The pollen wall has the uniqueness of a special endowment among plant morphosystems, being composed of an exine made up of a resistant compound, the sporo pollenin, and being organised to protect the male protoplast. At the same time, serving as a protective structure, the exine embodies in it such morphological characteristics that are reflective of the respective mother plant, by which the pollen unit has come to be increasingly used as an index in gaining information on the inter-relationships of plants. With this increase in the vista of application of pollen morphology new approaches in morphological analysis have been found leading to the emergence of newer areas of understanding in palynological science.

The present study of the pollen morphology of *Gloriosa*
advancements in optical technology, including electron microscopy, leading to new methods of studies. The replica method has been refined and simplified especially through the work of Rowley and his collaborators (Rowley and Flynn, 1966; Flynn and Rowley, 1967; Banerjee, 1967). In the case of various cultivars of *Linum usitatissimum*, the electron microscopy of the exine surface replica pictures showed significant differences in the nature and frequency of various sizes of surface islands (Nair and Sharma, 1975).

The introduction of scanning electron microscopy has come as a boon in studies of pollen morphology. There are numerous reports in the literature where scanning electron microscopy has been profitably utilised in resolving the differences in the morphology of various unipalynous taxa, such as microtaxa, cytotypes etc. (Grant, 1972; Albers, 1975; see Ferguson and Muller, 1976; Rajendra et al., 1978, etc.). In recent years, many aspects of the architecture and ontogeny of pollen grain walls have been elucidated by the application of scanning and transmission electron microscopy (Heslop-Harrison, 1968). Baksi (1976) showed that in genera *Gluta* and
Melanorrhoea, the application of SEM and TEM reveals interesting finer details of structure and sculpture of the pollen walls which provide the basis for the interpretation of the evolutionary development of the exine. Rowley and Jarai-Komlodi (1976) used SEM, TEM and light microscopy for the study of the critical features of the pollen morphology of Linum tenuifolium. Ravi Kumar et al., (1978) have demonstrated the significance of the use of SEM as well as LM in the study of supra surface and sub surface morphology respectively in Cajanus cajan. Therefore, it is clear that at the present day, the approach to pollen morphological analysis involves a wide variety of methods, the sum total of which should provide a considerably perfect picture of plant relationships.

In the present investigation on the pollen morphology of some taxa of Gloriosa and Amaryllis which belong to unipalynous taxa, information has been sought on various parameters such as exine ornamentation by both SEM and LM, occurrence of pollen shape forms, pollen size measurements (E and $E_1$ diameters), and the effect of acetolysis on $E$ and $E_1$ diameters. A comparison of the LM and SEM studies has revealed that by means of LM an understanding of the
exact pattern of the extreme surface is not reached and therefore, it is contended that the LM provides subsurface morphology, while the SEM provides the supra surface morphology. Combined data on LM and SEM have added a new dimension to the methodology of pollen morphological analysis. It has been found in the case of Gloriosa particularly, that the LM provides only a basic picture of striate ornamentation, while the SEM alone could provide the exact nature of the variations in the micromorphology of both the striae and lirae making the striate pattern. On the other hand, in the case of Amaryllis, the LM provides a basic picture of the variations in the shape, size, type of fusion and arrangement of the columella constituting the basic reticulate pattern, while the SEM has provided the variations in the supra surface morphology of the brochi constituting the reticulate pattern. Further, the data has helped in the understanding of the existence of morphotypes, the taxonomy and pollen morphological and cytopalynological evolution in the various taxa of Gloriosa and Amaryllis studied. The data on the study of the pollen morphology of the hybrids and their parents have also been utilized in demonstrating the potentiality of exine features as genetic
markers in the study of inheritance and gene expression during hybridization and also in understanding the relative roles of sporophytic and gametophytic complements in controlling exine patterns.

II THE CONCEPT OF MORPHOTYPES

Nair (1968) has suggested that any one pollen mass consists of "pollen strains" each characterized by a definite pattern of form and function. The idea emerged from direct and indirect evidences from the studies on pollen morphology and pollen germination. For example, in *Vitis vinifera* the pollen mass is composed of smaller and larger morphotypes and it was found that in 20% sucrose medium, the smaller grains germinate profusely, while the larger ones produce only incipient tubes (Nair et al., 1964). Similarly, Nair and Singh (1968) have reported that in *Allium cepa*, the pollen mass consists of spheroidal and elongate grains, which are respectively characterised by the central and lateral germination (with reference to colpus). Based on histochemical studies, Singh et al., (1976a) have concluded that in
Grotalarias juncea, small grains possess high percentage of germination and higher physiological activity than the larger ones. In the present study also, the differential pollen germination and tube growth responses in the pollen mass to various growth substances has been noted; also in G. virescens, when the grains were pretreated with CH + BM for 30 min and then transferred to BM, some small grains which normally does not germinate in BM, were found to produce small pollen tubes, while in the large grains the tube initiation was inhibited. This observation again confirms the existence of also pollen physiological strains. Nair (1969) proposed that pollen selection on a morphophysiological basis should be a prerequisite to breeding experiments.

The knowledge on the pollen morphology of cultivated plants shows that as a general rule, the nature of variations and the composition of morphotypes within any one taxon is of a very specific nature relating to any one of the character groups (rarely more than one character groups are involved); for example, the variations are with regard to the endocolpium in Citrus (Bamzai and Randhawa, 1965), exine ornamentation in Hibiscus (Nair, 1961), Linum and Brassica (Nair and Sharma, 1975 and 1976), strata in Canna (Nair, 1960b),
pollen size in *Zea mays* (Nair, 1962a), and shape types in *Allium cepa* (Nair and Singh, 1974), *Amaryllis* and *Hemerocallis* (Sharma, D, 1978).

It is always not possible to identify strains with a specific combination of form and function, but it is a common fact that the grains in any one pollen mass are constituted of various size classes and also of shape types. In addition to pollen variations, it has been observed that the effect of the chemical process of acetolysis on pollen size increase is very specific with regard to various taxa of cultivars, as has been demonstrated in the case of *Citrus* (Bamzai and Randhawa, 1965), vegetable crops (Nair and Kapoor, 1974), and also oil crops (Nair and Sharma, 1975, 1976). In the case of *Cajanus cajan*, a decrease in pollen size has been reported (Ravi Kumar et al., 1978).

The present studies also have clearly shown that in *Gloriosa* and *Amaryllis*, the pollen mass is generally constituted of three shape forms namely spheroidal, ellipsoidal and spindle shaped grains (expressed on the basis of the E diameter; ref. Text figs.2A-C). However, the percentage occurrence of each type in every taxon varies.
The spindle shaped grains almost as a rule, are morphologically sterile having no protoplasm.

In general, ellipsoidal grains form the dominant type in the taxa of Gloriosa. In G. superba (2x) and G. lutea the occurrence of spheroidal grains is relatively more (14.5-22.0%) and the spindle shaped grains are less (2.5-5.5%). On the other hand, ellipsoidal grains alone are present in G. richmondensis and G. virescens X G. carsonii and in the remaining tetraploid taxa of the genus, the spheroidal grains are less (0.0-7.0%) and the spindle shaped grains are also present in appreciable numbers (6.3-30.0%). Among the octoploid taxa, G. superba consisted of ellipsoidal (51.0%) and spindle shaped (4.0%) grains only, and G. magnifica consists of spheroidal, ellipsoidal and spindle shaped grains in 6.5, 83.4 and 10.1% respectively. (Table-V and Text fig. 22). However, G. richmondensis and G. virescens X G. carsonii are quite distinct in possessing only ellipsoidal grains.

