STUDIES IN THE PROTEACEAE

IX. Australian Proteeae

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The morphology, floral anatomy and embryology of four genera and about 25 species of Australian Proteeae are described. The affinities of the genera and their evolutionary status within the tribe are discussed. The probable polyphyletic origin of this tribe from Persoonieae-like ancestors is suggested.

Introduction

The Proteeae comprise 17 genera of which 4 occur in Australia and 13 in S. Africa. *Stirlingia* is endemic to West Australia, whereas the other genera are distributed in the manner shown in Table I.

Table I

Genus	Number of species		
	W. Australia	E. Australia	Tasmania
Adenanthos ..	18	1	–
Petrophila ..	36	5	–
Isopogon ..	26	6	1

Previous Work

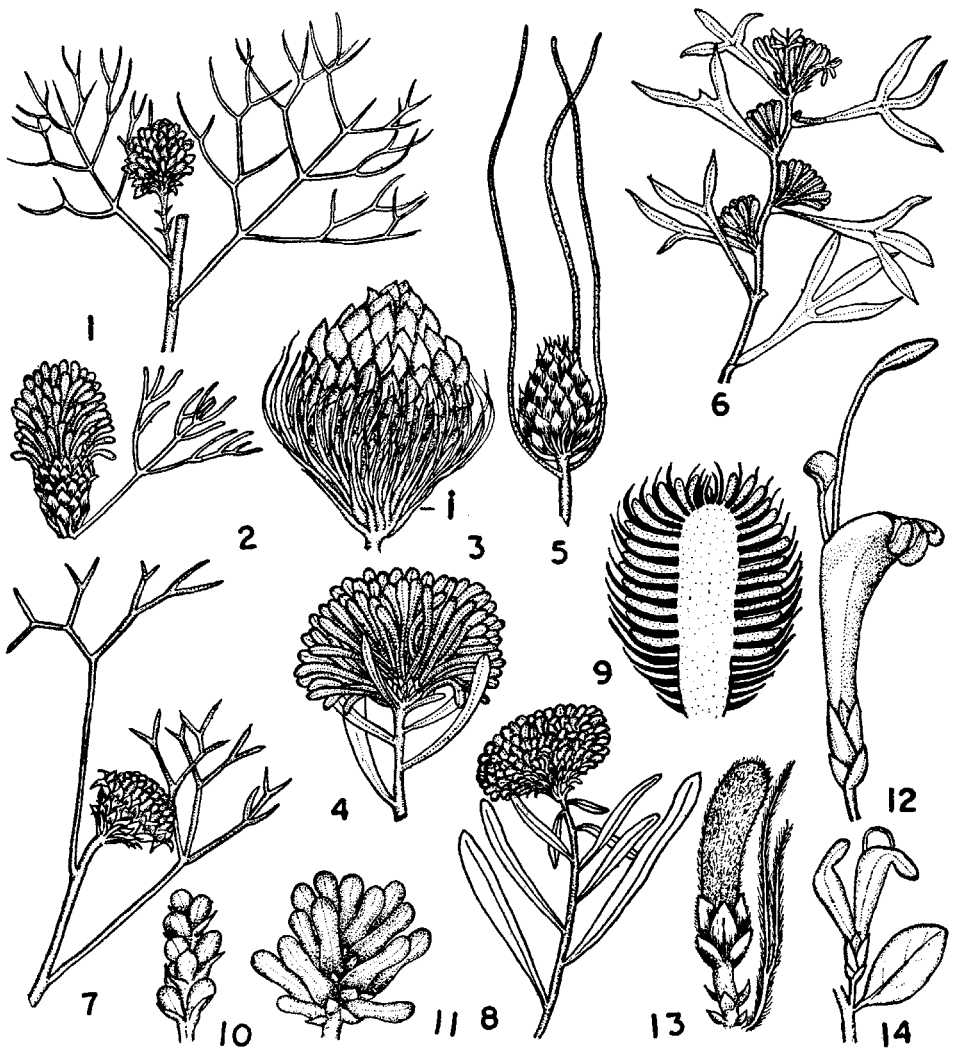
Haber (1959) studied the floral anatomy of four species, one of each Australian genus. Jordaan (1946) described the embryology of a few species of the African *Leucadendron* and *Leucospermum*. Venkata Rao (1957) studied the morphology, floral anatomy and embryology of several species of the Australian as well as African Proteeae.

Materials and Methods

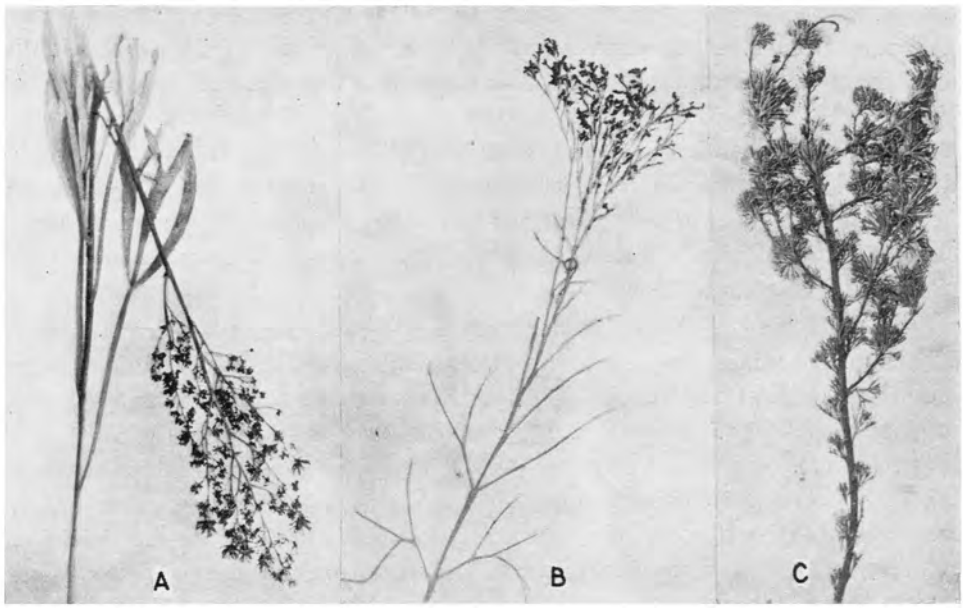
The material for the present study was collected by me from Australia and additional material was obtained from other sources. Formalin-acetic-alcohol was used as the fixative. Customary methods of dehydration and embedding were followed and sections were cut from 6 μ to 10 μ in thickness. The slides were stained in Delafield's haematoxylin.

Observations

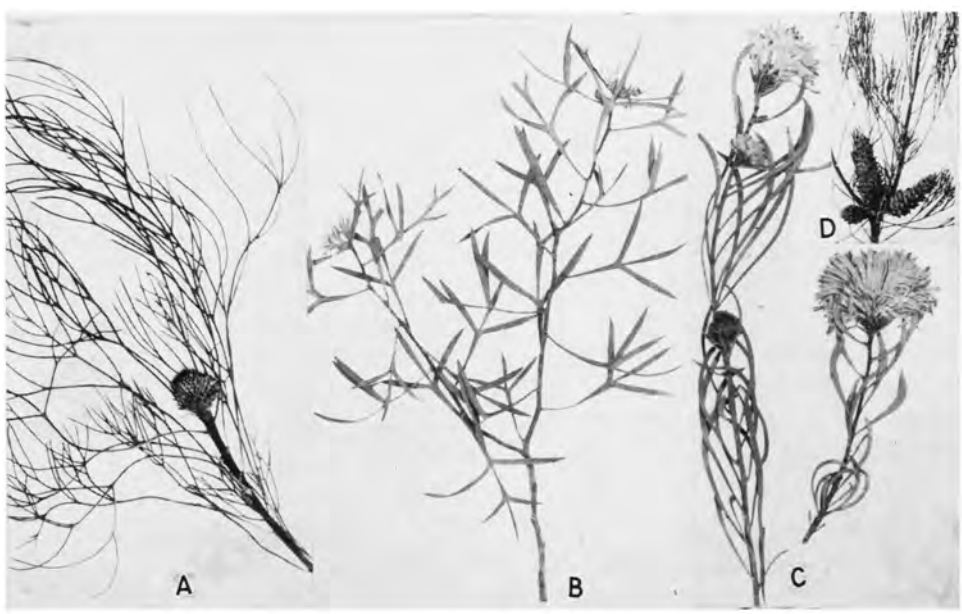
All the Australian Proteeae are distributed in temperate regions. The leaves show xeromorphic features and vary from bicompound to simple types even within genera. Bicompound leaves are noticed in *Petrophila pedunculcata*, *P. fucifolia* and *Isopogon teretifolia* (Figs. 1, 2, 7); the leaves are compound in *P. pulchella* and *I. anethifolius* (Plate XVIII A), lobed in *P. propinqua*



Figs. 1–14. Branches of some Australian Proteeae with inflorescences. 1, *Petrophila pedunculata*. ×½. 2, *P. fucifolia*. ×½. 3 and 4, young and older inflorescences of *P. linearis*. ×1; *i*—involucre of bracts. 5, *P. longifolia*. ×½. 6, *P. propinqua*. ×½. 7, *Isopogon teretifolia*. ×½. 8, *I. sphaerocephalus*. ×½. 9, L.S. inflorescence of *I. anethifolius*. ×2. 10, a spike of *Stirlingia tenuifolia*. ×3. 11, a spike of *S. latifolia*. ×2. 12, *Adenanthos barbigera*. ×3. 13, *A. sericea*. ×3. 14, *A. obovata*. ×2.



A—Branch with inflorescence of *Stirlingia latifolia* Steud.
B—Branch with inflorescence of *Stirlingia tenuifolia* Endl.
C—Branch with inflorescences of *Adenanthos meissneri* Lehm.



A—Branch with inflorescence of *Isopogon anethifolius* Knight.
B—Branch with inflorescences of *Petrophila propinqua* Br. var. *sericifolia*.
C—Branches, inflorescences and developing fruits of *Petrophila linearis* Br.
D—Branch with fruits of *Petrophila pulchella* Br.

