

MORPHOLOGY AND AFFINITIES OF *GLOSSOPTERIS*

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ABSTRACT

Reproductive organs of glossopterids, viz., *Eretmonia*, *Glossotheca*, *Kendostrobus*, *Lidgettonia*, *Partha*, *Russangea*, *Mooia*, *Rigbya*, *Denkania*, *Venustostrobus*, *Plumsteadostrobus*, *Dictyopteridium* and *Jambadostrobus* are briefly described. Their morphology and affinities are discussed. In the Permian of the southern hemisphere atleast two distinct orders of gymnosperms, viz., Pteridospermales and Glossopteridales were dominating the landscape.

G*LOSSOPTERIS* leaves from India and Australia were first recorded by Brongniart in 1828. From 1845 to 1905, a number of new species of *Glossopteris* were discovered from different continents of Gondwanaland. From 1905 to 1950 there were only a few records, but from 1950 onwards *Glossopteris* again attracted the attention of many palaeobotanists. At first, *Glossopteris* were regarded as ferns but later they turned out to be seed plants. In recent years our knowledge of the reproductive structures of glossopterids has increased to such an extent that one can get some idea as to what type of plants they were.

HABIT

Glossopteris were deciduous plants is evident from the abundance of isolated leaves found in the Permian deposits of Gondwanaland. Many believe that *Vertebraria* were roots of the trees bearing *Glossopteris* leaves. They were undoubtedly arborescent plants and many petrified woods described from Gondwanaland perhaps represent their stems. Growth rings are common in the fossil woods which point to prevailing seasonal growth periodicity. It is also certain that male and female reproductive organs were borne on different plants as in other groups of gymnosperms.

MALE REPRODUCTIVE ORGANS

Three types of sporangia bearing organs have been recognized under three different genera, viz., *Eretmonia* Du Toit, *Glossotheca* Surange & Maheshwari, 1970 and *Kendostrobus* Surange & Chandra, 1974. The first two

genera bore sporangia terminally on ultimate branches whereas the third genus bore sporangia crowded on a cylindrical axis.

Eretmonia Du Toit

Pl. 1, figs. 3, 4; Pl. 2, fig. 2; Pl. 3, figs. 2, 3

Fertile scale leaves of *Eretmonia* (see Chandra & Surange, 1977, text-fig. 1) are of different shapes and sizes and five species have been recognized on this basis. The fertile bracts are ovate (*E. ovooides* Surange & Chandra, 1974), spatulate with acute apex (*E. hingridaensis* Surange & Maheshwari, 1970), triangular (*E. emarginata* Chandra & Surange, 1977), diamond-shaped (*E. utkalensis* Surange & Maheshwari, 1970) and orbicular (*E. karanpurensis* Surange & Maheshwari, 1970). The sporangia are of *Arberiiella* type and produced two winged spores.

The venation pattern in fertile scales of all species is almost the same. There is no midrib but a few prominent bundles from the stalk enter the lamina and give out secondary veins, which branch two to three times, anastomose and form meshes as in *Glossopteris* leaves. In all species of *Eretmonia* net venation is clearly seen.

The fertile scales are stalked and after shedding the spores, the stalks get detached from the bract lamina. One pedicel arises from the stalk which divides into two equal daughter branches. Each branch then successively divides by repeated dichotomy and the ultimate branches bear one sporangium each at their tips and form a sporangial cluster. Thus two sporangial clusters are borne on one pedicel of one fertile bract.

The sporangia are oval to elliptical with fine parallel lines on the sporangial surface

and are of *Arberiella* type. Detached *Arberiella* type of sporangia are very common in the Permian deposits of Gondwanaland. Although, they look similar externally, it is quite likely that each species contain different type of spores. In two cases, one of the sporangium contained two winged *Faunipollenites* type of spore and other contained *Striatites* type.

Most of the fertile scales are convex on one side and concave on the other. It is also thick in the middle and thin at the margin. It must have acted as protective cover to sporangial clusters which were borne in its axil. Frequently detached sporangia are found preserved on the lamina of the fertile scale. At maturity the sporangial clusters must have opened out enabling the sporangia to shed their two winged spores.

It is true that *Eretmonia* has not been found attached to a *Glossopteris* leaf. But there is hardly any doubt that *Eretmonia* type of male reproductive organ belongs to glossopterids. The fertile bracts of *Eretmonia* are in no way different from fertile bracts of other reproductive organs assigned to Glossopteridales (Surange & Chandra, 1975). Moreover, *Glossopteris*-like net venation of the fertile bracts and their constant association with *Glossopteris* leaves further indicate their relationship with them.

Glossotheca Surange & Maheshwari

Pl. 1, figs. 1, 2; Pl. 3, fig. 1

This genus has three species and is known from India. It is on the same pattern as *Eretmonia* but differs from it in possessing more than one sporangia-bearing pedicels. All the three species are distinguished by their distinct fertile scales (see Chandra & Surange, 1977). *Glossotheca utkalensis* (Surange & Maheshwari, 1970) has a spatulate type of bract lamina with a long and stout stalk, *G. orissiana* (Surange & Chandra, 1974) has a rhomboidal bract and a short stalk and *G. immanis* (Chandra & Surange, 1977) has a bract large in size, oblanceolate with a short broad stalk. In *G. orissiana* and *G. immanis* four slender pedicels arise on the abaxial side of the stalk one below the other in a single row, some of them look as if arising from the midrib region of the bract lamina. In *G. utkalensis* three pedicels are seen. Each pedicel dichotomizes

immediately into two stout daughter branches as in *Eretmonia*. Each branch then further divides by repeated dichotomy so that possibly eight clusters of sporangia are formed on a single fertile scale. Sporangia are attached on the tip of the ultimate branches and they are of striated *Arberiella* type. The branching pattern of the pedicel is similar to that of *Eretmonia*. From the size of the pedicels and their branching, each cluster may contain not more than 32 sporangia. The sporangia are elliptical, oval and striated. Although, they look alike externally, they differ in size and perhaps in some other structural details and may have contained different types of spores. At present very few carbonized sporangia have been worked out (Chandra & Surange, 1977). The outer cells of the sporangium wall are thick-walled, more long than broad and twisted in various ways. These thickened cells give a striated appearance to the sporangium so characteristic of *Arberiella*. There is also a delicate layer of elongated cells. Sometimes spore mass is seen covered with a tissue with extremely thin-walled cells. The sporangium, therefore, appears to be multilayered and the dehiscence is perhaps longitudinal.

Isolated striated sporangia have been placed under the form genus *Arberiella* (Pant & Nautiyal, 1960). They are assigned to *Eretmonia*, *Glossotheca* and also to *Pteruchus*. Such sporangia have also been found attached to two rounded concave discs (attachment is different from *Eretmonia* & *Glossotheca*). There is, therefore, no doubt that the similar looking striated sporangia belonged to diverse plants. *Arberiella* type contain two winged spores. *A. africana* contains *Faunipollenites* type of spores and *A. vulgaris* contains *Lunatisporites* type. Other striated pollen grains found in masses inside the sporangia have not been identified with genera of dispersed spores.

