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ON THE ORIGIN OF SAXIFRAGA
NATHORSTI (DUSÉN) v. HAYECK

BY

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WITH 5 FIGURES IN THE TEXT

KØBENHAVN
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1. Introduction.

In 1933 TH. SØRENSEN in his paper on the Flora of East Greenland (pp. 77—84, Plate XII) gives a very interesting description of the endemic Northeast Greenland species *Saxifraga Nathorsti*. Other very thorough descriptions of this species may be found in the papers of DUSÉN (1901) and v. HAYECK (1905). According to v. HAYECK and SØRENSEN the species deserves to be considered a well-founded species. In respect of its morphology it is, however, distinctly intermediate between the purple-flowered *S. oppositifolia* L. (belonging to the *Porphyrion*-section) and the yellow-flowered *S. aizoides* L. (to the *Xanthizoon*-section). The colour of the flowers of *S. Nathorsti* varies according to SØRENSEN from sordid yellow (rather rare) to more or less deep red or purple, a sordid pink to flesh colour, however, being far the most frequent. Also with regard to its floescence and its ecology it is intermediate, suggesting a hybridogenous origin. v. HAYECK and SØRENSEN doubt this origin. v. HAYECK writes: "Der für eine Art aus der Sektion *Porphyrion* ganz befremdliche Habitus legt den Gedanken nahe, dass wir es mit einer Bastardform zu tun haben können. — — Eher wäre an einen Bastard mit *S. aizoides* zu denken. Aber diese hat fast freie Kelchzipfel, einen breiten Diskus und gelbe schmale einnervige Petalen, an welche Eigenschaften *S. Nathorsti* nicht die geringste Annäherung zeigt. Eine hybride Abkunft derselben können wir daher mit Sicherheit ausschliessen. — — — (Es) bleibt nur noch eine einzige Annahme übrig, nämlich die, dass *S. Nathorsti* aus *S. oppositifolia* durch Mutation entstanden sei." v. HAYECK's remark on the flower morphology is clearly not quite correct seeing that the petals are narrower and longer in *S. Nathorsti* as compared with *S. oppositifolia* (cf. fig. 1 and DUSÉN l. c. fig. on p. 36). SØRENSEN mentions the following arguments speaking against a hybrid origin: 1) the nuclear division of the PMC's takes place regularly, and 2) fructification is perfectly normal. The plant was found with mature seeds by the middle of August. On the other hand *S. Nathorsti* according to SØRENSEN grows especially in river beds and desiccated ponds and shows the greatest ecological agreement with *S. aizoides*. GELTING (1934, p. 126) mentions that HARTZ

by "cultivation experiments" found *S. Nathorsti* constant through several years and writes "hence it seems doubtful that it should represent the hybrid *S. oppositifolia* \times *aizoides*". HARTZ (in HARTZ & KRUSE 1911, p. 414), however, only says that specimens brought alive to Copenhagen later flowered every year and kept constant, "although somewhat luxuriating". Of interest are the remarks by HARTZ (l. c.) on the occurrence of the plant at Cape Seaforth. He found numerous specimens growing amongst *S. oppositifolia* and *aizoides*, but did not

