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CYTOTAXONOMY OF AMARYLLIDACEAE

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ABSTRACT

Chromosome numbers are now known for about 46 genera in the family Amaryllidaceae. The lowest basic number has been found to be 5 and the highest 30. Besides these two, 6, 7, 8, 9, 10, 11, 12, 14, 15, 16, 19, 23 and 29 have also been encountered of which 11 is found in majority of the genera. In a number of genera the derivation of one basic number from the other has been established. In the genus *Allium* largest number of species have been studied cytologically. The next largest is *Narcissus* followed by *Zephyranthes*, *Crinum*, *Hippeastrum* and *Lycoris* in that order.

B or supernumerary chromosomes have been observed in *Agapanthus*, *Allium*, *Crinum*, *Cooperia*, *Haemanthus*, *Hippeastrum*, *Lycoris* and *Narcissus*.

In this family repatterning of chromosomes through inversions (both para and pericentric), translocation, polyploidy (eu-, aneuo-, hetero-, auto-, and allopolyploidy) and hybridization have played prominent role in chromosome number evolution, karyotype alteration and speciation. In addition to this, gene mutation has also played significant part in speciation. Ready vegetative propagation has helped in maintaining sterile hybrids and those forms with numerical and structural changes of chromosomes. Apomixis has also been responsible in chromosome number evolution in some genera.

A consideration of taxonomic work done in Amaryllidaceae points out that Hutchinson's system of classification, based on the umbellate inflorescence rather than on the position of the ovary, has been found to be more phylogenetic but the amendments proposed by several workers for changes in tribal and generic level could be taken into consideration and in some cases may be justified.

INTRODUCTION

The family Amaryllidaceae is very interesting from cytotaxonomic point of view. Cytologically, most of the species belonging to this family have small number of large chromosomes and some species of the genus *Allium* are being extensively used for experimental studies involving physical and chemical agents. Taxonomically, the family has attracted added importance since the delimitation of the family by Hutchinson (1934, 1959) to only those members of petaloid monocotyledons, which have umbellate inflorescence.

CYTOTAXONOMIC CONSIDERATION

Hutchinson radically changed the concept of the differentiation of Liliaceae and Amaryllidaceae formerly based on the position of ovary and recognized the importance of the umbellate type of inflorescence as the unifying principle in Amaryllidaceae. For this reason, he included the tribes Agapantheae, Gilliesieae and Allieae in Amaryllidaceae, which were formerly placed in Liliaceae. On the other hand, he excluded the tribes Hypoxideae, Alstromerieae, Agaveae, Vellozieae and Conostyleae from Amaryllidaceae. Hutchinson's classification has been more or less supported by taxonomists and in many instances evidences have been brought forward by anatomists and cytologists to support him. As for example, Mckelvey and Sax (1933), Whitaker (1934) and Granick (1944) pointed out that *Yucca* and *Agave* are quite similar cytologically in having 5 pairs of large and 25 pairs of small chromosomes, yet the former was placed in Liliaceae and the latter in Amaryllidaceae by earlier taxonomists. On the basis of their cytological findings they urged for keeping them together. In Hutchinson's classification these two genera have been put together in Agavaceae. The genus *Furcraea*, which has cytological similarities (Whitaker, 1934) with *Yucca* and *Agave*, has also been grouped with these two genera by Hutchinson. Anderson (1940, vide Lawrence, 1951) on the basis of his studies on the floral anatomy of Liliales approved of Hutchinson's inclusion of Agapantheae, and Allieae in Amaryllidaceae. Cheadle (1942) also accepted the inclusion of Agapantheae, Allieae and Gillieseae in Amaryllidaceae on the basis of his anatomical work on monocotyledons. Maia (1941, vide Lawrence, 1951) through his studies on the pollen grain of some monocotyledons also came to the same conclusion. Lawrence (1951) commented that the classification based on the position of the ovary was not constant, since in the genera *Ophiopogon*, *Bomareae* and *Hemerocallis* of Liliaceae both superior and inferior ovaried plants are found and for this reason he expressed the opinion that the classification of Hutchinson, which was based on the type of inflorescence, was or more fundamental importance and stable in nature. Flory and Yarnell (1937) gave an account of chromosome numbers in the Hemerocallideae, Alstromeriales, and Amaryllidales following Hutchinson's classification but they supported

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Stout's (1932) view that so far as the basic number is concerned the genus *Hemerocallis* does not fit in Liliaceae, since it has a *n* number of 11, while an allied genus *Hosta* has a basic number of 30. On this ground they thought that further cytotaxonomic study of some genera in Amaryllidaceae might call for an inclusion of *Hemerocallis* in Amaryllidaceae. Earlier, Whitaker (1934) and Granick (1944) removed the genus *Hosta* from Hemerocalleae and placed it in the family Agavaceae.

Sato (1942) observed that his results of karyotype analyses in different genera of Liliaceae and related families agreed with Hutchinson's (1934) system of classification. He pointed out that the karyotypes of some genera in Liliaceae and Amaryllidaceae were similar in morphology, which according to him, showed that Hutchinson's classification based on the umbellate inflorescence was more reasonable than that based on the position of ovary. Through his studies on the karyotypes of *Phormium, Hosta, Hemerocallis, Leucocrinum, Hesperocallis, Dracaena* and *Cordyline* he supported Hutchinson's opinion that the Amaryllidaceae might have originated from the tribe Hemerocallideae of Liliaceae. Sato (1942) agreeing with Hutchinson, also suggested the transference of Alstroemerieae into Liliaceae but supported Nakai's (vide Sato 1942) modification of Hutchinson's system. Later, Flory (1944) gave another list of chromosome numbers in Hemerocallideae, Alstroemeriales, and Amaryllidales basing on Hutchinson's classification but took into account the changes suggested by some workers. Sharma and Ghosh (1954) not only supported the removal of the tribe Hypoxideae from Amaryllidaceae by Hutchinson but also accepted his creation of the family Hypoxidaceae. Mookerjea (1955) found cytological corroboration of Hutchinson's system in Amaryllidaceae, and later, working with some members of Liliaceae, Mookerjea (1956) did not agree to his inclusion of *Funkia* in Hemerocalleae. Traub (1957), while supporting the delimitation of the family by Hutchinson, proposed some new changes and presented a classification of the family Amaryllidaceae, which was a third revision of their (Traub, 1938 and Traub and Moldenke, 1949, vide Traub, 1957) earlier classifications. On the basis of morphological and cytological similarities with members of the tribe Allieae, Agapantheae and Gilliesiae, he removed the tribe Hemerocallideae from Liliaceae and placed it in Amaryllidaceae. He also divided the family Amaryllidaceae into three subfamilies and raised the number of tribes from 13 to 15, and shifted genera from one tribe to the other. Traub (1957) also criticised Darlington and Wylie's (1956) idea in keeping the tribes Allieae and Agapantheae in Liliaceae, although, in his opinion, the tribes Gillieseae and Hemerocalleae have been rightly placed by them in Amaryllidaceae. In Traub's (1957) system, basic numbers of chromosomes were also taken into account in the subfamily, tribal and generic level. Later on, Bose (1958*c*) commented on the taxonomic positions of the genera *Sprekelia* and *Lycoris* in the light of his cytological findings.

