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ASPECTS OF VERTEBRATE FOSSILS FROM PRANHITA-GODAVARI VALLEY WITH EMPHASIS ON DINOSAUR DISCOVERIES

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INTRODUCTION

I consider it a unique privilege and honour to deliver this lecture in honour of the late Professor M.R. Sahni, founder of Palaeontological Society of India, for whom I have had a deep esteem and regard.

Pranhita-Godavari (P.G.) valley has been the focus of detailed investigation by teams of Geological Studies Unit, Indian Statistical Institute (GSU-ISI), Calcutta for over last three decades. This sustained research work has contributed to better understanding of Gondwana Formations in the northern part of the valley. The work has also led to the discovery of new vertebrate faunal elements, including the Lower Jurassic dinosaur. Other vertebrates, no less interesting, have also been found. Most of the work has been published, including several syntheses (Jain, 1980a; Jain & Roychowdhury, 1987; Kutty *et al.* 1987; Bandopadhay, 1988; Jain, 1990). Research work by GSU-ISI is proceeding at a brisk pace and descriptions of a number of new faunal elements are in press. It is not intended to present another synthesis here but to piece together the knowledge gained from faunal elements about assemblage as whole and its impact on environment and ecology.

Geological work in the P.G. valley has been going on for nearly 150 years but the first detailed account, including stratigraphic description supported by geological map, was given by King (1881). The northern part of the P.G. valley has the most complete succession of Gondwana rocks. It has, therefore, been a happy hunting ground for geologists and palaeontologists. In addition to GSU-ISI, the Geological Survey of India (GSI) and Oil and Natural Gas Corporation Ltd. (ONGC) have also carried out independent work in this area. This has resulted in a revised stratigraphic column and geological map of this area. There are, at present, three different versions of geology of this area. A detailed discussion on this aspect has recently been given by Kutty, Jain and Roychowdhury, 1987.

The sequence of faunas in P.G. valley is almost uninterrupted and is the best known in any Gondwana basin in India. There are five faunas known from the northern part of P.G. valley: (1) Infra-Kamthi fauna, (2) Yerrapalli fauna, (3) Maleri fauna, (4) Dharmaram fauna and (5) Kota fauna. The GSU-ISI is the repository of newly discovered fossils by its teams.

INFRA-KAMTHI FAUNA

Kutty *et al.* (1987) have made a detailed analysis of Kamthis in the northern part of P.G. valley on the basis of lithological characteristics. The authors have recognized four lithozones in the Infra-Kamthi and Lower, Middle and Upper members in Kamthi. Only the lithozones 3 in the Infra- Kamthi and lower Kamthi have yielded vertebrate fossils which are inadequately known so far. Kutty (1972) described very briefly a new vertebrate fauna from lithozone 3 in Infra-Kamthi consisting of an endothiodont-dicynodont complex with an odd captorhinomorph in it. Also, it has two forms which are close to *Endothiodon* and *Cistecephalus*, both typical of the *Cistecephalus* zone of the Karroo sequence of South Africa. The fauna is readily correlated to that zone and can be dated as early Late Permian. The Lower Kamthi (*sensu* Sengupta, 1970) has yielded two reptilian fossil specimens from the basal siltstones by some local villagers from a quarry. The villagers, believing them to be representations of a deity, have started worshipping them and have constructed temples around them. However, diplomatic efforts by GSI have rescued one specimen which is available for study and examination. The specimen, apparently a counterpart, shows a near complete reptilian skeleton with only the anterior end and part of tail missing. The specimen is a little over 40 cm long. Only the occiput of the skull is visible which is low and wide. It is likely to be a dicynodont but does not seem to be either *Lystrosaurus* or any of the later Triassic forms. It may possibly belong to the fauna known from Infra-Kamthi zone 3, mentioned above. Kutty *et al.* (1987) have suggested that it may belong to a later Permian fauna, equivalent to *Daptocephalus* zone of the Karroo.

YERRAPALLI FAUNA

The Yerrapalli fauna has been discussed during last decade a number of times (Jain and Roychowdhury, 1987, Kutty *et al* 1987 and Bandopadhay, 1988). I am happy to tell that very active research work is currently

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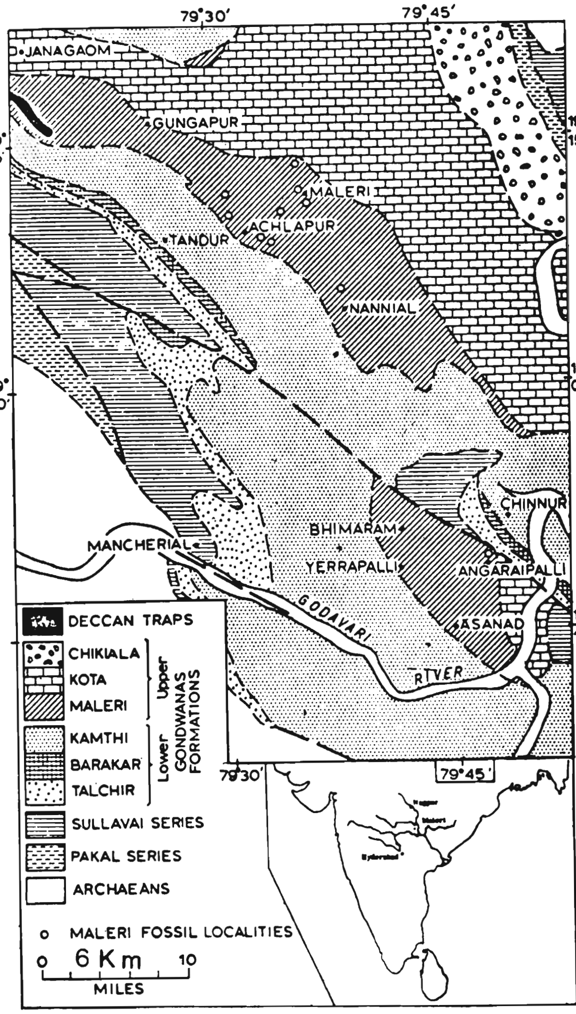

Fig. 1. Geological map of the northern part of the Pranhita - Godavari valley showing fossil localities in Maleri Formation and location of Yerrapalli Village. *Inset*: outline map of India showing river Godavari and its tributaries (From Jain, Robinson and Roychowdhury, 1964).

going on in ISI on this fauna and some of it is being reported here; some fossil sites are shown in fig.1.

The fauna was recognised (Jain *et al.*, 1964) initially on the basis of several new members of vertebrate fauna as distinct from Maleri, mostly fragmentary. Subsequently, as a result of concerted efforts, the new faunal members have been described in detail (Table 1). The fauna is now known to consist of a saurichthyid fish (Jain, 1984), the dipnoan *Ceratodus* (Chatterjee, 1967), temnospondyl *Parotosuchus* (Roychowdhury, 1970a), two dicynodonts - *Wadiasaurus* and *Rechnisaurus* (Roychowdhury, 1970b), rhynchosaur (*Mesodapedon kuttyi*) described by Chatterjee (1980a), cynodont (Chatterjee *et al.* 1969), at least two archosaurs (one protorosuchian and one ruisuchid) and a protosaurian (Jain & Roychowdhury, 1987).

Table 1 : Fossil Vertebrates from the Yerrapalli Formation.