Kendostrobus Surange & Chandra

Pl. 3, fig. 4

This male reproductive organ is organized on a different pattern. It is a long, narrow, cylindrical, cone-like organ, bearing sporangia. The cylindrical sporangia-bearing axis possesses very small, round protuberances on which 4 to 5 sporangia are attached in whorls. The whorls of sporangia in their

turn are carried on the axis in close spirals and appear crowded on the cone surface. The sporangia are large in size, one whorl occupying almost the entire breadth of the cone axis.

The sporangia are exannulate, oval to elongate and the sporangial surface is studded with oval to round depressions, giving it a spongy appearance. This type of sporangium in detached condition is described under a form genus *Lithangiium* (Pant & Nautiyal, 1960). The spores are stripped and monolete. Unmacerated spores show sculptine which is folded into curved ridges which are seen as longitudinal stripes in macerated spores.

The mode of attachment of sporangial whorls in close spirals is something like that of seeds in *Dictyopteridium* which is found attached on a *Glossopteris* leaf. However, neither a bract has been found in *Kendostrobus* nor it has been found attached to a *Glossopteris* leaf. In dispersed condition, it is widely reported from a number of places in the Raniganj. Its affinities are uncertain, but because of its association with *Glossopteris* and in the absence of any other plant to which it can be referred to, we believe that it could be a male reproductive organ of some glossopterid plant.

FEMALE REPRODUCTIVE ORGANS

CUPULATE FRUCTIFICATIONS

A number of cupulate reproductive organs have been discovered in recent years from the Permian deposits of India, South Africa and Australia. They are described under the genera *Lidgettonia*, *Partha*, *Denkania*, *Mooia*, *Rigbya* and *Russangea*.

Lidgettonia Thomas

Pl. 2, fig. 1

Lidgettonia was first described by Thomas (1958) from Lidgetton, Natal and later by Lacey *et al.* (1975) from Mooi River, both localities in South Africa. They were placed under one species, *Lidgettonia africana*. Another species, *L. mucronata*, is described from Orissa, India by Surange and Chandra (1974).

Lidgettonia is a female fructification consisting of a fertile bract with stalked seed bearing cupules. The bract lamina is small,

oblanceolate, spathulate-lanceolate or ovate-lanceolate, contracted at the base into a long stalk. The veins spread out from the base of the lamina, those in the middle running straight upwards and the rest fork and form anastomes right upto the margin. Cupules or cupulate discs are attached in two longitudinal rows by pedicels, arising from the abaxial surface of the basal part of the lamina. In Indian species, they number eight, but Lacey *et al.* reported 4-14 cupules. There is, however, some differences in the interpretation of the ovule bearing structure, due obviously to the imperfection of preservation. Lacey *et al.* interpreted them as cupules, 4 to 14 in number, open campanulate, sometimes appearing semicircular when compressed laterally or disc-like when compressed dorsiventrally. Surange and Chandra (1974) interpreted them as circular, fluted discs, on the under side of which small unwinged seeds are attached. The Indian and African specimens atleast represent two distinct species because the Indian species has unwinged seeds and the African species has winged *Samaropsis* type of seeds.

Partha Surange & Chandra

Pl. 2, fig. 4

This genus is a cupulate seed bearing reproductive organ and is represented by two species, viz., *P. indica* and *P. spathulata* (Surange & Chandra, 1973). The fertile leaf is oval spathulate with broad apex, measuring 3-4 cm in length. The petiole is long and broad. There is no midrib but a few strong veins run in the middle right up to the apex. The secondary veins arise from the outer veins, branch but anastomosing is rare, if not absent.

The cupules are borne in a single row, as against two rows in *Lidgettonia*, one below the other on short pedicels. Two pedicels arise near the base of the lamina (there may be one or two more) almost from the mid-veins. Four cupules are attached at the apex of each pedicels. Each cupule carries one seed. The seeds are winged.

Russangea Lacey, Dijk & Gordon-Gray

Pl. 3, fig. 5

This cupulate fructification is very similar to *Partha* and is described by Lacey *et al.*

(1975) from South Africa. The fructification consists of a petiolate fertile leaf bearing two scales, each with a single sessile seed. The shape of the fertile leaf is that of a narrow-ovate, petiolate, *Glossopteris* leaf. The venation is coarsely reticulate with vertically elongated meshes. There is no midrib but the central bundles pursue a close parallel course nearly to the apex. Two seed bearing scales are attached at the base of the lamina on its adaxial side by short stalks. The scales are expanded distally, beyond the point of attachment of the seed, but Lacey *et al.* do not consider them cupulate. The two seeds are oval and unwinged and are sessile on the scales.

Mooia Lacey, Dijk & Gordon-Gray

Pl. 2, fig. 3

It is yet another female fructification from South Africa consisting of a petiolated fertile leaf bearing two to four stalked, usually drooping, campanulate cupules. The lamina is spatulate or rhomboidal with spoon-shaped depression surrounded by a narrow margin of thin texture. There is no midrib. The secondary veins dichotomize and reticulation is found in large laminae. Two to four cupule bearing pedicels are borne near the base of the lamina, attached singly or in pairs or possibly more than two together in a single longitudinal row. The pedicel is upto 1 cm long and carries a single cupule at its apex. The cupules are often reflexed, drooping, lobed and of variable size. The cupule lobes are from four to eight, longitudinally striated with a fairly well-defined midline, acutely pointed, fused basally to form the "cup" of the cupule, often appearing in spiral sequence rather than a whorl. Seeds are borne probably one per cupule, flattened and scarcely winged. They are not *Samaropsis* type.

Rigbya arberioides Lacey, Dijk & Gordon-Gray

Pl. 2, fig. 5

This fructification has been described by Lacey *et al.* as problematical. This is a female fructification consisting of a stalk bearing a terminal aggregation of seed-bearing scales. The scales are long and

convex, each enveloping one seed at its base. The seeds are 3-5 mm long and 2.5-3 mm wide, ovoid, flattened, but not winged.

Rigbya arberioides is very similar to *Arberia winasica* White. But *Arberia* is much branched and not aggregated into a distinct head. Moreover, in *Rigbya* the terminal scales are at least partially surrounding the scales and hence cupulate.

Denkania Surange & Chandra

Pl. 3, fig. 6

This genus is represented by a single species (Surange & Chandra, 1973). The fertile leaf of this cupulate reproductive organ looks strikingly similar to a small *Glossopteris* leaf. It is a narrow linear form, measuring about 5 cm in length with 1 cm long petiole. The mid-veins in the lamina prominent, run parallel in the middle, becoming narrow towards the apex but remaining impressively broad, occupying almost the entire acute apex. The secondary veins arise from the outer straight veins, repeatedly branch and form small, narrow meshes.

The cupules in *Denkania* are borne erect on long pedicels on the abaxial side of the petiole in a single row, one below the other. A fertile leaf carries five to six cupules. The pedicel is 1-1.5 cm in length and the cupule is about 1 cm long and 6-7 cm broad. The large and massive cupule is carried almost erect on the stalk and so the stalk must have been provided with a fair amount of strengthening tissue. The cupule is oval in shape, lobed and the lobes may be three or more in number. One cupule probably carries one large seed and the seed is oval to elongate with a broad wing-like integument.

