

STUDIES IN THE PROTEACEAE

XIII. TRIBE GREVILLEAE

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The author revised Brown's Grevilleae (20 genera) and limited the tribe to 7 genera with zygomorphic flowers and biovulate carpels. The morphology of the vegetative and reproductive parts, floral anatomy and embryology of some species of all the 7 genera are described. The evolutionary trends within the tribe are discussed and they are correlated with the known chromosome numbers. Since the most primitive genera of the tribe (*Euplassa*, *Gevuina*) resemble the Persoonieae, the latter are considered to be ancestral to Grevilleae. Several of the evolutionary trends of the family attain their culmination within this tribe. All evidences point to the origin of the tribe under rain-forest conditions and their migration into open and arid regions. On the basis of species concentration and geographic distribution, East Australian region on a southern continent (Gondwanaland) is fixed as the probable centre of origin for the tribe and their present-day disjunct distribution is attributed to continental drift.

INTRODUCTION

The sub-family Grevilleoideae was divided by Brown (1810) into 3 tribes, the Banksieae (2 genera), Embothrieae (11 genera) and the Grevilleae (20 genera). This classification was accepted by Bentham (1870) and Engler (1894). However, while Banksieae and Embothrieae appear somewhat well defined due to the presence of ellipsoidal pollen grains and multiovulate carpels respectively, the Grevilleae seem to be a heterogeneous assemblage, comprising taxa with regular as well as zygomorphic flowers and biovulate as well as multiovulate carpels. In the revised classification, the author transferred the two genera with 4-ovuled carpels (*Darlingia* and *Buckinghamia*) to Embothrieae (*sensu lato*), raised *Orites* and *Lambertia* to the rank of separate tribes (Venkata Rao 1957, 1968b) and split the remaining taxa into two tribes, the Macadamieae (9 genera with regular flowers) and Grevilleae (7 genera with zygomorphic flowers).

Brough (1933) and Kausik (1942) studied the life history of *Grevillea robusta* and the latter author described vermiform endosperm haustorium; Kausik (1941) and Haber (1959) studied the floral anatomy of a few taxa. The author described the morphology, floral anatomy and embryology of

several species of *Grevillea* and *Hakea* and also the polymorphic pollen grains of *G. vestita* (Venkata Rao 1964, 1966a, 1966b, 1968a). The chromosome numbers in a few taxa have been reported by the author (Venkata Rao 1957), Ramsay (1963) and Johnson and Briggs (1963). Details regarding the numbers of species in each genus, their geographic distribution and the known chromosome numbers are given in Table I.

TABLE I

No.	Genus	<i>n</i>	<i>2n</i>	Author(s)	Number of species	Geographic distribution
1	<i>Euplassa</i> Salisb.				20	S. America
2	<i>Gevuina</i> Molina.		28	J and B*	3	1 E. Australia 1 New Guinea 1 Chile
3	<i>Kermadecia</i> Brongn. and Gris.				10	7 New Caledonia 2 Fiji, Samoa 1 New Hebrides
4	<i>Finschia</i> Diels.				4	New Guinea New Hebrides Palau, Aru
5	<i>Strangea</i> Meissn.		22	J and B	3	1 E. Australia 2 W. Australia
6	<i>Grevillea</i> R. Br.	10	20	VR,* R*	263	14 New Caledonia 2 New Guinea 1 Tasmania, rest East and West Australia
7	<i>Hakea</i> Schrad.	10	20	VR, R	124	c. 80 W. Australia 40 E. Australia 7 Tasmania of which 4 are com- mon with E. Australia

* J and B = Johnson and Briggs (1963); VR = Venkata Rao (1957); R = Ramsay (1963).

MATERIALS AND METHODS

This paper describes the morphology, floral anatomy and embryology of some species of all the 7 genera of the Grevilleaceae. Both herbarium specimens and materials fixed in formalin-acetic-alcohol were studied. Customary methods of microtechnique were followed and the materials were embedded in paraffin wax of 60 °C m.p. Sections were cut from 6 μ to 10 μ in thickness and stained in Delafield's haematoxylin or a combination of crystal violet and erythrocin.

OBSERVATIONS

External morphology

The Grevilleeae show much diversity in habit and morphological features of vegetative and reproductive parts. Sleumer (1955) describes that species of *Finschia* inhabiting the rain-forests and marshy regions of New Guinea are stately trees with buttressed stems and stilt roots. *Kermadecia vitiensis*, *Grevillea robusta*, *Hakea laurina*, *Gevuina avellana* and *Euplassa duquei* are also trees. Shrubs are very common; a few taxa like *Grevillea australis* and *Hakea corymbosa* are undershrubs. The largest leaves (in the tribe as well as in the family) are seen in *Gevuina avellana* and *Grevillea robusta* in



A—a branch of *Finschia carryi* with inflorescences.
 B—a twig of *Finschia chloraxantha* with cauliflorous inflorescences.
 C—a branch of *Strangaea linearis* with inflorescences and old fruits.

which they are bicomponent and measure about 35×25 cm. (Fig. 2). Pinnately compound leaves are found in species of *Gevuina*, *Euplassa*, *Kermadecia vitiensis*, *Grevillea banksii* and *Hakea adnata* (Figs. 1, 3, 4). In *Gevuina papuana* the leaves are generally compound with winged petioles, but show transition to lobed and entire ones on the same branch. Large simple leaves are seen in *Hakea victoriae* and *Kermadecia sinuata*. The leaves in several species of *Hakea* (e.g. *H. laurina*) and all the three species of *Strangaea* are narrow and isobilateral (Fig. 12; Plate XXXVIII C). In *Grevillea shepherdii* and some species of *Hakea* (*H. acicularis*, *H. microcarpa*) they are terete and markedly xerophytic. The culmination of reduction in the leaf is noticed in *Grevillea intricata* and *G. juniperina* in which they are microphyllous and



Figs. 1-21.

spinescent. *Hakea trifurcata* is interesting in showing dimorphism of leaf: expanded and terete leaves occur on the same branch.

