Chapter 10

Chromatid Abnormalities in Meiosis: A Brief Review and a Case Study in the Genus *Agave* (Asparagales, Asparagaceae)

Benjamín Rodríguez-Garay

Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/intechopen.68974

Abstract

The genus *Agave* is distributed in the tropical and subtropical areas of the world and represents a large group of succulent plants, with about 200 taxa from 136 species, and its center of origin is probably limited to Mexico. It is divided into two subgenera: *Littaea* and *Agave* based on the architecture of the inflorescence; the subgenus *Littaea* has a spicate or racemose inflorescence, while plants of the subgenus *Agave* have a paniculate inflorescence with flowers in umbellate clusters on lateral branches. As the main conclusion of this study, a hypothesis rises from the described observations: *frying pan-shaped* chromosomes are formed by sister chromatid exchanges and a premature kinetochore movement in prophase II, which are meiotic aberrations that exist in these phylogenetic distant species, *Agave stricta* and *A. angustifolia* since ancient times in their evolution, and this may be due to genes that are prone to act under diverse kinds of environmental stress.

Keywords: tequila, mescal, chromatid cohesion, centromere, inversion heterorozygosity, kinetochore

1. Introduction

The genus *Agave* is distributed in the tropical and subtropical areas of the world and represents a large group of succulent plants, with about 200 taxa from 136 species, and its center of origin is probably limited to Mexico [1]. It is divided into two subgenera: *Littaea* and *Agave* based on the architecture of the inflorescence; the subgenus *Littaea* has a spicate or racemose

inflorescence while plants of the subgenus *Agave* have a paniculate inflorescence with flowers in umbellate clusters on lateral branches (**Figures 1** and **2**) [1].

Agave is a young genus which originated 7.8 to 10.1 million years ago (Mya) [2]. A group of species of this genus, the subgenus *Littaea* is considered to be the most primitive of all *Agave* species as the spicate inflorescence is the most common among monocotyledons than the paniculate form of the subgenus *Agave* [1]. In this context, Eguiarte et al. [3] calculated that species of the subgenus *Littaea* group Striatae (*A. striata, A. dasyliriodes*) got separated about 8 Mya. It is important to mention that *A. stricta* also belongs to the Striatae group [1]. On the other hand, the same researchers found that *A. americana* that belongs to the subgenus *Agave* was separated about 2 Mya, thus being considered the subgenus *Agave* younger than the subgenus *Littaea*.

The groups Rigidae and Sisalanae that belong to the subgenus *Agave*, are commercially important due to their use for several purposes: (a) alcoholic beverages, such as tequila and mezcal; (b) natural long and hard fibers; and (c) steroidal and medicinal principles [2–4]. The *Agave* genus conforms a group of plant species of the Asparagaceae family (formerly Agavaceae) that belongs to the monocot class of angiosperms and because of

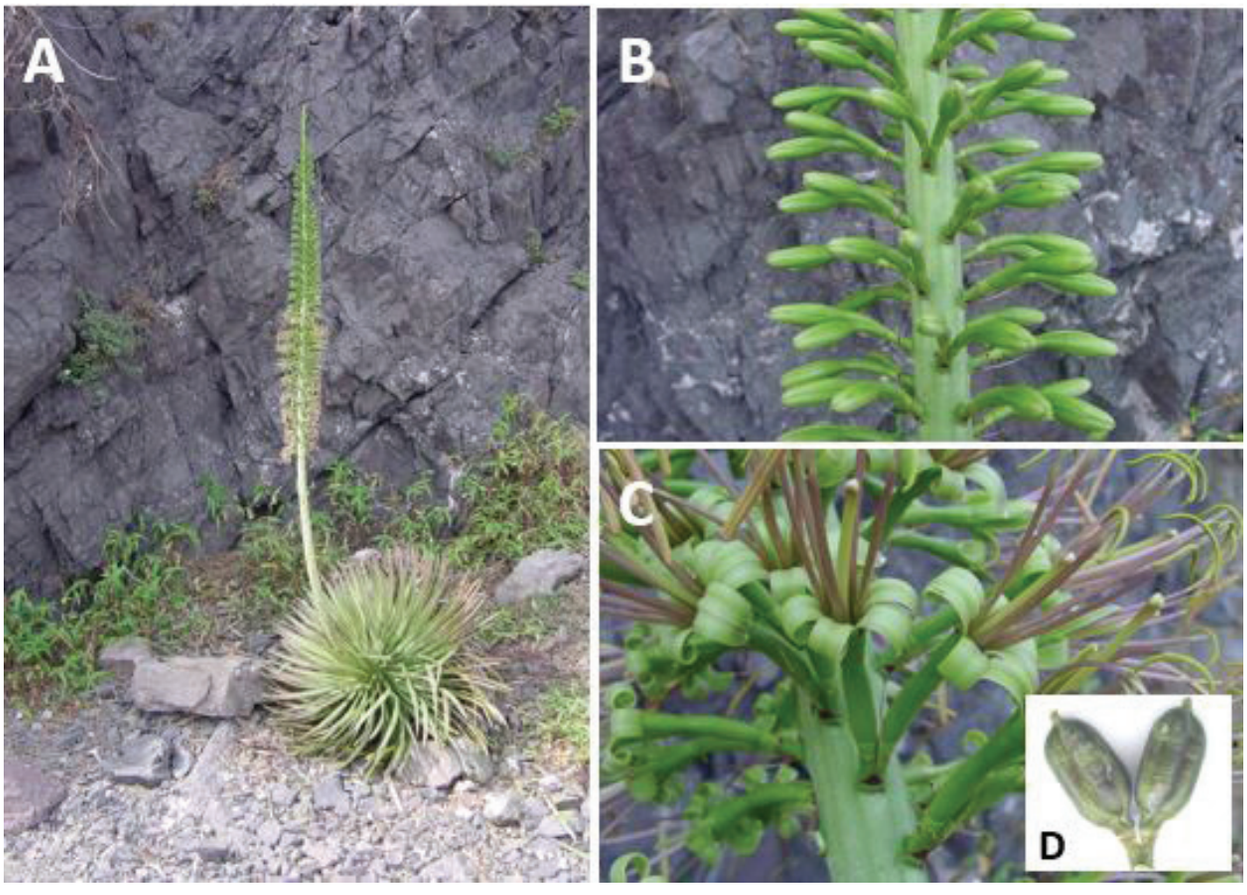

Figure 1. *Agave colimana* as an example of the subgenus *Littaea*. (A) Wild *A. colimana* plant growing in cliffs near the sea in the coast of the state of Jalisco, México. (B) Section of the spicate floral stalk showing the flower buds arranged in pairs. (C) Mature flowers arranged in pairs. (D) Immature fruits.

