Pollen Characters and Their Evolutionary Significance With Special Reference to the Flora of Karachi

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Abstract: The pollen morphology of 353 species from Karachi, belonging to 67 families of angiosperms, distributed in 58 dicots and 9 monocots were investigated by scanning electron microscope (S.E.M.) and light microscope (L.M.). Examination of these families revealed great pollen diversity in their qualitative and quantitative characters. However, from a phylogenetic and evolutionary point of view, polarity, symmetry, apertural types and exine sculpturing are the most important characters. In general, dicot pollen is relatively more specialized than that of monocots. Dicotyledons are generally characterized by radially symmetrical, isopolar, colporate, colpate and porate pollen, whereas monocotyledon are usually heteropolar, bilaterally symmetric, boat-shaped, monocolpate and monoporate pollen.

With few problematic exceptions, the pollen data supports the general classification. The relatively most primitive pollen type i.e. monosulcate (monocolpate), heteropolar, bilaterally symmetric pollen are restricted to the most primitive subclass of dicots i.e., Magnoliidae and to the monocots. In contrast to this, the highly advanced subclass Asteridae exhibits the greatest array of specialized pollen types, especially the family Compositae.

Key Words: Palynology, Evolutionary significance, Flora, Karachi.

Özellikle Karachi Florasına Bakarak Polenlerin Özellikleri ve Evrimsel Önemi


Az sayıda istisna ile, polen verileri genel sınıflandırmayı desteklemektedir. En basit polen çeşit izopolar, monosulcate (monocolpate) heteropolar, iki yönlü simetrik polen, dikotların en basit alt sınıfı olan Magnoliidae ve monokotlarla sınırlıdır. Buna karşılık olarak, hayli gelişmiş alt sınıf olan Asteridae polen türlerini ve daha özkese Compositae ailesini kapsar.

Anahtar Sözcükler: Palynology, evrimsel önem, Flora, Karachi.
Introduction

Palynology (from the Greek words, to sprinkle, fine meal; cognate with pollen flour or dust) is the study of pollen and spores (1). Palynology is unique in that one can obtain tremendous amount of information from a little material in a short time (1). The constant features and the sculpturing of the exine make pollen grains a highly recognizable object by which parent genera or even species may be recognized (2, 3). Application of pollen morphology in plant taxonomy is best evidenced in the flowering plants, especially in the angiosperms. The largest variety of pollen morphotypes occurs among the angiospermous plants (4).

With the advances in microscopy techniques, the knowledge from the scanning electron microscope is the most significant. Scanning electron microscopes provide an image of unequalled depth of field, which is ideal for comparative studies of pollen surface. Features observable only with an electron microscope provide useful characters relevant to the phylogeny of the angiosperms (5, 6). Nowadays, the field of palynology is making a tremendous contribution to the systematics and phylogeny of angiosperms because of the evolutionary trends in pollen wall stratification which provides an important source of phylogenetic information of major importance.

The Flora of Karachi is represented by 72 angiospermous plant families, c. 204 genera and about 430 species and a single gymnospermous species, viz., Ephedra ciliata Fischer. & Mey ex. C. A. Meyer (7–9).

The dicots are represented by 60 families, c. 146 genera and c. 251 species, and monocots by 12 families, 64 genera and c. 115 species.

The aim of this study was to find out the phyllogenetically important pollen characters and their major evolutionary trends within the Flora of Karachi.

Materials and Methods

Fresh polliniferous materials of 353 species were collected from the Karachi division and adjoining areas. However, in cases of non–availability of fresh material, herbarium (Karachi University Herbarium) material was also used. For the preparation of pollen slides, materials were processed by the standard acetolysis method of Erdtman (10), but for the thin walled pollen the material was directly examined in 1–2 drops of distilled water instead of acetolysis. However, when the herbarium materials were grasses, the anthers were soaked 1–2 minutes in KOH.

For light and scanning microscopy the material was divided into two parts. For scanning electron microscopy (S.E.M.), pollen material was mounted on a metallic stub, with a fine capillary tube and coated with gold, in a sputtering chamber (Ion–sputter JFC–1100), coating was restricted to 150Å, and S.E.M. examination was carried out with a Jeol (JSM–T–200) microscope.

