POLLEN MORPHOLOGY OF GENUS RUBUS L.  
PART III. STUDIES ON THE MALESIAN SPECIES 
OF SUBGENERA CHAMAEBATUS L. AND IDAEOBATUS L. 

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ABSTRACT  
The results of pollen morphology of Malesian Rubus species are presented. The pollen samples represented 2 subgenera; 2 species of subgenus Chamaebatus (R. calycinus, R. pectinellus) and 13 species of subgenus Idaeobatus (R. acuminatissimus, R. alpestris, R. archboldianus, R. chrysogaeus, R. copelandii, R. ellipticus, R. ferdinandi-muelleri, R. fraxinifolius, R. niveus, R. lorentzianus, R. macgregori, R. montis-wilhelmi, R. papuanus). The examination of these species has been made by SEM for the first time and also by LM. Detailed descriptions of the pollen grains are given. As in the majority of Rubus species, pollen grains of both subgenera are isopolar and trizonocolporate. The pollen grains were small for some species of the subgenus Idaeobatus only, medium for both subgenera: Chamaebatus and Idaeobatus. The thickest exine was observed among the species of subgenus Chamaebatus and in R. macgregori of subgenus Idaeobatus. The ornamentation of the studied pollen has shown a great variability. Except for the typical striate ornamentation of the genus, rugulate (R. archboldianus), striatescabrate (R. lorentzianus) and striate-rugulate (R. macgregori) ornamentation has been observed. 

New Guinean morphologically similar pinnate Rubus ferdinandi-muelleri, R. montis-wilhelmi, R. papuanus, have pollen with specific type of striate pattern, which is characterised by relatively high muri with variable thickness and lumina filled with granules. Some of their muri resemble baculate typical only for R. chamaemorus. The pollen morphology analysis leads to the conclusion that Rubus montis-wilhelmi and R. papuanus of subgenus Idaeobatus are the closest related species and morphologically very close to R. ferdinandi-muelleri. Since Focke placed the latter species in section Pungentes of the subgenus Idaeobatus, and the two first species were unknown to him – the authors suggest to include them into this section. 

Despite of the different origin and various types of leaves R. chrysogaeus, R. acuminatissimus and R. niveus have shown similarities in pollen morphology and are grouped together. On the basis of the same criteria, R. copelandii, R. ellipticus and R. fraxinifolius could have been grouped together, as well as R. alpestris and R. macgregori. Trifoliolate R. archboldianus and R. lorentzianus have not shown similarities of pollen ornamentation to each other and to the previous mentioned species. 

KEY WORDS: Rubus subgenus Chamaebatus, Idaeobatus, pollen morphology, SEM, LM. 

INTRODUCTION  
Continuing the review of Rubus pollen diversity among Malesian species, the subgenera Chamaebatus and Idaeobatus have been studied. The species of subgenus Chamaebatus occur in America (NW America and Mexico) and in Asia (China, Taiwan, Japan, Philippines, and Java). Among the five species distinguished by Focke (1911) in this subgenus, two species occur in Malesia. 

According to Kalkman’s description (Zande and Kalkman 1981), the small subgenus Chamaebatus comprises small creeping plants with simple, reniform to cordate lea-
ves, rarely more deeply incised. Stipules are free, flowers bisexual, solitary terminal, rarely 2-3 on erect laterals. Fruits are loosely cohering, becoming loose from the torus, when ripe. The area of distribution is disjunct.

Subgenus *Idaeobatus* includes about 100 species grouped in 9 sections (Focke 1911). The great majority is in Asia, Australia and islands in the Pacific Ocean. Some species occur in Africa and Madagascar and islands in the Indian Ocean. Few species are found in Central America and only one in Europe (*R. idaeus*). The Malesian species are mostly mountainous and are rarely found below 1000 m. Brambles of this subgenus are shrubs, erect or climbing. Leaves are palmately 3 to 5-foliolate, rarely simple. Stipules at the base of the petiole are persistent. Fruits occur in thyrsoid inflorescences. Fruits are cohering, becoming loose from the torus, when ripe. The species of subgenus *Idaeobatus* represent 4 sections distinguished in particular description of *Rubus* pollen. The present study describes the pollen of 13 species among the 18 dealt with by Kalkman and Zandee (1981). Pollen of the other 5 species was not available.

**MATERIAL AND METHODS**

Pollen samples were taken from dried material, present in the Nationaal Herbarium Nederland, Leiden. The method of preparing pollen for study was presented in previous papers (Tomlik-Wyremblewska 1993, 2000). The pollen morphological descriptions and the terminology used in the present paper are in accordance with those papers (Tomlik-Wyremblewska I.c.) and the literature quoted therein (Erdtman 1952; Ham 1990; Hebda et al. 1988; Hebda et al. 1987; Moore et al. 1991; Punt et al. 1974; Clarke et al. 1978; Heath 1984).

**Pollen Descriptions**

**SUBGENUS CHAMAEBATUS**

As mentioned before, only two species occur in Malesia, usually at altitudes between 750 and 2600 m in different types of forest.

The general morphology of *Rubus* pollen has been described already by Erdtman (1952), Reitsma (1966), Eide (1981), Moore et al. (1991), and also in the paper on *Rubus* subgenus *Rubus* and *Micranthobatus* pollen (Tomlik-Wyremblewska 1993, 2000). The latter general description pertains also to subgenus *Chamaebatus*. The differences are in the ornamentation of the pollen, development of the equatorial bridge and distinctness of the pori. The following presents description of the pollen of the individual species.