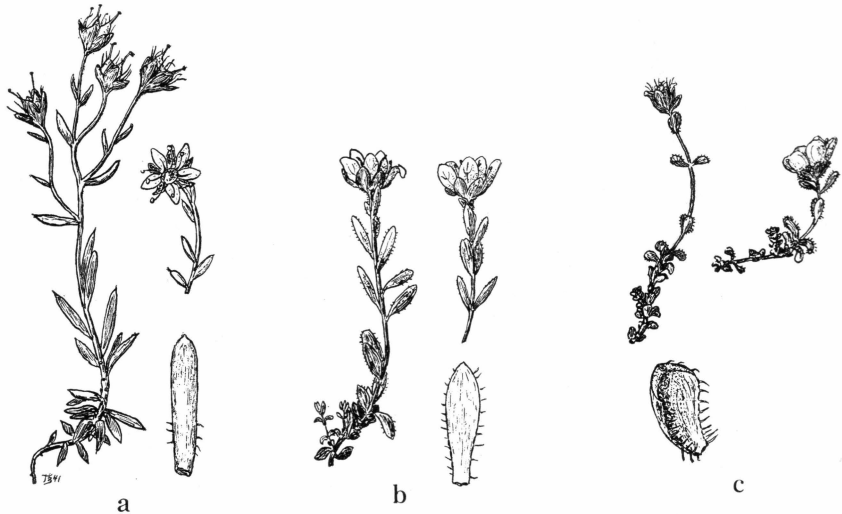


Fig. 1. a: *Saxifraga aizoides*, b: *Saxifraga Nathorsti*, c: *Saxifraga oppositifolia*. Habitus ($\times \frac{2}{3}$) and leaves of flowering shoots enlarged (a—b \times abt. 2, c \times abt. 3). All figures drawn from herbarium specimens from East Greenland.

see any ripe fruits on the plant (on the 25th of August) and he writes: "You think at first that you have a bastard of *S. oppositifolia* and *aizoides* before you."

Mag. scient. TH. SØRENSEN has fixed a great material of buds of *S. Nathorsti* and its supposed parent species. This material he kindly has handed over to the writer, who has made a cytological study of the three species. On the basis of SØRENSEN'S material from Traill Island in East Greenland of *S. Nathorsti* and *S. oppositifolia* and material from Finse (Norway) of *S. aizoides* (fixed by the writer) some orientating studies were made (BÖCHER 1938a, c), the chromosome numbers 13 for *S. aizoides* and *oppositifolia* and abt. 26 for *S. Nathorsti* being found. The opinion was advanced that the latter possibly was an allotetraploid species which had arisen after the doubling of the chromosomes of a hybrid *S. oppositifolia* \times *aizoides*. This theory accords well with the fertility of the species, and the sterility of the specimens found by

HARTZ may possibly indicate that the F_1 hybrid also occurs in East Greenland.

In the present paper the cytology of the three species will be treated in greater detail. As to the morphological characteristics reference is made to the floristic works mentioned above and to fig. 1, where some of the more important characteristics are visible. *S. Nathorsti* is intermediate as to shape, hairiness, and position of leaves, shape of sepals and petals (but in these characteristics closer to *S. oppositifolia*), number of flowers (it is sometimes 2-flowered) etc. According to verbal communication by Mag. scient. TH. SØRENSEN it is vegetatively rather robust and succulent; it may have a number of gigas-characters.

2. Technique.

The fixatives used were either CARNOY (Material from Finse and Traill Island) or a prefixation from abt. five to ten minutes in CARNOY followed by 24 hours fixation in NAVASHIN'S solution. The sections were cut 10—11 μ and stained in NEWTON'S Iodine-gentian violet (gentian violet from Anilin Comp. New York).

3. Cytological Observations.

A. Chromosome Numbers.

The following countings have been made:

Saxifraga aizoides. $n = 13$. Material from Norway and Copenhagen (Botanical Gardens) (SKOVSTED 1934).

$n = 13$. Material from Finse in Norway (BÖCHER 1938c).

$n = 13$. Material from Clavering Island, East Greenland (Granat-valley and the region round Granat-valley).

Saxifraga oppositifolia. $n = 13$. Material from Norway (SKOVSTED 1934).

$n = 13$. Material from Clavering Island (Eskimonæs).

$n = 13$. Material from Traill Island, East Greenland.

Saxifraga Nathorsti. $n = 26$. Material from Clavering Island (three localities).

$n = 26$. Material from Traill Island.

B. Morphology and Arrangement of Chromosomes During Meiosis.

a. *Saxifraga aizoides*. Fig. 2.