The inflorescences in *Grevillea robusta* and *Kermadecia vitiensis* are large terminal panicles; in *K. sinuata* and *Finschia chloraxantha* they are cauliflorous (Plate XXXVIII B). More commonly they are uniaxial pseudoracemes (Figs. 1, 3, 4, 12, 20; Plate XXXVIII A, B). In *Grevillea robusta* the flowers sometimes occur in groups of three or four at a node showing that the paired flower arrangement which is characteristic of all Grevilleoideae has not become fixed in this species. The inflorescence in *Hakea laurina* is a globose umbel of 200–300 flowers. In several species of *Hakea* and some species of *Grevillea* (*G. australis*, *G. linearis*) it is a small, few-flowered corymb. The three species of *Strangea* show interesting stages of reduction in the inflorescence; in *S. linearis* it is a lax panicle in which there are peduncles for flower pairs, pedicels for flowers, common as well as individual bracts for the flowers; some extra bracts are also found which show that reduction of some flower pairs has occurred (Figs. 12, 13). In *S. stenocarpoides* the peduncle shows two or three empty bracts at base and 2–3 flowers at the top placed singly at each node; there are neither common nor individual floral bracts (Fig. 15). In *S. cynanchicarpa* the short peduncle terminates in a single sessile flower which is surrounded at base by an involucre of 5–6 bracts (Fig. 19). Similar 1-flowered involucre heads, which mark the culmination of reduction in the inflorescence, are found in *Adenanthos* (Proteoideae) and *Lambertia uniflora* (Grevilleoideae) and provide good example of parallelism in evolution of the inflorescence in the two sub-families.

In *Euplassa* lateral peduncles as well as pedicels are found (Fig. 22) while in *Kermadecia* and *Gevuina* the flowers are nearly sessile but show lateral peduncles (Fig. 5). The bracts of the individual flowers are usually suppressed; the common bracts are either scaly or membranous (Figs. 10, 11, 13). The flowers are hermaphrodite, 4-merous and zygomorphic. The perianth is sepaloid or petaloid and polyphyllous; it is antero-posterior in the relatively primitive taxa (*Euplassa*, *Gevuina*) and diagonal in other genera; a transition is noticed in *Strangea* and *Kermadecia*. The stamens are shortly filamented and apiculate in *Euplassa*, *Kermadecia*, *Gevuina* and *Finschia* (Fig. 6); in others they are nearly sessile and non-apiculate. In *Hakea victoriae* and

Figs. 1–21. 1–9, *Gevuina* sp. 1, 2, *G. avellana* 1, a branch with inflorescence. $\times \frac{1}{2}$. 2, a leaf from the base of a branch. $\times \frac{1}{2}$. 3, a branch of *G. bleasdalei*. $\times \frac{1}{2}$. 4, a branch of *G. papuana*. $\times \frac{1}{2}$. 5–8, *G. bleasdalei*. 5, a flower pair. $\times 3$. 6, a stamen. $\times 6$. 7, 8, base and top of pistil. $\times 6$. 9, fruit of *G. avellana*. $\times 1$. 10, 11, *Hakea nitida*. 10, an inflorescence. $\times 2$. 11, a flower pair and common bract. $\times 3$. 12–19, *Strangea* sp. 12–14, *S. linearis*. 12, a branch with inflorescences. $\times 1$. 13, a flower pair. $\times 3$. 14, an open flower. $\times 4$. 15–18, *S. stenocarpoides*. 15, an inflorescence. $\times 2$. 16, a dehisced fruit. $\times \frac{1}{2}$. 17, a seed with testa removed on one side. $\times 1$. 18, an embryo. $\times 1$. 19, an inflorescence of *S. cynanchicarpa*. $\times 1$. 20, 21, *Finschia chloraxantha*. 20, a branch with inflorescence and fruits. $\times \frac{1}{2}$. 21, pistil and nectary. $\times 3$.

