STUDIES IN THE AGAVACEAE. I. CHROMOSOME MORPHOLOGY AND NUMBER OF SEVEN SPECIES

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Introduction

The position of the family Agavaceae has long been controversial. Hutchinson (1934), considering inflorescence type and habit more stable characters than ovary position, assigned to this group the most highly evolved tribes of the Liliaceae and Amaryllidaceae. This amounted to a resurrection of the old family Agavaceae (Endlicher, 1841; Lotsy, 1911), the nomenclatural type of which is the genus *Agave*. Hutchinson's decision has provoked much discussion among botanists. His arguments in refutation of the classical position are not numerous and may be quoted here: "In tracing out the relationships of Monocotyledons amongst themselves I have come to the conclusion that the character of the superior or inferior ovary has often been stressed too much and has led to artificial classification." He thus eliminated from consideration the single character separating the Liliaceae and Amaryllidaceae and continued, "To my mind the type of inflorescence is of much more importance than the superior or inferior ovary, and the result is a nearer approximation of allied genera." On this basis, he proposed an arrangement which transfers several genera from the two families and places them in others, for example, Agavaceae, Smilacaceae, Ruscaceae, and Trilliaceae. Characters cited by Hutchinson to separate the Amaryllidaceae from the Liliaceae include the presence of a scapose umbellate inflorescence, and involucres of two or more membranous bracts (rarely but one), true umbels being unknown in the Liliaceae.

To be sure, differences between these families are not profound; in many cases the primary distinction is one of habit. With respect to the family Agavaceae, Hutchinson wrote, "It is not clearly marked by any one character from the Liliaceae and is based mainly on habit."

The family Agavaceae includes plants with subterranean rhizomes, long or short stems which are usually arborescent with leaves in a basal rosette, the leaves narrow, thick, and fleshy, and entire or with a spinescent margin; inflorescence racemose or paniculate, the branches of the inflorescence with large bracts at their bases. Members of the family lack bulbs of the kind found among the Liliaceae and their inflorescences are never true umbels as in the Amaryllidaceae.

FIG. 1. A general view of the *Agave* section at the Jardín Bctánico, UNAM.

Contemporary with Hutchinson's work was the publication of the observations of McKelvey and Sax (1933) on the morphological and cytological affinities of *Yucca, Hesperaloë, Hesperoyucca, Cleistoyucca,* and *Samuela* (Liliaceae), and *Agave* and *Fourcraea* (Amaryllidaceae). Whitaker (1934) and Sato (1935) believed that *Yucca, Agave,* and related genera should be referred to a single group, since all possessed similar chromosomal patterns: 25 large and 5 small chromosomes. Thus, from a different point of attack, Hutchinson's thesis was corroborated.

On the basis of cytological evidence, most taxonomists are agreed on the necessity of a re-evaluation of the systematics of these groups. Some have suggested the erection of a greater number of families (Sato, 1942), other writers have considered the unification of the Amaryllidaceae and Liliaceae into a single family (Gómez-Pompa, 1963; Thorne, 1968), or the union of the two families while maintaining the family Agavaceae

