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Pollen Terminology

An illustrated handbook

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An illustrated Handbook

Michael HESSE, Reinhard ZETTER,
Heidemarie HALBRITTER, Martina WEBER,
Ralf BUCHNER, Andrea FROSCH-RADIVO,
Silvia ULRICH

GENERAL CHAPTER

ILLUSTRATED GLOSSARY

ALPHABETIC GLOSSARY

ANNEX

*In memory
of*

Jan MULLER and Wilhelm KLAUS,

*who played a prominent role
in the study of fossil and extant pollen.*

*There are more things in heaven and earth,
than are dreamt of in our philosophy.*

Preface

The principal aim in compiling this book was to provide the reader with first-hand information about the structure and outlook of the extremely manifold pollen in seed plants.

Pollen Terminology. An illustrated Handbook should not be seen as a mere collection of striking and/or informative light and electron micrographs. Each of the micrographs is intended to convey a specific message related to properties and functions of the pollen grains shown. The authors hope that the book will be useful for experienced researchers as well as for beginners in palynology, but also for medicine, biochemistry, or even for lawyers and artists as an aid and guide for the evaluation and interpretation of pollen features.

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assistance to offer; William W. Ruben
might care to offer; Pal Research Co
ology and Geography; "The question raised by
analysis the proper name to replace it by
and his suggestion to replace it by 'pollen'
much. We entirely agree that a new term
fact that pollen analysts normally inclu
of such plants as ferns and mosses we t
wider connotation than palynology (from Gre
therefore suggest palynology (from Gre
straw or sprinkle; cf. 'it's a lot' (r
Latin pollen, flour, dust): the stu
and their dispersal, and applications p-l-
that the sequence of consonants p-l-
a difference) and the general euphor
to our fellow soldiers in this field
coining of this new word by Mr. L.
College, Cardiff." (H.A. Hydc and
'Wales')

THE RIGHT WORD.

(H.A. Hydc and

"I have been toying with the
including most of the work on po
elements of soil and humus

... Chairman, Division of Paleobotany, August 30, 1944.

Dr. Antevy: 'Is pollen
pollen and its applications?
en science' interest us very
is needed but in view of the
ade in their counts the spores
think that some word carrying a
be called for. We would
ek Пд.Х.У.В. (paluno), to
palē), fine meal; cognate with
dy of pollen and other spores
s thereof. We venture to hope
n, (suggesting pollen, but with
y of the new word may commend it
J. D. Richardson, M.A., University
D. A. Williams, July 15, 1944.

... of micro-paleobotany' as
... also all minor
... remains which

layers of vegetative

GENERAL CHAPTER

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Introduction

Pollen Terminology. An illustrated Handbook is a collection of useful terms in palynology, well illustrated with light (LM) and electron microscope (EM) micrographs. The reader will not find an encyclopedic compilation of terms; in that respect see KREMP (1968). The focus is on the pollen of seed plants, predominantly angiosperms, while spores are considered only exceptionally. Therefore the terminology rarely includes spore or gymnosperm characteristics (e.g., leptoma, trilete mark).

Since 1994, the Glossary of Pollen and Spore Terminology, co-authored by Wim PUNT, Stephen BLACKMORE, Siwert NILSSON and Annick LE THOMAS, was the standard reference publication in palynological terminology. Then, in 1999 the online version by Peter HOEN (<http://www.bio.uu.nl/~palaeo/glossary/glos-int.htm>) appeared, with several additions. The online version was published by W. PUNT, P.P. HOEN, S. BLACKMORE, S. NILSSON and A. LE THOMAS in 2007 and provides informative schematic drawings containing the essentials of each term and colored to indicate the wall and aperture components, mostly using LM findings.

Although extremely useful for overview purposes, drawings cannot show the full

range of features. This can be achieved only with micrographs, which demonstrate – a picture is telling more than thousand words – the often stunning diversity of features. For that reason, the explanatory power of micrographs produced with scanning electron microscopy (SEM) and transmission electron microscopy (TEM) is used in the present volume. The numerous SEM micrographs illustrating the astonishing diversity of pollen ornamentation. Where important terms have appeared ambiguous or have been hitherto underrated, the term has been reviewed and brought into focus (e.g. harmomegathy, or pollen class versus pollen type).

It is self-evident that such a book cannot renounce the basics of palynology. In this context please consult standard textbooks in palynology, e.g., ERDTMAN (1952), FÆGRI and IVERSEN (1989) or BEUG (2004). The principles of pollen development and morphology are incorporated as separate chapters for purposes of clarity and in order to correctly interpret the detailed structures of the pollen wall and the full range of ornamentation.

Guidelines

The aim of this book is to provide a fully illustrated terminology and glossary of the most **important** palynological terms, including a substantial standardization of definitions. If terms are not considered here, then they appeared to us as insignificant, or they belong to the terminology of fern spores, which is not considered here. A comprehensive description of pollen grains with terms mentioned in "*Pollen Terminology. An illustrated Handbook*" is easily accomplishable.

A strict rationalization of terms on the basis of practical criteria has been attempted. For consistency, phrases are standardized as far as possible; for example, features of ornamentation are stereotypically defined as "**pollen wall with**", and pollen wall features (or pollen shape and size) as "**pollen grain with**".

Where it was necessary, definitions have been reworded, newly circumscribed, or brought into focus. In addition, consistent application of EM techniques and the nowadays better understanding of pollen features have made redefinition of some terms necessary. Moreover, we have classified terms according to applied techniques (LM, SEM, TEM) and their usage in morphological, anatomical and/or functional context. In chapter "Alphabetic Glossary" the entries are arranged alphabetically. The definitions are provided with numbers in bold referring to the respective page in chapter "Illustrated Glossary"¹ and numbers in square brackets referring to important literature (see chapter "Bibliography").

Emphasis is given to the numerous illustrations. The worldwide largest database on pollen, PalDat (<http://www.paldat.org/>) is the main source of pictures. Each term is illustrated with LM or EM pictures in order to point out the **character range** of a term (or,

more precisely, to show the full range of a single character). Brief information on the method of preparation is often provided. In preparing pollen for SEM micrographs, acetolysis was avoided as far as possible.

Underrated pollen conditions, e.g., the physical condition of the turgescient, life-like pollen, are considered. The SEM micrographs usually represent the turgescient condition, without further notice. Consequently, pollen grains are often shown in dehydrated stage, marked as "dry pollen". The deviating characters in turgescient and dry pollen grains are designated by descriptive pictorial terms such as cup-shaped, boat-shaped and aperture sunken.

Comments are provided where this may help in the application of a term or to qualify the circumstances in which it is used.

Self-explanatory general terms are usually not defined; in such cases the context is noted (e.g., circular, see **outline**). For more information on these see the appropriate page(s) in chapter "Illustrated Glossary".

Three categories of terms are used: important terms are printed in **bold** and are usually illustrated; terms of minor importance are printed in regular script, usually without illustrations (if necessary, terms in chapter "Alphabetic Glossary" are sometimes also illustrated in a footnote); terms printed in italics are not recommended and often provided with an explanatory comment.

The chapter "Illustrated Glossary" is subdivided into larger topics, e.g., "Shape and Size" or "Ornamentation". The terms themselves are listed according to their resemblance in order to provide the user with a side-by-side spectrum of similar characters. For a quick orientation please use the last page of "*Pollen Terminology. An illustrated Handbook*". It is a fold-out page with terms alphabetically arranged. Numbers indicate the page in chapter "Illustrated Glossary".

In contrast to chapter "Illustrated Glossary" the terms in chapter "Alphabetic Glossary" are throughout arranged alphabetically as the noun and the corresponding adjectival

¹ Please note: literature references are not necessarily the earliest publication in which the term was used. The comprehensive literature list (see chapter "Bibliography") includes beside the references more and other (and preferably recent) publications which have been selected as sources of further information.

form, if appropriate. Few terms are used exclusively as nouns or exclusively as adjectives. Sometimes two adjectival variants (-ate, -ar) are used but, if so, in two different meanings. For example: from the noun granulum (sculptural or structural element of differing size and shape, less than 1 µm in diameter) derive the two adjectival forms granular and granulate (both meaning "with granules"); these are corresponding terms used in two quite different contexts: **granular** describes a distinct type of infractum hence a **structural** feature whereas **granulate** refers to an ornamentation feature – a **sculpturing** element.

