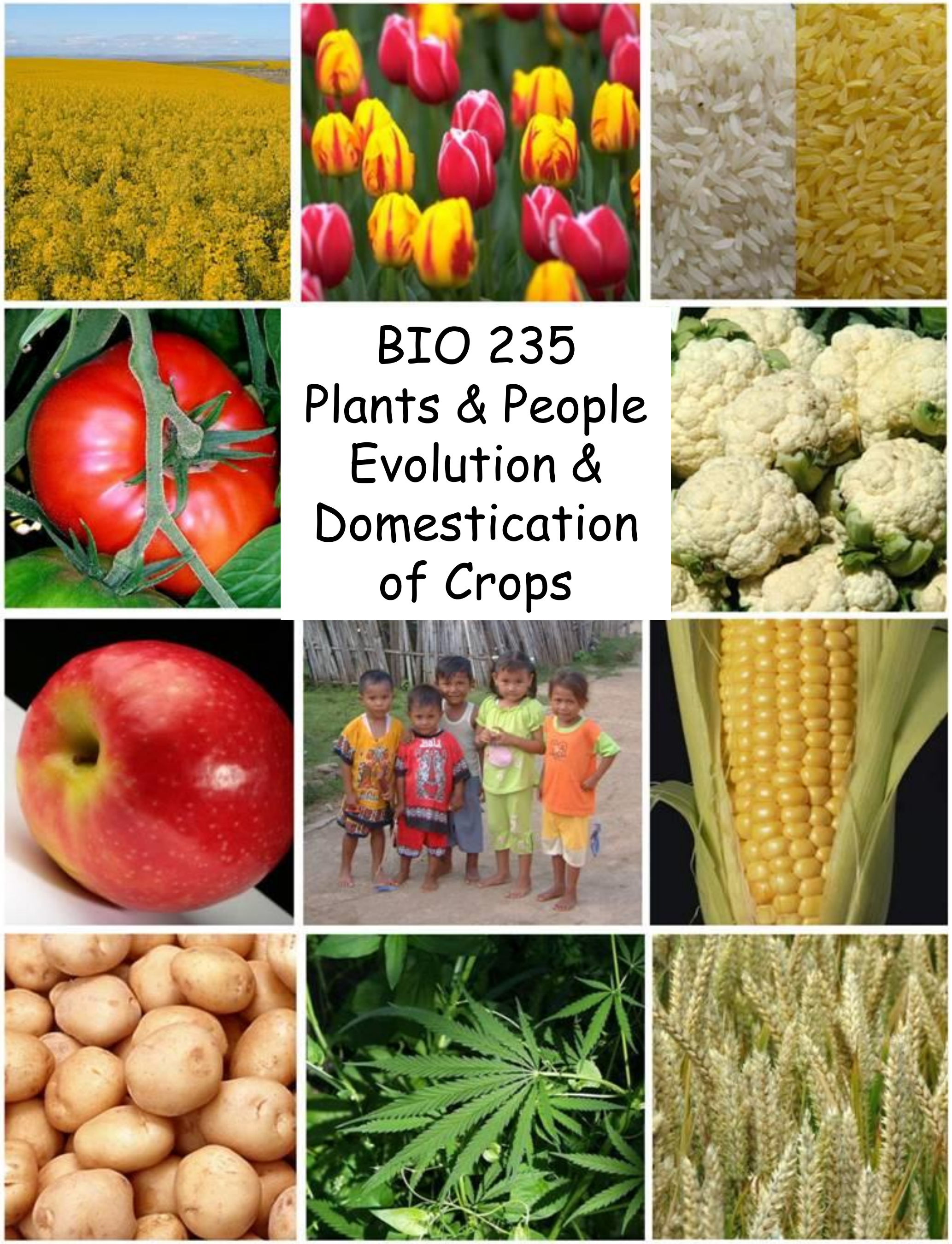

Lecture 4
How were Crops Domesticated?

- Crop domestication syndromes
- Indigenous knowledge and incipient domestication
- Darwin's variation under domestication; methodical and unconscious selection
- Molecular genetics of early crop domestication
- Definition of domestication

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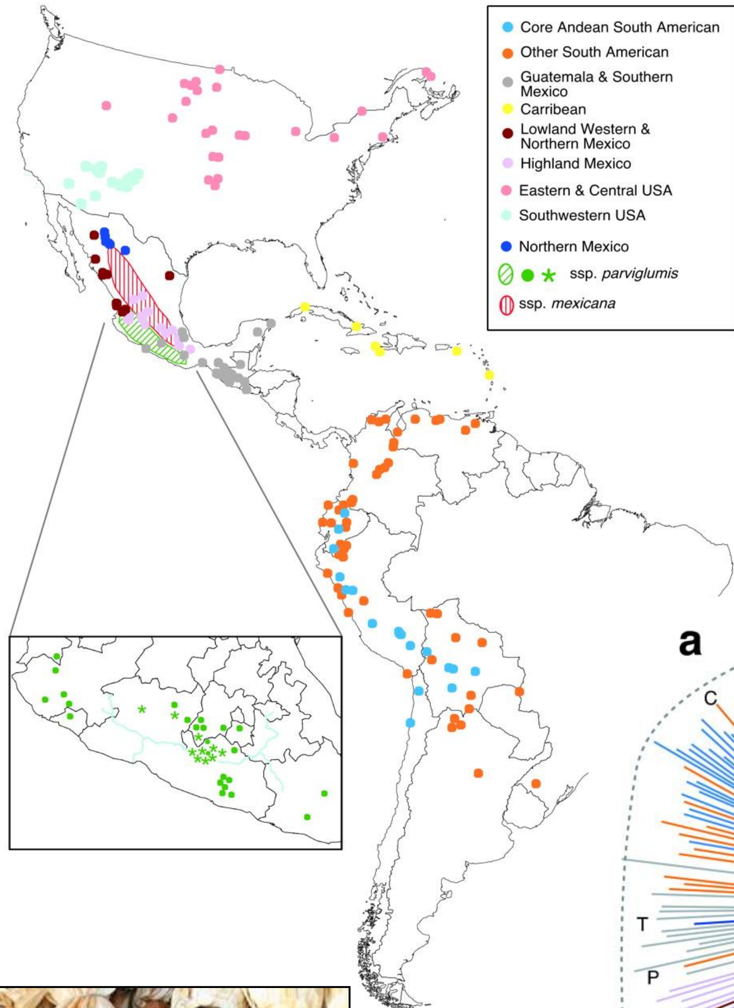
Maize – Genetic Data

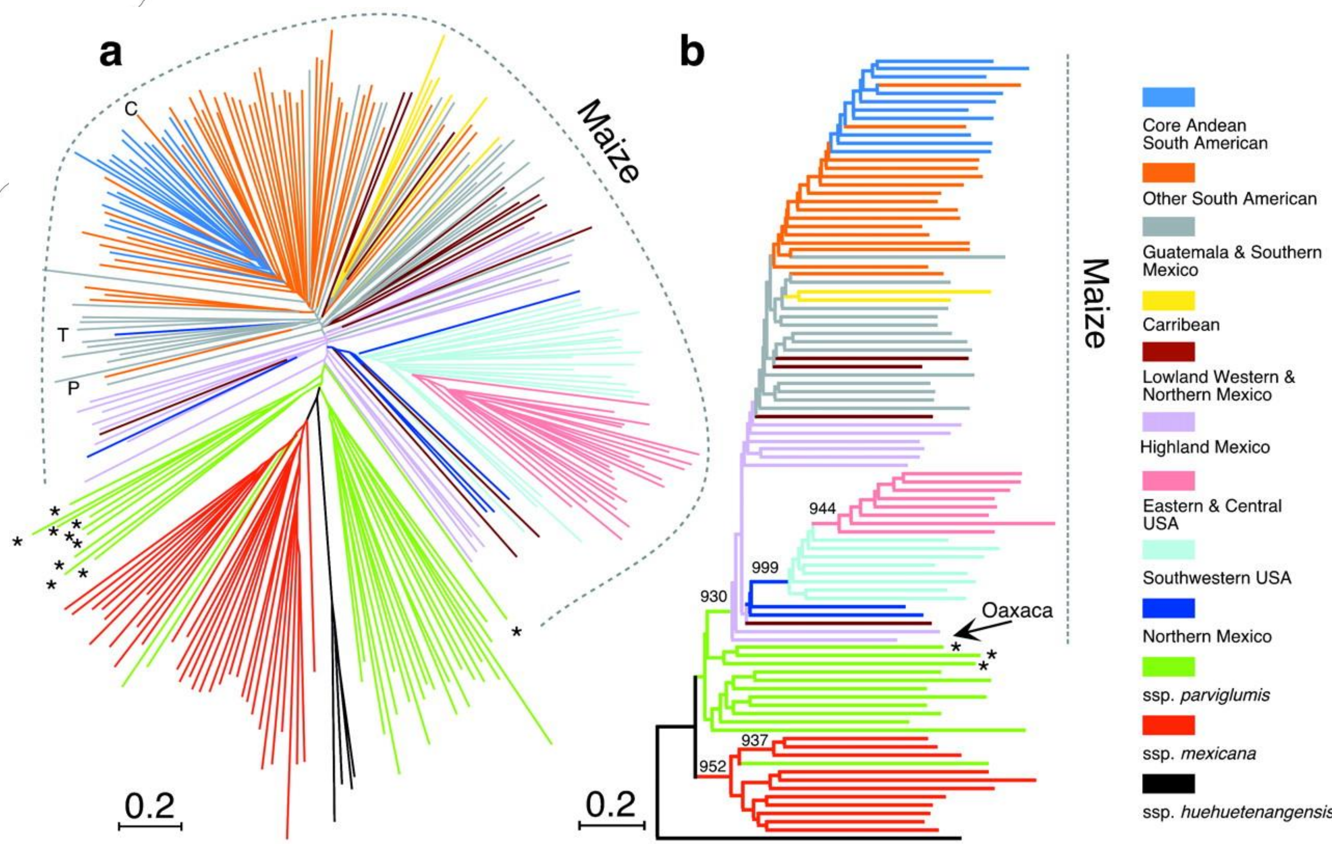
Annual teosinte – *Z. mays* ssp. *parviglumis* distributed in the Balsas Depression of southern Mexico

Maize accessions monophyletic & derived within teosinte suggesting a single domestication event & teosinte as progenitor.

Most closely allied teosinte is in the Balsas Depression

Earliest branching maize lineage from Oaxaca.



