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A Developmental Study of the Endocarp Tissue in the Fruits of Malus x zumi and Crataegus mollis, Two Representatives of the Family Rosaceae, Subfamily Maliodeae

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A DEVELOPMENTAL STUDY OF THE ENDOCARP TISSUE IN THE FRUITS OF MALUS X ZUMI AND CRATAEGUS MOLLIS, TWO REPRESENTATIVES OF THE FAMILY ROSACEAE, SUBFAMILY MALOIDEAE

(TITLE)

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THESIS

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INTRODUCTION

The purpose of this study is to investigate the development of the endocarp of the fruits of two representatives of the family Rosaceae, subfamily Maloideae. Malus x zumi, (Mats.) Rehd., (a hybrid of M. baccata var. mandshurica and M. sieboldii) an Asiatic flowering crab that is sometimes planted for ornament, is one of the representatives studied; the other is Crataegus mollis, (T. & G.) Scheele, the downy hawthorn, a common tree native to a large part of the Eastern United States.

A member of the order Rosales, the Rosaceae is a large family with approximately 115 genera and 3,200 species distributed throughout the world. Its members are characterized by four basic distinctions, according to Lawrence (1951). These are:

1. The usual presence of stipules.
2. A flower plan based on five (excluding the gynoecium), usually actinomorphic, and with numerous stamens.
3. A hypanthium formed from the fusion of the androecium and the floral envelopes resulting in a half-inferior or inferior ovary.
4. The absence or near absence of endosperm in the mature seed.

A subdivision of the Rosaceae, the Pomoideae, has been given tribe status (Bentham and Hooker, 1862; Fernald, 1950; Hutchinson, 1964) or subfamily status (Focke, 1891; Lawrence, 1951; Gleason and Cronquist, 1963) by various taxonomists. In this study the taxonomic treatment of the group by Gleason and Cronquist will be followed except that the subfamily name Maloideae will be used rather than the name Pomoideae. This follows the rules of the International Code of Botanical Nomenclature (Lanjouw, 1966), which specify that a subfamily name be based on a genus. As a taxonomic unit the Maloideae appears to stand out from other members of the Rosaceae by a common chromosome base of seventeen (Sax, 1931). Interrelationships between genera have been found through the following hybrids, as noted by Sax: Crataegus X Pyrus, Pyrus X Malus, Amelanchier X Sorbus, Sorbus X Aronia, Sorbus X Pyrus.

The morphological characteristics of the Maloideae, as presented by Weber (1964), are as follows:

> Trees or shrubs, unarmed or spiny. Leaves petiololate, alternate, simple or compound, with free stipules (at least on young shoots). Flowers regular, hermaphrodite (rarely unisexual by abortion), solitary, fasciculate or in terminal racemes, white, pink, or red. Calyx campanulate-urceolate with 5 persistent or deciduous lobes. Petals 5, unguiculate, inserted in the throat of the calyx. Stamens 10-60, inserted at the same level as the petals, filaments free, anthers introse with 2 locules. Disk laminate or fleshy, dry or nectariferous. Ovary formed of (1) 2-5 carpels, more or less adherent to the calyx on their abaxial side, completely fused with it at maturity. Ovules anatropous usually 2 (1 by abortion) in each locule, to indefinite Chaenomeles, Cydonia. Styles 1-5 terminal, free or connate at the base. Pollen tricolpate. Fruit fleshy, usually a pome (exceptionally a berry) formed of the hypanthium, the carpels becoming chartaceous or cartilaginous, sometimes dehiscing on the

> adaxial suture, to bony and indehiscent. Seeds ascending (or horizontal when numerous), testa coriaceous, or less often mucilaginous, raphe and chalaza apical (or subapical) endosperm lacking, embryo orthotropous with short and conical radicle and imperceptible plumule.

The genera included in the subfamily Maloideae which can be commonly observed in the Northeastern United States are the following: Malus, apple, crab apple; Pyrus, pear; Sorbus, mountain ash; Aronia, chokeberry; Amelanchier, juneberry or shadblow; Crataegus, hawthorn; Cotoneaster; Pyracantha, firethorn; Chaenomeles, Japanese or flowering quince.

In most genera of the subfamily Maloideae the inner portion of the pericarp is differentiated into one or more layers of cells with thickened and more or less lignified walls, giving the region either a cartilaginous or bony texture. The thickness of this layer and the degree of lignification of the cell walls vary among the genera of the subfamily. Most commonly the differentiated pericarp or endocarp cells qualify as sclerenchyma tissue due to their thick, lignified walls and simple pits. The isodiametric to moderately elongate form of these cells establishes them as sclereids rather than fibers, the other category of sclerenchyma.

Considerable confusion exists regarding the extent of the endocarp in various fruits. Commonly the term is defined in a rather indefinite manner as the inner wall or layer of the pericarp. It has been suggested by Sterling (1953) that a return to the original morphological defini-

tion of the endocarp as that tissue derived from the inner epidermis of the carpel would clarify the terminology of fruit structure.

REVIEW OF LITERATURE

On the basis of whether the endocarp structure in the mature fruit is cartilaginous or osseous, Lindley (1822) separated the pomoid genera into two fundamental groups as follows:

1. Endocarp cartilaginous: Pyrus, Chaenomeles, Cydonia, Amelanchier, Chamaemeles, and Raphiolepis
2. Endocarp osseous: Mespilus, Crataegus, Osteomeles, and Cotoneaster.

