

STUDIES IN THE PROTEACEAE

XIV. TRIBE MACADAMIEAE

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The tribe Macadamieae was erected by the author for nine genera of Brown's Grevilleeae which show regular flowers. In this article the morphology, chromosome number (one species), floral anatomy and embryology of several species belonging to all the nine genera are described. The present studies show that Macadamieae are a primitive, homogeneous tribe which resemble the Persoonieae of Proteoideae in several features and seem to be derived from them. The chromosome number of $n = 14$, reported in all the six genera of Macadamieae so far investigated, seems to be a tetraploid of $n = 7$ of *Persoonia* (Persoonieae). Due to species concentration, occurrence of morphological primitives, high degree of endemism and presence of genera common between East Australia and neighbouring islands, this region on a prehistoric continuous land mass (Pangaea or Gondwanaland) is considered to have been the probable centre of origin of the tribe. The present-day discontinuous distribution of the tribe in Australia and some Pacific islands (six genera), South America (two genera) and South Africa (one genus) is attributed to continental drift.

INTRODUCTION

The studies of the author have shown that Brown's (1810) Grevilleeae which comprise 20 genera are a heterogeneous assemblage of unrelated taxa. Genera with lax and dense inflorescences, regular and zygomorphic flowers and multiovulate and biovulate carpels have been grouped here. Brown's classification was accepted by both Bentham (1870) and Engler (1894). In his revision of classification, the author (Venkata Rao 1957a) made the following changes: (a) the two genera with multiovulate carpels (*Darlingia* and *Buckinghamia*) were transferred to (his) Telopeeae; (b) the two genera, *Orites* and *Lambertia*, were given the status of separate tribes; and (c) the remaining genera were split into two tribes, the Macadamieae (nine genera with regular flowers) and Grevilleeae (seven genera with zygomorphic flowers).

PREVIOUS WORK

In his taxonomic revision of the genus *Helicia*, Sleumer (1955) erected a new genus, *Heliciopsis*, for seven species which show dioecy and drupaceous

fruits. (This is the only genus among Grevilleoideae which shows dioecy). The range of *Heliciopsis* falls within that of *Helicia* (cf. Table I).

Kausik (1939) studied the floral anatomy and embryology of *Macadamia ternifolia* and Jordaan (1946) the embryology of *Brabeium stellatifolium*. The author (Venkata Rao 1957a, 1957b) investigated the floral anatomy, cytology and embryology of several members of the tribe. Haber (1959) described the floral anatomy of *Hicksbeachia pinnatifolia* and *Xylomelum pyriforme*. The haploid chromosome number of 14 (or the diploid number of 28) has been reported in six genera by de Vos (1943), Venkata Rao (1957a), Ramsay (1963) and Johnson and Briggs (1963). This points to the homogeneity of the tribe.

From a study of the floral anatomy of a single species of *Macadamia*, Kausik (1939) concluded that the nectary in Proteaceae is a 'reduced corolla on the verge of extinction'. This interpretation was accepted by Haber (1959) and Eames (1961) who therefore regarded the family as being derived by reduction from petaloideous ancestors. However, from comparative morphological and anatomical studies of the flower in a large number of taxa including several Macadamieae, the author (Venkata Rao 1967b) came to the conclusion that the nectary in Proteaceae is only an enation of the thalamus or other floral part and that the family is therefore primitively monochlamydeous.

MATERIALS AND METHODS

For the present studies, materials fixed in formalin-acetic-alcohol as well as herbarium specimens were used. For microtoming, the herbarium material was first soaked in distilled water for two to three days and then placed in 1 per cent solution of caustic soda in a paraffin bath at 60 °C and left overnight. It was then washed thoroughly in running water and treated like freshly fixed material. After following the customary methods of dehydration in alcohol series and infiltration with xylol, the material was embedded in paraffin wax of 60 °C m.p. Microtome sections were cut from 6 to 12 μ in thickness and stained in Delafield's haematoxylin or a combination of crystal violet and erythrocin.

Particulars regarding the number of species in each genus, their geographic distribution and the known chromosome numbers are shown in Table I.

OBSERVATIONS

External morphology—*Helicia erratica*, *Hicksbeachia pinnatifolia*, *Carnarvonia aralaefolia* and species of *Heliciopsis*, *Panopsis* and *Roupala* are rain-forest trees. *Macadamia tetraphylla* usually grows into a small tree but sometimes becomes shrubby due to suckering habit (Plate IA). Species of *Xylomelum* are shrubby and inhabit exposed regions. None of the Macadamieae is herbaceous.

