

POLLEN FLORA OF PAKISTAN -XLII. BRASSICACEAE

ANJUM PERVEEN, M. QAISER AND REHANA KHAN*

Department of Botany, University of Karachi, Karachi-75270, Pakistan

**Federal Urdu University of Science, Arts & Technology,
Gulshan-e-Iqbal, University Road, Karachi, Pakistan*

Abstract

Pollen morphology of 77 species belonging to 36 genera of the family Brassicaceae from Pakistan has been examined by light and scanning electron microscope. Pollen grains are usually radially symmetrical, isopolar sub-prolate to prolate, or prolate-spheroidal rarely oblate-spheroidal, tricolpate rarely 4-8 colpate. Sexine thinner or thicker than nexine. Tectum fine to coarsely reticulate with more or less regular pattern of muri or reticulate – rugulate. On the basis of tectal surface four distinct pollen types are recognized viz., *Arabis bijuga*-type, *Farsetia ramosissima*-type, *Draba lanceolata* –type and *Erysimum melicentae* – type.

Introduction

Brassicaceae is a cosmopolitan family of about 350 genera and 3000 species, occurring mainly in north temperate zone particularly in Mediterranean region (Mabberley, 1987). In Pakistan it is distributed by 92 genera and 250 species (Jafri, 1973). Cruciferae are annual, biennial and perennial herbs. Corolla is cruciform (4 petals arranged in cross manner. Some common members of Brassicaceae are species of *Brassica oleracea* (Broccoli, Brussels sprout, Cabbage, Cauliflower, Kale etc.). Oil is also extracted from the seed of *Brassica* species. Many Crucifers are cultivated as ornamentals like *Aubrieta deltoidea* (aubrieta), *Erysimum cheire* (wallflower), *Arabis* sp., (rock cress). Chiguriaeva (1973) examined the pollen morphology of the family Brassicaceae in relation to taxonomy. Javied & Naqshi (1975) also utilized pollen data in the classification of family Brassicaceae. Jonsell (1986) during monographic studies of Brassicaceae also examined pollen morphology of this family. Lahham & Al-Essawi (1987) examined the pollen morphology of the family Brassicaceae from Jordan. Pollen morphology of the family Brassicaceae has been examined by Erdtman (1963), Sharma & Nair (1973), Carter *et al.*, (1975). Moore & Webb (1978). The most comprehensive studies of Brassicaceae pollen is that of Rollins & Banerjee (1979). However, there are no reports on pollen of the family Brassicaceae from Pakistan. Present investigations are based on the pollen morphology of 77 taxa representing 36 genera of the family Brassicaceae by light and scanning electron microscope.

Materials and Methods

Pollen samples were obtained from Karachi University Herbarium (KUH) or collected from the field. The list of voucher specimens is deposited in KUH. The pollen grains were prepared for light (LM) and scanning microscopy (SEM) by the standard methods described by Erdtman (1952). For light microscopy, the pollen grains were mounted in unstained glycerin jelly and observations were made with a Nikon Type-2 microscope, under E40, 0.65 and oil immersion (E100, 1.25), using 10x eye piece. For

SEM studies, pollen grains suspended in a drop of water were directly transferred with a fine pipette to a metallic stub using double sided cello tape and coated with gold in a sputtering chamber (Ion-sputter JFC-1100). Coating was restricted to 150 Å. The S.E.M examination was carried out on a Jeol microscope JSM-2. The measurements are based on 15-20 readings from each specimen. Pollen diameter, polar axis (P) and equatorial diameter (E), aperture size, apocolpium, mesocolpium and exine thickness were measured (Tables 1-4).

The terminology used is in accordance with Erdtman (1952), Kremp (1965), Faegri & Iversen (1964) and Walker & Doyle (1975).

General pollen characters of the family *Brassicaceae*

Pollen grains usually radially symmetrical, isopolar, sub-prolate or prolate to prolate-spheroidal, rarely oblate-spheroidal, tricolpate often 4-8 colpate. Sexine thinner or thicker than nexine. Tectum fine to coarse reticulate or reticulate-rugulate. On the basis of tectum types, four distinct pollen types are recognized viz., *Arabis bijuga*-type, *Farsetia ramosissima*-type, *Draba lanceolata* – type and *Erysimum melicentae* - type.

