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THE OVARY, OVULE AND MEGAGAMETOPHYTE IN RHODODENDRON

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ABSTRACT. The ovary, ovule and megagametophyte at the mature gametophyte stage have been observed for, and compared among, 131 species chosen to represent all the subgenera, sections and most of the subsections of *Rhododendron*. Gametophyte and early endosperm development has been followed in 14 of the species. Considerable variation occurs in ovary size, shape, indumentum, carpel number, ovule number, placental characteristics, ovule orientation, wall thickness, etc. Similarly, the ovules, though basically alike in type throughout the genus, differ in size, shape, proportion of ovule occupied by the gametophyte, thickness of integument, length of micropyle, presence of appendages, etc., while the gametophytes, which all develop according to the Polygonum pattern and have a similar complement and arrangement of cells, do differ in size, proportions, amount of starch, some cellular details, etc. Although the indumentum types on the ovary show an essentially similar distribution among subgeneric taxa as do those on the leaves, it has not been possible to discern other features, singly or in clusters, which could serve to arrange groups of species in clearly distinguishable subgeneric taxa, whether newly erected ones or those presently recognized on other grounds. Wide variation occurs in most characters among the several species observed in each of the larger sections—*Vireya, Rhododendron* and *Hymenanthes*. Although the range of variation in any one section overlaps with that in the others, each section displays, *on the average,* a somewhat different expression of a set of ovary and ovule characteristics. *Vireya,* particularly, shows a number of features which regularly occur together in most species and are found only spasmodically, and individually, in species of other sections. The several subgenera and sections of the azalea complex, each represented by many fewer examples, are even more difficult to characterize on the basis of ovary and ovule.

INTRODUCTION

Many characteristics which have been studied in different species of *Rhododendron* have provided observations revealing character variation patterns that have served to supplement to a greater or lesser extent those of gross floral morphology in attempting to arrive at a natural classification of this large genus. These characteristics include the relationship between vegetative and floral buds (Maximowicz, 1870), leaf vernation in vegetative buds (Sinclair, 1937), dermal appendages (Cowan, 1950; Seithe, 1960, 1980), seeds (Kingdon-Ward, 1935, 1947; Hedegaard, 1968, 1980), leaf anatomy (Hayes *et al.,* 1951), wood anatomy on a limited scale (Cox, 1948), floral vascular anatomy on a limited scale (Copeland, 1943), nodal anatomy (Philipson & Philipson, 1968), cotyledon characteristics (Philipson, M. N., 1970, 1980; Hedegaard, 1968, 1980) and some chemical aspects (e.g. Reynolds *et al.,* 1969; Harborne & Williams, 1971; King, 1977; Evans *et al.,* 1980; Spethmann, 1980a,b, etc.). One broad category of characteristics which is known to show considerable diversity among angiosperms is embryology (Davis, 1966; Palser, 1975). There have been scattered observations of some embryological features in a few species of *Rhododendron* (Peltrisot, 1904; Creech, 1955; Veillet-

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Bartoszewska, 1959; Rudenko, 1964; Palser *et al.,* 1971; Yakobson, 1976), but the accumulated information is very limited and totally insufficient to show whether any aspect of embryology might add characteristics which could be used in attempts to clarify our understanding of the relationships among species of *Rhododendron.*

We have undertaken to try to fill some of this gap in the knowledge about *Rhododendron* by studying one broad aspect of the embryology of the genus, namely the ovule and its enclosed megagametophyte along with the ovary within which the ovules are borne. To have a basis for comparison, our observations have covered the ovary and ovule at the mature megagametophyte stage for 131 species distributed among all the subgenera, sections and almost all of the subsections recognized in the most recent revisions of the genus (Sleumer, 1966; Cullen & Chamberlain, 1978, 1979; Cullen, 1980; Chamberlain, 1982; Philipson & Philipson, 1982). In addition, for 14 of these species, again broadly distributed, we have followed development of the ovule and megagametophyte from just after initiation until shortly after fertilization when the endosperm had reached at least a four-celled stage. A summary of the species examined is given in Table 1.

TABLE 1
Number and taxonomic distribution of species examined in the genus *Rhododendron*

Classification[1]	Letter designation[2]	Number of species observed	
		Mature stage	Development
Subgen. *Rhododendron*	R		
Sect. *Vireya*	RV	16	1
(7 subsects [1 with 7 ser.])		(7 [4])	(1)
Sect. *Pogonanthum*	RP	3	1
Sect. *Rhododendron*	RR	42	5
(27 subsects)		(24)	(5)
Subgen. *Hymenanthes*	H		
Sect. *Ponticum*	HP	44	2
(24 subsects)		(21)	(2)
Subgen. *Azaleastrum*	A		
Sect. *Azaleastrum*	AA	2	1
Sect. *Choniastrum*	AC	2	0
Subgen. *Tsutsusi*	T		
Sect. *Tsutsusi*	TT	3	1
Sect. *Brachycalyx*	TB	3	0[3]
Sect. *Tsusiopsis*	TTs	1	0
Subgen. *Pentanthera*	P		
Sect. *Pentanthera*	PP	5	1
Sect. *Rhodora*	PR	2	0[3]
Sect. *Viscidula*	PV	1	0
Sect. *Sciadorhodion*	PS	4	1
Subgen. *Therorhodion*	Th	1	1
Subgen. *Candidastrum*	C	1	0[3]
Subgen. *Mumeazalea*	M	1	0[3]

[1] See text for sources of classification used.

[2] Letters used to identify subgenus and/or section in text and figure legends.

[3] Relatively complete development seen for one species.

The bulk of the information was obtained via light microscopic observations of serial cross and longi sections of the ovary cut 10–15μm thick and stained, in most cases, with safranin and fast green. To confirm and illustrate certain aspects, whole and dissected ovaries of a few species were prepared for, and observed under, the scanning electron microscope.

Not surprisingly in a genus which shows so much variation in gross morphology of the vegetative plant and inflorescence, there is a great deal of diversity in many of the aspects we observed, particularly of the ovary, but also of the ovule and even, though to a lesser extent, of the megagametophyte. To anticipate our conclusions, the variation in no single characteristic, or group of characteristics, is distinct or consistent enough to warrant recommending any major modification of the present classification. Thus, our discussion of the distribution of the different characteristics will be based on their occurrence in the taxa of the revised classification. Consideration of the many features of the *Rhododendron* ovary, ovule and megagametophyte, of those which vary and the extent of that variation, will start from the outside and work inward. The descriptions and comments are, of course, based on the particular species we have studied and may, or may not, be appropriate for other species which we have not seen, even though they may occur in the same infrageneric taxon.

THE OVARY

The pistil, which is the innermost organ of the *Rhododendron* flower, is superior and thus is clearly exposed by removing sepals, petals and stamens. In our study we essentially ignored the two upper parts of the pistil—the style and stigma—and concentrated on the basal ovary. The whole pistil is composed of several 'fused' carpels; externally the number of carpels is reflected in the number of lobes of the stigma and, in some species, by a fluting of the ovary which may be rather conspicuous, as in section *Choniastrum* A* (Fig. 3). although such lobing is often weakly expressed (Figs 4, 6, 10) or nonexistent (Fig. 1). Toward its apex the ovary normally narrows and in several species (sect. *Vireya* R, subsects *Maddenia* RR, *Boothia* RR, *Auriculata* HP and sect. *Choniastrum* A) joins the base of the style by a gradual or more abrupt taper (Fig. 9), but in most species it has a depression in the top, more or less deep, from which the style emerges (Figs 12, 13).

