Karyotype Alteration and Phylogeny. IV. Karyotypes in Amaryllidaceae with special reference to the SAT-chromosome*

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Introduction

Though the estimation of chromosome numbers in plants has since the last decade of the last century attracted the intense interest of plant cytologist, not so many plant species have yet been dealt with from the view points of phylogeny and karyotype alteration.

In Lycoris many chromosome numbers were found, namely L. sanguiflora $2n = 22 = 22i$, L. aurea $2n = 12 = 10V + 2i$, $2n = 13 = 9V + 4i$, $2n = 14 = 8V + 6i$, L. albiflora $2n = 17 = 5V + 12i$, L. squamigera $2n = 27 = 6V + 21i$, L. radiata $2n = 33 = 33i$. Take-naka (1930) and Inariyama (1931, 1932, 1933, 1937) interpreted those karyotypes by assuming that the V-shaped chromosome may be the result of a fusion of the two rod-shaped chromosomes (the i-chromosomes). This interpretation was also applied by the present writer in Leucojum (Sato 1937b). Besides the fusion of chromosomes the phenomena of fragmentation, elimination, translocation and other karyotype alteration were found in Scilla (Satô 1935a, 1936a, b).

In earlier reports we often find that the number of chromosomes was not exactly determined, this being partly due to the inadequate technique employed at that time and partly due to a prejudice as regards kindred taxonomic groups of plants. It will be sufficient to quote the somatic chromosome numbers of Agave and Hosta. Agave americana which was reported by Müller (1912) to have 20 chromosomes instead of $120 = 20L + 100S$ (cf. Satô 1935), that is, Müller overlooked one hundred short chromosomes. Again the haploid number of Hosta has been stated from the time of Strasburger until quite recently to be 24 instead of 30 (cf. Whitaker 1934, Satô 1935b, Ake-mine 1935, Yasui 1935, Matsuura and Suto 1935).

McKelvey and Sax (1933) have called attention to the existence of taxonomic and cytological similarities of the genera Yucca,
Hesperoyucca, Cleistyucca, Hesperoaloe and Samuela of the Liliaceae with the genera Agave and Fourcroya which belonged to a related family, Amaryllidaceae. Whitaker (1934) also reported that Polianthes and Fourcroya have exactly the same chromosome constitution as the Yucca-Agave karyotype (5 long and 25 short chromosomes). These observations when considered together with taxonomic resemblances, seem to indicate that the genera mentioned above are more closely related than it is shown by their classification into distinct families. Whitaker also remarked that Dasylirion (2n = 38) and Nolina (2n = 36) in the Yuccae and Doryanthes (2n = 36) in the Agavoideae possess karyotypes different from those of the Yucca-Agave type (cf. Satô 1935a p. 272).

The object of the present work is to analyze the karyotypes in the Amaryllidaceae from the standpoint of the karyotype alteration as in Lycoris (cf. Takenaka 1930, Inariyama 1931, 1932, 1933, 1937), Leucojum (cf. Satô 1937b) and Scilla (cf. Satô 1935a, 1936) and then to compare the various karyotypes in the Amaryllidaceae with the purpose of discovering a possible link between these genera and the Yucca-Agave karyotype.

Material and Methods

Almost all the materials used were obtained from pot plants, most of which were raised from the seeds imported by the Koisikawa Botanic Garden of the Tokyo Imperial University. For the species names the label names on the seed bag imported were adopted in most cases. The root-tips were fixed with Navashin’s solution, sometimes with Flemming’s fluid; the materials were embedded in paraffin, cut at a thickness of from fifteen to twenty micra, and stained after Newton’s gentian violet method.

Observations

The application of the hypothesis of SAT-chromosomes to the karyotype analysis was proposed by the present writer (Satô 1936b) and brought forth many favourable results in this investigation which revised the results which had reported absence, or more properly speaking which had overlooked the SAT-chromosomes, though the hypothesis itself may have been needful of modification by many recent workers in this line.

The varying observations on satellites in the literature were chiefly attributable to the difficulty of detecting the satellite in the Amaryllidaceae, for some satellites have a small amount of chromatin material and others have a short strand which connects the satellite
to mother chromosomes. The nucleoli in the telophase stage were counted carefully and then the SAT-chromosomes were observed in various stages with the expectation of finding the corresponding number. In the case of small satellites, the SAT-chromosome may be concluded by association with the persistent nucleolus in the prophase, for this expectation was found possible of fulfillment in the favourable cases of observation.

In the description of karyotypes the letters \( L, M \) and \( S \) signify respectively long, medium and short chromosomes and \( V, j \) and \( i \) are abbreviations respectively for V-shaped, bent and rod-shaped chromosomes. To distinguish the SAT-chromosomes from other chromosomes the suffix \( s \) or \( t \) is added on the shoulder of such the above-mentioned abbreviations, and then the former means the SAT-chromosome with a secondary constriction and the latter the SAT-chromosome with a trabant.

**Subfamily Amaryllidoideae**

*Amaryllideae-Haemanthinae*

1) *Haemanthus albiflos* \( 2n=16\ (2b)^{31}=2L^t+4M^t+4M+6S \) (Fig. 1)
2) *H. albiflos* var. *pubescens* \( 2n=16\ (2b)=2L^t+4M^t+4M+6S \) (Fig. 2)
3) *H. coccineus* \( 2n=16\ (2b)=2L^t+2M^t+6M+2S^t+4S \) (Fig. 3)
4) *H. Prince Albert* \( 2n=18\ (2b)=2L^t+2M^t+4M+10S \) (Fig. 4)

All these plants except the last species have 16 chromosomes, namely 2 long chromosomes with submedian constrictions, 8 medium chromosomes with subterminal ones and 6 short chromosomes each pair of which has median, submedian and subterminal constrictions respectively. The short arm of the long chromosome in *H. coccineus* is shorter than that in *H. albiflos* and *H. albiflos* var. *pubescens*, and one pair of short chromosomes with submedian constrictions in *H. albiflos* is comparatively longer than those of *H. albiflos* var. *pubescens* and *H. coccineus*, although the chromosome complement of the former is as a whole shorter than that of the latter two.

In *H. albiflorus* two pairs of medium chromosomes have satellites at their distal arms and one pair of long chromosomes also has satellites at its longer arms. In *H. albiflos* var. *pubescens* one pair of long chromosomes has satellites at its shorter arms and two pairs of medium chromosomes have satellites at their distal arms. In *H. coccineus* one pair of medium chromosomes has satellites at its proximal arms and one pair of short chromosomes with an extremely subterminal constriction also clearly shows comparatively large

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1) Throughout the present paper \( 16\ (2b) \) means that the number 16 is twice \( b \), the basic number of the group (cf. Sinotô 1929).
satellites at its proximal arms and one pair of long chromosomes also seems to have satellites at its shorter arms.

H. Prince Albert has 18 chromosomes, namely 2 long chromosomes with submedian constrictions, 6 medium chromosomes with subterminal ones and 10 short chromosomes three of which have subterminal constrictions and the remaining two pairs of which have submedian or median ones respectively. One pair of long chromosomes has satellites at its longer arms and one pair of medium

chromosomes has also satellites at its proximal arms. This karyotype may be derived from the other species such as *H. albiflos* (b = 8) either by fragmentation of medium chromosomes with satellites or by duplication of short chromosomes accompanying the same karyotypical changes mentioned above.

Such varying SAT-chromosomes in *Haemanthus* may be explained by the translocation of the satellite as in *Scilla* (cf. Satô 1936a,b), *Aloe* (cf. Satô 1937a), *Tricyrtis* (cf. Satô 1937d) and *Paeonia* (cf. Sinotô 1937, 1938), etc.

These karyotypes are very uncommon in Amaryllidoideae and seem to denote the absence of a karyotypical phylogenetic connection in this subfamily. These karyotypes resemble those of *Scilla* in the Liliaceae especially *Scilla peruviana* 2n = 16 = 2L + 8M + 2S' + 4S (cf. Satô 1935c) and *Alstroemeria* in Hypoxidioideae. The morphology of SAT-chromosomes may suggest a more intimate relation between *Haemanthus* and *Alstroemeria*.

Many species of this genus were already reported to have 16 somatic chromosomes by various previous workers (cf. Müller 1912; Heitz 1926; Woycicki 1927; Inariyama 1937), while Stenar (1925) reported an insufficient number of n = ca. 12 in *H. Katharinae*. Woycicki (1928) observed the same species *H. Katharinae* to be n = 9, 2n = 18 besides n = 8 and Inariyama (1937) reported also 2n = 18 in *H. Prince Albert* and explained this simply by a duplication of the short chromosomes, for he could not compare these karyotypes with each other in detail.

5) *Griffinia Blumenavia* 2n=77 (7b) (Fig. 6)

This plant has 77 chromosomes and seems to be heptaploid. This karyotype is clearly distinguished from the *Haemanthus* type and resembles those of *Clivia, Eucharis, Hymenocallis, Sprekelia* and *Hippeastrum*. SAT-chromosomes could not be observed on account of the large number of chromosomes.

Sometimes the somatic doubling of chromosomes was observed in the dermatogen cells indicating a large number of chromosomes such as 143 (Fig. 6b), etc. In the flatt dermatogen cell the nucleus divides into two daughter nuclei by mitosis in the direction of the short axis, so a cell-membrane can rarely be formed between two daughter nuclei on account of their extreme approximation. In the course of such a process the somatic doubling of chromosomes may occur and then chromosomal chimera may be formed by the successive divisions of such tetraploid cells. Such inference of somatic doubling was made by Miduno (1938) in *Cepharanthera* and *Epipactis*.

