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Early Eocene *Annona* fossils from Vastan Lignite Mine, Surat district, Gujarat, India: age, origin and palaeogeographic significance

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The family Annonaceae has Gondwanan affinity and is being reported from the Cambay Shale of Vastan Lignite Mine on the basis of well-preserved fruit (in counterpart), leaf and pollen grains. This finding is significant because it serves as yet another example of an angiosperm family found in South America and Africa that may have boarded the Indian raft when India was attached to Madagascar, reported on the basis of pollen from Kutch. The Vastan occurrences represent a continuous record from the Indian latest Cretaceous, through the Palaeocene, based on multiple vegetative entities. The well-preserved fruit is morphologically similar to *Annona palustris* L. At present the dispersal history of the family into India represents an origin in the Lower Cretaceous of North America with later dispersal to South America and Africa and then onto India, as it is recorded from the sedimentary beds associated with the Deccan Volcanics. Another angiosperm family, Dipterocarpaceae, is also found in Vastan, with a similar phytogeographic distribution.

Keywords: *Annona*, fossil leaf, fruit and pollen, lignite mine, phytogeography.

A well-known fossil hotspot, Vastan Lignite Mine is situated about 29 km northeast of Surat town (21°25′47″N, 73°07′30″E) in Surat District, Gujarat, India. The Cambay Shale stratigraphy, floral and faunal remains have been described in detail[1–11]. The present fossil material was collected from the Cambay Shale Formation of Vastan Lignite Mine. The rock is a claystone rich in fossil plants and mammals. It occurs about 1/2 m above the base of lignite seam 2. Cambay Formation of the Vastan Lignite Mine section is 20–145 m thick and consists of multiple lignite, carbonaceous shale and grey shale horizons (Figure 1). Fossil fruits, seeds, leaves and pollen grains of *Annona* and other associated fossils were recovered from the exposed section of the mine (Figure 1). The age of the fossiliferous succession in the Vastan Mine is considered as Early Eocene (~53 Ma) based on recorded index foraminiferal fossils assemblages, as well as age diagnostic dinoflagellate cyst assemblage[12,13]. Fossil fruit is small in size, measuring 2.8 cm width and 3.5 cm in height. In Indian geological record, Annonaceae has been found to appear first in the Late Cretaceous[14] and continued into the Palaeocene[15], spread in the Eocene and became dominant in the Miocene and there are also reports in archaeological sites[16].

The recovered fossil assemblages of fruits, leaves and pollen from Vastan are assigned to form species, *Annona eocenica* sp. nov., *Annona vastanensis* sp. nov. and *Matanomadhiasulcites* (*Liliciditees*) *maximus* Saxena respectively. Their systematic descriptions are as follows.

Fossil leaf

Order: Magnoliales, Family: Annonaceae.

Genus: *Annona* Linn., *Annona eocenica* n. sp. (Figure 2 *a–d*).

Material: Leaf impressions recovered from the grey coloured soft shale and devoid of the cuticles. BSIP Museum specimen nos 40018 (holotype), 40019, 40020 (paratype).

Locality: Vastan Lignite Mine, Cambay basin, Gujarat, Western India.

Horizon and age: Cambay Shale Formation, Early Eocene.

Etymology: This species is named after the age of the Cambay Shale Formation from where the specimens were recovered.

Diagnosis: Leaves asymmetrical; base obtuse; margin entire, venation pinnate, eucamptodromous; 4–5 pairs of secondary veins, alternate, branched, angle of divergence of secondary veins 55–60°; angle of origin of tertiary