According to SKOVSTED no differences were observed in his material from Norway and Copenhagen. The writer, too, was not able to see any difference between the Finse- and the Greenland material. The

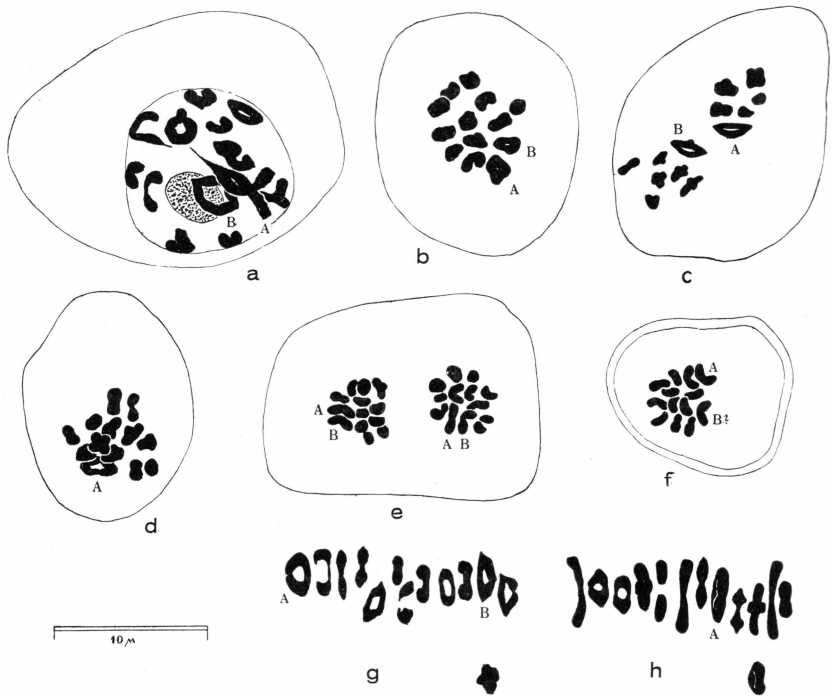


Fig. 2 a—h: *Saxifraga aizoides*. a: diakinesis; b—d: metaphase I, polar view or c obliquely sideways, in c two groups of bivalents and one isolated bivalent; e: metaphase II; f: first pollen division, metaphase; g—h: metaphase I, side view, bivalents separately drawn, one bivalent outside the equatorial plane.

size of the chromosomes varies in the material from all four localities, two pairs being larger than the rest of the complement. In the figures the two large bivalents are marked with A. and B. They are ringshaped and the corresponding chromosomes in the second division and the pollen division (fig. 2e, f) are medianly constricted. At metaphase I the bivalents do not lie in a plane. In very many cells one pair is placed outside the plate. This “non-congression” (cf. DARLINGTON 1937, p. 526) seems, however, as in the case of *Lychnis chalconica* (SOKOLOWA 1931) and *Ranunculus Thora* (BÖCHER 1938b) not to lead to an unequal distribution of the chromosomes. In one case (fig. 2c) the bivalents

are arranged in two groups each consisting of six pairs and one pair lying outside the equatorial plane.

b. *Saxifraga oppositifolia*. Fig. 3.

The 13 bivalents are somewhat smaller than those of *S. aizoides*. There are two to three larger bivalents which in many cells are ring-