*Rubus calycinus* D. Don

This species from Nepal and Java has medium-sized pollen grains (PxE: 33.6x22.8 µm), according to the Erdtman’s classification (Erdtman 1952), elliptical in meridional outline, P/E ratio is 1.34 (Fig. 1A; Figs 5, 6) and circular to 3-lobed in equatorial outline (Fig. 1B). The 3-lobed outline is rare because the colpi are not constricted (Fig. 1A, B).

**Apertures:** Ectoapertures – colpi long, ca 85% of polar axis, tapering towards the poles (Figs 1, 5). The widest part of the colpus is near the porus. The width is about 4.4 µm and is the largest of the examined species, which occur in Malesia: *Rubus calycinus* and *R. pectinellus*. It makes the colpus membrane very well visible. Colpus membrane granulated (Fig. 1B, marked by arrow). Margins of the colpus undifferentiated.

**Endoapertures – pori, distinct in some grains, usually covered by the equatorial bridge (Fig. 1A, arrow).**

**Exine:** The total thickness of the exine is 1.7 to 1.8 µm in the centre of mesocolpia. In LM (Fig. 6) and SEM examination (Figs 3, 4) indicates 3 sublayers: tectum with supratectal elements (Fig. 4A), infratectum – columnellae layer (Fig. 4B) and nexine (Fig. 4C) These layers have not been measured. The perforations are present on the tectum: there are mostly microperforations (Fig. 2).

**Ornamentation:** Finely striate both in LM and SEM. Muri oriented in different directions on the pole and in the mesocolpium area. In the apocolpium the muri are meandering, loose by laying on the perforate tectum; whereas in the mesocolpium, muri are oriented parallelly to the equator and often meandering, resembling a finger tip pattern (Figs 1, 2). Muri are mostly short and short, with high variation in thickness. They anastomose very often (the anastomose index is 4-5 connections per 10 µm length of a murus). The meandering muri separate the relatively wide grooves, where perforations in tectum are quite distinct (Figs 2, 3) and the muri often merge into the tectum. Muri anastomose by flat connections, which causes the characteristic pattern (Figs 1, 2).

*Rubus pectinellus* Maximowicz

This species from primary and secondary forest in the Philippines has small to medium pollen grains (PxE: 26.1x22.5 µm), elliptical to circular in meridional outline (P/E ratio 1.16) (Fig. 11), circular in equatorial outline (Fig. 7).

**Apertures:** Ectoapertures – colpi long, approximately 85% of polar axis, wide, not constricted, the equatorial bridge not closed, showing the porus very often. Colpus membrane well visible and granulated (Fig. 7).

Endoapertures – pori distinct, sometimes covered by the undifferentiated edges of the colpi.

**Exine:** The total thickness of the exine in the centres of mesocolpia is 1.9 µm. In LM examination 3 sublayers are distinct (Figs 11, 12). The exine sublayers have not been observed with SEM, but the perforate tectum is quite well distinct (Fig. 8).

**Ornamentation:** Striate both in LM and SEM examination (Figs 7-10). Muri running in different directions: parallelly in apocolpium and along the colpi; curving and meandering in the mesocolpia area (Figs 7, 8). Muri are compactly arranged, with narrow grooves in-between. They are short, equal in width and height, anastomosing often; the anastomose index is approximately 6-7 connections per 10 µm of a murus, the thickenings at the place of anastomoses are present. Density of the perforations is high and they are distinct in the tectum (Fig. 8).
Figs 1-6. *Rubus calycinus* pollen.
Fig. 1. (SEM). Pollen grains arranged in different direction; the equatorial view (A) and polar view (B) distinct; not constricted colpi, finely striate ornamentation, colpus membrana (arrow) and equatorial bridges distinct (arrow).
Fig. 2. (SEM). Details of striate ornamentation and muri features.
Fig. 3. (SEM). Cross-section of the exine in mesocolpium area. Magnification of the fragment marked.
Fig. 4. (SEM). Cross-section of the exine in mesocolpium area. The 3 sublayers distinct: A – tectum and supratablectal elements, B – infratectum: collumelate layer, C – nexine.
Fig. 5. (LM). Equatorial view, striate ornamentation on mesocolpium distinct (×1000).
Fig. 6. (LM). Equatorial view with stratification of the exine distinct (×1000).

**Remarks:** The pollen grains of the two representatives of subgenus *Chamaebatus* have two different patterns of ornamentation, not common with the species of already examined subgenera (Tomlik-Wyremblewska 1995, 2000).

**Subgenus Idaeobatus** (Focke) Focke
The general pattern of *Rubus* pollen (Erdtman 1952; Reitsma 1966; Punt et al. 1974; Clarke et al. 1978; Eide 1981; Heath 1984; Hebda et al. 1987, 1988; Moore et al. 1991;
Tomlik-Wyremblewska 1995, 2000) applies also to subgenus *Idaeobatus*. The particular diagnosis of the species are as follows:

**Rubus acuminatissimus** Hasskarl
Sect. *Rosae folii*

This species occurs in a very restricted area: in Java and Sumatra only. Its pollen grains are small (P×E: 19.7×14.2 μm); elliptical in meridional outline (Figs 13, 17); circular to trilobed in equatorial outline (Figs 13, 18).

**Apertures:** Ectoapertures – colpi long, 84.3% length of polar axis, with acute ends, often caused by constricted edges of the colpi (Figs 13, 14 arrow, 16, 17). Colpus membrane granulated, the equatorial bridges distinct and usually constricted (closed), which makes the porus area invisi-
Figs 13-18. Rubus accuminatissimus pollen.