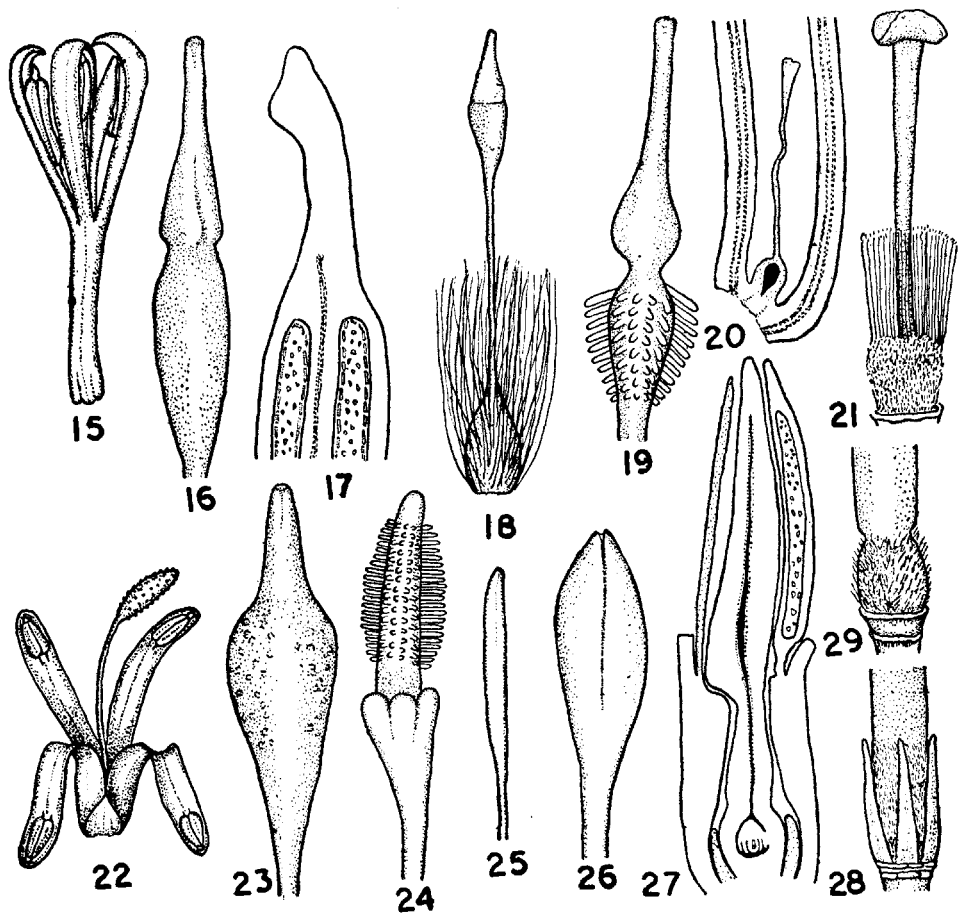
and *I. anemonifolius* (Fig. 6; Plate XVIII B) and simple in *P. longifolia*, *P. linearis* and *I. sphaerocephalus* (Figs. 4, 8; Plate XVIII C). Both simple and compound leaves occur in *Stirlingia* and *Adenanthos* (Figs. 13, 14; Plate XVII A–C).

In most members the leaves are isobilateral. In *I. buxifolius* well-developed spongy parenchyma is present. In the centric type of leaf, found in several species, 2 or 3 layers of palisade cells surround the angular parenchyma. Idioblasts are found in the mesophyll, which may be columnar (*Petrophila*) or stellate (*Isopogon*).

In *Stirlingia latifolia* the inflorescence is long, terminal, diffusely branched, with numerous inconspicuous flowers. In *S. tenuifolia* it is similar though smaller (Plate XVII A, B). Each ultimate branch is an elongated (*S. tenuifolia*) or globose spike (*S. latifolia*, *S. simplex*, *S. abratonoides*) with 15–50 flowers (Figs. 10, 11). Of these flowers some are hermaphrodite and others are male (Fig. 20). The axis of each spike terminates in a sterile apex with empty bracts or abortive flower buds. In *Petrophila* and *Isopogon* the inflorescences are simple and vary from large terminal, dense elongated or globose spikes to few-flowered, axillary, Compositae-like clusters (Figs. 1–8). Often the inflorescence axis is massive and terminates in a sterile apex (Fig. 9). The inflorescence is subtended by a multiseriate involucre of sepaloid bracts and bud scales (Figs. 3, 4). Since petaloid bracts are not noticed in any of the Australian Proteeae, the inflorescences stand at the level of sub-pseudanthia unlike in some African members. In *Adenanthos* a single flower stands at the end of a short lateral branch. The presence of empty bracts at the base of the stalk (peduncle) shows that some lateral axes have been suppressed (Fig. 13). The flower itself is either sessile (*A. cygnorum*) or nearly so (*A. barbigera*); its base is surrounded by 6–8 decussating or imbricating bracts (Fig. 12). That the flower is the sole survivor of a more elaborately constructed inflorescence is evident from the occasional development of an extra flower within the involucre (Fig. 14).

The floral organs arise in acropetal succession (Figs. 99, 100) as was also noticed in other members studied (Venkata Rao 1960, 1961). The flowers in all genera are bracteate, sessile, 4-merous and hermaphrodite. While in three genera the flowers are typically regular and remain straight till they open, in *Adenanthos* the style grows rapidly and curves through a slit in the perianth as a result of which the tip of the flower bud becomes reflexed (Fig. 14). In all genera the tepals are antero-posterior. They are sepaloid in *Stirlingia* and petaloid in other genera. In *Stirlingia* they are free to the base and somewhat persistent. In some species of *Petrophila* (*P. pulchella*, *P. fucifolia*) the tepals are free to the base while in other species like *P. linearis* and *P. rosea* and in *Isopogon* and *Adenanthos* they fuse to form a tube of variable length (Figs. 15, 22).

There are four antetepalous, epiphyllous stamens which show produced connectives in all genera except *Stirlingia* (Fig. 41). Where present, the connectives show precocious growth (Fig. 17). The anthers may be sessile or provided with short free part of filaments. In all species of *Isopogon* and in *P. rosea*, the anther is fused throughout its length with the tepal midrib. In species of *Adenanthos* belonging to *Stenolaema* section all the stamens of a flower are fertile; in species of *Eurylaema* section (e.g. *A. barbigera*) the anterior stamen is reduced to a filiform staminode (as in some species of the



FIGS. 15–29. Floral structure in Australian Proteeae. 15, 16, *Isopogon anethifolius*. 15, a flower. ×8. 16, style-end. ×10. 17, a young stamen of *Adenanthos barbigera* showing precociously developed staminal appendage. ×40. 18, pistil of *Isopogon trilobus*. ×10. 19, style-end of *I. sphaerocephalus*. ×10. 20, L.S. base of male flower of *Stirlingia latifolia*. ×25. 21, pistil of hermaphrodite flower of *S. latifolia*. ×10. 22, flower of *Petrophila pulchella*. ×10. 23, style-end of *P. biloba*. ×10. 24, style-end of *P. linearis*. ×10. 25, 26, style-ends of *Adenanthos cygnorum* and *A. barbigera* respectively. ×10. 27, L.S. flower bud of *A. barbigera*. ×15. 28, 29, *A. obovata*. 28, pistil and nectary. ×5. 29, pistil. ×5.

African genus *Protea*), making the flower structurally zygomorphic (Figs. 27, 86, 94, 97). Occasionally, one of the stamens in *Isopogon anethifolius* is noticed to be completely sterile (Fig. 70). In *Adenanthos* the flowers show four alternitepalous, somewhat prominent lobes for the nectary (Fig. 28). In other genera the flowers are glandless.

In all genera the ovary is sessile and studded with multicellular hairs (Figs. 18, 21, 29). These are deciduous in *Adenanthos* (Fig. 39) and persistent in other genera in which they function as coma. The style is terminal, somewhat massive in *Stirlingia* and *Adenanthos* and filiform in other genera (Figs. 22, 29). The stigma is large, peltate and discoid in *Stirlingia*, with the whole of its upper surface lined by 1-celled glandular hairs (Figs. 21, 41). In *Petrophila* and *Isopogon* it is punctiform and provided with short, 1-celled glandular hairs. In *I. anethifolius* there are no stigmatic hairs; the tip of the style shows a narrow canal which is lined by glandular cells (Fig. 16). Two types of stigma are noticed in *Adenanthos*: in section *Stenolaema* it is filiform while in *Eurylaema* it is club-shaped; in both types the stigma is seen as a furrow on one side (Figs. 25, 26, 86, 95). In *Petrophila* and *Isopogon* the 'style-end' is fusiform; it is either glabrous or studded with papillate or elongated hairs which seem to function like the 'pollen collecting apparatus' of some Grevilleoideae in holding the pollen grains which are shed from the markedly protandrous anthers (Figs. 19, 23, 24). The carpel is uniovulate in all genera. Occasionally carpels with two ovules are noticed in species of *Stirlingia* and *Isopogon* (Figs. 57, 78). The floral structure in the four genera is brought out in Fig. 30.

