POLLEN MORPHOLOGICAL EVIDENCE FOR SUBDIVISION AND AFFINITIES OF LECYTHIDACEAE

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SUMMARY

A subdivision of the pollen types encountered in *Lecythidaceae* is proposed. The presence of a demarcation line between an original colpate and a derived syncolpate pollen type is confirmed. The significance of pollen characters for taxonomic subdivision is evaluated and it is concluded that the subdivision proposed by Niedenzu in 1892 agrees best with the pollen evidence. Pollen morphology does not yet provide any clear indications of wider affinities of the family, except in a negative sense.

INTRODUCTION

In his monograph of the genus *Barringtonia* (*Lecythidaceae*), Payens (1967) stated, after reviewing the various proposals for subdivision by former authors, that 'a satisfactory taxonomic subdivision of the family is still wanting and may not even be possible'. Although some of these authors, notably Niedenzu (1892) and Pichon (1945), paid attention to pollen morphology, it was Erdtman (1952) who first pointed out that a clear demarcation line runs through the family, one part being characterized by the syntricolpate *Planchonia* pollen type, the other by the tricolpate *Lecythis* type. This evidence was not taken into account by Melchior (1964), who based his subdivision of the family on Pichon (1945).

In the following it will be attempted to evaluate the significance of this character for taxonomic subdivision in *Lecythidaceae* and in addition to comment briefly on the wider affinities of this family as far as these can be deduced from pollen morphology.

This note is dedicated to Professor Van Steenis on the occasion of his retirement and in grateful recognition of his promotion of palynological studies at the Rijksherbarium.

POLLEN TYPES

A preliminary account of the pollen morphology of the genus *Barringtonia* was already published in Payen's monograph (l.c., p. 169—171). Since then I have been able to extend my observations by studying the pollen of all species of the related genera *Careya*, *Chydenanthus*, *Combretodendron*, and *Planchonia*. Their pollen proved to be basically similar to that of *Barringtonia* and can be included in a *Planchonia* main type although the variability within this type is considerably larger than suggested by Erdtman (1952). A detailed account of this variability will form the subject of a later paper.

In addition, the pollen of the remaining genera of *Lecythidaceae*, as far as available, was cursorily examined, all proving to belong to the *Lecythis* main type. In the following scheme for which the subdivision of Niedenzu (1892) is adopted (table 1), a slightly revised subdivision of the pollen types in *Lecythidaceae* is presented[1]).

[1]) The opportunity is taken here to correct a most unfortunate error in Payens, l.c., p. 170: 'A. *Calyptrocalyx* main type' should read 'A. *Calyptrata* main type'.

TABLE I

II. PLANCHONIA MAIN TYPE (syncolpate)	PLANCHONIOIDEAE	A. Barringtonia calyptrata type (without marginal groove)	*B. calyptrata* *B. longifolia* *B. neocaledonica* *B. papeh* *B. procera*
		B. Barringtonia asiatica type (with marginal groove)	remaining species of *Barringtonia* *Careya* *Chydenanthus* *Combretodendron* *Planchonia*
I. LECYTHIS MAIN TYPE (colpate)	FOETIDIOIDEAE	*Foetidia*	
	NAPOLEONOIDEAE	*Asteranthus* *Crateranthus* *Napoleonea*	
	LECYTHIDIOIDEAE	*Bertholletia* *Cariniana* *Chytroma* *Corythophora* *Couratari* *Couroupita* *Eschweilera* *Grias* *Gustavia* *Holopyxidium* *Lecythis*	

From this scheme it will be clear that Erdtman's assertion that a pollen morphological demarcation line can be drawn within the family can be confirmed. However, before this fact can be utilized for taxonomic subdivision it is necessary to evaluate the character involved and to investigate whether any other characters are correlated with it.

First of all, the fact that the difference between the *Planchonia* and the *Lecythis* main pollen types is a qualitative one, viz. syntricolpate versus tricolpate, must be discussed. While in none of the species transitions have been observed, this of course does not imply that earlier in the phylogeny this has also not been the case. In fact, it is likely that the syntricolpate condition has been gradually derived from the tricolpate one. Evidence for this point of view can be found in recent observations on *Passifloraceae* pollen by Presting (1965) and Pacqué (oral communication) which show that varying degrees of syncolpatism may occur, even within one species and that, in that family at least, the syncolpate condition is a derived one. A second argument to consider the tricolpate condition as original can be based on the fact that this type characterizes the earliest Angiosperm pollen grains which occur in the early Cretaceous, while syncolpate types appear later in the geological record (Muller, 1970). Furthermore, the *Planchonia* and *Lecythis* main types differ in other characters also. In the *Lecythis* type, the grains are generally smaller, the polar axis rarely exceeding 45μ in length, the endoapertures are often more pronounced as in *Eschweilera*, *Foetidia*, *Grias*, and *Napoleona*, and the exine is generally of a more simple structure than is found in the *Planchonia* main type, being typically composed of a thin endexine, a layer of more or less distinct columellae, and a generally rather thin tectum which may be smooth (*Bertholletia*, *Couroupita*, *Eschweilera*, *Holopyxidium*), finely reticulate (*Chytroma*, *Couratari*, *Grias*, *Lecythis*, *Napoleona*), foveolate (*Foetidia*), or scabrate-verrucate (*Crateranthus*, *Gustavia*).

