

Taphonomy of some Gondwana vertebrate assemblages of India

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Abstract

The Gondwana formations of India, comprising a thick succession of Permo-Mesozoic continental sedimentary rocks, occur in rift basins formed within the Indian plate. Successions developed in some of the Gondwana basins namely—Pranhita–Godavari, Damodar, Satpura and Son–Mahanadi, contain an array of vertebrate fossil assemblages. Among the four basins, the Pranhita–Godavari basin contains vertebrate assemblages from Late Permian, Middle and Late Triassic and Early Jurassic sediments. An Early Triassic assemblage is known to occur in the Damodar basin. The Satpura basin has yielded a Middle Triassic assemblage while a Late Triassic assemblage is known from the Son–Mahanadi basin. All these assemblages are confined mainly to the fluvial red bed successions. Taphonomic aspects of some of the assemblages of these Gondwana basins are described here for the first time. On the basis of the nature of occurrences of the skeletal assemblages, six major taphonomic types (termed here as A–F) have been identified from the Gondwana basins of India. Type A includes complete articulated or semi-articulated skeletons. Type B exhibits disarticulated skeletons of a large number of monospecific individuals. Type C is characterized by disassociated bones of monospecific individuals in a “log jam” condition. Type D exemplifies disarticulated bone assemblage of mixed individuals, while isolated remains of single individuals belong to Type E. Type F typifies isolated fragmentary bones. Analyses of these skeletal assemblages provide considerable information of death, transportation and burial of the terrestrial vertebrates. These results, when integrated with the sedimentary features of the host rocks, provide additional palaeoenvironmental and palaeocological information.

Keywords: Taphonomy; Vertebrate; Permian; Triassic; Jurassic; Gondwana; India

1. Introduction

The last three decades have witnessed a spate of research by vertebrate palaeontologists and sedimentologists which has been aimed at a better understanding of death, transportation and burial of terrestrial vertebrates in different sedimentary facies. These

taphonomic studies, in combination with sedimentological data, provide additional insight into palaeoenvironmental, palaeocological, and palaeobiological studies (Efremov, 1940; Behrensmeyer, 1991; Speyer and Brett, 1991; Lopez, 1991). However, taphonomic information on Late Palaeozoic and Mesozoic vertebrate assemblages, with the exemption of Cretaceous dinosaurs, is scanty compared to similar studies on Cenozoic mammals. In India, geologists, naturalists and amateur enthusiasts have collected fossil vertebrates from different Gondwana horizons for a long time, but systematic collection including taphonomic

information started only recently (Robinson, 1958; Jain et al., 1962; Bandyopadhyay, 1988; Sengupta, 1990; Dasgupta, 1993a; Ray, 1997a).

The present authors have explored, excavated and collected fossil vertebrates from some of the horizons of the major Gondwana basins of India. Taphonomic data of the articulated, semi-articulated, scattered and isolated fossils were also carefully collected. Analyses of these data, along with their associated sedimentary features, have been used to interpret taphonomic histories of these assemblages.

2. Geological background of the Gondwana basins

The Gondwana formations of India contain a thick pile [maximum 4000 m (Veevers and Tewari, 1995)] of Permo-Mesozoic sedimentary rocks that are believed to have been deposited in rift basins formed within the Indian plate (Fox, 1931; Quersehi et al., 1968; Ramanamurthy and Parthasarathy, 1988; Veevers and Tewari, 1995; Biswas, 1999). The basins subsided between growing normal faults accommodating glacial, fluvio-glacial, fluvial and lacustrine sediments (Robinson, 1970; Veevers and Tewari, 1995). The initial basins were narrow and shallow in the earliest Permian giving rise to tectonically active grabens (or half grabens) accumulating thick pile of sediments (Krishnan, 1968). This model of thick accumulation of Gondwana sediments in block faulted basins was also corroborated by Dar and Viswanathan (1964) and Ahmad and Ahmad (1979). The NW–SE trending megastructure of the Pranhita–Godavari valley is, however, considered by Sreenivasa Rao (1994) to be a raft rather than a rift. Casshyap and Tewari (1988) suggested that prior to the rifting of the Indian plate, the Gondwana sedimentation in Peninsular India took place in linear intracratonic basins; these basins expanded areally through time as sedimentation progressed through Permian and Triassic.

During the period of accumulation of continental sediments in these faulted basins, marine incursions were suggested by some workers. Fox (1931) proposed a pathway from Salt Range in western India reaching to Umari in central India. While a westward connection through Narmada was proposed by Krishnan (1968), Ahmad (1970) visualized an incursion from south east through Mahanadi valley. These

marine influences were, however, small in amount as continental milieu prevailed mostly during the Late Permian and Triassic periods.

Deposition in these basins started with glacial sediments which were followed by carbonaceous sediments containing coal deposits of Permian age. Extensive red beds with alternation of sandstones and characteristic red mudstones/shales of variable thicknesses were deposited during the Late Permian (in some basins), the Triassic and, in one instance, also in the Jurassic. The Permo-Triassic/Jurassic succession is overlain uncomfortably by another suite of fluvial and lacustrine deposits of Early Cretaceous age. The Permian period of the Gondwana supergroup witnessed a severe glaciation event at the beginning of that period. As the environment was inhospitable to vertebrates, their record in the Early Permian is poor. As the Permian period advanced, the climate ameliorated. Although vegetation started flourishing, record of vertebrate life was still limited at the close of the Permian. However, during the Triassic the climate became warm and dry, which favoured terrestrial animals. This is evident from the diversified vertebrate assemblages recorded from Triassic red beds. No vertebrate remains have been recorded from the Early Cretaceous sediments in these basins although these are quite rich in plant remains. Hence, these are not discussed in this paper.

In India, the best occurrences of the Gondwana sediments are found in the Pranhita–Godavari basin, Damodar basin, Satpura basin and Son–Mahanadi basin (Fig. 1). A virtually continuous succession from Permian to Early Jurassic is available only in the Pranhita–Godavari basin (Fig. 2). Confirmed continental Jurassic sediments are present only in the Pranhita–Godavari basin. The Damodar and Satpura basins have a continuous succession spanning from Permian to the Early Triassic and early Middle Triassic, respectively (Fig. 2). The lower part of the Gondwana succession, containing glacial and fluvio-glacial sediments of the Talchir Formation and carbonaceous, fluvial and lacustrine sediments of the Barakar Formation is common to all the Gondwana basins (Fig. 2). However, such gross lithological similarity does not exist among the stratigraphically higher coeval formations across the basins.

The Pranhita–Godavari basin has produced the most vertebrate taxa. In this basin, vertebrate assemb-

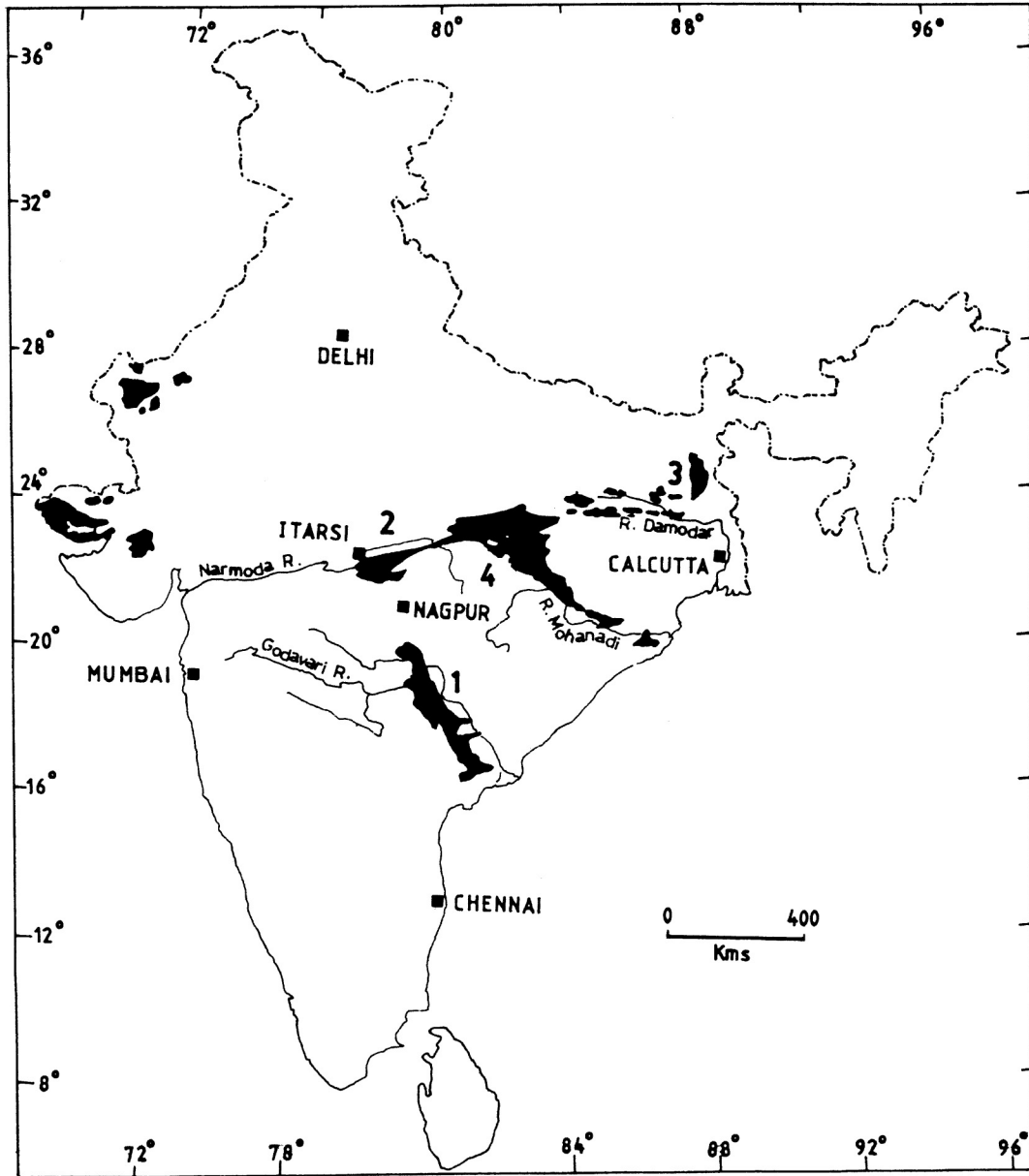


Fig. 1. Major Gondwana outcrops of peninsular India. (1) Pranhita–Godavari basin, (2) Satpura basin, (3) Damodar basin, (4) Son–Mahanadi basin.

lages are known from the Late Permian Kundaram Formation, Middle Triassic Yerrapalli Formation, Late Triassics Maleri and Dharmaram Formations and Early Jurassic Kota Formation. In the Damodar basin

of eastern India the Panchet Formation has produced an Early Triassic assemblage. A Middle Triassic and a Late Triassic vertebrate assemblage are known from the Denwa Formation of the Satpura basin and from

| Localities | | Pranhita-Godavari basin | Satpura basin | Damodar basin | |
|------------|--------|-------------------------|---------------|---------------|-------|
| Age | | | | | |
| JURASSIC | Middle | Yamanpalli | | | |
| | Early | Kota | | | |
| | | Dharmaram | | | |
| TRIASSIC | Late | Maleri | | | |
| | Middle | Bhimaram | | | Denwa |
| | | Yerrapalli | | | |
| | Early | Kamthi | Pachmarhi | Panchet | |
| | | | | | |
| PERMIAN | Late | Kundaram | Bijori | Raniganj | |
| | | | Motur | Barren | |
| | Early | Barakar | Barakar | Barakar | |
| | | Talchir | Talchir | Talchir | |

Fig. 2. Pre-Cretaceous Gondwana successions of the Pranhita–Godavari, Satpura and Damodar basins of India. Major vertebrate-bearing horizons are boldly outlined.

the Tiki Formation of the Son–Mahanadi basin, respectively. Taphonomic information of the Dharmaram faunal assemblage (Pranhita–Godavari basin) and the Tiki faunal assemblage (Son–Mahanadi basin) are not readily available, so we have excluded these from the present discussion. The taphonomic interpretation of the Kundaram faunal assemblage has been dealt with elsewhere (Ray and Bandyopadhyay, communicated).

