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Histogenesis polymorphism of the anther wall in some species of the *Rosaceae* family growing in the Ukrainian Carpathians

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Abstract. We studied 19 plant species of the Rosaceae family, belonging to 10 genera that grow in the Ukrainian Carpathians. Some of these species had not been previously subject to embryological studies. The polymorphism of the anther wall formation process (histogenesis) was confirmed. Because the existing classifications of anther wall development do not adequately capture the specific character of polymorphism in species of the Rosaceae family, the following three new variations were proposed within the dicotyledonous type: var. normal, var. *Rosa*, and var. *Crataegus*. The difference between these variations lies in the differentiation procedure of the middle layers and the peculiarities of tapetum differentiation. The performed studies highlight the need for further detailed investigation of the histogenesis of anther walls in species of the Rosaceae family, with the aim, among others, to establish the phylogenetic relationships between species that form anther walls in different ways.

Keywords: anther wall, embryology of angiosperms, histogenesis, Rosaceae, tapetum.

Introduction

The development, structure, and functioning of the male generative sphere in angiosperms are characterized by large polymorphism, leaving many questions that require more investigation. According to literary sources, microsporangium production has been examined in 150 of the 400 families (Teryokhin et al. 1994). Many classifications of microsporangium wall formation are based on the characteristics of parietal tissue formation. Davis (1966) suggested four different forms (centripetal, centrifugal, basic, and reduced) of microsporangium wall development. Teryokhin et al. (2002) classified the basic type as a complicated variation of the centripetal type, and the reduced type as a reduced variation of the centrifugal type. According to Shamrov et al. (2020), angiosperms have two forms of microsporangium wall layer formation: centrifugal and centripetal. Teryokhin et al. (1994) noted that the Rosaceae family showed polymorphism during this process. Along with sexual development, apomictic reproduction has been observed in several representatives of the Rosaceae, which is reflected in the peculiarities of the formation and functioning of both female and male generative structures of plants (Mandryk & Petrus 1985, Dickinson et al. 2007). In higher plants, sexual and asexual reproduction via seeds (apomixis) have evolved as alternate mechanisms (Tucker & Koltunow 2009). Apomixis, which results in the creation of clonal offspring, has long been recognized for its potential agricultural applications (Schmidt 2020).

The peculiarities of the geomorphology of the Ukrainian Carpathians determine the formation of the climatic gradient in the Tysa/Tisza River basin within the territory of Zakarpatska Oblast (Transcarpathian region), where, due to the changes of altitude above sea level from 2,061 m (Mount Hoverla) down to 102 m (Tchop/Csop) within less than 200 km, changes of vegetation bands can be observed from Alpine lawns to coniferous and deciduous forests, and to steppe (Karabiniuk et al. 2022, Roleček et al. 2022, Karabiniuk 2023). These environmental effects may be reflected in the reproductive strategies of plants prone to apomixis (Karunarathne et al. 2020). Karbstein et al. (2021) investigated the susceptibility of *Ranunculus auricomus* to apomixis based on the distribution of the plant. They found that sexual reproduction is more common in the southern zones, while apomixis is more common in plants from the more northern zones (Karbstein et al. 2021).

In terms of microsporangium development processes in Rosaceae plants, scientific sources show that in most species, the histogenesis of anther walls occurs efferently by dicotyledonous type (Mandryk & Petrus 1985); however, it is known that representatives of *Cydonia* and *Cerasus* genera exhibit the monocotyledonous type of anther wall formation - a developmental classification originally described in monocots but also occurring in other taxonomic groups (Abramyan 1979). According to different classification systems, this type is also referred to as the afferent type (Teryokhin et al. 1993). Several authors discuss the polymorphism of the anther wall structure, particularly the possibility of one to three layers and a one- or two-layer tapetum (Mandryk & Petrus 1985, Yao et al. 2022). There is literature describing the mechanism for some plants (Zou et al. 2013). Still, within the family Rosaceae, there is a lack of research on the differences in the formation of the anther wall between family members. Hasynets (2004, 2005, 2008, 2010) investigated the formation of anther walls of *Crataegus* and *Cotoneaster* species and determined that the anther wall of *Crataegus* plants consists of seven cell layers: epidermis, endothecium (fibrous layer), three middle layers, and two tapetal layers. Deviations were revealed in the division sequence: following the formation of the tapetum and secondary parietal layer, the latter again divided, leading to the appearance of two cell layers: the internal layer that was adjacent to the tapetum and the external middle layer, both of which were able to divide recurrently, forming two or three middle layers (Shamrov et al. 2021). One to three (but most frequently, two) middle layers reached maximum development at the synapsis stage of microsporocyte nuclei (Shamrov et al. 2021). Degeneration of the middle layers had occurred a bit earlier, during the ruination of the tapetum. The first to degenerate was the layer directly adjacent to it. The tapetum was of dual origin. The connective tissue was formed from the main parenchyma. Even though one part of the tapetal cells was derived from the primary archesporium (parietal layer) and the other part from the main parenchyma, they originated approximately simultaneously, developed synchronously, and hardly differed morphologically (Hasynets 2004, 2005, 2008, 2010).

