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Taxonomy and diversity of the genus *Glossopteris*

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ABSTRACT

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The speciation of *Glossopteris* leaves in Permian Gondwana of India is re-examined. It is based on study of thousands of specimens collected from Barakar Formation of Karanpura and Bokaro Group of Coalfields. The study of specimens of modern plants showing variation in shape and size of leaves within same species (sometimes within same plant) and survey of published literature, the author was fascinated to express the ideas about the parameters which may be helpful in speciation of the genus *Glossopteris*. Here, morphological characters have been critically analysed in order to find a reasonable basis for precise specific delimitations. The morphological circumscriptions have been further verified by characters of cuticle which have been taken as associated or supportive characters only. The size and shape of leaves have given secondary importance. The Diversity and the total number of species found in time and space have been tabulated.

Key-words— *Glossopteris*, Permian, Morphology, Cuticle, Speciation, Gondwana, India.

ग्लॉसोप्टेरिस वंश का वर्गीकरण विज्ञान तथा विविधता

शिवमोहन सिंह

सारांश

भारत के परमियन युगीन गोण्डवाना की *ग्लॉसोप्टेरिस* पत्तियों के जाति उद्‌भवन का पुनः परीक्षण किया गया. यह अध्ययन कोयला क्षेत्रों के करनपुरा एवं बोकारो समूह के बराकर शैलसमूह से एकत्र किए गए हजारों प्रादर्शों से किया गया है. कुछ प्रजातियों (कभी-कभी एक ही पौधे के भीतर) के अन्दर पत्तियों के आकार एवं आमाप में परिवर्तन प्रदर्शित करने वाले आधुनिक पौधों के प्रादर्शों का अध्ययन तथा प्रकाशित साहित्य का सर्वेक्षण करते हुए लेखक उन मानकों के बारे में विचार प्रकट करते हुए हर्ष का अनुभव करता है, जो *ग्लॉसोप्टेरिस* वंश के जाति उद्‌भवन में सहायक हुए हैं. यहाँ संक्षिप्त विशिष्ट परिसीमन हेतु औचित्यपरक आधार ज्ञात करने हेतु संरचनात्मक अभलक्षणों परिमितों का आलोचनात्मक विश्लेषण किया गया है. संरचनात्मक परिमितों को उन उपचर्मीय लक्षणों के लिए अभिप्रमाणित किया गया है, जिन्हें मात्र सहयोगी अथवा सहभागी लक्षणों के रूप में लिया गया है. पत्तियों के आकार एवं आमाप को द्वितीयक महत्त्व दिया गया है. विविधता तथा दिक् एवं काल में पाई गई प्रजातियों की कुल संख्या की तालिका निर्मित की गयी है.

संकेत शब्द— *ग्लॉसोप्टेरिस*, परमियन, संरचना विज्ञान, उपचर्म, जाति उद्‌भवन, गोण्डवाना, भारत.

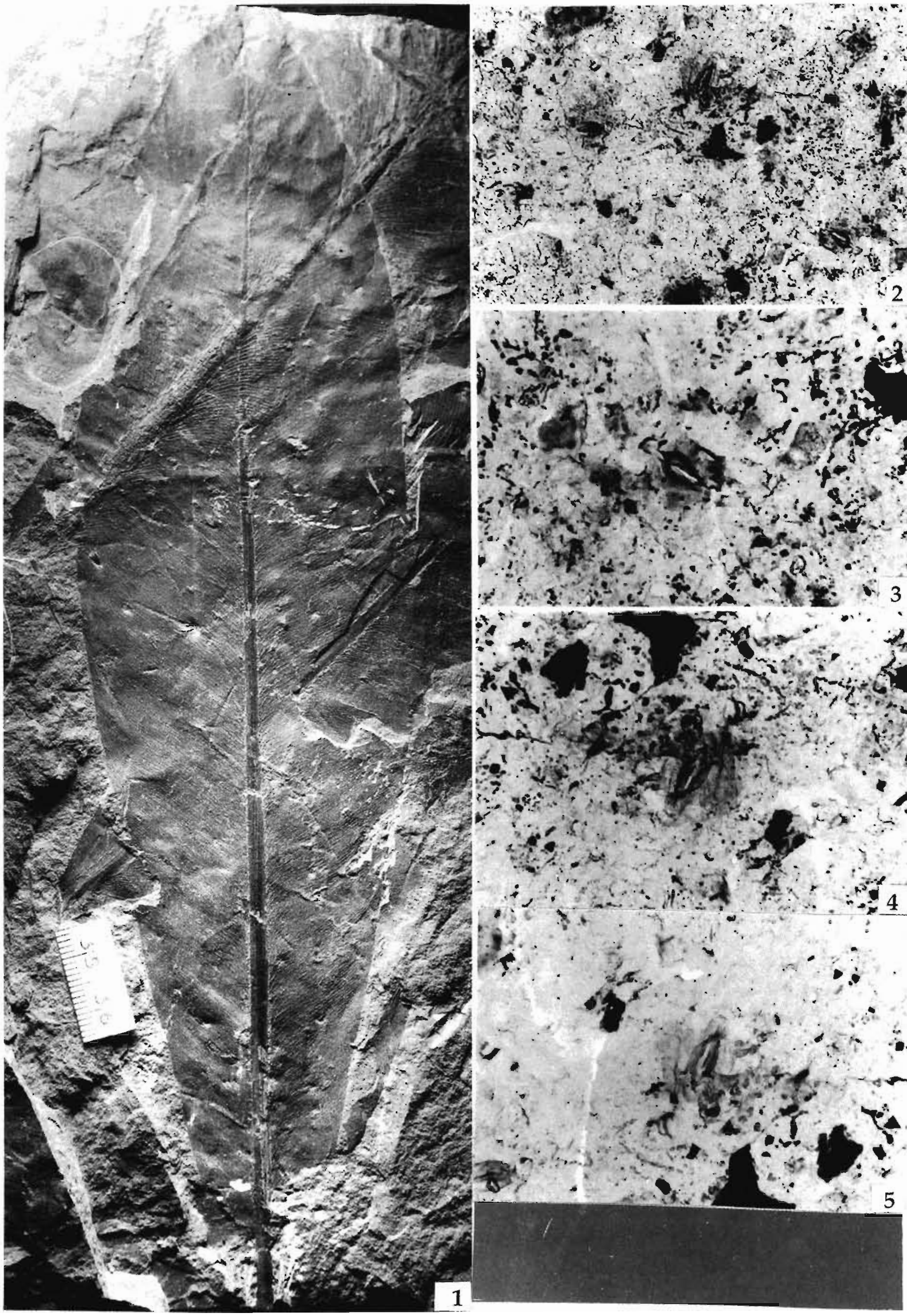

PLATE 1

INTRODUCTION

Though the genus *Glossopteris* is the most abundant of all plants in the Permian floras, it has not been circumscribed in definite species within a genus. The main reason for this was a complete lack of accepted criteria on which to base such classification. The first attempt in this direction was made by Arber (1905) whose system of specific circumscription has been widely followed. In view of earlier researches on the morphography and cuticular structure of leaves and on the nature of fructifications borne by these leaves; there is an apparent lack of agreement between the two systems of classification (Srivastava, 1957; Plumstead, 1958). Hence there is a greater need for further work in this direction and the evidences they obtained have to be correlated with those obtained by more critical studies on the fructification and the cuticular structures. Though the evidences provided by the cuticular and the fructifications are very important, their application is admittedly limited as most of the Lower Gondwana fossils occur more frequently as impressions. Hence the natural thing is to device a classification based on the morphographical characters. On the basis of morphography the retention of the taxonomic status of the present genus *Glossopteris* seems to be most advisable and advantageous inspite of the obvious difficulties sometimes encountered in determination of transitional forms. It is hoped that if due care is taken in identifying the specimens described in the Monograph of Chandra & Surange (1979), the cuticular species and the list of species given in Fig. 1 the most of the species will fit in one another and the number may become half. In the Karanpura & Bokaro Coalfields the circumscription of species made by studying more than one specimens and intensive observations have given 32 species (Thesis Shiv Mohan Singh, Contributions to the Early Permian flora of Karanpura and Bokaro Coalfields, 1998).

