POLLEN MORPHOLOGY OF THE GENUS *RUBUS* L. I. INTRODUCTORY STUDIES ON THE EUROPEAN REPRESENTATIVES OF THE SUBGENUS *RUBUS* L.

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ABSTRACT

The results of pollen morphology studies of 9 European *Rubus* species are presented in this paper (*R. apricus*, *R. armeniacus*, *R. divaricatus*, *R. fabrimontanus*, *R. gracilis*, *R. hirtus*, *R. laciniatus*, *R. nessensis* and *R. pedemontanus*). The examination is made by SEM observation for first time and also by LM. All examined pollen grains are small, isopolar and tricolporate. All grains, except for *R. armeniacus* and *R. gracilis* tend to have very long colpi. Equatorial bridges constricted, make the pores invisible in most of the species. *R. apricus*, *R. armeniacus*, *R. gracilis* and *R. pedemontanus* have the equatorial bridges stretched therefore the dark whole was only the trace of existing endoaperture. The sculpture of the grain confirms striate pattern and the orientation of the muri indicates the differences between the species; *R. pedemontanus* and *R. fabrimontanus* appear to have long, compact muri, parallelly orientated to the colpus; *R. nessensis* appears muri meandrically orientated, reminiscent of "finger prints" pattern with distinct thickenings in the place of connection and numerous narrow grooves with perforations. *R. hirtus* appears to have striate-scabrate sculpture because of granular elements (punctae) dispersed between the muri on all over the grain like the internal part of the exine. Shape and size turned out to be a poor criterion for identifying species.

KEY WORDS: *Rubus* subgenus *Rubus*, pollen morphology, SEM, LM.

INTRODUCTION

The study of *Rosaceae* pollen grain has a long story. First, pollenmorphological pattern for them was established by Erdtman (1952; 1954); Faegri and Iversen (1964), who's examinations were based on light microscopy observation (LM). The results of their studies were keys for the identification of particular subgenera among *Rosaceae*. Three "types" of pollen morphology based on the sculpture of *Crataegus*, *Geum*, and *Potentilla* have been distinguished. The pollen of genus *Rubus* was also described and its sculpture determined as striate pattern, excluding *R. chamaemorus* pollen, which sculpture was described as echinate (Erdtman l.c.; Faegri & Iversen l.c.; Demchenko 1965). Using LM observation, Reitsma (1966), established more pollenmorphological "types" in *Rosaceae*, corresponding with the almost particular genus, and introduced the term "subtype" for some genera or species with distinct pollen sculpture. Due to this classification 3 species representing genus *Rubus* were classified into *Rubus idaeus* type and *Rubus idaeus* subtype (striate pattern), while *R. chamaemorus* has been separated after his specific name as *R. chamaemorus* type (echinate pattern). These new terms were to help in pollen morphology distinguishing from each other by constant differences.

LM examination of *Rubus* pollen were carried out in Poland. (Stachurska et al. 1974-1975), but only the most charac-

teristic Linnean species were taken into consideration. 15 species were studied in Taiwan (Huang, Tseng Hieng 1972) and 15 brambles in Japan (Ikuse, 1955). The sculpture of pollen has been described as scabrate, granulate, reticulate, striate or showing a combination of these patterns.

The development of scanning electron microscope (SEM) technique, allowed to examine pollen morphology more truthfully. First SEM photographs of European *Rubus* have been published by Eide (1981a), where 4 Linnean species representing 3 subgenera of this genus have been described. From among the critical subgenus *Rubus*, 2 "good species" were studied: *R. thyrsanthus* Focke (actually *R. grabowskii* Wimmer ex Günther & al.) and *R. selmeri* Lindeb. (actually *R. nemoralis* P.J. Müller). Altogether 6 species were studied and SEM photographs indicated some differences between the pollen sculpture, except for *R. chamaemorus* sculpture, which appeared to be completely different and therefore has been studied separately (Eide, 1981b). Based on SEM method the pollen morphology of some *Rubus* cultivars were studied in America (Maas, 1971). In 1982 the pollen morphology of 30 Vietnam species, belonging to 2 subgenera, were described by Kosenko and co-authors (Kosenko & al., 1982).

Summarizing, the pollen morphology of the large genus *Rubus* has been examined on 6 European, 60 Asiatic species and some cultivars. The representatives of 5 from among 13 subgenera of genus *Rubus* have been described only (Focke,

1914; Kalkman 1987). The other 7 subgenera have not been revised yet. Therefore a more detailed study has to be carried out and that would be an intention of the author afterwards.

First, according to the latest researches of contemporary batologists (Weber, 1985; Edees, Newton, 1988; Zieliński 1993), pollen morphology of the critical subgenus *Rubus* could be examined. The aim of this work was to make an overview of pollen morphology (pollen sculpture) of the critical, mainly apomictic subgenus *Rubus* representatives. The characteristics based on the pollen grain sculpture might have been one more diagnostic feature helpful in verifying species of this complex subgenus.

MATERIAL AND METHODS

Open flowers of 9 examined *Rubus* species were collected in Poland from nature. Two among them were neophytes: *R. armeniacus* and *R. laciniatus*; while the others were native to Poland.

For light microscopy (LM) and scanning microscopy (SEM) examinations, ripe anthers were taken only. All samples were treated in the same way. Anthers were ground and acetolysed according to Erdtman (1960) for 3 minutes in acetolysis mixture, centrifuged and washed with acetic acid > 97%, ethyl alcohol 96% and ethyl alcohol 100%. Next the material was divided in two equal parts. One half was used for LM, the other for SEM.

For LM observation, pollen grains were mounted in glycerin jelly and sealed with Paraplast (Sherwood, St. Louis, quoted after van der Ham 1990). To avoid flattening and swelling of the grains, I followed the recommendations of Cushing (1961), Punt (1962) and van der Ham (1990). The observations and photography were performed with Nikon Biophot microscope and the photographs were taken with a Nikon AFX automatic camera system. The polar axis (P), equatorial axis (E) and exine thickness characteristics have been measured on 20 pollen grains in the centre of mesocolpium at 1000 magnification.