H. laurina the anthers are adnate throughout their length with the tepal midribs.

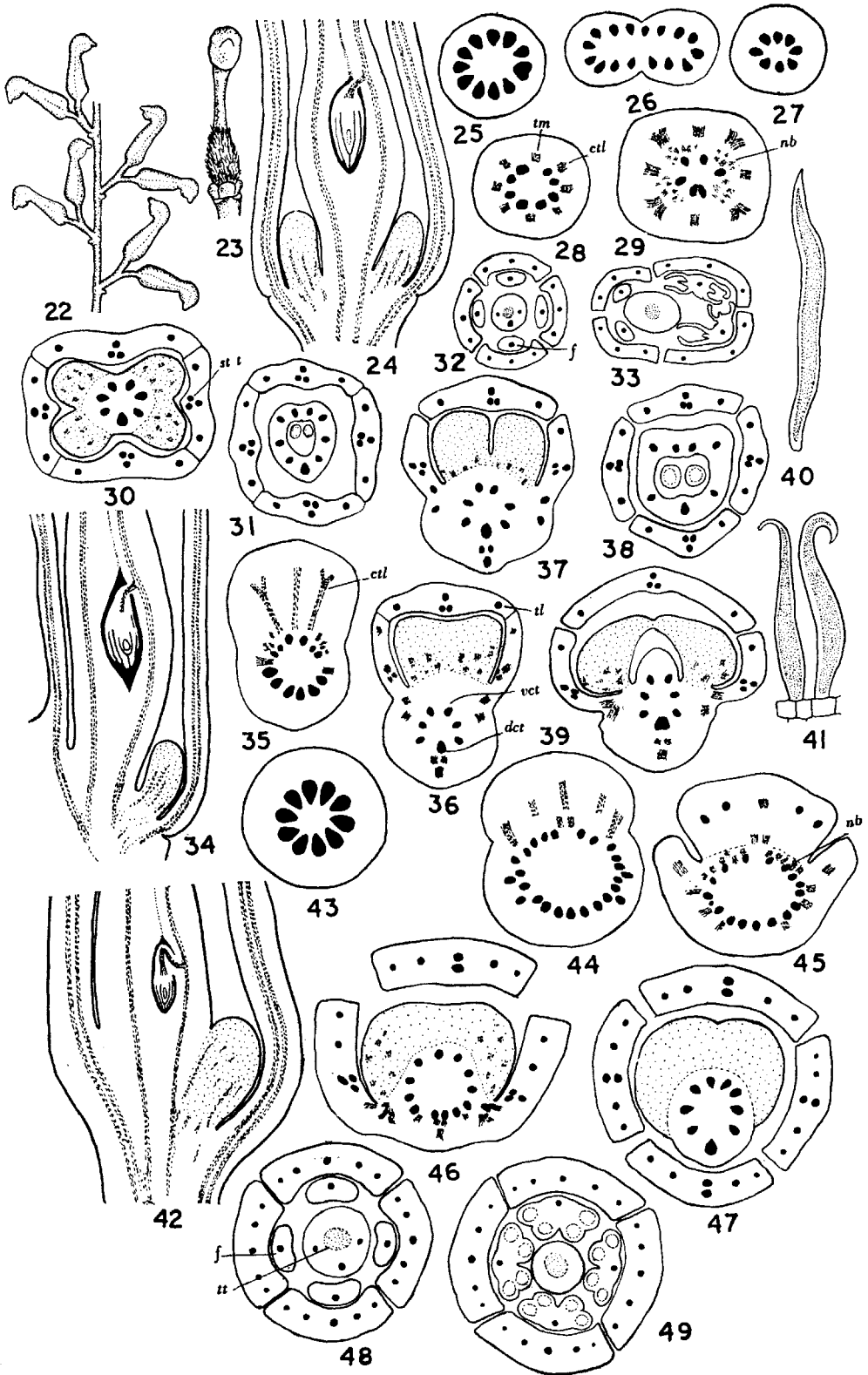
The ovary is either stipitate or sessile, sometimes both conditions being found in the same genus (*Strangea*, *Grevillea*). Puri (1967) considers the stipitate condition as relatively more primitive. The style-end is club-shaped in *Finschia* and *Kermadecia* and the stigma is devoid of a pollen-collecting apparatus (Figs. 21, 68); in other genera the stigma is lateral or oblique and subtended by a discoid pollen-collecting apparatus (Figs. 8, 14). All stages in the evolution of the pollen-collecting apparatus are noticed within *Grevillea* (Venkata Rao 1966b).

The flowers in all genera show a nectary. It consists of 4 separate lobes only in *Euplassa* (Figs. 23, 30), resembling the condition in some *Persoonieae*. In *Grevillea leucopteris* the lobes are connate into a massive perigynous ring. In other taxa it is incomplete, being 2-lobed in taxa with antero-posterior perianth, viz. *Gevuina*, *Kermadecia*, *Strangea stenocarpoides* and *S. cynanchicarpa*, or 3-lobed in those with diagonal perianth (Figs. 7, 21, 55, 60, 64, 65, 70). The nectary may be found either directly on the thalamus (Figs. 24, 34, 61) or adnate to the base of the perianth as in *Hakea crassifolia* or on the stipe or base of the ovary (Figs. 47, 58). In *H. neurophylla* and *Grevillea synaphae* the flowers are glandless due to complete reduction. The wide range of variation (sometimes within a genus like *Grevillea*) shows that it is not a morphological entity but only an enation of the thalamus or other floral organs.

Though the flowers are zygomorphic in all genera, the degree of zygomorphy varies. In *Euplassa* they are structurally regular but become slightly zygomorphic due to the curvature of the tip of flower bud. In other genera they become increasingly zygomorphic due to the structural modifications in one or more floral organs. The highest zygomorphy (in the tribe as well as in the whole family) is noticed in *Grevillea rosemarinifolia* due to oblique thalamus, gibbous perianth, strong curvature of the flower bud, structural modification of tepals of anterior and posterior sectors in size and shape, curved style, lateral stigma with pollen-collecting apparatus and incomplete, cushion-shaped nectary.

