Breeding Systems in New Zealand Plants

I. *Fuchsia*

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With three Figures in the Text

ABSTRACT

The three New Zealand *Fuchsia* species have heteromorphic flowers previously described as heterostyled. *F. excorticata* and *F. perscandens* are shown to be gynodioecious and *F. procumbens* trioecious. The frequencies of the two forms in several populations of *F. excorticata* are given.

I. INTRODUCTION

GYNODIOECY, or the occurrence of hermaphrodite and female plants in the same species, is an outbreeding mechanism of peculiar interest. On the one hand, the population can have a reliable seed source if hermaphrodite plants are self-fertilized, while, on the other hand, it may derive advantage from the offspring of the obligately cross-pollinated females. There are difficulties, however, in the maintenance of such a system in nature. The hazards of cross-pollination may lead to reduced seed setting on female plants, and thus to a reduced contribution of the genes of the female to the next generation. But more important still is the fact that, whereas in a dioecious species the two sexes contribute approximately equal amounts of chromatin to the next generation, in a gynodioecious species a hermaphrodite plant contributes approximately three times as much chromatin as a female. Genes causing male-sterility are thus in danger of decreasing in frequency, and if females are to survive in a population, some compensating mechanism must exist. Lewis (1941) has shown that where male-sterility is due to a dominant or recessive gene, the females cannot exist in a wild population unless they are more than twice as fertile as the hermaphrodite on the female side. However, Lewis also showed that with cytoplasmic control of male-sterility only a slight advantage in the females is necessary to maintain their frequency in a population.

According to Lewis (1942), more than 90 per cent. of the gynodioecious species so far recorded are in the Labiateae. This paper records gynodioecy in two of the New Zealand *Fuchsias* and describes trioecy in the third.

Although heteromorphic flowers are not described for these species by Munz (1943) in his monograph, New Zealand botanists have long been aware that different flower types exist. Hitherto the classification accepted has been

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given by Kirk (1892), who recognized three types of plant differentiated by their flowers, and called these 'long', 'mid', and 'short-styled', using the terms employed by Darwin (1877) for a tristylic species such as *Lythrum salicaria*. Although these positions of the stigma were determined in two species, by the degree of protrusion beyond the anthers, and not by the replacement of anthers at three different levels, Kirk believed the situation to be a true case of heterostyly. This confusion with true heterostyly has been maintained by Laing and Blackwell (1951), who introduce an account of Kirk's scheme by a description of heterostyly in *Primula*.

The purpose of this paper is to correct Kirk's descriptions and to provide information on breeding systems and natural populations.

II. *FUCHSIA EXCORTICATA*

F. excorticata is a small tree from 10 to 30 ft. in height, and is common throughout New Zealand. The flowers are pendulous with very small petals, and the species is gynodioecious.

Hermaphrodite flowers (Fig. 1). One mature flower was collected from each of 126 hermaphrodite trees on Banks Peninsula, Christchurch. The flower length, from top of ovary to apex of stigma, ranged from 24 to 51 mm. with a mean of 35·07±0·55. The degree to which the style protruded above the upper anther whorl, expressed as a percentage of style-length, ranged from nil to 33 per cent. In larger samples from six trees (number of flowers in parentheses), the corresponding figures were: 12–30 per cent. (67), 3–37 per cent. (73), 4–25 per cent. (25), 5–24 per cent. (40), and 4–33 per cent. (41).

It is clear from Kirk's descriptions that his 'short' and 'mid-styled' flower types are hermaphrodites. The 'short-styled' form is illustrated with the stigma at the same level as the upper whorl of stamens, while the flower illustrated as 'mid-styled' has the style protruding beyond the upper stamens for 30 per cent. of its length (Kirk, 1889). The right-hand pair of hermaphrodite flowers in Fig. 1 show the two extremes of style protrusion in a sample from one tree, and in this respect are almost identical with Kirk's two types. Kirk noted that it would not be difficult to find trees intermediate between these two types, and Cheeseman (1925) while accepting the two forms notes that they apparently grade into one another. I find it impossible to distinguish two distinct forms in the field, and as the 'mid' and 'short-styled' flowers can even be collected from the same tree, it is obvious that the classification is artificial.