For SEM observations, the drop of the alcohol-pollen suspension was placed on the aluminium stub. After evaporation of the alcohol, pollen grains were coated with gold, using a Polaron E 5100 series II sputter-coater. The sections of the pollen grains for SEM were made by Leitz freezing microtome according to Muller (1973) and coated with gold as the whole grain. The observations and photography were performed with JEOL JSM 5300 Scanning Electron Microscope at the Rijksherbarium of University in Leiden.

The photographs from SEM were useful for measurements of exine component thickness: nexine, columellae and tectum with supracteal elements, which have been taken in the centre of mesocolpium. Because of the difficulty of separating endoxine and ectoxine layers (especially the foot layer and endoxine) by SEM; the term "nexine" includes everything what is situated below the columellae and "tectum", everything above the columellae (Hebda & al., 1987; 1988). That simplification helps to interpretate the SEM image. The constitution of exine measurements are shown in drawing (Fig. B). Not all species however, could be measured in this way. In some pollen-crossing the subunits were undistinguishable, so the data were not presented in the Table 1.

The morphological description was concentrated mainly on striate sculptural pattern interpretation, because this type occurs frequently in *Rosaceae* and it is the main feature in distinguishing the groups of species (Reitsma, l.c.; Eide, l.c.).

The description terminology follows van der Ham (l.c.), Moore, Webb & Collison (1991), Punt & al. (1976-1991) and Hebda & al. (1987, 1988). The muri and their distribution on the tectum, the degree of branching was estimated on SEM photographs by counting the number of anastomoses along ten 5 µm segments. The data were presented as the range of anastomoses per 10 µm. The width and length of the muri have been measured finally. The pollen grains of the *Rubus* species are described according to taxonomy (Weber, l.c.; Zieliński, l.c.), whereas in the tables, they are presented in alphabetic order.

The drawings (Fig. A.; Fig. B) illustrate the main features which were taken to examinations and the descriptions are completed in Table 1. and Table 2. also for comparison of the species between each other.

Additional terminology:

Bridge (Faegri and Iversen, 1950, 1964, emend by Punt & al. 1980): the margins of the colpi are raised in the equatorial area and connected with each other, this connection forms a bridge over the colpus, dividing the ectoaperture into two parts.

Fastigium (Reitsma, l.c., 1970, emend by Punt & al. 1980): cavity in a colpate grain, caused by a separation of the inner part of the exine and the domed outer part of the exine in the area of endoaperture.

Fig. A. Trizonocolporate pollen grain of *Rubus* (x 2000). a: polar view; b: equatorial view. a – apocolpium, E – equatorial diameter, P – length of polar axis, ecto – ectoaperture, endo – endoaperture, eq – equatorial outline, m – mesocolpium, mer – meridional outline, n – mesocolpium.

Fig. B. Transsection of *Rubus* exine. (x 10 000); after Hebda & al. (1988); modified.

POLLEN MORPHOLOGY OF SPECIES

*Subgenus Rubus L.**Sectio Rubus**Subsectio Rubus**Rubus nessensis Hall*

Pollen grains are small; equatorial outline circular mainly, meridional outline elliptical (Figs. 1, 26; Table 2).

Apertures: Ectoaperture – colpus, long, extending 88% length of polar axis, narrow, tapering towards the pole, of acute ends. The widest part of the colpus is near the porus and measure up to 1,2 μm . Colpus membrane distinctly granulate, visible in SEM, particularly near the edges of the colpus (Fig. 2). Colpus is constricted at the equator and the equatorial bridge is present. Margins of the colpus undifferentiated. Endoaperture – porus indistinct, because of equatorial bridge and its margins constricted at the equator (Fig. 27).

Exine: Total thickness of the exine is 1,3-1,4 μm in the centres of mesocolpia. It is composed of 2 layers, visible in LM. The SEM subunits: nexine, columellae and tectum, were difficult to distinguish (Fig. 3), they are probably very thick. Perforate tectum with supratectal sculpturing distinct.

Ornamentation: Striate, both in LM and SEM examinations. The muri are short and long, approximately 1,5-3,8 μm ; not equal in width: 0,3-0,4 μm on their blunt, thick tops; often swirled and create distinct thickenings in the place of connections. The muri are arranged mostly longitudinally in the vicinity of colpus; on the mesocolpium, they are usually swirling and meandering, sometimes form pattern reminiscent of "finger prints" (Punt & al. 1976-1991). The individual muri running transversally on the poles. The grooves between the muri are shallow and narrow, sometimes twice as narrow as muri, parallelly orientated. Perforations between the muri measure up to 0,2 μm in diameter. Anastomoses range of 5-8 in a section of 10 μm length of the muri, are present under the thickenings (Figs 1-2).

*Rubus divaricatus P. J. Müll.**(R. nitidus Weihe & Nees)*

Pollen grains small; equatorial outline circular to 3-lobed, meridional outline elliptical (Figs 4, 28; Table 2).

Apertures: Ectoaperture – colpus is long and deep, extending approximately 90% length of polar axis, of acute ends. The edges of the colpus are undulated and colpus is constricted at the equator; the equatorial bridge is distinct with wide constricted margins. Edges of the colpus undifferentiated (Figs 4, 29). The colpus membrane covered with granulations (Fig. 4). Endoaperture – porus indistinct, hidden under the equatorial bridge.

Exine: Total thickness of the exine is 1,4-1,5 μm in the centres of mesocolpia. In LM examination 2 sublayers are seen (Fig. 28). SEM subunits have not been succeeded; however perforate tectum is distinct.