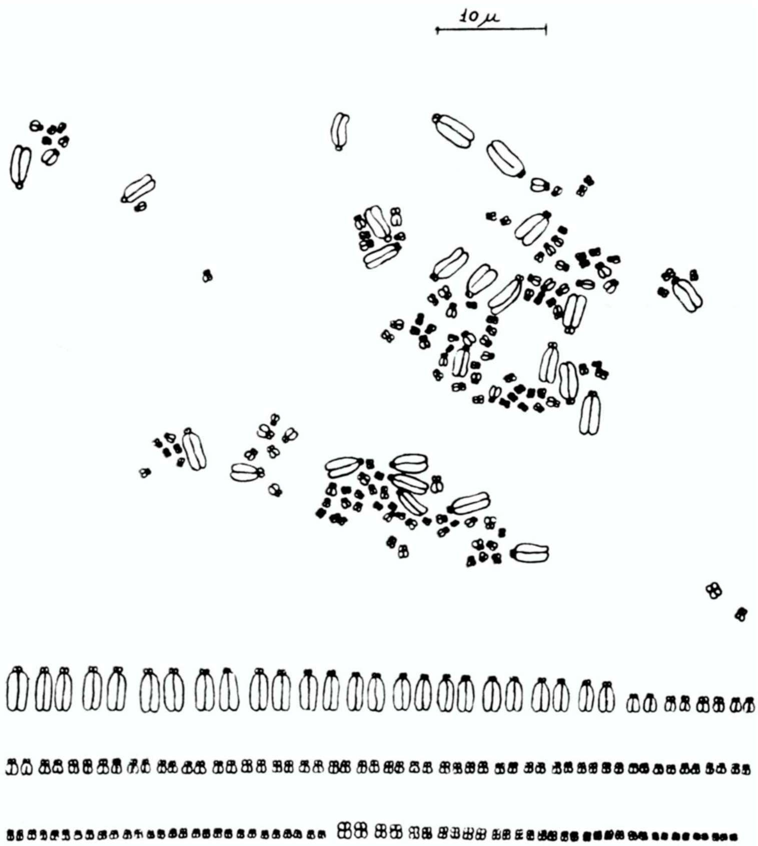

FIG. 2. Camera lucida drawings of the mitotic chromosomes of *Agave mapisaga*, **2n = 150.**

(Cronquist, 1968).

Cytological evidence enabling us to take a position is meager. In *Agave,* for example, chromosomal data are available for less than 20% of the species; moreover, several genera have yet to be analyzed (table 1). Equally important, however, is the development of study in other fields which will provide more information on these groups. For this reason, it was decided to begin work with the plants of the Botanical Garden of the Universidad Nacional Autónoma de México. The Garden possesses one of the richest collections of Agavaceae in the world (fig. 1), with nearly all Mexican genera and more than 100 species of the family in cultivation. The plants have been collected by the personnel of the Garden and careful records concerning origin have been maintained.

This paper presents the preliminary results of our work. We plan to

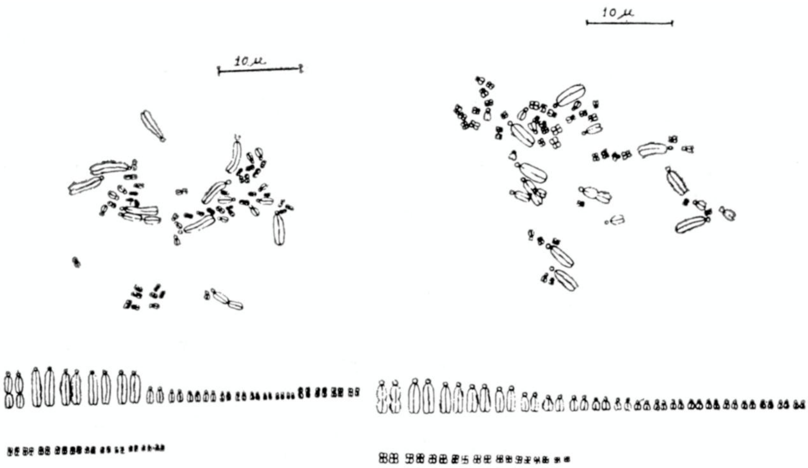

FIG. 3. Camera lucida drawings of the mitotic chromosomes of: A (left), *A. nizandensis*, **2n = 60**; B (right), *A. xalapensis*, **2n = 60.**

TABLE 1. A SUMMARY OF CHROMOSOMAL STUDIES OF THE GENERA OF AGAVACEAE FROM DIFFERENT AUTHORS.

L = long chromosomes, M = medium chromosomes, and S = short chromosomes.