There is a tremendous range in actual size of the ovary: in length from 1·5–12mm and in width from 1·1–6·5mm. The longer and wider dimensions rarely characterize the same species, although the shorter and narrower ones do so in several cases. This nonconformance reflects the wide variation in ovary shape. Generally the ovary is cylindrical or ovate with a diameter/length ratio of between 0·4 and 0·6 in almost half of the species examined. The slenderest ovaries have a ratio of about 0·2 (Fig. 9), while at the opposite extreme are those in which the width is greater than the length (ratio 1·2–1·5) in sect. *Azaleastrum* A. Both slender

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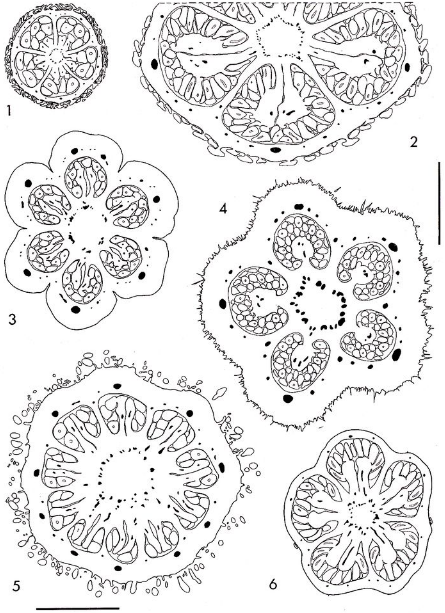
*Here, and following in text and figure legends, where the subgenus or section is not clear in the context of the sentence, identifying letters—listed in Table 1—are given to aid in recognizing the taxonomic placement of species, subsections or sections.

and squat ovaries are usually narrower toward the apex than through most of their length, so that the short ones do not really appear globose (Fig. 12). While sects *Vireya* R and *Rhododendron* R show a wide variation in ovary size (both length and width), rather small ovaries characterize sect. *Pogonanthum* R (Fig. 6) and the azalea complex (Fig. 12) (particularly sect. *Tsutsusi* T) with the exception of sect. *Choniastrum* A. Most species of subgen. *Hymenanthes* have rather large ovaries and none has a really small one. Slender ovaries tend to occur in sects *Vireya* R (Fig. 9) and *Choniastrum* A while squat ones are found in *Pogonanthum* R, *Viscidula* P, *Therorhodion* Th (Fig. 12) and *Mumeazalea* M as well as in *Azaleastrum* A. Both *Rhododendron* R and *Ponticum* H show a wide range in shape, although *Rhododendron* has more broad and fewer narrow ovaries than does *Ponticum*.

One of the most conspicuous features of the ovary when viewed from the surface is its indumentum. While in a few species (in *Vireya* R ([Fig. 26], *Ponticum* H ([Figs 13, 22, 25] and *Sciadorhodion* P) there are no, or very few, hairs on the ovary, most species do have dermal appendages, frequently abundant. Numerous categories of hairs have been described from leaves (Cowan, 1950; Seithe, 1960, 1980). We have not attempted to make the fine distinctions of these authors but have, instead, recognized five broad types: (1) scales (peltate hairs) (Figs 14, 15, 18); (2) glandular hairs (Fig. 16); (3) multiseriate hairs (Figs 19–21); (4) tufted hairs (more or less branched) (Figs 16, 17), and (5) unicellular, occasionally uniseriate, hairs (Figs 15, 18, 19). The hairs on the ovary are, in general, of the same type or types as those that occur on the leaves of the same species, although there may not be exact correspondence: some hair types may be missing and/or different ones added. For example, unicellular hairs are much more prevalent on ovaries than on leaves. Because leaf hairs play an important role in *Rhododendron* classification and there is a similarity of ovary hairs to leaf hairs, species can in many cases be placed into certain major subgroupings on the basis of hairs on the ovary.

Scales are present on ovaries of all but three of the species of subgen. *Rhododendron* (one glabrous [Fig. 26], one with only unicellular [Fig. 4] [both *Vireyas*] and one with only uniseriate [*Rhododendron*] hairs) and do not occur in any other subgenus (Figs 1, 2, 6, 9–11, 14, 15, 18, 24). They are never combined with either glandular or tufted hairs and in only one species are they combined with multiseriate ones. Tufted hairs are

FIGS 1–6. Cross-sectional diagrams of *Rhododendron* ovaries at mid-level; black areas are vascular bundles; Scale = 1mm. FIG. 1. *R. micranthum* RR; scales; locules large relative to ovary diameter; placenta small, cleft; few large ovules, none horizontal. FIG. 2. *R. leucaspis* RR; scales; five locules, large relative to ovary diameter; placenta deeply cleft and expanded; ovules all around placenta, inner lateral ones turn in. FIG. 3. *R. moulmainense* AC; glabrous; fluted; six locules, small relative to ovary diameter; placenta cleft, only slightly expanded; ovules all around placenta, none horizontal. FIG. 4. *R. commonae* RV; unicellular hairs; five locules, small relative to ovary diameter; placenta expanded but not cleft; ovules all around placenta, none horizontal. FIG. 5. *R. aberconwayi* HP; glandular and tufted hairs; ten locules, small relative to ovary diameter; placenta deeply cleft, only slightly or not expanded, extending to dorsal wall; ovules lateral only, none horizontal. FIG. 6. *R. anthopogon* RP; few scales and unicellular hairs; five locules, large relative to ovary diameter; placenta cleft and expanded; ovules all around placenta, lateral ones turn out.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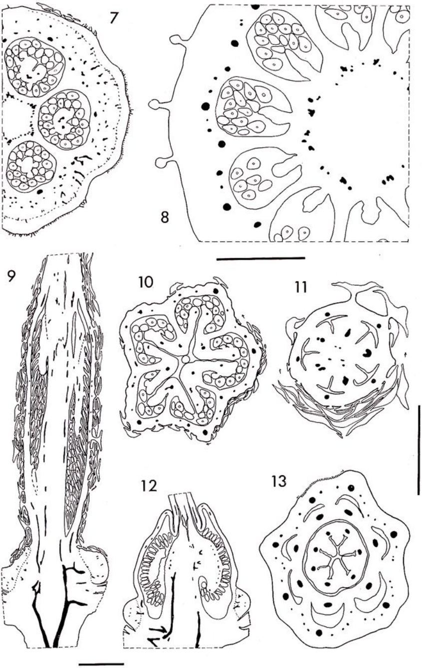
confined to the subgen. *Hymenanthes* (Figs 5, 16, 17) but are found in only about 60% of its species. Glandular hairs are found on ovaries of some, but not all, species of all non-lepidote taxa (Figs 5, 8, 16, 23) except *Therorhodion* Th. Except for *R. edgeworthii* RR, multiseriate hairs are not found on ovaries in any members of subgenera *Rhododendron*, *Hymenanthes*, *Azaleastrum*, *Therorhodion*, *Candidastrum* or *Mumeazalea*; they thus are restricted to subgenera *Tsutsusi* and *Pentanthera*. In the former subgenus the hairs of sects *Tsutsusi* (Fig. 21) and *Tsusiopsis* are easily distinguished from those of sect. *Brachycalyx* (Fig. 20) and of subgen. *Pentanthera* (Fig. 19) because they are flattened rather than rounded or irregular. Unicellular ovary hairs are broadly distributed throughout the genus, occasionally occurring alone (Fig. 4) but more commonly combined with one or more of the other types (Figs 15, 18, 19). In sect. *Vireya* R, with one exception (*R. konori*), the combination of scales and unicellular hairs (Fig. 18) is restricted to subsect. *Euvireya*; the hairs in this section are usually characterized by a prominent bulbous base. Unicellular hairs are found on the ovaries of more species in sect. *Rhododendron* R (Fig. 15) than in *Ponticum* H.

A nectary surrounds the base of the ovary. It is quite variable in shape and size and often forms a conspicuous feature of the total ovary (Figs 9, 12). Melva Philipson has presented this variability in her paper dealing with the *Rhododendron* nectary at this conference.

The ovary surface, in addition to bearing hairs, regularly has stomata which range in frequency from rather widely scattered to very common (Figs 16, 18, 28, 34, 35). In some species, and/or at an early age in their development, the guard cells may be essentially on the same level as the basic epidermal cells, but in many cases they are elevated, from slightly to considerably, above the surface (Fig. 28). The orientation of the guard cells may be irregular, but in a few species the long axis of each stoma tends to be at right angles to the vertical axis of the ovary, while in many more species it tends to be parallel to it (Fig. 34). The surface of the mature ovary of several species shows a range in size of stomata which appears to be related to time of initiation. In fact, it was evident that guard cells were in the process of being initiated in several of the species observed; these showed a complete range from guard-cell mother cells to completely mature guard cells with an open pore between them (Fig. 34).

