6. RECENT MODELLING OF THE MAJOR EVOLUTIONARY DEGREES OF EARLY ANGIOSPERM POLLEN TYPES

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Abstract

Following the most important steps of the DOYLE scheme concerning the angiosperm pollen evolution of each monocolpate, tricolpate and tricolporate pollen types three recent species were investigated. After heating the monosulcate angiosperm pollen grains (*Magnolia, Allium, Chamaedorea*) are similar to the early gymnosperm types. The investigated tricolporate pollen grains are heterogeneous in this point of view. At the heated tricolporate pollen grains the *Longaxones* character and the apertural area transformed in a more characteristic way. The parameters of the axes of the fresh and the heated pollen grains during one hour at 200 °C were compared.

Key words: Palynology, angiosperm *Longaxones,* high temperature effect.

Introduction

The origin of the early angiosperm pollen grains was the subject of several investigations, by several methods. A monograph was published by HUGHES (1976). KREMP (1978) in connection with the regional distribution of the first angiosperm pollen grains gave 8000 references used by the computer method. Among them 800 were useful. DOYLE (1977) published a scheme of the first stage of the evolution of the angiosperm pollen grains. Following this, the monosulcate – tricolpate/tricolporoidate – tricolporate – early *Brevaxones* stages, as the most important in this respect, were pointed out. Later KÉDVES (1981) added to this the following: P. 77: "The most important changes in the form and symmetry are as follows:

I. *Longaxones;* monosulcate – tricolpate – tricolporate
II. *Brevaxones;* tricolporate – triporate, triatriate, etc.
1. *Monosulcate* – tricolpate; change in number of the germinal apertures
2. *Tricolpate* – tricolporate; change in the character of the aperture
3. *Tricolporate Longaxones;* shortening of the polar axis."

Our first results on the high temperature effect on recent angiosperm pollen grains (KEDVES and KINCSEK, 1989) are surprising. Further papers on different concepts followed this one, and as it has been emphasized several times, a large research program is under elaboration.

The aim of this paper is to present the first results on the modelling with recent taxa of the high temperature effect of the most important evolutionary steps of the first angiosperm pollen grains.

Materials and Methods

Fresh and heated pollen grains during one hour at 200 °C were the subject of our investigations. The investigated species are the following:
Magnolia soulangeana SOULANGE—BODIN (Plate 6.1., figs. 1—4, text-fig. 6.1. and 6.2.)
Collected: Dr. L. TÉCSI in the Botanical Garden of the J. A. University on 6.4. 1989.
Allium ursinum L. (Plate 6.1., figs. 5—11, text-fig. 6.1. and 6.2.)
Collected: A. CSESZKÓ in the Mecsek Mountains on 3.9. 1989.
Chamaedorea elegans MART. (Plate 6.1., figs. 12—16, text-fig. 6.1. and 6.2.)
Collected: Dr. L. TÉCSI in the Botanical Garden of the J.A. University on 23. 3. 1989.
Helleborus odorus W. et KIT. (Plate 6.1., figs. 17—20, text-fig. 6.1. and 6.2.)
Collected: Dr. I. KINCSEK in the Botanical Garden of the J. A. University on 16. 3. 1989.
Salix caprea L. (Plate 6.1., figs. 21—25, text-fig. 6.1. and 6.2.)
Collected: Dr. I. KINCSEK in the Botanical Garden of the J. A. University on 10. 3. 1989.
Quercus robur L. (Plate 6.1., figs. 26—30, text-fig. 6.1. and 6.2.)
Collected: Dr. M. KEDVES in the Garden of Újszeged (cultivated) on 3. 4. 1989.
Potentilla arenaria BORKH. (Plate 6.1., figs. 31—34, text-fig. 6.1. and 6.2.)
Collected: Dr. I. KINCSEK in Bugac on 31. 3. 1989.
Spiraea media FR. SCHM. (Plate 6.1., figs. 35—39, text-fig. 6.1. and 6.2.)
Collected: Dr. L. TÉCSI in the Botanical Garden of the J. A. University on 6. 4. 1989.
Castanea sativa MILL. (Plate 6.1., figs. 40—47, text-fig. 6.1. and 6.2.)
Collected: Dr. L. TÉCSI in the Botanical Garden of the J. A. University on 21. 6. 1989.