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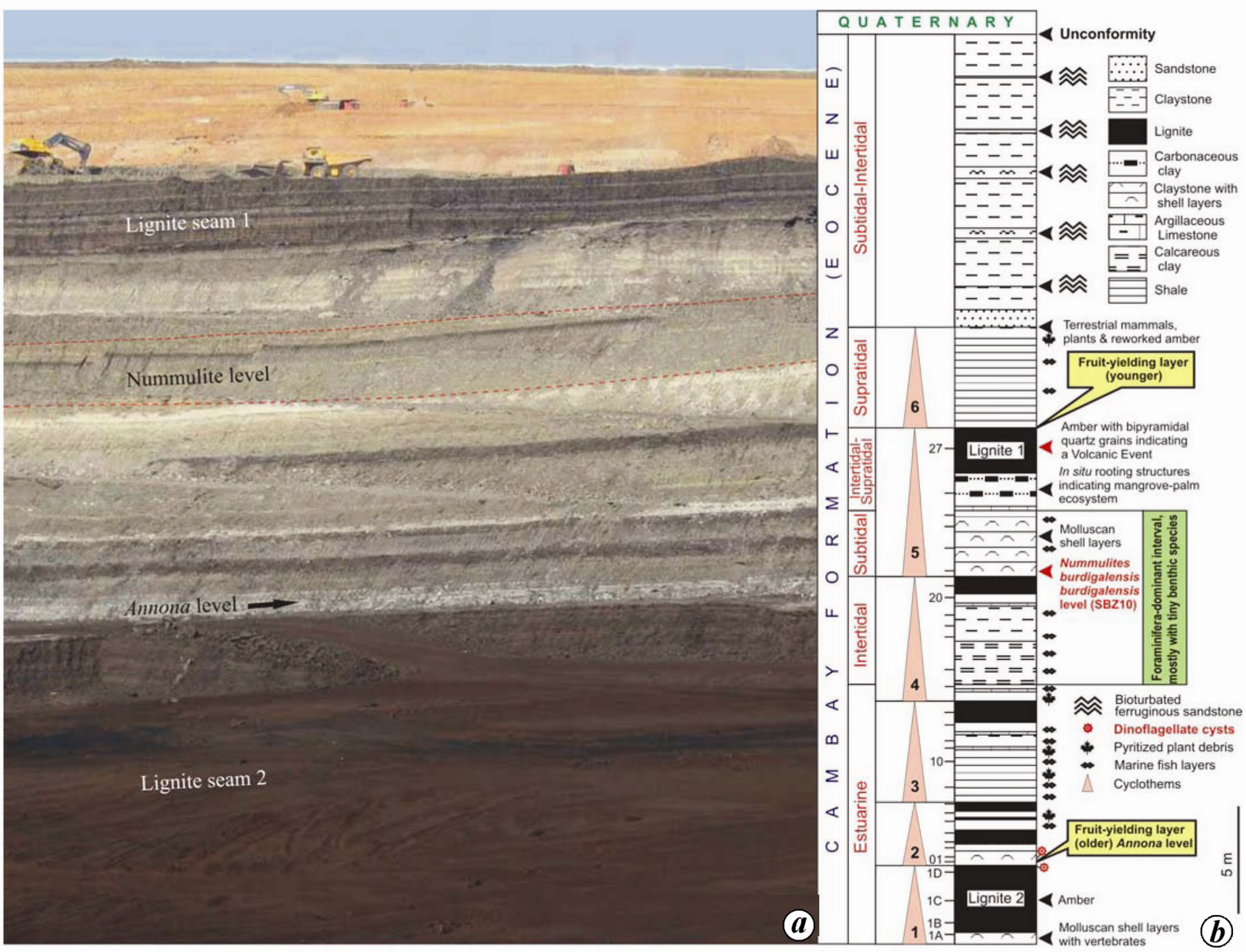

Figure 1. *Annona* level in the Vastan mine section. (***a***) and (***b***) showing *Annona* level in the Vastan mines and lithocolumn respectively.

veins RR, percurrent, straight to sinuous, usually alternate, oblique and close to distant.

Description: Leaves simple, slightly asymmetrical (width of the lamina on one side of midrib is greater than other side), seemingly elliptic in shape, preserved size 6.0 × 4.5 cm, 6.0 × 4.0 cm and 5.5 × 3.3 cm; apex not preserved; base obtuse; margin entire; texture thick chartaceous; venation pinnate, eucamptodromous; primary vein (1°) prominent, almost stout; secondary veins (2°) 4–5 pairs visible, 0.7–1.8 cm apart, alternate, seemingly unbranched, angle of divergence acute (55–60°), uniformly curved up and joined to their superadjacent secondary at acute angle, fine to moderate in thickness; tertiary veins (3°) still fine, angle of origin usually RR, percurrent, branched, straight to sinuous, predominantly alternate; oblique in relation to midvein, close to nearly distant. Further details could not be seen.

