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BARRIERS TO SEXUAL COMPATIBILITY IN RHODODENDRON

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ABSTRACT. The normal pollination process and pistil structure of *Rhododendron* are briefly described along with methods for observing pollen tube development within the pistil using epifluorescence microscopy. Characteristic pollen tube abnormalities and sites of arrest are distinguished for incompatible interspecific and intergeneric pollinations, with particular reference to crosses involving sect. *Vireya* as one parent. The germination characteristics of resulting intersubgeneric hybrid seed are compared with those of normal intrasectional hybrid seed. Juvenile indumentum of species and hybrid seedlings is examined to confirm hybridity, and the vigour of the hybrid seedlings is assessed as a guide to their future development.

INTRODUCTION

Although many families of flowering plants have dry stigmas, in *Rhododendron* (Ericaceae) the stigma surface, when receptive, is wet with a copious liquid exudate. Compatible pollen germinates in this stigmatic fluid and the pollen tubes penetrate through grooves in the stigma surface into a hollow mucilage-filled style down which they grow to enter the ovary and fertilize the ovules. Little is known about the physiology of pollination for the wet-stigma, hollow-style system of the Ericaceae (Shivanna, 1980). We have investigated both compatible and incompatible pollinations and here give results for pollinations involving *Rhododendron* sect. *Vireya* as one parent.

The technique used to observe pollen tube growth after pollination has been described by Williams *et al.* (1982), and is summarized in Fig. 1. Briefly, whole pistils were collected 7, 14 and 21 days after normal hand pollinations, fixed in 3:1 ethanol:acetic acid and stored in 70% ethanol. After transfer to 10% aqueous sodium sulphite the pistils were autoclaved and stained in decolorized aniline blue. They were then squashed in stain on a microscope slide and the coverslip sealed with petroleum jelly. The squashed pistils were examined using epifluorescence microscopy, the pollen tubes being located by the yellow fluorescence of the callose polysaccharide component of their walls and plugs. In addition to squash preparations hand-cut cross-sections of fresh, pollinated pistils were also used to study the pathway of pollen tube growth through the pistil in normal pollinations.

The structure of the pistil in *Rhododendron* is shown diagrammatically in Fig. 2 based on sections through the stigma, style and ovary of *R. dalhousiae*. Basically the pistils are 5-partite and symmetrical in cross-section, although some may be more than 5-partite and less strictly symmetrical. Grooves between the five stigma lobes are continuous with a 5-channelled stylar canal filled with a mucilaginous secretion which is continuous with the surface exudate of the stigma. At the base of the style the arms of the canal separate and each becomes the groove between two

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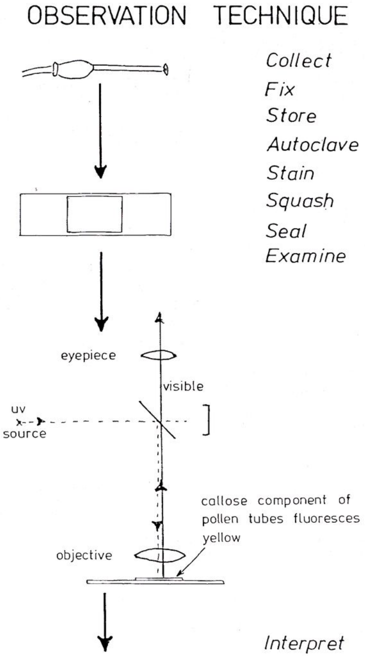


FIG. 1. Diagrammatic summary of the method used for epifluorescence miscroscopic examination of pollen tubes stained with decolorized aniline in pistil squashes of *Rhododendron* (see text).

