Pollen morphology and systematics in two subfamilies of the Ericaceae: Pyroloideae and Monotropoideae∗

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Abstract

Pollen of two subfamilies of the Ericaceae; Pyroloideae and Monotropoideae, was examined by electron microscopy. Palynological data revealed the followings: 1) In Pyroloideae Chimaphila is placed more apart from the other three genera, Moneses is situated between Chimaphila and Pyrola, and Orthilia is closely related to some Pyrola species; 2) In Monotropoideae a phylogenetic tree of North American taxa presented by Copeland (1941) is supported for the most part, and furthermore it is evident that the most primitive and/or distinct member is North American Alloptrop and the most advanced one is eastern Asiatic Monotropastrum humile; 3) Monotropa hypopithys is basically characterized by plesiomorphic 3–aperturate pollen in the Old World vs. apomorphic 2–aperturate pollen in the New World; 4) Two subfamilies have evolved the pollen morphology independently, i.e., a diversity of pollen units in the former subfamily and of aperture numbers in the latter.

Introduction

Pollen morphology based on the electron microscopy is one of the most important characters for evaluating the taxonomic system in the angiosperms. At this paper the pollen morphology within the two small subfamilies of the Ericaceae is treated. According to Stevens (1971) the Ericaceae is composed of six subfamilies (Fig. 1), among which subfamilies Rhododendroideae, Ericaideae and Vaccinioideae, have a lot of genera and species (over 500 spp.) characterized by shrubby habit. The Pyroloideae and Monotropoideae are small subfamilies (each having less than 50 spp.) and considered to be derived from the Vaccinioideae. They are characterized by herbaceous and half-shrubby habit. Sometimes these two are recognized as the family separated from the Ericaceae sens. str. (e.g. Cronquist, 1981). On the base of the absence of distinct features distinguishing them from the Ericaceae sens. str., recently taxonomists follow the Stevens’ opinion (Haber, 1985; Haber and Cruise 1974; Wallace, 1975a, b, 1987).

Ericaceae

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Representative genera</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhododendroideae</td>
<td><em>Rhododendron, Ledum</em></td>
<td>19</td>
<td>900</td>
</tr>
<tr>
<td>Ericaideae</td>
<td><em>Erica, Calluna</em></td>
<td>20</td>
<td>700</td>
</tr>
<tr>
<td>Vaccinioideae</td>
<td><em>Vaccinium, Gaultheria</em></td>
<td>50</td>
<td>11200</td>
</tr>
<tr>
<td>Pyroloideae</td>
<td><em>Pyrola</em></td>
<td>4</td>
<td>40</td>
</tr>
<tr>
<td>Monotropoideae</td>
<td><em>Monotropa</em></td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>Wittsteinioideae</td>
<td><em>Wittsteinia</em></td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Fig. 1. A system of the Ericaceae sens. lat. showing the size of six subfamilies. The system is according to Stevens (1971) and the numbers of genera and species are according to Kříža (1971), Stevens (1971), Wallace (1975a, 1987) and so on.

Materials and Methods

For LM, SEM and TEM observations, the pollen samples were obtained from the dried specimens deposited in the following herbaria: G, KYO, MO, P, RSA, SAPT, TI, TUS and TUSG. Abbreviations of the herbarium names except for SAPT are according to the Index Herbariorum, Pt. I (Holmgren, Keuken & Schofield, ed. 7, 1981), and for SAPT see “News and notes” in Taxon 32 : 703 (1983). Pollen was processed in accordance with the methods outlined by Takahashi (1986a, b, 1987c).

Results and Discussion

1. Pyroloideae

The subfamily Pyroloideae is composed of four genera: *Pyrola, Orthilia, Chimaphila* and *Moneses*. Among them both *Orthilia* and *Moneses* are monotypic, whereas *Chimaphila* consists of about six species and *Pyrola* about 30 species. All the members of the Pyroloideae are native to mainly
coniferous and deciduous broad-leaved forests of temperate and cool temperate regions of the Northern Hemisphere.