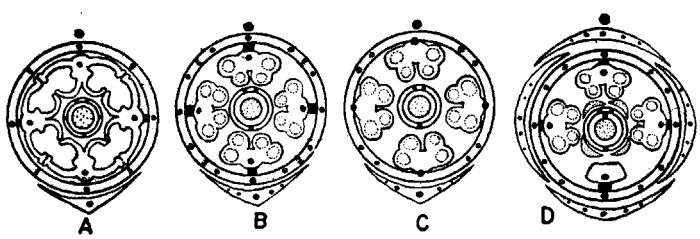


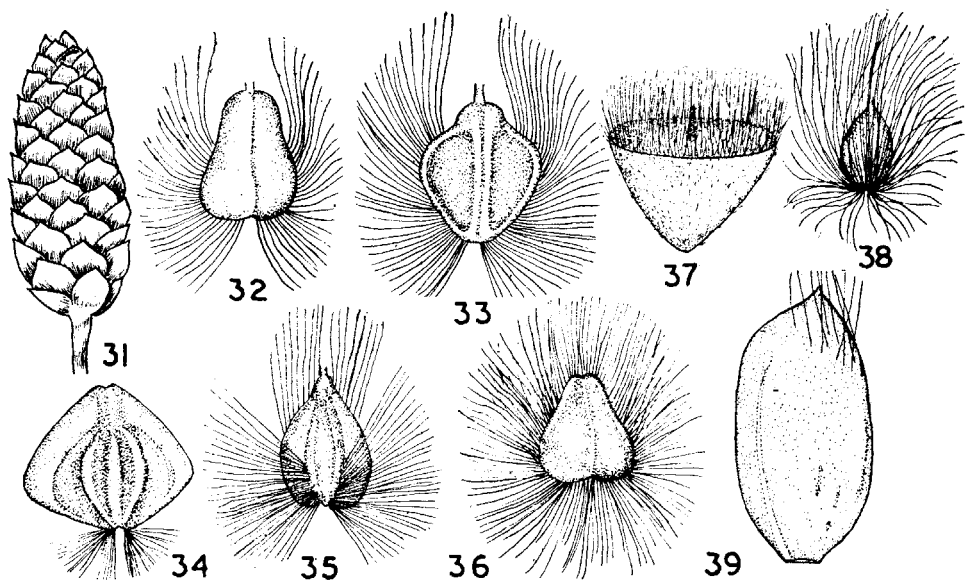
FIG. 30. Floral anatomical diagrams of Australian Proteeae: (A) *Stirlingia*; (B) *Petrophila*; (C) *Isopogon*; (D) *Adenanthos*.

Unlike in other genera, in *Petrophila* the bracts are accrescent; they give a pine-cone-like appearance to the infructescence (Fig. 31; Plate XVIII D). This provides an important feature of distinction from the allied genus *Isopogon* in which they are deciduous. The individual fruits in *Petrophila* are somewhat flat and ridged with the hairs showing localized distribution (Figs. 32–36). On the other hand, in *Isopogon* the fruits are ovoid and hairy all over (Fig. 38). The obconical, comose fruits of *Stirlingia* closely resemble the cypselas of Compositae (Fig. 37). The seeds in all genera are non-endospermic.

Floral Anatomy

From the ring of vascular bundles at the base of the flower, a single trace departs for the scaly bract in *Stirlingia* (Figs. 42, 46). In other genera in which the bracts are relatively large and sheathing, three or more traces arise from separate gaps in the floral stele and may show further branching (Figs. 61, 81). In *I. anethifolius* the bract receives a strand of sclerenchyma from the peduncle along with its vascular supply.

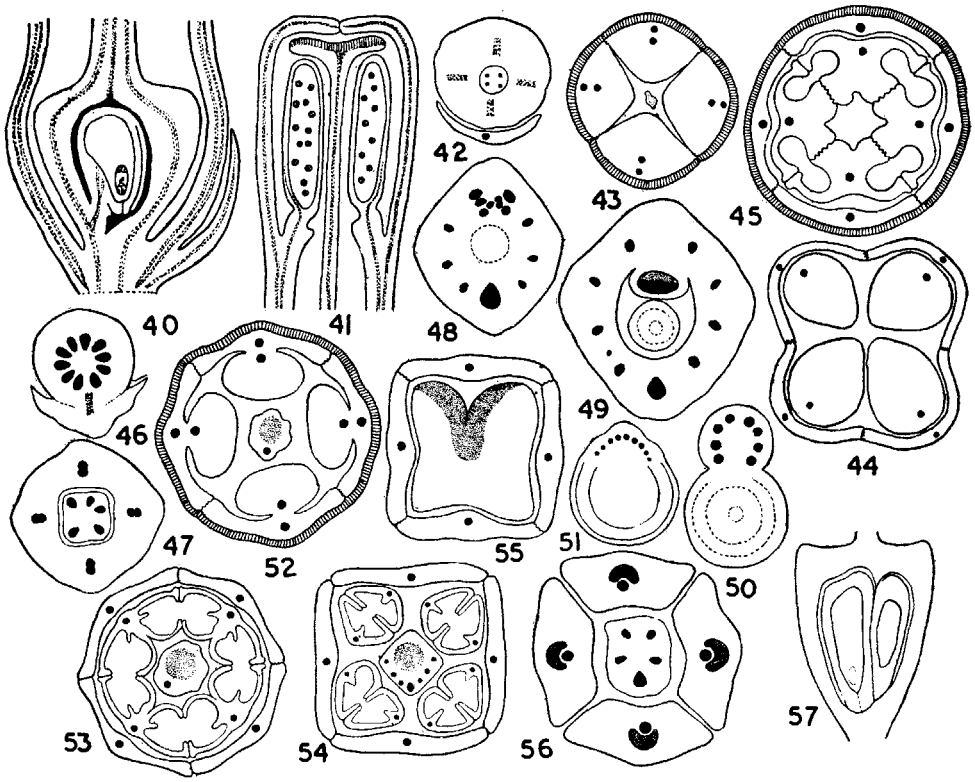
The flowers of *Stirlingia* are anatomically the simplest in the tribe. After the emergence of bract supply, four traces depart along the antero-posterior



FIGS. 31–39. Fruits in some Australian Proteeae. 31, 32, infructescence (×1) and fruit (×5) of *Petrophila peduncularis*. 33, *P. biternata*. 34, *P. heterophylla*. 35, *P. pulchella*. 36, *P. longifolia*. 37, *Stirlingia latifolia*. 38, *Isopogon anethifolius*. 39, *Adenanthos cygnorum*. 38, ×3; rest, ×5.

and lateral radii (Fig. 42). These represent the tepal midrib-cum-stamen cords; they divide tangentially close to their origin demarcating the tepal midrib to the outside and the staminal bundle to the inside (Figs. 43, 47). In *S. abrotanoides* the traces are accompanied by strands of sclerenchyma and division occurs at a relatively higher level (Fig. 56). Since the tepal midribs do not branch in *Stirlingia*, the tepals remain 1-bundled as was also noticed in *Symphyonema*, *Agastachys* and *Cenarrhenes* (Venkata Rao 1960). In *Petrophila* and *Isopogon*, 12 traces depart from the floral stele, three in each tepal sector. The median bundle of each group represents the tepal midrib-stamen trace while the lateral ones are the tepal marginals (Figs. 59, 71, 73). So the tepals in these genera are 3-traced as in most Proteaceae. In *Adenanthos*

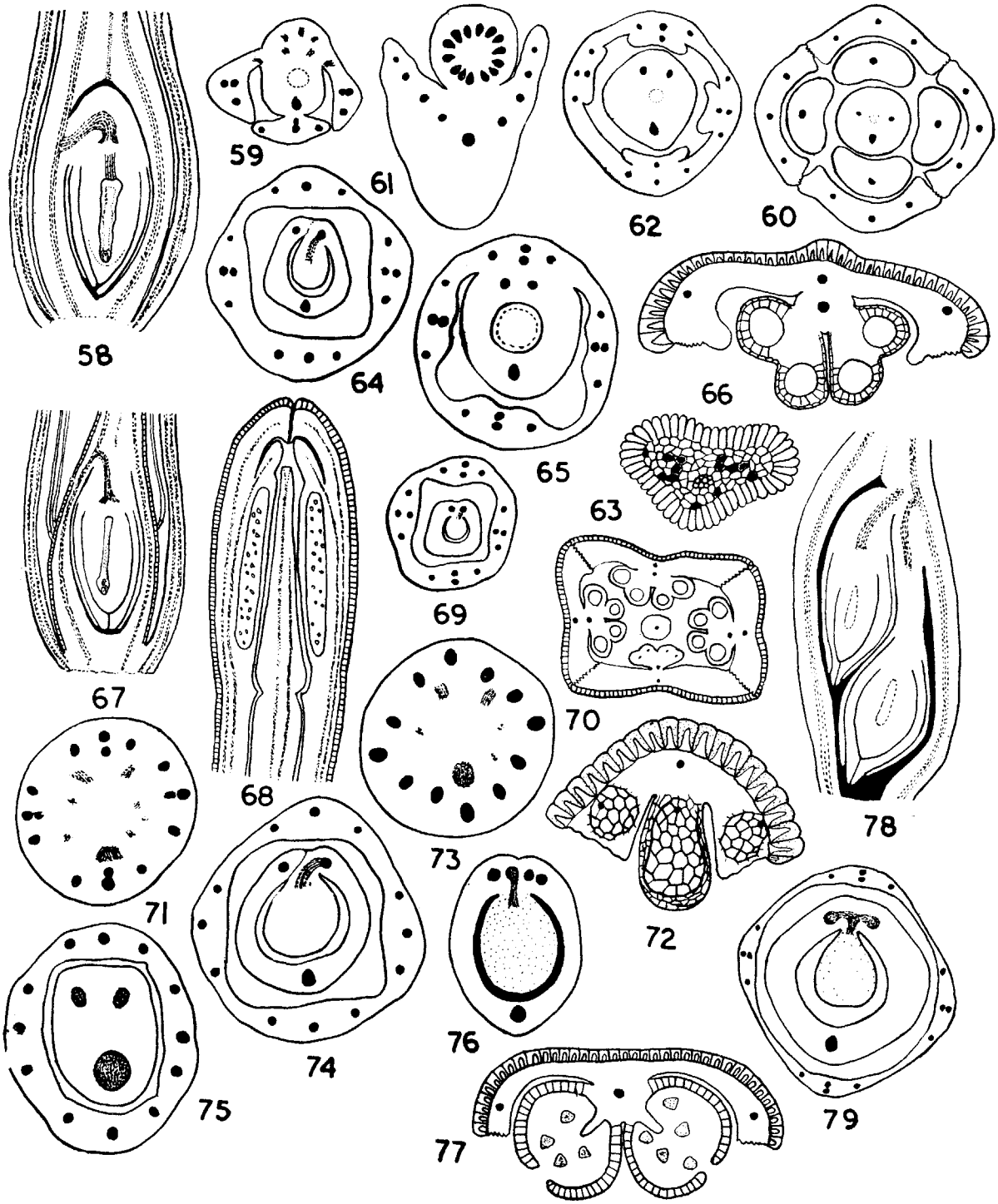
only eight traces arise, of which the four diagonal ones are the conjoint laterals and the alternate four the tepal midrib-stamen traces. These split close to



