



BIO 235  
Plants & People  
Evolution &  
Domestication  
of Crops



## Lecture 6 Hybridization, Polyploidy & Crop Domestication II -

- Strawberry
- Wheat
- Banana
- Potato
- Sugarcane
- Oil Seed Rape / Canola

Colin Hughes  
Institute of Systematic Botany  
[colin.hughes@systbot.uzh.ch](mailto:colin.hughes@systbot.uzh.ch)

# Lecture 5 - Serendipitous Backyard Hybridization & the Origin of Crops - Conclusions

Disturbed sites such as backyards, kitchen middens, and informal orchards are important sites for spontaneous hybridisation, where otherwise isolated plant species were brought into sympatry following cultivation.

For Guajes, Nopales & Maguey - three of the dominant perennial plants cultivated in south-central Mexico - predomestication cultivation has resulted in extensive artificial sympatry, and a complex series of geographically dispersed hybrids and polyploids.

In each case, there is evidence to suggest that the most prominent species in cultivation - *Leucaena leucocephala*, *Opuntia ficus-indica*, and *Agave tequilana*, have had hybrid origins most likely following cultivation.

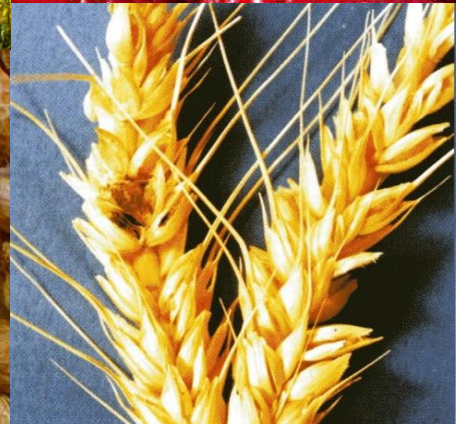
The simple step of bringing species together, casually or consciously in dump heaps and informal orchards has played a key role in domestication of these crops.

Incipient or semi-domesticates like these can provide powerful insights into the early stages of domestication





# Polyploidy & Crops

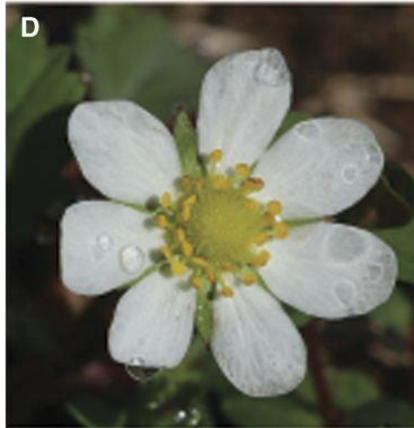




Wild  
Strawberries

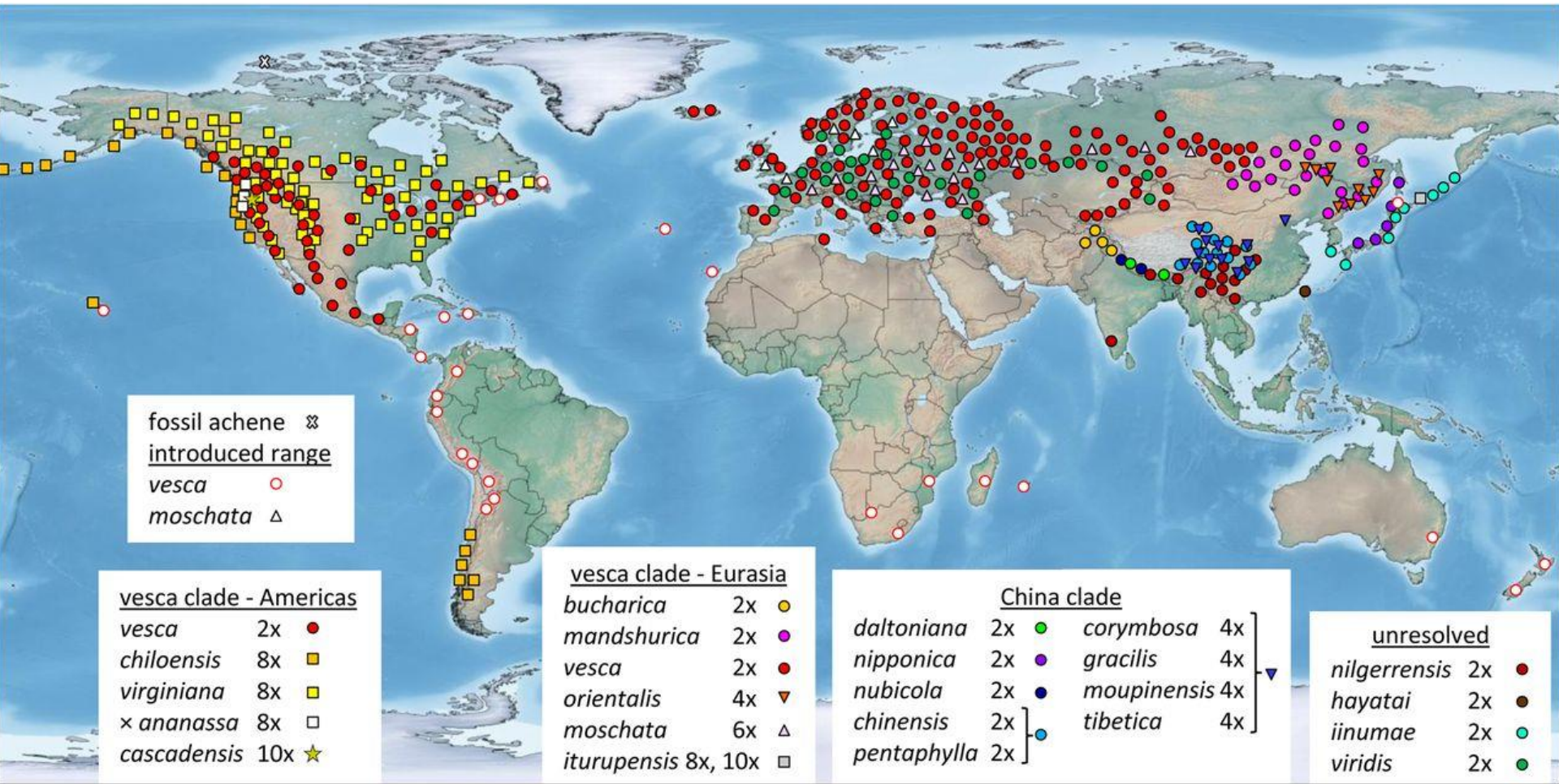
*Fragaria*  
Rosaceae

*F. vesca*  
*F. moschata*  
*F. viridis*

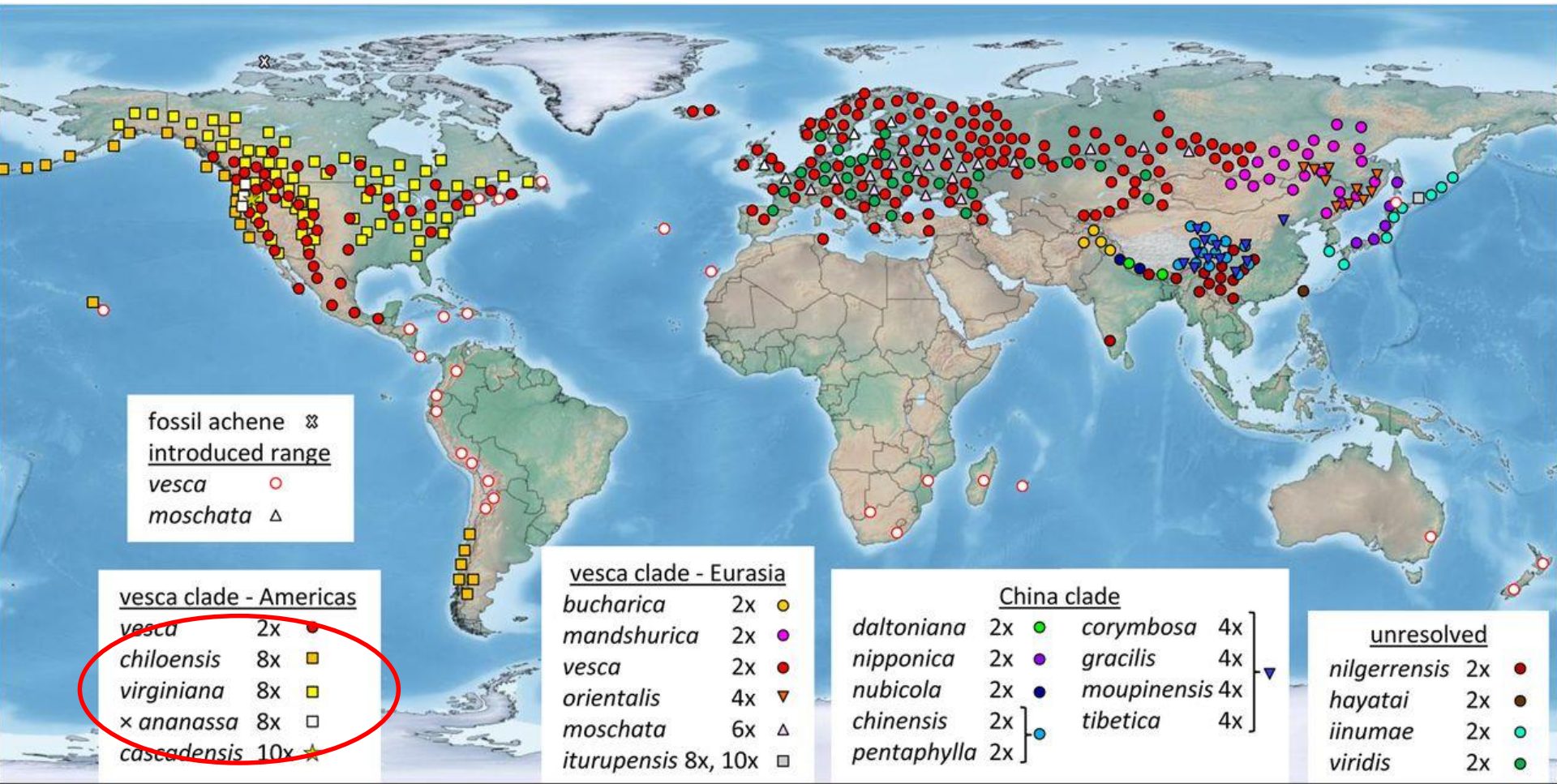




# Ployploidy & Geography of *Fragaria*



# Ployploidy & Geography of *Fragaria*







# Strawberry *Fragaria* - Rosaceae

*F. chiloensis* (Chile)  $2n=8x=56$



*F. virginiana* (USA)  $2n=8x=56$



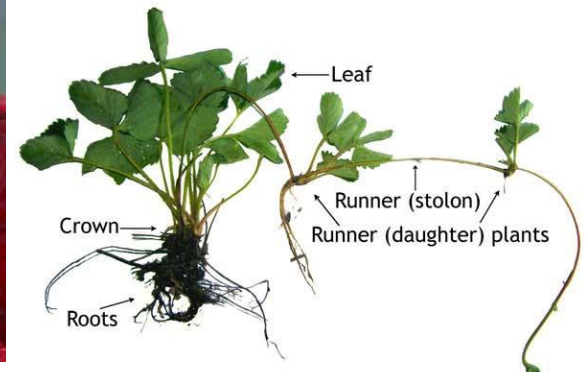
*F. xananassa* (Europe)  $2n=8x=56$



VIRGINIA STRAWBERRY  
*Fragaria virginiana* Duchesne  
ROSE FAMILY

Dioecious - separate  
male and female plants

Vegetative Propagation



# Strawberry - *Fragaria* - Rosaceae

- *F. vesca* cultivated in Roman & Greek times
- 1300s - *F. vesca*, *F. viridis* & *F. moschata* grown widely in Europe
- *F. chiloensis* - cultivated by native Mupache Indians in Chile
- 1714 - *F. chiloensis* - introduced from Chile to Europe by Frezier a French army spy
- 1600s - *F. virginiana* introduced to Europe & rose to importance in 1700s
- *F. virginiana* and *F. chiloensis* initially grown separately and only female plants of *F. chiloensis* introduced, but later pollinated by male *F. virginiana* plants
- 1750 - first *F. ×ananassa* hybrids arose spontaneously where Frezier's female *F. chiloensis* interplanted with males of *F. virginiana*.



*F. chiloensis* (Chile)  $2n=8x=56$

×

*F. virginiana* (USA)  $2n=8x=56$



*F. ×ananassa* (Europe)  $2n=8x=56$



Wheat - In 2007 world production of 607 million tonnes; second only to rice as main human food crop and ahead of maize, after allowing for use in animal feeds. Globally, wheat is the leading source of vegetable protein in human food, with a higher protein content than maize or rice.





