. 1982), all situated south of the Alpine-Himalayan chain, were, like SSEA at this time, also devoid of cervids. In contrast, the late Miocene locality of Maragheh in Iran, located north of the Taurus-Zagros Mountains, has yielded cervid remains (Tobien 1980; Bernor 1986; Ataabadi et al. 2013). Cervids are also documented in the late Miocene of Lufeng and Yuanmou in southern China, which is interesting considering that southern Chinese faunas were otherwise more similar to those of southern



Fig. 2.15 Cranium with antlers of '*Cervus*' *punjabiensis* from the upper Pinjor (Middle Pleistocene) of the Siwaliks (from Brown 1926). Views not to scale

Asia than to central or northern China (Dong and Qi 2013). Otherwise, it appears that cervids spread to Indonesia and the Philippines only later, in Pliocene to Pleistocene times (Reis and Garong 2001), never reaching Australia (until recent introduction by humans). Throughout most of their evolutionary history since the early Miocene, therefore, cervids were absent from SSEA, and their modern presence there can be traced no farther back than the late Pliocene (ca. 3 Ma). Extant cervids generally live in lowlands and it has been proposed that the ~10,000 km-long mountain belt resulting from the closure of the Neotethys Ocean impeded their southward dispersal (Brunet et al. 1984). High cervid species richness in modern SSEA implies high rates of diversification or immigration into the area since the latest Pliocene and early Pleistocene.

Muntjacs (*Muntjacus*, *Elaphodus*) are small deer that possess massive upper canines, superficially similar to those in tragulids, and distinguishing them from all other pecorans. With their reduced antlers and large upper canines, muntjacs have been proposed to represent primitive deer (Azanza 1993), but their molecular affinities with Cervinae (Gilbert et al. 2006; Hassanin et al. 2012) suggest morphological reversions that accompanied adaptation to a forest environment (Groves 2007). The oldest fossil muntjacs are known from the late Miocene (9–7 Ma) of southwestern China (Dong et al. 2004), suggesting the presence there of forested landscapes, in contrast to the desert climate that prevails in that area today and which probably developed as a result of increased uplift in the Tibetan Plateau in the Plio-Pleistocene (An et al. 2001).

Camelidae

Although the natural range of camelids today is restricted to parts of Asia, Africa, and South America, camelids first evolved in the Eocene of North America, where they remained endemic until their first dispersal into Eurasia and Africa in the late Miocene (Honey et al. 1998). Camelids entered South America in the early Pleistocene and went extinct in North America in the end Pleistocene megafaunal extinctions (Honey et al. 1998). Their North American fossil record is abundant and diverse, but they are otherwise rather rare components of fossil sites in Eurasia and Africa.

Falconer and Cautley (1836a, b, c, reprinted in Murchison 1868) described a fossil camel from the Siwaliks, which they named *Camelus sivalensis* (Fig. 2.16). These authors, along with Colbert (1935a, b), believed the Siwalik fossil camel was very similar to both the bactrian and dromedary camels alive today, which is surprising considering there are major differences between the two living species. Colbert (1935a, b) records *C. sivalensis* in the Pleistocene Pinjor Formation, while Nanda (2002, 2008) notes its presence in the preceding late Pliocene Tatrot Formation (ca. 3.6–2.6 Ma) as well. *Camelus antiquus*, first mentioned by Falconer and Cautley (1836a, b, c) and later described by Lydekker (1885), was taken by Matthew (1929) and Colbert (1935a, b) to be a synonym of *C. sivalensis*.

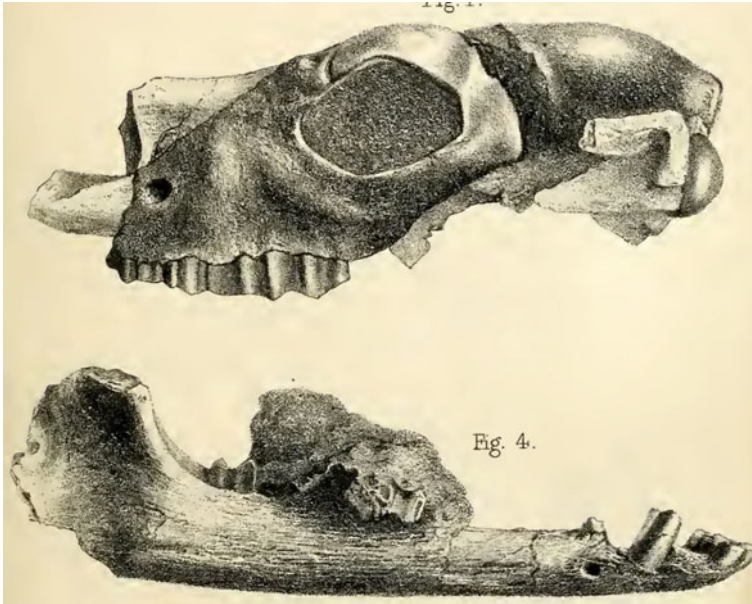


Fig. 2.16 *Camelus sivalensis*, a Pliocene-Pleistocene fossil camel from the Siwaliks (Falconer and Cautley 1836a, b, c; Murchison 1868, p. 18)

2.6.2 *Perissodactyla*

Living perissodactyls are limited to a few species of equids, rhinos, and tapirs, all of which today have restricted distributions. However, in the past, and especially during the Eocene, perissodactyls were much more diverse and widely distributed. Early perissodactyls may have originated from a taxon similar to *Radinskya* from the Paleocene of China (Froehlich 1999; Prothero and Schoch 2002). The earliest fossil perissodactyls (*Hyracotherium* spp.) appear at the beginning of the Eocene, almost simultaneously in Europe, Asia, and North America (Rose 2006). By the end of the early Eocene, perissodactyls had differentiated into lineages that would lead to equids, rhinocerotids, tapirids, and other extinct families. Perissodactyl diversity dropped steeply after the Eocene and, while competition with newly evolved ruminant artiodactyls has been proposed, the limited ability of perissodactyls to cope with increasingly dry and seasonal environments is more likely (Cifelli 1981a, b; Janis 1989).

