A STUDY OF GREAT-HEADED GARLIC IN ILLINOIS

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ABSTRACT. — Unusually large-bulbed *Allium* specimens, grown as a condiment in southern Illinois, were cloned, cytologically investigated, and found to belong to the sterile hexaploid ($2n = 48$) race of the great-headed garlic, *Allium ampeloprasum* L. var. *ampeloprasum*. Chromosomes and specimens are illustrated. Gross morphological data on clonal hexaploids, and from previous and newly reported collections of this "garlic", are tabulated.

Unusually large garlic-like *Allium* bulbs, grown in gardens for use as a condiment by people of Italian descent in Jackson Co., Illinois, were called to our attention in 1964. Several of these "giant" bulbs were obtained and cultivated as clones in Carbondale, outdoors and in a greenhouse, in order to have material to enable us to investigate the cytology and identity of the plants.

Cytological investigations comparing normal and colchicine-treated (conc. 0.05%) root tips of *Allium sativum* and of the "giant" taxon were made. In addition, smear preparations from anthers and paraffin-embedded, sectioned material from ovules of the "giant" taxon were used. Farmer, Navashin, Allen-Bouin, Zenker, and LaCour 2BE solutions were used as fixatives. Aceto-carmine, acetic-orcein, and Feulgen's squash technique were used as rapid stains. Paraffin-embedded material sectioned at 10 microns was stained by the following methods: Feulgen-light green, safranin-fast green, PAS-hematoxylin-picric acid, Fleming's triple stain, and LaCour's crystal violet.

In contrast to the 16 chromosomes counted in the diploid *Allium sativum*, 48 chromosomes were found in our hexaploid "giant" taxon (Figs. 1 and 2). This places the latter

FIGURE 1. 48 chromosomes at C. metaphase. Treated with 0.05% colchicine for 12 hours.

Upper arrow: One member of the homologous pair of chromosomes with a subterminal centromere.

Lower arrow: One member of the homologous pair of chromosomes bearing a constriction on the short arm. See also insert marked by double arrow.

FIGURE 2. 96 chromatids at C. anaphase. Cells treated with 0.05% colchicine for 12 hours.

FIGURE 3. C. metaphase showing approximately 60 chromosomes. Cells treated with 0.05% colchicine for 12 hours.

FIGURE 4. Metaphase and anaphase with slanted equatorial plates.

FIGURE 5. Metaphase with diagonally located equatorial plate. Note the crowded condition of the chromosomes and the narrow nucleoplasm ratio.

