

Origen y Evolución de los Sistemas de Determinación Sexual y Cromosomas Sexuales de Plantas

Genética, genómica y mejora vegetal

Febrero de 2023

Máster en Genética y Evolución
(Especialidad Agroalimentaria)



Rafael Navajas-Pérez

**UNIVERSIDAD
DE GRANADA**

ESTUDIOS GENÉTICOS Y GENÓMICOS EN PLANTAS DIOICAS CON CROMOSOMAS SEXUALES

- DETERMINACIÓN SEXUAL MEDIADA POR CROMOSOMAS SEXUALES

CARACTERIZACIÓN DE ESPECIES CON CROMOSOMAS SEXUALES HETEROMÓRFICOS (Enfoque citogenético-molecular).

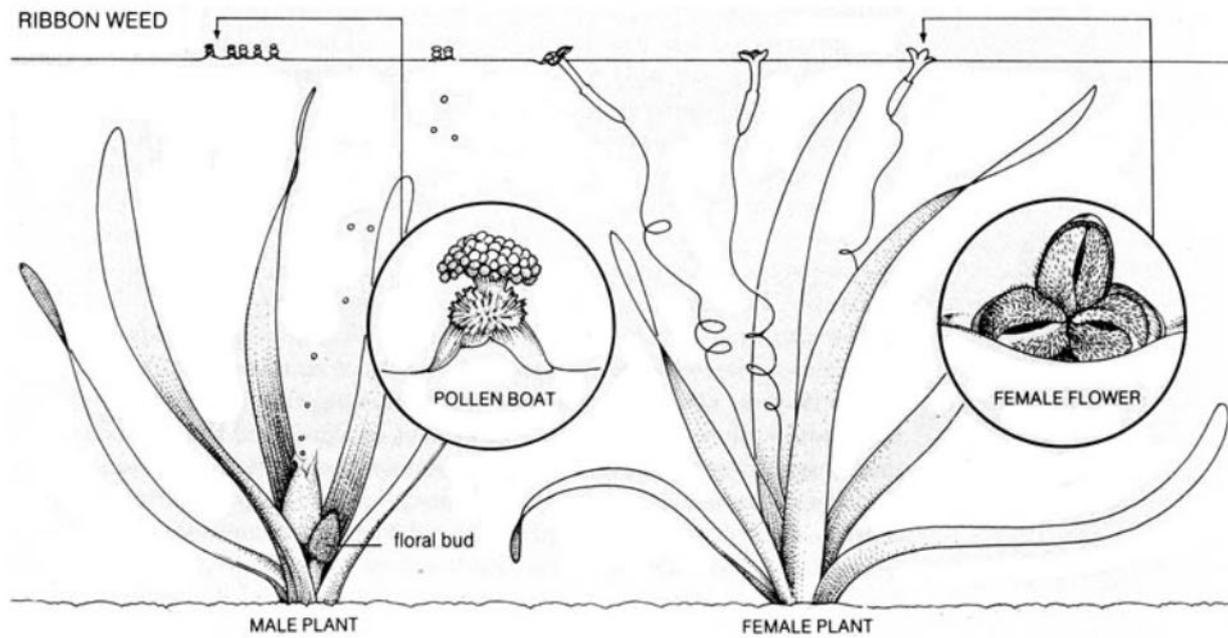
CARACTERIZACIÓN DE ESPECIES SIN HETEROMORFÍA CROMOSÓMICA (Enfoque genómico).

- CARACTERIZACIÓN DE GENES DETERMINANTES DEL SEXO

MODELO DE LAS DOS MUTACIONES

MODELO DE UNA MUTACIÓN





Sistema reproductivo de *Vallisneria spiralis*



Polinización Cruzada

Orquídeas, amor y mentiras

¿Cómo hacer para propagar los genes sin moverse del sitio?
Seduciendo a los animales, entre ellos a los humanos. Atraen a los polinizadores con artimañas y prometiendo sexo. Mira las fotografías de orquídeas de Christian Ziegler.

26 de septiembre de 2016, [National Geographic](#)





Murciélagos, la llamada de la flor

Algunas flores tropicales reflejan el sonido para que los murciélagos nectarívoros las encuentren con mayor facilidad.

16 de octubre de 2017, [National Geographic](#)

Polinización mediada por
murciélagos en
Marcgravia evenia



Foto de Merlin D. Tuttle



En Plantas...

- No existen **caracteres sexuales secundarios**. El dimorfismo sexual no es evidenciable en tejidos somáticos

- Las células de la línea germinal no se diferencian al principio del desarrollo, sus **órganos y gametos derivan de células somáticas**

- Se reproducen **vegetativamente**



Ambos sexos
juntos



Hermafroditismo



Sexos separados
en el mismo
individuo

en el espacio

en el tiempo

Monoecia

Dicogamia

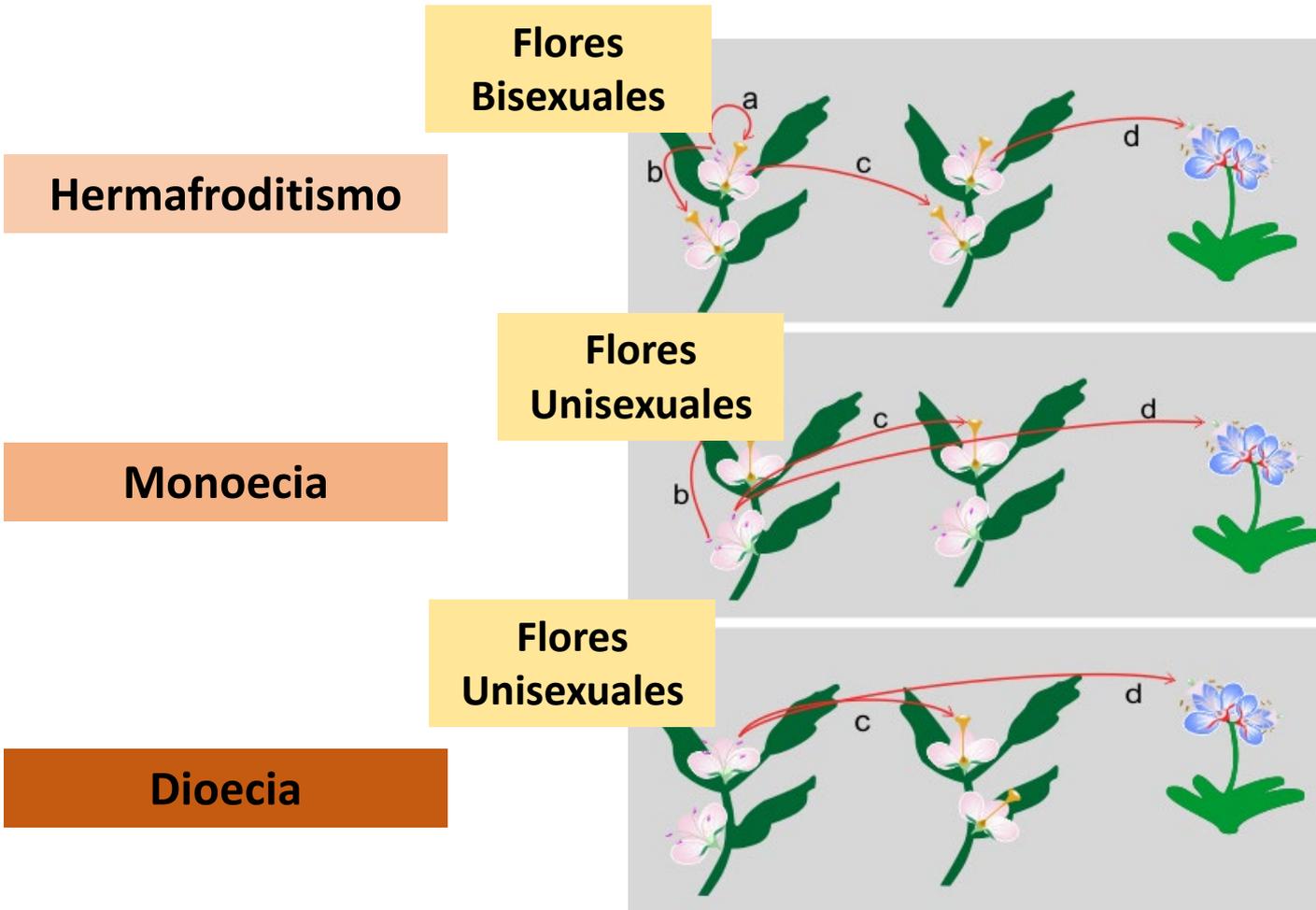
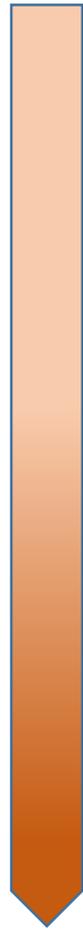


Individuos con
sexos separados



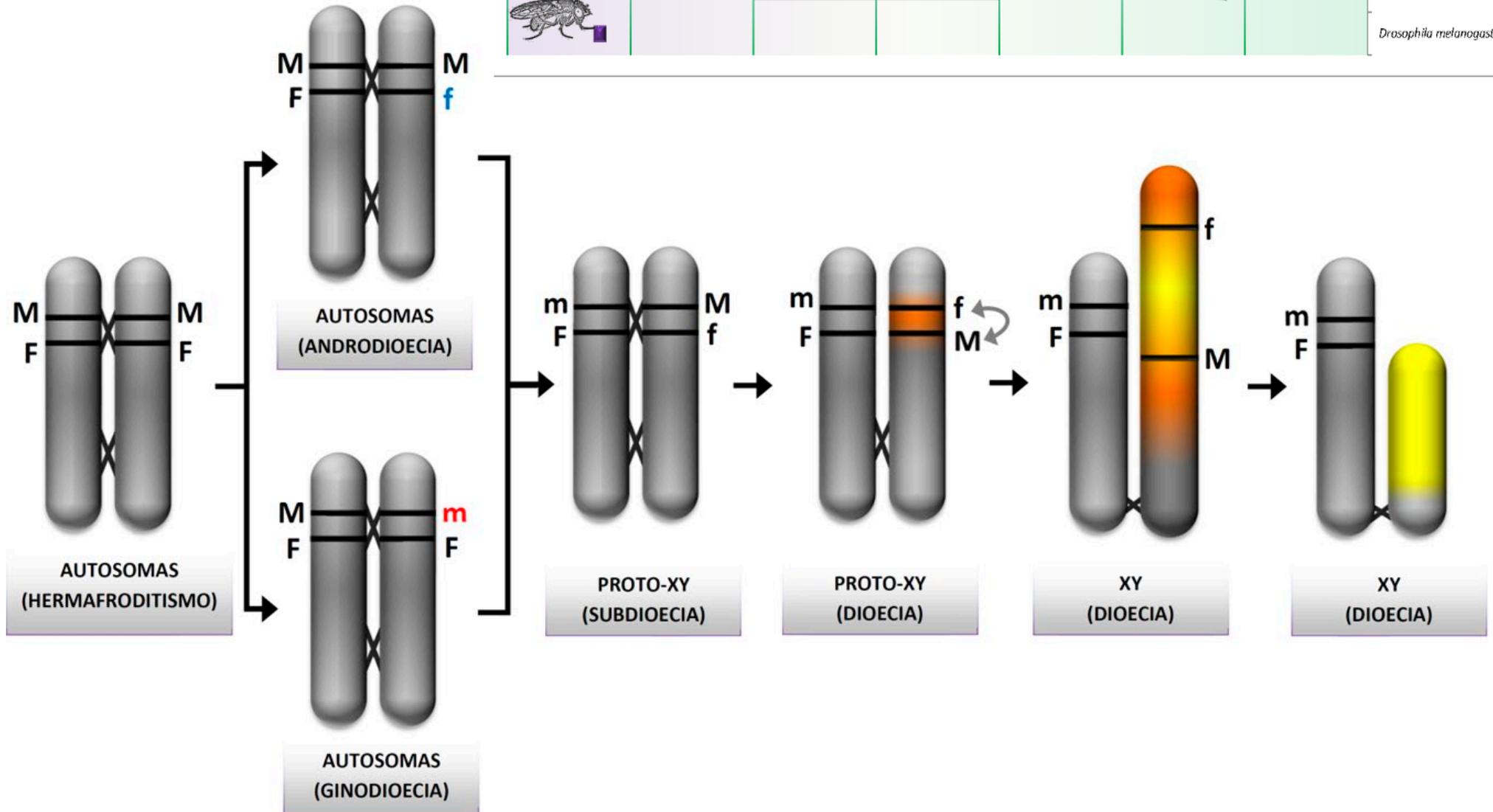
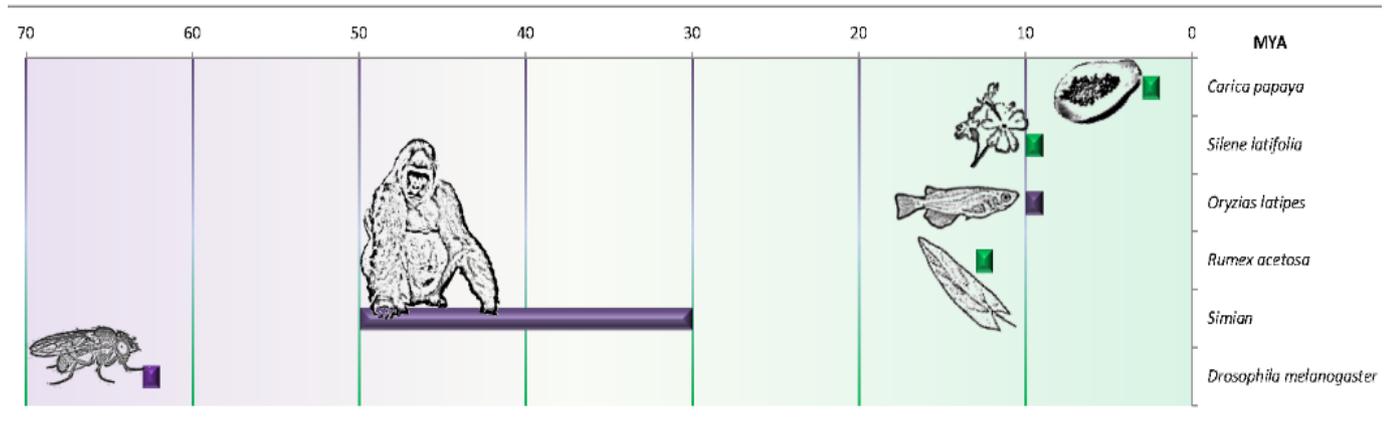
Dioecia





Modificado de:
<http://www.ufac.br/ppgespa/polen>

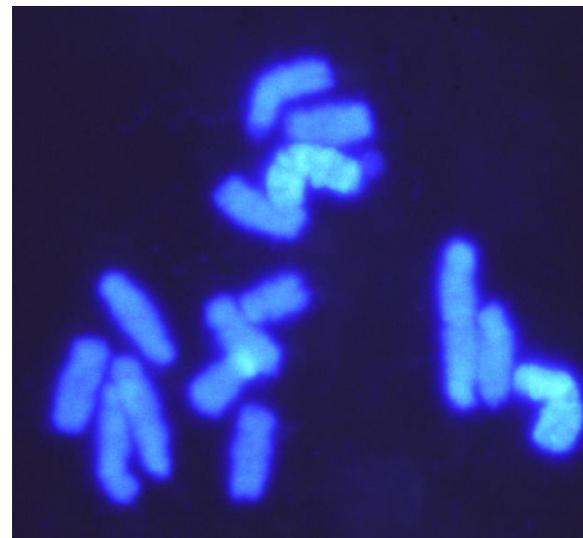
HIPÓTESIS DE PARTIDA

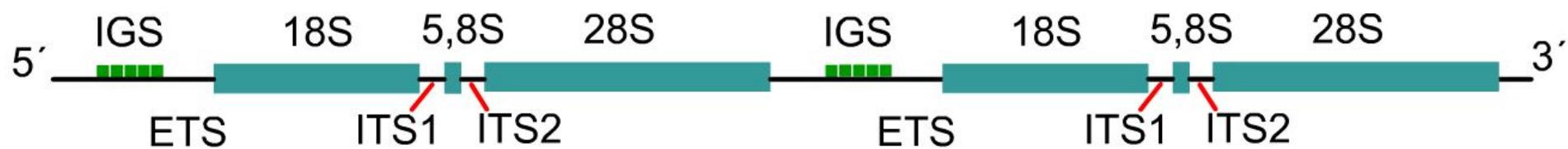


***CARACTERIZACIÓN DE ESPECIES CON CROMOSOMAS SEXUALES
HETEROMÓRFICOS (Enfoque citogenético-molecular).***

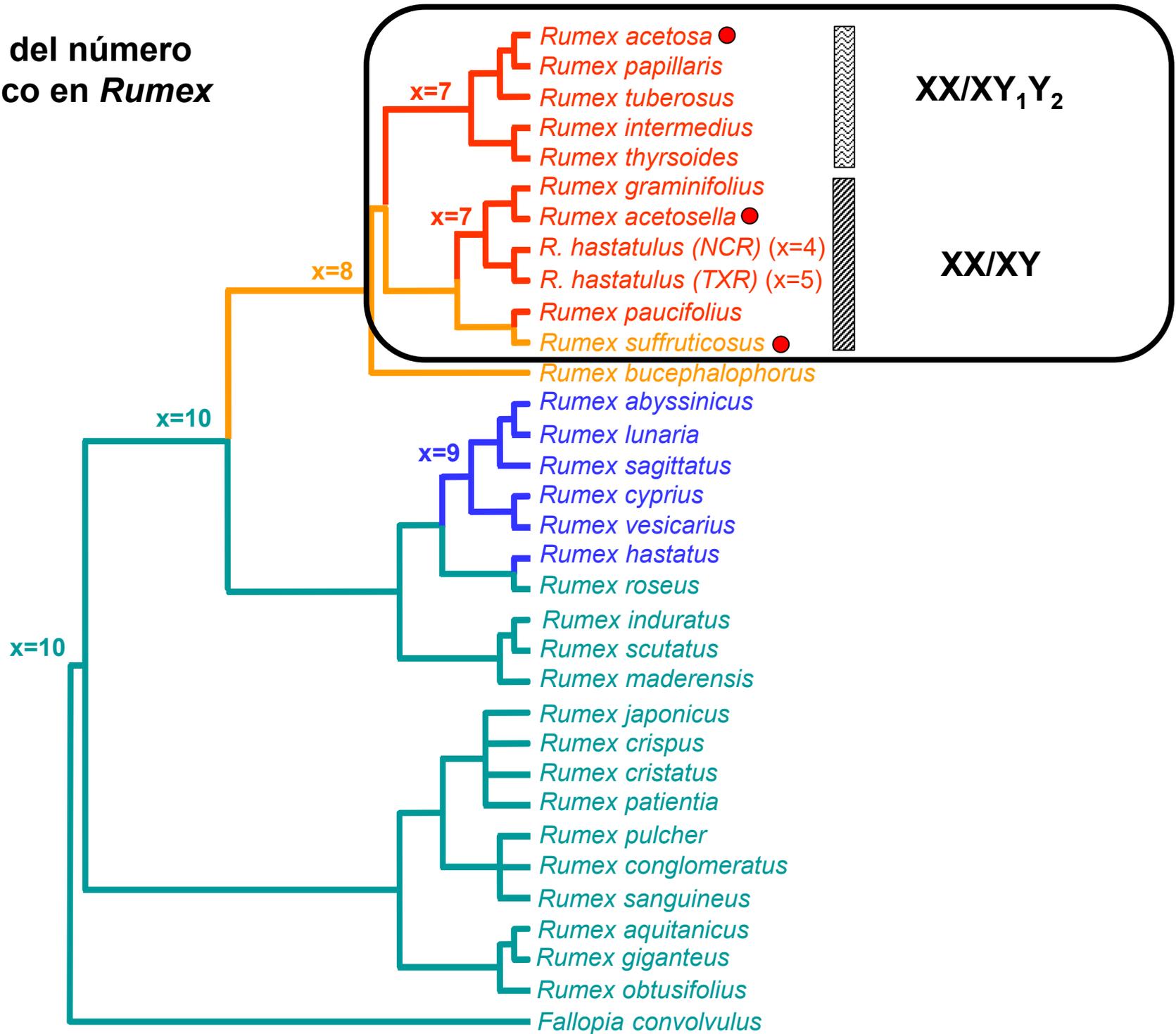


Origen y evolución de los cromosomas sexuales y de los sistemas de determinación sexual en el género *Rumex*.

