Swainsona 33: 75–102 (2020)

A preliminary survey of the leaf-indumentum in the Australian Pomaderreae (Rhamnaceae) using Scanning Electron Microscopy

Jürgen Kellermann[a,b]

[a] State Herbarium of South Australia, GPO Box 1047, Adelaide, South Australia 5001
Email: juergen.kellermann@sa.gov.au

[b] School of Biological Sciences, Adelaide, The University of Adelaide, South Australia 5005

Abstract: The tribe Pomaderreae (10 genera, c. 240 species) is almost endemic to Australia and defined within Rhamnaceae by the presence of 'stellate hairs'. This paper is the first to report observations on the leaf-indumentum of 33 species of the tribe with Scanning Electron Microscopy. Apart from simple hairs and papillae, three types of stellate trichomes were observed: fasciculate hairs, appressed stellate hairs and multiradiate hairs (sessile or stalked). The existence of stellate trichomes on the examined species of Pomaderreae was confirmed. Trichomes and indumenta are often variable within genera, as the type of indumentum may be more related to its function. Some groups of species in the genera *Cryptandra* Sm., *Pomaderris* Labill. and *Stenanthemum* Reissek have indumentum characters that seem to be more consistent and might be of value to elucidate relationships between taxa.

Keywords: Rhamnaceae, Pomaderreae, leaf morphology, trichomes, hairs, leaf surface, SEM

Introduction

Pomaderreae Reissek ex Endl. is the second largest tribe of Rhamnaceae. It was first described by Reissek (1840), but not accepted by subsequent botanists (e.g. Hooker 1862; Suessenguth 1953), until Richardson *et al.* (2000b) revised the suprageneric classification of the family. The tribe is now defined by the presence of 'stellate hairs' on stems, leaves and/or flowers; schizocarpic capsules with 1-seeded fruitlets are also a characteristic of, but not unique to, Pomaderreae.

The tribe is highly supported in all molecular analyses of the family (Richardson *et al.* 2000a; Onstein *et al.* 2015; Hauenschild *et al.* 2016, 2018; van Santen & Linder 2020), however the backbone of these phylogenies is not fully resolved and the exact relationship to other tribes is unknown. Pomaderreae seems to be most closely related to the tribe Colletieae (mainly distributed in South America, New Zealand and south-eastern Australia) and *Schistocarpaea johnsonii* F.Muell. (endemic to northern Queensland), as well as the *Alphitonia* Group (comprising the closely related genera *Alphitonia* Reissek ex Endl., *Granitites* Rye, *Jaffrea* H.C.Hopkins & Pillon and *Emmenosperma* F.Muell.; Hopkins *et al.* 2015).

Pomaderreae is virtually endemic to Australia, with only eight species of *Pomaderris* Labill. occurring in New Zealand. Most taxa are distributed in the temperate to semi-arid regions of south-western and south-eastern Australia, some occur in the tropical north of the continent and in the arid centre. Many species have xeromorphic adaptations, such as small, hard, revolute or conduplicate leaves, a dense indumentum or spines.

On-going molecular and morphological studies in the Australian Rhamnaceae have already resulted in the revision of the generic limits within Pomaderreae (Rye 1995a, 2001; Kellermann *et al.* 2005, 2006, 2007). There are currently approximately 240 species recognised in ten genera: *Blackallia* C.A.Gardner (1 species), *Cryptandra* Sm. (c. 55), *Papistylus* Kellermann, Rye & K.R.Thiele (2), *Polianthion* K.R.Thiele (4), *Pomaderris* (75–80), *Serichonus* K.R.Thiele (1), *Siegfriedia* C.A.Gardner (1), *Spyridium* Fenzl (c. 50), *Stenanthemum* Reissek (c. 30) and *Trymalium* Fenzl (13).

While all genera receive high support in molecular analyses of the tribe (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Kellermann & Udovicic 2008; Nge *et al.* 2019; see also Richardson *et al.* 2000a; Onstein *et al.* 2015; Hauenschild *et al.* 2016, 2018; Fig. 12), the relationship between the genera, i.e. within the tribe, are unresolved, with the exception of a sister relationship of *Siegfriedia* and *Pomaderris* and a close relationship of the three small genera, *Blackallia*, *Papistylus* and *Serichonus*. A relationship of *Trymalium* to *Pomaderris*/*Siegfriedia* is supported in some analyses (Onstein *et al.* 2015; Hauenschild *et al.* 2016).

When Labillardiére (1804) described the first two species of *Pomaderris*, he noted the presence of fasciculate trichomes. Stellate trichomes of *Pom. apetala* Labill. were first illustrated by Brongniart (1826), without realising that they were a common character of *Pomaderris* and related genera. Botanists, such as Fenzl

ISSN 2206-1649 (Print) • ISSN 2206-1657 (Online)

(1837), Steudel (1845) and Reissek (1848, 1857) were aware of the presence of stellate trichomes on Australian Rhamnaceae. Reissek (1840) even mentioned stellate indumentum as a generic character for *Pomaderris* and *Trymalium*, but not for *Cryptandra* and *Spyridium*. In his definition of Pomaderreae he also only included the former two genera.

It was Baillon (1875, 1880) who recognised that these genera "belonged to a distinct subseries, exclusively oceanic, [...] generally tomentose, with a simple or stellate, whitish or rusty down [i.e. indumentum]" (Baillon 1880: 61). Weberbauer (1895: 395) reported unpublished anatomical results by Emil Krause and stated that "der Besitz von Sternhaaren die australischen Gattungen *Pomaderris*, *Trymalium*, *Spyridium*, *Cryptandra* vor allen anderen […] auszeichnet" ["the presence of stellate hairs characterises the Australian genera *Pomaderris*, *Trymalium*, *Spyridium*, *Cryptandra* from all others"]. Four years later, Wildeman (1899: 31) describes *Pom. racemosa* as having "un tomentum forme de poils étoilés" ["an indumentum consisting of stellate hairs"] and illustrates one trichome in close-up. Grès (1901) confirmed these observations on *Pom. apetala* and *Pom. aspera* and published a detailed illustration of a cross section through a leaf including stellate trichomes (Fig. 1).

Gemoll (1902) and Herzog (1903) conducted detailed leaf anatomical examinations on all tribes of Rhamnaceae. Gemoll (1902) observed stellate trichomes on all 32 examined species of Pomaderreae and classified them into four types, grouped in two pairs (Table 1). Gemoll's results for the tribe are summarised in Table 2 (as they were so far largely inaccessible to researchers in Australia). Subsequent authors, for example Suessenguth (1953), generally agreed that the 'Australian stellate-haired Rhamnaceae' belonged to a distinct group within the family.

Since Gemoll (1902) and Herzog (1903) no studies have been published on leaf anatomy and the indumentum of the leaves of Pomaderreae. Observations are usually scattered through taxonomic papers and descriptions of new species (e.g. Walsh 1990; Rye 1995a, b; Walsh & Coates 1997; Thiele & West 2004; Thiele 2007; Kellermann & Barker 2012). Moore (1986) gave schematic drawings of the indumentum on leaves of New Zealand species of *Pomaderris*. Notable are the studies by Peacock (1987), who examined and photographed trichomes in the *Pom. aspera-apetala* complex, and Ross (1990) with her study on five species of *Pomaderris* in Queensland, in which she documents the indumentum of each species. The latter publication is the only one that gives detailed descriptions and illustrations (line drawings) of the indumentum.

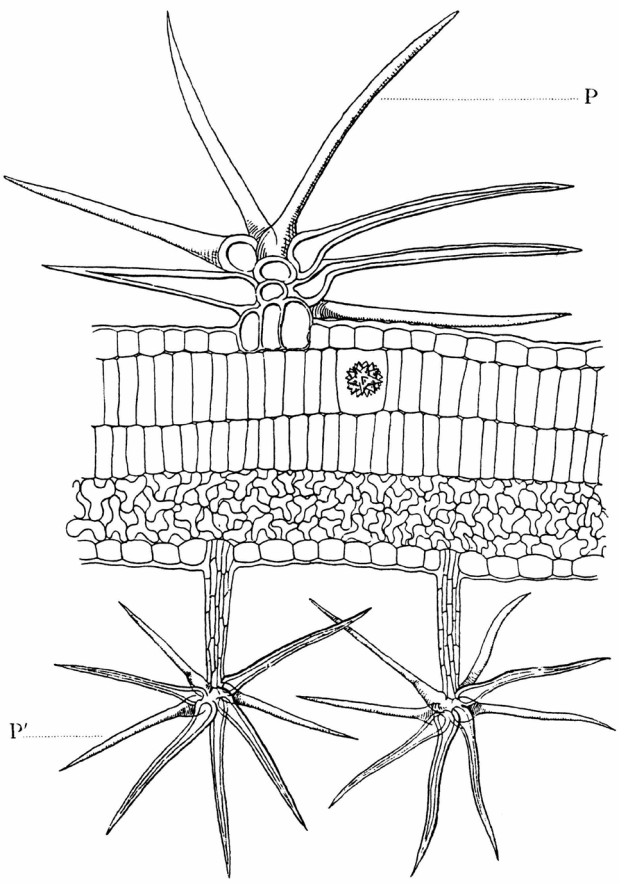

Fig. 1. Cross-section through leaf of *Pomaderris apetala*, showing multiradiate hairs on the upper surface (**P**) and dendroid hairs on the lower surface (**P'**). Reproduced from Grès (1901).

Table 1. The types of stellate trichomes reported by Gemoll (1902).

I – Stellate trichomes with a short stem/stalk:
IA – Stem narrow, inserted in epidermis
IB – Stem broad, multicellular, sitting on epidermis (only *Pomaderris apetala*)
II – Stellate trichomes with a long stem/stalk:
IIA – Stem consisting of long, stretched hair-cells, sitting on the epidermis (only *Spyridium coactilifolium*)
IIB – Stem made from numerous, specialised small cells, integrated in the epidermis (some *Pomaderris* spp.)

Different classification systems for plant hairs have been introduced, but terminology on trichomes and indumentum types is not standardised. Hewson (1988) uses two main categories: emergence and trichome. Emergences are defined as outgrowths that arise from more than one superficial cell and include papillae, tubercles, prickles or warts. Trichomes are outgrowths without vascular tissue that originate from one epidermal cell. They consist of hairs, bristles, prickles, scales and other hair-like outgrowths, and can be single- or multi-cellular.

Table 2. Trichomes reported by Gemoll (1902) for 32 species of Pomaderreae. Abbreviations: IA, IB, IIA, IIB, Gemoll's types of stellate trichomes (Table 1); +, trichome type is present; ?, questionable presence; Sgl., simple trichomes (L and S denote long and short simple trichomes); Pap., papillae. If Gemoll indicated the number of arms of trichome type IA, then this is indicated (e.g. '2, 4'). Gemoll's voucher specimens for most of the taxa can be found at the Herbarium in Munich, Germany (M).

Species name in Gemoll[1]	Currently recognised name	Lower surface of leaf						Nerves on lower surface						Upper surface of leaf					
		IA	IB	IIA	IIB	Sgl	Pap	IA	IB	IIA	IIB	Sgl	Pap	IA	IB	IIA	IIB	Sgl	Pap
Cryptandra obovata Sieber	*Pultenaea altissima* F.Muell. ex Benth.																		
C. sieberi Fenzl	*C. amara* Sm.											L						+	
C. arbutifolia Fenzl	*C. arbutifolia* Fenzl var. *arbutiflora*											L						+	
C. australis Sm.	*C. ericoides* Sm.	+						?										+	
C. leucopogon Meisn.	*C. leucopogon* Meisn. ex Reissek	+						?										+	
C. glabrata Stdl.	*C. arbutiflora* var. *tubulosa* (Fenzl) Benth.																	+	
C. mutila Nees	*C. mutila* Nees ex Reissek	+				S					S								
C. scoparia Reiss.	*C. scoparia* Reissek	+						?										+	
C. spinescens Sieber	*C. spinescens* Sieber ex DC.	+										L							
C. tomentosa Lindley	*C. tomentosa* Lindley	+						+				L	2, 3					+	
Pomaderris apetala Lab.	*Pom. apetala* Labill.		+		+	L			?		?	?				+			
Pom. discolor Vent.	*Pom. discolor* (Vent.) Poir	+										+	2, 3				+		
Pom. elliptica Labill.	*Pom. elliptica* Labill.	+										L					+		
Pom. phylliraeoides Sieb.	*Pom. phillyreoides* Sieb. ex DC.	+				+		+				+					S		
Pom. ferruginea Sieb.	*Pom. ferruginea* Sieb ex Fenzl	+										+					+		
Pom. lanigera Sims	*Pom. lanigera* (Andrews) Sieber ex Sims	+										L					+		
Pom. ligustrina Sieber	*Pom. ligustrina* Sieber ex DC.	+										L					+		
Pom. phylicaefolia Link.	*Pom. phylicifolia* Lodd. ex Link	+										L					S		
Pom. prunifolia Cunn.	*Pom. prunifolia* A.Cunn ex Fenzl	+									+						S		
Pom. racemosa Hook.	*Pom. racemosa* Hook. or *P. oraria* F.Muell.	+									+								
C. coactilifolia F.v.Müller	*Spyridium coactilifolium* Reissek			+											+				
C. eriocephala Hook.	*Sp. eriocephalum* Fenzl	+						+				L					S		
Trymalium globulosum Fenzl	*Sp. globulosum* (Labill.) Benth.	+						?									+		
C. gunii Hook.	*Sp. gunnii* (Hook.f.) Benth.	+						?											
C. obcordata Hook.	*Sp. obcordatum* (Hook.f.) W.M.Curtis	+						+				L							
Sp. parvifolium F.Müller	*Sp. parvifolium* (Hook.) F.Muell	+						?									+		
T. parvifolium F.Muell.	*Sp. parvifolium* (Hook.) F.Muell.	+											2, 4				+		
T. majoranaefolium Fenzl	*Sp. spadiceum* var *majoranifolium* (Fenzl) Benth.	+						?					2, 4				+		
C. ulicina Hook.	*Sp. ulicinum* (Hook.) Benth.	+																	
C. vexillifera Hook.	*Sp. vexilliferum* (Hook.) Reissek	+						?				+							
C. floribunda Steudl.	*T. ledifolium* Fenzl var. ledifolium	+						+				L	4						
T. floribundum Steudel	*T. odoratissimum* Lindl. subsp *odoratissimum*	+						?									+		
T. fragans Fenzl	Possibly *T. odoratissimum* Lindl.	+											2					+	

[1] The name "*Trymalium fragans* Fenzl" is of horticultural origin and could only be found in a list of cultivated species (Koch 1858), in some publications, the name is spelt "*Trymalium fragrans*" and attributed to "h. Kew" (Otto 1845, 1849); it is possibly identical with *Trymalium odoratissimum* Lindl. *Cryptandra obovata* Sieber ex DC. is actually a species of Fabaceae, *Pultenaea altissima* F.Muell. ex Benth. (Kok & West 2002).

Table 3. Sources of plant material used for SEM. ANBG: Australian National Botanic Gardens, Canberra.

