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EXTINCTION OF THE GENUS *GLOSSOPTERIS* BRONGNIART – A VIEW POINT

EXTINÇÃO DO GÊNERO GLOSSOPTERIS BRONGNIART – UM PONTO DE VISTA

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Resumo: A história dos eventos de extinção em massa testemunhados pela Terra afetaram processos evolutivos. A extinção da pteridosperma *Glossoperis* no Triássico (220 Ma.) é parte de um evento assim. Ela evidencia a inabilidade do gênero de evoluir adequadamente. Considerando os dados morfológicos e quantitativos das espécies indianas do gênero *Glossopteris*, as razões para sua extinção são sugeridas e discutidas. O assunto ainda suscita curiosidade quando as hipóteses evidenciam, até o momento, que não explicam, satisfatoriamente, a escala e grandeza da extinção de *Glossopteris*, que alcançou o seu auge no Permiano superior. Em adição às razões documentadas, a pobreza das frutificações de glossopterídeas, no Triássico, aponta em direção à possibilidade de que mudanças na habilidade de produzir sementes e no padrão de fertilidade da semente, definitivamente levaram ao desaparecimento da planta. Além disso, competição biológica, predação, fatores ambientais como clima árido hostil e outros fatores podem ter influído no extermínio dessa planta.

Palavras-Chave: *Glossopteris*; Extinção; Permiano; Triássico.

Abstract: History of earth witnessed mass extinction events that affected evolutionary processes. Extinction of pteridospermous *Glossopteris* in Triassic (220 Ma.) is part of one such event. It indicates the inability of the genus to evolve adequately. Taking into consideration, the morphological and numerical data on the Indian species of the genus *Glossopteris,* the reasons for its extinction are discussed. Various reasons have been attributed to this failure. The subject still evokes curiosity, as the assumptions put forward so far do not satisfactorily explain the scale and magnitude of extinction of *Glossopteris,* which had reached its zenith in Late Permian. In addition to the documented reasons, paucity of glossopterid fructifications in Triassic points towards possibility of changes in the seed production ability and seed fertility pattern, ultimately leading to the disappearance of the plant. Besides, biological competition, predation, environmental factors like hostile arid climate and other factors might have further influenced extermination of the plant.

Keywords: *Glossopteris;* Extinction; Permian; Triassic.

INTRODUCTION

Extinction is the inevitable lot of species - a fact attested by the fossils in museums. In the history of earth, there have been occasions when extinctions reached rare calamitous levels and permanently altered the nature of life. Extermination of *Glossopteris* is part of one such mass extinction event.

The genus *Glossopteris* Brongniart, which forms the bulk of the flora of Permian rocks of Gondwanaland, is widely distributed in India both horizontally and vertically. The leaves

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are preserved as impressions and compressions and occur in almost all the important basins of India. No petrified leaf is known from India.

The genus made its appearance in Talchir (Early Permian) where it is represented by a few species and later expanded in successive younger horizons, viz., Karharbari, Barakar, Barren Measures Succession and Raniganj. However, in Early Triassic, the number of species gradually declined and later perished. (Table 1)

Horizontally, the genus is widely distributed in Damodar, Son, Wardha-Godavari and Mahanadi valleys besides Satpura Basin and Rajmahal region (i.e., mainly eastern and central India). Despite the wealth of data accrued on the subject and some of the recent speculations made by various workers (Srivastava 1969, 1971, 1979; Banerji *et al.* 1976; Banerjee 1979a,b, 1987; Bose & Zeba-Bano 1979; Chandra & Surange 1979; Srivastava 1979, 1992; Chandra & Srivastava 1981, 1982; Bajpai & Tewari 1990; Tewari 1990, 1996a,b; Chandra 1992; Chandra & Singh 1992; Chandra & Tewari 1992; Maheshwari & Tewari 1992; Srivastava & Tewari 1996; Tewari & Srivastava 1996, 2000), the extermination of *Glossopteris* still evokes curiosity.

