Turczaninowia 28, 2: 101–111 (2025)
https://www.doi.org/10.14258/turczaninowia.28.2.10
http://turczaninowia.asu.ru

ISSN 1560–7259 (print edition)
TURCZANINOWIA
ISSN 1560–7267 (online edition)

УДК 582.948:581.458(94)

Micromorphological analysis of leaf trichomes in Australian species of Boraginales

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Keywords: Boraginales, distribution, glandular hairs, leaf morphology, scanning electron microscopy.

Summary. This study investigates the leaf trichome morphology of 27 species from 23 genera across seven families of Boraginales in Australia using scanning electron microscopy (SEM). We documented a wide diversity of trichome types, including glandular, non-glandular, bifurcate, and trifurcate forms. Trichome distribution varied considerably, ranging from sparse to densely packed across leaf surfaces. While some trichomes lacked surface ornamentation, most exhibited distinct protrusions, such as round, oval, or conical structures. Additionally, while filling a gap in the understanding of Boraginales leaf trichomes, this study reveals significant structural diversity and functional traits in Australian species. These traits offer a promising taxonomic tool for resolving classification ambiguities within the order.

Микроморфологический анализ листовых трихом у австралийских видов порядка Boraginales

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Ключевые слова: железистые волоски, морфология листьев, распространение, сканирующий электронный микроскоп, Boraginales.

Аннотация. В данном исследовании изучена морфология листовых трихом у 27 видов из 23 родов, относящихся к семи семействам порядка Boraginales в Австралии, с использованием сканирующей электронной микроскопии (СЭМ). Мы обнаружили значительное разнообразие типов трихом, включая железистые, нежелезистые, двураздельные и трехраздельные формы. Распределение трихом существенно варьировалось – от редкого до плотного покрытия поверхности листьев. Хотя некоторые трихомы не имели поверхностного орнамента, у большинства наблюдались выраженные выступы, такие как округлые, овальные или конические структуры. Данное исследование не только восполняет пробел в изучении листовых трихом Boraginales, но и выявляет значительное структурное разнообразие и функциональные особенности у австралийских видов. Эти признаки представляют собой перспективный таксономический инструмент для разрешения классификационных неясностей в пределах порядка.

Поступило в редакцию 11.04.2025
Принято к публикации 12.05.2025

Submitted 11.04.2025
Accepted 12.05.2025

Introduction

Australia, renowned for its unique biogeographical isolation and extreme environmental conditions, harbors a remarkable array of plant species adapted to diverse habitats (Lambers et al., 2020). The continent's vast expanse encompasses a mosaic of ecosystems ranging from arid deserts to lush rainforests, each characterized by distinct climatic regimes and soil compositions (Bowman et al., 2011). This environmental heterogeneity has fueled the evolution of a rich botanical diversity, with numerous endemic taxa exhibiting specialized morphological and physiological adaptations (Hopper, 2009).

Boraginales is an order of flowering plants comprising species with often bristly or hairy vegetative surfaces, including the well-known family Boraginaceae (Weigend et al., 2016). These species encompass a wide range of life forms, from ephemeral annuals to woody perennials, and occupy varied habitats spanning coastal dunes, montane forests, and arid outback regions (Thiele, al-Shehbaz, 2017). The taxonomy of Boraginales has been recently revised, with molecular phylogenetic studies (Chacón et al., 2016) redefining Boraginaceae s. str. and recognizing several segregate families. A comprehensive familial classification of Boraginales was proposed by Luebert et al. (2016), who recognized 11 distinct families, reflecting the order's morphological and ecological diversity. Although phylogenetic studies using lineage-specific and Angiosperms353 loci indicate that Namaceae can be integrated into Hydrophyllaceae and Lennoaceae is nested in Ehretiaceae (Cohen, 2025). Australia hosts more than 50 species of Boraginales, including 30 endemics and several naturalized introductions (Dimon, Renner, 2017).

Trichomes in Boraginales exhibit considerable diversity in form and function. Cronquist (1984) describes the family Boraginaceae as typically possessing stiff, bristly hairs, often with a roughened or barbed surface. Popov (1974) notes that trichomes in Boraginaceae can be either unicellular or multicellular, with some species exhibiting glandular hairs secreting aromatic compounds. Stanley and Ross (2002) highlight the presence of both simple and stellate trichomes in some genera, emphasizing their taxonomic significance. Starchenko (1991) briefly mentions the prevalence of coarse, scabrid trichomes in Far Eastern species. Verdcourt (1991) reports that tropical African Boraginaceae often feature glandular and non-glandular trichomes, sometimes aiding in water retention. Zhu et al. (1995) describe trichomes in Chinese Boraginaceae as variable, including both stiff, non-glandular types and softer, glandular forms, often contributing to species identification.

Leaf trichomes, specialized epidermal structures, play multifaceted roles in plant-environment interactions, including defense against herbivory, regulation of water loss, and modulation of light penetration (Wagner et al., 2014). The diverse forms and functions of trichomes have been extensively documented in various plant taxa worldwide, revealing intriguing patterns of adaptation and evolutionary convergence (Serna, Martin, 2006). Investigation of trichomes and their different characters play an essential role in identifying the relationships between angiosperm species, including the order Boraginales and the Boraginaceae family (Ghahremaninejad, 2004; Beilstein et al., 2006; Steyn, Van Wyk, 2021). Despite their ecological importance, comprehensive morphological analyses of trichomes within Boraginales remain scarce, necessitating pioneering studies to enhance our understanding of plant-environment interactions.