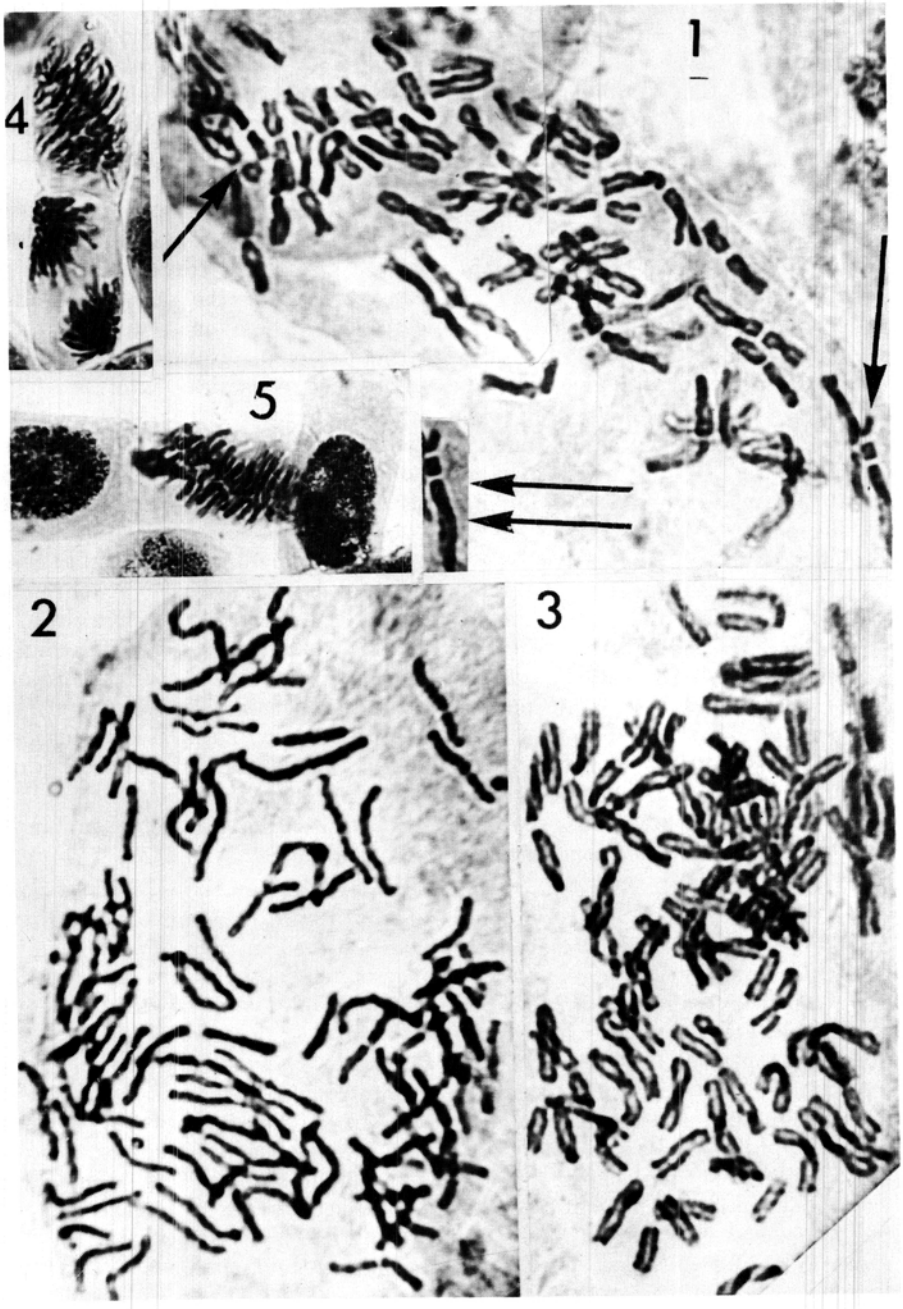

PLATE I.

taxon in section Porrum, (basic number x = 8) of the *Allium* genus. Occasionally, however, cells were found with chromosome numbers either higher or lower than 48, such as 34, 39, 40, 60, 62, and circa 74 (Fig. 3). This chromosomal instability is apparently caused by a noticeably lowered nucleus-cytoplasm ratio found in the cells of the hexaploid taxon. In fact, about 28% of the mitotic prometa- or metaphase configurations exhibited a slightly slanted or sometimes diagonally-positioned equatorial plate (Fig. 4). This alteration of mitotic geometry elongates the equatorial plate, and assures better accommodation during the lining up of the centromeres of the chromosomes. In relatively narrow cells, (Fig. 5) however, the long axis of the spindle becomes shorter, which in turn hinders the complete separation of the sister chromatids from each other. Incomplete separation of such chromatids was frequently observed. In some cells, this condition leads to the separation of chromatids into 3 or 4 groups which were found lying in tandem position in the narrow, long cells.

