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Corolla venation in Stylidiaceae

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Abstract

Corolla venation in 112 species of Stylidiaceae was studied using light microscopy. *Levenhookia*, *Phyllachne* and two annual species of *Stylidium* exhibit the simplest pattern of venation in which the midvein remains unbranched or, as observed in *P. colensoi*, branches once. In *Forstera*, *Oreostylidium* and the remaining species of *Stylidium*, the midvein branches at the base producing an almost palmate pattern that varies in complexity according to the species in question. In *Stylidium*, the labellum always has a simpler pattern of venation than its four larger counterparts; the midvein often remaining unbranched. A feature unique to the *S. scandens* complex is a vascular trace in the long basal labellum appendages. The throat appendages of 10 species were found to have a vascular supply.

Keywords: corolla, venation, Stylidiaceae, taxonomy, systematics

Introduction

The family Stylidiaceae comprises five genera and over 240 species that are characterized by the presence of a central floral column that bears the anthers and stigma at the apex. In the most prolific genus, *Stylidium*, the column is typically touch-sensitive, hence the common name of "trigger plants". The flowers in all family members are usually pentamerous, although some species of *Phyllachne* and *Forstera* are variable for this trait and have between five and nine corolla segments (Mildbraed 1908; Allan 1961; Curtis 1963). *Phyllachne*, *Forstera* and *Oreostylidium* all have corolla lobes that are regularly arranged and of similar size. The two remaining genera have a highly modified anterior petal, termed the labellum, which is hooded over the column in *Levenhookia*, and greatly reduced (yet morphologically diverse) in *Stylidium*. The corolla lobes in all genera are united at the base to form a corolla tube.

Gustafsson (1995) examined corolla venation patterns in five species of Stylidiaceae as part of a broader study on the petal venation trends within the Asterales and, in a systematic study on Stylidiaceae, Laurent *et al.* (1999) further investigated this character in an additional 20 species. Corolla venation patterns are shown in the illustrations from a recent taxonomic revision of *Stylidium* subgenus *Andersonia* (Bean 2000), although they are not specifically mentioned in the text. The present study examined corolla venation patterns in a broad range of species, with the aim of investigating differences in venation between the four larger corolla lobes and the labellum. The throat appendages (or paracorolla) located at the base of the corolla lobes in many species of *Stylidium* and *Levenhookia* were also examined for the presence of a vascular supply. This research forms part of a wider study on the systematics of Stylidiaceae.

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Methods

One hundred and twelve species were investigated, including representatives from all genera and each of the main morphological groupings within *Stylidium* (Table 1). Whole corollas were cleared in 70% ethanol and, where necessary, the labellum (which typically has a thickened area of tissue termed the boss) was cleared in 25% sodium hydroxide. Corolla venation patterns were then studied using light microscopy. Several flowers of each taxon were studied from one or more populations. Herbarium voucher specimens will be lodged at PERTH on completion of related research.

Results and Discussion

In all of the taxa examined, a solitary vascular trace feeds each of the corolla segments. The trace remains solitary in both *Phyllachne uliginosa* (Gustafsson 1995) and *P. clavigera* (Laurent *et al.* 1999); however, in *P. colensoi* the vein may branch once (Fig 1A). In contrast, the corolla veins in *Forstera tenella* are sparsely branched; the midvein diverges near the base of the corolla lobes and the lateral branches, which often branch again, extend towards the margins of the lobes (Fig 1B). This general pattern was first observed by Gustafsson (1995) and has also been recorded for *F. bidwillii* and *F. bellidifolia* (Laurent *et al.* 1999).

In accordance with previous observations, species of *Levenhookia* have a single unbranched vascular trace in both the corolla lobes and the hooded labellum (Fig 1C). An unbranched trace also occurs in both *Stylidium despectum* and *S. utricularioides* (Fig 1D) and is evident in the illustrations of *S. cordifolium* and *S. divergens* provided by Bean (2000).

In the majority of trigger plants, the vascular trace diverges at the base of each corolla lobe producing an

Table 1

Specimens of Stylidiaceae examined for the description of corolla venation patterns. Species are organized alphabetically under the groupings of Mildbraed (1908). Species in which a solitary vein was observed in the labellum are indicated with an asterix. JAW = J A Wege.

Phyllachne: *P. colensoi* (Hook f) Bergg JAW 189.

Forstera: *F. tenella* Hook f JAW 559.

Oreostylidium: *O. subulatum* (Hook f) Berggr JAW 558.

