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REVIEW

Style morphology and pollen tube pathway

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Abstract The style morphology and anatomy vary among different species. Three basic types are: open, closed, and semi-closed. Cells involved in the pollen tube pathway in the different types of styles present abundant endoplasmic reticulum, dictyosomes, mitochondria, and ribosomes. These secretory characteristics are related to the secretion where pollen tube grows. This secretion can be represented by the substances either in the canal or in the intercellular matrix or in the cell wall. Most studies suggest that pollen tubes only grow through the secretion of the canal in open styles. However, some species present pollen tubes that penetrate the epithelial cells of the canal, or grow through the middle lamella between these cells and subepithelial cells. In species with a closed style, a pathway is provided by the presence of an extracellular matrix, or by the thickened cell walls of the stylar transmitting tissue. There are reports in some species where pollen tubes can also penetrate the transmitting tissue cells and continue their growth through the cell lumen. In this review, we define subtypes of styles according to the path of the pollen tube. Style types were mapped on an angiosperm phylogenetic tree following the maximum parsimony principle. In line with this, it could be hypothesized that: the open style appeared in the early divergent angiosperms; the closed type of style originated in Asparagales, Poales, and Eudicots; and the semi-closed style appeared in Rosids, Ericales, and Gentianales. The open style seems to have been lost in core Eudicots, with reversions in some Rosids and Asterids.

Keywords Pollen tube pathway · Ultrastructure · Style · Stylar transmitting tissue

Introduction

The success of sexual reproduction of angiosperms depends on a series of interactions between the pollen grain and the different tissues of the pistil, including pollen germination on the stigma, the pollen tube growth and the guidance through style followed by a successful fertilization (Heslop-Harrison 1975a, b; Linskens 1986; Clarke et al. 1979; Gaude and Mccormick 1999; Acosta et al. 2007). Differences in the contribution of the sporophytic tissues that interact with the male gametophyte are observed along evolution, and were extensively studied in angiosperms (Whitehead 1969; Mulcahy 1979; Eriksson and Bremer 1992; Herrero 1992; Hormaza and Herrero 1992; Sargent and Otto 2004; Lora et al. 2016). These interactions will likely involve a complex cross talk, controlled by a genetic system that regulates the biochemical and molecular environments necessary: protein–protein or simple molecules such as water, ions, lipids, sugars, calcium (Cheung 1996; Gaude and Mccormick 1999; Acosta et al. 2007). A specialized set of tissues that interact with the pollen tube and facilitate its access to the female gametophyte evolved in angiosperms

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(Bell 1995; Herrero and Hormaza 1996; Sage et al. 2009; Williams et al. 2010). The functional attributes of the progamic phase are controlled by structural changes that exhibit considerable variation among species associated with differences in pollen–pistil interaction and their characteristics (Heslop-Harrison and Shivanna 1977; Erbar 2003; Edlund et al. 2004; Hiscock and Allen 2008; Williams 2009; Cruden 2009; Williams et al. 2016; Harder et al. 2016). Two of the most notable events are the specialization of a receptive surface in the stigma and the transmitting tissue (Endress and Igersheim 2000; Sage et al. 2009; Williams 2009; Endress 2011). In the stigma, some molecules that play a role in the interaction with pollen regulate the compatibility systems, such a self-incompatibility (SI). For instance, in *Brassica* L., locus SI encodes two proteins present on the surface of the stigma, a transmembrane tyrosine kinase receptor (SRK) and extracellular glycoprotein (SGL) (Stein et al. 1996). However, Acosta et al. (2007) found that a pollen–stigma adhesion in *Arabidopsis thaliana* L. is an interaction mediated by lipophilic molecules. In the open style of lily, adhesion molecules, pectin, and stigma/stylar cysteine-rich adhesion (SCA) are implicated in guidance (Lord 2003). In vitro assay results suggest that SCA alone may induce pollen chemotropism, playing a dual role in lily pollination: chemotactic in the stigma and haptotactic (adhesion mediated) in the style (Lord 2003). According to Lord (2003), there is a hierarchy of signaling events in pollen–pistil interactions starting at the stigma and ending at the micropyle, before pollen tubes can respond to ovule cues.

Cellular studies on this area are usually focused on individual pollen tube growth and their interaction with the stylar tissues (Malhó et al. 2006; Krichevsky et al. 2007; Moscatelli and Idilli 2009; Rounds et al. 2011; Dresselhaus and Franklin-Tong 2013). According to Harder et al. (2016), biochemical and cellular studies of pollen tube growth should consider heterogeneous conditions in styles, including the availability of space and other resources as well as pollen tubes interactions between them. Undoubtedly, these conditions should vary according to the morphology and cellular ultrastructure of the style. Hence, in this review, we explore the style types according to their morphology and anatomy in angiosperms in order to systematize this primordial information. We also highlight the advances on the pollen–style interactions and discuss the histology and ultrastructure of the styles types, considering their implications in the pollen tube paths.

Pollen tube growth and its interaction with the sporophytic tissues

During angiosperm reproduction, pollen grains form a tube that grows through pistil tissues to the ovule micropyle (Palanivelu et al. 2003). Details of the progression of the pollen tube through the gynoecium, beginning with germination of the pollen grain on the stigma and culminating with delivery of the sperm cells to the synergid of the embryo sac, are well established for many species (Knox 1984; Heslop-Harrison 1987; Bedinger et al. 1994; Cheung 1996; Wilhelmi and Preuss 1997; Lennon et al. 1998).

Studies on pollen tube growth are critical to understand the nature and regulation of sexual plant reproduction (Eberle et al. 2012). The pollen tube pathway evolved from an extragynoecial compitum to an internalized one through syncarpy. In the basal angiosperm lineages (the ANA grade of *Amborella* Baill., Nymphaeales, and Austrobaileyales) and the magnoliids, the carpels are generally free from each other, the style is very short or absent, and the compitum is in most cases extragynoecial, in species with either apocarpous or syncarpous gynoecia. Therefore, in many different species, the pollen tubes can start to grow before they reach the style, in the stigma–style interface (Endress 1982, 2015; Endress and Igersheim 2000). In contrast, most Eudicots and monocots show a syncarpous gynoecium in which the pollen tube, following stigmatic germination, traverses the style to reach the ovary locule and the ovule. As a result, stylar tissues constitute an internal compitum that allows pollen competition and selection (Endress 1982). The intragynoecial compitum offers greater advantages by providing favorable conditions and the necessary nutrition for pollen tubes (Labarca and Loewus 1972, 1973; Herrero and Dickinson 1981; Cheung et al. 1995; Wu et al. 1995; Herrero and Hormaza 1996). The evolution of distinct degrees of carpel closure and syncarpy evidently has impacted in the pollen tube track location (Endress 2015).