MULTIOVULATE FRUCTIFICATIONS

Between 1952 to 1958, Plumstead in a series of papers described reproductive organs of *Glossopteris* under five generic names, *Scutum*, *Lanceolatus*, *Hirsutum*, *Cistella* and *Pluma* attached on different species of *Glossopteris* leaves. Plumstead's nomenclature procedure was at variance with the International Code of Botanical Nomenclature which created a confusion. However, in 1958 she made it clear that *Scutum*,

Cistella, *Hirsutum*, etc. are not natural genera but they represent different types of fructification of glossopterids and should be grouped as Scutum type, *Cistella* type, *Hirsutum* type, etc. We agree with Plumstead's suggestion. The name *Scutum*, *Cistella* etc. have become well-known by usage and no purpose will be served by introducing new names for different types of glossopterid fructifications. It will only confound an already confused issue. Instead these groups could be raised to family level (Scuta-ceae, Cistellaceae, etc.) and the names *Scutum*, *Cistella* could be retained as form genera to include glossopterid fructifications of which structural details are not known. Majority of fructifications are preserved as impressions and there is, therefore, no chance of knowing any of their structural details. For such cases the form genera *Scutum*, *Cistella* etc. would be very useful. When a fructification is known in sufficient structural details, it could be described under a new name as a separate organ genus.

It is now well-recognized that *Glossopteris* is a very loose form genus and its speciation is very confusing. Add to it the imperfection of preservation and the task of specific identification becomes formidable. One can never be sure that one has correctly identified a species of *Glossopteris* even after several years of experience in dealing with the material. Therefore, when a fructification is found attached on a leaf of *Glossopteris* species, the name of the fructification should be given more importance and the name of the leaf could just become a synonym. The form genus *Glossopteris* should be retained to include only those leaves which are known morphologically but which cannot be assigned to a natural genus.

Recently, different types of glossopterid fructifications with structural details were described:

I. *Scutum* Type

Scutaceae

- (1) *Venustostrobus diademus* Chandra & Surange, 1977.
Leaf — *Glossopteris ghusikensis* Pant & Gupta, 1968.
- (2) *Venustostrobus indicus* Chandra & Surange, 1977.
Leaf — a new species of *Glossopteris*.

II. *Cistella* Type

Cistellaceae

- (1) *Plumsteadioctrobus ellipticus* Chandra & Surange, 1977.
Leaf — *Glossopteris gondwanensis* Pant & Gupta, 1971.
- (2) *Dictyopteridium feistmantelli* Chandra & Surange, 1976.
Leaf — *Glossopteris tenuinervis* Pant & Gupta, 1971.

III. *Hirsutum* Type

Hirsutaceae

- (1) *Jambadoctrobus pretiosus* Chandra & Surange, 1977.
Leaf — *Glossopteris contracta* Pant & Gupta, 1971.

Venustostrobus indicus Chandra & Surange

Multiovulate types of glossopterid fructification consisting of a seed bearing receptacle, is borne in the axil of a fertile bract. Both are attached by their common pedicel to the midrib of a vegetative leaf. The stalk of the fructification is obviously adnate to the midrib of the leaf in the axil of which it is borne. The seed bearing receptacle is thus placed between the fertile bract and the vegetative leaf. The fertile bract is veined, almost of the same shape and acts like a protecting spathe to the ovule bearing head.

The material of this fructification was interesting. A complete leaf of *Glossopteris* (a new species) was found covering underneath it what looked like an orbicular outline of a fructification attached to it. The material was a coalified compression. We, therefore, took successive cellulose pulls and studied them separately. This is what happened a thin coat of cellulose acetate removed the leaf which was on top of the fructification. The fructification thus exposed revealed small round seed-like bodies in a mass, badly compressed. When the second coat of cellulose acetate was applied, the mass of seed-like bodies were removed, exposing the veined fertile bract. The third pull removed the carbonized crust of the bract. Below that there was shale matrix.

There is no doubt that the fructification was attached to the vegetative leaf under which it was lying. The fructification was in the basal region where it should be and the orbicular outline was visible on both

sides of the midrib. Imprint of the seed mass made the leaf surface uneven.

When the first pull was macerated, tough cuticles of leaf, both from the abaxial and the adaxial sides, were recovered. When the third pull was macerated, it yielded the cuticles from the two sides of the fertile bract and were quite distinct from those of the leaf recovered from the first pull. The second pull after maceration yielded, besides a few pieces of leaf and bract, seed pieces with integument and nucellar tissue attached to them and quite a number of distinct cuticular pieces which we ascribed to the seed bearing axis or the receptacle.

The distinct cuticles of leaf and bract show that they are separate organs. Furthermore, the cuticles of the leaf to which fructification is attached and those of other vegetative leaves without fructification are identical, showing thereby that there is no difference between the two. The reproductive organ thus could be borne in the axil of any vegetative leaf of a shoot. If there is an axis on which the seeds are attached (as proved by a distinct type of cuticle) the entire reproductive organ cannot be dorsiventral as supposed by Plumstead and some other authors. On the other hand, the presence of a seed bearing axis or receptacle has been clearly demonstrated. Furthermore, if the seeds are arranged in close spiral, it cannot be a dorsiventral organ.

Venustostrobus diademus Chandra & Surange
Pl. 4, fig. 3

It is another Scutum type of fructification borne on a different type of leaf, *Glossopteris ghusikensis*. The multiovulate organ is attached by a short stalk to the midrib of a small, petiolate, open mesh type of leaf. It is circular to orbicular in outline and has a wide border, divided transversely into rectangular areas. Strongly veined fertile bract fits closely on the seed bearing head or receptacle.

The fructification bearing leaf is identical with *Glossopteris ghusikensis* described earlier by Pant and Gupta (1971) in external as well as cuticular characters. The protective bract has strong, prominent veins which fan out from the pedicel, branch and form narrow meshes. Two sides of the bract show two different types of cell

pattern. The nonstomatiferous surface has large, straight-walled cells and a few hair bases. The stomatiferous surface has much shorter, moderately thickened cells, stomata and highly thickened hair bases in large numbers. It appears that one surface of the bract possessed stiff hairs.

The seed bearing receptacle is orbicular in shape and carries spirally arranged sessile seeds. The cuticle of the receptacle has two types of cells. The cells around the seed are small, papillate, squarish with firm, dark coloured, thickened cell walls. The cells in between the seeds are large, thin-walled, non-papillate and contain stomata. Does the thickened layer below the seed help in shedding? The seed is small, roundish with chalazal end always found torned. The integument cells are large, arranged end to end and straight-walled. The cells at the micropylar end are elongated, narrow, slightly thickened and show slightly sinuous cell walls. The nucellar membrane is thin and show obscure cell outlines. The seed is filled with thick opaque tissue and often contain two winged pollen grains.

Jambadostrobus pretiosus Chandra & Surange
Pl. 4, fig. 2

It is a distinct type of multiovulate organ in which more than one seed bearing receptacles are attached on the midrib of a single leaf and the receptacles are naked in the sense that there is no protective fertile bract.

Jambadostrobus pretiosus is attached by a short stalk on the midrib of *Glossopteris contracta* Pant & Gupta, 1971. The leaf has been identified on both external as well as cuticular characters. The receptacle is 2-3 cm in length and 1 cm in breadth. It is elliptical or lenticular in shape, carrying large naked seeds on seed cushions in close spirals. The apex of the receptacle is drawn out like a beak, appearing like a crown. The margin is fairly broad, but not as broad as *Venustostrobus* and is divided by transverse markings left by the marginal seeds. The cuticle of the receptacle has small isodiametric, moderately thickened cells and the entire cuticle is covered with stripes of cuticular thickenings. The marginal cells are large and thin-walled. The stomata are arranged in small circles

where the cuticle is very thin or almost absent. This is a characteristic feature of the receptacle cuticle.