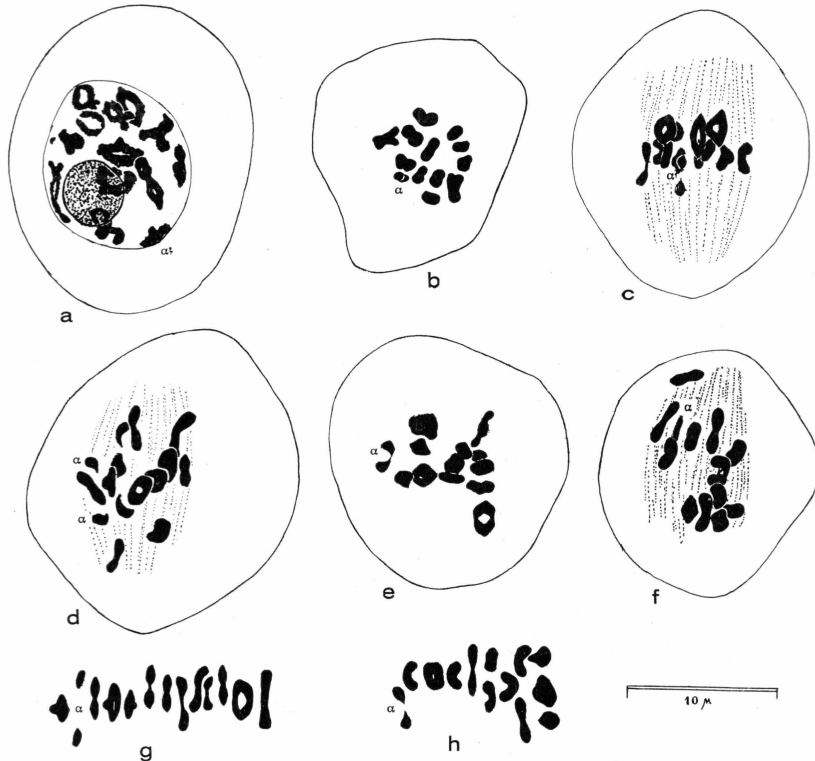


Fig. 3 a—h: *Saxifraga oppositifolia*. a: diakinesis; b—c: metaphase I, polar and side view; d—f: metaphase I, probably prometaphase; g—h: metaphase I, side view, bivalents separately drawn, in h five pairs outside the equatorial plane.

shaped. In all the cells it was possible to see one pair of very small size (*a* in the figures) and the corresponding small chromosomes are also visible in the premeiotic division figured in SKOVSTED'S paper. In most PMC'S this small pair divide before the rest. Only rarely this precocious separation takes place in two bivalents (fig. 3d). As in *Ranunculus* (LARTER 1932, BÖCHER 1938b) this behaviour may possibly be caused by a delayed onset of terminal affinity. Like *S. aizoides* the bivalents frequently were not arranged in a plane. The cells fig. 3d—f were found in pollensacks which also contained cells in diakinesis and, hence, they probably represent pro-metaphase stages. The first meta-

phase chromosomes showed no tendency of clumping as described by SKOVSTED in his material.

c. Saxifraga Nathorsti. Fig. 4.

The cells of this polyploid species are larger when compared with those of the diploid ones. At the first metaphase mostly 26 bivalents occur, but in a number of PMC's one tetravalent chromosome configuration was observed. The tetrasomes are in the figures marked with T. In the cells fig. 4 c, d, and h the four chromosomes are probably associated with quadruple chiasmata (cf. case 15 and 17 described by

