
SULCUS AND OPERCULUM STRUCTURE IN THE POLLEN GRAINS OF IRIDACEAE SUBFAMILY IXIOIDEAE¹

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ABSTRACT

Ixioideae, the largest and most derived of the four subfamilies of Iridaceae, is distinct in the family in having specialized pollen grains with tectate-perforate and scabrate sculpturing. This is in contrast to the prevailing tectate-reticulate exine in the rest of the family and its putative allies. In addition, most species have monosulcate grains with a 2-banded operculum, a feature that is probably synapomorphic for the subfamily. Exceptions among taxa with monosulcate grains having either a 1-banded or disorganized operculum are seen as most probably derived. Important exceptions to this pattern are *Micranthus*, which has zonasulcate grains with reticulate exine; one of seven species of *Thereianthus*, *T. racemosus*, which also has a reticulate exine except on the operculum; *Zygotritonia*, which has 3-aperturate inoperculate grains; and *Savannosiphon*, in which the grains have an irregular distribution of the exine and may be described as inaperturate but functionally omniaperturate. The origin of the operculum and the significance of the variation within Ixioideae is considered in relation to the systematics of Ixioideae.

Ixioideae, the largest of the four subfamilies of Iridaceae, are generally considered to have relatively uniform pollen grain morphology (Schulze, 1970, 1971; Goldblatt, 1990), and pollen has been accorded scant attention in systematic investigations of the 28 genera and ca. 860 species that are now considered to comprise the subfamily (Goldblatt, 1991). Like most petaloid monocots, pollen grains of Iridaceae are usually sulcate, and the exine is tectate-columellate. A reticulate surface pattern is probably basic for Iridaceae (Goldblatt, 1990; J. Walker, pers. comm.) and is the predominant or exclusive condition in Isophysidoideae, Nivenioideae, and Iridoideae, three of the four subfamilies recognized by Goldblatt (1990). However, in Ixioideae, most species of most genera have a perforate (micropunctate) and scabrate (spinulate) exine, a synapomorphy for the subfamily (Goldblatt, 1990, 1991). Within Ixioideae, *Syringodea* and *Crocus* have an imperforate scabrate exine, while in the relatively specialized *Micranthus* the exine is reticulate (Erdtman, 1952; Schulze, 1971). In *Syringodea* the grains are inaperturate and in *Crocus* inaperturate, spiraperturate, or poly-

rugoidate, clearly derived states for these two very specialized genera. The grains of *Micranthus* have been described as syncolpate by Schulze (1970).

A preliminary study of the pollen grains of *Micranthus* and the putatively closely related *Thereianthus* (Goldblatt, 1989a) to compare in detail the exine patterning revealed two unusual features. In *Thereianthus* there are discrete bands of exine in the sulcus, clearly separate from the rest of the exine. This structure, which accords with a broad definition of an operculum, is not present in *Micranthus*. The grains of the latter are zonasulcate (perhaps equivalent to Schulze's term syncolpate) in all three species. Independent study of the biology of North African species of *Romulea* (Bari, in prep.) revealed the presence of opercula in these species as well. These observations prompted us to examine the pollen grain aperture in a selection of species of all genera of Ixioideae. The size of Ixioideae precludes an examination of every species, but our results suggest that although the aperture is variable in the subfamily, its structure is constant within most genera so that a more thorough survey seems unnecessary except perhaps in the course

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of detailed systematic research. We have included observations of exine patterning and grain size as well as sulcus structure in our results.

MATERIALS AND METHODS

For examination of the sulcus, 80 species in 26 of the 28 genera (Tables 1, 2) of Ixiodeae were examined (*Crocus* and *Syringodea*, with imperforate grains, were not included in the survey). Information extracted from the literature for another five species (Radelescu, 1970a, b) is also included in Table 1.

Pollen grains from either fresh or herbarium material were placed on glass slides, rinsed briefly with 70% ethanol, and then mounted in Calberla's fluid (Ogden et al., 1974), which effectively re-expanded collapsed grains and stained the exine dark pink while leaving the rest of the grain unstained. Pollen was taken from herbarium specimens collected no more than 20 years ago whenever possible, as grains from older specimens were found to re-expand poorly, if at all. Grains were examined under the light microscope and measured within 48 hours of preparation for the following characters: aperture condition and presence and form of the operculum (Table 1); polar and equatorial diameter, sulcus width and length, operculum (if present) width and length, and interopercular distance when the operculum was 2-banded (Table 2). Measurements (Table 2) represent the mean of 5–10 grains. Descriptive terminology used follows Walker & Doyle (1975).

For grains examined under the scanning electron microscope (SEM), the following method was followed. Fresh grains were fixed in FAA, and dried grains from herbarium specimens were rehydrated by warming in 10% KOH for ca. 10 minutes. The grains from either source were then dehydrated directly in ethanol and critical-point dried before mounting and coating. Specimens were observed at an accelerating voltage of 15–20 kV.

OBSERVATIONS

APERTURE

All genera examined (Table 1) except *Micranthus*, *Savannosiphon*, and *Zygotritonia* have monosulcate pollen grains (Figs. 1A, B, 2–5). The sulcus is relatively broad and when expanded is usually as wide as the grain or nearly so (Table 2). *Syringodea* (10 spp.) and *Crocus* (80 spp.), which have specialized, inaperturate and inaperturate, spiraperturate, and polyrugoidate grains, respectively (Erdtman, 1952; Schulze, 1971; de Vos,

1974a; Mathew, 1982), were not included in our study.

Zygotritonia has grains with three elliptic apertures and thus is evidently trisulcate (Fig. 1C). The apertures are equidistant from one another and run almost the entire length of the ellipsoid grains.

The more or less spherical grains of the monotypic tropical African *Savannosiphon* have an irregular distribution of exine (Fig. 1D). The overall impression is of random distribution of irregularly shaped stained (exinous) patches of varying size and unstained (nonexinous) wall material. The grains are evidently inaperturate in morphological terms but probably functionally omniaperturate. Since grains of plants from two separate populations were examined, the possibility that our sampling was not representative seems unlikely.

