COMPLEX HYBRIDITY IN *ISOTOMA PETRÆA*
I. THE OCCURRENCE OF INTERCHANGE HETEROZYGOSITY, AUTOGAMY AND A BALANCED LETHAL SYSTEM

S. H. JAMES *
University of Sydney

1. INTRODUCTION

COMPLEX hybridity is a feature of a few groups of plants, particularly the Euoenotheras of North America. In all species which possess this genetic system the flowers are self pollinated. The correlation between complex hybridity and autogamy and its significance with regard to the maintenance of heterosis under conditions of strict inbreeding has long been recognised. The evolutionary mechanism whereby the components of the genetic system become associated is less well understood and two different hypotheses are current (Darlington, 1929, 1931, 1958; Cleland, 1936, 1960, 1962). In essence, Darlington maintains that complex hybridity is evolved via the sequential fixation of interchanges in the heterozygous condition under conditions of, and as a response to, imposed inbreeding. Cleland, however, asserts that in *Œnothera* at least, the system is initiated by the production of large interchange rings through the hybridisation of outbreeding races having different chromosome end sequences, the system subsequently becoming stabilised by the adoption of autogamy and a balance lethal system. *Isotoma petræa* F. Meull., an herbaceous species of the Lobeliaceæ, provides an example in nature in which the initial stages of the evolution of complex hybridity may be traced. As such, it appears to bridge the gap between *Œnothera*, which may be considered to be a " mature " case of complex hybridity, and the " incipient " complex hybridity exhibited by *Pæonia californica* (Walters, 1942) and other species in which interchange heterozygosity is frequent. This paper deals with genetic systems found in *Isotoma petræa* and the closely related *I. axillaris* Lindl. and *I. anæthifolia* Summerhayes.

2. MATERIAL AND METHODS

Wimmer (1953) in his monograph of the Lobeliaceæ groups ten Australian species along with one extra-Australian species into the section *Isotoma* of the genus *Laurentia*. However, Melville (1960) has discussed this taxonomic situation and supports the recognition of *Isotoma* as a genus including the ten Australian species only. The writer is in agreement with Melville's conclusions and follows his example in using the name *Isotoma* in lieu of *Laurentia*. Darlington (1963) in tabulating species in which all the chromosomes may be associated into a single interchange ring listed *Isotoma petræa* as *Laurentia perræa*.

* Present address: Botany Department, University of Western Australia.

Natural populations were sampled by raising seedlings progenies from open-pollinated plants and by making field collections of cytological materials. Anthers were fixed in acetic alcohol 1 : 3 for 6 to 24 hours and stored in absolute alcohol at about −10° C. Little deterioration of the stored material occurs over a year. Squash preparations were made in 2 per cent. orcein in 60 per cent. acetic acid. Crosses were carried out in the glasshouse. Emasculated and treated flower buds
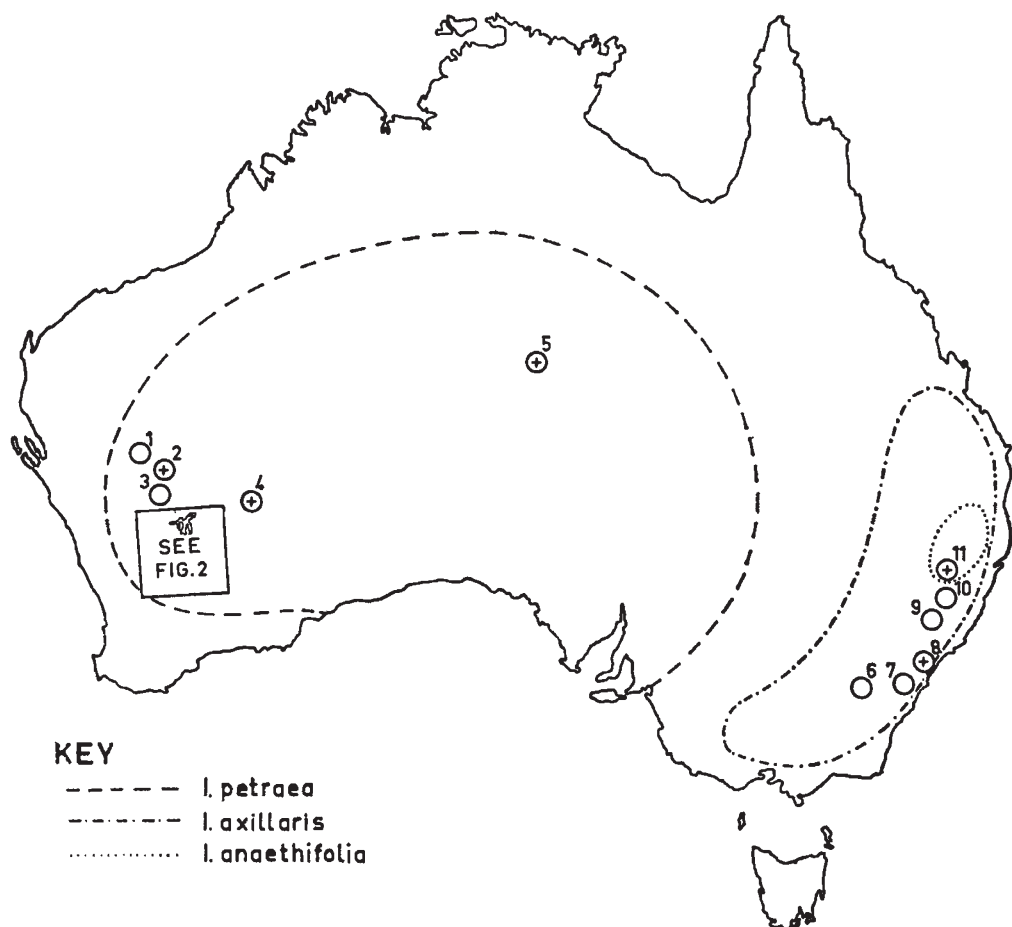
KEY

