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# Dinosaur coprolites from the Late Cretaceous (Maastrichtian) Lameta Formation of India: isotopic and other markers suggesting a C<sub>3</sub> plant diet

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## Abstract

A single locality of the Late Cretaceous (Maastrichtian) Lameta Formation at Pisdura in Central India has yielded a large number of coprolites attributed to titanosaurian dinosaurs. Internally the coprolites are dark grey and contain abundant plant tissues and other organic materials. The plant tissues are mostly of gymnospermous origin. In addition, remains of bacterial colonies, fungal spores and algae are seen in the macerated fraction under scanning electron microscope. The dark grey appearance is probably attributable to fine-grained organic matter within voids in tracheids or xylem. The average <sup>13</sup>C/<sup>12</sup>C ratio of the organic matter in the coprolites is -24‰ (relative to PDB) suggesting that plants of C<sub>3</sub> type were the main diet of their producers. A comparison of δ<sup>15</sup>N value (about 4‰ w.r.t. air) of the coprolites with that of faecal matter of modern herbivores and carnivores suggests that gut fermentation may not have been an active mechanism in the digestion process of titanosaurs.

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*Keywords:* coprolites; gut fermentation; stable isotopes

## 1. Introduction

Stable carbon and nitrogen isotopes in fossilized remains of animals can provide a valuable insight into their diet and the environment in which they lived (Ostrom and Fry, 1993; Koch et al., 1994; Koch, 1998). In particular, fossil faeces (coprolites) provide unique trophic perspectives on ancient ecosystems (Hollocher et al., 2001) as they represent fossilized residues from the digestive tract of animals. Since the stable isotope ratio of organic carbon in excreta closely represents the average composition of food sources it may be used to determine the relative amount of C<sub>3</sub> and C<sub>4</sub> plants in an

animal's diet (Vogel, 1978; DeNiro and Epstein, 1978; van der Merwe, 1986; Lee-Thorp et al., 1989). There is also a direct relationship between the trophic level and the nitrogen isotopic composition of the organic fraction (Minagawa and Wada, 1984; Sealy et al., 1987). This is mainly due to preferential catabolism and excretion of the lighter <sup>14</sup>N, resulting in an increase of δ<sup>15</sup>N values by approximately 3–5‰ for each trophic transfer along the food chain (Peterson and Fry, 1987). However, to decipher palaeo-diet a clear understanding of the isotopic fractionation in the biomineral is required and knowledge of the stable isotope ecology and bio-physiology of the extinct animal is needed.

Cretaceous strata in central India containing fluvial sediments known as the Lameta Formation include rich deposits of dinosaur fossils, among which are skeletons and eggs that have been investigated for physiological

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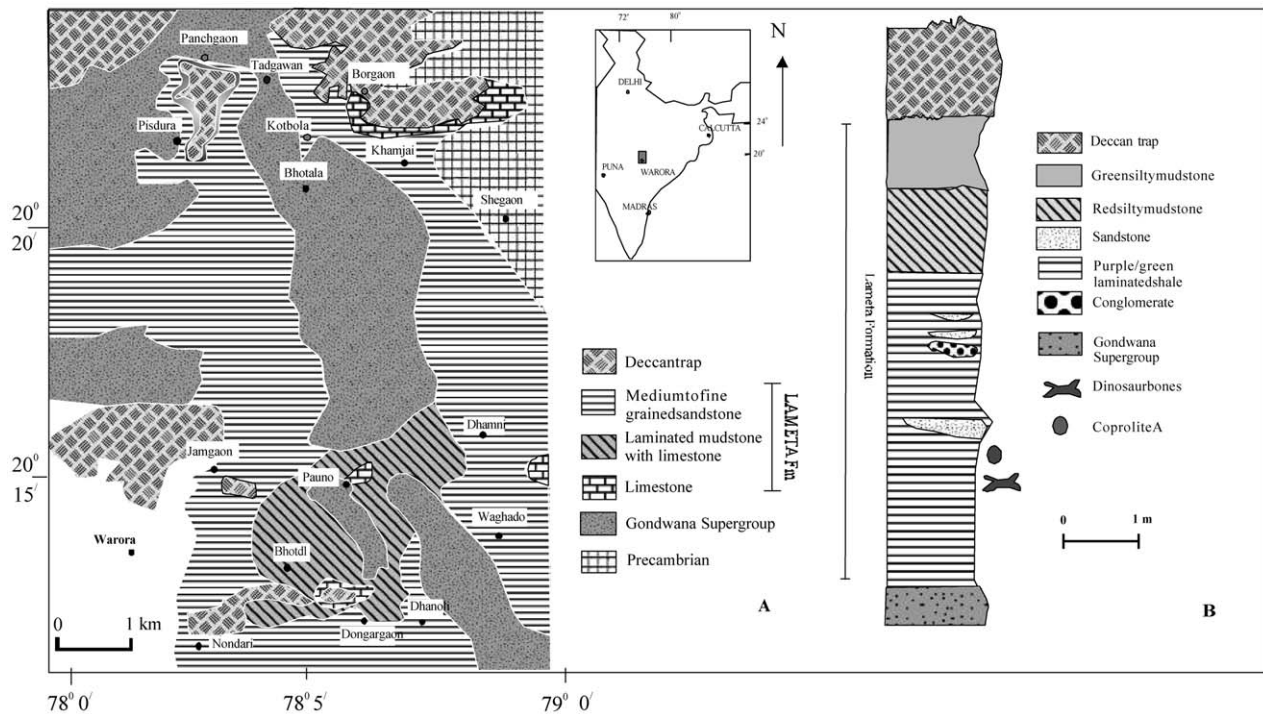