There is a cuticle on the ovary epidermis which can usually be seen in

FIGS 7–13. Diagrams of *Rhododendron* ovaries; Scales = 1mm (shorter scale for 9 & 12). FIG. 7. *R. hanceanum* RR; cross-section near base showing free downward lobe of placenta with ovules all around it, and vascularization to peripheral nectary; scales on ovary, unicellular hairs on nectary. FIG. 8. *R. fortunei* HP; cross-section near base below placenta showing placental stalk ridges; glandular hairs. FIG. 9. *R. fallacinum* RV; longisection showing tapered apex; scales; ovules tailed, all turn down. FIG. 10. *R. lepidotum* RR; cross-section toward apex showing unilocular area with small residuum of central tissue; scales. FIG. 11. *R. fallacinum* RV; cross-section at base of style with clefts not yet joined in centre; scales. FIG. 12. *R. camtschaticum* Th; longisection showing apical depression around style base; ovules essentially perpendicular to placenta and around downward lobe of placenta; shown glabrous but has some unicellular hairs. FIG. 13. *R. fulvum* HP; cross-section near top showing seven upward locular pockets in rim around central depression surrounding style with its angled canal; no hairs but epidermis highly papillate.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sections under the light microscope. It ranges in thickness from quite thin to thick. In certain species it can readily be seen, even with sections under the light microscope, that the cuticle is far from smooth and has a prominent ornamentation which shows as ridges projecting from the surface (Fig. 35). In other species the ornamentation is much less obvious, and it cannot be recognized at all in still others. A few observations with the scanning electron microscope confirm the existence of cuticular ornamentation with differing patterns, in some species very conspicuous and in others inconspicuous, suggesting that this is one aspect which might well repay study with the SEM. Our rough assessment of cuticular patterning, using only the light microscope, suggests that obvious ornamentation is characteristic of certain groups: for example, it is much more frequent on ovaries of subgen. *Hymenanthes* than of subgen. *Rhododendron* (none in sect. *Pogonanthum*). Similarly, cuticular patterns are marked in certain subgenera or sections of the azalea complex: in subgen. *Azaleastrum* with the exception of one species in sect. *Choniastrum,* in subgenera *Therorhodion, Candidastrum* and *Mumeazealea* and in sect. *Sciadorhodion* of subgen. *Pentanthera*. Such patterns cannot be seen in other sections of subgen. *Pentanthera* (except for slight indications in *R. glabrius* PP) or in any section of subgen. *Tsutsusi.*

When the ovary is opened, the number of carpels can be easily determined by the number of cavities or locules that surround the central axis (Figs 1–8, 11, 13, 22–24); the latter is solid for all or most of the length of the ovary. In the species examined, locule number ranges from 5 to 17. In all subgenera except *Hymenanthes* five is the most common number (Figs 1, 2, 4, 6, 10, 11, 24), but occasionally six can be found (sect. *Choniastrum* A [Fig. 3], subgen. *Mumeazalea* and species or individual specimens in other taxa) or, in a few of the largest ovaried species of sects *Vireya* R and *Rhododendron* R, seven. In contrast, only three of the species we examined in subgen. *Hymenanthes* have five locules, several have six, and most have higher numbers ranging up to 17 (Figs 5, 8, 13, 22, 23), with the average number for the subgenus being 8·4.

The locules are separated from one another for most or all of the ovary length by relatively narrow septa (Figs 1–8, 10, 22–24). The thickness of the outer ovary wall and the diameter of the central axis vary considerably, however, relative to the locules, so that the latter may occupy as little as 29% (*R. macabeanum* HP) to as much as 77% (*R. albiflorum* C) of the total ovary diameter. Although there may be considerable variation in this character among species within any one section, subgen. *Hymenanthes* (Figs 5, 8) and sects *Choniastrum* A (Fig. 3) and *Vireya* R (Fig. 4) average 48% or less for the proportion of locule to

FIGS 14–21. Scanning electron micrographs of *Rhododendron* ovary hairs. FIG. 14. *R. leucaspis* RR; scales, × 137. FIG. 15. *R. scabrifolium* RR; scales and unicellular hairs, × 88. FIG. 16. *R. caucasicum* HP; glandular and small tufted hairs, × 90. FIG. 17. *R. macabeanum* HP; tufted hairs, note that they are multiseriate at base with long free ends; × 77. FIG. 18. *R. vidalii* RV; scales and unicellular hairs, × 160. FIG. 19. *R. glabrius* PP; unicellular and multiseriate hairs, some with small gland-like tip, × 180. FIG. 20. *R. weyrichii* TB; multiseriate hairs, × 132. FIG. 21. *R. subsessile* TT; flattened multiseriate hairs, × 80.

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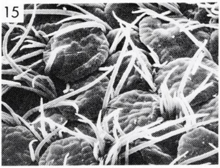

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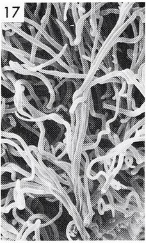

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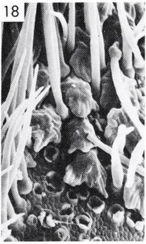

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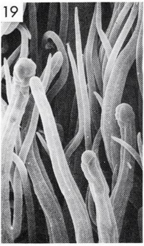

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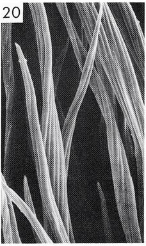

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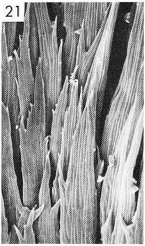
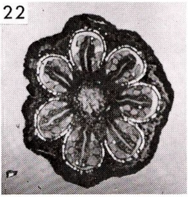


ovary diameter; in the other sections (except for *Viscidula* P) the proportion is quite a bit higher (Figs 1, 2, 6), in many close to or better than 60%. Whether the non-locule portion of the diameter is contributed primarily by outer wall, by the central axis, or by a combination of the two, varies. For example, in a number of species of subgen. *Hymenanthes* relatively small locules are arranged around a massive central axis and bounded outwardly by a moderately thick wall (Fig. 5). In *R. javanicum* RV, on the other hand, the central axis is rather narrow, while the outer wall is massive (Fig. 26).

The placenta on which the ovules are borne diverges into the locule from the central axis (Figs. 1–6, 9, 12, 22–24) along much of its extent. It projects more or less deeply toward the outer wall and may, or may not, have a free lobe downward below the area of its attachment to the axis (Figs 7, 12). Each placenta has an inner stalk or ovule-free portion (very short [Fig. 4] to moderately long [Fig. 2]) and an outer ovule-bearing part which may be only slightly broader than the stalk (Figs 3, 5, 22, 23) or be considerably expanded (Figs 2, 4, 24). It is usually divided, more or less deeply, into two halves (Figs 1–3, 5, 6, 22–24). The separation extends in as far as, or into, the central axis in the upper ovary or stylar base and usually becomes less and less deep lower in the ovary; a downward lobe may, or may not, show the cleft (Fig. 7). In sect. *Vireya* R (Fig. 4), subsects *Heliolepida* RR, *Caroliniana* RR and *Auriculata* HP and a few species of the azalea complex (mostly in subgen. *Pentanthera*) there is only a moderately shallow groove in the outer surface of the placenta for most of its length. As the placental clefts in the several locules of an ovary extend inward at the top of the ovary, they meet in the centre, occasionally around a small residual dome of tissue—sometimes vasculated—which soon disappears. When the junction occurs at a relatively low level where ovules are still being borne, the ovary becomes unilocular (Fig. 10) and the placentation can be considered parietal rather than axile as it is at lower levels. This is more prevalent among ovaries with a deep depression at the apex and upward placental lobes. Most

