Status of taphonomical studies in India: A review

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Taphonomy, a sub-branch of palaeontology, is defined as the study of the sequence of events beginning with the death of an organism and its subsequent deposition and fossilization. The present paper outlines important areas in which the work has been done on this subject and also attempts to review the Indian contributions.

The conditions of the burial and the preservation of nests and eggshell fragments of dinosaurs provide ample for taphonomic analysis. There is a need for experimental study on dispersal, disintegration, preservation and diagenesis of organic fossils. In puts from sedimentology are essential and only an interdisciplinary effort can result in any success to build the postmortem history of plants and animals.

Key-words— Palaeontology, Tophonomy, Fossilization.

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साराँश

भारत में जैवसादिकीय अध्ययन की स्थिति : एक समीक्षा

अशोक साहनी एवं असित जौली

जैवसादिकी, जो कि पुराजन्तुविज्ञान की एक शाखा है, में किसी जन्तु अथवा पौधे की मृत्यु से लेकर उसके परिरक्षण एवं अश्मन तक के घटना-क्रमों का अध्ययन किया जाता है। प्रस्तुत शोध-पत्र में इस विषय पर जो मुख्य-मुख्य शोध कार्य किये गये हैं पर प्रकाश डाला गया है तथा भारतीय योगदान की समीक्षा का प्रयास किया गया है।

डाइनोसोरो के अंडों के बाह्य आवरणों एवं अंडे रखने के स्थानों की परिस्थिति जैवसादिकीय विश्लेषण के लिए महत्वपूर्ण है। इस बारे में कार्बनिक जीवाश्मों के विकीरण, परिरक्षण एवं प्रसंघनन हेतु प्रायोगिक अध्ययन की आवश्यकता है। इसके लिए अवसादिकीय आँकड़े अति आवशयक हैं तथा अन्तर-विषयक प्रयासों से ही पौधों और जन्तुओं के जैवसादिकीय इतिहास की रचना की जा सकती है।

THE Golden Jubilee Celebrations of the Birbal Sahni Institute of Palaeobotany are almost coincident with another major event in the world of Palaeontology, namely the publication of the first monograph on Taphonomy by Efremov in 1940, who defined this sub-branch of palaeontology as the study of the sequence of events beginning with the death of an organism and its subsequent deposition and fossilization".

Taphonomy, as its Greek derived name implies, concerns the "Laws of burial' in the stricter sense and encompasses, in the broader context, all the environmental factors that affect or constitute the death-burial-fossilization-discovery history of any organism or group of organisms, individually or collectively. The present paper attempts to review the meagre work carried out in this field in India and attempts at focussing on those areas where work is essential in order to properly interpret the palaeoecology and biostratigraphy of a region. Wherever possible, examples from Indian palaeontology have been used, and this perspective is obviously biased towards vertebrate palaeontology where most of the work to date has been carried out.

Taphonomy includes three major approaches to obtain a better understanding of its major goals. These include "Aktuo- palaeontologie" (actualistic palaeontology) palaeoecological and sedimentological studies; and experimental work relating to the burial and disintegration of an organism.

The term actuo-palaeontologie was proposed by Richter (1928) and can be defined as the science of origin and present-day mode of formation of future fossils in the broadest sense. This is basically an application of the Principle of Uniformitarianism to palaeontological problems and is virtually synonymous with the term "neontology". Taphonomy is considered to be one of the most important subdivisions of actualistic palaeontology and has been actively followed by the German School of palaeobiologists. Weigelt (1935) in a classic paper applied data obtained from present day biologic and sedimentologic study to the preservation of Eocene vertebrates. Interestingly, inferences regarding the habits of Jurassic Sauropod dinosaurs, believed to live in herds, have been based on facies and ecological similarities to herding behaviour of elelphants and rhinos even though there is no evolutionary relationship between the reptiles and the mammals in question (Dodson, 1973).

The proper understanding of palaeoecological and sedimentological processes is essential in deciphering taphonomic overprinting or biases. The palaeoecologist is usually confronted with an enormously greater record in terms of time and facies variation and most of this is full of biases introduced by natural processes involved in the burial process. In fact, nearly all the lifetime attributes of ancient organisms can be better understood with the prior knowledge of their post-mortem history (Lawrence, 1968). The extent to which taphonomic overprinting can be removed is directly proportional to the level of accuracy of making palaeoecologic, palaeobiogeographic and evolutionary interpretations. One rather extreme option to remove the taphonomic bias is to treat fossils as an integral part of the sediment (Hill & Walker, 1972) and wherever possible to calculate and extrapolate the hydraulic conditions needed for transport of the preserved organic material. However, there are obvious lacunae in this approach: for instance, this method does not allow for floating carcasses that may ultimately settle down in fine grained sediments. To reiterate, each case has to be studied in its own perspective.