Fig. 13. (SEM). Pollen grains arranged in different directions. Polar view and equatorial view distinct.
Fig. 14. (SEM). Details of the ornamentation of the exine. Large grooves with perforations distinct.
Fig. 15. (LM). Polar view. Striate ornamentation on the polar area and apocolpium distinct, equatorial bridges not constricted, marked by arrow (×1000).
Fig. 16. (LM). Equatorial view. Striate ornamentation on the mesocolpium distinct (×1000).
Fig. 17. (LM). Equatorial view. Meridional outline with layers of the exine partly distinct (×1000).
Fig. 18. (LM). Polar view. Equatorial outline and stratification of the exine distinct, marked by arrow (×1000).

ble (Figs 13, 14, 16). In Figs 13, 15, the stretched bridge is visible, occasionally showing porus (marked by arrow). Colpus margins undifferentiated.

Endoapertures – pori: rarely visible, because of equatorial bridge (Figs 13 arrow, 14, 16).

Exine: Total thickness of the exine is 1.3 μm in the centres of mesocolpia (Figs 17, 18). In LM estimation 3 sublayers are distinct (Fig. 17), with SEM, sublayers have not been observed, but the perforate tectum is distinct (Figs 13, 14).

Ornamentation: Finely or loosely striate. Muri running perpendicularly to the colpi on mesocolpia and near the apocolpia, and meandering in the equatorial bridge surroundings. The arrangement of the muri is variable. Muri are equal in width, ca 0.18 μm, loosely laying on the tectum
and anastomosing; the anastomose index is approximately 5-8 connections per 10 μm length of a murus. They alternate with shallow grooves with distinct arranged perforations (Figs 13, 14).

**Rubus alpestris** Blume

Sect. Alpestris

This widely distributed species from Thailand, Sumatra, Borneo, Java, Celebes, Moluccas has medium-sized pollen (PxE: 30.6x26.6 μm); meridional outline slightly elliptical to almost circular (Figs 19, 23), (the P/E ratio is 1.15); equatorial outline triangular. In Figs 21, 24 the oblique view is shown only, but the observation in SEM allows to observe the shape of the grains in polar view.

**Apertures:** Ectoapertures – colpi long, ca 80% of polar axis (Table 1), with acute ends. The margins of the colpus undifferentiated, not constricted. Colpus membrane granulated and distinct (Fig. 19, arrow B). Equatorial bridges present, not constricted. Endoapertures – lalongate pori, distinct, not covered by the equatorial bridges (Fig. 19, arrows A).

**Exine:** The mean total thickness of the exine is about 1.9 μm in the centres of the mesocolpia and the apocolpia. In LM examination 3 sublayers are visible (Fig. 23). SEM photographs have not been taken, but many perforations in the tectum are distinct (Figs 19, 20).

**Ornamentation:** Striate with muri arranged in a meandering pattern. The muri surround the porus area, and curve, meander in the mesocolpium, which somehow resembles the “finger tips pattern” (Fig. 20). Muri are 0.2-0.25 μm wide, almost equal in width, they anastomose very often (the anastomose index is 6-7 per 10 μm length of a murus). Muri are sometimes covered, with microgranules. Microgranules are often present also in the grooves. Perforations and microperforations usually distinct, not hidden by muri (Fig. 20).

**Rubus archboldianus** Merrill & Perry

Unknown section

This New Guinean species, from eastern part of the island only, has medium-sized pollen grains (PxE: 29.6x29.5 μm); meridional outline circular and sometimes slightly elliptic (Figs 25, 28, 29); P/E ratio is 1.0; equatorial outline circular to triangular in LM examinations (Fig. 27).

**Apertures:** Ectoapertures – colpi long, 80.4% of polar axis (Table 1), with acute ends. Colpus margins undifferentiated, not constricted; equatorial bridge distinct, with not constricted margins, which makes the bridge “opened” (Figs 25, 27).

Endoapertures – pori lalongate, not covered by equatorial bridges (Fig. 25, arrow).

**Exine:** The mean total thickness of the exine is 1.6 μm in the centres of the mesocolpia. With SEM sublayers have not been observed. In LM examination 3 sublayers are distinct (Fig. 29, arrow).

**Ornamentation:** Rugulate, supratectal elements are arranged in groups, which are orientated in different directions. Between the muri slit-like spaces and perforations are present (Figs 25, 26).

**Rubus chrysogaeus** van Royen

Sect. Rosaefolii

This New Guinean species has small-sized pollen grains (PxE: 17.4x16.2 μm), (Table 1); meridional outline elliptical to circular (Figs 31, 33); equatorial outline circular to trilobed which could be observed with SEM only.

**Apertures:** Ectoapertures – colpi long, 82.2% of polar axis, with acute ends. Colpus margins constricted on whole its length and undifferentiated, but granulate colpus membrane is present. Equatorial bridges well developed, wide and distinct, their constricted margins making the porus invisible (Figs 31 arrow, 32).
Endoapertures – pori indistinct, hidden under the equatorial bridges (Figs 31, 32).

Exine: Total mean exine thickness is approximately 1.3 μm in the centres of mesocolpia. With SEM, sublayers have not been observed. The tectum has perforations of variable diameter (Fig. 31). In LM examination 3 sublayers are distinct (Fig. 33, arrow).

Ornamentation: Striate; muri are running mostly longitudinally, showing loosely arranged pattern with wide grooves, filled by perforations of different diameter. Muri are short, unequal in width, often merging with perforations at the basis of the muri (Fig. 31). Granules are distinct in the colpus surroundings. Muri often branched; anastomose index is 7-8 per 10 μm length of a murus.