Species	Locality	Voucher specimen
Blackallia nudiflora (F.Muell.) Rye & Kellermann	W.A.: Northampton	*J. Kellermann 260* (MEL)
Cryptandra amara Sm.	N.S.W.: Ebon Falls	*D.B. Foreman 2129* (MEL)
C. connata (C.A.Gardner) C.A.Gardner	W.A.: Brealya Well	*S. Patrick 2273* (PERTH)
C. dielsii C.A.Gardner ex Rye	W.A.: Trayning-Kellerberrin Rd	*J. Kellermann 292* (MEL)
C. intermedia (Rye) Rye	W.A.: Pobaderry Road	*J. Kellermann 311* (MEL)
C. intratropica W.Fitzg.	W.A.: King Edward River	*L.A. Craven & C.L. Brubaker 9163* (PERTH)
C. lanosiflora F.Muell.	ANBG 617457 Sect. 99F	*S. Fethers 8, I.R. Telford & S. Pedersen* (CANB)
C. mutila Nees ex Reissek	W.A.: S of Freemantle	*A.S. George 9185* (MEL)
Papistylus grandiflorus (C.A.Gardner) Kellermann, Rye & K.R.Thiele	W.A.: Peterwangi Hill	*J. Kellermann 274* (MEL)
Polianthion bilocularis (A.S.George) Kellermann	W.A.: Dongolocking	*S. Patrick 394* (PERTH)
Pol. collinum Rye	W.A.: Yalgoo	*A. Chant 9* (PERTH)
Pol. minutiflorum (E.M.Ross) K.R.Thiele	Qld: Coominglah State Forest	*A.R. Bean 9107 & G. Turpin* (CANB)
Pol. wichurae (Nees ex Reissek) K.R.Thiele	W.A.: Hi Vallee Farm, Badgingarra	*J. Kellermann 183* (MEL)
Pomaderris angustifolia N.A.Wakef.	Vic.: Barkly River	*E.A. Chesterfield 3524* (MEL)
Pom. apetala Labill.	Vic.: Mafeking	*R.J. Peacock 215* (MEL)
Pom. aspera Sieb. ex DC.	Vic.: Kalimna	*J. Stephen 6* (MEL)
Pom. brevifolia N.G.Walsh	W.A.: Ravensthorpe	*J. Kellermann 388* (MEL)
Pom. elliptica Labill.	Vic.: Wonga Park	*D.J. van Bockel 344* (MEL)
Pom. obcordata Fenzl	S.A.: Eyre Peninsula	*N.G. Walsh 3999* (MEL)
Pom. racemosa Hook.	Vic.: Kentbruck	*I. Hore-Lang s.n.* (MELU)
Serichonus gracilipes (Diels) K.R.Thiele	W.A.: Northampton	*J. Kellermann 262* (MEL)
Siegfriedia darwinioides C.A.Gardner	W.A.: Ravensthorpe	*J. Kellermann 391* (MEL)
Spyridium burragorang K.R.Thiele	ANBG c606176 Sect. 31	*S. Donaldson 903* (CBG)
Sp. daltonii (F. Muell.) Kellermann	Vic.: Grampians	*P. G. Neish 397* (MEL)
Sp. furculentum W.R.Barker & Kellermann	Vic.: near Little Desert	*A.C. Cochrane 71, N.G. Walsh & J.G. Eichler* (MEL)
Sp. globulosum (Labill.) Benth.	W.A.: Neerabup Natl Park	*J. Kellermann 172* (MEL)
Sp. parvifolium (Hook.) F. Muell.	Vic.: Grampians	*J. Kellermann 124* (MEL)
Stenanthemum centrale K.R.Thiele	N.T.: Palm Valley	*D.V. Matthews s.n.* (MEL)
St. leucophractum (Schldl.) Reissek	Vic.: Pink Lakes State Park.	*E.A. Chesterfield 1828* (MEL)
Trymalium ledifolium var. *rosmarinifolium* (Steud.) Benth	W.A.: Flynn State Forest, York	*J. Kellermann 294* (MEL)
T. monospermum Rye	W.A.: Narrogin	*L.W. Sage 1540* (MEL)
T. odoratissimum subsp. *trifidum* (Rye) Kellermannn, Rye & K.R.Thiele	W.A.: Two Peoples Bay Natl Park	*J. Kellermann 398* (MEL)
T. wayi F.Muell. & Tate	S.A.: E of Crystal Brook	*D.N. Kraehenbuehl 5194* (CANB)

Trichomes can form a sparse to dense indumentum on all above-ground parts of a plant. The indumentum on the upper and lower surface of the leaves is of particular importance due to the variety of functions that it performs. It has been traditionally used in taxonomic studies in Brassicaceae (e.g. Rollins & Banerjee 1976; Ančev & Goranova 2006), Fabaceae (e.g. Lackey 1978; Zarre 2003), Fagaceae (e.g. Jones 1986; Ávalos & Salinas 2003; Tschan & Denk 2012), Myrtaceae (e.g. Ladiges 1984), Solanaceae (e.g. Roe 1971, Granada-Chacón & Benítez de Rojas 2005) and other groups. Surveys of trichomes for the whole plant kingdom were published by Uphof (1962), Hummel & Staesche (1962) and Napp-Zinn (1973), however, information on Rhamnaceae and Pomaderreae is very limited in these books.

This paper examines, for the first time, the trichome diversity in Pomaderreae with Scanning Electron Microscopy (SEM). It gives an overview of the variation

of indumenta and types of trichomes observed in the tribe, using a selected sample of 33 species from all currently accepted genera, and draws some conclusions on the systematic usefulness of indumentum characters.

Materials and methods

Thirty-three species of Pomaderreae were examined using Scanning Electron Microscopy. Only material from herbarium specimens was used (Table 3).

The material was placed in silica gel overnight to remove residual moisture. Samples of leaves (both surfaces, and a cross-section), stems and stipules were mounted on aluminium stubs using double-sided carbon tabs and coated with gold using an Edward's S150B Sputter Coater. Samples were viewed under a Phillips XL30 Field Emission Scanning Electron Microscope.

Micrographs were taken of the upper and lower surface of the leaves and from cross sections. If no indumentum was present on the upper surface, pictures of epidermal features were taken at higher resolution. Three to five pictures were taken for each surface and typical examples for each species were chosen for Figures 3–11. Descriptions of the general indumentum and of the type of trichomes were written for each species. The results were also tabulated (Tables 4–6) and combined with Ross' observations on five Queensland species of *Pomaderris* (Ross 1990).

Data for the species examined is presented and discussed in alphabetical order, but in the figures, related taxa are grouped together.

Results

Classification of trichomes

The following types of trichomes were identified in this study. Nomenclature of trichomes was mainly adapted from Jones (1986); for general descriptions of indumentum, the terminology of Hewson (1988) is used. Glandular trichomes were not observed on Pomaderreae. The distinction between the three types of stellate trichomes *sensu lato* (fasciculate, appressed stellate and multiradiate trichomes) is somewhat arbitrary and intermediate forms may be observed. Figure 2 shows simplified drawings of the trichome types.

Simple hairs (Fig. 2A–D). Trichomes of this type can vary considerably in length. They are unicellular. The trichomes are usually straight (e.g. Figs 4F, 10E), but can also appear wavy or curly (Fig. 2B). Most of the simple trichomes examined are sessile when they emerge from the epidermis. Some species bear simple hairs that have a ***pedestal***, i.e. the trichome grows from a distinctive rounded base (Fig. 2C).

Papillae (Fig. 2E). Although not strictly trichomes, the presence and distribution of papillae on the upper surface of some species was noted (e.g. Figs 5B, 11J).

Fasciculate hairs (Fig. 2F–I). These trichomes consist of two or more elements that are only joined at the base, i.e. they include ***bifid hairs*** (Fig. 2I). As such, they are multicellular trichomes. The rays may be erect (e.g. Fig. 3C) or spread out to a varying degree. Fasciculate hairs can be sessile or borne on a pedestal (Fig. 2G).

Appressed stellate hairs (Fig. 2J–L). Stellate trichomes in a strict sense are characterised by the possession of three or more rays (arms) that radiate "from a common point of attachment in a fashion parallel, or nearly parallel, to the leaf surface" (Jones 1986: 263).

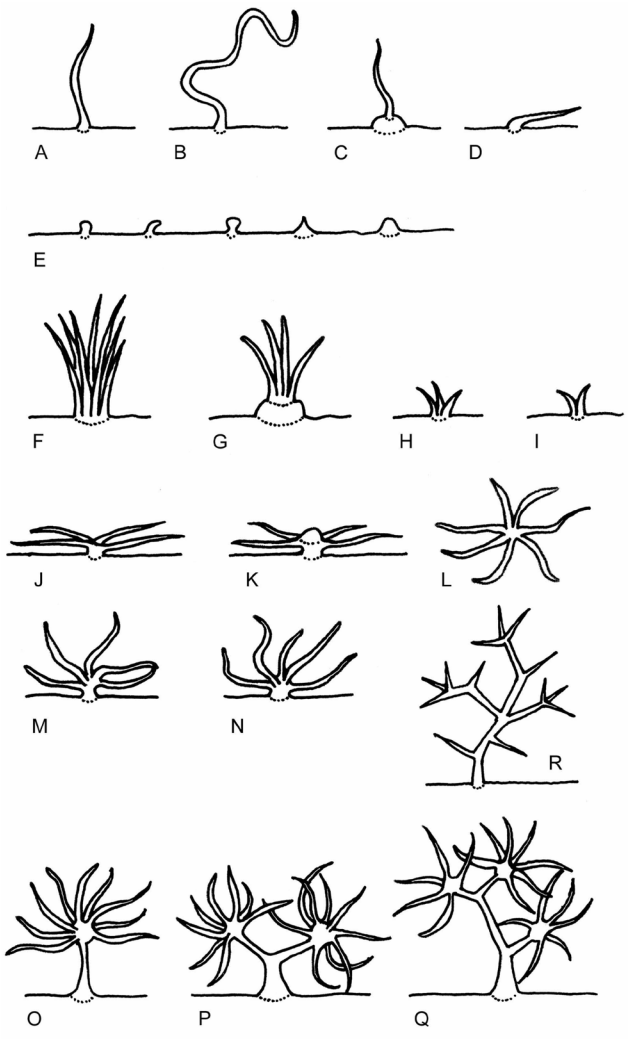

Fig. 2. Trichome classification. **A–Q** Trichome types in Pomaderreae. **A–D** Simple hairs: **A** straight trichome; **B** wavy or curly trichome; **C** trichome with pedestal; **D** appressed trichome. **E** papillae (several examples). **F–I** Fasciculate hairs: **F** trichome with many rays; **G** trichome with pedestal; **H** tri-fid hair; **I** bi-fid hair. **J–L** Appressed stellate hairs: **J** without umbo; **K** trichome with umbo (umbonate); **L** view from above. **M–Q** Multiradiate hairs: **M**, **N** sessile trichomes; **O** stalked multiradiate trichome; **P** dendroid multiradiate trichome with two heads; **Q** dendroid trichome with three heads. **R** True dendritic hair (not in Pomaderreae).

They appear to be multicellular. The trichomes can be sessile and appressed to the leaf surface (e.g. Figs 8F, 11L), or be elevated from the surface on a pedestal. In some species, an umbo (Fig. 2K), as defined by Rollins & Banerjee (1976), was present; this is a mound at the centre of the stellate trichome (Fig. 8F). To avoid confusion with the term 'stellate', which is usually used in a broad sense, these stellate trichomes *sensu stricto* are here termed 'appressed stellate hairs'.

Multiradiate trichomes (Fig. 2M–O). This type of trichome consists of several to many rays (arms) that originate from a (usually) rounded common base in a "variety of seemingly random directions" (Jones 1986: 264). Multiradiate trichomes can be sessile (e.g. Fig. 9A), possess a pedestal, or sit on a multicellular stalk (Fig. 9C, F).

Dendroid trichomes (Fig. 2P, Q). In some species this stalk can be branched and carry two to four multiradiate 'heads'. These trichomes are called here 'dendroid trichomes' (Fig. 9K, L), to distinguish them from true 'dendritic hairs' (e.g. Roe 1971; Fig. 2R).

Surface sculpturing

In species with glabrous or near glabrous upper surfaces, it was possible to record the sculpturing on the epidermis. The following terms are used to describe the surface:

Wrinkled. The epidermis is irregularly and randomly folded, without any discernible pattern (e.g. Fig. 6D).

Striate. There are more or less parallel or irregularly arranged ridges visible on the surface (e.g. Figs 4G, 11A).

Punctate. Each epidermal cell is covered with small warty emergences, which gives the whole cell surface a spotted appearance (e.g. Fig. 10D).

Description of foliar trichomes and surfaces for each species

An asterisk behind the name of a species indicates that only limited information was available from SEM. Data from Ross (1990) for six species of *Pomaderris* is incorporated into these descriptions. Some of this information is summarised in Tables 4–6.

Note that the descriptions provided here apply strictly to the specimens examined with SEM (Table 3). Some species may have varying levels of pubescens, especially on the upper leaf surface.

Blackallia nudiflora (Fig. 6G–I)

Upper surface: Glabrous, with deep wrinkles throughout.

Lower surface: Densely silky (to villose) indumentum of c. 300 μm long simple antrorse hairs overlying smaller appressed stellate hairs with 3–6 rays (rays 100–150 μm long), some trichomes are bifid. Leaves glabrescent with age, retaining only simple hairs on the lower surface.

Cryptandra amara (Fig. 10D–E)

Upper surface: Glabrous, epidermis punctate.

Lower surface: Glabrous. Midrib with sparse antrorse strigose simple hairs, c. 500 μm long.

Although stellate trichomes are absent on the leaves of *C. amara*, stellate trichomes are numerous on flowers and young stems of this species, indicating its correct placement in Pomaderreae.

Cryptandra connata (Fig. 11J–L)

Upper surface: Glabrous, folded (but this might be due to shrinkage in herbarium material), epidermis punctate.

Lower surface: Densely tomentose with 2–4-armed fasciculate hairs (rays 50–100 μm long) and 5–8-armed multiradiate trichomes (rays 50–100 μm long). Midrib with 2–4-armed appressed stellate hairs (rays 40–80 μm long) and 250–400 μm long antrorse simple hairs.

Cryptandra dielsii (Fig. 11D–F)

Upper surface: Sparsely to moderately tomentose to hispid with 30–50 μm long simple hairs. Epidermis punctate.

Lower surface: moderately to densely tomentose indumentum of entangled 5–6-armed multiradiate hairs (rays c. 150 μm long).

Cryptandra intermedia (Fig. 10G–I)

Upper surface: Densely to moderately papillose, especially in young leaves. There is a gradient from papillae to simple hairs and 4–6-armed fasciculate trichomes (each with arms 50–100 μm long). Epidermis punctate.

Lower surface: Moderately to densely tomentose with 6–8-armed multiradiate and appressed stellate hairs (rays c. 100 μm long, each).

Cryptandra intratropica (Fig. 10J–L)

Upper surface: Densely tomentose indumentum of (3–) 4–10-armed multiradiate trichomes (rays 50–100 μm long).

Lower surface: Densely tomentose indumentum of 7–10-armed multiradiate trichomes (rays 50–100 μm long) with rays seemingly more slender than on upper surface. Midrib additionally with scattered 200–300 μm long antrorse simple hairs.

Cryptandra lanosiflora (Fig. 11A–C)

Upper surface: Glabrous. Epidermis parallel striate.

Lower surface: Densely tomentose indumentum of 5–10-armed fasciculate trichomes (40–80 μm long). Midrib with 5–10-armed appressed stellate hairs (rays 40–60 μm long) and c. 500 μm long antrorse simple hairs.

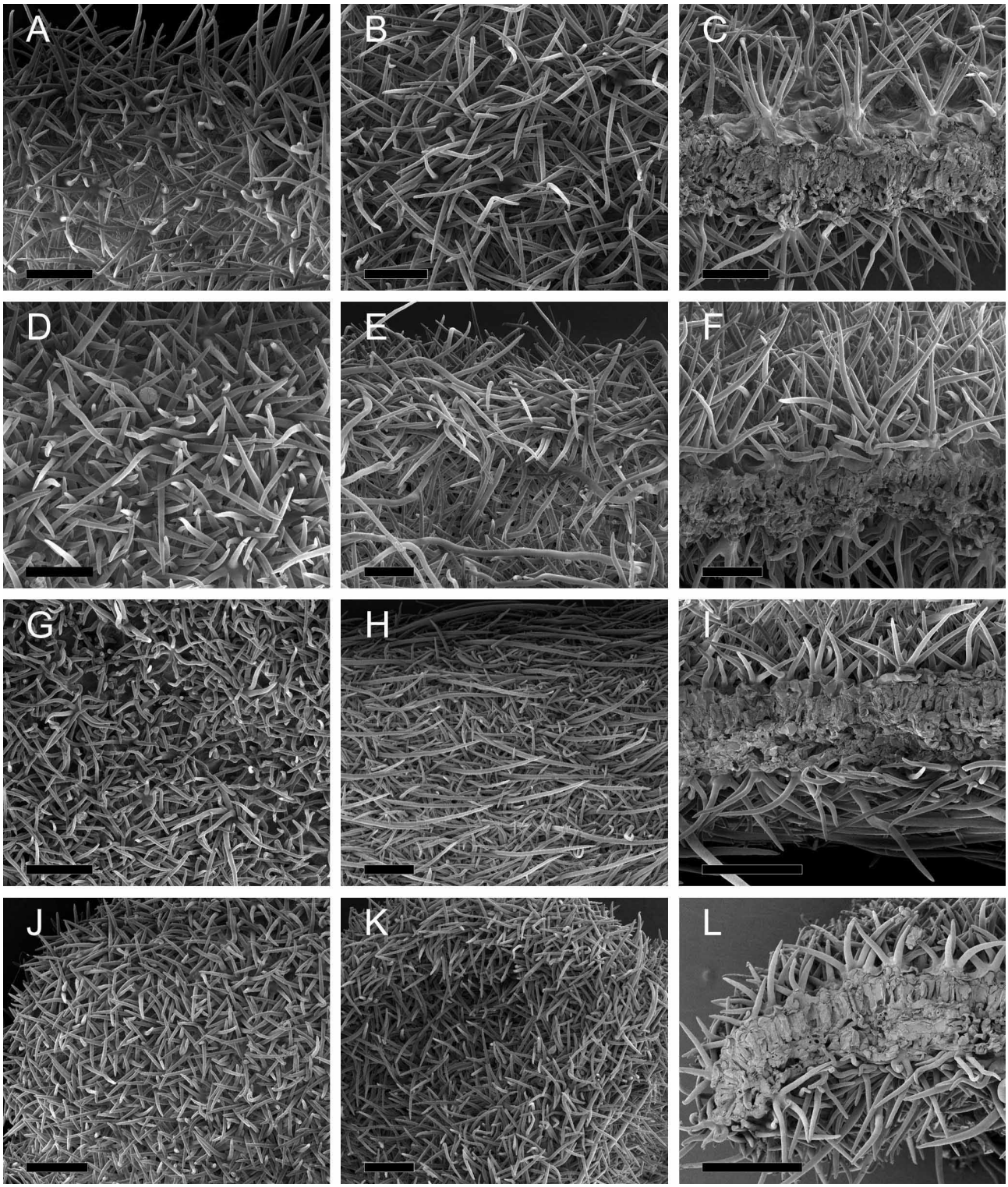

Fig. 3. Indumentum of leaves of *Polianthion*. **A–C** *Pol. wichurae*; **D–F** *Pol. bilocularis*; **G–I** *Pol. collinum*; **J–L** *Pol. minutiflorum*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm. Images first published in Kellermann *et al.* (2006).

Cryptandra mutila (Fig. 11J–L)

Upper surface: Sparsely papillose, surface slightly folded (but this might be due to shrinkage in herbarium material), epidermis punctate.

Lower surface: Glabrous. Midrib with sparse antrorse strigose simple hairs, c. 500 µm long, rarely with 4-armed appressed umbonate stellate hairs (rays c. 100 µm long).