The seeds are large in size and are *Platicardia bengalensis* type described by Pant and Nautiyal in dispersed condition. The outer cuticle of integument contain imprints of tetra- to octahedral crystals, some of them possessing short tails. The nucellar cells are thickened with deeply sinuous to zig-zag lateral walls.

Plumsteadiostrobos ellipticus Chandra
& Surange

Pl. 4, fig. 4

It is a Cistella type of fructification borne on the leaf of *Glossopteris gondwanensis* Pant & Gupta, 1971 attached by a short stalk to the midrib in the basal region. It consists of a seed bearing receptacle borne in the axil of a spathe-like protective fertile bract and possessing a common stalk by which it is attached to the midrib of the leaf.

The fertile bract is veined. There is no midrib, but a few parallel veins run in the middle and the secondary veins branch once or twice and form meshes. The bract yields one thick and one thin cuticle. The thin cuticle shows stomata. The receptacle cuticle has lense-shaped holes around which the cells are arranged in radial rows. The cuticle is also dotted with what looks like secretory cells or hair bases. The lenticular holes are the places where seeds are attached and through which vascular supply must have passed from the receptacle to the ovules. The seeds are arranged in close spiral. The seeds are *Pterygospermum rani-ganjense* described by Pant and Nautiyal, 1960 in dispersed condition. The outer covering of the seed expands into a wing, which is broad at the micropylar end and narrow at the chalazal end. The "wing" which is an extension of the integument is continued on either side of the micropyle. The cells of the outer integument contain crystalline imprints which are mostly hexagonal or rectangular and very characteristic of this seed. The nucellus is thickly cutinized and shows an excavated pollen chamber on top. Surface cells of the pollen chamber are elongated and have delicate wavy walls. Other cells of the nucellus are thin, elongated and deeply sinuous or

almost zig-zag. The winged pollen grains, generally seen inside the pollen chamber, are *Faunipollenites* type.

Dictyopteridium feistmanteli Chandra
& Surange

Pl. 1, fig. 1

There are two species of this genus, *Dictyopteridium sporiferum* Feistmantel, 1881 and *D. feistmanteli* Chandra & Surange, 1976 which is based on a compressed material.

The fructification is attached by a short stalk to the petiole, just at the base of the leaf of *Glossopteris tenuinervis* Pant & Gupta, 1971.

The fertile organ consists of a seed bearing receptacle borne in the axil of a stalked fertile bract which covers it like a protective spathe. The fertile scale is somewhat thick and stalked. A few parallel veins run in the middle like a midrib. The secondary veins branch and anastomose. The cuticle on one side of the bract has isodiametric cells with firm cell walls and numerous one-celled hairs or papillae. The other side has thin-walled rectangular cells and no hair at all. The receptacle is lanceolate and narrow and is covered with small round seed-cushions. They are arranged in close spirals, or some of them might appear as if arranged in arch. The receptacle cuticle is somewhat thick, covered with a network of stripes of cuticular thickenings. The cells are thin-walled and dotted with thickened, one-celled hairs. The seeds are attached on seed cushions. The seed is small, unwinged with pointed micropylar end. The cells at the micropylar end have wavy cell walls. The nucellar membrane is thin without any cellular markings.

DISCUSSION

Glossopterids are a class of seed plants is no longer in doubt. The problem of determining affinities among glossopterids, and their position among different groups of gymnosperms would be nearer solution if their reproductive structures are correctly interpreted. Different interpretations are in vogue. Plumstead (1952) interpreted the reproductive structure as pedicellate, flattened, dorsiventral cupule, the fertile half having a raised head, containing small oval

sacs and a fluted or striated wing. Later, she (1956) described the cupule as bisexual flower, the fertile half containing the seeds and the other half bearing bract-like staminate organs. Schopf (1976) agrees with Plumstead in regarding the reproductive organ as flattened, dorsiventral, bilaterally symmetrical structure, having different features on dorsiventral surfaces. He suggested a new term "fertiliger" for the reproductive structure, which consists of a leafy bract (the vegetative leaf on which the fructification is attached), a partially adnate stalk and a fertile head or capitulum. Surange and Chandra's interpretation is more akin to that of Edward's and Walton's in regarding the fertile heads as cone-like or strobilar. They regard the seed bearing central axis or receptacle essentially as cylindrical, oval or lenticular, bearing ovules in close spiral all round the axis and borne in the axil of a stalked, veined bract, which also acts like a protective spathe. The common stalk of bract and seed bearing receptacle is attached to the midrib of an ordinary leaf of *Glossopteris* to which it is partially adnate. Thus the reproductive structure is borne in the axil of a leaf and the seed bearing receptacle occupies a position in between the fertile bract and the vegetative leaf. The reasons for strobilar interpretation are as follows:

1. Compressions of the reproductive structure have shown that the veined bract and the seed bearing receptacle are *two separate organs* and not a single plant organ with veined adaxial and fertile abaxial surface. The veined bract yielded two types of cuticles, obviously one from its adaxial and the other from the abaxial surface. The receptacle yielded a distinct cuticle which is easily distinguishable from the bract cuticles. Therefore, two separate plant organs (and not one organ) are involved here.

2. Detached fertile bracts and detached seedless receptacles are found preserved separately. Hence, they are two separate organs. The cuticles of detached bracts are identical with the cuticles of bracts attached to fructification.

3. In one compression it was possible to remove the vegetative leaf, seed mass, the receptacle and the bract by successive cellulose pulls, showing thereby they are all separate and distinct organs.

4. The seeds are arranged in close spiral which is not possible if the fertile head was dorsiventral. Seeds still stuck together in spiral manner were found as such, or sometimes entangled with the receptacle cuticle on which they must have been borne.

5. Striated "wing" is nothing but the impressions left by seeds on the margin of the receptacle. The seeds are arranged one below the other as is seen in cases where although some seeds were shed, the others remained still sticking to the receptacle. The width of the "wing" depends upon the size of the seeds. The bigger the seed, wider is the "wing".

The seed bearing head is thus a strobilus without ovuliferous bracts. It can in no way be compared with a pteridospermous cupule. Therefore, no new term such as "fertiliger" is required to describe this simple multiovulate, strobilar type of *Glossopteris* reproductive structure. What Schopf (1976) calls as "fertile bract" is really an ordinary vegetative leaf which is in no way different from other similar leaves, externally as well as in cuticular structure. On the other hand, the veined part addressed to the fertile receptacle is truly a fertile bract and quite different in structure from a vegetative leaf.

It is not yet fully appreciated that the so-called glossopterids possessed two distinct types of reproductive structures. In one group the ovules were attached to megasporophyll or modified megasporophylls and could come nearer to the pteridosperms. These could be dorsiventral structures. The other group possessed a strobilar type of reproductive structure as shown clearly now by compressed material. The difficulty in understanding the glossopterid fructifications arises when one tries to interpret the strobilar type as cupulate or dorsiventral structure, drawing upon vague morphological terms, or even coining new morphological terms. It only adds to the confusion.