http://dx.doi.org/10.5772/intechopen.68974

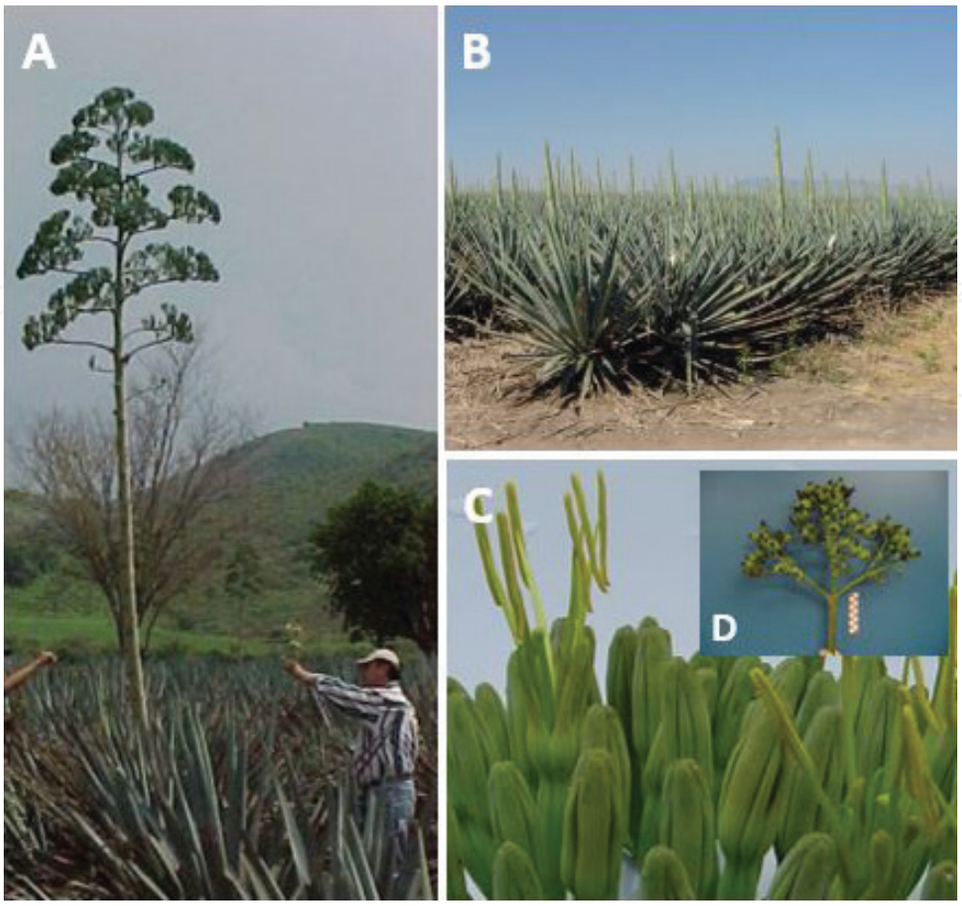

Figure 2. *Agave tequilana* as an example of the subgenus *Agave* growing near to the city of Guadalajara, Jalisco, México. (A) Mature plant of *A. tequilana* showing a paniculate inflorescence. (B) Commercial plantation with inflorescences in development ready to be cut off to allow the accumulation of sugars for the production of tequila. (C) Mature and immature flowers. (D) Immature fruits in a panicle.

its CAM metabolism and other botanical features, the genus *Agave* is gaining importance throughout the world to address the challenges that climate change is imposing with regard to food, medicine and bioenergy [4]. A good source of information about the taxonomy of the genus *Agave* is the book "Agaves of Continental North America" by Howard Scott Gentry [1].

The genus *Agave* is a semelparous perennial that produces flowers only once toward the end of its life cycle being 6–8 years for *A. tequilana* and *A. angustifolia* [5] and about 30 years for *A. Victoria-reginae* [6].

In *Agave* as in all Angiosperms, one of their main characteristics is that they possess seeds enclosed inside a fruit derived from the ovary of flowers [7]. Another important feature of angiosperms is that they have an alternation of generations in their life cycle (as in many other plants), divided in two phases: one diploid phase, which is called sporophytic, and the other haploid phase known as gametophytic phase [8–10]. The main function of the gametophytic phase is the production of haploid male and female gametes through the meiotic cell division [9, 11].

2. Meiosis (meiotic division)

The term "meiosis" (from the Greek word maiosis = μειωτικής which means reduction) was first proposed in 1905 by J. Bertland Farmer and J.E.S. Moore in reference to the nuclear division that was called "heterotype" by Walther Flemming, cell division which is responsible for the production of gametes in plants and animals [12].

Meiotic cell division is the key point process in the sexual reproduction of most of animal and plant species, through which haploid gametes are generated, and includes two successive divisions of the nucleus, where the first division is reductional and the second is equational; a failure in any or in both of these cell divisions produces chromosomal accidents which will be reflected in gamete viability or mutations that will appear in the progeny [13]. The objective of meiosis is to produce haploid gametes from original diploid cells and starts with the replication of DNA that produces four chromatids of each type of chromosome, two from the female parent and two from the male parent. These four chromatids are distributed into four final different nuclei [14]. In plants, male gametes or microgametophytes (pollen grains) are developed inside the anthers and are formed from a pollen mother cell, which undergoes a meiotic process that gives rise to a tetrad of haploid cells called microspores.

