

WERE THERE SIZE CONSTRAINTS ON BIOTIC EXCHANGES DURING THE NORTHWARD DRIFT OF THE INDIAN PLATE ?

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Contrary to the geophysical data, which envisaged a long period (about 100 Ma) of physical isolation for the Indian subcontinent during its northward journey, the palaeontological data from the Upper Cretaceous continental sequences (Deccan infra- and inter-trappean) of peninsular India unequivocally demonstrate the nonendemic nature of the biota with close biogeographic links to the southern as well as northern hemisphere continents. The Myobatrachinae frogs, pelomedusid turtles, titanosaurid and abelisaurid dinosaurs, and Sudamericidae mammals exhibit distinct Gondwanan relationships. In marked contrast, the pelobatid and discoglossid frogs, anguid lizards, alligatorid crocodiles, palaeoryctid mammals, ostracodes, and charophytes indicate Laurasian connection. The Gondwanan taxa have been considered as representing an immigration event before 80 Ma (time of separation of Madagascar from India) and possibly between 85-90 Ma that facilitated the exchange of fauna between South America and Indo-Madagascar via Antarctica and Kerguelen Plateau. As far as the Laurasian connection is concerned, it has been shown that the size of organisms had a significant control on the biotic exchanges between the Indian subcontinent and the Laurasian landmasses. Only small-sized taxa could participate in the northern biotic interchanges through filter corridor/sweepstakes mode of dispersal involving the Trans-Himalayan Arc, Kohistan-Dras island arc complex and some oceanic volcanic islands which have been destroyed in due course of time at the subduction zone south of the Asian mainland/Trans-Himalayan Arc.

Key Words: Deccan; Lameta/Infratrappean; Intertrappean; Laurasian; Gondwanan; Non-Endemic; Cretaceous; Palaeobiogeography; India

Introduction

The northward drift of the Indian plate and its final collision with Asia has been a subject of considerable debate ever since the plate tectonics concept emerged on the earth science scene. Conventional palaeogeographic maps based on geophysical data have shown that the Indian plate after its break-up from the Gondwanan landmasses in the late Jurassic (about 150-160 Ma ago) and until its collision with the Asian mainland in the Early Eocene (about 55 Ma ago), drifted northwards as an island landmass within the Tethys¹⁻⁶. Thus the Indian subcontinent was supposed to have remained physically cut off from other continental landmasses for over 100 Ma. The isolation of landmasses for such a long period of time would have a very dramatic effect on constituent populations. Following the continental

separation, a progressive genetic isolation of populations would take place and the same would be reflected in morphological divergence over a geologically appreciable period of time. Australia and Madagascar are two such examples. In the light of geophysical data, it had been argued in the past that the mammals did not evolve on the Indian subcontinent⁷, rather they had immigrated from Asia once a physical contact was established between India and Asia in the Middle Eocene as exemplified by the mammalian fauna of Subathu Formation and subsequently evolved into the modern fauna and flora⁸. Whether the Indian subcontinent supported an endemic biota or not during its northward migration, particularly during the Late Cretaceous, can only be ascertained by an objective analysis of Late Cretaceous terrestrial fauna and flora as land living organisms are not expected to cross large bodies of sea water.

In the last two decades, focussed palaeontological studies on the Infra- and Inter-Trappean beds of Peninsular India, enhanced our knowledge of Late Cretaceous biota and allowed us to make a reasonable assessment of the Late Cretaceous palaeobiogeography of the Indian subcontinent. The current article is aimed to present a clear picture on the biogeographic links of the Indian subcontinent during the Late Cretaceous period by presenting some new insights in conjunction with a synthesis of earlier works. In the following sections, an account of various continental Late Cretaceous sequences of India, their fossil content and biogeographic relationships, and possible dispersal routes is given.

Continental Upper Cretaceous Sequences of Peninsular India

The continental Upper Cretaceous sediments have a wide geographic distribution in peninsular India spread across the political boundaries of eight states and occur either as thick sequences (<50 m) beneath the Deccan basaltic flows (infratrappian/Lameta Formation) or as thin sedimentary strata (<5 m) sandwiched between the basaltic

flows (intertrappean beds) (Fig. 1). The distribution of Infra and Intertrappean beds follows the outcrop pattern of Deccan Traps and their exposures are found on the western, eastern, northern, southern, and central parts of the Deccan volcanic province. Besides, continental vertebrate yielding Upper Cretaceous strata (Kallamedu Formation) are also known from distinctly shallow marine sequences of Tiruchirapalli District, Tamil Nadu.

The Infratrappian (Lameta) sediments are primarily represented by sandstones, shales, limestones, mudstones, and siltstones, whereas the intertrappean beds consist of sandstones, cherts, cherty limestones, shales, mudstones, siltstones and marls. The Kallamedu Formation is predominantly represented by thick sandstone with subordinate clays and sandy clays. Some of these clay horizons have recently been identified as vitric tuff beds⁹. Based on palaeontological evidences from the Infra and Intertrappean beds and geochronological and palaeomagnetic data from the Deccan basaltic flows, a Maastrichtian age for the Infra- and Intertrappean beds and a short duration of about 4 Ma for Deccan volcanism has been suggested¹⁰.

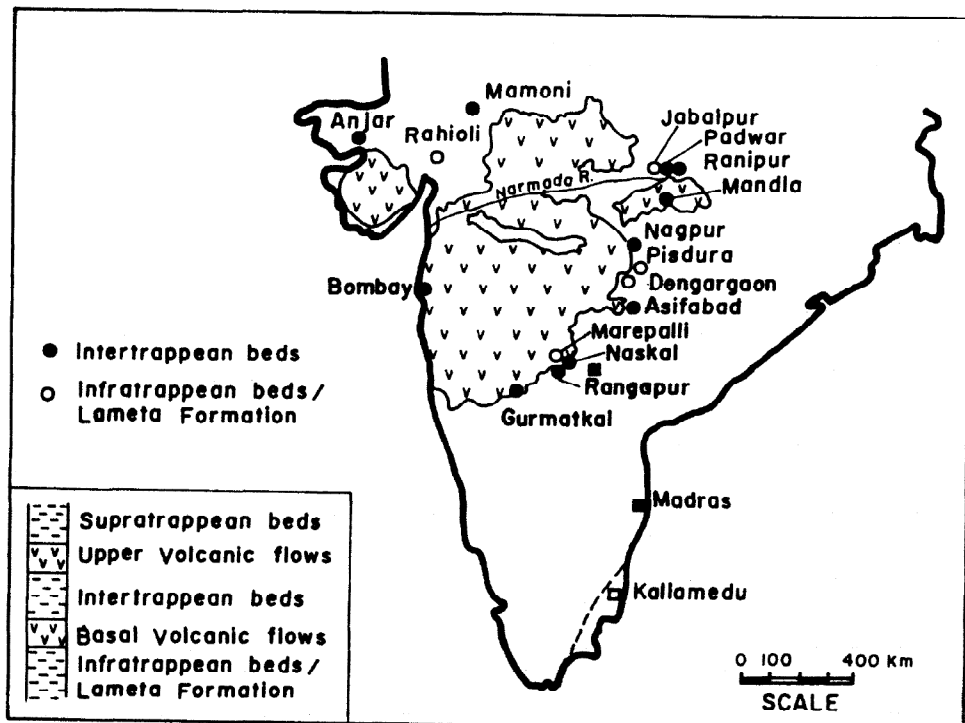


Fig. 1 Sketch map showing the location of continental Upper Cretaceous fossil-bearing sites in peninsular India.

The Ottakovil and Kallamedu Formations, which overlie *Globotruncana gansseri* bearing Kallankurichchi Formation, have been considered as Late Maastrichtian in age⁹. The faunal and floral list of the Infra- and Intertrappean beds and the Kallamedu Formation is given below.

Lameta Formation

The important localities from which the fossils have been recovered include Jabalpur¹¹⁻¹⁶, Pisdura-Dongargaon-Nand¹⁷⁻²², Rahioli²³⁻²⁷, and Marepalli - Auspalli²⁸⁻²⁹.

The Infratrappean biotic list comprises fishes: *Lepisosteus indicus*, *Igdabatis indicus*, *Rhombodus* sp., *Pycnodus lametae*, *Pycnodontidae* gen. et sp. indet., *Eoserranus hislopi*, *Osteoglossidae* gen. et sp. indet.; anurans: ?*Pelobatidae*; turtles: *Shweboemys pisdurensis*; crocodiles: *Alligatoridae* gen. et sp. indet.; dinosaurs: *Titano-saurus indicus*, *T. blanfordi*, *T. madagascarensis*, *T. colberti* (titanosaurids), *Indosuchus raptorius*, *Indosaurus matleyi* (abelisaurids), and many sauropod and theropod eggs and egg clutches; ostracodes: *Leiria jonesi*, *Mongolocypris* cf. *M. gigantea*, *Altanicypris bhatiai*, *Mongoli-anella palmosa*, *Eucypris* cf. *E. bajshintsavica*, *Frambocythere tumiensis tumiensis*, *Candona altanulaensis*, *Candona* cf. *C. hubeiensis*, *Cycloocypris transitoria*, *Cypridea* sp., *Cypridopsis bugintsavicus*, *Bisulocypris* sp., and *Darwinula* sp.; and charophytes: *Platychara perlata*, *P. compressa*, *P. raoi*, *P. rajahmundrica*, *Peckichara varians*, *Stephanochara* sp., *Nemegtichara grambasti*, *Harrisichara* sp.