In *Micranthus* the grains of all three species are evidently zonosulcate (Figs. 6, 8). The aperture is ca. 18–20 μm wide and forms a continuous band around the grain. We could not determine the orientation of the aperture but assume that it is polar rather than equatorial. There is a fair amount of scattered, granular exine material within the sulcus, usually concentrated close to the sulcus margins (Fig. 8).

OPERCULUM

In most of the genera with sulcate grains (Table 1) there are two narrow, linear to narrowly elliptic bands of exine within the sulcus (Figs. 1A, 2). By definition, this discrete exinous structure within the sulcus constitutes an operculum (cf. Kremp, 1965; Faegri & Iversen, 1964). The opercular exine appears to have the same microstructure as the rest of the grain (Figs. 2–5). These more or less parallel bands, occasionally joined at their ends, constitute an unusual structure that apparently does not occur in Iridaceae outside Ixiodeae. Included among the species listed in Table 1, we note from figures provided by Radelescu (1970a, b) that the following also have a 2-banded operculum: *Crocsmia* \times *crocsmiiflora* (Lemaire ex Morren) N.E. Br., *Gladiolus illyricus* Koch, *G. vandermerwei* (L. Bolus) Goldblatt & de Vos, *G. imbricatus* L., *Sparaxis tricolor* (Schneev.) Ker, and *Tritoniopsis pauciflora* (Jacq.) G. Lewis.

Exceptions to the above pattern among Ixiodeae with sulcate grains are as follows. All four species of *Ixia* examined and also *I. purpureo-rosea* G. Lewis (Radelescu, 1970a), *Anomatheca viridis* and *A. fistulosa* (but not the other three species of the genus), five of the seven species of *Thereianthus*,

TABLE 1. Pollen grain sulcus and operculum type for Ixioideae, including data from Radelescu (1970a, b). Collection information for the species examined here is included in the table. Taxa are arranged alphabetically by genus and species, following the most current taxonomy for the subfamily (Goldblatt, 1991). m/s = monosulcate; z/s = zonosulcate; t/c = tricolpate; s/u = structure uncertain (see text); 2/b = two-banded; 1/b = one-banded; d/o = disorganized; a = absent. All vouchers are housed at the Missouri Botanical Garden Herbarium (MO) unless stated otherwise. Total species per genus is indicated in parentheses after the genus name.

Taxon	Aper- ture	Operculum	Collection data
<i>Anomatheca</i> (5)			
<i>fistulosa</i> (Klatt) Goldblatt	m/s	1/b	Goldblatt 2359
<i>grandiflora</i> Baker	m/s	2/b	Jansen 7879
<i>laxa</i> (Thunb.) Goldblatt	m/s	2/b	ex hort. no voucher
<i>verrucosa</i> (Vogel) Goldblatt	m/s	2/b	Goldblatt 2933
<i>viridis</i> (Aiton) Goldblatt	m/s	1/b	Goldblatt 3640, 7190
<i>Babiana</i> (62)			
<i>dregei</i> Baker	m/s	2/b	Lavranos 22231
<i>stricta</i> (Aiton) Ker	m/s	2/b	Goldblatt 2322
<i>Chasmanthe</i> (3)			
<i>aethiopica</i> (L.) N.E. Br.	m/s	2/b	Goldblatt 1716
<i>Crocasmia</i> (8)			
<i>aurea</i> (Pappe ex Hook.) Planchon	m/s	2/b	Phillips 4670b
× <i>crocasmiflora</i> (Lem. ex Morren) N.E. Br.	m/s	2/b	Radelescu (1970a)
<i>Devia</i> (1)			
<i>xeromorpha</i> Goldblatt & Manning	m/s	2/b	Snijman & Manning 1194
<i>Dierama</i> (44)			
<i>cooperi</i> N.E. Br.	m/s	2/b	van der Zeyde 63
<i>mosscii</i> (N.E. Br.) Hilliard	m/s	2/b	Mauve & Venter 1
<i>pendulum</i> (L.f.) Baker	m/s	2/b	Dahlstrand 2896
<i>Duthieastrum</i> (1)			
<i>linifolium</i> (Baker) de Vos	m/s	2/b	Acocks 24202 (K)
	m/s	2/b	Acocks 460 (BOL)
<i>Freesia</i> (11)			
<i>occidentalis</i> L. Bolus	m/s	2/b	Goldblatt 4069
<i>refracta</i> (Jacq.) Klatt	m/s	2/b	Goldblatt 2841
<i>Geissorhiza</i> (82)			
<i>schinzii</i> (G. Lewis) Goldblatt	m/s	2/b	Goldblatt 3008
<i>scillaris</i> A. Dietr.	m/s	2/b	Walters 2616
<i>Gladiolus</i> (215)			
<i>abyssinicus</i> (Brongn. ex Lemaire) Goldblatt & de Vos	m/s	2/b	Lavranos & Collonette 20357
<i>callianthus</i> Marais	m/s	2/b	Keeley s.n.
<i>communis</i> L.	m/s	2/b	Martín Cacao & Fernández (1990)
<i>decoratus</i> Baker	m/s	2/b	Richards 18743 (P)
<i>dehnianus</i> Merxm.	m/s	2/b	Chase 8016 (P)
<i>dalenii</i> Geel	m/s	2/b	Ryding s.n. (UPS)
<i>erectiflorus</i> Baker	m/s	2/b	La Croix 1034
<i>grantii</i> Baker	m/s	2/b	Polhill & Paulo 1218 (P)
<i>gunnisii</i> (Rendle) Marais	m/s	2/b	Bally & Melville 15706
<i>illyricus</i> Koch	m/s	2/b	Radelescu (1970b), Martín Cacao & Fernández (1990)
<i>imbricatus</i> L.	m/s	2/b	Radelescu (1970b)
<i>italicus</i> Miller	m/s	2/b	Martín Cacao & Fernández (1990)

TABLE 1. Continued.