FIGS. 40–57. Floral anatomy of *Stirlingia* sp. 40–55, *S. latifolia*. 40, 41, L.S. base (×15) and top (×12) of flower bud. 42–45, floral anatomy of male flower. ×20. Explanation in text. 46–55, floral anatomy of hermaphrodite flower. 46, 47, T.S. base of flower bud. ×20. 48–49, T.S. ovary. ×30. 50–51, T.S. ovule. ×35. 52–55, T.S. bud at various heights. ×20. 56, T.S. hermaphrodite flower bud of *S. Abratonoides*. ×30. 57, L.S. 2-ovuled carpel of *S. simplex*. ×20.

their origin and demarcate the respective traces (Figs. 82, 83, 91). The connation of tepal marginals which is noticed in all the five species of *Adenanthos*

FIGS. 58–79. Floral anatomy of some Australian Proteeae. 58–66, floral anatomy of *Petrophila* sp. 58–60, *P. fucifolia*. 58, L.S. base of bud. ×25. 59, T.S. base of bud. ×25. 60, T.S. bud at level of filaments. ×20. 61–63, *P. seminuda*. 61, T.S. bud with bract. ×15. 62, T.S. base of bud. ×30. 63, T.S. filament. ×35. 64, T.S. bud of *P. biloba*. ×50. 65, T.S. bud of *P. linearis*. ×10. 66, T.S. tepal and stamen of *P. rosea*. ×50. 67–79, *Isopogon* sp. 67–70, *I. anethifolis*. 67, L.S. base of bud. ×20. 68, L.S. top of bud. ×30. 69, T.S. base of bud. ×30. 70, T.S. top of bud showing one sterile stamen. ×25. 71–72, *I. trilobus*. 71, T.S. base of bud. ×50. 72, T.S. tepal and attached staminal appendage. ×50. 73, 74, T.S. bud of *I. sphaerocephalus* at different heights. ×50. 75–78, *I. buxifolius*. 75, T.S. base of bud. ×50. 76, T.S. ovary showing origin of ovular supply. ×50. 77, T.S. tepal and stamen. ×50. 78, L.S. abnormal ovary with two ovules. ×55. 79, T.S. bud of *I. asper* showing origin of ovular supply. ×35.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studied (not described by Haber 1959) shows that this genus is more advanced than the other three genera. In *Stirlingia*, *Petrophila* and *Isopogon* the outer epidermis of tepals consists of radially elongated, sometimes thick-walled cells (Figs. 43, 45, 52, 68, 70, 77). The vascular bundles of tepals usually become associated with sclerenchyma towards the top (Fig. 72). In *Adenanthos* all the tepal tissue towards the top becomes sclerified (Fig. 94).

In most species the tepal midrib-stamen traces divide tangentially close to their origin so that the tepal and stamen show only congenital concrescence as in most Proteaceae (Figs. 47, 59, 69, 71, 87, 88, 96). In a few flowers of *Petrophila biloba* the common traces of the anterior and posterior sides are seen to remain undivided till about half the height of the perianth (Fig. 64). The staminal bundle may terminate in the connective or extend into the appendage (Figs. 17, 72). In *Isopogon* some variation is noticed in the extent of adnation between tepal and stamen. In *I. anethifolius* the whole of the anther is fused with the tepal midrib as in other species of the genus but the appendage remains free (Fig. 68); in other species even this part is adnate. In *I. anethifolius* and *I. asper*, though the anther is fused, the tepal midrib and staminal trace remain separate from the base (Figs. 65, 66, 70). This recalls the condition noticed in *Hakea laurina* and *H. victoriae* (Venkata Rao 1966). In *I. sphaerocephalus* and *I. buxifolis*, on the other hand, the common trace extends without dividing even into the produced connective. This marks the culmination of adnation between the tepal and stamen noticed in the family, which involves the organs as well as their traces, the like of which is not noticed elsewhere. In *Orites* the tepal midrib and stamen show complete adnation. However, the anther is free and the common trace characteristically enters the filament making the lamina above midribless (Venkata Rao 1963).

In *Stirlingia* the stamens show massive filaments which converge around the style and interlock by marginal papillae (Figs. 44, 45, 52); the cells of filaments show abundance of starch. Towards the top both the anther as well as the staminal bundle split completely into two parts (Figs. 53, 54). In *Adenanthos*, some species like *A. cygnorum* show massive interlocking filaments (Fig. 90) while in others like *A. barbigera* the anthers are nearly sessile. In some species of *Petrophila* the filaments are slender and lined by radially elongated cells, while in others they are massive and their outline can be followed for some distance downwards (Figs. 60, 62, 63). In *Isopogon* the filament is completely incorporated into the tepal tissue (Figs. 74, 75, 79).

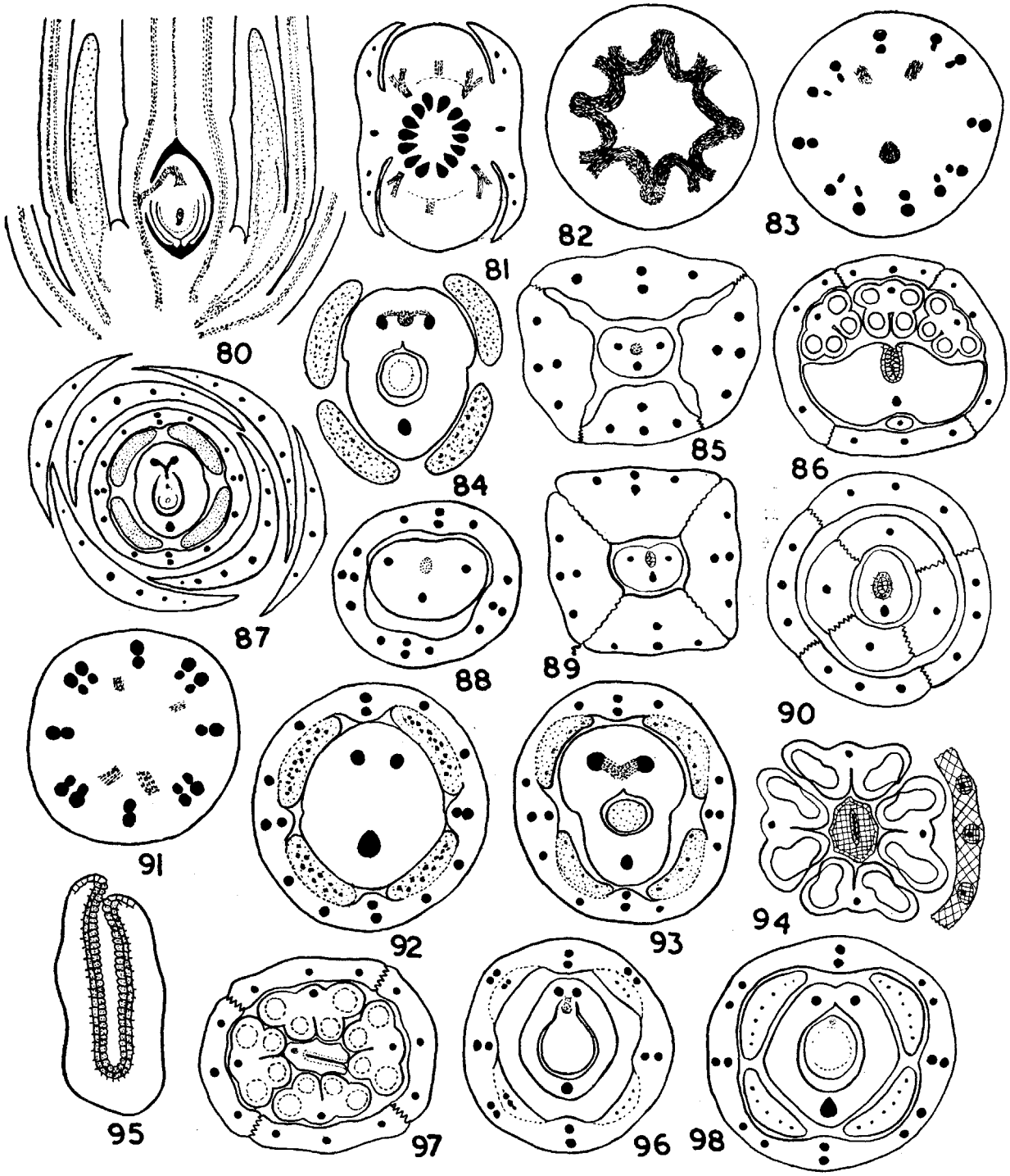
The nectary, which is noticed only in *Adenanthos*, is vascularized by strands derived from the tepal laterals. Soon after their demarcation each lateral gives off one strand towards the inside (Figs. 83, 91). The two strands derived from adjacent marginals enter one lobe of the nectary. They branch and form a row of bundles (Figs. 93, 96, 98) which fork higher up. The strands

thus derived form a row to the inside of each margin of the lobe (Figs. 84, 92). The strands fade out at about half the height of the lobes (Fig. 80). Each strand consists of thick-walled xylem-like cells but without any phloem. The rest of the gland consists of thin-walled richly cytoplasmic cells.

In *Stirlingia* the vascular bundles found at the base of the male flower are practically consumed in the formation of the tepal-stamen traces. The few vestigial strands that remain fade out at the base of the pistillode (Fig. 43). In the hermaphrodite flowers, several bundles remain over; these fuse suitably and form the five carpellary traces which branch further in the ovary wall (Figs. 47–49, 56). All bundles except the dorsal trace fade out towards the top of the ovary. The dorsal bundle, after traversing the style, divides and forms an arc of strands below the stigmatic disc (Figs. 52–54). In all species of *Stirlingia* studied, the sutures of the ovary stand antero-posterior (Fig. 56) but in some flowers of *S. latifolia* the ovary undergoes a torsion so that the sutures become diagonal (Fig. 47). A similar condition was noticed occasionally in *Cenarrhenes* (Venkata Rao 1960) but was characteristic of several species of *Orites* (Venkata Rao 1963).

