Journal of the Minnesota Academy of Science

Volume 43 | Number 1 Article 2

1977

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ABSTRACT-Pollen of 16 species and one variety of the Myricaceae was examined, including members of each of the genera proposed by Chevalier (1901) in addition to Canacomyrica (Guillaumin, 1939). Comparison of pollen characters within genera, within sections, between sections, and between genera suggests that the Myricaceae can be divided into four genera: Canacomyrica; Comptonia; Gale; and Myrica. The genus Myrica can be further divided into three sections; Cerophora, Faya, and Morella.

The Myricaceae is a cosmopolitan family containing about 56 species mostly represented in tropical or subtropical regions. Its classification at both the generic and specific levels has been variously interpreted (Abbe, 1974); but in this study Chevalier (1901) is followed. Thus the family is divided into three genera: Comptonia, a North American monotype; Gale, with four species distributed throughout the North temperate region; and Myrica, with 50 mostly tropical species. To these the poorly known monotype, Canacomyrica, from New Caledonia must be added (Guillaumin, 1939). The genus Myrica is further divided into three sections: sect. Morella, with seven species in East Asia; sect. Faya, with three species in warm, temperate North America and the Atlantic Islands: sect. Cerophora, subdivided into the Africanae with 26 species and Americanae with 14 species. The purpose of this study, then, is to determine whether the classification proposed by Chevalier can be supported on the basis of pollen morphology.

Pollen Preparation

Dried male inflorescences were obtained from herbarium sheets of either the collection of L.B. and E.C. Abbe, the United States National Herbarium, or the University of Minnesota. The acquisition numbers of all specimens were recorded and each sample was given a reference number in the pollen reference collection at the University. Samples were chosen so as to be representative of the proposed genera and sections as outlined by Chevalier, within the limits of availability. These are listed in Table 1 and include two of the four species of Gale; Comptonia peregrina; three of the seven species of sect. Morella (two from S.E. Asia and one from Japan); two of the species of sect. Faya (one from California and one native to the Atlantic Islands); four of the 26 species of sect. Cerophora-Africanae (representing S. Africa, tropical E. Africa, and Madagascar) and three of the 14 species of sect. Cerphora-Americanae (representing temperate-subtropical N. America, the Caribbean Islands, and tropical S. America). In addition, because male inflorescences of Canacomyrica were not available (indeed, mostly because of insufficient material the literature on this species is limited to several short taxonomic descriptions) dried female inflorescences were used in the hope that pollen might be found which had been trapped in the intact stigmatic regions.

The procedure used in pollen preparation is a modification of the methods outlined by Faegri and Iverson (1964) involving treatment with KOH and acetolysis and mounting in silicone oil, which is routinely used for the preparation of reference pollen in the Pollen Analysis laboratory at the University of Minnesota. A detailed description of the procedure can be obtained from the author upon request.

Three sets of permanent slides were made of each preparation, one of these, complete and documented, has been placed in the pollen reference collection of the University of Minnesota. Observations, measurements, and drawings were made at 1250x with a Wild M20 equipped with drawing tube and ocular micrometer.

The terminology used is that of Faegri and Iverson and is illustrated in Figure 1. Pore protrusion is defined to be the distance between the outside surface of the pore margin and a line connecting the edges of the intact endexine at the base of a pore. Endopore diameter is taken to be the length of the line connecting the edges of the intact endexine at the base of the pore. Shape is defined in the manner of Erdtman (1952) as polar diameter divided by equatorial diameter. Size is defined as the greatest diameter of the grain.

Examining Pollen Grains

The Myricaceae is a typically stenopalynous family, the pollen grains showing very little difference among genera, and indeed it is sometimes difficult to distinguish the pollen from that of several genera of the Betulaceae, especially Betula and Corylus (Figure 2). Thus there are few definitive characters and often the characters at hand are interrelated one with another.