Glossopteris and allied genera viz., *Gangamopteris, Rubidgea, Belemnopteris, Rhabdotaenia, Palaeovittaria, Maheshwariphyllum, Surangephyllum*, etc., are basically simple leaves. The typical flora of Triassic - the *Dicroidium* flora comprises various groups as, lycopodiales, equisetales (pteridophytes), pteridospermales, bennettitales, cycadales, coniferales, ginkgoales (gymnosperms), etc. The latter bear mostly compound pinnate leaves. The conditions in Triassic, though suited for compound pinnate leaves of gymnosperms by viz *Pterophyllum, Pteronilssonia* etc., were nevertheless

Age	Formation	No. of species
Triassic		30
Late Permian	Kamthi*	47
	Raniganj	66
Middle Permian	Barren Measures Succession	16
	Barakar	64
Early Permian	Karharbari	17
	Talchir	6

** Kamthi is equivalent to Raniganj Formation and is the name given to Late Permian rocks of Hinjrida Ghati Section, Handappa, Dhenkanal District, Orissa, India.*

TABLE 1: Numerical Distribution of ***Glossopteris*** *species during Permian of India.*
QUADRO 1: Distribuição quantitativa das espécies de ***Glossopteris*** *durante o Permiano na Índia*

Age	Shape	Apex	Base	Midrib	Venation Pattern and Meshes
Triassic	Ovate, Linear lanceolate, oblanceolate, narrow, elliptic, margins entire	Acute, obtuse	Acute decurrent, acute - normal	Distinct, persistent, stout or narrow	Venation dense or open, veins arched backwards, , meshes elongate, narrow, either uniform or broader near midrib
Late Permian Raniganj / Kamthi	Lanceolate, obovate, elliptic, oblong, cordate, ovate, circular, oblanceolate, orbicular, linear oblong, spathulate, oblong, lorate, elliptic, margins sometimes undulate or lobed	Acute, obtuse, acuminate, retuse, emarginate, mucronate	Attenuate, tapering, petiolate, cordate, round, obtuse, decurrent, cuneate, truncate, auriculate, acute – normal, obtuse – normal, obtuse - cuneate	Stout, persistent, strong distinct elevated, striated, sometimes gradually tapers in the apical region	Venation dense or open, veins arched, backwards, or at rightangle to midrib or radiating away from midrib, meshes sometimes short & broad near midrib and narrower near margin or small, narrow, elongate,trapezoidal or broad, pentagonal, polygonal
Middle Permian Barren Measures Succession Barakar	Linear,Lanceolate, oblanceolate, pandurate, elliptic,oblong, spathulate,linear, lorate, margins smooth	Acute, obtuse, rounded, retuse	Attenuate, petiolate, narrow, acute - normal, obtuse - cuneate	Either flat striated, evanescent with pits or strong stout, thick, elevated, distinct, persistent	Venation dense or open, veins either arched backwards or at right angles to midrib; meshes either narrow, elongate, trapezoidal or polygonal, hexagonal, pentagonal
Early Permian Karharbari Talchir	Spathulate,pandurate, oblong, lorate, lanceolate, linear, oblanceolate, narrow, obovate, elliptic, margins smooth, wavy undulate	Obtuse, rounded, sometimes retuse, notched	Narrow, simple, unspecialized, acute-cuneate, tapering, acute-normal, hastate	Flat, slender, evanescent, striated, sometimes very wide, distinct, sometimes persistent, sometimes present in basal 2/3 part	Dense venation, veins usually arched backward, sometimes horizontal, meshes narrow, elongate, trapezoidal, sometimes broad & short near midrib

Note: Name of the species have not been included as they are numerous and hold little significance for the present theme of the paper

TABLE 2: Morphological diversity in the genus ***Glossopteris*** *during Permian and Triassic.*
QUADRO 2: Diversidade morfológica no gênero ***Glossopteris*** *durante Permiano e Triássico.*

still congenial for the growth of simple *Glossopteris* leaves as is evident from versatility in morphological characters (Table 2).

An analysis of table 2 and review of the study of earlier workers show that the genus *Glossopteris* exhibits a great diversity in its external characters. The species found in older horizons viz., Talchir and Karharbari are pandurate, oblong, spathulate, lanceolate, oblanceolate in shape (the last four, however, occur throughout the lower Gondwana), with obtuse apices, narrow, simple, unspecialised bases (which may be petiolate), flat, evanescent and striated midrib, dense veins and narrow, trapezoidal meshes.