Following is a short account of the lithology and nature of succession of the Gondwana formations of the three main basins, from which sufficient taphonomic data is available.

2.1. The Pranhita–Godavari basin

The Gondwana succession of the Pranhita–Godavari basin occurs as a narrow rectilinear outcrop trending NNW–SSE and is bordered on both sides by Proterozoic and/or Archaean rocks. The overall dip of the succession is 5 to 12 degrees towards N and

NW. The general paleocurrent direction is toward the north (Sengupta, 1970; Veevers and Tewari, 1995).

In this basin, the succession from the Kundaram to Kota Formation (Fig. 2) is paleontologically the most interesting part. The Permian Kundaram Formation (250 to 450 m) is characterized by red mudstone, sandstone, sandstone–mudstone alternations and ferruginous shale. The sand bodies are laterally persistent, trough cross-stratified, exhibit unimodal paleocurrent directions and were formed by the lateral migration and avulsion of channels (Ray, 1997b). Abundant terrestrial vertebrate fossils have been found from the mudstone unit (Ray, 1999).

The overlying Kamthi Formation is characterised by siltstone, and ferruginous sandstone which is pebbly in places. The lower part of this formation is made up of a medium grained, poorly sorted argillaceous quartzose sandstone and thin sheets of sandy siltstone, while the upper part has coarse poorly sorted argillaceous yellowish brown sandstone with siltstone clasts and quartzite pebbles. Two specimens of a probable dicynodont have been found from the basal siltstone (Kutty et al., 1987).

The Yerrapalli, Bhimaram, Maleri, and Dharmaram Formations occur successively above the Kamthi Formation and, except for the Bhimaram Formation, these are all mud dominated red bed horizons. The red mudstones are believed to have been deposited from suspension in interchannel floodplain areas (Sengupta, 1970). An oxidising environment with warm, moist climate and seasonally distributed rainfall is indicated by the red mudstones (Robinson, 1970). Vertebrate fossils in these horizons (Tables 1 and 2) are mainly found in the red mudstones and in very rare instances in the sandstones.

The *Yerrapalli Formation* (400 to 600 m) is dominated by red to violet mudstone (approximately 80–85% mud) with scattered, thin (2 to 3 m thick) sheets of quartzose sandstone and relatively smaller lenticular sand bodies made up of caliche derived calcarenite/calcirudite (Dasgupta, 1993b). Small lenticular sandbodies enclosed within the mudstones (Fig. 3) represent fillings of small ephemeral channels wandering over an extensive floodplain. The parallel laminated sheet-like sandstones, which often display parting lineation, were probably deposited from sheet flows associated with episodic overbank flooding of ephemeral streams (Maulik and Chaudhuri, 1983).

Table 1
The Yerrapalli Fauna

| Fishes | |
|-----------------|--|
| Dipnoi | <i>Ceratodus</i> sp. |
| Actinopterygii | <i>Saurichthys</i> sp. |
| Amphibian | |
| Capitosauridae | <i>Parotosuchus rajareddyi</i> |
| Reptiles | |
| Dicynodontidae | <i>Wadiasaurus indicus</i> , <i>Rechnisaurus cristarhynchus</i> trirachodontid teeth |
| Cynodontidae | ? <i>Mesodapedon kuttyi</i> |
| Rhynchosauridae | ? <i>Erythrosuchus</i> sp. |
| Erythrosuchidae | new genus and species |
| Prolacertidae | new genus and species |
| Rauisuchidae | new genus and species |

The Bhimaram Formation is dominated by coarse, pebbly, yellowish brown feldspathic sandstone intercalated with abundant red mudstone; fragmentary vertebrate remains have been found from this horizon (Kutty et al., 1987). It is followed upward by the Maleri, Dharmarm and Kota Formations successively (Fig. 3). The average thickness of these three formations is 200 to 600 m (Kutty and Sengupta, 1989; Bandyopadhyay and RoyChowdhury, 1996).

The *Maleri Formation* (300 to 600 m) begins with a 100- to 150-m-thick red mudstone and passes upward into a succession of sandstone–mudstone alternations (Fig. 3). Sheet-like sandstones (3–6 m thick) alternate with relatively thicker mudstone intervals. The mudstones are dominantly red to brownish red and occasionally green, structureless and poorly lithified. The sandstones are quartzose, medium to coarse grained with subordinate feldspars, garnets and rock fragments. These are cross-bedded with overlapping channel fills forming multistoried packages; individual channel fills have a basal facies rich in mudclasts and transported bone fragments. Lenticular bodies of caliche-derived peloidal calcirudite/calcarenite are common (Sarkar, 1988). These appear either at the bottom of channel sand bodies or as solitary bodies enclosed in the mudstones.

The Dharmaram Formation (Fig. 2) has a thick basal sandstone followed by alternating series of sandstone and mudstone beds. Compared to the Maleri Formation, the sand bodies are thicker and the sand–mud ratio increases in the Dharmaram. Several

vertebrate fossils are noted from this formation (Kutty et al., 1987). The overlying *Kota Formation* is also rich in vertebrate fossils (Table 3). The lower part of the Kota includes 15 to 25 m thick, hard, compact and coarse sandstone, which is pebbly in places. This sandstone becomes finer and grades both laterally and vertically into mudstones which contain dinosaur remains (Fig. 3). The upper part of the Kota Formation includes marl and limestone beds (1 to 2 m thick). The limestone has yielded several aquatic and semi-aquatic vertebrates. This is followed upward by mudstone and ferruginous shale interbedded with sandstone. Rudra and Maulik (1994) suggested that the lower part of this formation was deposited by a meandering river system while a braided river system formed the upper part; the limestone facies was interpreted to be a lacustrine deposit.

2.2. The Damodar basin

The Gondwana rocks of the Damodar basin occur as isolated outcrops covering a large area trending almost E–W. Only the Panchet Formation of this basin (Fig. 2) is known to bear vertebrate fossils (Table 4).

Table 2
The Maleri Fauna

| Fishes | |
|------------------|--|
| Dipnoi | <i>Ceratodus hislopianus</i> , <i>C. virapa</i> , <i>C. nageswari</i> |
| Subholostean | (undescribed) |
| Xenacanthidae | <i>Xenacanthus indicus</i> |
| Amphibians | |
| Metoposauridae | <i>Metoposaurus maleriensis</i> |
| Chigutisauridae | <i>Compsocerops cosgriffi</i> <i>Kuttycephalus triangularis</i> |
| Reptiles | |
| Rhynchosauridae | <i>Paradapedon huxleyi</i> |
| Phytosauridae | <i>Parasuchus hislopi</i> a large <i>Rutiodon</i> -like form a small <i>Angistorhinus</i> -like form |
| Prolacertidae | <i>Malerisaurus robinsonae</i> |
| Herrerasauridae | <i>Alwalkeria maleriensis</i> |
| Aetosauridae | (undescribed) |
| Plateosauridae | <i>Massospondylus</i> sp. ? <i>Plateosaurus</i> sp. |
| Dicynodontidae | (undescribed) |
| Traversodontidae | <i>Exaerodon statisticae</i> |

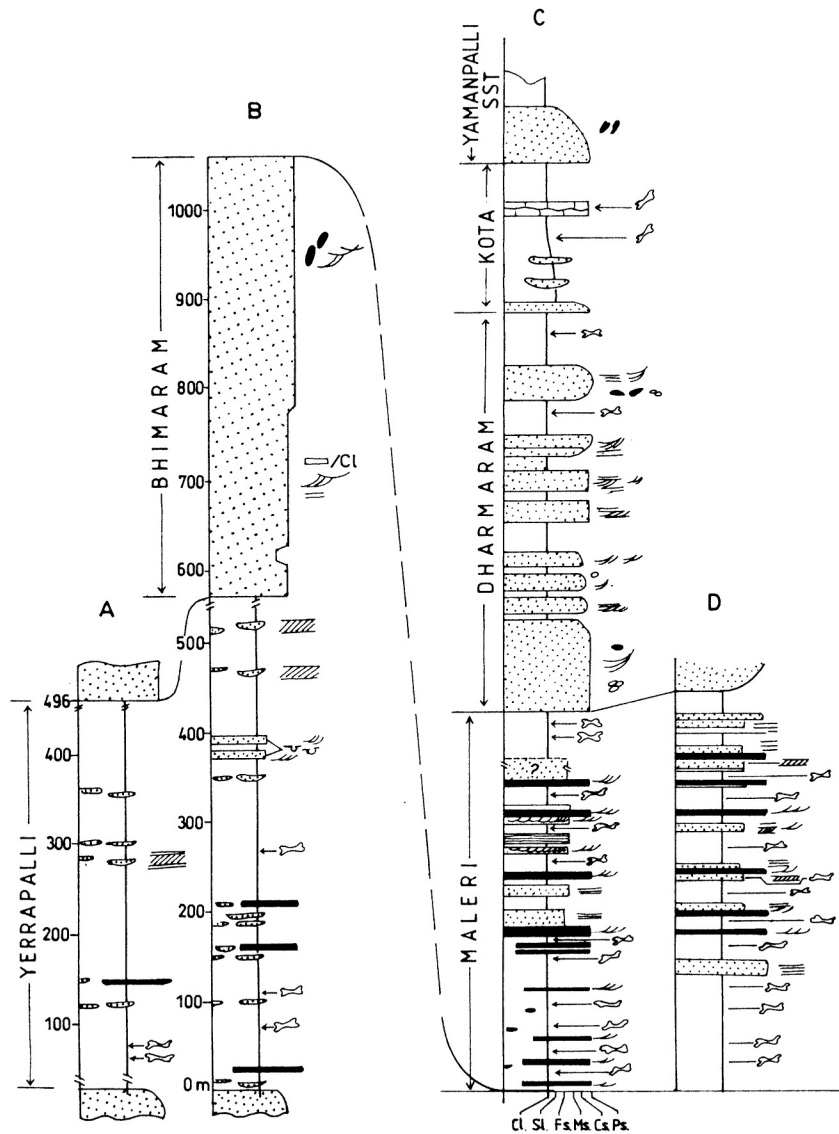


Fig. 3. Lithologs of the Triassic and Jurassic vertebrate-bearing formations of the Pranhita–Godavari basin (modified after Dasgupta, 1993b; Kutty and Sengupta, 1989; Bandyopadhyay and Roychowdhury, 1996). B is the lithologs of the Yerrapalli Formation near the type village Yerrapalli ($18^{\circ}49' 45''$ N and $79^{\circ}40' 50''$ E) and is that of the Maleri and Dharmaram Formations south of the village of Paikasigudem ($19^{\circ}16'$ N and $70^{\circ}31'$ E). A and D are additional logs of Yerrapalli Formation drawn close to B and Maleri Formation drawn close to the type village of Maleri ($19^{\circ}11'$ N and $79^{\circ} 40'$ E) respectively. (For index, see Fig. 5.)

