CHROMOSOME NUMBERS IN *CRASSULA*

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(With Twenty-eight Text-figures)

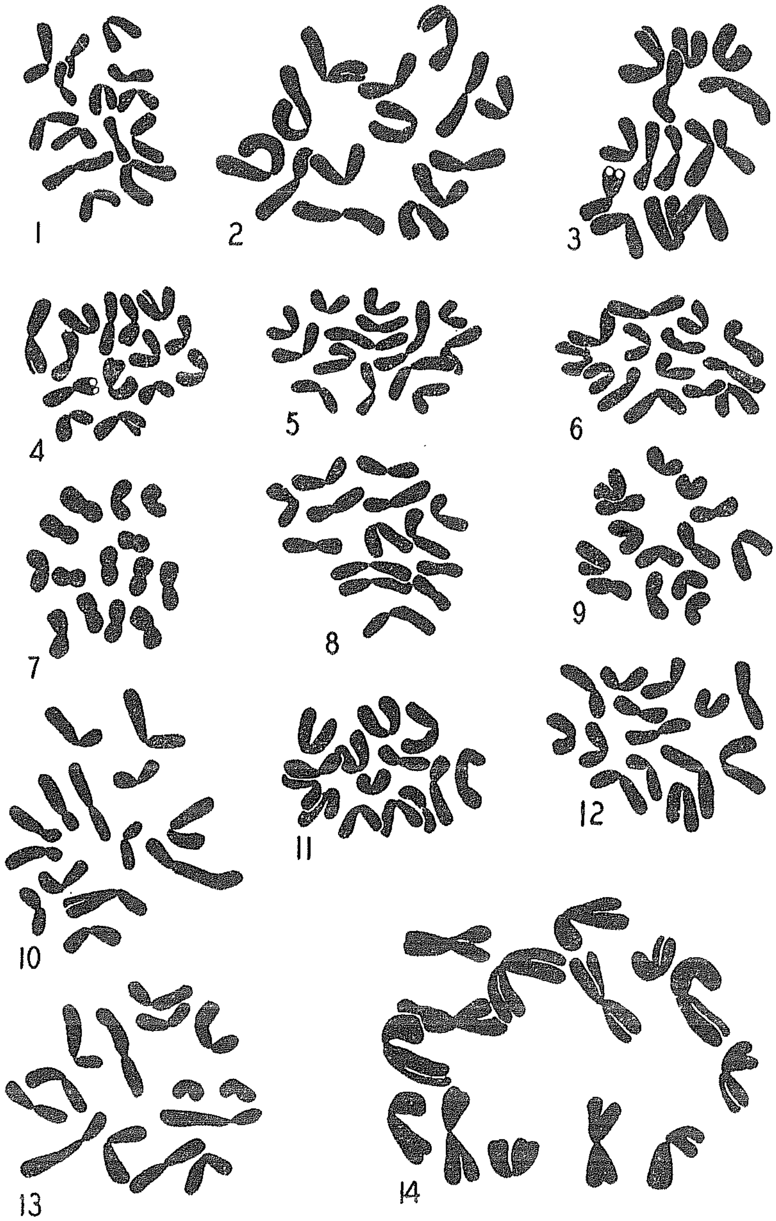
Introduction

Various writers have observed that the genera in the Crassulaceae are not well defined. In 1933, as an approach to an understanding of the phylogenetic relationships in the family, a cytological survey of the Crassulaceae was begun. It was planned, in so far as time and material would permit, to analyse, first in a preliminary, and finally in a detailed manner, the chromosomal situation existing in the several genera of the family, and to correlate that knowledge with the available taxonomic treatments of those genera. The purpose of the present paper is to report the introductory study of *Crassula* L.

