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RECORD OF *PRODEINOTHERIUM* (PROBOSCIDEA: MAMMALIA) FROM THE MID-TERTIARY DHARMSALA GROUP OF THE KANGRA VALLEY, NW HIMALAYA, INDIA: BIOCHRONOLOGIC AND PALAEOBIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT

We describe a rare fossil of a large-bodied mammal from the Dharmsala Group of the Kangra Valley of Himachal Pradesh. It is an isolated upper premolar of *Prodeinotherium*, a genus of an extinct proboscidean family. The find represents the highest trophic level taxon known so far from the Dharmsala and coeval horizons and is important towards understanding the pre-Siwalik large mammals of the Himalayan region of India. The Dharmsala Group has previously yielded a rodent and atypical fish remains (Tiwari and Bhandari, 2004 and 2005). Earlier, Tiwari *et al.* (1991) and Feist and Tiwari (1999) studied fairly diversified associated assemblage comprising aquatic elements such as chara gyragonites, ostracods, fishes, crocodiles, etc. The new record corroborates early Miocene age assigned earlier to the fossil-yielding horizons and extends the palaeogeographical expanse of *Prodeinotherium*, so far known from early Miocene horizons of Pakistan, by 400 km up to the Kangra Valley of Himachal Pradesh in the east.

Key words: *Prodeinotherium*, Dharamsala Group, Kangra Valley (Himachal Pradesh), Early Miocene Mammal, Proboscidea, Deinotheriidae

INTRODUCTION

An isolated cheek tooth of *Prodeinotherium*, an immigrant element of east African origin, is reported here for the first time from the mid-Tertiary Dharmsala Group of the Kangra Valley, Himachal Pradesh, India (Fig. 1). An attempt is made to present a systematic description of this form and to discuss its biochrono logic and palaeobiogeographic implications in the regional geological framework of the Lesser Himalaya. It is important in the context of recent palaeontological investigations on vertebrate fauna from the mid-Tertiary horizons of the Indian NW Himalaya, which are yielding new data and providing a palaeontological basis for refining the current geological models useful in the regional oil exploration activities.

The *Prodeinotherium*, though a primary consumer, is a taxon of highest trophic level of early Miocene terrestrial vertebrate community known from the Dharmsala Group and the Indian coeval horizons because of the absence of any carnivoran species; in a fully developed terrestrial vertebrate community the taxon ought to be below the secondary consumers' and predators' level in the trophic pyramid. In the local fauna, *Prodeinotherium* is represented by an isolated left upper third premolar that was recovered from the Traffic Check Post locality ($32^0$13.74'N: $76^0$18.46'E) on Dharmsala-McLeodganj Road (here after TCP locality; Fig. 1) by one of us (BCV).

Until now the deinothere material from the Indian subcontinent had been described as *Deinotherium* by previous workers (Cooper, 1922; Palmer, 1924; Osborn, 1936; Sahni and Tripathi, 1957; Dehm, 1963; Khan *et al.*, 1971; Sahni and Misra, 1975; West *et al.*, 1978; West and Munthe, 1981; Sahni and Gupta, 1984; Kumar, 1985). Some of the material pertains to *Prodeinotherium* which is small and comparatively less evolved in contrast to the relatively larger and more evolved genus *Deinotherium*. Now the smaller deinothere specimens collected earlier from the Miocene horizons of Pakistan are referred to *Prodeinotherium* comprising *P. pentapotameae* and *P. orlovii*, and the larger specimens with a wider geographic distribution in the Indian subcontinent are assigned to *Deinotherium indicum*. In the present work, the deinothere premolar from the Dharmsala Group is referred to *Prodeinotherium* on the basis of morphology and size; *Prodeinotherium* (pro - "before" "terrible beast") is an intermediate genus between *Chilgatherium* and *Deinotherium* of the family Deinotheriidae. Though *Prodeinotherium* was akin to a small elephant, it differed in anatomical details, for example, in having a pair of downward curving tusks on the lower jaw. In comparison to their successor *Deinotherium indicum*, both the Indian species of *Prodeinotherium* were not only smaller in size with shorter forelimbs but also differed in the details of the shape and form of the teeth.

