STUDIES IN THE PROTEACEAE

VIII. Morphology, Floral Anatomy and Embryology of
Grevillea R. Br.

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In this paper the morphology of the vegetative and reproductive parts, the
floral anatomy and embryology of several species of Grevillea are described.
Evolutionary trends within the genus are suggested and a comparison is
made with the allied genus Hakea.

INTRODUCTION

The genus Grevillea R. Br. belongs to the tribe Grevilleeae of the sub-
family Grevilleoideae of the Proteaceae. It is the largest genus of the family
with about 263 species. Of these, 14 are endemic in New Caledonia, two, viz.
G. papuana and G. elberti, in New Guinea, Malaysia and Celebes (Sleumer
1955) and one (G. australis) in Tasmania. The rest are distributed in East,
West and South Australia. Two of the E. Australian species (G. pinnatifida
and G. glauca) also extend into Malaysia. G. banksii (E. Australia) is culti-
vated in Malaysia as an ornamental plant while G. robusta is grown as a shade-
giving tree in coffee plantations in India. Grevillea is most closely related to
Hakea Schrad, all the 124 species of which are endemic in Australia. The
two genera are closely similar in habit, morphological features of inflorescence,
flower and seed and also in chromosome number of \( n = 10 \). Bentham (1870)
remarks that there is not a single organ in which the two genera are absolutely
distinct. Bentham divided the genus into 11 sections on the basis of the
structure of the inflorescence and flower, some of which are: Conogyne,
Anadenia, Manglesia, Eugrevillea, Calothrysus, etc.

PREVIOUS WORK

The genus received very little attention from botanists. Messeri (1929)
traced the development of the embryo sac in G. macrostachya and Brough
(1933) studied the life history of G. robusta. Since Brough used only micro-
tome sections, he missed the characteristic ‘vermiform’ type of endosperm
haustorium. Kausik (1942) described this structure in detail in G. robusta
using the dissection technique. Kausik (1939, 1941) also studied the embryology of *G. banksii* and the floral anatomy of *G. robusta*. Haber (1959) described the floral anatomy of *G. banksii* and *G. robusta* and favoured the view of Kausik that the nectary in the family represents the reduced corolla. I studied the floral anatomy of 15 species of *Grevillea* and came to the conclusion that the nectary represents only a glandular outgrowth of the thalamus (Venkata Rao 1957). Chromosome numbers (*n* = 10) have been reported by Ramsay (1963) in a few species. Cookson and Erdtman (Erdtman 1952) described the morphological features of the pollen grains in 10 species of *Grevillea* and I described the polymorphic pollen grains of *G. vestita* (Venkata Rao 1964b).

**Materials and Methods**

This paper deals with the morphology, floral anatomy, cytology (one species) and embryology of several species of *Grevillea* ranging from different geographic regions. Both fixed and herbarium materials were studied. Some of the materials were collected by the writer during his stay in Tasmania and Australia, and others were obtained from different sources which are acknowledged later. Customary methods of microtechnique were followed and the preparations were stained in Delafield’s haematoxylin or a combination of crystal violet and erythrocin. The endosperm development was followed both from sections and dissections. The cytology was studied from acetolacmoid smears of pollen mother cells.

**Observations**

*Habit and Leaf*

Species of *Grevillea* show much diversity in habit and morphological features of vegetative and reproductive parts; in fact no other genus of Proteaceae shows such a range of variation. In habit the species grade from lofty rain-forest trees like *G. robusta* to small undershrubs of exposed, arid situations like *G. australis*, though the majority are medium-sized shrubs of the 'bush'.

Large bipinnately compound leaf is seen in *G. bipinnatifida* and *G. robusta* (25×25 cm). All transitions are noticed from this type (Fig. 1) to the minute, microphyllous, spinescent leaves. The leaves in *G. acanthifolia* (Fig. 4) are compound; the pinnules are deeply lobed and spine-tipped, showing that the leaves are derived from bicomponent ones. In *G. banksii* (Plate XI, fig. 5) the leaf is once compound. In *G. synaphae* it is lobed and in *G. asplenifolia* it is deeply dentate (Figs. 5, 6); these facts point to their reduction from a compound leaf. Large, entire, mesophytic leaves as are seen in *G. victoriae* and *G. laurifolia* (Fig. 13) are somewhat rare. Elongated, ribbon-like leaves are seen in several species like *G. shepherdii* (Fig. 11), in which they are less
than ½ cm wide and 15–18 cm long. In most species the leaves are small, elliptic or linear, e.g. G. australis, G. buxifolia, G. rosmarinifolia and G. linearis (Figs. 8, 12; Plate XI, figs. 1–4, 6). In several species like G. alpina and G. lavendulacea with small leaves, the margins are strongly revolute and the undersurface is hairy (Fig. 15). The ecologically specialized compact, ‘acicular’ leaf seen in several species of Hakea and Orites acicularis (Venkata Rao 1963) is also found in some species like G. stenocarpa (Figs. 9, 10). However, in this species it is not cylindrical but ridged; it shows thick-walled epidermis and abundance of selerenchyma. Though usually reduction to the acicular condition is noticed at the level of simple leaf, it seems to be sometimes derived directly from the compound one as is evident from the terctely compound leaf in G. sericifolia and G. criostachya (Fig. 7). In G. intricata it shows only three narrow spine-tipped segments (Fig. 14). The minute, microphyllous leaf of G. juniperina (Fig. 3) which is a centimetre or less in length seems to represent the culmination of reduction in the leaf. The diversity and specialization in the leaf structure probably enabled the species of Grevillea to adapt themselves to different kinds of ecological situations and extend the range of the genus even beyond Australia.

Sometimes variation is noticed in the habit and nature of leaf within the same species due to differences in environment. Hooker (1860) distinguished seven different varieties in G. australis (Tasmania) according to the erect, spreading or prostrate habit, the length and breadth of the leaf and the degree to which the margins become revolute on drying. The ‘most remarkable’ variety is G. australis var. planifolia Hook. in which the leaf is 1-1½ cm long and 2-3 mm wide and the midrib is prominent on the upper surface unlike in other varieties.