In all the remaining genera the ovary is 3-traced as in *Bellendena* (Venkata Rao 1960) and the ovarian bundles do not branch. Though all bundles may enter the base of the style, only the dorsal bundle extends nearly to the stigmatic region (Figs. 60, 70, 75, 85, 86, 88–90). The style in all genera shows a core of elongated glandular cells of transmitting tissue which extends to the stigmatic region (Figs. 40, 41, 54, 55, 58, 67). In *Adenanthos* sp. the stylar tissue becomes sclerified towards the top (Fig. 94).

The vasculature of the ovule shows some variation in different genera. In some species of *Petrophila*, *Isopogon* and *Adenanthos*, the ovular trace arises from one ventral carpellary bundle. At this level, the margins of the ovary may fuse incompletely and even the epidermal layers may remain distinct (Figs. 64, 74). In *I. buxifolius*, in which the margins fuse to a greater extent, the second ventral is seen to give off a vestigial trace which fades out in the carpellary tissue (Fig. 76). In *I. asper* and *Adenanthos* sp. each ventral gives off one bundle; the two bundles thus formed fuse together and feed the ovule (Figs. 79, 84, 93). In all genera the funicular bundle branches slightly in the chalaza of the ovule (Figs. 125, 134, 138, 140, 145, 147). The vestigial or functional strand from the second carpellary marginal suggests that the 1-ovulate carpel in these genera is derived by suppression of the second ovule from a biovulate ancestral carpel such as is noticed in *Bellendena* and *Persoonia* and that the surviving ovule has captured the vascular supply of the suppressed one. This conclusion is justified by the occasional presence of an extra ovule in *Isopogon buxifolis* and *Stirlingia* sp. (Figs. 57, 78). The ovular attachment in *I. buxifolius* is strongly suggestive of that in *Persoonia* sp. (Venkata Rao 1960).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The vasculature of the ovule in *Stirlingia* differs markedly from that of the other three genera. A little above their demarcation, both ventral carpellary bundles branch and form a number of strands. These fuse together to form a single bundle which functions as the ovular trace. After entering the funicle the xylem spreads out fanwise and the bundle breaks up into 6–8 strands which form an arc in the raphe (Figs. 48–51). This probably suggests that the carpel in *Stirlingia* may have been derived from a multiovulate one like that seen in *Garnieria* of Persoonieae.

Microsporogenesis and Male Gametophyte

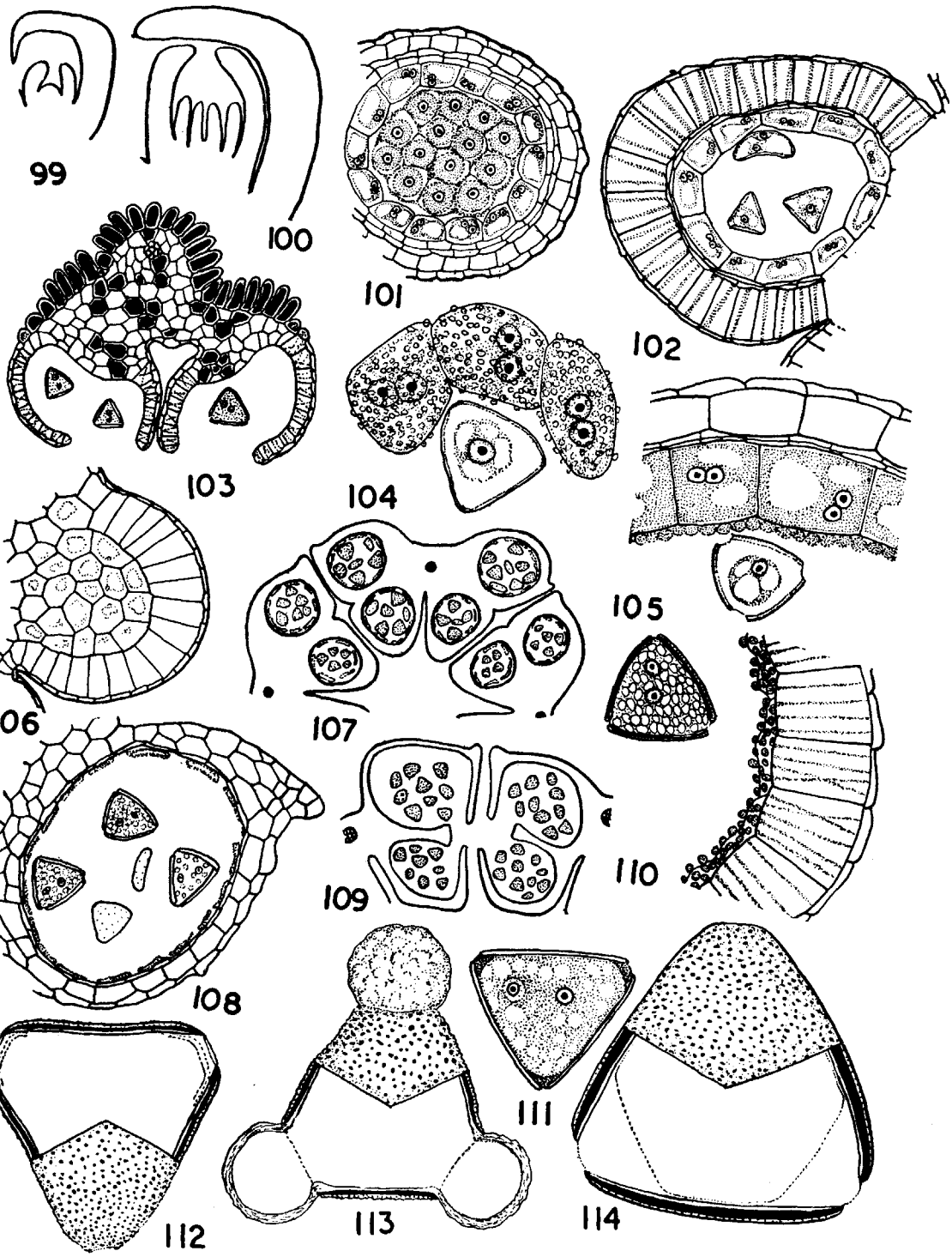
The anther wall comprises of five layers. In all genera, the endothecium develops fibrous thickenings (Figs. 102, 103, 110) except in *Stirlingia* (Fig. 108) where the epidermal cells persist and bring about the anther dehiscence. The tapetum is of the glandular type and the cells are commonly binucleate (Fig. 105). In *Adenanthos*, *Isopogon* and *Petrophila* ubish granules are seen on the outer tangential walls and increase with age (Figs. 104, 105, 110); these are not noticed in *Stirlingia*. Though the anther loculi in *Stirlingia* are described in ta .onomic works as being connate, ontogenetic studies disprove this. The anthers develop quite free from each other and dehisce individually (Figs. 107, 109). Due to shrinkage of their membranous walls the loculi become adpressed and simulate the coalesced condition (Fig. 53).

There is a secondary increase in the sporogenous cells (Fig. 101). Cytokinesis of the microsporocytes is simultaneous and the tetrads are tetrahedral. The pollen grains are shed in the 2-celled stage. In all genera the pollen grains are triangular, triporate, angulaperturate (Figs. 111–114), and are either oblately flattened or nearly sphaeroidal. The exine ornamentation ranges from granular to reticulate or slightly papillate condition. The germ pores are round and the intine usually protrudes slightly through them except in *P. teretifolia* in which it protrudes markedly forming knob-like swellings (Fig. 113).

Megasporangium

The bitegmic, crassinucellate ovules are orthotropous in *Petrophila* and *Isopogon* (Figs. 123, 125, 126, 131, 140); hemianatropous in *Adenanthos* (Figs. 145, 147) and anatropous in *Stirlingia* (Figs. 119, 121). Only the inner integument forms the micropyle.

FIGS. 80–98. Floral anatomy of *Adenanthos* sp. 80–86, *A. barbigera*. 80, L.S. base of inflorescence. ×25. 81–83, 85–86, T.S. bud at various heights. ×30. 84, T.S. ovary and nectary. ×50. 87–90, T.S. flower bud of *A. sericea* at various heights. ×25. 91–95, *A. cygnorum*. 91–94, T.S. bud. ×25. 95, T.S. stigma. ×50. 96-97, *A. meissneri*. ×25. 98, T.S. flower bud of *A. obovata*. ×25.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In *Stirlingia*, *Adenanthos cygnorum* and *A. sericea* the archesporium is multicellular; in other members studied it is 1-celled. The single cell or the hypodermally situated cells cut off the primary parietal cells while the deep-seated cells function directly as the megaspore mother cells (Figs. 116, 146). The parietal tissue, which consists partly of the cells derived from the primary parietal cell and partly of the nucellar cap (Fig. 132), shows much variation in the extent of development in different genera. In *Stirlingia* it becomes 3-layered by the tetrad stage of the ovule (Fig. 117); of these the inner two layers become crushed by the developing embryo sac (Figs. 118–120). In other genera the parietal tissue is thicker (Figs. 125, 126, 129, 130, 139, 140). The cells of the superficial layer become papillate in *Isopogon buxifolius* (Fig. 137). The most extensive parietal tissue is noticed in *I. trilobus*; it is 20–25 cells thick and an epistase of glandular, starch-bearing cells is organized above the embryo sac (Figs. 134, 135). Starch is also found in the nucellar cells of *Petrophila* and *Stirlingia* (Fig. 117). The embryo sac in *Stirlingia* is relatively small and ovoid; it is subtended by massive nucellus of large poorly cytoplasmic cells; a hypostase is not organized (Fig. 119). In other genera the embryo sacs are more elongated and are subtended by a hypostase of thick-walled cells (Figs. 126, 130, 138, 139, 144, 149); this is especially prominent in *Adenanthos cygnorum* (Fig. 147).

