Pollen morphological definitions and types

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Preface

The present article is a translation of Johs. Iversen and J. Troels-Smith: *Pollenmorphologische Definitionen und Typen,* whcih originally appeared both in a Danish and a German version. The Plates I-XVI are reproduced without changes; hence it was necessary to retain the Danish sign "÷" to indicate a minus, although this has a different meaning in English. The English text was read critically by Dr. M. Tooley, University of Durham, and by Dr. J. Troels-Smith and Mr. B. Brorson Christensen, The Danish National Museum, and was revised with reference to the Danish version, *Pollenmorfologiske definitioner og typer,* by Olivia C. Collin, The Geological Survey of Denmark.

Foreword

When research on pollen analysis began a generation ago, the structure of the pollen exine had already been explained in principle in the classic works of v. Mohl, Fritzche and Fischer. The rise of pollen analysis brought no new interest in questions of pollen morphology. Quite naturally, the first task of the new research became that of gaining an overall view of the most important episodes of post-glacial forest development. It was therefore at first sufficient to count the pollen of the most important genera of trees, which are – with certain exceptions – easily identifiable.

Today, the situation is different. The first aim of pollen statistical research has been achieved; the main features of forest development in northern

Europe have been traced. In order to progress, we must now take into account the pollen of other plants. This does not merely apply to vegetation study of epochs which had very little forest: even the problems of forest development themselves can be thoroughly illuminated only by an examination of pollen flora as a whole. Frequently, the pollen curves of herbaceous plants show evidence of important ecological connections, and thus become the key to a causal understanding of characteristic phases in forest development.

Naturally, any further progress in this field presupposes absolutely accurate pollen determinations. It can hardly be disputed that earlier standards in this respect were in general too low. The fact that *Salix* and *Artemisia* pollen were at one time confused with one another shows that research was content with a rather superficial examination of the form of the pollen grain in such cases. For reliable classification of pollen grains whose form is not especially characteristic, an accurate observation of the structural composition of the pollen exine is a *sine qua non*. Experience has shown that this creates considerable difficulties for the beginner, and that no one attains the necessary sharpness of eye without taking time to study the various pollen structures very thoroughly.

The beginner's best tactic is to work out precise descriptions of pollen grains. This forces one to observe accurately, and the eye becomes practised in grasping, quickly, all the essential traits. Even for the more advanced observer, descriptions of fossil pollen grains are a prerequisite for subsequent classification or for the documentation of classifications. Reports on finds of important or abstruse fossil pollen types are worthless without descriptions, drawings or photographs.

In our laboratories at the Danish Geological Survey and at the Danish National Museum, we have been working for a number of years on diagnoses of recent and fossil pollen types, both Quaternary and pre-Quaternary. Our terminology has evolved during the work, and was initially intended for use only in our laboratories. There are two reasons for the publication of these terms here: in the first place, the present work can be viewed as an introduction to an on-going series of communications on important pollen finds in post-glacial, late-glacial and Tertiary deposits, documented by diagnoses and photomicrographs; in the second place, it is the basis of the chapters on morphology and of the keys to classification in a book now in the press by Knut Faegri and Johs. Iversen[1].

In Section A, the pollen morphological definitions are discussed. This section is especially elaborate since we regarded it as important to cite all the possibilities that are included in a given concept, in order to make clear where to place divisions in practice. Section B on pollen morphological measure-

ments is also very detailed. This is not because we consider that size characteristics in general have great significance: on the contrary, these data are the last to which one should resort. But if one is to take measurements (and in certain cases this is necessary in order to distinguish between closely-related forms), then one must know exactly what one is measuring and how; otherwise one is groping in the dark[2]. This pollen typology makes no claim to represent a natural classification: it is entirely artificial, and its aim is the practical one of of making classification easier[3]. Clarity and simplicity were for us the essentials.

In our choice of terminology we have, in order to avoid misunderstanding, as far as possible avoided terms used by other authors in a sense different from ours. We may also refer readers to the works of Wodehouse, Potonié and Erdtman, which we have used extensively. Over the years, we have discussed the whole extent of the present work with our friend and colleague, Professor Dr. Knut Faegri, Bergen, and we owe many improvements to him. Conservator B. Brorson Christensen has been so kind as to prepare illustrations for all the concepts and types, thereby making them more readily accessible to others. Lektor A. Kragelund has advised us on matters of Latin terminology.

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Section A. Pollen morphological definitions

The following conventions are used in the abbreviations:

1. No hyphen is used when an entity is being considered; for example, in pollen morphological types: C_3P_3=Tricolporate.
2. A comma denotes that the abbreviation following the comma gives a more specific definition; for example, a part of a pore: P,op = operculum of a pore.
3. Parentheses are used when additional information is given elucidating the subject; for example, P(op) = pore with an operculum.
4. Hyphens precede an indication of dimensions; for example, P-M = the diameter of a pore. It can also be used for the indication of distance; for example, (P,1-P,1)-M, see page 15.

1. Orientation of the pollen grain

pol,ax = *axis poli* = polar axis: axis of symmetry in radio-symmetrical pollen grains. If more than one axis of symmetry occurs, only that which runs

through the centre of the pollen tetrad during the formation of the pollen grain is designated a polar axis. In such cases, the polar axis can be recognised only in pollen grains which occur in tetrads.

Po = *polus* = pole: point of intersection of the polar axis with the surface of the pollen grain.

aeq = *aequator* = equator: line of intersection between the surface of a pollen grain and a plane which passes through the centre of the polar axis and is perpendicular to it.

2. Colpi (Plate I)

C = *colpus:* an area which forms or surrounds the normal point of emergence of the pollen tube, and whose arbitrary length-breadth ratio is grater than 2. In relation to the surrounding exine, the colpus is designated in one of three ways:

C(ex = 0): by the absence of the exine
(for example, in consequence of the loss of an operculum);

C(mb): by thinning of the exine;
C(mb, ekt = 0): ektexine elements missing;
C(mb, ekt): ektexine elements present;

C(op): by the delimitation of a section of normal exine by a furrow or seam.

C,1 = *limes colpi* = edge of colpus: demarcation line of the colpus; *i.e.,* either the furrow or seam mentioned above – or, with a thinned or absent exine, the external limit of the lighter area thus caused.

C,ap = *apex colpi* = apex of the colpus.

C,mb = *membrana colpi* = membrane of the colpus: the thinned exine of a colpus.

C,op = *operculum colpi* = the thicker part of a colpus situated within a furrow or seam. The structure of the operculum is similar in nature to that of the remaining exine of the pollen grain.

C,med = *medianum colpi* the median of the colpus: a line which divides a colpus into two approximately symmetrical halves. A distinction is made between:

C,med,+ = *medianum colpi longitudinalis:*
the longitudinal median of the colpus;

C,med,÷ = *medianum colpi transversalis:*
the transverse median of the colpus.

C,cent = *centrum colpi* = the intersecting point of the medians.

mg = *margo:* an area which surrounds a colpus like a belt and which is

distinguished from the remaining exine of the pollen grain by deviations in the ektexine.

mg,l = *limes marginis* = edge of margo: external limit of the margo.

mg,ap = *apex marginis* = apex of the margo.

cost C = *costae colpi* = ridges of thickened endexine along a colpus.

tr C = *colpus transversalis* = transversal colpus: a colpus which intersects another colpus at a near right angle, and which is connected to the endexine.

cost tr = *costae transversales:* ridges of thickened endexine along the transversal colpus.

cost aeq = *costae aequatoriales:* two parallel encircling ridges of thickened endexine which occur on either side of the equator, such that the intervening space gives the impression of an equatorial colpus.

pseudo C = *pseudocolpus* : differs from a colpus in that it does not normally function as the point of emergence of the pollen tube. *Cf.,* pseudospore.

3. Pores (Plate I)

P = *porus* = pore: area which serves as normal point of emergence of the pollen tube and whose arbitrary length-breadth ratio is less than 2. The relation of the pore to the surrounding exine is designated in one of three ways:

P(ex = 0) = *diaporus* = open pore: when the exine is missing (for example, if the operculum has been lost);

P(mb): by thinning of the exine;

P(mb,ekt = 0): ektexine elements missing;

P(mb,ekt): ektexine elements present;

P(op): by the delimitation of a piece of normal exine by a furrow or seam.

P,l = *limes pori* = edge of pore: line demarcating the pore, *i.e.,* either the furrow or seam, or – with a thinned or missing exine – the outer limit of the lighter area thus caused.

P,mb = *membrana pori* = pore membrane: the thinned exine of a pore.

P,op = *operculum pori* = operculum of the pore: the thickened part of a pore, situated in a furrow or a seam. The structure of the operculum is similar in nature to that of the remaining exine of the pollen grain.

P,vest = *vestibulum pori* = a small, more or less well-defined, space created when the exine at the edge of the pore appears split in optical cross-section (foc. 5).

anl = *anulus:* an area which surrounds the pore like a ring, and which is distinguished from the rest of the exine of the pollen grain by differences in the ektexine; *e.g,* by a greater or lesser thickness of the ektexine.

If an anulus has concentric zones with different structure, these zones can be identified from the inside outwards: anl(1), anl(2) . . .

anl,l = *limes anuli* = edge of the anulus: external demarcation line of the anulus.

