Divergence time estimates of mammals from molecular clocks and fossils: Relevance of new fossil finds from India

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This paper presents a brief review of recent advances in the classification of mammals at higher levels using fossils and molecular clocks. It also discusses latest fossil discoveries from the Cretaceous – Eocene (66–55 m.y.) rocks of India and their relevance to our current understanding of placental mammal origins and diversifications.

1.   Introduction

In order to understand the rates of evolution and patterns in biogeography, precise estimation of divergence time of major taxonomic groups is very important. Traditionally species divergence time estimates were made using the time of first appearance of new species in the fossil record. However, there is always a time lag between the time of actual divergence and the first appearance in the fossil record as morphological distinction between two species is reflected in the fossil specimens much later than the genetic divergence. Further, a number of factors such as incomplete fossil record, misidentifications, and non-availability of precise age estimates for the fossil yielding horizons introduce many uncertainties into fossil based divergence time estimates. Based on good fossil record from 55-65 million year (m.y.) period and sudden appearance of many new groups of mammals, it is traditionally concluded that the origin and diversification of extant placental orders took place in the early Tertiary close to the Cretaceous-Tertiary boundary (KTB, 65 m.y. ago) following the extinction of dinosaurs (Alroy 1999; Benton 1999; Bromham *et al.* 1999; Foote *et al.* 1999; Novacek 1999; Archibald *et al.* 2001; Wible *et al.* 2007). An interordinal phylogenetic tree consisting of eight supraordinal clades, viz., (1) Epitheria (all living placentals except Xenarthra), (2) Preptotheria (all living placentals except Xenarthra and Lipotyphla), (3) Glires (Rodentia and Lagomorpha), (4) Archonta (Scandentia, Primates, Chiroptera, and Dermoptera), (5) Volitantia (Chiroptera and Dermoptera), (6) Cetungulata (Artiodactyla, Cetacea, Perissodactyla, Hyracoidea, Proboscidea, Sirenia), (7) Paenungulata (Hyracoidea, Proboscidea, Sirenia), and (8) Tethytheria (Proboscidea and Sirenia) was suggested for placental mammals based on morphology of fossils (Shoshani and McKenna 1998).

In the last decade and a half, mammalian phylogeny and lineage divergence dates underwent very rapid transformation with the extensive use of molecular clock methods. In molecular clocks, it is assumed that molecules evolve at a constant rate and longer the two lineages are separated from each other greater the genetic difference between them (Kimura 1968; Ohta and Kimura 1971). In the early stages, immunological differences between proteins were determined (Goodman 1975; de Jong *et al.* 1981; Miyamota and Goodman 1986), but in recent years mitochondrial and nuclear gene sequences have been widely used to understand placental mammal relationships at ordinal and supraordinal levels (Hedges *et al.* 1996; Springer *et al.* 1997; Kumar and Hedges 1998; Waddell *et al.* 1999a,b,c, 2001; Madsen *et al.* 2001; Murphy *et al.* 2001a; Scally *et al.* 2001; Eizirik *et al.* 2001; Waddell and Shelly 2003). Molecular studies suggested four supraordinal clades of placental mammals, namely, Afrotheria (Proboscidea, Sirenia, Hyracoidea, Tubilidentata, Macroscelidia, Tenrecomorpha), Xenarthra (Cingulata, Vermilingua, Folivora), Euarchontoglires (Glires – Rodentia and Lagomorpha, Euarchonta – Primates,