Inflorescence and Flower

As in vegetative parts, much diversity is noticed in the inflorescence which seems to have evolved mainly by reduction, as is noticed in the inflorescence of the family in general (Venkata Rao 1965a). The large, diffusely branched terminal inflorescence of G. robusta (Fig. 1) seems to be the nearest approach to the ancestral type. Though usually the flowers are arranged in pairs at each node as in all other Grevilleoideae, occasionally they are seen in groups of 3 or 4 at a node (Fig. 2). This shows that each flower pair is derived by reduction from a lateral branch system and, therefore, that the ancestral

inflorescence is a diffusely branched panicle with solitary flower arrangement. Evolution in the inflorescence seems to have led to the axillary position from the terminal and the few-flowered, compact smaller type from the diffuse, large, multiflowered one. Since the flowers are arranged in pairs at each node, the apparently racemose inflorescence noticed in some species like _G. banksii, G. synaphae, G. eriostachya_ is distinguished as a pseudoraceme (Figs. 4–7; Plate XI, fig. 5). It is interesting to notice that further evolution resulted in types similar to those which are derived from reduction of simple raceme, viz. pseudocorymb and pseudoumbel (Fig. 8; Plate XI, figs. 1, 4). Typical pseudospikes were not met with in the present studies. The flowers in some species like _G. acanthifolia_ and _G. eriostachya_ open in acropetal succession while in some others like _G. endlicheriana_ they open basipetally (Fig. 16); in still other cases all the flowers of an inflorescence may be at the same stage of development.

In all species of _Grevillea_ studied, the lateral peduncle of the flower pair is completely suppressed; at the most the two flowers may have a common base. So a pair of pedicellate flowers stands in the axil of a common bract (Figs. 17, 19). An involucre which is commonly present in the condensed inflorescences of _Hakea_ sp. is wanting in similar inflorescences of _Grevillea_ sp., though the sterile bracts found at the base of the inflorescences of some species like _G. crythmifolia_ may function as such. The common bracts for the flower pair may be small, scaly and inconspicuous as in _G. vestita_ (Fig. 22) or large and conspicuous as in _G. crythmifolia_ and _G. ilicifolia_ (Figs. 17, 18). In any case they are deciduous and do not form a permanent attractive apparatus. The bracts of the individual flowers are completely suppressed. In one abnormal flower pair of _G. asplenifolia_ (Fig. 20), however, the two flowers were partly fused at the base and show two bracts of which the outer one seems to be the common bract and the inner one derived by the fusion of the bracts of the individual flowers.

Figs. 16–45. Inflorescences and flowers of _Grevillea_ sp. 16, inflorescence of _G. endlicheriana_. x1. 17, young inflorescence of _G. crythmifolia_. x2. 18–19, _G. ilicifolia_. x8, part of inflorescence with common bracts. x1. 19, a bract and flower pair. x2. 20, an abnormal flower pair of _G. asplenifolia_; b1 and b2 common bract and individual bracts (fused). x2. 21, a flower bud of _G. oleoides_. x2. 22–26, _G. vestita_. 22, a part of the inflorescence with a flower pair. x2. 23, a flower bud. x3. 24, a stamen quite free from the tepal. x3. 25, a stamen adnate to tepal. x10. 26, pistil and nectary. x10. 27, a flower of _G. oystigma_. x1. 28–31, _G. leucopterus_ showing stages in development of flower. x2. 32–34, stages in the development of the flower of _G. wilsoni_. x2. 35–37, flower buds of _G. brachystylis_. x2. 38, base of pistil and nectary of _G. linearis_. x13. 39, 40, entire flower and perianth of _G. rosearitifolia_. x5. 41, part of style and stigma of _G. robusta_. x5. 42, stigmatic region of _G. viellardi_. x5. 43, part of style and stigma of _G. linearis_. x5. 44, stigma and pollen-collecting apparatus of _G. buxifolia_. x5. 45, stigma and pollen-collecting apparatus of _G. oystigma_. x20.
The flowers may be large (more than 2 cm long) and long pedicellate as in *G. rosemarinifolia* and *G. banksii* (Plate XI, figs. 2, 3, 5) or shortly pedicelled and minute as in *G. synaphae* and *G. stenocarpa* (Figs. 5, 9). In all species they are monochlamydeous, 4-merous and zygomorphic to a varying degree. In *G. intricata* and *G. vestita* the flower buds remain straight during development (Fig. 23) and the perianth is regular. The only feature of zygomorphy is the crescent-shaped nectary (Fig. 26). In some species like *G. linearis*, *G. oleoides* and *G. australis* the tip of the flower bud becomes reflexed; since the perianth parts are nearly similar, the flowers in these species are also slightly zygomorphic (Fig. 21). In other species like *G. leucopteris* and *G. wilsoni* the tip of the flower bud becomes strongly bent from the early stages of development (Figs. 28–33). In *G. rosemarinifolia* the tepals in the anterior and posterior sectors are markedly different in size and shape and the perianth is gibbous at base; so the flowers are strongly zygomorphic (Figs. 39, 40).

The perianth is polyphyllous but the tepals remain united in the upper part due to the interlocking of marginal hairs. The tepals are always diagonal in position though in one abnormal flower of *G. leucopteris* one tepal became anterior due to the partial union with the adjacent tepal (Fig. 62). The thalamus may be horizontal as in *G. oleoides*, *G. vestita* and *G. linearis* (Figs. 21, 23, 38) or slightly oblique as in *G. wilsoni* due to which the insertion of tepals becomes asymmetrical (Fig. 32). In *G. brachystylis* the levels of attachment of posterior and anterior perianth parts become separated by a good distance (Figs. 36, 37).

The stamens are antetepalous and all fertile. Though usually the filaments are adnate to the tepals, in some flowers of *G. vestita* they are found to be free to the very base (Figs. 24, 25). This feature is normally found only in one other member of the family, viz. *Bellendena montana* (Tasmania), and seems to represent the ancestral condition. The anthers are nearly sessile and non-apiculare. They are included in the concave laminae of tepals. There is a hypogynous nectary which is completely annular only in *G. leucopteris* (Fig. 31). In all other species it is incomplete, being formed by the fusion of three alternitepalous lobes, the fourth one on the anterior side being completely suppressed. According to the extent of its development it varies from a horseshoe-shaped structure to a cup-like or cushion-like or nearly spherical one (Figs. 34, 37, 38). Variations in the gland can be seen in figures on floral anatomy. The flowers of *G. synaphae* are devoid of nectary, probably due to complete reduction (Fig. 90).

Plate XI, Figs. 1–6. 1, a branch of *G. buxifolia* with inflorescences. 2, a branch of *G. rosemarinifolia* with inflorescence. 3, a branch of *G. rosemarinifolia* var. *divaricata* with inflorescence. 4, a branch of *G. australis* with inflorescences. 5, a branch of *G. banksii* with inflorescence. 6, a branch of *G. linearis* with inflorescences.
The gynoecium consists of a single carpel which may be stipitate or sessile. In some abnormal flowers of *G. vestita* two carpels were noticed. In some fruits of *G. banksii* an abortive pistil was noticed attached to the inside wall between the seeds (Figs. 261–264). In *G. intricata* and *G. vestita* the region above the ovary is somewhat swollen; it again narrows down and terminates in the stigma (Fig. 26). In other species the ovary terminates in a long or short style. Usually the pistil grows more rapidly than the perianth and emerges laterally through the split perianth. The stigma is held imprisoned by the laminae of tepals (Figs. 21, 23, 29–32). In *G. leucopteris* and *G. wilsoni* the style is much elongated and may be thrown into loops (Figs. 32–34). Probably it is thus kept turgid and spring-like and results in the explosive opening of the flower. In *G. brachystylis*, on the other hand, the pistil remains straight and the stigma emerges vertically through the top of the flower bud (Figs. 35–37).