The Tertiary sediments on the southernmost side of the Himalaya in NW sector largely comprise marine limestone and shale horizons of the Subathu Group (Palaeocene to middle Eocene) followed by the succeeding nonmarine horizons, namely, Murree and Siwalik in the Jammu region, Dharmsala and Siwalik in the Kangra Valley and Dagshai/Kasauli and Siwalik in the Simla region. The mid-Tertiary horizons, namely, Murree of Jammu, Dharmsala of Kangra Valley, and Dagshai/Kasauli of the Simla region are the regional names given to homotaxial horizons that are stratigraphically bracketed in the late Eocene-early Miocene time slice.

PREVIOUS WORK

The Dharmsala and the coevals, namely, the Murree and Dagshai/Kasauli of the NW Outer Himalaya of India, were studied in conjunction with the older Subathu and /or younger Siwalik horizons by previous workers who expressed a variety of opinions regarding environment of deposition and age range (Raiverman and Seshavataram, 1963; Bhandari and Agarwal, 1967; Chaudhri, 1968; Datta, 1969; Singh, 1978; Srivastava and Casshyap, 1983; Ranga Rao, 1986; Singh, 1996).

The Dharmsala and Dagshai/Kasauli horizons hitherto lack datable mammalian fossils, whereas Lower and Upper formations of the Murree Group have yielded mammalian remains (Khan *et al.*, 1971; Ranga Rao, 1986; Mehta and Jolly, 1989; Kumar and Kad, 2002 and 2003) which indicate early

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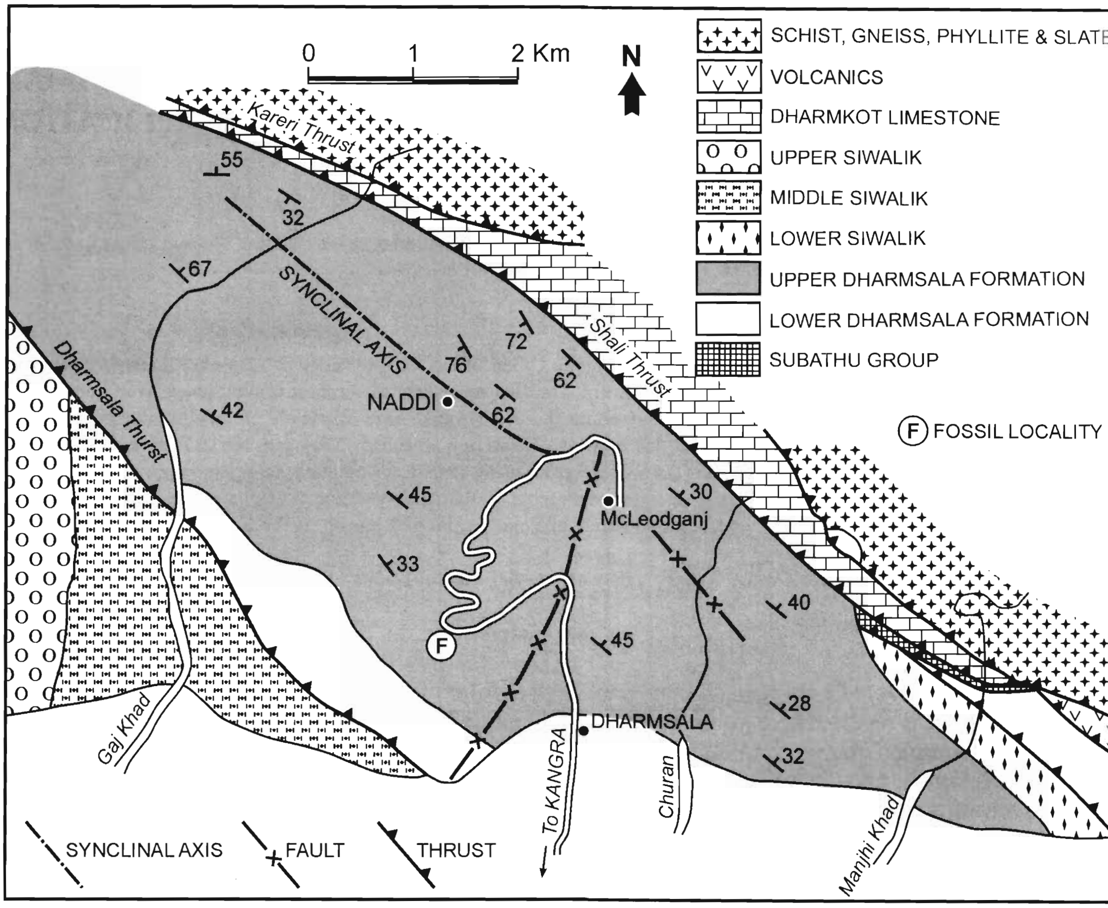

Fig. 1. Geological map of the Dharmsala area showing *Prodeinotherium* locality (after Kumar *et al.*, 1981).

