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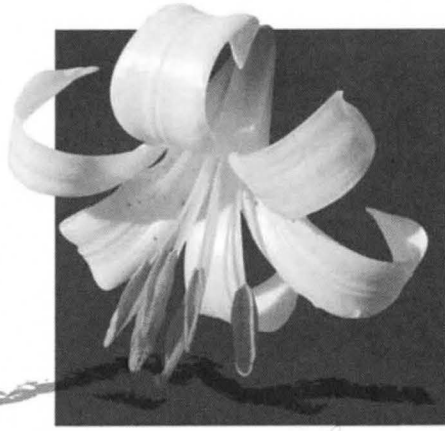


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MONOCOTS
Comparative Biology and Evolution
Excluding Poales

Pollen Evolution

THE OPERCULUM IN POLLEN OF MONOCOTYLEDONS

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ABSTRACT

Within monocotyledons, monosulcate pollen is the predominant type and probably represents the plesiomorphic condition, but considerable variation occurs in sulcus morphology. An operculum is an exine thickening that covers most of an aperture. Monocot opercula are usually associated with sulci, although they can occur in ulcerate apertures, as in Poaceae. There are several other aperture types closely related to the monosulcate-operculate type, and confusion occurs in the palynological literature between monosulcate-operculate, pontoperculate, disulculate, disulcate, and zona-aperturate (zonasulcate or zonosulcate) pollen. Transmission electron microscopy (TEM) was used to determine the distribution of the thick apertural intine and to accurately identify these aperture types. Operculate pollen most frequently was present in Asparagales (particularly Agavaceae, Doryanthaceae, Iridaceae, and Tecophilaeaceae), Liliales (particularly Liliaceae, Melanthiaceae, and Uvulariaceae), and relatively infrequently among commelinid monocots, except for some Arecaceae, Dasypogonaceae, and Poales. Thus, we conclude that opercula have probably evolved several times independently within monocots, particularly in taxa from dry or seasonally dry habitats, and that this adaptation may be related to their function in protecting the aperture. Two transformation series of related aperture types are proposed, one of which involves monosulcate-operculate pollen, although further testing will be required.

Key words: aperture, commelinids, lilioids, monocotyledons, monosulcate, operculum, pollen, transformation series.

INTRODUCTION

The monosulcate condition is the most common aperture type found in monocotyledons and is probably the plesiomorphic state (Furness and Rudall 1999). However, there is considerable diversity among monosulcate apertures. Sulci may be diffuse, extended, insulate (with scattered islands of exine), operculate, or with banded opercula (Halbritter and Hesse 1993). As Halbritter and Hesse (1993) pointed out, it is necessary to examine unacetolysed pollen in a turgid state to accurately observe details of the sulcus, since acetolysis causes the collapse of thin-walled monocot pollen and the removal of structures associated with the sulcus, including opercula.

Here we review the distribution of operculate pollen in monocots in a systematic context. In the palynological literature, the term “operculum” refers to an exinous thickening which covers a large part of an aperture (e.g., Punt et al. 1994). The operculum may be fused to the surrounding exine at both ends; apertures with this type of structure are termed “pontoperculate.” Since the pontoperculum effectively divides the sulcus into two, when viewed using scanning electron microscopy (SEM) such an aperture may be indistinguishable from the disulculate aperture type. Similarly, confusion may arise between monosulcate-operculate and zona-aperturate (zonasulcate or zonosulcate) apertures. The orientation of monocot pollen apertures cannot be determined without reference to the tetrad stage of pollen development, and examination of sections of fresh pollen using TEM is also necessary in order to determine the position of the thickened apertural intine and thus the type of aperture. There is therefore much confusion in the pollen literature about the application of the terms monosulcate-operculate,

pontoperculate, disulculate, disulcate, zonosulcate, and zonosulcate (or meridionosulcate).