The above discussion shows that although Hutchinson's (1934) new system of classification based on the umbellate inflorescence rather than on the position of the ovary has been found to be a more natural system, the amendments proposed by several workers for shifting tribes and genera could be taken into consideration and in some cases may be justified.

BASIC NUMBERS IN THE FAMILY AMARYLLIDACEAE

In the genus *Allium* largest number of species in the family Amaryllidaceae have been studied cytologically. The next largest is *Narcissus*, followed by *Zephyranthes, Crinum, Hippeastrum* and *Lycoris* in order. As regards the chromosome numbers, Table 1 shows that very varied chromosome numbers have been reported from *Allium, Zephyranthes, Hymenocallis* and some other genera.

A glance at Table 1 will also show that in this family the lowest basic number is 5, and the highest is 30. Besides these two, there are n=6, 7, 8, 9, 10, 11, 12, 14, 15, 16, 19, 23 and 29, of which 11 is found in majority of genera. In a number of genera the derivation of one basic number from the other has been established, as for example, Fernandes (1946) has shown that the basic number 10, in *Narcissus*, is derived from n=7, while in a genus like *Lycoris*, 6 or 11 could be taken as the original basic number, although Inariyama (1951*b*) has favoured 11 as the original basic number on the basis of fusion of rod chromosomes. On the other hand, if the fragmentation of V chromosomes is taken into consideration then 6 would be the original basic number in *Lycoris*. This aspect will be taken up in detail in the following discussion.

MECHANISM OF CHROMOSOME NUMBER EVOLUTION, KARYOTYPE ALTERATION AND SPECIATION IN AMARYLLIDACEAE

In Amaryllidaceae repatterning of chromosomes through inversions (both para and pericentric) and translocation, polyploidy (eu-, aneuo-, hetero-, auto-, and allopolyploidy) and hybridization have played prominent role in chromosome number evolution, karyotype alteration and speciation. Sato (1938) and others have discussed the importance of these mechanisms in evolutionary tendencies in Amaryllidaceae. In addition to this, gene mutation has also played significant part in speciation. In several genera, apomixis has also been a contributing factor. Ready vegetative propagation has helped in maintaining sterile hybrids and those forms with numerical and structural changes of chromosomes.

An attempt can now be made to analyse the ways these mechanisms have played their part in the different genera and species of Amaryllidaceae in which cytological studies have been done by several workers.

In *Agapanthus* somatic chromosome numbers of 30 and 32, coming from high basic numbers of 15 and 16 respectively, can be seen, but the possibility of these basic numbers arising from 6 and 8 cannot be ruled out in view of the suggestion of Bose (1958*c*) advanced in the genus *Sprekelia*. In that case one has to look for a polyploid series in *Agapanthus*. The aneuploid number 2n=29 reported by Riley and Mukherjee (1960) for *A. sp.* could have arisen by the loss of one chromosome from a 30 chromosome species or by the loss of three chromosome from a 12 chromosome species. In *Tulbaghia* only diploid species with a basic number of 6 has been found, and in *Bloomeria* only diploid numbers have been reported starting from a basic number of 9.

In *Allium* several factors have been responsible for evolutionary tendencies. Here, in addition to the finding of euploid series in the 7, 8 and 9 basic number groups, one gets aneuploid numbers like 19, 25 and 26. In any case, starting with these basic numbers one can have diploids, triploids, tetraploids and pentaploids in the 7 series, diploids, triploids, tetraploids, pentaploids, hexaploids and other higher ploidy in the 8 series and only diploids in the 9 series. Levan (1932, 1935) commented that in *Allium* a basic number of 8 has come about from a basic number of 7 through the fragmentation of a V chromosome into two. He also thought that n=7 was primitive and that n=8 was a derived one. Stebbins (1950) thought that there was an ascending basic type of aneuploidy in *Allium*. Levan's (1935) hypothesis that asymmetric chromosomes of *Allium* are derived from V shaped chromosomes through structural changes have been supported by many workers through their works in several genera of Amaryllidaceae, and the discussion to follow herewith will deal with this and other aspects of evolutionary tendencies in this family. Another interesting phenomenon observed in *Allium* is the occurrence of apomixis. The types of apomixis found in this genus have been discussed by Levan (1937) and Stebbins (1950). Levan (1937) also found a genetic basis of apomixis in an *Allium* species, and observed the formation of bulbils in polyploids, which helped in vegetative propagation but the diploids were devoid of bulbils. In addition to this, several workers have reported species hybrids in *Allium*: between *A. cepa* and *A. fistulosum* by Davis (1955), Emsweller and Jones (1945), Jones and Clarke (1942) and Levan (1941). Recently, Jones and Kehr (1957) reported interspecific crosses between *A. ascalonicum* and *A. fistulosum*. In all these cases amphidiploids were studied. Levan (1941) and Jones and Clarke (1942) observed spontaneously occurring amphidiploids in their crosses while Davis (1955) and Jones and Kehr (1957) produced amphidiploids from sterile F_1 hybrids.

In the allied genus *Nothoscordum* a similar evolutionary mechanism is going on like that observed in *Allium*. Here 8 and 9 are observed to be the basic numbers. In the 8 series diploid plants are found while in the 9 series, like *Allium*, only diploids are known. Aneuploid plants with 19 chromosomes have also been found. Beal (1932) has suggested that *Nothoscordum* might have taken its origin from *Allium*. Anderson (1931), Beal (1932), Levan (1935), Levan and Emsweller (1938) and Garber (1944) have discussed the mechanism by which fragmentation of V chromosomes has given rise to rod chromosomes causing an increase in the chromosome numbers in *Nothoscordum*. Levan and Emsweller (1938) observed the pairing of two *t* or terminally attached chromosomes with one *m* or medianly constricted chromosome. Moreover, the total length of each of these *m* chromosomes was found to be equal to that of two *t* chromosomes. These were evidences on which Levan and Emsweller (1938) drew the homology and derivation of two rods from one V by transverse fragmentation across the centromeric region. Garber (1944) thought that the original karyotype in *Nothoscordum* was with all V shaped chromosomes from which some of the V's fragmented to give rise to rod chromosomes and thus increased the chromosome number. In *Nothoscordum* one also finds apomitic triploids (Darlington and Wylie, 1956).

