POLLEN MORPHOLOGY OF THE GENERA *NORANTEA, SOUROUBEA* AND *RUYSCHIA* (MARCGRAVIACEAE)

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SOMMAIRE. — Etude de la morphologie du pollen de trois genres de Marcgraviaceae (*Norantea* AUBLET, *Souroubea* AUBLET et *Ruyschia* JACQUIN). On a pu établir neuf types polliniques dans le genre *Norantea* et trois groupes de pollen dans le genre *Souroubea*. Les pollens de *Ruyschia* n'ont pu être différenciés de ceux de *Souroubea*. On a distingué plusieurs tendances évolutives marquées chez *Norantea*. Ces tendances l'étaient moins chez *Souroubea*. Une clef des types polliniques a été ajoutée.

Introduction.

The study of the pollen grains of the Marcgraviaceae was undertaken to give additional information to the gross morphology of this family which is monographically studied by A. C. de ROON, taxonomist at the Botanical Museum and Herbarium, Utrecht.

The family is restricted to the Neo-tropics and comprises the following four genera : *Marcgravia* L., *Norantea* AUBLET, *Souroubea* AUBLET and *Ruyschia* JACQ. *Marcgravia* is the largest genus and the study of its pollen grains will be undertaken later. In the present paper the genera *Norantea, Souroubea* and *Ruyschia* are dealt with only. *Norantea* has about 30 species, *Souroubea* about 20 and *Ruyschia* about 7. All species were studied with the exception of those from which no pollen was available.

Material and methods.

MATERIAL.

The plant specimens were supplied by A. C. de ROON, who also took care of the identification and is responsible for the generic and

specific names in the text. Some new, undescribed species occurring in the present paper will be described in the near future.

All slides were prepared from herbarium sheets and these sheets were obtained from the following herbaria : C : Botanical Museum and Herbarium, Copenhagen ; E : Royal Botanic Garden, Edinburgh ; F : Chicago National Museum, Chicago, Ill. ; G : Conservatoire et Jardin Botanique, Genève ; K : The Herbarium, Royal Botanic Gardens, Kew ; LE : Herbarium of the Komarov Botanical Institute, Leningrad ; M : Botanische Staatssammlung, München ; MG : Museu Paraense Emilio Goeldi, Belem ; MO : The Missouri Botanical Garden, St.-Louis, Mo. ; NY : The New York Botanical Garden, New York, N. Y. ; P : Laboratoire de Phanérogamie, Muséum d'Histoire Naturelle, Paris ; R : Botanical Division of the National Museum, Rio de Janeiro ; S : Naturhistoriska Riksmuseet, Stockholm ; UC : Herbarium of the University of California, Berkeley, Cal. ; US : United States National Herbarium, Washington, D.C. ; VEN : Instituto Botanico, Caracas ; W : Naturhistorisches Museum, Wien.

Specimens investigated.

NORANTEA :

N. adamantium CAMBESS. — MACEDO *et al.* 4803 (US) ; Brasil.
N. albido-rosea GILG — TONDUZ 8087 (US) ; Costa-Rica.
N. anomala H. B. K. — BANG 1194 (F) ; Bolivia — CARDENAS 4581 (US) ; Bolivia — CUATRECASAS 18328 (F) ; Colombia — LEHMAN 8420 (F) ; Colombia.
N. aurantiaca SPRUCE ex WITTM. — GARCIA-BARRIGA 13687 (US) ; Colombia.
N. brasiliensis CHOISY — DUCKE et LIMA 78 (R) ; Brasil.
N. brachystachya (RUSBY) de ROON — BUCHTIEN 1857 (NY) ; Bolivia.
N. brenesii STANDLEY — BRENES 5570 (F) ; Costa-Rica.
N. coccinea DE ROON — MAGUIRE *et al.* 30687 (TYPE), (U) ; Venezuela.
N. cordaichida G. DON — CUATRECASAS 16005 (F) ; Colombia.
N. costaricensis GILG — SKUTCH 3441 (US) ; Costa-Rica — STANDLEY and TORRES 47658 (F) ; Costa-Rica — WHITE 40 (F) ; Panama — CUATRECASAS 23618 (F) ; Colombia.
N. cuneifolia DELP. — GLAZIOU 2937 (C) ; Brasil.
N. curva MACBR. — WILLIAMS 6999 (F) ; Peru — WILLIAMS 7480 (F) ; Peru.
N. delpiniana WITTM. — GARDNER 4454 (TYPE), (K) ; Brasil.
N. droseriformis RUSBY ex GILG. — BANG 1544 (TYPE), (F) ; Bolivia.

N. flammifera DE ROON — MAGUIRE *et al.* 53696 (U) ; Venezuela — AGOSTINI 402 (U) ; Venezuela.

N. glossostipa DE ROON — ANDRÉ 4682 (NY) ; Colombia.

N. goyasensis CAMBESS. — KRUKOFF 1468 (U) ; Brasil — MACEDO 3736 (NY) ; Brasil — PEREIRA 1773 (U) ; Brasil.

N. grandiflora DE ROON — TESSMANN 4699 (NY) ; Peru.

N. guianensis AUBL. — V. DOESBURG 217 (U) ; Suriname — MAGUIRE *et al.* 40151 (U) ; Brasil — OLIVEIRA 391 (IAN) ; Brasil — WESSELS BOER 359 (U) ; Suriname — WESSELS BOER 607 (U) ; Suriname.

N. ignescens DE ROON — MAGUIRE *et al.* 35109 (TYPE), (U) ; Venezuela.

N. japurensis MART. — CROIZAT 192 (NY) ; Venezuela — MAGUIRE *et al.* 31464 (U) ; Venezuela — MAGUIRE and WURDACK 34972 (U) ; Venezuela — MAGUIRE *et al.* 29038 (U) ; Venezuela — VELEZ 2416 (VEN) ; Venezuela.

N. jimenezii (STANDLEY) DE ROON — STANDLEY and VALERIO 49160 ; Costa-Rica.

N. magnifica GILG — SCOLNIK *et al.* 19 An 518 (US) ; Colombia.

N. micradenia DE ROON — CUATRECASAS 15456 (F) ; Colombia.

N. obovata G. DON — KANEHIRA 48 (F) ; Peru.

N. oxystylis BAILL. — CARDENAS 5129 (US) ; Bolivia — MANDON 793 (NY) ; Bolivia — WEDDELL 4611 (TYPE), (P) ; Bolivia.

N. paraensis MART. — SPRUCE 132 (NY) ; Brasil.

N. pedunculariS POEPP. et WITTM. — ASPLUND 13435 (US) ; Peru — BUCHTIEN 7611 (US) ; Bolivia — HURTADO L. 115 (US) ; Colombia.

N. aff. pedunculariS — ROSE and ROSE 23532 ; — SCHULTES and CABRERA 14589 (US) ; Colombia — SCHULTES and CABRERA 14931 (US) ; Colombia — ALLEN 3227 (MO) ; Colombia.

N. pendula LANJ. et v. HEERDT — B. W. 5682 (U) ; Suriname.

N. robusta DE ROON — Cuatrecasas 16790 (F) ; Colombia.

N. sessilis L. WILLIAMS — AUSTIN SMITH F. 1775, (F.) ; Costa-Rica.

N. sodiroi GILG — SODIROI s.n. (TYPE), (P) ; Ecuador.

N. spiciflora (JUSS.) KRUG et URBAN — DUSS 2302 (F) ; Guadeloupe — STEHLÉ 328 (NY) ; Guadeloupe.

N. subsessilis BENTH. — CUATRECASAS 22036 (F) ; Colombia.

N. tepuiensis DE ROON — STEYERMARK 93267 (U) ; Venezuela — STEYERMARK 60853 (F) ; Venezuela — STEYERMARK and DUNSTERVILLE 92472 (U) ; Venezuela.

N. weddelliana BAILL. — BANG 390 (NY) ; Bolivia — RAUTI-HIRSCH P 1350 (E) ; Peru.

SOUROUBEA :

S. bicolor (BENTH.) DE ROON — CUATRECASAS 17719 (F) ; Colombia.
S. corallina (MART.) DE ROON — PRANCE *et al.* 2748 (U) ; Brasil.
S. crassipes TRIANA et PL. — TRIANA s.n. (TYPE), (P) ;
S. aff. crassipes — DUKE 11275 (U) ; Colombia — BRISTAN 623 (U) ; Panama.
S. crassipetala DE ROON — DUCKE 1100 (MG) ; Brasil.
S. dasystachya GILG — CROIZAT 743 (NY) ; Venezuela — SCHUNKE 20 (UC) ; Peru — ULE 8422 (MG) ; Brasil.
S. exauriculata DELP. — LIEBMANN 333 (C) ; Mexico — MATUDA 1853 (U) ; Mexico — PURPUS 8631 (UC) ; Mexico.
S. fragilis DE ROON — BANG 2401 (M) ; Bolivia — VARGAZ 7342 (US) ; Peru.
S. gilgii A. RICHTER — GENTLE 4727 (herb. Lundell) ; Br.-Honduras.
S. guianensis AUBL. var. *guianensis* — MENNEGA 49 (U) ; Suriname — LINDEMAN 7857 (U) ; Suriname.
var. amazonica (MART.) DE ROON — PRANCE and SILVA 58796 (U) ; Brasil — PEREIRA 1857 (U) ; Brasil — JENMAN 2362 (U) ; Br.-Guiana — IRWIN *et al.* 48155 (U) ; Brasil.
var. bahiensis WITTM. — BELÉM and PINHEIRO 3031 (U) ; Brasil.
var. cylindrica WITTM. — MAGUIRE *et al.* 36211 (U) ; Venezuela — STEYERMARK *et al.* 95694 (U) ; Venezuela.
S. intermedia DE ROON — CUATRECASAS 21090 (F) ; Colombia.
S. loczyi (A. RICHTER) DE ROON ssp. *loczyi* — LUNDELL 6492 (S) ; Br.-Honduras — MATUDA 3679 (U) ; Mexico.
ssp. minima DE ROON — LÉON 2688 (M) ; Costa-Rica — ALLEN 1914 (GH) ; Panama.
S. pachyphylla GILG — SPRUCE 4469 (W) ; Peru (TYPE) — VIDAL-SÉNÈGE s.n. (P) ; Peru.
S. peruviana GILG — Y. MEXIA 8310 (U) ; Peru.
S. platyadenia (GILG) DE ROON — GLAZIOU 16365 (LE) ; Brasil.
S. stichadenia DE ROON — GAY s.n. (P) ; Peru.
S. sympetala GILG — ARISTEGUETA 4846 (U) ; Venezuela — BRETELER 4313 (U.) ; Venezuela.
S. aff. sympetala — TESSMANN 4798 (G) ; Peru — ASPLUND 14179 (US) ; Peru ; GENTLE 2895 (U) ; Br.-Honduras.
S. vallicola WOODSON ex DE ROON — ALLEN 3541 (U) ; Panama.
S. venosa SCHERY — ALLEN 3537 (U) ; Panama.
S. spec. — LAWRENCE 805 (S) ; Colombia.

