

*A Preliminary Report on the Manifestation of  
Characters in Reciprocal Hybridizations*  
*1. Matrocliny in Reciprocal F<sub>1</sub> Hybrids Between  
Silene Armelia and S. orientalis.*

By Kane NAKAYAMA

*Department of Biology, Faculty of Liberal Arts and Science, Shinshu University.*

(Received Dec. 26, 1964)

**I. Introduction**

It has been widely known that there are some divergences in characters between two reciprocal hybrids from crossings of different species or different ecotypes which are more or less remotely related to each other.

These divergences between reciprocals are presumed to be caused by some extranuclear hereditary factors which are contained in the female cytoplasm because the cytoplasm of F<sub>1</sub> hybrid, on the fertilization, is transmitted mainly from the female parent.

However, so far as hitherto is reported, the cytoplasmic effects are in most cases related to lethal or some deteriorating conditions of the reproductive processes such as male sterility, flower organ misbuilding, or severe inhibition which results in abnormal disharmonies in plant life. On the other hand, a matroclinous manifestation of morphological or physiological characteristics is also possibly to be expected, to be sure, within the range of normal life conditions of plants.

But, we have had up to now relative few instances available concerning to this subject.

In this paper, a preliminary examination is presented on the characters of reciprocal hybrids between a catchfly, *Silene Armelia*, and its related species, *S. orientalis* both belonging to *Caryophyllaceae*.

The genic analysis of individual characters concerned will be reported in the next issue of this journal.

In the present paper, for the sake of simplicity, Ar, Or, Ar×Or, and Or×Ar are applied as abbreviations for *S. Armelia*, *S. orientalis*, (*S. Armelia* ♀ × *S. orientalis* ♂) F<sub>1</sub> and (*S. orientalis* ♀ × *S. Armelia* ♂) F<sub>1</sub> respectively.

## II. Sources of materials

Plants which were used as parental materials for the present study were a common catchfly, *Silene Armelia*, and its related species, *S. orientalis*, belonging to *Caryophyllaceae*.

Plants of either species have a habit of growing as annual or biennial plants according to the conditions of temperature and day-length in our country.

1) *S. Armelia* has been naturalized for about one hundred years past, and now-a-days has a wide range of distribution in Japan.

The plants of this species, so far as the writer knows, consist of populations which are almost homogeneous in each character except in the color tone of petals and some other relatively minute characters.

An initial plant (symbolized as Ar-57) used for the genetical study, of *S. Armelia* was voluntarily picked out among a population naturally growing near Shinshû University at Matsumoto City, and was selfed in July, 1957.

The seeds thus obtained germinated in October 1957 in an incubator controlled at 25° C, and overwintered in a seedling box in a glasshouse.

These seedlings developed to plants showing no visible deviation from the parents, so one plant (symbolized as Ar-58) among them was chosen and was selfed as a plant material being typical of *S. Armelia* in May 1958.

2) Another plant material, *S. orientalis* was first presented by the Kyôto Botanical Garden in 1948, thereafter the progenies were produced by yearly selfings up to 1958.

## III. Observations

### 1. General appearance and growth habit of parental species.

#### a. Comparative aspects in seedling stage.

The germinated seeds of both species developed to form rosette plants before the beginning of November, 1958. At this season, one could easily distinguish between the two species through the following differences.

##### i) Shape and size of leaf-blade

Leaves of the rosette of *S. orientalis* are longer, slender necked than those of *S. Armelia*, and they have a trait toward the bending backward at the upper portion. (Fig. 1)

##### ii) Growing posture of leaf

The rosette-leaves of *S. Armelia* are characterized in the growing habit by keeping somehow horizontal in contrast to the appearance of more or less erect posture in those of *S. orientalis*. (Fig. 1 & 2)

That is, leaves of the latter species make a more acute angle with a

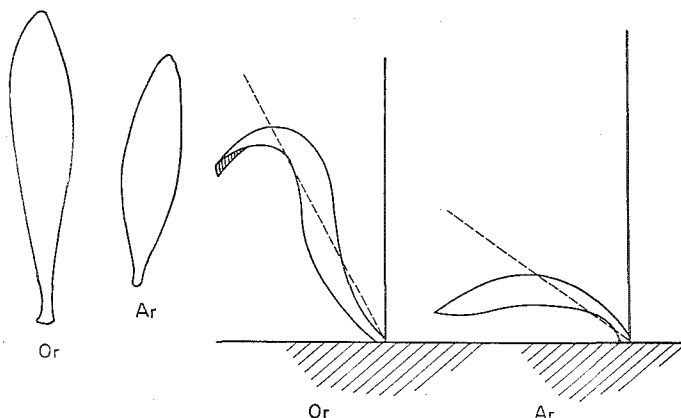


Fig. 1. Schematic view showing shape and growing posture of young rosette leaf.

perpendicular line drawn on the position of the plant than do those of the former species.