The characters chosen for study include: thickness of the ektexine; shape of the grain; size of the grain; exine sculpturing; extent of the pore's protrusion;

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diameter of the endopore. Three of the characters chosen are in some way related to the shape of the grain. The magnitude of the pore protrusion is included in the size of the grain. Likewise size is the denominator in the fraction used to determine the shape. Ideally, one would like to use independent characters in determining distinctions among taxa; however, preliminary observations indicated that the overall form of the grain is the most likely difference among genera, and thus the characters chosen should permit a quantification of these differences.

Ten grains of each species were scored for maximum equatorial and polar diameters, and either five or ten grains were scored for pore protrusion, endopore diameter, ektexine thickness, and sculpture. The range of possible values for each character was arbitrarily divided into three groups and assigned an index number of 1 to 3. Each species was then given an index number for each character, based on the average value obtained for that character. (Table 2).

Analysis of the Data

Table 2 shows the index value for each character of each species. To facilitate comparison the data are arranged according to the classification of Chevalier. Graphs were constructed of all the possible character combinations. These suggest that there might indeed be palynological evidence supporting Chevalier's classification. A composite graph can be seen in Figure 3. Size and shape are given on the abscissa and ordinate respectively. Each species is represented by a square within the correct block. The four remaining characters are indicated by the area included in each of the four quadrants of the square. Quadrant a represents endopore diameter, b is ektexine, c is the pore protrusion, and d is sculpture. An index value of 3 is represented by a completely filled quadrant, 1 is indicated by approximately one-fourth of the quadrant being included, and 2 is represented by the intermediate area.

A graph of this kind does not give an objective indication of the similarities within and between the genera in question. To do this, a simple mathematical procedure for computing the aggregate difference was employed (Anderson and Abbe, 1934). The differences between species within a genus were calculated from the data in Table 2 by the formula:

$$\text{Aggregate difference} = d12 + d22 + \ldots\ldots dn2$$

Thus, the aggregate difference between Gale palustris and G. hartwegii=

$$\sqrt{(3-2)_2+(3-2)_2+(3-3)_2+(2-3)_2+(2-3)_2(3-3)_2} = 20$$

This is scored under Intrageneric-Intrasectional differences in Table 3. The Intrageneric-Intersectional and Intergeneric differences are calculated in a similar manner and are also presented in Table 3.

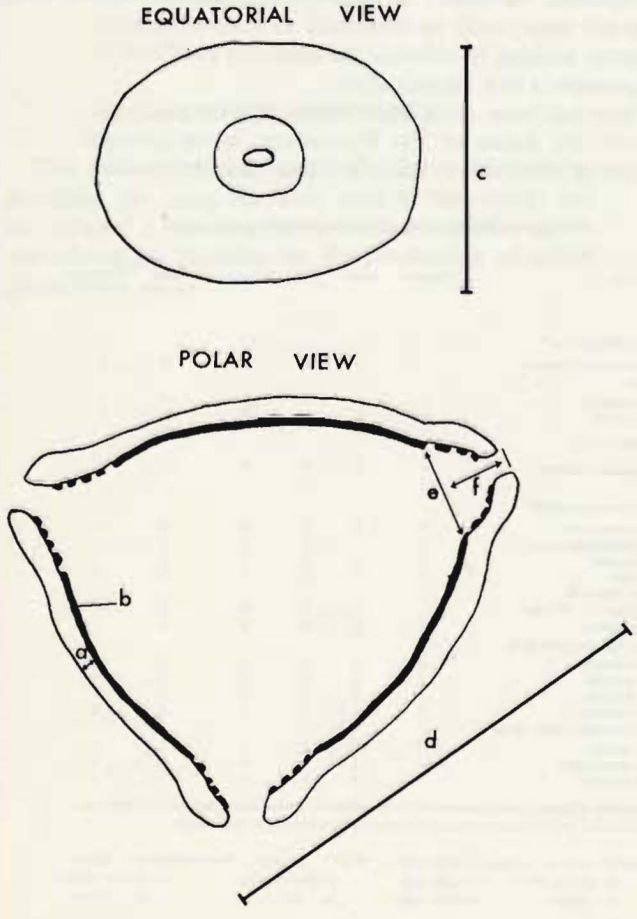


FIGURE 1.
Summary of Terminology: a) ektexine; b) endexine; c) polar diameter; d) equatorial diameter; e) endopore diameter; f) pore protrusion.