# Archaeobotanical evidence reveals the origins of bread 14,400 years ago in northeastern Jordan

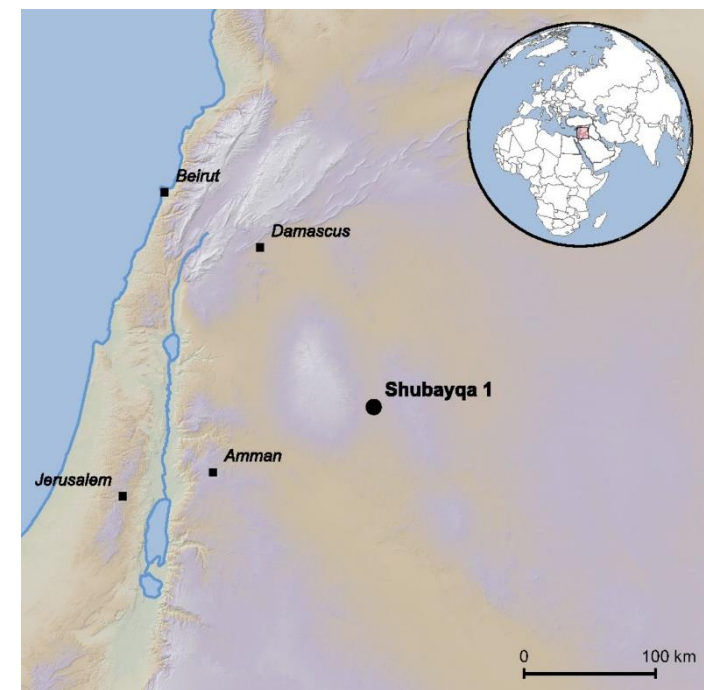
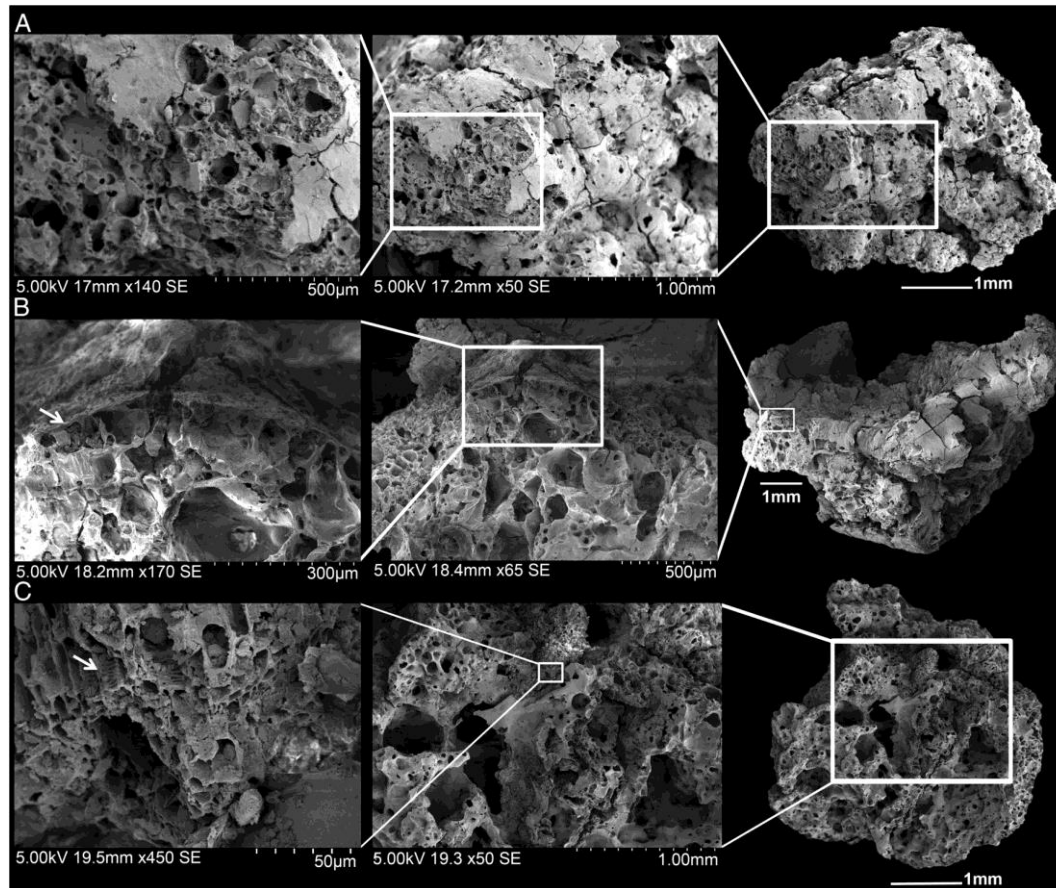
Amaia Arranz-Otaegui<sup>a,1</sup>, Lara Gonzalez Carretero<sup>b</sup>, Monica N. Ramsey<sup>c</sup>, Dorian Q. Fuller (傅稻峰)<sup>b</sup>, and Tobias Richter<sup>a</sup>

<sup>a</sup>Department of Cross-Cultural and Regional Studies, University of Copenhagen, 2300 Copenhagen, Denmark; <sup>b</sup>Institute of Archaeology, University College London, WC1H 0PY London, United Kingdom; and <sup>c</sup>McDonald Institute for Archaeological Research, University of Cambridge, CB2 3ER Cambridge, United Kingdom

Edited by Dolores R. Piperno, Smithsonian Institution, Washington, DC, and approved June 12, 2018 (received for review January 19, 2018)

**The origins of bread have long been associated with the emergence of agriculture and cereal domestication during the Neolithic in southwest Asia. In this study we analyze a total of 24 charred**

**phases at the center of Structure 1. The oldest fireplace is a large (approximately 1 m in diameter) circular structure made of flat basalt stones (Fig. 2). The contents of the fireplace were left**



Arranz-Otaegui et al. (2018)



## *Triticum* - 6 species, Middle East and trans-Caucasus

*T. monococcum* = diploid AA = Einkorn wheat - wild & domesticated

*T. urartu* = diploid AA - only wild - never domesticated

*T. turgidum* = tetraploid AABB = emmer (durum / pasta) wheat - wild & domesticated

*T. timopheevii* = tetraploid AAGG - wild & domesticated

*T. aestivum* = hexaploid AABBDD = bread wheat or common wheat - only domesticated - no wild populations (sometimes called *T. vulgare*)

*T. zhukoskyi* = hexaploid AAAAGG - only domesticated - no wild populations

## *Aegilops*

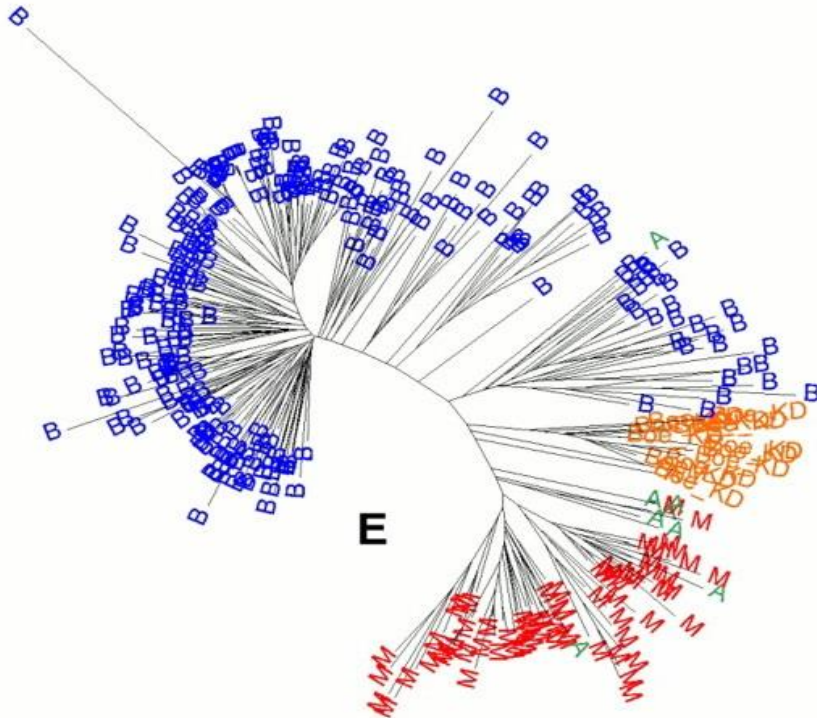
*A. tauschii* = diploid DD wild goat grass

## Origins of Einkorn Wheat - Genetic Data

**M** = Domesticated Einkorn wheat *Triticum monococcum* subsp. *monococcum* - the earliest cultivated wheat - monophyletic suggesting a single origin

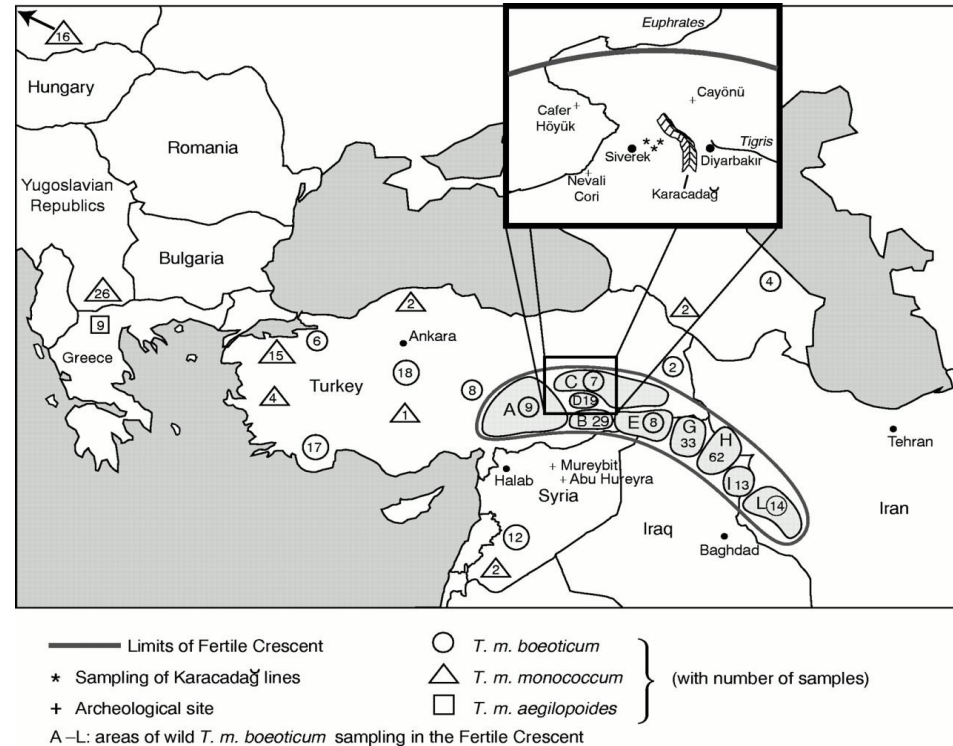
**B** = Wild progenitor *T. monococcum* subsp. *boeoticum*

**KD** = *boeoticum* accessions from the Karacadag Mtns of SE Turkey



## Origins of Einkorn Wheat - Archaeological Data

Abu Hureyra in NE Syria where the earliest evidence of farming domesticated einkorn around 9,500 BP has been found lies just 200km from Karacadag area where genetic data suggest einkorn wheat was first domesticated.



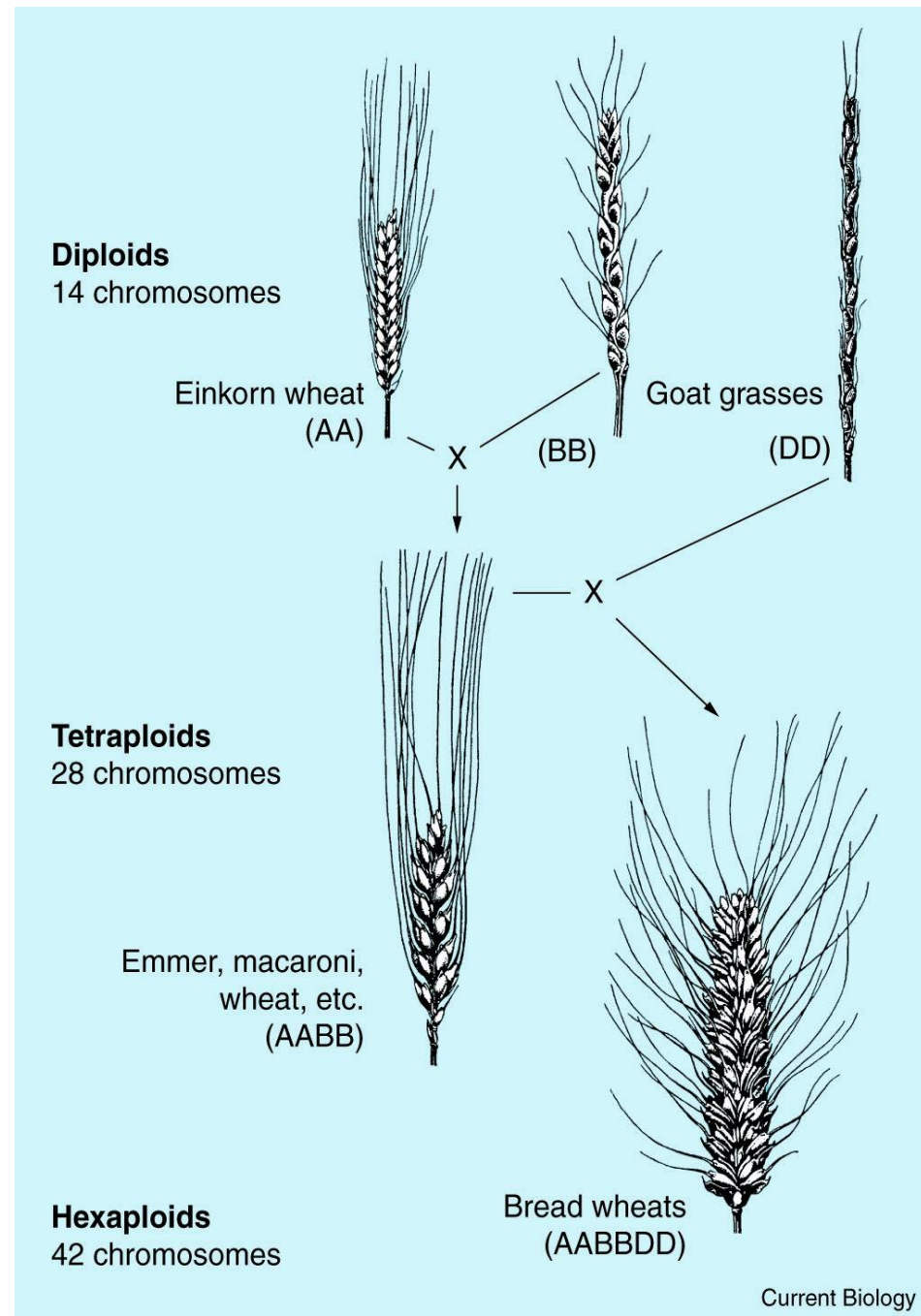


# Ploidy in Wheat

The ploidy levels of domesticated wheat species range from diploid,  $2n=14$ , to hexaploid,  $6n=42$ .

Wheats of all ploidy levels have been domesticated:

- Diploid einkorn AA - the earliest primitive, but now relic wheat, *T. monococcum* derived from wild *T. boeoticum*
- Tetraploid emmer AABB - the durum wheats used to make pasta, semolina and couscous, *T. turgidum* & *T. dicoccum* derived from *T. dicoccoides*
- Hexaploid bread wheats AABBDD, *T. aestivum* (*T. vulgare*), including spelt, *T. spelta*.



