1) The myrtalean group of families is primarily characterized by two distinctive wood anatomical features – the combination of bicollateral vascular bundles in the primary stem and vestured pits in the secondary xylem. Plants are mostly trees and shrubs and also herbs in a few member families.

2) Palynologically the order is very poorly investigated, great bulk being based on Light Microscopic examination, that too almost exclusively on alien taxa. The Indian group is almost uninvestigated.

3) The present study concerns 110 taxa (108 species) belonging to 42 genera representing the six families *sensu* Bentham and Hooker distributed in the South Indian region, mostly Kerala. The families studied are Rhizophoraceae, Combretaceae, Myrtaceae, Melastomaceae, Lythraceae and Onagraceae; and in addition one genus from Haloragaceae (included in the Myrtales in a later classification).

4) Polleniferous materials were collected from live plants from different localities of their distribution in the region. In recording the data, the
taxa are arranged according to Bentham and Hooker as contained in the Flora of British India by Hooker, which is the only comprehensive floristic work on Indian plants.

5) Morphological study of pollen grains was carried out by Light Microscopic (all taxa) and Scanning Electron Microscopic (62 species) observations. The pollen preparations were made by the acetolysis method following Erdtman (1952) and Nair (1960).

6) The exine of pollen grains embodies the morphological characteristics broadly categorized into (a) aperture (b) exine ornamentation (c) exine strata and (d) pollen size and shape in the order of importance. For pollen description the terminology proposed by Nair (1966) was followed. Pollen size was determined based on measurements of a random sample of 100 grains in each taxa. Pollen shape categories were determined following Walker and Doyle (1975) based on P/E x 100 values.

Salient features of pollen morphology (family wise) is briefly highlighted as under:

i) **Rhizophoraceae**: 7 species in 5 genera.

Aperture: 3-zonocolporate, with rectangular lolongate endoaperture. Endocolpium fused in species of *Rhizophora* and *Bruguiera*. Exine sculpturing is predominantly punctate; and
scrobiculate in one species. Pollen shapes varied from subprolate to prolate-spheroidal and oblate-spheroidal. High degree of homogeneity exists in pollen features.

ii) **Combretaceae:** 12 species in 6 genera.

Aperture: 3-zonocolporate, heterocolpate, endocolpium lolongate/circular; exine sculpturing rugulate, psilate, rugulate-verrucate, granular, reticulate. Pollen shape: prolate-spheroidal and oblate-spheroidal.

iii) **Myrtaceae:** 34 species and 11 genera.

Aperture: basically 3-zonocolporate and also 3,4,5- colporate; endoaperture faint or lolongate. Members exhibit syncolporate, colporate, syncolporate, parasyncolporate, longicolpate or brevicolpate apertures; exine sculpturing varied (psilate, granulate, areolate, rugulate, rugulate-verrucate, foveolate, macroreticulate). Genera *Barringtonia, Careya* and *Couroupita* stand out from the rest showing syncolpate, syncolporate or colporate apertures. The macroreticulate and granulate exine highly thickened polar cushions, costae colpi and apertural verrucae are also distinctive features in them. Pollen shape: oblate in most species, peroblate, prolate-spheroidal, prolate and spheroidal grains also occur.
iv) **Melastomaceae**: 25 species and 8 genera.

Apertures: 3-4-zonocolporate, heterocolpate with pseudocolpi in all except one with intercolpar concavities. Endoaperture: lalongate, faint or circular. Exine sculpturing varied (foveolate, rugulate, rugulate-fossulate, striate, granular, rugulate-granular, psilate-granulate, matted). Shape: varied (sub-prolate, prolate-spheroidal, oblate-spheroidal, spheroidal, sub-oblate).

v) **Lythraceae**: 19 species 9 genera.

Pollen morphology is highly heterogeneous with regard to aperture, endoaperture, exine sculpturing and shape.

Aperture: basically 3-zonocolporate, 3,4-colporate in a few, 3,4-syncolporate and 3-porate in one genus; endoaperture circular in majority, lalongate in a few and lolongate in one genus. Exine sculpturing highly variable (striate, rugulate, rugulate-psilate, granulate-rugulate, verrucate-rugulate, granulate, pebbly). The genus *Cuphea* stands out with syncolpate aperture, lolongate endoaperture and oblate shape; and also *Sonneratia* having porate aperture, prominent meridional ridges, apertural fields and psilate polar cushions.
vi) **Onagraceae**: 10 species and 3 genera.

