

Inheritance and Mechanism of Midrib Stripe and Anthocyanin Pigmentation in *Episcia*

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Keywords. air space, epistasis, foliage plant, leaf anatomy, variegation

Abstract. The presence of midrib striping and anthocyanin-rich foliage significantly enhances the aesthetic and commercial value of *Episcia cupreata*. Crosses among nine cultivars and their progeny were analyzed to investigate the inheritance patterns of leaf midrib striping and anthocyanin pigmentation. The results indicated that midrib striping is controlled by a dominant locus (*M*), which is epistatically suppressed by a dominant inhibitor (*S*) at a separate locus. Similarly, anthocyanin pigmentation is governed by a dominant locus (*A*), which is suppressed by a dominant inhibitor (*I*). Leaf anatomical structures were examined in the green-leaf, white-striped ‘Thad’s Yellow Bird’ and the brown-leaf, pink-striped ‘War Paint’ to elucidate the mechanisms underlying foliar variegation and coloration. In ‘Thad’s Yellow Bird’, air spaces were exclusively present in the white midrib regions, located between the epidermis and mesophyll, and absent in the green regions. In contrast, in ‘War Paint’, anthocyanins accumulated in the subepidermal layers of the pink midrib stripe, which also contained air spaces. In the brown regions, where air spaces were absent, anthocyanins localized in the mesophyll, predominantly within the spongy parenchyma cells.

Episcia (Gesneriaceae), a tropical flowering foliage plant, is widely used in interior decoration due to its aesthetic appeal. Leaf traits, such as the presence of midrib stripes and foliage color containing anthocyanins, play a significant role in its commercial value (Shalit 2000).

Midrib striping in foliage plants is typically controlled by dominant nuclear genes. For example, in *Dieffenbachia* ‘Wilson’s Delight’, the white midrib trait is governed by the *Wm* gene (Henny 1983); in *Dieffenbachia maculata* ‘Camille’, the lemon-yellow variegation is controlled by the *Pv^l* gene (Henny 1986); and in *Aglaonema nitidum* ‘Ernesto’s Favorite’, the silver-gray banding is determined by the *V^{ef}* gene (Henny 1992). In *Coleus blumei*, the albino midrib trait is controlled by a single locus (*A*), with the recessive *a* allele producing a pale midrib stripe (Rife 1944). Purple midrib coloration is governed by epistasis between the *P* and *I* loci: dominant *P* causes uniform purple leaves, while *pp* produces purple striping, and background leaf color depends on *I*. Selfed progeny of the

Purple cultivar segregate in a 12:3:1 ratio: uniform purple (*P_ _*), purple striped with dark green (*ppI_*), and purple striped with light green (*ppii*) (Boye and Rife 1938).

Anthocyanin inheritance has been documented in plants with variegated or diverse leaf coloration. In *Caladium*, anthocyanin pigmentation is typically controlled by single dominant nuclear genes: leaf spotting by *S* (Deng et al. 2008) and leaf blotching by *B* (Deng and Harbaugh 2009). Main vein color is determined by a single locus *V*

with three alleles: *V^r* (red) > *V^w* (white) > *V^g* (green) (Deng and Harbaugh 2006). In teosinte (*Zea mays*), crosses between subspecies *mexicana* and *parviglumis* revealed that purple sheath color is controlled by two independently inherited dominant loci, *B1* and *A3*, with *A3* acting as a dominant inhibitor of *B1*, which regulates anthocyanin synthesis in vegetative tissues (Lauter et al. 2004).

