Pollen structure and morphology

Struktura i morfologia pyłku

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Abstract

This paper presents literature, own observations and contemporary opinions about the structure and morphology of pollen grains. The structure of pollen was described in detail using the following parameters i.e. their shape and size, type and number, sculpturing and apertures of exine which may be very useful in identification and classification of pollen grains.

Key words: *pollen, structure, morphology, classification.*

Streszczenie

Na podstawie dostępnej literatury i badań własnych w pracy przedstawiono obecne poglądy na temat budowy i morfologii pyłków. Omówiono szczegółowo budowę pyłku koncentrując się na wybranych parametrach, tj. ich wyglądzie i rozmiarze, rodzaju i liczbie, a także ukształtowaniu ściany komórkowej i jej szczelinach, co jest szczególnie przydatne w identyfikacji i klasyfikacji pyłków.

Słowa kluczowe: *pyłki, budowa, morfologia, klasyfikacja.*

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Introduction

The pollen grain is the male gametophyte in gymnosperms and angiosperms, i.e. the structure that produces the male gametes and transfers them to the female part. The grains derive from the meiotic process of the pollen mother cells and at maturity usually consist of a bi or trinucleate cell surrounded by a wall that has the important function of protecting the microgamethophyte in its journey between male and female flowers. The pollen grain wall is very resistant to water loss and environmental injuries, primarily to avoid damage and desiccation during the aerial journey.

Each species elaborates a distinctive sculpture on the surface of the pollen grains, and there are also many other morphological characteristics that are useful for the pollen analyst in the classification of the pollen.

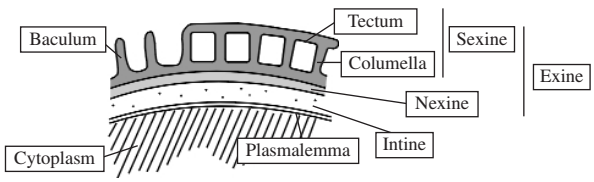

Fig. 1. Stratification of the pollen wall (Frenguelli et al., 1991)

Structure

In the living pollen grain, the wall is made up of two layers; the outer layer is called the **exine** and is composed of a very unusual substance, **sporopollenin**. The inner layer, or **intine**, is made up of cellulose and is very similar in construction to an ordinary plant cell wall. Under the light microscope, we can see the exine and it is this that carries all the morphological characteristics necessary for pollen identification.

The exine as a wall divided into an outer sculptured layer, **sexine**, and an inner unsculptured layer, **nexine** which covers the intine (fig. 1). The sexine may present different kinds of processes, more or less evident and with different shapes. In general pollen grains are formed in groups of four, each four resulting from the division of a single pollen mother cell. Usually these four cells become completely free at maturity, and we call these grains **monads**. Therefore, in certain genera or families, they are released in pairs, and we call this formation **dyads**, or they remain joined together forming a tetrad, e.g. many Ericaceae and Typhaceae. Larger aggregations occur, such as are found in some species of Acacia and certain orchids, and such groups are termed **polyads** (fig. 2).

Each pollen grain has a polarity because it exhibits opposite areas or poles as a consequence of its original position inside the tetrad. The polar axis is an imaginary line which passes through the pollen grain from the centres

of the opposite poles (fig. 3). The equator of the grain is the line which runs round the surface lying on the equatorial plane which perpendicularly bisects the polar axis. If the two poles are similar we have an „isopolar grain", while the grain is „eteropolar" when the two areas have different characteristics. Sometimes the two polar areas can not be identified and the pollen is „apolar".

For the identification of any grain there are three features to note: I) apertures, type and number, II) shape and size, III) exine sculpturing.

Apertures

Most pollen grains possess apertures, generally thin or missing parts of the exine through which the pollen tube emerges at germination on a compatible stigma.

