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THE RHODODENDRON NECTARY

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ABSTRACT. In all species of *Rhododendron* the nectary surrounds the base of the ovary. Considerable variation in its form exists among the species but broadly speaking, these variations fall into categories which correspond to the major subdivisions of the genus.

At the light microscope level, the nectary is seen to be well vascularized by repeatedly branched strands arising from traces supplying the ovary wall. These do not enter the secretory tissue but terminate at its inner face. The tissues of the nectary appear entirely parenchymatous and consist of two main types—heavily staining groups of cells alternating with very pale staining zones. Simple, unicellular hairs may arise on the outer walls of some epidermal cells, or rarely these may be uniseriate. The nectary bears numerous stomata of a modified type scattered over its surface.

At the ultrastructural level, considerable variation has been found in the thickness and form of the cuticle. Throughout the secretory tissue areas of heavily electron-dense cells occur containing phenolic compounds which may be absent from other cells or be present in only small amounts. Plastids are large and mitochondria have been found to show some virtually unique configurations. Autolysis of areas associated with phenolic substances proceeds rapidly in the fully open, actively secreting flower, and a possible mechanism for this process is suggested. The likely route of secreted nectar would appear to be from intercellular spaces through stomata to the nectary surface, rather than by way of the cuticle. A brief comparison of the nectariferous tissue of *Rhodoendron* with that of some other genera is made.

NECTARY FORM AND ITS TAXONOMIC SIGNIFICANCE

Nectaries may be classified as those occurring in flowers, the floral nectaries, and the extra-floral nectaries that may be found in some plants on aerial vegetative parts, e.g. on petioles and leaf bases, as in *Prunus* and *Passiflora*. They are not confined to flowering plants but can also be found in some ferns, e.g. *Pteridium* and *Photinopsis*.

In *Rhododendron* the nectary is of the floral type and in all species it surrounds the base of the ovary. Nevertheless considerable variation in form and anatomy occurs, and at least some of this variation can be linked to the taxonomy of the genus. In general, the nectary consists of a whorl of bulges at the basal part of the ovary wall, and these protrude between the bases of the stamen filaments. In species with five stamens (as in most azaleas) there are, therefore, only five nectary lobes, whereas in the rest of the genus there are usually between ten and twenty. When the stamens are as frequent as the carpels, each nectary lobe lies opposite a loculus, but when there are twice as many, two lobes correspond to each loculus.

Nectaries occur in three main types: (1) Type A, a rounded bulge, e.g. *R. jasminiflorum* (Fig. 1); (2) Type B, a broadly based bulge, e.g. *R. campanulatum* (Fig. 2); (3) Type C, a zone surrounding the lower part of the ovary only slightly raised above the ovary wall, e.g. *R. schlippenbachii* (Fig. 3). Although intermediate conditions occur, the distribution of these types among the subgenera is rather well defined.

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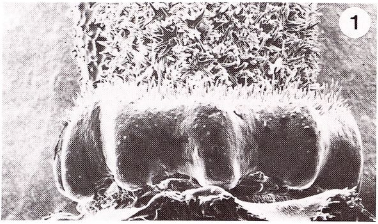
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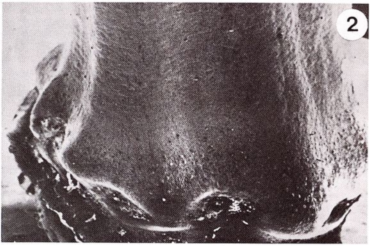
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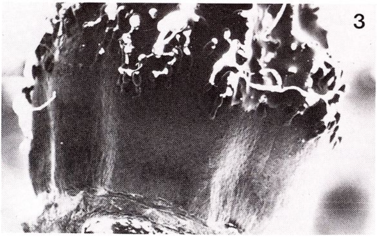
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In subgen. *Rhododendron* (lepidote species) the nectary is almost invariably the rounded bulge of Type A. In sect. *Vireya* the bulge is particularly distinct and rounded (Fig. 4) and in the large flowered *R. konori* it protrudes massively (Fig. 5). The most exceptional nectaries seen in the lepidotes are those of *R. trichocladum* (Fig. 6) and *R. lepidostylum* in which the nectary approaches Type C in form; both species are members of subsect. *Trichoclada,* a section aberrant in other respects.