Miocene age. This points to a late Eocene-Oligocene faunal gap in an apparently uninterrupted sequence. Other palaeontological data from these horizons lack the potential of resolving the issue of age range and related aspect of the late Eocene-Oligocene faunal gap/unconformity intervening between these horizons and the older Subathu (a mainly marine stratigraphic entity). The late Eocene-Oligocene faunal gap, however, has recently been explained in the light of latest sequence stratigraphic paradigm (Tiwari, 2005) as a manifestation of destruction of coastal vertebrate habitat. A few Lower Murree faunal reports (Ranga Rao, 1971; Khan, 1973) in fact described the Kalakot Zone fossil mammals which are now considered to be a part of the Subathu mammalian assemblage (Khan, 1975; Ranga Rao, 1986).

The Kasauli beds of the Dagshai and Kasauli formations in Simla Hills have yielded the fossil floral elements (Mathur *et al.*, 1996 and other references therein) as well as a rhinocerotid molar fragment showing wrinkled enamel and characteristic palaeohistological features (Arya *et al.*, 2004).

Records of previous palaeontological investigations in the Dharmsala Group started with report of vertebrate remains in the N/Q Boundary Seminar at Chandigarh (Verma and Verma, 1979). Subsequently, Kumar (1985), Dogra *et al.* (1985), Jolly *et al.* (1986), Tiwari *et al.* (1991), and Feist and Tiwari (1999) systematically studied and reported palaeobiological remains from the Dharmsala horizons. Recently, Tiwari and Bhandari (2004, 2005) reported discovery of an isolated ctenodactyloid rodent molar and *Dasyatis* fish remains from the TCP locality.

GEOLOGY OF THE AREA

The Dharmsala area is a part of foldthrust belt and is on the southern side of the Dhauladhar Range. The area comprises phyllites, schists and slates of Chandpur(?), limestone of Dharamkot, volcanics of Dharmsala and Tertiary sedimentary package assigned to Subathu, Dharmsala and Siwalik groups (Fig. 1). The Upper Dharmsala exposures forming core of syncline and otherwise dominate the scene in the area. There are three major east-west trending thrusts in the area. Dharmsala Thrust towards south delimits Dharmsala and Siwalik groups, whereas Shali Thrust juxtaposes Dharmkot Limestone with Dharmsala. Kareri Thrust (=Chandpur Thrust ?) in northern vicinity of Shali Thrust has brought Chandpur phyllites, schists and slates on the Dharmkot Limestone (Kumar *et al.*, 1981; Kumar, 1985).

The Tertiary geology of the Kangra Valley manifests interplay of eustatics, the Himalayan tectonics and sedimentation that has attracted numerous geologists. Gas and oil shows reveal great promise and thus the valley and nearby region is amongst the most studied Tertiary sectors of the NW Himalaya.

Regional lack of dip discordance between the Subathu and the under- and overlying horizons (Bhandari and Agarwal, 1967) indicates that the Himalayan tectonics, *sensu stricto,* did not play any role on the eastern side of the Hazara-Kashmir

