Sporne (1977) has reviewed the various methods employed to decide whether a character is primitive or advanced. Stevanov (1980) has listed certain criteria to be used to assign the evolutionary polarity of character-states.

On the basis of correlation of character-states Thanikaimoni (1970) has brought to light several phylogenetic trends in Palmae. Similar approach has been recently made for the Berberidaceae by Necham (1980, 1981). As for Theales, such a study seems to have been made only for the small family of Sarcolaenaceae (Straka 1963, 1964, 1971). The present study is the first major attempt to ascertain the phylogenetic trends within the Clusiaceae s.l. The various character-states of the leaf, flower, androecium, gynoecium, fruit and pollen found in the different genera are first arranged in hypothetical sequences which are then assessed in the light of the correlation of different character-states.

As most of the fossil pollen grains and leaves assigned to Clusiaceae are not distinct enough to make a categorical statement on their generic-relationship, I have sparingly used the fossil data in my assessment of the phylogenetic trends in Clusiaceae. As Kuller (1981) has rightly pointed out, some of the fossil pollen attributed to this family have to be studied in further detail and compared with the palynological data presented here.
Morphological sequences

After scrutinizing the data available in the various floras and monographs cited in the bibliography and supplementing them with personal observations, especially on the characters discussed below, I have recognized the following morphological sequences.

1. 

FOLLAR SEQUENCE : alternate → opposite

2. 

FLORAL SEQUENCE

 bisexual → polygamous → unisexual

3. 

androecial SEQUENCE

a) stamens on a flat floral axis:

filaments in 10 bundles → bundles fused into a tube
filaments basally fused
→ bundles simplified to a row of "free" filaments

5 fertile & 5 sterile bundles → 3 fertile & 3 sterile bundles

stamens on a well developed floral axis:

filaments long → filaments short or absent.

4. 

GYNOEcial SEQUENCE

style : 5 → 4 → 3 → 2 → 1 → 0

5. 

CARPOLOGical SEQUENCE

Capsule → Capsular drupe → drupe

→ Capsular berry → berry

6. 

PALYNOLOGICAL SEQUENCE

A. aperture

a. type : colporate → colpato → porate

pororate

b. number & position : 3 → 4-6 meridional

4-6 global

B. ectexine

a. tectum : tectum perforate → ± imperforate → intectate

b. infratectum : granulate → rugulate → columellate

C. form :

spheroidal to prolate (equatorial to longaxial) → oblate (breviangular)

D. size : medium (25-40 microns) → large (50-100 microns)

small (15-20 microns)
CORRELATION AND POLARITY OF CHARACTER STATES AND TRENDS EVOLUTION

WITHIN THE GLAIACEAE

An assessment of the phylogenetic trends existing within the Glaiaceae is made below by correlating the tentative sequences mentioned above. I have given suitable examples to illustrate the correlations and also to explain the exceptions.

1. POLAR TREND

In Glaiaceae, the alternate leaves are always associated with bisexual flowers and colporate pollen. They are never noticed in association with porate or pororurate pollen. The species with porate and pororurate pollen are always with opposite leaves. Further the species with unisexual flowers are also with opposite leaves. Hence I consider that alternate is the primitive condition and opposite is the derived state.

It is noteworthy that in Calophyllum, sclerophyllum and Paracentra sp. (Stevens 1980a) the leaves are alternate at the seedling stage and subsequently the opposite arrangements sets in. Probably this is a case of recapitulation of primitive ancestral condition in the early ontogeny of these species.

2. FLORAL TREND

The sequence bisexual ----> polygamous ----> unisexual seems to be confirmed by the fact that the bisexual genus Hypericum has a wide geographical distribution fitting with the age and area hypothesis. To a lesser extent this may also be said of the less advanced polygamous genus Lammas, which however is restricted to tropics, whereas Hypericum has extended also to the temperate regions. In the tribe Clusiaceae and Tovomiteae of relatively restricted distribution (probably consequent to their origin after the drift of the American and Afro-Asian land masses) the flowers are unisexual.

3. ANDROECIAL

Stamens in Clusiaceae are diversified into free, basally fused, polyadelphous and monadelphous types.

According to Corner (1946) the stamens in Clusiaceae arise in a centrifugal sequence and the fasciculate stamens cannot be considered as the relics surviving from an ancestral branched stamens.

On the basis of floral anatomical studies Robson (1972) concluded that the variation of the stamens in Clusiaceae can be explained satisfactorily by the Telome theory. According to him the fasciculate st;
are primitive and the free stamens are advanced. This could be achieved by the process of union, condensation and sterilization. A similar view point was also expressed by Leins (1975) who in addition proposed a possible derivation of diplostemonous and haplostemonous condition from polyandroous androecium through cyclisation and isomerisation.

Robson (1972) has suggested that basic type for Clusiaceae is represented by diplostemonous whorl of 10 distinct fertile bundles of stamens (eg. Decaphalangium) from which other conditions might have been derived in the following lines.

Filaments fused in 10 distinct diplostemonous bundles

- bundles fused into tube
- bundles basally fused
- bundles simplified into a row of stamens with long filaments
- filaments short or absent with 4 sessile anthers arranged on the floral receptacle or on a tube formed by the fusion of the filament
- one whorl of 5 antipetalous fertile bundles and one whorl of 5 antisepalous sterile bundles → one whorl of 3 antipetalous fertile bundles and one whorl of 3 antisepalous sterile bundles.