Taxon	Aper- ture	Operculum	Collection data
<i>melleri</i> Baker	m/s	2/b	Goldblatt et al. 8135
<i>muenzneri</i> Harms	m/s	2/b	Pawek 10432
<i>vandermerwei</i> (L. Bolus) Goldblatt & de Vos	m/s	2/b	Radelescu (1970b)
<i>Hesperantha</i> (ca. 65)			
<i>humilis</i> Baker	m/s	2/b	Goldblatt 6090
<i>radiata</i> (Jacq.) Ker	m/s	2/b	Goldblatt 6994
<i>Ixia</i> (45)			
<i>brevituba</i> G. Lewis	m/s	1/b	Goldblatt & Manning 8645
<i>polystachya</i> L.	m/s	1/b	Goldblatt 3254
<i>purpureorosea</i> G. Lewis	m/s	1/b	Radelescu (1970a)
<i>rapunculoides</i> Delaroché	m/s	1/b	van Berkel 140
<i>scillaris</i> L.	m/s	1/b	Goldblatt 2567
<i>Lapeirousia</i> (36)			
<i>arenicola</i> Schltr.	m/s	2/b	Compton s.n.
<i>coerulea</i> Schinz	m/s	2/b	Lavranos 22698
<i>erythrantha</i> Baker	m/s	2/b	Goldblatt 7515
<i>neglecta</i> Goldblatt	m/s	2/b	Goldblatt & Manning 9022
<i>Melaspheerula</i> (1)			
<i>ramosa</i> (L.) N.E. Br.	m/s	2/b	Low 943
<i>Micranthus</i> (3)			
<i>alopecuroides</i> (L.) Ecklon	z/s	a	Barker 4903 (NBG)
<i>junceus</i> (Baker) N.E. Br.	z/s	a	Winkler 166 (NBG)
<i>tubulosus</i> (Burm.f.) N.E. Br.	z/s	a	Goldblatt 8711
<i>Pillansia</i> (1)			
<i>templemannii</i> L. Bolus	m/s	2/b	Goldblatt 7907
<i>Radinosiphon</i> (1-2)			
<i>leptostachya</i> (Baker) N.E. Br.	m/s	2/b	Goldblatt 5933, 6864
cf. <i>leptostachya</i>	m/s	d/o	Goldblatt s.n.
<i>Romulea</i> (90)			
<i>bifrons</i> Pau	m/s	2/b-d/o	Moret & Bari 12-08
<i>bulbocodium</i> (L.) Sebast. & Mauri	m/s	2/b (joined)	Moret & Bari 313-89
var. <i>dioica</i> Batt.	m/s	2/b	Moret & Bari 413-89
<i>camerooniana</i> Baker	m/s	2/b	Gereau & al. 2828
<i>clusiana</i> (Lange) Nyman	m/s	2/b	Martín Cacao & Fernández (1990)
<i>columniae</i> Sebast. & Mauri	m/s	d/o	Moret & Bari 29-38
<i>engleri</i> Bég.	m/s	1/b-2/b (joined)	Moret & Bari 311-12
<i>ligustica</i> Parl.	m/s	2/b	Moret & Bari 52-88
<i>major</i> Schousboe	m/s	2/b (joined)	Moret & Bari 743-89
<i>monadelpha</i> (Sweet) Baker	m/s	2/b	Goldblatt 4036
<i>ramiflora</i> Ten.	m/s	2/b	Martín Cacao & Fernández (1990)
<i>rollii</i> Parl.	m/s	d/o	Moret & Bari 443-89
<i>rosea</i> (L.) Ecklon	m/s	2/b	Williams 2514
<i>stenopetala</i> Bég.	m/s	2/b	Moret & Bari 14-18
<i>Savannosiphon</i> (1)			
<i>euryphylla</i> (Harms) Goldblatt & Marais	s/u	s/u	Draper 14 (K); Pawek 7972
<i>Schizostylis</i> (1)			
<i>coccinea</i> Backh. & Harv.	m/s	2/b	Gibbs Russel 3016

TABLE 1. Continued.

Taxon	Aper- ture	Operculum	Collection data
<i>Sparaxis</i> (13)			
<i>bulbifera</i> (L.) Ker	m/s	2/b	Williams 430
<i>caryphyllacea</i> Goldblatt	m/s	2/b	Goldblatt 6162
<i>galeata</i> Ker	m/s	2/b	Goldblatt 7234A
<i>grandiflora</i> (Delaroché) Ker	m/s	2/b	Goldblatt 6270
<i>tricolor</i> (Schneev.) Ker	m/s	2/b	Radelescu (1970a)
<i>Thereianthus</i> (7)			
<i>bracteolatus</i> (Lam.) G. Lewis	m/s	1/b	Grant 4244; Goldblatt 9032
<i>ixioides</i> Lewis	m/s	1/b	Pillans 10276
<i>juncifolius</i> (Baker) G. Lewis	m/s	2/b	Esterhuysen 32359; Jackson s.n.
<i>longicollis</i> (Schltr.) G. Lewis	m/s	1/b	Compton 12413 (NBG)
<i>minutus</i> (Klatt) G. Lewis	m/s	1/b	Esterhuysen 35830; Goldblatt 5221
<i>racemosus</i> (Klatt) G. Lewis	m/s	2/b(-1/b)	Esterhuysen 16620 (BOL)
<i>spicatus</i> (L.) G. Lewis	m/s	1/b	Goldblatt 5396, 9032
<i>Tritonia</i> (28)			
<i>dubia</i> Ecklon ex Klatt	m/s	2/b	Goldblatt 4944
<i>pallida</i> Ker	m/s	2/b	Goldblatt 4167
<i>Tritoniopsis</i> (22)			
<i>pauciflora</i> (Jacq.) G. Lewis	m/s	2/b	Radelescu (1970a)
<i>pulchella</i> G. Lewis	m/s	2/b	Goldblatt 6839
<i>Watsonia</i> (52)			
<i>aletroides</i> (Burm.f.) Ker	m/s	2/b	Goldblatt 2858
<i>borbonica</i> (Pourret) Goldblatt	m/s	2/b	Goldblatt 7918
<i>marginata</i> (L.f.) Ker	m/s	2/b	Snijman 972
<i>Zygotritonia</i> (4)			
<i>bongensis</i> (Pax) Mildbr.	t/c	a	Fay 5544
<i>nyassana</i> Mildbr.	t/c	a	Faden & Faden 74/117

and one North African species of the predominantly southern African *Romulea* have grains with a single, narrowly elliptical band of exine in the center of the sulcus (Fig. 1B). This resembles the operculum of some genera of Tecophilaeaceae (Simpson, 1985). In *A. viridis*, *Thereianthus minutus* (Fig. 4), and *R. engleri* the opercular band of some grains lacks exine in the median center, suggesting the incomplete fusion of two separate bands. In one sample of *Radinosiphon leptostachya* the sulcus has exine fragments evenly scattered over its entire surface, while in three North African species of *Romulea* the operculum is sometimes partly (*R. bifrons*) to completely disorganized (*R. columnae*, *R. rollii*).