### iii) Leaf color

Leaves of two parental species are distinguishable with relative easiness from each other by the fact that a rosette of *S. orientalis* bears light or yellowish green leaves while that of *S. Armelia* ordinary green ones.

### b. Adult features of species

Among the plants of the two species in question, we could easily tell a plant of the one species from that of the other by the whole aspect even when seen from a distance.

Though there must be a wide range of morphological and physiological differences, following divergences were most noticeable in our genetical investigation.

i) The most remarkable difference in their outer appearances consists in the population density of flowers on a cyme and size of a cyme itself: *S. orientalis* has large, compact, bouquet-like cymes consisting of many, closely-crowded minute flowers, while the cyme of *S. Armelia* has a relative small number of flowers and is rather sparse and thin.

ii) *S. Armelia* shows an earlier development in turning from leaf-rosette to



Fig. 2. Growing postures of rosette seedlings, left : *S. orientalis* right : *S. Armelia*

stemmed stage than does *S. orientalis*, and begins to flower about ten days earlier than that.

iii) The stem of *S. Armelia* gives us a slender and rather feeble impressions while *S. orientalis* has the stem being relatively thick and robust.

To say more precisely, plants of *S. orientalis* have apparently less nodes on their stems than do *S. Armelia* plants, and especially their terminal internode just below the cyme is definitely thicker than that of the other species. These are the reasons that *S. orientalis* looks fairly stout.

iv) Leaves of *S. orientalis* are longer and more slender than those of *S. Armelia*, and have fairly flat surface in contrast to those of *S. Armelia* being apparently undulatory; Furthermore, former leaves are yellowish or light green in color while the latter are ordinary green as shown in their rosette stages.

## 2 *Matrocliny in reciprocal hybrids*

In June 1959, *S. Armelia* and *S. orientalis* were reciprocally crossed.

Though a time lag in flowering was found in *S. orientalis* as compared with *S. Armelia* as mentioned above, it was not so decisively that the author could not make crossing between them.

These two species are fairly compatible with each other, and a sufficient number of seeds were obtained to secure subsequent progenies irrespective of any kind of species used as female parent.

The seeds were sown in October 1959, and a week after they begun to germinate vigorously.

The seedlings of both reciprocal hybrids were grown and wintered in a glasshouse, and in January 1960 their rosette leaves were first measured.

### a) Growth and characters of leaves.

#### i) Growth of leaves.

For the purpose of understanding the developmental relation in leaf growth of each type, rosette leaves of the seedlings which germinated the preceding year were measured in January, April, and May 1960.

These results are presented in Table 1.

**Table 1.** Comparative leaf size in rosette seedlings of parents and reciprocal hybrids.

Date	Measurement	Parents and reciprocal hybrids			
		Ar	Ar × Or	Or × Ar	Or
January 10 1960	length	c. m. 4.00	c. m. 3.80	c. m. 2.60	c. m. 1.6
	width	1.40	0.95	0.70	0.5
	ratio of length/width	2.85	4.00	3.70	3.20

April	length	7.94	5.73	7.50	8.00
10	width	1.41	1.05	1.20	1.00
1960	ratio of length/width	5.63	5.46	6.25	8.00
May	length	7.10	6.80	9.70	11.20
10	width	3.00	2.50	2.60	2.20
1960	ratio of length/width	2.37	2.7	3.73	5.10

From the above table, it may be seen that the hybrids, irrespective of species used as female parent, showed in general an intermediate growth pattern of leaf between the two parental species in younger developmental stages.

Furthermore, more or less apparent matroclinous aspects may be expressly noticed concerning to the leaf length.

The width of leaf, excepting at very early stage of development, did not show any positive evidence for the matroclinous relation. This was also the case of the ratio of length/width of leaf.

In the leaves of rosette at the age of from three to four months some clear matroclinous tendency was detected in leaf length as well as in leaf width for the plants from crossings Ar×Or and Or×Ar.