If an anulus has concentric zones with different structure, the demarcation lines of such zones may be designated from the inside outwards: anl,l(1); anl,l(2) . . .

cost P = *costae pori:* the ring-shaped thickening of the endexine around a pore.

P,cent = *centrum pori:* centre of the pore.

pseudo P = *pseudoporus* = pseudo pore: deviates from a true pore in that it is not the normal point of emergence of the pollen tube.

lac = *lacuna:* a term which includes both pseudopores and pseudocolpi.

4. Intercolpia, interporia, and polar area

These concepts are only applicable to bi-polar pollen grains.

inter C = *intercolpium:* an area delimited by the edges of the colpi (or by the edges of the margo, if clearly defined margo-edges are present), and by the connecting lines of the apices of adjacent colpi.

inter C,med = *medianum intercolpii:* a line which divides an intercolpium into two approximately symmetrical halves.

inter C, cent = *centrum intercolpii:* point of intersection of the medians of an intercolpium.

inter P = *interporium:* area delimited by the edges og the pores (or by the edges of the anuli, if clearly defined anulus-edges are present) and by the lines which are tangential to the edges of two adjacent pores (or their anuli).

inter P,med = *medianum interporii:* a line which divides an interporium into two approximately symmetrical halves.

inter P,cent = *centrum interporii:* the point of intersection of the medians of an interporium.

polar = *area polaris* = polar area: an area which surrounds a pole and which is limited by the intercolpia or interporia.

5. Structure of the Exine (Plate II)

ex = *exina* = exine: the highly resistant external skin of the pollen grain, which may be composed of one or two layers.

matrix: the homogeneous fundamental substance of the exine.

gran = *granula:* sharply delimited granules, rods and similar structural elements which are embedded in or deposited upon the homogeneous basic substance.

end = *endexina* = endexine: the inner homogeneous layer of a double-layered exine.

ekt = *ektexina* = ektexine: the outer layer of a double-layered exine, consisting of granules which may or may not form a continuous surface.

tec = *tectum:* the external skin-like part of the ektexine which more or less entirely covers the endexine.

tec(perf) = *tectum perforatum:* tectum with holes.

col = *columellae:* ektexine elements (granules) which support the tectum like pillars.

col(simpl) = *collumellae simplices:* simple columellae.

col(dig) = *columellae digitatae:* distally branching columellae.

con(conj) = *columellae conjunctae:* columellae united distally in groups. The granules of intectate pollen grains may also be termed columellae if they occur in composite structures (*e.g.*, in a reticulum).

cav = *cavea:* hollow space in the exine created by the detachment of the ektexine from the endexine.

6. Sculpture of the exine (Plates III, IV and V)

Elementa punctualia: dot-shaped sculptural elements: the greatest diameter is less than twice as large as the smallest[4].

ver = *verrucae* = warts: the greatest diameter equals or exceeds the height[4]: the sculptural elements are neither pointed nor constricted.

gem = *gemmae* = grains: like verrucae, but proximally constricted.

bac = *bacula* = rod: the greatest diameter is less than the height[4]: the sculptural elements are neither pointed nor club-shaped.

cla = *clavae* = clubs: like bacula, but club-shaped.

ech = *echini* = spines: sharply-pointed sculptural elements. The greatest diameter can be larger or smaller than the height[4].

Elementa elongata: elongated sculptural elements: the greatest diameter is more than twice as large as the smallest. These sculptural elements can sometimes be created by the close juxtaposition of dot-shaped elements.

val = *valla* = ridges, crests, keels *etc.*, in various shapes: elongated, serpentine curves or with irregular outlines.

ret = *reticulum* = network: formed by the regular merging of elongated sculptural elements.

mur = *muri:* the walls of a reticulum.

pl,lum = *plateae luminosae:* the surface of the exine between sculptural elements.

lum = *lumina* (sing.: *lumen*): the meshes of a reticulum defined by the muri.

Section B. Pollen morphological measurements

The following abbreviations have been used in giving the various dimensions:

M = *mensura* = measurement: any measurement in general. M does not of itself denote any orientation with respect to the pollen grain. It is used in the following indications of size:

1. Dimensions of the pollen grain
2. Dimensions of the polar area
3. Interporial and intercolpial measurements
4. Dimensions of the pores and the colpi
5. Dimensions (thickness) of the exine

Lg = *longitudo* = length: a measurement parallel to the polar axis in bi-polar pollen grains; with this proviso, used as M.

Lt = *longitudo transversa* = breadth: a measurement perpendicular to the polar axis in bi-polar pollen grains; with this proviso, used as M.

D = *diameter:* a measurement parallel to the surface of the exine, but applicable only to structures and sculptures.

H = *altitudo* = height: a measurement perpendicular to the surface of the exine; applicable only to structures and sculptures

For more specific descriptions of these measurements, the following abbreviations have been used: + and ÷ denote respectively the largest and smallest measurement, where several are possible.

(÷) indicates that the measurement given is perpendicular to a corresponding + measurement.

foc 0–3 denotes that the measurement has been taken by observation of the surface of the pollen grain. For definitions of the various angles of view (foc 0–5), see p. 18.

foc 5 denotes that the measurement has been taken by observation of the pollen grain in optical cross-section.

Measuring pollen grains:

Practical guidelines for taking measurements:

1. All measurements are taken to the outer boundary (*limes exterior*) of the pollen grain (Plate X). The outer boundary is defined as the more or less rotation-ellipsoidal basic surface which bears the sculptural elements; however, in cases where the distal surfaces of the sculptural elements (seen in profile) constitute more than 50% of the outer demarcation line described, then this is taken as the outher boundary line of the pollen grain, and the corresponding more or less rotation-ellipsoidal surface is taken to be the outer boundary (Plate X).
2. When defective pollen grains are measured, this must be explicitly stated; *e.g.*, in the following manner:
   x = *exina fissa* = split exine.
   () = *exina crispa* = crumpled exine.
   (x) = *exina fissa et crispa* = exine both split and crumpled.

1. All pollen types (Plate VI):

M,+: the distance between two parallel planes which are tangential to the pollen grain and which are so arranged that the greatest possible distance is achieved between the planes.

M,(÷): the distance between two parallel planes which are tangential to the pollen grain and which are perpendicular to the two planes indicated by M,+.

If two or more different measurements can thus be obtained, then:

M,(÷),+ indicates the greatest measurement

M,(÷),÷ indicates the smallest measurement

In certain cases – for example, when the pollen grain is firmly embedded – one is obliged to take measurements from an arbitrary position. This can be indicated as follows:

M,+(fix) = M,+ when the pollen grain is fixed in an arbitrary position.

M,(÷)(fix) = M,(÷) when the pollen grain is fixed in an arbitrary position.

2. Bi-polar pollen grains (Plate VI):

Lg = *longitudo* = length: the length of the polar axis from pole to pole. For colpi, pores, intercolpia and interporia, *etc.*, Lg denotes a measurement parallel to the polar axis.

Lt = *longitudo transversa* = the breadth at the equator: the distance between two parallel planes which are tangential to the pollen grain at its equator and which are parallel to a plane of symmetry passing through the polar

axis; or else, a measurement at right angles to such a measurement, similarly in the equatorial plane.

If two or more measurements can be obtained thus, then:

Lt,+ denotes the largest measurement

Lt,÷ denotes the smallest measurement

For colpi, pores, intercolpia, interporia, *etc.*, Lt denotes a transverse measurement in the equatorial plane.

In cases where the greatest length and breadth of bi-polar pollen grains are not identical with the length of the polar axis or the breadth at the equator respectively, they can be indicated thus:

Lg,max = *maximum longitudinis* = maximum length: the distance between two parallel planes which are perpendicular to the polar axis and which are tangential to the pollen grain.

Lt,max = *maximum longitudinis transversae* = maximum breadth: the distance between two planes which are parallel to the plane of symmetry passing through the polar axis and tangential to the pollen grain; or else, a measurement at right angles to such a measurement and, similarly, perpendicular to the polar axis.

In cases where two or more different measurements can thus be obtained, then:

Lt,max,+ denotes the greatest

Lt,max,÷ denotes the smallest

Colpi measurements (Plate VII):

C-M,+ = length of colpus: length of longitudinal median of colpus

C-M,÷ = breadth of colpus: length of tranverse median of colpus

C-Lg = length of colpus in bi-polar pollen grains

C-Lt = breadth of colpus in bi-polar pollen grains

mg-M = breadth of margo: distance between edge of colpus and edge of margo

(C,ap-C,ap)-M: distance between apices of two adjacent colpi

(mg,ap-mg,ap)-M: distance between apices of two adjacent margines.

Pore Measurements (Plate VII):

P-M = Diameter of the pore. For pores that are not circular, the largest and smallest diameters can be denoted, respectively, thus:

P-M,+

P-M,÷

and for bi-polar pollen grains:
P-Lg
P-Lt
anl-M = breadth of the anulus: the distance between the edge of the pore and the edge of the anulus.
(P,l-P,l)-M: the distance between the edges of two adjacent pores.
(anl,l-anl,l)-M: the distance between the edges of the anuli of two adjacent pores.