Fig. 1. A, geological map of central India showing distribution of Lameta Formation and the localities of Pisidura and Dongargaon. B, section showing location of coprolites in the stratigraphic profile.

and morphological features (Mohabey et al., 1993; Sahni et al., 1994, 1996; Mahabey, 2001; Tandon and Andrews, 2001). The carbonate-rich Lameta deposits are often capped by hard Deccan lava which helped to preserve the dinosaurian fossils (Sahni et al., 1994; Tandon and Andrews, 2001). The age of Lameta Formation is Maastrichtian, based on the presence of remains of microvertebrates and other microfossil assemblages, palynostratigraphy, magnetostratigraphy and its field relationship with the Deccan Traps and associated inter-trappean sedimentary beds (Mohabey, et al., 1993; Sahni et al., 1994; Dogra et al., 1994, Hansen et al., 1996; Mohabey, 1996). Sarkar et al. (1991) analysed the stable isotope ratio of the carbonate phase of the dinosaurian egg shells obtained from the Lameta Formation of the Rahioli area of Gujarat and inferred a  $C_3$  plant diet for their producers. Matley (1939) was the first to describe a rich collection of coprolite segments from the Lameta Formation in the Pisidura area. A few coprolite fossils from this area have been compared with herbivorous dinosaur dung from the Two Medicine Formation of Montana (Chin, 1991; Hunt et al., 1992). The occurrence of Pisidura coprolites is restricted mainly to surface exposures where they occur as loose fragments except in a few cases where they are found embedded within the host rock (Matley, 1939). They are often associated with fossils of titanosaurs, pelomedusid turtle bones and non-marine molluscs. For the present paper, coprolite specimens

were collected from the Lameta sediments exposed near Pisidura and Nand-Dongargaon in central India (Fig. 1). Based on the size, shape, ornamentation and appearance, they were classified into four types by Matley (1939). Of these: (1) Type-A coprolites are large (up to 100 mm in diameter) and have a smooth surface without ornamentation; (2) Type-B (up to 64 mm in diameter) have a ribbed external surface; (3) Type-Ba are small (up to 25 mm in diameter) with a ribbed surface, and are coiled; (4) Type-C are small (20–25 mm diameter) with a smooth surface. Matley attributed the Type-A coprolites to titanosaurs on the basis of their large size and co-occurrence with skeletal remains of these dinosaurs. No evidence of the herbivore nature of their producers could be ascertained as the coprolite contents were reported to be unfossiliferous (Matley, 1939). However, recent work (Mohabey, 2001) on large number of Type-A coprolites has shown that they are enriched in plant tissues and other organic debris. Some of these were examined in the present study to characterise the carbon isotopic composition of organic residue and to identify the diet of the coprolite producers.