Megasporogenesis and Female Gametophyte

According to the number of archesporial cells in the ovule, one or more linear megaspore tetrads are formed (Figs. 117, 124, 131, 143). The lowest megaspore functions and forms the 8-nucleate embryo sac of the Polygonum type (Figs. 128, 133). More than one embryo sac develops to maturity (Figs. 120, 145, 147, 148). The synergids show rounded or hook-like protuberances on their free sides; a filiform apparatus is noticed in *Petrophila fucifolia* (Fig. 127). The polar nuclei fuse only at the time of fertilization. The three antipodal cells are inconspicuous and ephemeral.

Fertilization

The pollen grains germinate in a monosiphonous manner on the stigma and the generative nucleus divides while the pollen tube is passing through

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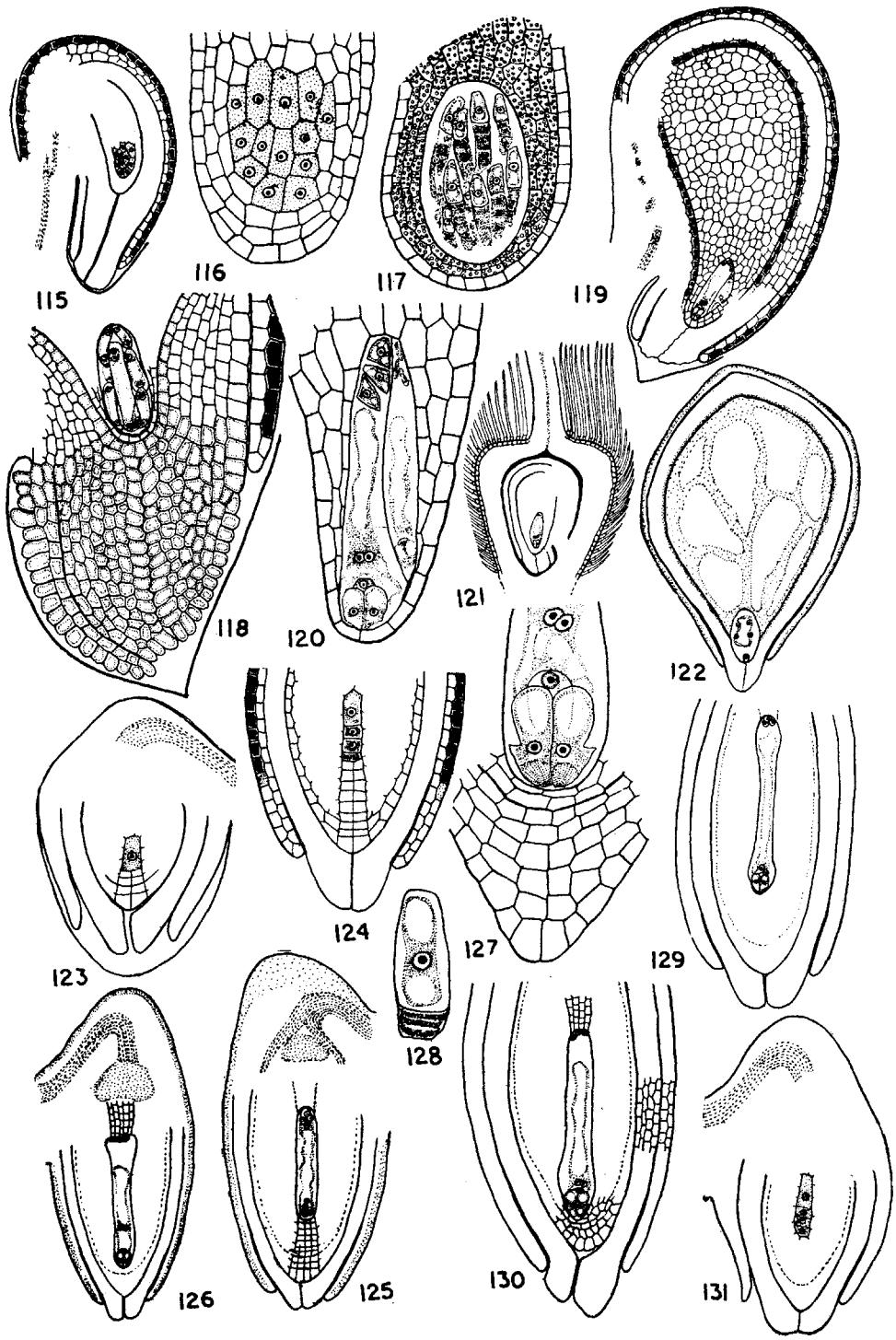
FIGS. 99–114. 99, 100, floral organogeny in *Stirlingia latifolia*. ×65. 101–114, microsporogenesis and male gametophyte in some Australian Proteeae. 101, T.S. anther loculus of *Isopogon anethifolius*. ×190. 102, T.S. anther loculus of *Adenanthos barbigera*. ×145. 103, T.S. mature anther of *Petrophila biloba*. ×90. 104, tapetal cells and microspore of *A. sericea*. ×300. 105, anther wall and microspore of *I. sphaerocephalus*. ×600. 106, T.S. sterile anther loculus of *P. fucifolia*. ×135. 107–109, anther development in *S. latifolia*. 107, 109, ×35; 108, ×120. 110, T.S. anther wall and pollen grain of *P. fucifolia*. ×300. 111, 112, young and old pollen grains of *A. sericea*. ×300. 113, pollen grain of *P. teretifolia*. ×480. 114, a pollen grain of *S. simplex*. ×600.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the style. Fertilization is porogamous. In one preparation the pollen tube is seen just penetrating the micropyle; the vegetative nucleus is seen at the tip of the pollen tube and the two male nuclei higher up (Fig. 138).

Endosperm and Embryo

The endosperm is nuclear (Figs. 136, 141). In *Stirlingia*, in which there is no hypostase, the cells of the nucellus show signs of degeneration early in seed development (Fig. 122); in other genera the hypostase persists as a podium while the remaining thin-walled cells degenerate (Figs. 141, 150, 152, 153). In all members studied the endosperm is relatively scanty and becomes cellular at a relatively advanced stage in seed development (Figs. 141, 151, 152, 154). In *Adenanthos cygnorum* the endosperm nuclei are aggregated at the chalazal end and fuse to form polyploid nuclei (Fig. 153).

The zygote divides transversely, both *ca* and *cb* thus formed give rise to the embryo which is devoid of a suspensor. The mature embryo shows a well-developed radicle and thick fleshy cotyledons.

Seed Coats and Fruit Wall

In *Stirlingia* the outer integument remains biseriate whereas the inner may become even 10-layered.

Mechanical tissues are developed in the fruit wall. Sclerenchyma develop below the ridges and in association with the vascular bundles in *Petrophila* (Fig. 156). There is no branching of the carpellary bundles in the fruit wall. In *Stirlingia* sp. the cells of the inner part of the pericarp become sclerified while in *P. longifolia* the cells of the median layers become sclerotic (Figs. 157, 161). In species of *Isopogon*, *Petrophila* and *Adenanthos* the innermost one or two layers of the pericarp become radially elongated and thick-walled and show tannin and druses (Figs. 155, 158–160).

Discussion

The Australian Proteeae show evolutionary diversification in morphological, floral anatomical and embryological features which is unparalleled in any other tribe of Proteaceae. In morphological features, variation is noticed

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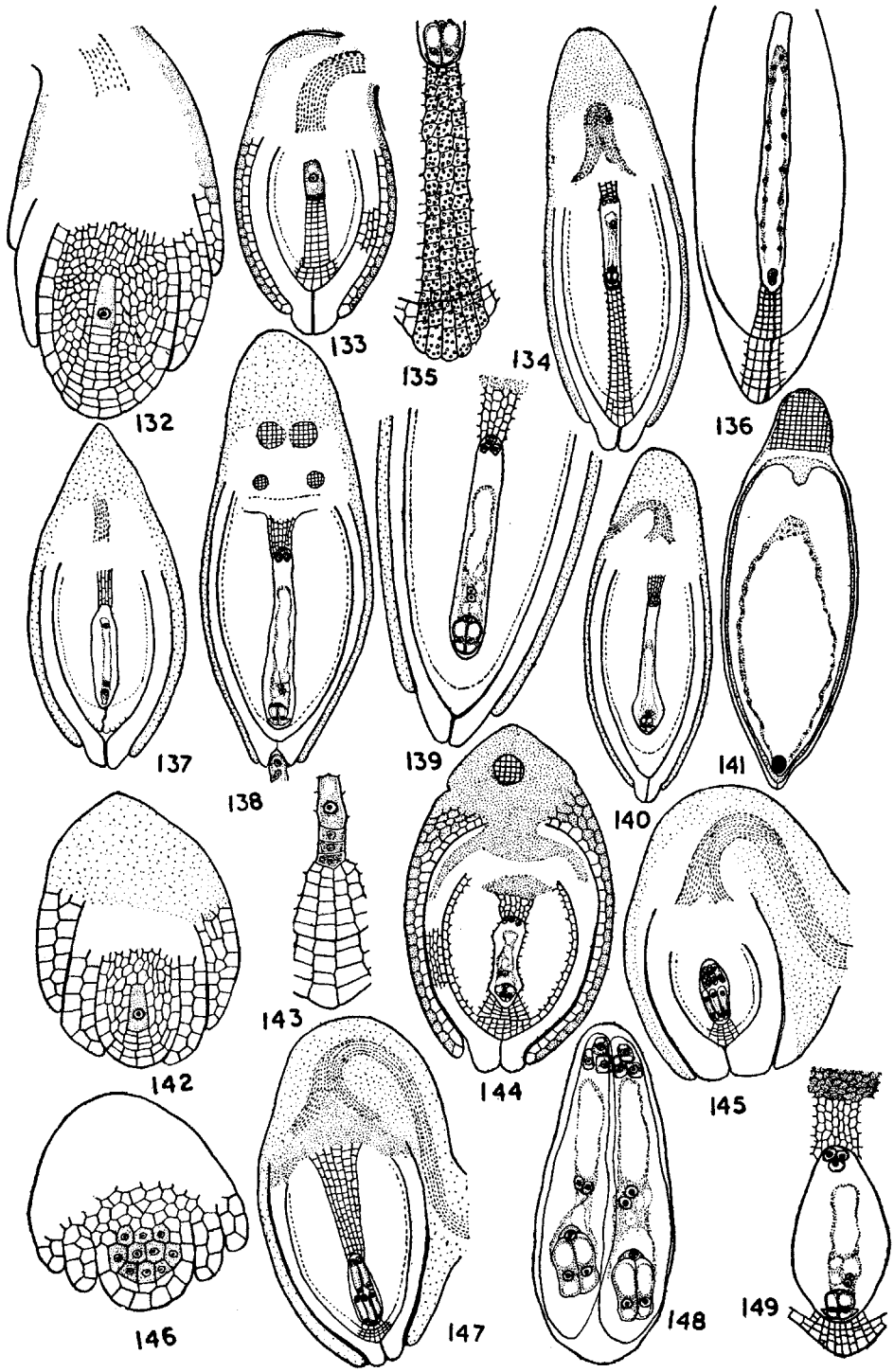
Figs. 115–131. Megasporogenesis and female gametophyte in some Australian Proteeae. 115–120, *Stirlingia latifolia*. 115, L.S. young ovule with megaspore mother cells. ×55. 116, nucellus from similar ovule. ×280. 117, nucellus with several megaspore tetrads; note starch in nucellar cells. ×225. 118, part of ovule with young embryo sacs and micropylar region. ×135. 119, L.S. mature ovule. ×45. 120, part of the above. ×180. 121, L.S. ovary of *S. abratonoides*. ×18. 122, L.S. developing seed of *S. simplex*. ×28. 123–131, *Petrophila* sp. 123–125, *P. seminuda*. 123, L.S. ovule with megaspore mother cell. ×110. 124, part of ovule with megaspore tetrad. ×135. 125, L.S. ovule with 8-nucleate embryo sac. ×55. 126, 127, *P. fucifolia*. 126, L.S. mature ovule. ×28. 127, upper part of nucellus and embryo sac. ×225. 128, 129, *P. squamata*. 128, one nucleate embryo sac. ×225. 129, L.S. part of mature ovule. ×110. 130, part of mature ovule of *P. rosea*. ×135. 131, L.S. ovule of *P. biloba* with megaspore tetrad. ×110.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from arborescent to under-shrubby habit, from large bicompound leaves with expanded leaflets to simple small, linear or terete ones. The inflorescence ranges from large, diffusely branched panicles with numerous, small, inconspicuous flowers, to conspicuous, axillary, 1-flowered, involucrate heads. However, the large panicles of *Stirlingia* cannot be taken as the ancestral type for Proteaceae because reduction is evident in the length of the ultimate flower-bearing axes, the number of flowers borne on them as well as the pedicels of flowers. The 1-flowered heads of *Adenanthos* mark the culmination of reduction not only in the Australian Proteeae but in the whole family. In *Spatalla* of the African Proteeae also a similar reduction is noticed but this occurs in the lateral branches; in none of the African taxa is the whole inflorescence reduced to a single flower. The other members of Proteaceae which show such 1-flowered, involucrate heads are *Strangea cynanchicarpa* of the Grevilleeae and *Lambertia uniflora* of Lambertieae (Grevilleoideae) and afford good examples of parallelism in the evolution of the inflorescence in the two sub-families.

