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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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both (Figure 1) which act in a cumulative way[29,35–37]. Abiotic factors that are responsible for the same are: mean temperature rise, anoxia, increased CO_2 concentration in the atmosphere, edaphic factors, climatic change, loss of provinciality and ecological niche. Biotic factors that are the causative agent for the phenomenon are symbiotic dissociation, diseases, reduction in primary productivity, nutrient scarcity, reduced vigour and intra- or inter-generic and specific competition. However, the most important factor for dwarfism, at the Permian–Triassic Boundary can be attributed to increased aridity, higher CO_2 concentration (about 2000 ppm) in the atmosphere and substantial rise in temperature (~ 8°C)[38]. A similar reduction in leaf width has been observed on well-preserved fossil leaves from the terrestrial Triassic–Jurassic sections in East Greenland and Scania, Sweden[39]. Comprehensive data generated on *Lepidopteris–Thaumatopteris* flora (Rhaetian–Hettangian) reveal the extent of high-temperature injury to leaves across the Triassic–Jurassic Boundary. The authors opine that volcanicity associated with the Central Atlantic Magmatic Province (CAMP, 199 ± 2.4 Ma) induced 'super-greenhouse' conditions resulting in a fourfold increase in atmospheric CO_2 and 3–4°C warming across the Triassic–Jurassic Boundary. The authors[39] further suggest that reduction in leaf size was to avoid lethally high leaf temperature. Increased SO_2 levels resulting from massive volcanism in the CAMP have also been implicated as a factor in reduced leaf size[40]. Experiments conducted on the nearest living equivalent taxa of the Triassic–Jurassic Greenland flora have revealed that fumigation by SO_2 resulted in leaf roundness as observed in the fossil flora. Therefore, rising SO_2 levels as a consequence of volcanism during the Permian–Triassic extinction event (PTEE) could also be a factor in reduced leaf size.

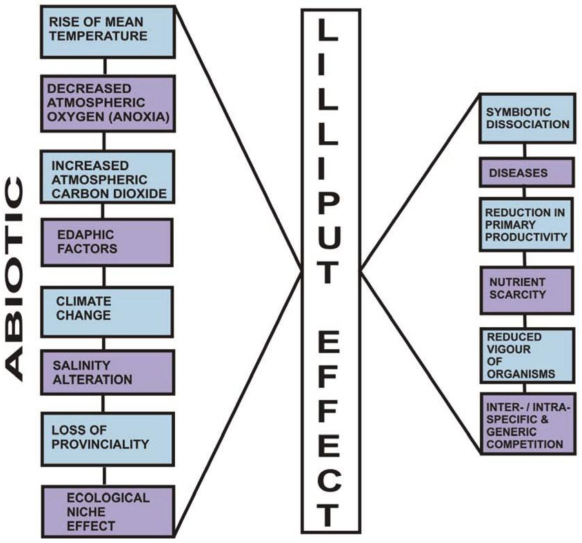

Figure 1. Possible biotic and abiotic factors responsible for 'Dwarfism and Lilliput effect'.

The PTEE that occurred ~ 252 Ma is the most severe and lethal event in the Earth's history. It witnessed the extinction of about 90% of all marine species and 70% of terrestrial species. The magnitude of floral extinction along with the overall change in diversity is more ambiguous. There are no major peaks in mass extinction for plants in the fossil record, excepting the Permian–Triassic Boundary[41]. Studies have revealed that the ecological instability in plant communities and their ultimate extinction was before or coincident with the peak of faunal extinction[31,42,43]. But, the effect on plants was much lesser compared to the marine and faunal records. However, some plants became extinct at the Permian–Triassic Boundary. Evidence shows that at the Permian–Triassic Boundary there was a sudden increase in pumping of massive volume of CO_2 into the atmosphere that led to the global warming and short-term production of acid rain[44]. This major catastrophic event affected the existing plant life. However, *Glossopteris* is the only plant taxon that could survive the event and is found beyond the Permian–Triassic Boundary in relative abundance. In fact, *Glossopteris* is an exceptional form that overcame the Permian–Triassic boundary mass extinction event and continued with reduced vigour in the early Triassic. Other associated late Permian plant taxa, viz. *Vertebraria*, *Gangomopteris*, *Phyllotheca*, *Dichotomopteris*, *Neomariopteris*, etc. could not sustain the extreme climatic conditions during the Permian–Triassic Boundary crisis.