Ornamentation: Shallowly striate in LM and SEM observations (Figs 4, 29). The muri are running mostly longitudinally, although they are arranged variable: they are swirling slightly along the mesocolpium and turning meandrically towards the edge of the colpus. The muri are short, equal in width, approximately 0,1 μm , of acute ends and blunt tops, often merge into the perforate tectum or connect in anastomoses. The anastomoses range is 3-4 per 10 μm length of the muri. The gro-

oves between the muri are short and narrow, sometimes as wide as the muri. Perforations between the muri are present.

*Subsectio Hiemales E.H. Krause**Series Rhamnifolii (Bab.) Focke**Rubus gracilis J. Presl & C. Presl**(R. villicaulis Koehler ex Weihe & Nees)*

Pollen grains are small, equatorial outline circular to sub-triangular (Fig. 5), meridional outline elliptical (Figs 6, 30).

Apertures: Ectoaperture – colpus, long, narrow, covers 86-90% length of polar axis, tapering towards pole, of acute ends. Colpi may occasionally connect on the pole (Fig. 5). The widest part of the colpus appears near the porus and measure up to 1,21 μm . The edges of the colpus are undulated and colpus is constricted at the equator. The equatorial bridge is distinct. The colpus membrane is covered with granulations. Endoaperture-porus, slightly distinct, partly hidden by equatorial bridge (Figs 6, 31). The fastigium as a result of splitting the exine apart, is visible at the equator (Fig. 31).

Exine: Total exine thickness is 1,5-1,6 μm in the centres of mesocolpia; composed of 2 layers in LM examination (Fig. 30). The SEM subunits of the exine appear as follows: nexine covers 0,3-0,4 μm , columellae 0,2-0,3 μm and tectum with supratectal elements varies from 0,6 to 0,7 μm thick (Figs 6, 7).

Ornamentation: Striate both in LM and SEM examination (Figs 5-6, 31). The muri are running longitudinally, slightly sinuous on the mesocolpium and parallel to the colpus in its surroundings. They are 2,5-5,5 μm long; equal in width, approximately up to 0,15 μm on their blunt tops. The ends of the muri are acute and the pairs of them often connect in anastomoses or merge into the perforate tectum separately. The anastomoses range is 3-7 along a section of 10 μm . The grooves between the muri are often as thick as the muri and almost as long, with the perforations measure up to 0,08-0,1 μm in diameter.

Rubus laciniatus Willd.

Pollen grains are small. Equatorial outline circular to 3-lobed; meridional outline elliptical (Fig. 8; Table 2).

Apertures: Ectoaperture – colpus, not long and narrow, extending 76% length of polar axis; shallow, of acute/obtuse ends, with edges undifferentiated. The colpus constricted at the equator and its edges undulated. The equatorial bridge is wide, well developed with margins constricted (Fig. 8). The colpus membrane as well as the edges of the colpi with distinct granulations (Fig. 9). Endoaperture – porus, indistinct because of the equatorial bridge and its constricted margins (Figs 8-9, 33).

Exine: The exine total thickness is 1,5-1,6 μm in the centres of mesocolpia; composed of 2 layers in LM examinations (Fig. 32). SEM subunits have not been succeeded, however the perforate tectum is quite well visible (Fig. 9).

Ornamentation: Finely striate apparent in LM (Fig. 33) and SEM study. The muri are running mostly longitudinally, some are parallel to the colpus. In the mesocolpium they appear slightly sinuous and swirled towards the colpus. The muri are low, short, ca 1,3-3,5 μm long, narrow, approximately 0,16 μm wide on their blunt tops with acute ends, which merge into the perforate tectum occasionally. They anastomose in a frequency of 3-7 along 10 μm . The grooves between the muri, twice as wide as the muri and sometimes wider, with distinct perforations and microperforations measure up to 0,1

μm in diameter. The singular punctae between and on the muri are rarely observed (Fig. 9).

Series Discolores (P. J. Müller) Focke

Rubus armeniacus Focke

Pollen grains are small, equatorial outline circular, meridional outline elliptical to circular (Figs 10, 34, Table 2).

Apertures: Ectoaperture – colpus relatively long, with obtuse ends, extending 87% length of polar axis, sometimes joined across the pole. The widest part of the colpus is 1,3-1,6 μm near the porus. Colpus occasionally constricted at the equator; wide, distinct equatorial bridge is present (Figs 10, 35). The margins of equatorial bridge stretched, but ragged and sometimes united, therefore the porus and pore area is slightly visible (Fig. 10). The colpus with granulate membrane appears and numerous granulations are spread along the edges of the colpus (Fig. 11). Endoaperture – porus partly distinct, covered by ragged exine material and hidden under the equatorial bridge.

Exine: Total thickness of the exine is 1,2-1,3 μm in the centres of mesocolpia; 2 sublayers are distinct in LM examination (Fig. 34). SEM subunits measurements appear as follow: nexine 0,3-0,4 μm , columellae 0,3-0,4 μm and tectum with supracteal elements 0,6-0,7 μm thick (Figs 12-13).

Ornamentation: Striate in LM and SEM examination. The muri are arranged in loosely striate pattern, running mostly meridionally. In the vicinity of the colpus, the muri appear straight and parallel in the comparison to the mesocolpium, where they are more curved and sinuous (Figs 11-12). The muri are narrow, 1,2-3,8 μm long; 0,16 μm wide on their blunt tops, of acute ends, which merge into perforate tectum or anastomose and form distinct, wide grooves. The range of anastomoses is 1-6 along 10 μm length of the muri. The grooves between the muri are shallow, up to 0,4 μm wide, with perforations and microperforations dense; 0,05-0,1 μm in diameter. The numerous microgranulations (punctae) between and on the muri are observed. They seem to be an integral part of the sculpture (Figs 10, 11, 12, 35).

Series Hystices Focke

Rubus apricus Wimm.

Pollen grains are small; equatorial outline circular, meridional outline elliptical (Figs 14-15, 36-37, Table 2).

