

Pollen morphology of *Curroria*, *Mondia*, *Socotranthus* and *Stomatostemma* (Periplocaceae)

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ABSTRACT

The pollen morphology of *Curroria* Planch., *Mondia* Skeels, *Socotranthus* Kuntze and *Stomatostemma* N.E. Br. was studied. All the genera are characterized by pollen grains arranged in tetrads. The arrangement of the grains may be rhomboidal, tetrahedral or decussate. The 4-6 pores present are restricted to the junction area of adjacent grains. The exine is smooth. Exine structure consists of an outer, homogeneous stratum (tectum) subtended by a granular stratum. The intine is well developed. The pollen grains of tetrads are connected by wall bridges (cross-wall cohesion). Except for small differences which may occur between species and genera in pollen size and arrangement of tetrads, the pollen is uniform in morphology.

UITTREKSEL

Die stuifmeelmorfologie van *Curroria* Planch., *Mondia* Skeels, *Socotranthus* Kuntze en *Stomatostemma* N.E.Br. is bestudeer. Al die genera word gekenmerk deur stuifmeelkorrels wat in tetraëdes gerangskik is. Die rangskikking van die stuifmeelkorrels kan romboïdaal, tetraëdries of kruisgewys wees. Vier tot ses porieë kom voor en hulle is beperk tot die aansluitingsgebied tussen aangrensende stuifmeelkorrels. Die eksien is glad en bestaan uit 'n buitenste homogene stratum (tektum) en granulêre stratum daaronder. Die intien is goed ontwikkel. Die stuifmeelkorrels van tetraëdes is verbind deur wandbrûe (dwarswandkohesie). Met die uitsondering van klein verskille tussen spesies en genera in stuifmeelgrootte en rangskikking van tetraëdes, stem die stuifmeelkorrels in morfologie ooreen.

INTRODUCTION

Periplocaceae and Asclepiadaceae are two closely allied families with several features in common. The former was a subfamily (Periplocoideae) of the latter, but raised to family status by Schlechter (1924), a concept followed by Bullock (1957), a well known expert in this group. The Periplocaceae is related to the Apocynaceae on the one hand and to the Asclepiadaceae on the other. All three families have in common a milky latex, flowers with coronas, fruits composed of paired follicles and seeds with comas of hairs. The Periplocaceae is distinguished by its spatulate pollen carriers and pollen grains united in tetrads. This contrasts with single-grained pollen and absence of pollen carriers in the Apocynaceae, and pollinia attached to wishbone-shaped translators in the Asclepiadaceae.

Of the 50 genera included in the Periplocaceae, approximately 20 occur in Africa. Among these *Raphionacme* Harv. is the largest with 35 species endemic to Africa (Verhoeven & Venter 1988) and one endemic to Arabia (Miller & Biagi 1988). *Raphionacme* is also the only herbaceous genus, although a number of its species are climbers. Most of the other genera are lianous and a small number are shrubs.

Little information is available on the pollen morphology of the Periplocaceae. Schill & Jäkel (1978) investigated representatives of the following Periplocaceae in their study on the pollinaria of the Asclepiadaceae: *Cryptostegia* R. Br., *Ectadiopsis* Benth., *Hemidesmus* R. Br., *Omphalogonus* Baill., *Parquetina* Baill., *Periploca* L.,

Raphionacme, *Tacazzea* Decne. and *Zygostelma* Benth. Data on tetrad size and number of pores for nine collections of *Raphionacme*, three species of *Periploca*, two species of *Tacazzea*, and one species of *Cryptostegia*, *Ectadiopsis*, *Hemidesmus*, *Omphalogonus*, *Parquetina* and *Zygostelma* are also given. Lebrun *et al.* (1984) in their identification of *Raphionacme bingeri* (A. Chev.) Lebrun & Stork, give SEM results on seven *Raphionacme* species. Verhoeven & Venter (1988) have examined the pollen of 35 *Raphionacme* species; Verhoeven *et al.* (1989), five *Tacazzea* species and the monotypic genus *Petopentia* Bullock; and Venter *et al.* (1990) three species of *Ectadium* E. Mey.