Although it appears that Lindley did not examine endocarp tissue in detail, his classification, in the opinion of Sterling (1964), appears to be in accord with other morphological evidence. Lindley also made the observation that the testa in the genera with osseous endocarp is membranaceous while in Pyrus it is cartilaginous.

One of the first to investigate the development of fruit of the family Rosaceae was Cave (1869). Cave's drawings and descriptions show the general development of the various tissue regions of the fruit wall, including the endocarp, of three genera: Rosa, Prunus, and Clematis. The latter genus is now commonly placed in the Ranunculaceae by most taxonomists rather than in the Rosaceae. No detailed study of any specific tissue was undertaken by Cave.

Probably the first serious developmental study of

endocarp tissue in the Maloideae was made by Tukey and Young (1942). Following through the development of the endocarp and other fruit tissues (pith and cortex) in the apple varieties McIntosh and Twenty Ounce, the study disclosed several interesting facts concerning endocarp development:

1. Endocarp tissue is the earliest of any tissue to mature (i.e., two to four weeks after flowering).
2. The endocarp is derived from a layer of cells immediately beneath the inner epidermis.
3. The cartilaginous endocarp tissue has a thickness of five to six cells but becomes progressively thinner and finally absent toward the ventral and dorsal vascular bundles.

The authors were unable to determine whether the layer which gave rise to the endocarp was derived from the inner epidermis several weeks before full bloom but speculated that this was the case since they had observed the same process in a related fruit, cherry.

Recently, Sterling (1964, 1965a, 1965b) has carried out extensive morphological research on the pistil structure of most genera commonly included in the Maloideae. The concepts of close relationship between genera and the relative primitiveness of the Maloideae have been augmented by Sterling's comparative study of carpel structure in the various genera of the subfamily. Sterling concluded from his research that evolutionary trends in the subfamily seem to point to a

fruit with completely fused ovular and wing bundles and other fused carpel parts.

MATERIALS AND METHODS

The two representatives used in the developmental study were *Malus x zumi* and *Crataegus mollis*. Floral and fruit specimens, obtained from the ornamental shrubbery collection of Eastern Illinois University, were collected at weekly intervals from April 26, 1966, through July 12, 1966, and placed in FAA preservative until prepared for sectioning. After being washed in two changes of fifty percent ethyl alcohol, the specimens were progressed through a graded tertiary butyl alcohol series and embedded in "Tissuemat" embedding wax. Transverse and longitudinal sections of the specimens were cut with a rotary microtome in thicknesses of twelve to twenty microns, depending on the hardness of the material. Some sectioning was attempted using a freezing microtome, but most of these sections were unsuccessful in the mature stages due to hardness of the material. Prepared sections were stained with safranin and fast green, according to the schedule presented by Johansen (1940). Permanent slides were made for subsequent observation.

Mature endocarp macerations were prepared by placing material in equal volumes of ten percent chromic acid and ten percent nitric acid at a temperature of thirty degrees centigrade for two to three days.

Drawings were prepared utilizing a Zeiss microscope and drawing apparatus.

OBSERVATIONS

To simplify descriptions and avoid repetition, two new terms will be utilized in connection with this study. The term primary endocarp will be used to indicate that part of the cartilaginous endocarp immediately contiguous to the inner epidermis and the term secondary endocarp as that part of the cartilaginous endocarp derived from parenchyma which differentiates after the primary endocarp.

Malus x zumi

At full bloom (based on material collected April 26, 1966), a cross section of the ovary reveals that the inner epidermal cells of the carpel have elongated horizontally along a line parallel to the inner surface of the carpel, except for two regions where the cells remain essentially isodiametric. One of these regions is in the vicinity of the dorsal vascular bundle where a partial dorsal septum is present, while the other is in the area of the ventral suture (Fig. 1).

By two weeks after full bloom (based on material collected May 10, 1966), the elongated epidermal cells measure approximately thirty microns in radial diameter and ten microns in tangential diameter, whereas those cells in the ventral suture and dorsal bundle regions measure ten by ten mi-

crens. The nucleus of these epidermal cells appears oval in shape and is oriented with its long axis parallel to the axis of the cell. Some of the elongated epidermal cells appear to have divided periclinally since the cells immediately adjacent to them have the same radial but smaller tangential diameters. Numerous inclusions, i.e. druses, are present throughout the developing fruit tissue but seem to be concentrated in the part of the carpel just external to the inner epidermis, especially in the area of the dorsal bundle (Fig. 1).

By approximately four weeks after anthesis (based on material collected May 24, 1966), the layer of elongated epidermal cells located about one-sixth of the circumference of the locule on each side of the dorsal bundle has increased to a thickness of three or four cells (Fig. 4), but this layer becomes progressively thinner toward the regions of the dorsal bundle and the ventral suture (Fig. 6). It could not be determined precisely whether this increase was due to differentiation of adjacent parenchyma or further division of the original elongated epidermal layer. The epidermal cells in the ventral suture region have not elongated (Fig. 7) while the cells in the dorsal bundle region appear to be elongating in a vertical direction parallel to the axis of the fruit and perpendicular to the elongated epidermal layer (Fig. 3). The parenchyma cells immediately adjacent to the elongated epidermal cells lack plastids and are smaller than those of neighboring parenchyma (Figs. 6 and 7).