As expected, the size of the nuclei of our hexaploid taxon was larger, and measured in Feulgen-stained material an average of 1552.5 cubic microns in volume, while the diploid measured only 597.1 cubic microns. Both of these averages were calculated from the measurement of 400 nuclei. Similarly, the size of the nucleoli increased noticeably. However, the average number of nucleoli per nucleus showed only a slight increase yielding an average of 2.34 in the hexaploid and 2.19 in the diploid. Out of the 48 chromosomes, 46 carried median or submedian centromeres, and 2 carried subterminal ones (Fig. 1, upper arrow). Two chromosomes which had submedian centromeres and a constriction on the short arm (Fig. 1, single and double arrow) were considered as nucleolar chromosomes. The presence of a third single chromosome with a median centromere bearing 2 constrictions on the same arm indicates that this taxon is karyotypically heterozygous. None of the chromosomes had a typical satellite. The low average number of nucleoli found in the hexaploid taxon is related to the fact that only 3 constrictions bearing chromosomes were present in this karyotype.

It is pertinent to note that a competition between nucleolar chromosomes discovered by Navashin (1934) in *Crepis* hybrids might eliminate not only the function, but also the nucleolar constriction of the functionally suppressed chromosomes. In our taxon a similar phenomenon may account for the low number of chromosomes carrying a nucleolar organizer.

Early degeneration of the sporogonial tissue, causing total sterility, was observed in the anthers. Abnormal pollen mother cells, heterogeneous in size and shape, were also found but only in a few cases. Apparently, some of the cells of the sporogonial tissue were able to differentiate to that level. However, meiosis was never observed in these abnormal pollen mother cells. Similarly, total sterility caused by early degeneration of the nucellar tissue was found on the female side, although in 4 cases we observed megaspore cells, and in one case an embryo sac-

like complex, containing pycnotic nuclei.

It is interesting to note that a similar large-sized garlic marketed in northwest India as a substitute for the normal garlic was collected by Khoshoo and Sharma (1957), and found to be also hexaploid and totally sterile on both the male and female sides. Khoshoo, Atal, and Sharma (1960) identified this taxon as *Allium ampeloprasum* Linn. The heterozygous karyotype contained only median and submedian centromeres, among which were 3 pairs of homologous chromosomes and 6 single chromosomes which carried nucleolar or secondary constrictions.

Ved Brat (1964) established 6 different types of nucleolar chromosomes in *Allium* genus. The section Porrum is characterized by two types, "Sativum" and "Scorodoprasum." Both types have a "median-submedian" centromere and one constriction, which is proximal in the "Sativum" type and "median-submedian" in the "Scodoprasum." In contrast to the findings of Ved Brat and Khoshoo, Atal, and Sharma, our taxon had a pair of chromosomes with a subterminal centromere (Fig. 1), only one pair of nucleolar chromosomes, plus a single chromosome with 2 secondary constrictions.

Male sterility is a well-known phenomenon in *Allium*, and the development of sterile anthers is frequently associated with the presence of viviparous bulbils which occur mixed with the flowers in the umbel. However, in our hexaploids, bulbils were never found.

The large size of the vegetative

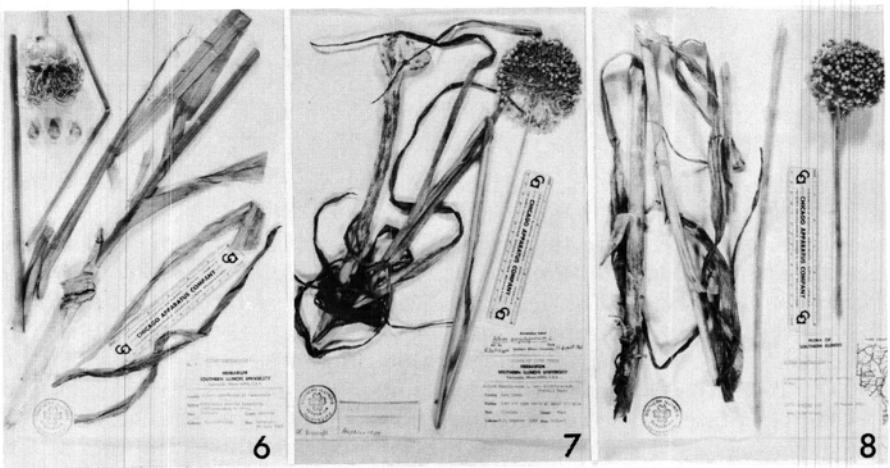

PLATE II.