Both the singular and the plural are given consistently for Latin terms. The English spelling of the Latin term is added (porus, pl. pori, engl. pore) if the English form is preferable.

Cross-references are given to terms that are **synonyms** (the preferable one is printed in bold) or that indicate the opposite condition (**antonyms**), e.g., homo- and heterobrochate.

Numbered literature references are given for each term in chapter "Alphabetic Glossary" and are not necessarily the earliest publication in which the term was used.

PUNT et al. (2007) provide the basis of the present terminology. Many terms in palynology were coined at a time when only LM observations were available. Mainly for historical reasons, inconsequent nomenclatural applications, enumerations of synonyms, and even differing definitions have been found for one and the same term.

During the 20th century questions of terminology became more and more problematic. The main reasons were the greatly increasing number of publications in palynology, dealing with sometimes insufficiently described or "uncommon" pollen features, and simultaneously the advent of manifold applied fields of palynology. For various reasons, nearly all authors used their own terminology. The situation became worse in the 1970s and 1980s, leading to a variety of terminological "schools".

Nonetheless, in the 1950s attempts were made to restrict the wording and to state the definitions of terms more precisely. A deserving, widely accepted but all-too-restricted list of pollen morphological terms and definitions was published as early as 1950 by IVERSEN and TROELS-SMITH. Later, KREMP (1968), in his famous encyclopedia, provided a monumental enumeration of all known terms.

Being aware of the danger that pollen terminology

tends to become foggy, REITSMA (1970) took the first resolute step to overcome this problem. A concise terminology now became available, though unfortunately not taking account of the range of variation of most of the palynological features, and without drawings or micrographs. FÆGRI and IVERSEN (1989, 4th ed.) restricted their glossary to terms exclusively used in their book. MOORE et al. (1991, 2nd ed.) provided a glossary of selected terms used in their pollen and spore keys. Standardization came with the glossary by PUNT et al. (1994), updated in 2007. The main advance of their concise and comprehensive terminology is the consistent usage of drawings and the critical comments on terms and usage.

Rules for Using Prefixes

If both a Greek and a corresponding Latin form exist for a prefix, then the Greek form is used consistently: panto- (not peri-), ekto- (not ecto-), or the Greek di- (dis-), and not the Latin bi- (bis-). There are few exceptions from this rule. If the Latin form is more widely used, then the term is treated as a nomen conservandum; for example, bisaccate is found exclusively in the literature and not the Greek form disaccate.

Some prefixes need a comment. **Micro** is used to denote features <1 µm: micro-reticulate, -echinate, -verrucate, -baculate, -clavate, -gemmate, -rugulate. However, some possible combinations are not applicable; for example, micro-striate or micro-perforate. Striae are not known to be <1 µm in length, and perforate by definition describes a feature <1 µm.

Terms not listed in the glossary belong to fern or moss spores, or are considered as obsolete, diffuse or redundant (e.g., multiplanar tetrad), superfluous (e.g., polylicate, because plicate pollen grains are always equipped with several to many plicae), or may be a permanent source of confusion (zon-, zona-, zoni-, zono-).

"*Pollen Terminology. An illustrated Handbook*" aims to clearly separate the types and classes of pollen. **Pollen type** is a general term categorizing pollen grains by distinct combinations of characters and is often used in connection with a distinct taxon (e.g., *Polygonum aviculare* type).

Pollen class² is an artificial grouping of pollen grains that share a single, distinctive character. Pollen classes refer to pollen units, to aperture form and location, or to an extremely distinctive ornamentation character. Classes include the terms polyads, tetrads, dyads, saccate, inaperturate, sulcate, ulcerate, colpate, col-

² "Pollen type" is sometimes (colloquially) misused; for example, *Croton* type, which is a distinct feature of ornamentation and is correctly termed *Croton* pattern.

porate, porate, synaperturate, spiraperturate, lophate, clypeate and plicate. These classes are useful in identification keys as they have a good diagnostic, although mostly no systematic, value. In general, a pollen grain may belong to more than one pollen class; in such cases the more significant feature should be ranked first (e.g., *Pistia*: plicate - inaperturate, *Hemigraphis*: plicate - colpate, *Typha*: tetrads - ulcerate, *Rhododendron*: tetrads - colpate).

Palynology

The Science of Pollen and Spores

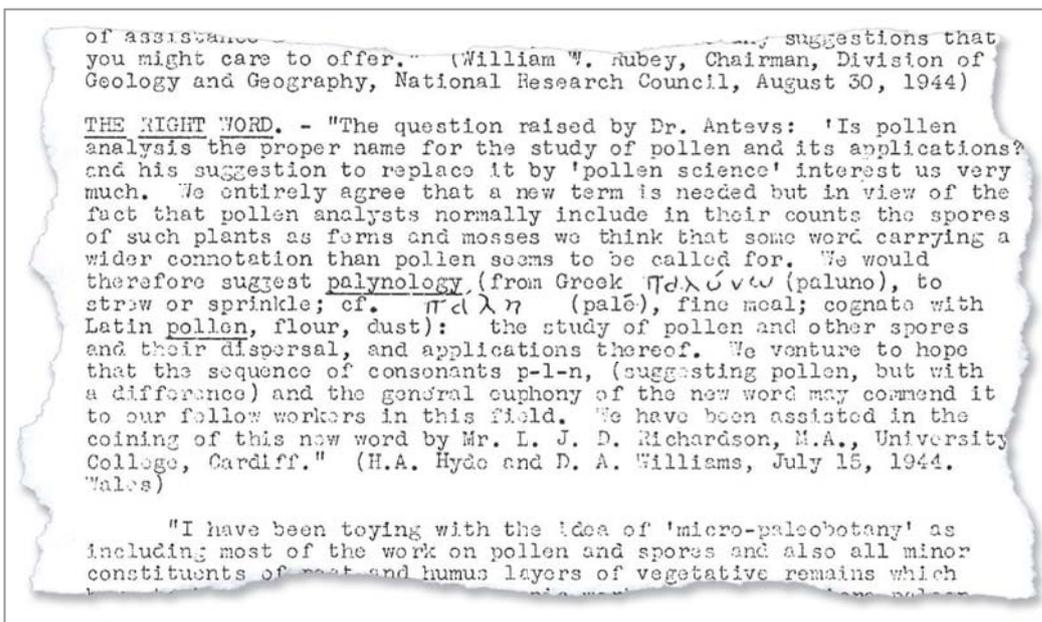
The term palynology was coined after a written discussion with Ernst ANTEVS and A. Orville DAHL in the Pollen Analysis Circular no.8 by HYDE and WILLIAMS (1944) and is a combination of the Greek verb paluno (παλύνω, "I strew or sprinkle"), palunein (παλύνειν, "to strew or sprinkle"), the Greek noun pale (παλη, in the sense of "dust, fine meal", and very close to the Latin word pollen, meaning "fine flour, dust") and the Greek noun logos (λογος, "word, speech").

Palynology is the science of palynomorphs, a general term for all entities found in palynological samples. A dominating object of the palynomorph spectrum is the pollen grain, the point of origin and the carrier for the male gametes (sperm cells).

What makes pollen grains so unique? Pollen grains represent an extra generation in seed plants, the highly reduced male gametophyte (the enclosing sporoderm and the cellular content, consisting of two or three cells, and the pollen tube). Pollen grains are therefore not simply parts of a plant, such as leaves or seeds, but are the

haploid counterpart of the much larger diploid plant body "as we see it in nature". During transport pollen grains are completely separated from the parent plant and perfectly adapted for their role – the transfer of male genetic material – and are able to resist hostile environmental stress on their way to the female flower parts. These tiny (male haploid) organisms usually have as variable parameters: the pollen shape and size, the number, type and position of apertures and the pollen wall with its extremely diverse structure and sculpture. The characters of these parameters in comparative pollen (and spore) morphology and plant systematics are at least as important as any other morphological character of the diploid generation.