In course of time of development, however, this relation became indistinct perhaps owing to the different stages of development of the types concerned.

The full grown plants of four types, Ar, Ar×Or, Or×Ar, and Or, showed leaf growth on each node as illustrated in Figs. 3 and 4,

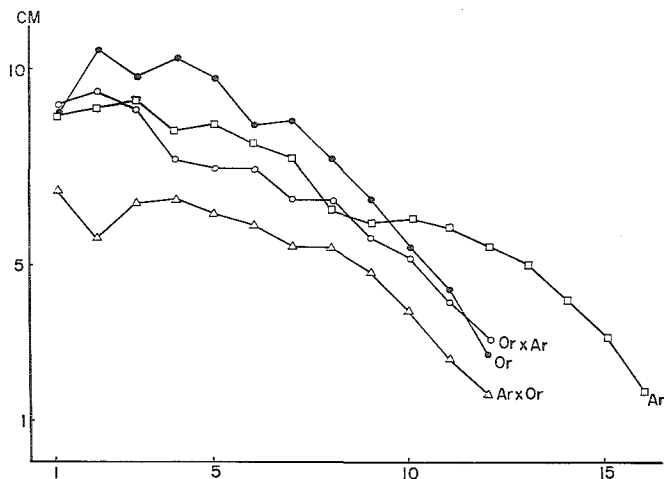


Fig. 3. Comparative leaf length in the order of node of main stem in parental and reciprocal  $F_1$  plants.

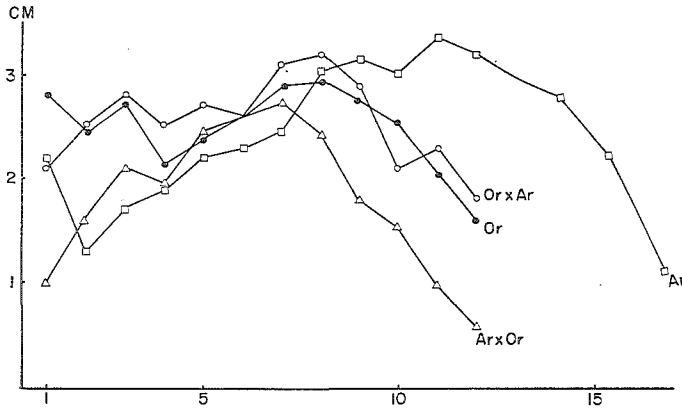


Fig. 4. Comparative leaf width in the order of node of main stem in parental and reciprocal  $F_1$  plants.

The comparative relation as to leaf growth was no more evidently confirmed in the adult plants.

ii) Leaf color and undulation of leaf.

It was observed that a plant having leaves of Or-type was, as a rule, yellowish light green in color, and that with Ar-type leaves was ordinary green.

Furthermore, the former was found to have flat leaves and the latter undulating ones.

Evidence which shows a parallelism of these two characters of leaf was obtained in the subsequent generations to  $F_2$  hybrids. And these two characters of leaf were also inherited with a matroclinous tendency between two reciprocals.

b) Forms of petal, flower and cyme.

The petal of *S. Armelia* is of cuneate, emarginate form, while that of *S. orientalis* is fusiform and acute.

These characteristics in petal form are reflected in the appearance of flower as a whole. (Fig. 5)

Crossings between the two species gave hybrids of intermediate forms in this respect, and plants from crossing Ar x Or were more or less similar to Ar, and those from Or x Ar looked to some extent like Or.

Thus here, the divergence of two reciprocal hybrids regarding to the petal form was evident.

The cyme of the hybrids from crossings between these species was found to be just intermediate between two parents showing some matroclinous aspect in size and form of it.

The character has a tendency to be inherited coupled with many other forms originate in either species.



Fig. 5. Diagrammatic comparison of petal and corolla forms of the two species and their reciprocal hybrids: from left to right, Ar, Ar×Or, Or×Ar, and Or.

### c) Diameter of stem

The wider diameter of the stem, especially of the uppermost internode, in the plant of *S. orientalis* gives a distinct appearance of this species as already mentioned.

The author measured the diameter of stems at three levels of plant height, namely the lowermost, middle, and uppermost internodes of a main stem of each plant just prior to the flowering season.

It was generally observed that the upper the internode is, the thinner may it be.