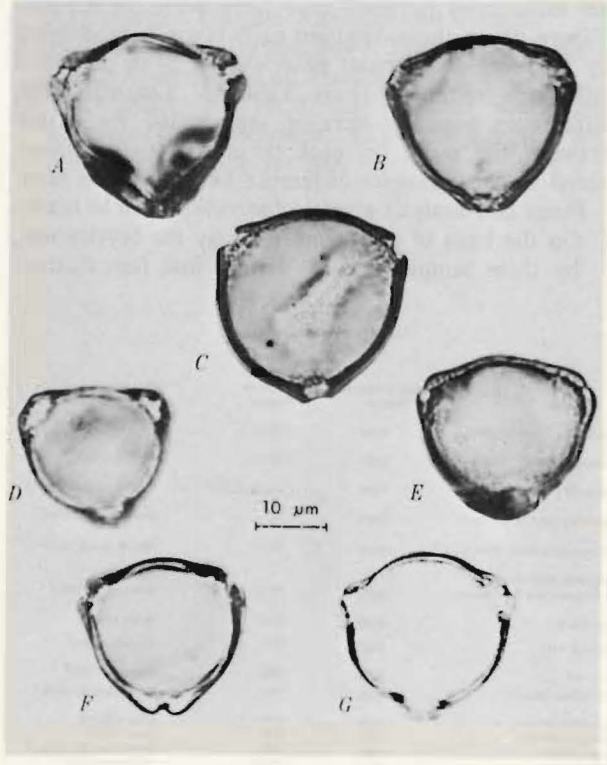


FIGURE 2.
Representative pollen grains of the Myricaceae: A) Myrica rugulosa; B) M. californica; C) Comptonia peregrina; D) canacomyrica monticola; E) M. cerifera; F) M. rubra; G) Gale palustris.

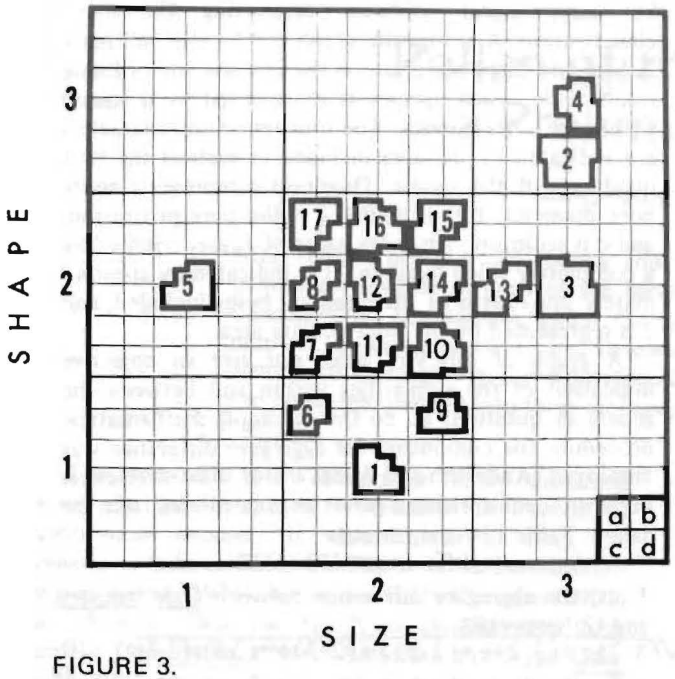


FIGURE 3.

Graphical representation of similarities between species of the Myricaceae. Quadrant a) endopore diameter; b) ektexine thickness; c) pore protrusion; d) sculpture.

See text for further explanation.