Faunal List	Geological Range
Fishes	
Chondrostei	
Saurichthys sp.	Triassic
Dipnoi	
Ceratodus sp.	Mesozoic
Amphibians	
Capitosaurs	
Paratosuchus rajareddyi	Early or Middle Triassic
Reptiles	
Dicynodonts	
Wadiasaurus indicus	Middle Triassic
Rechnisaurus cristarhynchus	Middle Triassic
Cynodonts	
Trirachodontid teeth	Early or Middle Triassic
Rhynchosaurs	
Mesodapedon kuttyi	Middle Triassic
Proterosuchians	
Undescribed genus and species	Early or Middle Triassic
Pseudosuchians	
Undescribed genus and species	Triassic
Protorosaurs	
Undescribed genus and species	Triassic

Among the Yerrapalli dicynodonts, *Rechnisaurus* is comparable with the stahleckriid *Dinodontosaurus* from South America of Middle Triassic age (Colbert, 1984) and *Wadiasaurus* with *Sangusaurus* from Ntavere Formation of Zambia, again of Middle Triassic age (Roychowdhury, 1970b). The rhynchosaurid *M. kuttyi* is undoubtedly very close to the form known from the Middle Triassic beds of Tanzania. Kasturi Sen (pers. comm.) is currently describing a prolacertid from Yerrapalli Formation which is somewhat similar to *Prolacerta* from Early Triassic of South Africa (*Lystrosaurus* zone). The animal, probably an insectivore was about 2-2.5 m long, endowded with a very long neck and having a sprawling to semi-sprawling posture. It was a terrestrial lowland form. Two individuals have been found is separate associations apart from a number of isolated skeletal elements. A new rauisuchid also from the same horizon is awaiting publication. This is similar to *Ticinosuchus* from Middle Triassic (Anisian) Grenzbitumen zone of Switzerland. The new form is about 2 metre long, again with a long neck. It is suggested that this reptile could attain a bipedal gait while in locomotion. It was a terrestrial higland form. Two rauisuchid individuals have been found in association with two prolecertid inidividuals in assemblage. How and why some Triassic reptiles occur as couples in the Indian Gondwanas remians a puzzle. Later on I will mention about phytosaur couple in Maleri.

MALERI FAUNA

Maleri fauna has been known for over a century (Lydekker, 1885) but almost all the fossils discovered in the 19th century and part of this century have been fragmentary. This resulted in the general impression that the Maleri sediments, particularly clays, are too friable to yield any associated material. Exploration and excavation techniques followed by GSU-ISI under the leadership of late Pamela Robinson, have resulted in the discovery of associated and articulated skeletons. These include skull and post-cranial material of rhynchosaur (*Paradapedon*) and two nearly complete and articulated phytosaur (*Parasuchus*) skeletons during mid-sixties. During last 4-5 years, the Southern Region of GSI has also reported finding of articulated rhynchosaur skeletons.

Following Huene (1940) and Colbert (1958), Kutty and Roychowdhury (1970) and Chatterjee and Roychowdhury (1974) have given succint account of Triassic vertebrates in India and their correlation with similar fauna elsewhere. During last two decades there have been conspicuous additions to our knowledge of Maleri fauna (Chatterjee, 1974,'78,'80,'87; Jain, 1980,1983; Kutty and Sengupta, 1989 and Sengupta 1995). Jain (1990) had given an account of Maleri fauna till the end of 1980's which now needs further updating, the most important addition being the increase in the knowledge of Maleri amphibians (Table 2)

The Maleri sediments are considered to have been deposited in a system of river valleys, with ridge sandstones implying river channel deposits and clays representing inter-channel flood plain. Fossils occur in clays, lime-pellet rocks and mound sandstones, though more commonly in clays. They show no evidence of appreciable transport before burial. The most important fossil localities are near the villages Maleri, Achalapur and Nannial (fig.1). Detailed geological map of Maleri Formation in relation to other Gondwana formations in the P.G. valley have been provided by Kutty *et al.* (1987) and Kutty and Sengupta (1989).

The fish fauna in the Maleri includes *Ceratodus* in abundance, an unnamed subholostean and a xenacanthid, *X. indicus*. Metoposaurid amphibian (*Metoposaurus maleriensis*), a rhynchosaur (*Paradapedon*), a phytosaur (*Parasuchus*), an eosuchian (*Malerisaurus*) and a cynodont (*Exaeretodon*) are other important members. Most noteworthy is the discovery of saurischain dinosaur (*Walkeria maleriensis*) from Adilabad district in red mudstones facies (Chatterjee, 1987). This has been considered as the earliest and most primitive dinosaur known from Asia. Recently, small and large brachyopid amphibian (chigutisaurids) and Rutiodon-like primitive phytosaurs have been discovered in Upper Maleri. It is believed that metoposaurids common in Lower Maleri have been replaced by chigutisaurid amphibians in the upper Maleri. These are also the latest known chigutisaurids anywhere (Kutty and Sengupta, 1989; Sengupta (1995).

Table 2: Fossil Vertebrates from the Maleri Formation.

Faunal List	Geological Range
Fishes	
Dipnoi	
Ceratodus virapa	Mesozoic
C. hunterianus	"
C. hislopianus	"
C. nageswari	"
Subholostean	
Unnamed genus and species	
Xenacanth	
Xenacanthus indicus	Late Triassic
Amphibians	
Metoposaurs	
Metoposaurus maleriensis	Late Triassic
Chigutisaurs	
Compsocerops cosgriffi	Late Triassic
Kuttycephalus triangularis	Late Triassic
Reptiles	
Cynodont	
Exaeretodon statisticae	Late Triassic
Rhynchosaur	
Paradapedon huxleyi	Late Triassic
Eosuchian	
Malerisaurus robinsonae	Late Triassic
Phytosaur	
Parasuchus hislopi	Late Triassic
Pseudosuchian	
Scutes similar to *Typothorax*	Late Triassic
Coelurosaur	
Walkeria maleriensis	Late Triassic
Prosauropod	
cf. *Massospondylus* sp.	Late Triassic

Remains of *Ceratodus* dental plates from Maleri Formation have been on record since nineteenth century (Oldham 1859, Miall 1878). These are fairly common even now. Although *Ceratodus* remains are fairly common over most parts of the world, these are largely represented by palatal and mandibular dental plates since the endoskeleton is largely cartilaginous. Maleri *Ceratodus* is no exception to this. However, collections in recent years have improved the understanding of Maleri dipnoans in several ways: (1) Larger collection has enabled re-evaluation of nineteenth century species, (2) Upper jaw material (associated palatal tooth with palatopterygoid) and lower jaw material (associated mandibular tooth and dentary) has added new osteological information (Jain,1986) and (3) finds of vomerine teeth in Maleri Formation (Jain, 1968), second anywhere in the world, have provided valuable information for comparison with *Neoceratodus*. At present, it would the best to consider three valid species from Maleri Formation: *C. hilopianus*, *C. hunterianus* and *C. nageswari*. Based on relative sizes of mandibular, palatal and vomerine teeth in *Neoceratodus forsteri* and Maleri *Ceratodus*, it appears that the latter had a mixed population of small, medium and large individuals; the largest may be 1-2 metre long (Jain, 1983,'90).

Presence of xenacanthid (= pleuracanth) fish from Maleri Formation was mentioned by Jain *et al* (1964) and the material described in detail later (Jain 1980). It is estimated that Maleri xenacanth, *Xenacanthus indicus* was about 1.2 metre long, predaceous and a swift swimmer. A small subholostean fish has been recorded (Jain, *et al.*, 1964) and commented upon (Jain 1980,1983). It is estimated that the fish was 6-8 cms long (Jain, 1990).

Labyrinthodont amphibians (metoposaurs) from Maleri Formation have been known for over a century (Lydekker, 1882,1885). Huene (1940) described some more material. All such material has been fragmentary. Roychowdhury (1965) gave a detailed account including a composite restoration of the skull of *Metoposaurus maleriensis* (fig.2). Most of the fossils were collected from a locality near Achalapur (fig. 1). These include various parts of skull, clavicle, interclavile, atlas, and other vertebrae, ischium and humerus. The described fossils suggest an amphibian of considerable size, though a skeletal restoration has not been made yet.

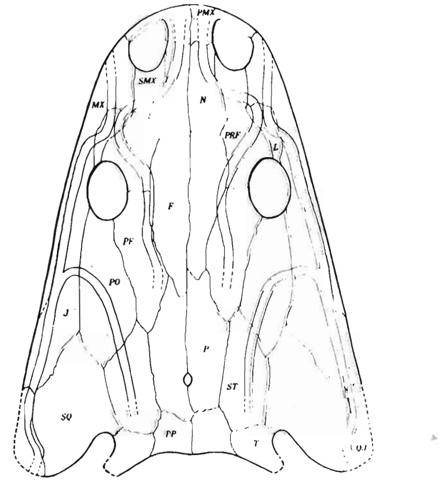

Fig. 2. A composite restoration of amphibian *Metoposaurus maleriensis* skull (dorsal view), from Maleri Formation (From Roychowdhury, 1965).