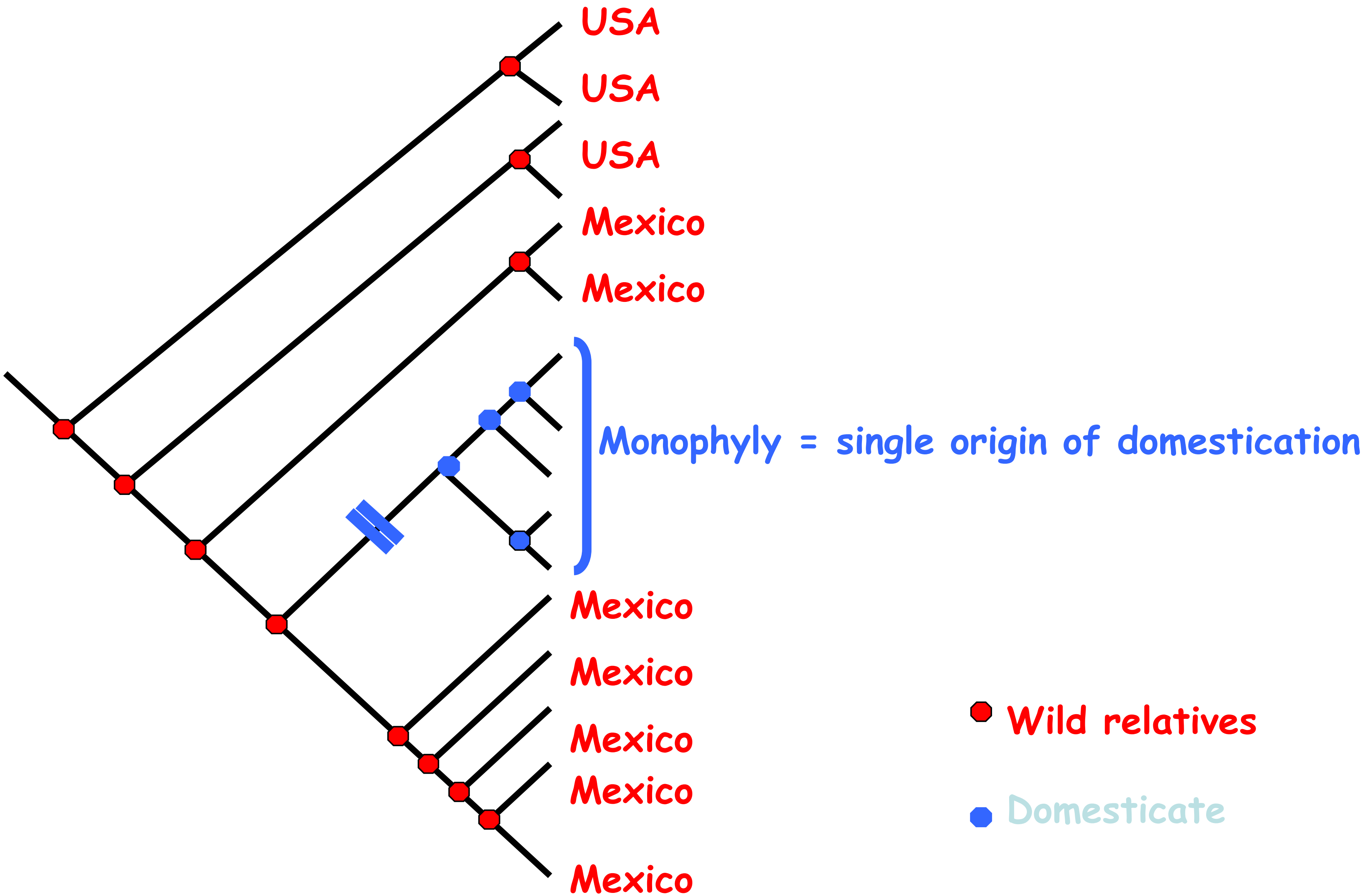


Matsuoka et al 2002 PNAS

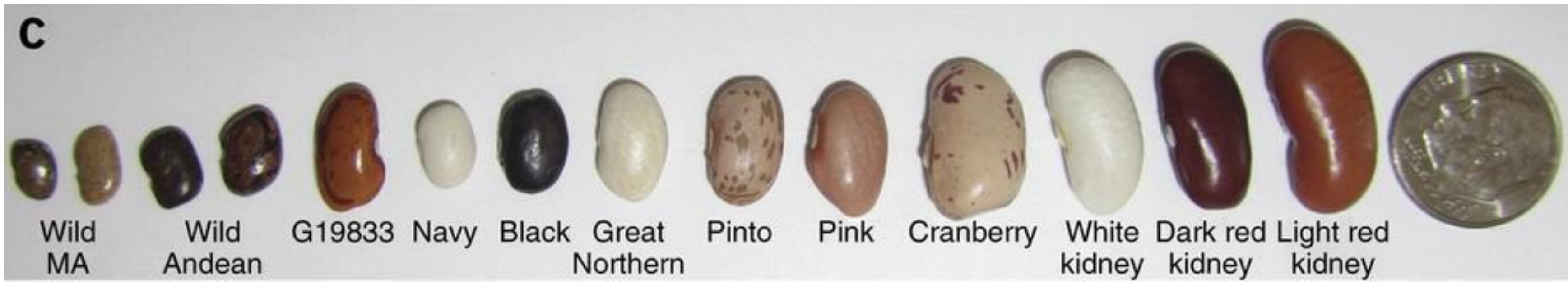
For this week:

Draw a phylogenetic tree that shows multiple independent origins of a crop

Monophyly = A group that contains all the descendents of a common ancestor



Common bean = *Phaseolus vulgaris* (Leguminosae)