There are two main shape types of apertures and they are named **pori** (pores) and **colpi** (furrows). Colpi are thought to be more primitive than pori and are elongate, furrow-like, with pointed ends: the ratio between the longitudinal and cross diameter is more than two. Pori are generally isodiametric or slightly elongated with rounded ends.

With a simplified terminology, irrespective of aperture position, pollens with only pori are called **porate**; with only colpi, **colpate**; with both pori and colpi in the same aperture, **colporate**. Grains rarely occur with both colpi and colpi+pori; these grains are named **heterocolpate**.

Pollen grains can be divided into groups on the basis of the number, position and characteristics of their apertures. The number of apertures varies from 0 to 40 or more and are indicated by attaching the prefixes **mono**-, **di**-, **tri**-, **tetra**-, **penta**-, **hexa**-, and **poly**- (more than six apertures), to colpate, porate and colporate. **Inaperturate** describes pollens without apertures. If the pori and colpi are arranged around the equator of the grain the prefix **zono**- (or **stephano**-) is used, while if they are scattered all over the surface this is indicated by the prefix **panto**-. The prefix **axi**- indicates apertures located at or near the pole (fig. 4).

Sometimes two or more colpi may be fused at the poles or elsewhere, and these are termed **syncolpate** grains. Other pollens (in Compositae Liguliflorae) either trizonocolporate or trizonoporate, have aperture systems obscured by large lacunae in the sexine, separated by high echinate ridges. This type is named **fenestrate** (fig. 5).

Those areas on a grain which are not occupied by apertures are given names depending on whether they are adjacent to pori or colpi. The area bordered by two colpi is called **mesocolpium**, and that bordered by two pori is called the **mesoporium**. If the pori or colpi are in the zono- arrangement, at each pole there is an area where no apertures occur. This polar area is called the **apocolpium** if the zonally arranged apertures are colpi, and **apoporium** if the zonally arranged apertures are pori (fig. 6).

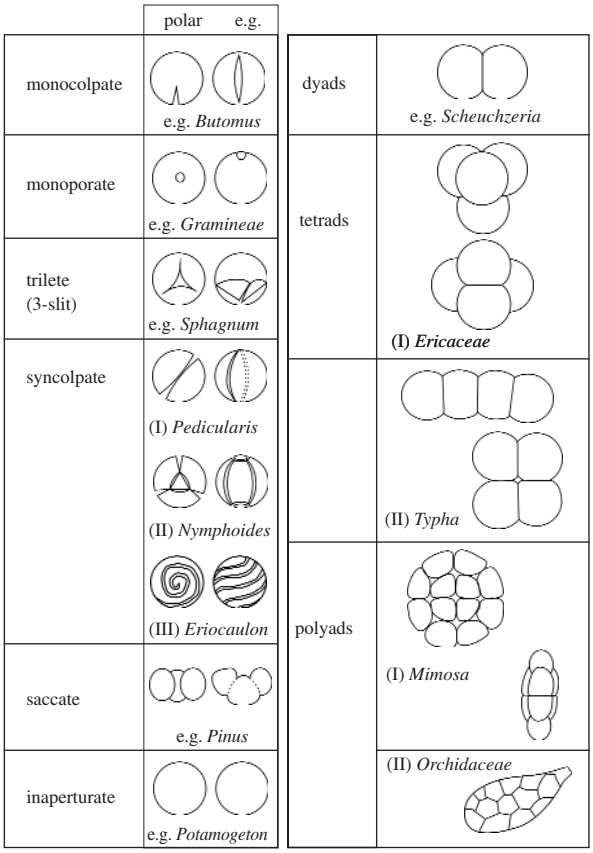

Fig. 2. Diagram showing the range of aperture number, position and character (Moore & Webb, 1978)