In species with a 2-banded operculum, the bands are separated from one another and from the sulcus margins by the pore membrane that remains unstained in our treatment. There may be scattered, small exine fragments concentrated in the midline of the unstained areas of the sulcus (Figs. 2–5).

The opercular bands are two-thirds to nearly as long as the sulcus and converge (rarely appearing fused) at their ends; thus, the interopercular space is widest in the center of the sulcus. The opercular bands range from 3.6–12.5 μm wide and are consistent in width within species and sometimes also within genera, but are fairly variable in length even within species.

GRAIN SHAPE AND SIZE

The grains of most species are typically broadly ellipsoid and slightly longer in equatorial than polar diameter, thus prolate (Table 2), but in a number of genera the grains are more or less globose. Grains of *Micranthus* and *Savannosiphon*, in particular, are spherical when fully expanded. Size is variable among species within genera as well as between genera. The smallest grains recorded are those of *Ixia scillaris* (32 \times 36 μm) and the largest those of *Savannosiphon* (106 \times 106 μm) and *Micran-*

thus tubulosus ($90 \times 90 \mu\text{m}$). Variation in size within genera may be extensive, notably in *Gladiolus* (Table 2), but so far we have found no taxonomic significance to size per se at the generic level, except that *Ixia* (Table 2) seems consistently to have the smallest grains. The genus stands out in the subfamily in this feature.

EXINE SCULPTURING

The exine of most genera of Ixioideae is tectate-columellate and usually has a perforate, sparsely scabrate tectum (described as punctitegillate or micropunctate and granulate, spinulate or verrucate). Our study did not focus on this aspect of the pollen because it has been extensively documented by Schulze (1970, 1971) using light and transmission electron microscopy and reported under the SEM for *Duthieastrum* (= *Duthiella*) (de Vos, 1974b), *Homoglossum* (now *Gladiolus*) (de Vos, 1976), *Tritonia* (de Vos, 1982), and *Pillansia* (Goldblatt & Stein, 1988).

Exceptions are the three species of *Micranthus* (Figs. 6–8) that have a reticulate tectum (Erdtman, 1952; Schulze, 1970, 1971), which *Thereianthus racemosus* has as well. The operculum of the latter, however, has a perforate exine. *Syringodea* and *Crocus* have an imperforate but sparsely scabrate tectum (Schulze, 1971; de Vos, 1974a).

Descriptions of the exine structure of pollen grains of *Thereianthus* and *Micranthus*, not before examined under the SEM, are as follows.

Thereianthus (Figs. 2–4). Exine tectate-columellate, tectum perforate (except *T. racemosus*), the perforations small (ca. $0.25\text{--}0.55 \times$ the width of the intervening tectum, *T. juncifolius*, *T. longicollis*), (ca. $0.75\text{--}1 \times$ the width of intervening tectum, *T. minutus*, especially on the proximal pole); finely scabrate; terminating abruptly at the sulcus (*T. minutus*) or broken into scabrate patches (especially *T. juncifolius*). In *T. racemosus*, tectum reticulate, lumina $2\text{--}3 \times$ width of the walls, becoming microreticulate at the sulcus margins with the walls as wide as the lumina; exine of the operculum perforate (perforations ca. $0.75\text{--}1 \times$ the width of the intervening tectum). Thus, except for *T. racemosus*, the exine of *Thereianthus* is typical of Ixioideae.

Micranthus (Figs. 6–9). Exine tectate-columellate, reticulate entirely or becoming microreticulate to perforate (Fig. 9) toward the margins of the sulcus (especially *M. tubulosus*), and forming isolated scabrate islands near the sulcus margins, the muri finely scabrate, lumina $1\text{--}3 \times$ the width of

the muri (*M. alopecuroides*), $1.3\text{--}4 \times$ (*M. juncus*), $0.75\text{--}22.2 \times$ (*M. tubulosus*), floor of the lumina containing pilae.

DISCUSSION

PHYLOGENETIC SIGNIFICANCE AND ORIGIN OF THE OPERCULUM

Operculate pollen has been mentioned as occurring in Ixioideae by Schulze (1970, 1971), who did not indicate which taxa had an operculum nor its specific form. However, figures published by Radelescu (1970a, b) show an operculum in the sulcus of a few species, drawn as somewhat diffuse exinous material. Referring to the operculum as “colpus ornamentation,” Radelescu did not describe its structure in detail nor did she include more than a few of the genera possessing an operculum in her survey. A 2-banded operculum is reported by Straka & Friedrich (1984) in *Gladiolus bojeri* (as *Geissorhiza bojeri*) and appears in the SEM micrograph of a pollen grain of a *Gladiolus* cultivar in Kress & Stone (1982). Martín Cacao and Fernández (1990) describe a 2-banded operculum in species of *Romulea* and *Gladiolus* that occur in Spain. The absence of any reference to an operculum (cf. Zavada, 1983) from other studies of the pollen morphology of Iridaceae is probably attributable to the examination of either acetolyzed or unexpanded grains.

The occurrence of an operculum in all 23 genera of Ixioideae that have monosulcate pollen grains (the basic aperture type for the subfamily), including members of all three tribes, makes it all but certain that an operculum is a synapomorphy for Ixioideae. The operculum is present in the 2-banded form in *Pillansia* (the only genus of Pillansieae), in three of the five genera of Watsonieae sensu Goldblatt (1989a, 1990), and in 18 of the 19 genera of Ixieae that have monosulcate pollen grains.