In the present study, an attempt has been made to decipher the changes in the various aspects of morphological traits of the species of *Glossopteris* from the late Permian and early Triassic succession of India. The above-mentioned formations with their respective geographical locations are shown in Figure 2.

The late Permian species of *Glossopteris* were studied from three different formations namely Bijori, Kamthi and Raniganj[8–15]; while for early Triassic, the Panchet Formation was taken into consideration[19–21]. The late Permian–Triassic sequences in different Gondwana basins of Peninsular India have been listed in Table 1. Lithology of the late Permian sediments of Raniganj Formation is characterized by predominantly fine-grained, occasionally feldspathic, micaceous, sometimes argillaceous, greenish-grey to whitish-grey sandstone. The sandstones of Raniganj Formation are frequently interbedded with micaceous siltstone. Grey as well as carbonaceous shales and coal seams are well developed. Lithologically the Bijori Formation comprises sandstones with micaceous shale and carbonaceous shales along with coal streaks. The lithological features as well as floral composition establish its homotaxis with the Raniganj Formation. The Kamthi Formation is predominantly composed of conglomerates, usually soft and argillaceous grits, fine-grained sandstone and shales. The floral assemblage is similar to that of the Raniganj Formation. The rocks of the early Triassic sediments of Panchet Formation are

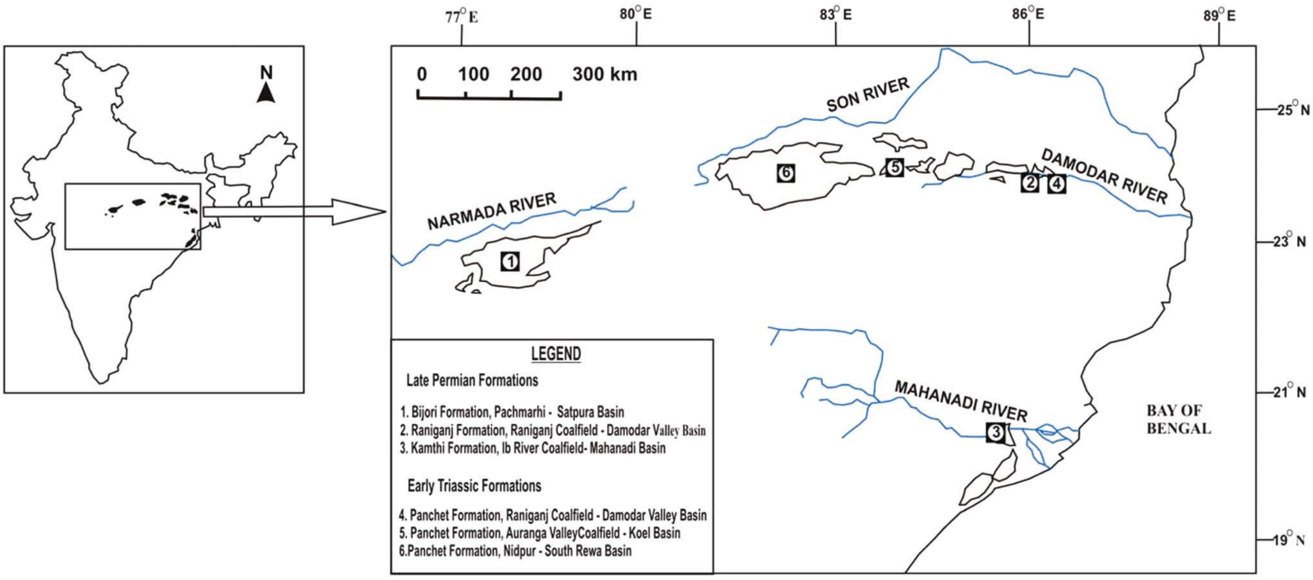

Figure 2. Map showing the different formations of Gondwana Basin[67,68] in Peninsular India from where the present analyses have been carried out.