In the process of pollen development, the microspore undergoes a nonsymmetric mitotic division giving rise to a vegetative and a generative cell. The generative cell undergoes a second mitotic division producing two haploid sperms. In the meantime, the vegetative cell remains without division and produces the pollen tube, which carries the sperms, and finally reaches the ovule for the process of fertilization [15].

On the other hand, the female gametophyte develops in the ovule. One megaspore mother cell is located in the center of the ovule, which after two meiotic cell divisions gives rise to a strand of four haploid cells or megaspores. In most of angiosperms three of these megaspores degenerate, however, the cell which is the closest to the chalaza survives as the functional megaspore, this enlarges and undergoes three mitotic divisions to form the embryo sac. In general, the embryo sac follows different patterns of development in different genera and species; however, the most common pattern consists of four types of cells: three antipodal cells (at the chalazal end), one central cell containing two polar haploid nuclei (that is generally located at the center of the embryo sac), and two synergid cells flanking the egg cell, all three positioned at the micropylar end [16].

2.1. Chromosomes and chromatids in meiosis

In the meiotic process, a single round of DNA replication is followed by two rounds of chromosome segregation that generate four haploid gametes from one diploid cell [17]. To accomplish this specialized chromosome segregation, sister kinetochores (contained in the region of the chromosome called *centromere*) are attached to microtubules emanating from a spindle pole to help with the reductional segregation of homologous chromosomes (*not* sister chromatids) in the first heterotype step of the meiotic division (**Figure 3**).

http://dx.doi.org/10.5772/intechopen.68974

Chiasmata occur between a homologous chromosome pair, and at least two of the four chromatids become unique, and different from those coming from the parents. There is the formation of bivalents in chiasmata, and this generates an adequate chromosome segregation in meiosis [21]. The chromatids that are conforming the unit called chromosome are called "sister chromatids". On the other hand, in most of organisms, homologous chromosomes have to be aligned in a precise linear manner with the help of the cytoskeleton formed by proteins that give motility to chromosomes and the intervention of the synaptonemal complex. In this manner, genetic recombination and the formation of chiasmata (stable connections between homologs formed at the sites of crossovers) take place [18]. The process of exchange of genetic material between homologous chromosomes is mediated by the action of recombination proteins and topoisomerase-like proteins that promote the breakdown of chromosomal DNA so that exchange can take place. Crossing over or recombination between sister chromatids is known as *sister chromatid exchange*. Thus, since they are identical, would not produce any new genetic variation. It has been found that chances of recombination of sister chromatids increase in meiotic cells of haploid yeast, while in mitotic cells, the chances are reduced. It is possible that several forms of ectopic recombination were favored by the lack of their genetic counterparts [19]. On the other hand, a wrong synapsis can have consequences during metaphase I, therefore, chromosomal segregation in anaphase I would occur incorrectly.

Sister chromatids are kept together by the action of the cohesin complex along the length of their arms and at their centromeres, and need to be held together in order to be segregated to opposite poles of the spindle in both mitosis and meiosis II. Sister chromatid cohesion is also involved in having homologous chromosomes together in meiosis I. Physical cohesion is dependent of the cohesin complex formed by several proteins for maintaining sister chromatids together, and the dissolution of sister-chromatid cohesion must be regulated precisely through specific control mechanisms that prevent the incorrect segregation of chromosomes [20], for example, the Spindle Assembly Checkpoint (SAC) complex that regulates the proper attachment of microtubules to kinetochores.

The cohesin complex is highly conserved in eukaryotes and is mainly composed of four conserved proteins found in yeast, animals and plants (reviewed in [21–25]). In mitosis as in meiosis, cohesins have a ring-like structure formed by SMC1, SMC2, α-kleisin (RAD21 / SCC1 in mitosis or Rec8 in meiosis) and SCC3, each element of the cohesin complex is of a key importance for proper segregation of chromosomes.

In mitosis, cell division depends on the correct separation of sister chromatids in anaphase and is accomplished by the attachment of microtubules (originated in opposite spindle poles) to sister kinetochores. Sister kinetochores are bi-oriented by being pulled to opposite poles (equational segregation) in a process of kinetochore-microtubule attachment called amphitelic. In this process that occurs in mitosis and meiosis II, sister-chromatids cohesion associated with chromatin is separated by the protease separase at the beginning of anaphase where chromosomes become bi-oriented (**Figure 3**) [26].

Kinetochores are protein complexes located at the centromeric region of the chromosome and regulate chromosome and chromatid movement, and plant kinetochores contain proteins