PAST STUDIES

Several experimental studies were undertaken in the past for understanding the burial of vertebrates, plants and invertebrates. For vertebrates one of the primary concerns is the hydraulic character of various skeletal elements and the determination of the size, shape, and volume, and mass dependence in terms of transportability and durability. Experimentation has also been carried out towards establishing the effects of subaerial exposure and the time required for disarticulation, decomposition and destruction of a vertebrate carcass. In a classic field study, Behrensmeyer (1975) determined decomposition stages for Kenyan larger animals such as hippopotami, suids, bovids and then applied this data for the Plio-Pleistocene assemblages. She studied the characteristics of bones as sedimentary particles, computing for bone size and density, their relative dispersal potential and the hydraulic equivalence of bones and quartz grains of various sizes.

Experimentation is not only confined to field conditions but has been replicated in flume experiments in the laboratory. A good example of this is the work of Voorhies (1969) who determined the sequence of element transport based on the initial velocity required to transport bone. He used *Canis* and *Ovis* to arrive at the definition of three transport groups which give the transportability index of various elements of a vertebrate animal. Similarly, experiments were undertaken on the hydrodynamics of microvertebrates by Dodson (1973) and the effect of stream abrasion on small mammal bones using tumbling barrels (Korth, 1979). The striking preservational differences between transported and digested bones were highlighted by Mellet (1974) who suggested a radically different theory for the accumulation of microvertebrates involving faecal droppings (scat). Scatological origin for many small vertebrate bones (especially rodents) is not well established and can be observed in modern owl pellets.

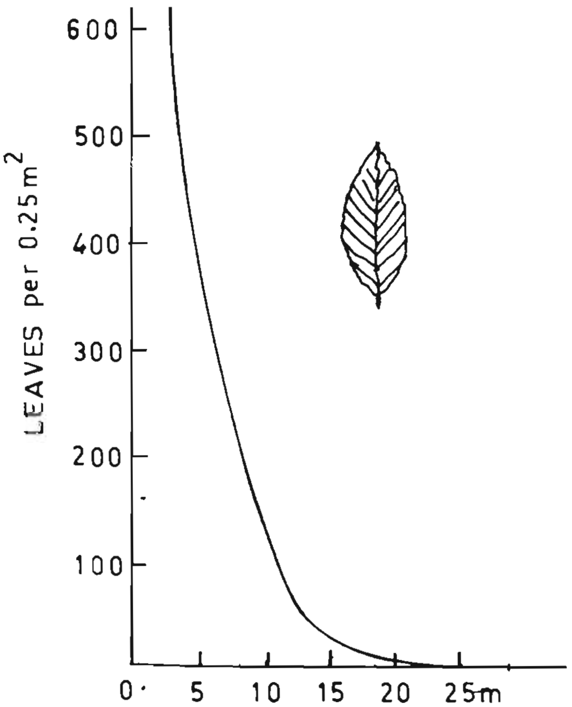
Field observations for "fossils in the making" have extended to defleshing studies of various carcasses of vertebrate animals defined by decomposition stages, 1-6, (Payne, 1965). He noticed a sharp difference of carcass defleshing: without insect activity (100 days) and with insect activity (8 days). Some semi-quantitative relations have also been suggested; Voorhies (1969) observed that decomposition rates are directly proportional to size and weight of the animal, while Johnson (1975) noted that decomposition was strongly temperature dependant. Korth (1979) noted for microvertebrates that four to fifth stage of decomposition lead to complete disarticulation and hence to transport as separate elements.

Relatively fewer studies have been conducted on an experimental basis on plant taphonomy. One of the most recent reviews in this context is the work of Ferguson (1985, 1993) who studied the dispersal of abcissed leaves and other plant material. He noted that the dispersal of plant material can be related to various factors including height of the source, the number of plants available for dissemination, the settling velocity of plant parts, the degree of exposure of source plants and the nature of terrain. He estimated that for a tree-canopy in a tropical and subtropical environment ranging in height from 20 to 60 m, leaves would be transported for less than 100 m from their source. However, storm conditions palpably alter these conditions and their quantitative control has yet to be effectively worked out. The distribution of leaves of *Carpinus betulus* is given in Text-figure 1.