Tapiridae

A single tapir species (*Tapirus indicus*) inhabits the Old World, and is restricted to Southeast Asia, namely the Malay Peninsula and Sumatra. The closest living relatives of the Asian tapir are to be found in Central and South America, and this hints at the broader geographic distribution that tapirs once enjoyed. Living tapirs are remarkably conserved in their morphological features and most classifications

include all four species into a single genus. This is remarkable given that molecular clock estimates put the divergence between them at about 30–20 Ma (Steiner and Ryder 2011). The earliest member of the tapir lineage (Tapiroidea) from the early Eocene of North America and Asia had many of the basic morphological features of this clade, and tapirs appear to have changed very little morphologically in the past 50 million years (Rose 2006). The main morphological changes since the early Eocene have primarily involved the development of the nasal trunk as recorded through the reduction in size of the nasal bones (Rose 2006). Their preferences for humid and forested habitats (less so *T. pinchaque*) may also be relatively unchanged since the Eocene, and perhaps their shrinking geographic distribution may have simply tracked the shrinking of tropical forest habitats in the later Cenozoic and especially during the late Neogene.

The earliest fossils assigned to Tapiridae (crown or stem) are from the middle Eocene of North America (Colbert and Schoch 1998; Rose 2006), while fossils assigned to *Tapirus* are as old as the middle Miocene of Europe (Heissig 1999) and the late Miocene of North America (Colbert and Schoch 1998). Tapiroids have been low in diversity since the Oligocene, and have generally declined in diversity since then (Schoch 1989; Colbert and Schoch 1998). They are relatively rare in the Neogene fossil record.

Fossil remains assigned to *Tapirus indicus*, though possibly representing multiple *Tapirus* species, are recorded from as old as the early Pleistocene, from southern China to Java (Hooijer 1947; Tong 2005). The extant species appears to have coexisted with at least one other, the giant tapir *Megatapirus augustus*, which is known from the late middle Pleistocene of southern China and SE Asia (Hooijer 1947; Tougaard 2001). This species differed from *Tapirus indicus* in its much larger size, being about 25 % larger in dental dimensions (Matthew and Granger 1923), which translates to about a doubling of body mass (our estimate based on the prediction equations in Janis 1990).

Rhinocerotoidae

Rhinocerotoids (amynodontids, hyracodontids, and rhinocerotids) were taxonomically and ecologically diverse during the Paleogene and early Neogene of Eurasia and North America. Since that time, hyracodontids and amynodontids have gone extinct and rhinocerotids have dispersed into Africa. The ancestry of rhinocerotoids is Holarctic and represented by *Hyrachyus*, an early to middle Eocene form that was widely distributed in Eurasia and North America (Prothero et al. 1986). In the Paleogene localities of Asia, rhinos outnumber all other ungulate mammals perhaps with the exception of tapiroids, another group of perissodactyls (generally smaller in size than rhinos) that flourished in Asia. Most Paleogene rhinos were hornless and the earliest horned rhinos possessed paired horns located at the tip of the nose. In rhinocerotids and hyracodontids, the upper third molar metastyle is reduced, resulting in a sub-triangular (to truly triangular in rhino) shape.

Amynodontidae

Amynodontids were ecologically diversified rhinocerotoids, with some resembling the hippopotamus (*Metamynodon*, with a body suggesting amphibious habits) and

others more tapir-like (*Cadurcodon*, probably with a tapir-like proboscis) (Wall 1980). Their mode of life and feeding adaptations remain poorly understood, as are the origins and affinities of the basalmost forms. Amynodontids are represented by around a dozen genera that extend from the middle Eocene to the late Oligocene. Several Asiatic forms are poorly diagnosed, but they all seem to have been hornless. They probably originated in Asia during the Eocene (Wall and Manning 1986), though their earliest representatives are from the early middle Eocene of North America, and reached their maximum diversity in Asia during the Eocene–Oligocene transition (Wall 1989). *Cadurcotherium* is one of the ‘Grande Coupure’ immigrants into Europe, and the latest representative of the family in Asia (Métais et al. 2009).

Hyracodontidae

Hyracodontids flourished in the Eocene and Oligocene of Asia (Prothero 1998a, b). Most of these were medium-sized and fairly cursorial ungulates with relatively elongate and gracile limbs. Across Asia, *Hyracodon* and *Forstercooperia* are the most common hyracodontids of the Eocene, while *Eggysodon* is the common taxon of the Oligocene. Among hyracodontids, the paraceratherines, including the emblematic *Paraceratherium* (= *Indricotherium*, *Baluchitherium*, from Pakistan, Central Asia, China, and Turkey) attained gigantic sizes, reaching about 7 m in height and maximum weights of 10–20 tons (Lucas and Sobus 1989; Fortelius and Kappelman 1993), making them, along with some fossil proboscideans, among the largest terrestrial mammals ever known (Fig. 2.17). Besides their large size, paraceratherines can be differentiated from other hyracodontids by a derived anterior dentition with conical incisors, such as *Paraceratherium*, which was characterized by enlarged, procumbent first upper and lower incisors and a loss of the remaining two incisors, the canine, and the first deciduous premolars. The earliest paraceratherines were small hyracodontids known from the middle Eocene of North America (*Forstercooperia*) and China (*Juxia*). Large paraceratherines appeared during the early Oligocene in Asia, reaching maximum sizes during the