The pollen grains are outstanding in Myrtales in possessing tetrads/polyads, presence of large central body and protruding (aspidote) apertures, presence of viscin threads on the exine, brevicolpate condition.

Aperture number varies (3 to 4) in *Ludwigia* and (2 to 5) in *Fuchsia*. Exine sculpturing predominantly rugulate; the genus *Trapa* is unique with prominent meridional ridges formed by folding of exinous material which passes over the colpi in contrast to other members.

8) **Special pollen features**

i) Heterocolpate: Presence of subsidiary colpi (Pseudocolpi colpi) or intercolpar concavities in addition to colpi.

ii) Pseudocolpi colpi (subsidiary colpi) occur in all members of families studied such as Combretaceae and Melastomaceae and in a few species of Lythraceae and intercolpar concavities in 2 genera of Myrtaceae and one in Melastomaceae. Pseudocolpi are not actual apertures, but conspicuous colpus-like thin parts of exine which is isomerous with aperture number in most cases and in a few double the number of aperture. They are harmomegathic in function.

iii) Intercolpar concavities are large in size than the pseudocolpi, and functionally similar.
iv) Meridional ridges: they occur in species of *Ludwigia* and *Trapa* (Onagraceae) and *Sonneratia* and *Lagerstroemia* (Lythraceae). They are thickenings of exine except in *Trapa* where it is formed by the folding of the exinous material and pass over the colpi and fused at the polar region in contrast to those found elsewhere in Myrtales where they alternate with the colpus.

v) Aspidote: These are conspicuously protruding aperture (papillose) characteristic of members of Onagraceae. In *Trapa* this is dome-shaped.

vi) Viscin threads: These are sporopollenin containing, long, flexible, nonelastic fibres basically located on the surface of the pollen grain, characteristic of members of Onagraceae.

vii) Longicolpate: The colpi are longer than the distance between their apices and poles.

viii) Syncolpate: These are colpi either straight without becoming wider or curved, meeting at the poles and forming a triangular area at the poles.

ix) Parasyncolpate: Here the colpi bifurcate at the poles and their branches meet and outline a triangular apocolpium.

x) Brevicolpate: Grains with the colpus length equal to or less than the distance between their ends and the poles.
9) The results of palynological study carried out are discussed along with available data on the group in relation to aspects such as pollen morphological analysis, pollen aperture evolution, palynology in relation to the systematics of the order, interrelationships, affinities and evolution of the Myrtales.

i) Rhizophoraceae: have tricolporate, radially symmetrical and isomerous pollen grains in all species. The colpi are long with smooth or granular membrane. Endoaperture is characteristically rectangular-lalongate; the endoapertures fused in *Rhizophora* and *Bruguiera*. The exine sculpturing is predominantly punctate. The family is stenopalynous and more or less homogeneous palynologically. The fused endoaperture of Rhizophoraceae has no counterpart in Myrtales.

ii) Combretaceae: very little palynological study on the family is known earlier. Basically Combretaceae pollen grains are tricolporate (rarely tetracolporate), heterocolpate, radially symmetrical and isopolar; endoaperture predominantly lalongate; mesocolpial extensions over the endoaperture noticed in species of *Terminalia* and *Calycoperis*. The exine sculpturing in the family is highly variable. This is predominantly rugulate, rugulate-verrucate, granular, reticulate and psilate. Pollen shape is also
variable. Earlier workers have pointed out gross similarity between Combretaceae and Melastomaceae and also to some members of Lythraceae and Penaeaceae. They also indicated several distinctive groups primarily based on the presence or absence of the pseudocolpi and exine sculpturing. But such a distinction could not be made out from the present data except however the heterocolpate pollen grains of Combretaceae was found to have gross similarity with those of Melastomaceae.

