SUGGESTIONS TOWARDS UNIFICATION OF DESCRIPTIVE TERMINOLOGY OF ANGIOSPERM POLLEN GRAINS

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SUMMARY

In this paper a descriptive terminology for angiospermous pollen grains studied with a light microscope is discussed. The requirements for terms have been formulated. On account of these the existing terms have been subjected to a close inspection. It appeared that it was necessary in few cases to introduce new terms. This was especially the case in the description of outlines in equatorial and polar view.

INTRODUCTION

Pollen morphology is a discipline with the primary goal to describe and classify pollen grains. The descriptions should be as much as possible free of subjectivism in order to classify. In fact it should be nothing else but a written picture of the pollen grains. The reader should be allowed to visualize the pollen grain as if it were seen under a light microscope. Furthermore in order to arrive at a maximal communication the description has to be short and distinct. It is often not possible however to describe a feature shortly and distinctly. Hence the description of a feature is replaced by a codeword or term. To my mind this is the background of all terminology. A term has value only in connection with its circumscription, in other words, when it is defined properly. It will be clear at once that a term can be a catchword only for one circumscription (definition). Two or more definitions for one term will cause confusions. Terms without a definition can be used only if these terms have been provided already by someone with a correct definition. However, with the understanding that these definitions may indicate nothing else but the original meaning of this term. The same applies to terms provided with an incorrect definition.

Naturally there are many features that can be studied with a limited number of methods only. Moreover, it is also possible that the results are dependant on the method used. From this it follows that also the descriptive terminology will depend on the research technic. For instance, terms defined by use of a light microscope cannot be used in transmission-electron-microscopical studies. Also the opposite is true. Terms defined with the help of a transmission electron microscope can not be used in light-microscopical studies.

Descriptive terminology also depends on the pre-treatment of the pollen grains. The characters of fresh, untreated pollen grains are often different from those of pollen grains treated with the acetolysis mixture or stained with a pigment.

It is not possible to have one terminology for both pollen grains and spores. It is even difficult to compare productively gymnospermous and angiospermous pollen grains. A comparison between angiospermous pollen grains and fern spores is particularly unproductive. Because the morphology of the "spores" of the groupes is so different, it seems better to treat the descriptive terminology of the Mycophyta, Bryophyta, the different phyla of the Pteridophyta, Gymnospermae and Angiospermae separately.

In this paper a descriptive terminology for acetolysed angiospermous pollen grains studied by means of a light microscope will be discussed. In doing this, I will try to use existing terms and avoid the introduction of new terms as much as possible. In many cases a choice between terms has to made. In deciding which term is to be preferred above other, the following requirements are important.

(*1*) The term should have one correct and unambiguous definition.

(*2*) Terms generally known and in common use are preferred above lesser-known terms or terms out of use.

(*3*) Terms associated with one of the modern languages should be dismissed, because they cannot be applied easily in every language. Therefore, terms with latin or greek roots are to be preferred.

In cases where existing terms do not meet any of the requirements new characters must be devised.

Following ERDTMAN (1969) I recommend to use a term only when the characters can not be described easily in plain words. Features that are rare in pollen grains should be described similarly.

Consulted literature

ANONYMOUS (1958), BEUG (1961), BRONCKERS (1968), EHRLICH (1958), ERDTMAN (1943, 1947, 1948, 1952, 1960a, b, 1964, 1966a, b, c, 1968, 1969), ERDTMAN and STRAKA (1961), ERDTMAN and VISHNU-MITRE (1958), ERDTMAN et al. (1961), FAEGRI (1956), FAEGRI and IVERSEN (1950, 1964, 1966), IVERSEN and TROELS-SMITH (1950), KREMP (1965), KUPRIANOVA (1956, 1965), KUPRIANOVA and ALESHINA (1967), KUYL et al. (1955), LARSON et al. (1962), MANTEN (1970), MULLENDERS (1955), NAIR (1962, 1966), PONS (1958), POPE (1925), POTONIÉ (1934), PUNT (1962), REITSMA (1966), ROWLEY (1959, 1960, 1962), SAAD (1963a, b), STRAKA (1964), TOMSOVIC (1960), VAN CAMPO (1955, 1957, 1958, 1960, 1961), VAN CAMPO et al. (1965), WAGENITZ (1955), WITTMAN and WALKER (1965), and WODEHOUSE (1935).

FEATURES OF POLLEN GRAINS

The features of pollen grains will be treated in five main groups: polarity, stratification of the wall, structure, apertures, shape.

Polarity

All pollen grains have a tetrad stage during development. It is at this stage that the polarity is determined. In each individual pollen grain of a tetrad two areas can be distinguished. One area, the proximal part, faces the centre of the tetrad. The other area, the distal part, is situated on the opposite side of the grain, away from the centre of the tetrad. The centre of each part is called pole, consequently pollen grains have a proximal and a distal pole. An imaginary straight line through the poles is called the polar axis and each plane through this axis is a polar plane. The borderline between the distal part and the proximal part of the pollen grain is the equator and the plane through the equator is called the equatorial plane. Each line in the equatorial plane, which intersects the polar axis, is called an equatorial diameter.

In studying pollen grains the equatorial plane can be faced towards the observer. Then it is said that the grain is looked upon in polar view. Alternatively when a polar plane faces the observer then it is said that the grain is looked upon in equatorial view.

The terms apolar and polar are from ERDTMAN (1952). In contrast to polar pollen grains, apolar pollen grains do not show a distinct polarity. According to him polar pollen grains are isopolar, heteropolar or paraisopolar (subisopolar) when the poles are respectively equal, unequal or more or less equal. The descriptions of this features are short and clear. Therefore, it is not necessary to provide them with a term.

Stratification of the wall

There is no group of pollen features on which more is published than the stratification of the wall. Originally the concepts were clear. At present this terminology is in a state of confusion, because terms have been changed needlessly and because existing terms have been redefined unnecessarily. Especially here terms often have a functional definition and more-over sometimes the same terminology has been used regarding different research technics.