In the present study pollen of *Curroria* Planch., *Mondia* Skeels, *Stomatostemma* N.E. Br. and *Socotranthus* Kuntze was examined with special reference to taxonomy. This paper thus constitutes part of a comprehensive palynological investigation and taxonomic revision of the African taxa of the Periplocaceae currently being undertaken by the authors.

Taxonomic aspects and distribution of genera

Curroria comprises five species. *C. decidua* Planch. is divided into three subspecies (Bullock 1953). With the exception of *C. decidua* subsp. *decidua* which occurs in southwestern Africa (Angola, Namibia and South Africa), all the other *Curroria* species and subspecies occur in the desert areas of east and northeast Africa (Tanzania, Kenya, Somalia, Ethiopia, with outlying stations in the Hadramawt and Socotra) (Bullock 1953). *Curroria* species are robust, erect shrubs or scramblers. The linear to spatulate leaves are borne in clusters on short shoots and opposite on long shoots. The petiole is absent or very short. Flowers are solitary or occur as few-flowered cymes in the axils of the leaves.

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Socotranthus is a monotypic genus. *S. socotranus* (Balf. f.) Bullock is found on the island of Socotra (Suqutra) east of the coast of Somalia. This is a large woody shrub of arid habitats. Its suborbicular leaves are opposite and the white flowers are grouped together in terminal cymes.

Mondia has two species, *M. ecornuta* (N.E. Br.) Bullock and *M. whitei* (Hook. f.) Skeels. Both species are lianas of moist forest in tropical and subtropical regions of Africa. They both bear large, cordate leaves and many-flowered axillary cymes. The flowers are showy, ranging from yellowish to reddish in colour.

Stomatostemma also comprises two species, *S. monteiroae* (Oliv.) N.E. Br. and *S. pendulina* Venter & D.V. Field. The first species is a climber with ovate leaves and large cymes of whitish-purple flowers, whereas the latter is a virgate shrub with linear leaves and large cymes of white flowers. Both species occur in dry forest.

MATERIAL AND METHODS

Pollen was obtained from herbarium specimens. For light microscopy (LM) pollen was acetolysed according to the method of Erdtman (1960), mounted in glycerine jelly and sealed with paraffin wax. Samples were examined with a Zeiss Photomicroscope. Measurements of tetrad size are based on a minimum of 15 tetrads per specimen. For scanning electron microscopy (SEM), pollen was

acetolysed, air-dried on stubs, coated with gold and examined with a Jeol Winsem 6400 microscope. For transmission electron microscopy (TEM) fresh material was used. Pollen carriers were fixed in 3% phosphate-buffered glutaraldehyde, postfixed in 1% osmium tetroxide, dehydrated in ethyl alcohol and embedded in Spurr's low-viscosity resin. Sections were cut with a glass knife, stained with uranyl acetate, followed by lead citrate, and examined with a Philips 300 electron microscope at 60 kV.

Pollen specimens examined

Curroria brevifolia Balf. f., no material available.

C. decidua subsp. *decidua* Planch., Warmbad, Namibia, Mar. 1986, Beukes 22 (BLFU); Mariental, Namibia, Sept.-Mar. 1959, Werdermann & Oberdieck 2261 (K); Usakos, Namibia, Feb. 1969, Jensen 93 (WIND); Ruacana Falls, Namibia, De Winter & Giess 7105 (WIND).

C. decidua subsp. *gillettii* (Hutch. & Bruce) Bullock, no material available.

C. decidua subsp. *volubilis* (Balf. f.) Bullock, Kishen, Socotra, Aug. 1956, Gwynne 96 (BM).

C. macrophylla A.R. Smith, Abd al Kuri, Somalia, Oct. 1966, Virzo A27 (K).

C. migiurtina (Chiov.) Bullock, no locality, no date, Collette 198 (K); Eil, Somalia, Nov. 1986, Lavranos & Carter et al. 24945 (K).

