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Comparative leaf epidermal characters for taxonomic clarification of the two varieties of *Pavetta tomentosa* (Rubiaceae) in Thailand

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Abstract. According to the latest taxonomic study of *Pavetta* L. in Thailand, 14 species and two varieties are recognised. However, this work was based mainly on morphological data and included some species with considerable morphological variation. Therefore, the taxonomic status of some species and infraspecific taxa is still uncertain and a re-evaluation is needed for clarification. This study focuses on whether the two varieties of *P. tomentosa* Roxb. ex Sm., *P. tomentosa* var. *tomentosa* and *P. tomentosa* var. *glabrescens* (Kurz) Bremek., are sufficiently distinct, as they are distinguished only by the degree of pubescence on various parts, with unclear boundaries between character states. To clarify the status of these taxa, we compared the leaf epidermis of representative individuals of *P. tomentosa* with different degrees of leaf hairiness using a peeling technique. The results revealed that *P. tomentosa* var. *tomentosa* and *P. tomentosa* var. *glabrescens* have similar leaf epidermal anatomy. No leaf epidermal anatomical characters were found that clearly support the recognition and separation of the two varieties.

Keywords: leaf epidermis, *Pavetta*, Rubiaceae, taxonomy

Introduction

Pavetta L. is a genus in the family Rubiaceae, most notably characterised by the presence of dark bacterial nodules or leaf galls, which occur in approximately 85% of its species (De Block *et al.*, 2015; Chantaranothai, 2021). Most species also bear attractive, whitish, 4-merous flowers with stigmatic lobes that are obscurely 2-lobed and mostly fused. In addition, they possess a single ovule per locule and hemispherical seeds with a large adaxial hilar cavity (De Block *et al.*, 2015; Chantaranothai, 2021).

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According to the most recent revision of *Pavetta* in Thailand by Chantaranothai (2021), 14 species (15 taxa) were recognised. *Pavetta tomentosa* Roxb. ex Sm. is one of the species reported in Thailand. It is distinguished from other species by its whitish tomentose, sparsely puberulous or glabrescent lower leaf surface and inflorescence (Chantaranothai, 2021). *Pavetta tomentosa* resembles *P. fruticosa* Craib in having sheath-like stipules and flowers with a corolla tube less than 2 cm long and a style less than 4 cm long. However, they differ in inflorescence type: *P. tomentosa* has more spreading inflorescences, whereas *P. fruticosa* produces compact ones (Chantaranothai, 2021). Among the 14 species of *Pavetta*, *P. tomentosa* is the only one with two recognised varieties: var. *tomentosa* and var. *glabrescens* (Kurz) Craib. The typical variety is characterised by tomentose hairs on the lower leaf surface and inflorescence, whereas var. *glabrescens* is distinguished by a sparsely puberulous to nearly glabrous lower leaf surface and sparsely puberulous inflorescence (Chantaranothai, 2021). However, the boundary between these two varieties remains unclear due to the continuous variation in hairiness, ranging from nearly hairless (glabrescent) to densely hairy (tomentose), rather than forming a clear-cut separation (Fig. 1). This raises the question of whether the two varieties of *P. tomentosa* are sufficiently distinct. To clarify their status, further studies beyond morphological analysis are required.

Hairiness (hair density) is a quantitative trait typically influenced by multiple genes or genomic regions (quantitative trait loci, QTLs). These contribute to continuous phenotypic variation and have been already identified in numerous plant species (Gao *et al*., 2018; Wang *et al*., 2024). In addition, besides genetic factors, environmental conditions can also influence hairiness in plants. Compared with the phenotypic plasticity of hairiness, leaf epidermal traits such as stomatal type, subsidiary cell arrangement, and cuticular features are generally less plastic than indumentum characters and have proven taxonomically informative in Rubiaceae and other angiosperms. Before the advent of molecular techniques, comparative studies of morphological and anatomical characters were fundamental in plant systematics, helping to elucidate plant diversity, evolution, and phylogeny (Endress *et al*., 2000; Janaćković *et al*., 2019). Anatomical features in particular, have proven particularly valuable in resolving identification challenges and clarifying taxonomic relationships (Metcalfe & Chalk, 1957; Karanović *et al*., 2015). The taxonomic significance of anatomical characters has been well documented in many plant groups, including the Rubiaceae (Piesschaert *et al*., 2001; Moraes *et al.,* 2009; Moraes *et al*., 2020; Poosongsee *et al*., 2025). However, anatomical studies of *Pavetta* remain limited. One of the few published studies since 1986 was conducted by Herman *et al.* (1986), who examined the petiole and leaf blade anatomy