The beds of the Early Triassic *Panchet Formation* (600–1000 m) dip at low angles (around 10°) towards N and NW in the area south of the Damodar river, and in the reverse direction to the north of the same river, indicating a gentle syncline (Gee, 1932). The overall

paleocurrent trend is toward NW to NE (Veevers and Tewari, 1995). Lithologically the *Panchet Formation* is a coarsening upward succession and has been divided into three parts (Robinson, 1970). The lower part (50–100 m) has micaceous, greenish or olive

Table 3
The Kota Fauna

| Fishes | |
|-----------------------|---|
| Semionotidae | <i>Lepidotes deccanensis</i> , <i>Paradapedium egertoni</i> , <i>Tetragonolepis oldhami</i> |
| Pholidophoridae | <i>Pholidophorus kingii</i> , <i>P. indicus</i> |
| Coelacanthidae | <i>Indocoelacanthus robustus</i> |
| Reptiles | |
| Kyantachelidae | <i>Indochelys spatulata</i> |
| Campylognathidae | <i>Campylognathus indicus</i> |
| Teleosauridae | a <i>Teleosaurus</i> -like form |
| Cetosauridae | <i>Barapasaurus tagorei</i> <i>Kotasaurus yamanapalliensis</i> |
| Mammals | |
| ? Kuehneotheriidae | <i>Kotatherium haldanei</i> , <i>K. yadagiri</i> |
| Morganucodontidae | Undescribed form |
| Amphidontidae | <i>Nakunodon paikasiensis</i> |
| ? Tinodontidae | <i>Indotherium pranhitai</i> |
| Sinoconodontidae | Undescribed genus and species |
| <i>Incertae sedis</i> | <i>Trishulotherium kotaensis</i> |

green coloured, well-laminated siltstone, interbedded with beds of yellow or buff coloured sandstones (0.5–4 m thick). The middle part (average 200 m) contains lenses of red or chocolate coloured laminated shaly siltstone (0.5–4.2 m thick) interbedded with buff coloured sandstones (2.5–23 m thick) while buff or pale grey sandstones with thin red shale layers dominate the upper part (300 to 400 m) (Fig. 4). The lower part is dominated by fine interchannel deposits. The middle part has both inferred channel and interchannel facies. The sediments in the upper part were deposited rapidly by a large, high-energy river channel (Robinson, 1970). The channel sand bodies in the upper part of the formation contain beds of small quartz pebbles, feldspar chips and mud clasts. Pockets of bone fragments are noted within this lithology.

2.3. Satpura basin

The Satpura basin has a more or less rectilinear outline caused by E–W trending faults. The basic geology is similar to other Gondwana basins. The Barakar Formation is followed upward by the Motur, Bijori, Pachmarhi and Denwa Formations in that order of succession (Fig. 2). The Late Permian Motur

Formation is dominated by thick red mudstone with interlayered lenses and sheets of sandstone and minor carbonaceous shale. Calcareous nodules occur within red mudstone in some places. Interestingly, not a single vertebrate bone has been recovered from the mudstone. The Bijori Formation is characterized by alternating argillaceous pale green to white coloured sandstone and carbonaceous shale. So far, only an isolated specimen of a temnospondyl, *Gondwanasaurus bijoriensis*, has been collected from this horizon. The overlying Pachmarhi Formation consists of thick beds of coarse, cross-bedded, poorly sorted sandstone, interbedded with red mudstone in some places, and thin layers of fine shale. Layers of white quartz pebbles are very common. Only some weathered temnospondyl fragments have been recovered from this horizon.

The early Middle Triassic *Denwa Formation* (300 to 600 m) gradationally overlies the Pachmarhi Formation and is dominated by red mudstone, which is silty in places and is interbedded with calcareous sandstone (Fig. 5). Maulik et al. (2000) have differentiated the Denwa Formation into two units. The lower unit is dominated by mudstone and lacks thick sand bodies (mud–sand ratio 4:1). The upper unit has alternating medium to fine grained sandstone bodies (3 to 15 m) and red mudstone (1.5 to 10 m) with mud–sand ratio 11:9. The upper unit has uncommon caliche derived calcirudites. The mean palaeocurrent direction of the lower unit is towards WSW and the upper towards WNW. Maulik et al. (2000) also

Table 4
The Panchet Fauna

| Amphibians | |
|------------------|---|
| Lydekkerinidae | <i>Lydekkerina panchetensis</i> |
| Capitosauridae | <i>Pachygonia incurvata</i> |
| Indobrachiopidae | <i>Indobrachiops panchetensis</i> |
| Trematosauroidae | <i>Gonioglyptus longirostris</i> , <i>G. huxleyi</i> |
| Lapillosidae | new genus and species |
| Reptiles | |
| Proterosuchidae | <i>Proterosuchus (Chasmatosaurus) indicus</i> |
| Dicynodontidae | <i>Lystrosaurus murrayi</i> <i>L. maccaigi</i> <i>L. rajurkari</i> <i>L. platyceps</i> |
| Cynodontidae | <i>Thrinaxodon bengalensis</i> |

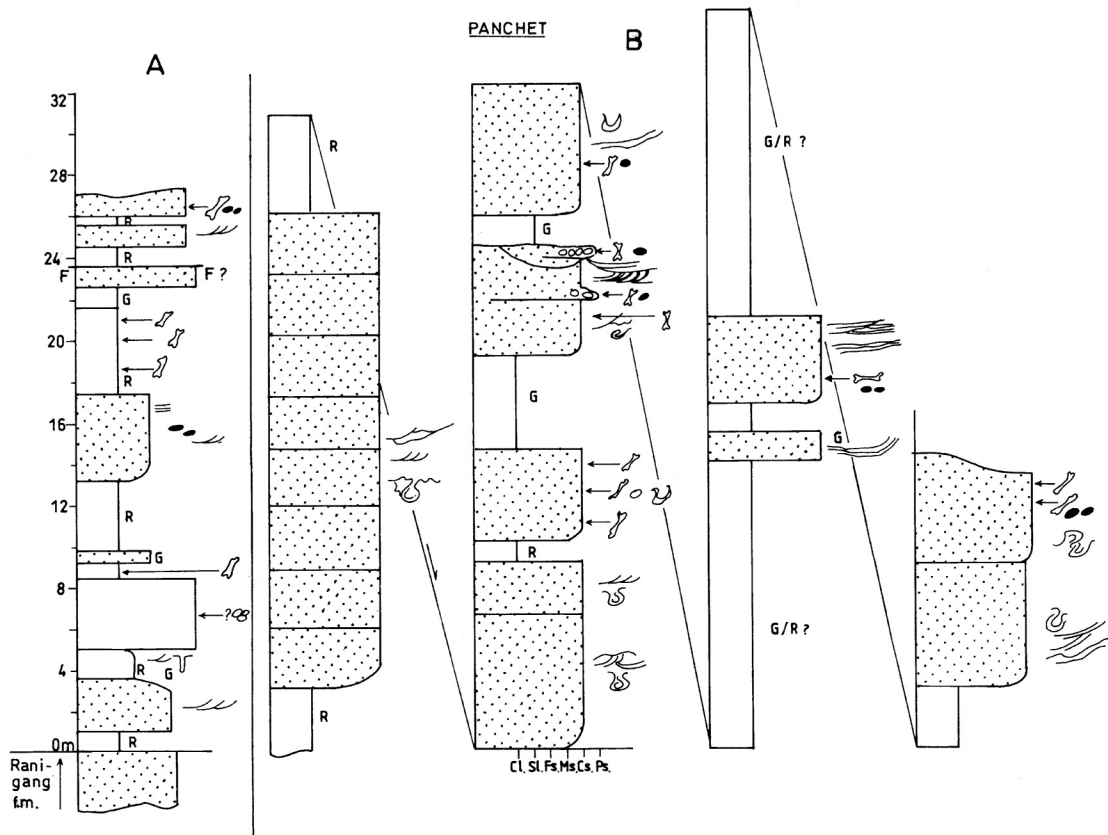


Fig. 4. Lithologs of the Early Triassic Panchet Formation of the Damodar basin. A is the lower part of the formation measured immediately east of village Saburbandh ($23^{\circ}36' 30''\text{N}$ and $86^{\circ}55' 42''\text{E}$). B is the lithologs of the upper part of the middle unit measured near the village Dumdumi ($23^{\circ}37' 50''\text{N}$ and $86^{\circ}53'\text{E}$). R is the red mudstone and G is the green mudstone and or fine sandstone. Deformed cross laminations and clay clasts are common associations with the vertebrate fossils of the sandstone. (For index, see Fig. 5.)

interpreted the upper unit as an alluvial plain characterized by sandy, braided channel belts and associated interchannel floodplains, while a network of meandering channels laterally separated by well-developed and stable interfluvial and floodplain areas is inferred to have formed the lower unit. Vertebrate fossils (Table 5) mainly occur in the mudstone although some are found in the calcareous sandstones of the upper part of this formation.

3. Taphonomic observations and interpretations

The Gondwana basins discussed briefly above contain seven vertebrate-bearing horizons of which

taphonomic information is available from five (Fig. 2). Most of the vertebrate bones are found in the red mudstones of the floodplain deposits. These floodplain deposits are mostly characterized by red mudstone interstratified with thin sandstone bodies and smaller lenses of calcirudite/calcareenite. Fossils are virtually absent in the large channel sand bodies but they are found, though sparingly, in the small lenticular channel fill bodies encased in the floodplain deposit. These smaller bodies presumably represent deposits of smaller, second order channels draining the floodplains. Red colouration indicates that the floodplains were well drained and deposition took place within an oxidising, well-aerated environment (Behrensmeier and Hook, 1992).