FIGURE 6. Specimen from a Carbondale-cultivated clone of *A. ampeloprasum* L. var. *ampeloprasum* known to be hexaploid and sterile. The stem is 12.3 dm tall; note large and small bulblets comprising bulb.

FIGURE 7. Specimen of *A. ampeloprasum* L. var. *ampeloprasum* which was growing spontaneously in Pope County, Illinois. The stem is 12.2 dm tall.

FIGURE 8. Specimen of *A. ampeloprasum* L. var. *ampeloprasum* cultivated in Pope County, Illinois. The stem is 15.4 dm tall.

TABLE 1. — Vegetative Characters of *A. ampeloprasum* L. var. *ampeloprasum*.

Specimen	Bulb Diameter (cm)	No. of Cloves in Bulb	Clove Length (cm)	Clove Diameter (cm)	Stem Height (dm)	No. of Leaves*	Leaf Length (dm)	Leaf Width (cm)
DeFilipps 1 (SIU)	4.5	8 (5 large & 3 small)	2.2-3.0 large; 1.2-1.6 small	1.5-3.0 large; 1.2-1.6 small	12.3	5	4.4-4.8	2.5-2.6
DeFilipps 2 (SIU)	5.5	4	2.6-4.0	1.6-3.0	13.5	7	3.9-4.1	1.2-1.7
Hopkins 1208 (SIU)	5.0	3 (incomplete bulb)	3.0-3.3	1.7-2.0	12.2	6	3.9-4.5	1.4-1.5
Wiley s.n. (SIU)	5.0	4	4.0-5.0	2.7-3.5	15.4	5	5.1	2.0-2.3
Fuller & Fisher 115 (F)	—	—	—	—	6.0 (incomplete specimen)	3	4.3	1.6
Khoshoo, Atal & Sharma's hexaploids (1960)	5.0-6.5	1; 4-6	3.0-4.5	—	8.9-9.0	—	3.0-3.5	1.5-1.7

* All specimens have flat leaves with scabrous margins and scabrous keel.

organs, the sterile flowers, and the absence of inflorescence bulbils make our material referable to the great-headed garlic, *Allium ampeloprasum* L. var. *ampeloprasum* (Fig. 6). This taxon grows wild in Europe, Southwest Asia, and North Africa (Hegi, 1909). It has been introduced into the United States, where it is cultivated for use as a condiment and as an ornamental (due to its large overall size), and escapes and persists near dwellings. It has been recorded from several states, including Tennessee (James, 1956), North and South Carolina (Ahles, Bell & Radford, 1958), Kentucky (Browne, 1963), Mississippi (Pullen, 1967), Alabama (Jones, 1968), and Illinois (Browne, 1963).

The basis for the previous Illinois record is *Fuller & Fisher 115 (F)*, collected in wet fields in the Union County State Forest in 1940. In 1968 this area was searched by the junior author and Mr. A. Skorepa, but no specimens were located. Two more recent Illinois collections are extant: *Hopkins 1208* (SIU), near an old home ¼ mile north of Lusk Creek Gorge, Pope Co. (Fig. 7), and *Wiley s.n.* (SIU), cultivated in a garden in Harrisburg, Pope Co. (Fig. 8). Details of the gross morphology of these two collections and from two plants from our hexaploid

TABLE 2.—Floral Characters of *A. ampeloprasum* L. var. *ampeloprasum*.

