STUDIES IN THE PROTEACEAE

1. TRIBE PERSooniEEAE

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ABSTRACT

Morphological floral anatomical, embryological and cytological (where fresh material was available) studies have been made in 6 genera and 25 species of the tribe Persooniaceae and the data have been made use of in discussing the inter-relationships among the genera and the evolutionary trends within the tribe.

Bellendena (n=5) and Persoonia (n=7) are the most primitive and the only diploid genera in the family. The remaining genera (Symphyomena n=10; Cenaarhenes, n=14; and Brabeium n=14) seem to be tetraploids on bases 5 and 7 respectively while Agastachys (n=13) seems to be a hypoploid.

The close similarity between the Australian and extra-Australian Persooniaceae points to a common ancestry for them. Due to species concentration and presence of the two diploid genera in East Australia, the latter is considered to be the probable centre of origin of the tribe wherefrom ancestral stocks seem to have migrated to other land masses.

INTRODUCTION

The family Proteaceae comprises 63 genera and about 1,400 species of trees and shrubs, with exstipulate, simple or compound, alternate or sometimes opposite or whorled leaves. Many species show xeromorphic features. The flowers occur singly or in groups in the axils of bracts in the subfamily Persoonioideae, in pairs in the Grevilloideae, and form racemose inflorescences. They are hypogynous, monochlamydeous, 4-merous and regular or zygomorphic. Though they are usually hermaphrodite, partial male sterility, gynodioecy and dioecy are noticed in a few genera. There are four valvate tepals which are sometimes petaloid and connate. These are antero-posterior in all Persoonioideae and the relatively primitive Grevilloideae, but diagonal to the bract in the more advanced genera of the latter. The four stamens are antetepalous, 4-locular, epiphyllyous and introrse, except in Conospermeae in which they are 2-locular and extrorse. In Stirlingia and Conospermeae, the anther loculi are connate. In several members there is a hypogynous nectary with 4 free alternatepalous lobes; these are sometimes fused into a cup and in the more advanced genera, the nectary becomes zygomorphic due to the suppression of one or two anterior lobes. The pistil is monocarpellary and stipitate or sessile; the style is either straight with simple, terminal stigma or curved with a lateral stigma situated at the middle of a discoid pollen collecting apparatus. The ovary bears either 4 or more ovules on marginal placenta, or two or one pendulous, lateral or basal ovules, the micropyle of which faces the base of the loculus. The fruit is indehiscent in the Persoonioideae, being a nut, drupe or samara; in the Grevilloideae it is usually a follicle with winged seeds. The seeds are mostly non-endospermic.

The large majority of the living Proteaceae are confined to the southern hemisphere; species of Protea and Faurea extend into temperate Africa. Helicia is the only genus of which a few species extend as far north as South Japan (Map I).

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Robert Brown (1810) divided the Proteaceae into two sub-families, the Nucamentaceae and the Folliculaires; he divided the former into 4 tribes and the latter into 3. Bentham (1870) accepted this classification since it was also in keeping with the geographic distribution of the family: the first sub-family occurs in S. Africa and second in S. America and both sub-families occur in Australia. Engler (in Engler and Prantl, 1894) while accepting Brown’s classification in principle, altered the names of the sub-families into Persoonioideae and Grevilloideae respectively. Engler’s views regarding evolution within the family are represented schematically in Fig. 1.

![Diagram of Proteaceae evolution]

Fig. 1.—Evolution within Proteaceae according to the views of Engler.

Recently Sleumer (1954, 1955a, 1955b) published some taxonomic accounts in which he redefined the limits of some genera of old and new world Proteaceae. He accepted, however, the classification of Engler and made no attempt at redefining the tribes. About 150 species have been added to the Australian Proteaceae since Bentham’s (1870) account (Mr. J. H. Willis of Melbourne Herbarium in a personal communication) and new species have been reported also from America (Jose, 1950). The following genera have been added since Engler’s publication: Hicksbeachia (Mueller, 1883), Musgravea (Mueller, 1890) Hollandaeca (Mueller, 1899), Placospernum (White and Francis, 1923), Austromuellera (White, 1930), Opistholepis (Smith, 1952) and Heliciopsis (Sleumer, 1955b). The systematic position of Musgravea and Austromuellera has not been fixed by their respective authors.

There is much diversity of opinion regarding the taxonomic position of the Proteaceae. Bentham and Hooker (1862–1883) include it in the series Daphnales of the Monochlamydeae along with the families Lauraceae, Thymelaeaceae, Elaeagnaceae and Penaeaceae. Engler (1894), Hutchinson (1926), Rendle (1952) and Lawrence (1955) place it by itself in the order Proteales. Lawrence (I.c.) summarises the opinions of the various taxonomists regarding the phylogeny and affinities of the family as follows: "Halleier accepted Engler’s view of primitiveness of the order and considered it derived from his Proberberidaceae. Bessey expressed doubt as to its relationship and placed it in the Sapindales as phylogenetically more advanced than the amertiferous families also assigned to the Rosales. Rendle, following Engler, placed the order between the Urticales and Sapindales noting that it was difficult to associate it phylogenetically with other orders. Hutchinson considered it a terminal taxon derived from stocks ancestral to the Thymelaeaceae".
Lawrence himself is of the opinion that the order is not basically primitive though it cannot yet be closely related to any existing order and concludes: "these views are divergent and are evidence of the need of much further study on the phylogeny of the order".

**Previous Work**

Cretaceous and tertiary fossils, supposed to belong to the Proteaceae, have been reported from different parts of the world including Greenland in the north and Grahamland in the south. Kausik (1943) reviewed the previous literature on the subject. Since then, Simpson has reported pollen of *Faurea, Petrophila* and *Lambertia* from the Tertiary of Scotland (Walton, 1953). Cookson (1950, 1953, 1956), Cookson and Duigan (1950), Cookson and Pike (1954) and Pike (1953) have described proteaceous pollen and fruits of *Bankia* from Tertiary of Australia. There is still much controversy regarding the occurrence of fossil Proteaceae in the northern hemisphere. This topic will be considered later in an article dealing with the origin of the family.

Chromosome numbers have been determined in 8 African genera by de Vos and about 15 Australian genera by Lancaster, and Blackwood (cf. Brock, 1954, and Darlington and Wylie, 1955).

Chattaway (1948a, 1948b) has studied the wood anatomy of about 30 genera of the family. The wood of *Bankia* and *Dryandra* which form a very natural tribe, the Banksieae, is not only distinctive from that of other tribes of the family but unique in showing radially aligned vascular tissue in the rays. Chattaway opines (in a personal communication) that in other tribes it is difficult to describe the wood as primitive or evolved or distinctive.

Kausik (1938b, 1940a, 1941) studied the floral anatomy of *Macadamia ternifolia* and *Grevillea robusta* and came to the conclusion that the perianth in the family represents the calyx and that the nectary is homologous to the corolla which is on the verge of extinction.

Embryological studies in the family are meagre. Development of the gametophytes has been studied by Ballantine (1909) in *Protea lepidocarpon*, Messeri (1928), Brough (1933), Kausik (1938a) in species of *Grevillea*, Kausik (1940) in *Hakea saligna* and by Jordaan (1946) and Garside (1946) in *Brabeium stellatifolium*.

Berry (1916) from fossil evidence, Lancaster (1952) from cytological studies and Levyns (1958) from a study of the phytochorographic distribution of the African Proteaceae, favour a northern origin of the family and its southward migration.

Due to the meagre cytological, floral anatomical and embryological studies, the Proteaceae remains one of the incompletely understood families of angiosperms.

The following points require clarification:

(a) **Morphological**: Are the flowers in Proteaceae primitively monochlamydeous or simple due to reduction? What is the nature of the perianth and the morphology of the nectary? What is the significance of the arrangement of the flowers regularly in pairs in Grevilleoideae?

(b) **Taxonomic**: How far are the tribes as at present constituted natural and homogeneous? Do all genera known to date fit into the existing tribes? What are the evolutionary tendencies among the tribes and within the family?

(c) **Phylogenetic**: Is the family monophyletic or polyphyletic? Monotopus or polytopus? What are its affinities and evolutionary potentialities?

(d) **Distributional**: How is the present disjunct distribution of the family to be accounted for? Does the present day geographic distribution or geological history throw any light on the time and place of origin of the family?