Table 2. Diameter of main stem in adult stage

Level of internode	Parents and reciprocal hybrids			
	Ar	Ar×Or	Or×Ar	Or
uppermost internode	m. m. 1.78	m. m. 2.25	m. m. 3.50	m. m. 3.38
middle internode	3.75	3.50	4.00	4.13
lowermost internode	6.13	4.50	6.00	6.25

From Tab. 2, it may be found that here again a matroclinous inheritance was evidenced because the plants belonging to *S. orientalis* and the hybrid Or♀×Ar♂ had a feature showing the distinct thick internode at uppermost level of stem.

Indeed, we could easily judge of plants of two types, Ar×Or and Or×Ar, by their appearance in this regard without fail.

#### d) Flowering time

On the basis of general matroclinous manifestation of characters in the species-hybrids here concerned, we can suppose some differences as to flowering time between Ar×Or and Or×Ar.

It was to be regretted, however, that owing to an unavoidable author's circumstance, an accurate observation which makes possible a detailed analysis of the flowering time could not be made.

Nevertheless, it is safe to say that the flowering time was, as far as the author had observed, found to be inherited being connected with other specific characters, e. g. leaf development, stem thickness and cymose form, etc.

Thus, the early flowering plants, as a rule, were found to have most features inhere in *S. Armelia*, and the late flowering ones impressed us as being of *S. orientalis* type.

It was the writer's guess, however, that there might hardly be apparent intermediate manifestation in anthesis of hybrid from the crossing Ar ♀ × Or ♂ or vice versa.

In this regard, further studies were required.

#### IV. Discussion

The evidence of cytoplasmic inheritance has hitherto been obtained in not a few plant genera e. g. *Sorghum*, *Circium*, *Funaria*, *Epilobium*, *Zea*, *Begonia*, *Petunia*, *Digitalis*, *Aquilegia*, *Oenothera*, *Streptocarpus*, *Triticum*, *Arachis*, *Beta*, *Allium*, *Gossypium*, and *Phaseolus*, etc.

Many studies intended to this field of research have often dealt with the problem along the line of some reproductive disharmonies, for example male-sterility, low fertilization capacity, or some morphological abnormality.

Concerning to the cytoplasmic hereditary effects controlling the growth or development native in the plant species, comparatively few reports are available, one of which is the paper by ASHRI (1964<sup>1)</sup> with the peanut.

According to him, in all crosses when a variety V4 was female parent, the F<sub>1</sub> hybrids were runners (trailing), while the reciprocal hybrids were bunch. He concluded that there are two plasmon types — one found only in V4 and another present in the other tested varieties. Furthermore, there are at least two genes designated Hb<sub>1</sub> and Hb<sub>2</sub> which interact differently with each other in each plasmon and with each plasmon. In the V4 plasmon the two genes are complementary, while in the second plasmon their dominant alleles or the recessive ones are additive. And in most cases, the same genotypes produce in conjunction with the different plasmon opposite growth habits.

Most cases of dissimilarities exhibited in reciprocal hybrids have been interpreted by the differences in so called "plasmon" which interacts with the genome to produce the characters.



But exceptionally, SCHWEMMLE (1964)<sup>21)</sup> explained the better and more quick seed germination when a light-green mutant of *Oenothera berteriana* was female parent than it was male parent by the term "predetermination". It was the reason that his experimental materials, the normal type of *Oenothera berteriana* and a light-green mutant were believed to have the same kind of cytoplasm.

The plant populations which here served comparable studies were species hybrids; therefore, it can be supposed that they have possibly mother cytoplasm which differ in the manner of interaction with the same hybrid genome.

Accordingly, the fact that the F<sub>1</sub> hybrids bear some more resemblances to their female parents than to male parents might be resulted from cytoplasmic influences of female parents on the manifestation of characters of F<sub>1</sub> hybrids.

With our case of the catchfly and it's related species, the genes responsible for the characters concerned were not yet analyzed, but the genome including these genes should be the same in two reciprocal hybrids.

Concerning to the results obtained here, many characters excepting the flowering time behaved phenotypically as intermediates, being more approximate to those of the female parents.

It may be noteworthy that a group of characters native in one parent species was apt to be inherited often collectively as a whole.