Intercolpium, interporium, and polar area measurements (Plate VIII)
inter C-M: the length of a median of an intercolpium
inter C-M,+: the length of the greatest median
inter C-M,÷: the length of the smallest median
inter C-Lg: the length of a median perpendicular to the equator (in bi-polar pollen grains)
inter C-Lt: the length of a median congruent with the equator (in bi-polar pollen grains)
inter P-M: the length of a median of the interporium
inter P-M,+: the length of the greatest median
inter P-M,÷: the length of the smallest median
inter P-Lg: the length of a median perpendicular to the equator (in bi-polar pollen grains)
inter P-Lt: the length of a median congruent with the equator (in bi-polar pollen grains)
polar-M = *mensura areae polaris* = measurement of the polar area: the longest diagonal or the longest side of a polar area.

Measurement of the exine[5] (Plate IX):
The thickness of the exine, the endexine, the ektexine and the tectum is measured in optical cross-section (foc 5). If, for the same pollen grain, several measurements can be obtained, then M,+ and M,÷ denote the greatest and smallest measurements respectively.
ex-M: the thickness of the exine.
ex-M,+: the maximum thickness of the exine.
ex-M,÷: the minimum thickness of the exine.
end-M: the thickness of the endexine.
end-M,+: the maximum thickness of the endexine.
end-M,÷: the minimum thickness of the endexine.
ekt-M: the thickness of the ektexine.
ekt-M,+: the maximum thickness of the ektexine.
ekt-M,÷: the minimum thickness of the ektexine.

tec-M: the thickness of the tectum.
tec-M,+: the maximum thickness of the tectum.
tec-M,÷: the minimum thickness of the tectum.
If desired, measurements can also be given for specific points on the pollen grain; for example, at the pole: ex(pol)-M.

Sculpture[6] and columella measurements (Plate IX):
Example of sculpture measurement: clava.
cla-D,+,(foc 0–3)
cla-D,÷,(foc 0–3)
cla-D,+,(foc 5)
cla-D,÷,(foc 5)
cla-H,(foc 5)
In the example given above, columella can be substituted for clava.

Lumina measurements:
lum-D,+
lum-D,÷

Section C. Pollen morphological size proportions

1. Absolute dimensions

a. The size of a pollen grain is denoted by the greatest measurement of the grain (M,+; Lg,max or Lt,max,+). According to Erdtman (1945), the following size categories can be distinguished:
p(<10μm) = *pollina perminuta* = very small pollen grains
p(10–25μm) = *pollina minuta* = small pollen grains
p(25–50μm) = *pollina media* = medium pollen grains
p(50–100μm) = *pollina magna* = large pollen grains
p(>100μm) = *pollina permagna* = very large pollen grains
b. Exine, sculpture and lumina measurements are denoted by the greatest measurements within each catagory (*c.f.,* pollen morphological measurements, p. 15): The following size-catagories can be distinguished:
M,+(<1μm) = *micro-* (*e.g.,* lum-M(<1μm) = micro-reticulate)
M,+(1–4μm) = *meso-*
M,+(>4μm) = *macro-*
c. Columella measurements are given according to the diameter of the thickest collumellae: the largest diameter of the unbranched part of the columella is measured. The following size-categories can be distinguished:

col-D,+(<0.5μm)
col-D,+(0.5–1.0μm)
col-D,+(1–4μm)
col-D,+(>4μm)

col(*incertae*) signifies that no clear columellae can be distinguished.

2. Relative Size

a. Pollen shape index. The pollen shape for bi-polar pollen grains can be expressed by the relation of length to greatest breadth (Lg/Lt,+ or – possibly – Lg/Lt,max,+). The following categories of shape can be distinguished (Erdtman 1943):

perprol	= *pollina perprolata:*	Lg/Lt,+ >2.00
prol	= *pollina prolata:*	Lg/Lt,+ 2.00–1.33
subsph	= *pollina subsphaeroidea*[7]:	Lg/Lt,+ 1.33–0.75
obl	= *pollina oblata:*	Lg/Lt,+ 0.75–0.50
perobl	= *pollina peroblata:*	Lg/Lt,+ <0.50

b. Polar area index (polar-I). The relative size of the polar area can be expressed by the relation of the measurements of the polar area (polar-M) to the greatest breadth of the pollen grain (Lt,+ or Lt,max,+): The following classes can be distinguished:

polar-I(0):	polar area absent
polar-I(<0.25):	polar area small
polar- I(0.25–0.50):	polar area medium
polar-I(0.50–0.75):	polar area large
polar-I(>0.75):	polar area very large

c. Exine index (ex-I). The relative thickness of the exine can be denoted by the relation between the greatest thickness of the exine (ex-M,+) and the greatest breadth of the pollen grain (M(÷),+; Lt,+ or – possibly – Lt,max,+).

ex-I(<0.05):	exine-index small
ex-I(0.05–0.10):	exine-index medium
ex-I(0.10–0.25):	exine-index large
ex-I(>0.25):	exine-index very large

Section D. Pollen morphological description

One great difficulty in the observation and description of a pollen is caused by the fact that the image which one sees under a microscope differs according to the depth of focus. A description can only be achieved in one of two ways: either the pollen grain is described exactly as one sees it under the microscope, or one describes it according to the interpretation of what has been seen. The first procedure, which is analytical, is cumbersome because the image in every focus has to be described separately. The second procedure, which is synthetic, produces a simple and organic description – but there is the risk that complex structures may be misunderstood and the resulting descriptions, misleading. In practice, both methods are used in combination. For the analytical description of a pollen grain, the following scheme may be applied:

A. Indicate the orientation of the pollen grain; *i.e.,* which part is facing upwards toward the observer (for example, a pole, a colpus or an intercolpium).

B. Indicate which part of the pollen grain is being described (for example, a wart or a pore).

C. Indicate the level of focus in relation to the upper or lower boundary of the pollen grain (*cf.,* pollen measurements, p. 12, and Plate X). This can be denoted in the following way:

foc 0: focusing above the outer boundary of the pollen grain (*cf.*, foc 1). Foc 0 can be further divided from the top downward into a, b, c, *etc.*; *e.g.*, foc 0,a.

foc 1: focusing on the outer boundary of the pollen grain. Small distances above and below the boundary can be indicated by ÷ (above) and + (below).

foc 2: focusing between foc 1 and foc 3. Foc 2 can be further divided from the top downward into a, b, c, *etc.*

foc 3: focusing on the inner boundary of the exine of the pollen grain; small distances above and below can be indicated by ÷ or +.

foc 4: focusing between foc 3 and foc 5. Foc 4 can be further divided into a, b, c, *etc.*

foc 5: focusing on the centre of the pollen grain; at this focus, the exine is seen sharply in profile. Small distances above and below can be indicated by ÷ or +.

foc ÷ 4 to ÷ 0: focus positions below the centre of the pollen grain, corresponding to those above but preceded by a ÷.

Section E. Pollen types

(Plates XI, XII, XIII, and XIV)

A.	Pollen grains in combination			
	B. Pollen grains combined in groups of more than four	1. Poly	= Polyadeae
	BB. Pollen grains combined in groups of four	2. Tetr	= Tetradeae
	BBB. Pollen grains combined in groups of two	3. Dy	= Dyadeae
AA.	Pollen grains single		
	B. One aperture, or none		
	C. Pollen grains with air sacs	4. Ves	= Vesiculatae
	CC. Pollen grains without air sacs		
	D. Colpus absent		
	E. Pore rudimentary or absent	5. Inap	= Inaperturatae
	EE. One clearly-defined pore	6. P_1	= Monoporatae
	DD. One colpus	7. C_1	= Monocolpatae
	BB. Two or more clearly-defined apertures		
	C. Without lacunae (pseudocolpi or pseudo pores)		
	D. Colpi present, no free pores		
	E. Colpi fused into rings, spirals, etc	8. C syn	= Syncolpatae
	EE. Colpi not fused, but discrete		
	F. Two colpi	9. C_2	= Dicolpatae
	FF. More than two colpi		
	G. Colpi without distinct pores or transversal colpi		
	H. All colpi are meridional		
	I. Three colpi	10. C_3	= Tricolpatae
	II. More than three colpi	11. C stp	= Stephanocolpatae
	HH. Not all colpi are meridional	12. C peri	= Pericolpatae
	GG. Colpi with pores or transverse colpi (sometimes one or two pores or transversal colpi may be absent)		
	H. All colpi are meridional		
	I. Three colpi	13. C_3P_3	= Tricolporatae
	II. More than three colpi	14. CP stp	= Stephanocolporatae
	HH. Not all colpi are meridional	15. CP peri	= Pericolporatae
	DD. Free pores present, colpi absent		
	E. Pores predominantly equatorial		
	F. Two to three pores		
	G. Two pores	16. P_2	= Diporatae
	GG. Three pores	17. P_3	= Triporatae
	FF. More than three pores	18. P stp	= Stephanoporatae
	EE. Pores not equatorial	19. P peri	= Periporatae
	CC. Lacunae (pseudocolpi or pseudopores) present		
	D. With pseudopores	20. Fen	= Fenestratae
	DD. With pseudocolpi		
	E. Some colpi with, others (pseudocolpi) without pores (free pores absent)	21. C het	= Heterocolpatae
	EE. With free pores	22. P extra	= Extraporatae

Section F. Pollen-sculpture types

(Plates III, IV, and V)

Abbreviations derive from the first three letters of each term.
(for example, psi = psilatus)

A. True sculptural elements absent
- B. Indentations absent or less than <1μm ..... psilatus
- BB. With holes or pits ≧ 1μm ..... foveolatus[8]
- BBB. With scattered, elongated hollows ..... fossulatus[9]

AA. Sculptural elements present, all dot-shaped
- B. All dimensions are <1μm ..... scabratus
- BB. At least one of the dimensions is ≧ 1μm
  - C. Sculptural elements not pointed
    - D. Greatest diameter > the height of the element
      - E. Without proximal constriction ..... verrucatus
      - EE. With proximal constriction ..... gemmatus
    - DD. Greatest diameter < the height of the element
      - E. Without distal thickening ..... baculatus
      - EE. With distal thickening ..... clavatus
  - CC. Sculptural elements pointed ..... echinatus

AAA. Sculptural elements present, all or some elongated
- B. Elements irregularly distributed, or without a predominant pattern ..... rugulatus
- BB. Elements predominantly parallel ..... striatus
- BBB. Elements arranged in a network ..... reticulatus

According to the distribution of the dot-shaped sculptural elements, two types can be distinguished:
inord = inordinatus: sculptural elements more or less randomly distributed.
ord = ordinatus: sculptural elements arranged in a pattern.