## The Near East & the Core Area of the Fertile Crescent

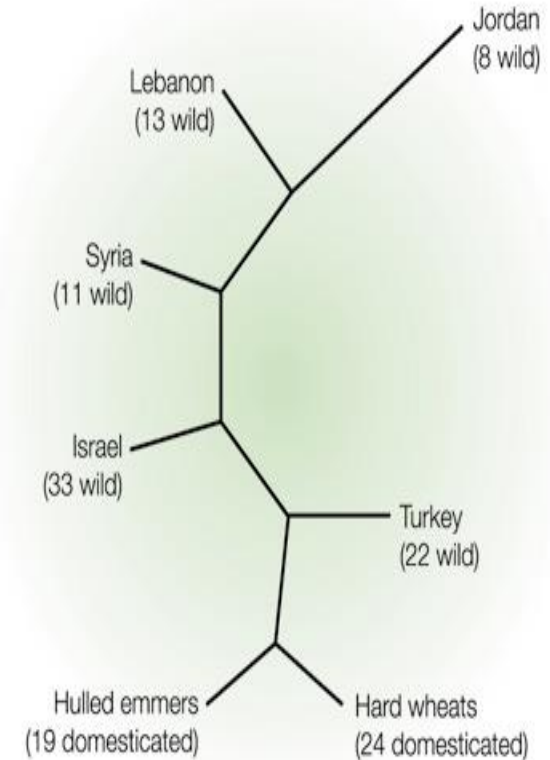


Archaeobotanical remains of 7 crops

Wild populations of einkorn & emmer wheat, pea, lentil & chickpea

Salimini et al. 2002

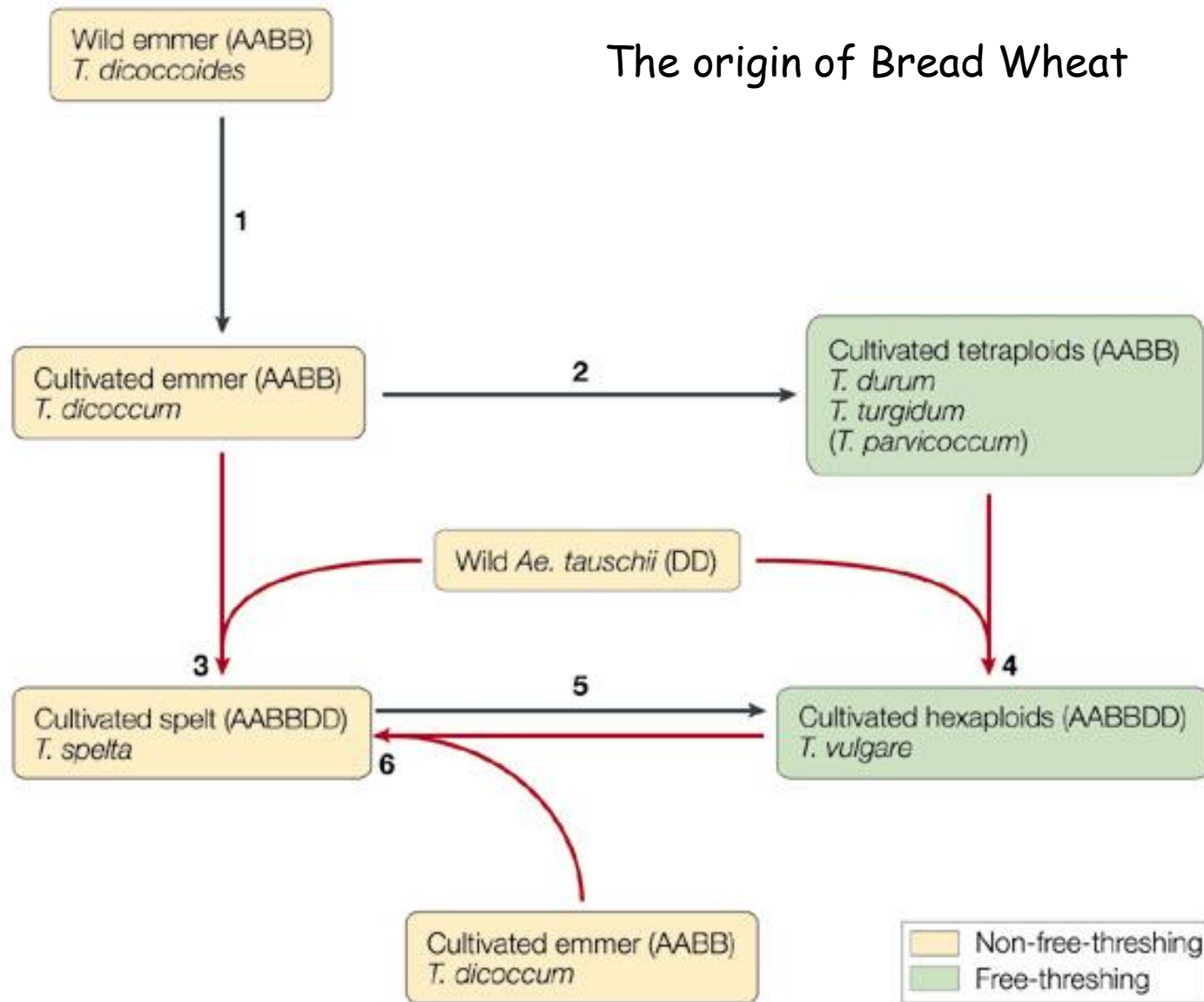
## Origin of tetraploid emmer wheat



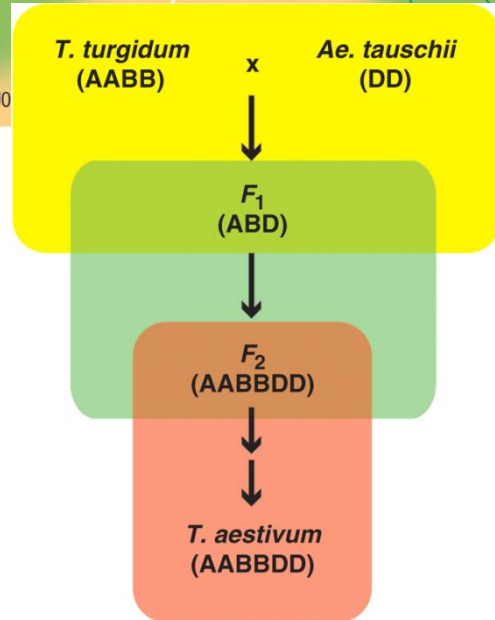
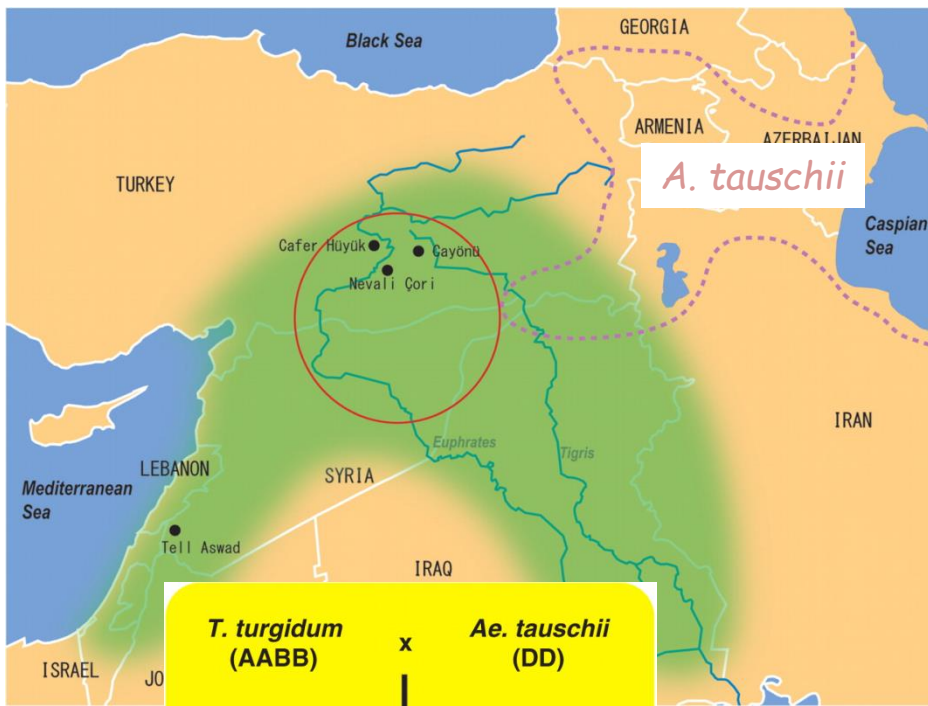
Genetic similarities (AFLPs) of cultivated tetraploid wheats *T. turgidum* (hulled emmer and hard durum wheat) to wild emmer populations from different regions, showing single origin and most closely related to wild emmer progenitors from Turkey



# The origin of Bread Wheat



Hypothesized routes for the origin of hexaploid wheat  
Black arrows = domestication events  
Red arrows = hybridization events



Human-mediated range expansion of *T. turgidum* into range of *A. tauschii*  
 Spontaneous hybridization in agricultural environment  
 Allopolyploid speciation of *T. aestivum*



*Aegilops tauschii*

Triploid F1 hybrid  
*T. turgidum* x *A. tauschii*

Spelt - *T. aestivum*  
 subsp. *spelta*

Bread wheat  
*T. aestivum* subsp.  
*aestivum*



# BANANALAND



BANANAS • SWEET • SATISFYING • SIMPLE TO SERVE



# Banana - *Musa* - Monocots, Zingiberales

c.50 species in S.E. Asia

Giant 3m tall herbs on edge of rainforests

Propagated by suckers

Centre of origin in New Guinea - Malaysia - Indonesia

Fourth most important crop in developing countries

Plantains are an important staple crop in the tropics







Sweet, satisfying & simple to serve  
& good for you!