— — — —   I. petraea

—·—·—·—   I. axillaris

················   I. anaethifolia

FIG. 1.—Distribution of *Isotoma* spp. in Australia. Symbols indicate the locations of populations examined. All are floating interchange populations. " + " included in the symbol indicates the positive identification of the " *axillaris* " chromosome end sequence in that locality.
        For locality names, refer to tables 1 and 2.

were covered with bags which were finally removed only after the style had withered away. Seed germination occurs after a prolonged dormancy period (about 4 months), the specific factors controlling germination being as yet unknown.

3. OBSERVATIONS

(i) Distribution

Isotoma petræa is found in rocky exposed situations throughout the Eremean province of Australia (fig. 1), typical habitat sites being

fissures in rocky cliff areas and on bald granite residuals (monadnocks) It is especially characteristic of the granite residuals which occur abundantly in the outer wheat belt of Western Australia. Because of this habitat preference, the species is particularly dissected in its distribution occurring in small populations which are precisely delimited and separated from neighbouring populations by distances of up to 20 miles. Populations initially visited in 1960 and revisited in 1962 were found to differ markedly in numbers of plants and luxuriance of growth. A single plant was found on one granite rock newly visited in 1962 (" 441 ", table 2). Other populations of less than a dozen plants have been recorded, but usually a population includes several hundred plants. Seed production is remarkably heavy. Individual capsules may contain up to 1000 ovules and an average sized plant may bear over a hundred flowers. The species therefore, is capable of increasing its numbers substantially given favourable climatic conditions. Presumably the observed variation in population numbers is dependent upon year to year climatic fluctuations.

The species is replaced eastwards by *I. axillaris* and *I. anæthifolia* which occur on elevated granitic outcrops throughout the highlands and western slopes of the Great Dividing Range. *I. axillaris* extends from central Queensland to central Victoria while *anæthifolia* is restricted to a small area near the New South Wales-Queensland border (fig. 1). The three species are morphologically quite distinct, being differentiated especially with regard to leaf shape. Capsule shape, and colour, shape and disposition of the corolla lobes are also constant differentiating characteristics. Synthetic *petræa* × *axillaris*, *petræa* × *anæthifolia* and (*petræa* × *axillaris*) × *anæthifolia* hybrids are quite fertile. The *anæthifolia* × *axillaris* cross has yielded ample seed, but the viability of this seed has not been tested. The three species are clearly very closely related, indeed the validity of their recognition as separate species is open to doubt.

(ii) *General cytological characteristics*

All three species are diploid throughout their range with the gametic chromosome number $n = 7$, a number basic to the Lobeliaceæ. No polyploids have as yet been found, though they do occur in other species of *Isotoma* and widely throughout the family.

The chromosomes are more or less isobrachial. Chiasma formation is terminally localised and the chiasmata are fully terminalised at first metaphase. Chiasma frequency is' approximately 1·95 per bivalent so that the chromosomes are generally associated as seven ring bivalents (plate I, (1)), though one or two rod bivalents occur in about 30 per cent. of P.M.C.s. These cytological attributes will be dealt with in detail in a subsequent paper. It may be said here, however, that *Isotoma* is cytologically preadapted to the occurrence and maintenance of interchange hybridity.

(iii) *Incidence and distribution of interchange hybrids*

Interchange hybrids occur widely throughout *petræa, axillaris* and *anæthifolia* (tables 1 and 2). Natural populations may be of two types with respect to interchange hybridity:

(a) *Floating interchange populations.* These are composed mainly of structural homozygotes but carry a proportion of heterozygotes. All populations of *anæthifolia* and *axillaris* so far examined are of this first type. In *petræa* such populations are characteristic of the greater portion of its distributional range. Although the data are insufficient

TABLE 1

Interchange hybrids in Isotoma petræa. *Analysis of progeny raised from seed collected in the field*

Locality	Parent no.	No. of progeny showing M-1 configuration				
		$7\,II$	$\odot_4$	$\odot_6$	$[\odot_6+\odot_6]$	$\odot_{12}$
Near Alice Springs (1, 5) *	1	6	2	1	...	...
	2	4	1	...	...	...
	4 others	11	...	...	...	...
Near Laverton (1, 4)	1	1	2	...	...	...
	2	...	1	...	...	...
	7 others	12	...	...	...	...
Pigeon Rock (2, 6)	1	...	...	3	...	...
	2	...	...	2	...	...
Berringbooding Rock (2, 10)	1	...	...	...	15	...
Near Bencubbin (2, 15)	1	...	...	...	...	5

* The figures in parentheses refer to map localities: the first number refers to figure and the second refers to locality numbered in that figure.

to give a precise measure of their frequency, the interchange hybrids compose approximately 10 per cent. of such populations but this frequency increases to 30-50 per cent. in some *petræa* populations near the western periphery of the species range.