SYSTEMATICS

Genus—GLOSSOPTERIS Brongniart 1828

Type species—GLOSSOPTERIS BROWNIANA Brongniart 1828

Glossopteris is the most abundant fossil in the Permian floras of the Southern Hemisphere, that during the period comprised Australia, Antarctica, Africa, South America, and India, and possibly also the Arabian Peninsula. *Glossopteris* is a genus of tongue-shaped fossil leaves which have a robust to flat midrib that gives off secondary veins that dichotomise and anastomose. The genus was first recognised by Adolphe Brongniart (1828), the father of Palaeobotany. He recognised two species in the genus, viz., *G. browniana* var. *australisica* from Australia, *G. browniana* var. *indica* from India and *G. angustifolia* also from India. Schimper (1869) raised var. *indica* to the status of a species as *G. indica*. Dana (1849), Bunbury (1861) and Feistmantel (1876-1881, 1886, 1890) described a number of species of *Glossopteris* from India and Australia. Zeiller (1896) reported for the first time the epidermal structure of a leaf he identified as *G. indica*. The results of investigations in the genus done in the nineteenth century were summarised by Arber (1905). Though sporadic work continued in the early part of the twentieth century, the investigation got an impetus in the 1950s onwards when a lot of data was generated not only on the morphography and taxonomy of the leaves but also on the cuticular features and attached/associated fructifications. In spite of all this, there is still a controversy about the characters on which speciation in the genus should be based. Most workers preferred to separate forms into different species on the basis of minor differences while others believed in maintaining a few species by merging different forms of leaves into one, if most of the characters of such leaves were the same. These two schools of speciation have been termed "splitters" and "lumpers", respectively (Plumstead, 1962).

Seward (1897, p. 317) believed that size and shape are extremely dangerous guides in specific delimitation. Seward (1910) went to extent of suggesting that speciation based on venation and generic delimitation on the basis of presence or absence of a midrib is not justified. Earlier Arber (1905), a strong supporter of maintaining a few species only, re-classified species distinguished by earlier workers into thirteen species only. According to him "there existed a considerable variation in the form and shape of the leaf of the genus *Glossopteris* and in the details of the nervation, even in the fronds in which there is reason to believe belonged to the same plant". He did not take into account the characters of midrib, nature of apex and angle of divergence of secondary veins from the midrib as characters suitable for specific delimitation. He did think that the only constant character for speciation was the openness or close-ness of the secondary veins and hence the shape of meshes. However, Maheshwari (1966) opined that without knowing the whole plant, it was not possible to know whether there was such a variation in the same plant or even in the

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PLATE 1

1. *Glossopteris karanpuraensis* Kulkarni 1971, Specimen no. BSIP-38836-B (1/4578 A1). Barakar Formation, shales associated with Naditoli Seam, Sirka Colliery, South Karanpura Coalfield, Bihar. x nat. size.

2-5. Cuticle of *Glossopteris karanpuraensis*, probably of the stomatiferous surface, showing barely discernible lateral cell walls, and spindle-shaped stomata. Specimen no. BSIP-38836-B (1/4578 A1). 2 x 200. 3-5 x 400.

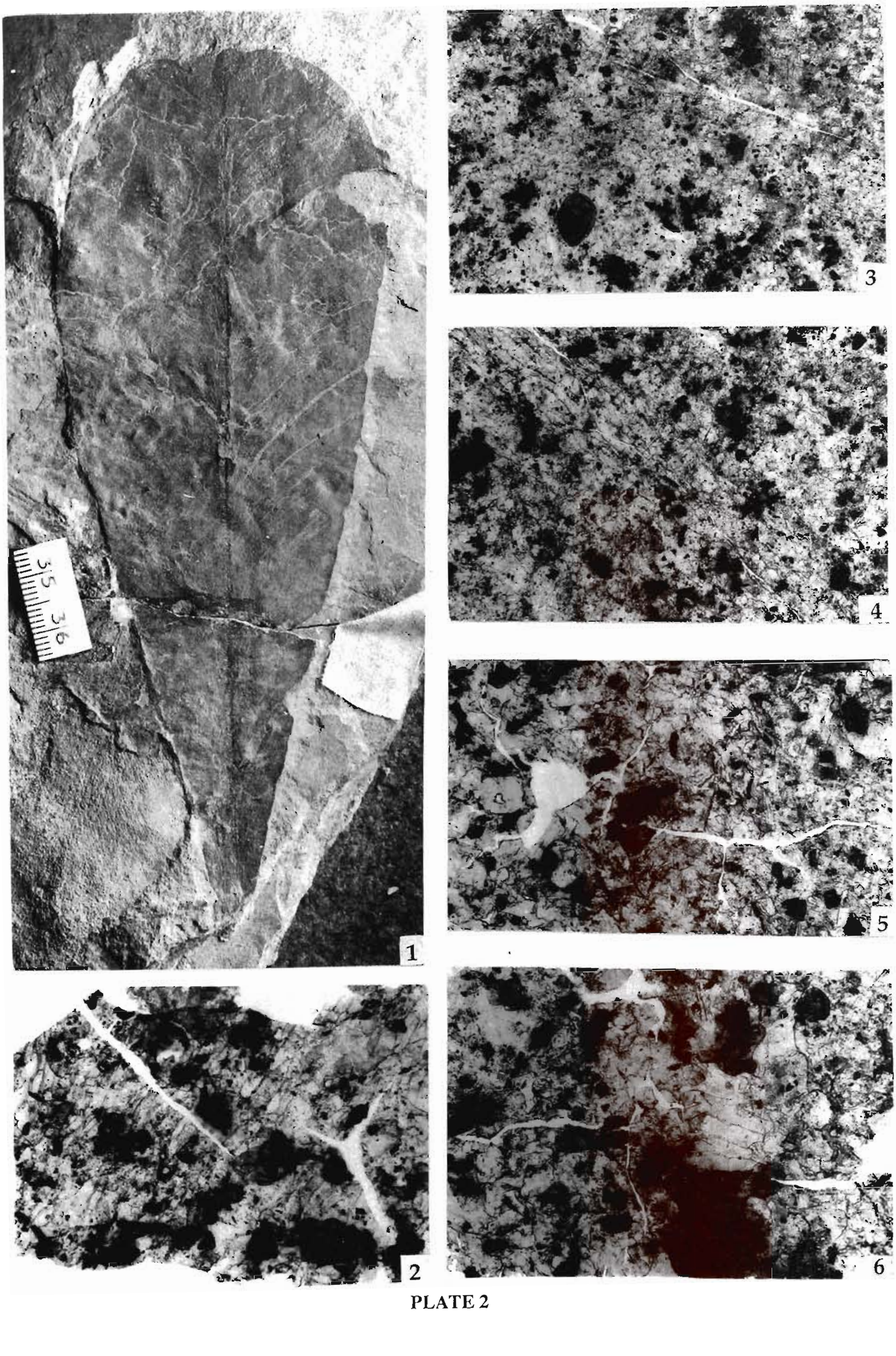

PLATE 2

same species of fossil leaves. He pointed out that in a character, the delimitation of its range is difficult and so the variation shall necessarily be an arbitrary one.