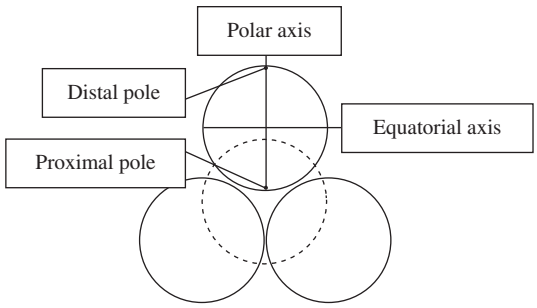

Fig. 3. A pollen tetrad with the terminology of the different parts of a grain (Frenguelli et al., 1991)

The exine often shows a slightly altered structure in the vicinity of apertures. When this happens, the aperture is said to be **bordered**. A sudden thickening or thinning of the sexine around a porus is called an **annulus**, and around a colpus is called a **margo**. Thickenings of the nexine around an endoaperture or below the edge of an ectoaperture are called **costae** (figs. 7–8).

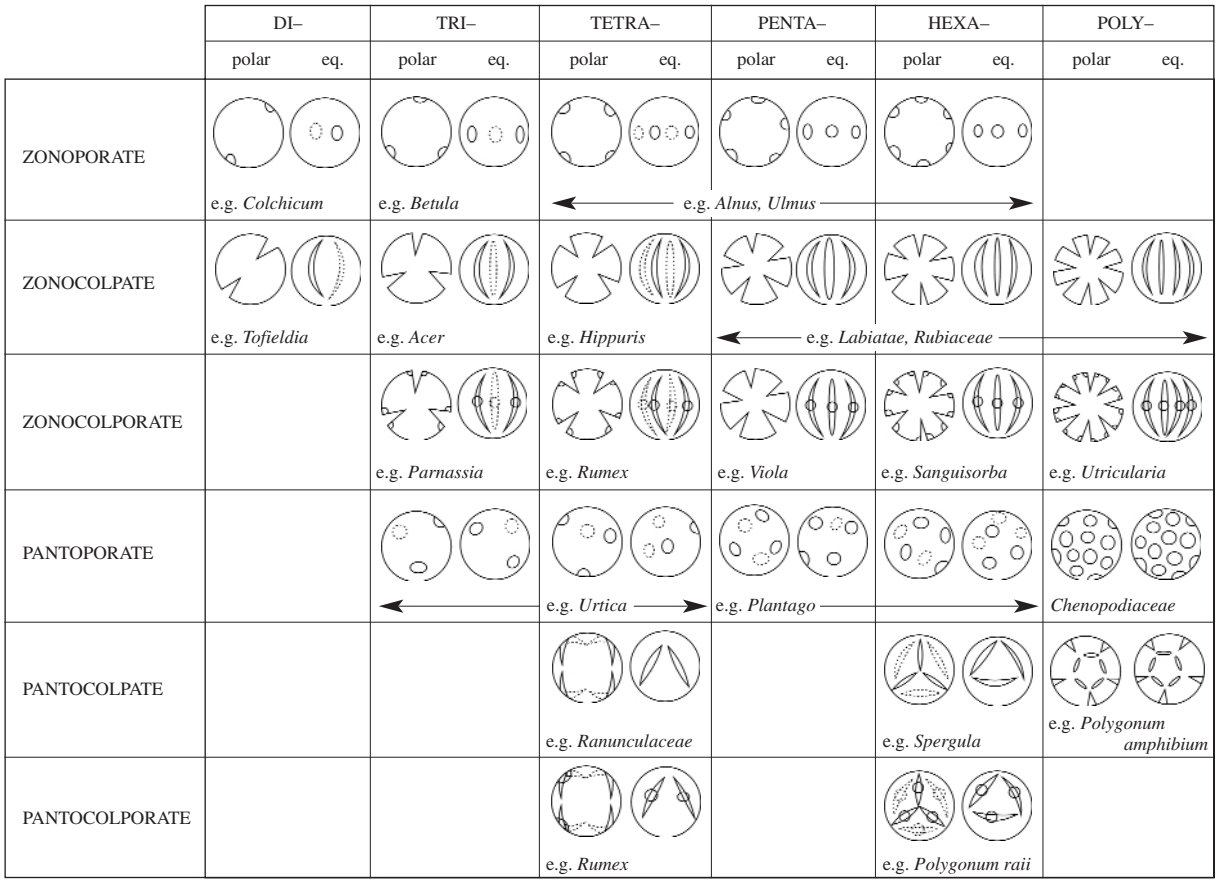

Fig. 4. Classification of pollen types upon the number and arrangement of apertures. Dotted lines indicate a different focal plane (Moore & Webb, 1978)