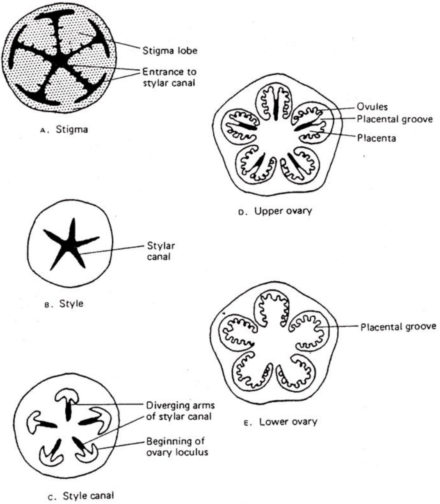
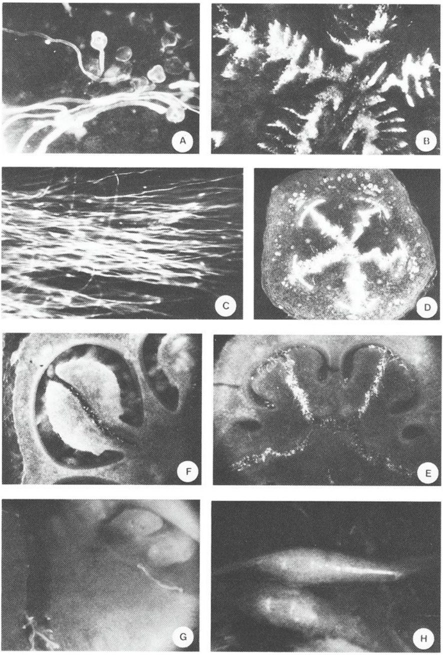


FIG 2. Diagrammatic cross-section of a pistil of *R. dalhousiae* at pollination. A, showing the surface covered with stigmatic exudate (light stipple) grading into stylar mucilage (solid black) at the top of the stylar canal. B & C, showing the black areas filled with mucilage. D, showing mucilage restricted to a tapering narrow strand in the inner region of each placental groove. E, showing the shallow placental groove at the base of the ovary that channels the pollen tubes out into the placental surface. (After Williams *et al.*, 1982).

placentae in one loculus of the ovary. The mucilage of the style canal extends into the ovary down the inner region of these grooves. At pollination the ovary loculus itself is not filled with mucilage, but a mucilaginous secretion appears to be present in the ovular micropyles. Ovules are attached so that the micropyles are close to the placental surface.

POLLEN TUBE BEHAVIOUR AFTER COMPATIBLE POLLINATIONS

Compatible pollen placed on the stigma germinates in the stigmatic secretion and pollen tubes grow across the stigma surfaces within the


A
B
C
D
F
E
G
H

exudate (Fig. 3A). Within 24 hours the pollen tubes have passed down into the style canal (Fig. 3B), and after several days (5–7 for many *Rhododendron* species), the tubes reach the base of the style (Fig. 3C, D). In the style compatible tubes are straight with thin-walled ends and regular callose plugs deposited at intervals behind the growing tips.

When the tubes reach the ovary (Fig. 3E), they grow vertically down the groove between the placentae of each loculus (Fig. 3F), progressively turning to emerge horizontally from the placental groove and grow across the surface of the placenta (Fig. 3G) to reach the ovular micropyles (Fig. 3H). Twenty-one days after compatible pollinations, fertilized ovules have visibly enlarged, but apart from an initial zygote callose wall no further callose is deposited in the embryo sac or micropylar region once embryo development has commenced.

POLLEN TUBE ARREST AFTER INCOMPATIBLE POLLINATIONS

In *Rhododendron* the pollination pathway is open via mucilaginous secretions from the stigma surface right into the ovary. Thus it would appear to provide an ideal germination and growth system for any pollen alighting on the stigma surface. However, we have found that discrimination against foreign pollen occurs in this mucilage at a number of points in the pathway from the stigma surface to the embryo sac within the ovule. For incompatible crosses within the genus *Rhododendron,* and between *Rhododendron* and closely related genera within the Ericaceae, arrest of pollen tubes may occur at any one of the inhibition points 1–7 shown in Fig. 4. Although arrest points 6 and 7 are presently only provisionally identified, in certain crosses tubes regularly enter the ovules without achieving fertilization. The site of arrest is characteristic of the species crossed but apparently not absolutely related to current taxonomic classification since certain crosses within *Rhododendron* show abortion on the stigma surface, whereas the pollen tubes of the ericaceous species *Kalmia latifolia* for example penetrate the styles of several *Rhododendron* species and the embryo sacs of *R. kawakamii.*

Arrested pollen tubes may show one or more of a range of characteristic cytological abnormalities depending on the species involved and the site of arrest within the pistil. These abnormalities fall into two major classes: errors in tip growth (Fig. 5) and anomalies in callose