TABLE I

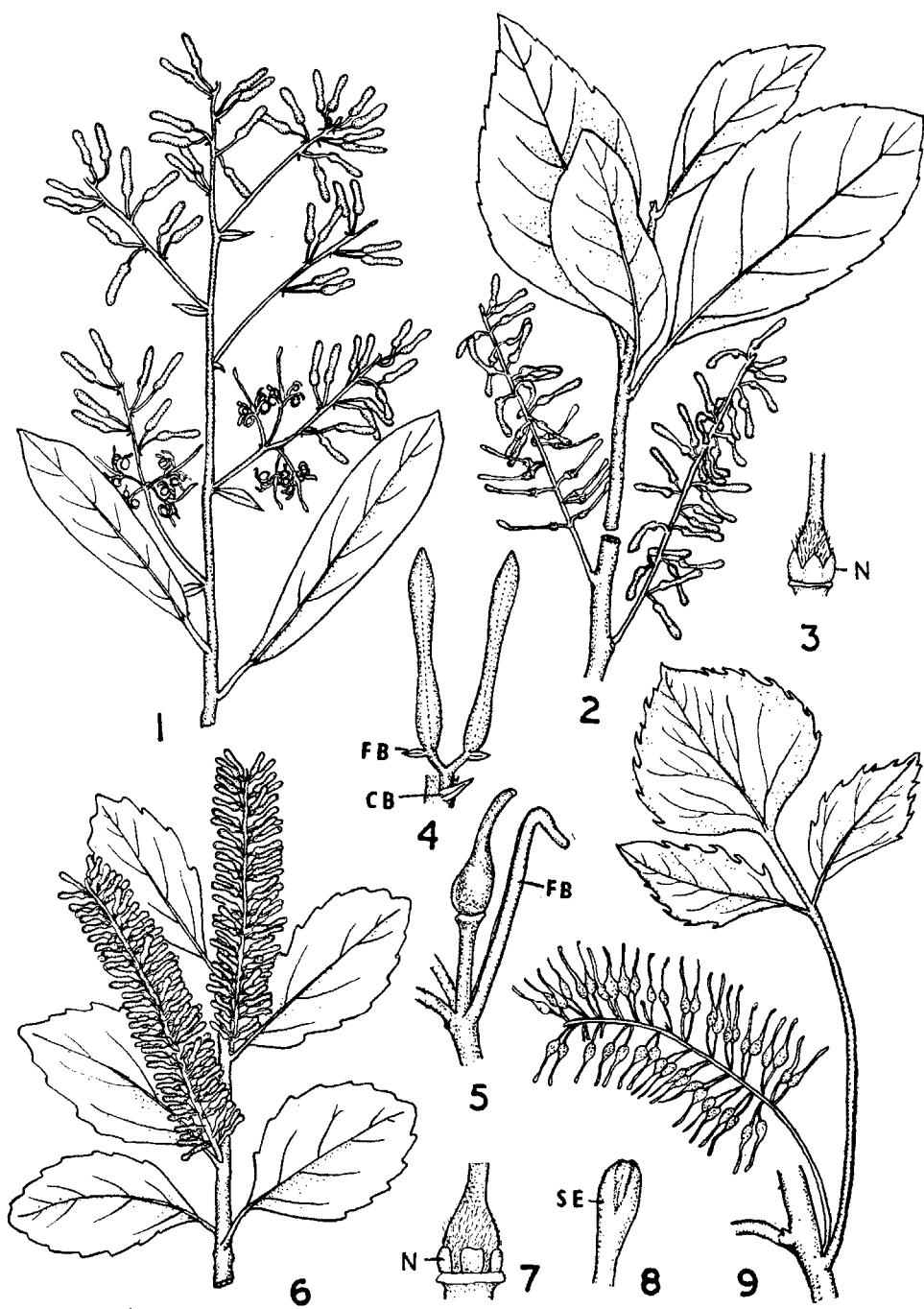
Genus	<i>n</i>	<i>2n</i>	Author	Number of species	Geographic distribution
<i>Brabeium</i> L. . .	14	-	dV*	1	South Africa
<i>Carnarvonia</i> F. Muell. . .	-	28	J and B*	1	Queensland
<i>Helicia</i> Lour. . .	14	-	J and B	88	9 East Australia; 44 New Guinea; rest in Borneo, Sumatra, Java, Ceylon, South India, Assam, China to South Japan
<i>Heliciopsis</i> Sleumer . .	-	-	-	7	Borneo, Java, Indo-China and Burma
<i>Hicksbeachia</i> F. Muell. . .	-	28	J and B	2	1 Queensland and 1 Queensland-New South Wales
<i>Macadamia</i> F. Muell. . .	14	-	VR*; R*	10	6 Queensland; 3 New Caledonia and 1 Celebes
<i>Xylomelum</i> Sm. . .	14	-	J and B	5	3 East Australia; 2 West Australia
<i>Panopsis</i> Salisb. . .	-	-	-	11	South America extending into tropics
<i>Roupala</i> Aubl. . .	-	-	-	55	South America extending into tropics

* dV = de Vos (1943); J and B = Johnson and Briggs (1963); VR = Venkata Rao (1957a); R = Ramsay (1963).

Hicksbeachia pinnatifolia has the largest leaf among the tribe. It is pinnately compound and resembles the leaf of *Beauprea pancheri* of Persoonieae. However, some extra leaflets are found where the pairs of leaflets are attached on the rachis (Fig. 15). This indicates that the leaf is probably derived by reduction from a pinnately bicomponent one. The leaves in *Carnarvonia aralaefolia* and *Roupala macrophylla* are digitately compound and show three to five leaflets (Fig. 9; Plate XLI, B); these seem to be derived by reduction from pinnately compound leaves. Though the leaves in some species of *Heliciopsis* are simple and entire, in some others they are dissected or lobed. In *Helicia erratica* and *Panopsis rubescens* the leaves are large, simple and mesophytic (Figs. 2, 14). In *Xylomelum* and *Macadamia* they are simple and coriaceous; internally they show several layers of palisade parenchyma, reduced spongy tissue and well-developed sclerenchyma in association with vascular bundles forming I-girders. Thus a series of transitional stages are met with from large compound and mesophytic leaves characteristic of rain-forest trees to sclerophyllous types typical of xerophytes. However, the acicular or terete leaf, which is seen in several tribes of Proteaceae like Conospermeae, Proteaeae, Oriteae and Grevilleaeae, is not noticed in any Macadamieae.



A, *Macarandia tetraphylla* Johnson showing shrubby habit due to suckering; B, a branch of *Macarandia tetraphylla* F. Muell. with inflorescences; C, fruits; D, branch of *Xylocarpus pyriformis* Knight with inflorescences; E, a branch of *Macarandia tetraphylla* F. Muell. with inflorescences.