6) *Clivia nobilis* 2n=44 (4b)=24L+4L'+16S (Fig. 5)
This species has 14 chromosomes and seems to be tetraploid or tetrabasic plant. Inariyama (1937) reported 22 chromosomes in both *Clivia miniata* and *C. nobilis*. 16 short chromosomes have median or submedian constrictions and the remaining long chromosomes subterminal ones. The chromosome sizes indicate so gradual a variation that there is no remarkable distinction between long and short chromosomes, unless the position of constriction is taken into account. The karyotype is distinctly different from that of *Haemanthus*, but is similar to those of the other genera of the Amaryllidoideae, especially *Hippeastrum*, *Hymenocallis* and *Sprekelia*. The SAT-chromosomes can not be easily observed, on account of the small size of the satellite and the large number of chromosomes. At any rate, we are convinced of the presence of four SAT-chromosomes in this species which has four nucleoli in the telophase nucleus. This SAT-chromosome with a subterminal constriction has a small satellite at the distal arm. In this point, the karyotype is particularly similar to that of *Hippeastrum*.

The chromosome number of *Clivia miniata* has been reported by van Camp (1924) to be 18 in haploid number, but this report is suspected after the present analysis of the karyotype which is in agreement with the results of Thornton (1930) and Inariyama (1937).

**Amaryllideae-Galanthinae**

7) *Galanthus nivalis* 2n=24 (2b) = 4L+12M+2M′+6S (Figs. 8, 9)
8) *G. nivalis* 2n=25 (2b+1) = 4L+13M+2M′+6S
9) *G. Elwesii* 2n=24 (2b) = 4L+12M+2M′+6S (Fig. 10)
10) *G. Elwesii* 2n=48 (4b) = 8L+24M+4M′+12S (Fig. 11)

Generally speaking the chromosome complement of *Galanthus* (2n = 24) may be divided into the following three classes, namely two pairs of long chromosomes with median constrictions (L chromosomes), seven pairs of medium chromosomes with submedian (or subterminal) constrictions (M chromosomes) and three remaining pairs of short chromosomes with median constrictions (S chromosomes). One pair of medium chromosomes with extremely subterminal constriction (M′ chromosomes) has a satellite at the proximal end of the chromosomes. Single-flowered and double-flowered races of *G. nivalis* from the Tōkyō-Nōsan-Syōkai Nursery have the typical chromosome complement (2n = 24 = 4L + 14M + 6S), while the same species from the Koisikawa Botanic Garden had 28 chromosomes (Fig. 7). One exceptional individual (2n = 25) belonging to the double-flowered race suggests the duplication of one medium chromosome. Some individuals of *G. Elwesii* are diploid (2n = 24) and the others tetraploid (2n = 48), having the typical karyotypes.
In this species two, three and four heteromorphic SAT-chromosomes have been observed suggesting the elimination of the satellite in the case of SAT-chromosomes (cf. Sato 1937b).

The karyotype of *Galanthus* may be explained by the duplication of long chromosomes in *Leucojum* type \((b = 11)\), though in spite of this it differs from the latter in having short chromosomes with submedian constrictions.

Heitz (1926) reported in three species of this genus and Perry (1932) in *G. nivalis* that the somatic chromosomes were 24 in number and also the haploid chromosome number of *Galanthus nivalis* was reported by Stenar (1925) to be 12 and by Transkowsky (1930) to be ten. These results except the last one are in accordance with the observation of the present case.

![Karyotypes in Galanthinae](image)

This karyotype is different not only from those of other *Galanthus* species but also from those of *Haemanthus* and *Clivia* mentioned above. Most chromosomes have median and submedian
constrictions and several shorter chromosomes have subterminal constrictions. Four satellited chromosomes exist in this complement. These SAT-chromosomes with subterminal constrictions have satellites at their proximal arms. This species has 28 chromosomes, while the basic number seems to be 14 and if the latter was 7, this plant would be tetraploid. This karyotype can not be so easily explained by the fusion or fragmentation of chromosomes as in the case of *Leucojum* (cf. Satô 1937b) and *Lycoris* (cf. Inariyama 1933, 1937) and also does not indicate the intimate relation to that of *Leucojum autumnale* \( (2n = 14) \).

11) *Leucojum vernum* \( 2n = 22 \) \( = 2L + 10M + 2M^t + 8S \)
12) *L. vernum* var. *carrathicum* \( 2n = 22 \) \( = 2L + 10M + 2M^t + 8S \) \( \text{(Fig. 14)} \)
13) *L. aestivum* \( 2n = 22 \) \( = 2L + 10M + 2M^t + 8S \) \( \text{(Fig. 12)} \)

These *Leucojum* species have 22 chromosomes in their somatic number and one pair of V-shaped chromosomes with median constrictions (L) is distinguished from the remaining ten pairs of rod-shaped chromosomes with subterminal constrictions. These ten pairs of chromosomes are divided into the following four classes: One pair of j (medium) chromosomes, one pair of \( M^t \) chromosomes with satellite, four pairs each of both i (medium) and S (short) chromosomes. This chromosome complement differs from those of *Clivia*, *Amaryllis*, *Nerine* and *Crinum* in that the chromosomes have extremely subterminal constrictions.

The same count of chromosomes has been given by Inariyama (1937) while the observations of Nagao and Takusagawa (1932) and Heitz (1926) seem to be insufficient on this genus and Overton's (1893) report that *Leucojum vernum* has \( n = 12, 2n = 24 \), seems to show a miscounting of the chromosomes.

14) *Leucojum autumnale* \( 2n = 14 \) \( = 2L^t + 8L + 2M^t + 2M \) \( \text{(Fig. 13)} \)

This plant has 14 chromosomes, namely five pairs of V-shaped chromosomes and one pair each of j and \( M^t \) chromosomes. Among the five pairs of V-shaped chromosomes one pair with median constrictions is homologous to the V-shaped chromosomes of other *Leucojum* species and the remaining four pairs of chromosomes have submedian constrictions. This karyotype is different from that of the other *Leucojum* species, but we take into consideration the morphological resemblances of these species and then the karyotype alterations such as fusion or translocation of chromosome (cf. Take-naka 1930 and Inariyama 1933 in *Lycoris*, Satô 1936 in *Scilla*), so that the four pairs of V-shaped chromosomes with submedian constrictions (the L chromosomes) may be derived from the result of fusion or translocation of the i- and S-chromosomes.
On close observation, four SAT-chromosomes were found, conforming to the four corresponding nucleoli of the telophase nucleus. One pair of newly discovered SAT-chromosomes is V-shaped with submedian constrictions and has a small satellite at its distal arms (cf. Satô 1937b).

The same chromosome number had been reported by Heitz (1926) in this species.

**Amaryllideae-Amaryllidinae**

15) *Nerine curviflora* 2n=22 (2b)=2L+10M+2M*+8S (Fig. 16)
16) *N. undulata* 2n=22 (2b)=2L+10M+2M*+8S (Fig. 15)
17) *N. humilis* 2n=33 (3b)=3L+15M+3M*+12S (Fig. 17)
18) *N. flexuosa* 2n=33 (3b)=3L+15M+3M*+12S (Fig. 20)
19) *N. sarniensis* 2n=33 (3b)=3L+15M+3M*+12S (Fig. 18)
20) *N. pudica* 2n=33 (3b)=3L+15M+3M*+12S (Fig. 19)

Nerine curviflora and N. undulata are diploid and have 22 chromosomes, namely one pair of long chromosomes with submedian constrictions, six pairs of medium chromosomes with submedian or subterminal constrictions, and four pairs of short chromosomes with median or submedian constrictions. One pair of medium chromosomes in N. curviflora has secondary constrictions at its proximal arms, while we can not observe such secondary constrictions in N. undulata which however seems to have a constricted point at the distal arm of one pair of medium chromosomes. The karyotype of N. undulata is generally speaking shorter than that of the other Nerine species and has many medium chromosomes with extremely subterminal constrictions.

Nerine humilis, N. flexuosa, N. sarniensis and N. pudica have 33 chromosomes and are triploids and further seem to be autotriploids, for the karyotype is entirely similar to that of N. curviflora with characteristic SAT-chromosomes.

The present finding confirms and supplements the previous observations made by Müller (1912), Heitz (1926) and Inariyama (1937). The last author gave the number as 2n = 33 in N. curviflora, but the karyotypical difference was not fully investigated and my observation mentioned above may show his mislabelling of the species name, for his material and mine were both obtained from the Koiskawa Botanic Garden.

21) Amaryllis Belladonna 2n=22(2b)=2L+10M+2Ms+8S (Fig. 21)
This karyotype resembles entirely that of Nerine curviflora. This count of chromosomes accords with that of Inariyama (1932, 1937), but differs from that of Fernandes (1930) who reported it to be 2n = 20 in this species.

22) Amaryllis alba 2n=39 (Fig. 23)
This plant seems to be hybrid and the phylogeny of this karyotype can not clearly be explained in the present paper, but this has 12 V-shaped long chromosomes and about 10 short chromosomes with subterminal constrictions and then seems to have three sets of the Zephyranthes type (b=6), the remaining chromosomes belonging to the Amaryllis type (2n = 39 = 6 × 3 + 21).

23) Amaryllis striatiflora (Zephyranthes?) 2n=12(2b)=8L+4M (Fig. 22)
This plant has 12 chromosomes, namely four pairs of V-shaped chromosomes with median constrictions and two pairs of bent chromosomes with submedian constrictions. This karyotype is similar to that of Zephyranthes and this species name must belong to Zephyranthes.
Amaryllideae-Zephyranthinae

24) Zephyranthes robusta 2n=12 (2b) = 8L+4M (Fig. 25)
25) Z. Tauberti 2n=12 (2b) = 8L+4M (Fig. 24)
26) Z. texana 2n=24 (4b) = 16L+8M (Fig. 27)
27) Z. Lindleyana 2n=24 (4b) = 16L+8M (Fig. 26)
28) Z. candida 2n=38 (6b+2) (Fig. 28)

Zephyranthes robusta and Z. Tauberti are diploids and have 12 chromosomes i.e., four pairs of V-shaped chromosomes with median constrictions and two pairs of chromosomes with submedian ones. Z. texana and Z. Lindleyana are tetraploids and probably autotetraploid plants and have 24 chromosomes indicating a similar karyotype to that mentioned above.