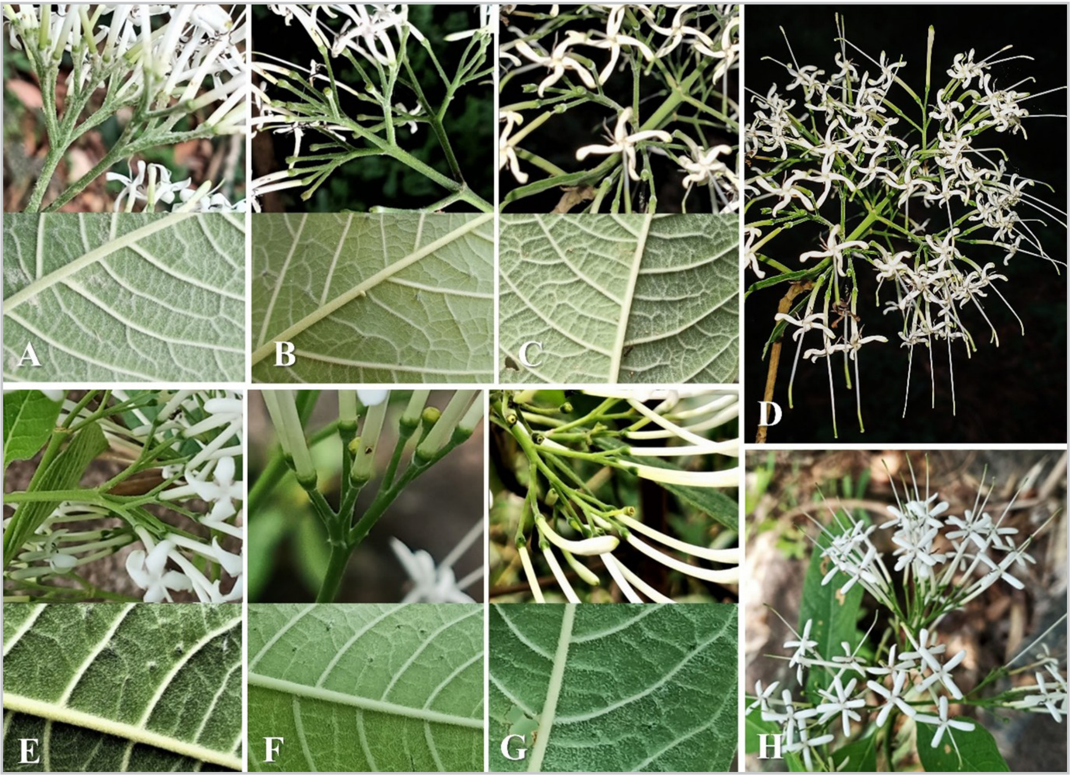

FIGURE 1. Inflorescence and lower leaf surface of *Pavetta tomentosa*: A–D. *P. tomentosa* var. *tomentosa* from the northern part of Thailand, Chiang Mai (T-CM); E–H. *P. tomentosa* cf. var. *glabrescens* from the southern part of Thailand, Songkhla (G-SKL).

of southern African *Pavetta* species. They reported several diagnostic features of the leaf blade with potential taxonomic significance, including the position of stomata, cuticle texture around stomata, structure of the leaf margin, number of palisade parenchyma layers, shape of the main vein, and presence or absence of non-glandular hairs.

For Thai species, Thangthong (2005) examined the leaf anatomy of eight *Pavetta* species, including *P. tomentosa* var. *tomentosa*, as part of his thesis. The results showed that anatomical characters were useful for species identification. However, the study did not compare the leaf anatomy of the two varieties of *P. tomentosa*, which could be useful for their taxonomic clarification. Therefore, the present study aims to compare the leaf epidermal characteristics of the two varieties to evaluate whether they should be treated as a single species.

MATERIALS AND METHODS

Plant materials

Field observations in Thailand were carried out to collect plant materials of *P. tomentosa* during its flowering period (April–November 2023). Species and variety identifications followed the key of Chantaranothai (2021). Voucher specimens were prepared and deposited in the KKU herbarium. Mature fresh leaves were collected from at least three representative individuals per population, whenever possible, covering a range of degrees of leaf hairiness for anatomical comparison. In some cases, samples were obtained from a single individual due to lack of available material. The population code and sample code as well as voucher specimens information are present in Table 1.

Leaf epidermal study

Leaf epidermal samples were prepared from the leaf blade using the epidermal peeling technique following Lersten & Curtis (2001). Mesophyll tissue was carefully removed with a razor blade, leaving only the adaxial and abaxial surfaces of epidermal layers. The epidermal tissues were stained with 1% aqueous safranin O and dehydrated through an ethanol series (50, 70, 95 and 100%), each step lasting 5 min. Samples were then transferred to a 1:1 (v/v) mixture of absolute alcohol and xylene for 10 min, followed by immersion in pure xylene for 15 min. Finally, the

TABLE 1. Sampling details of *P. tomentosa* individuals from Thailand included in this study.