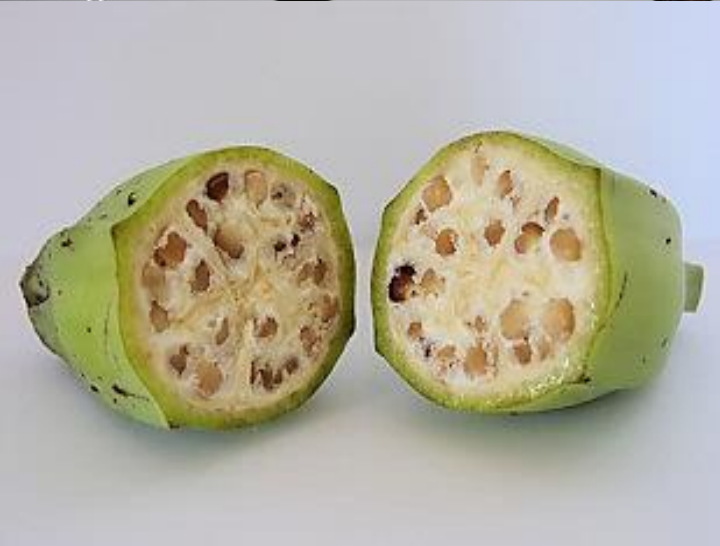








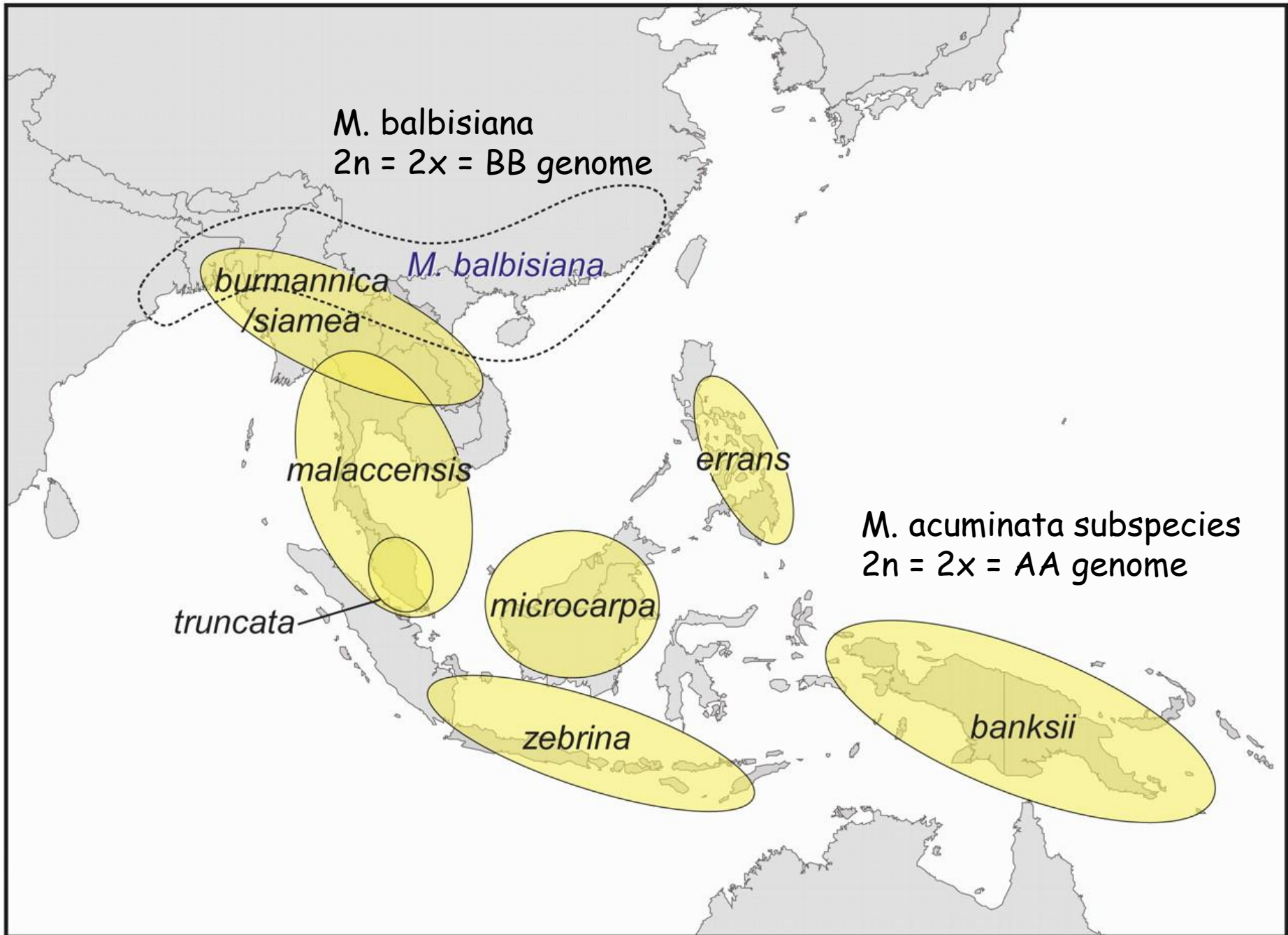
# Wild Bananas



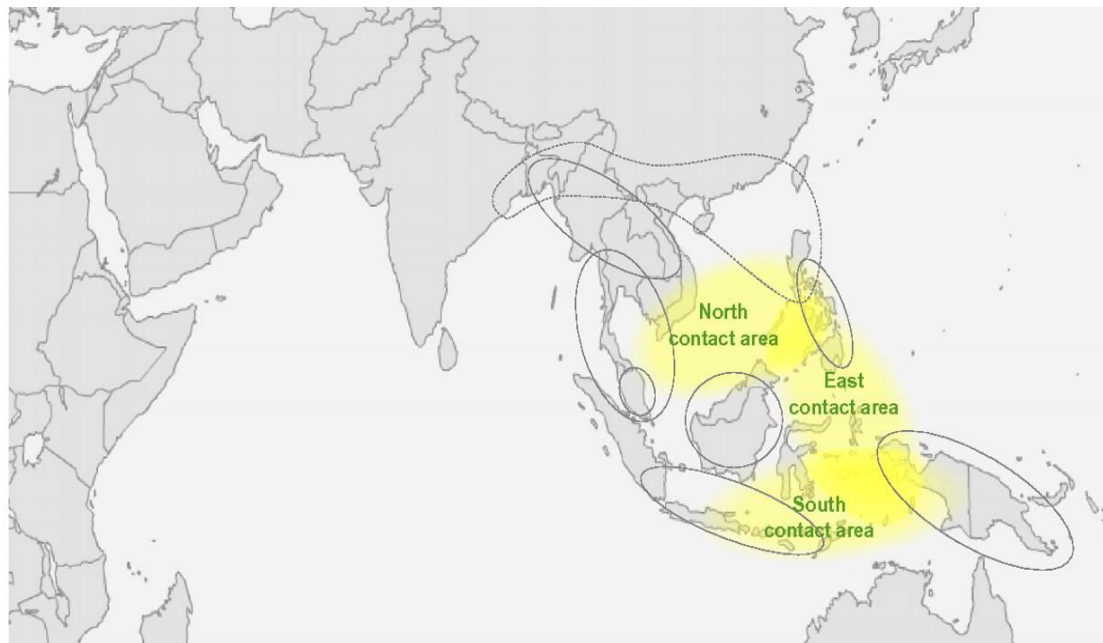
Wild diploid bananas *M. acuminata*  $2n=2x=22$  AA, and *M. balbisiana*  $2n=2x=22$  BB have seedy fruit with little starch and very little fleshy pith and no value as crops. Cultivated hybrids are seedless & parthenocarpic (i.e. fruit develops without seed development or pollination / fertilization). Domestication involved seed suppression, sterility and vegetative propagation







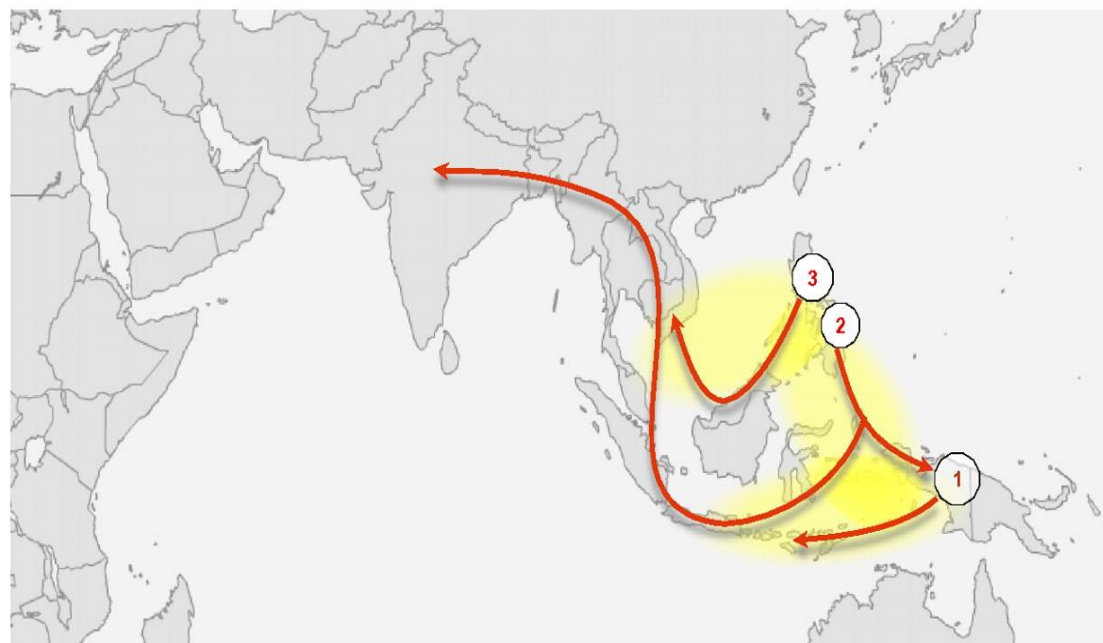
A



Three contact zones where AA subspecies hybrids arose

Most cultivars are wild collections made by farmers of spontaneously occurring mutants with parthenocarpic fruit production which were brought into cultivation and then multiplied and distributed by suckers.

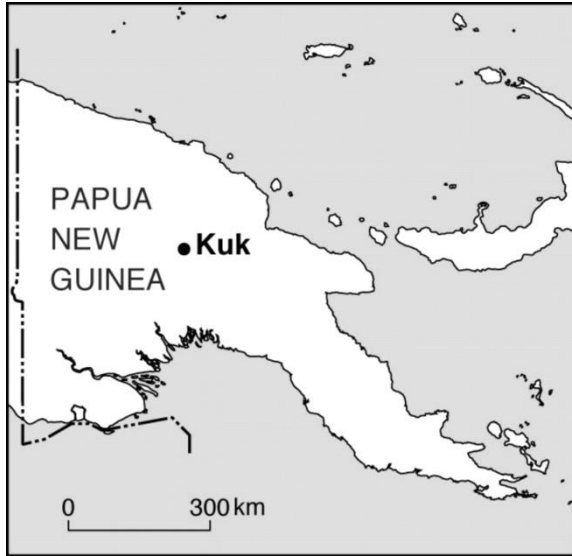
B



Hybridization events and mutations giving rise to the seedless parthenocarpic characters have occurred many 100s of times and spontaneous hybridization continues to produce new diversity.

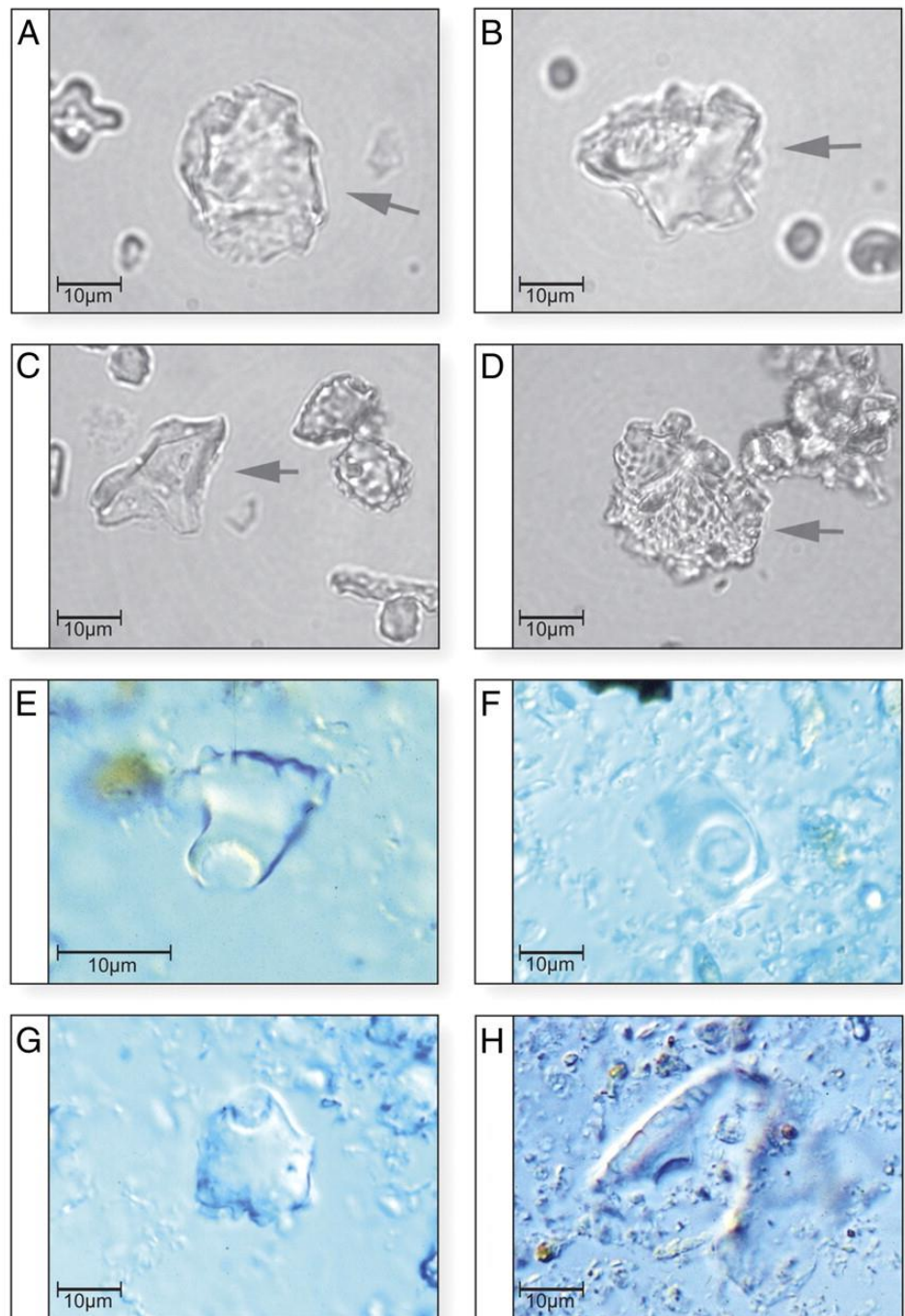


# Archaeological Evidence

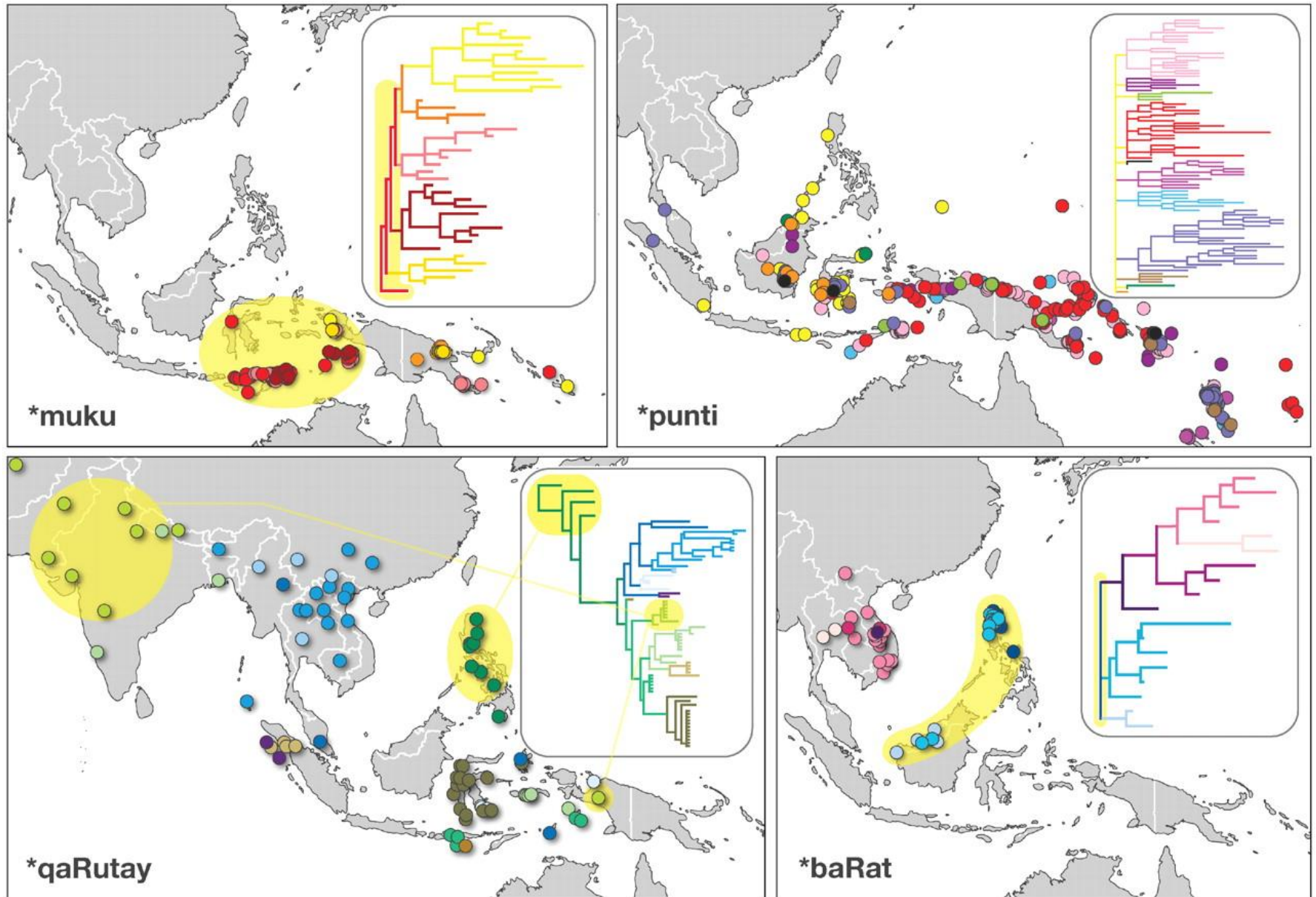


Leaf phytoliths matching *M. acuminata* subsp. *banksii* from archaeological excavations at Kuk Swamp, demonstrate that bananas were in cultivation in New Guinea 6,950-6,440 BP.

*Musa* leaf phytoliths from pottery remains in Nigeria in west Africa 2,790-2,300 BP, provide evidence for cultivation of exotic plantains in west Africa > 2,000 years ago.



