

A pretty problem: the flowers of *Vinca major* (Apocynaceae)

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Introduction

In this article I examine the floral biology of *Vinca major*, a familiar weedy plant with flowers nearly as complex as those of its relative the moth-plant, *Araujia hortorum* (Gardner 2017). It is suggested that only an inability to make much fruit is preventing *V. major* from becoming a serious pest.

Vinca major, native to Europe, is commonly known as periwinkle, or sometimes, larger periwinkle, to distinguish it from *V. minor* (rare in New Zealand). It is a herbaceous perennial of the 'cast iron' sort, being nearly immune to drought, insects and fungal diseases. Its sprawling stems root at the nodes and make a dense cover that excludes most lesser plants, including the seedlings of tree species.

Flora of New Zealand IV (Sykes 1988: 142) says that *V. major* is found in this country in waste places, "particularly in the shade", and also, that it is a "widespread escape from cultivation". I rather doubt this second statement. True, the plant was grown in the warmer gardens of 19th century Britain as an attractive exotic and could well have been brought to New Zealand as such. But I think that its vigour here would have soon made it unacceptable, even to sentimental gardeners.

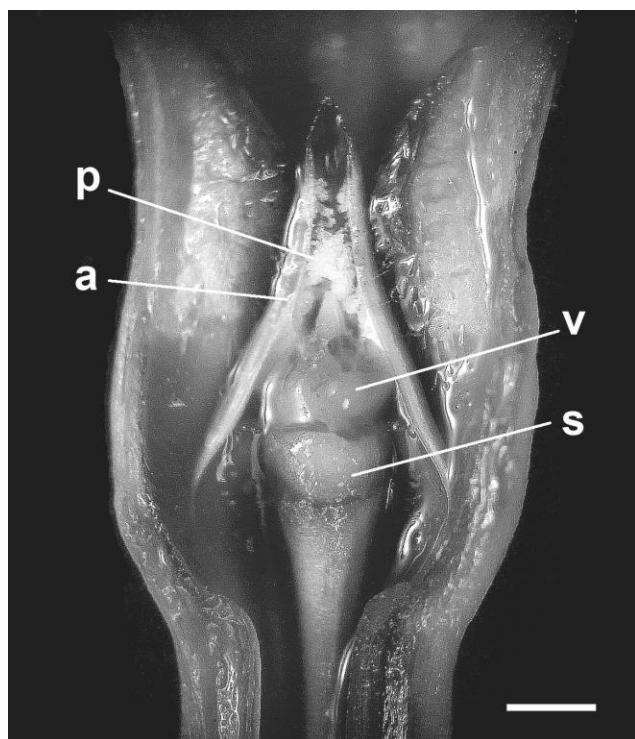


Fig. 1. *Trachelospermum jasminoides*. Upper part of corolla tube, opened to show anther cone and style-head. **a**, anther; **p**, pollen; **v**, viscin-producing part of style head; **s**, stigmatic zone. Anthers 4.5 mm long. Iodine solution added to provide contrast. Based on a cultivated plant; not vouchered. Scale bar 1 mm.

There is another reason to quibble about exactly which category of weed *V. major* belongs to: it does produce fruit and seeds. However, the frequency of the fruit may be very low compared to that of the flowers. The only two populations I have examined in this respect covered ten or more square metres and carried flowers from late October to mid-January. One then made at least two fruits, but the other, seemingly none at all.

Flower structure in Apocynaceae

Vinca major was one of the plants experimented on by Charles Darwin in his study of self- and cross-fertilization (Owens & Miller 2009). He found that seed was not formed when insects were excluded from the flowers but were when pollen from another plant was introduced on a needle (Darwin 1861: 552). Unfortunately, the (control) selfing experiments were not made, so the only conclusion to be drawn is that without insect visitation the plants are infertile.

Before considering what the natural pollinators of *V. major* might be we need to understand the structure of the apocynaceous flower. The family is a highly derived ('advanced') one and has a unique set of complex adaptations for insect-mediated outbreeding. These are elaborated on in the following paragraphs; for more detail see Fallen (1986).