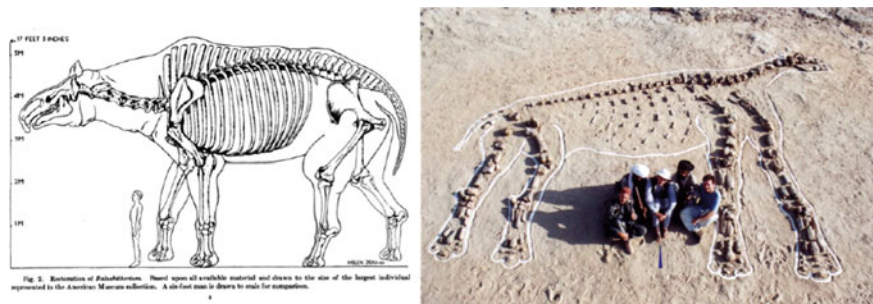


Fig. 2.17 The massive hyracodontid *Paraceratherium* as envisioned by Granger and Gregory (1935) (left), and a skeleton reconstructed in the field in the Bugti Hills showing the correct position and length of the neck (photo Mission Paléontologique Française au Balouchistan, MPFB)

late Oligocene and possibly persisting into the early Miocene. Paraceratherines appear to have possessed no sexual dimorphism, and were browsers in vast alluvial plains, dispersing often between Eurasia and North America (Radinsky 1967).

The sheer size of the gigantic paraceratherines (=indricotheres) raises functional and paleobiological problems (Fortelius and Kappelman 1993). For example, the cursorial ancestry of paraceratherines produced particular morphological features of the limbs (distinct from those of elephants) in response to the need to support such great body weight (over 15 tons in some individuals). Additionally, the quantity of plant matter (leaves or fruits) such a large animal would have to ingest daily to survive is a matter of question. Further investigation is required to better understand the extinction of these giants in the early Miocene, perhaps a result of climatic changes that took place in the Asian interior due to uplift of the Tibetan Plateau and shrinkage of the Paratethys Sea.

Rhinocerotidae

The five rhinoceros species living today are all in danger of extinction, but rhinocerotids comprised a large, diverse, and widespread clade throughout most of the Neogene. An important aspect of the evolutionary history of this clade involves the evolution of nasal horns and the transition from an older mode of combat using enlarged incisor tusks. The earliest fossil rhinocerotids (stem taxa) are known from the late Middle to Late Eocene of North America, Central Asia, and SSEA (Thailand and Vietnam) (Prothero 1998a, b; Antoine et al. 2003a, b; Böhme et al. 2013). These earliest rhinos did not have nasal horns, but instead had enlarged incisors forming a shearing complex with a chisel-like upper first upper incisor and a tusk-like lower second incisor. In contrast, all living rhinos have well-developed horns and incisors that are reduced (Asian species) or entirely lost (African species). The earliest horned rhino is the North American early Oligocene to early Miocene *Diceratherium*, which shows a morphological balance between the development of the horn and the incisor tusk complex (Heissig 1989; Prothero 1998a, b). Heissig (1989) reported that Asian rhinos use their tusk-like incisors to attack, and their horns only for interspecific combat, suggesting that rhino horns first evolved for sexual competition and display rather than defense.

Rhinos were diverse during the late Oligocene and Miocene of SSEA. All living rhinos belong to a single tribe, Rhinocerotini, but fossil rhinos represent a far greater diversity, with extinct clades such as Elasmotheriini, Aceratheriini, and Teleoceratini. *Brachypotherium* (Teleoceratini), for example, was a long-lived lineage, recorded from the early to the late Miocene of SSEA, from Pakistan to Thailand (Chaimanee et al. 2004; Chavasseau et al. 2006; Bhandari et al. 2010; Antoine et al. 2013). In the earliest Miocene (23–20 Ma) of the Bugti Hills, Pakistan, no less than nine separate rhino species have been found to co-occur in a single level (Antoine et al. 2010). Neogene Siwalik rhinocerotids were first described by Falconer and Cautley (1847), and subsequently by Matthew (1929), Colbert (1934, 1935a, b, 1942), E. Khan (1971), and A.M. Khan (2010), among others. Antoine et al. (2003a, b) reviewed the Paleogene record, and Antoine (2012) reviewed the Quaternary rhinocerotids of Southeast Asia.

Though only found in SSEA today, *Dicerorhinus* appears to have been a late-comer to the region, having perhaps first evolved in Central Asia and entering SSEA only sometime during the Pliocene, as evidenced by *Dicerorhinus gwebi-nensis*, a fossil species from the early Pleistocene of the Upper Irrawady in Myanmar (Zin-Maung-Maung-Thein et al. 2008, 2010). Fossils of the living Sumatran rhino (*Dicerorhinus sumatrensis*) are as old as the early Pleistocene or late Pliocene of southern China (Tong and Guérin 2009; Zin-Maung-Maung-Thein et al. 2010). Apparently, the Sumatran rhino's dentition has changed little from Oligocene taxa like *Lartetotherium* (Heissig 1989), reflecting the conservation of morphological features in this lineage. *Rhinoceros* on the other hand has a much older Neogene presence in SSEA (Zin-Maung-Maung-Thein et al. 2010). The oldest records of this genus may be *Rhinoceros* aff. *sivalensis* from the Siwaliks at 8.5 Ma (Fig. 2.18) (Badgley et al. 2008). *Rhinoceros* is believed to have descended from *Gaindatherium* (Colbert 1934, 1935a, b, 1942; Prothero et al. 1989), which is known from the Chitarwata Formation (23–20 Ma) in the Bugti region of Pakistan (Antoine et al. 2010) as well as in the Siwaliks from 16.0 to 7.3 Ma (Badgley et al. 2008). In general agreement with the fossil record, molecular estimates put the origin of the crown clade Rhinocerotidae at between 30 and 20 Ma, with

