

ON POLLEN AND SPORE TERMINOLOGY

G. ERDTMAN

Palynological Laboratory, Bromma (Sweden)

THE death of Professor B. Sahni severed a personal link between botanists in Sweden and those in India and deprived *scientia amabilis* of one of its paramount adepts, a scientist of a most modest and gentle nature, never desiring credit for himself, always considering the interests of the work first, unselfish and helpful to others in the highest degree.

Among other things Professor Sahni took a very active interest in pollen and spore research. This he often demonstrated, e.g. in his contribution "Palynology in India", presented in *Svensk Botanisk Tidskrift* 1948. In the last letter which I received from him, dated March 7th, 1949, Sahni asked me to acquaint spore workers in India with the terminology and nomenclature applied in pollen and spore investigations in Sweden. The following note is submitted in response to this request and as a tribute to the lasting memory of B. Sahni.

POLARITY

Cormophyte spores are usually produced in fours (tetrads) by spore mother cells. Polar axes of the spores (here and in the following "spores" mean pollen grains or spores, or both, according to the context) are those lines which pass through the centres of the spores towards the centre of the tetrad (or were so directed during the formation of the spores). The proximal pole of a spore is directed towards the centre of the tetrad; the distal pole faces the opposite direction.

Some spores are — as far as their wall is concerned — apolar, i.e. poles or special polar areas cannot be distinguished in individual spores after dismemberment of the tetrads. Cryptopolar spores have much the same appearance as apolar spores, but on closer examination they reveal a more or less distinct polarity (*Larix*, *Pseudotsuga*, *Equisetum*, and others).

Polar spores are isopolar, subsipolar or heteropolar. In isopolar spores an even plane (situated half-way between the poles

and cutting the polar axis at right angles) divides the spores into equal halves. The surface of the proximal half is known as the proximal face, the surface of the distal as the distal face. In heteropolar spores the two faces are pronouncedly dissimilar to each other with regard to apertures, etc. Subisopolar spores are \pm intermediate between isopolar and heteropolar. Their equatorial plane is usually more or less curved.

SYMMETRY

Spores are asymmetric or symmetric. In the first and rare case they are either non-fixiform (without fixed shape) or fixiform (with fixed shape). As a rule symmetric spores are either radiosymmetric or bilateral. Radiosymmetric spores have more than two vertical planes of symmetry or, if provided with but two such planes, always with equilong equatorial axes. Bilateral spores have two vertical planes of symmetry but, in contradistinction to the radiosymmetric spores with but two such planes, the equatorial axes are not equilong. It is occasionally a matter of some difficulty to determine whether a spore is radiosymmetric or bilateral (cf. e.g. the pollen grains of *Crypteronia*, *Eucryphia*, *Isoglossa*).

APERTURES

Spores are usually aperturate, i.e. provided with apertures, less frequently non-aperturate. Apertures are any openings or thin, more or less distinctly delimited areas which are or may normally be engaged in the discharging of the soft inner spore material or part of it. In the classification of apertures their position, shape, structure, number, and size have to be considered.

POSITION AND SHAPE

With regard to their position the apertures are polar, global, or equatorial. The polar apertures are monopolar (proximalipolar or distalipolar) or bipolar. Examples of proximalipolar apertures are the tetrad scars

(laesurae) of mosses and ferns. Monolete spores have one laesura, trilete spores three laesurae radiating from the proximal pole. Alete spores are devoid of laesurae. [In hilate spores the laesura(e) is (are) reduced to a \pm circular, indistinctly delimited aperture (hilum; cf. certain moss spores).]

To the distalipolar apertures belong the furrows, or sulci, of the pollen grains in many monocotyledonous and pseudocotyledonous plants. Sulci always reach or pass straight across the distal pole. Sulcate grains are either 1-sulcate (i.e. provided with one sulcus through the centre of which passes the polar axis), rarely trichotomosulcate (with three-slit sulcus), very exceptionally tetrachotomosulcate (with four-slit sulcus). A \pm distal, circular aperture, ulcus, may be derived from a sulcus or a sulcoid aperture. "Ulcus" means "wound", and like a wound an ulcus has either smooth (psilate) or ragged margins. Thus in Gramineae, Pandanaceae, etc., the ulcus is psilomarginate, whereas in certain species of Restionaceae its margin is \pm ragged.