Apertures: Ectoaperture – colpus, relatively short, extending 77% length of polar axis, of obtuse ends. The colpus edges are undulated, undifferentiated; colpus constricted at the equator. The colpi are 2,0-2,12 μm in their widest part near the equatorial bridge. The equatorial bridge distinct and wide with undulated margins, which are often constricted deep in the colpus. Colpus membrane covered with large granules. Endoaperture – porus partly distinct, because of equatorial bridge with margins constricted deep in the colpus (Figs 15, 37).

Exine: Total thickness of the exine is 1,6-1,7 μm in the centres of mesocolpia; 2 sublayers distinct in LM (Fig. 36). SEM micrographs of cross-section of the subunits have not been succeeded, but the perforate tectum is always present.

Ornamentation: Striate, both in LM and SEM observations. Muri are arranged loosely on the surface of the tectum. Their orientation is variable; they running mostly longitudinally in the centre of mesocolpium and turning to transversally near the poles of the grain and the inrolled edges of the mesocolpium. The muri are straight and sinuous, shallow, 2,2-5,6 μm

long and 0,21 μm wide on the blunt tops, with acute/obtuse ends, which often merge into perforate tectum or anastomose, creating remarkable wide grooves. The range of anastomoses is 4-8 a long of 10 μm length of the muri (Figs 14-15). Perforations and microperforations in grooves; measure up to 0,1 μm in diameter. The singular punctae between and on the muri are observed occasionally.

Series Glandulosi (Wimm. & Grab.) Focke

Rubus hirtus Waldst. & Kit. agg.

Pollen grains are small like previous examples; equatorial outline circular to subtriangular, sometimes 3-lobed; meridional outline elliptical (Figs 16, 38, Table 2).

Apertures: Ectoaperture – colpus is narrow and shallow, long, extending 86 % length of polar axis, with acute/obtuse ends with edges undifferentiated. Colpus constricted at the equator and makes the colpus membrane invisible, but it is probably granulate. The equatorial bridge wide, well developed with margins constricted. Endoaperture – porus is indistinct, because it is hidden under the equatorial bridge (Figs 16, 39).

Exine: Total exine thickness is 0,9-1,21 μm in the centres of mesocolpia, using LM, (Figs 17, 38). In apocolpium area exine measures up to 1,7 μm thick. The SEM subunits measurements present as follow: nexine 0,5-0,6 μm , columellae 0,5-0,7 μm and tectum with supracteal elements approximately 0,5 μm thick (Fig. 18).

Ornamentation: Scabrate in LM examinations (Fig. 39); more detail characteristics by SEM observations were taken, where the sculpture is striate-scabrate (Figs 16, 18). The muri are arranged mostly longitudinally; in the vicinity of the colpus, they are meandering and swirling towards its edges. The edges of mesocolpia are mostly finely inrolled. The muri are straight, slightly curved and branched, 2,5-4,5 μm long and 0,21 μm wide on their blunt tops. They often anastomoses on the top of columellae; the range is 4-7 along of 10 μm length of the muri (Fig. 18). The grooves between the muri approximately as wide as the muri and wider with perforations distinct, measure up to 0,1 μm in diameter. Numerous microgranulations (punctae) between and on the muri are present and they seem to be the integral part of the sculpture. The number of microgranulations increases on the equatorial bridges and near the colpi. Such distribution of sculpture elements indicates the striate-scabrate ornamentation.

Rubus pedemontanus Pinkw.

(Rubus bellardii Weihe)

Pollen grains are small, equatorial outline circular; meridional outline elliptical (Figs 19-20, 40-41, Table 2.).

Apertures: Ectoaperture – colpus relatively short, extending 78-80% length of polar axis, is narrow, shallow with obtuse ends. Colpus is partly constricted at the equator, 1,8 μm wide near the porus. (Figs 19-20). The equatorial bridge is present, not constricted with undulated and ragged margins. A lot of granules along the colpus edge as well as on the colpus membrane are observed (Figs 19-20). Endoaperture – porus, weakly distinct in a form of slit-like wholes, often hidden under the equatorial bridge, which is stretched and containing fragments of striate exine.

Exine: Total thickness of the exine is 1,6-1,7 μm in the centres of of mesocolpium, using LM. The SEM cross-sections appear the following thickness of the subunits: nexine

ca 0,5 μm , columellae 0,5 μm and tectum with suprategal elements 0,6 μm thick (Figs 22, 40).

Ornamentation: Finely striate, formed by long, parallel-sided muri, equal in width, running longitudinally and mostly parallel to the colpus (Figs 19, 20, 21, 22, 41). The muri are 4-5, 5 μm long and 0,25 μm wide on the blunt tops with acute ends, anastomosing rarely and creating long, narrow grooves. The grooves measure up to 0,2 μm wide; they are wider rarely with the comparison to *R. hirtus* and *R. apricus*. Perforations between the muri quite distinct and regular, sometimes partly hidden between them, measure up to 0,1 μm in diameter. There are singular punctae in the grooves and on the muri, irregularly spread all over the grain. Anastomoses range is 2-5 along of 10 μm length of the muri (Fig. 21).

Sectio Corylifolii Lindley

Subsectio Sepincoli (Weihe ex Focke) Hayek

Series Subradulae W.C. R. Watson

Rubus fabrimontanus (Sprib.) Sprib.

Pollen grains are small; equatorial outline circular, subtriangular, sometimes 3-lobed; meridional outline, elliptical (Figs 23, 42, Table 2).

Apertures: Ectoaperture – colpus is narrow and short, tapering towards pole, extending 70,6% length of polar axis, of acute ends. Colpus is constricted at the equator, the edges are not differentiated but slightly undulated. Equatorial bridge distinct with margins often constricted, filled up with large granules. Colpus membrane is also densely covered with granulations (Fig. 23). Endoaperture – porus indistinct, because of equatorial bridge, with margins often constricted. Large granules filling up the colpus at the equator. (Figs 23, 42).