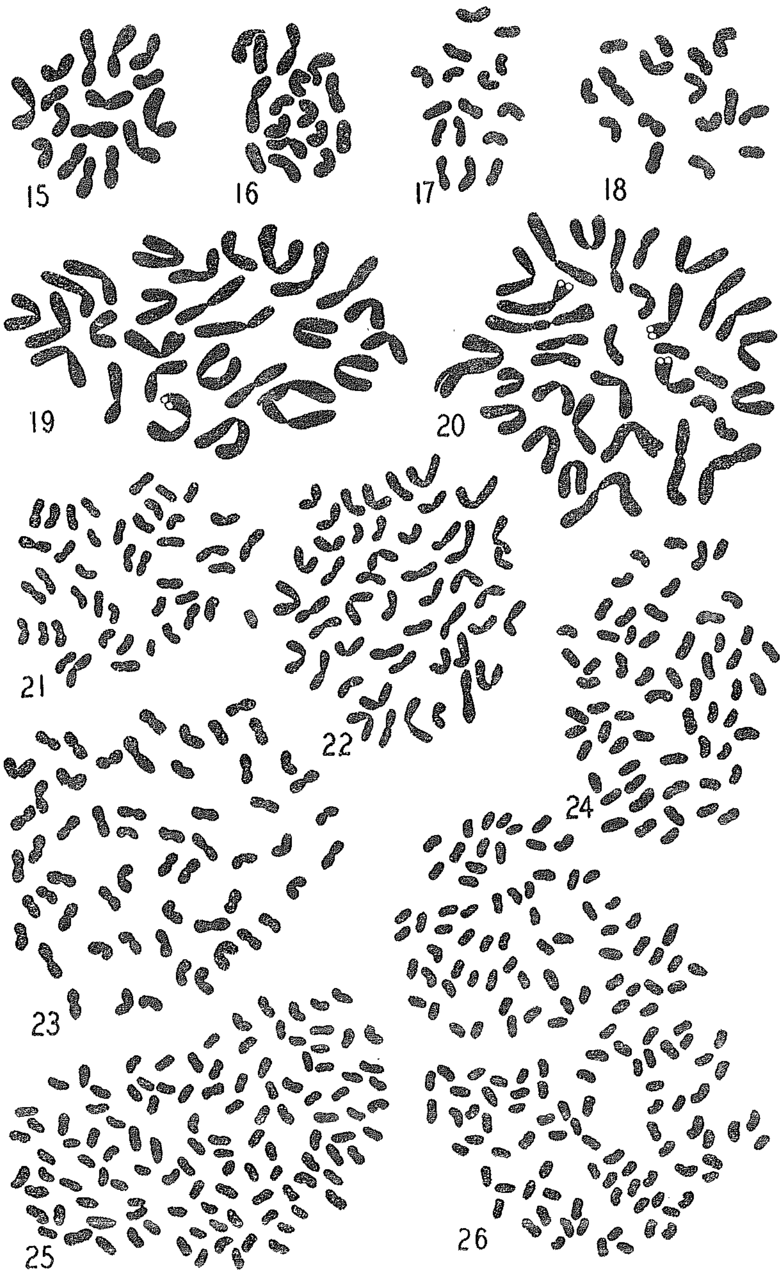
Estimates of the size of the Crassulaceae and of its individual genera vary considerably. According to *Index Kewensis*, *Crassula* is the second genus in size in the family, and *Sedum* is the first. *Crassula* includes, on the basis of that *Index*, 421 recognized species to which 166 others are reduced, 101 of these latter species being reduced from other genera. Similarly, sixty-five species of *Crassula* are reduced extra-generically. These figures afford an indication of the degree of systematic inexactitude that prevails in the demarcation of genera within this family. Berger (1930) reduces to *Crassula* some of the genera recognized in *Index Kewensis*, but he considers *Crassula* to include less than 300 species. About 230 of these species are in South Africa, a number in tropical—chiefly eastern—Africa, one in southern Arabia, several in Madagascar, and the members of section Tillaeoideae distributed throughout the world, but more particularly in the southern hemisphere.

Chromosome numbers for three species of the subfamily Crassuloideae were reported by Skovsted (1934); these species are marked by asterisks in the outline of the plants investigated. Numbers for twenty-seven additional species are given in this report.

The writer expresses appreciation to Dr Orland E. White, Director of the Blandy Experimental Farm, for criticism of this study.



Figs. 1–14. Fig. 1, *Rochea*. Figs. 2–14, *Crassula*. All metaphases except Fig. 14 whic is a drawing of prophase. All have $2n = 14$. $\times 3260$.

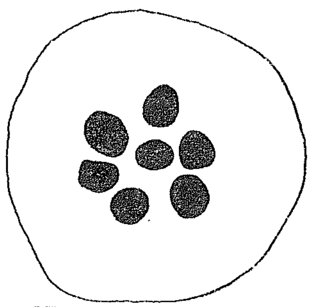


Figs. 15–26. All metaphases of *Crassula* species. Figs. 15–18, $2n=16$; Fig. 19, $2n=28$; Fig. 20, $2n=34$; Fig. 21, $2n=42$; Fig. 22, $2n=48$; Fig. 23, $2n=56$; Fig. 24, $2n=ca.\ 60$; Fig. 25, $2n=ca.\ 112$; Fig. 26, $2n=ca.\ 148$. $\times 3260$.