No.	Population code	Taxa	Sample code	Location (habitat)	Voucher specimens
1	T-CM	*P. tomentosa* var. *tomentosa*	INT1	Chiang Mai (Along the road side at high altitude)	*S. Sookcharoen 18* (KKU)
			INT4		*S. Sookcharoen 21* (KKU)
			INT5		*S. Sookcharoen 22* (KKU)
2	G-SKL	*P. tomentosa* cf. var. *glabrescens*	TON1	Songkhla (On the rocky area near the waterfall)	*S. Sookcharoen 1* (KKU)
			TON2		*S. Sookcharoen 2* (KKU)
			TON3		*S. Sookcharoen 3* (KKU)
			TON4		*S. Sookcharoen 4* (KKU)
			TON5		*S. Sookcharoen 5* (KKU)
			TON6		*S. Sookcharoen 6* (KKU)
3	TG-PCB	*P. tomentosa* cf. var. *glabrescens*	NN7	Phetchabun (Along the nature trail in the mixed deciduous forest)	*S. Sookcharoen 98* (KKU)
			NN16		*S. Sookcharoen 105* (KKU)
4	TG-BK	*P. tomentosa* var. *glabrescens*	PN	Bueng Kan (On the rocky area near the waterfall)	*P. Chantaranothai et al. 19-19* (KKU)

samples were permanently mounted on glass slides using DePeX mounting medium and examined under a compound light microscope (Olympus CH3, Optical Co., Ltd.). Adaxial and abaxial epidermal features, including epidermal cell shape, anticlinal wall pattern, stomatal type and trichome type, were investigated.

RESULTS

Overall, the leaf epidermal characters were highly similar among all examined individuals of both taxa. Our results indicate that representative individuals of var. *tomentosa* share all examined characters, including epidermal cell shape, anticlinal wall pattern, and trichome type and length, with all or at least some representative individuals of var. *glabrescens*. For the different characters between the two taxa, no consistent qualitative or quantitative differences were observed among representative individuals, as the characters show overlap and intermixing between representatives of the two varieties. The shared and overlapping characters, together with observed variation in some individuals, are described below. A summary of the anatomical comparison of the leaf epidermis between representative individuals of the two *P. tomentosa* varieties is provided in Table 2.

Adaxial leaf epidermis

Two epidermal cell shapes were observed in all examined individuals of both taxa. In *P. tomentosa* var. *tomentosa*, one individual (INT1) had irregular cells with undulate anticlinal walls (Fig. 3B), whereas the other two individuals (INT4 and INT5) exhibited jigsaw puzzle-like (Fig. 3A) intermixed with irregular shape cells. Similarly, the four *P. tomentosa* cf. var. *glabrescens* individuals from G-SKL (TON1, TON2, TON4 and TON5) showed irregular shaped cells with undulate to slightly sinuous anticlinal walls (Fig. 3D), while the individuals from G-SKL (TON3) exhibited jigsaw puzzle-like shaped cells. The var. *glabrescens* individual from TG-BK also showed irregularly shaped cells with undulate anticlinal walls (Fig. 3F). Non-glandular, unicellular trichomes were present in all individuals (Fig. 2), except for INT5 of var. *tomentosa*, which bare non-glandular, multicellular trichomes. In all individuals, trichomes were conical (Figs. 2A–B, 2D and 2F) or filiform (Fig. 2C), with lengths ranging from 10 to 450 µm. No stomata were found on the adaxial surface.

Abaxial leaf epidermis

As on the adaxial surface, two epidermal cell shapes were also observed on the abaxial surface. Irregular cells with undulate anticlinal walls occurred in some representatives of both taxa, including var. *tomentosa* (INT1) (Fig. 5A), cf. var. *glabrescens* (TON4, TON5 and TON6) and var. *glabrescens* (PN1) (Fig. 5D). In contrast, the remaining individuals displayed jigsaw puzzle-like epidermal cells with sinuous anticlinal walls, including var. *tomentosa* (INT4), cf. var. *glabrescens* (TON3, NN7 and NN16) (Figs. 5B–C). While, the intermixed of both irregular and jigsaw puzzle-like can be found in var. *tomentosa*

