STUDIES IN THE PROTEACEAE

V. Evolution of the Inflorescence

By C. Venkata Rao

Department of Botany, Andhra University, Waltair

THE Proteaceae is a monochlamydeous family with 63 genera and about 1,400 species. Of these, 37 genera belonging to both Proteoideae and Grevilloideae occur in Australia, 16 genera (15 of Proteoideae and one of Grevilloideae) in Africa and Madagascar, 8 genera (4 of which are common with Australia) in S. America, and 6 genera in Malaysia, New Caledonia, New Guinea and Pacific Islands. This is an ancient family: Proteaceous fossils are known with certainty from Tertiary of Australia and Antarctica. The Proteaceae are not definitely related to any other angiospermous family. Several taxonomists like Engler and Prantl (1894), Rendle (1952), and Lawrence (1955) place it singly in the order Proteales in the vicinity of Loranthaceae and Santalaceae. It is regarded as a primitive family which has undergone some specialisation in certain features. A study of the evolutionary trends in the inflorescence, which are unique in certain respects, lends support to this conclusion.

The large-leaved trees of marshy areas (*Finschia* of New Guinea) or of rain forests (*Austromuellera, Musgravea, Placospermum* of Australia) seem to represent the primitive habitual type for the family. From such a type evolution led to the development of other habitual types, *viz.*, the shrub and undershrub; this was accompanied by diversification of the leaf into the linear, lobed or dissected, sclerophyllous and microphyllous types which enabled the plants to colonise and inhabit diverse ecological situations including sandy waste lands abundantly available at that period (Andrews, 1916). Comparative studies of the inflorescence in the family show that the large, diffusely branched, multiflowered panicle is the primitive type of inflorescence and the small, compact few and 1-flowered forms, the derived ones. It is interesting to notice that reduction in the vegetative parts often proceeded concurrently with reduction in the inflorescences, not only in the whole family but within genera: *Grevillea robusta* is a lofty tree with large 2–3 times pinnate leaves and large diffusely branched paniculate inflorescences (Fig. 41) while *G. australis* is a small undershrub with small linear leaves and few-flowered corymbs (Fig. 43); *Dryandra floribunda* is a tree with umbellate multi-flowered inflorescences while *D. nivea* is a dwarf undershrub with much reduced, few-flowered compound heads.

PREVIOUS WORK

In the Proteaceae, the subfamily Proteoideae are characterised by the occurrence of solitary flowers and the Grevilloideae by the presence of flowers in pairs at each node, except in *Lambertia, Dryandra* and *Strangea* sp. in which a secondary solitary condition results due to the suppression of one flower from each pair. The writer (Venkata Rao, 1957) was the first to show that each flower pair of Grevilloideae represents a reduced lateral branch system and that the primitive type of inflorescence in the family, therefore, is a panicle. These conclusions were accepted by the subsequent workers. However, Haber (1959) believes that the paired-flower arrangement is the ancestral condition and that the solitary flowers of all Proteoideae are derived by reduction. Eames (1961) also seems to favour this view. On the other hand, the writer (Venkata Rao, 1957) as well as Johnson and Briggs (1963) think that the solitary flower of Proteoideae is ancestral to the paired-flower arrangement.

Since there have been no systematic and comprehensive studies of the inflorescence in the Proteaceae, the present study was undertaken.

MATERIALS AND METHODS

The present observations are based on fixed materials or herbarium specimens collected by the writer during his stay in or tour of Tasmania and Australia (1955-1957), or those obtained from other sources which are acknowledged later.

INFLORESCENCE AXIS AND FLOWER PAIRS

The flowers of Proteoideae occur singly either in the axils of vegetative leaves (Text-Figs. 33, 34) or bracts (Text-Figs. 1, 37, 39). Since the flowers show normal orientation with reference to the axis and bract, *i.e.*, similar to that noticed in other angiosperms (Text-Figs. 2, 32 *a*) the inflorescence axis and pedicel of Proteoideae present no problems in interpretation unlike in Grevilloideae.

The conclusion that each flower pair of Grevilloideae is a reduced branch system is based on several evidences, both morphological and anatomical. In *Strangea linearis* (E. Australia) the flowers occur in lax panicles (Text-Fig. 44). Each lateral branch (which is the least reduced among the Grevilloideae) shows an elongated axis arising in the axil of a scaly bract. At its top are found two pedicellate flowers each of which arises in the axil of a bract. One or more empty bracts are found at the top of the lateral axis; these give evidence for the suppression of some flowers of the lateral branch which has led to the paired arrangement of the flowers (Text-Fig. 3). Anatomical studies show that the lateral axis receives a single ring of vascular bundles from the primary axis. Close to its origin, this gives off a trace for the bract (Text-Fig. 4 *a*). Then the ring becomes transversely elongated and 2-lobed, coincident with an increase in the number of bundles due to splitting (Text-Fig. 4 *b*).

B-7
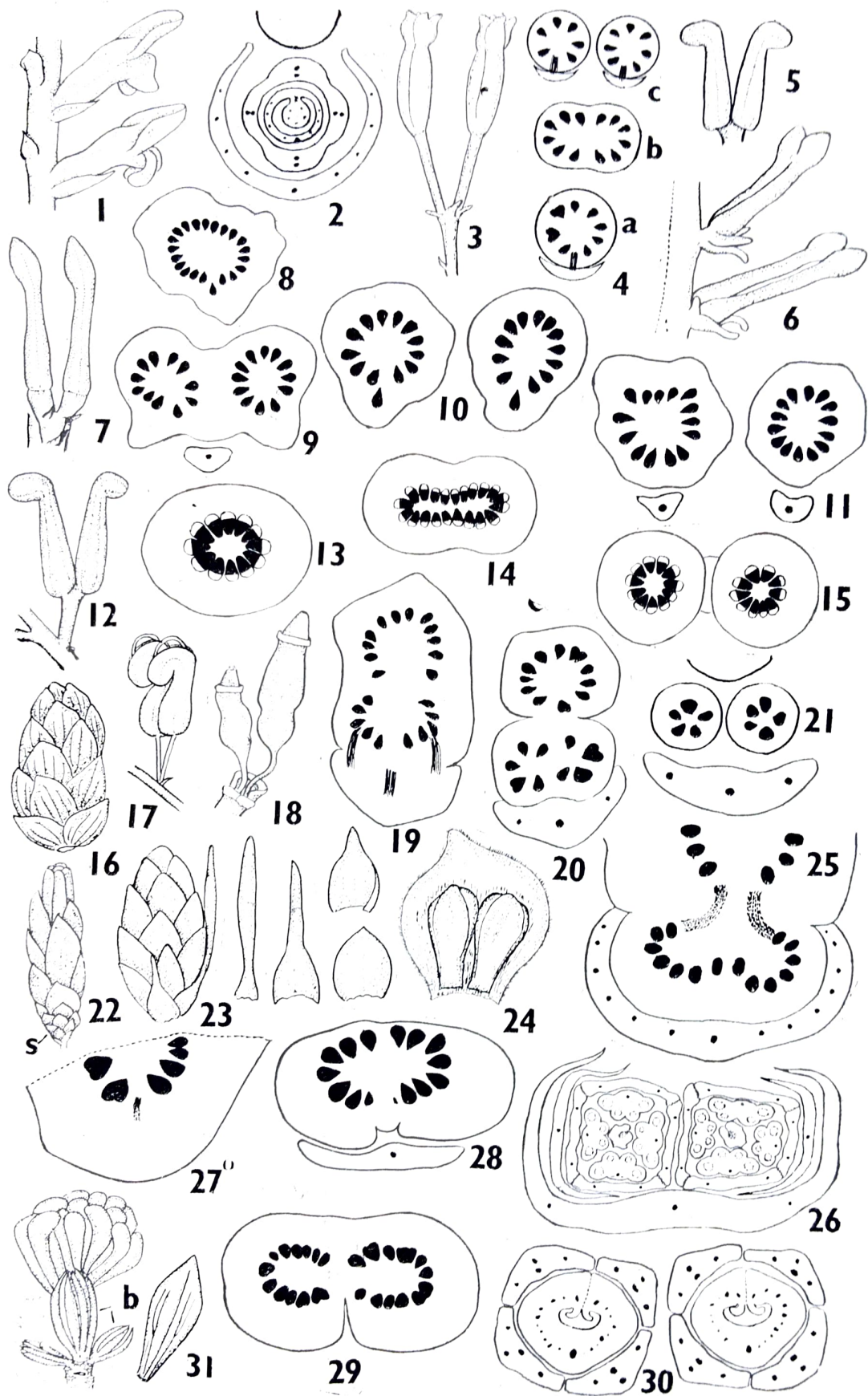
TEXT-FIGS. 1–31. Structure of the inflorescence in Proteaceae. Fig. 1. Part of the inflorescence of *Synaphea acutiloba*, ×3. Fig. 2. T.s. flower and bract of

Conospermum longifolium, ×40. Fig. 3. A flower pair of *Strangea linearis*, ×4. Fig. 4. *a–c*. Semidiagrammatic transverse sections of the lateral axis of the above. Fig. 5. A flower pair of *Cardwellia sublimis*, ×1. Fig. 6. Part of the inflorescence of *Musgravea stenostachya*, ×3. Fig. 7. A flower pair of *Austromuellera trinervia*, ×1. Figs. 8–11. T.S. lateral axis of the above, ×24. Fig. 12. A flower pair of *Gevuina avellana*, ×1. Figs. 13–15. T.s. stalk of the flower pair of the above, ×24. Fig. 16. Inflorescence of *Grevillea ilicifolia*, ×2. Fig. 17. A flower pair of *G. rosemarinifolia*, ×2. Fig. 18. Ovary from an abnormal flower of *G. vestita*, ×2. Figs. 19–21. T.s. base of flower pair of *G. rosemarinifolia*, ×35. Fig. 22. A young inflorescence of *Lambertia formosa*, ×1; *s*, bud scales. Fig. 23. A young inflorescence and its scales and bracts of *Orites acicularis*, ×1. Fig. 24. A bract and flower pair of *O. milligani*, ×3. Fig. 25. T.s. base of flower pair of the above, ×24. Fig. 26. T.s. flower pair of *O. acicularis*, ×24. Figs. 27–30. T.s. lateral axis and flower pair of *Telopea speciosissima*, ×20. Fig. 31. Inflorescence and one bract of *Hakea nitida*, ×2; *b*, vegetative buds in the axils of bud scales.

Finally it breaks up into two rings of bundles each of which gives off a trace for the bract of the individual flower and functions as the floral stele (Text-Fig. 4 *c*). Several other genera like *Hicksbeachia, Cardwellia* (Text-Fig. 5) and *Austromuellera* (Text-Fig. 7) show further stages in the reduction of the lateral axes and pedicels. In *Musgravea* these are much reduced and the flower pair is situated on a slight prominence but shows the common as well as the individual floral bracts (Text-Fig. 6). Where the lateral axes persist and the pedicels become suppressed as in *Kermadecia, Gevuina* (Text-Fig. 12) and *Euplassa* (Text-Fig. 95) the common stalk was mistaken by the earlier taxonomists to be 'fused pedicels' but the anatomical structure shows its axial nature (Text-Figs. 13–15). In several genera like *Grevillea* (Text-Fg. 17), *Telopea, Brabeium, Roupala*, etc., the lateral axes and individual floral bracts are so reduced that they are imperceptible in old inflorescences and pairs of pedicellate flowers stand in the axils of common bracts. In *Orites* (Text-Fig. 24) and *Darlingia* (Pl. I, Fig. 6) the pedicels are also reduced and the inflorescences are spikate. However, microtome sections of very young inflorescences reveal a common base for the flower pair, and individual floral bracts also in *Orites* (Text-Fig. 26). The anatomical features are closely similar to those of *Strangea linearis* though condensed in form (Text-Figs. 8–11; 19–21; 25–30).