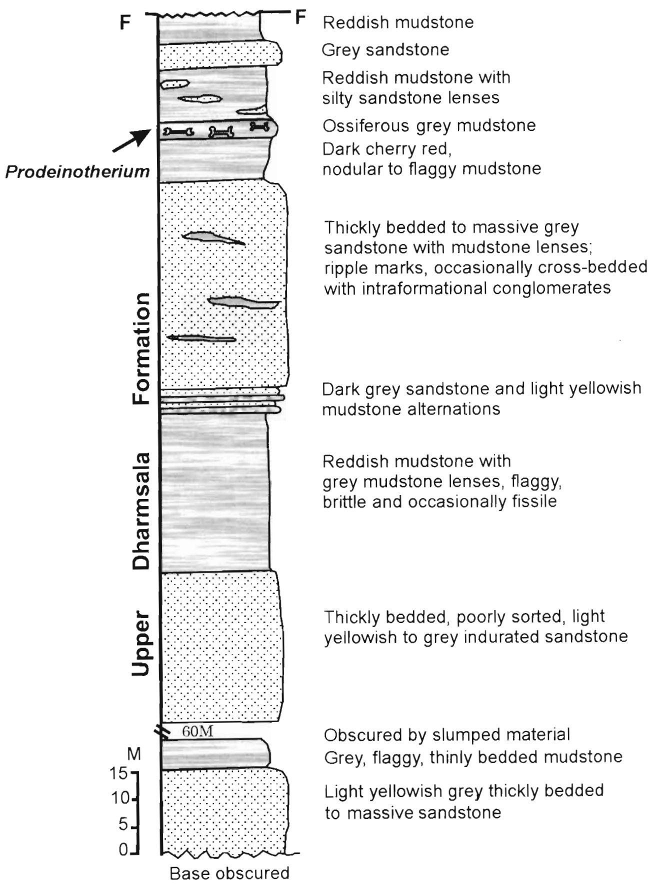

Fig. 2. Litholog of the TCP section showing the fossil-yielding grey mudstone horizon.

syntaxis in the Palaeocene-middle Eocene shallow marine plus nonmarine forced regressive phase (late Eocene to Oligocene) of sedimentation. Tiwari (2005) ascribes it to the global eustatic rise and fall in the sea level of that period. In the present context, regional tectonic stability at the onset of marine sedimentation has been identified earlier also on the basis of detailed facies analysis by Srivastava and Casshyap (1983). The foreland basin came into being in the region in the early Miocene as a consequence of regional component of thin skin tectonics due to subduction of Indian plate below the Asian plate that went on unabated and gave rise to successive southwardly prograding foreland basins.

Regarding the sedimentary record, the shallow marine Subathu Group having limestone and shale lithologies marks the beginning of the Tertiary sedimentation on broad coastal shelf (Srivastava and Casshyap, 1983) on the southern side of the proto-Himalayan landmass characterized by mature landscape and drainage (Singh, 1979; Tiwari, 2005). Exposures of the Subathu Group are very limited in the Dharmsala area and are confined to the Manjhi Khad section near Khaniyara. The succeeding mudstone and fine- to medium-grained sandstone horizons of the Dharmsala Group are subdivisible into Upper Dharmsala and Lower Dharmsala formations and consist of forced regressive barren units plus horizons marking the beginning of the foreland basin evolution in response to the regional tectonics activating MCT or its coeval event as a part of overall Himalayan Tectonics of that time. The Upper Dharmsala Formation is prominently exposed with many accessible sections now known to yield palaeobiological assemblage which constitute ancestral stock to some lineages in the younger Siwalik life forms. Arguably, the Siwalik foreland basin was sequel to activation of subsequent MBT or its precursor in the region and is adequately exposed in the vast expanse towards south up to the alluvial plains and is known to yield local faunal assemblages.

Tertiary stratigraphic sequence of the area along with under and overlying horizons is given in Table 1.

In the Dharmsala-McLeodganj Section, the Upper Dharmsala Formation is prominently exposed on the southern slope of the Dhauladhar Range. Predominantly, laterally persistent, medium-grained, light-coloured sandstone units of the Upper Dharmsala Formation are exposed in the expanse between Dharmsala and McLeodganj. However, a fossiliferous dark grey mudstone facies, uncommon in the Dharmsala Group, crops out in the high gradient nala right below the Traffic Check Post across the road (Figs. 1 & 2); the TCP section and the locality in the nala is around 4 km by road towards McLeodganj from Dharamsala. At this locality, the beds dip northeasterly with the dip amount varying from 40° to 50°. The fossil was recovered from the topmost level of the grey mudstone unit. GPS location of the TCP locality is 32°13.74'N: 76°18.46'E. In an adjacent nala too, towards the west in up dip direction and at a relatively higher altitude, the continuation of the dark grey mudstone facies is exposed.

SYSTEMATIC DESCRIPTION

Mirorder **Tethytheria** McKenna, 1975
Order **Proboscidea** Illiger, 1811
Family **Deinotheriidae** Bonaparte, 1841
Genus ***Prodeinotherium*** Ehik, 1930
Prodeinotherium orlovii (Sahni and Tripathi, 1957)
(Pl. I, figs. 1-5)

Deinotherium orlovii Sahni and Tripathi, 1957, p. 27, pl. 3.
Prodeinotherium orlovii (Sahni and Tripathi, 1957) Koufos *et al.*, 2003, p. 308.

Locality and Horizon: Traffic Check Post Locality, 4 km towards McLeodganj from Dharmsala via Cantonment. Horizon is the topmost level of the dark grey litho-unit of Upper Dharmsala Formation exposed in the high gradient nala below TCP on the road.