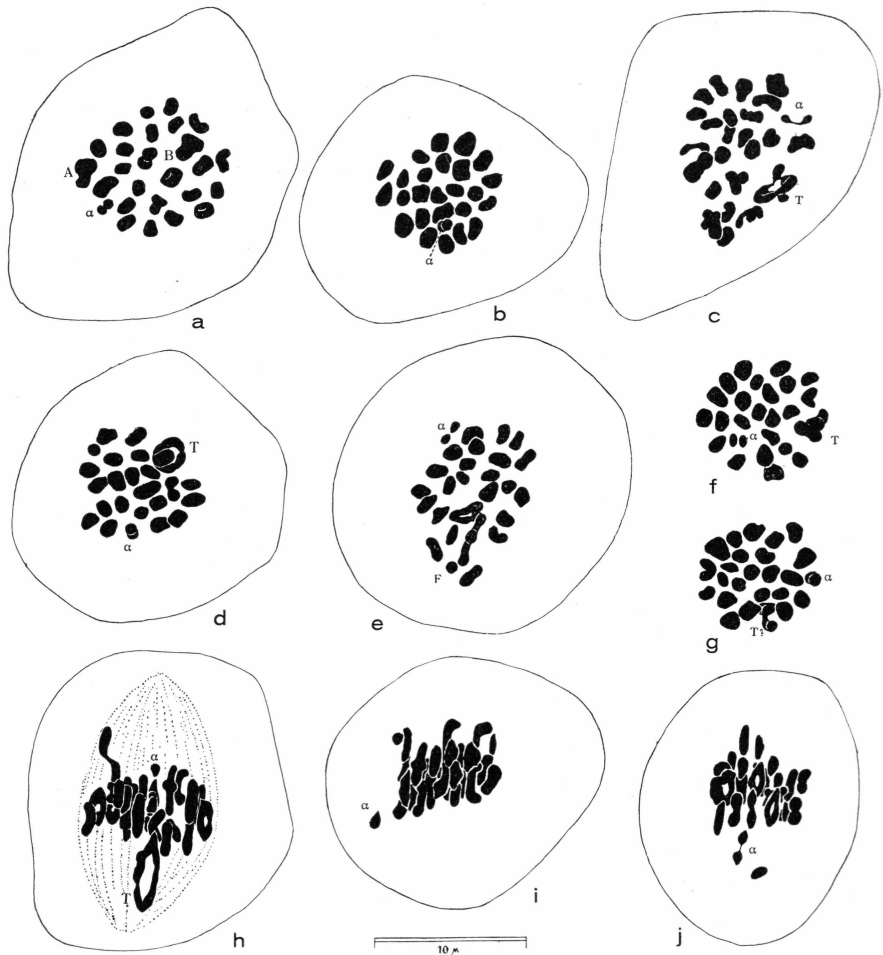


Fig. 4 a—j: *Saxifraga Nathorsti*. a—j: metaphase I, in c—d, f—h 24 bivalents and one tetravalent (T), in e: 26 bivalents and one big fragment (F) close to abnormally formed bivalent, in i one pair of pseudounivalents (α), in j one univalent.