Most species in subgen. *Hymenanthes* (elepidote species) have the broadly inserted cushion-like nectaries of Type B (Fig. 7). In some species the cushion is extended laterally to give a disc-like nectary, more or less separate from the base of the ovary (Fig. 8) or in other species the nectary protrudes only slightly, when it approaches Type C.

Nectaries in subgen. *Pentanthera* (Fig. 9) are all Type C (scarcely raised above the surface of the ovary.), with the one exception of *R. nipponicum* (Fig. 10), the sole representative of sect. *Viscidula.* In this species the extreme rounded form of the ovary contrasts markedly with the rest of subgen. *Pentanthera.* In view of its other curious features, particularly its pendulous bell-shaped corolla, the nectary emphasizes its distant relationship to other species. It is retained in its present position as it fits no other.

The removal of *R. schlippenbachii* and *R. quinquefolium* from sect. *Brachycalyx,* and their association with *R. pentaphyllum* and *R. albrechtii* as sect. *Sciadorhodion* of subgen. *Pentanthera,* has already been advocated on other grounds (Philipson, 1970; Philipson & Philipson, 1982). Nectary form gives further support to this proposal, for in sect. *Brachycalyx* the rounded nectary is of Type A (Fig. 11), thus making the flattened form of *R. schlippenbachii* and *R. quinquefolium* (Type C) aberrant in this section.

While the nectaries of sects *Brachycalyx* and *Tashiroi* of subgen. *Tsutsusi* are rather small and rounded (Type A), those of sect. *Tsutsusi* (Fig. 12) are more elongated, approaching Type C—but the number of examples examined is too few to support generalizations.

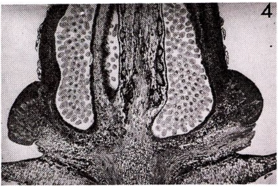
The nectaries of subgenera *Azaleastrum* (Fig. 13), *Candidastrum* (Fig. 14) and *Therorhodion* correspond to Type C, whereas those of subgen. *Mumeazalea* are closer to Type B. Table 1 summarizes these generalizations which show that nectary form has taxonomic usefulness.

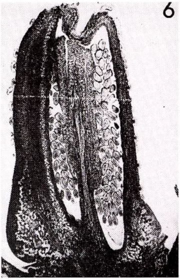
ANATOMY OF THE NECTARY

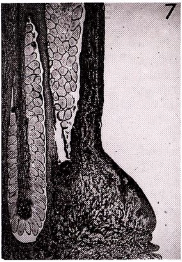
The nectary has a well-developed vascular system of repeatedly branched strands arising from the traces supplying the ovary wall. These strands display xylem elements with specially thickened walls but only phloem elements extend as far as the inner edge of the nectary tissue.

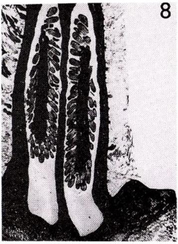
FIGS 1–3. Scanning electron micrographs of the lower portion of ovaries with nectaries. 1, *R. jasminiflorum* × 160; 2, *R. campanulatum* × 100; 3, *R. schlippenbachii* × 160. Exudate from glandular hairs on the ovary are responsible for the areas of flair.

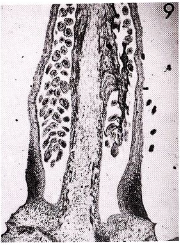
Notes and abbreviations for Figs 1–3, 16–25: B, enlarged nucleoids; D, dictyosome; E, endoplasmic reticulum (ER); H, phenolic material; I, intercellular space; L, lipid body; M, mitochondrion; N, nucleus; NO, nucleolus; P, plastid; R, ribosomes; V, vacuole; W, cell wall. SEM specimens used fresh and uncoated. TEM sections contrasted with $KMnO_4$.