Sulcoid apertures neither reaching nor passing across the distal pole may be termed sulculi (sing. sulculus, a small sulcus). They are situated in the distal face of the grain (sometimes even at or near the equator). A 2-sulcate pollen grain has two sulcoid furrows, parallel to each other, with the distal pole in the centre between the furrows. In 3-sulcate grains the sulculi stand in relation to the pole in much the same way as the sides of an equilateral triangle to the centre of the triangle. In zoni-sulcate grains, finally, the sulculi are confluent and the pole accordingly encircled by a continuous aperture zone.

Global apertures are spread uniformly over the spore surface. They are known as rugae if they are \pm elongate, or foramina in case they are circular or nearly so (i.e. the length is less than twice the breadth).

Equatorial or subequatorial, \pm circular apertures are known as pores (pori). Equatorial, elongate apertures with one of their axes (nearly always the longest) crossing the equator at right angles are termed colpi. [The surface of an ordinary colpate grain can be divided into the following areas: n mesocolpia (n : number of colpi) and two apocolpia. A mesocolpium is bounded by two adjacent colpi and two transversal lines drawn through the apices of the latter. The apocolpia (one at the

proximal, the other at the distal pole) make out the rest of the (non-apertural) surface. In a porate grain similarly n mesoporia and two apoporia can be distinguished.] If the colpi meet at both poles, the grains are syncolpate (and destitute of apocolpia); if they (or their \pm colpoid, non-equatorial parts) are bifurcate and the branches meet, leaving intact apocolpia of regular shape, they are parasyncolpate. Grains with six apertures in the same places as would have been occupied by the halves of three colpi, each bipartite from concrescence of its central part, are 3-diplodemicolpate. A grain with three demicolpi meeting at a pole offers an example of unipolar syndemicolpatism. A grain with 8 colpi arranged pairwise in four groups can be referred to as 4-geminicolpate, etc.

According to the above definitions a polycolpate grain is very different from a polyrugate grain. Yet there is a transition between colpi and rugae, since equatorial "colpi" do not infrequently converge in pairs. Such colpi may, if considered necessary, be referred to as rupi (sing. rupus; from "ru" in rugae and "pus" in colpus). A 6-rupate grain is consequently provided with six equatorial elongate apertures converging in pairs; in a 6-colpate grain the apertures do not converge, and in a 6-rugate grain they are usually situated in places corresponding to the sides of a tetrahedron.

Spiraperturate grains (cf. *Aphyllanthes*, *Berberis*, *Eriocaulon*, etc.) constitute a morphologically heterogeneous group. They are provided with spiral or spiraloïd apertures or with \pm aperturoïd weak sclerine streaks which are probably derived from colpi, rugae, or sulci, etc.

Under the provisional heading plicate grains may be classified a number of likewise \pm heterogeneous pollen types with folds or creases, etc., and which cannot be conveniently placed in any of the aperture classes previously mentioned (cf. e.g. the polypliate pollen grains in *Spathiphyllum*, *Ephedra*, and *Welwitschia*).

In spite of these definitions it may be difficult to classify indistinct apertures. In such cases it is advisable to use the letters "oid" either as a suffix to nouns or inserted in adjectives: a 3-colpoidate grain is thus provided with three colpoid apertures (colpoids), whereas a 1-letto-2-sulculoidate spore has one proximal laesura and two parallel distal grooves somewhat reminiscent

of two sulculi, at least in point of their position (cf. FIG. 4, PL. 108, in J. SCHOPF, "Pteridosperm male fructifications". *Ill. Geol. Surv.*, Rep. No. 142, 1949).