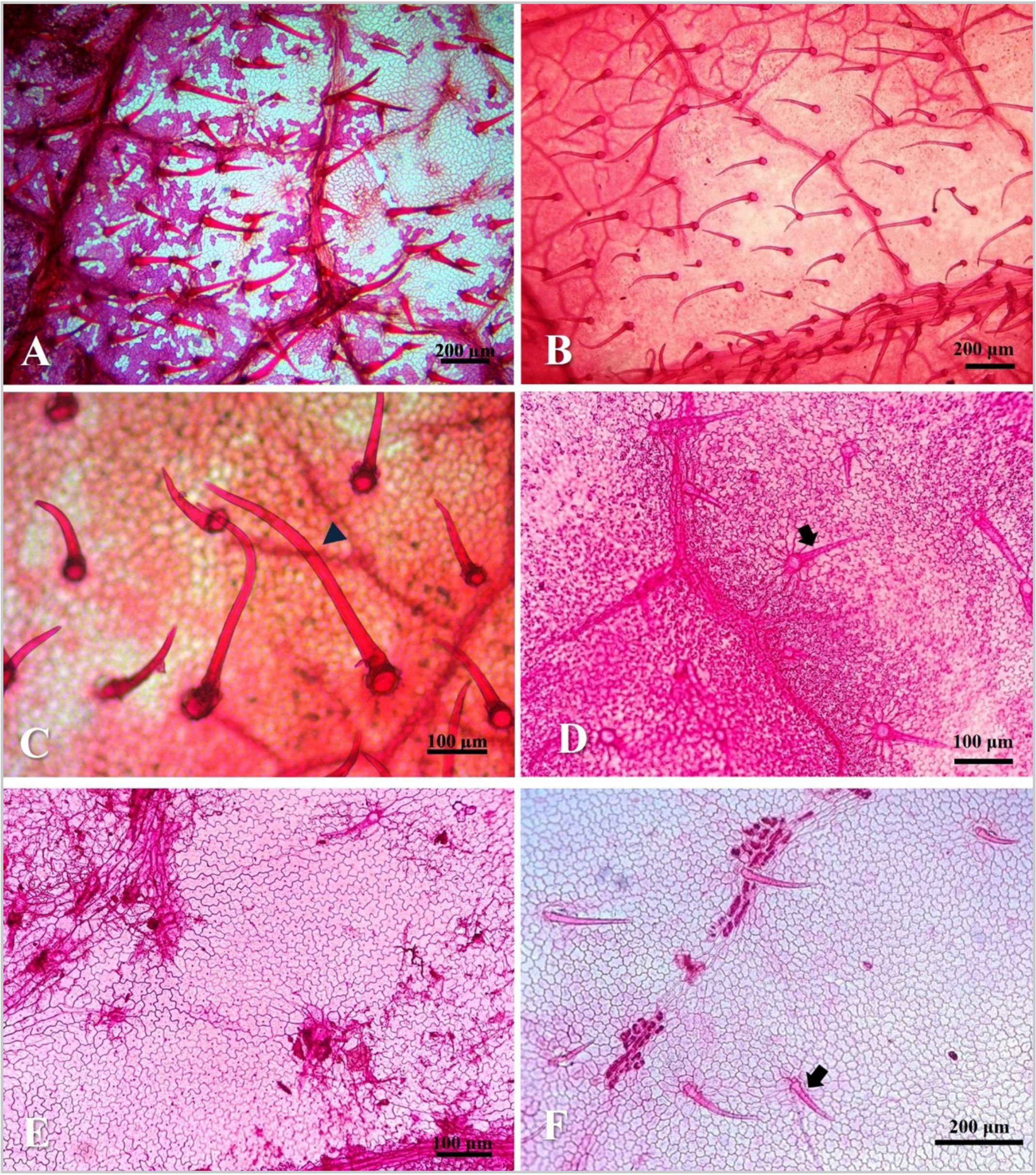

FIGURE 2. Adaxial surfaces of leaf epidermis under LM of *Pavetta tomentosa*: A. var. *tomentosa* from T-CM population; B–C. cf. var. *glabrescens* from G-SKL population; D–E. cf. var. *glabrescens* from TG-PCB population; F. var. *glabrescens* from TG-BK population. Black arrowheads indicate non-glandular, unicellular, filiform trichomes; black arrows indicate non-glandular, unicellular, conical trichomes.

TABLE 2. Anatomical comparison of the leaf epidermis among representative individuals of the two *P. tomentosa* varieties.

Population code	Taxa	Sample code	Epidermal cell shape		Anticlinal wall patterns		Trichome type		Trichome length (µm)	
			Ads	**Abs**	**Ads**	**Abs**	**Ads**	**Abs**	**Ads**	**Abs**
T-CM	*P. tomentosa* var. *tomentosa*	INT1	Irr	Irr	Undulate	Undulate	NUC	NMF	70–270	350–400
		INT4	Irr, Jig	Jig	Undulate to sinuous	Undulate to sinuous	NUC	NMF	20–320	180–400
		INT5	Irr, Jig	Irr, Jig	Undulate to sinuous	Undulate to sinuous	NMC	NMF	20–300	200–600
G-SKL	*P. tomentosa* cf. var. *glabrescens*	TON1	Irr	Irr, Jig	Undulate	Undulate to sinuous	NUC	NMF	10–200	300–500
		TON2	Irr	Irr, Jig	Undulate	Undulate to sinuous	NUC	NMF	50–150	400–450
		TON3	Jig	Jig	Sinuous	Sinuous	NUC	NUF	50–250	180–300
		TON4	Irr	Irr	Undulate	Undulate	NUF	NUF	120–450	300–400
		TON5	Irr	Irr	Undulate to slightly sinuous	Undulate	NUF	NUF	50–150	400–450
		TON6	Jig	Irr	Undulate to sinuous	Undulate	NUF	NUF	100–400	300–500
TG-PCB	*P. tomentosa* cf. var. *glabrescens*	NN7	Jig	Jig	Sinuous	Sinuous	NUC	NUF	50–150	200–600
		NN16	Jig	Jig	Sinuous	Sinuous	NUC	NMF	20–100	100–400
TG-BK	*P. tomentosa* var. *glabrescens*	PN1	Irr	Irr	Undulate	Undulate	NUC	NUF	100–200	120–200

