

PRINCIPAL POLLEN FEATURES IN THE ARUM LILIES (ARACEAE)

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SUMMARY: Araceae genera were screened for pollen morphological characters using TEM, SEM and LM. Pollen of Araceae is more diverse than previously reported. The manifoldness does not only concern the actual aperture configuration and the type of ornamentation, but especially - and rather unexpectedly - the pollen wall stratification. In most Araceae subfamilies the outermost pollen wall layer (the ektexine) is stable to acetolysis treatment. In contrast, in the most specialized subfamily, the Aroideae with more than two thirds of all Araceae genera, pollen grains show often an outermost layer, which is not resistant to acetolysis, and the mostly smooth pollen grains have an uncommonly spongy endexine, which is widely stable to acetolysis treatment. Pollen grains with a sporopolleninous ektexine should have a good chance to become fossil. This is valid for most subfamilies, however, in Aroideae there is a much smaller chance because of the lack of a stable ektexine layer, and the presence of a thick, inhomogeneous endexine. Most genera of the Araceae subfamilies Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, Lasioideae, Calloideae and in *Zamioculeas/Gonalopus* (Aroideae) have aperture pollen grains (mainly monosulcate, some disulcate), only few are lacking an aperture (i.e., the polyplcate pollen grains). Interestingly, the rare zonosulcate condition is found independently in two subfamilies: Monsteroideae and *Zamioculeas/Gonalopus* (Aroideae). No member of the subfamily Aroideae has aperture pollen grains. Moreover, the entire pollen surface is apertural in nature; such pollen should be called omniaperturate rather than inaperturate. Strikingly, at least 10 genera show a polyplcate condition and, therefore, share parallels with ephedroid (*Ephedra*) pollen. Surprisingly only two polyplcate genera have an acetolysis-stable outer layer, while the polyplcate condition of the other 8 genera is gone after acetolysis. The meagre fossil record of Araceae, and the potential confusion of any polyplcate Araceae with ephedroid pollen (recent or fossil) is evaluated in the light of these extraordinary pollen features.

KEY WORDS: Araceae, pollen, exine, ektexine, endexine, acetolysis.

RESUMEN: Se han analizado los caracteres de la morfología polínica en los géneros de Araceae usando MET, MEB y MO. Se ha encontrado más diversidad que la previamente descrita para el polen de Araceae. Los caracteres más llamativos no solo atañen a la configuración de la apertura y al tipo de ornamentación, sino especialmente a la estratificación de la pared polínica, algo bastante inesperado. En la mayoría de las subfamilias de Araceae el estrato más externo de la pared polínica (la ectexina) es resistente al tratamiento acetolítico. Por el contrario, en la subfamilia más especializada, las Aroideae con más de dos tercios de todos los géneros de Araceae, los granos de polen muestran frecuentemente un estrato externo que no resiste la acetolisis. Por lo que estos granos de polen, normalmente lisos, muestran al exterior una endexina esponjosa poco común que sí es estable bajo la acetolisis. Los granos de polen con una ectexina de esporopolenina deberían tener buenas oportunidades de fosilizar. Esto es válido para la mayoría de las subfamilias, sin

embargo, en Aroideae hay muchas menos oportunidades por la carencia de una ectexina resistente y la presencia de una gruesa y no homogénea endexina. La mayoría de los géneros de las subfamilias Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, Lasioideae, Calloideae y *Zamioculeas/Gonalopus* (Aroideae) tienen granos de polen aperturados (principalmente monosulcados, algunos disulcados), sólo unos pocos sin apertura (como algunos de los granos poliplicados). Es interesante que el poco frecuente carácter zonosulcado se encuentra independientemente en dos subfamilias: Monsteroideae y *Zamioculeas/Gonalopus* (Aroideae). Ningún miembro de la subfamilia Aroideae tiene polen aperturado. Además, toda la superficie del grano de polen es de naturaleza apertural, por lo que estos granos de polen deberían llamarse omniaperturados en lugar de inaperturados. Es de destacar que al menos 10 géneros muestran el carácter poliplicado y, por tanto, comparten caracteres en paralelo con el polen efedroide (*Ephedra*). Sorprende que sólo dos géneros poliplicados tengan un estrato externo estable bajo la acetólisis, mientras que el carácter poliplicado de los otros 8 géneros se pierde con esta. A la luz de estos llamativos caracteres, se evalúa el pobre registro fósil de Araceae y la potencial confusión de alguno de sus polenes poliplicados con polen de efedroide actual o fósil.

PALABRAS CLAVE: Araceae, polen, exina, ectexina, endexina, acetólisis.

INTRODUCTION

The Araceae, an herbaceous monocot family, are plants which are familiar to everyone, but paradoxically little known. Popular house plants include species of, e.g., *Monstera*, *Anthurium*, *Philodendron* or *Dieffenbachia*. The family is characterized by the distinctive inflorescence (a spadix with bisexual or unisexual flowers) subtended by a spathe. Many Araceae are famous for their specialized, unique pollination biology (e.g., *Arum*). Pollen is shed (mostly) as single grains, but is often loosely connected, thus forming threads (e.g., *Zantedeschia*).

Members of Araceae, currently including over 3,300 species in 105 genera (MAYO *et al.*, 1997, 1998), generally live in (sub-) tropical moist or wet habitats, only rarely in dry ones. Life forms are very diverse ranging from aquatics to terrestrial, and members may be climbing or epiphytic plants. The family is now regarded as basal in the monocots (Angiosperm Phylogeny Group, 1998). Concluding from the rise of the angiosperms in the (Early) Cretaceous, it is to be expected that the Araceae exists at least since Late

Cretaceous. However, the family has a poor fossil record in general (MAYO *et al.*, 1997). This depends mostly, but not exclusively, on the complete absence of woody parts. Its fossil pollen record is tiny, without on first sight sufficient reason.

The extraordinary poor pollen record depends not only on the life forms and the environmental conditions, which do not favor fossilisation. The main reason is on one hand the unique pollination mechanism (often a moist, warm kettle trap) and on the other hand the very uncommon wall stratification typical for many Aroideae (WEBER *et al.*, 1998, 1999). Only quite recently findings of Eocene fully zonate pollen grains could be related to distinct fully zonate Araceae (ZETTER *et al.*, in press.). Araceae pollen show a wide range of diversity with respect to pollen wall morphology and exine sculpturing (GRAYUM, 1992). Nevertheless, the tiny fossil record of Araceae pollen dates only from a few Eocene and Miocene palynomorphs, all attributed to *Spathiphyllum* because of their polyplcate appearance (VAN DER HAMMEN & GARCIA DE MUTIS, 1966; MÜLLER, 1981; MAYO *et al.*, 1997). This

discrepancy between the fact that Araceae are an old, basal branch of the monocots, and the paucity of published fossil pollen findings is intriguing (HESSE *et al.*, 1998).