DISTRIBUTION OF MONOSULCATE-OPERCULATE POLLEN IN MONOCOTYLEDONS

Operculate pollen is entirely absent from basal monocots, but relatively common in lilioid and commelinid monocots (Furness and Rudall 2003). Pollen of *Acorus* L. (Acoraceae), which is the basal monocot in most recent molecular analyses (e.g., Chase et al. 2000), is monosulcate without an operculum (Grayum 1992; Rudall and Furness 1997). Operculate pollen appears to be entirely absent from Alismatales. Many alismatids are inaperturate or have weakly defined apertures, or are porate with granular or spiny pore membranes (Chanda et al. 1988; Grayum 1992; El-Ghazaly and Rowley 1999; Furness and Rudall 1999, 2000). *Tofieldia* Huds. (Tofieldiaceae) is disulcate (Huynh 1976; Takahashi and Kawano 1989; Díaz Lifante et al. 1990) and zona-aperturate pollen occurs in some Araceae (Grayum 1992; Hesse et al. 2001; Zetter et al. 2001).

Lilioid Monocots

There are unconfirmed reports of monosulcate-operculate pollen in *Barbacenia* Vand. (Velloziaceae–Pandanales) and *Metanartheicum* Maxim. (Nartheciaceae–Dioscoreales) (Furness and Rudall 2003), although TEM sections are required to confirm the position of the thickened apertural intine. Within Liliales, operculate pollen is common in Alstroemeriaceae, Liliaceae, Melanthiaceae, and Uvulariaceae (Furness and Rudall 2003; Fig. 1–4), and is apparently a synapomorphy for Melanthieae–Melanthiaceae (Colosante and Rudall 2000; Rudall et al. 2000).