The fruit and seed also show much variation. In the relatively primitive taxa (*Euplassa*, *Gevuina* and *Finschia*) the fruits are rounded nuts (Figs. 9, 20). In *Grevillea* the fruit is a follicle which on dehiscence forms a single

FIGS. 22-49. Floral anatomy. 22-33, *Euplassa cantareirae*. 22, part of inflorescence. $\times 1$. 23, pistil and nectary. $\times 3$. 24, L.S. base of flower. 25, 26, T.S. lateral peduncle. 27, T.S. pedicel. 28-33, T.S. flower bud at various heights. 24-33, $\times 30$. 34-41, *Gevuina avellana*. 34, L.S. base of the flower. $\times 30$. 35-39, T.S. flower bud at different heights. $\times 25$. 40, 41, hairs from tepal and ovary wall respectively. $\times 80$. 42-49, *Kermadecia sinuata*. 42, L.S. base of flower bud. 43, T.S. pedicel. 44-49, T.S. flower bud at various heights. 42-49, $\times 8$. (*tm* = tepal midrib; *cll* = conjoint tepal lateral; *nb* = nectary bundles; *f* = filament; *tl* = tepal lateral; *vct* = ventral carpellary traces; *dct* = dorsal carpellary trace; *tt* = transmitting tissue; staminal trace.)



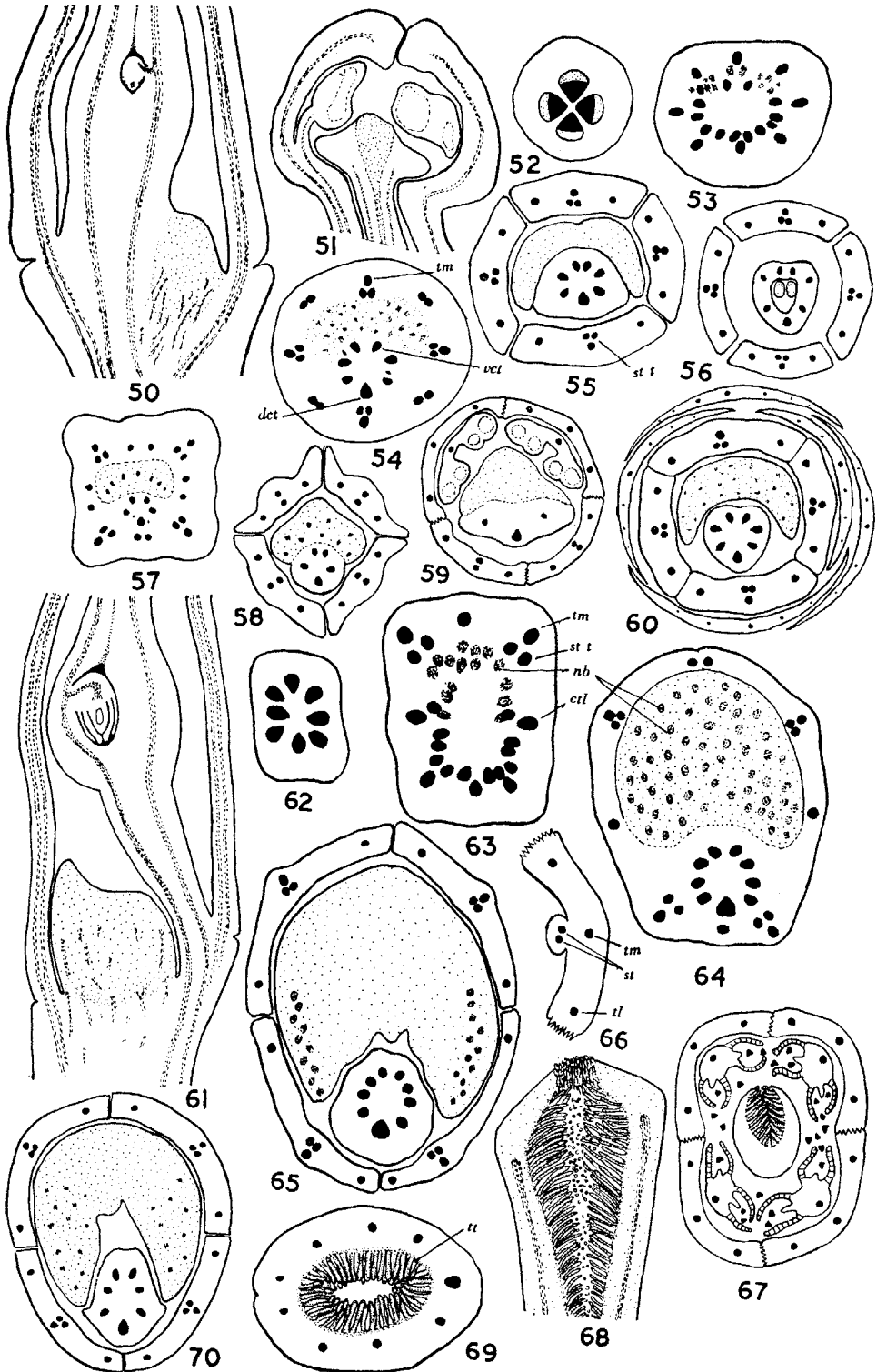
FIGS. 22-49.

concave valve. In *Strangea* it is relatively large and dehisces (capsule-like) into two valves which are smooth on the outside. In *Hakea* the fruit is very woody and splits characteristically into two plano-convex valves on the face of each of which one seed is left exposed. The outer surface of the valve may be smooth, warty or tubercular, these features being of taxonomic importance.

