

## Notes on Sexual Expression in Certain Species of New Zealand Coprosmas.\*

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IN creating the genus *Coprosma* for the two species *foetidissima* and *lucida*, J. R. and G. Forster (1776, pp. 137-8) include it in their section *Polygamia Dioecia*, and refer, with figures, to male, female, and hermaphrodite flowers. Of the ten species dealt with by A. Cunningham (1839, pp. 206-7) *C. acerosa* alone is described as dioecious. Raoul (1846, p. 23) described *C. robusta* as dioecious, while Hooker (1867, p. 110) says of the genus, "Flowers unisexual, often dioecious." Cheeseman (1887, p. 223) in his revision of the genus, states, "The flowers are unisexual, and the sexes are placed on different plants. Occasionally, however, a few male flowers are intermixed with the female, and *vice versa*. Some species, and especially *C. robusta* and *C. foetidissima*, now and then produce hermaphrodite flowers, to all appearances well developed and perfect, but which seldom mature fruit." Colenso (1889, p. 85) describes for his *C. pendula* (*C. crassifolia*, according to later authors) male, female, and hermaphrodite flowers, "the three kinds of flowers on one branchlet." He observes, "Another shrub was hermaphrodite, or more strictly speaking polygamous—the first, I think, I have ever known of this genus, so pre-eminently dioecious." Of his *C. coffaeoides* (*loc. cit.*, p. 88) he says, "Specimens of the *male* plant have been seen carrying *female* flowers at the top of the branchlet." Cheeseman (1925, p. 855) describes the genus as dioecious, without any statement about hermaphroditism.

We give here our observations on the incidence of abnormal, irregular, and hermaphrodite flowers in the various species of the genus *Coprosma* that have engaged our attention; assuming always that the normal plant is dioecious. The observations were made during the summer 1928-29 with the exception of those on *C. lucida*, which were started two years before.

For the purposes of this paper only the primary sexual characters—the presence of stamens or pistil—were used in determining the sexual position of a flower, but certain secondary characters were often useful in throwing early suspicion upon a plant. The chief of these were the stoutness of the bud and the width of the corolla in a male, and the more slender bud and narrower corolla of the female; the large number of flowers in more or less dense inflorescence in the male and the fewer flowers and somewhat lax inflorescence in the female.

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In the following descriptions of flowers, signs are often used with these meanings:—(F) flowers with well developed styles: (f) with poorly developed styles: (M) with well developed stamens: (m) with poorly developed stamens: (FM), (Fm), (Mf), (mf) flowers combining these characteristics.

1. *C. areolata* Cheesem.

This species was examined once near Foxton and several times near Palmerston North during the flowering season, September-October. No unusual cases were observed.

2. *C. acerosa* A. Cunn.

This species was examined on the Foxton sand-dunes twice during its flowering season, September-October, in its early and full flowering stages. Nothing unusual was observed.

3. *C. Cunninghamii* Hook. f. *i.e.* *C. propinqua* × *robusta*.

A hybrid swarm of this parentage was examined at Mt. Biggs near Feilding. No very detailed observations were made, but a short examination on more than one occasion revealed the presence of hermaphrodite flowers on the male plants. Usually these flowers are found on the plants that are in the early flowering stage. No evidence of hermaphroditism was noted in female plants. The F1 generation of *C. propinqua* ♀ × *robusta* ♂, which was produced artificially by Dr. H. H. Allan, and grown in the Feilding Agricultural High School garden, on observation gave similar evidence. Late in summer some of these plants known to be predominantly male were found bearing fruits. These differed, however, from those on female plants in having a wider calyx.

4. *C. depressa* Col. ex Hook. f.

This species was examined about its mid-flowering season, late December, on the Ruahine Ranges near Taihape. Many male plants were found bearing more or less numerous pistillate flowers, the ovaries of which were obscure. Nothing unusual was observed about the female plants.

5. *C. foetidissima* Forst. J. R. et G.

Towards the end of September only a single plant of this species was found in flower on the lower slopes of the Ruahines near Apiti. Of the two flowers open one was (M) with six stamens, and the other (F) with three styles. The general characteristics of the tree were those of a male. In mid-November (a little late, particularly for the male flowers) most of the female plants were pure female but many bore numerous (Fm) and even (FM) flowers intermingled with (F).