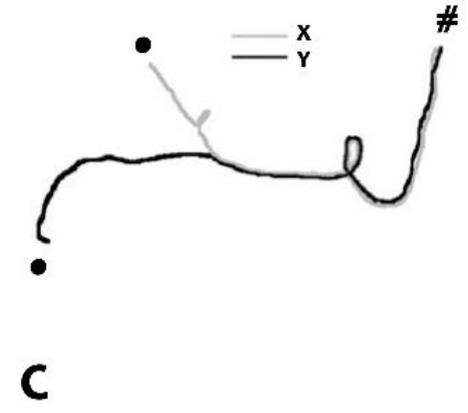
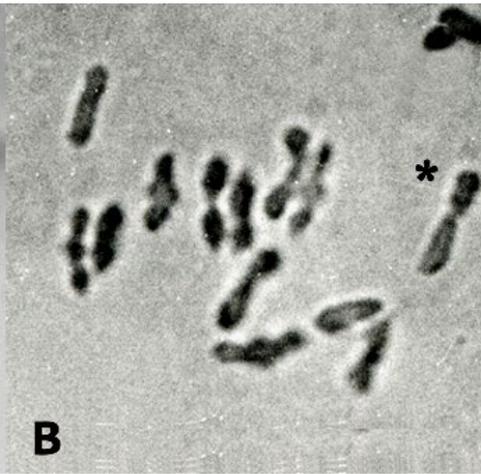
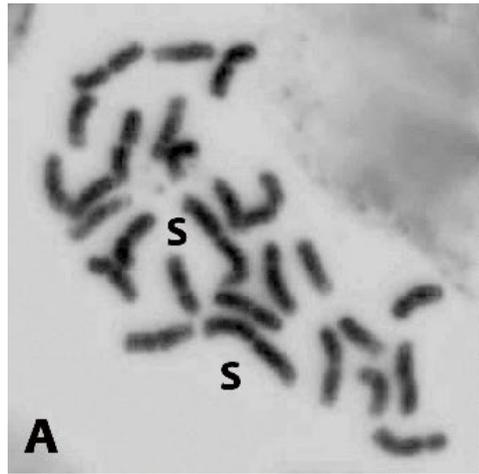




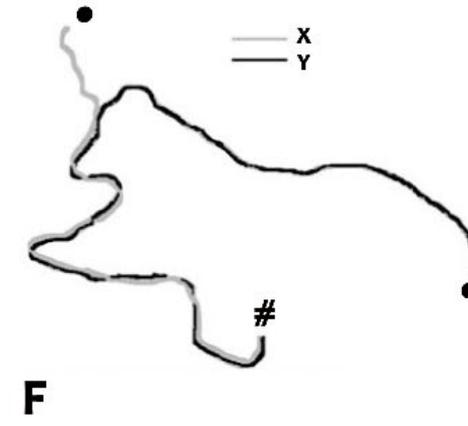
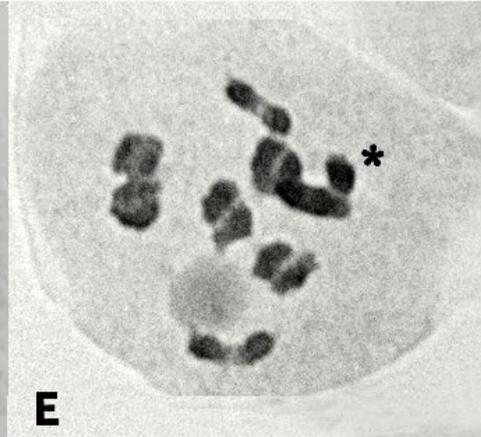
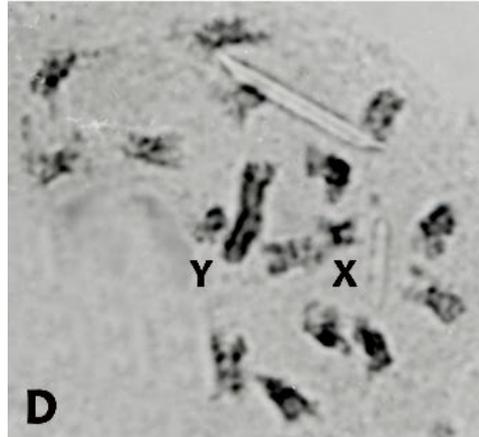
Evolución del número cromosómico en *Rumex*



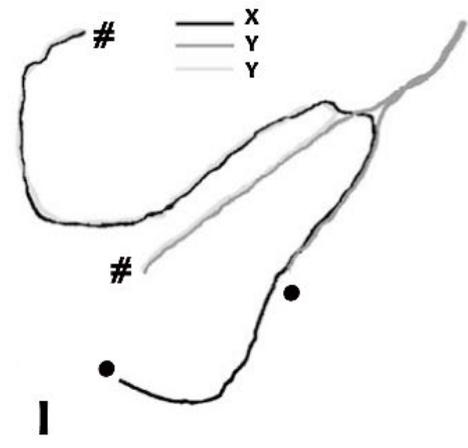
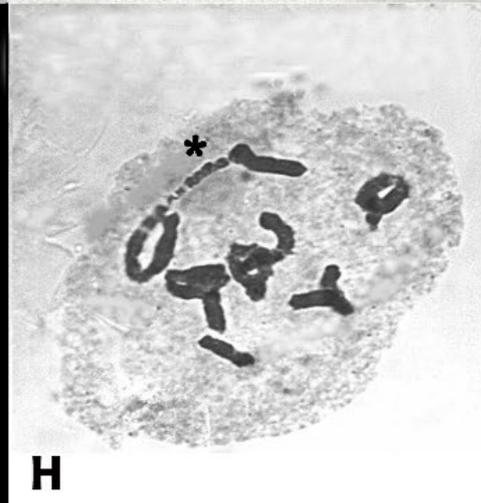
R. acetosella



R. suffruticosus

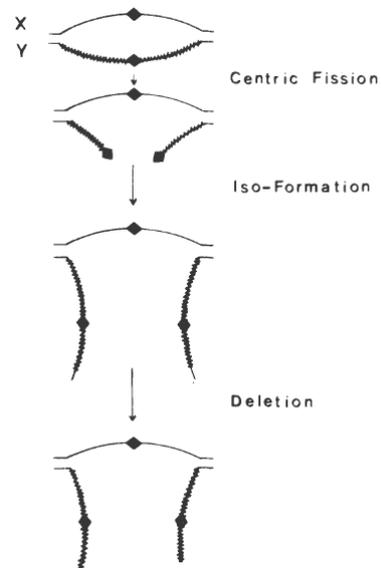
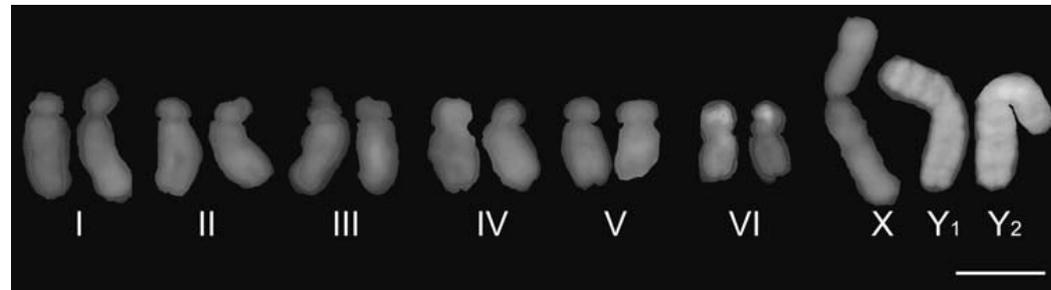


R. acetosa

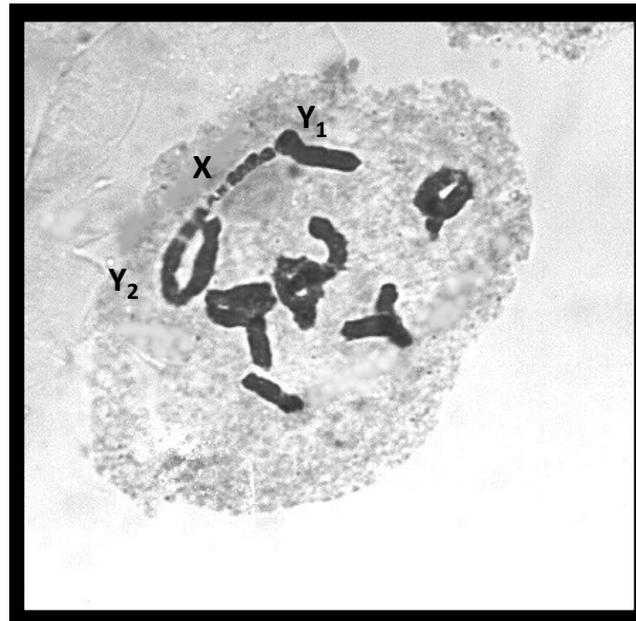


LOS SUPER-MACHOS DE *Rumex acetosa*

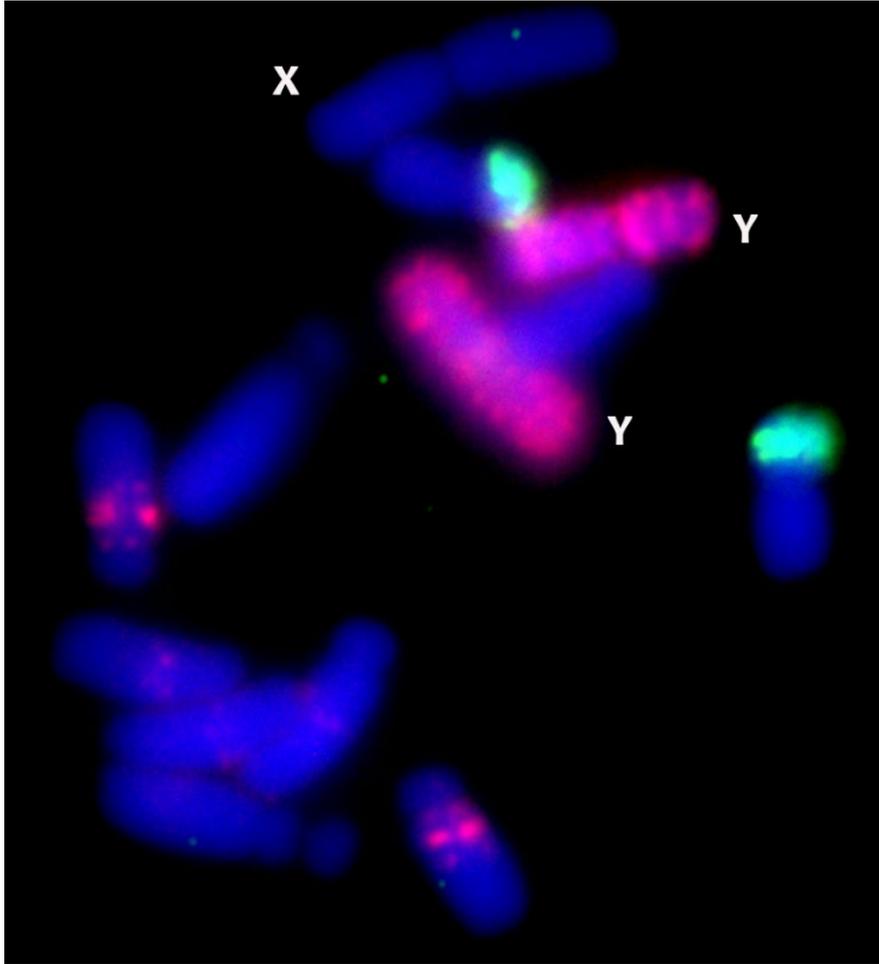
Navajas-Pérez et al., 2009



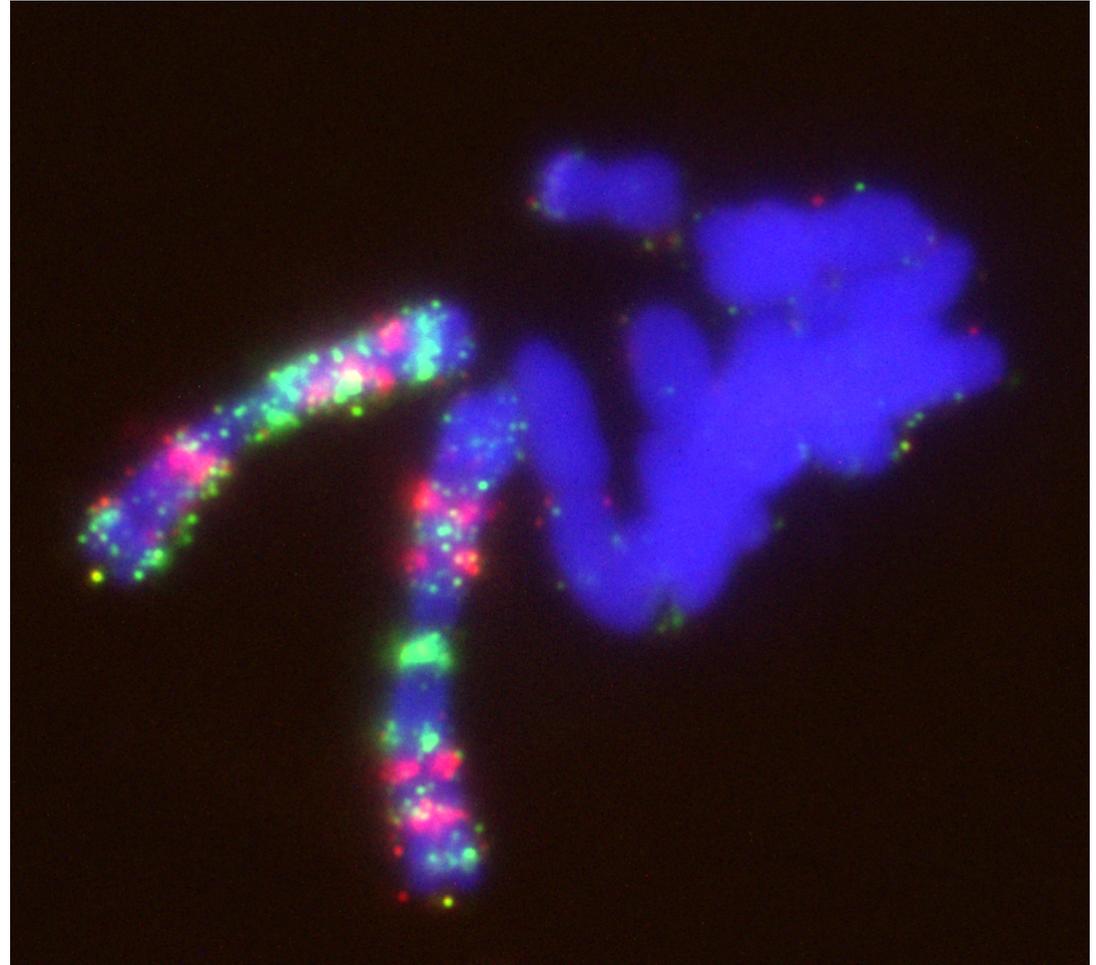
Ruiz Rejón et al., 1994



Papel del ADN repetido en la evolución de los sistemas de cromosomas sexuales.



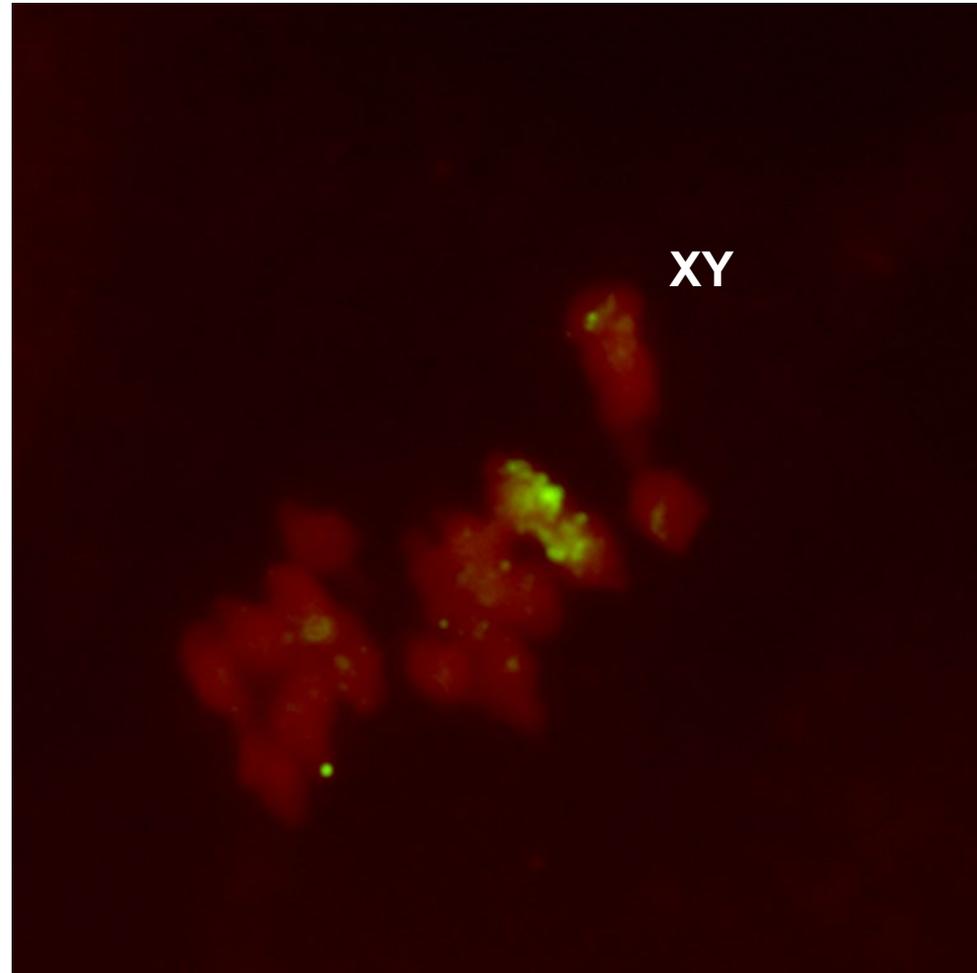
Presencia de las familias de ADN satélite **RAE-180** (rojo) y **RAE-730** (verde) en *Rumex acetosa*