Intertrappean beds

The most promising fossiliferous intertrappean localities are Gurmatkal³⁰⁻³¹, Naskal, Rangapur, Asifabad³³⁻⁴⁶, Nagpur, Bombay^{38,47-51}, Padwar, Ranipur⁵²⁻⁵⁴, Anjar⁵⁵⁻⁵⁸, and Mamoni⁵⁹.

The Intertrappean biota is represented by fishes: *Lepisosteus indicus*, *Lepidotes* sp., *Raja sudhakari*, *Rajiforme* indet., *Igdabatis indicus*, *Rhombodus* sp., *Pycnodontidae* gen. et sp. indet., *Osteoglossidae* gen. et sp. indet.; anurans: *Pelobatidae*, *Discoglossidae*, ? *Hylidae*, *Indobatrachus pusillus*; lizards: *Anguidae* gen. et sp. indet., snakes: *Indophis sahnii*, *Serpentes incertae sedis*; crocodiles: *Alligatoridae* gen. et sp. indet.; turtles: *Shweboemys pisdurensis*, *S. leithii*; dinosaurs: ?*Megalosaurus*, sauropod and ornithoid egg shells:

mammals: *Deccanolestes hislopi*, *Deccanolestes* cf. *D. hislopi*, *D. robustus*, *Sudamericidae* gen. et sp. indet.; ostracodes: *Leiria jonesi*, *Cytheridella strangulata*, *Candona altanulaensis*, *C. bagmodica*, *C. henaensis*, *Candoniella altanica*, *Altanicypris szzechuriae*, *Talicypridea biformata*, *Cypridea cavernosa*, *Mongolocypris longa*, ? *Cypridopsis bugintsavicus*, *Mongolianella palmosa*, *M. khamariniensis*, *Frambocythere tumiensis tumiensis*, *Timiriasevia* sp., *Bisulocypris* sp.; charophytes: *Platychara perlata*, *P. compressa*, *P. raoi*, *P. sahnii*, *P. rajahmundrica*, *Peckichara varians*, *Nemegtichara grambasti*, *Harrisichara muricata*, *Pseudoharrisichara* cf. *P. baytikshanensis*, *Stephanochara* cf. *S. levis*, *Grambastichara* sp., *Microchara* sp., *Chara* sp.; and molluscs: *Physa prinsepii*, *Lymnaea subbulata*, *Paludina normalis*, *Paludina* sp., *Unio deccanensis*.

Kallamedu Formation

A few poorly preserved bones and a tooth of a dinosaur were first reported by Blanford⁶⁰ from Kallamedu village, Tiruchirapalli District, Tamil Nadu. These fossils were referred to *Megalosaurus*. Following this, Matley⁶¹ documented fragmentary limb and girdle bones from the same locality and assigned them to *Titanosaurus* sauropod and an unidentified stegosaur. Yadagiri *et al.*⁶² made some new collections of dinosaur bones from the Kallamedu Formation which included ilium, pubis, ischium, femur and tibia of a theropod dinosaur and a humerus, armour plates and a coracoid bone of a supposed stegosaur dinosaur. However, Chatterjee & Rudra⁶ doubted the presence of stegosaurian remains in the Kallamedu collection.

Biogeographic Relationships

Since only non-marine taxa are useful in understanding the contiguity or isolation of landmasses in the geological past, exclusively those Infra and Intertrappean taxa which have some biogeographic value are taken into account. The most important taxa from biogeographic point of view are lepisosteid and osteoglossid fishes, leptodactylid, pelobatid and discoglossid frogs, pelomedusid turtles, anguid lizards, alligatorid crocodiles, titanosaurid, abelisaurid, and ankylosaurid dinosaurs, palaeoryctid and sudamericid mammals, ostracodes, and charophytes.

Fishes

The genus *Lepisosteus* is widely known from the Infratrappean as well as Intertrappean beds. Seven living species of gar fishes are confined to Central America, the Caribbean, and south-eastern North America. In the Cretaceous, the lepisosteids had a widespread distribution with fossil records from the Early Cretaceous of Niger⁶³ and Congo⁶⁴, the Campanian/Early Maastrichtian Los Alamos Formation⁶⁵, Upper Cretaceous Adamantina and Marilia Formations of Upper Bauru Group of Brazil⁶⁶⁻⁶⁷, Upper Cretaceous rocks of Colombia⁶⁸, Upper Cretaceous (Maastrichtian) El Molino Formation of Bolivia⁶⁹⁻⁷⁰, Albian Paluxy Formation, northcentral Texas⁷¹, Upper Cretaceous Lance Formation, Wyoming⁷², Upper Cretaceous (Campanian) Blufftown Formation, Western Georgia⁷³, and Upper Cretaceous of India^{18,33,48,74-75}. In the Indian subcontinent, the gars had persisted into the early Middle Eocene (Kuldana Formation) of Pakistan⁷⁶. More recently, Gottfried & Krause⁷⁷ reported *Lepisosteus* sp. from the Upper Cretaceous (Campanian) Maevarano Formation, Mahajanga Basin, Madagascar. Because of the wide geographic distribution of gars in the Cretaceous, it is assumed that this group must have evolved by the beginning of the break-up of Pangaea⁷⁷ and had a Pangean distribution in the late Mesozoic⁷⁸.

The Infratrappean osteoglossid fishes are known by squamules^{14,20,29}, whilst the Intertrappean osteoglossids are represented by squamules, dental plates, and otoliths^{32-33,35,48,56}. Besides these reports, dental plates and squamules of these fishes have also been described from the Middle Eocene Subathu Formation, Kalakot, India⁷⁹. Similar fossils are also known from the early Middle Eocene Kuldana Formation, Pakistan^{76,80}. So far, the osteoglossomorph fishes have been recorded from the Aptian Areado Formation, Brazil⁶⁶, Maastrichtian of Niger⁸¹, Bolivia^{69,82}, Palaeocene Santa Lucia Formation, Tuipampa, Bolivia⁶⁸, Palaeocene of Australia⁸³ and Europe⁸⁴⁻⁸⁵, Late Palaeocene of Turkey⁸⁶, Eocene of Sumatra⁸⁷, marine Ypresian of Morocco⁸⁸. From the northern continents, the osteoglossids have been reported from the Upper Jurassic - Lower Cretaceous Guyang Formation of Guyang Basin, Inner Mongolia and Madongshan Formation, Liupanshan Group, Ningxia, North China⁸⁹⁻⁹⁰, Upper Cretaceous (Campanian) Oldman Formation of

Alberta, Canada⁹¹, Palaeocene Paskapoo Formation of Alberta, Canada⁹², the Eocene of North America⁹³⁻⁹⁵, and the Middle Eocene Klondike Mountain Formation, Washington⁹⁶. Nelson⁹⁷ hypothesised a Gondwanan (African) origin for Osteoglossomorpha. Taverne⁹⁸ also arrived at a similar conclusion, but the attribution of Chinese *Lycoptera* to Hiodontiformes⁹⁹⁻¹⁰¹ compelled Patterson¹⁰² to suggest East Asia (China-Mongolia) as the centre of origin for osteoglossomorphs. However, the widespread distribution of fossil osteoglossomorphs on the northern and southern continents points towards a possible cosmopolitan distribution of this group at the end of Mesozoic Era.

Amphibians

The fossil frog *Indobatrachus pusillus* reported from the Intertrappean beds of Bombay is the only known fossil of the subfamily Myobatrachinae (Family Leptodactylidae) with extant members inhabiting Australia and New Guinea⁴⁹. *Indobatrachus* has been considered as a descendant of an older protodiscoglossid ancestor that reached India from a South American centre through northern Antarctica and South Africa⁴⁹.