FIGS 22–28. Cross-sections of *Rhododendron* ovaries and parts of ovary wall; Figs 22–25 taken under partially polarized light to show crystals. FIG. 22. *R. fulvum* HP, ×16; crystal-containing layer of carpel lining essentially complete in outer wall and through septa almost to central axis. FIG. 23. *R. barbatum* HP, ×16; crystal-containing layer of carpel lining fairly complete in outer wall but only at outer ends of septa; crystals also scattered in mid-mesophyll; glandular hairs on surface. FIG. 24. *R. leucaspis* RR, ×16; crystals in many cells of crystalliferous layer of carpel lining (small birefringent spots near locules), in placental stalks and central axis and in scattered mesophyll cells of wall (smaller birefringent spots). Large birefringent cells in wall are thick-walled sclereids. Broad dark area at left is upper part of nectary; scales on ovary wall not nectary. FIG. 25. *R. fulvum* HP, enlargement of portion from Fig. 22, ×98. Birefringent spots outside crystalliferous layer are tracheary elements in vascular bundles; mesophyll 'mixed', darkest cells contain tannins; epidermis papillate. FIG. 26. *R. javanicum* RV, ×39; many cells in outer half of very thick wall considerably enlarged; dark cells contain tannins; glabrous. Small flattened pieces in locule are sections of chalazal tails of ovules. FIG. 27. *R. serpyllifolium* TT, ×250; wall thin and lacks tannins; note portion of flattened multiseriate hair. FIG. 28. *R. weyrichii* TB, ×258; 'crystalliferous' layer of carpel lining clear but lacks crystals; mesophyll 'mixed', darkly stained cells contain tannins; note irregular multiseriate hairs. Five stomata in epidermis, not all in median section, are raised above general surface.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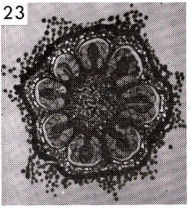
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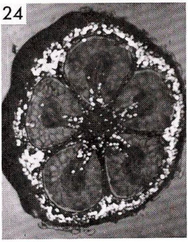
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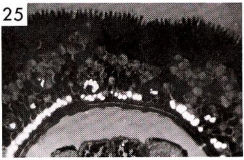
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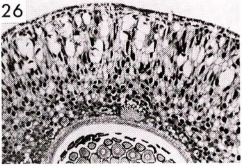
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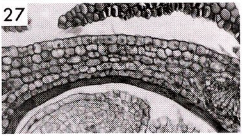
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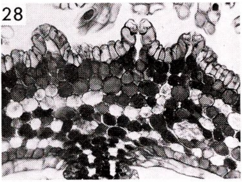
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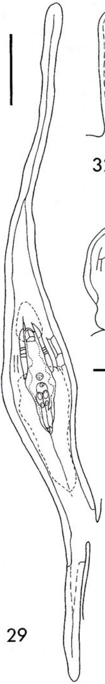
commonly the junction occurs at about the level of the uppermost ovules, but there are a number of species, some with a depression but others, particularly of sect. *Vireya* R, with a tapered apex, in which this junction occurs well above the level of the uppermost ovules in the very top of the ovary or base of the style (Fig. 11). In such species there is no unilocular portion of the ovary. Whatever the level at which the placental clefts meet one another, the central opening is continued upward as an angled canal through the style (Fig. 13). The stylar canal, the placental cleft and the placental lobes, but not the stalk, are covered by a layer of transmitting tissue along which pollen tubes grow from the stigma to the ovule.

The placental stalk is decurrent down the central axis in many species, in a number of them for a considerable distance. It projects more or less deeply into the locule as a narrow, or occasionally broad, ridge (Fig. 8). This placental stalk ridge occurs commonly, but not exclusively, in species with little or no downward placental lobe. It is absent in sects *Pogonanthum* R and *Azaleastrum* A, subgenera *Therorhodion* and *Candidastrum* and most species of sect. *Rhododendron* R and many of *Vireya* R. The ridge which occurs in several species of *Vireya* R, sect. *Tsutsusi* T and a few species of sect. *Rhododendron* R is inconspicuous (rather shallow and/or not long continued), but it is a conspicuous feature of the locules in most, but not all, species of subgen. *Hymenanthes* and also characterizes sects *Choniastrum* A, *Brachycalyx* T, and *Tsusiopsis* T and subgenera *Pentanthera* and *Mumeazalea.*

Stomata occur in the epidermis of the placental stalk in all species examined (Fig. 36). The guard cells may show no regular orientation but frequently tend toward a vertical alignment or, more rarely, a transverse one. Their abundance varies, but many species have a fairly large number, sometimes with two or even three pairs of guard cells in contact with one another (Fig. 36). The stomata are frequently somewhat larger than those on the ovary or nectary surface and the pore is usually wide open. Stomata may also occur elsewhere in the locule, such as on the central axis below the placenta, the dorsal carpel wall, the septum, and/or the upward locule pockets around the stylar depression, occurring in more species and in greater abundance in the latter two areas. Only rarely are they found on the placenta itself or on an ovule. Hairs, unicellular or occasionally uniseriate, also occur inside the ovary of several species. They

FIGS 29–36. *Rhododendron* ovules and stomata; Scales = 100μm (shorter scales for 29–33). FIGS 29–33. Longisection diagrams of selected ovules with micropylar end down. Indicated are integumentary epidermis, endothelium, number of layers in integument, area of starch around egg apparatus and micropyle, chalazal hypostase and mature or almost mature megagametophyte. FIG. 29. *R. javanicum* RV; both micropylar and chalazal tails. FIG. 30. *R. micranthum* RR; note 'frill' at micropylar end. FIG. 31. *R. calostrotum* RR; ovule from transition area on placenta and shorter and broader than usual; see Fig. 41. FIG. 32. *R. camtschaticum* Th. FIG. 33. *R. weyrichii* TB. FIGS 34–36. Ovary stomata. FIG. 34. *R. chrysodoron* RR; paradermal section of ovary wall surface, oriented vertically; guard cells apparently still being initiated. FIG. 35. *R. fulvum* HP; cross-section of ovary wall showing raised pair of guard cells, papillate epidermis and thick ornamented cuticle. FIG. 36. *R. carneum* RR; from longisection of ovary showing paradermal section of placental stalk surface; note that guard cells may be raised above surface and be in contact with one another.



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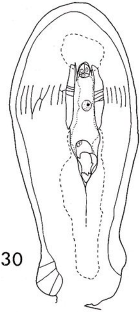

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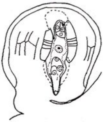

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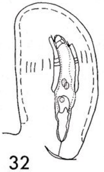

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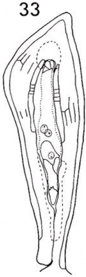

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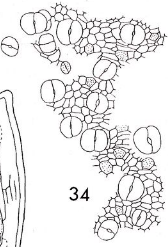

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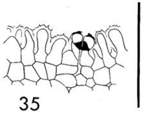

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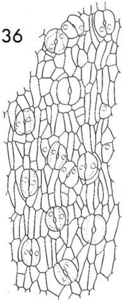

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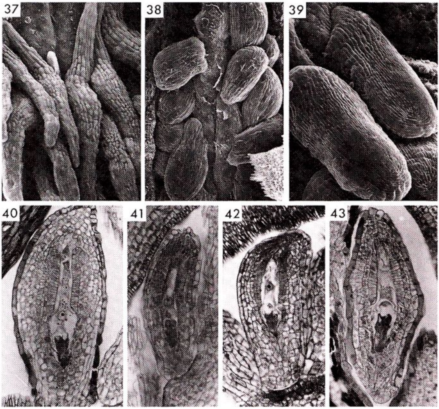

FIGS 37–43. Ovules in *Rhododendron*. FIGS 37–39. Scanning electron micrographs of whole ovules at top of placenta; top toward style. FIG. 37. *R. javanicum* RV, ×82; all ovules turn down sharply and have long micropylar (upward) and chalazal tails; groove above ovules is cleft in placenta. FIG. 38. *R. scabrifolium* RR, ×80. Ovules in transition area at top of placenta: topmost ovules turn up, lowermost down, with intermediate ones very variable in orientation; irregular line down centre is cleft between placental halves. FIG. 39. *R. quinquefolium* PS, ×105. All ovules inclined downward. FIGS 40–43. Longisections of ovules with mature or almost mature megagametophytes, micropylar end down. Dark stain in epidermal layer indicates presence of tannins. Endothelium shows as narrow radially elongated cells around chalazal portion of gametophyte, hypostase as slightly darker area around chalazal end; starch in micropylar part of ovule and/or in gametophyte may be distinguished in some cases by dark hilum. In gametophyte, note filiform apparatus (dark area at tip), lateral hooks and chalazal vacuoles in synergids; long vacuolate egg; rather small inconspicuous antipodal cells. FIG. 40. *R. fortunei* HP, ×178; this section lacks egg (in adjacent section); central cell has secondary nucleus within obvious micropylar bulge and many large starch grains. FIG. 41. *R. calostrotum* RR, ×172; secondary nucleus at endothelial constriction. FIG. 42. *R. anthopogon* RP, ×178; secondary nucleus well within chalazal portion of gametophyte. FIG. 43. *R. yunnanense* RR, ×163; polar nuclei, one obscured by starch, essentially at level of endothelial constriction; ovule starch extends to micropylar opening.

are found most frequently on or near the central axis close to the apex or base of the locule but also occur on the dorsal wall, septum, placental stalk and in the upper lobe. They may be few in number or may be very abundant in localized areas. In some species these hairs are short but in others they are long and project among the ovules.