Before 1956 the speciation of *Glossopteris* was based on morphography, i.e., external features of the leaf. Zeiller (1896) and Sahni (1923) described the epidermal and cuticular structures of the leaves of *G. indica* Schimper and *G. angustifolia* Brongniart, respectively. Srivastava (1957) made an effort to delimit species on the basis of cuticular characters. He described features of the cuticle in 16 species of *Glossopteris*, 6 species of *Gangamopteris* and one species of *Palaeovittaria*. Surange and Srivastava (1957) classified these 23 species in six groups on the basis of totality of cuticular features. They thought that these groups could be of generic rank. However, later workers have not followed this line of thinking. It may be mentioned here that Høeg and Bose (1960) found that morphographically similar leaves may have different cuticular types. Recently Maheshwari and Tewari (1992) have found that morphographically different leaves may have similar looking cuticles. These two observations need to be examined in detail, particularly in the light of Birbal Sahni's reluctance to accept features of the cuticle as very good indicators of specific variation.

Pant (1958) and Pant and Gupta (1968-1971) have described the cuticular features of a number of species of *Glossopteris* and *Gangamopteris*. According to these authors, one of the major characters which should be taken into account while differentiating the genera *Glossopteris* and *Gangamopteris* and also circumscribing a species is the midrib. According to Surange and Srivastava (1957), leaves of *Gangamopteris indica* Srivastava and *Gangamopteris cyclopterioides* Feistmantel are easily confused with *Glossopteris* because their median veins are more prominent, and forms like *Glossopteris longicaulis* Feistmantel and *Glossopteris decipiens* Feistmantel, where a midrib is seen only in the lower portion of the frond, can be mistaken for *Gangamopteris*. Maheshwari (1966) emphasised the fact that though, vertically running strands are found on the midrib of *Glossopteris* leaves yet, they never anastomose and in this sense are different from the median veins of the genus *Gangamopteris* which, though sometimes simulate a midrib, yet show definite anastomoses. Pant and Singh (1968) arrived at the conclusion that if the median region is ill-defined and if the cuticle of this region shows stomatiferous areas (meshes) bounded by non-stomatiferous areas (veins) like those of the lamina, and if it is otherwise not clearly differentiated from the cuticle of the lamina (in thickness or cell characters), the leaf may be assigned to *Gangamopteris*. Besides Pant and co-workers, Høeg and Bose (1960), Surange and Maheshwari (1962), Saksena (1963), Rigby (1966), Srivastava (1969, 1971), Banerjee (1971), Chandra and Surange (1977a, b), Rigby *et al.*, (1980), Chandra and Srivastava (1981) and Maheshwari and Tewari (1992) have reported on the cuticles of *Glossopteris* leaves.

The first *Glossopteris* fructification was described and illustrated by Feistmantel (1881). Though the lectotypes for the taxon *Dictyopteridium sporiferum* (Geological Survey of India, Calcutta, Museum Specimen 5210 figured by Banerjee 1973) does provide some evidence of probable attachment to a *Glossopteris* leaf, Feistmantel thought it was a fern pinnule. Zeiller (1902) reported *Ottokaria* (*Feistmantelia*) *bengalensis* now shown to be an ovaliferous capitulum with a long stalk and subtended by a *Glossopteris* leaf (Banerjee, 1978).

White (1908) established the genus *Arberia* for broadly incised, coriaceous or striate and thick nerved scale leaves whose distant recurvate and truncate lobes appear to owe their abrupt or even slightly ragged terminations to the detachment of some sort of bodies. Presumably reproductive in nature. His specimen came from *Gangamopteris* bed (Joaguim Branco Horizon, Rio Bonito Formation, Guata subgroup, Tubaro Group Rigby 1972a), northeast of Minas (now Lauro Muller). Santa Catarina, Brazil and were intimately associated with *Samaropsis* seeds and *Gangamopteris obovata* Carruthers leaves.

On the basis of association a relationship between *Arberia* and *Gangamopteris* was presumed. Rigby 1972b) interpreted *Arberia* as a fructification that bore large numbers of naked ovules on pinnate branchlets arranged laterally along a forked racheis.

However, the restoration of a mature specimen by Rigby (1972b, text fig. 2) and some of specimens illustrated by Appert (1977, pl. 36, fig. 2) Chandra & Srivastava (1981, pl. 1, fig. 1) and Anderson and Anderson (1985, pl. 103, fig. 1) show that the branching is pleiochasial.

Plumstead (1952, 1956a, b, 1958) described and illustrated a large number of fructifications in organic connection with leaves of *Gangamopteris, Glossopteris* and *Palaeovittaria*. Pant (1982) recognised 4 groups of Gondwana Gymnosperms, viz., Glossopteridales, Noeggerathiopsidales, Coniferopsida and incertae sedis. He remarked that the unique leaf attached fructifications of Glossopteridales may suggest some affinity with the Pteridosperms.

From time to time various diversified structures have been described as fructification of *Glossopteris* (Arber, 1905;

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PLATE 2

1 *Glossopteris communis* Feistmantel 1876, Specimen no. BSIP-38855 (8/4754), Barakar Formation, Dakara Colliery, North Karanpura Coalfield, Bihar. x nat. size.

2-5. Cuticle of *Glossopteris communis* Feistmantel, Specimen no. BSIP-38855 (8/4754). x 100.