The major of the Clusiaceae genera that show the above androecial specializations have the advanced opposite phyllotaxy.6

GYNOECIAL TREND

It appears that the ovary with five free styles represent the basic state from which single styled condition is derived through the process of fusion of the styles and by further step of the no style condition might have been realized. I find the 3–5 styled conditions represented in all the bisexual genera of the Hypericoidae and 2 genera of Bonnetioideae. Other genera of Bonnetioideae represent an exception since they are also bisexual but single-styled. This may be explained as a case of retention of basic bisexual condition and differential evolution of gynoecial characters associated with a comparable advance in androecial features. It may be noted that most of the unisexual genera of the subfamily Clusioidae have only 1 or no style. There again the 4–6 styled genera such as Tovomitidium, Faremambreae, Evettiopitis should be considered as exceptional cases wherein the primitive gynoecial trait is conserved but their floral characters evolved together with those of the androecium.

6 The genera Bonnetia, Kielmeyera, Meliania, Megaclisia, Notela, Nobakura and some species of Carissa which have advanced free filament condition associated with primitive androecial aspect seem like exception. In these cases the advanced androecial trend is associated with advanced gynoecial trend.
CARPOLOGICAL TREND

The most common type of fruit in Clusiaceae is the capsule (24 genera; the total will be 31 genera if we include the 6 genera with capsular drupe and the 1 with capsular berry) followed by the berry (14 genera) and the drupe (6 genera).

The most important functional aspect related to the structure of the fruit is its efficiency to release the seeds in a particular habitat where the taxon is present. According to Cronquist (1968) dehiscent fruit types are primitive and the indehiscent fruits have evolved many times by the suppression of the dehiscence. The most primitive type of capsular dehiscence is septicidal. Out of the 24 genera of Clusiaceae with capsular fruit 23 have septicidal dehiscence and one (Cretoxyllum) is with loculicidal dehiscence. The latter is said to be more efficient than the septicidal one and it is likely that this is a secondary trend of specialization within Clusiaceae.

All the genera with capsular fruits have the less specialised corporate pollen, which according to fossil evidence (Doyle 1966) represents a stage prior to that of pororurate and porate pollen. Several of these genera have bisexual flowers. The bisexual genera of Vigna have the advanced berry type (drupe in Evolvulus) and this is understandable because they are of recent origin and such are associated with other advanced character states like the reduction of some staminal bundle into sterile fascicles.

The presence of corporate pollen in the tribe Calophyllaceae with genera having drupaceous fruits represents an exception. Even though it has retained the primitive corporate state, the cariological advance is correlated with another evolutionary specialization namely the androecial evolution: basal fusion to simplification (free) of the staminal bundles.

The capsular drupe seem to be intermediate between the capsular and the drupe states. The capsular berry seems to represent a state in between the capsule and the berry. The capsular berry is associated with the simplified (advanced) free stamens and unisexual flowers. The capsular drupe is associated with simplified (free) or partly fused stamens.

It may be added that drupe represents a relatively less advanced state than berry since the drupaceous genera are either bisexual or polygamous (a few species of Calophyllum being exceptions).

Thus, the trend is:

Capsule → Capsular drupe → drupe
←------------------------------→ Capsular berry → berry.
PALYNOLOGICAL TRENDS

The principal palynological characteristics of phylogenetic significance are the type, number and position of the aperture and also the architecture of the non-apertural region. The form of the pollen (brevi- and longiserial) is also important (Van Campo 1966).

Aperture type: The most prevalent aperture type found is the colporate one with an equatorially elongated endaperture. From this basic type it is possible to visualize the derivation of the colporate and porate types on the one hand and the pororate on the other.

Colporate \(\longrightarrow\) pororate \(\longrightarrow\) colporate \(\longrightarrow\) porate
(simplified)

Among the fossils it is noteworthy that tricolporate condition appears earlier than the triporate condition (Doyle, 1969).

The pororate condition found in *Symposia* is associated with the advanced berry type of fruit and tubular androecium. All the porate genera are also found to have berry type of fruits and most of them exhibit also some androecial specialization. The simple apertures found in certain species of *Garcinia*, *Balboa* and *Chrysobalanus* seem to represent "simplified" apertures due to the lack of differentiation of the endapertures. This type is found only in genera with evolved type of androecium.

I have therefore grouped the simplified colporate condition found in certain species of *Garcinia* along with the porate condition in the table of distribution of character states given in page 165. It is noteworthy that similar simplification of aperture has been also reported in other families like *Icacinaceae* (Lobreaux Callen 1976) and *Leguminosae* (Guinet 1981).

Aperture number and position: The basic aperture number seems to be 3 for *Clusiaceae*. The genera with more than 3 apertures have only evolved type of fruit viz., berry. A secondary line of specialization is from meridional to global arrangement of the apertures, only when their number exceeds three. The periporate pollen are found so far only in the highly evolved *Garcinia*.

Ectexine: Two interesting trends of specialization of ectexine may be seen within the *Clusiaceae*.

- The tectum appears to be basically perforate and there is a minor trend towards the loss of perforations in a few genera of *Morombaceae* where the condition is positively associated with androecial specialization. Another
The line of secondary diversification is the loss of tegmen. This is seen in certain species of Clusioidae where it is associated with unisexual flowers and androecial specialization.

The presence of supratectal elements like spines and warts also seem to represent a derived state since they are found only in unisexual taxa.

b. The architectural trend in the organization of the infratectum appears to be as follows:

\[ \text{granulate} \rightarrow \text{rugulate} \rightarrow \text{columellate}. \]

This trend is tentatively presented here pending a thorough analysis of this trend on the basis of the TEM study of several genera.

