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Filament histology and anther dehiscence

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Several distinctive histological features of the stamen, especially of the filament, are described, some of these for the first time: for example, commonness of (a) mesarch xylem maturation, amphicribral bundles or else collateral strands with phloem considerably enveloping the xylem, and clustering of sieve elements of a bundle and their spatial separation from tracheary elements, (b) exclusively helical wall thickenings of tracheary elements and absence of sclerenchyma, (c) open stomata, a weakly developed cuticle, a prominent intercellular-space system, xylem lacunae, and (d) tannins and crystals. Some of the features in category (a) seem related to the nutritional needs of developing pollen grains in the anther. Features in category (b) are directly related to the usual expansion of the stamen, in particular the filament, before and at anthesis. Features in category (c) (and possibly (d)) probably promote a rapid loss of water or a disruption of the water supply to the anther, and therefore might facilitate anther dehiscence (these features could operate either in isolation or in unison). Tannins, crystals, and secretory structures have been implicated in the protection of pollen against predators.

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INTRODUCTION

The stamens of the vast majority of the approximately 225,000 species of flowering plants are dehiscent, their anthers releasing pollen grains by valves, by terminal pores or, typically, by lateral longitudinal (rarely transverse) slits (van Tieghem, 1891; Kerner von Marilaun, 1895; Staedtler, 1923; Schoenichen, 1924; Matthews & Maclachlan, 1929; Richter, 1929; Maheshwari, 1950; Eames, 1961; Puri, 1970). The endothecium (so-called fibrous layer, contractile layer or mechanical layer), a subepidermal layer (or layers) of cells with conspicuous secondary wall thickenings typically occurring in the inner and radial walls of a cell (but not in the outer periclinal or tangential wall), has

usually been implicated in the role of anther dehiscence; but its absence from some anthers clearly necessitates alternative means of pollen release. For example, disintegration of the anther wall generally occurs in taxa with poricidal anthers (e.g. Ericaceae, Melastomataceae, Epacridaceae, Solanaceae), whereas in others the pollen sacs open by longitudinal breaks (e.g. Orchidaceae, Araceae, Asclepiadaceae, Orobanchaceae). A typical fibrous layer is generally lacking in these taxa and also in certain aquatic ones (Hydrocharitaceae, Zosteraceae) and some cleistogamous flowers (see especially Staedtler, 1923; Matthews & Maclachlan, 1929).

Although it is generally acknowledged that the actual force resulting in dehiscence of anthers is in some manner related to the endothecium (when present), the exact physical mechanism for dehiscence still has not been adequately clarified (see Appendix, p. 311). Because of the presumed importance of the endothecium, previous anatomical attention (cf. the preceding references, those in the Appendix, and also Woycicki, 1924; Stejskal-Streit, 1939, 1940; Kenda, 1952; Wunderlich, 1954; Aleksandrov & Dobrotvorskaya, 1960; Periasamy & Swamy, 1964; Davis, 1966; Vasil, 1967) has focused largely on the anther, the distal portion of the stamen, and has neglected the histology of the filament, the proximal part of the stamen (Plate 1B-G).* Nevertheless, events involving dehiscence of the anther might be expected to be mediated by structural features of the filament since the former is dependent upon the latter for transport of water and nutrients.

As a result of a detailed and lengthy study (Schmid, 1977) based on analysis of some 1500 floral anatomical works (nearly 800 of which are cited in the bibliography of Schmid, 1977), as well as on original observations on over 600 species of angiosperms in some 145 families *sensu* Airy Shaw (1973), I discovered a number of hitherto unmentioned or largely neglected histological features of the stamen, especially of the filament. Since completion of my large and comprehensive study of staminal histology is not expected for some time, I intend the present paper as an interim statement on the histology of the stamen, particularly the filament, in order to stress certain novel histological features of the filament, some of which might shed light on the mode of anther dehiscence of various taxa. I thus hope not only to stimulate other floral anatomists to compile similar data, but also to encourage experimentally and physiologically inclined botanists to test some of the proposals presented in this report. Many of the statements herein are documented in Schmid (1977), but, as indicated previously, complete supportive and quantitative data will be given in a final report. (The species listed below (authorities for binomials appear in Schmid, 1977) are only a partial listing for most histological features.) Finally, although I am not directly concerned with the actual physical forces resulting in anther dehiscence, I take the opportunity in an Appendix to clarify some of the bibliographic and terminological confusion unfortunately encountered in many preceding discussions of anther dehiscence.