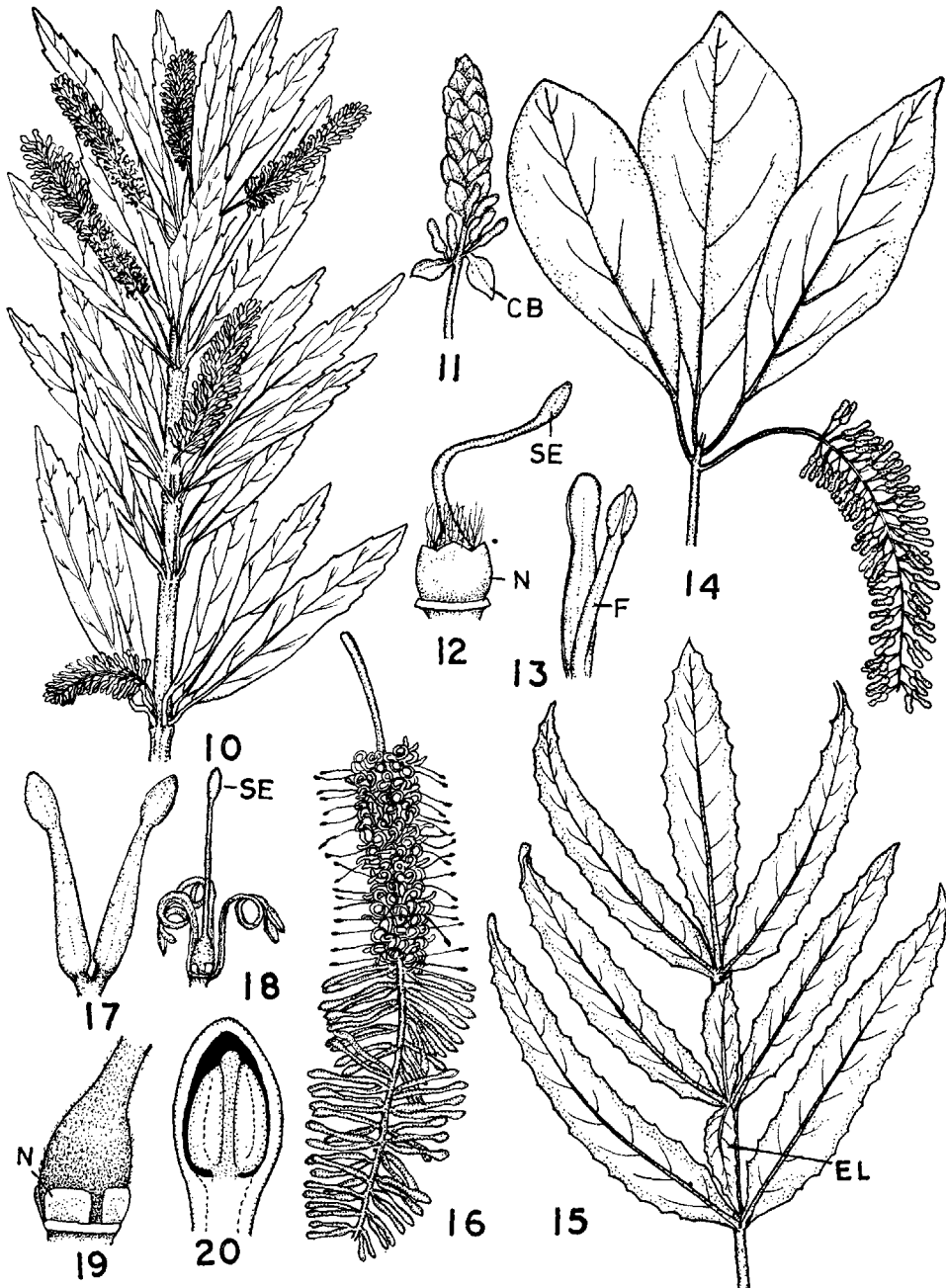


FIGS. 1-9. Branches, inflorescences and flowers of some Macadamieae. 1, a branch of *Panopsis multiflora*, $\times \frac{1}{2}$; 2-3, *Helicia erratica*: 2, branch with inflorescence, $\times \frac{1}{2}$; 3, base of pistil and nectary, $\times 2$; 4, a flower pair of *Helicia glabrescens*, $\times 2$; 5, part of lateral inflorescence of *Carnarvonia aralaefolia*, $\times 3$; 6-8, *Roupala impressiuscula*: 6, a branch, $\times \frac{1}{2}$; 7, base of pistil and nectary, $\times 2$; 8, style-end and stigma, $\times 2$; 9, a branch of *Roupala macrophylla*, $\times \frac{1}{2}$. (N, nectary; FB, floral bract; CB, common bract; SE, style-end.)

In most Macadamieae the leaves are alternate. In a few like *Macadamia tetraphylla* and *Brabeium* (Fig. 10) they are whorled, a condition considered to be more advanced than alternate.

The inflorescence in *Carnarvonia* represents the most primitive type not only in Macadamieae but among all Grevilleoideae. It is a diffusely branched panicle (Plate XLIB) in which pedicellate flowers occur either singly or in clusters of three to four at the ends of lateral peduncles. Each peduncle is subtended by a trifoliate, leaf-like bract while the flower itself shows a strap-shaped bract (Fig. 5). The paired-flower arrangement, which is noticed in all Grevilleoideae, is not found in *Carnarvonia*. In view of the presence of several primitive morphological features in the genus, it may be that the paired position has not yet evolved in it. The inflorescence in *Panopsis multiflora* is a diffusely branched terminal panicle in which the lateral peduncles are subtended by foliaceous bracts (Fig. 1); similar panicles are noticed in species of *Beauprea* (Persoonieae) though without paired arrangement of flowers (Venkata Rao 1960). In several species of *Helicia* the flower pairs show common peduncles, pedicels, common and individual floral bracts (Fig. 4); these depict the least reduced condition of the lateral branches among the tribe. In other genera, the common peduncle is nearly (*Hicksbeachia*, Fig. 17, *Xylomelum*) or completely reduced (*Brabeium*, *Macadamia*); the individual floral bracts are also suppressed so that pairs of pedicellate flowers stand in the axils of common bracts (Fig. 11). In *Xylomelum* the pedicels are also reduced (Plate XLIE). In most genera the bracts are small and scaly; in *Brabeium* they are larger and petaloid (Fig. 11). In all genera the inflorescences are in the shape of elongated axillary pseudoracemes (Figs. 2, 6, 9, 10, 14); in *Helicia erratica* they are also cauliflorous. Compact inflorescences are not noticed in any Macadamieae. On the basis of the presence of a compact, compound head inflorescence with well-developed petaloid involucre bracts, *Lambertia* was removed from Macadamieae and given a tribal status (Venkata Rao 1968). In some genera like *Roupala*, *Brabeium* and *Panopsis* all flowers of an inflorescence are at nearly the same stage of development (Figs. 6, 10, 14) while in others like *Hicksbeachia* they mature acropetally (Fig. 16).

The flowers in Macadamieae show much uniformity in structure. They are regular, 4-merous and hermaphrodite, except in *Heliciopsis* in which they are dioecious. The flower buds remain straight till they open; the perianth sometimes splits on one side to allow the style to curve through. The perianth consists of four strap-shaped segments which curl spirally in the open flowers (Fig. 18). In some genera like *Hicksbeachia* and *Xylomelum* the tepals are antero-posterior and lateral on the thalamus (Figs. 42, 43, 45) while in others like *Roupala*, *Panopsis* and *Brabeium* they are diagonal (Figs. 35, 39, 41). However, both conditions are noticed in different species of *Macadamia* and



FIGS. 10-20. Branches, inflorescences and flowers of some Macadamieae. 10-13, *Brabeium stellatifolium*: 10, a branch, $\times \frac{1}{2}$; 11, an inflorescence, $\times 2$; 12, pistil and nectary, $\times 3$; 13, a tepal and attached stamen, $\times 3$; 14, a branch of *Panopsis rubescens*, $\times \frac{1}{2}$; 15-20, *Hicksbeachia pinnatifolia*: 15, a leaf, $\times \frac{1}{2}$; 16, an inflorescence, $\times \frac{1}{2}$; 17, a flower pair, $\times 2$; 18, an open flower, $\times 2$; 19, base of pistil and nectary, $\times 4$; 20, top of tepal with the attached stamen, $\times 4$. (CB, common bract; SE, style-end; EL, extra leaflet; F, filament; N, nectary).

Helicia (Figs. 43, 44); in *M. tetraphylla* both conditions were found even in different flowers of the same inflorescence.