In the light microscopic observation, the pollen grains of a number of genera of Clusiaceae appear to have a poorly differentiated, \( \text{granular} \) (not columellate) construction. I find the somewhat \( \text{granulaty} \) to \( \text{rugulate} \) infratectal architecture in the genera of Moronoboeae, which are already shown to have specialized stamens. The fairly distinct columella are seen in a few genera like Araceae, where the number of staminal bundles are reduced to five and Viola where the fruits are of the evolved berry type.

Form: There seems to be a minor trend of palynological evolution from \( \text{spheroi}\)-
dal prolate to oblate form of the pollen. The former is most common among the coporate genera whereas the pororate and porate genera are generally found to have oblate pollen.

Size: The pollen grains that fall within the size range of 25-40 microns seem to represent the basic state. Both the smaller pollen (15-20 microns) and the larger ones (30-100 microns) seem to represent derived states. The smaller ones are especially common in the \( \text{Garcinea} \) and the larger in the \( \text{Moronoboea} \). In the relatively less specialized genera of Bonnetioidae like \( \text{Ploiarium} \) (bisexual with 5 styles) the pollen are medium sized: \( p = 39 \mu; B = 31 \mu \).

As it is evident from the foregoing discussion, the polarity of the character states are established on the basis of the following independent correlations avoiding circular reasoning. The interrelations, established after the analysis of the exceptions to these multiple correlations bring out the fact that the present day taxa represent different combinations of different evolutionary tendencies.
Correlation trends:

- **Floral trend**: Correlated with geographical distribution
- **Foliar trends**: correlated with floral trends
- **Androecial trends**: correlated with foliar trends
- **Gynoecial trends**: correlated with the floral trends
- **Carpological trends**: correlated with palynological and androecial trends

**Palynological trends**: correlated with fossil history, carpological, androecial and floral trends.
EVOLUTION OF SUBFAMILIES

According to the analysis of the polarity of character states presented here, the ancestor of Clusiaceae must have had the following combination of primitive character states: 5 bisexual flower, alternate leaves, polyadelphous stamens, styles, capsular fruit and tricolporate pollen.

All these primitive traits are present in the subfamily Rhetenioideae which seems to represent a condition similar to the hypothetical ancestor of Clusiaceae. The subfamily Hypericoidae also has all but one of these primitive character states namely the opposite leaves. The evolutionary differentiation of the subfamily Clusiaceae is portrayed in three of its tribes as follows:

- a change to berry type of fruit must have resulted in the origin of the tribe Moronobae;
- a change to drupaceous fruit must have caused the origin of the tribe Calophylineae;
- a change from capsule to berry accompanied by unisexuality must have lead to the development of Garcineae.

If we study the geographical distribution of the primitive character states in Clusiaceae, all the three subfamilies seem to have originated sometimes during the early Cretaceous, when tropical America, Africa, Madagascar, India and Australia were close to one another (Smith, Hurley & Briden 1981). Each of these land masses seems to have received a share of the early Clusiaceae stock. This hypothesis gain support from the fact that there are several primitive character states still preserved especially in the pantropical Hypericeae, Calophylineae and Garcineae which have continued to be present in the tropics.

* The cytological characters could not be included here since the available data covers only 10 genera. However it may be added that according to Robson and Adams (1966) the primary basic chromosome number is 7 and the evolution has progressed by the development of higher basic numbers 8,9,10, 11 and 12) as well as by the increase in ploidy.
The tribe Moronobae is found in tropical America, Africa and Madagascar on one side and New Caledonia on the other. It appears that the Miocene pollen of Tetracolporites reported from India (Navale 1962, Ramanujam 1966) belong to Moronobae. As no palynological work on Moronobae pollen was then available, Navale and Ramanujam have tentatively attributed these pollen to Meliacae where also we find tetradcolporate pollen. However, the absence of distinct columnelles in these fossil pollen grains (Ramanujam 1966) and the presence of thick endosculptured nexine as seen in the photographs published by Navale (1962) suggests that they belong to Moronobae and not to Meliacae.

The Eocene fossil pollen of Tetracolporites osmariensis (Couper, 1953) and T. palydus (Stover & Partridge, 1962) as well as the Miocene pollen of T. sp. (Playfair 1962) may also belong to Moronobae since it seems to have the peripheral thinning characteristic of certain Moronobae. Thus Moronobae appears to have had a wide fossil distribution.

Concerning the origin of the subfamily Bonnetioidae, which is presently concentrated in tropical America with an isolated genus (Ploiarium) in Malesia, it is quite likely that this is also of Cretaceous origin. It has more primitive character states than those of Clusioidae. If the Bonnetioidae affinity of the fossil pollen described under the name Kielmeyerspollenites is confirmed it would mean that this subfamily was present in India during the Eocene period.

**EVOLUTION OF GENERA**

In the light of the present study a brief note on the evolution of the genera of Clusiaceae is given below. The genera of Bonnetioidae are dealt first and they are followed by those of Hypericoideae and Clusioidae.

**PLOIARIIUM AND ARCHYTAEA**

Among the Bonnetiaceae, Ploiarium seems to have the most number of primitive traits. The genus Archytsea represents a slightly advanced state in that it has a single style where as Ploiarium has 5 styles. Further research is needed to explain the geographical gap between these two closely related genera.
These four closely related genera together represent a state more evolved than that of Archytera in that the number of locules in the ovary is reduced to three and the staminal bundles are simplified into free filaments. In this group of genera, Bonnetia and Nebulinaria seem to have slightly smaller pollen as compared to the other two genera.