The fruits in *Gevuina* and *Finschia* bear a single, large, rounded wingless seed; the embryos are large and rounded with fleshy cotyledons which store abundance of food. Netolitzky (1926) thinks that embryos which store food are relatively more primitive than those which do not. In *Strangea* the fruit bears a single, flat seed with a wing which extends on both micropylar and chalazal sides (Fig. 17). In *Grevillea* and *Hakea* the fruits are 2-seeded; the seeds are flat on the side of mutual contact and convex on the reverse. They are usually winged; the wing is samaroid in *Hakea* and symmetrical all round in *Grevillea*. The embryos in *Strangea*, *Grevillea* and *Hakea* are flat and show foliaceous cotyledons with basal lobes (Fig. 18).

Floral anatomy—The stalk of the flower pair in *Gevuina*, *Kermadecia* and *Euplassa* (morphologically a lateral peduncle) shows a ring of vascular bundles at base which expands laterally coincident with an increase in the number of bundles due to splitting. It becomes 2-lobed and finally splits into two rings, each of which functions as the stele of one flower (Figs. 25–27). The base of the pedicel in the different taxa shows four or more vascular bundles (Figs. 43, 52, 62). The origin and emergence of traces for floral organs occur either symmetrically or asymmetrically according as the thalamus is horizontal (Figs. 24, 28, 29, 50, 53, 54, 57) or oblique (Figs. 34–39, 42, 44–47, 63, 64). Only in *Kermadecia* the tepals (which are relatively massive) are 5-traced (Figs. 46–49); in others they are 3-traced. The tepal marginals in all taxa arise as conjoint traces. So, a whorl of 8 traces arises in all taxa except *Kermadecia* in which 16 traces arise. The nature of the traces varies according to the position of the perianth on the thalamus; in taxa with antero-posterior perianth, the traces given off along the antero-posterior and lateral radii function as the tepal midribs and the diagonal ones as the conjoint marginals while in those with diagonal perianth, the diagonal traces are the tepal midribs and the alternate ones the conjoint tepal laterals. In all taxa the conjoint

FIGS. 50–70. Floral anatomy. 50–60, *Strangea* sp. 50–56, *S. stenocarpoides*. 50, L.S. base of flower bud. $\times 35$. 51, L.S. top of flower bud. $\times 25$. 52, T.S. pedicel. 53–56, T.S. flower bud at different heights. 52–56, $\times 30$. 57–59, T.S. flower bud of *S. linearis*. $\times 30$. 60, T.S. flower bud of *S. cynanchicarpa* together with the involucre bracts. $\times 25$. 61–69, *Finschia chloraxantha*. 61, L.S. base of flower bud. $\times 25$. 62, T.S. pedicel. 63–65, 67, T.S. flower bud at different heights. $\times 30$. 66, T.S. tepal and the associated stamen. $\times 25$. 68, L.S. stigma. $\times 18$. 69, T.S. style. $\times 25$. 70, T.S. flower bud of *Finschia ferruginea*. $\times 20$. (*tm* = tepal midrib; *tl* = tepal lateral; *stt* = staminal trace; *nb* = nectary bundles; *ctl* = conjoint tepal laterals; *vct* = ventral carpellary traces; *dct* = dorsal carpellary trace; *tt* = transmitting tissue; *st* = stamen.)



Figs. 50-70.

laterals split radially close to their origin and demarcate the marginal bundles of adjacent tepals (Figs. 29, 35, 46, 54).

The staminal traces in all genera are organized as pairs of bundles which are given off along the tepal midrib radii and from the same gaps of floral stele; these traverse parallel to the tepal midribs in the limbs of tepals. The two bundles of each trace may fuse together either at the base of tepal or higher up or even just before entering the filament (Figs. 31, 46, 47, 55, 56, 59, 66). The lower the level at which the fusion occurs, the more evolved the condition is to be considered. Only in a few species of *Hakea* (*H. laurina*, *H. victoriae*) the staminal trace and tepal midrib arise as common traces. These split tangentially higher up and demarcate the respective bundles. Since in these species the anther is adnate with the tepal midrib the two bundles traverse parallel to each other in the tissue common between the tepal and stamen. This condition represents the maximum adnation between the tepal and stamen noticed in Grevilleae. The staminal bundle extends into the appendage of the connective where it is present. The stamens in *Euplassa*, *Kermadecia*, *Strangaea stenocarpoides* and *Finschia* sp. show short flat filaments (Figs. 32, 33, 48, 51), a condition which should be regarded more primitive than the nearly sessile condition of the anthers in *Grevillea* and *Hakea*.

After the emergence of tepal-stamen supply, the bundles of the floral stele abstrict some strands for the nectary, bend inwards and function as the carpel traces. Where the nectary is symmetrical, the nectary strands are cut off either all round the floral stele as in *Grevillea leucopteris* or from stelar bundles of four alternitetalous sectors as in *Euplassa* (Figs. 29, 30). In flowers with incomplete, 2- or 3-lobed nectaries they are derived from stelar bundles of the respective sectors (Figs. 54, 57, 58, 63, 64, 70). Usually the nectary bundles branch and terminate at about half the height of the nectary.