This study presents the first detailed scanning electron microscopy (SEM) investigation of leaf trichome diversity across 27 Australian Boraginales species (23 genera, 7 families), including native and non-native taxa. The research aims to characterize novel trichome morphologies and identify unique trichome characteristics to resolve taxonomic ambiguities and improve Boraginales classification. Additionally, the high diversity of leaf trichomes in the studied species highlights the high potential of Australia for the presence of species of this order.

Material and methods

Herbarium specimens representing 27 species of the order Boraginales were selected for analysis. The specimens were sourced from the herbaria of Muséum National d'Histoire Naturelle (P!) in Paris and the Naturhistorisches Museum (W!) in Vienna. Leaf samples with trichomes were carefully excised from the dried herbarium sheets and attached to SEM stubs with conductive adhesive tabs. Both adaxial and abaxial surfaces of the leaves were prepared for imaging. The samples were then coated with a gold-palladium alloy to improve conductivity and reduce charging effects during imaging. The preparation of the specimens involved gold sputtering using a HUMMER V apparatus and Imaging was conducted using a JEOL JXA 6610LV scanning electron microscope. High-resolution SEM analysis was conducted to examine the trichomes at various magnifications, capturing details such as shape, size (Short: less than 50 μm; Long: more than 50 μm), and surface texture. Multiple digital images were taken from different regions of each sample to ensure comprehensive coverage. Trichome characteristics including type (glandular or non-glandular), size, density, and distribution patterns, were documented for each species. Voucher table (Table 1) related to the information and barcode of the used specimens was also prepared. All herbarium acronyms used in this article comply with the authoritative online Index Herbariorum (Thiers, 2024).

Table 1. The voucher table of studied specimens

No.	Species	Collector and number	Barcode
1	*Amsinckia calycina* (Moris) Chater	Colin s. n.	W0107377
2	*Anchusa azurea* Mill.	Colin s. n.	W0107377
3	*Anchusa capensis* Thunb.	Colin s. n.	W0107377
4	*Borago officinalis* L.	Smaoui A. & aliis 0394	W0254115
5	*Buglossoides arvensis* (L.) I. M. Johnst.	Speta F. s. n.	W0254116
6	*Cerinthe major* L.	Grasl A. & Escobar P. 583	W0254110
7	*Coldenia procumbens* L. (Native)	E. de la Savinierre 721	W0118728
8	*Cordia myxa* L.	Karl R. s. n.	W0254097
9	*Cynoglossum amabile* Stapf et J. R. Drumm.	–	P04458113
10	*Cynoglossum creticum* Mill.	–	W0254123
11	*Echium candicans* L. f.	Vitek E. 97-15	W0254091
12	*Ehretia acuminata* R. Br. (Native)	–	W0254092
13	*Euploca strigosa* (Willd.) Diane et Hilger	–	W0254084
14	*Halgania anagalloides* Endl. (Native)	–	W0254130
15	*Halgania andromedifolia* Behr. et F. Muell. (Native)	–	W0254160
16	*Heliotropium arborescens* L.	–	W0254128
17	*Iberodes linifolia* (L.) M. Serrano, R. Carbajal et S. Ortiz	–	W0254129
18	*Lithospermum officinale* L.	Baily C. 856	W0254133
19	*Myosotis alpestris* F. W. Schmidt	Krendl F. s. n.	W0254148
20	*Myosotis australis* R. Br. (Native)	n. c. 4163	W0254067
21	*Neatostema apulum* (L.) I. M. Johnst	Escobar-Garcia s.n.	W0254048
22	*Nemophila menziesii* Hook. et Arn.	–	W0254050
23	*Pentaglottis sempervirens* (L.) Tausch ex L. H. Bailey	Riedl H. s. n.	W0254047
24	*Symphytum asperum* Lepech.	Voskanian H. T. & Vitek E. 03-1670	W0254162
25	*Trachystemon orientalis* (L.) D. Don	Aucher M. 39	W0254039
26	*Trichodesma zeylanicum* (Burm. f.) R. Br. (Native)	–	W0254025
27	*Wigandia urens* (Ruiz et Pav.) Kunth	–	W0254021

Results

A total of 27 species representing 23 genera within 7 families of the order Boraginales were examined for trichome morphology using SEM. Trichomes exhibited considerable diversity in size, shape, and structure across the sampled taxa. The majority of the species possessed trichomes, with variations observed both within and between families. Two main types of trichomes were identified among the studied species: glandular and non-glandular. Glandular trichomes were characterized by multicellular structures with glandular heads containing secretory substances, while non-glandular trichomes were typically unicellular or multicellular with pointed or branched tips. Table 2 shows the examined characteristics of the leaf trichomes of the studied species.

The results show that 74 % of the studied species have only non-glandular trichomes on their leaf surface. 14 % have both glandular and non-glandular trichomes. Only one of the studied species has only glandular trichomes. One species has bifurcate trichomes and one species has trifurcate trichomes. The distribution of trichomes on the surface of the studied species is mostly sparse and dense. Trichomes in 78 % of the studied species have surface decorations, most of these decorations are round and with a smaller percentage, oval type is observed. Also, in one species, the surface of the trichome is conical.