Foliage or vein coloration arises from several mechanisms, including variations in chlorophyll and pigment composition, air space distribution, epidermal structure, and surface appendages (Zhang et al. 2020). Variegation is typically categorized as either true, caused by a localized loss of chlorophyll or pigments (Hughes et al. 2014; Pao et al. 2020), or structural, resulting from anatomical features such as trichomes, scales, or air spaces (Sheue et al. 2012). Several plants, including *Arisaema erubescens*, *Gynostemma pentaphyllum*, *Impatiens wenshanensis*, and *Rubus corchorifolius*, exhibit a silvery-gray midrib stripe caused by air spaces between the epidermis and mesophyll cells (Zhang et al. 2020). These air spaces are present in the white or silver regions but absent in the green vein areas of *A. nitidum* ‘Curtisii’ (Fooshee and Henny 1990), *Begonia rex* (Zhang et al. 2009), and *Sinningia speciosa* (Kan et al. 2021), contributing to their variegated appearance. Additionally, pigment accumulation, such as anthocyanins, contributes to leaf variegation in species like *Aeschynanthus longicaulis* and *Colocasia esculenta* (Zhang et al. 2020).

The inheritance and mechanism of midrib striping and foliage coloration associated with anthocyanin pigmentation of *Episcia* remain unclear. In this study, nine *Episcia* cultivars were self- and cross-pollinated, and their progeny were assessed for midrib striping and leaf anthocyanin pigmentation. Additionally, microscopic examination of leaf tissue sections was performed to identify anatomical

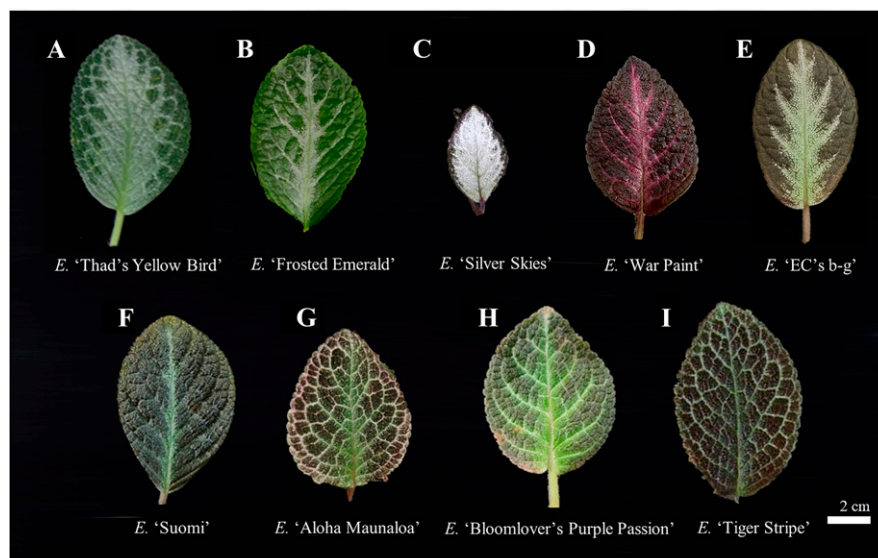


Fig. 1. Leaf traits observed in *Episcia* cultivars in this study. Midrib stripe: present (A–F) and absent (G–I). Anthocyanin pigmentation: present (C–I) and absent (A and B).

Received for publication 1 Aug 2025. Accepted for publication 27 Sep 2025.

Published online 20 Oct 2025.

This paper is part of the MS thesis by B.-X. L. The study was supported by the Ministry of Agriculture, Taiwan, under Project 114AS-4.1.5-FD-05.

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structures contributing to the observed variegation patterns.

Materials and Methods

Inheritance of midrib stripe and anthocyanin pigmentation. Rooted cuttings of *Episcia cupreata* were used in the study including nine cultivars: Thad's Yellow Bird, Frosted Emerald, EC's b-g, Suomi, Bloomlover's Purple Passion, Tiger Stripe, Silver Skies, Aloha Maunaloa, and War Paint (Fig. 1). Plants were grown in a plastic-covered greenhouse, and pollination was conducted between 0800 and 1200 HR. According to Shalit (2000), anthers were removed before flower opening. Once the style or stigma had fully extended, fresh pollen from the selected parent was applied to the stigma. Fruits were harvested 1 to 4 months after pollination, once they turned red and began natural cracking. Seeds were harvested, cleaned, and sown in soilless substrates (Potgrond H; UAB Klasmann-Deilmann Šilutė, Lithuania). Seedlings were raised in a controlled environment room maintained at $26 \pm 2^\circ\text{C}$, under a light intensity of $26 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density (PPFD), provided by white fluorescent lamps (Master TL5 HE 28 W/865; Royal Philips Co., Amsterdam, The Netherlands) for 12 h per day.