Papistylus grandiflorus (Fig. 6D–F)

Upper surface: Glabrous with deep wrinkles throughout, occasionally trichomes on midrib.

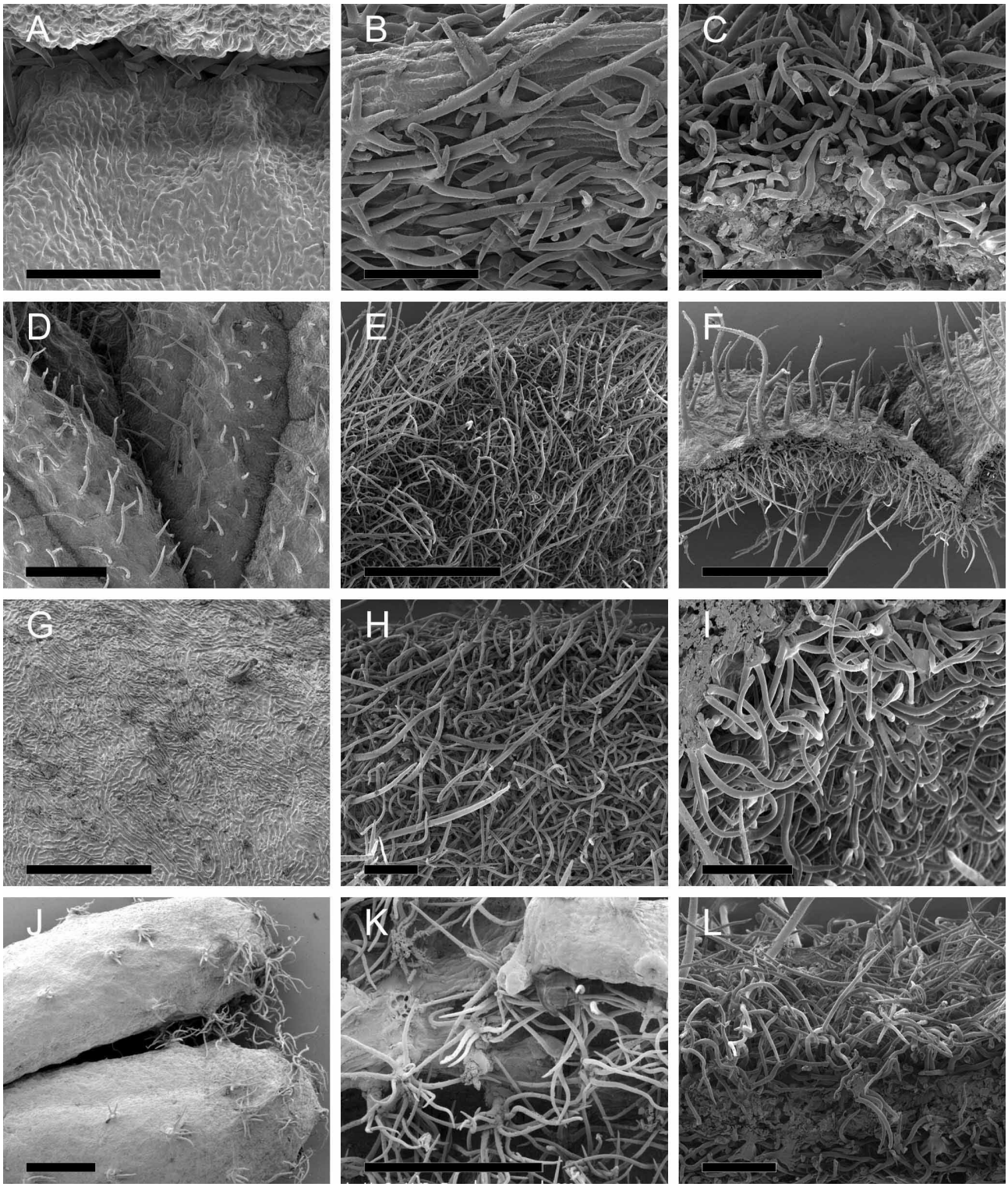

Fig. 4. Indumentum of leaves of *Spyridium*. **A–B** *Sp. globulosum*; **C–F** *Sp. parvifolium*; **G–I**, **L** *Sp. burragorang*; **J–K** *Sp. furculentum*. Vegetative leaves (**A–B**, **D–K**) and floral leaves (**C**, **L**). Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale A–C, G–I, K–L = 100 µm; D–F, J = 500 µm.

Lower surface: Densely silky (to villose) indumentum of c. 300 µm long appressed simple hairs overlying smaller umbonate appressed stellate hairs with possibly 4–6 rays (rays c. 200 µm long). The leaves glabrescent with age, retaining only a few trichomes on the lower surface and appressed antrorse trichomes along the midrib.

Polianthion bilocularis (Fig. 3D–F)

Upper surface: Densely tomentose indumentum of appressed stellate trichomes with 5–8 (–10) rays (rays 80–100 µm long) and slightly longer multiradiate hairs with 8–10 rays (rays 150–250 µm long).

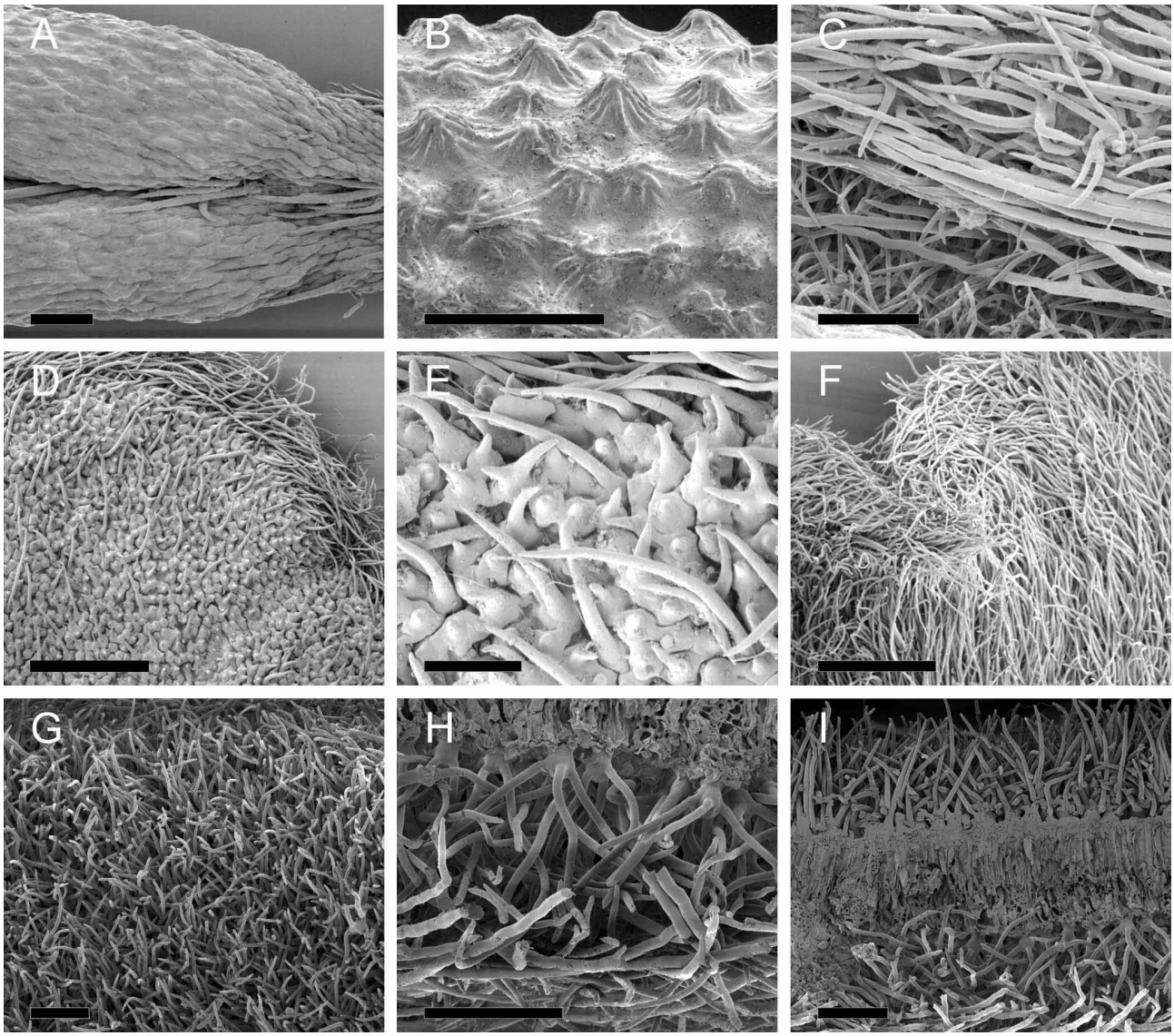

Fig. 5. Indumentum of leaves of *Spyridium* and *Stenanthemum*. **A–C** *Sp. daltonii*; **D–F** *St. leucophractum*; **G–I** *St. centrale*. Left column (**A**, **D**, **G**) & **B**, **E**, upper leaf surface; **C**, **F**, **H**, lower surface; **I**, cross section through leaf with upper leaf surface on top of the image. Scale A–C, E, G–I = 100 µm; D, F = 500 µm.

Lower surface: Densely tomentose to felty indumentum of appressed stellate trichomes with 6–8 (–10) rays (rays c. 100 µm long), slightly longer multiradiate hairs with 8–10 rays, each ray c. 200 mm long, and very long slightly wavy simple trichomes (c. 600 µm long).

Polianthion collinum (Fig. 3G–I)

Upper surface: Densely tomentose short indumentum of fasciculate trichomes with 2–4 (–8) rays (rays c. 50 µm long) and simple hairs of c. 50 µm length, both of which possess a slight pedestal.

Lower surface: Densely tomentose short indumentum of appressed stellate or slightly fasciculate trichomes with 4 rays, each ray 50–100 µm long overlain by c. 300 µm long antrorse simple hairs, which give the surface a velvety appearance.

Polianthion minutiflorum (Fig. 3J–L)

Upper surface: Densely tomentose indumentum of fasciculate trichomes with 2–6 rays (rays 50 µm long) and shorter 30–50 µm long simple hairs.

Lower surface: Densely tomentose indumentum of appressed stellate hairs with 4–8 rays of c. 100 µm in length, 4–8-armed multiradiate hairs (rays 100–200 µm long), and simple hairs that are appressed and 200–300 µm long along the midrib and c. 100 µm long elsewhere.

Polianthion wichurae (Fig. 3A–C)

Upper surface: Densely tomentose to felted indumentum of fasciculate trichomes with (5–) 8 (–10) rays (rays c. 100 µm long), which are slightly raised on a pedestal, and interspersed smaller simple hairs (c. 100 µm long).

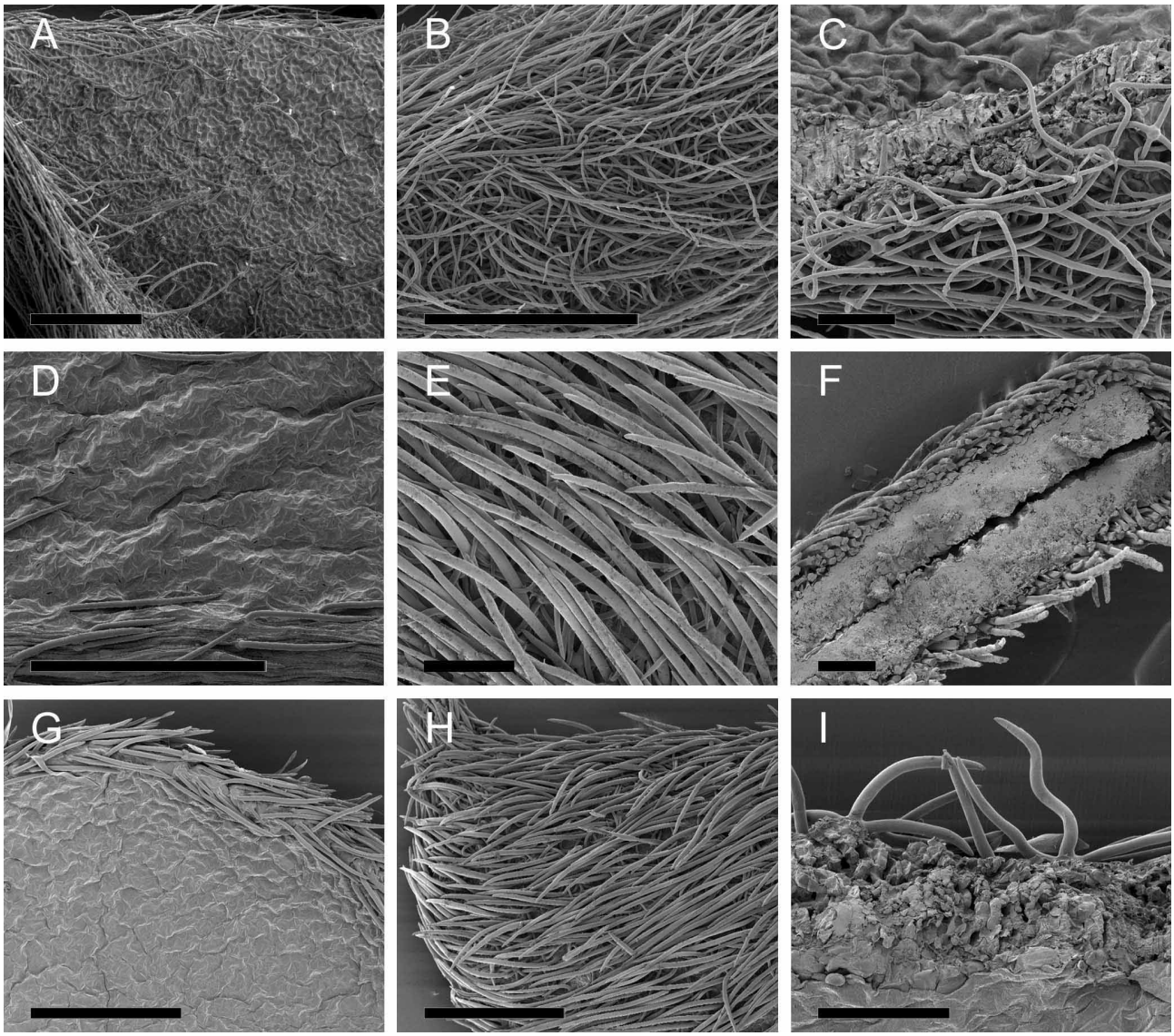

Fig. 6. Indumentum of leaves of species of three small Western Australian genera. **A–C** *Serichonus gracilipes*; **D–F** *Papistylus grandiflorus*; **G–I** *Blackallia nudiflora*. Left column (**A**, **D**, **G**), upper leaf surface; middle column (**B**, **E**, **H**), lower surface; right column, cross section through leaf with upper leaf surface on top of the image (**C**, **I**) or through conduplicate leaf (**F**). Scale C–F, I = 100 µm; A–B, G–H = 500 µm.

Lower surface: Densely to medium tomentose indumentum of multiradiate hairs with 8–10 arms, each arm c. 150 mm long.

Pomaderris angustifolia * (Fig. 8D–E)

Upper surface: Sparsely scattered 2–4-armed fasciculate hairs (rays c. 100 µm long) and 4–8-armed appressed stellate hairs with pedestal (rays c. 150 µm long). Surface pattern possibly striate.

Lower surface: Densely felted indumentum of 6–8-armed appressed umbonate stellate hairs (rays c. 100 µm long) and 4–8-armed multiradiate hairs with c. 200 µm long rays. Possibly some scattered simple hairs.

Pomaderris aspera (Fig. 9D–F, K–L)

Upper surface: Sparsely scattered 6–10-armed multiradiate hairs (rays 100–150 µm long). Surface irregular striate.

Lower surface: Densely felted indumentum of stalked and dendroid multiradiate trichomes with 6–40 rays per head (rays 200–250 µm long), and scattered c. 200 µm long simple hairs with pedestal. The surface can appear floccose when multiradiate heads break off.

Pomaderris apetala (Fig. 9A–C)

Upper surface: Scattered 10–20-armed multiradiate hairs (rays c. 200 µm in diameter). Surface smooth to irregular striate.

Lower surface: Densely felted indumentum of stalked and possibly dendroid multiradiate trichomes with 10–20 (–25) rays per head (rays 70–150 µm long) overlying 6–8-armed appressed umbonate stellate hairs (rays c. 70 µm long). The surface can appear floccose when multiradiate heads break off.