Table 1. The late Permian–Triassic sequences in different Gondwana basins of Peninsular India

Gondwana basins / Standard scale			Damodar Valley Basin	Koel Valley Basin	Rajmahal Basin	South Rewa Basin	Satpura Basin	Pranhita–Godavari Valley Basin	Mahanadi Valley Basin
Lower Jurassic						Hartala Hill Beds		Dharmaram Formation	Pathargarh Beds
Triassic	Upper	Rheatian				Tiki Formation			
		Norian			Dubrajpur Formation			Maleri Formation	
		Carnian	Supra-Panchet Formation	Mahadeva Formation		Parsora Formation	Bagra Beds	Bhimaram Formation	
	Middle	Ladinian					Denwa Formation		
		Anisian				Nidpur Beds	Pachmari Formation	Yerrapalli Formation	
	Lower	Sythian	Panchet Formation	Panchet Formation		Panchet Formation	Almod Formation	Mangli Beds	Sarimunda Hill Beds
Late Permian			Raniganj Formation	Raniganj Formation		Pali Formation	Bijori Formation	Kamthi Formation	Kamthi Formation

Table 2. Number of specimens of *Glossopteris* species analysed

Species of *Glossopteris*	Number of late Permian species studied	Number of early Triassic species studied
Glossopteris angustifolia	8	6
Glossopteris browniana	10	4
Glossopteris communis	12	8
Glossopteris conspicua	14	4
Glossopteris damudica	12	2
Glossopteris indica	10	6
Glossopteris retifera	8	4

Total number of specimens studied (n) = 108. Seventy four specimens from the late Permian. Thirty four specimens from the early Triassic.

clearly distinguishable from the underlying Raniganj Formation by the characteristic red shales, rich micaceous sandstones and absence of coal and carbonaceous shales. The lowermost beds of the Panchet Formation comprise shales and thin beds of greenish-brown mudstones, interbedded with micaceous greenish-grey siltstones[45].

Materials for the present study consisted of the illustrated, type and figured specimens of the *Glossopteris* species housed in the repository of Birbal Sahni Institute of Palaeobotany (BSIP), Lucknow, India. In all, 108 specimens preserved as impressions have been taken into consideration for the present analysis (Table 2). Based on various morphological traits of the leaf architecture,

Table 3. Comparative analysis of species of *Glossopteris* from different late Permian and early Triassic formations of India

Species of *Glossopteris*	Age/ formations	Morphological characters of leaf											
		Size						Midrib				Average concentration of veins	
		Maximum available length (cm)	Maximum available width (cm)	Shape	Apex	Base	Margin	Type	Thickness (mm)	Angle of emergence of secondary veins	Mesh type	Towards midrib (per cm)	Towards margin (per cm)
Glossopteris angustifolia	Late permian (Bijori/ Kamthi/ Raniganj formations)	13.0	2.00	Lorate-oblong to narrow-oblanceolate	Obtuse	Acute-cuneate	Entire	Medium to broad, flat, striated, evanescent towards apex	5.00	Emerge at 10–15°, fork once or more from midrib to margin	Elongated, oblong to linear-polygonal	18–25	12–15
	Early Triassic (Panchet Formation)	8.50	2.00	Oblanceolate to spathulate	Acute	Tapering towards base	Entire	Distinct, finely striated	2.00	Emerge at 15–20°, near base parallel to midrib	Broad, oblong, narrower near margin	20–30	15–23
Glossopteris browniana	Late Permian (Bijori/ Kamthi/ Raniganj formations)	16.4	5.60	Narrow oblong	Acute	Acute-cuneate	Entire	Thick at base, tapers gradually, distinct at apex	2.50	Emerge at 20–45°, slightly arched, reach the margin at an open angle	Narrow-broad, elongated polygonal meshes	22–40	25–45
	Early Triassic (Panchet Formation)	7.40	5.00	Lanceolate to spathulate	Acute	Tapering towards base	Entire	Distinct, flat, longitudinally ribbed, persists up to apex	1.50	Emerge at 35–45°, dichotomizing and anastomosing	Oblong-polygonal, narrower towards margin	10–12	18–20
Glossopteris communis	Late Permian (Bijori/ Kamthi/ Raniganj formations)	25.0	6.00	Narrow elliptic to oblong lanceolate	Acute	Acute-cuneate	Entire	Thick, flat, persists up to apex	3.00	Emerge at 10–18°, arching backwards	Long, narrow, oblong, polygonal	32–40	45–60