The species of younger horizons are usually lanceolate, elliptic, ovate, cordate in shape with acute, acuminate, retuse, emarginate apices; round cuneate, truncate, attenuate, auriculate bases; lobed margins (along with entire margins); stout persistent, strong, distinct, elevated midrib; fewer lateral veins apart from dense veins (course of veins is usually arched, sometimes at right angles to midrib or radiating away from midrib) and broad, pentagonal, hexagonal or polygonal meshes apart from trapezoidal, oblong meshes (Chandra & Surange 1979, Maheshwari & Tewari 1992).

The cuticular features, unlike external features, do not show any set pattern or an evolutionary trend and are rather inconsistent in their occurrence, for example, usually the cuticles are either hypostomatic or amphistomatic with differentiated cells over mesh and vein areas (cells over veins are elongate, narrow, squarish or irregular rectangular and arranged end to end in rows and those over meshes are usually polygonal and irregularly arranged - the midrib has a mixture of both these kinds of cells); straight anticlinal walls and unspecialised surface walls. However, sinuous, sinuous to straight, undulate or arched lateral walls and papillate surface walls (each cell with a single circular or dome shaped papilla or with numerous, small papillae) are of frequent occurrence. Laminated and pitted lateral walls and striated and mottled surface walls occur only in a few species of Raniganj (Upper Permian) Formation. Guard cells of stomata are normal in species of Karharbari, Barakar (Permian) and Lower Tiki (Triassic) formations; and thickened and sunken in species of Raniganj Formation (Upper Permian). Subsidiary cells are either with or without papillae. Papillae when present, usually overhang the guard cells, see Sahni (1923), Pant (1968), Pant & Gupta (1968, 1971), Pant & Singh (1971), Pant & Singh (1974), Tewari (1988, 1990), Maheshwari & Tewari (1992).

DISCUSSION

Climate has been identified, as the chief factor for the evolutionary failure of *Glossopteris* by various workers. It has been unanimously accepted that the genus *Glossopteris* and other allied elements arose as a result of glacigene event. See Lele (1976); Chandra & Chandra (1988), Maheshwari *et al.* (1988), Chandra (1992) and reached their acme in Late Permian with mellowing of climate. *Glossopteris* even survived severe arid conditions of Triassic. An analysis of table 2 shows gradual morphological adaptations and variations in different characters in order of superposition. In Triassic, though the number of species declined, the variations in characters are in no way less than those present in older horizons. This indicates adaptability of the genus towards the changing climate. The increased morphological diversity in the genus was perhaps in response to the climatic changes. However, survival of *Glossopteris* in hot arid conditions of Triassic is worth pondering. The logical questions then arises, that, was climate the sole cause for the extinction of the genus or were there other inter-related factors equally responsible as well.

Record of an extant leaf *Acrostichum aureum* Linn. of the family Polypodiaceae from South Andaman islands by Jafar & Kar (1996) also raises doubts about palaeo-environmental conditions under which the genus *Glossopteris* thrived. Accordingly, the leaves of *Acrostichum* are considered remarkably analogous to *Glossopteris* leaves. This plant typically grows in brackish or salt water and is an important element of mangrove community. Since *Glossopteris* is a fresh water form, and arose as a response to glacigene event, its striking similarity with the leaves of *Acrostichum*, which is adapted to present warm humid rain forests, needs serious consideration in climatic interpretations with respect to extinction of the former in Triassic. Chandra & Chandra (1988), however, are of the view that the parameters used for interpreting climate of modern plants, though used for determination of palaeoecology, have drawbacks of their own since there are always some limitations while dealing with fragmentary fossil evidences. According to them, interpretation of ecology from botanical structures can be very misleading and though evolution of certain structures may have resulted as response to a particular environmental condition, it is not always true that plants possessing these structures are found in the same environment. Chandra & Chandra (1988) derive support from the fact that identification and determination of species of fossil plants is often quite arbitrary and an assemblage may contain mixture of plants belonging to quite distinct habitats. However, there are several factors, which in combination can be linked to both development and extinction of *Glossopteris*. Raghubanshi *et al.* (1991, p. 89) are of the view that complex biological patterns are not the result of a single causal factor – "the effect of one factor may be overridden or modified by others." According to them, a number of features, viz., time, spatial heterogeneity, biological competition, predation, climatic stability, productivity, temporal heterogeneity, lithospheric complexity, environmental harshness and species energy hypothesis are responsible for species diversity or extinction. They further opine that stable climates allow the evolution of finer specializations and adaptations because of the relative constancy of resources than do areas with more erratic climatic regimes.