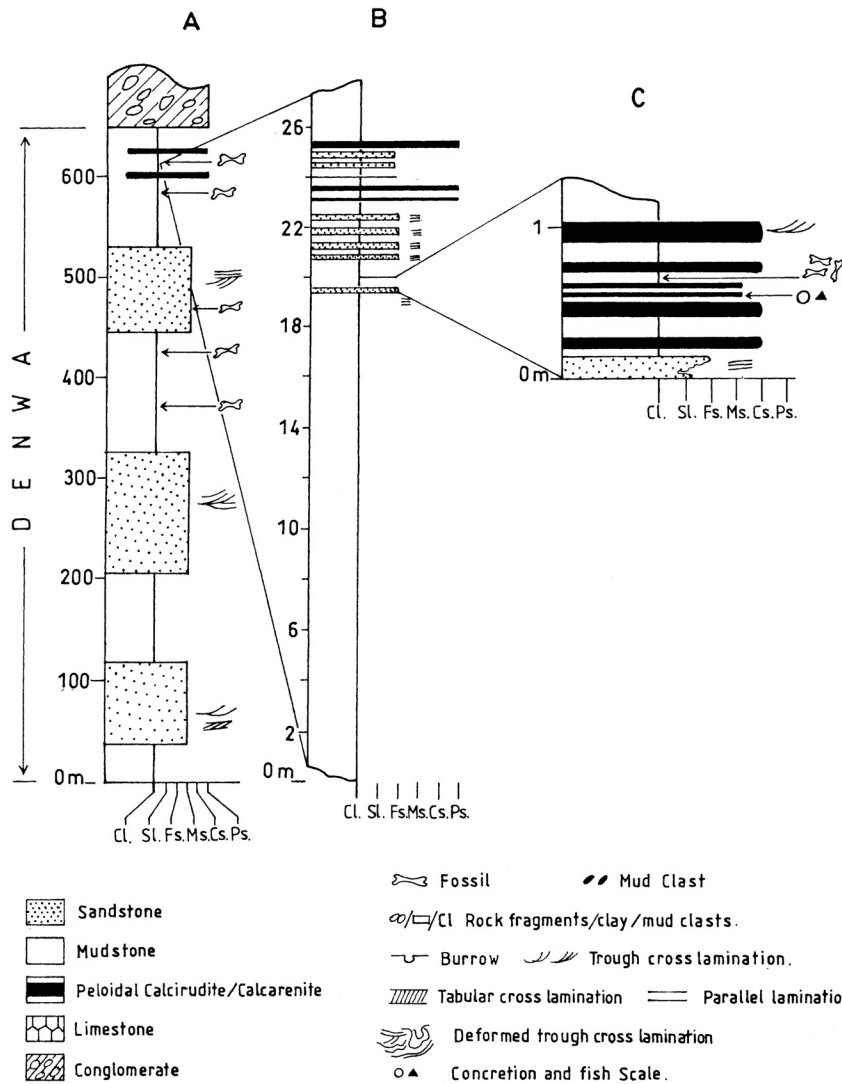


Fig. 5. Lithologs of the Middle Triassic vertebrate-bearing Denwa Formation of the Satpura basin (A modified after Maulik et al., 2000). B and C indicate the rich temnospondyl (represented by bone signs) and fish (represented by black triangle) association near the village Sahavan (22°38' N and 78°34' E).

The main taphonomic features which are considered here include articulation/disarticulation of the skeletons, number of species or genera, dominance of small/large bones, size (age spectrum) and orientation of the bones, sorting (hydraulic/other agents), completeness of the bones, degree of weathering or abrasion, horizontal or inclined bone bed and autochthonous/allochthonous accumulation. However, even

when considering all these features, the precise taphonomic meaning is sometimes difficult to understand. Apart from the known taphonomic biases (e.g., small/large bones, etc.), collection strategies in the field also affect taphonomic information. In the past, attention has been given to the more complete or nearly complete, less damaged, identifiable bones and this tendency leads to biased taphonomic information.

Table 5
The Denwa Fauna

| Fish | |
|-----------------|--|
| Dipnoi | <i>Ceratodus</i> sp. |
| Amphibians | |
| Brachyopidae | Undescribed genus and species |
| Capitosauridae | <i>Parotosuchus denwai</i> , <i>P. crookshanki</i> |
| Trematosauridae | a lonchorhynchine form |
| Reptiles | |
| Rhynchosauridae | Undescribed genus and species |
| Dicynodontidae | Undescribed genus and species |

Transported skeletal assemblages often do not provide precise information on the habitat of the related animal. Moreover, fossil assemblages cannot provide the total picture of a palaeocommunity, which in turn restricts the interpretation of the palaeoecosystems. Notwithstanding these shortcomings, taphonomic studies provide a lot of information on the palaeoenvironments, palaeoecology and palaeobiology of the fossils concerned.

On the basis of the mode of bone occurrences of the fossil, six taphonomic types of skeletal assemblages (Table 6) have been identified from the five

vertebrate-bearing Gondwana formations. The details of the taphonomic types are given below.

3.1. Type A: complete articulated or semi-articulated skeletal assemblage

Complete, articulated and semi-articulated skeletons of reptiles have been excavated from the red mudstones of the Maleri and Yerrapalli Formations (Table 6).

3.1.1. Complete articulated skeletons from the Maleri Formation

A pair of nearly complete articulated phytosaur skeletons (*Parasuchus hislopi*) was excavated from the red mudstones of the Maleri Formation (Chatterjee, 1978). Both these adult individuals (about 2.5 m in length) were found side by side lying on their ventral surfaces (Fig. 6). All the bones including the scutes were found articulated. This autochthonous pair was excavated from an area of about 6 m³ (3 × 2 × 1 m). One individual was found lying a little ahead of the other. The preservation is quite good and none of the bones shows any cracking, flaking, abrasion or surface marks. The curvature of the vertebral column indicates natural life-like posture. Interestingly, ingested bones of a small prolacertid, *Malerisaurus robinsonae*, were

Table 6
Taphonomic types of the skeletal assemblages of the different Gondwana basins

| Taphonomic types | Characteristic features | Stratigraphic formations | Gondwana basins |
|------------------|---|--|-----------------------------------|
| Type A | Complete, articulated or semi-articulated skeletal assemblages | (a) Late Triassic Maleri Formation | (a and b) Pranhita–Godavari basin |
| | | (b) Middle Triassic Yerrapalli Formation | (c) Damodar basin |
| | | (c) Early Triassic Panchet Formation | |
| Type B | Disarticulated monospecific skeletal assemblages | (a) Later Triassic Maleri Formation | (a and b) Pranhita–Godavari basin |
| | | (b) Middle Triassic Yerrapalli Formation | |
| Type C | “Log jam” association with disassociated monospecific skeletal assemblage | Early Jurassic Kota Formation | Pranhita–Godavari basin |
| Type D | Disarticulated and dispersed skeletal assemblages of mixed individuals | (a) Middle Triassic Yerrapalli Formation | (a) Pranhita–Godavari basin |
| | | (b) Middle Triassic Denwa Formation | (b) Satpura basin |
| Type E | Isolated disarticulated skeletal assemblages of single individuals | All vertebrate-bearing horizons | All Gondwana basins |
| Type F | Isolated skeletal fragments of different individuals | All vertebrate-bearing horizons | All Gondwana basins |

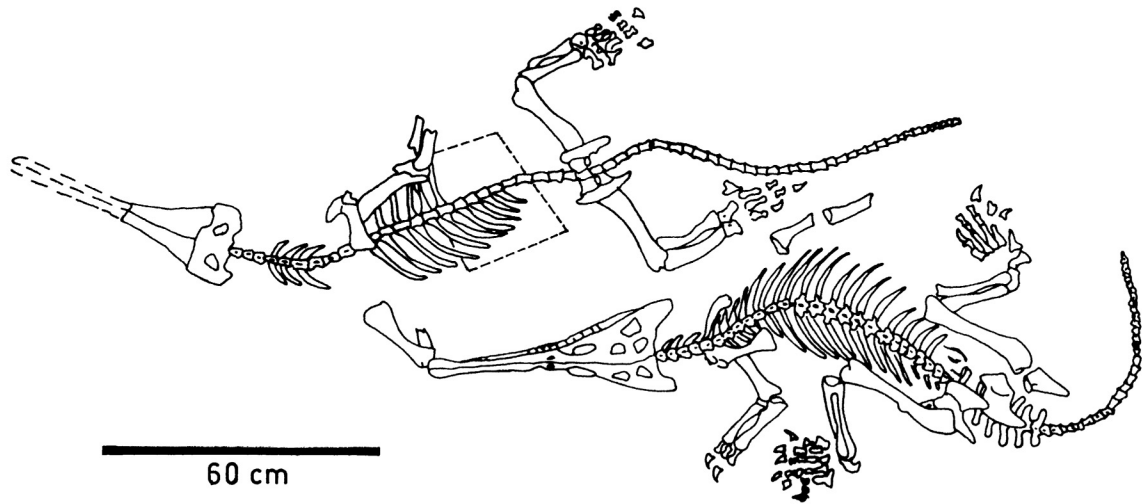


Fig. 6. Complete, articulated skeletons of *P. hislopi* (Maleri Formation) as occurred in the field (modified after Chatterjee, 1978).

found inside the rib cage of both these individuals (Chatterjee, 1980, 1986). The cranial parts of the skeletons of the prey were not entirely preserved but their postcranial bones were as well preserved as their predators; the centra of some of the dorsal and neck vertebrae were found articulated (Fig. 7). The occurrence of such articulated centra in the stomach of the phytosaurs led Chatterjee (1978) to postulate that apart from the skull, the predators gulped down the whole prey. The large phytosaurs possibly first crushed the head of the prey, which made the rest of the body easier to swallow.

3.1.2. Complete semi-articulated skeletons from the Yerrapalli Formation

From the red mudstones of the Yerrapalli Formation, two associated skeletons of prolacertids have been recovered along a gully slope from an area of about 1.5 m² (Figs. 8 and 9). One of them is an adult and almost complete while the other is small and incomplete and was found very near to the former. Both individuals belong to the same species (Dasgupta, 1993a). The adult animal was found lying in a life-like posture with its long neck stretched out. The skeletal elements are mostly articulated except for a few posterior cervical and anterior dorsal vertebrae and the left half of the pelvic girdle. As the skeleton

was stretched, there were some gaps in between axial elements (Fig. 8). Overall, most of the skeletal elements were found intact in a slightly disarticulated but associated condition. The skull is slightly crushed due to overburden pressure, whereas the postcranial bones are complete, being exceptionally well preserved, without any breakage or surface marks. The juvenile skeleton (Fig. 9) is rather incomplete; part of the skull, lower jaw and trunk vertebrae are disarticulated. The long neck shows a sinuous pattern of disposition. These bones are equally well preserved, complete, without any sign of any disturbances or damage.