Tribe	Genus	Karyotype
Hosteae	*Hosta* (Japan, China)	30 . . . 3n(4L + 1M + 25S)
Yucceae	*Yucca* (America)	30(5L + 25S)
	Hesperaloe (America)	30(5L + 25S)
	Clistoyucca (America)	30(5L + 25S)
	Samuela (America)	30(5L + 25S)
Dracaeneae	*Cordyline* (Tropics except Africa)	19 . . . 4n(2L + 17S)
	Cohnia (Madagasc. I., N. Caled.)	....
	Dracaena (Tropics)	19 . . . 5n(2L + 17S)
	Sansevieria (Africa, Asia)	20 . . . 6n(2L + 18S)
Phormiae	*Phormium* (N. Zealand)	16(4L + 12S)
Nolineae	*Nolina* (America)	18–19(6L + 13S)
	Calibanus (America)	....
	Dasylirion (America)	19(6L + 13S)
	Beaucarnea (America)	19 (?L + ?S)
Agaveae	*Agave* (America)	30 . . . 6n(5L + 25S)
	Furcraea (America)	30(5L + 25S)
	Beschorneria (America)	30(5L + 25S)
	Doryanthes (Australia)	24(2L + 22S)
Polyantheae	*Polianthes* (Trop. Amer.)	30(5L + 25S)
	Prochnyanthes (Mexico)	....
	Pseudobravoa (Mexico)	....
	Bravoa (Mexico)	30(5L + 25S)

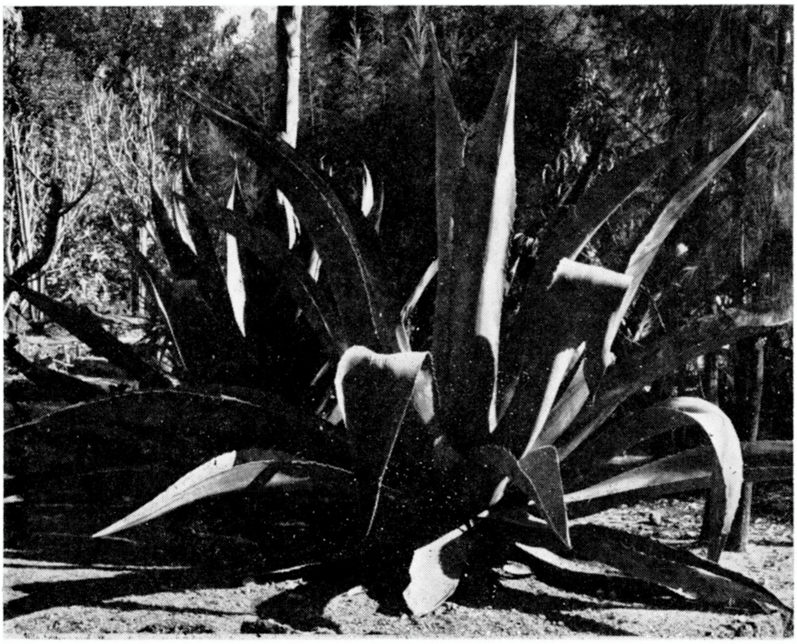

FIG. 4. *Agave mapisaga*, this species is the most common species cultivated for "pulque" in the Valley of Mexico.

assemble more data to facilitate a resolution of problems related to evolution and classification in this group.

On the basis of karyotype, it is possible to divide all genera included in the Agavaceae into two groups. In the first, including *Yucca* and *Agave*, somatic cells are characterized by 30 pairs of chromosomes, 5 of which are very large and 25 very small. The second group, with *Nolina*, *Dasylirion*, and allied genera, includes plants whose somatic cells contain 19 pairs of chromosomes without marked difference in size.

The study of the possible relationships between the two karyotypes of the family is especially interesting. Although the similarity of the karyotypes of *Yucca* and *Agave* supports the view that these genera are allied, the distinct karyotypes of the genera of the *Nolina* group seem to furnish a rationale for their segregation.