TABLE I—APERTURES AND CLASSIFICATION OF FOSSIL SPOROMORPHS

APERTURES (SITUATION, SHAPE)	LATIN NAMES OF	
	Apertures	Fossil sporomorphs (suggested "coenotypes")
Absent (Thin areas instead of apertures)	(nonaperturate)	Napites; - napites
	(Tenuitas) (-tenuate)	- tenuites
Polar		
<i>Proximalipolar</i>		
± Elongate	Laesura, -ae (-lete)	-letes, -lites
± Circular	Hilum (hilate)	Hilites
<i>Distalipolar</i>		
± Elongate	Sulcus, -i (-Sulcate)	-sulcites
± Circular	Ulcus (-ulcerate)	-Ulcerites
Global		
± Elongate	Ruga, -ae (-rugate*)	-rugites*
± Circular	Foramen, -ina (-forate*)	-foraminites*
Equatorial		
± Elongate	Colpus, -i (-colpate*)	-colpites*
± Circular	Porus, -i (-porate*)	-porites*

* In case of composite apertures "or" (in 'forate' 'aminor') is intercalated before -ate and -ites respectively.

Pollen grains with angular or lobate "amb" and provided with equatorial apertures may be either angul-, plan-, or foss-aperturate (cf. TEXT-FIG. 4). In the first case the centres of the apertures are situated on convex, more or less prominent parts of the amb, in the second case they are situated on ± plane (L. planus, flat, even), and in the third case on more or less concave parts (L. fossa, ditch) of the grains. [Amb (outline, circumference; L. ambitus, circumferentia) means the edge or boundary of a surface. This term should be used only when a sporomorph is viewed with one of the poles exactly uppermost, i.e. with the polar axis directed straightly towards the observer. In isopolar, not constricted grains the maximum amb coincides with the equator. Isopolar, equatorially constricted grains have two main amb. Besides of these it may sometimes be convenient to speak of the apo-mesocolpial amb, coinciding with the equatorial limit of an apocol-

pium in a colpate grain, etc. In heteropolar and in spherical, apolar sporomorphs only one amb, the largest, is usually spoken of.]

The apertures in 3-aperturate pollen grains are usually arranged either in accordance with Fischer's law, i.e. they meet two and two at six points in grains in tetrad arrangement, or according to Garside's law, i.e. they meet in threes at four points.

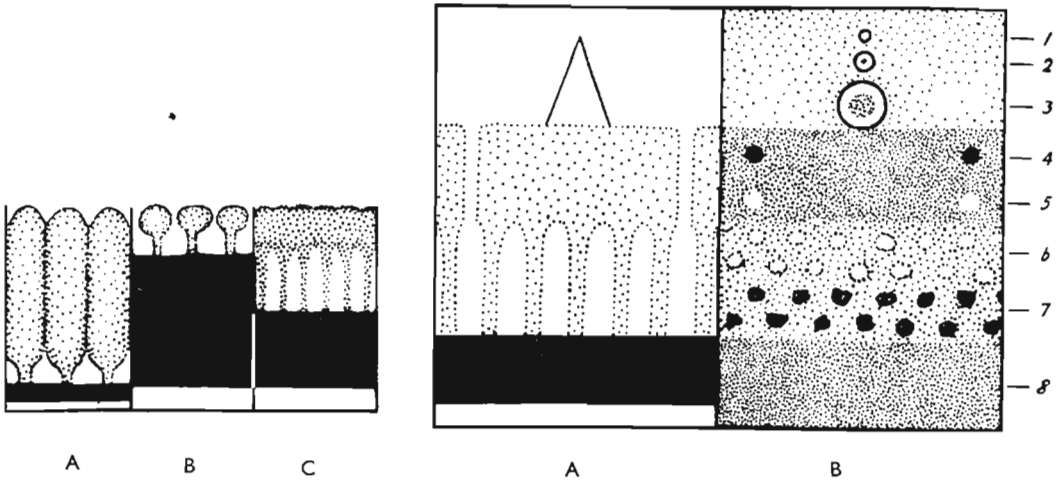
SIMPLE AND COMPOSITE APERTURES

With regard to their structure certain apertures (laesurae, hila, sulci, and sulculi) are simple, whereas others (colpi, rupi, rugae, foramina, and pori) are either simple or composite. Simple apertures are "thorough", i.e. formed so to speak by a succession of more or less congruent holes in the different sclerine layers. In composite apertures the successive openings (they are usually but two) are not congruent: the superficial parts of the apertures have the shape of colpi, rupi, rugae, foramina, or pori, whilst the underlying parts (deviating in shape, size, or both) are either circular, lolongate (longitudinally elongate; L. longus, long, and elongatus, extended), or lalongate (transversely extended; L. latus, broad). They thus exhibit the various shapes of a mouth and are accordingly termed ora (mouths; L. os, plur. ora). Grains with lalongate ora meeting laterally to form a continuous equatorial oral zone are zonorate (TEXT-FIG. 5: 9-10).