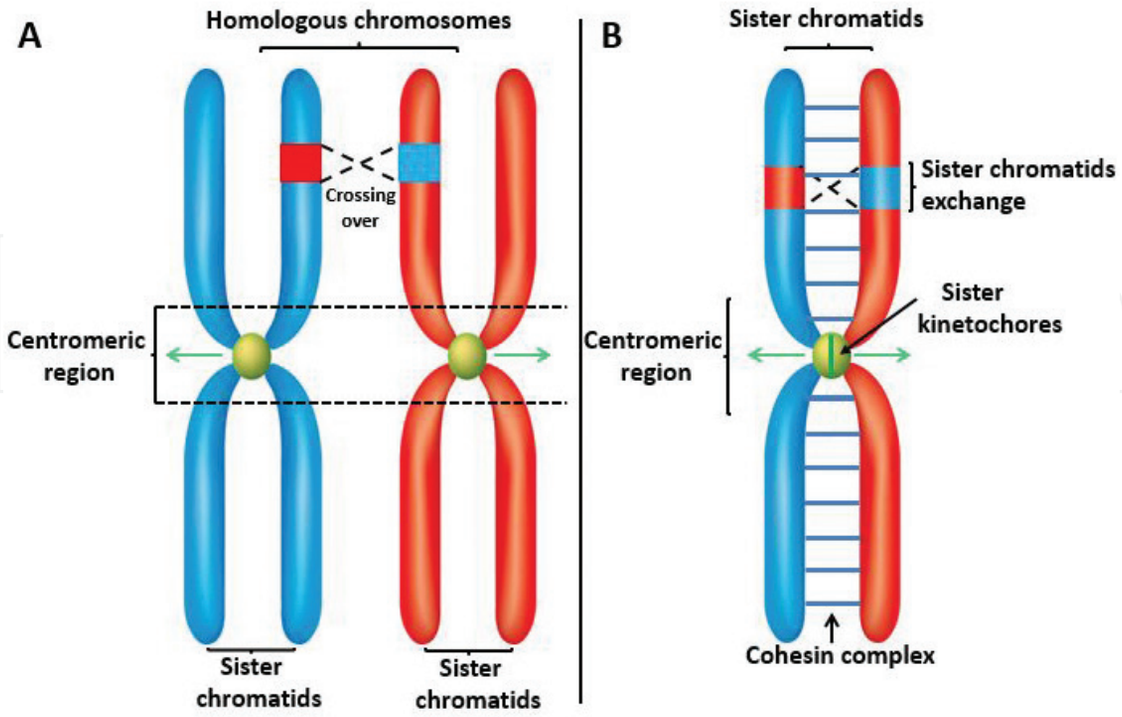

Figure 3. Schematic structure of chromosomes in meiosis. A) Homologous chromosomes showing sister chromatids, centromeric region and a crossing over. Balls represent the kinetochores and the arrows show their normal movement to opposite poles in Meiosis I. B) Metaphasic chromosome in Meiosis II showing the centromeric region which includes the kinetochores, the sister chromatids and the cohesin complex that holds together the sister chromatids. Also, an eventual sister chromatids exchange is represented. Again, the arrows show the process of normal movement of sister chromatids to opposite poles called *amphitelic bi-orientation*.

which are homologs to those found in animals and fungi kinetochores (reviewed in Ref. [27]). In this protein complex, CENH3 (a variant of histone H3) and CENPC interact internally with the centromere, while NCD80 and MIS12 interact with microtubules, and MIS12 is necessary for proper segregation of homologous chromosomes.

3. Agave cytogenetics: a case study

The genus *Agave* has been the object of cytological investigations only after 1933, since then, chromosome counts have been made on a large number of species. This genus has a bimodal complement of 10 large and 50 small chromosomes with a monoploid number of x = 30, and with varieties and species from diploid to hexaploid [5, 28–30]. Cave [31] reported regular meiosis in five diploid, two tetraploid and one hexaploid species, and irregular meiosis in two polyploids, with bridges and fragments at anaphase I. Similar cytological investigations were carried out in *Agave stricta* and *A. tequilana*, which are euploid species with the basic chromosome number of x = 30, and for which meiotic behavior heterozygous for paracentric inversions and subchromatid exchanges was described. The mentioned altered meiosis produced a number of aberrations, such as bridges and fragments at anaphase I and II [5, 32]. Also, in *A. stricta* loop chromatids were visible at prophase II, but not at metaphase II (see arrow in **Figure 4** [32]).

http://dx.doi.org/10.5772/intechopen.68974

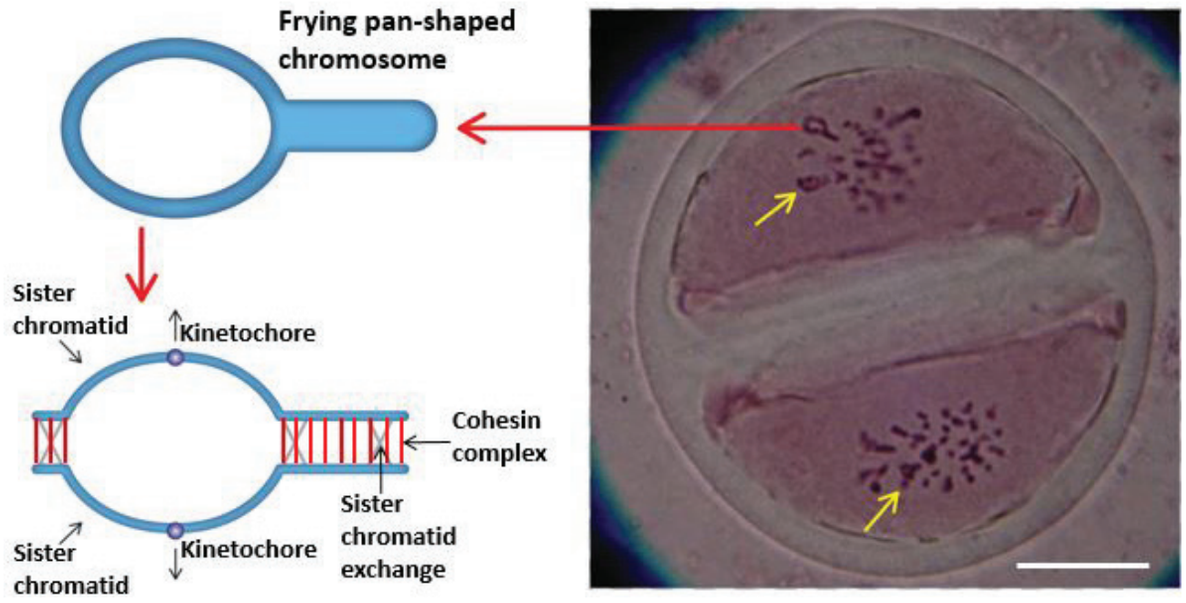

Figure 4. Schematic proposed hypothesis for the formation of *frying pan-shaped* chromosomes in prophase II of *Agave angustifolia*. White bar = 20 μm.