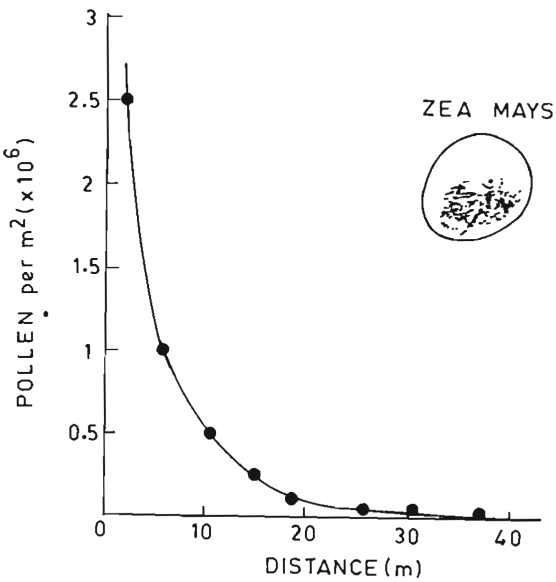
Pollen are relatively more widespread, largely because they are produced in greater numbers, may have evolved special structures to aid dispersal, and have low settling velocities. In one of the few quantitative studies on the subject, Raynor *et al.* (1972) illustrated the distribution of maize pollen away from its source (Text-figure 2).

The settling velocities of spores, pollen and unspecialized fruits and seeds are given in Text-figure 3 (after Ferguson, 1993). Leaves occupy an intermediate position between pollen and fruits.

Experiments have been undertaken to simulate specific conditions for the preservation of insects in lacustrine basins. A good example of this approach is the study by Martinez-Delclos and Martinell (1993). Tanks



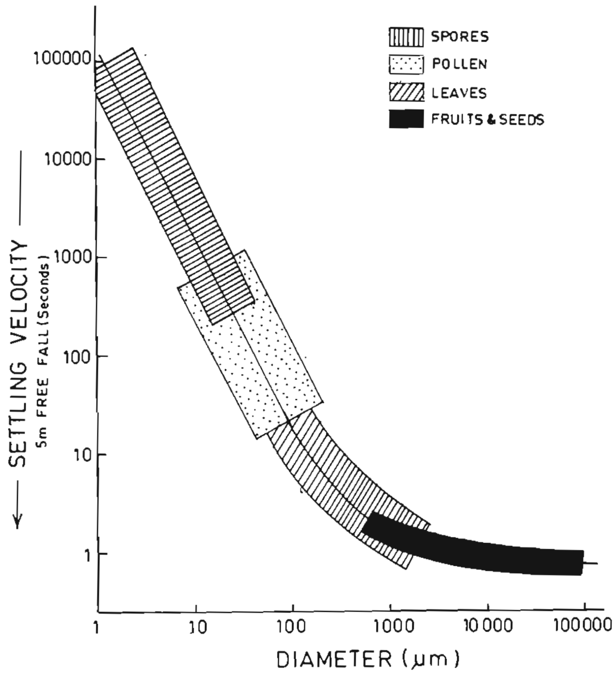
Text-figure 1 — Distribution of leaves in relation to distance from source (data and figure redrawn from Ferguson, 1985, 1993).



Text-figure 2 — Distribution of maize pollen from source (data and redrawn from Raynor *et al.*, 1972; Ferguson, 1993).

of 25 to 250 litres were specially constructed and filled with still, oxygenated freshwater to simulate lacustrine conditions. On death, terrestrial insects falling into water are usually incapacitated by the surface tension of water. Floating time naturally varies: in wasps, sinking usually takes place around the 10th day when they become fungus encompassed. In controlled conditions in the laboratory, insects that sink to the bottom can remain in an articulated condition for over one year. The Eocene fish and crabs from Bothia, described later on, are considered to have been buried under similar circumstances.