The supra-oral part of a composite aperture retains the name of the corresponding simple aperture. The grains with composite apertures are thus generally either colporate (TEXT-FIG. 5: 5-11), ruplicate, rugulate, foraminorate, or pororate (TEXT-FIG. 5: 2-4).

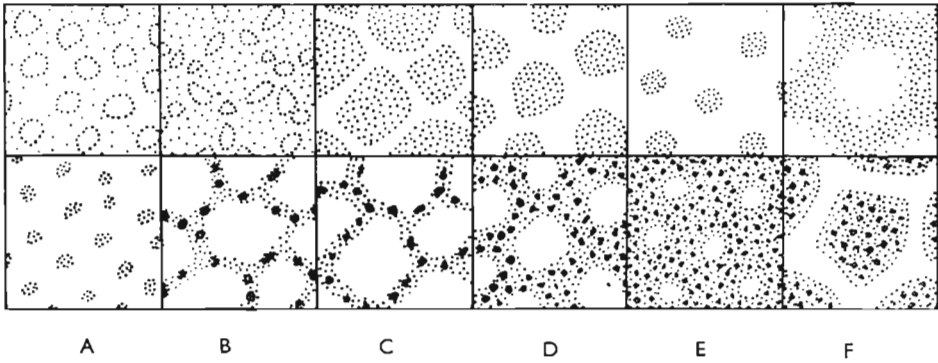
According to this terminology a grain with three oriferous colpi is 3-colporate, a grain with six oriferous rugae 6-rugulate, etc. A diorate colpus is provided with two ora. Further terms, as colporoidate (colporoidate), etc., do not call for special explanation.

The apertures are usually covered with aperture membranes. The membranes are psilate (smooth), granulate (provided with granules), crustate (thickly beset with coarse granules), etc. In certain apertures (colpi, rupi, rugae, pori, foramina, sulci, ulcera, sulculi) the membranes are sometimes conspicuously thickened (their margins excepted), often so as to assume fairly the same appearance as the inter-apertural