Table 2. Morphological characteristics of trichomes in Australian Boraginales

Family	Species	Types of Trichomes	Size	Distribution	Decoration shape	Decoration distribution
Boraginaceae	*Amsinckia calycina*	NG	L	S	Oval	S
	Anchusa azurea	NG & Tr	Sh	S	Round	VD
	Anchusa capensis	NG	Sh & L	S	Multi String	S
	Borago officinalis	NG	Sh & L	D	Oval	D
	Buglossoides arvensis	NG	Sh & L	D	Round	S
	Cerinthe major	NG	Sh	R or S	Oval	S
	Cynoglossum amabile	NG	Sh & L	VD	Round	D
	Cynoglossum creticum	NG	Sh & L	D	Round	D
	Echium candicans	NG	Sh & L	VD	Round	S
	Iberodes linifolia	NG	Sh	R		
	Lithospermum officinale	NG	Sh	VD	Round	R or S
	Myosotis alpestris	NG	Sh & L	S or D	Oval	S
	Myosotis australis	NG	Sh & L	D	Round	D
	Neatostema apulum	NG	L	R or S	Round	R
	Pentaglottis sempervirens	G & NG	Sh & L	D or VD		
	Symphytum asperum	G & NG	Sh & L	D or VD	Round	VD
	Trachystemon orientalis	NG	Sh	R		
	Trichodesma zeylanicum	NG	Sh & L	D or VD	Oval	S
Coldeniaceae	*Coldenia procumbens*	NG	Sh	R	Round	D
Cordiaceae	*Cordia myxa*	G & NG	Sh	S or D	Round	R or S
Ehretiaceae	*Ehretia acuminata*	G	Sh	R		
	Halgania anagalloides	B	Sh	S	Round	D
	Halgania andromedifolia	NG	Sh	R (adaxial) - VD (abaxial)		
Heliotropiaceae	*Euploca strigose*	NG	Sh & L	D or VD	Conical	D
	Heliotropium arborescens	G & NG	Sh & L	R or D	Round	S or D
Hydrophyllaceae	*Nemophila menziesii*	NG	Sh & L	S or D	Round	D
Namaceae	*Wigandia urens*	NG	L	VD		

Note. Abbreviations in the table are: NG – Non-glandular; G – Glandular; B – Bifurcate; Tr – Trifurcate; L – Long; Sh – Short; R – Rare; S – Sparse; – Dense; VD – Very dense.

Glandular trichomes

Among the studied species, glandular trichomes were observed in only five cases, which one is native and the rest are introduced to Australia. In *Ehretia acuminata* R. Br., the only native species in this group, in addition to the raised glandular cells, a kind of widened appendage similar to the basal part of some trichomes was observed, which lack raised trichome cell. Probably, these are a collection of secretory cells. Glandular trichome with multicellular base was also rarely observed. *Cordia myxa* L. displays unique glandular trichomes with bag-like, slightly wide cells lacking glandular activity in the end cell. *Heliotropium arborescens* L. presents rarely observed glandular trichomes with short bases. *Pentaglottis sempervirens* (L.) Tausch ex L. H. Bailey has glandular cells without a base or glandular trichomes with a short base and single cells. Glandular trichomes with a unicellular base were also rarely observed in *Symphytum asperum* Lepech. Figure 1 shows glandular trichomes in studied species.