Another evidence which shows that each flower pair is the sole survivor of a lateral branch system is given by the variation in the orientation of the flowers of a pair relative to each other and to the main axis. Three types of orientation are noticed: (1) In *Grevillea, Hakea, Strangea, Austromuellera, Oreocallis, Telopea* (Text-Fig. 30), etc., the ventral sutures of the carpels of both flowers are oriented normally, *i.e.*, at right angles to the respective bract (developed or suppressed). This type of floral arrangement can be derived by supposing that the two flowers found on the same side of the lateral axis have been brought together due to reduction and condensation (Text-Fig. 32 *b*). (2) Text-Fig. 32 *c* represents the orientation noticed in *Orites diversifolia* (Tasmania) in which the ventral sutures of the carpels of the flower pair face each other. This type of orientation seems to have resulted from the survival and approximation of two flowers found on the opposite sides of a lateral axis. (3) The condition noticed in *Banksia* (Text-Fig. 52)

is more difficult to interpret. In this position, the ventral sutures
of the carpels of a flower pair face the opposite directions. A similar
position is found also in *Dryandra* (Text-Figs. 56, 58), *Gevuina*, *Euplassa*,
Lomatia, *Hicksbeachia*, *Cardwellia* and *Opistholepis*. There are three
possible ways in which this condition could have been derived. Firstly,
it can be supposed that torsion of the ovaries occurred in the flower
pair of the first kind (*cf*. Solanaceae) through 90°. Torsion of the carpel
through 45° is commonly found in species of *Orites* (Text-Fig. 26) and
torsion through 90° is occasionally noticed in *O. acicularis*. Secondly,
it can be supposed that the flowers do not belong to the secondary axes
but to the tertiary axes. Just as the common bract is the bract for the
suppressed secondary axis, the bracts subtending the individual flowers
may be the bracts for the suppressed tertiary axes. According to this
view the bracts for the individual flowers are completely suppressed
and the carpels show normal orientation with reference to these suppressed
floral bracts (Text-Fig. 32 *d*).
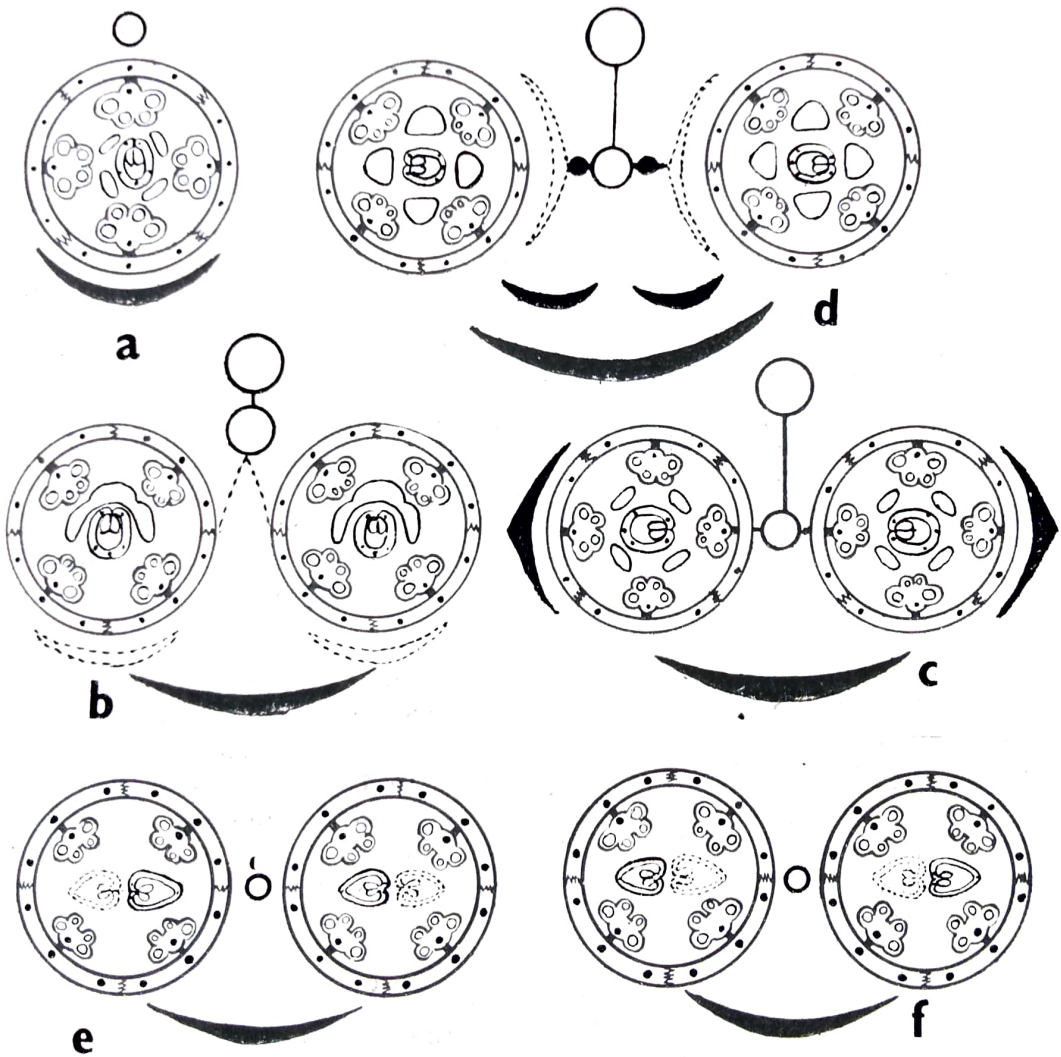
TEXT-FIG. 32 *a–f*. Diagrammatic representation of the flower positions in
Proteaceae. *a*. Flower position in *Persoonia*—Proteoideae; *b–d*, Flower positions

in Grevilloideae: *b, Grevillea; c, Orites diversifiolia; d,* explanation to *Banksia*-type of flower position; *e* and *f.* Derivation of the flower positions in *c* and *d* by reduction of carpels. Bracts and carpels seemed to have been suppressed are shown in dotted lines. [Antero-pasterior carpels (hypothetical) not shown.]

The above conclusion seems to be justified by the anatomical structure of the inflorescence axis in *Banksia* (which is described in detail in another article (*cf.* Venkata Rao, 1964). The axis is massive and shows a central ring of vascular bundles from which strands are given off towards the periphery (Text-Figs. 53, 54). These anastomose forming a mesh-like cortical vascular system. From each rhomboidal zone of the mesh, traces are given off for a pair of flowers and the associated bracts. This type of vasculature which is not noticed in any other member of the family shows that the vascular system of the secondary (and tertiary?) axes is incorporated in the primary axis.

However, though in *Dryandra* sp. also the inflorescences are condensed and the traces for flower pairs are organized within the cortex of the peduncle, a cortical vascular system is absent (Text-Fig. 57). In *Lomatia* the inflorescence is lax (Text-Fig. 46) and yet the carpels of the flower pair show *Banksia*-type of orientation. These instances show that the carpel position may have been derived in another manner and this brings us to the third alternative. In *Cercidiphyllum* sp. in which also a similar orientation of the carpels is noticed, Solereder (1900, quoted from Swamy and Bailey, 1949) interpreted that the ancestral flower possessed two transverse carpels with ventral sutures facing each other, and that the inner carpels (towards the axis) became suppressed. This could be possible in Proteaceae also. Though no vestigial organs or vestigial floral traces are noticed in normal flowers, occasionally abnormal flowers are met with in *Grevillea vestita* (Text-Fig. 18) and *Hakea laurina* with two separate carpels (Text-Fig. 63). Since these carpels are oriented antero-posteriorly in *H. laurina*, it is to be presumed that the ancestral flower possessed four carpels. Suppression of the antero-posterior and outer lateral carpels would result in *Banksia*-type of orientation (Text-Fig. 32 *c*) while suppression of the antero-posterior and inner lateral carpels would result in *Orites diversifolia*-type (Text-Fig. 32 *f*).

The diversity in orientation of the flower pairs in different genera of Grevilloideae shows that all flower pairs could not have arisen in the same manner and from similar ancestral stocks. These studies do not lend support to the view of Johnson and Briggs (1963) that the Grevilloideae are essentially monophyletic and monochronous. The writer feels that the different flower positions must have originated in different manners and at different levels from ancestral stock that already diversified to some extent.

EVOLUTION OF THE INFLORESCENCE IN THE AUSTRALIAN TAXA*

For tracing the evolution of the inflorescence of the Proteaceae a start can be made with the Proteoideae. Comparative studies of the

---

* All genera except the African and the American are included here.