C. volubilis (Schltr.) Bullock, Yaïda, Tanzania, Jan. 1970, Richards 25306 (K); Harrar, Ethiopia, Nov. 1970, De Wilde 7279 (WAG); Nyambiti, Tanzania, Mar. 1953, Tanner 1274 (BR).

Mondia ecornuta (N.E. Br.) Bullock, Pangani District, Tanzania, May 1950, Faulkner 558 (K); Kilifi District, Kenya, June 1973, Musyoki & Hansen 956 (K); Momyondzi, Congo, Nov. 1964, Bouquet 631 (P).

TABLE 1.—Diameter of pollen tetrads (μm)

Taxon		Tetrahedral	Rhomboidal
<i>Curroria</i>			
<i>brevifolia</i>		—	—
<i>decidua</i>			
subsp. <i>decidua</i>	1	32.5 (30–34) \pm 1.3 \times 31.3 (30–33) \pm 1.6	38 \times 28
	2	32.9 (30–36) \pm 1.4 \times 30.4 (27–34) \pm 2.1	34 \times 30
	3	32.0 (30–34) \pm 1.4 \times 30.9 (27–33) \pm 1.8	
	4	33.0 (30–36) \pm 1.2 \times 31.9 (30–33) \pm 0.9	
subsp. <i>gillettii</i>		—	—
subsp. <i>volubilis</i>	1	32.8 (30–36) \pm 2.3 \times 25.5 (24–28) \pm 1.0	36 \times 24
<i>macrophylla</i>	1	29.4 (27–35) \pm 3.1 \times 22.5 (22–24) \pm 1.1	36 \times 24
<i>migiurtina</i>	1	36.0 (31–41) \pm 2.8 \times 26.4 (22–28) \pm 2.1	41 \times 26
	2	33.9 (31–36) \pm 1.6 \times 25.3 (23–27) \pm 1.2	41 \times 24
<i>volubilis</i>	1	37.5 (29–42) \pm 4.0 \times 29.0 (27–32) \pm 1.6	44.5 (39–50) \pm 2.9 \times 28.5 (24–33) \pm 2.0
	2		46.3 (38–54) \pm 4.2 \times 28.5 (26–32) \pm 1.9
	3		48.5 (45–55) \pm 2.8 \times 27.5 (25–32) \pm 1.3
<i>Mondia</i>			
<i>ecornuta</i>	1	43.3 (41–46) \pm 1.7 \times 40.9 (38–42) \pm 1.4	53.3 (48–60) \pm 4.2 \times 46.7 (41–58) \pm 4.4
	2	43.9 (41–49) \pm 2.3 \times 39.6 (36–45) \pm 2.8	56 \times 42
	3	45 \times 42	57.3 (49–67) \pm 4.0 \times 44.6 (38–54) \pm 5.0
<i>whitei</i>	1	42.8 (39–45) \pm 2.1 \times 40.4 (36–44) \pm 3.2	
	2	41.4 (39–46) \pm 1.9 \times 40.0 (39–41) \pm 0.7	
<i>Socotranthus</i>			
<i>socotranus</i>	1	33.3 (28–36) \pm 2.9 \times 24.9 (22–27) \pm 1.8	
<i>Stomatostemma</i>			
<i>monteiroae</i>	1	52.7 (50–58) \pm 2.3 \times 51.5 (49–54) \pm 1.8	61 \times 51
	2	47.8 (45–50) \pm 1.5 \times 46.4 (43–50) \pm 1.8	55 \times 43
	3	44.7 (42–48) \pm 1.4 \times 42.2 (39–45) \pm 2.1	53 \times 39
<i>pendulina</i>	1	31.6 (29–35) \pm 1.9 \times 29.5 (27–32) \pm 1.4	39 \times 28