RUYSCHIA :

R. clusiifolia JACQ. — EGGERS 781 (M) ; Dominica.
R. phylladenia SANDWITH — Lankaster K 93 ;
R. tremadena (ERNST) LUNDELL — ARISTEGUETA 4636 (U) ; Venezuela — URIBE 3353 (NY) ; Colombia.

Species not investigated.

NORANTEA :

N. gigantophylla GILG — specimens with leaves only.
N. macrocarpa G. DON — specimens without good anthers ; e.g., dammaged by insects.
N. uleana PILGER — specimens with fruits only.

All species of *Souroubea* have been investigated.
No specimens were available of the following *Ruyschia* species ;
R. enervia LUNDELL
R. pavonii G. DON
R. pilophora TRIANA et PL.
R. valerii STANDLEY

Preparation method.

The pollen grains were prepared using the acetolysis method as described by REITSMA (1969). The mounted grains were covered by a cover slip which is supported by two granules of modelling clay, and afterwards sealed with paraffin (REITSMA, 1969).

Descriptions.

Descriptions have been made with the aid of a Leitz Ortholux microscope, Pl. apochr. obj. × 100/1.32 and an eye piece × 10, periplan. The photographs were taken with the use of a Pl. apochr. obj. 90/1.40 lens in combination with a Leitz Orthomat camera and a Leitz interference green filter, AL 546.

In this paper it is not attempted to give a statistical treatment of size measurements. The figures given under the P and E in the heading *Measurements* of the descriptions represent the size ranges of 5 or 6 pollen grains only. These figures cannot be trusted in a statistical point of view. From the results of Reitsma's study (1969) it is clear, that the size of a pollen grain highly depends on the preparation method followed. For this reason the values of the measurements should be considered as relative only.

Terminology.

The terminology used in this paper is mainly based on the terminology system as proposed by REITSMA (1970). In addition to the most commonly used terms, such as exine, colpus, etc., there are some other plain english words to describe certain characters which

need further explanation. The following list and figure (fig. 1) give additional information on the meaning of some of these subjective characters.

COLPUS	: *narrow* ;	usually at least 1 μ to 2 μ wide (1).
	slit-like :	ca 1 μ or less wide, margins parallel (2).
	long ;	in polar view colpi distinctly visible (3a). in equatorial view colpus ends not visible (3b).
	rather long ;	in polar view colpi just visible (4a). in equatorial view colpus ends just or just not visible (4b).
	short ;	in polar view colpi not visible (5a). in equatorial view colpus ends distinctly visible (5b).
ENDOCOLPUS	: *diffuse* ;	outer ends ; margins not meeting (7).
	tapering ;	outer ends ; margins meeting at the ends, shape of the endoaperture rhombic (6).
	middle part ;	thinned area in the middle part of the costae endocolpi ; situated between the colpus and the endocolpus on the crossing of these apertures ; can be circular or elliptic (8).
EXINE	: *thin* ;	thinner 1,5 μ.
	rather thin ;	1,5 μ - 2 μ.
	thick ;	2 μ - 3 μ.
	very thick ;	3 μ or thicker.
RETICULUM	: *coarse* ;	lumina wider 1,5 μ.
	fine ;	lumina smaller 1,5 μ.

In current literature the term « pollen type » is used by many authors in a sense which is more or less the same. However, the delimitations of all these pollen types are not always as sharp as they should be and the present author thinks it necessary to give a closer circumscription of the term « pollen type » as used in this paper. A sharp definition is the more necessary as besides the term pollen type, the concept « pollen group » is used as well.

A *pollen type* is a term which indicates that pollen grains can be distinguished from other pollen grains either by one distinct charac-

ter or by a combination of characters making the pollen grains distinctly different from other pollen grains. Consequently a pollen type must have sharp delimitations by its differential characters.

However, there are also cases in which the characters are highly variable or where the combination of characters shows gradual transitions into a combination of characters belonging to another group of pollen, so that the delimitations become vague. In such cases I prefer to speak of a pollen group and not of a pollen type.

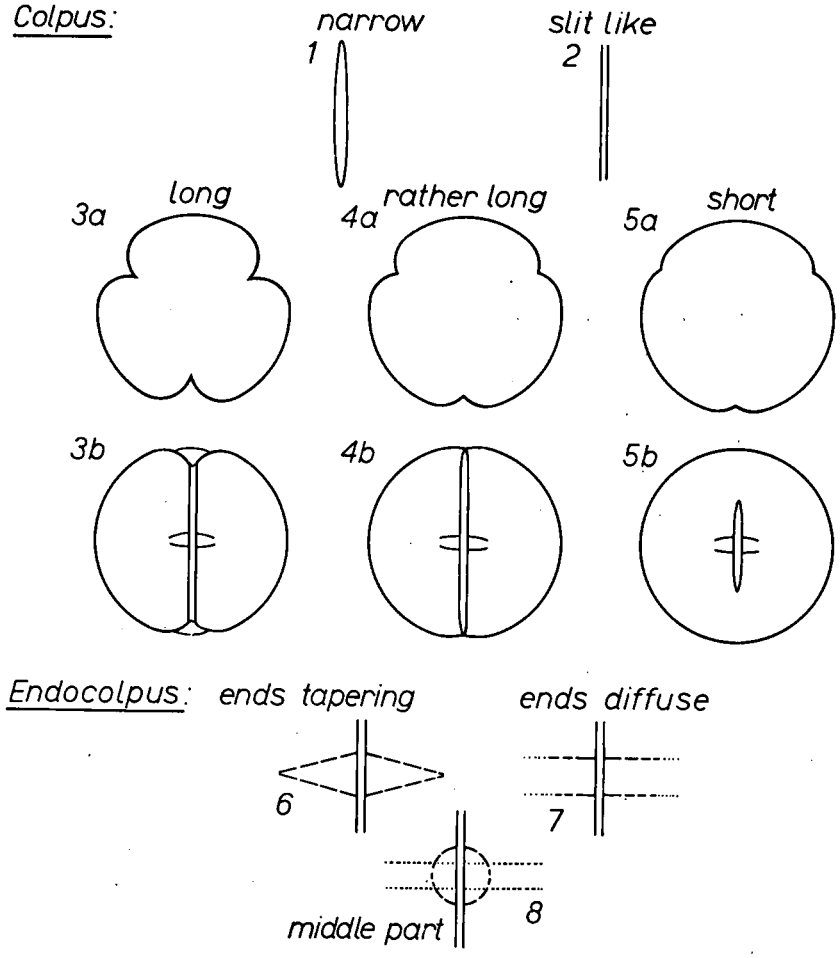


FIG. 1. — Explanation of some subjective « terms » — 1 - 5 ; *colpus* — 1. colpus narrow, margins slightly convex ; 2. colpus slit-like, margins ca parallel ; 3 - 5 ; length of the colpus, 3a - 5a ; colpus length in polar view ; 3b - 5b ; colpus length in equatorial view — 6 - 8 ; *endocolpus* — 6. ends tapering ; 7. ends diffuse ; 8. middle part in the costae endocolpus.

Key to the types.

1. a Pollen grains distinctly reticulate, coarsely or finely 2
   b Pollen grains not reticulate, however, often with a tectum perforatum 4
2. a Pollen grains usually coarsely reticulate ; lumina distinctly larger than 1 μ 3
   b Pollen grains only finely reticulate ; lumina usually ca 1 μ or less (*N. grandiflora*, rarely up to 1,5 μ) ..... *N. grandiflora* type. p. 212
3. a Muri thick, duplicolumellate. Colpi rather long. Pollen grains in polar view angular, sides distinctly convex .... *N. cuneifolia* type. p. 210
   b Muri thin, simplicolumellate. Colpi long. Pollen grains in polar view angular, sides only slightly convex, nearly straight ..... *N. delpiniana* type. p. 208
4. a Exine thick or very thick (2 μ or thicker). Pollen grains spheroidal, oblate spheroidal or suboblate 5
   Exine thin or rather thin (up to 2 μ). Pollen grains subprolate, prolate spheroidal, spheroidal, oblate spheroidal or suboblate 9
5. a Exine thick or very thick and sexine always distinctly thinner than exine 6
   Exine may be thick, but sexine about as thick as nexine or only slightly thinner 7
6. a Pollen grains spheroidal or only slightly oblate spheroidal ..... *N. japurensis* type. p. 216
   b Pollen grains distinctly oblate spheroidal or suboblate .. *N. anomala* type. p. 218
7. a Colpi short. Pollen grains distinctly oblate spheroidal ... *N. micradenia* type. p. 214
   b Colpi long or rather long and if rather short, then pollen grains not distinctly oblate spheroidal 8
8. a Pollen grains rather large, usually with one dimension larger than 25 μ ; usually spheroidal or only slightly oblate spheroidal. Distinct circular or elliptic middle part present ..... *N. weddelliana* type. p. 215
   b Grains small, not exceeding 25 μ. Grains slightly prolate spheroidal, spheroidal or slightly oblate spheroidal. Middle part indistinct or even absent ..... *N. oxystylis* type. p. 210
9. a Colpi short. Pollen grains usually distinctly oblate spheroidal (*N. robusta* spheroidal) 10

b Colpi long or rather long. Pollen grains usually prolate spheroidal, subprolate or spheroidal, rarely only slightly oblate spheroidal 11

10. a Exine rather thick (up to 2 μ). Tectum perforated .... *N. micradenia* type. p. 214

b Exine thin. Tectum without perforations .... *N. subsessilis* type. p. 215

11. a Exine rather thick or thick. Pollen grains spheroidal, sometimes slightly prolate spheroidal, sometimes oblate spheroidal ..... *N. oxystylis* type. p. 210

b Exine thin, rarely thick. Pollen grains usually prolate spheroidal or subprolate, less frequently about spheroidal and only rarely oblate spheroidal .... *Souroubea* and *Ruyschia*. p. 223

N. B. — Exact differences between the *N. oxystylis* type and *Souroubea* are difficult to trace. It is the combination of characters which supplies the difference between both groups.