Key to the pollen types

1. + Tectum reticulate-rugulate *Farsetia ramosissima*-type
 - Tectum fine-coarse reticulate 2
2. + Tectum finely reticulate *Arabis bijuga*-type
 - Tectum not as above 3
3. + Tectum medium reticulate *Erysimum melicentae* - type
 Tectum coarsely reticulate..... *Draba lanceolata* –type

Pollen type: *Arabis bijuga* - type (Fig. 1 A-C)

Pollen class: Tricolpate

P/E ratio: 108-140

Shape: Prolate-spheroidal to sub-prolate rarely prolate.

Apertures: Colpus long sunken with acute ends.

Exine: Sexine thicker than nexine.

Ornamentation: Finely reticulate more or less regular pattern of muri.

Measurements: Size: Polar axis P=16 (25.5) 32.5 µm and equatorial diameter E=15 (21.5) 28 µm, trilobed, with apertures on the angles of the outline of the grain in polar view, colpi 10 (15.5) 20 µm long. Exine 1.0 (1.5) 2.5 µm thick, sexine as thick as nexine. Tectum finely reticulate.

Species included: *Arabidopsis mollissima* (C.A. Mey) Busch, *A. traxacifolia* (T.And.) Jafri, *Arabidopsis wallichii* (Hook.f. Thoms.) Busch, *A. stricta* (Camb.) Busch., *Arabis amplexicaule* Edgew., *A. bijuga* Watt., *A. pterosperma* Edgew., *Bassica juncea* (L.) Czern., *B. napus* L.ssp. *napus*, *B. nigra* (L.) Koch., *B. oleracea* var. *botrytis* L., *B. oleracea* var. *capitata*, *B. rapa* ssp. *rapa*, *B. rapa* ssp. *campestris*, *Cardamine impatiens* L., *Chorispora sibirica* (L.) DC., *Douepia tortuosa* Camb., *Drabopsis verna* Koch., *Euclidium syriacum* (L.) R.Br., *Malcolmia scorpioides* (Bunge) Boiss.

Key to the species and group

1. + Pollen grains prolate-spheroidal *Douepia tortuosa* - subtype
(*Arabis pterosperma*, *Douepia tortuosa*, *Bassica juncea*, *Brassica napus* ssp.
napus, *B. nigra*, *B. rapa* ssp. *rapa*)
- Pollen grains sub-prolate to prolate 2
2. + Pollen grains subprolate *Arabidopsis mollissima*- subtype
(*Arabidopsis mollissima*, *A. traxacifolia*, *Arabis amplexicaule*, *A. bijuga*,
Brassica oleracea var. *capitata*, *B. rapa* ssp. *campestris*, *Cardamine impatiens*,
Chorispora sibirica, *Drabopsis verna*, *Euclidium syriacum* *Malcolmia*
scorpioides)
- Pollen grains prolate *Arabidopsis wallichii*-subtype
(*Arabidopsis wallichii*, *A. stricta*, *Brassica oleracea* var. *botrytis* L.)

Pollen type: *Erysimum melicentae* (Fig. 1D-F. Fig. 2 A & B).

Pollen class: Tricolpate

P/E ratio: 110-151

Shape: Sub-prolate to prolate rarely prolate-spheroidal

Apertures: Colpus long sunken with acute ends.

Exine: Sexine thicker or thinner than nexine.

Ornamentation: Medium reticulate with more or less regular pattern of muri.

Measurements: Size: Polar axis P=16 (24.5) 32.5 µm and equatorial diameter E=15 (21.5) 32 µm, (trilobed, with apertures on the angles of the outline of the grain in polar view, colpi 10 (15.5) 17.5 µm long. Exine 1.0 (1.96) 2.5 µm thick, sexine as thick as nexine. Tectum medium reticulate.

Species included: *Alliaria petiolata* (M.Bieb.) Cav. Grande, *Arabis saxicola* Edgew, *Alyssum desertorum* Staph, *Arabidopsis pumila* (Steph) Busch, *Cardaria drapa* (L.) Desv., *Cithareloma lehmannii* Bunge, *Coronocarpus didymus* (L.) Smith, *Diceratella canescens* (Boiss.) Boiss., *Goldbachia laevigata* (M.Bieb.) DC. *Eremobium aegypticum* (Spreng) Boiss., *Leptaleum filifolium* (Willd.) DC., *Malcolima strigosa* Boiss.