Section G. Types of pollen structure

A. Tectum absent ..... intec = intectatus
AA. Tectum present ..... tec = tectatus

For tectate pollen grains, the following structural types can be distinguished according to the distribution of the granulae below the tectum, by analogy with the sculptural types given above:

intra-bac ≷ intra-baculatus
intra-rug = intra-rugulatus
intra-str = intra-striatus
intra-ret = intra-reticulatus

Within the intra-baculatus type, two sub-types can be distinguished (*c.f.*, above):

inord = inordinatus
ord = ordinatus

Section H. Form, demarcation and structure of the apertures

(Plate XV)

Colpi

α = form

A. No irregularities at the equator
- B. Edges of the colpus turned neither outwards nor inwards ..... α 1
  - C. Colpus developed as a seam or very small fissure ..... α 1a
  - CC. Edges of colpus separated ..... α 1b
- BB. Edges of the colpus turned outwards or inwards ..... α 2
  - C. Edges turned inwards ..... α 2a
  - CC. Edges turned outwards ..... α 2b

AA. With irregularities at the equator in the form of constriction, fraying, or a bridge-shaped interruption.
- B. Constriction or fraying but no bridge-shaped interruption ..... α 3
  - C. With regular constriction at the equator, but no fraying.
    - D. Constriction not pronounced. The edges of the colpus form acute angles at the equator.
      - E. Length of the constricted section < the breadth of the colpus.
        - F. Constriction not S-shaped ..... α 3a
        - FF. Constriction is S-shaped ..... α 3b
      - EE. Length of the constricted section > the breadth of the colpus ..... α 3c
    - DD. Constriction pronounced. The edges of the colpus form obtuse angles or curves at the equator.
      - E. Length of the constricted section < the breadth of the colpus
        - F. Constriction not S-shaped ..... α 3d
        - FF. Constriction is S-shaped ..... α 3e
      - EE. Length of the constricted section > the breadth of the colpus ..... α 3f
  - CC. Colpus frayed at the equator. Constriction, if any, irregular.
    - D. Colpus irregularly constricted ..... α 3g
    - DD. Colpus not constricted ..... α 3h
- BB. Colpus completely interrupted at the equator by a bridge ..... α 4

β = demarcation

A. Margo absent
- B. Demarcation of the colpus diffuse, at least at the apices ..... β 1 (diffusus)
  - C. Diffuse demarcation in all directions ..... β 1a
  - CC. Diffuse demarcation only at the colpus apices ..... β 1b
- BB. Demarcation of the colpus distinct and rectilinear ..... β 2 (distinctus)
  - C. The apices of the colpus are pointed or sharp ..... β 2a
  - CC. The apices of the colpus are blunt or rounded ..... β 2b

AA. Margo present ..... β 3 (marginatus)
- B. Outer demarcation of the margo is diffuse ..... β 3a
- BB. Outer demarcation of the margo is distinct ..... β 3b

γ = structure

A. Operculum absent
- B. Colpus membrane absent or naked ..... γ 1 (nudatus)
- BB. Colpus membrane present and equipped with ektexine elements (granulae) ..... γ 2 (granulatus)

AA. Operculum present ..... γ 3 (operculatus)

Pores

α = form

1 - 4 seen in optical cross-section

A. Vestibilum absent
- B. Pore neither depressed nor raised ..... α 1
- BB. Pore depressed ..... α 2
- BBB. Pore raised ..... α 3

AA. Vestibulum present ..... α 4

a - d seen from above and in combination with a colpus

A. Pores not constricted into a figure-eight form
- B. Pores elongated in the direction of the polar axis - or of the colpus ..... α a
- BB. Pores with length and breadth approximately equal ..... α b
- BBB. Pores elongated at right angels to the polar axis or the colpus ..... α c

AA. Pores constricted into a figure-eight form ..... α d

β = demarcation

Anulus absent
- B. Demarcation of the pore diffuse in all or, possibly, two opposite directions ..... β 1 (diffusus)
  - C. Demarcation diffuse on all sides ..... β 1a
  - CC. Demarcation diffuse only on two opposite sides ..... β 1b
- BB. Demarcation of the pore distinct and regular ..... β 2 (distinctus)

AA. Anulus present ..... β 3 (anulatus)
- B. Outer demarcation of the anulus diffuse ..... β 3a
- BB. Outer demarcation of the anulus distinct ..... β 3b

γ = structure

Operculum absent
- B. Pore membrane naked or missing ..... γ 1 (nudatus)
- BB. Pore membrane present and equipped with ektexine elements (granulae) ..... γ 2 (granulatus)

AA. Operculum present ..... γ 3 (operculatus)

Section I. Groupings according to the number of apertures

In pollen grains with more than three apertures, the following groups can be distinguished according to the number of appertures:

4; 5–6; 7–12; 13–24; 25–48; >48.

Footnotes.

1. Faegri, Knut and Iversen, Johs.: Textbook of Modern Pollen Analysis, Ejner Munkcgaard, Copenhagen, 1950.
2. One of the authors (Troels-Smith) has taken measurements for a number of years with a view to illuminating variations in size within the same species, and also changes in size when various methods of chemical treatment have been applied. This material, which is to be published shortly, shows a quite extraordinary variation according to the method of treatment (*c.f.*, Brorson Christensen 1946). On the other hand, relative proportions in size between species show unexpectedly little change; *i.e.*, the relationship between, for example, *Corylus* and another pollen type remains relatively constant.
3. Such a typology is especially necessary where identifications are made with the aid of a punch-card system (see Plate XVI).
4. In sculptural and structural elements, a measurement parallel to the surface of the exine is termed "diameter"; a measurement perpendicular to the surface is termed "height".
5. All exine measurements apply to the exine *exclusive* of colpi, pores, lacunae, anuli, margines, and costae; *n.b.*, the outer boundary of the pollen grain – *c.f.*, p. 13.
6. That is, measurements of sculptural elements, abbreviated for the sake of convenience throughout.
7. The group of *subsphaeroidea* includes the classes of subprolate + spheroidal + suboblate in Erdtman 1943.
8. The dividing line between *foveolatus* and *reticulatus* has been established as follows: the diameter of the lumina is $\geqq$ the breadth of the surrounding muri (*reticulatus*); the diameter of the fovea is $<$ the smallest distance to the adjacent fovea (*foveolatus*).
9. The *fossulatus* types presupposes that the fossulae do not anastomose in such a way that sculptural elements (verrucae or valla) are formed.

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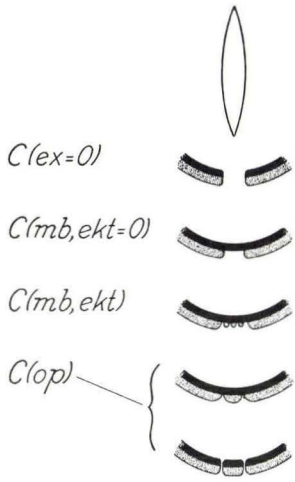
Index

Abbreviations

aeq	= aequator. aequatorialis	l	= limes
anl	= annulus, annulatus	lac	= lacuna
ap	= apex	Lg	= longitudo
ax	= axis	Lt	= longitudo transversa
bac	= bacula, baculatus	lum	= lumen, lumina, luminosae
C	= colpus	M	= mensura
C_1	= Monocolpatae	med	= medianum
C_2	= Dicolpatae	max	= maximum
C_3	= Tricolpatae	mb	= membrana
C_3P_3	= Tricolporatae	mg	= margo, margines
Cα; Cβ; Cγ	= cf. p. 21	mur	= muri
C het	= Heterocolpatae	obl	= oblata
C peri	= Pericolpatae	op	= operculum
C P peri	= Pericolporatae	p	= pollina
C P stp	= Stephanocolporatae	P	= porus
C stp	= Stephanocolpatae	P_1	= Monoporatae
C syn	= Syncolpatae	P_2	= Diporatae
cav	= cavea, cavatus	P_3	= Triporatae
cent	= centrum	Pα; Pβ; Pγ	= cf. p. 22
cla	= clavae, clavatus	P extra	= Extraporatae
col	= columellae	P peri	= Periporatae
conj	= conjunctae	P stp	= Stephanoporatae
cost	= costae	perobl	= peroblata
D	= diameter	perprol	= perprolata
dig	= digitatae	pl	= plateae
Dy	= Dyadeae	pol	= polus
ech	= echini, echinatus	polar	= area polaris
ekt	= ektexina	Poly	= Polyadeae
end	= endexina	prol	= prolata
ex	= exina	psi	= psilatus