In the present paper the chromosomal complements of seven species are described, six of which were hitherto unstudied.

MATERIALS AND METHODS

Two sorts of mitotic tissue were examined: stamen filaments and roots from adult plants cultivated in the Botanical Garden of the Insti-

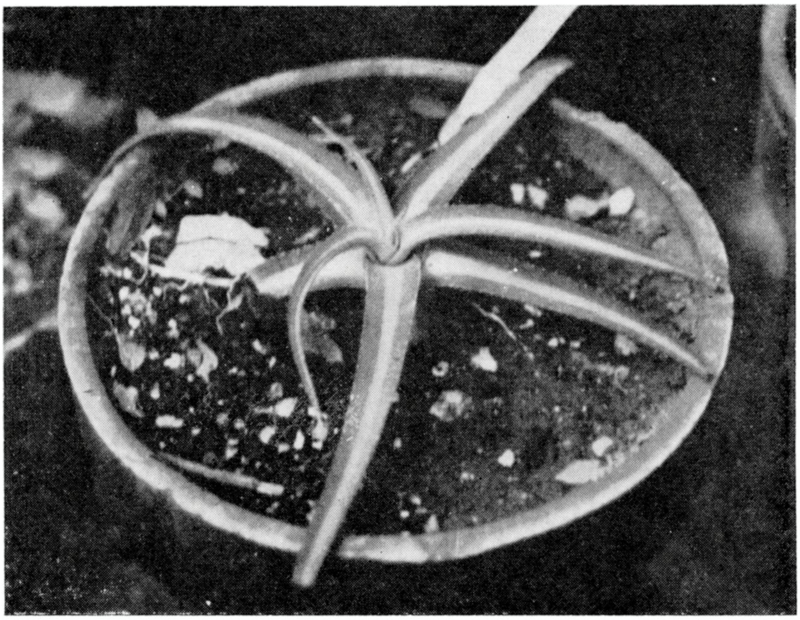

Fig. 5. *Agave nizandeniss* (from the type locality) growing in the Jardin Botánico, UNAM.

tuto de Biología of the Universidad Nacional Autónoma de México. Voucher specimens have been deposited in the Herbario Nacional del Instituto de Biología (MEXU). With both materials the Acetic-orcein-Janus green technique (Villalobos-Pietrini, 1965) was employed, making possible permanent preparations of cells held in metaphase by means of colchicine (C-metaphases).

RESULTS

Agave mapisaga Trel. **2n = 150 (25L + 125S).** ***Chimal 65,*** **Naucalpan**, State of Mexico. The chromosomal complex of this species identifies it as a pentaploid with 25 large submetacentric and 125 small metacentric and submetacentric, chromosomes (fig. 2). The plant is cultivated in the Valley of Mexico for the production of pulque (fig. 4).

This represents the second described pentaploid in the genus, the first being *Agave sisalana* (Sato, 1935). In *A. atrovirens,* Sato (1938) found 180 chromosomes (of which 30 were large and 150 small), corresponding to a hexaploid.

Agave nizandensis Cutak. **2n = 60 (10L + 50S).** *Chimal 29,* Nizanda, Oaxaca. The large chromosomes are submetacentric, one pair exhibiting secondary constriction. The small chromosomes are metacentric and submetacentric (fig. 3). This rather rare and infrequent species is from Nizanda, Oax. (fig. 5).