Abbreviations: Ads = Adaxial surface; Abs = Abaxial surface; Irr = Irregular shape; Jig = Jigsaw puzzle-like shape; NMC = Non-glandular multicellular, conical trichomes; NMF = Non-glandular, multicellular, filiform trichomes; NUC = Non-glandular, unicellular, conical trichomes; NUF = Non-glandular, unicellular, filiform trichomes.

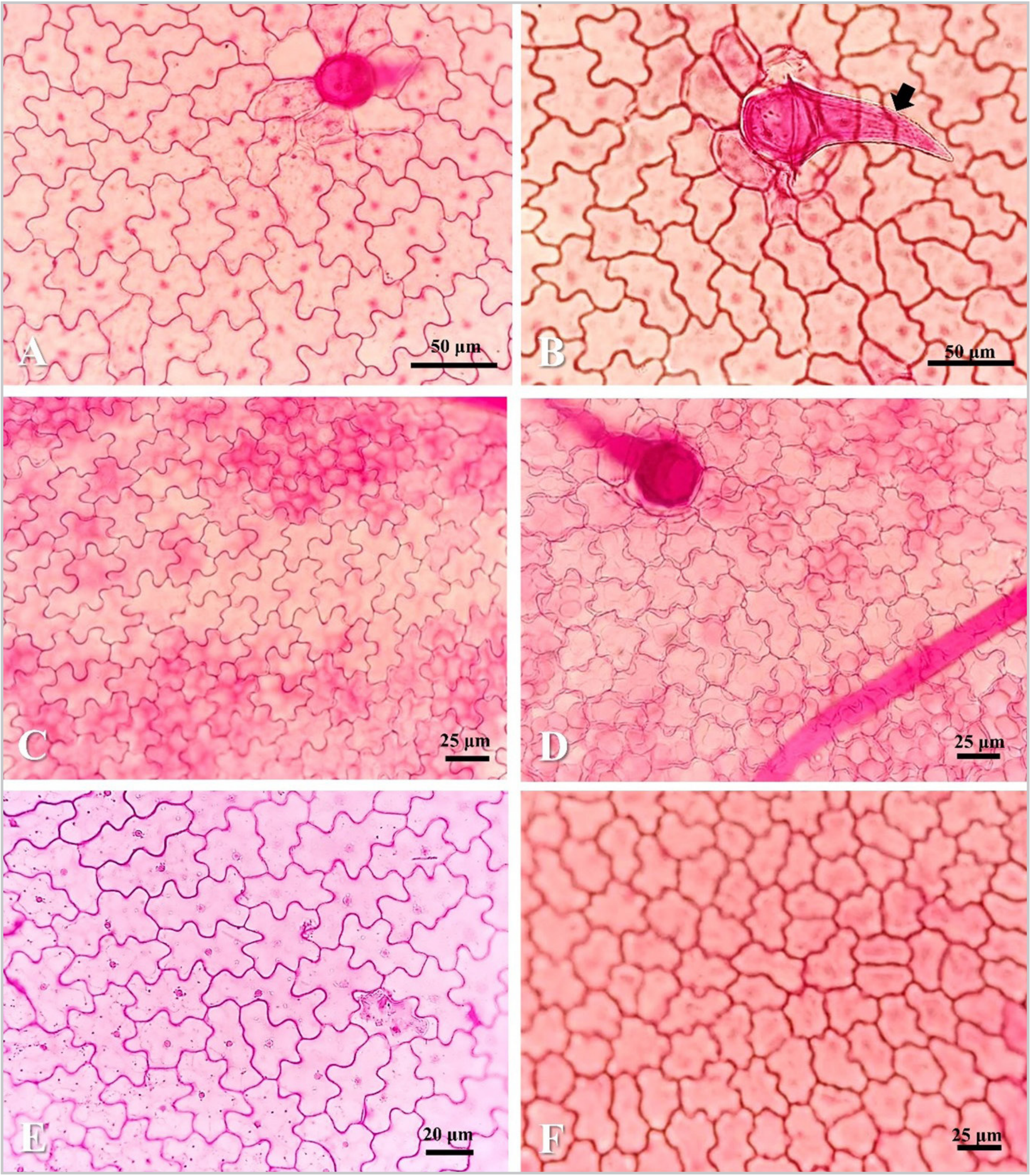

FIGURE 3. Adaxial surfaces of leaf epidermis under LM of *Pavetta tomentosa*: A–B. var. *tomentosa* from T-CM population; C–D. cf. var. *glabrescens* from G-SKL population; E. cf. var. *glabrescens* from TG-PCB population; F. var. *glabrescens* from TG-BK population. A. depict jigsaw puzzle-like intermixed with irregular shaped epidermal cells; C. & E. depict jigsaw puzzle-like shaped epidermal cells; B., D. & F. depict irregular shaped epidermal cells. Black arrows indicate non-glandular, unicellular, conical trichome with protuberances.