Taphonomy can be studied at various levels of organization ranging from the smallest (molecular) level to the level of the community and population (Taphonocoenose). At the molecular level, the preservation of organic matrix and soft parts is of great significance. It is now well established that besides exceptional preservation in resin and other deoxygenated materials, nucleic acids disintegrate with great rapidity and usually become un-indentifiable in two thousand years. Amino acids and lipids are more long-lived and may alter to more stabilized molecular structures. The best example of this is the conversion of the amino acid isoleucine to allisoleucine which is a left-handed molecule. Under constant temperature regimes, the con-



Text-figure 3 — Settling velocities of a variety of plant elements of different shapes, sizes and weights (based on the data of Ferguson, 1993 and modified accordingly).

version takes place at a constant rate and this allows for the age determination of parent organisms (Goodfriend, 1992). Syngenetic and early post-mortem diagenesis and phosphatization of soft tissue and foraminiferal shells have also been documented (Soudry, 1993). The largest number of taphonomic studies have been directed towards the individual level of organization. Those at the death assemblage level have usually been included in palaeoecological studies and provide important information of living habitats of the organisms and the transport history in case the taphnocoenose do not correspond to the biocoenose.

TAPHONOMICAL STUDIES IN INDIA

At present there are only a handful of papers dealing with the important subject of taphonomy in India. One of the first such studies was that of Badam *et al.* (1986). In this preliminary treatment of the taphonomy of the Pleistocene vertebrate faunas from central Narbada, an attempt was made to analyse the effects of scavenging, hydraulic sorting and disintegration due to subaerial exposure. Other works such as that of Bandopadhyay (1985) have tried to work out the taphonomy of Gondwana dicynodont reptiles from the Yerrapalli Formation but have really not provided a systematic basis for most of the conclusions drawn. The same applies for the Upper Siwalik faunas recovered from northeast of Chandigarh (Gaur, 1981; Gaur & Chopra, 1984). In the latter work, no attempt was made to reconstruct burial conditions, and most of the analysis has been carried out on the basis of palaeoecological parameters.

The taphonomy of Late Cretaceous dinosaur nesting sites in the central Indian localities along the Narbada River at Jabalpur and near Hathni, has recently been carried out (Jolly *et al.*, 1990; Sahni *et al.*, 1994; Sahni & Khosla, 1994). Recently, Sahni and Jolly (1993) have attempted a more detailed account of the accumulation and burial of the Middle Eocene mammalian assemblage at Sindkhatuti, represented by the Kalakot Zone of the Upper Subathu Formation, this study will be elaborated later in this paper.The only systematic work dealing with the taphonomy of plant material is the study by Tiwari *et al.* (1994). These authors have tried to account for the preservation of spores and pollen in various Phanerozoic sediments of the Gondwanas and Tethys Himalaya. The main focus of this paper is to document the early and late diagenetic stages which result in pronounced colour changes and microbial degradation of the exine. It is speculated that the pollen grains recovered from the Early Cretaceous Rajmahal pollen have been thermally degraded but no experimental demonstration of this relationship has been documented.

CASE HISTORIES

Some specific examples of case histories on the taphonomy of dinosaur nesting sites and Eocene mammals and other lagerstätten will be briefly discussed. It is beyond the scope of this paper to go into the details of each assemblage which have already been published: the taphonomy of dinosaur eggs and nesting sites (Jolly *et al.*, 1990; Sahni *et al.*, 1994; Sahni & Khosla, 1994), and the Sindkhatuti mammal assemblage of the Middle Eocene Kalakot Zone, Kashmir (Sahni & Jolly, 1993).