Materials and methods

Plants of twenty-five species from E. O. Orpet, Santa Barbara, Calif., and gift specimens of *Crassula Peglerae* from Reid Moran, La Canada, Calif., and of *C. arborescens* from the Valley View Greenhouses, Charlottesville, Va., were counted. Only one plant of a species was examined. Specimens from these plants will be placed in the Bailey Hortorium, Cornell University.

Aceto-carmine smears were used; Figs. 1–26 were drawn from smears of root tips and Figs. 27 and 28 from smears of anthers. Prior to smearing, the material was fixed for about 10 min. in Carnoy's fluid. Excellent preparations were obtained. The chromosomes of some of the species are favourable for morphological and structural study. Constrictions were often clearly present. All the drawings were made ×4900. A Zeiss microscope and Zeiss camera lucida were used in conjunction with Wratten filters.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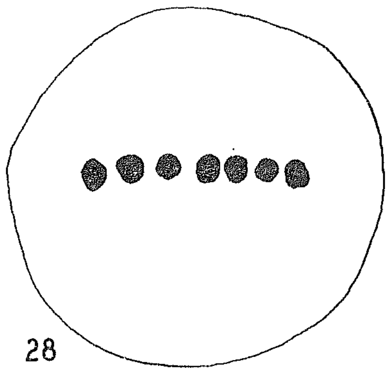
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Figs. 27 and 28. Fig. 27, $n=7$, 1st metaphase of pollen mother cell division in *C. hemisphaerica*. Fig. 28, $n=7$, pollen grain division in *C. Peglerae*. ×3290.

Observations

The species investigated together with their determined numbers are arranged below in accordance with Berger's (1930) monograph of the family:

Crassula L.

	n	Fig.	$2n$	Fig.
Sect. I. Tillaeoideae				
Div. 5. *Glomerata*				
*C. phanaceoides (Hochst.) Fisch. & Mey. (*Tillaea pharnaceoides* Hochst.)	8	—	—	—
Div. 7. *Lycopodioides*				
C. pseudolycopodioides Din. & Schinz.	—	—	16	16
Div. 9. *Corallina*				
C. corallina Thunb.	—	—	16	17
Crassula sp., near *corallina*	—	—	16	18

	n	Fig.	2n	Fig.
Sect. II. Stellatae				
Div. 2. *Spatulata*				
C. spatulata Thunb.	—	—	*ca.* 148	26
C. sarmentosa Harv.	—	—	*ca.* 60	24
Div. 3. *Lactea*				
C. multicava Lem.	—	—	*ca.* 112	25
Div. 4. *Arborescens*				
C. arborescens (Mill.) Willd.	—	—	42	21
Div. 5. *Cordata*				
C. cordata Thunb.	—	—	16	15
Sect. III. Tuberosae				
**C. nemorosa* Endl. (*C. nivalis* Harv.)	$\frac{44-46}{2}$	—	—	—
Sect. IV. Campanulatae				
Div. 1. *Acutifolia*				
C. tetragona L.	—	—	48	22
Div. 2. *Perforata*				
C. perforata Thunb.	—	—	14	12
Div. 3. *Harveyi*				
C. sarcocaulis Eckl. & Zeyh.	—	—	28	19
Div. 6. *Perfoliata*				
C. falcata Wendl.	—	—	14	3
C. perfoliata L.	—	—	14	9
Div. 9. *Ramuliflora*				
C. Peglerae Schönl.	7	28	14	8
Div. 10. *Setulosa*				
C. sedifolia N. E. Br.	—	—	14	10
C. Schmidtii Regel.	—	—	14	2
Div. 13. *Rosularis*				
C. rosularis Haw.	—	—	14	11
Crassula sp., near *rosularis*	—	—	14	13
**C. orbicularis* L.	7	—	—	—
Div. 14. *Turrita*				
C. nodulosa Schönl.	—	—	56	23
C. hemisphaerica Thunb.	7	27	14	6
C. barbata Thunb.	—	—	14	4
Div. 16. *Arta*				
C. deceptrix Schönl.	—	—	14	14
Sect. V. Sphaeritis				
Sect. VI. Globulea				
C. cultrata L.	—	—	14	5
Sect. VII. Pyramidella				
C. columnaris Thunb.	—	—	*ca.* 14	—

The material of *C. columnaris* was lost before the definite count for the species was made, but an approximate number of $2n=14$ was ascertained. Two species of *Crassula* not mentioned by Berger (1930) were also investigated: *C. rotundifolia* Haw., $2n=14$ (Fig. 7), and *C. nana* Schönl. & Baker, $2n=34$ (Fig. 20). *C. coccinea* L., considered by Berger to be *Rochea coccinea* (L.) DC., has $2n=14$ (Fig. 1).