Exine: Total exine thickness of the exine is 1,4-1,5 μm in the centres of mesocolpia. In LM observations, 2 distinct layers are appeared (Fig. 42). SEM subunits of exine are distinct and their thickness is presented as follow: nexine 0,35 μm , columellae 0,25-0,35 μm and tectum with sculptural elements 0,5 μm (Fig. 25).

Ornamentation: Striate in LM observations and finely striate in SEM. The muri are arranged meridionally and parallelly to the colpus. They are predominantly stright, parallel-sided, slightly curved, and equal in width, 4-6 μm long and 0,18 μm wide on their blunt tops. The muri are shallow and their ends anastomose more often than merging into perforate tectum. Pairs of the muri are frequently connecting and present compact pattern. The range of anastomoses is 1-3 along 10 μm length of the muri (Fig. 24). The grooves between the muri are long and very narrow, sometimes narrower than the muri are. Perforations and microporations, organized almost in one row, partly hidden by the muri, measure up to 0,1 μm in diameter. Occasionally singular punctae between and on the muri are observed.

DISCUSSION

Pollen grains of all *Rubus* species taken to the examinations were isopolar, radially symmetrical, 3-colporate like other *Rosaceae* pollen and clearly confirmed the previous investigation concerning with *Rosaceae* and *Rubus* pollen grains (Erdtman, 1962; Reitsma 1966; Eide 1981). The present studies were to fill up the information connecting with shape, size and morphology of the *Rubus* pollen grains in the light of

Reitsma's proposition of morphology for *Rubus idaeus* pollen subtype (1966).

SHAPE AND SIZE

The general outline of the grains were elliptical or suboblate in equatorial view; ratio P/E = 1,2-1,3 (Table 2) created this type of outline; circular to subtriangular in polar view. The glycerin jelly measurements (Table 2) indicated the range of variation in P, E, estimation and changes in shape and size. The equatorial outline seemed to be the most variable in *R. hirtus*, *R. laciniatus*, *R. gracilis* and it was connected often with the ability of constriction of colpus margins and distension caused by furrow expansion. *R. armeniacus* has shown the ability to distend, so the endoporus was visible despite of equatorial bridges. The harmomegathic state of the grain determined the shape of pollen, therefore it turned out to be a poor criterion for separating species.

The size of the grains of all taxa ranged between 20-28 μm in polar axis (P) and 15-23 μm in equatorial diameter (E), (Table 1). It classify the pollen types in the range of small grains (10-25 μm) according to Erdtman (1952). The biggest seemed to be *R. armeniacus*, *R. pedemontanus*, *R. fabrimontanus* and *R. divaricatus* the smallest one, due to P (polar axis length).

APERTURES

Ectoapertures: All examined *Rubus* pollen grains appeared to have long, acute or obtuse ended colpi, covering 70-90% length of polar axis, approximately 2,1 μm in their widest part near the pori (*R. apricus*). The longest colpi occurred in *R. divaricatus* and *R. nessensis* (88-90 %), the shortest in *R. fabrimontanus*. The furrows tapering to acute ends in *R. nessensis* and *R. gracilis*, rare joined across the pole. The colpus membrane was granulate in most species, although it was sometimes partly visible. This was caused by the constriction of the colpus along the whole its length (*R. gracilis*, *R. divaricatus*), or partly constricted colpus at the equator. Colpi constricted at the equator characterized the other examined species. This was the consequence of well developed equatorial bridges, which, with their constricted edges, made the pori and pore area invisible (*R. hirtus*, *R. laciniatus*, *R. apricus*). These bridges were quite wide in their attachment to the edges of the colpi. Sometimes the stretched bridges were observed (their edges were not completely constricted), accompanied with their granulated, ragged margins (*R. pedemontanus*, *R. armeniacus*). Among the other representatives, (*R. fabrimontanus*, *R. divaricatus*) the equatorial bridges were not so well developed and their margins were constricted deep in the colpus.

Endoapertures: Pori have not been seen, except *R. armeniacus* and *R. pedemontanus*, where some dark slit-like wholes between the granulate, ragged edges of the equatorial bridge were visible. But these information were not enough to withdraw the conclusion about the shape and size of endoapertures.

ORNAMENTATION

..."Sculpturing is the most important distinguishing character in rosaceous pollen" (Eide, 1981). Generally, sculpturing confirmed the Reitsma's *Rubus idaeus* pollen subtype, although the pollen differed in the type of striae and their orientation. The muri were narrow, parallel-sided, 1,2-5,6 μm long, more or less equal in width, approximately 0,15-0,25 μm wide on their blunt tops in most of the species, except for *R. nessensis*, where the muri were 0,3- 0,4 μm wide.

First type of the striate grain presented long, predominantly stright, slightly branched muri, usually parallel each other,

TABLE 1. Summary of the pollen characteristics of some *Rubus* taxa in Poland. Abbreviations according to drawings (Figs A, B).