The most remarkable floral features of the Apocynaceae are those of the stamens and style/stigma (Fig. 1). The five stamens are seated on the corolla tube, sometimes near its middle or low down. The filaments are usually short and robust. The five anthers are 'connivent', that is, they lie alongside one another and lean inwards to form a cone (our *Parsonsia capsularis* provides a familiar example). They are dart-shaped, with hardened sides that form 'guide rails' for probing insects (cf. *Araujia*). They have two pollen-sacs ('thecae') adaxially, each divided lengthwise into two lobes. The stamens do not change in position as the flower ages.

Pollen is shed from the anthers in the inwards direction, sometimes only from their upper part, because the lower part of the outer anther-lobes is often a sterile tail. The grains are usually quite smooth. Accumulating inside the anther-cone, they are prevented from falling to the bottom of the corolla by the conspicuously swollen apex of the style, the 'style-head'.

The complexity of the style-head was appreciated long ago and only rarely is it referred to just as a stigma. It generally has the form of a thick disc or

cone two or more times wider than the columnar part of the style below. Its lower rim may be flanged, or drawn out downwards as a 'pollen scraper' skirt. The upper rim may be flanged, or carry short hairs. Between the upper and lower rim lies the curved side of the head. In longitudinal section this is concave or flat, or convex (in the case of a conical style-head). It is responsible for one of the crucial features here, the production of 'viscin', an opaque, gummy sugar-polymer. The spread of viscin across to the upper part of the anther-filaments accomplishes three things: the anthers are kept in position; pollen is prevented from dropping past the sides of the style-head; and the near-continuous ring of viscin below the anthers enables pollen to be stuck onto the proboscis of a visiting insect.

Then where is the stigma? It seems this is not usually apparent by colour or texture, at least to the naked eye. It is generally situated on the lower half

of the style-head, immediately below the viscin-producing ring, as a continuous band or as five stigmatic zones. But sometimes it is situated right underneath the style-head, that is, between the pollen-scraper and the top of the style column. (see Notes 1 & 2 below).

Pollination is effected by an insect probing towards the base of the flower for nectar produced by the glands around the ovary. This activity, directed down between the sides of the anthers, is often guided by lines of colour that run from the corolla lobes down to the anther cone, and then by fluting of the corolla tube and/or vertical lines of retrorse hairs alternating with glabrous strips. When the proboscis is withdrawn from the lower part of the tube it picks up a covering of viscin and then pollen. On a visit to a second flower the mixture is scraped off on the lower part of the style-head, or adheres to the viscin ring. Insects able to reach the nectar will be rewarded for