Although trees cannot be differentiated by the relative positions of style and anthers, they may differ in flower size. Genetical studies are, of course, not practicable, so that an indirect approach must be made to determine whether this variation has a genetical basis. To minimize possible environmental effects, measurements of the tube (hypanthium) and of style-length were made in two hermaphrodite trees growing with their branches touching (Fig. 1, *a*–*b*). An analysis of variance (Table I) showed a significant difference between trees for both characters. Variation in stylar protrusion, on the other

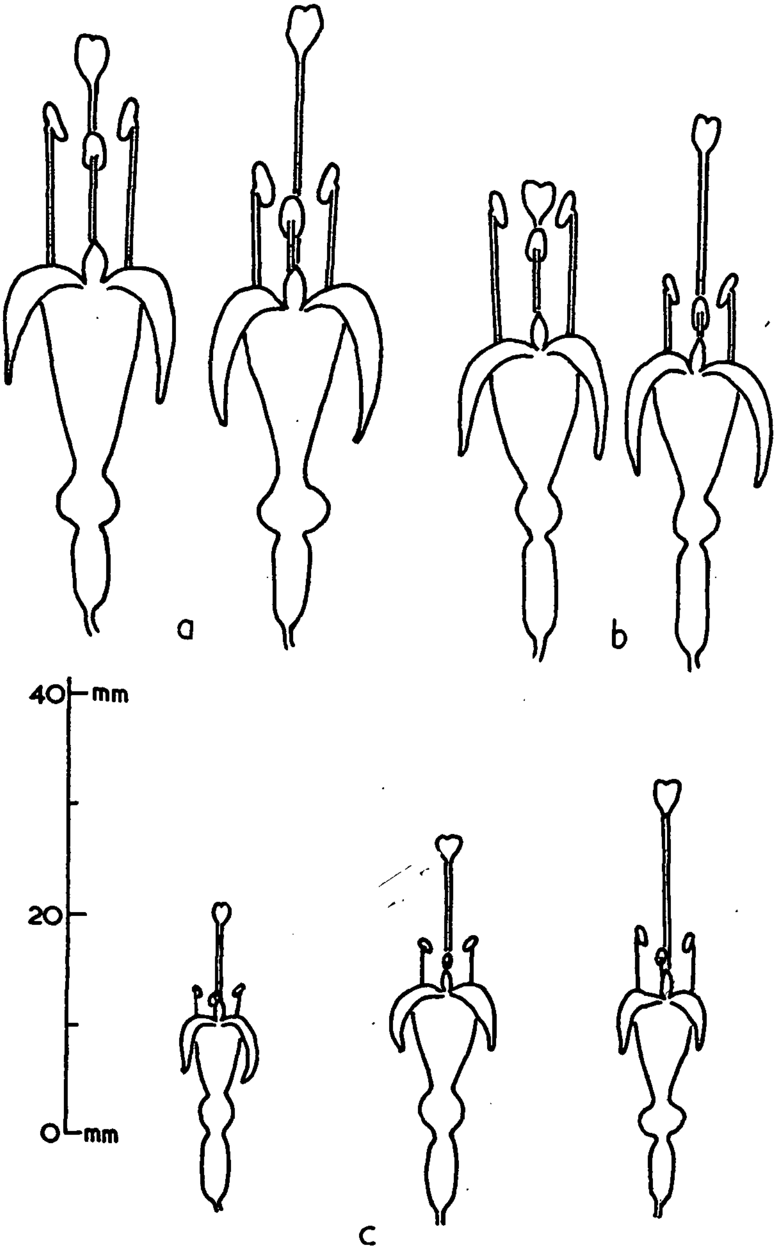

FIG. 1. *Fuchsia excorticata*. *a–b*, pairs of hermaphrodite flowers from two trees growing together, showing differences in style protrusion on the same tree, and differences in size between trees; *c*, female flowers from three trees.

hand, was not significantly different. The correlations between tube and style-length were 0·667 and 0·638 respectively, while those between tube-length and length of second stamen whorl were 0·661 and 0·606. In the original sample of 126 flowers the corresponding figures were 0·770 and 0·321. These rather loose correlations between the size of the floral parts could cause the variation in degree of style-protrusion observed (cf. Fig. 1*b*).

The observed variation in hermaphrodite flowers may be summed up as follows. Trees may differ in absolute length of style and tube, and this is probably under polygenic control. Within trees the degree of stylar protrusion varies, and this variation is approximately the same for all trees examined.