The canal and the transmitting tissue of the style provide an extracellular secretion that is incorporated into pollen tubes allowing a heterotrophic pollen tube growth (Labarca and Loewus 1973; Herrero and Dickinson 1981) that differs from the autotrophous pollen tube growth in the stigma (Herrero and Dickinson 1981; Stephenson et al. 2003). The stylar transmitting tissue is composed of highly secretory cells characterized by the production of an extensive extracellular matrix (ECM) (Sassen 1974; Lennon et al. 1998). The actual roles that this ECM plays in pollination are currently unknown, although functions proposed include mechanical and chemotropic pollen tube guidance (Knox et al. 1976; Knox 1984; Clarke et al. 1979; Heslop-Harrison 1987; Sanders and Lord 1989; Vennigerholz 1992; Cheung et al. 1995; Wu et al. 1995; Jauh and Lord 1995; Wilhelmi and Preuss 1996, 1997; Jauh et al. 1997; Malhó 1998; Wilhelmi and Preuss 1999; Shimizu and Okada 2000), as well as pollen tube nutrition (Kroh et al. 1970; Wu et al. 1995; Lind et al. 1996). Mainly carbohydrates and proteins compose the intercellular matrix (Knox 1984). There are also some pistil-specific glycoproteins (Herrero and Hormaza

1996). The transmitting tissue-specific glycoprotein (TTS) attracts pollen tubes and stimulates their growth; it adheres and incorporates into pollen tube walls (Cheung et al. 1995; Erbar 2003). This proposal is becoming increasingly accepted (Sanders and Lord 1989; Cheung 1996; Lord and Kohorn 1986; Wilhelmi and Preuss 1996; Lennon et al. 1998). Pollen tube growth is believed to be heterotrophic at the expenses of the stylar reserves (Herrero and Dickinson 1981). In many cases, the route of the pollen tubes depends on the structure of the transmitting tissue. In most species, the pathway is provided by the presence of thickened middle lamellae or by secretions produced by epithelial cells lining a canal (Crawford and Yanofsky 2008). However, other possible pathways were also described. For instance, pollen tubes were also observed growing through the cell wall and between the plasma membrane and the cell wall (Wilms 1980) and through the cytoplasm of the epithelial cells (Gotelli et al. 2012). This last report is an isolated case, and more studies are needed to confirm if the pollen tube can really pass through the plasmalemma.

A highly regulated tip growth of the pollen tube is required for plant fertility. Pollen tube growth is associated with several types of intracytoplasmic movements (Pierson and Cresti 1992; Mascarenhas 1993). A large number of secretory vesicles accumulate in the tip region and fuse with the apical membrane, providing new membrane and cell wall precursors to the growing pollen tube. A conspicuous mass of organelles moves along the pollen tube for the proper tip-directed elongation. Polarized growth is maintained mostly by two factors: the tip-to-base gradient of Ca^{2+} distribution within the pollen tube (Miller et al. 1992) and the cytoskeleton (Hepler et al. 2001). While the internal Ca^{2+} distribution could act as a factor of general control during tube elongation (Lenartowska et al. 2001; Ge et al. 2009; Hepler et al. 2012; Steinhorst and Kudla 2013), it seems likely that the cytoskeleton represents the molecular machinery that effectively moves vesicles and other organelles (Heslop-Harrison et al. 1988; Moscatelli et al. 1995). Suwinska et al. (2017) claimed that, in *Petunia* Juss. calreticulin is needed for the tip-focused Ca^{2+} homeostasis and for the actin cytoskeleton arrangement and function, required for several key processes involved in the pollen tube tip growth. It is believed that pollen germination and pollen tube growth depend on the presence of Ca^{2+} in the medium (Brewbaker and Kwack 1963). Zhao et al. (2004) described an increase of detectable levels of Ca^{2+} in the cytoplasm and vesicles near the pollen tube tip, in the transmitting tract extracellular matrix binding to the stylar cell and in the pollen tube walls after pollination in lily. Bednarska et al. (2005) reported that pollination induces an accumulation of Ca^{2+} in the apoplast of the stigma. According to Rosenfeldt and Galati (2009) the subcellular localization of Ca^{2+} ions in stigmas of species of *Oxalis* L. differs between developmental stages, being the highest during anthesis, but it is the same between different stylar morphs (heterostyly).

Stigma/style cysteine-rich adhesins (SCA) and plantocyanins are involved in pollen tube tip growth and guidance (Dong et al. 2005; Chae and Lord 2011; Qu et al. 2015), and chemocyanins appear to play a role in adhesion of the pollen tube to the stylar tissue (Park et al. 2000). Dowd et al. (2006) cloned the cDNA for PI-PLC of *Petunia inflata* R. E. Fr. named Pet PLC1, which is expressed in growing pollen tube. Pet PLC1 is involved in stabilizing the apical Ca^{2+} gradient normally required for directed tip growth and in maintaining actin dynamics associated with growth. These authors suggest that Pet PLC1 is an important element of the cellular machinery allowing pollen tube extension.

Other regulators of pollen tube tip growth include monomeric G-proteins (Fu et al. 2001; Wu et al. 2001; Chen et al. 2003; Gu et al. 2005). GABA (γ-amino butyric acid) is an extracellular signal for several cells; it is a neurotransmitter (Maitre et al. 2000) and a regulator of hormone secretion in endocrine organs (Gamel-Didelon et al. 2002; Satin and Kinard 1998). Plant cells can secrete GABA (Chung et al. 1992), and the *pop2* defect raises the possibility that GABA plays a signaling role in guiding pollen tubes. Palanivelu et al. (2003) described the role for GABA in pollen tube growth and guidance in *Arabidopsis*. They identified the *Arabidopsis POP2* gene as a GABA transaminase and demonstrated that decreased POP2 activity leads to increased levels of GABA throughout the ovule, coupled with aberrant growth and guidance of *pop2* pollen tubes.

Arabinogalactan glycoproteins (AGPs) are believed to have numerous functions for cell-to-cell interactive processes (Kreuger and van Holst 1993; Showalter 1993; Serpe and Nothnagel 1995) and constitute a major class of proteins in the extracellular matrix of the transmitting tissue and in the stigma exudates (Clarke et al. 1979; Gleeson and Clarke 1980). In *Nicotiana tabacum* L. a transmitting tissue-specific (TTS) protein belonging to the AGPs family attracts pollen tubes and promotes tube elongation (Wang et al. 1993; Cheung et al. 1995; Wu et al. 1995, 2000). AGPs act as a nutrient source as pollen tubes deglycosylate TTS proteins to free the carbohydrate from the protein backbone (Wu et al. 1995; Sanchez et al. 2004). However, the mechanism by which AGPs contribute to pollen tube guidance is not clear (Sommer-Knudsen et al. 1998; Higashiyama and Hamamura 2008; Hiscock and Allen 2008). In *Trithuria* Hook. F., AGPs have a similar role in the hairs that are homologous to the stigmatic papilla of most angiosperms and function as stigma and style (Prychid et al. 2011). Arabinogalactan proteins are also expressed in the ovule and in the synergids of other species (Pereira et al. 2014; Lopes et al. 2016). In *Malus domestica* Borkh. the secretion of glycoproteins on the obturator surface is concomitant with pollen tube arrival at this structure, and AGPs are depleted

after pollen tube passage, suggesting a role in regulating pollen tube access to the ovule (Losada and Herrero 2017). According to Okuda and Higashiyama (2010), cysteine-rich polypeptides (LUREs) secreted by the synergids cells are the key molecules at the last step of pollen tube guidance.

Styles types

In relation to its transmitting function and anatomy, styles can be classified into three different types: open, closed, or semi-closed (Johri 1984; Satina 1944; Knox 1984; Gasser and Robinson-Beers 1993). The open style is characterized by a canal lined with a glandular epidermis or epithelium and is more common among the monocots; the closed style, usually present in Eudicots, has a core of transmitting tissue; and, in semi-closed style, the transmitting tissue is limiting the stylar canal (Vasil and Johri 1964; Vasil 1974; Johri 1984).