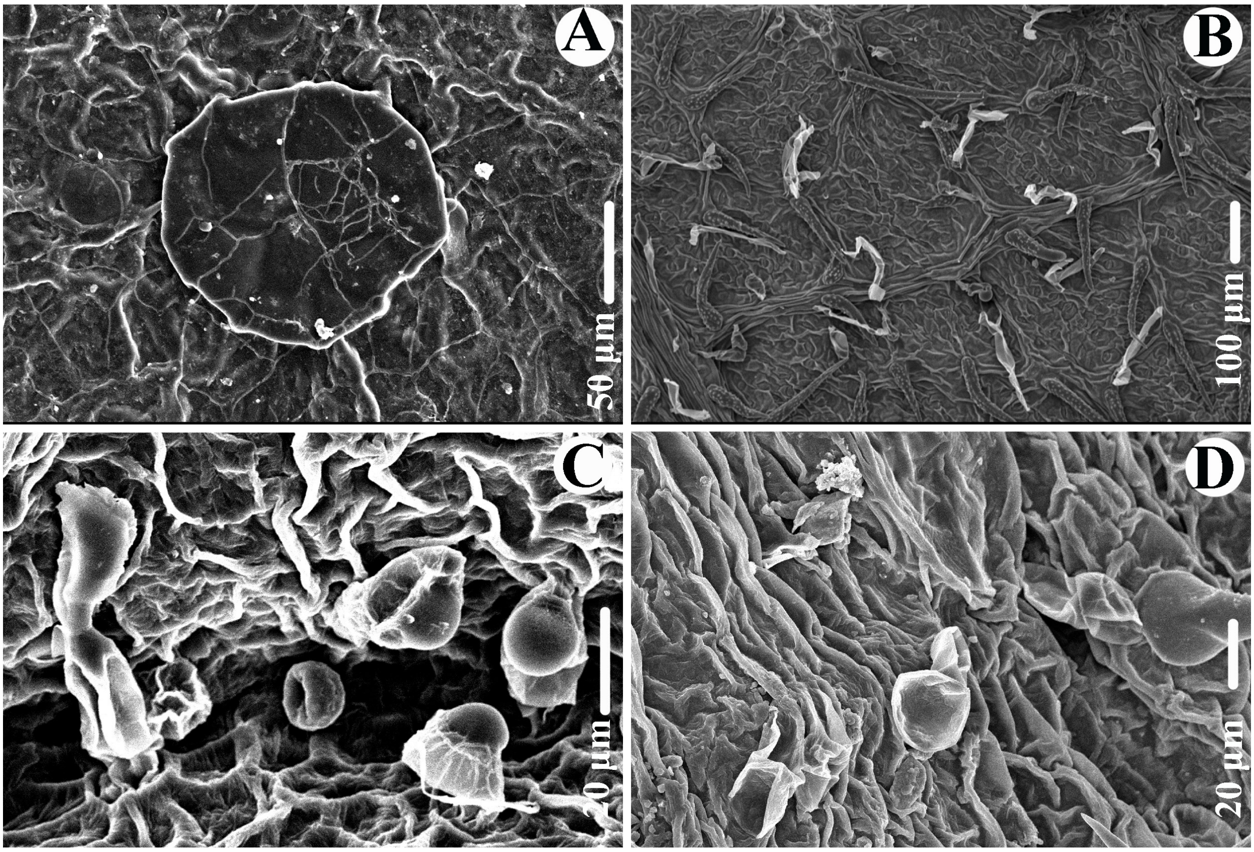

Fig. 1. Glandular trichomes in the studied species of Boraginales: A – *Ehretia acuminata*; B – *Cordia myxa*; C – *Pentaglottis sempervirens*; D – *Symphytum asperum*.

Non-glandular trichomes

Non-glandular trichomes, more abundant than glandular types, were widespread across the studied taxa. These trichomes exhibited diverse morphologies, ranging from simple unicellular hairs to complex multicellular forms, including short, long, bifurcate, trifurcate, and thorn-like types. Their density and distribution patterns varied among species. In Fig. 2, some types of non-glandular trichomes are shown.

A type of non-glandular trichome that is stronger and similar to a thorn is called thorn-like. This type of trichome was observed in some studied species, including both native and introduced species. In some cases, this type of trichome is present on the surface of the leaf along with other trichomes. For instance, in *Trichodesma zeylanicum* (Fig. 3A). In some cases, this type of trichome is the only type that covers the surface of the leaf. For example, in *Cerinthe major* L. (Fig. 3B), *Iberodes linifolia*, *Nemophila menziesii* (Fig. 3C), and *Trachystemon orientalis* (Fig. 3D).

Bifurcate and Trifurcate trichomes

Trichomes with two arms are called bifurcate and those with three arms are called trifurcate. Bifurcate type was observed in *Halgania anagalloides* (Fig. 4A), and trifurcate – in *Anchusa azurea* (Fig. 4B).

Non-glandular trichome decorations

The trichomes of most observed species have decorations on their surface. Most of them have created protrusions like a hemisphere on the surface of the trichome. Sometimes these bumps are slightly oval in shape. The distance of these protrusions from each other or in other words their density is also different in some species (Fig. 5). The trichomes of some species lack these frills. In Fig. 5, the leaf trichomes of two native species of genus *Halgania* can be seen, the trichomes of *Halgania anagalloides* have decorations, but the trichomes of the *Halgania andromedifolia* have no decorations.

