The Northwest European Pollen Flora, 33

FAGACEAE

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LITERATURE

Adams and Morton (1972), Colombo et al. (1983), Dupont (1975), Endress (1977), Erdtman (1943, 1952, 1963, 1969), Erdtman et al. (1961, 1963), Kedves (1982), Kuprianova (1965a, b), Kuprianova and Alyoshina (1972), McAndrews, Berti and Norris (1973), Monoszon (1954, 1961), Moore and Webb (1978), Nilsson, Pragłowski and Nilsson (1977), Olsson (1975a, b), Pragłowski (1962, 1982), Saënz de Rivas (1973, 1976), Șerbănescu-Jitariu (1977), Solomon (1983a, b), Surova (1975), Wodehouse (1935).

INTRODUCTION

The family Fagaceae is distributed world-wide although it is most characteristic of the temperate and subtropical zones of both hemispheres. The majority of species are large trees which play a dominant role in the vegetation of deciduous and evergreen forests. Many are economically important as timber trees.

The family comprises seven genera with altogether about 1000 species, but of these only ten species from three genera occur in Northwest Europe. The main genus is *Quercus* which accounts for eight species. Two of these, *Q. rubra* and *Q. palustris*, were introduced into Europe from North America some centuries ago and are now widely cultivated. In addition, *Q. pyrenaica* has been included in this account because its area of distribution, in the Iberian Peninsula and southern France, borders closely on that of the Northwest European Pollen Flora.

The pollen grains of the three genera *Quercus*, *Fagus* and *Castanea* are easily distinguished from one another by their structure and sculpture, as is well documented in the standard pollen keys for the area (Erdtman et al., 1961; Faegri and Iversen, 1975; Moore and Webb, 1978). Those keys do not subdivide the pollen of *Quercus* any further, but numerous attempts to do so are reported in the literature. These will be discussed in the comments on the *Q. robur* type.

Some characteristic features of the pollen morphology of the Fagaceae are as follows:

(1) Apertures

Castanea sativa and *Fagus sylvatica* both have well-developed endoapertures; the former an endocolpus and the latter an endoporus. Normally, the sexine is slightly extended across the ectocolpus above the endoaperture.

Traditionally, *Quercus* is included among those pollen types that lack an endoaperture, but there are reports in the literature that suggest that this view is mistaken. For example, Hyde and Adams (1958) and Smit (1973) both report the presence of endopori in *Q. cerris* and *Q. ilex*, whereas Richard (1970) describing *Q. rubra* and Planchais (1962) describing *Q. cerris* both use the term tricolporoid. One reason for this inconsistency may be the sexine extensions which are often present in *Quercus* grains, and can be so prominent that they extend from one side of the colpus to the other, thus obscuring the potential position of any endoaperture. Another reason may be the feature which was first described by Potonié (1934) as a "geniculus".

The geniculus is very characteristic of *Quercus* pollen and is unique to that genus within the Fagaceae, although it occurs in some members of other families such as *Fraxinus* in the Oleaceae. On the other hand, not all *Quercus* species show it; in *Q. dentata* from Japan it is absent. It takes the form of an equatorial bulge in the exine of the colpus [Van Campo and Elhai (1956) called it "accolade"], which is often associated with a splitting of the sexine from the nexine and a consequent rupturing of the latter. A vestibulum-like chamber is created in which, in equatorial view, the nexine forms two lateral "ears" (cf "fastigium" in Reitsma, 1970). Stanley and Kremp (1959) studied this phenomenon in a number of species, including *Q. prinoides*, and found that 90% of the grains showed a geniculus; but while it was strongly developed in some cases, there was only a slight bulge in others. They suggested that the geniculus has a function during the process of germination and speculated that it can be seen as an evolutionary intermediate between the colpate and colporate conditions. They concluded that if a geniculus is present and if the exine is split, the grain should be considered to have an endoaperture. Despite this, because of the lack of consistency, we have followed the standard convention and maintained the term tricolpate for *Quercus*.

(2) Ornamentation

Each of the three genera in Northwest Europe can be distinguished by its exine sculpture. *Castanea sativa* appears nearly smooth in the light microscope (LM). Kedves (1982), for example, referred to it merely as psilate, but it has a rugulate pattern in the scanning electron microscope (SEM). Visset (1972) called this "aspect rugulé".

