Studies of New Zealand Nothofagus

1. TAXONOMY AND FLORAL MORPHOLOGY

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SUMMARY

The taxonomic status of the species of New Zealand Nothofagus defined by Cockayne and at present accepted by New Zealand botanists is reviewed. Cockayne's clarification of the species was based on leaf morphology. Using these species, a detailed description is given of their floral morphology and mode of flowering. Hitherto this has been imperfectly known.

TAXONOMY

1. The Species

New Zealand botanical workers at present generally recognise five species of Nothofagus and two or more groups of hybrids. These were defined by Cockayne (1926). The history of the taxonomic work that preceded Cockayne's investigations and the synonymy of the species recognised by him follows.

The first collections of three species (i.e. species as at present understood) were made by Banks and Solander on Cook's first world voyage in 1769–71. Two further species were collected by A. Menzies, surgeon to the Discovery, which visited New Zealand in 1791.

Four of the above species were described in Solander's unpublished MSS., Primitiae Florae Novae Zelandiae, but no published description appeared until J. D. Hooker in 1844 described four of them under Fagus in Icones Plantarum. These were, F. fusca and F. solandri, both collected by Banks and Solander in 1769, F. menziesii and F. cliffortioides both collected by A. Menzies. The third species collected by Banks and Solander was included in one of two illustrations accompanying the description of F. fusca.

In his Flora Novae-Zelandiae, Hooker (1854) included the above four species with the addition of F. fusca var. colensoi, which he refers to one of the plates illustrating N. fusca in the Icones Plantarum. In his Handbook of the New Zealand Flora (1864) the same species were included, but var. colensoi of F. fusca was called var. β.

In 1850 Blume created the genus Nothofagus for the southern hemisphere beeches, and in 1873 Oersted placed Hooker's four species in Nothofagus. This generic name was however not adopted by New Zealand botanists until L. Cockayne commenced to use it in his writings from about 1910 onwards.

After the appearance of Hooker's Handbook, local botanists became active in collecting and describing plants, and the beeches did not escape their activities. Colenso (1884) described a new species, F. apiculata, and in the same year T. Kirk published the first comprehensive account of the New Zealand beeches. This included a de-
scription of another new species, F. blairii. T. Kirk, in his Forest Flora (1889), included all the species described to date and added two new varieties, *F. fusca* var. *dubia* and var. *obsoleta*. Colenso (1898) described a further species, *F. truncata*. Although this is undoubtedly the *F. fusca* var. *colensoi* of Hooker (1854), it is strange that Colenso made no reference to it.

Cheeseman, in his Manual of the New Zealand Flora (1906), included *F. menziesii*, *F. fusca*, *F. fusca* var. *colensoi*, *F. solandri*, *F. cliffortioides*, *F. blairii*, *F. apiculata*, and *F. apiculata* var. *dubia*. He included Colenso’s *F. truncata* under *F. fusca* var. *colensoi*, and, as will be seen, placed Kirk’s *F. fusca* var. *dubia* under *F. apiculata*, with which he also included Kirk’s *F. fusca* var. *obsoleta*. It was obvious from this treatment that confusion had arisen around *F. blairii*, *F. apiculata* and Kirk’s varieties of *F. fusca*. For example, Cheeseman referred to *F. apiculata* as “very closely related to *F. fusca*,” although the original descriptions of these two species were very dissimilar. *F. blairii* he likened to *F. solandri*, whereas the original description had likened it to *F. cliffortioides*.

Cockayne (1911) transferred *F. apiculata* Col. and *F. blairii* T. Kirk to *Nothofagus*.