FIG. 3. Normal aniline blue-stained pollen tubes on compatible stigmas. A, pollen tubes of *R. javanicum* on stigma surface. B, cross-section of a pollinated *Vireya* rhododendron pistil just below the stigma surface showing the upper part of the stylar canal delineated by the brightly fluorescent pollen tubes. C, normal pollen tubes of *R. konori* near the base of a compatible *Vireya* style. D–G, Transverse sections (T.S.) of a compatible self-pollinated *R. dalhousiae* pistil. D, T.S. near base of style showing the 5-armed canal delineated by fluorescent pollen tubes. E, T.S. of a pollinated *R. dalhousiae* pistil at top of ovary just above the level of ovules; the arms of the style canal, delineated by fluorescent pollen tubes, are separating to guide the pollen tubes into 5 ovary loculi. F–G, T.S. of a self-pollinated *R. dalhousiae* pistil at about mid-ovary: F, fluorescent pollen tubes in the placental groove of one ovary loculus; G, shows (at higher magnification) pollen tubes emerging from the placental groove onto the placental surface, among the ovules. H, ovule of the *Vireya* hybrid (*R. phaeopeplum* × *R. lochae*) × *R. zoelleri* compatibly entered by a pollen tube of *R. konori,* with a fluorescent tube fragrant visible in the micropyle.

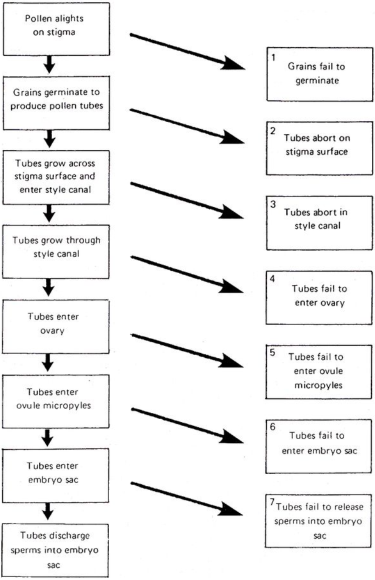


FIG. 4. Flow diagram indicating pollination sub-systems and related pollen tube arrest points observed in incompatible interspecific crosses of *Rhododendron*. Points 6 & 7 are included tentatively as confirmation will require serial sectioning of ovules to locate tubes in relation to the embryo sac. (After Williams *et al.*, 1982).

deposition on the external walls and in plugs. Errors of both types are frequently combined. For each interspecific cross the site of pollen tube arrest within the pistil is generally associated with a characteristic combination of tip growth and callose deposition anomalies.

For a particular pollen, the site of pollen tube arrest and the appearance of arrested tubes vary with the species of pistil through which

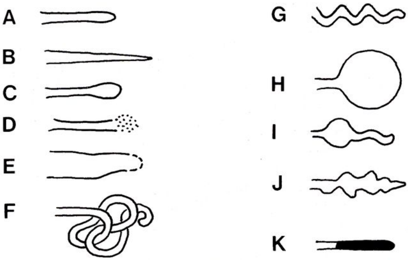


FIG. 5. Diagrammatic summary of the types of tip growth errors seen in arrested pollen tubes after incompatible interspecific pollinations in *Rhododendron*. A, Compatible; B, Tapered; C, Swollen; D, Burst; E, Wide-diameter; F, Coiling; G, Spiralling; H, Balloon-like; I, Swelling; J, Spiky; K, Terminal-callose.

the tubes are growing. For example, pollen tubes of *R. ellipticum* abort on the stigma surface of *R. aberconwayi,* in the style of *R. lindleyi,* and within the ovules of *R. occidentale*. Examples of pollen tube arrest in different regions of the pistil are shown in Fig. 6.

RESULTS OBTAINED FROM POLLINATIONS INVOLVING SECTION VIREYA AS ONE PARENT

Current *Rhododendron* taxonomy is based on the work of Sleumer (1949) together with his revision of sect. *Vireya* (1966, 1974). In his classification of the genus, he introduced eight subgenera based on the presence or absence of scales and the position of flower buds and foliage shoots. Following on the work of Cowan (1950), the investigation of indumentum by Seithe (1960, 1978) has shown that *Rhododendron* can be divided into three major groups which she calls 'chori subgenerum'. Chorus subgenerum *Rhododendron* is characterized by the presence of scales and simple hairs, chorus subgenerum *Hymenanthes* by the presence of glandular hairs and branched hairs and chorus subgenerum *Nomazalea* by the presence of simple hairs and glandular hairs, or, alternatively, the absence of scales and branched hairs. Chorus subgenerum *Rhododendron* corresponds to the 'lepidotes' and is further subdivided into three sections which include two major relatively homogeneous groups, sects *Rhododendron* and *Pogonanthum,* and sect. *Vireya.* Chorus subgenerum *Hymenanthes* corresponds to the major 'elepidote' group, which is again relatively homogeneous and well defined. Recently, revisions have been made within these two chori subgenerum; subsect. *Lapponica* by Philipson & Philipson (1975) and sects *Pogonanthum* and *Rhododendron* by Cullen (1980) and *Hymenanthes* by Chamberlain (1982). Chorus subgenerum