Through a light microscope the exine shows at least two layers. The inner layer is optically homogeneous. The outer layer often clearly stratified is separated from the inner layer by spaces. POTONIÉ (1934) called this inner layer intexine and the outer layer exoexine. ERDTMAN (1943) regarded these terms as unwieldy. He preferred to call the inner layer endexine and the outer one ektexine. Some years later, however, ERDTMAN (1948) changed these terms into nexine and sexine without clearly stating why. Perhaps he wanted to specify subdivisions of the inner and outer layer with the prefixes ekto-, meso- and endo-. Since for instance the terms ektoektexine and ektoendexine are very unwieldy, it was necessary to change the terms ektexine and endexine into the terms sexine and nexine. However, the definitions of these terms are completely identical. IVERSEN and TROELS-SMITH (1950) and FAEGRI and IVERSEN (1950) adopted ERDTMAN's 1943-terms ektexine and endexine. For some years the terms ektexine and endexine and the terms sexine and nexine thus were interchangeable. In 1956, however, Faegri redefined the terms endexine and ektexine on the basis of the staining capacity of the exine. He stated: "By suitable staining the outer part takes a strong colour, while the inner part remains almost or completely unstained. The ektexine I define as the part which takes the stain, the endexine as that part which remains unstained" (FAEGRI, 1956). Faegri was aware of the implications of his redefinitions for he writes: "if we define ektexine by means of its staining capacity, it is possible that it does not in all cases coincide with the sexine (ERDTMAN, 1952), but that there may exist staining elements also nearer to the centre of the grain than the bottom end of the columellae..." (FAEGRI, 1956). It will be clear that the boundary between endexine and ektexine is not in the same place as that between sexine and nexine. Later electron-microscopical investigations have showed that the upper part of the endexine (sensu prae-1956) has the same electron density as the ektexine (sensu prae-1956). There is even a distinct difference in origin of the endexine (sensu FAEGRI, 1956) and the remaining part of the exine (GODWIN et al., 1967, a.o.).

From 1956 on there are consequently two completely different definitions of the two layers of the exine, one on the basis of optical criteria, the other on the basis of chemical, physical or ontogenetical criteria. For this reason ERDTMAN (1966c) distinguishes between morphologically or topographically defined layers and layers that are morphogenetically defined. In this conception sexine and nexine (ERDTMAN, 1948 and later) and ektexine and endexine (sensu prae-1956) are morphologically defined layers, while ektexine and endexine (sensu FAEGRI, 1956) are morphogenetically defined layers.

In recent morphological literature both morphologically and morphogenetically defined terms are used.

Although in principle the limits between sexine and nexine and ektexine and endexine do not coincide, in practice these terms are treated as if they were interchangeable. A good example is found in the *Textbook of Pollen Analysis* by FAEGRI and IVERSEN (1964). They use the terms ektexine and endexine in the redefined form. They indicate, however: "Erdtman has later changed his terminology of exine stratifications as used in this book and he now divides exine into an outer sexine and an inner nexine. This division does not correspond with our ektexine-endexine division inasmuch as the sexine by definition, does not extend beyond the lower end of the columellae, no matter whether a foot layer is found or not. As a primary division we use the difference in chemical composition or physical state (as shown by staining reaction and electron micrographs) whereas Erdtman's division is a formal morphological one. In practice of pollen analysis the difference is trifling". However, when we compare the textplates I and III from the first edition (FAEGRI and IVERSEN, 1950, p.19 and 23) and the textplates I and III of the second edition (FAEGRI and IVERSEN, 1964, p.230 and 232), then it appears that the diagrammatic representations are quite similar. Although the terms ektexine and endexine, used in the first edition, are not synonymous at all with the terms ektexine and endexine, used in the second edition, this has no influence on the diagrammatic schemes of exine stratifications. This is rather inconsistent. Furthermore the statement: "In practice of pollen analysis the difference is trifling" is not exactly scientific.

From these considerations it will be clear that morphological definitions are preferably above chemical, physical or morphogenetical definitions. The terms described by KUPRIANOVA (1956), FAEGRI (1956), EHRLICH (1958), ROWLEY (1959, 1960, 1962), TOMSOVIC (1960), SAAD (1963a, b), VAN CAMPO et al. (1965) and KUPRIANOVA and ALESHINA (1967) are not strictly morphological and should be rejected. The terms exoexine–intexine (POTONIÉ, 1934), ektexine–endexine (ERDTMAN, 1943), sexine–nexine (ERDTMAN, 1948) and ectine–endine (NAIR, 1962, 1966) are the only four pairs of terms, which are morphologically defined, as far as I know. Of these I prefer sexine and nexine because they meet the requirements formulated on p.40. Of the other three possibilities the terms exoexine–intexine are not used anymore, the terms ektexine–endexine are, as mentioned above, defined in different ways and the terms ectine–endine are too scanty and ambiguous (ERDTMAN, 1960a, b).

Since nexine and exine are composed of different layers or zones, it is necessary to submit these two layers to a close inspection.

Nexine

Light-microscopically the nexine has a mostly homogeneous structure. Some authors, however, claim to have observed zones in the nexine. ERDTMAN (1952) described two zones, an outer ectonexine and an inner endonexine. VAN CAMPO (1955) even described three zones, an outer ectonexine, a middle mesonexine, and an inner endonexine. On the existence of these zones, however, there is no agreement. ERDTMAN (1968) interprets the endonexine as a "mere routine decoration" and Van Campo does not mention her three zones in later publications. Still we know from chemical and electron-microscopical investigations that the nexine is not homogeneous. There are at least two layers that can be distinguished by electron density and staining capacity. ERDTMAN (1960a, b) numbered these layers from outside to inside. The nexine 1 is identical with a.o. the foot layer (FAEGRI, 1956), ectonexine (AFZELIUS, 1955, 1956), pedium (ERDTMAN, 1966a, b) and bacularium (KUPRIANOVA and ALESHINA, 1967), but not identical with the ectonexine (ERDTMAN, 1952). The nexine 2 is identical with the endexine (FAEGRI, 1956). Some authors (RAJ, 1961; LARSON and SKARLA, 1961) described a third zone "endonexine". However, this zone appears to occur rarely. One should keep in mind that the endonexine sensu Raj is not identical with the endonexine (ERDTMAN, 1952) or with the nexine 3 (ERDTMAN, 1960a, b) since it is not really part of the nexine (ERDTMAN, 1968).

Layers or zones in the nexine thus can be described either with the prefixes ecto-, meso- and endo- or with the symbols, 1, 2 and 3. It is difficult to decide which kind of description is the best one. Perhaps it is better to use the symbols 1, 2 and 3 to delimitate the nexine. I want to stress the fact that the symbols indicate a topographical division of the nexine only. It is quite possible that for instance, the nexine 1 of one pollen grain is not identical with the nexine 1 of another pollen grain, but agrees more with the nexine 2 of that grain. It is thus not sufficient to mention the zones only. The components of each zone or layer should be described separately. Then after description a correlation of the zones may be attempted. It may be added that the use of symbols has the advantage that when more zones are discovered, there is an ample supply of symbols available. By sticking to the prefixes ecto-, meso- and endo- one certainly will run into topographically linguistical problems.