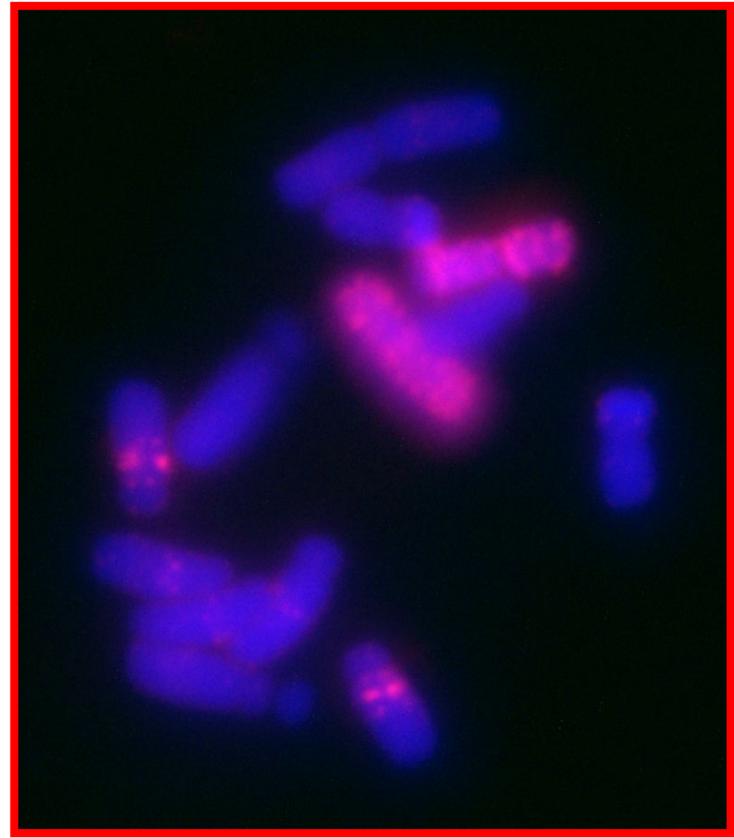
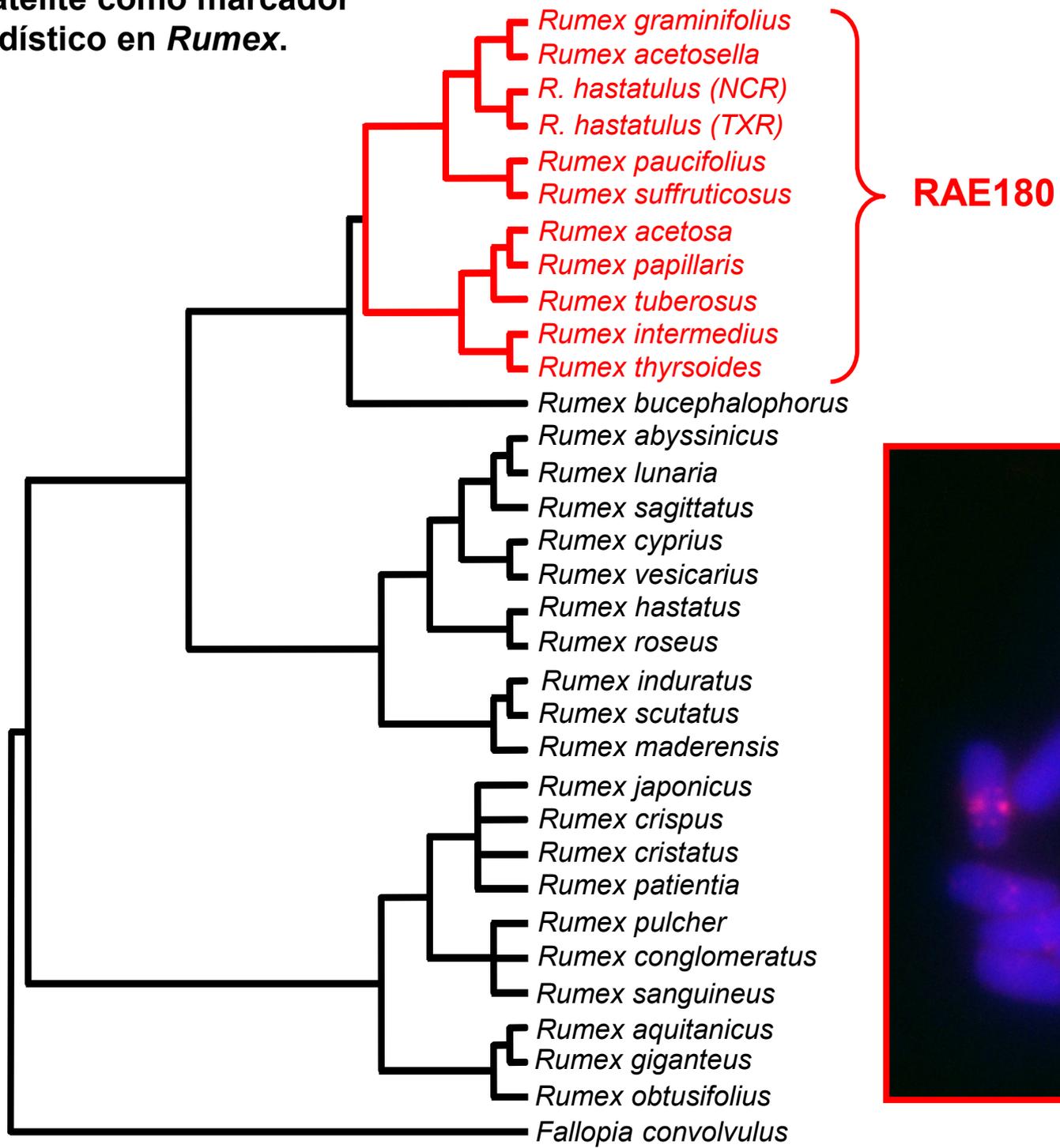
Presencia de la familia de ADN satélite **RAYSI** (rojo) y **RAE-180** (verde) en *Rumex papillaris*

Papel del ADN repetido en la evolución de los sistemas de cromosomas sexuales.

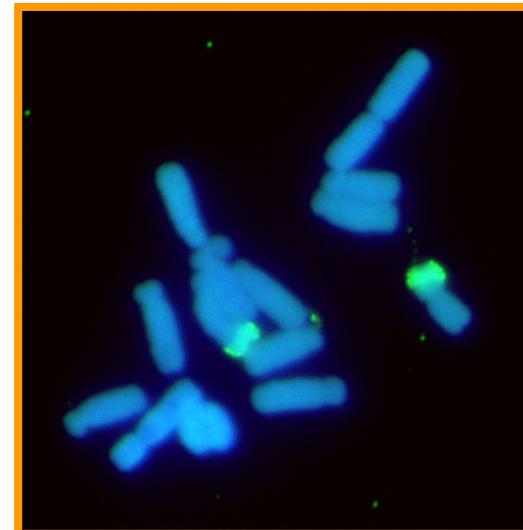
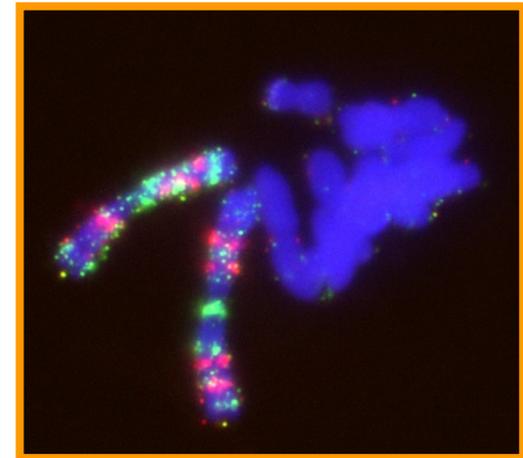
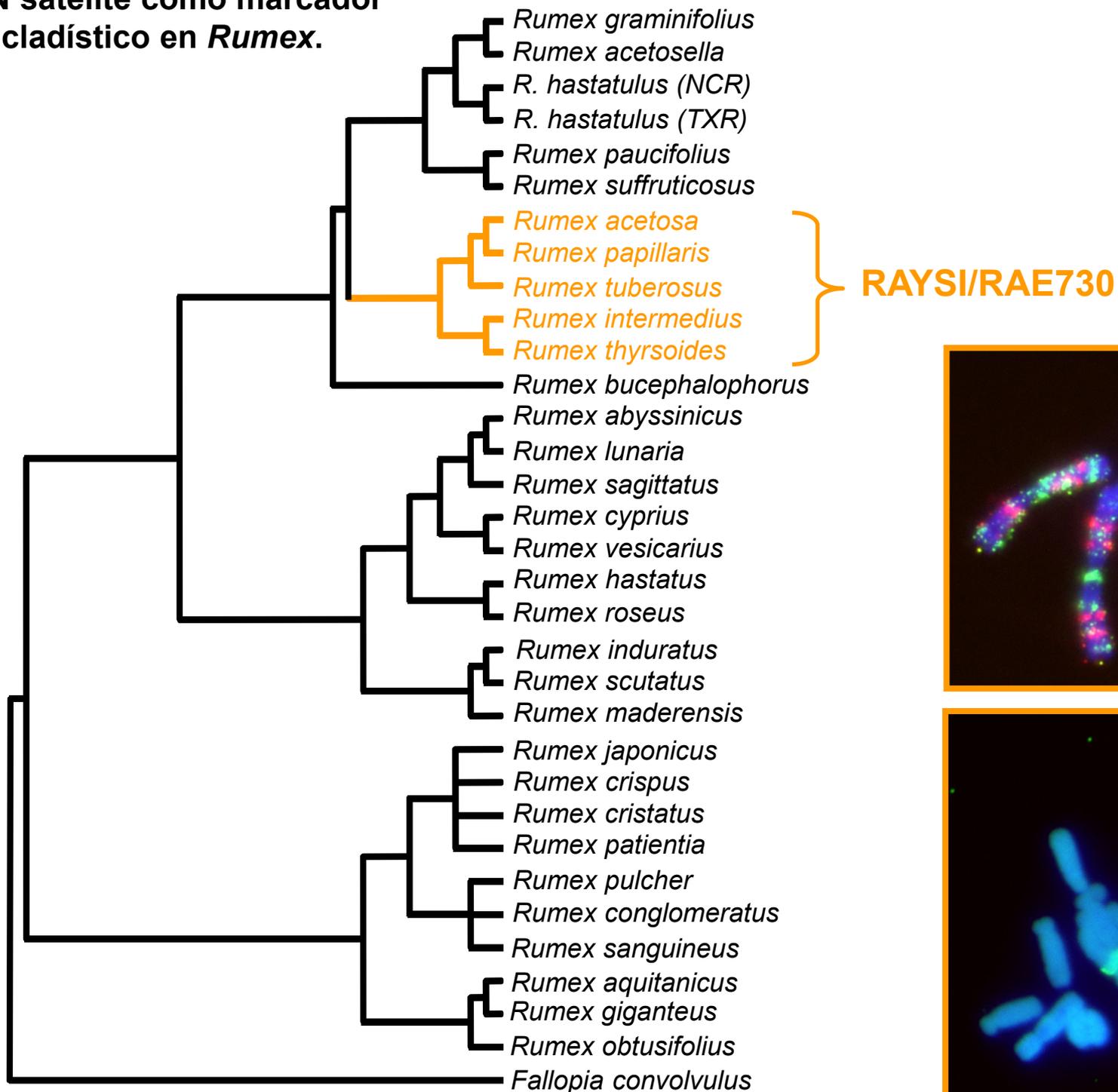
Presencia de la familia de ADN satélite **RAE-180** en *Rumex suffruticosus*



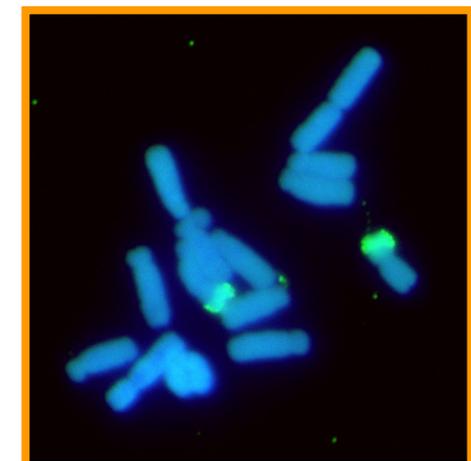
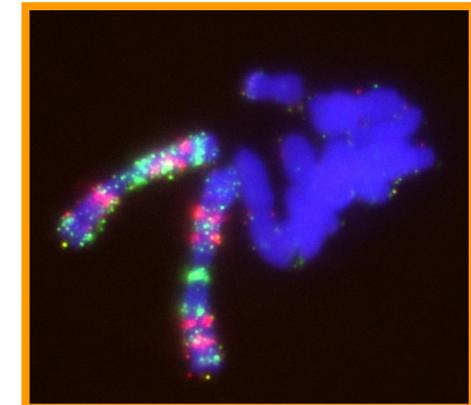
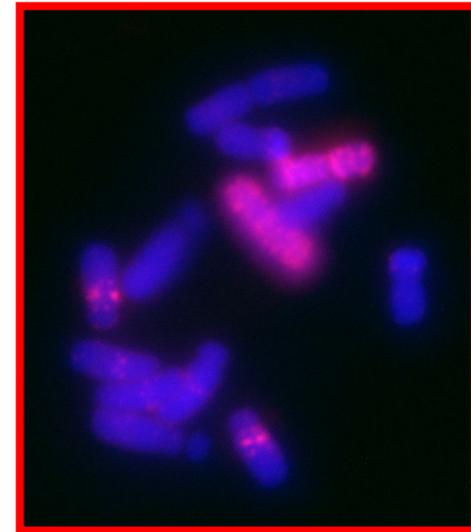
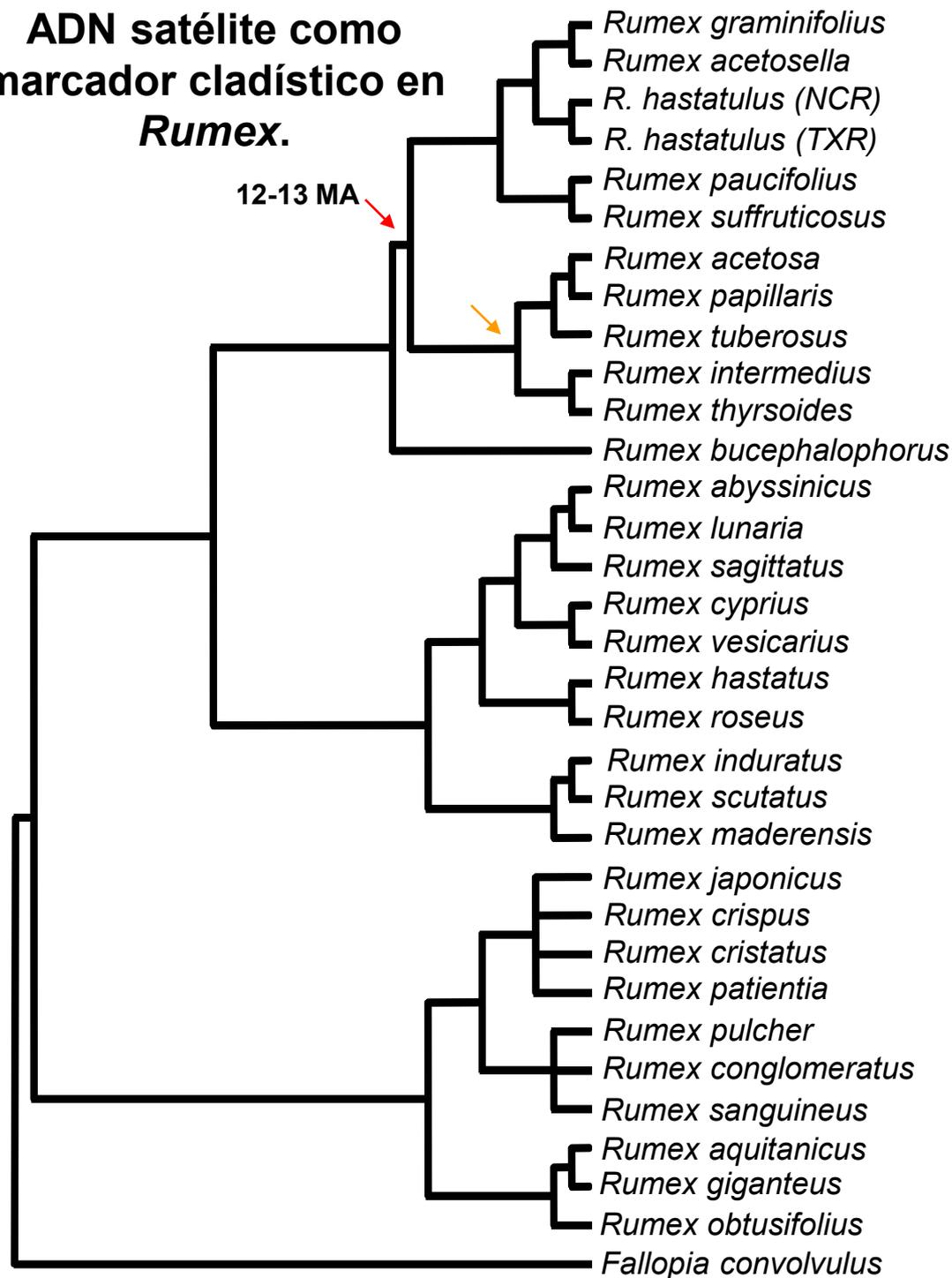
**ADN satélite como marcador
cladístico en *Rumex*.**

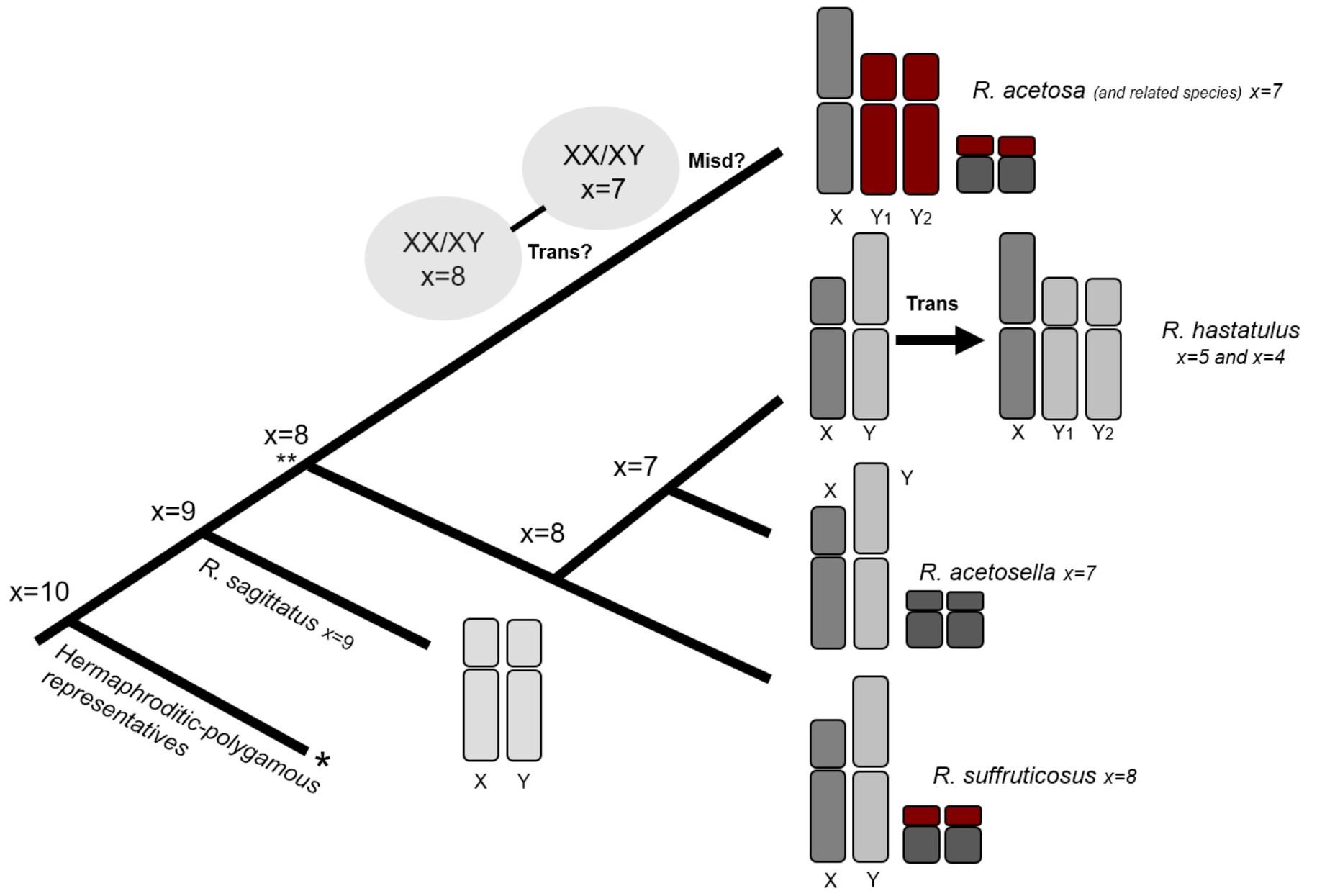


**ADN satélite como marcador
cladístico en *Rumex*.**



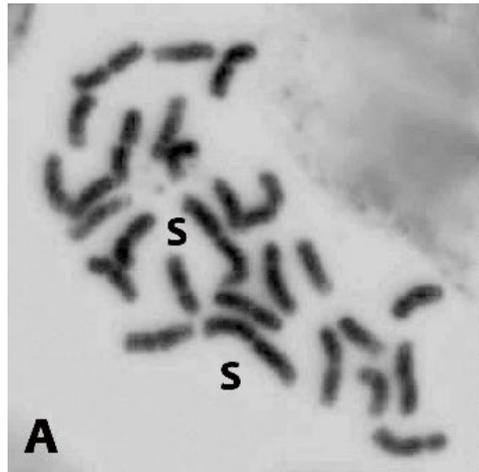
**ADN satélite como
marcador cladístico en
Rumex.**