For light microscopy a second part of the material was centrifuged for 3–5 minutes in 50% glycerine, which was decanted. The pollen material was mounted on slide in unstained glycerine
jelly. The slides were examined with a Nikon–Type–102, under (E40, 0.65) and oil immersion (E100, 1.25) using a x 10 eye piece. From each slide the polar axis of pollen, equatorial axis of pollen, aperture size and exine thickness were measured. Light microscope slides of all specimens are deposited at the palynological laboratory, Department of Botany at the University of Karachi.

The terminology used was in accordance with Erdtman (10) Faegri & Iversen (11); Kremp (12); Andersen & Bertelsen (13); Page (14); Solomon (15) and Walker & Doyle (1).

Observations

**Polarity and Symmetry of pollen grains**

The pollen grains examined were usually radially symmetrical, isopolar–apolar, rarely subisopolar and heteropolar (Fig. 1A–D). However, heteropolar grains were commonly found in monocotyledonous families compared with dicots, like Liliaceae, Pontederiaceae, Commelinaceae, Cyperaceae. A few dicots also had heteropolar pollen viz., Nymphaeaceae, Neuradaceae, Menyanthaceae and Sapindaceae.

**Shape**

Pollen grains were generally prolate–spheroidal to oblate–spheroidal or subprolate to prolate, rarely spheroidal or elliptic, often triangular as in Cyperaceae.

**Apertures**

In apertural types mostly colporate, colpate, porate rarely non–aperturate grains were observed. Apertures differed in number, position and structure. In some families namely Lythraceae, Acanthaceae and Boraginaceae more distinct heterocolpate grains were also found (Fig. 2 A–F). In addition, some miscellaneous types of aperture were also observed, such as in Neuradaceae *(Neurada procumbens* L.), Sapindaceae *(Cardiospermum helicacabum* L.) and Menyanthaceae *(Nymphoides cristata* (Roxb.) O. Ktze.),

**Exine sculpturing**

Similarly, exine sculpturing was also extremely varied, ranging from almost psilate, subpsilate, reticulate, rugulate, fossulate, foveolate, striate, scabrate, echinate and tubuliferous spinulose. However, some families viz., Acanthaceae, Boraginaceae, Convolvulaceae, Polygonaceae, Liliaceae, Typhaceae and Zygophyllaceae showed great diversity in their exine pattern. In contrast to this, families such as Rhamnaceae, Polygalaceae and Chenopodiaceae were fairly uniform in their exine pattern.

**Results and Discussion**

Palynology, although a relatively recent branch of plant sciences has already provided useful information for phylogenetic considerations. Pollen grains are usually categorized largely on the basis of their shape, size, apertural types, symmetry, polarity and exine sculpturing. However,
from a phylogenetic and evolutionary point of view, polarity, symmetry, apertural types and exine sculpturing are the most important pollen characters (1).

The pollen morphology of 353 species from 67 angiospermous families, belonging to 32 dicotyledons and 8 monocotyledon orders were investigated. The placement of families in different orders was according to the system of Takhtajan (16). The phylogenetic, evolutionary and taxonomic significance of different subclasses and orders with reference to various pollen characters such as shape, size, polarity, symmetry and exine patterns are separately discussed.

Figure 1. Scanning Electron micrographs of pollen grains. A. Cyperus atkinsoni C.B. Clarke, heteropolar pollen grain; B. Cardiospermum halicacabum L., sub–isopolar pollen grain; C. Ruellia petula Jacq., apolar pollen grain; D. Alychnosia capitata (Heyne ex Roth) DC., isopolar pollen grain. Scale bar = 10 µm.
Figure 2. Scanning Electron micrographs of pollen grains. A. Asphodelus tenuifolius Cavan, monocolpate pollen grain; B. Aristida adscensionis L., monoporate pollen grain; C. Suaeda vermiculata Forssk., panporate pollen grain; D. Merremia aegyptica (L.) Urban, tricolpate pollen grain; E. Indigofera sessiliflora DC., tricolporate pollen grain; F. Hygrophiila polysperma (Roxb.) T. Anders., heterocolpate pollen grain. Scale bar = 10 µm.
Dicotyledons

The present palynological data represent all the subclasses, except Hamamelididae (due to the non-availability of material).