Levenhookia: **L. leptantha* Benth JAW 194a, JAW 251; **L. pauciflora* Benth JAW 209, JAW 363, JAW 380; **L. preissii* (Sond) F Muell JAW 151, JAW 154; **L. pusilla* R Br JAW 100, JAW 179, JAW 360; **L. stipatata* F Muell JAW 96, JAW 120, JAW 512.

Stylidium* subgenus *Centridium (Lindl) Mildbr: **S. calcaratum* R Br JAW 7, JAW 196, JAW 500; **S. edentatum* Lowrie & Carlquist JAW 370, JAW 371; **S. perpusillum* Hook f JAW 248, JAW 364.

Stylidium* subgenus *Forsteropis (Sond) Mildbr: **S. imbricatum* Benth JAW 563; **S. leeuwinense* Lowrie & Kenneally JAW 522; **S. preissii* (Sond) F Muell JAW 66; **S. semaphorum* Lowrie & Kenneally JAW 523.

Stylidium* subgenus *Andersonia (R Br) Mildbr: **S. candellabrum* Lowrie & Kenneally JAW 483; **S. lobuliflorum* F Muell JAW 478, JAW 481; **S. ensatum* A R Bean JAW 470; **S. schizanthum* F Muell JAW 473, JAW 480.

Stylidium* subgenus *Tolypangium (Endl) Mildbr:

Section *Despectae* Mildbr: **S. despectum* R Br JAW 304, JAW 440; **S. inundatum* R Br JAW 138, JAW 274, JAW 416; **S. longitubum* Benth JAW 314; **S. obtusatum* Sond JAW 508; **S. periscelianthum* Erickson & Willis JAW 218, JAW 235; **S. pulchellum* Sond JAW 116, JAW 273; **S. roseo-alatum* Erickson & Willis JAW 118, JAW 281; **S. udusicola* Lowrie & Kenneally JAW 329; **S. utricularioides* Benth JAW 125, JAW 452.

Section *Debilia* Mildbr: **S. semipartitum* F Muell JAW 471, JAW 476.

Section *Floodia* Mildbr: **S. turbinatum* Lowrie & Kenneally JAW 477, JAW 484.

Section *Sparsifoliae* (Benth) Mildbr: *S. glandulosum* Salisb JAW 65.

Section *Repentes* Mildbr: *S. repens* R Br JAW 286; **S. sacculatum* (Erickson & Willis) Lowrie, A H Burb & Kenneally JAW 19.

Section *Guttatae* Mildbr: *S. guttatum* R Br JAW 119, JAW 175, JAW 461.

Section *Junceae* Mildbr: *S. junceum* R Br JAW 30, JAW 279; *S. laciniatum* C A Gardner JAW 185; *S. squamosotuberosum* Carlquist JAW 180.

Section *Verticillatae* (Benth) Mildbr: *S. galioides* C A Gardner JAW 375; *S. nonscandens* Carlquist JAW 21, JAW 219, JAW 224; *S. scandens* R Br JAW 297, JAW 377, JAW 423, JAW 443, JAW 462; *S. verticillatum* F Muell JAW 159.

Section *Echinospermum* Mildbr: *S. limbatum* F Muell JAW 256.

Section *Saxifragoideae* Mildbr: *S. aeonioides* Carlquist JAW 397; *S. albolilacinum* (Erickson & Willis) Lowrie & Carlquist JAW 222; *S. amoenum* R Br JAW 103, JAW 421; *S. articulatum* R Br JAW 162; *S. assimile* R Br JAW 178; *S. barleei* F Muell JAW 98, JAW 444; *S. brunonianum* Benth JAW 284, JAW 400; *S. carlquistii* Lowrie JAW 28, JAW 417; *S. carnosum* Benth JAW 490; *S. diuroides* Lindl JAW 31, JAW 287, JAW 418; *S. glabrifolium* Lowrie & Kenneally JAW 392; *S. lineatum* Sond JAW 110, JAW 122; *S. lowrieanum* Carlquist JAW 147, JAW 438; *S. luteum* R Br JAW 169, JAW 305; *S. maitlandianum* E Pritzel JAW 211; **S. pritzelianum* Mildbr JAW 524; *S. rupestre* Sond JAW 61, JAW 366; *S. spathulatum* R Br JAW 437; *S. squamellosum* DC JAW 355, JAW 390; *S. striatum* Lindl JAW 289; *S. violaceum* R Br JAW 163, JAW 428.