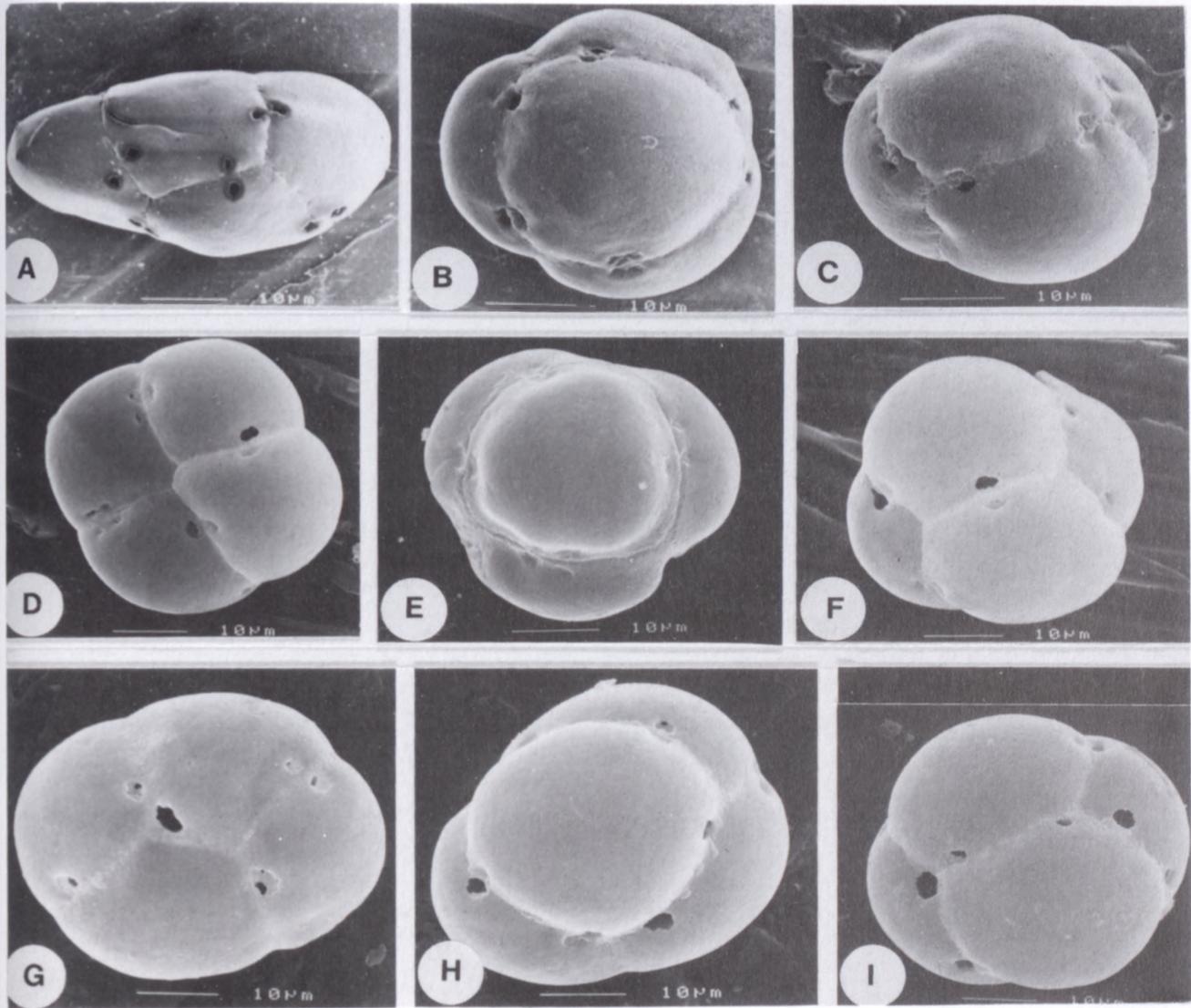


FIGURE 1.—SEM of tetrads of species. A, *Curroria volubilis*, Richards 25306 (K), rhomboidal tetrad. B, C, *C. decidua* subsp. *decidua*: B, tetrahedral tetrad, De Winter & Giess 7105 (WIND); C, decussate tetrad, Beukes 22 (BLFU). D–F, *Mondia whitei*: D, rhomboidal tetrad, Venter 9068 (BLFU); E, tetrahedral tetrad, Scheepers 1058 (PRU); F, decussate tetrad, Venter 9068 (BLFU). G–I, *Stomatostemma monteiroae*, Pooley 293 (NU): G, rhomboidal tetrad; H, tetrahedral tetrad; I, decussate tetrad. Scale bars = 10 µm.