The cupulate types were co-existing with the multiovulate strobilar types, although perhaps the cupulate types, like *Arberia* were present in the Karharbari Stage. The cupulate reproductive structures are organized on a different pattern and come closer to the pteridosperms, particularly the Triassic ones of the southern hemisphere. Here some of the structures like the one

described as *Ottokaria* by Pant (1977) and the petrified ovulate fructification described recently by Gould and Delevoryas (1977) where the seeds are borne on one side of a megasporophyll, may be dorsiventral organs such as *Lidgettonia* (Surange & Chandra, 1974) and some other cupulate fructifications described by us. The fertile bract or megasporophyll in cupulate fructifications is a small, specialized appendage with *Gangamopteris* type of venation and is not comparable to the ordinary vegetative leaves of multiovulate strobilar types on which the reproductive structures are borne. However, the mode of attachment of cupulate types appears to be similar to the multiovulate types, in the sense that the stalk of the cupules or cupulate disc is attached to the petiole or the midrib of the fertile bract in its basal region. Either the cupules are attached to the fertile bract individually by their stalks or there is a stalked cupulate disc to which ovules are attached. In cupulate types there is thus no aggregation of naked ovules on a central axis as in the multiovulate reproductive structures of Glossopteridales. It must be pointed out here that cupulate types have not so far been found attached to typical *Glossopteris* leaves. However, the net venation of the fertile bract is like *Gangamopteris* and the mode of attachment of the reproductive structure is also like glossopterids. There is also no leaf other than *Glossopteris* present in the material to which multiovulate types could be referred.

Thus in glossopterids of the southern hemisphere, there were atleast two distinct orders of gymnosperms, apart from *Buriadia* type of conifer-like plants, which were dominating the landscape. We would like to put the cupulate types, presuming that the ovules are borne on a modified frond, the megasporophyll, under the pteridosperms for the present and classify glossopterids as follows:

Order — PTERIDOSPERMALES

- Family — (1) Parthaceae
Partha
Russangea
- Family — (2) Lidgettoniaceae
Lidgettonia
- Family — (3) Denkanaceae
Denkania
Mooia

Order — GLOSSOPTERIDALES

- Family — (1) Cistellaceae
Dictyopteridium
Plumsteadiostrabus
- Family — (2) Scutaceae
Ottokaria
Venustostrobis
- Family — (3) Hirsutaceae
Jambadostrabus

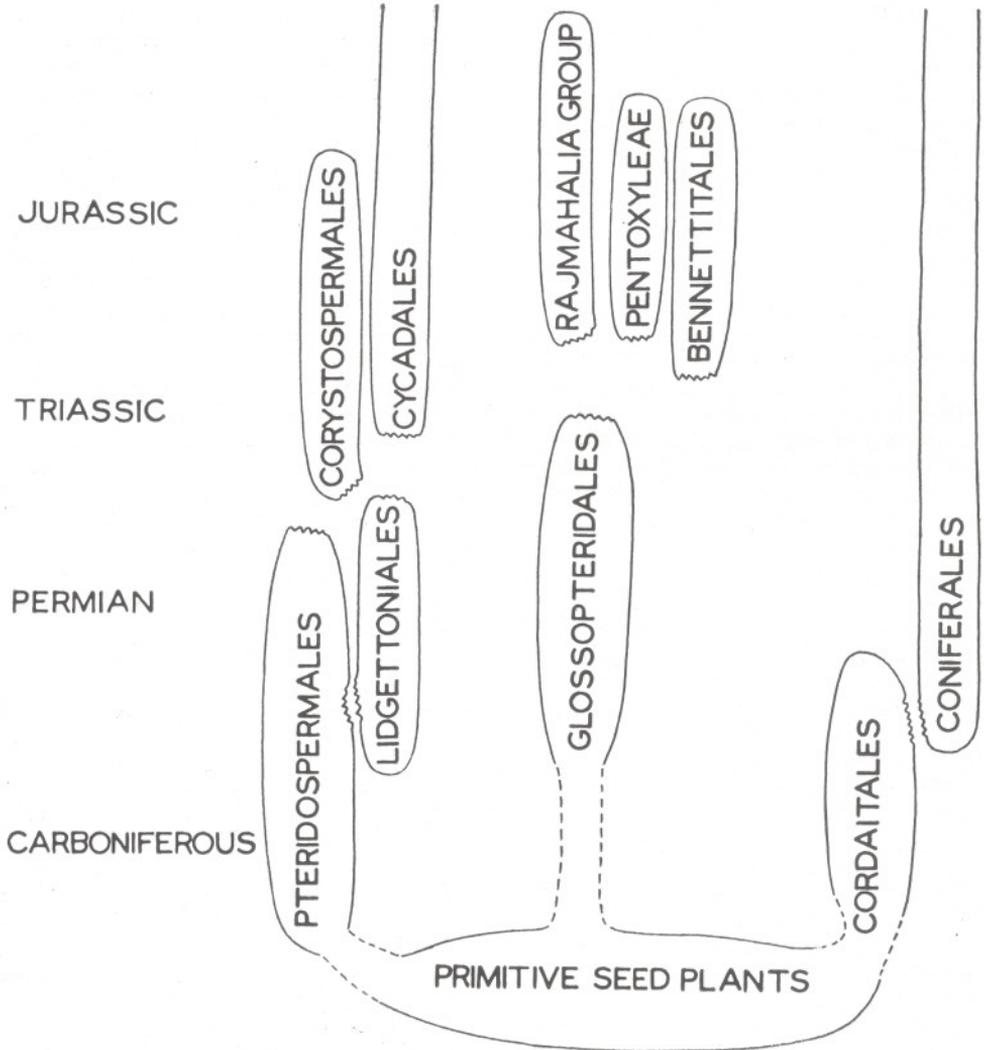
ORIGIN

The origin of the glossopterids is shrouded in mystery and it will remain so far the lack of fossil record immediately preceding the first appearance of *Glossopteris*. Before the Gondwana glaciation, the Lower Carboniferous *Rhaeopteris* flora was present in the southern hemisphere and immediately after the glaciation, or perhaps during the glaciation itself, *Gangamopteris-Glossopteris* flora had already come into existence. This is a gap in the fossil record and therefore, any phyletic model for glossopterid evolution would remain at best a speculation.

Perhaps the strongest point against the derivation of *Glossopteris* from the cordaites (Schopf, 1976) is the absence of true cordaites in the southern hemisphere. To attribute *Noeggerathiopsis* to Cordaitales on the basis of similarity in vegetative leaves is as good as attributing *Glossopteris* to ferns on the basis of venation. The ovulate fructification, *Arberia*, which is attributed by some authors to *Noeggerathiopsis*, is built on the same pattern as some of the later cupulate types of fructifications and could as well be put under the pteridosperms. If in *Arberia* the arrangements are pinnate, then the ovules could be considered as borne on modified frond. It is not definitely known what type of leaf bore *Arberia*. The other known reproductive structure of the same age, *Ottokaria* is attached definitely on the leaf of *Glossopteris communis* in the type specimen. We do not know what type of reproductive organs *Gangamopteris* possessed. So *Arberia* could as well belong to *Gangamopteris* or *Noeggerathiopsis*, the two genera then existing, apart from *Glossopteris*. All the three genera, *Gangamopteris*, *Glossopteris* and *Noeggerathiopsis* were thus co-existing (and so were *Arberia* & *Ottokaria*) and to derive one from the other does not appear plausible,

It clearly shows that the two distinct types of reproductive structures, one cupulate type as represented by *Arberia* and the strobilar multiovulate type as represented by *Ottokaria* were already present in the Lower Permian. The same two types, representing two orders, diversified and multiplied in the latter part of the Permian (Raniganj Stage). The origin of two types of reproductive structures therefore has to be traced back to the Middle Carboniferous period, particularly in the early seed plants, the fossil records of which are unfortunately missing in the Gondwanaland.