The scarcity of fossil Araceae pollen suggests that taphonomic conditions for their preservation differ from those required for the preservation of pollen types with stable exines. The textbook view that the outer part of the Angiosperm pollen wall (always) consists of a highly resistant organochemical substance, called sporopollenin, and will become a fossil as it stands, must be questioned, at least for many Araceae. The more basal subfamilies of Araceae show a sporopollenin-containing ectexine (with tectum, columellae, and a foot-layer) and usually a thin, more or less compact endexine. Strikingly, this is not the case in the largest subfamily, the Aroideae, where often an acetolysis-susceptible outer layer (lacking a subdivision in tectum, columellae and foot-layer) and a spongy, thick acetolysis-resistant endexine forms the sporoderm. A second characteristic feature of Aroideae pollen is the absence of apertures, while all other subfamilies of Araceae generally have aperturate pollen (with few, but significant exceptions).

The aim of this paper is to give an overview on the pollen wall diversity in the family Araceae and, to show the extraordinary type of pollen wall stratification within the subfamily Aroideae.

MATERIAL AND METHODS

The pollen material was obtained mainly from the Botanical Garden Munich, and also from the Greenhouses of the Botanical Garden of the University of Vienna. A large

sample of Araceae taxa was investigated (more than 60 species out of 47 genera from all subfamilies, cf. WEBER *et al.*, 1999). Only the following taxa are illustrated: *Staudnera colocasijfolia* K. Koch, *St. henryana* Engl., *St. assamica* Hooker f., *St. griffithii* Schott. For more pollen micrographs showing the high diversity the reader is referred to the papers by GRAYUM (1992), WEBER *et al.* (1998, 1999), and HESSE *et al.* (2000a, b).

Preparations for TEM and SEM were conducted in the same manner as described in WEBER *et al.* (1998) and in HESSE *et al.* (1999). Acetolysis was done following the Erdtman technique, but was also carried out on glass slides. Some pollen material was treated in 5 % boiling KOH for 20 minutes, independent of acetolysis.

RESULTS AND DISCUSSION

1. ARUM (AROIDEAE, ARACEAE) POLLEN: SMOOTH OR SPINY, THIS IS THE QUESTION

The case of *Arum* pollen with respect to its ornamentation is typical for quite different reports on the actual ornamentation. According to the applied preparation method (Tab. 1) *Arum* pollen was reported as to be either smooth or spiny. Especially after the application of acetolysis, a common method in palynology to clean the pollen surface, the pollen grains of *Arum*, but also of many other Araceae - Aroideae, was quite dissimilar (e.g., BEUG, 1961; BENZING, 1969; THANIKAIMONI, 1969; PACINI & JUNIPER, 1983). Only few authors, e.g., RAJ & SAXENA (1966) wonder about the appearance of their (acetolysed) *Pistia* material compared to Erdtman's description in 1952.

The main reason of differing reports on the actual surface ornamentation of many

Araceae pollen is the uncommon chemistry of distinct wall strata. The majority of Aroideae pollen shows an ornamentation, which is not made of sporopollenin, but of exclusively tapetum-derived substances (polysaccharidic, according to the Thiéry reaction); below this outer layer a thick, spongy endexine is present (WEBER *et al.*, 1998, 1999). In some taxa the surface ornamentation is not removed completely or immediately during acetolysis procedure (VAN DER HAM *et al.*, 1998). The effect of the acetolysis procedure depends on temperature and duration of the reaction. Remnants of the former ornamentation in distinct Aroideae pollen may depend on incomplete acetolysis procedure or treatment not at boiling temperature. Interestingly this conflicting reports were either ignored for a long time, or was usually explained in a simple manner: Araceae, especially Aroideae pollen grains often cannot withstand acetolysis.

Curiously enough, the clear statement in a leading scientific biological journal by PACINI & JUNIPER (1983) on *Arum* pollen wall stratification (... spaces ... filled with PAS positive material produced by the tapetum and formed spines on the exine“) failed - for any reason - make an impact to the Scientific community. Even one of the authors (Pacini) has mentioned this finding a single time again (in PARKINSON & PACINI, 1995:71). Similar reports by KUPRIANOVA & TARASEVICH (1984), and TARASEVICH (1990), respectively also made for many years nearly no impact to the Scientific Community. The publication in Russian may be an explanation. Only TAKHTAJAN (1997:581) is recalling these papers; he interpretes correctly the acetolysis-susceptible *Pistia*-exine as a separating feature between (his families of) Pistiaceae and Lemnaceae. However, he calls the feature as being singular for Pistiaceae only (!).

Recently research was focused upon this strange feature (VAN DER HAM *et al.*, 1998; WEBER *et al.*, 1998, 1999; HESSE *et al.*, 2000a-b).

2. TYPES OF POLLEN WALL STRATIFICATION IN ARACEAE (TAB. 2, FIGS. 1 & 2)

Araceae pollen walls differ significantly in morphological and chemical composition and are represented - to date - by two quite different types (each with two subtypes, WEBER *et al.*, 1998, 1999). Both types, and also the subtypes, have a different resistance to acetolysis and likewise to KOH treatment. With some precaution a quite different resistance to decay can be concluded. In the more “conventional“ type, represented by *Spathiphyllum*, the specific pollen ornamentation is preserved by the acetolysis-resistant ektexine. In the other type, represented by *Dracunculus*, only the highly unspecific, smooth endexine remains, and the specific pollen ornamentation is gone.

a) Pollen walls with an ektexine (Type 1 in WEBER *et al.*, 1999): A potassium hydroxide- and acetolysis-resistant, verrucate/reticulate, tectate/columellate, or thin and smooth ektexine upon a loosely packed endexine. Examples include: *Lysichiton*, *Anthurium*, *Calla*, *Spathiphyllum*, *Stenospermation*, and *Arisaema*. The ektexine may also be thin and smooth, as in *Spathicarpa* and *Caladium*. Note: in the latter four genera a thick, spongy endexine is present throughout. Figure 1 shows the situation.

b) Pollen walls without an ektexine (Type 2 in WEBER *et al.*, 1999). A thick, spongy, and to a certain extent acetolysis-resistant endexine is present. This endexine may either be covered by an ornamentation of polysaccharidic nature, which is not resistant to acetolysis or potassium hydroxide treatment, [e. g., in *Arum* (PACINI & JUNIPER, 1983; WEBER *et al.*, 1999); in *Sauromatum* (WEBER *et al.*, 1998); in *Pistia*

(WEBER *et al.*, 1999); and in *Dracunculus vulgaris*], or even may lack such a layer (e. g., in *Zantedeschia*, WEBER *et al.*, 1999). Figure 2 shows this uncommon stratification at hand of *Stuednera* pollen grains.