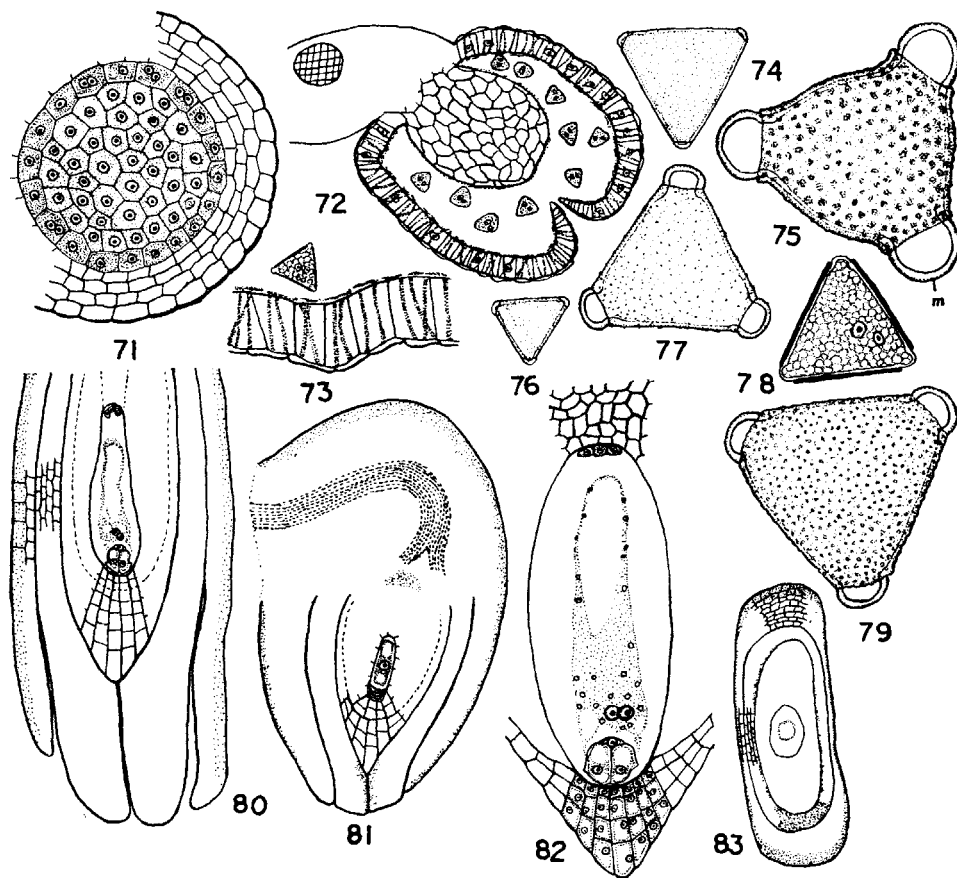
The carpels in all genera are five or more traced; 3-traced carpels are not noticed in Grevilleae. Three or more bundles extend into the style and traverse nearly to the stigma (Figs. 51, 59, 68, 69). The core of the style shows elongated glandular cells of transmitting tissue. Usually the style is solid (Figs. 48, 49) but in *Finschia* it shows a stylar canal which is lined by finger-shaped, 1-celled hairs (Fig. 69). These run continuously with similar hairs of the stigmatic region (Figs. 67, 68).

The floral organs show rust-coloured, 1-celled epidermal hairs (Figs. 40, 41).

Microsporangium, microsporogenesis and male gametophyte

The anther wall comprises the epidermis, well-developed fibrous endothecium, two middle layers and the tapetum which is of the glandular type (Figs. 71-73). There is a stomium at which the anther dehisces longitudinally. In *Strangaea*, *Finschia*, *Kermadecia* and some species of *Grevillea* (e.g. *G. vestita*) the sporogenous cells show a secondary increase (Fig. 71)

while in *Hakea* and some other species of *Grevillea* like *G. rosemarinifolia* they function directly as the sporocytes. In the latter case, only a few large pollen grains are produced per anther loculus while in others they are more numerous and small in size. The microspore tetrads are tetrahedral and cytokinesis of the sporocyte is brought about by simultaneous furrowing.



FIGS. 71-83. 71-79, microsporogenesis and male gametophyte. 71, T.S. young anther loculus of *Strangea stenocarpoides*. $\times 120$. 72, T.S. dehiscent anther lobe of *Finschia chloraxantha*. $\times 55$. 73, part of mature anther wall and a pollen grain of *Kermadecia sinuata*. $\times 120$. 74-79, pollen grains. $\times 800$. 74, *Gevuina bleasdalei*; 75, *Grevillea hilleana*; 76, *Strangea cynanchicarpa*; 77, *Kermadecia sinuata*; 78, *Euplassa cantareirae*; 79, *Finschia chloraxantha*. 80, L.S. micropylar part of ovule of *Kermadecia sinuata*. $\times 120$. 81-83, *Finschia chloraxantha*. 81, L.S. ovule with 1-nucleate embryo sac. $\times 75$. 82, L.S. part of nucellus with embryo sac. $\times 200$. 83, T.S. ovule. $\times 50$. (m = membrane.)

