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THE PLANT OF *GLOSSOPTERIS*[1,2]

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Introduction

Most of us can see the world of living plants as we move horizontally on Earth's surface or soar high up in the sky. In many respects it is a paradoxical world in whose study botanists, howsoever seasoned, become lured by formless chemical symbols and formulae and chemists are charmed by the form and structure of biological molecules.

Therefore bear with me if I extend this limited three dimensional world by introducing the fourth dimension and request you to descend down into the sands of time about 280 million years from now to the Carbo-Permian times when India, South Africa, South America, Australia and Antarctica were joined in a single land mass, hypothetically called Gondwanaland. The distinctive vegetation which inhabited Gondwanaland at the time is called the Glossopteris flora. A detailed knowledge of this flora is not only important for understanding the form, structure and ecology of its constituents but it would also be useful in desiphering the mode of formation of the energy rich extensive deposits of Lower Gondwana coal in these countries and in obtaining an overall picture of plant ancestors and plant evolution.

The leaves of *Glossopteris* are among the commonest fossils of the Glossopteris flora. Despite the fact that these leaves were recognized and named nearly a hundred and fifty years ago (Brongniart, 1828, 1828-38) and have even formed the basis of Melvills's Gonophyll theory, research on their structure, stems, reproductive parts and other organs has gained momentum only lately. Persistent gaps in the reconstruction of the plant of *Glossopteris* and what I believe to be the strong points and weaknesses of the recent contributions on the subject (including our own) have prompted me to present this reappraisal.

Stem, Root and Habit of the Plant

Stem atteched leaves of glossopterids have been described or mentioned by Bunbury (1861), Feistmantel (1881), Etheridge (1894), Zeiller (1896), Oldham (1897), Arber (1902), Seward (1910), Walton and Wilson (1932), Thomas (1952), Dolianiti (1954), Plumstead (1958), Pant (1967) and Pant and Singh (1974). Some of these authors, viz., Bunbury and Feistmantel mistook their foliage shoots for ferns or compound leaves and called them *Filicities*

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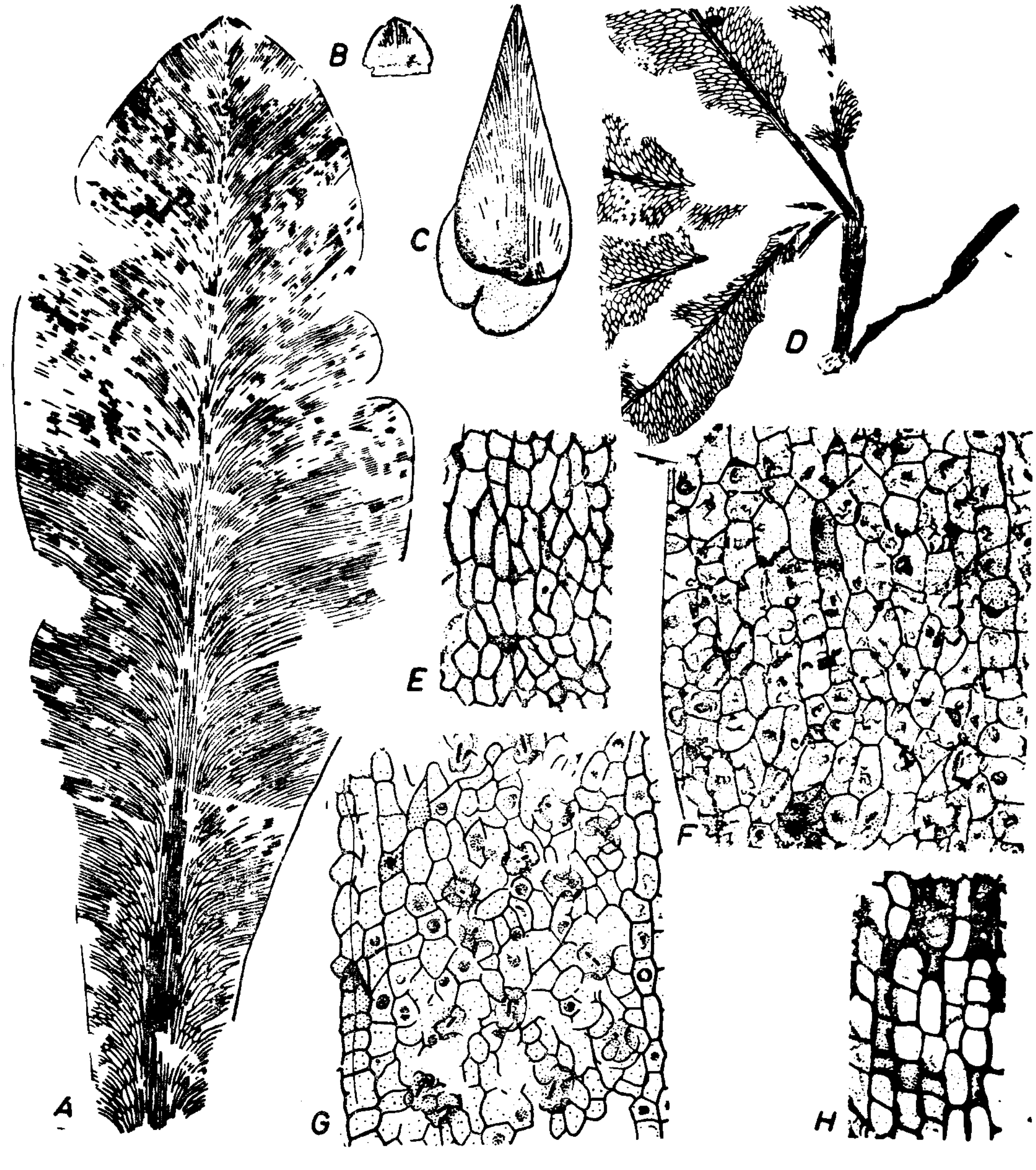

FIG. 1. A, leaf of *Glossopteris major* showing venation. B, C, scales attributed to *Glossopteris* (after Pant, 1958). D, foliage shoot of *Glossopteris maculata* (after Pant and Singh, 1974). E, F, upper cuticles of midrib and lamina, respectively. G, H, lower cuticles of lamina and midrib, respectively (A, E–H, after Pant and Singh, 1971).

and *Sagenoperis*, respectively. Among the remaining authors who identified the leaves as those of Glossopterids, Zeiller, Oldham, Arber and Dolianiti found them attached exclusively to axes of *Vertebraria indica* while the stems described by others lacked *Vertebraria* characters. Among such non-*Vertebraria* axes is a single foliage shoot described by Etheridge (1894) which shows rhomboidal leaf-base scars and an apical cluster of leaves. Other authors have described foliage shoots with smooth or longitudinally ribbed stems having apical clusters or laterally attached leaves. The arrangement of leaves in some of these axes was spiral but it was whorled in others (Fig. 1 D). All hitherto described foliage shoots of *Glossopteris* have slender axes with only a few leaves attached thereto. It has, therefore, been suggested (see Pant and Singh, 1974) that they could be of the nature of short shoots and the plants of *Glossopteris* and its allies were possibly large trees (Fig. 2 A). I have seen *Vertebraria* axes about 30 cm in diameter, in the roof shale of New Ghusick colliery at Raniganj and these may also indicate that *Glossopteris* was a large tree. Other authors have, however, suggested that *Glossopteris* is possibly a herb, a shrub or a small tree (Fig. 2 B) but it would be difficult to account for the thick axes of *Vertebraria* which was definitely an axis of *Glossopteris* and also for the enormous deposits of Lower Gondwana coal if we think that the most common constituents of the coal forming flora were herbs.

STRUCTURAL FEATURES OF AXES AND ROOTS

When Royle (1833) described axes of *Vertebraria*, he recognized two species, *V. indica* (Fig. 2 D) and *V. radiata* (Fig. 2 C). Later, it was pointed out by

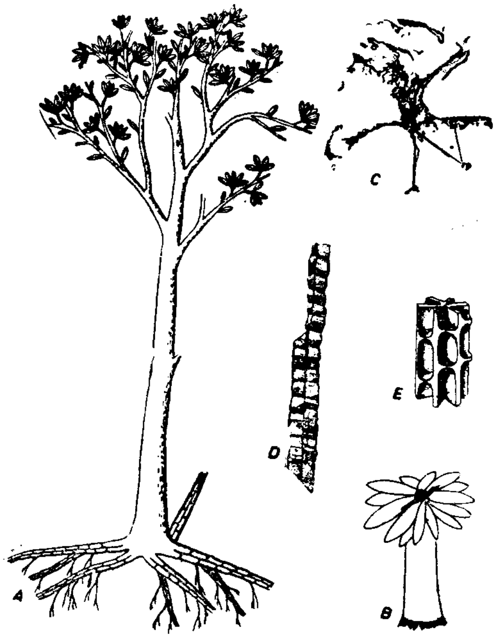

FIG. 2. A, B, hypothetical reconstruction of plants of *Glossopteris* (after Pant and Singh, 1974 and Rigby, 1969 respectively). C, D, E, *Vertebraria indica* "radiata" type vertically preserved axis with remains of large parenchyma cells by the side of xylem rays (after Pant, 1962). D, holotype showing horizontally preserved axis (after Pant, 1956), E. reconstruction of stele of *Vertebraria* (after Walton and Wilson, 1932).

Arber (1905b) and others that the two species actually represented two aspects of axes of the same kind, respectively preserved horizontally or vertically in relation to the bedding plane. Zeiller (1896) explained the occurrence of the characteristic rectangular areas in *Vertebraria indica* by assuming that they were the result of the squashing of a winged stem like that of the modern fern *Struthiopteris* while Oldham (1897) believed that the rectangular areas represented some kind of internal spaces. The structural details of *Vertebraria* were first investigated by Walton and Wilson (1932) and they found that the features of *Vertebraria* were only those of its rayed stele. They thought that the stele consisted of a number of vertical plates of xylem which were fused in the centre and also anastomosed here and there with adjacent plates to form broad parenchymatous rays. According to them the median groove or ridge in a *Vertebraria* represents the solid central core of the axis wherefrom all xylem plates radiated and the transverse septa are the regions where adjacent plates of xylem anastomosed (Fig. 2E). Pant (1956) confirmed the above observations on the basis of a *Stigmaria* preserved in the *Gymnostrobus* condition where also the radially compressed rays appeared like rectangular areas. In addition Pant (1956, 1962) found remnants of large celled parenchyma between the pycnoxylic plates of wood (Figs. 2C, 3B). The wood shows mainly primary xylem (Fig. 3E) but compact secondary wood usually showing tracheids with bi- or triseriate opposite pits (Fig. 3C). One of the characteristic features of tracheidal pitting is the occurrence of circular or oval groups of 3 to 9 bordered pits (Fig. 3G). The xylem rays are uniseriate commonly 1 to 4 cells high (Fig. 3F) but a few were up to 13 cells in height. Cross fields show 1 to 3 horizontally elongated oval simple pits (Fig. 3A). Remains of phloem are also seen (Fig. 3D). Facts do not justify recent attempts by Surange and Maheshwari (1962) and Maithy (1965) to recognize additional species of *Vertebraria* like *V. myelonis* and *V. gondwanensis*.