inflorescence in this subfamily show that the solitary pedicellate flowers distributed sparsely in the axils of the vegetative leaves represent the most primitive condition. Such flowers are found in several species of *Persoonia*, viz., *P. lancefolia, P. gunnii, P. juniperina* (Text-Fig. 33) and *P. saccata* (Pl. I, Fig. 1). Haber (1959) considers that all solitary flowers of Proteoideae are derived by reduction from paired-flower
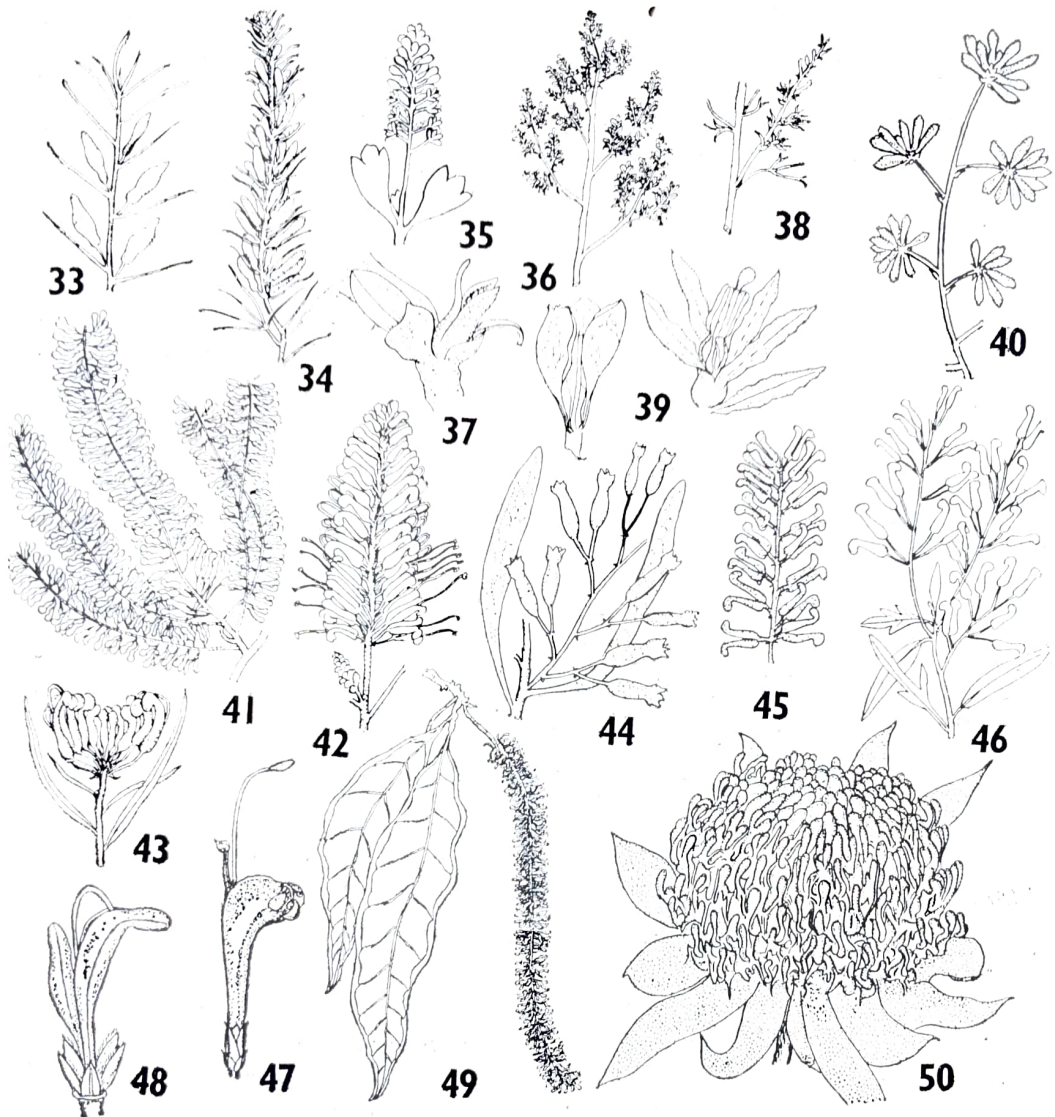
TEXT-FIGS. 33–50. Inflorescences in some Australian taxa. Fig. 33. A branch of *Persoonia juniperina*, ×1. Fig. 34. An inflorescence of *P. pinifolia*, ×1. Fig. 35. Inflorescence of *Bellendena montana*, ×1. Fig. 36. A branch of *Beauprea pancheri*, ×½. Fig. 37. Two flowers from the above, ×3. Fig. 38. A branch of *Symphyonema paludosum*, ×1. Fig. 39. A flower from the above, ×3. Fig. 40. Part of the inflorescence of *Stirlingia latifolia*, ×5. Fig. 41. Inflorescence of *Grevillea robusta*, ×1. Fig. 42. Inflorescence of *G. bipinnatifida*, ×1. Fig. 43. A branch with inflorescence of *G. australis*, ×1. Fig. 44. Inflorescence of *Strangea linearis*, ×3. Fig. 45. Inflorescence of *Gevuina bleasdalei*, ×1. Fig. 46. Inflorescence of *Lomatia diversifolia*, ×1. Fig. 47. Inflorescence of *Adenanthos obovata*, ×1. Fig. 48. An abnormal inflorescence of *A. meissneri* with two flowers, ×1. Fig. 49. Branch with inflorescence of *Finschia chloraxantha*, ×½. Fig. 50. Inflorescence of *Telopea speciosissima*, ×½.

arrangement noticed in Grevilloideae. Though no doubt reduction has played an important part in the evolution of the inflorescence in several angiosperms as also in Proteaceae, all solitary flowers cannot be regarded as the sole survivors of branch systems, unless there is definite evidence in support in the shape of some vestigial organs. For example in a few angiosperms like *Degeneria, Eupomatia* and *Annona*, the stalk of the solitary flower shows reduced scaly bracts which subtend either vestigial or well-developed buds thus giving evidence of reduction. In Proteaceae also in some members like the Australian *Adenanthos* and *Telopea truncata* and the African *Aulax* and *Spatalla* in which reduction has occurred, evidence is given by the occurrence of empty bracts (Text-Fig. 68). Since no such vestigial organs are found in association with the solitary flowers of *Persoonia* and other Proteoideae, these are to be regarded as primitively simple and not simple due to reduction.

Moreover, *Persoonia* belongs to the tribe Persoonieae which is considered by several taxonomists to be the most primitive tribe of the Proteaceae. This genus is also one of the three diploid genera of the family (the other two being *Bellendena* $n = 5$ and *Placospermum* $n = 7$ of Proteoideae). Its haploid chromosome number of 7 represents one of the two basic chromosome numbers in the family, all other genera of both subfamilies being polyploids and aneuploids on the two basic numbers 5 and 7. These facts also give evidence as to the probable direction in which evolution must have proceeded.

Aggregation of these sparsely scattered axillary flowers due to a shortening of the internodes seems to be the first step which led to the building up of a simple racemose inflorescence (Text-Fig. 64 *a, b*). Such a lax raceme is noticed in *Persoonia pinifolia* (Text-Fig. 34; Pl. I, Fig. 2). The inflorescence looks like a condensed vegetative branch; the leaves in the flowering region are similar to those of the vegetative branch but smaller in size and appear as if they are on their way towards evolution into bracts. Such a transformation is also noticed in other angiosperms like *Cleome* and *Gynandropsis* in which the vegetative leaves get progressively reduced towards the top of the axis till they become typical bracts.

The monotypic Tasmanian *Bellendena montana* shows long peduncled terminal racemes in which the flowers open in strict acropetal succession (Text-Fig. 35). However, the flowers are ebracteate; in fact this is the only member of Proteaceae with ebracteate flowers. This condition seems to have been derived from the ancestral raceme by a complete loss of leaves in the inflorescence region (Text-Fig. 64 b_1).†

---

† This, however, does not mean that *Bellendena* ($n = 5$) is derived by reduction directly from either *Persoonia* ($n = 7$) (or *Placospermum* $n = 7$) as Ramsay (1963) believes. Loss of entire chromosomes is not favoured in nature at the diploid level. Moreover *Bellendena* shows some essentially primitive features. This is the only member of Proteaceae with endospermic seeds; it is also the only member in which the tepals and stamens are completely free from each other. In all other Proteaceae the seeds are nonendospermic and the tepal and stamen show varying degrees of adnation. Since these evolutionary trends are considered to be irreversible it is not possible to derive *Bellendena* from any other living genus. It seems to represent another basic chromosome number, and another ancestral stock,

A process of elaboration now seems to have followed which led to the building up of the panicle. At first a number of branches bearing the racemes seem to be approximated due to a shortening of the terminal internodes. *Placospermum coriaceum*, the monotypic rainforest tree of N. Queensland (Pl. I, Fig. 9) shows a number of lax racemes clustered towards the ends of branches. This genus was placed by its authors (White and Francis, 1923) in a new tribe Placospermeae in the Grevilloideae on account of its multiovulate carpels, follicular fruits and winged seeds. The writer (Venkata Rao, 1957; 1961), however, recognising it as one of the most primitive genera of the family, shifted its position from Grevilloideae to the Proteoideae and placed it near the Persoonieae on the basis of its floral anatomical and morphological characters like the solitary flower, antero-posterior perianth and partial male sterility. This position is thoroughly justified by the cytological findings of Johnson and Briggs (1963). *Placospermum* is not only found to be a diploid with the same chromosome number ($n = 7$) but its chromosomes are similar to those of *Persoonia*.

Shortening of the internodes and reduction of the leaves subtending the racemes would result in a terminal long-stalked panicle (Fig. 64 c). Such an inflorescence is wholly hypothetical and is not noticed in any living member of Proteaceae. However, its plan is evident in *Leaupre* and *Garnieria* of New Caledonia (Persoonieae), *Stirlingia* (Proteeae) and *Conospermum* (Conospermeae) of Proteoideae. These inflorescences cannot be taken as the actual ancestral types because, as will be described later, reduction of some organs has already occurred in them.

After the attainment of the panicle, reduction seems to have been the main process whereby evolution progressed: reduction in the main peduncle, reduction in lateral axes, reduction in pedicels and reduction in the number of flowers in the partial as well as the whole inflorescence. Coincident with these processes there was aggregation, condensation and/or simplification of the inflorescence.

The bracts also play an important role in the evolution of the inflorescence by undergoing modification, reduction leading to ultimate elimination, or elaboration and specialisation into protective and attractive organs. In some like *Orites* (Text-Fig. 23) and *Hakea* sp. (Text-Fig. 31) the bracts are large while in others like *Franklandia* and *Stirlingia* (Text-Fig. 40) they are small and scaly. Sometimes variation is noticed within a genus (*cf.* Text-Figs. 16 and 17 of *Grevillea* sp:). In *Synaphea* (Text-Fig. 1), *Conospermum* (Text-Fig. 2), *Agastachys, Beauprea* (Text-Fig. 37) *Garrierea* and *Symphyonema* (Text-Fig. 39) the bracts are broad, clasping and multi-traced. In *Banksia* they are hirsute and persistent while in *Petrophila* they are accrescent and woody and give the infructescence a pine-cone like appearance. Good (1956) remarks that the development of an involucre is by far the most important single ingredient in the evolution of the highest type of inflorescence, the

pseudanthium (flower-like inflorescence) since it integrates all the component flowers. Involucres are noticed in the condensed inflorescences of both Proteoideae and Grevilloideae. The petaloid involucre which can be described as the climax functional form of the bract, is also noticed in a few genera of both subfamilies. However, all scaly structures subtending the inflorescences are not bracts. A few of the lowest ones are bud scales (modified leaves). This is evident from the occurrence of transitional stages and the presence of vegetative buds in their axils which later develop into branches (Text-Figs. 22, 23, 31, 51).

It is interesting to notice that among the Australian Proteoideae pedicellate flowers are noticed only in the three diploid genera, *viz.*, *Bellendena*, *Persoonia* and *Placospermum*. In all other genera the flowers are sessile. In *Beauprea*, reduction of the pedicels is not accompanied by reduction in the main and lateral axes; so the inflorescence is a long peduncled panicle of spikes and appears to be the nearest approach to the ancestral type (Text-Fig. 36). In *Conospermum* sp. reduction of the primary and/or secondary axes also occurs resulting in the formation of corymbose clusters of spikes. In *Stirlingia* the flower bearing region of the ultimate axes becomes completely reduced so that the flowers are aggregated into globose heads (Text-Fig. 64 *i*) the total inflorescence being a large, long-peduncled, lax panicle of heads (Text-Fig. 40). In *Cenarrhenes*, *Agastachys* (Pl. I, Fig. 11), *Synaphea*, *Symphyonema* (Text-Fig. 38) and *Garnieria* to some extent, the main peduncle is reduced and the spikes become aggregated into a terminal cluster.

Evolution of the inflorescence in other Australian Proteoideae seems to have proceeded along two lines: (1) condensation of the receptacle without much reduction in the number of flowers leading to multi-flowered heads and (2) reduction in the number of flowers in an inflorescence leading to 1-flowered heads.

In the less reduced forms of inflorescence of *Petrophila* (*e.g.*, *P. fucifolia*) and *Isopogon* (*e.g.*, *I. anethifolius*), the main axis is elongated or conical (Text-Fig. 64 *f*). Progressive reduction and flattening of the receptacle led to the evolution of the involucrate head as seen in *P. linearis* (Pl. I, Fig. 4; Text-Fig. 64 *g*, *h*). This represents the highest level of organisation in the Australian Proteoideae. However, as the involucre has not evolved into an attractive organ, the inflorescence stands at the level of subpseudanthium. Petaloid involucre has not evolved in any Australian Proteoideae.