# Linguistic Evidence



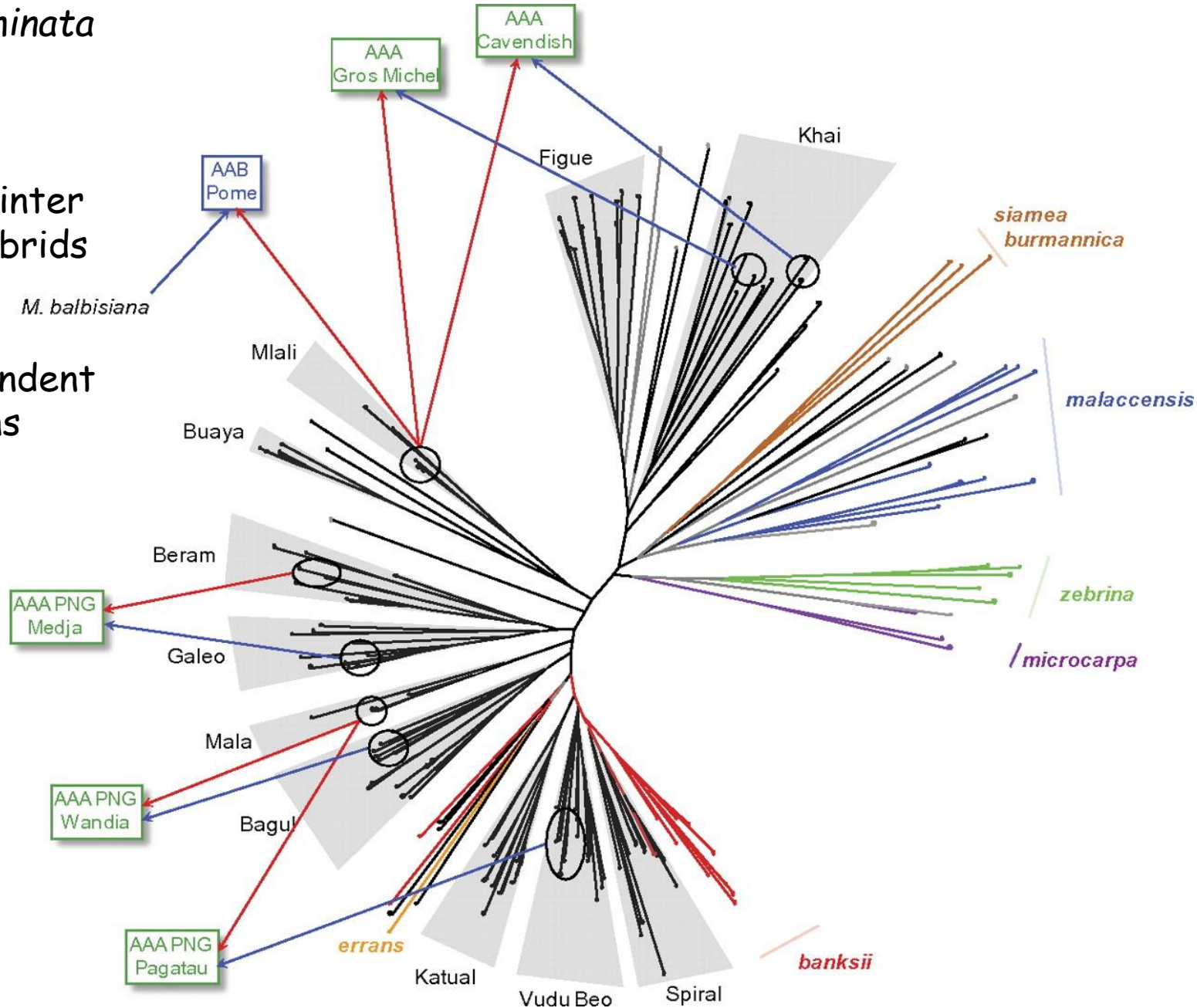


-Wild *M. acuminata* subspp.

-AA cultivars derived from inter subspecies hybrids

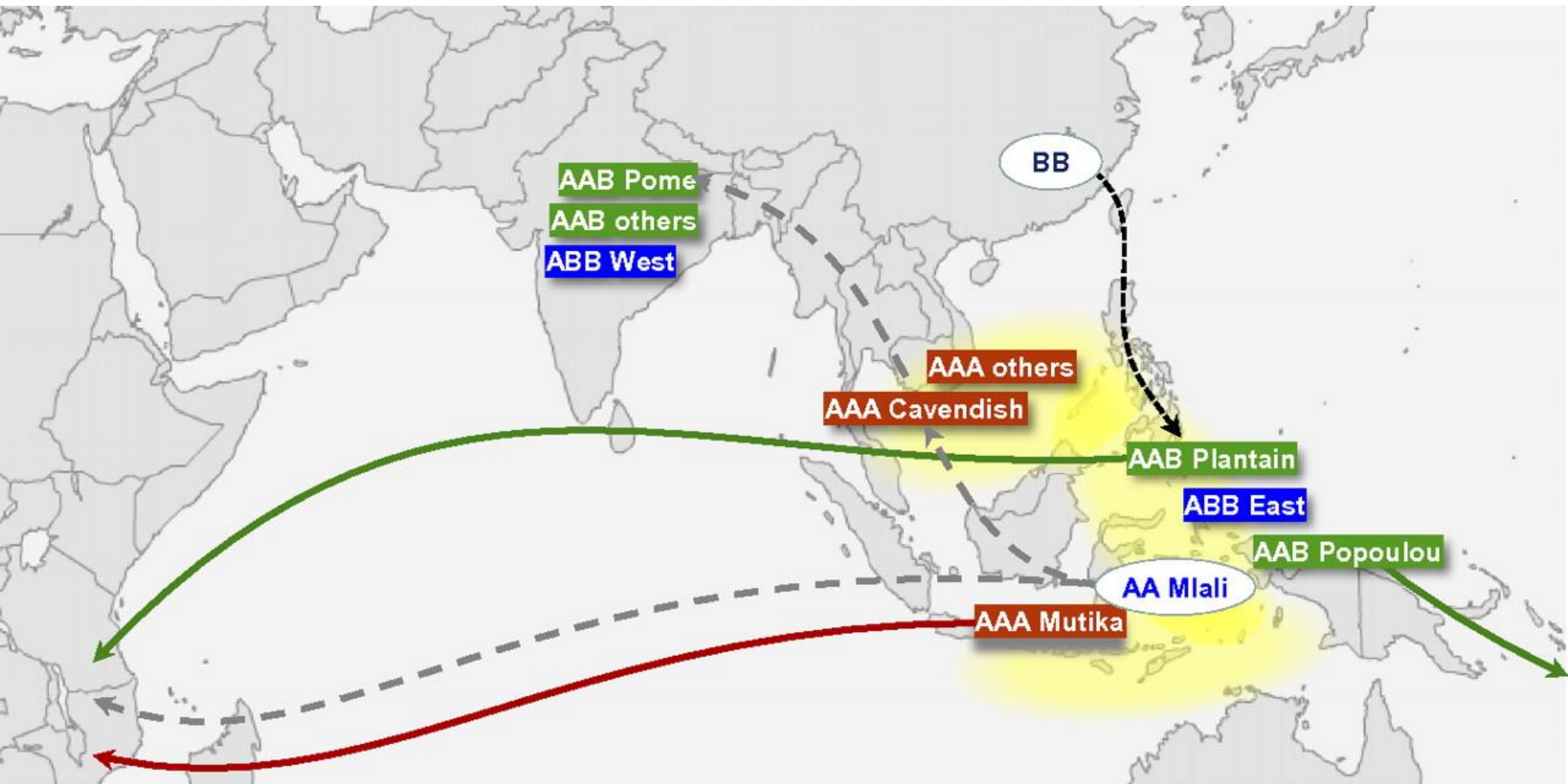
- many independent domestications

- AAA & AAB triploids



# Musa triploids

- three of these are remarkable because they are largely cultivated far from their regions of origin - African sweet AAA Mutika; African AAB plantains carried to Africa by Arab traders, as well as the Pacific AAB plantains





# Diversity of bananas & plantains in south India

Genome compositions:

- **a** = cultivar Red = AAA, a prized sweet desert banana cultivar
- **b** = Palayam Codan = AAB
- **c** = Njalipoovan = AB (unripe and ripe green and yellow) sweet desert banana with small fingers, thin skin and delicate flavour, but poor storage
- **d** = Robusta (Cavendish group) = AAA (these green bananas ripen without turning yellow when above 22C)
- **e** = Nendran = AAB, plantain used for cooking and making chips
- **f** = Peyan = ABB, used as a vegetable for curries and cooked snacks
- **g** = Poovan = AAB

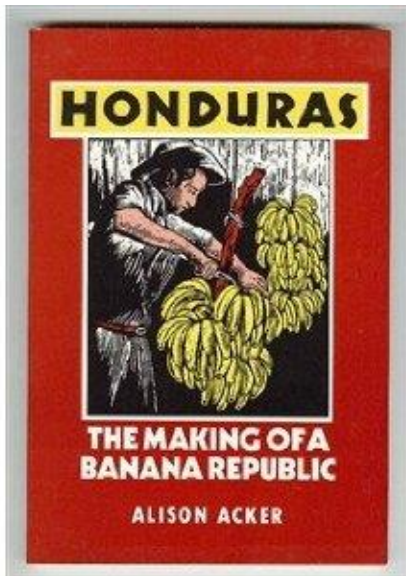
Heslop-Harrison & Schwarzacher (2007)

a a a b c cc dee e e e a f f g e e e e e





The Modern Banana in supermarkets and banana splits, is just one of numerous varieties found in the tropics - the Cavendish cultivar - genetically identical, uniform, possessing the same predictable pleasant taste and texture, and inevitably, susceptible to diseases. The previously dominant cultivar Gros Michel cultivar was decimated by a wilt fungus called Panama disease. Stuck with vegetative reproduction, disease and pest problems are especially problematic for bananas, and modern industrial scale commercial production is sustained mainly via enthusiastic applications of pesticides.





Rich in carbohydrates and energy.

A natural source of folate.

Full of vitamin C.

Low in calories.

Good source of niacin, vitamin B6 iodine and thiamin.

Good source of minerals.

No cholesterol whatsoever.

Completely fat-free.

Great source of protein.

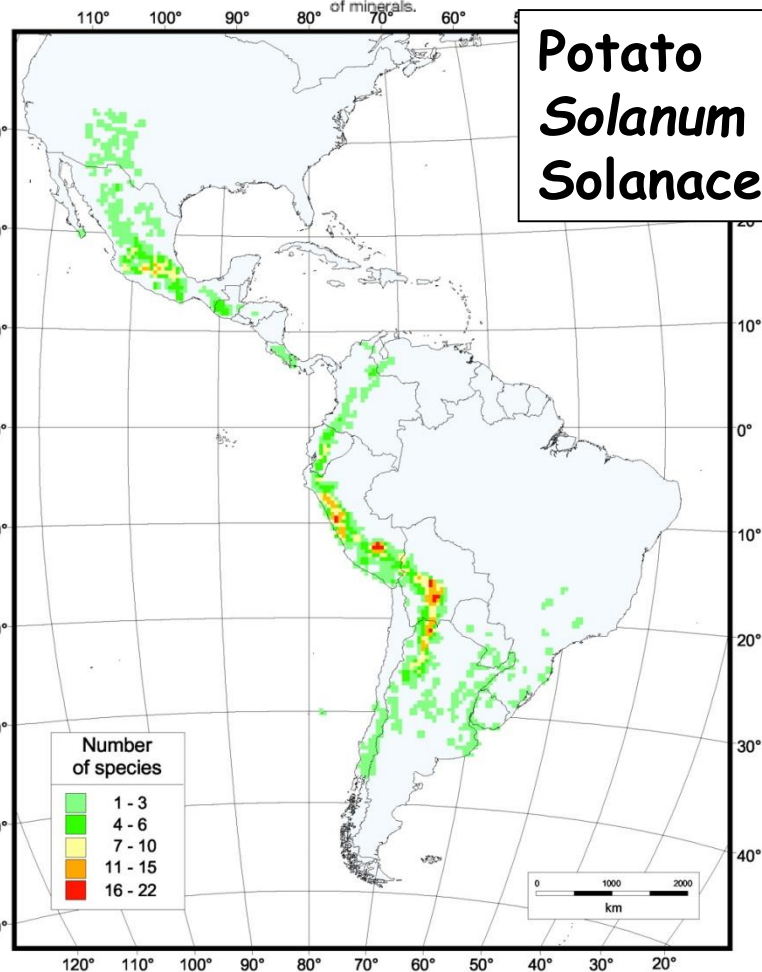
Natural, good-for-you dietary fibre.



# Potato

## *Solanum tuberosum*

### Solanaceae





*S. brevicaulis* complex

Selection

*S. stenotomum* complex X ?unknown species

2n

Chromosome doubling  
(polyploidy)