* This statement, of course, does not apply to studies of floral ontogeny and vasculature, which often have emphasized the filament. For convenience in discussion I am treating the stamen as composed of a distal anther and a proximal filament. Stamens of a number of taxa, however, are undifferentiated into an anther and a filament. The neoclassical concept of the flower regards such stamens as primitive.

OBSERVATIONS AND DISCUSSION OF STAMINAL HISTOLOGY

The dermal and fundamental tissue systems

As a rule, the filament is histologically much simpler than the other floral parts. The epidermis of both filaments and especially anthers may bear stomata (Plate 1A) (Kenda, 1952; Aleksandrov & Dobrotvorskaya, 1960) and trichomes, both hairs (*Platyspermation crassifolium, Tradescantia* spp., *Lamium amplexicaule, Nerium oleander*; *Bryonia dioica*—Barlow & Sargent, 1975) and especially papillae. The stomata may be either functional, opening and closing on a periodic basis, or else 'functionless' and permanently open (Plate 1A) (Kenda, 1952; Aleksandrov & Dobrotvorskaya, 1960).

The cuticle of stamens is typically minimal in extent (Plate 1A-C), usually less that 1.0 μm in thickness, but sometimes much thicker (e.g. 2.0 μm on the filament of *Moronobea* sp., up to 5.0 μm on the anther of *Nerium oleander*, 5.0-8.0 μm on the filament and 5.0 μm on the stomium of *Campsis radicans*). Not infrequently, the cuticle is unusually thickened at the stomium, but thin elsewhere on the anther (*Campsis radicans, Simmondsia chinensis*). In contrast, all other floral organs generally have a much more conspicuously developed cuticle reminiscent of that on leaves. These data are based on permanent microscope slides, but they are easily verified with Sudan W-stained hand sections of fresh floral material.

The ground tissue of stamens is parenchymatous. Filaments often have a prominent intercellular-space system (Plate 1B-E) (e.g. in *Bixa orellana, Ipomoea batatas, Heteropyxis natalensis, Cucumsis sativus, Campsis radicans, Dentaria laciniata, Paullinia jamaicensis, Tilia americana, Dodecatheon media, Calla palustris, Tradescantia ohiensis, Convallaria majalis, Trillium grandiflorum*), contrary to reports in the literature (Esau, 1965). Anatomists have generally overlooked this staminal feature; Straw's (1956) observation of conspicuous intercellular spaces in the filaments of *Penstemon* and Knoll's (1914) mention of the same for *Cistus* are the only previous reports I encountered.

Sclerenchyma is very rare in both anthers and filaments; but, if present (e.g. in Palmae, Gentianaceae, Nymphaeaceae and many Annonales—*Rollinia emarginata, R. laurifolia, Degeneria vitiensis*, Winteraceae, Myristicaceae, Himantandraceae, Magnoliaceae), it usually occurs as sclereids rather than as fibres (which are found in Palmae, Gentianaceae and *R. laurifolia*). For references to the preceding taxa, see Schmid (1977). Sclereids in stamens seem to be chiefly extra-vascular, whereas fibres are mainly vascular in origin. The isolated pockets of sclerenchyma apparently offer less resistance to staminal expansion than that produced by continuous strands of fibres. The predominance of taxa in the 'woody Ranales' in the preceding list suggests that staminal sclerenchyma might be an adaptation to beetle pollination and/or laminar stamens.

Hypodermal tissue of anthers, whether or not it constitutes part of the endothecium or so-called fibrous layer, may also be 'sclerified', 'sclerotic' or 'sclerenchymatous', for example in relatively primitive groups (Degeneriaceae, Himantandraceae, Magnoliaceae—Canright, 1962) and in relatively specialized ones, some of which have poricidal anther dehiscence (Tremandraceae,

Leguminosae, Acanthaceae—Matthews & Maclachlan, 1929; Pass, 1940; Schmid, 1977). Such hypodermal 'sclerenchyma' should be contrasted with the more deeply situated (occasionally vascular) androecial sclerenchyma discussed in the preceding paragraph, since these two types of sclerenchyma seem to be fundamentally different.