(b) *Multiple interchange populations.* At the extreme south-west of its range the local populations of *petræa* are composed of plants which are all multiple interchange heterozygotes. With only one exception (see below) a single meiotic configuration characterises all the individuals examined from any one population. So far, populations characterised respectively by $\odot_6$, $\odot_{10}$, $\odot_{12}$, $\odot_{14}$, $(\odot_6+\odot_6)$ and $(\odot_6+\odot_8)$ have been examined (plate I (2) to (7)). There is a marked tendency for the ring size, that is, the number of interchanges involved, to increase along a north-east to south-west line through the region occupied by the multiple interchange populations (fig. 2).

(iv) *The breeding mechanism*

All three species, *petræa*, *axillaris* and *anæthifolia* are characterised by a pollination mechanism which has been described in detail, for

TABLE 2

Incidence of interchange hybrids in Isotoma. *Analysis of field collections*

Species and Locality	No. of plants showing M-1 configuration								
	7II	$\odot_4$	$\odot_4+\odot_4$	$\odot_6$	$\odot_{10}$	$\odot_6+\odot_6$	$\odot_{12}$	$\odot_8+\odot_6$	$\odot_{14}$
I. petræa									
Rainbow Rocks, Mileura Station (1, 1) *	5	3	...	...	...	...	...	...	...
Hillview Station (1, 2)	6	2	...	1	...	...	...	...	...
Anketell North Breakaways (1, 3)	3	...	...	...	...	...	...	...	...
"589" (2, 1)	...	...	...	...	...	...	...	...	...
"495" (2, 2)	2	...	...	...	...	...	...	...	...
Yellowdine (2, 3)	1	...	...	...	...	...	...	...	...
Boondi (2, 4)	4	3	1	...	...	...	...	...	...
Bullabulling (2, 5)	10	...	...	...	...	...	...	...	...
Pigeon Rocks (2, 6)	...	...	...	13	...	...	...	...	...
"441" (2, 7)	...	...	...	...	1	...	...	...	...
"446" (2, 8)	...	...	...	...	...	3	...	...	...
Elackbutting Rock (2, 9)	...	...	...	...	...	...	1	...	...
Berringbooding Rock (2, 10)	...	...	...	...	...	7	...	...	...
3-mile Rock (2, 11)	1	...	...	...	9	...	...	...	...
12 m. West of Bullfinch (2, 12)	...	...	...	...	4	...	...	...	...
34 m. East of Muckinbudin (2, 13)	...	...	...	...	...	...	...	1	...
Moorine Rock (2, 14)	...	...	...	...	...	...	7	...	...
4 m. South of Bencubbin (2, 15)	...	...	...	...	...	...	9	...	...
Merredin (2, 16)	...	...	...	...	...	...	...	...	11
Muntagin (2, 17)	...	...	...	...	...	11	...	...	...
Yorkrakine Rock (2, 18)	...	...	...	...	...	...	2	...	...
Mt. Stirling (2, 19)	...	...	...	...	...	...	...	...	9
I. axillaris									
Moonbi Lookout (1, 10)	6	1	...	...	...	...	...	...	...
Murrurrundi (1, 9)	7	...	...	...	...	...	...	...	...
Kariong † (1, 8)	2	...	...	...	...	...	...	...	...
The Gib, Bowral (1, 7)	4	...	...	...	...	...	...	...	...
6 m. North of Bethungra	1	...	...	...	...	...	...	...	...
I. anæthifolia									
Gilgai (1, 11)	10	1	...	...	...	...	...	...	...

* See footnote to table 1.
† The two plants referred to here were obtained from a commercial native plant nursery—their origin being unknown.

axillaris, by Melville (1960). The syngenesious anthers from a tube into which the pollen is shed (fig. 3a). The style, with its closed stigma and ring of sub-stigmatic hairs form a brush which travels piston-like through the tube scraping out the pollen and subjecting it to pressure. At the apex of this tube there is a trap-door and lever mechanism formed by two enlarged bristles. When a vector depresses