Roots of *Vertebraria* were described by Pant (1958b) under the name *Lithorhiza tenuirama*. Slender branches of these roots show root tips and endogenous primordia of lateral rootlets. Some of these roots are attached to vertebrarias but others are borne on only slightly thicker root-like axes which lack rectangular areas but show *Vertebraria*-like xylem and large celled parenchyma. According to Schopf (1965), a petrified axis of *Vertebraria* has the features of a root rather than those of a stem. Since primitive roots and stems could be structurally alike, Pant and Singh (1974) point out that *Vertebraria* could represent the stele of either of these organs of *Glossopteris*. The resemblance between the xylem of *Vertebraria* and that of some *Glossopteris* stems as described by these authors lends support to this suggestion. One of our newly collected specimens shows a thinner leafy axis actually connected with a *Vertebraria* (Figs. 4A, B). Even the thinner axis seems to show obscure *Vertebraria*-like features and this favours the stem character of *Vertebraria*.

LEAVES

Leaves of *Glossopteris* may be small or large, commonly having a wide or narrow lamina with a pointed to a rounded apex. Their lamina gradually tapers towards the base and they are commonly sessile but some are petiolate (e.g., *G. petiolata*). A midrib is usually distinct up to the apex but in *G. decipiens* it may become obscure near the apex. Wherever details are recorded the midrib consists of a number of parallel longitudinal veins which may or may not be anastomosing. Their meshes may be narrow or wide. Early workers recognized species of *Glossopteris* on the basis of external form and venation but the work of Pant (1958a) made it clear that the same kind of venation could occur in leaves showing more than one kind of epidermal structure (Fig. 1A, E-H). Accordingly, structurally preserved leaves are now identified on the dual basis of

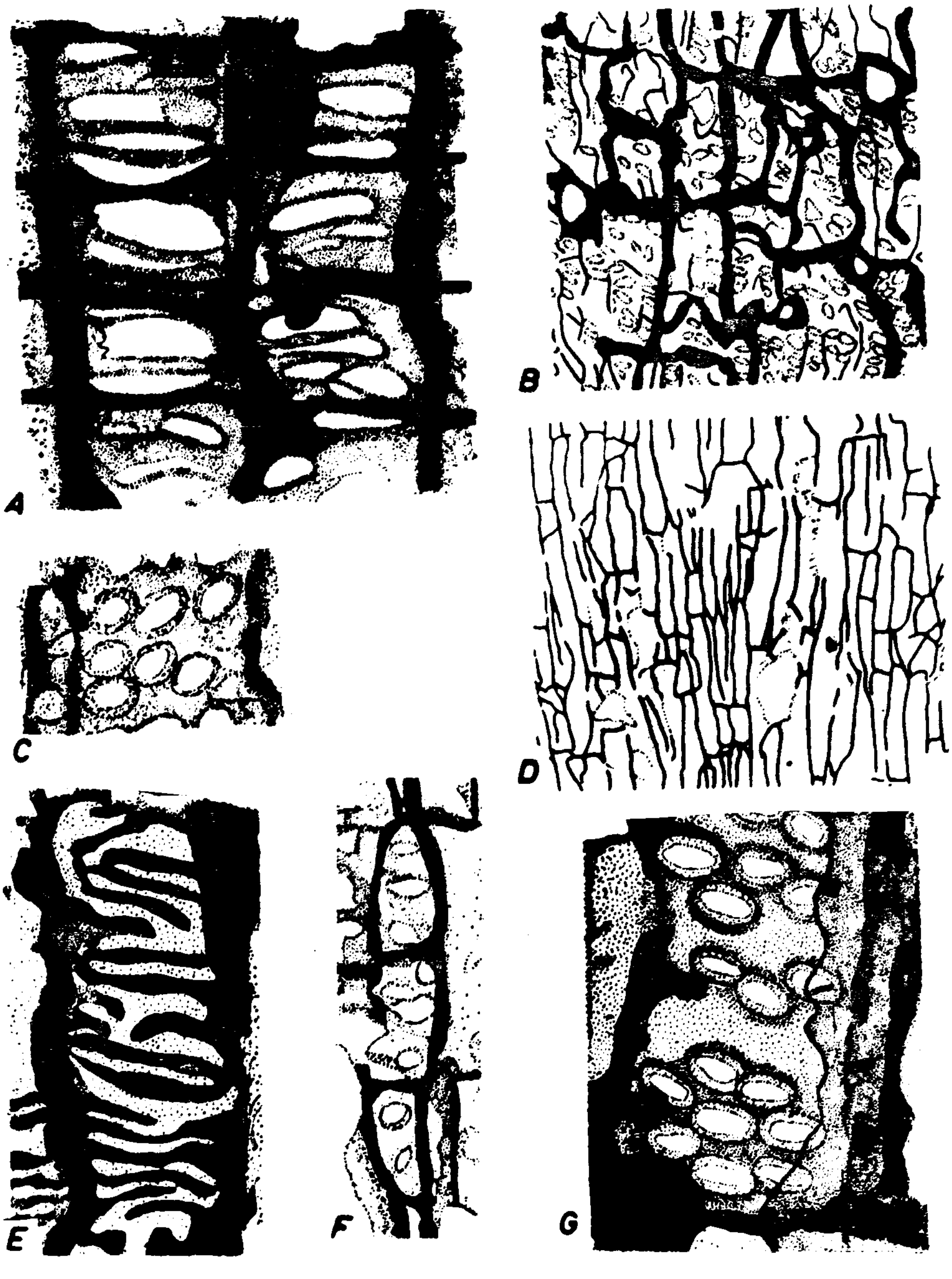

FIG. 3. A-G, *Vertebraria indica.* A, pit in ray fields. B, large parenchyma cells overlapping tracheids. C, tracheid showing triseriate pits. D, phloem-like cells. E, primary xylem tracheid, F, uniseriate ray in tangential section G, characteristic groups of bordered pits on the radial wall of a tracheid (after Pant and Singh, 1968).

external features and cuticular structure. Some species may show interstitial fibres, e.g., *G. fibrosa* or hairs, e.g., *G. hispida*. The leaves are typically dorsiventral. Although the leaves occur as compressions, their structural features have been carefully worked out by Pant and associates (Pant, 1958a; Pant and Gupta, 1968, 1971; Pant and Singh, 1971; Pant and Singh, 1974). The lower side of the lamina of some African leaves is described by Pant (1958a) as showing a raised midrib, side veins and slightly recurved margins but on the upper side it is flat, only the midrib region

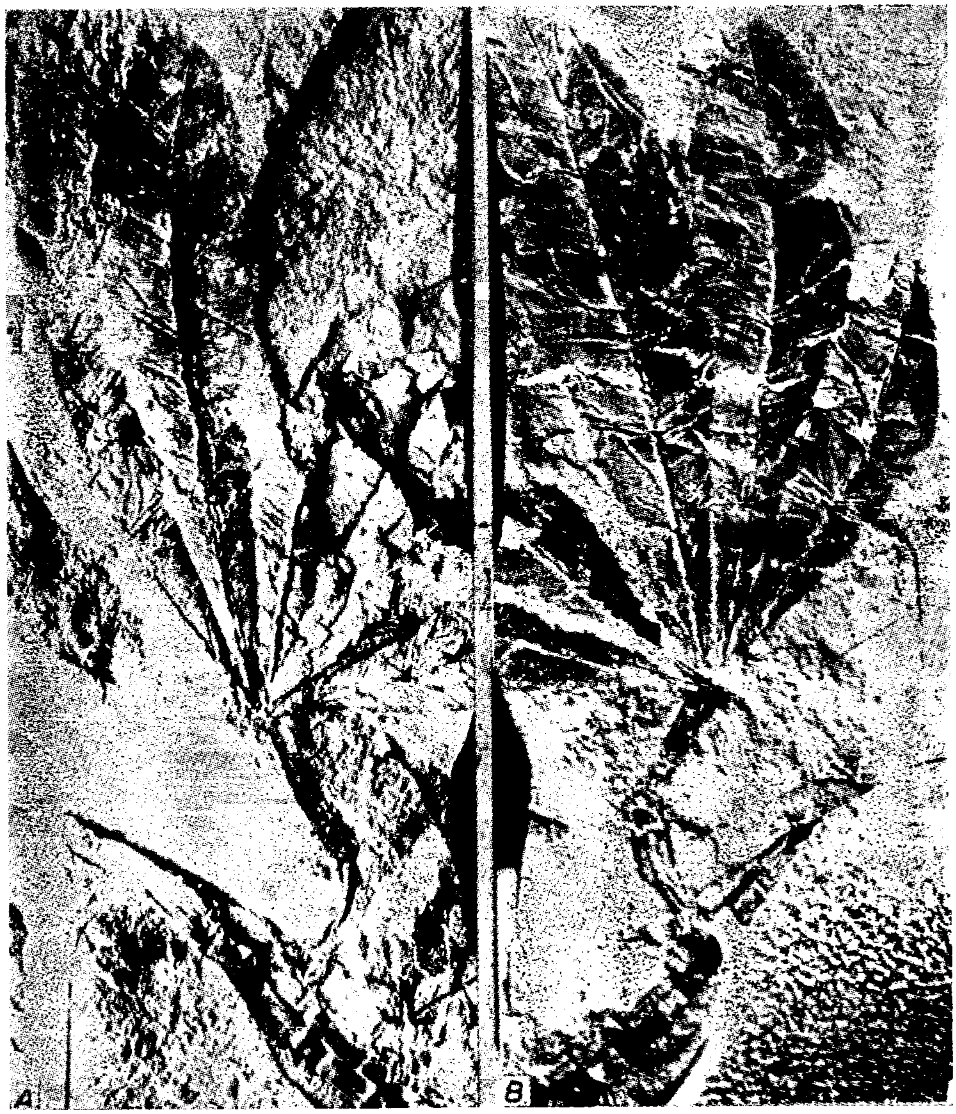

FIG. 4. *Vertebraria* axis with a short branch showing a branch of attached leaves of *Glossopteris sastrii*. X.8.

is slightly depressed. *Glossopteris* leaves are typically hypostomatic. Epidermal cells may be straight walled or sinuous-walled and the stomata are haplocheilic and irregularly dispersed between the veins. The subsidiary cells are usually papillate and the guard cells are generally sunken in a shallow pit. Epidermal peels show lateral and polar lignin lamellae of gymnosperm type. Some species show a hypodermis on the upper side or in the midrib region. The mesophyll was differentiated into palisade and spongy cells (see Fig. 5A, B). The midrib and the side veins show tracheids with scalariform thickenings but some tracheids of the midrib region may also have bordered pits.