## 2. Geological background and environment of deposition

The coprolite-bearing Late Cretaceous (Maastrichtian) Lameta Formation in the Pisidura-Dongargaon area rests unconformably on Precambrian basement or

Palaeozoic-Mesozoic sedimentary formations belonging to the Gondwana Supergroup, and is overlain by the Deccan volcanic sequence. The Lameta strata are conventionally considered as fluvio-lacustrine deposits (Hislop, 1859; Medlicot, 1872; Von Huene and Matley, 1933). However, a marine origin in places has been advocated based on the presence of fossil fishes such as *Apateodus striatus*, *Stephnodus libiscus* and *Igdabatis*, which are thought to indicate oceanic incursions during deposition of the sediments (Jain and Sahni, 1983; Sahni 1984). Mohabey and co-workers have undertaken detailed litho- and biofacies analysis of the sedimentary deposits in the Pisdura-Dongargaon area (Mohabey et al., 1993; Mohabey, 1996). Based on their study, an alluvial-limnic environment of deposition under semi-arid conditions was inferred for the Lameta Formation. They identified several distinctive subenvironments of deposition, including overbank, channel, paludal and lacustrine (Mohabey et al., 1993), and suggested that the sediments were pedogenically modified. Titanosaur skeletal remains, eggs and nests are well known in the Pisdura-Dongargaon area (Von Huene and Matley, 1933; Mohabey, 1996, 2001). In the Pisdura section, located nearly 13 km NNE of Warora (Fig. 1A), the Lameta formation comprises basal overbank red silty clays (Fig. 1B) associated with lenses and thin partings of planar and cross-bedded sandstone of lateral accretion type (Mohabey et al., 1993; Mohabey, 2001) and intercalated with thin (<20 cm thick) limey bands, paludal grey marl and laminated green and purple shales. The red clay becomes greenish and less silty towards the top and are capped by Deccan basalts. At this location all four types of coprolite are found in the limey bands within the red clays. The coprolites are associated with reworked skeletal remains of titanosaurs, pelomedusid turtles and well-preserved shells of the gastropod *Physa* and the bivalve *Unio*. The coprolite-bearing limey layer becomes exposed during the course of tilling of the fields and consequently a large number of coprolites appear on the surface (Mohabey, 2001). They show clear desiccation features, indicating that they were subaerially exposed for some time before being reworked and washed as float into the low lying area of the flood-plain. Diverse types of coprolite (Fig. 2) along with reworked and weathered titanosaurid skeletal remains occur as discrete objects in the overbank red silty clays exposed in the fields, a condition similar to that observed elsewhere during dinosaurian coprolite deposition (Thulborn, 1991). The association of coprolites with titanosaur and chelonia (pelomedusid) skeletal remains provides indirect evidence that the coprolite producers were titanosaurs and roamed near a 'marginal marine' environment. A large A-Type coprolite about 10 cm long was chosen for our study (Fig. 2). It contains black organic matter and fragments (1–2 cm) of plant tissues with an out-

side surface that was probably modified by beetles (Fig. 3).

### 3. Experimental methods

Particulate black organic matter from pieces of coprolite were isolated from the sample to avoid contamination from soil and modern organic matter (OM) attached to the outer surface. The carbonate matrix was dissolved in a 6M hydrochloric acid solution at room temperature; the resultant solution contained a suspension of OM and silt. The OM was separated by centrifuging the aqueous solution. The organic fraction, being hydrophobic, was separated by decantation. The residue was cleaned repeatedly (four times) with distilled water to remove the water-soluble fraction. The residual material was de-mineralized further using 50% HF at room temperature, first for 15 hours and then for another 3 hours. The excess HF and calcium and magnesium fluorides were removed by washing the residue with dilute HCl and then with distilled water. The material was dried at 40°C and stored in vials. The study was motivated by the assumption that a comparison of the carbon and nitrogen isotopic composition of organic residues from coprolite remains with those of faeces of living birds, reptiles and mammals might provide interesting information about dinosaur diet, and improve our understanding of the palaeobiology of these extinct animals, and lead to an appreciation of the trophic level of titanosaurs in the food web. Hence, we collected samples of faeces of several modern species from Ahmedabad zoo. While sampling, adequate care was taken to avoid risk of contamination from urine. Such a precaution is necessary since animal flesh and faeces are enriched in  $^{15}\text{N}$  compared to the diet while urinary nitrogen (both  $\text{NH}_3$  and urea) is depleted in  $^{15}\text{N}$  (Peterson and Fry, 1987). Each of these samples was treated separately to avoid any cross-contamination. They were dried at 50–60°C with an infrared lamp, and dried samples were crushed into powder for isotopic analysis.