Fig. 19. (SEM). Pollen arranged in different directions, mostly in equatorial view. Porus area (A), colpus membrane distinct (B), marked by arrows.
Fig. 20. (SEM). Details of striate ornamentation, showing especially the “finger-tips” pattern.
Fig. 21. (LM). Oblique view. Apocolpium area, acute ends of the colpi, striate ornamentation distinct (×1000).
Fig. 22. (LM). Equatorial view. Ornamentation on the mesocolpium distinct (×1000).
Fig. 23. (LM). Equatorial view. Outline of the grain, stratification of the exine distinct and pointed (×1000).
Fig. 24. (LM). Oblique view. Outline of the grain distinct (×1000).
Rubus copelandii Merill
Unknown section

This species is only known from some mountains in Philippines. Its pollen grains are small (PxE: 25.0x21.8 μm); equatorial outline circular to trilobed (Figs 34, 40); meridional outline elliptical (Figs 35, 39).

Apertures: Ectoapertures – colpi long, ca 80% of polar axis (Figs 34, 37-39), with round and acute ends (depending on the constriction of the margins). The colpus margin undifferentiated, colpus membrane granulate. The granulae are sometimes also on the margins of the colpus. The equatorial bridges present, with not constricted margins, which makes the bridges “opened” and layers of exine as well as the porus distinct (Figs 34, 35, arrows).

Endoapertures – pori lalongate, usually distinct (Figs 34, 35, arrows).

Exine: The mean total thickness of the exine is 1.55 μm in the centres of the mesocolpia. LM examination
shows 3 sublayers (Fig. 39, arrow); with SEM, sublayers have not been observed, although the perforate tectum is quite distinct (Figs 35, 36).

Ornamentation: Compactly striate. Muri running longitudinally, of equal width, almost not separated from each other; only slit-like grooves present (Figs 35-37, 41). Muri anastomose very often. The anastomosis index is 7-9 connections per 10 μm length of a murus. Thickenings are often present at connections (Fig. 36).

Rubus ellipticus J.E. Smith
Sect. Idaeanthi

This widely distributed species has small pollen grains (PxE: 20.38×15.31 μm). Equatorial outline trilobed, rarely circular; meridional outline elliptical (Figs 42, 43).

Apertures: Ectoapertures – colpi long, 81.7% of polar axis, with acute ends. Colpus margins constricted over their whole length, which makes the colpus membrane invisible; probably as in the other Rubus pollen the membrane is granulate. Like in other Rubus species, the colpus margins might be undifferentiated. Equatorial bridge present, well developed, with constricted margins (Figs 42, 44 arrows). Ectoapertures – pori indistinct, hidden under the equatorial bridges (Figs 42, 44).

Exine: The mean total thickness of the exine is 1.4 μm in the centres of the mesocolpia. LM examination shows 3 sublayers (Fig. 43). With SEM, sublayers have not been observed, but perforations in the tectum are distinct (Fig. 42).

Ornamentation: Compactly striate. Muri running longitudinally and curving towards the colpus slightly, of almost equal width, except for places of anastomoses. The anastomosis index is about 6-8 connections per 10 μm length of a murus. Muri are compactly arranged and the perforations are distinct in the grooves (Fig. 42).

Remarks: Regarding ornamentation, R. ellipticus is similar to R. copelandii, but the equatorial bridges are well developed and constricted.

Rubus ferdinandi-muelleri Focke
Sect. Pungentes

Pollen grains of this New Guinean species are small (PxE: 17.27×11.20 μm). Equatorial outline based on SEM observation circular to trilobed; meridional outline elliptical (Fig. 45A). Unfortunately SEM and LM photographs of polar view are not available.

Apertures: Ectoapertures – colpi long, 81% of polar axis, with rounded ends. Colpus margins undifferentiated and constricted along their length. A few granules are occasionally situated there. Colpus membrane granulate. Equatorial bridges have not been observed with SEM (Fig. 45A), but in LM they were visible (Fig. 47 arrow). Endoapertures – pori indistinct because of constricted colpus margins (Fig. 45).

Exine: The mean total thickness of the exine is 1.2 μm in the centres of the mesocolpia. LM examination shows 3 layers of the exine (Fig. 48). SEM, sublayers have not been
Figs 34-41. *Rubus copelandii* pollen.

Fig. 34. (SEM). Pollen grains in various arrangement. Porus well distinct and marked.
Fig. 35. (SEM). Oblique orientation of the grain. Striate ornamentation, not constricted bridges and porus distinct and marked.
Fig. 36. (SEM). Details of striate ornamentation.
Fig. 37. (LM). Equatorial view, Ornamentation on mesocolpium distinct (×1000).
Fig. 38. (LM). Equatorial view, equatorial bridges well distinct (×1000).
Fig. 39. (LM). Meridional outline of the grain in equatorial view. Stratification of exine distinct and marked (×1000).
Fig. 40. (LM). Equatorial outline of the grain in polar view (×1000).
Fig. 41. (LM). Polar view. Ornamentation on the polar area and apocolpium distinct (×1000).

observed, but perforations in the tectum are obviously recorded (Fig. 46).

**Ornamentation:** Striate-like pattern with elements arranged mostly longitudinally. Muri very thick and of irregular width, with many thickenings along the muri or at the places of connections. There are bacula-like elements along the colpus margins (Fig. 45B, arrow).

**Remarks:** Thick, irregular muri have not been observed in the subgenera *Micranthobatus*, *Chamaebatus*, *Idaeobatus* (Tomlik-Wyremblewska 1995, 2000).
**Figs 42-44. Rubus ellipticus pollen.**

Fig. 42. (SEM). Equatorial view and striate ornamentation of the grain, well developed bridges distinct.
Fig. 43. (LM). Meridional outline. Stratification of the exine distinct and marked (×1000).
Fig. 44. (LM). Equatorial view. Ornamentation and equatorial bridges constricted distinct (×1000).