Cheeseman in his 1925 Manual listed the same species as in his first Manual, but placed them under *Nothofagus*. The species position had become no clearer, but he did include a memorandum written by Cockayne on the occurrence of hybridism in New Zealand beeches. In his memorandum, Cockayne states that: “Hybridism occurs to an astonishing extent in the genus.” A few years later Cockayne’s investigations were more complete and in an article in Genetica (1926) he and Atkinson elaborated their ideas on the hybrid parentages. In the same year, in a monograph on the New Zealand Beech Forests (1926), he defined the species and hybrid groups as he considered them to be. This is the position as it is accepted to-day. The species considered to be valid by Cockayne, together with the synonymy noted in the preceding paragraphs, follow.


*Nothofagus menziesii* Solander’s MSS., Primitae Floraæ Novæ Zealandiæ (in edit.) Hooker fil. (1844), t. 652; (1853) i.p. 229; (1864) p. 249; T. Kirk (1889), p. 175, t. 89; T. F. Cheeseman (1906), p. 640.


*Betulodes fusca* Solander’s MSS. (in edit.).


*Myrtillioides conicaeus* Solander’s MSS. (in edit.).


Cliffortioides oblongata Solander’s MSS. (in edit.).


Nothofagus fusca var. colensoi T. F. Cheeseman (1926), p. 375.

The species and varieties considered invalid by Cockayne, Fagus blairii, F. apiculata, F. fusca var. dubia and var. obsoleta, were included by him in his hybrid groups. The question of beech hybrids will not be gone into in this paper. The extent of hybridism and its effect on speciation is a matter to be determined only by extensive population studies. It is sufficient to say now that Cockayne’s accepted species are distinct enough to accept them meantime as a basis for further studies.

Cockayne’s work did much to clarify the species position. N. menziesii had been recognised from the earliest times as distinct. Cockayne suggested that it did not enter into hybridism, and this together with the possession of a number of distinctive features noted later, suggested that it might belong to a separate section of Nothofagus. N. fusca in the form originally described by Hooker could also be recognised with reasonable certainty, though there were undoubtedly a number of forms. N. truncata could also be recognised as a good species; indeed, some wood-users, because of the difference of physical wood properties, had been sure of the segregation from N. fusca before the botanists. Unfortunately, many earlier botanists did not always recognise the difference, and some of their writings refer indiscriminately to the two species. Du Rietz (1930) made the distinction between N. fusca and N. truncata more certain by recording the presence of domatia on the back of the leaves of the former species and not of the latter. This has been checked in all herbarium specimens available and in a number of forests. Domatia have always been found in the axils of the lower one or two side veins of N. fusca where they join the midrib on trees and saplings above 6 ft.—10 ft. high. On seedlings or saplings below this height they are usually not present. They have not been found on any N. truncata leaves.

N. solandri and N. cliffortioides in their typical states had been recognised from earliest times, too, but in many places it was difficult to separate these two species, and again many botanical writings had confused them. Thus Cockayne and Atkinson (1926) write, “N. solandri is probably a compound species. It has been confused by all authors with N. cliffortioides and we confess that until close study of Nothofagus hybrids, we could not recognise for certain individuals of the two species. In any case, it is surprising that taxonomists who believed in ‘variable species’ should have kept
the two separate and not constituted a compound species with two varieties."

The recognition of hybridism cleared away the confusion that had arisen around *N. blairii*, *N. apiculata* and the varieties of *N. fusca*. As stated above, these were placed in hybrid groups.

2. Discussion

A more exact distinction between *N. solandri* and *N. cliffortioides*, the recognition of forms or sub-species within the species, and the determination of the status of hybrid groups remain the outstanding taxonomic problems of the New Zealand species of *Nothofagus*. Cockayne's final clarification, including the determination of hybrid groups, was based entirely upon leaf characters. His analysis undoubtedly served to carry our knowledge of the species a long way forward. Nevertheless, flower characters are of major importance in taxonomic work, so that a more thorough investigation of them was desirable, although the possibility of segregation on leaf characters alone has not been exhausted. The following section deals with the floral morphology of those species accepted by Cockayne. No mention will be made of the flowers from suspected hybrid trees, a matter left to a later paper.