1) Canacomyrica monticola; 2) Gale palustris; 3) G. hartwegii; 4) Comptonia peregrina; 5) Myrica esculenta; 6) M. esculenta; var. far.; 7) M. javanica; 8) M. rubra; 9) M. faya; 10) M. californica; 11) M. salicifolia; 12) M. pulullifers; 13) M. rugulosa; 14) M. cordlifolia; 15) M. cerifera; 16) M. pennsylvanica; 17) M. pubescens.

From these data, three-dimensional models showing the differences between taxa have been constructed (Figure 4). In these diagrams each taxon is represnted by a sphere of diameter proportional to its aggregate difference obtained from Table 3. Likewise, the differences between taxa is represented by a line between the mean for each taxon of length proportional to the aggregate difference between those taxa.

From this analysis several observations can be made:

1. On the basis of pollen morphology the Myricaceae, by these samples, can be divided into four distinct genera: Myrica; Gale; Canacomyrica; Comptonia. This conclusion is reached because the distance representing the difference between the midpoint of any two genera is sufficiently large so that the extremes of differences within a genus does not overlap that of another genus.
2. On the basis of the same reasoning as above, the genus Myrica can be divided into three sections: Morella; Faya; Cerophora.
3. The data suggest that there is probably a basis for the division of section Cerophora into two subsections: Africanae and Americanae.

On the basis of this investigation, the classification of the Myricaceae by Chevalier, above the species level, seems to be generally upheld, however there is still some doubt as to how the section Cerophora should be handled. The seven of forty species sampled indicate that although the aggregate differences between subsections is less than would be required for complete separation, there is a tendency towards two separate groups. The writer would propose that a greater number of species of this section be examined, as material permits, which also could be treated in the manner followed in this paper.

There is also the possibility that by using average values for each character at the species level, the differences between taxa are exaggerated because intra-specific variability is masked. Alternatively the expanded data could be submitted to a more rigorous computer analysis to calculate the similarity coefficients and generate a new classification.

There has been some controversy over the composition of the exine of the Myricaceae, some authors suggesting that there may be three layers involved

TABLE 1. Materials Investigated

Species	Pollen Reference Number	Laboratory Acquistion Number	Voucher number
Canacomyrica monticola Guill.	B346	M275	Abbe et al 12195 [1]
Gale palustris Lamk.	B325	M287	Abbe et al 3031 [1]
G. hartwegii S. Wats	B344	U of M 237252	Cogdon (June 30, 1885)[2]
Comptonia peregrina (L.) Coult.	B323	M9	Jacobs (june 2, 1940) [1]
Myrica esculenta Buch.-Ham. (s.l.)	B345	M218	Keng & Jumali 10127 [1]
M. esculenta Buch.-Ham. var. farquahariana (Wall.) Chev.	B324	M67	Kiah (Jan. 2, 1941) [1]
M. javanica Bl.	B338	M227	Meijer 22057 [1]
M. rubra S. et C.	B303	M71	Hatusima 6390 [1]
M. faya Ait.	B339	M282	Fosberg 41782 [3]
M. californica Cham.	B336	M6	Reeve (Apr. 6, 1940) [1]
M. salicifolia Hochst.	B335	M280	Brass 17221 [3]
M. pilulifera Rendle	B337	M281	Brass 16862 [3]
M. rugulosa Baill.	B341	M47	Bond (June 26, 1940) [3]
M. cordifolia L.	B326	M279	Hildebrandt 4054 [3]
M. cerifera Sw.	B342	M238	Jensen 279 [1]
M. pennsylvanica Loisel.	B343	U of M 418720	Sargent (May 25, 1950) [2]
M. pubescens Willd.	B340	M15	Daniel 2241 [1]