The pollen grains of seed plants and the spores of mosses and ferns share many homologies. However, although probably equivalent, the terminology of spore wall strata differs, mainly for historical reasons, from the terms used for pollen grains. Some elements and/or features of spores are unknown in pollen grains, e.g., the outermost wall layer in many fern spores, called the perine or perispore.



HYDE and WILLIAMS (1944)
The right word.
Pollen Analysis Circular 8: p. 6

A Brief History of Palynology

The Very Early Beginnings

Assyrians are said to have known the principles of pollination, but it is unclear if they recognized the nature and power of pollen itself. Greeks and Romans, and the Middle Ages up to the 16th century did not contribute substantially, as far as is known.

The Era of the Light Microscope

A comprehensive historical survey is found in WODEHOUSE (1935) and especially in DUCKER and KNOX (1985). Only the most important scientists can be mentioned here; the list is not exhaustive.

It was Nehemiah GREW who as early as 1662 in his famous work *"The Anatomy of Plants"* described the constancy of pollen form within the same species; in other words, he founded pollen morphology and was the first to recognize that all plants have "their" pollen. Carl von LINNÉ (1751) first used the term pollen (in Latin). During the 18th and the early 19th centuries there was considerable progress on pollen and the understanding of pollination. For example, Joseph Gottlieb KOELREUTER (1766), together with Christian Konrad SPRENGEL, the founder of flower ecology, perceived the importance of insects in flower pollination and found for the first time that the pollen grain has an important part in determining the characters of the offspring.

SPRENGEL (1793) was the first to recognize pores and furrows in the pollen wall; he also demonstrated the effects of cross pollination, of dichogamy, and distinguished between entomo- and anemophily.

Johannes PURKINJE (1830) and Franz Andreas (Francis) BAUER, among others, also made substantial contributions. BAUER is famous for his fine and exact drawings and watercolors of pollen, now held in the Botanical Library of the Natural History Museum, London. Only a few facsimiles have been published, e.g., in KESSELER and HARLEY (2004). Robert BROWN (1828, 1833) reported and confirmed BAUER's earlier work, and gave the first description of the origin of the pollen tube.

New and better microscopes enabled Hugo von MOHL (1834) and Carl Julius FRITZSCHE (1837) to separate clearly the principal layers of the pollen wall and to publish surveys on pollen morphology of many angiosperm families. The terms pollenin, exine and intine go back to FRITZSCHE. Johann Heinrich Robert GÖPPERT (1837) and Christian Gottfried EHRENBERG (1838) were the first to describe and depict fossil pollen grains. Eduard STRASBURGER (1882) achieved ground-breaking insights into the development and internal structure of pollen. Hugo FISCHER (1890) was the first to summarize the arguments for the phylogenetic value of pollen characters. Pollen statistics represented a first step towards an applied field of science and in 1916 Lennart von POST published the first pollen diagram (pollen profile).

The 20th century up to ca 1960 was dominated by the skilful use of the LM, with many new findings; for example, the LO-analysis, a method for analyzing patterns of exine organization by light microscopy: focusing at different levels distinct features appear bright (L = Lux) or dark (O = Obscuritas). Textbooks by Roger WODEHOUSE (1935), Gunnar ERDTMAN (1943, 1952, 1969), or Knut FÆGRI and Johannes IVERSEN (1950) summarized the knowledge on pollen at that time and to a great extent have maintained their value.

In the first half of the 20th century palynology as a predominantly basic science "went applied", giving rise to a series of diversifications. Applied fields, worldwide in use, include aeropalynology, biostratigraphy, copropalynology, cryopalynology, forensic palynology, iatropalynology, melissopalynology, paleopalynology, pharmacopalynology, among others.

The Era of the Electron Microscope

As pointed out by KNOX (1984, p. 204): *"The terminology applied to the pollen wall is daunting, especially as it has been developed from early light microscopy work, and then transposed to the images seen in the transmission and scanning electron microscopes"*.

Electron Microscopy with its two most important types, TEM and SEM, facilitated the major breakthrough in palynology: the ultrastructure of developing and mature pollen and the stunning visualization of pollen morphological characters.

During the 1950s and early 1960s considerable progress in TEM preparation methods (from fixation to microtomy and staining) took place. The resolving power of the TEM was the basis for new information on pollen grain ultrastructure and pollen development. Nevertheless, EM-based information on ornamentation details of pollen grains was rare up to the mid-1960s. Only TEM-based casts or replica methods were available, all of them with limited resolution and depth of focus (e.g., the single-stage carbon replica technique; ROWLEY and FLYNN 1966, FLYNN and ROWLEY 1967). The time-consuming and laborious TEM replica procedures were an obstacle to extensive surveys of pollen morphology and have now been successfully replaced by SEM (HARLEY and FERGUSON 1990).

Today barely conceivable, the introduction of SEM in palynology in the second half of the 1970s was a key innovation in the study of the fine relief of pollen surfaces. Advantages of SEM include the relatively simple and rapid preparation methods, the unsurpassed depth of focus revealing an overwhelming vividness and power. SEM was accepted in the very first moment as the quantum leap in EM (HAY and SANDBERG 1967). The first SEMs of pollen grains were published by THORNHILL et al. (1965) and ERDTMAN and DUNBAR (1966).

Since then palynologists have been provided with a plethora of beautiful micrographs. *"The scanning electron microscope has provided a greater impetus to palynology than any other technical development during the history of the subject."* (BLACKMORE 1992).

Nowadays the LM (with basic and advanced equipment) and the two main types of EM form an expedient combination of imaging techniques. The LM remains the workhorse method (TRAVERSE 2007; see the compendia by REILLE 1992, 1995 and 1998) but is limiting insofar as morphological and structural features at species level, not observable by LM but of diagnostic value, are routinely determinable only by SEM. The role of SEM as an essential part in illustrating exine sculpture and ornamentation cannot be overrated (HARLEY and FERGUSON 1990).

A Tentative Outlook

Nowadays, palynology, as an organismic-based science, can serve as an indispensable tool for various applied sciences, but clearly also can stand alone as one of the most developed basic sciences.

In general, compared to the diplont the male gametophyte in seed plants is yet poorly investigated. From at least 250,000 plant species only ca 10 percent have been studied with respect to pollen grain morphology, and regarding pollen grain anatomy it is much less.

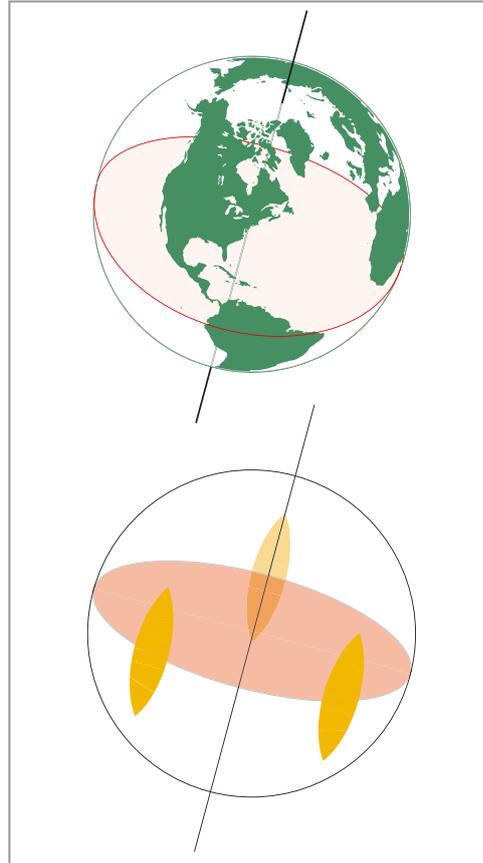
In the 21st century, no matter what role palynology will play, being a basic field of science or more probably a bundle of applied fields, a vital issue will be the increase of our knowledge of pollen grains and in this context the enhancement of pollen terminology. Modern palynologists, making use of LM as well as EM, need for descriptive matters a clearly defined and pictorial pollen terminology, covering the richness of features and the enormous spectrum of characters.

Pollen Morphology

A diagrammatic representation of the main morphological features of a palynomorph (preferably pollen grains or spores) is called **palynogram**. It includes parameters of symmetry, shape and size, aperture number and location, ornamentation and stratification.