Scandentia, and Dermoptera), and Laurasiatheria (Cetartiodactyla, Perissodactyla, Carnivora, Pholidota, Eulipotyphla, Chiroptera) (Waddell *et al.* 1999a,b,c). The basic structure of mammalian tree and divergence dates proposed by Waddell *et al.* (1999a,c) were supported by later works (Waddell *et al.* 2001; Madsen *et al.* 2001; Murphy *et al.* 2001a,b; Scally *et al.* 2001; Delsuc *et al.* 2002; Lin *et al.* 2002; Waters *et al.* 2007). In most of the cases, the molecular clock based species divergence time estimates are discordant with the divergence dates obtained from fossils, being older than or some times twice as old as fossil estimates. Contrary to estimates based on fossil data, the molecular divergence clocks inferred a range of 100–140 m.y. for the root of living placental mammalian groups (Kumar and Hedges 1998; Waddell *et al.* 1999a; Cao *et al.* 2000; Waddell *et al.* 2001; Springer *et al.* 2003) though it is not clear which modern crown-group orders originated in the Cretaceous (Waddell *et al.* 1999a). One of the reasons for this discrepancy is the assumption that there is no variation in the rate of molecular evolution in a lineage. However, the rate of molecular evolution is not constant over time and across taxa (Ayala *et al.* 1988; Bromham *et al.* 1999). A great amount of rate variation is known to occur among loci on a gene, between branches on a tree, and within a single lineage over time (Smith and Peterson 2002). To overcome this problem many recent molecular studies used concatenated sequences, multiple calibration points that span a range of divergence times, gene sequences exhibiting no heterogeneities, and various statistical methods (see Smith and Peterson 2002; Brochu *et al.* 2004). Although the gap between fossil record and molecular divergence estimates has been narrowed down using these methods (Eizirik *et al.* 2001; Madsen *et al.* 2001; Murphy *et al.* 2001b; Waddell *et al.* 2001; Springer *et al.* 2003) the mismatch still exists in many cases. More recent studies that used the refined molecular clock methodologies indicated that interordinal divergence of placental mammals took place in the Cretaceous but intraordinal splits of most mammalian orders occurred subsequent to KTB except for four orders viz., Lipotyphla, Rodentia, Primates, and Xenarthra (Springer 1997; Kumar and Hedges 1998; Springer *et al.* 2003). Earliest fossils of rodents, primates, and xenarthrans appear in the Palaeocene, whereas molecular phylogenies estimated intraordinal splits 1-16 m.y. before KTB for these groups (Springer *et al.* 2003).

Fossil evidence favours northern hemisphere origin for modern orders of mammals (Lillegraven 1974). On the contrary, molecular phylogenetic studies predicted the Gondwanan continents as centres of origin and Middle Cretaceous (105 m.y.) divergence for many placental orders (Hedges *et al.* 1996; Springer *et al.* 1997; Stanhope *et al.* 1998; Waddell *et al.* 1999c; Eizirik *et al.* 2001; Madsen *et al.* 2001; Murphy *et al.* 2001a) much before the appearance

of undoubted crown placental orders in the early Cenozoic (Foote *et al.* 1999; Novacek 1999; Meng *et al.* 2003; Asher *et al.* 2005; Wible *et al.* 2007). Waddell *et al.* (1999a) suggested that plate tectonics, particularly opening of South Atlantic ocean 95-110 m.y. ago, played an important role in shaping the phylogeny of placental mammals. Eizirik *et al.* (2001), on the other hand, invoked 105-80 m.y. trans-oceanic dispersals between Africa and Europe across Noah's Ark-like microplates or via South America that facilitated the arrival of boreoeutherian ancestor in the northern hemisphere. In the absence of fossil eutherian mammals in the Late Cretaceous of South America, this biogeographic model was opposed by the palaeontologists (Archibald 2003; Hunter and Janis 2006). Hedges *et al.* (1996) suggested that fragmentation of emergent land areas during the Cretaceous, not the sudden availability of ecological niches following the KTB mass extinction event, was responsible for the diversification of avian and mammalian orders and timing of these break-up events is correlatable with molecular clock estimates for the divergence of orders. It was further argued that the poor Cretaceous fossil record of mammals was the consequence of high sea level during the Middle and Late Cretaceous which resulted in about 25% less emergent land area than exists at present and proportionately reduced the area available for the deposition of terrestrial rocks