**Kielmeyeria**:  
The present study as well as that of Barth (1981) indicate that in some of the species of this genus the pollen are produced in permanent tetrad. According to Barth (1981) smooth to verrucate polyads are found in arid zone species of Kielmeyeria whereas the per-ripariate monads and polyads are frequent in the species of the humid regions. Thus, it appears that the tetrad character state represents a minor evolutionary trend linked with ecology and it is manifested at the level of species. It may be pointed out that Kielmeyeria stands out from the rest of the tribe by its orbicular to reniform embryo.

**Malurea and Marila**:  
According to Baretta Kuipers (1976) solitary vessels are primitive and multiple ones are advanced. Malurea has 'advanced' vessels and 'primitive' alternate leaves. On the other hand, Marila has 'primitive' vessels and 'advanced' opposite leaves. Thus these two genera represent each a combination of both primitive and advanced characters.

**Haplocathra and Caraipa**:  
These together constitute the tribe Caraipae of Bonnetioidae. Haplocathra with its staminal gland modified into appendages and with its libriform tracheids (Baretta Kuipers 1976) is more advanced than Caraipa.

**Hypericum and Santomaria**:  
The presence of Hypericum all over the tropics confirms its early differentiation during the Cretaceous when the tropical land masses were close to one another. It is quite likely that it reached Europe during the late Miocene when plant dispersal from Africa to Europe was possible. This genus must have had an access to the Sino-Japanese region more or less at the same time when India has acquired the present position. Eventually this genus has crossed Beringia to reach North America. Santomaria which is subtended to Central America showing close affinity with Hypericum bignoniifolius of Africa seems to have been derived along an evolutionary line different from that of Hypericum (Robbin 1981: 65162).
Vismia, Psorospermum and Harungana:

The tribe Vismiae seems to have originated in Africa from the Hypericaceae stock through a change from capsule to berry. This seems to have occurred sometimes during the Cretaceous when the proximity of South America to Africa permitted the dispersal of Vismia to America where it has differentiated into a distinct subgenus (with pubescent interstaminal glands; Bamps 1966). The origin of Harungana (with a change of the fruit into drupe) and of Psorospermum (with a reduction of the number of ovules per locule) must have been somewhere near the Southeastern region of Africa from where they must have spread to Madagascar. Probably this must have happened sometimes during Palaeocene by which time India had drifted away and hence these two genera could not invade it.

Cratoxylum, Elaea, Thouria and Triadenum:

The precursor tribe Cratoxyleae seem to have been differentiated at a time when Madagascar and the Indian subcontinent were closer to one another and eventually the genus Eliaeae must have evolved in Madagascar and Cratoxylum in India. The latter must have subsequently spread to Malesian and sino-Japanese territories. The genus Triadenum seems to have originated in the Asiatic region of the Indian subcontinent and reached North America via China and Japan crossing Beringia. The genus Thorneae of Central America on the other hand appears to be an offshoot of Cratoxylum (with which it shares floral and seed characters; Breedlove & McClintock 1976) and we need further investigation to support its spread from Malesia (Robson, 1981, fig. 59).

Calophyllum, Kamea, Parinacea, Ochrocarpus, Mesua and Pseudolepis:

Out of these six genera constituting the tribe Calophylleae, the genera Calophyllum and Kamea seem to have been differentiated fairly early in the evolution of Clusioidae and as such they are widely distributed in the tropics. Even though Calophyllum is presently absent in Africa it is noteworthy that fossils comparable to it have been reported from the Sahara region (cf. Prakash 1975). It was perhaps lost there due to the Pleistocene climatic deterioration (Moreau 1966). Further it seems to have been the precursor of the tribe Endodendrieae (comprising of Lebrunia and Endodendria) which must have originated in Africa rather recently since this tribe has no representation even in Madagascar. A similar recent genera-making seems to have taken place in Madagascar, where Ochrocarpus and Parinaceae have been produced as the offshoots of Kamea.

The genera Mesua and Pseudolepis seem to have been differentiated from the Indian stock of Calophyllum. Mesua* appears to have been more successful and it has spread to Malesia and New Guinea and further on also to Australia. Pseudolepis seems to be a neo-endemic, originated in the rain forests of South India, after the separation of Sri Lanka.

* Fossils resembling that of Mesua have been reported from the Tertiary beds of India (Ramanujan 1968, Lakshman 1964).
Commenting on the systematic position of *Poeclioneuron*, Baratta Kuipers (1976) pointed out that this genus has fibre tracheids like those of *Bonnetiaceae* and hence it could be placed in that family. This view is also shared by Nayar (1980). Even though it may have certain anatomical similarities with *Bonnetiaceae* (*Bonnetiaceae* being reduced into a subfamily of *Clusiaceae*), *Poeclioneuron* is basically a *Calophylleae* (a tribe of the subfamily *Clusiaceae*), since it has basal placentaion, opposite leaves and drupaceous fruits.

**ENODESMA AND LEBRUNIA:**

These two African genera have in common the apical placentaion. *Lebrunia* is rather less specialized both in palynological and in androecial characters than those of *Enodesmia*. These two genera must have originated from the *Calophyllum* stock (rather than *Mammea* which has calyptrate calyx) and that too recently since they have not reached even Madagascar.

**PLATONIA, MORONOBIA, PENTADESMA AND MONTROUZIERA:**

All these four genera are closely related to one another and share in common the character of stamens in bundles. Further their pollen are provided with a thinning of the nexine outside the costae (a feature is however absent in some species of *Enodesmia*). As stated earlier, fossil pollen grains comparable to the pollen of these genera seem to have been reported under the form genus *Tetracolporites*. A careful reinvestigation of these fossils might throw further light on the origin and evolution of these genera.