Key to the species and group

1. + Pollen grains prolate-spheroidal *Goldbachia laevigata*
- Pollen grains sub-prolate to prolate 2
2. + Pollen grains prolate *Alyssum desertorum*-sub-type
(*Alyssum desertorum*, *Arabis saxicola*, *Arbidopsis pumila*, *Cardaria drapa*)
- Pollen grains sub-prolate *Alliaria petiolata* -subtype
(*Alliaria petiolata*, *Cithareloma lehmannii*, *Coronocarpus didymus*, *Diceratella canescens*, *Goldbachia laevigata*, *Eremobium aegypticum*, *Leptaleum filifolium*,
Malcolima strigosa)

Pollen type: *Draba lanceolata*- type (Fig. 2 C-F; Fig. 3A-F; Fig. 4A-F)

Pollen class: Tricolpate

P/E ratio: 106-168

Shape: Prolate to subprolate rarely prolate-spheroidal

Fig. 1. Scanning Electron micrographs of pollen grains. *Arabis bijuga*: A, Equatorial view, B, Exine pattern. *A. pterosperma*: C, Polar view. *Leptaleum filifolium*: D, Equatorial view. *Cithareloma lehmannii*: E, polar view, F, Exine pattern. Scale bar = A, C, D & E = 10; B, F = 1 μm

Fig. 2. Scanning Electron micrographs of pollen grains. *Leptaleum filifolium*: A, Exine pattern. *Eremobium aegypticum*: B, pollen grains. *Isatis minima*: C, Equatorial view, D, Exine pattern. *Capsella burspastoris*: E., Polar view, F, Exine pattern. Scale bar =B, C & E = 10; A, D & F = 1 μ m

Fig. 3. Scanning Electron micrographs of pollen grain. *Boreava orientalis*: A, Equatorial view. *Euclidium tenuissimum*: B, Equatorial view, C, Exine pattern. *Farsetia hamiltonii*: D, Exine pattern, E, Equatorial view. *Alyssum desertorum*: F, Exine pattern. Scale bar = A, B & E = 10; C, D & F = 1 μm

Fig. 4. Scanning Electron micrographs of pollen grains. *Draba stenocarpa*: A, Exine pattern, B, Equatorial view. *Draba trinervia*: C, Polar view. *Christolea himalayensis*: D, Equatorial view, E, Exine pattern. *Barbrea intermedia*: F, Equatorial view. Scale bar = B –D & F= 10; A & E = 1 μ m

Apertures: Colpus long sunken with acute ends.

Exine: Sexine thicker than nexine.

Ornamentation: Coarsely reticulate.

Measurements: Size: Polar axis $P=16$ (27.5) $39.5\ \mu\text{m}$ and equatorial diameter $E=16$ (18.5) $22.1\ \mu\text{m}$, (trilobed, with apertures on the angles of the outline of the grain in polar view, colpi 10 (21.5) $32.5\ \mu\text{m}$ long. Exine 1.5 (2) $2.5\ \mu\text{m}$ thick, sexine as thick as nexine. Tectum coarsely reticulate.

Species included: *Alyssum desertorum* Staph, *Boreava orientalis* Jaub. & Spach, *Capsella bursa-pastoris* (L.) Medik., *Chorisporea bungeana* Fish & Mey, *Christolea himalayensis* (Camb.) Jafri, *Chorisporea tenella* (Pallas) DC., *Draba trinervis* Schultz, *D. altaica* (C.A. Mey) Bunge, *D. lanceolata* Royle, *D. melanopus* Kom., *D. stenocarpa* Hook. F. & Thoms. *Euclidium tenuissimum* (Pallas) B. Fedtsch., *Erysimum meilicentae* Dunn., *E. griffithianum* Boiss, *Farsetia hamiltonii* Royle, *Diceratella floccose* (Boiss.) Boiss., *Farsetia heliophila* Bunge ex Coss., *Isatis stocksii* Rech.f Boiss, *I. minima* Bunge, *Lepidium virginicum* L, *Matthiola macranica* Rech f., *Matthiola flavida* Boiss., *Malcolmia cabulica* (Boiss.) Hook. F. Thoms, *Malcolmia africana* (L.) R.Br., *Nasturtium officinale* R. Br., *Microsisymbrium flaccidum* Schulz.