Myrtaceae: In general Myrtaceae pollen is tricolporate, radially symmetrical and isopolar or heteropolar. In polar view they are triangular, goniotreme, with straight or curved sides and with acute or obtuse corners. The number of apertures varied from 3 to 4; endoapertures lalongate, faint or circular; intercolpar concavities present in some species. Based on nature of colpi three pollen types could be recognized such as (i) longicolpate (2) syn or parasyncolpate and (3) brevi or brevissimicolpate . Exine surface ornamentation is found to be varied.

Three genera (Barringtonia, Careya and Couroupita) have pollen quite different from other Myrtales and other core Myrtales. These three genera could be categorized into 2 groups based on pollen morphology. The first group (Barringtonia and
Careya) with larger pollen, macroreticulate exine sculpturing and syncolpate or syncolporate pollen and the second group (Couroupita) with smaller grains, colporate aperture and granulate sculpturing.

The Myrtaceae pollen does not appear to have any close similarities with other core families of Myrtales except superficial similarity with Onagraceae (shape of the grains as well as short colpi). Some similarity also exists with Lythraceae through the genus Cuphea.

iii) Melastomaceae: The pollen grains are generally monads but tetrads reported earlier. The grains are tricolporate (also tetracolporate in 2 genera), radially symmetrical, isopolar and spheroidal to subprolate in equatorial view and circular, hexagonal or triangular in polar view. Endoapertures lalongate, faint or circular; mesocolpial extensions over the endoaperture noticed in a few species. The exine sculpturing is variable. Based on the present data two groups could be recognized such as, (1) heterocolpate with pseudocolpi and (2) heterocolpate with intercolpar concavities. A third group was recognized by earlier workers with neither pseudocolpi nor intercolpar concavities.
iv) Lythraceae: the available pollen morphological data including the present indicate that Lythraceae have the most diverse pollen in the Myrtales. Much of the diversity concerns the aperture system; most genera with tricolporate grains, heterocolpate with six subsidiary colpi (4 species), grains with meridional ridges alternating with apertural fields, grains with syncolporate apertures and triporate apertures.

Diversity is also evident in exine sculpturing, pollen size and shape. Pollen diversity occurs at the intrageneric level as well (as in genus *Cuphea*) which is remarkably eurypalynous with great variation at sectional, subsectional, specific and varietal as reported by earlier workers who have recognized several structural pollen types on a harmomegathic stand point.

v) Onagraceae: the Onagraceae pollen studied have 3-zonoaperturate condition; also with variation in aperture number such as 2,3,4 or 5 in species of *Fuchsia* and 3 or 4 in *Ludwigia*. The grains are brevicolpate in *Ludwigia* and porate in *Fuchsia*. The characteristic pollen morphological attributes are large central body, apertural protrusions, viscin threads with different surface patterns and tetrads or poyads in some members.
The genus *Trapa* is distinguished by the 3-zonocolpate grains with three prominent meridional ridges and apertures protruding and swollen as elongated domes. *Trapa* bears unique features quite different from the rest of the Onagraceae.

Haloragaceae: Pollen of one taxon (*Myriophyllum* species) has been studied; the grains are isopolar, aspidote and crassimarginate with spinulate exine sculpturing. These features seem to deviate from core Myrtales especially due to the spinulate ornamentation.

10) Based on aperture character plant taxa, is broadly divided into two groups (i) stenopalynous and (2) eurypalynous. In the former the different sporomorphs are of the same basic type while in the latter they are of more than one type. Of the six myrtalean families, *sensu* Bentham and Hooker, all except Rhizophoraceae are eurypalynous in varying degrees. As far as aperture system is concerned the Myrtaceae are the most eurypalynous followed by Lythraceae and Onagraceae. Myrtaceae possess 3-zonosyncolpate, 3,4,5-zonocolporate, 3,4-zonosyncolporate and 3,4-zonoparasynocolporate grains while Lythraceae possess 3-zonoporate in addition and so also Onagraceae which have 2-zonoporate and 3,4,5-zonoporate in addition to 3,4-zonocolporate. Combretaceae has been the least eurypalynous family.
11) Morphological evolution of pollen grains: A tentative scheme of evolution of aperture morphoforms in the Myrtales is presented according to Nair’s order of aperture evolution. According to this scheme, the most primitive 3-colpate condition occurs only in Myrtaceae and Onagraceae while the 3-colporate in all the six families together with 4-colporate in Myrtaceae, Lythraceae, Onagraceae, Combretaceae and Melastomaceae. The most advanced porate condition (2 to 5-porate) occurs in members of the Onagraceae and 3-porate in one genus of Lythraceae. It appears that aperture evolution has most operated in the Lythraceae followed Onagraceae in which 3 to 4-colporate and 2,3,4,5-porate conditions occur. The more or less intermediate aperture condition may be noticed (syncolporate/parasyncolporate) in Myrtaceae and Lythraceae.