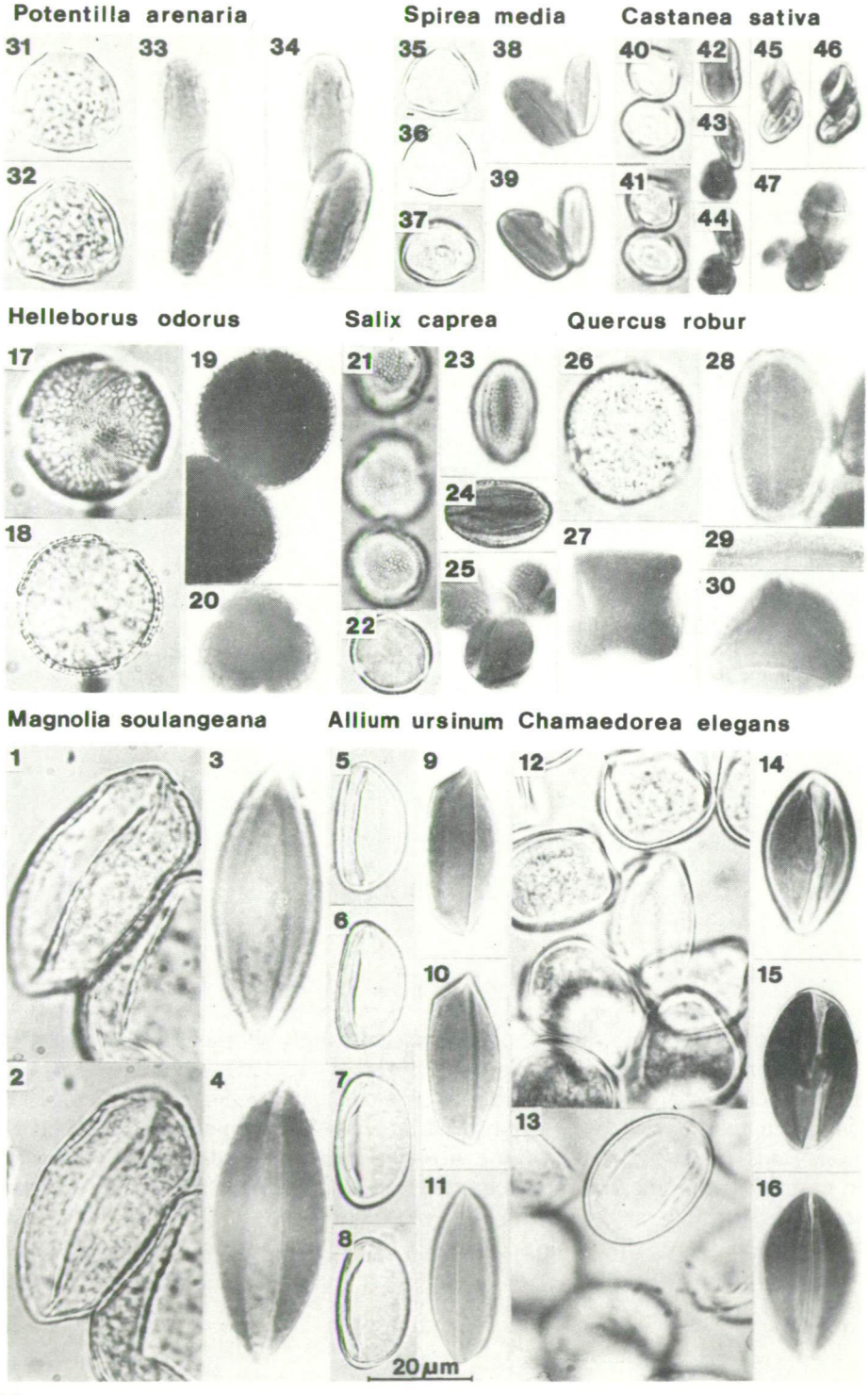
The fresh and the heated pollen grains were mounted in glycerin-jelly, hydrated at 39.6%. 200 specimens of each sample were investigated from the point of view of the qualitative and quantitative alterations. The polar axes in μm (Text-fig. 6.1.) and the values of P/E axis ratio (Text-fig. 6.2.) are illustrated.