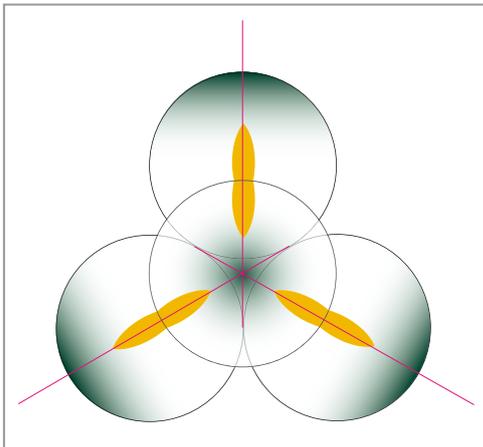
Polarity and Symmetry

Mature pollen is shed in **dispersal units**. The post-meiotic products either remain permanently united or become partly or usually completely disintegrated. In the latter case the dispersal unit is a single pollen grain, a **monad**; if the post-meiotic products remain united, **dyads** (a rare combination), **tetrads** or **polyads** (**massulae**, **pollinia**) are the result. **Pollinaria** are dispersal units of two pollinia including the sterile, interconnecting appendage.



Polar axis and equatorial plane

Tetrad stage orientation of microspores

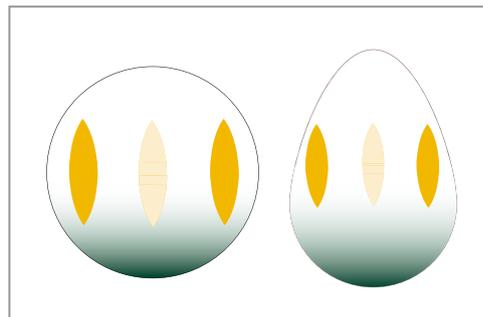


distal poles shaded green

microspore's center, perpendicular to the polar axis. Therefore, the **equatorial plane** divides the pollen grain into a proximal and a distal half.

Isopolar pollen grains have identical proximal and distal poles, thus the equatorial plane is a symmetry plane. In **heteropolar** pollen grains the proximal and distal halves are different.

Pollen shape and aperture location directly relate to pollen **polarity**, which is determined by the spatial orientation of the microspore in the meiotic tetrad and can be examined only in the tetrad stage. The **polar axis** of each microspore runs from the **proximal pole**, orientated towards the tetrad center, to the **distal pole** at the outer tetrad side. The **equatorial plane** is located at the



Polarity

left: isopolar

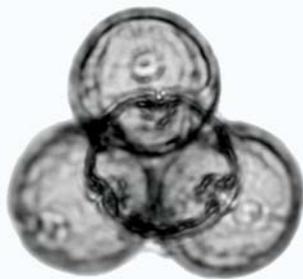
right: heteropolar

The various arrangements of the four microspores within permanent or disintegrating **tetrads** depend on the simultaneous or successive type of cytokinesis and on the type of intersporal wall formation. The spatial arrangement of microspores after **simultaneous** cytokinesis is usually a **tetrahedral tetrad**. This arrangement is of systematic relevance. The spatial arrangement of microspores after **successive** cytokinesis leads to different tetrad types without any systematic relevance: **planar** (tetragonal, linear, T-shaped) or non-planar (decussate or tetrahedral).

Tetrad arrangement

tetrad tetrahedral

Fagus sp.
Fagaceae, fossil
(exceptional finding)



10 μm

tetrad planar

Typha latifolia
Typhaceae

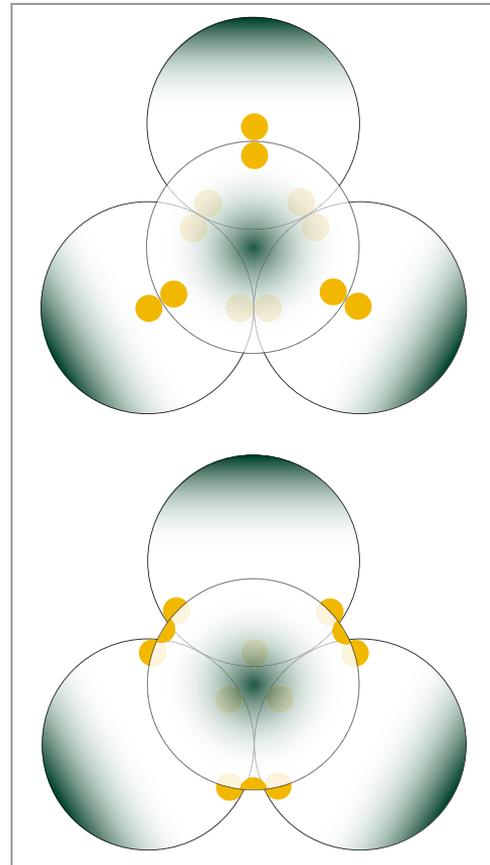


10 μm

In pollen grains with three apertures, two types of aperture arrangement occur after simultaneous cytokinesis (disintegrating or permanent tetrahedral tetrads). **Fischer's law** refers to the most frequent arrangement where the apertures form pairs at six points in the tetrad (e.g., Ericaceae, permanent tetrads). **Garside's law** refers to the unusual arrangement of apertures where they form groups of three at four points in the tetrad

(probably restricted to Proteaceae, no permanent tetrads).

Aperture arrangement

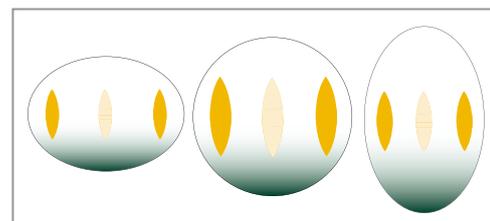


Fischer's law

Garside's law

Pollen **shape** refers to the **P/E-ratio**: the ratio of the length of the polar axis (P) to the equatorial diameter (E). In **spheroidal** (or **isodiametric**) pollen grains the polar axis is ± equal to the equatorial diameter. Pollen grains with a polar axis longer than the equatorial diameter are called **prolate**; grains where the polar axis is shorter than the equatorial diameter are described as **oblate**.

Pollen shape



left: oblate
mid: spheroidal
right: prolate

Pollen **size** varies from less than 10 µm to more than 100 µm. To indicate the pollen size the largest diameter is used. It also depends on the degree of hydration and the preparation method. Because of this and natural variation, a bandwidth designation is recommended. A diameter indication in the range of, e.g., less than 1 µm is not recommended.

The use of the following size categories may be helpful: very small (<10 µm), small (10–25 µm), medium (26–50 µm), large (51–100 µm) and very large (>100 µm).