Reduction in the number of flowers of the inflorescence to one is noticed in *Adenanthos* (Text-Fig. 64 *j*). In all species of this genus a single flower terminates a lateral branch. This flower is surrounded at base by 3 or 4 series of imbricating or decussating empty bracts which give evidence of reduction (Text-Fig. 47). This is also borne out by the occasional development of an extra flower within the involucre (Text-Fig. 48).
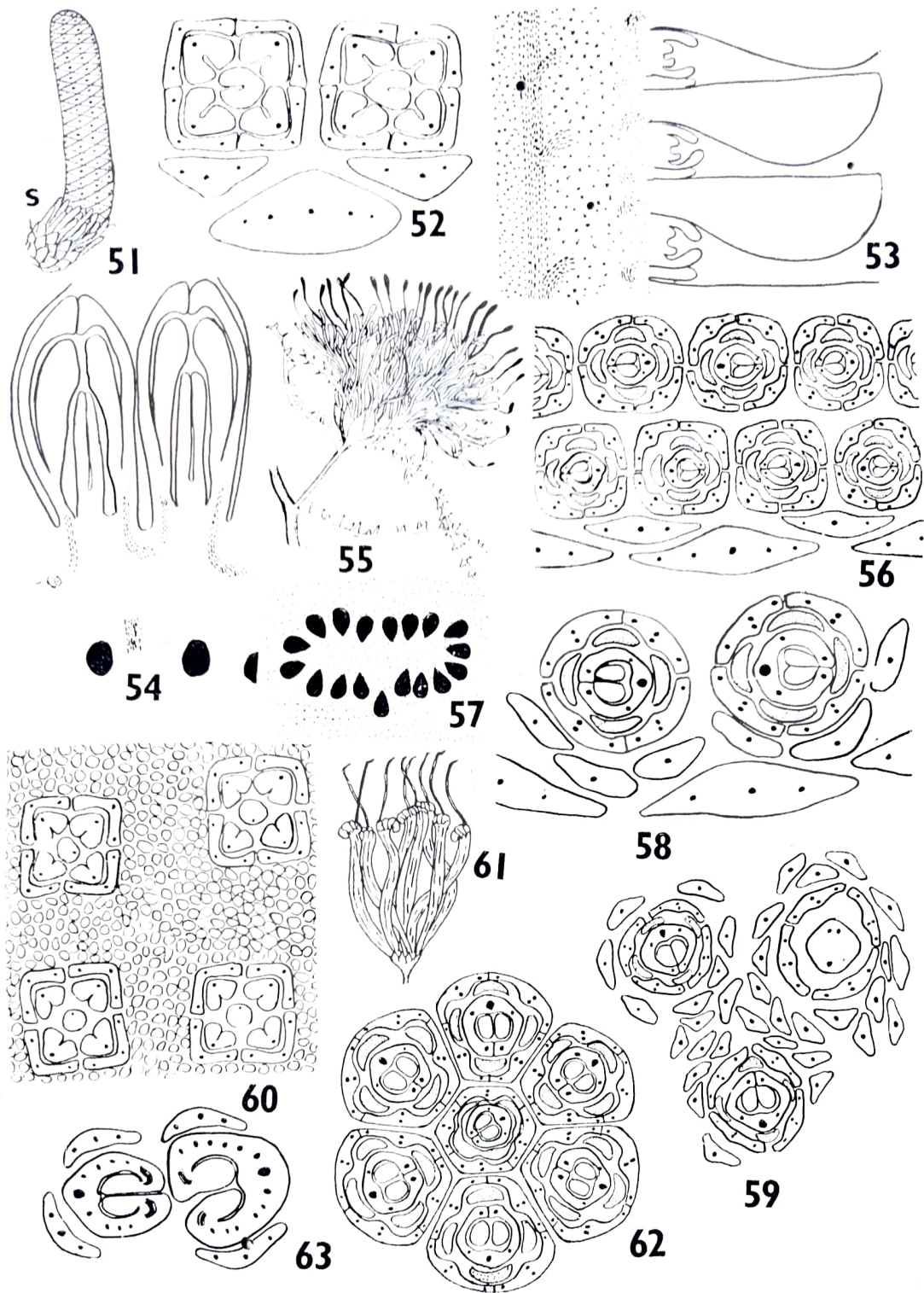
TEXT-FIGS. 51–63. Structure of the inflorescence in some Australian taxa. Fig. 51. A young inflorescence of *Banksia integrifolia*, ×1. s—bud scales. Fig. 52. T.s. flower pair of *B. marginata*, ×30. Fig. 53. L.s. young inflorescence of *B. marginata*, ×24. Fig. 54. T.s. inflorescence of *B. marginata*, ×24. Fig. 55. Inflorescence of *Dryandra polycephala*, ×2. Fig. 56. T.s. inflorescence of *D. floribunda*, ×12. Fig. 57. T.s. inflorescence axis of *D. armata*, showing organisation of trace for the common bract, ×24. Fig. 58. T.s. flower pair of *D. armata*, ×30. Fig. 59. T.s. inflorescence of *D. nivea*, ×12. Fig. 60. T.s. inflorescence of *D. speciosa*, ×30. Fig. 61. Inflorescence of *Lambertia multiflora*, ×1. Fig. 62. T.s. inflorescence of the above, ×6. Fig. 63. T.s. abnormal flower of *Hakea laurina*, ×30.

The inflorescences in Grevilloideae do not present the diversity of form which is noticed in Proteoideae. Since it has been shown that each flower pair characteristically noticed in Grevilloideae is a reduced branch system, it is evident that the solitary flower arrangement must have preceded the paired condition. The diffusely branched panicle with solitary flowers axillary to bracts is therefore taken as the ancestral type of inflorescence for the Grevilloideae (Fig. 64 c).

Carnarvonia aralaefolia the monotypic endemic of N. Queensland is the only member in which the flowers occur singly in bract axils; sometimes these become aggregated into loose clusters (Pl. I, Fig. 12). This genus was placed by Engler and Prantl (1898) in Grevilloideae because of its follicular fruits and winged seeds. It shows definite resemblance to *Macadamia* in its regular flowers and chromosome number ($n = 14$). The writer (Venkata Rao, 1957) therefore placed it in the Macadamieae. This genus seems to show the nearest approach to the ancestral condition from which the paired arrangement is derived by aggregation and reduction and became an established feature in the subfamily. As already described, the lax panicle of *Strangea lineari* represents the least reduced type among the Grevilloideae (Text-Fig. 64 k) and other genera show progressive reduction of lateral axes and pedicels (Text-Fig. 64 r, s). The plan of the diffusely branched ancestral panicle is still evident in *Grevillea robusta* (Text-Fig. 41), *Lomatia tinctor, L. polymorpha* (Text-Fig. 46) and *Kermadecia vitiensis* (Caledonia). Suppression of all branches except one led to the single axis inflorescence commonly noticed in a number of genera like *Gevuina* (Text-Fig. 45), *Finschia* (Text-Fig. 49), *Knightia* (Pl. I, Fig. 7), *Xylomelum* (Pl. I, Fig. 10), *Macadamia* (Pl. I, Fig. 13), etc. These simulate the simple racemes even in the acropetal arrangement of the flowers (Text-Fig. 42). That they have reduced panicles is, however, evident from the occurrence of flowers in pairs; so these are distinguished as pseudoracemes. In *Orites* and *Darlingia* (Pl. I, Fig. 6) the pedicels are completely reduced so that the inflorescences are pseudospikes (Text-Fig. 64 s).

Three main lines of evolution are apparent in the Grevilloideae, one in which the inflorescences, though showing some specialisation, still remain elongated or diffuse as is noticed in the tribes Macadamieae, Grevilleae, Oriteae, Musgraveae and Telopeae, the second in which the inflorescences become condensed and compact as in *Lambertia* (Macadamieae) and Banksieae and the third in which they become 1-flowered due to extreme reduction.

In a large number of genera of the first group of tribes the inflorescences are lax, *e.g., Hicksbeachia, Buckinghamia, Helicia, Heliciopsis, Opistholepis, Austromuellera, Knightia,* etc. Reduction of the internodes result in their becoming more compact and corymbose as in species of *Grevillea* (Text-Fig. 43), *Hakea* and *Oreocallis*. Complete reduction of the flower bearing region of the peduncle has led to the development of a special kind of inflorescence, the globose umbel (*cf.* the globose head of *Stirlingia*) as seen in *Stenocarpus* (Pl. I, Fig. 8) and *Hakea*
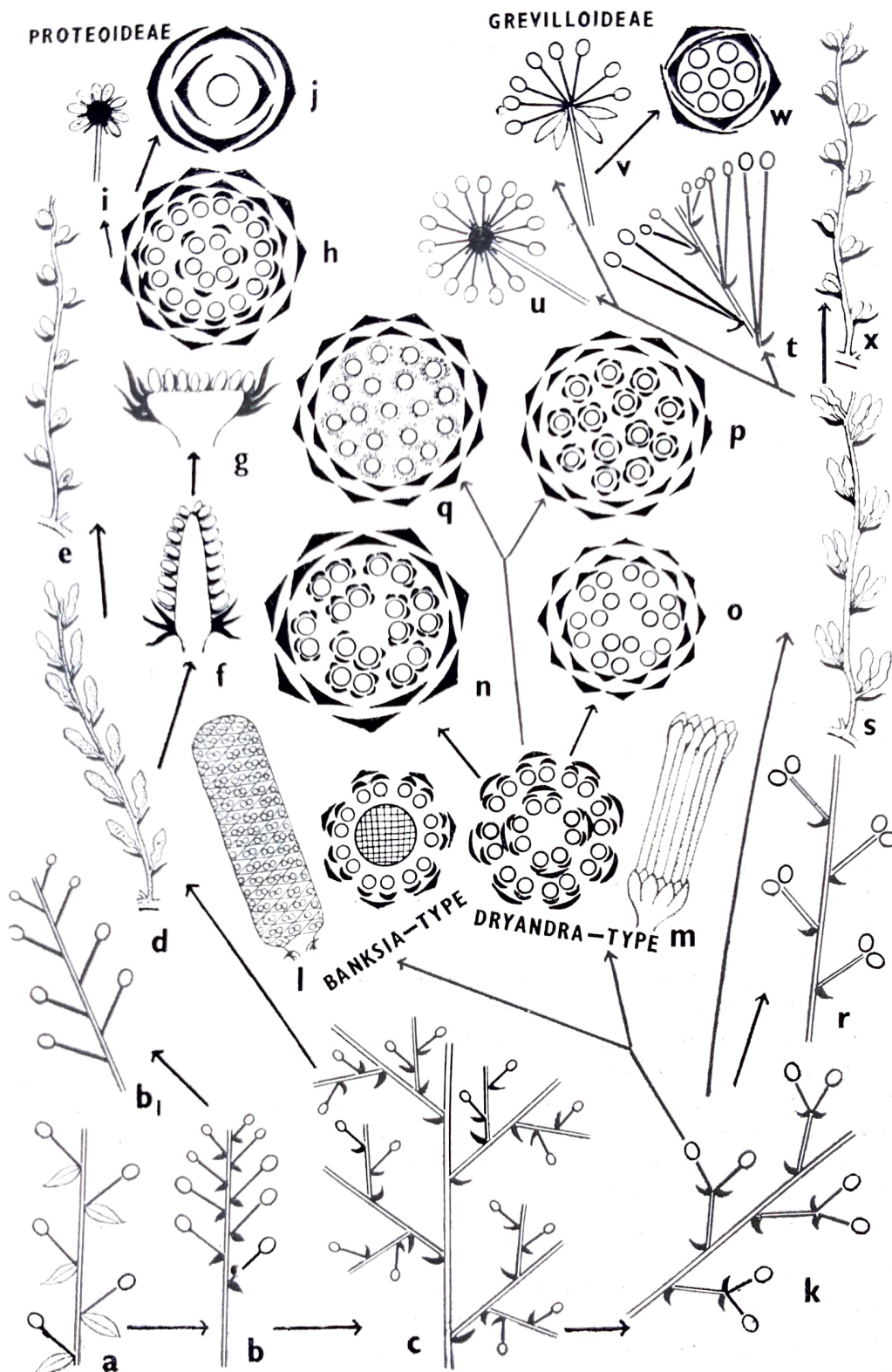
FIG. 64. *a–x*. Diagrammatic representation of the trends of evolution in the inflorescence of Australian taxa. *a.* Solitary axillary flower; *b.* Evolution of the raceme; *b₁.* Evolution of the bractless raceme (*Bellendena*); *c.* The hypothetical primitive panicle; *d–e.* Evolution of typical raceme and spike; *f, g, h.* Evolution of the involucrate head; *i.* The globose head (*Stirlingia*); *j.* 1-flowered head of *Adenanthos*;