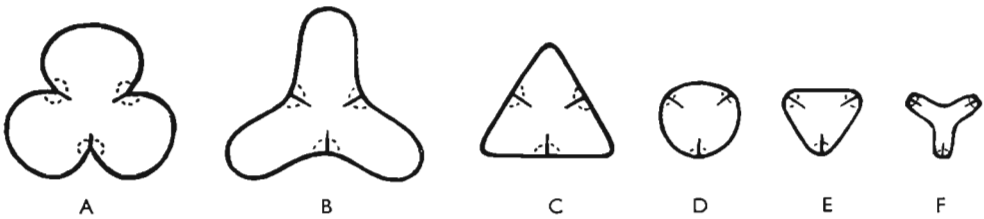


TEXT-FIG. 1

TEXT-FIG. 2

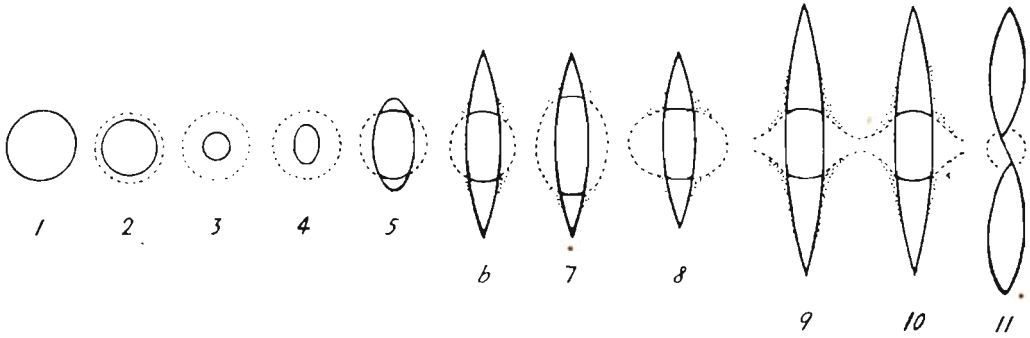


TEXT-FIG. 3

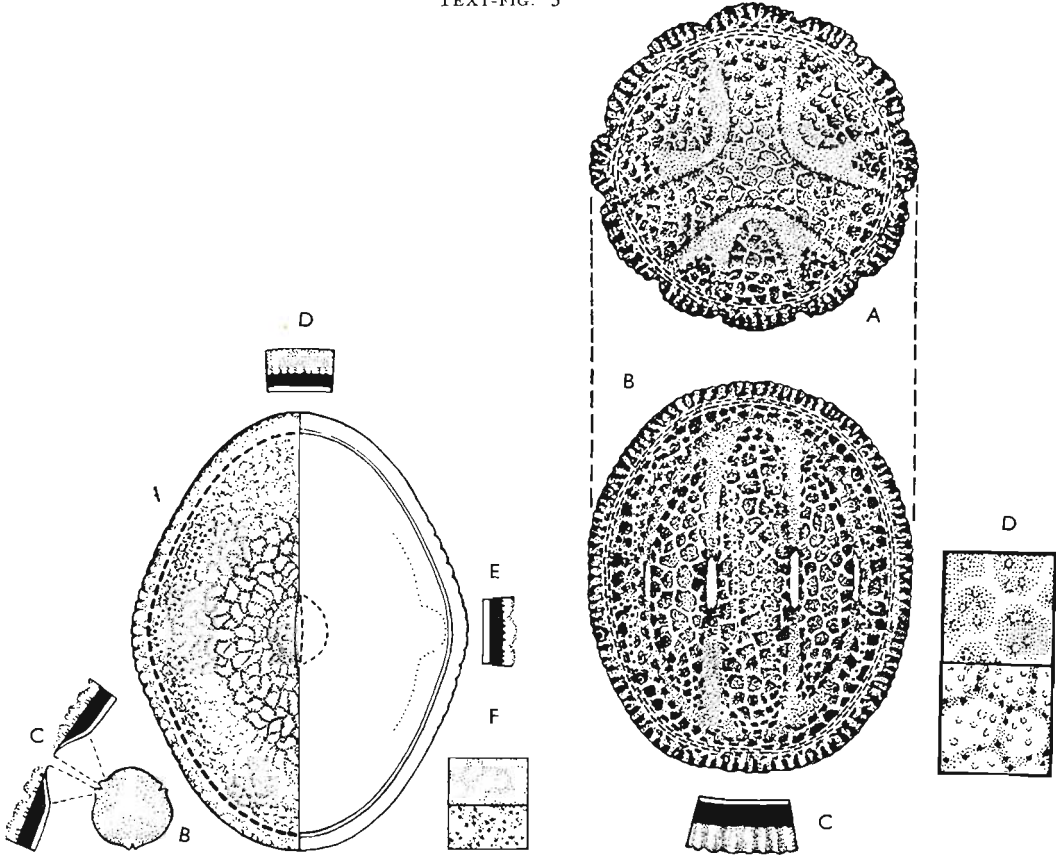


TEXT-FIG. 4

TEXT-FIG. 1 — SCLERINE STRATIFICATION. Endonexine covered by ectonexine (full black). Sexine elements (dotted) on top of nexine. TEXT-FIG. 2 — A, SCLERINE STRATIFICATION; B, LO-ANALYSIS OF SAME SCLERINE. 1-3, spinule; 4-5, ectosexine (tegillum with two puncta); 6-7, endosexine (bacula); 8, nexine; 4-7, sexine proper; 1-7, sculptine; 1-8, sclerine. TEXT-FIG. 3 — SEXINE PATTERNS (LO-ANALYSES). A, pilate sexine (LO); B, retipilate sexine (LO); C, reticulate sexine with simplibaculate muri (OL); D, transition from pattern C to pattern E; muri duplibaculate (OL); E, scrobiculate sexine (OL); F, areolate sexine (LO). TEXT-FIG. 4 — TRICOLPORATE GRAINS IN POLAR VIEW. POSITION OF COLPI IN: A, fossaperturate grain; B, "sinu-aperturate" grain; C, planaperturate grain; D, intermediate between C and E; E, F, angulaperturate grains.