Key to the species and group

1. + Pollen grains prolate-spheroidal *Isatis stocksii*-subtype (*Isatis stocksii*, *Isatis minima*)
 - Pollen grains not as above 2
2. + Pollen grains prolate *Capsella bursa-pastoris*. -subtype (*Capsella bursa-pastoris*, *Boreava orientalis*, *Chorisporea tenella*, *Malcolmia cabulica*)
 - Pollen grains sub-prolate *Matthiola macranica*-subtype (*Chorisporea bungeana*, *Christolea himalayensis*, *Draba trinervis*, *D. altaica*, *D. lanceolata*, *D. melanopus*, *D. stenocarpa*, *Euclidium tenuissimum*, *Erysimum meilicentae*, *E. griffithianum*, *Farsetia hamiltonii*, *Diceratella floccose*, *Farsetia heliophila*, *Lepidium virginicum*, *Matthiola macranica*, *Matthiola flavida*, *Malcolmia africana*, *Nasturtium officinale*, *Microsisymbrium flaccidum*)

Pollen type: *Farsetia ramosissima* - type (Fig. 5 A-G)

Pollen class: Tricolpate

P/E ratio: 102-113

Shape: Sub-prolate to prolate-spheroidal rarely prolate.

Apertures: Colpus long sunken with acute ends.

Exine: Sexine thicker than nexine.

Ornamentation: Reticulate – rugulate.

Measurements: Size: Polar axis $P = 14$ (23.5) $32.5\ \mu\text{m}$ and equatorial diameter $E=12$ (18) $24\ \mu\text{m}$, trilobed, with apertures on the angles of the outline of the grain in polar view, colpi 8.75 (16.5) $25.5\ \mu\text{m}$ long. Exine 1.5 (2) $2.5\ \mu\text{m}$ thick, sexine as thick as nexine. Tectum reticulate-rugulate.

Species included: *Barbarea vulgaris*, *Conringia planisiliqua* Fisch & Mey., *Crambe cardifolia* Steven, *Descurainia sophia* (L.) Webb. & Berth., *Diplotaxis griffithii* (Hook. f.

Fig. 5. Scanning Electron micrographs of pollen grains. *Diplotaxis harra*: A, Polar view, *D. griffithii*: B, Equatorial view, C, Exine pattern. *Crambe cordifolia*: D, Polar view. *Conringia planisliqua*: E, Equatorial view, F, Exine pattern, G, Polar view. Scale bar = A, B, D, E & G = 10; C & F = 1 μm

& Thoms.) Boiss., *Diptychocarpus strictus* (Fish.M.Beib.) Trautv, *Diploaxis harra* (Forssk.) Boiss, *Erysimum crassicaule* (Boiss.) Boiss., *Erysimum melicentae* Dunn., *E. repandum* L., *Farsetia ramosissima* Hochst. ex Boiss., *Malcolmia behboudiana* Rech.f., *Moricandia sinaica* (Boiss.) Boiss. *Lepidium aucheri* Boiss., *Isatis costata* C.A.Mey

Key to the species and group

1. + Pollen grains oblate-spheroidal.....*Isatis costata*
 - Pollen grains prolate-spheroidal or prolate to sub-prolate 2
2. + Pollen grains prolate *Erysimum crassicaule*-subtype (*Erysimum crassicaule*, *E. repandum*, *Barbarea vulgaris*)
 - Pollen grains sub-prolate *Diploaxis griffithii*-subtype (*Conringia planisiliqua*, *Crambe cardifolia*, *Descurainia sophia*, *Diploaxis griffithii*, *Diptychocarpus strictus*, *Diploaxis harra*, *Erysimum crassicaule*, *Erysimum melicentae*, *E. repandum*, *Farsetia ramosissima*, *Malcolmia behboudiana*, *Moricandia sinaica*, *Lepidium aucheri*)