Section *Lineares* (Benth) Mildbr: **S. arenicola* Carlquist JAW 255b, JAW 257; *S. caespitosum* R Br JAW 181; **S. ciliatum* Lindl JAW 102, JAW 420; *S. drummondianum* Lowrie & Carlquist JAW 192, JAW 326; *S. hispidum* Lindl JAW 158, JAW 278; *S. piliferum* R Br JAW 14, JAW 208; *S. spinulosum* R Br JAW 164, JAW 177.

Section *Squamosae* (Benth) Mildbr: *S. affine* Sond JAW 499; *S. albomontis* Carlquist JAW 56, JAW 79; *S. caricifolium* Lindl JAW 238; *S. crossocephalum* F Muell JAW 22, JAW 207; *S. hirsutum* R Br JAW 165, JAW 298; *S. leptocalyx* Sond JAW 29, JAW 513; *S. macranthum* Carlquist JAW 64, JAW 365; *S. maritimum* Lowrie, Coates and Kenneally JAW 491; *S. nungarinense* S Moore JAW 264, JAW 356; *S. pilosum* Labill JAW 373; *S. plantagineum* Sond JAW 301; *S. pseudohirsutum* Mildbr JAW 302; **S. scabridum* Lindl JAW 509; *S. schoenoides* DC JAW 84, JAW 348.

Stylidium* subgenus *Nitrangium (Endl) Mildbr:

Section *Sonderella* Mildbr: *S. divaricatum* Sond JAW 115, JAW 453; *S. kalbarriense* Lowrie & Kenneally JAW 198, JAW 317; **S. macrocarpum* (Benth) Erickson & Willis JAW 285; *S. ricae* Carlquist JAW 345; *S. tenuicarpum* Carlquist JAW 45, JAW 395; *S. torticarpum* Lowrie & Kenneally JAW 404, JAW 406.

Section *Appressae* Mildbr: **S. adpressum* Benth JAW 205, JAW 514; **S. choreanthum* Erickson & Willis JAW 255a, JAW 258.

Section *Thyrsiformes* (Benth) Mildbr: *S. bulbiferum* Benth JAW 516; *S. burbidgeanum* Lowrie & Kenneally JAW 405, JAW 409; *S. confluens* Banyard & James JAW 341, JAW 342; *S. crassifolium* R Br JAW 92, JAW 433; *S. dichotomum* DC JAW 40, JAW 454; *S. elongatum* Benth JAW 197, JAW 318; **S. eriopodum* DC JAW 294; *S. induratum* M Scott JAW 335; *S. lateriticola* Kenneally JAW 457; **S. leptophyllum* DC JAW 20, JAW 133; *S. merrallii* (F Muell) T Durand & B D Jackson James sn (Yannamooning Rock); *S. neglectum* Mildbr JAW 130, JAW 131; *S. pycnostachyum* Lindl JAW 132, JAW 408; *S. uniflorum* Sond JAW 48, JAW 139.

Section *Rhynchangium* Benth: **S. adnatum* R Br JAW 97, JAW 435, JAW 520; **S. falcatum* R Br JAW 87; **S. fasciculatum* R Br JAW 143, JAW 434; **S. rhynchocarpum* Sond JAW 141, JAW 313.