3.1.3. Interpretation of skeletal assemblages from the Maleri and Yerrapalli Formations

The natural life-like posture of the autochthonous Maleri phytosaurs and the Yerrapalli prolacertids in the floodplain fines indicates quick burial after death. From their life-like posture, it can be interpreted that these were trapped and partly bogged down in thick, sticky mud deposited over the floodplain. Muds with a porosity of 70–90% (50–80% water by volume) (Reike and Chilingarian, 1974; Weaver, 1989) might have forced these animals to subside gradually prior to death. The prolacertid skeletons might have been disturbed due to load adjustment of the host muds

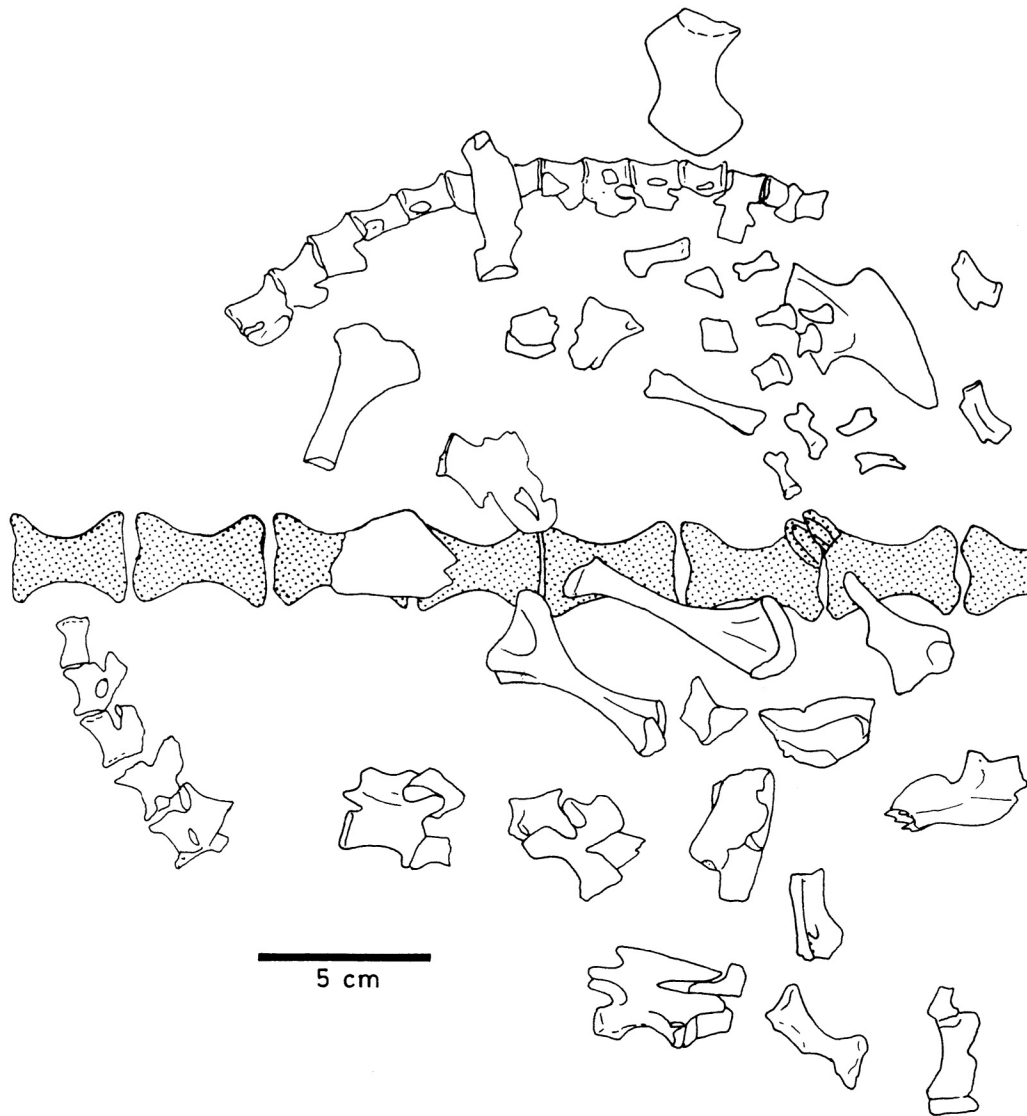


Fig. 7. Ingested bones of *M. robinsonae* (Maleri Formation) as found inside the rib cages of *P. hislopi* (modified after Chatterjee, 1980).

and were slightly disarticulated; parts of the skeleton of the juvenile prolacertid might have suffered winnowing by thin sheets of water currents. The complete bones in both cases indicate that the skeletons were neither trampled nor disturbed by scavengers. High sedimentation rates and quick burial prevented these skeletons from being disarticulated, fragmented, or abraded by physical processes. The time interval between death and burial must have been very short.

3.1.4. Complete articulated and semi-articulated skeletons from the Panchet Formation

Apart from the above two associations, articulated as well as semi-articulated but nearly complete skeletons of a dicynodont (*Lystrosaurus*) are known to occur in the red mudstones and olive green shale of the Panchet Formation of the Damodar basin (Robinson, 1958; Tripathi and Satsangi, 1963; Colbert, 1974). Data on these collections, such as the total

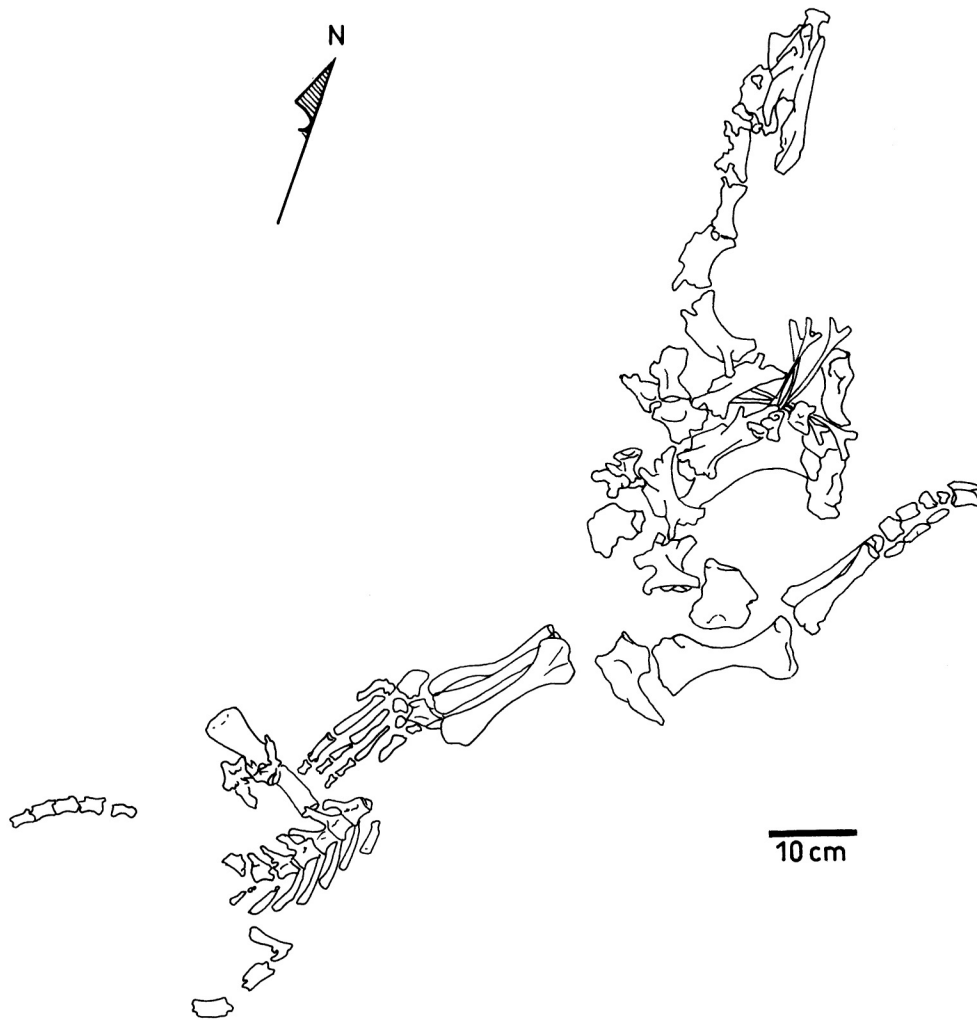


Fig. 8. Semi-articulated skeleton of the adult prolacertid (Yerrapalli Formation) as occurred in the field (modified after Dasgupta, 1993a).

area of the quarry, spatial distribution of the bones, or orientation of individual bones are not available. Robinson (1958) suggested that the gradual silting up of pools and lakes formed lenses of shales of varying thickness in the lower part of the Panchet Formation. In such conditions, terrestrial animals dying in or near the pools were buried without dismemberment. Though the reason for such occurrences of articulated and/or semi-articulated skeletons in the Panchet mudstone or shale is not very clear from Robinson's comment, it appears that the flood-plain pools and lakes were flooded while the animal

carcasses were covered quickly by suspended sediments.

3.2. *Type B: disarticulated monospecific skeletal assemblages*

Disarticulated skeletal assemblages of a large number of monospecific individuals have been found in the Maleri and Yerrapalli Formations of the Pranhita–Godavari basin (Table 6). However, the taphonomic interpretations of these cases are quite different from each other and are treated separately.



Fig. 9. Juvenile semi-articulated skeleton of the prolacertid (Yerrapalli Formation) found very near to the adult prolacertid (modified after Dasgupta, 1993a).

3.2.1. Disarticulated monospecific skeletal assemblage from the Maleri Formation

A graveyard of a large number of disarticulated and dispersed bones of metoposaurid amphibians (*Metoposaurus maleriensis*) was found in the red mudstones of the Maleri Formation (RoyChowdhury, 1965). These bones occur in an area of 50 m² (10 × 5 m) and were scattered. From this assemblage, 111 bones including fragmented cranial and postcranial bones, one complete skull, one partial skull and two rami of lower jaws were collected. The minimum number of individuals is estimated to be six based on six right humerii collection. Among the collected bones, 46 bones are fractured, 11 are fragmented but recognizable, 39 bones show flaking and 7 are broken beyond recognition; only 16 specimens are well preserved. Suncracks are common to all the bone elements but there are no tooth marks or perforations in any bone. The bones do not show any preferred orientation.

3.2.1.1. Interpretation. Three major size domains of the humerii can be differentiated in this assemblage;

the length of the largest humerus is 12.6 cm, which is smaller than the standard length of an adult metoposaurid. As the other two size domains are smaller as indicated by the humerus length, the entire skeletal assemblage may represent a population of smaller individuals of which all were juveniles. This monospecific association of juvenile metoposaurids indicates mass mortality. These amphibians were probably swept out of a river or pond during a flood and subsequently died. With the recession of flood, these carcasses were exposed on the floodplain for a considerable period during which they were stripped of flesh and subsequently the skeletons were disarticulated. The scattered nature of the bones indicates some depositional movement of the skeleton but not far from the site of death. These scattered disarticulated skeletons may owe their origin either to minor dispersive current action or scavenging and/or trampling. From the nature of bone preservation, it can be deduced that these disarticulated bones suffered long surface exposure when physical/environmental and biological agents dispersed and broke the bones. Trampling of scavengers within the abandoned channels disarticulated and broke the bones but at the same time enhanced the burial of disarticulated bones in the soft substrate, as observed elsewhere by Behrensmeyer (1991). Later these bones were gradually covered up by fine sediments. The time span between death and burial must have been longer than that of the previous cases.

3.2.2. Disarticulated monospecific skeletal assemblages from the Yerrapalli Formation

The Yerrapalli Formation has produced several lowland vertebrates (Table 1); of these the kannemeyeriid dicynodont, *Wadiasaurus indicus*, is very common. An assemblage of 754 bones, both cranial and postcranial, of a monospecific association of *W. indicus* has been excavated from the red mudstones of this horizon (Bandyopadhyay, 1988). The bone accumulation (Fig. 10) was found beside a modern streamlet and it can be assumed that a large number of bones have been lost to recent erosion. There are 6 occipital condyles, 43 femora (of which 23 are of left side and 4 probable pairs), 20 humerii (of which 13 are of right side and 2 probable pairs), 22 scapulae (of which 9 are of right side) and more than 200 vertebrae in the collection. From the number of left femora (23), it was estimated



Fig. 10. Excavation site of *W. indicus* (Yerrapalli Formation).

that at least 23 individuals were present at a single locality. The collected bones show significant size variation; for example the length of humeri ranges from 18.5 to 36.5 cm. From comparisons of bone measurement with respect to their numbers, it appears that within the group about 30% were juveniles or

young members. The skeletons were disarticulated, disassociated and dispersed (Fig. 11). This parautochthonous assemblage of bones occurs at one level and scattered over an area of about 144 m² (16 × 9 m). The bone distribution in the quarry map does not show any preferred orientation (Fig. 12). Some dis-



Fig. 11. Disarticulated bones of *W. indicus* (Yerrapalli Formation) as found in the excavation site.