Results

MONOSULCATE POLLEN TYPES

Magnolia soulangeana SOULANGE—BODIN
(Plate 6.1., figs. 1—4, text-fig. 6.1. and 6.2.)

Outline of the pollen grains after heating is strongly sharpened in contrast to the non-experimental material (Plate 6.1., fig. 3,4). This secondary form is similar to the associated pollen grains of *Wielandiella punctata* NATHORST 1909 following the monograph by POTONIÉ (1962). The variation-statistical graph of the polar axis (Text-fig. 6.1.) of the non-experimental and the experimental pollen grains has one maximum. A characteristic increasing of this character can be established at the heated material. The alteration of the P/E axis ratio is much more expressed, the "sharpening process" of the monosulcate forms is well established (Text-fig. 6.2.).


Potentilla arenaria
Spirea media
Castanea sativa
Helleborus odorus
Salix caprea
Quercus robur
Magnolia soulangeana
Allium ursinum
Chamaedorea elegans
MONOSULCATE TRICOLPATE TRICOLPORATE
20µm

◀ Plate 6.1.

1—4. *Magnolia soulangeana* SOULANGE—BODIN
1,2. Pollen grains without staining or heating.
3,4. Experiment No 587.
5—11. *Allium ursinum* L.
5—8. Pollen grains without staining or heating.
9—11. Experiment No 621.
12—16. *Chamaedorea elegans* MART.
12,13. Pollen grains without staining or heating.
14—16. Experiment No 563.
17—20. *Helleborus odorus* W. et KIT.
17,18. Pollen grains without staining or heating.
19,20. Experiment No 560.
21—25. *Salix caprea* L.
21,22. Pollen grains without staining or heating.
23—25. Experiment No 562.
26—30. *Quercus robur* L.
26. Pollen grains without staining or heating.
27—30. Experiment No 584.
31—34. *Potentilla arenaria* BORKH.
31,32. Pollen grains without staining or heating.
33,34. Experiment No 591.
35—39. *Spiraea media* FR. SCHM.
35—37. Pollen grains without staining or heating.
38,39. Experiment No 593.
40—47. *Castanea sativa* MILL.
40,41. Pollen grains without staining or heating.
42—47. Experiment No 718.

Allium ursinum L.
(Plate 6.1., figs. 5—11, text-fig. 6.1. and 6.2.)

The morphology of the fresh pollen grains is superficially similar to the monolete *Pteropsida* spores without perispore. This peculiar morphology can be observed at one part of the altered forms, in consequence of the high temperature (Plate 6.1., fig. 9,10). Others are similar to recent palm or monosulcate gymnosperm pollen grains. The variation-statistical graph of the polar axis is interesting (Text-fig. 6.1.). The non-experimental and the experimental material has one conspicuous maximum. The minimum value of the experimental material is not so far from the fresh pollen grains. In contrast to this, the character of the variation-statistical graphs of the P/E axis ratio of the fresh and the heated pollen grains (Text-fig. 6.2.) are different. The graph of the fresh pollen grains is similar to those of the polar axis, but the experimental one has several maxima, and the distance between the minimum and maximum values is much more larger than at the non-experimental.

Chamaedorea elegans MART.
(Plate 6.1., figs. 12—16, text-fig. 6.1. and 6.2.)

The sharpening of the pollen grains in consequence of the heating is well shown in Plate 6.1., figs. 14—16. These forms are very similar or identical with the experimental pollen grains of *Encephalartos transvenosus* STAPF et BURTT DAVY (KEDVES and AILER, 1990, p. 105, figs. 10—13). As regards the variation-statistical graphs of the polar axis (Text-fig. 6.1.), essentially a similarity can be established to those of *Allium ursinum*. But the P/E axis ratio is a little different in contrast to the previous.