After the elongated epidermal cells have ceased

enlargement, between four and five weeks after anthesis (based on material collected May 24, 1966, and May 31, 1966), lignification of cell walls begins as indicated by retention of the safranin stain. The lignification progresses rapidly so that by five weeks after full bloom cell walls occupy approximately one-fourth the diameter of the cell. At this point these cells measure one hundred and thirty microns in radial diameter by twenty microns in tangential diameter. Some tubular pits are visible in the thickening cell walls but are most discernable in the end walls of the maturing sclereids (Fig. 9). Protoplasm is still evident in the lumen of each cell. At the five week stage, the primary endocarp has reached its maximum thickness, varying from four to five layers of cells on each side of the dorsal bundle to approximately two layers near the ventral suture region. No lignification of the cells in the immediate vicinity of the ventral suture region occurs (Fig. 10).

Between five and six weeks after anthesis (based on material collected May 31, 1966, and June 7, 1966), the primary endocarp has undergone considerable thickening; those cells immediately adjacent to those of the primary endocarp have begun elongation and lignification of the cell walls, thus initiating the differentiation of the secondary endocarp (Fig. 9). In most cases, the direction of elongation is parallel to the axis of the fruit and perpendicular to the cells of the primary endocarp. On each side of the dorsal bundle the secondary endocarp cells are obliquely oriented toward the dorsal bundle rather than being perpendicular to

the primary endocarp (Fig. 8). Lignification of the secondary endocarp proceeds centrifugally, i.e., those cells nearest the primary endocarp lignifying first (Fig. 9).

By eight weeks after anthesis (based on material collected June 21, 1966), the limits of the secondary endocarp have been attained. Adjacent to the thickest portion of the primary endocarp it consists of five or six layers of sclereids (Fig. 11); while along each side of the carpel approaching the ventral suture region, it is composed of only two or three layers (Fig. 10). It is to be noted that the relative thickness of the secondary endocarp parallels that of the primary endocarp, except in the immediate vicinity of the dorsal bundle where the secondary endocarp is poorly developed. In carpel cross sections where only one ovule per locule can be seen or none has developed, a distinct fissure or fold can be observed in the endocarp near the dorsal bundle. At the thickest portion of the endocarp, i.e., on each side of the dorsal bundle, the entire endocarp measures approximately two hundred microns in thickness while in the region approaching the ventral suture it measures approximately ninety microns.

By approximately eleven weeks after flowering (based on material collected July 12, 1966), endocarp lignification is complete so that both primary and secondary endocarp sclereids are composed mainly of cell wall material with many of the walls showing concentric laminations. It could not be determined whether or not a protoplast was still present in the cell lumen. The ventral suture region has remained free

of any sclerenchymatous tissue, creating a gap of approximately four hundred microns in the cartilaginous endocarp (Fig. 10).

Crataegus mollis

At full bloom (based on material collected May 3, 1966), the inner epidermal cells of the carpel have elongated horizontally along a line parallel to the inner surface of the carpel as was observed in Malus x zumi. Similarly, the epidermal cells in the ventral suture region appear isodiametric (Fig. 2). However, unlike the corresponding cells in the carpel of Malus x zumi, the epidermal cells in the dorsal bundle region also undergo elongation. There is no evidence of a dorsal septum such as is found in Malus x zumi.

By two weeks after anthesis (based on material collected May 17, 1966), there are three to four layers of elongated cells extending around the carpel except in the region of the ventral suture where the cells remain essentially isodiametric. The elongated epidermal cells measure forty-five microns in radial diameter and ten microns in tangential diameter, while these cells in the ventral suture region measure approximately eighteen microns by eighteen microns (Fig. 2). It was not determined whether the increase in thickness of the layer of elongated cells lining the carpel was due to a periclinal division of the epidermal layer or to differentiation of adjacent underlying cells.

At this time the parenchyma cells outside of the develop-

ing primary endocarp, which are destined to become the secondary endocarp, can be differentiated from the cells of the cortex by their slightly thicker walls and smaller size (Fig. 13). Also, a band of smaller oval-shaped cells is evident between carpels (Fig. 2).

Between three and four weeks after anthesis (based on material collected May 24, 1966, and May 31, 1966), lignification of the cell walls of the primary endocarp begins. At this time, the primary endocarp consists of five to six layers of cells surrounding the entire carpel except in the region of the ventral suture, where the cells of the epidermal layer have elongated horizontally toward the center of the fruit (Fig. 18). At four weeks after anthesis, individual cells of the primary endocarp measure one hundred and forty microns in radial diameter by twenty microns in tangential diameter. It appears that lignification of the primary endocarp proceeds centrifugally (Fig. 18).

Lignification of the secondary endocarp begins after the cells have reached maximum size, between four and five weeks after full bloom (based on material collected May 31, 1966, and June 7, 1966). All cells do not develop secondary wall thickening at the same rate. Random clusters or groups of cells appear to lignify first; the remaining cells lignify later (Fig. 12). These cells are generally isodiametric in form and measure approximately fifty microns by fifty microns. In the region of the ventral suture, the lignifying cells of the secondary endocarp are smaller or elongated forming a definite

line which will be designated as the suture line (Fig. 18).