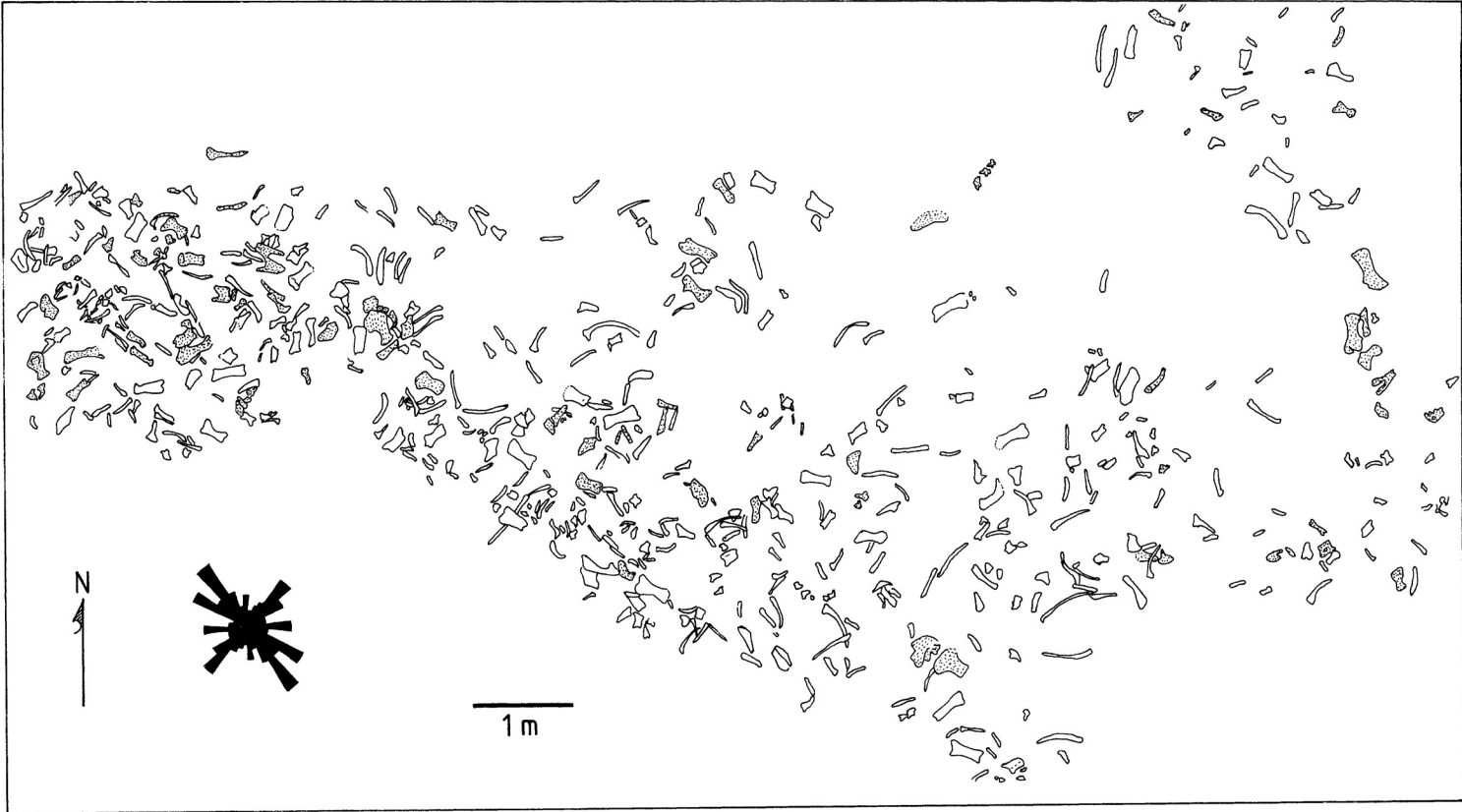


Fig. 12. Plan showing the distribution of *Wadiasaurus* bones as found in the excavation site. Better-preserved specimens are stippled (modified after Bandyopadhyay, 1988).

turbances of already disarticulated bones may have occurred due to the movement of thin sheets of water rather than by strong currents. Disturbances due to bioturbation cannot be ruled out. Apart from one complete skull, most of the skull elements were found in a disarticulated state. The postcranial bones including the ribs are mostly complete. However, a few limb bones are broken which may be due to scavenging and/or trampling (Hill, 1979; Voorhies, 1969). No signs of rolling, abrasion, tooth marks or perforations have been detected in any of the bones. Most of the bones show some fine cracks due to surface exposure.

3.2.2.1. Interpretation. From the age structure of such monospecific accumulation (30% juvenile versus adult animals), it was interpreted that *W. indicus* lived in a herd (Bandyopadhyay, 1988). This bone assemblage of such a herd indicates mass mortality probably due to some catastrophic event. Bandyopadhyay (1988) interpreted that after a flood, this herd of *Wadisasaurus* became trapped in the thick mud of a floodplain. The heavy build ($\sim > 100$ kg) of these animals might have contributed to their death. Subsequently, soft tissues decomposed and the skeletons were dismembered. These were later dispersed due to trampling and/or scavenging and also probably by low velocity water currents which were not strong enough to move the whole carcasses a long distance. Subsequently, the bones were covered by muds from later overbank flooding events.

An interesting palaeoecological interpretation of *W. indicus* may be made from the taphonomic observations of this bone assemblage. The skull and the collected maxillae from the excavation site are all found to be tuskless. Apart from this excavation site, there were about a dozen other localities in this horizon from which fossil bones of only one or two individuals of *W. indicus* have been found. The maxillae of these isolated individuals are tusked and the bones are comparatively quite robust with thickened nasals and maxillae. Bandyopadhyay (1988) considered these isolated individuals to be members of male *W. indicus*. It was interpreted that the female and juvenile members of *W. indicus* used to live in herds while their adult male members remained isolated and probably joined the herd only during mating seasons (Bandyopadhyay, 1988).

3.3. Type C: “log jam association” with dispersed monospecific skeletal assemblage

The Kota Formation of the Pranhita–Godavari basin has produced a large number of vertebrate assemblages (Table 3). Two dinosaurs and some micromammals have been collected from the mudstone of the lower part of the Kota Formation (see Section 2.1). A very rich layer of bones of the sauropod dinosaur, *Barapasaurus tagorei*, was found together with fossilized large tree trunks, just above the interface of a sandstone overlain by a mudstone lens (Jain et al., 1962, 1979). This dinosaur bone assemblage (Fig. 13), consisting of approximately 235 bones, includes only postcranial material and a few teeth of adult individuals. In the collection, the presence of six left femora indicates that there were at least six individuals. Except for one partially associated skeleton, the bones were disarticulated, disassociated and dispersed. This bone assemblage occurred in an area of about 276 m². Orientation of the bones is polymodal (Fig. 14) albeit with two strong modes. The majority of the bones were oriented nearly



Fig. 13. Mode of occurrence of bones of *B. tagorei* (Kota Formation) at the excavation site.

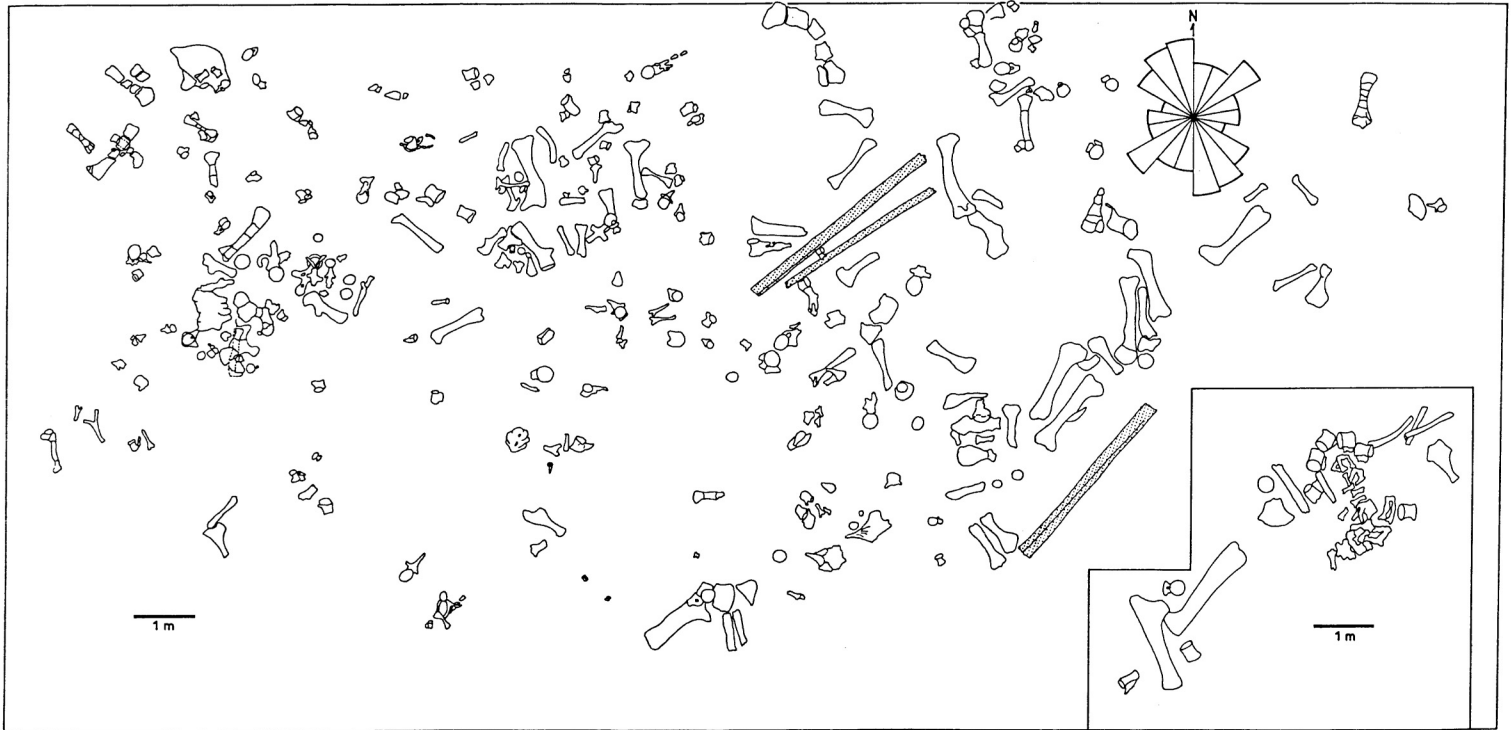


Fig. 14. Plan showing the distribution of bones of *B. tagorei* and fossil tree logs (stippled).

NNW–SSE while another set of bones along with logs were oriented NE–SW. The disarticulated bones are all complete and well preserved. A few limb bones were found to be broken but the shape and orientation remained intact, indicating these were broken after deposition. Behrensmeyer (1982, 1991) has experimented with more than 100 cow, horse and sheep bones and found that no breakage occurred when these were transported by natural rivers in sand and gravel bed-stream for several kilometers over a period of up to 12 years. The *Barapasaurus* bones show long fine sun cracks indicating brief surface exposure before burial but do not show any surface marks.