Discussion and Conclusions

Brassicaceae is a stenopalynous family (Erdtman, 1952). Pollen grains are generally prolate to sub-prolate or prolate – spheroidal rarely oblate – spheroidal, 3 - colpate often 4-8 –colpate as in *Erysimum stocksiana*. Tectum reticulate, reticulum varies from fine – coarse. Appel & Al-Shehbaz (2003) also reported tricolpate reticulate pollen in the family Brassicaceae. However, they reported sparsely spinulose and punctate tectum in the genus *Heliophila* and 10-colpate pollen in few genera of Brassicaceae. Erdtman (1963) divided the species of Brassicaceae into two pollen types on the bases of exine thickness. Moore & Webb (1987) classified the family in tricolpate with reticulate pollen. Khalik (2002) divided the family into three pollen types on the basis of lumina size. The generic delimitation based on pollen morphology is difficult. However, on the basis of tectal surface four distinct pollen types are recognized viz., *Arabis bijuga* – type, *Erysimum melicentae* - type, *Farsetia ramosissima* - type, *Draba lanceolata* - type. The *Arabis bijuga* – type is easily recognized by having finely reticulate pollen, 20 species are included in this pollen type viz., *Arabidopsis mollissima* (C.A. Mey) Busch, *A. traxacifolia* (T.And.) Jafri, *Arabidopsis wallichii* (Hook. f. Thoms.) Busch, *A. stricta* (Camb.) Busch., *Arabis amplexicaule* Edgew., *A. bijuga* Watt., *Arabis pterosperma* Edgew, *Brassica juncea* (L.) Czern., *B. napus* L., ssp., *napus*, *B. nigra* (L.) Koch., *B. oleracea* var. *botrytis* L., *B. oleracea* var. *capitata*, *B. rapa* ssp. *rapa*, *B. rapa* ssp., *campestris*. *Cardamine impatiens* L., *Chorispora sibirica* (L.) DC., *Douepia tortuosa* Camb., *Drabopsis verna*, *Euclidium syriacum* (L.) R.Br., *Malcolmia scorpioides* (Bunge) Boiss. This pollen type is further divided into three subtypes on the basis of pollen shape classes (see key to the species or species group). *Erysimum melicentae* – type is delimited by its medium reticulate tectum, 12 species have medium reticulate tectum such as *Alyssum desertorum* Staph, *Alliaria petiolata* (M.Bieb.) Cav. Grande, *Arabis saxicola* Edgew, *Arabidopsis pumila* (Steph) Busch, *Cardaria drapa*, *Cithareloma lehminii*, *Coronocarpus didymus* (L.) Smith, *Diceratella canescens* (Boiss.) Boiss., *Goldbachia laevigata* (M.Bieb.) DC., *Eremobium aegypticum* (Spreng) Boiss., *Erysimum melicentae* Dunn., *E. repandum* L., *E. griffithianum* Boiss., *Leptaleum filifolium* (Willd.)

DC., *Malcolima. strigosa* Boiss. This type also divided into two subtype based on pollen shape class (see key to the species and species group). *Draba lanceolata*- type is the largest among all the four pollen types (28 species). This pollen type is characterized by its coarsely reticulate tectum. viz., *Alyssum desertorum* Staph, *Boreava orientalis* Jaub. & Spach, *Capsella bursa-pastoris* (L.) Medik., *Chorispora bungeana* Fish & Mey, *Christolea himalayensis* (Camb.) Jafri, *Chorispora tenella* (Pallas) DC., *Draba trinervis* Schultz, *D. altaica* (C.A. Mey) Bunge, *D. lanceolata* Royle, *D. melanopus* Kom., *D. stenocarpa* Hook. F. & Thoms., *Euclidium tenuissimum* (Pallas) B. Fedtsch, *Erysimum melicentae* Dunn., *E. griffithianum* Boiss., *Farsetia hamiltonii* Royle, *Diceratella floccose* (Boiss.) Boiss., *Farsetia heliophila* Bunge ex Coss., *Isatis stocksii* Rech.f Boiss, *I. minima* Bunge, *Lepidium virginicum* L, *Matthiola macranica* Rech f., *Matthiola flavida* Boiss., *Malcolmia africana* (L.) R.Br., *Nasturtium officinale* R. Br., *Microsisymbrium flaccidum* Schulz., It is also divided into three subtype (see key to the species). *Farsetia ramosissima* - type is easily distinguished by its reticulate – rugulate tectum. Jonsell (1987) reported similar pollen in the genus *Farsetia* 13 species are included in this pollen type like, *Conringia planisiliqua* Fisch & Mey., *Crambe cardifolia* Steven, *Descurainia sophia* (L.) Webb. & Berth., *Diploaxis griffithii* (Hook.) & Thoms. Boiss., *Diptychocarpus strictus* (Fish. M. Beib.) Trautv, *Diploaxis harra* (Forssk.) Boiss, *Erysimum crassicaule* (Boiss.) Boiss. *Erysimum melicentae* Dunn., *E. repandum* L., *Farsetia ramosissima* Hochst. ex Boiss, *Malcolmia behboudiana*, Rech.f., *Moricandia sinaica* (Boiss.) Boiss. *Lepidium aucheri* Boiss. Like other three types this pollen type is also classified into two subtypes