In our research, we conducted a thorough analysis of the polymorphism observed in the anther wall formation process among 19 species within the *Rosaceae* family, revealing significant variability and distinctive characteristics in their developmental mechanisms that contribute to a better understanding of this polymorphic phenomenon (Shamrov et al. 2021). We hypothesize that the polymorphism observed in the histogenesis of the anther wall of the family Rosaceae does not conform to previous classification systems (Teryokhin et al. 1994, Davis 1966), and that it is therefore necessary to propose new variations that better reflect species differences and the relationships between developmental mechanisms. In our study, we aimed to establish a new taxonomic classification within the *Rosaceae* family based on the type of anther wall formation.

Materials and methods

We collected the plant material for this study between 1995 and 2020. Our research focused on 19 species from the Rosaceae family, representing 10 different genera. These species either grow naturally in various biotopes or are cultivated in Transcarpathia, Ukraine. By selecting species from different subfamilies within the Rosaceae family, we aimed to conduct a comparative analysis. The selection of these species was based on previous morphological, histological, and embryological research findings and observations. The species included in the experiment were: *Aruncus dioicus* (Walt.) Fern., *Filipendula vulgaris* Moench., *Filipendula denudata* (J. et C.Presl.) Fritsch, *Spiraea japonica* L., *Spiraea salicifolia* L., *Agrimonia eupatoria* L., *Alchemilla glabra* Neygenf., *Alchemilla flabellata* Buser., *Alchemilla deylii* Plocek., *Alchemilla subcrenata* Buser., *Alchemilla xanthochlora* Rothm., *Alchemilla monticola* Opiz., *Fragaria viridis* Weston., *Potentilla aurea* L., *Potentilla obscura* Willd., *Poterium sanguisorba* L., *Rosa canina* L., *Rosa corymbifera* Borkh., *Sanguisorba officinalis* L. For this study, we recorded material at several stages of development, including the formation of flower primordia, young and mature buds, and the onset and conclusion of flowering. The sample size comprised between 50 and 100 flowering shoots, randomly selected from natural populations or cultivated plantings of introduced species.

The sample was fixed at several developmental phases for cytoembryological investigation, ranging from flower primordial formation to mature pollen generation. The following fixing agents were used: chrome-aceto-formalin solution after Navashyn's (10:4:1), formalin aceto-alcohol (FAA) after Chamberlain (90:5:5), a mixture of formalin, acetic acid, and ethyl alcohol in a 10:7:1 ratio, and Carnoy's solution (ethyl alcohol and acetic acid in a 3:1 ratio) (see in Naumov & Kozlov 1954, Pausheva 1974, 1980, Carvalho et al. 2017). The microtome cuts ranged in thickness from 5 to 15 microns, depending on the developmental phase. The preparations were stained using Feulgen's iron hematoxylin, with cytoplasm colored with 0.5% solutions of eosin, erythrosine, and Bright Green (Pausheva 1980), and with gallocyanin-chrome stains following Einarson (Pearse 1962). The study was conducted using an OMAX light microscope with an A35100U photodetector.