Crystals occur in anthers of stamens (1) in the endothecium (*Muscaria* sp.), (2) in the tapetum (*Rudbeckia laciniata*; Labiatae, but apparently not *Satureia* spp.; Philydraceae; Commelinaceae; many Leguminosae—Buss and Lersten, 1972), (3) in sporogenous tissue (*Rudbeckia laciniata*), (4) intermixed with pollen (Liliaceae, Philydraceae, Bromeliaceae, Araceae, Lemnaceae, but rarely in dicotyledons, e.g. *Impatiens balsamina*) (Pohl, 1941; other references for preceding taxa in Schmid, 1977), and (5) in the connective and/or near the pollen sacs, frequently occurring in great profusion adjacent to pollen sacs (e.g. *Acmena smithii, Ampelopsis arborea, Casearia arborea, Conostegia* sp., *Hypelate trifoliata, Lamium amplexicaule, Marila* sp., *Moronobea* sp., *Mortonia scabrella, Paullinia jamaicensis, Rosa* sp., *Sambucus caerulea, S. canadensis, Spachea elegans, Syzygium aromaticum, Tilia americana*). Crystals are also found in filaments but here they are rarely in abundance.

Tannins often occur in stamens and then are usually abundant, especially in the epidermis (to which tannin may be restricted in the anther) (Plate 1C; *Acmena smithii, Ampelopsis arborea, Paullinia jamaicensis, Simmondsia chinensis, Casearia arborea, Cyrilla racemiflora, Coriaria* sp., *Drimys winteri, Tilia americana, Rourea paucifoliolata* and many other taxa).

In contrast, internal secretory structures (cells, cavities, and even laticifers, but apparently not ducts) are less common in stamens, especially in filaments (but occur in, for example, *Casearia arborea, Tilia americana* and *Cneorum tricoccum*). Even in taxa characterised by the presence of numerous secretory structures in their vegetative parts (Metcalfe & Chalk, 1950), secretory structures may be absent or sparse in stamens, although usually abundant in the gynoecium and especially the perianth parts. In contrast, the androecial secretory structures may be characteristic of certain taxa, e.g. Myrtaceae, many of which have one or more terminal secretory cavities in the anther (Schmid, 1972a).

Crystals, tannins, and secretory structures have been implicated in the protection of pollen against predators (Pohl, 1941; Uhl & Moore, 1973; Schmid, 1977). The protective functions of these chemicals have apparently been evolutionarily coordinated with each other (Schmid, 1977).

Collenchyma has rarely been reported in stamens, although it probably is commoner in these and in other floral organs than is generally appreciated (Schmid, 1977). On the other hand, I know of no cases of secondary activity (vascular or peridermal) occurring in stamens.

Staminal nectaries are rather common, but they may occur on both the filament and the connective (Fahn, 1974). The nectary may even take the form of glandular hairs, as on the filaments of *Penstemon* (Straw, 1956).

Vascular bundles of the filament and/or anther may be surrounded by one or more layers of tightly packed, thin-walled, parenchyma cells (Plate 1E, F), which in some cases (Plate 1H) appear very much like the bundle sheaths of

angiospermous leaves.* Bundle sheaths have been regarded as an endodermis (Esau, 1965), as have, in fact, comparable structures in flowers (Moll & Janssonius, 1923). In Plate 1H, cells of the bundle sheath exhibit plasmolysis similar to the 'band plasmolysis' of endodermal cells. Cells of the bundle sheath may contain druses or other crystals, as in the clove, *Syzygium aromaticum* (Schmid (unpubl.), Trease & Evans (1972) and other pharmacognostic literature therein) and in Schmid (1972c).

The vascular system

A single vascular strand traverses the filament in about 95% of the angiosperms (Wilson, 1942); and in both monocotyledons and dicotyledons it is very frequently amphicribral (Plate 1E-G) or else collateral with much phloem (Plate 1H), the phloem often enveloping the xylem to a considerable extent (resulting in so-called hemiamphicribral bundles) (Schmid, 1977). Schmid (1977) reports amphicribral bundles as occurring in 130 dicotyledonous and 26 monocotyledonous (especially Helobiae) families (*sensu* Airy Shaw, 1973). Prior to this study, there had been reports that monocotyledons lack amphicribral strands (discussion and references in Schmid, 1977).

In these bundle types there is usually more phloem present than xylem (Plate 1E-H). In fact, the xylic part of some stamen bundles may consist of only one or two tracheary elements per transection (e.g. in *Thismia americana, Lamium amplexicaule, Satureia* spp.; *Eugenia* spp.—Schmid, 1972a). Such an emphasis on phloem in stamens, as opposed to xylem, seems related to the nutritional needs of developing pollen grains in the anther (rationale in Schmid, 1977).