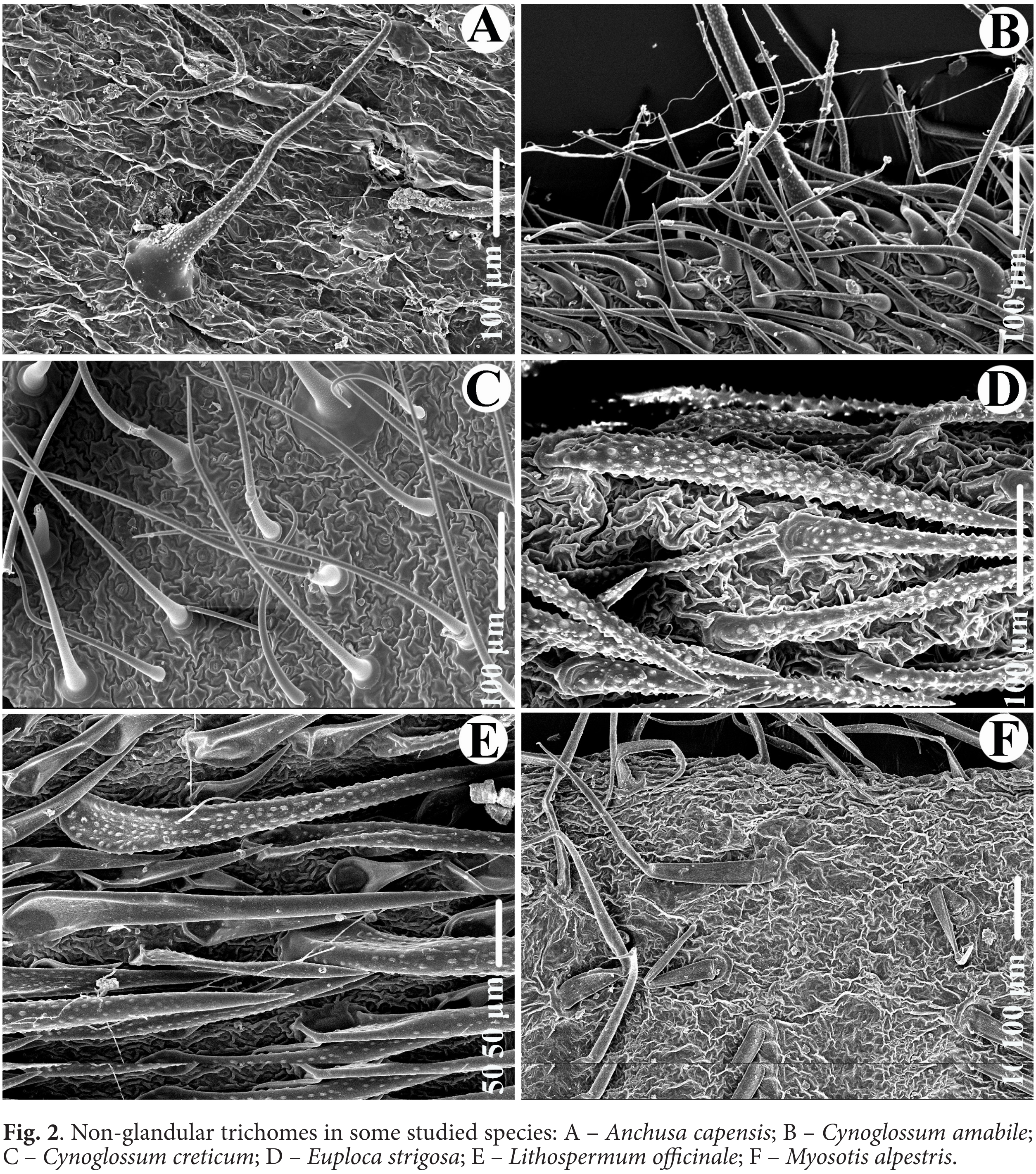

Fig. 2. Non-glandular trichomes in some studied species: A – *Anchusa capensis*; B – *Cynoglossum amabile*; C – *Cynoglossum creticum*; D – *Euploca strigosa*; E – *Lithospermum officinale*; F – *Myosotis alpestris*.

Trichome Distribution

The distribution and density of trichomes on the surface of the leaf can be seen with the naked eye most of the time. With a microscopic view, this variation is more visible in density (Fig. 6). In general, the distribution can be divided into four main types, although this division is relative, but almost all the studied species can be placed in these four parts.

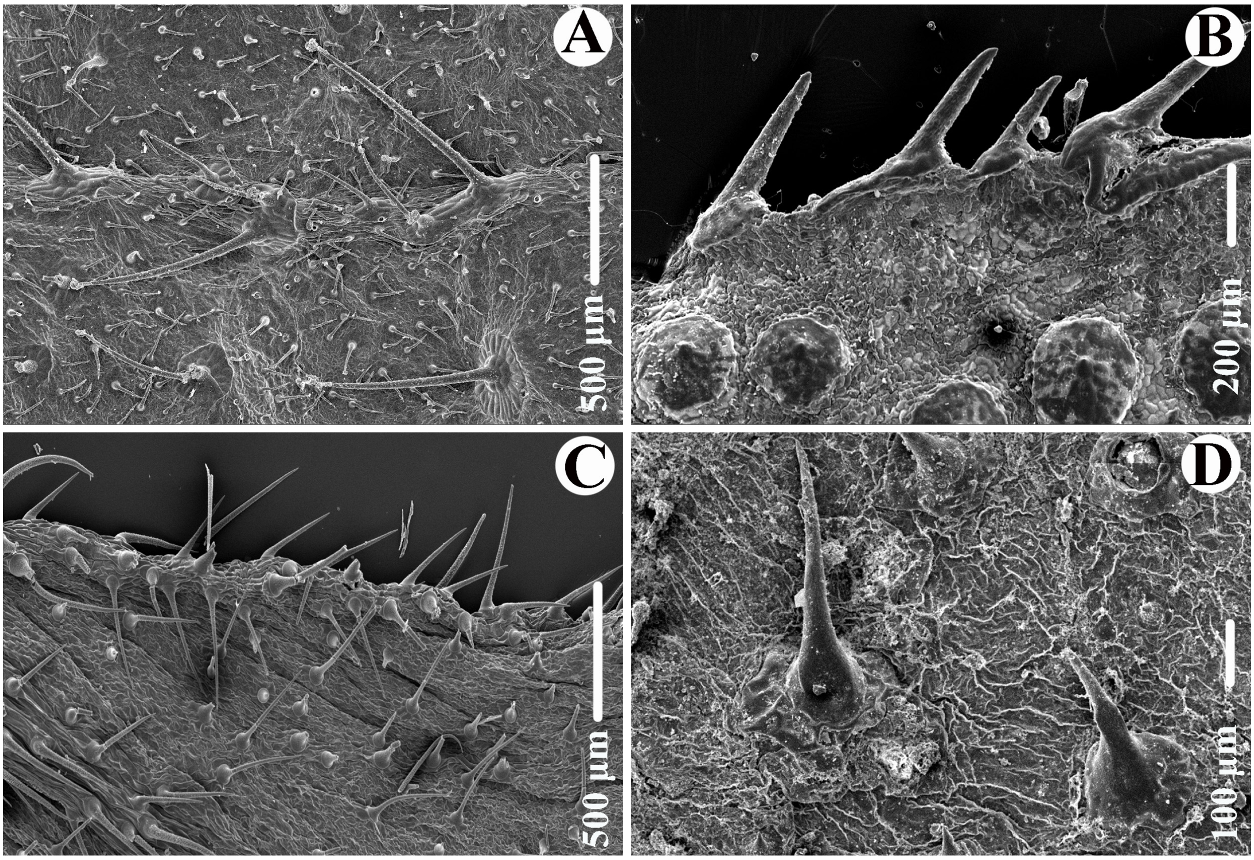

Fig. 3. Thorn-like trichomes: A – *Trichodesma zeylanicum*; B – *Cerinthe major*; C – *Nemophila menziesii*; D – *Trachystemon orientalis*.