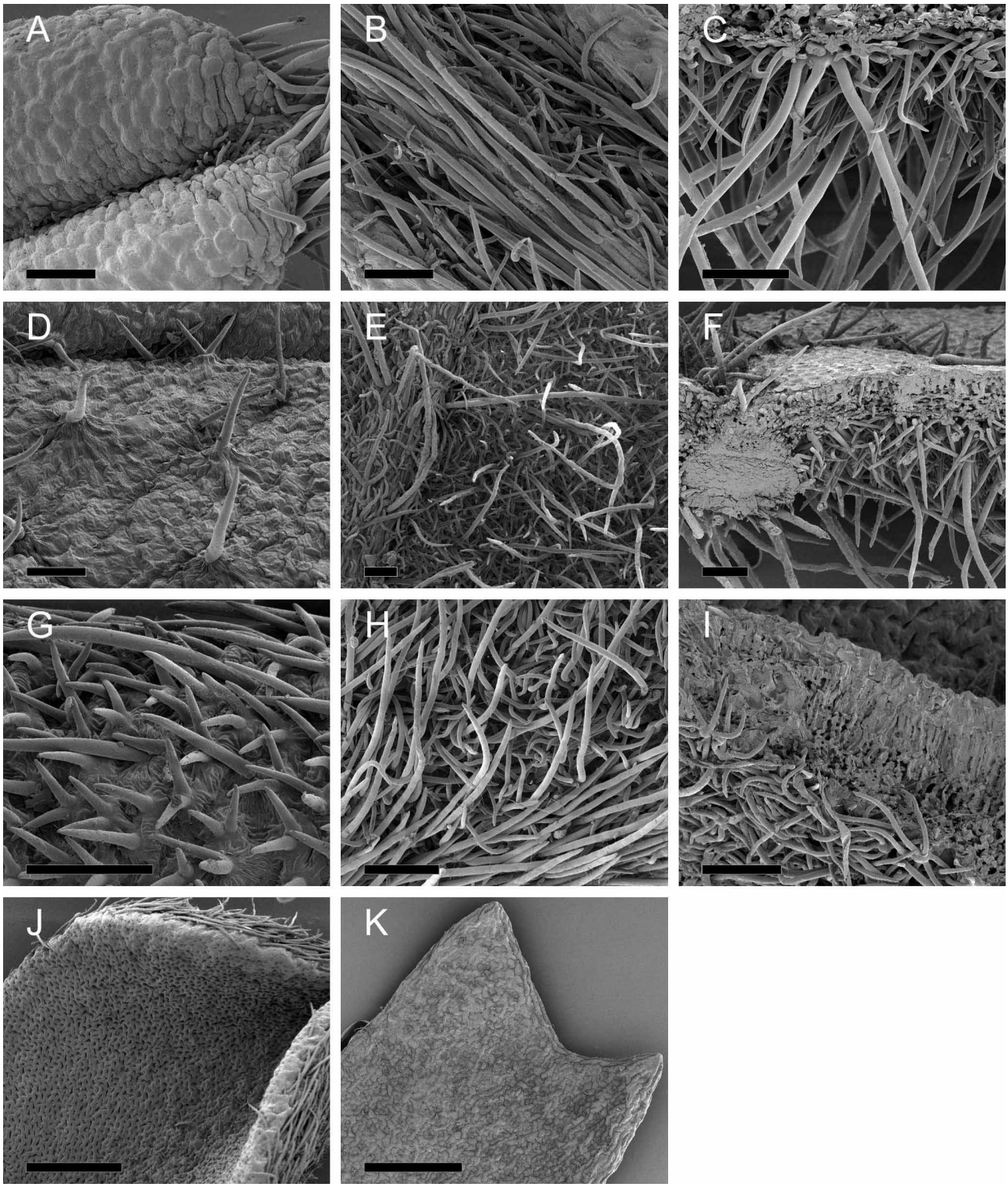

Fig. 7. Indumentum of leaves of *Trymalium*. **A–B** *T. ledifolium*; **C–F** *T. floribundum*; **G–J** *T. wayi*; **K** *T. monospermum*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**), cross section through leaf with upper leaf surface on top of the image. Scale A–I = 100 µm; J–K = 500 µm.

Pomaderris brevifolia (Fig. 8J–L)

Upper surface: Glabrous, surface with irregular wrinkles. Midrib with simple or bifid trichomes (50–100 µm long).

Lower surface: Silky indumentum of 200–300 µm long antrorse bifid hairs overlaying smaller 4-armed fasciculate and 4–8-armed appressed stellate hairs (with rays c. 50 µm long).

Pomaderris clivicola (data from Ross 1990)

Upper surface: Densely velvety indumentum of appressed stellate trichomes c. 100 µm long (possibly fasciculate trichomes with 4–5 rays).

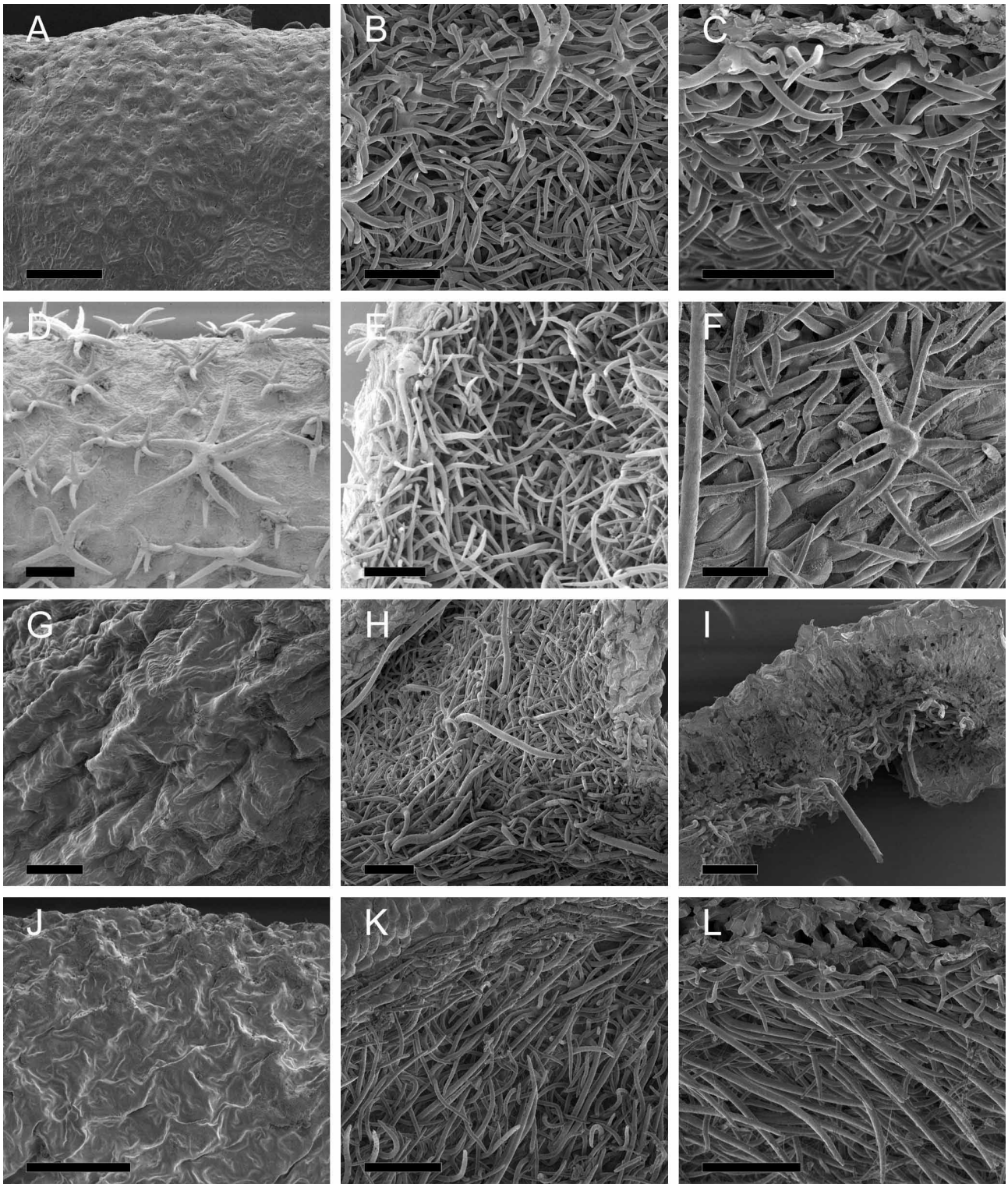

Fig. 8. Indumentum of leaves of *Pomaderris*. **A–C** *P. elliptica*; **D–E** *P. angustifolia*; **F–I** *P. obcordata*; **J–L** *P. brevifolia*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**) & **F**, lower surface; **C**, **I**, **L** cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm.

Lower surface: Densely pubescent with c. 200 µm long curved appressed stellate trichomes (possibly fasciculate with 8–10 rays) overlain by straight simple hairs (500–700 µm long).

Pomaderris elliptica (Fig. 8A–C)

Upper surface: Glabrous, pitted in the sunken centre of each epidermal cell.

Lower surface: Very densely tomentose to felted indumentum of intertwined appressed stellate trichomes with 6–8 rays (rays c. 100 µm long) and sometimed very sparse c. 100 µm long simple hairs. Midrib with 6–8-armed multiradiate hairs (rays 100–200 µm long).

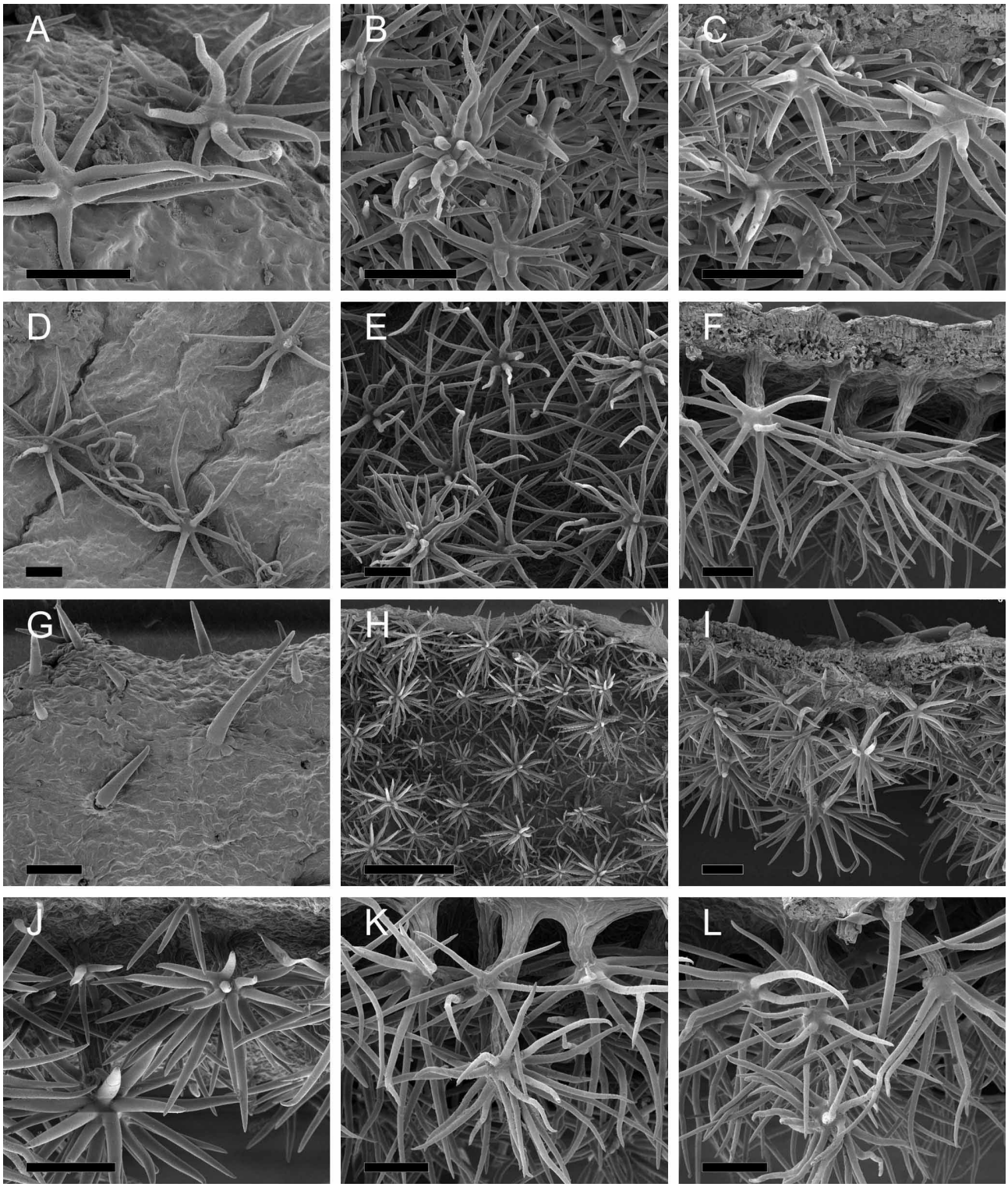

Fig. 9. Indumentum of leaves of *Pomaderris*. **A–C** *P. apetala*; **D–F**, **K**, **L** *P. aspera*; **G–J** *P. racemosa*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf with upper leaf surface on top of the image. Scale A–G, I–L = 100 µm; H = 500 µm.

Pomaderris lanigera (data from Ross 1990, who illustrated two variants)

Upper surface: Moderately densely pubescent with straight simple trichomes, 250–500 µm long.

Lower surface: Densely pubescent with appressed stellate hairs (arms c. 300 µm long) overlain by straight to curly 500–1000 (–2000) µm long simple hairs.

Pomaderris obcordata (Fig. 8F–I)

Upper surface: Glabrous, surface folded and parallel striate [but flat or nearly so in vivo; N.G. Walsh, pers. comm., May 2020]. Midrib with 4–8-armed appressed stellate trichomes (rays c. 100 µm long).

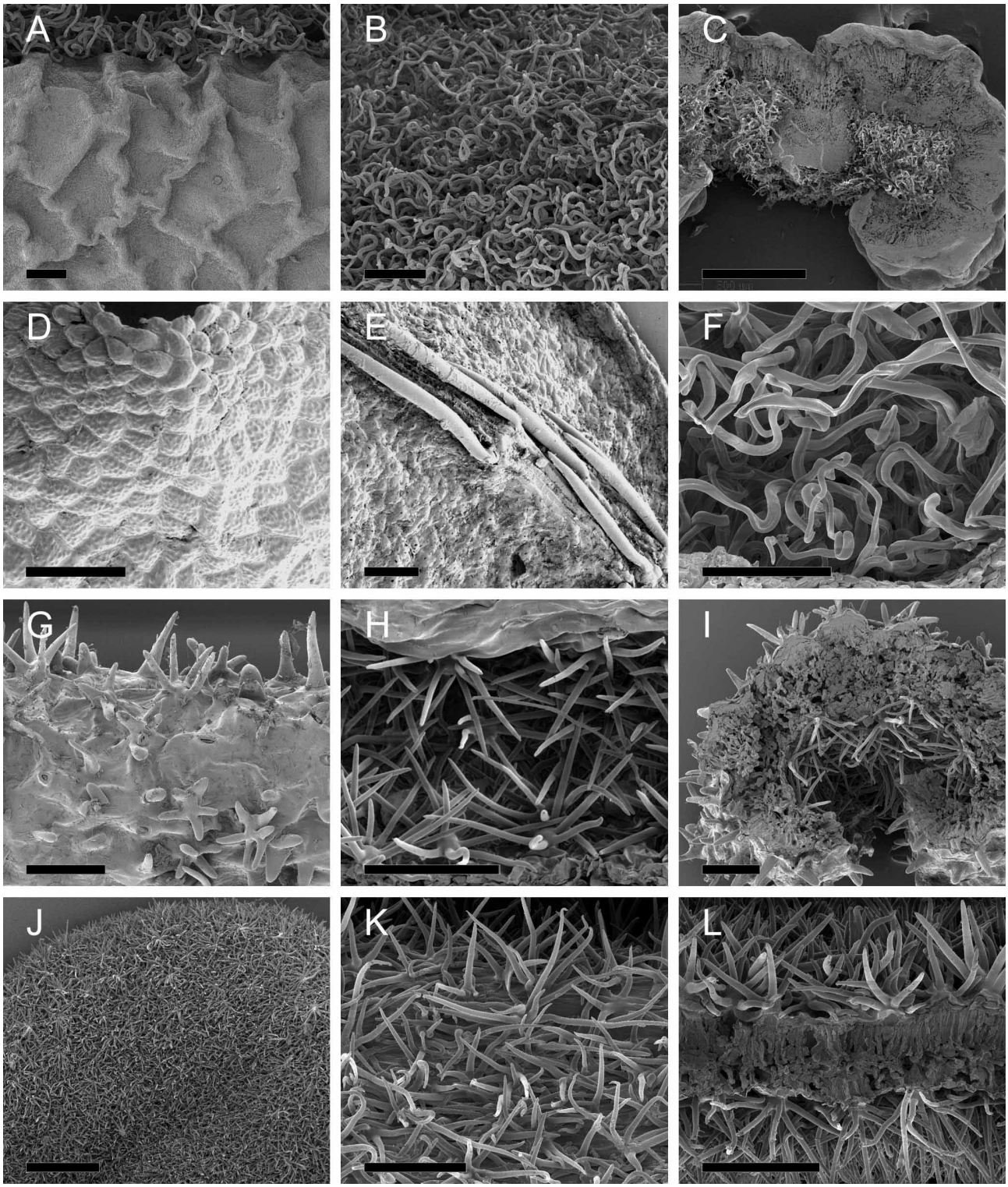

Fig. 10. Indumentum of leaves of *Siegfriedia* and *Cryptandra*. **A–C**, **F** *Si. darwinioides*; **D–E** *C. amara*; **G–I** *C. intermedia*; **J–L** *C. intratropica*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**), lower surface; right column (**C**, **F**, **I**, **L**), cross section through leaf (**L**, upper leaf surface on top of the image). Scale A–B, D–I, K–L = 100 µm; C, J = 500 µm.

Lower surface: Densely felted indumentum of 4–8-armed appressed stellate hairs, some umbonate (rays 100–150 µm long); midrib and secondary veins with sparse appressed stellate hairs and c. 400 µm long simple hairs.

Pomaderris prunifolia (data from Ross 1990)

Upper surface: Scabrous with stout simple (rarely divided) trichomes, 300–500 µm long [the surface may be also glabrous; Walsh 1999].