**SYMPHORIA:**

The genus *Symphoria* represents a relatively more advanced state than the rest of *Moronobea* both in its staminal character (filament fused into a tube) and pollen character (brevicolporate to pororate). The presence of a massive nexine in this genus is a feature also found commonly in many of the species of *Moronobea*. It is worth searching the pollen of this genus especially among the Miocene fossils of India.

According to the published opinion, *Symphoria* might have originated and evolved in Madagascar (Leroy 1978), reached the Nigerian coast by Eocene and crossed the Atlantic by Miocene (Germeraad et al. 1969; Kuller 1974). It is worth searching for the pollen of *Symphoria* type among the Miocene fossils of India before taking a final decision on this subject.
LOGOSPERMUM AND THYSANDERIFERUM:

The two genera are very closely related to one another and represent an extreme of the trend that lead to the reduction of style.

GARCINIA, RHEDIA, SEPTOGARCINIA AND TRIPETALUM:

The genus *Garcinia* is represented from Africa to Australia. In Africa it seems to have given rise to *Rheedia* (by the simplification of stamens), which spread from there to tropical America and Madagascar. Before *Rheedia* could reach India, the latter must have drifted. However the genera Septogardinia and Tripetalum appear to have been the offshoots of the Garcinias derived from Indian stock.

ALLANHELAKIA: This seems to have been a recent off-shoot of *Garcinia* in Africa.

DEOSPHALANGIUM:

According to Robson (1972) this genus, with two whorls of five staminal bundles represents a primitive state. The pollen of this genus is incompletely described by Melchior (1930) and it is worth further palynological study.

CLUSIONA:

This genus with the diversification of the staminal characters similar to that of *Garcinia* needs also further palynological study since the present one covers the pollen morphology of only 17 out of nearly 150 species.

FILOSPERMA:

This genus appears to have been derived from *Clusia* stock by the reduction in the number of ovules.

ORDISHITIS, GIPSHITIS, GLUSTELLA AND RENGERIA:

These four closely related genera appear to be the offshoot of *Clusia* and are palynologically very much similar to one another.

HAVERTIA AND HAVERTIOPSIS:

This pair of genera represents an extreme of the trend that lead to the reduction in the number of the stamens. Both these genera are evidently related to *Clusia*.

is considered as a section of *Garcinia* since the range of taxonomic variations noticed among the species of *Lanthochlamys* falls within that of *Garcinia*. This merger is also supported by Channaveeriah and
**TOVOMITA, DISTOVOMITA, TOVOMITOPSIS AND TOVOMITIDIUM**

These four genera appear to be the product of minor evolutionary diversification of the sepals and petiolar bases.

**CHRYSOCHLAMYDS AND BALBOA**

Both these genera appear to be palynologically more advanced than the other genera of Tovomites by their "porate-spinulate" pollen.
CLASSIFICATION AND KEY TO THE GENERA OF CLUSIACEAE s.l.

The family Guttiferae was created in 1789 by Jussieu and subsequently in 1836 Lindley called it as Clusiaceae based on the type genus Clusia. Both the names are valid as per the International code of botanical nomenclature.

The family Hypericaceae was created in 1789 by Jussieu and it was kept as a separate family by Choisy (1824) and Bentham & Hooker (1862) until Engler (1888) amended the description of Guttiferae to include it the Hypericaceae and also a few genera of Bentham and Hooker's Ternstroemiaceae.

While Choisy (1824), Vesque (1893) and Hutchinson (1969) have followed Jussieu's concept, Cronquist (1968) and Robson (1972, 1974) have favoured Englerian approach and this was also recently accepted by Takhtajan (1980).

The family Bonnetiaceae was created by Beauvisage (1920) to accommodate certain genera of Clusiaceae and it was accepted by Maguire (1972). Takhtajan (1980) expressed the opinion that this family is intermediate between Clusiaceae and Theaceae. According to Kubitzki (1978) the maintenance of Bonnetiaceae as a separate family is not justified.

In the present work, I have taken all the genera of Bonnetiaceae, Clusiaceae and Hypericaceae together and prepared a consolidated key based on the important diagnostic characters including pollen characters. My survey shows that these genera are closely inter-related and present different combinations of certain basic trends. There seems to be no special advantage in splitting them into different families particularly if the segregated families are to be placed next to one another.
Leaves opposite with 3 or 5 styles: s.f. HYPERICOIDEAE

Fruit capsule or berry in which case the interstaminal glands are absent
Petals white or greenish to pink or crimson, never yellow; trees or shrub (herbaceous only in Triadenum); venation pinnate never flabellate;
interstaminal glands always present: Cratoxyleae.

Petals yellow or orange never green; shrubs or herbs never trees;
venation flabellate to pinnate; interstaminal glands absent or rarely present: Hypericeae.

Fruit drupe or berry with interstaminal glands: Vismieae.
Leaves alternate with 0, 1, 3 or 5 styles or leaves opposite with 0, 1, 2, 4 or 6 styles.
Plants with bisexual flowers and capsular fruit: s.f. BONNETIOIDEAE
pollen with circular endospermat: Bonnetieae
pollen with transversely elongated endospermat: placenta in pairs: Kialmeyereae
placenta solitary: Carainesae

Plants either polygamous or unisexual or bisexual and in the last case the fruit is not capsular: s.f. CLUSIOIDEAE
placenta basal: Calophylleae
placenta apical: Endodesmieae
placenta parietal: Allenblackieae
placenta axile
flowers bisexual: Morenobeae
flowers unisexual or polygamous
fruit berry: Garcinieae
fruit capsule: Clusieae
fruit capsular drupe or capsular berry: Tovomiteae

* for Key to the genera see the following pages.
KEY TO THE GENERA OF GLESIACEAE s.l.
and their geographical distribution

**Tribe : Cratoxyloceae**

Ovary with 6–8 ovules and 3 true plus 3 false septa; styles and filaments villous – *Blasia* (S. Madagascar).