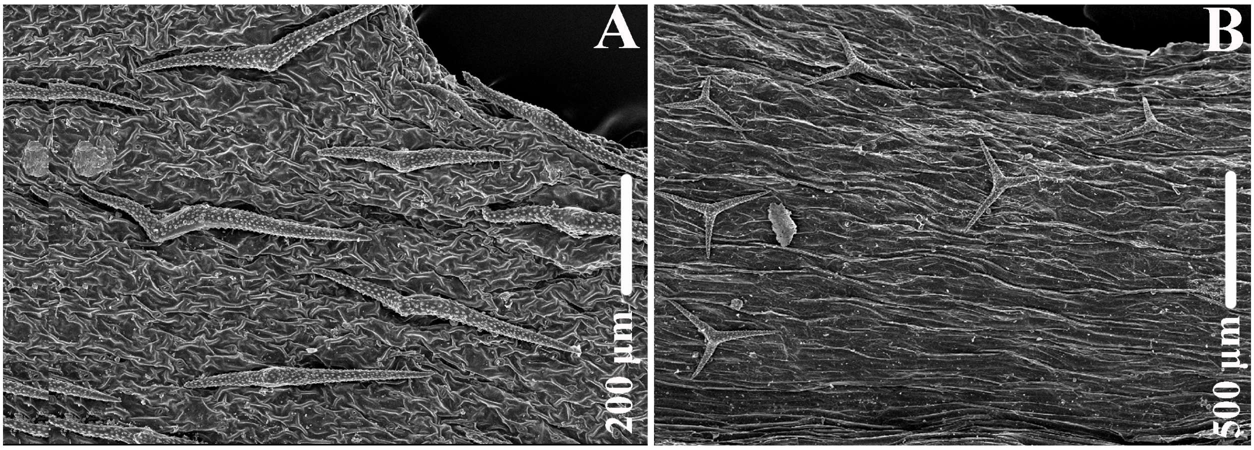

Fig. 4. Some different types of non-glandular trichomes: A – Bifurcate trichomes in *Halgania anagalloides*; B – Trifurcate trichomes in *Anchusa azurea*.

Discussion

This study underscores the critical role of scanning electron microscopy (SEM) in examining leaf trichomes among Australian species of Boraginales. The detailed morphological variation observed highlights the diagnostic value of trichomes, reinforcing their utility as reliable taxonomic tools for distinguishing and classifying closely related species. Given their structural complexity and species-specific patterns, trichomes often serve as key characters in plant taxonomy, shedding light on species boundaries and evolutionary relationships.

The findings presented here are in line with growing recognition of trichome morphology in taxonomic and evolutionary studies. For instance, trichome traits were pivotal in the description of a new species of *Nama* from Arizona, USA (Crawford, Rink, 2024). Similarly, in the genus *Cryptantha*, these traits have facilitated the recognition of three new species and supported more accurate classification within Boraginales (Rebman, Simpson, 2022). Such examples underline the consistent relevance of trichomes in delimiting taxa across geographic regions.

Despite the longstanding acknowledgment of trichome diversity in Boraginales, detailed investigations using SEM remain relatively limited. However, recent taxonomic efforts have increasingly incorporated SEM-based analysis of leaf pubescence. For example, König et al. (2015) used SEM to effectively differentiate *Cynoglossum* species in Nepal, while Dimon and Renner (2017) employed trichome morphology to support the description of a new *Cynoglossum* species and its subsequent transfer to Hackelia in Australia. A similar study used trichomes to characterize a newly described *Cynoglossum* species from Turkey (Sutorý, 2024). These studies exemplify the enhanced resolution that SEM can provide in taxonomic treatments. Research on trichomes in various Boraginales families continues to affirm their taxonomic significance. Nazari and Ghahremaninejad (2024, 2025a, b) demonstrated that trichome morphology, captured through SEM, reveals clear interspecific distinctions within Heliotropiaceae, Cordiaceae, and Ehretiaceae. Similarly, the identification of *Onosma satensis* as a new species from eastern Turkey relied heavily on microscopic trichome images as a distinguishing character (Firat, Binzet, 2021). Similar to our study, Madika and Moteetee (2022) investigated South African *Cynoglossum* trichomes, highlighting their diversity, taxonomic significance, and utility in species identification. Both studies underscore the potential of trichomes for resolving taxonomic ambiguities within Boraginales.

Additional studies further underscore the systematic relevance of trichomes. Zeraatkar et al. (2022) used SEM to reveal consistent trichome features within species that varied sufficiently between taxa to inform species delimitation and infrageneric relationships. Likewise, Troshkina (2022), in her examination of 34 taxa of *Geranium*, reported novel trichome types, reinforcing their diagnostic utility. By examining both non-native (28) and native (6) species, this study establishes a foundational comparative framework for future research. This dual focus not only broadens our understanding of trichome diversity in Australia's flora but also opens avenues for exploring adaptive traits in introduced species. Such comparisons offer valuable insights into the ecological roles and evolutionary significance of trichome variation.

In conclusion, this research advocates for the broader integration of SEM in taxonomic and phylogenetic studies within Boraginales. The detailed characterization of trichome traits presented here provides a stepping stone for future investigations, contributing to a deeper understanding of species relationships, evolutionary pathways, and biogeographic patterns. Ultimately, such studies will support the refinement of classification systems across Boraginales and related plant groups.