In the taxa of Amaryllis presently studied, any one of the three shape forms constitute the dominant type (Table-IX and Text fig.34). For example, in A. sp.
Cv-44 (2x) and *A. vittata* (2x and 4x) the spheroidal grains constitute the dominant type (54.0, 58.0 and 39.0% respectively), while in Cv-12 (2x) and *A. vittata* (3x), the spindle shaped grains form the dominant type (63.5 and 65.4% respectively). On the other hand in *A. belladonna* hybrid group (2x, 3x and 4x) the ellipsoidal grains constitute the dominant type (48.0 - 59.0%) followed by spindle shaped grains (22.5 - 37.5%) and spheroidal grains (10.6 - 25.4%) in the order of their occurrence. Further, the range and average E and E1 diameter of these three shape forms are also found to vary significantly in all of the taxa of *Gloriosa* and *Amaryllis* presently studied (Table, VI - VIII and X-XIII and Text figs. 23 and 35).

The data on the percentage increase in E and E1 diameters due to acetylation is also quite distinct in the different shape morphotypes of the above two genera (ref. Table VI-VIII and X-XIII). Thus, the concept of morphotypes as applied here refers mainly to the three shape classes showing differences also in their size range and average size, and their response to acetylation.
III POLLEN POLYMORPHISM

In most examples of polymorphic pollen, the different pollen types produced by a single species are regular and conform to a limited number of morphological patterns, each of which possesses a limited and restricted variability. This is true whether the polymorphism is associated with a breeding system (heterostyly) as in Waltheria (Kohler, 1973, 1976), Japsonia (Ornduff, 1970), Primula (Punt et al., 1974), etc., or with geographical isolation as in Alangium chinense (Reitsma, 1970). The present studies of the pollen morphology of the hybrid *G. superba* X *G. lutea* (2x) showed a picture of great morphological changes in the pollen mass having a varied combination of morphological characters in any one grain (Note: pollen grain were collected from the anthers of a single flower).

However, the pollen polymorphism in the hybrid *G. superba* X *G. lutea* did not conform to the limited or uniform variations in the pollen morphology. The variations are very irregular as against the normal parental pollen types. Apart from monads, there are also dyads
occurring at maturity. The pollen mass in the hybrid is constituted of 17% spheroidal grains, 13% ellipsoidal grains and the rest of the 70% being spindle shaped and its variations (sterile).

Most of the abnormalities are confined to spheroidal grains which are very large in size (33.5 x 28.0 μm to 61.5 x 59.0 μm) as compared to those in the rest of the genus presently investigated. The abnormalities are related mostly to aperture types (ref. Text fig. 19A - L) such as:

1. Gigantiporate-operculate, the size of the operculum varying from 25 x 25 μm to 45 x 42 μm,
2. Normaliporate operculate,
3. Pontoperculate, the area of the attachment of operculum to the general surface being small or large, straight or zig zag or in other configurations,
4. Trichotomo colpate,
5. Trichotomo-operculate, the trichotomous aperture occurring in the centre of the operculum.
On the other hand, the ellipsoidal and spindle shaped grains possess fundamentally monocolpate apertures with variations in shape and size of the colpi, so that two grains rarely look alike and the grains are also of various sizes. The categories of pollen types listed above by no means exhausts the forms which were produced, but merely represents some basic types and the grains being much more asymmetric.

Exine ornamentation is of a mixed type, there being striato reticulate, rugulate (corrugate) forms. Apparently all the types have their origin in the basic striate form from which by division or fusion of striae the various other forms have originated. It is in the spheroidal grains that the multiplicity of ornamentation types occur similar to the occurrence of various apertural types. In some cases, the ornamentation varies from one area to other in the same grain. It is of great significance to note that the spheroidal grains having basic operculate type apertures in the hybrid have been reported for the first time in the genus *Gloriosa* and are totally absent in the various species of the genus presently investigated or in the previous reports (Sharma, 196?). In fact, the pollen type characteristic of the genus is the ellipsoidal with monocolpate apertures.
Clarke (1976) observed that in the various species of Hypericum, the deviations were confined to aperture number and configuration. But in the present study, the abnormalities in the pollen grains of the hybrid *G. superba* x *G. lutea* are related to pollen shape forms, aperture types as well as exine ornamentation. The factors which normally determine pollen aperture configurations and contain them within the narrow limits of variability do not seem to operate in the hybrid *G. superba* x *G. lutea* (2n = 22). Normally when species produce more than one pollen type they do so regularly and predictably. But this is not so in the present hybrid, where a single anther or a single flower contains a range of irregular grains forming different categories and give the impression of being produced more or less at random rather than following a predetermined plan.

Drastic variations in pollen size (large and small grains) in some hybrids and mutants have been shown to be due to the variation in the number (reduced or more) of chromosomes in the microspore resulting from abnormal meiosis (Rogers and Harris, 1969; Pal and Khoshoo, 1972;
Tara and Namboodiri, 1976). Dover (1972), and Mujeeb et al., (1978) have reported that in some grasses, the tetraporate pollen were formed due to meiotic disturbances leading to abnormal cross cell wall formation. Heslop-Harrison (1972) also observed that in Lilium, when the spindles of either both the divisions or of the second division are blocked by colchicine treatment or by centrifugation, the meiocyte as a whole or the partially fused dyads respectively are formed, which develop into large sized individual spores with normal exine pattern- ing; the colpus in such a spore is totally absent or it may develop randomly often in an irregular form. Thomas (1970) in a study of polyploid cultivars of Hypericum patulum concluded that the large pollen grains are pro- duced from dyads which are formed due to the failure of the second meiotic division, while the small grains are derived from the normal tetrads. Clarke (1975), based on his study of 40 species of Hypericum having irregular pollen with varying aperture number and configuration, suggested that the production of such grains is often associated with faulty meiosis.

The results of the present investigation on the pollen morphology of the hybrid G. superba x G. lutea
are in close agreement with the conclusions of the above workers. Narain (1972) also indicated that because of the genetical and morphological distinctness of *G. superba* (2x) and *G. lutea* (2x), the crosses between the above two species were often a failure. However, in a single instance, the cross was successful resulting in a hybrid which showed a lot of meiotic abnormalities and high male sterility (personal communication).

It seems likely that in the hybrid *G. superba* x *G. lutea* also the large spheroidal grains with new apertural types are the result of irregularities in meiosis and consequently are produced from the meiocytes or dyads, almost at random rather than being the result of selection. In fact, a large number of dyads were also seen in the pollen mass of the hybrid. Therefore, the variations in the pollen types of the hybrid different from those characteristic for the genus, may be the result of spatial variations after meiosis during pollen grain development. The abnormalities could thus be attributed to physical and genetical imbalance of *G. superba* and *G. lutea* parental chromosomes during meiosis. The fact, that no species in the genus *Gloriosa* has similar apertural types or large sized grains reinforces the above view of formation of irregular pollen types.
IV ASPECTS OF CYTOPALYNOLOGY

There are several reports where palynological studies have been made in conjunction with cytological studies. Literature is replete with example where a general correlation between polyploidy or chromosome number and the pollen size has been shown (Akerberg, 1942, Sun, 1946a & b; Nissen, 1950; Love, 1952; Derman, 1957; Gould, 1953, 1957, 1959 and 1963; Kapadia and Gould, 1964; Powell, 1965, Levin, 1968; Besett and Crompton, 1968; Kessler and Larson, 1969; Sreerangaswami and Raman, 1973). In fact, a reasonably sure test of colchicine is the increase in pollen grain size. For sometime, taxonomists and cytologists have been using mature pollen size in samples from herbarium sheets as a method for surveying the extent of polyploidy within certain taxa (Stebbins, 1950).