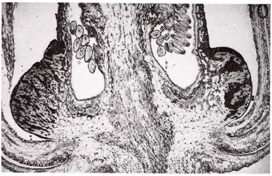


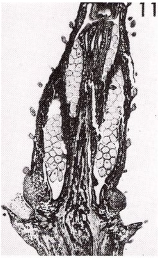


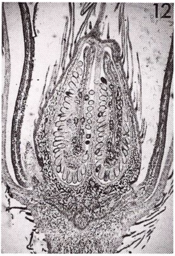


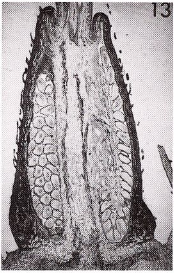


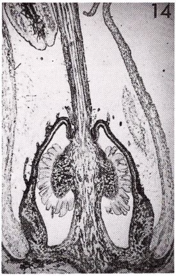
FIGS. 4–9. Sections of ovaries showing types of nectaries (all × 18): 4, *R. jasminiflorum*; 5, *R. konori*; 6, *R. trichocladum*; 7, *R. thomsonii*; 8, *R. beanianum*; 9, *R. vaseyi*.











FIGS 10–15. Sections of ovaries showing types of nectaries (all × 18): 10, *R. nipponicum*; 11, *R. reticulatum*; 12, *R. yedoense*; 13, *R. leptothrium*; 14, *R. albiflorum*; 15, *R. roxieanum*.

TABLE 1
Distribution of Nectary Types within the genus *Rhododendron*

Subgenus	Section	Type A (rounded bulge)	Type B (broadly-based bulge)	Type C (only slightly raised)
Rhododendron		+		
Hymenanthes			+	
Pentanthera	Sciadorhodion			+
	Rhodora			+
	Viscidula	+		
Tsutsusi	Tsutsusi			+
	Tashiroi	+		
	Brachycalyx	+		
Azaleastrum				+
Candidastrum				+
Mumeazalea			+	
Therorhodion				+

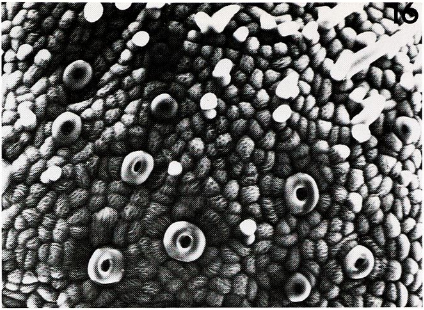
The epidermis of the nectary is provided with abundant, modified stomata which act as outlets for the nectar (Fig. 16). Frequently the surface also bears unicellular hairs on the upper third or half, and the indumentum of the ovary wall (if any) may extend downwards onto the upper part of the nectary (Fig. 16).

The tissues of the nectary are entirely parenchymatous and typically comprise two broad types of cells whose arrangement is extremely variable. One type contains much phenolic material (staining purple or red in safranin), while the other type is devoid of phenolics, or at least stains much less deeply. The two cell types are usually distributed in alternating zones. Mostly the phenolic zones predominate, with the clear zones forming isolated islands or bands which do not, or only rarely, reach the epidermis, resulting in a more or less continuous zone of phenolic-bearing cells below the epidermis. Another common arrangement is for the bands of clear cells to be as predominant as the phenolic tissue and to extend to the epidermis (Fig. 10). It is more unusual for the whole nectary to consist of clear nonphenolic cells (e.g. *R. roxieanum*; Fig. 15), and quite rare for it to consist entirely of phenolic cells (e.g. *R. vaseyi*).

These anatomical types show some taxonomic correlation, but intergrade too much for it to be clear cut. However, it can be said that nectaries with uniformly clear cells are found only within some species of subgen. *Hymenanthes*.