These plants indicate that the basic number of Zephyranthes is 6 which connects with the 11 in Lycoris found by Inariyama (1932). In Zephyranthes there are no plants which have a basic number of 11, but this karyotype (b = 6) may be either derived from those karyotypes (b = 11) by a karyotype alteration such as fusion or translocation of chromosomes as in Lycoris (b = 6, 11) and Leucojum (b = 7, 11) or be derived from the Leucojum type (b = 7) by a karyotype alteration such as elimination of one pair of chromosomes.

Z. candida has 38 chromosomes and seems to have 2 extra chromosomes in addition to hexaploid complements of this set.

In Z. Tauberti the karyotype was traced in detail, with the expectation of finding two SAT-chromosomes corresponding to the two nucleoli of the telophase, but in the present observation the SAT-chromosomes could not be determined, though many secondary constrictions have been found at the middle point of one arm or distal end of the V-shaped chromosomes.

These observations confirm the results of Pace (1913) in *Z. texana* (n = 12) and Inariyama (1937) in *Z. candida* (2n = 38) and *Z. carinata* (2n = 48), but differ from that of Yamamoto (1930) in *Z. candida* where he found 36 somatic chromosomes.

29) *Sternbergia lutea* 2n=22(2b)=4L+2S'+16S (Fig. 29)

This species has 22 chromosomes, namely two pairs of long chromosomes and nine pairs of short chromosomes with subterminal constrictions, of which one pair has satellite at its proximal arms. One pair of long chromosomes has median constrictions and another pair of long chromosomes has submedian constrictions.

Previous workers reported various chromosome numbers in this species. Yamamoto (1930) found that this species has 12 chromosomes. Nakajima (1936) also found 16 (2n) in the root-tips. The present finding is not in accordance with those of the cases mentioned above, but accords with that of Inariyama (1937).

**Amaryllideae-Crininae**

30) *Crinum lineare* 2n=22(2b)=2L+10M+2M*+8S
31) *C. lineare* var. *album* 2n=22(2b)=2L+10M+2M*+8S (Fig. 36)
32) *C. Moorei* 2n=22(2b)=2L+10M+2M*+8S (Fig. 30)
33) *C. Moorei* var. *album* 2n=22(2b)=2L+10M+2M*+8S (Fig. 31)
34) *C. latifolium* 2n=22(2b)=2L+10M+2M*+8S (Fig. 32)
35) *C. capense* 2n=22+2ff (2b+2ff)=2L+10M+2M*+8S+2ff (Fig. 33)
36) *C. gigas* 2n=22(2b)=2L+10M+2M*+8S (Fig. 34)
37) *C. asiaticum* var. *japonicum* 2n=22(2b)=2L+10M+2M*+8S
38) *C. Rattrayii* 2n=22(2b)=2L+10M+2M*+8S (Fig. 35)
39) *C. macrantherum* 2n=33(3b)=3L+15M+3M*+12S (Fig. 37)

The chromosome number of *Crinum* is 22 in most species studied, except *C. macrantherum*, and the karyotype is similar to those of *Nerine* and *Amaryllis*. One pair of long chromosomes with submedian constrictions, six pairs of medium chromosomes with submedian or subterminal constrictions constitute this karyotype which differs from those of *Nerine* and *Amaryllis* in having characteristic SAT-chromosomes. The SAT-chromosome in *Crinum* has the secondary constriction at its proximal arm. In any case, the karyotype of *Crinum* is similar to those of *Nerine* and *Amaryllis*.

In *Crinum capense* two fragments were found in addition to the ordinary chromosome complement. *C. macrantherum* has 33 chromosomes and seems to be autotriploid.

This count of chromosomes is in agreement with the results reported by Inariyama (1932, 1937), Nagao and Takusagawa (1932),
Matsuura and Sutô (1935) and Suita (1937), but is not in accordance with those of Stenar (1925) who reported \( n = \text{ca. 12} \) in *C. latifolium*. Sugiura's (1936) observation was also erroneous due to a counting of the SAT-chromosome as two chromosomes.

40) *Cyrtanthus obliquus* \( 2n=22 (2b)=2L+8M+4M'+8S \) (Fig. 38)

This species has 22 chromosomes, namely one pair of long chromosomes with submedian constrictions and six pairs of medium chromosomes with subterminal constrictions and four pairs of short chromosomes of which one pair has median constrictions and remaining three pairs have subterminal ones. Two pairs of medium chromosomes have satellites at their proximal arms and the one pair has a larger satellite than the other. Another pair of medium chromosomes has clearly defined secondary constrictions at its long arms near the spindle fibre attachment. This karyotype differs from those of *Nerine* and *Crinum* in regard to the absence of SAT-chromosomes with secondary constrictions and short chromosomes with median constrictions, except for one pair. Presence of short chromosomes with median constrictions make for a clear distinction between this karyotype and the *Leucojum* type.

Taylor (1924) reported \( n = \text{ca. 16} \) in *Cyrtanthus parviflorus*, but this number is doubtful and contradicts the present findings.

**Narcisseae-Eucharidinae**

41) *Eucharis grandiflora* \( 2n=68 (6b+2)=6L+26M+36S \) (Fig. 41)

This species has 68 chromosomes, namely 6 long chromosomes with submedian constrictions, 26 medium chromosomes with subterminal constrictions and 36 short chromosomes with median ones, and may be derived from the duplication of 2 medium chromosomes in hexaploid with the most familiar karyotype \( (b=11) \). The SAT-chromosome can not easily be observed on account of the largeness of the chromosome number and one medium chromosome with satellite at the proximal arm was illustrated in Fig. 41, which was the best of the SAT-chromosome in this subfamily.

Svensson-Stenar (1925) reported that *Eucharis Amazonica* had ca. 45 in haploid number.

42) *Hymenocallis littoralis* \( 2n=46 (2b) \) (Fig. 39)

43) *H. lacera* \( 2n=69 (3b) \) (Fig. 40)

The karyotype of *Hymenocallis* is similar to that of *Crinum*, though the chromosome size is much smaller than in the latter and *H. littoralis* has 46 chromosomes of which ca. 14 are short chromosomes with median or submedian constrictions. Two pairs of comparatively long chromosomes with submedian constrictions have
secondary constrictions in their longer arms and seem to be SAT-chromosomes. This SAT-chromosome is different from those of other genera in having a secondary constriction in its longer arm and also from that of *Crinum* in having a submedian constriction. This SAT-chromosome suggests a derivation from the translocation.

or inversion of other typical SAT-chromosomes. At any rate, the presence of a few chromosomes with subterminal constrictions reminds us that this type does not have so intimate relation to either the *Zephyranthes* karyotype \( b = 6 \) or the *Amaryllis* type \( b = 11 \), but seems to have some karyotypical resemblance to *Crinum*, *Clivia*, *Griffinia* and *Sprekelia*. *H. lacera* has 69 chromosomes and seems to be triploid. The presence of a SAT-chromosome with satellite suggests the deficiency or translocation of a characteristic SAT-chromosome with secondary constriction. From the result of the present observation the basic number of *Hymenocallis* is concluded to be 23 which is derived from \( b = 11 \) by duplication, and secondarily balanced as in *Campanula* \( (n = 8, 16, 17, 34, 51) \), cf. Gaiser 1930, 1933), *Dahlia* \( (n = 8, 18) \), cf. Lawrence 1929), *Pyrus* \( (n = 8, 17) \), cf. Darlington and Moffett 1930, Moffett 1931) and *Scilla* \( (n = 8, 9, 17 \) etc., cf. Satō 1935c).

Nagao and Takusagawa (1932) reported that the same species (*H. rotata* = *H. lacera*) has 40 chromosomes in haploid number, but in view of the present karyotype analysis the writer is led to believe that they were mistaken in counting univalents as bivalents in meiosis which is a common event in the case of a triploid.

**Narcisseae-Narcissinae**

44) *Narcissus Jonquilla* \( 2n = 14(2b) = 10L + 2M + 2Mt \) (Fig. 43)
45) *N. Pseudonarcissus* \( 2n = 14(2b) = 11L + 1M + 2Mt \) (Fig. 44)
46) *N. incomparabilis auratus* \( 2n = 14(2b) = 12L + 2Mt \) (Fig. 42)
47) *N. poeticus* \( 2n = 21(3b) = 18L + 3Mt \) (Fig. 45)

The basic number of chromosomes in these species is 7 as already reported by de Mol (1922, 1926, 1928), Nagao (1929, 1933) and Fernandes (1931a, b, 1934). The karyotypes of these species are very similar to each other and to understand these karyotypes, the following explanation may be made in the case of *N. Jonquilla*.

\( L_1, L_2 \) Two pairs of long chromosomes with subterminal constriction which correspond to \( L_p \) of Fernandes. The long arms of these chromosomes, especially L's have secondary constrictions near the spindle fibre attachment. \( L_3 \) One pair of long chromosomes with subterminal constrictions, corresponding to \( L_m \) of Fernandes, of which the long arms are smaller than \( L_1 \) and \( L_2 \). \( L_4 \) One pair of long chromosomes with submedian constrictions which corresponds to \( l_1 \) of Fernandes. \( L_5 \) One pair of long chromosomes with subterminal constriction which can be distinguished only with difficulty from \( L_1 \) and \( L_2 \) and which corresponds to \( l_p \) of Fernandes.
M₁ One pair of medium chromosomes with subterminal constrictions which corresponds to Pᵥ of Fernandes. M₂ One pair of medium chromosomes with subterminal constrictions having satellite at the proximal arms. This corresponds to Pᵥ⁺ of Fernandes.