Characteristics of the dorsal wall at about mid-level have been recorded from cross-sections of ovaries containing mature ovules. This wall can be subdivided into three regions: an epidermis, the mesophyll which encloses the vascular bundles near its inner edge, and a carpel lining. The epidermal cells range from slightly tabular to radially elongate and from flat on the surface (Figs 26, 27) to papillate for more than half of their length (Figs 25, 35). The mesophyll usually consists of parenchyma cells only and ranges in thickness from as few as three layers in *R. malayanum* RV and *R. serpyllifolium* TT (Fig. 27) to as many as 24 in *R. griffithianum* HP. The number of layers tends to be lowest in sects *Pogonanthum* R, *Rhodora* P, *Viscidula* P and subgenera *Therorhodion* and *Candidastrum* and highest in subgen. *Hymenanthes* and sect. *Choniastrum* A. Sect. *Vireya* R is very variable in this regard, while sect. *Rhododendron* R tends to have relatively few layers except in subsects *Maddenia* and *Boothia*. Cell size is variable both among species and, in a number of them, even within the wall of a single ovary. In the latter case cell size may range from smallest near the lining to largest under the epidermis or the largest cells may occur in mid-mesophyll. A few species are beginning to show maturing sclereids in the wall mesophyll at the mature ovule stage (Fig. 24), but such cells occur in more species and in greater abundance after fertilization has occurred. The carpel lining in almost all species consists of three different layers (Figs 25–28), each of them initially one cell thick. At the mature ovule stage cells in each of the inner two lining layers are starting to divide periclinally in many species so the layers may be one, one–two, two or rarely two–three cells thick. The layer adjacent to the locule is composed of cells very shallow vertically and tangentially elongated; cells of the second layer are also shallow but less elongated, while those of the third layer, which is rarely more than one cell thick, are essentially isodiametric. The lining layers extend to the central axis through the septa; in the latter they are separated from similar layers of the adjacent locule by just a few mesophyll cells.

Tanniniferous compounds are common in cells of the ovary wall of most species. At one extreme are those species in which there appear to be no tannins (Fig. 27) and at the other those in which all cells stain heavily. Most species, however, have varying numbers of 'clear' cells scattered among tanniniferous ones (Figs 25, 26, 28). In most of these 'mixed' ovary walls the epidermis and/or one to three or four hypodermal layers are usually tanniniferous (Figs 25, 28). The one layer which is most commonly composed entirely or almost entirely of non-tanniniferous cells is the third layer of the lining, that closest to the mesophyll (Figs 25, 26, 28). Within the mesophyll the greatest concentration of 'clear' cells usually occurs about midway between lining layers and epidermis (Figs 25, 28). Crystals, either prismatic ones or druses, or both, are found in certain cells of the ovary in many, but not all, species. Their most characteristic location is in the clear cells of the third layer of the carpel lining (Figs 22–25). There their appearance may be restricted largely to the outer wall (Fig. 23) but may also continue for varying distances through the septa (Figs 22, 24) and even into the placental stalk in some species (Fig. 24). In fewer species and cells, crystals may also be present in some of the non-tanniniferous cells of the mesophyll (Figs 23, 24), usually those about midway between epidermis and lining. In a few species they occur in the placenta or in the central axis (Fig. 24). There are only a few species in the azalea complex which have more than a few scattered crystals. No regular distributional pattern could be recognized in other taxa.

THE OVULE

Within each locule ovules are attached to the placenta. Variation occurs in number of ovules per locule, their orientation, and the portions of the placenta to which they are attached. In no species is there a single ovule per locule; the lowest number is found in *R. micranthum* RR which has about 12 per carpel and the highest, close to 2000, in *R. nuttallii* RR and *R. konori* RV. The average number of ovules per carpel is higher in sect. *Vireya* R than in any other taxon and the lower numbers are more prevalent in sects *Pogonanthum* R, *Tsutsusi* T, *Pentanthera* P, *Sciadorhodion* P and subgen. *Candidastrum*. Sect. *Rhododendron* R shows a wide range in ovule number, being high in subsects *Maddenia* and *Edgeworthia* and rather low in *R. hirsutum* and *R. trichanthum* as well as very low in *R. micranthum*. Ovule number varies, but much less widely, in subgen. *Hymenanthes*.

Initially the young ovule stands at essentially right angles to the placental surface on which it is borne and its anatropous curvature is away from the center of the locule toward the septa on either side; thus the ovules on the two halves of the placenta turn in opposite directions. During subsequent development this basic orientation is often modified. In some species there is little change and the ovules continue to be perpendicular, or close to perpendicular, to the placental surface (Figs 6, 12), but more usually they become tilted up or down to a greater or lesser extent. In all species of sect. *Vireya* R (Figs 9, 37) and all or most species of subsects *Maddenia, Edgeworthia, Moupinensia, Lapponica, Micrantha, Boothia* and *Camelliiflora* (all of sect. *Rhododendron* R) plus an occasional species in other subsections (Fig. 39), all ovules are oriented downward and, where the angle is particularly steep, overlap like shingles (Fig. 9). In the majority of species, however, varying numbers of ovules at the top turn up while the rest turn down (Fig. 38). The change in direction may be abrupt or gradual and ovule shape and orientation can be quite variable in the 'transition' area (Fig. 38). There is a tendency in sect. *Rhododendron* R for only the few uppermost, usually not more than the upper one-quarter, of the ovules to tilt upward, while in *Ponticum* H close to half of the ovules do so and in sect. *Choniastrum* A the number approaches two-thirds or more.

In addition to the variability in vertical orientation, the ovules may show a different horizontal orientation relative to the central axis and placental stalk. In those species where the ovules are essentially perpendicular to the placenta, or in the transition region in those species where some tilt up and others down, ovules (only the innermost or more) on the sides or inner surface adjacent to the placental stalk may turn in so that the micropylar opening is 'tucked in' (Fig. 2), while in other species they turn out so that the micropylar opening is 'exposed' (Fig. 6). In a few species the lateral ovules may be perpendicular. No correlation between these different orientations and sections could be recognized.

In subgenera *Therorhodion, Candidastrum, Mumeazalea,* and sect. *Tsutsusi* T and in most species of subgenera *Rhododendron* and *Pentanthera* ovules are borne on both the sides and outer surface of the placenta between the placenta and septa and placenta and dorsal wall (Figs 1–4, 6, 10, 24). In sect. *Tsusiopsis* T and in most species of sect. *Brachycalyx* T and subgen. *Hymenanthes,* as well as one species of *Sciadorhodion* P, however, they are borne only on the sides of the placenta and are absent from the outer surface which extends all the way to the dorsal wall (Figs 5, 22, 23). In some species, several in *Ponticum* H and a few in *Rhododendron* R and *Vireya* R, there are no outer ovules in the top of the locule, but toward the base, where the placenta projects less deeply into the locule, some do occur. In those species with a downward placental lobe, ovule attachment continues on the base of the lobe and may extend up its inner surface between the placenta and central axis (Figs 7, 12). There are a few species, with small placentae, in which all the ovules are borne on the outer surface (*R. micranthum* RR [Fig. 1], *R. quinquefolium* PS).

The ovule in *Rhododendron* starts as a narrow nucellus which early begins to bend to the side and soon becomes anatropous. A single integument is initiated by division of epidermal cells several cells back from the tip of the nucellus; it continues to grow until it extends beyond and closes over the nucellus to form the micropyle, which often becomes quite long (Figs 29, 30). With the differentiation of sporogenous tissue, the nucellus is restricted to a single epidermal layer on the sides and at the micropylar end. Later this layer breaks down completely so that the mature ovule has only a very few nucellar cells remaining at the chalazal end (Figs 29–33, 40–43). Those cells of the inner layer of the integument which had surrounded the nucellus differentate as an endothelium (Figs 29–33, 40–43). In many species, usually starting at the chalazal end rather early in development, tannins are deposited in outer epidermal cells of the integument which, thus, often becomes quite distinct from the other integumentary layers (Figs 40, 43). Starch occurs in integumentary cells, except for the endothelium and usually the epidermis, appearing fairly early in development as a few small grains which increase in size and number, usually reaching greatest abundance before the ovule is mature and decreasing in frequency to maturity and post-fertilization. In most species starch persists longest around the egg apparatus and along the micropyle (Figs 29–33, 40–43). During development, cells around the chalazal end of the gametophyte usually become more conspicuous because their cytoplasm is more dense and/or their walls stain more heavily (Figs 29–33, 40–43); this may be considered a ‘cytoplasmic’ hypostase. In some species appendages, particularly micropylar and chalazal tails, are already well developed by the time the ovule is mature (Figs. 29, 37).