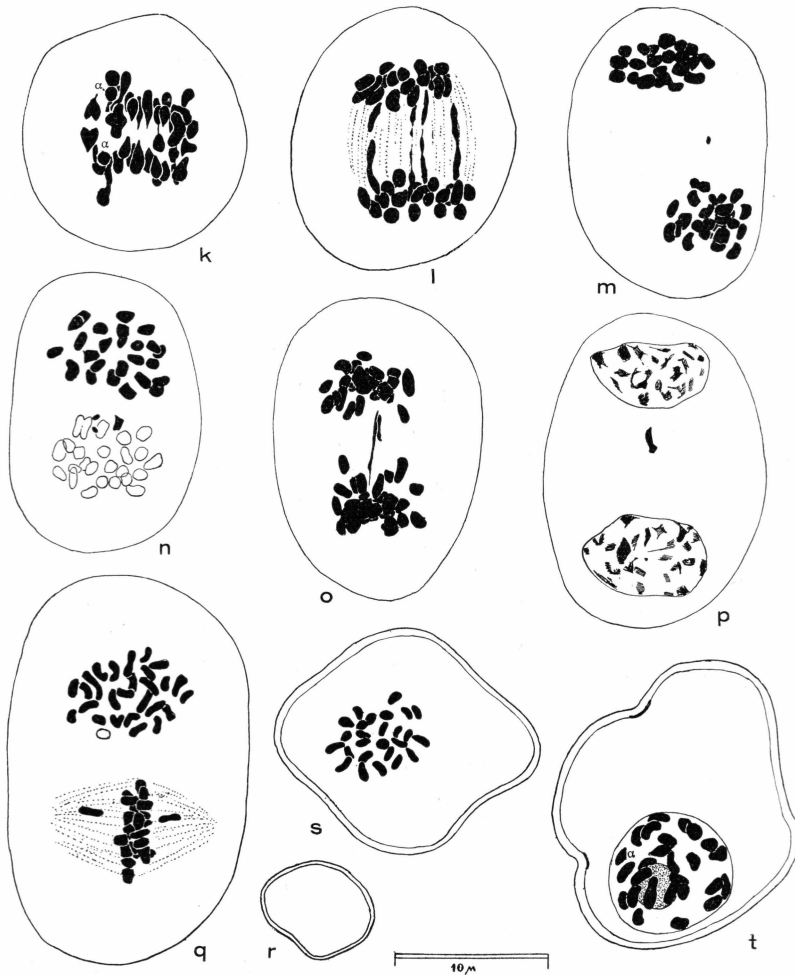


Fig. 4 k—t: *Saxifraga Nathorsti*. k: anaphase I, early stage with four unseparated bivalents; l—o: late anaphase I showing bridges and fragments, in o inversion bridge with fragment, in l laggard bivalents and perhaps chromatid bridge; p: interkinesis with excluded chromosome; q: metaphase II, in both plates one chromosome (not *a*) moves precociously to the poles; r: dwarf pollen grain; s: first pollen division, early anaphase; t: first pollen division, prophase.

DARLINGTON l. c. fig. 40). In the cell fig. 4g the chromosomes may possibly form a chain with three chiasmata.

In very many PMC's meiosis proceeds without any irregularity. The chromosomes which were lying outside the equatorial plane were mostly bivalents or pseudounivalents but in some cases their size and position indicate univalents or fragments. In the cell fig. 4e 26 pairs and one big fragment (F) occurred, the latter being situated close to one of the larger bivalents which was very long and abnormally shaped

probably almost like an angle. In two cells small fragments were placed near chromatid bridges thus indicating crossing over and inversion (fig. 4 o). In some cases it was not possible to distinguish lagging bivalents from chromatid bridges (cf. fig. 4 l). In the late anaphase fragments were observed in a number of cells, but fragmentation is not of common occurrence in the plant. The fragments may be formed by breakage of the bridges and during the prophase after crossing over between non-homologous chromosomes. In the interkinesis (fig. 4 p) the bridges have generally disappeared, only small fragments and possibly parts of bridges being left in the cytoplasm.

In all cells studied one pair (α) was very small and separated before the rest. The behaviour and size of this pair agrees completely with the small pair of *S. oppositifolia*. In the cell fig. 4 a two very large bivalents are visible; they probably represent the two large bivalents A and B of *S. aizoides*. It was, however, in most cells not possible to distinguish the latter from the other somewhat smaller pairs.

Most pollen-sacks contained only normal tetrads or pollen grains. In some cases up to 10 % pentads and in other cases up to 5 % dwarf pollen were found. In one anther a degeneration of the PMC's probably caused by irregularities during the prophase took place.

4. Discussion and Conclusions.

The theory of the hybrid origin of *Saxifraga Nathorsti* is supported by the following facts:

1) In respect of morphology, biology, and ecology *S. Nathorsti* occupies an intermediate position between *S. oppositifolia* and *S. aizoides*.

2) The chromosome number $n = 26$ for *S. Nathorsti* is the sum of that of its supposed parent species, which have $n = 13$. Thus the possibility of an origin of *S. Nathorsti* after doubling of the chromosomes of a hybrid is great.

3) The size and morphology of the chromosomes in *S. Nathorsti* correspond with those of the supposed parents. In all cells only one small pair with precocious separation as in *S. oppositifolia* is visible and sometimes it is also possible to distinguish two big pairs which probably are the A and B pairs of *S. aizoides*. Hence, *S. Nathorsti* is not autopolyploid and has not originated from duplication of the chromosome complement of *S. oppositifolia*.