**Floral Morphology**

1. The Genus

In separating *Nothofagus* from *Fagus*, Blume (1850) gave the following description of the flowers of the former genus (translation):

"Flowers monoecious. Male on solitary peduncles, ternate, naked. Perianth campanulate, irregularly spread, 5–7 lobed. Stamens 4–40 inserted at the base of the perianth; filaments filiform, simple; anthers erect, bilocular, separated by an excurrent connective. Female inflorescence: buds axillary, solitary, subnude, usually completely sealy with subquadripartite or profoundly quadripartite involucere, three-flowered. Perianth edge superior, short, six-toothed, or in the central flower, four-toothed. Ovary inferior, three winged or, in the central flower, laterally compressed, 3, rarely 2 locular. Ovules two per locule, pendulous from the central apex—'ex apice anguli centralis pendula'—anatropous. Styles short; stigmas the same number as locules, subulate.'" Subsequent descriptions in standard works such as Bentham and Hooker's *Genera Plantarum* (1883) are brief and add nothing new to our knowledge of the floral structure of the genus.

The most comprehensive description of the flower morphology and flowering habit of the genus has recently been given by Langdon (1947), who studied the comparative morphology of a number of Australian, South American and New Zealand species as well as the newly discovered ones from New Guinea. This worker was however faced with the difficulty of working on preserved and herbarium material only. No fresh material was available to her.

2. The New Zealand Species

At the beginning of this study it was apparent from the discrepancies between the descriptions given by Hooker (1844), Kirk (1889), Cheeseman (1925) and others, that flowering and flowers of the New Zealand species were imperfectly known. Male flowers were
reasonably described because they are fairly conspicuous and often collected. Female inflorescences and flowers were generally inadequately described, and most of the descriptions had obviously been drawn up from developing cupules. Some were grossly inaccurate. A comparison of all the flower descriptions available shows that, hitherto, these have been of little use for the diagnosis of species.

There follows detailed descriptions for the New Zealand species accepted by Cockayne (1926). Before this is set out a general account summarising this detail will be given. The material upon which the following descriptions are based was obtained from a wide range of habitats. The detailed descriptions were however based upon one tree only for each species, though deviations found in other material have been noted. The localities from which material was examined and the herbarium particulars of the "type" trees is given under the separate species' descriptions. As the flowers are very small, all examinations were made under a X7 to X20 binocular microscope. To examine particular points, sectioning was sometimes resorted to. *Nothofagus* collections in all the main New Zealand herbaria were also examined. Leaf characters of the "type" trees are set out in the table on p. 368.*

**General Description of Floral Characteristics**

The species are monoecious, the staminate and pistillate flowers being borne normally in the spring on the same vegetative shoot as it expands from the opening bud. The bud is characteristic; the general pattern is an oval or somewhat pointed structure covered with 15–20 imbricating oval scales, arising spirally, but arranged in approximately four rows. The upper part of the bud may be formed of the stipules to the unfolded leaves. The lowermost scales are smaller than the uppermost. At the point of attachment of the scales and of the stipules there are characteristic multicellular resinous glands. These are small (Fig. 2) and long-cylindrical in shape, consisting of long radiating cells surrounding central vascular tissue.

As a flowering bud opens, peduncles bearing usually 1–3 staminate flowers appear singly in the axils of the uppermost scales or lowermost leaves which lie near the top of the bud. Immediately above the staminate flowers sessile or sub-sessile pistillate inflorescences are borne singly in the axils of the leaves. Above these, a normal leafy shoot with minute vegetative buds in the axils of the leaves, develops. The bud scales are caducous and the staminate flowers and peduncles carrying them drop after the pollen is shed, so that later there appear to be vegetative shoots carrying pistillate inflorescences only.