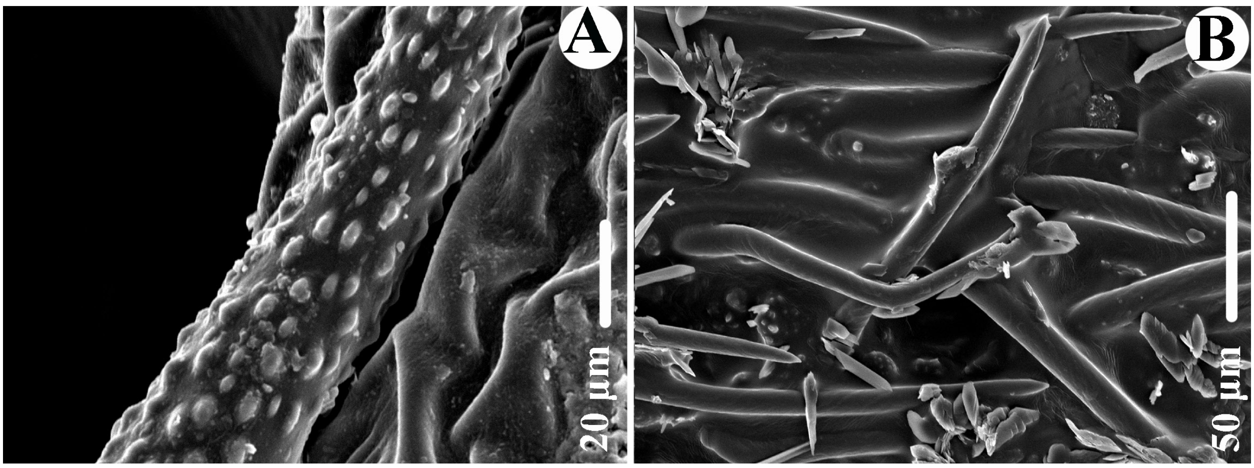

Fig. 5. The presence and absence of decorations on the leaf trichome surface: A – *Halgania anagalloides*; B – *Halgania andromedifolia*.