French beans

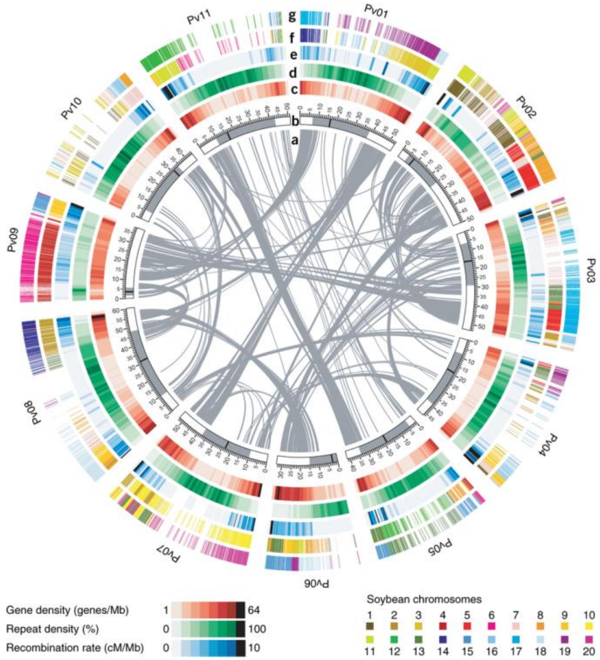

Kidney beans

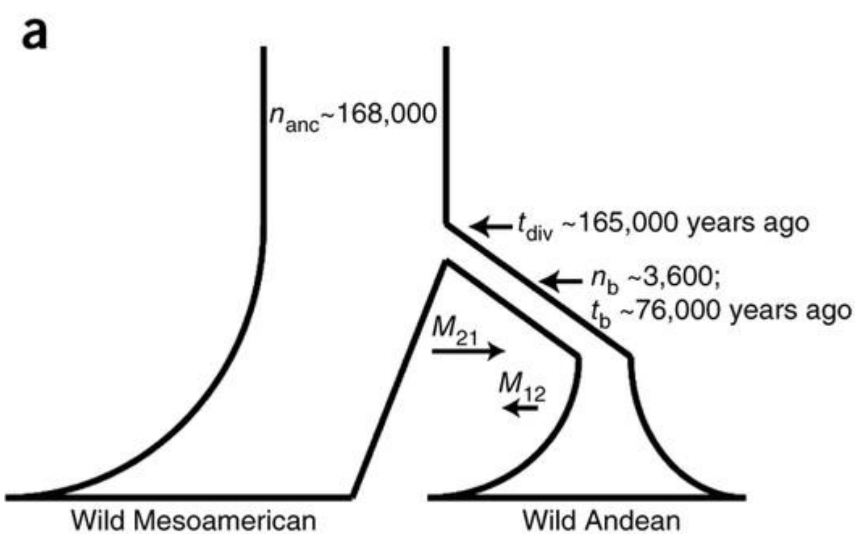

String beans


Pinto beans

1/3 of dietary protein in some parts of Africa and the Americas

Independent domestication of Phaseolus in Mexico & the Andes

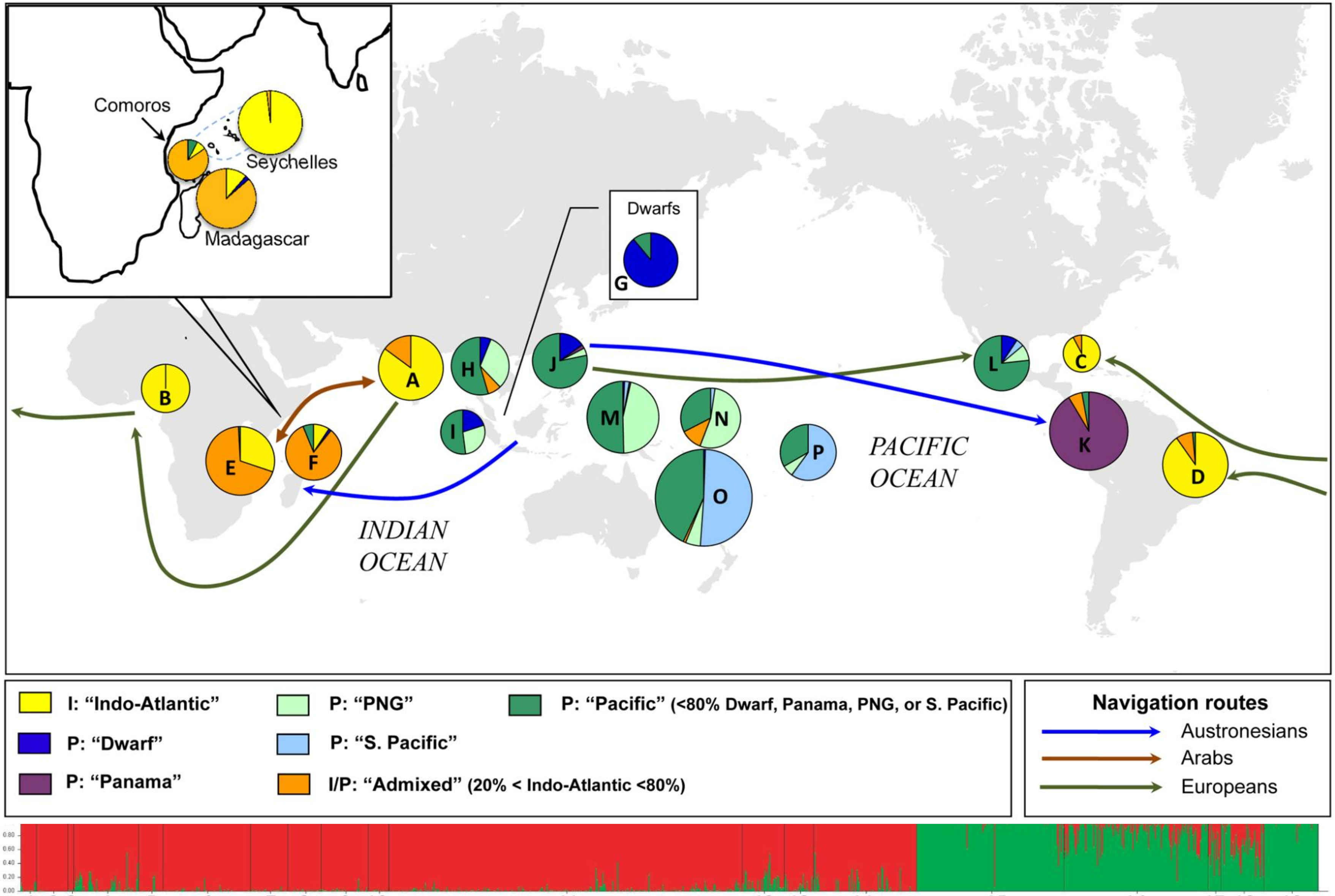




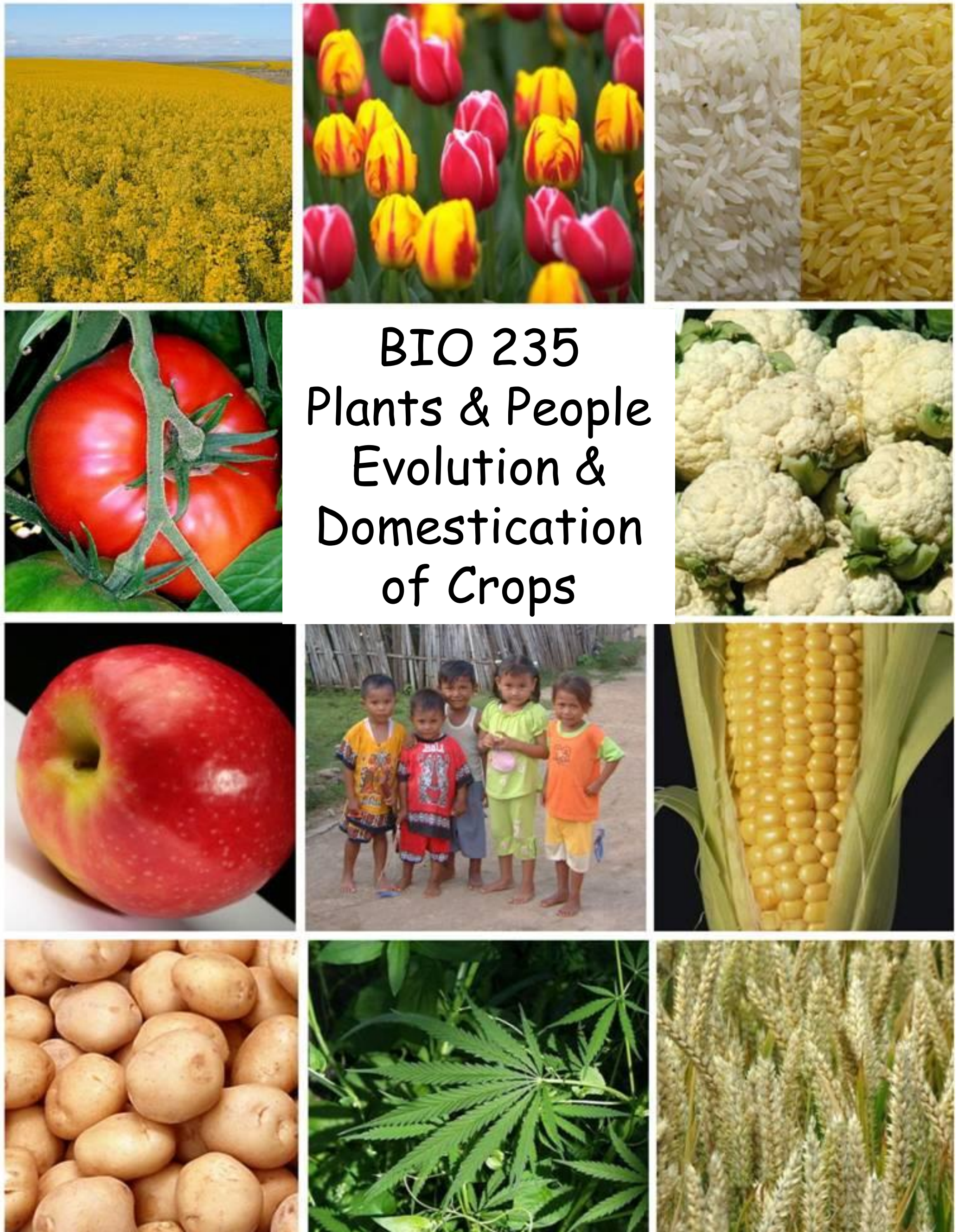
Gaut (2014); Schmutz et al. (2014)

Coconut – *Cocos nucifera*
Palmae / Araceae

Two independent origins of cultivated coconut *Cocos nucifera*



Gunn et al (2011)



BIO 235
Plants & People
Evolution &
Domestication
of Crops

Lecture 4
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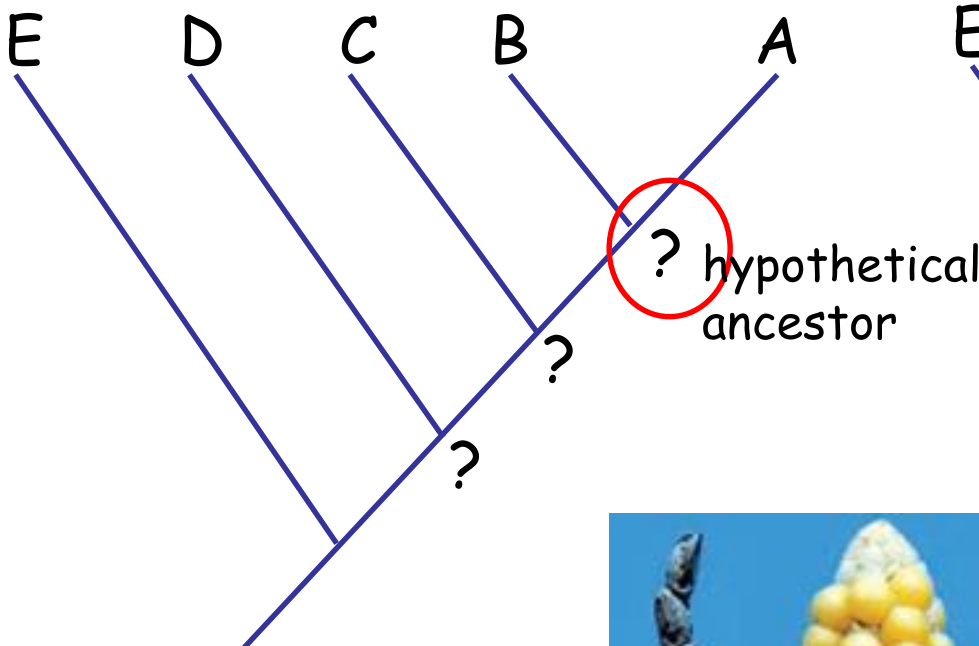
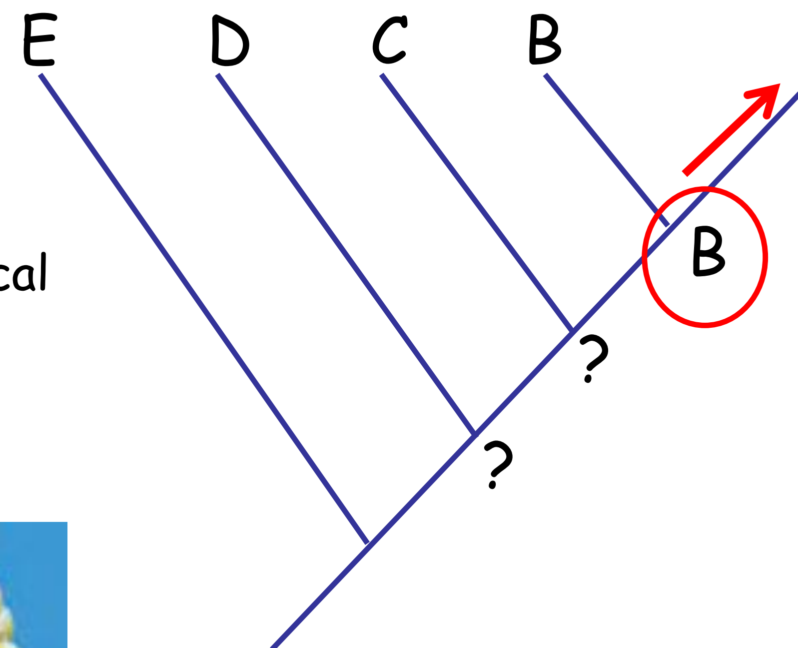
Crop domestication and phenotypic change