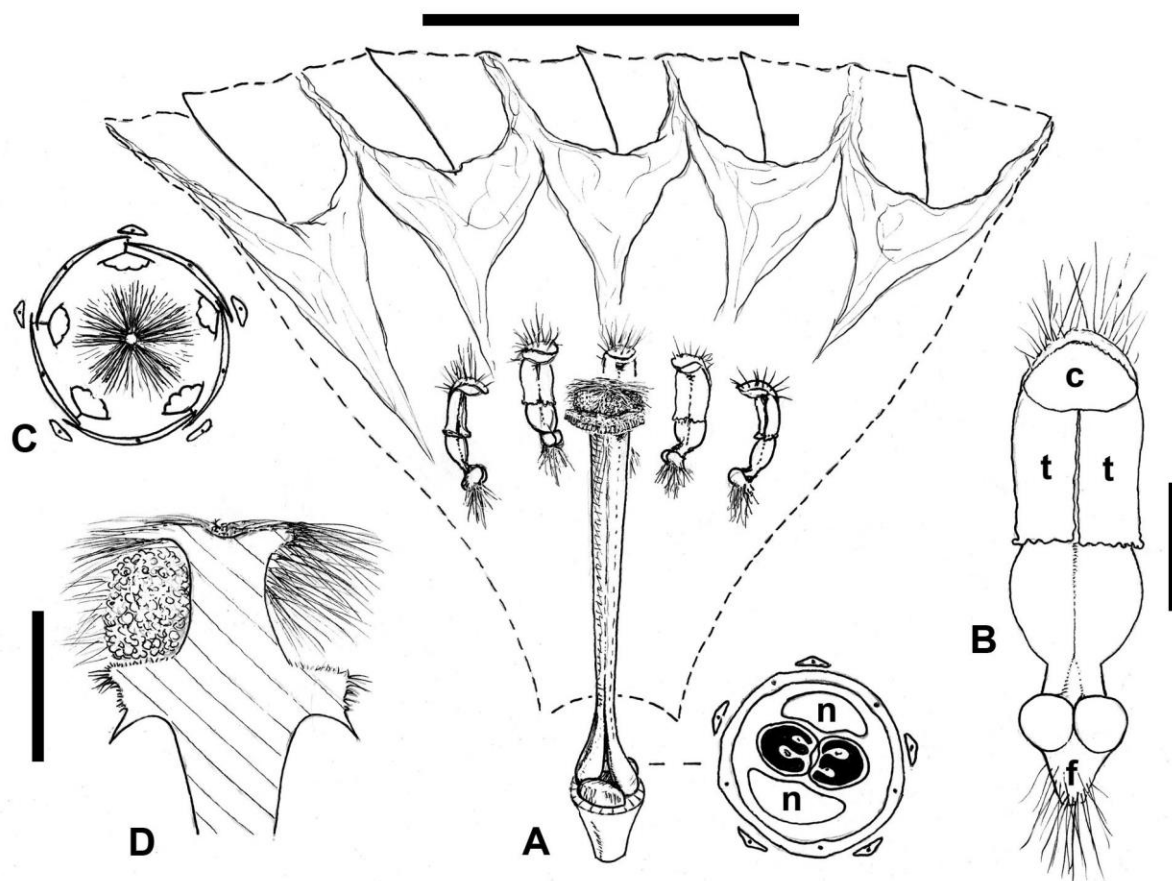
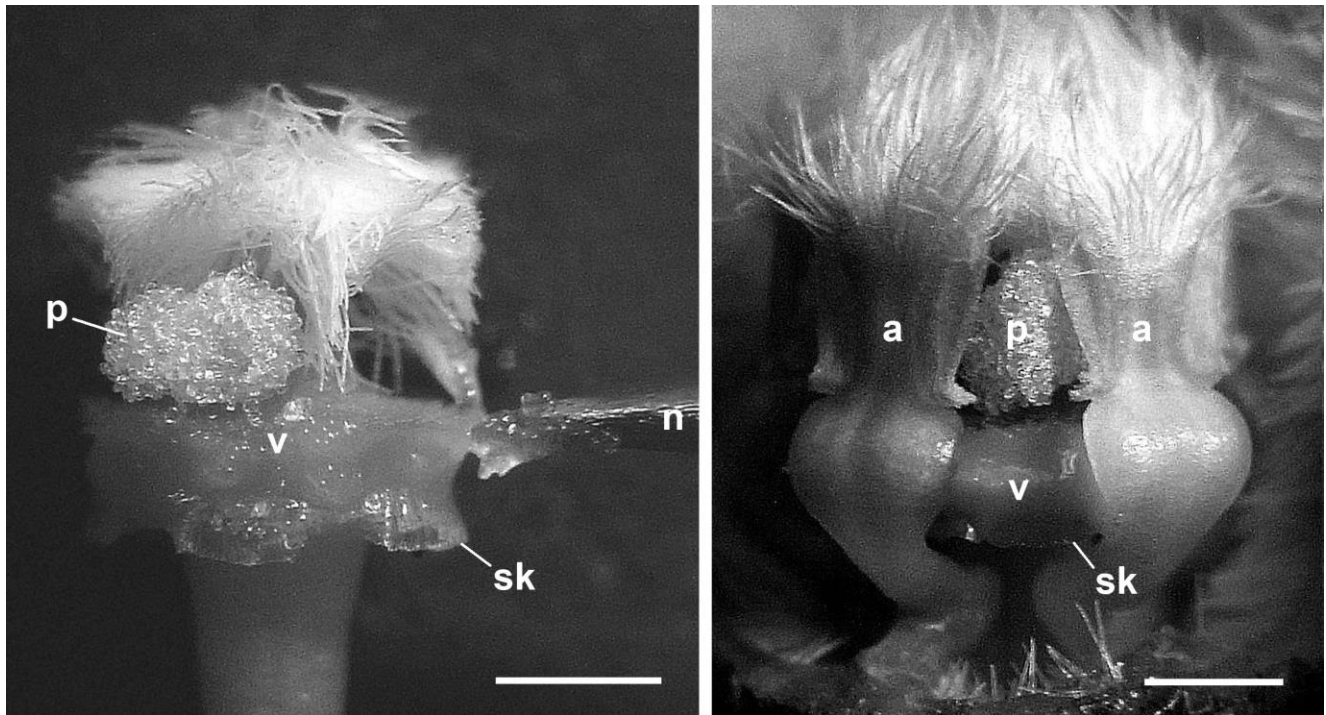