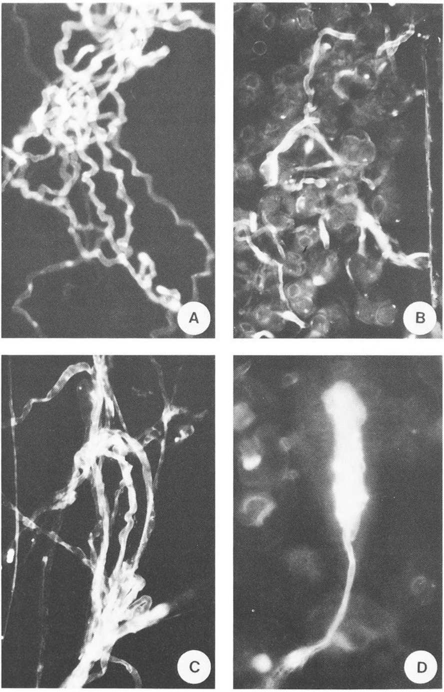


FIG. 6. Growth errors in pollen tubes. A, distortion and arrest of incompatible pollen tubes of *R. morii* at the base of the style of (*R. phaeopeplum* × *R. lochae*) × *R. zoelleri*. B, incompatible pollen tubes of *R. ellipticum* arrested on the stigma of *R. aberconwayi*. C, distortion and arrest of pollen tubes of *R. laetum* × *R. aurigeranum* in the ovary of *R. retusum*. D, coiled overgrowth of pollen tube within an ovule of *R. kawakamii*.

Nomazalea corresponds to the 'azalea complex', a heterogeneous grouping, which, in some sense, contains those species which do not fit into the other chori subgenerum. At present it contains three subgenera, *Pentanthera, Tsutsusi* and *Azaleastrum,* but revision of this group has introduced changes (Philipson & Philipson, 1982). The problems of classification within this complex have been outlined by W. R. Philipson (1978), who makes the point that subgen. *Pentanthera,* the deciduous azaleas, form a relatively united group and sect. *Tsutsusi,* the evergreen azaleas, likewise form a distinct group. Sect. *Brachycalyx,* which consists of deciduous or semi-deciduous azaleas, can, he says, be regarded 'as a deciduous parallel of sect. *Tsutsusi*'. The remaining subgenus *Azaleastrum* does not include rhododendrons that are commonly thought of as azaleas; the characteristic which unites them being the lateral position of their inflorescences. The two major groups, sects *Choniastrum* and *Azaleastrum* are, however, each relatively homogeneous.

There are known barriers to compatibility (Kehr, 1977) between the three chori subgenerum, and within subgen. *Rhododendron* between sect. *Vireya* and the remaining two sections. There are further barriers within sections, some of which involve difference in degree of polyploidy. A simplified chart which summarizes *Rhododendron* taxa and major barriers to compatibility is shown in Fig. 7, where taxa not used in the present work have been omitted. Regions where polyploidy occurs frequently are shown hatched but species selected for the present series of pollination are diploids where ploidy is known. In using this chart to display our results, it is important to note that some of our groups contain few or only one species owing to restricted availability of flowering materials, so that sect. *Choniastrum* (A_3) contains only *R. ellipticum,* and subsection *Pseudovireya*

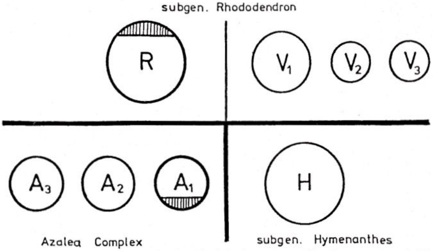


FIG. 7. Simplified chart representing the *Rhododendron* taxa used in the present work. The dividing lines represent the strength of the breeding barriers. Taxonomic groups in which polyploidy is known are shown with a cross-hatched sector. R, sect. *Rhododenron.* V, sect. *Vireya*: V_1, all but subsect. *Pseudovireya* ; V_2 subsect. *Pseudovireya* (tropical); V_3 subsect. *Pseudovireya* (temperate). H, sect. *Hymenanthes.* A, Azalea Complex: A_1 sect. *Pentanthera*; A_2 sect. *Tsutsusi*; A_3 sect. *Choniastrum.*