Fen	= Fenestratae	ret	= reticulatus
fix	= fixus	rug	= rugulatus
foc	= focus	sca	= scabratus
fos	= fossula, fossulatus	simpl	= simplices
fov	= foveolatus	subsph	= subsphaeroidea
gem	= gemmae, gemmatus	str	= striatus
gran	= granula	tec	= tectum, tectatus
H	= altitudo	tec(perf)	= tectum perforatum
I	= index	Tetr	= Tetradeae
Inap	= Inaperturatae	tr	= transversalis
inord	= inordinatus	val	= valla
intec	= intectatus	ver	= verrucae, verrucatus
inter C	= intercolpium	Ves	= Vesiculatae
inter P	= interporium	vest	= vestibulum
intra e	= intra-baculatus e		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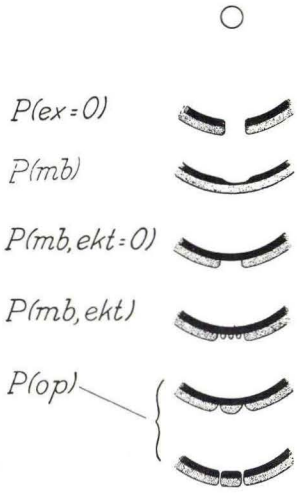
C(mb,ekt=0)
C(mb,ekt)
C(op)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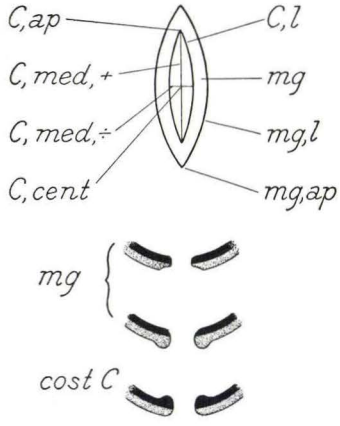
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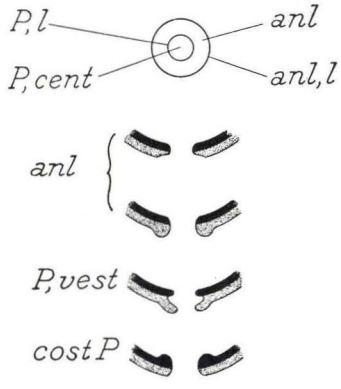
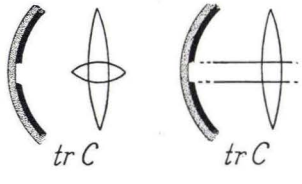
C,l
C,med,+
mg
C,med,÷
mg,l
C,cent
mg,ap
mg
cost C


P,l
anl
P,cent
anl,l
anl
P,vest
cost P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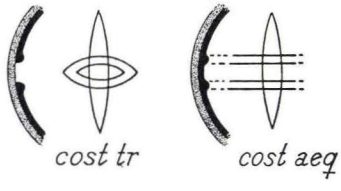
tr C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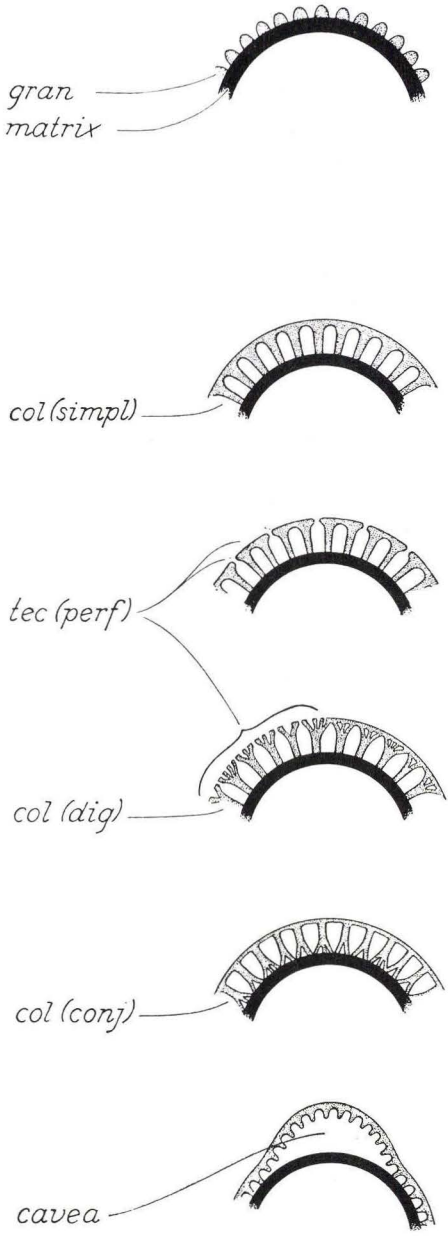
cost aeq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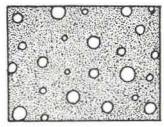
matrix
col (simpl)
tec (perf)
col (dig)
col (conj)
cavea

psi



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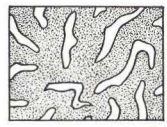


fos

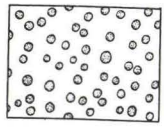
ver

gem

bac

cla

ech



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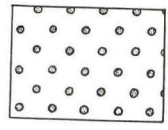