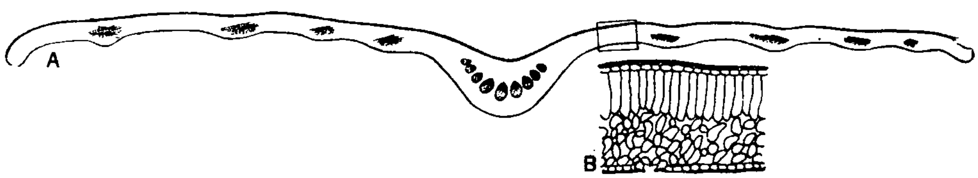

FIG. 5. A, reconstructed transverse section of a *Glossopteris* leaf. B, a portion of the same magnified to show details.

SCALE LEAVES

Rounded and lanceolate scales (Fig.1B, C) with a broad truncated or cordate base have been described by Feistmantel (1881, 1882), Zeiller (1896, 1902), Seward (1897, 1904), Arber (1905a, 1905b), Seward and Sahni (1920), Walkom (1921, 1922, 1928), Walton (1929), Pant (1958a) Lacey, Van Dijk and Gordon Gray (1974) and others. Some of these are found in close association with *Glossopteris* and wherever visible their venation is described as similarly reticulate although a midrib may be clear or obscure. Pant (1958a) was able to extract a few of these carbonised scales from the rock matrix. They showed a thick substance with scarious margins Some of them showed a interstitial fibres and when macerated they yielded non-stomatiferous cuticles with short cutinized hairs on the convex surface. Pant (1958a) attributed his scales to *Glossopteris fibrosa* on account of their close association and structural similarity with that species. He was also able to confirm that these and other transferred scales from Australia contained no sporangia and both their surfaces and cuticles were smooth without any scars or indications of the attachment of any reproductive organs. These facts and the occurrence of some scales in a bud-like group led Pant to conclude that these organs are of nature of vegetative bud scales which protected young parts and fell off during the growing season.

FRUCTIFICATIONS

More than thirty form genera of fructifications have been attributed to *Glossopertis* and allied leaves. Some of these are reportedly unisexual (male or female) while others are supposed to be bisexual. For convenience in discussion the present account deals with these under the following headings:—

(a) Associated detached fructifications which have never been reported in organic connection with *Glossopteris* leaves.

(b) Attached fructifications (some of these may also occur detached).

ASSOCIATED DETACHED FRUCTIFICATIONS

Many different kinds of fructifications have been attributed to *Glossopteris* on grounds of association. Some of these are species of the same kind of organs which are, in other cases, seen attached. These will be covered in the accounts of attached fructifications but there are others which have been attributed to *Glossopteris* only on account of close association in widely scattered localities (none of them are reported attached) and these are discussed below:—

Seed bearing organs and seed.—According to Rigby (1972) *Arberia minasica* (White 1908) and some species of *Dolianitia* described by Millan (1967) are possibly the seed bearing organs (see Fig. 6G, H, I) of leaves of *Glossopteris*,

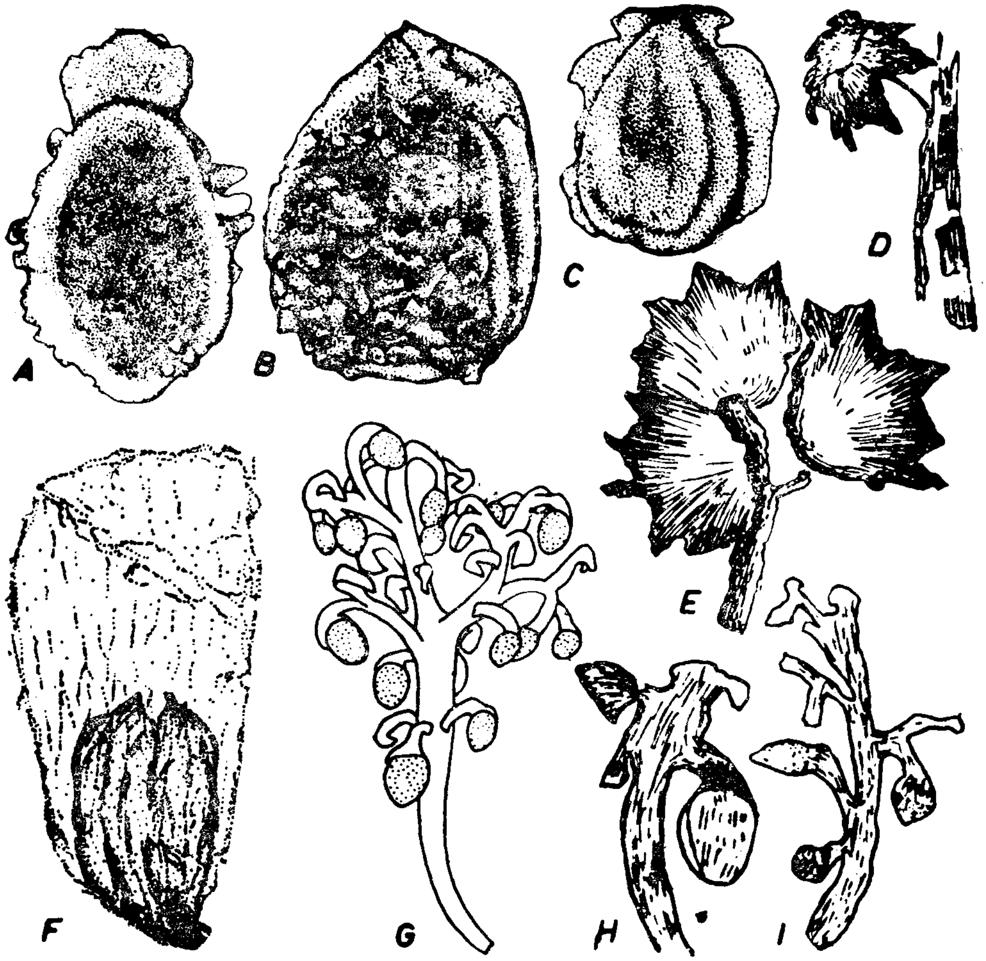

FIG. 6. A, *Stephanostoma crystallinus*. B, *Platycardia bengalensis*. C, *Pterygospermum raniganjense* (all after Pant and Nautiyal, 1960). D, E, *Mooia lidgettonioides* (drawn from photographs in Lacey, Van Dijk and Gordon-Gray, 1975). F, *Indocarpus* (after Surange and Chandra, 1975). G, reconstruction of *Arberia minasica* (after Rigby, 1972). H, I, *Dolianitia crassa* (after Millan, 1957).

Gangamopteris alliance which are associated with them. Except for showing attached seed-like bodies their structural details are unknown. Two similar fructifications are *Derbyella* White (1901) from Brazil and *Rigbya arberioides* Lacey, Van Dijk and Gordon Gray;(1974, 1975) from Natal there is neither any certainty about their being male or female nor about their affinities. Under the name *Dictyopteridium sporiferum* Surange and Chandra (1973a) have described structures regarded as seed-bearing receptacles of *Glossopteris* which occur in association with seeds and masses of structurally preserved seeds like those described earlier by Pant and Nautiyal (1960). They have also described typical specimens of *Dictyopteridium sporiferum* which look rather different from the presumed seed-bearing receptacles. These authors have suggested that *Dictyopteridium sporiferum* was a cone-like seed bearing fructification protected on one side by a spathe-like a midrib under the name *Isodictyopteridium costatum*.

Among dispersed seed-like impressions attributed to the glossopterids are *Nummulospermum* (Walkom, 1921) and *Indocarpus* (see Fig.6F and Surange and Chandra, 1974d) and seeds attributed to *Mooia, Lidgettonia, Rusangea* and others whose internal structure is unknown. A few other dispersed seeds called *Platycardia* (Fig.6B), *Pterygospermum* (Fig. 6C) *Stephanostoma* (Fig. 6A) and *Semenites* (Pant and Nautiyal, 1960) are structurally preserved and their fibrous integument and its outer and inner cuticles as well as the free nucellar membranes and megaspore membranes have been deseribed. They show micropylar canals at the narrower end and chalazal holes on the opposite side. Their micropylar canals and pollen chambers are often filled with two winged pollen grains of *Striatites* type (Fig. 7A, B, C).

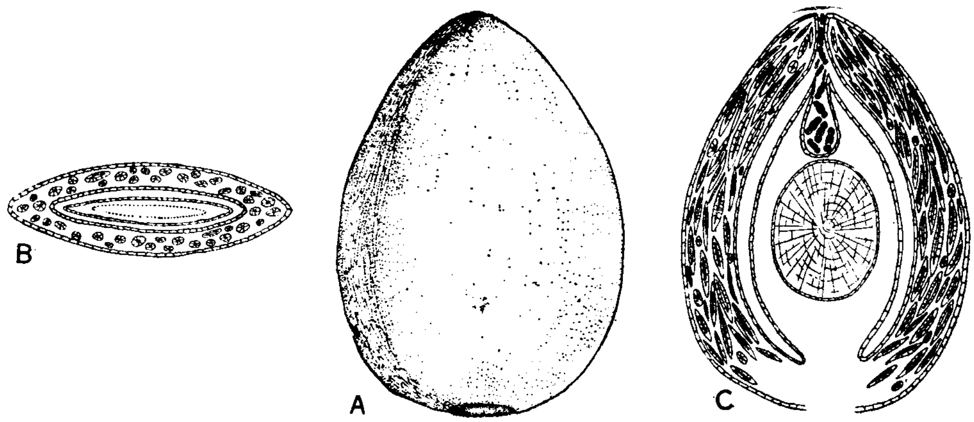

FIG. 7. A, reconstruction of a seed of *Platycardia*. B, C, reconstructed transverse and longitudinal section, respectively of the same (the surface processes are not shown).

sterile organ (Fig.10A). On the contrary Holmes (1974) believes that it was a sporangium bearing organ. Holmes has also described similar looking bodies with

Arber (1905a, b) described some "sporangium-like organs of *Glossopteris*" as attached to scale leaves. Thomas and Mrs. Thomas (1925) thought these were ramental scales. Many other authors have also described similar bodies ocurring in association with *Glossopteris* from various parts of Gondwanaland. Pant (1958a) found that there was no evidence of attachment of these bodies in Arber's specimens and other similar scales but he discovered that undehisced specimens of these bodies were full of two-winged pollen grains of *Striatites* type and thus they were proved to be sporangia (Fig. 8H, 11B).