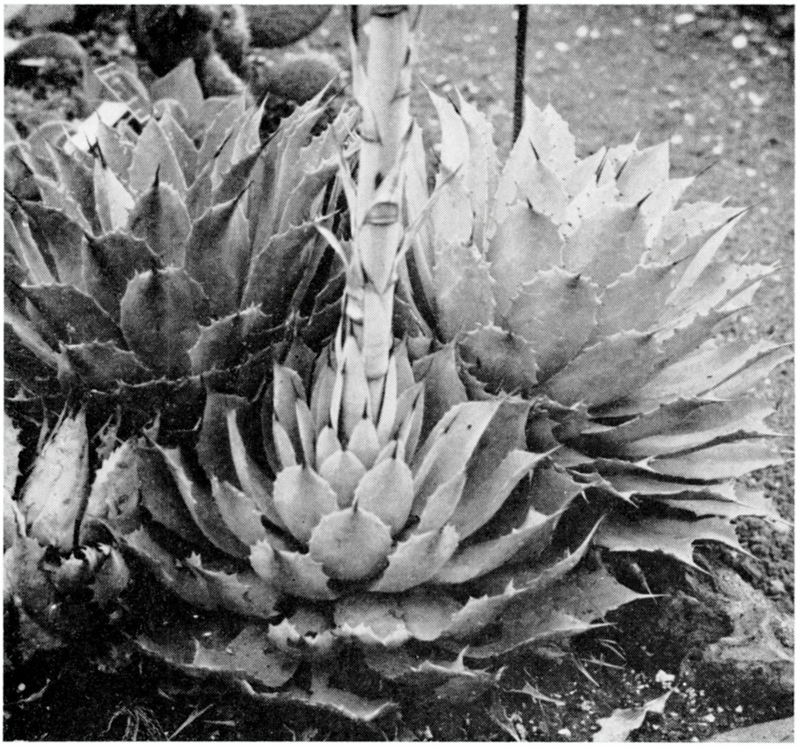

FIG. 6. *Agave verschaffeltii* (from Tehuacán, Pue.) growing in the Jardin Botánico, UNAM.

Agave verschaffeltii Lem. **2n = 60 (10L + 50S).** *Chimal 37,* Tehuacán, Puebla. The large chromosomes are submetacentric; one pair exhibits secondary constriction. The small chromosomes are metacentric and submetacentric. This species is abundant in the State of Puebla, near Tehuacán (fig. 6).

Agave xalapensis Roezl. **2n = 60 (10L + 50S).** *Chimal 2,* Xalapa, Veracruz, Botanical Garden No. *5363.* As in the preceding species, the large chromosomes are submetacentric, one pair with secondary constriction, and the small metacentric and submetacentric (fig. 3). These results agree with those obtained by Granick (1944) for the same species. The plant was collected on the basalt flow east of Xalapa (fig. 7).

Dasylirion serratifolium (Schult.) Zucc. **2n = 38 (12L + 26M).** *Chimal 36,* Oaxaca. There are 12 large submetacentric chromosomes and 26 metacentric and submetacentric and metacentric medium-sized chromosomes present (fig. 9).

The same chromosome number was reported for *Dasylirion longissimum* (Whitaker, 1934; Sato, 1942), *D. taxanum* and *D. wheeleri* (Sato,

FIG. 7. *Agave xalapensis* (from the lava beds near Xalapa) growing in the Jardin Botánico, UNAM.

1936), and *D. acrotriche* (Sato, 1942). The species is native in the state of Oaxaca (fig. 8).

Yucca lacandonica Gómez-Pompa & Valdés. **2n = 60 (10L + 50S).** *Chimal 74,* Botanical Garden No. *6929.* The 10 large chromosomes are submetacentric; the 50 small chromosomes are metacentric and submetacentric (fig. 10). This is the only representatives of the genus in the humid tropics known as an epiphyte (Gómez-Pompa and Valdés, 1962) (fig. 12).