Apertures

The many facets of an allegedly simple character

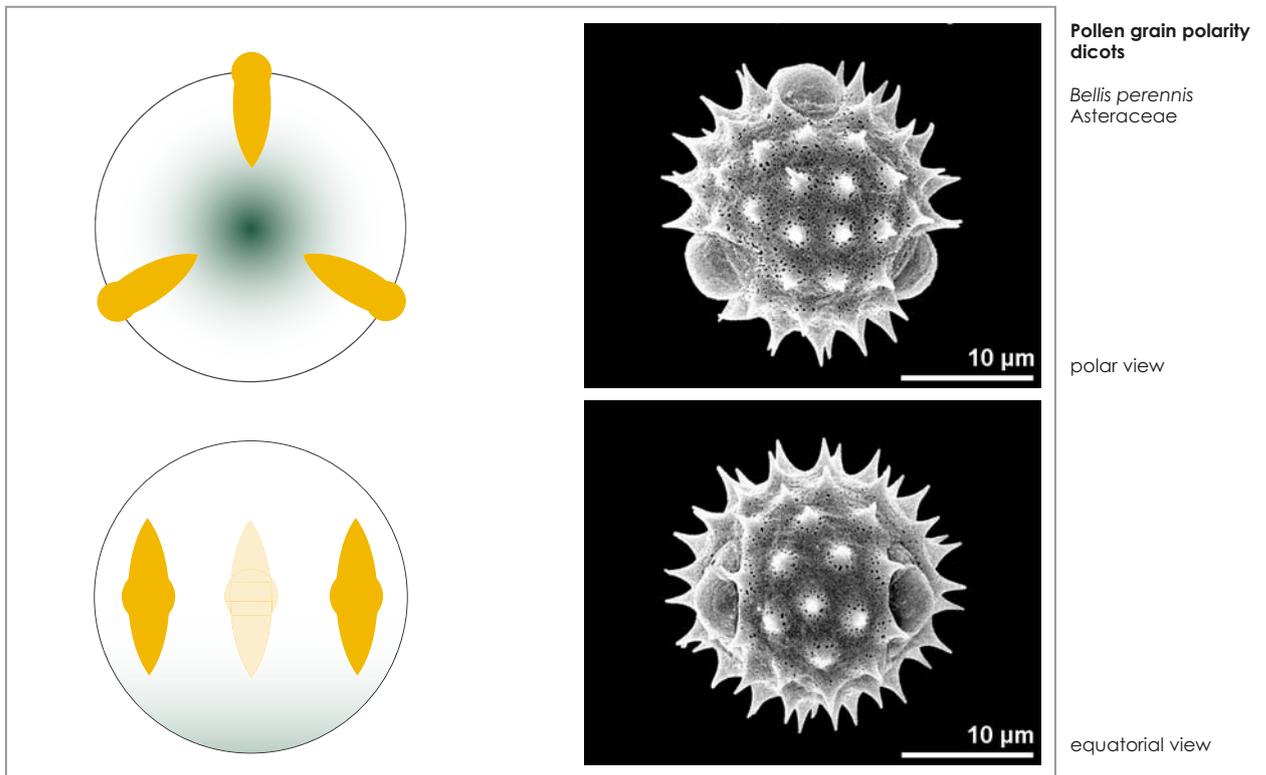
Nomenclature and Typology

An **aperture** is a region of the pollen wall that differs significantly from the rest of the wall in its morphology and/or anatomy, and is presumed to function usually as the site of germination and to play a role in harmomegathy. Pollen grains lacking

an aperture are called **inaperturate**. The aperture definition fits both angiosperm and gymnosperm pollen, but in gymnosperms the type of aperture usually differs from that in angiosperms, since often a **leptoma** is present. Note: unless stated otherwise, the following sections deal with angiosperm aperture constructs only.

The polarity of the pollen determines the aperture terminology. A circular aperture is called a **porus** if situated equatorially or globally; if situated distally it is called an **ulcus**. An elongated aperture is called a **colpus** if situated equatorially or globally; if situated distally it is called a **sulcus**. A combination of porus and colpus is termed a **colporus**; colpi are situated only equatorially or globally. Colpi and colpi (colpi and pori) may be present simultaneously in some taxa; this condition is called **heteroaperturate**. A circular or elliptic aperture with indistinct margins is a **poroid**.

The number of equatorial apertures (pori, colpi, colpori) is indicated by the prefixes di- or tri-. However, tetra-, penta- or

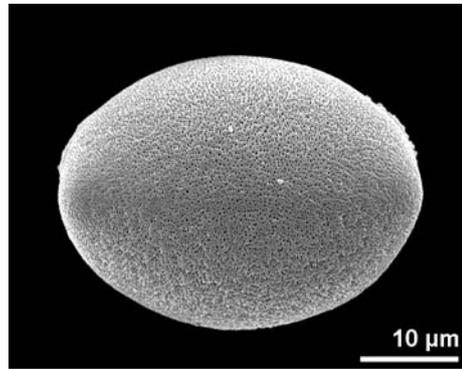
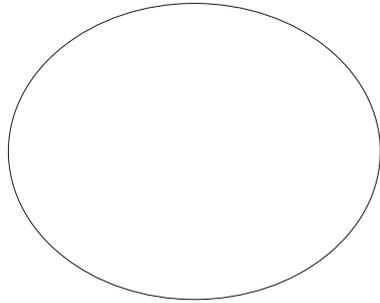


Pollen grain polarity
monocots

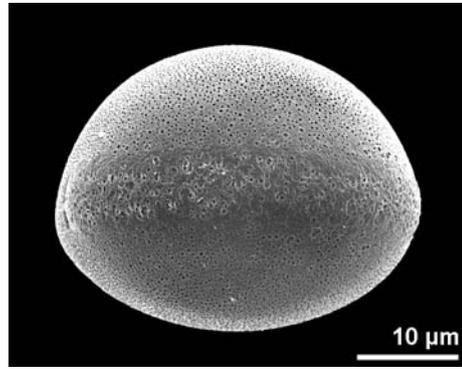
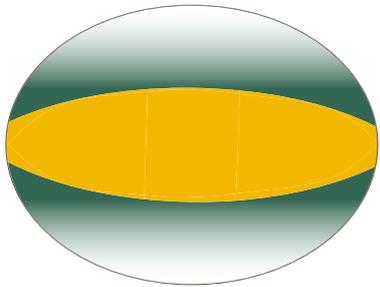
Allium paradoxum
Alliaceae



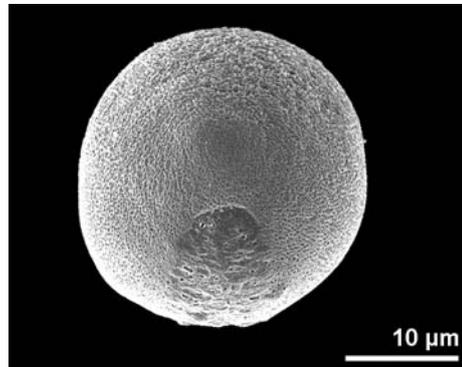
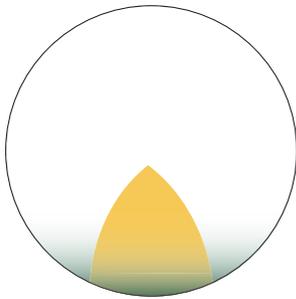
proximal polar view



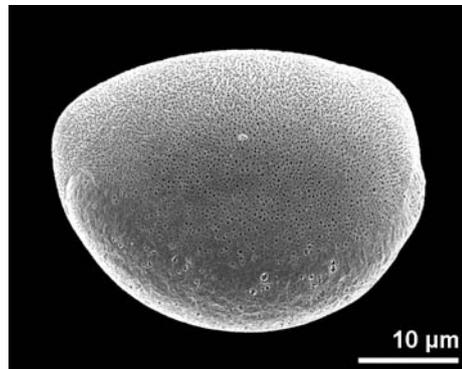
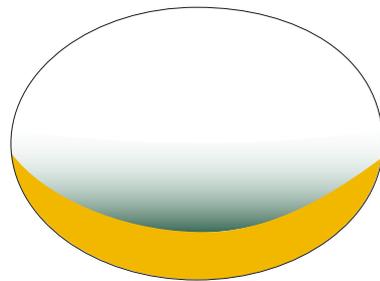
distal polar view



equatorial view



equatorial view



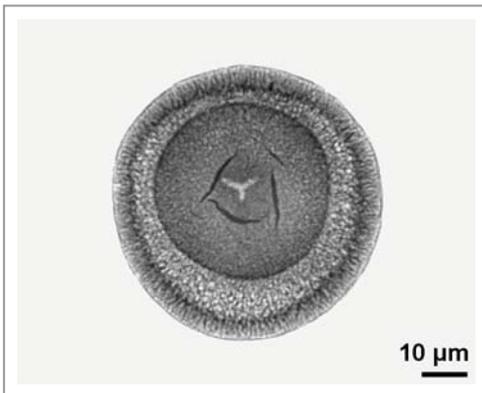
hexa- are sometimes used. (Writing numbers instead of prefixes is in common use, e.g., 4-porate or tetraporate, 6-colpate or hexacolpate. "Pollen Terminology. An illustrated Handbook" prefers the use of prefixes.) Any pollen grain with more than three apertures at the equator is also called **stephanoper-
turate** (**stephanoporate**, **stephanocolpate**, **stephanocolporate**). Pollen grains with globally distributed apertures are called **pantoaperturate**.

The polarity gives rise to the polar and the equatorial view. In dicots there is usually one polar and one equatorial view. In monocots, due to the mostly distal aperture, there are four views: a proximal polar, a distal polar, and two different equatorial views.