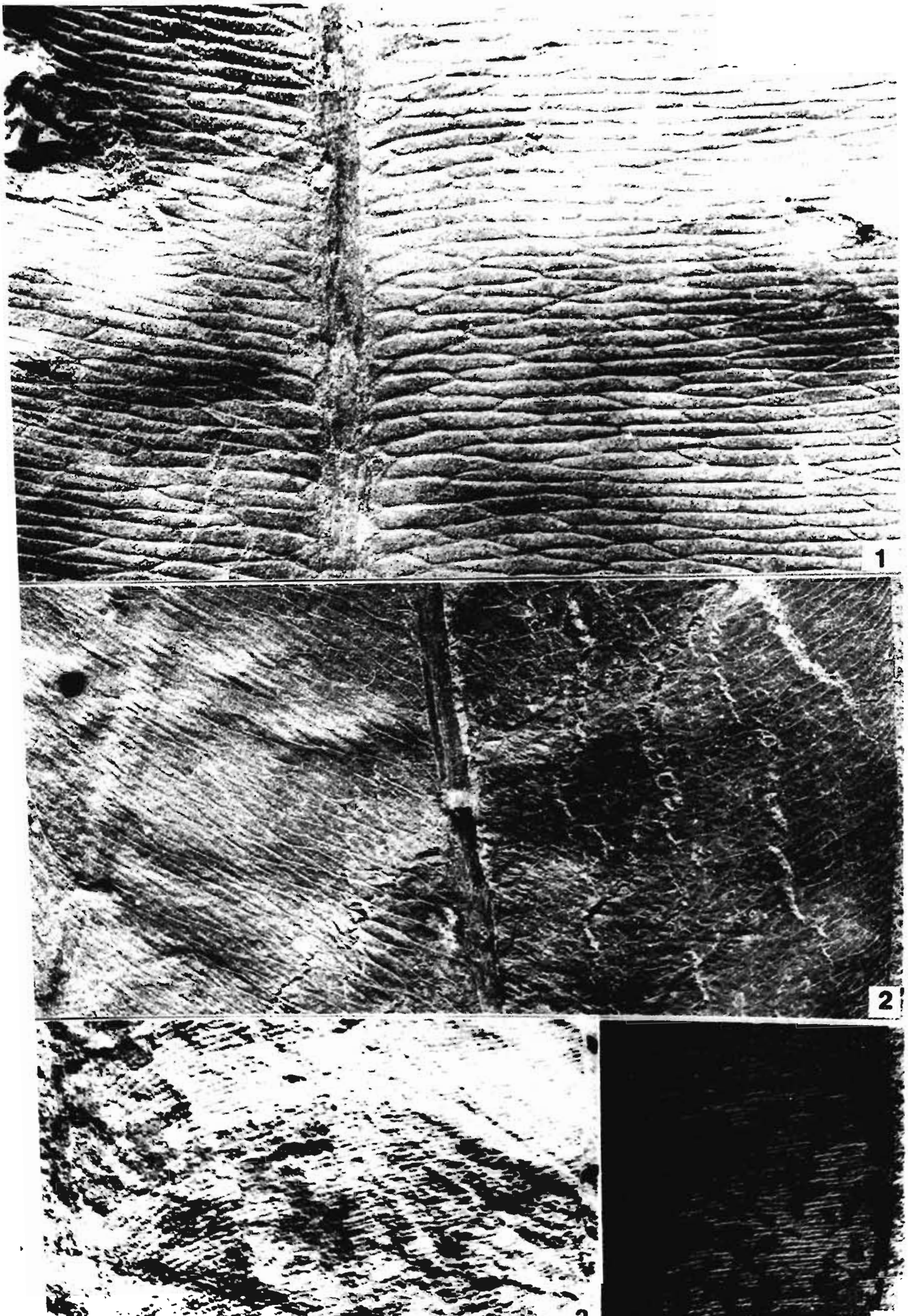

PLATE 3

Walkom, 1928; Dutoit, 1927; Sen, 1954, 1955a, b, 1956; White, 1962). The first attached fructification was figured by Zeiller (1902, pl. 4, fig. 9) under the name *Ottokaria bengalensis* which is attached to a *Glossopteris indica* type of leaf. Later on a large number of attached fructifications have been described (Plumstead, 1952, 1956, 1958; Sen, 1955a, b; Rigby, 1962; Maheshwari, 1966; Pant, 1982; Anderson & Anderson, 1985).

Some important records of attached fructification with genus *Glossopteris* are *G. browniana, G. damudica, G. decipiens, G. indica, G. jamottei, G. longicaulis, G. retifera (=elongata), G. stricta, G. tortuosa* var. *vaolanse, G. angustifolia.*

Chandra and Surange (1979) produced a monograph on the "Revision of the Indian species of *Glossopteris*" in which the species of *Glossopteris* have been classified on the basis of external characters alone. These authors considered that the size, shape, midrib, lateral veins and their behaviour are characters of diagnostic value in differentiating one species from another.

Maheshwari and Tewari (1992) are of view that the genus *Glossopteris* should be classified on the basis of both morphographical and cuticular characters. Among morphographical features, they have taken shape, nature of apex, base and margin, nature of midrib, density of lateral veins, and shape and size of meshes for speciation. Among cuticular characters, shape and arrangement of cells, cell walls, stomatal type, orientation and distribution of stomata, type of guard cells, and stomatal index have been considered useful criteria.

In the present study, the speciation of genus *Glossopteris* is based on morphography and cuticular features. Here, morphographical characters have critically analysed in order to find a reasonable basis for precise specific delimitations. Morphographical circumscriptions have been further verified by characters of the cuticle wherever available. Thus for specific circumscription, the characters of the cuticle have been taken as associated or supportive characters only.

Morphographical characters

The morphographical characters which are considered important from the point of view of specific circumscription are:

(a) Shape of the leaf
(b) Margin of the lamina
(c) Apex
(d) Base
(e) Nature of midrib
(f) Venation pattern

(a) Shape of the leaf:

The leaves vary in shape, having a varied length/width ratio. The leaves may be :

1. Linear, e.g., *G. formosa*
2. Linear-lanceolate, e.g., *G. angustifolia*
3. Lanceolate, e.g., *G. indica*
4. Lanceolate-spathulate, e.g., *G. indica*
5. Spathulate, e.g., *G. browniana*
6. Oblong, e.g., *G. emarginata*
7. Obovate, e.g., *G. retusa*
8. Cordate, e.g., *G. sahnii*
9. Obcordate, e.g., *G. spathulata*

In modern plants, however, it has been observed that the shape of the leaf shows considerable variation within the same

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PLATE 3

1. *Glossopteris danae* Maheshwari & Tewari 1992, Specimen no. BSIP-38830 (35/5004), Jharkhand Colliery, West Bokaro Coalfield (Venation x 3).
2. *Glossopteris karanpuraensis* Kulkarni 1971, Specimen no. BSIP-38838 (21/5004A), Jharkhand Colliery, West Bokaro Coalfield (Venation x 3).
3. *Glossopteris raniganjensis* Chandra & Surange 1979, Specimen no. BSIP-38849 (13/4998), Sirka Colliery, South Karanpura Coalfield (Venation x 3).
4. *Glossopteris clarkei* Feistmantel 1878, Specimen no. BSIP-38827 (9/4752), Gidi-C Colliery, South Karanpura Coalfield (Venation x 3).

PLATE 4 See Page No. 340

1. A twig of modern plant *Morus alba* showing variation in shape of the leaves.
2, 4. A modern plant *Millettia* sp. showing variation of leaves in two branch of the same plant.
3. A twig of modern plant *Ixora arborea* of showing variation in shape of the leaves.

PLATE 5 See Page No. 341

1-4. A modern Algae *Grateloupia indica (Red Algae)* showing variation in shape of the thallus structure within the same species. Collected from Okha, Gujarat, January 1999 by DB Sahoo.