k. the primitive lax Grevilloid panicle (*Strangea*); *l. Banksia*-type of inflorescence; *m.* Ancestral *Dryandra*-type of inflorescence; *n. D. armata*-type; *o. D. floribunda*-type; *p. D. nivenia*-type; *q. D. speciosa*-type; *r. Gevuina*-type of inflorescence; *s.* Typical pseudoraceme; *t.* Corymb; *u.* The spherical umbel; *v.* Umbel with petaloid involucre (*Telopea*); *w.* Head with petaloid involucre (*Lambertia*); *x.* Pseudospike of *Orites*.

laurina. In all the above described forms, since the inflorescence is elongated or globose, there is no scope for the evolutionary specialization of the involucre. A typical involucre is seen only in *Telopea* sp. The inflorescence in this genus is a lax hemispherical umbel subtended by a large petaloid involucre. In *T. speciocissima*, the waratah of New South Wales, the inflorescence is large and bears more than a hundred flowers (Text-Fig. 50) while in *T. truncata*, the Tasmanian waratah, there are only 25–30 flowers (Pl. 1, Fig. 5). Evidence of reduction of flowers in this species is given by a sterile prolongation of the inflorescence axis beyond the flower-bearing region with a number of vestigial bracts.

Along the second line *Lambertia* shows a very highly organized inflorescence. The flowers are sessile and placed compactly on a slightly convex receptacle (Text-Fig. 61). Their number is reduced to 7 in *L. formosa*. The head (compound) is surrounded by a series of bud scales and petaloid involucral bracts (Text-Fig. 22). Anatomical studies have shown that the stele of the peduncle which is 5-angled at the base, gives off a number of traces for the scales and bracts and becomes 6-lobed in outline. As the bundles of the outer arcs form the traces for the circumference whorl of 6 flowers, the lobing becomes accentuated. The vascular bundles situated in the bays come together and form a ring which functions as the stele of the central flower. So unlike in other Grevilloideae, the flowers in *Lambertia* are arranged *singly* at each place. Common bracts as well as bracts for the individual flowers are completely suppressed (Fig. 62, 64 *w*).

The maximum amount of condensation of the inflorescence among the Grevilloideae is attained in the tribe Banksieae. However, the two component genera *Banksia* and *Dryandra* show two different lines of evolution. In *Banksia* the inflorescences are massive, cone-like or hemispherical, and present a stereotyped structure. The thick axis bears numerous small flowers (1,000–1,500 in *B. serrata*), arranged in pairs. Each flower pair is subtended by a common bract and a pair of 'bracteoles' (Text-Fig. 53). No variation is noticed in the position of the flowers of a pair or the bracts in the species studied. An involucre is present in some species like *B. integrifolia* (Text-Fig. 32) but since the inflorescence is elongated, it serves to protect it only in the very young condition and is therefore poorly developed. Though great condensation has occurred in the evolution of the *Banksia*-type of inflorescence, it shows several archaic features, *viz.*, absence of a well-developed involucre, massive inflorescence axis which incorporates the vasculature of the lateral axes, the presence of a large number of flowers, their constant occurrence in pairs and the presence of large bracts and bracteoles for all flower pairs (Text-Fig. 64 *l*).

The inflorescences in *Dryandra* are more condensed and Compositae-like than those of *Banksia* because the receptacle is convex or flat and the involucre is relatively better developed, though it still remains sepaloid (Text-Fig. 55). The inflorescence also shows greater range of variation than that noticed in any other genus of Grevilloideae. Two lines of evolution have become apparent from the study of the few species: (i) suppression of one flower from each pair and resultant reduction in the total number of flowers per inflorescence, and (ii) suppression or elaboration of the common bract into an involucel.

Due to the great condensation of the inflorescence, paired arrangement of the flowers is not externally evident in the inflorescences of *Dryandra* as it is in *Banksia*. However, anatomical studies have shown that in *D. floribunda*, *D. armata* and *D. polycephala* (?) the flowers are arranged in pairs. Though in none of the species examined the flower pair shows both common as well as individual bracts, their existence may be taken as the ancestral condition on analogy with *Banksia* (Text-Fig. 64, *m*). In *D. floribunda* the flowers are slightly pedicellate while they are sessile in *D. nivea* and *D. speciosa*. In *D. floribunda* the circumference pairs of flowers show common bracts while these are suppressed from the inner series (Text-Figs. 56, 64 *o*). In *D. armata* a trace for the common bract is first given off from the stele of the flower pair (Text-Fig. 57). The broad common bract into which it enters first splits into three segments and later into six. These form an involucel which surrounds the flower pair on three sides (Text-Fig. 58). The involucel is completed by that of the adjacent flower pair (Text-Fig. 64 *n*). In *D. nivea* the flowers are solitary and the bract splits into a number of segments which completely encircle the flower (Text-Figs. 59, 64 *p*). So each inflorescence is a compound head of 1-flowered, involucelled heads. *D. speciosa* represents the culmination of the process of reduction in this line. The flowers are sessile, few in number and arrange on a flat receptacle. Bracts for the flowers are completely suppressed. One of the flowers of each pair is suppressed and the surviving flower becomes surrounded by hairs. So each inflorescence is an involucrate compound head of 1-flowered hairy heads (Text-Figs. 60, 64 *q*).

The third line of evolution, *viz.*, reduction of the inflorescence to a single flower is illustrated by the W. Australian species of *Strangea*. While the inflorescence is *S. linearis* (E. Australia) is a diffuse panicle in which the flowers are dedicellate and paired and the flower pairs show peduncles and common as well as individual bracts, the inflorescence in *S. stenocarpoides* is a peduncled umbel with only 2 or 3 flowers. The presence of one or two empty bracts on the peduncle and the origin of the flowers singly give evidence of reduction. *S. cynanchicarpa* represents the culmination of the process of reduction. There is a single sessile flower at the end of a short peduncle. Five or six empty bracts surround the base of the flower showing that the single flower is the sole survivor of a more elaborately constructed ancestral inflorescence.

Some trees of Grevilloideae like *Kermadecia* (New Caledonia), *Austromuellera* (Pl. 1, Fig. 3) and *Knightia* (New Zealand; Pl. 1, Fig. 7) show cauliflory. This condition is considered to be a primitive feature according to the Durian Theory (Corner, 1949). However, Eames (1961) is inclined to believe that it is a feature of specialisation in relation to ornithophily and seed dispersal.

Evolution of the Inflorescence in African Taxa

Out of the 16 genera of Proteaceae represented in Africa, 15 belong to the Proteoideae and one (*Brabeium**) to the Grevilloideae. Of the Proteoideae, *Dilobeia* (Madagascar) belongs to the tribe Persoonieae and the rest to the Proteeae. So the Proteeae have undergone greater diversification than in Australia where the tribe is represented only by 4 genera. Likewise, the inflorescence in the African Proteeae, while showing parallelism in evolution with the Australian section, has also undergone greater diversification and specialisation.

No African genus shows the solitary pedicellate flowers axillary to the leaves such as are found in the Australian *Persoonia*. In all genera inflorescences are organised. The inflorescence of *Dilobeia* appears to be the nearest approach to the ancestral type in this section. It is an axillary, diffusely branched, long-stalked panicle (Text-Fig. 65) resembling to some extent that in *Beauprea* (New Caledonia). Though the paniculate plan is evident, it cannot be taken to be the ancestral type because as in *Beauprea*, reduction has already occurred of the pedicels so that the branches are spikate (Text-Fig. 56). (It is significant that the most primitive type of inflorescence among the African section should occur in a member of Persoonieae. The chromosome number in *Dilobeia* may throw further light on the actual nature of the ancestral stock that entered Africa and Madagascar which seem to have been united in the remote past.) In *Aulax umbellatus* the male inflorescences occur in terminal clusters or axillary fascicles of racemes (Text-Fig. 67). Each raceme shows a number of sterile bracts below and pedicellate flowers above (Text-Fig. 68). The female inflorescences are solitary, sessile involucrate heads (Text-Fig. 69). The occurrence of branches in an umbellate cluster shows that reduction has occurred of the main axis. The empty bracts also show that reduction has occurred in the number of flowers in each raceme. Combining the two types of inflorescence found in *Dilobeia* and *Aulax* and working backwards, we can visualise the diffusely branched panicle with racemose branches containing solitary flowers axillary to the bracts as the ancestral inflorescence for the African section of Proteaceae (Text-Fig. 89 *a*).