Affinity: The diagnostic features of the present fossil leaves are slightly asymmetrical in shape, obtuse base, entire margin, eucamptodromous venation, acute angle of divergence of secondary veins, RR angle of origin of tertiary veins with percurrent, straight to sinuous and close to distant pattern. These features collectively suggest its modern affinity with the leaves of the genus *Annona* L. of the family Annonaceae. A critical examination of the herbarium sheets of all the available species of this genus has been made to find out the specific affinity of the fossil leaves. After consultation of a variety of herbarium sheets of different species, it has been concluded that the leaves of *Annona palustris* Linn. (C.N.H. Herbarium sheet no. 13558), show closest affinity with the Vastan leaves. However, the modern leaves of *A. squamosa* Linn. (C.N.H. Herbarium no. 3744) and *A. reticulata* (C.N.H. Herbarium sheet no. 4290) also show similarity in shape and size to some extent, but differs in the nature and arrangement of the secondary and tertiary veins.

So far, two fossil leaves of *Annona*, *A. koilabasensis*[17] and *Annona miocenica*[18] showing close affinity with *A. laurifolia* Linn and *A. reticulata* Linn. respectively, have been recorded from Siwalik sediments of Nepal. *A. koilabasensis*[17] can be distinguished in being lobate shape with wide acute angle of divergence of secondary veins. However, *A. miocenica*[19] differs from the present fossil in being narrow elliptic shape with bigger size (10.5 × 3.5 cm). The tertiary veins are closely placed in the present fossils. In view of these differences, the present