In *Brodiaea* many chromosome numbers have been reported and the basic numbers of 5, 6, 7 and 8 are all represented by polyploid series. Burbanck (1941) suggested the basic number for *Brodiaea* as 6, and a derived basic number 9 for *Dickelostemma* (*Brodiaea*). The somatic number of 48 chromosomes found in *Brevoortia* could be taken as derived from a basic number of 6. In *Milla* Sato (1942) found a somatic number of 39 chromosomes, which he thought was a triploid species. In *Miersia chilensis* Cave and Bradley (1943) found structurally altered types in microspore divisions. Here, some microspores had nine pairs of rod chromosomes and one pair of V chromosomes while other microspores had nine pairs of rods, one 7 and two rods. In these cases they took both fusion of two rods to form a V, and the fragmentation of a V to form two rods into consideration and suggested the possible ways they might have come about through inversion and translocation. However, they pointed out that for the origin of V chromosomes, reciprocal translocation was more likely than just the fusion of two rods. In *Miersia chilensis* Cave and Bradley (1943) also found the pairing of a V chromosome with two rod chromosomes in metaphase I, like that observed in *Nothoscordum* by previous workers. In *Galanthus* a high basic

number with 12 chromosomes has been recorded and starting with this one gets diploids, triploids and tetraploids. In addition to this, aneuploids with 25 and 28 chromosomes have also been observed by Sato (1938) in *G. nivalis*. He thought that the karyotype of *Galanthus* might have come about by the duplication of the long chromosomes of the allied genus *Leucojum* (n=11). In *Sternbergia* diploids and triploids are seen from a basic number of 11. In this genus aneuploid types with somatic numbers of 20 and 24 have also been observed. The triploids in *Galanthus* and *Sternbergia* might have originated by the crossing of 2x and 4x or *vice versa*. In *Leucojum* although majority of species have multiples of 11 in their somatic complement, 7, 8 and 9 could also be taken as the basic numbers here. Sato (1938) assumed that in this genus fusion of rod chromosomes, like that found in *Lycoris*, might be playing the role. Stern (1949, vide Darlington, 1956) reported an interesting observation on the distribution of the species of *Leucojum* in relation to the basic number of chromosomes. In this genus he found the somatic chromosome number increasing from 14 to 16 to 18 to 22 as the species progressed from Morocco to parts of Northern Europe.

In *Amaryllis, Brunsvigia* and *Nerine*, 11 is the predominant basic number but in addition to this one finds, 9 as another basic number in *Amaryllis*. Starting with the 11 series diploids, tetraploids and hexaploids have been seen in *Amaryllis*, diploids in *Brunsvigia* and diploids and triploids in *Nerine*. This shows that polyploidy has played significant role in the evolutionary tendencies in these genera. But apart from this, other mechanisms also seem to be contributing. For instance, in *Amaryllis alba*, Sato (1938) found a somatic count of 39 chromosomes and thought it to be a hybrid with chromosomes being contributed from *Zephyranthes* and *Amaryllis*. In *Nerine* aneuploid numbers, such as 2n=24, 26 and 28 have been observed. In addition to this 2n=22-26 have been reported in the garden forms of this genus (Darlington and Wylie, 1956). One of the ways polyploid and aneuploid types could come about has been evident from the present author's observation in *N. sarniensis*. In this species unreduced microspores with n=33 have been observed in majority of pollen grains. In addition to this, n=27, 21, 17, 16, 12 and 11 have also been found. The origin of new chromosome numbered plants, through the crossing of one of these male gametes with normal gametic number from the female side, cannot be overemphasized.

In the next tribe Crineae a diploid count has been made in *Chlidanthus* starting with a basic number of 10. In the allied genus *Crinum* great many species have been investigated and majority of them have diploid numbers starting with n=11. Sato (1938) reported a triploid count in *C. macrantheum* and Bose (unpub.) found triploid individuals in *C. rattrayi*. Gouws (1949, vide Darlington and Wylie, 1956) reported a somatic count of 72 chromosomes in *C. bulbispermum*, which is an aneuploid in the otherwise euploid series. Sato (1942) reported a hybrid between *Crinum moorei* and *Amaryllis belladonna* and Sharma and Bhattacharyya (1956) found 2n=22 in *Crinum ammocharoides*, which they suggested to be a hybrid between *Crinum* and *Amaryllis*. They also pointed out the strong affinity in breeding behaviour of *Crinum* with *Amaryllis*. In *Ammocharis* a diploid number of 22 chromosomes has been found and it also has a basic number of 11 chromosomes. The genus *Cyrtanthus* is very interesting from cytological point of view. There are not only different basic numbers here (n=7, 8, 9, 10 and 11) from that observed in *Crinum* and *Ammocharis* but also the karyotype is different. Aneuploidy by means of structural changes of chromosomes could be taken as the mechanism responsible for the change in basic number in several species of this genus. Polyploidy has possibly played no role in speciation and chromosome number evolution in *Cyrtanthus*. In *Vallota*, only diploid chromosome number has been reported with 16 somatic chromosomes.

Zephyranthes of the tribe Zephyrantheae is very active and interesting genus. In this genus various chromosome numbers have been reported in the several species studied. Here, in the euploid series starting with a basic number of 6 one gets diploid, triploid, tetraploid, hexaploid and other higher ploidy; from a basic number of 7 diploid, tetraploid, hexaploid and other higher ploidy; and from a series with 11 chromosomes, diploid, tetraploid and pentaploid types only. In addition to this, aneuploid numbers like 25, 38, 43 and 45 etc., are also found. Sato (1938) presumed that *Z. candida* (2n=38) was a secondary polyploid from a 6 series. These aneuploids could also come about by alteration of chromosome numbers through fragmentation and other means or by hybridization. Flory (1959) concluded that *Z. puertoricensis* (2n=25) was a pentasomic tetraploid (4x+1) arising through the union of n × 2n gametes. It might be mentioned here that Coe (1954) observed that in *Z. longifolia*, within a single root tip, cells were found with extra chromosomes and also with deficient chromosomes, which he called aneusomaty following Duncan's (1946, vide Coe, 1954) terminology. Sharma and Ghosh (1954) observed that in a tetraploid variety of *Z. mesochola* in addition to the normal somatic number of 48 chromosomes, 2n numbers of 42, 60, 66 and 72 were present, the numbers being always a multiple of 6. It would be worthwhile to investigate the mechanism operating here. As regards the role of hybridization, Flory (1954) pointed out that the aneuploid *Z. ajax* (2n=43) was a hybrid between *Z. citrina* and *Z. candida*, which readily backcrossed to each of these putative parents, and gave rise to seedlings