Three models – *explosive*, *long fuse*, and *short fuse* – have been proposed to explain placental mammal diversification with respect to the K/T boundary (65 m.y.) which marks the extinction of dinosaurs (Archibald and Deutschman 2001) (figure1). The *explosive* model suggests that both interordinal and intraordinal diversifications of placental mammals took place within a short time span of 10 m.y. immediately after the K/T boundary as the ecological niches vacated by dinosaurs were available for mammals (Simpson 1945; Foote *et al.* 1999; Wible *et al.* 2007). This model recognizes most of the Cretaceous eutherians as stem groups which played no significant role in the origin and diversification of modern placental orders. As a vast majority of fossils of modern placental mammals occur in post-Cretaceous rocks, many palaeontologists are in favour of this model (Foote *et al.* 1999; Benton 1999; Wible *et al.* 2007). The *long fuse* model assumes that the interordinal divergences occurred in the Cretaceous, but intraordinal diversifications were predominantly post K/T boundary phenomena with a few placed within the Cretaceous (Archibald 1996; Nessov *et al.* 1998; Archibald *et al.* 2001). The *short fuse* model favours both interordinal and intraordinal diversifications deep in the Cretaceous period soon after the appearance of eutherians. Majority of molecular studies supported deep time interordinal divergences about 105 m.y. ago in the Cretaceous and extension of several intraordinal clades well back into the Late Cretaceous compatible with the *short fuse* model (Springer 1997; Kumar and Hedges 1998; Penny *et*

al. 1999; Eizirik *et al.* 2001; Murphy *et al.* 2001a). However, some recent molecular studies using maximum likelihood and Bayesian phylogenetic methods suggested that four orders (Lipotyphla, Rodentia, Primates, Xenarthra) had intraordinal splits in the Cretaceous about 1-16 m.y. prior to the KTB and thus favour the *long fuse* model (Springer *et al.* 2003). As against this, Waddell *et al.* (2001) pointed out that molecular divergence time estimates do not agree with each other for the simple reason that different workers use different calibration points. They emphasized the fact that pre-Cretaceous placental groups should be directly recognizable from fossils. By applying new procedures for divergence time estimation, such as multidimensional vector

space (MVS) representation method to detect convergent evolution at molecular level, Kitazoe *et al.* (2007) estimated the root of placental mammals at 84 m.y. as against 122 m.y. from earlier works. The new method of Kitazoe *et al.* (2007), which takes into account the effects of both abrupt rate change and convergent evolution, raised doubts not only on the need of *long fuse* model to explain the absence of modern placental mammals prior to 75 m.y. but also on the validity of vicariant plate tectonic models proposed to explain the geographic distribution of the four major groups of placental mammals (Kumar and Hedges 1998; Bromham *et al.* 1999; Waddell *et al.* 1999a,d; Cao *et al.* 2000; Lynch and Conery 2000; Benton and Ayala 2003; Springer *et al.* 2003).
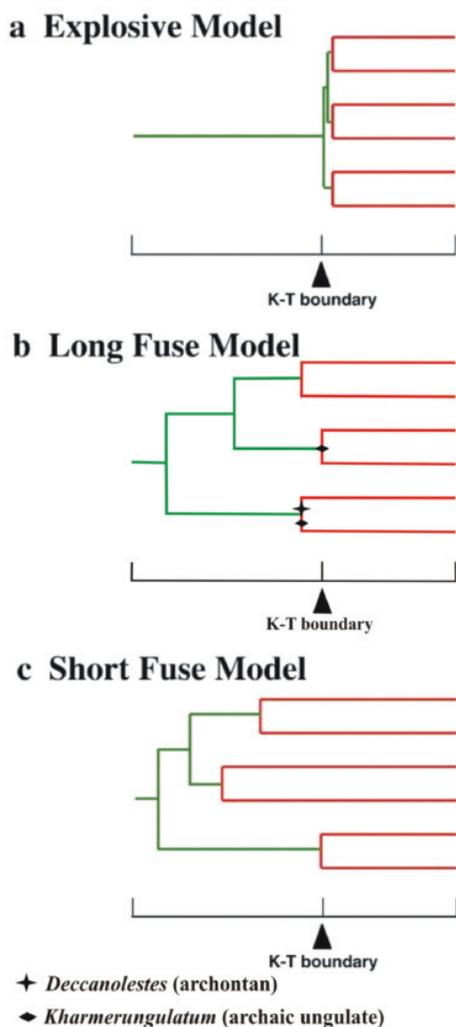
2. Fossil record from India