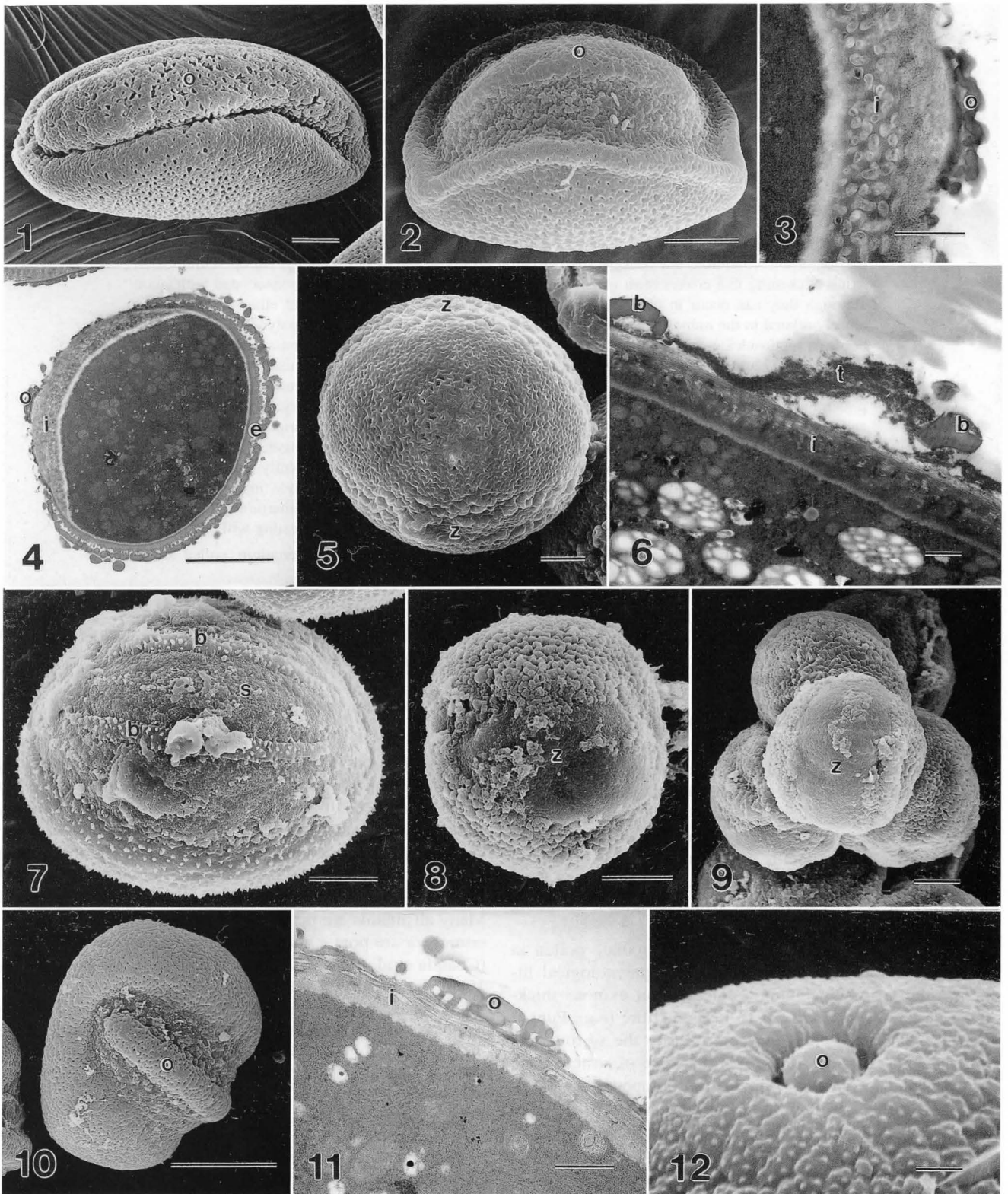


Fig. 1-12.—Operculate and related pollen apertures in monocots.—1. *Erythronium elegans* P. C. Hammond & K. L. Chambers (Liliaceae–Liliales), monosulcate-operculate pollen (SEM).—2-4. *Zigadenus venenosus* S. Wats. (Melanthiaceae–Liliales).—2. Monosulcate-operculate pollen (SEM).—3. Detail of the sulcus with an operculum with layers of thick intine, including a channelled layer, beneath (TEM).—4. Section showing the operculum, thick apertural intine and non-apertural exine with a prominent foot layer.—5. *Iris reticulata* M. Bieb. (Iridoideae–Iridaceae–Asparagales), zona-aperturate (zonasulcate) pollen (SEM).—6-7. *Gladiolus tristis* L. (Ixioidae–Iridaceae–Asparagales).—6. Detail of the sulcus with two exine bands with thick intine beneath (TEM).—7. Monosulcate-operculate pollen with a two-banded sulcus (SEM).—8-9. *Aristea ecklonii* Baker (Nivenioideae–Iridaceae–Asparagales).—8. Zona-aperturate pollen (SEM).—9. Tetrad of zona-aperturate (zonasulcate) grains (SEM).—10. *Odontostomum hartwegii* Torr. (Tecophilaeaceae–Asparagales), monosulcate-operculate

Within Asparagales, operculate pollen is relatively rare in the higher asparagoid clade, but occurs in representatives of several families of the lower asparagoid grade, including Iridaceae (Fig. 5–9), Orchidaceae, Hypoxidaceae, Tecophilaeaceae (Fig. 10, 11), and Doryanthaceae (Furness and Rudall 2003). Nair and Sharma (1965) also reported monosulcate-operculate pollen in *Dianella* Lam. (Hemerocallidaceae), although we found only trichotomosulcate pollen in this genus (Rudall et al. 1997). Monosulcate-operculate pollen is a synapomorphy for six genera of Tecophilaeaceae (Simpson 1985b; Fig. 10, 11). Pollen apertures are diverse within Iridaceae, including highly variable apertures within the genus *Aristea* Sol. ex Aiton (Nivenioideae: Goldblatt and Le Thomas 1992b, Goldblatt et al. 2004; Fig. 8, 9), and operculate pollen occurs in three subfamilies. For example, in Iridoideae there appears to be a gradation from monosulcate-operculate (e.g., *Hermodactylus* Mill.) to zonosulcate (*Iris danfordiae* (Baker) Boiss., *I. reticulata* M. Bieb.: Goldblatt and Le Thomas 1992a; Furness and Rudall 2003; Fig. 5). Many members of Iridaceae subfamily Ixioidae have pollen with an operculum composed of two separate bands of exine which is probably synapomorphic for the subfamily, although a variety of other aperture types also occur including monosulcate with one-banded opercula or with insulae, and zona-aperturate, spiraperturate, polyrugate (sensu Erdtman 1952), triaperturate and inaperturate types (Goldblatt et al. 1991; Fig. 6, 7).