Pant's African specimens of these sporangia were borne terminally on selender repeatedly forked stalks (Fig. 8F, G) but he also described two slightly concave disc-like organs from Australia which too were found in association with *Glossopteris*. Detached sporangia of the kind described by Pant (1958a) were subsequently named *Arberiella* (Pant and Nautiyal, 1960) but since no name has so far been given to the disc-like organs, they are here designated *Nesowalesia edwardsii* gen. et. sp. nov." with the following diagnosis: Concave disc-shaped organs with *Arberiella* type of sporangia attached on concave side, convex side smooth. Holotype V. 24233 (Fig. 11A), Horizon and Locality Lower Gondwana of Newcastle, New South wales, Australia. The generic name refers to the locality and the species is named after Mr W. N. Edwards in grateful memory of the help he rendered me at the British Museum (Nat. Hist.) London. The discs are reminiscent of northern *Potoniea* but the mode of attachment of sporangia is presently unknown although it could have been similar. The close association of *Glossopteris, Arberiella* and *Striatites* pollen as well as the seeds which they pollinate (*Platycardia, Pterygospermum, Stephanostoma* and *Semenites*) in widely scattered parts of Gondwanaland is an argument in favour of their belonging to *Glossopteris.*

Lately, Surange and Chandra (1974b) have described a stalked strobilus, *Kendostrobus cylindricus* (Fig. 8A) bearing *Lithangium surangei* type of sporangia with unwinged spores which are named *Kendosporites*. After presuming *Kendostrobus* to be a gymnospermous cone these authors suggested that it might have belonged to the Glossopteridales because that was the dominant group of gymnosperms during the lower Gondwanas.

ATTACHED FRUCTIFICATION

Feistmantel (1886) and Sen (1955) reported vague rounded scars on leaves of *Glossopteris* and assumed that these were fern-like sori. No sporangia or spores were described. The preservation of some of these leaves, e.g., those described by Sen is admittedly so poor that even the veins are obscure. Moreover, other features of *Glossopteris* leaves suggest that they were possibly gymnospermous and these reports may be rejected as worthless.

Among other fertile organs may be mentioned two stalked cupules (see Fig. 9L and Pant and Singh, 1974) which are exceptional in being attached to a stem in the axils of leaves of *Glossopteris taenioides* Feist. The structure of the rounded bodies contained in the cupules is unknown. All other hitherto described organically connected fructifications of *Glossopteris* are leaf borne. This important specimen leads me to two conclusions: firstly it shows that such other fructifications of *Glossopteris* which seem to arise from leaf midribs may also be axillary shoots which have fused with the midribs of the subtending bracts as in *Tilia* and secondly it shows that the fertile side of the fructification was adaxial and away from the subtending leaf although a

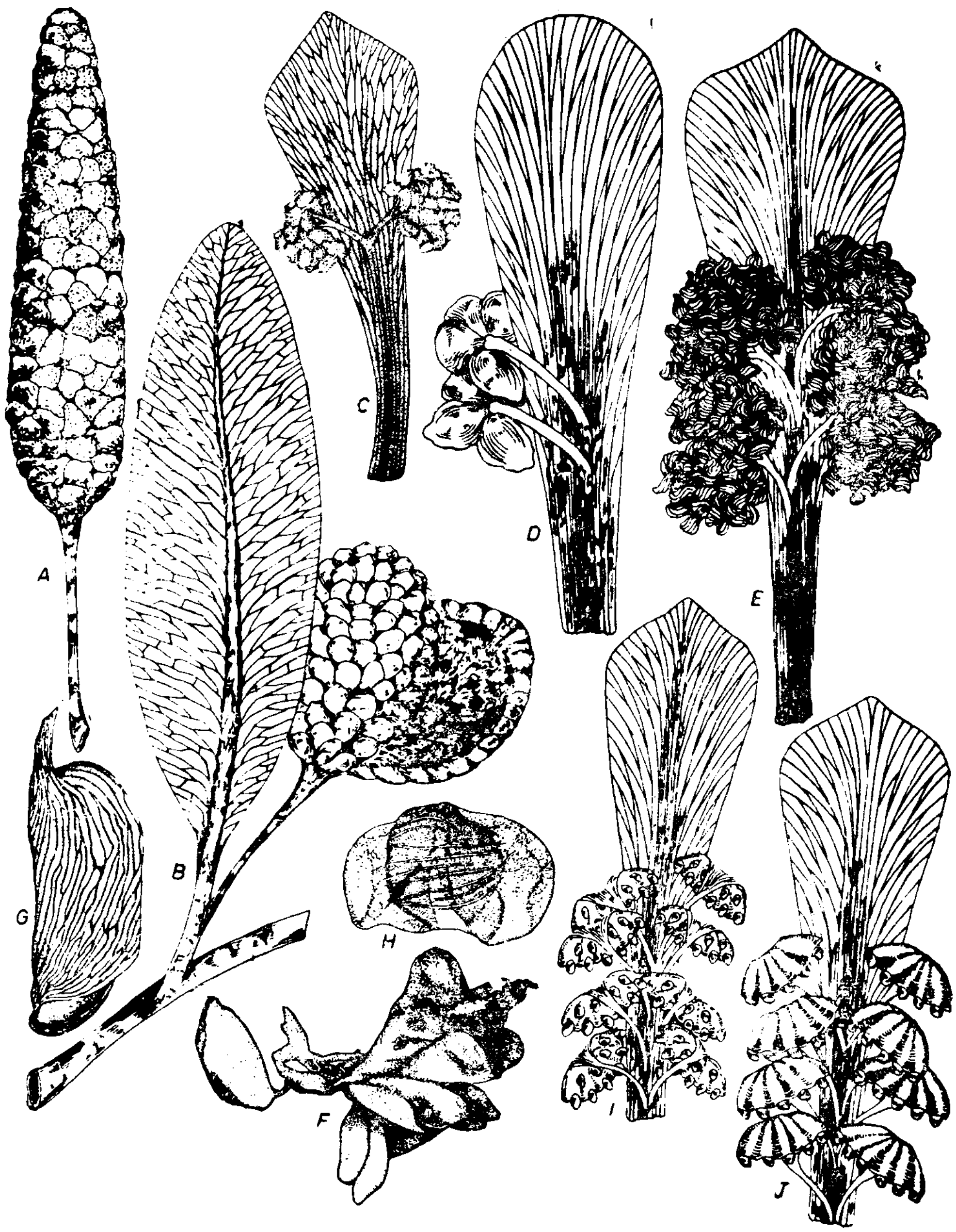

FIG. 8. A–E, I, J, reconstructed fructifications (after Surange and Chandra, 1975). F-G, *Arberiella africana* (after Pant, 1958). H, *Striatites* pollen grain of *Arberiella vulgaris* (after Pant and Nautiyal, 1960). A, *Kendostrobus*. B, *Scutum*. C, *Eretmonia*, D, *Partha*. E, *Glossotheca*, F, group of sporangia attached to repeatedly branched stalks. G, a single dehisced sporangium. H, pollen grain (*Striatites* type dissected out of a sporangium of *Arberiella vulgaris*, I, J, *Lidgettonia* cupule in two views (the leaf is, however, presented in the same view).

detached fertile *Glossopteris* called *Australoglossa* (see Eig. 10 C and Holmes 1974) shows the fertile side of the fructification turned towards the lamina (see also Schopf, 1976) but a closer examination of the photograph and figure suggests that the petiole of the leaf was bent and came on the reverse side of the fructification and the petiole was also twisted in such a manner that the leaf is seen dorsiventrally flattened while the fructification presents a lateral view. Accordingly, I believe that the correct orientation of the stem, leaf and fructification is seen only in the specimens of *G. taenioides* described by Pant and Singh (1974).

The first person to have noticed a fructification whose stalk was clearly traceable up to the midrib of a *Glossopteris* leaf was Zeiller (1902) but since he found this in a single specimen he cautiously discounted it as a chance overlap of the two organs. Regarding it separate, Zeiller called the fructification, *Ottokaria bengalensis* and identified the leaf as *Glossopteris indica* (Fig. 12 A). However, in 1952 when Plumstead reported a large number of similarly attached fructifications, it became at once clear that Zeiller's *Ottokaria* too must have been attached to the midrib of *G. indica*. In fact, Plumstead's paper (1952) seems to have turned the tide against all caution, converting judicious conservetism into ready credulity. Even chance overlaps or bodies which seemingly lie clear of leaves have since been unhesitatingly accepted as attached fructifications of the glossopterids.

Up to date more than a dozen genera of fructifications have been described as attached to leaves of various species of *Glossopteris* or to fertile *Glossopteris*-like scales or bracts. As was pointed out by Edwards (1952) and others it is unfortunate that even when the fructifications are found attached to *Glossopteris* leaves they have been given separate generic titles. Separate names would, however, be necessary for diverse leafy bracts with attached fructifications termed "fertiligers" by Schopf (1976). Some of the genera of fertile organs are: *Australoglossa* Holmes, *Denkania* Surange and Chandra, '*Eretmonia*' du Toit, *Glossotheca* Surange and Maheshwari, *Hirsutum* Plumstead, *Isodictyopteridium* Holmes, *Lanceolatus* Plumstead, *Lidgettonia* Thomas, *Mooia* Lacey, van Dijk and Gordon-Gray, *Ottokaria* Zeiller, *Partha* Surange and Chandra, *Plumsteadia* Rigby (=*Cistella* Plumstead), *Pluma* Plumstead, *Rusangea* Lacey, van Dijk and Gordon-Gray and *Senotheca* Banerjee.