TRICOLPATE POLLEN GRAINS

Helleborus odorus W. et KIT.
(Plate 6.1., figs. 17—20, text-fig. 6.1. and 6.2.)

No qualitative changes have happened at this species after heating (Plate 6.1., fig. 19,20). The variation-statistical graphs of the polar axis of the non-experimental and experimental pollen grains have their maximum at the same value in μm (Text-fig. 6.1.). However, a diminution of the per cent of the maximum value of the experimental material can be established. This is the trend at the variation-statistical graphs of the P/E axis ratio, too (Text-fig. 6.2.).

Salix caprea L.
(Plate 6.1., figs. 21—25, text-fig. 6.1. and 6.2.)

The most important alteration was the increasing of the polar axis in consequence of the high temperature (Plate 6.1., figs. 23—25). The approximatively globular forms altered into *Longaxones* type. The increasing of the polar axis can be well shown in Text-fig. 6.1. Moreover the graph of the P/E axis ratio of the fresh and the experimental pollen grains well represents this process (Text-fig. 6.2.)

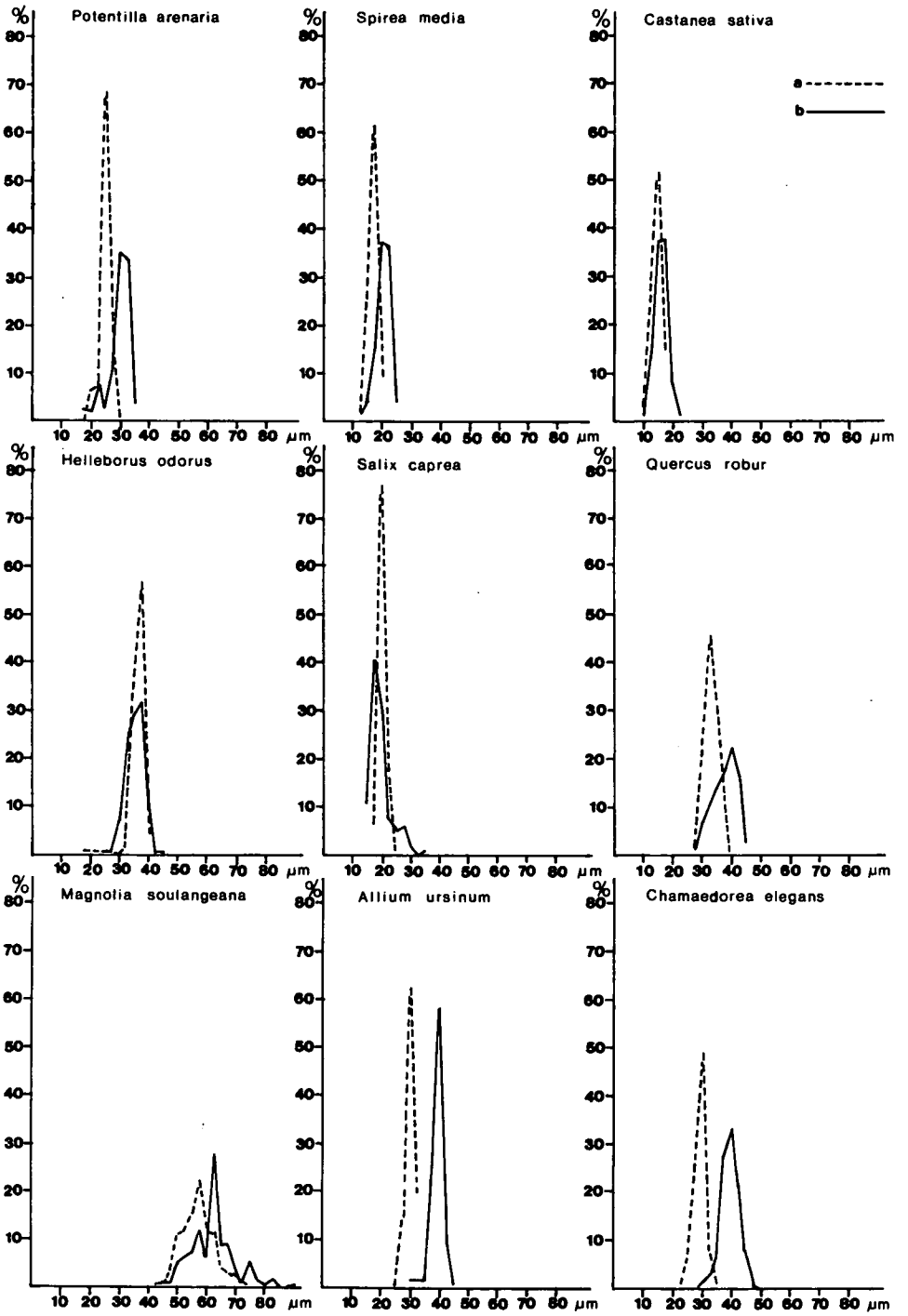
Quercus robur L.
(Plate 6.1., figs. 26—30, text-fig. 6.1. and 6.2.)