The region of the style immediately below the stigma (= style-end) has a special function to perform in relation to pollination in accordance to which it becomes modified. In several species it develops into a discoid platform called the 'pollen-collecting apparatus' on which the pollen grains from the protandrous anthers are shed long before the flower bud opens. The presence of the pollen-collecting apparatus is an important taxonomic character. It is also noticed in the relatively advanced taxa of only one other tribe, viz. Telopeeae. Within the genus *Grevillea* evolution can be traced from the unspecialized simple conical style-end as seen in *G. robusta* (Fig. 41) to the well-developed discoid structure as is noticed in *G. rosearinifolia* (Fig. 39). In *G. viellardi* and *G. rubiginosa* (New Caledonia) there is a rim-like outgrowth below the conical style-end (Fig. 42). In *G. intricata*, *G. vestita* and *G. trifida*, though the style-end is still elongated and conical, it is subtended by a thick annular rim (Fig. 26). In *G. synaphae* the stigma has a similar form but the rim becomes thinner and broader (Fig. 90). Further evolution seems to have led to the broadening of the platform into a discoid organ and the reduction of the stigmatic region to a papillate structure situated at its centre (Fig. 43). In *G. brachystylis* the pollen-collecting apparatus is ovate while in *G. buxifolia* it shows a prominent horn-like outgrowth (Figs. 37, 44). In *G. oxystigma* and *G. pilulifera* it is somewhat swollen (Figs. 27, 45).

The position of the stigma shows some variation. In *G. intricata* and *G. vestita* the stigma is held erect. In *G. brachystylis* the style and pollen-collecting

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apparatus are held erect but the stigma is lateral (Fig. 37). In several species like *G. wilsoni* and *G. rosemarinifolia* the style is slightly or strongly curved and the stigma is lateral or oblique in position. It may be held directly above the gland (Figs. 27, 33, 39) or the stigma may face away from the flower as in *G. synapheae* and *G. trifiida*. Probably the position of the stigma changes during the maturation of the flower so as to facilitate cross-pollination.

The extent of hairiness varies: in *G. leucopteris* the flowers are glabrous; in *G. oxystigma* they are studded with stiff 1-celled hairs; in some species hairs may be found on the perianth (Fig. 94) while in still others they may be found only on the pistil.

**Fruit and Seed**

The ovary bears two collateral, hemianatropous or nearly anatropous ovules attached laterally at about the middle of the loculus on marginal placent (Figs. 148, 185, 205). The fruit is usually spherical or ellipsoid with a persistent style (Figs. 187, 204, 230, 265, 287, 288) and offers an important feature of distinction from the allied genus *Hakea*. It is smooth and does not show any protuberances that are commonly noticed on the fruits of *Hakea*. It dehisces only on one side to form a boat-shaped, woody follicle. In *Hakea*, on the other hand, it dehisces completely into two woody, plano-convex valves. Usually both ovules develop into seeds though one of them may sometimes abort. The seeds are either devoid of a wing or provided with a symmetrical membranous outgrowth all round the body of the seed (Figs. 211, 231, 260). The terminal wing characteristic of several species of *Hakea* is relatively less common (Fig. 268).

**Floral Anatomy**

The floral anatomy of about 25 species of *Grevillea* has been studied. The different species show slight variation about a basic ground plan.

The pedicel in different species receives a ring of 4-8 vascular bundles (Figs. 48, 57, 80) or a ring of several bundles as in *G. wilsoni*. These branch
and increase in number in the region of the thalamus (Fig. 49). Depending on
the horizontal or oblique nature of the thalamus, the traces for the perianth
arise either symmetrically all round the floral stele as in G. australis, G. robusta
and G. sericea (Fig. 65) or asymmetrically as in G. leucopteris, G. ilicifolia
and G. rosemarinifolia (Figs. 56, 58, 70, 79, 81). In all species studied the
tepal marginals are connate. A whorl of eight traces is first given off from
the floral stele for the perianth; of these the four diagonal ones are the tepal
midribs and the four alternate ones the conjoint marginals (Figs. 50, 86).
The conjoint traces split radially within the cortex of the thalamus to form
the marginal bundles of adjacent tepals (Figs. 50, 58, 81). Since the midrib
and marginal bundles traverse without branching, the tepals in all cases are
3-bundled.

As in several other members of the family, the staminal traces are
organized characteristically as pairs of bundles from the same gaps caused by
the tepal midribs (Figs. 58, 81). These emerge into the bases of tepals along
with the tepal midribs. At this level they have the orientation shown in
Fig. 51. They fuse together to form a single concentric bundle either at
the base of the tepal or higher up (Figs. 54, 61, 63, 67, 72, 82). The condition
in which the fusion occurs at a low level should be considered relatively more
advanced than one in which fusion occurs higher up. In all species studied
the tepal and stamen show only congenital concrescence; no case of complete
adnation of the tepal midrib and stamen traces has been noticed. Though
the anthers are sessile or subsessile the outline of the filaments can be followed
for some distance below the separation of the stamen (Fig. 52). In some
flowers of G. vestita the filaments are found to be quite free (Figs. 46, 53).

The ovary in the different species is provided with a long or short stipe
(Figs. 46, 50, 65, 70, 90); in a few species it is nearly sessile (Fig. 79). I feel
that reduction in stipe is a sign of evolution. After the emergence of traces
for the perianth and stamens, the bundles of the floral stele bend inwards
and function as carpel supply after giving off some strands for the nectary.
The pistil receives 5, 7, 9 or more traces which may branch further in the
ovary wall (Figs. 52, 60, 64, 67, 71, 74, 77, 83, 89, 92). The ventral carpellary
bundles usually remain separate though in G. vestita they fuse together for a
short distance (Fig. 53). Three or more carpellary bundles extend into the
style nearly to the stigmatic region (Figs. 47, 55). The core of the style is
filled with elongated glandular cells of transmitting tissue (Fig. 68).