The sieve elements of stamen bundles generally occur separated from the tracheary elements by phloic-xylic parenchyma and/or by undifferentiated provascular tissue (Plate 1E-H), the latter frequently even occurring in filaments examined at or after anthesis. Both tracheary elements and sieve elements are usually narrow (Plate 1E-H), and the latter often occur in a bundle (no matter whether it is collateral, bicollateral or amphicribral) in multiple clusters (Plate 1E-G), rather than in continuity as in vegetative organs of both seed plants and cryptogams. These features are typical of all floral organs, but especially of stamens and carpels (Schmid, 1977). A number of these observations have not been previously noted in the literature.

The direction of primary xylem maturation is commonly mesarch in filaments and anthers (Plate 1E-G), and is typically so in amphicribral bundles or in collateral strands with phloem considerably enveloping the xylem (records in Schmid, 1977). Previous reports of mesarchy in flowers (see Schmid, 1977) have been few, and it has generally been thought to indicate vestigiality and/or a relationship of angiosperms with the ferns or certain gymnosperms; but mesarchy in angiosperms seems instead to have a developmental basis rather than a functional or phyletic one (Schmid, 1977).

* Compare, for example, Plate 1H with figures of leaf transections of *Zea mays* in Esau (1965) and O'Brien & Carr (1970). Unlike the leaves and floral bracts, however, the staminal bundle sheath lacks chloroplasts.

The secondary wall patterns of tracheary elements are almost exclusively of the extensible annular or especially the helical type. The general absence of other, non-extensible types of wall thickening is related to the usual expansion of the stamen, in particular the filament, at anthesis (rationale in Schmid, 1977).

Vascular bundles of anthers and especially filaments often contain conspicuous xylem lacunae (Plate 1G), which may involve most or all of the xylem of a bundle.* Such xylem lacunae, which have been previously and incidentally noted in only two of some 1500 papers on floral anatomy that I examined (Anderson (1970) for *Chrysothamnus;* Jäger (1961: 477) for *Prunus*), involve completely unrelated taxa of both monocotyledons and especially dicotyledons: *Maranta leuconeura, Thismia americana, Mosquitoxylum jamaicense, Rhus lanceolata, Bixa orellana, Euonymus alatus, Cneorum tricoccum, Coriaria* sp., *Cornus* sp., *Cyrilla racemiflora, Geranium pusillum, Ribes rotundifolium, Floerkea proserpinacoides, Spachea elegans, Ficus rubiginosa, Bontia daphnoides, Myoporum sandwichense, Oxalis crassipes, Ipomopsis arizonica, I. macombii, I. spicata, I. thurberi, Claytonia caroliniana, Chaenomeles lagenaria, Prunus americana* or *angustifolia, Simmondsia chinensis, Siparuna* sp., *Petunia* sp., *Guaiacum officinale.* These lacunae are generally an age phenomenon related to the expansion of the filament at anthesis, (1) since they are more often present or more conspicuously present in the flowers of a plant than in its buds (e.g. *Euonymus*), and (2) since in species with many stamens (e.g. *Prunus*) they are better developed in the older than in the younger stamens of a flower. Xylem lacunae are often more conspicuous in the basal parts of filaments, which typically undergo more movement or expansion than the distal parts. Both the vascular bundle and the vascular trace of a stamen may have such lacunae, especially in epipetalous/sympetalous taxa where the lacuna in the trace may occur deep in the corolla (e.g. *Ipomopsis* spp., *Petunia* sp.).

Features possibly related to anther dehiscence

Dehiscence of anthers is largely a desiccatory process (references in initial paragraph and in Appendix). Therefore, any histological features promoting a rapid loss of water from the stamen or a disruption of the water supply to anthers might facilitate anther dehiscence. Such histological features would clearly be more critical if they occurred in the filament rather than in the anther, since all water and nutrients transported to the latter must traverse the former.

The stamen, in particular the filament, seems to be well adapted to promote rapid loss of water once the necessary developmental stage (i.e. pollen maturation) is achieved. The weakly developed cuticle (Plate 1A-C) would thus be significant in this respect after the protective perianth parts unfold at anthesis. Stomata present on stamens (Plate 1A) may be 'functionless' and possibly permanently open as in hydathodes (Kenda, 1952; Aleksandrov &

* I have also occasionally seen xylem lacunae in the bundles of petals (e.g. *Rosa* sp.), carpels (the style of *Maranta leuconeura,* the fruit of *Simmondsia chinensis*) and ovules (Umbelliferae). Conceivably, xylem lacunae in carpellary bundles may aid in the dehiscence of capsular fruits, since such lacunae would disrupt water transport and thus help in the desiccation of the fruit.