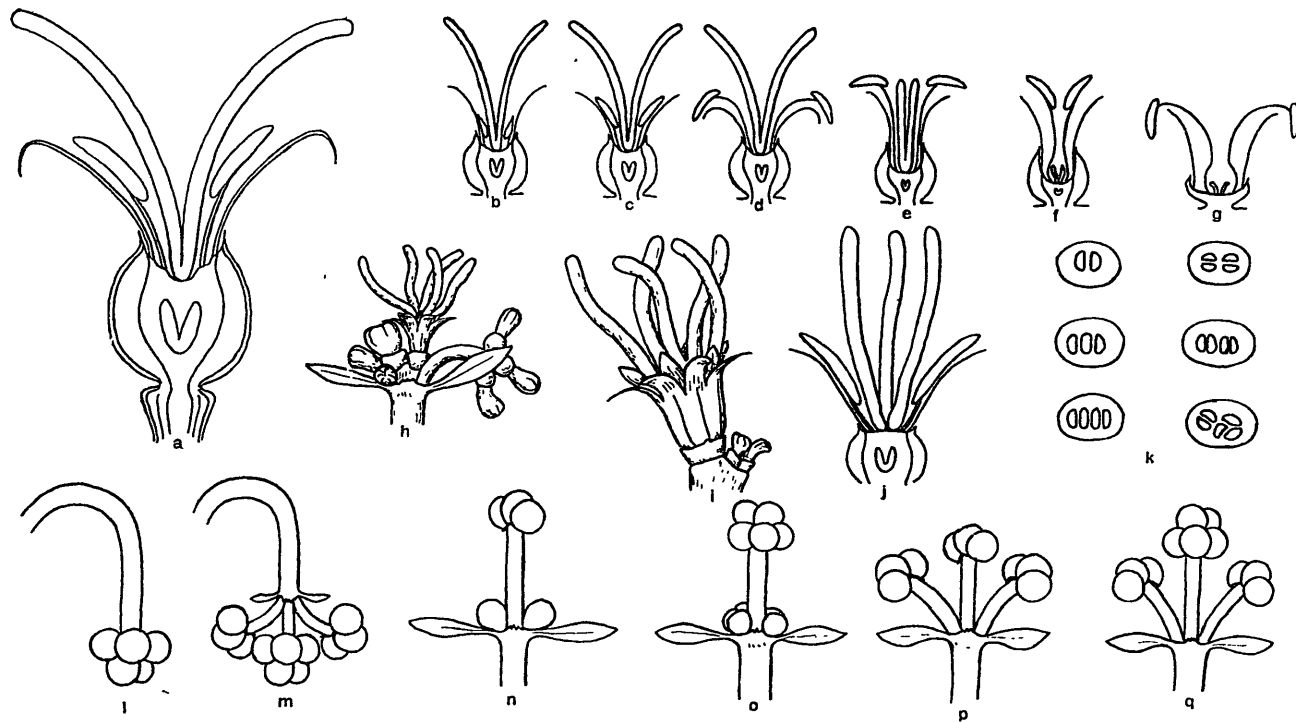


FIG. 1.—*Coprosma lucida*.

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|-------------|--|-------------|--|
| a.          | Diagram of a section of a hermaphrodite flower.                    | i.          | A single flower from this inflorescence. |
| b.          | Diagram of a section of a flower nearest in form to a pure female. | j.          | A section of the same flower.            |
| g.          | Diagram of a section of a flower nearest in form to pure male.     | k.          | Sections of two- to five-pyrened fruits. |
| c, d, e, f. | Diagrams of intermediate forms.                                    | l, m.       | Diagrams of male inflorescences.         |
| h.          | An inflorescence from a polygamous plant,                          | n, o, p, q. | Diagrams of female inflorescences,       |

**6. *C. grandifolia* Hook. f.**

Late in August a plant was observed in flower and fruit. Some flowers examined were distinctly (Fm) even approaching (FM). Another plant was female but bore at least one (FM) flower. When the flowering season began again at the end of the following March, numerous plants were examined at Tiritea, near Palmerston North. Only a few hermaphrodite (Fm) flowers were found on a female plant. Anthers in these flowers appeared to be sterile, though well developed. No trace of hermaphroditism was detected on male plants by naked-eye examination. Yet under the microscope every male flower was found to have ovules and styles, the former being about .25 mm. long and the latter about .5 mm. No true female flower was found to have any trace of stamens. The following is the count of the male and female plants examined as they were observed in the field:—male 47, female 43, sex not definite 15. This suggests that the sexes are fairly evenly distributed.