Lower surface: Densely pubescent with appressed stellate (possibly multiradiate) trichomes with rays c. 300–400 µm long and dendroid multiradiate trichomes (rays 400–500 µm long), especially on veins and midrib.

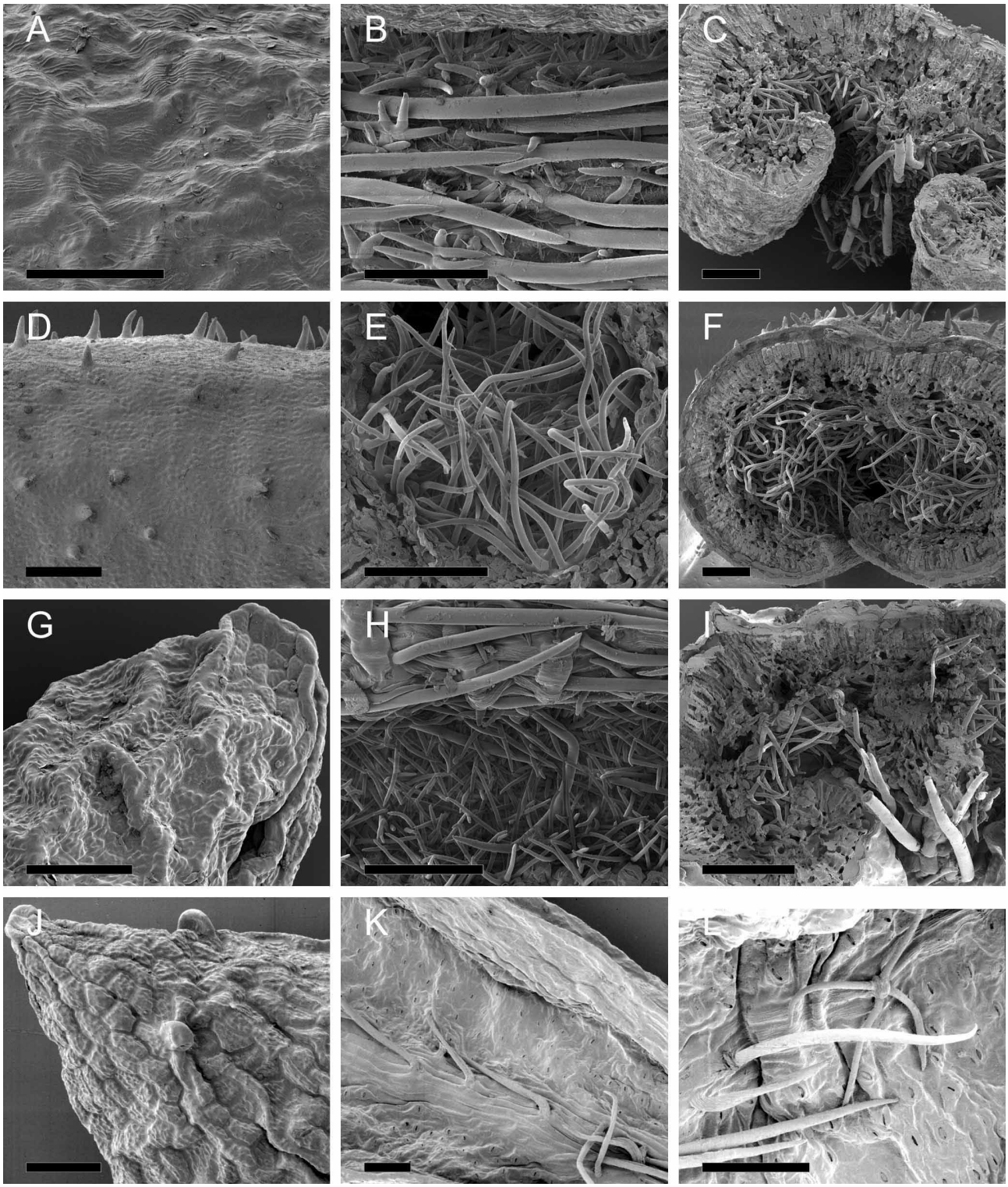

Fig. 11. Indumentum of leaves of *Cryptandra*. **A–C** *C. lanosiflora*; **D–F** *C. dielsii*; **G–I** *C. connata*; **J–L** *C. mutila*. Left column (**A**, **D**, **G**, **J**), upper leaf surface; middle column (**B**, **E**, **H**, **K**) & **L**, lower surface; **C**, **F**, **I**, cross section through leaf with upper leaf surface on top of the image. Scale = 100 µm.

Pomaderris racemosa (Fig. 9G–J)

Upper surface: Sparsely tomentose to hirsute with 100–200 µm long simple hairs that easily break off and leave the base of the trichome behind. Surface smooth to slightly wrinkled with some ridges radiating from the base of the trichomes [the surface may also be glabrous; Walsh 1999].

Lower surface: Indumentum of two layers of stalked trichomes (appearing floccose): tall stalked multiradiate hairs with 6–30 rays (rays c. 200 µm long) and umbonate stalked to sessile appressed stellate hairs with 4–6 rays (each ray 50–100 µm long). These trichomes overlay long simple hairs (up to 100 µm) and 3–4-armed fasciculate hairs (rays c. 70 µm long).

Pomaderris tropica (data from Ross 1990)

Upper surface: Densely velvety indumentum of appressed stellate trichomes, rays c. 100 µm long (possibly fasciculate with 3–4 arms).

Lower surface: Densely pubescent with (possibly 8–10-armed) appressed stellate trichomes (each ray c. 200–300 µm long), overlain by appressed, straight simple hairs, 500–700 µm long.

Pomaderris vellea (data from Ross 1990)

Upper surface: Densely velvety with straight simple hairs, c. 200 µm long, occasionally the trichomes are basally divided.

Lower surface: Densely pubescent with curly simple hairs, c. 500–600 µm long [these almost certainly overlay stellate hairs, similar to the closely related *Pom. lanigera* (above); N.G. Walsh, pers. comm., May 2020].

Serichonus gracilipes (Fig. 6A–C)

Upper surface: Sparsely pubescent with c. 200 µm long erect simple hairs. The leaf surface is deeply wrinkled throughout.

Lower surface: Densely pubescent to villose indumentum of c. 400 µm long wavy simple hairs overlaying appressed stellate hairs with a distinct umbo, with 4–6 rays (each 100–200 µm long).

Siegfriedia darwinioides (Fig. 10A–C, F)

Upper surface: Glabrous, deeply folded, epidermis with a striate surface pattern.

Lower surface: Densely felted and matted indumentum of 2- to possibly 4-armed very long and curly fasciculate hairs (rays at least 200–500 µm long). Exact measurements were impossible due to the matted nature of the indumentum.

Spyridium burragorang (Fig. 4G–I, L)

Upper surface: Glabrous, surface irregular striate. Floral leaf with a densely felted indumentum of intertwined, slightly curly 6–8-armed multiradiate hairs (rays c. 100 µm long) and 200–300 µm long interspersed simple hairs.

Lower surface: Densely felted indumentum of intertwined curly 6–8-armed multiradiate hairs (rays 100–150 µm long) and up to 1000 µm long simple hairs on midrib and margins.

Spyridium daltonii * (Fig. 5A–C)

Upper surface: Glabrous, densely papillose to verrucose, with a somewhat striate pattern of ridges emanating from the centre of each wart-like protuberance.

Lower surface: Densely felted indumentum of stellate trichomes with rays c. 50–150 µm long (the exact type of hair was not observed with SEM), interspersed long simple hairs, 200–400 µm long. Midrib with long antrorse simple trichomes (400–600 µm long) and (2–)3–6-armed antrorse comb-like appressed stellate hairs (rays 100–200 µm long).

Spyridium furculentum * (Fig. 4J–K)

Foliar trichomes of this species are all stalked multiradiate hairs with (4–) 6–10 rays, which are placed on a broad multicellular pedestal.

Upper surface: Glabrous, except for some sparsely scattered trichomes (rays c. 150 µm in length). Floral leaves not examined.

Lower surface: Sparse to medium dense cover of trichomes (rays c. 200 µm long) on lower lamina and midrib.

Spyridium globulosum (Fig. 4A–B)

Upper surface: Glabrous, surface ± smooth. Midrib with 60–80 µm long simple hairs. Floral leaves not examined with SEM.

Lower surface: Densely felted indumentum of entangled multiradiate hairs with 6–8 rays (rays c. 100 µm long). Midrib less hairy, with smaller 4–8-armed appressed stellate hairs (arms 50–100 µm long) and long simple hairs, 500–1000 µm long.

Spyridium parvifolium (Fig. 4C–F)

Upper surface: Sparsely pubescent to hispid indumentum of simple hairs on a pedestal, 150–500 µm long. Surface irregularly striate. Floral leaves have additionally a very dense felted indumentum of entangled multiradiate hairs with 6–8 rays (rays c. 150 µm long).

Lower surface: Very dense, felted to pubescent indumentum of (6–) 8 (–10)-armed multiradiate trichomes (rays 150–200 µm long) with interspersed very long simple hairs (c. 1000 µm long), which are denser on midrib and leaf margin.

Stenanthemum centrale (Fig. 5G–I)

Upper surface: Densely tomentose indumentum of 2–4-armed fasciculate hairs with pedestal (rays 150–200 µm long) and interspersed simple hairs of the same length.

Lower surface: A dense indumentum of silky antrorse long simple hairs, 500–600 µm in length, overlying intertwined 4-armed multiradiate hairs of medium density (rays c. 150 µm in length).

Stenanthemum leucophractum * (Fig. 5D–F)

Upper surface: Densely papillate; the papillae may develop into the pedestals of fasciculate hairs, if rays develop. Sparsely tomentose with fasciculate hairs, 2–4 rays (each ray c. 100 µm long) and interspersed simple hairs 150–250 µm long.

Lower surface: Villous to silky indumentum of more than 500 µm long simple hairs. Possibly appressed stellate hairs below, but not visible on SEM images.

***Trymalium ledifolium* var. *rosmarinifolium* *** (Fig. 7A–B)

Upper surface: Glabrous, epidermis parallel-striate. Midrib with 50–100 µm long trichomes; type of hair not visible on SEM.

Lower surface: Densely tomentose to felted indumentum of possibly multiradiate hairs (rays 100–200 µm long) and 200–500 µm long simple hairs. Midrib moderately covered with 4–8-armed appressed, sometimes umbonate stellate hairs (rays 50–100 µm long), and 200–500 µm long simple antrorse hairs.

Trymalium monospermum (Fig. 7K)

Upper and lower surface: Completely glabrous, surface wrinkled. Epidermis covered with a glaucous thick layer of wax.

Trymalium odoratissimum* subsp. *trifidum (Fig. 7C–F)

Upper surface: Sparsely pubescent indumentum of 200–400 µm long simple hairs. Midrib with V-shaped bifid fasciculate hairs, with rarely up to 4 rays (rays 100–400 µm long) [becoming glabrous with age and usually described as such; Rye 1995b]. Epidermis parallel-striate.

Lower surface: Densely tomentose to felted indumentum of 4–8-armed multiradiate trichomes (rays c. 400 µm long) and 500–1000 µm long simple hairs. Midrib moderately covered with 4–9-armed appressed umbonate stellate hairs (rays 100–150 µm long) and simple hairs that are slightly longer than the ones on the lamina (c. 1000 µm).

Trymalium wayi (Fig. 7G–J)

Upper surface: Young leaves moderately to densely tomentose with simple and V-shaped bifid fasciculate hairs, with rarely up to 4 rays (rays c. 50 µm long), becoming glabrous with age, hairs in older leaves only persisting on midrib. Surface deeply wrinkled and grooved. Epidermis parallel-striate.

Lower surface: Moderately dense silky indumentum of 400–500 µm long simple hairs overlaying very dense entangled 4–6 (–8)-armed appressed stellate hairs with umbo (rays 50–150 µm long). Simple hairs denser at midrib.

General observations

Simple hairs

Simple hairs were found on leaves of all examined species, except *Cryptandra intratropica*, *Pomaderris apetala* and *Trymalium monospermum*. It is possible to divide these simple hairs into two categories: erect and appressed hairs.

Erect hairs can be small, persistent and up to 100 µm long, as observed on the upper surface of *Cryptandra dielsii* (Fig. 11D) and *C. intermedia* (Fig. 10G). Tall erect hairs are c. 100–400 µm long on the upper surface and up to 1000 µm long on the lower surface of the leaf. In many species they were found on both surfaces. Frequently, they wear off on the upper surface with age and only persist in the impressed midrib. For example in *Stenanthemum gracilipes* (Fig. 6A, C), or in *Pomaderris racemosa* (Fig. 9G), scars of broken-off trichomes can be observed. On both, the upper and the lower surface, erect simple hairs occur interspersed with stellate trichomes (e.g. Figs 4F, 7F, 9L). In three species, the erect simple hairs had a distinctly raised base (pedestal): *Pom. aspera* (Fig. 9F), *Spyridium parvifolium* and *Polianthion collinum*.

Appressed hairs are mostly antrorse and 200–1200 µm long, in some cases they are up to 2000 µm long. They arise only on the lower surface and are usually conspicuous on the midrib (e.g. Figs 4B, 10E, 11B), secondary veins (if present) and leaf margins (e.g. Figs 5D, 6G). They may also be interspersed with stellate trichomes on the leaf lamina (Fig. 8K) or produce a dense villous or silky indumentum overlaying smaller stellate trichomes (e.g. Figs 7F, 8H).

Some simple hairs have a slightly wavy or curly appearance (e.g. Figs 5C, 8B). In *Stenanthemum leucophractum* (Fig. 5E) and *Cryptandra intermedia* (Fig. 10G) there appears to be a gradient from simple to bifid and stellate trichomes.

Papillae

Different kinds of papillae were observed on the upper surface of leaves. In *Cryptandra intermedia* (Fig. 10G) and *C. mutila* (Fig. 11J), papillae were round emergences, scattered on the upper surface. *Spyridium daltonii* had dense conical papillae that were marked with a distinctly striate surface pattern (Fig. 5B). In one species, *Stenanthemum leucophractum*, it appeared that the papillae were actually the pedestals of fasciculate hairs that failed to develop rays (Fig. 5D, E). As such there seemed to be a gradient from papillae to pedestals with rudimentary rays and then to fully developed fasciculate hairs.

Stellate trichomes

The presence of stellate trichomes is confirmed as a synapomorphy of the tribe Pomaderreae (Richardson *et al.* 2000b; Medan and Schirarend 2004). Three types of stellate trichomes were distinguished in this study: stellate, fasciculate, and multiradiate hairs. They could be found on leaves of all species, except *Cryptandra amara* and *Trymalium monospermum*. In *C. amara*, stellate trichomes are present on other parts of the plant, such as stems and flowers, whereas *T. monospermum* is the only species in Pomaderreae to be completely glabrous throughout (Rye 2000). Herzog (1903) reported fasciculate hairs on some species of *Rhamnus* L. (tribe Rhamneae), but Johnston & Johnston (1987) commented that these were just closely spaced simple hairs. Specialised two-armed hairs occur in *Sageretia* Brongn. (Johnston 1974 labelled them “medifixed hairs”; Medan and Schirarend 2004), but these were not observed in Pomaderreae.

Table 4. Indumentum cover of the lower surface of leaves of Pomaderreae as observed with SEM. Results from Ross (1990) are shaded in grey. The length of simple hairs or the rays of stellate hairs is designated by diamonds: ♦, < 50 µm; ♦♦, 50–150 µm; ♦♦♦, 150–250 µm; ♦♦♦♦, 250–400 µm; ♦♦♦♦♦, 400–800 µm; ♦♦♦♦♦♦, 800–1200 µm. The number of rays per stellate hair is indicated. Appr., appressed; D, dendroid trichome; M, hairs only on midrib; P, trichome with pedestal; W, wavy or curly hair. An asterisk after the species name indicates that only limited information was available from SEM.