As cell walls thicken between five and six weeks after anthesis (based on material collected June 7, 1966, and June 14, 1966), many simple pits can be observed in both the primary and the secondary endocarp sclereids (Figs. 17 and 18). Lignification and thickening of the cell wall continues, resulting in a series of layers or laminations as each cell lumen becomes progressively smaller with the straight tubular pits coalescing to form a branched or ramiform type of pitting (Fig. 15). At the middle lamella, the pit canals of each sclereid are aligned with those of adjoining sclereids forming pit pairs.

By nine weeks after full bloom (based on material collected July 5, 1966), the cell walls of the primary and secondary endocarp sclereids have thickened so that the lumen of each cell occupies about one-fourth the diameter of the cell (Fig. 15). The entire sclerenchymatous endocarp now forms a generally uniform shell or pit structure enclosing the seeds (Fig. 16). This shell averages approximately six hundred and fifty microns in thickness and is slightly thinner (five hundred and fifty microns) on its abaxial side. Parenchyma cells adjacent to the outer surface of the secondary endocarp are smaller and slightly oval in shape. Between each lignified shell of secondary endocarp, five or six layers of unlignified cells are present. These cells are much smaller than neighboring sclereids and are elongated horizontally toward the axis of the fruit. At least four minor vascular bundles, in

addition to the major dorsal bundle, are trapped within the thickened secondary endocarp (Figs. 14 and 17). These bundles appear to be functional and relatively undisturbed by the adjacent sclerenchymatous tissue.

DISCUSSION AND CONCLUSIONS

The results of the developmental study conducted on the endocarp of Malus x zumi agree in general with those obtained by Tukey and Young (1942) in their study of the apple varieties McIntosh and Twenty Ounce. The elongation of the inner epidermal cells of the carpel and the absence of elongation of the inner epidermal cells in the ventral suture and dorsal bundle regions are shared by Malus x zumi and the two clones of cultivated apple. Likewise, the gradual reduction in thickness of the mature endocarp as it approaches the ventral suture region is a common characteristic. In contrast, Tukey and Young did not mention the presence of endocarp in the dorsal bundle region, a condition very evident in Malus x zumi. Also it should be noted that Tukey and Young did not report an endocarp region in the apple varieties McIntosh and Twenty Ounce equivalent to what has been designated as the secondary endocarp in Malus x zumi. It should be emphasized that the cells of the secondary endocarp in Malus x zumi are oriented in a different plane than those of the primary endocarp. Based on the investigation of Tukey and Young, it would appear that all of the endocarp cells of the apple varieties used in their study are oriented with their long axes in a horizontal plane.

In addition, it might be noted that the observation (reported by Tukey and Young) that the endocarp, which they called the cartilaginous pericarp, was derived from a layer of cells immediately underlying the inner epidermis could not be confirmed in the developmental study of Malus x zumi.

The fruits of both Crataegus mollis and Malus x zumi show two distinct cartilaginous endocarp regions: a primary endocarp composed of several layers of elongated sclereids lining the inner surface of the carpel, and a secondary endocarp region derived from parenchyma adjacent and external to the elongated sclereids. In the ventral suture region of Malus x zumi, there is a lack of development of primary and secondary endocarp tissue creating a gap in the cartilaginous endocarp, while in Crataegus mollis this region becomes sclerenchymatous. The entire cartilaginous endocarp of Crataegus mollis enclosing the seeds attains an average thickness of six hundred and fifty microns; while the cartilaginous endocarp of Malus x zumi where present is much less extensive measuring from two hundred microns to ninety microns in thickness. In both species, cell wall thickening and lignification in both primary and secondary endocarp sclereids are pronounced.

Two distinct lines of evolutionary development within the subfamily Maloideae seem to be evidenced by the endocarp structure of the two representatives studied. In one line, represented by Malus x zumi, it appears that the protective layers of the seed have evolved through lignification of the testa, the endocarp becoming "open" or poorly developed. In

the divergent line, represented by Crataegus mollis, seed protection has evolved through a thickened lignified endocarp completely "encapsulating" the seeds, the seed coat remaining non-lignified and membranaceous.

Most botanists accept the definition of the typical pome fruit as an accessory fruit with a fleshy exocarp and "leathery" endocarp, such as the apple (Hill et al., 1960; Wilson and Loomis, 1967). It appears that the fruit of Crataegus mollis contains a completely sclerenchymatous ovary within the floral tube. This observation is based on the fact that the dorsal bundle is entrapped in the secondary endocarp, which extends to the margin of the floral tube. If this is true, the above definition of a pome fruit must be altered or the genus Crataegus be given tribe status.