In a previous article, the writer (Venkata Rao, C. 1957) postulated the criteria of taxonomic value made use of in the revision of the family by him, and also
### Table I

**Materials studied**

<table>
<thead>
<tr>
<th>No.</th>
<th>Genus</th>
<th>Total no. of species</th>
<th>Geographic distrbn.</th>
<th>Species examined</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td><em>Bellendenia</em> Br.</td>
<td>1</td>
<td>Tasmania</td>
<td><em>B. montana</em> Br.</td>
<td>! Tasmania</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. virgata</em> Br.</td>
<td>F.H. Mr. L. S.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. nutans</em> Br.</td>
<td>Smith, Queensland</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. salicina</em> Pers.</td>
<td>do</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. ferrarinea</em> Sm.</td>
<td>do</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. myrtilloides</em> Sieb.</td>
<td>do</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. ozyccoccoides</em> Sieb.</td>
<td>do</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. lanceolata</em> Andr.</td>
<td>N.S.W.</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. pinnifolia</em> Br.</td>
<td>N.S.W.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. linearis</em> Andr.</td>
<td>N.S.W. and</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. chamaepence</em> Lhotk.</td>
<td>N.S.W. R.H.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. rigida</em> Br.</td>
<td>do</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. caleyi</em> Br.</td>
<td>N.S.W. and</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. microcarpa</em> Br.</td>
<td>Vic. R. H.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. longifolia</em> Br.</td>
<td>do</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. saundersiana</em> Kipp.</td>
<td>do</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. saccata</em> Br.</td>
<td>!do</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. juniperina</em> Labill</td>
<td>!Tas.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. gunnii</em> Hook.f.</td>
<td>!Tas.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>P. toru</em> Br.</td>
<td>H. New Zealand</td>
</tr>
<tr>
<td>3.</td>
<td><em>Cenarrhenes</em> Labill.</td>
<td>2</td>
<td>Tasmania</td>
<td><em>C. nitida</em> Labill.</td>
<td>!Tasmania</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td><em>Agastachys</em> Br.</td>
<td>1</td>
<td>Tasmania</td>
<td><em>A. odorata</em> Br.</td>
<td>!Tasmania</td>
</tr>
<tr>
<td>5.</td>
<td><em>Symphyotheca</em> Br.</td>
<td>2</td>
<td>N.S.W.</td>
<td><em>S. paludosum</em> Br.</td>
<td>R.H.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>S. montana</em> Br.</td>
<td>H. Melbourne Herbarium</td>
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<tr>
<td>7.</td>
<td><em>Garnieria</em> Brongn. et. Gris.</td>
<td>1</td>
<td>New Caledonia</td>
<td>Nil</td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td><em>Diloehia</em> Thou.</td>
<td>1</td>
<td>Madagascar</td>
<td>Nil</td>
<td></td>
</tr>
<tr>
<td>9.</td>
<td><em>Brabeium</em> L.</td>
<td>1</td>
<td>S. Africa</td>
<td>Nil</td>
<td></td>
</tr>
</tbody>
</table>

**Abbreviations used:** 
- 'collected by the writer; R.H. = Rodway Herbarium; F.M. = fixed material; 
- H = herbarium specimen; N.S.W. = New South Wales, Vic. = Victoria.

The author gave a synopsis of the new classification. In the present studies he proposes to describe his observations on cytology, morphology, floral anatomy and embryology of a large number of members examined and discuss the various problems posed above.
The present studies were made on fresh material collected by the writer during his stay and tour of Tasmania and Australia and also materials obtained from other sources which are acknowledged below. Where fresh material was not available, herbarium material was used for morphological and floral anatomical studies. The genera, number of species in each genus, their geographic distribution, the species examined and their source are given in Table 1.

For cytological studies, aceto-carmoyloid smears of flower primordia, root tips and young anthers were examined. Microtome sections stained in Crystal Violet according to the schedule given by Darlington and LaCour (1955) were also used. For floral anatomical and embryological studies, materials fixed in formalin acetic alcohol or even in 70 per cent alcohol were used with satisfactory results. Delafield’s Haematoxylin, Safranin and Fast Green or Crystal Violet and Erythrocyan were used as stains. For a study of endosperm haustoria whole mounts were made according to the method given by Kausik (1938, 1942). Studies in anatomy of vegetative parts were also made in a few cases; both microtome and free hand sections, stained in Safranin and Fast Green were used.

Where herbarium material was used, it was soaked overnight in 5 per cent teepol solution for morphological investigations. For microtoming, the material was kept in 1 per cent solution of caustic soda at 50°C for 12–24 hours, washed thoroughly and then treated like freshly fixed material.

Cytology

Though Bentham (1870) described the stamens in Bellendena montana as 'all perfect', the writer noticed that it shows a gynodioecious system of sex distribution i.e., the occurrence of male sterile (functionally female) and hermaphrodite flowers on separate plants. Unlike in the gynodioecious species of New Zealand Fuchsia (Godley, 1955), the flowers in Bellendena are morphologically indistinguishable. In Proteaceae, partial male sterility (i.e., sterility of one or more stamens of a flower) is noticed in Persoonia hakeaeforvis, Adenanthos sp., Synaphea, Conospermum, Placocarpum and Protea sp. and dioecy in Leucadendron and Heliciopsis, but Bellendena is so far the only member in which gynodioecy is reported.

A study of populations of Bellendena growing on Mt. Wellington and Mt. Field National Park showed female percentages ranging from 34.5 to 48.0 as shown in Table 2.

Table II

Gynodioecy in Bellendena montana

<table>
<thead>
<tr>
<th>No.</th>
<th>Locality</th>
<th>Male sterile plants</th>
<th>Total population studied</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Percentage</td>
<td></td>
</tr>
<tr>
<td>1.</td>
<td>Mt. Wellington/Summit</td>
<td>45</td>
<td>45.0</td>
</tr>
<tr>
<td>2.</td>
<td>do First Marsh</td>
<td>40</td>
<td>34.5</td>
</tr>
<tr>
<td>3.</td>
<td>Mt. Field National</td>
<td>Park–Dobson Huts</td>
<td>47</td>
</tr>
<tr>
<td>4.</td>
<td>do Wombat moor</td>
<td>59</td>
<td>48.0</td>
</tr>
</tbody>
</table>

Gynodioecy is a stable genetic system which promotes outbreeding since the female flowers must necessarily be fertilised by the hermaphrodites. It is reported in several unrelated families of angiosperms viz., Acanthaceae (Santiera hortensis)
Compositeae (*Circium oleraceum*), Labiatae (*Origanum vulgare*) and Gramineae (*Lolium perenne*). Allen (1940) believed that gynodioecy is derived from hermaphroditism and is transitional to dioecy, but Lewis (1942) considered it to be an independent sexual system and not a step towards dioecism because in Labiatae which contains about 90 per cent of the reported gynodioecious species, there are

**Figs. 2-18.**—Figs. 2-9. *Bellendena montana.* Fig. 2. Mitotic metaphase plate from section of root tip, c.v. stain. Fig. 3 Mitotic metaphase plate form smear of root tip after cold treatment; note banded appearance of the chromosomes. Fig. 4. Late prophase from p.m.c. Fig. 5. Metaphase I showing terminal association and precocious separation of homologues of a pair. Fig. 6. Late anaphase I showing formation of a fragment. Fig. 7. Telophase I showing division of fragment into chromatids. Fig. 8. Anaphase II showing formation of a fragment. Fig. 9. A polyad of microspores. Figs. 10 and 11. *Persoonia juniperina.* Fig. 10. A mitotic metaphase plate from tapetal cell. Fig. 11. Metaphase I from p.m.c. Figs. 12 and 13. *P. gunnii.* Fig. 12. Metaphase I from p.m.c. Fig. 13. Late anaphase II. Figs. 14-16. Genarrhenes nitida. Fig. 14. Mitotic metaphase plate from a tapetal cell. Figs. 15 and 18. Prophase I and Metaphase II from p.m.c. Figs. 17 and 18. Agastachys odorata. Fig. 17. Mitotic metaphase plate from cell of flower primordium. Fig. 18. Metaphase I from p.m.c.
no dioecious species at all. From the classical experiments of Correns (1928) which showed that both the females and hermaphrodites breed true, it was believed that gynodioecism is under the control of a permanent cytoplasmic particle or plasmagene. However, from a study of the breeding system in *Origanum vulgare*, Lewis and Crowe (1956) conclude that gynodioecism in this species is controlled by two independent genes.

The chromosome numbers in *Bellendena montana* as determined from squashes of young anthers and root tips are $n=5$ and $2n=10$. The chromosomes range from 4–62 in length and are relatively thick (Fig. 2). One pair is distinctly longer than the rest and shows a sub-median constriction; one pair is short and the rest intermediate in size. No secondary constrictions or trabants are noticed. Such simple karyotypes are usually seen in primitive plants. Chromosomes of the root tips after 24 hours of cold treatment at 0°C showed a banded appearance suggesting the presence of heterochromatic segments (Fig. 3) as Smith-White (1955) also found in *Leucopogon juniperinus*.

In the majority of the p.m.c. pairing and disjunction of chromosomes are normal and 1–4 chiasmata are noticed in each bivalent (Fig. 4). The X-α frequency obtained from a count in 10 cells chosen at random is 2.1 per pair. In less than 1 per cent of the cells, one pair of chromosomes showed irregular pairing which ranged from a slight terminal association and precocious separation (Fig. 5) to the absence of pairing. In a few cases a chromosome bridge and a fragment are noticed during anaphase I or II (Figs 6 and 8), which show that one of the pairs is heterozygous for an inversion. The fragment forms micronuclei and super-numerary microspores after or without division into chromatids so that polyads with 5–7 microspores were noticed (Figs. 7 and 9). The spores formed by the micronuclei and those formed by nuclei deficient in the full chromosome complement give rise to sterile pollen grains. These form less than 10 per cent of the grains of fertile anther loculi. Lawson (1930) reported the occurrence of larger percentages of sterile pollen in several mainland species of the Proteaceae.

The chromosome numbers in *Persoonia gunnii* and *P. juniperina* as determined from squashes of young anthers, are $n=7$ and $2n=14$ (tapetal cells). The chromosomes are relatively thicker and longer than those of *Bellendena* and showed no secondary constrictions or trabants (Fig. 10). Pairing and disjunction of chromosomes are normal (Figs. 11–13). Lancaster (1952) reported the same numbers in some mainland species of *Persoonia*. She also found that a secondary constriction occurs in one of the pairs near to the centromere.