The nectary is the most variable organ of the flower. Though Kausik
(1941) described that the gland in G. robusta is non-vascular, I found that in
all species examined including G. robusta (Fig. 84) it is profusely vascularized.
In G. leucopteris it is thick and annular and receives vascular strands from all
bundles of floral stele (Figs. 59–61). In all other species it is incomplete and
zygomorphic. In the less reduced forms like G. vestita and G. crythmifolia it
shows lobing also (Figs. 53, 72). When horseshoe-shaped the gland receives its vascular supply from stelar bundles in the posterior and lateral sectors (Figs. 63, 69, 75–77, 88, 91). In other species it shows a tendency for reduction in the lateral sectors and in extreme cases like G. obtusifolia and G. rosemarinifolia it becomes spherical (Figs. 73, 74, 79, 82). In such cases its vascular strands are derived only from stelar bundles of the posterior sector. In all cases the vascular strands branch and give rise to a brush of strands (Figs. 83, 84). These usually fade away in the upper part of the gland where they appear as pseudoveins (Fig. 89). In some species like G. leucopteris, G. sericea, G. thelaminiana, G. australis and G. buxifolia the gland is quite free from the stipe as well as the perianth (Figs. 61, 67, 83, 89, 93). In G. obtusifolia, G. sphaecellata and G. phyllicoides it is adnate to the base of the stipe (Figs. 74–76) while in G. pinnatifida (Fig. 78) it is adnate to the base of the perianth. In G. rubiginosa, G. viellardi, G. endlicheriana, G. quercifolia, G. wilsoni, G. asplenifolia and G. banksii the margins of the horseshoe-shaped gland fuse with the stipe so as to enclose a cup-shaped cavity in which probably nectar is stored (Figs. 63, 86–88, 91, 92). In G. pilulifera the margins of the gland are strongly incurved and form a deep cup by their fusion with the stipe (Fig. 85). In G. ilicifolia it is in the form of a cup which is adnate to the base of the perianth as well as stipe (Figs. 70, 71). In G. synaphae it is completely reduced (Fig. 90). The gland is made up of richly protoplasmic cells interspersed by tannin-bearing cells; these become evident much below the level of separation of the floral organs (Figs. 64, 66, 84).

Though variable in shape, the nectary always stands to the inside of tepal-stamen whorl and receives its vascular supply after the emergence of the tepal and stamen traces. Neither its position nor its shape, vasculature and origin give any evidence of its homology to the corolla as Kausik (1941), Haber (1959) and Eames (1961) thought. It seems to be only a glandular outgrowth of the thalamus such as is found in several other angiospermous families.

**Organogeny**

The floral organs in G. ilicifolia arise in acropetal succession (Figs. 95–97) as was also noticed in *Cunarrhenes*, *Synaphea* and *Banksia* (Venkata Rao 1960, 1961, 1964a). The pistil arises as an open cup. The upper part narrows to enclose a cavity. As it elongates, the loculus and stylar canal become differentiated. The tip expands early to form the pollen-collecting apparatus while the sub-terminal part forms the style and the basal part, the ovary and stipe (Figs. 70, 98, 99). The stylar canal progressively narrows till it disappears and the cells at the core develop into the transmitting tissue. The ovules arise as collateral hump-like outgrowths on marginal placenta. The young ovules appear somewhat pendulous though later on they become erect with growth (Figs. 70, 99).
Microsporogenesis and Male Gametophyte

The archesporium differentiates at four places in the anther primordium when it shows slight lobing. In *G. vestita*, which shows secondary increase in sporogenous cells, 2-3 cells differentiate at each place while in other species like *G. rosemarinifolia* in which the primary sporogenous cells function directly as the spore mother cells a plate of 6-8 cells is differentiated at each place. The archesporial cells divide periclinal and form the primary parietal cells to the outside and the primary sporogenous cells to the inside (Fig. 102). By repeated divisions in the primary parietal cells and their derivatives the anther wall becomes 5-6 layered below the epidermis (Fig. 103). As the anther grows the epidermal cells become stretched and tangentially flattened; the sub-epidermal layer develops into the fibrous endothecium, the innermost into the tapetum and the 2-3 middle layers eventually become crushed (Figs. 100, 101, 108). The tapetum is of the secretory type; its cells are usually binucleate and tangentially flattened or radially elongated (Figs. 100, 107). There is a definite stomaium composed of small cells where the anther wall joins the septum. Dehiscence occurs here longitudinally (Fig. 112). Since the septum is composed of somewhat thick-walled cells it persists for some time after the dehiscence of the anther (Fig. 113) as was also noticed in some other genera like *Agastachys*, *Persoonia* and *Banksia* (Venkata Rao 1960, 1964a).

In *G. vestita* the primary sporogenous cells divide mitotically and increase in number (Venkata Rao 1964a). So 10-15 cells are seen in transverse sections of anther lobus which has a rounded outline (Fig. 55) as in *Persoonia*. In other species in which there is no secondary increase, the lobus looks oblong in transverse section and the cells stand in a single row. They appear relatively few for the size of the lobus. This leaves enough space for the pollen grains which are generally large in size. As the anther grows the microspore mother cells separate out from each other and become invested by a callose sheath which persists till the formation of microspore tetrads (Fig. 100). During the meiotic divisions the pairing and disjunction of

chromosomes occur normally; 10 bivalents are noticed in *G. rosenmarinifolia* var. *divaricata* (Figs. 104, 105). The same number has been reported in some more species of *Grevillea* by Ramsay (1963). The microspores are commonly arranged in tetrahedral tetrads and cytokinesis of the sporocytes is brought about by simultaneous furrowing as was also noticed in other species with triangular pollen grains (Venkata Rao 1965b).

The microspore nucleus divides while the cytoplasm is still scanty and vacuolated. A small lenticular cell is formed against the flat side (Figs. 108, 110). In *G. oleoides* in which the microspores remain together till this time the generative cell is seen to be formed against the free side (Venkata Rao 1965b). As the pollen grains grow the generative cell rounds up and migrates into the vegetative cytoplasm. The sheath of hyaline generative cytoplasm stands out clearly from the deep-staining vegetative cytoplasm in the beginning but, as starch accumulates in the vegetative cytoplasm, it becomes obscure (Figs. 106, 118). The generative nucleus assumes an ellipsoidal shape and is relatively smaller than the vegetative nucleus. The pollen grains are shed in the 2-celled condition.

In all species of *Grevillea* studied, the pollen grains are triangular, triporate and angulaperturate. In *G. vestita*, in addition to the triangular grains, polymorphic grains with 4–8 germ pores are also noticed (Venkata Rao 1964b). Among the species studied, the smallest grains occur in *G. vestita* and *G. synaphae* (Fig. 111) and the largest in *G. leucopteris*. The exine in some species is as thick as the intine but usually it is much thicker and divisible into the outer sculptured, thinner sexine and the inner thicker nexine. The sculpturing of the sexine varies from granular to reticulate and pitted types (Figs. 111, 114). In grains with wide germ pores the intine protrudes strongly through them and becomes covered by a 'membrane' which shows a precocious development (Fig. 109). The membrane is attached in the region of the ora between the intine and exine (Figs. 115–118); it seems to be protective in function and shows ornamentation like the exine. During germination of the pollen grains it is said to be thrown off as a lid (Erdtmann 1952).