Connel & Orias (1964) suggest that combined with the factor of climatic stability, increased productivity would increase species diversity. This hypothesis states that everything being equal, as environment increase in productivity, diversity will increase. Thus, environment during Upper Permian was highly favourable for productivity of *Glossopteris* as is also supported by reports of number of fructifications during this period, as Surange & Maheshwari (1970), Surange & Chandra (1975), Chandra & Surange (1977a,b,c,d,e), Banerjee (1979a,b) and Tewari (1996a,b).

Habitats with a more complex or variegated structure contain more species than do simpler habitats. Raghubanshi *et al.* (1991) are of the view that coexistence of more complex environment, i.e. the more heterogeneous and complex the physical environment is, the more complex and diverse will be the plant and animal communities. Ananthakrishnan (1999, pp. 356-357) is of the similar consideration.

According to him, "species living in heterogeneous environment show considerable phenotypic plasticity adding to fitness of individuals in diverse environment. In such heterogeneous environments, there are adaptive advantages to the genomes that allow for environmentally induced expression of phenotypes. Hence taxa are the units that contain genetic diversity and the units that make up ecological diversity. This results in cladistics". Since the Permian Period observed extremely cold to milder conditions with varying rainfall and other associated ecological conditions, it can be assumed that the physical environment during this period was quite complex and heterogeneous and hence favoured existence of different structurally diverse *Glossopteris* species.

POSSIBLE FACTORS RESPONSIBLE FOR EXTINCTION OF *GLOSSOPTERIS*

The increased morphological diversity of *Glossopteris* during Late Permian raises doubts regarding currently accepted reasons for the extinction of the genus. The plant that was so well possessed with simple as well as highly complex structural morphology and that too, in different climatic conditions of Permian and Triassic, i.e., from cold to warm arid, surely would have been critically affected by factors other than the climate as well to reach its extermination.

Climate induced mutational changes

Seward (1922, 1924) was of the opinion that the onset of catastrophic climatic changes in the geological past, like sudden rise of temperatures during widespread volcanic upheavals during some periods might have been responsible for large-scale extinction of old forms and abrupt appearance of new forms. According to Sahni (1937a,b, 1939), radiations, chemicals, sudden heating and chilling, etc., can induce mutations responsible for disappearance of previous vegetation and appearance of newer flora. Pant (1988) was of the similar view and held responsible mutational changes for incoming of new elements. According to him, "some old forms adapted themselves for the changed conditions and continued their existence with dwindled strength of numbers". Accordingly, catastrophic climatic events destroy biota and hence relatively little time is available for evolution of plant communities. There is also a possibility of ecological and evolutionary saturation.

Seed sterility

Compared to Permian, there are relatively few reports of occurrence of glossopterid fructifications from Triassic (Bose *et al.* (1977) and Banerji & Bose (1977). Scarcity of glossopterid fructifications in Triassic suggests that environment was not favourable for propagation of *Glossopteris*. Another reason might be the sterility of the seeds, i.e. the seeds might have lost their fertility and hence fewer *Glossopteris* species were produced.

Microspatial heterogeneity, soil toxicity

Another factor is microspatial heterogeneity i.e., type of soil, soil particle size, topography, lithology, soil pH, soil texture, temperature, etc. Extinction of the plant in Triassic may also be attributed to the fact that the changed soil environment was not suited for its growth. Possibility of certain toxins present in the soil adversely affecting the survival chances of the plant cannot be denied.

Biological competition

Biological competition is another important factor. As competition increases, organisms become more specialized and niche size decreases, causing an increase in species diversity. (MacArthur 1965, 1972). This might have happened during Raniganj Formation (Upper Permian) when maximum number of species with a greater range of diversity in structural features existed. However, in Triassic, the genus could not compete with the new elements and only those species thrived which were more resistant and adaptable.