Smears of the p.m.c. of *Cenarrhenes nitida* showed 14 bivalents and tapetal cells showed $2n=28$ (Figs. 14–16). The chromosomes are short and somewhat thick. Meiotic divisions proceed normally.

In *Agastachys odorata* the chromosome numbers are $n=13$ and $2n=26$ (Figs. 17 and 18). The meiotic divisions proceed normally. The chromosomes are thinner than those of *Bellendena* and more elongated than those of *Cenarrhenes*.

**Inflorescence and Flower**

In several species of *Persoonia* (e.g., *P. saccata* and *P. juniperina*), the flowers are solitary axillary and diffusely scattered (Plate XVIII, 8, 9). In *P. pinifolia* they are aggregated into terminal racemes in which region the leaves are small and bract like (Plate XVIII, 10). *In Symphyomena* and *Bauera* the inflorescence is a lax panicles (Plate XVII, 6; Figs. 36 and 42), while the spikes are more closely clustered in *Cenarrhene* and *Agastachys* (Plate XVII, 3, 4, Plate XVIII 7). It is a simple raceme in *Bellendena* (Plate XVII, 1, 2).

The flowers are ebracteate only in *Bellendena*. The young inflorescence is covered over and protected by a group of bud scales (modified leaf bases) which
are left behind as the inflorescence elongates (Figs. 19–22). In other genera there are relatively large and persistent bracts (Figs. 37, 39, 44 and 46).

The flowers in all genera are actinomorphic (cf. Fig. 26). They are zygomorphic only in Picnostylis section of Persoonia (e.g., P. saundersiana and P. saccata) due to the presence of saccate perianth and curved style (Figs. 30–33). In Bellendena, Persoonia and Agastachys the flowers are glandless. In other genera there is a hypogynous nectary with 4 alternitepalous, vascularised lobes (Figs. 27, 29, 38, 40, 45 and 47). The stamens are free from the tepals only in Bellendena (Figs. 23 and 54). In all other genera they are adnate to the bases of tepals (Figs. 25, 31). In Symphyonema the filaments are connate at the top (Fig. 44). In Agastachys, Symphyonema and Amblyanthera section of Persoonia, the stamens are non-apiculate (Figs. 25 and 28). In other members they have produced connectives (Figs. 31, 32, 34). In Cenarrhenes nitida and Beauprea paniculata, the connective of the posterior stamen is elongated and tapering (Figs. 46, 110 and 122). In Bellendena and Persoonia the ovary is stipitate. It is sessile or nearly so in other members. There are two orthotropic pendulous ovules in Bellendena (Fig. 24) Persoonia and Symphyonema. In other genera there is a single ovule per carpel, which is pendulous in Cenarrhenes and Agastachys and lateral in Beauprea (Fig. 38). The style is terminal and stigma simple (Figs. 27 and 43), or hook like (Fig. 35). In Agastachys it is 2-lobed (Fig. 41). The fruit is a 1-seeded achene in Bellendena, a succulent drupe in Persoonia and Cenarrhenes (Plate XVII, 5; II, 9, 10) and a samara in Agastachys (Figs. 270, 271).

Organogeny

The floral organs arise in acropetal succession (Figs. 48–51). The margins of the carpel fuse incompletely in the young ovary (Figs. 52, 53, 156 and 157). The line of fusion remains distinct for some time during the growth of the ovary (Figs. 62 and 72).

Floral Anatomy

In Agastachys the stele of the peduncle is 3-angled. Since the vascular supply for the flowers is abstracted from each of the ridges (Fig. 100), the flowers stand in three vertical rows. The bract is 1-traced in Persoonia and Beauprea (Figs. 80, 111 and 117), and 3-traced in Symphyonema, Cenarrhenes and Agastachys. The traces cause separate gaps in the floral stele (Figs. 90–93). In Cenarrhenes, unlike in Agastachys, the bract laterals depart earlier than the bract midrib (Figs. 101, 103, 123–125).

The pedicel shows either 4 vascular bundles as in Bellendena and Beauprea pancheri (Figs. 55 and 117) or a ring of more than 4 bundles or a siphonostele as in Persoonia sp. which breaks up into 4 arcs (Figs. 67 and 80). In Symphyonema there are only 3 vascular bundles at the base of the flower which increase in number by splitting in the thalamus region (Figs. 88–90). The flowers in Bellendena present the simplest structure anatomically. The 4 bundles of the pedicel bend outwards in the thalamus; strands are given off from the margins of the lateral and anterior bundles (Figs. 56 and 57). These bend inwards, fuse suitably and reorientate as 3 carpellary traces (Fig. 58). There is no branching of the bundles in the ovary wall or pericarp. The 4 peripheral bundles divide tangentially into 2 each. The outer bundles thus formed function as the tepal traces; each expands tangentially and divides into 3 bundles, which traverse as the midrib and marginals (Figs. 58–60). The inner ones function as staminal traces; these are concentric for most part and quite free from the tepal bundles from the base (Figs. 60 and 61). The ventra
carpellary bundles give off ovular traces (Figs. 62) and fade out towards the base of the style. The dorsal bundle extends to the top of the style and becomes associated with patches of sclerenchyma (Figs. 63 and 64). The core of the style is filled with glandular transmitting tissue (Fig. 65).

In other members studied, though the floral structure is essentially similar, some variations are noticed. The tepals are antero-posterior in all Persooniaceae studied. In Persoonia and Beauprea paniculata, the tepals are 3-bundled as in Bellendena (Figs. 68–70, 75–77, 82–85, 118–121). In others the tepal trace traverses the tepal without branching (Figs. 93–96, 98, 102–104, 109, 115, 126–128). The staminal trace is usually organised as a pair of bundles to the inside of the tepal trace (Figs. 68, 74, 75, 78, 79, 83 and 112). The twin bundles of each trace fuse together either before or after emergence into the tepal (Figs. 69, 82, 93, 103 and 113). In any case they do not unite with the tepal trace so that the tepal and stamen show only congenital connescence but not true adnation (Figs. 66, 87, 99, 110 and 122). The stamens in all members show distinct filaments (Figs. 106, 107, 114, 120, 121 and 128). The filaments in Symphyomena are flat and become connate by marginal hairs (Figs. 96 and 97) as the tepals do in all Proteaceae. In Persoonia vaccata (Fig. 86), Cenarrhenes and Beauprea sp. the staminal bundle extends into the produced connective.

In P. vaccata usually the two bundles of each staminal trace fuse together just below the level of separation of the filament from the tepal. In one abnormal flower, however, the bundles of the lateral traces not only remained separate but entered the filaments of independent stamens so that the flower showed six stamens and not the customary four (Fig. 83–85).

In Persoonia sp. the lobes of the nectary are vascularised by strands derived either from the main stele or from the tepal laterals or from staminal trace (Figs. 69, 74–76 and 81). In Cenarrhenes and Beauprea they are derived from the outer margins of the vascular bundles in the alternitepalous sectors of floral stele (Figs. 112, 113, 118, 119, 125 and 126). As these bundles branch further in the base of the gland, 4–7 strands are noticed in each lobe (Figs. 70, 71, 76, 82, 116 and 127). The vascular bundles are surrounded by richly protoplasmic and tannin bearing cells (Fig. 71).

In Beauprea paniculata the carpel is 3-traced as in Bellendena (Fig. 114). In Persoonia and Symphyomena it is 5-traced while in Cenarrhenes it is 7-traced and there may be further branching in the ovary wall. The dorsal bundles and sometimes the median dorsals also extend into the style (Figs. 73, 97, 106, and 115).

EXPLANATION OF FIGURES

Figs. 19–53.—Figs. 19–46. Floral structure in Persooniaceae. Figs. 19–24. Bellendena montana. Fig. 19. L. S. young inflorescence and surrounding bud scales, ×8. Fig. 20. A twig with inflorescence, ×8. Fig. 21. A cleared leaf showing venation, ×1. Fig. 22. Bud scales, ×8. Fig. 23. Flower with two tepals removed, ×4. Fig. 24. L.S. mature ovary, ×40. Figs. 25–35. Persoonia sp. Fig. 25. L. S. flower bud of P. lanceolata, ×8. Figs. 26–29. P. tora, Fig. 26. An open flower, ×2. Fig. 27. Pistil and nectary, ×8. Fig. 28. A tepal and the attached stamen, ×4. Fig. 29. A lobe of the nectary, ×8. Figs. 30–33. P. saccata. Fig. 30. A flower bud, ×2. Fig. 31. L. S. flower bud, ×4. Fig. 32. A tepal and attached stamen, ×2. Fig. 33. Pistil and nectary, ×2. Figs. 34 and 35. P. microcarpa. Fig. 34. A tepal and attached stamen, ×3. Fig. 35. Pistil, ×3. Figs. 36–40. Beauprea sp. Fig. 36. A branch with inflorescence of B. paniculata, ×4. Fig. 37. A flower, ×4. Fig. 38. L. S. ovary and nectary ×60. Figs. 39 and 40. B. paniculata. Fig. 39. A flower bud, ×4. Fig. 40. Ovary and nectary, ×4. Fig. 41. Pistil of Agastachys, ×25. Figs. 42–44. Symphyomena yaludorum. Fig. 42. A branch with inflorescence, ×1. Figs. 43 and 44. Pistil and flower, ×10. Figs. 45–53. Cenarrhenes nitida. Fig. 45. Pistil and nectary, ×6. Fig. 46. Flower after removing tepals, ×6. Fig. 47. L. S. ovary and one lobe of nectary, ×15. Figs. 48–51. Stages in the organogenesis of flower, ×30. Figs. 52 and 53. T. S. ovary and style, ×25.
Although in species of *Peroonia* the carpel is usually two ovulate, in an abnormal ovary of *P. saccata*, three ovules were seen (Figs. 31 and 221). This resembles the carpel of *Garnieria* (New Caledonia), the only genus of Persooniaceae to show the multiovulate condition. In the 2-ovulate carpels, the ovular traces are derived alternately from both ventrals. In *Cenarrhenes* and *Beauprea*, though the second ovule is suppressed, the marginal bundle that fed it still persists. In the former a parenchymatous protuberance (vestigial ovule) is noticed on the sterile carpellary margin (Figs. 239 and 241), and occasionally a normal second ovule is developed (Figs. 258). This shows that the uniovulate condition is derived by suppression of the extra ovules. The vasculature of the carpel in *Agastachys* is interesting in this connection. It is atypical in showing 4 traces which traverse as the dorsal, 2 median laterals and one ventral bundle, there being no bundle in the sterile carpellary margin (Figs. 103 and 104). From this it is evident that in *Agastachys* reduction has gone further; the second ovule as well as the marginal that had been
feeding it are completely suppressed. The surviving marginal directly functions as the ovular trace (Fig. 105). The dorsal bundle fades at the base of the style and each of the median laterals extends into one lobe of the stigma (Figs. 106–108). There is no branching of the ovarian bundles even in the fruit wall (Fig. 271).