Species	Size Px E µm	Meridional. outline	Equatorial. outline	Equatorial. bridge	Apertures	
					Pori and pore area	Colpi
<i>R. apricus</i>	22,4 x 18,3	elliptical	circural	Equatorial bridge present, and wide;	indistinct;	colpus constricted at the equator; 2,1 µm wide; with undulated edges; membrane of the colpus, granulate; colpi extending 77% length of polar axis;
<i>R. armeniacus</i>	24,9 x 20,1	slightly elliptical to circular	circular	equatorial bridge present, wide, with margins stretched and ragged, occasionally constricted;	porus and pore area slightly distinct;	long, sometimes joined across the pole; 1,3-1,6 µm wide; constricted at the equator; colpus membrane granulate; extending 87% length of polar axis;
<i>R. divaricatus</i>	21,3 x 16,6	elliptical	circular to 3-lobed	equatorial bridge present, with edges constricted deep in the colpus;	the pore area and porus not visible;	long, wide, the colpus edge strong undulated; granulate membrane of the colpi; 90% length of polar axis;
<i>R. fabrimontanus</i>	23,7 x 19,0	elliptical	circular, subtriangular to 3-lobed	equatorial bridge wide, with margins constricted at the equator;	pore area and porus invisible;	colpi are narrow with acute ends, shallow; edges not differentiated; colpus with granulate membrane, short, extending 70,6% length of polar axis;
<i>R. gracilis</i>	23,7 x 18,1	elliptical	circular to subtriangular	equatorial bridge present with margins constricted;	pore area slightly distinct, porus indistinct;	long, narrow, 1,2 µm in the widest part; acute, sometimes joined across the pole; edges of the colpus undulated; granulate membrane of the colpus distinct; extending 86-90% length of the polar axis;
<i>R. hirtus</i>	21,6 x 16,9	elongated elliptically	circular to subtriangular	equatorial bridge present, wide and well developed with margins constricted at the equator;	pore area and porus indistinct;	long, narrow and shallow, acute/obtuse ends; edges of the colpus slightly undulated colpus constricted at the equator, with granulate membrane; extending 86% length of polar axis;
<i>R. laciniatus</i>	22,7 x 18,2	elliptical	circular to 3-lobed	equatorial bridge present, wide, well developed; its margins are constricted at the equator;	pore area and porus invisible, hidden under the equatorial bridge;	not long, shallow with obtuse ends, constricted at the equator; edges undulated, colpus membrane with large granulations; extending 76% length of polar axis;
<i>R. nessensis</i>	21,4 x 17,6	slightly elliptical	circular	equatorial bridge present;	pore area and porus indistinct;	long, shallow, narrow with acute ends; 1,2 µm in the widest part; granulate membrane of the colpus; extending 88% length of polar axis;
<i>R. pedemontanus</i>	23,6 x 19,6	elliptical	circular	equatorial bridge present, with margins stretched, granulated, ragged and undulated;	porus and pore area weak distinct, visible in a form of slit-like whole between the equatorial bridge and its edges;	short with obtuse ends; 1,8 µm in the widest part; edges of the colpi undulated; colpus constricted at the equator; membrana with numerous granulations; extend 78% length of polar axis;

Ornamentation	The orientation of the muri	Anastomoses range per 10 μm	Exine thickness (μm)	Exine subunits thickness (μm)	Morphological variability
striate, often shallowly striate, muri are loosely lying on the tectum surface; perforations and microperforations in grooves between the muri;	variable: in the mesocolpium they are sinuous and arranged almost transversally; parallel to the colpus near the colpus area; muri are 2,1-5,6 μm long; 0,21 μm wide;	4-8	1,6-1,7	not measured	little; in degree of porus shape (in the meaning of constricted and unconstricted equatorial bridges;
striate; perforations and microperforations in the grooves between the muri, dense and distinct; microgranulations (punctae) are spread on all over the grain occasionally;	mostly arranged longitudinally; the muri not compact; some stright are parallel to the colpus; the other curved and sinuous, interweave each other; narrow, 1,2-3,8 μm long and 0,16 μm wide;	1-6	1,2-1,3	columellae: 0,3-0,4 nexine: 0,4-0,5 tectum+supratectal elements (microgranulations): 0,6-0,7	very regular in shape, sometimes colpi united on the pole, not constricted equatorial bridges;
shallowly, finely striate; muri swirling slightly; perforations and microperforations in grooves between the muri;	the arrangement of the muri variable: swirling slightly along the mesocolpium and turning meandrically towards the edge of the colpus;	3-4	1,4-1,5	unknown	little variation in shape;
finely striate; the muri are long; create compact pattern with long narrow grooves in between; numerous perforations and microperforations dense, partly hidden between the muri;	the muri orientated meridionally, parallel to the colpus; they are narrow and very compact, parallelly orientated each other; 4-6 μm long, 0,18 μm on their blunt tops;	1-3	1,4-1,5	columellae: 0,25-0,35 nexine: 0,35-0,4; tectum: 0,4-0,5	very regular pollen grains; little variation, sometimes pollen grains are collapsed;
striate; the muri and the grooves about the same width in slightly sinuous arrangement; perforations and microperforations distinct between the muri;	the muri mostly parallel to the colpus; slightly sinuous on the mesocolpium; swirling on the poles; 2,5-5,5 μm long and 0,15 μm wide with obtuse ends often merge into perforate tectum;	3-5	1,5-1,6	columellae: 0,24-0,3 nexine: 0,35-0,4 tectum: 0,6-0,7	little variation in shape;
striate-scabrate; long, branched muri form wide grooves with perforations; numerous punctae between and on the muri are distinct, dispersed on all over the grain and fill up the scabrate sculpture;	muri orientated mostly longitudinally; meandering in the vicinity of colpus; they are stright and curved; 2,0-4,5 μm long, 0,21 μm wide;	4-7	mesocolpium: 0,9-1,2 apocolpium: 1,6-1,7	columellae: 0,5-0,7 nexine: 0,5-0,6 tectum: 0,5-0,6	not so much variation; grains could collapse in glycerin jelly
finely striate; the muri are narrow and slightly compact; the grooves wider than the muri with numerous microperforations and perforations; some singular punctae betwen and on the muri are distinct;	muri running longitudinally, forming slightly sinuous pattern; they are parallel each other and to colpus; short, narrow, 1,3-3,5 μm long; 0,16 μm wide, with blunt tops;	3-7	1,5-1,6	unknown	regular, distinct, equatorial bridges without variation;
striate; the arrangement of the muri reminiscent of „finger prints” pattern especially on the mesocolpium area; distinct thickenings in the place of anastomosing; the grooves are narrow with numerous perforations;	the muri not compact; orientated irregularly; running parallel to the colpus and meandering on the mesocolpium; short, 1,5-3,8 μm long and 0,3-0,4 μm wide on the top of thickenings;	5-8	1,3-1,4	difficult to differentiate;	regular and tend to have small variation in size and the composition of colpi;
finely, shallowly striate; formed by stright parallel-sided, compact muri and narrow grooves; perforations between the muri;	muri are mostly orientated longitudinally, parallel to each other and to the colpus; they are 4-5,5 μm long and ca 0,25 μm wide on the blunt top;	2-5	1,5-1,6	columellae: 0,5-0,6 nexine: 0,4-0,5 tectum: 0,5-0,6	very regular in shape, distinct, short colpi, equatorial bridges partly constricted;