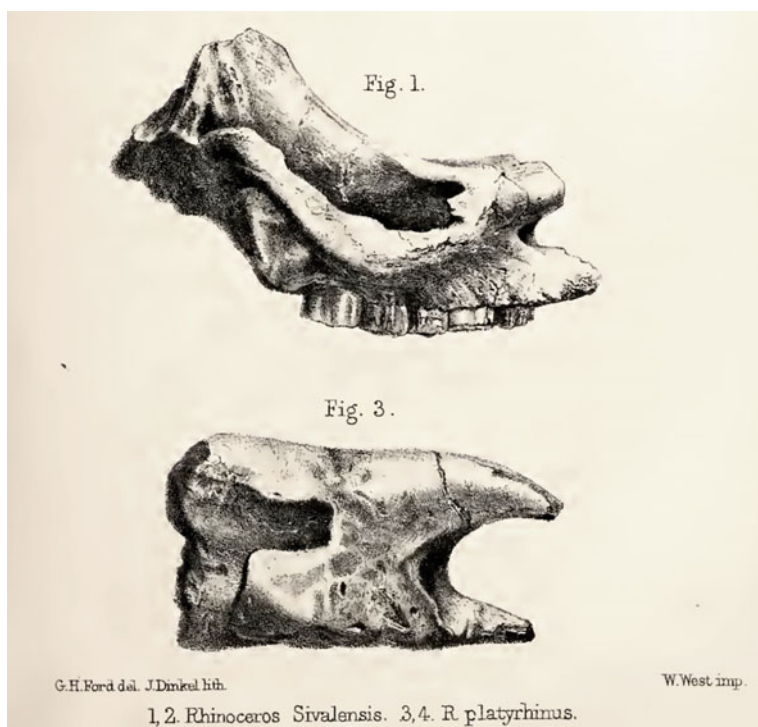


Fig. 2.18 Fossil skulls of *Rhinoceros sivalensis* and *Punjabitherium platyrhinus* from the Pleistocene (Pinjor) Siwaliks, both in lateral view (from Murchison 1868, p.14)

Rhinoceros and *Dicerorhinus* having been separated for just as long (Steiner and Ryder 2011).

Equidae

Equids are represented today by horses, zebras, and donkeys. Equids hold a special place of importance among humans, as the horse and donkey have supported agrarian and nomadic civilizations since the mid-Holocene. Today, nondomesticated equids in SSEA are basically limited to the endangered Asiatic wild ass, *Equus hemionus* (the kiang—*Equus kiang*—can be found in northernmost India, but its range is essentially in the Tibetan highlands). In SSEA, the IUCN (www.iucnredlist.org) records only a single wild population of the Asiatic wild ass, located in northwestern India.

The oldest recognized fossil (stem) equid is *Sifrihippus sandrae* (previously *Hyracotherium sandrae*) from the earliest Eocene (ca. 55.5 Ma) of North America (Froehlich 2002). Most of the evolutionary history of equids took place on the North American continent, so much so that the first appearances of progressive equid clades in the Old World are recognized as important biochronological events. Among these was the appearance of *Anchitherium* in the early Miocene (MN 3) in Europe and Asia, with anchitheriids equids persisting in the Old World until the early late Miocene (Bernor and Armour-Chelu 1999). Anchitheriids are not, however, recorded in SSEA (Bernor and Armour-Chelu 1999).

A second major dispersal event was the ‘*Hipparion* Datum,’ marking the spread of hipparionin equids from North America and into Eurasia and Africa at around 11 Ma. One of the earliest Old World occurrences of hipparionin equids is from the Siwaliks at 10.7 Ma (Barry et al. 2002; Badgley et al. 2008). A number of fossil equid species from the Siwaliks were named by Falconer and Cautley (1849), Lydekker (1882a, b), and Pilgrim (1910a, b), with revisions by Matthew (1929), Colbert (1935a, b), Hussain (1971), MacFadden and Woodburne (1982), and Bernor and Hussain (1985). *Hipparion* makes its last appearance in SSEA in the Tatrot fauna, dating to about 3.3–2.7 Ma (Barry et al. 1982; Dennell et al. 2006), which is significantly earlier than its last appearances in Africa and North America, where it survived into the middle and late Pleistocene, respectively (MacFadden 1998; Bernor et al. 2010).

The third major dispersal out of North America was that of *Equus*, the genus to which all modern equids belong. The evolution of *Equus* also took place in North America, tracing back to an ancestor like *Dinohippus* of the North American late Miocene (Bernor and Armour-Chelu 1999; Prothero and Schoch 2002). The first appearance datum of *Equus* in Eurasia is at 2.6 Ma, and it appears simultaneously in Europe and the Siwaliks (Lindsay et al. 1980; Barry et al. 1982; Bernor and Armour-Chelu 1999), and shortly thereafter in Africa (Bernor et al. 2010). *Equus* differs from its numerous fossil relatives in several respects, but most easily observed among these may be the extreme reduction of the lateral metapodials, leaving only a single large and central element (metapodial III), and the great increase in tooth crown height, permitting extremely high rates of tooth wear as might occur with grass-feeding, especially in dry and dusty environments.