Agave angustifolia belongs to the subgenus *Agave* group Rigidae and is used for Mezcal production in México. The chromosome behavior in the meiosis of *Agave* species has been previously reported [5, 32–33]. Frequently, in diverse plant species, the formation of dicentric bridges and acentric fragments in Anaphase I is known as a result of inversion heterozygosity. In *A. tequilana*, the analysis of Pollen Mother Cells in anaphase I (A-I) has shown cells with normal and irregular A-I with side arm bridges (SAB), cells with one bridge and one fragment, anaphases with one or two lagging chromosomes and acentric fragments. Also, in anaphase II (A-II) some cells showed bridges, all of them leading to the production of shrunken or empty pollen grains [5].

The plant material used in this study consisted of immature anthers from the inflorescence of a plant which was an offshoot taken from a mother plant originally collected in the year 2006 in the vicinity of Sayula, Jalisco, México. This plant was called "224" as is referred in the field books and diverse files at the Plant Biotechnology Unit-CIATEJ and grown at the CIATEJ campus located in the city of Guadalajara, Jalisco, México. Fresh anthers from young buds were collected on June 2014, selected and fresh squashed in 1% acetoorceine. The best cells for meiotic chromosome analysis were photographed using an Olimpus BH2 microscope coupled with a digital Sony camera.

As the most outstanding results in this study, several aberrant meiotic divisions could be observed in the male gametogenesis. Some of the most frequent aberrations were bridges formed in anaphase I mainly due to heterozygous inversions and probably due to sister chromatid exchanges. A striking finding was a couple of *frying pan-shaped* chromosomes in each cell of several diads in prophase II before entering anaphase II (**Figure 3**),, which were highly similar to those previously reported for *Agave stricta* (see arrow in **Figure 4**) [32], a species that belongs to the subgenus *Littaea* group Striatae.

As reviewed above, the genus *Agave* is divided into two subgenera: *Littea* and *Agave*, whose most important difference is the morphology of their inflorescence, being racemose for *Littaea* and paniculate for *Agave* [1]. Also, it has been mentioned that the subgenus *Littaea* is considered to be the most primitive of the two and both separated by a span of several million years [2, 3].

On the other hand, the formation of *frying pan-shaped* configurations may be explained by putative sister chromatid exchanges, where chiasma type junctions in different points of the chromosome held the sister-chromatids and remained joined at the site of the exchange as it has been explained for regular chiasmata in a model for achiasmate homologous chromosome segregation (**Figure 5**) [34]. The phenomenon of sister-chromatid exchange may be viewed as a mechanism of double-strand break repair in plants and in general in eukaryotes. These breaks may be the product of errors caused by endogenous or exogenous kinds of stress such as reactive oxygen species (ROS), radiation [36, 37], and many other environmental kinds of stress imposed by climate change [38, 39]. Also, with regard to the cohesin complex, an example of ROS action is in the induction of loss of cohesion and chromosome errors in mammals, mainly in human females causing the phenomenon called *maternal age effect* which is produced in oocytes [40].

Furthermore, an alternative explanation for the formation of *frying pan-shaped* chromosomes is the putative aberrant loss of cohesion of arms and/or in the centromeric region of sister chromatids in meiosis II. Nowadays, it is known that the centromeric cohesin complex is protected by the

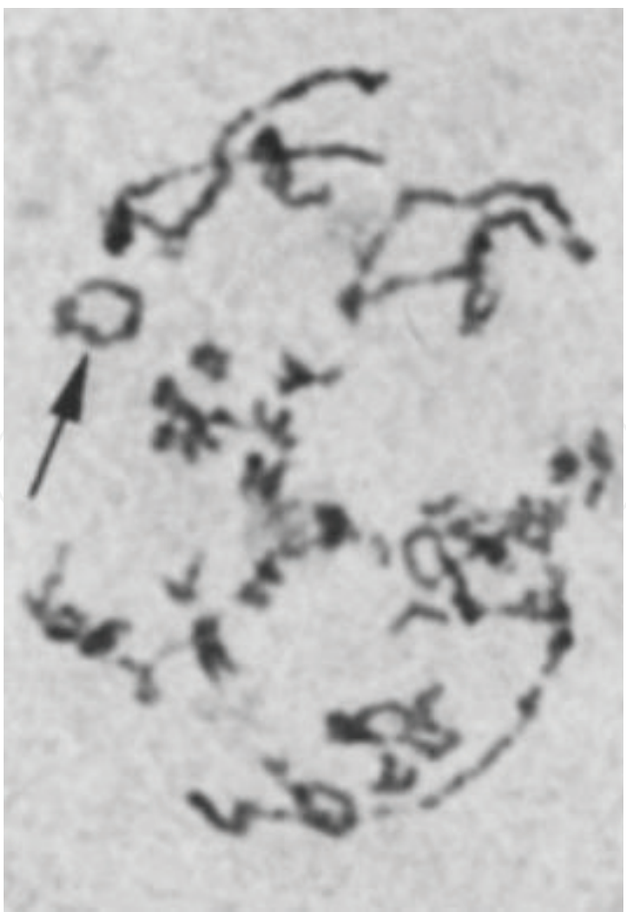

Figure 5. P II. Loop chromatid (arrow). The unaffected short arms can be seen, left. *Source:* Brandham [32]. With permission of Springer.

http://dx.doi.org/10.5772/intechopen.68974

protein Shugoshin (Sgo1) (which means *protective deity* or *guardian* in the Japanese language). In meiosis I, sister chromatids are maintained together by the cohesin complex that contains the Rec8 subunit. At this stage, separase destroys Rec8 in the chromosome arms, while Shugoshin protects Rec8 at the centromeres. In meiosis II, the state of kinetochores of being stretched may cause Shugoshin destruction, and sister chromatid separation is facilitated by cleavage of Rec8 by separase [41]. The mechanisms of cohesion action and Shugoshin protection seem to be conserved across species such as in fission yeast and plants [23, 41, 42]. In addition, the cohesion of sister chromatids depends on an acyltransferase called Eco1/Ctf7 [43], however, this enzyme is not required for cohesin loading on DNA, but it is necessary once cohesion has been established. It has been shown that an important function of Eco1 is the acetylation of cohesin on two lysine residues that are located in the ATPase head of the SMC3 domain. Mutations of lysine residues in yeast to non-acetylated amino acid residues caused defects in cohesion [44, 45].