Female flowers (Fig. 1). A sample of one flower from each of 32 trees on Banks Peninsula gave flower lengths ranging from 19 to 31 mm. with a mean of 26·7±0·05. Thus most female flowers are smaller than hermaphrodites, a point not illustrated by Kirk (1889). The difference in flower size between female trees growing in proximity can be quite obvious, and would be expected if this character is under polygenic control.

TABLE I

Analysis of Variance for Tube and Style Length in Two Neighbouring Trees of F. excorticata

Tube length.	df.	s.s.	m.s.	F.
Between trees	1	643·49	643·49	329·5
Within trees .	138	269·45	1·953	—
Total . .	139	912·94	—	—

Style length.	df.	s.s.	m.s.	F.
Between trees	1	3,649·56	3,649·56	411·3
Within trees .	138	1,224·58	8·874	—
Total .	139	4,874·14	—	—

As the tiny staminodes project for only about 2 mm. above the tube, the style is very prominent and Kirk described it as 'long-styled', but as shown above it is usually shorter than in hermaphrodite flowers.

Pollination. Pollen was examined from three trees and found normal. This conflicts with observations by Beer (1921), who included *F. excorticata* in a list of species having irregular pollen development or all sterile pollen. It is possible that female flowers were studied.

Fruiting is always prolific, and artificial pollination showed that hermaphrodite flowers are self-fertile. Bagged female flowers set no fruits, and as these females gave hybrids when crossed with *F. procumbens*, the possibility of apomixis is ruled out. Cross-pollination by two nectar-seeking native birds, the tui and bell-bird, has also been recorded as important (Potts, 1870; Myers and Atkinson, 1923), but cross-pollination by wind is probably more difficult, as the pollen is held together by mucilage in masses, and is only blown with difficulty from the dehisced anther.

Natural populations. F. excorticata grows from sea-level to about 3,800 ft., and extends throughout New Zealand, covering 12 degrees of latitude. The populations in Table II are listed from north to south, and cover as much of the distribution area as was practicable. They extend over 9 degrees of latitude and include three populations from high altitudes, the remainder being from between sea-level and 1,000 ft. Each count was obtained by walking through bush for distances up to a mile and scoring all trees bordering the road.

TABLE II

Frequency of Flower Types in Natural Populations of F. excorticata

Population.	Miles from previous station.	Hermaphrodite.	Female.	Total.	Percentage females.
North Island:					
1. Auckland; Filters Rd. and Mt. Atkinson . .	—	56	38	94	40·42
2. Ruahine Range; Track to Rangiwahia Ski Club Hut (3,000–3,800 ft.) . . .	210	58	26	84	30·95
3. Wellington; Khandallah Reserve .	120	69	16	85	18·82
South Island:					
4. Queen Charlotte Sound; Momorangi Bay . .	30	64	26	90	28·88
5. Nelson; Wairoa Gorge . .	50	55	26	81	32·10
6. Nelson; Maruia Springs Hotel (2,300 ft.) . .	80	56	21	77	27·27
7. Christchurch; Summit Rd., Banks Peninsula . .	110	126	32	158	20·25
8. Taramakau River; below Harper's Pass (2,000–2,500 ft.) . . .	80	151	72	223	32·29
9. Aickens Rly. Station	10	103	42	145	29·00
10. Dunedin; Leith Valley . .	200	105	41	146	28·08
11. Dunedin; Highcliffs, Otago Peninsula . . .	8	79	31	110	28·18
12. Bluff; coastal track .	120	97	4	101	4·12
Total . .	—	1,019	375	1,394	—

The numbers of the two types in samples from twelve districts are given in Table II. In eight of these, from widely separated districts and different altitudes, the frequency is remarkably uniform, ranging from 27·27 to 32·29 per cent. of female plants. An explanation of the frequencies observed must await knowledge of the genetic basis of male-sterility and of the relative 'fitness' of the two types. Genetical experiments would take many years with this tree, but a short-cut is being explored using artificial hybrids between the different types of *F. procumbens* and *F. excorticata.* Undoubtedly the female type has been present in this species for a considerable time, and the high frequencies observed in all but one sample must indicate a greater 'fitness' of female plants, if male-sterility should prove to be controlled by a single gene. Two of the components of 'fitness' are the number of seeds produced and their percentage germination. Only a rough measure of the first variable will be possible, as each tree may produce some hundreds of many-seeded edible fruits. It may be noted that Kirk considered that the 'long-styled' trees (females) produced the most fruits.