Dobrotvorskaya, 1960); such stomata could then accelerate water loss. The epidermal cells of anthers usually become disorganised near or at anthesis (many observations, both personal and in the literature), so that the endothecium becomes the outermost functional wall layer of the anther. A prominent intercellular-space system in the ground tissue (Plate 1B-E) might tend to enhance the rate of gaseous movement. (Straw (1956) observed conspicuous intercellular spaces in the filaments of *Penstemon* but was unable to assign any "adaptive significance . . . to this peculiarity".)

Expansion of the filament typically results in considerable disruption of the xylem, an effect perhaps facilitated in those stamens having relatively few tracheary elements (see above). With extreme extension and cessation of function of the tracheary elements, xylem lacunae may result (Plate 1G). The water supply to the anthers therefore would be disrupted, since such lacunae presumably do not function in conduction. Comparable protoxylem lacunae in stems of monocotyledons apparently have not been suspected of transporting water, although this function has been proposed for protoxylem lacunae in shoots of *Equisetum* (Bierhorst, 1958). Significantly, the 'wilted' mutant of maize exhibits severe signs of wilting during most of its growing season. Since its stem metaxylem differentiates very late (Postlethwait & Nelson, 1957), the wilting of the plant must mean that conduction does not occur via the protoxylem lacunae.

All the preceding events directly affect the water regime of the filament and anther and, acting either in unison or in isolation, they could effect a progressive drying out of the anther and its consequent dehiscence (see Appendix for proposed physical mechanisms). Other histological features might also be related to anther dehiscence. Crystals are usually mentioned as having this capability, but there is little supportive evidence for this notion (Schmid, 1977). Finally, a role for tannins and/or secretory structures in dehiscence also should not be dismissed out of hand, although the evidence here too is very slight.

It should be noted that vascular tissue often increases considerably in amount distally in the connective of the stamen (e.g. in *Eugenia* spp. and *Syzygium* spp.—Schmid, 1972a). Here tracheary elements strongly resemble the storage tracheids ('Speichertracheiden') described in vegetative and reproductive organs (Pass, 1940; Foster, 1956). Conceivably, these elements may store water in the anther and thus safeguard against premature desiccation and dehiscence.

In the foregoing discussion the desiccation causing anther dehiscence is considered as resulting from evaporation of water. In contrast, Burck (1906) suggested that anthers of many flowers lose considerable amounts of water not by transpiration, but rather by withdrawal of the water internally to other tissues, particularly nectaries. Thus, nectar secretion has the dual effect of not only attracting pollinators but also creating in the anther wall conditions of hydrostatic tension leading to dehiscence of the anther. Unfortunately, this ingenious and little-known hypothesis could not be confirmed by subsequent investigators (Hannig, 1910; Schmid & Alpert, 1977). In addition, any xylem lacunae in the filament (Plate 1G) would clearly prevent such retransport of water.

CONCLUSIONS AND SUMMARY

Since most structures have (or had) adaptive significance, it follows that they generally have a functional basis (see Schmid, 1977). On the other hand, it is quite easy to fall prey to teleological speculation or interpretation, since direct observational or experimental evidence is generally lacking for such presumed functional significance. Of the various histological features of anthers and especially filaments described above, some appear to have clear adaptive significance and others to have probable functional significance, while still others have no apparent significance. For example, the near universal occurrence in stamens of exclusively helical (or sometimes annular) secondary wall thickenings of tracheary elements and, possibly, the rarity of sclerenchyma seem clearly to be related to the usual expansion of the stamen, in particular of the filament, before and at anthesis. In contrast, the evidence for concluding that amphicribral bundles or else collateral strands with phloem considerably enveloping the xylem are related to the nutritional needs of developing pollen grains in the anther is less direct, although still quantitatively significant (see Schmid, 1977). Surely the very common occurrence of such strands in the stamen and in the placental supply, and their scarcity elsewhere, are strongly indicative of this function? This suggestion, in fact, is supported by the very limited experimental evidence available (see Schmid, 1977). Although it has become popular to attribute protective and other functions to tannins, crystals and secretory structures (Pohl, 1941; Uhl & Moore, 1973; Schmid, 1977, and the many references therein), such a conclusion, however reasonable it might seem, is based largely on circumstantial evidence; and virtually no experimental evidence has been adduced to support it. As will be shown below, there is a similar lack of experimental evidence to support the assumption that certain histological features aid in the dehiscence of the anther. Finally, certain structural features have no apparent function. This appears to be the case with mesarchy, and its commonness in the stamen may be simply a developmental 'by-product' or concomitant of amphicribral or hemiamphicribral bundles. Likewise, the usual clustering of sieve elements, especially in amphicribral bundles, and their spatial separation from tracheary elements are difficult to explain on any functional basis.