Specimen	Umbel Diameter (cm)	Pedicel Length (cm)	Tepal* Length (mm)	Pistil Length (mm)	Style Length (mm)	Filament Condition	Seeds
DeFilipps 1 (SIU)	9	4.5	4.5	4.0-4.5	2.5-3.0	inner 3 with appendages	none
DeFilipps 2 (SIU)	8	3.5-4.5	4.5	4.0-4.5	2.5-3.0	inner 3 with appendages	none
Hopkins 1208 (SIU)	8.5	4.0	4.5-5.5	4.0-4.5	3.5-4.0	inner 3 & outer 3 with appendages	few, shriveled
Wiley s.n. (SIU)	8.5	3.0-3.5	4.0	4.0	2.0-3.0	inner 3 with appendages	few, shriveled
Fuller & Fisher 115 (F)	7.5	3.0	4.2-4.5	3.5-4.0	3.0	outer 3 with appendages	none
Khoshoo, Atal & Sharma's hexaploids (1960)	—	—	—	—	—	inner 3 & outer 3 with appendages	none

* All specimens have outer 3 tepals verrucose-scabrate; inner 3 often not or weakly verrucose-scabrate.

clone, *DeFilipps 1* (SIU) (Fig. 6), and *DeFilipps 2* (SIU) are given in Tables 1 and 2.

Two current studies of cultivated *Alliums* differ in their circumscription of *A. ampeloprasum*. Jones & Mann (1963) prefer to treat this species as composed of three entities: great-headed garlic, leek, and kurrat, indicating that they were probably derived from the same wild parent. Millan (1952) separates the kurrat (*A. kurrat*, Schweinfurth ap. Krause) from *A. ampeloprasum*, the latter including the great-headed garlic (*A. ampeloprasum* L. var. *ampeloprasum*) and the leek (*A. ampeloprasum* L. var. *porrum* (L.) Gay). These taxa may be differentiated, according to Millan (1952), as follows:

1. Umbel with bulbils.
   2. Bulbs without cloves (bulblets) ..... *A. kurrat*
   2. Bulbs with cloves (bulblets) ..... *A. sativum*
1. Umbel without bulbils.
   3. Plants with bulbs; bulbs with large and small cloves; flowers sterile .... *A. ampeloprasum* var. *ampeloprasum*
   3. Plants with an enlarged

base, but without bulbs; flowers fertile ....*A. ampeloprasum* var. *porrum*.

Previous cytological studies have shown that *A. ampeloprasum* var. *ampeloprasum* (sensu Millan, 1952) exists in three forms or races: Diploid with 2n = 16 (Renzoni, 1964), tetraploid with 2n = 32 (Maude, 1940; LaCour, 1945; Ved Brat, 1965), and hexaploid with 2n = 48 (Khoshoo & Sharma, 1957; Khoshoo, Atal & Sharma, 1960; Ved Brat, 1965.) In the reported hexaploids the source of investigated material was India, and the two former articles (1957, 1960) reported total sterility of flowers, whereas the latter reported vivipary. Ved Brat (1965) noted tetraploid *A. ampeloprasum* as being a sexual outbreeder and hexaploids as viviparous asexually.

According to our study of living specimens, this taxon in Illinois is hexaploid and sterile, and thus cannot breed sexually. However, no bulbils were found in any inflorescences, so reproduction by vivipary is excluded. In Illinois this variety is reproduced vegetatively from bulblets from the underground bulb, which is usually compound. Simple-bulbed plants have been observed in our study, as well as by Khoshoo & Sharma (1957), Khoshoo, Atal & Sharma (1960), and Millan (1952).

Khoshoo, Atal & Sharma (1960) noted that *A. ampeloprasum* var. *ampeloprasum* is karyotypically heterozygous. The heterozygosity, which may have arisen either after its origin or more probably as a result of hybridization between karyotypically dissimilar forms preceding the institution of polyploidy, is maintained by the vegetative reproduction, which has been discussed by Galil (1965, 1966). At present it is not possible to comment on the origin of the hexaploid race and/or its relationship to other races until detailed studies of all the karyotypes concerned are available, a conclusion also reached by Khoshoo, Atal & Sharma (1960).

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