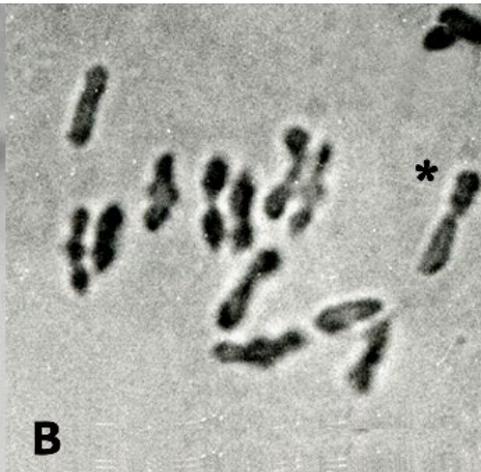




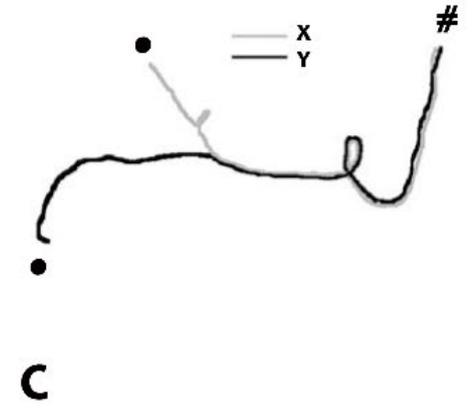
R. acetosella



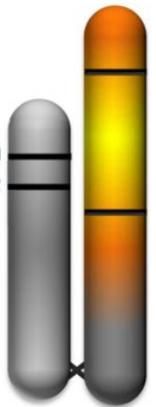
A



B



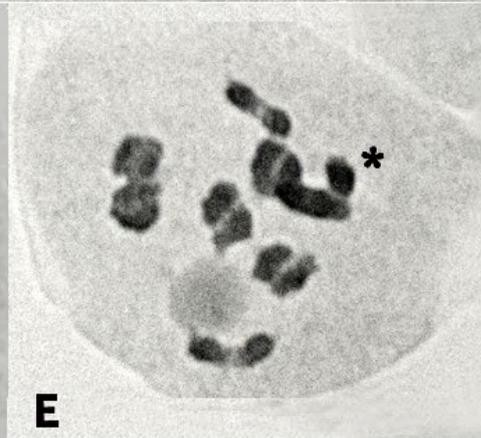
C



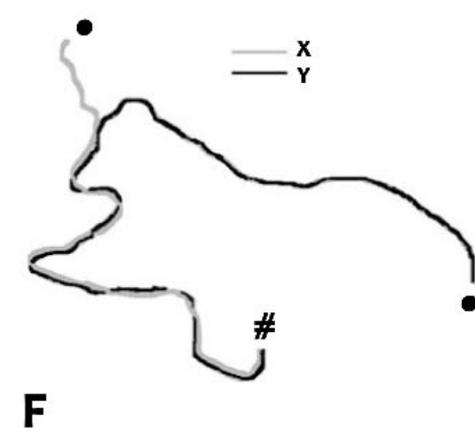
R. suffruticosus



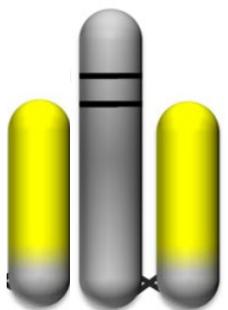
D



E



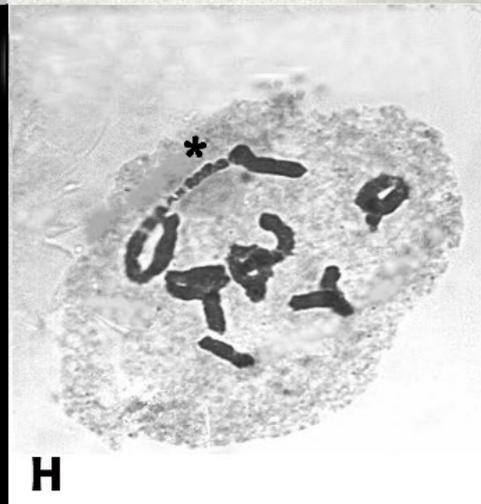
F



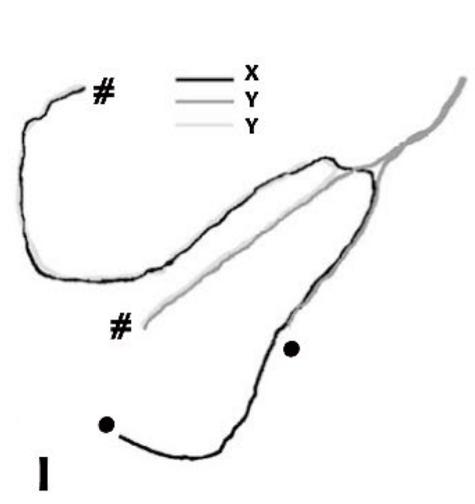
R. acetosa



G



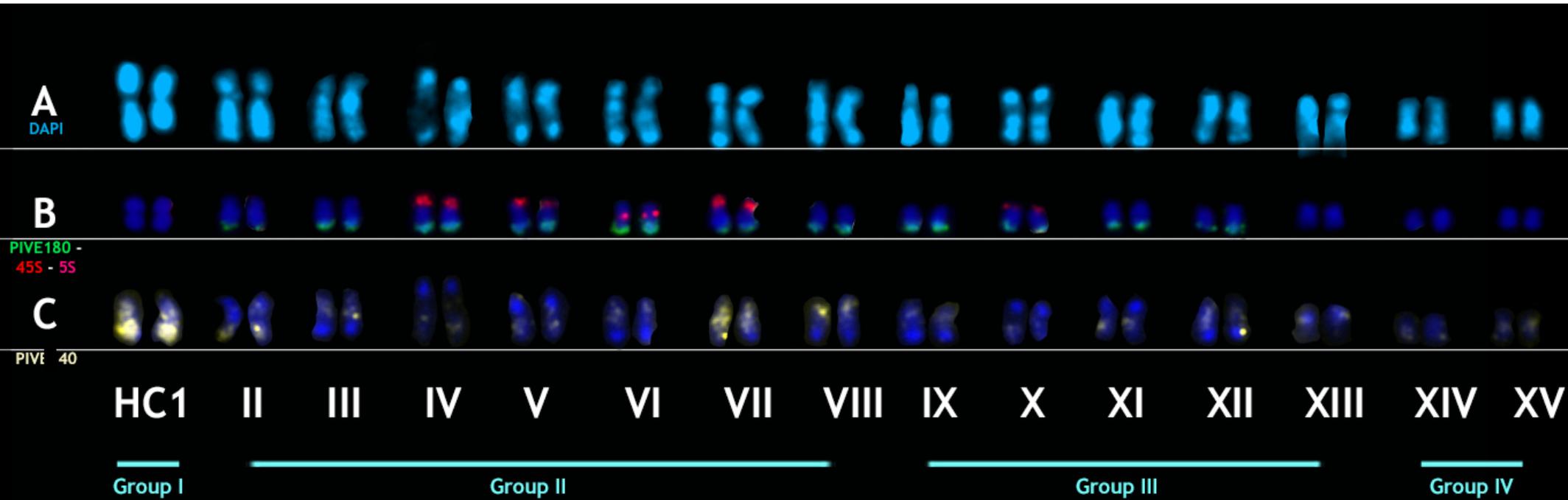
H



I

***CARACTERIZACIÓN DE ESPECIES CON CROMOSOMAS SEXUALES
HETEROMÓRFICOS (Enfoque citogenético-molecular).***

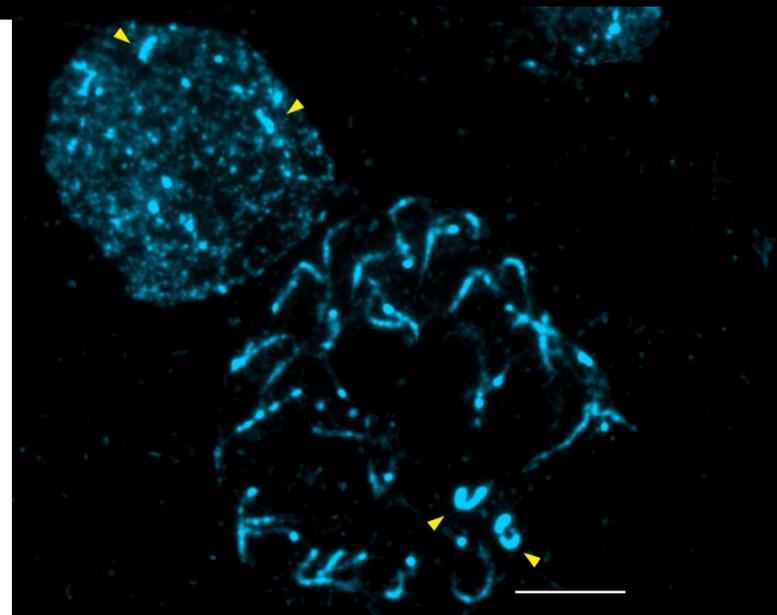




PIVE-40 Evolutionary Pattern



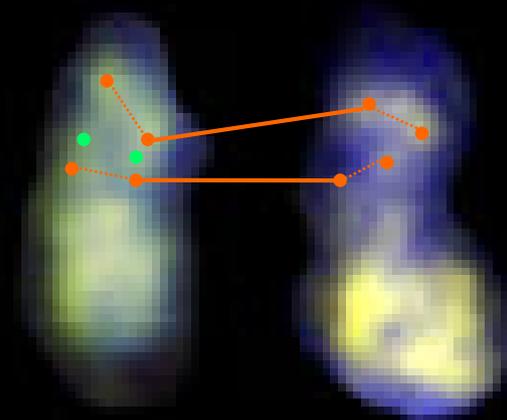
HORs (High Order Repeats)