Within Orchidaceae (Asparagales), which are putatively the sister family to all other Asparagales (e.g., Fay et al. 2000), operculate pollen is restricted to the subfamilies Cypripedioideae (in all four genera: Burns-Balogh and Hesse 1988) and Apostasioideae. One genus of Apostasioideae, *Neuwiedia* Blume, has operculate pollen, while the other, *Apostasia* Blume, has a sulcus with insulae (Newton and Williams 1978; Schill 1978; Furness and Rudall 2003). *Pauridia* Harv. (Hypoxidaceae) has disulcate pollen although most Hypoxidaceae are monosulcate, and monosulcate-operculate and disulcate apertures may form part of a transformation series of homologous apertures (Rudall 2002; Rudall and Bateman 2002).

In the higher asparagoid clade, opercula are rare or absent, with the exception that several genera of Agavaceae have pontoperculate pollen and some have a sulcus that appears to be intermediate between operculate and pontoperculate (Alvarez and Köhler 1987; Ambwani and Kumar 1993). Some Laxmanniaceae have zonosulcate apertures (Chanda and Ghosh 1976), although aperture orientation requires confirmation by examination of tetrads, and sections showing the position of the thickened intine have not been examined to date. Disulcate apertures are a synapomorphy for tribe Amaryllideae (Amaryllidaceae: Schulze 1984; Snijman and Linder 1996).

Commelinid Monocots

Opercula are common in Poales, in which they characterize Anarthriaceae, Ecdiocoleaceae, and Poaceae, which all have ulcerate apertures (Linder and Ferguson 1985; Fig. 12). The operculum in Poaceae often becomes detached in acetolysis. Operculate pollen also occurs in some species of *Tillandsia* L. (Bromeliaceae–Poales: Halbritter 1992) and *Xyris* (Xyridaceae–Poales: Rudall and Sajo 1999). Extended sulcate, zona-aperturate, and disulcate apertures occur in Rapateaceae (Carlquist 1961). Opercula are absent from most other commelinids apart from *Calectasia* R. Br. (Dasygogonaceae: Chanda and Ghosh 1976), and *Chamaerops* L., possibly *Iriartella* H. A. Wendl., and *Sclerosperma* G. Mann & H. A. Wendl. (Arecaceae: Furness and Rudall 2003; Harley and Dransfield 2003). In many Commelinales the pollen sulci have scattered exine elements on the surface: granules, scabrae, verrucae, or insulae (Poole and Hunt 1980; Simpson 1983, 1985a, 1987). Pontederiaceae (Commelinales) have disulcate pollen (Simpson 1987; Ressayre 2001).