Results

We observed that meristematic stamen ribs were established at the early development stages of the flower of *Sanguisorba officinalis* (Fig. 1A- C). Later, anther lobes are formed in the stamen ribs. All species in this study had tetrathecal anthers, with the cells joined into two thecae.

In the sub-epidermal layer of the future anther theca, an initial archesporium with 3–5 cells on a transverse cut was set. The size of the cells in the initial archesporium was larger than that of the adjacent cells; they had thick cytoplasm with large nuclei and nucleoli.

As a consequence of periclinal divisions, the primary archesporial cells gave rise to the secondary archesporial (sporogenous) and primary parietal cells (Fig. 2A).

When dividing periclinal, the primary parietal cells formed the tapetum and the secondary parietal layer (Fig. 2B-E). The secondary parietal layer was divided periclinal, resulting in two middle layers. The upper middle layer towards the center formed the middle layer, and outwards from the center, it formed the endothecium. This way of forming middle layers was typical for the studied species of the *Filipendula* genus (Fig. 3 A-B).

Another way of dividing the secondary parietal layer, namely, periclinal division with the formation of the endothecium and the middle layer, is also possible. Such was observed, for instance, in representatives of the *Agrimonia* (Fig. 2A), *Sanguisorba* (Fig. 2B-E), *Poterium,* and *Alchemilla* genera.

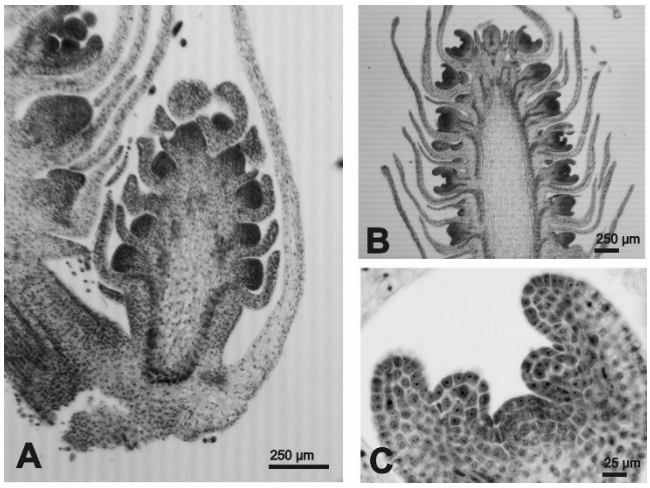

Figure 1. Initial inflorescence stage and flowers in *Sanguisorba officinalis* L: A - formation of flowers in the lateral inflorescence (Scale – 250 µm); B - formation of flower elements (Scale – 250 µm); C - a flower of inflorescence under large amplification (Scale – 25 µm).