**Figs 45-48. Rubus ferdinandi-muelleri pollen.**

Fig. 45. (SEM). Pollen grain in oblique (B) and equatorial (A) view.
Fig. 46. (SEM). Details of the striate ornamentation; irregular muri distinct.
Fig. 47. (LM). Oblique orientation of the grain. Ornamentation on the mesocolpium distinct (×1000).
Fig. 48. (LM). Oblique orientation of the grain, outline and stratification of the exine distinct and marked (×1000).

**Rubus fraxinifolius** Poiret

Sect. *Rosaeoii*

This widely distributed species has small pollen grains (P×E: 17.9×14.9 μm); equatorial outline circular (Figs 49C, 54), meridional outline elliptical (Figs 49A, 53); (P/E index: 1.3), (Table 1).

**Apertures:** Ectoapertures – colpi long, 88% of polar axis, with acute ends. Colpus margins undifferentiated, fi-
nely undulated, constricted slightly in the equator. Equatorial bridges relatively poorly marked, which makes the porus visible (Figs 49, 52). Endoapertures – pori lalongate, partly hidden by equatorial bridge (Fig. 49, marked by arrow). Microgranules are often visible in porus and colpus surroundings (Figs 49, 50).

**Exine:** The mean total thickness of the exine is 1.3 μm in the centres of the mesocolpia. LM and SEM examination shows 3 distinct units: nexine, infractectum (columellate layer) and tectum with supratectal elements on SEM (Fig. 50 arrow) and LM (Figs 53, 54 arrows).
Ornamentation: Striate pattern with muri arranged meanderingly (Figs 49-52). The anastomosis index is average 7-9 per 10 μm length of a murus. Grooves with perforations and often filled with microgranules (Fig. 50).

*Rubus niveus* Thunb. (collected as *R. leucocarpus* Arnott) Sect. *Idaeanthi*

This widely distributed species in Malesia and continental Asia has small pollen grains (PxE: 24.95×18.9 μm). In LM and SEM examinations, equatorial outline circular to trilobed, what could be seen in oblique view also on Fig. 56; meridional outline elliptical (Figs 55, 58); P/E ratio 1.3.

Apertures: Ectoapertures – colpi long, 81.6% of polar axis, with acute ends. Colpus margins undifferentiated, slightly constricted along their length. Colpus membrane granulate; granules are distinct also on the colpus margins. Equatorial bridges hardly marked (Figs 55, 57, marked by arrows).

Endoapertures – pori not distinct, because of constricted colpus margins (Fig. 55).

Exine: Mean total thickness of the exine is 1.4 μm in the centres of the mesocolpia. LM examination shows 3 layers of the exine (Fig. 58). SEM sections have not been observed, although SEM details show a perforate tectum (Fig. 55).

Ornamentation: Loosely striate. Muri are arranged mostly longitudinally, turning towards the colpi. Muri separate wide grooves, filled with perforations. Muri anastomose 3-5 times in the length of 10 μm of a murus. They are equal in width except for the place of the connections, where thickenings are occasionally observed (Fig. 55). Granules are observed in the grooves along the colpus margins.

*Rubus lorentzianus* Pule

Unknown section

This New Guinean species has medium-sized pollen grains (PxE: 34.5×24.3 μm); equatorial outline circular to trilobed (Fig. 62), meridional outline elliptical (Figs 59, 60, 64, Table 1).

Apertures: Ectoapertures – colpi long, 86.2% of polar axis, with acute ends, constricted along all their length. Colpus margins undifferentiated. Colpus membrane granulate. Equatorial bridges distinct; their margins are constricted (Figs 59, 65 arrow).

Endoapertures – pori indistinct because of usually “closed” equatorial bridges (Figs 59, 63, 65).

Exine: Mean total thickness of the exine is 1.6 μm in the centres of the mesocolpia (Table 1, Figs 62, 64, marked by arrows). Details of exine stratification unknown, but the perforate tectum is distinct (Fig. 61).

Ornamentation: Striate-scabrate with muri running mostly perpendicular to the polar axis, although some change of arrangement of the muri can be observed, especially around the equator (Figs 59, 60, 63). Muri are thin in comparison to the previous species, equal in width, loosely arran-
Fig. 59. (SEM). Group of the pollen in oblique and equatorial view. Equatorial bridges constricted deep in the colpus.
Fig. 60. (SEM). Equatorial view of the grain. Striate-scabrate ornamentation distinct.
Fig. 61. (SEM). Details of the striate-scabrate ornamentation.
Fig. 62. (LM). Polar view, equatorial outline of pollen, stratification of the exine distinct and marked (×1000).
Fig. 63. (LM). Equatorial view, ornamentation distinct (×1000).
Fig. 64. (LM). Meridional outline of pollen in equatorial view, stratification of the exine distinct (×1000).
Fig. 65. (LM). Equatorial view, equatorial bridges constricted, marked by arrow (×1000).

Remarks: One of the biggest pollen grains among the examined species.

R. macgregori F. von Mueller
Unknown section
The occurrence of this species is restricted to mountains in Celebes and Papua New Guinea. Pollen grains are ± medium-sized (PxE: 29.8×28.9 μm), equatorial outline circular to trilobed, what could be seen on Fig. 68 and 71; meridional outline circular to slightly elliptical (Fig. 66). P/E ratio 1.03 shows circular shape of the grain (Table 1).
Apertures: Ectoapertures – colpi long, with acute ends, 80.2% of polar axis, usually constricted along the ends. Colpus margins undifferentiated and folded inwards (Figs 66, 69). Colpus membrane granulate. Equatorial bridges distinct with their margins constricted (Fig. 66, 69 arrows).

Endoapertures – pori indistinct because of equatorially constricted bridges (Fig. 66, marked by arrow).

Exine: The total thickness of the exine is 2.0 μm in the centres of the mesocolpia (Figs 70, 71). Exine is composed of 3 sublayers. Tectum perforate; perforations 0.1-0.15 μm in diameter, often covered by muri (Fig. 67).