POLLEN MORPHOLOGY OF THE GENUS *NORANTEA*.

General description of *Norantea* pollen grains.

Pollen class : The pollen grains are usually 3-zonocolporate, a few species show very low percentages of 4-zonocolporate pollen grains.

Shape : The outline of the pollen grains in polar view is usually triangular, with obtuse angles or sometimes nearly circular. The sides are varying in convexity and always inward bent at the angles, where the colpi are situated. The outline of the pollen grains in equatorial view is usually elliptic (e.g., *N. oxystylis* type), sometimes slightly truncate (e.g., *N. anomala* type).

P:E ratio : The pollen grains are often oblate spheroidal or spheroidal, sometimes prolate spheroidal and rarely suboblate.

Apertures : Ectoapertures : The pollen grains have distinct colpi which are always narrow, and often slit-like. The length of the colpus varies from long, via rather long to short. The colpi are always more or less sunken and they are accompanied by distinct costae. The colpus membrane is nudate. *Endoapertures* : The endocolpi are lalongate and can be narrow or rather broad. The outer ends are usually diffuse, less often tapering. The margins are thickened into distinct costae. In the middle part of the endocolpus, where the colpus crosses the endocolpus, there is usually a thinned area present in the costae endocolpi. This middle part is either circular or slightly lalongate elliptic.

Exine : The exine is usually thick or very thick and less frequently rather thin (e.g., ca. 1,5 μ in the *N. subsessilis* type). The exine is sometimes as thick as the nexine, but usually distinctly thinner than the nexine. The thickness of the sexine does not vary much, but it is usually the nexine which supplies the varying factor in the thickness of the exine. The columellae are always short and usually rather indistinct in optical section. Some pollen grains, however, do show a distinct pattern at high focus (LO pattern) ; e.g., the *N. weddelliana* type. The pollen grains are either reticulate or tectate. Two types show a distinct reticulum with wide lumina (*N. delpiniana* type and *N. cuneifolia* type). A fine reticulum is present in the *N. grandiflora* type. The other types are tectate. The tectum is always smooth and can be either closed or provided with perforations.

Description of the *Norantea* pollen types.

N. delpiniana type
(Pl. I, fig. 1-4).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; Pollen grains distinctly triangular, with obtuse angles, sides convex, nearly straight. Outline in *equatorial view* ; grains circular to slightly elliptic, not truncate. *P:E ratio*; grains slightly prolate spheroidal to slightly oblate spheroidal.

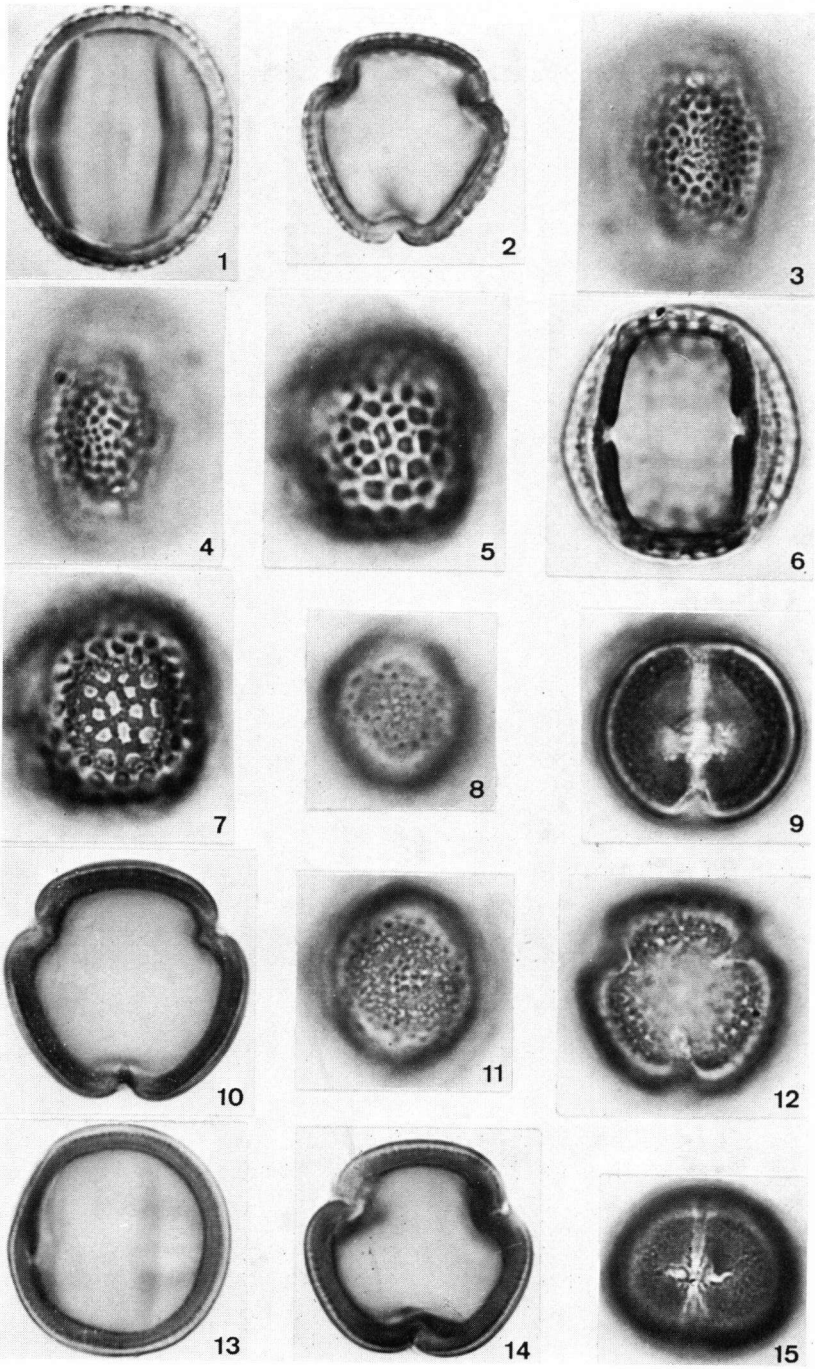
Apertures : Ectoapertures ; colpi long, slit-like, sunken and with distinct costae colpi. *Endoapertures* ; endocolpi lalongate, narrow, small, rather indistinct, without middle part and with distinct costae endocolpi.

Exine : Exine thick (ca. 2 μ). Sexine thinner than nexine. Columellae short and rather indistinct in optical section. Reticulum present, coarse ; muri rather thin, simplicolumellate ; lumina distinct, very irregular, decreasing towards the colpi ; up to 3 μ.

Measurements : P = 18,5-21 μ ; E = 17,5-20 μ.

PLATE I (× 1600).

FIG. 1 - 4. *Norantea delpiniana* — 1, optical section, equatorial view ; 2. optical section polar view ; 3. reticulum at low focus ; 4. reticulum at high focus. — FIG. 5 - 7. *Norantea cuneifolia* — 5. reticulum at high focus ; 6. equatorial view, two colpi ; 7. reticulum at high focus. — FIG. 8 - 12. *Norantea adamantium* — 8. tectum perforatum at high focus ; 9. endocolpus with circular middle part ; 10. optical section of polar view ; 11. columellae at low focus ; 12. ends of colpi in polar view — FIG. 13-14. *Norantea oxystylis* (Mandon 793) — 13. optical section of equatorial view ; 14. optical section of polar view — FIG. 15. *Norantea brasiliensis* — small, narrow endocolpus with indistinct circular middle part.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Species : N. delpiniana WITTM.

Comment : The *N. delpiniana* type has some affinities with the *N. cuneifolia* type. On the other hand the type is without doubt related to the *N. oxystylis* type (see below). The most important difference with the latter type is the distinct reticulum. In the *N. oxystylis* type the pollen grains are tectate ; however, this tectum can be perforated.

N. cuneifolia type
(Pl. I, fig. 5-7).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; grains slightly triangular, with obtuse angles ; sides convex. Outline in *equatorial view* ; grains circular or slightly rectangular with slightly truncate lateral sides and obtuse angles. *P:E ratio* ; grains ca. spheroidal to slightly oblate spheroidal.

Apertures : Ectoapertures ; colpi rather long, narrow, but not slit-like, sunken and with distinct costae colpi. *Endoapertures* ; endocolpi lalongate, narrow, small, rather indistinct, with distinct costae endocolpi, without a special middle part or with an indistinct one.

Exine : Exine thick (ca. 2 μ). Sexine as thick as nexine or only slightly thinner. Reticulum present, coarse ; muri thick, duplicolumellate ; lumina up to 3,5 μ, irregular, decreasing towards the colpi, columellae short and indistinct in optical section.

Measurements : P = 20,5-24,5 μ ; E = 22-25 μ.

Species : N. cuneifolia DELP.

Comment : The *N. cuneifolia* type has several characters in common with the *N. delpiniana* type (e.g., distinct reticulum, small and indistinct endoaperture). On the other hand, some important differences, such as shape, length of the colpi and the number of columellae in the muri of the reticulum keep both types apart. The type also shows some affinity to the *N. grandiflora* type ; e.g., reticulum and absence of a distinct middle part in several species of the latter type.

N. oxystylis type
(Pl. I, fig. 8-15 ; Pl. II, fig. 6 and 8).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; pollen grains distinctly angular with obtuse angles. Sides convex, outline in *equatorial view* ; grains circular or elliptic, not truncate at the lateral sides. *P:E ratio* : grains slightly prolate spheroidal, to slightly oblate spheroidal.

Apertures : Ectoapertures ; colpi long or rather long, slit-like, sunken and with costae colpi. *Endoapertures :* lalongate endocolpi, narrow, with distinct costae endocolpi, sometimes with an indistinct circular middle part.

Exine : Exine thick ; about 2 μ. Sexine as thick as nexine or slightly thinner. Columellae short and indistinct in optical section. Tectum present, smooth, sometimes with numerous, distinct perforations (*N. oxystylis, N. adamantium*).

Measurements : P = 18-25 μ ; E = 19-23 μ.

Species : N. adamantium Camb., *N. brachystachya* (RUSBY) de ROON, *N. brasiliensis* CHOISY, *N. oxystylis* BAILL.