At this species heterogeneous and peculiar qualitative alterations have been observed. These are as follows.

i. The elongated *Longaxones* type (Plate 6.1., fig. 28, 29).
ii. *Brevaxones*-like forms (Plate 6.1., fig. 27,30).

Text-fig. 6.1. ▶

Variation-statistical graphs of the polar axis of the investigated pollen grains.
a: Fresh pollen grains.
b: Experimental pollen grains.


Potentilla arenaria
Spirea media
Castanea sativa
a
b
Helleborus odorus
Salix caprea
Quercus robur
Magnolia soulangeana
Allium ursinum
Chamaedorea elegans
%
μm

Inside this group plicate triaperturate (Plate 6.1., fig. 30) and tetra-aperturate forms (Plate 6.1., fig. 27) have been observed. These preservation forms are of early *Normapolles*-like types. The increase of the polar axis is well illustrated with the variation-statistical graphs of the non-experimental and the experimental pollen grains (Text-fig. 6.1.). A remarkable difference can be established. This is the same at the P/E axis ratio (Text-fig. 6.2.).

TRICOLPORATE POLLEN GRAINS

Potentilla arenaria BORKH.
(Plate 6.1., figs. 31—34, text-fig. 6.1. and 6.2.)

The alteration of the axis symmetry is extremely characteristic at this species. The contrast of the apertural area in the equatorial region is well shown (Plate 6.1., fig. 33,34). The alteration of the polar axis and the P/E axis ratio are very remarkable. Particularly the variation-statistical graph of the P/E axis ratio of the fresh and experimental pollen grains respectively is quite different.

Spiraea media FR. SCHM.
(Plate 6.1., figs. 35—39, text-fig. 6.1. and 6.2.)

As regards the qualitative and the quantitative alterations, these are essentially the same as the previously discussed species.

Castanea sativa MILL.
(Plate 6.1., figs. 40—47, text-fig. 6.1. and 6.2.)

At this species there are also not so conspicuous differences in the tendencies of the qualitative and quantitative characteristic features, including alterations. As one difference in contrast to the previous two species, the more *Longaxones* character of the fresh material can be pointed out. The experimental material (Plate 6.1., fig. 42—47) is very similar to several fossil tricolporate pollen grains which occur in the Upper Cretaceous and the Tertiary sediments.