Styles and pollen tube pathways in basal angiosperms

In the early divergent angiosperms, the precise pathway of the pollen tubes is known for a few species. In *Brasenia* Schreb., *Cabomba* Aubl., *Nymphaea* L., *Victoria* Lindl. *Austrobaileya* C. T. White, *Illicium* L., *Trimenia* Seem., *Tasmannia* R. Br. ex DC., and *Annona* L. a stylar, canal is distinct at least at some part of the stylar region, and it is coated by uniseriate epithelium with uninucleate secretory cells (Orban and Bouharmont 1995; Endress and Igersheim 1997; Bernhardt et al. 2003; Frame 2003; Lyew et al. 2007; Sage et al. 2009; Taylor and Williams 2009; Lora et al. 2010; Williams et al. 2010; Galati et al. 2016, table 1). The pollen tubes enter the stylar canal in these taxa; however, they do not necessarily start their growth in it. In *Cabomba caroliniana* A. Gray pollen tubes first grow through the intercellular lamella of the substigmatic ground stylar tissue adjacent to the stigmatic papillae and then grow into the stylar canal (Galati et al. 2016). In the syncarpous gynoecium of *Nymphaea*, the stylar portion (no true style) is also composed by a solid tract formed by the postgenitally fused epidermis, determining intercellular growth of the pollen tubes at this region (Orban and Bouharmont 1995; Williams et al. 2010). Many pollen tubes displace freely within the canal rich in secretion in *Nymphaea* and *Cabomba* (Williams et al. 2010; Galati et al. 2016), whereas only one to three of them can penetrate the short and narrow stylar canal in *Annona* (Lora et al. 2010). *Trithuria* (Hydatellaceae) is devoid of a style but long stigmatic papillae function as a style. In this genus, the pollen tubes penetrate the hair cuticle and grow through the outer layer of the cell wall (Prychid et al. 2011).

In *Amborella trichopoda* Baill., the pollen tube grows through a continuous line of secretion from stigma to the open stylar canal and the ovarian cavity (Endress and Igersheim 2000; Williams 2009). The brief style presents a secretory canal not bounded by a distinct epidermal layer, so it was considered as semi-closed (Williams 2009). According to Sage et al. (2009), the cuticular matrices from adjacent stigmatic papillae become fused during development, forming a stigmatic matrix that structurally resembles a "solid style" in other angiosperms. Enfolding of the carpel margins in the pseudostyle offers protection to the growing pollen tube (Lyew et al. 2007) and to a minor amount of ECM present over the secretory slit. The role of the pseudostyle is more or less similar to that of the usual compitum in confining the pollen tube growth along the secretory path and regulating the number of pollen tubes (Erbar 2003). The pathway in the stylar region is in most cases intercellular, through the extracellular matrix between the loose secretory cells bordering the canal, and only in few occasions pollen tube enters the stylar canal if proceeds from a pollen grain just above its open mouth (Williams 2009). Similar growth pattern of pollen tubes is reported in *Trimenia* Seem. in which the two surfaces of the carpel are appraised to each other and secretion is also present, but the pollen tube grows intercelullarly between subepithelial cells (Bernhardt et al. 2003). This partly hidden pollen tube growth pattern is similar to that reported in Winteraceae (Canellales) (Frame 2003), Schisandraceae (Austrobaileyales) (Lyew et al. 2007) and other basal angiosperms (Endress and Igersheim 2000; Bernhardt et al. 2003; Thien et al. 2003; Lora et al. 2010, 2016). *Sarcandra* Gardner and *Chloranthus* Sw. (Chloranthaceae, Chloranthales) also possess a stylar canal delimited by an epithelium, but pollen tubes elongate intercellulary within the extracellular matrix of the inner tangential wall of the canal epidermal cells (Hristova et al. 2005).

Open styles

Open type styles are characterized by a canal lined with a glandular epidermis or secretory epithelium (Tilton and Horner 1980; Ciampolini et al. 1981; Dickinson et al. 1982). They are mostly present in monocots (Johri 1984, table 1); however, there are reports of Eudicots with open styles too (Gotelli et al. 2012, table 1). The ultrastructure of the epithelial cells was studied in some species, and it is characterized by the presence of abundant rough endoplasmic reticulum, usually with cisterns parallel to the external tangential wall, vacuoles, many mitochondria, plastids that contain well-developed grana and lipidic globules inside, numerous dictyosomes, and vesicles (Rosen and Thomas 1970; Vasilev 1970; Clarke et al. 1977; Tilton and Horner 1980; Ciampolini et al. 1981; Owens et al. 1984; Lord and Kohorn 1986;

Leins and Erbar 2005; Reinhardt et al. 2007; Castro et al. 2008; Gotelli et al. 2012; Galati et al. 2016).

Ciampolini et al. (1981) found that the inner tangential walls of *Citrus x limon* (L.) Osbeck were formed by two layers: the original wall and the inner one formed by subsequent deposition of abundant materials of different origin. Localized wall expansions or wall ingrowths toward the interior of the cell were also found in the epithelial cells of *Lilium* L. (Rosen and Thomas 1970; Vasilev 1970), *Gladiolus* L. (Clarke et al. 1977), *Ornithogalum caudatum* Jacq. (Tilton and Horner 1980), *Strelitzia reginae* Aiton (Kronestedt and Walles 1986), *Sternbergia* Waldstein & Kitaibel (Ciampolini et al. 1990), *Ornithogalum sigmoideum* Freyn & Sint. (Ismailoglu and Ünal 2012) and, *Discaria americana* Gillies & Hook. (Gotelli et al. 2012). This is a common characteristic of transfer cells (Gunning and Pate 1969; Pate and Gunning 1972). According to Tilton and Horner (1980) the increase in surface area in transfer cells facilitates intracellular transport and transfer of the secretion products into the canal.

The stylar canal of *Polygala vayredae* is surrounded by metabolically active cells and has lipid rich mucilage (Castro et al. 2008). In *Cabomba caroliniana* the ultrastructure of the glandular epidermal cells shows abundant mitochondria, plastids, RER, and dictyosomes (Galati et al. 2016). Considerable dictyosomic activity was observed in *Citrus limon* (Ciampolini et al. 1981) and in *C. caroliniana* (Galati et al. 2016). Ismailoglu and Ünal (2012) described the ultrastructure of the open style of *Ornithogalum sigmoideum* and considered that the presence of abundant endoplasmic reticulum, dictyosomes, mitochondria, plastids, and ribosomes would indicate the secretory function of these cells. The presence of ER, active dictyosomes, and abundant starch-containing plastids in epithelial cells is correlated with the synthesis and secretion of proteins, polysaccharides, and lipids required for pollen tube growth (Tilton and Horner 1980; Kandasamy and Kristen 1987; Ciampolini et al. 1990; Ciampolini and Cresti 1997). The presence of abundant and active dictyosomes is linked to the synthesis and secretion of polysaccharides (Ciampolini et al. 1988), while there is a close relationship between lipid accumulation and the presence and activity of ER with abundant plastids (Ismailoglu and Ünal 2012).