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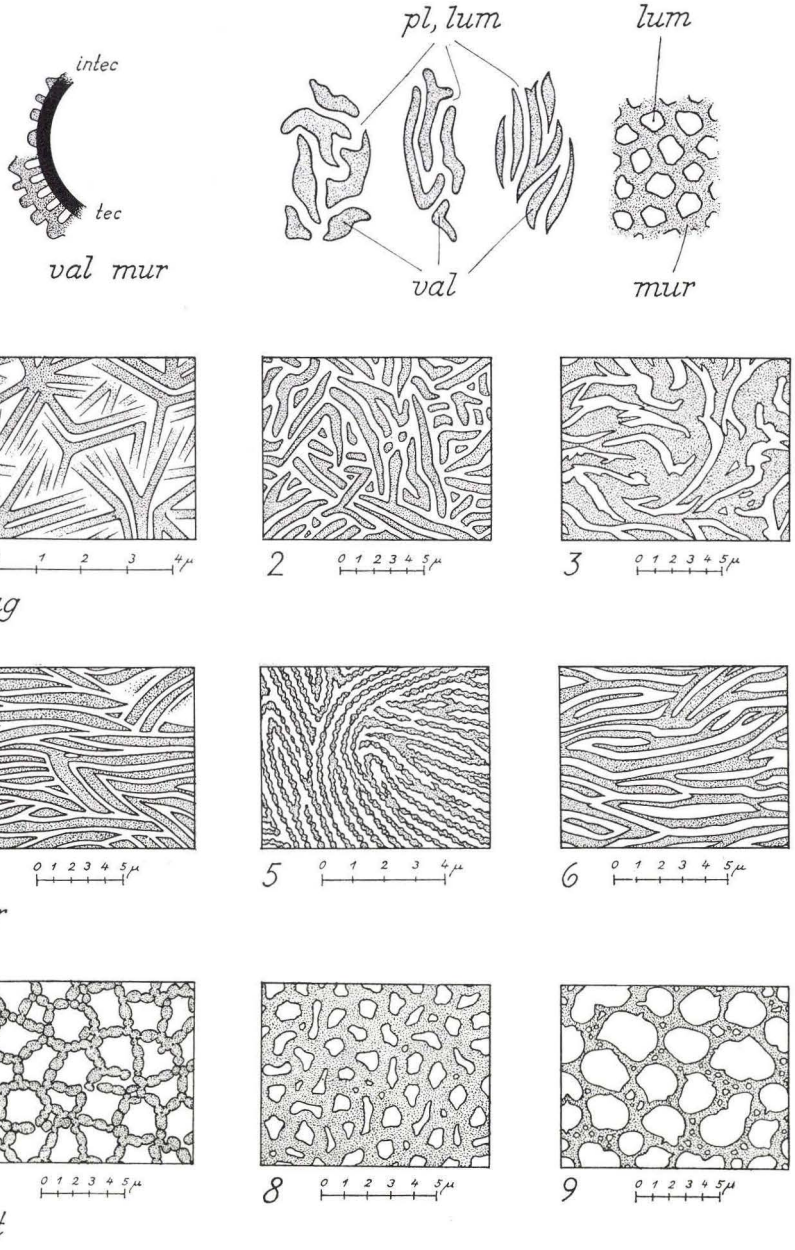
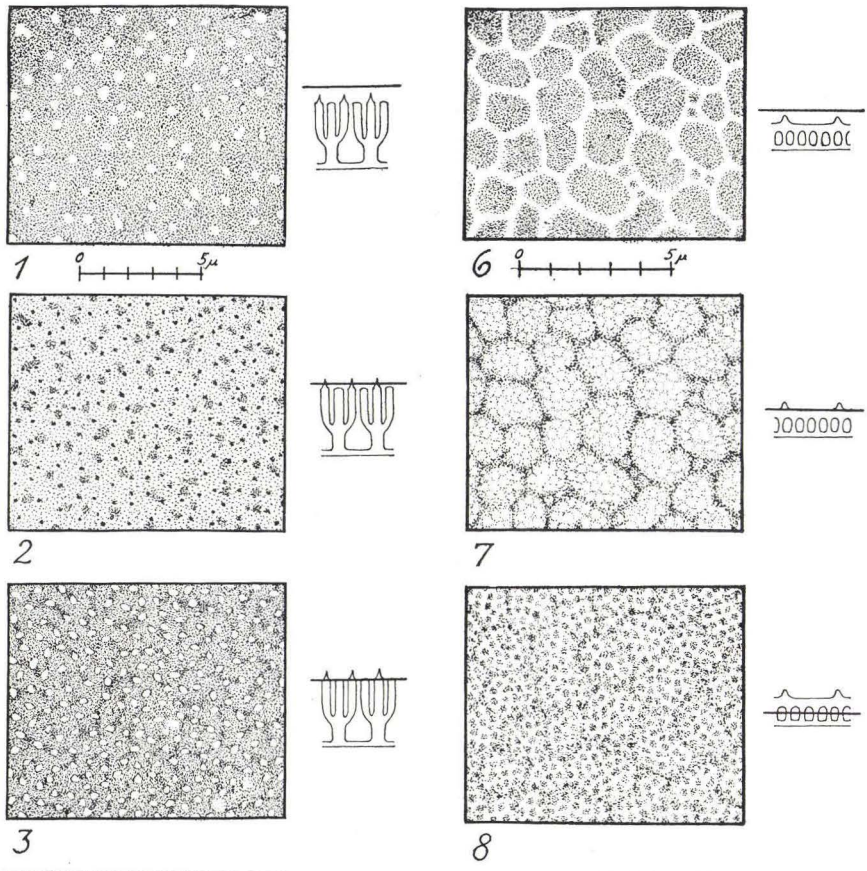
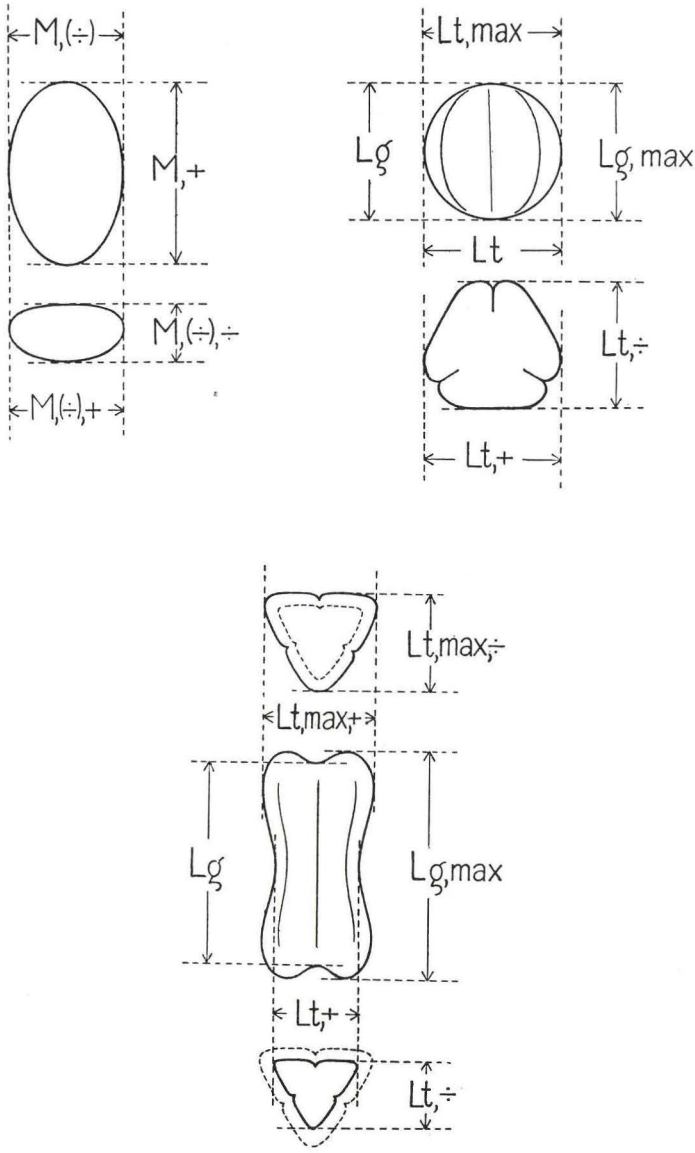


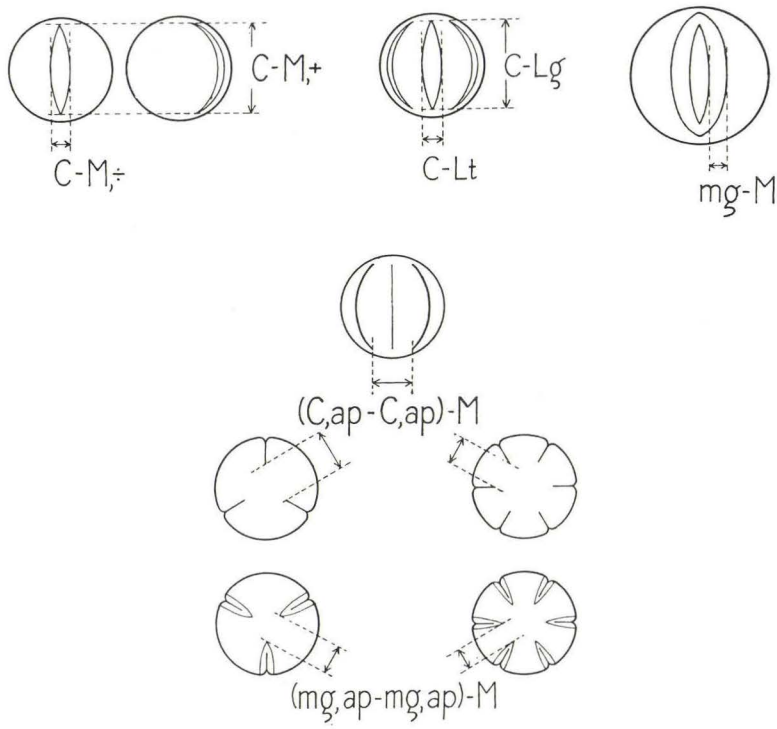
1. Sedum rosea (L) SCOP. *2. Nymphoides peltata* (S. G. GMEL.) O. K. *3. Prunus insititia* L. *4. Menyanthes trifoliata* L. *5. Acer pseudoplatanus* L. *6. Saxifraga oppositifolia* L. *7. Iris pseudacorus* L. *8. Lysimachia thyrsiflora* L. *9. Thesium ebracteatum* HAYNE.



6—8. Galeopsis tetrahit L.

1—5. Stellaria longipes GOLDIE.


M,(÷)
M,+
M,(÷),÷
M,(÷),+
Lt,max
Lg
Lg,max
Lt
Lt,÷
Lt,+
Lt,max,÷
Lt,max,+
Lg
Lg,max
Lt,+
Lt,÷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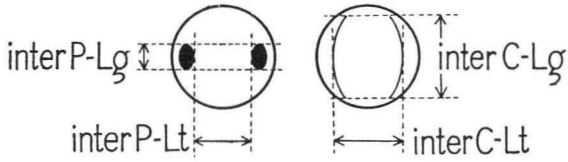
C-M,÷
C-Lg
C-Lt
mg-M
(C,ap-C,ap)-M
(mg,ap-mg,ap)-M
P-M
P-M,+
P-M,-
P-Lg
P-Lt
anl-M
(anl,l-anl,l)-M
(P,l-P,l)-M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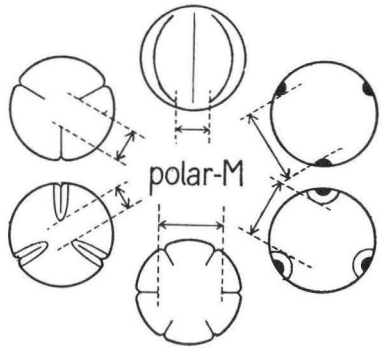
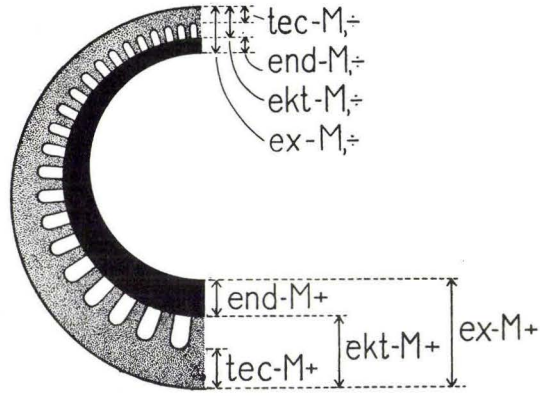
inter P-Lt
inter C-Lg
inter C-Lt