Molecular systematics



Ancestor – descendent relationships



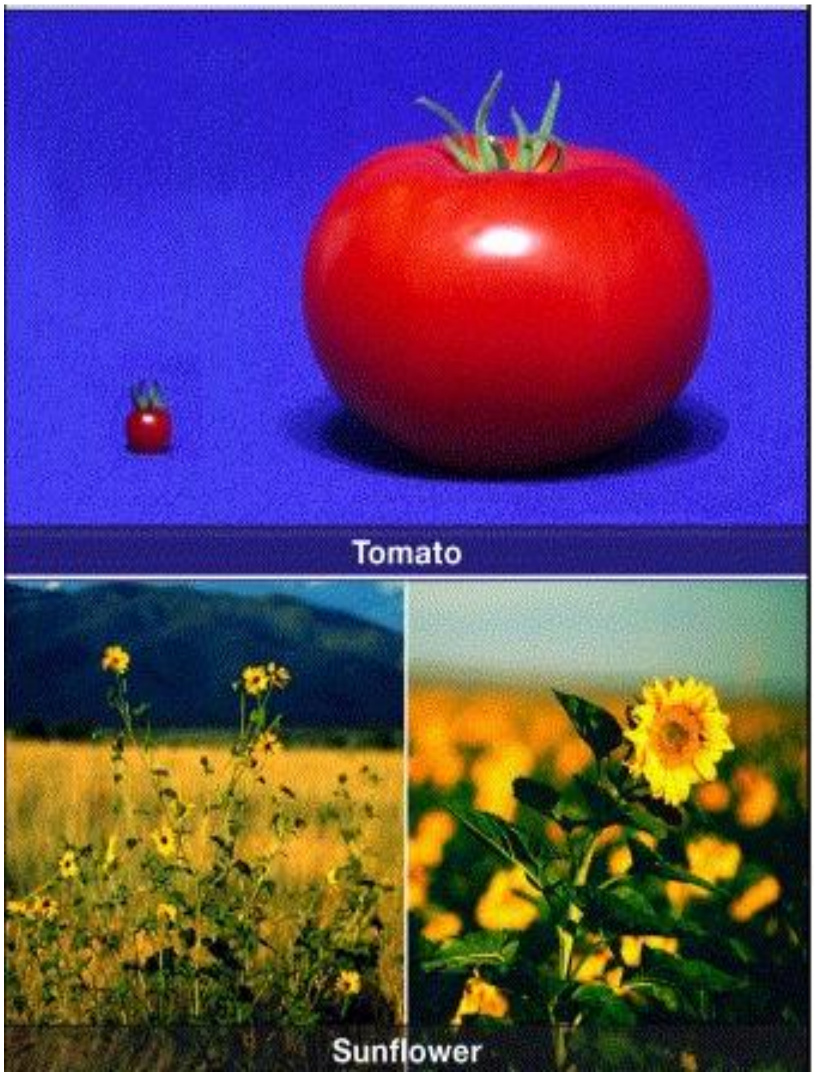
teosinte maize

B → A

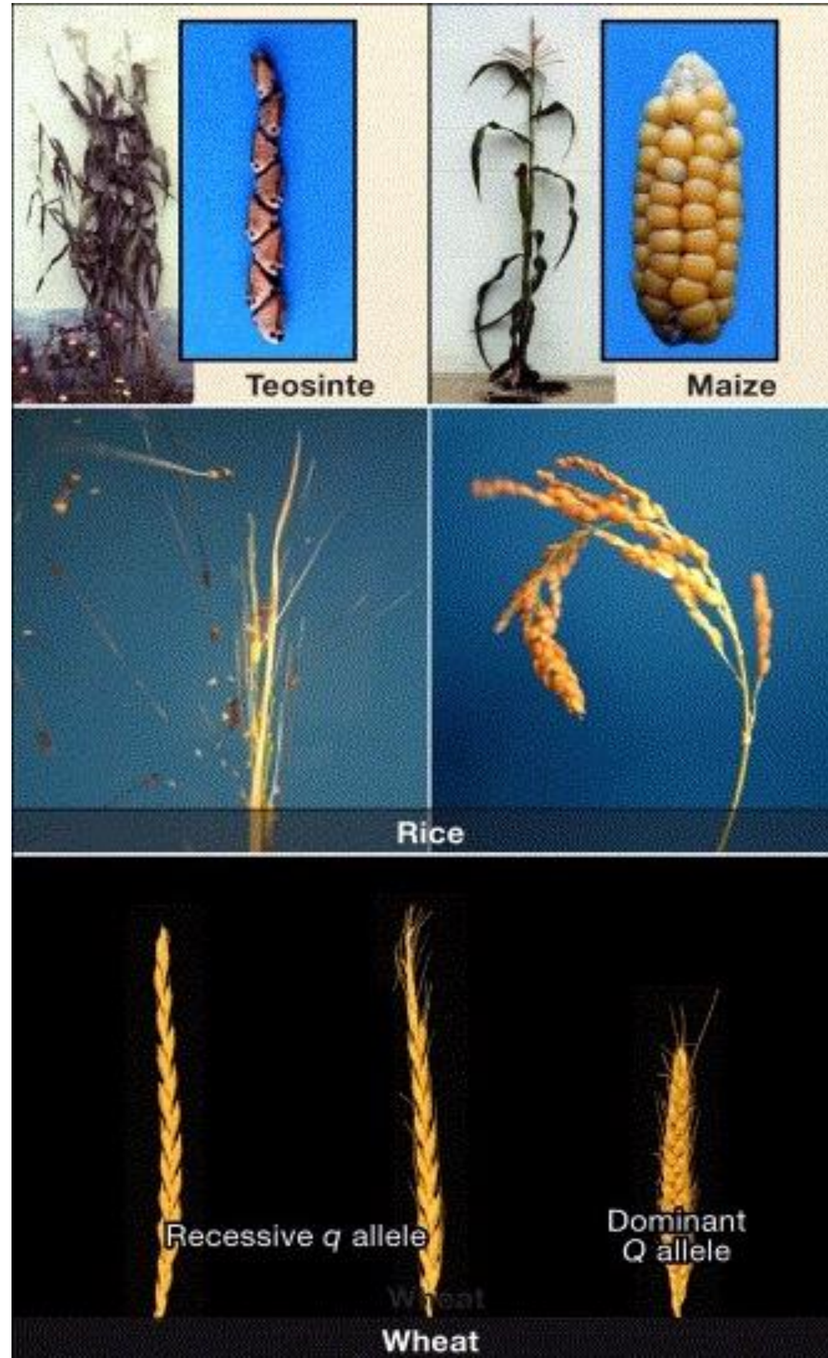
Domestication Syndrome of Crop Plants

Doebley et al 2006 Cell

Wild Domesticated



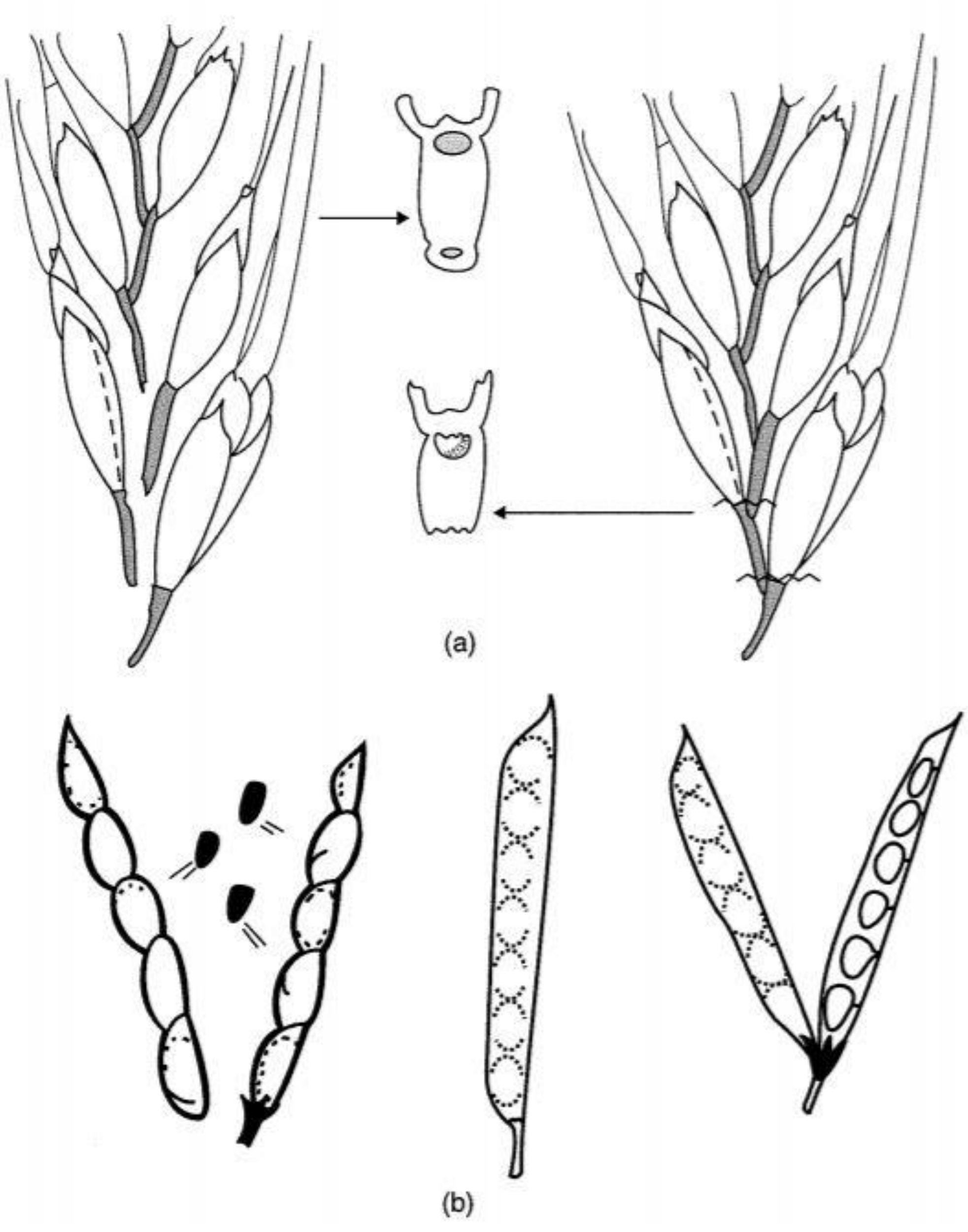
Wild Domesticated



Domestication Syndrome of Crop Plants

- **Gigantism** – larger fruits or grains (often fewer fruits or grains)
- **Suppression of seed dispersal** - seeds remain attached to the plant for easy harvest by humans
- **Secondary metabolites** - biochemical changes – decrease in bitter substances in edible structures
- Changed growth form – more robust plants
- Changed life form - > determinate growth and increased apical dominance; shifts from perennial to annual habit
- Changed breeding system
- Physiological changes
  - Loss of seed dormancy
  - Changes in photoperiod sensitivity
  - Synchronized flowering
- Changed ploidy level

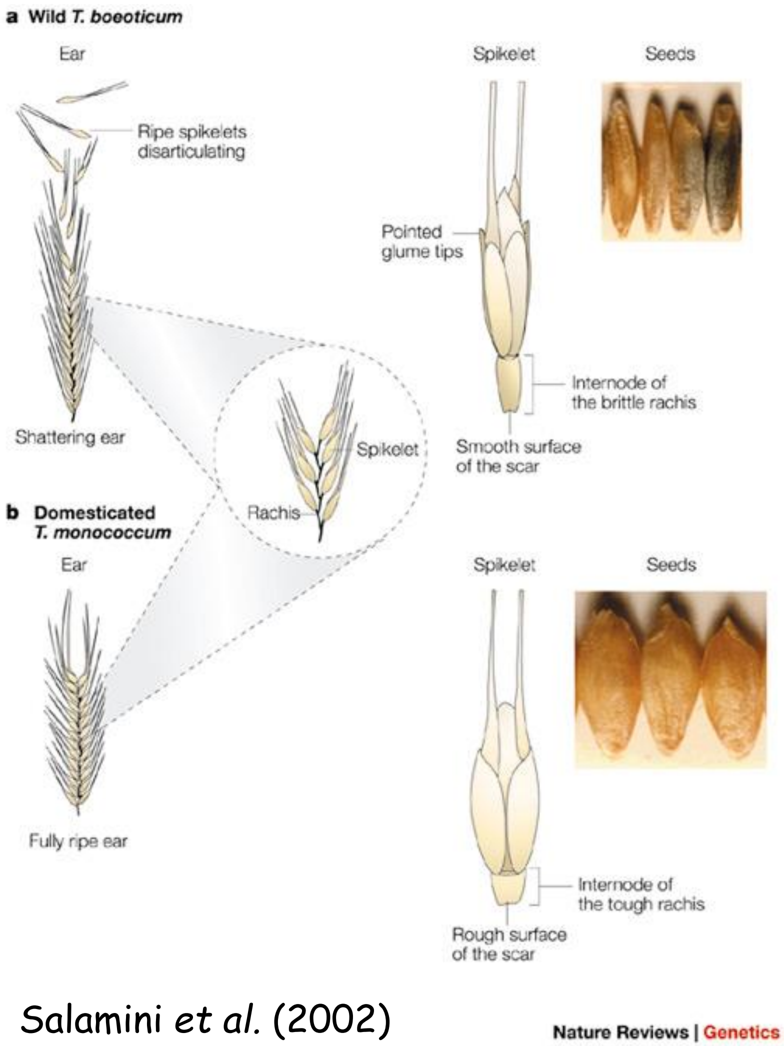
Shattering to non-shattering in grasses and legumes



Dominance of non-shattering genotypes = full domestication

Fuller & Allaby (2010)

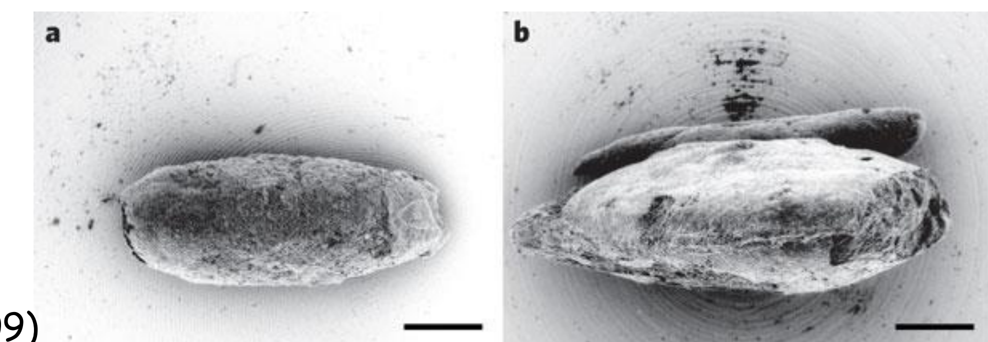
Phenotype of wild vs domesticated cereals



Salamini *et al.* (2002)

Einkorn wheat spikelets, or ears, with two rows of seeds:

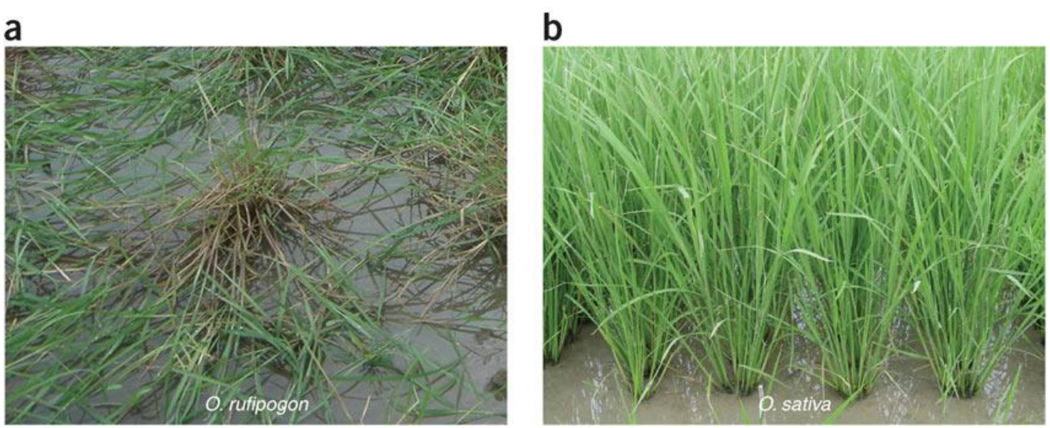
- Seed size increase in domesticated forms
- Non-shattering spiklets due to a tough rachis that holds the seeds together in a harvestable and threshable ear
- Leaf-like structures that protect the seed – called glumes – are attached tightly to the seed or fused to it in wild forms whereas they release the seed in the more advanced domesticated forms, which are therefore termed 'free-threshing' or naked.