Sexine

The stratification of the sexine is very heterogeneous. On the nexine we find mostly pillar-like elements. They are called columellae by IVERSEN and TROELS-SMITH (1950) and bacula by ERDTMAN (1952). In the terminology of IVERSEN and TROELS-SMITH (1950) bacula are also present. In their sense both bacula and columellae are pillar-like elements. However, columellae support other sexine elements, while bacula do not support anything. In the sense of Erdtman all pillar-like elements are indicated with the term baculum. In my opinion the terms columellae and bacula are preferable above baculum as a general term, because there is a difference between supporting and non-supporting elements.

Each individual columella can support sexine elements. Such processes are called pila, each consisting of a columella and an apical swollen part (caput). If pila are found on the nexine then the pollen grain is said to be intectate. Columellae can also support a more or less closed sexine layer. When this closed layer is found outside the exine it is called tectum. The pollen grain then is tectate. It is also possible that groups of columellae support more or less separated plates.

Other elements of different shapes can of course also be found in the sexine like scabrae, echinae, clavae, verrucae and gemmae. Since these terms rarely are disputed, they will not be discussed here.

However, we run into problems when the sexine is divided in more than two layers. Fig.1 will clarify this. On the left side is the terminology of ERDTMAN

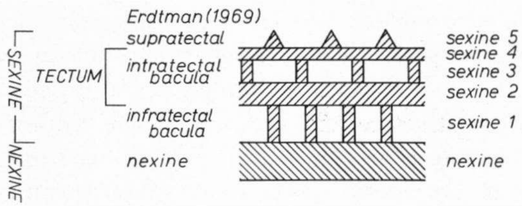

Fig.1. A diagrammatic representation of a topographical stratification of the exine. The terminology used to describe this stratification as used by ERDTMAN (1969) is on the left hand side of the figure, while that used by the present author is on the right hand side.

(1969), on the right side that of the present author. According to Erdtman the inner layer of the sexine consists of infratectal bacula whereas the rest of the sexine is called tectum. In the tectum intratectal bacula are present. On the tectum echinae are found. Such a division of the sexine is based clearly on an interpretation. A possible interpretation is that the tectum had a very solid structure during development. For this reason cavities arose in the tectum. If we accept this interpretation then the relics of the closed layer have to be called intra-tectal bacula, if the relics have the shape of pillars by coincidence. An other interpretation is also possible. Let it be supposed that the sexine consisted originally of a columellae layer and a tectum and that pila were present on that tectum. The capita of these pila may have fused during development resulting in a second tectum. In this case Erdtman's intratectal bacula should be called supratectal bacula with regard to the primary tectum or infratectal bacula with regard to the secundary tectum.

It is clear that such a terminology is based on interpretation, and must be rejected therefore (see p.40). A more objective description would be to number the visible layers of the sexine from inside to outside with the symbols 1, 2, 3, etc. The structure of each layer should be described separately. After the description one may attempt to interpret the structure of the wall. According to this method the description of the structure of the wall should be as follows: sexine composed of 5 layers. Sexine 1 and sexine 3 consists of columellae. Sexine 2 and sexine 4 consists of a closed layer without any visible differentiation. Sexine 5 consists of spine-like processes (echinae).

The term tectum is not used in this description. However, it is possible to call the outer most closed layer (here sexine 4) tectum. The definition of the term tectum then should be: outermost closed layer of the sexine.

Structure

In the present study no difference is made between structure and sculpture. POTONIÉ (1934) tried to give sharp differential definitions of these two terms. According to FAEGRI and IVERSEN (1964) the term structure covers all the characters due to the form and arrangement of the individual elements in intectate pollen types and to the form and arrangement of the exine elements inside a tectum. The term sculpture indicates the external geometrical features without reference to their internal construction. From these two definitions it appears that it is not always possible to distinguish between structure and sculpture. Even POTONIÉ (1934) admitted that structure and sculpture pass into each other. FAEGRI and IVERSEN (1964) state that "unless one is very careful, it is easy to confuse structure and sculpture". For these reasons it seems better to exclude the terms structure and sculpture from pollen grain terminology. Here structure will be used as a mere word, not as a term.

Sexine layers may consist of parts of sexine material separated from each other by spaces not filled up with sexineous material. Often these elements are arranged in a definite pattern, when seen from above. Of course the number of patterns is principally infinite and from this it will be clear at once that not all structure patterns can be named with a term. There are, however, patterns that occur so frequently that it is useful to have a term at hand.

A pattern that occurs often is a network. The structure elements (muri) surround spaces of different shapes (lumina). This pattern is called reticulate. Striate patterns come into existence when structure elements run parallel of each other. Generally the spaces are called striae and the structure elements lirae or valla. Patterns between reticulate and striate are called rugulate. ERDTMAN (1969) states that logically nothing contradicts the use of the terms muri and lumina in the description of striate patterns. Of course a similar reasoning can be held for rugulate patterns. The terms lumina and muri indicate only the spaces and the structure elements in patterns formed by spaces and structure elements.

ERDTMAN (1952) introduced the term brochus. A brochus is defined as: "consisting of a lumen and the adjoining half of the muri which separate that particular lumen from other lumina". This term is not so useful since it is difficult to determine the half of the muri in many cases.

The structure patterns mentioned so far may occur in various layers of the sexine. This can be an important feature. The localisation can be indicated with the prefixes eu-, supra- and infra-. If the elements which form the structure pattern are found on the nexine and if the grain is intectate, the prefix eu- can be used. If the elements which form the structure pattern are found between two closed layers of the sexine or between a closed layer of the sexine and the nexine, the prefix infra- can be used. If the structure elements which form the structure pattern are found on the outermost layer of the sexine, the prefix supra- can be used.

The muri may consist of columellae and sexine material that is supported by them. If the muri consists of one row of columellae, one may coin the muri simplicolumellate. Muri consisting of two rows of columellae are duplicolumellate and muri consisting of three or more rows are pluricolumellate.

Apertures

Pollen grains can show gaps or thin parts in the exine, which usually permit the living content to leave the pollen grain at germination. These special preformed parts are called apertures. Unfortunately the definition of the term aperture is not purely morphological, but partly physiological. It is impossible to determine the opening for normal exit of the cytoplasm of a pollen grain, when the grain has been acetolysed, in other words when the cytoplasm has gone. For this reason PUNT (1962) defined an aperture as: "any weak preformed part of the exine". REITSMA (1966) defined it: "a thinning or a missing of a part of the exine". Erdtman (personal communication, 1966) criticised this. He noted this definition also covers lumina. But no one will be inclined to call lumina apertures. A better morphological definition is: preformed thinnings or missings of parts of the exine, independant of the pattern of the exine. Of course the apertures themselves can be arranged in a pattern.