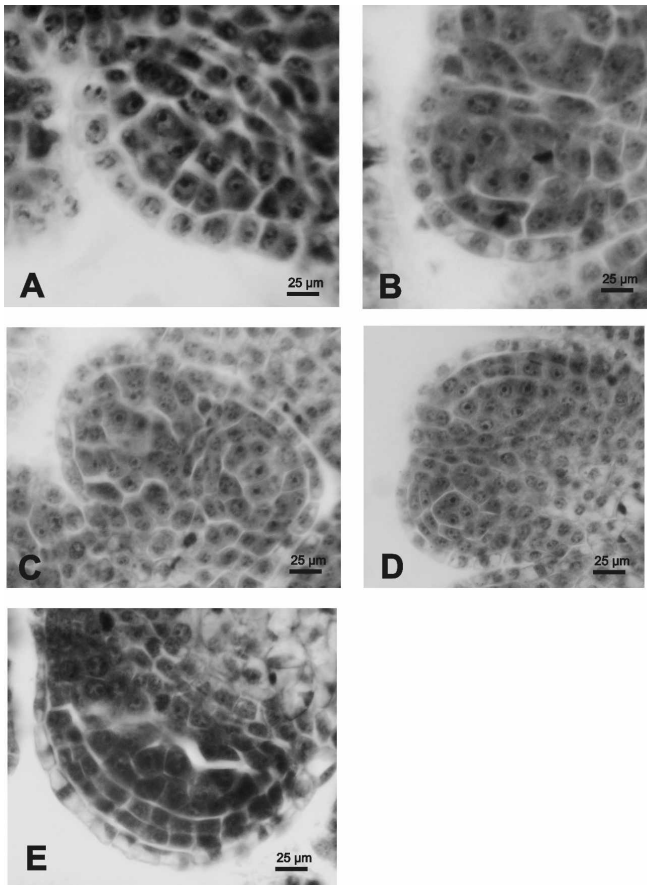

Figure 2. Initial stages of anther wall formation. A.- *Agrimonia eupatoria* L. Division of primary archesporium to secondary archesporial and primary parietal layers (Scale – 25 µm); B.- *Sanguisorba officinalis* L. Beginning of division of primary parietal layer to secondary parietal layer and tapetum (Scale – 25 µm); C.- *Sanguisorba officinalis* L. Division of primary parietal layer to secondary parietal layer and tapetum (Scale – 25 µm); D.- *Sanguisorba officinalis* L. Primary parietal layer divided to secondary parietal layer and tapetum (Scale – 25 µm); E.- *Sanguisorba officinalis* L. Secondary parietal layer divided into middle layer and endothecium (Scale – 25 µm).

The number of middle layers may vary among representatives of the *Rosaceae* family. In some of the species studied (*Agrimonia eupatoria*, *Sanguisorba officinalis*, species of the *Alchemilla*, *Potentilla*, and *Rosa* genera), alongside the typical histogenesis of the anther wall, we observed the formation of two (Fig. 3 A-K) or, in species of the *Rosa* genus, three middle layers by division of one layer formed from the secondary parietal layer (Fig. 3 L-M).