Chigutisaurid amphibians (Brachyopids) have been the most important addition to the Maleri fauna. Kutty and Sengupta (1989) mentioned the presence of a large and a small chigutisaurids. The material has been described in detail recently (Sengupta, 1995). In the past the only known chigutisaurids have been from Australia and South America. The recognition of two faunal zones in the Maleri Formation (Kutty and Sengupta, 1989) has been largely on the basis of occurence of metoposaur and chigutisaurid amphibians. Metoposaurids dominant in Lower Maleri are apparently replaced by chigutisaurids in Upper Maleri, accompanied by disappearance of some other reptilian forms. Possessing enormous skulls, one form *Compsocerops cosgriffi* (skull 30x40 cms) known by at least 3 well preserved skulls was about 2 metre long (fig.3A) Indication of carnivorous feeding habits is indicated by strong dentition. These animals had streamlined body with agile movements, mostly feeding on small fish and probably other small invertebrates. The other form (*Kuttycephalus triangularis*) is known by only one skull and other fragments. The skull (fig. 3B) appears

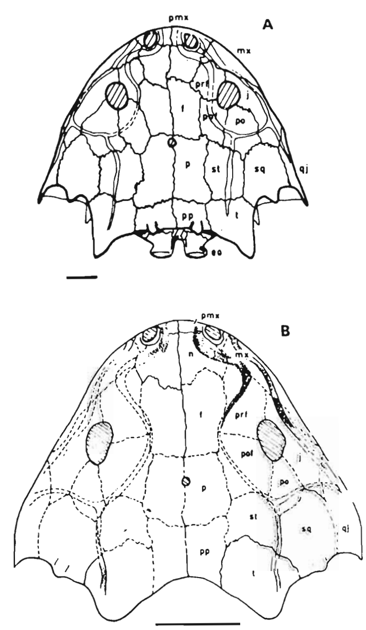

Fig.3. The chigutisaurid amphibians from Maleri Formation; A. *Compsocerops cosgriffi*, skull, dorsal view and B. *Kuttycephalus triangularis* restoration of the skull, dorsal view (From Sengupta, 1995).

to be shorter and narrower (14x22 cms) than other chigutisaurids, bearing resemblance to rhytidosteid skull. Its dentition was feeble and was smaller than the former.

Maleri reptiles are rich in diversity and include several sauropsids, one saurischian dinosaur and one therapsid. Chatterjee (1974, '78, '80, '82, '87) in a series of excellent monographs has given modern osteological account of some members. Early papers have been reviewed and commented repeatedly (Jain *et al.*, 1964; Kutty, 1969; Kutty and Roychowdhury, 1970; Jain and Roychowdhury, 1987, and Jain 1990). The better known members are a rhynchosaur (*Paradapedon huxleyi*), a phytosaur (*Parasuchus hislopi*), an eosuchian (*Malerisaurus robinsonae*), a saurischian dinosaur (*Walkeria maleriensis*), and a traversodont cynodont (*Exaeretodon statisticae*). Poorly known elements include an aetosaur (scutes resembling *Typothorax*), a thecodontosaur and a coelurosaurid dinosaur.

Paradapedon huxleyi (fig. 4, top) is represented by associated material from a locality near Nannial (fig. 1) and cranial material from several localities between Maleri and Achlapur (Chatterjee, 1974). The restored reptile, about 1.4 metre long, reveals a curvature of the backbone, a slight upcurving of the neck and presence of gastralia in addition to the usual features of vertebrae of rhynchosaurs. The orbits are directed upwards and forwards. Osteological features suggest that the animal was not adapted to an aquatic mode of life. The diet of rhynchosaurs has been speculated for over a century because of unique pattern of dentition. It is believed currently that *P. huxleyi* used tongs of premaxillae and dentaries to gather the bivalve shells (mussels) abundant in Maleri. The hinder part of the jaws was used to crack the shells and the numerous small projecting maxillary teeth to hold the shells in the mouth. The reptile also enjoyed vegetable food such as rhizomes and seeds, if available. The heavy built, blunt claws and premaxillae do not suggest a predatory hunter, though it may have been a carrion-feeder at times. Geology Museum at Indian Statitical Institute, Calcutta has on display, since mid 1960's, an articulated skeleton of *P. huxleyi* (Majumder, 1974). Discovery of an associated articulated skeleton of *P. huxleyi* from Maleri has also been announced by GSI Hyderabad in early 1990's.

Parasuchus hislopi (fig. 4, *middle*) now known by two complete skeletons (Chatterjee 1967, '78), collected during 1965-66, from a fossil locality in the vicinity of Mutapuram village, close to Nannial (fig1). These are the most complete skeletons of parasuchians discovered anywhere in the world. The twin phytosaur skeletons were lifted *in situ* from the field by making a large wooden crate on the site. Transport of crate to the campsite and subsequent shipping to Calcutta created unprecedented logistic problems which were sorted out ingeniously. The restored skeleton of *P. hislopi*, about 2.7 m long, suggests a quadrupedal gait with the body off

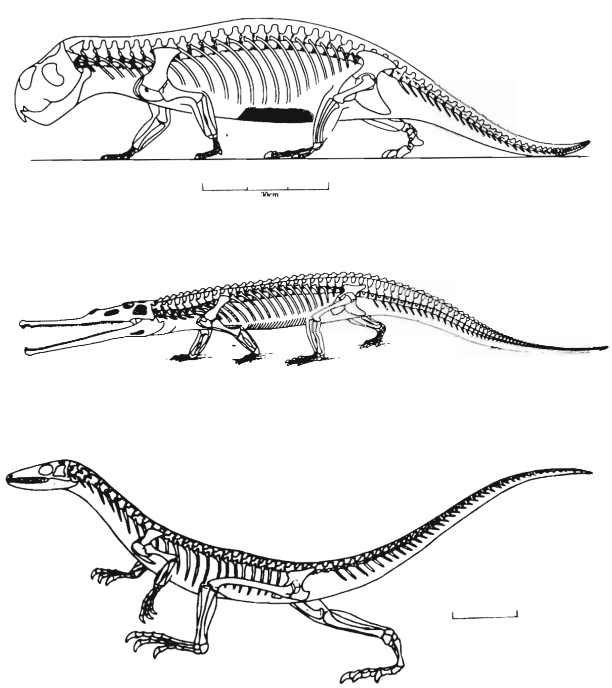

Fig.4. Some reptiles from Maleri Formation; top, *Paradapedon huxleyi* restoration of skeleton (from Chatterjee, 1974); middle, *Parasuchus hislopi*, restoration of skeleton (from Chatterjee, 1978); and bottom, *Malerisaurus robinsonae*, restoration of skeleton (from Chatterjee,1980); scale bar= 15 cm.

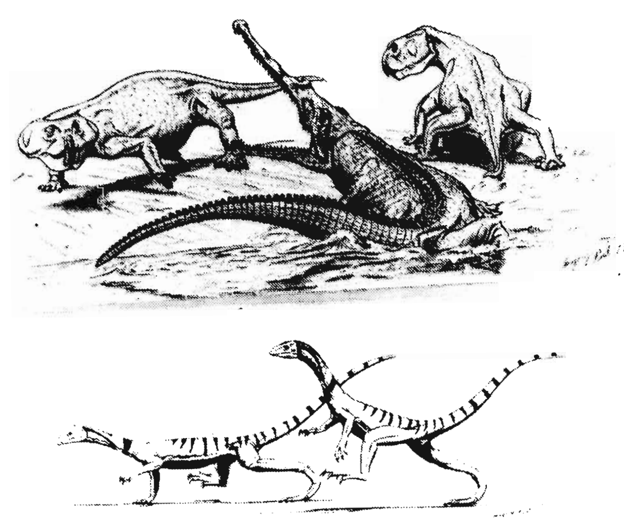

Fig.5. Life-like restorations of some Maleri reptiles; *top*, the rhynchosaur pair (*Paradapedon huxleyi*) in natural semi-aquatic environment with phytosaur, *Parasuchus hislopi* (By Gregory Paul, from Chatterjee, 1980a) and *bottom*, the eosuchian *Malrisaurus robinsonae* in running posture, showing quadrupedal and bipedal gait (By Gregory Paul, from Chatterjee, 1980).

the ground. It was provided with a covering of dermal armour consisting of two rows of elongated paramedian scutes, supplemented by small subcircular lateral scutes. It is surmised that Maleri phytosaur was a formidable carnivore (fig. 5, *top*) since jaws were provided with numerous sharp-pointed conical teeth. It is believed that phytosaurs, like the crocodiles, had a 25^0 of binocular vision which offered good distance judgement to strike the prey precisely. Also, like crocodiles the phytosaurs were able to keep totally submerged in water, keeping the eyes and nostrils just above surface.