In marked contrast to the Gondwanan relationship of *Indobatrachus*, two other families of frogs-Discoglossidae and Pelobatidae-described from the Intertrappean beds of Naskal³⁹ and Nagpur⁴⁷, respectively, indicate distinct Laurasian affinities. Mohabey & Udhoji²⁰ have briefly mentioned the occurrence of Pelobatidae in the Upper Cretaceous Lameta sediments of Nand area. Since no descriptions or illustrations have been provided, the identification of Lameta pelobatids needs to be authenticated. The living members of the family Discoglossidae reside in Europe (*Discoglossus*, *Bombina*, *Alytes*, *Baleaphyrne*), Middle East (*Discoglossus*), North-western Africa (*Discoglossus*, *Alytes*), Asia (*Bombina*), and Southeast Asia (*Barbourula*). The fossil record of discoglossids is biased towards Laurasia with known occurrences from the Middle Jurassic of England (*Eodiscoglossus oxionensis*)¹⁰³, Upper Jurassic (*E. santonjae*)¹⁰⁴ and Hauterivian-Barremian (*Wealdenbatrachus jucarensis*)¹⁰⁵ of Spain, Albian of Texas¹⁰⁶, Late Turonian-Coniacian of Asia (*Gobiates*)¹⁰⁷, *Kizylkuma antiqua*, *Aralobatrachus robustus*, *Saevesoederbergia egredia*, *Procerobatrachus paulus*, *Estesina*

*elegans*¹⁰⁸), Upper Cretaceous of Montana (*Scotiophryne pustulosa*)¹⁰⁹, *Paradiscoglossus americanus*¹¹⁰, Spain¹¹¹, Baja California (*Scotiophryne*)¹¹⁰, Middle Palaeocene Tongue River Formation, Montana (cf. *Scotiophryne*)¹¹², Upper Palaeocene of Cernay, France¹¹³, and Miocene of North Caucasus¹¹⁴. In the absence of a dorsal crest and in the development of dorsal tubercle and postero-dorsal extension of supra-acetabular expansion, the discoglossid ilia from the Intertrappean beds of Naskal resemble those of extant genus *Alytes* and the Coniacian-Santonian discoglossid ilia from Uzbekistan¹⁰⁸. The extant and extinct members of the family Pelobatidae follow the same distribution pattern as the discoglossids except for the fact that the fossil record of the former group is known from the Cretaceous and living pelobatids also occur in North America. The pelobatids are known from the Upper Cretaceous rocks of Asia (*Eopelobates leptocolaptus*¹¹⁵, *E. sosedkoi*¹¹⁶) and North America (*Eopelobates* sp.)¹¹⁷, Middle Eocene of Europe (*E. hinschei*), Oligocene of Asia (*Macropelobates*)⁴⁷, Lower Oligocene of South Dakota (*E. grandis*)¹¹⁸, Upper Oligocene or Lower Miocene of Czechoslovakia (*E. bayeri*)¹¹⁹, and Lower Miocene of Germany (*E. anthracimus*)¹²⁰.

The fossil record is, however, silent on the time of immigration of pelobatids and discoglossids from Eurasia to NW Africa, a small territory of which houses some living members of these groups. Recently, Asher & Krause¹²¹ indicated the presence of doubtful pelobatid frog remains in the Upper Cretaceous rocks of Madagascar. If this identification is confirmed with additional well preserved material in future, our current view on the distribution of this group needs a revision. Prasad & Rage⁴⁴ reported a humerus and ilium with morphology reminiscent of the family Hylidae from the Intertrappean beds of Naskal. Because of the poor state of preservation, these authors did not commit on the hylid assignment of these specimens. Before this find, hylids were definitively known from the Lower Oligocene of Canada¹²² and probably from the Middle Palaeocene of Brazil¹²³.

Lizards

Several vertebrae with morphology reminiscent of *Anguis* (subfamily Anguinae) and *Anniella*

(subfamily Anniellinae) represent the lizard family Anguinae in the intertrappean fauna⁴⁴. Estes¹²⁴ advocated a Laurasian (North American) origin for anguid lizards. Until now, the oldest anguid lizard has been reported from the Campanian of North America (*Odaxosaurus*)¹²⁴. In Asia, this group is known from the Upper Cretaceous Djadochta Formation (*Isodontosaurus gracilis*)¹²⁵, Upper Eocene rocks of Mongolia (*Placosaurus mongoliensis*)¹²⁶⁻¹²⁷ and from China¹²⁷ (*Placosaurus* sp). In Europe also, the members of this family first appear in the fossil record of Lower Eocene deposits (*Campinosaurus woutersi*)¹²⁸. The extant taxa of Anguinae occur in North America, Europe, Asia, North Africa, West Indies and South America.

Turtles

Pelomedusid turtles have been recorded from both Infra (*Schweboemys pisdurensis*)^{17,129} and Intertrappean beds (*Schweboemys pisdurensis*⁵⁶, *S. leithii*¹³⁰). Broin¹³¹ was of the opinion that the Indian pelomedusids represent *Schweboemys-Stereogenys* group of Podocnemidinae, a branch of common African - South American pelomedusid trunk, which persisted on the Indian subcontinent in isolation and had given rise to several post-Cretaceous pelomedusids. Hence the Indian pelomedusids may be considered as part of a Gondwanan stock that boarded the Indian plate before its separation from Africa contrary to the cosmopolitan distribution favoured for this group by Krause & Hartman¹³².

Crocodiles

Dental remains of crocodiles referable to the family Alligatoridae are known to occur both in the Infra²⁰ and Intertrappean beds^{36,75}. The fossil record shows that Alligatoridae is a Laurasian group with distribution in the Upper Cretaceous-Pliocene of Europe, Palaeocene, Miocene, and Recent of Asia, and Upper Cretaceous-Recent of North America. The most important fossil finds are from the Upper Cretaceous Oldman Formation, Canada (*Albertochampsia langstoni*), Hell Creek Formation, Montana, U.S.A. (*Brachychampsia montana*)¹³³, Upper Cretaceous of Europe¹³⁴, Palaeogene of North America (*Allognathosuchus*, *Ceratosuchus*), China (*Eoalligator*)¹³³. Extant members of this group also inhabit North America and China.

Dinosaurs

Large bones belonging to titanosaurid (*Titanosaurus indicus*, *T. blanfordi*, *T. colberti*, *T. madagascarensis*), abelisaurid (*Indosuchus raptorius*, *Indosaurus matleyi*), and possibly ankylosaurid (?*Lametasaurus indicus*) dinosaurs and sauropod and ornithoid eggs are known from the Lameta Formation, whereas few isolated bones, teeth and egg shells occur in the intertrappean beds. The Lameta titanosaurid eggs closely resemble those of France and Spain¹⁶. Jain and Bandyopadhyay²² considered *Antarctosaurus septentrionalis* reported from the Lameta beds of Jabalpur¹¹ as a junior synonym of *Titanosaurus indicus*. Similarly, *Laplata-saurus madagascarensis* has also been transferred to *Titanosaurus madagascarensis*¹³⁵⁻¹³⁶. The titanosaurid dinosaurs have previously been reported from the Early and Late Cretaceous of Niger¹³⁷, Albian of Malawai (*Malawaisaurus dixeyi*)¹³⁸⁻¹³⁹, Cenomanian of Egypt (*Aegyptosaurus*)¹⁴⁰ and Sudan¹⁴¹, Turonian and Santonian of Kenya¹³⁶, Albian-Cenomanian of Argentina (*Andesaurus delgadoi*)¹⁴², Upper Cretaceous rocks of Argentina and Uruguay (*Titanosaurus*, *Antarctosaurus*, and *Laplata-saurus*^{11,143}, *Saltasaurus loricatus*¹⁴⁴), Bauru Group of Brazil¹⁴⁵, and Madagascar (*Titanosaurus madagascarensis*)^{11,146}, Lower and Upper Cretaceous of South Africa and Upper Cretaceous of Morocco¹³⁷, Upper Cretaceous rocks of Fontllonga, Spain¹⁴⁷, Upper Cretaceous of Provence, southern France (*Titanosaurus indicus*)¹⁴⁸, Spain (*T. indicus*)¹³⁵, and Transylvania¹⁴⁹, and Late Maastrichtian of south-western U.S.A. (*Alamo-saurus*)¹⁵⁰.

Similarly Abelisaurids have so far been recorded from the Albian (*Carnotaurus sastrei*)¹⁵¹, Senonian (*Xenotarsosaurus bonapartei*)¹⁵² and Early Maastrichtian (*Abelisaurus comahuensis*)¹⁵³ of Patagonia, Campanian Maevarano Formation of Madagascar (*Majungasaurus crenatissimus*)¹⁵⁴, Upper Cretaceous Bauru Group of Brazil¹⁴⁵, Late Cretaceous of France (*Taracosaurus salluvicus*)¹⁵⁵ and Spain¹¹¹. Sampson *et al.*¹⁵⁴ considered *Majungasaurus crenatissimus* from the Campanian of Madagascar as a sister taxon of *Indosuchus raptorius* of the Upper Cretaceous Lameta Formation (India). On the whole, the Upper Cretaceous titanosaurid and abelisaurid dinosaurs of India compare well with those of South America, Madagascar, and southern Europe.