Predation factor

Another factor, worth pondering is - was Mesozoic fauna responsible for extinction of *Glossopteris*? End of Permian witnessed massive extinction of insects resulting in disappearance of six orders and over half of all families of insects. Renewal at order and family level was initially particularly slow (Anderson 1999, p.45). The fauna that came into existence Triassic onwards, in all probabilities required altogether different vegetation to feed upon. In this context, support is gained from Ananthakrishnan (1999, p. 358) who is of the view that "Evolutionary innovations in plant defenses and insect feeding habits seemed to have spurred their adaptive radiation. Escalation of plant defenses has resulted in increased diversity and plant feeding has stimulated insect diversification with changes in chemical profiles exerting different behavioral interactions." According to him, taxonomic and functional aspects of community structure incorporated in food web for energy flow are equally important. Insects and plants are integral part of complex web of multi species interactions. There is a possibility that *Glossopteris* was unable to acquire proper defenses against the Triassic fauna and hence perished. However, Pianka (1966) and Raghubanshi *et al.* (1991) are of the view that whereas, vegetation complexity is directly determined by climatic factors, it is only indirectly related to the faunal diversity.

Time and space factor

Another hypothesis, which supports coexistence of a number of species, is time and space related i.e. longer the growing season, more the diversity (Pianka 1966; Raghubanshi *et al.* 1991). However, Anathakrishnan (1999) suggests that long term temporal aspects of species diversification can be assessed only from phylogenesis and evidence of phylogenesis is available from molecular characterization. The potential of molecular phylogenesis in revealing evolutionary radiation is important i.e. genetic makeup of an organism plays an important role in its growth, development, climax and extinction.

Geomorphological complexity

Cracraft (1985) opines that the rate of speciation is affected by the rate of change of lithospheric evolution operating through geomorphological complexity. Increase in lithospheric complexity is directly proportional to species diversity. He is also of the view that there is an increased probability of extinction with respect to an increase in environmental harshness. Environmental rigour is a measure of physiological stress felt by the populations. According to Raghubanshi *et al.* (1991, p. 92) "Since rate of biological diversification is a function of balance between rates of speciation and extinction, lithospheric complexity together with environmental harshness is responsible for species diversity gradients.”

Solar energy factor

Turner *et al*. (1988) have given solar energy hypothesis for species richness and diversity. According to them, the species richness is directly related to the availability of solar energy. Hence, the diversification of organisms is directly proportional to active absorption of solar energy. On the contrary, if solar energy absorption ceases, they disappear. *Glossopteris* might have undergone certain physiological changes in Triassic, which negatively influenced its solar energy absorption ability.

CONCLUSION

Analysing the above discussed theories, assumptions and evolutionary principles, it can be conclusively said that a combination of factors were responsible for the extinction of *Glossopteris* in Triassic. Species always respond to and try to adjust according to the changing environment. Dynamics of the changing climate during the Triassic is well accepted. The morphological diversity, which evolved over time in *Glossopteris*, bears testimony to the efforts made by the genus to adapt itself to the changing conditions. Inspite of all these adaptations, the genus perished. It is quite possible, that it failed to change enough, or was forced to change in a self destructive nature due to pressures and influences exerted by the then changing environment. Many such factors having potential to change the morphology, physiology, reproductive biology and genetic composition of the plant, etc., were present. Changing ratio of flora to flora, flora to fauna, temperature variation, solar radiation level, composition and relative ratios of different atmospheric gases, dynamics of various gas cycles (like nitrogen cycle, CO_2-O_2 cycle, etc.) in the nature, soil composition, soil toxins, humidity level, concentration of various elements and chemicals in water and soil, the herbivorous faunal population, resistance level of the plant and its chemical composition, all individually, collectively and in combination, were responsible for bringing about morphological and physiological changes in the plant. One such important physiological factor that could have adversely affected the survival chances of *Glossopteris* is change in seed production and/or fertility pattern. A combination of the then climatic and environmental factors could have triggered permanent changes in the genetic make up of the plant so that it stopped producing seeds or produced sterile seeds. Scarcity of glossopterid fructifications in the Triassic is a strong pointer to this. Alternatively, the dry arid climate of Triassic may have proved too hostile to seed germination, resulting ultimately in its extermination over passage of time.

Holistic interpretation of the *Glossopteris* extinction phenomenon indicates that during Triassic, following interrelated events with potential to affect the biodiversity were happening almost simultaneously:

a) continental drift
b) inevitable temperature changes due to (a)
c) change in land pattern, texture and composition due to (a)
d) change in humidity level due to (a) and (b)
e) drastic extinction of insects
f) advent of dinosaurs

Not much is known about the microclimate, which brings changes in the morphology and physiology of the life forms and critically affects their survival potentialities. It is proven that a change of more 1ºC in the minimum or maximum temperature brings about calamitous changes in the environment and biodiversity (Raunkier *et al*. 1934). Massive extinction of terrestrial and marine fauna during Upper Permian - Triassic might have brought sudden changes in the overall spatial heterogeneity and various gas cycles of the nature and exerted physiological stress on the genus, which was at its zenith during Permian.