The twin phytosaur skeletons provided a unique opportunity to understand, articulate and analyse the detailed osteological and biological features of the reptile. The two skeletons were found so closely associated that they soon become known as the "loving couple." During the removal of the soft, clay-like matrix from their skeletons, it soon became clear that they had also eaten a similar last meal. Within the rib-cage of each were found dismembered skeletons of small rhynchosaurs, and almost articulated skeleton (one each) of another smaller reptile (described next). Chatterjee (1980) suggests an interesting predator-prey relationship : small prey was gulped down whole but if the prey was too large to be swallowed whole it was reduced to pieces. Death of the predator shortly after eating is proved by the articulated nature of the meal as it was not processed for digestion. It is suggested that the prey was probably poisonous.

Malerisaurus robinsonae (fig. 4, *bottom*; fig. 5, *bottom*), an eosuchian, was discovered as the presumable gastric content of twin skeletons of phytosaurs (Chatterjee, 1980), as stated above. *Malerisaurus* belongs to a group of still poorly known and poorly understood Permo -Triassic reptiles that includes the ancestors of the lizards themselves. It was of considerable size, some 1.3 m long, notable for its rather large hind-limbs. Restoration of the animal suggests a small gracile reptile with moderate size skull, elongate neck, short trunk and a long tail. Chatterjee (1980) has portrayed the animal in two alternative postures: the animal may have had a very long stride, capable of cursorial progression; it could probably climb trees or take to water when alarmed. The diet was mainly insectivorous as indicated by unspecialized teeth. It probably lived in densely forested, lowland environment with lakes or flood-plains.

A saurischain dinosaur has been added to the Maleri vertebrate record by Chatterjee (1987). It is a small podokesaurid theropod, similar to *Procompsognathus* of Germany, *Coelophysis* of North America and *Syntarsus* from Zimbabve and North Ameria. The material was found in red mudstone facies near Nannial village, Adilabad dist., A.P. This predacous biped was small and slenderly built, with elongated neck and proportionately long forearms. *Walkeria maleriensis* has been considered as the earliest and most primitive dinosaur so far known from Asia. A restoration of this dinosaur has so far not been published.

A traversodont cynodont, recognised through the presence of characteristic gomphodont post-canine teeth, has been known from Maleri (Chatterjee and Roychowdhury, 1974). However, Chatterjee (1982) has established it taxonomically as *Exaeretodon statisticae* based on fossils found in "red clay facies" near Venkatapur village in the Maleri formation. The material consists of skull fragments representing two individuals. Like other advanced cynodonts, *Exaeretodon* shows mammalian attributes of complex crown patterns and accurate occlusion between cheek teeth. The teeth are differentiated into incisors, canines and "molariform" post-canines. These are most prolific and cosmopolitan groups of mammal-like reptiles during Triassic. They are not ancestral to mammals but have independently developed precise occlusion between cheek teeth closely parallel to later mammals.

A few more forms, including an armoured aetosaur and two more phytosaurs are suspected to the present in Maleri fauna as suggested by fragementary remains (Kutty *et al.*, 1987)

Records of coprolites from Maleri are as old as the dipnoan fish remains. In fact, the fish teeth and coprolites have been known to occur together at a site near Maleri (fig. 1). King (1881) recognised two types of coprolites: (1) short cylindrical spiral and those with (2) rudely discoid coil. Matley (1939) in his detailed account suggested that since *Ceratodus* is known to have a spiral valve the spiral coprolites can be "attributed to *Ceratodus* with much confidence". I had an opportunity to examine a fairly large collection of such coprolites collected by me and my colleagues. In addition, I also succeeded in importing an intestine of *Neoceratodus forsteri* from Australia, since there is a ban on the export of the whole fish. I dissected it to find out the exact nature of the spiral valve. I also obtained data and photographs of the excrement of *N. forsteri* from Australia. The external morphology and thin sections of spiral coprolites were compared with the data from *N. forsteri* and it was concluded that these coprolites are neither "fossilized excrement," "fossilized intestinal content" nor "enterospirae" of *Ceratodus* but may belong to an as yet undetermined member of Maleri fauna (Jain, 1983). The second type, which includes round, oval or ellipsoidal coprolites found from a site near Achalapur (fig. 1), has been examined by Sohn and Chatterjee (1979). It has been suggested that these coprolites are possibly droppings on the ground because a few specimens show surface cracks and their large size suggests that they came from a large animal, e.g., a rhynchosaur.

Invertebrate faunal record from Maleri is very poor. A freshwater mussel (unionid *Tikhia*) has been known (Sahni and Tewari, 1958). Sohn and Chatterjee (1979) have isolated a faunule of ostracods from rounded coprolites. The ostracods belong to the families of Darwinulacea; the material has been discussed in open nomenclature due to poor preservation. *Darwinula* is basically a non-swimming fresh-water species found in muddy substrate. The floral record from Maleri is equally poor. Fragments of petrified wood of *Dadoxylon, Araucarioxylon* and *Mesembrioxylon* have been recorded (Pascoe, 1959).

Interpretation of palaeoecological conditions of Maleri fauna have been largely based on sedimentological studies and palaeontological data. Robinson(1964) suggested a subtropical monsoon type of climate with fairly high year-round temperatures and a dry season alternating with a season of rainfall. Sengupta (1970) interpreted cross-bedded and arcuate lenses of calcareous sandstones intercalated with red clays as abandoned older channels of a main stream, which were left behind in the interchannel flood plain as cut-off meanders. The finer clay fractions may have been deposited on the water-logged flood plains besides the river channel during waning period. The absence of dessication cracks, foot prints and signs of evaporites indicate that the climate was probably not arid. Sarkar (1988) made a petrological study of Maleri "lime-pellet -rocks" and suggested that Maleri geomorphic set up was characterised by insufficient relief and possibly a gentle slope with low seasonal rainfall in a semi-arid climate.

The presence of abundant unionids, aquatic fishes and semi-aquatic tetrapods indicates that Maleri was a well-watered country, at least seasonally. The Maleri ceratodonts probably fed on aquatic plants as well as mussels, the shell of the latter was discarded before ingesting the soft parts. The rhynchosaur, *Paradapedon* must be living near water holes since its diet consisted mainly of rhizomes and mussels (fig. 5, *top*). The phytosaur, *Parasuchus* had a mode of life and habits of recent crocodiles (Chatterjee, 1978). They were mainly catching swift-swimming fishes by sidewise sweep of the head. As an arch predator it also fed on medium-sized rhynchosaurs as well as bipedal archosaurs. Due to great disparity of limb size, *Malerisaurus* indicates fast, erratic bipedal locomotion on land. It probably lived most of the time on a river flood plain or marshy land near to streams and lakes. The saurischian dinosaur (*Walkeria*) was active, predaceous theropod with bipedal gait. The cynodonts are also regarded as very active animals capable of fast locomotion on land. The Maleri cynodont (*Exaeretodon*) was an advanced herbivore of large size, having feeding habits similar to modern herbivorous mammals. The overall impression of Maleri environment is of a well watered country, teeming with a variety of aquatic vertebrates and invertebrates and surrounded by well forested landscape. Amphibious, terrestrial and even arboreal vertebrates inhabited the surroundings near water holes.

THE DHARMARAN FAUNA

The vertebrate fauna from the Dharmaram Formation is still inadequately known but is essentially an archosaur fauna (Kutty, 1969). There are at least two saurischians, both prosauropods; one is a large plateosaurid and the other a small thecodontosaurid. In addition, there is an ornithischian and a sphenosuchid in the fauna. None of the typical Maleri faunal members have been found in this formation.

The fauna is late Triassic in age. In discussing the age of Dharmaram fauna, Kutty (1969) noted that the changes between the Dharmaram and Maleri faunas are similar to changes found between the Knollenmergel and Rhatsandstein on the one hand, and the Keuper horizons below on the other in the German-type Triassic sequence. The Dharmaram fauna is provisionally considered to be late Norian to Rhaetian age.