Proximal germination is unknown in seed plants and is restricted to **spores**, which germinate at the **tetrad mark**, the so-called **laesura** (extensive overview: TRYON and LUGARDON 1991).

Pre-(prae-)pollen (microspores of certain extinct seed plants) is characterized by proximal and distal apertures, and by presumed proximal germination, producing motile spermatozoids.

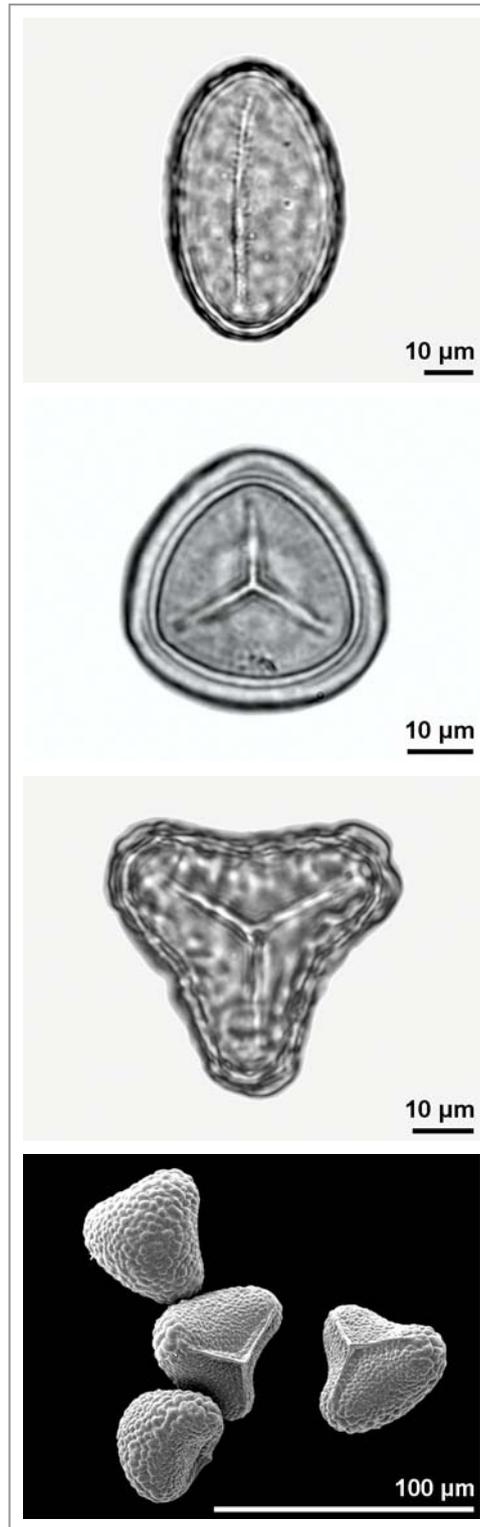
Pre-pollen



polar view

Apertures are normally covered by an exinous layer, the **aperture membrane**. **Aperture membranes** can be **ornamented**, e.g., covered with various exine elements, or can be **smooth**. In contrast, an **operculum** is a thick, coherent exine shield and covers the aperture like a lid.

In general, aperture membranes are infolded in dry pollen state; after acetolysis the aperture membrane may be lost.



Tetrad mark in spores

Polypodium sp.
Polypodiaceae, fossil
monolete tetrad mark
polar view

Sphagnum sp.
Sphagnaceae, fossil
trilete tetrad mark
polar view

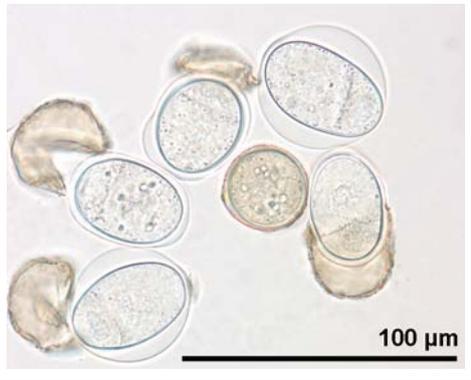
indet.
Pteridaceae, fossil
trilete tetrad mark
polar view

Cryptogramma crispa
Pteridaceae
trilete tetrad mark

Taxoid pollen germination

Cephalotaxus sp.
Cephalotaxaceae

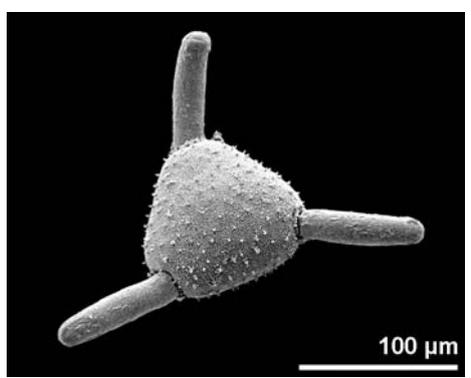
exine shedding prior to
pollen tube formation



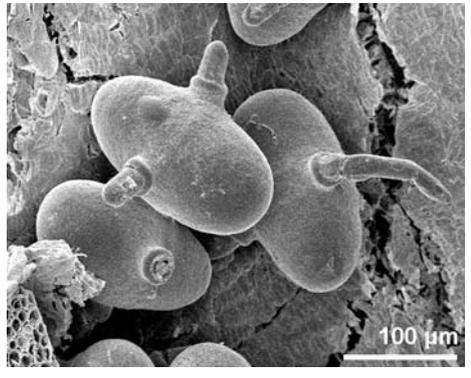
fresh pollen in water

Instant pollen tubes

Scabiosa caucasica
Dipsacaceae



Morina longifolia
Morinaceae



Number, type and position of apertures are genetically determined and usually fixed within a species; however, it may sometimes vary (e.g., number of apertures in stephanoaperturate pollen grains).

Structure and Function

The aperture usually acts as the (exclusive) **germination** site. Pollen tubes in inaperturate angiosperm pollen are produced without a preformed exit zone. In **taxoid** pollen the exine ruptures during hydration at a specialized region, the tenuity, ulcus, or papilla in the center of a circular leptoma and is subsequently shed.

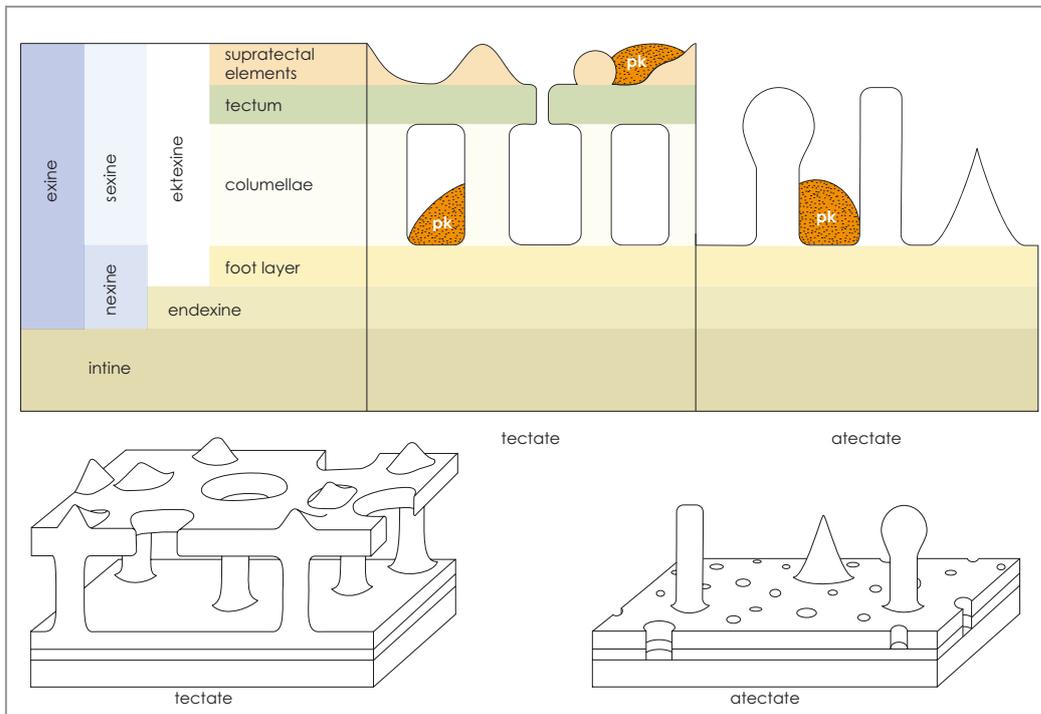
The intine including the protoplast is released and a pollen tube can be formed anywhere (resembling functionally an inaperturate pollen grain). Furthermore some angiosperm taxa shed the exine before pollen tube formation, e.g., in some Annonaceae.