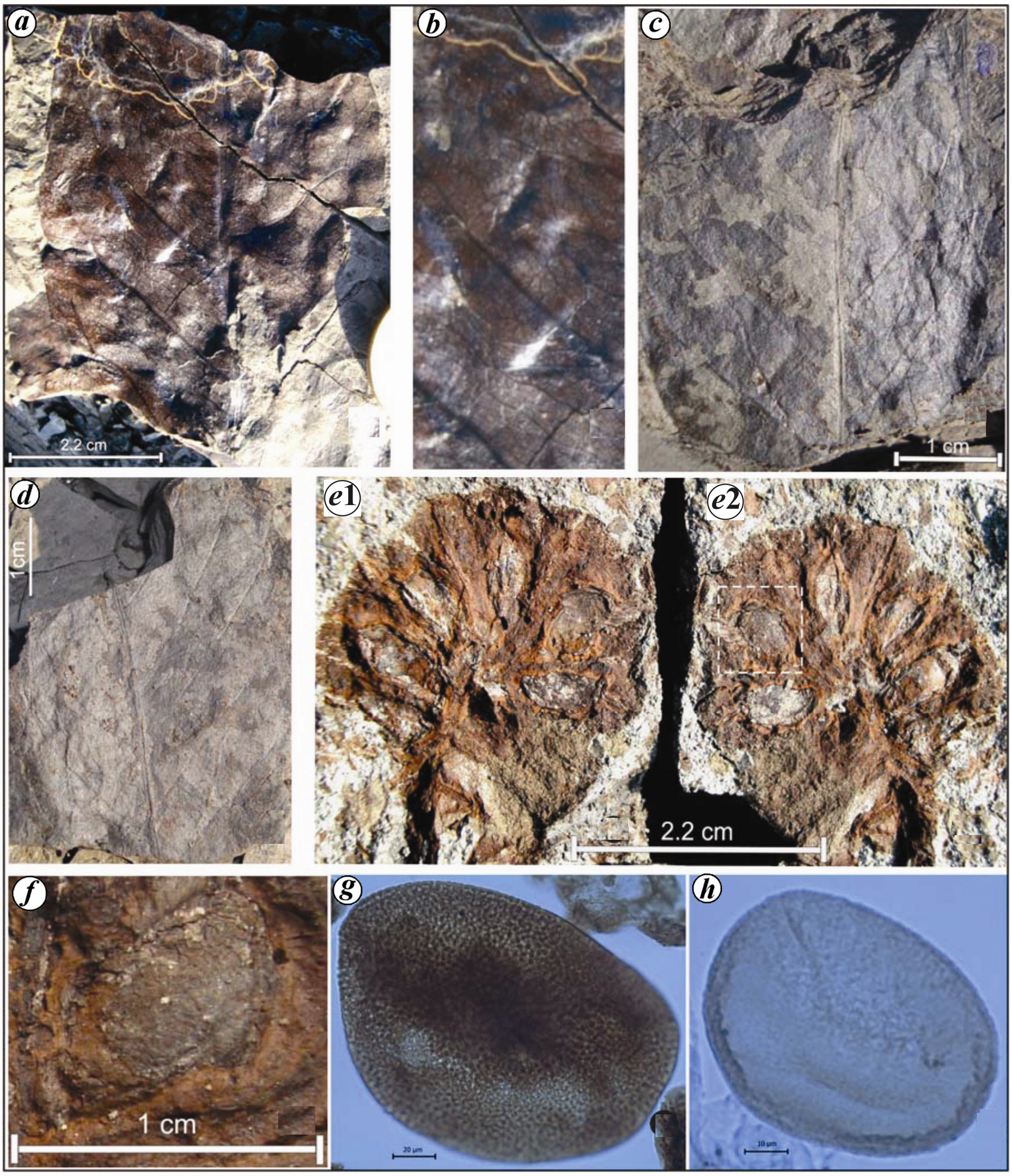

Figure 2. Early Eocene fossil fruit, leaf and pollen of the genus *Annona* from Vastan Lignite Mine, Gujarat. ***a–d***, *Annona eocenica* n. sp. Leaf impressions. ***a***, BSIP40018 (Holotype); ***b***, Enlarged view of (***a***) showing details of venation pattern of secondary and tertiary veins; ***c***, BSIP40019 and (***d***) BSIP40020 (Paratype); ***e*1**, ***e*2**, *Annona vastanensis* n. sp. fossil fruit of *Annona* (***e*1**) BSIP40121 (Holotype), (***e*2**) BSIP40122 (paratype). ***f***, Enlarged view showing nature of seed BSIP40122 (paratype); ***g***, *Matanomadhiasulcites (Lilicidites) maximus* Saxena pollen grains (specimen no. BSIP40123); ***h***, Modern pollen of *Annona (A. sqaumosa)*.

fossil leaves have been reported under the new form species, *A. eocenica.*

Fossil fruit

Annona vastanensis n. sp. (Figure 2 *e*1, *e*2 and *f*).

Material: Two specimens of fruit impression; one is with counterpart and broken open like in a cross-section. BSIP Museum no. 40121 (holotype), 40122 (paratype).

Locality: Vastan Lignite Mine, Cambay basin, Gujarat, western India.

Horizon and age: Cambay Shale Formation, Early Eocene.

Etymology: The specific epithet has been assigned after the name of mine (Vastan) from where the fossil fruits were collected.

Diagnosis: Fruit ovate to spherical, 4.3 × 3.3 cm in size; syncarps; eight small fruits having one seed in each;

seed elliptic to oblong having maximum size of 1.2 × 0.6 cm, thalamus distinct.

Description: Fruit broken, ovate to spherical, 4.3 × 3.3 cm; syncarps, containing many (eight visible) small fruits with one seed, seed bean-like, elliptical to oblong; maximum length 1.2 cm and width 0.6 cm; fruit skin thin; rachis or thalamus present in the fruit; distinct; all the fruits are attached to the thalamus.

Affinity: Shape, size and other characteristic features of the present fossils such as their syncarpouss nature containing many small fruits with elliptic to oblong seed in each fruit and their arrangement on the rachis strongly suggest the affinity of Vastan fruits with the modern fruits of the genus *Annona* L. of the family Annonaceae. Among the species of *Annona*, the most common ones such as *A. reticulata*, *A. squamosa*, *A. palustris*, *A. muricata* and *A. cherimola* have been compared with the observed fossil fruits. The fruits of all the above species are so similar that it is difficult to differentiate one from the other, only on the basis of morphology. However, keeping in view the shape, size of the fossil fruits and seeds and their number and arrangement on the rachis, it has been concluded that it shows closest affinity with the modern fruits of *A. palustris* Linn. (C.N.H. Herbarium sheet no. 13557).