4n

*S. tuberosum* - andigena group

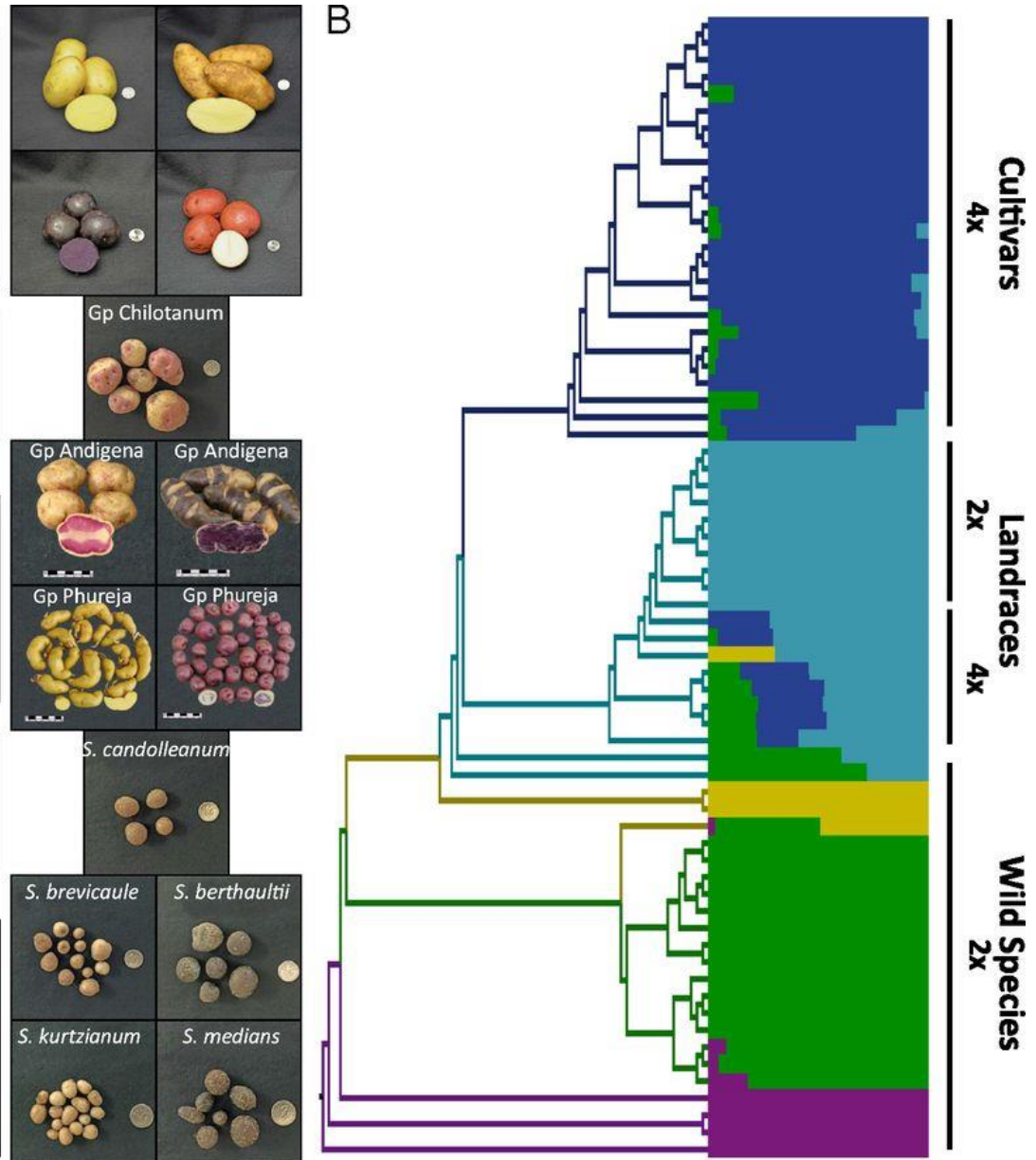
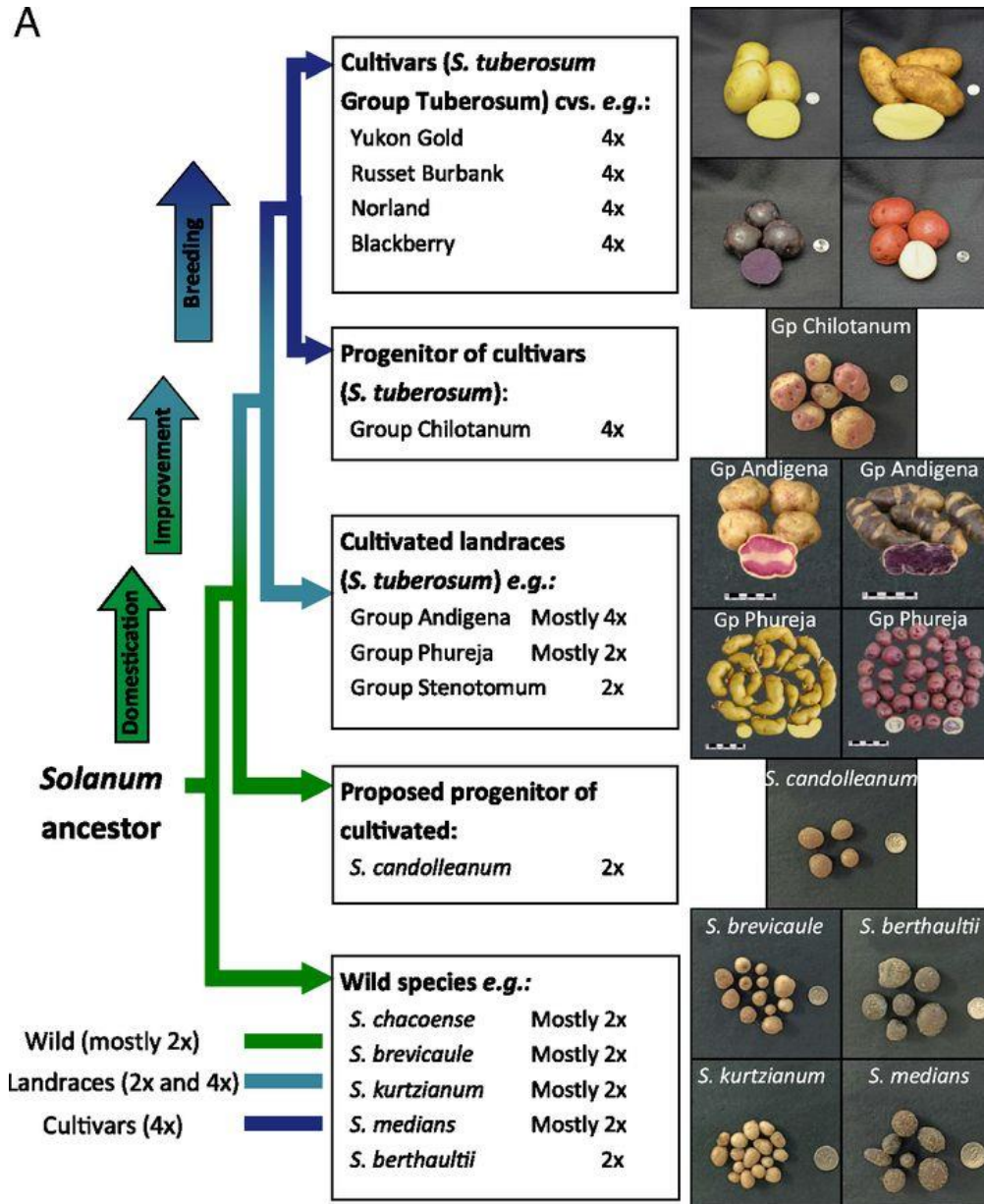
Multiple backcrossing  
(Introgression)

many diploid species X andigena group

*S. tuberosum* subsp. *tuberosum*



# The Complex Evolutionary History of the Potato



# Genome diversity of tuber-bearing *Solanum* uncovers complex evolutionary history and targets of domestication in the cultivated potato

Michael A. Hardigan<sup>a</sup>, F. Parker E. Laimbeer<sup>b</sup>, Linsey Newton<sup>a</sup>, Emily Crisovan<sup>a</sup>, John P. Hamilton<sup>a</sup>, Brienne Vaillancourt<sup>a</sup>, Krystle Wiegert-Rininger<sup>a</sup>, Joshua C. Wood<sup>a</sup>, David S. Douches<sup>c</sup>, Eva M. Farré<sup>a</sup>, Richard E. Veilleux<sup>b</sup>, and C. Robin Buell<sup>a,1</sup>

<sup>a</sup>Department of Plant Biology, Michigan State University, East Lansing, MI 48824; <sup>b</sup>Department of Horticulture, Virginia Polytechnic University and State University, Blacksburg, VA 24061; and <sup>c</sup>Department of Plant, Soil, and Microbial Sciences, Michigan State University, East Lansing, MI 48824

Edited by Esther van der Knaap, University of Georgia, and accepted by Editorial Board Member June B. Nasrallah October 5, 2017 (received for review August 21, 2017)

Cultivated potatoes (*Solanum tuberosum* L.), domesticated from wild *Solanum* species native to the Andes of southern Peru, possess a diverse gene pool representing more than 100 tuber-bearing relatives (*Solanum* section *Petota*). A diversity panel of wild species,

adopted into the global diet and is the third most important food crop for direct human consumption ([faostat3.fao.org](http://faostat3.fao.org)), providing food security in Asia and South America (9, 10).

The adaptability of potato to diverse growing conditions stems

- (i) Autopolyploidization of early diploid land races (sections *Stenotomum* and *Phureja*) via unreduced gametes resulted in the cultivated Andean tetraploids, *S. tuberosum* group *Andigena*,  $2n=4x=48$ , the initial Andean domesticated potatoes.
- (ii) Migration south to coastal Chile resulted in long-day-adapted *S. tuberosum* group *Chilotanum*,  $2n=4x=48$ , which provided the genetic background for commercial cultivars across the world.
- (iii) A large number of the over 100 tuber-bearing wild relatives (*Solanum* section *Petota*) which ranges from the SW U.S.A. to S. Chile have contributed to the genomes of commercial potato cultivars via introgression. Including: (a) diploid Peruvian land races of *S. candolleanum*, *S. medians*, and *S. raphanifolium*; (b) Bolivian tetraploids, *S. brevicaulis*, *S. leptophyes*, and *S. microdontum*; (c) Argentinian tetraploids, *S. bethaultii*, *S. chacoense*, *S. gourlayi*, *S. kuntzianum*, *S. spegazzinii* and *S. vernei*.



Up to five species cultivated together in fields in S Peru / Bolivia, alongside several other wild / weedy species

Highly sophisticated and complex systems of indigenous selection and use of potato varieties e.g. for drought / frost resistance to avoid risks - Andean farmers are growing (and conserving) genetic diversity

Formation of spontaneous hybrids following juxtaposition in cultivation has been vitally important in potato domestication





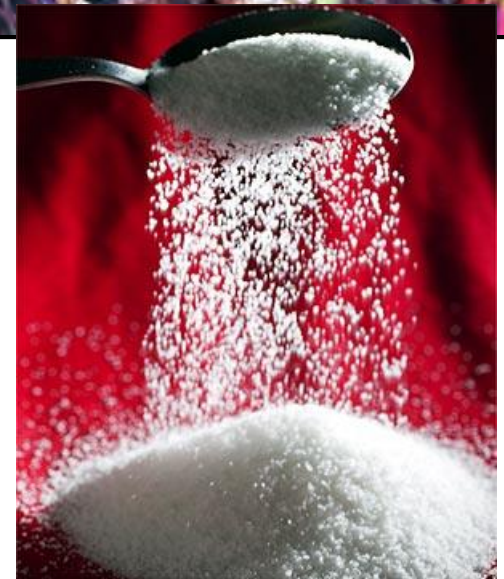
# Sugarcane

*Saccharum officinarum* x *S.spontaneum*

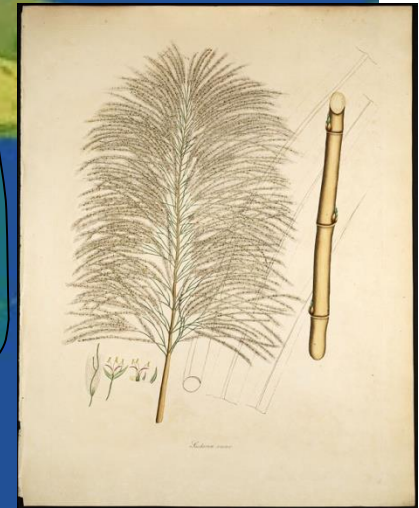
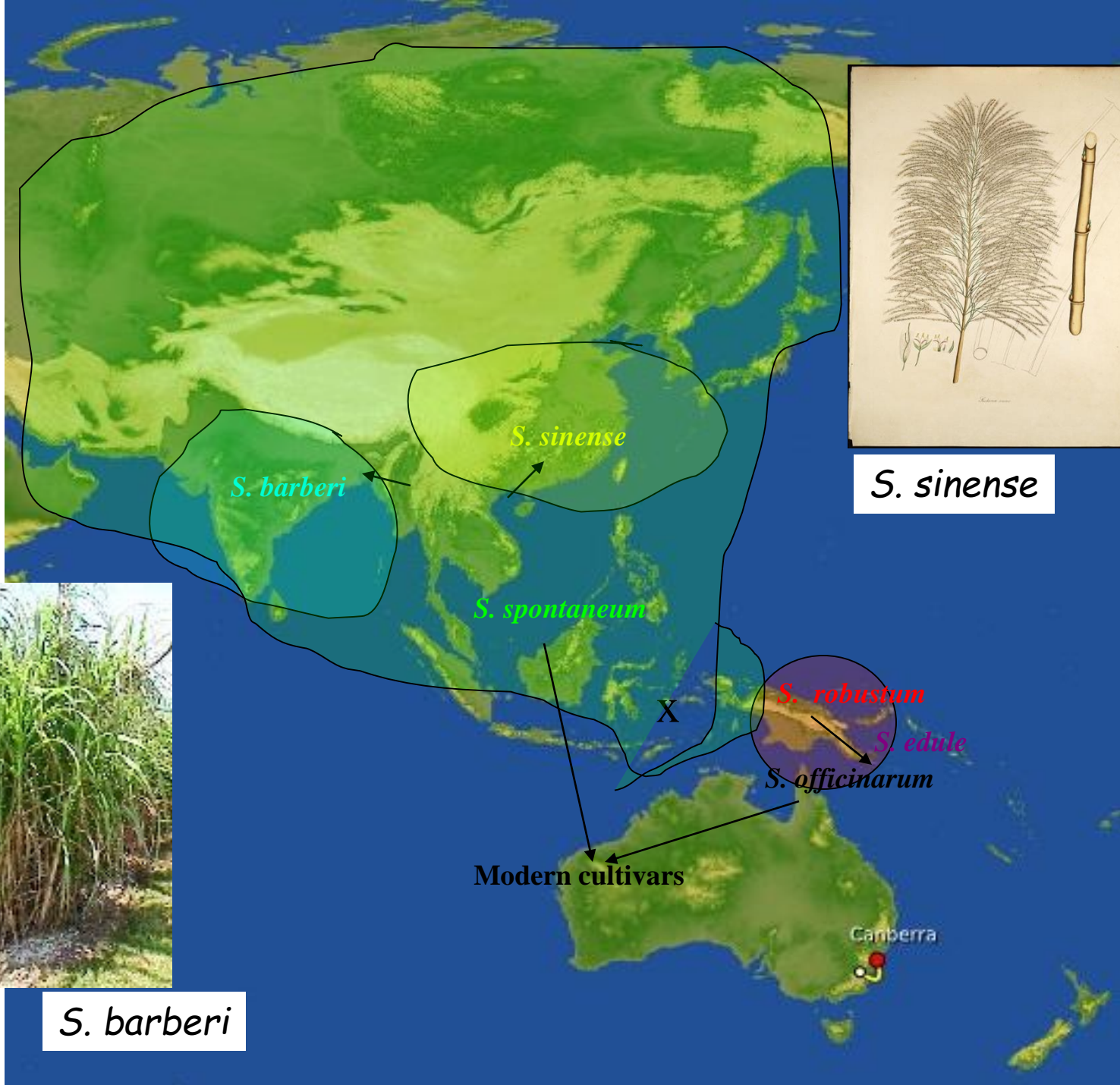
Poaceae: Andropogoneae:



Sugar:  
the 'unnecessary  
food'.... yet  
Europe imports >  
1 billion tones  
each year