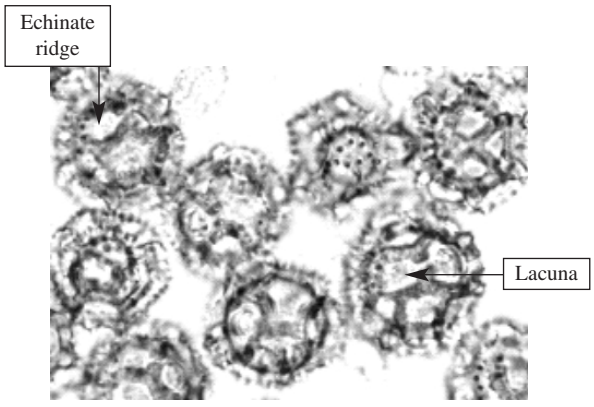

Fig. 5. Fenestrate pollen of Taraxacum

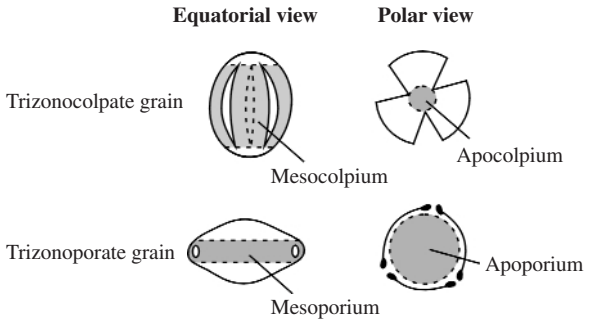

Fig. 6. Examples of how grains with different aperture types would appear in polar and equatorial view and how the apertures partition the surface of the grain into areas which are given names for descriptive purposes (Moore & Webb, 1978)

In some grains the two layers of the exine become separated from one another in the vicinity of the apertures. The cavity so formed is commonly found around pori and is called a **vestibulum**. Other grains have the central part of the aperture membrane with a sexine layer as thick as that occurring on the main body of the grain. This thickened centre is called an **operculum** (fig. 7). Most of the Pinaceae family have

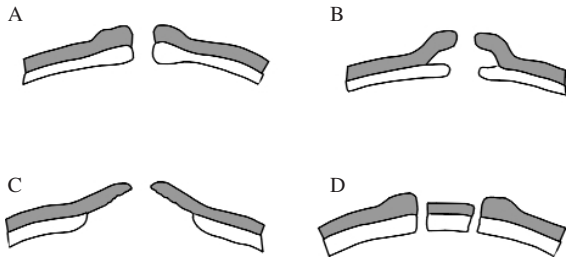

Fig. 7. Examples of exine features associated with pori: A, porus with a **costa** (*Gramineae*); B, porus where sexine separates from nexine to form a **vestibulum** (*Betula*); C, porus with an **annulus** formed by a slight thickening of the sexine; D, porus with an **operculum** (thickening of the middle of the aperture membrane) and an **annulus** (sexine thickening) (*Plantago*); (Moore & Webb, 1978)

air sacs which are brought about by the separation of the sexine from the nexine: **saccate grain** (fig. 2).