The early diversification of placental mammalian orders in the Cretaceous as inferred by molecular data needs to be confirmed by the fossil record which shows a very high diversity only after the K/T boundary. The mismatch between molecular clock estimates and fossil record implies that either the fossil record is incomplete or molecular divergence clocks are not reliable, or both. If the molecular clocks are not in error, why are we missing the stages representing early divergence in the fossil record? One of the reasons for this could be the difficulty in recognizing ancestral members of a lineage which may not reflect the defining characters of the crown group, which is further compounded by the fragmentary nature of Cretaceous fossil record, mostly known by teeth. To explain this mismatch, Cooper and Fortey (1998) invoked what they termed as "phylogenetic fuse" which assumes that a comparatively unknown phase of structural innovation detectable in the genome occurred tens of millions of years before it could be manifested in the fossils. Alternatively, it was argued that many modern mammalian orders were widely distributed near the K/T boundary and their previously restricted ranges remain poorly sampled in areas like Africa and India (Waddell *et al.* 1999c). Foote *et al.* (1999) stated that "Modern eutherian lineages diversified in regions that have no known Late Cretaceous mammals (such as Africa, Australia, and Antarctica) and suddenly dispersed widely during the early Tertiary. This "Garden of Eden" hypothesis is testable with intensive exploration of the fossil record of the regions in question". This implies that early mammals representing the crown groups are yet to be discovered on less explored areas of former Gondwanaland. Much of the existing fossil record is heavily biased towards the northern hemisphere. This is mainly because of a large number of palaeontologists working in the northern hemisphere and the location of early mammal yielding sites in North America, Asia and Europe. Sites yielding fauna of small terrestrial

Figure 1. Three models (**a**, *explosive*, **b**, *long fuse*, **c**, *short fuse*) of diversification of placental mammals. Green lines represent interordinal diversifications, red lines represent intraordinal diversifications (redrawn after Archibald and Deutschman 2001 and Springer *et al.* 2003). Note that **b** also shows the pre-K/T boundary occurrence of 'euarchontan-like' basal placental (*Deccanolestes*) and archaic ungulate (*Kharmerungulatum*).

vertebrates of Late Cretaceous age are not very common outside the Late Turonian and Coniacian and Campanian - Maastrichtian of North America and Asia whereas these sites are very limited from Europe, South America, Madagascar and India. Continental vertebrate fossil yielding sites of Late Cretaceous age are yet to be discovered from Africa and Australia. In recent years, many research groups started work on early mammal sites in the southern continents, particularly in Africa, Madagascar, South America and India, with the objective of improving the fossil record and our understanding of early mammalian evolution. The discovery of oldest tribosphenic mammals, which represent the basal stock for placentals and marsupials, in rocks as old as 167 m.y. (Middle Jurassic) from Madagascar (Flynn *et al.* 1999) and slightly younger Late Jurassic rocks of South America (Rauhut *et al.* 2002) implies that many new discoveries are awaited from the southern continents. Although Late Cretaceous terrestrial vertebrate fossil sites of India and Madagascar have been explored in recent years, the full potential of these beds is yet to be realized.

In the last one and half decades, intensive exploration work for early mammals from the Late Cretaceous (67-65 m.y.) and Early Eocene (55 m.y.) rocks of India resulted in the discovery of many new mammalian groups. In the following section, the significance of Late Cretaceous and Early Eocene mammals is discussed in the context of recent molecular phylogenies.