At maturity (megagametophyte mature) the ovule, which is longer than broad and rather round or oval in cross-section, varies considerably in size in different species of *Rhododendron.* The longest are 0·46–0·41mm in length (without tails) and the shortest 0·18–0·21mm. The widest (halfway between chalazal end and micropylar opening) are 0·20–0·15mm and the narrowest 0·07–0·08mm wide. As with the ovaries, only in a very few species do the longer and wider ovules or the shorter and narrower ones occur in the same species; that is, there is considerable variation in shape (see Figs 29–33, 37–43). Although the shape of the ovules may vary within a single locule depending primarily on their position on the placenta (compare Figs 31, 41), the majority are relatively constant in their proportions. The peculiar ovules are almost always those in the transition area and a few larger ones may occur at the base of the placenta. The ratio of diameter to length ranges from 0·22–0·65 with a great deal of variation within sect. *Rhododendron* R and subgen. *Hymenanthes*. Sect. *Vireya* R shows much less variation, with ovules in all species being relatively slender (ratio 0·22–0·35, average 0·27) (Figs 29, 37). Among the azalea complex, sects *Brachycalyx* T (Fig. 33), *Rhodora* P, subgenera *Candidastrum* and *Mumeazalea* have moderately slender ovules, while in sections *Choniastrum* A, *Tsusiopsis* T, *Viscidula* P and subgen. *Therorhodion* (Fig. 32) they are moderately broad with those in sects *Tsutsusi* T, *Pentanthera* P, *Sciadorhodion* P (Fig. 39) and *Azaleastrum* A being intermediate. There appears to be little correlation between ovule and ovary size: in many cases the largest ovules are not found in the largest ovaries nor the smallest in the smallest. For example, the ovules in the very small ovary of *R. micranthum* RR are among the largest (Figs 1, 30). The correlation between ovule number and ovary size is much better: the two largest ovaries (*R. konori* RV and *R. nuttallii* RR) have the most ovules and the three lowest numbers of ovules occur in three of the smaller ovaries (Fig. 1). There is, of course, very close correlation when ovule number and size together are compared to ovary size.

The megagametophyte which is contained within the ovule occupies a greater or lesser proportion of the ovule length (see Figs 29–33, 40–43). Those gametophytes that are shortest (30–38% of ovule length) occur primarily in sect. *Vireya* R (Fig. 29), while those that are proportionately long (84–68%) belong to species in the azalea complex (Fig. 32), although in different sections. This wide variation in gametophyte/ovule length ratios is rather closely correlated with the length of the micropyle. The longest micropyles are found in sect. *Vireya* R (Fig. 29) which also has the shortest gametophytes. All species which have the longest gametophytes relative to ovule length have rather short micropyles (Fig. 32) and those that have the proportionately shortest micropyles have gametophytes long relative to ovule length.

Tails develop, by some cell division and considerable cell elongation, from both the micropylar and chalazal ends of the ovules in species of sect. *Vireya* R. At the mature ovule stage these tails vary in length from quite short in *R. lochae* to very long in several others (Figs 29, 37). Ovules in a few other species, primarily in subgen. *Hymenanthes* and sects *Pentanthera* P and *Choniastrum* A, show a slight beginning of some chalazal extension (Fig. 40). Almost all of these species are ones which have chalazal ornamentation on their seeds. A ‘frill’ may develop around the micropylar end of the ovule by radial elongation of a few epidermal cells (Fig. 30). This is most noticeable on ovules of species with micropylar ornamentation of their seeds (e.g. species of subgen. *Hymenanthes*, subsects *Maddenia* and *Edgeworthia* of sect. *Rhododendron* R and in sects *Choniastrum* A, *Tsusiopsis* T and *Pentanthera* P.

Considerable diversity among species occurs in details of ovular structure, as well as in general size and proportions. The epidermis, though it commonly is tanniniferous (Figs 40, 43), may have little or no tannin in some species (Figs 41, 42), and in those species in which it is present the stain in the cells ranges from rather pale to very intense (Fig. 40). Similarly the degree of differentiation of the endothelium and of the hypostase varies considerably. In its most highly differentiated state the endothelium, which surrounds only the chalazal one-half to two-thirds of the gametophyte (Figs 29–33, 40–43), is made up of highly cytoplasmic narrow cells elongated at right angles to the surface of the gametophyte. In a relatively weakly differentiated endothelium the cells are only slightly narrowed, not much deeper than those adjacent to them, and almost as vacuolate as other integumentary cells. A conspicuous, or inconspicuous, endothelium is not characteristic of all species in any section, although it tends to be less distinct in sect. *Vireya* R and rather well-developed in subgen. *Hymenanthes*. It is well-defined to moderately clear in all species of the azalea complex except in four species of subgen. *Pentanthera* (from three different sections).

The hypostase (Figs 29–33) is most conspicuous when both the walls and cytoplasm stain more heavily than in other cells (Figs 40, 42, 43). In some species only the walls or only the cytoplasm stains more heavily, while in still others a differentiated zone is difficult to recognize. Again, no section is characterized throughout by a distinct, or a weak, hypostase, although there is a tendency for it to be more conspicuous in sects *Vireya, Pogonanthum* and *Rhododendron* (all subgen. *Rhododendron*) and less obvious in the azalea complex.

The number of integumentary cell layers between the endothelium and the epidermis varies from two to six (rarely eight) in different species; thus the integument ranges from four to eight (ten) cells in thickness (Figs 29–33, 40–43). The basic number can be determined in any plane but that of the raphe (joint funiculus-integument) where the ovule is thicker. Again, no particular number characterizes the ovules of all species in any section, but it commonly is four to five in *Vireya* R, four to six (rarely ten) but mostly five in *Rhododendron* R, five to six (rarely eight) in *Ponticum* H, with the highest average number (six to eight) occurring in *Sciadorhodion* P. The differences in number of integumentary layers accounts for some of the differences in ovule size but not all of it; differences in cell size also contribute to the variation.

Integumentary starch is usually conspicuous in the mature ovule (Figs 40, 43). The grains are often rather large and usually stain blue-green with the safranin-fast green stain used. The number per cell ranges from few to several, and the size of the grains and of the zone in which they occur also varies. In all but one species they surround the egg apparatus and, in many, also extend along the micropyle for varying distances, in a few all the way to the mouth. The starch may occupy a narrow zone immediately adjacent to the gametophyte and micropyle (Figs 31, 33) or it may extend for varying distances out to, but normally not including, the epidermis (Figs 29, 43). No particular pattern of starch distribution, size or abundance could be recognized as being characteristic of any individual taxon.

THE MEGAGAMETOPHYTE

Megasporogenesis and development of the megagametophyte occur concurrently with development of the ovule and are the same in general pattern in all species. They have been illustrated for *R. yunnanense* RR by Palser *et al.* (1971) and by Yakobson (1976) for *R. luteum* PP, *R. mucronulatum* RR and *R. catawbiense* HP. Development starts by the differentiation of a single hypodermal cell at the tip of the young nucellus as the archesporium; it is often the terminal cell of a row of two or three cells surrounded by the nucellar epidermis. The archesporial cell enlarges to become the megaspore mother cell directly. The latter undergoes meiosis to form first a dyad and then a tetrad which is almost always linear with the chalazal spore larger than the three micropylar ones. The micropylar spores disintegrate while the chalazal one enlarges. Disintegration of the nucellus starts laterally coincidentally with spore degeneration. Three mitotic divisions occur in the functional spore giving rise to eight nuclei occurring in two groups of four at opposite ends of the gametophyte and separated by a large vacuole. Nucellar degeneration is usually complete by the four-nucleate stage and the gametophyte starts to elongate into the micropyle. Cell formation follows closely on the last mitosis, resulting in the formation of three rather small antipodal cells at the chalazal end, an egg apparatus consisting of an egg and two synergids at the micropylar end, and a large central cell with two polar nuclei. Development thus corresponds to the Polygonum pattern (Maheshwari, 1950). The only variations which occur during development in different species are related to the timing of certain events, not in the basic pattern. For example, the mature megagametophyte is very much larger than the functional spore; the increase in size may be gradual throughout development in a few species, while in others it occurs primarily at one stage or another—in *R. yunnanense* RR between the eight-nucleate and mature stages. As another example, by an early two-nucleate stage in the gametophyte of *R. micranthum* RR the micropyle has closed and become very long, while in a species such as *R. camtschaticum* Th the integument at the same stage has usually not yet closed over the nucellus to form the micropyle. No consistent pattern was recognized in such variations.