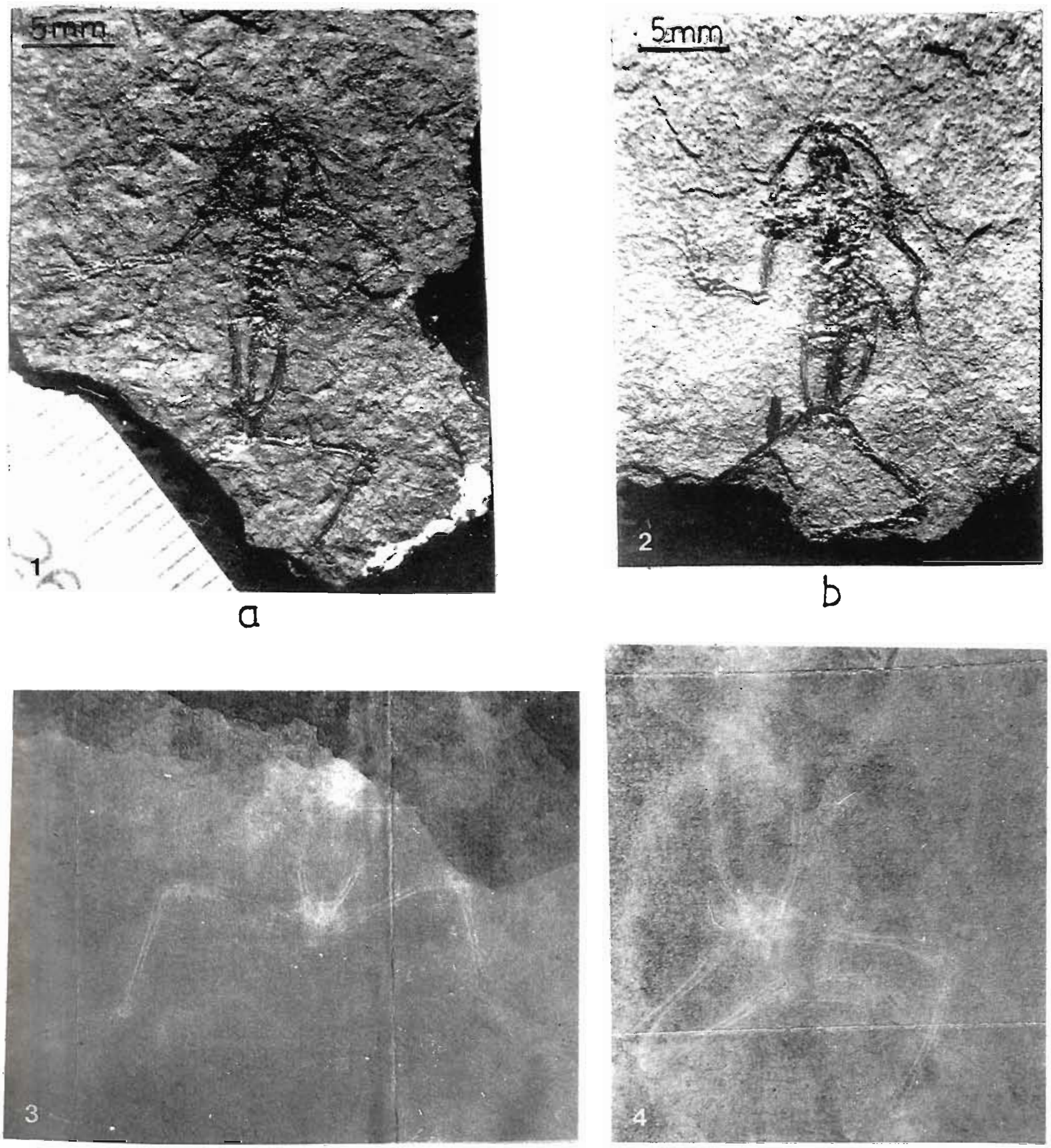


PLATE 1

1, 2. Fossil frogs from the Bombay intertrappeans (specimens courtesy of S. Singh, 1995). 3,4. X-ray micrographs illustrating skeletal outlines of the frogs.

Assemblages associated with the Deccan volcano-sedimentary sequences

The dinosaur (sauropod) nesting sites of the Late Cretaceous Lameta Formation are well known and have excited interest, as these are one of the most extensive nesting sites recorded to date extending over 10,000 sq km in discontinuous outcrops; they are specific to a particular lithology, i.e., a sandy carbonate bed which shows characteristic pedogenic features and contain nests with eggs varying in number from 3 to 13.