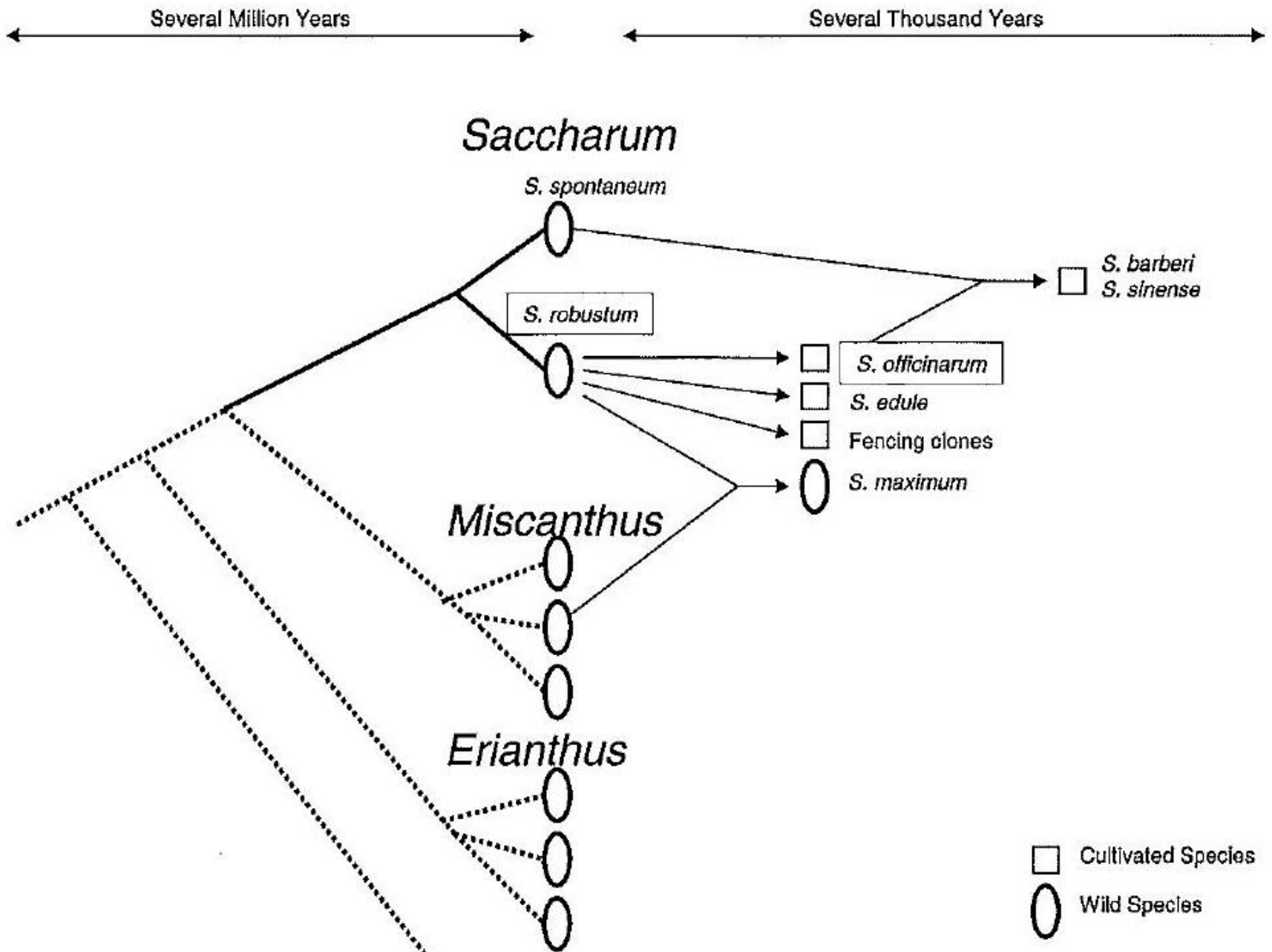




*S. sinense*



*S. barberi*

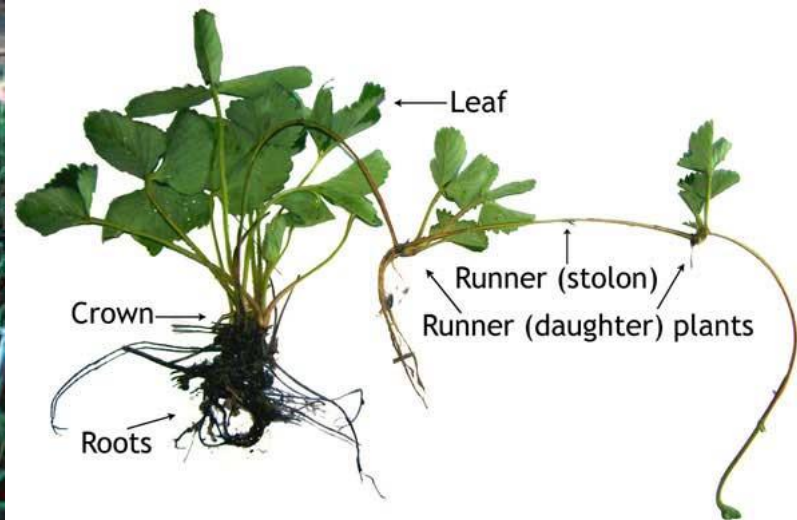




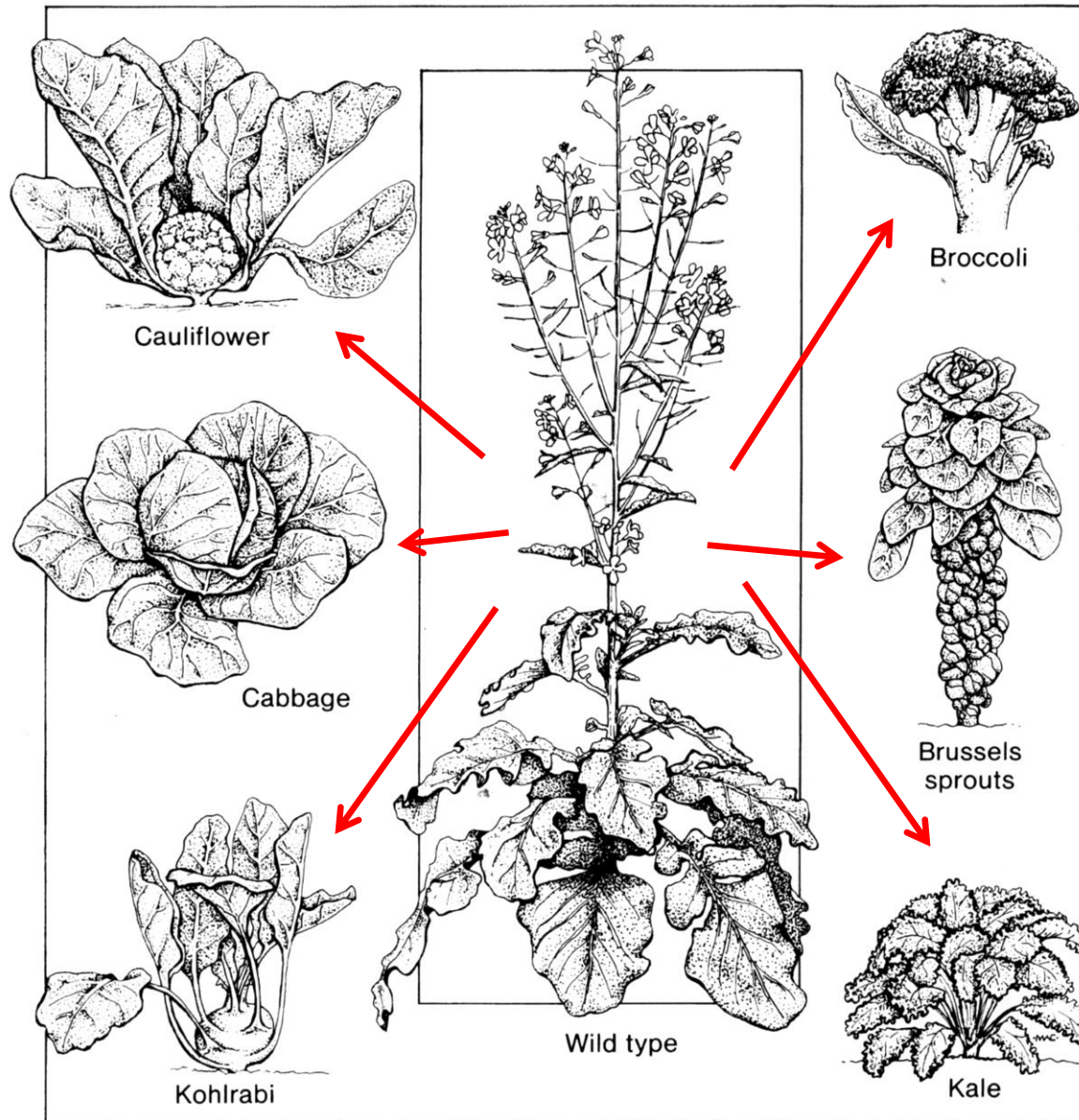
# Vegetative Propagation & Polyploid Domesticates

- How does the mode of crop reproduction (ie. Clonal vs. seed setting) contribute to the genetics of domestication?

Opuntia, Agave, strawberry, potato, banana, sugarcane are all vegetatively propagated - polyploids can be immediately replicated



Crops originating from *Brassica oleracea* subsp. *oleracea* -  $2n=2x=18$



*Brassica oleracea* subsp. *oleracea* - native along coasts of Europe from Greece to England

Leafy kales - recorded in cultivation in Greece at least 2500 years ago

Early cabbage in Germany c.1000 years ago

Cauliflower - northern Europe c. 500 years

Broccoli - eastern Mediterranean c. 500 years

Brussels Sprouts - spontaneous mutation in France in 1750

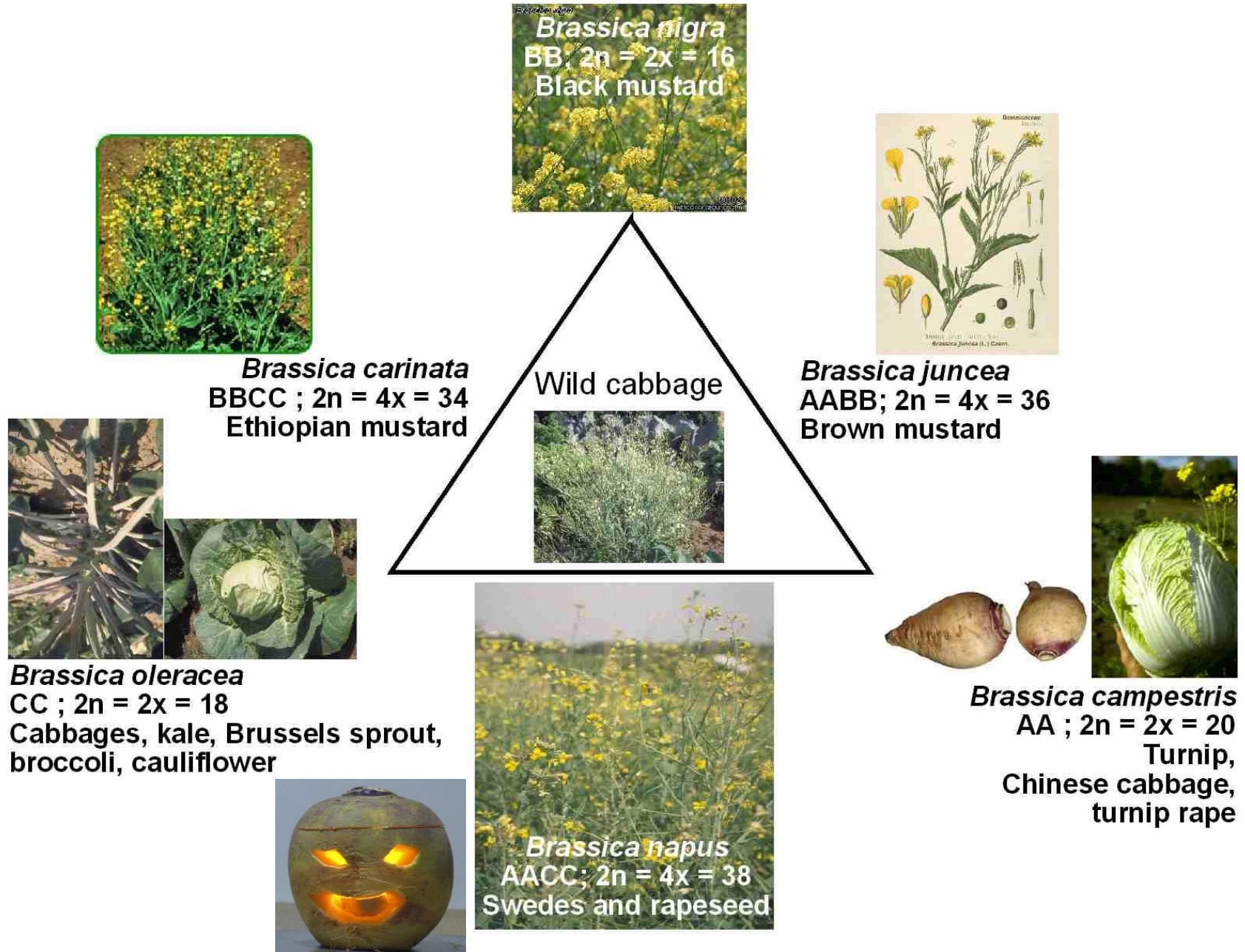


# Turnip - *Brassica campestris* - $2n=2x=20$



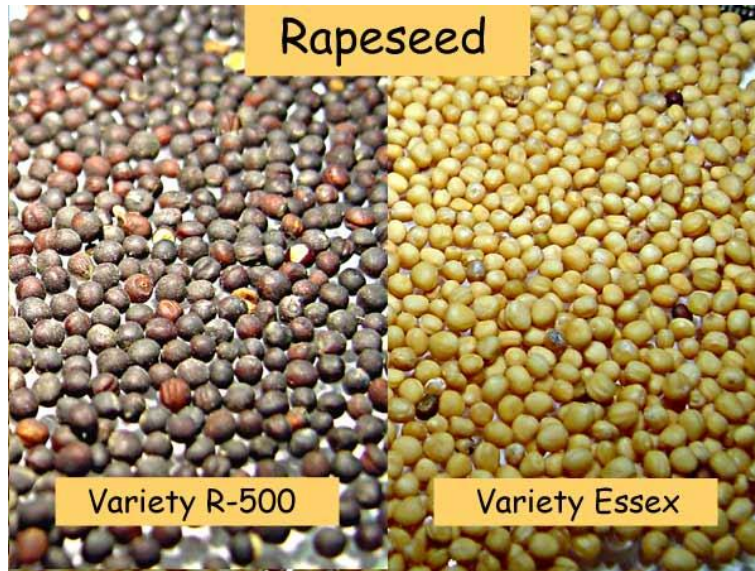
- First cultivated Brassica
- Used for seed oil from as early as 4,000 BP
- Domesticated repeatedly from wild populations across Eurasia where often found as a weed in fields of wheat