It is believed that the presence of phenolics (or tannins, as they are also known) in the leaves of many woody plants acts as a barrier against both insect and herbivore predation (Harborne, 1977). A similar function may be ascribed to these substances when they occur in nectaries which, to predators, must be a highly nutritious tissue. The hydrolysable tannins, derivatives of simple phenolic acids, combined with the sugar glucose, are secondary compounds. It seems reasonable to assume that nectar secretion is not confined to non-phenolic cells, but is carried out by both types.

Scanning electron micrographs of the outer surface of the *Rhododendron* nectary may reveal the presence of a cuticle which in some



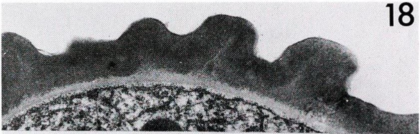


FIG. 16. *R. griersonianum.* Surface of nectary showing stomata, and wrinkled cuticle of epidermal cells. A few unicellular hairs are present on the upper part of the nectary. SEM, × 2400.

FIGS. 17–19. Sections of outer surface of nectary as viewed under the TEM: 17, *R. campanulatum* × 21000; 18, *R. cinnabarinum* × 26000; 19, *R.* 'Albatross' × 28000.

species gives a wrinkled appearance due to its irregular contours (Fig. 16). In section, the cuticle of *R. campanulatum* is thick, with a strongly convoluted surface (Fig. 17). It is composed of two layers, an outer lamellate, and an inner reticulate layer (Wattendorff and Holloway, 1980). This is not the case in all rhododendrons, for there appears to be a variation in the form of the layer covering the epidermal cells, e.g. the nectary cuticle of *R. cinnabarinum* is moderately thick with both flat and irregular profiles above the epidermis (Fig. 18), while in a hybrid of subsect. *Fortunea, R.* 'Albatross', the cuticle is narrow and flat-surfaced (Fig. 19), and the two-layered structure does not occur.

ULTRASTRUCTURE DURING ACTIVE SECRETION

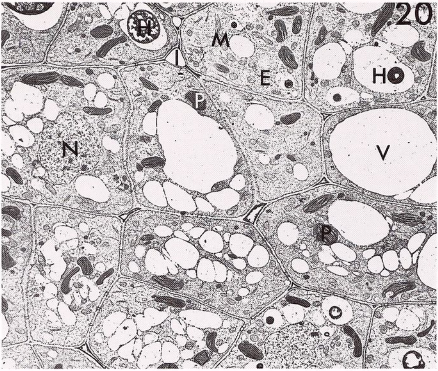
The parenchymatous tissue of two actively secreting nectaries is described below, the first being from an area of electron translucent cells in the nectary of *R. campanulatum,* and the second, from an area in the nectary of *R.* 'Albatross', where many cells were heavily electron dense due to the presence of phenolic substances. These substances may cause sectioning problems due to imperfect fixation, or have a masking effect on cell organelles.

In *R. campanulatum* electron-lucent cells lie in groups among heavily electron-dense subepidermal cells and are typically parenchymatous (Fig. 20). They are small with dense cytoplasm and many small, or fewer, larger vacuoles, some of which contain phenolic deposits. Nuclei are relatively large with prominent nucleoli. Mitochondria, oval to somewhat elongated in shape, are numerous, and plastids, with thylakoids and some grana, are prominent. Lipid droplets occur in small numbers; dictyosomes are also present but not apparently numerous. Ribosomes are difficult to distinguish within the coarse granularity of the cytoplasm. The endoplasmic reticulum (ER) occurs mainly as short to medium lengths of rough ER, and plasmodesmata occur plentifully in the walls. Intercellular spaces are numerous and usually contain an electron dense deposit in varying amounts. Vascular traces do not penetrate the secretory tissue although phloem cells may come within a few cells of its inner periphery.

In *R.* 'Albatross' phenolic substances are abundant throughout and in many cells give negative staining effects which often reveal organelle detail (Fig. 21). More often their electron density effectively masks cytoplasmic content.