In this paper I stress a number of features of the stamen such as open stomata, a weakly developed cuticle, a prominent intercellular-space system, and xylem lacunae. Some or all of these may play a role in anther dehiscence, since such features would tend to promote a rapid loss of water or a disruption of the water supply to the anther. Clearly, however, many flowers (e.g. protogynous ones, or ones having the perianth reduced or absent) may not conform to these generalisations, and certainly some of the features stressed here may have additional functions. Intercellular spaces in filaments, for example, might facilitate movement of the stamen, although this idea is sheer speculation.

The model of anther dehiscence presented here might also be criticised on the grounds that in many plants the filament remains 'fully turgid' for an appreciable time after the dehiscence of the anther. Such 'turgidity' would admittedly be inconsistent with the filament dehydration mechanism that I propose; but the counter-argument is: Is such 'turgidity' really turgidity (when

water is present in large amounts) or merely cell rigidity due to cell walls and other factors (when water is not necessarily present in large amounts)? Unfortunately, experimental data to answer this criticism are not available.

The model of filament histology and anther dehiscence presented above may be significant in at least two further ways. (1) The desiccation that results in anther dehiscence probably also results in the common dehydrated appearance of mature pollen grains as manifested in both their cytoplasm and their retracted cell walls (Grady L. Webster, pers. comm., 1975; observations based on various taxa, especially Euphorbiaceae). This dehydration apparently increases the dispersal capability of the pollen. Once the pollen lands on the stigma, it can absorb various stigmatic fluids, so that the well-known volumetric changes or so-called harmomegathy (see Payne, 1972) can result. (2) Similar desiccatory, histological features may occur in other groups of vascular plants in which microsporangia are borne on slender, filament-like sporangiophores or microsporophylls (e.g. *Equisetum, Ginkgo, Cephalotaxus, Taxus, Torreya, Ephedra, Welwitschia*). Perhaps the analogy should not be pushed too far, however, because there are numerous anatomical differences between the anthers of the angiosperms and the microsporangia of the other vascular plants. For example, in the gymnosperms the fibrous layer, which is technically exothecium rather than endothecium, is derived from the epidermis, whereas in the angiosperms it is derived from a subepidermal layer (or layers) (Periasamy & Swamy, 1964; Foster & Gifford, 1974). Nevertheless, in the microsporophylls or sporangiophores of *Equisetum* (the sporangiophores of *E. arvense* and *E. telmateia* also have xylem lacunae), *Ginkgo* and *Ephedra* the occurrence of tracheary elements with only extensible helical wall thickenings (Schmid, unpubl. data) suggests that in the lower vascular plants mechanisms similar to those in anthers may operate for sporangial dehiscence.

The stamen provides an ideal structure for both anatomical and physiological investigations (see Schmid, 1977) and for attempts to interpret floral structure from a functional and ecological viewpoint (*sensu* Carlquist, 1969; Schmid, 1972b, 1977; Uhl & Moore, 1973). Critical studies correlating pollen development with development of the filament and anther are urgently needed. Most developmental studies to date, however, have focused on earlier stages of the flower, whereas palynological and embryological investigations have concentrated on cytological events and have largely disregarded histological features. The novel histological features of the filament stressed in the above discussion are admittedly circumstantial evidence for a role in anther dehiscence. They are presented, however, to provide a structural prelude to detailed physiological experiments (using radio-active tracers and other means) and ultrastructural studies which, it is hoped, will follow.

APPENDIX ON MECHANISMS OF ANTHER DEHISCENCE

The dehiscence of anthers is, of course, a desiccatory process. The process has been characterized as being effected by a hygroscopic and/or a cohesion mechanism (references in next paragraph). Hygroscopic (imbibition) mechanisms depend entirely upon volumetric changes in cell walls, whereas cohesion mechanisms involve volumetric changes in cell lumina, the cell walls undergoing largely passive deformation. The latter mechanism primarily

involves cohesive forces between water molecules in the cell lumen, but the adhesive forces between the water and the cell wall are also important; dehiscence occurs when the cohesive forces are exceeded. In a hygroscopic mechanism, adhesive rather than cohesive forces are predominant. In both mechanisms the cells are dead; but in a cohesion mechanism their walls are usually thin (or at least one wall is thin if each of the other five walls of a cell are partly or entirely thickened), whereas in a hygroscopic mechanism the walls are usually thick, the antagonistic action of walls of the same or different cells eventually supplying the movement. Heat and internal pressure have also been implicated in anther dehiscence (Zarr, 1972).