Ornamentation: Faintly rugulate or irregularly rugulate-striate. Muri arranged in triangular groups, of different orientation, usually close together. Grooves narrower than the mu-
Figs 72-78. *Rubus montis-wilhelmi* pollen.

Fig. 72. (SEM). Different arrangement of pollen: Oblique position (A), equatorial position (B).
Fig. 73. (SEM). Equatorial view of pollen. Ornamentation of the exine distinct, porus marked.
Fig. 74. (SEM). Details of striae ornamentation, granulate membrane distinct and marked (arrow).
Fig. 75. (LM). Equatorial outline of pollen. Stratification of the exine distinct and marked (×1000).
Fig. 76. (LM). Equatorial view of pollen, ornamentation distinct (×1000).
Fig. 77. (LM). Meridional outline of pollen in equatorial view (×1000).
Fig. 78. (LM). Polar view of the grain. Ornamentation of the polar area distinct (×1000).

Fig. 79. (SEM). Pollen in different arrangement: Oblique (A) and equatorial (B) view. Porus distinct and marked.

Fig. 80. (SEM). Details of ornamentation. Irregular muri and “baculae-like” elements.

Fig. 81. (SEM). Details of ornamentation. Irregular muri and “baculae-like” elements in higher magnification marked.

Fig. 82. (LM). Equatorial outline of pollen (A), stratification of the exine distinct and marked, ornamentation of pollen in oblique view, polar area distinct (B) (×1000).

Fig. 83. (LM). Equatorial view of pollen, ornamentation distinct (×1000).

Fig. 84. (LM). Meridional outline of pollen in equatorial view (×1000).

Fig. 85. (LM). Polar view of pollen, ornamentation on the polar area distinct (×1000).
ri and elongated, filled up by perforations. Muri are short, L-shaped or striate, 1.3-3.5 μm long, sometimes anastomosing; the range is 1-3 per 10 μm length of a murus (Figs 66, 67).

**Remarks:** Pollen of very regular shape and very thick exine. This type of ornamentation has been reported in my studies on *Rubus* pollen for the first time.

*Rubus montis-wilhelmi* van Royen
Unknown section
This bramble from New Guinea has small pollen grains, Px:E: 17.2x16.6 μm (Table 1), of very regular shape, almost without variation (Table 1); equatorial outline circular to 3-lobed (Figs 72A, 75), meridional outline almost circular, P/E ratio 1.04 (Table 1, Figs 72B, 73, 77).

**Apertures:** Ectoapertures – colpi long, 90.1% length of polar axis, with acute ends. Colpus margins undifferentiated and distinct, rarely folded inwards. Colpus is not constricted, the equatorial bridge very faintly developed, not constricted (stretched or opened) (Figs 72, 73). The granulate colpus membrane is quite distinct (Figs 73, 74, marked by arrow).

Endoapertures – pori not covered by the equatorial bridge, distinct in SEM and LM observations, usually lalongate in shape (Figs 72, 73, marked by arrows). SEM photos show pori covered by granules (Figs 72, 73).

**Exine:** Total thickness of the exine is 1.3 μm in the centres of the mesocollia. In LM examination 3 sublayers are distinct (Figs 75, marked by arrow, 77). These layers have not been measured, but a perforate tectum is distinct (Figs 73, 74). Perforations are up to 0.2 μm in diameter and situated in the grooves.

**Ornamentation:** Striate, with distinct, relatively thick comparing with the previous species, high muri, loosely arranged on the tectum, usually running longitudinally. Muri are short and do not anastomose. Perforations of different diameter are filling up relatively wide grooves (Fig. 74).

**Remarks:** Pollen grains very uniform in size and shape, comparable with pollen of *R. papuanus*.

*Rubus papuanus* Schlechter ex Diels
Unknown section
This species occurs in eastern part of New Guinea. Pollen grains are small, (Px:E: 17.8x17.2 μm), very regular in shape and almost without variation (Table 1, Fig. 79). Equatorial outline circular to trilobed (Figs 79A, 82A). Meridional outline circular, P/E ratio 1.03 indicates almost spherical shape (Figs 79B, 84).

**Apertures:** Ectoapertures – colpi short, ca 75% length of polar axis, with acute ends. Colpus is not constricted; equatorial bridges faintly developed, stretched. The porus area distinct. Membrane of the colpus granulate; granules are big (Fig. 79).

Endoapertures – pori lalongate and distinct (Fig. 79, marked by arrow).

**Exine:** Total thickness of the exine is 1.2 μm in the centres of the mesocollia (Figs 82A, 84). In LM examination 3 sublayers are distinct. These layers have not been measured, but a perforate tectum is distinct (Figs 80, 81). Perforations are less than 0.1 μm in diameter and are situated in the grooves.

**Ornamentation:** The surface of the pollen presents not a regular sculpture. It could be classified as a mixture of striate and granulate-baculate pattern (Figs 79-81, 82B, 83, 85). The granules are different in size, some of them are so big as baculae in baculate pattern in *R. chamaemorus* (Fig. 81, marked by arrows).

**Remarks:** Pollen grains very uniform in size and shape, comparable with pollen of *R. montis-wilhelmi*.

**DISCUSSION**

The Malesian *Rubus* species grouped in the subgenera *Chamaebatus* and *Idaeobatus*, as described by Zandee and Kalkman (1981), present a rather great diversity both in size and in shape of their pollen grains. All species examined have the *Rubus* pollen type. They are isopolar, radially symmetrical, 3-colporate, according to Erdtman (1952), Reitsma (1966) and Eide (1981). The main ideas on pollen morphology of the examined species are presented below.