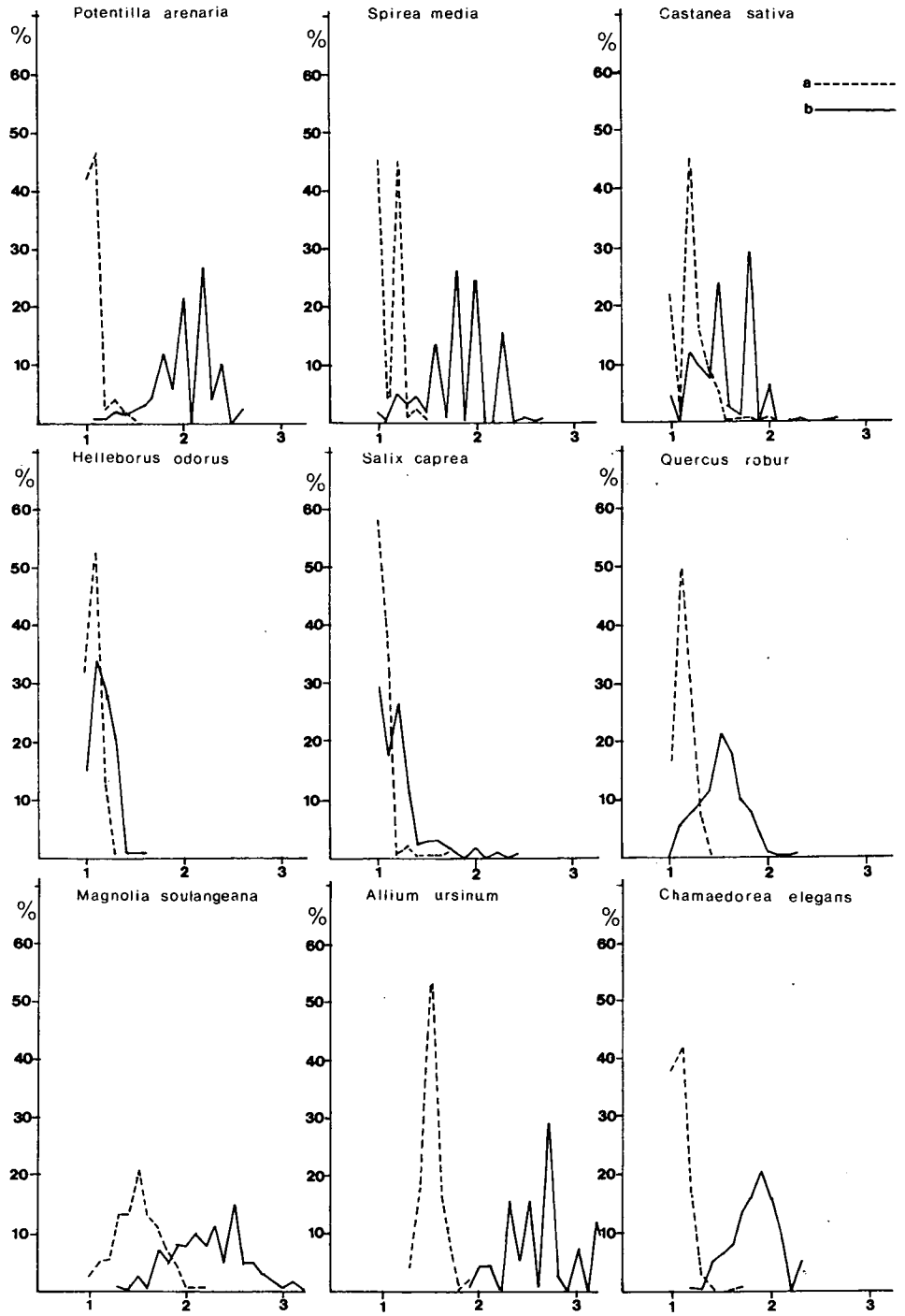
Discussion and Conclusions

The qualitative results of the secondary alterations, as it was emphasized at the first results, too, (KEDVES and KINCSEK, 1989) are heterogeneous in character.

All the investigated monosulcate pollen grains from the *Dicotyledonopsida* and the *Monocotyledonopsida*, after heating are similar to the early monosulcate *Gymnospermatophyta* type. In this respect, the altered forms of *Magnolia*

Text-fig. 6.2. ▶

Variation-statistical graphs of the P/E axis ratio of the species investigated.
a: Fresh pollen grains.
b: Experimental pollen grains.


Potentilla arenaria
Spirea media
Castanea sativa
a
b
Helleborus odorus
Salix caprea
Quercus robur
Magnolia soulangeana
Allium ursinum
Chamaedorea elegans
%
60
50
40
30
20
10
1
2
3

soulangeana (dicot.) and *Chamaedorea elegans* (monocot.) can be pointed out. But the altered forms of *Allium ursinum* are similar to *Cycadales* and to some *Palmales*, too.