The only counts of gynodioecious populations of which I am aware are the brief records given by Darwin (1877) which show little regularity in the proportions of the two forms. Two populations of *Thymus serpyllum* had 12 and 0 females respectively among hundreds of plants, and three populations of *Nepeta glechoma* contained, respectively, all females, all hermaphrodites, and a preponderance of hermaphrodites. Two small counts of *Echium vulgare* gave 11 females, 4 hermaphrodites, and 14 females, 16 hermaphrodites, 2 intermediates. *Cnicus palustris* and *acaulis, Plantago lanceolata,* and *Scabiosa arvensis* are recorded as having a preponderance of hermaphrodites.

III. *FUCHSIA PERSCANDENS*

This species was described by Cockayne and Allan (1927). It is not common, and is a slender scrambling liane, which can form compact bushes in exposed situations. The flowers are pendulous with tiny petals, and could be conveniently described as smaller copies of the flowers of *F. excorticata.*

Allan (1927) described a flower type which is hermaphrodite. He writes, however, 'I have not seen more than one type (long-styled) of floral structure in *F. perscandens*'. This is not the correct use of the term 'long-styled' in Kirk's sense, as he applied it to plants which are actually females.

I have collected flowers from both hermaphrodite and female plants in the Riccarton Bush, Christchurch, and these are illustrated in Fig. 2. As in *F. excorticata,* the females are smaller than the hermaphrodites.

IV. *FUCHSIA COLENSOI*

The validity of this species requires further investigation. Allan (1927) notes that the description was not based on a type specimen, but on a collection of variable material, and that natural hybrids of *F. excorticata* and *F. perscandens* could conform to the description of *F. colensoi.* He suggests, however, that one or more true shrubby forms may exist.

I have examined a hybrid swarm of *F. excorticata* × *perscandens* in the Riccarton Bush, Christchurch, containing plants which would be referred to *F. colensoi,* and find that both hermaphrodite and female plants exist. The flowers are similar to those of *F. excorticata.*

V. *FUCHSIA PROCUMBENS*

This is a very slender-stemmed, trailing species, and is confined to the coast in the north of New Zealand where it is not common. The flowers contrast with the two previous species in being erect, apetalous, and having the two whorls of anthers at almost the same level. After examining herbarium specimens and eleven populations, it was found that this species is trioecious. The forms described have retained their differential characters for three seasons in a glass-house.

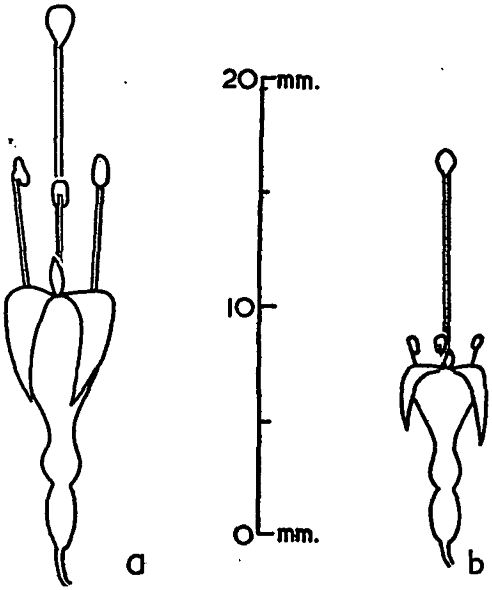

FIG. 2. *Fuchsia perscandens. a*, hermaphrodite flower; *b*, female flower.

Hermaphrodite (Fig. 3). The characteristic flowers of such plants have a large globose stigma about 2 mm. in diameter and level with the anthers. Intermixed with these one may find flowers with aborted stigmas, and in these aberrants the styles vary in length, from those of normal height to those which reach only to the mouth of the tube. Hermaphrodite flowers are self-fertile, and by the end of a season these plants are covered with fruits. The imperfect flowers set no fruits.

This form was known to Cheeseman (1914) and probably to Kirk, as is shown by their remarks on fruit-setting. It was not, however, distinguished from the type A male of this paper, and both forms were called 'mid-styled' (Kirk, 1892).

I have found this in only one population, growing with the type B male.

Male, type A (Fig. 3). This differs from the hermaphrodite in having slightly shorter stamens and a stigma which is only $\frac{3}{4}$ mm. in diameter. The stigma is almost always level with the anthers, and often shrivels when the flowers open.