Taxon	Indumentum	Simple	Fasciculate	Appr. stellate + umbo	Appr. stellate	Multiradiate	Multiradiate + stalk
Polianthion wichurae	medium-dense tomentose					♦♦♦ 8–10	
Pol. bilocularis	dense tomentose to felted	♦♦♦♦♦ W			♦♦ 6–8 (–10)	♦♦♦ 8–10	
Pol. minutiflorum	dense tomentose	♦♦, M ♦♦♦♦			♦♦ 4–8	♦♦♦ 4–8	
Pol. collinum	dense tomentose (-velvety)	♦♦♦♦			♦♦ 4		
Spyridium globulosum	dense felted	M ♦♦♦♦♦			M ♦♦ 4–8	♦♦ 6–8	
Sp. parvifolium	felted-pubescent	♦♦♦♦♦♦				♦♦♦ (6–) 8 (–10)	
Sp. burragorang	dense felted	M ♦♦♦♦♦♦				♦♦ 6–8 W	
Sp. furculentum *	sparse-medium	(?)					♦♦♦ (4–) 6–10
Sp. daltonii	dense felted	♦♦, M ♦♦♦♦♦			M ♦♦ (2–) 3–6	♦♦ 2?–6?	
Stenanthemum leucophractum *	villous-silky	♦♦♦♦–♦♦♦♦♦				(?)	
St. centrale	silky strigose	♦♦♦♦♦				♦♦♦ 4	
Serichonus gracilipes	dense pubescent to villose	♦♦♦♦ W		♦♦–♦♦♦ 4–6			
Papistylus grandiflorus	dense sliky (to villose)	♦♦♦♦		♦♦♦ (4–)6			
Blackallia nudiflora	silky (to villose)	♦♦♦♦	♦♦ 2		♦♦ 3–6		
Trymalium ledifolium *	dense tomentose-felted	♦♦♦–♦♦♦♦		M ♦♦ 4–8		♦♦–♦♦♦	
T. floribundum	dense tomentose-felted	♦♦♦♦♦♦		M ♦♦ 4–9		♦♦♦♦ 4–8	
T. wayi	moderate-dense silky	♦♦♦♦♦		♦♦ 4–6 (-8)			
T. monospermum	glabrous, glaucous						
Pomaderris angustifolia *	dense felted	(?)	♦♦ 6–8			♦♦♦ 4–8	
Pom. elliptica	dense tomentose-felted	♦♦	♦♦ 6–8			M ♦♦–♦♦♦ 6–8	
Pom. apetala	dense felted		♦♦ 6–8				♦♦–♦♦♦ 10–20 (–25) D?
Pom. aspera	dense felted (floccose)	♦♦♦ P					♦♦♦ (6–) 10–40 D
Pom. racemosa	floccose	♦♦	♦♦ 3–4	♦♦ 4–6 S			♦♦♦ 6–30
Pom. clivicola	dense pubescent	♦♦♦♦♦				♦♦♦ 6–8	
Pom. prunifolia	dense pubescent		?			♦♦♦ 10	♦♦♦♦ 12
Pom. lanigera form 1	dense pubescent	♦♦♦♦♦–♦♦♦♦♦♦ W	♦♦♦♦ 4				
Pom. lanigera form 4	dense pubescent	♦♦♦♦♦–♦♦♦♦♦♦	♦♦♦♦ 4				
Pom. vellea	dense pubescent	♦♦♦♦♦ W					
Pom. tropica	dense pubescent	♦♦♦♦♦	♦♦♦–♦♦♦♦ 8–10				
Pom. obcordata	dense felted	M ♦♦♦♦♦		♦♦ 4-8	♦♦ 4–8		
Pom. brevifolia	silky		♦♦♦♦ 2, ♦♦ 4		♦♦ 4–8		
Siegfriedia darwinioides	dense felted-matted	(?)	♦♦♦–♦♦♦♦♦ 2 W				
Cryptandra amara	glabrous, M strigose	M ♦♦♦♦♦					
C. intratropica	dense tomentose	M ♦♦♦–♦♦♦♦				♦♦ 7–10	
C. intermedia	moderate to dense tomentose				♦♦ 6–8	♦♦ 6–8	
C. mutila	glabrous, M strigose	♦♦♦♦♦		♦♦ 4 (rare)			
C. lanosiflora	dense tomentose	M ♦♦♦♦♦	♦–♦♦ 5–10		M ♦–♦♦ 5–10		
C. dielsii	moderate-dense tomentose	(?)				♦♦♦ 5–6	
C. connata	dense tomentose	M ♦♦♦♦	♦♦ 2–4		M ♦♦ 2–4	♦♦ 5–8	

Table 5. Indumentum cover of the upper surface of leaves of Pomaderreae as observed with SEM. Results from Ross (1990) are shaded in grey. The indumentum of floral leaves is reported in square brackets. The length of simple hairs or the rays of stellate hairs is designated by diamonds: ♦, < 50 µm; ♦♦, 50–150 µm; ♦♦♦, 150–250 µm; ♦♦♦♦, 250–400 µm; ♦♦♦♦♦, 400–800 µm; ♦♦♦♦♦♦, 800–1200 µm. The number of rays per stellate hair is indicated. Appr., appressed; M, hairs only on midrib; P, trichome with pedestal; W, wavy or curly hair. An asterisk after the species name indicates that only limited information was available from SEM.

Taxon	Indumentum	Papillae	Simple	Fasciculate	Appr. stellate	Multiradiate
Polianthion wichurae	dense tomentose-felted		♦♦	♦♦ (5–) 8 (–10) P		
Pol. bilocularis	dense tomentose				♦♦ 5-8 (–10)	♦♦♦ 8–10
Pol. minutiflorum	dense tomentose		♦	♦ 2–6		
Pol. collinum	dense tomentose		♦ P	♦ 2–4 (-8) P		
Spyridium globulosum	glabrous		♦♦			
Sp. parvifolium	sparse pubescent-hispid [dense felted, intertwined]		♦♦♦–♦♦♦♦♦ P			[♦♦♦ 6–8 W]
Sp. burragorang	glabrous [dense felted, intertwined]		[♦♦♦]			[♦♦ 6–8 W]
Sp. furculentum *	scattered					♦♦–♦♦♦ (4–) 6–10
Sp. daltonii	glabrous					
Stenanthemum leucophractum *	tomentose	dense	♦♦♦	♦♦ 2–4 P		
St. centrale	dense tomentose		♦♦♦	♦♦♦ 2–4 P		
Serichonus gracilipes	sparse pubescent		♦♦♦			
Papistylus grandiflorus	glabrous, some on M		♦♦ rare			
Blackallia nudiflora	glabrous					
Trymalium ledifolium *	glabrous			M ♦–♦♦ ?		
T. floribundum	sparse pubescent		♦♦♦–♦♦♦♦	M ♦♦–♦♦♦♦ 2 (–4)		
T. wayi	moderate-dense tomentose			♦♦ 2 (–4)		
T. monospermum	glabrous (glaucous)					
Pomaderris angustifolia *	scattered			♦♦ 2–4	♦♦♦ 4–8	
Pom. elliptica	glabrous					
Pom. apetala	scattered					♦♦♦ 10–20
Pom. aspera	scattered					
Pom. racemosa	sparse tomentose-hirsute		♦♦–♦♦♦			
Pom. clivicola	dense velvety			♦♦ 4–5		
Pom. prunifolia	scattered, scabrous		♦♦♦♦			
Pom. lanigera form 1	moderate pubescent		♦♦♦♦–♦♦♦♦♦			
Pom. lanigera form 4	moderate pubescent		♦♦♦			
Pom. vellea	dense velvety		♦♦	♦♦ 2 rare		
Pom. tropica	dense velvety			♦♦ 3–4		
Pom. obcordata	glabrous					
Pom. brevifolia	glabrous M only			♦♦ 1–2		
Siegfriedia darwinioides	glabrous					
Cryptandra amara	glabrous					
C. intratropica	dense tomentose					♦♦ (3–) 4–10
C. intermedia	papillose	moderate-dense	♦♦	♦♦ 4–6		??
C. mutila	papillose	sparse				
C. lanosiflora	glabrous					
C. dielsii	tomentose-hispid		♦			
C. connata	glabrous					

Table 6. Surface sculpturing on the upper surface of leaves of Pomaderreae as observed with SEM. Due to trichome cover on the surface, the surface could not be examined in *Polianthion*, *Stenanthemum* and *Cryptandra intratropica*. An asterisk after the species name indicates that only limited information was available from SEM. Abbreviation: +, presence of type of sculpturing; ?, questionable presence.

Taxon	Wrinkled	Irregular striate	Parallel striate	Punctate	Punctate centre of cells
Spyridium globulosum	+				
Sp. parvifolium		+			
Sp. burragorang		+			
Sp. furculentum *		?			
Sp. daltonii		+			
Serichonus gracilipes	+				
Papistylus grandiflorus	+				
Blackallia nudiflora	+				
Trymalium ledifolium *			+		
T. floribundum			+		
T. wayi			+		
T. monospermum					
Pomaderris angustifolia *		possibly	possibly		
Pom. elliptica					+
Pom. apetala		+			
Pom. aspera		+			
Pom. racemosa		+	possibly radiating from hair base		
Pom. obcordata			+		
Pom. brevifolia		+	+		
Siegfriedia darwinioides		+	+		
Cryptandra amara				+	
C. intermedia				+	
C. mutila				+	
C. lanosiflora			+		
C. dielsii				+	
C. connata				+	

Gemoll (1902) did not distinguish different stellate trichomes, but listed them all under his type IA (Table 2). He reported stellate trichomes with a long multicelled stalk (type IIB) in some species of *Pomaderris*, and with a short multicelled stem (type IA) on the upper surface of *Pom. aspera*. This type IA is possibly a reduced version of type IIB, since in *Pom. aspera* the actual heads of the multiradiate hairs do not differ, only the length of the stalk (Fig. 9D, F). *Spyridium coactilifolium* Reissek, for which Gemoll reports a unique type of trichome (type IIA), was not examined in this study. Similarly, Ross (1990) only distinguishes between sessile and stalked stellate trichomes. The results of these studies are confirmed here with SEM.

Fasciculate hairs were found on nearly all species of *Trymalium*, *Siegfriedia*, *Pomaderris*, *Blackallia*, some species of *Cryptandra* and *Stenanthemum*, and *Polianthion collinum*. The number of rays per hair and the size and shape of fasciculate hairs were variable and ranged from bifid hairs to hairs with 10 rays, but usually 2–8 rays were present. The hairs were mainly observed on the lower surface of the leaf, but in *Trymalium* (e.g. Fig. 7G), *St. leucophractum* (Fig. 5D, E) and *St. centrale* (Fig. 5G, I) they were exclusively found on the upper surface.

Appressed stellate hairs were usually found in combination with other trichomes. They were present as a bottom layer of trichomes in a multi-layered indumentum, and often hidden by the overlaying trichomes. Only in two of the studied species, *Polianthion bilocularis* (Fig. 3D, E) and *Pomaderris angustifolia* (Fig. 8D), appressed stellate hairs were recorded on the upper surface. In 17 other species examined with SEM (Tables 4, 5), appressed stellate trichomes were found on the lower surface; in six of these species only on the midrib and veins. Umbonate appressed stellate hairs were seen on nine of the examined species, including all species of *Trymalium* examined, *Serichonus gracilipes*, *Papistylus grandiflorus*, *Pomaderris obcordata*, *Pom. racemosa* and *Cryptandra mutila*.

Multiradiate trichomes were among the most common trichomes observed, and are usually part of the indumentum of the lower surface of the leaf. Four species were observed to always have multiradiate hairs on the upper surface: *Polianthion bilocularis*, *Pomaderris apetala*, *Pom. aspera* and *Cryptandra intratropica*. Additionally, the floral leaves observed in *Spyridium parvifolium* and *Sp. burragorang* also carried multiradiate hairs on the upper surface. In Pomaderreae, multiradiate trichomes have 4–20 rays. ***Stalked multiradiate trichomes*** were detected on only three species: *Pom. aspera*, *Pom. apetala* and *Pom. racemosa* (Fig. 9). They are identical with Gemoll's type IIB that he reported for *Pom. apetala* (Gemoll 1902) and had multiradiate 'heads' crowded with (6–) 10–40 rays per head. In *Pom. aspera* and possibly *Pom. apetala* the multiradiate trichomes are dendroid with up to three 'heads' (Fig. 9K, L).

Spyridium furculentum has a different kind of stalked multiradiate hair. It has 6–10 rays on a not very well developed 'head' and sits on a broad multicellular base (Fig. 4K). This type of hair is possibly similar to the trichomes of type IIA, reported by Gemoll (1902) for *Sp. coactilifolium*, since the two species are closely related (Kellermann & Barker 2012).

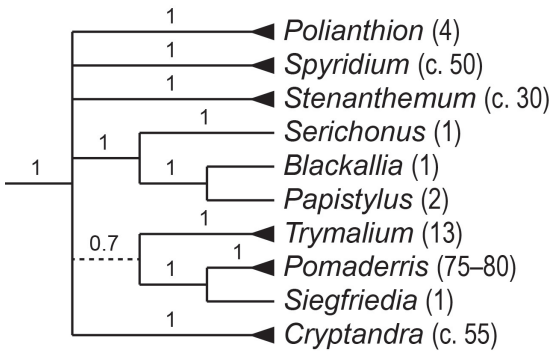

Fig. 12. Summary phylogeny of Pomaderreae, abridged from the Bayesian analysis of the family by Hauenschild *et al.* (2018), using molecular data from 15 DNA regions. Posterior probability is indicated above branches. Nodes with support below 0.7 are collapsed; support below 1 is indicated by a dashed line. Triangles show that more than one taxon was used for the analysis. Species numbers for each genus are indicated in brackets.

Surface sculpturing

The sculpturing on the upper epidermis could not be examined in species with a dense indumentum on the upper surface, i.e. it was not recorded for seven of the 32 examined species (Table 5).

The surface had a distinctly ***wrinkled*** appearance in *Blackallia nudiflora*, *Spyridium globulosum*, *Serichonus gracilipes* and *Papistylus grandiflorus* (Figs 4A, 6A, D, G). It was ***punctate*** in *Cryptandra amara*, *C. connata*, *C. dielsii*, *C. mutila* and possibly *C. intermedia* (Figs 10D, G, 11D, G, J). *Pomaderris elliptica* also displayed a punctate surface (Fig. 8A), however, the punctate surface of each epidermal cell was distinctly sunken, compared to the slightly raised or level surface in the other species. All remaining species had a ***striate*** surface pattern, which was parallel in three species of *Trymalium*, *Pom. obcordata* and possibly *Pom. brevifolia* (Figs 7A, D, G, 8G, J), and irregularly striate elsewhere.

Some of these wrinkles, folds and striations could also be an artefact of drying. However, this could not be ascertained, as fresh material was not available for comparison.

Trichome distribution in Pomaderreae

The distribution of trichomes in the tribe is discussed below, using the clades and genera resolved in phylogenies of the tribe (Kellermann *et al.* 2005; Ladiges *et al.* 2005) and most recent molecular analyses of the family (Hauenschild *et al.* 2016, 2018). A summary phylogeny of the tribe is depicted in Fig. 12.

Polianthion ('Bilocular Clade' of Kellermann *et al.* 2006; Fig. 3)

Characteristic for the four species of this genus is the densely tomentose indumentum of stellate trichomes on both surfaces of the leaf. The upper surface is covered by very short erect fasciculate hairs in *Polianthion minutiflorum* and *Pol. collinum*, and slightly longer ones in *Pol. wichurae*. These three species also have interspersed short simple hairs among the stellate trichomes. *Polianthion bilocularis* has a dense cover of entangled small appressed stellate and larger multiradiate hairs on the upper surface; the presence of simple hairs could not be ascertained. The lower surface of *Pol. wichurae* was covered only by multiradiate trichomes, whereas the other three species had a cover of appressed stellate, multiradiate and simple hairs. These simple hairs were up to 600 µm long in *Pol. bilocularis*. In *Pol. collinum* they were overlying the stellate indumentum of the lower surface, giving the leaf a velvety appearance. *Cryptandra intratropica* is the only other species examined with such a dense indumentum on both leaf surfaces. Its indumentum is similar to that

in species of *Polianthion* in density, but it only seems to consist of multiradiate trichomes. Due to the dense trichome cover, the epidermis could not be examined; in *Pol. wichurae* it is possibly wrinkled (Fig. 3C).

Spyridium (Fig. 4, 5A–C)

Species of *Spyridium* typically have a dense indumentum of stellate and simple trichomes on the lower surface of the leaf. The upper surface is glabrous or sparsely hairy; some species have floral leaves, which are covered with a dense white indumentum.

The upper surfaces of *Spyridium globulosum*, *Sp. burragorang* and *Sp. daltonii* are totally glabrous, the indumentum of *Sp. parvifolium* ranges from glabrous (Walsh 1999) to hispid (in the specimen examined; Fig. 4D, F) on the upper surface and *Sp. furculentum* has sparse stellate trichomes. In *Sp. globulosum* the epidermis has a wrinkled appearance, while in the remaining four species it appears irregularly striate (Fig. 4G). The upper surface of leaves of *Sp. daltonii* is densely covered in conical papillae. The indumentum of floral leaves was observed in *Sp. parvifolium* and *Sp. burragorang*. In both cases it consisted of very dense intertwined multiradiate and simple hairs with curly or spiralling rays (Fig. 4C, L).

The indumentum on the lower surface is composed of multiradiate hairs in all species examined. The distinct multiradiate hairs of *Spyridium furculentum*, which are located on a large base (as mentioned above), have also been reported in the related species *Sp. coactilifolium*, *Sp. coalitum* Kellermann & W.R.Barker, *Sp. fontis-woodii* Kellermann & W.R.Barker, *Sp. halmaturinum* (F.Muell.) F.Muell. ex Benth. and *Sp. scabridum* (Tate) Kellermann & W.R.Barker (Kellermann & Barker 2012). Appressed stellate hairs are visible on the midrib of *Sp. globulosum* and *Sp. daltonii*. Very long erect and spreading simple hairs (up to 1000 µm) were interspersed on the lower surface of *Sp. parvifolium*, becoming denser on the midrib and margins (Fig. 4E, F). The remaining species, except *Spyridium furculentum*, also had long simple hairs on the midrib of the lower surface; additional short simple hairs were found on *Sp. burragorang*.

Gemoll (1902) examined nine species of *Spyridium*, eight of which had stellate hairs of type IA on the lower surface (Table 2), only *Sp. coactilifolium* had trichomes of the unique type IIA.

Stenanthemum (Fig. 5D–I)

Two species of *Stenanthemum* (as defined in Rye 2001; Thiele 2007) were examined. The lower surface is covered in a characteristic densely silky-villous indumentum of long simple hairs, which are overlaying 4-armed multiradiate trichomes. The long simple hairs reach on to the upper surface along the margins. In *St. centrale*, the upper surface is covered with densely arranged erect 2- or 4-armed fasciculate hairs and occasional simple hairs. The upper surface of *St. leucophractum* appears densely papillose-tuberculate with occasional trichomes, however, close examination reveals that the papillae seem to be the bases of simple and fasciculate hairs that failed to develop rays (see above). Long simple hairs overlaying small stellate trichomes on the lower surface have been reported for most species of *Stenanthemum* (Rye 1995a, 2001; Thiele 2007) and seem to be characteristic for the genus.

