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 had been known fragmentally, until 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 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-acetocarmine
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.

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 pre-
liminarily 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 (Tischler 1937, Wulff 1937). On the chromosome number of Bryophyllum calcinum Salisb., Tylor (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. angustifolium; 3, 4, S. Siebodi; 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 acetocarmine preparations, others from material fixed with Carnoy's fluid. x ca. 2000. (Explanation in Table I).
Table I.

<table>
<thead>
<tr>
<th>Section</th>
<th>Plant name</th>
<th>Japanese name</th>
<th>Sources</th>
<th>Chromosome number</th>
<th>Other investigators</th>
<th>No. of text-figs</th>
</tr>
</thead>
<tbody>
<tr>
<td>*S. Rhodiola var. elongatum MAXIM.</td>
<td>Rhodiola *8. var. elongatum MAXIM.</td>
<td>Hoso-bano-iwabenkei</td>
<td>Mt. Teine(1)</td>
<td>11, 22</td>
<td></td>
<td>11, 22</td>
</tr>
<tr>
<td>S. verticillatum L.</td>
<td>S. verticillatum L.</td>
<td>Mitubabenkei</td>
<td>Jiozankei(10)</td>
<td>11, 22</td>
<td></td>
<td>11, 22</td>
</tr>
<tr>
<td>S. cuscutinum PRAGER</td>
<td>S. cuscutinum PRAGER</td>
<td>Hidakamisebaya</td>
<td>cultivated(10)</td>
<td>11, 22</td>
<td></td>
<td>11, 22</td>
</tr>
<tr>
<td>S. Sieboldi Sweet</td>
<td>S. Sieboldi Sweet</td>
<td>Misebaya</td>
<td>&quot;</td>
<td>24, 25</td>
<td></td>
<td>24, 25</td>
</tr>
<tr>
<td>S. spectabile BOR.</td>
<td>S. spectabile BOR.</td>
<td>&quot;</td>
<td>&quot;</td>
<td>25, 25</td>
<td></td>
<td>25, 25</td>
</tr>
<tr>
<td>Plant A</td>
<td>Plant A</td>
<td>&quot;</td>
<td>&quot;</td>
<td>51, 51</td>
<td></td>
<td>51, 51</td>
</tr>
<tr>
<td>Telephium</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>50, 50</td>
<td></td>
<td>50, 50</td>
</tr>
<tr>
<td>&quot; B</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>50, 50</td>
<td></td>
<td>50, 50</td>
</tr>
<tr>
<td>S. alboroseum BAKER</td>
<td>S. alboroseum BAKER</td>
<td>Benkeisō</td>
<td>Jiozankei(10)</td>
<td>11, 22</td>
<td></td>
<td>11, 22</td>
</tr>
<tr>
<td>*S. yezoensis MIYABE et TATEWAKI</td>
<td>*S. yezoensis MIYABE et TATEWAKI</td>
<td>Ezomisebaya</td>
<td>Jiozankei(10)</td>
<td>11, 22</td>
<td></td>
<td>11, 22</td>
</tr>
<tr>
<td>S. sordidum MAXIM.</td>
<td>S. sordidum MAXIM.</td>
<td>Titippabenkei</td>
<td>Mt. Iide in Yamagata Prefecture</td>
<td>24</td>
<td></td>
<td>24</td>
</tr>
<tr>
<td>Aizoon</td>
<td>S. kamtschaticum FISCH et MEYER</td>
<td>Kirinsō</td>
<td>Kamakura in Kanagawa Prefecture cultivated(10)</td>
<td>32</td>
<td>2n=64</td>
<td>16</td>
</tr>
<tr>
<td>S. sp. [S. kamtschaticium FISCH et MEYER]</td>
<td>S. sp. [S. kamtschaticium FISCH et MEYER]</td>
<td>&quot;</td>
<td>Jiozankei(10)</td>
<td>16, 32</td>
<td></td>
<td>16, 32</td>
</tr>
<tr>
<td>*S. kamtschaticum FOR. angustifolium KOMAROV</td>
<td>*S. kamtschaticum FOR. angustifolium KOMAROV</td>
<td>Hosoba-exokirinsō</td>
<td>Jiozankei(10)</td>
<td>16, 32</td>
<td></td>
<td>16, 32</td>
</tr>
<tr>
<td>S. Aizoon L.</td>
<td>S. Aizoon L.</td>
<td>Hosobano-kirinsō</td>
<td>Mt. Taisetu in Hokkaido</td>
<td>64</td>
<td></td>
<td>64</td>
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<tr>
<td>Seda Genuina</td>
<td>S. reflexum L.f.</td>
<td>Taitogome</td>
<td>cultivated(10) from Libge Yamagata</td>
<td>Ca. 112</td>
<td>2n=48, 2n=68</td>
<td>21</td>
</tr>
<tr>
<td>*S. orysteolium MAKINO</td>
<td>*S. orysteolium MAKINO</td>
<td></td>
<td></td>
<td>112, 47</td>
<td></td>
<td>112, 47</td>
</tr>
<tr>
<td>Cotyledon malacophylla PALL</td>
<td>Cotyledon malacophylla PALL</td>
<td>Aonoiwarenge</td>
<td>Jiozankei(10)</td>
<td>12, 12</td>
<td></td>
<td>12, 12</td>
</tr>
<tr>
<td>C. sp. (C. spinosa L.f)</td>
<td>C. sp. (C. spinosa L.f)</td>
<td></td>
<td>Jiozankei(10)</td>
<td>12, 12</td>
<td></td>
<td>12, 12</td>
</tr>
<tr>
<td>Bryophyllum calcinum SALISS.</td>
<td>Bryophyllum calcinum SALISS.</td>
<td>Seironbenkei</td>
<td>cultivated(10)</td>
<td>40</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td>B. proliferum BOWIE</td>
<td>B. proliferum BOWIE</td>
<td>&quot;</td>
<td>cultivated(10)</td>
<td>34</td>
<td></td>
<td>34</td>
</tr>
</tbody>
</table>