Figs. 119–136. Megasporogenesis and female gametophyte in *Grevillea* sp. 119–124. *G. ilicifolia*. 119, ovule primordium with archesporium. ×400. 120, ovule primordium with megaspore mother cell and integument initials. ×200. 121, ovule with full-grown megaspore mother cell. ×120. 122, nucellus with megaspore tetrad. ×250. 123, ovule with young embryo sac. ×80. 124, part of ovule with full-grown embryo sac. ×100. 125–129, *G. endlicheriana*. 125, ovule with full-grown megaspore mother cell. ×160. 126, ovule with megaspore tetrad. ×120. 127, nucellus from above. ×250. 128, nucellus with 1-shaped tetrad of which one megaspore is forming 1-nucleate embryo sac. ×400. 129, part of ovule with 4-nucleate embryo sac. ×160. 130, ovule of *G. cryphanthifolia* with 4-nucleate embryo sac. ×100. 131–134, *G. australis*: 131, ovule with megaspore mother cell. ×160. 132, nucellus with megaspore tetrad. ×250. 133, micropylar part of nucellus with full-grown embryo sac. ×280. 134, ovule with full-grown embryo sac. ×100. 135, ovule of *G. oleoides* with linear tetrad. ×80. 136, micropylar part of mature ovule of *G. trifida*. ×120.
Ovule

In all species studied the ovules are bitegmic and crassinucellate. They arise in a somewhat pendulous manner (Figs. 120, 163, 171, 172). The mature ovules in some species like G. viellardi, G. leucopteris, G. trifida and G. vestita are attached towards the base of the loculus and are nearly anatropous (Figs. 138, 140, 158, 161, 202) while more commonly (e.g. G. ilicifolia, G. crythmifolia) they are attached at about the middle of the loculus and are hemianatropous (Figs. 123, 130, 134, 144, 154, 166, 180, 185, 206).

The integument initials become demarcated soon after the differentiation of the archesporium in the ovule primordium (Figs. 120, 172). Both the integuments remain biseriate till about the formation of the 1-nucleate embryo sac. In some species like G. australis the outer integument remains biseriate even in the mature ovule (Fig. 134), while in others it becomes more layered especially in the micropylar region (Figs. 124, 182). The inner integument usually becomes 3-4 layered (Figs. 126, 135, 158, 178, 206). In the mature ovules of G. banksii the cells of the middle layer become radially elongated (Fig. 267) while in G. rosemarinifolia they divide and increase the thickness of the inner integument especially in the micropylar region (Fig. 182). Since the ovules are collateral and appressed against each other (Fig. 148) they look plano-convex in transverse sections. The cells of the outer integument are tangentially compressed at the sides of the ovule but are in radial rows in the marginal portion (Fig. 164) which develops into a seed wing in several species (Figs. 211, 260). In some members the wing develops from the chalazal region of the ovule (Fig. 268) and becomes noticeable from the early stages of development (Figs. 125, 126, 151, 174). The cells of the epidermal layers of the integuments and chalazal wing accumulate tannin (Figs. 146, 147, 154). In G. leucopteris and G. synaphae the ovules do not show a chalazal wing. The integuments in several species are not only free from each other but cover the nucellus loosely (Figs. 123, 166, 259).

The micropyle is formed only by the inner integument; the outer integument does not cover up completely even in the seed stage (Figs. 194, 202).
The inner integument grows more rapidly than the outer and forms the micropyle at the tetrad- or 1-nucleate stage of the embryo sac (Figs. 135, 146, 176, 178). In *G. leucopterus* a micropyle is not formed even in the mature ovule. The nucellar cells protrude and come directly into contact with the locular epidermis (Figs. 160, 162). The micropyle is usually elongated and straight though in *G. rubiginosa* it is slightly curved (Fig. 138). It stands close to or in contact with the glandular cells of the locular epidermis (Fig. 136).

The archesporium of the ovule consists of a single hypodermal cell in all species except *G. rosemarinifolia*. This divides periclinally and cuts off the primary parietal cell to the outside and the megaspore mother cell to the inside (Figs. 119–121). In *G. rosemarinifolia*, in which the archesporium is multicellular, only the hypodermal cells cut off the parietal cells while the deep-seated cells function directly as megaspore mother cells (Figs. 172, 173, 175). In both cases the primary parietal cells divide periclinally and form 3-4 layers of parietal tissue. The cells of the nucellar epidermis also divide periclinally from early stages of ovule development and give rise to 2-3 layered nucellar cap (Figs. 147, 150, 155, 156, 174). All cells of parietal tissue and some layers of nucellar cap become crushed by the enlarging embryo sac; one or more layers of the nucellar cap persist even in the seed stage (Fig. 257). One characteristic feature of *Grevillea* (not noticed in the allied genus *Hakea*) is that the cells of the nucellar cap in the micropylar region become elongated and glandular from early stages of ovule development (Figs. 122, 127, 133, 153, 182, 183). They stain more deeply than the surrounding cells though rarely they may be scantily cytoplasmic (Fig. 128). The superficial cells are usually markedly elongated and sometimes papillate (Figs. 132, 160, 177). The cells seem to facilitate the entry of pollen tubes into the ovules. The outline of the nucellus may be rounded as in *G. leucopterus* or elongated and beak-like (Figs. 124, 136, 149, 184). The nucellar cells of the mature ovule surrounding the embryo sac usually fall apart and create a space due to which the embryo sac can be easily dissected out at this and subsequent stages (Figs. 165, 232). In some species like *G. buxifolia* the antipodal end of the embryo sac extends to the chalaza (Fig. 154), while in others like *G. endlicheriana* and *G. vestita* several nucellar cells stand below the antipodal end of

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Figs. 155–170. Megasporogenesis, female gametophyte and fertilization in *Grevillea* sp. 155–158, *G. vestita*. 155, nucellus with megaspore mother cell. ×250. 156, ovule with megaspore dyad. ×100. 157, nucellus with 1-nucleate embryo sac. ×120. 158, ovule with 2-nucleate embryo sac. ×80. 159–162, *G. leucopterus*. 159, part of nucellus with linear tetrad. ×550. 160, micropylar part of ovule with 2-nucleate embryo sac. ×160. 161, ovule with 4-nucleate embryo sac. ×60. 162, part of ovule with embryo sac. ×120. 163–167, *G. banksii*. 163, young ovule with megaspore mother cell. ×160. 164, T.S. mature ovule. ×50. 165, part of nucellus showing embryo sac. ×160. 166, ovule with embryo sac. ×30. 167, micropyral part of ovule showing entry of pollen tube. ×100. 168, ovule of *G. synapheae* with megaspore mother cell. ×200. 169, L.S. stigma of *G. trifida* with germinating pollen grain. ×30. 170, L.S. stigma of *G. crythamnifolia*. ×20.
the sac. These become thick walled and form a sort of hypostase (Figs. 129, 157).