In contrast, the large (45—60μ polar diameter) grains of the *Planchonia* main type generally lack a clearly defined endoaperture, while the syncolpate ektoapertures often show a number of specialized structures in the marginal zones. Especially striking in this respect are the polar thickenings occurring in the *Barringtonia asiatica* type. The exine structure on the mesocolpia may show a heavy tectum with funnel-like depressions, supported by columnate structures, comparable to the *Tilia* structure type described by Chambers and Godwin (1961) and Praglowski (1971). However, simple exine structures also occur in the *Planchonia* main type and it is especially the *Barringtonia calyptrata* type which must be considered as least evolved and which approaches certain representatives of the *Lecythis* main type and especially the pollen of *Crateranthus*. As can be seen on Plate I, where the pollen of two representatives of the *B. calyptrata* type is compared to that of *Crateranthus congolensis*, in both the columellae are rather conspicuous and regularly distributed, supporting a medium thick, almost smooth tectum (figs. 5, 6). An additional striking point of similarity is the presence of scattered verrucae on the apertural membranes (figs. 4, 7, 8). This is a feature which occurs frequently in the *Planchonia* main type, but in the *Lecythis* main type so far only has been encountered in *Crateranthus* pollen.

As already stated, the step from tricolpate (fig. 7) to syntricolpate (fig. 1), which is the main difference between the pollen grains of *Crateranthus* and the two representatives of the *Barringtonia calyptrata* type shown, although at present qualitatively definable, need not be a fundamental one. Moreover, the general construction of the ektoapertures (apart from the syncolpatism) and the absence of marginal grooves and of distinct endoapertures are further points of agreement. The highly complex pollen of the *Barringtonia asiatica* type is much less similar and probably represents a separately evolving side branch in the phylogeny of the family.

In this connection it is of interest to review briefly the geographical distribution of the pollen types. The *Planchonia* main type is restricted to the Old World tropics, ranging from Africa and Madagascar to the west Pacific. The *Lecythis* main pollen type is found in the American tropics, tropical Africa, and Madagascar. The genus *Crateranthus* is African, while the *Barringtonia calyptrata* type is restricted to New Guinea, North Australia, the Solomon Islands, Fiji, and New Caledonia. It is obvious that this distribution pattern does not support the idea that the latter group could be closely related to *Crateranthus*, unless one assumes a relict distribution for the *B. calyptrata* type.

On the other hand, the transatlantic distribution of the *Lecythis* main pollen type agrees well with the view that this may be close to the ancestral pollen type of the family. The origin of the *Planchonia* main type could then have been in Africa, presumably at a time when transatlantic migration was not possible any more. In this connection it is of interest to mention that the earliest pollen grains which can be assigned to the *B. asiatica* type date from the Paleocene of Borneo (Muller, 1970) and from the Eocene of India (Venkatachala & Kar, 1968), while Payens (l.c., p. 172) cites fossil wood of *Barringtonia* from the Eocene of India. Puzzling in this context is a recent record of fossil *Barringtonia* leaves from the Eocene of Alaska (Wolfe, 1972).

In conclusion, it would appear that the two main pollen types could be utilized, in combination with macromorphological characters, for a subdivision of the family, since they probably reflect a Cretaceous split in the phylogeny, with one branch finding its main development in South America and to a lesser extent in Africa, while the other branch has probably migrated eastwards from Africa, establishing a second centre of diversification in the Indo-Pacific area.

TAXONOMIC SUBDIVISION

From the subdivisions of *Lecythidaceae* reviewed by Payens, it is only that of Niedenzu (1892) which fully agrees with the pollen morphological evidence in the recognition of a subfamily *Planchonioideae* in which, as shown on the scheme showing the subdivision of pollentypes, all the genera are grouped, characterized by the *Planchonia* main pollen type. The other three subfamilies, *Foetidioideae*, *Napoleonoideae*, and *Lecythidioideae* are marked, as far as known at present, by the *Lecythis* main pollen type.