Secretions found in stylar canals are usually rich in polysaccharides and proteins. Secretion products found in the canal of *Citrus* L. (Ciampolini et al. 1981), *Strelitzia reginae* Aiton (Kronestedt and Walles 1986), and *Ornithogalum sigmoideum* (Ismailoglu and Ünal 2012), consist of insoluble polysaccharides, proteins, and lipids. In *Lilium* (Labarca and Loewus 1973), *Annona* (Vithanage 1984), *Sternbergia* (Ciampolini et al. 1990), and in *Cabomba caroliniana* (Galati et al. 2016) secretions show a weak reaction for proteins but are rich in polysaccharides. According to van Went and Willemse (1984), the secretion products of the canal epithelial cells in open styles are compared with the extracellular matrix of the transmitting tissue in closed styles. Galati et al. (2016) supported this by claiming that secretion in *C. caroliniana* has a notable fibrillar structure, similar to a cell wall.

In *Gladiolus*, the mucilaginous secretion is accumulated between the epithelial cell wall and the cuticle that covers the canal epithelial cells. The pollen tube penetrates the cuticle and grows through the secretion (Clarke et al. 1977; Pandey 1997).

In some species of Rhamnaceae pollen tubes do not always grow through the canal. In *Discaria americana* pollen tubes grow through the middle lamella located between epithelial and subepithelial canal cells and not through the canal (Gotelli et al. 2012). In *D. americana* and *Colletia spinossisima* J. F. Gmel., pollen tubes can move through different routes: They can grow through the secretion in the canal, through the middle lamella between epithelial and subepithelial cells of the stylar canal, and through the cytoplasm of subepithelial cells (Gotelli et al. 2012).

According to Gotelli et al. (2012) ultrastructural differences between the epithelial cells of the canal can be correlated with different pollen tubes paths. The presence of epithelial and subepithelial cells with cytoplasm rich in organelles and a copious secretion in the lumen of the canal could favor growth of the pollen tubes both through the cytoplasm of these cells and the canal. Conversely, very vacuolated epithelial cells, with transfer cell characteristics, abundant amyloplasts, and limited canal secretion, may lead pollen tubes to grow through the thickened middle lamella between the epithelial and subepithelial cells, which it would probably be the most favorable medium.

Closed styles

The structure of closed styles is known for several species, such as *Lycopersicum peruvianum* (L.) Mill. (Cresti et al. 1976), *Malus communis* Desf. (Cresti et al. 1980), *Primula vulgaris* Huds. (Heslop-Harrison et al. 1981), *Olea europaea* L. (Ciampolini et al. 1983), *Zephyranthes candida* (Lindl.) Herb. and *Z. citrina* Baker (Ghosh and Shivanna 1984), *Hypericum calycinum* L. (Ciampolini et al. 1988), *Nicotiana sylvestris* Speg. (Kandasamy and Kristen 1987; 1990), *Pyrus serotina* Rehder (Nakanishi et al. 1991), *Brugmansia suaveolens* (Humb. & Bonpl. Ex Willd.) Bercht. & J. Presl. (Vennigerholz 1992; Hudak et al. 1993), *Smyrnium perfoliatum* L. (Weber 1994), *Tibouchina semidecandra* (Mart. & Schrank ex D.C.) Cogn. (Ciampolini et al. 1995), *Vitis vinifera* var. *vinifera* Raf. (Ciampolini et al. 1996), *Karwinskia parvifolia* Rose (Hanackova and Piñeyro Lopez, 1999), *Oxalis paludosa* A. St.-Hill., *O. hispidula* Zucc., and

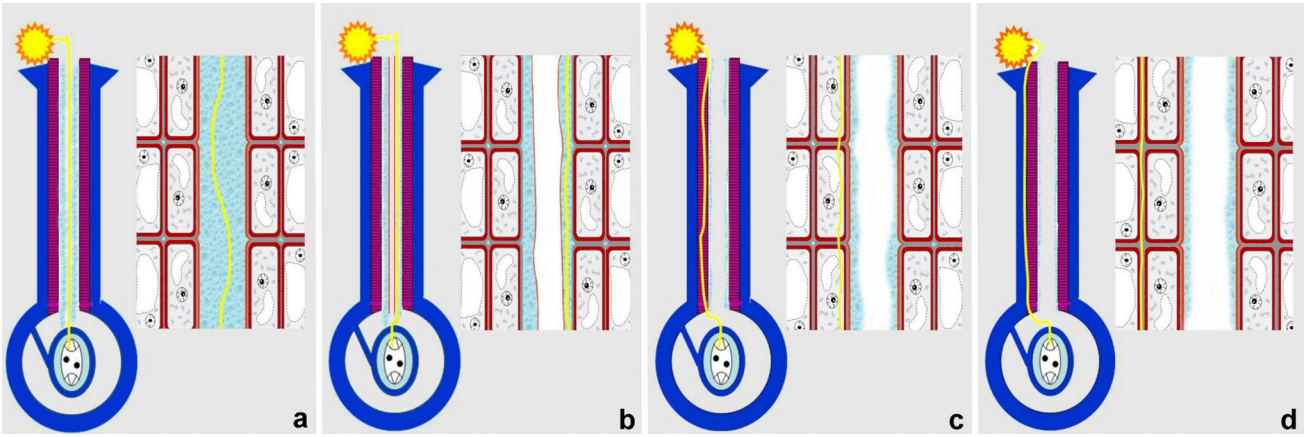

Fig. 1 Pollen tube pathways in open styles. **a** General aspect and detail of pollen tube growing through the secretion in the canal. **b** General aspect and detail of pollen tube growing through the secretion accumulated between the cuticle and the wall of the epithelial cells. **c** General aspect and detail of pollen tube growing through the cytoplasm of subepithelial cells. **d** General aspect and detail of pollen tube growing through the middle lamella between epithelial and subepithelial cells of the stylar canal (**b**)

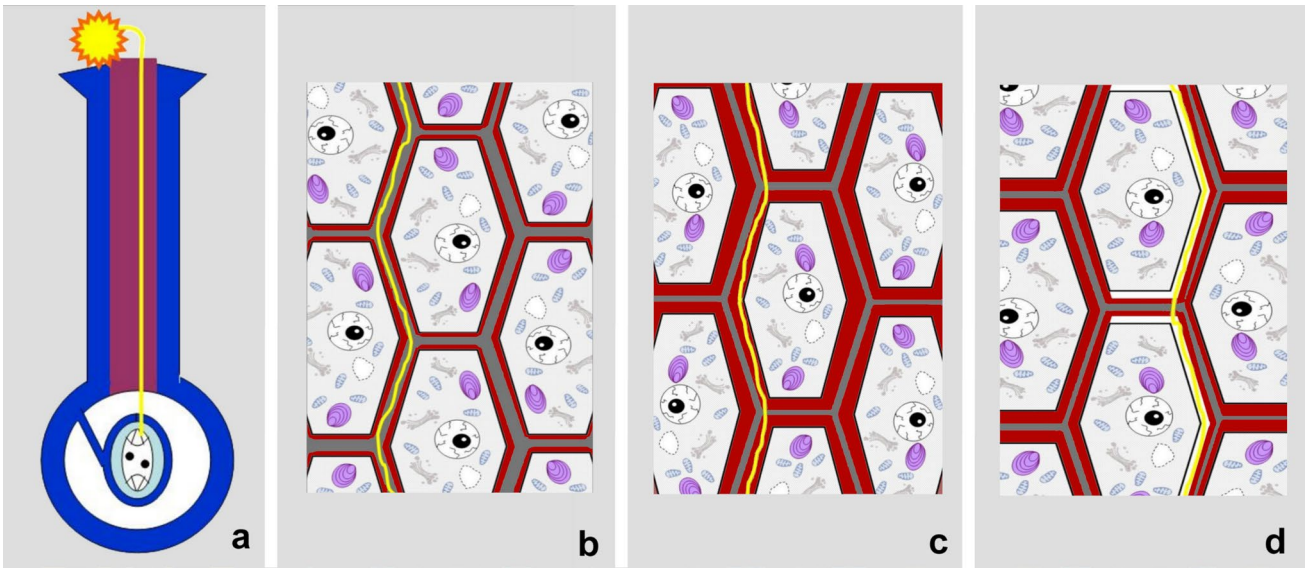

Fig. 2 Pollen tube pathways in closed styles. **a** General aspect. **b** Detail of pollen tube growing through the intercellular matrix of the transmitting tissue. **c** Detail of pollen tube growing through the thickened cell walls of the transmitting tissue. **d** Detail of pollen tube growing between the plasma membrane and the cell wall of the transmitting tissue cells