In Cenarrhenes, though normally the ventral suture points to the posterior side (Fig. 128), sometimes a tendency is noticed for the torsion of the ovary (Fig. 129).

**Microsporogenesis and Male Gametophyte**

In all species studied, the anthers are 4-locular. The primary archesporium differentiates as 1 or 2 rows of hypodermal cells in each lobe. These divide periclinally forming the primary parietal cells to the outside and the primary sporogenous cells to the inside. The former give rise to 4–5 layers of wall cells below the epidermis (Figs. 130, 131 and 147). The sub-epidermal layer develops into the fibrous endothecium and the innermost into the tapetum of the secretory type (Figs. 133, 151 and 154). The septum between the anther loculi persists for some time after the dehiscence of the anther; in Agastachys there is no distinct septum (Figs. 154).

There is a secondary increase of the sporogenous tissue of the anther (Figs. 130, 131 and 147). Microspore tetrads are usually tetrahedral. Cytokinesis is of the simultaneous type and is brought about by furrowing. In all genera studied, the pollen grains are triporate and triangular except in P. saccata (Fig. 143) in which they are nearly spherical. The exine is smooth in Beauprea and Bellenda (Figs. 146 and 152). In others it ranges from finely granular to markedly reticulate pattern (Figs. 135, 136, 138 and 153). The intine may be uniformly thick as in P. juniperina, P. saundersiana and P. lanceolata (Figs. 134, 136 and 138) or thicker in the region of the germ pores and slightly or markedly protruding through them as in Cenarrhenes, P. salicina, P. linearis, and P. myrtilloides (Figs. 132, 135, 140 and 141). In P. virgata, P. ferruginea, P. oxyoccoides and P. microcarpa the intine protrudes through the germ pores and forms knob like swellings (Figs. 137, 142, 144 and 145). Pollen grains which are hemi-spherical on one side are noticed in P. lanceolata (Fig. 139). The pollen is 2-celled at the shedding stage. The generative cytoplasm is devoid of starch and is seen as a hyaline sheath around the generative nucleus in the earlier stages (Fig. 155). Later, the generative nucleus becomes ellipsoidal (Fig. 134 and 137) and the generative cytoplasm becomes obscure.

In pollen sterile anthers of Bellenda the microsporocytes degenerate without undergoing meiotic divisions. During early prophase I they separate out from each other, become covered with a thick wall and begin to show signs of degeneration. The cytoplasm of the tapetal cells also disintegrates and the cells become filled with droplets of deep staining material (Figs. 148 and 149). The hypodermal cells of the anther wall do not develop fibrous thickenings and the anthers do not dehisce (Fig. 150).

**Ovule**

The ovule primordia arise transverse to the ovarian loculus and become pendulous with growth (Figs. 156, 158–160, 168, 223 and 228). The funicles of the ovules in Bellenda and Persoonia (Fig. 222) are relatively longer than those of Cenarrhenes and Agastachys (Figs. 245, 246 and 248), while the funicle of the laterally attached ovule of Beauprea is much shorter (Fig. 252). In Persoonia, the funicle of one ovule is much longer than that of the other and this difference facilitates the accommodation of the ovules in the space of the loculus (Fig. 223). The vascular bundle of the funicle branches in the chalaza and forms a ring of bundles (Figs. 199,
211 and 233). The ovules are orthotropous, bitegmic and crassinucellate (Figs. 218–220). The inner integument arises earlier than the outer (Figs. 161–163, 237–239). In the mature ovules, the outer integument remains biseriate while the inner becomes about 4 cells thick. The inner alone forms the micropyle which is usually long and straight (Figs. 165, 168, 208, 211 and 249). In Persoonia sp. the micropyles press against the side or base of the loculus and become bent or asymmetrical (Fig. 222). In the multiovulate carpel of P. saccata the integuments and micropyyle are not normally formed due to exigencies of space (Fig. 221). The primary parietal cell of the ovule gives rise to 4-5 layers of parietal tissue; the cells of nucellar epidermis may also divide periclinally and form a nucellar cap (Figs. 165, 224, 240, 247 and 252). Three or more layers of these cells persist in the mature ovules and developing seeds (Figs. 169, 212 and 250). In Bellendena they not only persist till a late stage in seed development but become glandular (Figs. 184–186). In Bellendena and Persoonia sp. the cells of nucellus around the antipodal end of the embryo sac become thick walled and form a postament in the developing seeds (Figs. 174, 176, 224, 230–233). A transverse section of the postament of Bellendena shows some cells radiating from it (Fig. 177). In Persoonia sp., Agastachys and Beavurea, the antipodal end of the embryo sac extends to the chalaza. In Cenarrhones and P. lanceolata, it is separated from the chalaza by several layers of nucellar cells. A hypostase of elongated regularly placed cells extends between the antipodal end of the sac and the chalaza. The cells are thick walled in Persoonia species (Figs. 230–232) but thin walled and glandular in Cenarrhones nitida (Figs. 245 and 256). Tannin is accumulated in the cells of the chalaza and outer epidermis of the outer integument and inner epidermis of the inner integument.

Megasporogenesis and Female Gametophyte

The archesporium of the ovule consists of the single hypodermal cell (Figs., 161 and 227). This cuts off the primary parietal cell (Fig. 251) and functions as the megaspore mother cell which becomes elongated and tapering when full grown (Figs. 162, 163, 207, 229 and 239). A linear tetrad of megaspores is formed (Figs. 164, 208, 241–244); the lowest megaspore functions and forms the embryo sac according to Polygonum-type (Figs. 165, 166, 209, 210 and 232). The synergids show filiform apparatus and rounded or hook like protuberances on their free sides (Fig. 167). The polar nuclei do not fuse before fertilization (Fig. 170). The antipodals are inconspicuous but persist till a few endosperm nuclei are formed (Fig. 173). The cytoplasm of the embryo sac shows starch.

Fertilization

Bellendena, Cenarrhones and Agastachys are very showy when in flower. The flowers of Bellendena give out a foetid smell which is attractive to some insects. The flowers are protandrous and the pollen is shed on the stigma long before the

Explanation of Figures

Figs. 66–86. Persoonia sp. Figs. 66–73. P. juniperina. Fig. 68. L. S. flower bud. Figs. 67–70 and 73. sections at various heights through flower bud. Fig. 71. T. S. a lobe of the nectary. Fig. 72. T. S. carpel. Figs. 74–76. Semidiagrammatic transverse sections of flower bud of P. lanceolata. Fig. 77. T. S. flower bud of P. virgata. Figs. 78 and 79. P. gunnii. Figs. 80–82. P. pilosifolia. Figs. 83–86. P. saccata. Figs. 83–85. Sections through an abnormal flower with six stamens. Fig. 86. T. S. appendage of stamen. n. s. = nectary strands; st.t. = staminal trace; n. = lobe of nectary. Fig. 66. × 8; Figs. 67–70, 72 and 77. × 40; Fig. 71, × 160; Figs. 73, × 35 Figs. 78 and 79, × 28; Figs. 80–82, × 20; Figs. 83–85, × 6; Fig. 86, × 35. (Explanation in text).
flowers open. Self sterility prevents self fertilization. Pollen grains are caught among the glandular stigmatic hairs (Fig. 225) where they germinate in a monosiphonous manner (Figs. 171 and 172). The transmitting tissue of the style facilitates the passage of pollen tubes. In several species of Persoonia the transmitting tissue is biseriate (Fig. 206) and the cells adjoin the glandular tissue lining the loculus. In P. saccoata the transmitting tissue is more extensive (Fig. 226). In Bellendena the ovules hang freely in the loculus so that the pollen tubes have to bridge a gap in order to reach the micropyles (Fig. 24). In Beaupea and Agastachys the micropylies stand close to or in contact with the base of the loculus. In Persoonia sp. the glandular cells of the loculus adjacent to the micropyle proliferate and form some glandular tissue which functions as an obturator (Figs. 205, 212, 230 and 231). In Cenarrhenes, the epidermal cells of the inner integument around the micropyle become papillate and come in contact with similar cells lining the base of the loculus. Together they seem to facilitate the passage of pollen tubes (Fig. 245). After fertilization the micropyte in Cenarrhenes becomes conical and fits into the funnel shaped base of the loculus; the surrounding cells become glandular and seem to assist in the nutrition of the embryo sac (Fig. 253, 257 and 260).

