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, Potthoideae, Monstroideae, Lasiotidae, Calloideae and in Zamiocu/ea/Gonatopus (Aroideae) have aperturate pollen grains (mainly monosulcate, some disulcate), only few are lacking an aperture (i.e., the polyplicate pollen grains). Interestingly, the rare monosulcate condition is found independently in two subfamilies: Monstroideae and Zamiocuccas/Gonatopus (Aroideae). No member of the subfamily Aroideae has aperturate 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 polyplicate condition and, therefore, share parallels with ephedroid (Ephedra) pollen. Surprisingly only two polyplicate genera have an acetolysis-stable outer layer, while the polyplicate condition of the other 8 genera is gone after acetolysis. The meagre fossil record of Araceae, and the potential confusion of any polyplicate 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, SEM 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 ektexina) 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 si es estable bajo la acetolisis. Los granos de polen con una ektexina de esporopollenína deberían tener buenas oportunidades de fósilizar. Esto es válido para la mayoría de las subfamilias, sin...
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 Aroidaceae (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 polylicate appearance (Van der Hammen & Garcia de Mutis, 1966; Muller, 1981; Mayo et al., 1997). This
Principal pollen features in the Arum Lilies (Araceae)

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 exine (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 Aroidae, where often an acetoysis-susceptible outer layer (lacking a subdivision in tectum, columellae and foot-layer) and a spongy, thick acetoysis-resistant endexine forms the sporoderm. A second characteristic feature of Aroidae 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 Aroidae.

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: Steudnera colocasiifolia K. Koch, St. henryanana Engl., St. assimica 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 Erdman 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 (Aroidae, 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 - Aroidae, 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 Erdman’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 Aroidae pollen shows an ornamentation, which is not made of sporopollenin, but of exclusively tapetum-derived substances (polysaccharidic, according to the Thiery 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 Aroidae 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 Aroidae 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 Lernnaceae. 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 ekteexine. 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 ekteexine (Type 1 in Weber et al., 1999): A potassium hydroxide- and acetolysis-resistant, verrucate/reticulate, tectate/columellate, or thin and smooth ekteexine upon a loosely packed endexine. Examples include: Lysichiton, Anthurium, Calla, Spathiphyllum, Stenospermatum, and Arisaema. The ekteexine 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 ekteexine (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 Steudhiera 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 apertural 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, Lasiioideae and Calloideae, but is found also in few taxa with unisexual flowers, Zamia culeas and Gonatopus, i.e., two of the three perigoniate Aroideae genera (sensu Mayo et al., 1997). The third member of the perigoniate Aroideae, Stylochaeton, shows a thin, slightly lamellated endexine below a continuous, thin, intact ektexine. This striking difference to the pollen stratification of Zamia culeas/Gonatopus was one of the arguments, together with several morphological arguments to propose a new subfamily, the Zamia culeadoideae (Bogner & Hesse, in publ.). The pollen grains of the remaining Araceae with unisexual flowers, i.e. the aperigoniate 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, Oronto-

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<tr>
<th>Aroideae (Araceae)</th>
<th>Ornamentation before acetolysis</th>
<th>Ornamentation after acetolysis</th>
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<tr>
<td><strong>Arinae</strong> (tribe)</td>
<td>Thanikaimoni 1969: spiny</td>
<td>Thanikaimoni 1969: smooth</td>
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<td></td>
<td>Reille 1992: smooth</td>
<td>smooth</td>
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<td></td>
<td>Tarasevich 1990: plicate</td>
<td>Tarasevich 1990: smooth</td>
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<tr>
<td></td>
<td>Kuprianova &amp; Tarasevich 1984: plicate</td>
<td>Kuprianova &amp; Tarasevich 1984: smooth</td>
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<td></td>
<td>Erdman 1952: plicate</td>
<td>Raj &amp; Saxena 1960: smooth to obscure</td>
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**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., Steudnera (Fig. 2), with few exceptions, e.g., zonosulcate in Zamioceleas and Gonatopus, proposed for a new subfamily Zamioeleadaceae (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 Zamioceleas/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 & Priestant, 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; Elsk, 1971; Hovinga, 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 Aroidae) sensu Mayo et al. (1997), has stable, acetylisis-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: Pettitt, 1980; or Cymodoceaceae: McConchie et al., 1982; Pettitt 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 Meere 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 acelolysis 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 Aroidae, 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

<table>
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<tr>
<th>Spathiphyllum</th>
<th>Dracunculus</th>
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<td><strong>Before acelolysis</strong></td>
<td><strong>after acelolysis</strong></td>
</tr>
<tr>
<td>ektexine</td>
<td>present tectum, columellae and foot-layer</td>
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<tr>
<td>endexine</td>
<td>present</td>
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<td>intine</td>
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**TABLE 2:** Pollen wall stratification in main pollen types of Araceae, before and after acelolysis.