Out of the above fructifications *Eretmonia, Glossotheca* are described as unisexual and male, *Australoglossa, Denkania, Mooia, Partha, Plumsteadia* and *Senotheca* as unisexual and female, *Lanceolatus, Hirsutum, Scutum,* and *Ottokaria* sensu Plumstead are supposed to be bisexual and *Lidgettonia* sensu Thomas and *Pluma* Plumstead are regarded as having either male or female fructifications. The chief features of the various kinds of fructifications are discussed below —

(i) *Male fructifications.*—Under the name *Eretmonia natalensis* du Toit (1332) described impressions of a few detached spoon-shaped stalked structures which appeared to him as having "contained" sporangium-like bodies of Arber in their hollows. Pant (1962) suggested that Du Toit's *Eretmonia* could represent lonceolate scales viewed upside down. However, the sporangium bearing nature of *Eretmonia* is now indubitably established by Lacey, van Dijk and Gordon Gray (1974, 1975) on the basis of well preserved specimens showing branched sporangiferous stalks attached to scale-like bodies with anastomosing veins. The scales are just like those seen in Du Toit's *Eretmonia* and the sporangia are described as being of *Arberiella* type (see Pant, 1958a and Pant and Nautiyal, 1960). After a detailed statistical analysis of the various forms of *Eretmonia* in their collection Lacey et al., recognised only a single species, *E. natalensis* but Surange and Maheshwari (1970) and Surange and Chandra (1974 b, 1975) have described four species of the genus from India. They show stalks, sporangia and scales like those of the African *Eretmonia* and are reconstructed as showing repeatedly branched stalks attached to the midrib region of small scale leaves with *Glossopteris*-like reticulate venation (Fig. 8C). Ultimate branches of the stalks are described as ending in striate sporangia, like those of *Arberiella* Pant and Nautiyal (1960). Apparently the Indian species of *Eretmonia* may be similar to the African material described by Lacey et al., Surange and Maheshwari (1970) and Surange and Chandra (1974b, 1974c, 1975) have also described fructifications, which appear to be very similar to their *Eretmonia*, under the names *Glossotheca utkalensis* and *G. orissiana* (Fig. 8E).

(ii) *Female fructifications.*—The fructifications of *Australoglossa walkomii* have been mentioned already. They show clear impressions of *Cordaicarpus* type of seeds (Fig. 9C).

Surange and Chandra (1973b) described impressions of fertile seed-bearing leaves under the name *Denkania indica*. The reconstruction shows a *Glossopteris*-like leaf with a number of long stalks attached to the midrib (Fig. 10D). Seed-like bodies seen terminating the stalks are interpreted as uniovulated cupules. The fructification called *Rusangea elegans* by Lacey, van Dijk and Gordon-Gray (1974, 1975) are somewhat similar to those of *Denkania* but in place of its uniovulate cupules, the stalks of *Rusangea* are described as bearing uniovulate scales.

Surange and Chandra (1973c) have described yet another kind of female fructifications bearing stalks in a single row under the name *Partha* (Fig. 8D). These authors think that the terminal structure of the stalks of *Partha* could possibly be a group of uniovulate cupules or alternatively a disc-like cupule on the underside of which are attached four seeds. A similar genus showing usually drooping four to eight lobed campanulate cupules possibly bearing seeds is *Mooia lidgettonioides* (see Fig. 6D, E and Lacey, van Dijk and Gordon-Gray, 1974, 1975). The cupules may be compared with the discs of *Ledgettonia* and Lacey et al., even suggest a comparison with *Eretmonia natalensis*.

Fructifications called *Plumsteadia* Rigby = (*Cistella* Plumstead) are described as having two halves, a female half with oval sacs and a protective half of harder tissue but both are without a wing (Fig. 9G).

Unisexual fructifications which could be either male or female.—

Plumstead (1958) believes that some fructifications called *Pluma* may be ovulate but others bearing the same name could be microsporangiate (Fig. 9D, E). The photographs and figure of what she believes to be a male fructification appears to be a laterally compressed cupule (Fig. 9D). Under the name *Lidgettonia natalensis*, Thomas (1958) described some *Glossopteris*-like fertile scales bearing a number of stalks with peltate heads or cupules (Fig. 9F). He found detached seeds and sporangia in association with these organs and thought that some lidgettonias could have borne seeds on

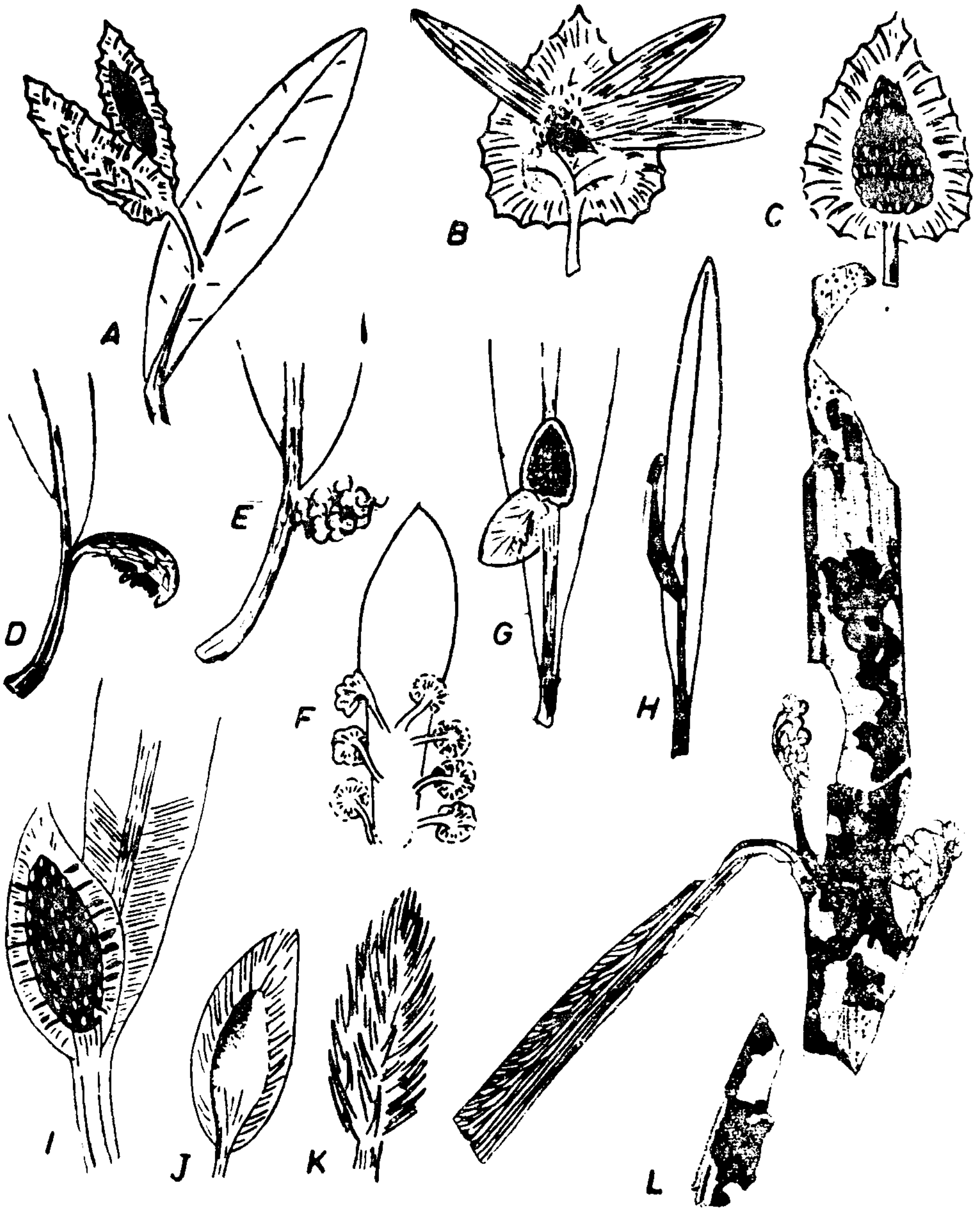

FIG. 9. A, bivalved cupule of *Scutum*. B. inside of male half and C, inside of female half of the same. D, E, *Pluma* mature male and female fructifications, respectively. F, *Lidgettonia africana*. G, *Plumsteadia* showing protective half and inside of mature female half. H, *Lanceolatus*, cupule protecting growing fructification. I, *Hirsutum* showing inside of female half. J, same showing inside of male half after shedding pollen grains. K, same showing male half with pollen organs. L, stem attached fructification of *Glossopteris taenoides* (A-E, G-K, after Plumstead, 1958; F, after Thomas, 1958; L, after Pant and Singh, 1974).

their cupules while others sporangium bearing. However, according to Lacey, van Dijk and Gordon-Gray (1974. 1975) and Surange and Chandra (1974a) *Lidgettonia* is exclusively a seed bearing organ which has been reconstructed by the latter as a half umbrella-like organ (Fig. 8 I, J).

Supposed bisexual and bivalved fructifications

Plumstead (1952) described two kinds of fructifications under separate generic names *Scutum* (Fig. 9A, B, C) and *Lanceolatus* (Fig 9H) although they were found attached to leaves of different species of *Glossopteris*. In the discussions appended to the above paper Edwards, Lakhanpal, Kräusel and Jongmans were critical of the nomenclature adopted by Plumstead wherein she violated two articles of the International Code of Botanical Nomenclature by referring attached organs to new genera and by using adjectival epithets for generic names. Subsequently, Plumstead (1956a, 1956b, 1958) reviewed and extended her observations by adding three more similarly named genera and by redescribing and reinterpreting her old forms and *Ottokaria*. All these fructifications except *Pluma* were now described as bivalved structures. Some of them like *Scutum*, *Lanceolatus* and *Hirsutum* were assumed to be bisexual where one valve was presumably bearing "male bracts" and the other the seeds. None of her fructifications shows any trace of carbon and the interpretations are therefore largely conjectural. Pant (1962) has already pointed out that there is no reason to believe that the two counterparts of the same fossil which showed its two different faces were the two valves of a bivalved bisexual structure. Surange and Chandra (1974d) also believe that *Scutum* had two halves but suggest that it was like a spadix inflorescence with a spathe-like veined scale protecting a seed bearing radially organised cone-like receptacle (Fig. 8B). Plumustead's interpretation of *Lanceolatus* as bearing its seeds on the leaf surface and their being covered by a cupule "which in addition to its protective function bore staminate organs for a short period" assumes a similar scale-like organ. The fructification called *Hirsutum* (Fig. 9I, J, K) appears to be quite like *Scutum* but its presumed male half is described as being hairy in the young conditions and bearing "filamentous pollen organs" which are shed on maturity.