Although megalosaurids have been reported

from the Kallamedu Formation⁶⁰ and the intertrappean beds^{36,156-157} nothing can be said about their biogeographic relationship as the fossils are either fragmentary in nature or represented by isolated teeth. Moreover, the referral of isolated theropod teeth from India to "*Megalosaurus*" is based on close morphological similarity to "*Megalosaurus crenatissimus*"¹⁴⁶ of Upper Cretaceous of Madagascar. But more recently, "*Megalosaurus crenatissimus*" has been transferred to *Majungasaurus crenatissimus*, associated with family Abelisauridae¹⁵⁴. Therefore, the presence of "*Megalosaurus*" in the Upper Cretaceous rocks of India is not firmly established.

The fossil record of titanosaurids and abelisaurids demonstrates that these two groups were dominant in the dinosaur fauna of the Gondwanan continents and were either absent or played a subordinate role to the hadrosaur, ceratopsian, and tyrannosaurid dominated fauna of Laurasia. There is nothing unusual about their occurrence in southern Europe as many faunal interchanges are supposed to have taken place between NW Africa and Iberia via Alboran and Apulian microplates during Late Cretaceous low sea levels¹⁴⁹. The presence of ziphodont mesosuchian crocodiles with close relationship to the South American and African Late Cretaceous trematochampsids in the European Eocene has also been linked to this episode of faunal exchanges¹⁵⁸. Gheerbrant¹⁵⁹ also invoked a Late Cretaceous/Early Tertiary episode of faunal interchange to explain the presence of Laurasian palaeoryctids in the Palaeocene of Morocco. Likewise, Bonaparte & Kielan-Jaworowska¹⁶⁰ considered the occurrence of titanosaurid sauropods in the south-western U.S.A. as an evidence in support of Late Cretaceous faunal interchange with South America. Besides titanosaurids and abelisaurids, ankylosaurid remains have been documented from the Lameta sediments of Rahioli¹⁶, but no descriptions or illustrations have been provided by these authors. The referral of *Lametasaurus indicus* from the Lameta beds of Jabalpur^{11,161} to ankylosaurs has been doubted¹⁶²⁻¹⁶³. Even if their existence in the Late Cretaceous of India is established, ankylosaurids are of little biogeographic significance as this group of dinosaurs are known to occur in both Gondwanan and Laurasian landmasses¹⁶⁴. Bajpai *et al.*⁵⁷ described ornithoid egg shells with close affinities to Lacvisoolithidae

and Subtiliolithidae families of Late Cretaceous Nemegt Formation, Mongolia from the intertrappean beds of Anjar.

Mammals

Until now, two groups of mammals - Palaeoryctidae and Sudamericidae have been documented from the Intertrappean beds of India^{34,42-43,46,165}. Palaeoryctidae is a Laurasian family of insectivore mammals with widespread distribution in the Upper Cretaceous-Palaeocene rocks of North America¹⁶⁶⁻¹⁶⁷ and the Upper Cretaceous strata of Mongolia¹⁶⁸, and Cenomanian, Turonian, and Coniacian deposits of Uzbekistan¹⁶⁹. The Indian Late Cretaceous palaeoryctid mammals (*Deccanolestes hislopi* and *D. robustus*) are closer to North American *Cimolestes* and *Procerberus* in certain derived characters. The palaeoryctid mammals (*Cimolestes*, *Palaeoryctes*, *Aboletylestes*) have also been recorded from the Upper Palaeocene (Thanetian) Adrar Mgorn locality, Ouarzazate Basin of Morocco¹⁷⁰⁻¹⁷¹. Briggs¹⁷² misquoted Prasad and Sahni³⁴ to show that a close relationship exists between the Moroccan and Indian palaeoryctids. Therefore, it needs to be stressed here that the Moroccan palaeoryctids compare with those of India in primitive characters only and no phylogenetic relationship has been established between the two. The Moroccan forms are supposed to have immigrated from North America via Southern Europe at about the Cretaceous-Tertiary boundary¹⁵⁹. Krause *et al.*⁴⁶ described a highly specialised group of mammals (Sudamericidae, Gondwanatheria) from the Upper Cretaceous (Campanian) Maevarano Formation of Madagascar and the Upper Cretaceous Intertrappean beds of Naskal in peninsular India. The gondwanatheres are multituberculate or multituberculate-like mammals previously known from the Late Cretaceous and Palaeocene of Argentina¹⁷³. Absence of gondwanatheres in other Gondwanan continents has been cited to show that these mammals are endemic to South America¹⁷³. The latest reports from Madagascar and India refute this view and instead favour cosmopolitan distribution for this group of mammals in Gondwanan continents facilitated by biogeographic links between South America and Indo-Madagascar through Antarctica and Kerguelen Plateau⁴⁶.

Ostracodes

The Infratrappean non-marine ostracode

assemblage includes many forms, such as *Mongolocypris cf. M. gigantea*, *Altanicypris bhatiai*, *Eucypris sp.*, *Candona altanulaensis*, *Cycloocypris transitoria*, *Mongolianella palmosa*, and *?Cypridopsis bugintsavicus*, similar to the Upper Cretaceous ostracode assemblage IV of Sifangtai and Mingshui Formations of Singliao Basin¹⁷⁴.

The other members of the Lameta assemblage also exhibit close resemblance to contemporaneous fauna from Mongolia and China. The Lameta *Eucypris* is very close to *Eucypris bajshintsavica* known from the Upper Cretaceous rocks of Bayshingtoav region of southeastern Mongolia, whereas *Candona cf. C. hubeiensis* approaches in its morphology the Upper Cretaceous *C. hubeiensis* of Central Hubei, China¹⁵. Besides these taxa, *Frambocythere tumiensis tumiensis*, which has also been recorded from the intertrappean beds, was first recorded from the Upper Cretaceous of Spain and subsequently its other subspecies from the Montian of Belgium³⁸. Likewise, the intertrappean ostracode fauna, which is remarkably similar to that of Lameta Formation, consists of many species, such as *Candona altanulaensis*, *C. bagmodica*, *Candoniella altanica*, *Altanicypris szczechuriae*, *Talicypridea biformata*, *Cypridea cavernosa*, *?Cypridopsis bugintsavicus*, *Mongolianella palmosa*, and *M. khamariniensis*, which are common to that of Upper Cretaceous Nemegt Formation of Mongolia³⁸.

This assemblage is also identical to *Talicypridea-Cypridea-Candona* assemblage from the Campanian-Maastrichtian Wangshi Group and from the Upper Cretaceous Jaiding Group, Southern Sichuan and Northern Guizhou Provinces, China³⁸. Similarly, *Mongolocypris longa*, *Mongolianella khamariniensis*, *Candona henaensis*, *Cypridea cavernosa*, and *Talicypridea sp.* present in the intertrappean fauna were first documented from the Upper Cretaceous strata of Xining and Minhe Basins of China¹⁷⁵. *Paracandona jabalpurensis* of the Lameta Formation and *Leiria jonesi* and *Cytheridella strangulata* of the Intertrappean beds have been considered endemic species to peninsular India³⁸. However, according to these authors, the genus *Leiria* has wide distribution in the Late Mesozoic rocks of Europe and Asia. Similarly, *Paracandona* is also known from the Late Cretaceous of Belgium (*Paracandona belgica*)¹⁷⁶. *Timiriasevia* and

Bisulocypris reported from the Intertrappean beds of Gurmatkal³¹ range from Jurassic to Late Cretaceous in age and may have cosmopolitan distribution. The latter genus has recently been documented from the Lameta sediments of Nand-Dongargaon areas²⁰. Therefore, the freshwater ostracode fauna of the Infra and Intertrappean beds exhibits taxonomic relationship not only at generic level, but also overwhelmingly at species level to the Upper Cretaceous ostracode assemblages of Nemegt Basin, Mongolia and several inland lacustrine basins of China.

Charophytes

Bhatia *et al.*³⁷ and Srinivasan *et al.*³¹ discussed the biogeographic affinities of the Intertrappean charophytes. According to these authors, *Platychara raoi*, *P. sahnii*, and *P. rajahmundrica* are endemic to India. The genus *Platychara* is abundant in the Late Cretaceous lacustrine deposits of North America, Europe, South America, and possibly China³⁷. The genus has also persisted into the Early Palaeocene of N. America¹⁷⁷ and Europe¹⁷⁸⁻¹⁷⁹. *Platychara perlata* with known distribution from the Upper Cretaceous to Palaeocene of South America and Mexico is a cosmopolitan taxon. In contrast *P. compressa* has been recorded from the Upper Cretaceous to Palaeocene of U.S.A., Canada and Europe. The genus *Peckichara* occurs in the Maastrichtian of France and Spain, but its species *P. varians* has so far been documented from the Palaeocene - Early Eocene of Europe³¹. Correspondingly, *Harrisichara muricata* and *Stephanochara levis* are confined to the Palaeocene of Europe (France and Belgium), but at generic level *Harrisichara* has been reported from the Upper Cretaceous rocks of Nemegt Basin, Mongolia. Similarly *Grambastichara* sp. is also comparable to *Grambastichara bailanteensis* described from the Cretaceous-Tertiary transitional sequences of the Shalamulum area of inner Mongolia³¹. Bhatia *et al.*³⁷ described a new species of *Nemegtichara* (*N. grambasti*) from the Intertrappean beds of Rangapur. This genus was first documented from the Palaeocene-Eocene rocks of Nemegt Basin, Mongolia and later on from the Turonian - Maastrichtian - Palaeocene - Eocene sequences of China³⁷. Similarly, the genus *Microchara* has a junior synonym in *Gobichara* reported from the Palaeocene of Mongolia¹⁸⁰.