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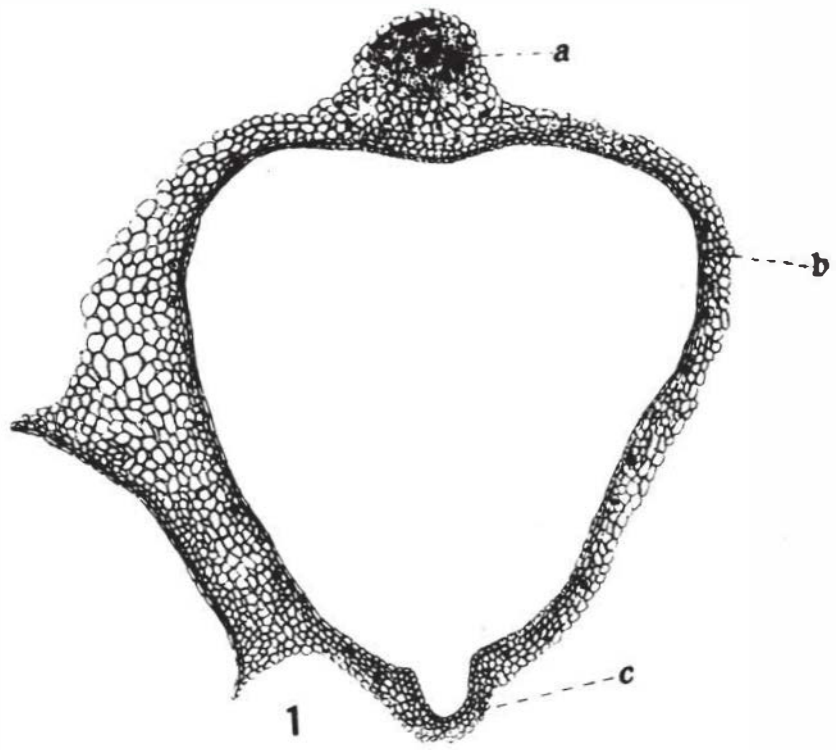
Fig. 1. *Malus x zumi* carpel in cross section two weeks after anthesis. The inner epidermal cells have elongated (b), except for those epidermal cells in the regions of the dorsal bundle (a), and the ventral suture (c), which remain isodiametric. X 85.

Fig. 2. *Crataegus mollis* carpel in cross section two weeks after anthesis. Most of the inner epidermal cells (b), including those of the dorsal bundle region (a), have elongated, with only those of the ventral suture region (c) remaining isodiametric. A layer of differentiated cells (d) separates the carpels. X 85.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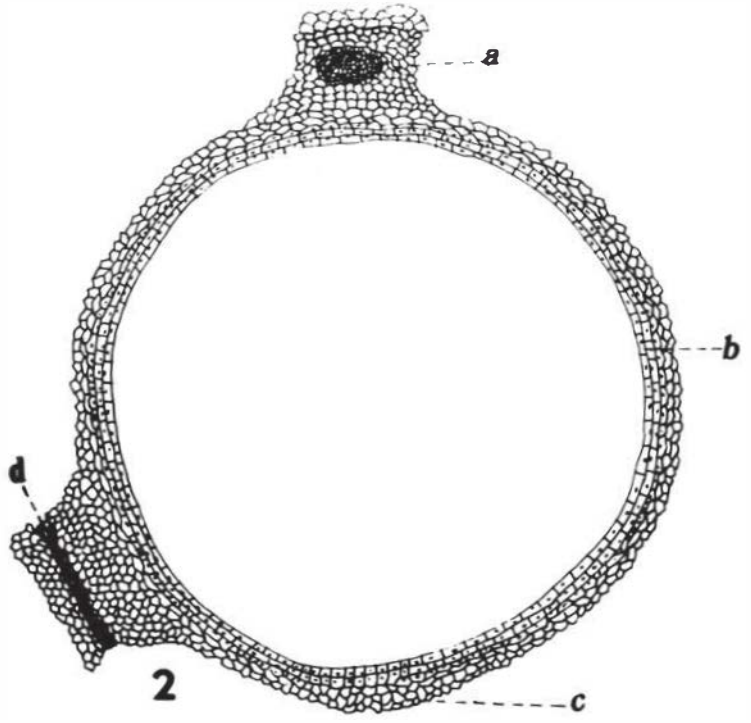
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Fig. 3. Cross section of Malus x zumi carpel at approximately four weeks after anthesis, showing ovule (c) and dorsal bundle (d). Primary endocarp cells (b) have elongated vertically in a plane parallel to the fruit axis. X150.

Fig. 4. Cross section of Malus x zumi carpel and ovule (c) four weeks after anthesis, illustrating development of primary endocarp (b). Parenchyma cells (d) that will differentiate into a sclerenchymatous secondary endocarp are distinct in appearance from those neighboring parenchyma cells that will remain undifferentiated. X150.

Fig. 5. Malus x zumi ovary in cross section.

Fig. 6. Cross section of Malus x zumi carpel and ovule (c), four weeks after anthesis, in the region of the ventral suture. The primary endocarp cells (b) show developing secondary walls while secondary endocarp cells (d) remain undifferentiated. X150.

Fig. 7. Cross section of Malus x zumi carpel and ovule (c), four weeks after anthesis, in the ventral suture region. Primary endocarp cells (b) have failed to elongate in immediate ventral suture region. X75.