2.1 *Late Cretaceous mammals*

Cretaceous mammals are known from the sedimentary rocks sandwiched with the Deccan volcanic flows of peninsular India designated as 'intertrappean beds'. So far, mammals have been reported from the intertrappean beds of Upparhatti (Gokak District, Karnataka state), Naskal and adjoining areas (Rangapur, Bacharam) in Rangareddi District, Andhra Pradesh state, and Kisalpuri (Dindori District, Madhya Pradesh state) (figure 2). These intertrappean beds were deposited in fluvio-lacustrine basins in a coastal-plain setting. A Late Cretaceous (Maastrichtian) age was assigned to the mammal yielding intertrappean beds based on Maastrichtian fish fauna, ostracods, and palynofossils (Singh *et al.* 2006; Prasad *et al.* 2007a,b; Wilson *et al.* 2007). The intertrappean mammals represented by three groups, viz., eutherians (*Deccanolestes hislopi* Prasad and Sahni 1988, *D. robustus* Prasad *et al.* 1994, *Sahnitherium rangapurensis* Rana and Wilson 2003, *Kharmerungulatum vanvaleni* Prasad *et al.* 2007b), gondwanatheres (*Bharattherium bonapartei* Prasad *et al.* 2007a), and haramiyids (*Avashishta bacharamensis* Anantharaman *et al.* 2006) are generally found in association with disarticulated microscopic remains (microvertebrates) of fish, amphibans, lizards, snakes, turtles and crocodiles, and additionally dinosaurs at Kisalpuri.

2.2 *Early Eocene mammals*

Although Lower Eocene rocks are known from a number of sites in western India, the Lower Eocene Cambay Shale Formation exposed in Vastan lignite mine, Surat District, Gujarat state (figure 2) has yielded a diversified assemblage of mammals consisting of artiodactyls, perissodactyls, primates, insectivores, proteutherians, apatotherians, rodents, bats, lagomorphs, hyaeonodontids and arctocyonid condylarths (Bajpai *et al.* 2005a,b, 2007, 2008, 2009; Rose *et al.* 2006, 2008; Smith *et al.* 2007; Rana *et al.* 2008; Bajpai *et al*. 2009). The Vastan mammal assemblage has been dated as earliest Eocene (Sparnacian, 55-54 m.y.) in age based on dinoflagellate cysts (Garg *et al.* 2008). On lithological grounds and fossil associations, shallow marine to backshore lagoonal environment was suggested for the mammal-bearing horizons of Cambay Shale (Sahni *et al.* 2006).

Pertinent to the present discussion is the fossil record of rodents from the Indian subcontinent as rodents are expected to provide the best calibration point for the placental tree (Waddell 2008). The oldest rodents of the Indian subcontinent are known from the Lower Eocene strata of Barbora Banda site in Pakistan (de Bruijn *et al*. 1982) and the Lower Eocene Cambay Shale of Vastan lignite mine, western India (Bajpai *et al*. 2007; Rana *et al*. 2008). Of these two sites, the rodent teeth from the Vastan lignite mine represented by reasonably good number of specimens have been assigned to the European subfamily Ailuravinae (Family Ischyromyidae). Because of the occurrence of primitive ailuravine rodents in the Lower Eocene rocks of India, Rana *et al*. (2008) speculated on the possible origin of this subfamily in South Asia rather than in Europe. However, the current fossil data which is very limited does not offer enough support for such a conclusion. Moreover, the fossil record from the Palaeocene-Eocene boundary and Palaeocene is unknown from the Indian subcontinent. Future exploration of some of the Deccan intertrappean beds dated as Early Palaeocene may throw some light on the Palaeocene mammal fauna of India.

3. Significance of new fossil finds

Based on fossils and morphology, primates, tree shrews (Scandentia), colugos or flying lemurs (Dermoptera), bats (Chiroptera) and extinct early Tertiary Plesiadapiformes were placed in the supraordinal group Archonta (McKenna and Bell 1997). Recent molecular phylogenetic studies, excluded bats from this alliance and the group as such was redesignated as Euarchonta (Waddell *et al.* 1999b) closely related to Glires (rodents and lagomorphs). Euarchonta and Glires were included in Euarchontoglires (Murphy *et al.* 2001b) or formally in Supraprimates (Waddell *et al.* 2001), one of the four major placental clades. Ankle bones of Late

Figure 2. Map of India shows the Late Cretaceous (Upparhatti, Naskal, Rangapur and Kisalpuri) and Early Eocene (Vastan) mammal-yielding sites (after Sahni and Prasad 2009).