That is, green relatively short undulating leaf, cuneate and emarginate petal, thinly flowered cyme, early flowering, short diameter of uppermost internode, all characteristic of *S. Armelia* on the one side, and yellowish green long flat leaf, fusiform and acute petal, large compact cyme, late flowering, wide diameter of uppermost internode, all native in *S. orientalis* on the other side were observed as a group respectively in F<sub>1</sub> hybrids.

Though a reliable presumption could not be made owing to the insufficient number of plants, there was practically no plant which combined characters of one parent with those of the other.

For the time being, whatever the relations between genes and characters in question may be, it may safely be said that the matroclinous conditions of several characters in F<sub>1</sub> hybrids here studied may attribute to the cytoplasmic effects or factors inherent in the parental species.

The detailed account on the genetical analyse of each character concerned will be stated in the next issue of this journal.

## V. Summary

1. For the purpose of affording more examples in evidence of cytoplasmic inheritance in flowering plants, differential manifestations of characters were studied in reciprocal crosses between *Silene Armelia* and *S. orientalis* belonging to *Caryophyllaceae*.

2. Though the  $F_1$  hybrids were more or less intermediate in many characters, a matrocliny was observed in reciprocal crosses as to following characters:

- form of petal
- size and flower-density of cyme
- flowering time
- size and form of leaf
- diameter of stem (especially that of uppermost internode)

Thus in many characters concerned, (*S. Armelia* ♀ × *S. orientalis* ♂)  $F_1$  had a resemblance to female parent *S. Armelia* and (*S. orientalis* ♀ × *S. Armelia* ♂)  $F_1$  looked in some way like to *S. orientalis*.

3. This cytoplasmic control on the characters was already detected at the leaf-rosette stage of few months age, and seemed to maintain throughout the whole period of plant life up to the anthesis.

#### References

- 1) ASHRI, A. (1964) Intergenic and genic-cytoplasmic interactions affecting growth habit in peanuts. *Genet.*, 50, 363-372.
- 2) CASPARI, E. (1948) Cytoplasmic inheritance. *Adv. in Genet.*, 2, 1-66.
- 3) CHANDRARATNA, M. F. and SAKAI M. (1960) A biometrical analysis of matroclinous inheritance of grain weight in rice. *Hered.*, 14, 365-373.
- 4) COOPER, D. C. (1952) The transfer of desoxyribose nucleic acid from the tapetum to the microsporocyte at the onset of meiosis. *Amer. Nat.*, 86, 219-229.
- 5) DELLINGSHAUSEN, M. v. (1935) Permeabilitätsstudien an zwei genetisch verschiedenen Plasmen. *Planta.* 23, 604.
- 6) FUKASAWA, H. (1953) Studies on restoration and substitution of nucleus in Aegilotriticum 1. Appearance of male-sterile durum in substitution crosses. *Cytologia*, 18, 167-175. (1957) Nucleus substitution and restoration by means of successive backcrosses in wheat and its related Genus *Aegilops*. *Jap. Jour. Bot.*, 17, 55-91.
- 7) FÜRSTAUER, R. (1940) Untersuchungen über die Beziehungen zwischen Photoperiode, Lichtintensität sowie Temperatur und der Plasmavererbung bei *Epilobium*. *Jahrb. wiss. Bot.* 89, 412.
- 8) HINDERER, G. (1936). Versuche zur Klärung der reziproken Verschiedenheiten von *Epilobium*-Bastarden. II. Wuchsstoff und Wachstum bei reziprok verschiedenen *Epilobium*-Bastarden. *Jahrb. wiss. Bot.*, 82, 669.
- 9) KIHARA, H. and YAMADA, I. (1942) Ein Fall von Plasmonwirkung auf das artfremde Genom. *Seiken Ziho* 1, 38-45. (1961) Cytoplasmic male sterility of common wheat. *Nat. Inst. Gen. Japan. Ann. Rept.* 12.
- 10) LEHMANN, E. (1932) Der Anteil von Kern und Plasma an der reziproken Verschiedenheiten von *Epilobium*-Bastarden. 2., *Pflanzenzücht*, 17, 157-172.
- 11) LEWIS, D. (1953) The rouge tomato : a problem in nuclear, cytoplasmic and environ-