An individual staminate flower consists of a shallow-lobed bell-shaped perianth, except for *N. menziesii* flowers, which have widely spreading, glandular-toothed perianths. Stamina vary from 9–36—the higher numbers in *N. menziesii* only—and are attached by fine filaments in a group to the base of the perianth. The filaments grow until the anthers are exerted, or partly exerted at dehiscence. Anthers are bilocular and deliase lengthwise; the connective is excurrent and forms a blunt apiculate tip.

The pistillate inflorescence, usually referred to as a cyme, consists of 1–3 flowers surrounded by a cupule (fig. 1). This cupule has
<table>
<thead>
<tr>
<th>Leaf Characters</th>
<th>\textit{N. fusca}</th>
<th>\textit{N. truncata}</th>
<th>\textit{N. solandri}</th>
<th>\textit{N. cliffortioides}</th>
<th>\textit{N. menziesii}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shape</td>
<td>Broadly ovate, cuneate base, petiolate</td>
<td>Broadly ovate, cuneate base, petiolate</td>
<td>Elliptic oblong, cuneate base, shortly petiolate</td>
<td>OVate triangular, acute or sub-acute, shortly petiolate</td>
<td>OVate deltoid, shortly petiolate</td>
</tr>
<tr>
<td>Size</td>
<td>3–4 cm. long ± 2 cm. wide</td>
<td>2.5–3.5 cm. long ± 2 cm. wide</td>
<td>1.2–1.5 cm. long, 0.7–0.8 cm. wide</td>
<td>1–1.5 cm. long, 0.7–1 cm. wide</td>
<td>1–1.2 cm. long ± 1 cm. wide</td>
</tr>
<tr>
<td>Margin</td>
<td>6–8 deep, acuminate teeth on each side</td>
<td>8–12 shallow blunt teeth on each side</td>
<td>Margin entire</td>
<td>Margin entire</td>
<td>Coarsely doubly crenate</td>
</tr>
<tr>
<td>Venation</td>
<td>3–4 distinct pairs veins</td>
<td>5–6 distinct pairs veins</td>
<td>Distinct on ab-axial surface only, 3–4 pairs veins</td>
<td>Obscure</td>
<td>Obscure</td>
</tr>
<tr>
<td>Domatia</td>
<td>1–2 hairy ab-axial domatia in axils of lowermost veins</td>
<td>Domatia absent</td>
<td>Domatia absent</td>
<td>Domatia absent</td>
<td>1–2 hairy, ab-axial domatia at base of leaf</td>
</tr>
<tr>
<td>Hairiness</td>
<td>A few short hairs</td>
<td>A few short hairs</td>
<td>Greyish-white tomentose on ab-axial surface</td>
<td>Greyish-fulvous tomentose on ab-axial surface</td>
<td>Petiole hairy</td>
</tr>
</tbody>
</table>
a thickened base of regular parenchymatous tissue. From the base, 3–4 rows of unequal sized bracts, referred to by some workers as bracteoles, are given off. These are grouped in 3–4 segments. Some investigators (Langdon, 1947) maintain that these bracts or bracteoles correspond to secondary and tertiary units of a compound cyme. This view was based by Langdon on a detailed investigation of the vascular system in the cupule and flowers. Embedded in the cupule tissue are cells, often numerous, containing calcium oxalate. Between the bracts, and between the innermost bracts and flowers, are glands similar to those on the bud scales and stipules (fig. 2).

From the central portion of the cupule 1–3 di- or trimerous flowers arise. When three are present, two are lateral and trimerous and one median and dimerous. Each flower consists of somewhat enlarged club or tongue-shaped spreading stigmas and very short thickish styles joined just above a slightly enlarged ovary. At the junction of the styles there is a poorly developed perianth, usually present as a rim, and scarcely visible to the naked eye. Successive cross-sections examined under the microscope show this perianth to be 6-partite in the trimerous flowers and 4-partite in the dimerous flowers. The tissue of the perianth is continuous with that of the ovary. The inferior ovary is two- or three-angled, and at these angles the perianth is lobed. In *N. menziesii* these lobes are glandular. The tissue of the ovary and cupule is continuous. At the time of fertilisation the ovules
and the locules are usually just commencing to form. There is one locule corresponding to each style, and in each locule are two pendulous ovules which become anatrapous.