(INT5), cf. var. *glabrescens* (TON1 and TON2). Non-glandular, multicellular, filiform trichomes were present in all individuals of *P. tomentosa* var. *tomentosa* (Figs. 4A–B), and also in some *P. tomentosa* cf. var. *glabrescens* individuals from G-SKL (TON1 and TON2) (Fig. 4C) and TG-PCB (NN16). In contrast, the remaining cf. var. *glabrescens* individuals, including one from TG-PCB (NN7) (Figs. 4D–E) and four from G-SKL (TON3, TON4, TON5 and TON6), had non-glandular, unicellular, filiform trichomes, similar to those in *P. tomentosa* var. *glabrescens* from TG-BK (Fig. 4F). Trichomes varied in length and were mostly longer than those on the adaxial surface, ranging from 100 to 600 μm. Paracytic stomata were present in all individuals of both taxa (Fig. 5).

DISCUSSION

According to Thangthong (2005), the leaf epidermis of *P. tomentosa* was described only for representatives of var. *tomentosa*. In the present study, by examining additional individuals of var. *tomentosa* and including representatives of *P. tomentosa* cf. var. *glabrescens* and var. *glabrescens*, more detailed leaf anatomical characters were observed and described beyond those reported in Thangthong (2005). Based on his work, the adaxial surface of the leaf epidermis was characterised by irregularly shaped cells with undulate anticlinal walls (described as jigsaw puzzle-like in the present study), whereas the abaxial surface was irregular cells with slightly sinuous anticlinal walls. The present study revealed additional variation, with epidermal cells exhibiting both irregular and jigsaw puzzle-like shapes. Anticlinal wall patterns varied more widely, ranging from undulate to sinuous. As in Thangthong (2005), paracytic stomata was observed only on the abaxial surface. Non-glandular trichomes, either unicellular or multicellular uniseriate (2–6 cells), were also reported in Thangthong's study. In the present study, similar trichome types were observed, occurring in both conical and filiform shapes. Trichome length was also documented, ranging from 10 to 600 μm. Notably, the ultrastructure of the trichome surface showed protuberances, which are normally visible only under SEM but were observable through LM in one individual from the T-CM population (Fig. 3B). A similar feature was also reported in the leaf anatomy of some southern African *Pavetta* species (Herman *et al.*, 1986).

Apart from the difference in hairiness on the lower leaf surfaces among the studied individuals of *P. tomentosa*, their leaf epidermis was very similar. This included the shape and anticlinal wall pattern of epidermal cells, the type and length of trichomes, and the type and position of stomata. Although some variation in these characters was observed, it was not enough to clearly separate the two taxa. These results show slight variation and overlap in anatomical characters, which is consistent with the morphological similarity in populations of the two varieties of *P. tomentosa*. Morphological variation is often caused by phenotypic plasticity, a natural phenomenon referring to environmentally