**7. *C. lucida* Forst. J. R. et G.**

This species provides abundant material for the present subject, and has been under observation for several years. What makes it of outstanding interest is this: that so far not a single flower from either male or female plant has been found entirely free from styles or stamens respectively. A 'male' flower invariably has at least a rudimentary pistil, a 'female' at least immature or rudimentary stamens. In what follows with regard to *C. lucida* we mean by a male or female flower one in which the sex mentioned is functioning and the opposite sex is expressed to a minimum extent. Besides these types there are an indefinite number of intermediates, which join the extremities in a more or less perfect series of hermaphrodite flowers.

Two trees bearing definitely hermaphrodite flowers are known. The flowers appear to be protogynous. The corolla is as wide as in the male flowers and the filaments are as long as the corolla tube, while the anthers appear to be perfect, at least in some flowers. In many flowers the anthers do not reach maturity, but wither away with the styles. In others they are sterile and poorly developed. No pollen was actually observed being shed by any flower, though often an appreciable crop of fruit is produced. Inasmuch as a careful search failed to reveal any species of *Coprosma* flowering at the same time as *C. lucida*, it is highly probable that pollen was produced by hermaphrodite flowers.

One bush of *C. lucida* was different from all others observed. It was polygamous. Male and female inflorescences with almost perfect unisexual flowers were scattered along the branches, intermingling with other flowers, giving a complete hermaphrodite range. No type of flowers definitely predominated. Among the hermaphrodite flowers were female flowers with anthers well developed though sterile, flowers with both organs well developed, male flowers with large though hollow ovaries, and immature ovules and stigmas. The peduncles of the female inflorescences were almost invariably glabrous, while those of the male inflorescence were often exceedingly pubescent.

There are many other irregularities noted in this species. The ovary frequently has more than two ovules—3, 4, or 5—and the

number corresponds to the number of styles. Six corolla lobes and six stamens appears to be the normal number, but sometimes this number increases even up to ten (whether the flower is 'male' or 'female'). Fairly often the filaments of two or more stamens are united. Even anthers may be so joined. Sometimes the styles are united almost throughout their length. Frequently flowers were found with the ovaries united, but all other parts free. Male flowers were found with two sets of stamens in the same corolla.

8. *C. propinqua* A. Cunn.

This species was examined once only in a swamp near Foxton where it abounds. Plants were seen in various stages of flowering, but nothing unusual was observed.

9. *C. repens* Hook. f.

This species was examined at the same time as *C. depressa*. The male plants were in an advanced stage of flowering, while the female were just in bud. A noteworthy feature is that male plants cover large areas while female are only to be seen here and there in small patches. Many drupes were examined and found invariably to contain four pyrenes.

10. *C. retusa* Hook. f.

This species was observed throughout its flowering season, November-December, in hedges at Palmerston North and also at Wellington in mid-December. In the latter place only several apparently perfect hermaphrodite flowers were found on a female plant.

11. *C. rhamnoides* A. Cunn.

The following observations were made chiefly near Feilding, but were supplemented considerably by others near Bunnythorpe, Palmerston North, Foxton and several other localities.

A forest remnant near Feilding contains numerous examples of this species, varying in height up to 6 or 8 feet, but chiefly as low growing and densely divaricating shrubs. In late August and early September the plants were in full flower when a considerable number of observations were made. As a result, it was found again that male plants frequently bore pistillate flowers, and that sometimes it was practically impossible to determine which sex was most manifest in the plant. There was some evidence of the formation of fruit on trees predominantly male; indeed, ripe fruit was collected from such plants. The majority of the irregular plants were noted in the first 30 examined. The examination of the following 70 or 80 was more hurried, and a plant classed as male or female if no flowers showing the characteristics of the opposite sex were observed in a rapid survey. It is possible that some irregularities thus escaped observation. It is also possible that, as in the case of some other species, the pistillate flowers on male plants disappear early. The count of the plants examined in this locality is as follows:—true male 55, males with some pistillate flowers 14, true female 34, sex not expressed or mixed 5. This analysis incidentally shows the great predominance of males over females (in proportion of 2 to 1).