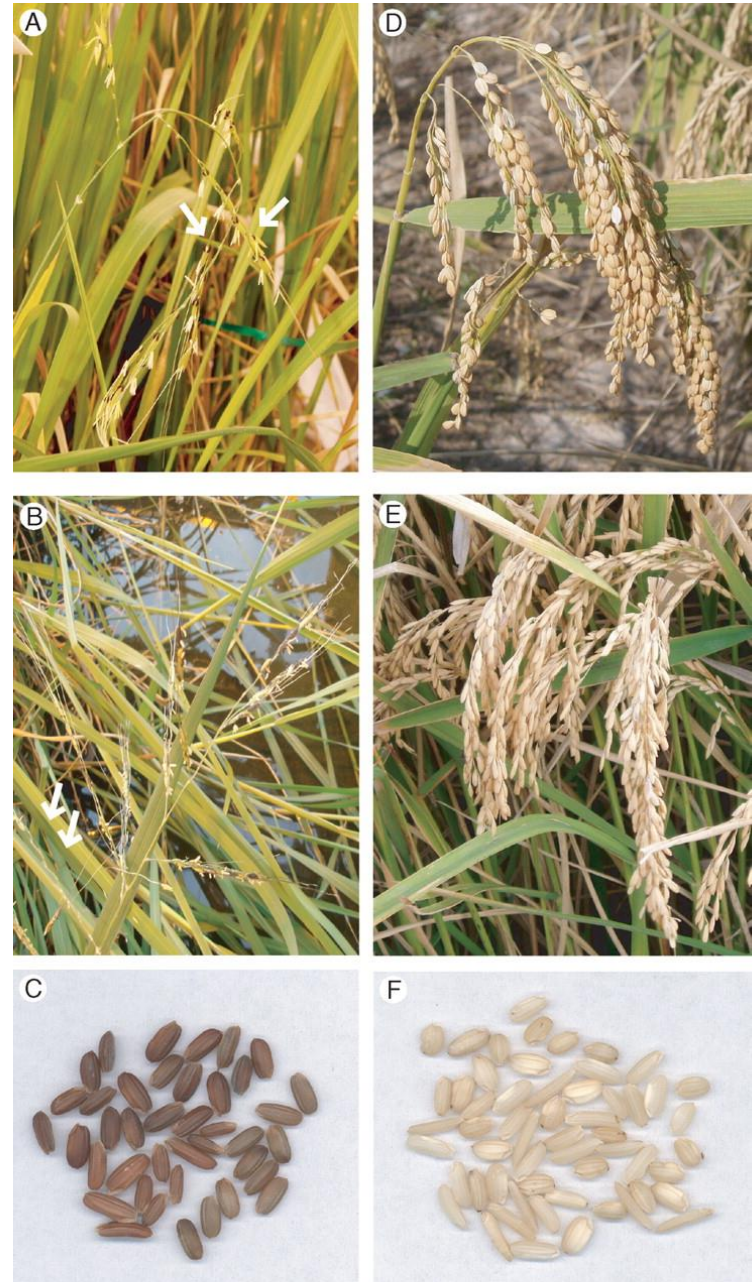


Purugganan & Fuller (2009)

Rice: changes during domestication

- Perennial to annual
- Shattering to non-shattering seeds, critical for effective harvesting, and the hallmark of domestication
- Disparate to synchronized seed maturation
- Awns to lack of awns
- Prostrate habit to erect habit providing improved plant architecture and increased yields
- Many to fewer tillers
- Low yield to high yield
- Seed dormancy to reduced seed dormancy

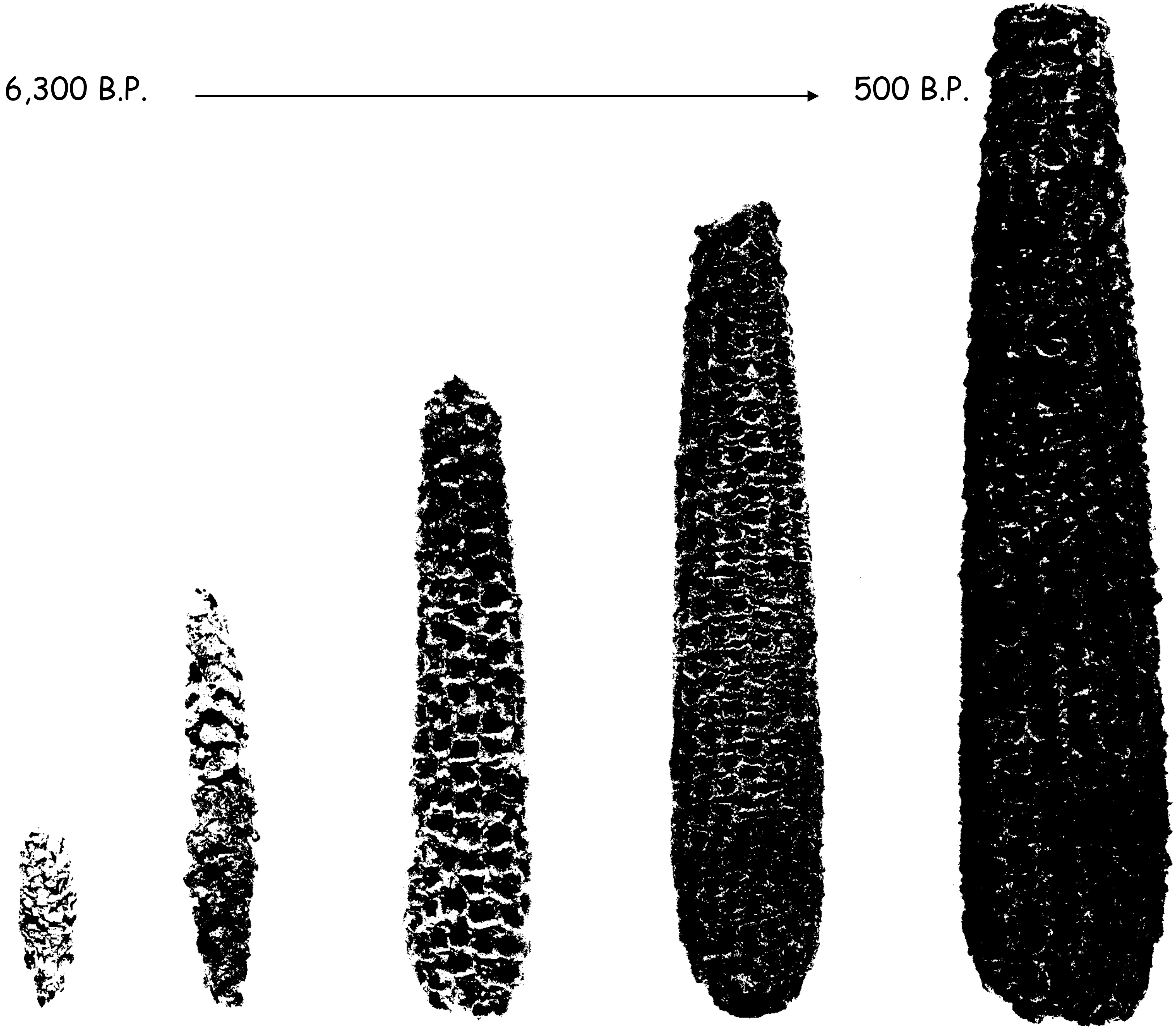




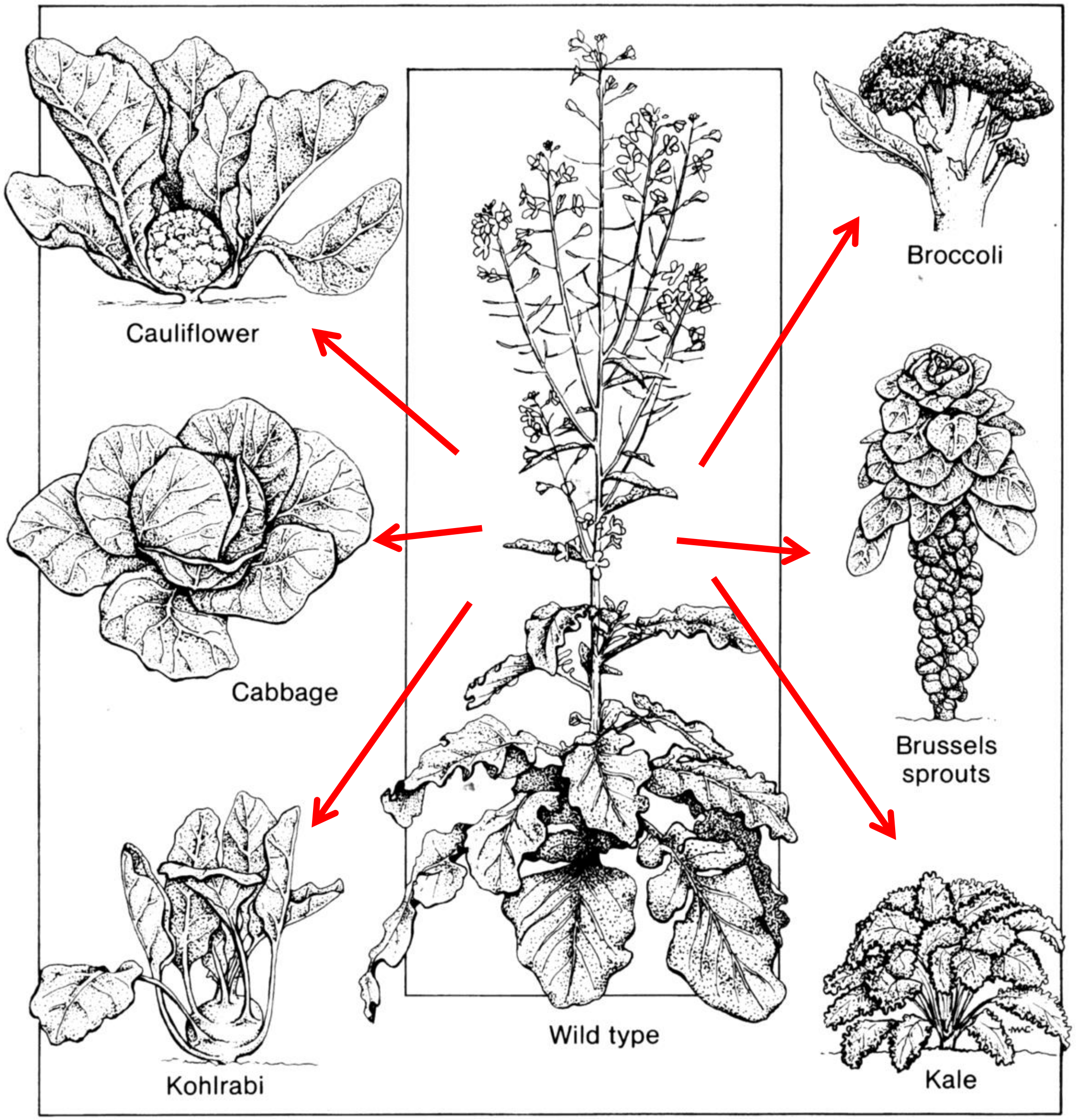
Teosinte spike

Annual teosinte

Modern hybrid corn


6,300 B.P.
500 B.P.

Crops originating from *Brassica olearacea* subsp. *oleracea*



Brassica oleracea subsp. oleracea – native along coasts of Europe

Broccoli – hundreds of tiny unopened flower buds with arrested inflorescence development.

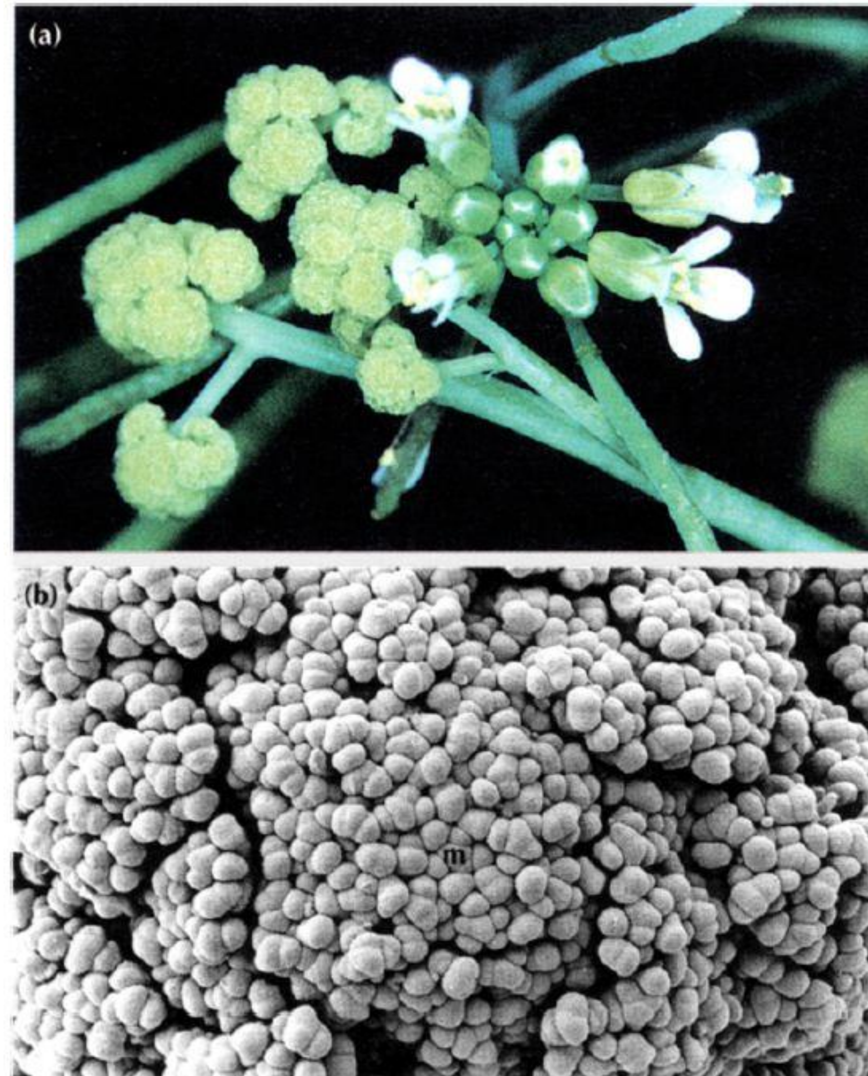
Cabbages – large tightly curled ball of leaves packed into a congested head