Pichon's subdivision, dating from 1945, includes the genus *Foetidia* in a subfamily *Planchonioideae*, although he has noticed a difference in pollen between *Foetidia* (smooth pollen) and the other genera (ornate pollen). If we check the macromorphological characters utilized by these two authors for their subdivisions, it appears that the genera included by Niedenzu in *Planchonioideae* are characterized by the presence of petals, filaments which are more or less connate at the base, an undivided stigma, a placenta which is not peltate, and ovula in a vertical row, while *Foetidia* lacks petals, has the filaments free or nearly so, a divided stigma, and a peltate placenta with the ovules in a horizontal circle. If the pollen character is added to this list it will be clear that the demarcation line between the tribe *Foetidieae* and the rest of the *Planchonioideae sensu* Pichon is deeper than between *Planchonieae*, *Barringtonieae*, and *Combretodendreae*. It is therefore suggested that *Foetidieae* are restored to subfamily rank, as originally proposed by Niedenzu.

AFFINITIES

The wider affinities of *Lecythidaceae* are more difficult to trace on pollen morphological evidence. Under the assumption that the syncolpate *Planchonia* main pollen type is the

derived one, it would appear that the tricolpate *Lecythis* type should be considered as close to the ancestral type. Essentially this is similar to the basic tricolpate-reticulate pollen type which is widespread among Angiosperms and which dates back to the lowermost Cretaceous (Muller, 1970).

Of the families which have at various times been proposed as being closely related to *Lecythidaceae*, *Myrtaceae* are the most prominent in the older literature (cf. Payens l.c., p. 161) and it is striking that in this family syncolpate grains dominate, although in all other respects these small, thinwalled, oblate grains are unlike the syncolpate *Planchonia* type pollen grains. It is probable that syncolpatism has arisen independently in both *Lecythidaceae* and *Myrtaceae* and does not indicate close relationship.

Miers (1875) accepted affinities with *Rhizophoraceae*, which are characterized by small tricolporate pollen grains with a tendency to equatorial fusion of the distinct endoapertures, a type which is not similar to the *Lecythis* main type.

Niedenzu (1892) also denies any relationship with *Myrtaceae* and suggests relationship with *Rhizophoraceae* and *Sonneratiaceae*. Pollen morphologically, however, there is not the slightest resemblance between *Lecythidaceae* and the latter family (cf. Muller, 1969).

Takhtajan (1959) retains *Lecythidaceae* in the *Myrtales*, postulating affinities to *Sonneratiaceae*, *Rhizophoraceae*, and *Myrtaceae*.

Cronquist (1968), finally, suggests affinities to *Malvales* or, through common ancestry, possibly to *Theales*, denying at the same time any relationship with *Myrtales*. This, of course, offers ample scope for comparison since many families belonging to the former orders are characterized by tricolpate-reticulate pollen types.

In conclusion, pollen morphology so far does not give any clear indication of the wider affinities of *Lecythidaceae*, except in a negative sense. However, the *Lecythis* pollen type has not yet been studied in detail and when this is done new clues may be found.

REFERENCES

CHAMBERS, T. C., & H. GODWIN, 1961. The fine structure of the pollen wall of Tilia platyphyllos. New Phytol. 60: 393—399.

CRONQUIST, A. 1968. The evolution and classification of flowering plants. London: 201—202.

ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Stockholm: 222—225.

MELCHIOR, H. 1964. Lecythidaceae, in Engler's Syllabus der Pflanzenfamilien, ed. 12, 2: 353—355.

MIERS, J. 1875. On the Barringtoniaceae. Trans. Linn. Soc. Bot. 1: 47—118.

MULLER, J. 1969. A palynological study of the genus Sonneratia (Sonneratiaceae). Pollen et Spores 11, 2: 223—298.

—— 1970. Palynological evidence on early differentiation of Angiosperms. Biol. Rev. 45: 417—450.

NIEDENZU, F. 1892. Lecythidaceae, in Engler & Prantl, Die Natürlichen Pflanzenfamilien, 3, 7: 26—41.

PAYENS, J. P. D. W. 1967. A monograph of the genus Barringtonia (Lecythidaceae). Blumea 15: 157—263.

PICHON, M. 1945. Le genre Combretodendron et les Lécythidacées. Not. Syst. 12: 192—197.

PRAGLOWSKI, J. 1971. Reticulate and allied exines. Grana 11: 79—86.

PRESTING, D. 1965. Zur Morphologie der Pollenkörner der Passifloraceen. Pollen et Spores 7, 2: 193—247.

TAKHTAJAN, A. 1959. Die Evolution der Angiospermen. Jena: 225—226.

VENKATACHALA, B. S. & R. K. KAR, 1968. Fossil pollen comparable to pollen of Barringtonia from the Laki sediments of Kutch. Pollen et Spores 10, 2: 335—339.

WOLFE, J. A. 1972. An interpretation of Alaskan Tertiary Floras, in Graham, Floristics and palaeo-floristics of Asia and Eastern North America. Amsterdam: 201—233.