O. articulata Savigny (Rosenfeldt and Galati 2000), *Cynara cardunculus* L. (Duarte et al. 2006), *Passiflora edulis* fo. *flavicarpa* O. Deg. (Souza et al. 2006), *Olea europaea* (Serrano et al. 2008), *Oxalis pes-caprae* L. (Signorini et al. 2014), *Allionia choisyi* Standl., *Boerhavia diffusa* var. *leiocarpa* (Heimerl) C. D. Adams, *B. pulchella* Griseb., *Bougainvillea campanulata* Heirmel, *B. praecox* Griseb., *B. stipitata* Griseb., *Mirabilis jalapa* L., *M. ovata, Pisonia zapallo* var. *guaranitica* Toursark, *P. zapallo* var. *zapallo* Griseb., *Pisoniella arborescens* var. *glabrata* Kuntze (Nores et al. 2015).

According to Ciampolini et al. (2001) in almost all non-graminaceous species characterized by a closed style, the transmitting tract of the style is very distinct. The transmitting tissue in a closed style can be either loosely arranged or in a more compact structure, depending on the amount and quality of the intercellular spaces (Johri 1984). These intercellular spaces can be filled with interstitial material containing phenolic compounds, tannins polysaccharides and pectic substances, commonly referred to as extracellular matrix (ECM) or intercellular matrix (IM) (Sanders and Lord 1992; Cheung et al. 1995; Raghavan 1997; Shivanna et al. 1997; Mollet et al. 2000). The extracellular matrix has greater electron density than the cell walls due to its amorphous nature (Raghavan 1997). This mucilaginous matrix

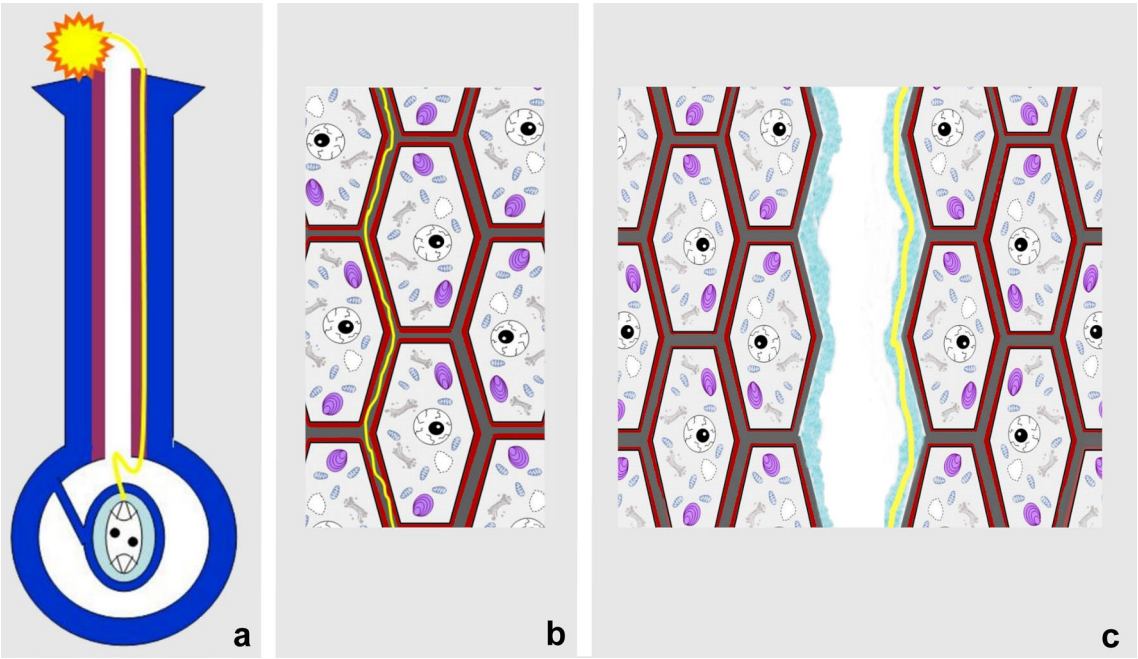

Fig. 3 Pollen tube pathways in semi-closed styles. **a** General aspect. **b** Pollen tube growing through the intercellular matrix of the transmitting tissue. **c** Pollen tube growing through the secretion in the canal

facilitates and guides pollen tube growth (Clarke et al. 1977; Rosenfeldt and Galati 2009).

In *Lycopersicum peruvianum* the development of the transmitting tissue goes through two phases: first the main part of the extracellular matrix, consisting of pectins, is formed; then, the cells form an extensive rough endoplasmic reticulum and proteins are incorporated in the extracelular matrix (Cresti et al. 1976). In *Petunia*, *Lycopersicum* and *Malus* the intercellular spaces are equally filled throughout the whole diameter of the transmitting tissue, but the intercellular substance in *Vitis* L. increases from the periphery to the center of the transmitting tissue where the cuticle of both carpels is joined. This phenomenon is especially prominent near the ovary resulting in a real cavity or canal (Ciampolini et al. 1996). The primary axes of the pistils of *Pennisetum* Rich. (Heslop-Harrison and Heslop-Harrison 1980), *Zea* L. (Heslop-Harrison et al. 1984), and *Oryza* L. (Ciampolini et al. 2001) lack a well-defined transmitting strand. Many cell layers surrounding the vasculature represent the transmitting tissue. The cells of the transmitting tissue in these cereals are polygonal in cross section, and plasmodesmata are present in the longitudinal as well as in transverse walls. In rice the ECM is confined to the corners of the cells of the transmitting tissue (Ciampolini et al. 2001). The components of the ECM in rice seem to be secreted by exocytosis, as indicated by the discharge of the contents of vesicles by fusion with the plasma membrane. In *Secale* L. and *Hordeum* L. (Heslop-Harrison and Heslop-Harrison 1980), paramural bodies discharging vesicle swarms into the adjacent intercellular spaces of the axes have been frequently observed. Heslop-Harrison and Heslop-Harrison (1980) suggest that the paramural bodies form a granulocrine secretory system producing the constituents of the ECM (Ciampolini et al. 2001).