From the most primitive subclass Magnoliidae (16, 17) members of two orders viz. Aristolochiales (Aristolochiaceae) and Nymphaeales (Nymphaeaceae) were examined. The members of family Aristolochiaceae studied here were characterized by having non-aperturate grains. However, 1-sulcoidate, or 2-sulcoidate grains have also been reported from this family (10). The pollen morphology of Nymphaceaeae was extremely distinct from the rest of the dicotyledonous families studied by the presence of monocolpate, heteropolar, bilateral symmetric grains, whereas Erdtman (10) and Walker (18) reported 2–3 sulcate grains in the Nymphaea genus.

The presence of the most primitive types of pollen grain viz. boat-shaped, monosulcate grains clearly indicates the primitive nature of order Nymphaeales (Magnoliidae) (16, 19–24). These primitive types of pollen were restricted to the subclass Magnoliidae and monocots. Walker (18) suggested that in the two different families of the Magnoliidae viz. Chloranthaceae and Aristolochiaceae monosulcate pollen evolved into polycopate (or polyporate) pollen i.e., pollen with more than 3–colpi or pores, via an inaperturate intermediary form without going through a tricolpate stage.

From the subclass Ranunculidae, members of 3 orders: Nelumbonales, Ranunculales and Papaverales were examined. This subclass was characterized by tricolporate rarely tricolporate, isopolar grains, which are a relatively more advanced type than monocolpate and non-aperturate pollen (Table 1). Ranunculidae are considered the first tricolpate-derived subclass, a basic type from which other types have been derived (18, 1). Within Ranunculidae, Nelumbonales seemed to be a relatively more primitive order than Ranunculales and Papaverales. Nelumbonales (Nelumbonaceae) showed a definite link with the subclass Magnoliidae (Aristolochiaceae more than 60 µm in diameter), by the presence of large grains (68–97 µm in diameter Nelumbo nucifera Gaertn). In Ranunculales (Menispermaceae Cocculus pendulus (Forssk.) Diels) small, tricolporate grains with reticulate tectum were present (25). Nevertheless, Papaverales (Argemone maxicana L.) pollen were characterized by having coarsely reticulate tectum, with spinulose like projections. This pollen type was in a slightly more advanced condition than that of Ranunculales.

Within Caryophyllidae (3 orders: Caryophyllales, Polygonales and Plumbaginaceae were examined) the majority of the families had colporate grains. However, porate and colporate grains were also observed.

Caryophyllales is the best example of a large natural association of families. These families are united by remarkably uniform characters of placenta, ovule, and embryo (26). Betalains, a distinctive class of pigments are also found in many families of Caryophyllales. However, in Molluginaceae and Caryophyllaceae anthocynins are present (27).

Pollen morphology, more specifically the presence of a scabrate punctate tectum in the majority of the taxa examined in the order Caryophyllales, clearly suggest the close relationship
Table 1. General pollen characters of dicotyledon subclasses according to the Takhtajan (1969) system of classification.

<table>
<thead>
<tr>
<th>Dicotyledons subclasses</th>
<th>Polarity</th>
<th>Shape</th>
<th>Apertures</th>
<th>Tectum</th>
</tr>
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<tbody>
<tr>
<td>Magnoliidae</td>
<td>Heteropolar</td>
<td>boat-shaped–or spheroidal</td>
<td>monocolpate, rarely non-aperturate</td>
<td>usually foveolate–fossulate rough reticulate</td>
</tr>
<tr>
<td>Ranunculidae</td>
<td>isopolar</td>
<td>oblate spheroidal or prolate–spheroidal</td>
<td>3–colpate or colporate</td>
<td>reticulate or fossulate</td>
</tr>
<tr>
<td>Caryophyllidae</td>
<td>isopolar apolar</td>
<td>mostly spheroidal rarely oblate–spheroidal to prolate–spheroidal</td>
<td>mostly pantoporate colpate rarely 3–colporate</td>
<td>scabrate often reticulate or tubuliferous spinulose</td>
</tr>
<tr>
<td>Dilleniidae</td>
<td>isopolar rarely apolar</td>
<td>mostly subprolate rarely prolate–spheroidal to oblate–spheroidal</td>
<td>mostly 3–colpate colpate or porate</td>
<td>reticulate or echinate rarely fossulate or foveolate often subpsilate</td>
</tr>
<tr>
<td>Rosidae</td>
<td>isopolar rarely apolar</td>
<td>prolate–spheroidal subprolate or prolate</td>
<td>3–colpate, polycolpate rarely porate and heterocolpate</td>
<td>mostly reticulate often subpsilate or striate</td>
</tr>
<tr>
<td>Asteridae</td>
<td>isopolar rarely apolar</td>
<td>prolate to subprolate prolate–spheroidal to oblate spheroidal</td>
<td>mostly 3–colpate or heterocolpate rarely colpate or porate</td>
<td>usually echinate or echinolophate spinulose, subpsilate scabrate or reticulate</td>
</tr>
</tbody>
</table>