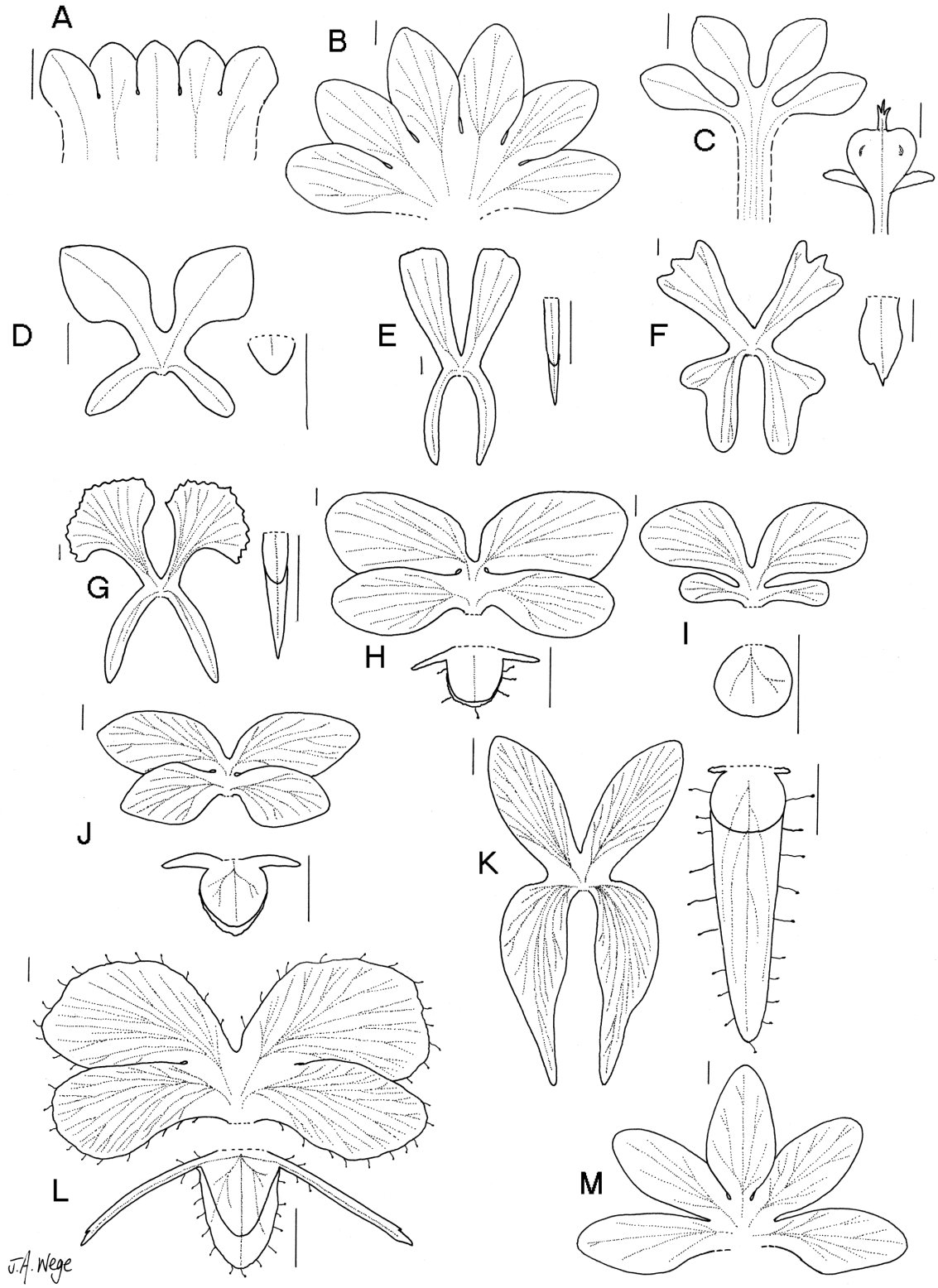

Figure 1. Corolla venation patterns in Stylidiaceae. Where present, the labellum has been detached and drawn separately at a different scale: in vertically-paired flowers it is positioned to the right of the four main corolla lobes, whereas in laterally-paired flowers it is situated underneath. Scale bars at 1 mm. **A:** *Phyllachne colensoi*; **B:** *Forstera tenella;* **C:** *Levenhookia preissii*; **D:** *Stylidium utricularioides*; **E:** *S. obtusatum*; **F:** *S. calcaratum*; **G:** *S. choreanthum*; **H:** *S. fasciculatum*; **I:** *S. burbidgeanum*; **J:** *S. glandulosum*; **K:** *S. crossocephalum*; **L:** *S. scandens*; **M:** *Oreostylidium subulatum*.

almost palmate pattern that varies in complexity across the genus (Figs 1E-L). In those species that bear corolla lobes of unequal size, the smaller lobes often have a solitary vein whilst their larger counterparts have a branched pattern (*e.g.* Fig 1E; *cf* Figs 3G, 5C & 7F of Bean 2000). The largest flowers, such as those belonging to subgenus *Tolypangium* sections *Squamosae* and *Verticillatae*, have the most complex pattern of venation with a number of branches occurring along the midvein and at the tips of the lateral branches (*e.g.* Figs 1K & 1L). As recorded by Laurent *et al.* (1999), *Oreostylidium* has a branching venation pattern similar to that found in *Forstera* and many species of *Stylidium* (Fig 1M).

The labellum in *Stylidium* has a simpler pattern of venation than the larger corolla lobes and in many species the trace is unbranched (Table 1; Fig 1D-H). Alternatively, the midvein branches at the base to produce two lateral veins that may divide again (Figs 1I & 1J). Additional branching occasionally occurs along the length of the midvein (Fig 1K). *Stylidium scandens* is unique in having prominent lateral veins that extend along the length of the basal appendages (Fig 1L).