The genus *Fagus* was studied in detail by Hanks and Fairbrothers (1976) who described the ornamentation of *F. sylvatica* as "scabrate; element rods distinguishable with modified conical ends, distal ends partially fused, proximal roots show fusion; interrod areas not clearly defined". Praglowski (1962) described the sculptural elements as spinules, based on LM observations only,

but later (1982) he replaced it by vermicular-rugulose, now based on SEM observations. In the LM, *Fagus sylvatica* appears finely scabrate, with the underlying columellae very clear and densely packed in cross-section.

In the LM, the ornamentation of *Quercus* species can be divided into two kinds: indistinctly scabrate and distinctly scabrate-verrucate. In the SEM the two members of the first type, *Q. cerris* and *Q. ilex*, appear scabrate and micro-rugulate respectively. All the other *Quercus* species have a scabrate-verrucate pattern. This is described in more detail under the *Quercus* pollen type.

Another characteristic of *Quercus* species that applies to all except *Q. cerris* is the aggregation of columellae into groups. In cross-section at low focus these appear as dark patches against a lighter background. The individual columellae can sometimes be seen as solitary black spots within the dark patches. The patches are variable in size and in clarity.

SPECIMENS EXAMINED

- Castanea sativa* Miller — Austria: Buysman 348 (U); England: Sowerby 299 (BM); France: Billot 2531 (BM), Murray s.n. (BM); Germany: W. and P.J.M. Maas 87 (U), Reitsma s.n. (fresh material Anno 1966), Swart 1963 (U); The Netherlands: Cult. Hort. Bot. Baarn 115 (U), Reitsma s.n. (fresh material Anno 1965); Sweden: Granvik s.n. (BM), Johansson s.n. (BM).
- Fagus sylvatica* L. — England: Jackson s.n. (BM), Whealler 243 (U); France: Gadeceau s.n. (BM); Germany: s.c. 1584 (U); The Netherlands: Kok-Ankersmit 5 (U), Punt s.n. (fresh material Anno 1967, idem Anno 1969), Swart s.n. (U), s.c. fresh material Anno 1951 and 1963, Vroman s.n. (BM); Sweden: Ahlberg s.n. (BM), Hasslow 633 (BM).
- Quercus cerris* L. — Austria: Buysman 406 (U); England: Bangerter s.n. (BM), Lousley s.n. (BM); France: Billot 2362 (BM), Lloyd s.n. (BM), Lousley s.n. (BM); Hungary: Visser 241 (U); The Netherlands: Cult. Boom 5985 (L).
- Q. ilex* L. — Austria: Buysman 17 (U); England: Britton Ref. No. 653 (BM), Gerrans 1165 (BM); France: Billot 1328 (BM), Lanjou et al. 28 (U), Mansel Pleydell s.n. (BM), Marais 757 (BM), Vijk s.n. (L); Portugal: Kostermans and Kruij 554 (U); Spain: Exc. Biol. Stud. Utrecht 1951-721 (U).
- Q. palustris* Muenchhausen — The Netherlands: Cult. Hort. Bot. Baarn 14 (U); U.S.A.: Conrad 761 (L), Umbach 5263 (U).
- Q. pedunculata* Ehrhardt = *Q. robur*.
- Q. petraea* (Mattuschka) Lieblein — Austria: Kramer and Westra 4010 (U); England: Jackson s.n. (BM), Mull Survey No. 662 (BM), Redgrove s.n. (BM), Rilstone s.n. (BM); France: Lawalrée 16088 (BM), Pourtier et al. 134 (BM); Italy: Behrendsen s.n. (U); The Netherlands: De Smidt s.n. (U); Wales: Lewis 776 (BM).
- Q. pubescens* Willdenow subsp. *pubescens* — Austria: Groves s.n. (BM); France: Billot 3897 (BM), Deséglise 279 (BM), Gadeceau s.n. (BM), Kotschy 96 (U), Paillot s.n. (BM), Vegter and Thomas 201 (U); Yugoslavia: Ferman and Van Hille 336 (U).
- Q. pyrenaica* Willdenow — France: Kotschy 92 (U); Portugal: Kostermans and Kruij 802 (U); Spain: Exc. Biol. Stud. Utrecht 1964-449 (U).
- Q. robur* L. subsp. *robur* — Belgium: Lawalrée 10455 (BM); England: Foggitt 1392 (BM), Gerrans s.n. (BM); France: Gadeceau s.n. (BM), Urqel 99 (U); Italy: Buysman 1624 (U); The Netherlands: Arnolds 1303 (U), Hoogland 40 (BM), Kramer s.n. (BM), s.c. 24 (U), Punt s.n. (fresh material Anno 1951, idem Anno 1960); Sweden: Norrman s.n. (BM).
- Q. rubra* L. — The Netherlands: Punt s.n. (fresh material Anno 1966); U.S.A.: Buysman 1899 (U), Suksdorf s.n. (L).
- Q. sessiliflora* Salisbury = *Q. petraea*.