Material: An isolated left upper third premolar (LP^3; WIF/A 1064); the isolated tooth of the *Prodeinotherium* from the TCP locality bears the Wadia Institute of Himalayan Geology Repository no WIF/A 1064 and will be in the personal care of BCV till he finally hands it over to the Institute for posterity and till such time cast of the molar will occupy the number allotted to the original specimen.

Description: The isolated premolar (WIF/A 1064) is complete and well preserved; it measures 52 mm in length and 57 mm in width in occlusal view with the crown height of 30 mm (maximum 40 mm at postero-labial corner, i.e. metacone). Three lophs, namely protoloph, ectoloph and metaloph, are present on the premolar. Transverse lophs attain maximum height on their lingual edges. While the protoloph is slightly convex towards anterior side, the metaloph is straight and heads, little beyond ectoloph, towards postero-labial beginning of the posterior cingulum. The protoloph is more developed than the metaloph. A centrally deep and labially wide transverse enamel valley between protoloph and metaloph is closed by ectoloph on labial side and has a constricted lingual opening with slight obstruction from enamel beads on the cingulum

Table 1: Stratigraphic sequence in the Dharmsala area.

Group / Formation		Lithology	Age and remarks
Glacial deposits		Alluvium, boulder beds, terrace deposits, moraines and erratics	Sub Recent to Pleistocene, conspicuous huge granite boulders
Siwalik Group	Upper Middle Lower	Boulder beds, medium to coarse grained sandstone, shales and claystone	Lower Pleistocene to middle Miocene. fossil remains known and are being studied
Dharmsala Group	Upper Lower	Medium to fine grained sandstone, shales and claystone	Lower Miocene, faunal control is not robust
Subathu Group		Limestone, claystone, shales and quartzite	Middle Eocene to lower Eocene/ Palaeocene, was also a part of provenance as we are getting reworked foraminifer clusters
Dharmkot Limestone		Limestone, dolomite with salt marl at base	
Dharmsala Traps		Green to grayish green	Lesser Himalayan Precambrian -- early Cambrian horizons comprising bedrocks and provenance for Tertiary horizons in the area
Chandpur		Phyllites, schists and quartzits	
Dhauladhar Granite (intrusive)		Granite with xenoliths	

that is confined to the opening there. These obstructing enamel beads are the distinguishing features of the upper third premolar of *Prodeinotherium orlovii* setting it apart from the homologous tooth of *Prodeinotherium pentapotamiae* which has otherwise comparable size and crown morphology. On the anterior and posterior sides, cingula are well developed but the posterior one is damaged on postero-labial corner. Preserved portions of the roots reveal that the tooth was four-rooted and the two roots at lingual border were distinctly closer to each other than the other two on the labial side. The tooth, like other deinothere teeth, is least worn and lends credibility to the supposition that the taxon fed on succulent, non-abrasive tree vegetation. However, WIF/A 1064 has characteristic wear facets of a deinothere P^3 corroborating the functional aspect elaborated by Harris (1975). The lingual edge of the ectoloph has a wear facet due to shearing by labial edge of the ectolophid of the lower first premolar. And the lower fourth premolar's anterior buttress of protolophid occludes against the posterolingual edge of the ectoloph and thereby gave rise to a wear facet there. Further, Harris (1975) is of the view that though premolars possess shearing function but their primary role remains lateral guidance of the mandible and to limit its forward movement. And thus slight morphological variations on the anterior most cheek teeth, i.e. P^3s were rightly adjudged worth distinguishing species in the habitat in the conservative deinotheres (Sahni and Tripathi, 1957).

Remarks: Deinothere teeth are readily identified as they differ appreciably in size and morphology from other Tertiary mammals (Harris, 1973) and our cheek tooth (WIF/A 1064) from the Dharmsala Group is no exception; it has been identified on