HC1



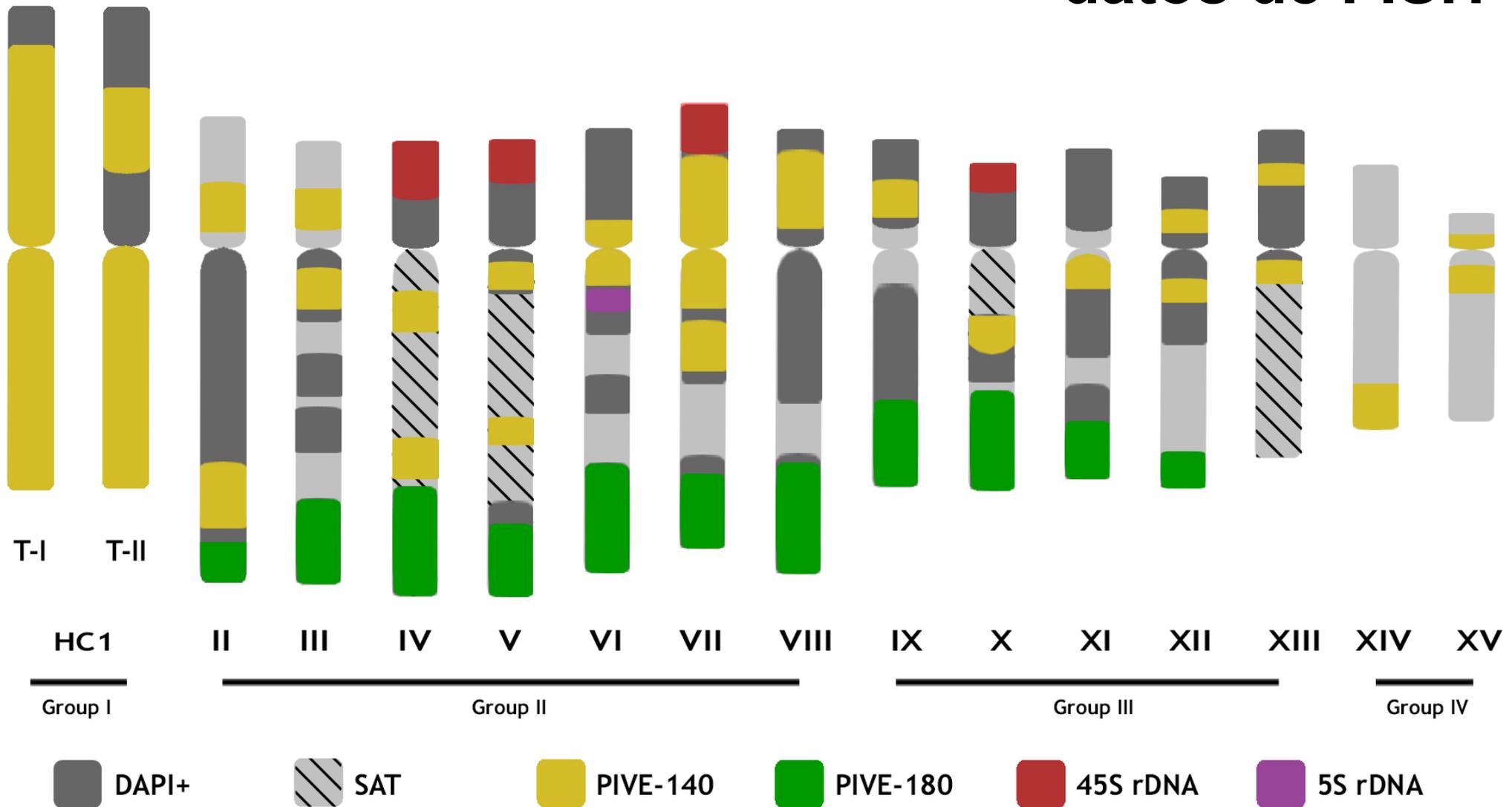
Type-I/Type-I

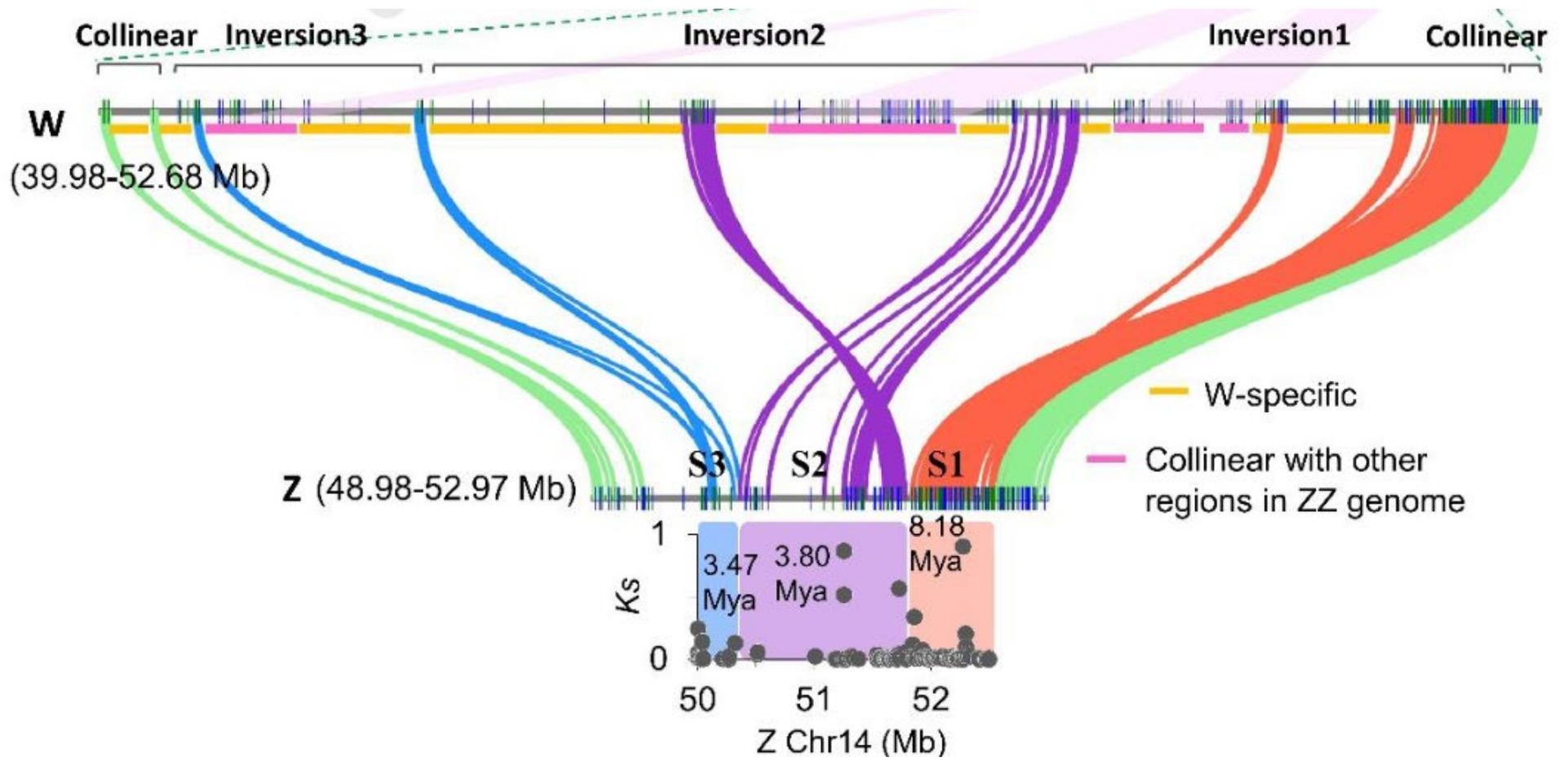


Type-I/Type-II



Idiograma de *Pistacia vera* L. a partir de los datos de FISH





***CARACTERIZACIÓN DE ESPECIES SIN HETEROMORFÍA
CROMOSÓMICA (Enfoque genómico).***

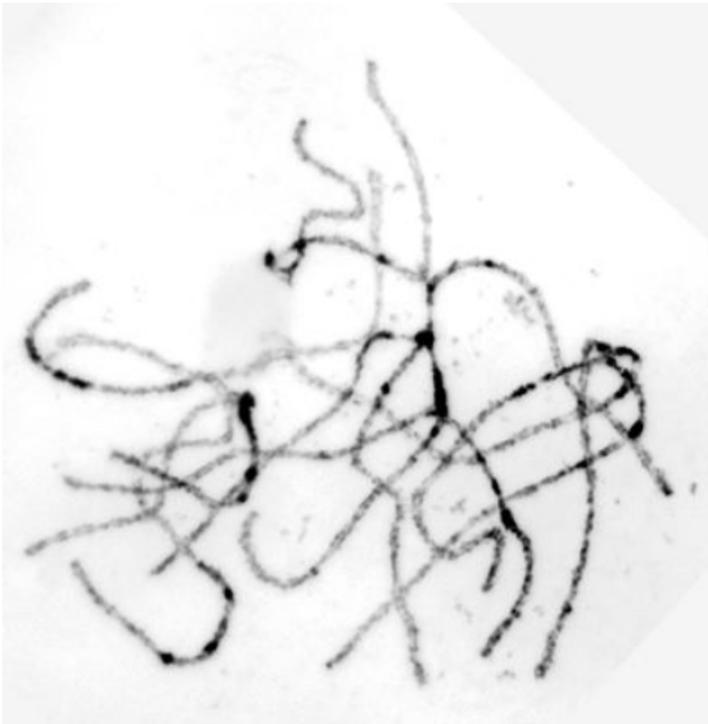


TRIOECIA EN PAPAYA

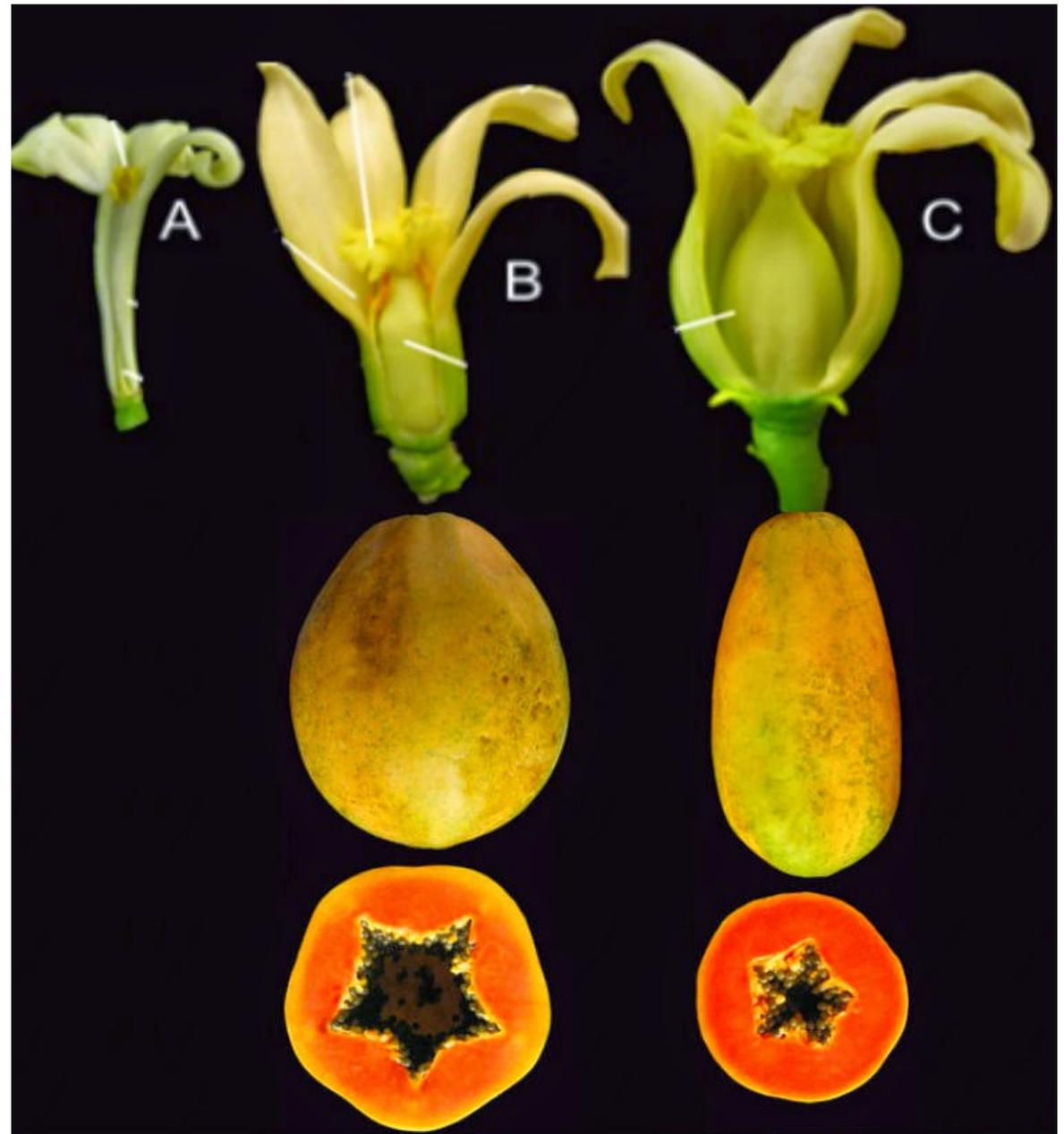
(A): Flor masculina

(B): Flor hermafrodita y su fruto

(C): Flor femenina y su fruto



Fuente: Ming et al., 2008



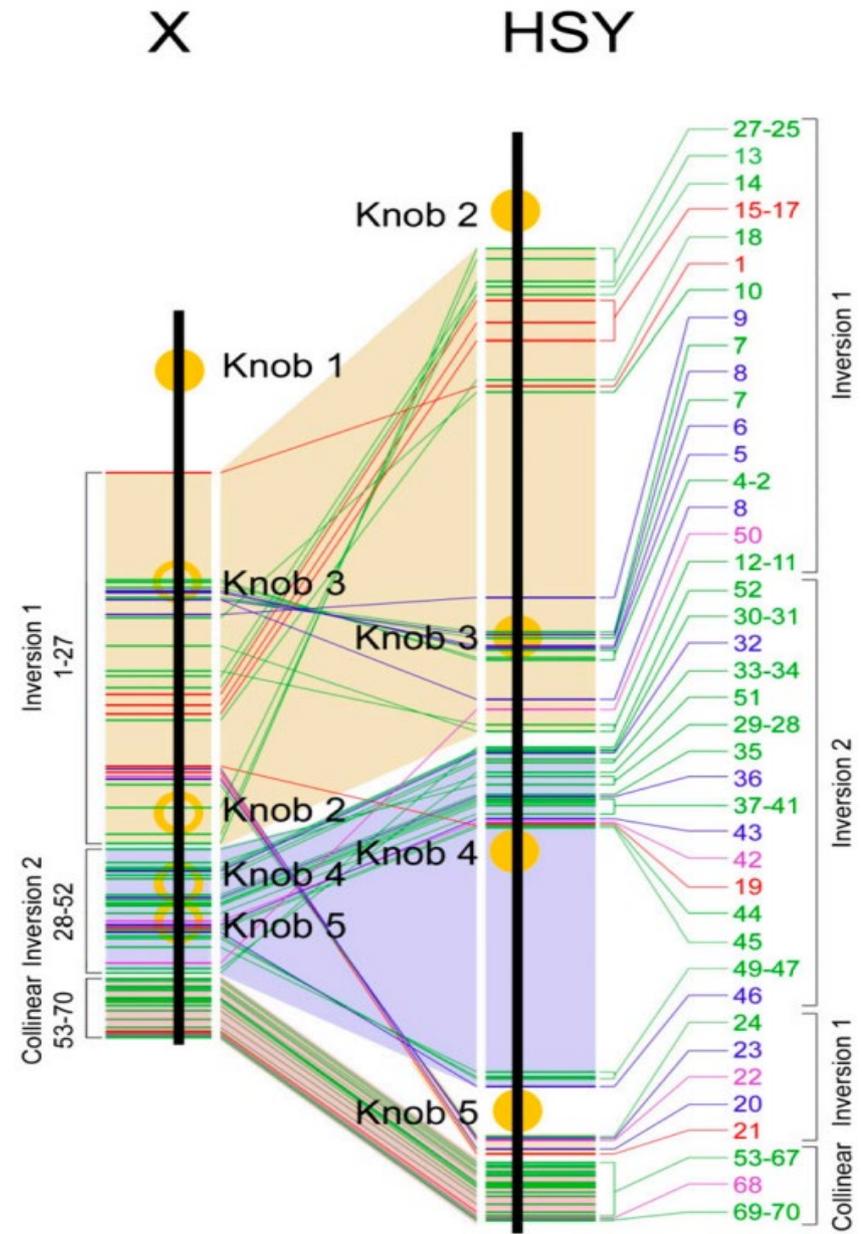
Presencia de dos inversiones en la región HSY

Inversión I: 7 MA

Inversión II: 2 MA

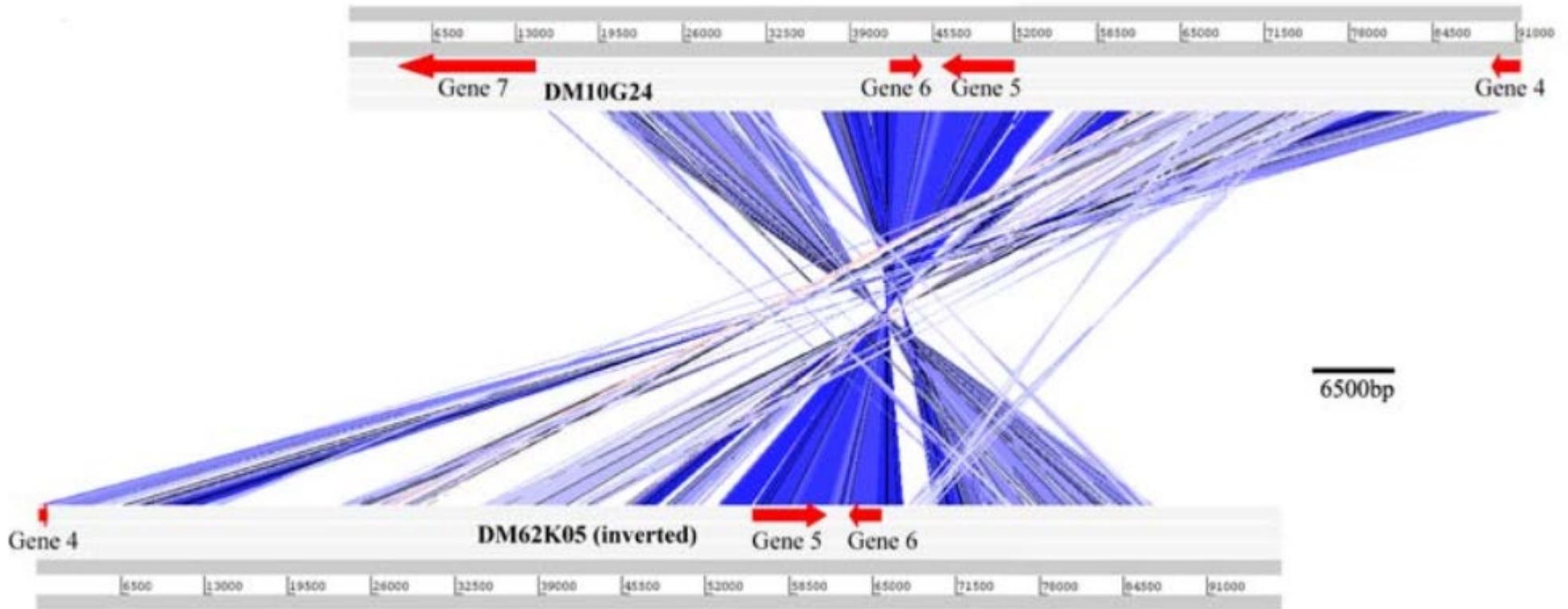


Fuente: Ming et al., 2008

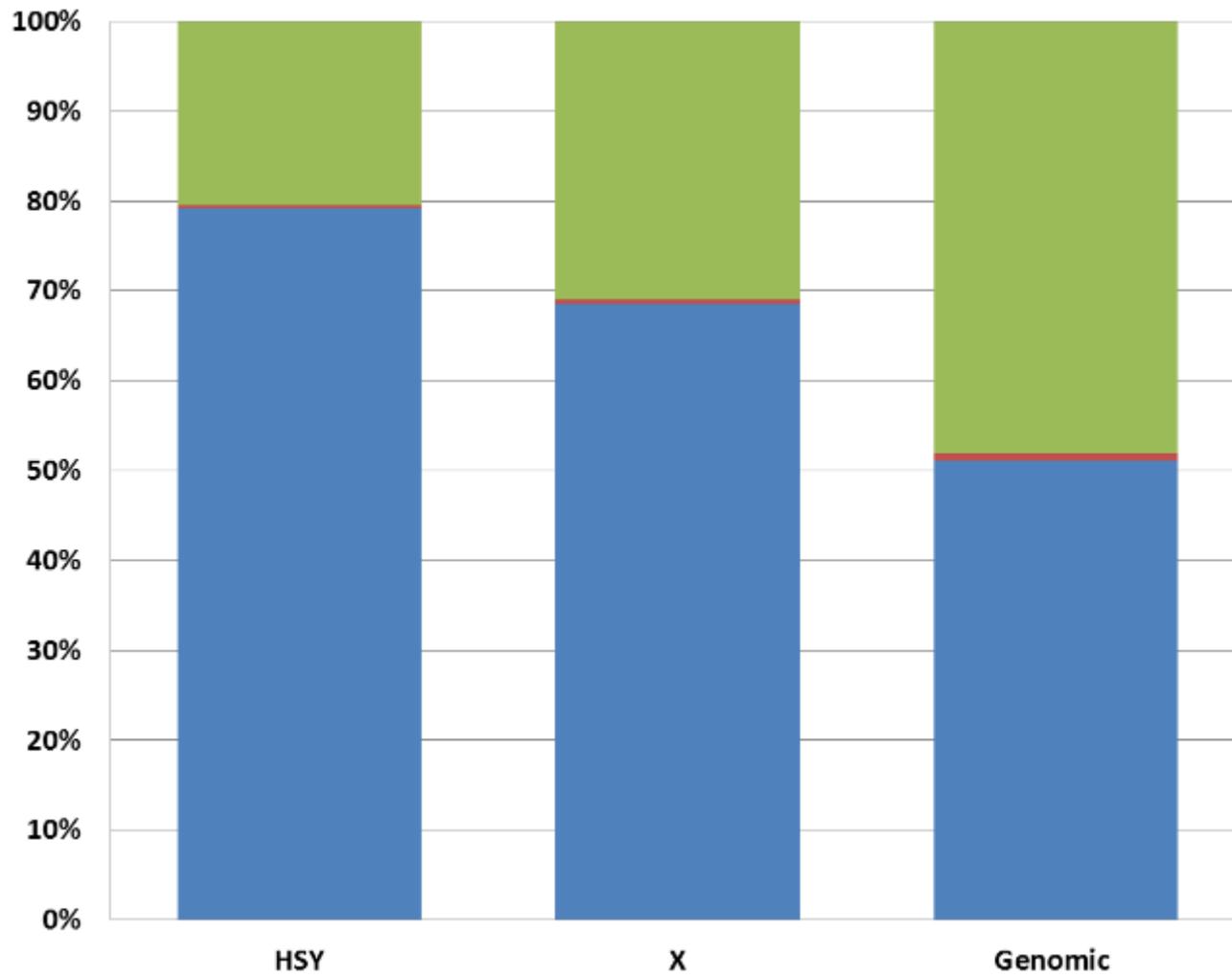


Fuente: Wang et al., 2012

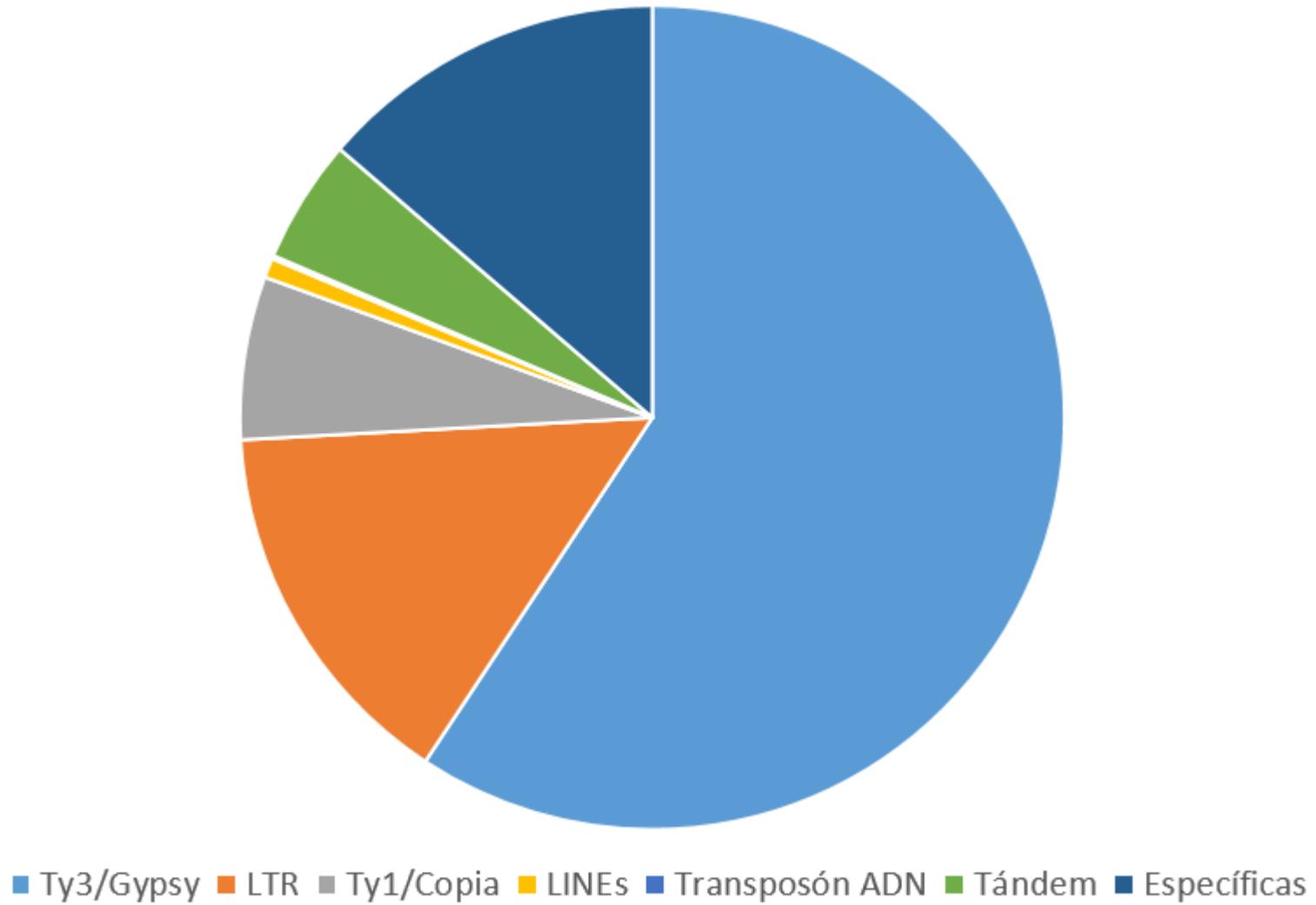
Comparación de secuencias BAC de la región determinante del sexo correspondiente al cromosoma X y al cromosoma Y de papaya



Expansión de la cromatina del Y: 8,1 Mb vs 3,5 Mb



Secuencias Repetidas en el Genoma de Papaya



CARACTERIZACIÓN DE GENES DETERMINANTES DEL SEXO

Diferenciación de Verticilos

Perianto

Verticilo #1: Cáliz

Parte más externa de la flor. Protege los verticilos interiores, sobre todo cuando la flor aún no se ha abierto. Se compone de sépalos, normalmente verdes y de naturaleza herbácea.

Verticilo #2: Corola

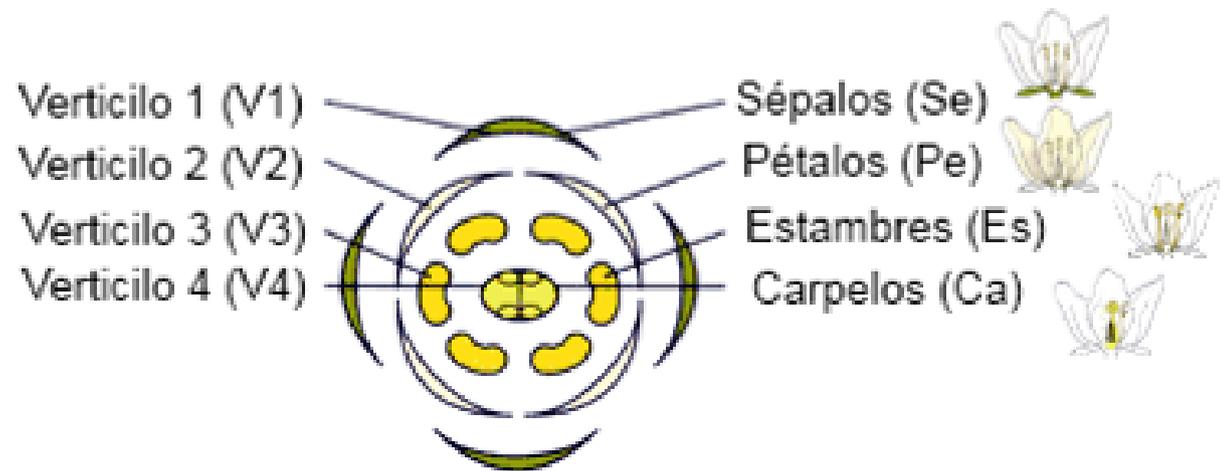
A continuación del cáliz. Está formado por los pétalos de la flor, que sirven de protección pero, sobre todo, tienen como función la de atraer polinizadores. Pueden presentar diversa coloración.

Verticilo #3: Estambres

A continuación de la corola. Este verticilo da lugar a los órganos reproductores masculinos.

Verticilo #4: Carpelos

Ocupa la posición central de la flor. Da lugar a los órganos reproductores femeninos, incluyendo el ovario que se transformará, tras la fecundación, en fruto.