THE KOTA FAUNA

Kota fauna (Table 3) has been investigated in great detail and several published accounts are available (Jain, 1980; Jain and Roychowdhury, 1987; Kutty, Jain and Roychowdhury, 1987). The fauna is dominated by a variety of fish, reptiles and mammals, apart from invertebrates and some plants. The semi-onotid fishes are commonest in occurrence and have been known for over a century. Collections by GSU-ISI of these fishes during sixties have led to re-assessment. Now *Lepidotes deccanensis, Paradapedium egertoni* and *Tetragonolepis oldhami* are recognised, indicating a Liassic age for Kota. *Pholidophorus* is represented by *P. kingii* and *P. indicus*. The coelacanth, *Indocoelacanthus robustus*, from Kota is an important record of this fish from India. Crocodilian scutes have been known since 1852 by Owen but only recently these have been recognised as teleosaurids and regarded as earliest representatives of this family. The flying reptile, a pterosaurid (*Campylognathoides indicus*) from Kota is a valuable record indicating Liassic age. In addition, it gives evidence of such reptiles in Gondwanaland as well because mostly these have been known from Laurasian continent.

Table 3 : Fossil Vertebrates from Kota Formation.

Faunal List	Geological Range
Fishes	
Semionotidae	
Lepidotes deccanensis	Liassic
Paradapedium egertoni	Liassic
Tetragonolepis oldhami	Late Liassic
Pholidophoridae	
Pholidophorus kingii	Liassic
P. indicus	
Coelacanthidae	
Indocoelacanthus robustus	Uncertain
Reptiles	
Dimorphodontidae	
Campylognathoides indicus	Liassic
Sauropod dinosaur	
Barapasaurus tagorei	Early Jurassic
Teleosauridae	
Scutes and other fragments	Uncertain
Mammals	
Symmetrodonts	
Kotatherium haldanei	Uncertain
Trishulotherium kotaensis	Uncertain
Indotherium pranhitai	Uncertain
Nakunodon paikasiensis	Uncertain

A few more comments on above fauna would be in order. *Lepidotes deccanensis* (fig.6) has been recognised after a long and detailed examination based on ISI collections for over a decade. Some of this collection was taken to the British Museum (Natural History), London,

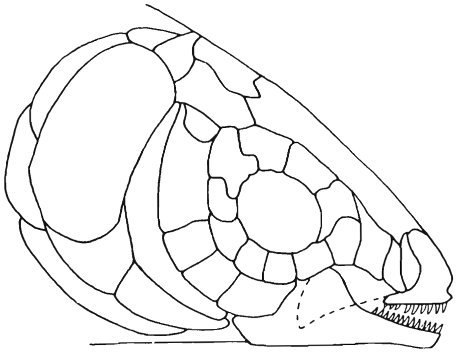

Fig.6. Restoration of the skull of *Lepidotes deccanensis*, the lanceolate semi-onotid fish from the Kota Formation (From Jain, 1983a).

to compare with the type material. It may be mentioned that Egerton (1851, '54, '78) had erected four species, *L. longiceps, L. breviceps, L. pachylepis* and *L. calcaratus*, in addition to already known *L.deccanensis* Sykes,1851. In an analysis (Jain, 1983) it was found that Egerton's species distinctions were not valid. All specimens of the genus so far obtained from Kota are now assigned to *L.deccanensis*. Throughout its long history, species of the genus *Lepidotes* appear to have been able to colonise marine or freshwater environment. Species of the genus occur in brackish to freshwater Rhaetic, in marine Upper Lias, in the marine Oxfordian and Kimeridgian, in brackish to freshwater Purbeckian, in freshwater Wealden, and in both marine (British) and freshwater (Brazilian) Cenomanian. While there is no doubt that the genus, regarded as a whole, was euryhaline, the question whether individual species were euryhaline remains open. It seems reasonable to postulate that species of *Lepidotes* were osmotically adaptable and could withstand at least moderate concentration of the waters of the Kota lake. A sedimentological study of the Kota limestones (Rudra, 1982) shows that Kota limestones are: (1) lake deposits and (2) the deposition was under freshwater evaporite condition. *L. deccanensis* gives evidence of its morpholgical resemblance to *L. elvensis* from European Lias, suggesting a Liassic age for Kota Formation (Jain, 1983).

Among the hypsisomid (deep-bodied) semi-onotids *Dapedium* and *Tetragonolepis* from Kota Formation have been recognised since nineteenth contury (Sykes, 1851; Egerton, 1854, '78). *Dapedium* has been known from Rhaetic to Upper Liassic in Europe. The Kota "*Dapedium*", however appeared quite different in morphological proportions to the European "*Dapedium*". It was found (Jain, 1973) that Kota '*Dapedium*' had a higher value for the depth of the body below lateral line canal, a much smaller length and depth of head as a percentage of body length (15-16%), less heavily osssified skull bones and a fewer number of suborbitals as compared to European *Dapedium*. *Paradapedium* (Jain, 1973) was erected after prolonged discussions with Dr. Bob Schaeffer and Dr. E.I. White on the issue. It seems that *Paradapedium* (fig. 7 *top*) need not be geolgically younger or older than *Dapedium* but may be an ecological substitute for *Dapedium* in Asia. The second hypsisomid fish *Tetragonolepis*, known by 3 species from Kota (*T. oldhami, T. rugosus* and *T. analis*) was also re-examined in the light of new collections (Jain, 1973). A proper definition of *T. oldhami* (fig. 7, *bottom*) has been, possible; the other two species, *T. rugosis* and *T. analis* have been rejected as these are based on fragmentary material. The restricted geological distribution of *Tetragonolepis* and its presence

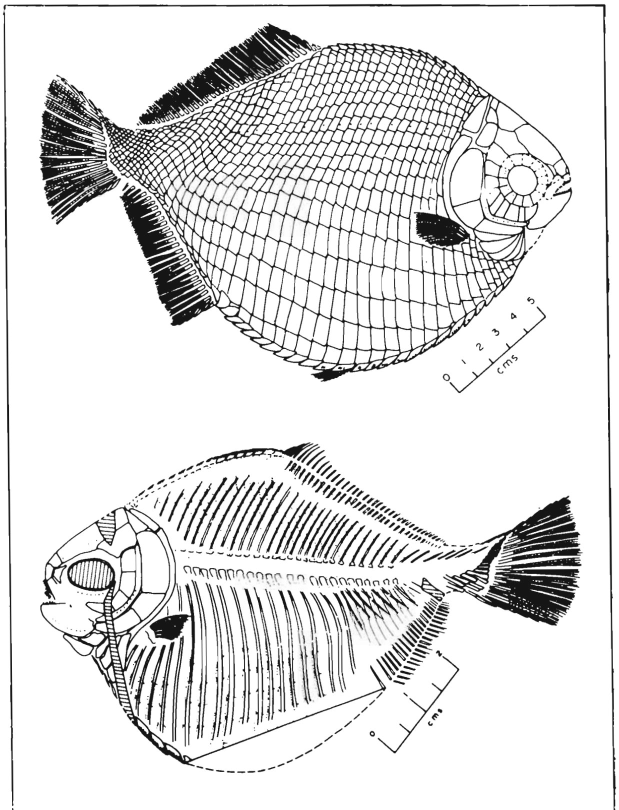

Fig.7. Restoration of the hypsisomid semi-onotid fishes from Kota Formation; top, *Paradapedium egertoni* and bottom *Tetragonoleois oldhami* (From Jain, 1973).

in Kota Formation is a valuable evidence of Upper Liassic age.

In view of the rarity of coelacanth fish remains from Asia, except a single poorly known record of *Sinocoelacanthus* from China, the finding of coelacanth remains in the field season of 1962-63 from Kota Formation was exciting. However, this material was poor. In subsequent years, as a result of concerted prospecting efforts, considerable material was obtained. On the basis of these fossils it has been possible to recognize the new monotypic form *Indocoelacanthus robustus* (Jain, 1974), shown in Fig 8, *top*. It is estimated to be slightly larger than *Holophagus*. In view of the composition of the fauna and suggested Lower Jurassic age of the Kota Formation, it is of interest to note that another coelacanth genus, *Lualabaea* from Zaire (Stanleyville stage= Middle to Upper Jurassic) is a freshwater form similar to *Indocoelacanthus*.