TABLE 2. The measurements of examined *Rubus* pollen grains in glycerine-jelly. The abbreviations of P, E are explained in drawings (Figs A, B); Sp, Se indicates the standard deviation of P and E respectively.

Species	P x µm	Range P µm	Sp	E x µm	Range E µm	Se	P/E	Exine µm
<i>Rubus apricus</i>	22,4	19-25	2,4	18,3	16-21	1,6	1,2	1,6-1,7
<i>Rubus armeniicus</i>	24,9	22-28	1,8	20,1	18-21	1,1	1,2	1,2-1,3
<i>Rubus divaricatus</i>	21,3	20-24	1,1	16,6	15-21	1,4	1,3	1,4-1,5
<i>Rubus fabrimontanus</i>	23,7	21-26	1,6	19,0	17-21	1,3	1,3	1,4-1,5
<i>Rubus gracilis</i>	23,7	22-25	1,0	18,1	16-20	1,3	1,3	1,5-1,6
<i>Rubus hirtus</i>	21,6	21-24	1,5	16,9	16-18	0,9	1,3	0,9-1,2
<i>Rubus laciniatus</i>	22,7	19-27	4,61	18,2	16-19	1,0	1,3	1,5-1,6
<i>Rubus nessensis</i>	21,4	19-24	1,2	17,6	14-20	1,5	1,2	1,3-1,4
<i>Rubus pedemontanus</i>	23,6	21-27	1,5	19,6	16-23	1,7	1,2	1,4-1,5

compact and arranged meridionally. They anastomosed very rare, nearly twice. The grooves were long and narrow, often as wide as the muri. Perforations distinct, but sometimes partly hidden between muri and measure up to 0,15 µm in diameter (*R. pedemontanus* and *R. fabrimontanus*). Very similar ornamentation was presented by *R. laciniatus*. The muri were shorter than the previous examples, parallel each other, slightly sinuous orientated along the mesocolpium.

The second sculptural type presented *R. apricus* and *R. armeniicus*. The muri appeared predominantly curved. They were loosely lying on the surface of the tectum. The orientation of the muri was variable: in the vicinity of colpi, the muri were running meandrically and somewhat parallelly; on the mesocolpium, they were more transversally orientated. The frequency of anastomoses was variable and high: 1-8 per 10 µm length of the ridge. The grooves between the muri were shallow and wider than muri very often (sometimes 4 times wider than muri and measure up to 0,4 µm in width). Perforations were well distinct and numerous punctae between and on the muri, especially for *R. armeniicus*, were observed. The same type of ornamentation, but with more compact, also transversally orientated muri appeared *R. gracilis* and *R. divaricatus*.

The separate, third type of striate ornamentation occurred in only one species – *R. nessensis* hitherto. The muri appeared short; 1,3-3,8 µm long, curved, distinctly thickened in the place of connections, arranged in meanders especially on the mesocolpium, resembling the "finger prints" pattern (Punt, l.c.). The grooves between the muri were very narrow with distinct perforations in the tectum.

The last type of sculpture, has been separately described for *R. hirtus*. The ornamentation presented striate-scabrate pattern. The muri were orientated mostly longitudinally. They were stright and curved, branched, anastomosed often (4-7 along 10 µm length of the ridges), creating remarkable wide grooves (Figs 16, 18, Table 1). The grooves between the muri, were filled up with numerous punctae, which were the integral part of exine. Perforations were also distinct. This type of *Rubus* pollen ornamentation has not been reviewed yet.

EXINE

The glycerin jelly measurements showed not so much variation in exine thickness in the centres of mesocolpia. The range was 1.2-1.7 µm for different species. The thickest exine seemed to have *R. apricus*. *R. hirtus*, *R. nessensis* and *R. fabrimontanus* had the thinnest exine among the examined species. The results of SEM subunits measurements are presented in Table 1. There was not distinct variation between nexine thickness in all species; *R. hirtus* and *R. pedemontanus*, appeared to have relatively high collumelae layer (0,5-0,7 µm) in the comparison to *R. gracilis* and *R. fabrimontanus*: 0,24-0,35 µm; (Table 1, Figs 17, 22; 6, 25). Tectum layer with supratectal elements was distinctly thick for *R. armeniicus* and *R. gracilis* (Table 1; Figs 6, 12, 13; 30, 34). The thickness of the exine was variable for grain: thicker on the poles and thinner in mesocolpium area as it was showed for *R. gracilis* (Fig. 6) and *R. hirtus* (Table 1).

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EXPLANATION OF PLATES

Rubus pollen, SEM and LM photographs. On different photo bar is referred to magnification.

Figs 1-3 (SEM); 26, 27 (LM). *R. nessesensis* Hall. Polar view of the grain, (1). Distinct thickenings in the place of anastomosing of meandering muri (*arrow*) (2). Undifferentiated layers of exine (3). Meridional outline, thin exine (26). Striate ornamentation with meandering muri, thickenings (*arrow*). Equatorial bridge is visible (27).

Figs 4 (SEM); 28, 29 (LM). *R. divaricatus* P.J. Müll. Polar and equatorial view of the grain, undulated colpus edge, granulate membrane of the colpus, equatorial bridge with margins constricted deep in the colpus (4). Meridional outline of the smallest grain, (28). Finely striate sculpture (29).