Other authors, McKelvey and Sax (1933), Whitaker (1934), Sato (1935), and Watkins (1936), in examining different species of *Yucca,* encountered the normal somatic chromosome number of **2n = 60.** On the other hand, Sharma and Sarkar (1964), in a study of the karyotypes of five species of *Yucca,* some of which had been described, reported a variation of **42** to **52** chromosomes in somatic cells. Although Sharma and Sarkar reported secondary constrictions in one of two pairs of chro-

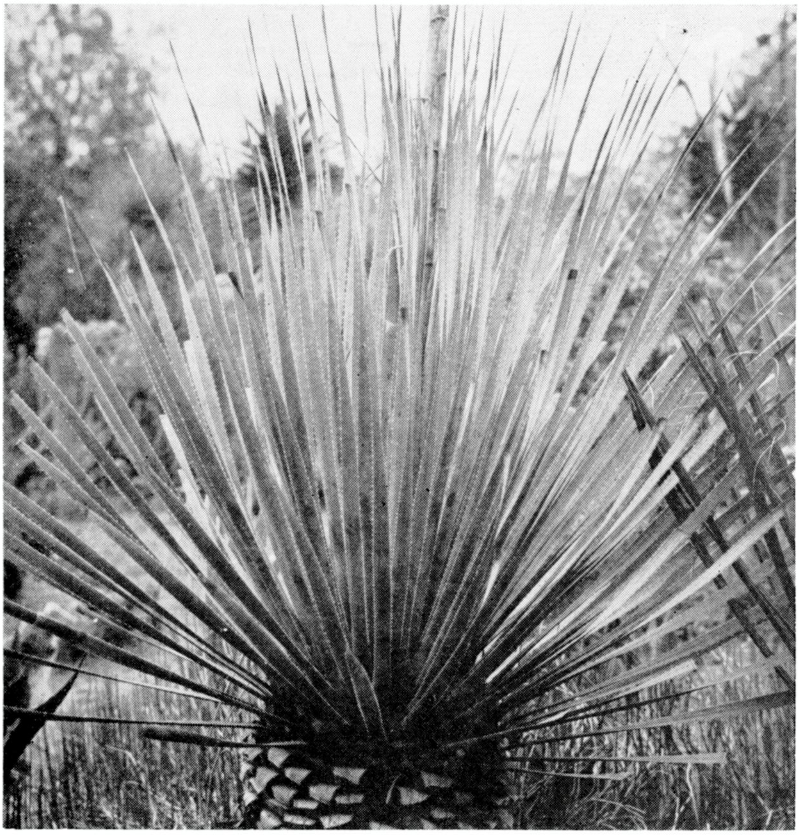

FIG. 8. *Dasylirion serratifolium* (from Oaxaca) growing in the Jardin Botánico, UNAM.

mosomes, in our examination of *Yucca lacandonica* no secondary constrictions were located, a fact which may prove to be of great interest in an understanding of the karyotype evolution of *Yucca*. The plants studied originated in Teapa, Tabasco.

Hesperaloë funifera (Koch) Trel. **2n = 60 (10L + 50S).** The large chromosomes are submetacentric, and the small chromosomes are metacentric and submetacentric (fig. 11). The same chromosome number was reported by McKelvey and Sax (1933) for *H. parviflora*. The plants studied were collected in San Luis Potosí (fig. 13).

DISCUSSION

On the basis of the chromosomal analyses performed, we can corroborate the presence of a very asymmetric karyotype with the uniform chromosome number of **2n = 60** in the genera *Agave, Yucca* and *Hesperaloë,* confirming their close relationship. On the other hand, we have