The predation of the *Glossopteris* by the then fauna, might be a potential reason for its dwindling population. Extinction of *Glossopteris* and advent of giant dinosaurs may not be just a co-incidence. The food chain of nature, if disturbed massively, has tremendous potential to bring about catastrophic changes.

Apparently, the genus flourished during Permian. However, later towards the Early Triassic, changes in the micro environment, geology, temperature, floral and faunal population, humidity level, solar radiation level etc., exerted physiological stress on the genus. The genus either proved slow to respond, or failed to respond with adequate levels of morphological, structural, physiological and genetic changes. Alternatively, the interrelated dynamics, rapidity and complexity of the above mentioned factors induced unfavorable changes in the physiology and genetics of the plant and finally the genus succumbed to these pressures and perished. The evolving giant herbivorous fauna could have hastened the demise of *Glossopteris* in Triassic.

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REFERENCES

ANANTHAKRISHNAN, T.N. 1999. Multidimensional links in biodiversity research. In: integrated exercise. *Curr. Sci.*, **77:** 356-358.

ANDERSON, J.M. 1999. Biodiversity Past. in: ANDERSON JM (ed). *Towards Gondwana Alive*, Gondwana Alive Society, National Botanical Institute, Pretoria, South Africa, p. 44-45.

BAJPAI, U. & TEWARI, R. 1990. Plant fossil from upper beds of Raniganj Formation in Jharia Coalfield. *The Palaeobotanist*, **38:** 43-48.

BANERJEE, M. 1979a. Glossopteridean fructifications: 2. On the revision of *Ottokaria* Zeiller and the occurrence of *O. raniganjensis* Banerjee from the Raniganj Formation (Upper Permian) of India. *Indian J. Earth Sci.*, **5:** 129-140.

BANERJEE, M. 1979b. Seed-bearing glossopteridean fertile organs. In: LASKAR, B. & RAJA RAO, C.S. (eds). INTERNATIONAL GONDWANA SYMPOSIUM, 4º, Calcutta, 1977 Papers, **1:** 122-132.

BANERJEE, M. 1987. A study of the frequency of megaplant fossils in Raniganj Formation (Upper Permian) of Raniganj Coal Field, India. *Geol. Surv. India Spec Publ.* (11), **1** Section -2 (Gondwana): 261-288.

BANERJI, J. & BOSE, M.N. 1977. Some Lower Triassic Plant Remains from Asansol Region, India. *The Palaeobotanist*, **24:** 202-210.

BANERJI, J.; MAHESHWARI, H.K.; BOSE, M.N. 1976. Some plant fossils from the Gopad River Section near Nidpur, Sidhi District, Madhya Pradesh. *The Palaeobotanist*, **23:** 59-71.

BOSE, M.N.; BANERJI, J.; MAITHY, P.K. 1977. Some plant remains from Ramkola-Tatapani Coalfield, Madhya Pradesh. *The Palaeobotanist*, **24:** 108-117.

BOSE, M.N. & ZEBA-BANO. 1979. On some cycadophytic leaves from the Jabalpur Series. *The Palaeobotanist*, **26:** 1-9.

CHANDRA, S. 1992. Changing patterns of the Permian Gondwana vegetation. *The Palaeobotanist*, **40:** 73-100.

CHANDRA, S. & CHANDRA, A. 1988. Vegetational changes and their climatic implications in coal-bearing Gondwana. *The Palaeobotanist*, **36:** 74-86.

CHANDRA, S. & SINGH, K.J. 1992. The genus Glossopteris from the Late Permian beds of Handappa Orissa. *India Rev. Palaeobot. Palynol.*, **75:** 183-218.

CHANDRA, S. & SRIVASTAVA, A.K. 1981. A new species of *Glossopteris* from the Barakar Formation of Lower Gondwana of India. *The Palaeobotanist*, **27:** 166-173.

CHANDRA, A. & SRIVASTAVA, A.K. 1982. Plant fossils from the Talchir and coal-bearing formations of South Rewa Gondwana Sequence and their biostratigraphic significance. *The Palaeobotanist*, **30:** 143-167.