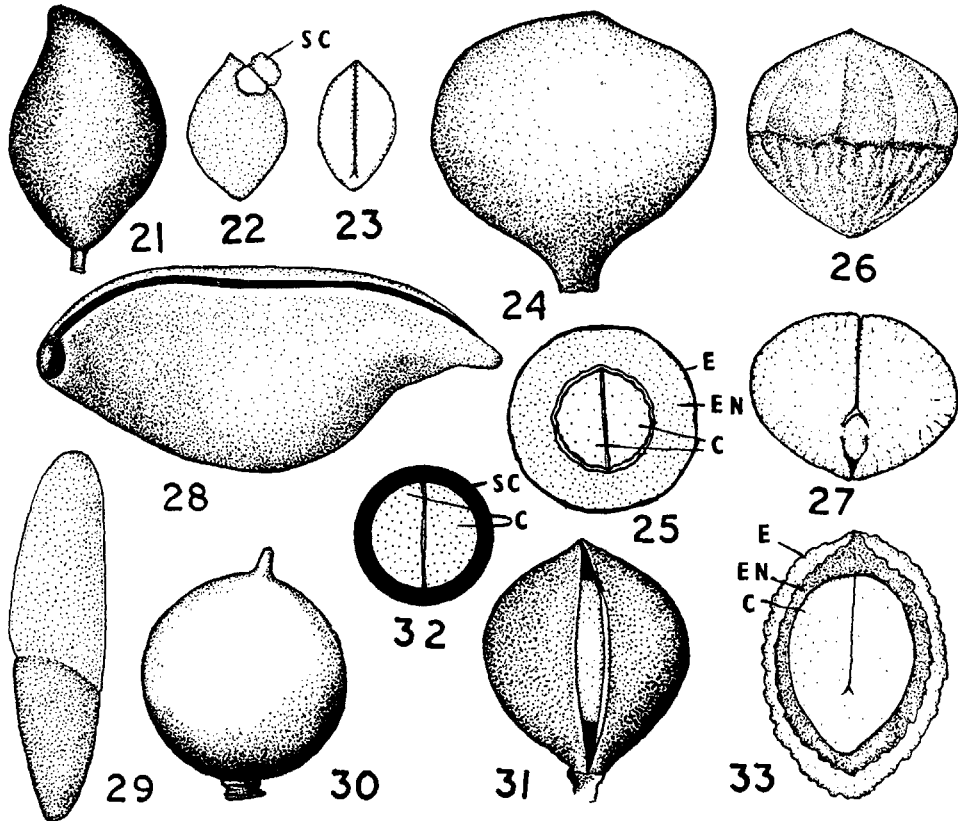
The stamens are epiphyllous, introrse and appendaged in all genera. Usually they show a free part of the filament. In *Brabeium* the filaments are elongated, strap-shaped and coil spirally in the open flowers as the tepals do. They are attached only slightly at the base of the tepal (Figs. 13, 34, 35) and recall the condition noticed in some flowers of Persoonieae (*Persoonia* and *Cenarrhenes*). In *Xylomelum* and *Hicksbeachia* the filaments are adnate to the tepal tissue throughout their length so that the anthers are nearly sessile (Fig. 20). This condition is to be regarded as relatively more advanced and is noticed only in *Grevillea* and *Hakea* (Venkata Rao 1969b).

The ovary in all genera is nearly sessile and covered by dense 1-celled hairs (Figs. 3, 7, 19). These are deciduous in *Panopsis*, *Macadamia* and *Helicia* so that the fruits are glabrous; in *Roupala* and *Brabeium* they are persistent and form a velvety covering on the fruit. The carpels are bi-ovulate in all genera (Figs. 43, 44). The style is terminal and straight. In *Carnarvonnia* it is tapering and the stigma simple and punctiform as is noticed in some Persoonieae like *Bellendena*, *Persoonia* and *Cenarrhenes* (Fig. 5). In all other genera the stigma is cleft-like and subtended by a fusiform style-end (Figs. 8, 12, 18).

The flowers are glandless only in *Carnarvonnia* in which respect it resembles primitive genera like *Bellendena* and *Symphyonema* (Persoonieae). *Carnarvonnia* is the only genus among Grevilleoideae to show glandless flowers. In some genera like *Roupala*, *Hicksbeachia* and *Xylomelum* the flowers show a nectary of four symmetrical, free lobes (Figs. 7, 19, 39, 42, 45) while in others like *Brabeium* and *Panopsis* the lobes are connate to form a ring or cup (Figs. 12, 35, 41). Both conditions are noticed in different species of *Macadamia* and *Helicia* (Figs. 3, 43, 44). In all Macadamieae the nectary remains symmetrical.

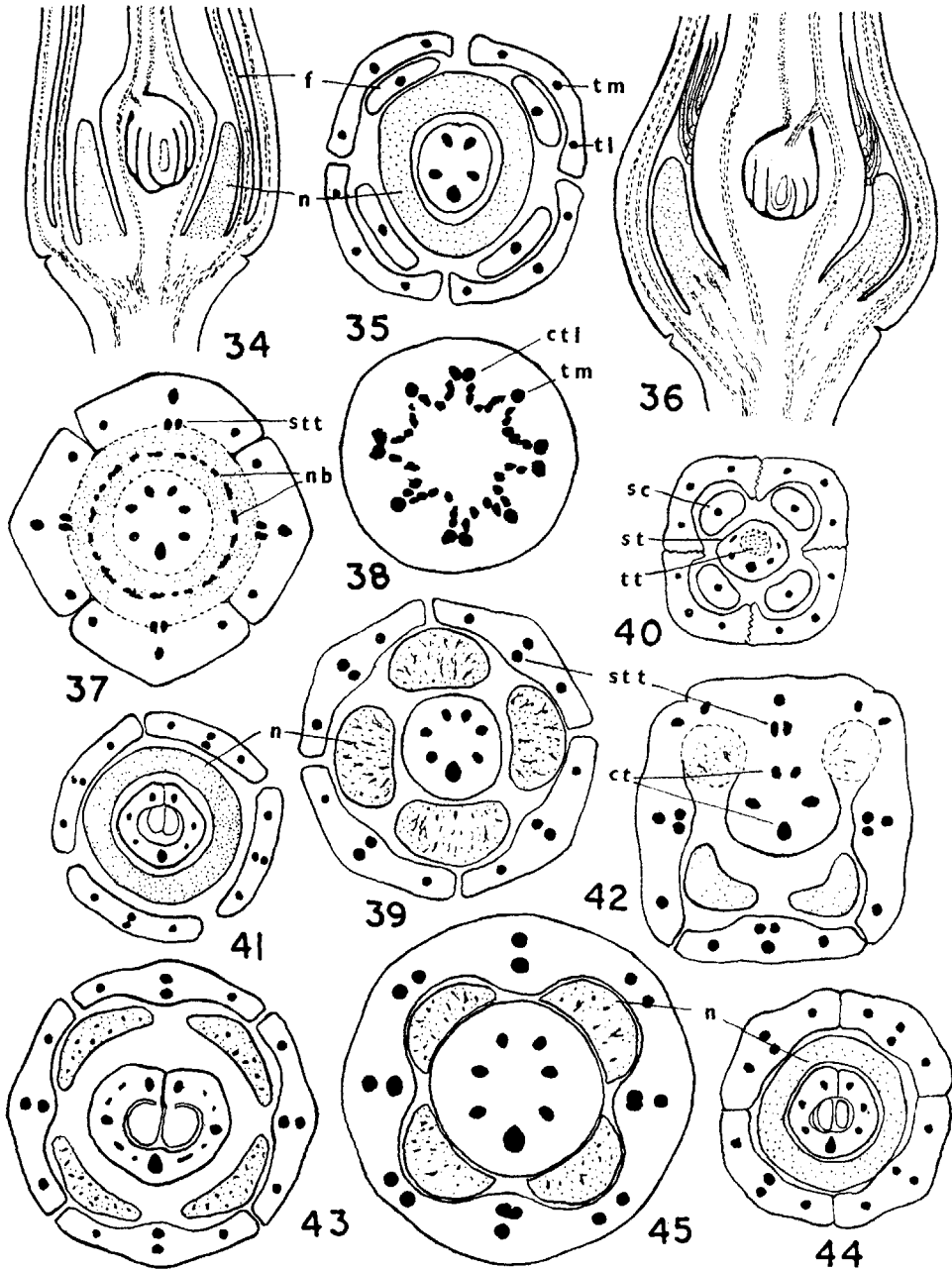
The fruit and seed in Macadamieae show considerable variation; in general they are large (Figs. 21, 24, 30). The fruit in *Xylomelum pyriforme* is the largest in the family and weighs 500 gm or more as against the fraction of a gram of the weight in *Agastachys* and *Bellendena*. The fruits in *Heliciopsis* and *Hicksbeachia* are typical drupes with a thick succulent exocarp and stony endocarp (Fig. 33). In *Brabeium* also the fruits are drupaceous but the exocarp, which is fleshy in the young fruit, becomes corky as the fruit matures. In some species of *Macadamia* and *Helicia* the fruits start development as drupes but become dry when mature. The exocarp becomes a thin skin-like covering for the thick coriaceous endocarp (Fig. 25). Some other species of *Helicia* and *Macadamia* show transition from nuts to follicles; they dehisce tardily on the ventral suture but often fail to liberate the large rounded seeds (Fig. 31). In *Roupala*, *Carnarvonnia* and *Xylomelum* the fruits are woody