As far as we are aware, there is no prior fossil fruit record from the Tertiary sediments of India. However, some fruit pieces and seeds resembling *A. squamosa* and *A. reticulata* have been reported from archeological sites dated from 200 BC to AD 300 at Sanghol, Punjab and from the successive horizons, datable from about 1700/1600 to 200 BC of Tokwa in the Vindhyan region of southeastern Uttar Pradesh (UP)[16]. As the fruits are fragmentary, it is not possible to compare with fossils. In view of this the present Vastan fossil fruits have been assigned to a new species, *A. vastanensis.*

Pollen grain

Matanomadhiasulcites (*Liliciddites*) *maximus* Saxena[18] (Figure 2 *g*).

Diagnosis: After Saxena[18] (Kar[20]). Pollen grain oval–elliptical, 135–205 × 90–145 μm, monosulcate, sulcus may be distinct or indistinct, wide, extending from pole to pole. Exine 2–3 μm thick, generally retipilate to reti-baculate, pilla/baculla 3–8 μm, long.

Description: Pollen grains mostly with equally broad lateral ends, very large in size, 170–160 × 120–125 μm, sulcus mostly distinct, sometimes broader, tapering at ends. Exine 2–4 μm, thick, reticulated pila, 1.2 μm long, 0.8–1 μm broad, sometimes interspersed with bacula, pila closely placed, 1.5 μm apart, forming negative reticulum in surface view, lumina 4.5–5 μm.

Specimen BSIP Museum no. 40123.

Locality: Vastan Lignite Mine, Cambay basin, Gujarat.

Horizon and age: Cambay Shale, Early Eocene.

Remarks: The present fossil pollen is compared with extant pollen of the available species of *Annona* (*A. squmossa*). They show almost all comparable characters such as shape, sulcus, similar exine pattern, pilla of almost same size, except for the size of pollen which as a whole is larger (170–160 × 120–125 μm), than their modern (72 × 57 μm) counterpart (Figure 2 *h*). The presence of *Annona* fossil pollen (*Matanomadhiasulcites*) further supports the presence of *Annona* in the sediments.

Annona, the second largest genus of the family Annonaceae contains approximately 137 species of trees and shrubs, distributed in the tropical region of America, Brazil and Africa[21,22]. Five species of *Annona* are known to have been introduced in India[23], among which *A. palustris* L. (syn. *A. glabra* L.) is naturalized and confined only to the west coast of peninsular India, commonly along backwaters of Kumarkom Bird Sanctuary, Kerala. Its fossil record from the neotropics is richer compared to that from the Southeast Asian region[24,25]. Based on both fossil leaves and fruits, this genus includes 15–20 fossil species[24]. The oldest species comes from the Dakota Sandstone (Lower Cretaceous), and another species is found in the Late Cretaceous or Early Eocene of the Rocky Mountain Province. It is well documented from Tertiary sediments of America, England, Italy, Chile, France and Bohemia. The other known fossils of Annonaceae comprising wood, seeds and pollen are from the Maastrichtian of India, Nigeria and Colombia respectively, and leaves from Palaeocene–Eocene of western India[14,15,26]. The present records of both mega and micro fossils of *Annona* from the Early Eocene of Vastan Lignite Mine of India, fully support Gondwanan affinity and the family may have originated much earlier during late Cretaceous. The other supporting evidence for a west Gondwanan affinity of Annonaceae is substantiated by the occurrence of more primitive pollen of early stalk of this family, whereas most Asian taxa have more derived pollen morphology[27]. None of the fossils found from Cretaceous flora of Laurasia could unambiguously be assigned to the family Annonaceae. The precise date of origin of Annonaceae, which is the largest living family among the magnoliid group of early divergent angiosperm, is still being conjectured. The estimated age of anaxagorea, probable ancestral stalk of Annonaceae is determined to be around 90.6 + 1.3 Ma (ref. 28). While another report suggests it is between 82 and 91 m.y. ago (ref. 27). These estimated ages for Annonaceae are more than those indicated by the record of fossil seed from a Maastrichtian of Nigeria and pollen from Columbia[29,30]. While treating the origin of Anaxagorea to be from South America or Africa, it is expected that these ancestral sites of the area of distribution of this taxa might be dated at above 82 Ma (ref. 31). The continental drift is inferred to account for the amphi-Atlantic range of *Anaxagorea* and transported on the northward rafting India. Further, the long-distance dispersal from Africa to South America and vice versa also played a role[31]. The migration of taxa between Africa and South America could have been possible after their break-up about 90–105 m.y. ago through short-distance dispersal over water[32] and up to the Maastrichtion via filter dispersal through island chains of the Rio Grande Rise-Walvis Ridge and the Sierra Leone Rise[33–36]. The common eastern Asian and eastern North America disjunction pattern may have had multiple origins throughout the Tertiary, during which many taxa could have migrated between Asia and North America via the Bering land bridge or the North Atlantic land bridge[35–38].