with 40, 41, 42 and 45, and these were to some extent fertile. Intergeneric crosses between *Zephyranthes* and *Cooperia* have been reported by Lancaster (1912). However, Sharma and Bal (1956) questioned the status of *Cooperanthes pereyi* (Lancaster, 1912) as a hybrid. They based their doubts from the study of its somatic chromosomes, where according to them, no indication of its hybrid nature was detected but they suggested the necessity of more investigation in this direction. Flory (1958) also reported intergeneric hybrids between *Zephyranthes* and *Cooperia*. In addition to polyploidy and hybridization, apomixis has also accelerated some of the evolutionary tendencies in *Zephyranthes*. Brown (1951) has recognized a wide range of apomiotic forms in *Z. texana*, such as:— agamospermy, diplospory, parthenogenesis, gametophytic apomixis and pseudogamy. Coe (1954) reported apomixis in *Z. brazosensis* and Flory (1954) also recognized the role of parthenogenesis in *Zephyranthes*.

In the allied genus *Cooperia*, Coe (1953) found pseudogamous apomixis and semigamy in *C. pedunculata*. In this genus diploid and tetraploid types have been recorded starting with a basic number of 12, but in view of Bose's (1958c) and Flagg's (1960) suggestions 6 could be taken as the original basic number here. Aneuploid counts of 54 and 69 have also been observed. In another closely allied genus, *Habranthus*, an euploid series has been established, which goes up to such a high number as 2n=108 (Flory and Flagg, 1958), beginning with a basic number of 6. Another basic number, 11, has also been represented here. Again, aneuploid numbers have been found in several species. For example, Sato (1938) reported an aneuploid type in *H. andersoni* (2n=21) and he suggested the elimination of one chromosome (2n−1) here. Flory and Flagg (1958) reported 2n=54 in *H. incaica* but pointed out that this individual could also be *Zephyranthes flammea* (*Pyrolorion flammeum*), and they found a diploid species (*H. juncifolium*) starting from a basic number of 7. They also reported hybrids between *H. brachyandrus* × *H. robustus*. Traub's ×*H. floryi* (12×24) has 2n=18 chromosomes. Since the finding of apomictic forms in *Atamosco texana* (*Habranthus texanus*) by Pace (1913), Coe (1954) observed apomixis in *H. andersoni* var. *texanus*. Flory (1954) has also recognized the role of parthenogenesis in this connection. It might be pointed out that in *Cooperia* and *Habranthus* an evolutionary mechanism is manifested similar to that seen in *Zephyranthes*. The situation in *Sternbergia*, which also belongs to this tribe, has been discussed earlier.

Griffinia of the tribe Haemantheae has a high chromosome number (2n=77) which Sato (1938) suggested to be a heptaploid coming from a basic number of 11. In *Clivia*, most of the species investigated have originated from a basic number of 11, and diploid and tetraploid types are represented. Whittlake (1940, vide Darlington and Wylie, 1956) reported 2n=18 for *C. cyrtanthiflora* (*miniata* × *nobilis*).

The genus *Haemanthus* is very interesting from cytological point of view. It has a very different karyotype from the rest of the species of Amaryllidaceae in which cytological studies have been reported. This karyotype is that which Darlington (1956) calls bimodal chromosome complement. In this type of bimodality characteristic of the genus *Haemanthus*, one finds sharply contrasted long and short chromosomes without the presence of intermediate types. The basic numbers in this genus are n=8 and 9, and only diploid numbers of these basic sets are present. Sato (1938) commented that the karyotype in *Haemanthus* is similar to that found in *Alstremeria*. Sharma and Bal (1956) reported the finding of heteromorphic pair of chromosomes in *H. kalbreyeri*. Karyotype alteration in *Haemanthus* could be concluded to have come about by structural changes of chromosomes only. In *Leptochiton* a diploid count has been reported starting from a basic number of 12 but the original basic number could have been 6. In *Pancratium* 11, 12 and 23 might be suggested as the basic numbers. Starting with 11, one gets diploid and tetraploid types, and only tetraploid type in the 12 series. The somatic number of 46 found in *P. speciosum* by Inariyama (1937) could have originated from a basic number of 23 since this basic number is found in several genera of the tribe Eucharideae. In *Pamianthe* and *Elisena* this high basic number (n=23) is represented by diploid types only.

The situation in *Ismene* and *Hymenocallis* is somewhat similar to that observed in *Zephyranthes*. In *Hymenocallis* very many chromosome numbers have been reported. Taxonomically this genus is a difficult one (Flory and Schmidhauser, 1957). Sato (1938) proposed a basic number of 23 in *Hymenocallis*, which he thought was derived from n=11 by duplication and then was secondarily balanced. Other basic numbers here are 6, 10, 19, and of course 11. All these basic numbers are represented by an euploid series but aneuploid types are also present to a great extent. Apart from this, inconstancy of chromosome numbers is prevalent in this genus. For instance, Snoad (1955) failed to find a constant count of chromosomes in *H. calathina* in mitotic stages (2n=23-86), while Sharma and Bal (1956) could not find a constant number in *H. concinna*, among the small number of root tips studied by them. The significance of this inconstancy has been discussed by Sharma and Sharma (1957). The occurrence of metacentric and telocentric chromosomes in different taxa (Flory and Schmidhauser, 1957) indicate the role of structural changes in chromosome number evolution in this genus. Flory (1958) has also pointed out the part played by hybridization and apomixis is evolu-

tionary tendencies in *Hymenocallis*. In *Eucharis*, 11 has been suggested to be the basic number by Sato (1938), and he thought that the somatic number of 68 in *E. grandiflora* is secondarily balanced from a multiple of 11. If this suggestion is accepted then *Phaedranassa carmioli* (2n=46) is also secondarily balanced and the basic number 23 found here has also originated from an 11 series.