- mental control. *Hered.*, 7, 337-360.
- 12) LINDEGREN, C and LINDEGREN, G. (1946) The cytogene theory. *Cold. Spr. Har. Sym.* 11, 115-129.
  - 13) MATHER, K. et al. (1958) Cytoplasm in sexual reproduction. *Nature*, 182.
  - 14) MICHAELIS, P. (1937) Untersuchungen zum Problem der Plasmavererbung. *Protoplasma*, 27, 284. (1938) Über die Konstanz des Plasmons. *Z. ind. Aps. Ver.*, 74, 435. (1954) Cytoplasmic inheritance in *Epilobium*. *Advan. in Genet.* 6., 288-394.
  - 15) OWEN, F.V. (1945) Cytoplasmically inherited male-sterility in sugar beets. *J. Agr. Res.*, 71, 423-440.
  - 16) RHOADES, M. M. (1943) Genic induction of an inherited cytoplasmic difference. *Proc. Nat. Acad. Sci.* 29, 327-329. (1950) Gene induced mutation of a heritable cytoplasmic factor producing male sterility in maize. *Proc. Nat. Acad. Sci.*, 36, 634-635.
  - 17) ROSS, H. (1939) Über die physiologischen Ursachen der Verschiedenheiten einiger reziproker *Epilobium*-Bastarde, insbesondere die Beteiligung von Wuchsstoff. *Ber. Deut. Bot. Ges.* 57, 114.
  - 18) RUDORF, W. (1939) Entwicklungsphysiologische Grundlagen der Pflanzenzüchtung. *Handbuch d. Pflanzenzüchtung*, 1, 210, *Verlag Parey, Berlin*,
  - 19) SAKAI, K., IYAMA, S. and NARISE, T. (1961) Biometrical approach to the cytoplasmic inheritance in autogamous plants. *Bull. Intern. Sta. Inst.* 38 (Pt III)
  - 20) SCHWARTZ, D. (1951) The interaction of nuclear and cytoplasmic factor in the inheritance of male sterility in maize, *Genet.* 36, 676-696.
  - 21) SCHWEMMLE, J. (1964) Die Keimung von Samen aus reziproken Kreuzungen der *Oenothera berterriana* und *Oe. odorata* jeweils mit ihren hellgrünen Mutanten. *Ber. Deut. Bot. Ges.*, 77, 189-195.
  - 22) SHUMWAY, L. K. (1964) An apparent case of cytoplasmic inheritance of abnormal plants in maize. *Genet.* 50.
  - 23) SMITH, H. H. (1962) Studies on the origin, inheritance, and mutation of genic-cytoplasmic male sterility in *Nicotiana*. *Genet.* 47, 985-986.
  - 24) SPARROW, A. H. and HOMMOND, M. R. (1947) Cytological evidence for the transfer of desoxyribose nucleic acid from nucleus to cytoplasm in certain plant cells. *Amer. Jour. Bot.* 34, 439-445.
  - 25) SPIEGELMAN, S. (1946) Nuclear and cytoplasmic factors controlling enzymatic constitution. *Cold Spr. Har. Sym.* 11, 256-277.
  - 26) VILLERTS, A. (1942) Über die Verschiedenheit reziproker Artbastarde in der Gattung *Begonia*. *Jour. Genet.* 43, 223-236.

#### Explanation of Plates

- Pl. 1 : Fig. 1 Leaf-rosette stage of *S. Armelia*.  
 Fig. 2 Ditto (*S. Armelia* ♀ × *S. orientalis* ♂) F<sub>1</sub>.  
 Fig. 3 Ditto *S. orientalis*.  
 Fig. 4 Ditto (*S. orientalis* ♀ × *S. Armelia* ♂) F<sub>1</sub>.
- Pl. 2 : Fig. 1 A comparison in the flowering stem among *S. Armelia* (left), (*S. Armelia*

♀ × *S. orientalis* ♂) F<sub>1</sub> (middle), and *S. orientalis* (*right*).

N.B. the cymes and uppermost internodes of the three types of plant.

Fig. 2 Cymes of *S. Armelia*.

Fig. 3 Cymes of *S. orientalis*.

Pl. 3 : Fig. 1 Flowering view of *S. Armelia*.

Fig. 2 Ditto (*S. Armelia* ♀ × *S. orientalis* ♂) F<sub>1</sub>.

Fig. 3 Ditto *S. orientalis*.

Fig. 4 Ditto (*S. orientalis* ♀ × *S. Armelia* ♂) F<sub>1</sub>.