Pollen wall stratification with respect to its distribution within the Araceae.

The pollen walls may consist of an acetolysis-resistant, elaborated ektexine with an endexine below, which is thin in non-apertural areas, but thick and inhomogeneous in aperture regions. This manner of pollen wall stratification is typical for all subfamilies (according to MAYO *et al.*, 1997, 1998) with bisexual flowers, the Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, Lasioideae and Calloideae, but is found also in few taxa with unisexual flowers, *Zamioculcas* and *Gonatopus*, i.e., two of the three perigyniate Aroideae genera (sensu MAYO *et al.*, 1997). The third member of the perigyniate Aroideae, *Stylochaeton*, shows a thin, slightly lamellated endexine below a continuous, thin, intectate

ektexine. This striking difference to the pollen stratification of *Zamioculcas/Gonatopus* was one of the arguments, together with several morphological arguments to propose a new subfamily, the Zamioculcadoideae (BOGNER & HESSE, in publ.). The pollen grains of the remaining Araceae with unisexual flowers, i.e. the aperigyniate Aroideae, which represent the bulk of what is commonly called "Ayum Lilies", are generally characterized by an equally thick, spongy, widely acetolysis-resistant endexine. Very uncommonly this endexine is covered either by a skin-like, acetolysis-resistant ektexine, or an outer stratum, which is not resistant to acetolysis. For additional discussion and review see HESSE *et al.* (1999) and HESSE *et al.* (2000a, 2000b).

3. APERTURE TYPES

GRAYUM (1992) presented an exhaustive paper on pollen wall features in Araceae, including the apertural configuration. In the subfamilies Gymnostachydoideae, Orontio-

Aroideae (Araceae)	Ornamentation before acetolysis		Ornamentation after acetolysis	
Arinae (tribe)	Thanikaimoni 1969:	spiny	Thanikaimoni 1969:	smooth
<i>Arum</i> ssp.	Pacini & Juniper 1983: Grayum 1992:	spiny spiny	Pacini & Juniper 1983 Beug 1961: Erdtman 1952: Reille 1998:	smooth smooth smooth smooth
<i>Ambrosina bassii</i>	Grayum 1992:	striate-plicate	Reille 1992: Benzing:	smooth verrucate
<i>Pistia stratiotes</i>	Thanikaimoni 1969: Tarasevich 1990: Kuprianova & Tarasevich 1984: Erdtman 1952:	plicate plicate plicate plicate	Thanikaimoni 1969: Tarasevich 1990: Kuprianova & Tarasevich 1984: Raj & Saxena 1966:	smooth smooth smooth smooth to obscure
<i>Ariopsis</i> sp.	Grayum 1992:	spiny	Tarasevich 1990:	smooth
<i>Alocasia</i> sp.	Grayum 1992:	spiny	Tarasevich 1990:	smooth
<i>Zomicarpa</i> sp.	Grayum 1992:	spiny	Tarasevich 1990:	smooth

TABLE 1: Some Araceae with differing ornamentation before and after acetolysis treatment.

deae, Pothoideae, Monsteroideae, Lasioideae and Calloideae, we find mostly monosulcate pollen, but rarely also diporate, zonosulcate (in Monstereae) and inaperturate. In the Aroideae (sensu MAYO *et al.*, 1997), pollen is inaperturate, e.g., *Stuednera* (Fig. 2), with few exceptions, e.g., zonosulcate in *Zamioculcas* and *Gonatopus*, proposed for a new subfamily Zamioculcadoideae (BOGNER & HESSE, in publ.). It is worthy to note that the spectacular zonosulcate type was „invented“ (at least) two times in the Araceae. The zonosulcate pollen grains in Monstereae are only superficially similar to those of *Zamioculcas*/*Gonatopus* (Aroideae) (cf. HESSE *et al.*, 2000b.)

Terminological note: omniaperturate versus inaperturate

Araceae pollen grains lacking apertures are often called inaperturate (e.g., GRAYUM, 1992; FURNESS & RUDALL, 1999). PUNT *et al.* (1994) propose the term inaperturate for pollen grains without apertures (*Populus* and *Taxus* as examples), while omniaperturate in their sense designates such pollen grains, where the whole surface is apertural in nature.

In our view, inaperturate is not synonymous with omniaperturate, and omniaperturate is no subsumption of inaperturate. Inaperturate is a morphological term, while omniaperturate points towards a function, and thus is a functional term. Following THANIKAIMONI (1978, 1984), pollen of *Stylochaeton* and of other Araceae with „inaperturate“ pollen should be clearly designated as omniaperturate (WEBER *et al.*, 1999:429). The entire pollen surface of *Stylochaeton* is apertural in nature, no morphological aperture is present, and the intine is uniformly thickened. The pollen tube can be formed everywhere. The exine is reduced, as always in omniaperturate grains, and splits in various manner but is generally

not detached; this feature is restricted to Angiosperms and is found especially in monocots (cf. MUELLER-STOLL, 1956). Thus we prefer the term omniaperturate in describing the Araceae pollen grains lacking apertures. The term inaperturate should be restricted to those few cases, when the exine splits and gets completely detached. This feature is found only in Gymnosperms (e.g., *Taxus*: MUELLER-STOLL, 1948; *Ephedra*: EL-GHAZALY *et al.*, 1998; or *Gnetum*: MAHESHWARI & VASIL, 1961:80). In superficially similar angiosperm cases, e.g., in *Populus* or *Tulipa*, the split exine does not get completely detached: often small parts of the exine remain.

4. ANGIOSPERM POLLEN: ITS RESISTANCE TO DECAY (WITH SPECIAL REFERENCE TO ARACEAE)

STEWART & ROTHWELL (1993:14) point out that the degree of preservation depends especially on the amount of tissue decay that occurred prior to fossilization. On the one hand, the individual resistance to pollen decay depends on the respective chemism and consistence of the pollen wall strata, and to a lesser degree on the apertural condition. Only a few experiments have been done to evaluate the selective destruction of exines by chemical (REITSMA, 1969; ROWLEY & PRUANTO, 1977) or mechanical treatment (CAMPBELL, 1991). On the other hand, of course the degree of preservation depends also on environmental factors (e. g., soil types), or post-depositional alterations, but published data and considerations in this direction are likewise rare (GERMERAAD *et al.*, 1968; ELSIK, 1971; HAVINGA, 1971, 1984; TRAVERSE, 1988; ROWLEY *et al.*, 1990; STEWART & ROTHWELL, 1993; all also for review). Furthermore, questions concerning polymerization and stability of sporopollenin remain widely unsettled. Both aspects will be discussed in the following paragraphs.