---

* Previously when material of *Brabeium* was not available, the writer placed the genus in the tribe Persoonieae (Venkata Rao, 1960), basing his conclusions on the available descriptions. Now after examination of herbarium material he is convinced that *Brabeium* belongs to the Grevilloideae since it shows the characteristic paired flower arrangement. The elongated pseudoracemes, the regular flowers, the indehiscent fruit and above all the haploid chromosome number of 14 show that the genus is closely related to *Macadamia* and is therefore placed in the tribe Macadamieae.
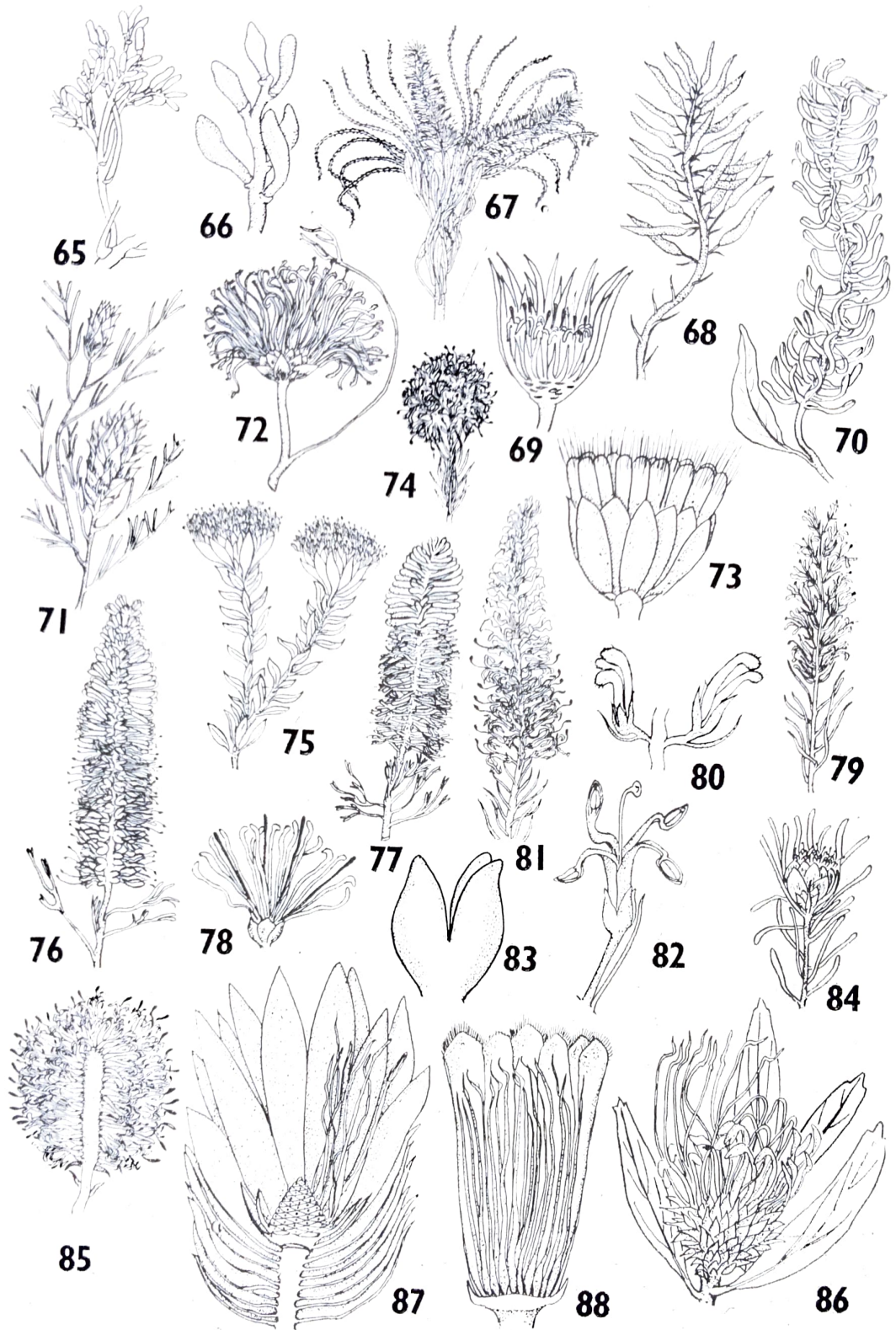
TEXT-FIGS. 65–88. Inflorescence in some African taxa. Fig. 65. Inflorescence in *Dilobeia chouarsii*, $\times \frac{1}{2}$. Fig. 66. A spike from the above, $\times 1$. Fig. 67. Male inflorescence of *Aulax umbellatus*, $\times \frac{1}{2}$; flowers are shown only for two branches. Fig. 68. A raceme from the above, $\times 1$. Fig. 69. Female inflorescence of *A. umbellatus*, $\times 1$. Fig. 70. A spike of *Faurea usambarensis*, $\times \frac{1}{2}$. Fig. 71.

A branch with inflorescence of *Serruria rostellaris*, ×1. Fig. 72. Inflorescence of *S. cygnea*, ×2. Fig. 73. A compound head of *S. brevifolia*, ×3. Fig. 74. Inflorescence of *Sorocephalus lanatus*, ×1. Fig. 75. A branch with inflorescence of *Distella serpyllifolia*, ×1. Fig. 76. Inflorescence of *Nivenia spikata*, ×1. Fig. 77. A pseudospike of *Paranomus medius*, ×1. Fig. 78. A 4-flowered head of *P. sceptrum*, ×2. Fig. 79. Inflorescence of *Spatallopsis confusa*, ×1. Fig. 80. Part of the above, ×2. Fig. 81. Inflorescence of *Spatalla cericea*, ×1. Fig. 82. A lateral head of *S. golpini*, ×½. Fig. 83. An involucre of *S. mollis*, ×4. Fig. 84. Inflorescence of *Leucadendron maimianum*, ×½. Fig. 85. L.s. inflorescence of *L. tortum*, ×3. Fig. 86. Inflorescence of *Leucospermum catheninae*, ×½. Fig. 87. L.s. inflorescence of *Protea cynaroides*, ×½. Fig. 88. L.s. inflorescence of *P. nerifolia*, ×½.

From this ancestral panicle, reduction in various lines seems to have led to the evolution of the different types of inflorescences found in the existing genera. Four lines of evolution can be traced: (1) reduction of pedicels not accompanied by reduction of the inflorescence axis or number of flowers, leading to the spikes (Text-Fig. 89 *b, c*); (2) reduction of pedicels accompanied by progressive flattening of the receptacle resulting in pseudanthia (Text-Fig. 89 *d–g*); (3) reduction of pedicels and number of flowers on the branches leading to compound pseudoracemes, pseudospikes and compound heads (Text-Fig. 89 *h–m*); and (4) the Grevilloid tendency of paired flower arrangement (Text-Fig. 89 *n, o*).

Coincident with these processes there is evolutionary specialisation of the bracts into protective and attractive organs.

As in the Australian section, pedicellate flowers are rare in the African section also and are noticed only in two genera, *viz.*, *Aulax* and *Faurea*. In some species of *Faurea* the inflorescences are racemose while in others they are spikate (Text-Figs. 70, 89 *b, c*), elongated and multi-flowered.

In the second line of evolution the relatively primitive types of inflorescence as seen in *Serruria rostellaris* (Text-Fig. 71) and *Leucadendron* sp. (Text-Figs. 84, 85) show sessile flowers arranged on an elongated axis (Text-Fig. 89 *d*). In the more evolved forms the receptacle becomes progressively shortened and the heads become surrounded by a multiseriate involucre (Text-Fig. 89 *e*). Such heads are noticed in *Sorocephalus* sp. (Text-Fig. 74), *Leucospermum* (Text-Fig. 86), *Diastella* (Text-Fig. 75), etc. Since the involucre in these inflorescences remains sepaloid and the flowers retain individual bracts (Text-Fig. 89 *h*) they are to be described as subpseudanthia. In species of *Protea* the receptacle becomes further flattened and dilated; the involucral bracts become large and petaloid and bracts for the individual flowers are completely suppressed. So the inflorescences become more compact and Compositae-like pseudanthia which sometimes attain considerable size (Text-Figs. 87, 88, 89 *f*). The most advanced level of organisation, however, is attained in *Mimetes* and *Orothamnus*. The number of flowers in an inflorescence becomes reduced (to four in some species) and the involucral bracts become more petal-like in form and texture (Text-Figs. 89 *g*, 90, 91).

B—8
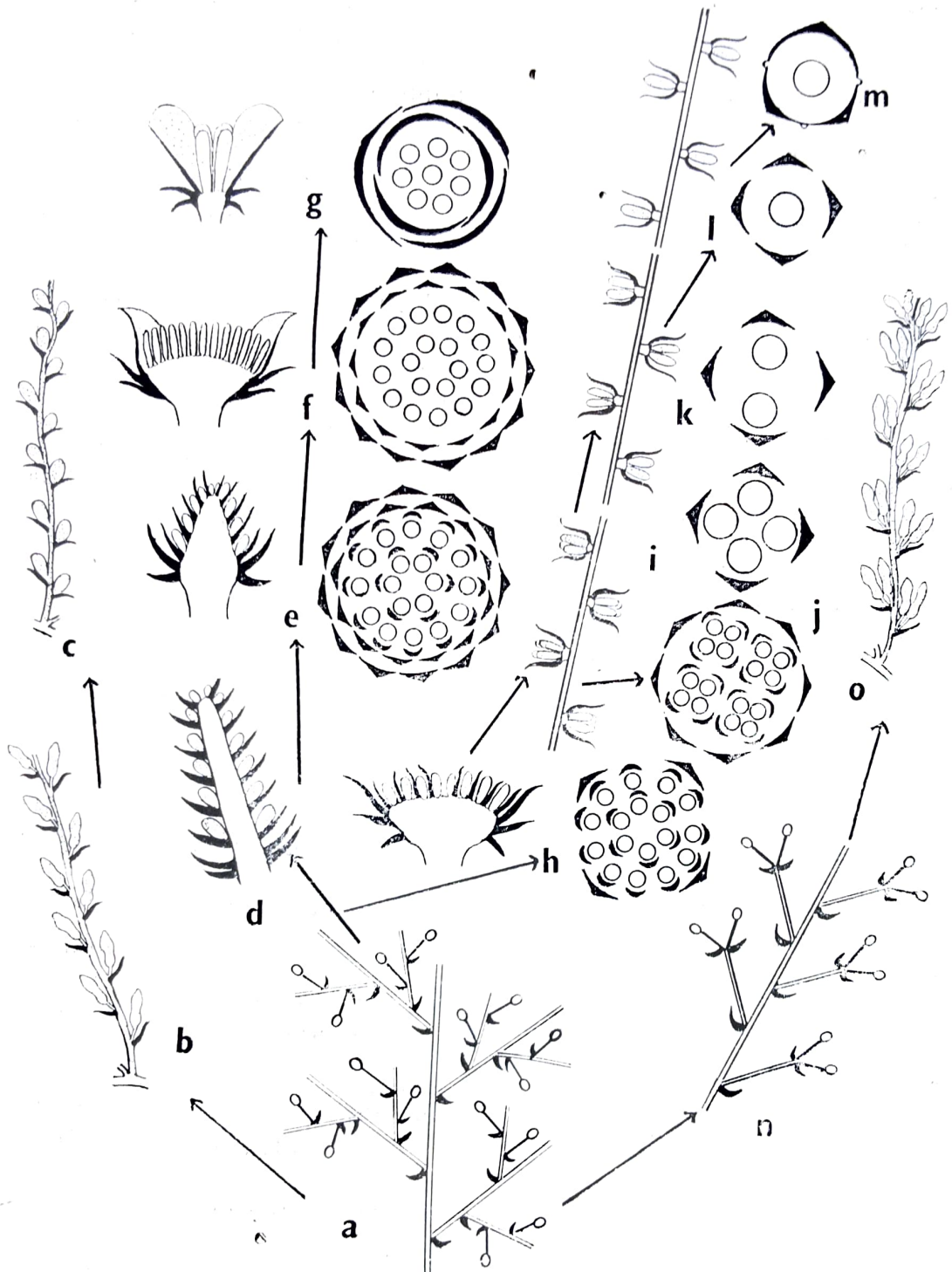
TEXT-FIG. 89. *a–o.* Diagrammatic representation of the trends of evolution in the inflorescence of African taxa. *a.* The primitive panicle; *b.* the raceme; *c.* The spike; *d–e.* Elongated condensed spike and head; *f. Protea*-type of pseudanthium; *g.* Few-flowered head with petaloid involucre (*Mimetes*); *h. Serruria*-type of head; *i.* Compound pseudoraceme of *Nivenia*; *j.* Compound head of *Serruria brevifolia*; *k. Spatallopsis*-type of pseudoraceme; *l. Spatalla*-type of pseudoraceme; *m.* 1-flowered head of *S. mollis*; *n, o.* Grevilloid pseudoracemes.