**Detailed Description of Floral Characteristics**

**Nothofagus fusca** (Hook. f.) Oerst. (Figs. 1–6 and 23)

[Tree growing in the Maitai Valley, ten miles from Nelson, in mixed *N. fusca*, *N. solandri* and *N. truncata* forest. (Botany Division Herbarium No. 59532.) Material was also examined from the Wellington Botanical Gardens (cultivated) and from near Greymouth.]

1. **Mode of Flowering.** From 1–7 slender, glabrous peduncles up to 4 mm. long, each bearing 1–3 or rarely 5 sub-sessile, staminate flowers appear singly in the axils of the upper bud scales. The lowermost peduncle is usually 1-flowered and the peduncles above 2–3-flowered. The flowers are normally borne on the top of the peduncle, though peduncles with one or two lateral branches each bearing flowers are to be found on some trees.

Above the staminate flowers from 1–5 sessile pistillate inflorescences appear in the axils of the developing leaves. At the time of reception they are very small and partly hidden by the leaves and stipules.

2. **Staminate flowers.** Sessile, with a bell-shaped perianth 5 mm. long. Perianth with five shallow, obtuse lobes at the rim, and prominent veins ending in each lobe; membranous and sparsely hairy. Stamens 8–11, the higher number usually in the uppermost flowers. Anthers about 3 mm. long, exserted beyond the perianth at pollination. Filaments slender, fixed in a group at the base of the perianth. Anthers basi-fixed, biocular, dehiscing lengthwise, reddish. The connective excurrent, forming a blunt tip. Yellow or straw coloured anthers may also occur. All colours may appear in the same population of trees, but each tree is uniform for one colour.

3. **Pistillate inflorescence.** Sessile, greenish, ovoid, about 3 mm. long by 2 mm. wide; a few sparse hairs on the base. Cupule 4-partite with four large segments and smaller bracts on the inside and outside of these. Tips of segments attenuate. Glauds present between the segments and bracts. Cupule enveloping the flowers. Inflorescence normally three-flowered, having two lateral and one central flower.

4. **Pistillate flowers.** The two lateral flowers of the inflorescence are trimerous with three styles and a three locular ovary. Central flower bimerous, flattish, with two styles and a two-locular ovary. Styles very short, with sparse hairs. Stigmas tongue-shaped, grooved on top, somewhat fleshy, spreading, straw-coloured; styles and stigmas of the central flower somewhat larger than those of the two lateral flowers. What might be termed a perianth ridge is present at the base of the styles. This ridge is inconspicuously 6-partite in the lateral flowers and 4-partite in the central flower. It is adnate with the tissue of a small inferior ovary. In each lateral flower the ovary has three sharply projecting incipient wings, and in the central flower the ovary has two such wings. The tips of the wings correspond with division of the perianth.

**Nothofagus truncata** (Col.) Cockayne. (Figs. 7–11 and 24.)

[Tree from Butterfly Creek, near Wellington, in mixed *N. truncata*,
**Figures 3-6**—*Nothofagus fusca* flowering. **Fig. 3**—Twigs bearing spring flowering shoots; × 1. **Fig. 4**—A terminal spring shoot with staminate flowers. St, stipule; l, unexpanded leaf. × 2. **Fig. 5**—Staminate flowers. × 2. **Fig. 6**—Pistillate inflorescence. × 7.
N.M. Adams.

