A Cytological Study on the Genus *Sedum*, with Remarks on the Chromosome Numbers of Some Related Plants

By

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(With 46 Text-figures)

According to PRAEGER (1921), the genus *Sedum* constitutes a large group in *Crassulaceae,* containing about five hundred of known species and is most widely distributed throughout the Northern Hemisphere. Concerning the karyological studies of this genus, chromosome numbers of only five species[1] had been known fragementally, untill the chromosome numbers of twelve species were reported by BALDWIN in 1935. BALDWIN (1936) furthermore studied the chromosome numbers of eight species, one variety and one hybrid, and gave some consideration of the section *Telephium* of the genus from the cyto-phyletical point of view.

The present study[2] deals with a karyological research on eleven species, one variety and one form in the genus *Sedum,* and also on some species of the related genera *Bryophyllum* and *Cotyledon.*

The materials used were collected in various districts; in the vicinity of Sapporo and Mt. Taisetu in Hokkaido; Mt. Iide and Yamagata in Yamagata Prefecture; Kamakura in Kanagawa Prefecture; and also obtained from the experimental gardens of our Laboratories and the botanical gardens of our University in which several species from various sources are being cultivated.

For determining the somatic chromosomes, root-tips were fixed with NAWASHIN's chromo-acetic solution and sectioned by the usual paraffin method. For the meiotic chromosomes in the PMCs, iron-acetocarmin smears were made in addition to the paraffin section, the fixative being CARNOY's fluid. The slides made by paraffin section, both root-tips and PMCs, were stained with iron-alum haematoxylin.

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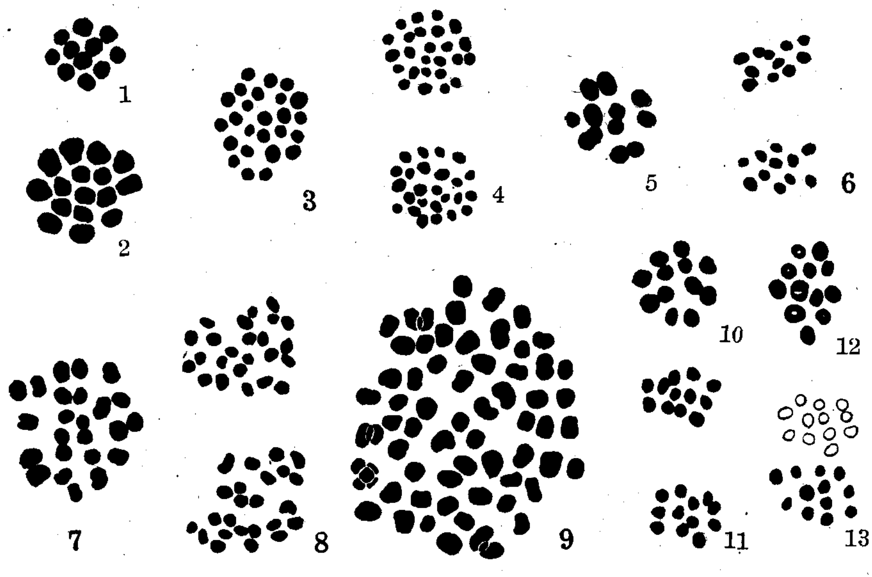
1) *S. alboroseum, S. Iwarenge, S. corleum* (SUGIURA 1931, 1936); *S. Rhodiola* (LEVAN 1933); *S. Mexicanum* (SKOVSTED 1934, cited from TISCHLER's list).

2) This study has been done during 1935, a part of which was reported preliminarily in the same year with the writer's former name TÔRU TOYOHUKU.

Observations

1) Chromosome numbers. Chromosome numbers counted were summarized in Table I, in which all species observed were grouped into four sections after PRAEGER's system. Some species signed with asterisk in Table I are not included in PRAEGER's monograph.

The writer (1935) before reported that chromosome number of *S. acre* L. is $2n=16$, but afterward the plant investigated by him was found to be quite different from *S. acre* L. though the species name of this plant observed by the writer could not be identified. Accordingly, the chromosome number of $2n=16$ which had been given for *S. acre* L. by the writer is erroneous and the chromosome number of *S. acre* is omitted from the present Table I. Chromosome number of *S. acre* L. has been reported to be $n=24$ (TISHLER 1937, WULFF 1937). On the chromosome number of *Bryophyllum calcinum* SALISB, TAYLER (1926) has reported that it is probably $2n=40$ or possibly $2n=38$. The chromosome number of this plant was determined to be $2n=40$ in the present study. (Fig. 23).