Cretaceous eutherian mammal *Deccanolestes* were reported from the sedimentary beds associated with Deccan volcanic flows of India (Prasad and Godinot 1994; Godinot and Prasad 1994). Ankle bone morphology provides important information about attachment surfaces for muscles and tendons and hence the functional adaptations of the animal during its life and phylogenetic relationships. Based on tarsal bone morphology, it was inferred that *Deccanolestes* was

adapted to an arboreal mode of life. As its tarsal morphology closely approaches that of early primates and as living and fossil tree shrews are known from India, it was inferred that India was a center of origin for archontans (Prasad and Godinot 1994; Godinot and Prasad 1994). Since dental material, on which *Deccanolestes* was based, was originally assigned to palaeoryctoids, a northern hemisphere group of insectivorous mammals (Prasad and Sahni 1988; Prasad *et al.* 1994), it was inferred that archontans originated from a palaeoryctoid stock. It is only the primitive tritubercular dental morphology of *Deccanolestes* which stands against its inclusion in Archonta or as an archontan ancestor. Latest comparisons with Late Palaeocene mammalian faunas of North Africa and Europe (Prasad *et al.* in press), however, indicated close taxonomic relationship of *Deccanolestes* to *Afrodon germanicus* and *A. chleuhi* (Russell 1964; Gheerbrant 1988, 1995). The taxonomic affinities of Adapisoriculidae, the family to which *Afrodon* is referred, has been a subject of debate ever since its description and was placed in Lipotyphla as recently as in 1995 by Emmanuel Gheerbrant. The more recent work by Storch (2008) based on associated postcranial bones from the Late Palaeocene Walbeck locality in Germany considered adapisoriculids as plesiadapiform primates rather than lipotyphlan insectivores. The close resemblance of *Deccanolestes* teeth to those of *Afrodon*, the adapisoriculid from northwest Africa and Europe now regarded as an euarchontan, further support the euarchontan affinities of *Deccanolestes*. The latest study that involved comparison of *Deccanolestes* postcranial bones to those of a number of eutherian taxa viz. condylarths, cimolestans, nyctitheriids, plesiadapiforms, dermopterans, scandentians, and euprimates considers it as an 'euarchontan-like arborealist' with a postcranial morphology closely comparable to plesiadapids (Boyer *et al.* 2009). The oldest record of plesiadapiforms comes from the Palaeocene of North America (*see* Bloch *et al.* 2007). The latest discovery of oldest definitive anthropoid primate (*Anthrasimias*) from the Early Eocene Cambay Shale, Vastan lignite mine, Gujarat dated at 55-54 m.y. suggested India as an important center for the diversification of primates of modern aspect (euprimates) in the Early Eocene (Bajpai *et al.* 2008). The co-occurrence of antropoid primates with omomyoid and adapoid primates in the Early Eocene further points to an ancient diversification of haplorrhines and strepsirrhines possibly in the Palaeocene or Cretaceous as indicated by molecular phylogenies (Bajpai *et al.* 2008). The presence of oldest euarchontan-like basal placental group in the Late Cretaceous and the definitive oldest anthropoid primate in the Early Eocene of India points to the possible origin of this placental group a few million years before the K/T boundary congruent with molecular data (Waddell *et al.* 1999a; Waddell *et al.* 2001; Waddell and Shelley 2003; Janečka *et al.* 2007). The adapisoriculid (*Afrodon*) affinity

of *Deccanolestes* has additional implications for the Late Cretaceous palaeobiogeography of India. *Deccanolestes* in its primitive dental morphology as compared to *Afrodon* and older age appears as a basal euarchontan stock from which *Afrodon* may have evolved. It thus implies the existence of a biogeographic connection between India and Africa or Europe, or both during the Cretaceous-Tertiary transition.