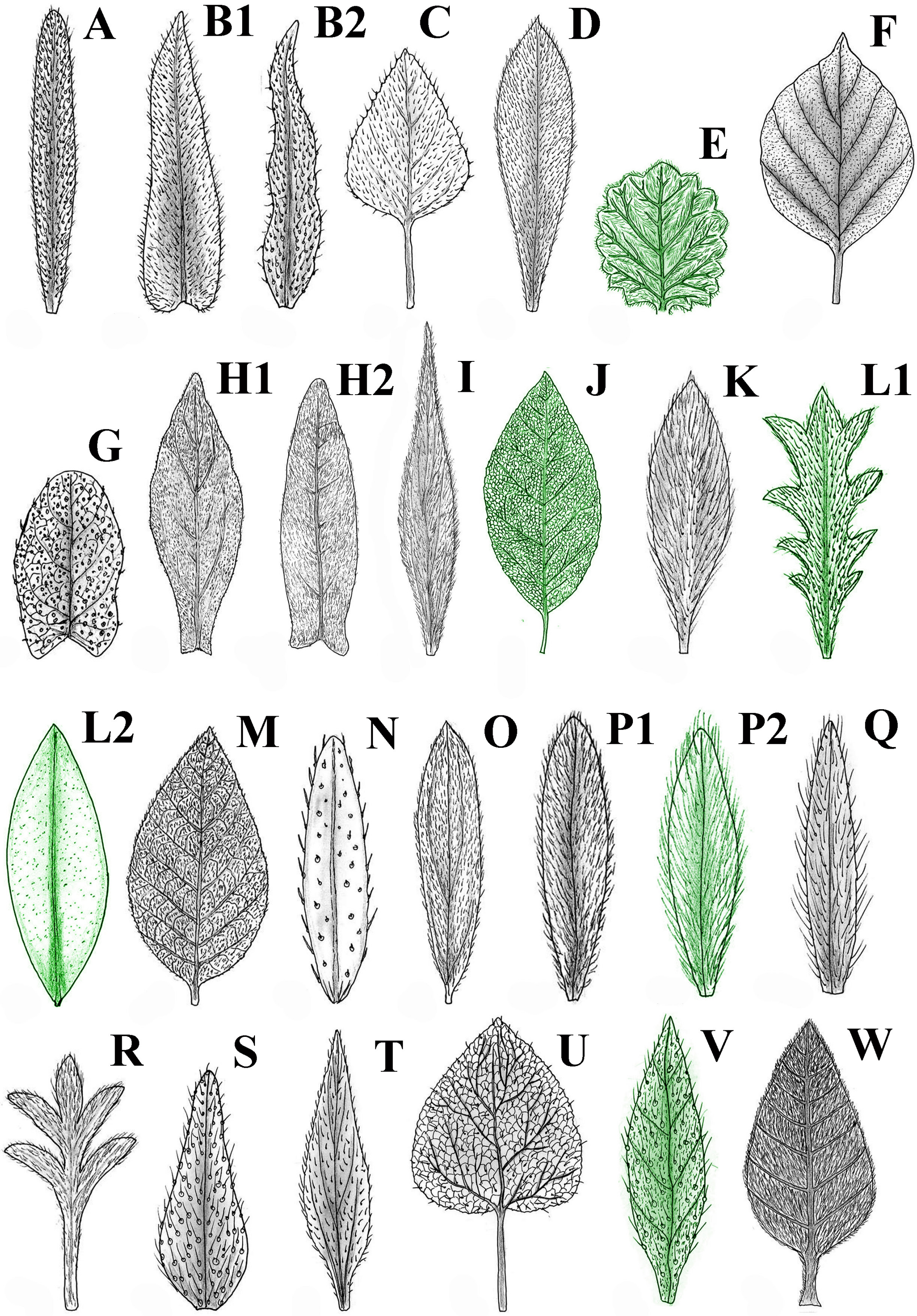

Fig. 6. The distribution of the trichomes on the leaf surface of the studied species of Boraginales (The colored ones are native to Australia): A – *Amsinckia calycina*; B1 – *Anchusa azurea*; B2 – *A. capensis*; C – *Borago officinalis*; D – *Buglossoides arvensis*; E – *Cerinthe major*; F – *Coldenia procumbens*; G – *Cordia myxa*; H1 – *Cynoglossum amabile*; H2 – *C. creticum*; I – *Echium candicans*; J – *Ehretia acuminata*; K – *Euploca strigosa*; L1 – *Halgania anagalloides*; L2 – *H. andromedifolia*; M – *Heliotropium arborescens*; N – *Iberodes linifolia*; O – *Lithospermum officinale*; P1 – *Myosotis alpestris*; P2 – *M. australis*; Q – *Neatostema apulum*; R – *Nemophila menziesii*; S – *Pentaglottis sempervirens*; T – *Symphytum asperum*; U – *Trachystemon orientalis*; V – *Trichodesma zeylanicum*; W – *Wigandia urens* (Drawn by Hamid Nazari).

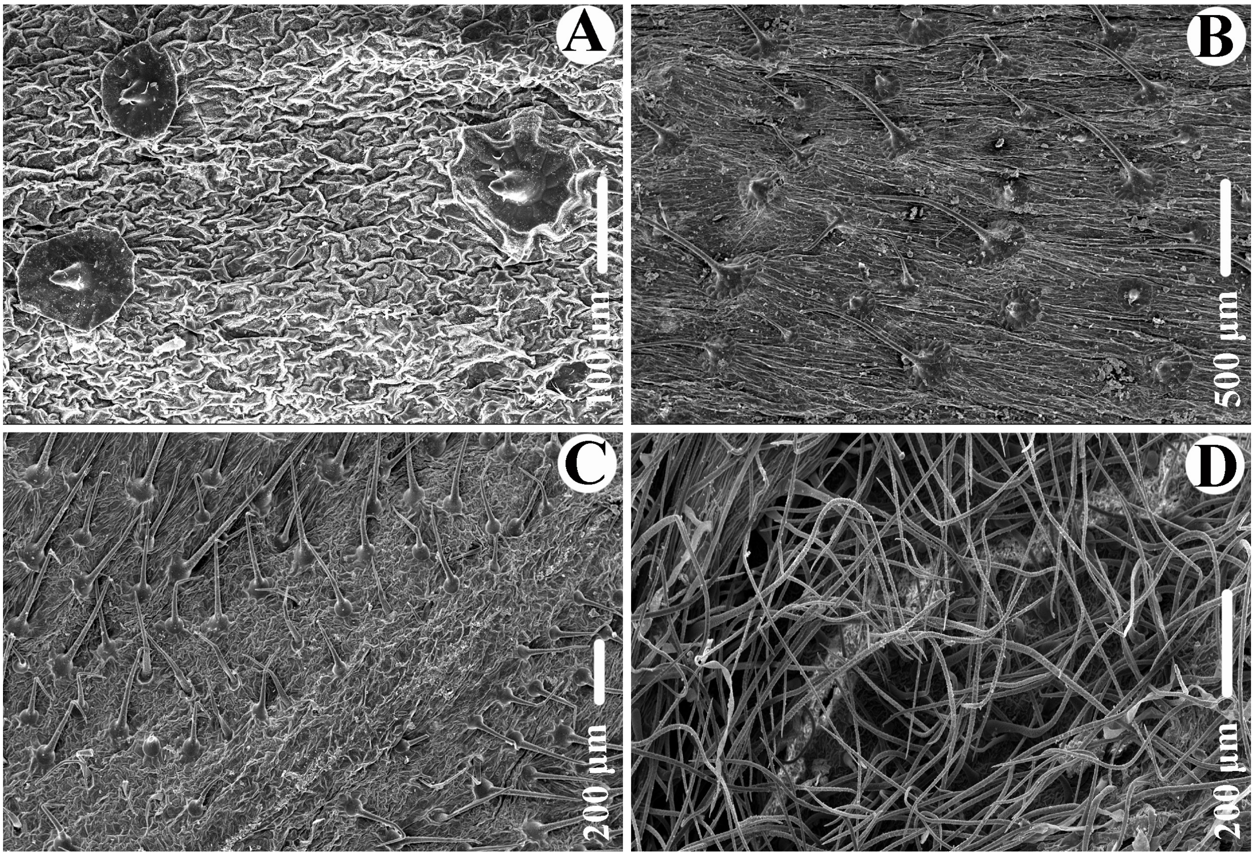

Fig. 7. Types of trichome distribution: A – Rare in *Iberodes linifolia*; B – Sparse in *Anchusa capensis*; A – Dense in *Buglossoides arvensis*; D – Very dense in *Coldenia procumbens*.

Acknowledgments

We thank Heimo Rainer, Astrid Hille, Andreas Berger, Tanja Schuster, and Johannes Walter (Department of Botany, Natural History Museum of Vienna) for their support. Special thanks to Wenke Wegner (SEM specialist, Natural History Museum of Vienna) for training and supervision in microscopic imaging. We gratefully acknowledge W Herbarium and P Herbarium for access to their botanical resources.

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