or flicks these bristles, it is dusted by pollen forcibly ejected from the tube. Eventually, the style grows through the anther tube, the stigmatic lobes separate and the receptive surfaces are presented in a position favourable for the receipt of pollen from similar vectors (fig. 3, *b* and *c*).
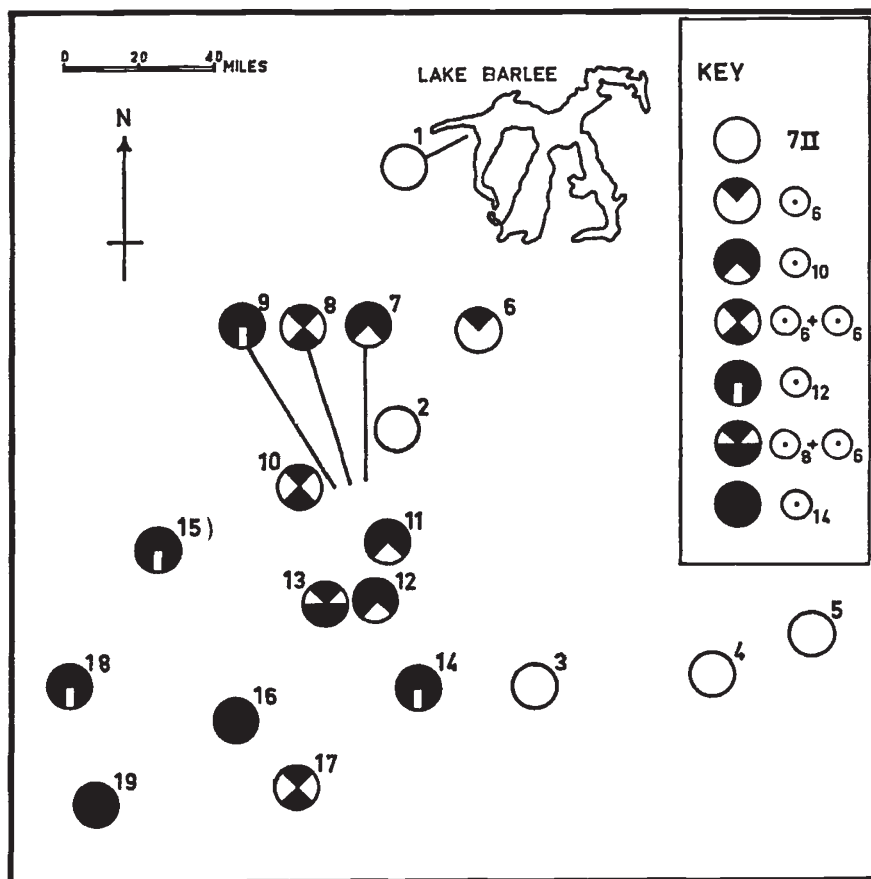

Fig. 2.—Distribution of floating and multiple interchange populations in Western Australia. The open circle (7II symbol) indicates a floating interchange population: interchange hybrids may be present. Other symbols indicate the multiple interchange populations (complex hybrid populations) in which the plants are uniformly of a single meiotic configuration.

    For locality names, refer to tables 1 and 2.

    Self pollination is characteristic of all these populations and it has been observed also in material from Anketell (fig. 2, population No. 3).

    The *axillaris* chromosome end sequence has been identified as one of the gamete genotypes in populations 6 and 11.

The above description represents a very slight variation of the usual Lobeliaceæ mechanism. It is clearly a mechanism favouring cross-pollination.

In *Isotoma petræa*, however, this mechanism is frequently short-circuited so that self-pollination is achieved. It is usually found that the stigmatic lobes part precociously within the anther tube and

emerge only partly or not at all (fig. 3, *d* and *e*). As a result of this, self-pollination occurs. Plate I, fig. 8 illustrates mature capsules from which fully formed seeds have been shed and upon which are still attached the dried remains of the flowers. It can be seen that in each case the anther tube is quite intact and that the stigmatic lobes have never emerged. Self-pollination must have occurred.

The versatility of the pollination mechanism in *I. petræa* is apparently dependent upon weather conditions. In hot dry weather, as is usual
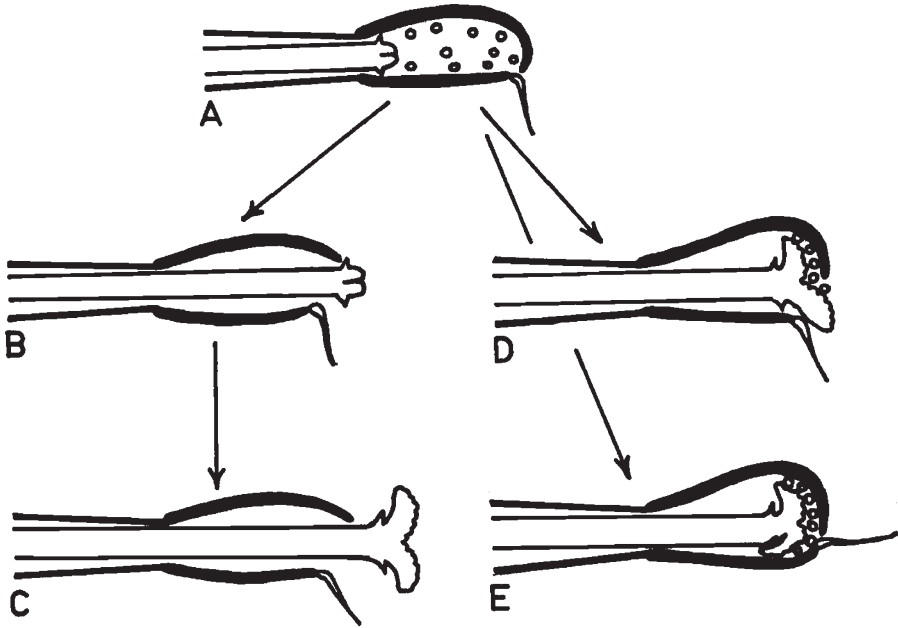
FIG. 3.—Pollination versatility in *Isotoma*. See text for details.

in the natural habitat, self-pollination is the rule. In cooler, more moist weather, protrusion of the stigmatic lobes is frequently observed. Another response indicating dependence upon environmental conditions, is the protrusion of the style in unopened buds in material stored in polythene bags (*i.e.* in cool, very humid conditions). The physiological basis of the pollination versatility has not been investigated. However, it has been observed that in the multiple interchange populations and at least six of the floating interchange populations (fig. 2) self pollination is responsible for the bulk of the seed formation.