(*Contd*)

Table 3. (*Contd*)

		Morphological characters of leaf											
		Size						Midrib				Average concentration of veins	
Species of *Glossopteris*	Age/ formations	Maximum available length (cm)	Maximum available width (cm)	Shape	Apex	Base	Margin	Type	Thickness (mm)	Angle of emergence of secondary veins	Mesh type	Towards midrib (per cm)	Towards margin (per cm)
	Early Triassic (Panchet Formation)	11.0	4.60	Lanceolate to spathulate	Acute	Tapering towards base	Entire	Distinct, flat, tapering towards apex	2.50	Emerge at 30–35°, dichotomizing and anastomosing	Narrow-elongated, equal width throughout the lamina	24–26	34–36
Glossopteris conspicua	Late Permian (Bijori/ Kamthi/ Raniganj formations)	11.0	4.20	Oblong to oblanceolate	Indiscernible	Indiscernible	Entire	Flat, persistent	2.00	Emerge at 20–35°, straight course to margin	Long, broad, pentagonal to hexagonal, uniform	7–10	9–15
	Early Triassic (Panchet Formation)	6.50	3.60	Obovate	Acute	Tapering towards base	Entire	Distinct, evanescent towards apex	1.50	Emerge at 35–40°, travel straight to margin	Large, broad, oblong-polygonal, narrower near margin	4–6	6–8
Glossopteris damudica	Late Permian (Bijori/ Kamthi/ Raniganj formations)	18.2	6.30	Elliptic	Obtuse	Not preserved	Entire	Thick, persistent, evanescent towards apex	5.00	Emerge at 50–70°, straight course to margin	Broad, polygonal, narrow near margin, short near midrib	10–13	30–32
	Early Triassic (Panchet formation)	3.00	2.70	Indiscernible	Indiscernible	Indiscernible	Entire	Distinct, strong	1.25	Emerge at 45°, after emergence bends sharply and continues up to margin	Oblong-polygonal	4–6	9–14

(*Contd*)

Table 3. (*Contd*)

		Morphological characters of leaf											
		Size						Midrib				Average concentration of veins	
Species of *Glossopteris*	Age/ formations	Maximum available length (cm)	Maximum available width (cm)	Shape	Apex	Base	Margin	Type	Thickness (mm)	Angle of emergence of secondary veins	Mesh type	Towards midrib (per cm)	Towards margin (per cm)
Glossopteris indica	Late Permian (Bijori/ Kamthi/ Raniganj formations)	31.0	3.50	Narrow elliptic	Acute	Acute	Entire	Distinct, persists up to apex	5.00	Emerge at 12–20°, veins anastomosing	Broad near midrib, narrow towards margin	22–35	35–48
	Early Triassic (Panchet Formation)	7.00	3.40	Oblanceolate to spathulate	Obtuse	Tapering towards base	Entire	Distinct, thinning out towards apex	4.00	Emerge at 30–40°, dichotomizing and anastomosing to form meshes	Broad, smaller near midrib and narrow, elongated	12–14	16–20
Glossopteris retifera	Late Permian (Bijori/ Kamthi/ Raniganj formations)	14.0	4.50	Narrow oblanceolate to linear	Acute to obtuse	Acute to acute-cuneate	Entire	Persistent medium-broad, flat, evanescent towards apex	3.00	Emerge at 20–30°, run straight to margin	Broad, short, pentagonal-hexagonal	6–9	12–18
	Early Triassic (Panchet Formation)	6.00	3.20	Obovate	Acute	Indiscernible	Entire	Distinct, longitudinally ribbed	2.00	Emerge at 45°, dichotomizing and anastomosing	Oblong-polygonal meshes	10–11	12–14