The secretory tissue in *R.* 'Albatross' has been found to possess exceptionally long mitochondria (Figs 21–24) of a size and configuration that suggest that they may be parts of an organelle of complex structure. These bizarre organelles may be very narrow along their length but with enlarged ends. Nucleoids are represented by unusual distended areas, or bulbous structures, in which DNA fibrils can be detected. These long mitochondria may be found partly or completely encircling a vacuole or nucleus, and often appear to be intimately associated with plastids. Their juxtaposition to nucleus, vacuole or plastid could indicate a physiological or biochemical association, or be fortuitous, because of the unusual length of the organelle.

The majority of plastids in *R.* 'Albatross' are large and broad, often with a simple thylakoid system and few grana stacks. They contain also



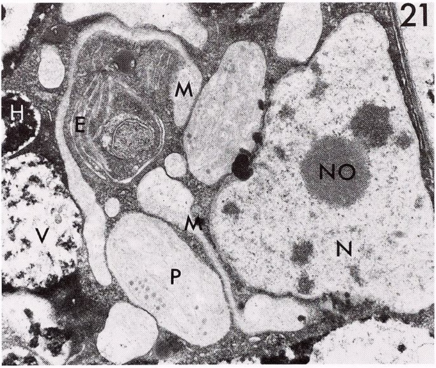
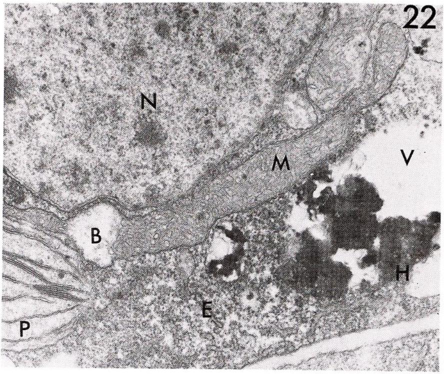
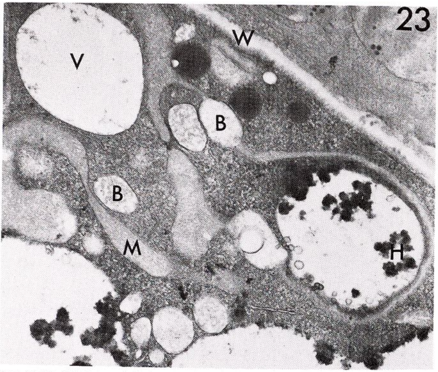


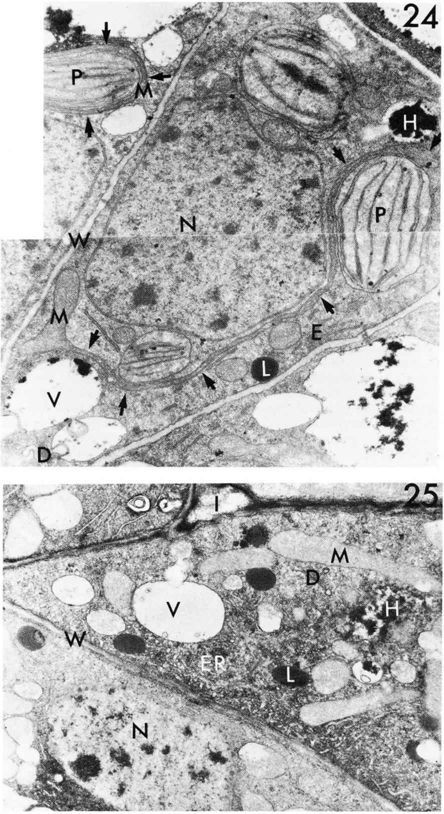
FIG. 20. *R. campanulatum*. Secretory tissue. Parenchymatous cells from an area immediately below the epidermis that is comparatively free of phenolic substances. × 8000.

FIG. 21. *R*. 'Albatross'. Secretory cell from an area immediately below the epidermis that is heavily electron-dense due to the presence of phenolic substances. These give a negative staining effect to the organelles in the cytoplasm. × 47000.





FIGS. 22–23. *R.* 'Albatross'. 22, Portion of a long mitochondrion in a secretory cell. ×51000. 23, Mitochondrial complex with enlarged nucleoid areas from a heavily electron dense cell. ×34000.