During germination, usually a single pollen tube is formed. However, sometimes tube-like structures ("instant pollen tubes") are simultaneously formed in the anther or very quickly in shed pollen immediately after water contact. Their production is interpreted as a pre-germinative process (BLACKMORE and CANNON 1983).

Pollen Wall

In general, **the pollen wall (sporoderm)** of seed plants consists of two main layers: the outer **exine** and the inner **intine**. The exine consists mainly of **sporopollenins**, which are acetolysis- and decay-resistant biopolymers. The intine is mainly composed of cellulose and pectin. Commonly, the pollen wall in apertural regions is characterized by the reduction of exinous structures or by a deviant exine, and a thick, often bilayered intine.

Two layers within the exine are distinguished: an inner endexine and an outer ektexine. The ektexine consists of a basal



Pollen wall stratification

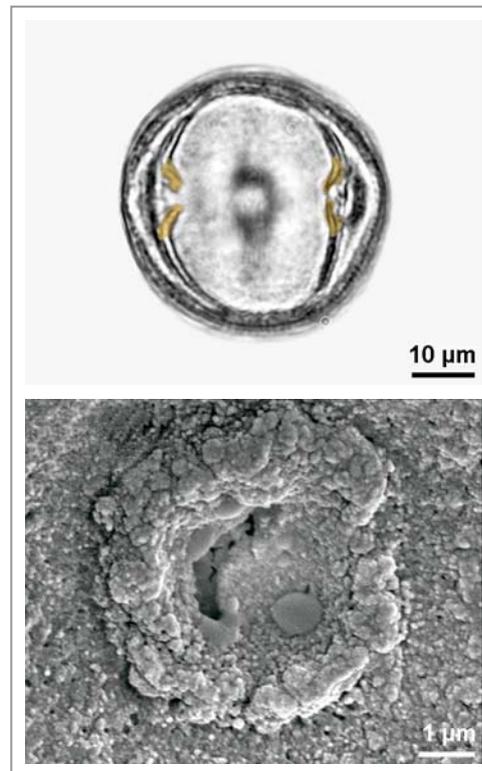
pk: pollenkitt

foot layer, an **infratectum** and a **tectum**, the endexine is a mainly unstructured, single layer. There are many deviations from this principal construction: layers may be thickened, variably structured, or lacking. In apertural regions the pollen wall is characterized by a different exine construction.

The terms **sexine** for the outer, structured, and **nexine** for the inner, unstructured exine layer are widely used in light microscopy, but do not fully correspond to ekt- and endexine, respectively.

The angiosperm pollen wall

The **ektexine** consists in general of **tectum**, **infratectum** and **foot layer**. The outer layer, the more-or-less continuous tectum, can be covered by supracteal elements. The infratectum beneath is **columellate** or **granular** (a second layer of columellae may form an internal tectum). The foot layer may be either continuous, discontinuous or absent. The **endexine** may be characterized as continuous or discontinuous, spongy or compact, is present overall, only in apertures, or even completely absent. Some typical deviations of the wall thickness are named with special terms: **arcus**, **annulus**,



Costa

Nyssa sp.
Nyssaceae, fossil
equatorial view

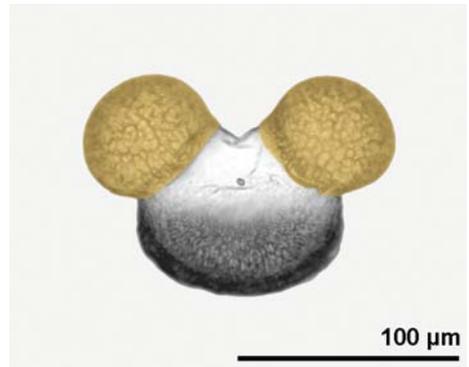
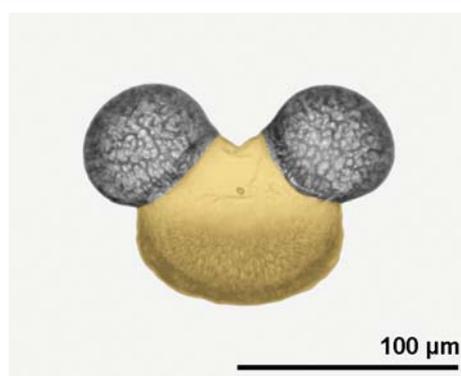
Austroboxus nitidus
Picrodendraceae, fossil
broken grain,
thickening around the
endoaperture

tenuitas (see "Illustrated Glossary") and **costa** (a thickening of the nexine/endexine bordering an endoaperture).

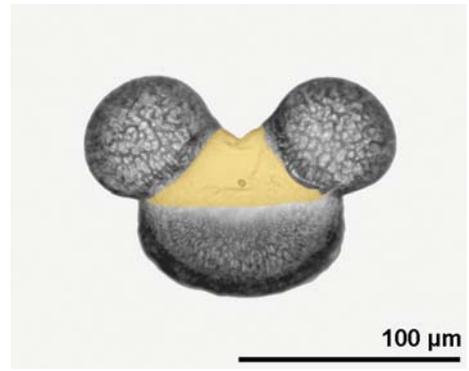
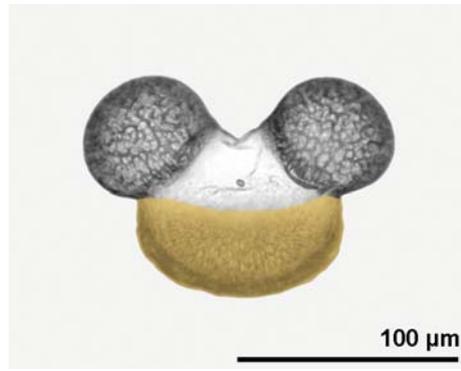
**Pollen terminology
in saccate
gymnosperm pollen**

Abies sp.
Pinaceae, fossil
equatorial view

left: corpus
right: sacci



left: cappa
right: leptoma

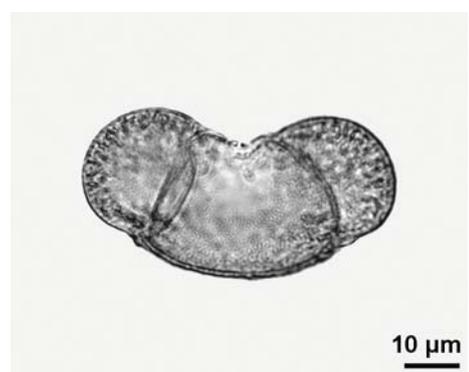
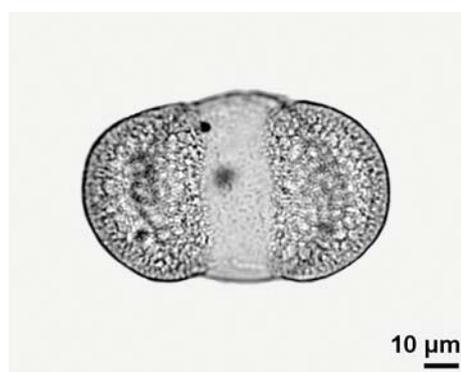


**Pollen types
in saccate
Pinus pollen**

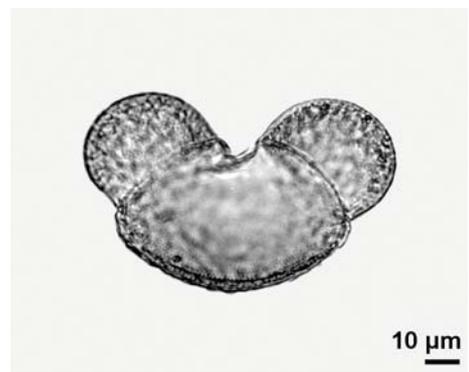
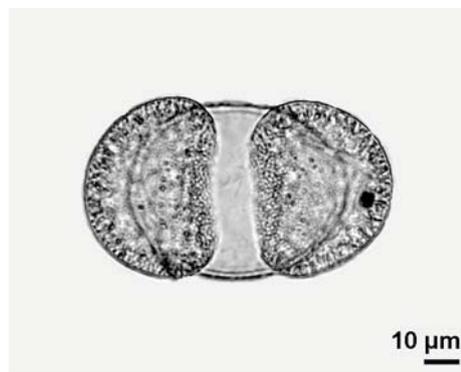
Pinus sp.
Pinaceae, fossil

left: polar view
right: equatorial view

Haploxyton-pollen-type



Diploxyton-pollen-type



Extreme examples of variable ektexine design include massive forms lacking almost any subdivision or stratification, extremely reduced forms, or even their complete absence.