Erdtman (1952) observed that in the members of Labiatae, the pollen grains are 3-zono colpate in 2-celled pollen and 6-zono colpate in 3-celled ones. There are several cases where the pollen grain size as well as aperture number has been correlated with ploidy levels (Maurizio, 1956; Dahl and Rowley, 1956; Kuzdowiez, 1958;
Duigan, 1961; Dyansagar, 1965; Geslot and Medus, 1971; Punt et al., 1974). There are also many reports where several other characters such as the details of exine ornamentation, exine excrescences, exine strata, total apertural area and so on have been correlated with polyploidy (Bronckers, 1963; Lewis, 1964, 1965a; Kessler and Larson, 1969; Albers, 1975).

There are several reports where the palynological data has been shown to agree with the phyletic trends found in the sporophyte on the basis of morphology, distributional pattern and chromosome number and size (Lewis, 1964, 1965a & b; Khoshoo, 1978). Nair and Sharma (1966-67) observed the occurrence of varying degrees and combinations of apertural types in the various ecotypes and cytotypes of *Sisymbrium irio* complex and have inferred the cytopalynological relationships and evolution of pollen morphotypes in conjunction with the genetic constitution as proposed on the basis of the experimental data of Khoshoo (1960 & 1963). Taylor and Levin (1975) while studying the pollen morphology of Polemoniaceae concluded that pollen phylogeny is completely compatible with chromosome phylogeny in the family.
In the present study also, an attempt has been made to gain knowledge on the changes brought about in the various features of pollen morphology by the increase in ploidy level and also to understand the cytopalynological evolution of exine patterns in the cytotypes of *Gloriosa* and *Amaryllis*.

1. POLLEN MORPHOLOGY OF CYTOTYPES

In the diploids, *G. superba* and *G. lutea*, the exine ornamentation being striato-reticulate and striato undulate punctate respectively are of an advanced type. Among the tetraploids *G. carsonii* has a striato-reticulate pattern, while *G. virescens* and *G. richmondensis* have striato fossulate ventriculate and striate patterns respectively. Among the octoploids, *G. superba* and *G. magnifica* are characterized by striato-punctate and striato-ciss-cross foveolate patterns respectively and almost similar situations as in the octoploids occur also in the tetraploid hybrids namely *G. carsonii* x *G. virescens* and *G. virescens* x *G. carsonii* which has been termed striate-pan-punctate and striato intertwined foveolate respectively. Similarly the striato reticulate pattern is an advanced feature in morphological evolution which occurs in the diploid *G. superba* as well as tetraploid *G. carsonii*. 
Thus, the above data shows that the evolution of exine ornamentation does not fully conform with the pattern of increasing ploidy level in the genus *Gloriosa*. It is therefore, felt that the species investigated may have independent origins from a hypothetical species of the genus along three lines namely, the diploid line, the tetraploid line, and octoploid line, on each of which there are species at various stages of evolution (ref. Text fig. 21). However, in the case of *G. superba*, the diploid species possess striato-reticulate exine pattern, the striae surface being plane and non punctate, while the octoploid species is characterized by the occurrence of puncta on the fossulate striae, which in terms of morphological evolution is an advanced condition.

On the other hand, in the taxa of *Amaryllis* presently studied, it has been noted that the diploid taxa possess retipilate to simple reticulate exine patterns having various stages of union of columella islands, while the triploid and tetraploid taxa are characterized by a distinct reticulate condition having complete muri with fully fused columella heads and distinct micro brochi and mega brochi which are considered as relatively advanced stages of morphological evolution (ref. Text. fig. 33).
Thus, in the case of *Amaryllis* the evolution of exine ornamentation could be correlated with the increasing ploidy level, which is in contrast with the finding with regard to *Gloriosa*.

It has been pointed out earlier in the discussion that the higher frequency of ellipsoidal grains in the monocolpate forms represent primitiveness while that of the spheroidal grains represents advancement. The data on the studies of the occurrence of shape types in the taxa of *Gloriosa* indicates that in general, the ellipsoidal grains constitute the dominant type in all the cytotypes, presently studied. The spheroidal grains are relatively more and the spindle shaped grains are less in the diploid taxa, when compared to the tetraploid and octoploid taxa. However, the tetraploid taxa have more ellipsoidal grains than the diploids, and also the tetraploid taxa *G. richmondensis* and *G. virescens* X *G. carsonii* possess only ellipsoidal grains (ref. Table V and Text fig.22). Thus, the data on the occurrence of shape types also agrees with the data on the evolution of exine ornamentation in the sense that the above data do not correlate with the pattern of cytological evolution. On the other hand, all the three shape forms are present in all the
taxa of *Amaryllis* presently studied and that any one of
the three shape forms dominate in each taxa (Table IX
and Text fig. 34). Thus, there is no correlation between
the occurrence of shape types and ploidy level in the
taxa of *Amaryllis* unlike the case of exine ornamentation
in the genus.

With regard to pollen size, the data on the taxa
of *Gloriosa* suggests that the average E diameter (Uc) of
the ellipsoidal grains of both diploid and tetraploid
taxa are more or less same (29.1 - 32.0 \( \mu m \)) while that of
octoploid taxa are higher (34.1-38.6 \( \mu m \)) which is in
confirmity with the general belief that the pollen size
increase is related to the increase in ploidy level. In
*Amaryllis*, the average E diameter of ellipsoidal grains
varies from 58.5-62.5 \( \mu m \) in the diploid taxa, from 60.7 -
65.6 \( \mu m \) triploid hybrids and from 68.4-75.7 \( \mu m \) in the
tetraploid taxa (ref. Text fig. 23) which again confirms
the increasing pollen size with increasing ploidy level.

The data on the response of ellipsoidal grains
to the process of acetolysis reveals that in the taxa
of *Gloriosa* there is no significant correlation between
the response of acetolysis and ploidy level and some taxa
show more increase and some show less increase in $E$ diameter of ellipsoidal grains due to acetolysis. (ref. Text fig. 24). In general, there is more increase in $E$ diameter due to acetolysis than that of $E_1$ diameter (except in $G. \text{superba} \times G. \text{lutea}$ and $G. \text{richmondensis}$).

In **Amaryllis**, the two diploid taxa namely Cy-44 and $A. \text{vittata}$ showed more increase in $E_1$ diameter while the rest of the taxa showed more increase in $E$ diameter. In general the tetraploids showed more increase in $E$ diameter than the diploids and triploid taxa (ref. Text fig. 36). Thus, there is no clear cut correlation between the effect of acetolysis and the ploidy level. Therefore, it appears that the effect of acetolysis depends more on the type of exine ornamentation and the mode of arrangement of wall material rather than on the ploidy level.

2. POLLEN MORPHOLOGY AND BIOSYSTEMATICS

The bearing of pollen/spore morphology in biosystematics has been demonstrated with regard to **Pteris vittata** (Verma, 1966-67), **Girtrullus vulgaris** var. *fistulosus* (Khooshoo and Vij, 1963), in some members of subtribe Deschampsiiinae of Poaceae (Albers, 1975). Lewis (1965b) found that the data on the pollen morphology and
evolution in Hedyotis sub genus Edrisia agree with the phyletic trends found in the sporophyte on the basis of the results from morphology, chromosome number and size, and distribution, and further the data support and add to an earlier phylogenetic scheme proposed for the sub genus. De (1968) correlated the palynology of Acanthaceae with cytological and anatomical studies in tracing the affinity and phylogeny of the family. Johnson (1973) studied the pollen morphology in African species of Swertia (Gentianaceae) in relation to chromosome number and found that the species of Swertia could be pollen morphologically divided into three groups as has been already divided into three groups by Hedberg (1957). In the present investigation of the pollen morphology of the taxa of Gloriosa and Amaryllis, an attempt has been made to see whether the results of the present study are in agreement with the conclusions reached based on the cytogenetical studies by Narain (1972).