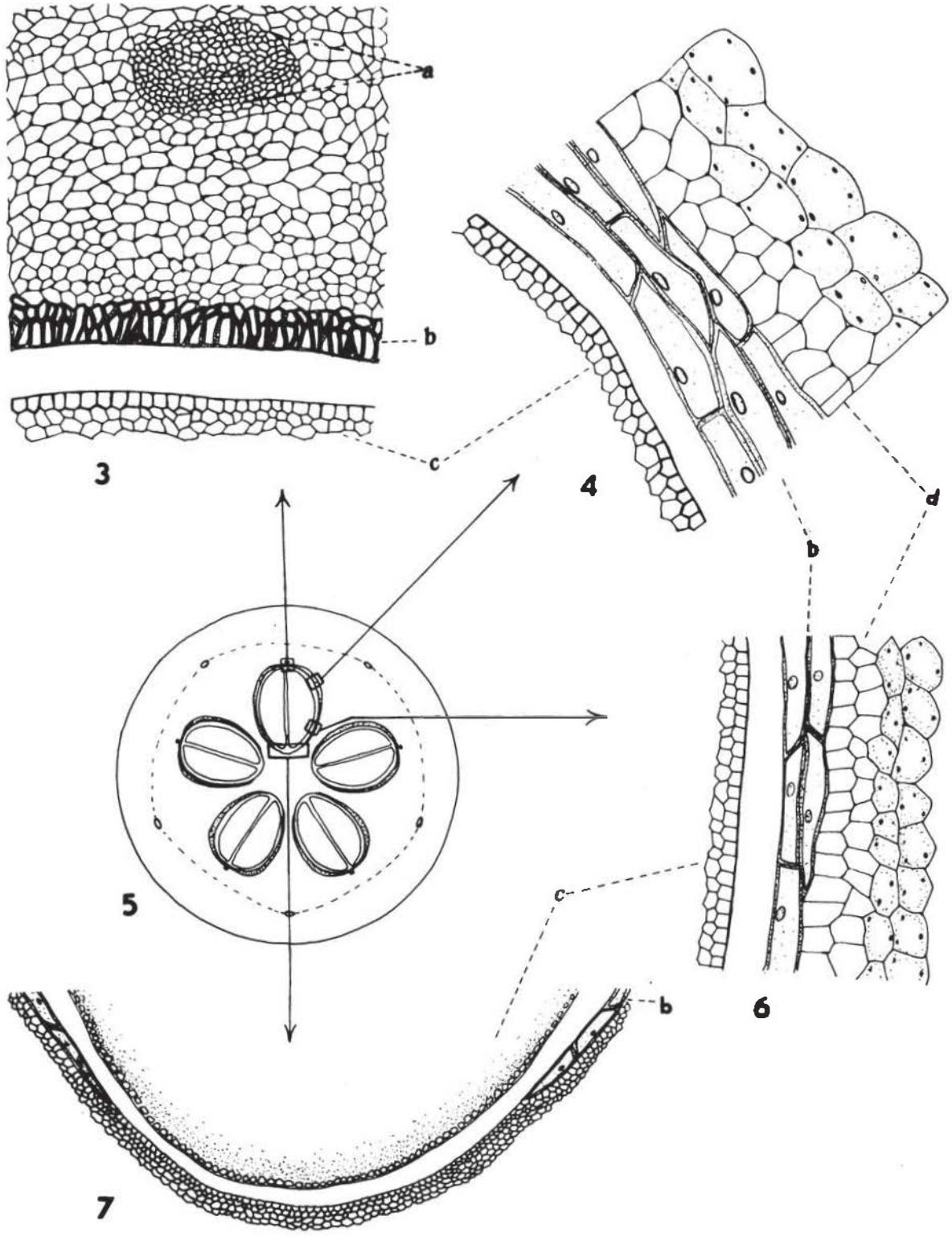
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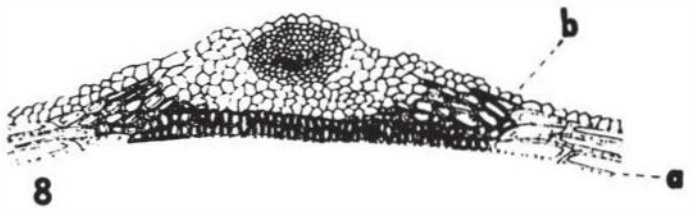
Fig. 8. Cross section of Malus x zumi carpel, six weeks after anthesis in the region of the dorsal bundle. Secondary endocarp sclereids (b) show oblique orientation, in relation to primary endocarp sclereids (a). X 75.

Fig. 9. Cross section of Malus x zumi carpel six weeks after anthesis, illustrating vertical elongation of secondary endocarp cells (b). Secondary endocarp cells adjacent to primary endocarp sclereids thicken before other secondary endocarp cells. X 150.

Fig. 10. Cross section of Malus x zumi carpel, eight weeks after anthesis, in ventral suture region. Primary endocarp sclereids (a) and secondary endocarp sclereids have not developed in immediate ventral suture region. X75.

Fig. 11. Cross section of thickest endocarp region of Malus x zumi carpel, eight weeks after anthesis. Cell walls of primary endocarp sclereids (a) have undergone extensive thickening and lignification. Secondary endocarp (b) has attained maximum thickness. X 150.



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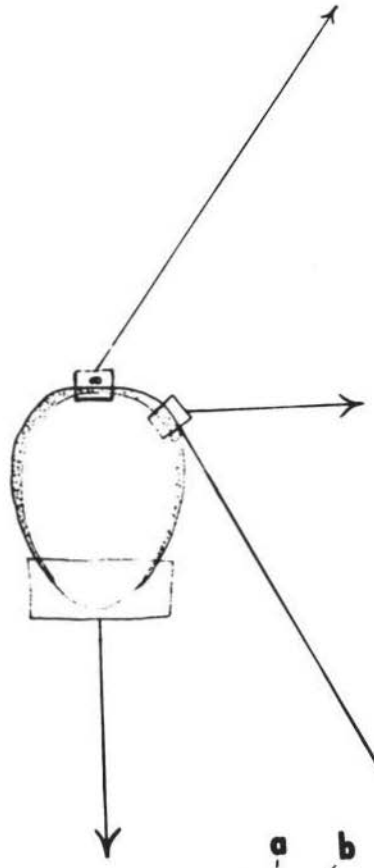