Once the progenies developed two pairs of leaves, they were transplanted into 9-cm pots containing a mixture of two parts peatmoss (Fafard No. 1; Conrad Fafard, Agawam, MA, USA), one part perlite (#3; Nanhai Vermiculite Industrial Co., New Taipei City, Taiwan), and one part vermiculite (#2; Nanhai Vermiculite Industrial Co.). Progenies were grown in a plastic greenhouse with an average temperature of 27°C , a 12-h daylength, and PPFD of $128 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, conditions conducive to *Episcia* growth (Dole and Wilkins 2005; Harbaugh et al. 1981). The plants were fertilized biweekly with $1 \text{ g}\cdot\text{L}^{-1}$ of a 15N-4.4P-24.9K soluble fertilizer (Peters 15-10-30; Scotts, Marysville, OH, USA) and were watered as needed. When the progeny developed five or six mature leaf pairs exhibiting stable leaf characteristics, the presence of midrib stripe and anthocyanin pigmentation was recorded in various self- or cross-combinations. χ^2 analysis was used to test the goodness-of-fit between observed and expected segregation ratios for each trait. The χ^2 value and corresponding probability (P value) were calculated to determine statistical significance.

Observation for midrib stripe and anthocyanin pigmentation. Recently fully expanded leaves of 'Thad's Yellow Bird' (green leaf with white midrib stripe) and 'War Paint' (brown leaf with pink midrib stripe) were collected. Free-hand sections were cut manually with a razor and mounted in water. Paraffin sections were prepared by fixing tissues in FPGa solution (formalin:propionic acid:glycerol:ethanol = 1:1.3:7), dehydrating through a graded *tert*-butyl alcohol series (10% to 75%), embedding in paraffin wax, sectioning at 10 to 12 μm on a rotary microtome, clearing in a xylene-ethanol series, and staining

Table 1. Segregation of leaf midrib stripe in progeny of *Episcia* crosses.

Cross (cross no.) ⁱ	Midrib stripe		Tested ratio	χ^2	<i>P</i>
	Present	Absent			
Present × present					
Thad's Yellow Bird ⊗ (1)	124	0	1:0	0	1
Frosted Emerald ⊗ (2)	144	0	1:0	0	1
Silver Skies ⊗ (3)	72	0	1:0	0	1
War Paint ⊗ (4)	72	0	1:0	0	1
Thad's Yellow Bird × EC's b-g (5)	147	0	1:0	0	1
Thad's Yellow Bird × Suomi (6)	139	0	1:0	0	1
War Paint × Frosted Emerald (7)	72	0	1:0	0	1
War Paint × Silver Skies (8)	144	0	1:0	0	1
Present × absent					
Frosted Emerald × Bloomlover's Purple Passion (9)	0	89	0:1	0	1
Silver Skies × Aloha Maunaloa (10)	69	75	1:1	0.25	0.62
Absent × present					
Bloomlover's Purple Passion × Suomi(11)	0	124	0:1	0	1
Tiger Stripe × Frosted Emerald (12)	67	68	1:1	0.01	0.93
Tiger Stripe × EC's b-g (13)	50	46	1:1	0.17	0.68
Absent × absent					
Tiger Stripe ⊗ (14)	14	45	1:3	0.05	0.82
Aloha Maunaloa ⊗ (15)	0	72	0:1	0	1

¹Numbers in parentheses serve as cross-references within the text.

$\otimes$ indicates self-pollination.

with 1% safranin and 0.1% fast green. Sections from both variegated and nonvariegated regions were observed under a microscope (Eclipse E600; Nikon, Tokyo, Japan), and images were captured using a microscope digital camera (MicroFire; Olympus America, Melville, NY, USA).