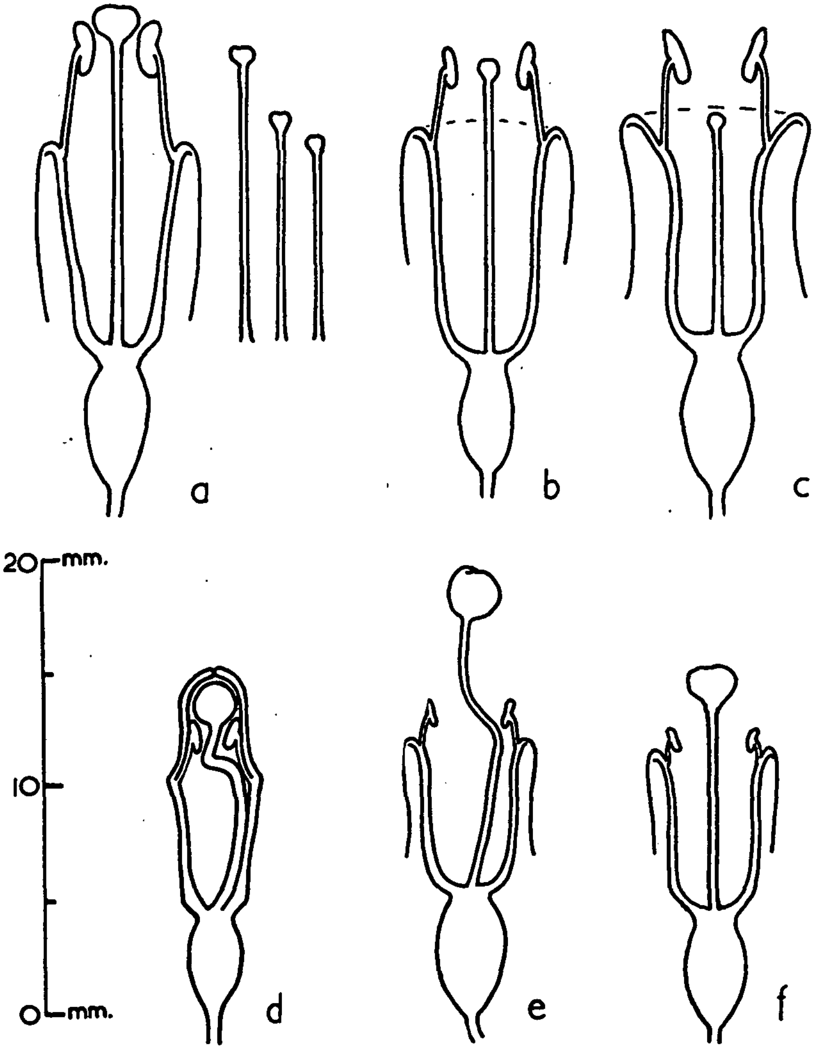

FIG. 3. *Fuchsia procumbens*. *a*, hermaphrodite flower, and styles of male flowers occasionally formed on hermaphrodite plants; *b*, male, type A; *c*, male, type B (*F. kirkii*); *d*, section of flower bud of female, type B; *e*, female, type B; *f*, female, type A.

With one exception, mentioned below, these flowers have never set perfect fruits on selfing or crossing. It is possible, however, to obtain parthenocarpic fruits with persistent flowers. The following observations were made:

(*a*) Six mature flowers with shrunken stigmas on self-pollination gave three parthenocarpic fruits with persistent flowers.

(*b*) Five flowers, with unshrunken stigmas when bud-pollinated, yielded four parthenocarpic fruits with persistent flowers.

(*c*) Of 84 flowers on an isolated plant, only 1 produced a fruit and this was parthenocarpic.

(*d*) Ten flowers used as females in a cross with a hermaphrodite gave two fruits which were parthenocarpic with persistent flowers.

(*e*) In 1950 an isolated plant in the field at Ngahau produced about 100 flowers, and the one fruit set contained seeds.

Thus the cause of female-sterility is probably due to some characteristic of the stigma. Possibly functional ovules are present, but are rarely fertilized.

Cheeseman's illustration (1914) is of a flower with an unshrivelled stigma.

Two populations were found pure for this type, and in a third it grew with the female, type B.