(v) Preliminary crosses

A number of crosses involving individuals from floating interchange populations, multiple interchange populations and derived hybrids are recorded in table 3. Each individual in the cross is described as follows: species, M-I configuration, name of population of origin as indicated in tables 1 and 2 and in figs. 1 and 2. Where

derived hybrids are involved their derivation is given in full. Where two individuals of similar M-I configuration from a single population are separately used, these are differentiated as (a) and (b). The

TABLE 3

Cross no.	Details of cross	Progeny cytologically analysed						
		7II	$\odot_4$	$\odot_4+\odot_4$	$\odot_6$	$\odot_8$	$\odot_{10}$	$\odot_{12}$
1.	*axillaris* 7II Kariong × *petræa* 7II Simpson's Gap	3	...	...	...	...	...	...
2.	*petræa* 7II Hillview × *axillaris* 7II Kariong	4	...	...	...	...	...	...
3.	7II (*petræa* $\odot_4$ Laverton × *petræa* 7II Laverton) × *axillaris* 7II Kariong	4	...	...	...	...	...	...
4.	*petræa* $\odot_4$ Laverton × *petræa* 7II Laverton	8	10	...	...	...	...	...
5.	*petræa* $\odot_4$ Laverton 1 × *petræa* $\odot_4$ Ormiston Gorge	...	...	1	...	...	...	...
6.	*petræa* $\odot_4$ Ormiston Gorge × *petræa* $\odot_4$ Emily Gap *	1	...	...	...	...	...	...
7.	*petræa* $\odot_6$ Pigeon Rock × *axillaris* 7II Kariong †	8	...	...	1	...	...	...
8.	7II (*petræa*) $\odot_6$ Pigeon Rock × *axillaris* 7II Kariong) × *anethifolia* 7II Gilgai	1	...	...	...	...	...	...
9.	*petræa* $\odot_{10}$ 3-mile Rocks (a) × *axillaris* 7II Kariong	...	2	...	...	...	5	...
10.	*petræa* $\odot_{10}$ 3-mile Rocks (b) × 7II (*petræa* $\odot_6$ Pigeon Rock × *axillaris* 7II Kariong)	2	...	...	...	...	...	...
11.	*petræa* $\odot_{12}$ Bencubbin × *petræa* 7II Laverton	...	...	...	10	1	...	...
12.	*petræa* $\odot_{12}$ Bencubbin × *axillaris* 7II Kariong	...	...	...	1	2	...	...
13.	*petræa* 7II " 495 " × *petræa* $\odot_{12}$ Bencubbin	...	...	...	1	1	...	...
14.	*petræa* $\odot_{14}$ Merredin × *axillaris* 7II Kariong	...	...	9	...	...	6	...
15.	*petræa* $\odot_{14}$ Merredin × *anethifolia* 7II Gilgai	...	...	2	...	...	2	...
16.	*petræa* 7II " 495 " × *petræa* $\odot_{14}$ Merredin	...	...	1	...	...	1	1 ‡
17.	*petræa* ($\odot_6+\odot_6$) Berringbooding Rock × *axillaris* 7II Kariong	...	...	...	...	...	4	...
18.	*petræa* $\odot_{10}$ 3-mile Rock (a) × *petræa* $\odot_{12}$ Bencubbin	...	...	...	...	5	8	...
19.	*petræa* $\odot_{12}$ Bencubbin × *petræa* $\odot_{10}$ 3-mile Rock (a)	...	...	...	...	3	1	...

* Both " Ormiston Gorge " and " Emily Gap " are localities, included under " Near Alice Springs " in table 1.

† This progeny also included an $\odot_6+\odot_6$ obviously due to error; either a stray seed or stray pollen grain.

‡ Unreliable result; the $\odot_{12}$ probably not a true progeny plant.

progeny cytologically analysed and recorded are comparatively few in number, but irregular results, such as the ($\odot_6+\odot_6$) in the progeny of cross 7 and the $\odot_{12}$ in the progeny of cross 16 are sufficiently rare to indicate an otherwise high degree of reliability.

4. DISCUSSION

Isotoma petræa is rectricted to rocky areas throughout the arid interior of Australia, occurring in small discrete populations. Individual populations are effectively isolated, on a short term view, and migration and genetic exchanges between them must be restricted. The isolation of individual populations, their variable size (particularly any occasional decimation) and above all, their pollination mechanism must contribute to an exceedingly high degree of inbreeding within the populations.

Over the bulk of the distributional range of all three species, the populations are of the floating interchange type; that is, structural homozygotes predominante. Crosses between structurally homozygous plants from all three species and from widely separated localities have always yielded structurally homozygous progeny (table 3, crosses 1, 2, 3 and 8). The segmental arrangement of the chromosome ends, therefore, is constant throughout all the homozygotes used since they were all tested against *axillaris* 7II Kariong, a plant obtained from a commercial native plant nursery at Kariong in New South Wales. Altogether, this chromosome and sequence has been positively identified, in structural homozygotes, from five floating interchange populations, and as one of the gamete genotypes in two multiple interchange populations (figs. 1 and 2). Its occurrence in a sixth floating interchange population (495) seems highly probable (compare crosses 11, 12, 14 and 15 with 13 and 16 in table 3). The results of crosses involving small rings which have not been directly compared with *axillaris* 7II Kariong or its equivalent, *e.g.* table 3, crosses 5 and 6, are compatible with an hypothesis of minimal deviation from that sequence.