namely size, shape, apex, base, midrib, angle of emergence of secondary veins, mesh type and average concentration of veins, the present analysis has been done on seven species of *Glossopteris*, viz. *G. angustifolia*, *G. browniana*, *G. communis*, *G. conspicua*, *G. damudica*, *G. indica* and *G. retifera*. These species continued their existence in Indian Gondwana sediments right from the Permian up to the early Triassic. Xeromorphic features, viz. thick cuticle, sunken stomata and stomatal papillae are usually found in the early Triassic plant taxa, e.g. *Lepidopteris* and *Dicroidium*. As evident from the fossil record, xeromorphic features have not been reported in any species of *Glossopteris* known from the early Triassic of India. However, xeromorphic features of plants cannot be interpreted purely in terms of possible antitranspirant properties. Certain features such as sunken stomata and stomatal papillae earlier regarded as antitranspirant in function, are now considered as adaptations for the growth of plants in high precipitation environments, serving a water-repellent role. Various xeromorphic features possibly served different functions and these properties act in combination, such as water repellence and resistance to toxic atmospheric gases and volcanic dust, etc. and may account for the development of xeromorphic features in a number of Mesozoic plants. Therefore, the use of these xeromorphic characters as indicators of palaeo-environmental aridity in the Mesozoic plant taxa needs supporting evidence from sedimentology, geochemical analysis, climate modelling and examination of modern ecological analogues[46].

The studied impression specimens of *Glossopteris* are from well-known late Permian and early Triassic outcrops of peninsular Indian Gondwana basins, which are palynologically well dated. In the Gondwana sequence of Peninsular India, the Permian–Triassic Boundary is yet to be demarcated by absolute age

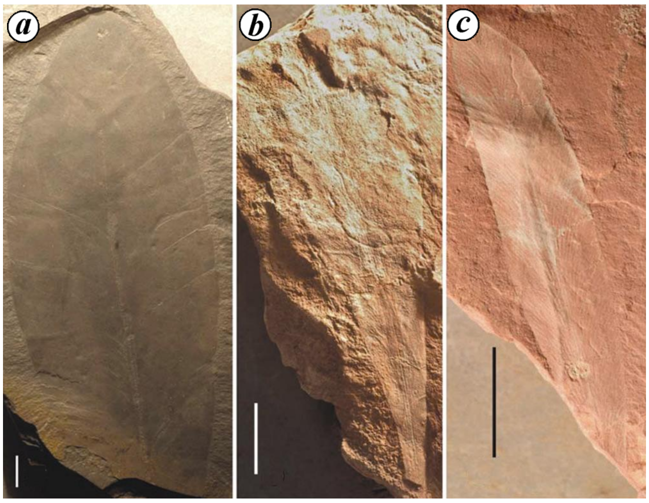

Figure 3. Size variation of species of *Glossopteris* from the late Permian and early Triassic sequence of India. ***a***, *G. communis* from the late Permian (Raniganj Formation) of Raniganj Coalfield, West Bengal; BSIP specimen number II/629. ***b***, *G. communis* from the early Triassic (Panchet Formation) of Deobar, Jharkhand; BSIP specimen number 35181/1246. ***c***, *G. angustifolia* from the early Triassic (Panchet Formation) of Deobar, Jharkhand; BSIP Specimen Number 35180/1246 (scale bar = 1.0 cm).