TEXT-FIG. 5



TEXT-FIG. 6

TEXT-FIG. 7

TEXT-FIG. 5 — OUTLINES OF EQUATORIAL APERTURES. 1, simple aperture (porus); 2-11, composite apertures; 2-4, apertures in pororate grains; 5-11, apertures in colporate grains; 9-10, apertures in colporate, synorate grains. TEXT-FIG. 6 — POLLEN GRAIN OF *Sonneratia Griffithii*. Grains 3-colporate (brevicolpate), subprolate ($52 \times 40 \mu$); sexine + areolate; polar sexine thicker, equatorial sexine thinner than nexine. A, pollen grain (lateral view), surface (left) and section (right) $\times 1000$; B, pollen grain (polar view) $\times 250$; C-E, exine stratification $\times 2000$; F, LO-analysis. Upper detail figure: sexine pattern at high, lower detail figure: the same at low adjustment of the microscope. Analytical illustrations like this Text-fig. are known as "palynograms". TEXT-FIG. 7 — POLLEN GRAIN OF *Passiflora maculifolia*. A, polar view $\times 1000$; B, lateral view $\times 1000$; C, sclerine stratification $\times 2000$; D, LO-analysis (sculptine reticulate, \pm isobrochate, muri simplibaculate, lumina provided with small rods or granules).

sclerine. Thus is formed the operculum of an operculate ulcus, foramen, porus, colpus, sulcus, etc. Apertures with elongate opercula with the ends (apices) merging with the extra-apertural sclerine are pontoperculate (L. pons, bridge; ex. *Dendropoterium*).

NUMBER, SIZE, ETC.

According to common practice Greek figures or prefixes are used when stating the number of apertures (mono-, di-, tri-, tetra-, penta-, hexa-, hepta-, octa-, nona-, deca-, hendeca-, dodeca-, . . . poly-). A pollen type with an \pm inconstant, low number of \pm equidistantly distributed circular apertures can be referred to as oligoforate.

Extreme length, size, etc., can be given Latin denominations, e.g. longi- (long), brevi- (short), grandi- (large), parvi- (small), lati- (broad), angusti- (narrow), crassi- (thick), tenui- (thin). A longicolpate-parvorate grain is thus colporate and provided with very long colpi and minute ora. A brevicolpate-grandorate grain is shown in Text-fig. 6 (cf. also 5 : 5). Text-fig. 6C exhibits a tenuimarginate colpus in equatorial section.

SPORODERM

SPORODERM STRATIFICATION

The spore wall (sporoderm or sporodermis; cf. BISCHOFF, 1833) usually consists of two main strata, an inner soft (malacodermatous) layer, the intine [FRITZSCHE, 1837; synonyms: endospore, tegmen interius, intinium, endosporium; the term "endine" would fit better than "intine" in the series intine (endine) - exine - perine; "intine", however, has priority and has always been in use since Fritzsche's days], and an outer, hard (sclerodermatous) layer, the sclerine (ERDTMAN, 1948; synonyms: sclerospore, sclerinium, sclerosporium).

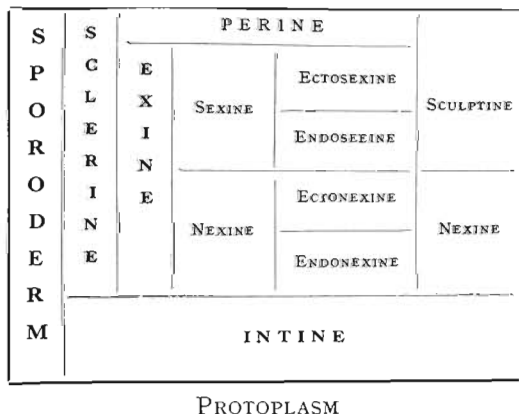
Sclerine is many times, but not always, synonymous with exine (FRITZSCHE, 1837; synonyms: exospore, extine, tegmen exterius, exinium, exosporium). In the spores of certain plants, however, it also comprises an outer layer, perine (perispore; perinium, perisporium). The presence of this layer seems to be due to the activity of a periplasmodium with perinigenous properties. The physico-chemical qualities of the perine differ more or less from those of the exine. It is, however, sometimes difficult, parti-