Comment : The pollen grains of the *N. oxystylis* type are without doubt related to those in the *N. delpiniana* type (p. 208). The main difference is the distinct reticulum in the latter type, while in the former type the pollen grains are tectate. On the other hand, there is a striking resemblance between the pollen grains of the *N. oxystylis* type and those occurring in *Souroubea* (p. 223). The size, the P:E ratio, which is often prolate spheroidal, and especially, the long or rather long colpi give the pollen grains in the *N. oxystylis* this remarkable resemblance to the *Souroubea* pollen grains. Some species, however, already show a tendency to a P:E ratio which is spheroidal or even oblate spheroidal and in most grains the exine is thick (ca. 2 μ). But, the most striking difference is the small and narrow endocolpus in the *N. oxystylis* type, while those occurring in *Souroubea* are certainly more conspicuous.

N. oxystylis and *N. adamantium* resemble each other by the distinct tectum perforatum, which is sometimes tending towards a fine reticulum.

N. brasiliensis is slightly different because of its closed tectum and more oblate pollen grains. However, BARTH (1963) studying another specimen (REITZ and KLEIN 334) gives a P:E ratio which is spheroidal or slightly prolate spheroidal and this is in agreement with the P:E ratio of the other species of the group. Moreover, all other characters mentioned by BARTH are in close agreement with those found in the present study.

N. brachystachya, although placed in this type, differs in some characters. The tectum is closed (as in *N. brasiliensis*) and the colpus length is shorter than in any other species in the type. However, the narrow and small endocolpus and the absence of a special middle part, together with the characters of the exine points into the direction of the *N. oxystylis* type. The species of the *N. oxystylis*

type can be differentiated by the following table with differential characters :

Name	Colpi	Middle part	Tectum perfor.	Shape in polar view
N. brachystachya	rather long	—	—	slightly angular
N. brasiliensis	long	—	—	distinctly angular
N. Oxystylis	long	—	+	distinctly angular
N. adamantium	long	+	+	distinctly angular

N. grandiflora type
(Pl. II, fig. 1, 2 and 4).

Pollen class : Pollen grains 3-colporate ; rarely 4-colporate in some species.

Shape : Outline in *polar view* ; grains only slightly or distinctly triangular with obtuse angles, sides convex, outline in *equatorial view* ; circular or elliptic to slightly rectangular, sometimes slightly truncate at the poles. *P:E ratio* ; grains spheroidal to oblate spheroidal.

Apertures : Ectoapertures ; colpi rather long or short, narrow or slit-like, sunken, with distinct costae colpi. *Endoapertures* ; lalongate endocolpi, usually rather broad, outer ends diffuse, distinct costae endocolpi ; middle part present or absent, if present then either circular or lalongate elliptic.

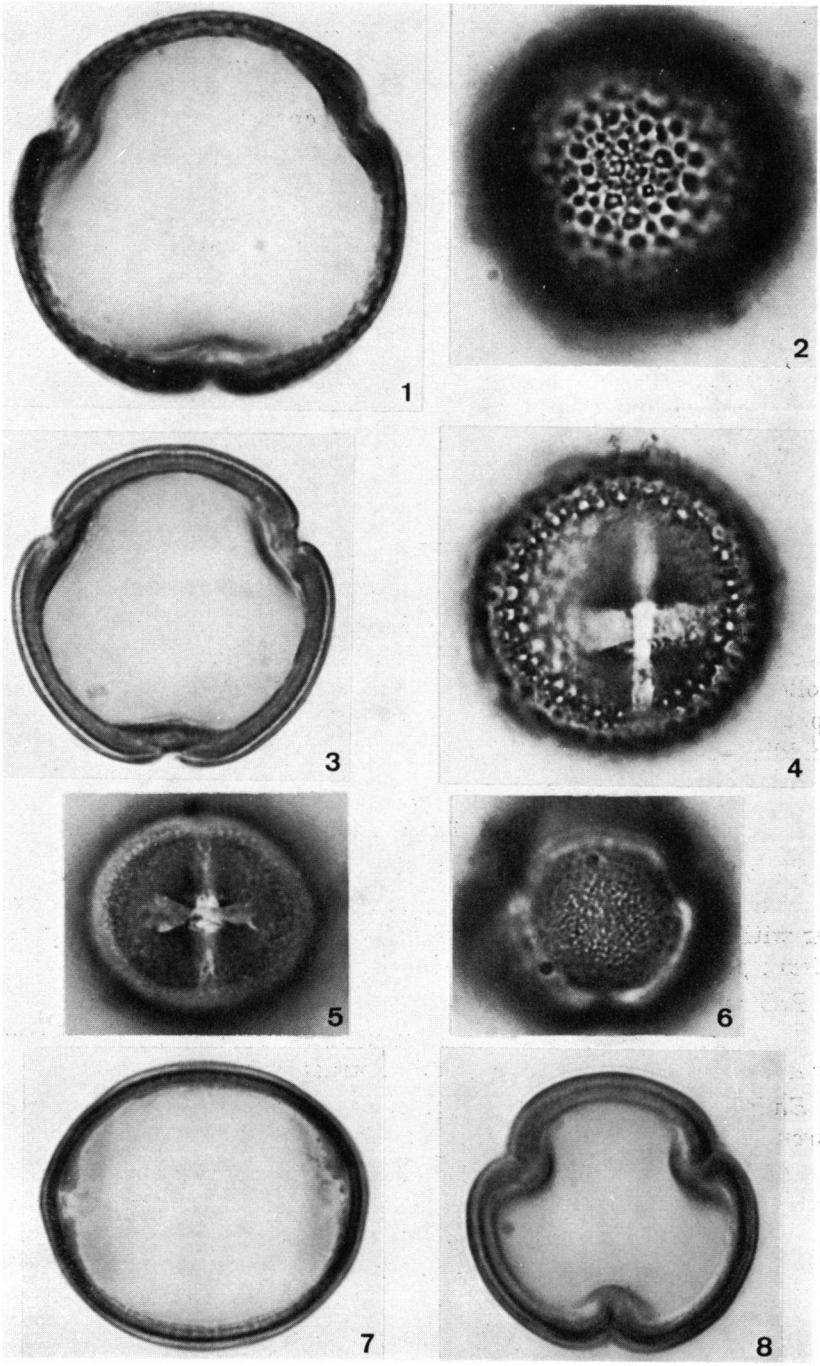
Exine : Exine rather thin or thick (1,5 - 2,5 μ). Sexine as thick as nexine or slightly thinner. Columellae short and rather indistinct in optical section. Reticulum fine or very fine, but always distinct ; muri thick, duplicolumellate ; lumina irregular, decreasing towards the colpi, usually ca. 1 μ wide or less.

Measurements : P = 21 - 32 μ ; E = 22 - 32 μ.

Species : N. curva MACBR., *N. glossostipa* de ROON, *N. grandiflora* de ROON, *N. obovata* G. DON, *N. pendula* LANJ. et v. HEERDT, *N. peduncularis* POEPP. et WITTM., *N. spiciflora* (JUSS.) KRUG et URBAN.

PLATE II (× 1600).

FIG. 1, 2, 4. *Norantea grandiflora* — 1. optical section of polar view ; 2. reticulum at high and low focus ; 4. endocolpus with diffuse outer ends, rather broad. — FIG. 3, 5, 7. *Norantea micradenia* — 3. optical section of polar view ; 5. rather long colpus, circular middle part in the endocolpus ; 7. equatorial view, elliptic outline — FIG. 6, 8. *Norantea brachystachya* — 6. O-L pattern at low focus ; 8. polar view in optical section.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Comment : This type is rather heterogeneous. The most important character, which all species have in common, is the fine reticulum. However, the species show marked differences in some other important characters e.g., the thickness of the exine and the middle part of the endocolpus. If these latter two characters are considered differential characters, then the species can be arranged according to the following table :

Name	Exine		Middle Part		
	thin	thick	lacking	o	○
N. curva	+				+
N. obovata	+				+
N. grandiflora		+			+
N. peduncularis		+		+	
N. pendula		+		+	
N. glossostipa		+	+		
N. spiciflora	+		+		

From this table it is clear, that *N. curva* and *N. obovata* are morphologically related and that *N. peduncularis* and *N. pendula* show some morphological affinities as well. *N. curva* and *N. obovata* have pollen grains, which resemble those of the *N. subsessilis* type (p. 215). Both groups of pollen have a rather thin exine and a circular middle part in the endocolpus.

N. micradenia type
(Pl. II, fig. 3, 5 and 7).

Pollen class : Pollen grains 3-colporate ; rarely 4-colporate.

Shape : Outline in *polar view* ; pollen grains only sightly triangular with obtuse angles, sides distinctly convex. Outline in *equatorial view* ; pollen grains distinctly elliptic, not truncate.

P:E ratio : oblate spheroidal.

Apertures : Ectoapertures ; colpi usually rather long or in some grains short, narrow, sunken, with distinct costae colpi.

Endoapertures ; lalongate endocolpi, narrow, with an indistinct circular middle part and distinct costae endocolpi.

Exine : Exine rather thin (1,5 - 2 μ). Sexine as thick as nexine or only slightly thinner. Columellae short and indistinct in optical section. However, a distinct LO pattern is visible at high focus. Grains tectate ; tectum smooth and with more or less distinct perforations.

Measurements : P = 23-26 μ ; E = 26 - 30 μ.

Species : N. micradenia de ROON.

Comment : The *N. micradenia* type shows several affinities with the *N. subsessilis* type (see below). Both types have : 1. an elliptical outline in equatorial view ; 2. a P:E ratio which is distinctly oblate spheroidal ; 3. a circular middle part in the endocolpus. In the *N. micradenia* type, however, the exine is somewhat thicker, the colpi are longer and there is a distinct LO pattern visible.

N. subsessilis type
(Pl. III, fig. 3 and 4).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; grains circular or only slightly angular, with obtuse angles, sides distinctly convex. Outline in *equatorial view* ; usually distinctly elliptical, not truncate. *P:E ratio* ; grains oblate spheroidal or rarely spheroidal (*N. robusta*).

Apertures : Ectoapertures ; colpi short, narrow, but not slit-like, not or only slightly sunken, with costae colpi. *Endoapertures* ; lalongate endocolpi rather broad, usually with a distinct circular middle part. In *N. sodiroi* this middle part is elliptic. Distinct costae endocolpi present.

Exine : Exine thin or rather thin (1,5 - 2 μ). Sexine as thick as nexine or slightly thinner. Columellae short and indistinct in optical section. At high focus usually no LO pattern visible. Tectum smooth, without perforations.

Measurements : P = 20 - 26 μ ; E = 23 - 27 μ.

Species : N. albido-rosea GILG, *N. robusta* de ROON, *N. sodiroi* GILG, *N. subsessilis* BENTH.