DISCUSSION

Monosulcate-operculate pollen is primarily a monocot character, since opercula are rare in other basal angiosperms with monosulcate pollen. However, opercula are not restricted to monocots, as they occur on the colpate or colpate-derived apertures of some eudicots (though they are sometimes removed by acetolysis), including some Caryophyllaceae, some Euphorbiaceae, and some Rosaceae (Erdtman 1952; Eide 1981; Lobreau-Callen et al. 2000). Within monocots, opercula are particularly characteristic of the orders Asparagales (especially lower asparagoids), Liliales, and Poales, and have thus probably evolved several times, perhaps as a result of similar selection pressures (Fig. 13). The function of the operculum is probably to shield the cytoplasm from desiccation via the pollen aperture, although it may also provide protection against entry of pathogens such as bacteria and fungi via the aperture. Protection from dehydration could account for the presence of opercula in many species from relatively dry (or seasonally dry) habitats, such as many Iridaceae and Tecophilaeaceae. Opercula are noticeably absent from Alismatales and Zingiberales (Fig. 13), which occur in moist or wet habitats, and often have inaperturate (omniaperturate) pollen (Furness and Rudall 1999). Blackmore and Barnes (1986) demonstrated that in *Crococmia* × *crococmiiflora* (Lemoine ex Anonymous) N. E. Br. (Iridaceae) the operculum assists in sealing the large sulcus, which folds inwards during dehydration. Opercula may occur in either insect-pollinated or wind-pollinated species. In Poaceae, which are wind pollinated, there is a reduced aperture that is almost completely covered by the operculum.

The operculum is a specialized region of exine that is

←

pollen (SEM).—11. *Tecophilaea cyanocrocus* Leyb. (Tecophilaeaceae–Asparagales), detail of the sulcus with an operculum with thick intine beneath (TEM).—12. *Oryzopsis paradoxa* Nutt. (Poaceae–Poales), detail of the operculate ulcus (SEM). Other notations: b = exine band, e = exine, i = intine, o = operculum, s = sulcus, t = tapetal material, z = zona-aperture. (Fig. 1, 5, 7–10, bar = 10 μm; Fig. 2, 4, bar = 5 μm; Fig. 3, 6, 11, 12, bar = 1 μm.)

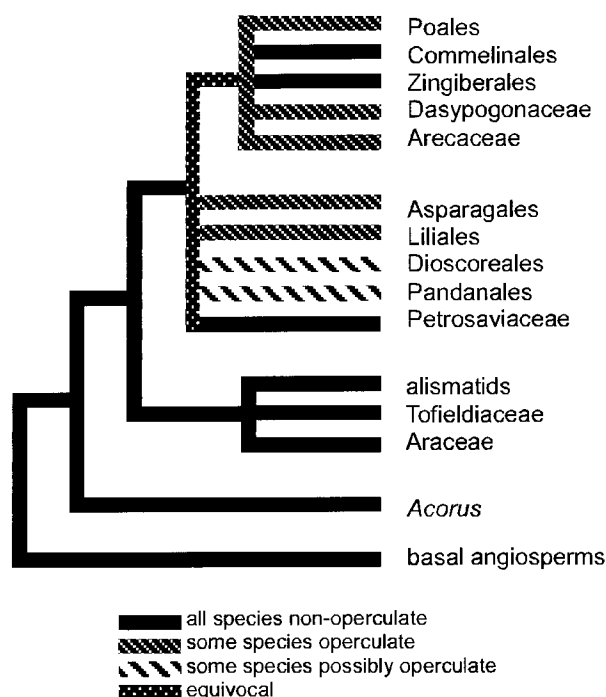


Fig. 13.—Operculate pollen mapped on a diagram of monocot relationships, with orders as in the Chase et al. (2000) classification.

usually thinner and has a simpler structure than the exine elsewhere on the pollen grain. For example, in *Zigadenus* Michx. (Melanthiaceae–Liliales) the operculum lacks the thick foot layer of the remaining exine (Furness and Rudall 2003; Fig. 3, 4). The operculum rests on top of a thick, often channelled, apertural intine and in this way a pontoperculate grain can be distinguished from a disulcate one. Disulcate pollen has two distinct apertures separated by thin non-apertural intine (e.g., *Pauridia*, Hypoxidaceae–Asparagales: Simpson 1983). In zona-aperturate pollen the intine is thick and often channelled beneath the ring-like aperture and thin beneath the exine of the rest of the grain (e.g., *Aristea ecklonii* Baker, *Iris reticulata*, Iridaceae–Asparagales: Furness and Rudall 2003). The operculum in Poaceae is associated with a structure known as the *Zwischenkörper*, a lenticular body composed of pectic polysaccharides located between the operculum and the intine, which hydrates at germination and presses away the operculum before the pollen tube tip emerges (Heslop-Harrison and Heslop-Harrison 1980).