Although the throat appendages typically lack a vascular supply, veins are present in the conspicuous wing-like appendages of species belonging to *Stylidium* subgenus *Forsteropsis* and in subgenus *Tolypangium* sections *Verticillatae* and *Squamosae* (Table 2; Fig 2). The wing-like appendages are attached to the base of the anterior corolla lobes and, where present, the vascular supply originates from the main trace entering the anterior corolla lobe. The additional tooth-like throat appendages attached to the posterior petals of these species do not receive a vascular supply.

Table 2

Species of *Stylidium* in which the throat appendages (paracorolla) have a vascular supply. S = solitary vein; B = branching vein.

Subgenus	Section	Species	Vasculature
Forsteropsis		*S. leeuwinense*	S
Tolypangium	*Verticillatae*	*S. galioides*	S or B
		S. scandens	S or B
	Squamosae	*S. affine*	S
		S. caricifolium	B
		S. hirsutum	S or B
		S. macranthum	B
		S. maritimum	S or B
		S. nungarinense	B
		S. pseudohirsutum	S

Within each of the above-mentioned subgeneric groupings there is often variation in the presence of and the pattern of throat appendage venation. Within subgenus *Forsteropsis*, the wing-like throat appendages in *S. leeuwinense* have a solitary vein and those in *S. semaphorum* and *S. imbricatum* have no vascular supply, whilst *S. preissii* lacks the wing-like appendages altogether. Within section *Squamosae*, the vascular trace may be absent (*e.g. S. crossocephalum*, *S. leptocalyx*, *S. pilosum*), remain solitary (*e.g. S. pseudohirsutum*) or branch into two to four traces (*e.g. S. caricifolium*, *S. macranthum*). Similar variation is also evident within section *Verticillatae* with the vascular trace absent in

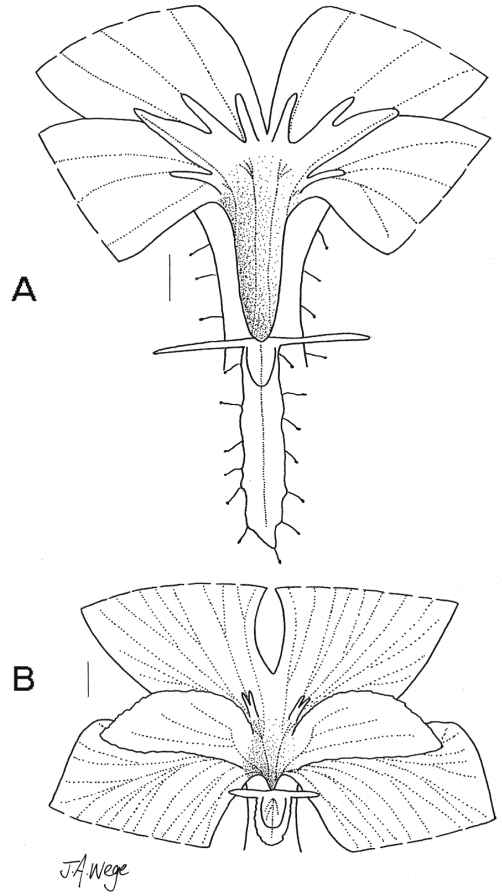

Figure 2. Examples of throat appendage (paracorolla) venation in *Stylidium*. Scale bars at 1 mm. **A:** *S. leeuwinense*; **B:** *S. maritimum*.

S. nonscandens and *S. verticillatum*, but present and typically branched in *S. scandens*. Interestingly, two yellow-flowering populations of *S. scandens* (JAW 423 and JAW 443) lack basal labellum appendages and have a solitary throat appendage vein. Throat appendage and labellum venation patterns may provide useful characters to taxon delimitation in a revision of this group. However, given that the morphology of the labellum and the throat appendages can be variable within and between populations of the same species (Raulings 2001; personal observations) the venation patterns should be assessed across more populations to determine whether they are taxonomically reliable characters. This is a salient point given that flowers of *S. galioides*, a species known from only one locality, were found here to have throat appendages with either a solitary or a branched vascular trace. This variation was also evident between populations of *S. hirsutum* and within populations of *S. maritimum*.

The different patterns of corolla venation described here are yet another example of the immense diversity found within Stylidiaceae and particularly within *Stylidium*. Venation patterns may provide useful characters in the study of systematic relationships within

the family and potentially in the definition of species boundaries.

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