Male, type B (Fig. 3). The tube and anther length are the same as in type A, but the style is always short, never showing beyond the mouth of the tube. This is Kirk's 'short-styled' form. The stigma has the same size and characteristics as the type A male.

Four selfed flowers set no fruit. Kirk, writing of three localities in which only this form had been recorded, stated: 'At Tryphena Bay Professor Hutton and myself examined hundreds of flowers but saw no trace of fruit; subsequently I had the same experience at Mine Bay and again at Whangaruru.' On a plant at Tryphena which set some 150 flowers I found only one fruit towards the end of the season and this contained seeds. Thus these flowers are like the type A males, in being able to set a rare 'illegitimate' fruit due to some cause as yet unknown.

This was the second flower-type discovered, and was first collected by Kirk in December 1867 'on the beach of Great Barrier Island' (Hooker, 1871). The locality was almost certainly Tryphena. The only form then known was the one described in this paper as type A female, and which was already named *F. procumbens*. Specimens from Great Barrier were sent to Hooker who first considered them merely another sexual form of *F. procumbens*, but finally described it under the new name of *F. kirkii* (Hooker, 1871), and gave an excellent illustration of a flower. Munz (1943) has retained *F. kirkii* as a species. However, Kirk (1892) realized that this form was wrongly classified, and since then New Zealand taxonomists have rightly assigned it to *F. procumbens*. It may be found growing intermixed with the female, and seed from these females gives females and '*F. kirkii*' in approximately equal proportions.

This type was found in five populations. In two it grew alone; in two it was intermixed with the female type A, and in one with the hermaphrodite.

Female, type A (Fig. 3). The flowers are approximately two-thirds the size of the preceding types. Because of the shorter tube and tiny staminodes the style protrudes, and this led Kirk to classify the flower as 'long-styled'. A typical plant had style-lengths ranging from 10 to 13 mm. The stigma is always large and globose, and of the same type as in the hermaphrodite. The flowers set no fruit in isolation but are fertile with pollen from males and hermaphrodites.

This was the first type of flower recorded and is the common form of the female. It has been excellently illustrated by W. J. Hooker (1842). The illustrations of Kirk (1892) and Cheeseman (1914), on the other hand, give no indication of the smaller size of the flower or of the large stigma.

Two populations have only this type; in two others it grows intermixed with the type B male.

Female, type B (Fig. 3). This differs from the previous type in having a longer style, which, on the one plant available, ranged from 12 to 17 mm. in length. The style becomes bent when confined within the small female flower-bud, and the distortion persists in mature flowers. These styles are almost as long as those of the hermaphrodite. I have found this variant in only one population, growing with the type A male.

VI. BREEDING SYSTEMS IN THE GENUS

The three New Zealand *Fuchsia* species belong to the *Skinnera* section of the genus. It would be of interest if heteromorphic flowers occur in *F. cyrtantroides* of Tahiti, which is the one other species of this section. The type specimen is hermaphrodite (Moore, 1942). Miss Marie C. Neale, botanist at the Bishop Museum, Honolulu, has kindly examined for me the four sheets of this species in their herbarium (1315, 1341, 17005, and a collection by M. L. Grant), and all are from hermaphrodite plants. Considering, however, the small number of specimens seen, it is possible that female plants may yet be found in this species.

This isolated Pacific section of the genus is probably not unique among the *Fuchsias* in having gynodioecious species. Within the *Encliandra* section, which is distributed from Mexico to Panama, Munz (1943) describes the flowers of seven species as hermaphrodite, four species as 'perfect or pistillate', one species as 'perfect or imperfect', one as 'dioecious or polygamous', and three as dioecious.

When the genetical basis of the differences in flower type in *F. procumbens* is known, it may provide information as to the way dioecy has evolved in the genus, and also whether or not gynodioecy has played a part in the process.

SUMMARY

1. *F. excorticata* and *F. perscandens* are gynodioecious, and female flowers are smaller than hermaphrodites.
2. Differences in flower size between hermaphrodite plants and also between females in *F. excorticata* are probably under polygenic control.
3. Of twelve widely separated populations of *F. excorticata*, eight showed female percentages between 27·27 and 32·29, the remaining percentages being 40·42, 20·25, 18·82, and 4·12.
4. *F. procumbens* is trioecious, and two style lengths have been found in males and females. The type B male has previously been described as *F. kirkii*.
5. Gynodioecy probably occurs also in the *Encliandra* section of the genus.

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