Apertures can have various outlines. It does not make sense to provide all these outlines with terms. Only those that occur so frequently are to be provided with terms. The majority of the apertures of angiospermous pollen grains have a circular or elliptic outline. Circular or faintly elliptic apertures are called pori. Oblong elliptic apertures are called colpi. The limit between faintly and oblong elliptic is arbitral and is placed mostly at a length/breadth ratio of 2. If the length/breadth ratio is smaller than 2 the aperture is called a porus, it is called a colpus if the ratio is larger than 2.

Apertures can be situated either in the sexine or in the nexine. Apertures situated in the sexine are generally called colpi or pori depending on the length/breadth ratio. With regard to apertures situated in the nexine there is much disagreement. ERDTMAN (1952) speaks of ora, a term not based on any outline. FAEGRI and IVERSEN (1950, 1964) and IVERSEN and TROELS-SMITH (1950) speak of colpi transversales if the length/breadth ratio is larger than 1 and of pores if the length/breadth ratio is equal to 1. VAN CAMPO (1958) distinguished apertures situated in the sexine (ectoapertures) and apertures situated in the nexine (endoapertures). Also REITSMA (1966) speaks of endocolpus and endoporus depending on the length/breadth ratio. Which term is the best one? Erdtman's term os can be used very well. It fulfils all requirements (see p.40). However, a disadvantage is that the term os does not take in consideration the outline, as is the case with apertures situated in the sexine. An additional disadvantage is that the term can be used only for nexine apertures associated with sexine apertures. Nexine apertures not associated with sexine apertures may not be indicated with the term os. The terms colpus transversalis and pore can not be used, since the definitions of pores and colpi in the nexine do not correspond with the definitions of pori and colpi in the sexine. Furthermore, the term colpus transversalis consists of two words, a feature that should be avoided as much as possible. Thus the terms endocolpus and endoporus remain. They are also terms which fulfil the requirements (see p.00) and the objections raised regarding the term os do not apply.

Other objections can be raised against the terms endocolpus and endoporus. One may say that there are fundamental, functional or whatever non-morphological differences between elliptic apertures in the sexine and elliptic apertures in the nexine. It may be that differences are present, but the outline of the apertures is entirely similar. Since pollen morphology is a descriptive discipline, in which functional or any other non-morphological differences are not to be taken in consideration, it is completely justified to give similar names to apertures with equal outlines in spite of a different localisation, or a different function.

Another objection against these terms may be of a linguistic nature. The words ecto- and endo- are of greek origin and the words aperture, porus and colpus of latin origin. It is especially Erdtman who values linguistics very highly. A consistent usage may be right, but it is very difficult to sustain it. Even ERDTMAN (1969) uses the greek prefix eu- and the suffix -oid in combination with latin words. One should not forget that terminology is nothing else but a collection of technical words, which are derived from various languages. If one will use only words derived from either greek or latin, he should realise that a majority of terms must be replaced. Furthermore many terms are not based on real greek or latin words, but on so-called botanical Greek or Latin. In this way one makes of terminology an independant discipline, which originally is meant as an expedient for communication. And I believe that nobody wishes this.

Summarizing, one can state that first of all the outline of the aperture should be described. After this the localisation of the apertures should be described with the prefixes ecto- and endo-. Among apertures colpus and porus are frequently occurred outlines.

Other outlines also occur like ringshaped, spiralshaped, dumb-bellshaped and rectangular. It is not necessary to create in these cases special terms, since they can be described easily. One may speak of a spiralshaped, a dumb-bell-shaped, or a rectangular ecto- or endoaperture. Ringshaped endoapertures were called "Ringfurchen" by WAGENITZ (1955), "colpi equatoriales" by FAEGRI and IVERSEN (1950, 1964) and "endocingulus" by REITSMA (1966). It may be better to abandon all these terms and to use a description.

In the work of ERDTMAN (1952) one often meets the terms colpoid and oroid. He defines colpoid as an aperture approximately similar to colpi and oroid as inner part, more or less similar to an os. However, the limits between a colpus and a colpoid and between an os and an oroid are very faint. Later (ERDTMAN, 1969), he dropped the term colpoid, together with terms as ruga, rupus, sulcus and sulculus. But the term oroid still exists.

Pollen grains can have either ectoapertures or endoapertures or combined ecto- and endoapertures. Combined ecto- and endoapertures are called compound apertures, while the others are called simple apertures. In compound apertures there are two possibilities concerning the situation of the endoaperture with regard to the ectoaperture.

(*1*) The longest axis of the endoaperture is perpendicular to the longest axis of the ectoaperture (lalongate endoaperture).

(*2*) The shortest axis of the endoaperture is perpendicular to the longest axis of the ectoaperture (lolongate endoaperture).

If the ectoaperture and the endoaperture are congruent one often speaks of a simple aperture in practice, although in principle the aperture is compound.

Pollen grains with simple apertures are called colpate, if the ectoaperture is a colpus and porate, if the ectoaperture is a porus. Pollen grains with compound apertures are called colporate, if the ectoaperture is a colpus and pororate, if the ectoaperture is a porus. In practice the terms colporate and pororate are used only, when the ectoapertures are not congruent. If the ecto- and endoapertures are congruent, one considers them simply as colpate and porate pollen grains, depending on the length/breadth ratio of the apertures.

From this it will be evident that the outline of the ectoaperture determines the terminology. It follows that pollen grains without ectoapertures must be called inaperturate. It is, however, possible that endoapertures can be present in inaperturate pollen grains.

The number of apertures in a pollen grain can be indicated by attaching the prefixes mono-, di-, tri-, tetra-, penta- and hexa- before the terms colpate, colporate, porate and pororate. More than six apertures can be indicated by using the prefix poly-.

The ectoapertures can be arranged over the surface of a pollen grain in various ways. Very often the ectoapertures are changed in an equatorial zone. This is indicated by the prefix zono- (ERDTMAN et al., 1961). Another possibility is that the ectoapertures are regularly scattered over the surface of the grain. This is indicated with the prefix panto- (ERDTMAN et al., 1961). FAEGRI and IVERSEN (1950, 1964) use the prefixes stephano- and peri-. A choice is difficult, but it seems better to use the prefixes zono- and panto-. Polyzonoaperturate pollen grains are grains with more than six ectoapertures, situated in a equatorial zone. Polypantoaperturate pollen grains are grains with more than six ectoapertures, scattered over the surface of the grain. Pentazonoaperturate grains are grains with five apertures, situated in an equatorial zone. Pentapantoaperturate pollen grains are grains with five ectoapertures, scattered over the surface of the grain.