Pleistocene fossil *Equus* is recorded from the Pinjor fauna of the Siwaliks as *Equus sivalensis* and *E. namadicus* (Falconer and Cautley 1849; Colbert 1935a, b; Barry et al. 1982; Nanda 2002; Dennell et al. 2006; Nanda 2008), and in Myanmar as *E. yunnanensis* (Nanda 2008). There are overlapping records of both *E. namadicus* and the living Asiatic wild ass (*E. hemionus*) in the late Pleistocene of India (Chauhan 2008; Nanda 2008). The record of Indian fossil *Equus* is reviewed and discussed by Badam (1977) and Badam and Tewari (1974). Ironically, after over 50 million years of evolution in the North American continent, equids went extinct there in the latest Pleistocene megafaunal extinction, only to be reintroduced to the Americas by European colonialists in the fifteenth and sixteenth centuries.

Molecular phylogenetic analyses indicate a clade uniting onagers, asses, and zebras (Steiner et al. 2012). The fossil *Equus sivalensis* has been may be closely related to the living Asiatic ass (Prothero and Schoch 2002). If correct, this would indicate the separation between Asian and African asses may have already been in place by the early Pleistocene.

Chalicotheriidae

Chalicotheres are an extinct group of large and strange perissodactyls with no living analog. They were characterized by the possession of claws rather than hooves and low-crowned teeth that indicate a leaf-eating diet (Fig. 2.19). The earliest chalicotheres probably appeared in the Early Eocene of Asia (Mongolia) and North America, and were well represented in both continents by the Middle Eocene (Rose 2006). Chalicotheres are quite rare in fossil assemblages, so their evolutionary history and interrelationships are difficult to piece together, including also the story of their Pleistocene extinction.

The schizotheriine chalicotheres *Phyllotillon naricus* is recorded in the Oligocene and early Miocene Chitarwata Formation in Pakistan (Forster-Cooper 1920; Métais

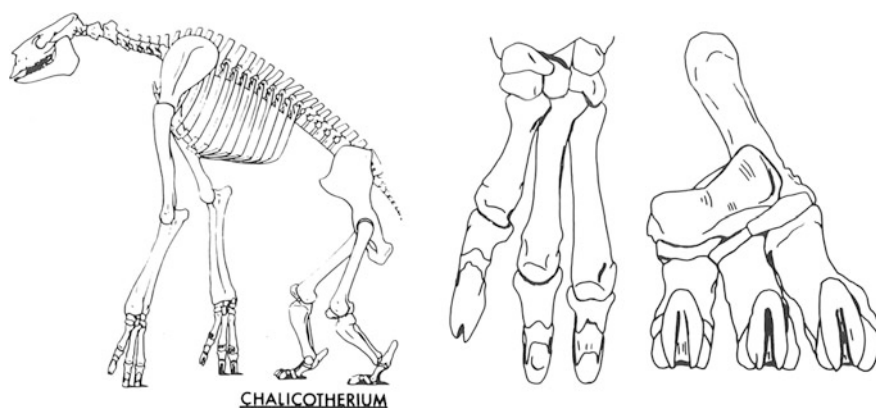


Fig. 2.19 Skeleton, hand, and foot of *Chalicotherium grande*, closely related to *Chalicotherium salinum* from the late Miocene of Pakistan. Species of *Chalicotherium* had long forelimbs, short hindlimbs, and large claws (from Zapfe, 1979 in Coombs 1989)

et al. 2009; Antoine et al. 2013). *Chalicotherium* is first recorded in the early Miocene of Africa, Europe, and Asia, and survives into the late Miocene. These were large animals marked by long forelimbs and shortened hindlimbs in gorilla-like proportions, and may have lived in forested habitats and adopted bipedal postures for browsing from trees, with the claw being used to hook onto branches (Fig. 2.19) (Coombs 1989). In SSEA, '*Chalicotherium*' *pilgrimi* is recorded in the early Miocene Chitarwata Formation in Pakistan (Métais et al. 2009; Antoine et al. 2013), and *Chalicotherium salinum* is recorded in the Siwaliks at 12.9–8.0 Ma (Forster-Cooper 1922a, b; Pickford 1982; Barry et al. 2002; Badgley et al. 2008; Khan et al. 2009). Further reports of Miocene chalicotheres from SSEA come from Thailand, southern China, and Myanmar (Chavasseau et al. 2009a, b and references therein).

Young SSEA chalicotheres are represented by *Anisodon* (= *Nestoritherium*) *siwalense* from the Pleistocene Pinjor (Falconer and Cautley 1843; Colbert 1935a, b) and *Nestoritherium/Anisodon* sp. from the Pleistocene of the Irrawady Formation in Myanmar (Takai et al. 2006). These records may represent the last appearance of chalicotheres (see Coombs 1989, Fig. 24.4).

2.6.3 Proboscidea

The order Proboscidea is named for the characteristic nasal proboscis (trunk), made up of a fused nose and upper lip. The earliest fossil Proboscideans are recognized from the earliest Eocene (around 55 Ma) of Africa (Gheerbrant and Tassy 2009; Sanders et al. 2010). Though the first appearance of proboscideans in Eurasia has been given important biochronological significance (Madden and Van Couvering 1976; Van Couvering and Berggren 1976), the timing of their dispersal from Africa remains poorly constrained. The early recognition of Proboscidea almost simultaneously in Europe, Asia, and North America has been termed as the 'Gomphotherium Datum,' or the Proboscidean Datum Event (PDE), and was long considered a reliable biochronologic marker dated at 17.5 Ma, with the implication that any non-African assemblage bearing proboscidean remains could not be older than the late early Miocene. Tassy (1990), however, cast serious doubt on the consistency of such a datum, and Antoine et al. (2003a, b) reported the occurrence of an elephantoid incisor from the late Oligocene Bugti Member. Lindsay et al. (2005) also pointed out remains of an indeterminate elephantoid in the lower Chitarwata Formation at Zinda Pir. The presence of elephantoids in the Oligocene of Pakistan confirms intermittent trans-Tethyan dispersals during the Paleogene as hypothesized by several authors (e.g., Ducrocq 1997; Gheerbrant et al. 2001; Gheerbrant and Rage 2006).