Although for morphopalynological reasons (A. Le Thomas, pers. comm.) it may be preferable to see the 2-banded operculum as having arisen from a 1-banded operculum, the pattern in extant Ixioideae suggests that a 2-banded operculum is ancestral in the subfamily, and this is congruent with what is known about relationships within Ixioideae (Goldblatt, 1990, 1991; Rudall & Goldblatt, in press). The 1-banded operculum of *Ixia* and some species of *Romulea*, *Anomatheca* (all Ixieae) and *Thereianthus* (Watsonieae) must therefore be regarded as derived. The occurrence of the 1-banded operculum is scattered in the subfamily and none

TABLE 2. Pollen grain characteristics of selected Ixiodeae (voucher information as in Table 1). Measurements for interopercular distance are only for grains with a double-banded operculum; those with a single operculum are scored n/a (nonapplicable) for the character. Measurements were taken only from normal-looking grains and are the mean of 5–10 measurements for each feature. Equatorial diameters are measured across the length of the sulcus. All measurements in microns.

Taxon	Grain diameter		Sulcus		Operculum		Inter- opercular distance
	Pole	Equator	Width	Length	Width	Length	
<i>Anomatheca</i>							
<i>fistulosa</i>	57	58	43	>58	4.8	43	n/a
<i>grandiflora</i>	66	76	48	>76	8.4	67	7.2
<i>laxa</i>	60	64	48	>64	7.2	63	9.6
<i>verrucosa</i>	53	61	34	>61	4.8	48	8.4
<i>viridis</i>	76	87	58	>87	12.5/6.3	60	n/a/2.4
	51	59	34	>59	12.1	39	n/a
<i>Babiana</i>							
<i>dregei</i>	63	67	43	>67	6.6	51	12.1
<i>stricta</i>	76	89	48	>89	7.2	58	10.8
<i>Chasmanthe</i>							
<i>aethiopica</i>	52	59	34	53	8.4	48	9.6
<i>Crocasmia</i>							
<i>aurea</i>	43	57	48	>57	4.8	48	12.1
<i>Devia</i>							
<i>xeromorpha</i>	46	52	34	>52	3.6	35	8.4
<i>Dierama</i>							
<i>cooperi</i>	46	53	29	>53	4.8	39	6.0
<i>mossii</i>	48	51	41	>51	6.0	41	9.6
<i>pendulum</i>	68	65	60	>65	10.4	58	16.9
<i>Duthieastrum</i>							
<i>linifolium</i>	55	75	51	>75	7.9	70	12.1
<i>Freesia</i>							
<i>refracta</i>	51	58	36	>58	6.5	41	10.8
<i>Geissorhiza</i>							
<i>schinzii</i>	89	96	65	>96	8.5	43	19.3
<i>scillaris</i>	44	48	36	>48	4.8	35	11
<i>Gladiolus</i>							
<i>abyssinicus</i>	60	65	43	>65	8.4	58	8.4
<i>callianthus</i>	75	82	43	>82	8.4	68	12.1
<i>decoratus</i>	59	60	31	>66	5.1	44	8.8
<i>dehnianus</i>	37	40	31	>40	6.6	42	5.9
<i>erectiflorus</i>	60	71	53	>71	9.6	51	9.6
<i>grantii</i>	50	53	47	>53	5.9	47	7.4
<i>muenzneri</i>	43	48	40	>48	7.2	27	7.2
<i>melleri</i>	47	58	34	>58	6.0	48	7.2
<i>Hesperantha</i>							
<i>humilis</i>	51	51	43	>51	4.5	38	12.5
<i>radiata</i>	48	48	27	>48	4.1	36	6.0
<i>Ixia</i>							
<i>brevituba</i>	32	36	24	>36	4.8	27	n/a
<i>polystachya</i>	34	38	23	>38	9.6	36	n/a
<i>rapunculoides</i>	37	41	27	>41	8.4	36	n/a
<i>scillaris</i>	30	41	27	>41	6.6	39	n/a

TABLE 2. Continued.

Taxon	Grain diameter		Sulcus		Operculum		Inter-opercular distance
	Pole	Equator	Width	Length	Width	Length	
<i>Lapeirousia</i>							
<i>arenicola</i>	67	72	48	>72	6.0	60	15.7
<i>coerulea</i>	55	55	36	>55	4.8	36	9.1
<i>erythrantha</i>	51	65	38	>65	3.6	53	7.2
<i>Melasphaerula</i>							
<i>ramosa</i>	55	61	34	>61	4.9	53	7.2
<i>Micranthus</i>							
<i>tubulosus</i>	90	90	18–20	n/a	n/a	n/a	n/a
<i>Pillansia</i>							
<i>templemannii</i>	63	67	65	>67	9.6	60	9.6
<i>Radinosiphon</i>							
<i>leptostachya</i>	64	71	36	>71	6.2	71	8.2
<i>Romulea</i>							
<i>camerooniana</i>	55	60	48	>60	6.0	41	8.4
<i>monadelpha</i>	43	62	24	>62	5.3	43	9.6
<i>rosea</i>	46	63	25	>63	4.8	43	7.2
<i>Savannosiphon</i>							
<i>euryphylla</i>	106	106	n/a	n/a	n/a	n/a	n/a
<i>Schizostylis</i>							
<i>coccinea</i>	48	55	30	>55	7.2	43	4.8
<i>Sparaxis</i>							
<i>bulbifera</i>	70	77	48	>78	8.9	60	12.7
<i>grandiflora</i>	58	67	46	67	6	65	15.7
<i>Thereianthus</i>							
<i>juncifolius</i>	65	70	41	65	6.0	57	7.2
	79	76	43	>76	6.6	58	9.6
<i>minutus</i>	55	70	53	>70	19.9	58	n/a
<i>racemosus</i>	43	58	51	>58	4.8	43	8.4
<i>spicatus</i>	68	71	55	>71	12.1	65	n/a
<i>Tritonia</i>							
<i>pallida</i>	59	70	36	>70	6.0	53	8.4
<i>Tritoniopsis</i>							
<i>pulchella</i>	54	59	53	±59	9.6	53	15.6
<i>Watsonia</i>							
<i>aletroides</i>	63	71	58	>71	12.5	60	16.9
<i>borbonica</i>	87	101	58	>101	8.9	60	10.4
<i>marginata</i>	63	69	68	>69	8.4	55	18.1
<i>Zygotritonia</i>							
<i>bongensis</i>	63	70	17	>70	n/a	n/a	n/a
<i>nyassana</i>	48	57	12	>57	n/a	n/a	n/a

of the genera in which it occurs is especially primitive. *Romulea* is probably a particularly specialized genus. Moreover, the closest relatives of genera with a 1-banded operculum have a 2-banded operculum.