Comment : The *N. subsessilis* type comprises a remarkable homogeneous group of species. The type does not have much affinity with the other *Norantea* types. It is characterized by the short colpi and thin exine. The only pollen grains which show some similarity with the *N. subsessilis* type are present in the *N. grandiflora* type (*N. curva* and *N. obovata*) and in the *N. micradenia* type (p. 214).

N. weddelliana type
(Pl. III, fig. 1-2 and 7-8).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; pollen grains angular, with obtuse angles, sides convex. Outline in *equatorial view* ; usually circular, sometimes elliptic.

P:E ratio ; grains usually spheroidal, sometimes oblate spheroidal.

Apertures : Ectoapertures ; usually rather long colpi, rarely short or long ; usually narrow, but not slit-like, distinctly sunken, with costae colpi.

Endoapertures : usually rather broad, lalongate endocolpi, with diffuse outer ends ; middle part either slightly elliptic (lalongate) or circular. Distinct costae endocolpi present.

Exine : Exine thick (2-3 μ). Sexine as thick as or only slightly thinner than nexine, rarely distinctly thinner. Columellae short and rather indistinct in optical section. However, in surface view a distinct LO pattern is present. Tectum smooth, usually with perforations (many or few), sometimes without perforations.

Measurements : P = 23 - 29 μ ; E = 23 - 30 μ.

Species : N. costaricensis GILG, *N. jimenezii* (STANDL.) DE ROON, *N. weddelliana* BAILL.

Comment : This type might be regarded as a heterogeneous one. However, the combination of characters makes the type readily distinguishable. The most important characters for the classification of this type are the P:E ratio (usually spheroidal), the distinct granules in surface view (LO pattern) and the sexine which is almost always as thick as nexine or only slightly thinner (some specimens of *N. costaricensis* excepted). In these aberrant specimens of *N. costaricensis* the sexine is distinctly thinner than the nexine. By this character the specimens have some relationship with the *N. japurensis* type (*N. tepuiensis*). Other characters, such as the thickness of the exine, the length of the colpi and the LO pattern, keep these specimens in the *N. weddelliana* type nevertheless.

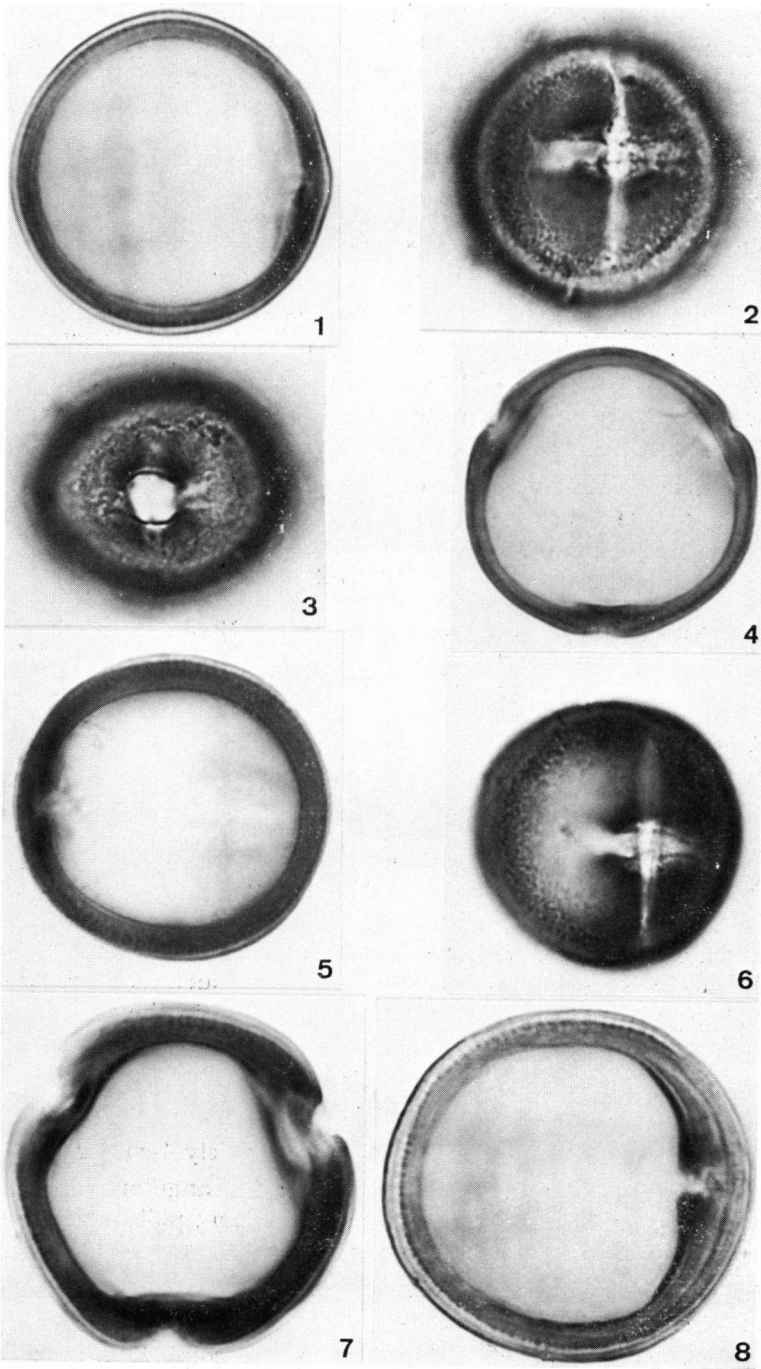
N. japurensis type
(Pl. III, fig. 5 and 6 ; Pl. IV, fig. 1 and 2).

Pollen class : Pollen grains 3-colporate.

Shape : Outline in *polar view* ; distinctly angular, with obtuse angles, sides convex. Outline in *equatorial view* : circular or elliptic to rectangular, often slightly truncate.

PLATE III (× 1600).

FIG. 1 - 2. *Norantea weddelliana* (Bang 390) — 1. optical section of equatorial view, exine thick, sexine ca as thick as nexine or slightly thinner ; 2. endocolpus with elliptic middle part. — FIG. 3 - 4. *Norantea subsessilis* — 3. short colpus and circular middle part in the endocolpus ; 4. optical section of polar view, rather thin exine. — FIG. 5 - 6. *Norantea brenesii* — 5. optical section of equatorial view, sexine distinctly thinner than nexine ; 6. short colpus, endocolpus with elliptic middle part. — FIG. 7 - 8. *Norantea costaricensis* — 7. Standley 47658, optical section of polar view, sexine distinctly thinner than nexine ; 8. Skutch 3441. optical section of equatorial view, sexine about as thick as nexine.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P : E ratio : spheroidal to slightly oblate spheroidal.

Apertures : *Ectoapertures* ; rather long or short colpi, narrow, usually slit-like, sunken, with distinct costae colpi. *Endoapertures* ; rather broad, lalongate endocolpi with diffuse or tapering outer ends ; middle part either circular or elliptic (lalongate) ; with distinct costae endocolpi.

Exine : Exine usually very thick, sometimes thick (2,5 - 3,5 μ). Sexine always distinctly thinner than nexine. Columellae short and rather indistinct in optical section. In surface view sometimes a rather distinct LO pattern is present, but more often this pattern is not distinguishable. Tectum smooth, without or with perforations.

Measurements : P = 24 - 31 μ ; E = 24 - 31 μ.

Species : *N. brenesii* STANDLEY, *N. japurensis* MART., *N. tepuiensis* DE ROON.

Comment : The species of this type can be differentiated by the following table with differential characters :

Name	Endocolpus						Perforations
	Outer ends		Colpus		Middle part		
	tap.	diff.	broad	narrow	○	o	
N. brenesii		+		+		+	−
N. japurensis....	+			+	+		− or few
N. tepuiensis....		+	+		+		+

This group of species has pollen grains which show some affinity with the *N. weddelliana* type (p. 215) ; e.g., shape, features of the endocolpus and the size of the grains. On the other hand, a close relationship with the *N. anomala* type cannot be denied, especially with those species having large pollen grains such as *N. guianensis* and *N. goyasensis*. The only difference is found in the shape.

N. anomala type
(Pl. IV, fig. 3 - 8).

Pollen class : Pollen grains 3-colporate ; rarely 4-colporate.

Shape : Outline in *polar view* ; pollen grains angular, with obtuse angles, sides convex. Outline in *equatorial view* ; pollen grains elliptic to rectangular, often slightly truncate.

P : E ratio : oblate spheroidal to suboblate.

Apertures : Ectoapertures ; rather long or short colpi ; narrow, slit-like, slightly sunken ; with distinct costae colpi. *Endoapertures* ;

rather broad or narrow endocolpi, lalongate, with diffuse or tapering outer ends ; middle part either circular or elliptic (lalongate) ; distinct costae endocolpi present.

Exine : Exine very thick or thick (2,5 - 3,5 μ). Sexine always thinner than nexine. Columellae rather indistinct and short in optical section ; also in surface view there is usually no LO pattern present. Tectum smooth, with or without perforations.

Measurements : P = 18 - 29 μ ; E = 20 - 31 μ.

Species : N. anomala H. B. K., *N. aurantiaca* SPRUCE ex WITTM., *N. cordaichida* G. DON, *N. droseriformis* RUSBY ex GILG, *N. goyasensis* CAMB., *N. guianensis* AUBL., *N. paraensis* MART., *N. sessilis* L. WILLIAMS, *N. coccinea* DE ROON, *N. flammifera* DE ROON, *N. ignescens* DE ROON.

Name	Middle part		Size			Endocolpus	
	○	o	large	med.	small	◇	=
N. sessilis	+				+		+
N. aurantiaca	+				+		+
N. flammifera Maguire et al. 53696	+				+		+
N. aff. peduncularis Schultes et al. 14589	+				+	+	
N. anomala		+			+		+
N. coccinea		+			+		+
N. cordaichida		+			+		+
N. paraensis		+		+			+
N. droseriformis	+ or	+		+		+	
N. ignescens	+			+			+
N. flammifera Agostini 402		+		+		+	
N. guianensis		+	+			+	
N. goyasensis		+	+			+	

Comment : The *N. anomala* type can easily be recognised by the thick to very thick exine, a sexine which is distinctly thinner than the nexine, and by the characteristic shape. Within the type three features show a variation which might be of importance for a further classification of the type.

1. The middle part circular or elliptic (lalongate).
2. The size of the grains. Most species have pollen grains with an equatorial diameter not exceeding 24 μ (small) ; some others have distinctly larger grains and these have a polar axis of at least 24 μ (large) ; however, both groups are not sharply delimited from each other, some species show pollen grains which are transitional (medium).