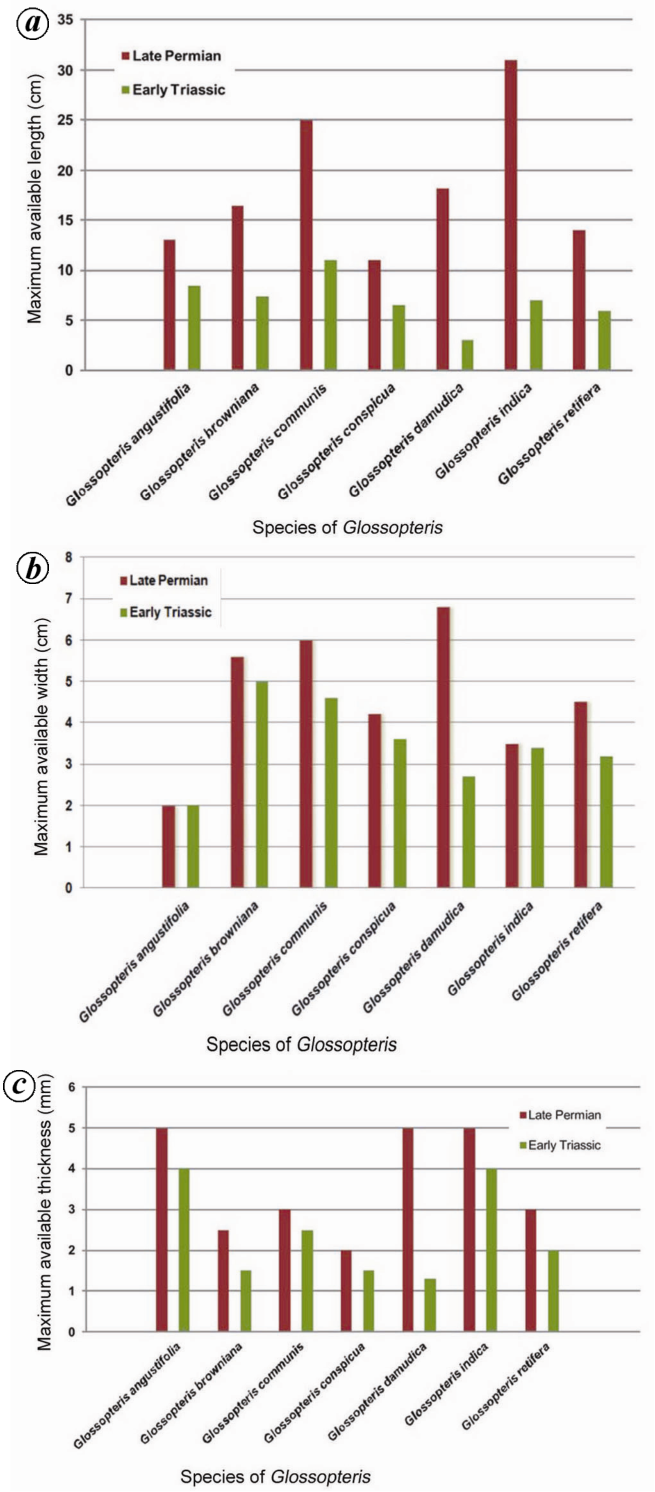

Figure 4. Graphical representation of variation of (***a***) laminar length, (***b***) laminar width and (***c***) midrib thickness in species of *Glossopteris* from late Permian and early Triassic sequences of India.

determination[47]. However, the transition from Permian to Triassic is well documented by both plant megafossils and microfossils. High-resolution palynostratigraphy from the localities from where the specimens have been studied is well established. The late Permian palynoassemblage is characterized by *Densipollenites magnicorpus* zone and the early Triassic palynoassemblage is represented by *Falcisporites–Klausipollenites* zone[48–51].

The necessary measurements of the impressions of *Glossopteris* leaves were done from the original material. Illustrations of the already published papers of the original authors also have been taken into consideration. If any character of the leaf is not clear enough, it has been left as indeterminable. The results of the analysis are presented in Table 3. Evidences from the study conducted on the seven species of *Glossopteris* leaves clearly support the fact that there is indeed a reduction in the dimension of the lamina in the post-Permian sequence of India (Figure 3). The species from the early Triassic sequences are characterized by leaves possessing reduced laminar area with smaller length (Figure 4 *a*) and width (Figure 4 *b*) and narrower thickness of midrib (Figure 4 *c*) in comparison to those of the underlying Permian sequences. Dimensions of the studied *Glossopteris* leaf specimens (length and width) have been given in the form of a cluster diagram (Figure 5).

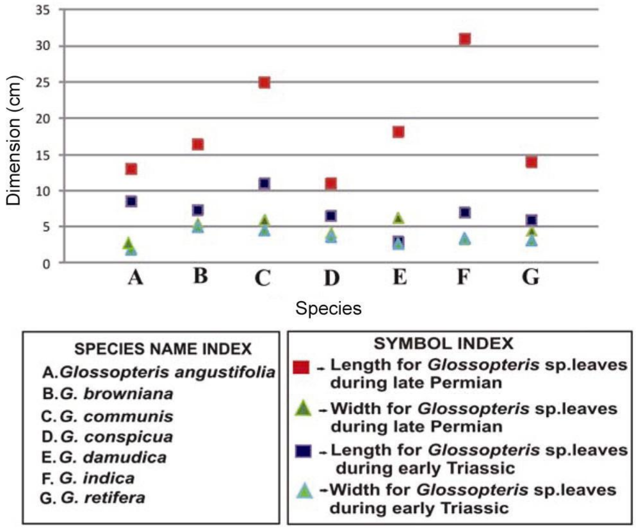

Figure 5. Dimensions of the studied *Glossopteris* leaf specimens (length and width) in a cluster diagram.