The typical angiosperm aperture shows a thick, bilayered **intine**.

The Gymnosperm Pollen Wall

The "Gymnosperms" comprise cycads, *Ginkgo*, conifers and Gnetales. The gymnosperm pollen wall differs from that in angiosperms in two characters: 1. the endexine is always **lamellate** in mature pollen stages. 2. the infratectum is never columellate. The four gymnosperm classes exhibit diverse, special constructions of the apertures.

The principal stratification (ektexine, endexine and intine) of the gymnosperm pollen wall is identical to that of angiosperms. A tectum is present in all cycads, in *Ginkgo*, in all Gnetales, but not in all conifers: in some taxa the tectum is completely lacking (sculpture elements are situated on the foot layer). The infratectum is either **alveolate** or **granular** but never columellate.

A special terminology is applied to saccate pollen, i.e., Pinaceae and Podocarpaceae. The **saccus** is a large hollow projection from the **corpus**, the central body of saccate pollen grains. It is a typical deviation of the pollen wall conformation, composed only by the exine with an alveolate infrastructure. Most frequently, two sacci are present, in some taxa even three, or only a single one. Saccate pollen grains show on the proximal side of the corpus a region termed **cappa**, and on the distal side a thinned region, the **leptoma**.

In *Pinus* two pollen types are recognized as of systematic value. The **Haploxylon-pollen-type** is characterized by pollen grains with broadly attached half-spherical air sacs – in LM the leptoma shows remarkable thickenings (black spots). The **Diploxylon-pollen-type** is characterized by pollen grains with narrowly attached, spherical air sacs - the leptoma does not show any thickenings.

Structure and Sculpture

The internal construction of the pollen wall is its **structure**; ornamenting elements on the pollen surface (ornamentation) are summarized under the term **sculpture** or sculpturing. However, it is not always possible to distinguish between structure and sculpture (e.g., free-standing columellae).

Ornamentation

This general term in palynology is applied to surface features. All the ornamenting features (**areola**, **clava**, **echinus**, **foveola**, **fossula**, **granulum**, **gemma**, **plicae**, **reticulum**, **rugulae**, **striae**, **verruca**) are artificial categories that mark extremes within a broad morphological series and are therefore regarded as extremely variable; nevertheless, they are important in pollen description.

For practical purposes a distinct feature can be subdivided into ornamenting elements extending 1 μm in diameter, or if smaller then marked with the prefix **micro-**.

Combinations of sculptural elements are common. Frequently a specific ornamentation is difficult to describe only in words because of the high plasticity of its ornamenting elements. A typical micrograph characterizes sculptural elements to a much higher degree.

The arrangement of ornamenting elements on the pollen surface is very often disparate, particularly in apertural regions. Pollen coatings like **pollenkitt** or **tryphine** may obscure the ornamentation.

Harmomegathy

Harmomegathic Effect (Wodehouse Effect)

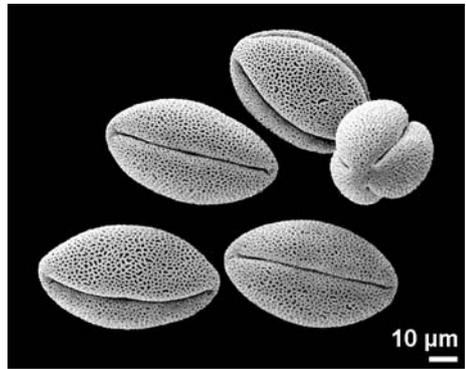
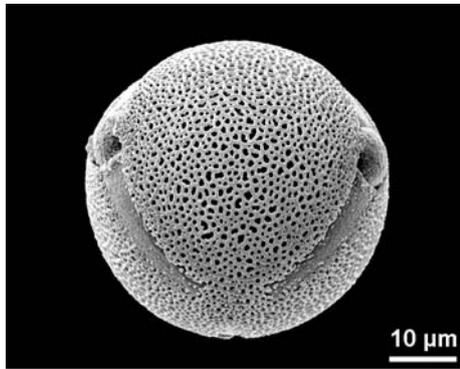
All living pollen grains are able to absorb and release water; thus, each living grain exists in two morphologically different states: the **dry** and the **hydrated** condition. Harmomegathic mechanisms, e.g., infolding of the pollen wall, accommodate the change of the osmotic pressure in the cytoplasm during hydration or dehydration.

Harmomegathic effect

Cistus creticus
Cistaceae

left: spheroidal

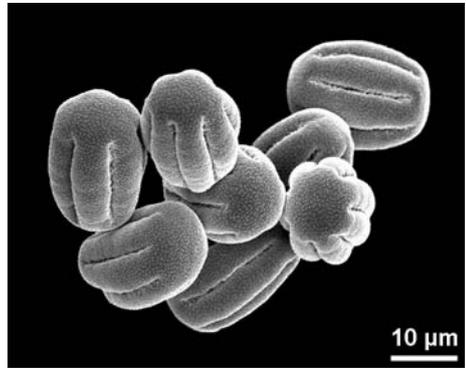
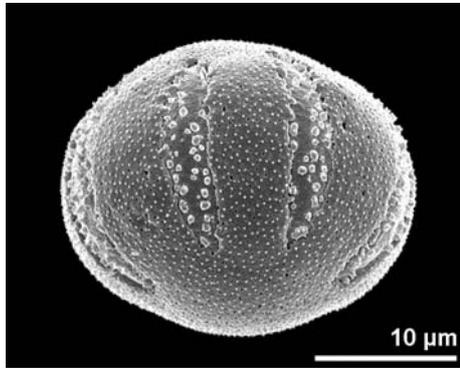
right: dry pollen
prolate, lobate



Galium rotundifolium
Rubiaceae

left: oblate

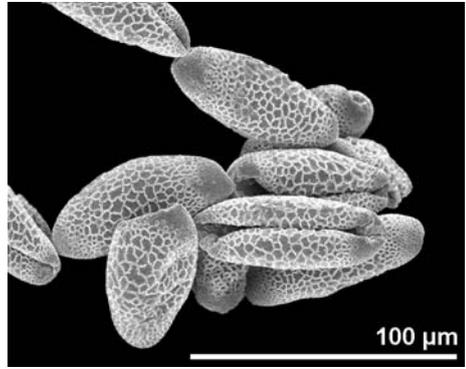
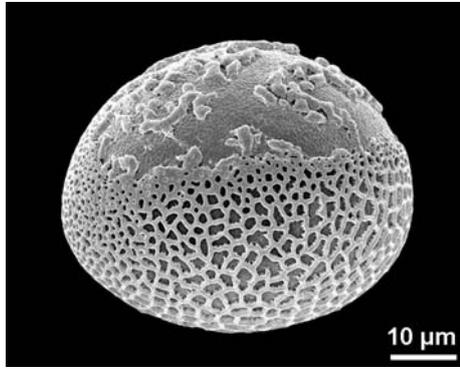
right: dry pollen
prolate, lobate



Vriesea pabstii
Bromeliaceae

left: oblate

right: dry pollen
boat-shaped



Lamiastrum montanum
Lamiaceae

left: spheroidal

right: dry pollen
prolate, outline elliptic