The third line of evolution is characterized by reduction in the number of flowers on the lateral branches and their aggregation with or without reduction in the main and/or lateral axes. The involucre which has evolved into a protective and attractive organ in the second line not only remains sepaloid but undergoes reduction into a uniseriate few-membered whorl. *Serruria* is a synthetic genus between the second and third lines of evolution and depicts all types of inflorescence from elongated spikes (Text-Fig. 71) to condensed, few-flowered compound heads. In *S. cygnea* (Text-Figs. 72, 89 *h*), *S. elongata*, *S. nightii* and *S. fucifolia* each head bears more than 20 flowers while in *S. adscendens* the head shows only 10 5 flowers. In *S. brevifolia* each partial head bears only 4 flowers which are surrounded by 4 involucral bracts; these are aggregated into a compound head (Text-Figs. 73, 89 *j*). In *Nivenia spicata* and *Paranomus medius* also the partial inflorescences are 4-flowered heads surrounded by 4 involucral bracts but these are placed on an elongated main axis to form a pseudospike (Text-Figs. 76 78; 89 *i*). Further stages of reduction are noticed in *Spatallopsis* and *Spatalla*. In *Spatallopsis confusa* the total inflorescence is a pseudoraceme (Text-Fig. 79). Each partial inflorescence is a peduncled head with only 3 or 2 flowers but surrounded by 4 involucral bracts which shows that reduction of the flowers has occurred (Text-Figs. 80, 89 *k*). Typical 1-flowered heads arranged in pseudoracemes are found in all species of *Spatalla* examined, *viz.*, *S. gracilis*, *S. panilis*, *S. golpini*, *S. sericea* and *S. mollis*. Each head is peduncled and arises in the axil of a bract. The flower is surrounded at the base by an involucre of 4 bracts so that it looks like a typical pedicellate, 4-merous, dichlamydeous flower (Text-Figs. 81, 82, 89 *l*). In *S. mollis* the involucre consists only of 3 segments which fuse at the base forming a 2-lipped cup (Text-Figs. 83, 89 *m*). This represents the culmination of the process of reduction in the African Proteeae. These 1-flowered involucral heads of *Spatalla* are closely similar to those of the Australian *Adenanthos* and *Strangea cynanchicarpa* except that the bracts are fewer and show tendency for connation.

In *Brabeium* the inflorescence consists of axillary fascicles of pseudoracemes (Text-Fig. 92). This condition seems to have arisen by the suppression of the main peduncle of an ancestral panicle (*cf. Aulax* of Proteoideae). In each pseudoraceme, pairs of pedicellate flowers stand in the axils of common bracts, there being no sign of the lateral axes or bracts for the individual flowers (Text-Fig. 93). So the inflorescence looks like that of *Macadamia*. The paired flower arrangement seems to have been derived along lines similar to those in the Australian section (Text-Fig. 89 *n, o*).

EVOLUTION OF THE INFLORESCENCE IN AMERICAN TAXA

All the 8 genera of the American Proteaceae belong to Grevilloideae, 4 being common with Australia. Since the paired flower arrangement is common to all genera, the diffusely branched panicle with racemose branches bearing flower pairs, can be taken as the ancestral type for
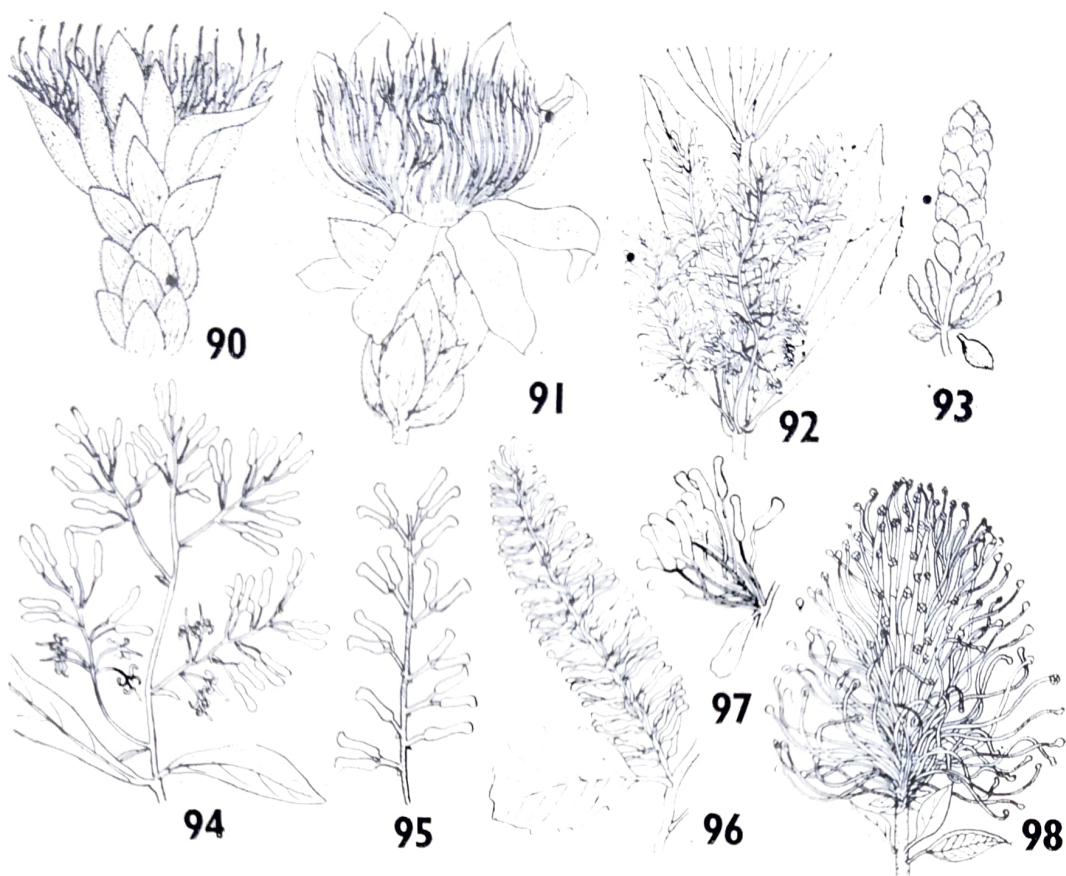
TEXT-FIGS. 90–98. Figs. 90–93. African taxa. Fig. 90. Inflorescence of *Mimetes pauciflora*, ×½. Fig. 91. Inflorescence of *Orothamnus zeyheri*, ×½. Fig. 92. A branch with inflorescence of *Brabeium stellatifolium*, ×½. Fig. 93. A pseudoraceme from the above, ×1. Figs. 94–98. Inflorescence in some American taxa. Fig. 94. Inflorescence in *Panopsis multiflora*, ×1. Fig. 95. Inflorescence of *Euplassa meissneri*, ×1. Fig. 96. Inflorescence of *Roupala impressiusculata*, ×1. Fig. 97. Inflorescence of *Lomatia dentata*, ×1. Fig. 98. Inflorescence of *Embothrium coccineum*, ×1.

the American section. Such an inflorescence is found in *Panopsis multiflora* (Text-Fig. 94) and *Lomatia hirsuta*. Reduction of all branches but one led to the uniaxial inflorescence noticed in *Gevuina*, *Euplassa* (Text-Fig. 95), *Roupala* (Text-Fig. 96), etc. While in *Gevuina* and *Euplassa* the pedicels are suppressed and the lateral axes persist, in others the lateral axes become suppressed and pedicels persist. In *Orites* both the lateral axes as well as pedicels become suppressed so that the inflorescences are pseudospikes as in the Australian species of the genus. In *Lomatia dentata* (Text-Fig. 97) since the main axes as well as the lateral axes become completey suppressed, the inflorescence is an umbellate cluster of long pedicelled flowers. Only in *Oreocallis* and *Embothrium* the main axis of the inflorescence shows some reduction which results in the development of corymbose clusters (Text-Fig. 98); an incipient involucre is noticed in *Embothrium*. No compact types of inflorescence have evolved. So the inflorescence in the American section shows very low level of organisation.

DISCUSSION

One feature which is interesting as well as significant regarding the inflorescence in the Proteaceae is that its structure is fairly constant within a genus and sometimes within a tribe. Often the structure is so characteristic that a genus can be readily identified by a look at the inflorescence: *e.g.*, the panicle of heads of *Stirlingia*, the 1-flowered heads of *Adenanthos* and *Spatalla*, the condensed cones of *Banksia*, the involucrate heads of *Dryandra* and *Protea* and the umbels of *Telopea*. In a few genera like *Grevillea* there is a slight range of variation but in others like *Banksia* it presents a stereotyped structure and it looks as though evolution has stood still from the Tertiary times. The structure of the inflorescence, therefore, seems to be a well-fixed character which offers a dependable evidence for understanding the evolutionary trends in the family.

Two main views have been expressed regarding the phylogeny and evolution of the inflorescence in the angiosperms: (1) that the solitary axillary flower is the simple ancestral type and the complex forms are derived by aggregation and condensation (Parkin, 1914) and (2) that the complex types like the panicle (Nageli, 1884; Celakovsky, 1892; Pilger, 1922) or the dichasium (Woodson, 1935; Rickett, 1944) represent the primitive ancestral condition and the simpler types are derived by reduction. However, evolution of the inflorescence in all angiospermous families may not fit into these frames and more than one process may have been operative. Intensive studies of the inflorescence in any taxon can only reveal the pattern of evolution in that particular taxon. Comparative studies have shown that in Proteaceae both processes were operative: there was an initial process of elaboration which was subsequently followed by reduction, condensation or simplification. The general remark of Eames (1961) that: " if the solitary flower is primitive there must have been extensive building up to the paniculate inflorescence followed frequently by reduction to simple clusters and solitary flowers which represent a highly specialised condition ", beautifully summarises the evolution of the inflorescence in the Proteaceae.

A general survey of the inflorescence among the angiosperms shows that reduction has played a more vital part in its evolution than elaboration. This reduction has not been sporadic and haphazard but continued and systematic and resulted in a definite pattern of structure. Often similar inflorescences evolved in distantly related or unrelated taxa. Studies in the Proteaceae have brought to light several such parallelisms not only within the family but with other angiospermous families.

One feature of reduction relates to the number of flowers in the inflorescence. In several families this led to the retention of a definite number of flowers on the main or lateral axes. Retention of more than one flower on each lateral axis is noticed in several families. The apparently simple male catkins of some Amentiferae are seen to be reduced

panicles in which the flowers are arranged in cymules (groups of three).
A similar arrangement is seen in Santalaceae in which sometimes the
number of flowers becomes reduced to two at each node. In several
palms belonging to the tribe Ceroxylinae, *e.g.*, *Howea, Cocos, Caryota*
and *Areca* the flowers are arranged in triads, the central female being
flanked by two males. Each group is interpreted as a lateral branch
system (Venkata Rao, 1959). In Proteaceae retention of two flowers
on each lateral branch has become a universal feature in the Grevilloideae
while in the African Proteeae, four flowers are retained on a branch in
species of *Serruria, Nivenia* and *Paranomus*.