of these families i.e., Nyctaginaceae, Molluginaceae, Aizoaceae, Portulacaceae, Caryophyllaceae (including Illecebraceae), Amaranthaceae and Chenopodiaceae. The pollen of Nyctaginaceae and Portulacaceae was different from that of Chenopodiaceae, Amaranthaceae and Caryophyllaceae in having a tubuliferous and spinulose type of tectum. Pollen grains of Aizoaceae and Molluginaceae were quite similar and were sometimes indistinguishable from each other. Both families had uniformly tricolpate pollen grains with a scabrate–punctate tectum. However, similar types of grain were also observed in Cometes surattensis Burm. f. belonging to the Illecebraceae family (formerly included in Caryophyllaceae). In contrast to this, caryophyllaceous grains were different from those of Molluginaceae and Illecebraceae. Caryophyllaceae and Molluginaceae are more closely related families and more or less similar type of grains are present in both the families (27). However, the present pollen data are insufficient to comment on the above contention. Amaranthaceae and Chenopodiaceae have long been considered closely related families by having congested inflorescences with small, reduced flowers, 2–3 carpelled, unilocular ovary. In Chenopodiaceae and Amaranthaceae all the taxa have exclusively panporate
Figure 3. Scanning Electron micrographs of pollen grains. A. Polygala eriocarpa DC., pollen grain showing psilate tectum; B. Suaeda vermiculata Forssk., pollen grain showing scabrate tectum; C. Farsetia jacquemontii Hook. f. thomson, pollen grain showing reticulate tectum; D. Prosopis cineraria (L.) Druce, pollen grain showing foveolate tectum; E. Ipomoea aquatica Forssk., pollen grain showing echinate tectum; F. Andrichne aspera Spreng, pollen grain showing striate tectum. Scale bar = A–D & F = 1 μm; E = 10 μm.
grains (27–30), and both have a scabrate punctate often spinulose tectum. Similarly, the size and shape of the grains in both the families are also not very different.

A definite evolutionary trend from colpate to polyporate condition through polycolpate was clearly seen in many members of Caryophyllales, thus in Aizoaceae, Molluginaceae, Illecebracae and *Polycarpae spicata* Wight & Arn. (Caryophyllaceae) tricolpate grains were found, while in the family Portulacaceae and in the genus *Spergularia* of Caryophyllaceae pantocolpate grains were found, whereas families like Amaranthaceae, Chenopodiaceae and Nyctaginaceae had predominately pantoporate grains. Similar phylogenetic series of apertural changes in the order Caryophyllales have also been reported by Van Campo (31).

Polygonales were more specialized by having compound (tricolporate grains, in addition to simple (porate, colpate) grains, the tectum also varied from reticulate–scabrate types. Takhtajan (16) suggested that the Polygonaceae are probably derived from the same stock as the Caryophyllales. However, our palynological data do not support this contention in spite of the fact that Polygonaceae are a fairly large and a eurypalynous family. Nevertheless, palynology supports the idea of monotypic order within Caryophyllidae and Polygonales seem to be misfits in this subclass.

The present palynological studies reveal that the pollen characters in Plumbaginaceae are more or less unique, especially the exine pattern i.e. coarsely reticulate with striate mural wall. The creation of a separate monotypic order Plumbaginales by Takhtajan (16) and Dahlgren (32) seems to be justified on a palynological basis as well.