Narain (1972) reported that the diploid species G. superba and G. lutea are genetically well differentiated from each other, G. superba having 8 V + 14 J chromosomes with 2 satellites associated with a submedian pair, and G. lutea having 8 V + 8 L + 4 J + 2 I chromosomes with
2 satellites associated with the terminal chromosome. Further, the two species are also morphologically distinct from each other, G. superba attaining a height of about 300-800 cm and G. lutea about 190-200 cm in height. The flowers of the two species are also quite different from each other in their colour and in a few other characters (Narain, 1972). The present study of the pollen morphology of the two species also support the observations of Narain (1972) owing to the fact that the pollen grains of G. superba (2x) and G. lutea are markedly distinct from each other. For example, the exine pattern is striato reticulate in G. superba and striato undulate punctate in G. lutea. The effect due to acetolysis in E and E₁ diameters of ellipsoidal grains is +30.2 and -0.9% respectively in G. superba and +50.3 and +29.5% respectively in G. lutea.

Thus, because of their genetical and morphological distinctness, the crosses between the G. superba (2x) and G. lutea (2x) were often a failure (Narain, 1972). However, in one instance, the cross was successful resulting in a hybrid which showed considerable meiotic abnormalities and a high degree of sterility (personal communication).
The present pollen morphological study of the above hybrid *G. superba* × *G. lutea* (2n = 22) showed a picture of great morphological variations in the pollen mass. Many dyads, very large sized grains, and other varied types of abnormalities were noticed. The details will be discussed in the later pages in connection with pollen polymorphism.

Narain (1972) showed that the three tetraploid species namely *G. virescens*, *G. carsonii* and *G. richmondensis* are karyotypically almost the same having 16 V + 16 L + 8 L + 4 I chromosomes, being exact multiple of the basic karyotype found in *G. lutea* (2x), but having a few differences in their respective chromosome associations and flower colour. However, the present study of the pollen morphology of the above tetraploid species show that the exine pattern is striato-fossulate-ventriculate in *G. virescens*, striato- reticulate in *G. carsonii* and plain striate with dissected and zig zag striae in *G. richmondensis*, and the above exine patterns are at different levels of morphological evolution. Besides, in *G. carsonii* all the three shape forms occur, whereas in *G. virescens* only ellipsoidal (73%) and spindle shaped grains (27%) are present and in *G. richmondensis* only the ellipsoidal ones are represented. However, the differences in E diameter
of ellipsoidal grains (Uc) are not quite distinct, being 25.3 µm in G. carsonii, 29.14 µm in G. virescens, and 31.4 µm in G. richmondensis. But with regard to the increase due to acetolysis in the E diameter of ellipsoidal grains, the three tetraploid species are quite distinct from each other being + 25.0%, + 49.4%, and + 40.0% respectively. Thus, the present study amply provide a picture of pollen morphological distinctness of the three tetraploid species contrary to the cytogenetical similarities reported for the three species by Narain (1972).

The hybrids between the above three tetraploid species namely G. virescens × G. carsonii, G. carsonii × G. virescens, and G. virescens × G. richmondensis were reported by Narain (1972) as morphologically intermediate but from horticultural point of view superior than their parents. In flower colour, the three hybrids show dominance of G. virescens (parent) than the other parental species. Karyotypically also they are similar to their parents. The reciprocal hybrids of G. virescens and G. carsonii are also similar with regard to meiotic features, pollen fertility, seed fertility, etc. However, the hybrid G. virescens × G. richmondensis has reduced
pollen fertility (66.3%) and is also seed sterile. The present studies show that in pollen morphology, the two reciprocal hybrids differ from each other as well as from that of their parents very distinctly. For example, in *G. virescens* × *G. carsonii*, the exine pattern is striato-intertwined-foveolate, while in *G. carsonii* × *G. virescens*, the same is striate pan-punctate. Further, in the former, only ellipsoidal grains are present unlike its parents, and in the latter, all the three shape forms are present as in its female parent *G. carsonii*. However, there are no significant differences in E diameter of ellipsoidal grains (Uo) and in its response to the process of acetylation in the two hybrids. Therefore, the present studies of the pollen morphology of the above two reciprocal hybrids differ from their cytogenetical data as reported by Narain (1972). On the other hand, the exine pattern in *G. virescens* × *G. richmondensis* is striato-fossulate with partially intertwined striae which is an intermediate condition between the two parents. Further, only ellipsoidal and spindle shaped grain (70 : 30) are represented in the hybrid as in the female parent *G. virescens*. But, the E diameter of ellipsoidal grains (Uo) is more and its (E diameter) increase due to acetylation is less in
the hybrid, as compared to its parents (Table VII).
The present studies are considerably in agreement with
the cytogenetical observations of Narain (1972) that the
hybrid G. virgescens x G. richmondensis show characters
intermediate between its parents.

With regard to the octoploid species of Gloriosa,
Narain (1972) reported that the somatic complement of
G. superba (2n = 88) is exact multiples of the basic
karyotype of diploid G. superba, while that of G. magni-
ifica (2n = 88) is exact multiples of that diploid G. lutea.
However, the above data is not fully supported by the
pollen morphology, because the exine pattern is striato-
fossulate punctate in G. superba (8x) and striato reticu-
late in diploid G. superba (2x); similarly in G. magnifica
(8x), striato-criss cross-foveolate condition is seen,
whereas in G. lutea (2x), striato undulate-punctate exine
pattern is found. Thus, the exine patterns of the diploid
and octoploid taxa of Gloriosa are found to vary. However,
the exine patterns in both diploids and tetraploids are
considered as belonging to advanced condition and are at
the same level of pollen morphological evolution. Further
in the case of Amaryllis also, the diploid and tetraploid
taxa of A. belladonna and A. vittata differ from each other
distinctly in pollen morphology although cytological
similarities have been reported by Narain (1972).
V POLLEN MORPHOLOGY OF HYBRIDS AND THEIR PARENTS

While the effect of polyploidy on pollen morphology and pollen size is reasonably well known, that of mutation and hybridisation, either single or in combination, is not properly worked out (Khoshoo, 1978). In recent years, much attention has been focussed on the study of pollen morphology of the mutants, hybrids and their parents, with a view to gain knowledge on the nature of hybridity and genetical mechanisms at such micromorphological levels (Rogers and Harris, 1969; Mepham, 1970; Grant, 1972; Tara and Namboodiri, 1974; Srivastava, 1976a & b 1978; Srivastava et al., 1977; Mair et al., 1977; Rajendra et al., 1978; Ravi Kumar et al., 1978).

In the present investigation, the pollen morphology of diploid and tetraploid hybrids and their parents of Gloriosa and that of diploid parents of Amaryllis have been studied. Various parameters such as exine ornamentation, occurrence of shape types, E diameter of ellipsoidal grains (Uo) and its response to acetolysis have been considered for pollen morphological analysis. The data with regard to the diploid hybrid group of Gloriosa has already been
discussed earlier in connection with pollen polymorphism. The tetraploid hybrid group of *Gloriosa* consists of 3 tetraploid parental species namely, *G. virescens*, *G. carsonii* (producing reciprocal hybrids) and *G. richmondensis* (male parent) and 3 hybrids. The two reciprocal tetraploid hybrids namely *G. virescens* × *G. carsonii* and *G. carsonii* × *G. virescens* are characterized by entirely new exine ornamentation patterns different from each other and also from that of their parents. For example, in *G. virescens* × *G. carsonii* the exine pattern is striato-intertwined foveolate type and that in *G. carsonii* × *G. virescens* is pan-punctate striate whereas in the parents the same is striato-fossulo-ventriculate in *G. virescens* and striato- reticulate in *G. carsonii*. Further, the striae are arranged in a single tier in the parents while they are in double tier in the above hybrids. However, in the hybrid *G. virescens* × *G. richmondensis* the exine ornamentation is striato-fossulate with partially intertwined striae which condition is intermediate between the plain striate pattern of the male parent *G. richmondensis* and the striato-fossulo-ventriculate pattern of the female parent *G. virescens*. Further, the data with regard to the occurrence of shape types, E diameter of ellipsoidal grains (Uo) and their response to acetolysis (ref. Text fig.22-24)
shows that in each of the characters, the three tetraploid hybrids resemble one or the other parents or intermediate between the parents which suggests that the pollen grains of the hybrids have assumed in total a new morphology different from their respective parents.