Ovary with more than 12 ovules, with 3 true and no false septa; styles and filaments glabrous.

- Herbs : seeds without wing or appendage – *Triadenum* (E. Asia : Assam–Japan, N.E. America)
- Shrubs or trees; seeds winged or with appendages: ovules & styles glabrous
  - Placentation incompletely axile – *Cratoxyllum* (Assam, S. China, Malesia)
  - Placentation completely axile – *Thornea* (Mexico, Guatemala)

**Tribe : Hypericeae**

Staminodes 5 alternating with 5 fertile fascicles – *Santomasia* (Mexico, Guatemala)

Staminodes either absent or very rarely 3 alternating with 3 fertile fascicles – *Hypericum* (tropical and temperate zones, absent from some lowland tropical areas, rare in Australasia)

Fruit berry

- Ovule 1 per locule : *Macrosernum* (trop. Africa & Madagascar)
- Ovule 5–8 per locule : *Vismia* (trop. Africa & trop. America)

Tribe: Bonnetiaceae

ovary 3-locular; stamens free
leaves with distant pinnate venation: *Bonnetia* (trop. S. America & W. Indies)
leaves with close parallel venation
peduncle strongly two edged (ancipitus) and exceeding the subtending leaves; bracts conspicuous; pachycaulous treelet: *Nehlinaria* (Venezuela)
peduncle terete and shorter than the subtending leaves; bracts inconspicuous or lacking; non pachycaulous shrubs or small trees
plant non lactiferous; seeds glabrous; anthers oblong: *Neoboeoconia* (Venezuela)

plant lactiferous; seeds hirsute; anthers linear: *Nectaeae* (Venezuela, Colombia)

ovary 5-locular; stamens pentadelphous
style 1: *Archytasea* (Guyana)
Style 5: *Plotarum* (S. E. Asia, W. Malaysia, Moluccas, New Guinea)

Tribe: Kielmeyereae

embryo orbicular reniform; pollen often in tetrads: *Kielmeyera* (Brazil)
embryo straight; pollen in free monads (eumonads)
anthers distinctly 4 celled, introrse; vessels in multiples, leaves alternate; ovary 3-locular: *Makura* (trop. S. America)
anthers 2 celled; latrorse; vessels solitary; leaves opposite;
 ovary 4-5 locular: *Marila* (trop. C. & S. America)

Tribe: Caraipaeae

anthers eglandular; silica grains present; libriform tracheids present: *Haploclathrea* (Brazil)
anthers glandular; silica grains absent; libriform tracheids absent: *Caraipa* (trop. S. America)
Tribe: Calophylleae

Calyx calyptrate

4 carpelled ovary, style 1-4, stigma 4: *Paranephenea* (Madagascar)
2 carpelled ovary, style 1, stigma 2

stamens free to monadelphous: *Kazmea* (Pantropical)
stamens polyadelphous: *Ochrocarpus* (Madagascar)
calyx not calyptrate

leaves with reticulate venation; fruit dehiscent drupe
style 1: *Marua* (Indomalaysia & Australia)
style 2: *Poecilemacon* (S.W. India)

leaves with parallel venation; fruit indehiscent drupe: *Calophyllum*
(Pantropical except Africa)

Tribe: Endodesmiae

stamens fused only at the base; pollen longicolporate: *Lebnumia* (trop. C. Africa)
stamens fused into a 5 lobed tube; pollen brevicolporate: *Endodesmia*
(trop. C. & W. Africa)

Tribe: Allanblackiae

1 genus only: *Allanblackia* (trop. Africa)

Tribe: Moronobeae

style short or absent

fruit stipitate, pericarp ligneous, ribbed; bracteate: *Lorostemon*
(trop. S. America)

fruit sessile, pericarp not ligneous, not ribbed; ebracteate:

*Thysanostemon* (Br. Guiana)

style: long and distinct

filaments fused into a tube; anthers in 5 groups at the summit: *Symponia*
(trop. S. America, Africa & Madagascar)

filaments fused into 5 discrete bundles

interstaminal glands fused to form a 5 lobed disc

stamens more than 50 per bundle, vertically arranged, multiseriate,
ovary not spirally grooved: *Platonia* (Brazil & Guyana)
stamens 3-5 per bundle, spirally twined around the ovary, uniseriate;
ovary spirally grooved: *Moronoea* (trop. S. America)

interstaminal glands free,

filaments in each bundle fused only at the base; *Pendesema* (trop. Africa)

filaments in each bundle fused completely: *Kontrastiera* (New Caledonia)

is merged into *Mesua* by Kostermans (1969) who has however not transferred

*Ekafe*, *K. pacifica*, *K. morio*, *K. Subatoma* Kosterm. studied by me.
Tribe : Garcineae

stamen free : *Rheedia s.l.* (incl. section Texacentrum of *Garcinia*) (trop. C. & S. America, W. Indies, Africa, Madagascar)

stamen monadelphous or polyadelphous

flowers tetramerous or pentamerous

fruit not ribbed : *Garcinia s.s.* (Africa, Madagascar, Asia & Australia)

fruit ribbed : *Septogarcinia* *a.* (W. Sumbawa Is.)

flowers trimerous : *Trinetalum* (New Guinea)

N.B. The free stamened *Garcinia livingstonii* and *G. pachyclada* are transferred to *Rheedia*. See p. 36.97.