Looking at the reproductive structures in various groups of fossil and living gymnosperms, it appears likely that the evolution in seed plants diversified at least in three directions quite early in its history (Lower Carboniferous?), almost at its beginning. The three main lines suggested are (i) Pteridosperm—Cycad complex, (ii) Glossopterid complex, possibly giving rise to Pentoxyleae and Cycadofilicales, and (iii) Cordaitan—Conifer complex. Text-fig. 1 illustrates a tentative working hypothesis suggesting possible evolutionary lines in seed plants.



TEXT-FIG. 1

Three distinct evolutionary complexes possibly arose from the primitive seed plants. One was pteridosperm complex, the second was cordaitalean complex, and the third was glossopterid complex. The first perhaps gave rise to groups like Lidgettoniales, Corystospermales and other groups of pteridosperms. From this group perhaps arose the Cycadales. The second complex gave rise

to Coniferales and possibly Ginkgoales. The glossopterid complex perhaps gave rise to *Rajmahalia* type of plants and the southern hemisphere Pentoxyleae. The bennettitalean "flower" might have also arisen from the multiovular type of reproductive structure like that of the Glossopteridales. At least aggregation of ovules on a receptacle was first achieved in Glossopteridales.

REFERENCES

- BRONGNIART, A. (1828). *Histoire des Végétaux fossiles ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe*. Paris.
- CHANDRA, S. & SURANGE, K. R. (1976). Cuticular studies of the reproductive organs of *Glossopteris* Part 1. *Diclyopteridium feistmanteli* sp. nov. attached on *Glossopteris tenuinervis*. *Palaeontographica*, **156B** (4-6): 87-102.
- CHANDRA, S. & SURANGE, K. R. (1977). Cuticular studies of the reproductive organs of *Glossopteris* Part 2. *Cistella* type fructification *Plumsteadiostrobos ellipticus* gen. et sp. nov., attached on *Glossopteris taenioides*. Feistmantel. *Palaeobotanist*, **23** (3): 16-174.
- CHANDRA, S. & SURANGE, K. R. (1977). Cuticular studies of the reproductive organs of *Glossopteris*. Part—3. *Jambadostrobos* and *Venustostrobos* borne on *Glossopteris* leaves. *Palaeontographica*, **164B** (4-6): 127-152.
- CHANDRA, S. & SURANGE, K. R. (1977). Cuticular studies of the reproductive organs of *Glossopteris* Part-4. *Venustostrobos indicus* sp. nov. *Palaeobotanist*, **24** (3): 149-160.
- CHANDRA, S. & SURANGE, K. R. (1977). Fertile bracts and scales of *Glossopteris* fructifications from the Lower Gondwana of India. *Palaeobotanist*, **24** (3): 195-201.
- CHANDRA, S. & SURANGE, K. R. (1977). Some scale leaves and sporangia from the Raniganj Coalfield, India. *Palaeobotanist*, **24** (3): 245-253.
- FEISTMANTEL, O. (1880-81). The fossil flora of the Gondwana System (Lower Gondwanas)-2. The flora of Damuda-Panchet divisions. *Palaeont. indica*, ser. XII, **3** (2): 1-149.
- GOULD, R. E. & DELEVORYAS, T. (1977). The biology of *Glossopteris*. Evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringa*, **1**: 387-399.
- LACEY, W. S., DIJK, D. E. & GORDON-GRAY, K. D. (1975). Fossil plants from the Upper Permian in the Mooi River district of Natal, South Africa. *Ann. Natal Mus.*, **22** (2): 349-420.
- PANT, D. D. (1977). The plant of *Glossopteris*. *J. Indian bot. Soc.*, **56** (1): 1-23.
- PANT, D. D. & GUPTA, K. L. (1968). Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part—I. *Palaeontographica*, **124B** (1-3): 45-81.
- PANT, D. D. & GUPTA, K. L. (1971). Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart Part—II. *Palaeontographica*, **132B** (1-4): 130-152.
- PANT, D. D. & NAUTIYAL, D. D. (1960). Some seeds and sporangia of *Glossopteris* Flora from Raniganj Coalfield, India. *Palaeontographica*, **107B** (1-3): 41-64.
- PLUMSTEAD, E. P. (1952). Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. geol. Soc. S. Afr.*, **55**: 281-328.
- PLUMSTEAD, E. P. (1956). On *Ottokaria*, the fructification of *Gangamopteris*. *Trans. geol. Soc. S. Afr.*, **59**: 211-236.
- PLUMSTEAD, E. P. (1958). Further fructifications of the Glossopteridae and a provisional classification based on them. *Trans. geol. Soc. S. Afr.*, **61**: 51-76.
- SCHOPF, J. M. (1976). Morphologic interpretation of fertile structures in Glossopterid gymnosperms. *Rev. Palaeobot. Palynol.*, **21**: 25-64.
- SURANGE, K. R. & MAHESHWARI, H. K. (1970). Some male and female fructifications of Glossopteridales from India. *Palaeontographica*, **129B**: 178-191.
- SURANGE, K. R. & CHANDRA, S. (1973). *Diclyopteridium sporiferum* Feistmantel female cone from the Gondwana of India. *Palaeobotanist*, **20** (1): 127-136.
- SURANGE, K. R. & CHANDRA, S. (1973). *Denhania indica* gen. et sp. nov. A Glossopteridean fructification from the Lower Gondwana of India. *Palaeobotanist*, **20** (2): 264-268.
- SURANGE, K. R. & CHANDRA, S. (1973). *Partha*, a new type of female fructification from the Lower Gondwana of India. *Palaeobotanist*, **20** (3): 350-360.
- SURANGE, K. R. & CHANDRA, S. (1974). *Lidgettonia mucronata* sp. nov. a female fructification from the Lower Gondwana of India. *Palaeobotanist*, **21** (1): 121-126.
- SURANGE, K. R. & CHANDRA, S. (1974). Fructifications of *Glossopteris* from India. *Palaeobotanist*, **21** (1): 1-17.
- SURANGE, K. R. & CHANDRA, S. (1974). Further observations on *Glossotheca* Surange & Maheshwari, a male fructification of Glossopteridales. *Palaeobotanist*, **21** (2): 248-254.
- SURANGE, K. R. & CHANDRA, S. (1974). Some male fructifications of Glossopteridales. *Palaeobotanist*, **21** (2): 255-266.
- SURANGE, K. R. & CHANDRA, S. (1975). Morphology of the gymnospermous fructifications of the Glossopteris flora and their relationship. *Palaeontographica*, **149B** (5-6): 153-180.
- THOMAS, H. H. (1958). *Lidgettonia*, a new type of fertile *Glossopteris*. *Bull. Br. Mus. (nat. Hist.) geol.*, **3** (5): 179-189.