3. Endocolpi tapering or with diffuse outer ends and then rather broad. According to these features the table on p. 219 can be composed.

Evolutionary trends in *Norantea*.

In a previous paper on *Phyllanthus* (PUNT, 1967), the author regarded 3-colporate, reticulate pollen grains as the most primitive pollen grains in that genus. According to taxonomic studies in *Norantea*, the most primitive species happen to have 3-colporate, reticulate pollen grains as well (*N. delpiniana*, *N. cuneifolia*). Of course, pollen grains which are 3-colporate have to be considered advanced (VAN CAMPO, 1966). VAN CAMPO also stated, that « breviaxe pollen » might be primitive and, indeed, her pollen examples seem to point to such a conclusion. However, in *Phyllanthus* as well as in Marcgraviaceae, it is more likely that pollen grains with a P : E ratio larger than 1,0 (longiaxe) are more primitive than those with a P : E ratio smaller than 1,0.

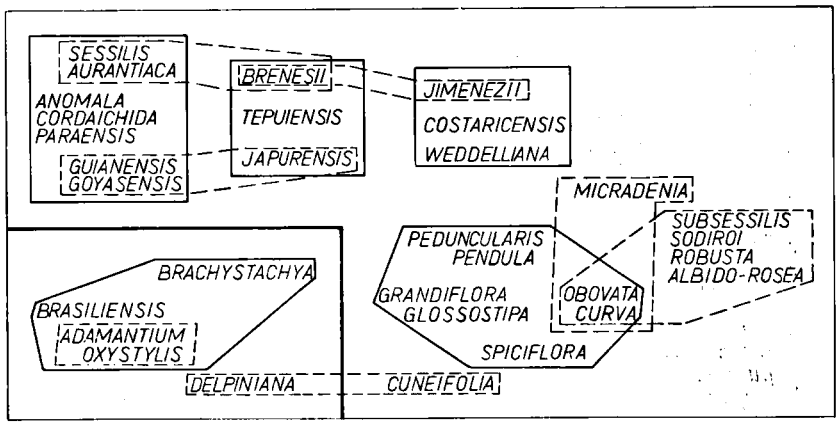
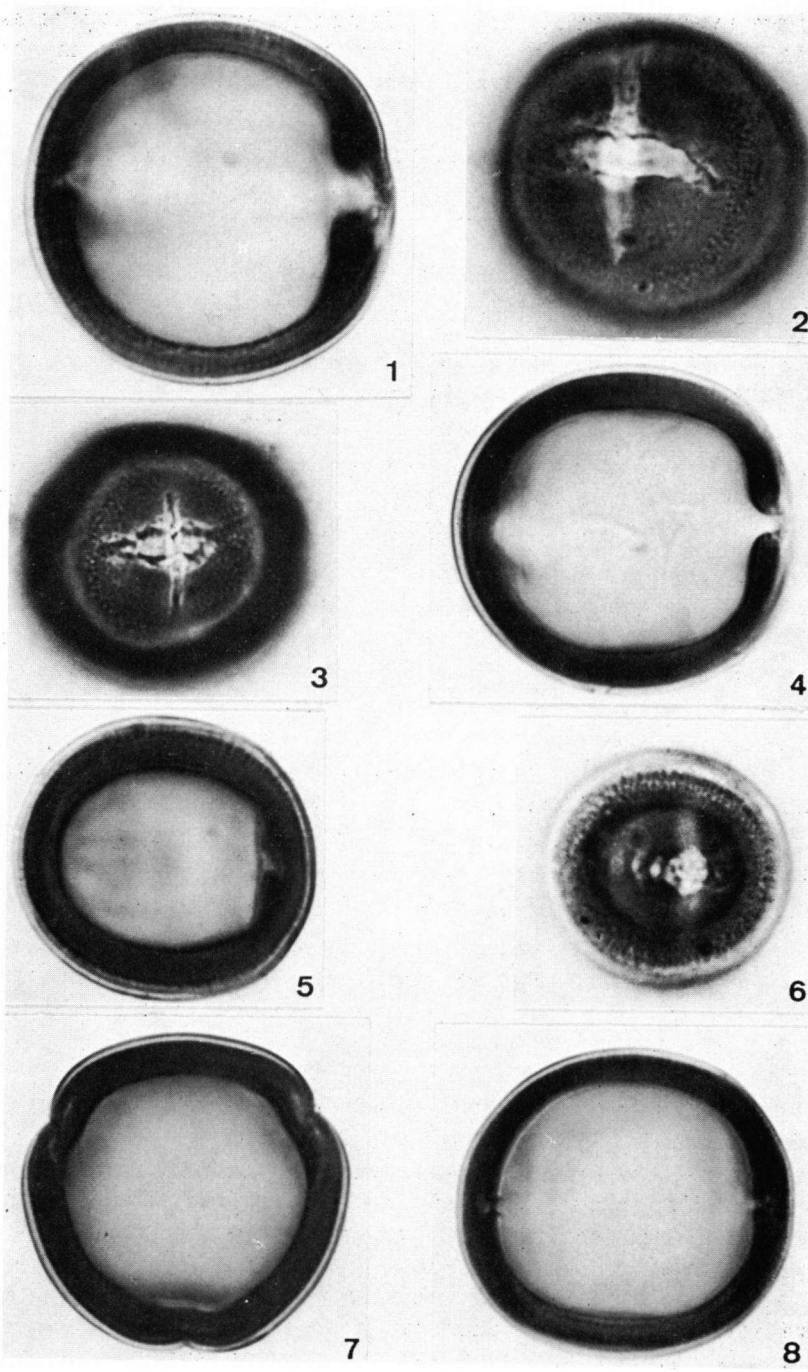


FIG. 2. — Scheme of pollen morphological relationships of *Norantea* species based on evolutionary trends. The heavy line devides the species into two groups which do not have much in common with each other. The thick lines enclose species belonging to the same type. The interrupted lines enclose species which do not belong to the same type, but show distinct pollenmorphological relationships.

PLATE IV (× 1600).

FIG. 1 - 2. *Norantea japurensis* (Maguire 31464) — 1. optical section in equatorial view, outline slightly truncate ; 2. short colpus and endocolpus with circular middle part and tapering outer ends. FIG. 3, 7, 8. *Norantea guianensis* (Oliveira 391) — 3. short colpus, endocolpus with slight elliptic middle part and with tapering outer ends. 7. optical section of polar view ; 8. optical section of equatorial view, outline slightly truncate. — FIG. 4. *Norantea goyasensis* (Macedo 3736) — optical section of equatorial view — FIG. 5 - 6. *Norantea aurantiaca* — 5. equatorial view, optical section, very thick exine and distinctly thinner sexine than nexine ; 6. short colpi, endocolpus with middle part.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If we accept pollen grains of *N. delpiniana* and *N. cuneifolia* as being primitive, then the pollen-morphological characters in the other pollen grains are advanced, and the following evolutionary trends may be constructed :

1. Reticulum : coarse ⟶ finely reticulate ⟶ tectum.
2. P : E ratio : prolate spheroidal ⟶ spheroidal ⟶ { oblate spheroidal. / suboblate.
3. Colpi : long ⟶ rather long ⟶ short.
4. Endocolpus : without middle part ⟶ { elliptic middle part. / circular middle part.
5. Exine : rather thin ⟶ thick ⟶ very thick.
6. Sexine : about as thick as nexine ⟶ distinctly thinner than nexine.

If these trends are taken as a starting point, then it is possible to compose a scheme as given in fig. 2. In this scheme the morphological features change gradually from primitive to advanced.

Following the trends, it is clear, that morphological change of the pollen grains might have followed three lines :

1. The first, short line beginning with the *N. delpiniana* type and ending in the *N. oxystylis* type. In the latter type *N. oxystylis* and *N. adamantium* are more primitive than *N. brasiliensis.*
2. The second, somewhat larger line begins with the *N. cuneifolia* type and ends in the *N. subsessilis* type via the species *N. curva* and *N. obovata* of the *N. grandiflora* type.
3. The third, and longest line also begins with the *N. cuneifolia* type, but it ends in the *N. anomala* type, via some species in the *N. grandiflora* type, the *N. weddelliana* type and the *N. japurensis* type.

It is not certain if the *N. micradenia* type has to be reckoned to the second line or to the third line. The type shows some resemblance to the *N. subsessilis* type but also to some species in the *N. grandiflora* type. However, the sexine is not reticulate and for this reason its position is intermediate between the two types.

Most interesting is the presence of a secondary aperture in the endoaperture. The endoaperture is always an endocolpus and in the more primitive species (*N. delpiniana, N. cuneifolia*) there is only this single, simple endocolpus. However, in more advanced species (e.g., *N. brenesii, N. anomala, N. brasiliensis*) in the middle part of the aperture, just below the crossing with the ectoaperture, an extra aperture is visible which can have either a circular or an elliptic (lalongate) shape. This feature is also present in some spe-

cies of *Souroubea* (p. see below), but it was not observed in *Ruyschia* species.

Following the evolutionary trends in its morphological change, it is quite evident, that two groups of pollen grains have evolved. One group with the *N. delpiniana* type and *N. oxystylis* type is still rather primitive and does not show much variation in its characters. On the other hand, the second group (with all other types in it) shows a broad scale of variable characters and the most advanced pollen grains of this group do not show much resemblance to the pollen grains of the first group.

POLLEN MORPHOLOGY OF THE GENUS *SOUROUBEA*.

General description of the *Souroubea* pollen grains.

(Pl. V, fig. 1 - 10 ; Pl. VI, fig. 3 - 9).

Pollen class : The pollen grains are usually 3-zonocolporate, a few species show very low percentages of 4-zonocolporate pollen grains, which are loxocolporate.

Shape : The outline of the pollen grains in polar view is usually triangular, often with obtuse angles (e.g., *S. peruviana*) and sometimes acute angles (*S. guianensis p.p.*). The sides are varying in convexity. In most species the angles are situated at the colpus area. In some species, however, the sides are so much convex, that the inner margin of the exine show obtuse angles not in the colpus area, but in the middle of the mesocolpia (*S. bicolor* group). The outline of the pollen grains in equatorial view is usually elliptic or less frequently circular. Few species show pollen grains which are rectangular obtuse in equatorial view. In these species the lateral sides are truncate.

P : E ratio : The pollen grains are in most cases prolate spheroidal or subprolate. They are sometimes spheroidal and rarely oblate spheroidal (e.g., *S. sympetala, S. loczyi* ssp. *minima*).