STATUS OF TAXA WITH 1-BANDED OPERCULA

The single opercular band in *Anomatheca fistulosa* and the single or nearly single band in *A. viridis* are noteworthy, for these two species are

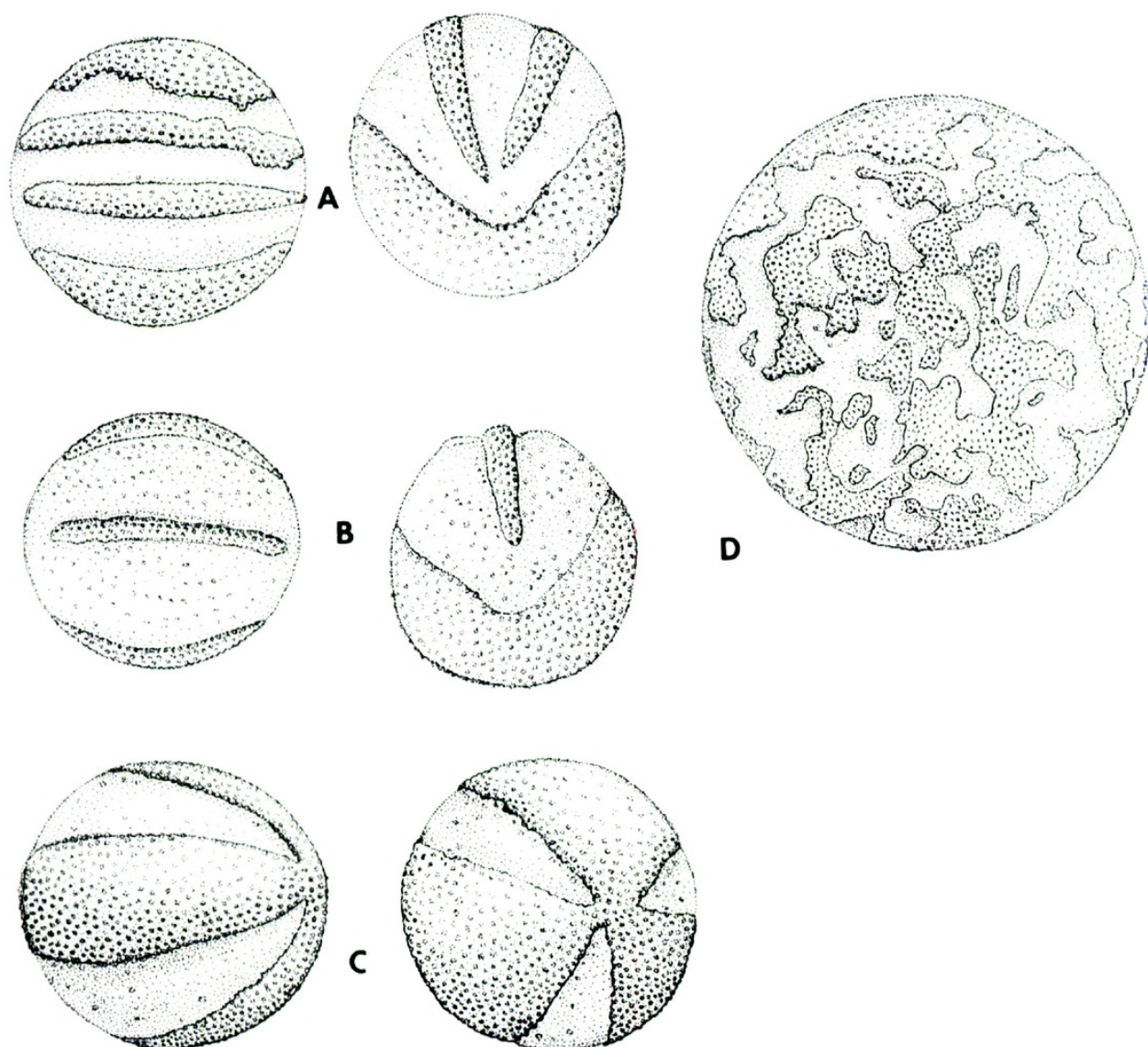


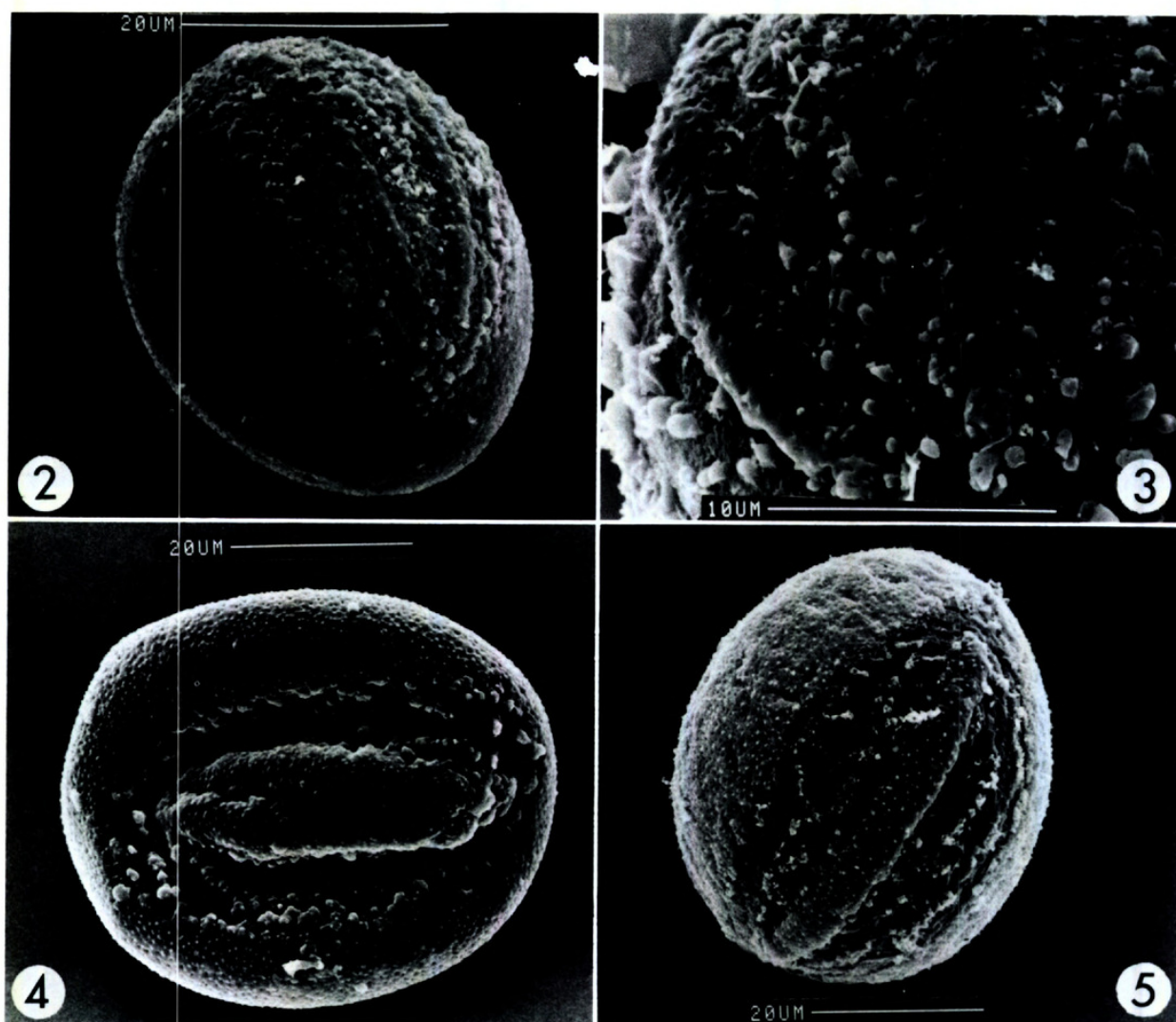
FIGURE 1. Expanded pollen grains of Ixiodeae in polar and equatorial view (except for D), showing sulcus types. — A. *Anomatheca laxa*, monosulcate grain with double banded operculum. — B. *Ixia brevītuba*, monosulcate grain with single banded operculum. — C. *Zygotrīttonia bongensis*, triaperturate grain, the apertures without opercula. — D. *Savannosiphon euryphylla*, omniaperturate grain. For dimensions of grains see Table 2.

unusual members of the genus and are evidently taxonomically isolated from the other species of *Anomatheca* and the closely related *Freesia* (Goldblatt, 1972). The two species seem derived in the genus, *A. fistulosa* having a long perianth tube and flowers solitary on the branches, and *A. viridis* having a green perianth and autogamous reproduction. The possibility that these two species are united by the 1-banded operculum, or are misplaced in *Anomatheca*, should be considered in future studies of this genus. It seems reasonable to regard the 1-banded operculum in *A. fistulosa* and *A. viridis* as derived within the genus on the grounds explained above and because of their own specialized features.

The infrageneric variation in the opercular mor-

phology in *Thereianthus* probably also has taxonomic significance. *Thereianthus juncifolius*, which has a 2-banded operculum, is isolated in the genus because of its lax inflorescence, but the possibility that it is misplaced is remote. The other species of *Thereianthus*, *T. racemosus*, which has a 2-banded operculum, may be primitive in the genus. It stands out morphologically in having small flowers with a short perianth tube (a plesiomorphic character in the genus). It should be considered less specialized than the long-tubed and often zygomorphic-flowered members of the genus, all of which have a 1-banded operculum. Thus, in this genus the hypothesis that the 2-banded operculum is the basic state also seems likely.

In the largely southern African genus *Romulea*



FIGURES 2-5. Sulcate pollen grains of Ixioidae.—2. *Pillansia templemannii* with 2-banded operculum.—3. Aperture detail in *P. templemannii*.—4. *Thereianthus minutus*, sulcate grain with 1-banded operculum with the median lacking exine.—5. *Lapeirousia neglecta*, sulcate grain showing operculum (one of the two bands has exfoliated) and scattered exine debris lying on the aperture membrane. Scale bar = 20 μm (2, 4, 5); = 10 μm (3).