In this study, a putative premature loss of sister kinetochores and chromatid cohesion may be the cause of the *frying pan-shaped* chromosomes.

Finally, as a result of these meiotic errors in prophase II, aberrant anaphase II showed stretched bridges which at the end produced unbalanced meiotic end products: pollen grains (**Figures 6** and **7**).

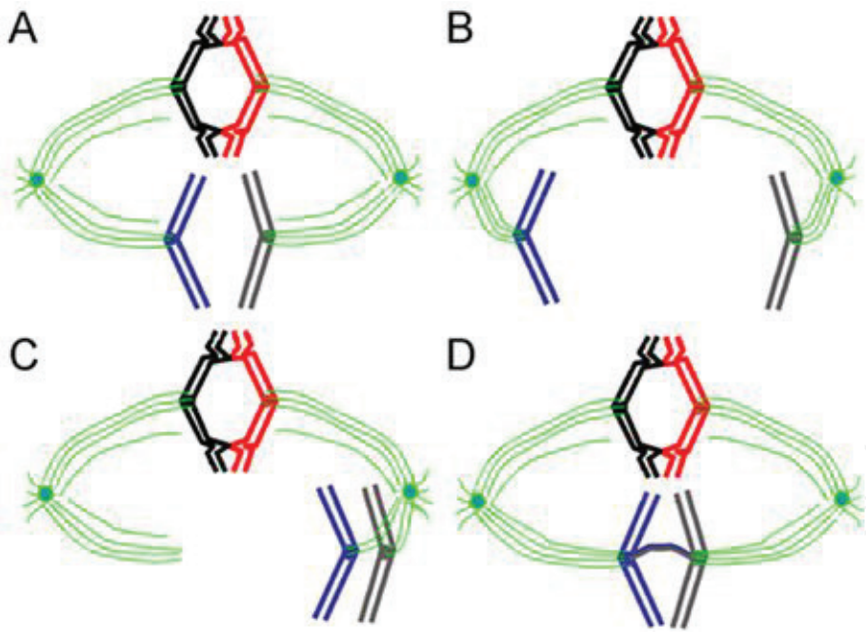

Figure 6. Model for achiasmate chromosome segregation. (A) Chiasmate homologs (red and black) are locked together by crossovers, whereas the sister chromatids are held together by cohesins (not shown). Achiasmate homologs (blue and gray) are not locked together by crossovers. Spindle (green) attachments to kinetochores (solid circles) are stabilized by tension created by pulling forces that draw chiasmate homologs to opposite poles. (B) Achiasmate chromosomes were thought not to be locked with their homologs and are able to move prematurely to one or the other spindle pole. (C) As shown by Hughes et al. [35], achiasmate homologs can be found on the same side of the metaphase plate. This is the first demonstration that this configuration can occur, and it suggests that achiasmate homologs can move in unison. (D) In addition, heterochromatic DNA threads between achiasmate homologs can be observed. These threads may provide chiasma-like function that lock homologs together and allow tension to be established between these nonexchange homologs. This tension is used by spindle forces to move achiasmate chromosomes along the spindle, orient them, make them join the mass of chiasmate chromosomes congressed at the metaphase plate, and ultimately ensures proper segregation). *Source:* Bosco [34]. With permission of Dr. Giovani Bosco.

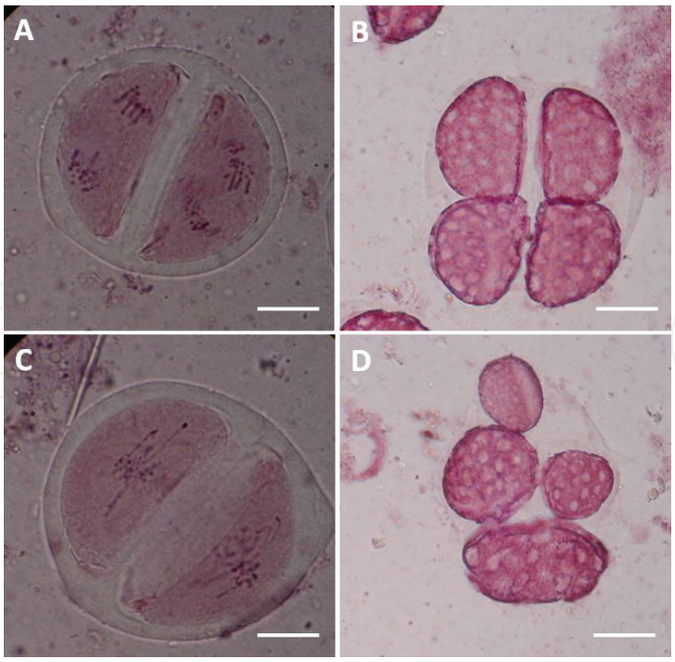

Figure 7. Consequences of normal and abnormal Meiosis II in *Agave angustifolia*. (A and B) Normal anaphase II producing normal pollen grains. (C and D) Abnormal anaphase II as a product of the abnormal sister chromatids behavior showed in **Figure 4**. Unbalanced products (pollen grains) are produced with a high and low genetic load. White bar = 20 μm.

As the main conclusion of this study, a hypothesis rises from the described observations: *frying pan-shaped* chromosomes are formed by sister chromatid exchanges and a premature kinetochore movement in prophase II, which are meiotic aberrations that exist in these phylogenetic distant species, *Agave stricta* and *A. angustifolia* since ancient times in their evolution, and this may be due to genes that are prone to act under diverse kinds of environmental stress [46].

Acknowledgements

This article was published with funds from Fideicomiso 2017 Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco (CIATEJ). The author thanks J.M. Rodríguez-Domínguez, J.R. Trinidad-Cruz, B. Tirado-Pérez, and A.M. Barranco Guzmán for reviewing the manuscript and helpful suggestions, and H. Rodríguez-Julián for the artwork of **Figures 3** and **4**.