The overwhelming majority of angiosperm pollen grains, including the subfamilies of Araceae (except Aroideae) sensu MAYO *et al.* (1997), has stable, acetolysis-resistant exines. Such pollen should be found widely unmodified in the fossil record. For a long time it was generally accepted that pollen walls have to consist of an extremely resistant organic polymer, called sporopollenin, one of the most resistant chemicals in nature. However, it is well known that in a few Angiosperm families with peculiar pollination ecology pollen grains completely lack an exine (e. g., in some taxa of the Hydrocharitaceae: PETTIT, 1980; or Cymodoceaceae: McCONCHIE *et al.*, 1982; PETTIT *et al.*, 1984; all also for review), or the respective exines are extremely thin and highly reduced (e. g., in Callitrichaceae: MARTINSSON, 1993; in Strelitziaceae: ROWLEY *et al.*, 1997; or Lauraceae: VAN DER MERWE *et al.*, 1990; HERENDEEN *et al.*, 1994; all also for review). Their pollen walls are generally not resistant to decay, and these pollen grains may not be present in the actual fossil record. However, this "all-or-nothing" classification is an oversimplification. A third, different kind of pollen wall stratification is found within Araceae. This wall type is characterized - as shown above- by a thick, spongy endexine, often with an outer exine layer lacking any resistance to acetolysis or related methods used in palynology (e.g., treatment with 5 %

boiling KOH). Its stability is intermediate between the resistant tectate-columellate type of stratification and the extremely fragile, exine-less type mentioned above.

The peculiar environmental condition and pollination ecology of many Araceae: at least in part responsible for the poor fossil record of Araceae pollen?

Araceae are found preferably in tropical to subtropical climates, relatively few in temperate to even subarctic regions. Dominating habitats are tropical to subtropical (freshwater) swamps or ponds or river margins, or warm eutrophic soil (only few taxa prefer dry areas). Most probably all Araceae are strictly entomophilous, often possessing kettle traps (in German literature referred as Kesselfallenblumen). So long-distance pollen transport is not expected. Pollen of many bisexual Araceae taxa lacking kettle traps may fall down into water or on soil surface, or remain, as in most Aroideae, within the inside of the kettle trap. The kettle trap is characterized by an extreme microclimate, and microbial attack may start very soon. The degree of microbial attack is also high in humid, warm environments. Consequently, pollen degradation (but not necessarily, as might be expected, exine corrosion! cf. ROWLEY *et al.*, 1990) may occur very rapidly. However, this degradation, especially exine corrosion, will be generally

	<i>Spathiphyllum</i>		<i>Dracunculus</i>	
	Before acetolysis	after acetolysis	Before acetolysis	after acetolysis
ektexine	present: tectum, columellae and foot-layer	unmodified	PAS-positive layer, not called an ektexine by Weber <i>et al.</i> (1998)	absent
endexine	present	unmodified	present	present, but modified
intine	present	absent	present	absent

TABLE 2: Pollen wall stratification in main pollen types of Araceae, before and after acetolysis.

lower if a stable ektexine is present, but will take place to a greater extent especially if "weak points" (less stable, fragile sporoderm regions) with are present. The pollen walls of the majority of Araceae have indeed some fragile regions, which may reduce their chance to become fossil. The fully zonate ("hamburger-like") condition of some principally stable pollen grains with an acetolysis-resistant ektexine could be seen as one weak point: such pollen generally separate into halves during acetolysis (However, quite recently findings of Eocene fully zonate pollen could be related to fully zonate Araceae pollen types, (ZETTER *et al.*, in press.). A second weak point may be the spongy endexine of most Aroideae: this type of endexine tends to swell enormously during acetolysis, and therefore may split. In some cases (e.g., Monstereae) such acetolysed pollen indeed show an unmodified endexine. Hence, the spongy endexine in Araceae may have a greater degree of stability than one might expect.

The presumed fossilization potential of Araceae pollen walls

The meagre fossil record of Araceae is enigmatic. The reasons may be found either in the conflicting reports on pollen morphology (unconspicuous, often smooth or collapsed palynomorphs are overlooked or misinterpreted), but also on the often poor fossilization potential of such pollen grains. The degree of preservation depends on the amount of tissue decay that occurred prior to fossilization and of course also on environmental factors. The individual resistance to pollen decay is influenced especially by characteristics of the respective pollen wall stratification, and - to a lesser degree - by the apertural condition.

The various types of pollen walls in Araceae are without doubt variably resistant

to decay. Araceae pollen with an ektexine survive the acetolysis treatment intact as most dicot pollen does. However, taxa without an ektexine do not survive acetolysis. While the spongy endexine is, in principal, acetolysis-resistant (WEBER *et al.*, 1998; VAN DER HAM *et al.*, 1998), it swells greatly and may split during acetolysis. If the endexine remains intact it has a fair chance of becoming fossilized. Thus so far unrecognized Araceae pollen with this type of endexine should be present in the actual fossil record and therefore should be found (but often in a surprisingly modified form).

One can hardly avoid questions about the extremely poor fossil pollen record of Araceae taxa with a stable, acetolysis-resistant ektexine. The many monosulcate pollen grains typical for the basal subfamilies of Araceae in particular should have a good fossilization potential. However, the presence of an extended sulcus of many pollen grains, e.g., in *Lysichiton*, may be another fragile or weak point. It is worthy to note that this pollen type has almost no fossil record (only SRIVASTAVA & BINDA, 1991, associate dispersed Eocene palynomorphs with *Pothos* pollen, which has a stable ektexine, somewhat representative for this pollen type). The probably significant exception is *Spathiphyllum*: the continuous ektexine in the plicae and the lack of any aperture may cause a high resistance to decay. In contrast, the zonosulcate grains, found within the *Zamioculeas/Gonalopus* and independently in the *Monstereae*, probably have a smaller fossilization chance. In the non-apertural regions the exine consists of a massive ektexine (with imperforate tectum, short columellae, and a compact foot-layer), and a thin, slightly spongy endexine. The weak point of these zonosulcate („fully zonate“)

pollen grains could be represented by the zonosulcus: a thick, bilayered, distally tubular intine is covered by the endexine only. According to GRAYUM (1992) and HESSE *et al.* (2000b) after acetolysis the *Monstereae* pollen grains split into halves. Interestingly this is not the case in the zonosulcate grains of *Zamioculcas* and *Gonatopus*, because a

thin ectexine layer covers the endexine in the aperture region (HESSE *et al.*, 2000b). Hence, the zonosulcate condition may be more stable than first supposed. Recently, findings of Eocene fully zonate pollen grains or "pollen halves" were related to Araceae (ZETTER *et al.*, in press.), which was tentatively done earlier by THANIKAIMONI *et al.* (1984).