Órganos reproductores

Genetic interactions among floral homeotic genes of *Arabidopsis*

JOHN L. BOWMAN, DAVID R. SMYTH* and ELLIOT M. MEYEROWITZ†

Division of Biology 156-29, California Institute of Technology, Pasadena, California 91125, USA

*Permanent address: Department of Genetics and Developmental Biology, Monash University, Clayton, Victoria 3168, Australia

† Author for correspondence

Nature **353**, 31–37 (5 September 1991) | doi:10.1038/353031a0

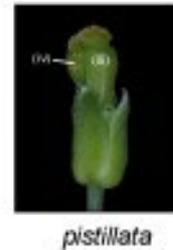
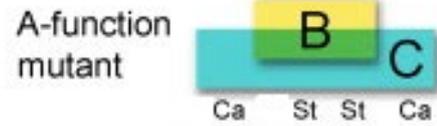
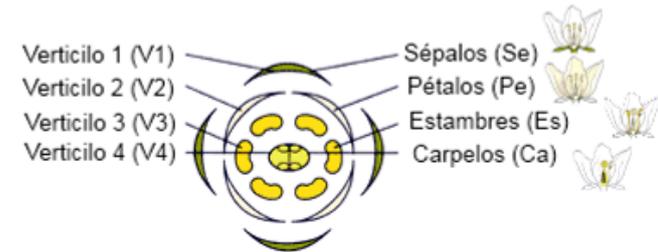
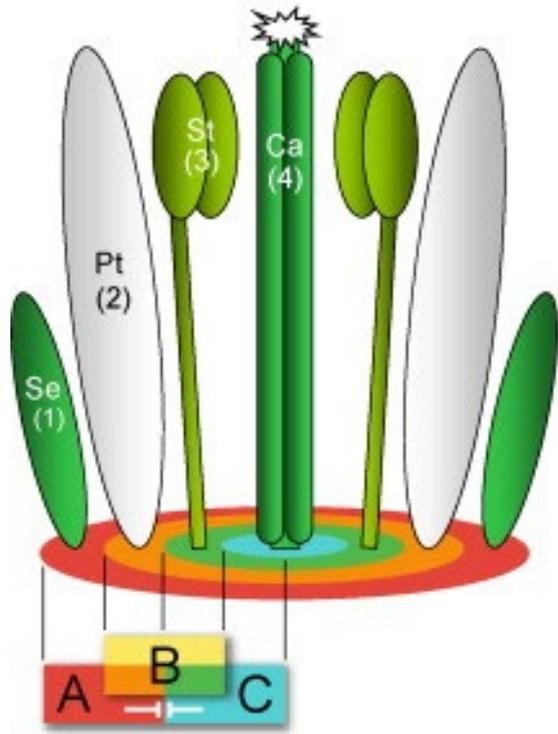
1 The war of the whorls: genetic interactions controlling flower development

Enrico S. Coen & Elliot M. Meyerowitz*

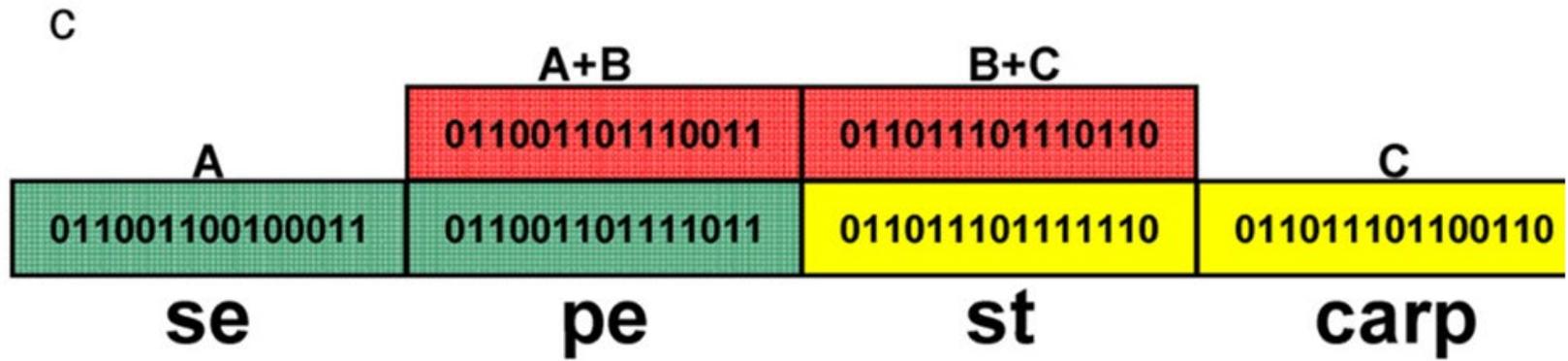
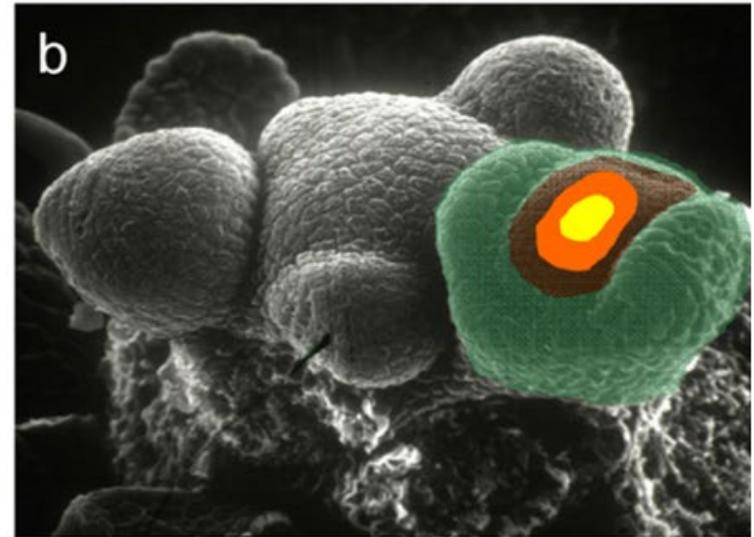
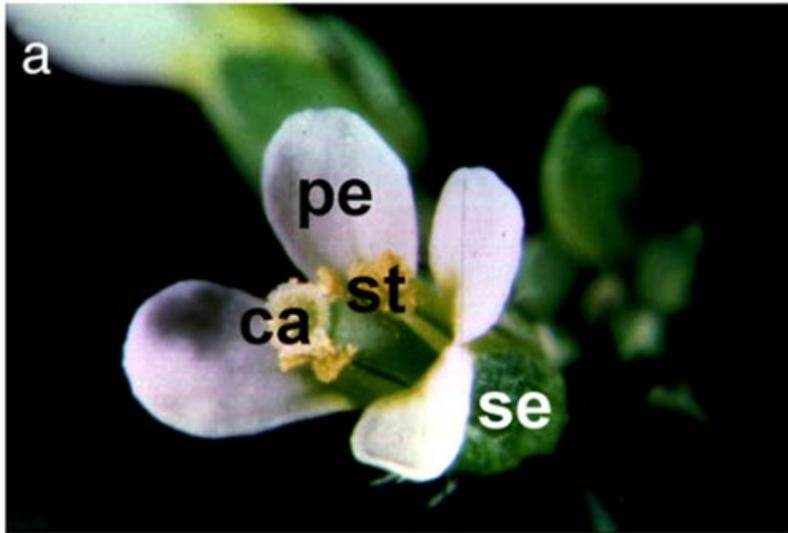
The analysis of mutations affecting flower structure has led to the identification of some of the genes that direct flower development. Cloning of these genes has allowed the formulation of molecular models of how floral meristem and organ identity may be specified, and has shown that the distantly related flowering plants *Arabidopsis thaliana* and *Antirrhinum majus* use homologous mechanisms in floral pattern formation. [▲ Top](#)

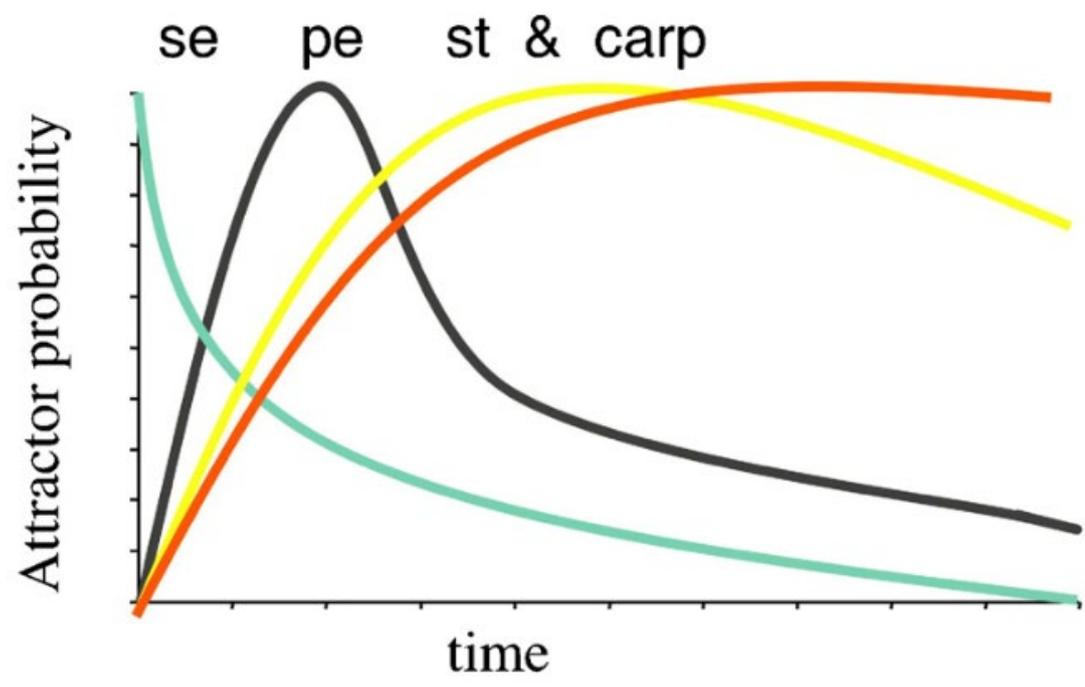
Mutantes simples y
dobles para genes
homeóticos en
Arabidopsis

A (APETALA2, AP2),
B (APETALA3 y PISTILLATA, AP3/PI)
C (AGAMOUS, AG).



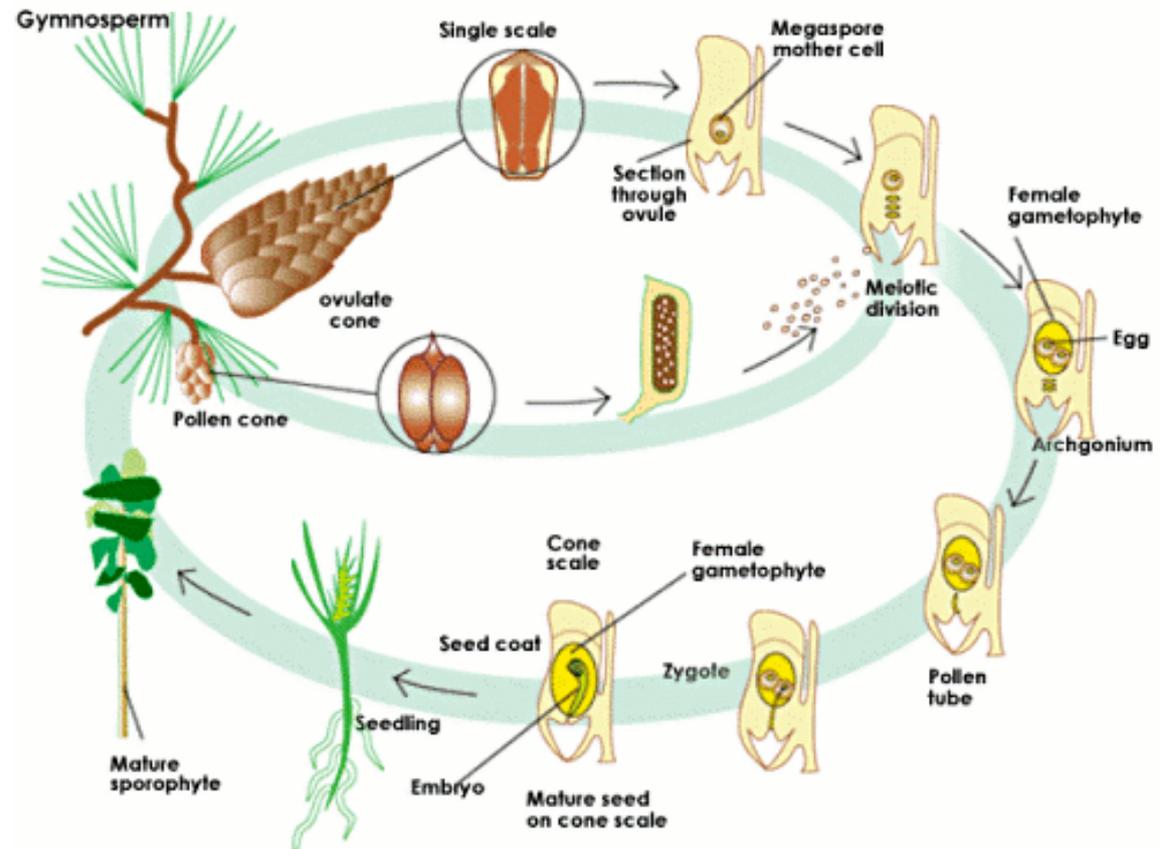
A (APETALA2, AP2),
B (APETALA3 y PISTILLATA, AP3/PI)
C (AGAMOUS, AG).

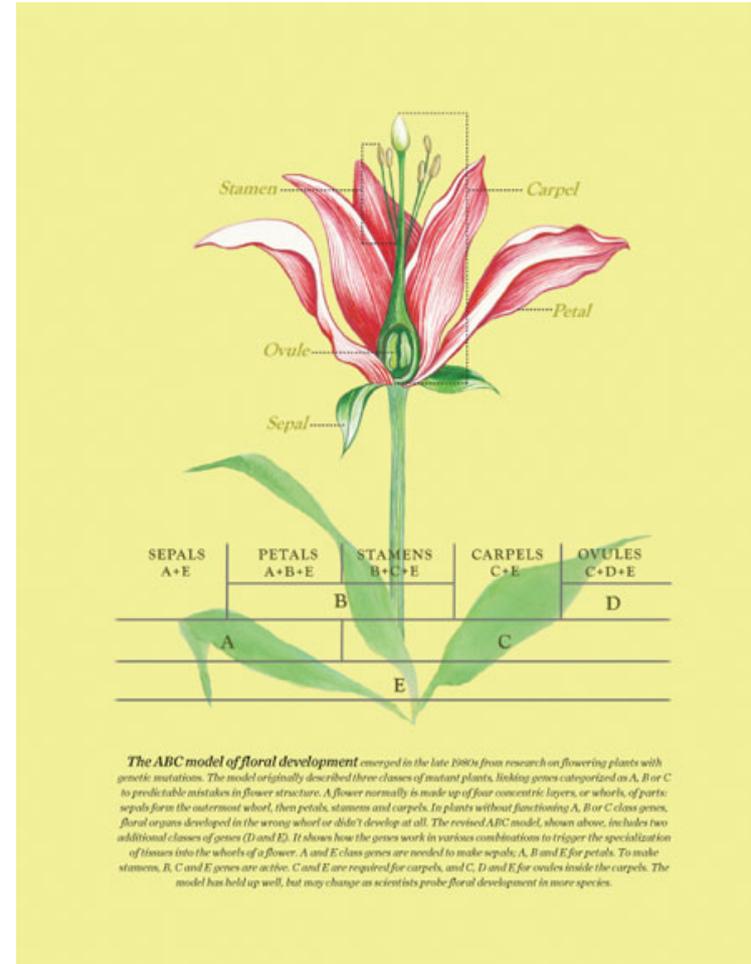
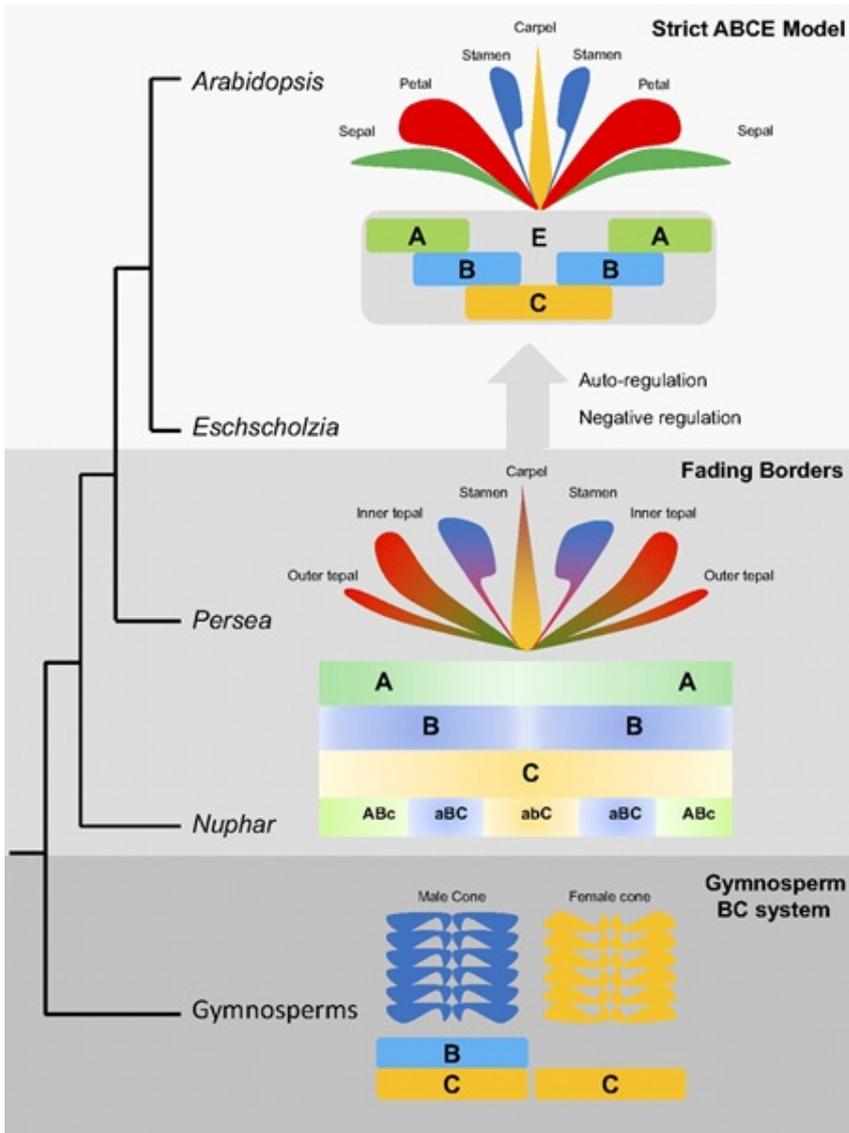




Aparición de las Angiospermas y diversificación de la estructura floral

Función de **B** y **C** estaría presente en el ancestro común de las plantas con semilla. Ha debido ocurrir un cambio en la función de **B** y **A** ha debido adquirir nuevas funciones.





<http://www.pnas.org/content/107/52/22570.full.pdf>

Negative Regulation of the Arabidopsis Homeotic Gene *AGAMOUS* by the *APETALA2* Product

Gary N. Drews, John L. Bowman,
and Elliot M. Meyerowitz
Division of Biology
California Institute of Technology
Pasadena, California 91125

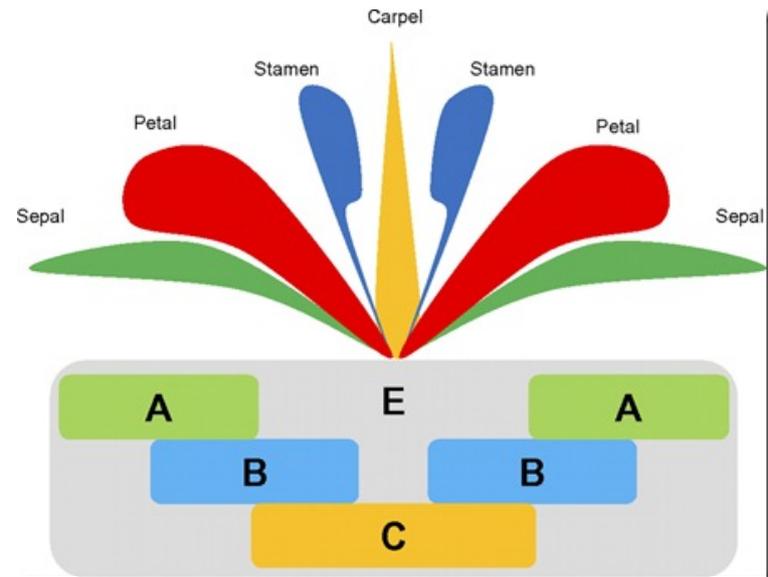
Nature **405**, 200–203 (11 May 2000) | doi:10.1038/35012103; Received 21 January 2000; Accepted 28 February 2000

B and C floral organ identity functions require *SEPALLATA* MADS-box genes

Soraya Pelaz¹, Gary S. Ditta¹, Elvira Baumann², Ellen Wisman² & Martin F. Yanofsky¹

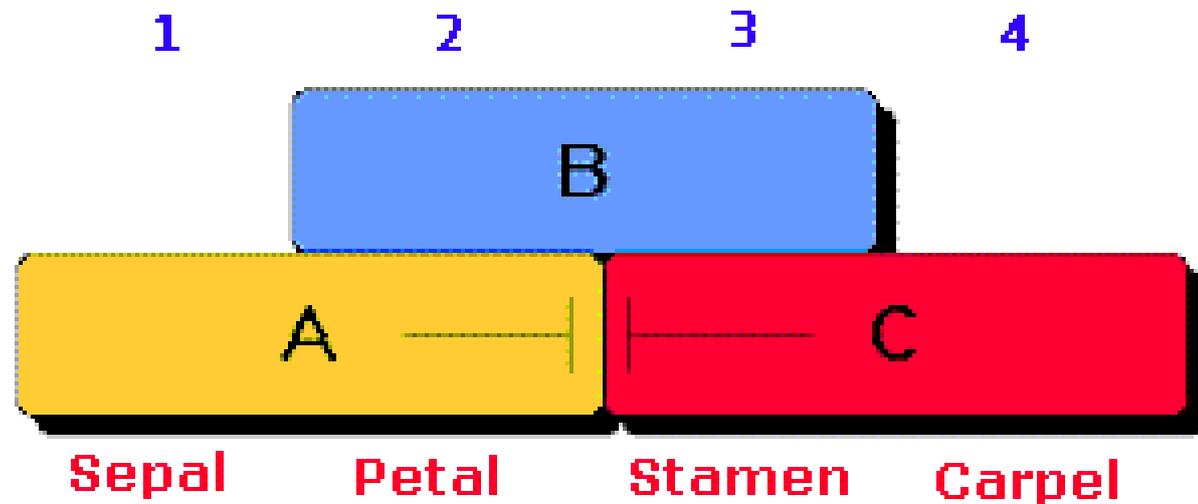
1. Section of Cell and Developmental Biology, La Jolla, California 92093-0116, USA
2. Max-Planck-Institut für Züchtungsforschung, Carl-von-Linné-Weg 10, 50829 Köln, Germany

E: *SEPALLATA*

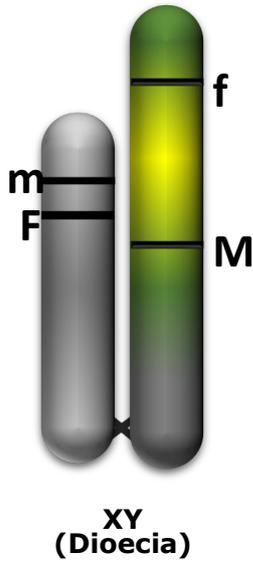


Genes determinantes del sexo en plantas

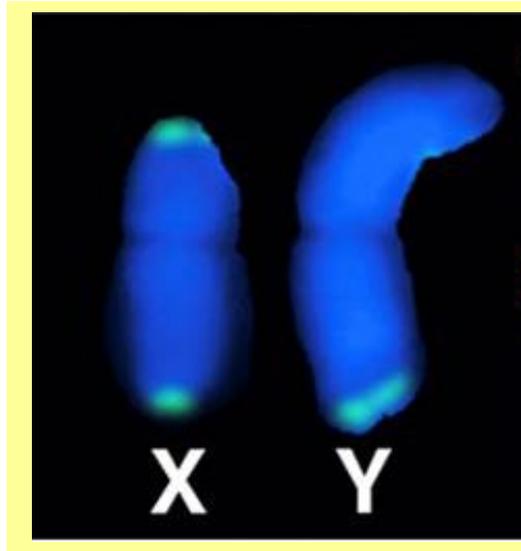
En *Silene latifolia* el gen *SIAP3* (homólogo de *APETALA3*) se encuentra en los cromosomas sexuales. Tal como demuestra el estudio de ARNm, existe un patrón diferencial de expresión: el alelo Y se expresa fundamentalmente en estambres y pétalos, mientras que el alelo X se expresa en pétalos, estilos y ovarios.