From the foregoing discussion, it is apparent that

the Infra and Intertrappean fossil assemblages do not indicate any marked endemism, rather they exhibit either Laurasian or Gondwanan connections. The Myobatrachinae frogs, pelomedusid turtles, titanosaurid and abelisaurid dinosaurs, and sudamericid mammals demonstrate Gondwanan affinities, whereas pelobatid and discoglossid frogs, anguid lizards, alligatorid crocodiles, palaeoryctid mammals, ostracodes, and charophytes suggest a Laurasian connection. So far, the strongest evidence for the Late Cretaceous Laurasian connection for India is offered by the ostracode fauna which includes many taxa identical at generic and even species level to those of Mongolia and China. On the other hand, the lepisosteid and osteoglossid fishes, and ankylosaurid dinosaurs had cosmopolitan distribution in the Late Cretaceous.

Possible Biogeographic Connections

There has been a general agreement among the palaeontologists and geologists on the non-endemicity of biota in the northward drifting Indian plate. However, a notable difference of opinion continues to prevail concerning the possible dispersal routes for the biotic interchanges. The presence of Gondwanan and Laurasian elements in the Late Cretaceous of India has been accounted in markedly different ways by different workers. Sahni¹⁸¹ and Sahni *et al.*¹⁸² discussed the entire gamut of Late Cretaceous faunal exchanges between Africa-India-Asia and came to the conclusion that Gondwanan taxa might have reached the Indian plate via Mascarene Plateau, Chagos and Laccadive aseismic ridges of the Indian Ocean. These authors also favoured dispersal of Laurasian taxa into India through Iran-Afghanistan microplates and Kohistan-Dras island arc systems that lay north of Greater India. But Chatterjee¹⁸³ discounted the model suggested for the southern connection on the grounds that these volcanic island chains came into existence only from Tertiary to Recent times.

Alternatively, Briggs¹⁷² made an attempt to explain strong relationships of the Indian Late Cretaceous fauna and flora with those of Africa and Laurasia. He concluded that by Early Cretaceous India was isolated from Africa and Madagascar, and by Middle Cretaceous, it had moved close to North Africa (Somali peninsula); or alternatively it occupied the gap between Northeast Africa and

Eurasia, which facilitated a dispersal route involving a direct connection from India to North Africa and with an intermittent or sweepstakes passage across the Tethys to Eurasia. A somewhat similar conclusion was arrived at by Chatterjee¹⁸³ to explain the African elements in the Late Cretaceous (65 Ma ago) of India. According to him, in the Late Cretaceous Karachi was adjacent to Socotra microcontinent at the northeast tip of Somalia and a greater part of south-western Arabia was emergent forming a dispersal corridor between India and Africa for terrestrial vertebrates. Regarding the Laurasian taxa, he suggested that the central part of Afghanistan (Dasht-i-Margo block) along with east central Iran (Lut block) formed a large microcontinent that maintained a land connection with Eurasia in the north and a dispersal corridor with Greater India through Kashmir region. The models advocated by Briggs¹⁷² and Chatterjee¹⁸³ for the African connection of the fauna are not acceptable as the palaeogeographic reconstructions show that the Indian subcontinent was widely separated from Africa, moving in a northeastward direction during the Late Cretaceous period^{8,184-187}.

Krause & Maas¹⁸⁸ maintained that the Indian subcontinent was adjacent to the eastern margin of Madagascar prior to magnetic anomaly 33b (Campanian) and Africa was faunistically linked with Madagascar at this time. These authors hypothesised that one or more groups of placental mammals boarded the Indian subcontinent in the Late Cretaceous from eastern Africa via Madagascar followed by a period of isolation during the Palaeocene when the Indian plate was drifting northeastwards through the Tethys. During this period of isolation, many groups of mammals, such as the Artiodactyla, Perissodactyla, Adapidae, Omomyidae, Hyaenodontidae and Anthracobunidae, had developed endemic taxa as evident from the Middle Eocene Kuldana and Domanda Formations of Pakistan and the Upper Subathu Formation of India. Contrary to most mammalian palaeobiogeographic reconstructions, which favoured mammalian immigrations from Central Asia to India after subaerial contact was established between India and Asian mainland in the early Eocene, Krause & Maas¹⁸⁸ suggested that the dispersals were from India to Asia. This palaeobiogeographic model implies that the placental mammal *Deccanolestes* from the Upper

Cretaceous Intertrappean beds was an immigrant from the African mainland via Madagascar. Besides immigrants, we cannot rule out the indigenous evolution of mammals in the Mesozoic of India in the light of recent discoveries of triconodont mammals from the Upper Triassic¹⁸⁹ and Lower Jurassic¹⁹⁰ deposits of peninsular India. One of the author's (GVRP) ongoing work on the early Jurassic mammals of India indicates much more diversity and the presence of eupantotheres cannot be ruled out. In a more recent paper, Krause *et al.*⁴⁶ justified the occurrence of highly derived Late Cretaceous South American mammal (Sudamericidae) in both India and Madagascar by invoking a late early Cretaceous (88-90 Ma) dispersal route from South America to India-Madagascar through Antarctica and Kerguelen Plateau which might have lasted as late as 80 Ma. The same biogeographic link might have been used by other Gondwanan elements, such as titanosaurid and abelisaurid dinosaurs, to make their appearance in the Late Cretaceous of India.

Contrary to the palaeobiogeographic models proposed by Briggs¹⁷² and Krause and Maas¹⁸⁸, Jaeger *et al.*¹⁹¹ based on lack of significant endemism and the occurrence of Laurasian pelobatid frogs, palaeoryctid mammals, and Mongolian charophytes in the Late Cretaceous of India, advanced a new hypothesis suggesting that the Indian subcontinent was close to Asia at the end of Cretaceous that facilitated the dispersal of non-marine biota across ephemeral land routes. The early India/Asia collision (Cretaceous/Tertiary boundary age) concept of Jaeger *et al.*¹⁹¹ received an added impetus from the subsequent discoveries of alligatorid crocodiles^{36,75}, discoglossid frogs³⁹, anguillid lizards⁴⁴, ostracodes^{38,59}, and charophytes^{31,37} of typical Laurasian affinity from the infra and intertrappean beds of peninsular India. Sahni and Bajpai¹⁹² and Prasad *et al.*¹⁹³ also favoured the early India/Asia collision model to account for the existence of Eurasiatic elements in the Late Cretaceous of India. Prasad *et al.*¹⁹³ while discussing the palaeobiogeographic significance of the Infra and Intertrappean biota observed that the Infratrappian biota have Gondwanan affinity possibly representing relics from former Gondwanaland, whereas the Intertrappean biota exhibit distinct Laurasian affinities. Based on the absence of Laurasian taxa in the Infratrappian beds, they concluded that the physical contact

between India and Asia was not achieved by the time of deposition of Infratrappean sediments. But more recent works have shown that the Infratrappean biota also contains many Laurasian elements, for instance ostracodes, charophytes, alligatorid crocodiles, and a doubtful pelobatid frog^{15,20}. Additional and more important evidence for the early India/Asia collision model was furnished by palaeomagnetic studies of southern, central and northern parts of Ninetyeast Ridge in the Indian Ocean¹⁸⁷. According to these authors, Greater India was extended 650 km beyond the present day outline of Northern Kohistan Suture and Greater India's north-western margin crossed the equator at or before 65 Ma and arrived in the equatorial to low northern latitude belt. Further, they concluded that reduction in the rate of India's northward movement at 55 Ma coincides with reduction in the spreading rate of the central Mid-Indian ridge at magnetic anomaly MA24 and this slow down in India's northward motion was taken for completion of eastward propagating India/Asia suturing process. Klootwijk *et al.*¹⁹⁴ arrived at a similar conclusion based on the palaeomagnetic data from the Chitral region (Eastern Hindukush).