In *Hippeastrum* two basic numbers are represented (9 and 11). In the 9 series one gets only diploids, but in the 11 series, diploids, triploids, tetraploids and heptaploids are present. The situation in this genus is similar to that found in *Amaryllis*. Aneuploid types are also observed in *Hippeastrum* (2n=43 and 49). In *Sprekelia*, after Bose's (1958*c*) finding of 2n=60, c. 120, c. 150 and c. 180 chromosome number individuals, an apparently aneuploid series has been established. F_1 seedlings obtained from a cross between 2n=c. 180 × 2n=60 (Bose, 1961) indicate one of the ways in which individuals with different chromosome numbers have arisen. A count of the chromosome number in the F_1 seedling of this cross showed c. 120 chromosomes. It has been observed that in this monotypic genus, bulbs with 2n=60 chromosomes are highly fertile and set seed, while the higher chromosome number individuals are sterile and set seed very rarely. It might be mentioned here that in *Sprekelia* the highest chromosome number (2n=c. 180) of the family *Amaryllidaceae* has been recorded. Earlier reports show counts between 2n=c. 110 and c. 121, but only Mookerjea (1955) observed a constant somatic number of 116.

Lycoris is another interesting genus from the cytological point of view. In all the 14 taxa studied chromosomes have been found to be very large in size and small in number and they could be broadly divided into easily distinguishable V and rod shaped elements. Inariyama (1931, 1932, 1937, 1951*a*, 1951*b*) speculated that either fusion of two rods to form a V or the fragmentation of a V to form two rods has been responsible for the evolution of chromosome number, karyotype alteration and speciation in this genus. Sato (1939) also took into consideration the part played by fusion and fragmentation of chromosomes in karyotype evolution in *Lycoris*. However, Inariyama (1951*b*) concluded that a species with 22 rod chromosomes gave rise to all other types in *Lycoris* with different constitution of V and rods in them through the fusion of rod chromosomes, but he pointed out that for the evolution of karyotype in *Lycoris*, the part played by fragmentation of chromosomes could not be ignored (from *L. aurea* with 10 V and 2 rod chromosomes). Darlington (1956) took both these mechanisms into consideration to explain the karyotype evolution in *Lycoris*. Bose (1957, 1958*a*, 1958*b*, 1059*a*, 1959*b*) recognized the importance of these mechanisms in karyotype alteration in the species of *Lycoris*. In the preceding part of this discussion it was pointed out that Cave and Bradley (1943) also suggested these mechanisms (fusion and fragmentation) to be responsible for chromosome alteration in *Miersia chilensis*. They commented that, for the origin of V chromosomes, reciprocal translocations were more likely a mechanism than fusion of two rods. The role of translocation in bringing about karyotypic change and its importance in speciation has been reviewed by Burnham (1956). Swanson (1958) pointed out that there is no example of direct fusion of two rods chromosomes to form a V chromosome in the plant kingdom like that which has been amply demonstrated in *Drosophila* (Patterson and Stone, 1952).

At any rate, if the structure of the centromere, as described by Lima-de-Faria (1952, 1954), and the four points of breakage of certain regions in the structure of the centromere as suggested by Marks (1950), are taken into consideration, then one could visualise the ways a V chromosome might give rise to two rods (telecentric), which could remain functional. In *Lycoris*, in those species where one gets rods of the nearly terminal centromeric type (*L. aurea, L. traubii*, etc.) only, one can see them originating directly from the V's. But in those cases where subterminally constricted rods are present, Cave and Bradley's (1943) hypothesis, that telocentric rods could be converted into subterminally constricted rods through inversion, could be taken into account. In several species of *Lycoris* Inariyama (1951*a*) has observed metaphase I pairing of two rod chromosomes with one V chromosome. Similar configurations have been observed by Levan and Emsweller (1938) in *Nothoscordum bivalve*, by Cave and Bradley (1943) in *Miersia chilensis* and by Darlington and LaCour (1950) in *Campanula persicifolia*. In this species, Darlington and LaCour (l.c.) found both stable and unstable telocentric chromosomes. The stable telocentrics, which occurred in natural populations, were found to pair regularly, while the unstable ones, arising from metacentric chromosomes by misdivision, gave rise to isochromosomes. They also pointed out that the difference in behaviour of telocentric chromosomes depend on the structure and stability of their centromere. Unstable telocentrics, on the other hand, undergo secondary misdivision to give rise to supernumerary isochromosomes, which in turn may be stable as in *Nicandra* (Darlington and Janaki Ammal, 1945*b*) or semistable as in *Sorghum* (Darlington and Thomas, 1941) and *Poa* (Muntzing, 1948). If these supernumeraries are still unstable (Darlington and LaCour, 1950) they are either lost by tertiary misdivision or fragmentation or remain as supernumerary broken telocentrics and unequal isochromosomes, as has been observed in *Secale* by Muntzing (1944) and in *Zea* by Darlington and Upcott (1941).

The above discussion shows the mechanisms by which karyotype alteration could come about in the

various taxa of *Lycoris* studied (through fusion and fragmentation of chromosomes). In addition to this one also observes the role of gene mutation in the differentiation of 12 chromosome types of *L. aurea* and *L. traubii* (Bose, 1958*a*). Somatic numbers of 13, 14, 15, 16, 17, 27, 29+1B and 30 could also come about through hybridization. For instance, successful interspecific crosses in *Lycoris* have been reported by Inariyama (1951*b*) from a cross between *L. straminea* (2n=16) and *L. sprengeri* (2n=22), and also from a cross between *L. aurea* (2n=14) and *L. radiata* var. *pumila* (2n=22). Inariyama (1951*b*) also suggested the hybrid origin of *L. albiflora* (2n=17) and *L. squamigera* (2n=27) occurring in nature. *Lycoris albiflora* was believed by him to be originating from a cross between *L. radiata* var. *pumila* (2n=22) and *L. aurea* (2n=12) and *L. squamigera* from a cross between a diploid gamete of *L. straminea* (2n=16) and haploid gamete of *L. sprengeri* (2n=22). As evidence for these assumptions, he pointed out the morphological and karyological resemblances of *L. albiflora* with *L. straminea* var. *rosea* and *L. sprengeri*. Creech (1952) obtained seeds from a cross between a seed producing clone of *L. radiata* and *L. aurea* and the chromosome number in the F_1 seedling was counted to be 2n=19. Traub and Moldenke (1949) reported a cross between *L. traubii* and *L. radiata* and Traub (1957) described mature F_1 plant of this cross and pointed out the intermediate nature of this hybrid in so far as the leaf and flower character of the parents were concerned. These facts clearly show that in *Lycoris*, except the finding of apomictic forms, gene mutation, repatterning of chromosomes (translocations and inversion by fusion and fragmentation), polyploidy and hybridization have played active role. Extensive hybridization work and meiotic studies might reveal the nature of polyploidy and origin of the several taxa.