Apertures : Ectoapertures : The pollen grains have long or rather long colpi which are often slit-like or nearly so. The colpi are usually distinctly sunken and they are always accompanied by distinct costae. The colpus membrane is nudate. *Endoapertures* : The endocolpi are lalongate and they vary from narrow to rather broad. The outer ends are either diffuse or tapering. The margins have distinct costae. Some species show a more or less distinct middle part in the endocolpus which is situated just under the crossing with the colpus. This middle part is circular in shape.

Exine : The exine is usually rather thin (ca. 1,5 μ) and only few species show a rather thick one (up to 2 μ). The sexine is either as

thick as the nexine or slightly to distinctly thinner than the nexine. The columellae are short and rather indistinct in optical section. Some pollen grains, however, show a LO pattern at high focus. The pollen grains are always tectate. The tectum is smooth and don't show any processes. In many cases the tectum is provided with perforations.

Measurements : P = 19 - 30 μ ; E = 15 - 26 μ.

Discussion of the *Souroubea* pollen groups.

Souroubea pollen grains show a basic set of constant characters which make them readily distinguishable from *Norantea* pollen grains. However, most of these characters vary more or less and comparing the pollen grains of all species with each other, it is difficult to trace any system in the variability. It seems reasonable to suggest that within certain limits the pollen grains of *Souroubea* may vary into many directions thus giving rise to a number of short morphological series which are difficult to distinguish.

The most important, fairly constant characters (basic set) are :

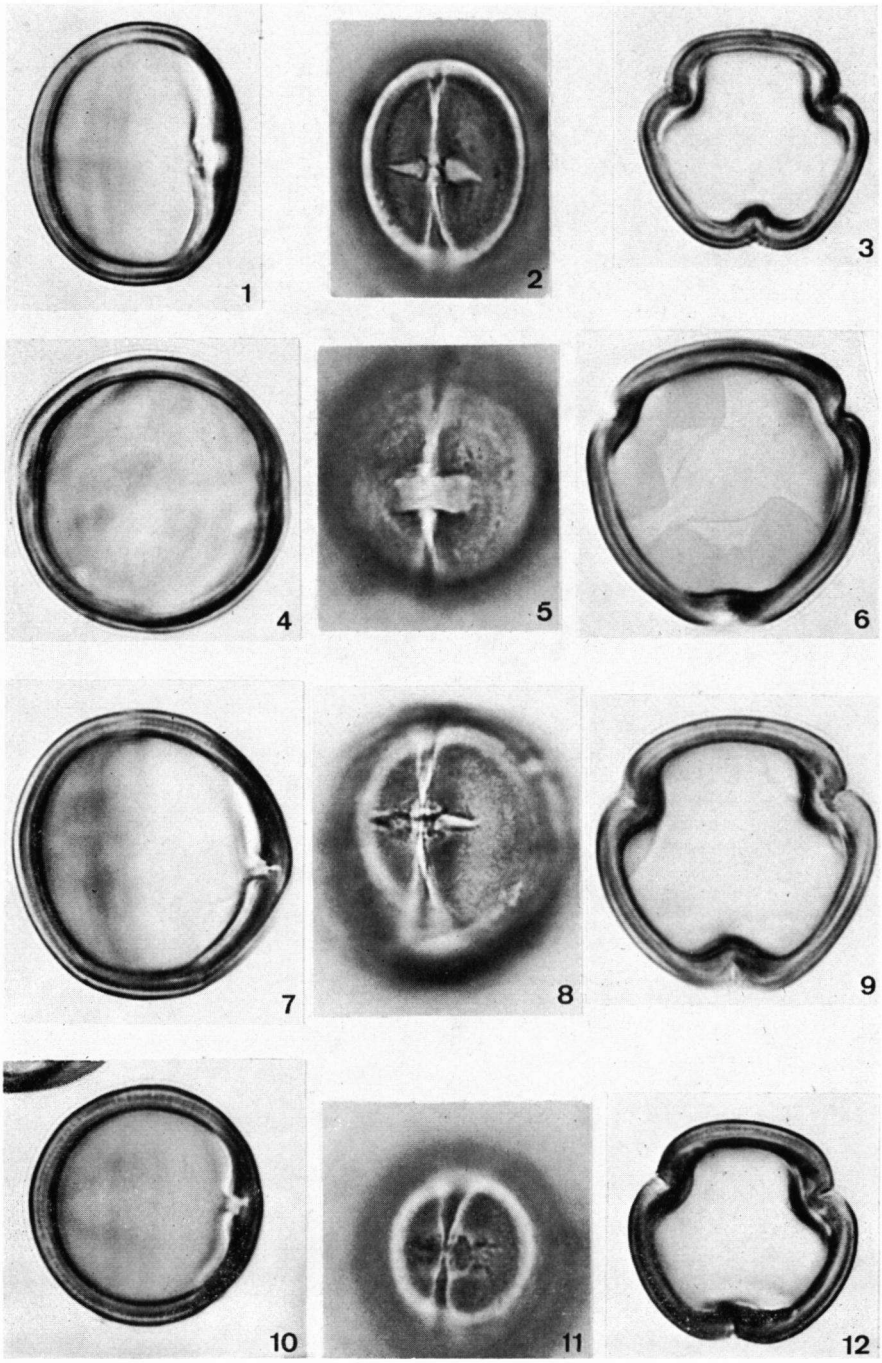
1. Pollen grains tricolporate ; longest axis usually short (i.e., usually not exceeding 25 μ).
2. Colpi always narrow, usually slit-like ; always long or rather long with distinct costae colpi.
3. The endoapertures are always lalongate endocolpi and show distinct costae endocolpi.
4. Exine rather thin (usually ca 1,5 μ ; sometimes up to 2 μ).
5. All grains are tectate, and this tectum can be perforated.
6. Columellae short and rather indistinct.
7. Pollen grains in polar view always angular.

Characters which vary more or less are :

8. The P : E ratio varies from subprolate via prolate spheroidal to slightly oblate spheroidal. The majority of the grains, however,

PLATE V (× 1600).

FIG. 1 - 3. *Souroubea peruviana* — 1. equatorial view, optical section, sexine about as thick as nexine ; 2. endocolpus without middle part, outer ends tapering ; 3. polar view, optical section, distinct angular outline. — *Souroubea guianensis* (Lindeman 757) — FIG. 4 - 6. equatorial view ; slightly truncate at lateral sides ; 5. endocolpus without middle part, with parallel margins ; 6. polar view, optical section. — FIG. 7 - 9. *Souroubea guianensis v. amazonica* (Prance 58796) — 7. equatorial view, optical section ; 8. endocolpus with circular middle part and tapering outer ends ; 9. equatorial view, optical section. — FIG. 10 - 12. *Souroubea loczyi* ssp. *loczyi* (Lundell 6492) — 10. equatorial view, optical section, circular outline ; 11. endocolpus with circular middle part ; 12. polar view, optical section.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possesses a polar axis which is larger than the equatorial diameter.

9. In polar view the angles are usually situated in the colpus area, however, sometimes the sides are so much convex, that the inner margin of the exine shows obtuse angles in the middle of the mesocolpia.
10. Endocolpus usually narrow (ca 2 μ or less) ; sometimes relatively broad (up to 3 μ).
11. Shape of the endocolpus ; margins often tapering to the outer ends, but in several species the margins are parallel with diffuse outer ends.
12. Thickness of the sexine ; sexine often about as thick as nexine, but in most cases slightly to distinctly thinner than nexine.
13. The presence of a middle part in the endocolpus. This feature, rather common in *Norantea* pollen grains, is not common at all in *Souroubea*, and if present usually indistinct.

According to the variability of some characters it is possible to distinguish three morphological groups. However, the delimitations of these groups being rather weak and being based on characters of minor importance, it seems better to avoid the term pollen type.

On the basis of the following differential characters three pollen groups have been distinguished :

S. peruviana group.

Pollen grains in polar view angular with the angles situated in the colpus area. Middle part in the endocolpus absent.

Species : *S. dasystachya, S. fragilis, S. gilgii, S. guianensis* v. *guianensis, S. guianensis* v. *bahiensis, S. guianensis* v. *cylindrica, S. pachyphylla, S. peruviana, S. platyadenia, S. sympetala pp., S. vallicola, S. venosa, Ruyschia clusiifolia, R. tremadena, R. phylladenia.*

S. stichadenia group.

Pollen grains in polar view angular with the angles situated in the colpus area. Middle part in the endocolpus present.

Species : *S. crassipes, S. exauriculata pp., S. guianensis v. amazonica, S. loczyi v. loczyi, S. loczyi v. minima, S. stichadenia, S. sympetala p.p.*

S. bicolor group.

Pollen grains angular. Sides so much convex, that the inner margin of the exine show obtuse angles in the middle of the mesocolpia. Middle part in the endocolpus absent or indistinct.

Species : *S. bicolor, S. corallina, S. crassipetala, S. exauriculata, p.p., S. intermedia.*

Evolutionary trends in *Souroubea*.

Distinct evolutionary trends as occurring in *Norantea* (see p. 220) are certainly less clear in *Souroubea*. In *Souroubea* most of the trends as occurring in *Norantea* are either not important at all or at least less well-marked. In the next lines the *Souroubea* features are discussed in comparison with the *Norantea* trends.

Trend 1. Reticulum. Not any species in *Souroubea* shows a reticulum and for this reason this trend is not important. All species are tectate and the only weak trend may be that several species show a tectum perforatum.

Trend 2. P : E ratio. The shape of the pollen grains in equatorial view may be of importance as there is a large variation with regard to the P : E ratio. Prolate spheroidal and subprolate grains are predominant and the most primitive shape might be one of these two. In that case the trend runs in two directions : one way from subprolate to prolate (*S. fragilis, S. dasystachya*) and the other way from prolate spheroidal to spheroidal and oblate spheroidal (*S. sympetala, S. guianensis*).

However, there is an obvious trend in the polar view which is not present in the *Norantea* species. Some species have pollen grains with angles not situated in the colpus area, but because of the convexity of the sides show obtuse angles in the middle of the mesocolpia. This feature is most prominent in *S. bicolor* and *S. exauriculata* (LIEBMANN 333). Besides this remarkable character, the other species from the *S. bicolor* group show two more characters which they have in common. A. In equatorial view the lateral sides run parallel (sides truncate). B. The outer ends of the endocolpus are diffuse and the endocolpus is rather broad. The latter two features can be present in some species of the *S. peruviana* group and *S. stichadenia* group, as well, but never in combination with the remarkable above mentioned polar view.

The described trend of the three joint characters might be the most important one in *Souroubea*, but it is not at all a clear one.