In the case of *Amaryllis*, three hybrid groups namely *A. sp.*, hybrid group, *A. belladonna* hybrid group, and *A. vittata* hybrid group have been studied. With regard to *A. sp.*, hybrid group, basically reticulate and isobrochate exine ornamentation with uni- to bi-seriate columella islands in the muri is characteristic of the female parent Cv-44, and retipilate and isobrochate exine pattern with broken brochi are characteristic of the male parent Cv-12, while in the hybrid Cv-44 X Cv-12, retipilate pattern with large isomorphous broken brochi as that of male parent is found but in addition, uni- to bi-seriate columella islands in the muri, a feature of the female parent is also found. In addition luminar columella islands are also found in the hybrid pollen. This indicates that the exine pattern in the hybrid combines features of both the parents, the male features being more than those of the female parent. Besides, size change E brought about in ellipsoidal grains of the hybrid
to the process of acetolysis resembles that of the male parent; even with regard to the occurrence of shape types and E diameter of ellipsoidal grains (Uc) the hybrid is intermediate between the parents. Thus the pollen grains of the hybrid appear to be a new morphotype when compared to its parents.

In the case of *Agave belladonna* hybrid group, analysis of the data indicates that the triploid hybrid pollen possess characters of both the parents in exine ornamentation, those of the tetraploid female parent being more than those of the diploid male parent. With regard to other characters also the pollen of the hybrid has been observed to resemble either of the parents or intermediate (ref. Tables IX & XI Text figs. 34-36), which again suggests that the pollen of the hybrid is a new morphotype different from those of its parents.

Similarly, *A. vittata* hybrid group also, the exine ornamentation of the hybrid has been observed to possess more features of the tetraploid female parent and also few new additional exine ornamentation features. The constitution of shape forms is completely different in the pollen mass of the hybrid than that of its parents; however, the E diameter of ellipsoidal grains (Uc) and its
response to acetolysis the hybrid pollen are intermediate between its parents (ref. Tables IX & XII Text figs.34-36). Thus in this case also, the pollen of the hybrid can be considered to be a distinct new morphotype.

Grant (1972) observed that the pollen grains of the intergeneric hybrid \((2n = 44)\) namely, Zea mays \((2n=20)\) x Tripsacum dactyloides \((2n = 72)\), exhibits a wall sculpture which is intermediate between the extremes of the parents. It seems that the 10 chromosomes of Zea as against 36 in Tripsacum parent \((1:4)\) have enough influence to modify the typical Tripsacum exine pattern to a noticeable extent. On the other hand, the 82 chromosome hybrid T. dactyloides \((2n = 72)\) x Z. mays \((2n = 20)\) exhibits a wall sculpture which is indistinguishable from that of octoploid Tripsacum. In this hybrid, the 10 maize chromosomes are outnumbered by 72 Tripsacum chromosomes \((1:8)\) in terms of genome. Under these conditions the maize chromosomes have little effect on exine sculpturing as compared with the 46 chromosome hybrid, where the genome balance is 4:1 Tripsacum to Zea. Therefore, Grant (1972) concluded that the pollen grains of the hybrids between Zea and Tripsacum exhibited markedly different exine
sculpturing depending up on their chromosome numbers and the ratio of Zea to Tripsacum genome present.

In the present study also in the two intraspecific triploid hybrids of A. belladonna and A. vittata (2n=33), the chromosomes of the diploid parent (2n=22) are out numbered twice by those of the tetraploid female parent (2n=44) in terms of genome (1:2). Therefore, in the exine pattern of the A. belladonna hybrid (2n=33), the characters of the female parent are more in number with a few characters of the male parent. Thus, a few exine characters of the male parent have been expressed in the above hybrid pollen, even though the chromosomes of the male parent are less (n=11). In the triploid hybrid of A. vittata also the exine pattern characters of the female parent have been expressed clearly where as those of the male parent have not been expressed. On the other hand, some new additional characters which are altogether absent in the parents, have been found in the hybrid. It appears therefore, that in the case of A. vittata hybrid, the chromosomes of the male parent (n=11) have not enough influence to express atleast some of its exine characters, all the same they appear to have enough influence to bring about new characters in association with those of the
female parent (m=22). Thus, the present studies are also in agreement with the conclusions of Grant (1972) that the exine pattern of the hybrid depends on the ratio of the parental genome constitution in the hybrids.

Recently, the potentiality of pollen morphological features as genetic markers in the studies of inheritance and gene expression in hybridization, has been demonstrated in a few cases. Quiros (1975) observed that in the pollen grains of the hybrid *Lycopersicon esculentum* × *Solanum pennellii*, the genes of *S. pennellii* (male parent) are dominant over those of *L. esculentum* for pollen size and spine shape and its density; however, for pollen shape, and spine size the genes of *L. esculentum* are dominant over those of *S. pennellii*. Rajendra et al., (1978) reported that the pollen grains of the polyhaploids namely *Hordeum vulgare* × *Secale cereale* and *H. vulgare* × *Triticum turgidum* are intermediate with regard to exine pattern having few characters of both the parents. Recently Ravi Kumar et al., (1978) also showed that in the pollen grains of an intervarietal hybrid of *Cajanus cajan*, the genes of the female parent for brochi characters and colpi lips are dominant over those of the male parent while the genes of the male
parent for muri characters and endocolpium are dominant over those of the female parent. Similarly, the present investigation of the pollen morphology of the *Amaryllis* hybrid groups also indicates the potentiality of pollen morphological features as genetic markers in studies of inheritance and gene expression. For example, in the pollen grains of the diploid *A*. sp., hybrid Cv-44 x Cv-12, the genes of the male parent for retipilate condition and large isomorphous brochi, are dominant over those of the female parent, and however the genes of the female parent for uni- to bi-seriate columella islands in the muri are dominant over those of the male parent; with regard to the effect of acetolysis on the E diameter of ellipsoidal grains, the genes of the male parent are dominant in the hybrid; and with regard to the occurrence of shape forms, the genes of the female parent for spheroidal grains and those of the male parent for ellipsoidal grains appear to be co-dominant in the diploid hybrid.

In the pollen grains of *A. belladonna* triploid hybrid, the genes of the tetraploid female parent for reticulate exine, unbroken brochi, uniseriate, distinct and narrow muri and circular columella islands are dominant over those of the diploid male parent whereas the genes
of the male parent for loose muri are dominant over those of the female parent. However, the genes of the female parent for large unbroken brochi and those of the male parent for small broken brochi are probably co-dominant in the hybrid and hence the large unbroken and small broken brochi are present in almost equal proportions in the hybrid. In general, the exine pattern of the hybrid seems to be dominant with regard to many female characters, but in other characters such as E diameter of ellipsoidal grains (Uo) and its response to acetolysis, the genes of the male parent appear to be dominant in the hybrid, although in the occurrence of three shape types the genes of one or the other parent are dominant or else an intermediate situation prevails in the hybrid.