Sometimes ectocolpi anastomose. This happens mostly at the poles. But it may occur also in other places. Pollen grains with anastomosing ectocolpi are called syncolpate or syncolporate depending on the simple or compound nature of the aperture.

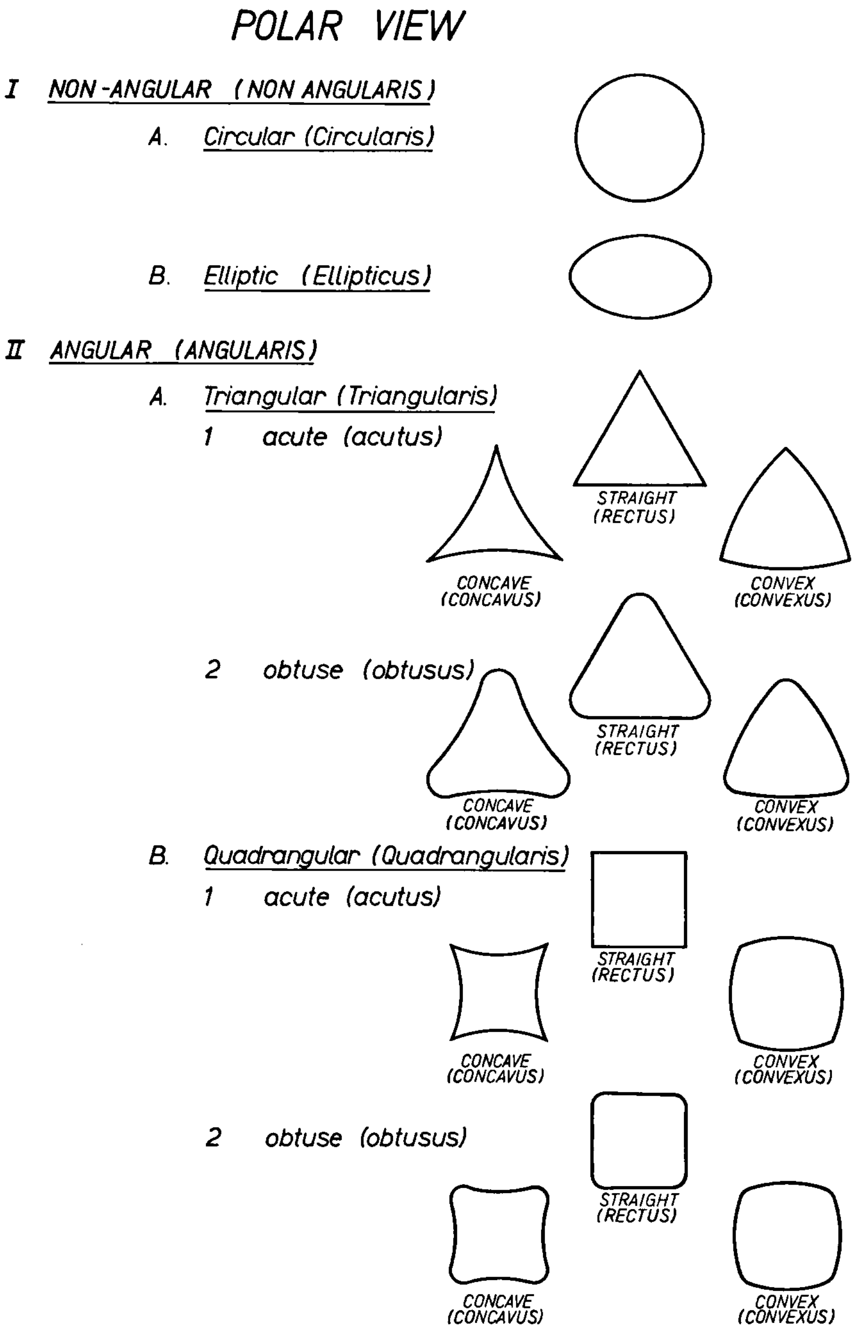

Fig.2. Non-angular, triangular and quadrangular outlines of symmetrical pollen grains in polar view.

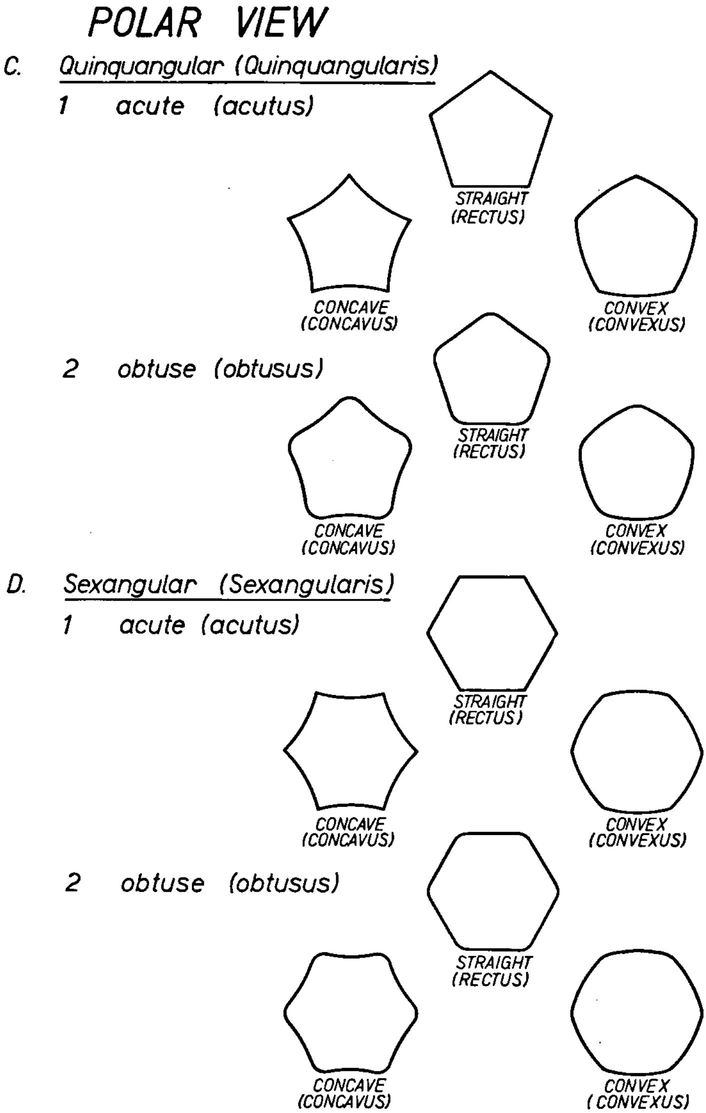

Fig.3. Quinquangular and sexangular outlines of symmetrical pollen grains in polar view.