polar-M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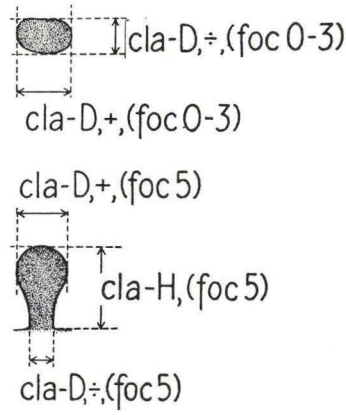
tec-M+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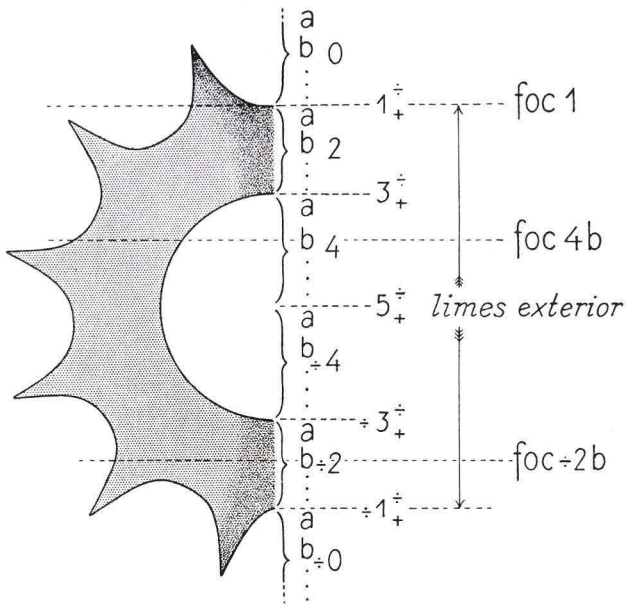
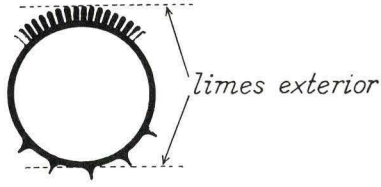
cla-H,(foc 5)
cla-D,÷,(foc 5)


a
b 0
1 ÷ +
foc 1
a
b 2
3 ÷ +
a
b 4
foc 4b
5 ÷ +
limes exterior
a
b ÷ 4
÷ 3 ÷ +
a
b ÷ 2
foc ÷ 2b
÷ 1 ÷ +
a
b ÷ 0


limes exterior

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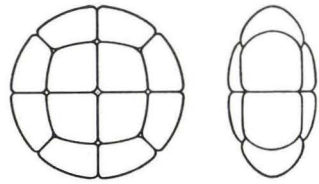
Polyadeae



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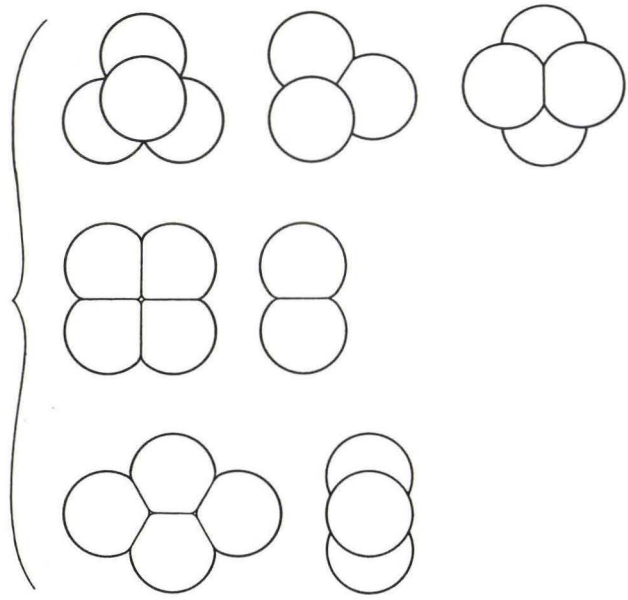

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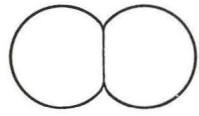
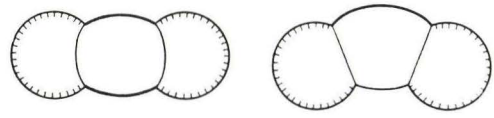
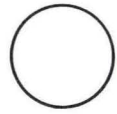
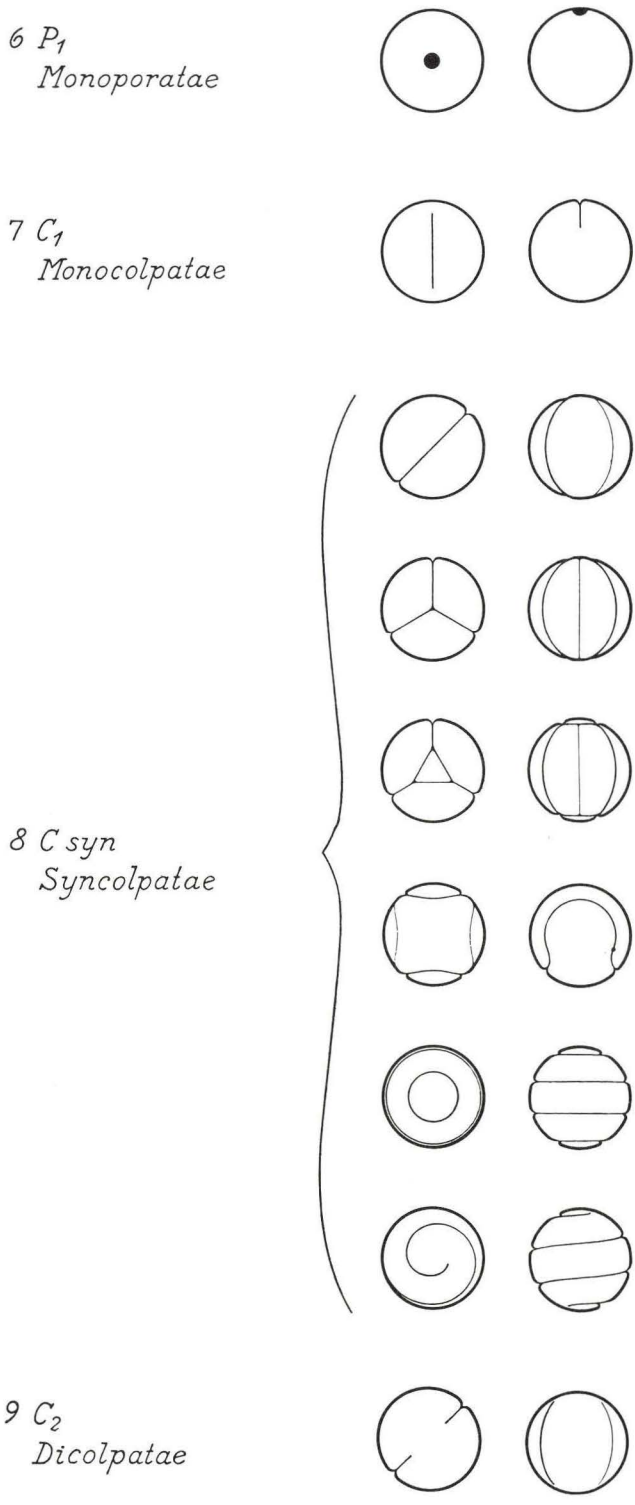