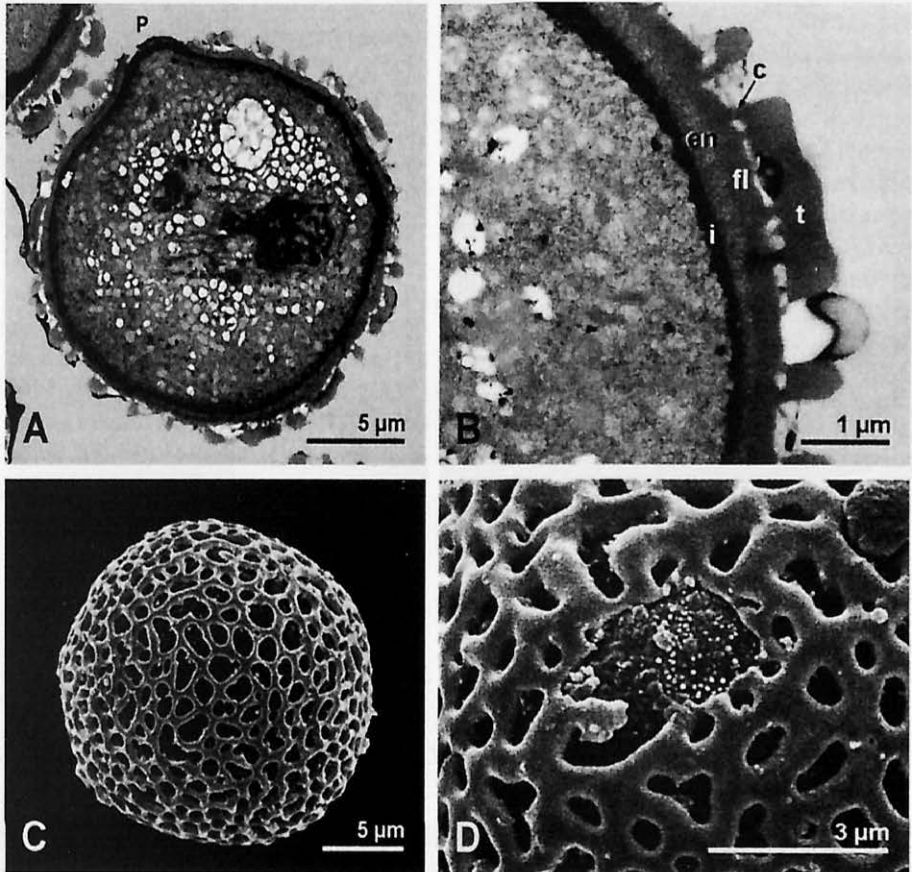


FIGURE 1. *Anthurium radicans* K. Koch. Porate, reticulate pollen grains in SEM and TEM view. A, pollen grain in cross section. P porus. B, detail of cross-sectioned pollen grain. Pollen wall stratification: t tectum, c columellae, fl foot-layer, en spongy endexine, i electron-dense intine. C, individual pollen grain. D, detail, with porate aperture.

The second type of pollen grains with an acetolysis-resistant layer upon the spongy endexine generally may have a much smaller fossilization potential. During acetolysis the dimension of the pollen grain enlarges enormously. The endexine quickly swells and often get ruptured indicating that the endexine cannot stand completely this chemical stress. Pollen of this type should have a considerable fossilization potential only if the spongy endexine is covered by an acetolysis-resistant ectexine. Generally the ectexine is more resistant to microbiological attack than the endexine. As in *Caladium* or *Spathicarpa*, the endexine remains covered by the ectexine, and does not split or swell (our unpubl. results). If found as a fossil such pollen would typically form inconspicuous smooth (collapsed) ovoids or bean-shaped bodies. These products of partial decay may be perhaps misinterpreted as fungal spores (BEUG, 1961). But without knowledge of the potential dramatic change from spiny to psilate pollen surface at least such smooth palynomorphs will not be recognized as Araceae pollen.

The third type of pollen grains should behave in a different manner: the spiny, or verrucate, or striate pollen ornamentation of many Aroideae is made of polysaccharidic substances (WEBER *et al.*, 1998, 1999), not resistant to acetolysis and thus has surely no fossilization potential. In contrast the smooth spongy endexine, which is present in all Aroideae, probably has some fossilization potential. It shows a restricted resistance to acetolysis: the diameters of these ovoids or spheres are enlarged, but simultaneously the pollen grains often collapse and may rupture. So, if resistant to decay and found in dispersed form, the pollen remnants may appear as ruptured, collapsed, inconspicuous bodies.

5. A CLOSE LOOK ON A SPECIAL CASE: THE POLYPPLICATE CONDITION IN VARIOUS ARACEAE, EPHEDRA AND "EPHEDROIDS" AS A MATTER OF CONVERGENCE

Dispersed polyplicate ephedroid pollen occur in sediments ranging from Lower Permian to Recent and are especially abundant in the Mid-Cretaceous, but also common in the Tertiary (e.g., KRUTZSCH, 1961; TAKAHASHI *et al.*, 1995; and especially CRANE, 1996; for review and discussion). Of the numerous ephedroids only three genera have been examined using the Transmission Electron Microscope (TEM): *Ephedripites mediolobatus* Bolkhovitina (TREVISAN, 1980), *E. virginiaensis* Brenner and *E. multicostatus* Brenner (KEDVES, 1994), *Equisetosporites chinleana* Daugherty (ZAVADA, 1984; POCOCK & VASANTHY, 1988), and *Cornetipollis reticulata* Pocock & Vasanthy (POCOCK & VASANTHY, 1988), all from Laurasian localities. The ephedroid pollen grains from the Lower Cretaceous of Brazil, a Gondwana locality, are most similar to *Ephedripites* (OSBORN *et al.*, 1993). Sometimes ephedroid pollen are found *in situ*, for example, attached to the Early Cretaceous pre-flower organ of *Vithimantha* (KRASSILOV, 1997). Fossil ephedroid pollen grains may represent an artificial group (OSBORN *et al.*, 1993). However, ephedroid grains may share affinities with various modern taxa and the Gnetales or Araceae in particular. Therefore, it was questioned if some of the presumed Gnetalean dispersed pollen grains might be confused with angiosperm polyplicate pollen grains.

Polyplicate, inaperturate pollen grains (in part strongly resembling the various "ephedroid" types) exist in several recent gymnosperm and angiosperm taxa (surprisingly within two subfamilies of the Araceae 10 genera with polyplicate pollen exist). Polyplicate pollen grains of Araceae (*Spathiphyllum*, *Holochlamys*, *Amorphophallus*, *Pseudodra-*

contium, *Arisarum*, *Ambrosina*, *Stuednera*, and *Pistia*), and Ephedraceae (*Ephedra*) were analysed with regard to their pollen walls. From the position of a palynologist working stratigraphically it is understandable that (almost) all dispersed polyplicate pollen grains are called "ephedroids", and often considered as related with Gnetales.