After *Allium* the largest number of species have been studied in *Narcissus*. In the other two genera of the tribe *Narcisseae*, *Tapeinanthus* and *Cryptostephanus*, only one species in each has been studied. In *T. humilis* Wylie (1952) reported a somatic number of 28, while in *C. vansonii* Gouws (1949, vide Wylie, 1952) found a somatic number of 24, but Darlington and Wylie (1956) have listed 2n=28 for this species (*C. vansonii*, Gouws, 1949). Wylie (1952) on chromosome morphological evidence took the 2n=28 species of *Tapeinanthus* to be closer to n=10 (11) species of *Narcissus*. Nagao (1929, 1933) and Fernandes (1946) have dealt on the evolutionary tendencies in *Narcissus*, while Wylie (l.c.) has given an account of the same in garden forms. Fernandes (1934) has offered a revised classification of the genus and has later (1951) pointed out that in the classification of *Narcissus* basic chromosome number and breeding behaviour can suggest a better classification than any other system proposed earlier. The works of these authors have shown that the processes responsible for the evolution in *Narcissus* are, gene mutation, chromosome alteration, polyploidy and intra- and intergroup crossing in both wild and cultivated forms. Wylie (l.c.) has classified the species in *Narcissus* in the following types: Sexually reproducing, clonal hybrids and fertile hybrids. Out of the two basic numbers suggested for this genus (7 and 10), majority of the species have n=7, while *N. tazetta* and two other closely related species have n=10 or occasionally 11. Recently, Sharma and Sharma (1961) have reported the finding of 2n=24 and 28 chromosome numbered types in *N. tazetta*. Only in *N. bulbocodium*, polyploid series with diploids, triploids, tetraploids, pentaploids and hexaploids have been found. Fernandes (1946) presumed that the basic number 10 was derived from the basic number 7, and Wylie (l.c.) suggested that in *Narcissus* a basic number of 10 could come about from a basic number of 7 through fragmentation near the centromere of a median or submedian chromosome since in the species with 7 as the basic number all the chromosomes have median or submedian primary constrictions, while those species with basic numbers of 10 or 11, 8 subterminally constricted chromosomes are present. Aneuploid types (2n=15, 17, 26 and 29) have also been reported in this genus by some workers. The findings of Nagao (1929, 1933), Fernandes (1934, 1951) and Wylie (1952) have also shown that in *Narcissus* several types, which were originally taken to be distinct species, are mere natural hybrids. Fernandes (1951) and Wylie (1952) pointed out that several diploid parents have contributed towards the improvement of *Narcissi* varieties. Wylie concluded that although polyploidy is rare in the species of *Narcissus* still it is responsible for the origin of garden forms. Sometimes tetraploids arise directly from diploids but oftentimes one gets triploids, and from the same, tetraploids arise. Unreduced gamete formation has been responsible for this evolution of garden forms. Darlington (1956) clarified the way through which segregation following polyploidy in hybrids has contributed towards the origin of garden varieties of Narcissi.

The above discussion shows that in Amaryllidaceae euploidy, aneuploidy, hybridization and apomixis have played significant role in the evolution of chromosome number. Changes in basic number have originated mainly through aneuploidy, which in turn has been brought about by structural changes of chromosomes. The part played by hybridization in change of basic number has also been recognized. The loss or gain of chromosome number and corresponding to it the decrease or increase in basic number and intra or interspecific chromosomal polymorphism has been attributed to fusion or fragmentation of chromosomes. In some genera this mechanism (fusion or fragmentation) is the chief source of intra and inter-specific chromosomal polymorphism and speciation, while in others

euploidy has been the contributing factor in speciation. In some dynamic genera, gene mutation, polyploidy, hybridization and apomixis have participated fully in the evolutionary tendencies, while in others only a few of such mechanisms have been responsible. It seems that in a genus like *Lycoris*, structural changes of chromosomes have been the dominant factor in speciation. Starting with an ancestral karyotype with all rod-shaped chromosomes (which has been found in several species) one can see the evolution of V shaped chromosomes (by fusion of two rods) in several species in this genus. On the other hand, when one starts with an ancestral karyotype with all V shaped chromosomes (which has not been found yet), the evolution of rod shaped chromosomes (by fragmentation) in several species in this genus becomes apparent. This process is operative in the diploid level but somewhere along the line, triploidy has intervened, and here again one finds the same mechanism playing the part. This is illustrated in the following diagram:

DIPLOID

22R * ⟶ 20R+1 V ⟶ 18R+2V ⟶ 16R+3V ⟶ 14R+4V ⟶ 12R+5V ⟶ 10R+6V ⟶ 8R+7V * ⟶ 6R+8V * ⟶ 4R+9V * ⟶ 2R+10V *

11V ⟶ 10V+2R * ⟶ 9V+6R * ⟶ 8V+6R* ⟶ 7V+8R * ⟶ 6V+10R * ⟶ 5V+12R * ⟶ 4V+14R ⟶ 3V+16R ⟶ 2V+18R ⟶ 1V+20R

TRIPLOID

33R * ⟶ 31R+1V * ⟶ 29R+2V ⟶ 27R+3V * ⟶ 25R+4V* ⟶ 23R+5V ⟶ 21R+6V* ⟶ 19R+7V ⟶ 17R+8V ⟶ 15R+9V ⟶ 13R+10V ⟶ 11R+11V ⟶ 9R+12V ⟶ 7R+13V ⟶ 5R+14V ⟶ 3R+15V ⟶ 1R+16V

16V+1R ⟶ 15V+3R ⟶ 14V+5R ⟶ 13V+7R ⟶ 12V+9R ⟶ 11V+11R ⟶ 10V+13R ⟶ 9V+15R ⟶ 8V+17R ⟶ 7V+19R ⟶ 6V+21R * ⟶ 5V+23R ⟶ 4V+25R* ⟶ 3V+27R * ⟶ 2V+29R ⟶ IV+31R *

** Indicates karyotypes which have been observed in the Lycoris species.*

It is evident from the above diagram that the ancestral types in the V-series are yet to be found. The sterility and fertility of the odd numbered ancestral types with 2n=11 (11V) and 2n=17 (16V +1R) chromosomes are also to be considered. But a careful look at the same diagram shows that many odd numbered sterile species have already been found both in the diploid and triploid series, with various combinations of rod shaped and V shaped chromosomes, as for example in the diploid series with 2n=13 (9V+4R) chromosomes and in the triploid series with 2n=27 (6V+21R) chromosomes. On the basis of these findings it can be hoped that most if not all of the karyotypes in the diploid and triploid series may be discovered when more taxa of *Lycoris* are brought under investigation. It may further be emphasized that, through hybridization between taxa with different karyotypes, so far studied, new karyotypes (those which have not been found) may originate. At any rate, the above diagram illustrates clearly that in *Lycoris*, evolution of chromosome number, karyotype alteration and speciation did not involve the addition of any extra chromosomal elements both at the diploid and tetraploid level.