CHANDRA, S. & SURANGE, K.R. 1977a. Fertile bracts and scales of *Glossopteris* fructifications from Lower Gondwana of India. *The Palaeobotanist*, **24:** 195-201.

CHANDRA, S. & SURANGE, K.R. 1977b. Cuticular studies of the reproductive organs of *Glossopteris*. Part II. *Cistella type fructification - Plumstaediostrobus ellipticus* gen. et. sp. nov. attatched on *Glossopteris taenioides* Feistmantel. *The Palaeobotanist*, **23:** 161-175.

CHANDRA, S. & SURANGE, K.R. 1977c. Some scale leaves and sporangia from Raniganj Coalfield, India. *The Palaeobotanist*, **24:** 245-253.

CHANDRA, S. & SURANGE, K.R. 1977d. Cuticular studies of the reproductive organs of *Glossopteris* Part III – Two new female fructifications – *Jambadostrobus* and *Vensustostrobus* – borne on *Glossopteris* leaves. *Palaeontographica*, **B164:** 127-152.

CHANDRA, S. & SURANGE, K.R. 1977e. Cuticular studies of the reproductive organs of *Glossopteris*. Part IV. *Vensustostrobus indicus* sp. nov. *The Palaeobotanist*, **24:** 149-160.

CHANDRA, S. & SURANGE, K.R. 1979. Revision of the Indian species of *Glossopteris*; *Monograph 2*, pp. 1-291. Birbal Sahni Institute of Palaeobotany, Lucknow, India.

CHANDRA, S. & TEWARI, R. 1992. *A catalogue of fossil plants from India. Part 2. Palaeozoic and Mesozoic megafossils*. Birbal Sahni Institute of Palaeobotany, Lucknow, India.

CONNEL, J.H. & ORIAS, E. 1964. The ecological regulation of species diversity. *Am. Nat.*, **98:** 399-414.

CRACRAFT, J. 1985. Biological diversification and its causes. *Ann. Missour. Bot. Gdn.*, **72 :** 794-822.

JAFAR, S.A. & KAR, R.K. 1996. Glossopterid Flora: A case for Wetland Mangrove Vegetation? in: INTERNATIONAL GONDWANA SYMPOSIUM, 9º, Gondwana Nine, Hyderabad 1994, India, **1:** 331-338.

LELE, K.M. 1976. Palaeoclimatic implications of Gondwana floras. *Geophytology*, **6:** 207-229.

MACARTHUR, R.H. 1965. Patterns of species diversity. *Biol. Rev*., **40:** 510-533.

MACARTHUR, R.H. 1972. *Geographical Ecology*; Harper & Row, New York.

MAHESHWARI, H.K. & TEWARI, R. 1992. Epidermal morphology of some Indian species of the genus *Glossopteris Brongniart*. *The Palaeobotanist*, **39**: 338-380.

MAHESHWARI, H.K.; BAJPAI, U.; TEWARI, R. 1988. Climatic reflections in the Permian vegetation of Indian peninsula. in: ULBRICH H. & ROCHA CAMPOS AC (eds). GONDWANA SEVEN, Instituto de Geociências Universidade de São Paulo, *Proceedings*, pp. 549-556.

PANT, D.D. 1968. On the stem and attachment of *Glossopteris* leaves. *Phytomorphology*, **17** : 351-369.

PANT, D.D. 1988. The origin, rise and decline of Glossopteris Flora , with notes on its palaeographical northern boundry and age. *The Palaeobotanist*, **36**: 106-117.

PANT, D.D. & GUPTA K.L. 1968. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part 1. *Palaeontographica*, **B124**: 45-81.

PANT, D.D. & GUPTA K.L. 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part 2. *Palaentographica*, **B132:** 130-152.

PANT, D.D. & SINGH, K.B. 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. *Palaeontographica*, **B135:** 1-40.

PANT, D.D. & SINGH, R.S. 1974. On the stem and attachment of *Glossopteris* and *Gangamopteris* leaves. Part II. Structural features. *Palaeontographica*, **B147:** 42-73.

PIANKA, E.R. 1966. Latitudinal gradients in species diversity : a review of concepts. *Am. Nat.*, **100:** 33-46.

RAGHUBASNHI, A.S.; SINGH, J.S.; VENKATACHALA, B.S. 1991. Environmental change and biological diversity : Present, past and future. *The Palaeobotanist*, **39:** 86-109.