What about a possible confusion concerning "ephedroids" (dispersed recent and fossil pollen of the *Ephedra*-type including the fossil form genera *Ephedripites* and *Equisetosporites*) and *Spathiphyllum*? According to HUYNH (1975) *Ephedra* and *Spathiphyllum* share six parallel features, including the (alleged) same tetrad arran-

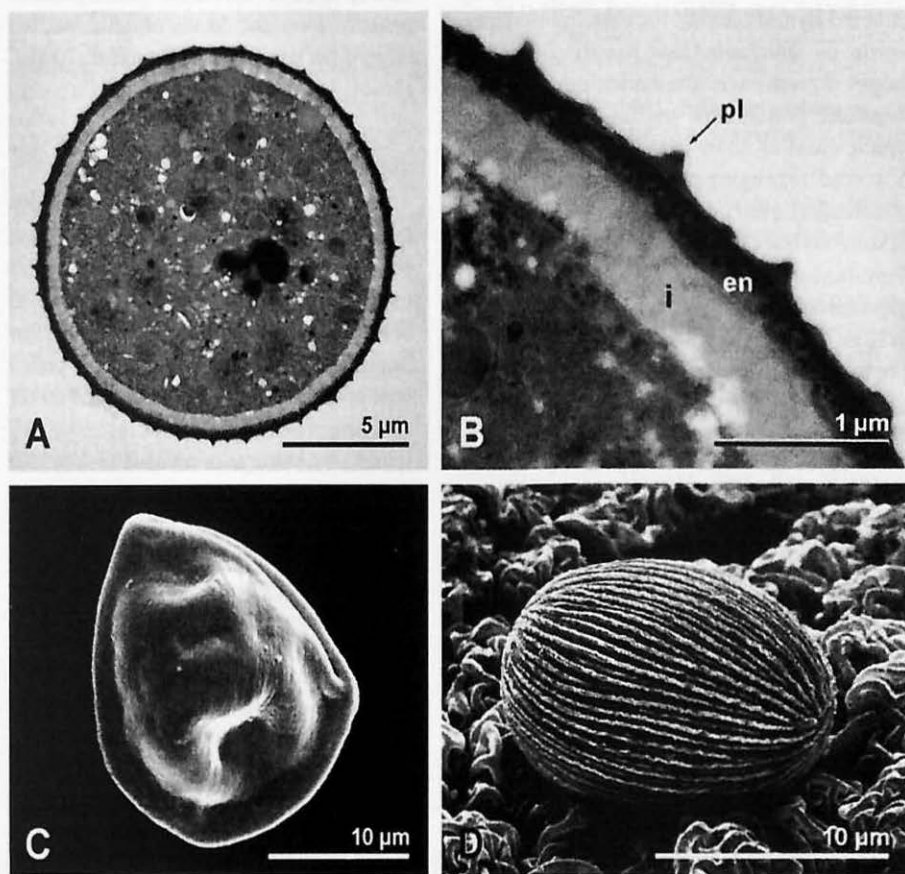


FIGURE 2. *Steudnera* ssp. Omniperturate, polyplicate pollen grains in SEM and TEM view. A, *Steudnera griffithii* Schott. Pollen grain in cross section. B, *St. griffithii* Schott. Detail of cross-sectioned pollen grain. Pollen wall stratification: pl acetolysis-susceptible plicae (ribs) in cross-sections, en spongy endexine, i intine. C, *St. colocasiifolia* K. Koch. Acetolysed pollen grain. D, *St. henryana* Engl. Pollen grain before acetolysis.

gement. In fact there are only four parallel features: 1. the presence of acetolysis-resistant ridges, 2. the whole exine is resistant to decay, 3. the evenly thick intine, and 4. the inaperturate condition. However, the two genera are separated by five different features: 1. ridges not columellate (*Ephedra*) versus columellate ridges in *Spathiphyllum*, 2. endexine lamellated and evenly thickened (*Ephedra*) or not lamellated and thin (*Spathiphyllum*), 3. in *Ephedra* the endexine is always totally covered by the continuous ektexinous ridges, while in *Spathiphyllum* the discontinuous ridges do not cover the endexinous grooves, 4. plicate pollen caps in *Ephedra* absent or much smaller than in *Spathiphyllum*, and 5. tetrad arrangement in *Ephedra* mostly tetrahedral (EL-GHAZALY *et al.*, 1998), in *Spathiphyllum* isobilateral (HUYNH, 1975; THANIKAIMONI, 1969). So confusing *Spathiphyllum* and *Ephedra* pollen grains is unlikely: at least form and nature of the ridges and the presence of the distinct "caps" in *Spathiphyllum* are clearly separating features.

HESSE *et al.* (2000a) compile their findings together with the published informations by EL-GHAZALY & ROWLEY (1997), EL-GHAZALY *et al.* (1998), GRAYUM (1992), HUYNH (1975), LUGARDON *et al.* (1987/88), REILLE (1992, 1998), THANIKAIMONI (1969), VAN DER HAM *et al.* (1998), and ZAVADA (1990). It was clearly demonstrated that the various polyplcate types are merely superficially similar. The polyplcate pollen grains distinctly differ in various morphological details and especially within the Araceae in the uncommon chemical composition of the ridges. It is concluded that the Araceae polyplcate pollen grains have either a low fossilization potential and - if at all preserved - will be found in a highly modified form (e.g., *Pistia*, *Ambrosina* and *Steudnera*, as smooth, ruptured bodies, respectively). MULLER (1981) pointed out that

pollen from *Ambrosina* is "expected" to occur in a polyplcate condition, but in fact this pollen, if at all preserved, will not appear in a polyplcate, but in a psilate condition! In contrast, as all *Ephedra*-*ephedroids* only the pollen grains of the Araceae genera *Spathiphyllum*, *Holochlamys*, and probably *Arisarum* have high fossilization potential: they should be found as polyplcate grains in the fossil record. But a "mix-up" of these pollen grains with *Ephedra* or *ephedroid* pollen grains is unlikely: form and details of the respective ridges differ significantly (HESSE *et al.*, 2000a).

CONCLUSION AND OUTLOOK

An investigation of recent and especially fossil, dispersed pollen material by TEM is time consuming and exhaustive. Nevertheless important palynological features can be found only if using the TEM with its analytical strength. A non-sporopollenin outer pollen wall layer seems to be a unique feature of Aroideae pollen: the nature of the respective spines, ribs, verrucae or whatsoever is neither ontogenetically nor chemically homologous to corresponding features of other taxa as, e.g., *Spathiphyllum* (Monsteroideae, Araceae: WEBER *et al.*, 1999), and this might be valid for - so far known - all other angiosperms.