Pollen tubes in style, locule and ovule were seen in several species. The pollen tubes (often more than one) enter the ovule via the micropyle. The sperm nuclei are small and fuse rapidly with the egg and secondary nuclei to form the zygote and primary endosperm nuclei. Initiation of endosperm development follows closely on fertilization with each nuclear division being followed by cell division, so endosperm development conforms to the Cellular pattern (Maheshwari, 1950), despite certain earlier reports to the contrary (i.e. a Nuclear development: Peltrisot, 1904; Creech, 1955). Cellular endosperm development in *Rhododendron* has previously been described for *R. yunnanense* RR by Palser *et al.* (1971), for *R. ferrugineum* RR by Veillet-Bartoszewska (1959) and for *R. luteum* PP, *R. mucronulatum* RR and *R. catawbiense* HP by Yakobson (1976). The first divisions are transverse so that the first four cells are linearly arranged. The next divisions are longitudinal in the two central cells at least and often in the micropylar one as well; the chalazal cell may also divide vertically but frequently the division is transverse. Subsequent divisions are less regular. Even by an eight-celled stage in the endosperm the zygote has not yet divided, only started to elongate toward the area of the endothelial constriction.

As is not surprising when the ovules vary considerably in size, there is a rather wide range among species in length and width of the mature megagametophyte. The shortest (0·10–0·11mm) are all in subgen. *Rhododendron* (two *Vireya,* two *Pogonanthum* and four *Rhododendron*), while the longest (0.28–0.21mm) are mostly from the azalea complex—all of sects *Sciadorhodion* P, *Viscidula* P and subgen. *Candidastrum*—but one each from sect. *Rhododendron* R and subgen. *Hymenanthes*. There is fair agreement between long ovules and long gametophytes, particularly in sect. *Sciadorhodion* P, but the *Vireyas* R are a notable exception. As was pointed out earlier, in this section the gametophyte tends to be short relative to ovule length and the micropyle long (Fig. 29). When measured within the endothelium, gametophyte width also varies among species (0·012–0·057mm). The narrowest are scattered in subgenera *Rhododendron* and *Hymenanthes* and in only one azalea (*R. canadense* PR), while the widest are in *Hymenanthes* and the azalea complex. As can be seen from the length and width dimensions, the gametophytes are always narrower than long (Figs 29–33, 40–43), but some are more so than others with the percentage of width to length ranging from 9–29%. The gametophytes are, therefore, basically narrower than the ovules (width/length 19–65%). There does not appear to be any regular correlation between relative slenderness or broadness of the gametophyte and that of the ovule; while *R. fallacinum* RV with one of the slenderest ovules also has a slender gametophyte and *R. ovatum* AC a broad gametophyte in a broad ovule, the reverse is also found: two of the slenderest ovules (in *Vireya* R) have a broad gametophyte and one of the broadest gametophytes (in *Ponticum* H) occurs in a slender ovule. On the average, the gametophyte is proportionately broad in sects *Pogonanthum* R (Fig. 42), *Azaleastrum* A and *Pentanthera* P and slender in subgenera *Therorhodion* (Fig. 32) and *Mumeazalea* and sects *Rhodora* P and *Brachycalyx* T (Fig. 33). *Vireya* R, *Rhododendron* R and *Ponticum* H are highly variable.

The megagametophyte has two portions: a chalazal one bounded by the endothelium and a micropylar one, containing the egg apparatus, anterior to the endothelial constriction (Figs 29–33, 40–43). The micropylar portion is that which elongated into the micropyle after nucellar degeneration and has often expanded there at the expense of adjacent integumentary cells, so that it appears, and often is, wider than the chalazal section. The ratio of the width of the chalazal portion to that of the micropylar ranges from about 40% to well over 100% in which case the chalazal end is wider than the micropylar. Where the percentage is lower, the gametophyte has an obvious micropylar bulge (Fig. 40). Wide variation in this relationship occurs within all taxa. The micropylar portion is generally a little shorter than the chalazal (micropylar length/total length 35–50% in most species) (Figs 29–33, 40–43); in only four species does the micropylar portion comprise 30% or less of the total gametophyte, while in 16 species the micropylar is actually a little longer than the chalazal portion (51–57% of the whole). Again, there appears to be considerable variability within sections but, on the average, the micropylar part forms a somewhat larger proportion of the gametophyte (47%) in sect. *Rhododendron* R than it does in subgen. *Hymenanthes* (40%).

Since the egg apparatus is contained within the micropylar portion of the gametophyte, it is not surprising to find that the proportion of the total gametophyte occupied by the egg apparatus also varies—from 24–58%—and that percentages are rather similar for micropylar portion to whole and egg apparatus to whole. The egg apparatus may occupy only part of the micropylar portion, however, and may even project a short way beyond the endothelial constriction into the chalazal end; thus, there is not an exact correspondence between the relation of egg apparatus to the whole gametophyte and of micropylar portion to the whole. The comparatively shortest egg apparati tend to be found in ovules in which the micropylar portion forms a relatively large proportion of the whole and the comparatively longest to be found in ovules in which the micropylar portion forms a smaller proportion of the whole. It is difficult to see any real correlation between proportion of the micropylar bulge occupied by the egg apparatus and taxonomic groups, although there are some slight tendencies.

There is some variation in characteristics of individual cells making up the gametophyte, but again no correlation of these with taxon can be discerned. Examples of the types of diversity that occur include the following (see Figs 29–33, 40–43). The synergids are large with a filiform apparatus at the micropylar end which varies considerably in size among species, as do the hooks which occur laterally on these cells. The egg may project only a little beyond, but more commonly well beyond, the synergids. In a relatively small number of species the egg has some starch grains. The two polar nuclei fuse before fertilization in almost all species, and the position of the secondary nucleus varies from within the micropylar bulge with the egg apparatus in a few species (Fig. 40), through close to the endothelial constriction in many (Figs 29, 32, 33, 41, 43), to well within the chalazal portion in several (Figs 30, 31, 42). Starch is commonly present in the central cell around the secondary nucleus (or rarely polar nuclei) (Figs 40, 43); it varies widely in size of grains and abundance. Those grains which occur in the central cell and egg rarely stain, in contrast to those in the integumentary cells around the egg apparatus. The antipodal cells, which are usually small and rather vacuolate, are often partially or wholly degenerated by gametophyte maturity. The three cells vary in their arrangement, usually being two chalazal to one micropylar (2+1) (Figs 29–31, 40, 43) or the reverse (1+2) (Figs 32, 42) and only rarely linear.

DISCUSSION

It should be apparent by now that, in spite of a number of rather consistent basic features, a great deal of diversity in many characteristics of the ovary, ovule and megagametophyte can be found among species of *Rhododendron*. It would be nice if this diversity, or at least some aspects of it, were consistent enough in distribution to provide characteristics that would be useful in classification. Other than the indumentum on the ovary, however, a feature of the vegetative plant which has been widely used for classification of *Rhododendron,* only one group of characters appears together consistently enough to be considered fairly diagnostic. The tapered top of the ovary, scales with or without unicellular (or occasionally uniseriate) hairs with bulbous bases, five carpels (one or two more only in very large ovaries), comparatively shallow rounded placenta only lobed on the outer surface with the locules connected only in the extreme top of the ovary or in the base of the style, all ovules directed downward, ovules long and slender with few integumentary layers and both micropylar and chalazal tails, and the gametophyte short plus the micropyle long relative to ovule length all occur quite regularly in species of sect. *Vireya* R. In addition, in this section other features tend to be present, although they are less consistent: ovary long and slender, locule size rather small as compared to wall and/or central axis thickness, considerable tannin, placental stalk ridge none or inconspicuous, little or no cuticular ornamentation, ovules all around the placenta, ovule number comparatively high as related to size of ovary locule, egg apparatus usually close to half the length of the gametophyte, hypostase usually conspicuous and endothelium relatively inconspicuous. The occurrence of such an extensive group of characteristics among species of *Vireya* confirms and strengthens the uniqueness of this group of species.