Retention of one flower on the main or lateral axes is also noticed
in some families like Graminae, Amarantaceae and Compositae. In
several grasses each lateral inflorescence (spikelet) is represented by
a single fertile flower. In the Amarantaceae the apparently solitary
flower is seen to be the sole survivor of a branch system so that the spike
is in reality a reduced panicle. The parallelism between Proteaceae
and Compositae is particularly close not only in the structure of the
inflorescence but in the trends of its evolution. Several genera like
Serruria, Sorocephalus, Leucadendron, Petrophila and *Isopogon* show
Compositae-like pseudanthia with sepaloid involucres; the heads of
Protea, Mimetes, Orothamnus and *Lambertia* with petaloid involucres
resemble those of *Helichrysum* of Compositae. Reduction in the number
of flowers of an inflorescence to one is noticed in *Corymbium* of Compo-
sitae and *Strangea cynanchicarpa* and *Adenanthus* of Proteaceae.
The compound heads of *Serruria brevifolia* and *Dryandra armata* are
similar to those of *Sphaeranthus* while the compound head of *Dryandra
speciosa* with 18-flowered hairy heads is closely similar to *Echinops* of
CFmpositae.

Interesting parallelisms in the evolution of the inflorescences are
noticed within the family between: (*a*) the involucrate subpseudanthia
of the Australian *Isopogon* and *Petrophila* and the African *Serruria,
Leucospermum, Sorocephalus*, and *Diastella*; (*b*) the development of
1-flowered involucrate heads in *Adenanthos* and *Strangea cynanchicarpa*
of Australia and *Spatalla* of Africa; (*c*) the reduction in the number
of flowers to two in the partial inflorescences of Grevilloideae and to
four in the African Proteoideae; (*d*) the development of petaloid
involucres in *Protea, Orothamnus* and *Mimetes* of African Proteoideae
and *Telopea* and *Lambertia* of the Australian Grevilloideae.

The study of the inflorescence in the Proteaceae lends full support
to the conclusions regarding the origin and spread of the family derived
from other evidences. The writer (Venkata Rao, 1957) suggested that
the family probably arose in Australia. While only Grevilloideae are
represented in America, and the Proteoideae and only one genus of
Grevilloideae in Africa, in Australia, both subfamilies as well as all
the tribes (except the unigeneric S. American Embothrieae) are repre-
sented. The presence of large number of genera and species (37 genera
out of 63 and 950 species out of 1,400) and the occurrence of a number

of monotypic endemics in Australia are also significant. Cytological observations have shown that all the three diploid genera are confined to Australia and that the remaining genera of both subfamilies are polyploids or aneuploids on bases 5 and 7. Morphological studies have shown that Persoonieae are the most primitive tribe and in several features stand close to the ancestral stock (Venkata Rao, 1957, 1960). Out of the 8 genera which constitute this tribe, Australia has 5 genera, New Caledonia has three of which one (*Cenarrhenes*) is common with Australia, and Madagascar has one. Proteaceous fossils are also known with certainty from Australia; the European fossils ascribed to Proteaceae are now proving to belong to Myricaceae (Budantsev, 1959; Kotlaba, 1961). So applying all the criteria which are used for deciding the centre of origin of a taxon, *viz.*, species concentration, cytological evidence including the occurrence of diploids, occurrence of primitives (morphological), endemism, palaeontological evidence and geographical distribution, one has to conclude that Australia must have been the original home of this family, from where ancestral stocks must have migrated to S. America and Africa.

The most primitive condition of the inflorescence which is supposed to be ancestral, *viz.*, the presence of solitary flowers axillary to vegetative leaves, is found only in the Australian *Persoonia*; genera of other land masses show organisation of inflorescences. It is significant that the least reduced paniculate inflorescences are found in addition to the genera of Australian Persoonieae, in *Beauprea* of New Caledonia and *Dilobeia* of Madagascar. This shows that the ancestral stock of Proteaceae entered these land masses at a very early period of diversification. The fact that there is one genus of Grevilloideae in Africa also (which itself belongs to a relatively primitive tribe, the Macadamieae) shows that by this time diversification occurred to the level of the subfamilies. No genera of Proteaceae are, however, common between Australia and Africa. The presence of 16 genera in Africa shows that speciation has been independent and vigorous, especially in the tribe Proteeae which has a larger number of genera and species here than in the mother country. Africa was, therefore, a secondary centre of evolution for the family; since probably the conditions were congenial, diversification of one particular taxon occurred to a greater extent. The situation is closely similar to what obtains in the Asclepiadaceae. The distribution of the primitives of this family (*cf. Frerea* in India) shows that the family is extra-African in origin (Good, 1953). But Africa was a secondary centre of diversification in which the tribe Stapelieae is particularly well developed.

America seems to have received its stock after diversification occurred not only into the two subfamilies but to the generic level. Four of the American genera are common with Australia, but since the American group was geographically and genetically isolated, independent speciation occurred so that no species are common. Diversification of the American stock led to the evolution of four more genera. *viz.. Roupala, Panopsis, Euplassa* and *Embothrium,*

Observation of the inflorescences in the genera common between America and Australia shows that they are similar in the two groups of species, *cf.* the spikes of *Orites*, the corymbs of *Oreocallis*, the diffuse panicles of *Lomatia* sp. and the pseudoracemes with persistent lateral axes of *Gevuina*. This shows that the characteristics of the inflorescence already became well established in the genera by the time the ancestral stock reached America. The presence of pseudoracemes in the remaining genera, *viz.*, *Roupala*, *Panopsis* and *Euplassa* shows that the ancestral stock was akin to the Macadamieae which is regarded as a primitive tribe among the Grevilloideae. The inflorescence in *Embothrium* is similar to that in *Oreocallis* and the genus seems to have diverged early from an ancestral stock with regard to its pollen grains.

SUMMARY

A survey of the inflorescences in all the 63 genera of the Proteaceae has been made and the evolutionary trends are discussed. From comparative studies (supported by cytological evidence) the solitary flowers scattered sparsely in leaf axils are taken to represent the ancestral condition. An initial phase of aggregation is supposed to have led to the evolution of the raceme and panicle. The panicle is believed to be the basic type from which evolution by reduction and condensation or simplification led to the different types of inflorescence found in both Proteoideae and Grevilloideae.

The evidence of evolutionary trends in the inflorescence is examined in conjunction with other evidences in matter of the probable origin and spread of the family.

REFERENCES

ANDREWS, E. C. 1916. The geological history of the Australian flowering plants. *Amer. J. Sci. IV Ser.* **42**: 171–232.

BUDANTSEV, L. J. 1959. Oligotsenovaia flora severnogo Priaral'ia. *Probl. Bot,* **4**: 190–252. (quoted from Johnson and Briggs, 1963),

CELAKOVSKY, L. F. 1892. Gedanken über eine zeitgemässe Reform der Theorie der Blutenstande. *Engler's Bot. Jb.* **16**: 33–51.

CORNER, E. J. H. 1949. The Durian Theory. *Ann. Bot., Lond. N.S.* **13**: 367–414.

EAMES, A. J. 1931. *Morphology of the Angiosperms.* McGraw-Hill, N.Y.

ENGLER, A. AND PRANTL, K. 1894. *Die natürlichen Pflanzenfamilien,* Tiel 3, Leipzig.

GOOD, R. 1953. *The Geography of Flowering Plants.* Longmans, London.

————. 1956. *Features of Evolution in Flowering Plants,* Longmans, London.

HABER, J. M. 1959. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. I. Some Australian taxa. *Phytomorphology* **9**: 325–58.

JOHNSON, L. A. S. AND BRIGGS, B. G. 1963. Evolution in the Proteaceae. *Aust. J. Bot.* **11**: 21–61.

KOTLABA, F. 1961. Taxonomicko-nemenklaToricke poznamky k fosilni *Comptonia difformis* (Sternb.) Berry a recentni *Comptonia asplenifolia* (L) Aiton. *Preslia* **33**: 130–40.

LAWRENCE, G. M. L. 1955. *Taxonomy of Flowering Plants,* N.Y.

NAGELI, C. W. VON. 1884. *Mechanisch-physiologische Theorie der Blute Abstammungslehre.* München.

PARKIN, J. 1914. The evolution of the inflorescence. *J. Linn. Soc. (Bot.)* **42**: 511–63.

PILGER, R. K. F. 1922. Über Verzweigung und Bluthenstandsbildung bei den Holzgewachsen. *Bibl. bot. Stuttgart* **23**: 1–38. (quoted from Haber, 1959).

RAMSAY, H. P. 1963. Chromosome numbers in the Proteaceae. *Aust. J. Bot.* **11**: 1–20.

RENDLE, A. B. 1952. *Classification of Flowering Plants* **2**: Dicotyledons. London.

RICKETT, H. W. 1944. The classification of inflorescences. *Bot. Rev.* **10**: 187–231.

SWAMY, B. G. L. AND BAILEY, I. W. 1949. The morphology and relationships of *Cercidiphyllum. J. Arnold Arbor.* **30**: 187–210.

VENKATA RAO, C. 1957. Cytotaxonomy of the Proteaceae. *Proc. Linn. Soc. N.S.W.* **82**: 257–71.

————. 1959. Contributions to the embryology of Palmae. II. Ceroxylinae *J. Indian bot. Soc.* **38**: 46–75.

————, C. 1960. Studies in the Proteaceae. I. Tribe Persoonieae. *Proc. nat. Inst. Sci. India* **26B**: 300–37.

————. 1961. Studies in the Proteaceae. II. Tribes Placospermeae and Conspermeae. *Ibid.* **27 B**: 126–51.

————. 1964. Studies in the Proteaceae. IV. Tribes Banksieae, Musgraveae and Embothrieae. *Ibid.* **30 B**: 197–244.

WHITE, C. T. AND FRANCIS, W. D. 1923. A new genus of Proteaceae from N. Queensland. *Proc. R. Soc. Qd.* **35**: 79–81.

WOODSON, R. E. JR. 1935. Observations on the inflorescence of the Apocynaceae. *Ann. Mo. bot. Gdn* **22**: 1–48.

Explanation of Plate I

Figs. 1–13

FIG. 1. A branch of *Persoonia saccata* with flowers (W. Australia).

FIG. 2. A branch of *Persoonia pinifolia* with inflorescence (N.S.W.).

FIG. 3. A branch of *Austromuellera trinervia* with inflorescences (N. Queensland).

FIG. 4. An inflorescence of *Petrophila linearis* (W. Australia).

FIG. 5. An inflorescence of *Telopea truncata* (Tasmania), a yellow mutant.

FIG. 6. A branch of *Darlingia speciosissima* (N. Queensland).

FIG. 7. A branch with inflorescences of *Knightia excelsa* (New Zealand).

FIG. 8. An inflorescence of *Stenocarpus umbellatus* (N.S.W.).

FIG. 9. A branch of *Placospermum coriaceum* with inflorescences (N. Queensland).

FIG. 10. A branch of *Xylomelum pyreforme* (W. Australia).

FIG. 11. A branch of *Agastachys odorata* (Tasmania).

FIG. 12. A branch of *Carnarvonia aralaefolia* with flowers (N. Queensland).

FIG. 13. A branch of *Macadamia ternifolia* (E. Australia).