Fig. 2. *Vinca major*, floral features. Based on a plant wild in Fowlds Park, Mt Albert; not vouchered. **A.** Flower (sepals and most of each corolla lobe removed; hairs of corolla tube not shown). A lobed corona alternates with the petals. The ovary is superior, of two carpels that fuse above to form the style. Section on lower right shows the two nectary glands (**n**) and the parietal placentation of the carpels. Scale bar 1 cm. **B.** Stamen (dehiscent), viewed adaxially and slightly from below, in outline. The top of the anther, and the basal part of the filament, are set with bristly hairs. Below the top of the anther, above the pollen sacs, is a pale thickened structure (**c**), like a flat hollow cushion. **t**, thecae (pollen sacs), **f**, the base of the filament, set with hairs directed down and inwards. Scale bar 1 mm. **C.** Floral diagram. Note that the style-head has five denser groups of hairs, which are directed towards the stamens and form the sides of the "alcoves" into which pollen will be shed. **D.** Style-head in longitudinal section. The "alcove" on the left, sectioned medially, contains a pollen mass. The lower part of the head has an orange, scarios 'pollen scraper' skirt, and above it a wide viscin-producing ring, bearing hairs that become longer towards the upper rim of the disc. Location of transmission tissue not detectable in hand-sections. Scale bar 1 mm.



Figs. 3 & 4: *Vinca major*, style head and anthers, from a plant in Fowlds Park, Mt Albert. Scale bars 1 mm. **3** (left). Style head, with a needle (**n**) pulling away viscin (**v**) from its concave edge. **p**, pollen mass; **sk**, 'pollen scraper' skirt. **4** (right). External view of two post-dehiscence anthers (**a**) and style-head. A pollen mass (**p**) visible, below which appears the wide viscin-producing ring of the style-head (**v**), and below it the 'pollen scraper' skirt (**sk**).

this service, but even shorter-tongued ones, that can only reach a little past the style-head, will be able to carry out a few cross-pollinations before learning that they have nothing to gain from such visits.

Flowers that need to be cross-pollinated often have quite a long life-span. So, it is not hard to imagine that, after a week or more of wind and rain and perhaps an episode or two of inappropriate behaviour by visitors, a small amount of a flower's pollen might fall downwards to reach the stigmatic zone. In the Apocynaceae a self-incompatibility mechanism may often prevent this from leading to seed being formed. Detailed studies are few, but it seems likely that, as in the sister-family Asclepiadaceae, a 'late-acting' incompatibility is involved, that is, the self-pollen can germinate and grow down the style and into the ovules, but here the process stops.