The fruits and seeds of *Annona* reported earlier[16] from Vindhyan terrains of southeastern UP during 1700/1600–200 BC suggest its indigenous status in the Indian subcontinent since much earlier times. This is contrary to the general belief that it is an exotic taxon and introduced here only in the recent past. Occurrence of fossil leaves of this genus during middle Miocene period (+12 Ma)[17,19], further suggests that *Annona* had naturalized even much earlier. The present finding suggests a relook into all these views and emphasizes its long continuous existence in this region since a much earlier geological period.

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Dwarfism and Lilliput effect: a study on the *Glossopteris* from the late Permian and early Triassic of India

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The 'Lilliput effect' represents the phenomenon whereby there is a pronounced reduction in the size of biota associated with the aftermath of mass extinction. This fact has been supported by the evidence of dwarfism both in invertebrates and vertebrates recorded after the end-Permian mass extinction event. The extinct genus *Glossopteris* belonging to seed ferns Glossopteridales is one of the best known fossil taxon that flourished during the Permian and continued its existence till Triassic. In contrast to the Permian, the Triassic was a time when greenhouse conditions with an increased temperature and widespread aridity prevailed as evidenced by the global dataset. The new set of environmental conditions in the Triassic posed a major challenge for the existing *Glossopteris* lineage, whereby the smaller forms (dwarfs) with reduced leaf surface area continued and sustained. The present study from different late Permian and early Triassic formations of India is aimed at unravelling the changes in morphological traits of seven species of *Glossopteris* leaves whose existence continued surpassing the Permian–Triassic mass extinction event.

Keywords: Dwarfism, extinction event, *Glossopteris*, Lilliput effect, Permian–Triassic boundary.

GLOSSOPTERIS is one of the best known taxon belonging to the extinct order of the seed ferns Glossopteridales (family Glossopteridaceae). It is one of the first fossil plants described and named by Brongiart[1,2]. The name implies lanceolate to tongue-shaped entire leaves, which are characterized by a prominent midrib and reticulate secondary venations[2–5]. It has been extensively recorded from the once united southern hemisphere called 'Gondwana', which comprised of India, Australia, New Zealand, South America, Africa and Antarctica.

The origin of the glossopterids took place in the southern hemisphere around the beginning of the Permian ~ 290 Ma (ref. 6). *Glossopteris* is considered as the stratigraphic marker for the Permian throughout all the Gondwana continents. Its existence continued up to the Triassic and there is one report of its doubtful occurrence in the Jurassic[7].

The late Permian megafossil assemblage of India (Bijori Formation, Kamthi Formation and Raniganj Formation) is dominated by larger-sized species of *Glossopteris*[8–15]. They were broadleaved and presumed to be deciduous, capable of living in a wide range of fluviolacustrine subenvironments[12,13,16,17]. In contrast, species of *Glossopteris* recorded from the early Triassic (Panchet Formation) were comparatively smaller in dimension than the underlying Permian[18]. The leaves of early Triassic sediments had a reduced surface area which was adapted to withstand the extreme climatic condition[19–21].

The 'Lilliput effect' represents the phenomenon whereby there is a pronounced reduction in the size of the biota associated with the aftermath of mass extinction event[22–25]. After a particular extinction event, the biotic crisis is normally represented in two major ways: (i) the larger forms which are structurally specialized species tend towards extinction[26,27] and (ii) species whose size decreases (dwarfism) tend to continue[28,29]. The 'Lilliput effect' has been established for the end-Permian Mass Extinction Event (EPME). This fact is supported by the evidence of dwarfism of invertebrates[30,31] and relatively few records of vertebrates[32–34]. A single factor cannot be held responsible for the phenomenon of dwarfism, i.e. 'Lilliput effect'. Factors that are responsible for this phenomenon can be either biotic or abiotic or a combination of

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