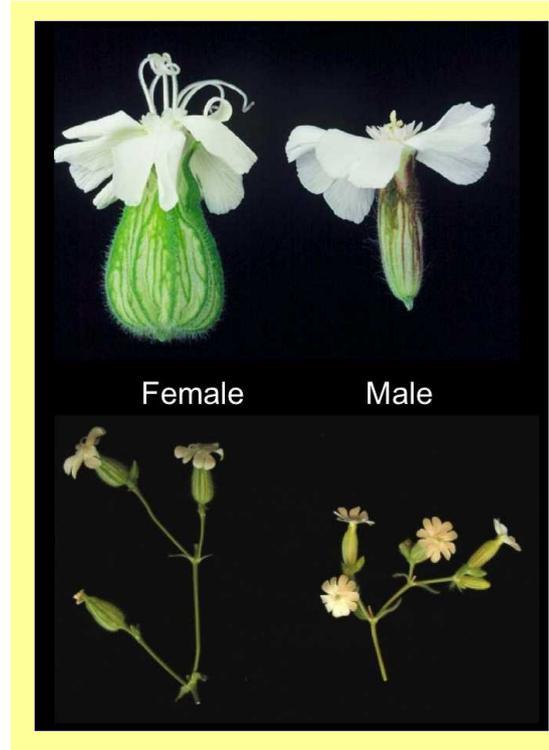
Silene latifolia



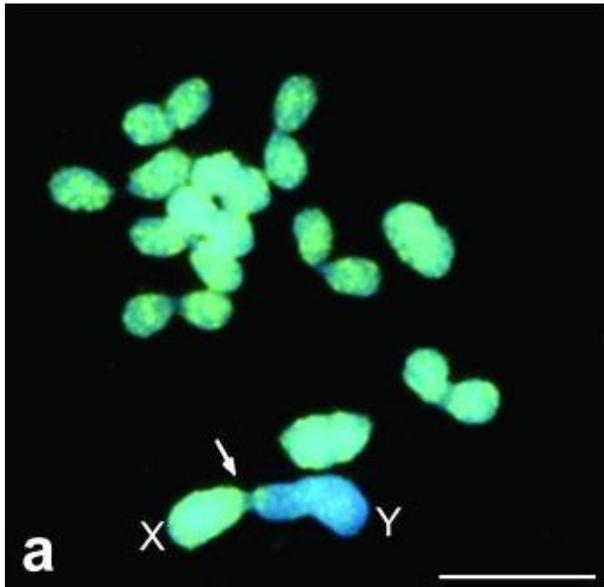
Acumulación de
Secuencias
Repetidas



Matsunaga, 2009

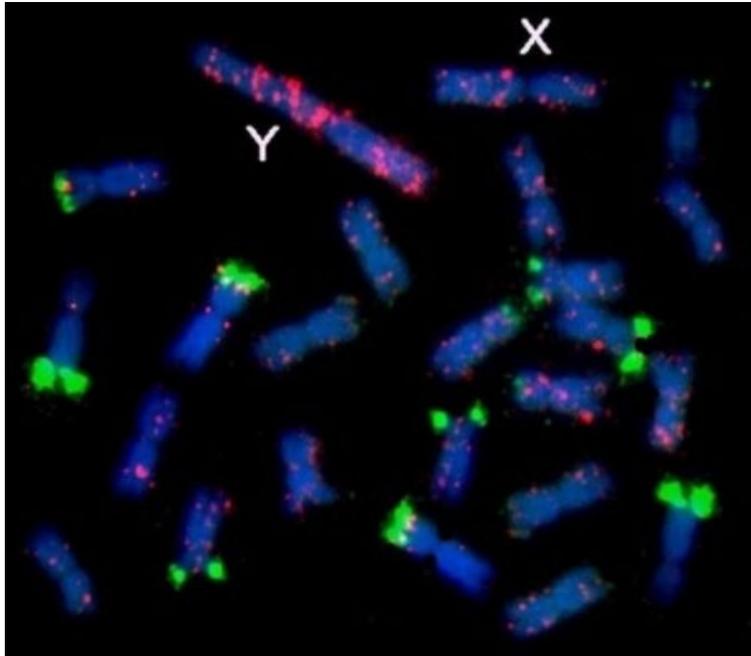


Silene latifolia

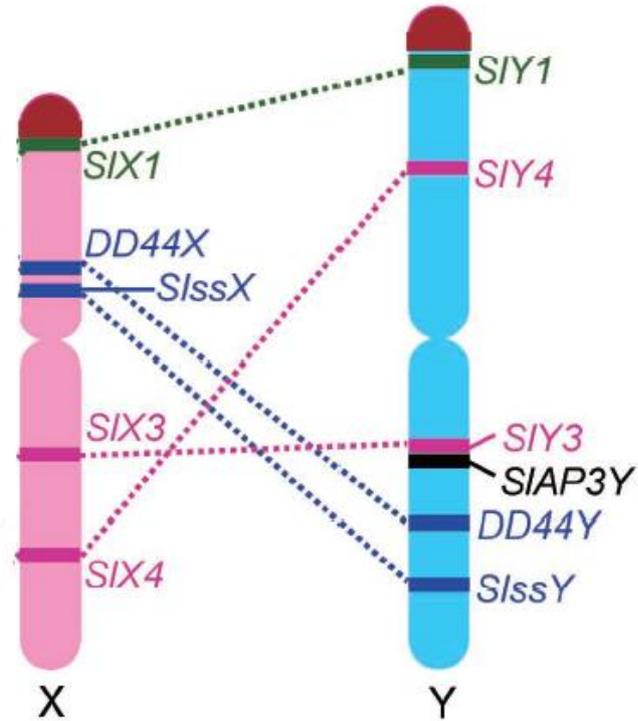


Existe diferenciación a nivel morfológico
(**Cromosomas Heteromórficos**)

Silene latifolia



Vyskot et al.



YY no viables

Existen
**reordenaciones
cromosómicas,
inactivación de
genes del Y y
moderado nivel de
degeneración
molecular**

CARACTERIZACIÓN DE GENES DETERMINANTES DEL SEXO
MODELO DE LAS DOS MUTACIONES



Modelo de las dos mutaciones

Charlesworth & Charlesworth, 1978

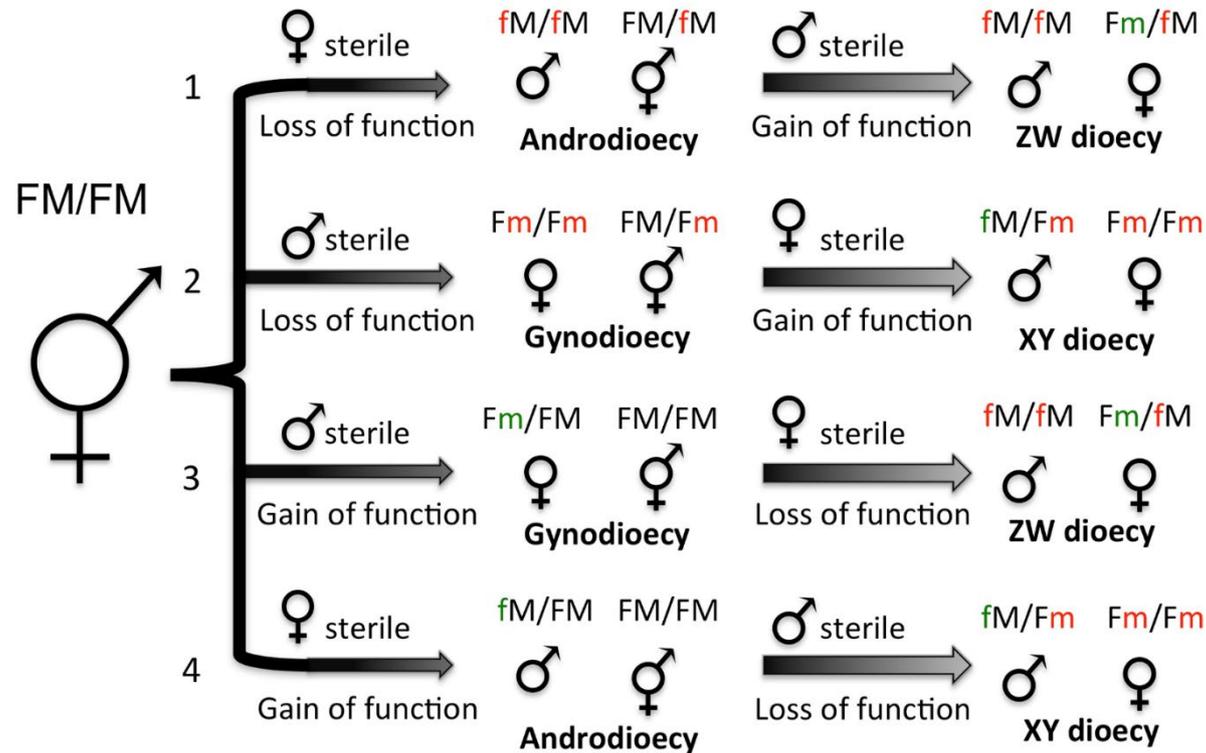


Figure 2. Evolutionary pathways from hermaphroditism to separate sexes. Shown are two-step pathways involving intermediate male- and female-sterile individuals. Loss-of-function mutations (red) are assumed to be recessive, while gain-of-function mutations (green) are assumed to be dominant. Ancestral alleles are in black. M, male fertility allele; m, male sterility mutation; F, female fertility allele; f, female sterility mutation. Because loss of function mutations (red) are almost 50 times more frequent than gain of function mutations (green) in flowering plants, we would expect pathways 1 (e.g., some poplar species) or 2 (e.g., papaya) to arise earlier. Furthermore, transitions through gynodioecy, pathways 2 and 3 (e.g., strawberry) allow females to completely avoid inbreeding depression, while transitions through androdioecy are more costly because males must compete with hermaphrodites for fertilization and do not have any of their own ovules to fertilize. These theoretical arguments help to account for the prevalence of gynodioecy and the XY chromosome system (via pathway 2) observed in plants; nevertheless, all four pathways may be biologically relevant, although no known examples for pathway 4 currently exist.

THE ROLE OF ANDRODIOECY AND GYNODIOECY IN MEDIATING EVOLUTIONARY TRANSITIONS BETWEEN DIOECY AND HERMAPHRODITISM IN THE ANIMALIA

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Akron, Ohio 44325-3908

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Sólo **9 animales ginodioicos**, pertenecientes a alguno de los *fila* más antiguos de invertebrados: 2 esponjas (Porifera), 3 anémonas (Cnidaria), 1 coral (Cnidaria), 1 gusano sipuncúlido (Sipuncula), 1 poliqueto (Annelida) y un vertebrado (el pez mixino).

Un total de **115 especies animales**, pertenecientes a los *fila* de artrópodos, anélidos y cordados, son **androdioicas**: 2 cnidarios, 27 nematodos, 1 nemertino, 72 crustáceos, 3 insectos, 7 anélidos y 3 vertebrados.

Two Y-chromosome-encoded genes determine sex in kiwifruit

Takashi Akagi^{1,2,8*}, Sarah M. Pilkington³, Erika Varkonyi-Gasic³, Isabelle M. Henry⁴, Shigeo S. Sugano^{2,5}, Minori Sonoda¹, Alana Firl⁴, Mark A. McNeilage³, Mikaela J. Douglas³, Tianchi Wang³, Ria Rebstock³, Charlotte Voogd³, Paul Datson³, Andrew C. Allan^{3,6}, Kenji Beppu⁷, Ikuo Kataoka⁷ and Ryutaro Tao¹



PLANTAS HERMAFRODITAS

Pérdida de función

Primera mutación en el gen M

Proto-X en las plantas femeninas



GINODIOECIA

Friendly Boy

The presence of the FrBy gene was male-specific in a wide variety of Actinidia species and the X chromosomes do not carry any FrBy homologue.

Fasciclin domain typically involved in cell adhesion.

Ganancia de función

Segunda mutación en el gen suF

Proto-Y en las plantas masculinas



DIOECIA

Shy Girl

A Y-encoded cytokinin response regulator, **SyGI**, acts as suppressor of female development (SuF).

This gene represses gynoecium development at a very early flower developmental stage, via negative regulation of cytokinin signalling

Ligamiento



Sistema XY

**DIOECIA | Plantas
Masculinas**

Delección
SyGI



HERMAFRODITAS

**DIOECIA | Plantas
Femeninas**

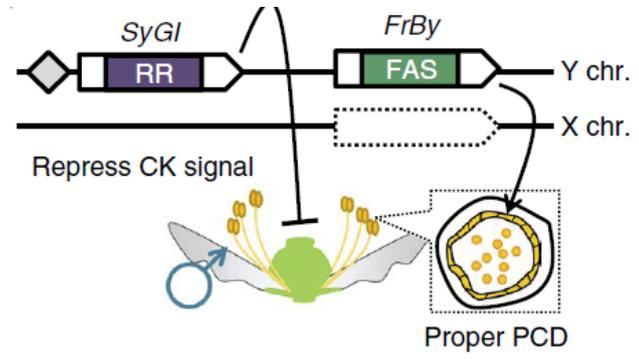
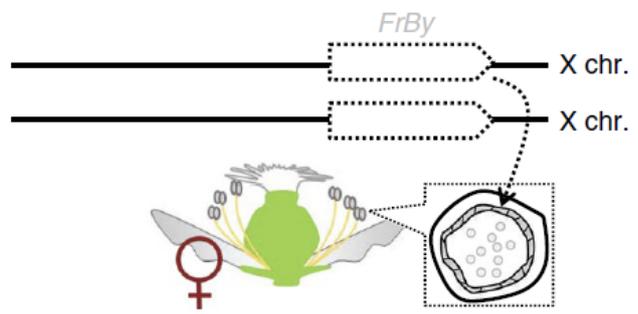
Expresión
FrBy



HERMAFRODITAS

These results clearly indicate that Y-encoded *SyGI* and *FrBy* act independently as the SuF and M factors in kiwifruit, respectively, and provide insight into not only the evolutionary path leading to a two factor sex-determination

The MSY includes the two sex determinants and highly repetitive sequences, which is consistent with the structure of MSY in other plants or animals





suF

M/suM

Log1-LIKE

CPY703/GPAT3



SOFF

TDF1



VviYABBY3

VviINP1



Corrected: Author correction

ARTICLE

DOI: 10.1038/s41467-018-06375-y

OPEN

Genus-wide sequencing supports a two-locus model for sex-determination in *Phoenix*

Maria F. Torres^{1,2}, Lisa S. Mathew³, Ikhlak Ahmed¹, Iman K. Al-Azwani³, Robert Krueger⁵, Diego Rivera-Núñez⁶, Yasmin A. Mohamoud³, Andrew G. Clark⁷, Karsten Suhre⁴ & Joel A. Malek^{1,3}

The Plant Cell, Vol. 32: 1790–1796, June 2020, www.plantcell.org



BREAKTHROUGH REPORT

Sex Determination by Two Y-Linked Genes in Garden Asparagus^{OPEN}

Alex Harkess,^{a,b,1} Kun Huang,^c Ron van der Hulst,^d Bart Tissen,^a Jeffrey L. Caplan,^c Aakash Koppula,^{a,f} Mona Batish,^{a,f} Blake C. Meyers,^{a,g} and Jim Leebens-Mack^b



ARTICLE

https://doi.org/10.1038/s41467-020-16700-z

OPEN

The genetic basis of sex determination in grapes

Mélanie Massonnet¹, Noé Cochetel¹, Andrea Minio¹, Amanda M. Vondras¹, Jerry Lin¹, Aline Muyle², Jadran F. Garcia¹, Yongfeng Zhou², Massimo Delledonne³, Summaira Riaz¹, Rosa Figueroa-Balderas¹, Brandon S. Gaut^{2,5} & Dario Cantu^{1,5}



Evidence of Recombination Suppression Blocks on the Y Chromosome of Date Palm (*Phoenix dactylifera*)

Maria F. Torres¹, Yasmin A. Mohamoud², Shameem Younsunju², Karsten Suhre¹ and
Joel A. Malek^{2,4*}

1. Recessive male-sterility mutation (M to m). Deletion of CYP703 and/or GPAT creates females - Gynodioecy

2. Reduction of recombination. Chromosomal rearrangement in Proto-Y reduces recombination with Proto-X

3. Dominant female-suppressing mutation (f to Su^f). Duplication and translocation of autosomal LOG to Proto-Y. Addition of LOG^{Su} creates males.

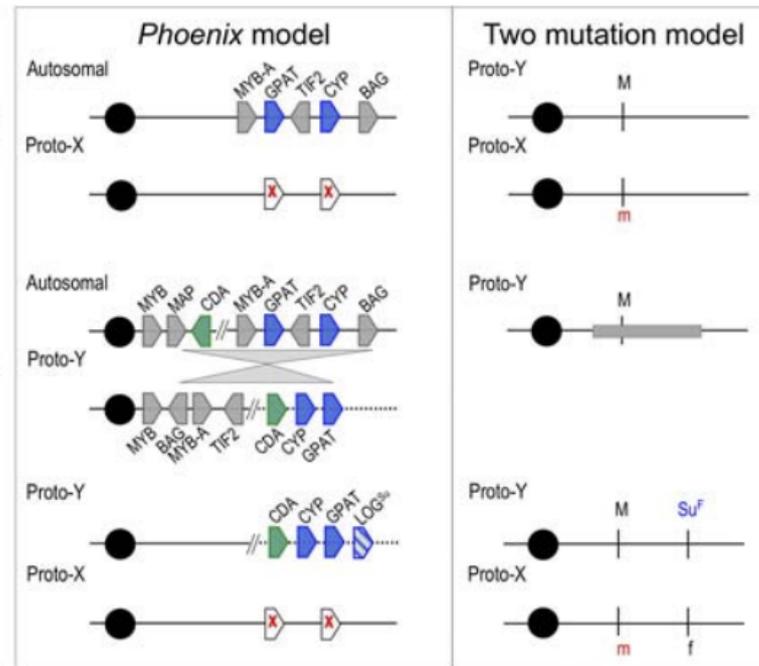


FIGURE 1 | A proposed step-wise model of evolution in the *Phoenix* (including Date Palm) sex-determination region compared with the two-gene model for sex determination (adapted from Charlesworth et al., 2005). Two genes are deleted from Proto-X (white pentagons with red x), a later rearrangement (gray triangles) relocates multiple genes and a final duplication and translocation of a gene (pentagon with blue lines) with potential female-suppressing characteristics (LOG^{Su}) creates males and females. Gene abbreviations and gene IDs MYB: LOC105059740, MAP: LOC105059742, CDA: LOC105059743, MYB-A: LOC105059783, GPAT (GPAT3): LOC105059961, TIF2: LOC105059784, CYP (CYP703): LOC105059962, BAG: LOC105059785. Cytidine deaminase (CDA) was the only gene with male-conserved kmers present in both male and female individuals.