The flower of *Vinca*

The ancestral member of the Apocynaceae was probably a woody tropical plant. As a herbaceous temperate genus, then, *Vinca* would be expected to have flowers with highly derived features, and in fact both its male and female parts have become unique (Figs. 2–4). The anther-cone is formed largely by the orange, bristly, expanded tops of the anthers. Underneath each of these, above the two, short, pollen-bearing thecae, there is a flattened, hollow and firm-textured 'cushion', a modification of either the upper part of the thecae or the connective apex. Like the tuft of

bristles sported by the top of the anther, it may serve to guard the pollen from robber-insects.

When the pollen thecae dehisce, their lower edge turns upwards as a short stiff rill and just catches onto the upper rim of the style-head. Presumably this is a positioning aid. Similarly, the slight indentation at the apex of the 'knee' part of the strongly geniculate filament sits against the columnar part of the style immediately below the style-head. Lastly in this list of modifications, just below the thecae the filament expands sideways into a pair of slightly cupular flaps, which contact the viscin-producing part of the style-head and would help contain the viscin's spread. All these features can be seen in Figs. 2–4.

The *Vinca* style-head is just as remarkable. Here is the description by Darwin (1862: 552):

"The pistil ... is a curious object, consisting of a style, thickening upwards, with a horizontal wheel on the top; and this is surmounted by a beautiful brush of white filaments. The concave tire of the wheel is the stigmatic surface, as was very evident when pollen was placed on it, by the penetration of the pollen tubes [Note 3]. The pollen is soon shed out of the anthers and lies embedded in [five] little alcoves in the filamentous brush above the stigma."

The projection of the pollen inwards onto the style-head is of some interest. Firstly, the "alcoves" alternate with the anthers, so the pollen mass in

each comes half from the anther on the left and half from the one on the right. In my observation though, the five masses are not clearly bipartite, as if their emplacement had been quite forcible.

Pollination ecology in New Zealand

The flowers of this plant remain open for quite a long time, perhaps a couple of weeks, and this suggests that they need to be cross-pollinated. What might the pollinators of *V. major* in New Zealand be, and could their rarity explain why only a low amount of fruit is made?

Blue-coloured flowers of temperate regions typically have bees as their co-evolved pollinators. Knuth (1909: 87) lists several kinds of bee as visitors to the plant in Europe. In New Zealand, only one of our introduced bumblebees, *Bombus hortorum*, has a tongue long enough (c. 1 cm) to reach the nectar of the *V. major* flower, although the smaller bumblebees and the honey-bee are of a size that would allow them to insert their heads down into the flower and probe some way past the anthers and the style-head. However, my casual observation of one local colony failed to detect any pollinators at all. Nor are any bee-visitors to *V. major* listed by Donovan (2007).

Also, our local colonies of periwinkle, if they have spread clonally by 'garden discard' mode, would mostly be of the same incompatibility genotype. Then, even if insect visitors were quite numerous, cross-fertilization would be a rare event. On this scenario, the rather few fruits produced at the present time would mostly represent failures of the incompatibility system.

Unfortunately, new genotypes could be introduced to New Zealand under varietal or cultivar names, on the supposition that no threat is posed since "the species is already in the country". This could bring about a great increase in the amount of fruit produced. The shade-tolerant nature of the plant could then result in it becoming a serious weed of native forests.

Acknowledgements

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Notes

Note 1: To find the stigmatic zone one could try to observe the penetration of pollen tubes into the style-head, but it is easier to test sections of the latter for particular enzymes or locate in these sections the position of the 'transmission tissue', down which the pollen tubes must grow (Fallen 1986).

Note 2: It is surprising how hard it is to ascertain from the literature just where the stigma of any particular apocynaceous plant is located — even some modern Floras omit this information (Forster 1996) or contain erroneous statements (Smith 1998). In particular, the two horn-like processes often present on the top of the style-head resemble stigmas, but a little thought shows how unlikely it is that they could be: always enclosed by the anther cone, and covered by self-pollen, they could only be reached by foreign pollen in exceptional, disruptive circumstances.

Note 3: Some more Darwin-bashing: since modern authorities place the stigmatic zone of *Vinca* on the underside of the style-head, it seems that what he saw was the germination of the pollen grains rather than the penetration of the tubes into the style-head tissue. The experiment needs repeating.

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