RAUNKIER, C.; EGERTON, F.N.; GILBERT-CARTER, H. 1934. Life Forms of Plants and Statistical Plants Geography (History of Ecology Series), Oxford University Press.

SAHNI, B. 1923. On the structure of the cuticle in *Glossopteris angustifolia* Brongn. *Rec. Geol. Surv. India*, **54:** 268-270.

SAHNI, B. 1937a. Speculations on the climates of the Lower Gondwanas of India, in: INT. GEOL. CONG., XVIII, Moscow 1937, pp. 257-258.

SAHNI, B. 1937b. Revolution in the plant world. *Proc Nat. Acad. Sci. India*, **7:** 46-60.

SAHNI, B. 1939. Recent advances in Indian palaeobotany (Presidential Address Bot. Sec.). in: INDIAN SCI. CONGR., 25th, Calcutta, Pt. II, Lucknow University Studies no. 2. *Proc*.

SEWARD, A.C. 1922. *A summer in Greenland*. Cambridge.

SEWARD, A.C. 1924. The leaf records of plant life (Presidential Address: Geol.Soc., London) Q. Jl. *Geol. Soc. London*, **80:** 61-98.

SRIVASTAVA, A.K. 1979. *Studies in the Glossopteris Flora of India* – 44. Raniganj plant megafossils and miospores from Auranga Coalfield, Bihar. *The Palaeobotanist*, **26:** 72-94.

SRIVASTAVA, A.K. 1992. Plant fossil assemblages from the Barakar Formation of Ranignaj Coalfield, India. *The Palaeobotanist*, **39:** 281-302.

SRIVASTAVA, A.K. & TEWARI, R. 1996. Plant fossils from the Barakar Formation, Auranga Coalfield, Bihar. *Geophytology*, **26:** 83-88.

SRIVASTAVA, S.C. 1969. Two new species of *Glossopteris* from the Triassic of Nidpur, Madhya Pradesh, India. In: SANTAPAU, H *et al.* (eds). *J. Sen Memorial Volume*. Bot. Soc. Bengal, Calcutta, p. 299-303.

SRIVASTAVA, S.C. 1971. Some gymnospermic remains from the Triassic of Nidpur, Sidhi District, Madhya Pradesh. *The Palaeobotanist*, **18:** 280-290.

SRIVASTAVA, S.C. 1979. The Triassic Flora of Nidpur, India. in: LASKAR, B. & RAJA RAO, C.S. (eds.), INTERNATIONAL GONDWANA SYMPOSIUM, 4º, Calcutta, 1977, Papers, **1**: 105-108.

SURANGE, K.R. & CHANDRA, S. 1975. Morphology of the gymnospermous fructifications of Glossopteridales from India. *Palaeontographica*, **B129:** 178-192.

SURANGE, K.R. & MAHESHWARI, H.K. 1970. Some male and female fructifications of Glossopteridales from India. *Palaeontrographica*, **B129:** 178-192.

TEWARI, R. 1988. *Contribution to the Palaeobotany of Permian Gondwana of India.* Ph.D. thesis vols. 1 & 2, Kanpur University, Kanpur, India.

TEWARI, R. 1990. Epidermal morphology of Permian Gondwana gymnosperms; *The Palaeobotanist*, **38:** 39-42.

TEWARI, R. 1996a. Glossopterid fructifications from Upper Permian of India. A morphological correlation. *The Palaeobotanist*, **45:** 315-323.

TEWARI, R. 1996b. Palaeobotanical investigations from the Raniganj Formation of the Jharia Coalfield. in: INTERNATIONAL GONDWANA SYMPOSIUM, 9º, Gondwana Nine, Hyderabad, 1994, **1**: 135-142.

TEWARI, R. & SRIVASTAVA, A.K. 1996. Plant fossils from the Barakar Formation, Jharia Coalfield, Bihar. *Geophytology*, **25:** 35-39.

TEWARI, R & SRIVASTAVA A.K. 2000. Plant fossil assemblage from Talchir Formation Auranga Coalfield, Bihar, India. *The Palaeobotanist*, **49:** 23-30.

TURNER, J.R.G.; LENNON, J.J.; LAWRENSON, J.A. 1988. British bird species distributions and the energy theory. *Nature*, **335:** 541.