Figs 5-7 (SEM); 30, 31 (LM). *R. gracilis* J. Presl & C. Presl. Polar view showing colpi, fused on the pole (5). Cross-section of exine, the details are distinct (7). The pore with equatorial bridge, meridionally and sinuously orientation of the muri (5, 6). Meridional outline (30). The apparent striate pattern, equatorial bridges with margins constricted (31).

Figs 8-9 (SEM); 32-33 (LM); *R. laciniatus* Willd. Equatorial and diagonal view of the grain; well developed equatorial bridge and sinuous orientation of the muri are shown (8). Details of the sculpture; frequency of anastomosing and some microgranulations are seen on Fig. 9. Meridional outline, endoaperture, (*arrow*) (32). Details of the sculpture (33); apparent striate pattern, variable orientation of the muri, (*arrow*). Equatorial bridge well developed, (*arrow*), (33).

Figs 10-13 (SEM); 34, 35 (LM). *R. armeniacus* Focke. Polar and equatorial view, showing not completely constricted colpi, some of them almost fused on the pole (10). Distinct microgranulations along a colpus edge and microgranulations (punctae) spread on all over the surface (11). Variability in the muri orientation (4); Densely perforated tectum and cross-section through the exine, (12, 13). Meridional outline (34); Striate ornamentation with distinct punctae on the surface and equatorial bridge (*arrow*), (35).

Figs 14-15 (SEM); 36-37 (LM). *R. apricus* Wimm. Polar view, showing partly transversal orientation of the muri (14); equatorial view, well developed equatorial bridge with margins constricted, (15). Meridional outline, exine thickness and colpi distinct (36). Sculpture of the grain, equatorial bridge not completely constricted, visible (*arrow*), (37).

Figs 16-18 (SEM); 38-39 (LM). *R. hirtus* Waldst. & Kit. agg. Equatorial view, showing wide, very well developed equatorial bridges with constricted edges (*arrow*) (16). Straight and curved orientation of muri, filled up by numerous punctae, create the striate-scabrate pattern (18). The cross-section of the exine, (17). Meridional outline, regularly elliptical (38). Striate-scabrate sculpture is visible in a view of dark punctae, (*arrow*) and equatorial bridge (39).

Figs 19-22 (SEM); 40-41 (LM). *R. pedemontanus* Pinkw. Diagonal view of the grain (19). Equatorial view of the grain, undulated edges of the colpi, equatorial bridge, (20). Details of the sculpture, meridionally orientated, compact muri with perforation in between (21). Cross-section of the exine, (22). Meridional outline showing endoapertures (40). The details of the sculpture e.g. the bridges (41).

Figs 23-25 (SEM); 42-43 (LM). *R. fabrimontanus* (Sprb.) Sprb. Equatorial view with equatorial bridges; the granulate membrane of the colpus (23). Meridional orientation of the muri, parallel each other; compact muri, separated by narrow grooves with dense perforations (24). The cross-section of the exine (25). Meridional outline of the grain (42). Apparent finely striate pattern and equatorial bridge constricted (43).

Figs 1-7 (for description see p. 9)

Figs 8-13 (for description see p. 9)

Figs 14-19 (for description see p. 9)

Figs 26-31 (for description see p. 9)

Figs 32-37 (for description see p. 9)

Figs 38-43 (for description see p. 9)

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MORFOLOGIA PYŁKU RODZAJU *RUBUS* L. I.WSTĘPNE BADANIA NAD EUROPEJSKIMI PRZEDSTAWICIELAMI PODRODZAJU *RUBUS* L.

STRESZCZENIE

W niniejszej pracy przedstawiono wyniki badań nad morfologią pyłku 9 Europejskich gatunków jeżyn (*Rubus* L.: *R. apricus*, *R. armeniacus*, *R. divaricatus*, *R. fabrimontanus*, *R. gracilis*, *R. hirtus*, *R. laciniatus*, *R. nessensis* i *R. pedemontanus*). Badania te opierały się na analizie mikroskopowej skaningowej po raz pierwszy dla tego rodzaju w Polsce oraz na analizie ziarn pyłku pod mikroskopem świetlnym. Wszystkie obserwowane ziarna pyłku były małe, izopolarne, trójbruzdowe z porami w bruzdach w płaszczyźnie równika. Wszystkie ziarna pyłku jeżyn, za wyjątkiem *R. armeniacus* i *R. gracilis* miały długie bruzdy (colpi). Zaciśnięte mostki równikowe ziarn pyłku spowodowały, że pory (pori) były niewidoczne u większości gatunków. U gatunków: *R. apricus*, *R. armeniacus*, *R. gracilis* i *R. pedemontanus* mostki równikowe były rozciągnięte i dlatego widoczny był ciemny otwór jako ślad istniejącej pory. Urzeźbienie ziarn pyłku potwierdziło wzór *striate* (prążkowany) a orientacja prążków (*muri*) wskazała na różnice pomiędzy gatunkami; ziarna pyłku *R. pedemontanus* i *R. fabrimontanus* posiadały długie, zwarte *muri* o przebiegu południkowym i równoległe zorientowane do bruzdy. Urzeźbienie *R. nessensis* ukazało *muri* ułożone meandrycznie, przypominające wzór „linii papilarnych”, z wyraźnymi zgrubieniami w miejscach połączeń oraz liczne, wąskie, perforowane przestrzenie pomiędzy prążkami (*grooves*). Powierzchnia ziaren *R. hirtus* ukazała prążkowanymi-ziarnistą (*striate-scabrate*) skulpturę z powodu ziarnistych elementów (*punctae*) rozproszonych na całej powierzchni ziaren, będących jakby integralnymi częściami egzyny. Kształt i wielkość ziarn okazały się słabym kryterium dla identyfikacji gatunków.