The surface of zonoaperturate grains is split up by the ectoapertures in areas. At each pole there is an area, where no ectoapertures occur. These two areas are called apocolpium or apoporium depending on the outline of the ectoapertures. Also the zone in which the ectoapertures are situated, is divided by the ectoapertures into various areas. Each area is bordered by two adjacent ectoapertures.

This area is called mesocolpium if the ectoapertures are colpi and mesoporium if the ectoapertures are pori.

The part of the nexine that forms the bottom of the ectoapertures is called aperture membrane. Again one can distinguish between a colpus membrane and a porus membrane. The membrane can be either smooth (nudate) or set with scattered sexine elements (granulate). If a closed sexine layer lies over the aperture membrane and if the margin of this covering layer is completely or partly isolated from the rest of the sexine by an uncovered part of the aperture membrane, then this layer is called operculum.

The ectoapertures and endoapertures can be bordered by thickenings or thinnings of the exine. A sudden thickening or thinning of the sexine around an ectoporus is called annulus and around an ectocolpus it is called margo. Principally annulus and margo are the same and may be replaced by one term. However, these terms are so common, that I do not object to their continued use. Thickenings of the nexine around an endoaperture or below the edge of an ectoaperture are called costae. One may speak of costae ectocolpi, ectopori, endocolpi, endopori, etc.

In the area of the apertures two layers of the exine can be separated from each other by a cavity. This cavity is called a vestibulum in porate grains and a fastigium in colporate grains.

Shape

Pollen grains have a three-dimensional shape, which mostly is radially symmetric. It is difficult to detect a three-dimensional shape by means of a light microscope. Therefore, one generally describes the outline of the grain in polar and in equatorial view, thus the outline in a plane. Two completely different terminological systems exist to describe the outline, i.e., that of ERDTMAN (1952) and that of KUYL et al. (1955).

Erdtman compares the shape of a pollen grain with a rotation ellipsoid, in which the polar axis is the axis of rotation. On account of this he describes the outline in equatorial view as the ratio between the polar axis (P) and the maximum breadth (E); the P/E ratio. The maximum breadth is mostly identical with the equatorial diameter. Erdtman divides the various P/E ratios in different shape-classes, which he calls perprolate, prolate, subprolate, spheroidal, suboblate, oblate, and peroblate. The outline in polar view, indicated with the term amb, in Erdtman's terminology, is described with the terms angular or circular.

Kuyl et al. describe more outlines than Erdtman does. In equatorial view they maintain the terms oblate and prolate of Erdtman, but they use the term spherical for circular outlines. Apparently these authors do not pay any attention to the P/E ratio classes. They describe the outline of a grain with the terms circular, oval, rhomboidal and rectangular. All these outlines can be described further with the terms constricted, compressed and depressed. In polar view they describe outlines with terms as semiangular, subangular, hexagonal, lobate and semilobate.

On closer inspection it is evident that the two systems both have drawbacks. Not all shapes of pollen grains can be compared with an ellipsoid of rotation. In polar view one often meets difficulties when using these systems. The angular amb can often be described more exactly, while for instance four- and five angular outlines cannot be described with the system of Kuyl et al.

If we base our considerations on the principle that outlines must be described in a plane, it is not difficult to find a good system. For a description of outlines in a plane there exist already many proposals, such as the proposals set by the SYSTEMATICS ASSOCIATION COMMITTEE FOR DESCRIPTIVE BIOLOGICAL TERMINOLOGY (1962). Since it is difficult and unnecessary to classify asymmetrical forms in a system, these forms will not be dealt with here.

Polar view (Fig.2, 3)

The basis for the description of the outline in polar view are angular and non-angular forms. Non-angular forms are either circular, elliptic, ovate or lanceolate. In angular forms there are three variable characters, i.e., the number of the angles, the outline of the angles and the form of the sides. The number of angles varies from three to numerous. This is indicated by putting the number of the angles before the term angular. For instance, 3-angular, 4-angular, 5-angular, etc. The angles can be acute or obtuse. The sides can be straight, concave or convex.

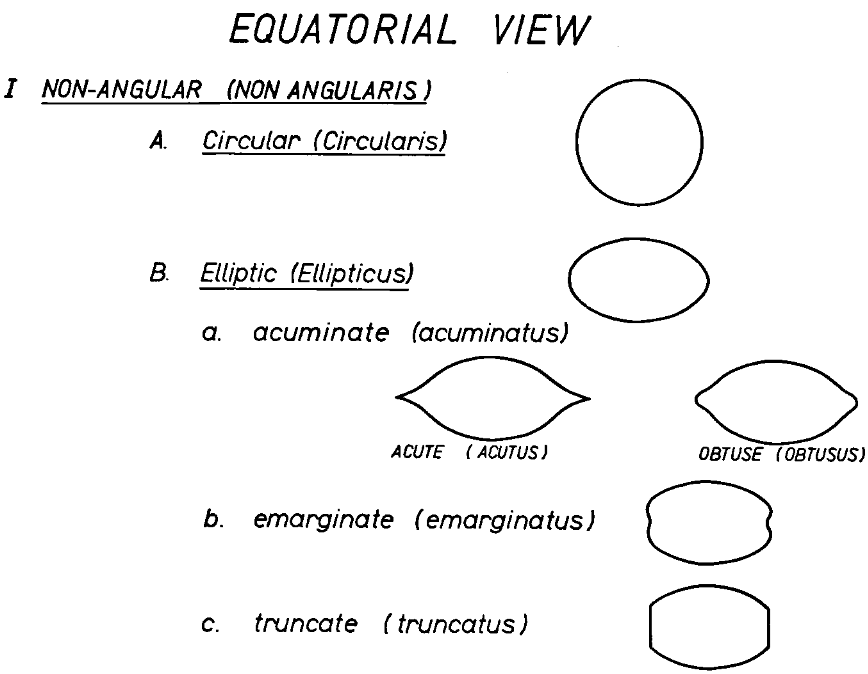

Fig.4. Non-angular outlines of symmetrical pollen grains in equatorial view.