Figs. 7-11—*Nothofagus truncata* flowering. Fig. 7—Twig bearing axillary and terminal spring shoots. × 1. Fig. 8—Spring shoot bearing staminate flowers and a pistillate inflorescence. × 2. Fig. 9—Longitudinal section of a pistillate inflorescence showing b, base of cupule; se, cupule segments and bracts; f, pistillate flowers. Fig. 10—Staminate flowers. × 3. Fig. 11—Unexpanded spring shoot tip showing arrangement of stipules (s†) and young leaves (l) enclosing pistillate inflorescence (p†). × 6.
N. solandri forest. (Botany Division Herbarium No. 61889.) Material was also examined from other localities near Wellington, from Nelson and from Greymouth.]

1. Mode of flowering. As the flowering buds expand, from 1–7 sparsely hairy peduncles, up to 1 cm. long, each bearing 1–3 sub-sessile staminate flowers appear singly in the axils of the upper bud scales. The topmost peduncle is frequently subtended by a leaf. The lowermost peduncle often bears a solitary flower, and the following peduncles 3 flowers each.

Above the staminate flowers from 1–5 sessile pistillate inflorescences appear in the axils of the developing leaves. At the time of reception they are small and partly hidden by the leaves and stipules.

2. Staminate flowers. Sub-sessile, with a bell-shaped perianth, 4 mm. long by 2–3 mm. wide at the top. Perianth with 5 shallow lobes, each lobe obtuse, dark tipped; membranous to sub-membranous between the lobes. Stamens 10–13. Anthers about 3 mm. long, exserted beyond the perianth at pollen-shed; yellow. Colour of the anthers may vary from yellow to dark orange. All colours may appear in the same population of trees, but each tree is uniform for one colour.

3. Pistillate inflorescence. Sessile, greenish, ovoid. about 2 mm. long by 1.75 mm. broad, a few short hairs at the base. Cupule 4-partite, with four large segments and smaller bracts on the inside and outside of these Tips of segments acute. Glands present between the segments and bracts. Cupule enveloping the flowers. Inflorescence normally three-flowered, having two lateral and one central flower.

4. Pistillate flowers. These are the same as in N. fusca with the exception of the stigmas, which are always less grooved on top.

Nothofagus solandri (Hook. f.) Oerst. and N. cliffortioides (Hook. f.) Oerst.

The flowering and flower characters of these two species correspond in so many ways that they will be set down in a comparative table.

<table>
<thead>
<tr>
<th>N. solandri</th>
<th>N. cliffortioides</th>
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<tr>
<td>[Tree from Butterfly Creek, near Wellington, growing in a mixed forest of N. solandri and N. truncata (Botany Division Herbarium No. 63914) Material was also examined from other localities near Wellington, from Greymouth and from Nelson.] (Figs. 12–13, 25.)</td>
<td>[Tree from Lake Manapouri. (Botany Division Herbarium No. 63953) Material also examined from Hartley Springs and Kaitol.] (Figs. 16–20, 26.)</td>
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</tbody>
</table>

1. Mode of flowering

From 1–4 very short, sparsely hairy peduncles each bearing 1–2 staminate flowers appear singly in the axils of the upper bud scales; some or all peduncles may be in the axils of the lowermost young leaves.

Above the staminate flowers 1–2 sessile pistillate inflorescences appear in the axils of young leaves. At the time of reception they are small and partly hidden by the young leaves and their stipules.

From 1–3 very short, sparsely hairy peduncles each bearing 1–2 staminate flowers appear singly in the axils of the lowermost young leaves.

Above the staminate flowers usually 1 sessile pistillate inflorescence appears in a leaf axil. At the time of reception it is very small and partly hidden.
Transactions.

N. solandri 2. Stamine flower
Sessile; with wide, hemispherical perianth, 2 mm. long by 3 mm. wide, with 4–5 shallow lobes. Perianth membranous; white with reddish tinge. Stamens 8–17. Filaments short, slender, included within the perianth. Anthers 2.5 mm., about ½ exserted; dark red.