follicles (Fig. 28; Plate XLIC, D). Thus Macadamieae show a continuous series of transitional stages from succulent drupes to typical follicles.



FIGS. 21-33. Fruit and seed in Macadamieae. 21-23, *Brabeium stellatifolium*: 21, a fruit, $\times 1$; 22, 23, entire seed and L.S. seed, $\times 1$. 24-27, *Helicia erratica*: 24, entire fruit, $\times 1$; 25, T.S. fruit, $\times 1$; 26, entire seed, $\times 1$; 27, L.S. seed, $\times 1$; 28, 29, *Xylomelum pyriforme*: 28, a dehiscenced fruit, $\times \frac{1}{2}$; 29, a seed, $\times \frac{1}{2}$; 30, a fruit of *Panopsis mucronata*, $\times 1$; 31, 32, *Macadamia tetraphylla*: 31, a dehiscenced fruit, $\times 1$; 32, T.S. seed, $\times 1$; 33, L.S. fruit of *Heliciopsis* sp., $\times \frac{1}{2}$. (SC, seed coats; C, cotyledons; E, exocarp; EN, endocarp).

In all taxa the seeds are non-endospermic and fleshy (megaspermous) and store abundance of food materials in their fleshy cotyledons (Figs. 22, 25, 27, 32, 33). They are spherical (or hemispherical when two seeds develop in one carpel) in *Macadamia* (Fig. 32), oblong in *Heliciopsis* (Fig. 33), top-shaped and rugulose in *Helicia erratica* (Fig. 26) and somewhat flattened in *Brabeium* (Fig. 23). In *Xylomelum* and *Carnarvonnia* they are flat and show a terminal membraneous wing (Fig. 29). In general the seed coat is thin and flimsy but in *Macadamia* it is 3-4 mm thick and makes the seed one of the hardest among angiosperms (Fig. 32).



FIGS. 34-45. Floral anatomy of Macadamieae. 34, 35, L.S. and T.S. base of the bud of *Brabeium stellatifolium*; 36, L.S. base of the bud of *Macadamia tetraphylla*; 37, T.S. bud of *M. minor*; 38-40, *Roupala brasiliensis*, T.S. of bud at different levels; 41, T.S. bud of *Panopsis multiflora*; 42, T.S. bud of *Xylomelum pyriforme*; 43, T.S. bud of *Helicia glabrescens*; 44, T.S. bud of *H. erratica*; 45, T.S. bud of *Hicksbeachia pinnatifolia*. All figs. $\times 25$. (*f*, filament; *n*, nectary; *tm*, tepal midrib; *tl*, tepal lateral; *cti*, conjoint tepal lateral; *stt*, staminal trace; *nb*, nectary bundles; *sc*, connective of stamen; *st*, style; *tt*, transmitting tissue; *ct*, carpellary traces.)

The arborescent habit, large compound mesophytic leaves, cauliflory, drupaceous fruits and megaspermous seeds are characteristics of plants of rain-forests while the shrubby habit, sclerophyllous leaves, follicular fruits and winged seeds are typical of vegetation of arid regions. So morphological evidence points to the ancestral stock of Macadamieae having originated under rain-forest conditions and migrated into open, arid regions.

The seed kernels of *Macadamia* are edible. Different species like *M. tetraphylla* and *M. integrifolia* are cultivated in Australia and Hawaii (on a larger scale). Attempts are being made to grow them in the Nilgiris.

Floral anatomy—The common stalk of the flower pair in *Helicia erratica* shows a ring of vascular bundles at the base from which a trace arises for the common bract. Then the ring expands laterally and becomes deeply two-lobed coincident with an increase in the number of vascular bundles due to splitting. One trace is given off from each lobe for the individual bract of the flower after which the bundles form two complete rings one for each flower. Thus anatomy gives evidence that the common stalk is a lateral peduncle and the flower pair is a reduced branch inflorescence. This fact is also borne out by the difference in orientation of the flowers of a pair relative to each other in different genera of Macadamieae.

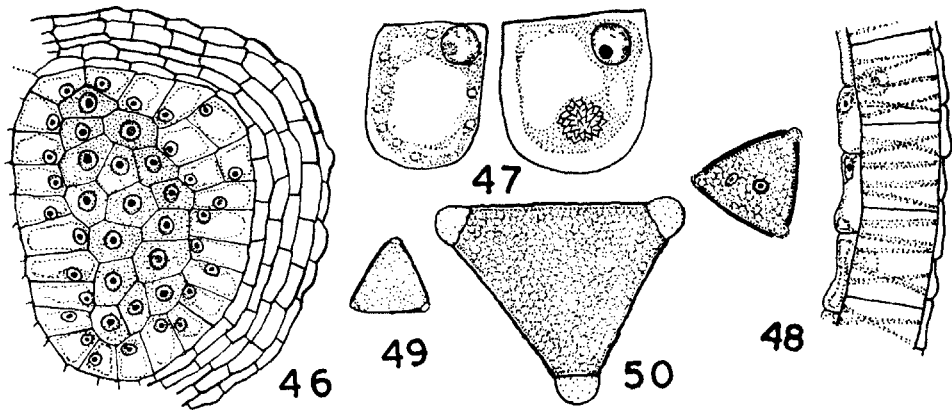
The pedicel shows a ring of about eight vascular bundles which branch and increase in number in the thalamus. Depending upon whether the thalamus is horizontal (*Brabeium*, *Macadamia*) or oblique (*Xylomelum*) the origin and emergence of floral traces are either symmetrical (Figs. 34, 36, 38) or asymmetrical (Fig. 42). The tepals are 3-traced; since the tepal marginals are connate in all members, eight traces depart as the first whorl from the floral stele. Four of these are the conjoint tepal laterals and the alternate four the tepal midribs, their morphology depending upon the position of the tepals on the thalamus. The conjoint tepal laterals split close to their origin and demarcate the marginal bundles of adjacent tepals (Fig. 38).