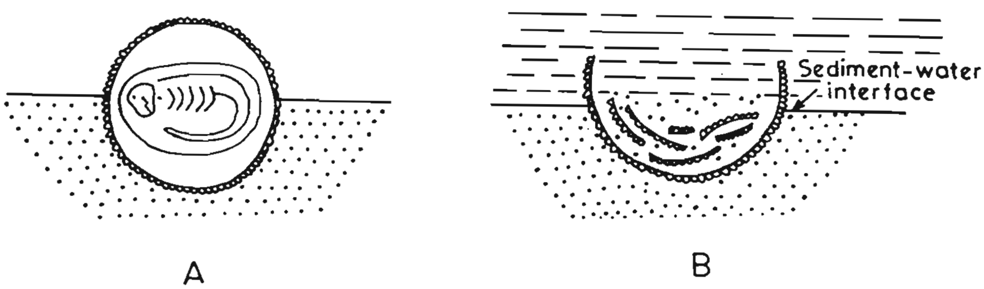
Taphonomic analyses have been directed towards understanding the conditions of the burial and preservation of nests and eggshell fragments. The eggs are believed to have been preserved by rapid matrix cementation in mainly arenaceous fluvial sediments in which they were laid down (Jolly *et al.*, 1990; Sahni *et al.*, 1994). This process involves the burial and preservation of eggs (usually with thick calcified shells (1-3 mm) in palaeosols undergoing calcretization and being wetted by episodic sheetwash flooding. Recently, Sahni and Khosla (1994) have recorded collapse structures in eggs. The collapse structures are represented by concentric arrangement of egg-shell fragments after breakage and fracture of the egg-shell. The collapse structures are believed to have formed during the burial process as the eggs were submerged by a sheetwash event leading to the death of the embryo. Chips of the broken shell gravitated downwards in a wet muddy medium (Text-figure 4). The preservation of nests is in sharp contrast to the accumulation of eggshell fragments which are considered to be largely transported material. The preservation of the Lameta Formation itself can be ascribed to the sudden blanketing by the Deccan Basalts and its continuous unroofing during Tertiary (Text-figure 5). The preservation of Lameta dinosaurian nesting sites is mainly conincidental on the fact that the thin Lametas are exposed in discontinuous patches, wherever the overlying basalts have been eroded away. This is particularly true of areas where rivers such as the Narbada, have incised their way into basement rock.

Though poorly studied as yet, the taphonomy of the Bombay intertrappean frog beds offers interesting possibilities on the influence of volcanic eruptions and episodic mass mortality events. X-ray micrographs (Pl. 1, figs 3,4) offer another technique for determining the orientation of delicate bones without disturbing matrix. Singh (1995) attempted to relate mass burial events of frogs (Pl. 1, figs 1, 2) found on the same bedding plane to episodic eruptions and input of pyroclastics from nearby volcanic source.

Eocene Lagerstätten and mammalian assemblages

Lagerstätten constitute exceptionally well preserved biotas and the assemblages from the Fuller's Earth (Lower Eocene) sequences of Rajasthan are testimony of these biotas which are preserved in a fine-grained calcareous mud of a lagoon. Similar basinal environments are well known in other localities, such as the classic Solenhofen Limestone. The preservation of these biotas suggests accumulation in calm, still lagoons with a minimum of bacterial activity. However, the disruption of the scales of the fish–*Eoluvarus* and the associated presence of small crabs (Pl. 2, fig. 1) are quite interesting.

The taphonomy of an Middle Eocene mammalian assemblage from the topmost member of the Subathu Group at Kalakot has been worked out in respect to several factors including hydraulic properties of sediment (quartz grain-size equivalents, minimum number of individuals, frequency of occurrence of individual skeletal elements, Voorhies Transport Groupings, orien-



Text-figure 4 — Collapsed structures in Late Cretaceous dinosaur eggs from Lameta Formation of India. **A**, Egg with embryo; **B**, Egg collapses as water from a sheet flood event prevents oxygen interchange leading to the death of the embryo. Shell fragments gravitate to the bottom.

tation of long bone axes in oriented blocks (Pl. 2, fig. 2), body size distribution of the recovered mammals at Sindkhatuti (Text-figure 6) and other factors related to sedimentological conditions. It has been proposed that the Sindkhatuti mammal assemblage was exposed to subaerial weathering before being covered by silts of a flood event. During still stand, an ash fall occurred. The fish component associated with the mammalian remains was probably introduced at this time as the analysis of the sediment grain-size coefficient corresponds to the quartz grain-size equivalent of the fish skeletal elements. Scales of the osteoglossid fishes obtained from this horizon have Liliaceae pollen entrapped in their pore spaces (Pl. 2, figs 3, 4).