*Vol. 11 (2000)*
lower if a stable ektesixne 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 acetoysis-resistant ektesixne could be seen as one weak point: such pollen generally separate into halves during acetoysis (However, quite recently findings of Eocene fully zonate pollen could be related to fully zonate Araceae pollen types, (Zettaer et al., in press.). A second weak point may be the spongy endexine of most Aroidea: this type of endexine tends to swell enormously during acetoysis, and therefore may split. In some cases (e.g., Monstereae) such acetoysed 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 the character 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 ektesixne survive the acetoysis treatment intact as most dicot pollen does. However, taxa without an ektesixne do not survive acetoysis. While the spongy endexine is, in principal, acetoysis-resistant (Weber et al., 1998; Van der Ham et al., 1998), it swells greatly and may split during acetoysis. 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, acetoysis-resistant ektesixne. 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 Pothis pollen, which has a stable ektesixne, somewhat representative for this pollen type). The probably significant exception is Spathiphyllum: the continuous ektesixne 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 ektesixne (with imperfectate 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 zonosuleus: 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 zonosulate grains of Zamioculcas and Gonatopus, because a thin ektextine layer covers the endexine in the aperture region (Hesse et al., 2000b). Hence, the zonosulate 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).

The second type of pollen grains with an acetyolysis-resistant layer upon the spongy endexine generally may have a much smaller fossilization potential. During acetylolysis 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 acetylolysis-resistant extexine. Generally the extexine is more resistant to microbiological attack than the endexine. As in Caladium or Spathicarpa, the endexine remains covered by the extexine, 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 Aroidae is made of polysaccharidic substances (Weber et al., 1998, 1999), not resistant to acetylolysis and thus has surely no fossilization potential. In contrast the smooth spongy endexine, which is present in all Aroidae, probably has some fossilization potential. It shows a restricted resistance to acetylolysis: 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 POLYPLICATE CONDITION IN VARIOUS ARACEAE, EPHEDRA AND "EPHEDRIDS" 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): Ephedrites mediodobatus Bolkhovitina (Trevisan, 1980), E. virginiaensis Brenner and E. multiradiatus Brenner (Keedy, 1994), Equisetosporites chinleana Daugherty (Znada, 1984; Pockock & Vasanthy, 1988), and Concretipollis reticulata Pockock & Vasanthy (Pockock & Vasanthy, 1988), all from Laurasian localities. The ephedroid pollen grains from the Lower Cretaceous of Brazil, a Gondwana locality, are most similar to Ephedrites (Osborn et al., 1993). Sometimes ephedroid pollen are found in situ, for example, attached to the Early Cretaceous pre-flower organ of Vitimpantha (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, inaperture pollen grains (in part strongly resembling the various "epheidroid" 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, Steudnera, 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 Huyhn (1975) Ephedra and Spathiphyllum share six parallel features, including the (alleged) same tetrad arran-

Hesse, M.

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), Lugardoni 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 polyplicate types are merely superficially similar. The polyplicate 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 polyplicate 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 Steudhera, as smooth, ruptured bodies, respectively). Muller (1981) pointed out that pollen from Ambrosina is "expected" to occur in a polyplicate condition, but in fact this pollen, if at all preserved, will not appear in a polyplicate, 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 polyplicate 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-sporopolleninous outer pollen wall layer seems to be a unique feature of Aroidae pollen: the nature of the respective spines, ribs, verrueae or whatsoever is neither ontogenetically nor chemically homologous to corresponding features of other taxa as, e.g., Spathiphyllum (Monoteroidae, 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.
Principal pollen features in the Arum Lilies (Araceae)

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, acetylolicy-resistant ectexine, or more often from originally spiny, verrucate or polypticate pollen grains with an acetylolicy-susceptible ornamentation. Those 'overlooked' palynomorphs should be typical for many Aroidae, representing two thirds of all Araceae genera.

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Principal pollen features in the Arum Lilies (Araceae)


Hesse, M.