We propose two transformation series of monocot aperture types: (1) monosulcate, monosulcate-operculate, pontoperculate, disulcate, zonosulcate (Fig. 14; see Series A) and (2) monosulcate, extended sulcate, disulcate, zonosulcate (meridionosulcate) (Fig. 14; see Series B). In the first series (Fig. 14, Series A), if the thickened intine beneath the operculum of a pontoperculate grain is lost, and the exine of the operculum becomes thicker, disulcate apertures will result. These changes could equally work in the opposite direction. Thus, monosulcate-operculate pollen may give rise to pontoperculate, disulcate, and zonosulcate or vice versa, and these aperture types can occur within single species, as in *Agave americana* L. and *A. wightii* L. (Ambwani and Kumar 1993). Relatively simple changes in the proportions of exine and intine would enable these transformations to take place

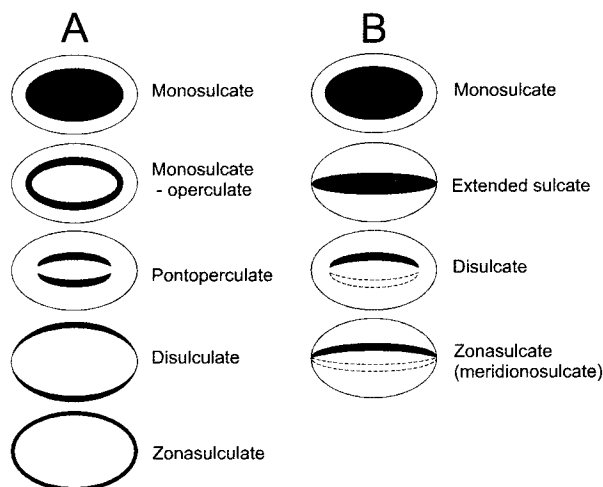


Fig. 14.—Two proposed transformation series of pollen apertures, Series A and B, all in distal polar view. Series A includes monosulcate-operculate pollen.

and the developmental controls affecting exine and intine production in pollen require further investigation. There may also be a separate transformation series between monosulcate (non-operculate) and both disulcate and zonosulcate types (Fig. 14, Series B). Disulcate apertures are relatively rare in monocots but occur in *Tofieldia* (Tofieldiaceae–Alismatales), in which Huynh (1976) demonstrated the presence of sulci at both the distal and proximal poles. Extension of either a single sulcus (with extended sulcate as an intermediate condition) or two sulci around the grain would produce the zonosulcate (meridionosulcate) condition.

The developmental controls giving rise to an operculum are unknown, but the position of the operculum may relate to that of the microtubule organizing centers (MTOCs) during meiosis. Sheldon and Dickinson (1983, 1986) disrupted meiosis in microsporocytes of *Lilium* L. (Liliaceae), which has monosulcate pollen, using centrifugation or colchicine treatment, then cultured them to maturity. Some microsporocytes underwent only the first meiotic division to produce dyads rather than tetrads; these developed a sulcus with an “island” of exine in the center, similar to a monosulcate-operculate aperture. Sheldon and Dickinson demonstrated that in “normal” *Lilium* pollen the location of the MTOC at the second meiotic division corresponds with the sulcus position, but in pollen with only one meiotic division the MTOC corresponds with the patterned exine in the center of the sulcus. The relationship between the MTOCs and the operculum of monosulcate-operculate Liliaceae such as *Erythronium* L. would be an interesting topic for future investigation.

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