cularly when dealing with pollen grains, to decide whether a certain sporoderm layer or sporoderm element is perinous or exinous. At least some details of the sporoderm sculpturing in certain pollen types are probably perinous. As long as this cannot be definitely proved it is advisable to classify perine under the same heading — sculptine (ERDTMAN, 1948; L. sculptinium) — as the outer, sculptured part of the exine. This part is termed sexine [ERDTMAN, 1948 (from "s" in sculptured, and "exine"); L. sexinium or exinium sculpturatum]. Synonym: "Ueberzug der Exine" [FRITZSCHE, 1837, p. 31; cf. also p. 32: "Sehr verschiedenartig sind die Bekleidungen, mit welchen die Membran überzogen ist; sie bestehen entweder in einem körnigen, oder in einem zelligen Ueberzuge, welche theils durch die verschiedenen Grösse und Verbindung der Körner, theils durch die Art der Entstehung der zelligen Textur interessante Modificationen darbieten, und dadurch noch viel mehr variiren, dass sie bald mit Stacheln oder Warzen versehen sind, bald ohne diese vorkommen"]. Fritzsche did thus not (in contradistinction to statements by Faegri and Iversen, 1950, and Iversen and Troels-Smith, 1950) use the term "granula" in descriptions of the "Ueberzug der Exine" (cf. FRITZSCHE, l.c., p. 24: "Die kleinen Oeltröpfchen und Amylumkörner machen nun die sogenannten Granula des Pollen aus . . ."). Further synonyms: Exo-exine (POTONIE, 1934); ektexine, ektexinium (ERDTMAN, 1943).

The sexine often exhibits two layers, an inner [endosexine; synonym: "Isolierschicht" (POTONIE, 1934)] and an outer [ectosexine; synonyms: Exolamelle (POTONIE, 1934), tectum (FAEGRI & IVERSEN, 1950)]. These terms are further explained below under "Sculptine Patterns".

The inner, non-sculptured part of the exine is known as nexine (ERDTMAN, 1948; from "n" in non-sculptured, and "exine"; L. nexinium, exinium nonsculpturatum). Synonyms: Intexine? (FRITZSCHE, 1837, p. 28), "Membran der Exine" (FRITZSCHE, l.c., p. 31; in contradistinction to the statement by Iversen and Troels-Smith, 1950, p. 51, Fritzsche did not use the term "matrix" in descriptions of this membrane), Int-exine (POTONIE, l.c.), endexine (ERDTMAN, 1943, p. 41). The nexine usually exhibits an outer, not very refractive zone (ectonexine) and an inner, more refractive zone (endonexine; ERDTMAN, 1948).

TABLE 2 — SPORODERM STRATIFICATION



SCULPTINE PATTERNS

Among flowering plants one of the basic elements of the sexine appears to consist of small drumstick-shaped rods [pila (POTONIE, 1934)], projecting at right angles from the nexine surface. Each pilum has a head (caput) supported by a rod-like neck (baculum). The bacula of a baculate sexine are usually straight and unbranched. The capita form the upper part of the sexine (the ectosexine), the bacula the lower, basal part of it (endosexine). If the capita coalesce or if — hypothetically — a layer of some sort should be formed on the top of the pila, enveloping the capita whilst leaving the bacula free, a tegillum (small roof) is formed. [The term tectum is used in descriptions of thick, \pm stratified tegilloid layers (cf. Compositae, etc.).] A tegillate sexine is crassitegillate if the ectosexine is at least twice as thick as the endosexine, tenuitegillate if it is at least twice as thin as the latter. It is referred to as punctitegillate if it is provided with small perpendicular holes (puncta). Punctitegillate sexine occurs in the pollen grains of many plants and can be easily studied, e.g. in the large grains of *Opuntia* subgen. *Cylindropuntia*. The upper surface of a tegillum is usually psilate (smooth) or slightly undulating. It is sometimes beset with sculptural elements in the shape of granules (granula), warts (verrucae), spines (spinae), spinules (spinulae), etc. In saccate pollen grains, i.e. grains provided with air-sacs (sacci), as well as in subsaccate grains (provided with "air-sacs in statu nascendi" in the shape of small bladders or irregular waves and crests), the bacula locally lose

their foothold in the nexine (cf. e.g. *Grevillea* spp., *Oenothera* spp., *Pterocephalus papposus*, *Trapa*, etc.).