The Late Cretaceous-Early Tertiary India/Asia collision model of Jaeger *et al.*¹⁹¹ was questioned by some workers¹⁹⁵⁻¹⁹⁷ on the grounds that the evidences from pelobatid and discoglossid frogs, and palaeoryctid mammals are inadequate for establishing a direct northern contact with Asia in the Late Cretaceous. Rather they favoured the traditionally accepted Early Eocene age for achieving a definite subaerial contact between India and Asia. Although some doubts have been raised by these authors on the identifications of anuran remains with Pelobatidae and Discoglossidae families, Rage and Jaeger¹⁹⁸ convincingly defended the earlier taxonomic treatment of these taxa. According to Thewissen & McKenna¹⁹⁶ and McKenna¹⁹⁷, the Lameta pelobatids might have reached the Greater India from Africa when the former landmass maintained a connection with Seychelles Block or the Horn of Africa on the west or northwest via now destroyed island arcs or Deccan basaltic pile itself. A somewhat similar explanation has also been forwarded for the Infratrappean *Deccanolestes*, in view of the occurrence of palaeoryctid mammals in the Late Palaeocene of Morocco¹⁷⁰⁻¹⁷¹ and a primitive therian mammal (*Tribotherium africanum*) with

alleged close relationship to *Prokennalestes* of Mongolia in the Early Cretaceous of Morocco¹⁹⁹. Contrary to McKenna's¹⁹⁷ conclusion, no close phylogenetic relationship has been shown to exist between *Tribotherium* and the Early Cretaceous *Prokennalestes*¹⁹⁹. Moreover, the current plate kinematic reconstructions showed a wide body of marine water separating the Greater India from Africa throughout the former's northward migration until its collision with mainland Asia¹⁸⁵⁻¹⁸⁷. Owing to these reasons, the palaeobiogeographic models favouring a western connection for Greater India with Africa are not sustainable. Further, it needs to be emphasised that contrary to the views held by Thewissen & McKenna¹⁹⁶⁻¹⁹⁷ and Krause & Hartman¹³², the fossil taxa of Laurasian affinities in the Infra and Infratrappean beds include not only anurans and mammals, but also anguillid lizards, alligatorid crocodiles besides the most important ostracode and charophyte assemblages. In fact, the ostracodes are identical to those of Upper Cretaceous deposits of Mongolia and China even at species. These fossil groups have been completely overlooked by the above authors in their biogeographic analysis of Late Cretaceous biota of India.

In the light of existing fossil data from Africa, the early India/Asia collision model of Jaeger *et al.*¹⁹¹ appears highly attractive as it provides the best possible explanation for the Laurasian taxa in the Late Cretaceous of India. However, we cannot ignore the fact that the fossil record of Africa is incomplete and extensive field prospecting is needed before arriving at meaningful biogeographic conclusions. Moreover, conflicting opinions exist on the date of initiation of collision between India and Asia. Patriat and Achahe¹⁸⁵ postulated that the initial collision between India and Asia took place at about 52-50 Ma ago as inferred from the dramatic reduction in the northward movement of Indian plate around this time. Contrary to the palaeomagnetic results of Klootwijk *et al.*^{187,194} which envisaged completion of suturing along the entire Himalayan chain by 55 Ma after the collision being initiated around 65 Ma ago, new structural and sedimentological data from Zaskar shelf area favour a relatively younger age for India/Asia collision. Searle *et al.*²⁰⁰, based on structural and stratigraphic studies of the northern continental margin of India, came to the conclusion that all the ophiolitic belts along the northern

Indian plate margin were emplaced on this margin during the Late Cretaceous or at the Cretaceous-Tertiary boundary. Following the ophiolite obduction phase, stable shallow marine conditions prevailed not only along the Zaskar shelf, but also all along the Indus suture. As per these authors, the cessation of marine sedimentation with Kesi Formation and the onset of continental sedimentation with red beds and fluvial conglomerates (Chulung-La Formation) at about 54 Ma (Ypresian) mark the closure of Tethys in this region. These continental beds conformably overlie the lowermost Eocene Nummulitic limestones which also occur all along northern Indian plate margin from Salt Range and Hazara to as far as southern Tibet²⁰⁰. A similar age (54 Ma) has also been favoured for the final closure of Tethys in Ladakh and diachronous ages for collision from west to east on the basis sedimentary history along the northern Indian continental margin in Ladakh Himalaya²⁰¹. Treolar²⁰² argued that the 65 Ma event identified by Klootwijk *et al.*^{187,194} does not necessarily date the initiation of India/Asia collision, instead marks a temporary hiatus in the northward path of India caused by the emplacement of ophiolites on to the leading edge of the Indian plate and collision must have occurred sometime between 65 and 55 Ma ago. On the basis of subsidence history of the stratigraphic section on Zhepure Mountain on the northern flank of Everest, Rowley²⁰³ suggested that the initiation of collision began probably closer to 45 Ma or even later. In the Zaskar and Hazara regions of Indo-Pakistan, about 1200 km west of Zhepure Mountain along the India-Asia suture, the date for the initiation of collision is stratigraphically well constrained at 51.8 Ma²⁰⁴. Further west of Zaskar and Hazara, extensive biostratigraphic analysis of sediments overlapping the suture between the Indian subcontinent and fragments of old oceanic terrains from Waziristan and Kurram in Northwest Pakistan led Beck *et al.*²⁰⁵ to suggest an age after 66 and before 55.5 Ma for the beginning of India/Asia collision. These new data favour diachronous initiation of collision from west to east along India-Asia suture zone and reject either collision at K/T boundary or isochronous initiation of collision in the Early Eocene. Although cooling history of metamorphic rocks along Higher Himalaya-Swat and Hazara²⁰⁶, Suru Valley, Zaskar²⁰⁷, Tibet²⁰⁸ and eastern Nepal²⁰⁹ - indicates

diachronous collision events from west to east, Searle *et al.*²⁰⁰ assumed that no diachroneity occurs in view of the similarity in stratigraphic data from Waziristan (Pakistan) and Ladakh (India). Recently, Lee & Lawver²¹⁰ suggested a Middle Palaeocene (58 Ma) land connection between India and Asia based on the reduction of drift rate from 17 cm/year in the Late Cretaceous to 11 cm/year in the Middle Palaeocene. Therefore, there is no unequivocal evidence to demonstrate that subaerial contact between the Indian plate and Asia (including microcontinental fragments accreted to its southern margin) was achieved by the end of Cretaceous.

New Insights

In view of the existing discordances in dating the India/Asia collision event, there is a need to consider alternative faunal dispersal mechanisms and/or routes which would provide a credible explanation for the presence of Laurasian taxa in the Late Cretaceous of the Indian subcontinent. Although it is not possible to make propositions regarding the dispersal mechanisms with a great degree of confidence, there are certain clearer pointers to some general conclusions. From the biogeographic point of view, one significant aspect—the size control on dispersal of fauna and flora—has been grossly overlooked in the past. A detailed analysis of the Infra and Intertrappean fauna and flora demonstrates the presence of three important palaeocommunities viz., terrestrial, lacustrine/fluvial, and mixed (Table I). Of these, dinosaurs are the largest animals of the terrestrial community. The Lameta dinosaurs have been documented not only by large bones of titanosaurids, and abelisaurids, but also by sauropod and ornithoid egg clutches. In comparison, the Intertrappean dinosaurs are known only by a few isolated teeth, bones, and egg shell fragments whose taxonomic position is not clear, therefore are of uncertain biogeographic affinity. As discussed earlier, the Lameta titanosaurids and abelisaurids are of unmistakable Gondwanan affinity and are supposed to have arrived from South America making use of a dispersal route followed by sudamericid mammals (i.e. South America-Antarctica-Kerguelen Plateau-Indo-Madagascar). The presence of another Gondwanan vertebrate group, the pelomedusid turtles, in the Infra and

Table I

Important Palaeocommunities viz. terrestrial, lacustrine fluvial, mixed and marine communities are classified as under:

Terrestrial Community	Lacustrine/fluvial Community	Mixed Community	Marine Community
<i>Frogs:</i>	<i>Fishes:</i>	<i>Frogs:</i>	<i>Fishes:</i>
?Hylidae	<i>Lepisosteus indicus</i>	Pelobatidae	<i>Igdabatis indicus</i>
<i>Lizards:</i>	Osteoglossidae	Discoglossidae	<i>Rhombodus</i> sp.
Anguidae	Ostracodes:	Myobatrachinae	<i>Raja sudhakari</i>
<i>Dinosaurs:</i>	<i>Leiria jonesi</i>	Crocodyles:	Rajiforme indet.
<i>Titanosaurus indicus</i>	<i>Cytheridella strangulata</i>	Alligatoridae	<i>Pycnodus lametai</i>
<i>T. madagascarensis</i>	<i>Candona altanulaensis</i>	Turtles:	Pycnodontidae
<i>T. colberti</i>	<i>C. bagmodica</i>	<i>Shweboemys pisdurensis</i>	<i>Eoserranus hislopi</i>
<i>Indosuchus raptorius</i>	<i>C. henaensis</i>	<i>S. lethii</i>	
<i>Indosaurus matleyi</i>	<i>Candoniella altanica</i>		
<i>Megalosaurus</i>	sp. <i>Altanicypriis szcechurae</i>		
Mammals:	<i>A. bhatiai</i>		
<i>Deccanolestes hislopi</i>	<i>Talicypridea biformata</i>		
<i>D. robustus</i>	<i>Cypridea cavernosa</i>		
Sudamericidae	<i>Cypridea</i> sp.		
	<i>Mongolocypriis longa</i>		
	<i>Mongolocypriis</i> cf. <i>M. gigantea</i>		
	<i>Mongolianella palmosa</i>		
	<i>M. khamariniensis</i>		
	<i>Frambocythere tumiensis</i>		
	<i>Cyclocypriis transitoria</i>		
	? <i>Cypridopsis bugintsavicus</i>		
	<i>Candona</i> cf. <i>C. hubeiensis</i>		
	<i>Eucypriis</i> cf. <i>E. bajshintsavica</i>		
	<i>Bisulocypriis</i> sp.		
	<i>Timriasevia</i> sp.		
	Charophytes:		
	<i>Platychara perlata</i>		
	<i>P. compressa</i>		
	<i>P. raoi</i>		
	<i>P. sahnii</i>		
	<i>P. rajahmundrica</i>		
	<i>Peckichara varians</i>		
	<i>Nemegtichara grambasti</i>		
	<i>Harrisichara muricata</i>		
	<i>Stephanochara</i> cf. <i>S. levis</i>		
	<i>Pseudoharrisichara</i> cf. <i>P. baytikshanensis</i>		
	<i>Grambastichara</i> sp.		
	<i>Microchara</i> sp.		
	Molluscs:		
	<i>Physa prinsepii</i>		
	<i>Lymnaea subbulata</i>		
	<i>Paludina normalis</i>		
	<i>Paludina</i> sp.		
	<i>Unio deccanensis</i>		

Intertrappean beds demands no explanation as the ancestral stock of this group was supposed to have boarded the Indian plate well before the separation of India from Africa¹³¹.

On the other hand, the Infra and Intertrappean taxa of Laurasian affinity, such as pelobatid and

discoglossid frogs, anguid lizards, alligatorid crocodyles, palaeoryctid mammals, ostracodes and charophytes, are relatively very small in size. The individuals of all the vertebrate groups barring the alligatorid crocodyles could not have exceeded the size of a domestic rat. The crocodyles also appear to

be small in size as a vast majority of the teeth by which they have been identified is less than 5 mm in height. The ostracode carapaces are less than 2 mm and the chara gyrogonites are less than 1 mm in size. On the whole, very small-sized fauna and flora of terrestrial and lacustrine habitats were involved in the Late Cretaceous biotic interchanges between India and Asia. The question that now arises is what was the most likely reason behind the preferential dispersal of small-sized organisms? The most plausible explanation one could offer is that the kind of dispersal mechanism adopted by small-sized animals is not suitable for the migration of large-sized animals. Possibly there was no continuous land connection between India and Asia in the Late Cretaceous without which the large animals could not have crossed the marine barriers. McKenna²¹¹ maintained that the past distribution of animals and plants is not governed by the time of separation or connection of continental blocks. Other factors may also play an important role in biotic distributions. As pointed out by McKenna²¹¹, within major bodies of marine water which act as strong barriers for land based biota, there may exist a number of lesser barriers, such as aseismic elements, sea-floor spreading elements that act as an isthmian filter or intermittently maintained connection allowing some organisms to filter through (filter corridors). Alternatively, over long distances of water, sweepstakes dispersal may result in unbalanced and stray immigrants of usually small size rafting across the barrier. Therefore mixing of continental biotas of two converging continental blocks would take place initially by sweepstakes mode of dispersal when their coasts are approaching each other, through a filter corridor when the landmasses made contact at some place, and through a continuous stable corridor finally when the contact is fully established.

The charophyte taxa exhibit affinities to those of Europe as well as Mongolia. However, the striking similarity of the ostracode fauna of the Infra- and Intertrapean beds to that of Mongolia and China even at specific level, the recovery of only a couple of these species from Europe, and their total absence from the African Cretaceous deposits do not favour any other dispersal route except the one directly from the north of Greater India. In view of the equivocal evidence for the end Cretaceous suturing of Indian and Asian landmasses, the only

dispersal mechanisms which can provide a convincing explanation for the Central Asian and Chinese species in the Late Cretaceous of India are the filter corridors/sweepstakes. The Trans-Himalayan Arc-Trench system represented by the Kohistan magmatic arc in Pakistan, Ladakh arc in India, and Gangdise arc in Tibet may have played an important role in providing a filter corridor for the Laurasian biota. These magmatic arcs had already established subaerial contact with Asia by the end of Cretaceous. But on the southern margin of these arc-trench systems, shallow marine conditions prevailed during the Late Cretaceous^{200-201, 212}. However, subaerial exposure of Zanskar shelf sediments due to intermittent fall in sea level at a rate greater than the rate of subsidence has been noted at the Cretaceous-Tertiary boundary²¹³. The latest report of sharks and rays from the Upper Cretaceous (Maastrichtian) Tremp Formation at Suterranya and Fontllonga 6, south-central Pyrenees, Spain²¹⁴ favours a close biogeographic link between India and Eurasia in the Late Cretaceous. The fossil fish assemblage from this locality includes the genus *Igdabatis* which was earlier reported from the Maastrichtian of Niger (*Igdabatis sigmodon*⁸¹) and India (*Igdabatis indicus*^{41,215}). The new myliobatid dental material from Spain has been assigned to the Indian species, *Igdabatis indicus* (Prasad and Cappetta⁴¹), because of identical morphology and is supposed to be very distinct from the African species, *I. sigmodon*. Likewise, *Rhombodus* sp., which represents the family Rhombodontidae, in the Spanish material compares well with *Rhombodus* sp. 2 of Prasad and Cappetta⁴¹. Since the living members of rays have adopted to benthic habits in shallow waters and are not known to cross deep oceanic barriers, the presence of two common species in India and Europe has been interpreted as an evidence for Late Cretaceous shelf connection between the two landmasses in the northern region²¹⁶. Hence the new data from Spain when viewed in conjunction with the data from India indicates that the Tethys Sea was probably very shallow and was reduced to a narrow channel in the Late Cretaceous enabling the dispersal of non-marine small-sized biota across intermittent and subaerially exposed landmasses. Soler-Gijón & López-Martínez²¹⁶ favoured a dispersal route between Greater India, extending 1500 km to the north of its present northern margin^{210,217}, and Asia through intermediate

continental fragments, such as Gondwanan Mount Victoria, Sikuleh, Natal Semitau, and Southwest Borneo, now part of Southeast Asia. This proposal is somewhat similar to one of the biogeographic models put forward by Prasad *et al.*¹⁹³ to account for the Laurasian taxa in the Late Cretaceous of India. Prasad *et al.*¹⁹³ speculated that Sundaland (South Yunan, Indochina, Thailand and Shan Plateau), located north of Greater India before its displacement towards ESE over 1000 -1500 km in the Tertiary²¹⁸⁻²¹⁹ in combination with the Trans-Himalayan Arc system may have formed an important dispersal route from north to south. However, the amount of extrusion involved is disputed²²⁰. More recently, Huchon *et al.*²²¹ opined that Indochina was never located north of the Indian subcontinent, rather it was situated northeast of the eastern syntaxis and thus the eastward extrusion should not exceed 600 km.