Sprouts – secondary shoots with small heads of congested leaves

Kohlrabi – swollen stems

Cauliflower – undifferentiated arrested inflorescence meristems

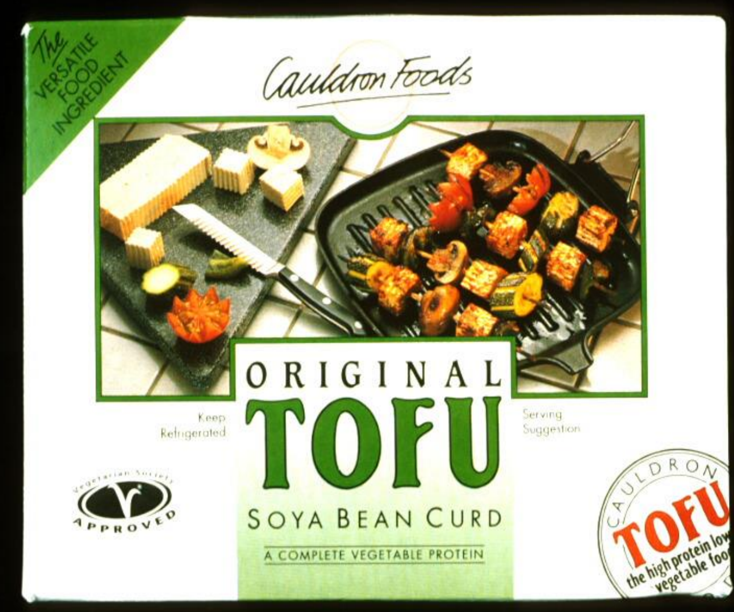
<u>Cauliflower</u> – closely packed *geometric* cluster of undifferentiated inflorescence meristems – an arrested meristem – maintained in a vegetative state. A mutation in the *Cal* gene is enough to convert *Arabidposis* into a plant that resembles a miniature cauliflower



Smith (1995) Current Biology

Pulses = Legumes

Edible, highly nutritious staple food crops with high crude protein contents



Pulses - Leguminosae

- Arachis – peanut - Andes
- Cajanus – pigeon pea - Asia
- Cicer – chickpea – Fertile Crescent
- Glycine – soy bean - China
- Lens – lentil – Fertile Crescent / Mediterranean
- Phaseolus – beans – Mesoamerica & Andes
- Pisum – pea – Fertile Crescent
- Vigna – mung bean – Africa

Domestication syndrome of legumes: indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination, nearly annual life history, reduced levels of seed alkaloids

Seeds of pulse crops from archaeological sites (left) and modern domesticated varieties (right)

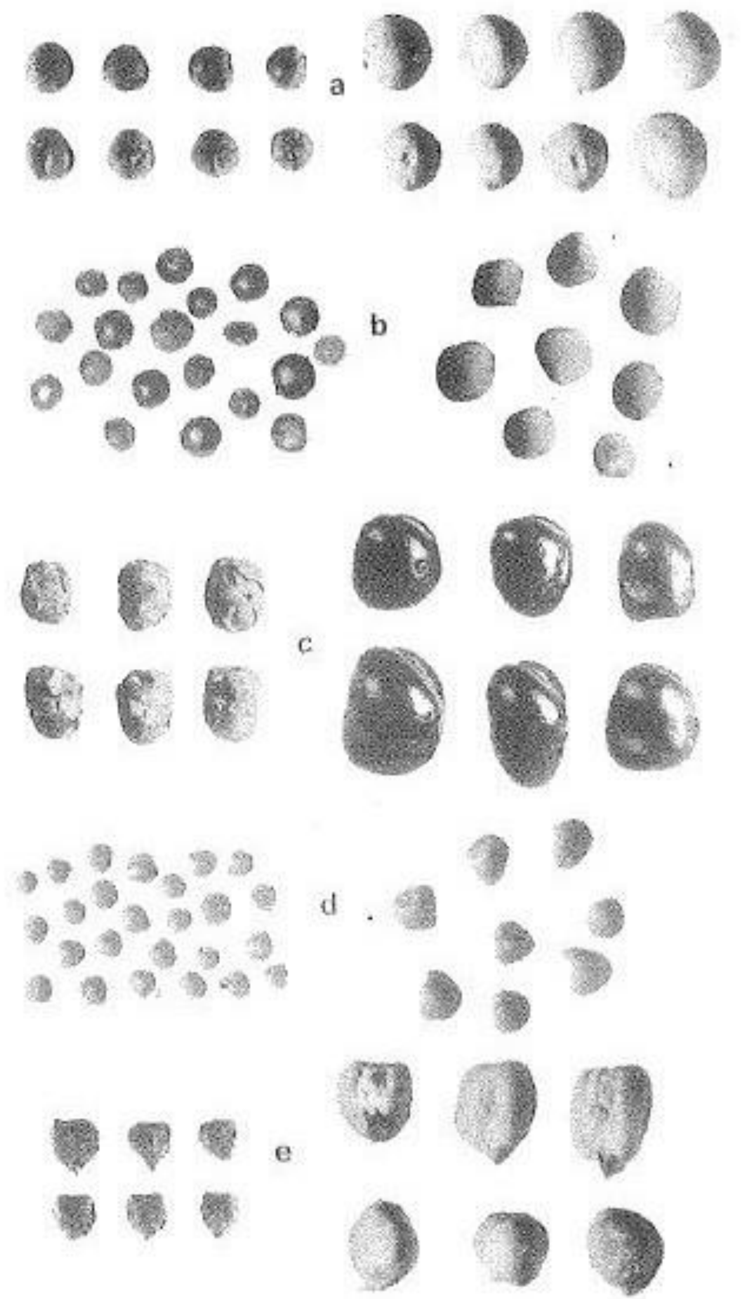
Pea - *Pisum sativum*

Lentil - *Lens culinaris*

Faba bean - *Vicia faba*

Bitter vetch – *Vicia ervilia*

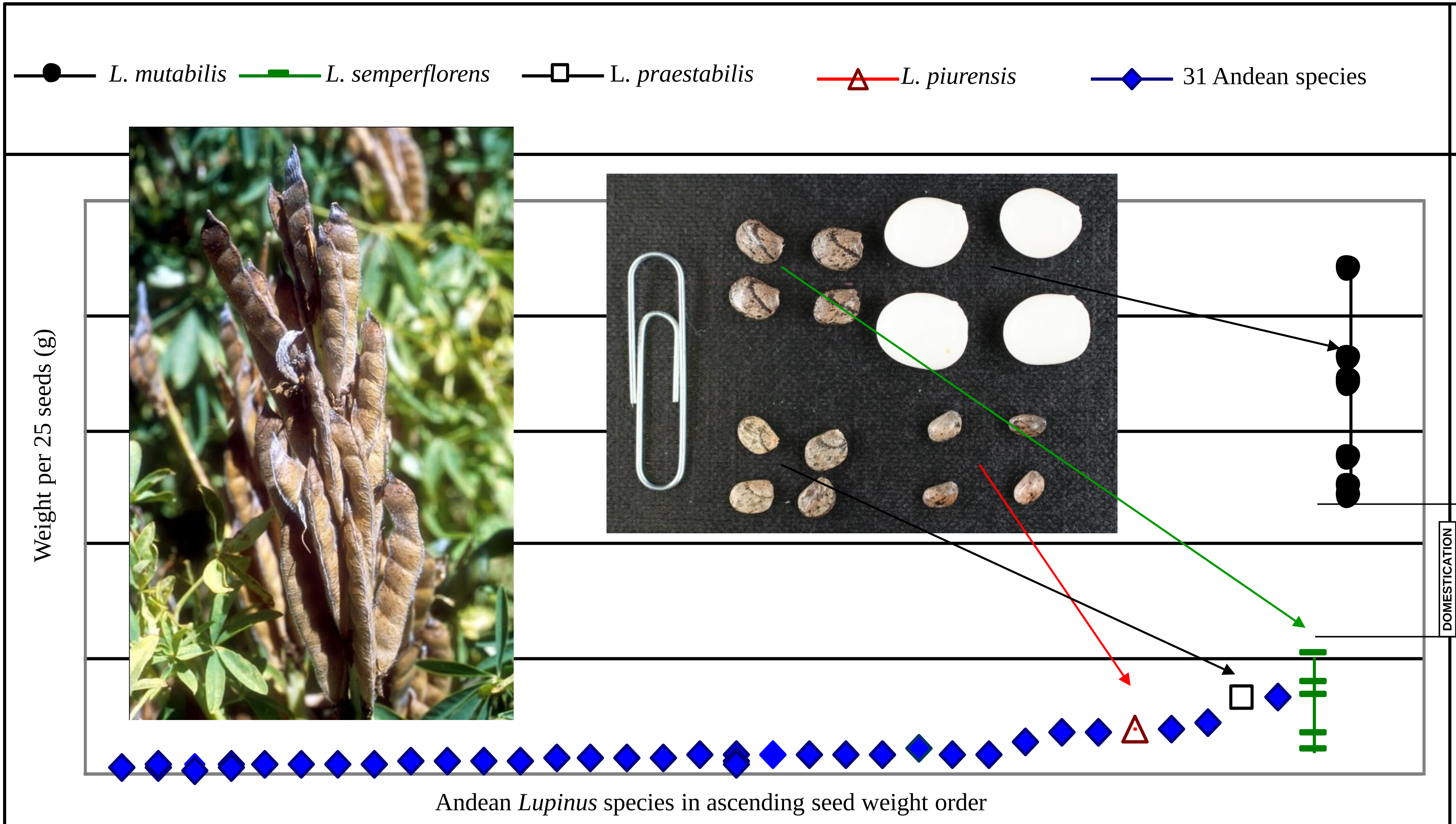
Chickpea - *Cicer arietinum*



Tarwi / Chocho
Lupinus mutabilis (Leguminosae)