A striate sexine pattern is formed by a lateral union of pila (or their capita) standing in rows. A reticulate sexine (cf. TEXT-FIG. 3C) is formed by a similar coalescence of pila arranged to certain patterns, usually \pm hexagonal. A reticulum consists of meshes (brochi). Certain grains, not very frequently met with, are oligobrochate (provided with few meshes), others polybrochate (provided with a large number of meshes). Distinction can also be made between isobrochate and heterobrochate reticula; in the latter — but not in the former — brochi of \pm widely differing sizes are often adjacent.

A reticulum is also said to consist of walls (muri) and spaces (lumina) between the walls. According to the number and arrangement of bacula in the muri it is possible to distinguish between simplibaculate (TEXT-FIG. 3C), duplibaculate (TEXT-FIG. 3D), and multibaculate (TEXT-FIG. 3E) muri (bacula arranged in one, two, or several rows respectively). If the muri are not supported by individual bacula but by bacularia (groups of \pm fused bacula), they may be termed simpli-, dupli-, or multibaculariate, according to the arrangement of the bacularia. In an angustimurate reticulum the thickness of the muri is one-fifth or less of the diameter of the lumina; in a latimurate reticulum it is as thick as the diameter of the lumina or thicker.

The lumina in typical reticulate grains are usually \pm polygonal. Large, circular lumina are termed foveolae (cf. ERDTMAN, 1947, p. 106) and very small, circular lumina scrobiculi (POTONIE, 1934, p. 12). The mureoid ridges between the foveolae are sometimes finely reticulate. Foveolate grains are rare whereas scrobiculate grains are met with in several families, e.g. Restionaceae.

Muri are not always continuous. If — as in *Cuscuta lupuliformis* and many liliaceous plants — they are composed of \pm isolate pila in polygonal arrangement (cf. TEXT-FIG. 3B), the pattern is retipilate. In ornate grains the muri are curved, occasionally interrupted and irregularly branched, forming ornaments of different patterns.

Pollen grains are, finally, said to be areolate (cf. TEXT-FIG. 3F) if the sexine is chiefly or exclusively confined to areas (areolae) which as to size and position correspond to the lumina of a reticulate sexine.

The above terms may be compounded when describing complex sexine features: thus in a striati-reticulate pattern the reticulate arrangement is slightly blurred by a striation. Many of the terms are more or less vague. A large reticulum, e.g. in the pollen grains of *Cobaea*, may for instance not be strictly homologous with the fine reticulate patterns in many other plants, e.g. *Pogostemon auricularia*. This suffices to set out the great difficulties to be faced in the study of sculptine patterns, difficulties which can only be overcome by detailed investigations of particularly favourable objects and with the application of new methods, e.g. electron microscopy.

LO-ANALYSIS

A sculptine like that in Text-fig. 2A exhibits different patterns at different adjustments of the microscope. At high adjustment small white islands produced by the spinules are seen (TEXT-FIG. 2B:1). When focusing a slightly lower level, the same islands turn \pm dark (TEXT-FIG. 2B:2, 3). At medium adjustment very small dark islands appear,

produced by the puncta in the tegillum (TEXT-FIG. 2B:4). They later become bright (TEXT-FIG. 2B:5). At low adjustment numerous small white islands, caused by the bacula, appear and later likewise turn dark (TEXT-FIG. 2B:6, 7). These patterns are referred to as S-, T-, and I-patterns respectively (S: suprattegillar, T: tegillar, I: infrattegillar). In pattern analyses made according to this method it would seem convenient to record the first shade of every system of islands (and not that of the channels) as they appear at successive adjustments of the microscope from high to low. Even if it is impossible to elucidate any sculptine details in sporoderms seen in optical section, it may sometimes be possible to establish — by "LO-analysis" (L: lux, light; O: obscuritas, darkness) of a sculptine surface — whether the sporoderm in question is provided with LO-, OL-, or still more complicated patterns. Immersion objectives are necessary for observations of this kind. Nevertheless, the method of penetrating the sculptine and describing the patterns in the way just mentioned is often difficult and hazardous.

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