The Dras arc complex of the Indus Suture Zone (Ladakh Himalaya), comprising three structural units—Suru Unit, Naktul Unit and Nindam Formation - from west to east, has been interpreted as an oceanic volcanic arc that formed a larger arc assemblage along with Kohistan arc²²². Based on 79 Ma age deformation in Dras unit 1 in the Suru valley, the known accretion age of 80 Ma for the Kohistan arc with the southern margin of Asia, and lack of evidence for deformation in the eastern most Dras unit (Nindam Formation), these authors suggested that the Kohistan-Dras arc complex converged obliquely on the southern margin of Asia/Trans-Himalayan arc resulting in diachronous collision. Thus in the eastern part, the Nindam Formation, representing the distal fore arc apron was left as an offshore high and was only deformed after collision with the Indian plate in the early Tertiary²²². Recently, Sinha and Mishra²²³

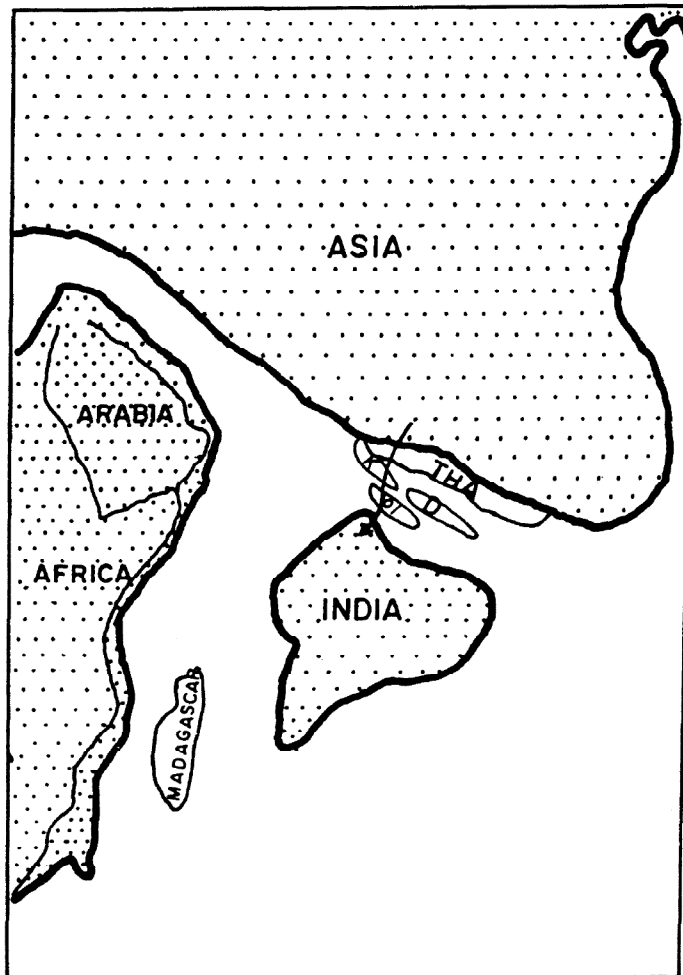


Fig. 2 Possible dispersal route between Greater India and Asia at the end of Cretaceous period (modified after Jaeger *et al.*¹⁹¹)

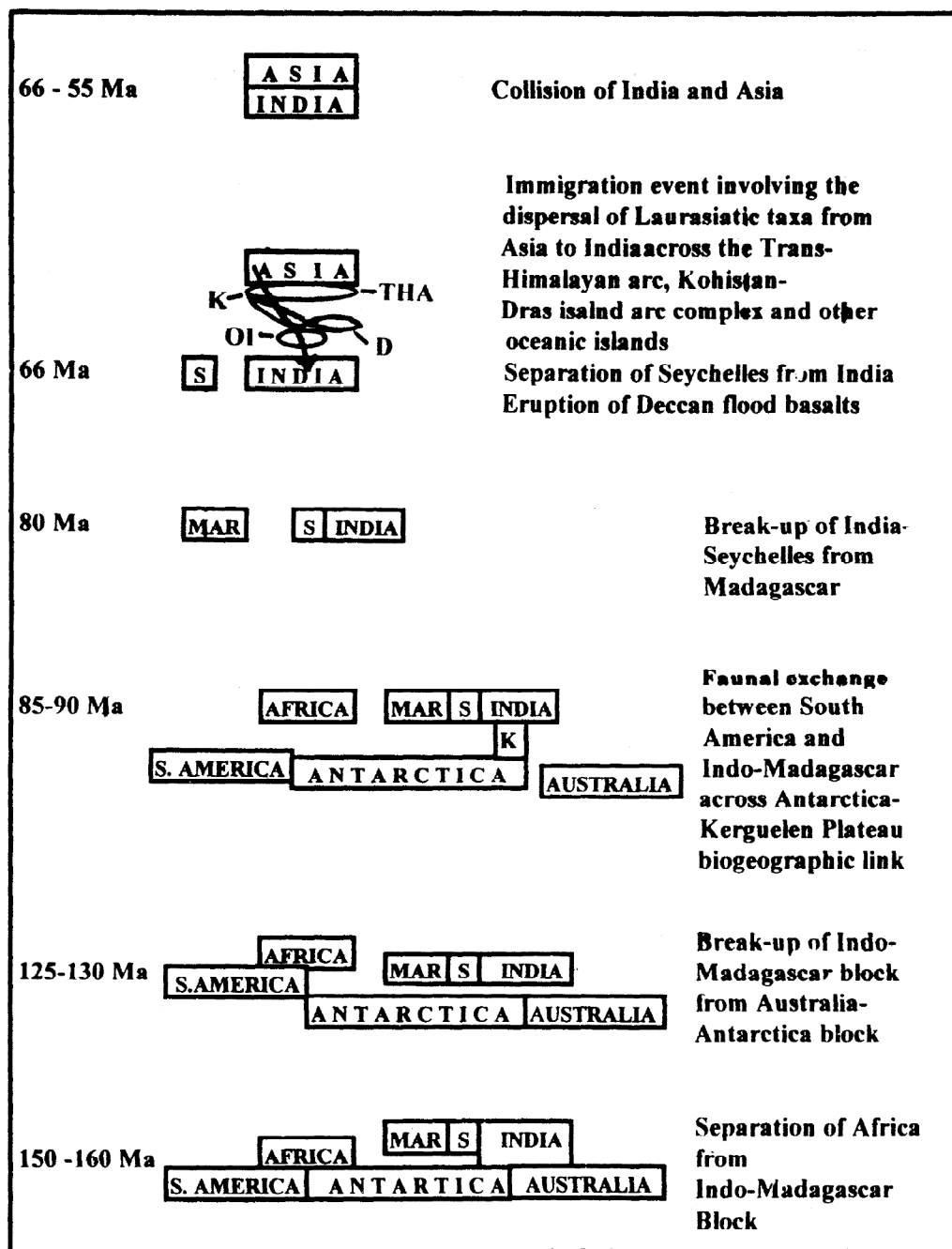


Fig. 3 A simplified graphical presentation of various plate tectonic and faunal exchange events during the northward flight of India. MAR = Madagascar, S = Seychelles, THA = Trans-Himalayan Arc, K=Kohistan island arc, D = Dras island arc, OI = Oceanic volcanic island (Dates based on Storey *et al.* 1995, Beck *et al.* 205, Krause *et al.* 47).

considered the tectonic blocks of volcanics and gabbro imbricated with turbidites along the melange zone between Shergol and Bodhkhharbu, western part of Ladakh, in the light of petrographic and geochemical parameters as relicts of oceanic islands which had erupted in the Neotethys at about

75 Ma. According to these authors, when such volcanic islands reached the trench along the southern margin of Trans-Himalayan arc, initially there was temporary choking of the subduction zone, but continued convergence resulted in dismemberment of the oceanic island and

imbrication of island fragments with trench fill turbidites. The additional data from the Indus Suture Zone have tempted us to speculate that the Kohistan-Dras arc complex, which was welded in the western part to the southern margin of Asia/Trans-Himalayan arc, together with certain oceanic volcanic islands to its south in the shallow Tethys as suggested by Sinha and Misra²²³ facilitated the dispersal of Laurasiatic elements into the Indian plate by filter corridor/sweepstakes mode of dispersal (Fig. 2). Palynological data from the tuffaceous shales associated with Dras volcanics near Shergol also indicate proximity of this belt to the Indian subcontinent. Based on a palynological assemblage dominated by palm pollen, particularly *Nipa*, and rare *Ephedra*, Mathur and Jain²²⁴ suggested a coastal-plain, brackish water environment and a common floral province extending from Tamil Nadu (southern India) through Kutch, Rajasthan (western India) as far north as Dras volcanics in the Palaeocene.

In conclusion, the palaeontological data from the Upper Cretaceous sequences of peninsular India demonstrated that the Indian subcontinent during its northward journey towards Asia maintained biogeographic links both with the Gondwanan and Laurasian landmasses. After its separation from Africa around 150-160 Ma ago and subsequent divergence from Australia and Antarctica at about 125-130 Ma, a dispersal corridor was established

between India/ Madagascar and South America via Antarctica and Kerguelen Plateau. This biogeographic connection, which was responsible for the faunal exchange between South America and Indo-Madagascar, such as the immigration of titanosaurid & abelisaurid dinosaurs, and Sudamericidae mammals, was achieved by 85-90 Ma and possibly maintained at least up to 80 Ma. At the Cretaceous/Tertiary boundary, the Indian plate, which had already undergone a fast rate of drift, moved farther northwards approaching the southern margin of Asia, but still a substantial body of shallow Tethys separated it from Asia. At this stage, many Mongolian, Chinese, North American and European biota of relatively small size reached India through filter corridor/sweepstakes mode of dispersal, making use of the Trans-Himalayan Arc-Kohistan-Dras island arc complex and some other oceanic islands south of these which have possibly been consumed at the subduction zone south of Asia. This biotic exchange preceded the final collision of India after 66 Ma and before 55 Ma (Fig. 3).

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