On the other hand, in the pollen grains of *A. vittata* triploid hybrid, the genes of the tetraploid female parent for compound reticulum, unbroken brochi and circular columella islands are dominant over those of the diploid male parent. However, there are also other additional new characters such as the regular shape and size of the microbrochi, straight and even muri, and the fusion of columella along their full
height, perhaps because of the interaction of the concerned genes of the parents in the hybrid. Further the constitution of the shape forms in the pollen mass of the hybrid is completely different from that of its parents and also the E diameter of ellipsoidal grains (Uc) and its response to acetolysis is intermediate between its parents. Therefore, the totality of the data suggests that in *A. vittata* triploid hybrid, though the genes of the female parent are dominant over those of the male for many characters, it appears however, that some genes of the parents interact together to produce some additional new characters in the hybrid and in some characters an intermediate situation between the parents prevails.

Thus, the results of the present study only demonstrates clearly the potentiality of exine features as genetic markers in the studies of gene expression and inheritance in hybridization. However, it is to be noted that more refined techniques and well planned experiments have to be executed selecting properly defined, clear cut and inheritable characters, which will serve to offer information on the actual genetic mechanisms operating, the number and type of genes controlling each exine character, their mode of inheritance and so on.
VI CONTROL OF EXINE PATTERNING

The exine ornamentation of the pollen grain is one of the unique features among plant cell walls. These exine patterns are so precise, distinct and genetically stable within the taxa that they are being used as important diagnostic marker characters. At the present day the major sequences of pollen wall ontogeny and the architectural principles upon which the exine structure is based are reasonably well understood (Heslop-Harrison, 1971b). However, there has been a controversy as to whether the exine patterning is controlled by the gametophytic (haploid) genome (Heslop-Harrison, 1962; Godwin, 1968) or by the sporoplytic (diploid) genome (Heslop-Harrison, 1978) and the problem has been a matter of high speculation.

Vasil and Aldrich (1971) have reported the occurrence of pronounced invaginations and evaginations of the nuclear envelope during the early tetrad stage, indicating vital nucleo-cytoplasmic exchange at the time of patterning and the possibility of microspore nuclear involvement in the synthesis and/or transport of pollen wall precursors. Similar observations have been also made on pine microspore tetrads (Dickinson and Bell, 1970; Willemsel, 1971).
Waterkeyn and Bienfait (1970) have suggested that the special callose wall surrounding the early tetrads constitutes a hollow template or mould for the deposition of the primexine matrix and this callose seems to play an effective though indirect part in the establishment of the very first exine patterning. It is clear that the callosic deposits of the special wall do not play any active role. Callose is a dead, extra cellular secretion which may be locally accumulated by the activity of the living cytoplasm and according to a pre-established programme. This hypothesis needs actual experimental proof (Vasil, 1971).

However, many experimental evidences support the concept of the control of exine pattern by microspore mother cell (sporophyte) genome. It has been realised that the study of the development and morphology of pollen grains of hybrids and their parents offers a means of investigation of the genetic control of exine patterns in the sense that the study gives clues for the relative roles of sporophytic and gametophytic compliments in controlling pollen exine characters. In this connection, it may be pointed out that segregation of characters takes place during meiosis and its immediate
segregational products are pollen grains and megaspores. As is true of all other characters, pollen characters are also controlled by genes as is clear from Demerec's classical work on maize heterozygous for starch and waxy gene pair. The segregation is apparent in pollen grains as the grains containing starchy gene, stain blue with iodine, while those containing waxy gene, stain red. The proportion of the two types is 1:1 (Sinnott, Dunn and Dobzansky, 1958). The most important characteristic is that in pollen grains such segregation can be observed one generation in advance. This is also true of xenia, a phenomenon associated with endosperm colour due to the influence of pigment carrying gene in the pollen grains. Because of double fertilization, xenia appears one generation in advance. There are also cases such as the colour of the pollen grains where the pigment is in the microspore protoplast, one might expect a direct haploid control of pollen and hence in suitable hybrids, segregation might be expressed by different coloured pigments in one and the same anther (c.f. Godwin, 1968). Thus, after hybridization such segregation takes place in $F_1$ generation itself in the pollen grains (gametophyte) as against the case in sporophyte, where segregation takes place in $F_2$ generation.
Therefore, it has been argued that in the study of the pollen morphology of hybrids and their parents, gametophytic control would be indicated by some segregation of exine characteristics towards the condition in the two parental species, while sporophytic control would be revealed by the production of a uniform type. With the above view in mind, some studies have been carried out in recent years (Henderson, 1972; Quiros, 1975; Ravi Kumar, et al., 1978).

In the present investigation, it has been demonstrated clearly that the reciprocal tetraploid hybrids (2n=44) namely G. virescens × G. carsonii and G. carsonii × G. virescens possess striato- intertwined foveolate and pan punctate striate exine patterns respectively which are entirely new exine patterns when compared to its parents where striato fossulo-ventriculate and striato reticulate exine patterns occur in G. virescens and G. carsonii respectively, on the other hand the hybrid G. virescens × G. richmondensis is characterised by striato fossulate exine pattern with partially intertwined striae which is somewhat intermediate combining the characters of both of its parents.
Similarly in the A. sp., diploid hybrid Cv-44 x Cv-12, the exine pattern combines the features of both the parents. For example, the retipilate pattern and large isomorphous broken brochi are features of the male parent and the uni-biseriate columella islands in the muri is a feature of the female parent. In the same way, in A. belladonna triploid hybrid the reticulate exine, unbroken large brochi, distinct narrow muri, and uniseriate circular columella islands are characters of the tetraploid female parent, whereas the small brochi, loose muri are characters of the diploid male parent. Again in A. vittata triploid hybrid, the exine pattern shows the dominance of female characters such as the compound reticulum, unbroken brochi and circular columella islands, but possess a few new additional characters such as the regular shape and size of the microbrochi, straight and even muri and the fusion of columella along their full height.

Therefore, it is clear from the above data that the pollen grains of the hybrids of Gloriosa and Amaryllis possess exine ornamentation of new morpho forms which are either different from those of its parents or combine
characters of both the parents. It is necessary to point out that the above characteristic exine patterns are uniform in each material and no segregation into parental types could be observed in any of the hybrids presently investigated.

Similar observations were made by Crane (1963) for Dryopteris hybrids; by Schulze (1965) for presumed hybrid populations of Siphonostylis; by Hendersen (1972) for the hybrid Meconopsis × Cockeri; by Grant (1972) for hybrids between Zea and Tripsacum by Quiros (1975) for an intergeneric hybrid between Lycopersicon and Solanum; by Rajendra et al., (1978) for intergeneric hybrids of Hordeum, Secale, and Triticum; and by Ravi Kumar et al., (1978) for an intervarietal hybrid of Cajanus cajan. There are also reports of the dominance of either female characters as in the pollen of Erythrina hybrid (Nair et al., 1977) or male characters as in the pollen of an intergeneric hybrid Cotyledon grandiflora × Echeveria sp., (Mamatha Rao et al., 1979).

All the above reports record the occurrence of a uniform type of pollen morphology in the hybrid pollen. There is no record of any instance of segregation of pollen type with regard to exine characters in any one
tetrad or anther (Godwin, 1968). However, the occurrence of male (high %) and female (small %) pollen types have been recorded in the hybrids of Corchorus, Tagetes and Cajanus (Srivastava, 1976 a & b, 1978) and in the hybrid Amaranthus spinosus x dubius (Srivastava et al., 1977). Khoshoo (1978) comments on the above observations of Srivastava that the significance of the above ratios is not clear in terms of the genetic constitution. Therefore, it appears that the segregation of pollen morphotypes into two parental types is yet to be established beyond reasonable doubt.