The pollen tube enters the ovule porogamously and usually a synergid becomes effected when it enters the embryo sac (Figs. 170 and 254); in Cenarrhenes, remnants of such synergids are seen by the side of growing embryos. In Bellendena the pollen tubes are narrow and ephemeral; in Cenarrhenes they are relatively wider and more persistent.

**ENDOSPERM**

The endosperm is of the nuclear type. It becomes cellular first around the embryo when the latter is a small globular mass (Fig. 174), by a process of indentation. In Bellendena and Persoonia, nuclear fusions occur in the antipodal endosperm resulting in polyploid nuclei (Fig. 177 and 213). The nucleus standing close to the postament is especially large and seems to be concerned in the nutrition of the embryo sac (Fig. 178). An exactly similar situation is noticed in some Sterculiaceae e.g., Abroma augusta and Pentapetes phoenicea (Venkata Rao, 1953). There is no aggressive enlargement of the embryo sac after fertilization in Bellendena and Persoonia, the digestion of the nucellus being slow and prolonged. The endosperm in the antipodal region in Bellendena remains nuclear for a long time. Ultimately the whole of the endosperm becomes cellular. The cells in the antipodal region contain large polyploid nuclei. The endosperm is even in outline and does not show papillate haustorial cells as are reported in Macadamia ternifolia (Kausik, 1938b).

Mature seeds of Bellendena are endospermic. The endosperm cells are packed with starch and other reserve materials. The number of layers of endosperm cells surrounding the embryo varies in the different parts of the seed, the endosperm

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**EXPLANATION OF FIGURES**

Figs. 87-109. Figs. 87-98. Symphyomena montanum. Fig. 87. L. S. flower bud. Figs. 88-96 and 98. Sections at various heights through flower bud. Fig. 97. Section through the tube formed by filaments and style. Figs. 99-109. Agastachys odorata. Fig. 99. L. S. flower bud. Fig. 100. T. S. peduncle showing origin of floral stels. Figs. 101-109. Sections through flower bud at various heights. Fig. 105. T. S. ovary at the level of attachment of ovule. Fig. 108. T. S. stigma. b.m. = bract midrib; b.l. = bract laterals; st.t. = staminal trace; t.t. = tepal trace. Figs. 87, 87; Figs. 88-98 and 98, 80; Fig. 97, 80; Fig. 99, 80; Figs. 100, 101, 103, 104, 106, 107 and 109, 80; Fig. 102, 80; Fig. 105, 80; Fig. 108, 80. (Explanation in text.)
C. VENKATA RAO: STUDIES IN THE PROTEACEAE

Figs. 110–129.—Figs. 110–115. **Beauveria paniculata.** Fig. 110. L. S. flower bud. Figs. 111–115. T. S. at various heights through flower bud. Fig. 116–121. **Beauveria penchari.** Fig. 116. L.S. base of flower bud. Figs. 117–121. T. S. at various heights through flower bud. Figs. 122–129. **Cenarthrome nitida.** Fig. 122. L. S. flower bud. Figs. 123–129. T. S. at various heights through flower bud. b.m. = bract laterals; b.m. = bract midrib; st.t. = staminal trace; t.t. = tepal trace. Figs. 110–121, × 25: Fig 116, × 35; Figs. 122–129, × 12.
being thicker around the radicle than around the cotyledons (Figs. 196 and 197). In one young seed, though the embryo was normal, there was no trace of endosperm (Figs. 190 and 191). In Persoonia, the seeds are non-endospermic or only a trace of endosperm persists.

In Cenarrhenes nitida the enlargement of the ovule after fertilization is sudden and pronounced. This results in a transverse rupture of the nucellus at about the middle of its height and sometimes the inner integument also becomes involved (Figs. 255 and 257). As the seed grows, a lenticular cavity develops which becomes filled with a clear nutritive fluid. As already described, there is a hypostase of elongated, thin-walled, glandular cells below the embryo sac which stands out distinctly from the large, isodiametric, scantily cytoplasmic, light staining cells constituting the rest of the nucellus. During seed development, the cells of the hypostase fall apart giving rise to an irregular space which serves to connect the antipodal end of the sac with the nucellar cavity (Figs. 258, 259 and 261). The endosperm is scanty and does not extend into the enlarging nucellar cavity. This cannot, therefore, be described as ‘endosperm haustorium’ in the strict sense. A somewhat similar condition is described by Jordaan (1946) in the S. African Brabeium stellatifolium. The endosperm in C. nitida remains nuclear even at the stage shown in Fig. 261. It is doubtful if it ever becomes cellular. The nucellus persists for sometime and functions as the perisperm. In the mature seed both the endosperm and perisperm become absorbed and the seed cavity is filled by the large succulent embryo (Figs. 268 and 269).

**Embryo**

The fertilised egg does not rest for a prolonged period. The first division of the oospore is transverse and results in the basal cell cb and the terminal cell ca (Fig. 262). The next division is longitudinal in both cells and results in a tetrad of cells in two tiers (Figs. 179, 180, 263 and 264). The derivatives of both ca and cb enter into the embryo proper, there being no suspensor (Figs. 181–185, 214, 234-236, 265-267). In B. montana, sometimes the lowest cell of the embryo presents a glandular appearance (Fig. 184); since this comes into intimate contact with the glandular nucellar cells, it seems to function in absorption of food materials. The embryo development in all Persoonieae studied keys out to Penaea variation of Asterad type (Johansen, 1950).

The mature embryo in Bellendena and Cenarrhenes shows a well developed radicle and two thick cotyledons. The cells of the embryo are packed with food materials. The cotyledons do not show the basal lobes that are characteristic of genera like Grevillea and Hakea (Fig. 198).

**Seed and Fruit**

The mature seed of Bellendena is fusiform and slightly flattened parallel to the fruit; it is 5–6 mm. long and c. 2 mm wide at the middle. In the mature ovule the outer integument is biseriate and the inner 4 cells thick (Fig. 201). After fertilization, both the integuments increase in thickness, the outer becoming 5 layered and the inner 6-7 cells thick (Fig. 202). The maximum thickness of the testa is attained in seeds with embryo just showing cotyledon primordia. The coats of mature seed are devoid of mechanical tissue. Several layers of both integuments break down (Fig. 203) and mature seed coats show only two layers: the innermost layer of tannin filled cells belonging to the testa and the palisade like layer of thin walled cells belonging to the tegmen (Fig. 204). The seed coats of Cenarrhenes are also flimsy.
The style in *Bellendena* is persistent. Though it is at first terminal, as the ventral margin of the fruit grows more rapidly than the dorsal, it becomes bent and ultimately fits into a depression at the summit of the fruit (Figs. 192-194). The pericarp consists of 5-6 layers of thin walled parenchyma surrounded by strongly cutinised epidermal layers, there being no mechanical tissue (Fig. 200). The mature fruit is obovate, dry and light and apparently wind dispersed. A membranous wing develops to the outside of the ventral margin (Fig. 195). The fruit does not show any dehiscence mechanism; decay of or mechanical injury to the brittle pericarp seems to result in liberation of the seed.

In *Persoonia* the fruit is a small succulent drupe with persistent style (Fig. 215). After fertilization, the glandular cells lining the loculus proliferate and produce a tissue which completely envelopes the seeds (Figs. 216 and 217). The ovary wall shows two zones: the outer of tannin filled cells which ultimately develops into the succulent epicarp and the inner zone and the tissue surrounding the seeds which form the stony endocarp.

In *Cenarrhenes*, the fruit is a purplish spherical drupe (Plate XVII, 5) The ovary wall shows two distinct regions from early stages (Figs. 47 and 253). The outer zone consists of scantily cytoplasmic, light staining cells; this develops into the succulent epicarp; the inner consisting of small richly protoplasmic cells develops into the stony endocarp (Figs. 268 and 269).

In *Agastachys* the fruit is a small 3-winged samara. Two larger wings develop to the outside of the median dorsals and a small wing to the outside of the dorsal bundle (Figs. 270 and 271).

**Sterility**

There is good fruit set in *Bellendena*; an inflorescence contains 50-80 flowers of which 50 percent or more give rise to fruits (Plate XVII, 2). In *Cenarrhenes* and *Agastachys* there is relatively less fruit set (Plate XVII, 5) and sometimes all the flowers of an inflorescence wither away without forming a single fruit. Sometimes in apparently normal fruits, the seed cavity was found to be empty.