Coprolite fragments belonging to the category of large A-type were examined under a scanning electron microscope (SEM: JEOL JSM 25S) and the images were recorded on Polaroid film. The coprolite samples were disintegrated using 1M sodium ethylenediaminetetraacetate (EDTA) at a pH of 10 and several components were isolated after dispersion of disintegrated material in water. Individual fractions were examined to identify capillary cores of xylem, woody tissue, and pollen.

In order to determine the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the organic fraction, samples were loaded in a 10-cm-long quartz break seal tube along with CuO (wire form) and an Ag strip. The quartz tube was evacuated, sealed and combusted at 700°C for six hours. Evolved  $\text{CO}_2$  was

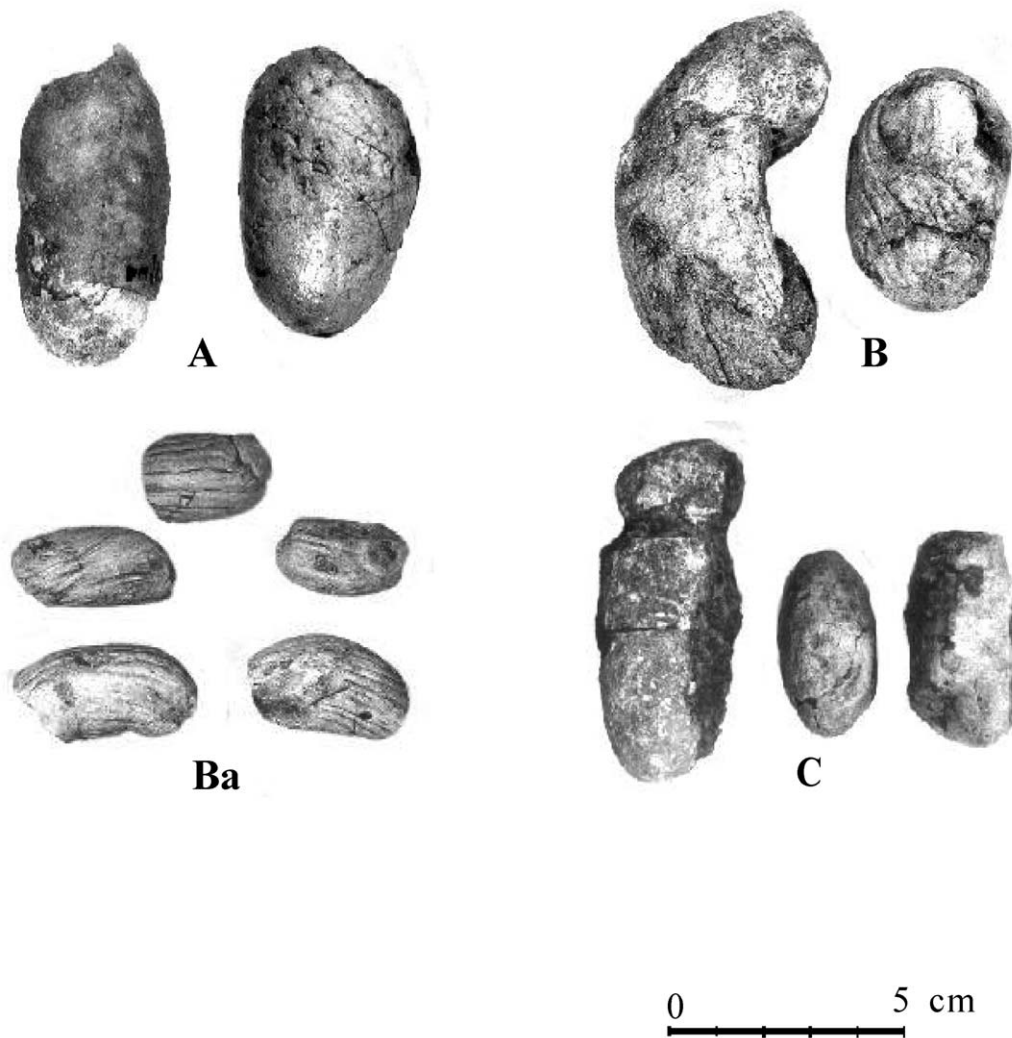


Fig. 2. A–D, four different classes of coprolite, Types A, B, Ba and C, respectively, collected from Pisdura. The Type-A specimens were used for isotopic analyses.