Structually preserved fructifications

Unfortunately none of the above mentioned attached or presumably attached fructification described by Plumstead (1952, 1956a, 1956b, 1958), Surange and Maheshwari (1970), Holmes (1973), Lacey, van Dijk and Gordon-Gray (1974, 1975) and Surange and Chandra (1973a, b, c, 1974a, b, c, d) shows any trace of carbon. Accordingly their structural details and determination of their rounded marks or other features as cupules, seeds, sporangia, stigma or micropyles cannot be confirmed. The only exceptions among such fructifications are *Ottokaria* and certain *Scutum*-like organs described by Mukherjee, Banerjee and Sen (1966) and some linear fructifications with a median groove called *Senotheca* Banerjee (1969) which lie over midribs of *Glossopteris* leaves and *Ottokaria*-like heads (Fig. 10B) described by Pant and Nautiyal (1965, 1966). However, the structural details of the holotype of *Ottokaria* as described by

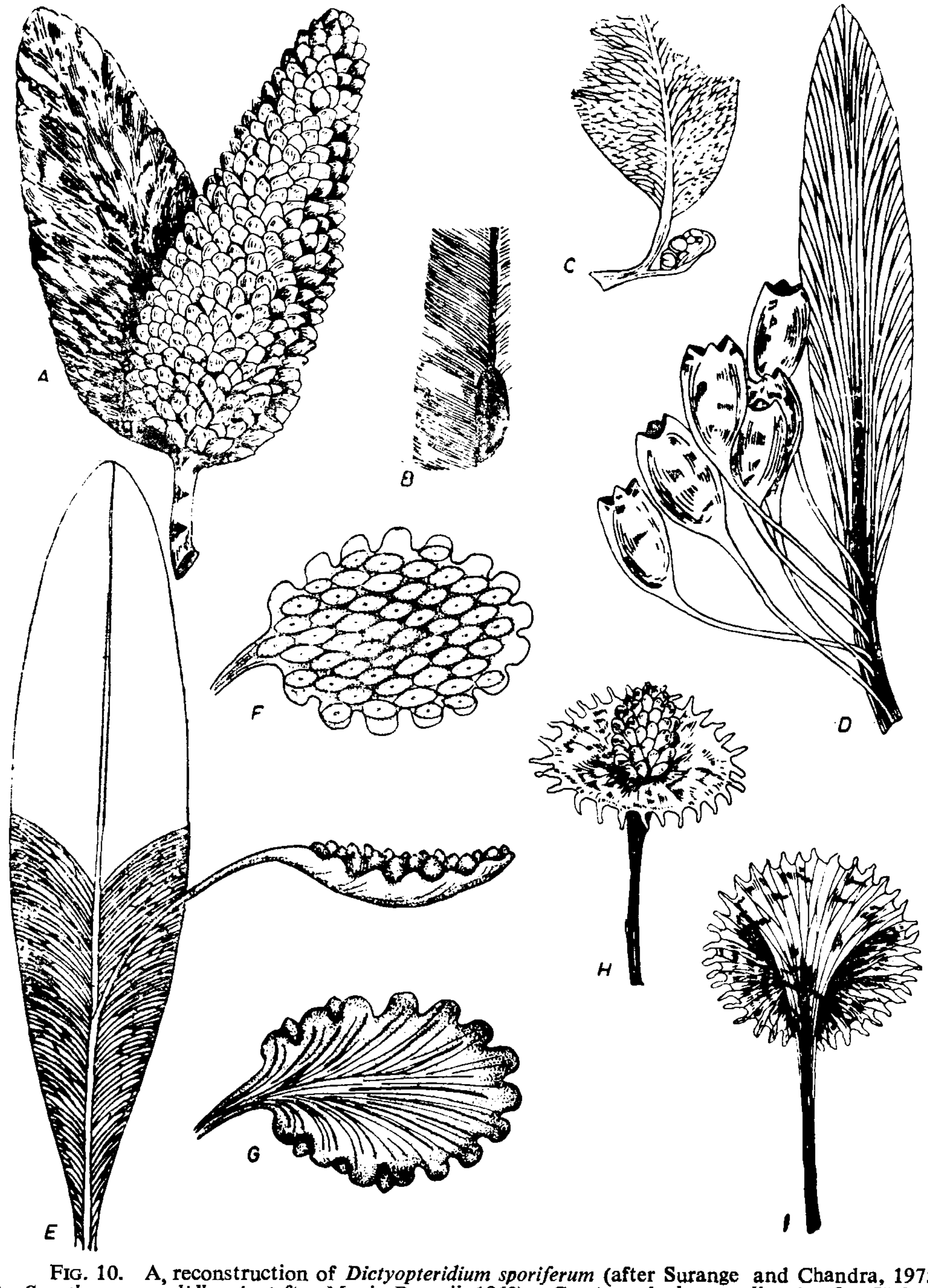

FIG. 10. A, reconstruction of *Dictyopteridium sporiferum* (after Surange and Chandra, 1975). B . *Senotheca murulidhensis* (after Manju Banerji, 1969). C, *Australoglossa walkomii* (after Holmes, 1974). D, reconstruction of *Denkania* (after Surange and Chandra, 1975), E, F, reconstruction of *Glossopteris* leaf bearing an *Ottokaria* (presenting a side view). F, G, *Ottokaria* heads showing fertile and sterile side respectively (E, F, G, after Pant and Nautiyal) H, I, two views of an *Ottokaria* reconstruction (after Surange and Chandra, 1975).

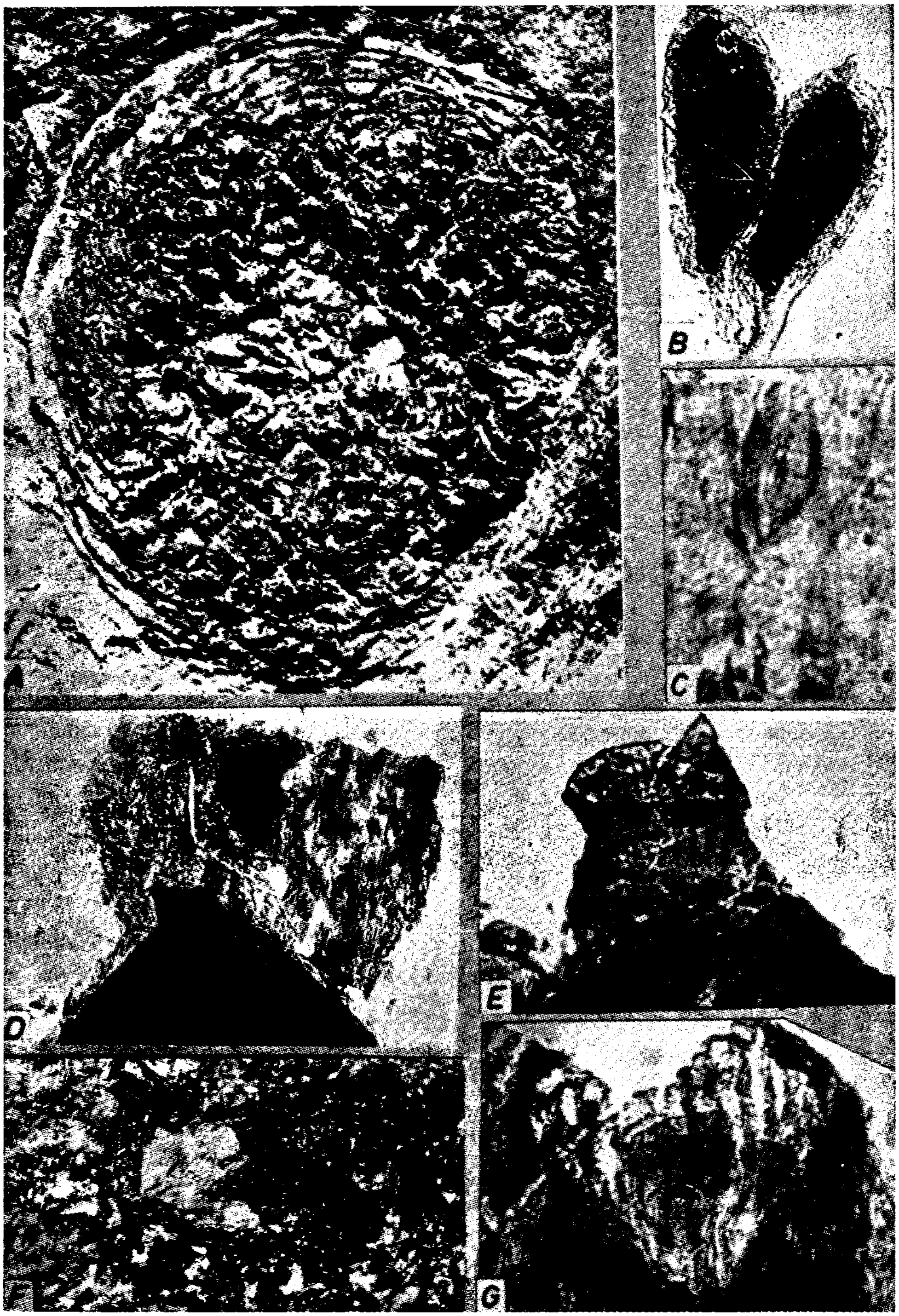

FIG. 11. A, holotype of *Nesowalesia edwardsii* gen. et sp nov No. V. 24233. B, undehisced sporangia of *Arberiella africana*. C, cuticle of the lower side of a disc of *Ottokaria* showing a stoma. D, micropylar portion of dark nucellar cuticle of a seed of *Ottokaria* with attached cuticle of wing or micropylar funnel. E, micropylar tube of a seed, nucellar cells around pollen chamber of a seed of *Ottokaria* showing two winged pollen grains inside. F, carbonised substance at the periphery of an *Ottokaria* disc showing a compressed seed whose mud filled nucellus appears white.