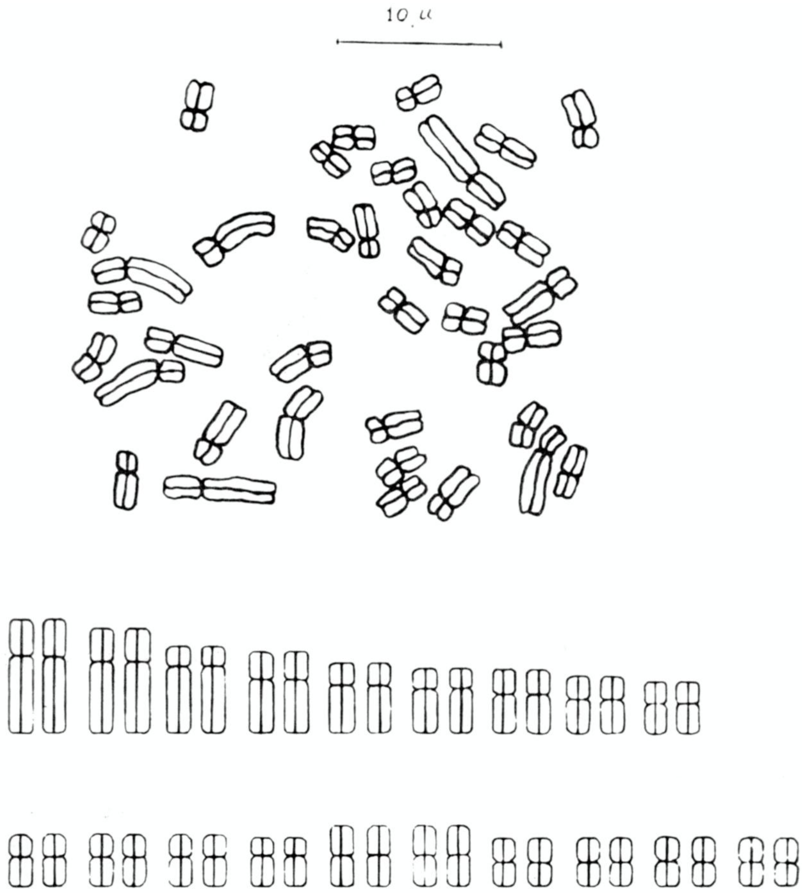

FIG. 9. Camera lucida drawings of the mitotic chromosome of *Dasylirion serratifolium*, **2n = 38.**

in the genus *Dasylirion* with **2n = 38** a number similar to that of other genera in the tribe Nolineae such as *Nolina* (Cave, 1964) and *Beaucarnea* (Flory and Varma, 1960).

The information obtained during our research and from a survey of the literature does not support the circumscription of the family Agavaceae proposed by Hutchinson. The family includes two groups which are well defined chromosomally and with little apparent phylogenetic relationship. Further, they are morphologically and geographically diverse, indicating a long independent evolutionary history.

From a taxonomic point of view, this conclusion seems to weaken the already weak case for maintaining the Agavaceae as a distinct family, especially since it shares many characters with the Liliaceae and Ama-

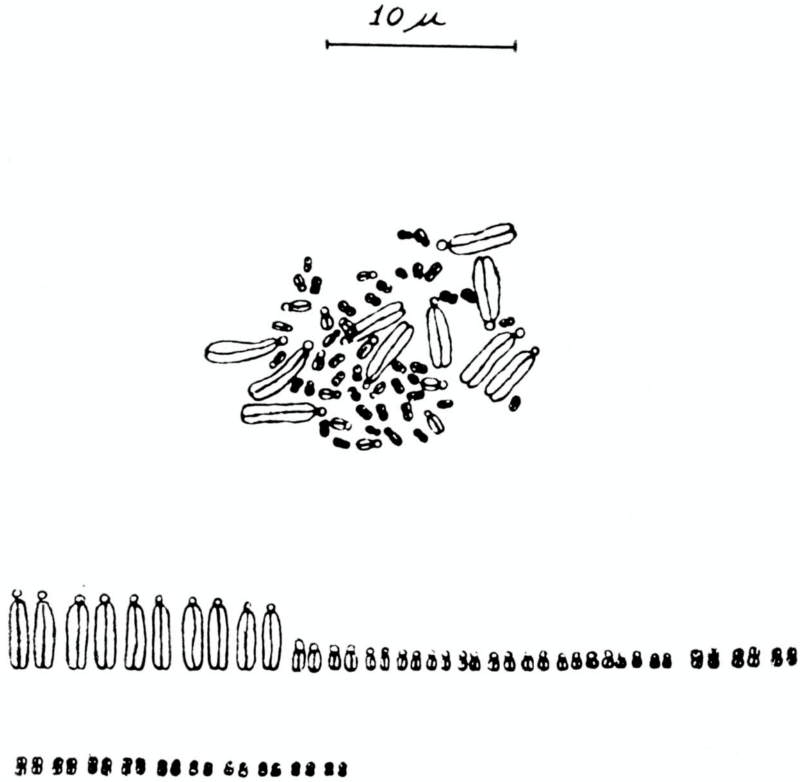

FIG. 10. Camera lucida drawings of the mitotic chromosomes of *Yucca lacandonica*, **2n = 60.**