There is a great diversity of the pollen unit within the subfamily (Fig. 2). Orthilia pollen is a monad, i.e., pollen grains are separated from each other. This feature is ubiquitous in the angiosperms. In Pyrola and Moneses, four grains derived from a pollen mother cell, are united into a pollen tetrad. This is unusual palynological feature in the angiosperms but the majority of species of the Ericaceae are characterized by the pollen tetrad. On the other hand Chimaphila pollen is a polyad, adjacent tetrads are loosely connected each other. This pollen unit, polyad is a first record from the Ericaceae (Takahashi, 1986b).

In Orthilia the aperture is 3–colpor(oid)ate characterized by the narrow and long colpi with verrucate sculpture. In Pyrola the aperture is 3–colporoidate forming concurrent colpi between

![Fig. 2. Pollen grains of four genera of the Pyroloideae. A. Orthilia secunda, monad showing verrucate exine sculpture and long narrow colpi; B. Pyrola asarifolia, tetrad showing rugulate exine sculpture and narrow concurrent colpi; C. Moneses uniflora, tetrad showing short and wide concurrent colpi; D. Chimaphila maculata, polyad showing psilate exine sculpture and ill demarcated colpi. Scale bars = 10 μm.](image-url)
adjacent grains, and colpus is commonly narrow with scarcely verrucate sculpture. In Moneses the aperture is 3–colpate characterized by comparatively wide and short colpi with verrucate sculpture. The aperture in Chimaphila is 3–colpate with colpi discontinuous from adjacent ones due to the loose connection between the pollen grains. Each colpus is not well demarcated as in the former genera.

Within the genus Pyrola exine sculpture on the distal face varies from verrucate through rugulate to psilate (Takahashi, 1986a, 1987b). Orthilia pollen is characterized by verrucate sculpture similar to that in some species of Pyrola; e.g., P.minor, P.grandiflora (Takahashi, 1987a). In Moneses the sculpture shows rugulate to psilate sculpture. Most species of Chimaphila have distinct psilate exine sculpture except for C. domingensis (Takahashi, 1986b).

From Orthilia through Pyrola and Moneses to Chimaphila, total exine, especially tectum increases in thickness and the exine sculpture changes from verrucate through rugulate to psilate. Furthermore Orthilia exine is characterized by reduced and thin columellae.

Pollen morphological features in four genera of the Pyroloideae are summarized in Fig. 3. In an ancestral stock of this group; Vaccinioideae, pollen tetrad is most common, therefore evolutionary trends from tetrads to monads and polyads respectively, are presumed. Furthermore taking the aperture feature, the exine sculpture and structure into consideration, close relationships among four genera based on pollen morphology are shown as lines connected between the genera.

So far, there have been two main opinions on the phylogenetic relationships among four genera of the Pyroloideae (Fig. 4). Above-mentioned palynological evidence is not well consistent with these opinions in either case. The evidence suggests that Chimaphila is comparatively distinct genus from the other three genera, Moneses is placed as an intermediate between Chimaphila and Pyrola,

![Diagram](R-P/4)

**Fig. 3. Palynological features of four genera of the Pyroloideae.** The meanings of abbreviated characters are as follows: V- verrucate, R- rugulate, P- psilate exine sculpture, 1-4- the degree of the exine thickness (larger numbers indicate thicker exine). Close relationships are shown by connected lines.
and *Orthilia* is related to some *Pyrola* species.

2. Monotropoideae

This subfamily is composed of 10 genera and 13 species (Wallace, 1975a, 1987). Seven of 10 genera are monotypic, therefore we can expect a great diversity in pollen morphology within this subfamily. The Monotropoideae are characterized by their mycotrophic achlorophyllous habit and reduced scale-like leaves. *Monotropa hypopithys* has the broadest range of distribution in the Monotropoideae, covering mainly temperate region of the Northern Hemisphere. The other species except for two *Monotropa* species have a somewhat limited distribution to either North America or eastern Asia.
Detailed result on the pollen morphology of this subfamily was recently published (Takahashi 1987c). In this paper, therefore, brief outlines are discussed. Every taxon examined until now has monads, therefore a diversity of the pollen unit is not found in the subfamily. On the other hand there is a variation in the aperture numbers. Aperture numbers are mainly two, three and four, shown in the polar view of the pollen grains in four representative genera (Fig. 5). Intraspecific