N. cliffortioides
Sessile; with wide, hemispherical perianth, 2 mm. x 2 mm., with 4–5 shallow lobes. Perianth membranous, white with reddish tinge. Stamens 8–14. Filaments short, slender, included within the perianth. Anthers 2.5 mm. long, about ½ exserted; dark red.

3. Pistillate inflorescence
Sessile, about 2 mm. long by 1.5 mm. broad; very hairy, making structure of young cupule almost indistinguishable. Upon dissection, shown to be 3-partite. Enveloping flowers except for stigmatic lobes.

Inflorescences normally 2, but may be 1–3 flowered. If 2 flowered, 1 is trimerous and one dimerous.

4. Pistillate flowers
Stigmas club-shaped, reddish. Styles very short with sparse hairs. Styles and stigmas of the dimerous flowers larger than those of the trimerous.

Perianth ridge present at the base of the styles; inconspicuously 6-partite in the trimerous and 4-partite in the dimerous flowers; adnate with the tissue of a small inferior ovary.

Ovary sparsely hairy, 2- or 3-angled, each angle with an incipient wing. The tips of the wings correspond with divisions of the perianth.

Nothofagus menziesii (Hook. f.) Oerst. (Figs. 21–24 and 27.)
[Tree from Prettybridge, near Nelson, growing in mixed N. menziesii, N. fusca. forest. (Botany Division Herbarium No. 59528.) Material from Greymouth and Lower Hutt (cultivated) also examined.]

1. Mode of flowering. From 1–4 short, sparsely hairy peduncles 2–3 mm. long, each bearing a single, terminal stamineate flower, appearing singly in the axils of the upper bud scales.

Above the stamineate flowers from 1–4 shortly stalked pistillate inflorescences are borne in the axils of the developing leaves. At the time of reception they are small and partly hidden by the young leaves and stipules.

2. Stamineate flowers. Sessile, somewhat heart-shaped, 5 mm. long by 6 mm. broad, including the anthers. Perianth membranous, spreading, sparsely containing the stamens; consisting of two unequal lobes; larger lobe adaxial; each lobe cut into segments; perianth margin sparsely hairy. Stamens 30–36. Filaments up to 1.5 mm. long. Anthers up to 2.5 mm. long, dull red at the top, greenish below. Some trees have straw-coloured anthers.

3. Pistillate inflorescence. Each borne on very short, densely hairy stalk, oval, about 2 mm. long by 1.5 mm broad. Cupule with a marked basal portion, from the sides of which two leaf-like bracts are
Figs. 12-15—*Nothofagus solandri* flowering. Fig. 12—Twig with axillary spring shoots bearing staminate flowers. × 1. Fig. 13—Unexpanded spring shoot tip with young leaves (l) and stipules (st) surrounding a pistillate inflorescence (p). × 8. Fig. 14—Spring shoot with two staminate flowers (s) in the axils of young leaves and pistillate flowers (p) above. × 4. Fig. 15—Pistillate inflorescence subtended by a young leaf and stipules. × 10.
Figs. 16–20—*Nothofagus cliffortioides* flowering. Fig. 16—Twig with spring shoots bearing staminate flowers. × 1. Figs. 17 and 18—Spring shoots with staminate flowers (S) and above them pistillate inflorescence (P). Tip of shoots unexpanded, with (st) stipules and (l) young leaves. × 4. Fig. 19—Staminate flower. × 5. Fig. 20—Pistillate inflorescences showing the larger stigmas of the dimerous flower and smaller stigmas of the trimerous flower. × 8.
given off, each bearing three glands. Cupule with four larger segments each with four rows of gland-capped bracts. Inflorescence three-flowered, but almost as often two-flowered, with the central flower showing various stages of abortion.