4 Ves
Vesiculatae



5 Inap
Inaperturatae




6 P_1
Monoporatae
7 C_1
Monocolpatae
8 C syn
Syncolpatae
9 C_2
Dicolpatae

10 C_3
Tricolpatae

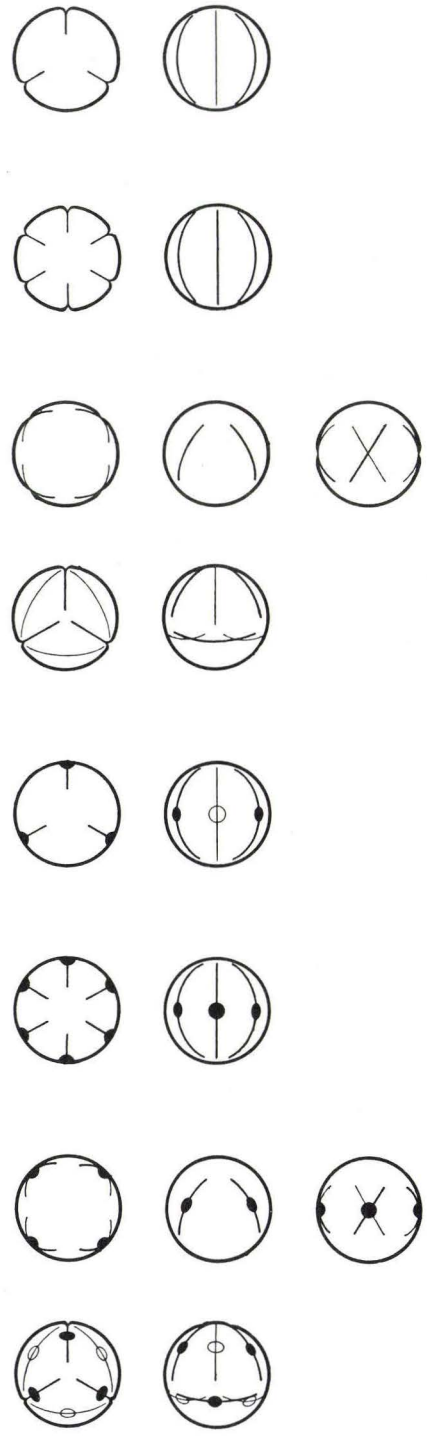
11 C stp
Stephanocolpatae

12 C peri
Pericolpatae

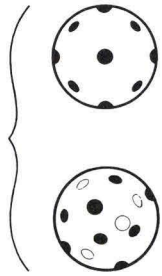
13 C_3P_3
Tricolporatae

14 CP stp
Stephanocolporatae

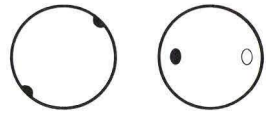
15 CP peri
Pericolporatae



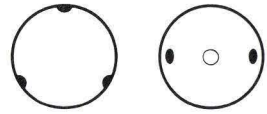
19 *P peri*
Periporatae



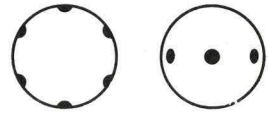
16 P_2
Diporatae



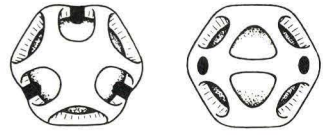
17 P_3
Triporatae



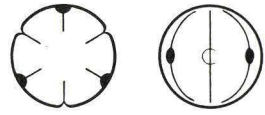
18 *P stp*
Stephanoporatae



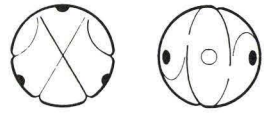
20 *Fen*
Fenestratae

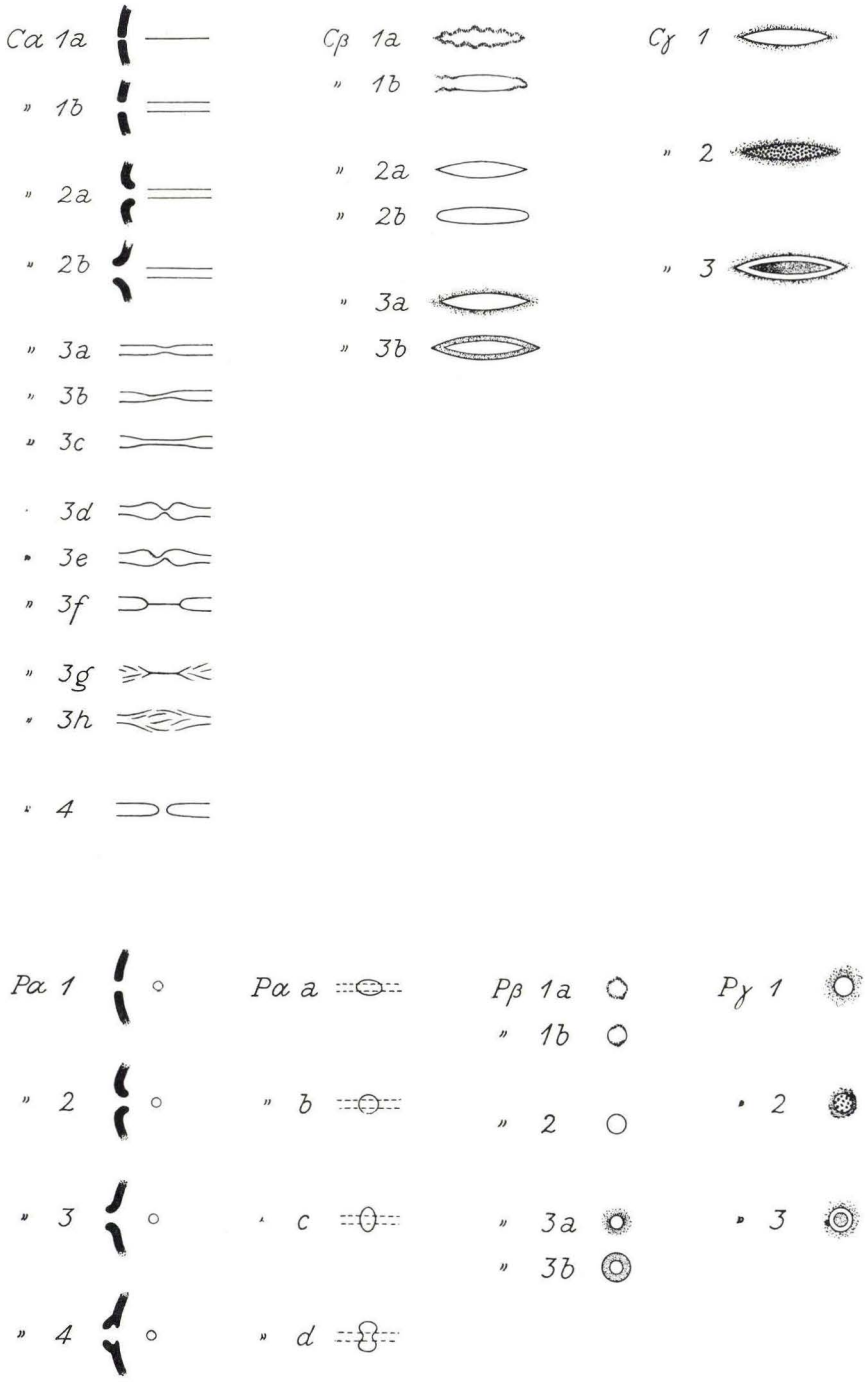


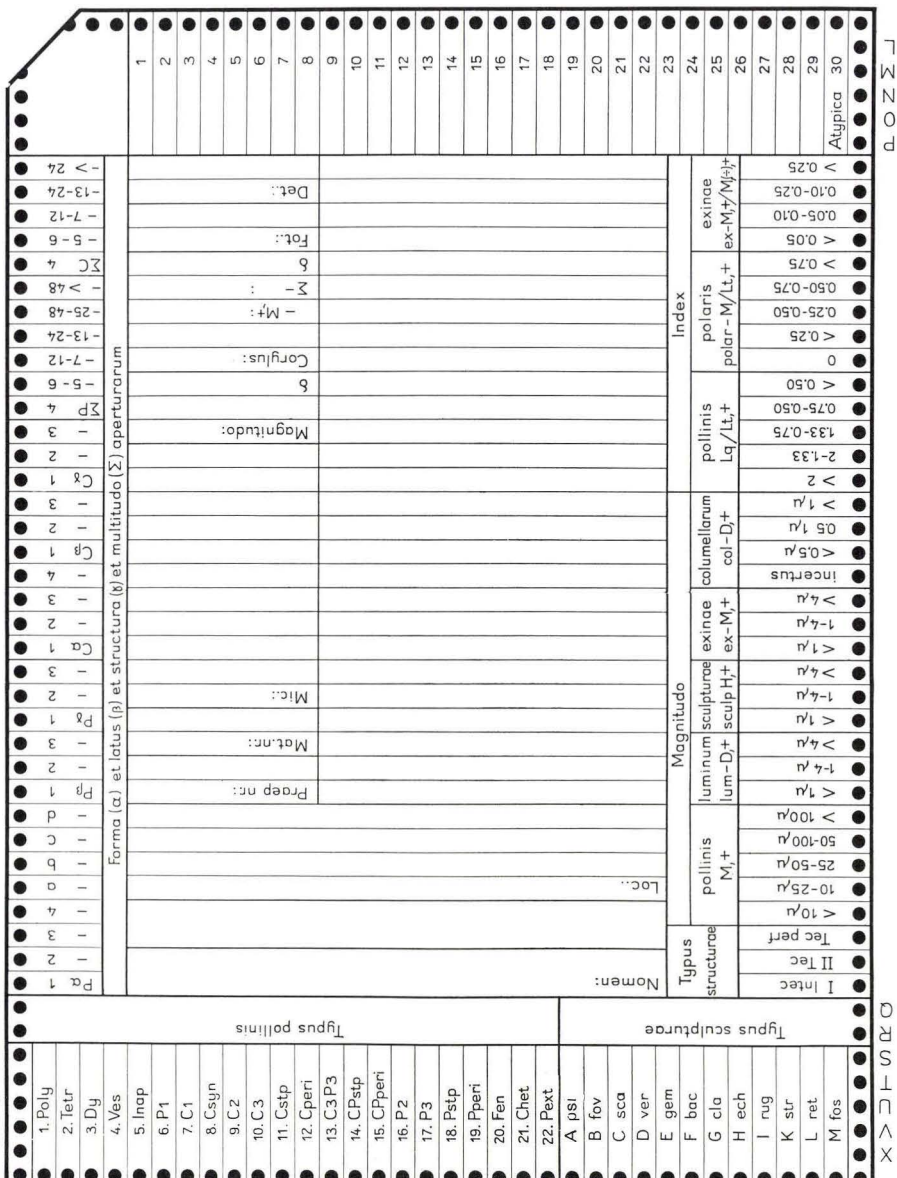
21 *Chet*
Heterocolpatae



22 *P extra*
Extraporatae




Cα 1a
" 1b
" 2a
" 2b
" 3a
" 3b
" 3c
" 3d
" 3e
" 3f
" 3g
" 3h
" 4
Cβ 1a
" 1b
" 2a
" 2b
" 3a
" 3b
Cγ 1
" 2
" 3
Pα 1
" 2
" 3
" 4
Pα a
" b
" c
" d
Pβ 1a
" 1b
" 2
" 3a
" 3b
Pγ 1
" 2
" 3



Punch Card for description and registration of unidentified fossil pollen grains, and for use in the construction of a "Key" to recent pollen flora. See Clark 1938, Faegri and Iversen, 1950.