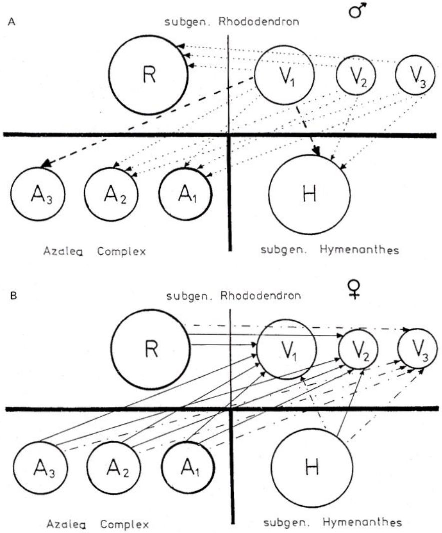


FIG. 8. Results of intersubgeneric pollinations (based on Fig. 7). A, crosses with a *Vireya* species as pollen parent. Dotted lines indicate pollen tubes arrested within the style or at the base of the style. Dashed lines indicate crosses in which pollen tubes entered the ovary without entering the ovules. No crosses of this type showed ovule entry by pollen tubes or seed set. B, results of crosses with a *Vireya* species as seed parent. Broken lines indicate pollen tubes arrested at style base or in the ovary without entering ovules. Solid lines indicate crosses in which pollen tubes entered the ovules.

contains only *R. retusum* and *R. quadrasianum* var. *rosmarinifolium* from tropical regions (V_2) and *R. kawakamii* var. *flaviflorum* from temperate regions (V_3). Further, in sect. *Rhododendron* (R) we used only representatives from subsect. *Maddenia*.

Fig. 8A shows the results of our pollinations made with a sect. *Vireya* pollen parent. In all but two of these pollinations, pollen tubes were arrested within the style or at the base of the style. In the two exceptional crosses pollen tubes entered the ovary but did not enter the ovules. No

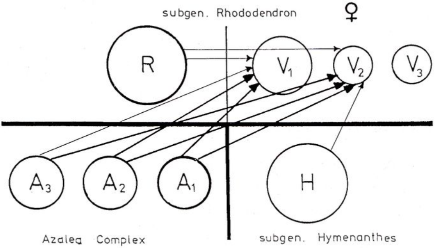


FIG. 9. Results of those pollinations in which *Vireya* ovules were entered by pollen tubes after intersubgeneric pollinations (crosses shown by solid lines in Fig. 8B). Fine lines indicate ovule entry without production of viable seed. Heavy lines indicate crosses from which viable seed was obtained.

capsules developed and no seed was obtained from any of these pollinations using a *Vireya* pollen source.

Figs 8B & 9 show the results of pollinations made on sect. *Vireya* pistils. In incompatible combinations pollen tubes aborted at the base of the style, in the ovary, or within the ovules. Arrest at the style base was associated with *R. kawakamii* var. *flaviflorum* (V_3). (In this series of pollinations V_2 was represented by *R. retusum* because of the difficulty found in emasculating *R. quadrasianum* var. *rosmarinifolium* without selfing). Five types of pollination set viable seed (V_1 pollinated by A_1 and A_2, and V_2 pollinated by A_1, A_2 and A_3). In four pollinations the ovules were entered without producing viable seed: *R. retusum* (V_2) × *R. arboreum* (H) gave seed which contained no embryos; *R. retusum* (V_2) × *R. burmanicum* (R) gave seed, 45% of which contained embryos but failed to germinate; *R. sessilifolium* (V_1) × *R. ellipticum* (A_3) and [(*R. phaeopeplum* × *R. lochae*) × *R. zoelleri*] (V_1) × *R. formosum* (R) both produced no seed.

Though both are in subsect. *Pseudovireya*, the behaviour of *R. retusum* and *R. kawakamii* var. *flaviflorum* as seed parents is quite different. When *Rhododendron* pollen is applied to *R. retusum*, seed is usually obtained though it may not be viable. However, no seed has been obtained from *R. kawakamii* var. *flaviflorum* with any pollen which we have tried except its own and that of *R. santapaui* (subsect. *Pseudovireya* temperate).