*N. Jonquilla* has 14 chromosomes, namely 10 long and 4 short chromosomes and its karyotype is formulated as follows, 2n = 14 = 2L₁ + 2L₂ + 2L₃ + 2L₄ + 2L₅ + 2M₁ + 2M₂ or according to Fernandes 2n = 14 = 2Lₚ₁ + 2Lₚ₂ + 2Lₘ + 2l₁ + 2l₂ + 2Pᵥ + 2Pᵥ⁺

*N. Pseudonarcissus* has also 14 chromosomes, namely 11 long and 3 short chromosomes. This observation accords with that of Fernandes but contradicts that of de Mol and Nagao which showed 10 long and 4 short chromosomes. The chromosome morphology is, generally speaking, similar to that of *N. Jonquilla* except for one long chromosome (Lₘ) with submedian constriction which corresponds to lₘ of Fernandes. He could not observe 2 satellited chromosomes but only one in this species, while my observation clearly demonstrates 2 SAT-chromosomes. Accordingly, the karyotype of this species is 2n = 14 = 4Lₚ + 2Lₘ + 2l₁ + 1l₂ + 1Pᵥ + 2Pᵥ⁺


*N. incomparabilis auratus* has 14 chromosomes, being diploid. The morphology of the somatic chromosomes can not be easily distinguished, for they are comparatively long except for one pair of short chromosomes with satellites (Pᵥ⁺). Fernandes demonstrates 11 long and 3 short chromosomes in this species and the heterozygo-
ticity of both chromosome types. The asymmetry of the chromosome complement of this species seems to show a hybrid origin from *N. Pseudonarcissus* and *N. poeticus*. Many taxonomists (Fiori and Pasletti, Rouy, etc.) have considered this question and already advanced this opinion.

*N. poeticus* has 21 chromosomes, namely 18 long chromosomes and 3 short satellite ones. In this species 3 SAT-chromosomes can be easily observed, though one SAT-chromosome has an extremely small satellite, while other type of short chromosomes (M₁) without satellite can not be observed.

48) *N. tazetta* var. *papyraceus* 2n=22(2b+2) = 8L + 2M + 4M₁ + 8S (Fig. 46)

49) *N. tazetta* var. *suisen* 2n=32(3b+2) = 13L + 5M + 4M₁ + 10S (Fig. 47)

*N. tazetta* var. *papyraceus* has 22 chromosomes, namely four pairs of long, three pairs of medium and four pairs of short chromosomes and these have subterminal constrictions except for one pair of short chromosomes with median constrictions. Among the three pairs of medium chromosomes, one pair is comparatively longer than the rest (M₁ or P₁ of Fernandes). The remaining two pairs of medium chromosomes (M₂) have satellites at their proximal arms.

*N. tazetta* var. *suisen* has 32 chromosomes, namely 13 long, 9 medium and 10 short chromosomes. Among 9 medium chromosomes with subterminal constrictions, 3 (M₁) are comparatively longer than the rest and 4 (M₂) have satellite at their proximal arms while the remaining 2 have no satellite. The chromosome complement suggests that this species consists of two sets of an 11-basic plant such as *N. tazetta* var. *papyraceus* (8L + 6M + 8S) and one set of a 10-basic plant (5L + 3M + 2S).

**Narcisseae-Pancratinae**

50) *Pancratium ilyricum* 2n=44(4b)=20L+4M+20S (Fig. 48)

This plant is tetraploid and has 44 chromosomes, namely 20 long chromosomes with median constrictions, 4 medium chromosomes with submedian ones and 20 short chromosomes with subterminal ones. This karyotype is characterized by the existence of many long chromosomes with median constrictions.

The chromosome numbers in this genus have been reported to be 2n = 90–100, ca. 90 by Heitz (1926) and ca. 45, 40–45 and 2n = 18 or 20 by Fernandes (1930) and 2n = 46 by Inariyama (1937) in the other species. These count are not in agreement with the present observation.
51) *Sprekelia formosissimum* 2n=110–117 (Fig. 49)

This karyotype resembles that of *Hymenocallis* and many metaphase plates counted showed more than 100 chromosomes, for example 117 chromosomes are illustrated in Fig. 49. The karyotype is not clear as regards its origin. Inariyama (1937) stated that this species has ca. 110 chromosomes in its somatic number, but the writer doubts this number, in view of the case of *Eucharis* and *Hymenocallis*.

52) *Hippeastrum vittatum* 2n=44(4b)=24L+4L'+16S (Fig. 50)

53) *H. rutilum* 2n=44(4b)=24L+4L'+2S'+14S (Fig. 51)

Generally speaking this karyotype resembles those of *Clivia*, *Nerine* and *Crinum*, and has 44 chromosomes of which 16 short chromosomes have median or submedian constrictions and the remaining 28 long chromosomes have subterminal ones.

The SAT-chromosome of the former species is similar to those of *Clivia* in which were found 4 SAT-chromosomes and 4 nucleoli corresponding. Suita (unpublished) distinctly observed 2 satellites and 2 nucleoli in the primary division of pollen grain in this species, thus supporting the present result. The latter species has 6 nucleoli.
in the telophase and 6 SAT-chromosomes corresponding to them, namely 2 short chromosomes with satellite besides one set of 4 SAT-chromosomes. Consequently, *H. rutilum* may be allotetraploid judging from the presence of such SAT-chromosomes.

*Hippeastrum vittatum* has been reported by Nagao and Takusagawa (1932) to have 2n = 46 chromosomes and Inariyama (1937) to have 2n = 44. Heitz (1926) had already reported that the haploid chromosome number of *H. rutilum* was 22–24.

54) *Habranthus Andersoni* 2n=21(2b−1)=2L+9M+3Mt+7S (Fig. 52)

This species has 21 chromosomes, namely 2 long chromosomes with submedian constrictions, 12 medium chromosomes with subterminal constrictions and 7 short chromosomes with subterminal constrictions but one which has a median constrictions. This karyotype suggests the elimination of one short chromosome with a median constriction, and is similar to those of *Nerine*, *Crinum* and *Cyrtanthus*. The SAT-chromosome of this species has a satellite at its proximal arm, while the secondary constrictions of SAT-chromosomes exist at the proximal arm in *Nerine* and at the distal arm in *Crinum*. On close observation, three SAT-chromosomes were found two (one pair) of which has large satellites, while the remaining one has a small satellite at both of its proximal arms. The latter SAT-chromosome and another medium chromosome have each no homologues. The latter is longer than the former SAT-chromosome and may be derived from the fusion or translocation between this SAT-chromosome and small chromosome with median constriction.

This karyotype is entirely similar to that of *Cyrtanthus*, when the karyotype alteration mentioned above is taken into consideration. This conclusion may be supported by the presence of one pair of medium chromosomes with secondary constriction.

55) *Lycoris squamigera* 2n=27=6V+21i (Fig. 53)

This species has 27 chromosomes, namely 6 V-shaped chromosomes with median constrictions and 21 rod-shaped chromosomes with subterminal constrictions. If these V-shaped chromosomes were counted as two rod-shaped chromosomes, this species would have 33 rod-shaped chromosomes. These observations were already made by Takenaka (1930) in this species and by Inariyama (1932, 1934, 1937) even in other species (*L. sanguinea* 2n = 22 = 22i, *L. aurea* 2n = 12 = 10V + 2i, 2n = 13 = 9V + 4i, 2n = 14 = 8V + 6i, *L. straminnea* 2n = 16 = 6V + 10i, *L. albilflora* 2n = 17 = 5V + 12i, *L. radiata* 2n = 33 = 33i). Three SAT-chromosomes with extremely subterminal or terminal constrictions have satellites at their proximal
arms. Nishiyama’s report (Nishiyama 1928) that *L. squamigera* has 33 chromosomes in its somatic number is apparently erroneous.