M. whitei (Hook. f.) Skeels, Duiwelskloof, South Africa, Nov. 1960, Scheepers 1058 (PRU); Bloemfontein (glasshouse), South Africa, Dec. 1984, Venter 9068 (BLFU).

Socotranthus socotranus (Balf. f.) Bullock, Aola, Socotra, Mar. 1953, Popov 275 (BM).

Stomatostemma monteiroae (Oliv.) N.E. Br., Josini, South Africa, Nov. 1983, Venter 8988 (BLFU); Umfolozi Game Reserve, South Africa, Dec. 1961, Ward 3921 (PRE); Ndumu Game Reserve, South Africa, Dec. 1968, Pooley 293 (NU).

S. pendulina Venter & D.V. Field, Namina, Mozambique, July 1962, Leach & Schelpe 11441 (K).

RESULTS

Pollen morphology

The pollen grains in the four genera are united in tetrads, with the grains arranged rhomboidally (Figures 1A, D, G; 2A, D, G), tetrahedrally (Figures 1B, E, H; 2B, E, H) or decussately (Figures 1C, F, I; 2C, F, I; 3). The number of pores of individual grains of the tetrads may vary, but the morphology and position are the same for all the genera investigated. The pores are round, oval or irregular and

are restricted to the junction area of adjacent grains. Pores are sometimes covered with a thin layer of exine material.

Curroria

Pollen grains are arranged rhomboidally (Figures 1A; 2A), tetrahedrally (Figures 1B; 2B) or decussately (Figures 1C; 2C). In *C. volubilis* (Schltr.) Bullock the most common arrangement is rhomboidal, whereas in the other species it is tetrahedral and decussate. Size of tetrads varies from 27–42 × 22–34 µm (tetrahedral) to 34–55 × 24–33 µm (rhomboidal) (Table 1). Individual grains of tetrads have 4–6 pores.

Mondia

Pollen grains are arranged rhomboidally (Figures 1D; 2D), tetrahedrally (Figures 1E; 2E) or decussately (Figures 1F; 2F). Although rhomboidally arranged grains are present, the most common arrangements are tetrahedral and decussate. Size of tetrads varies from 39–49 × 36–45 µm (tetrahedral) to 48–67 × 38–58 µm (rhomboidal) (Table 1). Individual grains of the tetrads have 4–6 pores.