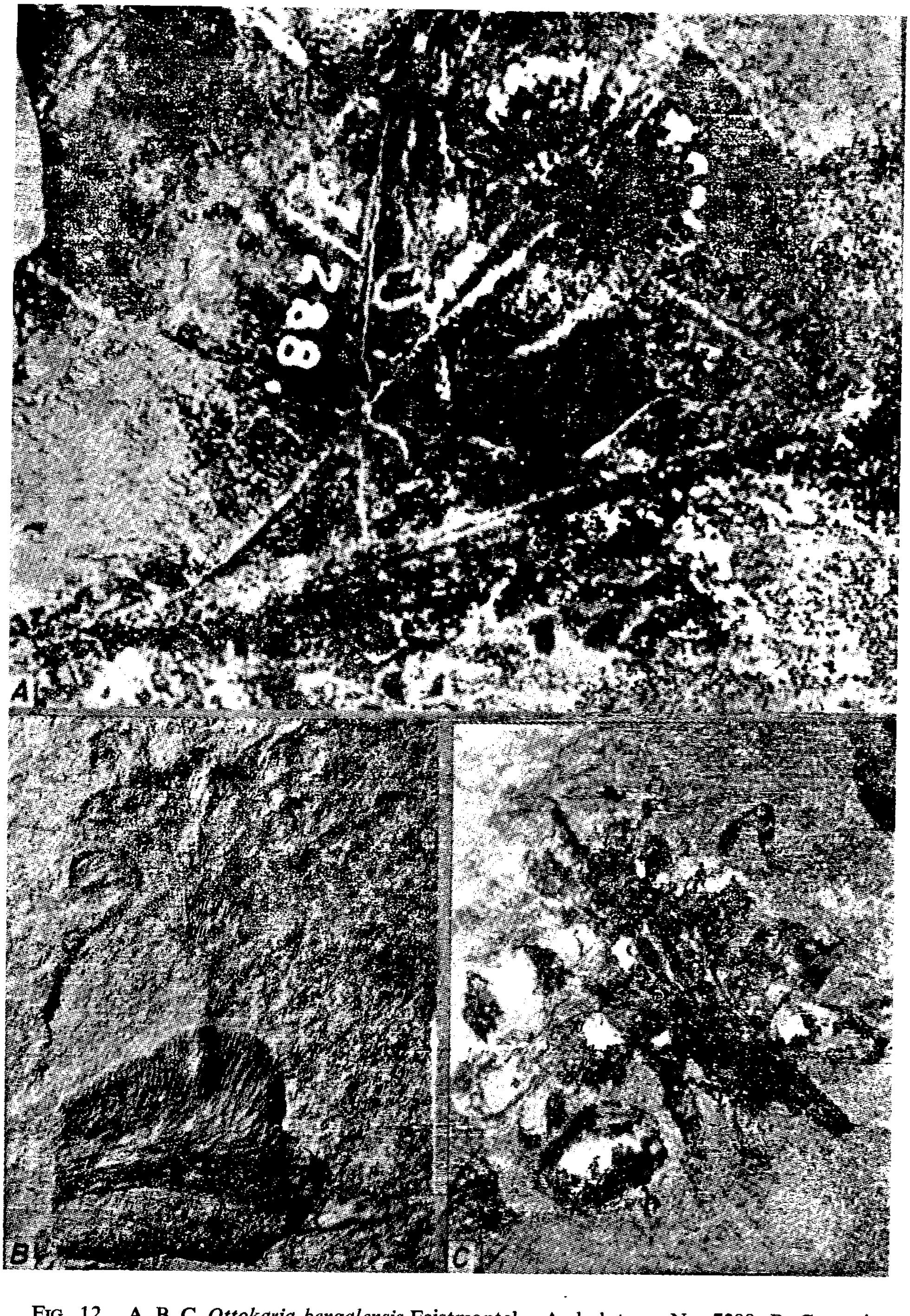

FIG. 12. A, B, C, *Ottokaria bengalensis* Feistmantel. A holotype No. 7288. B, C, specimens showing attached seeds.

Mukherjee, Banerjee and Sen are far from being clear since only a few spores were described but no sporangia were seen. The spores could be wind-blown *Sporae dispersae*. Some seed-like bodies were found in the *Scutum*-like organs and in *Senotheca* but the morphology of the fructifications and the insertion of seeds are unknown.

This leaves us only with a *Ottokaria*-like heads described by Pant and Nautiyal (1965, 1966). Subsequent collections have swelled their number to more than 200 and my colleague Dr D. D. Nautiyal and I have now almost completed the investigation of their structure. The main results of this work are summarized below:

All the fructifications show a terminal head and a slender stalk. The stalks in some of our specimens (which are from the same locality as the holotype) are clearly traceable up the midribs of *Glossopteris* leaves which show fibres and veins like those of *G. fibrosa* Pant (externally they are just like *G. indica* to which Zeiller's *Ottokaria* is attached and this is shown by the continuance of uninterrupted files of cells in the carbon (see Pant and Nautiyal, 1966) but the lamina in our leaves is narrower. Near the disc the stalk becomes slightly wider as in the type of *Ottokaria*. These fructifications have been collected from the type locality of *Ottokaria* (Zeiller, 1902) and although slightly smaller they are all essentially similar to it. The form of the head is, however, somewhat variable. Some of the variations seem to be the result of compression in different planes in the same type of fossil or its state of preservation but others are possibly different. However, the fructification which we described as resembling *Ottokaria* are in no way similar to *Arberia* as was assumed by Rigby (1972) without a first hand examination of our specimens.

The heads of all the fructifications in our collection are seed bearing and many show preserved seeds in situ. Transfers of the fructifications have convincingly shown that the seeds are attached to slightly concave spoon-like cupules which show sterile lobes at the margins. The convex surface of the cupule is presumably adfoliar (towards the leaf) and sterile. Often it shows radiating fibres and veins with occasional anastomoses and its stomatiferous epidermis shows elongated rectangular cells which radiate in the direction of the veins. The cuticle of the fertile surface of the disc is delicate. The seeds are comparable with those of *Pterygospermum* and *Platycardia* but slightly larger. Like the detached seeds the attached ones are also pollinated by two winged pollen grains.

As outlined above our study of *Ottokaria* has covincingly shown that it is a dorsiventral organ (see Fig. 10 E-G) which is neither bivalved and bisexual as suggested by Plumstead (1958) nor radially symmetrical as presumed by Surange and Chandra. (Fig. 10H, I).

AFFINITIES OF *GLOSSOPTERIS*

The attachment of seemingly diverse fructifications to the leaves of *Glossopteris* is generally regarded as suggesting that the form genus *Glossopteris* is an unnatural conglomerate of a number of natural genera. As described by Plumstead (1968) the occurrence of apparently similar fructifications in *Glossopteris*, *Gangamopteris* and *Palaeovittaria* may suggest that the boundaries between these form genera too are unnatural. Perhaps we would be able to determine the natural boundaries between the various glossopterids only when we have come to know the structure of their various parts and then we may also be able to put them to better use in understanding the formation and stratigraphy of the coaliferous rocks which they have formed.

The occurrence of a resistant cuticle in *Glossopteris* leaves and gymnosperm type of lignin lamellae in their stomata as well as the gymnosperm type of wood in *Vertebraria* had so far been used as arguments for regarding *Glossopteris* as a gymnosperm. The occurrence of gymnospermously pollinated exposed seeds attached to our leaf attached ottokarias finally proves that *Glossopteris* was a gymnosperm.

Surange and Chandra (1975) have suggested that leaves of *Glossopteris* may belong to two rather different groups of gymnosperms, viz., the Pteridospermales and the Glossopteridales. Under the Pteridospermales they include *Lidgettonia, Denkania* and *Partha* which are all interpreted as cupulate fructifications. On the other hand their Glossopteridales include leaf attached fructifications of *Scutum, Dictyopteridium* and *Ottokaria.* They believe that *Scutum* and *Dictyopteridium* have multiovulate radially organised cone-like receptacles protected by spathe-like protective scales although convincing arguments in favour of such an interpretation of the morphology of these organs are lacking. Surange and Chandra suggested that *Ottokaria* too had a radially organised cone like receptacle with a funnel-like cover at the base. The covering has been compared with *Rajmahalia paradoxa* Sahni and Rao. However, as our structurally preserved material shows, the discs of *Ottokaria* heads may be compared on the contrary, with some multiovulate cupules of pteridosperms, e.g., *Calathospermum* but the seeds in *Ottokaria* are less protected. Although not at all related a parallel may be drawn between *Calathospermum* versus *Ottokaria* and the hypanthodium of a fig versus a flat disc of *Dorstenia.* In fact if the *Potoniea*-like Australian discs, described by Pant (1958), also belong to *Glossopteris*, the male and female organs of the plant would appear to be similar and comparable with those of pteriodosperms.

Even though similar attachment of a cupule stalk to the midrib of a simple leaf is unknown in other seed ferns its being borne on a leaf is a pteriodospermous feature. Perhaps we could continue to keep these plants among the pteridosperms in the manner of the Caytoniales, Corystospermaceae and Peltaspermaceae, the attachment of whose "megasporophylls" and "microsporophylls" is unknown. However, if the fructification is axillary as seen in *G. taeniodes* (Pant and Singh, 1974) and as sometimes assumed for *Scutum*, etc., it would undoubtedly suggest that the Glossopteridales are very different.

Harris' meaningful remark (see Plumstead, 1952), "Such strange plants should not be placed in the Pteridosperms...... They would just as well be included in the Angiosperms" seems to have led Plumstead (1958) astray, first to imagine that her fructifications were bivalved and bisexual and then to suggest that the Glossopteridales may have given rise to the angiosperms. As I have already pointed out, *Glossopteris* is now in all respects a gymnosperm and there is also nothing to show that its fructifications are bivalved and bisexual. Any direct relationship between the Glossopteridales and the angiosperms is therefore out of question.

Speculating on the affinities of the glossopterids, Schopf (1976) derives them from the Cordaitales. The main arguments advanced in favour of the idea are presumed similarities between the supposed fructification of *Noeggerathiopsis* (whose Cordaitean affinities are uncertain), *Cordaianthus* and glossopterid fructifications and between foliar boundles and seeds of glossopterids and Cordaitales. However, the foliar bundles and seeds of cycads and Cordaitales also have simiarities but so far no one has seriously suggested a connection between them.

Schopf (1976) has in addition derived the Gnetales from the Glossopteridales but again without valid reasons. Unfortunately our knowledge of these very strange plants is presently so poor that we can only make plausible guesses about their reconstructions and affinities and further work is an urgent necessity.

And now let me end my talk by offering you my very best thanks for the great honour you have done me by electing me to the high office of the President of our Society for this year. I also take this opportunity to thank our Honorary Secretary, Prof. Y.S. Murty, Honorary Treasurer and Business Manager, Prof. L.P. Mall, other office bearers and honourable members of the Executive Council for their efficient handling of the affairs of the Society which made the burden of my duties as President imperceptible.

And lastly I thank you all for the patient hearing you have given me.

References

ARBER, E.A.N. 1902. On the Clarke collection of fossil plants from New South Wales. *Quart. J. Geol. Soc.* **58**: 1-26.

——. 1905a. On the sporangium like organs of *Glossopteris Browniana* Brongn. *Quart. J. Geol. Soc. Lond.* **61**: 324-328.

——. 1905b. *Catalogue of the Fossil Plants of the Glossopteris Flora in the Department of Geology, British Museum (Nat. History)* lxxiv + 255p.p. London.

BANERJEE M. 1969. *Senotheca murulidihensis* a new glossopteridean fructification from India associated with *Glossopteris taeniopteroides* Feist. *J. Sen. Mem. Vol*: 359-368.

BRONGNIART, A. 1828. *Prodrome d'une Histoire des Vegetaux fossiles.* VIII+223 pp. Paris.

——. 1828-38. *Histoire des Vgetaux fossiles, ou recherches botaniques et geologiques sur les vegetaux renfermes dans les diverse couches du Globe.* 2 vols. Paris.

BUNBURY, C.J.F. 1861. Notes on a collection of fossil plants from Nagpur Central India. *Quart. J. Geol. Soc. Lond.* **17**: 325-346.

DOLIANITI, E. 1954. A flora do Gondwana inferior em Santa. Catarina, 4, O. Genero *Vertebraria. Nots. prelim. Estud. Div. Geol. Miner. Bras.*, **81**: 1-5.