### Table 1. Comparison of the karyotypes in subfamily Amaryllidoideae

<table>
<thead>
<tr>
<th>Species</th>
<th>Karyotypes (2n)</th>
<th>Basis</th>
<th>Nucleoli</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Haemanthus albiflos</em></td>
<td>16 = 2L+4M+4M+6S (2b)</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>H. albiflos var. rubescens</em></td>
<td>16 = 2L+4M+4M+6S (2b)</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>H. coccineus</em></td>
<td>16 = 2L+2M+6M+2S+4S (2b)</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>H. Prince Albert</em></td>
<td>16 = 2L+2M+4M+6S (2b)</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>Griffonia Blumenavia</em></td>
<td>77 (6b)</td>
<td>11</td>
<td>—</td>
</tr>
<tr>
<td><em>Clivia nobilis</em></td>
<td>44 = 2L+4L+16S (4b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>Galanthus nivalis</em></td>
<td>28</td>
<td>7?</td>
<td>4</td>
</tr>
<tr>
<td><em>G. nivalis</em></td>
<td>24 = 4L+12M+2M+6S (2b)</td>
<td>12</td>
<td>2</td>
</tr>
<tr>
<td><em>G. nervosus</em></td>
<td>25 = 4L+13M+2M+6S (2b+1)</td>
<td>12*</td>
<td>2</td>
</tr>
<tr>
<td><em>G. Elwesii</em></td>
<td>24 = 4L+12M+2M+6S (2b)</td>
<td>12</td>
<td>2</td>
</tr>
<tr>
<td><em>G. Elwesi</em></td>
<td>45 = 8L+24M+4M+12S (4b)</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td><em>Lecocotomum autumnale</em></td>
<td>14 = 2L+8L+2M+2M (2b)</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td><em>L. vernalis</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>L. vernalis var. carraticum</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>L. aestivum</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>Nerine curviflora</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>N. undulata</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>N. humilis</em></td>
<td>33 = 3L+15M+3M+12S (3b)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>N. fleurets</em></td>
<td>33 = 3L+15M+3M+12S (3b)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>N. sarniensis</em></td>
<td>33 = 3L+15M+3M+12S (3b)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>N. pulchra</em></td>
<td>33 = 3L+15M+3M+12S (3b)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>Amaryllis Belladonna</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>A. alba</em></td>
<td>39</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. striatiflora</em> (Zephyranthes?)</td>
<td>12 = 8L+4M (2b)</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td><em>Zephyranthes robusta</em></td>
<td>12 = 8L+4M (2b)</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td><em>Z. Taverti</em></td>
<td>12 = 8L+4M (2b)</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td><em>Z. texana</em></td>
<td>24 = 16L+8M (4b)</td>
<td>6</td>
<td>—</td>
</tr>
<tr>
<td><em>Z. Lindleyana</em></td>
<td>24 = 16L+8M (4b)</td>
<td>6</td>
<td>—</td>
</tr>
<tr>
<td><em>Z. candida</em></td>
<td>38 (6b+2)</td>
<td>6*</td>
<td>—</td>
</tr>
<tr>
<td><em>Sternbergia lutea</em></td>
<td>22 = 4L+2S+16S (2b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>Crinum lineare</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. lineare var. album</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. Moorei</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. Moorei var. album</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. latifolium</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. capense</em></td>
<td>22 = 2L+10M+2M+8S+2F (2b+2F)</td>
<td>11*</td>
<td>2</td>
</tr>
<tr>
<td><em>C. gigas</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. Rattrayii</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. asiaticum var. japonicum</em></td>
<td>22 = 2L+10M+2M+8S (2b)</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><em>C. macrantherum</em></td>
<td>33 = 3L+15M+3M+12S (3b)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>C. Pandanus obliquus</em></td>
<td>22 = 8L+8M+4M+12S (2b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>Eucharis grandiflora</em></td>
<td>68 = 6L+26M+36S (6b+2)</td>
<td>11*</td>
<td>—</td>
</tr>
<tr>
<td><em>Hymenocallis littoralis</em></td>
<td>46 (2b)</td>
<td>23</td>
<td>4</td>
</tr>
<tr>
<td><em>H. lacera</em></td>
<td>69 (3b)</td>
<td>23</td>
<td>6</td>
</tr>
<tr>
<td><em>Narcissus Jonquilla</em></td>
<td>14 = 10L+2M+2M+2M (2b)</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td><em>N. Pseudonarcissus</em></td>
<td>14 = 11L+1M+2M (2b)</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td><em>N. incompatibilis auratus</em></td>
<td>14 = 12L+2M (2b)</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td><em>N. poeticus</em></td>
<td>21 = 18L+3M (3b)</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td><em>N. tazetta var. papyraceus</em></td>
<td>22 = 8L+2M+4M+8S (2b+2)</td>
<td>10*</td>
<td>4</td>
</tr>
<tr>
<td><em>N. tazetta var. suisen</em></td>
<td>32 = 13L+5M+4M+10S (3b+2)</td>
<td>10*</td>
<td>4</td>
</tr>
<tr>
<td><em>Pancratium iyiicum</em></td>
<td>44 = 20L+4M+20S (4b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>Sprekelia formosissima</em></td>
<td>ca. 117</td>
<td></td>
<td>—</td>
</tr>
<tr>
<td><em>Hippeastrum vittatum</em></td>
<td>44 = 2L+4L+16S (4b)</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td><em>H. ruticum</em></td>
<td>44 = 2L+4L+2S+14S (4b)</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td><em>Habranthus Anderson</em></td>
<td>21 = 2L+9M+3M+7S (2b+1)</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td><em>Lycoris squamigera</em></td>
<td>27 = 6V+18I+3I</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>
Subfamily Agavoideae

56) _Brava geminiflora_ 2n=60 (2b)=10L+50S (Fig. 54)

This species first reported in this genus has 60 chromosomes, namely five pairs of long chromosomes with terminal or extremely subterminal constrictions and twenty-five pairs of short chromosomes. This karyotype is of the so-called _Yucca-Agave_ type and described in the other genera by McKelvey and Sax (1933), Whitaker (1934) and Satô (1935).

57) _Polianthes tuberosa flore-pleno_ 2n=60 (2b)=10L+50S (Fig. 56)

This plant has the same karyotype as the other genera _Brava, Agave, Fourcroya_ and _Beschorneria_. Somatic doubling of chromosomes was observed in this species which showed 20 long chromosomes and about 100 short ones.

Whitaker (1934) had already found that _Polianthes tuberosa_ (n=30) had 30 chromosomes in reduced number.

58) _Agave vivipara_ 2n=60 (2b)=10L+50S (Fig. 60)
59) _A. lutea_ var. _heterocentra_ 2n=60 (2b)=10L+50S
60) _A. univittata_ 2n=60 (2b)=10L+50S (Fig. 59)
61) _A. Verschaffelti_ 2n=60 (2b)=10L+50S (Fig. 58)
62) _A. Zapupe_ 2n=90 (3b)=15L+75S (Fig. 61)
63) _A. americana_ 2n=120 (4b)=20L+100S
64) _A. americana_ var. _albo-marginata_ 2n=120 (4b)=20L+100S
   (2n=240 (8b)=40L+200S) (Fig. 62).
65) _A. americana_ var. _variegata_ 2n=120 (4b)=20L+100S
66) _A. sisalana_ 2n=150 (5b)=25L+125S (Fig. 63)
67) _A. atrovirens_ 2n=180 (6b)=30L+150S (Fig. 64)
68) _Agave_ sp. 2n=60 (2b)=10L+50S
69) _Agave_ sp. 2n=120 (4b)=20L+100S

_Agave vivipara, A. lutea_ var. _heterocentra, A. univittata_ and _A. Verschaffelti_ each have 60 chromosomes, and _A. americana, A. americana_ var. _albo-marginata_ and _A. americana_ var. _variegata_ have 120 chromosomes. The former four species are dibasic plants (2b) and the latter are tetrabasic plants (4b). The somatic doubling of chromosomes was observed in _A. americana_ var. _albo-marginata_ and the chromosome numbers counted were 236 = 38L + 198S, 226 = 40L + 186S and so on. These numbers seem to be derived from the original number 240 (8b) = 40L + 200S which may be octoploid.

_A. Zapupe_ has 90 chromosomes, namely 15 long and 75 short chromosomes and seems to be a triploid or tribasic plant (3b) as in _A. candelabrum_ (cf. Doughty 1936, Inariyama 1937).
A. *sisalana* has 25 long chromosomes and more than 100 short chromosomes, for example $147 = 25L + 122S$, $141 = 25L + 116S$ and so on. This species appears to be of the formula $150 = 25L + 125S$ (5b) and to be a pentaploid or pentabasic plants (cf. Inariyama 1937). A. *atrovirens* has 30 long chromosomes and more than 100 short chromosomes, for example $167 = 30L + 137S$. This species appears to be of the formula $180(6b) = 30L + 150S$ and to be a hexabasic plant as in *A. Gilbeyi* (cf. Vignoli 1936) and *A. Ghiesbrechti* (cf. Vignoli 1937). Unknown species which perhaps belong to the genus *Agave* also have the same karyotype as mentioned above.

Müller (1912) reported that *A. americana* had only 20 chromosomes. This calculation was probably made on insufficient observation or more properly speaking he counted only long chromosomes. Based on the present analysis of the karyotype the results of Müller (1912) and Schaffner (1909) that *Agave virginica* is $n = 12$ and $2n = 24$ are suspected and need reinvestigation. The same reference may be admitted in the case of *A. sisalana* which was reported previously $n = 7$, $2n = 14$ by Catalano (1929, 1930). Heitz (1926) also reported that *Agave* had 50 chromosomes instead of 60. The present observation accords with those of McKelvey and Sax (1933), Satô (1935a), Vignoli (1936, 1937), Doughty (1936) and Inariyama (1937).

70) *Fourcroya gigantea* $2n=60 (2b)=10L+50S$ (Fig. 57)

71) *F. pubescens* $2n=60 (2b)=10L+50S$

These plants also have the *Yucca-Agave* karyotype and this result (cf. Satô 1935a) conforms with those of Whitaker (1934) and Inariyama (1937).

72) *Beschorneria tubiflora* $2n=60 (2b)=10L+50S$ (Fig. 55)

This species also belongs to the same group as *Agave*. According to Müller (1912) another species *Beschorneria superva* has ca. 50 somatic chromosomes and this result may be explained as being $2n = 60$. Koerperich (1930) gives $2n = 60$ in *Beschorneria Yuccoides* and this accords with the present observation.

73) *Doryanthes Palmeri* $2n=48 (4b)=4L+44S$ (Fig. 67)

74) *D. Guilfoylei* $2n=48 (4b)=4L+44S$ (Fig. 66)

75) *D. excelsa* $2n=48 (4b)=4L+44S$ (Fig. 65)

*Doryanthes Palmeri* has 48 chromosomes, namely 4 long and 44 short chromosomes. Whitaker (1934) reported the same species as having 36 chromosomes. If we take into consideration the karyotype given here and Whitaker’s result, this species would be autotetraploid and the plant dealt with by Whitaker would be triploid. *Doryanthes Guilfoylei* and *D. excelsa* have also 48 chromosomes, namely 4 long...
and 44 short chromosomes and seem to be allotetraploid judging from the presence of two pairs (L₁ and L₂) of long chromosomes. One arm of the long chromosomes with median constriction may translocate to the small chromosome, so that 2 long chromosomes with subterminal constrictions (L chromosomes of Yucca-Agave type) may result and vice versa. Such karyotype alteration may explain the relation between the Yucca-Agave type and Doryanthes type, although a considerable difference is shown in the chromosome size.