KEY TO THE POLLEN TYPES

1. a. Pollen grains with distinct endoapertures2
- b. Pollen grains without distinct endoapertures. *Quercus robur* type
2. a. Endoaperture a porus; P/E ratio semi-transverse to suberect; grains large ($P > 30 \mu\text{m}$) *Fagus sylvatica* type
- b. Endoaperture a colpus; P/E ratio semi-erect to erect; grains small ($P < 20 \mu\text{m}$) *Castanea sativa* type

Castanea sativa type

Pollen class: 3-Zonocolporate.

P/E ratio: Semi-erect to erect.

Apertures: Ectoaperture — colpus, long, narrow, sunken; margins distinct, regular; ends acute; colpus membrane occasionally with irregular granules; fastigium absent; sexine extensions above endoaperture usually present; costae colpi absent. Endoaperture — colpus, lalongate, elliptic in outline; margins distinct, straight; ends acute or irregularly diffuse, sometimes with horns; costae distinct, narrow.

Exine: Thin. Sexine equally thick, or slightly thicker than nexine. Sexine subdivisions weakly developed. Sexine 1 an indistinct layer, columellae not visible. Sexine 2 a tectum, about as thick as sexine 1.

Ornamentation: Psilate in LM. Vaguely rugulate in SEM. In cross-section columellae not visible, or only weakly so.

Outlines: Equatorial view — elliptic. Polar view — angular, with convex mesocolpia, or more or less circular.

Measurements: Glycerine jelly — P 15–20 μm ; E 10–13 μm ; P/E ratio (1.19–)1.31–1.50. Exine up to 1.5 μm thick. Apocolpium index 0.29–0.36. Silicone oil — P 14–16 μm ; E 11–12 μm ; P/E ratio 1.20–1.42.

Species: *Castanea sativa*.

Comments

This type is easily distinguished from other types in the family by its much smaller size, its endocolpus and its semi-erect to erect P/E ratio. Furthermore, this type differs in the thickness of the exine and the rather smooth appearance of the grains in LM, in contrast with the clearly sculptured grains of the *Fagus* and *Quercus* types. Its endocolpus, especially at the ends, is less regular than the endoaperture of *Fagus sylvatica*.

Fagus sylvatica type

Pollen class: 3-Zonocolporate.

P/E ratio: Subtransverse, less often semi-transverse or adequate, rarely suberect.

Apertures: Ectoaperture — colpus, usually short, or sometimes rather long, rather broad, slightly sunken; margins distinct, irregular; ends rounded to

subacute; colpus membrane smooth to scabrate-verrucate in LM; fastigium absent; sexine extensions usually absent, sometimes indistinctly present. Endoaperture — porus, circular or lalongate-elliptic in outline; margins distinct, convex; ends rounded, obtuse, rarely acute; costae distinct, narrow, decreasing towards the ends of the pori.

Exine: Medium thick. Sexine up to twice as thick as nexine, thicker at poles. Stratification not always distinct. Sexine 1, when visible, of very short columellae. Sexine 2 a tectum slightly thicker than sexine 1. Sexine 3 of fine scabrae.

Ornamentation: Finely scabrate in LM; scabrae of uniform size, irregularly distributed; in SEM scabrae appear to be elongated, branched, with rounded ends and partially fused together. Columellae in cross-section clearly present in L-O analysis, densely packed, but irregularly arranged.