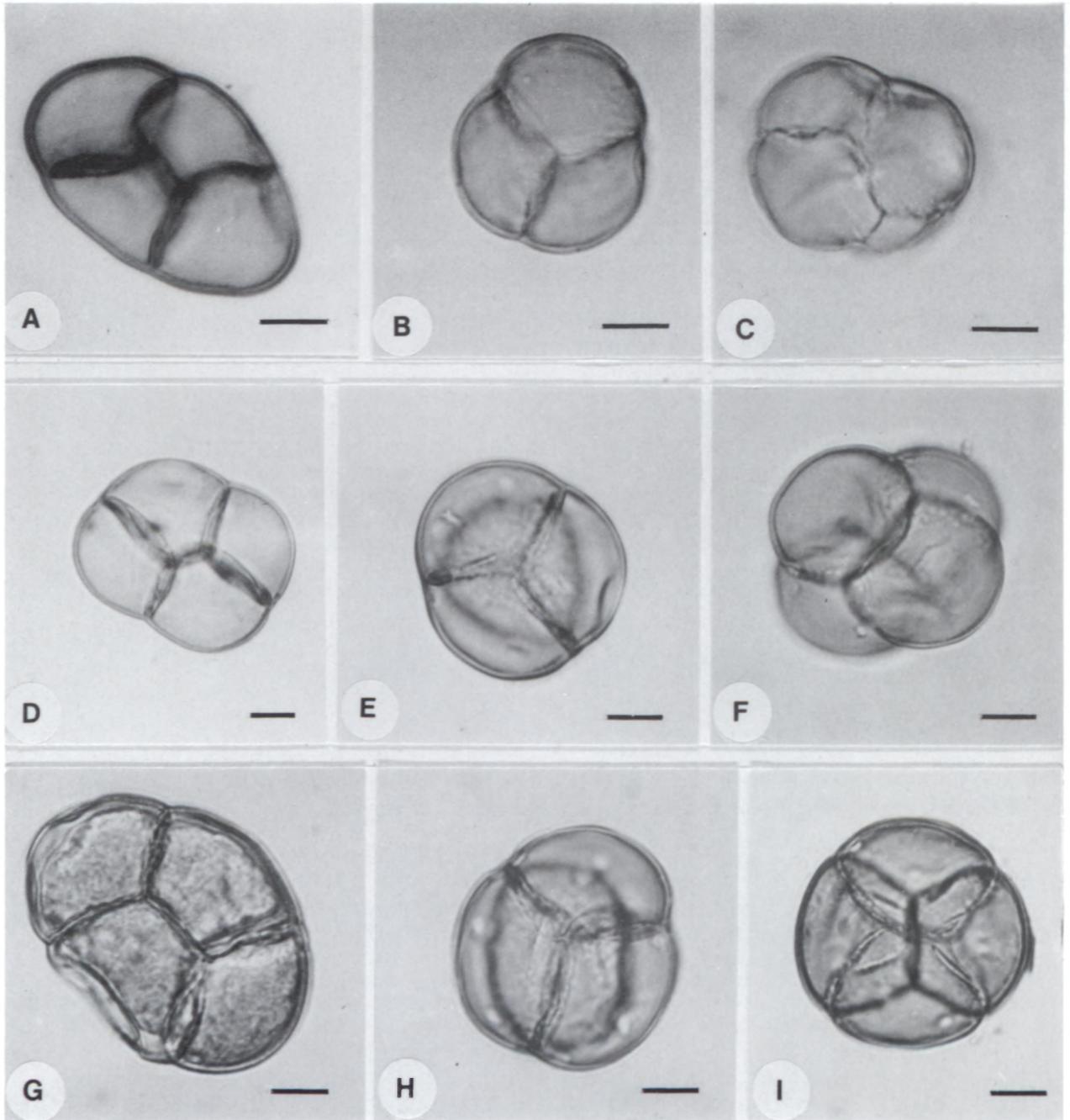


FIGURE 2.—LM photographs of tetrads of species. A, *Curroria volubilis*, Richards 25306 (K), rhomboidal tetrad. B, C, *C. decidua* subsp. *decidua*, Beukes 22 (BLFU): B, tetrahedral tetrad; C, decussate tetrad. D, E, *Mondia ecornuta*, Faulkner 558 (K): D, rhomboidal tetrad; E, tetrahedral tetrad. F, *M. whitei*, Venter 9068 (BLFU), decussate tetrad. G–I, *Stomatostemma monteiroae*: G, rhomboidal tetrad, Venter 8988 (BLFU); H, tetrahedral tetrad, Pooley 293 (NU); I, decussate tetrad, Pooley 293 (NU). Scale bars = 10 μ m.

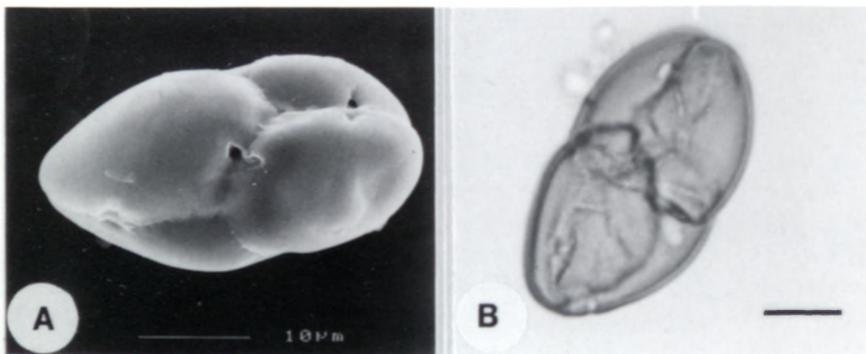


FIGURE 3.—Decussate tetrad of *Socotranthus socotranus*, Popov 275 (BM). A, SEM; B, LM photograph. Scale bars = 10 μ m.