Figs. 1–13. The meiotic chromosomes of PMCs in some species of *Sedum* and *Cotyledon*; **1–3, 5, 7, 9, 10** and **12**, first metaphase; **4, 6, 8** and **11**, second metaphase; **13**, first anaphase; **1**, *S. verticillatum*; **2**, *S. kamschaticum* for. *angstifolium*; **3, 4**, *S. Sieblodi*; **5, 6**, *S. yezoense*; **7, 8**, *S. cauticolum*; **9**, *S. Aizoon*; **10, 11**, *Cotyledon malacophylla*; **12, 13**, *C.* sp. (*C. spinosa*?). **2** and **9** from acetocarmin preparations, others from material fixed with CARNOY's *fluid*. ×ca. 2000. (Explanation in Table I).

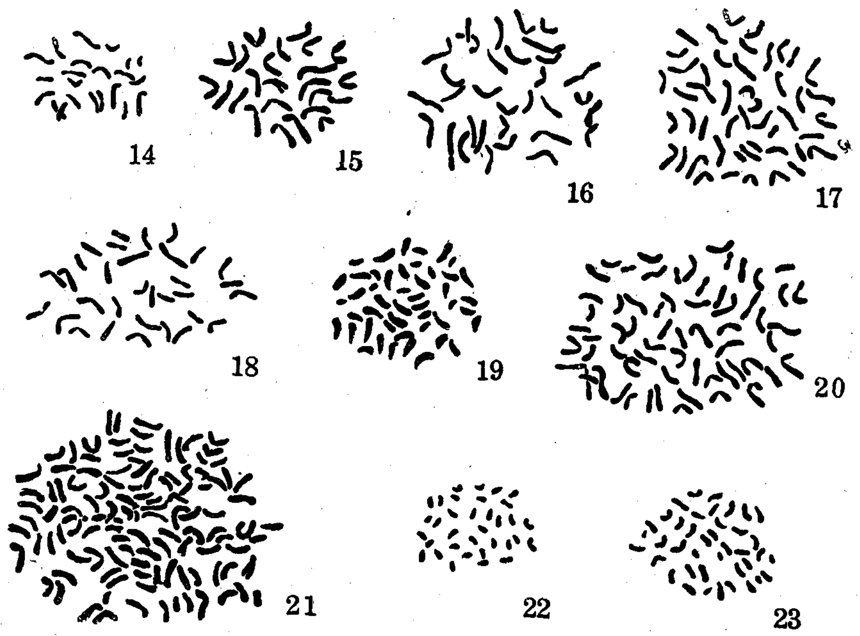
Table I.

Section	Plant name	Japanese name	Sources	Chromosome number *n*	Chromosome number 2*n*	Other investigators	No. of text-figs.
Rhodiola	**S. Rhodiola* var. *elongatum* MAXIM.	Hosobano-iwabenkei	Mt. Teine[1]	11	22 22		42–46
Telephium	*S. verticillatum* L.	Mitubabenkei	Jiozankei[1]	11	22		1, 14
	S. cauticolum PRAEGER	Hidakamisebaya	cultivated[2]	24			7, 8
	S. Sieboldi SWEET	Misebaya	”	25		$n=25$, $2n=50$ BALDWIN ('36)	3, 4
	S. spectabile BOR. Plant A		”	irregular	51	$n=25$, $2n=50$ BALDWIN ('36)	36–39
	” B		”	25			41
	S. alboroseum BAKER	Benkeisô	”	abnormal	50	$n=24$ SUGIURA ('36) $2n=48$ SUGIURA ('31) BALDWIN ('36)	24–34
	**S. yezoense* MIYABE et TATEWAKI	Ezomisebaya	Jiozankei[1]	11			5, 6
	S. sordidum MAXIM.	Titippabenkei	Mt. Iide in Yamagata Prefecture		24		15
Aizoon	*S. kamtschaticum* FISCH et MEYER	Kirinsô	Kamakura in Kanagawa Prefecture		32	$2n=64$ BALDWIN ('36)	16
	S. sp. {*S. kamtschaticum?*		cultivated[3]		48		17
	S. sp. {		”		64		20
	**S. kamtschaticum* for. *angustifolium* KOMAROV	Hosoba-ezokirinsô	Jiozankei[1]	16	32		2, 18
	S. Aizoon L.	Hosobano-kirinsô	Mt. Taisetu in Hokkaido		64		9
Seda Genuina	*S. reflexum* L.?		cultivated;[2] from Liège?		Ca. 112	$2n=48$, $2n=68$ BALDWIN ('36)	21
	**S. oryzifolium* MAKINO	Taitogome	Yamagata		47		19
Cotyledon malacophylla PALL		Aonoiwarenge	Jiozankei[1]	12			10, 11
C. sp. (*C. spinosa* L.?)			cultivated[2]	12			12, 13
Bryophyllum calcinum SALISB.		Seironbenkei	cultivated[2]		40	Probably $2n=40$ TAYLER ('26)	23
B. proliferum BOWIE			”		34		22