The pollen grains in all genera are triangular, triporate, angulaperturate and 2-celled at the shedding stage (Figs. 74-79). Starch is accumulated in the cytoplasm of the pollen grain. The intine is as thick as the exine or thinner and protrudes slightly or markedly through the germ pore. In species of

Grevillea and *Hakea* in which the germ pores are wide, it forms knob-like swellings which are covered over by special protective membranes (Fig. 75). The ornamentation of the exine ranges from granular to papillate and spinescent patterns. In their large size and complex exine ornamentation, the pollen grains of *Grevillea* and *Hakea* conform to the most highly evolved type in Proteaceae. The pollen grains of *Grevillea vestita* are unique in being polymorphic; they show 3-8 germ pores according to which they vary from triangular to wheel-shaped structures (Venkata Rao 1964).

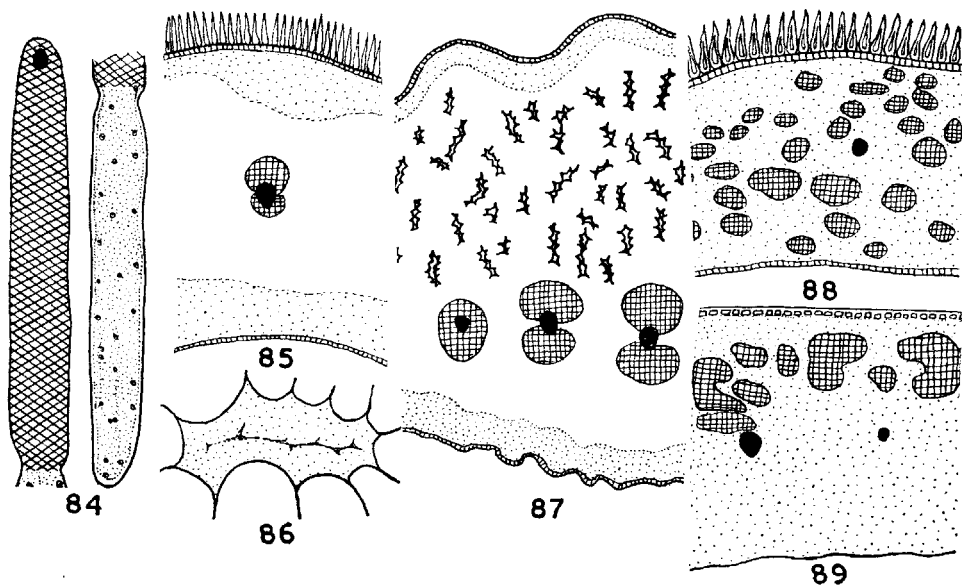
Megasporangium, megasporogenesis and female gametophyte

The ovules in all genera are bitegmic and crassinucellate. In *Euplassa*, *Gevuina*, *Strangea* and *Kermadecia* they are orthotropous and pendulous while in *Finschia* and most species of *Grevillea* and *Hakea* they are hemianatropous and lateral. In a few species of *Grevillea* (e.g. *G. trifida*) they are anatropous and basal, which seems to be the most highly advanced condition in the family. The funicular vascular bundle branches and forms a ring of strands in the chalaza (Fig. 81). The outer integument is biseriate and the inner usually 3-4 cells thick. In *Finschia chloraxantha* the outer integument is 8-10 cells thick at the margins and thinner elsewhere (Fig. 83). Only the inner integument forms the micropyle (Figs. 80, 81). The parietal tissue consists partly of the derivatives of the primary parietal cell and partly of the nucellar cap (Figs. 80, 81). A hypostase of thick-walled cells is usually found below the embryo sac (Fig. 82).

The female archesporium consists of a single hypodermal cell. In *Grevillea rosemarinifolia* it is multicellular and several embryo sacs are formed in an ovule (Venkata Rao 1966a). The embryo sac develops according to the Polygonum type (Figs. 81, 82). A filiform apparatus is noticed in some species of *Grevillea*. The two polar nuclei fuse only at the time of fertilization. The antipodals are usually inconspicuous and ephemeral; in some species of *Grevillea* they are seen to persist till the early stages of endosperm development. Starch grains are noticed in the embryo sac of some species of *Grevillea* and *Finschia chloraxantha* (Fig. 82).

Endosperm—Fertilization is porogamous. The endosperm is of the Nuclear type. The endosperm nuclei formed after the first free nuclear divisions become distributed throughout the embryo sac. The micropylar part then becomes cellular while the rest of the endosperm remains free nuclear and functions as the haustorium. In *Strangea cynanchicarpa* the endosperm haustorium is of a simple type and does not show either aggressive growth or secondary haustorial lobes (Fig. 84); it resembles the haustorium in *Orites revoluta* and *Knightia excelsa* (Venkata Rao 1967). Complex haustoria which show aggressive growth and secondary haustorial lobes are seen in *Grevillea* and *Hakea* (Venkata Rao 1966b, 1968a). Mature seeds are non-endospermic.

Pericarp—In *Grevillea* and *Hakea* sclerenchyma is noticed both in association with the vascular bundles and as additional strands distributed either near to the outer surface of the pericarp or throughout its thickness (Figs. 88, 89). The epidermal hairs of the ovary wall are persistent in some taxa. Eventually all the parenchyma become thick-walled and lignified and the pericarp becomes very woody.