Fig. 14 is a drawing of late prophase. Figs. 1–26, exclusive of Fig. 14, are drawings of metaphases. Fig. 27 shows seven bivalents at 1st metaphase of a pollen mother cell division in *C. hemisphaerica*. Meiosis in this species is regular. Fig. 28 presents the metaphase chromosomes

($n=7$) of a pollen division in *C. Peglerae.* At this stage in this species the chromosomes are characteristically arranged in a single line; little deviation from this "rowed" alignment was observed in about a hundred pollen grains examined.

The range in $2n$ numbers is wide within this genus: 14–*ca.* 148. This latter number is the highest yet reported for the family. Since the plate from which the final count was made required a minimum amount of interpretation, 148 is probably correct. This number, however, falls into few regular series and is divisible by neither 7 nor 8: which numbers seem to be basic for two lines of evolution in the genus. In some of the species, those represented by Figs. 13 and 20 for example, the members of the chromosome complement are so morphologically different that the individual chromosomes can be distinguished without difficulty. Among the higher polyploids, no members of the complement can be recognized with certainty. In comparison with the diploid species ($2n=14$ or 16), the polyploid species *C. sarcocaulis* (Fig. 19) and *C. nana* (Fig. 20) show little or no reduction in the size of their chromosomes. Some of the diploid species (Figs. 17 and 18) have smaller chromosomes than these polyploid species.

Discussion

That an attempt to arrive at the basic chromosome number of a taxonomic group from consideration of a small fraction of the species within that group might lead to erroneous conclusions was emphasized by Babcock (1934). The validity of that emphasis is appreciated. Though only about 10 per cent of the *Crassula* species have been studied, a peculiar cyto-taxonomic situation seems to justify at the present time certain conclusions with reference to basic numbers in the genus. Schönland, as referred to by Berger (1930), regards Tillaeoideae as the oldest section of *Crassula.* Fröderström (1929) retains the generic rank of Tillaea which largely constitutes Tillaeoideae and considers it to be the probable origin of the historically known Crassulaceae: "The annual species of this genus are scantily distributed over almost the whole globe, whereas the rest of the genera of the family are more or less limited to certain regions; the floral characteristics in this genus represent also the prototype of the real or apparent abortions in the flower, which occur in the rest of the genera of the family. . . ." It is significant, in view of these attitudes toward Tillaeoideae, that this section appears to be founded upon a basic number of 8 while the remainder of the genus appears to fall, for the most part, into a 7 series. This situation is revealed by an analysis of the list of the investigated species as given above.

Chromosome numbers for four species from three of the nine divisions of section Tillaeoideae have been determined. Each of these species has 16 somatic chromosomes; the presence of an 8 series is thus suggested.

Five species from four of the six divisions of section Stellatae have been investigated. Their chromosome numbers do not form a regular series. Numbers divisible by 8 ($2n=16$, *C. cordata*) and 7 ($2n=42$, *C. arborescens*) are present. Stellatae may be transitional between an 8 series in Tillaeoideae and a 7 series, as discussed below, in Campanulateae. Some of the species in Stellatae, however, fit neither series. *C. spatulata* could be regarded as a secondary polyploid of a 21-ploid condition of the 7 series, but since the other species, *C. sarmentosa*, in the same taxonomic division has *ca.* 60 chromosomes, such a hypothesis is at present unwarranted. *C. multicava* with about 112 chromosomes would fit into either of the two series mentioned; the high chromosome number and a similar chromosome size and morphology indicate the relationship of this species to *C. spatulata* and *C. sarmentosa*. Parenthetically, it is suggested that an increase in number of chromosomes may occur in roots growing out from the callus tissue that often results from propagation by cuttings. Rather frequent instances are on record of such a change in number of chromosomes in buds that arise from callus tissue.

In section Tuberosae, *C. nemorosa* is the only species that has been studied cytologically. Meiosis in this species is irregular; a definite n number was not determined. The section is not separated into divisions.