Although their evolutionary relationships have not been precisely defined, it is quite clear that *petræa*, *axillaris* and *anæthifolia* are very closely related, being completely interfertile, and they have a common chromosome end sequence. This is a primitive sequence which predates the morphological divergence of the three species and which stretches some 2000 miles across the Australian continent. Subsequently in this series of papers, this primitive chromosome end sequence will be referred to as the " *axillaris* " sequence.

Interchange heterozygosity is prevalent in natural populations of all three species. In the floating interchange populations more than one interchange may occur in a single population, since $\odot_6$ and $(\odot_4 + \odot_4)$ individuals occur. Also, different populations may be characterised by different interchanges, since crosses between *petræa* $\odot_4$'s have yielded $(\odot_4 + \odot_4)$ progeny (table 3, cross 5).

It has been noted above that the general cytological features of the group are those generally accepted as being characteristic of species in which interchange hybridity naturally occurs. It is clear, therefore, that the capacity for the origin and maintenance of interchange heterozygosity is a primitive feature of the group and that it is a

longstanding component of the genetic systems of all the three species. One must assume that a variety of chromosome end-sequences have been in existence during the group's history. However, as shown above, a primitive sequence has persisted since before the divergence of the three species and has spread across the Australian continent. The new structural arrangements, in floating interchange populations, are ephemeral in that they have rarely, if ever, replaced the basic " *axillaris* " sequence in the homozygous condition. It is possible however, that certain local populations may be characterised by new homozygous arrangements, but no evidence of this has been obtained.

The multiple interchange populations are virtually monomorphic with respect to the M-1 configuration characterising component plants. Progeny raised from seed collected in natural populations and from selfings under controlled conditions have been found to exhibit the maternal chromosome configuration. This fact in particular applies to seed obtained from $(\odot_6 + \odot_6)$ plants where, in the absence of a balanced lethal mechanism, only one-quarter of the progeny from selfings would be expected to have the two-ring constitution. Since all fifteen sibs examined proved to be of this type (table 1), it is concluded that a balanced lethal mechanism is operative in eliminating the structurally homozygous progeny. The single structural homozygote in the 3-mile Rock population, otherwise composed of $\odot_{10}$ plants, cannot deny the occurrence of a balanced lethal system. The plant in question may be due, for example, to migration from a neighbouring floating interchange population, it may be a relic of a floating interchange population previously inhabiting the rock or it may be an alethal segregate following crossing-over in a differential segment. Crosses between multiple interchange heterozygotes and structural homozygotes characteristically yield twin-hybrids, that is, the progeny so obtained exhibits one of two M-1 configurations according to the gamete received from the multiple interchange heterozygote (table 3, crosses 7 to 16). Reciprocal crosses yield identical results. Thus, both gamete types are transmissable via the pollen grain and both are transmissable via the embryo sac. The lethal system must operate, therefore, through zygotic rather than gametic elimination.

The multiple interchange heterozygotes, then, are true breeding in nature and are maintained thus by a substantially if not entirely autogamic breeding mechanism and by a balanced lethal system operating through zygotic elimination of the structurally homozygous forms. The plants are indeed *complex heterozygotes* and are entirely comparable in their genetic system with previously described complex hybrids such as *Œnothera lamarckiana*.

The spatial distribution of the complex heterozygotes, with the smaller rings to the north-east and the larger rings to the south-west suggests a single origin of the genetic system. It would appear that the system originated as small rings, in the Lake Barlee area (fig. 2)

and has migrated throughout populations to the south-west, territorial expansion being associated with increasing ring size. This suggestion is in agreement with a number of other observations. In the first place, the primitive and transcontinental *axillaris* chromosome end sequence is present as one of the complexes in the Pigeon Rock $\odot_6$ complex hybrid population (cross 7, table 3). That is, $\odot_6$ Pigeon Rock differs from the ancestral structural homozygotes by a minimal number of two interchanges. The *axillaris* sequence also occurs as one of the complexes in $\odot_{10}$ 3-mile Rocks (*b*) (cross 10); again, there is a minimal deviation from the *axillaris* sequence involved. Similarly, in $\odot_{12}$ Bencubbin the complexes differ from *axillaris* by two and three interchanges repsectively (crosses 11 and 12) and those of $\odot_{14}$ Merredin differ from *axillaris* by two and four interchanges respectively (crosses 14 and 15). Hence, in these four complex hybrids, it appears that the multiple interchange rings have been achieved through the fixation, in the heterozygous condition, of a minimal number of interchanges upon a primitive *axillaris* sequence.