(1) Collected in the vicinity of Sapporo, (2) cultivated in the experimental gardens of our Laboratory, (3) cultivated in the botanical gardens of our Unversity; from Amur?

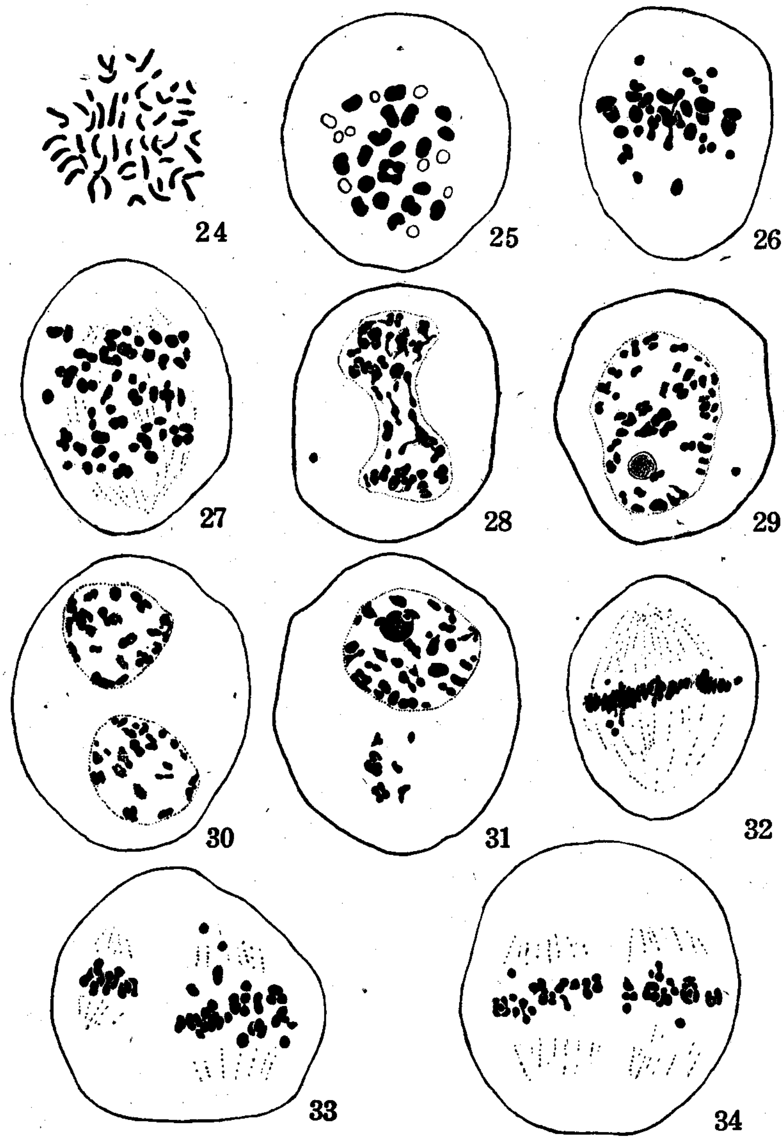
2) Irregeular meiosis. The meiotic process is normal in the majority of the materials except *S. alboroseum*. The secondary pairing, which will be discussed later, is met with in many plants: especially in *S. Rhodiola* var. *elongatum*, (Figs. 42, 43), *S. cauticolum* (Fig. 7), *S. yezoense* (Figs. 5, 6), *S. spectabile* (Figs. 38, 40, 41) and *Cotylodon malacophylla* (Fig. 10).