The presence of active dictyosomes, ribosomes, rough endoplasmic reticulum, and vesicles in cells of the transmitting tissue can be associated with the synthesis and secretion of polysaccharides and pectin (Jensen and Fisher 1969; Cresti et al. 1976; Ciampolini et al. 1995; Duarte et al. 2006; Souza et al. 2006; Rosenfeldt and Galati 2009). Transmitting tissue in *Nicotiana tabacum* is chlorophyllous, and its cells contain numerous mitochondria, dictyosomes, RER, amyloplasts, ribosomes, as well as crystal-containing microbodies and myelin-like formations (Bell and Hicks 1976). Rosenfeldt and Galati (2000) claim that starch is commonly present in the peripheral parenchyma of the transmitting tissue and is consumed by the pollen tube during growth and not by the cells that contain it. Plasmodesmata are observed in the transmitting cell walls of several species: *Petunia hybrida* E. Vilm. (Sassen 1974), *Nicotiana tabacum* (Bell and Hicks 1976), *Lycopersicum peruvianum* (Cresti et al. 1976), *Tibouchina semidecandra* (Mart. & Schrank ex DC.) Cogn. (Ciampolini et al. 1995), *Corylus avellana* L. (Ciampolini and Cresti 1997), *Oryza sativa* L. (Ciampolini et al. 2001), *Oxalis paludosa*, and *O. hispidula* (Rosenfeldt and Galati 2009). The cell walls of the transmitting tissue of *O. paludosa* and *O. hispidula* have ingrowths surrounded by the plasma membrane. Similar observations were made

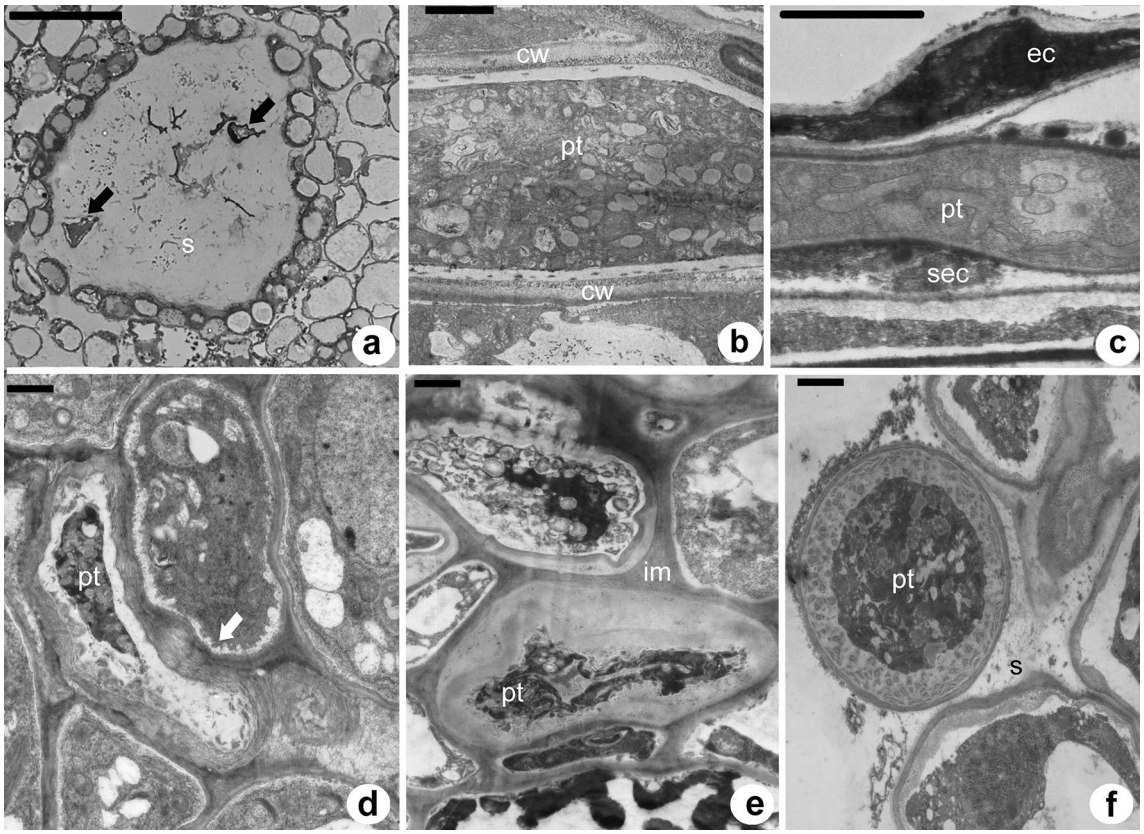

Fig. 4 **a** Bright field microscope. **c–f** TEM. **a–c** Open styles. **d** Closed style. **e**, **f** Semi-closed style. **a** Transversal section of pollen tubes (arrows) growing through the secretion (s) in the canal of *Cabomba caroliniana* [reproduced by permission from Galati et al. (2016) Protoplasma 253:155–162]. **b** Pollen tube (pt) growing through the intercellular matrix between the epithelial and subepithelial cells in *Discaria americana*; cw: cell wall [reproduced by permission from Gotelli et al. (2012) Plant Syst Evol https://doi.org/10.1007/s00606-012-0665-x]. **c** Pollen tube (pt) growing through subepitelial cells (sec) in *Colletia paradoxa*. The cytoplasm of the epithelial cell (ec) shows abortion signs [imagines modified and reproduced by permission from Gotelli et al. (2012) Plant Syst Evol https://doi.org/10.1007/s00606-012-0665-x]. **d** Pollen tube (pt) growing through the intercellular matrix of *Condalia buxifolia.* **e** Pollen tube (pt) growing through the intercellular matrix of *Ziziphus mucronata* [reproduced by permission from Gotelli et al. (2017) Protoplasma https://doi.org/10.1007/s00709-017-1167-z]. **f** Pollen tube (pt) growing through the secretion of *Ziziphus mucronata* [reproduced by permission from Gotelli et al. (2017) Protoplasma https://doi.org/10.1007/s00709-017-1167-z]. Scale bars: **a** 50 µm; **b–f** 1 µm

in *P. hybrida* by Herrero and Dickinson (1981). According to these authors, this characteristic associated with the plasmodesmata assures a great efficiency in the cellular exchange. These wall ingrowths resemble the "transfer cells" described by Gunning and Pate (1969). Wardini et al. (2007) claim that the progression of wall ingrowths deposition is positively correlated with intracellular sucrose concentrations. Intracellular sucrose is likely to increase in the transmitting tissue cells before anthesis. Ciampolini et al. (1996) suggest that the presence of plasmodesmata strengthens the hypothesis that they are involved in transduction of signals from the ovary and in the control of pollen tube growth.