INTERSUBGENERIC HYBRID SEED OBTAINED; ITS GERMINATION AND INITIAL SEEDLING DEVELOPMENT

Viable intersubgeneric seed was produced on *Vireya* seed parents in a total of seven crosses involving pollen parents in sects *Tsutsusi*, *Pentanthera* and *Choniastrum*:

(a) *Vireya* × sect. *Tsutsusi* (A_2).

(i) The cross (*R. laetum* × *R. aurigeranum*) × *R. indicum* produced some viable seed whose germination percentage was only 0·1% compared with 36% for (*R. laetum* × *R. aurigeranum*) selfed and 18% for the intra-*Vireya* cross (*R. laetum* × *R. aurigeranum*) × *R. retusum* (Fig. 10 top). From the cross with *R. indicum* a total of eight hybrid seedlings survived to ventilation 33 days after sowing the seed. Thereafter they declined, and 20 weeks after sowing there were no surviving seedlings.

(ii) *R. retusum* × *R. simsii* produced viable seed with 0·8% germination. Three weak seedlings were obtained. Two have died and the third is not expected to survive.

Vireya × *Tsutsusi* hybrids were also reported by Messrs Veitch & Sons as reported by Henslow (1891), and by Holttum (1941). Veitch produced the hybrid *R.* 'Lord Wolseley' × *Azalea indica* 'Stella'. The seed parent is [(*R. jasminiflorum* × *R. javanicum*) × *R. brookeanum* var. *gracile*] × *R. javanicum*, a third generation sect. *Vireya* hybrid, the pollen parent is in sect. *Tsutsusi* and probably an *R. indicum* or *R. simsii* hybrid. One seedling was flowered and Henslow gives a description of the foliage and a description and sketch of the truss. These descriptions are consistent with the plant not being a true *Vireya* × *Tsutsusi* hybrid and suggest *Vireya* × *Vireya*. The brief description of a dwarf sister-seedling which attained the height of 5 inches after 7 years and never flowered does suggest that a true hybrid was obtained in this case. Holttum used *R. longiflorum* as the seed parent and two varieties of *R. indicum* as the pollen parent. He reported that the seeds gave poor germination, the plants were weak and none survived.

(b) *Vireya* × sect. *Pentanthera* (A_1).

Five crosses were made which produced viable seed:

(i) (*R. intranervatum* × *R.* 'Souvenir de J. H. Mangles') × *R. periclymenoides* (*R.* 'Souvenir de J. H. Mangles' is a third generation sect. *Vireya*, Veitch hybrid). This cross gave seed with a germination percentage of about 1% compared with 26% for the hybrid *Vireya* female parent selfed, and 50% for a compatible intra-*Vireya* cross of the female parent with *R. konori* (Fig. 10 middle). A total of 42 hybrid seedlings were obtained with very variable vigour. After 12 months, a few seedlings had normal vigour but most had low vigour with a propensity for the leaves to develop brown necrotic lesions and abscise earlier than expected. At the time of writing 11 seedlings survive and although current development suggests that while some of the more vigorous individuals may grow to maturity, the weaker seedlings are unlikely to survive.

(ii) (*R. intranervatum* × *R.* 'Souvenir de J. H. Mangles') × *R. japonicum* (*glabrius*) gave seed with 0·2% germination and a single rather weak seedling which is still surviving at the time of writing.

(iii) (*R.* 'Dr. Hermann Sleumer' × *R. herzogii*) × *R. bakeri*. (*R.* 'Dr. Hermann Sleumer' is a natural *R. phaeopeplum* hybrid). This cross gave seed with a germination percentage of 0·3–1% compared with 14–26% for an intra-*Vireya* cross to (*R. laetum* × *R. aurigeranum*) using the same seed parent (Fig. 10 bottom). A total of 34 hybrid seedlings were obtained from