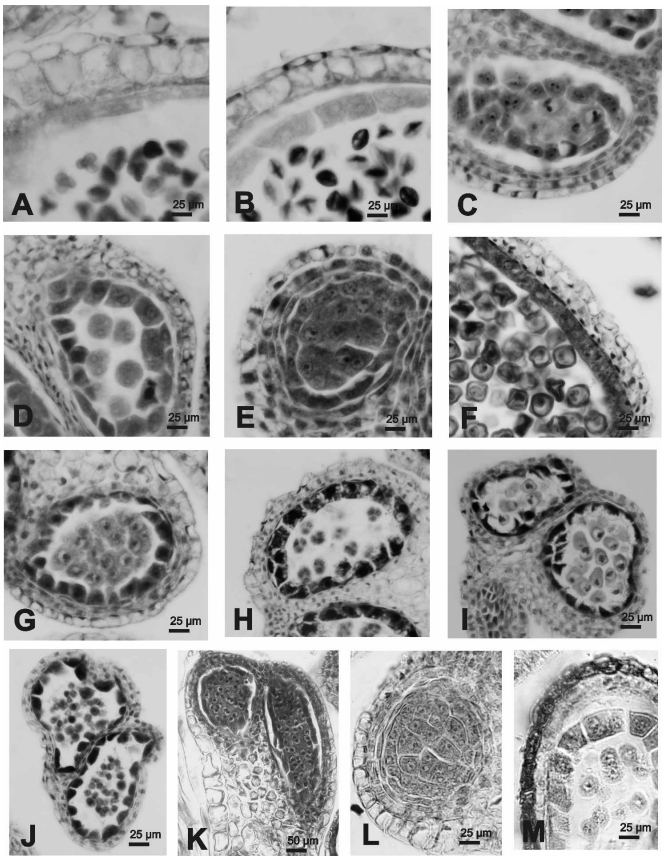

Figure 3. Structure of formed anther wall in some of the reviewed species of the Rosaceae family: A.- *Filipendula denudata* (J. et C. Presl.) Fritsch. A well-formed anther wall. Beginning of degeneration of the middle layers. Microspores (Scale – 25 µm); B.- *Filipendula denudata* (J. et C.Presl.) Fritsch. The middle layers degenerated. Microspores (Scale – 25 µm); C.- *Agrimonia eupatoria* L. A well-formed anther wall. The microsporocytes proceeded to meiosis (Scale – 25 µm); D.- *Agrimonia eupatoria* L. Beginning of degeneration of the middle layers. Microspore tetrads (Scale – 25 µm); E.- *Sanguisorba officinalis* L. A well-formed anther wall. The microsporocytes proceeded to meiosis (Scale – 25 µm). F.- *Sanguisorba officinalis* L. Beginning of degeneration of the middle layers. Microspores (Scale – 25 µm); G.- *Poterium sanguisorba* L. A well-formed anther wall. The microsporocytes proceeded to meiosis (Scale – 25 µm); H.- *Poterium sanguisorba* L. Beginning of degeneration of the middle layers. Microspore tetrads (Scale – 25 µm); I.- *Alchemilla monticola* Opiz. A well-formed anther wall. The microsporocytes proceeded to meiosis. First signs of anther degeneration observed (Scale – 25 µm); J.- *Alchemilla monticola* Opiz. Beginning of degeneration of the middle layers and tapetum. Abortive microspore tetrads (Scale – 25 µm); K.- *Potentilla obscura* Willd. A well-formed anther wall. The microsporocytes proceeded to meiosis (Scale – 50 µm); L.- *Rosa canina* L. A well-formed anther wall and sporogenous tissue (Scale – 25 µm); M.- *Rosa canina* L. Degeneration of the middle layers. Binuclear tapetum. The microsporocytes proceeded to meiosis (Scale – 25 µm).

In species of the *Sanguisorbeae* tribe (*Agrimonia eupatoria, Sanguisorba officinalis, Poterium sanguisorba, and Alchemilla sp.*), while the secondary archesporium was still in the pre-meiotic state, the young anther tapetal cells contained one nucleus with a nucleolus. The cytoplasm of these cells was not yet weakly vacuolated. Microsporocyte nuclei transfer into the early prophase of the first meiotic division coincided with the mitotic division of the tapetal cell nuclei. The division occurred without deviations from the norm, although no phragmoplasts or cell walls formed between the newly formed nuclei. All tapetal cells contain two nuclei (seldom, one nucleus). Binuclearity of the tapetal cells was also noted for the other reviewed species belonging to Spiraeoideae (*Aruncus dioicus* (Walt.) Fern (Fig. 4H), *Spiraea japonica* L.f., *S. salicifolia* L.) and Rosoideae (*Rosa canina* L., *R. corymbifera* L.) (Fig. 3L-M; Fig. 4G).

The tapetum is of the secretory type in all the analyzed species. The first signs of tapetum degeneration were observed during the formation of microspore tetrads, while the tapetum fully degenerated at the stage of microspore nucleus division.

Differentiation of the endothecium occurred somewhat later than in the other anther wall tissues. At later stages, the cells became strongly vacuolated, cell sizes increased, and secondary fibrous thickening appeared in their membranes. By the time the flower buds unfurled, the cell protoplasts had disappeared, and the endothecium had the form of a fibrous layer.

The epidermal layer of the anther lobe was represented by strongly vacuolated cells. During the differentiation of other layers, its morphology changed little. As pollen grains matured, the cell cytoplasm was strongly vacuolated; thereupon, the protoplast fully degenerated. When the anthers were opening, their walls consisted of an endothecium with remnants of epidermis; the other layers had by then been absent (Fig. 4).