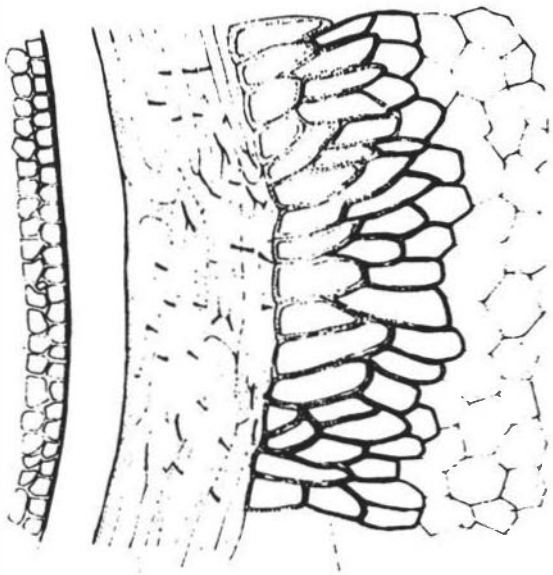

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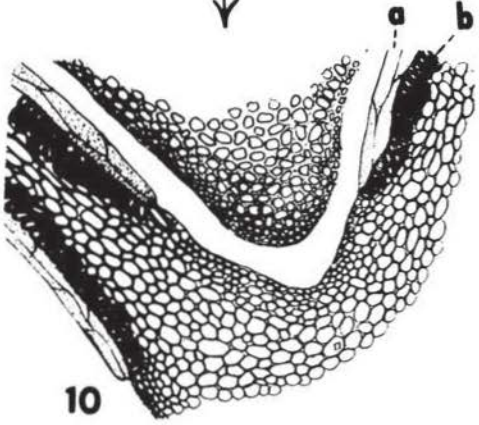

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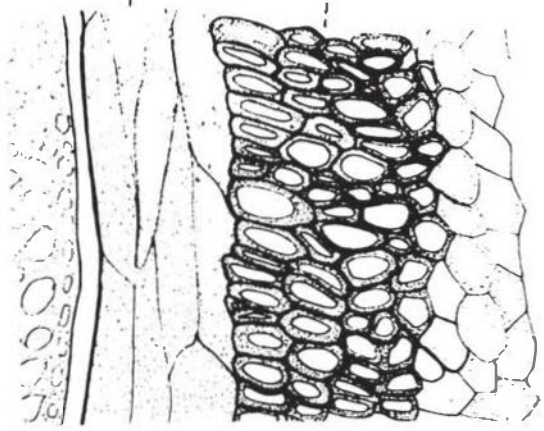

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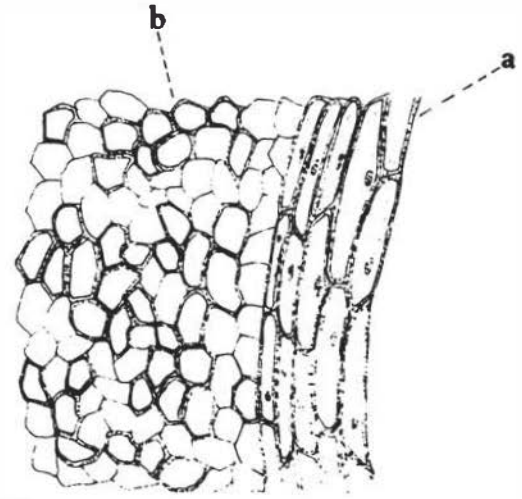
Fig. 12. Cross section of Crataegus mollis carpel, five weeks after anthesis, illustrating random cell differentiation of secondary endocarp (b). Elongated cells of primary endocarp (a). X75.

Fig. 13. Cross section of Crataegus mollis carpel and ovule (c), three weeks after anthesis in the region of the dorsal bundle (b). X75.

Fig. 14. Cross section of Crataegus mollis carpel, illustrating vascular bundle trapped in mature secondary endocarp. X150.

Fig. 15. Mature secondary endocarp sclereids of Crataegus mollis, illustrating laminated wall structure and ramiform pits. X300.



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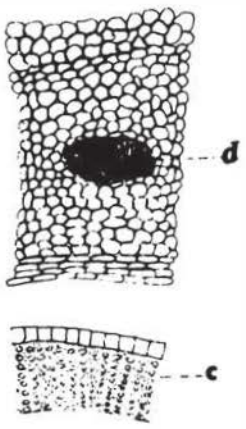

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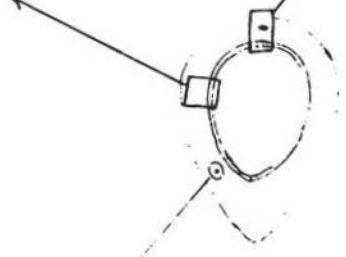