The ovule receives a single vascular bundle. In ovules in which a chalazal wing develops, this curves into it (Figs. 126, 135, 151, 174). In *G. leucopteris* the vascular bundle shows a loop-like bend in the chalazal region (Fig. 161). In *G. viellardi*, *G. rubiginosa* and *G. linearis* the chalazal bundle branches and forms a ring of strands (Figs. 138, 140, 144) as was also noticed in *Bellendena* and *Persoonia* (Venkata Rao 1960).

**Megasporogenesis and Female Gametophyte**

In all species except *G. rosemarinifolia* the archesporium consists of a single hypodermal cell. This divides periclinally to form the primary parietal cell to the outside and megaspore mother cell to the inside (Figs. 119–121). The megaspore mother cell is elongated and tapering (Figs. 131, 142, 155, 168) and megaspore tetrads linear (Figs. 122, 137, 143, 152, 158). Only in one case a 1-shaped tetrad was noticed in *G. endlicheriana* (Fig. 128). The lowest megaspore always functions and gives rise to the embryo sac according to the Polygonum type. In *G. rosemarinifolia*, in which several megaspore mother cells function, several embryo sacs are formed (Fig. 178, 179). Sometimes the medianly placed megaspore mother cell is more precocious (Figs. 176, 177). In such cases the surrounding sporogenous cells may fail to complete the further stages of embryo sac development. However, they elongate a good deal, become tubular and persist during the seed development (Figs. 181, 183, 184, 219, 222). The mature embryo sac may be narrow and elongated (Figs. 134, 154, 184) or fusiform (Figs. 140, 144, 186) or ellipsoidal in shape (Fig. 162). The antipodal end of the sac may be narrower than the remaining part (Fig. 138) or continuous with it (Fig. 165). The synergids may be ellipsoidal or hooked on the free side (Figs. 145, 162); in some species like *G. rubiginosa* they show filiform apparatus (Figs. 141, 165). The two polar nuclei lie closely pressed against each other in the vicinity of the egg; in *G. viellardi* they are sometimes found nearer to the antipodals (Fig. 139). They fuse together only at the time of fertilization. In *G. leucopteris* their nucleoli show crystals as was also noticed in some Palmae (Venkata Rao 1959).

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**Figs. 171–184. Megasporogenesis and female gametophyte in *G. rosemarinifolia* var. *divaricata*.** 171, L.S. young pistil with ovule primordium. ×20. 172, loculus of ovary with ovule primordium showing multicellular archesporium and integument initials. ×200. 173, 174, ovules with megaspore mother cells. 173, ×250; 174, ×80. 175, nucellus of ovule with megaspore mother cells. ×250. 176, ovule showing a median linear tetrad. ×80. 177, nucellus from above. ×250. 178; 179, ovule and nucellus with 1-nucleate embryo sacs. 178, ×50; 179, ×250. 180, ovule with several embryo sacs. ×30. 181, part of ovule with developing embryo sacs. ×250. 182, a slightly tangential section of ovule showing micropyle and developing embryo sacs. ×100. 183, part of nucellus showing a median embryo sac. ×160. 184, micropylar part of nucellus with mature embryo sac. ×160.
The three antipodals are richly cytoplasmic and persist till the early stages of seed development (Figs. 192, 200, 220, 241). They usually lie as free cells at the tip of the sac, though sometimes they are cut off from the sac as distinct cells (Figs. 240, 256). Starch grains are sometimes noticed either in the cytoplasm of the embryo sac as in G. obtusifolia or in the nucellar cells (Figs. 149, 181, 183). Much sterility is seen in the ovules of G. vestita; megaspore mother cells or tetrads commonly degenerate.

**Fertilization**

In Grevillea species the stigmas are of two types: those which are situated at the end of a conical style-end and those which are papillate and subtended by a discoid pollen-collecting apparatus. In the immature pistil the transmitting tissue fills the core of the style compactly and extends to the stigma. As the pistil matures the cells of transmitting tissue in the region of the pollen-collecting apparatus separate out and form a space below the stigma (Fig. 170). Such a space is not seen in conical stigmas (Fig. 169). The pollen grains caught among the stigmatic hairs germinate in a monosiphonous manner and the pollen tubes traverse through the transmitting tissue of the style. They creep along the glandular cells of the locular epidermis and enter the ovules porogamously (Fig. 167). They are somewhat wide and persistent (Fig. 257). The pollen tube enters a synergid which stains more deeply henceforth (Fig. 233).

**Endosperm**

The endosperm is of the nuclear type. The nuclei formed as a result of the first few divisions become distributed throughout the sac though they are placed more closely in the micropylar region (Figs. 198, 199, 220, 233). After about a dozen nuclei are formed the endosperm around the fertilized egg becomes cellular (Figs. 202, 259). Further growth of the cellular part occurs by cell divisions while in the nuclear part free nuclear divisions continue to occur. This part may remain permanently nuclear or it may become partly cellular at a late stage in seed development.

The 'vermiform appendage' of G. robusta has become classical. The present studies of the endosperm development in six species of Grevillea show

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Figs. 185–205. Endosperm and seed development in Grevillea sp. 185–197, G. endlicheriana. 185, L.S. ovary. ×25. 186, embryo sac. ×80. 187, a fruit. ×1. 188, embryo with three cotyledons. ×4. 189, a normal embryo. ×4. 190, a 4-celled embryo. ×300. 191, 192, micropylar and chalazal parts of young endosperm. ×250. 193, developing endosperm. ×40. 194, L.S. seed with endosperm. ×30. 195–197, stages in development of endosperm. 195. ×30; 196, 197. ×7. 198–205, G. trifida. 198–201, stages in the development of endosperm. ×60. 202, L.S. young seed. ×40. 203, micropylar part of young seed. ×40. 204, a fruit. ×1. 205, L.S. young fruit. ×12.
that there are less specialized as well as more specialized types than this and a sort of evolution can be traced in the different types of endosperm haustoria.

Soon after fertilization there is a rapid growth of the embryo sac as well as the seed. Several nucellar cells immediately around the embryo sac become absorbed so that the sac lies loosely in the cavity of the seed (Figs. 194, 202, 259). A few layers of tangentially flattened nucellar cells stand at the periphery of the seed (Fig. 203), and persist for some time.

For purposes of description the endosperm can be divided into three zones: (i) the upper cellular part immediately around the growing embryo, (ii) the lower cellular part and (iii) the nuclear part. The upper cellular part consists of small, richly protoplasmic, uninucleate cells. This can be described as an 'inert' region because in all species studied it remains smooth in outline and does not show any signs of haustorial activity. The nucellar cells around this zone persist for a long time. The lower cellular part and the nuclear part exhibit various degrees of haustorial activity either by directly functioning as haustorium or by developing secondary haustorial outgrowths which are varied in structure and development in different species.