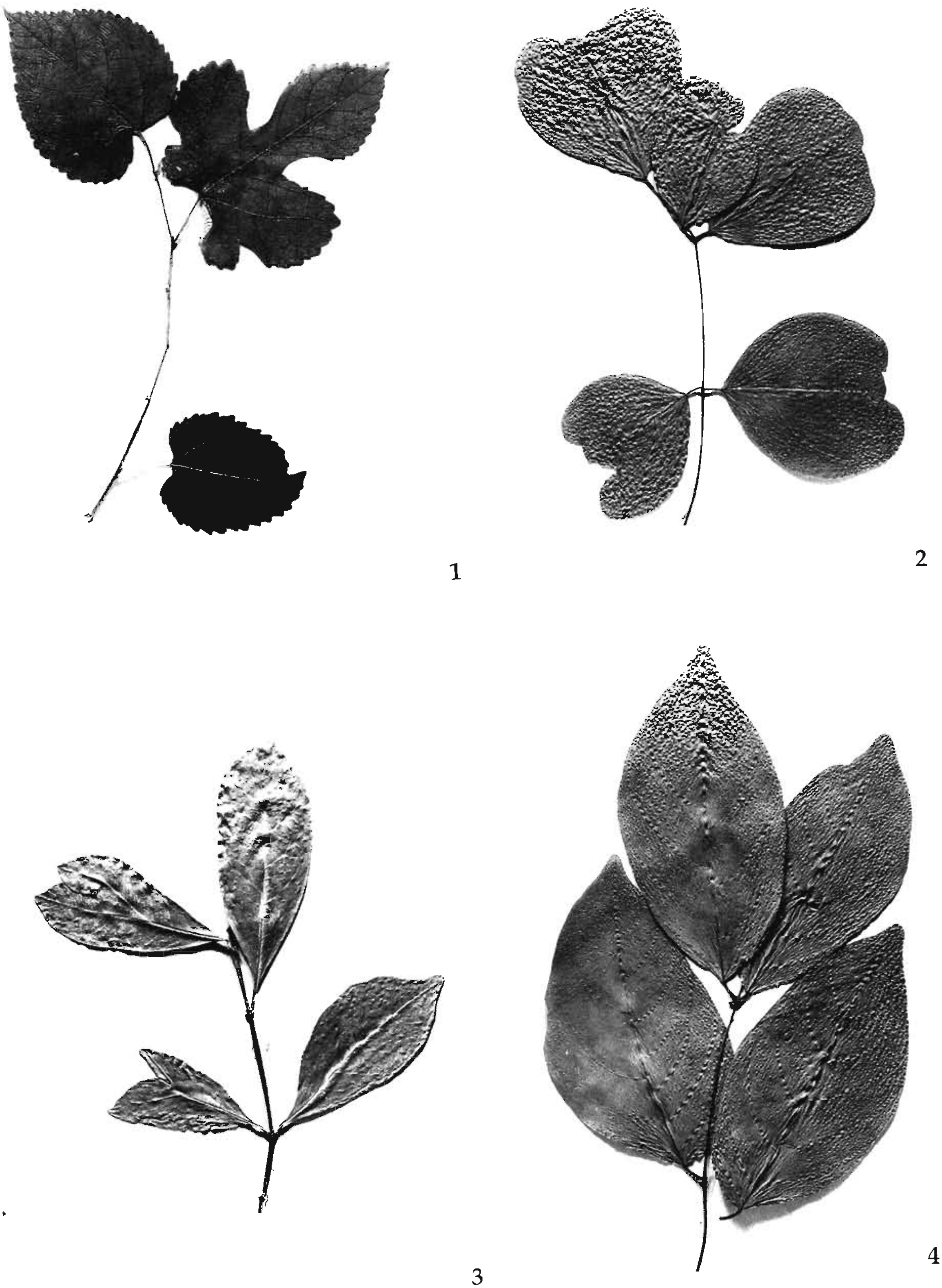

PLATE 4

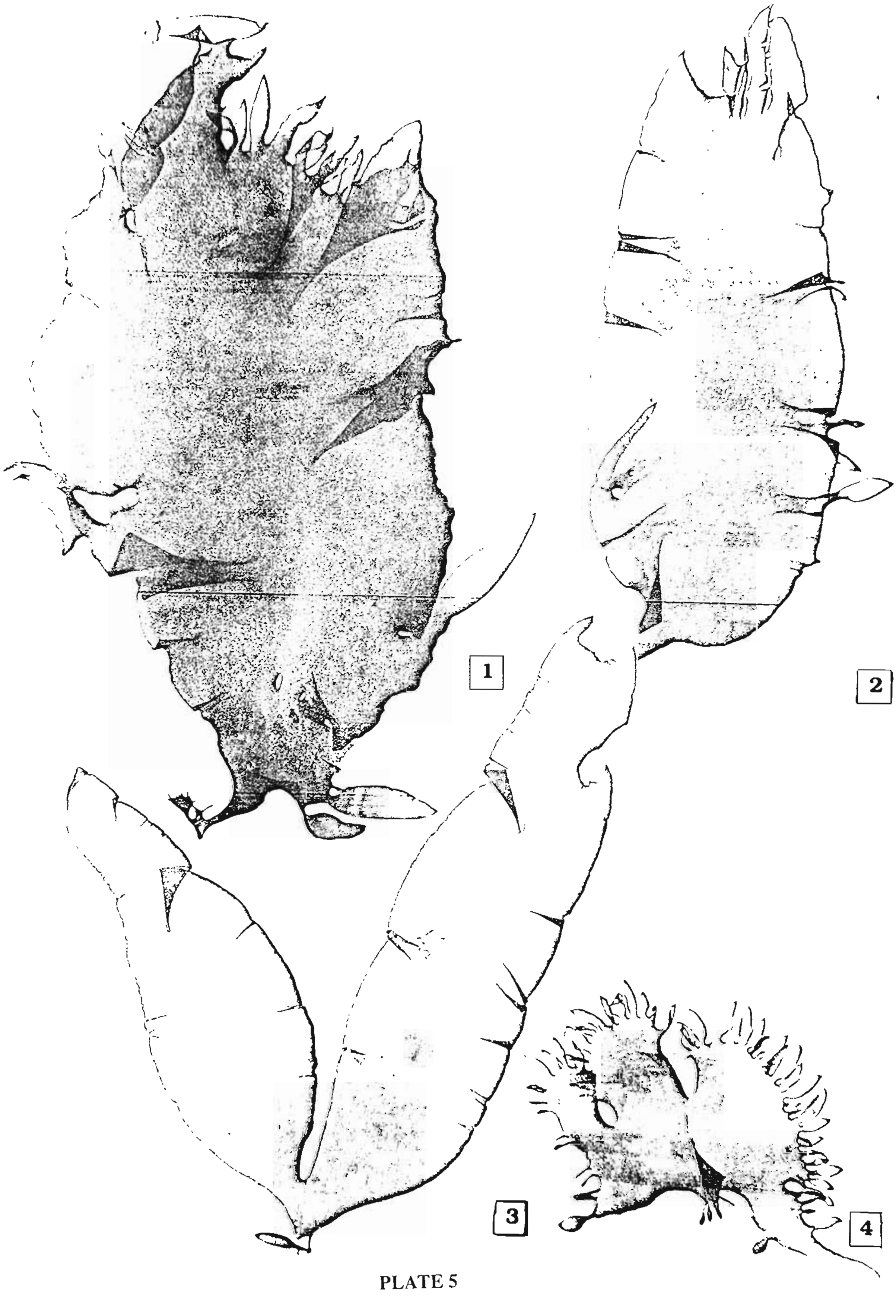

PLATE 5

species (Pl. 4·1-4; Pl. 5·1-4). Therefore, this character/ feature has only secondary importance.

(b) Margin of the lamina:

Almost invariably the leaf margin is continuous and smooth, sole exception being *G. retusa*.

(c) Apex:

Apex may be acute, acuminate, obtuse, retuse or driptip. This character is important only when wide differences are present, otherwise this character is of little importance, e.g., *G. emarginata* (emarginate apex) and *G. retusa* (retuse apex-cum-notched margin)

(d) Base:

The leaves of a species may either be sessile or petiolate, their being no intra-specific variation. As such this character whenever preserved is usually important for species delimitation when taken together with other characters.

(e) Nature of midrib:

The midrib which forms the main vascular supply of the leaf shows considerable variation in various species. It may continue from the base of the leaf up to the apex or may dissolve into secondary veins after some distance from the base, in which case it is said to be evanescent. The midrib may look to be solid and stout or flat and insignificant. This character seems to be taxon specific. In case where the midrib is flat, vertically running striations resembling the secondary veins may be found but these never anastomose and in this sense are different from the median veins of the genus *Gangamopteris* McCoy. Sometimes the midrib is pitted throughout the length. These pits possibly represent bases of outgrowths, such as, hairs or spines. Earlier workers mistook this feature as representing the fertile stage.

(f) Venation pattern: (Pl. 3·1-4)

The most important character in specific delimitation as already emphasised by Arber (1905) and Maheshwari (1966) is the nature of the secondary veins and the meshes formed by them.

(a) Angle of origin:

(i) Veins arise almost perpendicular to the midrib, e.g., *Glossopteris taeniopteroides* Feistmantel, *G. euryneura* Maheshwari.

(ii) Veins arise at acute angles from the midrib. Degree of emergence of the veins is species specific. This situation occurs in majority of species.