**Shape and size**

The equatorial outline of the grains is circular to 3-lobed, whereas the meridional outline is mainly elliptical and sometimes circular. The exceptions are *Rubus archboldianus, R. montis-wilhelmi* and *R. papuanus* (subgenus *Idaeobatus*) which have an almost circular meridional outline* (Table 1) and a spherical shape.

The size of the grains is in the range from small to medium. The medium-sized class is represented by the species of subgenus *Chamaebatus* and some of subgenus *Idaeobatus*, e.g.: *Rubus alpestris, R. archboldianus, R. loorentzianus* and *R. maccgregori*. The size of the medium-sized grains is 28-38 μm for the polar axis “P” and 25-31 μm for the equatorial diameter “E” (Table 1). The other grains should be classified as small according to Erdtman (I.c.). The largest pollen was found in *R. loorentzianus* (range Px:E: 32.3-32 μm×24-28 μm, average 34.5±26.2 μm), whereas the smallest was observed in *R. montis-wilhelmi* (Px:E: 17.2x16.6 μm), *R. papuanus* (Px:E: 17.7x17.2 μm) and in *R. chrysogaeus* (Px:E: 17.4x16.2 μm). The most uniformly-sized grains are presented by *R. montis-wilhelmi* (the standard deviation is only 0.16 μm for polar axis). The most variable pollen in size belongs to *R. calycinus* and *R. pectinellus*, both of subgenus *Chamaebatus*, and to *R. alpestris, R. ellipticus* and *R. loorentzianus* of subgenus *Idaeobatus*, where the standard deviation for polar axis (P) is from 1.55 to 2.18 μm (Table 1). Both LM and SEM examinations show the variation between and within the species. The P/E index indicates the ellipsoid grains in the most of the species except the circular grains described above.*

**Apertures**

Ectoapertures: Except *Rubus papuanus* (ca 75% length of polar axis), all examined *Rubus* species tend to have long colpi measuring 81-85% length of the polar axis. Colpi are approximately 4.4 μm wide in the widest part. The
longest colpi occur in *R. lorentzianus*, which cover 86.2% length of polar axis; the shortest in *R. papuanus*: 75% length of polar axis. The furrows taper into acute ends in most of the examined species. The colpus membrane is granulate in all species, which is distinct in SEM microphotographs. Equatorial bridges are present in all species, although in some of them they are not well developed. In such species as *R. pectinellus*, of subgenus Chamaebatus, and *R. montis-wilhelmi* and *R. papuanus*, of subgenus Idaeobatus, there are almost no bridges. Membrane granules cover the pore area. The bridges are stretched (opened) in such species as *R. alpestris*, *R. archboldianus* and *R. copeelandii* of subgenus Idaeobatus. *R. calycinus* of subgenus Chamaebatus shows the equatorial bridge constricted deep in the colpus. The other species of subgenus Idaeobatus show well developed equatorial bridges, often constricted deep in the colpus.

Endoapertures: Alongate pori were found in *R. pectinellus*, of subgenus Chamaebatus, and in *R. alpestris*, *R. archboldianus*, *R. copeelandii*, *R. montis-wilhelmi* and *R. papuanus*, of subgenus Idaeobatus. In the other species, pori are hidden under the equatorial bridges and they are not seen neither in LM nor in SEM.

**Exine**

The exine thickness in the centres of the mesocolpia measured in glycerine-jelly showed variation. The range was 1.22–2.04 μm for different species. The thickest exine was observed in *Rubus pectinellus*, of subgenus Chamaebatus, and in *R. macgregorii*, of subgenus Idaeobatus (Table 1); whereas the thinner exine was found in *R. papuanus* of subgenus Idaeobatus. The thickness of the exine depends partly on height of the suprathecatal elements, which differs from species to species.

**Ornamentation**

The species studied generally show the striate pattern. Variation was present in subgenus Idaeobatus, where species showed several modifications of the striate pattern. Some of these patterns have not been reported earlier for Rubus.

1. *Rubus archboldianus* – rugulate pattern, suprathecatal elements arranged in groups, oriented in different directions.
2. *R. lorentzianus* – striate-scabrata pattern, muri alternating with relatively wide “grooves”, which could be described here as lumina, filled with granules. Muri are not running longitudinally, mostly perpendicular to the polar axis.
3. *R. macgregorii* – faintly rugulate or irregular striate-rugulate pattern, muri arranged in triangular groups.
5. *R. ferdinandi-muelleri* *R. montis-wilhelmi*, *R. papuanus*, – striate pattern with muri of variable length, width and height, sometimes grooves filled with granules of different size, or high and short muri resembling the baculae in baculate pattern are present (*R. papuanus*).

**CONCLUSIONS**

The pollen of *Rubus* of subgenus Chamaebatus represented by two Malesian species (*R. calycinus* and *R. pectinellus*) shows a striate ornamentation pattern with diversity in the orientation of the muri, their width and the anastomosing pattern. The species of this subgenus are small, mostly herbaceous to slightly woody plants, with creeping stems and simple leaves, occurring in disjunct mountain areas. *R. calycinus* comes from the Himalaya region (Nepal), NE India, N Burma, S China and E Java, whereas *R. pectinellus* occurs mainly in south-eastern part of China, Taiwan, Japan and Philippines. From the morphological point of view of pollen, they could be regarded as related species, although their area of distribution is not the same.