3.3.1. Interpretations

The monospecific bone assemblage of *B. tagorei* indicates that these animals suffered mass mortality due to some catastrophic event. It can be assumed that a herd of *Barapasaurus* died in a flood and the carcasses were transported by floodwater for a distance. There is so far no record of any other tetrapod fossil material from the mudstones of the lower part of the Kota Formation; hence no other skeletal materials was found in association of this *Barapasaurus* assemblage. The associated tree logs were most likely uprooted in the flood event and were transported together with *Barapasaurus*. Subsequently, these carcasses became entangled with the tree trunks, decomposed and disarticulated. The sauropod skulls being lighter were fragmented and washed away while the heavier postcranial bones were left behind along with the tree trunks. This bone assemblage was exposed on the surface for some time and subsequently buried by silty and clayey flood plain deposits. From the bone orientation (Fig. 14), it appears that the relatively small bones were transported with their long axes parallel to the paleocurrent direction while the larger bones and tree trunks were rolled with their major axis oriented NE–SW, perpendicular to the flow. The latter NE–SW orientation conforms to the general north-westerly palaeocurrent direction of the Kota Formation (Rudra and Maulik, 1994).

3.4. Type D: disarticulated skeletal assemblages of mixed individuals

Disarticulated skeletons of more than one animal are found to occur together in the Yerrapalli Forma-

tion of the Pranhita–Godavari basin and in the Denwa Formation of the Satpura basin. The taphonomic interpretations of these cases are treated separately.

3.4.1. Disarticulated mixed skeletal assemblages from the Yerrapalli Formation

About 100 m away from the excavation site where two prolacertid skeletons were found (see Section 3.1.2), a mixed assemblage of two different reptiles—a prolacertid and a raulisuchid has been excavated from the red mudstones. There were 155 disarticulated bones of which 63 belong to a raulisuchid and 92 belong to a prolacertid assemblage. Analysing the assemblage, Dasgupta (1993a) concluded that there was more than one adult individual of prolacertid reptile, similar to material from the adjacent site, and an adult raulisuchid. The skeletons were completely disarticulated and dispersed. The bones occurred in an area of about 4 m², without any preferred orientation (Fig. 15). The prolacertid bones were more scattered than the raulisuchid ones. Apart from a few limb bones of the prolacertids, most of the other bones were found to be complete, very well preserved and did not show any external damage. Some of the limb bones are somewhat flattened, probably due to overburden.

3.4.1.1. Interpretation. The preservation of the bones and the mode of occurrence of the Yerrapalli prolacertid and raulisuchid assemblage indicate that these animals also suffered a similar fate (trapped in floodplain muds) to those of the prolacertids of the previous site (Section 3.1.2). The possibility of predation or scavenging can be ruled out due to lack of any perforation, chew marks or other surface damage in the prolacertid bones; on the contrary, the bones are quite well preserved. However, it is conceivable that after the inferred flood event the predator may have ventured out onto the floodplain in pursuit of the trapped prolacertid and became trapped itself in the cohesive mud and eventually died. The skeletons were exposed for some time when they were disarticulated and disassociated by physical and/or biological agents. The time span between death and burial was most likely longer than that of the complete semi-articulated prolacertid of the adjacent site (Section 3.1.2).



Fig. 15. Plan showing the distribution of the disarticulated bones of prolacertids and rausuchid (Yerrapalli Formation) (modified after Dasgupta, 1993a).

3.4.2. Disarticulated mixed skeletal assemblage from the Denwa Formation

The temnospondyl amphibians dominate the faunal association of the Denwa Formation of the Satpura basin (Table 5). As stated earlier, mudstones dominate the upper part of the Denwa Formation; two localities with disarticulated bone assemblages of two different animals have been identified from this mudstone unit. These are discussed separately.

3.4.2.1. Mixed skeletal assemblage of capitosaurids and dipnoans.

An exceptionally rich accumulation of capitosaurid amphibians (*Parotosuchus*) has been noted in a thick (1–1.5 m) mudstone band with thin lenses (~20 cm) of fine sandstone between calcirudite lenses (Fig. 5C). Just 1 m ESE of this accumulation, there are stacks of dipnoan fishes in the same stratigraphic level. The capitosaurid assemblage mainly comprises skulls, with few postcranial ele-

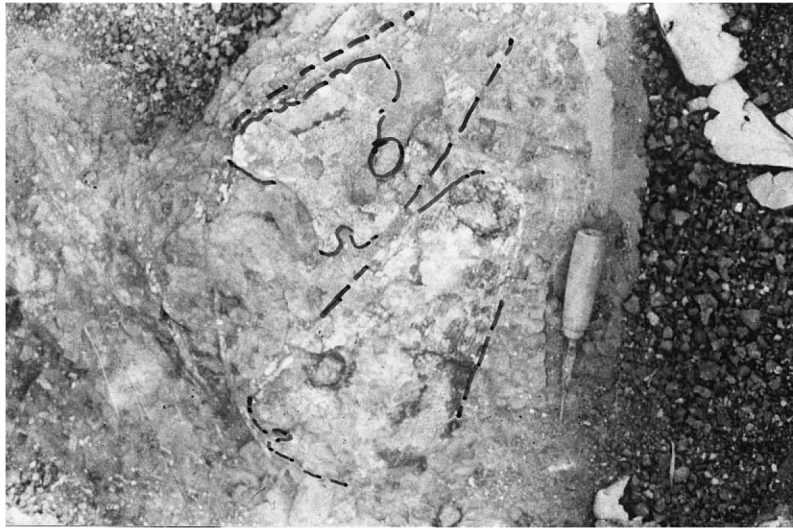


Fig. 16. Disarticulated skulls of *Parotosuchus* (Denwa Formation) as occurred in the excavation site.

ments (Fig. 16). Twelve disarticulated skulls of the capitosaurids (six complete or almost complete, some with mandibles) and a few postcranial bones including five clavicles, three interclavicles, rib fragments including rib heads, a few intercentra and some limb bones have been excavated. Among the skulls, the largest one is 46.9 cm long while the smallest measures 27 cm. Demographically, it appears that this bone assemblage has adults, subadults and juveniles. Most of these skulls are stacked almost one above the other within a small area of 2×6 m. The bones are little weathered without any surface mark or signs of rolling or abrasion; minor cracking can be seen indicating that these skulls were exposed for a brief period before burial. The complete edges of these randomly oriented skulls also rule out scavenging or trampling.

Possible reasons for such an association of adult and juvenile capitosaurids and dipnoans in a vertically stacked preservation is not yet discernable. Excavation is still being continued at this locality. Detailed sedimentology of this horizon as well as geochemical study of the mudstone is in progress.

3.4.2.2. Mixed skeletal assemblages of dicynodonts and rhynchosaur. An association of small, perhaps juvenile bones of dicynodonts and a rhynchosaur has been found in the red Denwa mudstones. The bones

include mainly the squamosals, snout, dentary, articular and almost all the girdle and limb bones of dicynodonts and some fragmentary skull bones and postcranial material of a rhynchosaur. Disarticulated and disassociated skeletons of dicynodonts of two different sizes (two right ischia measuring 9 and 11.5 cm in length, respectively) and a rhynchosaur occur in a small area of about 3 m^2 . These bones occur in a scattered manner without any preferred orientation, and are well preserved. Most of the postcranial material is complete and does not show any bone modifications like cracking, trampling, surface marks, abrasion or polishing. The skull elements such as the squamosals, snout and dentary also do not show any bone damage. The skull bones, especially the dicynodont squamosals, and some of the postcranial bones such as dicynodont ischia and rhynchosaur tibia are slightly flattened.

3.4.2.3. Interpretation. These small, juvenile reptiles (dicynodonts and rhynchosaur) of the Denwa palaeocommunity suffered death probably due to becoming trapped in mud. The disarticulated but not dispersed bones indicate that these animals were not moved far from the site of death. According to Behrensmeyer (1978), small, juvenile animals usually weather more rapidly than large animals and their

carcasses are destroyed faster by carnivores. However, the well-preserved bone condition in both these cases indicate that they were rapidly buried (Behrensmeyer, 1982).

3.5. Isolated disarticulated skeletal assemblages of single individuals

These assemblages, represented by skulls, skulls with mandibles or rarely skulls with postcranial material (with varying degree of disarticulation) have been reported from almost all the vertebrate-bearing horizons of the Gondwana basins. Taphonomic observations have been made on skeletal assemblages from the Yerrapalli and Maleri Formations of Pranhita–Godavari basin and from the Denwa Formation of the Satpura basin.

3.5.1. Isolated skeletal assemblage from the Maleri Formation

Several isolated skeletal assemblages occur in the red mudstones of the Maleri Formation. Among them, a complete but disarticulated skeleton of a reptile (rhynchosaur) and two chigutisaurid amphibian skulls with lower jaws are noteworthy.

3.5.1.1. *Isolated disarticulated but complete skeletal assemblage.* The skeleton of a rhynchosaur (*Paradapedon huxleyi*) has been excavated from the Maleri red mudstones (Chatterjee, 1974). The skeleton, belonging to a small individual, was found disarticulated but associated in a slightly dispersed condition (Fig. 17). This para-autochthonous assemblage occurs in an area of about 4 m². The material, including the skull and a number of postcranial bones,

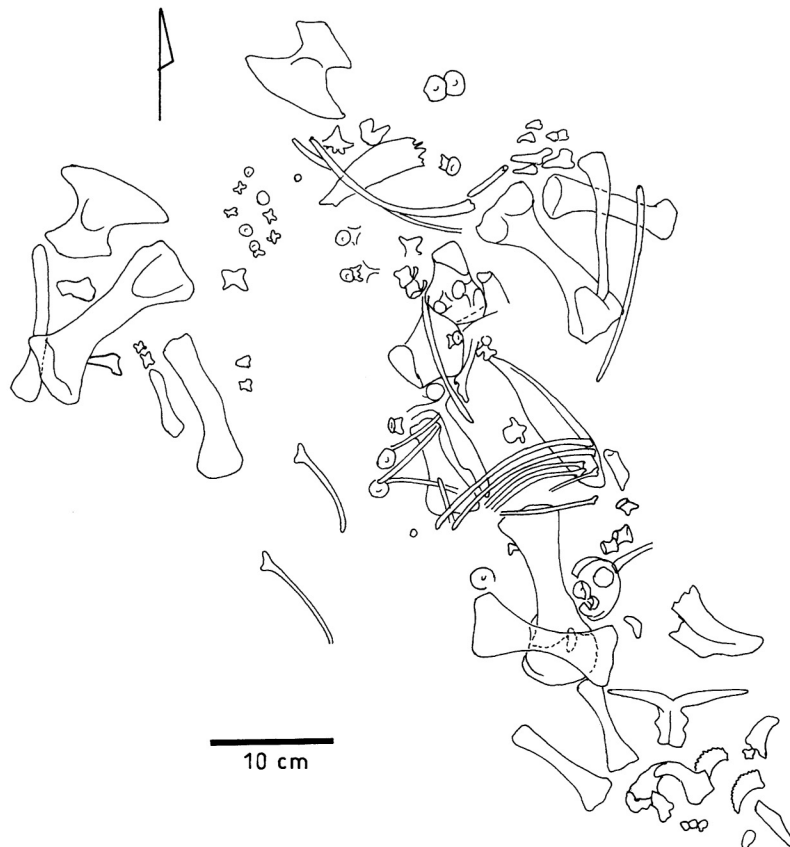


Fig. 17. Plan showing the disarticulated bones of *P. huxleyi* (Maleri Formation) (modified after Chatterjee, 1974).

was well preserved. Although the skull elements came apart along the sutures, the postcranial bones, including the very fragile ribs, were complete. Apart from fine sun cracks, the bones do not show any sign of abrasion or external damage. The disassociated condition of the bones indicates minor movement by physical agents but dispersion due to biological agents is doubtful.