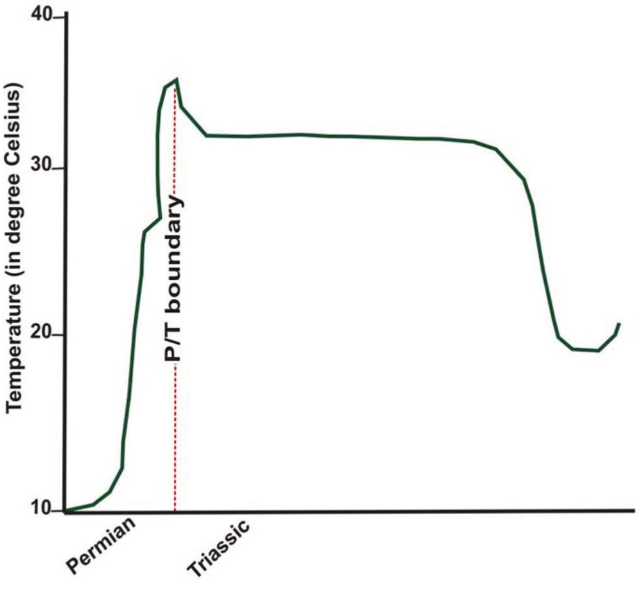

Figure 6. Temporal variation of mean temperature during Permian and Triassic periods[55].

Modern-day high-resolution regional palaeoecological studies have proved the myth wrong, which stated that the mass extinction event had little macroecological or evolutionary consequence for terrestrial plants[38]. The early Triassic (Panchet Formation) in India witnessed more arid or semi-arid climate in comparison to the Permian. The early Triassic experienced greenhouse conditions with a warmer phase (Figure 6) due to global rise of temperature coupled with episodes of intense volcanism[52–56]. The reduced size of the lamina is one of the strategies adapted by the plants during the adverse condition in early Triassic when there was indeed a shortage of essential nutrients in the soil, in addition to seasonal dry climate, irregular rainfall and widespread aridity. The leaves possessed cuticles with sunken stomata since the atmosphere during the early Triassic had higher levels of CO_2 and lower O_2 levels[57–60] (Figure 7). The *Glossopteris* flora of late Permian was adapted to temperate, cool and moist environments[60,61]. The phenomenon of dwarfism as evidenced in *Glossopteris* has been observed only up to the early Triassic, which is represented by the Panchet Formation. During the middle to late Triassic, typical *Dicroidium* flora associated with *Lepidopteris* takes over the preceding *Glossopteris* flora.

Records of plant fossils substantiate the evidence that numerous physiological, reproductive and behavioural traits enabled the smaller sized plant species to persist in extreme climatic conditions[38,62–66]. With the onset of new

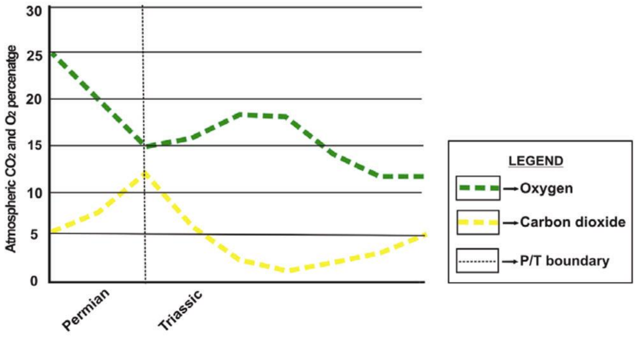

Figure 7. Temporal variation in atmospheric CO_2 and O_2 during the Permian and Triassic periods[56,58].

environmental conditions during the early Triassic, surpassing the major extinction event, the smaller sized features of glossopterids became prevalent and continued their existence, though, during the late Triassic they gradually became extinct.

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