Author details

Benjamín Rodríguez-Garay

Address all correspondence to: brodriguez@ciatej.mx

Plant Biotechnology Unit, Research Center for Assistance in Technology and Design of the State of Jalisco, El Bajío del Arenal, Zapopan, Jalisco, México

References

[1] Gentry HS. Agaves of Continental North America. Tucson, Arizona: The University of Arizona Press; 1982. p. 670

[2] Good-Avila SV, Souza V, Gaut BS, Eguiarte LE. Timing and rate of speciation in Agave (Agavaceae). Proceedings of the National Academy of Sciences of the United States of America. 2006;**103**:9124-9129. DOI: 10.1073/pnas.0603312103

[3] EguiarteLE, Souza V, Silva-Montellano A. Evolucion de la familia Agavaceae: filogenia, biología reproductiva y genetica de poblaciones. Boletín de la Sociedad Botánica de México. 2000;**66**:131-150

[4] Rodríguez-Garay B. Somatic embryogenesis in *Agave* spp. In: Loyola-Vargas VM, Ochoa-Alejo N, editors. Somatic Embryogenesis: Fundamental Aspects and Applications. Switzerland: Springer International Publishing AG; 2016.pp. 267-282. DOI: 10.1007/978- 3-319-33705-0_16

[5] Ruvalcaba-Ruiz D, Rodríguez-Garay B. Aberrant meiotic behavior in *Agave tequilana* Weber var. azul. BMC Plant Biology. 2002;**2**:10. DOI: 10.1186/1471-2229-2-10

[6] Obledo EN, Barragán-Barragán LB, Porfirio Gutiérrez-González, Ramírez-Hernández BC, Ramírez JJ, Rodríguez-Garay B. Increased photosynthetic efficiency generated by fungal symbiosis in *Agave victoria-reginae*. Plant Cell, Tissue and Organ Culture. 2003;**74**:237-241. DOI: 10.1023/A:1024046925472

[7] Li W, Ma H. Gametophyte development. Current Biology. 2002;**12**:R718-R721. DOI: http://dx.doi.org/10.1016/S0960-9822(02)01245-9

[8] Haig D. New perspectives on the angiosperm female gametophyte. Botanical Review. 1990;**56**:236-274. DOI: 10.1007/BF02858326

[9] Fan YF, Jiang L, Gong HQ, Liu CM. Sexual reproduction in higher plants I: fertilization and the initiation of zygotic program. Journal of Integrative Plant Biology. 2008;**50**:860-867. DOI: 10.1111/j.1744-7909.2008.00705.x

[10] Ma H, Sundaresan V. Development of flowering plant gametophytes. Current Topics in Developmental Biology. 2010;**91**:379-412. DOI: 10.1016/S0070-2153(10)91013-2.2010

[11] Yadegari R, Drews GN. Female gametophyte development. Plant Cell. 2004;**16**:S133–S141. DOI: http://dx.doi.org/10.1105/tpc.018192

[12] Farmer JB, Moore JES. On the meiotic phase (reduction divisions) in animals and plants. Journal of Cell Science. 1905;**s2-48**:489-558

[13] Gómez-Rodríguez VM, Rodríguez-Garay B, Barba-Gonzalez R. Meiotic restitution mechanisms involved in the formation of 2n pollen in *Agave tequilana* Weber and *Agave angustifolia* Haw. SpringerPlus. 2012;**1**:17. DOI: 10.1186/2193-1801-1-17

[14] Petronczki M, Simons MF, Nasmyth K. Un Ménage à Quatre: The molecular biology of chromosome segregation in meiosis. Cell. 2002;**112**:423-440. http://dx.doi.org/10.1016/S0092-8674(03)00083-7

[15] Mc Cormick S. Control of male gametophyte development. Plant Cell. 2004; **16**:S142–S153. http://dx.doi.org/10.1105/tpc.016659

[16] Gutiérrez-Mora A, González-Gutiérrez AG, Rodríguez-Garay B, Ascencio-Cabral A, Li-Wei L. Plant somatic embryogenesis: Some useful considerations. In: Sato K, editor. Embryogenesis. Rijeka, Croatia: InTech; 2012. pp. 229-248. DOI: 10.5772/36345

[17] Tanaka K, Watanabe Y. 2007. Sister chromatid cohesion and centromere organization in meiosis. In: Egel R, Lankenau D.-H, editors. Recombination and Meiosis. Genome Dyn Stab 2. Berlin Heidelberg: Springer-Verlag; 2007. pp. 57-79. DOI: 10.1007/7050_2007_027/ Published online: 23 June 2007

[18] Roeder GS. Meiotic chromosomes: It takes two to tango. Genes & Development. 1997;**11**: 2600-2621. DOI:10.1101/gad.11.20.2600

[19] Loidl J, Nairz K. Karyotype variability in yeast caused by nonallelic recombination in haploid meiosis. Genetics.1997;**146**:79-88

[20] Bickel SE, Orr-Weaver TL. Holding chromatids together to ensure they go their separate ways. BioEssays. 1996;**18**(4):293-300. DOI: 10.1002/bies.950180407

[21] Zamariola L, Tiang CL, De Storme N, Pawlowski W, Geelen D. Chromosome segregation in plant meiosis. Frontiers in Plant Science. 2014;**5**:279. DOI: 10.3389/fpls.2014.00279

[22] Remeseiro S, Losada A. Cohesin, a chromatin engagement ring. Current Opinion in Cell Biology. 2013;**25**(1):63-71. http://dx.doi.org/10.1016/j.ceb.2012.10.013

[23] De K, Sterle L, Krueger L, Yang X, Makaroff CA. Arabidopsis thaliana WAPL is essential for the prophase removal of cohesin during meiosis. PLoS Genetics. 2014;**10**(7):e1004497. DOI:10.1371/journal.pgen.1004497

[24] Yuan L, Yang X, Christopher A. Makaroff CA. Plant cohesins, common themes and unique roles. Current Protein & Peptide Science. 2011;**12**(2):93-104. DOI: 10.2174/1389 20311795684904