purified and separated for analysis using a GEO 20-20 mass spectrometer. The reproducibility of measurements was determined by analysing the PRL laboratory standard UCLA glucose ( $\delta^{13}\text{C} = -9.9\text{‰}$  relative to PDB) along with each set of samples. Details of the procedure are given in Ghosh et al. (2001). Some of the samples were re-analysed to check the reproducibility of measurements. In a separate experiment,  $\delta^{15}\text{N}$  of the organic residue was measured. Residual matter was combusted at  $850^\circ\text{C}$  in the presence of  $\text{CuO}$ , silver chips (to remove  $\text{SO}_2$  evolved from sulphur compounds), and a few pieces of high-purity thin Cu wire in an evacuated quartz tube.  $\text{CO}_2$  and  $\text{N}_2$  evolved during combustion were separated cryogenically in a glass vacuum line.  $\text{N}_2$  was further purified by passing through a U tube containing Cu wire at  $650^\circ\text{C}$  and collected in the sample bottles containing a molecular sieve. The IAEA N-2 standard  $[(\text{NH}_4)_2\text{SO}_4]$  was analysed as the international reference standard ( $\delta^{15}\text{N}$  of IAEA N-2 is 20.85‰ with

respect to air nitrogen). Isotopic ratios of carbon and nitrogen are presented in the usual  $\delta$  notation in units of per mil (‰) with respect to the international standard V-PDB and air-nitrogen respectively, and are reproducible within  $\pm 0.1\text{‰}$  and  $\sim 0.3\text{‰}$  at  $1\sigma$  level.

#### 4. Composition

Most of the coprolite specimens comprise clays that are either silicified or micritised. A few were found to be enveloped by a 0.5–1-mm-thick ferruginous or calcite coating. The samples investigated were found to be phosphate-rich (23 wt.%). Red clay particles were often found adhering to the surface of the specimens or inside shrinkage cracks, fractures and gas vesicles within the coprolites. A few specimens of Type-A coprolites contain visible plant tissues and other organic matter. Such specimens studied in thin section as well as in randomly

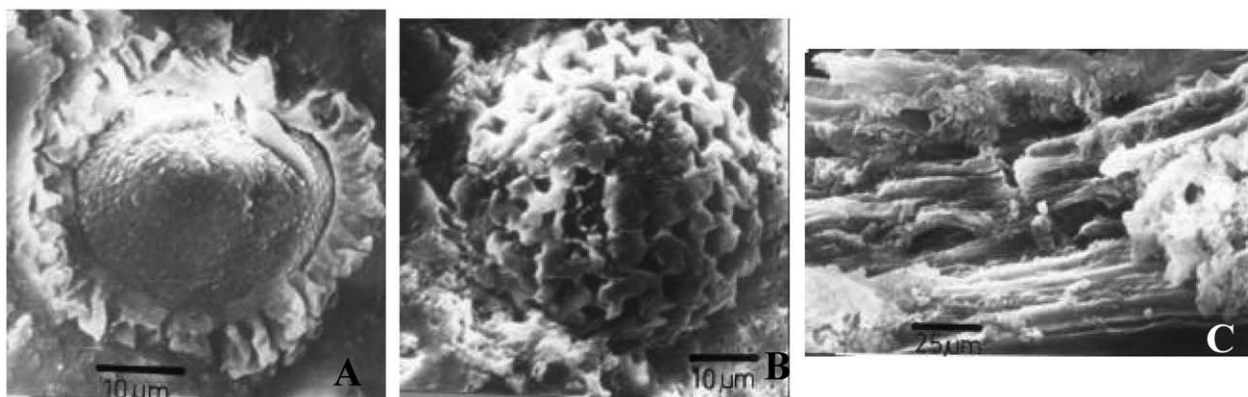


Fig. 3. Scanning electron microscope (SEM) images of in situ material from fractured surfaces of coprolites. A, possible spore species, *Gabonisporis vigourouxii*, characteristic of Maastrichtian palynological assemblages (Sahni et al., 1996). B, a fractured specimen of spore *G. vigourouxii* SEM. C, residual fraction containing organic fragments of plant material resembling woddy tissue.