The species of subgenus Idaeobatus have been classified into nine sections according to Focke (1911, 1914). The Malesian species do not belong to one section and according to Zandee and Kalkman (1981), on the basis of morphological features, they can be grouped as follows:

1. Species with pinnate leaves, represented by *Rubus* chrysogaeus and *R. fraxinifolius*, belong to section Rosaefoli, and *R. ferdinandi-muelleri* to section Pungentes. *R. montis-wilhelmi* and *R. papuanus* were not known to Focke, so they have no place in any section.
2. Species with trifoliolate leaves, occurring in rather restricted areas: *R acuminatissimus* (Sumatra, Java), *R. copeelandii* (Philippines: Prov. Luzon), *R. archboldianus*, *R. lorentzianus*, *R. macgregorii* (New Guinea). Except for *R. acuminatissimus*, which was placed in section Rosaefolii, these species were unknown to Focke.
3. Species related to the latter group and belong to section Alpestres: *R. alpestris*. It has 5-foliolate palmate leaves and it was placed in this section by Focke (l.c.).
4. The remaining Malesian species: *Rubus niveus* with pinnate leaves and trifoliolate *R. ellipticus* share the feature of a dense, woolly felt underside of the leaflets, and have therefore been placed in section Ideanthi, but in different series. According to Zandee and Kalkman (l.c.) they are not very closely related each other.

In the light of macromorphological division, presented above, the pollen morphology and the relation between the species could be revised. On the basis of pollen morphology the following relation between the species of subgenus Idaeobatus is proposed and presented in Fig. 86.

**COMMENTS**

The macromorphological division proposed by Zandee and Kalkman (1981) does not always agree with the micro-morphological one, based on the ornamentation pattern of the pollen.

1. As closely related species may be regarded New Guinean *Rubus montis-wilhelmi* and *R. papuanus*, species unknown to Focke (l.c., Zandee and Kalkman l.c.), which have pinnate leaves. This is confirmed by a similar ornamentation pattern of the exine.
2. New Guinean *Rubus ferdinandi-muelleri* with pinnate leaves, from the section Pungentes presents a similar pattern of the pollen ornamentation and may be regarded as related with the two species mentioned above. On the basis
of macromorphology and pollen morphology the common systematical position of the three species: *R. ferdinandi-muelleri*, *R. montis-wilhelmi* and *R. papuanus* in the section *Pungentes* has been proposed.

3. *R. acuminatissimus*, *Rubus chrysogaeus*, from section *Rosaefolii*, the former with pinnate leaves, whereas the latter with trifoliolate leaves, and *R. niveus* of section *Ideanthi*, have almost the same type of exine ornamentation and may be grouped together. This does not agree with the macromorphological division proposed by Zandee and Kalkman (I.C.).

4. *Rubus ellipticus* with trifoliolate leaves of section *Ideanthi*, trifoliolate *R. copelandii*, and *R. fraxinifolius* with pinnate leaves from section *Rosaefolii* have very similar ornamentation patterns. This demonstrates that apparently unrelated species may share similar pollen patterns.

5. Trifoliolate *Rubus macgregori* from New Guinea and widely distributed *R. alpestris* have the same exine pattern; 5-foilate palmate *R. alpestris* belongs to section *Alpestre*, whereas the systematic position of the former is unknown.

6. The trifoliolate *Rubus archboldianus* from New Guinea and trifoliolate *R. lorentzianus* could not be placed in any of mentioned groups because they have completely different patterns of ornamentation.

The studied samples were taken from the following herbarium specimens stored in the Naionala Herbarium Nederland at Leiden. Photographs of the pollen grains presented in this article were taken from material indicated with an asterisk (*).

**SPECIMENS INVESTIGATED**

- *Rubus acuminatissimus*
  - *Rubus alpestris*
    - Sumatra. Aceh. Mt. Leuser, 2200 m, van Steenis 8532, 9123 (*), 9706.
  - *Rubus archboldianus*
    - *Rubus chrysogaeus*
      - New Guinea. Papua New Guinea. Morobe Distr., Edie Creek, alt. 2430 m, Womersley NGF 24680, L 66389 (*).
    - *Rubus calycinus*
      - Asia. Nepal. Tahshindu., alt. 2400 m, van Steenis (1972) (*).
    - *Rubus copelandii*
      - Philippines. Luzon. Mt. Pulog, alt. 2350-2450 m, Zandee 104 901 (*).
    - *Rubus ellipticus*
      - Thailand, Leo Kay Province, Tonkin Pres de Pakha Fang, alt. 1100 m, Pollane 17246 (*).
    - *Rubus ferdinandi-muelleri*
      - New Guinea. Papua New Guinea. Western Higl. Distr., Wabag Subdistr. Merimanta, alt. 2430 m, Hoogland & Schodde 6739, 6920; Womersley NGF 9512 (*).
    - *Rubus fraxinifolius*
      - Borneo. Sabah. Kinabalu Sabah National Park; Ranau Distr., alt. 1800 m, Badak SAN 32325 (*), Kadir A 1661, Poore H 141.
    - *Rubus lorentzianus*
    - *Rubus macgregori*
      - New Guinea. Papua New Guinea. Central Distr., Mt. Victoria, Craven 2861, Croft LAE 61609, van Royen 10 798; Tapini Subdistr., alt. 3800 m, Zandee 4312 (*).
    - *Rubus montis-wilhelmi*
      - New Guinea. Papua New Guinea. Western Higl. Distr., Kubor Range, alt. 3220 m, Vink 16 118, 16 159 (*).
    - *Rubus niveus*
      - Collected as *Rubus leucocarpus* from Ceylon Ceylon. Central Province. Nuwara Eliya Distr., Kanda-pole, alt. 2000 m, Tirvengadan, Jaysuriya 1976 (*).
    - *Rubus papuanus*
    - *Rubus pectinellus*
      - Philippines. Luzon Mountain Province, Bontoc, Vanoverbergh 563; Mt. Polis, Britton PNH 1973; Mt. Pulog, Jacobs 7102, Steiner 2062; Mt. St. Thomas, van Steenis 18574 (*).
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LITERATURE CITED