[25] Peters JM, Nishiyama T. Sister chromatid cohesion. Cold Spring Harbor Perspectives in Biology. 2012;**4**:a011130. DOI: 10.1101/cshperspect.a011130

[26] Yamagishi Y, Sakuno T, Goto Y, Watanabe Y. Kinetochore composition and its function: Lessons from yeasts. FEMS Microbiology Reviews. 2014;**38**:185-200. DOI: http://dx.doi.org/10.1111/1574-6976.12049

[27] Yu HG, Dawe RK, Hiatt EN, Dawe RK. The plant kinetochore. Trends in Plant Science. 2000;**5**:543-547. DOI: http://dx.doi.org/10.1016/S1360-1385(00)01789-1

[28] Pinkava DJ, Baker MA. Chromosome and hybridization studies of Agaves. Desert Plants. 1985;**7**:93-100. http://hdl.handle.net/10150/554212

[29] Moreno-Salazar SF, Esqueda M, Martínez J, Palomino G. Tamaño del genoma y cariotipo en *Agave angustifolia* y *A. rhodacantha* de Sonora, México. Revista Fitotécnia Mexicana. 2007;**30**(1):13-23. http://www.revistafitotecniamexicana.org/30-1.html

[30] Palomino G, Martínez J, Méndez I, Cepeda-Cornejo V, Barba-González R,Rodríguez-Garay B. Nuclear genome size and cytotype analysis in *Agave parviflora* Torr subsp. flexiflora Gentry & Berger (Asparagales, Asparagaceae).Caryologia. 2015;**68**(3):159-168. http://dx.doi.org/10.1080/00087114.2015.1032575

[31] Cave MS. Cytological observations on some genera of the Agavaceae. Madroño. 1964; **17**:163-170

[32] Brandham PE. Inversion heterozygosity and sub-chromatid exchanges in *Agave stricta*. Chromosoma. 1969;**26**:270-286. DOI: 10.1007/BF00326522

[33] Doughty LR. Chromosome behaviour in relation to genetics of *Agave*. I. Seven species of fibre agave. Journal of Genetics. 1936;**33**(2):198-205. DOI: 10.1007/BF02982532

[34] Bosco G. When segregation hangs by a thread. PLoS Genetics. 2009;**5**(2):e1000371. DOI:10.1371/journal.pgen.1000371

[35] Hughes SE, Gilliland WD, Cotitta JL, Takeo S, Collins KA, et al. Heterochromatic threads connect oscillating chromosomes during prometaphase I in Drosophila Oocytes. PLoS Genetics. 2009;**5**(1):e1000348. DOI:10.1371/journal.pgen.1000348

[36] Puchta H. The repair of double-strand breaks in plants: mechanisms and consequences for genome evolution. Journal of Experimental Botany. 2005;**56**:1-14. DOI:10.1093/jxb/eri025

[37] González-Barrera S, Cortés-Ledesma F, Wellinger RE, Aguilera A. Equal sister chromatid exchange is a major mechanism of Double-Strand break repair in yeast. Molecular Cell. 2003;**11**:1661-1671. DOI: http://dx.doi.org/10.1016/S1097-2765(03)00183-7

[38] Rodríguez-Garay B, Gutiérrez-Mora M,González-Gutiérrez AG. Climate change reaches the tequila country. In: Gutiérrez-Mora A, editor. Rodríguez-Garay B, Contreras-Ramos SM, Kirchmayr MR, González-Ávila M (Comps.). Sustainable and Integral Exploitation of Agave; 2014. ISBN: 978-607-96619-1-5. Published online: December 22, 2014. DOI: 10.13140/RG.2.1.2524.6882

[39] Paital B, Panda SK, Hati AK, Mohanty B, Mohapatra MK, Kanungo S, Chainy GBN. Longevity of animals under reactive oxygen species stress and disease susceptibility due to global warming. World Journal of Biological Chemistry. 2016;**7**(1):110-127. DOI: http://dx.doi.org/10.4331/wjbc.v7.i1.110

[40] Perkinsa AT, Dasa TM, Panzeraa LC, Bickela SE. Oxidative stress in oocytes during midprophase induces premature loss of cohesion and chromosome segregation errors. Proceedings of the National Academy of Sciences of the United States of America. 2016;**113**(44):E6823–E6830. DOI: 10.1073/pnas.1612047113

[41] Clift D, Marston AL. The role of shugoshin in meiotic chromosome segregation. Cytogenetic and Genome Research. 2011;**133**:234-242. DOI: 10.1159/000323793

[42] Hamant O, Golubovskaya I, Meeley R, Fiume E, Timofejeva L, Schleiffer A, Nasmyth K, Cande WZ. A REC8-dependent plant shugoshin is required for maintenance of centromeric cohesion during meiosis and has no mitotic functions. Current Biology. 2005;**15**:948-954. DOI: 10.1016/j.cub.2005.04.049

[43] Unal E, Heidinger-Pauli JM, Koshland D. DNA double-strand breaks trigger genome-wide sister-chromatid cohesion through Eco1 (Ctf7). Science. 2007;**317**:245-248. DOI: 10.1126/science.1140637

[44] Ben-Shahar TR, Heeger S, Lehane C, East P, Flynn, H, Skehel M, Uhlmann F. Eco1-dependent cohesin acetylation during establishment of sister chromatid cohesion. Science. 2008;**321**:563-566. DOI: 10.1126/science.1157774

[45] Unal E, Heidinger-Pauli J.M, Kim W, Guacci V, Onn I, Gygi SP, Koshland DE. A molecular determinant for the establishment of sister chromatid cohesion. Science. 2008;**321**:566-569. DOI: 10.1126/science.1157880

[46] Harrison CJ, Alvey E, Henderson IR. Meiosis in flowering plants and other green organisms. Journal of Experimental Botany. 2010;**61**(11):2863-2875. DOI:10.1093/jxb/erq191