Therefore, the uniform occurrence of new pollen exine morpho forms in the hybrids, different from their respective parents in the genera Gloriosa and Amaryllis and the absence of segregation into parental exine morpho forms supports the concept of Heslop-Harrison (1968,1971), that the exine pattern is controlled sporophytically by the diploid compliment of the pollen mother cell. Similar conclusions have been arrived at by Henderson (1972), Quiros (1975), and Ravi Kumar et al., (1978) based on their study of pollen morphology of parents and hybrids.
The studies on the development of irregular pollen have shown that typical exine development takes place in reduced, unreduced, and tetrakaryotic cells as well as in atypical and abortive spores (Wodehouse, 1935; Drahozwal, 1936; Rogers and Harris, 1969; Mepham, 1970; Pal and Khoshoo, 1972; Heslop Harrison, 1972; Tara and Namboodiri, 1974). Thus it is clear that exine controlling factors are effective in the microspores irrespective of their size of chromosome content. The present study of the pollen morphology of the sterile diploid hybrid *G. superba* × *G. lutea* (*2n = 22*) has also shown that normal exine formation takes place in all the pollen grains of the above hybrid even though there are several meiotic abnormalities, resulting variations in chromosome content (more or reduced) and also various apertural forms, some times dyads or even unreduced meioocytes developing into pollen grains. Thus all the above studies suggest that intervention of the spore nucleus is not required for exine pattern formation and that the cytoplasm already carries the basic programme for exine pattern before the nuclear divisions and that the programme can be carried through whatever the fate of the microscope nuclei.
There are many instances in literature indicating the association of the dimorphism in pollen (pollen size to exine pattern) with heterostylous flowers (see, Kohler, 1973 & 1976, Ornduff, 1970; Punt et al., 1974 etc). The pollen differences associated with heterostyly behave as though they were determined exclusively by the diploid parental genome (sporophytic), since all the spores in an anther share the same exine features (Heslop-Harrison, 1968). In Primula melacoides in which self incompatibility is sporophytically controlled, Pandey and Troughton (1974) observed a strong relationship between the dimorphic sculpturing of the pollen grains in pin and thrum flowers and the incompatibility system and indicated that the dimorphic sculpturing of the pollen grains is also sporophytically controlled.

The above records show that many experimental evidences based on various approaches, support the concept of sporophytic control of exine patterning. However, when exactly the genes concerned with exine patterning are transcribed from the sporophytic genome and in what form the templates are stored in the cytoplasm of the microspore, are not clearly known. However, considerable progress has been made in the last few years in understanding the cellular control of wall patterning. Heslop-
Harrison (1968) has observed that in Lily, the primexine formation begins soon after the cleavage following meiosis II, a normal ribosome population is not yet fully restored in the spores at this time, but the polyribosomes do become associated with the sites of future probaculae and thus it appears as if the very earliest pre occupation of the spore cytoplasm were to establish a protein synthetic system concerned with these aspects of wall growth. Heslop-Harrison (1968) has suggested that the read out of exine information precedes the meiotic division and so is accomplished in the diploid PMC. The information is carried through meiosis either in the form of long lived messenger RNA or in the form of already synthesized special protein moiety. Apparently, these are retained in the cytoplasm enclosed by double membrane units during meiotic prophase which remains free from the general clean up taking place in the remaining part of cytoplasm (Dickinson and Heslop-Harrison, 1977).

Still it is not clearly understood how the biochemical information is translated into the morphogenetic control exerted by the cytoplasmic membranes. Perhaps one of the ways of understanding the mechanisms is to
probe the structural and biochemical differences at the cytoplasmic level in meiocytes which produce pollen with normal and aberrant walls.

VII POLLEN MORPHOLOGY IN RELATION TO TAXONOMY AND EVOLUTION

A volume of literature is available on the importance of pollen morphology in the taxonomy, phylogeny and evolution of plants at various levels, such as families, subfamilies, tribes, genera, species and varieties (Wodehouse, 1935; Erdtman, 1965; Vishnumit, 1964; Nair, 1965a, 1966, 1970; Chanda, 1966; Van Campo, 1966). In such considerations, the germinal apertures are of primary importance and there are also other characters in which taxonomic and evolutionary phenomena are expressed. Pollen morphology also aids in distinguishing the species within a genus. The germinal apertures were taken as the basis for distinguishing the species of *Anemone* (Erdtman, 1952). The exine ornamentation is also of great significance in the diagnosis of species (Nair, 1966). The spine on the ectexine of 3-zono eolporate grains of *Abutilon* show variations in their length, tips, basal cushion etc, to be of help in
separating the various Indian species (Nair 1962b).
The variations in the aperture and eotine ornamentation have been shown to be of use in Bauhinia spp. (Nair and Sharma, 1962). In umbelliferae with 3-zono colporate pollen, the nature of the endocolpium and ectocolpium has been found to be of diagnostic value in species identification (Cereceau, 1959). Similar observations have been made with regard to the genus Citrus (Nair and Mehra, 1961). Baksi (1976) studied the pollen morphology of the species of Gluta and Melanorrhoea in relation to taxonomy and evolution within the genera. Nair (1970) discussed the principles in the trends of pollen morphological characters. Further the evolutionary significance of exine has been vividly discussed by several workers (see, Ferguson and Muller, 1976).

In the present studies on the pollen morphology of various taxa of Gloriosa and Amaryllis, SEM pictures have provided the fundamental basis for the differentiation of the taxa, although there are other characters to substantiate the differentiation based on SEM pictures. In Gloriosa, the exine surface has basically striate pattern composed of ridges (striae) and lumina (lirae).
In the various taxa investigated, the striae and lirae showed considerable variation resulting in the occurrence of various ornamentation patterns characteristic of each taxon. The striae, in the basic form may be considered as an even, straight ridge with no inter-connections thereby having uninterrupted lumina. In other cases, the ridge may be uneven and become dissected and interconnected with adjacent striae on one hand, or become closer and fused thereby reducing the size and depth of the lumina. In yet other cases, the striae are in two tiers and produce an intertwined or criss cross pattern. In some cases, the striae are punctate. These differences have served to provide a basis for differentiation of the taxa of *Gloriosa* as given below (see also Text fig.2).

1. Exine surface with plain striae,
   -- (Hypothetical).

2. Exine surface with zig-zag and dissected striae,
   -- *G. richmondensis* (4x).

3. Exine surface striato-fossulate-ventriculate or vermiculate,
   -- *G. virescens* (4x).

4. Exine surface striato- reticulate,
   -- *G. superba* (2x)
   -- *G. carsonii* (4x).
5. Exine surface with partially intertwined-fossulate striae, -- *G. virescens* × *G. richmondensis* (4x).

6. Exine surface striato-intertwined foveolate,

   -- *G. virescens* × *G. carsonii* (4x).

7. Exine surface striato-criss-cross foveolate,

   -- *G. magnifica* (8x).

8. Exine surface with punctate intertwined striae,

   -- *G. carsonii* × *G. virescens* (4x).

9. Exine surface with punctate striae,

   -- *G. superba* (8x).

10. Exine surface striato-undulate-punctate,

    -- *G. lutea* (2x).