Variation is seen in floral structure from typically regular flowers to structurally zygomorphic ones, from hermaphrodite to partially male sterile and unisexual ones, from glandless to glanded flowers, from free tepals to those connate into a tube, from stamens with large massive free part of filament to sessile anthers completely fused with tepal, from appendaged to non-apiculate stamens, from simple unspecialized style-end to specialized one with hairs which function as the 'pollen-collecting apparatus'. The ovary in all genera is sessile which is considered to be a more advanced condition than the stipitate (Puri 1967). The fruit ranges from glabrous drupes to small dry samara or comose types. Viewed against the phylogenetic background of the family (Venkata Rao 1967*a*, *b*), the drupe (which is reminiscent of rain-forest conditions) seems to be the primitive type and the dry small fruits, which show adaptations to wind dispersal, the more evolved types.

Anatomically, the flowers show evolution in connation, adnation, reduction and amplification of floral traces and organs. Evolution is noticed

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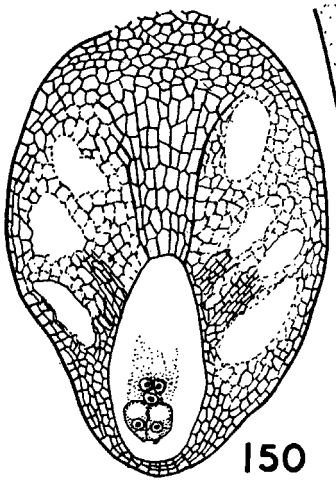
FIGS. 132–149. Megasporogenesis and female gametophyte in some Australian Proteeae. 132–141, *Isopogon* sp. 132–136, *I. trilobus*. 132, L.S. young ovule with megaspore mother cell. ×180. 133, L.S. ovule with 1-nucleate embryo sac. ×90. 134, L.S. mature ovule showing epistase. ×55. 135, part of the above; note starch grains in cells of epistase. ×135. 136, L.S. young seed. ×85. 137, L.S. fertilized ovule of *L. sphaerocephalus*. ×30. 138, L.S. mature ovule of *L. asper* showing entry of pollen tube. ×55. 139, L.S. lower part of ovule of *I. buxifolius*. ×90. 140, L.S. mature ovule of *I. anethifolius*. ×35. 141, L.S. young seed of *L. drummondi*. ×15. 142–149, *Adenanthos* sp. 142–144, *A. barbigera*. 142, L.S. ovule with megaspore mother cell. ×135. 143, megaspore tetrad with overlying parietal tissue. ×180. 144, L.S. mature ovule. ×70. 145, L.S. ovule of *A. sericea* with several 2-nucleate embryo sacs. ×55. 146–148, *A. cygnorum*. 146, L.S. young ovule showing several megaspore mother cells. ×125. 147, L.S. ovule with developing embryo sacs. ×70. 148, two mature embryo sacs from one ovule. ×225. 149, part of ovule of *A. obovata*. ×90.



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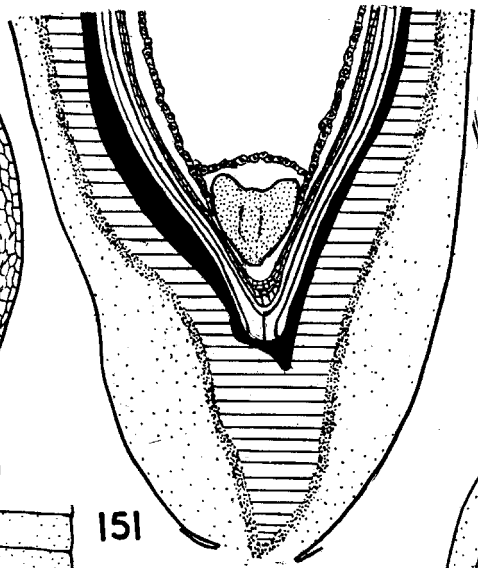

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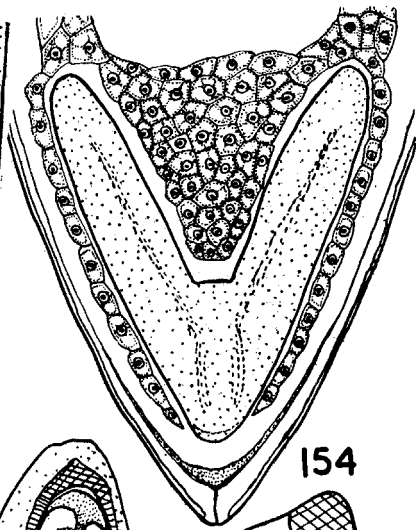

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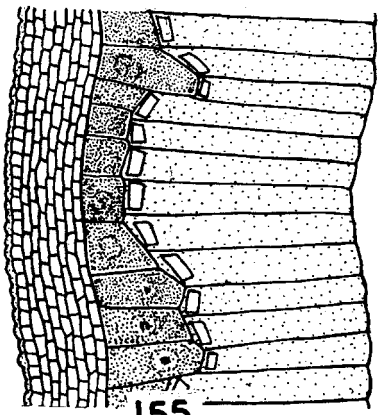

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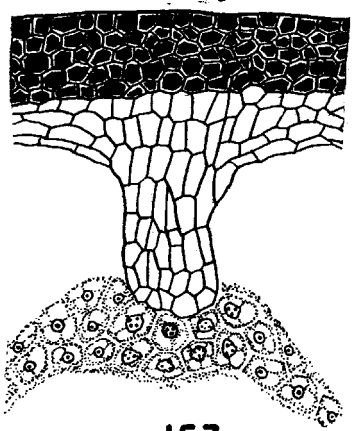

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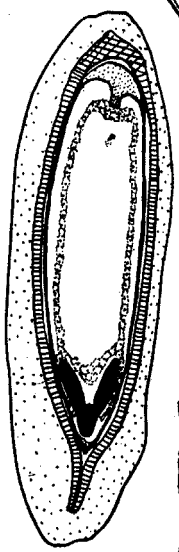

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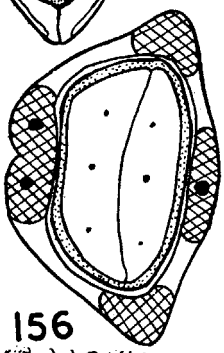

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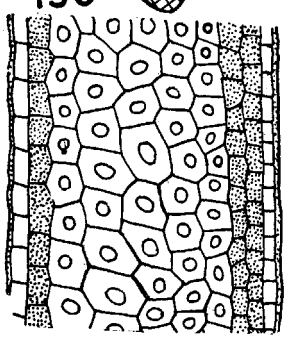

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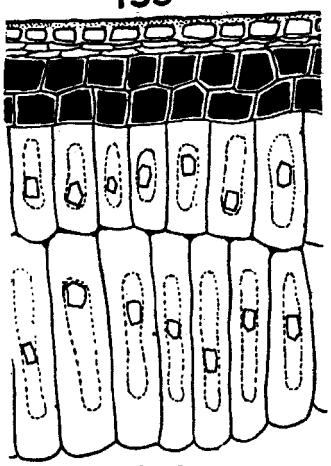