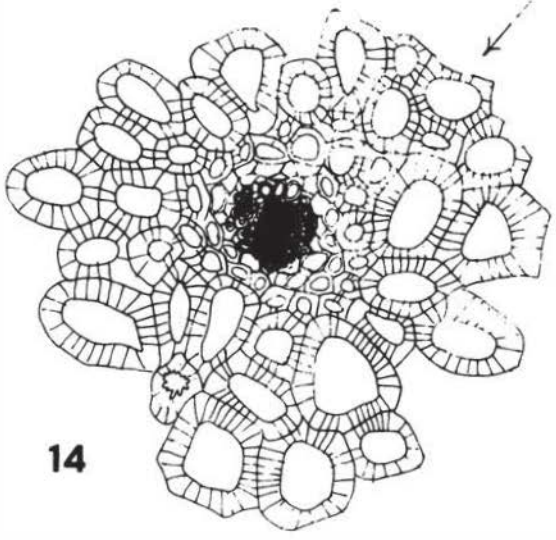

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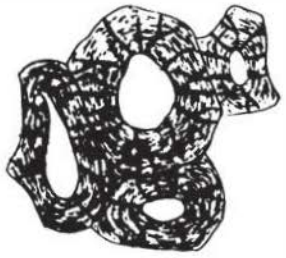

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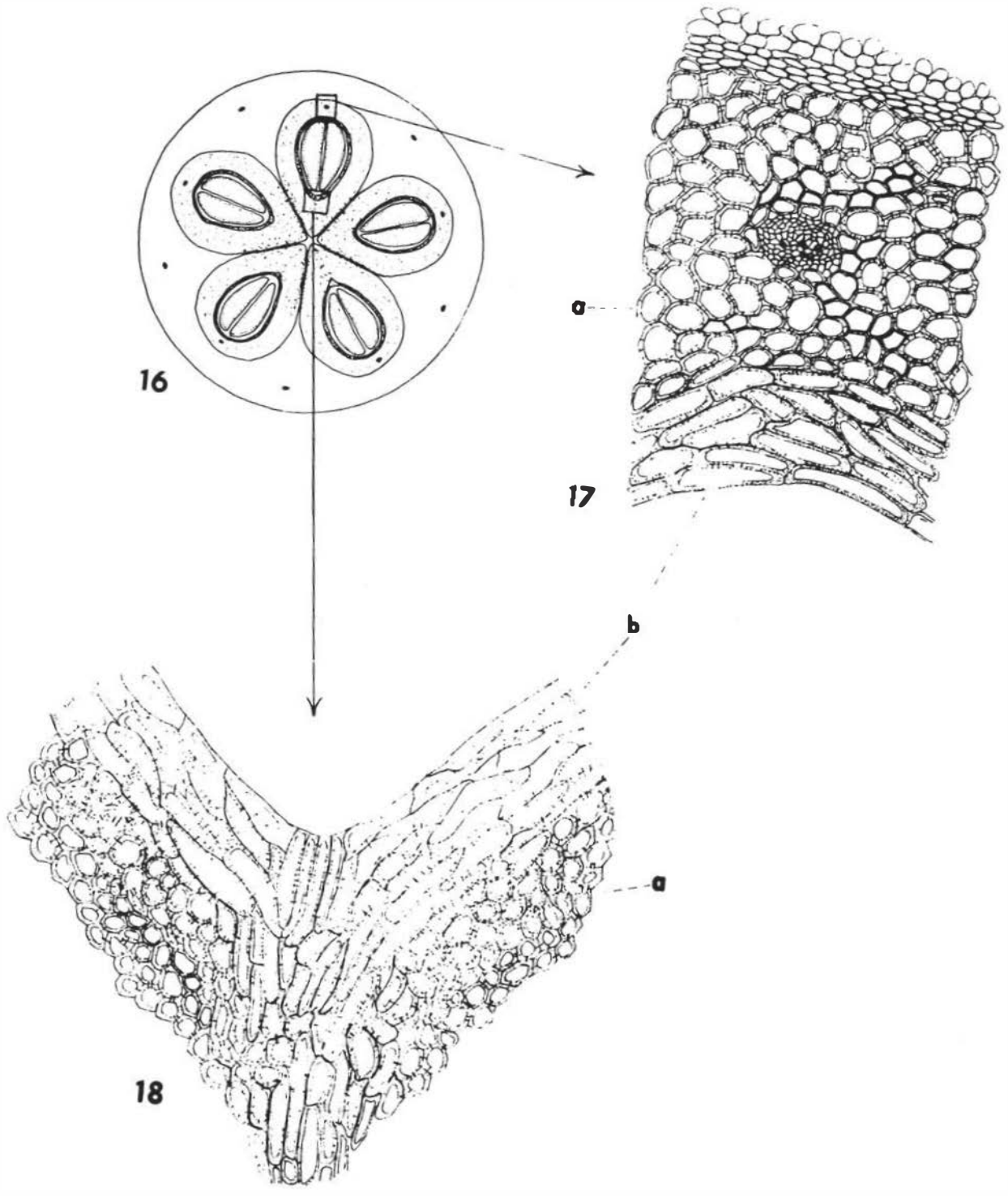
Fig. 16. Crataegus mollis ovary in cross section.

Fig. 17. Cross section of Crataegus mollis carpel six weeks after anthesis in the region of the dorsal bundle. Elongated sclereids of primary endocarp (b) show considerable thickening. Secondary endocarp (a) extends beyond dorsal bundle. X75.

Fig. 18. Cross section of Crataegus mollis carpel six weeks after anthesis in the region of the ventral suture. Primary endocarp sclereids (b) have elongated along with secondary endocarp sclereids (a) forming suture line. Those primary endocarp sclereids adjacent to the locule show a greater degree of cell wall thickening than other primary endocarp sclereids. X75.


16
a
17
b
a
18