(b) Course of veins:

(i) Veins almost straight, e.g., *G. intermittens* Feistmantel; *G. jonesii* Walkom, *G. mitchelii* Walkom.

(ii) Veins arched, e.g., *G. indica* Schimper, *G. communis* Feistmantel, *G. browniana* Brongniart.

(iii) Veins arched and sinuous, e.g., *G. verticillata* Thomas.

(c) Vein density:

The per centimeter concentration of the veins has also been given importance. For example, in both *G. taeniopteroides* and *G. euryneura* the secondary veins are almost perpendicular to the midrib but in the latter case the number of veins per centimeter is much less as compared to the former. This difference is verified by the flexuous nature of the secondary veins in the latter, unlike the former where the veins follow an almost straight course.

(d) Vein anastomoses:

(i) In some species the veins anastomose infrequently, e.g., *G. taeniopteroides*, *G. intermittens*.

(ii) In most species veins anastomose frequently, e.g., *G. browniana, G. formosa* Feistmantel, *G. elongata* Dana, etc.

(e) Frequency of veins dichotomies:

(i) In some species the secondary veins dichotomise just once or twice and then follow an almost parallel course, e.g., *G. parallela* Feistmantel.

(ii) Secondary veins dichotomise several times and hence the concentration of veins at the margins is much higher than near the midrib, e.g., *G. browniana, G. indica, G. linearis Bunbury*, etc.

(f) Shape of meshes:

The shape of the meshes formed by the secondary veins depends considerably on the number of dichotomies, concentration of the veins, as well as the number of anastomoses. Meshes may be:

broad and open, e.g., *G. conspicua* Feistmantel
narrow and elongate, e.g., *G. communis* Feistmantel
elongate-polygonal, e.g., *G. browniana* Brongniart
polygonal, e.g., *G. elongata* Dana, *G. formosa*
trapezoid, e.g., *G. tortuosa* Zeiller

Cuticular characteristics: (Pl. 1-2)

It is not often that leaves with a carbonified crust (leaf compressions) are present. Very seldom the carbonified crust, on maceration, yields well-preserved cuticles. But whenever satisfactorily preserved pieces of cuticle are recovered these provide valuable secondary data for species delimitation. Some of the characters of the cuticle that have been taken into consideration for speciation are :

(i) The presence of stomata on one (hypostomatic) or both (amphistomatic) the surfaces of the leaf. In the species of the genus *Glossopteris* amphistomatic cuticle is unusual.

(ii) Shape and arrangement of cells—The vein and mesh areas may be decipherable on the cuticle through arrangement of the cells. The cells over the veins are usually narrow, elongate, rectangular or squarish and arranged end-to-end in longitudinal rows. The cells in the mesh areas are polygonal, rectanguloid or very rarely trianguloid and squarish and do not show a regular arrangement.

(iii) Cell walls—The anticlinal and periclinal walls of the cells may be straight, slightly undulate or sinuous. The surface walls may be smooth or papillate; the number of papillae may be numerous or only one. When the papillae are many in number they are usually small and rounded.

(iv) Distribution and orientation of the stomata—The Stomata occur only in mesh areas and are usually haplocheilic and anamocytic (irregular number of subsidiary cells). The stoma may have only one ring of encircling cells (monocyclic), rarely two rings (dicyclic); sometimes the encircling cells may partly cover the stoma. Usually the stomata do not exhibit any regularity in distribution and orientation.

(v) Types of guard cells—The guard cells may be normal or sunken. The nature of the stomatal pore usually can not be very well deciphered in fossil cuticles.

(vi) Stomatal index—It refers to the number of stomata in a unit area. The formula that is used to work out the stomatal index is:

$$\text{Stomatal index} = \frac{\text{Number of stomata}}{\text{Number of stomata} + \text{Number of epidermal cells}} \times 100$$

It is said to be highly variable within a species thus its diagnostic value, remains doubtful.

Generic Diagnosis (from Maheshwari & Tewari, 1992):

Leaves simple, sessile or petiolate; entire or slightly notched in the upper half; shape, size, apex and base variable; midrib prominent, flat or elevated, persistent or evanescent, when flat, with longitudinally running parallel striations or pits or sometimes both, anastomoses of striations absent; lateral veins arching from the midrib at acute angles, arched or more or less straight, dichotomising and anastomosing variously to form meshes of various shapes and sizes, density of veins usually lesser near midrib than near the margin.

Leaf cuticle usually hypostomatic, rarely amphistomatic, either undifferentiated or differentiated into vein and mesh areas on both the surfaces, cells over veins narrow, elongated, rectangular or squarish, arranged end-to-end in linear rows; cells in mesh areas varying in shape and size and arranged irregularly, lateral walls of cells usually straight, sometimes undulate or sinuous, surface walls mostly unspecialised, sometimes granulate or papillate, trichomes generally absent; stomata haplocheilic, present only in mesh areas, distributed and oriented irregularly, stomatal index variable, stomatal apparatus mostly monocyclic, rarely dicyclic or amphicyclic, guard cells sunken or normal, subsidiary cells unspecialised or with papillae overhanging guard cells. Cells over midrib squarish or rectangular, arranged in rows, stomata usually absent over midrib.

Habit of *Glossopteris*

The habit of the plant which bore *Glossopteris* leaves is little known. Seward (1931, p. 247) proposed its habit as "shrubs". Plumstead (1958, p. 92) opined that "it is probable that they were deciduous, woody plants with an arborescent habit, and that the leaves, flowers and fruits were borne on short shoots, a few of which developed into long shoots to form branches". Earlier it was suggested that the genus *Vertebraria* is one of the stems which bore such leaves (Dolianiti, 1954; Surange & Maheshwari, 1962; Pant, 1962). These leaves were borne on stems either in tight spirals (Surange & Maheshwari, 1962, text-figure 8) or in pairs (Dolianiti, 1954, figure 1). However, it has now been conclusively shown that *Vertebraria* is a root axis (Schopf, 1965). It is possible that all *Glossopteris*-bearing plants were not arborescent. In the Talchir and Karharbari Formations no petrified wood has yet been recovered. The climate was relatively cool and not much coal was formed. During this period it is probable that *Glossopteris*-bearing plants were shrubby in nature. In the late Early and Late Permian petrified wood is assigned to the *Glossopteris*-bearing plants on the basis of association. In one case this association seems to be indoubitable. In the shales associated with the topmost seam of the Raniganj Formation in the Raniganj and Jharia Coalfields, and below the Kumarpur and Mahuda Sandstone Members, respectively, one finds an almost pure association of the leaf *Glossopteris shailae* Bajpai and the wood *Araucarioxylon kumarpurensis* Singh & Bajpai (Bajpai, 1987; Bajpai & Singh, 1986; Bajpai & Tewari, 1990). Banerjee *et al.* (1991) have reported a *Glossopteris* plant *in-situ* from the Barakar (=Karharbari) Formation of Saharjuri Coalfield. The specimen is said to show branched stems bearing *Glossopteris* leaves and vertical *Vertebraria* roots with spreading branches.