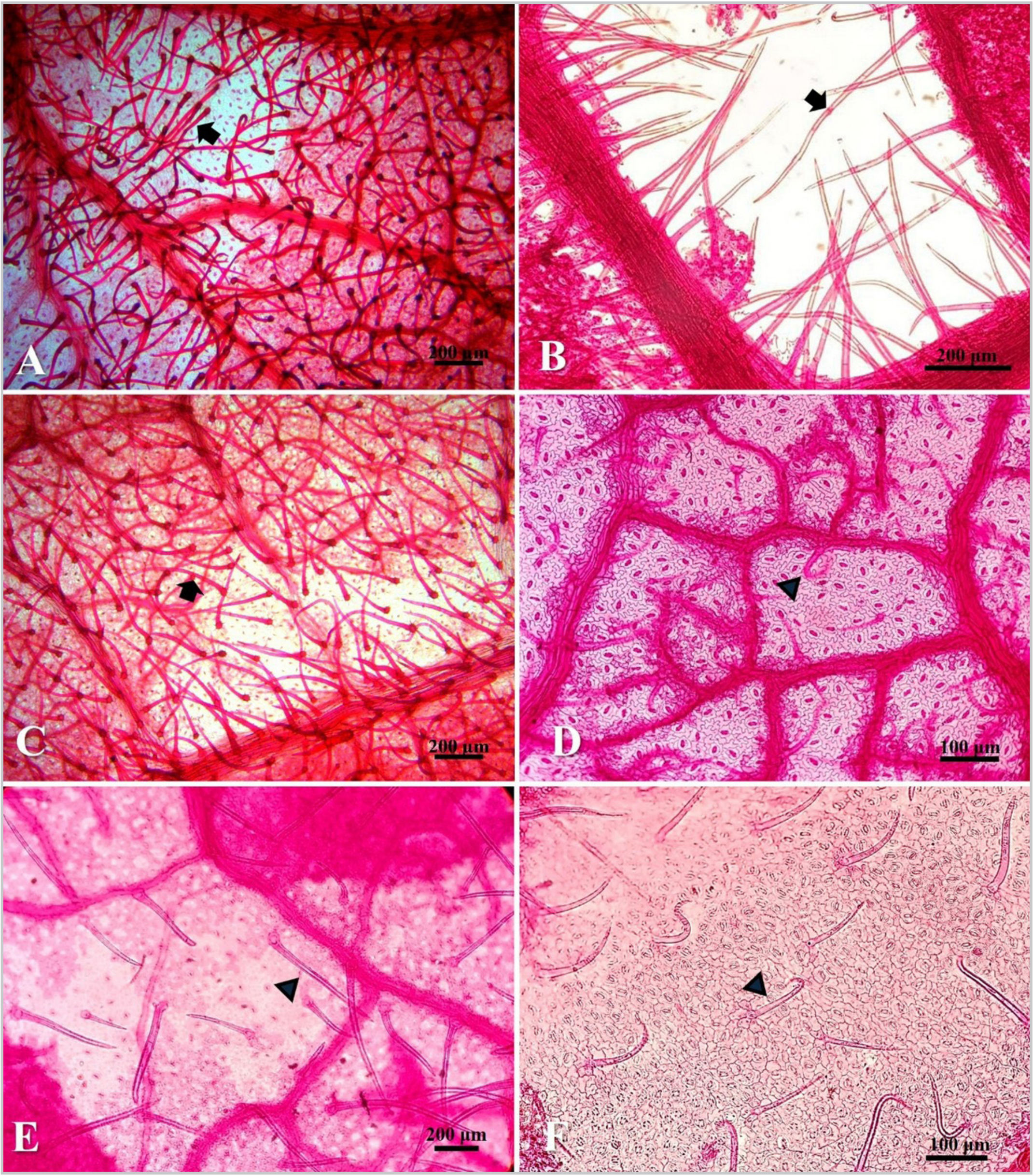

FIGURE 4. Abaxial surfaces of leaf epidermis under LM of *Pavetta tomentosa*: A–B. var. *tomentosa* from T-CM population; C. cf. var. *glabrescens* from G-SKL population; D–E. cf. var. *glabrescens* from TG-PCB population; F. var. *glabrescens* from TG-BK population. Black arrow indicate non-glandular, multicellular, filiform trichomes; black arrowheads indicate non-glandular, unicellular, filiform trichomes.

induced variation that can affect the morphological, physiological and behavioural traits of an organism (Sommer, 2020). It is also considered a reflection of adaptive evolution (Franks *et al.*, 2014; Wang & Zhou, 2021; Wang *et al.*, 2021). In plants, many studies have shown the influence of environmental factors on morphology. For example, Li *et al.* (2015) studied the relationship between leaf traits of Chinese jujube (*Ziziphus jujuba* Mill.) and annual temperature and precipitation. They found that several leaf features, such as shape and size, were correlated with local precipitation and temperature (Li *et al.*, 2015).

In the case of hairs, they play an important role in biotic defenses from herbivory and fungal infections and against abiotic stress such as drought, heat, freezing, excess light and UV radiation (Hauser, 2014). Ramesar-Fortner *et al.* (1995) grew individuals of four Arctic *Festuca* species under different temperature and water conditions and found that leaf hair density in each species varied with the environment. Rogers (1979) studied the antibiosis resistance of *Phaseolus vulgaris* L. to the bean fly, *Ophiomyia phaseoli* (Tryon). The number of viable eggs per plant was significantly correlated with leaf hairiness, stem diameter and internode length. Low egg counts were associated with high leaf hair density, thin stems and long internodes. Skelton *et al.* (2012) investigated whether leaf pubescence in Cape Proteaceae functions as a xeromorphic trait or as protection against radiation. They found a positive association between leaf hairiness and temperature, suggesting that leaf pubescence is more likely to protect against excessive sunlight and heat than to serve as an adaptation to drought. Similarly, the variation in hairiness, ranging from glabrescent to densely tomentose, observed among *P. tomentosa* populations may reflect responses to environmental factors such as sunlight, temperature, soil composition or other local conditions. For example, the T-CM population represents *P. tomentosa* var. *tomentosa*, while the G-SKL population represents *P. tomentosa* cf. var. *glabrescens*. These two populations are geographically distant, with T-CM located in northern Thailand and G-SKL in the south. The T-CM individuals were found along roadsides in higher-latitude areas with cooler temperatures, whereas the G-SKL individuals were collected from rocky sites near a waterfall. These different environmental conditions may influence leaf and inflorescence traits, especially hairiness. The leaves and inflorescences of T-CM individuals were densely tomentose, consistent with the diagnostic characters of var. *tomentosa* (Figs. 1A–C) described in previous studies. In contrast, G-SKL individuals also had densely tomentose leaves, similar to var. *tomentosa*, but their inflorescences were sparsely puberulous, as in var. *glabrescens* (Figs. 1E–G). In addition to environmental influences, leaf hair density is often affected by genetic variation within species (Zaiter *et al.*, 1990; Ågren & Schemske, 1992). Another minor difference between these two populations is the twisting of corolla lobes in the T-CM population (Fig. 1D), whereas in the G-SKL population, the lobes are either straight or curved (Fig. 1H).