Starch grains are noticed in endosperm cells only in the early stages (Fig. 257); the cells of mature endosperm do not show any visible products of storage. As the embryo enlarges it absorbs the endosperm immediately around it so that it becomes reduced to a thin filmy layer. The lower part of the endosperm lasts longer and probably serves as a secondary reserve (Figs. 216, 229). Mature seeds are non-endospermic.

Often both ovules of an ovary develop into seeds but occasionally one of them becomes abortive. The embryo sacs in such cases elongate enormously and may show some endosperm cells and nuclei but, since the fertilized egg degenerates, they cease to grow sooner or later (Figs. 218, 221, 254, 255).

Among the species studied, the endosperm in *G. endlicheriana* seems to be the least specialized. The antipodal end of the mature embryo sac, which is narrow in the mature ovule, widens after fertilization so that the sac becomes uniformly tubular (Figs. 186, 191, 192). After cell wall formation in the upper part, both the cellular and nuclear zones of endosperm grow. For some time the cellular part remains narrow and cylindrical while the nuclear part widens out and becomes ovoid (Figs. 193, 194). Such a shape of nuclear part is not noticed in other species of *Grevillea* studied but is common in species of *Hakea*. In due course the cellular part also widens and becomes ovoid (Figs. 195, 196).

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During the later stages of seed development growth of the endosperm is confined to the cellular part. The nuclear part ceases to grow. Since its proximal part gradually becomes cellular, it gets relatively smaller and smaller. As it does not grow aggressively it does not show worm-like folds. In the mature seed it remains as a small, narrow, tubular appendage and is tucked away beneath the cellular part (Fig. 197). Since the endosperm does not show haustorial activity in any region, it remains smooth in outline.

The fusiform embryo sac of *G. trifida* widens after fertilization (Figs. 198, 199). In the early stages the nuclear part of the endosperm is ovoid as in *G. endlicheriana* (Fig. 200); later it grows aggressively and becomes thrown into worm-like folds (Fig. 201). Since older material was not available the fate of the cellular and nuclear parts of endosperm in this species could not be ascertained.

In *G. bipinnatifida* both the cellular and nuclear parts of endosperm grow rapidly and become uneven in outline due to the development of secondary haustorial lobes. Unlike in the above two species the nuclear part tapers and ends in a narrow tube; it becomes thrown into folds from early stages (Figs. 207–209). After some time the nuclear part ceases to grow and becomes cut up into multinucleate cells (Fig. 210). In general features the endosperm development in *G. bipinnatifida* resembles that in *G. robusta*.

In *G. alpina* though the mature embryo sac is fusiform, the micropylar and chalazal parts of the sac becomes bulged and the median part remains narrow and tubular after fertilization (see endosperm of sterile seed, Fig. 218). The micropylar part becomes cellular and the tubular part becomes thrown into folds. Several finger-shaped and sac-like secondary haustorial lobes arise from the lower part of the cellular region (Figs. 212, 213). With growth these lobes coalesce togethe and form a mesentery-like covering around the nuclear part. From the early stages the surface of endosperm in this species presents an uneven outline since the haustorial lobes are slightly or markedly papillate (Figs. 214–216). The distal end of the nuclear part remains sac-like even in the mature endosperm and terminates in a narrow tube (Fig. 217).

The mature ovule in *G. rosemarinifolia* var. *divaricata* shows a number of developed and undeveloped embryo sacs of which the medianly placed one is more conspicuous and has its micropylar end extending beyond those of others (Fig. 219). This sac has better chances of fertilization than the rest. In all seeds dissected only one developing endosperm was noticed. The fertilized embryo sac remains tubular, elongates rapidly and shows an early

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Figs. 219–231. *G. rosemarinifolia* var. *divaricata*. 219, embryo sacs from a mature ovule. ×80. 220, early endosperm. ×80. 221, embryo sacs from sterile seeds. ×20. 222, undeveloped embryo sacs from a developing seed. ×20. 223–228, stages in development of endosperm. 223, 224, ×30; 225, 226, ×20; 227, ×30; 228, ×12. 229, endosperm and embryo from mature seed. ×5. 230, a fruit. ×1. 231, a seed. ×2.
curvature (Fig. 220). Both the cellular and nuclear parts grow for a long time and show great haustorial activity. (Probably some of these folds belong to the undeveloped embryo sacs.) The nuclear part grows rapidly and becomes thrown into a number of folds which recall the folds of the intestine in the bowels (Figs. 223–326). Some haustorial lobes also develop from the lower part of the cellular region, coalesce and envelop the folds of the vermiciform appendage (Fig. 226). The non-functional embryo sac which also elongate a good deal are pushed down into the chalazal region by the growing endosperm, where they lie huddled together till a late stage in the seed development (Fig. 222). In the older stages only the cellular endosperm grows and the nuclear part shrinks away and does not become cellular (Figs. 227, 228).

Table I

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<th>No.</th>
<th>Length of cellular part in μ</th>
<th>Length of nuclear part in μ</th>
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Among the species studied, the endosperm in *G. banksii* shows the greatest haustorial activity. The ellipsoidal embryo sac becomes ovoid after fertilization, grows rapidly and shows signs of folding even before the micropylar part becomes cellular (Figs. 232, 233). Both the nuclear and cellular parts show continued growth as is evident from the measurements of the respective regions at different stages of development given in Table I.

Haustorial lobes develop from the lower part of the cellular region but do not coalesce together (Figs. 234–239). So this part becomes more and more uneven in outline. These secondary haustorial lobes proliferate in an interesting manner. The cytoplasm around a nucleus rounds up. It then

undergoes free nuclear division and forms a cyst-like coenocyte (Figs. 245, 246). The cytoplasm then undergoes cleavage and forms a number of uninnucleate naked cells which later may secrete cell walls (Figs. 244, 247). Thus bunches of cells are formed, some cells of which may repeat the above process of proliferation (Fig. 250). At first the nuclear part is tubular and even in outline (Figs. 242, 243). Later, particular nuclei in this region also initiate the formation of secondary haustorial lobes as in the cellular region due to which this part also becomes uneven (Figs. 248, 249). With growth, more and more of this part becomes cellular and shows haustorial lobes (Figs. 251, 252).

Embryo

The fertilized egg divides transversely and forms ca and cb. Both of these cells divide and contribute to the formation of a suspensorless embryo (Figs. 190, 257, 283). So the embryo development keys out to the Penaea variation of the Asterad Type as was also found in the previously studied members of the Proteaceae. The mature embryo is flat with two foliaceous cotyledons with prominent basal lobes (Figs. 189, 216, 229, 269). In G. endlicheriana embryos with three cotyledons were occasionally noticed (Figs. 188, 197).