S. alboroseum BAKER, in which 50 somatic chromosomes were counted, showed very irregular meiotic division. In first metaphase, many univalents which lay apart from the equatorial plane were observed, it was, however, difficult to discern them from fragments, because of the chromosomes of this material being considerably small. The frequency of univalents which were various in different cells could not be determined statistically, but



Figs. 14–23. The somatic chromosomes of some species of *Sedum* and *Bryophyllum*; **14**, *S. verticillatum*; **15**, *S. sordidum*; **16**, *S. kamschaticum* (japanese species); **17** and **20**, *S. kamschaticum*? (foreign species); **18**, *S. kamschaticum* for. *angstifolium*; **19**, *S. oryzifolium*; **21**, *S. reflexum*?; **22**, *Bryophyllum proliferum*; **23**, *B. calcinum*. ca. × 2000. (Explanation in Table I).

they seemed to be ranging from about 8 to 15, mostly over 10. Multivalent-like-chromosomes were very rarely observed (Fig. 25). The plate in Fig. 25, in which all the components are easily discernible, is probably composed of 18 bivalents, 10 univalents and one quadrivalent. The most peculiar abnormality observed at the following stage was the frequent formation of restitution nuclei (Figs. 28–29) which were originally described in *Hieracium* by ROSENBERG (1927). It is probably due to the existence of numerous lagging chromosomes at the first anaphase (Fig. 27). The



Figs. 24–34. The irregular meiosis of *S. alboroseum* having 50 somatic chromosomes; **24**, somatic chromosome; **25**, **26**, first metaphase, the former is polar view, the latter is side view; **27**, first anaphase; **28**, **29**, the formation of restitution nuclei; **30**, **31**, first telophase. **32–34**, second metaphase.

formation of two normal nuclei at first telophase (Fig. 30) is rather rarer than other irregular cases, and sometimes several chromosomes are excluded in cytoplasma (Fig. 31). Abnormal processes also take place in the second division. Fig. 32, in which only one equatorial plane is seen in the second division, seems to be derived from the restitution nuclus found at the previous first anaphase. Besides this, unequal sized plates in the second division were frequently met with (Fig. 33). As the result of the meiotic irregularities mentioned above, the formation of sporads is generally unusual (Fig. 35), although normal sporads are rarely observed. The interior of pollen sacks of this plant was completely empty. This fact shows that the pollens may degenerate by the way of their developmental process. Although the cause why such meiotic abnormalities of this plant were raised is unexplainable, it is, however, supposed that this plant may be a hybrid in origin. For this species the chromosome number of $n=24$ (SUGIURA 1936) or $2n=48$ has been counted by SUGIURA (1931) and BALDWIN (1936). In the latter's material also several univalents occurred at first metaphase, though the process of meiotic division was not described.

In one plant of *S. spectabile* BOR. which has been cultivated in experimental gardens of our Laboratories 51 somatic chromosomes were counted (Fig. 36). In the meiosis of the plant frequently 24 bivalents and one multivalent, probably trivalent (Figs. 37, 38 and 39) or rarely 25 bivalents