EXPLANATION OF PLATES

PLATE 1

1. *Glossotheca immanis* Chandra & Surange. $\times 2$.
2. *Glossotheca utkalensis* Surange & Maheshwari. $\times 2$.
3. *Eretmonia hingridaensis* Surange & Maheshwari. $\times 2$.
4. *Eretmonia emarginata* Chandra & Surange. $\times 2$.
5. *Rigbya arberioides* Lacey *et al.* Pencil drawing made from photographs of specimens NM 1644a and NM 1669 of Lacey *et al.*, 1975. $\times 2$.

PLATE 2

1. *Lidgettonia mucronata* Surange & Chandra. $\times 2$.
2. *Eretmonia karanpurensis* Surange & Maheshwari. $\times 2$.
3. *Mooia lidgettonioides* Lacy *et al.* Pencil drawing made from photograph of specimen NM 1476b of Lacey *et al.*, 1975. $\times 2$.
4. *Partha spatulata* Surange & Chandra. $\times 2$.

PLATE 3

1. *Glossotheca orissiana* Surange & Chandra. $\times 2$.
2. *Eretmonia ovooides* Surange & Chandra. $\times 2$.
3. *Eretmonia utkalensis* Surange & Maheshwari. $\times 2$.
4. *Kendostrobus cylindricus* Surange & Chandra. $\times 2$.
5. *Russangea elegans* Lacey *et al.* Pencil drawing made from specimens NM 1361a and NM1363a of Lacey *et al.*, 1975. $\times 2$.
6. *Denkania indica* Surange & Chandra. $\times 2$.

PLATE 4

1. *Dictyopteridium feistmanteli* Chandra & Surange. $\times 2$.
2. *Jambadostrobus pretiosus* Chandra & Surange. $\times 2$.
3. *Venustostrobus diademus* Chandra & Surange. $\times 2$.
4. *Plumsteadostrobus ellipticus* Chandra & Surange. $\times 2$.

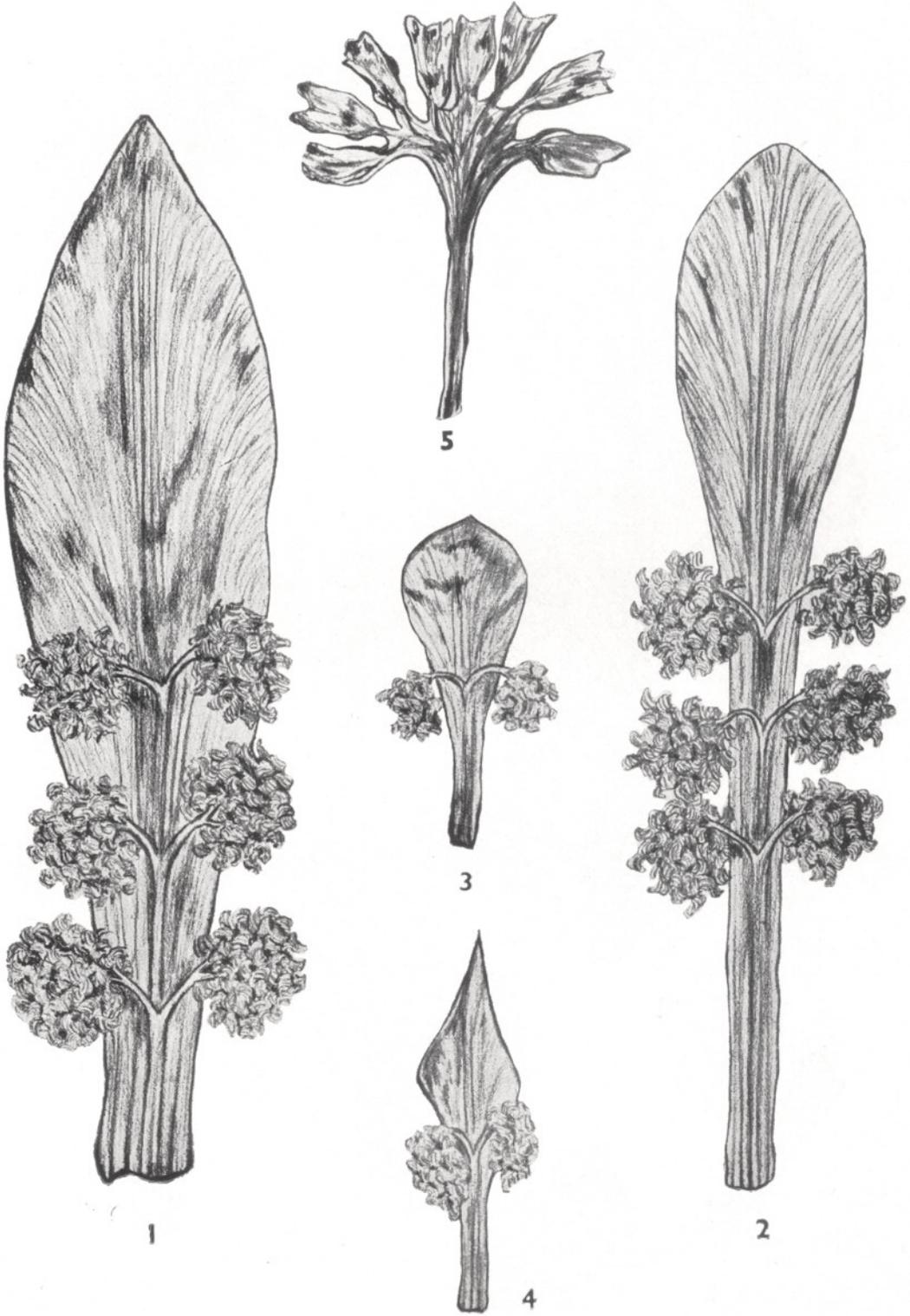
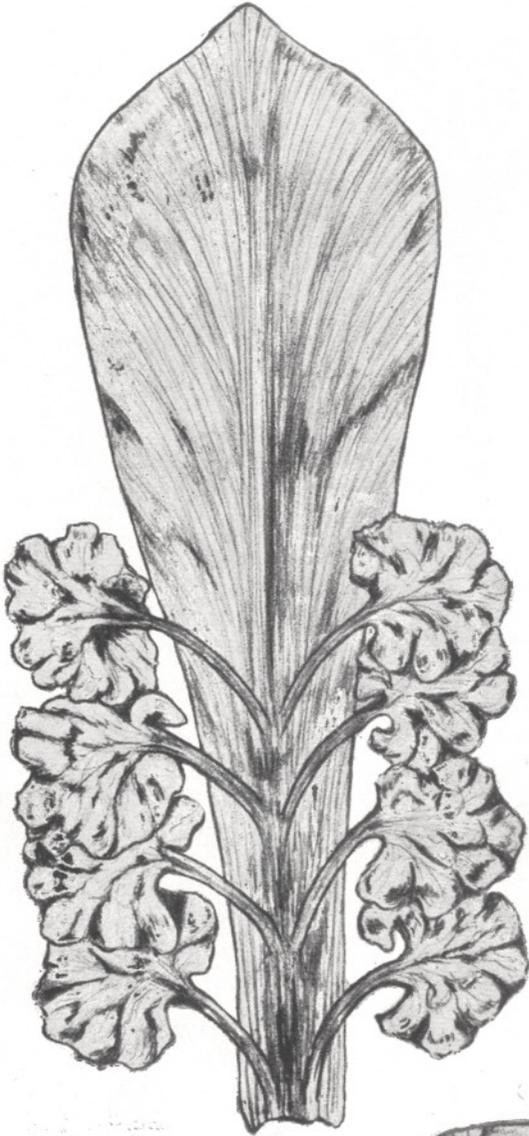