Proboscideans were of high diversity and wide geographic range, often with numerous sympatric species co-occurring at sites in Eurasia, Africa, and North America from the middle Miocene up to the latest Pleistocene. The end Pleistocene extinction of mammoths, mastodons, and other species left behind only the tropical species of *Loxodonta* and *Elephas*. Proboscideans have a relatively well-studied

Neogene fossil record, and the African record is well investigated with respect to ecological evolution and the evolution of grazing and browsing behaviors (Cerling et al. 1999; Uno et al. 2011; Lister 2013).

Elephantidae

Elephants are unique and peculiar animals. Elephants replace their teeth in a ‘conveyor-belt’ type replacement, with serial eruption, wear, and ejection of teeth one by one from the front of the tooth row, a version of the delayed dental eruption common to Afrotheres (Asher and Lehmann 2008). Living elephants are distinguished from many of their fossil relatives in the advanced development of their teeth, particularly the height of the tooth (hypsodonty) which presumably increased in order to sustain the higher rates of tooth wear demanded by a rougher diet. Strangely enough, living elephants subsist mainly on browse or mixed browse-graze diets, while most of their fossil relatives over the past six million years consumed much more grass than would have been expected from their dental evolution alone (Cerling et al. 1999).

Elephants are also important vectors of local ecological change. African elephants are known to destroy trees, making large clearings in forests, and often seriously changing the balance of trees to grassland habitats in local environments. While effects on habitats are also noted in Asian elephants, these are generally much less severe (Sukumar 2003). An important aspect of elephant ecology is their behavior, which is socially organized. In both African and Asian elephants, sexual size dimorphism is marked, and male and female social roles differ. Herds of varying size (five to 20 or more individuals—termed family units), are made up of closely related females and their young, and led by an older female (the matriarch). Upon reaching sexual maturity, males leave their family unit and lead basically solitary lives, meeting up with the female-dominated groups occasionally for mating. While proboscideans have a long and rich fossil record, almost nothing is known about their social behavior from the bone fossils themselves. Rather, one of the few clues to the antiquity of elephant social structure comes from a unique late Miocene trackway site in the United Arab Emirates (Bibi et al. 2012). The trackway site preserves footprints of a herd of proboscideans of varying sizes that walked together across what was a muddy and relatively featureless landscape. The site also fortuitously preserves the trackway of a lone individual that, by its large size, was probably made by a male. At around seven million years in age, these fossil trackways provide direct evidence for social herding and possible sexual segregation in late Miocene proboscideans.

Like rhinos and tragulids, the Asian elephant (*Elephas maximus*) has its closest living relatives in Africa, and is a surviving remnant of a once much more widespread and diverse clade of mammals. In fact, the earliest records of *Elephas* spp. are in the early Pliocene of Africa (Sanders et al. 2010). The lineage had spread to Eurasia by the late Pliocene, making its first appearance in Siwalik faunas at around 3.6 Ma with *Elephas planifrons* (Nanda 2002). This is followed by *E. hysudricus* and *E. platycephalus* alongside several species of *Stegodon*, *Stegolophodon*, and *Anancus* after 2.6 Ma (Nanda 2002, 2008). Kundal and Kundal

(2011) report a possible middle Pleistocene occurrence of *Elephas maximus* from Jammu Province, India. '*Elephas*' *celebensis* (= *Archidiskodon celebensis*) is a dwarf elephant recorded from the early Pleistocene (<2.5 Ma) Walanae Fauna of the island of Sulawesi (Hooijer 1949, 1964; van den Bergh et al. 2001a, b). If belonging to *Elephas*, then '*E.*' *celebensis* would represent at least a single dispersal event of this lineage as far southeast as Sulawesi, with subsequent insular dwarfing.

Extant wild Asian elephants were estimated to number between 40,000 and 50,000 individuals in 2006 (Sukumar 2006) though these estimates may not be very accurate (Blake and Hedges 2004). Besides occupying the southern and south-eastern Asian mainland, *Elephas maximus* is also known from the islands of Sri Lanka, Sumatra, and the northeastern tip of Borneo. Genomic analyses indicate that the Bornean, Sumatran, and Peninsular Malaysian populations all form distinct haplotypes indicating repeated incursions of the Sunda Shelf in the middle and late Pleistocene (Fernando et al. 2003).

Non-Elephantid Proboscideans

Extant African and Asian elephants are relatively closely related members of a single family, Elephantidae, to which also the famous mammoth (*Mammuthus*) belongs. The fossil record, however, documents the presence of a much greater diversity of proboscideans until the relatively recent past. Several non-elephantid proboscideans are recorded from the fossil record of SSEA. Deinotheres (Deinotheriidae) attained massive sizes and were characterized by a peculiar pair of down-curving lower tusks and relatively simple lophodont teeth suited to a browsing diet (Göhlich 1999; Sanders et al. 2010). Deinotheres are known from as early as the late Oligocene of Africa (Sanders et al. 2004), spreading to Eurasia in the early Miocene. In SSEA, deinotheres are represented by *Prodeinotherium* spp. from the early Miocene of Pakistan, and *Deinotherium* spp. from the middle and late Miocene of Pakistan and India (Forster-Cooper 1922a, b; Barry et al. 2002; Bhandari et al. 2010; Antoine et al. 2013).