Outlines: Equatorial view — elliptic to circular. Polar view — circular.

Measurements: Glycerine jelly — P 38–42 μm ; E 42–50 μm ; P/E ratio 0.84–0.96(–1.03). Exine 2–3 μm . Apocolpium index 0.50–0.61. Silicone oil — P 38–39 μm ; E 40–41 μm ; P/E ratio 0.91–0.95.

Species: *Fagus sylvatica*.

Comments

The single species of this type is characterized by its large grains, its usually short, but rather broad colpi and its distinct endoporus. The endoporus is often lalongate-elliptic in outline, but this feature is variable and it can be circular. In the LM the ornamentation is finely scabrate with distinct, crowded columellae, but when the higher magnification of the SEM is used, the details shown are complex and irregular and therefore hard to describe accurately. The scabrae are typically elongated and are often partially fused together.

Both Hanks and Fairbrothers (1976) and Praglowski (1982) assigned all the species of the genus *Fagus* to a single pollen type. Hanks and Fairbrothers claimed that each of the eleven species that they studied can be distinguished by their ornamentation with the aid of the SEM. The quality of their plates as reproduced makes it hard to confirm this claim and the very clear illustrations given in Miyoshi (1982) suggest that the ornamentation of *Fagus sylvatica* is very similar to that of species such as *F. crenata* and *F. japonica*. This problem is discussed in more detail by Praglowski (1982).

At the LM level, Hanks and Fairbrothers suggest that the size of the grains, and of their colpi and endoapertures are all important for specific identification. The size of grains is, however, notoriously variable since it can be altered significantly by preparation techniques. Here again, Praglowski, who uses a wider range of characters, is probably a safer guide.

Quercus robur type

Pollen class: 3-Zonocolpate.

P/E ratio: Subtransverse to semi-erect.

Apertures: Ectoaperture — colpus, long, narrow, slightly sunken, often covered at equator by sexine extensions (geniculi); margins distinct, irregular; ends acute to narrowly obtuse; colpus membrane smooth to irregularly granular in LM. Endoaperture — absent to clearly developed. Exine split only in equatorial area or nearly up to the apocolpium. Nexine ears absent, poorly developed or long and distinct.

Exine: Of medium thickness throughout, or somewhat thicker at poles. Sexine two to three times as thick as nexine. Sexine of even thickness throughout or thicker at poles. Sexine 1 of short columellae, sometimes indistinct. Sexine 2 a tectum, equal in thickness to sexine 1 or thicker, less often slightly thinner. Sexine 3 of scabrae or scabrae and verrucae.

Ornamentation: Indistinctly scabrate or clearly scabrate with verrucae in LM. Verrucae more or less circular in outline, in an irregular pattern. In SEM micro-rugulate, scabrate or scabrate-verrucate, the verrucae beset with small, rounded processes. Perforations of the tectum may be scarce or abundant (SEM). Columellae distinct or indistinct in L-O analysis, in a weakly striate pattern, detached or aggregated in coherent groups of varying size and form (dark patches).

Outlines: Equatorial view — elliptic with flattened apocolpia, to circular, sometimes obtusely elliptic because of protruding sexine extensions at equator. Polar view — angular with convex mesocolpia to circular.

Measurements: Glycerine jelly — P 22–37 μm ; E 19–35 μm ; P/E ratio 0.92–1.27. Exine 1.5–3 μm . Apocolpium index 0.23–0.55. Silicone oil — P 21–37 μm ; E 18–33 μm ; P/E ratio 0.94–1.33(-1.37).

Species: *Quercus cerris*, *Q. ilex*, *Q. palustris*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica*, *Q. robur*, *Q. rubra*.