Shape and size

Pollens are three-dimensional structures and usually they are spherical or ovoidal, but other shapes also exist. If the pollen grains are regarded as more or less regular rotating ellipsoids with the polar axis as the rotation axis, and it is possible to define the pollen on the basis of the ratio between the length of the polar axis (P) and the equatorial diameter (E). When P/E >2.00 the pollen is called perprolate, therefore in order: prolate (P/E=2.00–1.34), subprolate (P/E=1.33–1.15), prolate spheroidal (P/E=1.14–1.01), spherical (P/E=1), oblate-spheroidal (P/E=0.99–0.89), suboblate (P/E=0.88–0.76), oblate (P/E=0.75–0.50) and peroblate (P/E<0.50) (fig. 9).

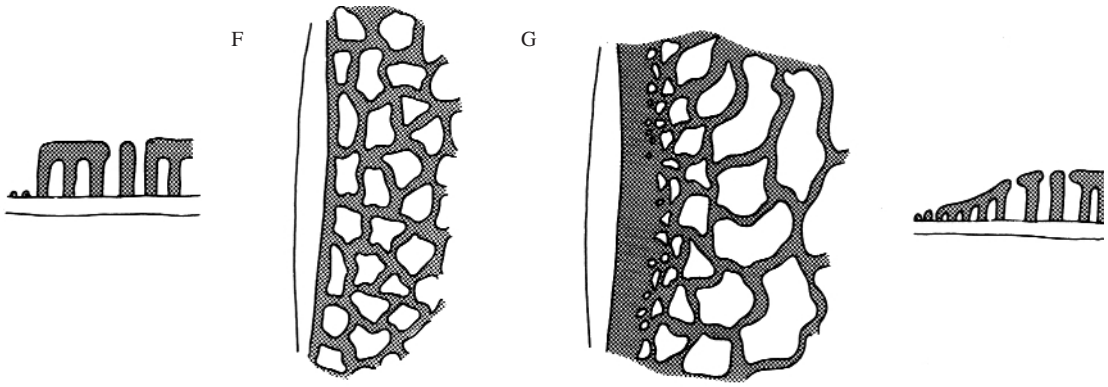

Fig. 8. Examples of exine features associated with colpi: F, Colpus without a border or margo, the lumina of the reticulum remain the same size right up to the colpus edge and the sexine also remains the same thickness right up to the colpus edge (*Fraxinus*); G, colpus with a **margo**, the lumina become smaller towards the colpus edge and disappear at the edge, giving a tectate margin while he sexine becomes gradually thinner towards the colpus edge (*Salix*); (Moore & Webb, 1978)

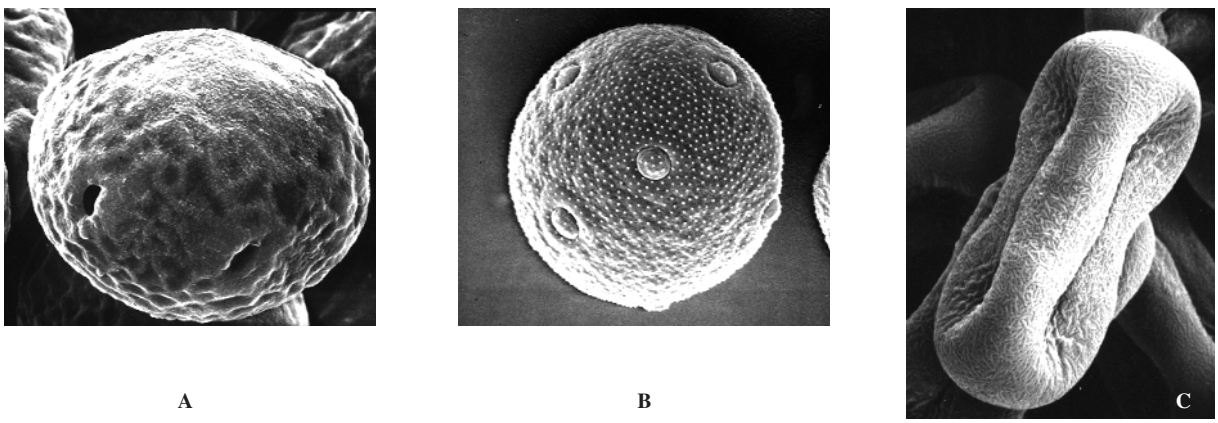

Fig. 9. Examples of pollen shape: A, oblate (*Ulmus*); B, spheroidal (*Plantago*); C, prolate (*Tordylium*)