In some of the hybrids tested, however, redundant interchanges, that is, interchanges beyond the $n-1$ necessary to build up a ring of $2n$ chromosomes (Darlington and Gairdner, 1938), do occur. Thus, the two complexes of $\odot_{10}$ 3-mile Rock (*a*) are one and four interchanges removed from *axillaris* while the ($\odot_6 + \odot_6$) Berringbooding Rock has one complex four interchanges removed from *axillaris* and the second complex at least one interchange removed. Redundant interchanges may well be expected in the sequential elaboration of the rings for a variety of reasons; in particular, they are probably important in the achievement of mechanical stability of the chromosome rings at meiosis.

Secondly, reciprocal crosses between pairs of complex heterozygotes (crosses 18 and 19) have yielded twin hybrid progenies identical with respect to M-1 configurations. This is in agreement with the operation of the lethal system described above and it also indicates that both populations, Bencubbin and 3-mile Rock, are characterised by the same lethal system. It is probable that the one basic lethal system is operative throughout all the complex hybrid populations. If this is so, a single origin of the genetic system must be inferred.

It is clear from the pollination mechanism of other species of *Isotoma* and of the Lobeliaceæ in general, that cross-pollination must have characterised the ancestral *Isotomas*. Where cross-pollination and out-breeding is fostered in a species, heterosis is invariably a component in the genetic system. Hence, where inbreeding has been imposed on such a system, adjustments must be made if the species is to survive; either the genetic architecture must be reorganised so that heterosis is no longer a component in the genetic systems— that is, in terms of Mather (1943) the polygenic balance must be changed from a relational to an internal balance, or else systems of conservation of genetic heterozygosity must be adopted. Clearly,

complex hybridity provides an effective system of preservation whereby genetic heterozygosity may be maintained even under the strictest inbreeding. It would seem that the situation in *Isotoma petræa* admirably demonstrates the evolutionary principle enunciated by C. D. Darlington (1958) that " any species forced to inbreed at the edge of its range, and having the right type of chromosomes and of meiosis, will make use of interchange hybridity and fix it to preserve general hybridity and to make itself into a permanent hybrid ".

5. SUMMARY

1. In *Isotoma petræa* the typical Lobeliaceæ pollination mechanism has been modified so that in many south-western populations at least, autogamy is achieved.

2. *Isotoma* species are pre-adapted for the maintenance of interchange heterozygosity by virtue of their general cytological features. Interchange heterozygosity occurs widely throughout *I. petræa, I. axillaris* and *I. anæthifolia*.

3. There is a basic karyotype (chromosome end sequence) common to *petræa, axillaris* and *anæthifolia* and it is transcontinental in distribution. There is no evidence to indicate that this karyotype has been replaced by new sequences to any significant extent.

4. Complex hybridity has evolved in the extreme south-western population through a process of sequential fixation of interchanges in the heterozygous condition. The complex hybrids are true breeding being stabilised by a balanced lethal mechanism operating through zygotic elimination of the structural homozygotes.

5. It seems clear that the complex hybrid genetic system has evolved under conditions of, and as a response to, a high degree of inbreeding in the natural populations.

6. REFERENCES

CLELAND, R. E. 1936. Some aspects of the cytogenetics of *Œnothera*. *Bot. Rev.*, **2**, 316-348.

CLELAND, R. E. 1960. A case history of evolution. *Proc. Indiana Acad. Sci.*, **69**, 51-64.

CLELAND, R. E. 1962. The cytogenetics of *Œnothera*. *Adv. in Genetics*, **11**, 147-237.

DARLINGTON, C. D. 1929. Ring formation in *Œnothera* and other genera. *Jour. Genet.*, **20**, 345-363.

DARLINGTON, C. D. 1931. The cytological theory of inheritance in *Œnothera*. *Jour. Genet.*, **24**, 405-474.

DARLINGTON, C. D. 1958. *The Evolution of Genetic Systems*. Oliver and Boyd, London.

Plate I

1-7. Meiotic configurations in *I. petræa*.

1. 7II ; 2. $\odot_6$ Pigeon Rock ; 3. $\odot_{10}$ 3-mile Rock ; 4. $\odot_{12}$ Bencubbin; 5. $\odot_6$+chain of 8 34m E. Muckinbudin ; 6. $\odot_6$+$\odot_6$ Muntagin ; 7. $\odot_{14}$ Merredin (all *ca*. ×2300).