Results and Discussion

Inheritance of midrib stripe. Self-pollination (crosses 1 to 4; Table 1) and cross-pollination (crosses 5 to 8) of midrib-striped cultivars resulted exclusively in progeny exhibiting midrib striping, suggesting that these cultivars are homozygous at the locus controlling the trait. Crosses between midrib-striped and nonstriped cultivars generally produced a 1:1 segregation ratio of striped to nonstriped progeny (crosses 10, 12, and 13), supporting the hypothesis

that midrib striping is controlled by a single dominant allele at a locus designated *M*. However, crosses involving the nonstriped 'Bloomlover's Purple Passion' and midrib-striped cultivars (crosses 9 and 11) yielded only nonstriped progeny, suggesting that 'Bloomlover's Purple Passion' may carry a dominant modifier or inhibitor gene *S*. A two-gene model is proposed: one gene (*M*) confers striping, while a second gene (*S*) inhibits *M*; both genes exhibit complete dominance.

Self-pollination of the nonstriped 'Tiger Stripe' resulted in a 1:3 segregation ratio of striped to nonstriped progeny (cross 14), while self-pollination of the nonstriped 'Aloha Maunaloa' produced only nonstriped progeny (cross 15). According to this model, 'Aloha Maunaloa' likely has the genotype *Ssmm*, explaining its uniform nonstriped selfed progeny and segregating F_1 when crossed. 'Silver Skies' is likely

Table 2. Segregation of leaf anthocyanin pigmentation in *Episcia* crosses.

Cross (cross no.) ⁱ	Anthocyanin pigmentation		Tested ratio	χ^2	<i>P</i>
	Present	Absent			
Present × present					
Tiger Stripe ⊗ (16)	59	0	1:0	0	1
Aloha Maunaloa ⊗ (17)	72	0	1:0	0	1
Silver Skies ⊗ (18)	72	0	1:0	0	1
War Paint ⊗ (19)	72	0	1:0	0	1
Silver Skies × Aloha Maunaloa (20)	144	0	1:0	0	1
Tiger Stripe × EC's b-g (21)	147	0	1:0	0	1
Bloomlover's Purple Passion × Suomi(22)	139	0	1:0	0	1
War Paint × Silver Skies (23)	96	0	1:0	0	1
Present × absent					
Tiger Stripe × Frosted Emerald (24)	67	68	1:1	0.01	0.93
War Paint × Frosted Emerald (25)	45	51	1:1	0.38	0.54
Absent × present					
Frosted Emerald × Bloomlover's Purple Passion (26)	45	44	1:1	0.01	0.91
Thad's Yellow Bird× EC's b-g (27)	67	80	1:1	1.15	0.28
Thad's Yellow Bird × Suomi (28)	73	66	1:1	0.35	0.55
Absent × absent					
Frosted Emerald ⊗ (29)	44	100	1:3	2.37	0.12
Thad's Yellow Bird ⊗ (30)	0	124	0:1	0	1

¹Numbers in parentheses serve as cross-references within the text.

$\otimes$ indicates self-pollination.

ssMM, as it is consistently striped and shows no segregation. This model also accounts for the 1:3 ratio in ‘Tiger Stripe’ (*SsMM*), and the uniform striping observed in other cultivars such as Thad’s Yellow Bird, Frosted Emerald, War Paint, EC’s b-g, and Suomi, all likely having the genotype *ssMM*. ‘Bloomlover’s Purple Passion’ is homozygous dominant for the *S* gene (*SS*), but its genotype for the *M* gene cannot be conclusively determined from the current crosses; analysis of an F_2 generation may be necessary to clarify its genetic makeup.