Fig. 5. Polar view of the pollen grains of representative four genera of the Monotropoideae. A. Monotropis odorata, 2-colpor(oid)ate pollen; B. Allotropa virgata, 3-colpor(oid)ate pollen; C. Pleurocospora fimbriolata, 4-colpor(oid)ate pollen; D. Monotropastrum humile, 3-porate pollen. Arrow heads indicate the aperture. Scale bar = 10 μm.
Table 1. A summary of the palynological characters in nine taxa in the Monotropoideae. In exine sculpture the meanings of the abbreviated characters are as follows: V-verrucate, R-rugulate, P-pilate, FV-fine verrucate, FR-fine rugulate exine sculpture.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of apertures</th>
<th>Shape of aperture</th>
<th>Exine sculpture</th>
<th>Sexine thickness</th>
<th>Horizontally oriented exine sub-layer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peterspora</td>
<td>4</td>
<td>colpus</td>
<td>W-R</td>
<td>thick</td>
<td>-</td>
</tr>
<tr>
<td>Sarcoles</td>
<td>4</td>
<td>colpus</td>
<td>R-R</td>
<td>thick</td>
<td>-</td>
</tr>
<tr>
<td>Allotropa</td>
<td>3</td>
<td>colpus</td>
<td>V-R</td>
<td>thick</td>
<td>-</td>
</tr>
<tr>
<td>Pleuricospora</td>
<td>4(5)</td>
<td>colpus</td>
<td>P</td>
<td>thick</td>
<td>+</td>
</tr>
<tr>
<td>Monotropis</td>
<td>2</td>
<td>colpus</td>
<td>P</td>
<td>thick</td>
<td>+</td>
</tr>
<tr>
<td>Monotropa hypophysis</td>
<td>3&amp;2</td>
<td>colpus(porus)</td>
<td>P</td>
<td>thick</td>
<td>-</td>
</tr>
<tr>
<td>Monotropa uniflora</td>
<td>3(2,4)</td>
<td>colpus&amp;porus</td>
<td>FV-FR</td>
<td>thin</td>
<td>-</td>
</tr>
<tr>
<td>Monotropastrum humile</td>
<td>3-4</td>
<td>porus</td>
<td>FV-FR</td>
<td>very thin</td>
<td>-</td>
</tr>
<tr>
<td>Hemitomes</td>
<td>2</td>
<td>colpus(porus)</td>
<td>P</td>
<td>thick</td>
<td>-</td>
</tr>
</tbody>
</table>

variation of the aperture numbers are also revealed in four taxa (Tab. 1). A remarkable point is that we can never find the infraspecific variation composed of exclusively two and four. So, we can scarcely or not presume that four aperturate pollen grains are originated from the two aperturate grains by multiplication, or two from four by reduction. Three aperturate condition is most common in the Ericaceae, it is reasonable to presume evolutionary trends from three aperturate pollen grains to two four aperturate grains, respectively.

In Monotropa hypophysis infraspecific variation of the aperture numbers may be correlated to the distribution area (Fig. 6). Most North American samples are characterized by two aperturate pollen, on the other hand. Old World samples have more wide variation in the aperture numbers and are mainly characterized by three aperturate pollen. As stated above, two aperturate pollen is regarded as apomorph and three aperturate pollen as plesiomorphic within this subfamily.

Palynological features including the aperture numbers, the aperture shape, the exine sculpture, the sexine thickness, and the presence of horizontally oriented exine sub-layer, are also summarized in Table 1. Copeland (1941) presented a phylogenetic tree of the North American Monotropoideae mainly based on the anatomical characters. Generally speaking, the present palynological evidence supports her phylogenetic tree composed of two main branches. Furthermore the followings are newly revealed: eastern Asiatic Monotropastrum humile having 3-4-porate pollen with reduced sexine is the most advanced member and North American Allotropa having 3-colp(orida)ate pollen is the most primitive and/or distinct member in the subfamily.
Fig. 6. Intraspecific variation of the aperture numbers in *Monotropa hypopithys*. One circle shows a variation within one individual.
References


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