Numbers for fifteen species from nine of the seventeen divisions of section Campanulatae have been determined. Two other species, *C. rotundifolia* ($2n=14$) and *C. nana* ($2n=34$), should probably be included in this section. If these two species are included, the following series founded upon a basic number of 7 is present: 14–28–34–48–56. The frequency of distribution for these forms would be: 13 diploids, 1 tetraploid, 1 pentaploid (a derivative of 35), 1 heptaploid (a derivative of 49), and 1 octaploid. The species with 34 and 48 chromosomes could be included in an 8 series, but because of the morphology of their chromosomes and their intimate taxonomic relationship to the members of this 7 series, they are more logically placed in it.

No species from section *Sphaeritis* and only one each from section *Globulea* and section *Pyramidella* have been studied. A determination of $2n=14$ for each of these two species gives evidence of a possible 7 series in these two sections.

Representative species from *Crassula* have been investigated; some correlation with the taxonomy of the genus is exhibited by the chromosome numbers determined. The data, therefore, appear to warrant the following conclusions. If, as suggested by Fröderström (1929), Tillaea is restored to the rank of a genus, the primary basic number of *Crassula* is 7. If Tillaea is included within *Crassula*, the primary basic number of *Crassula* must be considered to be 8, and in the evolution of the genus a descending chromosome series of 8–7 has functioned with the secondary development of a predominant multiple series of 7–14–28, etc. The descending series is "usually intergeneric and seldom inter- and intraspecific"; the multiple series is usually "intra- and interspecific, rarely intergeneric" (Wanscher, 1934). Wanscher's observations favour the retention of Tillaea as a genus. It is so recognized in *Index Kewensis* where it has assigned to it fifty-five accepted species.

As established by Berger (1930), the subfamily Crassuloideae includes besides *Crassula* four restricted genera: *Rochea* with four species, *Dinacria* with three species, *Vauanthes* with one species, and *Pagella* with one species. *Rochea coccinea* has 14 somatic chromosomes. From this evidence, and since the genus consists of only four species, it may be assumed that *Rochea* has a basic number of 7. None of the other three genera have been investigated. The most ancient members of this subfamily belong to section Tillaeoideae of *Crassula* and have basically 8 chromosomes; the primary basic number of Crassuloideae must, therefore, be concluded to be 8, from which a more evolutionally effective number of 7 has originated. Consequently, in this subfamily a primary basic number of 8 has been lowered to 7. Within the closely related families, Saxifragaceae and Rosaceae, a basic number of 7 has been raised to 8 in the subfamilies Saxifragoideae and Rosoideae (Schoennagel, 1931).

The present data do not allow the formulation of definite conclusions concerning the origin of the family. A number of chromosomal series have contributed to its development; it may be polyphyletic in origin. *Crassula* possesses at least two series. Skovsted (1934), after determining the chromosome numbers of fifteen species from five genera of this family, states that "not less than five different chromosome numbers or series have been found". Investigations so far made on *Sedum* (about 10 per cent of the species have been studied) reveal an *n*-chromosome range from 6–64 with twenty-six intermediate numbers; more than one line of chromosomal evolution has been operative in the development of the genus (Baldwin, 1936). A detailed analysis of section Tillaeoideae will perhaps give an insight into the initial evolution of the Crassulaceae.

SUMMARY

Chromosome numbers for twenty-six species of *Crassula* are reported in this paper. Numbers for three other species have been reported by another investigator. The $2n$-numbers exhibit a range of 14–*ca.* 148. This latter number is the highest known for the family.

Tillaeoideae is the oldest section of the genus. The species counted from this section have 16 somatic chromosomes. The other species are distributed taxonomically throughout the rest of the genus and belong predominantly to a 7-chromosome series: 14–28–35–42–48–56. It is assumed that if Tillaeoideae is restored to generic rank as Tillaea, the primary basic number for *Crassula* is 7 and, if Tillaeoideae is retained as a section, the primary basic number of *Crassula* is 8 although most of its species belong to a 7 series.

The subfamily Crassuloideae includes besides *Crassula* four small genera. Only one species from these four genera has been examined; *Rochea coccinea* has 14 somatic chromosomes. *Rochea* is assumed to have a basic number of 7. In the evolution of this subfamily a descending chromosome series of 8–7 has functioned, and a multiple series of 7–14–28, etc., has arisen secondarily and dominated the development of this taxonomic group.

No conclusions relative to the origin of the Crassulaceae can be definitely reached at the present time, but the chromosomal studies so far made indicate that in the development of this family several lines of chromosomal evolution have been operative.

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