Socotranthus

Pollen grains are arranged decussately (Figure 3) or tetrahedrally, very seldom rhomboidally. The decussate arrangement differs from that observed in other genera, in that the cells are arranged more parallel to each other and not perpendicular. Size of tetrads varies from $28-36 \times 22-27 \mu\text{m}$ (tetrahedral) (Table 1). Individual grains of the tetrads have 4-6 pores.

Stomatostemma

Pollen grains are arranged rhomboidally (Figures 1G; 2G), tetrahedrally (Figures 1H; 2H) or decussately (Figures 1I; 2I). The most common arrangements are tetrahedral and decussate. Size of tetrads varies from $29-58 \times 27-54 \mu\text{m}$ (tetrahedral) to $39-61 \times 28-51 \mu\text{m}$ (rhomboidal) (Table 1). Individual grains of the tetrads have 4-6 pores.

Exine structure

The exine is smooth and covered with a thin electron-dense layer (Figure 4A, arrow). Exine structure consists of an outer, homogeneous stratum (tectum) subtended by a granular stratum (Figure 4B). The tectum and granular stratum have the same electron density but the granular stratum has an irregular appearance because of channels which occur throughout it. The two layers are separated by a discontinuous line of osmiophilic substance. The fibrillar intine is well developed. The internal walls have the same structure as the exterior wall. Wall bridges consisting of intine and granular layer occur between adjacent grains (Figure 4C). The intine wall bridges indicate the position of pores in the internal wall of acetolysed pollen grains.

DISCUSSION

Compound pollen grains occur in more than 56 families of angiosperms (Erdtman 1945; Walker & Doyle 1975; Knox & McConchie 1986). The cohesion mechanisms in mature polyads were discussed by Knox & McConchie (1986). The cohesion of compound pollen occurs by attachment of the tectum (simple cohesion) or by connecting wall bridges (cross-wall cohesion). In cross-wall cohesion wall bridges are present in the common wall between adjacent grains, and these bridges comprise intine and granular layer in the Periplocaceae.

Pollen tetrads and polyads are common in a number of families and have been used in systematic treatments to separate genera and species (Oldfield 1959; Skvarla *et al.* 1975; Takahashi 1986). In the Mimosoideae extensive use of tetrads and polyads is made to separate genera (Guinet 1981a, b; Niezgodá *et al.* 1983). In the Periplocaceae, *Raphionacme* can be distinguished palynologically from the other genera by the 8-16 pores per pollen grain (Verhoeven & Venter 1988) as against 8-10 in *Baseonema* Schltr. & Rendle and 4-6 in the other genera. The monotypic *Petopentia natalensis* (Schltr.) Bullock can be distinguished from the other genera by the presence of linear and T-shaped tetrad arrangements (Verhoeven *et al.* 1989). In *Tacazzea*, *T. tomentosa* Bruce differs significantly from the other species by the width of the rhomboidal tetrads (Verhoeven *et al.* 1989).