No other group of characteristics occurs together so consistently nor is any other of the existing subgeneric or sectional taxa as sharply characterized by features of the ovary, ovule and megagametophyte. In the larger sections—*Rhododendron* R and *Ponticum* H—the range of variation in most characteristics is wide, although if the expression of many characteristics among all the species in these sections is averaged, certain tendencies are recognizable. In sect. *Rhododendron* R scales are almost always present on the ovary and are combined with unicellular hairs in many species. Except in subsects *Maddenia* and *Boothia* the slightly elongated ovaries are depressed at the summit. Locule number is usually five; the placenta is expanded and divided into distinct halves through most of its length with the clefts often joining in the top of the ovary to form a unilocular zone; ovules usually occur on the outer surface of the placenta as well as on the sides. In all or most species of seven subsections all the ovules tilt downward, but in the others at least a few and occasionally as many as one-quarter tilt upward at the top. Only rarely is there a conspicuous placental stalk ridge and usually little or no cuticular ornamentation can be seen. The ovules are very variable but tend to be moderately small and moderately broad with the gametophyte moderately short relative to ovule length and to have a moderately long micropyle; the number of integumentary layers is relatively low. The egg apparatus is relatively large as related to total gametophyte length.

In subgen. *Hymenanthes* the ovary indumentum consists of tufted and/or glandular hairs, only occasionally combined with unicellular ones. Except in subsect. *Auriculata* the ovary, which tends to be moderately slender, is depressed at the summit. Cuticular ornamentation is normally conspicuous. Locule number is almost always more than five, frequently much higher, and the locules occupy less than half the diameter of the ovary. The placenta is usually little expanded, extending to the dorsal wall with ovules only on the sides, and a placental stalk ridge is generally conspicuous. In most species approximately half the ovules tilt up and half down. Again, ovules are very variable but they tend to be moderately long and broad with a moderately long micropyle and moderately high number of integumentary layers. The gametophyte, which is moderately slender, occupies a moderately small portion of the ovule length and the egg apparatus forms a comparatively smaller proportion of the gametophyte length. It must be remembered that, although general tendencies have been pointed out for sect. *Rhododendron* R and subgen. *Hymenanthes,* there are conspicuous exceptions to the characters enumerated.

The other sections—*Pogonanthum* R and all those of the azalea complex—were represented in our study by a smaller number of species (one to five). These sections or subgenera comprise many fewer species, however, and the representation of the monotypic and some other very small taxa was 100% (sects *Tsusiopsis* T, *Rhodora* P, *Viscidula* P, *Sciadorhodion* P, subgen. *Candidastrum, Mumeazalea*). Because of the small numbers and the rather wide variability in some characteristics within a taxon (as ovule size in sect. *Rhodora* P or ovary shape in subgen. *Azaleastrum*), we feel rather uncertain about generalizations for the several taxa of the azalea complex. Thus, only those features which may be relatively consistent will be listed.

Ovaries in *Pogonanthum* R are small and rather broad, with a short style arising from a depression at the summit. Scales occur, occasionally combined with unicellular hairs. There are only five locules which are relatively large. A placental stalk ridge and cuticular ornamentation are lacking. Ovules, which are relatively few in number and occur all around the placenta, are small and moderately broad.

Ovaries in sect. *Azaleastrum* A are small and squat (broader than long), depressed at the summit, with both glandular and unicellular hairs. Cuticular ornamentation is conspicuous. There are only five locules which are moderate in size. The ovules are usually at right angles to, and all around, the placental surface and are moderately small. There is no placental stalk ridge. In *Choniastrum* of the same subgenus, in contrast to *Azaleastrum,* the ovaries are fluted, long and slender, and taper into the style; there are six relatively narrow locules and a conspicuous placental stalk ridge. More of the ovules, which are all around the placenta, tilt up than down and they are broader than most others in the genus.

Sect. *Tsutsusi* T has small moderately narrow ovaries depressed at the top with many flattened multiseriate, and occasional glandular or unicellular, hairs. There is no cuticular ornamentation. In the five locules small moderately broad ovules are attached all around the placenta; most tilt down but usually a few at the top tilt up. In relation to the short ovule length the gametophyte is short and the egg apparatus occupies a large proportion of that length. In both *Brachycalyx* and *Tsusiopsis* of the same subgenus the ovaries are somewhat larger but they have a similar shape and five locules, which in these sections are large, as well. In *Tsusiopsis* the multiseriate hairs are flattened as in *Tsutsusi,* but in *Brachycalyx* they are either lacking (one species) or rounded or irregular in cross-section. Glandular hairs also occur, alone or with the multiseriate hairs; in one species of *Brachycalyx* the terminal glands are few and small. There is no cuticular ornamentation but a placental stalk ridge is clearly present. Ovules occur only on the sides of the placenta, or in one species of *Brachycalyx* where they occasionally are attached on the outer surface of the placenta, they turn sharply to the sides. In *Brachycalyx* the ovules tend to be moderately large and relatively narrow.

In subgen. *Pentanthera* (sects *Pentanthera, Rhodora, Viscidula* and *Sciadorhodion*) all ovaries tend to be moderately short, depressed at the summit and clothed with glandular hairs. There are five locules and placental stalk ridges are conspicuous. In sects *Pentanthera* and *Rhodora* multiseriate and unicellular hairs are combined with the glandular. Except in sect. *Sciadorhodion* moderately small ovules are attached all around the placenta. Most other ovule characters in these sections vary, although *Viscidula* has a very short micropyle. In *Sciadorhodion* the ovules are among the largest found in the genus, with the largest number of integumentary layers. The gametophytes are the longest found, with the egg apparatus forming a smaller proportion of total gametophyte length. *Sciadorhodion* is the only section of subgen. *Pentanthera* to show conspicuous cuticular ornamentation.

In the three very small subgenera—*Therorhodion, Candidastrum* and *Mumeazalea*— ovaries are small, squat and depressed at the summit with glandular and/or unicellular hairs. The cuticle is clearly ornamented. Ovules are borne perpendicularly to the surface all around the placental halves. Only in *Mumeazalea* are there more than five locules (six) and a conspicuous placental stalk ridge. Ovule characteristics are rather intermediate and somewhat dissimilar among these subgenera with those of *Therorhodion* being most distinctive. In this subgenus the ovules are small and among the broadest (relative to length) found in the genus; the gametophyte is slender and, as it is long compared to ovule length, there is a short micropyle.

Thus, although many features of ovary, ovule and megagametophyte of *Rhododendron* show considerable variation in their expression, this diversity is really useful taxonomically only in characterizing species of sect. *Vireya*. While there are tendencies in the other sections, the range of variability overlaps too much among sections to allow clear characterization.

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QUESTIONS

Chamberlain: I am particularly interested in the tapering versus non-tapering ovary. One of the examples of a tapering ovary that Prof. Palser has quoted is in subsect. *Auriculata*. It is of interest because otherwise this subsection is only an extension of subsect. *Fortunea*. I also wonder if she has looked at those species of subsect. *Neriiflora* that apparently have ovaries that are intermediate between the tapering and non-tapering types?

Palser: We did look at four species of subsect. *Neriiflora* and in none of these did we find variation in the depth of the depressions. However, these depressions may not have been particularly deep. The ones that seemed closest to what you might call intermediate, sometimes just turning in slightly, or going up quite gradually, were restricted to subsect. *Auriculata* and to subsections of subgen. *Rhododendron*. However, we looked at a rather small number of species and there may well be exceptions.

Cullen: You do find a tapering ovary in *R. auritum* in subsect. *Tephropepla* as well.

Palser: Yes, this is possible. This is a species that we did not look at. You will notice that sect. *Choniastrum* is characterized by tapering ovaries as well.

Stevens: The question that those that work on *Vireya* rhododendrons seem to be resolutely avoiding is just how the vireyas link on to the rest of the genus. Although some species should be removed from *Vireya* altogether, it does generally seem that they are a natural group. Your results suggest, and I think that we could extend this to other characters too, that the vireyas may form a group co-ordinate with the rest of subgen. *Rhododendron*, and that the vireyas stand alone on many of their characters.

Palser: This is right. In most respects the vireyas seem to be more distinct in a wide variety of characters, including the flavonoids. I therefore think that this is a good possibility. Sixteen out of say 200 species is not very many.

Rouse: There seems to be a very wide range in the number of ovules per locule and, finally, per capsule.

Palser: Yes. I did not include the number of ovules per locule because there is some question as to the accuracy of our estimates. Our original estimates range from 12 in *R. micranthum* up to over 2000 in *R. nuttallii*, with almost anything in between. There are only a few with over 1000 but there are many in the range of 100–500 per locule. This is a very wide range. In actual numbers per ovary the range is widest in sect. *Rhododendron*. It is narrower in subgen. *Hymenanthes* and the number tends to be smaller in the Azalea complex. As far as we can tell there is little correlation between ovule number and the size of the ovary. For instance, *R. micranthum* has one of the smallest ovaries and yet one of the largest ovules, but the total number of ovules is very small.