Close to the origin of the tepal midribs and from the same gaps pairs of bundles are given off which function as the staminal traces as in most genera of Proteaceae (Fig. 42). Each pair enters the base of a tepal where they fuse to form the single staminal trace (Figs. 37, 42, 43). This runs parallel to the tepal midrib in the limb of the tepal and emerges into the filament when this separates out (Figs. 35, 41). Though the filament and tepal tissues are fused, their traces always stand separate; sometimes the outline of the filament can be followed on the tepal below the attachment of the anther. Adnation of the stamen and tepal traces was never noticed in any of the Macadamieae. The staminal bundle may terminate in the connective itself or extend into the appendage (Fig. 40).

After the emergence of the staminal traces, the stelar bundles of the alternitpalous sectors emit some strands to the outside which feed the nectary

(Fig. 37). These may branch further (Fig. 39) but always terminate at about half the height of the nectary (Fig. 36). No such strands are noticed in the nectary of *Brabeium*. The remaining bundles of the stele reorientate as five to seven carpellary traces which traverse the ovary wall after slight branching (Fig. 43). The carpellary margins are incompletely fused especially at the level of ovule attachment and their epidermal layers run continuous (Fig. 44). Three or five bundles of the ovary enter the base of the style but only the dorsal bundle runs to the top. The core of the style is filled with glandular cells of transmitting tissue (Fig. 40).

Microsporogenesis and male gametophyte—Of the five layers of anther wall, the epidermis shrinks and the sub-epidermal layer enlarges considerably and functions as the fibrous endothecium (Fig. 48); the two middle layers get crushed and absorbed and the innermost layer functions as the secretory tapetum. In all members of Macadamieae studied, the tapetal cells were seen to remain 1-nucleate as was also reported by Kausik (1939) in *Macadamia ternifolia*. In *M. minor* each full-grown tapetal cell shows a plate-like or sphaeroidal crystal of calcium carbonate (druse), a feature not noticed in any other Proteaceae. After the formation of microspore tetrads, these crystals disappear and the cytoplasm of the tapetal cell shows some globular bodies which do not stain with iodine (Fig. 47). The cells of the connective show abundance of tannin and starch.



FIGS. 46-50. Microsporogenesis and male gametophyte in Macadamieae. 46, T.S. anther lobe of *Hicksbeachia pinnatifolia*, $\times 300$; 47, tapetal cells (dissected out) of *Macadamia minor*, $\times 750$; 48, T.S. anther wall and a pollen grain of *M. minor*, $\times 450$; 49, 50, pollen grains of *Helicia erratica* and *Xylomelum occidentale* respectively, $\times 450$.

The archesporium consists of one to two rows of hypodermal cells in each of the four lobes of the anther. These form by periclinal division the primary parietal cells to the outside and the primary sporogenous cells to the inside. There is a secondary increase of sporogenous tissue in all members studied

(Fig. 46). Meiotic divisions in the microsporocytes proceed normally; 14 bivalents were noticed in *Macadamia tetraphylla* during meiosis I. The microspore tetrads are tetrahedral and cytokinesis is brought about by simultaneous furrowing.

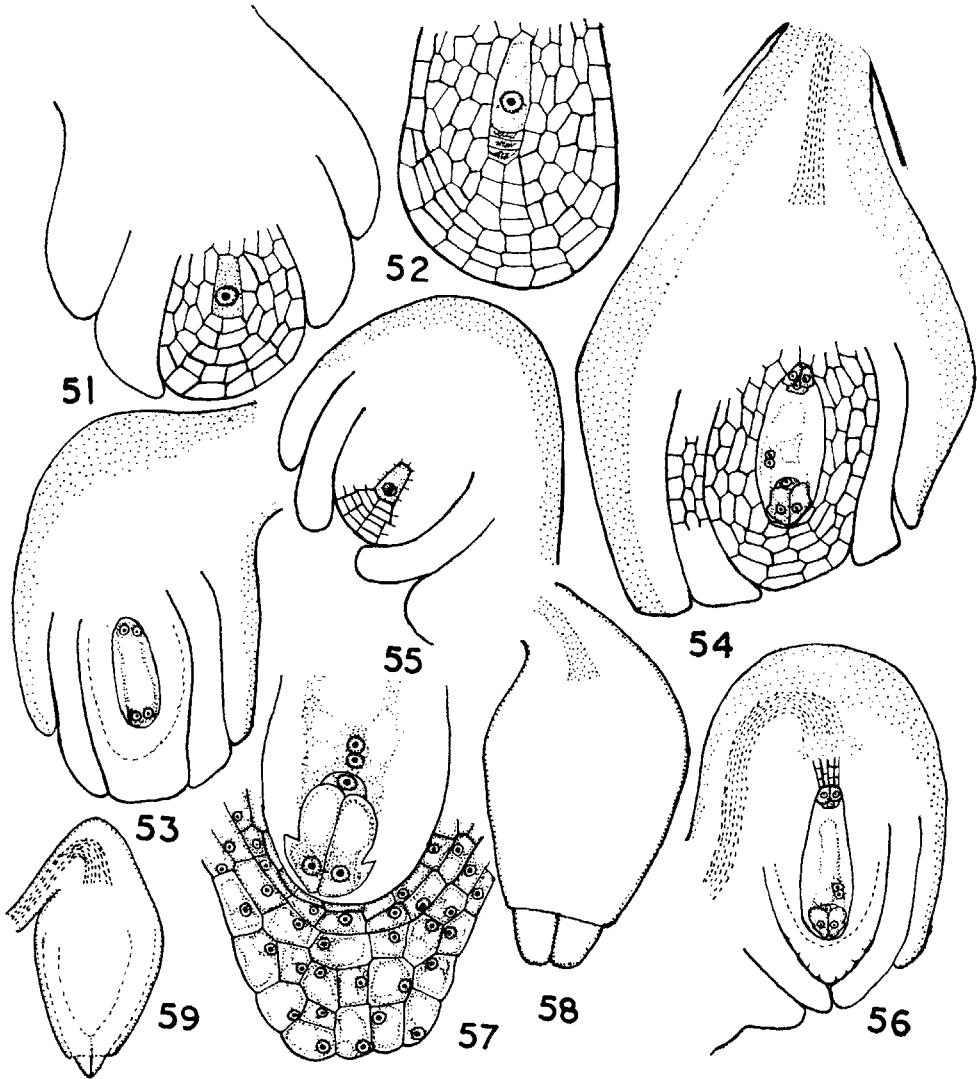
In general, the pollen grains in Macadamieae show several features which are regarded as primitive from comparative studies (Venkata Rao 1965). They are small in size, smooth-walled, triangular, triporate, angulaperturate, with narrow germ pores. The pollen grains of *Helicia erratica* are the smallest and those of species of *Xylomelum* the largest in the tribe (Figs. 49, 50). In *Xylomelum* the pollen grains show wide germ pores through which the intine protrudes forming knob-like swellings as was noticed in *Petrophila teretifolia* (Venkata Rao 1969a). The pollen grains are shed at the 2-celled stage; the vegetative cytoplasm stores abundant starch.