### Table 2. Comparison of the karyotypes in subfamily Agavoideae

<table>
<thead>
<tr>
<th>Species</th>
<th>Karyotypes (2n)</th>
<th>Basis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bravaea gemniflora</td>
<td>60 = 10L+50S (2b)</td>
<td>30</td>
</tr>
<tr>
<td>Polianthes tuberosa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>flore-pleno</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agave vivipara</td>
<td></td>
<td></td>
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<tr>
<td>A. lutea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>var. heterocentra</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. univittata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. Verschaffeltii</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. Zapupe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. americana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. americana var. albo-marginata</td>
<td>120 = 20L+100S (4b)</td>
<td>30</td>
</tr>
<tr>
<td>A. americana var. albo-variegata</td>
<td>120 = 20L+100S (4b)</td>
<td>30</td>
</tr>
<tr>
<td>A. sisalana</td>
<td>150 = 25L+125S (5b)</td>
<td>30</td>
</tr>
<tr>
<td>A. atrovirens</td>
<td>150 = 30L+150S (6b)</td>
<td>30</td>
</tr>
<tr>
<td>Agave spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agave spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foucroya gigantea</td>
<td>60 = 10L+50S (2b)</td>
<td>30</td>
</tr>
<tr>
<td>F. pubescens</td>
<td>60 = 10L+50S (2b)</td>
<td>30</td>
</tr>
<tr>
<td>Beschormeria tubiflora</td>
<td>60 = 10L+50S (2b)</td>
<td>30</td>
</tr>
<tr>
<td>Doryanthes Palmeri</td>
<td>48 = 4L+44S (4b)</td>
<td>12</td>
</tr>
<tr>
<td>D. Guifoyei</td>
<td>48 = 4L+44S (4b)</td>
<td>12</td>
</tr>
<tr>
<td>D. excelsa</td>
<td>48 = 4L+44S (4b)</td>
<td>12</td>
</tr>
</tbody>
</table>

### Subfamily Hypoxidoideae

76) *Alstroemeria chilensis* 2n=16 (2b)=2L+2L₁+4S+8S (Fig. 69)

This species has 16 chromosomes, namely two pairs of long chromosomes with submedian constriction and six pairs of short chromosomes of which four pairs have subterminal constrictions and the remaining two pairs have submedian ones. One pair of long chromosomes has a satellite at the short arm, one pair of short chromosomes has a satellite at the proximal end and another pair of short chromosomes has also a satellite at the distal end.

This karyotype is similar to those of *Haemanthus* in the Amaryllidoideae particularly in so far as the SAT-chromosomes are concerned.

77) *Alstroemeria pulchella* 2n=16 (2b)=2L+2L₁+2S+10S (Fig. 68)

Generally speaking this species has shorter chromosomes, with the exception of the long pair, than those of *A. chilensis* and also has 16 chromosomes, namely one pair of long chromosomes with submedian constriction, one pair of medium chromosomes with subterminal constrictions and six pairs of short chromosomes of which four pairs have almost terminal constrictions, one pair has a subterminal constriction and the remaining one pair has a median one.
One pair of short chromosomes with an extremely subterminal constriction has a satellite at its proximal end. One pair of medium chromosomes has a secondary constriction at its distal arm and seems to be a SAT-chromosomes. This karyotype is in accordance with those described by Whyte (1929) in many other species of this genus. Comparison of karyotypes of *A. chilensis* and *A. pulchella* suggests that the medium chromosome with a secondary constriction in *A. pulchella* may be derived by the inversion of a short arm with a satellite of the long chromosome in *A. chilensis*.

The chromosome number of the genus *Alstroemeria* was reported to be \( n = 8 \), and \( 2n = 16 \) in many other species (cf. Strasburger 1882, 1888; Guignard 1884, 1889, 1891; Taylor 1926; Whyte 1929), while Svensson-Stenar (1925) only reported that the haploid number of *Alstroemeria pittacina* (*A. pulchella*) is nine.

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**78)** *Bomalia salsilla* \( 2n = 18 \) (2b) = \( 2L + 4S + 12S \) (Fig. 70)

This species has 18 chromosomes, namely 2 long chromosomes with median constrictions and 16 short chromosomes of which six pairs have extremely subterminal constrictions while the remaining two pairs have subterminal and median constrictions respectively. Two pairs of short chromosomes with extremely subterminal constrictions have satellites at their shorter arm. This karyotype is similar to those of *Alstroemeria*, though the chromosome sizes are much
smaller than in the latter. This karyotype may be derived from the *Alstroemeria* type by duplication of 2 short chromosomes with extremely subterminal constrictions. These karyotype alterations may explain the phylogenetic similarities of karyotypes among *Alstroemeria* (b = 8), *Bomalia* (b = 9) and *Curculigo* (b = 9, 10) etc.

The present karyotype analysis is in agreement with the results reported by Whyte (1929).

Table 3. Comparison of the karyotypes in subfamily Hypoxidoideae

<table>
<thead>
<tr>
<th>Species</th>
<th>Karyotypes (2n)</th>
<th>Basis</th>
<th>Nucleoli</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alstroemeria chilensis</em></td>
<td>16 = 2L+2L^t+4S^t+8S (2b)</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>A. pulchella</em></td>
<td>16 = 2L+2M^t+2S^t+10S (2b)</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td><em>Bomalia salsilla</em></td>
<td>18 = 2L+4S^t+12S (2b)</td>
<td>9</td>
<td>4</td>
</tr>
</tbody>
</table>

Discussion

(1) Karyotype analysis and the hypotheses of karyotype alteration

The object of karyotype analysis is in part to compare the various karyotypes in allied groups and to consider the morphological resemblances among them in order if possible to get evidence of the phylogenetic relations of karyotypes. Accordingly, in the case of the karyotype analysis all sorts of possibilities of karyotype alteration must be taken into consideration and then a conclusion drawn as to the relation of the karyotypes. The hypotheses of karyotype alteration such as the dislocation hypothesis (cf. Navashin 1932), the structural hybridity (cf. Darlington 1929) and the “Chromosomenverkürzung” (cf. Delaunay 1926) have been discussed and supported by many previous investigators in this line and the present observations also refer to such hypotheses of karyotype alteration.

Amaryllidoideae have very similar karyotypes and most genera of them have a basic number of 11 (b = 11), while some genera have a basic number other than 11, namely *Haemanthus* b = 8, 9, *Leucojum* b = 7, 11, *Galanthus* b = 12, *Zephyranthes* b = 6, *Hymenocallis* b = 23, *Narcissus* b = 7, 10 and *Lycoris* b = 6, 11, while the basic number of *Sprekelia* could not be determined in the present case. Generally speaking, the resemblance of the karyotypes in the Amaryllidoideae is explicitly observable and in *Leucojum* the karyotypical relation between plants with b = 7 and with b = 11 may be explained by reference to the phenomenon of translocation; while in *Zephyranthes* the karyotype (b = 6) may have resulted from elimination of one pair of chromosomes from the *Leucojum* type (b = 7). In *Galanthus* the karyotype (b = 12) may be derived from the *Leucojum*
type (b = 11) by the duplication of one pair of long chromosomes; in *Hymenocallis* the karyotype (b = 23) may be explained as a result of secondary balance from a plant with b = 11. *Narcissus* with b = 10 may be produced by the elimination of one pair of chromosomes from the 11-series and those with b = 7 may be the result of such karyotype alteration as translocation or fusion in *Leucojum* (cf. Sató 1937b) and in *Lycoris* as Inariyama (1933, 1937) has suggested the plant with b = 6 is derived from the plant with b = 11 by the fusion of chromosomes. The karyotype of *Haemanthus* is far from resembling the species reported here and rather resembles those of *Scilla* in the Liliaceae and of *Alstroemeria* in the Hypoxidioideae. When SAT-chromosomes are taken into consideration, the karyotype of *Haemanthus* is similar to that of *Alstroemeria*. The karyotype of *Sprekelia* could not be determined on account of the large number of chromosomes, but the morphology was resembling that in the other genera, so that the karyotype phylogeny may be drawn by more elaborate observation.

The chromosome sizes indicate considerable variation in different genera and species. As a whole, the chromosomes of *Haemanthus* and *Lycoris* are long, those of *Leucojum, Galanthus, Crinum, Sternbergia* and *Pancratium*, etc. are medium and those of *Nerine undulata, Hippeastrum, Clivia, Habranthus, Cyrtanthus, Hymenocallis, Eucharis* and *Sprekelia* are short.

The different species with the same basic number have also different karyotypes and the species of the same genera often show different karyotypes especially as in *Haemanthus, Nerine, Narcissus* and *Hippeastrum*, and rarely the same one as in *Crinum*. The karyotype

![Fig. 71. Various karyotypes in *Haemanthus*, as represented by the basic chromosome sets, the chromosomes being shown slightly diagrammatized. a, *Haemanthus albiflos* (2n = 16). b, *H. albiflos var. pubescens* (2n = 16). c, *coecineus* (2n = 16). d, *H. Prince Albert* (2n = 16).]
Fig. 72. Various karyotypes in Amaryllidoideae, as represented by the basic chromosome sets, the chromosomes being shown slightly diagrammatized. a, Clivia nobilis (2n = 44). b, Galanthus Elwesii (2n = 24). c, Leucojum aestivum (2n = 22). d, L. autumnale (2n = 14). e, Nerine undulata (2n = 22). f, N. curviflora (2n = 22). g, Amaryllis Belladonna (2n = 22). h, Zephyranthes Tauberti (2n = 12). i, Sternbergia lutea (2n = 22). j, Crinum Moorei (2n = 22). k, Cyrtanthus obliquus (2n = 22). l, Hymenocallis littoralis (2n = 46). m, Narcissus Jonquilla (2n = 14). n, N. tazetta var. papyraceus (2n = 22). o, Pancratium illyricum (2n = 44). p, Hippeastrum vittatum (2n = 44). q, Habranthus Andersoni (2n = 21). r, Lycoris.
of *Nerine undulata* is smaller than that of the other *Nerine* species and besides this the SAT-chromosome of the former has a secondary constriction at its long arm, while the latter has this constriction at its short arm. A similar observation in various genera is interpreted by the dislocation hypothesis of Navashin (1932).