The above ornamentation forms do provide the basis for gaining an understanding of the morphological evolution of the exine ornamentation in the taxa investigated (Text fig. 20). The plain striate form is the basic one from which two lines marked by the single tier forms and double tier forms have evolved. Along the single tier line, the first stage is marked by the dissected and zigzag striae form, from which have evolved the punctate and non-punctate lines respectively. The non-punctate line seems to have become resolved into two lines of evolution namely, the striato-fossulate-ventriculate line.
and the striato-reticulate line. The punctate line is constituted of three forms namely, punctate from which have evolved the striae punctate and striato undulate punctate forms. Along the double tier line, partially intertwined foveolate, intertwined foveolate and criss-cross foveolate forms have evolved.

In the case of *Amaryllis* the exine surface is basically reticulate with muri having various stages of union of pila heads leading to a complete muri condition, in addition to which, are muri with small luminar areas (microbrochi). It has been possible to build a scheme of morphological evolution of exine pattern starting from the retipilate condition with connate columella islands to those with full muri beset with luminar areas through various stages of fusion of columella heads (see Text fig.32). From the retipilate form two lines namely simple retipulate forms and compound reticulate forms have evolved.

The data on the exine ornamentation of the cyto-types, species and hybrids of *Amaryllis* have provided a basis for their differentiation which is described as follows:
1. Sub retipilate and isobrochate exine with large brochi having various stages of fusion of pila heads. ---- *A. vittata* (2x).

2. Retipilate (A) and isobrochate exine pattern with large brochi having uneven murus margins and greater fusion of columella heads, ---- *A. sp. Cv-12* (2x).

3. Retipilate (B) and isobrochate exine with large brochi having plain murus margins and heteromorphous columella islands in the lumina, ---- *A. sp. Hybrid Cv-44 x Cv-12* (2x).

4. Retipilate (C) exine with dominantly small brochi and even muri, ---- *A. belladonna* (2x).

5. Simple reticulate (A) and isobrochate exine with large brochi, ---- *A spl. Cv-44* (2x).

6. Simple reticulate (B) and heterobrochate exine with large and small brochi in almost equal proportions, ---- *A. belladonna* (3x).

7. Compound reticulate (A) exine, dominantly large brochate with few small brochi here and there, ---- *A. belladonna* (4x).

8. Compound reticulate (B) exine with rows of microbrochi separating the megabrochi of regular and size, ---- *A. vittata* (3x).

9. Compound reticulate (C) exine with rows of microbrochi surrounding the megabrochi of irregular shapes and sizes, ---- *A. vittata* (4x).
Apart from the exine surface morphology, there are also other characters such as the occurrence of shape morphotypes, pollen size, including the effect of acetylalysis on $E$ and $E_1$ diameters etc., but the exine ornamentation being a true projectile of the fundamental differences, there is hardly any purpose served in collating the above data with less important characters.

In a recent analysis of shape morphotypes, Nair and Chaturvedi (1978) observed the occurrence of the spheroidal and the elongate forms as a regular feature in the taxa of angiosperms having monocolpate apertures, the degree of differences between the shape forms has been found to be of taxonomic and phylogenetic significance. Considering the morphological evolution of apertures correlated with that of shape classes, the elongate forms with a furrow is the normal rule in the monolete spore form of pteridophytes. The same holds good with the pollen grains of the present day cycadales. It is therefore imperative that the elongate form is more primitive and that the spheroidal one has appeared later in the line of monocolpate taxa of angiosperms. In considerations of morphological evolution of shape classes among the monocolpate taxa of angiosperms, the higher
frequency of elongate form may be considered to project
the primitiveness while the higher frequency of spheroi-
dal represents advancement.

In the present study, both spheroidal and the
elongate forms do occur in the various taxa of Gloriosa
and Amaryllis. The elongate form is constituted of
grains with a higher or lower E diameter according to
which they are designated as ellipsoidal or spindle
shaped. The spindle shaped grains as a rule, are mor-
phologically sterile. In general, the ellipsoidal grains
constitute the dominant type in the taxa of Gloriosa,
while the spheroidal grains occur in small percentages
(ref. Table V and Text fig. 22). The spheroidal grains
occur relatively more (14.5 - 22.0%) in the diploid
taxa such as G. superba, G. lutea and their hybrid
G. superba x G. lutea while in other taxa with higher
ploidy levels (4x and 8x), the spheroidal grains are
absent in all except three taxa where they occur in
small percentages (5.0-7.0%). The pollen of G. richmon
densia and the Hybrid G. virensens x G. carsonii are
constituted of only ellipsoidal grains which shows that
the two taxa are mostly primitive among the taxa of
Gloriosa presently studied and the rest of the tetraploid and octoploid taxa appear to be more primitive than the diploid taxa with regard to the occurrence of shape forms. On the whole, the high dominance of the ellipsoidal form may perhaps be considered to suggest the position of the genus Gloriosa at a lower phylogenetic level within the family Liliaceae as suggested by Nair and Chaturvedi (1978).

It is is also significant to point out that all the grains (100.0%) are ellipsoidal in G. richmondensis in which the striation is of the fundamental 'plain striate' type, while in the most advanced striatopunctate form as in G. superba (8x) the ellipsoidal grains are as low as 51.0%. The above correlation may be considered to suggest that the higher frequency of ellipsoidal grains do mark the primitive level of evolution and the lower frequency of the type marks a higher evolutionary level.

On the other hand, in the taxa of Amaryllis any one of the three shape forms are dominant in each taxon. However, in general in A. belladonna hybrid group the ellipsoidal grains are dominant (48.0-59.0%) whereas in A. vittata hybrid group, the spheroidal grains are
dominant (39.0-58.0%) (except an *A. vittata* hybrid).

Nonetheless, the spheroidal grains do occur in relatively more percentage in the taxa of *Amaryllis* than those of *Gloriosa* (ref. Table X and Text fig.34). The above data suggest the position of the genus *Amaryllis* at a higher phylogenetic level within the family Amaryllidaceae. Besides, the taxa of *A. belladonna* appear to be more primitive than the rest of the taxa presently studied.

In *Gloriosa*, the furrow form of aperture occurs in both the elongate and spheroidal grains, but in the latter, the central region of the furrow is wide. The same holds true for *Amaryllis* also. However, in the diploid interspecific hybrid *G. superba* × *G. lutea*, the spheroidal grains possess basically circular aperture with an operculum which condition is of an advanced level in evolution as such situations occur in advanced families like grasses (Porate). Nair and Sharma (1963) have observed the occurrence of spheroidal grains with pore like (megasporat) apertures in *Cocos nucifera* and further Sharma (1967) observed a similar condition in several monocot families.

The data with regard to B diameter (Uo) of ellip-
soidal grains shows that the diploid and tetraploid taxa of *Gloriosa* are more or less nearer to each other suggests
that the genus as a whole is a very natural one and this fact is also further substantiated by the occurrence of the basic striate pattern in the genus. On the other hand, in *Amaryllis*, the E diameter of ellipsoidal grains (Uc) vary from 58.0 - 62.5 \( \mu m \) in the diploid taxa, 60.7 - 65.6 \( \mu m \) in the triploid taxa, and 68.4 - 75.7 \( \mu m \) in the tetraploid taxa which shows increasing trend in pollen size with increasing ploidy level.

The increase in E diameter due to acetolysis of ellipsoidal grains is higher in the basal species namely *G. richmondensis* and *G. virescens* and lesser in more advanced ones such as *G. carsonii*, *G. superba* and *G. magnifica*. Further, it is of significance to point out that the same in the hybrids has been less (+ 21.0 to + 27.5\%). Apparently, the plain striate condition allows distention by being not restricted by cross bars (striae bridges), while in others, the distension is brought down by more complex striations which include both the two tier striae and the bridging of the lirae. However, in *Amaryllis*, the tetraploid taxa, showed more increase in E diameter of ellipsoidal grains than the diploid and triploid taxa.