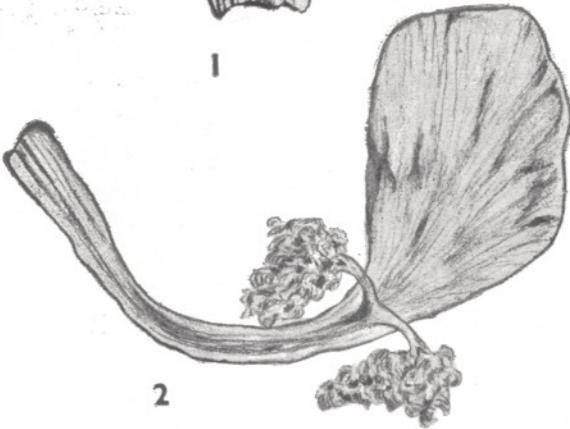
PLATE 1



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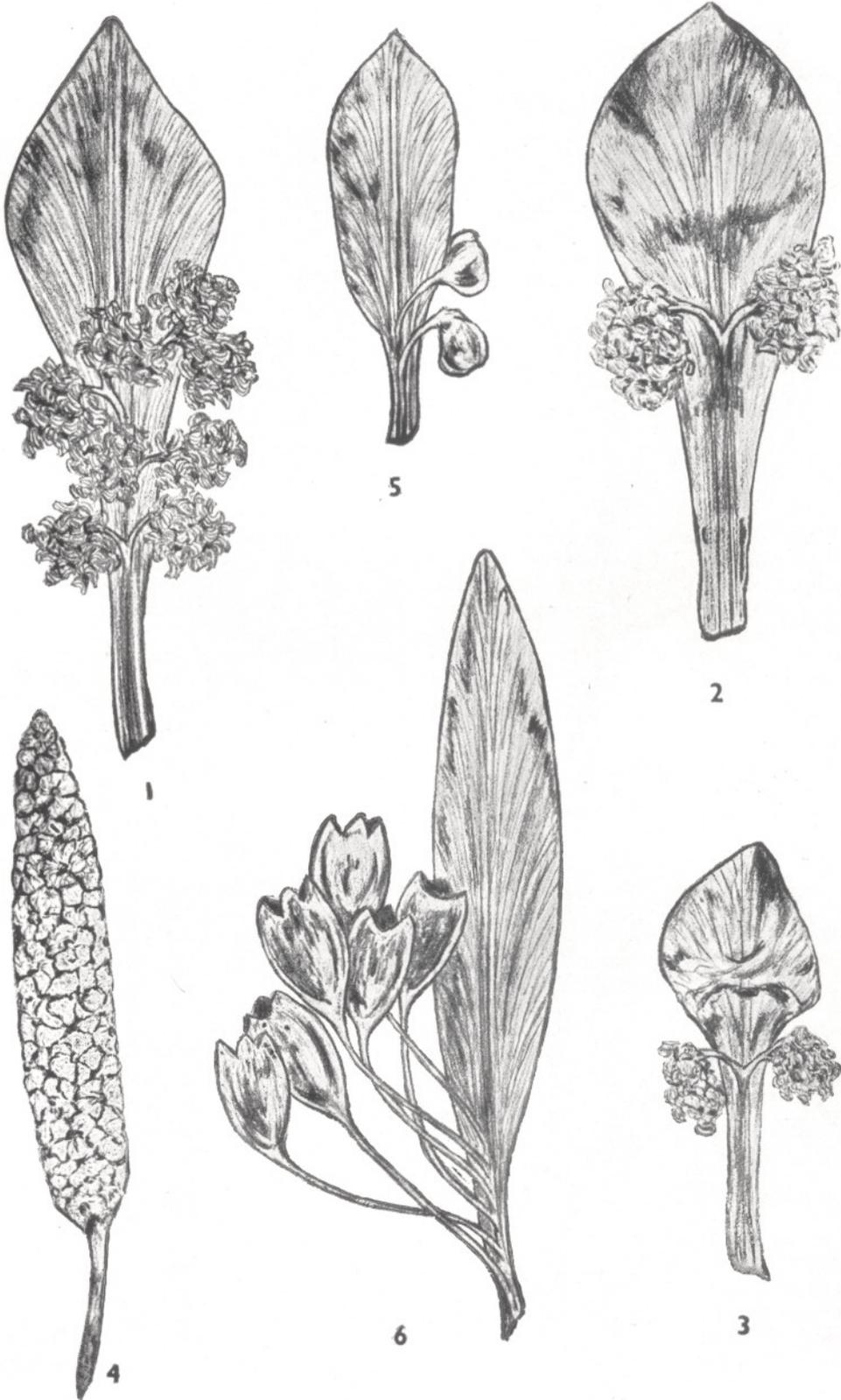


PLATE 3

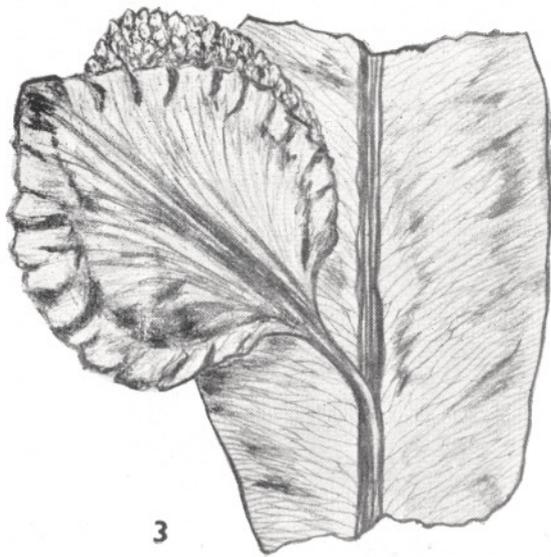
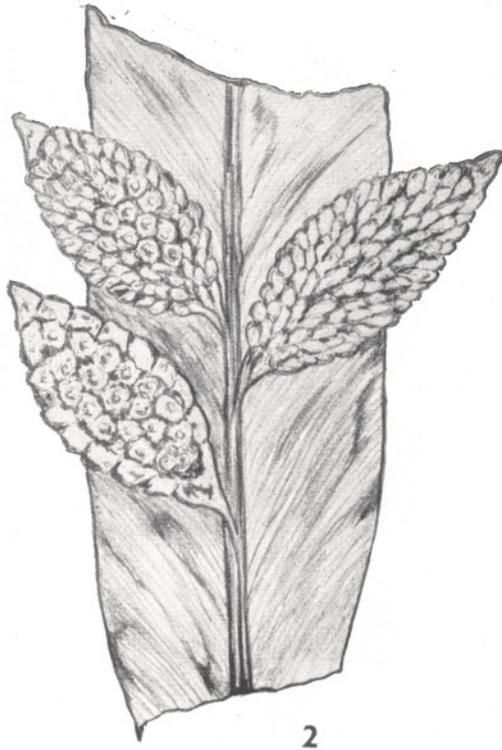


PLATE 4