Our results indicate that the midrib stripe trait in *Episcia* is controlled by two independently inherited genes, one acting as an inhibitor of the other, with both exhibiting complete dominance (Table 1). A two-gene epistatic inheritance model for midrib anthocyanin pigmentation has also been reported in *C. blumei* (Boye and Rife 1938). In variegated *Vitis* hybrids, the trait is governed by epistatic interactions between two recessive loci, *Lvar1* and *Lvar2* (Olson et al. 2022). This contrasts with midrib striping in *Dieffenbachia* and *Aglaonema*, where the trait is controlled by a single dominant nuclear gene (Henny 1983, 1986, 1992).

Inheritance of anthocyanin pigmentation. Selfing and crosses between cultivars showing visible anthocyanin pigmentation (cyanic) in leaves consistently produced only cyanic progeny (crosses 16 to 23; Table 2). In contrast, crosses between cyanic and acyanic cultivars yielded a 1:1 cyanic to acyanic segregation ratio (crosses 24 to 28). Selfing of the acyanic ‘Frosted Emerald’ produced a 1:3 cyanic to acyanic ratio (cross 29), while selfing of another acyanic ‘Thad’s Yellow Bird’, resulted in only acyanic progeny (cross 30). These patterns, particularly from crosses 27, 28, and 30, support a two-gene epistatic model in which the proposed *A* gene controls anthocyanin pigmentation and the proposed *I* gene inhibits it; both genes exhibit complete dominance. Based on segregation in selfed and crossed progeny, two acyanic cultivars, namely Thad’s Yellow Bird and Frosted Emerald, are inferred to have the genotypes *liaa* and *liAA*, respectively. The cultivars consistently producing cyanic progeny including ‘Tiger Stripe’, ‘Aloha Maunaloa’, ‘Silver Skies’, ‘War Paint’, ‘EC’s b-g’, ‘Bloomlover’s Purple Passion’, and ‘Suomi’ are most likely *iiAA*.

Leaf anthocyanin pigmentation in *Episcia* is governed by two independently inherited genes exhibiting complete dominance and epistatic interactions (Table 2). A similar two-gene model involving epistasis has been reported in teosinte (*Z. mays* subsp. *mexicana* and *Z. mays* subsp. *parviglumis*) (Lauter et al. 2004). This contrasts with the inheritance of single dominant nuclear genes controlling leaf spotting and blotching in *Caladium* (Deng et al. 2008; Deng and Harbaugh 2009).

Observation for midrib stripe and anthocyanin pigmentation. In ‘Thad’s Yellow Bird’, anatomical analysis revealed that air spaces between the epidermis and mesophyll cells were present exclusively in the white regions but absent in the green regions. Furthermore, the palisade mesophyll in the white areas consisted of smaller, more densely packed