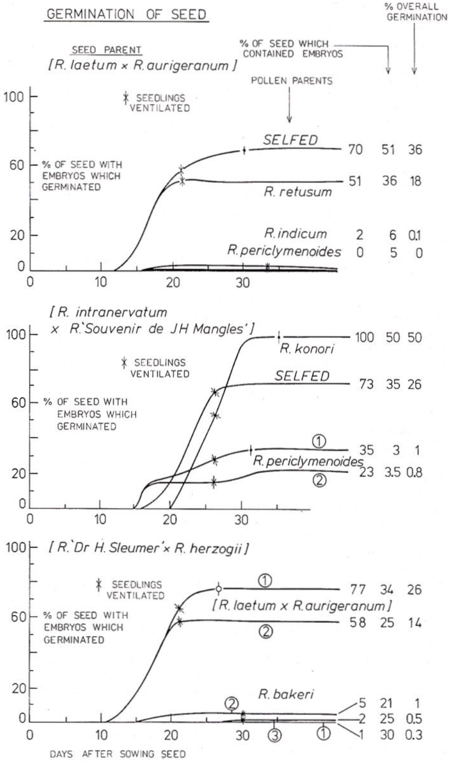


FIG. 10. Proportion of embryo-containing seeds which germinated following hybrid and selfed pollination of 3 *Vireya* seed parents. Percentage plotted against time after sowing.

the cross to *R. bakeri*. Initially vigour was variable but generally low. At the time of writing 17 survivors show a wide range of vigour and it can be expected that the stronger seedlings are capable of growing into mature plants.

(vi) *R. retusum* × *R. periclymenoides* (*R. nudiflorum*), involving subsect. *Pseudovireya*, produced viable seed with 4–12% germination, and a total of 41 hybrid seedlings. At the time of writing all survive but only seven show good vigour.

(v) *R. retusum* × *R. japonicum* (*glabrius*) produced seed with 3·8% germination. Six hybrid seedlings were obtained of which four have died and the remaining two are unlikely to survive.

The cross between an evergreen *Vireya* and a deciduous azalea is not one that would be expected to result in viable seed, and we know of no previous reports of the production of such hybrids.

(c) *Vireya* × sect. *Choniastrum* (A_3).

R. retusum × *R. ellipticum* gave viable seed with 1% germination and a total of 11 seedlings. At the time of writing eight seedlings remain of which only two show reasonable vigour.

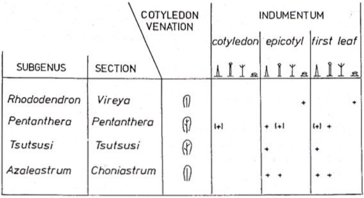
(d) More recently seed has been obtained from an additional intersubgeneric cross of a vireya seed parent to a pollen parent in the azalea complex, subgen. *Tsutsusi*, sect. *Tsusiopsis*. The cross: [(*R. macgregoriae* × *R. lochae*) × *R. macgregoriae*] × *R. tashiroi* gave seed with less than 0·05% germination and a single hybrid seedling which still survives at the time of writing.

SEEDLING CHARACTERISTICS RELATED TO TAXONOMIC GROUPING

We have seen how the investigation of indumentum of mature plants has played its part in the development of *Rhododendron* taxonomy. Here, our interest is in the characteristics of the cotyledons, epicotyl and first foliage leaves of young seedlings, since these may allow us to confirm the hybridity of seedlings arising from intersubgeneric pollinations.

Philipson (1970, 1978) investigated the taxonomic relationships of cotyledon venation and hair or scale types. She showed for four taxonomic sections that the venation of the cotyledons may consist of a midrib only, a midrib with simple lateral veins, or a midrib with a reticulation of veins (Fig. 11). (Note that the pattern for sect. *Choniastrum* is based on a single species, *R. ellipticum*). The cotyledons and first foliage leaves bear a restricted number of trichome types compared to the mature plant. Seithe (1978) lists these as: juvenile transparent scales, simple acute hairs, glandular hairs, and juvenile branched hairs. Fig. 11 shows the distribution of these trichome types among four sections based on Philipson (1970, 1978), the drawings of Hedegaard (1980) and our own observations. Sect. *Virya* seedlings have glabrous cotyledons and only scales on the first foliage leaves.

In the present work all intersubgeneric seedlings raised on *Vireya* seed parents after crossing to pollen parents in sects *Tsutsusi, Pentanthera* and *Choniastrum* showed glandular hairs and a lack of scales on the first



\+ Present on all or almost all species in the section

(+) Frequently observed on species in the section

FIG. 11. Chart showing cotyledon venation and juvenile hair types found on cotyledons, epicotyl and first foliage leaves for the taxonomic groups used in the present study. Symbols used for juvenile indumentum in column headings are: (left to right) simple hair, stalked glandular hair, branched hair, and scale.