DU TOIT, A.L. 1932. Some fossil plants from the Karoo system of South Africa. *Ann. S. African Mus.* **58**: 369-393.

EDWARDS, W.N. 1952. *A guide to the fossil plants of the British Museum (Nat. Hist.)* 2nd Ed. London.

ETHERIDGE, R. 1894. On the mode of attachment of the leaves or fronds to the caudex in *Glossopteris* with remarks on the relation of the genus to its allies (with a note on its stratigraphical distribution in Australia by by T.W. Edgeworth David.). *Proc. Linn. Soc. N.S.W.* **9**: 228-258.

FEISTMANTEL, O. 1881. The fossil flora of the Gondwana system–3, (2 and 3). The flora of the Damuda and the Panchet Divisions. *Palaeont. Indica.* Calcutta (12): 1-149.

——. 1882. The fossil flora of the Gondwana system–4 (i), The fossil flora of the Rewah Gondwana Basin. *Palaeont. Indica.* Calcutta (12): 1-52.

——. 1886. The fossil flora of the Gondwana system–4 (2). The fossil flora of some of the coalfields of Western Bengal 2. *Palaeont. Indica.* Calcutta (12): 1-66.

HOLMES, W.B.K. 1974. On some fructifications of Glossopteridales from the Upper Permian of N.S.W. *Proc. Linn. Soc. N.S.W.* **98**: 131-141.

LACEY, W.S., D.E. VAN DIJK, AND K.D. GORDON-GRAY, 1974. New Permian *Glossopteris* Flora from Natal. *African J. Science.* **70**: 154-156.

——., ——., AND ——1975. Fossil plants from the Upper Permian in the Mooi river district of Natal, South Africa. *Ann. Natal. Mus.* **22** (2): 349-420.

MAITHY, P.K. 1965. Studies in the Glossopteris flora of India–26. Glossopteridales from the Karharbari beds, Giridih coalfield, India. *Palaeobotanist*. **13**: 248-263 (1964).

MAHESHWARI, H.K. 1965. Studies in the Glossopteris flora of India-23. On two fructifications from Raniganj stage of the Raniganj coalfield, Bengal. *Palaeobotanist*. **13**: 144–147.

MILLAN, J.H. 1967. Novas frutificacoes na flora Glossopteris do Gondwana inferior do Brasil. *Dolianitia* gen nov. *Div. Geol. Min. Not. Prel. Est.* **140**; 1-19.

MUKHERJI, S., M. BANERJI, AND J. SEN, 1966. Further glossopteridean fructifications from India. *Palaeontographica* B. **117**: 99-113.

OLDHAM. R.D. 1897. On a plant of *Glossopteris* with part of the rhizome attached, and on the structure of *Vertebraria*. *Rec. Geol. Surv. India*. **30**: 45-50.

PANT, D.D. 1956. On the two compressed Palaeozoic axes; *Stigmaria ficoides* in the *Gymnostrobus* condition and *Vertebraria indica*. *Ann. Bot.* (N.S.). **20**: 419-429.

——. 1958a. The structure of some leaves and fructifications of the Glossopteris flora of Tanganyika. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.* **3**: 127-175.

——. 1958b. Structure of some roots and spores from Lower Gondwana (Permo-Carboniferous) of E. Africa. *Vijnana Parishad Anusandhan Patrika* **1**: 231-234.

——. 1962. Some recent contributions towards our knowledge of Glossopteris flora. *Proc. Summer School of Botany*, Darjeeling: 302-319.

——. 1967. On the stem ond attachment of *Glossopteris* leaves. *Phytomorphology*. **17**: 351-359.

PANT, D,D. AND K.L. GUPTA, 1968. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Bgt. Párt 1. *Palaeontographica B.* 124: 45-81.

——., AND ——. 1971. Cuticultar structure of some Indian Lower Gondwana species of *Glossopteri* Bgt. Part II. *Palaeontographica B.* **132**: 130-152.

PANT, D.D., AND D.D. NAUTIYAL, 1960. Some seeds and sporangia of Glossopteris flora from Raniganj coalified, India, *Palaeontographica* B. **107**: 41-64.

——. 1965. Seed-bearing *Ottokaria*-like fructifications from India. *Nature*. 207 (4997): 623-624.

——. 1966. On two peculiar fossils from Karbarbari stage, India. *Symposium of Floristics and Stratigraphy of Gondwanaland*; 98-101.

PANT, D.D., AND K.B. SINGH, 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Bgt. Part 3. *Palaeontographica, B.* **135**: 1-40.

PANT, D.D. AND R.S. SINGH, 1968. The structure of *Vertebraria indica* Royle. *Palaeontology*, **11**: 643-653.

——., AND ——, 1974. On the stem and attachment of *Gangamopteris* and *Glossopteris* leaves Part II-structural features. *Palaeontographica*, B. **147**: 42-73.

PLUMSTEAD, E.P. 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. Geol. Soc. S. Africa*, **55**: 281-329.

——. 1956a. Bisexual fructifications borne on *Glossopteris* leaves from South Africa. *Palaeontographica*. B. **100**: 1–25.

—— 1956b. On *Ottokaria*, the fructification of *Gangamopteris*. *Trans. Geol. Soc. S. Africa* **59**: 211-234.

——. 1958. Further fructifications of the Glossopteridae and a provisional classification based on them. *Trans. Geol. Soc. S. Africa* **61**: 52-74.

RIGBY, J.F. 1962. Occurrence of Glossopteridae fructifications at Baralaba, Queensland, and their evolution. *Nature*. **195**: (4837) 196-198.

——. 1968. The conservation of *Plumsteadia* Rigby 1963 over *Cistell* a Plumstead 1958. *Bol. da Sociedade Brasileirada Geologia*, **17** (1): 93.

——. 1972. On *Arberia* White, and some related Lower Gondwana female fructifications. *Palaeontology*. **15**: 108-120.

ROYLE J.F. 1833. *Illustrations of the botany and other branches of the natural history of the Himalayan Mountains and of the flora of Cashmere*. 2 vols: ixxxii 472 p.p. London.

SCHOPF, J.M. 1965. Anatomy of the axis in *Vertebraria*. Geology and palaeontology of the Antarctic. *Antarctic Res. Ser.* 6, *Am. Geophys. Union*: 217-228.

——. 1976. Morphologic interpretation of fertile structures in glossopterid gymnosperms. *Review of Palaeobotany and Palynology*. **21**: 25-54.

SEN, J. 1955. On some male fructifications referable to *Glossopteris* and the systematic position of the genus. *Proc. natn. Inst. Sci. India*, **21** (B): 48-51.

SEWARD, A.C. 1897. On the association of *Sigillaria* and *Glossopteris* in South Africa. *Quart. J. Geol. Soc. Lond.* **53**: 315-338.

——. 1904. Report on collections of Natal fossil plants from the Ecca coal series Umhlali on the North-East coast of Natal. *Rept. Geol. Surv. Natal & Zaluland, Landon*, **2**: 97-101.

——. 1910. *Fossil Plant*. 2. Cambridge, XXII+624 pp.

——. AND B. SAHNI, 1920. Indian Gondwana plants: a revision. *Palaeont Indica*. Calcutta (n.s.) **7** (**1**): 1-54.

SURANGE, K.R. AND S. CHANDRA, 1973a. *Dictyopteridium sporiferum* Feistmantel-female cone from the Lower Gondwana of India. *Palaeobotanist*, **20**: 127-136.

——., AND —— 1973b. *Denkania indica* gen. et sp. nov.–Glossopteridean fructification from the Lower Gondwana of India. *Palaeobotanist*, **20**: 264-268.

——., AND —— 1973c. *Partha*—a new type of female fructification from the Lower Gondwana of India. *Palaeobotanist*. **20**: 356-360.

——., AND —— 1974a. *Lidgettonia mucronata* sp. nov.–a female fructification from the Lower Gondwana of India. *Palaeobotanist*. **21**: 121-126.

——., AND —— 1974b. Some male fructifications of Glossopteridales. *Palaeobotanist*. **21**: 255-266.

——., AND —— 1974c. Further observations on *Glossotheca* Surange and Maheshwari. A male fructification of Glossopteridales. *Palaeobotanist*. **21**: 248-254.

——., AND —— 1974d. Fructifications of Glossopteridae from India. *Palaeobotanist*, **21** (1): 1-17.

——., AND —— 1975. Morphology of the gymnospermous fructifications of the Glossopteris flora and their relationships. *Palaeontographica*, B. **149**: 153-180.

——., AND MAHESHWARI, H.K. 1970. Some male and female fructifications of Glossopteridales from India. *Palaeontographica*. B. **129**: 178-192.

THOMAS, H.H. 1952. A *Glossopteris* with whorled leaves. *Palaeobotanist*. **1**: 435-438.

——. 1958. *Lidgettonia* a new type of fertile *Glossopteris*. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol*. **3**: 177-189.

——., AND THOMAS. 1925. On the ancestry of the Caytoniales. *Rep. Brit. Assoc. Adv. Sci. London* (*3rd Meeting*)*:* : 364.

WALKOM, A.B. 1921. On *Nummulospermum* gen. nov., the probable megasporangium of *Glossopteris–Quart. J. Geol. Soc. London*. **77**: 289-295.

——. 1922. Palaeozoic floras of Queensland, Pt. I. The flora of the Lower and Upper Bowen series, *Queensld. Geol. Surv. Publn*. **73**: 1-64.

——. 1928. Notes on some additions to the *Glossopteris* flora in New South Wales. *Proc. Linn. Soc. N.S.W.*, Sydney. **53**: 555-564.

WALTON. J. 1929. The fossil flora of the Karroo system in the Wankie District, Southern Rhodesia, *Bull. Geol. Surv S. Rhodesia*, Salisbury. 15: 62-75.

WALTON, J., AND WILSON, J.R. 1932. On the structure of *Vertebraria–Proc. R. Soc. Edinb*. **52**: 200-207.

WHITE, D. 1908. Fossil flora of the Coal Measures of Brazil in White, I.C. *Commissao estudos das Minas de Carvao de Pedra do Brazil Rio de Janerio.*: 337-617.

WHITE, M.E. 1964. Reproductive structures in Australian Upper Permian Glossopteridae. *Proc. Linn. Soc. N.S. Wales*. **88**: 386-391.

ZEILLER, R. 1896. Etude sur quelques fossiles, en particulier *Vertebraria* et *Glossopteris* des environs de Johannesburgh (Transvaal). *Bull. Soc. Geol. Fr*. **24**: 349-378.

——. 1902. Observation sur quelques plantes fossiles des Lower Gondwanas. *Palaeont. indica*, Calcutta (n.s.) **2**: 1-40.