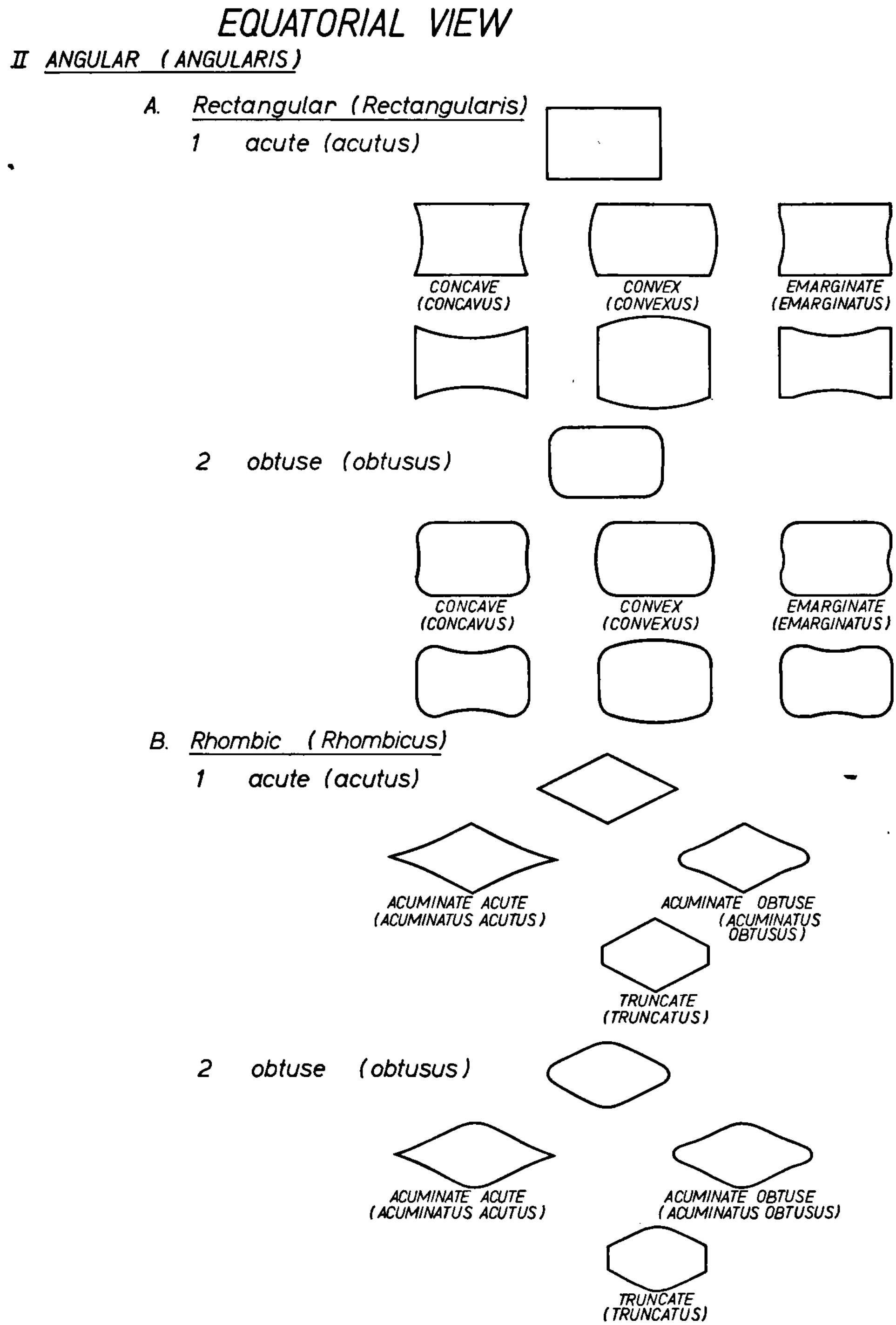

Fig.5. Angular outlines of symmetrical pollen grains in equatorial view.

Each radially symmetric outline can be described with these variable characters.

The situation of the apertures has to be indicated separately and independently of the outline. The apertures are situated either in the angles (axillary) or between the angles (interaxillary), when pollen grains are zonoaperturate.

Equatorial view (Fig.4, 5)

The basis for the description of the outline in equatorial view were also angular and non-angular forms. Non-angular outlines can be either circular or elliptic. Often the term oval is used instead of elliptic. Since the word oval has various meanings in different languages, it is rejected here. The ends of an elliptic form can lie further than was expected from the course of the sides. This is called acuminate. The sides of an elliptic form can be either introverted (emarginate) or flattened (truncate). Angles, if present, can be either acute or obtuse. The basic forms of angular outlines can be either rectangular of rhombic. Mostly the term rhomboidal is used instead of rhombic. Since rhomboidal indicates a three-dimensional shape and rhombic a two-dimensional outline, the term rhomboidal has to be rejected. In all cases the angles can be acute or obtuse. The sides are either straight, concave or convex. In rhombic forms the ends may be acuminate or truncate.

With this system the polar axis (P) and the equatorial diameter (E) are not taken into consideration. The P/E ratio, introduced by Erdtman, should be indicated separately, as well as the P/E ratio class. But now the difficulty arises that the terms of Erdtman cannot be used without comment. These terms are based partly on a rotation ellipsoid. There are two possibilities. Either Erdtman's terms are maintained and must be redefined or new terms must be introduced. Erdtman is not much inclined to redefinitions, I agree and, therefore, it might be better to introduce new terms (see Table I). The terms erect and transverse have been borrowed from leaf morphology. However, no term exists for a P/E ratio equal to 1. Tentatively the term adequate is used here.

TABLE I

RELATION BETWEEN THE POLAR AXIS (P) AND THE EQUATORIAL DIAMETER (E)

P/E ratio class	*P/E*
Pererect (pererectus)	>2
Erect (erectus)	1.33–2
Semi-erect (semi-erectus)	1.14–1.33
Suberect (suberectus)	1 –1.14
Adequate (adaequatus)	1
Subtransverse (subtransversus)	1 –0.88
Semi-transverse (semi-transversus)	0.88–0.75
Transverse (transversus)	0.75–0.50
Pertransverse (pertransversus)	<0.5