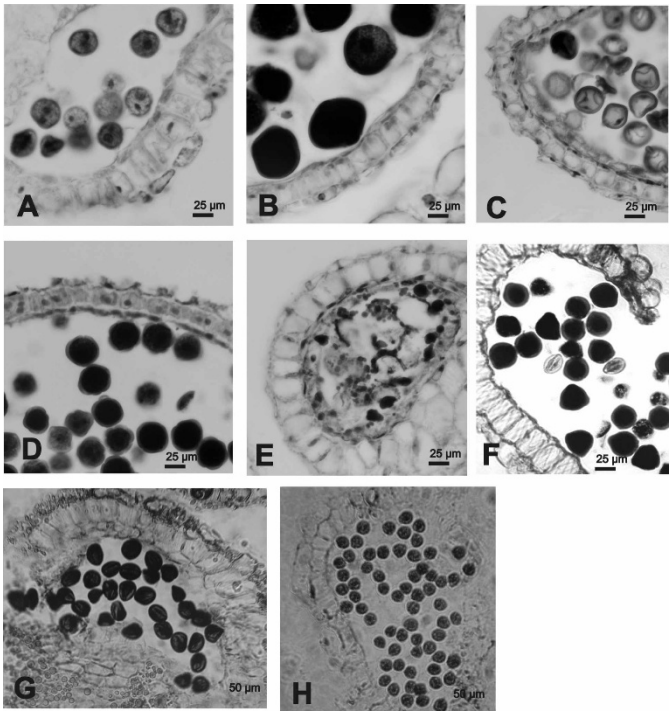

Figure 4. Mature anther wall structure in the reviewed species of the Rosaceae family: A.- *Filipendula denudata* (J. et C. Presl.) Fritsch. (Scale – 25 µm); B.- *Agrimonia eupatoria* L. (Scale – 25 µm); C.- *Poterium sanguisorba* L. (Scale – 25 µm); D.- *Sanguisorba officinalis* L. (Scale – 25 µm); E.- *Alchemilla monticola* Opiz. (Scale – 25 µm); F.- *Fragaria viridis* L. (Scale – 25 µm); G.- *Rosa canina* L. (Scale – 50 µm); H.- *Aruncus dioicus* (Walt.) Fern. (Scale – 50 µm)

Discussion

Despite its pivotal role in producing viable pollen and facilitating the release of pollen grains from anther locules—key steps for successful pollination—recent research has largely overlooked the developmental morphology of the anther wall in flowering plants (Shamrov et al. 2020). This gap is especially significant within the Rosaceae family, where the development of the anther wall is particularly intriguing. This interest arises from their remarkable reproductive diversity, which includes sexual reproduction, apomixis, vegetative propagation, and various combinations of these methods (Dickinson et al. 2007, Tucker & Koltunow 2009).

Foundational studies in embryology have significantly contributed to our understanding of how the microsporangial wall forms in the Rosaceae family. The most comprehensive of these is the five-volume *Comparative Embryology of Flowering Plants* (Yakovlev 1981, 1983, 1985, Batygina & Yakovlev 1985, 1990), with a chapter in Volume III, authored by Mandryk and Petrus (1985), addressing Rosaceae. Their findings highlight a dominant dicotyledonous pattern of anther wall formation, characterized by the development of one or two middle layers, and the presence of polyploid nuclei within tapetal cells in certain species. Our current research not only confirms these earlier observations in several taxa but also uncovers new developmental patterns, including intermediate histogenetic forms and consistent polyploidization of tapetal nuclei in specific lineages.

In particular, first Kolesnyk (1994) and then Saffari et al. (2020) observed a four-layered anther wall and binucleate tapetum in *Agrimonia eupatoria*, features which align closely with what we have documented in the var. *Rosa* variant. However, our investigation also revealed broader histological variation, such as the presence of polyploid tapetal cells previously unreported in the literature. Macková (2020) similarly noted stable tetraploidy and facultative apomixis in *Cotoneaster*, where our data show a distinctive three-layered middle zone and polyploid tapetum in the var. *Crataegus* variant. Such consistency in cytological features may indicate developmental stabilization linked to apomictic reproduction.

Our findings in *Crataegus* and *Cotoneaster* also resonate with Talent's (2009) evolutionary framework, which associates polyploidy with gametophytic apomixis in Maloid Rosaceae. Although our research did not directly address apomixis, the structural variation observed lends support to the idea of inherent reproductive adaptability in these genera. Comparable patterns were reported by Aldasoro et al. (1998) in *Sorbus*, a genus noted for its high polyploidy and frequent hybridization, which often result in intermediate morphotypes. This outcome was mirrored by the variation we recorded in tapetal structure and wall layering.

Phylogenetic analysis by Vamosi and Dickinson (2006) further demonstrated that polyploidy is widespread across *Crataegus*, *Cotoneaster*, and *Rosa*, potentially correlating with increased species richness. The developmental differences we observed in the tapetum and wall layers may thus represent underlying anatomical mechanisms that support such diversification.