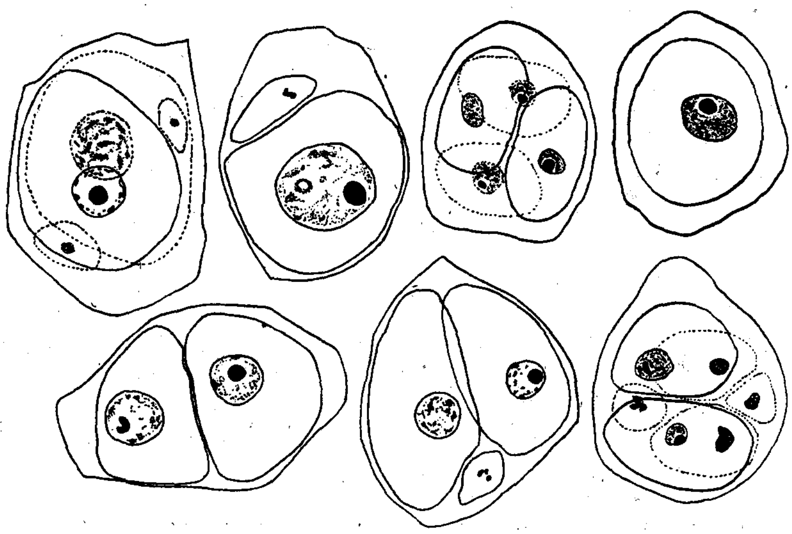


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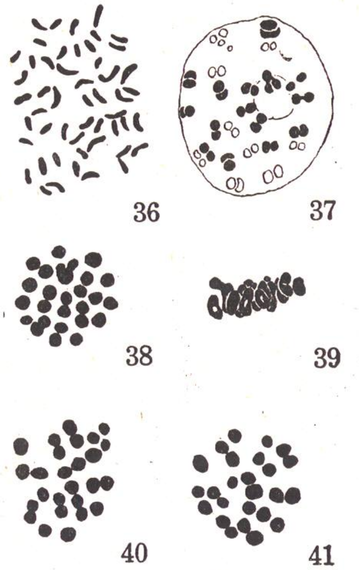
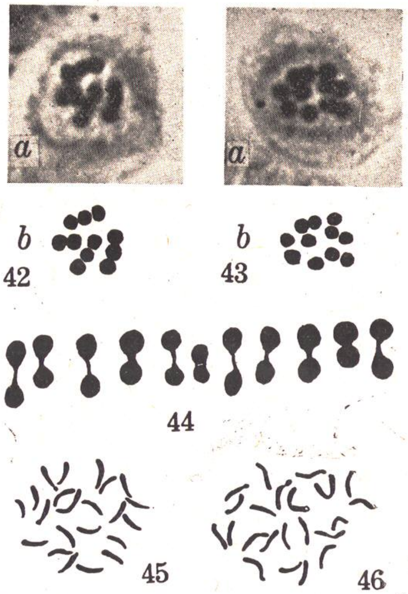
Fig. 35. Usual and unusual sporads of *S. alboroseum.* ca. ×1400.

and one univalent (Fig. 40) were met with at first metaphase of PMCs. A quadrivalent-like-chromosome was observed in one first metaphase but this is doubtful, since the secondary pairing is too remarkable and the chromosomes were crowded in this plate.



Figs. 36–41. *S. spectabile.* **37–40,** meiotic chromosomes in one plant having 51 somatic chromosomes (Fig. 36); **37,** diakinesis, one trivalent is seen; **38, 39,** first metaphase in which one multivalent is seen; **41,** first metaphase of other plant of same species, regularly 25 were counted. ca. × 2000.



Figs. 42–46. *S. Rhodiola* var. *elongatum*, **42, 43,** two PMCs at first metaphase; **42** (a, b) and **43** (a, b) show the two types of secondary pairing, **42,** maximum type $3(3)+1(2)$; **43,** $3(2)+2(1)+1(3)$; **44,** Early anaphase chromosomes, which were arranged to make clear each pair of chromosome; **45** and **46,** male- and female-complements of somatic chromosomes respectively, **42–43, 45–46** ca. × 2000. **44** ca. × 3500.

This plant showed very heigh pollen-sterility of about 70–90%, in spite of the process of meiotic division being relatively regular. In another plant of the same species, 25 were counted regularly at the first metaphase of PMCs (Fig. 41), secondary pairing, however, was also observed in this plant. BALDWIN (1936) has determined the chromosome number of it to be $n=25$ or $2n=50$ in six lines of this species gathered from various sources.

3) On the chromosomes of one dioecious plant. There are some dioecious plants in this genus, of which *S. Rhodiola* DC. has been reported to be X-Y type in male plant by LEVAN (1933). The writer could not discern such heterochromosomes at meiotic division of *S. Rhodiola* var. *elongatum* MAXIM. (Fig. 44), however, the comparable analysis of somatic complements in both male and female plants could not be made, because the chromosomes of this plant are very small (Figs. 45, 46).

Consideration

So far as the writer has observed, no common basic number throughout this genus could be determined. The section Aizoon, however, comprises a regular number series of chromosomes with the lowest number of 16: a series $2n=32$, 48 and $n=64$ in inter- and intra-species, though the species investigated are yet few. BALDWIN (1936) also observed the fact that a polyploid series with a basic number of 12 (or 6) exits in the section *Telephium*. He suggested that 12 (or 6) is a primary basic number and the reduced numbers 10 and 11 found in this section are secondary basic numbers. BALDWIN (1939) has pointed out frequent instances of the intra-specific polyploidy in many species: *S. Ternatum, S. album, S. anglicum, S. dasyphyllum* and *S. hispanicum*. This is, cytophyletically, an interesting fact as well as the phenomenon of secondary association described later on in this paper.

Table II. Type and frequency of the secondary pairing in *Sedum Rhodiola* var. *elongatum*.