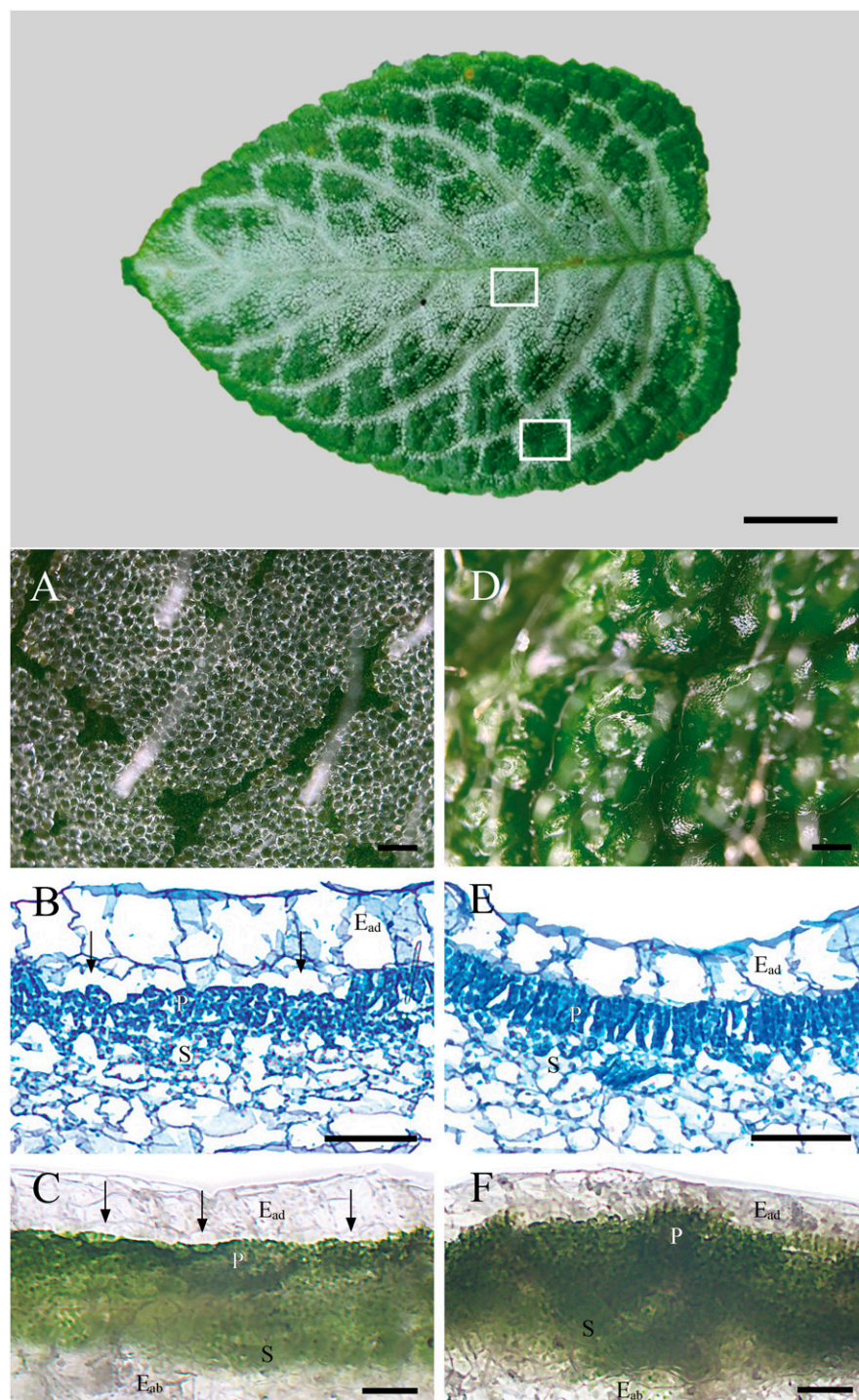


Fig. 2. Macroscopic and microscopic observation of white (A–C) and green (D–F) leaf regions of *Episcia* ‘Thad’s Yellow Bird’. (A and D) Surface views. (B and E) Paraffin sections. (C and F) Freehand cross-sections. Black arrows indicate air spaces. Bars indicate 200 μ m in A and D and 100 μ m in B, C, E, and F. E_{ad} = adaxial epidermis, E_{ab} = abaxial epidermis; P = palisade tissue; S = spongy tissue.

cells, whereas in the green regions, the palisade cells were larger and more loosely arranged (Fig. 2B, 2C, 2E, and 2F). These structural differences likely account for the appearance of a white midrib stripe on the adaxial leaf surface, which is more translucent and lighter, exhibiting significantly higher light reflectance compared with the adjacent green tissues (Fig. 2A and 2D). Sheue et al. (2012) attributed the variegation mechanism to the presence of air spaces,

explaining that, according to Snell’s Law, the refractive index differences in the white regions lead to altered light refraction and increased reflectance, contributing to the observed visual characteristics. Several plants, including *A. erubescens*, *G. pentaphyllum*, *I. wenshanensis*, and *R. corchorifolius*, exhibit a silvery-gray midrib stripe, resulting from air spaces between the epidermis and mesophyll cells (Zhang et al. 2020). This structural white variegation, associated with air spaces, has also