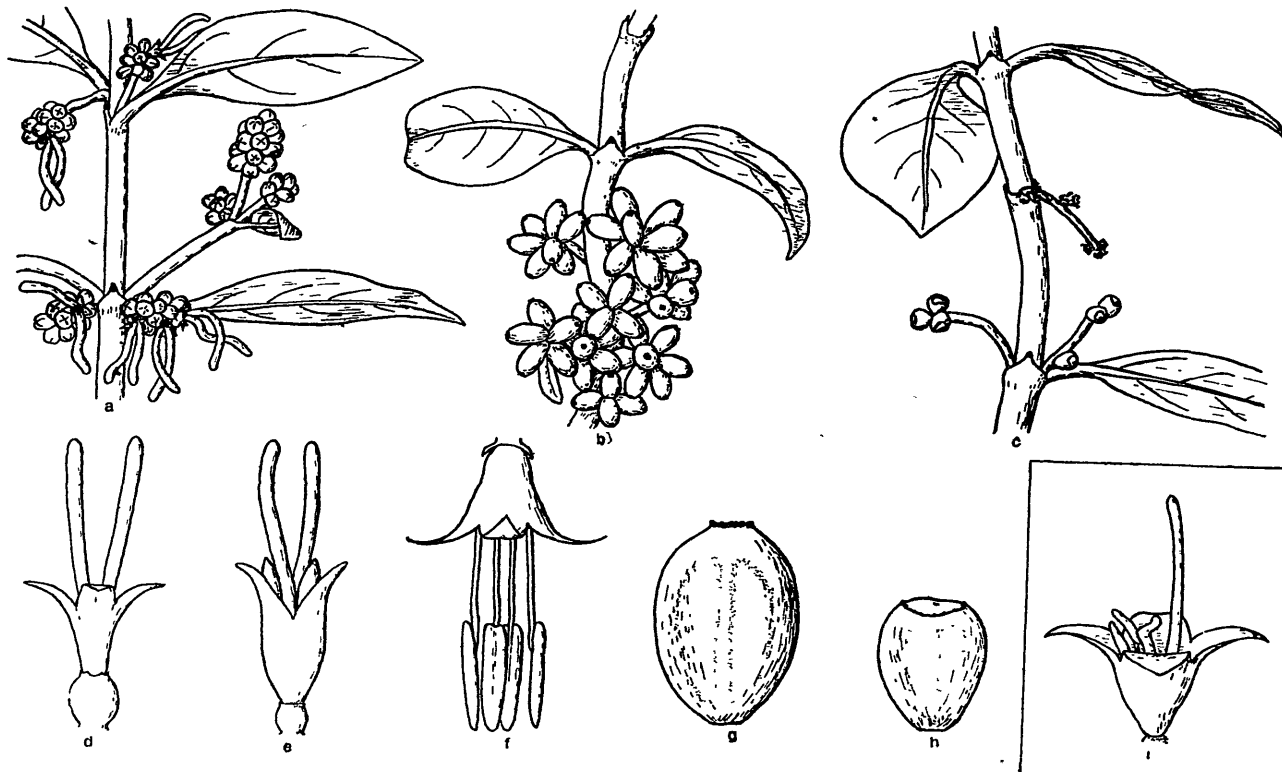


FIG. 2.—*Coprosma robusta*.