From the subclass Dilleniidae members of 8 orders viz., Theales, Violales, Cucusbitales, Capparales, Tamaricales, Primulales, Malvales and Euphorbiales were examined.

Unlike previous subclasses, in Dilleniidae tricolporate (compound) grains were fairly common (Table 1). According to Doyle (33), and Muller (21) tricolporate grains are in fact numerically dominant in the modern dicot flora, and it seems to be more specialized than the preceding subclass. Nevertheless, in two families of Capparales, viz. Brassicaceae, Resedaceae and in the whole order of Tamaricales tricolporate grains were present.

The creation of a separate order Tiliales by some authors such as, Hutchinson (34), seems to be justified on palynological grounds also.

Malvales is more advanced than the remaining orders above, because of the presence of echinate, predominantly Pantoporate grains. Similar grains were also found in some Sterculiaceae. The pollen morphology of both families are closely related to each other. However, the pollen of Tiliaceae was totally different from these two families by the presence of non–echinate, reticulate, tricolporate grains (*Corchorus* L, *Grewia* L). Nevertheless, pollen grains of Tiliaceae were quite compatible with those of Euphorbiaceae. Agreement includes the prolate–subprolate shape, small to medium sized and finely reticulate to coarsely reticulate sculpturing. Takhtajan (16) indicated that the Euphorbiaceae, have features in common with both primitive Violales and Malvales and may have arisen from an ancestral group between them.
From Rosidae, the pollen morphology of 9 orders: Rosales, Fabales, Myrtales, Hippuridales, Rutales, Sapindales, Geraniales, Polygalales, and Rhamnales were investigated.

Rosidae are a relatively advanced subclass in the Takhtajan and Cronquist system of classification compared with Caryophyllidae and Dilleniidae. Palynologically, it has a mixture of primitive and advanced pollen types; for instance, more specialized heterocolpate and polycolporate zonoaperturate grains were found in Myrtales (Lythraceae–*Ammannia baccifera* L.) and Polygalales (*Polygala*) respectively. However, relatively primitive and unusual trends were also seen. The oblate triangular grains of Sapindaceae (*Cardiospermum helicacabum* L.) had a triradiate scar in the centre, and subsaccate heteropolar grains were found in Neuradaceae (*Neurada procumbens* L.).

Within the subclass Asteridae, 6 orders: Gentianales, Polemoniales, Scrophulariales, Lamiales, Campanulales, and Asterales were examined.

Asteridae is the most advanced subclass (16, 17). It is morphologically the best defined subclass of dicotyledons. With very few exceptions, the flowers are basically pentamerous with connate or much reduced calyx, and sympetalous, mostly zygomorphic corolla.

The pollen morphology also supports the above idea. For instance, the most specialized heterocolpate grains, which are rare in the subclass Rosidae (*Ammannia baccifera* L. (Lythraceae)) are fairly common in Asteridae as in Acanthaceae (*Peristrophe paniculata* (Forssk.) Brummitt, *Hygrophila polysperma* (Roxb.) T. Anders), Boraginaceae (*Heliotropium* L.).

The Lamiales are very near to and derived from Scrophulariales (16). Similarly, Yamazaki (35) also pointed out that in embryogeny Scrophulariales and Lamiales seem to be fairly uniform compared with the Polemoniales, but pollen morphologically, Lamiales are more similar to Polemoniales compared with Scrophulariales, more especially the family Labiatae in which colpate grains were found (colpate grains were also present in the Polemoniales), while in Scrophulariaceae usually tricolporate grains were found. However, Argue (36) reported tricolpate grains in several Scrophulariaceaeous genera in the tribe Gratioleae.

Within the Asteridae family, Compositae showed highly specialized pollen types and show a new level of complexity in their exine structure ranging from simple echinate to echinolophate tectum (Table 1).

Apart from their highly specialized pollen types, the Asteridae exhibited great pollen diversity, even within the same family viz., Acanthaceae, Boraginaceae and Convolvulaceae, especially the family Acanthaceae in which almost all types of aperturates grain occurred. In addition, exine stratification was also varied from species to species, ranging from simple reticulate, as in *Blepharis sindica* Stocks ex T. Anders. to more specialized lophoreticulate in *Barleria prionotis* L., *B. hochstetteri* Nees.