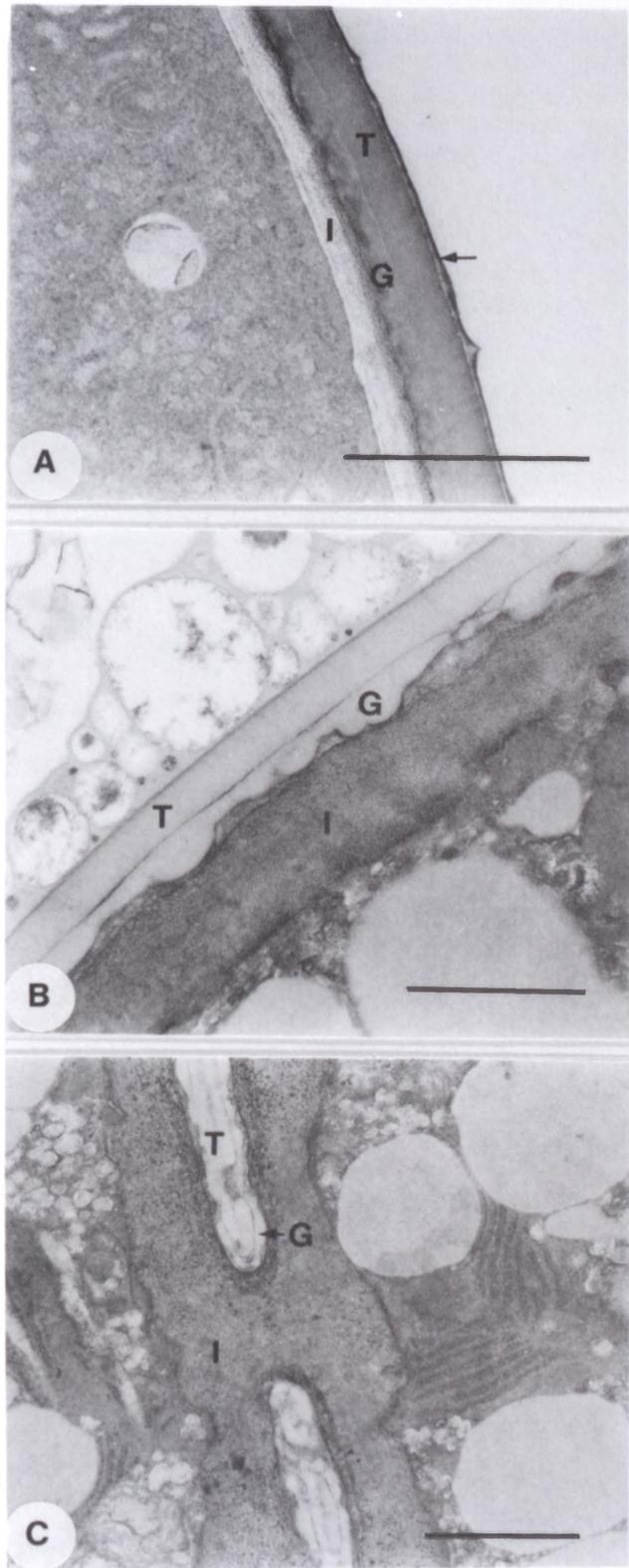


FIGURE 4.—A, B, TEM of pollen wall: A, *Curroria decidua* subsp. *decidua*, Beukes 22 (BLFU); B, *Mondia whitei*, Venter 9068 (BLFU). C, *M. whitei*, Venter 9068 (BLFU), internal wall. G, granular stratum; I, intine; T, tectum. Scale bars = $1 \mu\text{m}$.

The present study shows that *Stomatostemma pendulina* differs in tetrahedral size ($32 \times 30 \mu\text{m}$) from *S. monteiroae* ($48 \times 47 \mu\text{m}$). In *Curroria*, *C. volubilis* differs from the other species in that rhomboidal tetrad arrangement is predominant. *Socotranthus* can be identified by the unusual decussate arrangement of the tetrad.

The exine structure, consisting of a solid stratum (tectum) subtended by a granular stratum, appears to be without much variation in the representatives of the Periplocaceae studied thus far. The exine structure shows a resemblance with the general exine structure in the Apocynaceae. In the Apocynaceae the granular stratum is however, more variable, e.g. consisting of elements of unequal size and shape; subtended by a sole; larger granules towards the base and partly fused to a sole; faintly defined and delimited stratum with irregular voids containing traces of osmiophilic material (Nilsson 1986; 1990).

Although small differences may occur, the pollen morphology of the taxa investigated is rather uniform and thus of little value in the distinction of the species and genera investigated. The different, predominantly rhomboidal arrangement of the pollen tetrads of *Curroria volubilis* may indicate that this species should be placed in a different genus. It is significant that other floral characteristics show that *C. volubilis* does not belong in *Curroria* or to any of the genera investigated but to a new genus.

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