FIGS. 84-89. 84-86, *Strangea cynanchicarpa*. 84, endosperm. $\times 12$. 85, T.S. young pericarp. $\times 30$. 86, a thick-walled 'cell' from old pericarp. $\times 85$. 87, T.S. pericarp of *S. stenocarpoides*. $\times 13$. 88, T.S. pericarp of *Grevillea acanthifolia*. $\times 25$. 89, T.S. pericarp of *G. endlicheriana*. $\times 30$.

Thick-walled cells of a special type are noticed in *Strangea*. In the young fruit sclerenchyma are noticed only in association with the vascular bundles; the remaining pericarp consists of thin-walled parenchyma with cellulose walls (Fig. 85). As the fruit grows, cell wall material (which stains lightly with safranin) becomes deposited on the parts of cell walls abutting on an intercellular space. Such 'cells' are usually described as tubular collenchyma (Fig. 86). These are 4- or 5-sided to start with; as more and more cell wall material becomes deposited, the adjacent cells become wedged apart and the intercellular space extends. The material continues to be deposited on the walls of the newly exposed cells. Thus these 'cells' grow and become caterpillar-like as the pericarp becomes older (Figs. 86, 87). Such thick-walled cells are noticed characteristically in all the species of *Strangea* but are not seen in any other genus of Proteaceae studied.

DISCUSSION

From the account given above, we can not only trace the evolutionary trends within the Grevilleae but formulate the characteristics of the ancestral stock. The ancestral Grevilleae seem to have been large rain-forest trees with large, compound, mesophytic leaves; large terminal paniculate inflorescences which were sometimes cauliflorous; small nearly regular flowers; large indehiscent nuts; large wingless seeds, and rounded fleshy embryos. The relatively primitive genera of the tribe (*Euplassa*, *Gevuina*) resemble closely the Persoonieae suggesting their origin from this tribe. In several features the two genera, *Grevillea* and *Hakea*, mark the culmination of the evolutionary tendencies not only within Grevilleae but in the whole of Proteaceae. The following trends of evolution are evident within the tribe:

TABLE II

No.	Primitive	Evolved
1	Large trees of rain-forests	Shrubs and undershrubs of exposed spaces
2	Large, bicompond or compound, mesophytic leaves	Small, simple, acicular or spinescent, xerophytic leaves
3	Diffuse, terminal panicles with more than two flowers on lateral branches	Uniaxial pseudoracemes with paired flowers, or small few-flowered corymbs or 1-flowered involucrate heads
4	Flowers inconspicuous, nearly regular with sepaloid, antero-posterior perianth	Flowers strongly zygomorphic with petaloid, diagonal perianth
5	Stamens with short free part of filaments and produced connectives	Stamens nearly sessile, not appendaged
6	Ovary stipitate; stigma simple, terminal	Ovary sessile; stigma lateral, subtended by pollen-collecting apparatus
7	Nectary symmetrical, either 4-lobed or ring-like	Nectary zygomorphic, incomplete, 2- or 3-lobed
8	Fruit indehiscent, globose nut	Fruit flattened, follicle or 'capsule'
9	Embryo rounded with thick, fleshy cotyledons	Embryo flat with thin foliaceous cotyledons
10	Floral organs and traces free	Floral organs and traces showing connation and adnation
11	Pollen grains small, numerous with smooth exine	Pollen grains large, few per loculus, exine intricately ornamented
12	Ovules orthotropous, pendulous from the top of loculus	Ovules hemianatropous and lateral or anatropous and basal.

The cytological evidence corroborates the conclusion drawn on morphological grounds that Persoonieae are the nearest to the ancestral stock of Grevilleeae. The Persoonieae contain, in addition to some polyploids, the two diploid genera, *Bellendena* ($n = 5$) and *Persoonia* ($n = 7$); both 5 and 7 seem to be the basic numbers in the family though $n = 14$ is found more commonly. In Grevilleeae, $n = 14$ is found in the relatively primitive genus *Gevuina* (the chromosome number in *Euplassa* is not known); $n = 11$ is found in the relatively more advanced *Strangea* and $n = 10$ (which is the smallest haploid chromosome number in the Proteaceae) in the two most highly evolved genera, *Grevillea* and *Hakea*. Morphological evolution, therefore, seems to have been accompanied by a reduction in chromosome numbers.

The distribution pattern of the genera of Grevilleeae throws some light on the probable centre of origin of the tribe. *Hakea* and *Strangea* are wholly endemic to Australia being distributed in East and West Australia; *Euplassa* is wholly endemic to S. America. *Grevillea*, with the major number of species centered in Australia, extends to the neighbouring islands New Guinea and New Caledonia. *Gevuina* is common to East Australia, New Guinea and S. America. *Kermadecia* and *Finschia* are not Australian but are found in Pacific islands. Out of the 7 genera, therefore, four are found in E. Australia, three in W. Australia, two in S. America and two in the islands off east coast of Australia. E. Australia shows community at the generic level with the neighbouring islands as well as with far off S. America, which W. Australia does not. So, E. Australian region on a once connected land mass (Gondwanaland) seems to be the probable centre of origin for the tribe. The Persoonieae from which the Grevilleeae are supposed to have originated are also better represented in this region than elsewhere. The present-day disjunction of the tribe seems to have been brought about due to continental drift. When S. America separated from the common land mass, it seems to have received the primitive stock.

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