In *Bellendena* and *Persoonia*, though the carpel is 2-ovulate the fruits are commonly 1-seeded, 2-seeded ones being very rare. In *Bellendena* both the ovaries become fertilised and start development as seeds. Later, in several cases the two seeds were seen to become fused by webbing together of their integuments. The rapid elongation of one seed results in dislodging the other and therefore to the degeneration of the latter. Shrunken remnants of such seeds are often found attached to the functional seeds (Figs. 175 and 194). However, in some other cases seeds are seen to degenerate without any apparent cause. The process of degeneration may start even at a late stage when the seed is showing a large globular embryo. In one young seed which was still attached to the placenta, the integuments and nucellus were showing signs of degeneration but the endosperm was

**Explanation of Figures**

_Figs. 130–155._ Microsporogenesis and male gametophyte in *Persoonia*. Figs. 130–132. *Cenarrhenes nitida*. Figs. 133–145. *Persoonia* sp. Figs. 133 and 134. *P. juniperina*. Fig. 135. *P. salicina*. Fig. 136. *P. saundersiana*. Fig. 137. *P. virgata*. Figs. 138 and 139. *P. lanceolata*. Fig. 140. *P. linearia*. Fig. 141. *P. myrtillodes*. Fig. 142. *P. ferruginea*. Fig. 143. *P. succata*. Fig. 144. *P. oxyocccoides*. Fig. 145. *P. microcarpa*. Fig. 146. *Beauprea paniculata*. Figs. 147–152. *Bellendena montana*. Figs. 148–150. Sections through pollen sterile anthers. Figs. 153. *Symphogenema paludosum*. Figs. 154 and 155. *Agastachys odorata*. Figs. 130, 131, 134, 137, 143, 147, and 148, × 270. Figs. 132, 133, 135, 139, × 500; Figs. 136, 140, 141, 142, 144, 145, × 335; Figs. 136, 149, × 480; Figs. 146, × 720; Figs. 150, 151, × 120; Figs. 152, 153, 155, × 1200. Fig. 154, × 100.
showing nuclear divisions (Figs. 187-189). The endosperm in this case is probably parasitising on the sporophytic tissues. In *Persoonia* sp. the integument of the functionless ovule was found fused to the false septum (Fig. 233). The enlargement of the fruit probably resulted in breaking off the funicle from the placenta and therefore led to the degeneration of the seed.

**Discussion**

The present studies support Engler’s (1894) conclusion that the Persoonieae are the most primitive tribe of the Proteaceae. The members show a large number of primitive morphological, floral anatomical, embryological and cytological features. However, a comparative study of the different genera shows that some evolution has taken place within the tribe. These evolutionary trends are discussed in the following pages.

The members studied show evolution in vegetative features. *Cenarrheneae* and *Agastachys* are confined to the rainforests or their fringes in Tasmania. Though usually shrubby, they attain the size of trees on the west coast. Some species of *Persoonia* (e.g. *P. longifolia*) are trees and others shrubby. Species of this genus show wide range and inhabit diverse situations from sea level to c. 2,000’ altitude. Both species of *Symphyomena* are undershrubs endemic in New South Wales. *Bellendena montana* is a gregarious shrub which inhabits sub-alpine meadows of Tasmania above 3,500’ altitude. The climate in such places is cool and moist throughout the year and the soil is covered by snow in winter months.

The leaves in *Symphyomena* are 2-3 times pinnatisect (Fig. 42). They are palmately 3-lobed, 3-traced, somewhat succulent and externally veinless in *Bellendena* (Figs. 20 and 21), expanded, simple, and dentate in *Cenarrheneae* and *Beauprea* and succulent and entire in *Agastachys*. In *Persoonia* they range from acicular (*P. sacca* and *P. pinifolia*) to oblong-lanceolate form (*P. lanceolata* and *P. toru*). In several species they show xeromorphic features: the edges of the narrow, small, spine tipped leaves of *P. juniperina* are held vertically (cf. Plates XVII and XVIII).

In several species of *Persoonia* the flowers are solitary axillary and diffusely scattered. *P. pinifolia* shows the evolution of inflorescence (and bract) by the aggregation of flowers towards the ends of branches. The leaves in this region are acicular like the vegetative leaves but smaller and bract-like in appearance. In *Beauprea* and *Symphyomena* the inflorescence is a lax panicle. It is more condensed in *Cenarrheneae* and *Agastachys* due to the suppression of the peduncles. The bracts in these genera are relatively large and persistent.

The ebracteate, pedicillate, regular, glandless flowers of *Bellendena* with stamens completely free from the tepals, and stipitate ovary seem to represent the most primitive floral structure. Evolution is noticed in the different members in the suppression of pedicel, introduction of a bract and its persistence, adnation of tepals and stamens, connation of filaments, suppression of the appendage of the

**Explanation of Figures**

Figs. 156-170. *Bellendena montana*. Figs. 156 and 157. T. S. through young ovary and style. Figs. 158-160. L. S. through ovary at different stages of development. Fig. 161. Ovule primordium with aril sporium. Figs. 162 and 163. Ovules with megaspore mother cell. Fig. 164. Nucellus with linear tetrad. Fig. 165. L. S. ovule with 2-nucleate embryo sac. Fig. 166. Nucellus with young embryo sac. Fig. 167. Micropylar part of mature embryo sac. Fig. 168. Ovule with mature embryo sac. Figs. 169 and 170. Nucellus and micropylar part of embryo sac from above. Figs. 156-158, x100; Figs. 159 and 160, x75; Figs. 161, - 164 and 170, x360; Figs. 165 and 168, x180; Fig. 166, x270; Fig. 167, x600; Fig. 169, x130.
stamen and stipe of the ovary, development of vascularised nectar, tendency towards zygomorphy of the flower and attainment of partial male sterility. The ancestral carpel seems to be multiovulate, a condition still found in *Garnieria* (Persooniaceae) and in other tribes of the family viz., Placophoraeae, Embothriaceae and Telopeaeae. The abnormal multiovulate carpel noticed in *Persoonia succata* seems to be atavistic. The 2- and 1-ovulate conditions in other *Persoonia* seem to be derived by suppression of the extra ovules. Evidence for the suppression of the second ovule is found in *Cenarrhenes* in the shape of a vestigial ovule on the sterile carpellary margin and in the occasional development of a normal second ovule. In *Agastachys*, the second ovule as well as the marginal bundle feeding it are completely suppressed. The fruits in *Bellendena* do not show any mechanical tissue or dehiscence mechanism or any special adaptations for dispersal. In *Agastachys* the fruit is a small samara adapted for wind dispersal, while in *Persoonia* and *Cenarrhenes* they are attractive drupes adapted for bird dispersal.

In general there is an elaboration of floral stele by an increase in carpellary traces and intercalation of vascular supply for the nectary, though reduction is also noticed in suppression of tepal marginals or one ventral bundle in *Agastachys*. The stamens become adnate to the tepals but the union does not involve their traces. The organisation of the staminal traces as a pair of bundles to the inside of the tepal midrib is interesting. A similar antitepalous position and twin bundled staminal trace are noticed in *Helicanthus elastica* (Johri, Agrawal and Garg, 1957) and *Nuyssia* sp. (Narayana, 1958) of Loranthaceae. The significance of this peculiar staminal trace will be discussed later.

The 3-traced carpel noticed in *Bellendena* and *Beaupea* sp. seems to be primitive and the 5- and 7-traced carpels of *Persoonia* and *Cenarrhenes* seem to be driven by an elaboration as suggested by Eames (1931).

The morphology of the perianth is linked with that of the nectary. If the nectary could be homologised to the corolla of a dichlamydeous flower, the perianth could be equated to the calyx. The 4 alternitepalous lobes of the nectary seen in *Persoonia*, *Cenarrhenes* and *Beaupea* offer a tempting comparison to the petals of a dichlamydeous flower. But in S. African *Brabeium*, (and Macadamieae) the lobes of the nectary unite to form a cup situated between the tepal-stamen whorl and the pistil and not in the position of the corolla of a dichlamydeous flower. In Grevilleae and Telopeaeae, the lobes of the nectary are not only connate but the nectary becomes zygomorphic due to the suppression of one or two anterior lobes. If the nectary is to be homologised to the corolla, then it must be conceded that apetalous (cf. the glandless flowers of *Bellendena*, *Symphomyema* and *Agastachys*), polypetalous, gamopetalous and zygomorphy of the corolla have been attained within the family. The nectary is non-vascular in Oriteae and *Banksia* sp. In the Persooniaceae it is vascularised by strands derived either from tepal laterals or staminal traces or outer margins of intertepalous sectors of floral stele. In no

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**EXPLANATION OF FIGURES**

Figs. 171–191.—Endosperm and embryo development in *Bellendena montana*. Fig. 171. Stigmatic hairs and germinating pollen grains. Fig. 172. A germinating pollen grain. Fig. 173. A fertilized embryo sac. Figs 174 and 175. L.S. developing seeds. Fig. 176. L.S. part of seed showing antipodal endosperm and postament. Fig. 177. T.S. postament. Fig. 178. L.S. postament and some endosperm. Figs. 179–185. Stages in the development of the embryo. Fig. 186. Tip of radicle and some endosperm and mucellar cells. Fig. 187. L.S. degenerating seed. Figs. 188 and 189. Micropylar and antipodal parts of embryo sac from the above. Fig. 190. L.S. abnormal seed devicid of endosperm. Fig. 191. Micropylar part of the above. Fig. 171, x 130; Fig. 172, x 620; Figs. 173 and 177, x 270; Figs. 174 and 175, and 190, x 80; Figs. 176 184, 188, 189, and 191, x 160; Figs. 178, x 600; Figs. 179–183, x 210; Figs. 185 and 187, x 60.
Figs. 192–204.—Bellendena montana. Figs. 192–194. Developing fruits. Fig. 195. T. S. fruit. Fig. 196. L. S. seed. Fig. 197. T. S. seed. Fig. 198. Entire embryo. Fig. 199. T. S. chalazal part of the seed showing ring of strands formed by division of ovular trace. Fig. 200. Section of pericarp. Fig. 201. T. S. integuments of mature ovule. Figs. 202–204. T. S. of coats of developing and mature seeds. Figs. 192, 193, and 195, ×10; Fig. 194, ×4; Figs. 196–198, ×6; Figs. 199 and 200, ×75; Figs. 201–204, ×340.