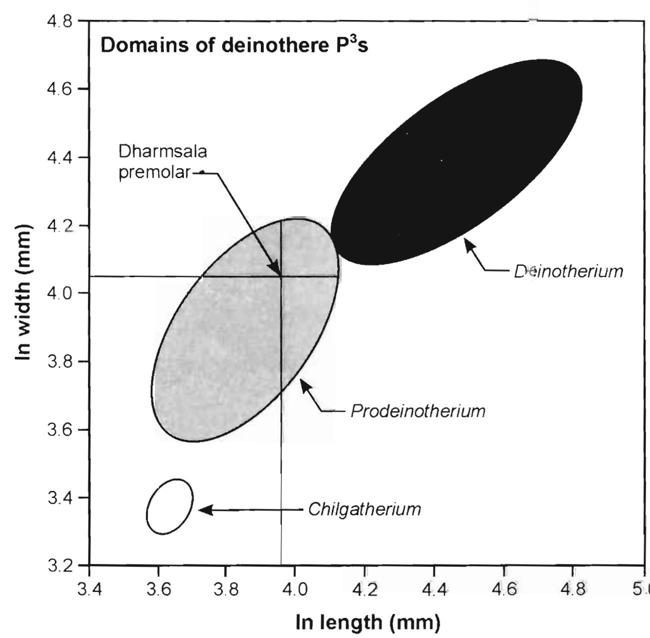

Fig. 3. Position of the premolar (WIF/A 1064) of *Prodeinotherium orlovii* in the domains of P^3s of deinotheres in natural log of length vs. width plot (after Sanders *et al.*, 2004).

EXPLANATION OF PLATE I

1. Occlusal sketch of ***Prodeinotherium orlovii***, left upper third premolar (WIF/A 1064) showing elements of descriptive terminology.

2-5. ***Prodeinotherium orlovii***, LP^3 (WIF/A 1064); 2. Occlusal view; 3. Lingual view; 4. Anterior view; 5. Posterior view showing partially obliterated cingulum; all the views were taken following magnesium oxide coating by smoking the premolar over the burning Mg ribbon.

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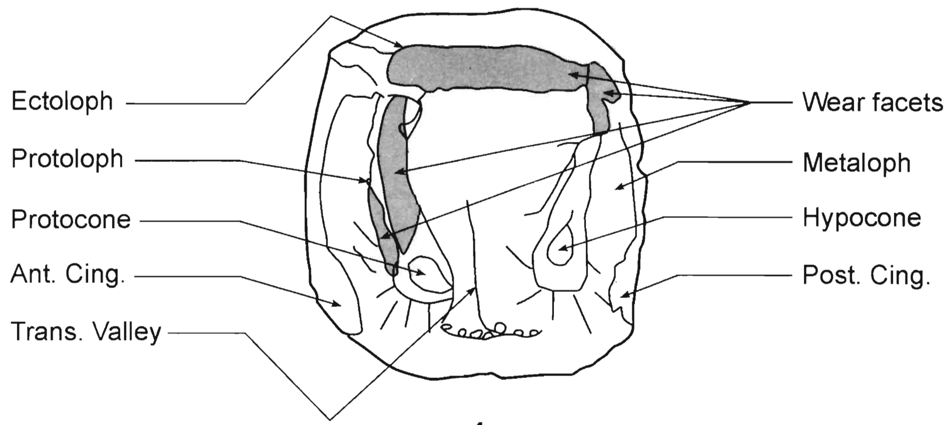

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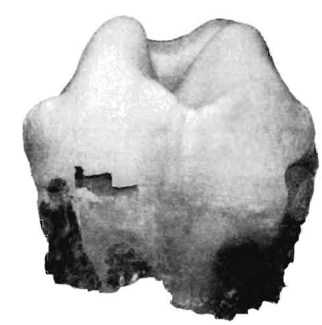