12) Systematic considerations: great deal of controversy exists between and among the various systematic treatments of the order Myrtales. Bentham and Hooker’s treatment is the most comprehensive among the classical, according to which the order comprises six families such as Rhizophoraceae, Combretaceae, Myrtaceae, Melastomaceae, Lythraceae and Onagraceae. This composition has been subjected to significant degree of shuffling and reorganization in subsequent modern treatments.
In the families of the Myrtales *sensu* Bentham and Hooker, the most reorganized are Rhizophoraceae, Lythraceae and Myrtaceae. A modest attempt is made to view the merits of the major revisionary treatments of the order, in the light of evidences from available palynological information.

Of the various modern treatments the most comprehensive and largely accepted is the one of Dahlgren and Thorne which include 14 families in the Myrtales, Onagraceae, Trapaceae, Lythraceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomaceae, Psiloxylaceae, Heteropyxidaceae and Myrtaceae.

Rhizophoraceae: The main controversy is regarding the inclusion of the family Rhizophoraceae in the order. The questionable monophyly of the family is further complicated by the debatable placement of Anisophylleaceae in the family. The lack of vested pits and internal phloem in members of Rhizophoraceae argues against the inclusion of the family in the Myrtales, despite the palynological attribute tricolporate pollen consistently present in the family.

There are suggestions of ordinal rank (Rhizophorales) or a place in the Cornales to this by certain modern taxonomists. Although members of Rhizophoraceae possess tricolporate pollen as is very common in the other
myrtleaceous families, the possession of punctate ornamentation in the
Rhizophoraceous members which is seldom known in any of the
myrtleaceous taxa, together with another palynological feature, the fused
endoapertures that are rectangular-lolongate, both totally unknown in the
core families of the Myrtales swings heavily against a place for
Rhizophoraceae in the myrtleaceous complex, despite the solitary, seemingly
favourable attribute of tricolporate pollen.

Combretaceae: is one of the large families of the Myrtales, uniformly
treated as a core member of the order in almost all taxonomic treatments,
both classical and modern. The characters available from various
biological systems in pollen morphology show a high degree of
resemblance with other sister families of the order. The heterocolpate
pollen grains of Combretaceae show broad similarities to Melastomaceae
and Lythraceae. All known treatments agree in considering Combretaceae
as a coherent group in the myrtleaceous complex.

Myrtaceae: is characterized by tricolporate often syncolporate grains
lacking pseudocolpi except for Psiloxylaceae and Heteropyxidaceae
centred on two alien genera *Psiloxylon* and *Heteropyxis* (included in
Myrtaceae) the family apparently has no connection with other families in
the Myrtales.
The taxonomic rank of *Psiloxylon* and *Heteropyxis* has long been debated as to whether these two should be treated as part of Myrtaceae or as separate families.

Myrtaceous pollen does not appear to have any close similarity to other core Myrtales except for some superficial similarity existing between pollen of *Cuphea* (Lythraceae).

Genera *Barringtonia*, *Careya* and *Couroupita* that belong to Myrtaceae *sensu* Bentham and Hooker has been subsequently given a separate identity under the family hold of Lecythidaceae. The observation of syncolpate, syncolporate and colporate pollen grains which is in consensus with earlier reports together with the peculiar exine sculpturing (macroreticulate) appears to suggest the separation of these genera under a family cover Lecythidaceae earlier suggested by modern taxonomic treatments.