The *Yucca-Agave* karyotype prevails in Agavoideae and the popyploidy (2b, 3b, 4b, 5b, 6b) of this type shows its stability. The karyotype does not demonstrate clearly any phylogenetic similarity to the various karyotypes in both Amaryllidoideae and Hypoxidioideae. The karyotype of *Doryanthes* (b = 12) is a possible connecting link between these genera and the *Yucca-Agave* karyotype, if we take into consideration the possibility of the karyotype alteration such as translocation.

The karyotypes of *Alstroemeria* and *Bomalia* in the Hypoxidioideae show a resemblance to those of *Haemanthus*, but have no intimate relation with any others.

When the karyotypes in the Liliaceae have been thoroughly investigated, we will be able to draw a more exact conclusion from the present observation.

1. Fusion. The fusion of chromosomes produces a new linkage group, namely a new karyotype. The karyotypes in *Leucojum*, *Narcissus* and *Lycoris* may be explained by such karyotype alteration, unless they are attributed to either translocation or fragmentation.

2. Fragmentation. The chromosome fragment was observed in *Crinum capense* and the karyotypes in *Narcissus* such as *N. tazetta* var. *papyraceus* (2n = 22) and *N. tazetta* var. *suizen* (2n = 32) are also attributed to the fragmentation of chromosomes (cf. Nagao 1933).

3. Duplication. The karyotype of *Galanthus* (2n = 24) may be interpreted in conformity with the duplication of long chromosomes from the 11-series. The exceptional individual of *G. nivalis* (2n = 25) is also explained by such a process and the structure of *Zephyranthes candida* (2n = 38) (b = 6) and *Eucharis grandiflora* (2n = 68) (b = 11) may be attributed to the same karyotype alteration. The karyotype of *Hymenocallis* (b = 23) may be derived from the plant with b = 11 by the action of such a process and then secondarily balanced. The karyotypes of *Haemanthus Prince Albert* (b = 9) and *Bomalia* (b = 9) may be formed by the duplication of short chromosomes from the common *Haemanthus* type (b = 8).

4. Translocation. Three pairs of SAT-chromosomes in *Haemanthus* have different combinations (2Lt + 2Mt + 2St; 2Lt + 4Mt) in respect of different species. The SAT-chromosome of *Nerine*
undulata has a secondary constriction at its distal arm, while those of the other Nerine species have such a constriction at their proximal arms. The satellites exist at the distal arms in Clivia and Hippeastrum, and at the proximal arms in Leucojum, Galanthus, Sternbergia, Cyrtanthus, Narcissus and Habranthus. These facts suggest the translocation of chromosome segment or satellites of SAT-chromosomes. The same inference may be admitted in the cases of Crinum, Amaryllis, etc.

The translocation of the satellite occurs very frequently in Haemanthus, Aloe (cf. Satô 1937a; Resende 1937a, b), Tricyrtis (cf. Satô 1937d), Paeonia (cf. Sino-tô 1937, 1938), etc. and these phenomena are partly due to the fragility of the satellite. Most satellites consist of heterochromatin which constitutes the inert (or more properly speaking chromocentral) region of X- and Y-chromosomes in Drosophila and is more fragile than the other active or euchromatic region. For this reason, the occurrence of translocation, inversion or the other chromosome changes are frequently found in the heterochromatic region in Drosophila and seven different types of Y-chromosome were observed by Dobzhansky (1937) in Drosophila pseudoobscura. The variation of SAT-chromosomes is not only a simple result of easy detection, but may also be attributed partly to the fragility of the "région nucléologénique".

(5) Inversion. The relation between the chromosomes with a median constriction and those with a subterminal constriction may be attributed to such karyotype alteration or to translocation.

The medium chromosome with a secondary constriction in Alstroemeria pulchella may be derived from the inversion of the short arm with a satellite of a long chromosome in A. chilensis. The relation between various SAT-chromosomes may be explained partly in the light of this alteration.

(6) Elimination. The elimination of the short chromosome with a median constriction was observed in Habranthus Andersoni (2n = 21). The karyotype of Zephyranthes (b = 6) suggests the
elimination of one pair of long chromosomes from the *Leucojum* type \((b = 7)\). The *Narcissus* plant with \(b = 10\) may indicate the elimination of one pair of chromosomes from the common karyotype \((b = 11)\) of the other genera, though the case of the *Narcissus* such as *N. tazetta* var. *papyraceus* \((2n = 22)\) is explained by fragmentation (cf. Nagao 1933).

(7) **Deficiency.** The deficiency of the satellite was observed in *Galanthus, Habranthus, Narcissus*, etc. The heteromorphic SAT-chromosomes are also explained on the basis of such a karyotype alteration.

(8) **“Chromosomenverkürzung”** Various karyotypes with the same basic number often show a gradual shortening or elongation of chromosomes especially in the species belonging to the same genus. For instance, the karyotypes of *Haemanthus albiflos, H. albiflos* var. *pubescens* and *H. coccineus* offer evidence of such a karyotype alteration as seen in *Muscari* (cf. Delaunay 1926) and *Aloinae* (cf. (Satô 1937a). The same inference may be possible in the case of *Nerine, Narcissus* and *Alstroemeria*.

(2) **Genotypic control of the karyotype alteration and the secondary balance**

“In a far less satisfactory state is the problem of the cause of these changes in the process of evolution. The potent source of artificially induced changes in chromosome structure, X-ray, is acknowledged to be a most insignificant factor as regards mutation under natural conditions (cf. Muller 1930). The same also hold true for structural chromosome changes. The aging of seeds, advanced by Navashin (cf. Navashin and Gerassimova 1936), cannot be recognized as a factor of general biological significance. The formation of structurally new chromosomes as a result of distant hybridization (cf. Müntzungs 1934; Sveshnikova 1936) assumes the existence of karyo-structural difference between the species crossed.

In a number of reported instances of the spontaneous origin of structural chromosome changes they were connected with the alteration of karyological balance as a result of hybridization (cf. Poole 1931; Navashin 1934) or of trisomic (cf. Belling and Blakeslee 1924; Lesley and Frost 1928; Lesley and Lesley 1929) or monosomic condition.” (cf. Levitskij 1937).

According to Levitskij the families which showed a large number of deviations in *Crepis capillaris* are inclined to produce such deviations, this inclination being especially marked in some particular individuals in these families. This “inclination” can scarcely be inter-
interpreted in any way than genetically, i.e., as due to definite peculiarities of the genotype. Since these peculiarities appeared only in the progeny of certain of the plants subjected to X-radiation, they are apparently the result of X-ray-induced mutations, which brought about genotypically determined instability of the chromosomes and which were transmitted through the female gametes to the F₁.

Such genotypic control of the karyotype alteration accounts in a natural way for the marked difference as regards such changes in different sections of the taxonomic system. Various karyotype alterations of species of Haemanthus, Leucojum, Narcissus, Lycoris and Alstroemeria stand in contradistinction to their complete absence in the divergence of the genera, Yucca, Bravoa, Polianthes, Agave Four-croya and Beschorneria (so-called Yucca-Agave karyotype). The fundamental reconstruction of the chromosomes of Drosophila miranda, as compared with those of the chromosomes of the closely related D. pseudoobscura (cf. Dobzhansky and Tan 1936), stands in contradistinction to the comparatively insignificant differences in this respect between D. melanogaster and D. similans (c. Pătău 1935). The same facts can be easily shown in the different genera of the Amaryllidoideae.

On the other hand, the genotypic control represents a factor which may explain in a natural way the general occurrence of structural changes of chromosomes in both the animal and plant kingdoms.

Generally speaking, polyploidy had been commonly found in Amaryllidaceae and the species with the stable karyotypes such as the Yucca-Agave type necessarily have many euploids, while the species with the unstable karyotypes such as Narcissus and Lycoris show various aneuploids. The former type includes only the multiples of the basic chromosome numbers, but the latter includes various derivatives of different basic chromosome numbers as a result of karyotype alterations such as duplication, translocation, fusion, fragmentation, inversion, and elimination.

In the Amaryllidaceae diploid plants prevail in many species, and triploids were found to occur in Nerine, Crinum, Hymenocallis, Narcissus and Agave, tetraploids in Clivia, Galanthus, Zephyranthes, Pancratium, Hippeastrum, Agave and Doryanthes, pentaploid and hexaploid in Agave and heptaploid in Griffinia.

Many unbalanced karyotypes were reported in various horticultural and cultivated plants. The karyotype of Amaryllis alba (2n = 39) seems to be derived as a result of hybridization. The karyotype of Habaranthus Andersoni (2n = 21) may denote the process of change from the 11-series to the 10-series such as Narcissus tazetta by elimination or a similar karyotype alteration.
More striking is the fact that the karyotype of *Hymenocallis* (b = 23) is clearly shown as the secondary polyploid from the 11-series. The karyotype of *Zephyranthes candida* (2n = 38) also demonstrates secondary balance from the 6-series. *Eucharis grandiflora* (2n = 68) is the same example in the 11-series.

"The distinction between secondary polyploidy and structurally changed polyploidy (i.e., polyploidy followed by fragmentation or fusion) is important, because the first means an important change in genetic balance, while the second means little or no change of this kind." (cf. Darlington 1932 p. 225). Not only the first type but also the second have been discovered in the Amaryllidaceae. From the consideration of karyotype alteration detailed in the previous paragraph, it follows that the possibility always lies open for variation to occur by a change in proportion, either by reduplication of segments of chromosomes or of whole chromosomes. If such a change in proportion were successfully accomplished, it would yield a new secondary balance having a different phenotypic expression from the primary, ancestral type. Evidence of this probably universal type of variation is only beginning to appear, for the reason that the necessary inference are elaborate ones.