Important and interesting alterations have been observed at the investigated tricolpate pollen grains. The most common alteration, namely the increasing of the polar axis, was observed at the pollen grains of the genus *Salix*. But the "morphological neutrality" of the pollen grains of *Helleborus odorus* in spite of heating, and the extremely interesting secondary forms at the pollen grains of *Quercus robur* can be pointed out. There are *Longaxones* and *Brevaxones* characters among the secondary altered pollen grains. These latter mentioned genuses (*Helleborus* and *Quercus*) and their taxonomically connected forms may be the subject of further investigations. At other species of the genuses *Helleborus* and *Quercus* it is a question that these have also the same or similar characters in connection with the secondary influences. Is the nearly non-altered polar axis at the pollen grains of *Helleborus odorus* the consequence of the relatively thick pollen wall? Similar secondary phenomenon was observed at the spores of *Equisetum arvense* L. (KEDVES, TÓTH and FARKAS, 1991). The diameter and the wall thickness ratio and the characters of the secondary altered forms may also be a problem to be investigated later.

The investigated tricolporate forms are the most homogeneous in contrast to the previously discussed ones. But it seems that the results of the investigations in the future will bring more interesting complementary data.

Finally, it is necessary to touch the question of the distance between the minimum and maximum values of the variation-statistical graphs. This characteristic feature was previously used in another respect. In connection with this problem the relation of this character to the evolutionary and taxonomically important secondary alterations will also be a problem to be investigated. Our present results in this point of view are as follows.

Polar axis

		minimum	maximum	deviation
Potentilla arenaria	0	17.5 µm	30.0 µm	12.5 µm
	591	17.5 µm	35.0 µm	17.5 µm
Spiraea media	0	12.5 µm	20.0 µm	7.5 µm
	593	12.5 µm	25.0 µm	12.5 µm
Castanea sativa	0	10.0 µm	17.5 µm	7.5 µm
	718	10.0 µm	22.5 µm	12.5 µm
Helleborus odorus	0	17.5 µm	40.0 µm	22.5 µm
	560	27.5 µm	45.0 µm	17.5 µm
Salix caprea	0	17.5 µm	25.0 µm	7.5 µm
	562	15.0 µm	35.0 µm	20.0 µm
Quercus robur	0	27.5 µm	40.0 µm	12.5 µm
	584	27.5 µm	45.0 µm	17.5 µm
Magnolia soulangeana	0	42.5 µm	75.0 µm	32.5 µm
	587	42.5 µm	90.0 µm	47.5 µm
Allium ursinum	0	25.0 µm	32.5 µm	7.5 µm
	621	30.0 µm	45.0 µm	15.0 µm
Chamadorea elegans	0	22.5 µm	35.0 µm	12.5 µm
	563	30.0 µm	47.5 µm	17.5 µm

P/E axis ratio

		minimum	maximum	deviation	increasting
Potentilla arenaria	0	1.0	1.6	0.6	
	591	1.1	2.6	1.5	0.9
Spiraea media	0	1.0	1.5	0.5	
	593	1.0	2.7	1.7	1.1
Castanea sativa	0	1.0	2.0	1.0	
	718	1.0	2.7	1.7	0.7
Helleborus odorus	0	1.0	1.3	0.3	
	560	1.0	1.6	0.6	0.3
Salix caprea	0	1.0	1.7	0.7	
	562	1.0	2.4	1.4	0.7
Quercus robur	0	1.0	1.4	0.4	
	584	1.0	2.3	1.3	0.9
Magnolia soulangeana	0	1.0	2.2	1.2	
	578	1.3	3.4	2.1	0.9
Allium ursinum	0	1.3	1.9	0.6	
	621	1.9	3.4	1.5	0.8
Chamaedorea elegans	0	1.0	1.7	0.7	
	562	1.2	2.3	1.1	0.4

At this moment it is not so easy to interpret these data but probably these will be useful after the complementary investigations.

Acknowledgements

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