4) The occurrence of only one quadrivalent configuration indicates that autosyndesis takes place in most bivalents. This is in accordance

with the fact that the two supposed parent species belong to different sections within the genus. In the intersectional hybrid *Saxifraga granulata* × *rosacea* the chromosomes were mainly present as bivalents together with a varying number of univalents (PHILP 1934). In the corresponding tetraploid *S. Potternensis* pairing was almost complete and probably owing to differential affinity only one to two quadravalents occurred (WHYTE 1930). The pairing in the supposed *S. oppositifolia* × *aizoides* is perhaps rather incomplete as in the intersectional hybrid *Saxifraga Andrewsii* (SKOVSTED 1934).

5) In *Saxifraga Nathorsti* fragmentation occurs probably caused partly by breakage of chromatid bridges partly as a result of crossing over taking place in homologous segments of non-homologous chromosomes. This behaviour is described in a number of species-hybrids (e. g. *Crepis divaricata* × *dioscoridis*, MÜNTZING (1934); *Allium cepa* × *fistulosum*, LEVAN (1941)) but occurs also in structural hybrids (cf. GEITLER 1937 and DARLINGTON 1937, p. 274) and autotetraploids produced experimentally (WESTERGAARD 1940). In the genus *Ranunculus* it was only found in the tetraploid species with irregular meiosis (*R. auricomus* and the very irregular Greenland material of *R. reptans*, BÖCHER 1938b). Fragmentation was not observed in the parents of the *Crepis* hybrid mentioned and the same is the case with the two species of *Saxifraga* which probably gave rise to *S. Nathorsti*. The formation of bridges and fragments gives no evidence for the hybrid nature of *S. Nathorsti*, but the occurrence of these structures suggests in this case a hybridogenous origin. As in the allotetraploid *Allium cepa* × *fistulosum* (LEVAN 1941) they occur only now and then and may be caused by incidental allosyndetic pairing.

The polymorphy of *Saxifraga Nathorsti* (re variation in colour of the flowers see Introduction) is explained by its structural hybridity. It is very probable that chromosomes of opposite parents occasionally pair in quadrivalents or bivalents and pass to opposite poles. Variation in the proportions of the chromosomes of the parent species may be the result. In certain cases viable deviating pollen grains caused by unequal division of quadrivalents, fragmentation, or exclusion of chromosomes may perhaps also give rise to variation in the offspring.

In *Saxifraga Nathorsti* we have in all probability a new case of allopolyploidy (amphidiploidy). Other cases may be found in WINGE (1932), MÜNTZING (1931, 1936) and DARLINGTON (1937). The phenomenon is not limited to cultivated plants or hybrids produced experimentally. A number of previously known species, e. g. *Galeopsis tetrahit* (MÜNTZING), *Spartina Townsendii* (HUSKINS 1931), *Pentstemon neotericus*

(CLAUSEN 1933) and *Iris versicolor* (ANDERSON 1936) must certainly in common with *Saxifraga Nathorsti* have arisen after duplication of the chromosomes of hybrids.

DARLINGTON (1928) has pointed out, that the more intersterile the two parents of an allotetraploid species, the more fertile and true-breeding is the resulting progenies. *Saxifraga Nathorsti* belongs very probably to the most fertile and stabilised allopolyploids. The age of species may be great seeing that icefree areas may have existed in many localities in Greenland through at least the last glaciation (cf. GELTING, l. c. p. 126 and the writer 1938a). The rather large area of the species in Northeast Greenland (see SØRENSEN, l. c. fig. 4, and SEIDENFADEN & SØRENSEN, 1937) indicates also that the species formation took place early. Thus there has probably been time enough for a stabilisation of the species through selection of the more suitable and stabilised types. In the case of the allotetraploid *Saxifraga Potternensis* and the tetraploid plants of *Saxifraga tridactylitis* × *adscendens* the first generations showed a tendency towards greater stabilisation (WHYTE 1930, DRYGALSKI 1935) and the same may apply to *Saxifraga Nathorsti*.

The writer wishes to express his sincere thanks to Mag. scient. TH. SØRENSEN for the interesting material of *Saxifraga Nathorsti* and its parent species.

Copenhagen, March 1941.

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