Monocotyledons

The pollen in monocots is less specialized than that of dicots, particularly in their apertural types. Simple apertural grains were fairly common viz., monocolpate, porate or sometimes even with ill–defined apertures (Table 2). However, the monocots’ pollens showed great variation in
their exine pattern. Walker & Doyle (1) suggested that, like Magnoliidae, the monocotyledons were basically a monosulcate group. Takhtajan (16) pointed out that the ancestors of the monocots were dicotyledonous plants with primitive monocolpate pollen.

The pollen data of monocots included in the present treatise, were representative of all the four subclasses, distributed in 8 orders, and 9 families.

Only one order, Potamogetonales of Alismidae, had apolar monoporate grains which are more advanced than monocolpate grains. Nevertheless, the latter type is fairly common in all the four subclasses of monocots (1).

Palynologically, Liliidae seems to be relatively unspecialized within the subclasses of monocots, because of the presence of boat–shaped, bilaterally, symmetric, monocolpate pollen, which are the ancestral pollen type in angiosperm (as described previously).

From Liliidae, two families Liliaceae and Pontederiaceae of the order Liliales were examined. The palynological findings support Takhtajan’s (16) suggestion that the Pontederiaceae is related to Liliales by the presence of heteropolar, monocolpate pollen grains.

Within Commelinidae, 4 orders (Juncales, Cyperales, Commelinales and Poales) were examined. The pollen morphology of the Commelinidae is most striking and is a more specialized subclass of monocots than the preceding subclasses (1); for instance, the order Poales is more specialized than the remaining orders by having apolar, porate grains. Cronquist (17) placed the grasses and sedges in the order Cyperales. Takhtajan (16) trealid grasses and sedges under two distinct orders, Poales and Cyperales, respectively. Palynology supports the interpretation of Takhtajan, because Poales (Gramineae) is distinctly separated from Cyperales (Cyperaceae), by having apolar, porate (mono–tri) grains.

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<th>Shape</th>
<th>Apertures</th>
<th>Tectum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alismidae</td>
<td>apolar</td>
<td>spheroidal</td>
<td>non–aperturate</td>
<td>reticulate</td>
</tr>
<tr>
<td>Liliidae</td>
<td>heteropolar</td>
<td>mostly boat–shaped</td>
<td>monocolpate or bicolpate</td>
<td>reticulate or reticulate–rugulate</td>
</tr>
<tr>
<td>Commelinidae</td>
<td>heteropolar</td>
<td>boat–shaped or</td>
<td>mostly monoporate</td>
<td>scabrate or scabrate/areolate</td>
</tr>
<tr>
<td></td>
<td>apolar</td>
<td>spheroidal often</td>
<td>rarely monosulcate</td>
<td>rarely spinulose</td>
</tr>
<tr>
<td></td>
<td></td>
<td>triangular</td>
<td>(monocolpate)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>miscellaneous type</td>
<td></td>
</tr>
<tr>
<td>Arecidae</td>
<td>apolar often</td>
<td>spherical</td>
<td>monoporate</td>
<td>reticulate or fossulate, rugulate</td>
</tr>
<tr>
<td></td>
<td>tetrads</td>
<td></td>
<td></td>
<td>often spinulose</td>
</tr>
</tbody>
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Takhtajan (16) indicated that the Cyperales is evidently derived directly from the most primitive Juncaceae. However, in Juncaceae tetrads were observed. Walker & Doyle (1) suggested that the pseudomonads (cryptotetrads) of Cyperaceae are apparently evolved from premanent tetrads, since the only family that has pseudomonads (Cyperaceae) appears to be related to the family Juncaceae. However, within Commelinidae, relatively the least specialized pollen commonly occurs in Commelininales, which are quite compatible with the Liliidae pollen type; both have monocolpate grains, but Commelinidae are distinct from Liliidae by having a spinulose tectum.

Within Arecidae, two orders (Arales and Typhales) were examined. Pollen morphologically, Arecidae is a relatively advanced order of monocots. Both in the families Lemnaceae and Typhaceae, porate grains were found. However, the family Typhaceae were extremely variable in their pollen types.

References


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