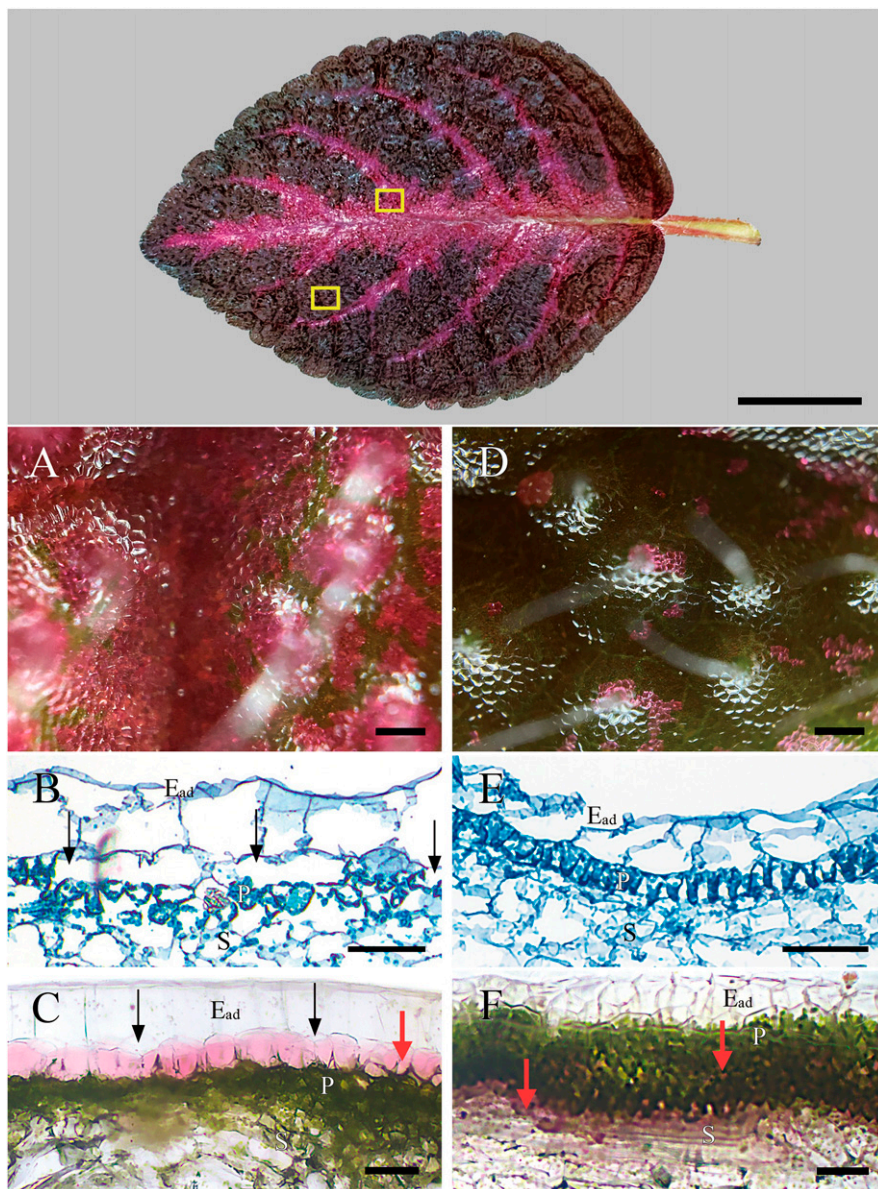


Fig. 3. Macroscopic and microscopic observation of pink (A–C) and brown (D–F) leaf regions of *Episcia* ‘War Paint’. (A and D) Surface views. (B and E) Paraffin sections. (C and F) Freehand cross-sections. Black and red arrows indicate air spaces and anthocyanin-rich regions, respectively. Bars indicate 200 μm in A and D and 100 μm in B, C, E, and F. E_{ad} = adaxial epidermis; P = palisade tissue; S = spongy tissue.

been documented in *Aglaonema* (Fooshee and Henny 1990), *Begonia* (Sheue et al. 2012), and *Sinningia* (Kan et al. 2021). Structural white

variegation may represent an adaptive mechanism to low-light conditions, enhancing the plant’s ability to capture available irradiance

(Sheue et al. 2012). This mechanism likely underlies the ability of *E. cupreata* to thrive in forest understory environments (Wiehler 1978) or low light conditions (Harbaugh et al. 1981; Li and Yeh 2025).