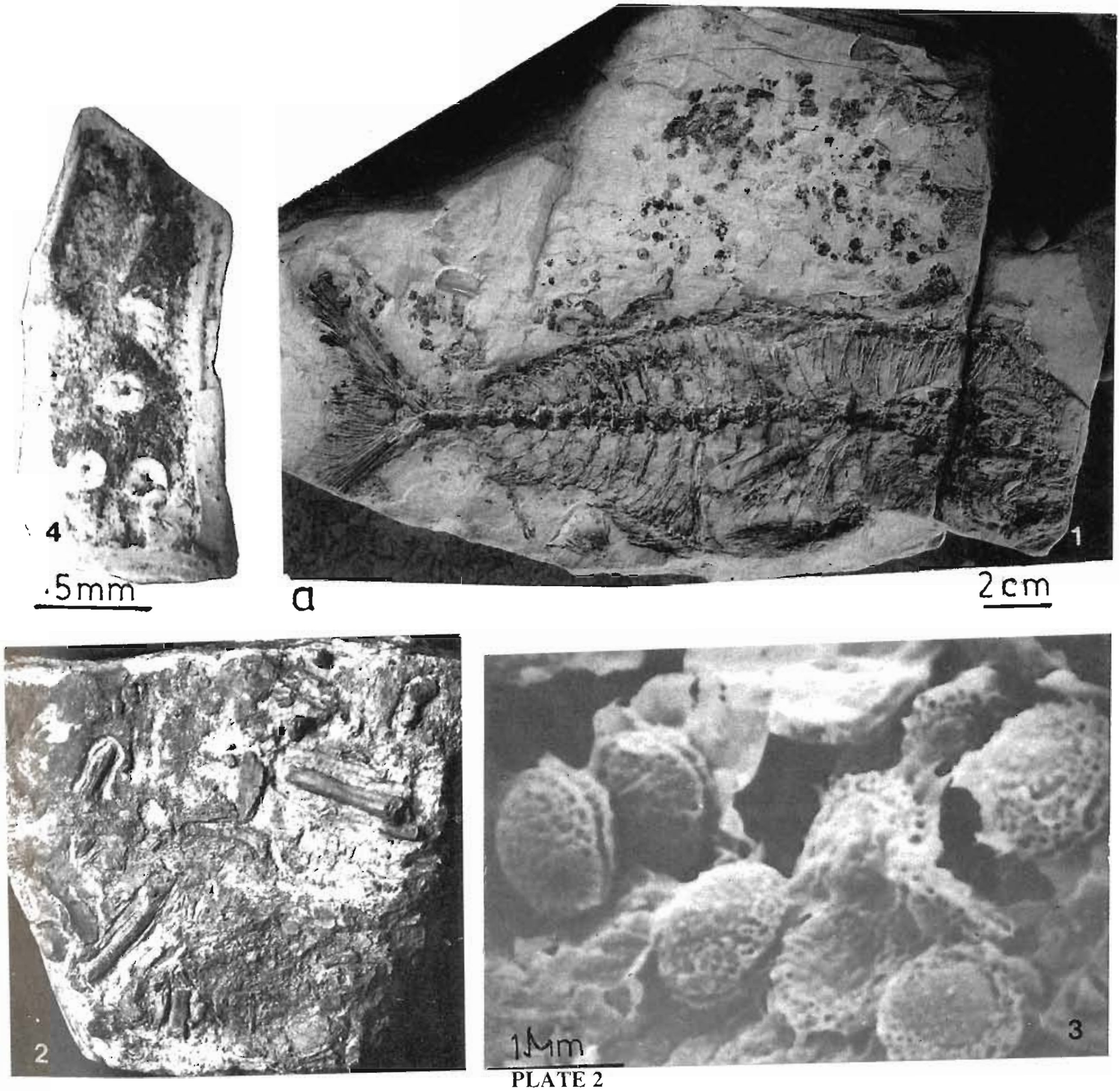
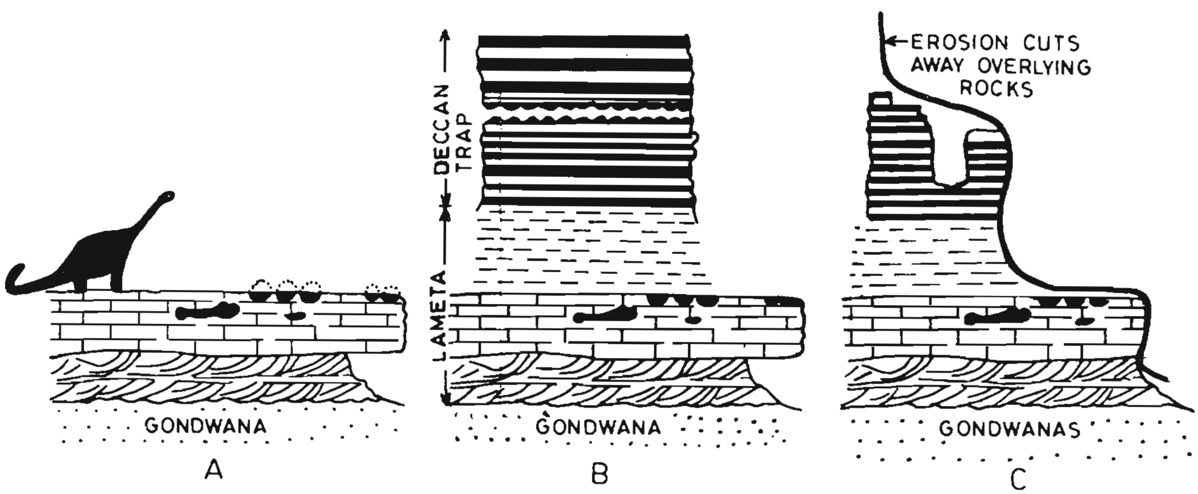