GLOSSARY

Annulus: zone around an ectoporus formed by a sudden thinning or thickening of the sexine or by any other sexine structure, different from the remaining sexine.
Aperturate: pollen grain provided with one or more ectoapertures.
Aperture: any preformed thinning or missing of a part of the exine, independant of the pattern of the exine.
Apocolpium (pl. apocolpia): area at each pole of a pollen grain delimited towards the equator by a transverse line drawn through the polar ends of the ectocolpi.
Arcus (pl. arcus): band-like, locally thickened part of the exine usually extending in sweeping curves from aperture to aperture.
Aspis (pl. aspides): shield-shaped exine area surrounding an ectoaperture and protruding as a rounded dome from the general surface of a pollen grain.
Baculum (pl. bacula): pillar-like process, always longer than broad and higher than 1 μ.
Caput (pl. capita): apical swollen part of a pilum.
Clava (pl. clavae): process higher than broad, slightly tapering towards the base, higher than 1 μ.
Colpate: pollen grain provided with one or more ectocolpi.
Colporate: pollen grain provided with one or more ectocolpi, each combined with one or more endoapertures (N.B. ectoaperture and endoaperture are not congruent).
Colpus (pl. colpi): elliptic aperture with a length/breadth ratio higher than 2.
Columella (pl. columellae): pillar-like element, supporting a layer, a part of a layer or crowned by a single element.
Compound aperture: ectoaperture combined with one or more endoapertures (N.B. apertures not congruent).
Costa (pl. costae): thickening of the nexine near an aperture.
Costae ectocolpi: thickening of the nexine below the edge of an ectocolpus.
Costae ectopori: thickening of the nexine below the edge of an ectoporus.
Costae endocolpi: thickened edge of an endocolpus.
Costae endopori: thickened edge of an endoporus.
Distal part: part of a pollen grain that faces in opposite of the centre of the tetrad during meiosis.
Distal pole: the centre of the surface of the distal part.
Duplicolumellate: muri consisting of two rows of columellae.
Echina (pl. echinae): spinelike process, always higher than 1 μ.
Ectoaperture: aperture in the sexine.
Ectocolpus (pl. ectocolpi): elliptic ectoaperture, with a length/breadth ratio higher than 2.
Ectoporus (pl. ectopori): circular or faintly elliptic ectoaperture, with a length/breadth ratio smaller than 2.
Endoaperture: aperture in the nexine.
Endocolpus (pl. endocolpi): elliptic endoaperture, with a length/breadth ratio higher than 2.
Endoporus (pl. endopori): circular or faintly elliptic endoaperture, with a length/breadth ratio smaller than 2.
Equator: borderline of the distal and proximal part.
Eureticulate: pollen grain provided with structure elements standing in a reticulate pattern on the nexine.
Eurugulate: pollen grain provided with structure elements in a rugulate pattern standing on the nexine.
Eustriate: pollen grain provided with structure elements in a striate pattern standing on the nexine.
Exine: the part of a pollen wall outside the intine.
Fastigium (pl. fastigia): cavity in a colporate grain, caused by a separation of the nexine and the domed sexine, in the area of the endoaperture.
Gemma (pl. gemmae): process, constricted at its base, always higher than 1 μ, the diameter is equal or larger than the height.
Inaperturate: pollen grain without ectoapertures.
Infrareticulate: pollen grain with a reticulate pattern, situated between the nexine and a closed sexine layer, or situated between two closed sexine layers.

Infrarugulate: pollen grain provided with a rugulate pattern, situated between the nexine and a closed sexine layer or situated between two closed sexine layers.
Infrastriate: pollen grain provided with a striate pattern, situated between the nexine and a closed sexine layer or situated between two closed sexine layers.
Intectate: pollen grain without a tectum.
Intine: the cell wall proper (cellmembrane), inner layer of a pollen wall.
Lalongate: the longest axis of an endoaperture of a compound aperture is perpendicular to the longest axis of the ectoaperture.
Lolongate: the shortest axis of an endoaperture of a compound aperture is perpendicular to the longest axis of the ectoaperture.
Loxoaperturate: zonoaperturate pollen grain with ectoapertures converging in pairs (loxocolpate, loxocolporate and loxoporate).
Lumen (pl. lumina): space between muri.
Margo (pl. margines): zone around an ectocolpus formed by a sudden thinning or thickening of the sexine or by any other sexine structure different from the remaining sexine.
Mesocolpium (pl. mesocolpia): area delimited by two adjacent ectocolpi and by transverse lines drawn through the polar ends of these ectocolpi.
Murus (pl. muri): ridge separating two lumina.
Nexine: inner united homogeneous layer of the exine.
Operculum (pl. opercula): closed part of the sexine which is found on the aperture membrane and which is completely or partly isolated from the rest of the sexine by an uncovered part of this membrane.
Pantoaperturate: pollen grain with ectoapertures scattered over the whole surface (pantocolpate, pantocolporate, pantoporate and pantopororate).
Pilum (pl. pila) process consisting of a pillar-like part (columella) and an apical swollen part (caput).
Pluricolumellate: muri consisting of three or more rows of columellae.
Polar axis: a straight line connecting the distal and the proximal pole of a pollen grain.
Porate: pollen grain provided with one or more ectopori.
Pororate: pollen grain provided with one or more ectopori, each provided with one or more endoapertures (apertures not congruent).
Porus (pl. pori): circular or faintly elliptic aperture, with a length/breadth ratio smaller than 2.
Proximal part: part of a pollen grain that faces towards the centre of the tetrad during meiosis.
Proximal pole: the centre of the surface of the proximal part.
Reticulate: pollen grain provided with reticulum.
Reticulum (pl. reticula): network formed by muri and lumina.
Rugulate: pollen grain provided with an irregular pattern of lumina and muri.
Scabra (pl. scabrae): element of different shape, smaller than 1 μ.
Sexine: outer layer of the exine.
Simplicolumellate: muri consisting of one row of columellae.
Striate: pollen grain provided with a regular pattern of approximately parallel lumina and muri.
Suprareticulate: pollen grain provided with elements in a reticulate pattern standing on a tectum.
Suprarugulate: pollen grain provided with elements in a rugulate pattern standing on a tectum.
Suprastriate: pollen grain provided with elements in a striate pattern standing on a tectum.
Syncolpate: pollen grain with anastomosing ectocolpi.
Syncolporate: pollen grain with anastomosing ectocolpi of compound apertures.
Tectate: pollen grain provided with a tectum.
Tectum (pl. tecta): outermost closed layer of the sexine.
Tectum perforatum: tectum provided with some small holes.
Trichotomocolpate: a three-slit aperture.
Verruca (pl. verrucae): wart-like process always broader than high and always higher than 1 μ.
Vestibulum (pl. vestibula): cavity inside an ectoporus, caused by a separation of two layers of the exine.
Zonoaperturate: pollen grain provided with ectoapertures and situated in an equatorial zone (zonocolpate, zonocolporate, zonoporate, zonopororate).

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