B OR SUPERNUMERARY CHROMOSOMES

One of the most interesting things observed in Amaryllidaceae is the finding of very small chromosomes in several genera. A glance at Table 2 will show that they have been reported in *Agapanthus, Allium, Crinum, Cooperia, Haemanthus, Hippeastrum, Lycoris* and *Narcissus*. These are found in addition to the normal somatic complements. These types of chromosomes have been designated by various names, such as, B-chromosomes, supernumerary chromosomes, accessory chromosomes, etc., by different workers (Randolph, 1941, Muntzing, 1945, 1949, 1954, Ostergren, 1947, Frost, 1956). Darlington and Janaki Ammal (1945a) included all these chromosomes under the terminology of *f* or fragment chromosomes, but later on, Darlington and Wylie (1956) changed the terminology, and designated them as B-chromosomes.

In *Agapanthus* Riley and Mookherjee (1960) reported the occurrence of two fragments in *A. orientalis*, which were found only in emerging radicals but were absent in later stages and also in the root tips from the bulbs while in *A. sp.*, they were found in all stages. A somewhat similar situation was found by Milinkovic (1957) in rye, where supernumerary chromosomes, which were seen in primary roots and in pollen mother cells, were absent in the adventitious roots. It would be interesting to study the behaviour of these fragments in meiotic stages of these *Agapanthus* species. In *Allium cernuum* Levan (1932) reported the finding of accessory chromosomes.

Grun (1959) also observed small euchromatic accessory chromosomes in *A. cernuum*. He found that these accessories were without any visible constrictions but large accessory chromosomes with metacentric constrictions were also present. He pointed out that because of non-disjunction of these accessories during mitotic cell divisions, different cells had variable number of accessories in them. Recently, Sharma and Aiyangar (1961) observed a very remarkable phenomenon in *Allium stracheyi*. The diploid individuals of this species have 2-10 B-chromosomes in addition to the normal somatic number of 14 chromosomes, but these B-chromosomes are not present in the polyploid plants. Diploid bulbs of the species, which are found in the temperate regions, when brought down to the tropical climate, became polyploid in a month and the B-chromosomes were lost, which they ascribed as due to the effects of temperature

differences. In some cells of the polyploid plants 1-3 B-chromosomes were found. Their observations were made in the root tip cells of *A. stracheyi* and it would also be desirable to observe the behaviour of these B's in meiotic stages. Darlington's (1956) observation that the B's are present in the diploids and are absent in the polyploids can be taken into consideration in this connection.

In *Crinum longifolium* (*capense*) Sato (1938) observed two fragments. He also found two fragments in *Haemanthus albiflos*. In *Hippeastrum equestre* Mookerjea (1955) observed two fragments. In *Lycoris incarnata* Bose (1958b) observed one B or supernumerary chromosome to be present. This had a subterminal primary constriction and was probably euchromatic. In *L. radiata* Bose (1962) found an individual with a B or supernumerary chromosome. This species has usually 2n=22 and 33 chromosomes but one individual had 2n=31R+1V+1B or supernumerary chromosome. In *Narcissus* B or supernumerary chromosomes have been mostly reported by Fernandes (1947) and Wylie (1952). Both eu- and heterochromatic B chromosomes have been observed here. In this genus the behaviour of B-chromosomes has been studied in great detail and Fernandes (Darlington, 1956) has shown that plants with B-chromosomes are very successful in competing with their relatives which have no B-chromosomes. Fernandes also observed that in *N. bulbocodium* B-chromosomes delay flowering. Furthermore, Fernandes (1949) pointed out that in *N. bulbocodium* due to the action of a single gene, euchromatic supernumerary chromosomes change to heterochromatic one. Muntzing (1950) has suggested further investigation of this interesting observation by Fernandes (1949).

As regards the origin of these B or supernumerary or accessory chromosomes although no direct evidence is available, Darlington's (1956) hypothesis that they arise from A or normal chromosomes by misdivision of the centremere seems plausible. He also speculated that they could originate through meiotic irregularities. The origin of fragments from A chromosomes have been observed by Darlington and Thomas (1941) in *Sorghum* and by Muntzing (1948, 1949) in rye. Muntzing and Lima-de-Faria (1949, 1953) studied the structure of the standard fragment and its derivatives in rye, and secured evidence for the origin of two isochromosomes from the standard fragment. Fernandes (1946, 1947) found both eu- and heterochromatic B-chromosomes to be present in *N. bulbocodium*, while Wylie (1952) found both types to be present in different species of *Narcissus*.

It may be pointed out here that extensive studies in these B or supernumerary chromosomes are needed, which should include studies specially in the meiotic and pollen mitotic stages. Another line of study should include geographical distribution of taxa in which these chromosomes have been located. Hybridization between types with B's and those without B's should be attempted to study their pairing relationships, if any, with A's. Lastly, the chromaticity of B or supernumerary chromosomes in different species should be studied in detail.

CONCLUSIONS

A review of the cytotaxonomic studies carried out in the family Amaryllidaceae by several workers shows that diversification in this family has been effected through gene mutation, chromosome repatterning by fusion and fragmentation (through translocation and inversion), polyploidy (eu-, aneu-, hetero, auto-, and allo-), hybridization and apomixis. In some genera, all of these mechanisms have been operating, while in others most of these have been responsible, while in still others only a few of these have been playing a part. In addition to this, hetero- or euchromatic B or supernumerary chromosomes, found in some genera, have played additional role. It may be pointed out here that although in many genera detailed knowledge is available as regards somatic chromosome numbers and karyotypes, meiotic studies are lacking in most of the genera. It is hoped that in future more attention will be directed to this aspect. This will give one a better picture of the evolutionary tendencies operating in the family. The pairing behaviour of chromosomes at meiosis of the taxa in which polyploid series have been reported, should be thoroughly studied, in order to find out the nature of polyploidy.