PLATE 2

1. Fossil fish in the Lower Eocene Fuller's Earth deposits of Rajasthan Note the disarticulated scales of fish and small crabs around the specimen

2 Bone-bearing block from Sindkhatuti, Kalakot showing lack of preferred orientation for the long bones

3, 4 Osteoglossid scale with Liliaceae pollen filling some of the pores.



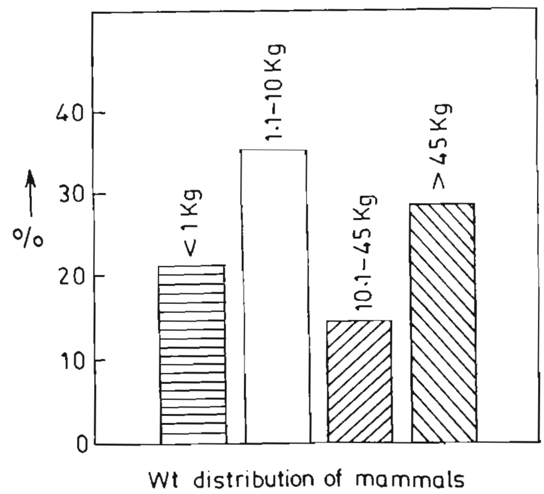
Text-figure 5 — Sequence of events leading to the burial and discovery of the Lameta dinosaur nesting sites. A, Burial of eggs and nests in a pedogenically modified sandy carbonate horizon represented by alluvial plain sediments of a semi-arid region. B, Sudden blanketing of the egg-bearing horizon by Deccan basalts. C, Unroofing of the basalt through erosion extending 65 million years of time. The sandy carbonate bed stands out in relief as it is resistant to weathering.

Withdrawal of flood waters led to further exposure, desiccation, incipient soil formation with the development of calcareous nodules, and subsequent re-flooding. It is believed that the highly site selective occurrence of the mammals whereby some localities are dominated by medium-sized artiodactyls and others by larger rhinoceratoids suggests catastrophic mass mortality by a flood event. This hypothesis is also borne out by the unusually high occurrence of young individuals identified by the common presence of deciduous dentitions in the large collection of teeth and bones recovered by screen washing (Sahni & Jolly, 1993).

In an interesting and pioneering contribution to aktuo-palaeontologie, Singh (1978) documented lebensspuren (recent tracks, trials and burrows) on the braid bars of Ganga River near Kanpur and Allahabad. He described the traces made by lamellibranchs, crabs, insects and earthworms. Such studies serve a useful purpose in understanding ichnofossils and need to be pursued vigorously.

CONCLUSIONS

Taphonomic studies are an integral part of palaeontological studies but have not been given their due status in India. The burial and post-mortem conditions reveal important details of the living habits of the organisms and the depositional conditions prevailing in the basin. Inputs from sedimentology are essential and only an interdisciplinary effort can result in any success. So far, there are very few studies related to marine invertebrate



Text-figure 6 — Percentage weight distribution of mammals in the Sindkhatuti mammal assemblage, Kalakot Zone, Subathu Formation, Middle Eocene, Jammu and Kashmir.

taphonomy and there is hardly any data on aktuopalaeontolgie in spite of a variety of recent basinal environments in the country. Although several studies have described ichnofossils in the fossil record, there is hardly any documentation of this activity in recent rivers, lakes, mud flats and other accessible areas of study. An interdisciplinary effort is essential to identify problems in taphonomy and to develop models for the burial and preservation of fossil biotas.

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