Further, the discovery of a definitive Late Cretaceous ungulate mammal (*Kharmerungulatum vanvaleni* Prasad *et al.* 2007b) with affinities to archaic ungulates (condylarths), which were considered ancestral to some extant and extinct ungulate groups, from the Late Cretaceous rocks of peninsular India raises the question – Was India a centre of origin for archaic ungulates? The occurrence of endemic perissodactyls (cambaytherids, Bajpai *et al.* 2005a) and artiodactyls (raoellids) (the latter is regarded as sister taxon to whales, Thewissen *et al.* 2007) in the Early and Middle Eocene (55-50 m.y.) rocks of India respectively, implies these groups may have been derived from an archaic ungulate of Late Cretaceous-Early Palaeocene age. But the available fossil material for *Kharmerungulatum* is very limited and well preserved and complete material is needed to firmly establish its affinities. As the oldest ungulate-like mammals (zhelestids) come from the Late Cretaceous rocks of Middle Asia (Nessov *et al.* 1998), alternatively it can also be argued that *Kharmerungulatum* was an immigrant from the Asian stock of zhelestids. However, no phylogenetic relationship has been established between zhelestids and archaic ungulates.

Molecular phylogenies indicated that the split of Lagomorpha into extant families Ochotonidae (pikas) and Leporidae (rabbits and hares) took place either around Middle Eocene (~40-45 m.y.) with a confidence interval of ~36 to 55 m.y. (Waddell *et al.* 2001; Kitazoe *et al.* 2007) or Late Eocene (Douzery *et al.* 2003; Asher *et al.* 2005). However, Springer *et al.* (2003) suggested that basal split within Lagomorpha occurred 10-15 m.y. after K/T boundary at about 51 m.y. ago. Until recently, the oldest lagomorph was from the late Early or early Middle Eocene of Central Asia (Russell and Zhai 1987; Shevyreva 1995; Lopatin and Averianov 2006; Li *et al.* 2007). The latest report of tarsal bones of Lagomorpha from the Lower Eocene Cambay Shale of Vastan Lignite Mine, Gujarat (India), dated at 55-54 m.y. based on benthic foraminifers and dinoflagellate cysts (Garg *et al.* 2008), predates the oldest known record of lagomorphs from Asia by several million years (Rose *et al.* 2008). These authors inferred that Vastan lagomorph ankle bones with gracile adaptations of extant leporids are suggestive of Lagomorpha split into Ochotonidae and Leporidae prior to 54 m.y. which is slightly older than that of molecular estimates.

Although whales were considered to have evolved from a terrestrial group of mammals, there was no consensus on

the possible ancestral group. Based on morphological data, they have often been related to creodonts (hyaenodonts), ungulates, seals, and mesonychid condylarths (archaic ungulates) with majority of works favouring mesonychid origins (*see* Thewissen *et al.* 2001). But molecular studies, on the other hand, favoured a close relationship with artiodactyls, the even-toed ungulates, especially with hippopotamids (Gatesy *et al.* 1996). Subsequent fossil discoveries supported molecular phylogenetic studies. Thewissen *et al.* (2001) and Gingerich *et al.* (2001) based on postcranial remains of Early Eocene whales (Pakicetidae, Protocetidae) from India and Pakistan favoured an artiodactyl ancestry. Fossil record of Artiodactyla and Cetacea accords well with molecular clock estimates for the divergence of these two groups. Documentation of *Himalayacetus,* the oldest cetacean, from 53.5 m.y. old rocks of the Subathu Formation, Himachal Pradesh, India (Bajpai and Gingerich 1998) and *Diacodexis*, the oldest artiodactyl from the earliest Eocene (55 m.y.) rocks of North America and Europe (e.g. Gingerich 1989) is more or less in agreement with a minimum age of 52 m.y. with a confidence interval of ~49-61 m.y. (Waddell 1995) assigned for the hippo-cetacean divergence based on molecular clock estimates (Waddell *et al.* 2001; Springer *et al.* 2003). Although whales first appear in the Early Eocene, hippopotamids appear much later in the fossil record about 15.6–15.8 m.y. ago (Behrensmeyer *et al.* 2002). As the whale-hippo divergence date is well constrained by the molecular data, the missing fossils of hippopotamids between 15–52 m.y. is possibly an issue of finding older fossils.