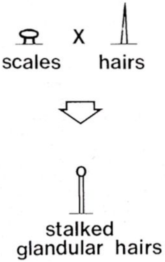


FIG. 12. Diagram depicting juvenile indumentum as an indicator of hybridity after pollination of *Vireya* seed parents with pollen of species from other subgenera. (See FIG. 13).

foliage leaf (Fig. 12). For certain hybrid seedlings occasional simple hairs were present in addition to glandular hairs. The lack of scales and presence of hairs are characteristics of the pollen parents and therefore indicate true hybrids. In sect. *Tsutsusi* the first foliage leaf has only simple acute hairs. However, in the hybrid [(*R. laetum* × *R. aurigeranum*) × *R. indicum* (*Tsutsusi)*] the hairs were glandular, suggesting that the stalked

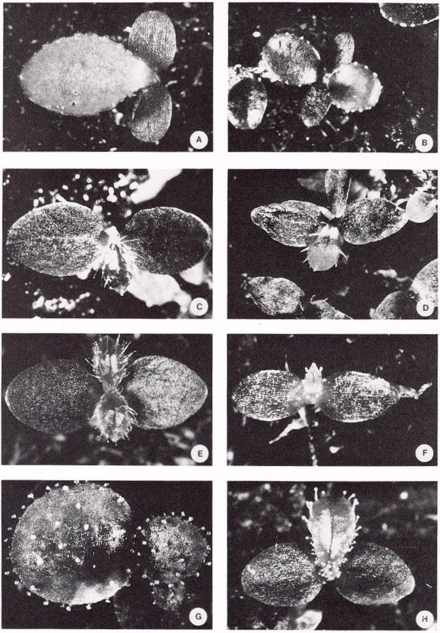


FIG. 13. Juvenile indumentum on *Vireya*, non-*Vireya* and hybrid seedlings. A & B, *Vireya* seedlings to show scales: A, *R. konori*; B, (*R. laetum* × *R. aurigeranum*) × *R. retusum*. C–E, 'Azalea' seedlings to show hairs: C, *R, simsii* (subgen. *Tsutsusi*); D, *R. bakeri* (subgen. *Pentanthera*); E, *R. ellipticum* (subgen. *Azaleastrum*). F–H, intersubgeneric hybrids to show stalked glandular hairs: F, (*R. laetum* × *R. aurigeranum*) × *R. indicum*; G, (*R.* 'Dr H. Sleumer' × *R. herzogii*) × *R. bakeri*; H, *R. retusum* × *R. ellipticum*.

glandular hair may represent a genetic intermediate between scales and simple hair forms. Examples of the juvenile indumentum in selected species and hybrids are shown in Fig. 13.

CONCLUSIONS

1. Incompatible crosses may fail at several different stages of pollination within the flower pistil.
2. The same pollen may fail at different points in pistils of different species.
3. Intersubgeneric crosses involving *Vireya* are more likely to succeed if *Vireya* is the seed parent, and if the pollen parent is from the 'azalea complex'.
4. In intersubgeneric hybrid seedlings, the structure of the leaf hairs can confirm hybridity.

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QUESTIONS

G. Ring: I would like to report two instances of crosses of Vireyas with hardy rhododendrons in the United States. One was accomplished by using a temperature of 110°F with high humidity for 3 hours during pollination. The second involved a form of *R. brachycarpum* from Finland which was found to be exceedingly fertile and would accept pollen from almost any other rhododendron.

Rouse: We have tried not to fool the Vireyas so far but we plan to investigate compatibilities under artificially high temperatures. We have made crosses between species of *Rhododendron* and other genera of the Ericaceae, between *Ledum* & *Rhododendron* and *Kalmia* & *Rhododendron* for instance. We have not been successful though we know that others have been. I used *R. retusum* because that species accepts all pollen that is put on it and produces seed, not always viable, when crossed with species from the other subsections of sect. *Vireya.* On the other hand, *R. kawakamii* does not accept pollen from other species, even those in its own subsection, only from itself.

Cullen: I would like to congratulate Dr Rouse for his slides of pollen tubes.

Rouse: All these slides were the work of Dr Williams.

D. Leach: The Dutch, in an effort to produce yellow-flowered Azaleas of the Obtusum series, have made a number of successful crosses between them and the Vireyas. They have also sent me a photograph of a hybrid between *R. keiskii* and a Vireya.

Rouse: We have only used subsect. *Maddenia* successfully. I did try *R. augustinii* of subsect. *Triflora* but no seed was produced. We only used *R. ellipticum* from sect. *Choniastrum* but if we had used *R. moulmainense* or some other species from the same section we might not have achieved the same result.