3.5.1.2. Remains of isolated skulls with mandibles. Of the two chigutisaurid amphibian skulls with lower jaws (*Compsocerops cosgriffi*), one skull with articulated lower jaw was found lying on its dorsal surface in the gully slope of a recent streamlet in a thick mudstone unit (12 to 15 m) (Sengupta, 1990). Few parts of the skull were broken. The skull was found stuck obliquely in the red mudstone; roots of a small recent tree actually held the skull tightly and one of the roots passed through the pineal opening. These roots prevented the skull from being washed away. The postcranial elements probably were eroded. The other skull is partially complete; fitting fragments of the skull were collected from a thin mud lens alternating with fine to medium sandstone or coarse caliche derived calcirudite/calcarenite. One ramus of the lower jaw was found underneath the skull fragment. The skull roof elements were fragmented along sutures. Dispersed postcranial material occurs near this skull.

3.5.2. Isolated skulls or mandibular remains from the Denwa Formation

Isolated large capitosaurid amphibian skulls (*Parotosuchus*) with or without mandibles, and a brachyopid amphibian skull with mandible occur in the red mudstone, while a few mandibles of capitosaurids were found in the calcareous sandstone of the Denwa Formation. Large and medium sized isolated postcranial bones of dicynodonts have also been excavated at different localities. Four isolated single adult *Parotosuchus* skulls have been collected from different Denwa localities. These are complete, without any surface marks, abrasion or any breakage, although fine cracks and flaking are common, which may be due to short-time surface exposure. One isolated ramus of a mandible and several isolated fragments of mandible and teeth of *Parotosuchus* were found in the fine to medium calcareous sandstone.

3.5.3. Isolated skulls from the Yerrapalli Formation

From the red mudstones of the Yerrapalli Formation, a single adult individual of a capitosaurid (*Parotosuchus*) and of a dicynodont (*Rechnisaurus*) have been collected from two different localities. The capitosaurid is represented by a nearly complete skull roof associated with the right ramus of the mandible and an interclavicle, whereas the dicynodont is represented only by the skull and dentary symphysis. The capitosaurid skull (*P. rajareddy*) is not complete; a major part of the skull roof is lost but the skull margin is complete. The right ramus of the mandible is reasonably complete and less damaged (RoyChowdhury, 1970a).

On a gully slope of the Yerrapalli red mudstone, a partly exposed skull of another dicynodont, *Rechnisaurus cristarhynchus*, was excavated (RoyChowdhury, 1970b). Parts of the skull were found actually in the gully, a little removed from their original site but these could be fitted on to the skull. Most of the occiput and the zygomatic arches were probably washed away. Breaks along the sutures of some parts of the skull and some broken skull elements such as the anterior part of the orbit indicate long exposure on the surface. Some skull elements such as part of the prefrontals, lacrymals, jugals and squamosals were probably washed by recent running water.

3.5.3.1. Interpretation. Occurrences of such single isolated individuals without any nearby vertebrate remains in different localities of a horizon indicate attritional death. The carcasses suffered various degrees of exposure, weathering and movement. It has already been mentioned that water movement is not unexpected in the well-drained floodplain deposits. As a result, disarticulated, comparatively lighter bones become transported leaving behind heavier skulls and/or mandibles and other fragmentary bones.

The disarticulated Maleri rhynchosaur was exposed to the surface for some time. The bones show a preferred orientation (NNW–SSE) (Fig. 17) indicating that they were moved by thin sheets of flowing water. However, not a single bone element including the small digit bones was removed by water. The bones were later covered up by fine sediments. The time interval between death and burial was short but must have been longer than the articulated phytosaur or semi-articulated prolacertid skeletons (Section 3.1).

The isolated Maleri chigutisaurid, Denwa capitosaurid, Yerrapalli capitosaurid and the Yerrapalli dicynodon skulls were probably dispersed by physical agents. Virtual lack of postcranial material of the Yerrapalli capitosaurid led RoyChowdhury (1970a) to speculate that the carcass was scavenged by predators, which might also be the case for the other animals. The lighter postcranial materials were transported from the site while the large skulls, being the heavier part of these skeletons, could not move far and were buried with or without the lower jaws. The lower jaws were further fragmented through the symphyseal region in some cases. Being large and quite resistant, the lower jaws have high preservation potential; these were disarticulated probably due to intense postmortem activity (Holz and Barberena, 1994). Frequent findings of isolated lower jaws led Weigelt (1927) and Schaefer (1962) to suggest that the ligamentous connection with the skin tissue of the skull loosens in time in floating/resting carcasses, and these usually got disarticulated within 20 to 30 days provided the carcasses were not affected by biotic agents. The bone condition of these isolated skulls implies that the skeletons were exposed to the surface for a long time before burial. The flattened condition of the skull roof of the Yerrapalli capitosaurid as well as the individual skull elements indicate that these were fragmented along the sutures probably due to overburden pressure after the burial.

3.6. Type F: isolated skeletal fragments of different animals

Fragmentary bones are common to all the vertebrate producing horizons of the Indian Gondwana basins. Of these, bone fragments from the Early Triassic Panchet Formation of the Damodar basin have important taphonomic connotations.

The Panchet mudstones yield only reptilian bones (Table 5), whereas reptilian as well as amphibian bones are found in the sandstones. The fossils preserved in Panchet sandstones are essentially “channel lags” (sensu Behrensmeyer, 1988) comprising both fragmentary cranial and postcranial material sorted due to hydraulic action and winnowing (Behrensmeyer, 1991). However, these fragments occur throughout the sandbodies and are particularly concentrated in the pockets along with coarser grains and

clasts. The areal distribution of these bone fragments and the exact percentage of different bones of particular animals are difficult to calculate.

Among the bone fragments in the Panchet sandstone, the larger ones (> 5 cm) belong to reptilians, whereas the smaller (< 5 cm), which constitutes the majority of the fragments, are mostly amphibians. Of the smaller-size group, two types of bone fragments occur in two different modes. One has a longer axis that is either tabular or cylindrical and the other is spherical or a shorter cylindrical form. The modal length of the specimens is around 1.5 cm. The vertebral elements of dicynodonts (*Lystrosaurus*) and the post glenoid mandibular part of the temnospondyls occur in this size and shape range.

3.6.1. Interpretation

Disarticulated fragmentary bones indicate a long postmortem-preburial period. It can be interpreted that these Panchet vertebrates suffered death due to severe flooding and the carcasses of different animals were transported together for a while. With the recession of flood, the small amphibians as well as the reptiles were de-fleshed and disarticulated due to long exposure in a subaerial environment. Bones of small animals mostly disintegrate faster than those of larger animals (Behrensmeyer, 1978). Scavengers also play an important role in such high degree breakage (Bown and Krauss, 1981). These small fragments were later transported either due to water movement in the channel or later floods, and finally buried in the channel sediments.

4. Concluding remarks

Among the Indian Gondwana basins, the Pranhita–Godavari can be identified as the most important for fossil vertebrates in several respects. First, a complete succession is present in this basin from Permian to Early Jurassic (Fig. 2). Secondly, at least five vertebrate-bearing formations have been identified. Thirdly, maximum taphonomic information is available from this Gondwana basin, although taphonomic data from all the horizons or all the faunal associations (e.g., association of fishes, turtle and crocodile from the limestone of the Kota Formation or the screen washed micromammals from the mud-

stone) are still awaited. The other Gondwana basins provide comparatively less information on the palaeo-communities and less taphonomic data.

Meandering rivers with large floodplains and cyclic flooding perhaps due to heavy rainfall, and alternating dry and humid conditions are common climatic conditions in the Triassic and Jurassic of Gondwana. Depending upon such climatic conditions, most of the animals of the palaeo-community, especially the lowland vertebrates, were forced to migrate. After a flood some animals might have tried to migrate for food or for a more habitable environment, which could easily have resulted in their becoming trapped in mud.

Most of the vertebrate bones are found in the red mudstones, which are indicative of well-drained and well-aerated floodplain deposits (Behrensmeyer and Hook, 1992). The red mudstones are interstratified with thin sandstone bodies and smaller lenses of calcirudite/calcarenite, which can probably be interpreted as crevasse-splay and reworked paleosol deposits. Fossil occurrences are rather scarce in the large channel sandbodies but sparingly occur in small lenticular channel fill bodies encased in the pervasive floodplain deposit. These smaller bodies presumably represent deposits of smaller second order channels draining the floodplains.

Bone accumulations occur in the “channel-fill” mode (bones occurring in fine grained to mixed fills of abandoned channels) and in a “channel-lag” preservation (in coarse sediments near the bases of active channels) though the majority of the bone accumulations are found in between the two modes (*sensu* Behrensmeyer, 1988). In the “channel-fill” mode, bones are mostly autochthonous to para-autochthonous with respect to local channels which are abandoned, having been subject to sporadic, waning flow with minor reworking of bank and bedload sediments. The bone accumulations in the “channel-lag” are allochthonous representing large areas of drainage system; the related channels represent active drainages with recurring energetic flow and reworking of banks and bedload deposits.

Six taphonomic types (Table 6) ranging from extremely well preserved, complete, articulated skeleton to scattered, isolated, fragmentary bones have been identified in Indian Gondwana basins. Of these, the articulated to semi-articulated skeletons of Type A are rare and it is quite possible that the skeletons of the

individuals were buried quickly with a minimum time interval between death and burial. Disarticulated skeletal assemblages of a large number of monospecific individuals of Type B indicate mass mortality probably due to some catastrophic event, and the time interval between death, dismemberment and burial must be longer than Type A. The “log jam association” of the dinosaur bones of Type C is a special case which indicates obstruction of transported skeletons by logs and suggests a considerable gap between death and burial. The occurrences of disarticulated and dispersed skeletal parts of small mixed individuals of Type D also indicates group-death, but the time interval between death and burial is more or less the same as that of Type B. Skeletal assemblage of isolated single individuals of Type E represents the attritional death assemblage. Type F, which is characterized by fragmentary isolated bones was quite common in almost all the vertebrate-bearing horizons and it is likely that such carcasses witnessed more than one flood event with very long surface exposure.

From the analysis of the above six taphonomic types, it is evident that apart from natural death, mortality rate became higher seasonally during repeated flood events; the carcasses were transported and deposited later while some of the animals which could survive floods bogged in the muddy substrate. Death of animals due to severe aridity is not yet recorded from the Indian Gondwana sediments.

Finally, it can be said that at present only six taphonomic types of fossil skeletal assemblages have been identified from the Indian Gondwana scenario. It is expected that more information will be forthcoming from the rest of the vertebrate-bearing horizons and the number of taphonomic types of vertebrate assemblages will increase in the future.

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