The structure of the transmitting tissue determines the path of pollen tubes from stigma to ovules, along a path of least mechanical resistance (Jensen and Fisher 1968; Vasil 1974; Heslop-Harrison 1999; Signorini et al. 2014). In several taxa such as *Petunia* (Van der Pluijm and Linskens 1966; Sassen 1974), *Diplotaxis* DC. (Kroh and Munting 1967), *Capsella lythrum* (Sassen 1974), *Lycopersicum* (Cresti et al. 1976), *Nicotiana* (Bell and Hicks 1976), *Raphanus raphanistrum* L. (Hill and Lord 1987), *A. thaliana* (Lennon et al. 1998), *Borago officinalis* L. and *Heliotropium europaeum* L. (Ghorbel and Nabli 1998), *Quercus suber* L. (Boavida et al. 1999), *Oxalis articulata*, *O. hispidula* and *O. paludosa* (Rosenfeldt and Galati 2009), and *O. pes-caprae* (Signorini et al. 2014), pollen tubes grow through the extracellular matrix of the transmitting tissue of the style. In *Gossypium* L., pollen tubes penetrate and grow through the thickened cell walls of the transmitting tissue as in *Helianthus annus* L. (Jensen and Fisher 1970; Gotelli et al. 2010). In spinach,

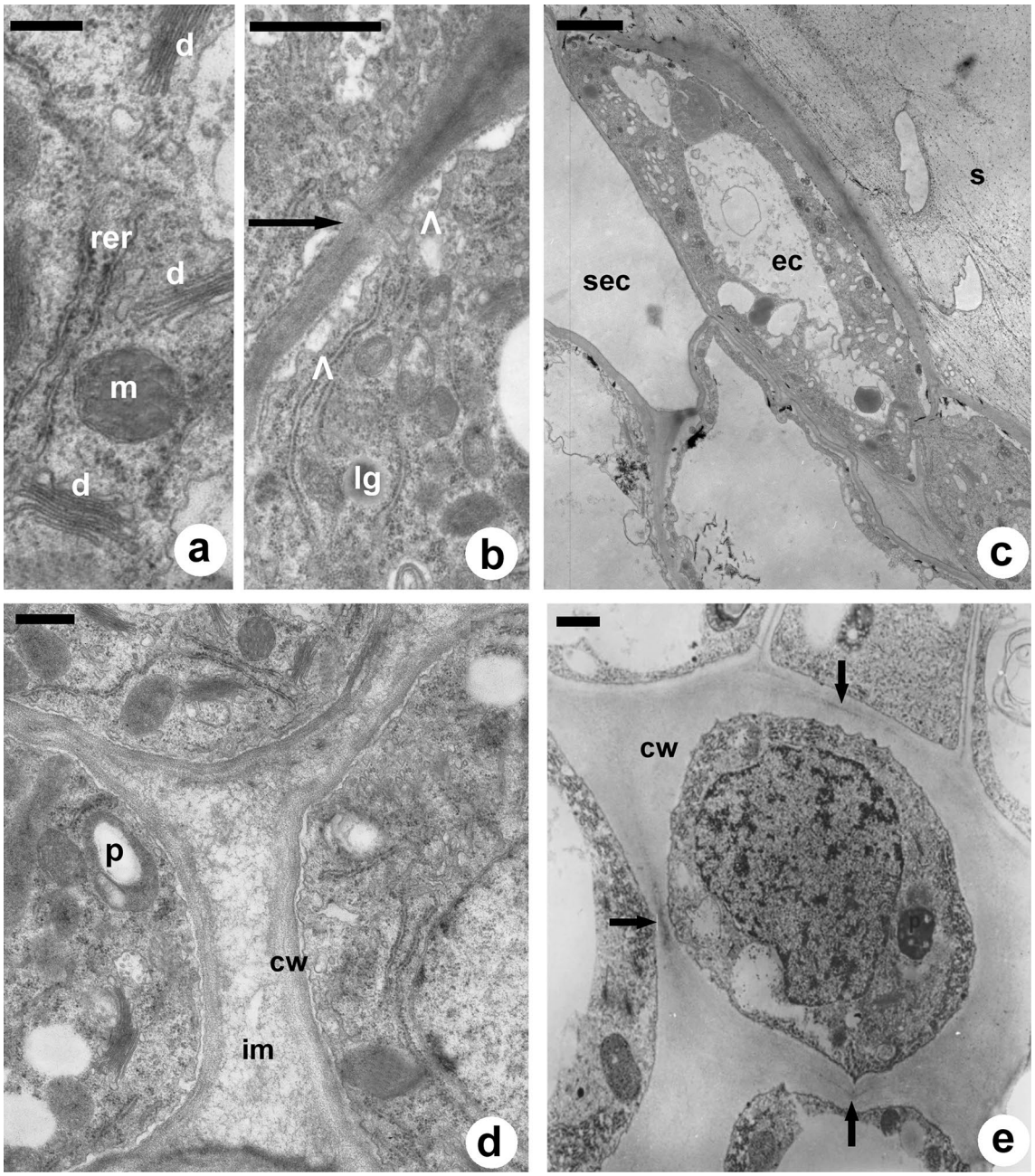

Fig. 5 **a**–**e** TEM. **a**, **b** Detail of cytoplasm of transmitting tissue cells in *Condalia buxifolia*. rer: rough endoplasmic reticulum, m: mitochondria, d: dictyosome, arrow: plasmodesmata, arrow head: cell wall ingrowths [imagines modified and reproduced by permission from Gotelli et al. (2017) Protoplasma https://doi.org/10.1007/s00709-017-1167-z]. **c** Detail of open style of *Cabomba caroliniana* showing secretion (s), ephitelial (ec) and subepithelial (epc) cells [reproduced by permission from Galati et al. (2016) Protoplasma 253:155–162]. **d** Detail the transmitting tissue of closed style in *Condalia buxifolia* showing intercellular matrix (im), the cell wall (cw) and organelles (p: amyloplast, m: mitochondria, rer: rough endoplasmic reticulum). **e** Detail the transmitting tissue of semi-closed style in *Helianthus annus* showing thickened cell wall (cw) and thin intercellular matrix (arrows) [reproduced by permission from Gotelli et al. (2010) Biocell 34: 133–138]. Scale bars: **a** 0.25 µm; **b**, **d** 0.5 µm; **c** 2 µm; **e** 1 µm

pollen tubes can grow intercellularly through the outer part of the cell wall or between the plasma membrane and the cell wall (Wilms 1981). It is not known how pollen tubes penetrate and pass the cell wall. One possibility is the presence of enzymes that degrade cell walls. As pollen tubes grow within the cell walls, the cytoplasm of the penetrated cells slowly degenerates.


EARLY ANGIOSPERMS
ANITA GRADE
MAGNOLIDS
MONOCOTS
COMMELINDS
EUDICOTS
CORE EUDICOTS
ROSIDS
EUROROSIDS I
EUROROSIDS II
ASTERIDS
EUASTERIDS I
EUASTERIDS II
AMBORELLALES
NYMPHAEALES
AUSTROBAILEYALES
CHLORANTHALES
CANELLALES
PIPERALES
LAURALES
MAGNOLIALES
ACORALES
ALISMATALES
PETROSAVIALES
DIOSCOREALES
PANDANALES
LILIALES
ASPARAGALES
ARECALES
POALES
COMMELINALES
ZINGIBERALES
CERATOPHYLLALES
RANUNCULALES
SABIALES
PROTEALES
TROCHODENDRALES
BUXALES
GUNNERALES
DILLENIALES
SAXIFRAGALES
VITALES
ZYGOPHYLLALES
CELASTRALES
MALPIGHIALES
OXALIDALES
FABALES
ROSALES
CUCURBITALES
FAGALES
GERANIALES
MYRTALES
CROSSOSOMATALES
PICRAMNIALES
SAPINDALES
HUERTEALES
MALVALES
BRASSICALES
BERBERIDOPSIDALES
SANTALALES
CARYOPHYLLALES
CORNALES
ERICALES
GARRYALES
GENTIANALES
LAMIALES
SOLANALES
BORAGINALES
AQUIFOLIALES
ASTERALES
ESCALLONIALES
BRUNIALES
APIALES
PARACRYPHIALES
DIPSACALES
Amborellaceae
Cabombaceae, Nymphaeaceae
Austrobaileyaceae, Schisandraceae, Trimeniaceae
Chloranthaceae
Winteraceae
Saururaceae
Hernandiaceae, Monimiaceae, Gomortegaceae, Lauraceae
Annoncaceae
Acoraceae
Posidoniaceae, Tofieldiaceae
Petrosaviaceae
Nartheciaceae
Velloziaceae
Liliaceae
Iridaceae, Asparagaceae
Amaryllidaceae
Arecaceae
Eriocaulaceae
Poaceae
Pontederiaceae
Strelitziaceae
Ceratophyllaceae
Berberidaceae
Sabiaceae
Nelumbonaceae
Proteaceae
Trochodendraceae
Didymelaceae, Buxaceae
Myrothamnaceae, Gunneraceae
Dilleniaceae
Hamamelidaceae
Vitaceae
Krameniaceae
Celastraceae
Passifloraceae, Hypericaceae
Oxalidaceae
Polygalaceae
Fabaceae, Caesalpiniaceae
Rosaceae
Rhamnaceae
Coriariaceae, Begoniaceae
Betulaceae
Geraniaceae
Melastomataceae, Lythraceae
Staphylaceae
Rutaceae
Burseraceae
Anacardiaceae
Tapisciaceae
Malvaceae
Brassicaceae
Berberidopsiaceae
Loranthaceae
Amaranthaceae, Nyctaginaceae
Cornaceae
Ericaceae
Primulaceae
Garryaceae
Eucommiaceae
Asclepiadaceae
Oleaceae
Solanaceae
Boraginaceae, Ehretiaceae
Cardiopteridaceae
Asteraceae
Bruniaceae
Apiaceae
Paracryphiaceae
Adoxaceae