(1) Collected in the vicinity of Sapporo, (2) cultivated in the experimental gardens of our Laboratory, (3) cultivated in the botanical gardens of our University; from Amur!!
2) **Irregular 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 *Cotyledon 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 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
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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 cytoplasm (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 nucleus 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. x1400.
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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. x 2000.

This plant showed very high 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 Levä (1933). The writer could not discern such heterochromosomes at meiotic division of \textit{S. Rhodiola} var. \textit{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 \textit{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: \textit{S. Ternatum}, \textit{S. album}, \textit{S. anglicum}, \textit{S. dasyphyllum} and \textit{S. hispanicum}. This is, cytologically, 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 \textit{Sedum Rhodiola} var. \textit{elongatum}.

<table>
<thead>
<tr>
<th>Number of types</th>
<th>Pairing type</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3(3)+1(2)+0(1)</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>3(3)+0(2)+2(1)</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>2(3)+2(2)+2(1)</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td>2(3)+1(2)+2(1)</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>2(3)+0(2)+5(1)</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>1(3)+3(2)+2(1)</td>
<td>18</td>
</tr>
<tr>
<td>7</td>
<td>1(3)+2(2)+4(1)</td>
<td>9</td>
</tr>
<tr>
<td>8</td>
<td>1(3)+1(2)+6(1)</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>1(3)+0(2)+8(1)</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>0(3)+4(2)+3(1)</td>
<td>6</td>
</tr>
<tr>
<td>11</td>
<td>0(3)+3(2)+5(1)</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>0(3)+2(2)+7(1)</td>
<td>2</td>
</tr>
<tr>
<td>13</td>
<td>0(3)+2(2)+9(1)</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>0(3)+0(2)+11(1)</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>65</strong></td>
</tr>
</tbody>
</table>
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,\textsuperscript{1)} so far as it is recognized as the most supportable explanation \begin{flushleft}
\textsuperscript{1)} The theory of secondary association of chromosomes was originally advocated by \textsc{Darlington} (1928) and systematized by \textsc{Lawrence} (1931). \textsc{Matsura} (1935), afterward, has explained the mechanism of this phenomenon. Furthermore this phenomenon was analysed statistically in various plants by \textsc{Sakai} (1935), \textsc{Nandi} (1936), \textsc{Catcheside} (1937) and \textsc{Haga} (1938) etc. It has been recently made clear by many workers of our Laboratory (\textsc{Matsura} 1939) that this phenomenon is widely distributed in plant kingdom.
\end{flushleft} of it that this phenomenon represents the homology of chromosomes to some extent.

A small statistical analysis of this phenomenon was made on \textit{S. Rhodiola} var. \textit{elongatum} having the chromosome number of \textit{n=11} (Table II). As shown in Table II, the maximum type of the secondary pairing of this plant is \textit{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 \textit{A\textsubscript{1}A\textsubscript{2}A\textsubscript{3}, B\textsubscript{1}B\textsubscript{2}B\textsubscript{3}, C\textsubscript{1}C\textsubscript{2}C\textsubscript{3}, D\textsubscript{1}D\textsubscript{2}}, accordingly this plant may be a secondarily balanced polyploid which derived from the original genom of only \textit{A}, \textit{B}, \textit{C} and \textit{D}. It is interesting to notice that the supposed basic number of \textit{4} found in \textit{S. Rhodiola} var. \textit{elongatum} is connectible to the section \textit{Aizoon}, \textit{Telephium} and other sections. In this genus \textit{Sedum}, the secondary pairing has been reported also in \textit{S. maximum}, a tetraploid race of \textit{S. ternatum} (\textsc{Baldwin} 1936 a, b) and \textit{S. acre} (\textsc{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. \textsc{Baldwin} (1939) afterward has reported ranging low numbers of chromosomes in even one section: \textit{Telephium}, \textit{n-number} of 10, 11 and 12; \textit{Eurasiafrica Orthocarpa}, of 6, 7 and 8; \textit{Eurasiafrica Kyphocarpa}, of 5, 6 and 7. The existence of such ranging numbers in one section seems also very suggestive on secondary polyploidy, though \textsc{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 (\textit{S. oryzifolium} and one plant of \textit{S. spectabile}) and showing the meiotic irregularities may be preserved and propagated.
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 cytologically.

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 Levam.

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

Literature cited


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