Melastomaceae: has been treated as a major core family of the Myrtales in all taxonomic treatments of the order. The family possesses stable characteristic states with respect to various biosystems including palynology. Palynological evidence is very much in favour of treating Melastomaceae and Memecylaceae as a comfortably single family as against their suggested segregation on other grounds.
Lythraceae: has been subjected to great deal of taxonomic restructuring based on various disciplines including palynology. Infrageneric variation in palynologic characters is remarkable in *Cuphea*.

Major deviation from the taxonomic treatment of Bentham and Hooker is the recognition of familial and subfamilial rank given to genera such as *Sonneratia*, *Duabunga* and *Punica*. Present palynological results appear to suggest that *Sonneratia* and *Punica* stand out from the rest of the genera of Lythraceae and more so *Sonneratia*; hence on palynological grounds familial and subfamilial rank assigned to them appears very much justified. Moreover the palynological distinction in *Sonneratia* appears to be strong enough to this being given a familial rank rather than subfamilial.

Onagraceae: this is a very distinctive family, on several grounds from other Myrtales whose relationships have been widely debated. The distinctiveness of Onagraceae is supported by several morphological synapomorphies pertaining especially to pollen morphology characterized by viscin threads and unique exine sculpturing.

The genus *Trapa* has been included in the Onagraceae by Bentham and Hooker. The pollen grains of *Trapa* are triangular and have three meridional ridges. In view of the distinction of pollen grains from other Onagraceae, (absence of viscin threads, the meridional ridges formed by
the exine folding) appear to provide palynological support for the separation of *Trapa* from Onagraceae and family rank assigned to the genera.

Interrelationships, evolution and affinities of Myrtales: based on a constellation of character attributes it has been pointed out that myrtalean ancestors were probably woody plants with alternate or opposite leaves with teothy margin, stem with bicollateral vascular bundles and vessel elements with vestured pits. It is also held that the ancestral forms of myrtales would have been similar to certain extant Lythraceae. In a cladistic presentation of the probable evolution of Myrtales there is a contention that myrtalean-ancestors are represented in Psiloxylaceae, Heteropyxidaceae and Myrtaceae.

The great concordance of pollen morphology of Psiloxylaceae, Heteropyxidaceae and Myrtaceae suggest that this rather peculiar type evolved from proto-myrtaceous ancestors and later gave rise to superficially simpler kinds. The kind of pollen known in Cretaceous is suggestive that this group of families may have differentiated from the myrtalean ancestors very early.

Onagraceae seem to have deviated rather strongly from other Myrtales, and probably may have evolved as a later evolutionary line at an early stage.
It is likely that families such as Trapaceae would have evolved from an Onagraceous evolutionary line. The pollen grain shape and pollen wall structure of Onagraceae apparently corroborate this. An alternative is that Onagraceae was derived from protolythraceous ancestors.

It is possible that the characters associated with the pollen grains of Onagraceae along with many other distinctive features may be suggestive that the family was derived early from ancestral Myrtales.

The remaining families of the Myrtales sensu Dahlgren and Thorne form a coherent group, most families being characterized by heterocolpate pollen grains with pseudocolpi. It is likely that pseudocolpi may have evolved along several phyletic lines within the Myrtales.

It is possible that *Trapa* may have diverged strongly from other Myrtales and other plausible ancestral types.

Oliniaceae agree with Combretaceae in several respects. The two unigeneric families Alzateaceae and Rhynchocalycaceae share a number of wood anatomical characters which make them closely allied.

The families that are allegedly related to myrtales are Thymelaeaceae, Haloragaceae, Rhizophoraceae, Lecythidaceae, Elatinaceae etc. The consensus view is that Haloragaceae comprises a fairly isolated family although possessing a number of myrtalean attributes. The porate pollen
grains and spinulate exine may be suggestive that the family is not strongly allied to Myrtales.

Concerning the relationships and affinities of Myrtales with other orders, there is no agreement. However, it is generally agreed that the order is more or less related Rosiflorae including Rosales and Saxifragales.

Numerous studies (morphological, anatomical, embryological, biochemical, palynological, phytochemical and molecular) has been conducted by a host of workers on the Myrtales and yet a convincing consensus concerning the interrelationships among the families of the order and its phylogeny and evolution and its affinities remain elusive.

......ROGER......