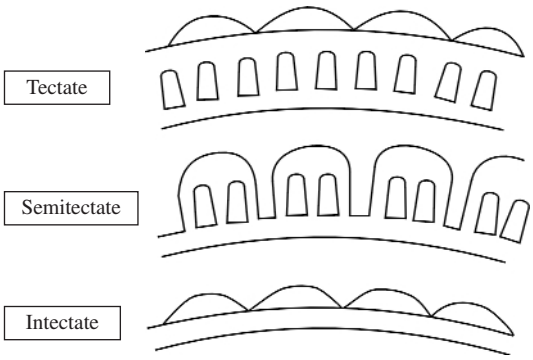

Fig. 10. Diagrams of different tectum arrangements

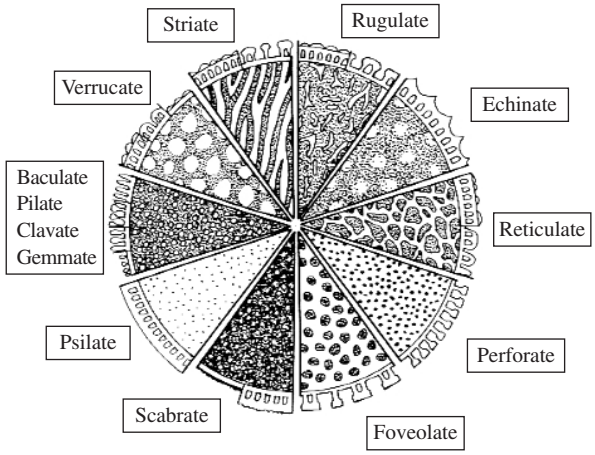

Fig. 11. Sexine sculpturing types; the raised areas are shown light and the lower areas are shown dark. Sometimes the same sculpturing type is produced by different sexine structures (tectate; semitectate; intectate) (Frenguelli et al., 1991)

The size of pollen grains varies from about 5 μm in the forget-me-not to 200 to 300 μm in the pumpkin. The following groups are normally used: very small grain, in which the diameter is less than 10 μm; small, in which the diameter in 10–24 μm; medium size, 25–49 μm; large, 50–99 μm; very large, 100–200 μm; gigantic, the diameter of which is greater than 200 μm. The airborne pollen grains normally range from 10 μm to 80 μm.

Sculpturing

The different sculpturings on the surface of pollen grains result from the architecture of the sexine. In the „columellate" structural type, typical of angiosperms pollen, the sexine is composed of small radially directed rods that sit on the nexine and are called **columellae**, supporting a roof or tectum which may be perforated or sculptured in characteristic ways. The tectum may be complete (**tectate grains**), partially dissolved (**semitectate grains**) or completely absent (**intectate grains**) (fig. 10).

In the intectate grain the rods are called **bacula** if they are cylindrical in shape, but in other cases they have different shapes and they are called **clavae** if they are club-shaped, **pila** if they have swollen heads, or **gemmae** if they are short and globular. Sometimes the sculptural elements may be in the shape of small hemispherical warts (**verrucae**) or tiny flakes (**scabrae**) or other small elements (**granules**) (Fig. 11).

In some tectate and semitectate types the heads of the columellae are connected in two directions to form a **reticular** pattern. The reticulum walls are called **muri** and the spaces between the walls **lumina**. A **striate** sexine pattern is formed by a lateral union of columellae and the muri run parallel to one another. The intermediate situation between these is called **rugulate** pattern. The tectum sometimes has perforations of various shape or size, and sculptures upon it are described on the basis of their shape in the same way as infra-tectal types (clavae, bacula, etc.).

References

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