Megasporangium, megasporogenesis and female gametophyte—The ovules are bitegmic and crassinucellar in all Macadamieae. They are commonly orthotropous or hemianatropous (*Roupala*) and either pendulous from the top of the loculus or slightly lateral (Figs. 51, 58, 59). Such a variation is seen within *Macadamia* (Figs. 53, 54) as was also noticed in *Aulax* (Venkata Rao 1970). In *Helicia* the ovules are basal and anatropous (Figs. 55, 56). Comparative studies show that this is the most highly evolved condition in the Proteaceae and is found only in a few genera like *Stirlingia* and *Grevillea* (Venkata Rao 1967a, 1969a). As in other Proteaceae, only the inner integument forms the micropyle in most genera. However, in all species of *Macadamia* examined, both integuments stand only as high as the nucellus so that a micropyle is not formed even in the mature ovules (Figs. 53, 54) and the pollen tube penetrates the naked nucellus directly. The outer integument is usually 2-layered (three to four cells thick in *Macadamia*) and the inner integument is three to four cells thick. The cells of the nucellar epidermis divide periclinally and form a nucellar cap (Figs. 51–55). In *Helicia erratica* a hypostase of thick-walled cells is noticed below the embryo sac; the cells of nucellus above the embryo sac are richly protoplasmic (Figs. 56, 57). Tannin is found in the cells of the integuments and chalaza.

A single hypodermal archesporial cell is noticed in each ovule. The megaspore mother cell becomes deep seated due to the development of parietal layers and nucellar cap (Figs. 51, 55). The megaspore tetrads are linear (Fig. 52) and development of the embryo sac conforms to the *Polygonum* type. The synergids are hooked and the polar nuclei fuse only at the time of fertilization. The three antipodal cells are ephemeral.

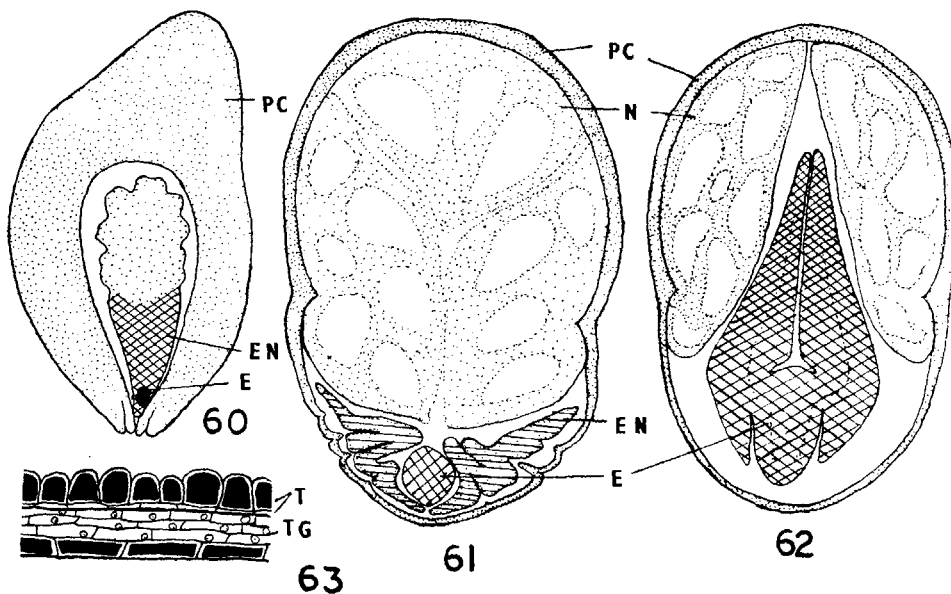
Seed development—The seed development was followed in *Macadamia tetraphylla* and *Helicia erratica*. The endosperm is of the nuclear type. In *Macadamia* the nucellus is absorbed quickly after fertilization and the endosperm extends into the seed cavity. It shows an early differentiation into

the cellular and nuclear regions. The nuclear part shows only slight haustorial activity as is evident from its scanty lobing (Fig. 60). In *Helicia erratica* the embryo sac expands mostly to the sides and the endosperm occupies the space thus formed. The endosperm is relatively scanty and the nucellus (perisperm), which persists till an advanced stage even after the whole of the



FIGS. 51-59. Megasporogenesis and female gametophyte in Macadamieae. 51-53, *Macadamia minor*: 51, L.S. young ovule with megaspore mother cell, $\times 300$; 52, L.S. nucellus with linear tetrad, $\times 300$; 53, L.S. ovule with 4-nucleate embryo sac, $\times 150$; 54, L.S. mature ovule of *M. tetraphylla*, $\times 265$; 55-57, *Helicia erratica*: 55, L.S. young ovule with megaspore mother cell, $\times 180$; 56, L.S. mature ovule, $\times 180$; 57, L.S. micropylar part of nucellus and embryo sac, $\times 450$; 58, entire ovule of *Hicksbeachia pinnatifolia*, $\times 75$; 59, entire ovule of *Roupala brasiliensis*, $\times 50$.

endosperm is absorbed, seems to function as the important source of food (Figs. 61, 62). This recalls the condition in *Cenarrhens nitida* of Persoonieae, which was regarded as very primitive (Venkata Rao 1967c).



FIGS. 60-63. Seed development in some Macadamieae. 60, L.S. developing seed of *Macadamia tetraphylla*, $\times 20$; 61, 62, L.S. developing seeds of *Helicia erratica*; 61, $\times 15$; 62, $\times 10$; 63, T.S. seed coats, $\times 180$. (PC, perichalazal region; EN, endosperm; E, embryo; N, nucellus; T, testa; TG, tegmen.)