KEY TO THE SPECIES

1. a. Pollen grains indistinctly scabrate; scabrae small, $\leq 0.6 \mu\text{m}$ 2
 - b. Pollen grains distinctly scabrate-verrucate; scabrae passing into verrucae, up to 1.5 μm in diameter; in SEM scabrae beset with rounded processes. 3
2. a. Polar view angular; grains small (P 22–28 μm); columellae and dark patches indistinct; in SEM elements elongated micro-rugulate (dispersed rice hulls). *Quercus ilex*
 - b. Polar view circular; grains large (P 30–37 μm); columellae indistinct or distinct, but detached; dark patches small; in SEM, elements of regular, small size with longitudinal grooves on them, micro-verrucate *Quercus cerris*
3. a. Distinct dark patches of verrucae at low focus, medium to large, up to 2 μm long (*Quercus rubra* group) 4
 - b. Dark patches of verrucae at low focus small to medium-large, up to 1.2 μm long, or, rarely, absent. (*Quercus robur* group) 5
4. a. Apocolpium index usually large (0.30–0.50), geniculus distinct and exine usually split *Quercus palustris*
Quercus rubra

- b. Apocolpium index 0.25–0.35, geniculus usually not split. *Quercus pyrenaica*
- 5. a. Dark patches of verrucae at low focus absent or very small. *Quercus pubescens*
- b. Dark patches always present, usually medium-large, sometimes small *Quercus petraea*
Quercus robur

Comments

This pollen type is distinguished from both the other types of the family by the absence of a clear endoaperture and by a scabrate-verrucate exine. It is intermediate between the *Castanea* and *Fagus* types in size and form. Most *Quercus* grains are further characterized by a typical equatorial bulge in the colpus exine, the geniculus.

Differentiation of the species within the genus has always attracted much attention from pollen morphologists. Van Campo and Elhai (1956) and Planchais (1962) used the LM to distinguish between five of the species mentioned above, mainly on features of ornamentation and structure. These results were incorporated in a pollen key by the latter. Later studies, however, many using the SEM, raised doubts about the results. The variation within species was shown to be considerable while many of the differences between species were comparatively slight. This is particularly true of *Quercus robur*, *Q. petraea* and *Q. pubescens* which have been studied intensively because of their significance in studies of vegetation history (Pilcher, 1968; Dupont and Dupont, 1972; Olsson, 1975b).

By means of phase contrast microscopy, Van der Spoel-Walvius (1963) was able to distinguish two pollen types among the five common Northwest European species. These types were based on sexine characters. Subsequently Dupont and Dupont (1972) confirmed these results in the SEM and linked the two pollen types with the distinction between evergreen and deciduous species. The phase contrast observations of Yamazaki and Takeoka (1959) were also in agreement. Studying a large number of European *Quercus* species in the SEM, Smit (1973) concluded that three pollen types could be recognized; his classification corresponds with the taxonomic arrangement of Schwarz (1936–1939) of the genus. By and large, Smit's results have been corroborated by the recent observations made by Colombo et al. (1983). They also correspond with the three groups recognized here, the ornamentation being micro-rugulate, indistinctly scabrate or scabrate-verrucate.

Of the species studied here, only *Q. ilex* has a micro-rugulate ornamentation. It has in the SEM a supratectal pattern of small elongated elements, up to 0.4 μm long which Yamazaki and Takeoka (1959) referred to as "dispersed rice hulls" and Dupont and Dupont (1972) called "microrugules". In LM an indistinctly scabrate pattern is apparent, caused by an aggregation of these elements into protruding clusters (Smit, 1973). The ornamentation of this type somewhat resembles that of *Fagus sylvatica*.

Quercus cerris is the only species with an indistinctly scabrate pattern (scabrae <0.6 μm). It takes a more or less intermediate place between the

micro-rugulate type and the scabrate-verrucate type. In the SEM, however, the elements of the exine differ from those of *Q. ilex* as well as those of all other Northwest European *Quercus* species. The elements are small, densely packed and provided with longitudinal grooves. *Q. cerris* belongs to the *Q. suber* type of Smit (1973) together with *Q. suber*, *Q. crenata* and several other Mediterranean species of the genus.

The remaining Northwest European species have a distinct scabrate-verrucate type of ornamentation, in both the SEM and the LM. It consists of scabrae (Dupont and Dupont, 1972: microverrucae; Smit, 1973: microverrucae with rounded spinuloid processes) gradually merging into verrucae (Van der Spoel-Walvius, 1963: scabrae; Smit, 1973: microverrucae), in an irregular pattern. The verrucae and larger scabrae are provided with small rounded elements.