EXPLANATION OF FIGURES

Figs. 205–220. Persoonia sp. Figs. 205–217. P. juniperina. Fig. 205. L. S. ovary. Fig. 206. Transferring tissue of style. Fig. 207. Section of ovule with megaspore mother cell. Fig. 208. Section of ovule with megaspore tetrad. Fig. 209. Nucellus with developing embryo sac. Fig. 210. Nucellus with young embryo sac. Fig. 211. L. S. young seed showing postament. Fig. 212. L. S. micropylar part of fertilised ovule and adjacent glandular obturator. Fig. 213. L. S. antipodal part of embryo sac showing postament and some endosperm. Fig. 214. A young embryo. Fig. 215. A fruit. Figs. 216 and 217. L. S. loculus and T. S. fruit showing tissue developed from glandular cells of locular epidermis. Figs. 218–220. Entire ovules of P. toru, P. microcarpa and P. saundersiana respectively. Fig. 205, ×60; Figs. 206–210, 212–214, ×160; Fig. 211, 216 and 217, ×25; Fig. 215, ×3; Fig. 218, ×35; Fig. 219, ×60; Fig. 220, ×25.
case is it fed by independent traces which cause gaps in the floral stele like those of tepals. Therefore, neither the position, nor the morphology nor the vasculature of the nectary give any evidence of its homology to the corolla. It seems to be only a glandular nectar secreting outgrowth of the thalamus. Similar outgrowths are also found in some other monochlamydeous and dichlamydeous families. Since the nectary cannot be homologised to the corolla of a dichlamydeous flower, the perianth cannot be equated to the calyx. The flower seems to be primitively monochlamydeous and the perianth parts are best designated as tepals.

The Persoonieae show close resemblance in embryological features: 5-6 layered anther wall with hypodermal endothecium and tapetum of the secretory type, 3-porate, triangular, 2-celled pollen, transmitting tissue in the style, crassinucellate, bitegmic ovules in which the inner integument is more massive than the outer, an elongated micropyle formed by the inner integument, branching of the funicular vascular bundle in the chalaza, Polygonum—type of embryo sac development, fusion of the polar nuclei at the time of fertilization, inconspicuous antipodals nuclear type of endosperm, development of the embryo according to Peneae variation of Asterad type, and flimsy seed coats. Evolution is noticed in the reduction of the length of the funicle and the lateral attachment of the ovule, development of special devices which facilitate the progress of pollen tubes (obturator), and tendency towards the formation of 'endosperm' haustorium. Bellendena is the only member in which the seeds are endospermic; in other Persoonieae as well as in the rest of the family they are non-endospermic.

As is commonly noticed in other angiosperms, evolution has not progressed at the same rate in all floral organs in any genus or species. In Picnostylis section of Persoonia, for example, zygomorphy of the flower has been attained due to the development of a saccate perianth and curved style, but the flowers retain primitive features in the presence of pedicel, fusion of the twin bundles of the staminal trace at a relatively high level, conspicuous vascularised appendage for stemen and stipe for the ovary.

Several of the evolutionary tendencies noticed in the Persoonieae become established and accentuated in other tribes of the family and form their important characteristics, e.g., adnation of stamen and tepal culminates in the complete union of their traces in Oriteae; connation of filaments results in connation of the anther lobes in Conospermeae; connation of the lobes of the nectary leads to its zygomorphy in Grevilleae, Telopeae and Embothrieae; curved style and lateral stigma lead to the development of a pollen collecting apparatus in Spatalka of Proteaceae, Grevilleae Telopeae and Embothrieae; zygomorphy of the flower becomes accentuated in Grevilleae, Telopeae and Embothrieae partial male sterility in Conospermeae, torsion of the ovary in the Oriteae and development of a well defined endosperm haustorium in several genera of the Grevilloideae.

**Explanation of Figures**

Figs. 221–236.—Persoonia sp. Figs. 221–226. P. saccata. Fig. 221. L. S. abnormal ovary with 3 ovules. Fig. 222. L. S. ovule with 2-nucleate embryo sac. Fig. 223. L. S. loculus of mature ovary showing attachment of the ovules (from 2 sections). Fig. 224. Nuclue with mature embryo sac. Fig. 225. Glandular stigmatic hairs. Fig. 226. T. S. style with transmitting tissue. Figs. 227–229. P. gunnii. Fig. 227. Ovule primordium with archesporium. Fig. 228. Loculus of ovary. Fig. 229. L. S. young ovule with megasporang mother cell. Figs. 230–232. P. lanceolata. Fig. 230. L. S. young ovule with adjacent part of the loculus showing glandular epidermal cells. Fig. 231. L. S. mature ovule and glandular obturator; Fig’ 232. Nuclue with 4-nucleate embryo sac. Figs. 233–236. P. pinifolia. Fig. 233. L. S. part of fruit with a normal and a degenerating ovule. Figs. 234–236. Stages in development of the embryo; Figs. 221, 222 x 75; Figs. 223, 226, 228 x 35; Figs. 224, 225, 229, 232 x 160; 227 x 270; Figs. 230, 231, x 60; Fig. 233, x 6; Figs. 234–236, x 360.
The sum of morphological, floral anatomical and embryological evidence points to *Bellendena* being the most primitive member of the Persooniaceae which probably escaped extinction by continuing to inhabit situations similar to those under which it originally evolved. Australia and adjacent islands did not experience the drastic effects of glaciation and several examples of the most primitive fauna and flora persist there till today, e.g., the fresh water shrimps of Tasmania, the egg laying mammals of Australia. Five of the nine vesselless angiosperms are endemic in New Guinea and New Caledonia (Bailey, 1949). *Bellendena* may be another such paleo-endemic.

Lancaster (1952) thought that 7, the haploid chromosome number of *Persoonia* represents the basic number in the family and that \( n = 14, 13, 12, 11 \) and 10 noticed in other genera of the family represent reduction series derived by stepwise loss of one chromosome. The presence of \( n = 10 \) in highly evolved genera like *Grevillea* and *Hakea* was thus explained but the same number in *Symphomyrtus* (Persooniaceae) could not be accounted for. The writer, however, feels that the cytological data lend support to the conclusions drawn from morphological, floral anatomical and embryological evidence that evolution within the family has been progressive.

*Bellendena* (\( n = 5 \)) and *Persoonia* (\( n = 7 \)) have the smallest chromosome numbers in the family. The karyotypes of the two genera are very simple and closely similar with long and thick chromosomes which show median or sub-median constrictions and no trabsants. The two genera show close resemblance also in the formation of a postament during seed development, structure of the endosperm with nuclear fusions in the antipodal region, presence of a large polyploid nucleus close to the postament and also the causes which lead to the sterility of the functionless seed. These are the only diploid genera in the family. There seem to be two possibilities for the derivation of their chromosome numbers: \( n = 5 \) might have been derived from \( n = 7 \) by loss of two chromosomes or \( n = 7 \) might have been derived from \( n = 5 \) by the addition of two chromosomes. The latter alternative seems to be more probable since at the diploid level addition of chromosomes is more favoured in nature. Moreover, *Persoonia* shows several features which prove that it is the derived genus, viz., a vascularised nectary, adnation of tepals and stamens, suppression of the produced connective (*Amblyanthora* section), tendency towards zygomorphy of the flower (*Picnostylis* section), tendency towards the suppression of the second ovule, non-endospermic seed and a specialised drupeaceous bird dispersed fruit. Though some of the simpler morphological features (e.g., absence of the nectary) can be interpreted as being due to reduction, there are others which are generally agreed upon as being irreversible e.g., adnation of stamen and tepal, tendency towards zygomorphy of the flower and non-endospermic seed. *Persoonia*, therefore seems to be the derived genus. The increase in chromosome number in this genus seems to have led to great speciation, adaptability and tolerance capacity to diverse ecological conditions. While five out of the nine genera of Persooniaceae are monotypic endemics, *Persoonia* with 72 species shows wide range and variety in habitat. In fact it is the only living genus of Proteaceae which is represented in East and West Australia, Tasmania and New Zealand.

**Explanation of Figures**

Figs. 237–252.—Figs. 237–245. *Cenarrhenes nitida*. Figs. 237, 238, 239 and 241. L. S. through ovules at various stages of development. Fig. 240. Nucellus showing formation of megaspore dyad. Figs. 242 and 243. Formation of linear tetrad of megaspores. Fig. 244. Formation of 2-nucleate embryo sac. Fig. 245. L. S. ovule with mature embryo sac. Figs. 246–250. *Agastachys odorata*. Fig. 246. L. S. ovary with young ovule. Fig. 247. L. S. ovule with 1-nucleate embryo sac. Fig. 248. Entire ovule. Fig. 249. L. S. mature ovule. Fig. 250. Micropylar part of the embryo sac and the overlying nucellar cells. Figs. 251 and 252. L. S. ovules of *Beauvosa paniculata*. Figs. 237, 240, \( \times 270 \); Figs. 238, \( \times 135 \); Figs. 239, 241, 249, \( \times 85 \); Figs. 242, 243, 250, \( \times 390 \); Fig. 244, \( \times 600 \); Figs. 245, 246, and 248, \( \times 60 \); Fig. 247, \( \times 160 \); Figs. 251 and 252, \( \times 600 \).
Bellendena and Persoonia seem to provide two types of floral structure (one without and one with nectary) and also two basic chromosome numbers. As in most angiospermy families, polyplody and aneuploidy led to the evolution of the genera and tribes. This is accompanied by a diminution of chromosome size which is also noticed in other angiosperms e.g., diploid and polyploid species of Dianthus. Symphyonema (n=10) and Cenarrhenes (n=14) seem to be tetraploids, on bases 5 and 7 respectively; \( n=13 \) of Agastachys seems to be a hypoploid on \( n=14 \). It is interesting to notice that in the last genus reduction in floral structure is found in association with reduction in chromosome number. Several physiological changes are known to accompany polyplody (Munzing, 1935; Stebbins, 1940; Blakeslee, 1941). The presence of a specialised method of nutrition in the shape of an ‘endosperm’ haustorium in Cenarrhenes seems to be one such.