Most workers now accept a cohesion mechanism for anther dehiscence (see especially Hannig, 1910; Steinbrinck, 1915, and his many earlier works; Haberlandt, 1924; Straka, 1962, and von Guttenberg, 1971) rather than a hygroscopic mechanism (accepted by Leclerc du Sablon, 1885; Schips, 1913, and Haberlandt, 1914, among others—see preceding references). Straka (1962) characterized anther dehiscence as resulting from continuous cohesion movements with passive water loss. Canright (1952) believed that both cohesion and hygroscopic phenomena probably play a role, but said that the quantitative factor of each was still problematical. In fact, German workers (e.g. Hannig, 1910; Haberlandt, 1924, and von Guttenberg, 1971: 97), admit that the wall structure of the endothecium corresponds to a hygroscopic mechanism and that this makes possible an exact functioning of the primary cohesion mechanism.

It should also be noted that in the earlier, more widely circulated, English translation of Haberlandt's book (Haberlandt, 1914), a hygroscopic mechanism for anther dehiscence was accepted and that, consequently, many English-speaking botanists, who apparently are unfamiliar with the subsequent German editions (1918, 1924) of Haberlandt's book, in which a cohesion mechanism was accepted, frequently describe anther dehiscence as resulting from a hygroscopic mechanism.

Confusion has obviously arisen between the preceding designations of 'hygroscopic mechanism' and 'cohesion mechanism', in part because numerous botanists, instead of adopting a strict physico-chemical definition of 'hygroscopic' as 'absorption of moisture', adopt the wider botanical usage (*sensu* Jackson, 1928) and define 'hygroscopic' loosely as referring to volumetric changes that result from either water loss *or* water uptake. (In fact, turgor mechanisms, which involve volumetric changes in the cell protoplast and hence must involve live cells, have also been described as hygroscopic.) Because of this loose usage, and because wherever there is water there must be both adhesive and cohesive forces involved, it seems best to avoid characterizing the mechanism of anther dehiscence as either hygroscopic or cohesive, although reference to operative cohesive and adhesive forces seems acceptable, indeed necessary. A similar recommendation applies to sporangial dehiscence in cryptogams (see Ingold, 1939, 1965) and to fruit/seed dispersal in angiosperms (see Fahn & Werker, 1972; Fahn, 1974), which have also been described as resulting from cohesion or hygroscopic mechanisms.

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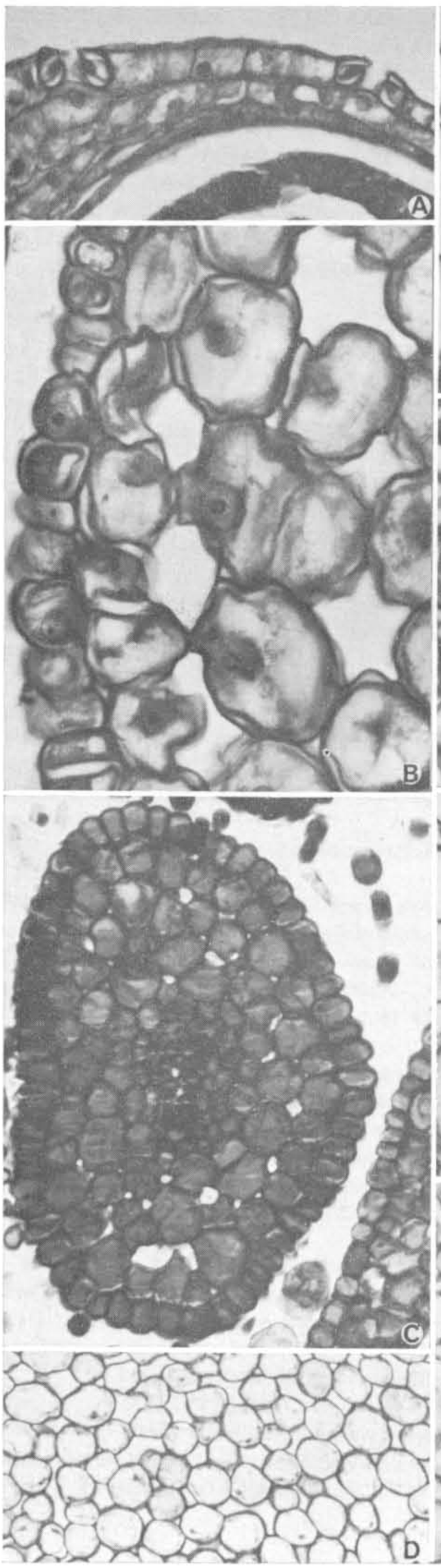