In ‘War Paint’, microscopic sectioning revealed that air spaces were present only in the pink regions and absent in the brown regions (Fig. 3B and 3E). Anthocyanins accumulated in the subepidermis of the pink stripe with air spaces, while in the brown region without air spaces, anthocyanins were located in the mesophyll, mainly in the spongy parenchyma cells (Fig. 3C and 3F). The combination of anthocyanin distribution and light refraction by the air spaces likely explains why the pink midrib stripe appears lighter compared with the adjacent brown tissues on the adaxial leaf surface (Fig. 3A and 3D). A nongreen leaf region, characterized by both air spaces and pigments, has been documented in various variegated ornamentals, including *Begonia pseudodryadis*, *Ludisia discolor*, *Saxifraga stolonifera*, and *Sonerila cantonensis* (Zhang et al. 2020). Anthocyanins function as antenna pigments in the photosystem, protecting the photosynthetic apparatus from photoinhibition (Taiz and Zeiger 2010). This protective role likely explains why *Episcia* cultivar with anthocyanin pigmentation exhibit greater tolerance to high light conditions compared with green cultivar (Li and Yeh 2025).

Conclusions

In *Episcia*, leaf midrib striping is conferred by the dominant *M* allele, but this phenotype is suppressed by the dominant *S* allele; thus, the striped phenotype is observed only in *ssM* genotypes. Similarly, pigmentation requires the dominant *A* allele and the absence of the dominant inhibitor *I*, occurring exclusively in *iiA* genotypes. All other allele combinations result in either nonstriped or acyanic phenotypes. The genotypes of nine cultivars for these traits are summarized in Table 3. The presence and distribution of anthocyanin, combined with light refraction caused by the air spaces, likely account for the observed foliar variegation and color patterns. These findings on the inheritance of midrib striping and pigmentation, along with the underlying anatomical mechanisms, provide valuable insights for improving breeding strategies and facilitating the development of cultivars with desirable leaf traits.

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Table 3. Phenotype and proposed genotype of *Episcia* cultivars used in this study.

Cultivar	Midrib stripe		Anthocyanin pigmentation	
	Phenotype	Genotype	Phenotype	Genotype
Thad’s Yellow Bird	Present	<i>ssMM</i> ¹	Absent	<i>liaa</i> ¹¹
Frosted Emerald	Present	<i>ssMM</i>	Absent	<i>liAA</i>
Silver Skies	Present	<i>ssMM</i>	Present	<i>iiAA</i>
War Paint	Present	<i>ssMM</i>	Present	<i>iiAA</i>
EC’s b-g	Present	<i>ssMM</i>	Present	<i>iiAA</i>
Suomi	Present	<i>ssMM</i>	Present	<i>iiAA</i>
Aloha Maunaloa	Absent	<i>Ssmm</i>	Present	<i>iiAA</i>
Bloomlover’s Purple Passion ¹	Absent	<i>SS</i> _	Present	<i>iiAA</i>
Tiger Stripe	Absent	<i>SsMM</i>	Present	<i>iiAA</i>

¹Two possible genotypes (*ssMM* and *ssMm*) produce progeny with midrib striping, while other genotypes (*SS* _ , *Ss* _ , and *ssmm*) produce progeny without midrib striping.

¹¹Two possible genotypes (*iiAA* and *iiAa*) produce progeny with anthocyanin pigmentation on the leaves (cyanic), while other genotypes (*II* _ , *Ii* _ , and *iiAA*) produce acyanic progeny.

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