Where the change of balance is concerned with whole chromosomes its occurrence seems to be confined to polyploids. Thus the 18-series arises in *Dahlia* secondary to the 8-series (cf. Lawrence 1929) and the 17-series in the Rosaceae secondary to the 7-series (Darlington and Moffett 1930; Moffett 1931).

Various karyotypes in the Amaryllidaceae indicate polyploidy and the secondary balance, and further investigation will probably show that the secondary polyploidy and other variation due to change in balance (such as reduplication of segments) are important elements in the species formation.

**3) The relation between SAT-chromosomes and nucleoli**

According to Heitz (1931) the nucleoli in the telophase originate in the strand which connects the satellites (or chromosome segments) with their mother chromosomes, namely the SAT-chromosomes. Consequently the number, size and position of the nucleoli in the telophase have to correspond with those of the SAT-chromosomes. This explanation has been found applicable to the observations made in *Haemanthus, Clivia, Galanthus, Nerine, Amaryllis, Crinum, Cyrtanthus, Hippeastrum, Narcissus, Habranthus, Alstroemeria and Bomalia*. The secondary constrictions in *Zephyranthes, Cyrtanthus, Habranthus* and *Narcissus* seem however to have no relation to the origin of the nucleoli. The same thing had already been found to be
the case in *Drosophila* (cf. Heitz 1933; Kaufmann 1934), *Scilla* (cf. Satō 1936b), *Aloinae* (cf. Satō 1937a; Resende 1937a, b) and *Narcissus* (cf. Fernandes 1936). The satellited chromosomes have no relation to the nucleoli in *Labiatae* (cf. Bushnell 1936) and *Lobelia* (cf. Okuno 1937), though the writer believes that these latter observations are doubtful owing to the alternative possibility of separation or non-separation between the satellited chromosome and the nucleoli in the early stage.

Since McClintock (1934) described the peculiar case of the SAT-chromosomes in *Zea mays*, it became necessary to modify or extend the hypothesis of SAT-chromosomes. Matsuura (1935) reported that the long chromosome (A) of *Trillium kamschaticum* became attached to the nucleolus at the time of the primary division of the pollen grain and Fernandes (1936) also made a similar observation in the case of *Narcissus bulbocodium*, that is, that the chromosome without a satellite associated with the nucleolus. The latter author explained these chromosomes without a satellite by postulating a “région nucléologénique” Recently Matsuura reported that in *Trillium* not only a long chromosome (A) but also a short chromosome (E) attach to the nucleolus at the chromosome ends (Matsuura 1938), while Resende (1937) observed many satellites of extremely small size in *Trillium* and a large number of nucleoli than was expected from the count of SAT-chromosomes.

Such confusion might have resulted partly from the inadequate technique employed and partly from the extremely smallness of the satellites. As shown in *Haemanthus*, the extremely small satellite can only be observed in favourable cases and the connection of the persistent nucleolus to the chromosome end is an indication of SAT-chromosomes with small satellites. Consequently, this nucleolar chromosome connected to the persistent (and soon vanishing) nucleolus may be concluded with certainty to be a SAT-chromosome with an extremely small satellite. In inadequately fixed materials or unfavourable case, the satellites of SAT-chromosomes can hardly be observed, probably owing to the coiling of the satellites altogether with their mother chromosomes in the process of chromosome contraction or spiralization. This postulate is based on the coiling of the satellite which follows separation from the persistent nucleolus.

McClintock (1934) and Fernandes (1936) suggested that the “région nucléologénique” consisted of heterochromatin in *Zea* and *Narcissus* respectively, and these observations can be confirmed in many species of Amaryllidaceae. When the SAT-chromosome has a secondary constriction instead of a satellite, the deeply stained body which consists of heterochromatin can not be observed on the surface.
of the nucleoli and consequently too rapid a conclusion must be avoided. Heitz (1929, 1932) previously showed that the chromocentres consisting of heterochromatin have no relation with the nucleolus. Many chromocentres free from the nucleoli are observed in *Leucojum autumnale* besides four satellites on the surface of the nucleoli.

In *Paeonia* four pairs of SAT-chromosomes have small, sometimes extremely small, satellites at their distal ends and four pairs of nucleoli corresponding were observed in the telophase, while besides these nucleoli one group of ten chromocentres was found in the probable position of the spindle fibre attachments in the telophase and even in the resting stage (cf. Sinotô 1937, 1938).

As regards the nature of heterochromatin, Heitz (1932) could not distinguish it from euchromatin when using Feulgen's nucleal reaction instead of haematoxylin, but the chromocentres are clearly distinguished from euchromatin (cf. Schaeide 1936) in *Scilla sibirica* (Satô unpublished) in the case of Feulgen's staining, although the chromocentres were deeply stained and fine unravelled threads connecting each chromocentre were also stained faintly. Such an observation supports the view that the chromocentre is preserved in the state of chromonemata without unravelling in the telophase and the resting stage.

The connecting strand of the SAT-chromosome seems to be lengthened by the tension between the SAT-chromosome and the persistent nucleolus and this tension may result from some agent such as an electric repulsion of both materials. This repulsion seems to be correlated with the size of the satellite in most cases, and the SAT-chromosome with a large satellite or a long connecting strand was also attached to the persistent nucleolus in *Gasteria* (cf. Satô 1936b, 1937a), *Galanthus* (cf. Satô 1937c), etc. But one pair of small satellites was newly distinguished by its connection with the persistent nucleolus in *Leucojum autumnale*, although only one SAT-chromosome with a longer connecting strand was often attached to the nucleolus even in this exceptional case. This repulsion may separate a SAT-chromosome or a nucleolar chromosome from the nucleolus and *vice versa*. This phenomenon is one of the reasons which have mislead many investigators to conclude that there was an absence of relationship between the SAT-chromosome and the nucleolus.

Though four nucleoli were observed in *Leucojum vernum*, *L. aestivum* and *Sternbergia lutea* only two SAT-chromosomes were found during the present observation. This is probably due to the presence of another pair of nucleolar chromosomes which either SAT-
chromosomes with extremely small satellites or a nucleolar chromosome (in the strict sense) without a satellite or secondary constriction. The SAT-chromosomes in Zephyranthes could not be determined in spite of the presence of many secondary constrictions. In Agavoideae, the long chromosome of the Yucca-Agave karyotype was attached occasionally to the persistent nucleolus. These observations can not easily be explained for the present. At any rate, the presence of SAT-chromosomes can be emphasized, though the hypothesis itself has to undergo modification in order to reconcile it with the finding on the nucleolar chromosome.

Summary

(1) The karyotypes of nineteen genera in the Amaryllidoideae, namely Haemanthus (2n = 16, 18), Griffinia (2n = 77), Clivia (2n = 44), Galanthus (2n = 24, 25, 28, 48), Leucojum (2n = 14, 22), Nerine (2n = 22, 33), Amaryllis (2n = 22), Zephyranthes (2n = 12, 24, 38), Sternbergia (2n = 22), Crinum (2n = 22, 33), Cyrtanthus (2n = 22), Eucharis (2n = 68), Hymenocallis (2n = 46, 69), Narcissus (2n = 14, 21, 22, 32), Pancratium (2n = 44), Sprekelia (2n = ca. 117), Hippeastrum (2n = 44), Habranthus (2n = 21) and Lycoris (2n = 27) have been analyzed from the point of karyotype alteration (cf. Table 1). Many genera such as Griffinia, Clivia, Leucojum, Nerine, Amaryllis, Sternbergia, Crinum, Cyrtanthus, Pancratium, Hippeastrum, Habranthus and Lycoris have the 11-series of chromosomes, in other word 11 is their basic number of chromosomes which indicates the intimate relationship existing between these karyotypes. More striking is the fact that various karyotypes belonging to the same genus, for instance Leucojum (b = 7, 11), have been explicitly explained by the dislocation hypothesis of Navashin (1932). By further reference to this hypothesis it may be possible to suggest the derivation of karyotypes in other genera.

(2) The karyotypes of Hymenocallis (2n = 46, 69) and Eucharis (2n = 68) clearly indicate their derivation from the 11-series by the duplication of chromosomes and the secondary balance. The similar secondary polyploid appeared in Zephyranthes (b = 6), i.e., Z. candida (2n = 38). All genera except Haemanthus in the Amaryllidoideae may be concluded to have some karyotypical resemblances, when the karyotype alteration such as fusion, fragmentation, duplication, translocation, inversion, elimination and deficiency have been taken into consideration. The karyotypes of Haemanthus resemble those of Scilla in the Liliaceae or Alstroemeria in the Hypoxidioideae.
(3) The karyotypes of five genera in the Agavoideae, namely Bravoa, Polianthes, Agave, Fourcroya and Beschorneria are similar (so-called the Yucca-Agave karyotype) (5 long and 25 short chromosomes) (cf. Table 2). The karyotype of Doryanthes (4 long and 44 short chromosomes) is different from the Yucca-Agave type, but some similarities are suggested, although difference in chromosome sizes can clearly be detected. The karyotypes of the Agavoideae are generally speaking different from other ones in the Amaryllidaceae and rather resemble those of Yuccae in the Liliaceae.

(4) The karyotypes of Alstroemeria (2n = 11) and Bomalia (2n = 18) in the Hypoxidoideae are similar to those of Haemanthus (2n = 16), especially in respect to the SAT-chromosomes.

(5) The hypothesis of the SAT-chromosome has been adopted in the present analysis of karyotypes in the Amaryllidaceae and has brought about successful results. Various hypotheses of karyotype alteration were discussed and such karyotype alterations are concluded to be genotypically controlled (cf. Levitskij 1937). The genotypic control of karyotype alteration and the secondary balance seem to play an important role in the process of evolution.

(6) The relation between the nucleoli and the SAT-chromosomes was discussed and the hypothesis of the SAT-chromosome was extended to reconcile it with the conception of the nucleolar chromosome. The presence of the SAT-chromosome was emphasized by the observation of satellites or secondary constrictions in many species which had usually been overlooked or neglected by previous investigators.

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