Mammutids, represented by *Zygolophodon*, are recorded in SSEA from the late early Miocene to the early late Miocene of Pakistan (Tassy 1983a, b, c; Chavasseau et al. 2009a, b; Antoine et al. 2013). Gomphotheriids, represented by diverse taxa including *Gomphotherium*, *Protanancus*, *Tetralophodon*, and *Choerolophodon*, are recorded from the Miocene of Pakistan, Thailand, and southern China (Tassy 1983a, b, c; Chavasseau et al. 2009a, b; Antoine et al. 2013).

Stegodontid proboscideans, as represented by *Stegolophodon*, are recorded from the middle Miocene of Thailand and from numerous late Miocene localities in Thailand, the Siwaliks, and southern China (Tassy 1983a, b, c; Tassy et al. 1992; Saegusa et al. 2005; Chavasseau et al. 2009a, b; Thasod et al. 2012). In the Pleistocene, stegodontids are represented in Southeast Asia by many different insular dwarfed species of *Stegodon*, as recorded from Sulawesi, Flores, Timor, Mindanao, and Luzon among others (Hooijer 1953, 1964; van den Bergh et al. 2001a, b, 2008; Meijer et al. 2010). The smallest among these, *Stegodon sondaari* from Flores at 900 ka, weighed around 300 kg (Van den Bergh 1999; van den Bergh et al. 2008). In early Pleistocene of Sulawesi, *Stegodon* co-existed with another 'pygmy elephant',

'*Elephas celebensis* (Hooijer 1949, 1964; van den Bergh et al. 2001a, b). *Stegodon* survived into the late Pleistocene in Southeast Asia, and into the Holocene in southern China (Saegusa 2001, van den Bergh et al. 2008).

Proboscidean diversity in SSEA, as for so many other herbivorous groups reviewed here, was much higher throughout the Neogene than it is today. The dynamic Southeast Asian island archipelago in particular appears to have been a landscape of proboscidean diversification.

2.7 Modern Large Herbivore Faunas: Continental Comparisons

With around 85 living large herbivore species (83 of which are found in SSEA, Table 1.1), the Indomalayan Realm is about 25 % less species-rich than the Afrotropics (~106 species), but more than three times as rich than the Neotropics (~25 species). These numbers become astounding, however, when one considers that the land area of the Indomalayan Realm is only a third the size of sub-Saharan Africa, and less than half the size of the Neotropics. This extraordinary richness of herbivores in SSEA relies greatly on Southeast Asia and the southeastern island archipelago, a hotspot of speciation and endemism. Other reasons are the effects of the end Pleistocene extinctions, which took out a much larger proportion of South America's large mammals than it did Africa's or southern Asia's.

Sub-Saharan African large herbivore fauna may be diverse (106 species in 8 families), but is overwhelmingly dominated by bovids (88 species). The Neotropical large herbivore fauna is species-poor (25 species in 4 families) but is overwhelmingly dominated by cervids (16 species). An obvious major difference between these two continental areas is that the Afrotropics have no cervids, while the Neotropics have no bovids (Fig. 2.20). Like the Afrotropics, the Indomalayan Realm is very diverse (85 species in 9 families) but in contrast to both the Afro- and Neotropics, species richness in Indomalaya is much more evenly distributed among mammalian families, with the richest family (Bovidae) comprising only a third of the total (30 spp). Also in contrast to both the Afrotropics and the Neotropics, the Indomalayan Realm is home to both bovids and cervids. Taken together, these clades comprise 60 % of SSEA species richness, which approaches the African and South American ratios for bovids and cervids, respectively.

However, it should be kept in mind that the modern taxonomic diversity of the Indomalayan Realm is a relatively recent, Pleistocene or Holocene, configuration. For example, while absent there today, we know that species of hippopotamids and giraffids were to be found in SSEA through most of this area's Neogene history. In contrast, cervids only dispersed into the region in the early Pleistocene (discussed above).

From the late Miocene Siwaliks of northern Pakistan, some 55 species of large herbivores in 11 families are recorded between 11 and 5 Ma (Badgley et al. 2008).