Another line of investigation should include the study of heterochromatin. The importance of this line of investigation has been pointed out by Swanson (1957) who showed that, for a change in basic number without the intervention of polyploidy, Darlington's (1937) scheme as modified by Stebbins (1950) that the gain or loss of a chromosome could come about only by the gain or loss of a centromere and in order to effect this, inertness (heterochromatin) or activeness (euchromatin) of the chromatic substance close to the centromere plays a part, should be taken into consideration. The original postulation of Navashin (1932) that a centromere cannot arise *de novo* is of fundamental importance in this connection. The finding of structural alteration (fusion and fragmentation) of chromosomes, and the B or supernumerary chromosomes, in this family, attach added importance for the study of heterochromatin. Swanson (l.c.) also pointed out that the cytochemical approach made by Mirsky and Ris (1951), through their work on the evolutionary significance of DNA content of animal cells, should be included in any study of karyotype evolution along with other criteria. Recently, Sharma and Sharma (1959) have discussed the issues which could be considered in speciation

and phylogenetic studies. Artificial hybridization work to know more about the nature of species and group relationship should be attempted on a large scale. Another line of approach should be to find out the occurrence and types of apomixis in the various taxa and last but not the least, investigation on the cytogeography of different species, specially the area of distribution of a polyploid genus or species, in which a polyploid series has been discovered.

Cytotaxonomically, delimitation of the family Amaryllidaceae by Hutchinson (1934, 1959) has been justified but the suggestions advanced by some workers for the inclusion of Hemerocalleae in Amaryllidaceae and for necessary changes in the tribal level, may be justified.

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TABLE 1

Chromosome numbers in different tribes and genera of Amaryllidaceae

Tribes and Genera*	Range in 2n number	Basic number **
AGAPANTHEAE		
Agapanthus	29, 30, 30+2B, 32, 32+2B	15, 16
Tulbaghia	12	8
ALLIEAE		
Bloomeria	18	9
Allium	14, 16, 16-22, 16-100, 16-108, 17, 18, 19, 21, 24, 25, 26, 28, 28-32, 32, 40	7, 8, 9
Nothoscordum	16, 16-22, 18, 19, 24	8, 9
Brodiaea	10, 10-12, 12, 14, 30, 36, 42, 72	5, 6, 7, 9
Milla	39	13 ?
Brevoortia	c.40, 48	8
CILLIESTEAE		
Miersia	20, 21	10(11)
GALANTHEAE		
Galanthus	24, 25, 28, 36, 48	12
Lapiedra	22	11
[*Sternbergia*]	20, 22, 24, 33	10, 11, 12
Leucojum	14, 16, 18, 22	10, 11, 12
AMARYLLIDEAE		
Amaryllis	12, 18, 22, 39, 44, 66	6, 9, 11
Brunsvigia	22	11
Anoiganthus	16	8
Ungernia	24	12
Nerine	22, 22-26, 24, 26, 28, 33, 36	11, 12
CRINEAE		
Chlidanthus	20	10
Crinum	22, 22+2B, 33, 72	11
Ammocharis	22	11
Cyrtanthus	14, 16, 18, 20	7, 8, 9, 10
Vallota	16	8
Ungernia	24	12
ZEPHYRANTHEAE		
Zephyranthes	12, 14, 18, 22, 24, 25, 28, 38, 42, 44, 44-50, 45, 46, 46-48, 48, 49, 54, 55, 55-59, 56, 58, 60, c.96	6, 7, 11
Cooperia	24, 48, 54, 69+1B	12
Sternbergia	20, 22, 24, 33	10, 11, 12
HAEMANTHEAE		
Buphane	22	11
Clivia	18, 22, 44	9, 11
Griffinia	77	11
Haemanthus	16, 16+2B, 18	8, 9
IXIOLIRIEAE		
Ixiolirion	24	12
EUCHARIDEAE		
Hyline	20	10
Pamianthe	46	23
Pancratium	22, 44, 46, 48	11, 12, 23
Leptochiton	24	12
Elisena	46	23
Ismene	45, 56, 74-80, 104-110	7, 8, 10
Hymenocallis	38-40, 42, 44, 46, 48, 50, 52, 54-69, 70, c.84 88-98	6, 10, 11, 19, 23
Eucharis	44, 68	11
Eurcyles	20	10
EUSTEPHIEAE		
Phaedranassa	46	23
HIPPEASTREAE		
Hippeastrum	18, 22, 22+1B, 33, 43, 44, 49, 77	9, 11
Sprekelia	60, 116, c.117-121, c.120, c.150, c.180	29, 30
Lycoris	12, 13, 14, 15, 16, 17, 22, 27, 29+1B, 30, 32+1B, 33	6, 7, 8, 11, 15
NARCISSEAE		
Cryptostephanus	28	14
Tdpeinanthus	28	14
Narcissus	14, 14+1B, 14+0–2B, 14+0–4B, 15, 17, 20, 21, 22, 24, 26, 29, 30, 33, 35, 42, 50	7, 10, 11

* Based according to Hutchinson's (1934, 1959) system of classification.

** Includes original and derived basic numbers.

TABLE 2

B or supernumerary chromosomes in Amaryllidaceae

Taxa	2n	Author
Agapanthus orientalis	32+2 B	Riley and Mookerjee 1960
A. sp.	30+2 B	Riley and Mookerjee 1960
Allium cernuum	14+variable B	Levan 1932
A. cernuum	14+variable B	Grun 1959
A. stracheyi	14+2–10 B	Sharma and Aiyanger 1961
Crinum longifolium (capense)	22+2 B	Inariyama 1937
Cooperia brasiliensis	69+B	Traub 1945
Haemanthus albiflos	16+2 B	Sato 1938
Hippeastrum equestre	22+f	Mookerjea 1955
Lycoris incarnata	29+1 B	Bose 1958c
L. radiata	32+1 B	Bose 1962
Narcissus asturiensis	14+0–2 B	Wylie 1952
N. bulbocodium Hoop petticoat	14+0–4 B	Fernandes 1949
N. bulbocodium v. *citrinus*	14+0–2 B	Fernandes 1949
N. calcicola	14+0–2 B	Wylie 1952
N. cyclamineus	14+0–1 B	Wylie 1952
N. juncifolius	14+1 B	Fernandes 1939
N. minor v. *pumilis*	14+1 B	Wylie 1952
N. bernardi (ps. nar × post) (hybrid species)	14+1 B	Wylie 1952

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