FIGS. 24–25. *R.* 'Albatross'. 24, Cell from secretory tissue containing an unusually long mitochondrion that appears to be intimately associated with two plastids; a similar association is shown in the cell, upper left; arrowheads follow lengths of mitochondria; × 14400. 25, Irregular profiles of endoplasmic reticulum, sometimes branches are abundant near the wall of a secretory cell; long mitochondria are also present; × 36000.

plastoglobuli and small ribosomes. Lipid droplets, dictyosomes releasing vesicles from their ends, and ribosomes, all occur as cell constituents but are usually difficult to detect because of the densely packed nature of the cytoplasm. Vacuoles containing variable amounts of substance of a presumably phenolic nature are invariably present. Nuclei often show a large amount of heterochromatin and the nucleolus is large and prominent (Fig. 21). Bundles of long parallel fibrils, perhaps of a proteinaceous nature, have been observed within the nucleus and also may be found lying in the cytoplasm outside it. The ER may occur as short strands, or in parallel and rather long stacks and in this case always associated with vacuoles. In other areas (Fig. 25) a convoluted and branched form of ER occurs which may be similar to the smooth ER in the secretory cells of some other genera., e.g. in the farina-producing glands of *Primula*. Often these short vesicular and tubular forms lie in an area of heavy electron density between a vacuole and a bounding ER cisterna.

TOXICITY OF RHODODENDRON NECTAR

It is well known that the leaves of many rhododendrons are poisonous to animals and that the nectar of many, but apparently not all species contains a poisonous constituent. Leach (1972) published an historical survey of the effects of the toxin, acetylandromedol, on man and animals, while the same toxin, also known as grayanotoxin was identified in the leaves of *R. aurigeranum* (sect. *Vireya*) after cattle fatalities and at least one human poisoning in New Guinea (Abberton, Gough & Keast, 1980). The toxic agent, a diterpene, causes vertigo, vomiting, marked lowering of blood pressure, respiratory depression, loss of consciousness and finally death from respiratory failure. When it occurs in rhododendron nectar it is presumably present throughout the plant.

MODE OF SECRETION

The general presence of stomata over the surface of *Rhododendron* nectaries indicates that nectar reaches the surface through these pores. However, steps in the secretion of nectar from the secretory cells prior to its appearance on the surface of the nectary are a matter of speculation based on an interpretation of the ultrastructure.

It is generally accepted that nectar is a modification of the sugar solution which is produced in the green parts of plants, and is transported throughout the plant in the phloem of the vascular system. The sugar solution of the sieve tubes is unloaded close to the nectary tissue from where it is transported by the ER via a symplastic route, i.e. through the cytoplasm and plasmodesmata of intervening cells, to the secretory cells. Somewhere along this route, or in the secretory cells themselves, the phloem sap becomes modified to a specific composition—sucrose may be inverted to a greater or lesser extent to its hexose monomers, glucose and fructose; amino acids may be modified or withdrawn; potassium ions are removed, and deterrent substances, such as phenolics and anti-oxidants, may be incorporated.

The substance brought to the secretory cell by the ER must later be secreted from that cell either enclosed in membrane-bound vesicles (granulocrine secretion) or in a free molecular form (eccrine secretion). In a granulocrine system, sugars are transported to the plasmalemma by vesicles of ER or dictyosome origin, and vesicle contents are released into the cell wall by fusion of vesicle and plasmolemma membranes. It has been postulated that vesicles from ER (e.g. in *Lonicera*; Fahn & Rachmilevitz, 1975), from dictyosome cisternae (e.g. in *Diplotaxis* and *Helleborus*; Eymé, 1966) or from both (e.g. in *Musa*; Fahn & Benouaiche, 1979), may be intimately associated with secretion from nectary cells.