Three small genera from Western Australia (Fig. 6)

Kellermann *et al.* (2007) described three closely related genera of Pomaderreae: *Blackallia*, *Serichonus* and *Papistylus*. Three species from these genera were examined in this study; the leaf morphology of these species is very similar.

The upper surface of the leaves is wrinkled. Young leaves of *Serichonus gracilipes* (Fig. 6A) and *Papistylus grandiflorus* (Fig. 6D) are moderately covered with simple hairs, which are erect and antrorse, respectively. Leaves become glabrous with age, except for a few hairs remaining at the midrib. *Blackallia nudiflora* (Fig. 6G) has a glabrous upper surface.

The lower surface in all three species is moderately covered with small appressed stellate hairs, which are umbonate in *Se. gracilipes* and *Pap. grandiflorus*; an umbo was not observed in *B. nudiflora*, but in addition, bifid fasciculate hairs were present in this species. These stellate trichomes are covered by a dense silky to villous layer of long antrorse simple hairs, which are straight and closely appressed in *Pap. grandiflorus* and *B. nudiflora*, but in *Se. gracilipes* they appear to be slightly undulating or wavy. The surface of the former two species becomes glabrous with age, whereas in *Se. gracilipes* the indumentum is persistent.

The indumentum on the leaves of these three species is very much alike and a close relationship of *Se. gracilipes*, *Pa. grandiflorus* and *B. nudiflora* can be confirmed from these observations. The hair cover is similar to species of *Stenanthemum*, however, in this genus the upper surface is not glabrous but densely papillose or tuberculate, with or without 2–4-fid trichomes; furthermore, the underlying layer of stellate trichomes on the lower surface is much denser.

Trymalium (Fig. 7)

Four species of *Trymalium* were examined with SEM. *Trymalium monospermum* (Fig. 7K) is an exception within Pomaderreae, as it is the only species that is totally glabrous on all parts of the plant. The leaf surfaces, however, are covered with a conspicuous glaucous layer of wax. As such, this species is not discussed in the following description of trichomes.

The upper surface of the leaves in the remaining species of *Trymalium* is glabrous or moderately to densely covered with erect simple or bifid fasciculate trichomes. With age, the upper surface tends to become glabrous

with only a few hairs remaining on the midrib (e.g. Fig. 7G, J). In leaves, which are otherwise glabrous on the upper surface (Fig. 7A), the midrib also carries hairs. The upper surface in *Trymalium ledifolium*, *T. odoratissimum* subsp. *trifidum* and *T. wayi* displays a parallel striate pattern; no surface sculpturing is discernible in *T. wayi*.

The lower surface has a densely tomentose to felted indumentum in *Trymalium ledifolium* (Fig. 7B, C) and *T. odoratissimum* (Fig. 7E, F), consisting of multiradiate hairs with long patent simple hairs. The midrib of these two species has appressed umbonate stellate hairs lying under long antrorse simple hairs.

The lower surface of *T. wayi* (Fig. 7H, I) consists of a layer of entangled umbonate appressed stellate hairs overlayed by long silky simple hairs. This type of indumentum is also found in *Stenanthemum* and might have developed due to similar selection pressures in these species, since molecular results, inflorescence, floral and fruit characters clearly place *T. wayi* in *Trymalium*. The difference in indumentum might, however, reflect the position of *T. wayi* as a geographically isolated taxon within the genus.

Pomaderris (Fig. 8–9)

With c. 75 species, *Pomaderris* is the largest genus of Pomaderreae. The results of SEM examinations of seven species were augmented with observations by Ross (1990) on five species of *Pomaderris* from Queensland. As can be expected in such a large genus, the indumentum varies quite considerably.

The upper surface of leaves in *Pomaderris* can be smooth and glabrous (*Pom. elliptica*, Fig. 8A), glabrous and wrinkled (*Pom. obcordata* and *Pom. brevifolia*, Fig. 8G, J), although this might be an artefact of drying of thicker leaved species (N.G. Walsh, pers. comm.). The upper indumentum consists of silky to hispid simple (Fig. 9G; Ross 1990) or stellate hairs (Fig. 8D; Ross 1990). The indumentum cover on the upper surface also varies within species, e.g. some forms of *Pom. prunifolia* may be glabrous (N.G. Walsh, pers. comm.) and not bear simple hairs as reported by Ross (1990: Fig. 1A). All species examined by SEM seem to have a parallel or irregularly striate surface pattern, with the exception of *Pom. elliptica*. In this species every epidermal cell is somewhat sunken in the middle and conspicuously punctate.

The indumentum on the lower surface contains both stellate and simple hairs, but five species had stellate hairs only (*Pomaderris apetala*, *Pom. brevifolia*, *Pom. clivicola*, *Pom. prunifolia* and *Pom. tropica*; the latter three not examined with SEM, data from Ross 1990). Simple hairs are very few and sparse in *Pom. elliptica* (see Walsh 1999); often this species is described as being devoid of simple hairs. *Pomaderris vellea* was reported by Ross (1990) to have only an indumentum of long curly simple hairs. However, the simple hairs in that species are extremely dense and completely obscure the underlying layer of stellate hairs (N.G. Walsh, pers. comm.). *Pomaderris brevifolia* appears to have long simple hairs on the lower surface, but these are actually bifid fasciculate hairs.

Walsh & Coates (1997) published an infrageneric classification for *Pomaderris*. Specimens from all but two of the seven sections, sect. *Flabellares* N.G. Walsh and sect. *Annulares* N.G. Walsh, were examined by SEM. Sect. *Biloculares* N.G. Walsh is now a synonym of *Polianthion* (Kellermann *et al.* 2006). Some of these sections, however, are not natural groups, but seem to be para- or polyphyletic assemblages (Kellermann *et al.* 2005; Chen *et al.* 2019). The indumentum characteristics of the lower surface of the leaves given by Walsh & Coates (1997) for the sections were confirmed by SEM in nearly all cases:

Sect. *Psilogyne* N.G.Walsh (represented by *Pomaderris angustifolia*) had a mixture of stellate and simple trichomes, concordant with their definition (Walsh & Coates 1997).

Sect. *Apetalae* N.G.Walsh (represented by *Pomaderris apetala* and *Pom. aspera*) is reported to have stellate trichomes only (Walsh & Coates 1997), but this was only the case in *Pom. apetala*. The lower surface of *Pom. aspera* also may have interspersed erect simple hairs (Fig. 9F, L), which are often not reported (e.g. Walsh 1999).

The largest section, sect. *Pomaderris*, accommodates species with a wide variety of indumenta. It is defined to have a trichome cover "of simple and stellate hairs (rarely stellate hairs only)" (Walsh & Coates 1997: 29). This is corroborated by SEM in *Pom. racemosa* and *Pom. elliptica*, and by the observations of Ross (1990) on *Pom. clivicola*, *Pom. lanigera*, *Pom. prunifolia* and *Pom. vellea*.

Sect. *Umbelliflorae* N.G.Walsh was represented in this study by two species, *Pomaderris brevifolia* from Western Australia and *Pom. obcordata* from southern Australia. Both species have a very similar indumentum of stellate and simple hairs, which agrees with the description of Walsh & Coates (1997), but molecular analyses do not place these two species as sister taxa (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Hauenschild *et al.* 2016, 2018). They are found in two geographically separated clades with species from Western Australia and south-eastern Australia.

Sect. *Flabellaris* is reported to have only a cover of stellate trichomes on the lower surface (Walsh 1990; Walsh & Coates 1997); no species from this section were examined with SEM.

Sect. *Annulares* is defined as having stellate and simple hairs on the lower surface of the leaves (Walsh & Coates 1997). This is confirmed by Ross (1990) in the description of *Pomaderris tropica*, but the illustration of

the lower surface (Ross 1990: Fig. 1E) does not show the simple trichomes reported for that species.

A striking feature of three species examined by SEM, *Pomaderris apetala*, *Pom. aspera* and *Pom. racemosa*, is the presence of stalked multiradiate and dendroid hairs with multiradiate 'heads' (Fig. 9) on the lower surface of the leaves. Gemoll (1902) observed trichomes of type IIB on *Pom. apetala*, *Pom. prunifolia* and *Pom. racemosa* (Table 2). Ross (1990) reports stalked trichomes for *Pom. prunifolia* and Moore (1986) lists stalked trichome types for *Pom. aspera*, *Pom. paniculosa* subsp. *novae-zelandiae* (L.B.Moore) N.G.Walsh, *Pom. edgerleyi* Hook.f. (as *Pom. prunifolia* var. *edgerleyi* (Hook.f.) L.B.Moore) and *Pom. rugosa* Cheeseman.

In *Pomaderris apetala* these hairs have short stalks and heads with 10–20 (–25) rays (Fig. 9C). The observation of "dense sessile stellate hairs" by Walsh (1999: 91) is probably due to the fact that the short stalks are hard to identify under a dissecting microscope. Long-stalked multiradiate hairs are found in *Pom. aspera* and *Pom. racemosa*, the heads of both species having more rays than *Pom. apetala*. Dendroid multiradiate hairs are recorded in *Pom. aspera* (Fig. 9K, L) with up to three 'heads' per trichome.

Walsh & Coates (1997) do not group these species with stalked or dendroid hairs together, but place *Pomaderris apetala*, *Pom. aspera*, *Pom. paniculosa* and *Pom. rugosa* into sect. *Apetalae*. *Pomaderris prunifolia*, *Pom. oraria* and *Pom. racemosa* are arranged in sect. *Pomaderris*. This corresponds with an indumentum of sparse multiradiate hairs on the upper leaf surface of the species placed into sect. *Apetalae* and the presence of simple trichomes on species from sect. *Pomaderris* (Fig. 9G; Walsh 1999). The molecular analyses (Kellermann *et al.* 2005; Ladiges *et al.* 2005; Hauenschild *et al.* 2016, 2018) only included three of these taxa, *Pom. oraria*, *Pom. edgerleyi* and *Pom. rugosa*; resolution within *Pomaderris* was limited. Whether the stalked and dendroid trichomes have arisen twice independently or only once, should be the subject of future research.

Siegfriedia (Fig. 10A–C, F)

Sister taxon to *Pomaderris* is the monotypic genus *Siegfriedia* (Kellermann *et al.* 2005; Hauenschild *et al.* 2016, 2018). The upper leaf surface of *Si. darwinioides* is glabrous with deep folds (Fig. 10A); the epidermis displays a strigose pattern. The lower surface of the species is covered in a very dense, intertwined, often felted and matted indumentum of long curly bifid and four-armed fasciculate hairs that fill the cavity within the revolute leaf (Fig. 10B, C, F).

The indumentum of *Siegfriedia* is unique in Pomaderreae, and has not been observed in any other species. Although flower and fruit morphology, as well as the molecular results indicate a close relationship of *Pomaderris* and *Siegfriedia*, this cannot be ascertained from this survey of leaf trichomes. *Siegfriedia darwinioides* is very distinctive in many vegetative and floral characteristics, indumentum being only one of many (Rye 1996).

Cryptandra (Fig. 10C–L, 11)

Seven species were examined of *Cryptandra*. *Cryptandra connata*, previously included in the genus *Blackallia*, displayed indumentum characteristics comparable to other species of *Cryptandra*. This is confirmed by the results of molecular analysis (Kellermann *et al.* 2005; Hauenschild *et al.* 2016, 2018).

The upper surface for all except one of the species examined, *Cryptandra intratropica*, is typically glabrous or sparsely pubescent. *Cryptandra amara*, *C. connata* and *C. lanosiflora* have a totally glabrous surface. Some papillae are found on *C. mutila* (Fig. 11J) and *C. dielsii* has a cover of sparse hispid erect simple hairs (Fig. 11D). *Cryptandra intermedia* has a moderate to dense indumentum of simple and fasciculate hairs on the upper surface. The indumentum of *C. intratropica* only consists of dense multiradiate hairs. The irregular nature of these trichomes (in regards to ray length and thickness or degree of spreading of the rays) is comparable to *C. intermedia*, but different from the uniform trichomes covering the upper surface of *Polianthion wichurae* or *Pol. minutiflorum* (Fig. 3C, L).

Epidermal sculpturing of the surface was observed in all species, except *Cryptandra intratropica*, due to the dense cover of trichomes on the upper surface. Parallel striate patterns are present on *C. lanosiflora* (Fig. 11A). The five remaining species have a characteristic punctate pattern on all cells of the epidermis (e.g. Figs 10D, 11D, G, J). This punctate surface is different to the one observed in *Pomaderris elliptica*, since in that species the centre of each epidermal cell seems to be slightly sunken (Fig. 8A; see above).

Two types of indumentum were found on the lower surface of *Cryptandra* species. The lower surface of *Cryptandra amara* and *C. mutila* is totally glabrous, with only a few appressed antrorse simple hairs along the midrib. The exception was one appressed stellate trichome with umbo present on the *C. mutila* specimen examined (Fig. 11L). This is the first report of stellate hairs on *C. mutila*, which so far was thought to be one of only a few species of Pomaderreae without stellate hairs (K.R. Thiele, pers. comm.).

The remaining taxa have a moderate to dense indumentum of stellate trichomes (fasciculate, appressed stellate and multiradiate hairs) on the lower surface. The leaf is usually closely revolute and obscuring the lower surface. In *Cryptandra dielsii* and *C. intermedia* the lower surface is totally obscured (Figs 10H, I, 11E, F), whereas in *C. lanosiflora* and *C. connata* the midrib is exposed and then covered with long antrorse simple hairs (Fig. 11B, C, H, I).

Cryptandra intratropica has more or less flat leaves with a dense stellate indumentum on the lower surface of the leaf (Fig. 10K, L). Morphologically, it is closely related to *C. filiformis* A.R.Bean and *C. triplex* K.R.Thiele ex Kellermann, two species of *Cryptandra* that share the dense stellate indumentum with *C. intratropica*, in addition to inflorescence and floral characteristics (Kellermann 2006).

Conclusion

The indumentum of the leaves of Pomaderreae was examined with Scanning Electron Microscopy for 32 species. Although this was only a limited sample set, preliminary conclusions can be drawn on the taxonomic significance and function of the trichomes.

A dense indumentum on the lower surface of the leaves was found in nearly all taxa. The main function of these hairs may be the prevention of water loss, which is particularly important in arid ecosystems (Ehleringer 1984). In many Pomaderreae species that occur in arid or semi-arid environments, this is paired with xerophytic, strongly recurved or revolute leaves, which fully or partly obscure the lower surface, e.g. in *Cryptandra dielsii* (Fig. 11F), *Siegfriedia darwinioides* (Fig. 10C) or *Spyridium furculentum* (Fig. 4K).

Species of *Stenanthemum* (Fig. 5H, F), *Serichonus gracilipes*, *Papistylus grandiflorum* and *Blackallia nudiflora* (Fig. 6B, E, H), *Trymalium wayi* (Fig. 7H) and *Polianthion collinum* (Fig. 3H), which grow in similar arid conditions, meet this environmental challenge with incurved conduplicate leaves (e.g. Fig. 6F) that are covered in a dense layer of long appressed simple hairs on the lower surface (the outer surface in conduplicate leaves). This silky or villous layer is usually white, grey or silver in colour, presumably reflects the sunlight, and therefore decreases the amount of radiation absorbed by the leaf (Holmes & Keiller 2002). This effect is reinforced by folded leaves, i.e. only very little sunlight is actually received by the upper (inner) surface of the leaves. A decrease in leaf temperature also helps to reduce transpiration (Johnson 1975).

Many species of *Pomaderris*, *Trymalium* and *Spyridium* occur in mesic environments, e.g. *T. odoratissimum* in the forests of south-west Western Australia. These species have larger leaves, which are covered in a variety of indumenta. Prevention of water loss during the summer months might be one explanation for the development of complex stalked and dendroid trichomes of *Pom. aspera* or *Pom. racemosa* (Fig. 9). However, an additional explanation for the development of these hairs could be defence against predators (Johnson 1975), which find it much easier to eat the large soft leaves of *Trymalium* or *Pomaderris*, compared to the xerophytic hard leaves of, for example, *Cryptandra* or *Siegfriedia*. The deposition of eggs may be obstructed by trichomes (Levin 1973). There is also evidence that leaf indumentum protects against parasitic algae, fungi and bacteria (Johnson 1975).

The indumentum on the upper surface of the leaves is more variable within genera and even within species (*cf.* Ross 1990 for *Pom. prunifolia*). Many species of *Spyridium* and *Stenanthemum* develop floral leaves around the inflorescences. These special leaves are covered in a conspicuous white, dense and felty indumentum and are thought to attract pollinators to the flowers. The minute flowers within one head-like inflorescence of *Spyridium* and *Stenanthemum* (containing up to 50 flowers in some species) usually bloom over a long period, with only one or two flowers being open at a time. Attracting possible pollinators with 2–6 floral leaves seems to be a better expenditure of resources for the plant, than producing large showy individual flowers. In a way, taxa with floral leaves mimic the appearance of capitula of Asteraceae.

A dense cover of stellate hairs on the upper surface of the leaves is also present in a number of unrelated taxa that occur in the tropical north of Australia, such as *Cryptandra filiformis* (Bean 2004), *C. intratropica* (Fig. 10J, L), *Pomaderris tropica* (Ross 1990) or *Polianthion minutiflorum* (Fig. 3J, L). It is possible that this is in response to higher exposure to sun and increases the reflectance of the leaves.