Seed Development

In all species studied, the ovule receives a single vascular bundle. In G. trifida, G. banksii and G. alpina, after fertilization a strand is given off from the funicular vascular bundle from the region where it bends upwards into the funicle. This traverses in the outer integument nearly to the micropyle (Figs. 205, 259, 282). This seems to feed the outer integument which becomes thick and fleshy in all species. In the mature ovule of several species the funicular vascular bundle is seen to branch in the chalaza and form a ring of strands (Figs. 138, 140). In G. alpina, the strands formed by the branching of the funicular bundle become prominent in the seed stage (Figs. 270–274). In the region of the chalaza they become arranged in a ring but lower down they come to lie in a single row (Figs. 275, 276). In Bellendena and Persoonia (Venkata Rao 1960) in which the ovules are pendulous and attached one above the other, the seeds are cylindrical and the vascular

Figs. 248–267. G. banksii. 248, 249, older stages in endosperm development. 248 x40; 249, x20. 250, a proliferating secondary haustorial lobe from the cellular region. x60. 251, 252, cell formation and development of haustorial lobes in the nuclear endosperm haustorium. 251, x20; 252, x80. 253, 254, endosperm from young fertile and sterile seeds of the same fruit. x80. 255, endosperm from an older sterile seed. x20. 256, antipodals from the above. x120. 257, embryo, endosperm and nucellus from a developing seed; note the persistent pollen tube. x160. 258, T.S. seed. x12. 259, L.S. young seed. x30. 260, a seed. x3. 261, L.S. fruit showing sterile pistil between developing seeds. x3. 262, the sterile pistil. x5. 263, 264, L.S. lower and upper parts of the sterile pistil. x12. 265, a fruit. x1. 266, 267, parts of outer and inner integuments of ovule soon after fertilization. x250.
strands formed by the branching of the funicular vascular bundle are arranged in a ring. The arrangement of the strands in a ring in the upper part and in a row in the lower part in *G. alpina* seems to be an adaptive modification resultant of the collateral attachment of the ovules and their mutual compression. Several multicellular glands are noticed in the region of the chalazal wing of *G. alpina* (Figs. 272–275, 280).

In all species studied, the mature ovule shows an outer integument which is 2-3 layered and relatively thinner than the inner. Its cells are scantily cytoplasmic and show traces of tannin while those of the inner integument are more richly cytoplasmic. After fertilization the outer integument not only becomes thicker due to addition of more layers but its cells lose tannin. The cells of the inner epidermis become especially prominent by their larger nuclei and richer cytoplasm (Fig. 266). In older seeds of *G. alpina* and *G. banksii* the outer integument becomes 8-9 layered. The cells of the inner epidermis which are tangentially flattened at first become radially elongated and look like the palisade layer though they remain thin walled. They show prominent raphides; some or all the cells of the outer layers accumulate tannin (Figs. 284, 286). The cells of the testa towards the side of the funicle are irregularly arranged, smaller, more richly cytoplasmic and show abundance of raphides (Fig. 285). The testa forms a loose mantle around the body of the seed (Figs. 258, 277–279). Probably this permits accommodation of the rapidly growing seed.

In *G. banksii* the cells of the median layer of the inner integument become radially elongated after fertilization but their cell walls remain flimsy (Fig. 267). As the seed grows, the inner integument becomes crushed out at the sides of the seed though in the micropylar region it lasts longer (Figs. 277, 282). Likewise, the nucellar cells at the sides of the seed become crushed out earlier than those in the chalazal region (Figs. 281, 283).

In the mature seed the cells of the testa become dry and membranous. Since there is no mechanical tissue, the seed coats are flimsy.

**DISCUSSION**

From the comparative studies in the different aspects of several species of *Grevillea*, the evolutionary trends within the genus can be visualized. The lofty rain-forest tree like *G. robusta* with large compound leaf and large,
terminal, diffusely branched inflorescence seems to represent the ancestral type from which the dwarf undershrub of arid and exposed situations like *G. australis* with small simple leaf and few-flowered, axillary, corymbose inflorescences, seems to be derived by reduction in the vegetative and reproductive parts. The diversity in habit and the specialization in the leaf seem to have led to adaptation to different ecological situations and increase in the range of the genus. Combining the primitive floral characters noticed in different species of *Grevillea* like regular perianth, horizontal thalamus, straight flower bud, occasional presence of stamens quite free from the tepals, stipitate ovary (*G. vestita*), annular nectary (*G. leucopteris*), straight style and simple terminal stigma (*G. robusta*) we can visualize the nature of the ancestral stock from which the genus is derived. Evolution of the flower led to strong zygomorphy of the flower with gibbous perianth, its oblique insertion, the tepals markedly different in the anterior and posterior sectors, incomplete reduced nectary (sometimes absent) which is adnate either to the base of perianth or ovary, sessile stamens adnate to tepals, sessile pistil, strongly curved style (and flower bud) with small lateral stigma with well-developed discoid pollen-collecting apparatus. Evolutionary specialization is also noticed in pollen and endosperm haustoria.

Comparative studies of the different genera of the family show that *Grevillea* and *Hakea* are the most advanced genera. Though *Grevillea* has evolved parallel to *Hakea* in several respects, it seems to be less specialized in certain features. Shrubs and undershrubs with specialized acicular leaves and compact, corymbose inflorescences are more common in *Hakea*. In seed and fruit characters, *Hakea* shows greater specialization. The pollen grains in *Grevillea* are more varied in shape and size showing that the genus is less homogeneous than *Hakea* in which they are more stereotyped. Floral anatomically *Grevillea* stands at a lower level than *Hakea*: no species of *Grevillea* show complete adnation of the tepal midrib and stamen traces such as is noticed in species of *Hakea* like *H. laurina* and *H. victoriae* (Venkata Rao 1966).

Bentham (1870) remarks that there is not a single character in which *Grevillea* and *Hakea* are absolutely distinct. However, embryological studies revealed two features which appear to be distinctive. One is the presence of radially elongated glandular nucellar cells below the micropyle in species of *Grevillea* and their absence in all species of *Hakea* studied. The second is the generally narrow or tubular endosperm haustorium which is thrown into vermiform folds in *Grevillea* species and the presence of wide, sac-like nuclear part of endosperm in all species of *Hakea* (*studied by me*).

All species of *Grevillea* and *Hakea* so far studied show the chromosome number of \( n = 10 \). This is the smallest haploid chromosome number in the polyploid genera of the family, the others being \( n = 14, 13, 12 \) and 11.
Comparative studies in the family show that morphological evolution is accompanied by reduction in chromosome numbers.

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