Number of types	Pairing type	Frequency
1	3(3)+1(2)+ 0(1)	3
2	3(3)+0(2)+ 2(1)	1
3	2(3)+2(2)+ 2(1)	16
4	2(3)+1(2)+ 2(1)	8
5	2(3)+0(2)+ 5(1)	0
6	1(3)+3(2)+ 2(1)	18
7	1(3)+2(2)+ 4(1)	9
8	1(3)+1(2)+ 6(1)	1
9	1(3)+0(2)+ 8(1)	0
10	0(3)+4(2)+ 3(1)	6
11	0(3)+3(2)+ 5(1)	1
12	0(3)+2(2)+ 7(1)	2
13	0(3)+2(2)+ 9(1)	0
14	0(3)+0(2)+11(1)	0
Total		65

When one considers the basic number of chromosomes in plants or a group of plants, one of the important clues, besides the finding of the polyploid series as above mentioned, is the phenomenon of secondary pairing,[1] so far as it is recognized as the most supportable explanation of it that this phenomenon represents the homology of chromosomes to some extent.

A small statistical analysis of this phenomenon was made on *S. Rhodiola* var. *elongatum* having the chromoseme number of $n=11$ (Table II). As shown in Table II, the maximum type of the secondary pairing of this plant is 3(3)+1(2) (Fig. 43, a, b). The combinations derivable from the maximum type are limited to theoretically fourteen types, and other types, indeed, were not observed. These above facts suggest that the genom of this plant is composed of $A_1A_2A_3$, $B_1B_2B_3$, $C_1C_2C_3$, D_1D_2, accordingly this plant may be a secondarily balanced polyploid which derived from the original genom of only A, B, C and D. It is interesting to notice that the supposed basic number of 4 found in *S. Rhodiola* var. *elongatum* is connectible to the section *Aizoon, Telephium* and other sections. In this genus *Sedum,* the secondary pairing has been reported also in *S. maximum,* a tetraploid race of *S. ternatum* (BALDWIN 1936 a, b) and *S. acre* (TISHLER 1937). This fact leads one to suppose that the secondary polyploidy, in addition to regular polyploidal change, has been playing a great rôle in the evolution of this genus. BALDWIN (1939) afterward has reported ranging low numbers of chromosomes in even one section: *Telephium,* n-number of 10, 11 and 12; *Eurasiafica Orthocarpia,* of 6, 7 and 8; *Eurasiafica Kyphocarpia,* of 5, 6 and 7. The existence of such ranging numbers in one section seems also very suggestive on secondary polyploidy, though BALDWIN has not mentioned it.

When we consider the phylogeny or evolution of this genus from the cytological point of view, it must be furthermore noticed that the vegetative propagation is possible in many plants of this genus. Consequently, the plants having the odd somatic number (*S. oryzifolium* and one plant of *S. spectabile*) and showing the meiotic irregularities may be preserved and propagated.

1) The theory of secondary association of chromosomes was originally advocated by DARLINGTON (1928) and systematized by LAWRENCE (1931). MATSUURA (1935), afterward, has explained the mechanism of this phenomenon. Furthermore this phenomenon was analysed statistically in various plants by SAKAI (1935), NANDI (1936), CATCHSIDE (1937) and HAGA (1938) etc. It has been recently made clear by many workers of our Laboratory (MATSUURA 1939) that this phenomenon is widely distributed in plant kingdom.

Here the writer wishes to express his cordial thanks to Prof. H. Matsuura under whose guidance the work has been carried out. He is also indebted to Prof. M. Tatewaki, of the Department of Agriculture in our University, for his kindly suggestions on the materials. The present study was aided by a grant from the Scientific Research Fund of the Department of Education to which his sincere thanks are also due.

Summary

1) Eleven species, one variety and one form of the genus *Sedum* and some species of two related genera were studied cytologicaly.

2) A polyploid series with the lowest number of 16 was found in the section *Aizoon* of the genus *Sedum*, though the plants studied are yet few.

3) Some irregular meioses, especially on *S. alboroseum*, were described.

4) The meiotic and somatic chromosomes of one dioecious plant (*S. Rhodiola* var. *elongatum*) were investigated. In this variety the author could not observe such heterochromosomes as described in the male plant of *S. Rhodiola* DC. by Levan.

5) Secondary pairing is remarkable in several species, of which *S. Rhodiola* var. *elongatum* was discussed in some detail.

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