Depending on the form of the verrucae (only in the SEM), a further division can be made. *Q. robur*, *Q. petraea* and *Q. pubescens* have well-defined verrucae, which are clearly distinct from the tectum and scabrae, and beset with indistinct rounded elements. *Q. rubra*, *Q. palustris* and *Q. pyrenaica*, on the other hand, have vaguely defined verrucae, which merge into the tectum and scabrae and are beset with distinct, rounded elements. In this group, and also in *Q. cerris*, perforations of the tectum are abundant, but in the remaining four species perforations are more scarce.

The two main features used for a subdivision of the genus in the LM are the ornamentation and the presence at low focus of dark patches. *Q. ilex* and *Q. cerris* can be distinguished satisfactorily from the rest by the small size of their scabrae. In the remaining group of species, clear scabrae and verrucae are present, and even if the size of the scabrae somewhat resembles that in *Q. ilex* and *Q. cerris*, those scabrae are much more distinct. Because of differences in the size and density of the dark patches of columellae, the scabrate-verrucate group can be further separated. Overlap in this feature is, however, possible, which sometimes makes identification difficult.

Further identification to the species level is mainly based on size and form of the grains in the case of *Q. ilex* and *Q. cerris*. These features often show a high degree of variation within species, but their use can be justified in this case because the differences are substantial. A further differentiation between *Q. pyrenaica* and *Q. rubra* and *Q. palustris* is based on a set of features of which the apocolpium index is the most clear. *Q. rubra* and *Q. palustris* show only slight differences, and are therefore kept together. The differences in the remaining three species are minimal, as had already been demonstrated in the literature mentioned above.

Some remarks on relationships can be made. Within this group of species, *Q. ilex* is clearly differentiated because of its essentially different ornamentation. This coincides with the fact that it is the only evergreen species. Of the remaining scabrate or scabrate-verrucate species, *Q. cerris* can be split off because of its lack of verrucae, the regular distribution of its densely packed scabrae and its usually circular outline. The scabrate-verrucate group can be further divided into two groups (the *Q. rubra* group and the *Q. robur* group)

based on differences in the form of the verrucae and density of tectum perforations (SEM). The resemblances between *Q. pyrenaica* and the American natives *Q. rubra* and *Q. palustris* are striking. This suggests a parallel evolutionary development. Further subdivision of the *Q. rubra* group, with *Q. rubra*, *Q. palustris* and *Q. pyrenaica*, and the *Q. robur* group, with *Q. robur*, *Q. petraea* and *Q. pubescens*, is not supported by pollen morphology except on the basis of measurements. It would be unwise to read anything of significance into these.

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Plate descriptions (all plates $\times 2000$, except where otherwise stated)

PLATE I (p. 98)

Castanea sativa L. (figs.1—2 Swart 1963; figs.3—6, 8 Billot 2531; fig.7 Buysman 348)

1. Scanning electron micrograph; equatorial view, rugulate ornamentation ($\times 5000$).
2. Scanning electron micrograph; polar view ($\times 5000$).
3. Equatorial view; cross-section, sexine above endoaperture slightly raised.
4. Polar view; cross-section.
5. Equatorial view; cross-section, costae distinctly visible.
6. Equatorial view; colpus and endoaperture.
7. Ornamentation at polar area at low focus.
8. Endoapertures with horns; costae narrow, but distinct.

PLATE II (p. 99)

Fagus sylvatica L. (Whealler 243)

1. Scanning electron micrograph; polar view.
2. Scanning electron micrograph; ornamentation ($\times 10\,000$).

PLATE III (p. 100)

Fagus sylvatica L.

1. Polar view; cross-section.
2. Equatorial view; cross-section.

PLATE IV (p. 101)

Fagus sylvatica L. (fig.1. Vroman s.n.; figs.2—5 Whealler 243)

1. Scanning electron micrograph; section of the exine, very short columellae and more or less smooth inner contour of the nexine ($\times 10\,000$).
2. Endoaperture; elliptic, lalongate endoporus; relatively long ectocolpus.
3. Endoaperture; circular endoporus; short ectocolpus.
4. Ornamentation at high focus.
5. Ornamentation at low focus.