CARACTERIZACIÓN DE GENES DETERMINANTES DEL SEXO
MODELO DE UNA MUTACIÓN



Pathways for making unisexual flowers and unisexual plants: Moving beyond the “two mutations linked on one chromosome” model¹

Susanne S. Renner^{2,3}

Epigenetic Regulation of the Sex Determination Gene *MeGI* in Polyploid Persimmon ^{OPEN}

Takashi Akagi,^{a,b,1} Isabelle M. Henry,^c Takashi Kawai,^a Luca Comai,^c and Ryutaro Tao^a

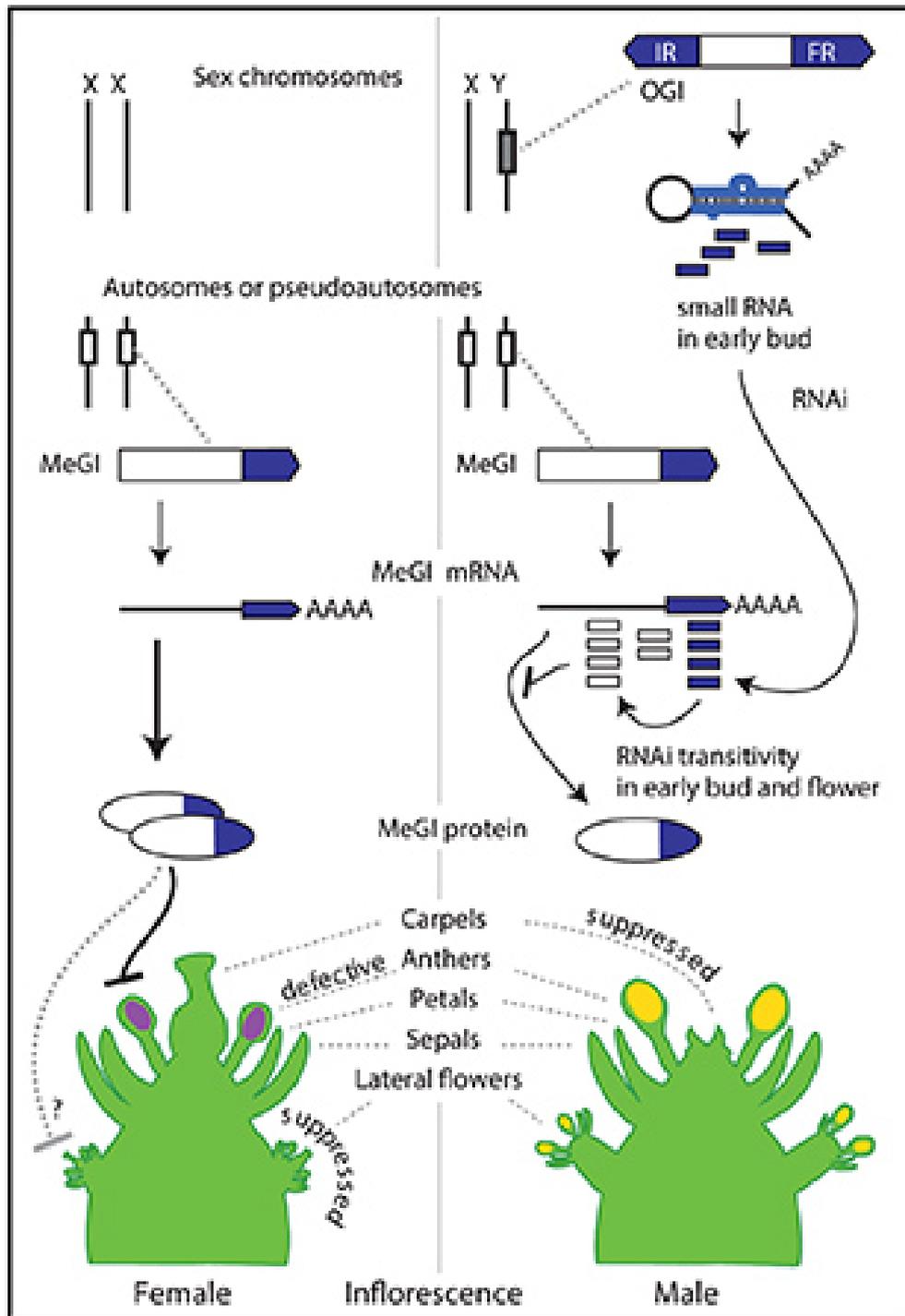
^aLaboratory of Pomology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

^bJST, PRESTO, Kawaguchi-shi, Saitama 332-0012, Japan

^cDepartment of Plant Biology and Genome Center, University of California, Davis, California 95616

ORCID IDs: 0000-0001-9993-8880 (T.A.); 0000-0002-6796-1119 (I.M.H.); 0000-0003-2642-6619 (L.C.)





MeGI, Male Growth Inhibitor (también, pie de árbol femenino)

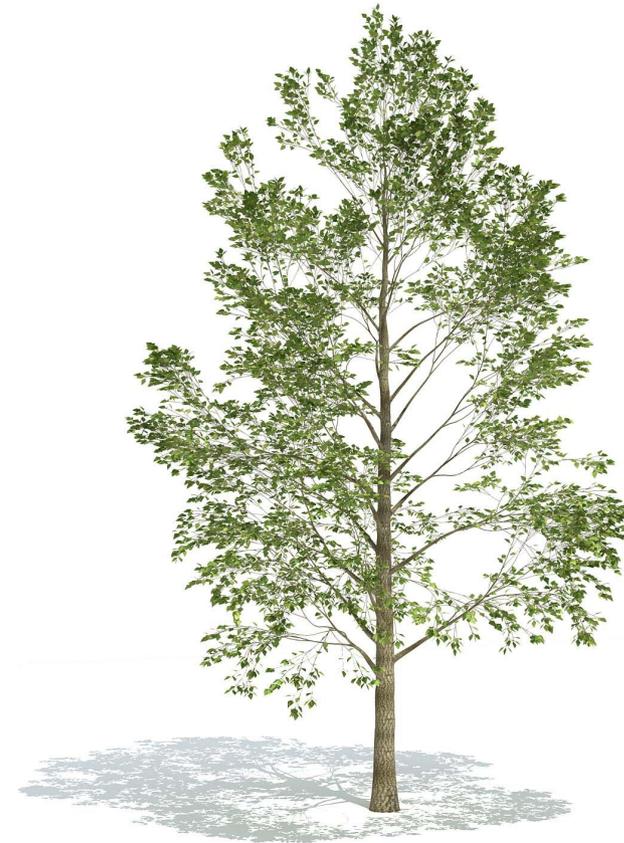
OGI, Oppressor of meGI (también, pie de árbol masculino)



Default Sex and Single Gene Sex Determination in Dioecious Plants

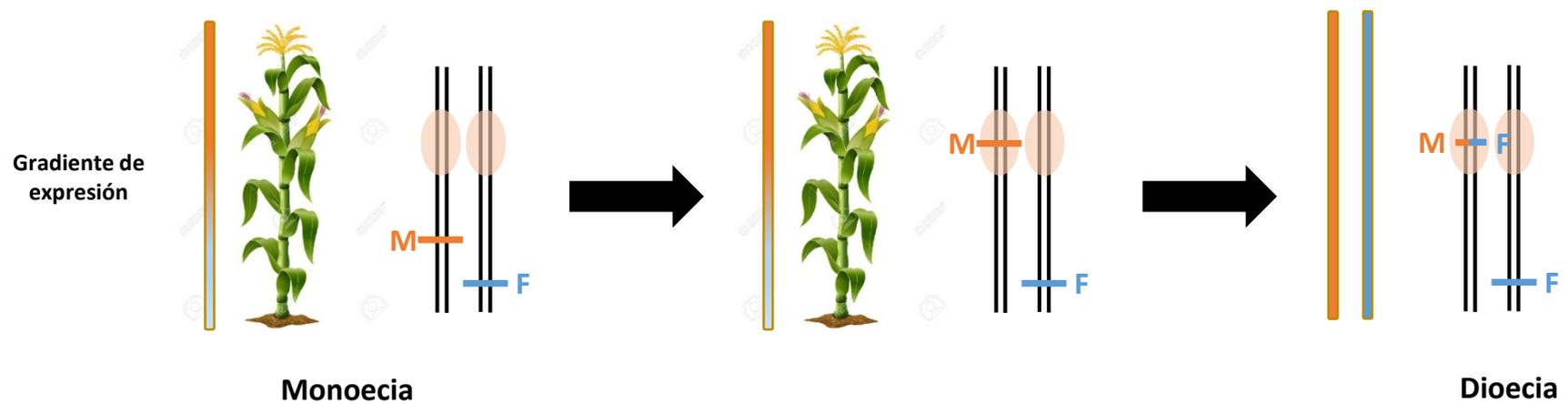
Quentin Cronk^{1*} and Niels A. Müller²

In poplar, the feminizing factor **popARR17** acts as a “master regulator”, analogous to the mammalian masculinizing factor SRY.



Pathways for making unisexual flowers and unisexual plants: Moving beyond the “two mutations linked on one chromosome” model¹

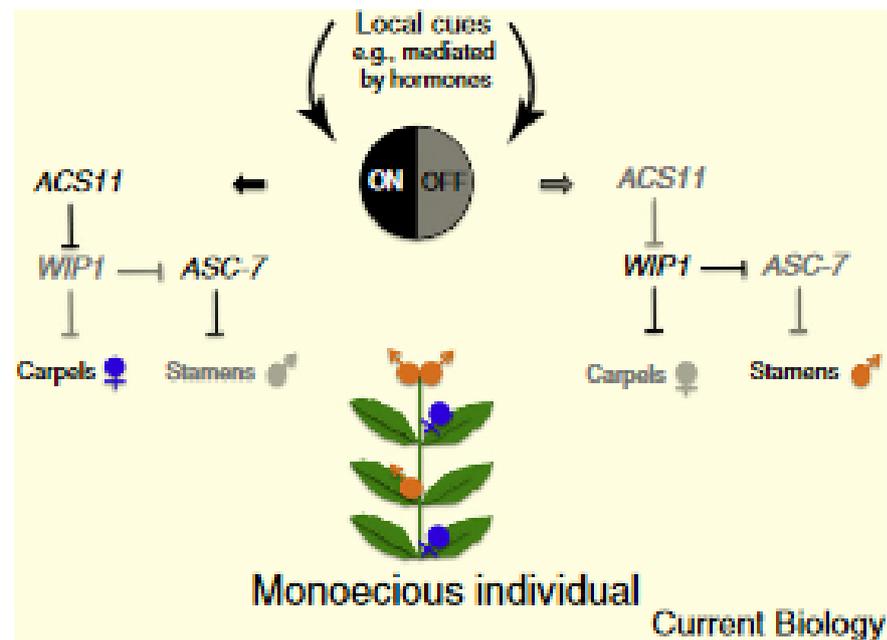
Susanne S. Renner^{2,3}



Sex Determination: Separate Sexes Are a Double Turnoff in Melons

Current Biology 26, R157–R179, February 22, 2016

Wen-Juan Ma and John R. Pannell*





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A three-genome phylogeny of *Momordica* (Cucurbitaceae) suggests seven returns from dioecy to monoecy and recent long-distance dispersal to Asia

Hanno Schaefer*, Susanne S. Renner

Systematic Botany and Mycology, University of Munich (LMU), Menzinger-Str. 67, D-80638 Munich, Germany

monoecy/paradioecy/dioecy pathway

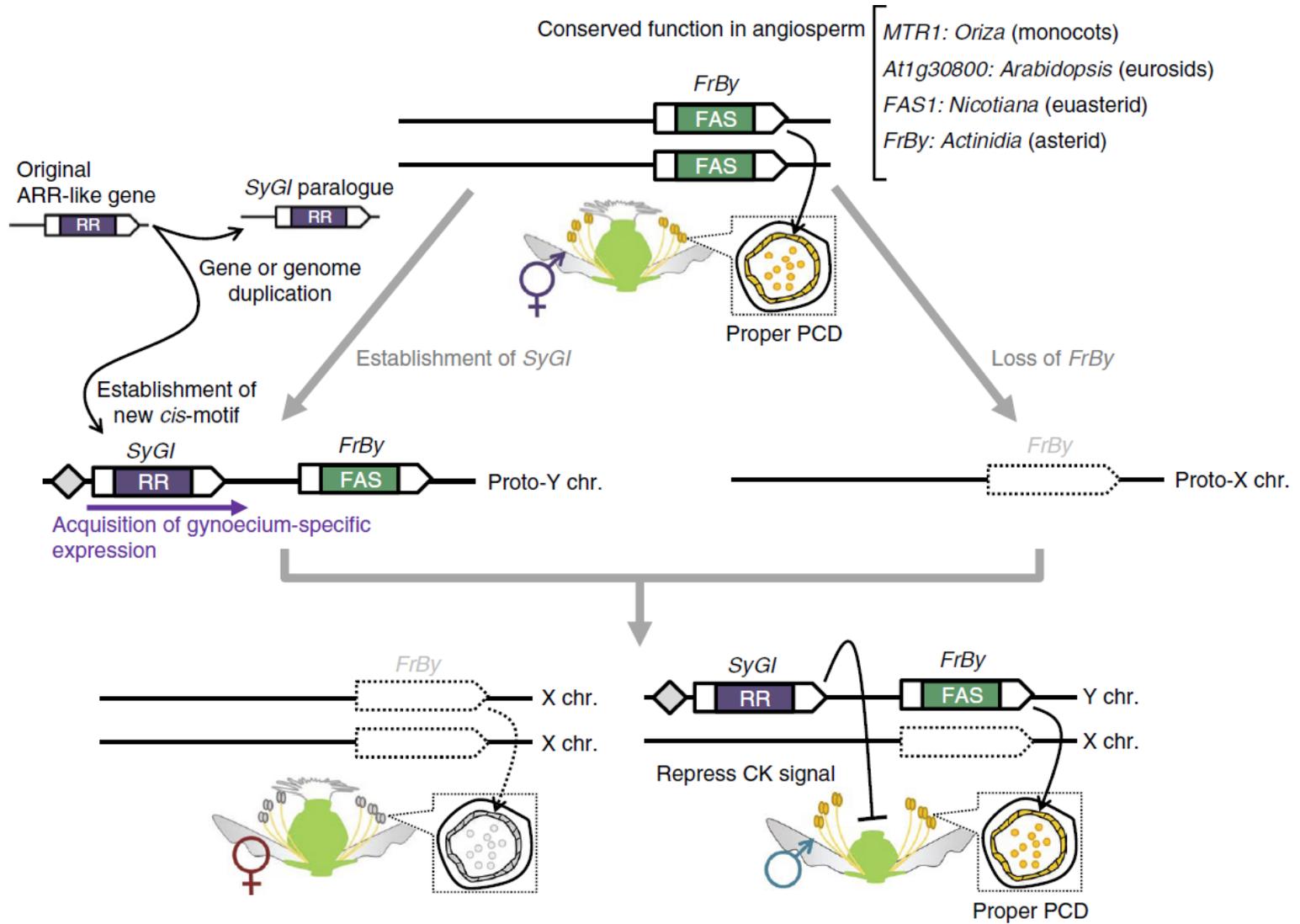


Ontology terms involving PCD and phosphorylation signals were highly enriched (Supplementary Table 3). Not only PCD, but also abundant phosphorylation signals are indispensable for proper tapetum maturation and degradation^{22–24}. Furthermore, an orthologue of *Tapetal Development and Function 1* (*TDF1*) or *MYB35*, a key gene in tapetum maturation in Arabidopsis and one of the two sex determinants in dioecious garden asparagus^{13,25,26}, was detected as one of the male-biased DEGs in kiwifruit, although this gene (Acc30672.1) was not located within the MSY (Supplementary Table 2 and Supplementary Fig. 5).

Our evolutionary analyses suggested that the function of *FrBy* might be conserved across the angiosperms. To investigate their function, we first used the CRISPR/Cas9 gene-editing system in two distantly related model plants, *A. thaliana* and *N. tabacum* (Supplementary Table 4). Although the Arabidopsis genome includes three paralogues of *FrBy*, only one, AT1G30800, was in the cluster that was conserved across Brassicaceae species (Fig. 1a). In Arabidopsis the AT1G30800 null lines (Supplementary Fig. S6) were self-sterile, with low pollen germination rates (Fig. 2g), but could successfully produce seed after being crossed to control male plants (Fig. 2a–e). The null line showed substantial delay in tapetal layer degradation (Supplementary Fig. 7), which is consistent with the development of female kiwifruit plants (Supplementary Fig. 1)^{18,19}. On the other hand, the absence of AT1G30800 had no significant effect on female reproductive function ($P > 0.1$; Supplementary Fig. 8). In *N. tabacum*, knockout mutation of the *FrBy* orthologues, *FAS1a/b* (*fas1*) (Supplementary Fig. 9), resulted in male sterility, with substantial reduction in pollen germination rate, and was accompanied

by a delay in tapetum degradation. The other organs, including the gynoecium, showed no differentiation compared to the control plants (Fig. 2h–o). The transgenic *N. tabacum* lines expressing the kiwifruit SuF gene, *SyGI*, under the control of its native promoter (p*SyGI-SyGI*) exhibited female sterility⁶. Reciprocal crossing using control plants (p*SyGI-SyGI*) and *fas1* indicated that *SyGI* and *FAS1* independently promote gynoecium and androecium development, respectively (Fig. 2p). Importantly, male function in a *fas1* null line could be complemented by introduction of the kiwifruit *FrBy* under the control of its native promoter (Fig. 2q,r; Supplementary Fig. 10), indicating that *FrBy* can act to maintain male fertility via proper tapetum degradation in *N. tabacum*. These results all suggest that *FrBy* is likely to be the male-promoting factor and that the two sex-determining genes, *SyGI* and *FrBy*, work independently for female and male fertility, respectively, in kiwifruit. Furthermore, our phylogenetic and evolutionary analyses indicated that the function of this fasciclin-like monophyletic gene is highly conserved across angiosperm species.

Reference genome sequences for kiwifruit have been assembled from female (2A+XX) cultivars^{21,27}, but the Y chromosome of kiwifruit (or *Actinidia* spp.) has not been sequenced to date. Here, we constructed the whole-genome reference sequence of a male cultivar, Soyu, which is one of the main pollinizers used in Japan. The sequences were assembled using 10X Genomics Supernova v.1.2.2, which is based on a long haploblocking method suitable for assembly of highly heterozygous diploid genomes²⁸. Downstream genomic analysis for the Soyu cultivar was conducted on the ‘pseudo-haploid’ version of the whole-genome assembly.



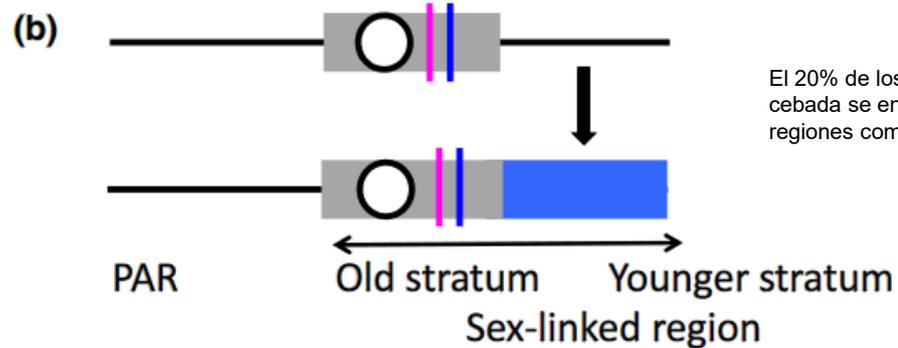
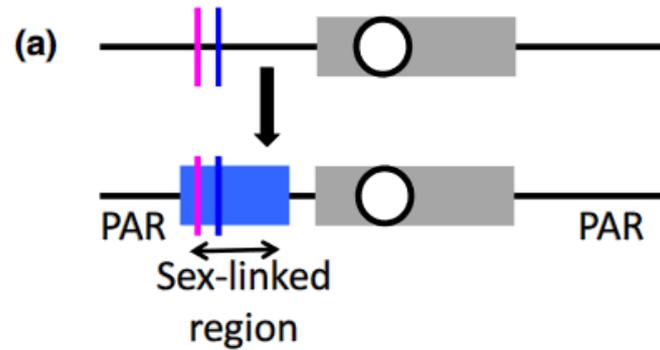
Pero ¿Cómo de modernos son los cromosomas sexuales de plantas?

El tiempo que hace que dos regiones dejaron de recombinar se puede estimar comparando genes presentes tanto en el cromosoma X como en el cromosoma Y, teniendo en cuenta el reloj molecular y la tasa de sustituciones sinónimas o silenciosas.

El cese de la recombinación es **posterior** a la acumulación de regiones determinantes del sexo.

El cese de la recombinación es **anterior** a la acumulación de regiones determinantes del sexo.

Aparición de un gen determinante del sexo en una región distinta.



El 20% de los genes de la cebada se encuentran en regiones como ésta.