- a. A flowering shoot from a male plant showing hermaphrodite flowers  
 b. A fruiting shoot from a female plant.  
 c. A fruiting shoot from a male plant.  
 d. Diagram of a female flower.  
 e. Diagram of a hermaphrodite flower,

- f. Diagram of a male flower.  
 g. Diagram of a fruit from a female plant.  
 h. Diagram of a fruit from a male plant.  
 inset. *C. rhamnoides*, an abnormal flower from a male plant,

There was considerable diversity in the development of the ovary in the pistillate flower or male plants. There are various forms, from that of a perfect ovary surmounted by a calyx down to a mere trace of a calyx. One or two, as a rule, and rarely all four stamens are present in such a flower; they are, however, usually sterile. Commonly these flowers have only one style or a perfect or an imperfect one, which is either shrivelled or short. Rarely both styles are well developed. Ripe fruit is sometimes to be seen on the male plants. Male flowers also occur on the female plants, but they are few in number. One case is known to us where pollen was shed from such a flower. Several polygamous trees were observed, in which it was impossible to say which sex was predominant. Both unisexual and hermaphrodite flowers, together with various gradations, were freely intermingled along the branches. On one tree the early flowers were polygamous, and an abundant crop of fruit was set, but all the later flowers were purely male.

12. *C. rigida* Cheesem.

One tree bearing hermaphrodite flowers was seen in early flowering season, in August. In the following month numerous specimens were examined around Feilding and Palmerston North, but no more evidence of hermaphroditism was revealed.

13. *C. robusta* Raoul.

The observations on this species were made on garden plants in Feilding and on wild plants in the Manawatu area generally.

With the start of the flowering season, at the end of August, very many flowers on male plants opened to show large perfect styles and only immature non-extended stamens, though with fertile anthers. Many of these flowers were found to have perfect, though somewhat smaller than normal, ovaries; the majority, however, had no trace of ovary. As the season advanced, fewer and fewer hermaphrodite flowers would open, until they entirely disappeared. Numerous plants were examined, with almost always the same result. With two exceptions, close examination of a male plant early in the flowering season would bring to light some irregularity, such as either a pure female or a hermaphrodite flower. Of the numerous female plants examined all were pure except two; on one a single sterile male flower was found; on another a single and almost sterile hermaphrodite flower. Three plants were quite exceptional. Though their buds had the appearance of males, they produced nothing but (F) and (Fm) flowers during September. Later on, however, pure male flowers appeared and soon covered the trees. A few months later these trees produced a fairly good crop of fruit. The latter differed somewhat from those of true female plants, being smaller in size and possessing a wider calyx.

14. *C. rotundifolia* A. Cunn.

This species was examined on several occasions and in several localities of the Manawatu district during its flowering season, September-October. Only one pistillate flower was found on a male plant. The styles appeared to be good, though the ovary was obscure.