# Brassica & the triangle of U (1935)





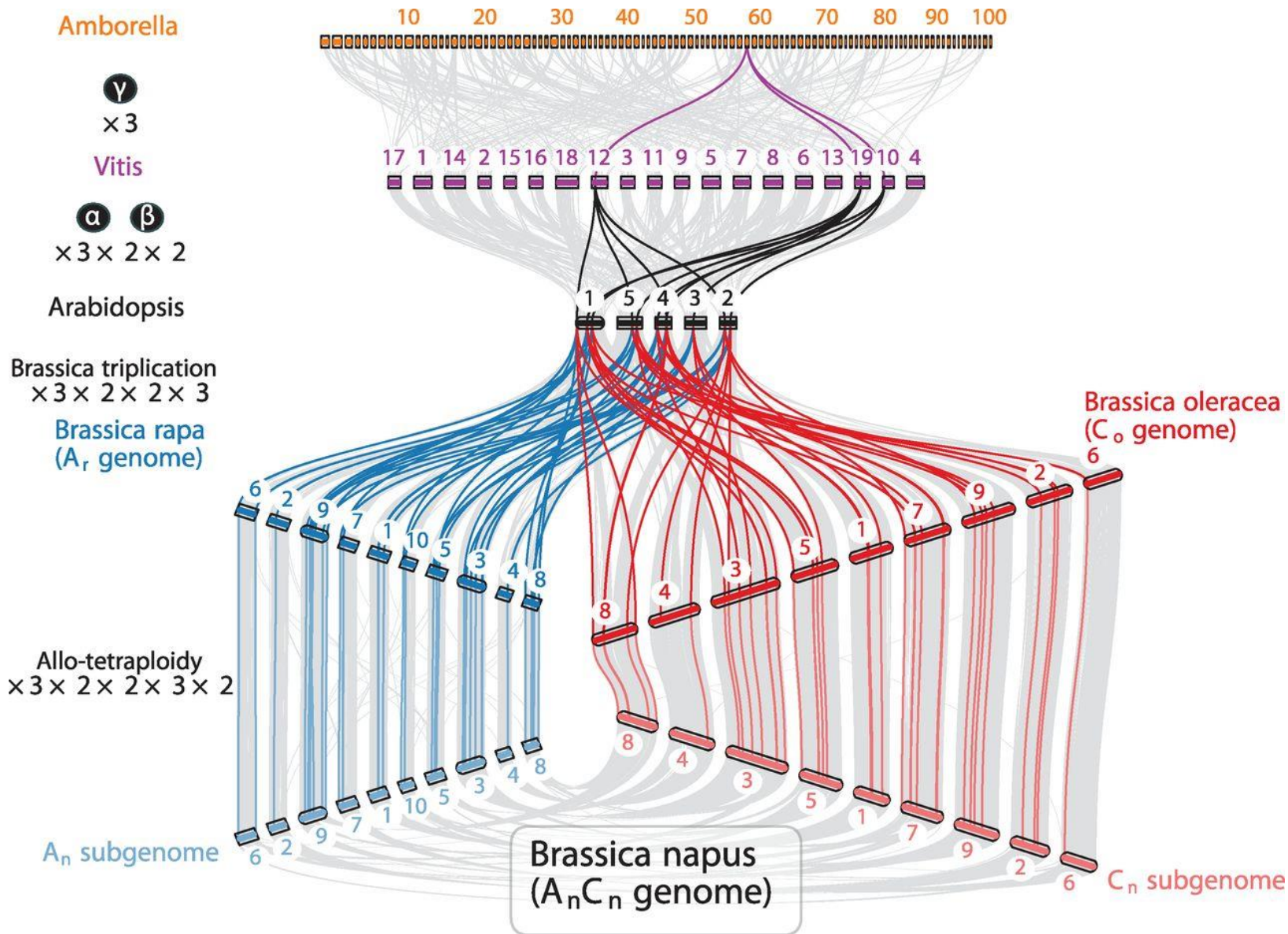
# Oil Seed Rape / Canola - *Brassica napus*



*Brassica napus* is a polyploid:  $2n=38$  AACC  
Derived from a hybrid between:

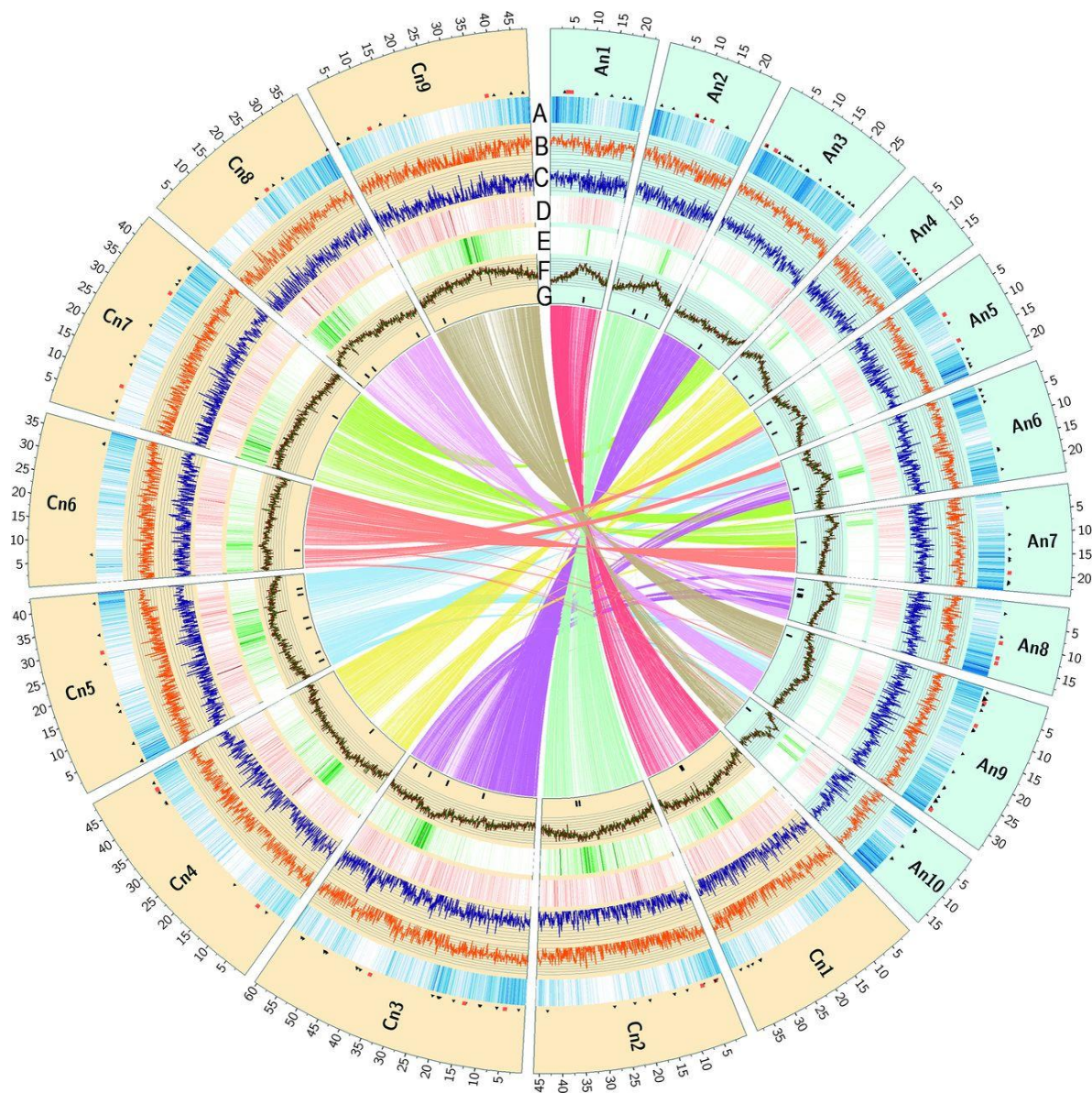
- Kale - *B. oleracea*:  $2n=18$  CC domesticated at least 2500 years ago in Europe
- Turnip - *B. campestris*:  $2n=20$  AA - domesticated c.4000 years ago in Mediterranean
- recent introgressive hybridization between these two species and oil seed rape

# The genome of the recent allopolyploid (neopolyploid) *Brassica napus*





# The genome of the recent allopolyploid (neopolyploid) *Brassica napus*



# The genome of the recent allopolyploid (neopolyploid) *Brassica napus*

Oilseed rape (*Brassica napus* L.) was formed ~7500 years ago by hybridization between *B. rapa* and *B. oleracea*, followed by chromosome doubling, i.e. via allopolyploidy.

Together with more ancient polyploidizations, this conferred an aggregate 72× genome multiplication since the origin of angiosperms and high gene content.

In the *B. napus* genome the constituent  $A_n$  and  $C_n$  subgenomes are engaged in subtle structural, functional, and epigenetic cross-talk, with abundant homeologous exchanges.

Incipient gene loss and expression divergence have begun.

Selection in *B. napus* oilseed types has accelerated the loss of glucosinolate genes, while preserving expansion of oil biosynthesis genes.

These processes provide insights into allopolyploid evolution and its relationship with crop domestication and improvement



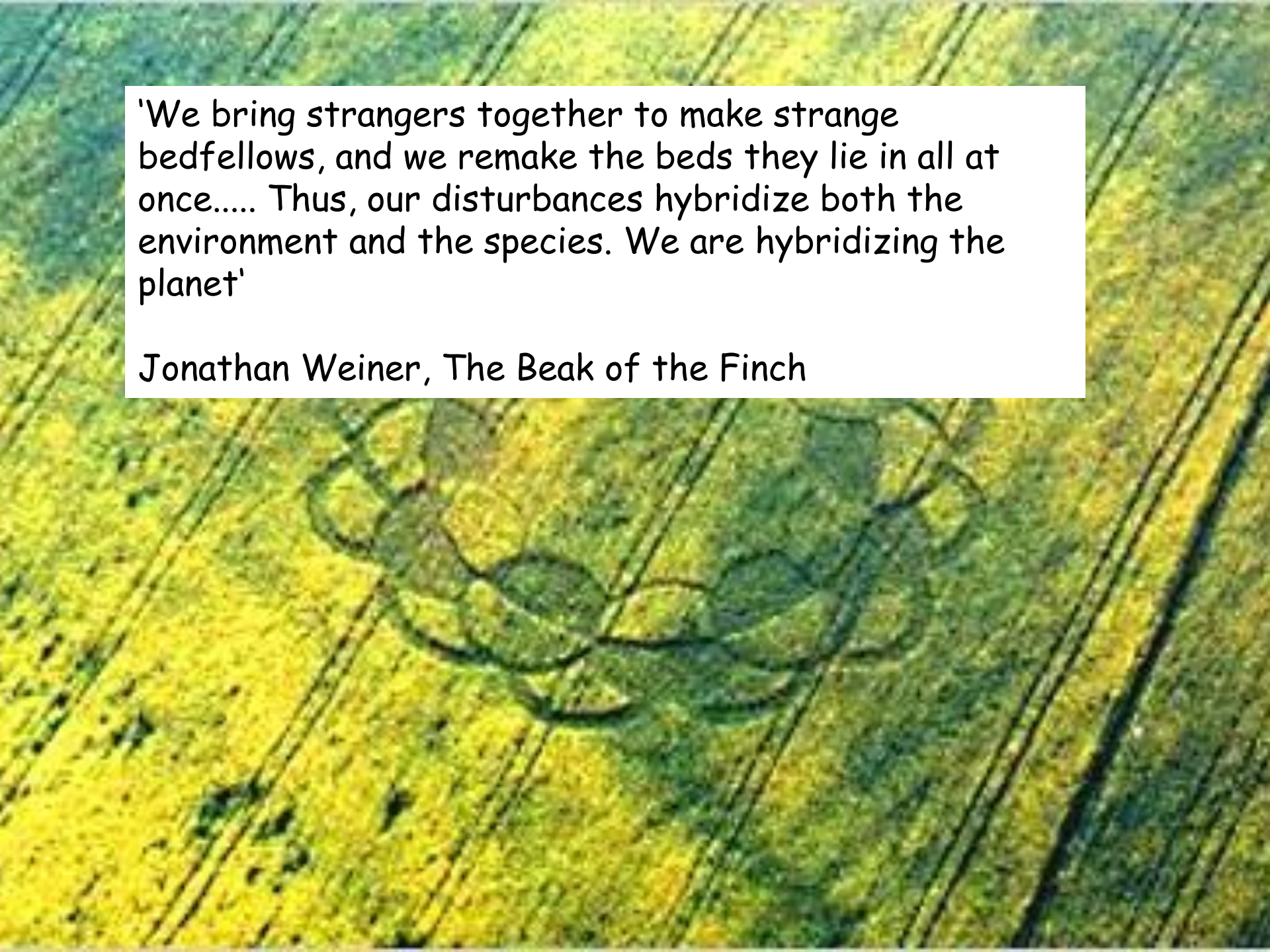




# Hybridization, Polyploidy & Crop Domestication - Conclusions

- Many of our most important crops are polyploids
- The origins in terms of where, when, how many times and from what progenitors, of several of these are highly complex, involving multiple sequential cycles of hybridization and multiple sets of wild species and early domesticates, and as yet incompletely understood - e.g. potato, banana, sugarcane
- For at least two of these - strawberry and bread wheat - there is evidence to suggest anthropogenic origins in cultivation
- For the others - potato, banana, sugarcane & canola - there is abundant circumstantial evidence that serendipitous hybridization following early cultivation, translocation and incipient domestication played an important part in generating the diversity that we see today amongst the set of important crops.
- There are many other hybrid / polyploid crops - citrus, tobacco, peanut, oca, kiwi fruit.....





'We bring strangers together to make strange bedfellows, and we remake the beds they lie in all at once..... Thus, our disturbances hybridize both the environment and the species. We are hybridizing the planet'

Jonathan Weiner, *The Beak of the Finch*







# Announcements

Botanic Garden Fruit Market - Obstsortenmarkt  
27 Oktober 2017: 11.00 - 17.00 Uhr im  
Botanischen Garten der Universität Zürich  
Detailed program on OLAT  
[www.bguz.uzh.ch](http://www.bguz.uzh.ch)



Course Assignment - *What do We Eat Today?* - 6 November 2017