4. **Pistillate flowers.** The two lateral flowers of the inflorescence are trimerous with three styles and a three-locular ovary. Central flower bimerous, flattish, with two styles and a two-locular ovary. Stigmas tongue-shaped, spreading. Styles very short. Perianth ridge present at the base of the styles. This ridge is 6-partite on the lateral flowers and 4-partite on the central flowers. The perianth is adnate with the tissue of the inferior ovary. In each lateral flower the ovary has three incipient wings and in the central flower the ovary has two such wings, but a third may sometimes be present; when it is, two lie in the same place. The wings are tipped with large glands.

**Discussion**

From the previous descriptions the following points arise:—

1. The five species of New Zealand southern beech upheld by Cockayne are distinct in floral morphology.

2. They can be divided into three different groups:—
   a) *N. fusca* and *N. truncata*, in which the staminate are sometimes, and the pistillate inflorescences are always triflorous; the pistillate flowers in the inflorescence are arranged as two lateral and trimerous and one central and dimerous; and the staminate flower colours vary from yellow to orange;

   b) *N. solandri* and *N. clifortioides*, in which both the staminate and pistillate inflorescences may have single flowers or be biflorous (rarely triflorous in *N. solandri*); the pistillate flowers may be dimerous and the staminate flower colour is red;

   c) *N. menziesii* is readily separated by several distinct characters, the most important of which are the glandular nature of the pistillate cupule, the spreading perianth of the staminate flower and the numerous stamens. The pistillate inflorescence is triflorous and arranged as in the *N. fusca* and *N. truncata* group, but the central flower is, as often as not, aborted. Staminate flowers are invariably borne singly.

3. The two species with somewhat similar, toothed leaves, *N. truncata* and *N. fusca*, confused by earlier botanists, but separated by Cockayne, have small but distinct flower differences. The peduncles of the staminate flowers are longer in the former species and the stigmas are not so markedly grooved.

4. The two entire leaved species, *N. solandri* and *N. clifortioides*, between the typical leaf forms of which are many intermediates, are very similar in floral morphology. There is an important difference between trees with typical leaf forms—not checked in intermediate forms—that the pistillate flowers of *N. solandri* are very hairy and those of *N. clifortioides* are hairy on the base only and are viscid.

5. Floral characters which readily separate *N. menziesii* from the other species are noted under (2) above.

6. The postulate of Langden (1947), based on a study of vascular organisation, that the floral morphology of southern beeches is basically trimerous seems to apply to the New Zealand species. The pistillate flowers of all species are basically trimerous, but suppression has evidently taken place in the central flowers until they are truly
Figs. 21-24.—Nothofagus menziesii flowering. Fig. 21—Twig with spring shoot bearing staminate flowers. × 1. Fig. 22—Spring shoot with staminate flowers and unexpanded tip. × 4. Fig. 23—Staminate flower. × 7. Fig. 24—Pistillate inflorescence. × 12.
Figs. 23–27—Pistillate inflorescences and flowers of New Zealand Nothofagus species. Fig. 23—N. fusca; a, inflorescence; b, trimerous flower; c, dimerous flower. Fig. 24—N. truncata. Fig. 25—N. solandri. Fig. 26—N. cliffortioides. Fig. 27—N. menziesii.
bimerous with two stigmas and two locules. Occasionally three wings, two lying in one plane, are to be seen in the central flower of *N. menziesii*. In the inflorescence itself suppression has taken place in *N. solandri* and *N. cliffortioides* until one or two flowers are missing. It has proceeded furthest in *N. cliffortioides*, for this species frequently has but one flower and never three, whereas *N. solandri* may have one to three, but usually has two. In *N. menziesii* the central flower is frequently represented as an aborted structure. It is interesting to note that the reduction in the number of flowers per inflorescence is most marked amongst the New Zealand southern beech species. In other southern beeches it is only present in the South American, *N. punilo*, which has constantly one trimerous flower per cupule.

(7) The different floral characters of the New Zealand beeches are of importance phytogeographically because they have their counterparts in the Tasmanian, Australian and South American species. This aspect will be dealt with in a separate paper.

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References
