Digitalis purpurea	m
Galium aparine	o
G. parisiense ssp.anglicum	o
Geranium robertianum	o
Lotus angustissimus	m
L. pedunculatus	p
Mentha pulegium	p
M. suavolens	o
Mimulus moschatus	o
Myosotis caespitosa	o
Nasturtium officinale	m
Parentucellia viscosa	m
Plantago hirtella	o
P. lanceolata	m
R. conglomeratus	o
R. obtusifolius	o
R. pulcher	o
Sagina apetala	o
S. procumbens	o
Sherardia arvensis	o
Stellaria alsine	o
S. media	o
Trifolium pratense	o
T. repens	m
Verbascum thapsus	o
Verbena bonariensis	p
V. officinalis	o

DIOECY IN GENIOSTOMA LIGUSRIFOLIUM

J.A. Rattenbury

In their descriptions of *Geniostoma ligustrifolium* (pigwood, hangehange) Allan, Cheeseman and other New Zealand botanists make no mention of sexual differentiation of the flowers although Cheeseman reports that members of the family (*Loganiaceae*) to which this species belongs, sometimes bear flowers which are unisexual by abortion. Species of *Geniostoma* from Java are reported as being gynodioecious (perfect-flowered plants and female-flowered plants).

Examination of several populations in the Auckland province has indicated that individual plants bear flowers that are either female or (apparently) hermaphrodite, (Figs. 1 and 2). In the former, sterile (empty) pollen sacs are present. The pistils are undistinguishable in the two types of flower. Because of the small size, the floral differentiation appears to have been missed.

Studies of these populations and detailed examination of the flowers at high magnification have revealed the following facts:

1. Only female flowers set seed (extremely rare exceptions may occur).

2. Female-flowered plants are fewer than males (about three females to five males or 37½% female).

3. Pollen from the apparently hermaphrodite flower is shed from the pollen sacs before the flower opens and is deposited virtually in its entirety on its own stigmatic surface, almost completely smothering the surface of the latter (Figs. 3 and 4).

4. Insects are powerfully attracted by the strongly fragrant flowers to the nectaries which are situated at the base of the style immediately under the capitate stigma.

5. Some good sized plants exist which appear to be non flower bearing, although this could be a question of age, season or environmental conditions.

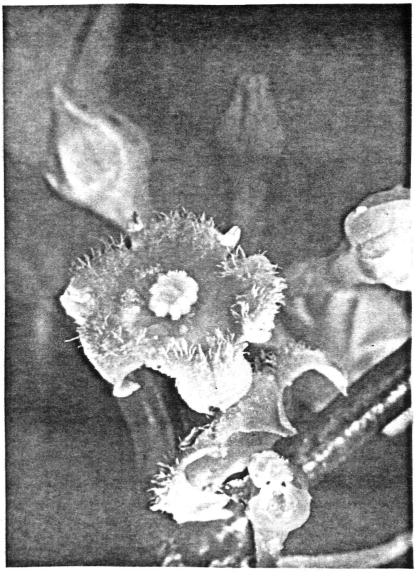

FIG. 1: "Male" flower showing coating of pollen on stigma and well-developed anthers.

FIG.2: Female flower showing pollen-free stigma and reduced (sterile) anthers.

FIG. 3: Section of "male" flower with normal-appearing ovules.

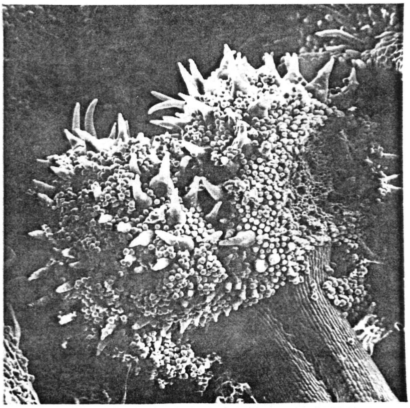

FIG. 4: Stigma of "male" flower showing dense covering of pollen grains.

From these few observations it is possible to speculate on the nature and origin of the breeding system in this species.

Although the mechanics of the pollinating process seem designed to ensure self-pollination in the perfect flowers, absence of seed set in these plants indicates that either the female organs are non-functional (sterile) or that a genetic self-incompatability system exists preventing self-pollination. Furthermore, the excess of its own pollen physically or physiologically prevents access by pollen from other (compatable) flowers. Observation of two seed pods on a single "hermaphrodite" plant resulting from infrequent penetration of the pollen barrier may support the second alternative, although rare apomictic seed development (without fertilisation) could have occurred. The effect of this process, whichever it is, is to make all such flowers functionally male, and the species truly dioecious in its breeding system.

Current thinking suggests the ancestors of many, if not most, dioecious plants, were perfect (bisexual). Mutations in such hermaphrodite plants which led to premature pollen discharge and deposition on the stigma would only have been selectively advantageous because they led to an improved process of insect pollination by placing the pollen supply closer to the nectaries and thus ensuring that insects visiting the latter both collect and deposit pollen. The result of selection favouring these functional males would be a build-up in the numbers in wild populations.

The evolution of purely female plants would be an advantage to the species since such plants would not have their resources wasted in pollen production and more energy could be devoted to seed-production.

The problem of the origin of female flowers has a complex genetical base, the more so as the ratio of male to female plants is not one-to-one. Two genes, at least, are involved and certain genetic combinations will need to be sterile and/or produce flowerless plants. It is possible to construct a genetic model on this basis which, over three or four generations of free interbreeding, results in about 37% females in the population, no matter what proportions of genetic types were initially present. This figure is consistent with field observations, especially as flowerless plants are not uncommon in most populations.