The alternative method, eccrine secretion, has been suggested as operating in the nectaries of red clover (Eriksson, 1977) and *Aptenia* (Meyberg & Kristen, 1981). In this process, nectary sugars leave the cell in an unpackaged or free molecular form and must pass through the barrier afforded by the plasmalemma by a mechanism of active membrane transport, which is transport against a concentration gradient and one requiring energy. The nectary of *R.* 'Albatross' is well provided with the means of producing ample energy, in its possession of exceptionally long mitochondria. In *R. campanulatum,* mitochondria are numerous and sometimes quite long although they do not show the attenuated form of those of *R.* 'Albatross'.

From the lack of any great abundance or predominance of either ER or dictyosomes, it would appear that in the two nectaries examined here, nectar is more likely to leave the secretory cells in a free molecular form rather than in membrane-bound vesicles.

Once outside the plasmalemma, nectar is able to move unhindered in the so-called 'free-space' of cell walls and in the intercellular spaces, and passes along this apoplastic route, until it finds its way out through the stomatal openings onto the nectary surface.

Whatever the means of moving nectar from the secretory cell to the nectary surface may be, nectar droplets accumulate and lie at the base of the corolla or fill the pouches there. It should be noted that these processes are synchronized with the advancing maturity of the young flower—a mechanism of which we are still largely ignorant.

While the nectary may only be an unobtrusive bulge at the base of the ovary, it still plays an important role in the successful reproduction of the plant and therefore in the continuation of the line. The presence of its secretion attracts pollinators, and the composition of this secretion performs a major part in the determination of desirable pollinators and the rebuffal of those that are undesirable. It is enough for the taxonomist that the nectary shows variation in form which can be related to the major subdivisions of the genus. The complexities of the mechanism of nectar production, however, must await eludication by membrane biophysicists and biochemists, and our high magnification studies of the subcellular structure of secretory cells will provide the setting against which form will be endowed with function.

ACKNOWLEDGEMENTS

Morphological details and their taxonomic implications result from a joint study on the embryology of *Rhododendron* by B. F. Palser, W. R. Philipson and M. N. Philipson.

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QUESTIONS

Cullen: You saw elongated mitochrondria in *R.* 'Albatross' and in no other species of rhododendron?

Philipson: Nothing quite as elongated as that.

Cullen: What about its parents; did you look at them?

Philipson: I have not looked at its parents but at others in that subsection. They do not seem to be quite as long but any EM study is long term and involved, and it does take a long time to get results like this.

Cullen: You don't think that this could be an effect of hybridization?

Philipson: I have not read of any ultrastructure effect of hybridization.

Rouse: Do you know at what stage in the floral development the nectar is released and at what stage it stops? I did not quite gather if it was a continuous process or whether it comes to an abrupt stop after a short time. Is it replenished as the pollinator removes the nectar?

Philipson: In *Rhododendron* I believe it is stored in the inter-cellular spaces just below the surface of the nectary and is released as the flower opens. We do not know the mechanism by which it is released on to the surface. I think that there are cells in which nectar production is delayed so that if you draw off nectar it will be replenished. I have drawn it off over a period of a couple of days and it is still being replenished at the surface but in smaller amounts. However, it is no longer released after a day or two.

Kores: At what stage in the development of the nectaries were they actively secreting nectar?

Philipson: The flowers were mature.

Kores: Have you any evidence that the actual constituents vary in rhododendrons?

Philipson: No, I have done no work on that but I would very much like to. Baker & Baker have reported, I think for *Rhododendron ferrugineum,* that the nectar has a high proportion of sucrose. It is usually broken down into glucose and fructose. The amino acid composition may be more specific and could be more telling.

Cullen: I would just like to add that Professor Harborne has examined a number of rhododendrons but he has not yet published his results. Apparently quite a high proportion had nectar that contained sucrose instead of the six-carbon sugars and quite a range of amino acids, some of them quite uncommon, but he could not make any particular taxonomic sense out of them.

Philipson: Has he covered a wide range of species?

Cullen: Yes, he must have looked at two hundred species.

D. Leach: I wonder if you have examined *Rhododendron carolinianum*. It is most receptive before the flower has opened and this seems rather an odd situation if the nectar is produced after the flower opens.

Philipson: I have not looked at that species. There is an awful lot of work yet to be done.