Table 1

Carbon and nitrogen isotopic composition of faecal pellets of few selected animals compared with the type-A coprolite from Pisdura.

Samples details	$\delta^{13}\text{C}_{\text{PDB}}$ (‰)	$\delta^{15}\text{N}_{\text{AIR}}$ (‰)	Digestive mechanism/Food	Diet
Coprolite A	$-24.2 \pm 0.7$ (4)	4.1	Probably no fermentation	C <sub>3</sub> type
Bird	-24.3	3.9	No gut fermentation/Herbivorous	C <sub>3</sub> type
Deer	-24.5	5.8	Fore gut fermentation/Herbivorous	C <sub>3</sub> type
Camel	-27.9	7.7	Fore gut fermentation/Herbivorous	C <sub>3</sub> type
Goat	-26.4	6.2	Fore gut fermentation/Herbivorous	C <sub>3</sub> type
Buffalo	-12.4	7.4	Fore gut fermentation/Herbivorous	C <sub>4</sub> type
Tiger	-16.1	13.3	Hind Gut fermentation/Carnivorous	Mixed
Leopard	-15.5	12.7	Hind Gut fermentation/Carnivorous	Mixed

fractured surfaces by electron microscopy, showed the presence of plant debris (probably a residue of undigested food), and numerous siliceous sponge spicules and diatoms. Such occurrences probably denote either an intake of water contaminated with microbiota or foreign materials. A wide variety of plant materials, such as pollen and spores, cuticles, woody tissues of conifers and cycads, were observed. In addition, microbiota resembling bacterial colonies, fungal spores and algal remains were noted in the samples.

The specimens were also investigated using scanning electron microscopy on several fractured surfaces. The scanned images show presence of spore-pollen species of several taxa, including possibly that of *Gabonisporis vigourouxii* (Fig. 3A, B), a characteristic species of Indian Maastrichtian polynomorph assemblages known from several intertrappean localities (Sahni et al., 1996). In addition, there are indications of the presence of woody tissues (Fig. 3C).

This microscopic evidence suggests that the producers were mainly herbivorous animals capable of cropping trees, a suggestion that was verified independently by the carbon and nitrogen isotopic composition of the organic matter preserved in the Type-A coprolite samples.

## 5. Inference from isotopic studies

The  $\delta^{13}\text{C}$  values of organic matter from four specimens of Type A coprolite are presented in Table 1. The  $\delta^{15}\text{N}$  value measured in one of the samples is 4.1‰ (Fig. 4). Although the overall carbon isotopic composition of animal tissues is determined mainly by the diet, considerable variation exists among different components of an animal's body. For example, bones are 2–6‰ enriched in  $^{13}\text{C}$  relative to diet, while lipids and fats are 2–8‰ depleted in  $^{13}\text{C}$ . The  $^{15}\text{N}$  enrichment of tissues relative to diet is mainly owing to excretion of isotopically light nitrogen in urine. Studies on cattle, fish and zooplankton show that animal tissues and faeces are enriched in  $^{15}\text{N}$  relative to the diet, but urinary nitrogen (both  $\text{NH}_3$  and urea) is depleted in  $^{15}\text{N}$  (Minagawa and Wada, 1984). For example, cow urine is 1–4‰ depleted in  $^{15}\text{N}$  while cattle faeces are 2‰ enriched in  $^{15}\text{N}$ , and milk and blood are 4‰ enriched in  $^{15}\text{N}$ . The mass balance requirement is thus satisfied as the urinary output of lower  $^{15}\text{N}$  values are compensated by  $^{15}\text{N}$  enrichment in body tissues and faeces.