An announcement about the discovery of a "fossil bird" from Kota Formation was made in the popular press (*India Today*, 16-31 May, 1979). The discovery was attributed to P.Yadagiri (G.S.I. Hyderabad) and it was reported that " the find is the first record of a Mesozoic fossil bird in India and is being claimed as the oldest fossil bird". In comprison to *Archaeopteryx*, it was stated that "while the *Archaeopteryx* measures 15 cm from skull to tail, the Kota fossil bird's skull alone is about 16 cms." An apportunity was provided to me to re-examine the specimen sometimes after the publication of above report. I came to the conclusion that there has been a gross error in the interpretation of the specimen (Jain, 1980). The specimen had been placed front-side backwards. In the new position, bones labelled as "frontal", " quadrate" and "wish bone" show familiar features of gular, opercular and cleithrum of a coelacanth fish. The skull is quite comparable to *Indocoelacanthus* from Kota (fig.8, *top*) and matches in morphology of gulars, opercular and cleithrum. Moreover, the size of the alleged "bird" skull is very close to that of *L. robustus*.

Good crocodilian material, including skull, has been obtained from Kota Formation confirming century-old report of presence of crocodilian scutes. These are the earliest representative of teleosaurid crocodiles anywhere. A report on the new material is yet to be published. The presence of a turtle in Kota has also been

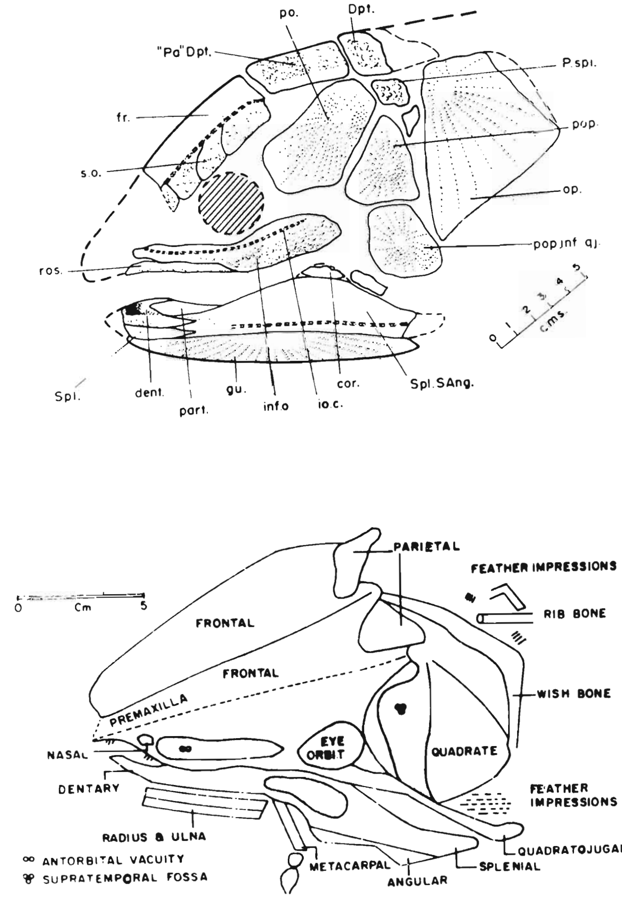

Fig.8. *Top*, Restoration of the skull of coelacanth fish, *Indocoelacanthus robustus*, from Kota Formation (from Jain, 1974) and *Bottom*, the so-called "Kota Bird" from Kota Formation (From *India Today*, with permission of Editor); for comments please see text.

confirmed. My own collection has been rather fragmentary and I had restrained myself from describing it. However, I was glad to see an entire carapace and plastron exhibited in the Indian Museum as exhibit of the month during 1980's. It was also reported in popular press. I understand that the material had been collected by GSI (Calcutta) and will be described in future. It would be the earliest record of a turtle from India. The flying reptile, a pterosaurid (*Campylognathoides indicus*) from Kota Formation was described by me (Jain, 1974 a). Further prospecting in Kota beds during next decade did not yield any further material. However, further laboratory preparation of the block containing part of the jaw has revealed another undescribed fragment with teeth. It appears that the two pieces might fit together and give a better picture of the entire jaw.

The discovery of sauropod dinosaurs from Kota Formation has been a major breakthrough in our understanding of the early evolution of sauropod dinosaurs. For a long time, it had been believed that gigantism in sauropods developed during Upper Jurassic and continued into Cretaceous. The early Jurassic sauropod history had been sketchy due to fragmentary nature of fossils known. As such, the discovery of a graveyard of sauropod dinosaurs in India, of Liassic age, published in *Nature* (Jain *et al.*, 1962) as a leading article aroused much interest. Nearly 10 tonnes of fossil bone material (300 skeletal elements) was lifted from the field and brought to Calcutta for further laboratory work and study. During next 15 years, several more field expeditions were conducted for more material. This fully developed sauropod exhibiting gigantism was named *Barapasaurus tagorei* (Jain *et al.*, 1975). A skeletal mount was put on display in 1977 coinciding with the 4th International Gondwana Symposium held at Calcutta. At present, this is the only display of a mounted dinosaur skeleton in India. A scale model of this dinosaur, along with *Triceraptops* was exhibited as a float during Republic Day Parade in 1995.

B. tagorei from Kota Formation (Plate I) has attracted much attention from palaeontologists, some placing it in a separate family as Barapasauridae (Halstead and Halstead, 1981; Lambert, 1990), others preferring to keep it within Vulcanodontidae (McIntosh, 1990). My colleagues and I have not yet taken a position in this regard (in print), pending the publication of a detailed

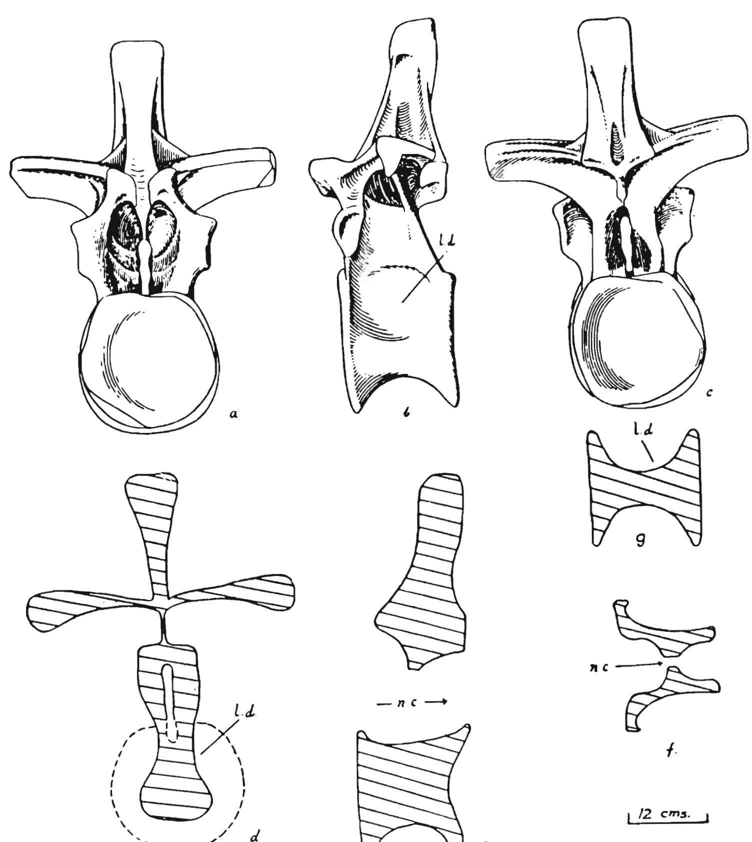

Fig.9. Posterior dorsal vertebra of *Barapasaurus tagorei*, (a) anteriror view, (b) lateral view, (c) posterior view (d) transverse section, (e) sagittal section, (f) horizontal section through neural canal and (g) horizontal section of centrum (From Jain, Kutty, Roychowdhury and Chatterjee, 1979).