A specially interesting feature in both taxa studied is the development of the perichalazal region of the seed. In *Macadamia* the integuments practically do not show any growth after fertilization and remain distinct only for a short distance around the micropyle (Fig. 60) which is formed at the seed stage. The rest of the seed is the result of enormous growth of the perichalazal region. This forms the massive seed coat which, therefore, is not homologous to the seed coats (testa and tegmen) of other Proteaceae. All cells of the coat become highly sclerified. In *Helicia* also the perichalazal region shows much growth. This region is thicker and is marked off from the region formed by the integuments by a transverse infolding (Figs. 61, 62) which is evident even on the surface of the seed (Fig. 26). The seed coats are flimsy and consist of 2-layered testa and 4-layered tegmen (Fig. 63).

DISCUSSION

From the above account it is clear that the Macadamieae form a homogeneous tribe with well-defined features, viz. predominantly arborescent habit, compound or expanded leaves, paniculate or pseudoracemose inflorescences,

presence of lateral peduncles and/or pedicels for flowers, common bracts for flower pairs, regular flowers, straight flower buds, slight adnation between tepal and stamen, their traces remaining free, apiculate stamens, symmetrical nectary of four free or connate lobes, sessile hairy ovary, straight style, simple terminal stigma, indehiscent or tardily dehiscent fruits and large fleshy seeds. In most of the above features which are essentially primitive, the Macadamieae show close resemblance to Persoonieae (Proteoideae) from which they seem to be derived. This conclusion is also supported by cytological evidence: the haploid chromosome number of 14 reported in six genera of Macadamieae seems to be a polyploid of $n = 7$ of *Persoonia* (Persoonieae).

The Macadamieae show some features of evolution that are noticed in other tribes of Grevilleoideae, and also interesting transitional stages which indicate that they are a primitive stock in which some evolutionary modifications have already occurred, as shown in Table II.

TABLE II

Primitive	Transitional	Advanced
Rain-forest trees		Shrubs of open spaces
Large, compound, mesophytic leaves	Lobed or dissected leaves	Small, simple, sclerophyllous leaves
Large paniculate, terminal inflorescences		Unbranched, axillary pseudo-racemes
Leaf-like bracts		Simple scaly bracts
Solitary and clustered flowers		Flowers in pairs
Flower pairs with peduncles, pedicels and common and individual floral bracts		Flower pairs without common peduncles and/or pedicels and floral bracts
Perianth antero-posterior and lateral on thalamus		Perianth diagonal
Filament nearly free from tepal		Filament adnate throughout its length
Nectary absent	Nectary of four free lobes	Nectary ring- or cup-like
Style tapering, stigma simple and punctiform		Stigma cleft-like, subtended by fusiform style-end
Small pollen with narrow germ pores		Large pollen with wide germ pores and protruding intine
Orthotropous ovules pendulous from top of locules	Orthotropous or hemianatropous lateral ovules	Anatropous, basal ovules
Succulent drupes	Drupaceous nuts	Follicles
Large fleshy rounded seeds with abundance of stored food		Small flat dry seeds with samaroid wing

Johnson and Briggs (1963) remark that the tribe Macadamieae 'is not marked off by any particular combination of advanced features and is scarcely a natural tribe', and that it was retained by them 'simply as a convenient receptacle for many genera which share reduction to two ovules'. However,

the tribe was not delimited by the author on the basis of advanced characters; in fact, it was regarded as the most primitive tribe of the Grevilleoideae (as it combines the largest number of primitive features) and placed as the first of its tribes (Venkata Rao 1957a, 1957b). The reason why Johnson and Briggs are not able to recognize it as homogeneous and natural tribe is because they have meddled with the integrity of the tribe by excluding one genus (*Carnarvon*) and including two other genera (*Kermadecia* and *Gevuina*) which were placed in Grevilleae by the author.

Johnson and Briggs (1963) suggest the exclusion of *Carnarvon* from Macadamieae (though they did not define its position in their scheme) because 'its inflorescence suggests an earlier independent divergence'. However, the morphological features of the genus and its chromosome number of $n = 14$ definitely point to the genus belonging to Macadamieae. The arborescent habit, compound leaf, paniculate inflorescence, leaf-like bracts, solitary and clustered pedicellate flowers, their glandless condition, tapering style and punctiform stigma mark it off as the most primitive genus among the Macadamieae and a good connecting link with the Persoonieae.

In suggesting the inclusion of *Kermadecia* and *Gevuina* in Macadamieae Johnson and Briggs (1963) have ignored the most important characteristic on which the tribe was erected by the author, viz. the regular flower. In both the above genera the flowers are zygomorphic due to a 2- or 3-lobed nectary (*Kermadecia*) or a curved style with discoid pollen-collecting apparatus (*Gevuina*). So it is evident that the genera do not fit into Macadamieae.

On the basis of morphological features (habit, leaf, fruit and seed characters), it was concluded that the ancestral Macadamieae originated under rain-forest conditions and migrated into the open, arid regions. From their geographic distribution some conclusions can be drawn regarding the probable centre of origin of the Macadamieae and the causes which led to their present-day discontinuous distribution. Six out of the nine genera are found in Australia, of which three are endemic; two endemic genera are found in South America and one monotypic genus in South Africa. The (morphologically) most primitive genera, *Carnarvon* and *Hicksbeachia*, are found in Australia; the extra-Australian genera resemble the relatively advanced genera of Australia. These facts suggest Australia as the probable centre of origin of the tribe. The distribution pattern of the taxa within Australia gives more definite clue to the place of origin. All the six genera are represented in East Australia, of which two (*Carnarvon* and *Hicksbeachia*) are endemic here; *Xylomelum* is the only genus found in West Australia and even this has more species in East (3) than in West (2) Australia. Some of the East Australian genera are represented in the neighbouring islands—New Caledonia, Celebes (*Macadamia*) and New Guinea (*Helicia*). *Helicia* is the largest genus of Macadamieae and has the widest range not only among the tribe but in the whole family. It is the only

genus which extends farthest into the northern hemisphere up to South Japan. Some authors like Berry (1916), Sleumer (1954) and Ramsay (1963) believe that the Proteaceae originated in the north and migrated into the south and that the distribution pattern of *Helicia* suggests the path of migration into Australia. However, the concentration of the family as well as the Macadamieae in Australia and the species concentration of *Helicia* itself in New Guinea strongly point to the origin of the taxa in the south and their northern extensions. The range of *Heliciopsis* falls within that of *Helicia*; the genus resembles *Helicia* in most features and differs from it only in dioecy and pericarp structure. *Heliciopsis*, therefore, seems to have originated from *Helicia* by gene mutations.

The species concentration in East Australia, occurrence of primitives of the tribe, endemism and community at the generic level which it shows with neighbouring islands, strongly point to East Australian region on a once continuous land mass (Pangaea or Gondwanaland) being the most probable centre of origin for the Macadamieae. Geologists like du Toit (1937) and Carey (1955) think that the continents of Australia, South America and Africa and the Pacific islands (New Guinea, New Caledonia, etc.) formed parts of this continent. Probably the ancestral Macadamieae were spread over such a continent by the time fragmentation started and the stocks became isolated when the land masses drifted apart.

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