Tribe : Clusieae

stamens not in bundles

stamens 4

anthers sessile on a lobed synandrium : *Havetia* (Colombia)

anthers sub-sessile on a short floral axis

filament basally fused : *Havetionia* (trop. C. & S. America)

stamens 5-20

filaments basally fused, floral axis not lobed : *Quadematopus* (trop. S. America)

filaments completely fused, floral axis lobed

androecium umbraculiform

petals imbricate : *Quapova** (trop. S. America)

petals contorted : *Clusiella** (C. & S. America)

androecium not umbraculiform : *Renggeria* (trop. S. America)

stamens more than 20

ovules 2 per locule : *Filosperma* (Colombia)

ovules many per locule : *Clusia* (trop. C. & S. America)

stamens in 10 distinct bundles : *Decaphalanquium* (Peru)

* If we accept K’s stamens description of the fruit of *Septogarcinia* as fleshy "dehiscent fruit", this becomes not only a distinct genus but also a link between *Garcineae* and *Clusieae*.

**Quapova** is a berry according to Maguire (1961) although Engler (1925) has grouped it along with other capsular genera. Likewise *Clusiella* is considered as a berry according to D’Arcy (1980). A study of the mature fruits of these two genera might eventually show them to be a capsular type.
Tribe : Tovomiteae

outer sepals fused partially (at the base) or completely
petioles with large basal axillary structures : Dystovomita (Panama)
petiole bases lacking axillary structures : Tovomita (trop.C. & S. America)

outer sepals free
stamens free :
  style absent : Tovonitopsis s.l. (incl. sections Choristemon & Heterandra
  of Chrysochlamys) (trop.C. & S. America)
  style present : Tovomitidium (Brazil)

stamens monadelphous
  stamens many : Chrysochlamys s.s. (section Adelphia only) (trop.S. America)
  stamens few : Balboa* (Colombia)

*Balboa is said to be a fleshy fruit. Pending confirmatory study it is
considered here as capsular berry.
AFINITIES OF CLUSIACEAE s.l.

According to several botanists, Clusiaceae belong to Thoreales (Cronquist 1968, Takhtajan 1969, 1979 & Dahlgren 1975, 1980). Erdtman (1952) has signalled the palynological affinities of this family with Korokaviaceae, Quinaceae and Theaceae. I give below my analysis of the affinities of Clusiaceae with a few select families.

Theaceae: As shown on page 184, Clusiaceae and Theaceae have similar trends of specialization and their maximum expression is found in Clusiaceae. Even though polypetalous condition is common to both, a tendency towards sympetaly is developed in Theaceae (as Camellia, Ternstroemia and Eurya) and this does not occur in Clusiaceae. A notable difference is the presence of the resin canals in the sub-family Clusioidae, which is unknown in Theaceae.

The tribe Camelliaeae appears to be the most primitive among the tribes of Theaceae in having capsular fruit associated with bisexual flowers, colporate pollen and alternate leaves in most of the genera. These appear also to be the ancestral characters of Clusiaceae as shown by my analysis of the polarity of the character states. I therefore support the view that the Theaceae and Clusiaceae have differentiated from a common stock.

Quinaceae: This is a family of 4 genera, of which only one (Oling) has been studied palynologically. According to Erdtman (1952) Oling does show affinity with Clusiaceae and on anatomical grounds, Metcalfe and Chalk (1950) have suggested that this genus should be placed between Calophyllum and Clusia. The tricolporate pollen found in all these three genera does not contradict this view. However, the study of the pollen of the other 3 genera belonging to Quinaceae must be studied before taking a final decision whether it should be merged into Clusiaceae or maintained as a separate family, because of the presence of the characters such as hairy seeds and stipulate-pinnate leaves in Quinaceae.

Marasmiaceae: My study confirms the opinion of Erdtman (1952) that this family, having the same basic tricolporate pollen type, does have palynological affinity with Clusiaceae. In fact, similar trends of gynoecial evolution are found in both the families, which in addition have in common free stamens and berrics.
Dipterocarpaceae: Dipterocarpaceae and Clusiaceae have in common the "Y" shaped tilioid tectal perforations. I have shown this feature especially in Vismia (fig. 513) and for Dipterocarpaceae. I would like to cite the case of Monotocoidae, which also has the colporate pollen, similar to that of Clusiaceae. These two families have in common several wood anatomical features (similar type of vessels, pitting of fibres and silica crystals; in addition both have resin canals: Parameswaran 1979).

The sub family Dipterocarpoidea have colporate grain without endexine (endaperture absent). Such a condition is not seen in Clusiaceae. Although the apertures in the pollen of certain genera may be described morphologically as colpi should in phylogenetic consideration be treated on par with "pores" (since they are simplified colporate apertures wherein the colporate fraction is lost by reduction).

The Dipterocarpaceae seem to have specialized in the seed dispersal by wind through the development of winged fruits; whereas the Clusiaceae have progressed towards the fruit dispersal by birds and animals through the development of berries. However in certain species of Hypericum with capsular fruit we come across winged seeds dispersed by wind.

Sarcolaenaceae (Claoenaceae): Erdtman (1952) has pointed out that similar pollen tetrads are found in Kielmeiera of Clusiaceae and the genera of Sarcolaenaceae. The works of Straka (1963, 1964, 1971) brought to light a very characteristic elaboration of exine architecture in Sarcolaenaceae pollen tetrads. This is not followed up in Clusiaceae, in which the "tetrads evolutionary line" seems to have bluntly stopped with the genus Kielmeiera. It may be pointed out that my study extends to as many as 16 of the 20 species of Kielmeiera and it is possible that the remaining 4 species would also turn out to be palynologically similar to the ones studied by me.