Sometimes seemingly well established textbook views should be abandoned, in our case that the outermost pollen wall layer with its often typical ornamentation must consist of sporopollenin and thus must be found more or less unmodified, either in modern pollen floras or even in the fossil record. As every experienced palynologist knows, such insignificant palynomorphs may be easily overlooked, therefore not realizing the possible taxonomic value, or may be supposed as an artifact.

Special attention is called to many inconspicuous, smooth, often collapsed or ruptured grains, sometimes resembling fungal or fern spores. A smooth ovoid or sphere may be deriving either from pollen grains with a thin, smooth, acetolysis-resistant ectexine, or more often from originally spinose, verrucate or polyplicate pollen grains with an acetolysis-susceptible ornamentation. Those "overlooked" palynomorphs should be typical for many Aroideae, representing two thirds of all Araceae genera.

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REFERENCES

- ANGIOSPERM PHYLOGENY GROUP (1998). An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85:531-553.
- BENZING, L. (1969). *Beitrag zur Klärung der Verwandtschaftsverhältnisse der Tribus Araceae (= Aroideae-Araceae) auf vergleichend-blütenmorphologischer Grundlage.* Dissertation Universität Mainz.
- BEUG, H.J. (1961). *Leitfaden der Pollenbestimmung.* G. Fischer, Stuttgart.
- CAMPBELL, I.D. (1991). Experimental mechanical destruction of pollen grains. *Palynol.* 15:29-33.
- CRANE, P.R. (1996). The fossil history of the Gnetales. *Int. J. Plant Science* 157(6 Suppl.):S50-S57.
- EL-GHAZALY, G. & ROWLEY, J.R. (1997). Pollen wall of *Ephedra foliata*. *Palynol.* 21:7-18.
- EL-GHAZALY, G.; ROWLEY, J.R. & HESSE, M. (1998). Polarity, aperture condition and germination in pollen grains of *Ephedra* (Gnetales). *Plant Syst. Evol.* 213:217-231.
- ELSIK, W.C. (1971). Microbial degradation of sporopollenin. In: J. BROOKS; P.R. GRANT; M.D. MUIR; P. VAN GIJZEL & G. SHAW (eds). *Sporopollenin*, pp. 480-511. Academic Press, London.
- ERDTMAN, G. (1952). *Pollen morphology and plant taxonomy.* Angiosperms. Almqvist & Wiksell, Stockholm.
- FURNESS, C.A. & RUDALL, P.J. (1999). Inaperturate pollen in Monocotyledons. *Int. J. Plant Sci.* 160:395-414.
- GERMERAAD, J.H.; HOPPING, C.A. & MULLER, J. (1968). Palynology of Tertiary sediments from tropical areas. *Rev. Palaeobot. Palynol.* 6:189-348.
- GRAYUM, M. (1992). Comparative external pollen ultrastructure of the Araceae and putatively related taxa. *Monogr. Syst. Bot. Missouri Bot. Gard.* 43:1-167.
- HAVINGA, A.J. (1971). An experimental investigation into the decay of pollen and spores in various soil types. In: J. BROOKS; P.R. GRANT; M.D. MUIR; P. VAN GIJZEL & G. SHAW (eds). *Sporopollenin*, pp. 446-479. Academic Press, London.
- HAVINGA, A.J. (1984). A 20 year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. *Pollen Spores* 26:541-558.
- HERENDEEN, P.S.; CREPET, W.L. & NIXON, K.C. (1994). Fossil flowers and pollen of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Syst. Evol.* 189:29-40.
- HESSE, M.; WEBER, M. & HALBRITTER, H. (1998). Why is fossil Araceae pollen so rare? *Palyno-Nytt* 37:6-7.

- HESSE, M.; WEBER, M. & HALBRITTER, H. (2000a). A comparative study of the polyplicate pollen types in Arales, Laurales, Zingiberales and Gnetales. In: M.M. HARLEY; C.M. MORTON & S. BLACKMORE (eds). **Pollen and Spores: Morphology and Biology**, pp. 227-239. Royal Botanic Gardens, Kew.
- HESSE, M.; WEBER, M. & HALBRITTER, H. (1999). Pollen walls of Araceae, with special reference to their fossilization potential. **Grana**: 38:203-209.
- HESSE, M.; BOGNER, J.; HALBRITTER, H. & WEBER, M. (2000b). Palynology of the perigyniate Aroideae: *Zamioculcas*, *Gonatopus* and *Stylochaeton* (Araceae): **Grana**: in press.
- HUYNH, K.-L. (1975). Quelques phénomènes de polarité du pollen à plis multiples du genre *Spathiphyllum* (Araceae). **Beitr. Biol. Pflanzen** 50:445-456.
- KEDVES, M. (1994). Transmission electron microscopy of the fossil gymnosperm exines. **Szeged**.
- KRASSILOV, V.A. (1997). **Angiosperm origins: morphological and ecological aspects**. Pensoft, Sofia and Moscow.
- KRUTZSCH, W. (1961). Über Funde von "epheidroidem" Pollen im deutschen Tertiär. **Geol.** 10:15-53.
- KUPRIANOVA, L.A. & TARASEVICH, V.T. (1984). The ultrastructure of the surface of pollen grain wall in some genera of the family Lemnaceae and the related genera of the family Araceae. **Bot. Zhurn.** 69:1656-1662.
- LUGARDON, B.; LOBREAU-CALLEN, D. & LE THOMAS, A. (1987/88). Structures polliniques chez les Araceae - I, tribu des Spathiphyllaeae. **J. Palynol.** 23-24:51-57.
- MAHESWARI, P. & VASIL, V. (1961). *Gnetum*. Council of Scientific and Industrial Research, New Delhi.
- MARTINSSON, K. (1993). The pollen of Swedish *Callitriche* (Callitrichaceae) - trends towards submerge. **Grana** 32:198-209.
- MAYO, S.J.; BOGNER, J. & BOYCE, P.C. (1997). **The Genera of Araceae**. The Royal Botanic Gardens, Kew.
- MAYO, S.J.; BOGNER, J. & BOYCE, P.C. (1998). Araceae. In: K. KUBITZKI (ed.). **The Families and Genera of Vascular Plants. Monocotyledons: Alismatanae and Commelianaee (except Gramineae)**, pp. 26-74. Springer, Berlin.
- MCONCHIE, C.A.; KNOX, R.B.; DUCKER, S.C. & PETTITT, J.M. (1982). Pollen wall structure and cytochemistry in the seagrass *Amphibolis griffithii* (Cymodoceaceae). **Ann. Bot.** 50:729-732.
- MUELLER-STOLL, W.R. (1948). Zytomorphologische Studien am Pollen von *Taxus baccata* L. und anderen Koniferen. **Planta** 35:601-641.
- MUELLER-STOLL, W.R. (1956). Über das Verhalten der Exine nonaperturater Angiospermen-Pollen bei Quellung und Keimung. **Grana Palynol.** (N. S.) 1:38-58.
- MULLER, J. (1981). Fossil pollen records of extant Angiosperms. **Bot. Rev.** 47:1-142.
- OSBORN, J.M.; TAYLOR, T.N. & DE LIMA, M.R. (1993). The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. **Rev. Palaeobot. Palynol.** 77:171-184.
- PACINI, E. & JUNIPER, B.E. (1983). The ultrastructure of the formation and development of the amoeboid tapetum in *Arum italicum* Miller. **Protoplasma** 117:116-129.
- PARKINSON, B.M. & PACINI, E. (1995). A comparison of tapetal structure and function in pteridophytes and angiosperms. **Plant Syst. Evol.** 198:55-88.
- PETTITT, J.M. (1980). Reproduction in seagrasses: nature of the pollen and receptive surface of the stigma in the Hydrocharitaceae. **Ann. Bot.** 43:237-271.
- PETTITT, J.M.; MCONCHIE, C.A.; DUCKER, S.C. & KNOX, R.B. (1984). Reproduction in seagrasses: pollen wall morphogenesis in *Amphibolis antarctica* and wall structure in filiform grains. **Nord. J. Bot.** 4:199-216.