Trend 3. Colpi. Unlike the colpi in *Norantea* pollen, there is only a slight variation in the length of the colpi in pollen of *Souroubea*. The length is either long or rather long and consequently this trend is an unimportant one in *Souroubea*.

Trend 4. Endocolpus. In *Souroubea* the endocolpus shows several variable features. One of them (the middle part) might have some value as trend, but from the other ones it is far from obvious to decide in which direction the trend goes. In the lines below trends

are given, but they have to be considered suggestions of the author which cannot be proved by clear data.

1. Pollen grains without middle part ⟶ Middle part present ; either circular or elliptic.
2. Outer ends tapering ⟶ Outer ends parallel.
3. Width narrow ⟶ Width rather broad.

The occurence of a middle part in the endocolpus is certainly a more advanced character than the absence of this feature. The same trend occurs in *Norantea* in which genus the direction of this trend could be established without difficulty. The other two characters have less values as evolutionary trend but are of importance for the identification and grouping of the pollen grains.

Trend 5. Exine. The exine in pollen grains of *Souroubea* shows little variation in thickness and is therefore of no value as evolutionary trend.

Trend 6. Sexine. Usually the sexine is as thick as the nexine or only slightly thinner. In a few species the sexine is distinctly thinner than the nexine (e.g., *S. crassipes, S. guianensis*). Without doubt thickening of the nexine is also occurring in *Souroubea,* but this feature is not as striking as in *Norantea.*

POLLEN MORPHOLOGY OF THE GENUS *RUYSCHIA.*

General description of the *Ruyschia* pollen grains.

(Pl. VI, fig. 1 and 2).

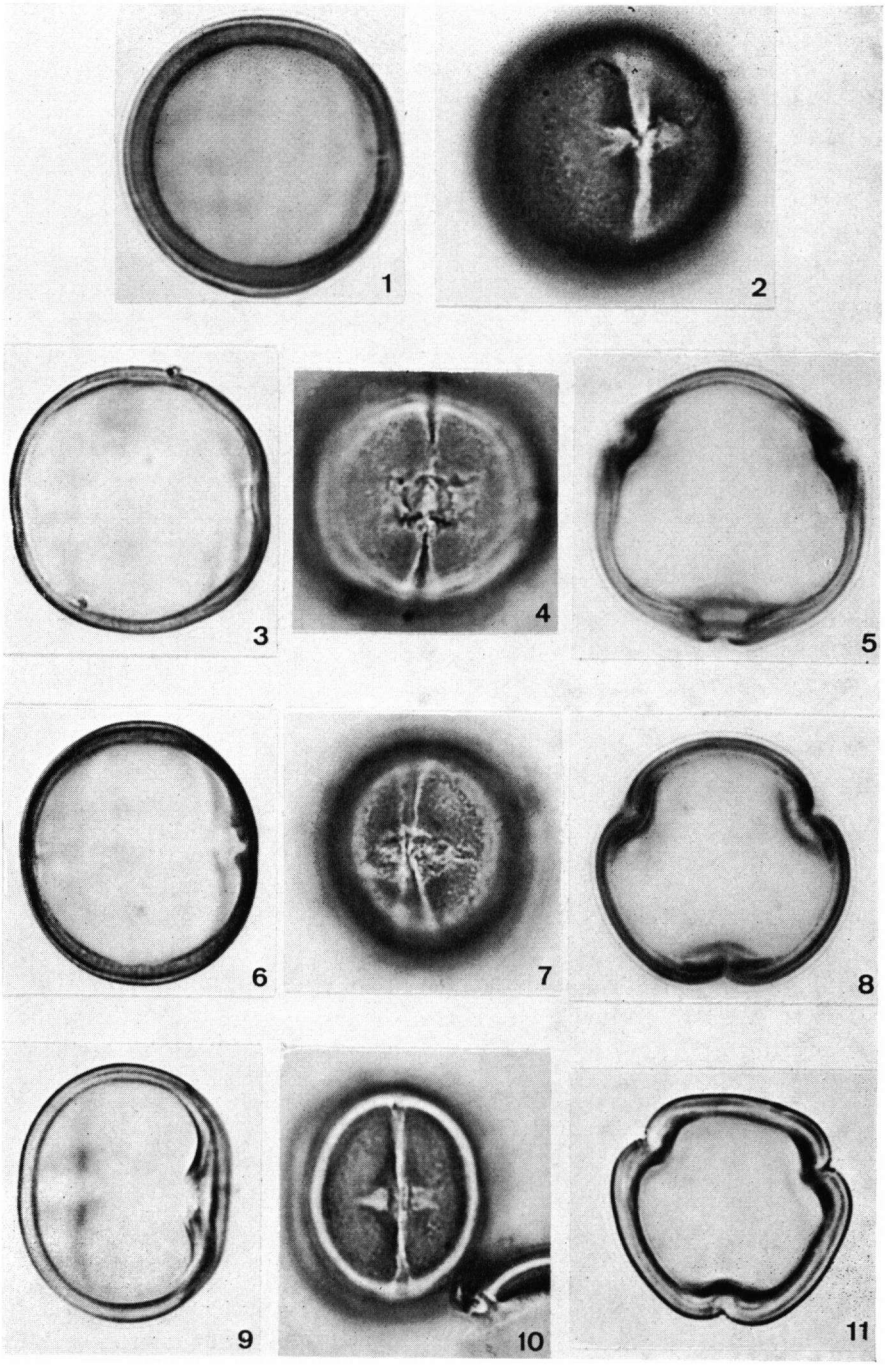
Pollen class : Pollen grains 3-zonocolporate.

Shape : The outline of the pollen grains in polar view is triangular, with obtuse angles. The sides are convex and inward bent at the angles where the colpi can be found. The outline in equatorial view is usually elliptic, and sometimes obtuse rectangular. In the latter case, the lateral sides only are slightly truncate.

P : E ratio : The pollen grains are slightly to distinctly prolate spheroidal.

PLATE VI (× 1600).

FIG. 1 - 2. *Ruyschia clusiifolia* — 1. equatorial view, optical section ; 2. endocolpus. — FIG. 3 - 5. *Souroubea bicolor* — 3. equatorial view, optical section, thin exine, truncate outline at lateral sides ; 4. endocolpus, rather broad, with indistinct circular middle part and parallel margins ; 5. polar view, optical section, outline with obtuse angles in the middle of the inside of the convex sides. — FIG. 6 - 8. *Souroubea stichadenia* — 6. equatorial view, optical section ; 7. endocolpus with circular middle part and tapering outer ends ; 8. polar view, optical section. — FIG. 9 - 11. *Souroubea platyadenia* — 9. polar view, optical section ; 10. endocolpus, without middle part, with tapering outer ends ; 11. polar view optical section.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Apertures : Ectoapertures : The colpi are long, narrow to slit-like and only slightly sunken. They are accompanied by distinct costae. *Endoapertures :* The lalongate endocolpus is narrow or rather broad and has tapering or parallel outer ends. The distinct costae which are accompanying the endocolpi lack a special middle part as described in the *Norantea* and *Souroubea* pollen grains (p. 222).

Exine : The exine is rather thin or thick (up to ca 2 μ). The sexine is about as thick as the nexine or distinctly thinner. The columellae are short and rather indistinct in optical section. In high focus, however, usually a rather distinct LO pattern is visible. The grains are tectate. This tectum is smooth and usually completely closed, but occasionally provided with perforations.

Measurements : P = 18 - 26 μ ; E = 17 - 24 μ.

Discussion of the *Ruyschia* pollen grains.

Pollen grains of the genus *Ruyschia* resemble much those occurring in the genus *Souroubea*. The long colpi, narrow and tapering endocolpus without middle part and especially the P : E ratio which is prolate spheroidal, bring the pollen grains nearest to *S. gilgii*, *S. pachyphylla* and *S. venosa*. All three mentioned species belong to the *S. peruviana* group (p. 226).

Conclusions.

Norantea : 1. The pollen grains in the genus *Norantea* are usually different from those occurring in *Souroubea* and *Ruyschia*. Some of the characters which never occur in the latter two genera are : A. Reticulate grains. B. Short colpi. C. Thick or very thick exine. Some other characters are exceptions in the genera *Souroubea* and *Ruyschia* but occur regularly and more distinctly in the genus *Norantea* : D. Pollen grains with a P : E ratio which is spheroidal, oblate spheroidal or suboblate. E. Sexine distinctly thinner than nexine. F. The presence of an elliptic or circular middle part in the endocolpus.

2. Nine pollen types have been established. These types could be differentiated with distinct characters.

3. Several evolutionary trends can be distinguished in *Norantea*. These trends are obvious and have been used to make a scheme in which the pollen types gradually change from primitive to advanced.

4. Following the trends it is possible to compose three lines of pollen-morphological change (fig. 2). A. A short line, beginning with the *N. delpiniana* type and ending in the *N. oxystylis* type. B. A larger line, beginning with the *N. cuneifolia* type and ending in the

N. subsessilis type via the species *N. curva* and *N. obovata* of the *N. grandiflora* type. C. The longest line also begins with the *N. cuneifolia* type, but it ends in the *N. anomala* type via some species of the *N. grandiflora* type, the *N. weddelliana* type and the *N. japurensis* type.

Souroubea and Ruyschia : 1. Pollen grains of *Souroubea* can be distinguished from those of *Norantea* by taking together several characters. Some of these characters are : P : E ratio : larger 1 ; tectum ; colpi long or rather long ; exine rather thin. The pollen grains of *Ruyschia* can not be differentiated from those of *Souroubea.*

2. Three pollen groups have been distinguished with the aid of a few rather obvious characters. However, there are so many transitions and the delimitations are so vague, that the term pollen type has been rejected for these groups.

3. The *S. stichadenia* group and *S. bicolor* group are the smallest ones. They are based on one or two special characters. The *S. peruviana* group comprises most of the other species and consequently is rather heterogeneous.

4. Evolutionary trends may be distinguished. However, being only few in number and weak in comparison with those occurring in *Norantea,* these trends cannot be used for distinct series.

Summary.

A pollen-morphological study has been carried out on three genera of the Marcgraviaceae (*Norantea* AUBLET, *Souroubea* AUBLET and *Ruyschia* JACQUIN). Nine pollen types in *Norantea* and three pollen groups in *Souroubea* could be established. The pollen grains of *Ruyschia* could not be differentiated from those of *Souroubea.* Several distinct evolutionary trends have been distinguished in *Norantea.* These evolutionary trends were less distinct in *Souroubea.* A key to the pollen types has been given in addition.

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