monograph. Here I would like to reiterate some interesting biological features of the nerve cord as interpreted from dorsal and sacral vertebrae (Jain *et al.*, 1979). The posterior dorsal vertebrae have been excavated extensively below the base of transverse process and between infra-diapopyseal laminae (fig, 9). The excavation is so deep that in the anterior mid-dorsals and posterior dorsals, there is only a thin bony wall separating the excavations of two sides. The anterior and posterior faces of the neural arches around neural canal are excavated into large concavities. The opening of the neural canal is pushed closer to each other. The neural canal itself is narrow and tall in cross section. The concavities of the anterior and posterior faces of the arch are not equal on the two sides, i.e., there is a distinct assymmetry. The most interesting feature of the nerve cord, probably unique to *B. tagorei*, is evidenced in the post-mid dorsals. Here the anterior and posterior faces of the arch are normal, i.e., unexcavated or only slightly excavated. In between, the neural canal becomes rather narrow, deeply sunk on the centrum ventrally, and opening dorsally into a large cavity through a narrow slit-like opening (fig,10) The edges of the slit-like opening at either ends are not at the same level but sags down in the middle. Some modifications of this dorsal cavity have been mentioned by us (Jain *et al.*, 1979). The modifications suggest that the spinal cord in *B.tagorei* in the sacral region would probably look like a string of beads. The presence of a dorsal cavity, however, defied any reasonable explanation. Whether it housed an enlargement of the spinal cord or whether they are pleurocoels on the neural arch remains debatable. It is clearly not a modification adopted by later sauropods. We have analysed many pecular features of *B. tagorei* and made a suggestion that it made one of the earliest attempts at gigantism as evidenced by its skeleton. But the neural canal region suggests attempts at specialization not followed by later sauropods. As such, it could be considered an offshoot from the main line of sauropod evolution. An account of Indian dinosaur discoveries in the context of world-wide reports up to mid 1980's has been given (Jain, 1989).

Discovery of early Jurassic mammals from Kota Formation during 1981-85 by GSI teams at Hyderabad and Calcutta is a valuable addition to the early mammalian history of Indian peninsula. The material belongs to four new taxa of symmetrodonts and, as expected, is in the form of isolated teeth (Table 3). The precise relationship with other symmetrodonts is at present uncertain. Datta (1981) erected *Kotatherium* and Yadagiri, (1984) erected *Trishulotherium* and *Indotherium*, all assigned to kuehnotherid symmetrodonts. An amphidontid symmetrodont, *Nakunodon*, has also been identified from Kota Formation (Yadagiri, 1985). In addition, I understand that some further new material of mammalian teeth has been found and is in the process of publication. The paucity of early mammals from Gondwanaland and sparse records of early Jurassic mammals from all over the world makes the discoveries of Kota mammals extremely important.

Estherids and ostracods dominate among invertebrates. GSI has also reported occurrence of fossil insects in a richly fossiliferous band of limestone in Kota Formation. Although taxonomic assessment of the

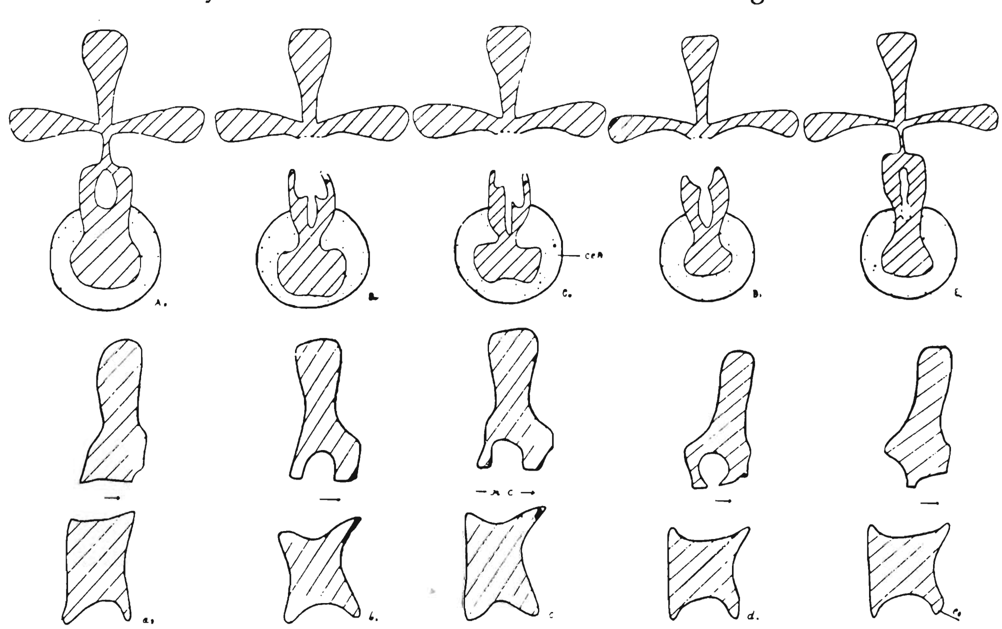

Fig.10. Transverse (A-E) and sagittal (a-e) sections of dorsal vertebrae of *Barapasaurus tagorei* to show the modifications of the neural canal (From Jain, Kutty, Roychowdhury and Chatterjee, 1979).

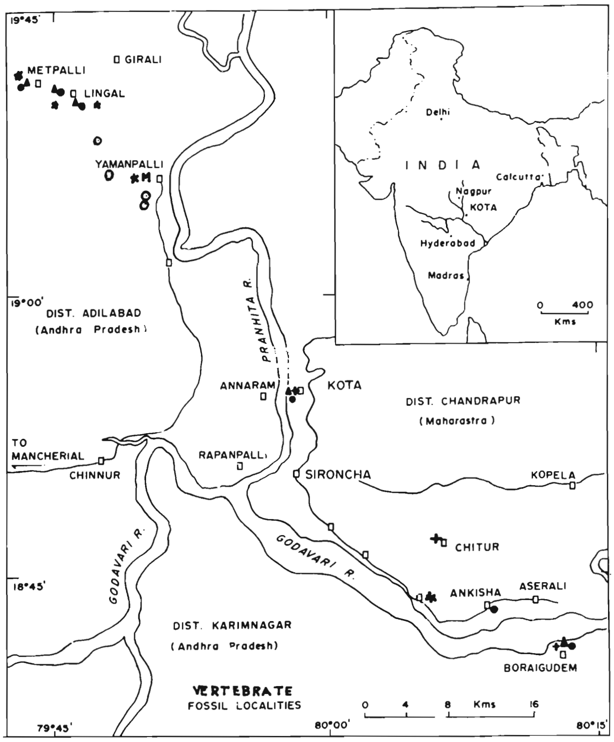

Fig.11. Main vertebrate fossil localities in the Kota Formation; *inset*, map of India showing P.G. valley river system and location of village Kota. The semi-onotid (•), coelacanth (Δ), pholidophorid (o), dinosaur(*), pterosaur (+) and mammalian (m) lolcalities are marked (From Jain, 1980a).

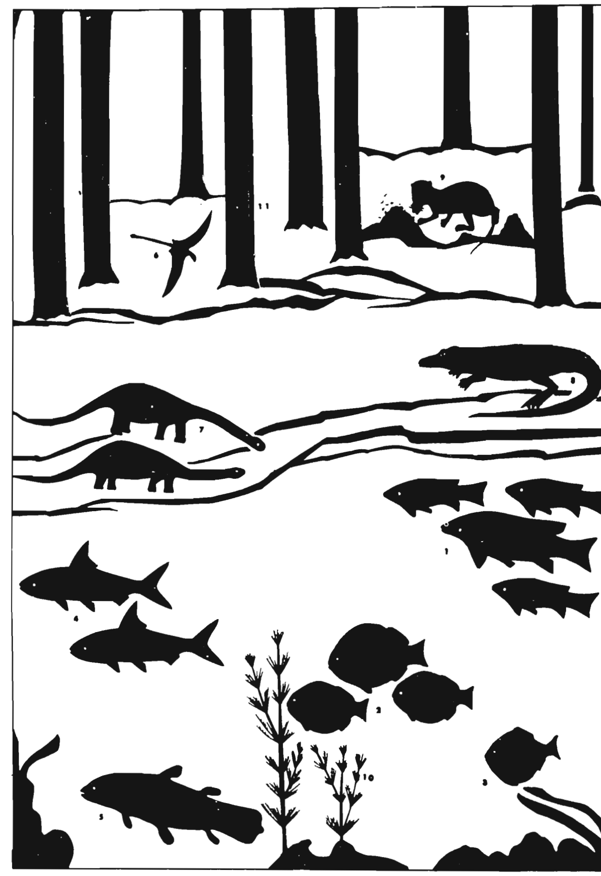

Fig.12. An attempted restoration of the main Kota fossil assemblage in silhoutte to indicate suggested ecological roles (not to scale). 1. *Lepidotes deccanensis*, 2. *Paradapedium egertoni*, 3. *Tetragonolepis oldhami*, 4. *Pholidophorus* kingii and *P. indicus* 5. *Indocoelacanthus robustus*, 6. *Campylognathoides indicus*, 7. *Barapasaurus tagorei*, 8. teleosaurid crocodile,9. Kota mammal, 10. Charophytes and 11. Fossil woods (From Jain, 1980a).