Additionally, Chen et al. (2020) linked male sterility in *Rosa sterilis* to delayed tapetal degeneration and nutrient deficiencies. The presence of a multilayered tapetum and polyploid nuclei in *Crataegus* highlights the importance of precise tapetal regulation for successful microspore development, underscoring the broader functional significance of tapetal differentiation across the *Rosaceae*. Çetinbaş and Ünal (2015) described anther wall development in *Crataegus tanacetifolia*, noting the presence of 2–3 middle layers and a multinucleate secretory tapetum undergoing programmed cell death. These findings correspond with our general observations in *Crataegus*, although our data provide further evidence of histogenetic diversity and

widespread polyploidy.

Recent reevaluations of classical anther wall development typologies have also emerged. Early frameworks by Batygina et al. (1963) and Davis (1966) introduced and refined the dicotyledonous (efferent) developmental model, later expanded into a binary afferent–efferent classification by Teryokhin et al. (1993, 1994). However, these did not adequately address developmental polymorphism. More recent work by Shamrov et al. (2020) and Åstrand et al. (2021) has underscored the variability within traditional categories, pointing to a need for revision based on molecular and cellular data. Our identification of three distinct morphogenetic variants within Rosaceae provides new anatomical evidence to support this reevaluation.

In our study, all investigated species had tetrasporangiate (tetrathecal) anthers, with a eusporangiate origin of the archesporium (Goebel 1887). Based on the patterns observed, we propose three histogenetic variations in Rosaceae:

- var. normal (Fig. 5A) is characterized by the typical occurrence of anther wall histogenesis by dicotyledonous type (Davis 1966) with gradual efferent separation of layers and the formation of a one-layered predominantly binuclear tapetum (some cells may have remained mononuclear). We noted this variation in the following genera: *Filipendula*, *Aruncus*, and *Spiraea*.
- var. *Rosa* (Fig. 5B) differed from var. normal in the fact that the secondary parietal layer singled out the endothecium and the middle layer, from which two (less frequently, three) middle layers were formed. In this variation, like in the previous one, the tapetum was one-layered and predominantly binuclear. We noted this variation for the following genera: *Agrimonia*, *Sanguisorba*, *Alchemilla*, *Rosa*, *Fragaria*, and *Potentilla*.
- var. *Crataegus* (Fig. 5C) differs from var. normal in the fact that, similarly to var. *Rosa*, the secondary parietal layer singled out the endothecium and the middle layer, from which two middle layers were formed, of which the inside layer (most frequently) divided once again, leading to the formation of three middle layers. Unlike the previous variation, in this case, the tapetum was two-layered with cell polyploidization (Hasynets 2004, 2005, 2008, 2010). We noted this variation for the following genera: *Crataegus* and *Cotoneaster*.

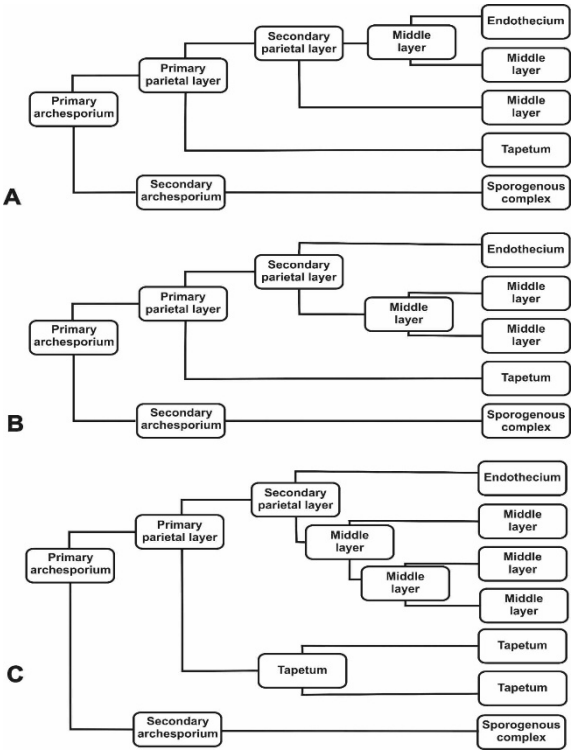

Figure 5. Anther wall variation and histogenesis patterns for the reviewed species of the *Rosaceae* family. A. – var. normal; B. – var. *Rosa*; C. - var. *Crataegus*

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