PLATE V (p. 102)

Quercus cerris L. (Buysman 406)

1. Scanning electron micrograph; equatorial view.
2. Scanning electron micrograph; ornamentation ($\times 10\,000$).
3. Equatorial view; distinct sexine extensions (geniculi).
4. Polar view; cross-section.
5. Narrow colpus with sexine extensions covering the endoaperture.
6. Ornamentation at low focus.

PLATE VI (p. 103)

Quercus ilex L. (Buysman 17)

1. Scanning electron micrograph; equatorial view.
2. Scanning electron micrograph; polar view.
3. Scanning electron micrograph; ornamentation ($\times 10\,000$).
4. Equatorial view; colpi without sexine extensions.
5. Equatorial view; cross-section.
6. Polar view; cross-section.
7. Ornamentation at low focus.
8. Ornamentation at high focus.

PLATE I (*Castanea sativa* type)

PLATE II (*Fagus sylvatica* type)

PLATE III (*Fagus sylvatica* type)

PLATE IV (*Fagus sylvatica* type)

PLATE V (*Quercus robur* type: *Q. cerris*)

PLATE VI (*Quercus robur* type: *Q. ilex*)

PLATE VII (p. 105)

Quercus petraea (Mattuschka) Lieblein (figs. 1—3 Behrendsen s.n.; fig. 4—5 Kramer and Westra 4010)

1. Scanning electron micrograph; polar view.
2. Scanning electron micrograph; equatorial view.
3. Scanning electron micrograph; ornamentation ($\times 10\ 000$).
4. Polar view; cross-section.
5. Equatorial view; cross-section.

PLATE VIII (p. 106)

Quercus petraea (Mattuschka) Lieblein (de Smidt s.n.)

1. Ornamentation at low focus.
2. Ornamentation at high focus.

Quercus pubescens Willdenow (Ferman and Van Hille 336)

3. Equatorial view; cross-section.
4. Ornamentation at low focus.
5. Ornamentation at high focus.
6. Polar view; cross-section.

PLATE IX (p. 107)

Quercus pubescens Willdenow (Ferman and Van Hille 336)

1. Scanning electron micrograph; equatorial view.
2. Scanning electron micrograph; polar view.
3. Scanning electron micrograph; ornamentation ($\times 10\ 000$).

Quercus robur L. (Arnolds 1303)

4. Scanning electron micrograph; equatorial view, distinct extensions.
5. Scanning electron micrograph; polar view.

PLATE X (p. 108)

Quercus robur L. (Arnolds 1303)

1. Polar view; cross-section.
2. Narrow colpus; distinct sexine extensions over the endoaperture.
3. Ornamentation at low focus.
4. Equatorial view; cross-section.
5. Scanning electron micrograph; ornamentation ($\times 10\ 000$).

PLATE XI (p. 109)

Quercus pyrenaica Willdenow (Exc. Biol. Stud. Utrecht Spain 1964—449)

1. Equatorial view; cross-section.
2. Ornamentation at polar view; low focus.
5. Scanning electron micrograph; equatorial view.
6. Scanning electron micrograph; ornamentation ($\times 10\ 000$).

Quercus palustris Muenchhausen (Conrad 761)

3. Ornamentation at equatorial view; low focus.
4. Equatorial view; cross-section.

PLATE XII (p. 110)

Quercus palustris Muenchhausen (Conrad 761)

1. Scanning electron micrograph; equatorial view.
 2. Scanning electron micrograph; ornamentation ($\times 10\ 000$).
- Quercus rubra* L. (Buysman 1899)
3. Scanning electron micrograph; equatorial view.
 4. Equatorial view; cross-section.
 5. Ornamentation at low focus.
 6. Scanning electron micrograph; ornamentation ($\times 10\ 000$).

PLATE VII (*Quercus robur* type: *Q. petraea*)

PLATE VIII (*Quercus robur* type: *Q. petraea*, 1–2; *Q. pubescens*, 3–6)

PLATE IX (*Quercus robur* type: *Q. pubescens*, 1–3; *Q. robur*, 4–5)

PLATE X (*Quercus robur* type: *Q. robur*)

PLATE XI (*Quercus robur* type: *Q. pyrenaica*, 1—2, 5—6; *Q. palustris*, 3—4)

PLATE XII (*Quercus robur* type: *Q. pyrenaica*, 1–2; *Q. rubra*, 3–6)