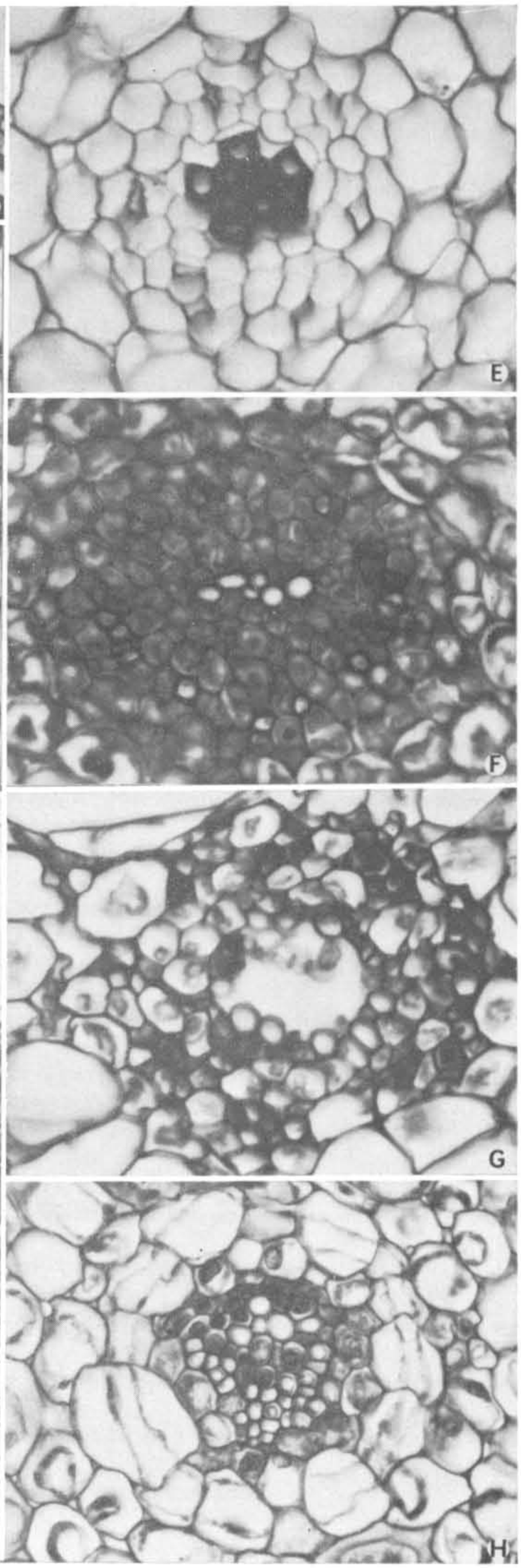

R. SCHMID

(*Facing p.* 315)

EXPLANATION OF PLATE

PLATE 1

Transections of anthers (A, H) and filaments (B-G) of stamens of flower buds showing: stomata (A), weakly developed cuticle on epidermis (A-C), prominent intercellular-space system (B-E), tannin (C), endodermoid bundle sheath (H), mesarch amphicribral bundles (F-G), endarch collateral bundle with emphasis on amount of phloem (H), bundles with clusters of sieve elements spatially separated from the tracheary elements by phloic-xylic parenchyma and/or by undifferentiated provascular tissue (E-H), and xylem lacuna (G). Fig. E is of herbarium material; all others of pickled material. Contrast of photographs enhanced by Kodak Wratten filters 15 (A-C, F-H) or 22 (D, E).

Taxa depicted: A. *Iris versicolor.* × 270. B. *Dentaria laciniata.* × 480. C. *Paullinia jamaicensis.* × 250. D. *Campsis radicans.* × 126. E. *Heteropyxis natalensis.* × 620. F. *Guaiacum officinale.* × 600. G. *Petunia* sp. × 640. H. *Zea mays.* × 425.