material has not been made, it is indicated that blattids, coleopteran and hemipteran insects are present (see Jain, 1980a). Large logs of wood without any leaves or fructification were found during dinosaur excavation in 1961. In addition, charophytes have been recorded. The rich and varied faunal and floral assemblage of Kota has enabled us to reconstruct and understand the palaeoenvironment and palaeo-ecology during early Jurassic times in P.G. valley. Vertebrate fossil localities in the Kota Formation are shown in fig, 11 and an attempt has been made to depict Kota fauna in silhouette in fig, 12.

Cretaceous dinosaurs : Cretaceous dinosaurs from Central India have been known for over a century. Some 15 taxa belonging to theropods, sauropods and ornithischians were identified by pioneering workers such as Lydekker, von Huene and Matley. However, most of the material had been rather fragmentary. During last two decades, new sites of Cretaceous dinosaurs have been located in western and southern India.

A review of these discoveries could be the subject of a separate lecture in itself. Here I would like to refer to certain important landmarks in this connection. Chatterjee(1978) re-examined a part of Barnum Brown collection from Lameta Formation lodged in American Museum of Natural Hestory, New York and recognised two carnosaurs (1) *Indosaurus matleyi*, a megalosaur and (2) *Indosuchus raptorius* a tyrannosaur. Yadagiri and Ayyasami (1979,'87) described a new stegosaurian from South India and a carnosaur from Kallamedu Formation (Maastrichtian) of Tamil Nadu. Berman and Jain (1982) described the braincase of a small sauropod dinosaur from the Lameta Group at Dongargaon. Attempts to obtain associated and articulated skeletons have also been made. One associated skeleton of a sauropod titanosaurid from this site was obtained during 1984-86 field season. A study of this material has been completed and is awaiting publication (Jain and Bandhopadhay, *in press*).

Long strides have been made in understanding the egg-laying behaviour of Cretaceous dinosaurs in India. Starting from the collection of fragmentary egg shells (Jain and Sahni, 1983,' 85; Vianey-Liaud *et al.*, 1987), the focus has shifted to obtaining entire eggs, nests and nesting sites. Several sites rich in dinosaur eggs have been discovered between Jabalpur and Ahmedabad. Srivastava *et al.* (1986) and Tripathi (1986) have made a detailed study of ultrastructure of dinosaur egg clutches. Reseach work up to late 1980's was reviewed by me (Jain, 1989a) and Sahni (1989). More recently, Sahni *et al.* (1994) have made a very extensive review of all the Upper Cretaceous dinosaur egg sites from peninsular India.

CONCLUDING REMARKS

The study of fossil vertebrates from the P.G. valley has assumed special importance for several reasons. It has a fairly unbroken succession of Gondwana rocks. It is unique among the Indian Gondwanas in having five distinct vertebrate faunas from the northern part of the valley. There are indications that there might be two more faunas (Kutty *et al.*, 1987). There is sufficient overlap of this faunal sequence with those from other Gondawanaland areas on the one hand and Laurasian sequences on the other. This provides for a tie-up of the former with the latter. Detailed documentation of the fauna, coupled with sedimentological studies in many cases, has enabled us to reconstruct palaeobiology of the fauna against the backdrop of palaeoenvironment with some precision. There is a need for more work in southern part of P.G. valley about which little is known. Similarly detailed work in other Gondawana basins in India is urgengly required so that the faunal history of Indian Gondwana is understood in proper perspective.

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EXPLANATION OF PLATE

Plate - I

Barapasaurus tagorei, sauropod dinosaur skeleton from the Kota Formation, Pranhita-Godavari valley, India, on display at the Geology Museum, Indian Statistical Institute, Calcutta.

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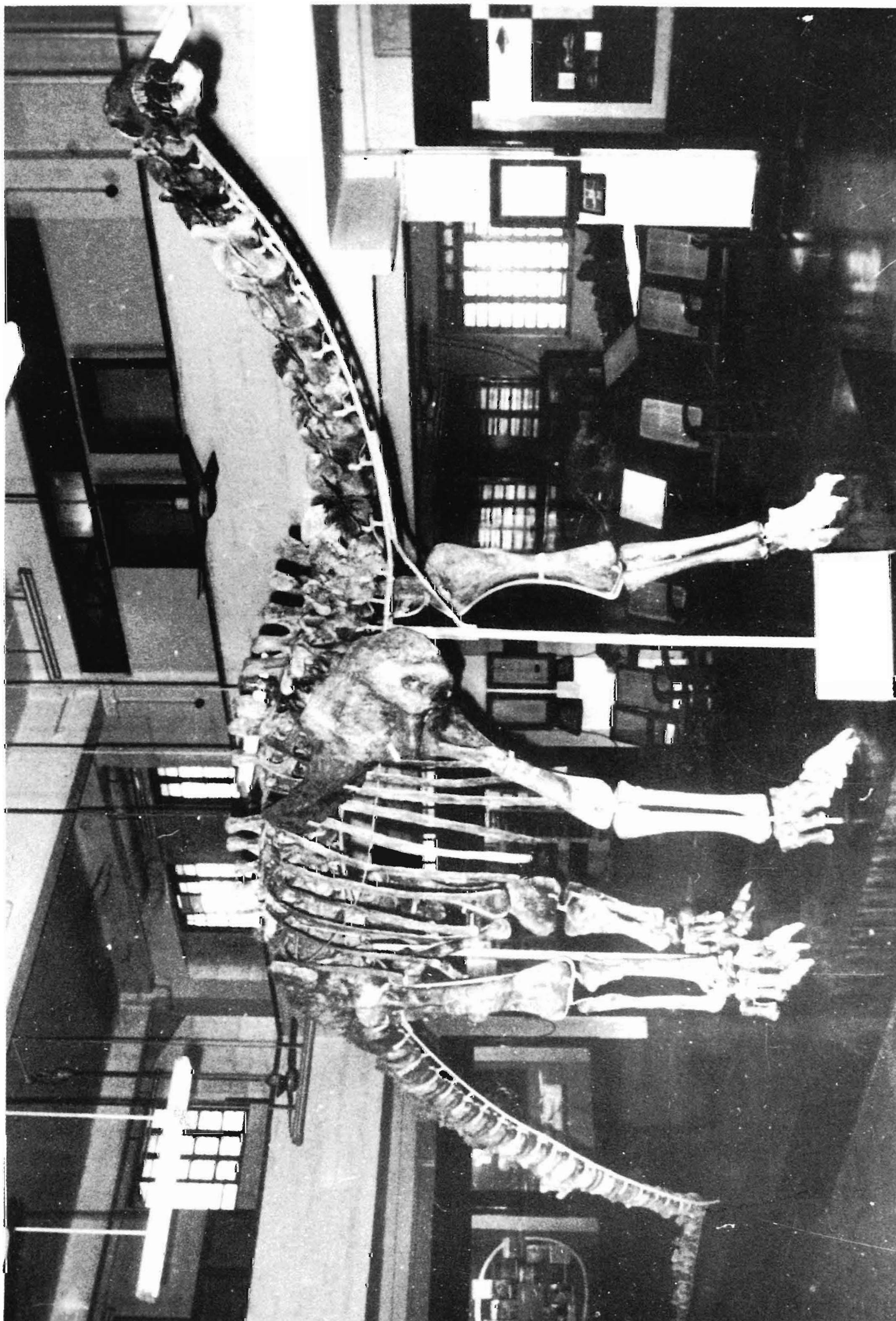
Plate I



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