◂**Fig. 6** Type of style mapped in a phylogenetic tree according to APG IV and APweb following the maximum parsimony principle. : open style, : closed style, : semi-closed style, : lost of open style, : lost of closed style, : lost of semi-closed style

Semi-closed styles

The transmitting tissue in semi-closed styles is characterized by production of a fluid intercellular matrix between its cells and pollen tubes generally grow through the highly specialized matrix (de Graaf et al. 2001). However, pollen tubes growing through the secretion in the canal were observed in *Ziziphus mucronata* Willd. (Gotelli et al. 2017). The ultrastructure of semi-closed styles is known for a few species: *Trifolium pratense* L. (Heslop-Harrison and Heslop-Harrison 1982a, b), *Caesalpinia pulcherrima* (L.) Sw. (Owens et al. 1995), *Asclepias exaltata* L. (Sage and Williams 1995), *Vigna adenantha* (G. Mey.) Maréchal, Mascherpa & Stainier (Castro and Agulló 1998), *Ceiba insignis* (Kunth) P. E. Gibbs & Semir (Rosenfeldt and Galati 2000), and *Ziziphus mucronata* Willd., *Z. jujuba* Mill., *Paliurus spinachristi* Mill. and *Hovenia dulcis* Thunb. (Gotelli et al. 2017).

In *Vigna adenantha* the distal portion of the style is closed and gradually passes to the semi-closed condition. One or a few layers of transmitting tissue surround the canal of the style (Castro and Agulló 1998). The transmitting tissue of *Ceiba insignis* has thin primary walls that are separated by massive deposits of amorphous material, and contain numerous mitochondria, endoplasmic reticulum of rough type, ribosomes and amyloplasts (Rosenfeldt and Galati 2000). Transmitting tissue cells of *Asclepias exaltata* have a peripheral cytoplasm with some mitochondria, numerous plastids with starch grains, dictyosomes and several lipidic globules. These characteristics indicate a secretory function and proteins, and insoluble carbohydrates are secreted (Sage and Williams 1995). In *Caesalipinia pulcherrima* (Owens et al. 1995) and in the species above mentioned, pollen tubes grow through the intercellular matrix of the transmitting tissue but do not enter the canal (Sage and Williams 1995; Castro and Agulló 1998; Rosenfeldt and Galati 2000; Gotelli et al. 2010). In *Colophospermum mopane* (J. Kirk ex Benth.) J. Léonard (Jordaan et al. 2002) and *Scutia buxifolia* Hutch. & M.B. Moss (Gotelli et al. 2017), the style has a lysigenous canal. In the first species, this canal is bordered by several layers of large vacuolated parenchyma cells containing starch and polyphenolic substances that constitute the body of the style. Pollen tubes grow through the transmitting tissue, which is rich in starch and phenolic substances (Jordaan et al. 2002).

Conclusions

Different pollen tube pathways have been described for several species. Although there is a tendency for pollen tubes to grow through the canal in open styles and through the intercellular matrix in closed and semi-closed styles, there are other possible pathways. Therefore, the pollen tube's route cannot be deduced by the type of style and more ultrastructural studies at different developmental stages of the style are needed. In this review, subtypes are defined according to the pollen tube pathway.

Type I (open style):

Subtype I A: pollen tubes grow through the secretion in the canal (Figs. 1a, 4a).
Subtype I B: pollen tubes grow through the secretion accumulated between the cuticle and the wall of the epithelial cells (Fig. 1b).
Subtype I C: pollen tubes grow through the middle lamella between epithelial and subepithelial cells of the stylar canal (Figs. 1c, 4b).
Subtype I D: pollen tubes grow through the cytoplasm of epithelial cells (Figs. 2b, 4c).

Type II (closed style, Fig. 2a):

Subtype II A: pollen tubes grow through the intercellular matrix of the transmitting tissue (Figs. 2b, 4d).
Subtype II B: pollen tubes grow through the thickened cell walls of the transmitting tissue (Fig. 2c).
Subtype II C: pollen tubes grow between the plasma membrane and the cell wall of the transmitting tissue cells (Fig. 2d).

Type III (semi-closed styles, Fig. 3a):

Subtype III A: pollen tubes grow through the intercellular matrix of the transmitting tissue (Figs. 3b, 4e).
Subtype III B: pollen tubes grow through the secretion in the canal (Figs. 3c, 4f).

The secretory characteristics present in epithelial and transmitting tissue cells, such as a dense cytoplasm with abundant mitochondria, RER, dictyosomes, and plasmodesmata, with or without transfer cells characteristics (Fig. 5a, b), are related with the secretion where pollen tube grows. This secretion can either be represented by the substances in the canal (Fig. 5c), in the intercellular matrix (Fig. 5d), or in the cell wall (Fig. 5e).

The morphology of the style has received little attention. Although there are studies on flower morphology and anatomy of many species of angiosperms, authors do not usually describe the type of style. However, all orders, with the exception of Picramniales and Escalloniales, have at least one type of style either described, mention or photographed. This trait was mapped in a phylogenetic tree according to APG IV and APweb (Fig. 6) following the maximum parsimony principle and information was detailed in Table 1 (supplementary material). According to this, it could be hypothesized that the open style appeared in the early divergent angiosperms. The closed type of style originated three times, in Asparagales, Poales, and Eudicots, and the semi-closed style appeared three times in Rosids, Ericales, and Gentianales. It could also be hypothesized that the open style was lost in core Eudicots, with reversions in some Rosids and Asterids orders (Fig. 6). However, since the information is limited to a few species, we cannot assure if other types of styles are represented in a specific order.

Author contribution statement MG made the bibliographic review and wrote the manuscript. EL and MZ read the manuscript, revised and completed the information. BG revised and corrected the manuscript. MG and BG made the figures.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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