Pollen morphologically the family is more closely related to Tamricaceae where both families have tricolpate pollen with reticulate tectum (Qaiser & Perveen, 2004). Erdtman (1952) reported that the family is more close to family Capparaceae. However, Capparaceae is eurypalynous family, in this family tricolporate pollen are common (Perveen & Qaiser, 2001). Pollen morphology confirms the homogeneous nature of the family.

References

- Appel, O and I.A. Al-Shehbez. 2002. Cruciferae. In: *The families and genera of vascular plants* (Ed.): K. Kubitzki. V. Flowering plants Dicotyledons, Malvales, Capparales and Non-Betalain Caryophyllaceae. C. Bayer. 75-174. Springer-Verlag, Berlin Heidelberg, New York.
- Carter, A.L., S.T. Willams and T. Mcneilly. 1975. Scanning electron microscope studies of pollen behaviour on immature and mature brussels sprout (*Brassica oleracea* var. *gemmifera*) stigmas – *Euphytica*, 24: 133-141.
- Chiguriaeva, A.A. 1973. Pollen morphology of Cruciferae in pollen and spore morphology of recent plants (in Russian) – Proc. 3rd Int. Palynology Conf., Acad. Sci. USSR. 93-98. 3P1.
- Erdtman, G. 1952. *Pollen Morphology and Plant Taxonomy. Angiosperms*. Chronica Botanica Co., Waltham, Massachusettes.
- Erdtman, G., J. Praglowski and S. Nilsson. 1963. *An Introduction to a Scandinavian Pollen Flora. II* Almqvist & Wicksell, Stockholm.
- Faegri, K. and J. Iversen. 1964. *Test book of Pollen Analysis*. Munksgaard, Copenhagen.
- Javeid, G.M. and A.R. Naqshi. 1976. Pollen grains as an aid to taxonomy of Brassicaceae. Int. Symp. Physiology of sexual reproduction in flowering plants. Dept. Bot. Punjab Agricultural University Abstract A-6.
- Jonsell, B. 1986. A monograph of *Farselia* (Cruciferae). *Acta. Univ. Ups. Symb. Bot. Up Sal* 25(3): 1-107.
- Khalik, K.N.A 2002. *Biosystematic studies on Brassicaceae* (Cruciferae) in Egypt. Ph.D.

- dissertation.
- Kremp, G.O.W. 1965. *Encyclopaedia of Pollen Morphology*. Univ. Arizona Press, Tuscon, U.S.A.
- Lahham, J.N. and D. Al-Eisawi. 1987. Pollen morphology of Jordanian Cruciferae. *Mitt. Bot. Staatssamml. Muchen*, 23: 355-375.
- Mabberley, D.I. 1987. *The Plant Book*. Camb. Univ. Press, Cambridge, New York.
- Moore, P.D. and J.A. Webb. 1978. *An Illustrated Guide to Pollen Analysis*. Hodder and Stoughton, London.
- Perveen, A. and M. Qaiser. 2001. Pollen Flora of Pakistan-XXXI. Capparidaceae. *Turk., J. Bot.*, 25: 389-395.
- Qaiser, M. and A. Perveen. 2004. Pollen Flora of Pakistan-XXXVII Tamaricaceae. *Pak. J. Bot.*, 35(1): 1-18.
- Rollins, R.C. and M.A.U.C. Banerjee. 1979. *Pollen of Cruciferae*- Cambridge, M.A. Busey. Institution of Harvard University.
- Sharma, R.R. and P.K.K. Nair. 1973. A study on pollen production in *Brassica* L. *Palynological Bull. V.J.*, (2): 62-66.
- Walker, J.W. and J.A. Doyle. 1975. The basis of Angiosperm phylogeny: Palynology. *Ann. Mo. Bot. Gard.*, 62: 666-723.

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