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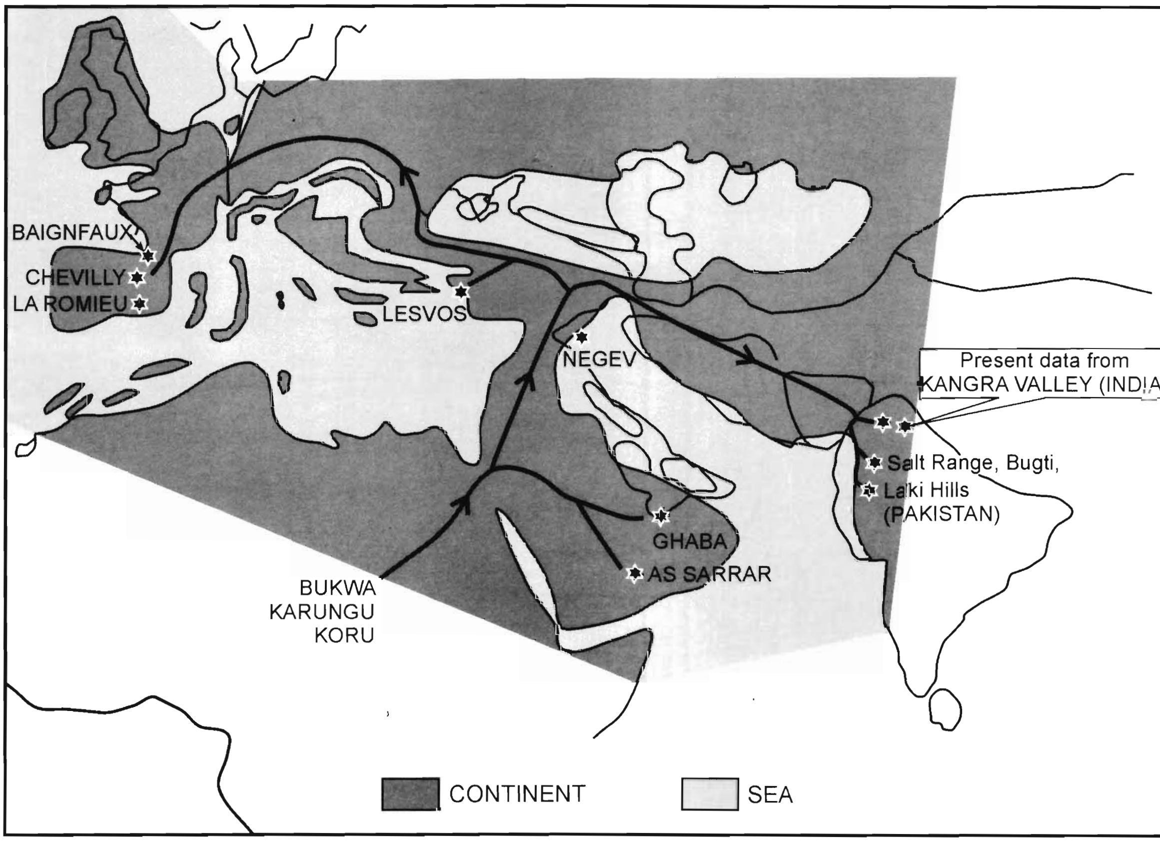

Fig. 4. Distribution of *Prodeinotherium* in three continents, namely, Africa (place of origin and radiation), West Asia, and Europe portraying inferred routes of migration (after Koufos *et al.*, 2003).

the basis of occlusal dimensions and morphology as left upper third premolar of *Prodeinotherium.* Furthermore, it falls in the domain of *Prodeinotherium* in the bivariate plot of natural log-transformed length versus width of the deinothere taxa done on the basis of larger sample size (Sanders *et al.*, 2004; Fig. 3).

Deinothere lineage follows Cope's Rule that relates evolution with increase in size which is plausibly beneficial in proliferation of the group on many counts (Alroy, 1998). Deinothere upper molars and premolars are similar to the dentition of tapirs but are easily distinguishable because of the lack of parastyle and much bigger size; parastyle is a characteristic feature of *Tapirus* and lack of this feature precludes the possibility of the premolar in our collection to be that of a tapir (Haowen Tong, *pers. comm.*). Above all, it compares well with a left P^3 (GSI Type No. A596) that was described by Sahni and Tripathi (1957) as a part of the type material for *D. orlovii.* P^3s of *P. pentapotamiae* are morphologically distinct in having a spouted projection of lingual cingulum at the opening of transverse enamel valley instead of having the obstructing lingual enamel beads as described above in our Dharmsala P^3 referred to *Prodeinotherium orlovii.* Further, P^3 of *Deinotherium indicum* is distinctly bigger besides having cingula on anterior, lingual, and posterior sides of the premolar and hence distinguishable from the P^3 of *P. orlovii.*

A *Deinotherium* sp. molar fragment (isolated cusp, VPL/M 1651) recorded independently earlier by Kumar (1985) from this section may be referred to *P. orlovii* since its assignment was purely on the premise that *Deinotherium* was the only deinothere genus recorded from the Indian subcontinent.

DISCUSSION

The genus *Prodeinotherium* belongs to the Deinotheriidae, a proboscidean family of uncertain taxonomic position that keeps it in focus of future research (Shoshani and Tassy, 2005). The Proboscidea is held as an African order as it originated and diversified there and its different lineages emigrated up to far off negotiable equatorial continents (Osborn, 1936) in two or more phases (Tassy, 1990; Antoine *et al.*, 2003). *Prodeinotherium* appeared in the Indian subcontinent at the beginning of the Burdigalian (~20.5 Ma) and is taken as an evidence of the supposed short-time early connection of Africa and Asia (Koufos *et al.*, 2003).