It is well known that the majority of land plants fall into two categories based on photosynthetic pathways,

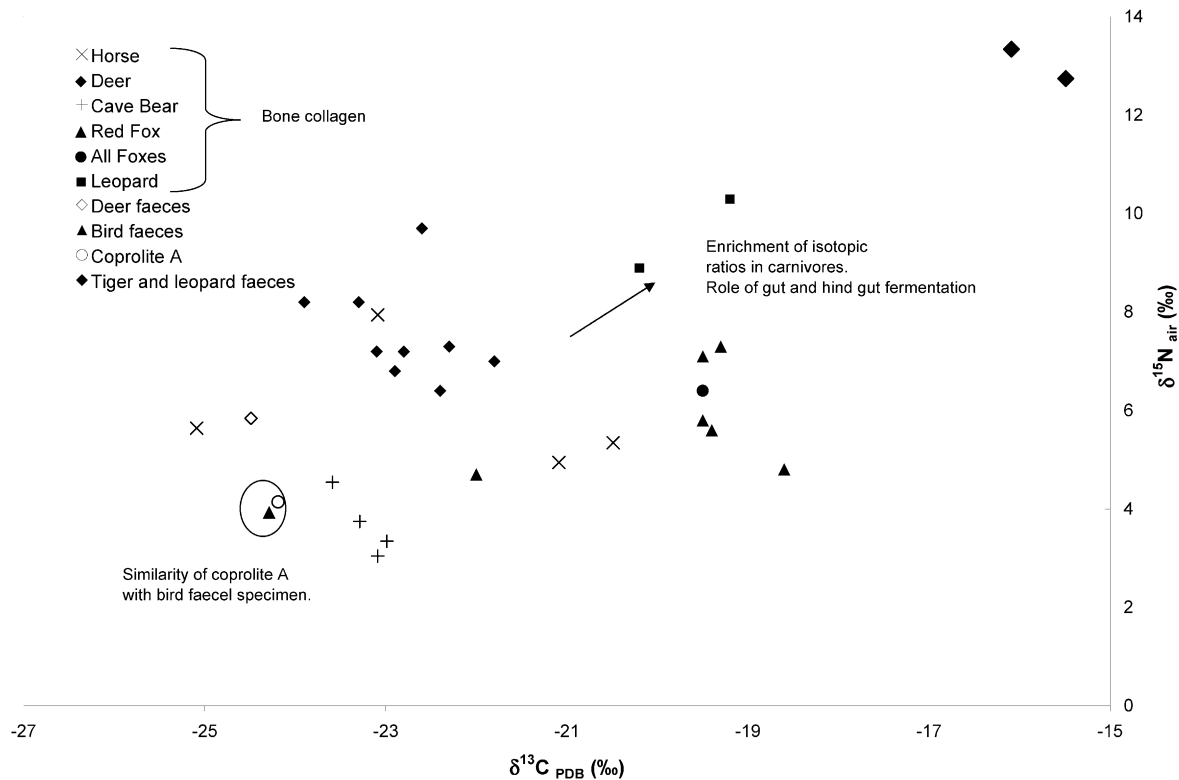


Fig. 4. Plot showing the range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition of bone collagen of widely different animals (taken from Bocherens et al., 1999) also plotted in the figure are the ratios of faeces (animals from Ahmedabad Zoo) and a coprolite OM (average of four samples) analysed in the present study.

namely  $\text{C}_3$  and  $\text{C}_4$ , which are characterized by distinct carbon isotopic signatures (Ehleringer, 1989).  $\text{C}_3$  plants have a unimodal distribution around a mean of  $-26\text{‰}$  while  $\text{C}_4$  plants are enriched, having a mean  $\delta^{13}\text{C}$  value around  $-12\text{‰}$ . The carbon isotopic ratio of the organic matter within the coprolite falls under the category of  $\text{C}_3$ -type vegetation. This result confirms the observation made in a previous study in which  $^{13}\text{C}$  composition of dinosaurian eggshell fragments from the Pisdura locality (Sarkar et al., 1991) was analysed to identify the diet of sauropod titanosaurs.

The nitrogen content of the samples varies considerably within the organic fraction. The appreciable yield in two of those samples processed for stable isotopic analysis allowed measurement of nitrogen isotopic composition. The nitrogen in the organic matter is probably derived from the organic tissue, bone collagen and bacteria (Hollocher et al., 2001). In the case of the coprolites examined, direct evidence for collagen or bacterial components was not found. However, debris of organic tissues is visible in some of the SEM micrographs. With this background, we compared the nitrogen isotopic ratio of coprolite organic matter with bone collagen and tissue of different animals and faeces of four widely different species.