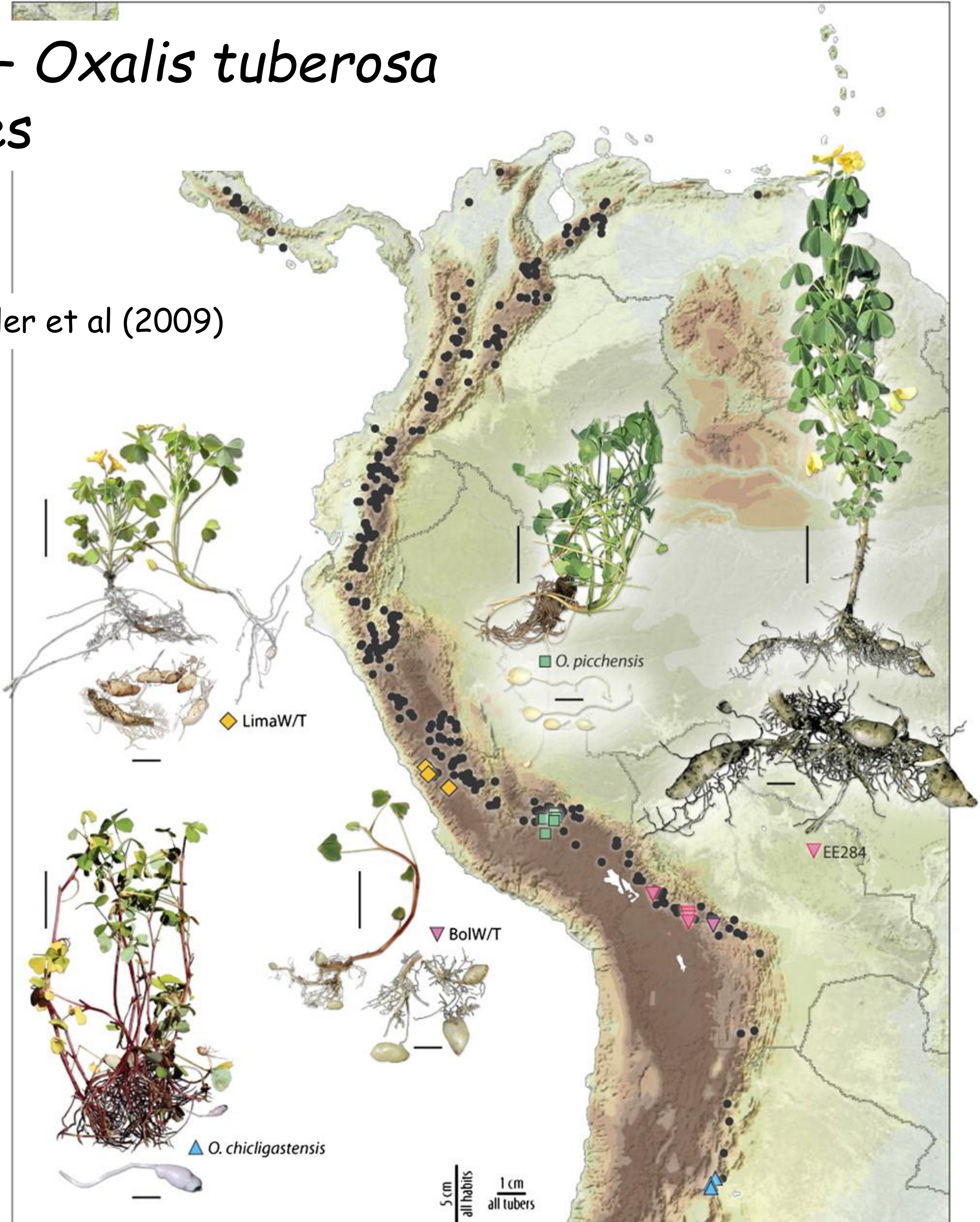
Tarwi - *Lupinus mutabilis* in the Andes

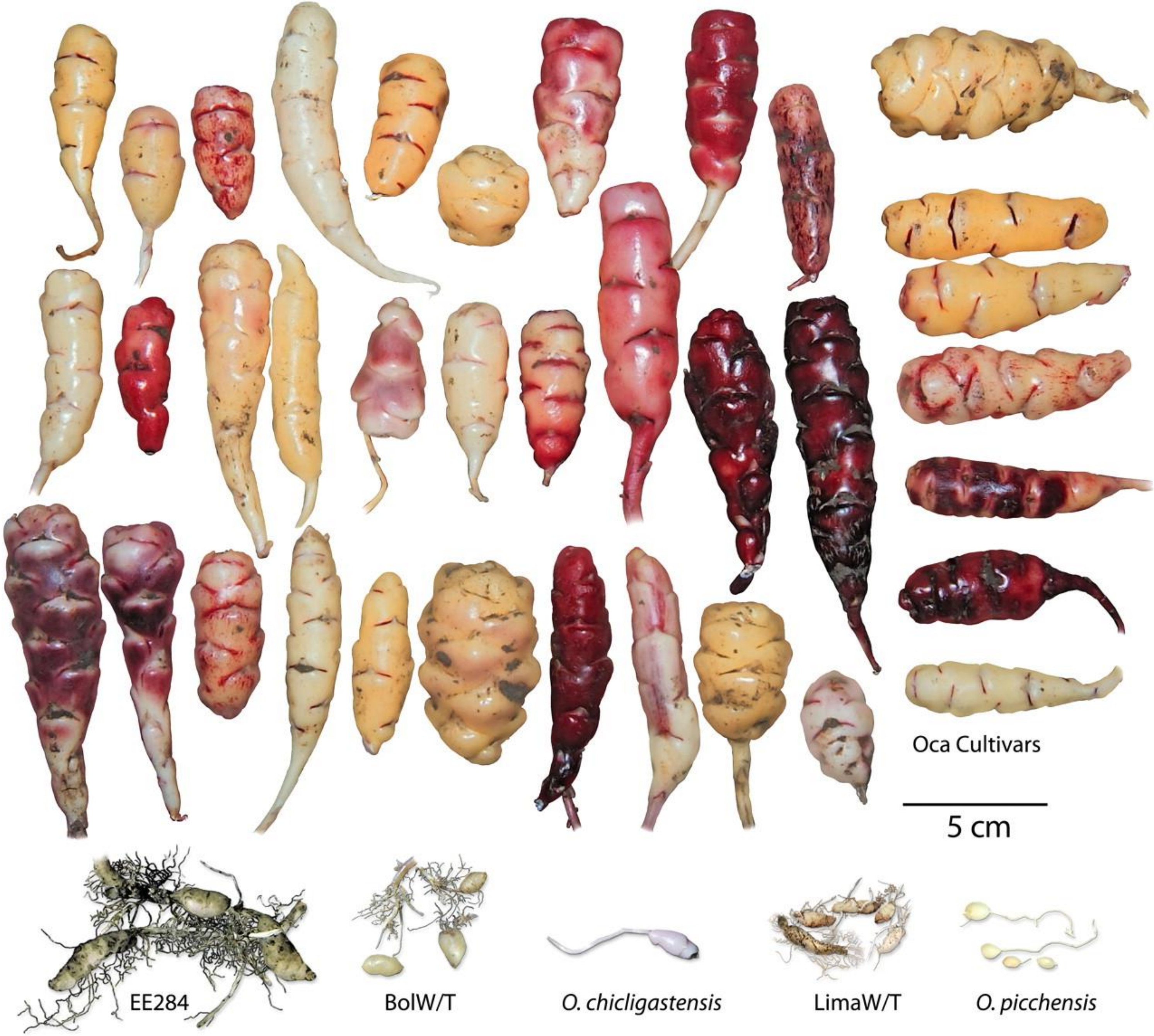
Exhibits typical legume domestication syndrome traits of indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination and growth, and nearly annual life history, but retains higher seed alkaloid levels than other lupins.



Oca – *Oxalis tuberosa* Andes

Emshwiller et al (2009)

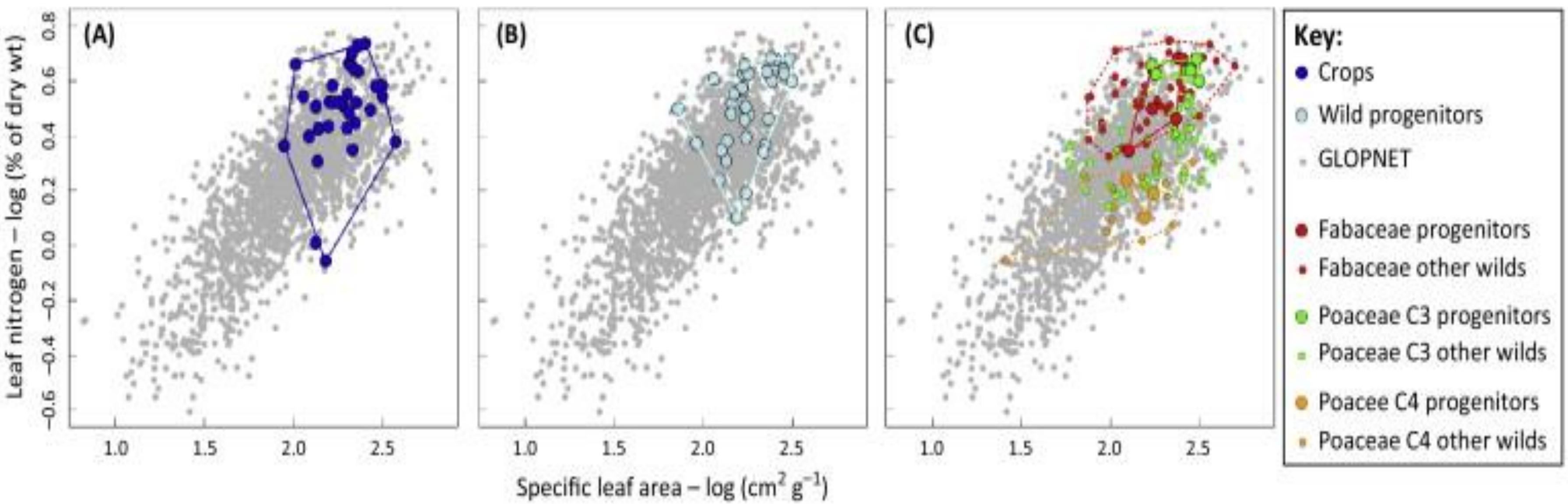




Emshwiller et al (2009)

Quantitative Plant Functional Traits

Specific Leaf Area and Leaf Nitrogen Content of Crops, their immediate wild relatives and wider botanical diversity – distinctive resource-use trategies of crop plants



TRENDS in Ecology & Evolution

Microbes digest domesticated crop leaf litter faster than litter from their corresponding wild relatives

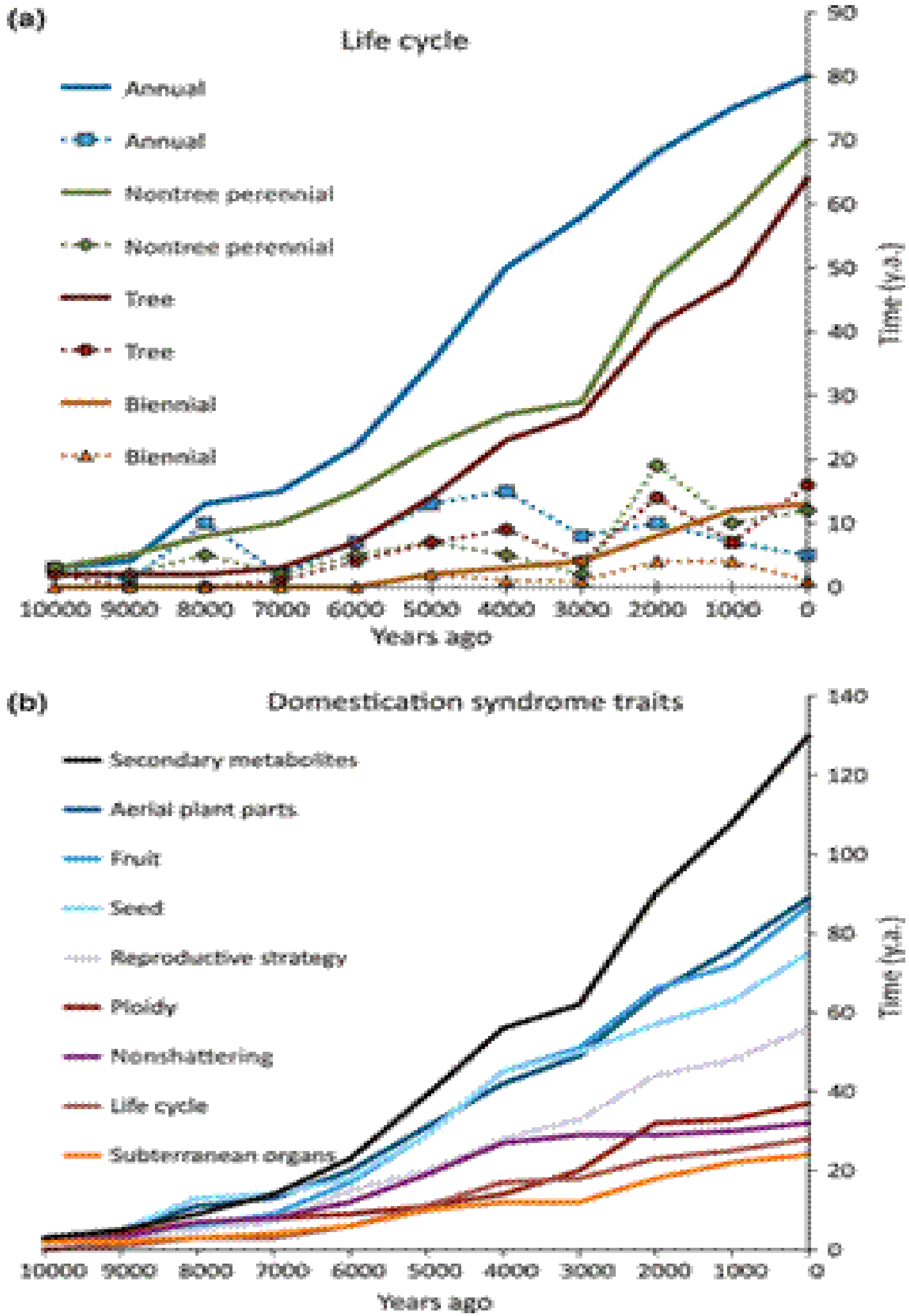
Milla et al. (2015)