	PERMIAN																		TRIASSIC	
	INDIA							AUSTRALIA N.S. Wales					S. AFRICA				S. AMERICA		ASIA	
Glossopteris species	ANTARCTICA	MEDAGASCAR	Talchir	Karharbari	Barakar	Barren Measures	Raniganj, Kamthi	Muree Series	New Castle Series	Victoria	Queensland	Tasmania	Cape Colony	Natal	Orang River colony & Transvaal	Zimbabwe	Brazil	Argentina	India, Panchet	Tonquin
Glossopteris acuminara							+													
G. acuta							+		+											
G. ampla	+			?	+	+	+		+		+	+	+	+		?				
G. angustifolia	+			+	+	+	+				+	+	+	+	+				+	+
G. angusta			+	+																
G. anthrophylloides							+													
G. arberi					+		+													
G. asansolensis					+															
G. barakarensis					+		+													
G. bengalensis							+													
G. browniana	+	+		+	+	+	+	+	+		+	+	+	+	+	?			+	+
G. brongniartii							+													
G. bunburyana					+															
G. churiensis					+															
G. clarkei					+			+												
G. communis	+	+	+	+	+	+	+				+			+				+	+	
G. contracta							+													
G. cordiformis							+													
G. cordata							+		+											
G. damudica	+	+			+	+	+						+							
G. danae (G. danae)					+															
G. daenaeoides							+													
G. divergens							+													
G. decipiens			+	+	+	+	+				+		?							
G. dhenkanalensis							+													
G. deogarhensis					+															

Fig. 1—Distribution of *Glossopteris* species in Time and Space

G. ednae					+											
G. elegans								+		+						
G. emarginata					+		+									
G. euryneura					+		+									
G. formosa	+				+		+			+						
G. feistmantelii							+									
G. fibrosa							cf.									
G. frondosa							+									
G. gangamopteroides									+							
G. gigas					+		+									
G. giridihensis				+												
G. ghusikensis							+									
G. gondwanensis							+									
G. gopadensis															+	
G. harrisii							+									
G. hingridaensis							+									
G. ingens					+		+									
G. intermedia					+		+								cf.	
G. indica	+	+	+	+	+	+	+	?	+	+	+	+	+	+	+	+
G. inequalis							+									
G. intermittens					+				+							
G. isolateralis															+	
G. jayantiensis					+											
G. karanpuraensis					+											
G. karharbariensis			+	+												
G. kusumiae					+											
G. kamthiensis							+									
G. lanceolatus							+									
G. leptoneura				?	+		+									
G. longifolia					+		+									
G. longicaulis	+			+			+					+			+	
G. linearis					+		+									
G. maculata							+									
G. manjuiae					+											
G. major					+		+									
G. maheshwari							+									
G. mohudaensis							+									
G. musaefolia							+									
G. nautiyalii							+									
G. nephroedicus							cf									
G. obovata sp. nov.					+											
G. ovata											+					
G. obscura					+		+									
G. oldhami					+		+									
G. orbicularis	+						+									
G. pandurata					+		+									
G. pantii					+		+									
G. papillosa															+	

G. parallela				+		+		+	+						
G. petiolata						+									
G. primaeva							+								
G. pseudocommunis				+		+									
G. pseudotortuosa sp. nov.				+											
G. pseudostricta sp. nov.				+											
G. radiata						+									
G. recurva		+													
G. reticulata						+									
G. roylei			+												
G. rectinervis								+							
G. rewanensis						+									
G. retifera (=*G. elongata*)				+	+	+					+	+	+	+	+
G. rhabdotaenoides				+		+									
G. reticulum								+		+					
G. retusa						+		+							
G. sahnii						+									
G. saksenae				+											
G. sastrii						+									
G. schopfii				+											
G. searsolensis						+									
G. senii						cf									
G. schimperii				+											
G. singularis						+									
G. spathulata						+					+				
G. spathulo-cordata	+		+							+					
G. srivastavae				+	+	+									
G. stenoneura				+	+	+									
G. surangei						+									
G. shailae				+		+									
G. subtilis						+									
G. syaldiensis				+											
G. stricta	+			+		+					?	+			+
G. taeniopteroides				+				+							
G. tatei												+			
G. tenuifolia						+									
G. taenioides			+			+									
G. transversalis						+									
G. tortuosa				+		+			+		cf.				
G. utkalensis						+									
G. varia						+									
G. venustus						+									
G. verticillata						+									
G. vulgaris						+									
G. waltonii				+		+									
G. wilkinsoni								+	+						
G. zeilleri		+	+	+											

GLOSSOPTERIS FLORA	Talchir	Karharbari	Barakar	Kulti	Raniganj	Kamthi	Bijori	Pali	Pachware	Hinjir	Maiture	Hirapur	Parsorsa
Neomariopteris lobifolia			+*		+				+		?		
Glossopteris angustifolia		+	+	+	+	+	+	+	+	+	?	+	
G. arberi			+*		+	+							
G. barakarensis			+		+								
G. browniana		+	+	+	+	+	+	+	+	+	?		?
G. clarkei			+*		+								
G. communis		+	+	+	+	+	+	+	+	+	?		
G. danae (=*G. damudica*)		+	+	+	+		+	+	+	cf		?	
G. decipiens		+	+	?	+								
G. elongata			+	+	+		+	+	+	+	?		
G. emarginata			+		+			+					
G. euryneura			+*		+								
G. indica	+	+	+	+	+	+	+	+	+	+	+		+
G. intermedia			+		+								
G. intermittens			+		+			+					
G. karanpuraensis			+										
G. linearis			+		+								
G. longifolia			+*		+								
G. major			+*		+								
G. oldhami			+*		+								
G. obscura			+*		+								
G. obovata sp. nov.			+*										
G. pseudostricta sp. nov.			+										
Glossopteris pseudotortuosa sp. nov				+*									
G. raniganjensis			+	+	+	+	+						
G. shailae			+*		+								
G. stenoneura			+		+			+					
G. tortuosa			+*	+	+								
G. taeniopteroides			+*		+								
G. tenuinervis			+		+								
G. vulgaris			+*		+								
G. waltonii			+*		+								
G. zeilleri		+	+*		+								
Gangamopteris sp. cf. *G. buriadica*		+	+	+*		?							
G. obovata		+	+										
Palaeovittaria sp.			+		+								
Gonophylloides (=*G. cistella*)			+										
Scutum			+		+								
Cordaicarpus	+	+	+*										
Pantophyllum gidiense sp. nov.			+*										
Euryphyllum whittianum		+	+										
Kawizophyllum dunpathriensis			+										
K. barakarensis sp. nov.			+*										
Ginkgopsid			+										
Vertebraria indica	+	+	+	+	+	+	+	+	+	+	+		
Equisetalean axes	+	+	+	+	+	+	+	+	+	+	+		
Incertae sedis			+*										

Fig. 2—Vertical distribution of flora of present study in Indian Gondwana (* + indicates new contribution)

Glossopteris Species	North Karanpura				South Karanpura						West Bokaro Coalfields									
	Dakara	K.D. Heslong	Ray	Karkata	Sirka	Religara	Gidi-A & C	Bhurkunda	Saunda	Urimari	Jharkhand	Pundi	Kuju	Kedla	Tapin	Saruberа	Ara	Topa	Ghato	Pindra
Glossopteris arberi					+															
G. angustifolia					+			+												
G. browniana	+				+															
G. barakarensis											+									
G. clarkei			+				+													
G. communis	+	+			+	+	+		+	+	+		+					+	+	+
G. danae					+						+									
G. decipiens	+						+			+							+			
G. elongata											+									
G. emarginata					+															
G. euryneura					+															
G. indica	+	+			+	+	+				+			+	+					
G. intermedia					+															
G. intermittens												+					+			
G. karanpuraensis					+	+		+	+		+									
G. linearis			+								+					+				
G. longifolia					+															
G. major					+		+	+			+									
G. oldhami							+													
G. obscura	+				+		+													
G. obovata sp. nov.			+		+	+	+													
G. pseudotortuosa sp. nov.			+		+	+	+				+									
G. pseudostricta sp. nov.					+	+	+			+										
G. shailae						+	+													
G. stenoneura	+					+														
G. raniganjensis					+															
G. tenuinervis					+		+													
G. tortuosa					+															
G. taeniopteroides					+															
G. vulgaris					+		+				+									
G. waltonii			+	+	+			+			+		+						+	
G. zeilleri								+												

Fig. 3—Colliery-wise distribution of *Glossopteris* species

Diversity in *Glossopteris*

Glossopteris diversified rapidly once established after glaciation. There were two major phases of diversification, viz: in Barakar and Raniganj Formations. In these periods maximum number of species diversified to occupy almost every kind of terrestrial habitat. Over the whole long period, plant communities have been evolved. Diversification has occurred as a result of competition between plants. There are fragmentary plant fossils of *Glossopteris* from Talchir Formation and comparatively some better were recovered from Karharbari Formation. These plants were successful in unsupporting environment. They probably required several adaptations: mechanical strength to support them in the air to expose light catching surfaces, an anchoring system to prevent them being blown over, a conducting system to supply water to all parts of plants, a system for obtaining mineral nutrients, a means of restricting water loss in the desiccating environment of the air, a means of reducing and dispersing on land.