ryllidaceae and is thus not easily separable from them. We are inclined to support Thorne (1968) in a unification of the three families in one, although we are aware of the difficulties engendered by such an arrangement, and to make a separation into subfamilies. Without doubt, it will be necessary to have more information from other sources (morphology, genetics, biochemistry) to achieve an arrangement of subfamilies which best reflects the phylogenetic relationships of the included groups.

ABSTRACT

A chromosomal study of the following species is presented: *Agave mapisaga*, *A. nizandensis*, *A. verschaffeltii*, *A. xalapensis*, *Dasylirion serratifolium*, *Hesperaloë funifera*, and *Yucca lacandonica*. Some observations concerning the systematics of the Agavaceae in the light of chromosomal studies are made. The union of the Amaryllidaceae and Liliaceae is discussed.

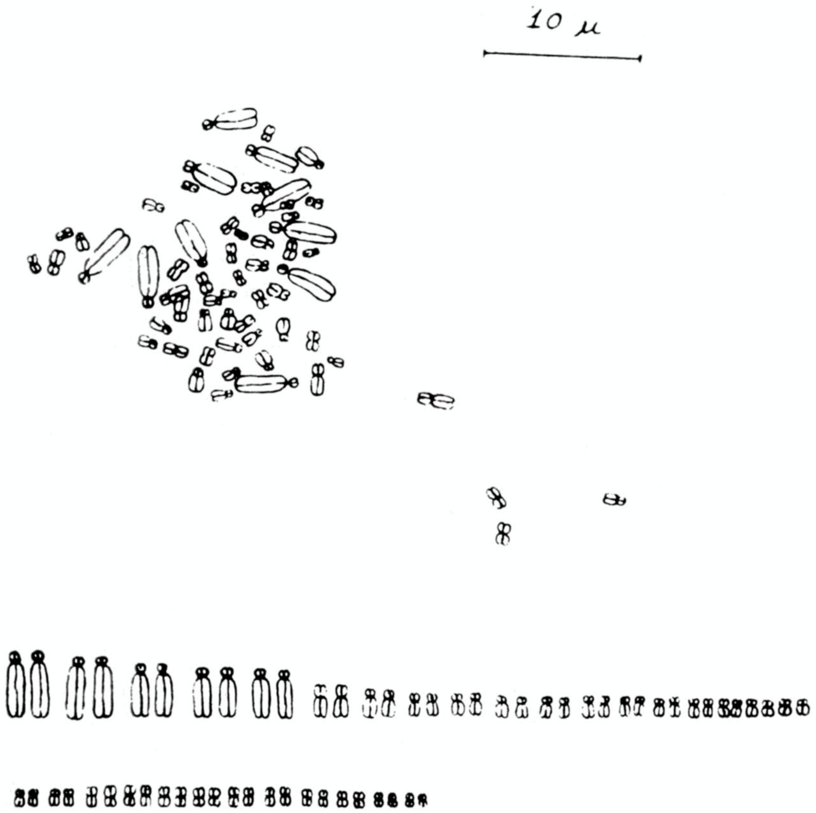

FIG. 11. Camera lucida drawings of themitotic chromosomes of *Hesperaloe funifera*, **2n = 60.**

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FIG. 12. *Yucca lacandonica* in its natural habitat in the state of Chiapas.

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FIG. 13. *Hesperaloe funifera* (from San Luis Potosí) growing in the Jardin Botánico, UNAM.

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