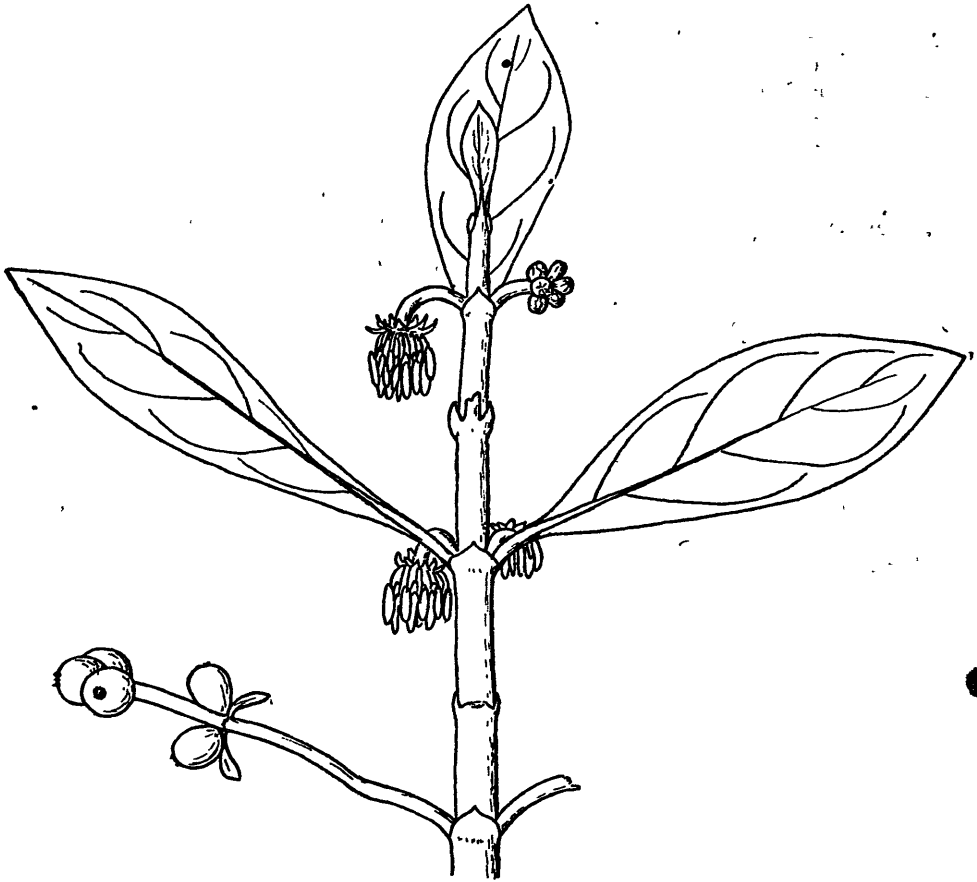


FIG. 3.—*Coprosma lucida*.

A flowering and fruiting branchlet from a polygamous plant.



15. *C. tenuifolia* Cheesem.

Preliminary observations were made on a cultivated specimen at the Feilding Agricultural High School. In mid-August it was observed to be bearing (1) male flowers with anthers fully developed, (2) female flowers with styles fully developed, and (3) hermaphrodite flowers chiefly with extended styles and non-extended filaments, the anthers being plump and apparently fertile. The ovaries, however, were generally non-existent in such flowers. Some flowers were noted at random on 20th August as follows:—(1) three (Fm) flowers in a whorl, (2) (MF) one stamen protruded four short, two styles half protruded, (3) (Fm) three styles, (4) (m) five stamens with short filaments, (5) three (Mf) flowers on the same branchlet, (6) (M?), (7) (m), (8) (F), (9), (Fm) (10) (Mf). At this time only a few flowers were open. At the end of August the plant was almost completely in flower and almost completely male. Only two irregular flowers were observed. One showed a single poorly developed style and a single sickly stamen; another a five-lobed corolla, five perfect stamens, and two well developed styles, but there was no development of ovary. Later on about twenty ripe fruit were collected, which had peculiarly wide calyces. At the end of September and early in October, the species was studied in its native haunts nearer the mountains, about Kimbolton and Rangiwahia. Considerable evidence of hermaphroditism was collected, and this despite the fact that the flowering period, and particularly so with the male plants, was almost over. Of many female plants examined most were found to bear some hermaphrodite flowers. As a rule these had well developed pistils and only two stamens on short filaments. One tree, however, which was predominantly female, bore numerous hermaphrodite flowers with all four stamens, which showed all stages of development. In this case it was evident that the flowers were of protogynous nature. Five male plants were also examined, and of these two bore some hermaphrodite flowers, which, however, appeared to be protandrous. The season, however, was then too far advanced to make a more careful observation on this point.

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TABULATED SUMMARY.

Species.	No. of Plants Examined.	Male Plants with Abnormal Flowers.	Female Plants with Abnormal Flowers.	Polygamous Plants.	Pollen Shed by Female Plant.	Ripe Fruit on Male Plant.	Season of Observation.
Areolata	Many	None	None	None	None	None	Throughout.
Acerosa	Many	None	None	None	None	None	Early and Mid.
Cunninghamii*	Not many	Few	One	None	None	Few	Throughout.
Depressa	Many	Few	None	None	None	—	Early.
Foetidissima	Many	Two	Four	None	None	—	Late (mainly).
Grandifolia	Many	None	Three	None	None	None	Throughout.
Lucida	Twelve	Two	Nine	One	Two	None	Throughout.
Propinqua	Many	None	None	None	None	—	Mid.
Repens	Many	None	None	None	None	—	Early.
Retusa	Many	None	One	None	None	—	Mid (mainly).
Rhamnoides	Many	Many	Few	Six	One	Many	Throughout.
Rigida	Many	One	None	None	None	—	Late (mainly).
Robusta	Many	Almost all	Two	None	None	Many	Throughout.
Rotundifolia	Few	One	None	None	None	None	Throughout.
Tenuifolia	Not many	Several	Several	None	None	One	Late (mainly).

\**C. robusta* × *propinqua* (art. hybrid) is included.