The earliest picture of the plant community comes from present study of Barakar Formation of Karanpura and Bokaro Coalfields. These includes *Glossopteris*, *Gangamopteris*, *Palaeovittaria*, *Pantophyllum*, *Euryphyllum*, *Kawizophyllum* etc. There were many short herbaceous species viz., *Neomariopteris lobifolia* and a new fossil (*Incetae sedis*). *Glossopteris*, *Gangamopteris* and *Palaeovittaria* were small shrubs or small trees. In these genera leaves are in spiral and whorls. *Euryphyllum*, *Pantophyllum*, *Kawizophyllum* were probably tree habit. The great adaptive radiation in genus *Glossopteris* reaches its fullest expression in the Raniganj Formation. *Glossopteris indica*, *G. angustifolia*, *Vertebraria indica* and Equisetalean axes have wide longitudinal distribution from Talchir to Parsora. *G. browniana*, *G. communis*, *G. elongata* and *G. stenoneura* have comparatively narrow distribution from Karharbari/Barakar to Hinzir/Maitur (Figs 1, 2, 3). *G. barakarensis*, *G. decipiens*, *G. emarginata*, *G. euryneura*, *G. intermedia*, *G. karanpuraensis*, *G. linearis*, *G. longifolia*, *G. major*, *G. oldhami*, *G. obscura*, *G. obovata*, *G. raniganjensis*, *G. tortuosa* etc. show maximum diversity in Barakar and Raniganj Formations. *Glossopteris* flora owing to high degree of inaccessibility, had escaped from complete transformation and hence exhibits high magnitude of bio-diversity at species level. Since the data is lacking at the level of gene and ecosystem, so bio-diversity at this level is avoided. Probably genome of *Glossopteris* modified according to time and space and different species of *Glossopteris* ranges from Triassic to Parsora. The variation in shape and size within species of genus *Glossopteris* was due to mutation. Up to the Parsora "Nature" conserved their germplasm which was the basis of diversity. The climax community of this genus naturally remains stable until another environmental change occurs. Bio-diversity-rich support area probably supply massive amounts of nutrients to livestock to maintain local hydrological cycle. Diversity provides a base for ecologically sound system. *Glossopteris ampla*, *G. angustifolia*, *G. browniana*, *G. communis*, *G. indica* and *G. stricta* have world-wide distribution (Fig. 1).

DISCUSSION & CONCLUSION

The species of this geological past genus is often confused with each other due to close similarities in their appearances. Most of the work published in the past was based on either morphological features (Size, Shape, Base, Apex) or cuticular features and in this way a large number of *Glossopteris* species have been created. In present study both the features together have been taken as reliable parameters during identification and speciation. Large number of closely related species have been minimised by making the species complexes (e.g., *G. arberi*............ *G. zeilleri* (Thesis Shiv Mohan Singh, 1998). Species complexes can be compared to the mountainous terrain where the major hills are named. In fact the method of naming the peaks is akin to the way we name the species. The names of the hills for instance are not referred to the peaks alone but to the whole domain of the hill. A small shoulder or a sub peak on the major peak belong to the major hill and any two hills can be clearly separated only if there is distinct valley between them.

Species complexes can be similarly considered as morphometric terrain's with species as the hills, varieties as the shoulders within the species domains. In other words in this view species are not merely peaks (means) but are population domains isolated by reproductive valleys. However as not all hills are distinctly isolated, not all morphometric peaks would be completely separated offering challenges to the taxonomists.

Arber suggested that as the classification of *Glossopteris* is an artificial one it would be better to maintain comparatively few species by grouping together those species which differ in one or two characters but are not sufficiently dissimilar in the aggregate of their characters. He also doubted the usefulness of creating varieties or sub-species and in this connection he is amply supported by Edwards (1928, p. 325) who says "..... I think that the custom of applying varietal names to isolated fossil leaf impressions is to be deprecated.... The use of trinomial nomenclature does not appear to add to the convenience of this artificial classification." While the tendency to create varieties or sub-species is to be deprecated it is equally true that a genus, howsoever artificial has to be critically resolved into various specific components, whatever their number. Seward (1897) has very rightly observed that "while endeavouring to avoid dangerous and unscientific practice of needlessly multiplying specific names, we must be careful to bear in mind the possibility of carrying too far the system of linking together distinct types by a long series of intermediate forms." Arber was infact more interested in reducing the number of species by linking together, which resulted in a conglomeration of many distinct types under fewer names which sometimes became so unwieldly as to be of no stratigraphical value. His *Glossopteris browniana* may particularly be cited as an example where different and distinct forms were huddled together, e.g., *G. parallela, G. linearis, G. taeniopteroides*, etc.

Further researches have, however, shown the unsatisfactory nature of Arber's broad based specific circumscriptions. They go a long way in supporting Feistmantel's "liberal" circumscription of the species. It is interesting to note that so far almost none of the species delimited by Feistmantel have been contradicted by cuticular studies or on fructification evidence. In fact some of Feistmantel's species need even further delimitation as is evident from the works of Srivastava (1957), Pant (1958) and Høeg & Bose (1960) on the epidermal structures and of Plumstead (1956) on the fructifications. As an example may be cited the *G. indica* type of leaf which has been found to possess many different types of epidermal structures, e.g., *G. indica, G. communis, G. jamottei, G. arberi, G. hispida* and *G. fibrosa*. Here it is not meant to say that the above species are morphographically indistinguishable from the typical *G. indica* leaf. However, this distinction between these species can only be accomplished when we leave aside Arber's "broad-based" system and take into account all the important morphographical characters whether gross or minute. Maheshwari (1965) mentioned that *G. brownii* also seems to be a complex species as is evident from the different types of fructifications borne by such leaves. Singh *et al.* (1999) studied the taxonomic problems of *Berberis lycium* complex. They supported that the cuticular studies are as an additional parameter to distinguish the infra-specific variations within closely related taxa.

It seems that these leaves had a generalized pattern. Hence it is important that take into account all recognizable characters - whether gross or minute - and they should be critically analysed in various ways in order to find a more reasonable and precise basis for specific delimitations. Morphographic circumscriptions can be further verified by other evidences such as cuticular, if and when they are available. An example is the case of *G. fibrosa* Pant. Ordinarily this leaf would have been placed in *G. indica* but by detailed observations the interstitial veins were discovered which lead to the creation of this species. This specific circumscription was supported by characters of the epidermis.

On the basis of the study of several hundred specimens from the Barakar Formation of the Damuda series and a survey of the published literature it has been found that in specific circumscriptions aggregate of characters should be taken into account and attempt must always be made to verify difference in one character by other characters too.

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