A plot of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ratios of bone collagen and faeces from variety of herbivorous and carnivorous animals is given in Fig. 4. The stable isotopic ratios of the bone collagen of different modern animals are known (Bocherens et al., 1999). These data are plotted along with the results from the analyses of faeces of several animals collected from Ahmedabad zoo (both herbivorous and carnivorous). The faeces data show a broad similarity with the collagen fraction of similar herbivorous animals. Several studies have indicated that the carbon and nitrogen isotope ratios in the solid excreta of animals resemble that of tissue and the bone collagen fraction (Peterson and Fry, 1987). This allows us to compare the isotopic ratios from coprolites and faeces with the available data on bone collagen of different animals. Fig. 4 shows the distribution of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in the collagen fraction according to the taxon or trophic level. The  $\delta^{13}\text{C}$  values are lower for herbivores such as the cave bear compared to foxes, brown bears and other carnivores. The  $\delta^{15}\text{N}$  values are significantly different from each other. For carnivores, there is an increase in  $\delta^{15}\text{N}$  with a progressive rise in the trophic level. The coprolite samples fall between the data on bird faeces and cave bear collagen and occupy the lowest level in the plot. The  $^{13}\text{C}$  and  $^{15}\text{N}$  compositions of

the coprolite samples suggest that the main food of the producer was terrestrial plants (DeNiro and Epstein, 1981) and provides strong additional evidence of herbivorous diet in this species. The C/N ratio of 18 also closely matches values of typical land plants.

Additional information about the mode of digestion is provided by the nitrogen isotope ratios. In animals the food digestion process takes place mainly in the stomach or in the intestine, the two processes being known as gut fermentation and hind gut fermentation respectively. In the case of ruminants, fore gut fermentation is also an important process where carbohydrates are transformed by microbiotic fermentation via pyruvate into short chain fatty acids. Since carbohydrates, e.g. glucose, cannot penetrate the rumen epithelium, metabolically needed glucose is re-synthesized mainly by the process of glyconeogenesis. Carbon and nitrogen isotopes together can be used as a tool to characterize the processes responsible for the digestion in animals and, therefore, can be used as an index of gut fermentation. In a study on cattle, a slight increase (ca. 2‰) of  $^{13}\text{C}$  composition of organic matter in the faeces compared to their feed has been observed (Jones et al., 1979). In a separate study, the  $^{15}\text{N}$  composition of faeces of modern ruminants (Minagawa and Wada, 1984) has shown nitrogen isotopic discrimination during fore gut fermentation. Gut and hind gut fermentation usually enriches the nitrogen isotope ratio to a much higher level owing to the participation of bacteria in the breakdown of food in the stomach. The coprolite organic matter analysed here shows a slightly enriched  $\delta^{13}\text{C}$  value of  $-24.1\text{‰}$  compared to the mean  $\delta^{13}\text{C}$  value of  $\text{C}_3$  plants ( $-26\text{‰}$ ). The  $\delta^{15}\text{N}$  value of coprolite organic matter also matches that of modern ruminants (Minagawa and Wada, 1984). This suggests that gut and hind gut fermentation was probably not a dominant process in sauropod dinosaurs. This inference is in contrast to that based on the weak dentition of most sauropods (Wilson and Sereno, 1998; Farlow, 1987). The carbon and nitrogen isotope ratios of coprolite OM shown in Fig. 4 are similar to those of birds. This suggests that sauropod dinosaurs occupied a trophic level similar to that of birds (Aves) and ruminants when compared with the modern food-chain and were mainly dependent on plants in their diet. Their digestive mechanism might have resembled that of modern ruminants.

## 6. Conclusion

This study characterizes coprolites found in the Cretaceous Lameta Formation of central India. The investigated specimens from Pisdura belong to the Type-A category based on surface ornamentation. We observed plant and other organic fragments in the acid insoluble fraction separated from the samples. Stable

isotopic analyses (both carbon and nitrogen isotopes) of the coprolites help in deciphering the diet and provide an indication of their digestive mechanism. The mean carbon isotope ratio of  $-24.1\text{‰}$  provides strong evidence of  $\text{C}_3$  type plant material in the coprolites, supporting the earlier conclusion of a herbivorous diet for sauropods drawn by Sarkar et al. (1991). In addition, the  $\delta^{15}\text{N}$  value of  $4\text{‰}$  gives a strong indication that herbivory in titanosaurs lacked the gut fermentation process seen in modern large herbivorous mammals.

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