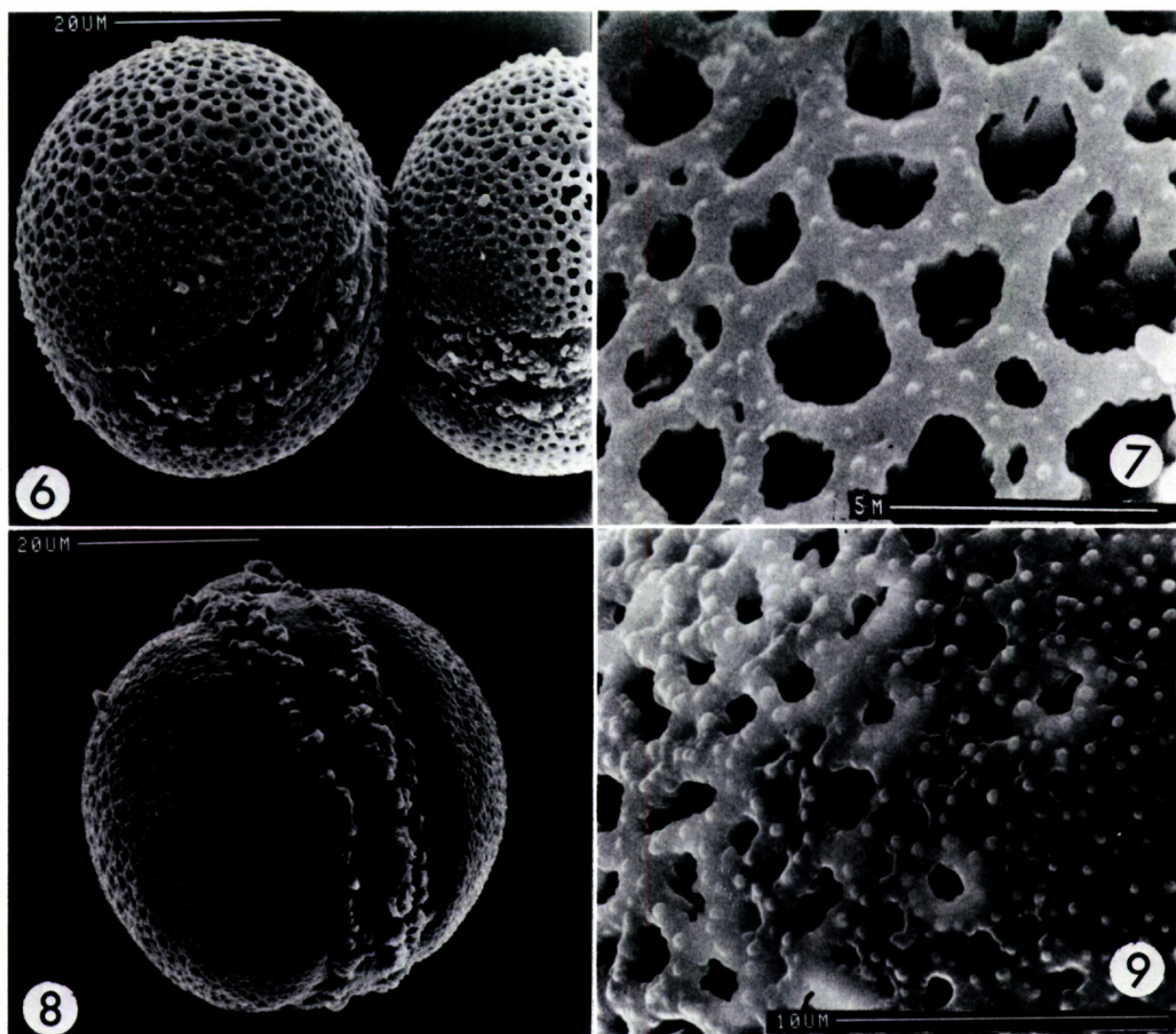
(whose close relatives are also southern African), only a few North African species are so far known to have a 1-banded or disorganized operculum, although pollen of few of the southern African species have been examined. A 1-banded operculum is thus presumably derived in the genus, but as far as we know there are no morphological or other reasons to view the species with a 1-banded operculum as specialized or derived from ancestors with a 2-banded operculum.

The only genus that seems consistently to have a 1-banded operculum is *Ixia*, and this is presumably an apomorphy for the genus. Lewis (1962) regarded *Ixia* as most closely related to *Dierama*. *Dierama*, which has a 2-banded operculum, is apparently less specialized in its evergreen habit but derived in its pendulous flowers and possibly also in its unusual leaf anatomy (Rudall & Goldblatt, in press; Goldblatt, in prep.).

SIGNIFICANCE OF THE ZONASULCATE APERTURE AND RETICULATE EXINE IN *MICRANTHUS*

Zonasulcate grains (previously described as syncolpate by Schulze, 1970) and a reticulate exine are almost certainly both apomorphic for *Micranthus*, evidently a fairly derived genus of Watsonieae (Goldblatt, 1989a).

Micranthus is undoubtedly correctly placed in Ixioidae despite its reticulate or largely reticulate exine, which corresponds to the patterning in other subfamilies of Iridaceae. In this connection, the transition from reticulate to microreticulate to perforate exine toward the sulcus margins, noted in preparation of *M. alopecuroides* and *M. tubulosus*, seems noteworthy. In Iridoideae with reticulate exine structure, perforate exine does not occur adjacent to the aperture (e.g., Goldblatt & Manning, 1989). The reticulate exine of *Micranthus* thus



FIGURES 6–9. Pollen grains and exine detail of *Micranthus*.—6. *M. alopecuroides*, whole grains showing exine fragments in the aperture.—7. *M. junceus*, detail of exine sculpture.—8. *M. tubulosus*.—9. Detail of transition from microreticulate to perforate exine in *M. tubulosus*. Scale bar = 20 μm (6, 8); = 5 μm (7); = 10 μm (9).

appears best regarded as a reversal to the basic state for the family.

Likewise, we consider the reticulate exine of *Thereianthus racemosus* a specialization for the species. The possibility that this character is shared with *Micranthus* must be seriously considered. The two genera are closely related (Goldblatt, 1989a), and the suggestion that they may be congeneric seems supported by this shared exine character. However, the unusual zonosulcate aperture of *Micranthus* seems to isolate it effectively from *Thereianthus*, despite their shared karyology, unusual leaf insertion, and similar corm, fruit, and seed morphology (Goldblatt, 1991).

The absence of intermediates between the sulcate-operculate and zonosulcate apertures in the subfamily makes exact interpretation of the aperture of *Micranthus* impossible. The aperture may have evolved through an extension of the sulcus

around the grain through the distal pole and the loss of the operculum. Alternatively, the aperture may have been pushed into an equatorial position by the enlargement of the operculum to match the size of the other part of the exine (thus zonisulcate).

SIGNIFICANCE OF TRI-APERTURATE AND POLYRUGOIDATE GRAINS

The trisulcate grains of *Zygotritonia* are remarkable for Iridaceae and probably for the monocots. We speculate that the tri-aperturate condition may have evolved from an ancestor with a double-banded operculum by the enlargement of the opercular bands, and the displacement of the membrane areas away from the polar part of the grain toward the equator. *Zygotritonia* is a specialized genus (Goldblatt, 1989b) and must be derived from stock

that had a sulcus with a double-banded operculum. Whatever the phylogeny of this unusual aperture type, it is clear that *Zygotritonia* is additionally isolated in the subfamily by its specialized pollen grains.

The remarkable pollen grains of *Savannosiphon* reinforce our appreciation that the genus, segregated from *Lapeirousia* by Goldblatt & Marais (1979), is quite distinct from the palynologically uniform (as far as is known) *Lapeirousia*.

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