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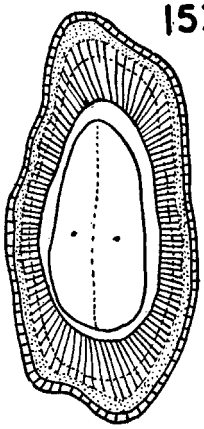

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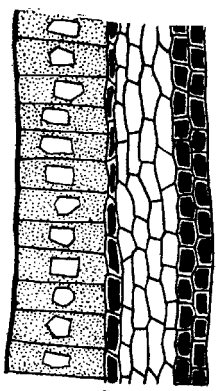

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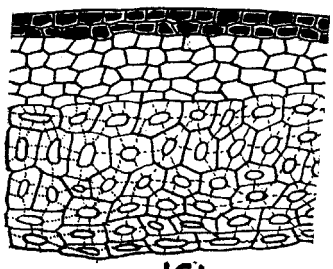

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from small, scaly, 1-traced bracts to large, clasping, woody, persistent, multi-traced ones. The tepals with three separate traces seem to represent the primitive condition (*Petrophila* and *Isopogon*); from this condition evolution proceeded in two directions, viz. connation of tepal marginals (*Adenanthos*) and reduction of tepal marginals (*Stirlingia*). Though in several members the tepal and stamen show only congenital concrescence, in some species of *Isopogon*, the stamen and tepal traces show complete adnation as nowhere else in the family. The carpel ranges from 3-traced to 5-traced condition with further branching of the ovarian bundles. The introduction and vascularization of a nectary involves elaboration of floral stele. The vasculature of the ovule in different genera shows interesting stages which are suggestive of the origin of the uniovulate condition from the multiovulate one such as is seen in *Garnieria* of Persoonieae.

In embryological features also evolution is noticed from the primitive to advanced conditions. A fibrous endothecium is not organized in *Stirlingia*, the anther dehiscence being brought about ectokinetically (as in gymnosperms) by the persistent epidermal cells. In other genera the anther dehiscence is endokinetic as in most angiosperms, being brought about by a well-developed fibrous endothecium. The pollen grains range from small, smooth-walled types with narrow germ pores, which seem to represent the primitive type in the family, to large grains with complex exine ornamentation and wide germ pores through which the intine protrudes forming knob-like swellings, similar to those met with only in the most highly evolved genera, *Grevillea* and *Hakea* (Venkata Rao 1965*a*, *b*). The ovules range from orthotropous type pendulous from the top of the loculus (*Isopogon* and *Petrophila*) to hemianatropous laterally attached (*Adenanthos*) and anatropous, basal type (*Stirlingia*). The presence of orthotropous ovules in all genera of Proteoideae, including the three diploid ones, and also the relatively primitive genera of the Grevilleoideae, shows that this is the relatively primitive condition. Anatropous ovules are rare in Proteaceae and are noticed, in addition to *Stirlingia*, only in some species of *Grevillea* and *Hakea*. From comparative studies it is evident that concurrent with evolution from orthotropous to anatropous condition, migration of the ovule attachment occurred from the top to the base of the loculus. A similar migration is visualized by Bechtel (1921) in Urticaceae and by Murty (1952) in Piperaceae. Much variation is seen in the structural features of the ovules. In *Stirlingia* the embryo sacs are small and ovoid; the nucellus

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FIGS. 150–161. Seed and fruit structure in some Australian Proteeae. 150–155, *Adenanthos cygnorum*. 150, nucellus from a mature ovule at the time of fertilization. ×75. 151, basal part of developing fruit. ×25. 152, L.S. older fruit. ×6. 153, chalazal part of seed showing podium and endosperm. ×95. 154, micropylar part of seed. ×30. 155, part of pericarp. ×45. 156, T.S. fruit of *Petrophila longifolia*. ×10. 157, part of pericarp from above. ×100. 158, T.S. fruit of *P. seminuda*. ×10. 159, part of pericarp from above. ×45. 160, pericarp of *Isopogon drummondi*. ×95. 161, pericarp of *Stirlingia latifolia*. ×60.

below the embryo sac is massive and consists of large parenchymatous cells, there being no hypostase. The parietal tissue is limited to only 3 layers. In other genera the embryo sacs are more elongated and are subtended by a hypostase of thick-walled cells; the parietal tissue is more prominent and in some species shows an epistase of starch-bearing cells. The archesporium is 1-celled or multicellular, variation being sometimes noticed within a single genus like *Adenanthos*. It is difficult to decide which condition is more primitive because both types are found in the relatively primitive (Ranunculaceae, Rosaceae) as well as advanced families (Rubiaceae, Compositae). In all genera the endosperm is scanty and remains nuclear for a long time; the massive nucellus seems to be the chief source of nutrition. This recalls the condition in some genera of Persoonieae like *Cenarrhenes* and it stands in marked contrast to the abundant, aggressive type of endosperm found in several Grevilleoideae and seems to represent the primitive type (Venkata Rao 1967*a*, *b*).

Stirlingia seems to be the most primitive genus among the Australian Proteeae since it shows the largest number of primitive morphological and floral anatomical features. It resembles closely *Cenarrhenes* (Persoonieae) in: terminal paniculate inflorescences, small, 1-traced bracts, polyphyllous, 1-bundled tepals, slight adnation between tepal and stamen, massive free parts of filaments for stamens which converge around the style, 5-traced, 1-ovuled sessile carpels, occasional torsion of the ovary into a diagonal position on the thalamus, structural features of ovule, viz. broad micropylar region with papillate superficial cells, small ovoid embryo sac, large nucellus of parenchymatous cells subtending the embryo sac, scanty parietal tissue, scanty endosperm and functioning of the nucellus as perisperm. However, *Stirlingia* shows features of advance over *Cenarrhenes* in its under-shrubby habit, non-apiculate stamens, basal anatropous ovule and small comose fruit.

Petrophila and *Isopogon* resemble *Bellendena* and *Persoonia*, the two diploid genera of Persoonieae, in their regular flowers, appendaged stamens, 3-traced tepals, 3-traced carpels, orthotropous ovules pendulous from the top of the loculus, and their structural features, viz. conical micropylar region, well-developed parietal tissue including nucellar cap, elongated embryo sac and presence of a hypostase of thick-walled cells. However, *Petrophila* and *Isopogon* show advance in connation of tepals, adnation of tepals and stamens as well as their traces, uniovulate sessile ovary, specialized stigmas with devices for pollen collection, comose fruits and non-endospermic seeds.

Adenanthos seems to be the most specialized genus among the Australian Proteeae. While showing resemblances to *Petrophila* and *Isopogon* in features like 3-traced tepals, 3-traced carpels and achenial fruits (some species), it shows features of advance in its 1-flowered, involucrate inflorescences, connation of tepal marginals, hemianatropous, lateral ovules, structurally

zygomorphic flowers with partial male sterility and presence of vascularized nectary.

The close resemblance of the genera of Australian Proteeae to different genera of Persoonieae shows that they may have originated polyphyletically from the Persoonieae or that both taxa had common ancestors. All genera of Australian Proteeae are characterized by $n = 13$ (Ramsay 1963). This number seems to be an aneuploid on bases 7 and 14 found in Persoonieae. Since there is no change in chromosome numbers within the tribe, it is evident that diversification occurred due to gene mutations at the sub-microscopic level.

In taxonomic works, the anther loculi of *Stirlingia* are described as connate. As this is a rare phenomenon noticed in only one other tribe of Proteaceae, viz. Conospermeae (*Conospermum* and *Synaphea*), some phylogenetic significance was attached to it by Engler (1894). Since in *Stirlingia* all stamens of a flower are fertile and in Conospermeae they show partial male sterility, Engler derived Conospermeae from *Stirlingia* (= *Simsia*)-like ancestors. Johnson and Briggs (1963) go a step further and suggest that *Stirlingia* be removed from Proteeae and placed in Conospermeae. However, in advocating this regrouping, the authors have ignored all other evidences from comparative morphology and cytology, particulars of which are given in Table II.

TABLE II

Stirlingia	Conospermeae
1. Flowers regular, hermaphrodite or unisexual by abortion	Flowers strongly zygomorphic, partially male sterile
2. Anthers 4-locular, introrse	Fertile anthers bilocular, extrorse
3. Anther loculi do not coalesce	Anther loculi coalesce due to a breakdown of the intervening wall layers
4. Ovules basal, anatropous	Ovules orthotropous, pendulous
5. $n = 13$	$n = 11$

The description of connation of anther loculi in *Stirlingia*, to which such phylogenetic significance was attached, was based only on observation of the exomorphic features. However, the present studies in ontogeny of stamens show that this appearance is unreal and that coalescence of anther loculi of the kind noticed in Conospermeae does not occur in *Stirlingia*. So the suggestion of transference of *Stirlingia* to Conospermeae seems to be unwarranted since it would not only obscure the affinities of *Stirlingia* but make the Conospermeae, an otherwise most homogeneous and natural tribe, a heterogeneous assemblage.

The Proteeae are the only tribe of Proteaceae in which more genera occur outside Australia than within. The close similarity between Australian and African sections of the tribe in morphological, floral, anatomical and embryological features, the parallelism in their evolutionary trends and the common chromosome number of $n = 13$ in both sections (de Vos 1943) show that the two groups must have been derived from common ancestors. However, no genera are common between the two continents. This shows that separation of the ancestral stocks occurred quite early in the phylogenetic history of the tribe, i.e. before diversification took place to the generic level. Genetic and geographic isolation seems to have contributed to independent speciation. As in other tribes, in Proteeae also the most primitive members occur in Australia and the derived forms in Africa. This shows that the ancestral stocks must have originated in the Australian region on a once connected land mass (Pangaea or Gondwanaland). Spread to S. Africa must have occurred when this land mass fragmented and the continents drifted apart. Probably due to the presence of more favourable conditions and less species pressure in Africa, diversification of the tribe occurred to a greater extent than in Australia. Africa, therefore, seems to have been a secondary centre of diversification for the Proteeae. A similar phenomenon is visualized in tribe Stapelieae of Asclepiadaceae (Good 1953).

Acknowledgements

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