A comparative study of the Australian and extra-Australian Persooniaceae brings to light several points of interest. The genus Cenarrhenes is common to Tasmania and New Caledonia, and Persoonia between Australia (including Tasmania), and New Zealand. There is close resemblance between Cenarrhenes nitida (Tasmania) and Beauprea (New Caledonia) in morphological and floral anatomical features. The elongated tapering connective of the posterior stamen is strikingly similar in both genera. This feature is also shared by Persoonia falcata (E. Australia). These points show that the Australian, New Caledonian and New Zealand Persooniaceae must have had common ancestry. The discontinuous distribution of Persoonia and Cenarrhenes can be ascribed to ancient dispersals by birds (as both have succulent drupes), and/or to the existence in the past, of land connections between the land masses which are now separate. Geological history shows that they formed a continuous continent in ancient times and that the islands have broken asunder and drifted apart since Cretaceous (Carey, 1938, 1955).

Levynns (1958) suggested that the monotypic S. African Brabeium stellatifolium might belong to the Grevilleoideae, placing too much stress on the whorled leaves. One important feature which distinguishes the Grevilleoideae from the Persooniaceae is the occurrence of the flowers regularly in pairs in bract axils. In Brabeium the flowers occur in groups. This feature is never noticed in Grevilleoideae but is found in some Persooniaceae viz., Paramonous and Spatyalopsis of S. African Proteaceae. The stamens in Brabeium are described as being free from tepals; this feature is noticed only in Bellendena of the Persooniaceae. Brabeium, therefore seems to be belonging to Persooniaceae in which Engler had placed it. The genus resembles other Persooniaceae in the presence of 3-porate pollen, 2 orthotropic pendulous ovules and their structural features, embryo without suspensor, non-endospermic seeds and flimsy seed coats. The ‘endosperm’ haustorium of Brabeium is also closely similar to that of Cenarrhenes (data from Jordaan, 1946). However, Brabeium shows advance in the formation of the lobes of the nectary into a cup. The haploid chromosome number of 14 in Brabeium (Darlington and Wylie 1955) is of particular interest since it coincides with that of Cenarrhenes (Tasmania). The close similarity between S. African and Australian Persooniaceae points to their common ancestry. The

**Explanation of Figures**

Figs. 253–271.—Figs. 253–269. Cenarrhenes nitida. Fig. 253. L. S. mature ovary. Fig. 254. A fertilised embryo sac and adjacent cells. Fig. 255–261. L. S. young seeds in different stages of development. Fig. 258. L. S. loculus with two normally developed ovules. Fig. 260. Micropylar part of young seed and adjacent cells of loculus. Fig. 262–267. Stages in development of the embryo. Figs. 268 and 269. L. S. and T. S. of fruit. Figs. 270 and 271. Entire fruit and T. S. fruit of Agastachys odorata. Figs. 263 and 264, x10; Figs. 265 and 266, x 215; Figs. 267 and 268, x35; Figs. 269, 270, 271. x100, Fig. 261, x3. Figs. 255, x 75; Figs. 262–266, x 360; Fig. 267, x 240; Figs. 268, 269 and 270, x 4; Fig. 271, x 15.
probable causes which led to the distribution of the ancestral stocks between the two continents, now widely separated, will be discussed later.

The floral structure and chromosome number in *Dilobelia* (Madagascar) might prove useful in throwing some light on the nature of the ancestral stock that entered this land mass.

![Diagram of evolutionary relationships in the tribe Persooniaceae](image)

**Fig. 272.**—Evolution within the tribe Persooniaceae according to the views of the writer.

The region which shows the greatest concentration of species is generally regarded as the probable centre of origin of a taxon (Cain, 1944; Good, 1953). Out of the 9 genera and c. 90 species which constitute Persooniaceae, 5 genera and c. 77 species are found in Australia (and two more in the adjacent New Caledonia). As Good (1953) rightly points out and illustrates in the case of Asclepiadaceae species concentration alone should not be relied upon but the distribution of the primitives should also be taken into account in fixing the centre of origin of a taxon. Usually diploids, being more primitive and less adaptable than their polyploid derivatives, will have limited range and do not stray far from the place of their origin while their
polyploid derivatives have greater spread e.g., *Tradescantia* (Anderson, 1937). The two diploid genera of the *Proteaceae* (*Bellendena* and *Persoonia*) are confined to Australia. Australia, therefore, seems to be the centre of origin of the tribe *Persooniaceae*.

Within Australia, all the 5 genera of the *Persooniaceae* are found in East Australia including Tasmania, which seems to have been connected with the mainland in the past (Crocker and Wood, 1947; Browne, 1945), while only *Persoonia* is represented in West Australia. Even within this genus, there are more species in East (43) than in West (27). East Australia, therefore, seems to be the centre of origin of the tribe *Persooniaceae*, wherefrom ancestral stocks probably migrated to the other land masses.

It is interesting to notice that in *Persoonia* as well as 11 other genera of the *Proteaceae* common between East and West Australia, there are no species common between the two zones. This leads one to the conclusion that there existed in the past a pan-Australian flora, as Diels (1906) also believed. After evolution has occurred to the generic level, ecological and geographical barriers seem to have been created between the two regions which led to independent speciation. Geological history shows that during Cretaceous, the central part of Australian continent was under sea so that the land presented the form of two long islands, eastern and western (Crocker and Wood, 1947).

All the 7 species of *Picnostylis* section of *Persoonia* are mainly confined to W. Australia, only *P. falcata* extending to N. Australia and Queensland. This section which contains the only species with zygomorphic flowers among *Persooniaceae*, therefore, seems to have evolved in W. Australia. A detailed study of the cytology and distribution pattern of the *Epacridaceae*, another typically Australian family led Smith-White (1948) to a similar conclusion; he observes: "the genera that are endemic in W. Australia are usually specialised relatives of the eastern ones, and data do not suggest W. Australia as the source of the whole group".

Evolution within the tribe *Persooniaceae* as visualised by the writer is represented in Fig. 272.

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**Postscript:** When this paper was in press, the article of Haber (Phytomorphology, 1959 pp. 325–358) appeared. While there is general agreement between the present writer and Haber in the evolutionary trends in the inflorescence and flower, there is difference of opinion in the interpretation of the morphology of the nectary. Haber interpreted the nectary as corolla and therefore that the flower is dichlamydeous or monochlamydeous by reduction. In addition to the arguments presented in this paper, the writer wishes to add the following to substantiate his view that the proteaceous flower is fundamentally monochlamydeous.

17
In interpreting the ‘glands, discs and scales’ as corolla or modified form of it, Haber has not properly weighed the evidence of their position. Though in the polyphyllous condition the lobes of the nectary occur in the position of petals, in the gamophyllous state, the gland stands inner to the tepal-stamen whorl. The writer is doubtful whether the corolla can or does occur inner to an epiphyllous staminal whorl in any angiosperous family.

It is generally accepted that gamophyll and zygomorphy of the corolla are progressive and irreversible changes. It is difficult to imagine how a change can occur during the process of reduction “from a gamophyllous corolla to scale-like organs or to glands” (Haber, p. 355).

In the families in which strong zygomorphy of the corolla has been attained, tubular or polyphyllous conditions are not usually noticed. A great diversity is seen in the structure of the nectary in the Proteaceae, not only within the family but even within genera e.g., Grevillea. In *G. leucopterus* the gland is annular; in *G. cryphaea* it is more than semiannular with a small lobe at the back of the stipe; in the majority of species it is semiannular and strongly zygomorphic while in *sympyphae* it is absent. Such a variety is not seen in the corolla within a single family but is noticed in the structure of the nectary e.g., Cruciferae. The writer therefore feels that the nectary is not homologous to the corolla but to the gland of a dichlamydeous flower.

**References**


Lawrence, C. M. L. (1955). Taxonomy of Flowering Plants, N.Y.


1. *Bellendena montana* (Mount Wellington, Tasmania) in full bloom.
2. A branch with inflorescences; inset is a branch with fruits.
3. *Cenarrhenes nitida* (Florentine, Tasmania) in full bloom.
4. A branch with inflorescences.
5. A branch with fruits.
6. A branch of *Symphyomena montana* (New South Wales) with inflorescences.
7. A branch of *Agastachys odorata* (Florentine, Tasmania) with inflorescences.
8. A branch of *Persoonia sessilis* with flowers (W. Australia).
9. A branch of *P. juniperina* (Tasmania) with flowers; inset is a branch with fruits.
10. A branch of *P. pinifolia* (New South Wales) with flowers; inset is a branch with fruits.
11. A branch of *P. lanceolata* (N. S. W.) with flowers.
12. A branch of *P. loru* (New Zealand) with flowers.