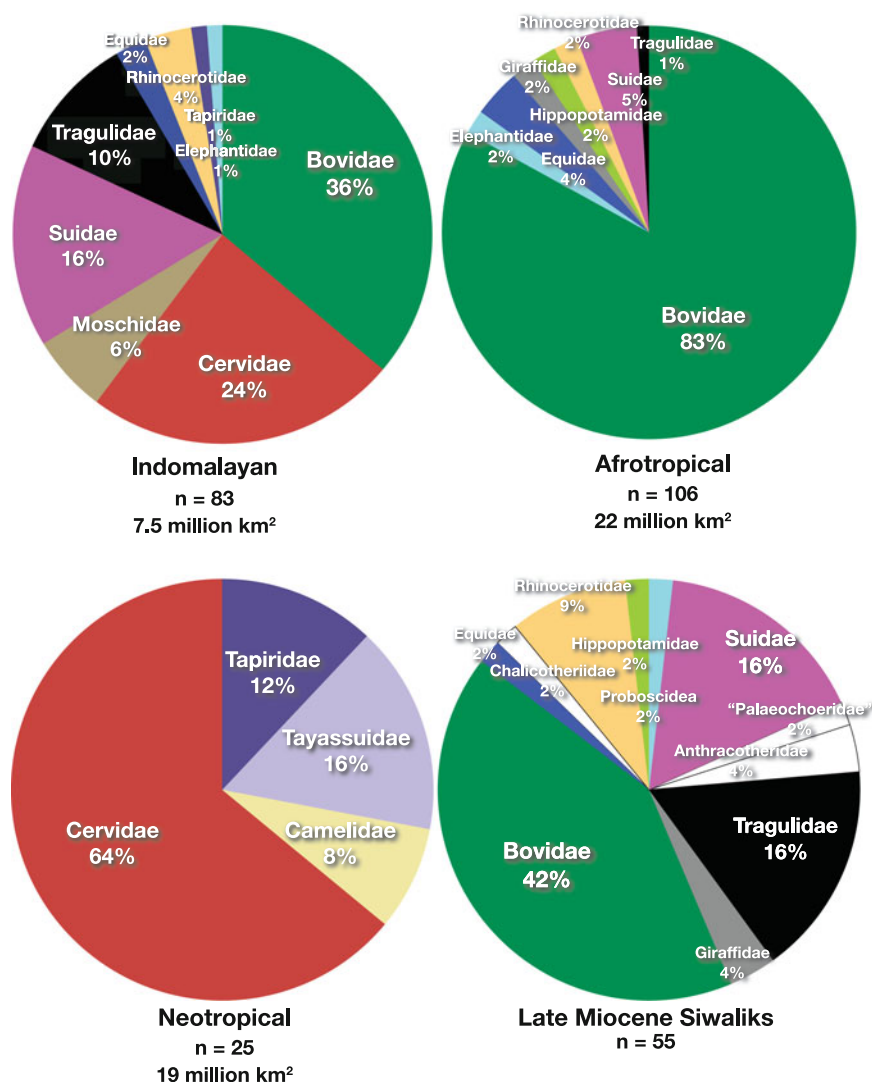


Fig. 2.20 Comparison of taxonomic diversity among the large herbivore faunas of the Indomalayan, Afrotropical, and Neotropical Realms, and to the late Miocene fauna (11–5 Ma) of the Siwaliks of northern Pakistan (faunal list of Badgley et al. 2008). Similarities between Indomalaya today and in the late Miocene include high proportions of bovids, suids, and tragulids

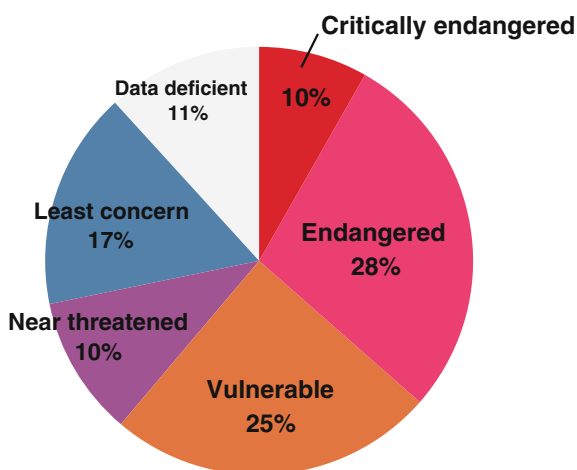
This rough estimate spanning 6 million years of evolution from a small geographic area allows only a superficial comparison with the modern day tropical diversity (Fig. 2.20). Even so, the late Miocene of northern Pakistan still shows some similarities to the modern Indomalayan Realm, namely in the high proportions of bovids, tragulids, and suids. The lack of cervids, and the presence of hippopotamids, giraffids, and several entirely extinct families are obvious and major differences.

2.8 Conclusion: The Future of SSEA's Large Herbivores

This chapter has covered many of the geological and faunal changes that have taken place in South and Southeast Asia during the Cenozoic. These changes have been many, and in many respects the modern representation and diversity of large herbivores is very different today than it was in the Miocene, Pliocene, or even the late Pleistocene. However, many elements of this evolutionary history are familiar far back in time, including the relative isolation and distinctiveness of the Indomalayan Realm from surrounding continental areas since at least the middle Miocene, and the endemic species ‘factory’ of the Southeast island archipelago since at least the early Pleistocene.

While naturally reoccurring faunal change and extinction induced by tectonic or climatic changes may be a central part of any evolutionary history, today we are witnessing the effects of a less natural type of faunal change, or at least one that is being wrought by a relatively newly arrived vector: humans. Over the past few thousand years, humans have altered global environments to the point of producing species extinctions at a rate that is comparable to some of the largest mass extinctions of the past 600 million years (Barnosky et al. 2011). Interestingly, SSEA did not suffer large herbivore losses as extreme as in mainland Eurasia, the Americas, or Australasia with the first arrivals of humans there in the late Pleistocene. Perhaps this was because, like Africa, humans and their fossil relatives had long been present in SSEA and so their effects on the landscape might have developed more gradually. Many large mammals, however, have suffered extreme range reductions since the late Pleistocene (Louys 2012a, b), and today over half the extraordinarily rich assemblage of large herbivores of the Indomalayan area is threatened or in danger of extinction (Grenyer et al. 2006; Fig. 2.21). Probably every single one of these threatened species has been put in this position by human hunting, deforestation, and the effects of dumping and pollution. These pressures

Fig. 2.21 Conservation status of extant SSEA large herbivore species (IUCN Red List). Of the 85 Indomalayan species, 52 are vulnerable or in danger of extinction



will only be compounded by the effects of ongoing global warming, such as global sea level rise and the inundation of low-lying islands. Southeast Asia, a particularly fragile region on account of its small islands and large number of endemics, stands to lose some 85 % of its mammal species by the end of the twenty-first century (Sodhi et al. 2010).

The evolutionary history of SSEA's large herbivores has been shaped by extinction probably just as much as it has been shaped by speciation. The fossil record informs us that local or global biotas have always rebounded following major extinction events, though always in a permanently altered state. With the ongoing human-induced mass extinction and with current rates of habitat and species loss, we might ask whether SSEA's faunas might ever be able to recuperate to preindustrial levels, and if so, in what kind of altered state.

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