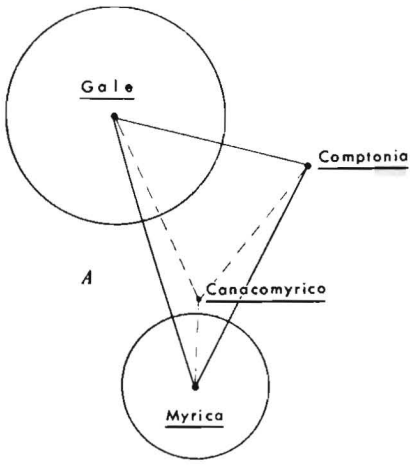
1 Personal herbarium of L.B. and E. C. Abbe
2 Herbarium of the University of Minnesota
3. United States National Herbarium

TABLE 2. Index Numbers of Selected Species for the Six Characters Examined

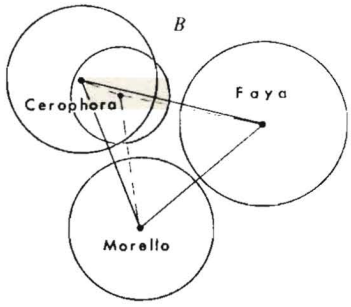
Species	Ektexine	Shape	Size	Sculpture	Pore Protrusion	Endopore Diameter
CANACOMYRICA (1/1) [1]						
Canacomyrica monticola	1	1	2	2	2	2
GALE (2/4)						
Gale palustris	3	3	3	2	2	3
G. hartwegii	2	2	3	3	3	3
COMPTONIA (1/1)						
comptoria peregrina	2	3	3	3	1	1
MYRICA sect. Morella (3/7)[2]						
Myrica esculenta	2	2	1	2	2	1
M. esculenta var. farq.	1	1	2	1	2	1
M. javanica	2	2	2	1	2	1
M. rubra	2	2	2	1	2	1
sect. Faya (2/3)						
M. Faya M. faya	1	1	2	2	2	1
M.californica	1	2	2	2	3	2
sect. Cerophora-Afr. (4/26)						
M. salicifolia	2	2	2	1	2	3
M. pilulifera	1	2	2	1	2	3
M. rugulosa	2	2	3	1	3	1
m. cordifolia	2	2	2	1	3	2
sect. Cerophora-Amer. (3/14)						
M. cerifera	2	2	2	1	3	2
M. pennsylvanica	1	2	2	2	3	2
M. pubescens	2	2	2	1	2	2

1 The number of species of each taxon studied is indicated by the fraction following the genus of section name.
2 In Myrica sect. Morella one of nine recognized varieties of M. esculenta also was examined.

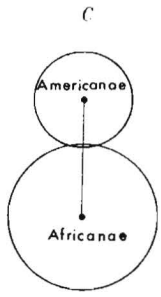
Ektexine 1 = 1.0 um; 2 = 1.0 - 2.0 um; 3 = 2.0 um
Shape 1 = 1.00 - 0.88; 2 = 0.88 - 0.75; 3 = 0.75 - 0.50
Size 1 = 25.0 um; 2 = 25.0 - 30.0 um; 3 = 30.0 um
Pore Protrusion 1 = 2.0 um; 2 = 2.0 - 3.0 um; 3 = 3.0 um
Sculpture 1 = strongly scabrate; 2 = scabrate; 3 = faintly scabrate
Endopore Diameter 1 = 7.0 um; 2 = 7.0 - 8.0 um; 3 = 8.0 um



A. Summary of intergeneric differences.



B. Summary of intrageneric differences, genus Myrica.



C. Intersectional differences, section Cerophora.

(Erdtman, 1943). Whether there is a varying number of layers involved could be precisely determined by mounting in resin, thin sectioning, and examining with the electron microscope. Pollen of all the species in this study has been prepared in such a way as to make similar infiltration possible. If a structural differentiation of the exine into three parts does indeed exist in some cases, this may serve as another character to differentiate the taxa.

ACKNOWLEDGEMENTS

The writer wishes to thank Dr. Ernst C. Abbe for providing the plant materials used in this study, and Dr. Edward J. Cushing for providing technical advice and laboratory facilities for the preparation of pollen grains.

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