- POCOCK, S.A.J. & VASANTHY, G. (1988). *Cornetipollis reticulata*, a new pollen with angiospermoid features from Upper Triassic (Carnian) sediments of Arizona (U.S.A.), with notes on *Equisetosporites*. *Rev. Palaeobot. Palynol.* 55:337-356.
- PUNT, W.; BLACKMORE, S.; NILSSON, S. & LE THOMAS, A. (1994). *Glossary of Pollen and Spore Terminology*. University of Utrecht, Utrecht.
- RAJ, B. & SAXENA, M.R. (1966). Pollen morphology of aquatic Angiosperms. *Pollen Spores* 8:49-55.
- REILLE, M. (1992). *Pollen et spores d'Europe et d'Afrique du Nord*. Laboratoire de botanique historique et palynologie, Marseille.
- REILLE, M. (1998). *Pollen et spores d'Europe et d'Afrique du Nord*. Supplement II. Laboratoire de botanique historique et palynologie, Marseille.
- REITSMA, T. (1969). Size modification of recent pollen grains under different treatments. *Rev. Palaeobot. Palynol.* 9:175-202.
- ROWLEY, J.R. & PRIJANTO, B. (1977). Selective destruction of the exine of pollen grains. *Geophytology* 7:1-23.
- ROWLEY, J.R.; ROWLEY, J.S. & SKVARLA, J.J. (1990). Corroded exines from Havinga's leaf mold experiment. *Palynol.* 14:53-79.
- ROWLEY, J.R.; SKVARLA, J.J. & CHISSOE, W.F. (1997). Exine, onciform zone and intine structure in *Ravenala* and *Phenakospermum* and early wall development in *Strelitzia* and *Phenakospermum* (Strelitziaceae) based on aborted microspores. *Rev. Palaeobot. Palynol.* 98:293-301.
- SRIVASTAVA, S.K. & BINDA, P.L. (1991). Depositional history of the early eocene Shumaysi formation, Saudi Arabia. *Palynol.* 15:47-61.
- STEWART, W.N. & ROTHWELL, G.W. (1993). *Palaeobotany and the Evolution of Plants* (2nd edition). Cambridge University Press, Cambridge.
- TAKAHASHI, M.; TAKAI, K. & SAIKI, K. (1995). Ephedroid fossil pollen from the Lower Cretaceous (Upper Albian) of Hokkaido, Japan. *J. Plant Res.* 108:11-15.
- TAKHTAJAN, A. (1997). *Diversity and Classification of Flowering Plants*. Columbia University Press, New York.
- TARASEVICH, V.F. (1990). Palynological evidence of the position of the Lemnaceae family in the system of flowering plants. *Bot. Zhurn.* 75:959-965.
- THANIKAIMONI, G. (1969). Esquisse palynologique des Aracées. *Inst. Fr. Pondichéry, Trav. Sec. Sci. Tech.* 5:1-31.
- THANIKAIMONI, G. (1978). **Pollen morphological terms: proposed definitions. I.** Proceedings of the IV International Palynological Conference Lucknow 1, pp. 228-239.
- THANIKAIMONI, G. (1984). Omniperturate Euphorbiaceae pollen with striate spines. *Bull. Jard. Bot. Belg.* 54:105-125.
- THANIKAIMONI, G.; CARATINI, C.; VENKATACHALA, B.S.; RAMANUJAM, C.G.K. & KAR, R.K. (1984). Selected Tertiary Angiosperm pollens from India and their relationship with African Tertiary pollens. *Inst. Fr. Pondichéry, Trav. Sec. Sci. Tech.* 19:1- 92.
- TRAVERSE, A. (1988). *Palaeopalynology*. Unwin Hyman, Boston.
- TREVISAN, L. (1980). Ultrastructural notes and considerations on *Ephedripites*, *Eucommiidites* and *Monosulcites* pollen grains from Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen Spores* 22:85-132.
- VAN DER HAM, R.W.J.M.; HETTERSCHIED, W.L.A. & VAN HEUVEN, B.J. (1998). Notes on the genus *Amorphophallus* (Araceae). 8. Pollen morphology of *Amorphophallus* and *Pseudodracontium*. *Rev. Palaeobot. Palynol.* 103:95-142.
- VAN DER HAMMEN, T. & GARCIA DE MUTIS, G. (1966). The Palaeocene pollen flora of Colombia. *Leidse Geol. Med.* 35:105-116.

- VAN DER MERWE, J.J.M.; VAN WYK, A.E. & KOK, P.D.F. (1990). Pollen types in the Lauraceae. *Grana* 29:185-196.
- WEBER, M.; HALBRITTER, H. & HESSE, M. (1998). The spiny pollen wall in *Sauromatum* (Araceae) - with special reference to the endexine. *Int. J. Plant Sci.* 159:744-749.
- WEBER, M.; HALBRITTER, H. & HESSE, M. (1999). The basic pollen wall types in Araceae. *Int. J. Plant Sci.* 160:415-423.
- ZAVADA, M. (1984). Angiosperm origins and evolution based on dispersed fossil pollen ultrastructure. *Ann. Missouri Bot. Gard.* 71:444-463.
- ZAVADA, M. (1990). The ultrastructure of three monosulcate pollen grains from the Triassic Chinle formation, western United States. *Palynol.* 14:41-51.
- ZETTER, R.; HESSE, M. & FROSCH-RADIVO, A. (2001). Early Eocene zona-aperturate pollen grains of the *Proxapertites* - type with affinity to Araceae. *Rev. Palaeobot. Palynol.* (in press).