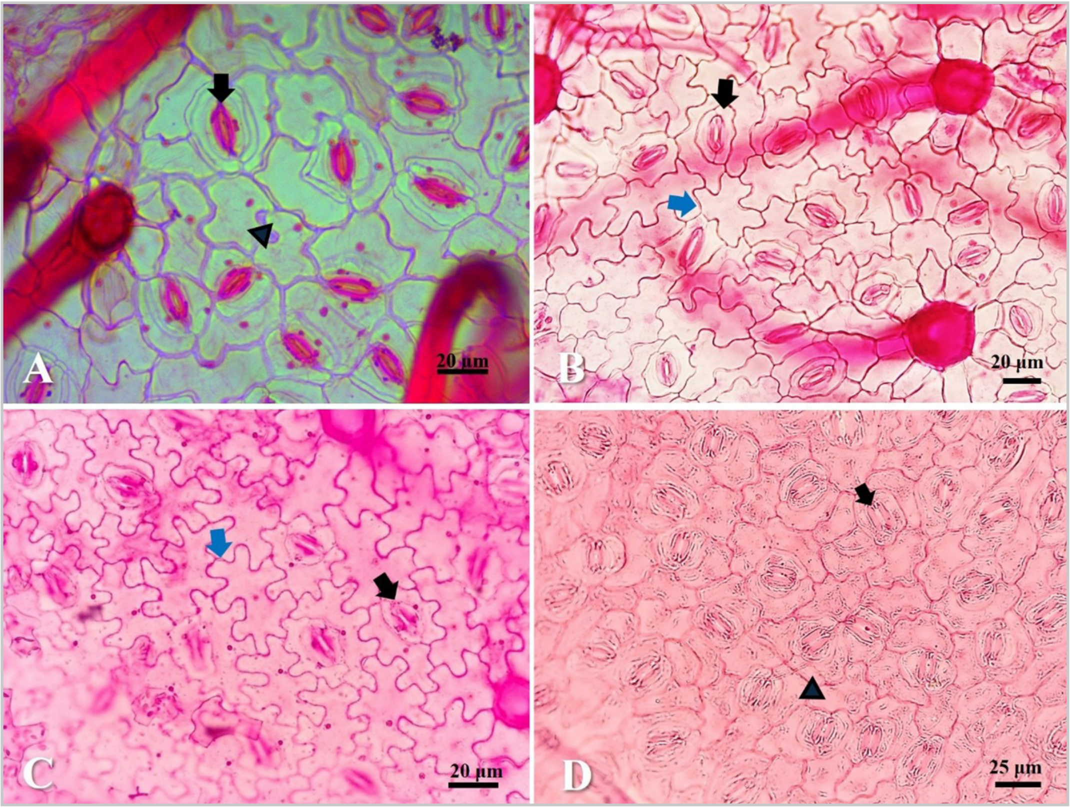

FIGURE 5. Abaxial surfaces of leaf epidermis under LM of *Pavetta tomentosa*: A. var. *tomentosa* from T-CM population; B. cf. var. *glabrescens* from G-SKL population; C. cf. var. *glabrescens* from TG-PCB population; D. var. *glabrescens* TG-BK population. Black arrows indicate paracytic stomata; black arrowheads indicate irregular shaped epidermal cells; blue arrows indicate jigsaw puzzle-like shaped epidermal cells.

CONCLUSION

Based on leaf epidermal characters, the two varieties of *P. tomentosa* showed similar or overlapping characters in all individuals examined. This finding therefore supports merging the two varieties. However, as the present study is an investigation based only on leaf epidermal anatomical evidence, additional data from other anatomical studies (*e.g.* transverse sections of the leaf blade and petiole), as well as molecular data will be necessary to confirm and support the treatment of the two varieties as a single species without recognised varieties. The lack of anatomical differences observed in this study leads to the hypothesis for our subsequent population genetic study that examining genetic diversity and genetic structure may reveal that the populations of the two varieties are not clearly differentiated. If confirmed, this would provide additional evidence for merging the two varieties.

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