Besides mammals, some other groups of animals and plant also suggest India as a centre of origin in the Cretaceous. The recent discovery of phytoliths of grasses (tiny microscopic silica crystals which grow inside plant cells and can survive digestion of animals) from the fossil dung of Late Cretaceous dinosaurs extended back the time of origin for grasses well back into the Cretaceous (Prasad *et al.* 2005). The five types of phytoliths (of Poaceae subclades) found in the dinosaur fossil dung represent very highly evolved forms, suggesting that they diverged well before the Cretaceous. Prior to this, the oldest definitive records of grasses are from the Palaeocene (between 60 and 55 m.y.) rocks of South America and Africa (Jacobs *et al.* 1999). Molecular clock estimates on the other hand suggested 83 m.y. for the origin of crown group Poaceae (Janssen and Bremer 2004). Another example for early evolution of plants on the Indian plate is the latest finding of oldest freshwater diatoms from the Late Cretaceous of India (Ambwani *et al.* 2003).

If the molecular divergence estimates are true, many modern orders of mammals may have originated in the Cretaceous and began radiating before the extinction of dinosaurs. Intensive search in the Gondwanan continents, particularly in Africa, Australia and India may improve the fossil record and may lead to many new discoveries that will have important bearing on biogeographic origins of mammals and many other animal and plant groups. In coming years, refined molecular clock estimates combined with new fossil discoveries and palaeobiogeographical data would help us in understanding the tempo and mode of evolution in a better way and inferring the placental tree with a greater degree of confidence.

4. Summary

Improved molecular clock estimate techniques and many new fossil discoveries in recent years narrowed the gap between the fossil record and molecular divergence estimates of mammals. Fossil discoveries of oldest whales (Thewissen *et al.* 2001, 2007; Gingerich *et al.* 2001), lagomorphs (Rose *et al.* 2008), anthropoid apes (Bajpai *et al.* 2008) from the Indian subcontinent are close to the molecular clock estimates. The occurrence of 'euarchontan-like' mammals (Prasad and Godinot 1994) and archaic ungulate (Prasad *et al.* 2007b) in the Late Cretaceous of India (65 m.y.) extends back in time the fossil record for these groups. The new mammalian finds from the Indian subcontinent and the recent reports of oldest agamid lizards, grasses and freshwater diatoms hint at the possibility of the Indian plate serving as one of the Gondwanan centres of origin for many animal and plant groups during its northward journey as a Noah's Ark. This, however, needs to be further tested with well preserved fossil material representing a large spectrum of animal and plant groups and firm establishment of phylogenetic relationships of the mammalian taxa in a cladistic framework. Until now, no Palaeocene mammals were documented from the Indian subcontinent. Exploration for more Cretaceous mammal-yielding sites to understand the diversity of Cretaceous mammals in India and intensive search for mammals from the Palaeocene, an important time frame during which placental mammals underwent rapid diversification, would help us in better understanding the early evolution of placental mammals in India and the possible phylogenetic links between the Cretaceous and Eocene mammals, if any. Additionally, focused search for Late Cretaceous mammals in other less explored Gondwanan continents, such as Australia, Madagascar and Africa, will pave the way towards a better resolution of phylogenetic relationships of Gondwanan mammals and Late Cretaceous biogeographic patterns.

by Peter J Waddell has greatly improved the content of the paper. The author is thankful to Peter J Waddell for making available some latest articles dealing with the phylogeny of mammals and to K Praveen Karanth for his useful suggestions on the manuscript. Thanks are due to Omkar Verma for drawing the figures.

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