Caryocaraceae: While commenting on the position of this family in Theales, France & de Silva (1975) commented that the pollen of Caryocar is quite similar to that of Kielmeiera of Clusiaceae. If we compare the TEM photomicrographs of the pollen of Caryocaraceae published by Barth (1966) with the ones given here for Kielmeiera (figs. 591-594) we may note that in both the cases the infratectum ranges between granulate to columnellate condition, although the endexine in the former is not as endosculptured as in the latter. The thickening of the exine noticed especially at the polar region of the Caryocaraceae pollen appears to be mainly due to the thickening of the tectum, whereas the slight polar thickening of the exine of certain Hypericoideae is mainly due to the presence of the "Y" shaped tilioid tectal perforations.

* In some highly evolved Dipterocarpaceae the fruits are dispersed by animals or water (Maur, 1978)
to the increase in the height of the infructescial columnella. Even though both the families have the basic colporate pollen of two Theaceae type, I consider that in view of the above differences they are not to be placed next to one another. While Caryocaraceae has differentiated into a compound-leaved family from the Theaceae stock, the Clusiaceae remained as a simple-leaved family.

**Flacourtiaeaceae**: As Keating (1973) has pointed out the Flacourtiaeaceae pollen are similar to that of Ochnaceae (Miller 1969). In both, one finds a certain tendency towards the striate tectal surface and this is unknown in Clusiaceae.

That tricolporate condition is basic to Flacourtiaeaceae suggests that it does have palynological affinity with Theaceae. The Flacourtiaeaceae seems to have made an attempt to parallel to that of certain Kerriobaccaceae (Clusiaceae) in developing tetracolporate pollen but without the characteristic nexinal thickening.

**Halphiaceae**: Lobrecus Callen (1967) has suggested possible palynological affinities between Halphiaceae and Clusiaceae, underlining the common presence of small tricolporate grains with thin exine and the large pollen with thin nexine. She has drawn at the same time our attention to the fact that the apertures are different from those of Halphiaceae. To support the relation between Clusiaceae and Halphiaceae she mentioned that one should note the common presence of foliar glands, again drawing caution over the fact that the origins of these glands are quite different.

Even though these two families have similar tricolporate pollen type, the palynological trends of Clusiaceae presented here are not comparable to those of Halphiaceae elaborated by Lobrecus-Callen. In my opinion, Halphiaceae with their fringed petals, jointed petals and stipulate leaves belong to an altogether different circle of botanical affinity.

**Asteropeiaceae**: This family was created by Takhtajan to accommodate a single genus, Asteropeia, previously considered as a member of Theaceae (Cronquist 1968) but placed in his system next to Theaceae.

According to Nagyere (1972) it should be included in Bonnetiaceae which is now a subfamily of Clusiaceae. On the basis of anatomical studies Baretta Kuipers (1976) suggested to it a position near the Bonnetiaceae.
I have studied the pollen of *Asteronea multiflora* Thouars (collected by J.K. Hildebrandt 3315, Feb 1880, Madagascar, M°) and described below the pollen: tricolpate (rarely 2-colpate), breviartal (r=19-24 μ, B=25-30 μ), sexine: 0.8 μ, nexine: 0.8 μ; spinulate with supratenal spines (0.3 x 0.8), t = 10 μ; colpi with spinulate operculoid membrane bordered by narrow smooth margins; costae absent.

In another species of *Asteronea amblyocardia* Tul., Erdtmann (1952) has observed 3-colporate or 6-rugate, spinulate pollen with spinulate aperture membrane.

It is noteworthy that Erdtmann has expressed some doubt about the presence of endosperm by his statement "colporate." Hence, I have carefully examined the central part of the nonacetolysed aperture of the related *Asteronea multiflora* and failed to note any endosperm. The intine was uniformly thickened all over the colpus without any central oncoid differentiation. I therefore conclude that *Asteronea* is colpate. A study of the non acetolysed pollen grains of *A. amblyocardia* may prove it to be also 3-colpate.

As far as I know, a distinct colpate-spinulate pollen similar to that of *Asteronea* does not occur in Clusiaceae and in fact it is unknown in any of the families cited under the Thalca by Cronquist. The colpate condition found in Dipterocarpaceae is never associated with spines.

Further detail study of *Asteronea* pollen with SEI and TEM may throw some light on the botanical affinity of this genus, endemic to Madagascar.
AFFINITIES BETWEEN THEACEAE AND CLUSIACEAE AND THEIR EVOLUTIONARY DIVERSIFICATIONS

**Character States**

1. Leaf: a: alternate; b: opposite
2. Flower: a: f; b: f; c: f; d: f
3. Stamen: a: polyadelphous
   - b: basally fused
   - c: free
   - d: monadelphous
4. Style: a: 5-6; b: 4; c: 3; d: 2; e: 1; f: 0
5. Fruit: a: capsule; b: capsular drupe & drupe
   - c: capsular berry & berry
6. Pollen: a: 3 colporate; b: 4-6 colporate
   - c: 3-5 pororate; d: 3-6 pororate
   - e: 4-6 pororate

**Diagram:**
- Tribe Ternstroemiaceae
- Tribe Camelliaeae
- Tribe Asteropoeae
- Tribe Hypericoideae
- Tribe Clusioideae
- Tribe Theaceae
- Tribe Clusiaceae