8. Mature capsules from which seeds have been shed and which still have dry floral parts attached. The anther tubes, though swollen, are still intact : the stigmas have never protruded and self-pollination must have occurred. Material from a floating interchange population near Boondi (×4).
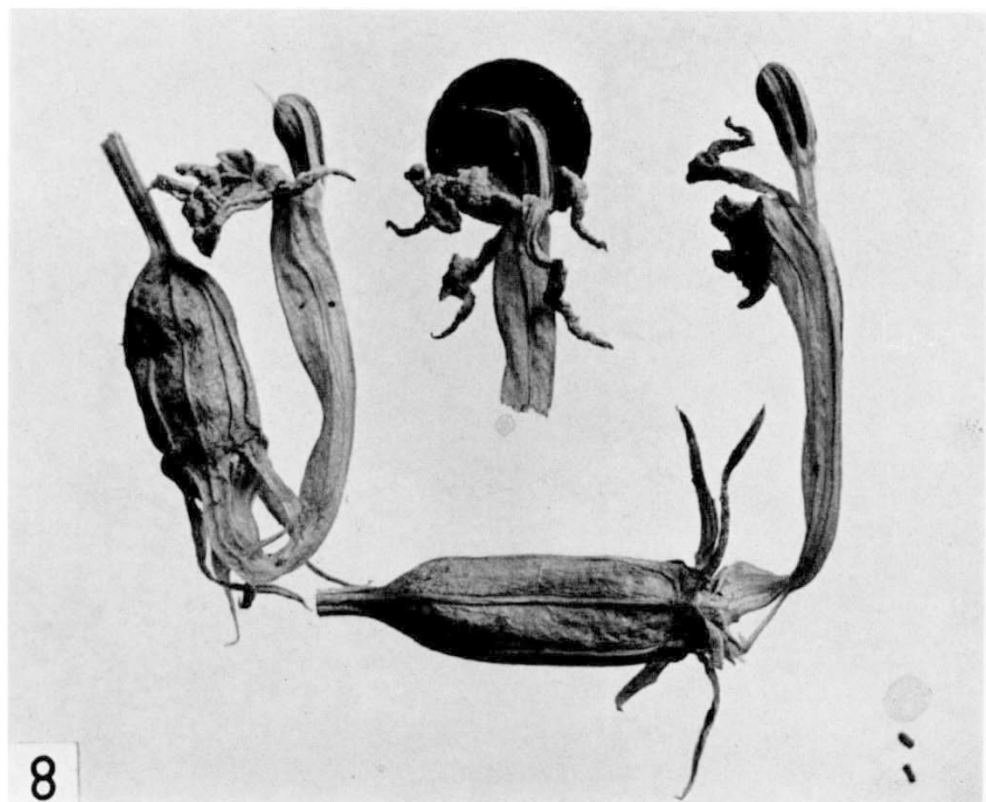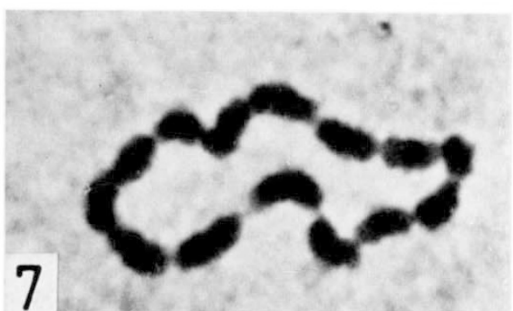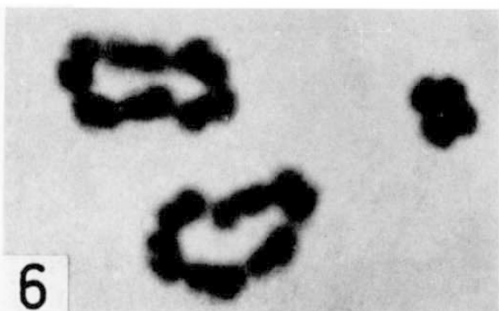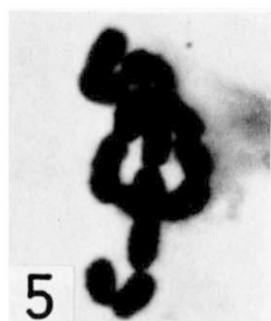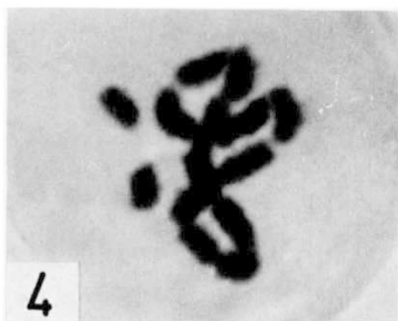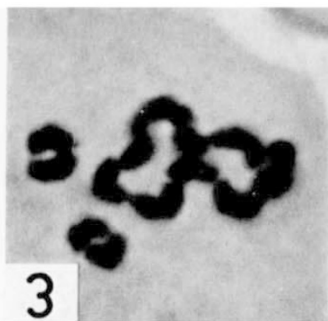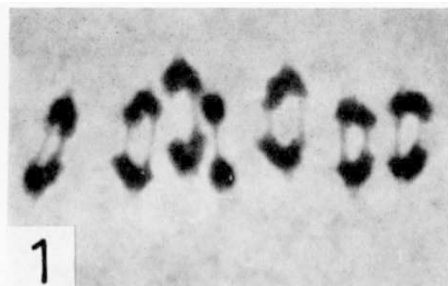
DARLINGTON, C. D. 1963. *Chromosome Botany and the Origins of Cultivated Plants.* Allen & Unwin, London.

DARLINGTON, C. D., AND GAIRDNER, A. E. 1938. The variation system in *Campanula persicifolia. Jour. Genet., 35,* 97-128.

MATHER, K. 1943. Polygenic inheritance and natural selection. *Biol. Review, 18,* 36-64.

MELVILLE, 1960. Contributions to the flora of Australia. VI. The pollination mechanism of *Isotoma axillaris* Lindl. and the generic status of *Isotoma* Lindl. *Kew Bull., 14,* 277-279.

WALTERS, J. L. 1942. Distribution of structural hybrids in *Pæonia calificornica. Amer. J. Bot., 29,* 270-275.

WIMMER. 1953. Campanulaceæ—Lobelioideæ II. *Pflanzenreich,* Heft 107.