PLATE 1



Fig 1



Fig 2



Fig 3

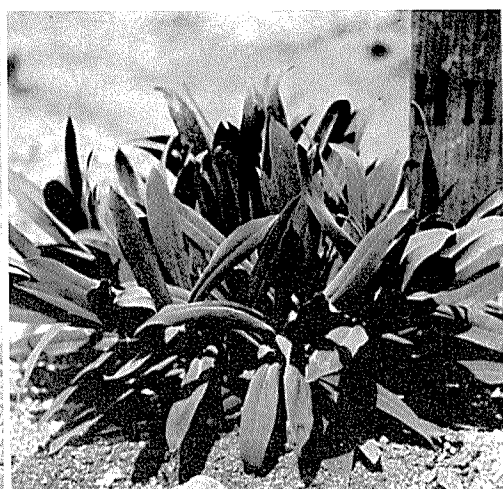


Fig 4

PLATE 2

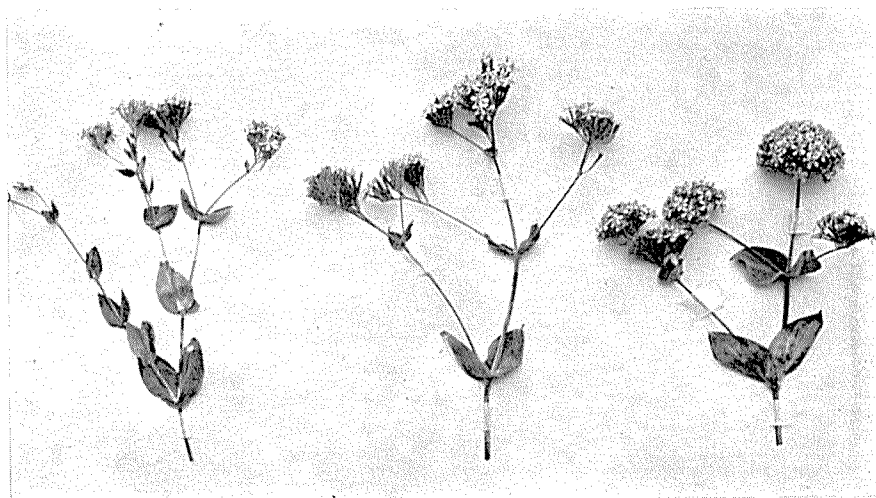


Fig 1



Fig 2



Fig 3

PLATE 3



Fig 1

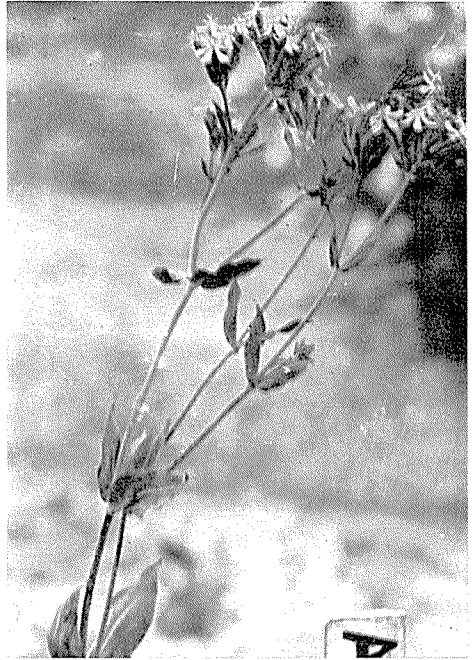


Fig 2



Fig 3

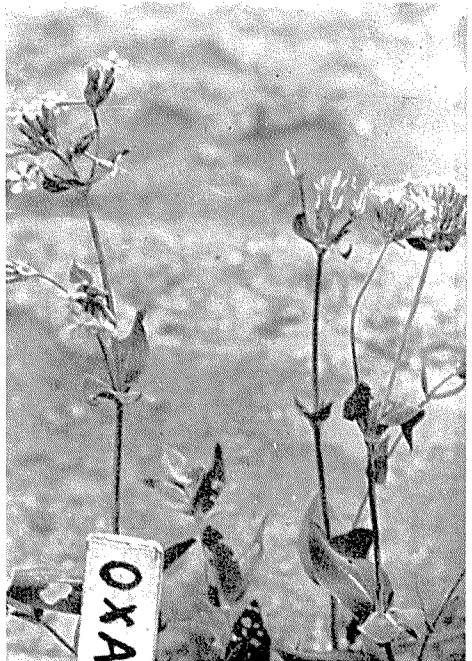


Fig 4