Deinotheriidae, an early Palaeogene lineage of the order, has now three established genera, namely, *Chilgatherium, Prodeinotherium* and *Deinotherium* (Sanders *et al.*, 2004). *Prodeinotherium* was larger and more specialised than its Oligocene predecessor *Chilgatherium* and emigrated to Europe and the Indian subcontinent in Asia in early Miocene (Fig. 4). The genus flourished for several millions of years but was replaced in the later part of Miocene by *Deinotherium* with larger body size and cursorial adaptations (Harris, 1973). *Prodeinotherium* and *Deinotherium* are known from the Miocene horizons of the Indian subcontinent, whereas the most primitive and small-sized deinothere taxon *Chilgatherium* apparently did not emigrate anywhere and remained in Africa.

In view of the updated systematics, *Prodeinotherium* is represented by *P. orlovii* (Sahni and Tripathi, 1957), *P. pentapotamiae* (Falconer, 1868), *P. bavaricum* (von Meyer, 1831), *P. hobleyi* (Andrews, 1911). An Interesting point to note is that only the former two species, *P. orlovii* and *P. pentapotamiae,* are exclusive to the Indian subcontinent. Both were replaced, most likely through *in situ* evolution, by larger species *Deinotherium indicum* which is again exclusive to the subcontinent. European and Indian subcontinent species of *Prodeinotherium* are distinct from each other plausibly as a manifestation of the late and early phases of radiations to these places respectively. For better resolution, that is, which species gave rise to *D. indicum,* we need more and better Indian deinothere collection from the well-established Miocene sections.

Deinothere fossils, now assigned to *Prodeinotherium*, are known from the NW part of the Indian Subcontinent, to be precise, from the Laki Hills in Sind, Bugti Hills in Baluchistan, and Salt Range in Attock (Sahni and Tripathi, 1957). However, the large deinothere species of the subcontinent, that is, *Deinotherium indicum* was far more widespread, reaching up to Nepal in the east and Piram Island in the Cambay Basin in the south besides being known from Haritalyangar (Bilaspur) and the Kangra Valley in Himachal Pradesh, India (West and Munthe, 1981; Sahni and Misra, 1975; Sahni and Gupta, 1984). To the best of our knowledge, this is the first record of the *Prodeinotherium orlovii* from India as the type material described by Sahni and Tripathi (1957) of the taxon is from the Kamlial horizons of the Lower Siwalik Subgroup in Attock District (33^0 52' N: 72^0 20' E) of Pakistan, approximately 400 km from Dharmsala towards WSW. This systematic study is significant as it describes the first large mammal fossil from the Dharmsala Group-putatively coeval to the Murree and Dagshai/Kasauli horizons of NW Himalaya; it is pertinent to mention here that question-marked deinothere report from the Laren beds of the Upper Murree in India is based on molar fragments (Khan *et al.,* 1971).

SUMMARY

1. As per records today, Kangra Valley was the easternmost abode of the relatively less cursorial immigrant deinothere *Prodeinotherium*; all previous records of the genus are from across the Hazara-Kashmir Syntaxis. However, the record of a younger, more evolved and cursorial form *Deinotherium* are known from the far off places up to Nepal towards the east and Piram Island towards south in western India.
2. Conjecturally, *Prodeinotherium* remained restricted to the basins proximal to the coastal areas having closed forest, whereas better cursorial traits in *Deinotherium indicum* enabled them to inhabit the areas far from coasts (e.g. *Deinotherium indicum* in Dang Valley, Nepal). Presence of *Dasyatis* in the Dharmsala assemblage, too, apparently supports the 'proximal to coastal areas' contention.
3. Occurrence of *Prodeinotherium* of early Miocene age from the basal horizons of the Upper Dharmsala Formation substantiates earlier age constraining the basis of chara (Feist and Tiwari, 1999) and lends support to the hypothesis, arguing for revival of terrestrial vertebrate habitat with basic trophic levels (basic biomass + primary consumers) because of initiation of foreland basin (*sensu stricto*; due to regional thrusting) in the early Miocene. The earlier coastal habitats of the Subathu Basin which supported the terrestrial vertebrate community of multiple trophic levels in the region, vanished because of eustatically driven, forced regression in the middle Eocene (Tiwari, 2005).

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