It is interesting to note that the only species in Pomaderreae that is totally glabrous, *Trymalium monospermum*, has a conspicuous glaucous, waxy epidermis (pers. obs.) and adapted to the arid environment by increasing surface wax production instead of a dense indumentum. It is not known, whether other species of Australian Rhamnaceae have waxy leaves.

Trichomes and indumenta on leaves of species of Pomaderreae are not always constant within genera or groups of species, but often variable, a fact that might reflect the development of indumenta being mostly associated with their function rather than with the phylogeny of species. However, in some groups, such as *Stenanthemum*, *Cryptandra* or the three small genera *Blackallia*, *Serichonus* and *Papistylus*, indumentum characters seem more constant and might be of value when defining genera and elucidating relationships between taxa. The examination of more species with SEM is needed to complete the data-set and to be able to draw firm conclusions on the taxonomic significance of leaf indumentum in the 'Australian stellate-haired Rhamnaceae'.

Acknowledgments

Jocelyn Carpenter and Dr Simon Crawford (School of Botany, The University of Melbourne, now incorporated into the School of Biosciences) introduced me to SEM and assisted with the preparation of specimens. The Directors of CANB, MEL and PERTH provided access to specimens and gave permission to remove

plant material. I am grateful to the Director of the Australian National Botanic Gardens (ANBG), Canberra, for permission to collect leaf material from their living collections. Collection permits and free access to FloraBase were provided by the Western Australian Department of Environment and Conservation (now Department of Biodiversity, Conservation and Attractions). Dave Albrecht (NT, now CANB) and D.V. Matthews (Alice Springs) organised plant material of *Stenanthemum centrale*. Hellmut Toelken (AD) and Neville Walsh (MEL) are thanked for commenting on earlier drafts of this paper. Most of the research was undertaken during PhD studies at The University of Melbourne, supervised by Pauline Ladiges and Frank Udovicic, and supported by a Melbourne Research Scholarship, the Sophie Ducker Postgraduate Scholarship and the Dawson Bursary from the University of Melbourne. This study was in part supported by a Melbourne University Research Development Grant to P.Y. Ladiges; it is written in preparation of the *Flora of Australia* treatment of Rhamnaceae, funded by Research Grants from the Australian Biological Resources Study (ABRS).

References

Ančev, M. & Goranova, V. (2006). Trichome morphology of eleven genera of the tribe Alysseae (Brassicaceae) occuring in Bulgaria. *Willdenowia* 36: 193–204.

Ávalos, S.V. & Salinas, A.D. (2003). Los tricomas foliares en la caracterización de un grupo de especies del género *Quercus*, sección *Lobatae* (Fagaceae). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica* 74: 5–15.

Baillon, H. (1875). Monographie des Célastracés et des Rhamnacées. In: *Histoire des plantes* 6: 1–92. (Hachette & Cie.: Paris).

Baillon, H. (1880). Rhamnaceae. In: *Natural History of Plants* 6: 52–94. (L. Reeve: London).

Bean, A.R. (2004). New species of *Cryptandra* Sm. and *Stenanthemum* Reissek (Rhamnaceae) from northern Australia. *Austrobaileya* 6: 917–940.

Brongniart, A.T. (1826). *Mémoire sur la famille des Rhamnés*. (Didot le Jeune: Paris). [Republished without the preface in *Annales des sciences naturelles* 10: 320–385, pl. 12–17, 1827].

Chen, S.H., Guja, L.K. & Schmid-Lebuhn, A.N. (2019). Conservation implications of widespread polyploidy and apomixis: a case study in the genus *Pomaderris* (Rhamnaceae). *Conservation Genetics* — doi.org/10.1007/s10592-019-01184-2.

Ehleringer, J. (1984). Ecology and ecophysiology of leaf pubescence in North American desert plants. In: Rodriguez, E., Healey, P.L. & Mehta, I. (eds), *Biology and chemistry of plant trichomes*, pp. 113–132. (Plenum Press: New York).

Fenzl, E. (1837). Rhamneae. In: Endlicher, S.F.L., Bentham, G., Fenzl, E. & Schott, H. (eds), *Enumeratio plantarum quas in Novae Hollandiae ora austro-occidentali ad Fluvium Cygnorum et in Sinu Regis Georgii collegit Carolus liber baro de Hügel*, pp. 20–27. (F. Beck: Vienna).

Gemoll, K. (1902). Anatomisch-systematische Untersuchung des Blattes der Rhamneen aus den Triben: Rhamneen, Colletieen und Gouanieen. *Beihefte zum Botanischen Centralblatt* 12: 351–424.

Granada-Chacón, W.A. & Benítez de Rojas, C. (2005). Morfología de tricomas foliares en especies de *Solanum* sección *Acanthophora* (Solanaceae), presentes en Venezuela. *Sida, Contributions to Botany* 31: 1675–1694.

Grès, L. (1901). *Contribution a l'étude anatomique et microchimique des Rhamnées*. (P. Brodard: Coulommiers).

Hauenschild, F., Matuszak, S., Muellner-Riehl, A.N. & Favre, A. (2016). Phylogenetic relationships within the cosmopolitan buckthorn family (Rhamnaceae) support the resurrection of *Sarcomphalus* and the description of *Pseudoziziphus* gen. nov. *Taxon* 65: 47–64.

Hauenschild, F., Favre, A., Michalk, I. & Muellner-Riehl, A.N. (2018). The influence of the Gondwanan breakup on the biogeographic history of the ziziphoids (Rhamnaceae). *Journal of Biogeography* 45: 2669–2677.

Herzog, T. (1903). Anatomisch-systematische Untersuchung des Blattes der Rhamneen aus den Triben: Ventilagineen, Zizypheen und Rhamneen. *Beihefte zum Botanischen Centralblatt* 15: 95–207.

Hewson, H.J. (1988). *Plant indumentum: a handbook of terminology*. (Bureau of Flora and Fauna: Canberra).

Holmes, M.G. & Keiller, D.R. (2002). Effects of pubescence and waxes on the reflectance of leaves in the ultraviolet and photosynthetic wavebands: a comparison of a range of species. *Plant, Cell and Environment* 25: 85–93.

Hooker, J.D. (1862). Rhamneae. In: Bentham, G. & Hooker, J.D. (eds), *Genera plantarum* 1: 371–386. (A. Black: London)

Hopkins, H.C.F., Pillon, Y., Stacy, E.A. & Kellermann, J. (2015). *Jaffrea*, a new genus of Rhamnaceae endemic to New Caledonia, with notes on *Alphitonia* and *Emmenosperma*. *Kew Bulletin* 70: article 42 (19 pp.).

Hummel, K. & Staesche, K. (1962). Die Verbreitung der Haartypen in den natürlichen Verwandtschaftsgruppen. In: Zimmermann, W. & Ozenda, P.G. (eds), *Handbuch der Pflanzenanatomie* IV(5): 209–250. (Gebrüder Borntraeger: Berlin).

Johnson, H.B. (1975). Plant pubescence: an ecological perspective. *The Botanical Review* 41: 233–258.

Johnston, M.C. (1974). Revision of *Scutia* (Rhamnaceae). *Bulletin of the Torrey Botanical Club* 101: 64–72.

Johnston, M.C. & Johnston, L.A. (1987). Rhamnus. *Flora Neotropica Monograph* 20.

Jones, J.H. (1986). Evolution of Fagaceae: the implications of foliar features. *Annals of the Missouri Botanic Garden* 73: 228–275.

Kellermann, J. (2006). *Cryptandra triplex* K.R.Thiele ex Kellermann, a new species of Rhamnaceae (Pomaderreae) from Arnhem Land, Northern Territory. *Austrobaileya* 7: 299–303.

Kellermann, J. & Barker, W.R. (2012). Revision of the *Spyridium bifidum-S. halmaturinum* complex from South Australia and Victoria. *Muelleria* 31: 26–58.

Kellermann, J., Rye, B.L. & Thiele, K.R. (2006). *Polianthion*, a new genus of Rhamnaceae (Pomaderreae) from Western Australia and Queensland. *Australian Systematic Botany* 19: 169–181.

Kellermann, J., Rye., B.L. & Thiele, K.R. (2007). *Blackallia*, *Serichonus* and *Papistylus*: three closely related genera of Rhamnaceae (Pomaderreae) from south-western Australia. *Nuytsia* 16: 299–315.

Kellermann, J. & Udovicic, F. (2008). Large indels obscure phylogeny in analysis of cpDNA (trnL-F) sequence data: Pomaderreae (Rhamnaceae) revisited. *Telopea* 12: 1–22. [Proceedings of the ASBS conference 'Plant diversity in the tropics', Cairns].

Kellermann, J., Udovicic, F. & Ladiges, P.Y. (2005). Phylogenetic analysis and generic limits of the tribe Pomaderreae (Rhamnaceae) using internal transcribed spacer DNA sequences. *Taxon* 53: 619–631.

Koch, K. (1858). Bericht über die größere Frühjahrs-Austellung am 11 April 1858. *Verhandlunges des Vereines zur Beförderung des Gartenbaues in den Königlich Preußischen Staaten Neue Reihe* 6: 52–65.

Kok, R.P.J. de & West, J.G. (2002). A revision of *Pultenaea* (Fabaceae). 1. Species with ovaries glabrous and/or with tufted hairs. *Australian Systematic Botany* 15: 81–113.

Labillardière, J.J.H. de (1804). *Novae Hollandiae plantarum specimen*. (Paris).

Lackey, J.A. (1978). Leaflet anatomy of Phaseolae (Leguminosae: Papilionoideae) and its relation to taxonomy. *Botanical Gazette* 139: 436–446.

Ladiges, P.Y. (1984). A comparative study of trichomes in *Angophora* Cav. and *Eucalyptus* L'Hérit. – a question of homology. *Australian Journal of Botany* 32: 561–574.

Ladiges, P.Y., Kellermann, J., Nelson, G., Humphries, C.J. & Udovicic, F. (2005). Historical biogeography of Australian Rhamnaceae, tribe Pomaderreae. *Journal of Biogeography* 32: 1909–1919.

Levin, D.A. (1973). The role of trichomes in plant defence. *The Quarterly Review of Biology* 48: 3–15.

Medan, D. & Schirarend, C. (2004). Rhamnaceae. In: Kubitzki, K. (ed.), *The Families and Genera of Vascular Plants* 6: 320–338. (Springer: Berlin and Heidelberg).

Moore, L.B. (1986). *Pomaderris* revisited. *Tane* 31: 139–143.

Napp-Zinn, K. (1973). Blattanatomie der Angiospermen: Entwicklungsgeschichtliche und topographische Anatomie des Angiospermenblattes (Anatomie des Blattes II.A). In: Linsbauer, K., Tischler, G. & Pascher, A. (eds), *Handbuch der Pflanzenanatomie* VIII(2A), part 1. (Gebrüder Borntraeger: Berlin).

Nge, F.J., Biffin, E., Kellermann, J. & Waycott, M. (2019). Biogeography of Pomaderreae (Rhamnaceae) across the ditch: Multiple dispersal events from Australia to New Zealand [poster]. In: Meudt, H. & Elliot, R. (eds), *Taxonomy for Plant Conservation – Ruia mai i Rangiātea: Joint Conference of the Australasian Systematic Botany Society (ASBS) and the New Zealand Plant Conservation Network (NZPCN), 24–28 November 2019*, p. 67. (Museum of New Zealand, Te Papa Tongarewa: Wellington).

Onstein, R.E., Carter, R.J., Xing, Y., Richardson, J.E. & Linder, H.P. (2015). Do Mediterranean-type ecosystems have a common history?—Insights from the Buckthorn family (Rhamnaceae). *Evolution* 69: 756–771.

Otto, E. (1845). *Verzeichniss einer Auswahl von im Freien ausdauernden Bäumen, Gesträuchen und Staudengewächsen, so wie von Hauspflanzen welche im Hamburgischen botanischen Garten abgegeben werden können*. (J.A. Meissner: Hamburg).

Otto, E. (1849). Auswahl schön oder selten blühender Pflanzen im botanische Garten zu Hamburg während des Monats März 1849. *Neue allgemeine deutsche Garten- und Blumenzeitung* 5: 216–218.

Peacock, R.J. (1987). *Variation in the* Pomaderris apetala-aspera *complex*. GradDipSci (Hons) thesis, University of Tasmania.

Reissek, S. (1840). Rhamneae. In: Endlicher, S.F.L (ed.), *Genera plantarum secundum ordines naturales disposita*, pp. 1094–1104. (Fr. Beck: Vienna).

Reissek, S. (1848) [1846–1847]. Rhamneae: synopsis specierum Novae Hollandiae austro-occidentalis. In: Lehmann, J.G.C., *Plantae Preissianae sive enumeratio plantarum quas in Australasia occidentali et meridionali-occidentali annis 1838-1841 collegit Ludovicus Preiss* 2: 279–291. (Meissner: Hamburg).

Reissek, S. (1857). Plantae Muellerianae: Rhamneae. *Linnaea* 29: 265–96.

Richardson, J.E., Fay, M.F., Cronk, Q.C.B., Bowman, D. & Chase, M.W. (2000a). A phylogenetic analysis of Rhamnaceae using *rbc*L and *trn*L-F plastid sequences. *American Journal of Botany* 87: 1309–1324.

Richardson, J.E., Fay, M.F., Cronk, Q.C.B. & Chase, M.W. (2000b). A revision of the tribal classification of Rhamnaceae. *Kew Bulletin* 55: 311–340.

Rollins, R.C. & Banerjee, U.C. (1976). Trichomes in studies in Cruciferae. In: Vaughhan, J.G., MacLeod, A.J. & Jones, B.M.G, *The Biology and chemistry of the Cruciferae*, pp. 145–166. (Academic Press: London).

Roe, K.E. (1971). Terminology of hairs in the genus *Solanum*. *Taxon* 20: 501–508.

Ross, E.M. (1990). *Pomaderris* Labill. (Rhamnaceae) in Queensland,1. *Austrobaileya* 3: 309–317.

Rye, B.L. (1995a). New and priority taxa in the genera *Cryptandra* and *Stenanthemum* (Rhamnaceae) of Western Australia. *Nuytsia* 10: 255–305.

Rye, B.L. (1995b). New and priority taxa in the genera *Spyridium* and *Trymalium* (Rhamnaceae) of Western Australia. *Nuytsia* 10: 119–140.

Rye, B.L. (1996). A synopsis of the genera *Pomaderris*, *Siegfriedia*, *Spyridium* and *Trymalium* (Rhamnaceae) in Western Australia. *Nuytsia* 11: 109–131.

Rye, B.L. (2000). *Trymalium monospermum* (Rhamnaceae), a new species from south-western Australia. *Nuytsia* 13: 339–343.

Rye, B.L. (2001). A taxonomic update of *Stenanthemum* (Rhamnaceae: Pomaderreae) in Western Australia. *Nuytsia* 13: 495–507.

Steudel, E.G. (1845) [1844–1845]. Rhamneae Brown. In: Lehmann, J.G.C., *Plantae Preissianae sive enumeratio plantarum quas in Australasia occidentali et meridionali-occidentali annis 1838–1841 collegit Ludovicus Preiss* 1: 182–189. (Meissner: Hamburg).

Suessenguth, K. (1953). Rhamnaceae. In: Engler, H.G.A. & Prantl, K.A.E., *Die Natürlichen Pflanzenfamilien* (2nd edn) 20d: 7–173. (Duncker & Humblot: Berlin)

Tschan, G.F. & Denk, T. (2012). Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, *Quercus* subsection *Galliferae* (Fagaceae): Implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* 169: 611–644.

Thiele, K.R. (2007). Two new species of Australian *Stenanthemum* (Rhamnaceae: Pomaderreae). *Journal of the Adelaide Botanic Gardens* 21: 63–70.

Thiele, K.R. & West, J.G. (2004). *Spyridium burragorang* (Rhamnaceae), a new species from New South Wales, with new combinations for *Spyridium buxifolium* and *Spyridium scortechinii*. *Telopea* 10: 823–829.

Uphof, J.C.T. (1962). Plant hairs. In: Zimmermann, W. & Ozenda, P.G. (eds), *Handbuch der Pflanzenanatomie* IV(5): 1–206. (Gebrüder Borntraeger: Berlin).

van Santen, M. & Linder, H.P. (2020). The assembly of the Cape flora is consistent with an edaphic rather than climatic filter. *Molecular Phylogenetics and Evolution* 142: 106645.

Walsh, N.G. (1990). The *Pomaderris oraria* F.Muell. complex in Australia. *Muelleria* 7: 267–287.

Walsh, N.G. (1999). *Pomaderris*. In: Walsh, N.G. & Entwisle, T.J. (eds), *Flora of Victoria* 4: 85–109. (Inkata: Port Melbourne)
Walsh, N.G. & Coates, F. (1997). New taxa, new combinations and an infrageneric classification in *Pomaderris* (Rhamnaceae). *Muelleria* 10: 27–56.
Weberbauer, A. (1895). Rhamnaceae. In: Engler, H.G.A. & Prantl, K.A.E. (eds), *Die Natürlichen Pflanzenfamilien* III(5): 393–427. (Wilhelm Engelmann: Leipzig)
Wildeman, É. de (1899). *Pomaderris racemosa* Hook. *Icones selectae horti Thenensis* 1: 31–34, pl. VIII.
Zarre, S. (2003). Hair micromorphology and its phylogenetic application in thorny species of *Astragalus* (Fabaceae). *Botanical Journal of the Linnean Society* 143: 323–330.