Domestication syndrome of crop plants

203 domesticated crops

Average of 2.8 traits per crop

Meyer et al. (2012)



Definition of Domestication

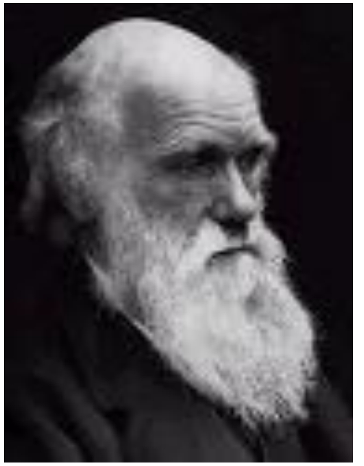
Plant Domestication = Genetic modification of a wild species to create a new form of plant altered to meet human needs

Fully Domesticated = For some, but not all crops, domesticated crops are completely dependent on humans and unable of propagating in the wild

True Domesticates

- For some crops domestication means they are rendered no longer capable of reproducing themselves naturally
- Maize, cauliflower and bananas are examples of highly modified crops that depend on man for their continued propagation and survival.
- The ultimate control of plants by humans, and an extreme manifestation of the sorts of changes that humans have brought about in plants.
- Other crops are less drastically modified and can revert to the wild and become self-propagating weeds.

Charles Darwin's 1883 studies of variation and selection - *The Variation of Animals and Plants under Domestication.*

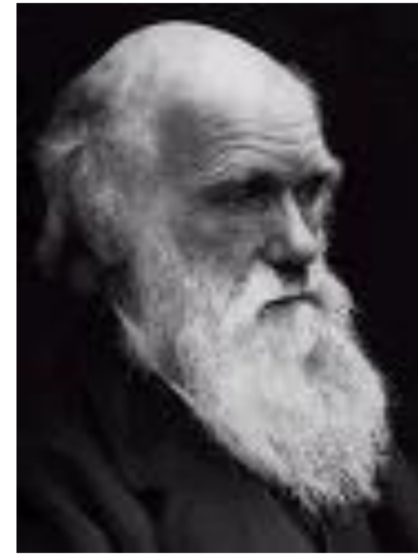


Darwin used plant domestication as a proxy for evolution under selection

'I often asked myself how these many preculiar animals and plants had been produced: the simplest answer seemed to be that the inhabitants of the several islands had descended from each other, under on-going modification in the course of their descent...... But it long remained to me an inexplicable problem how the necessary degree of modification could have been affected, and it would have remained thus for ever, had I not studied domestic productions and thus acquired a just idea of the power of selection.' (Orign of Species, 1875)

Darwin's Pigeons

'While man does not cause variability, he can select, preserve and accumulate the variations provide by nature in almost any way he chooses, and thus he can certainly produce a great result'. Charles Darwin's 1868 studies of variation and selection - *The Variation of Animals and Plants under Domestication*



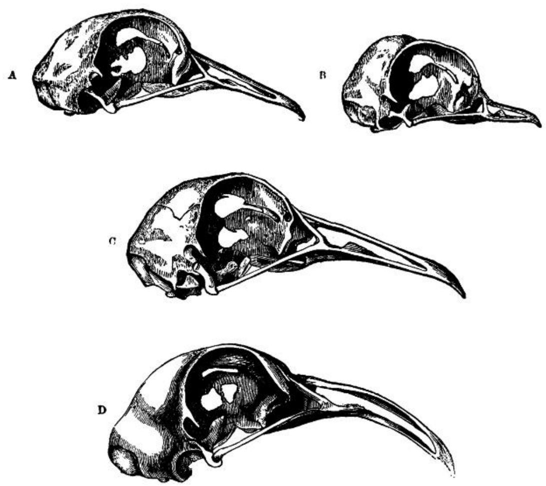
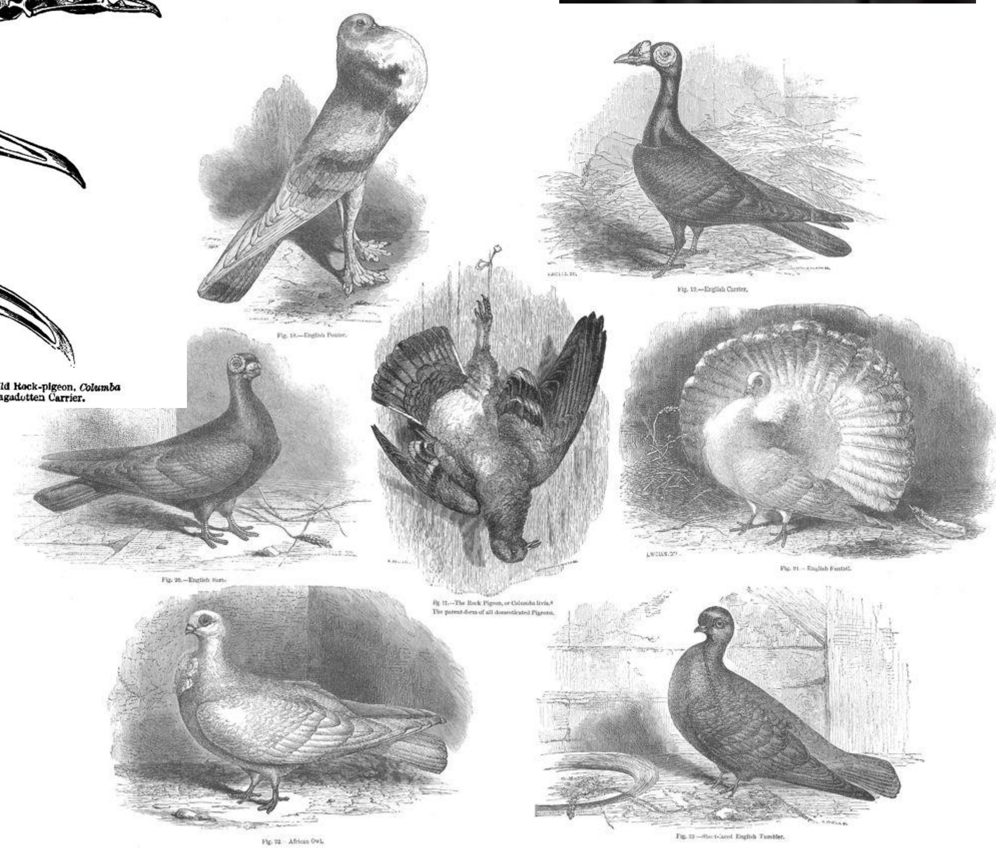
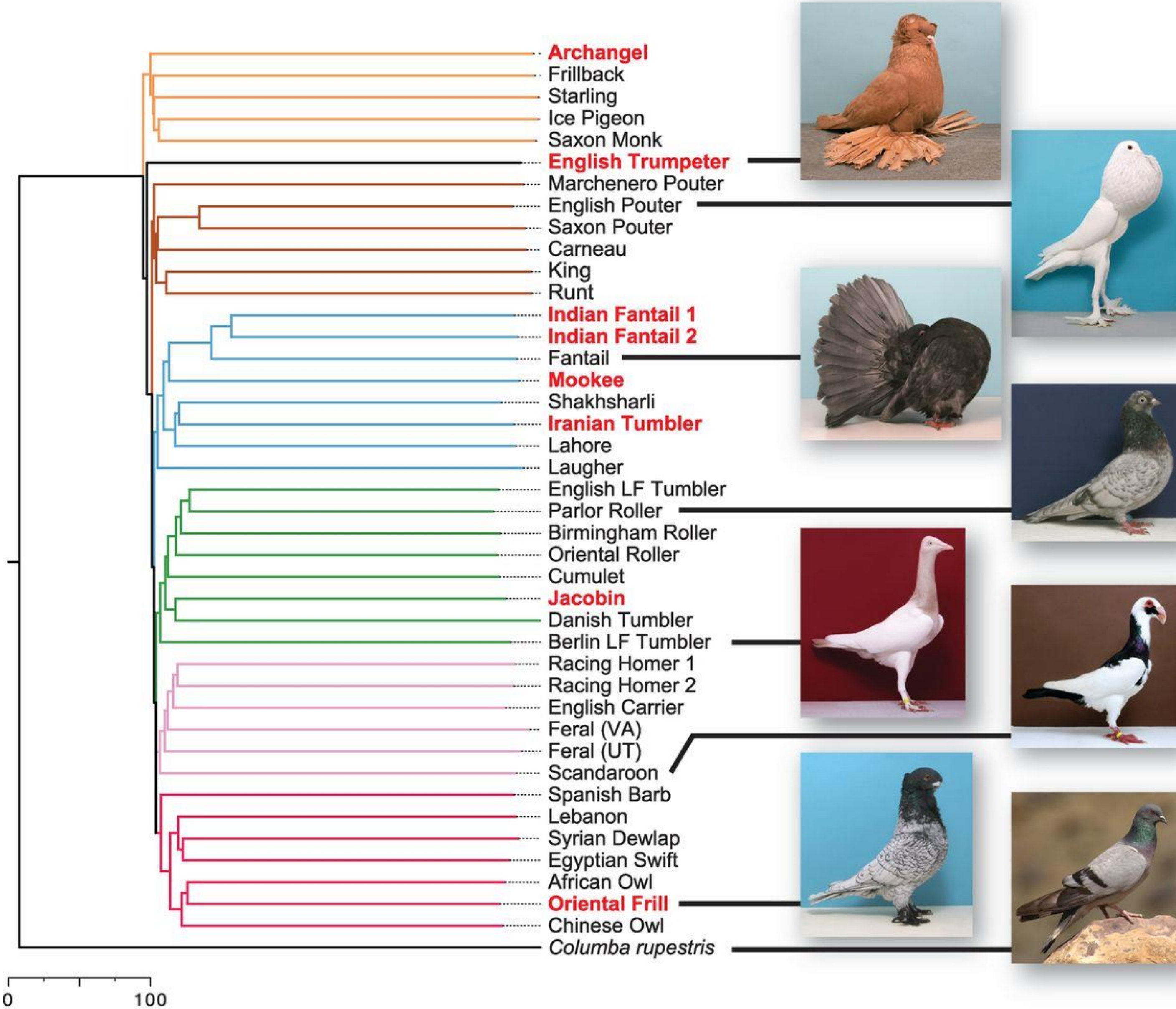


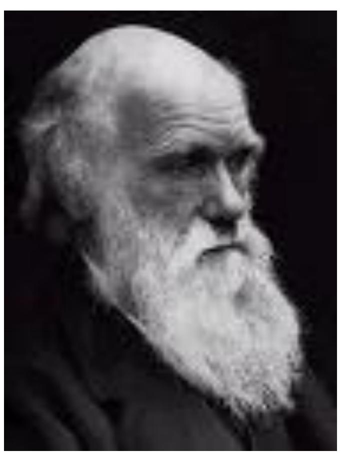
Fig. 24.—Skulls of Pigeons viewed laterally, of natural size. A. Wild Rock-pigeon. *Columba livia.* B. Short-faced Tumbler. C. English Carrier. D. Bagadotten Carrier.



Domestication of Pigeons

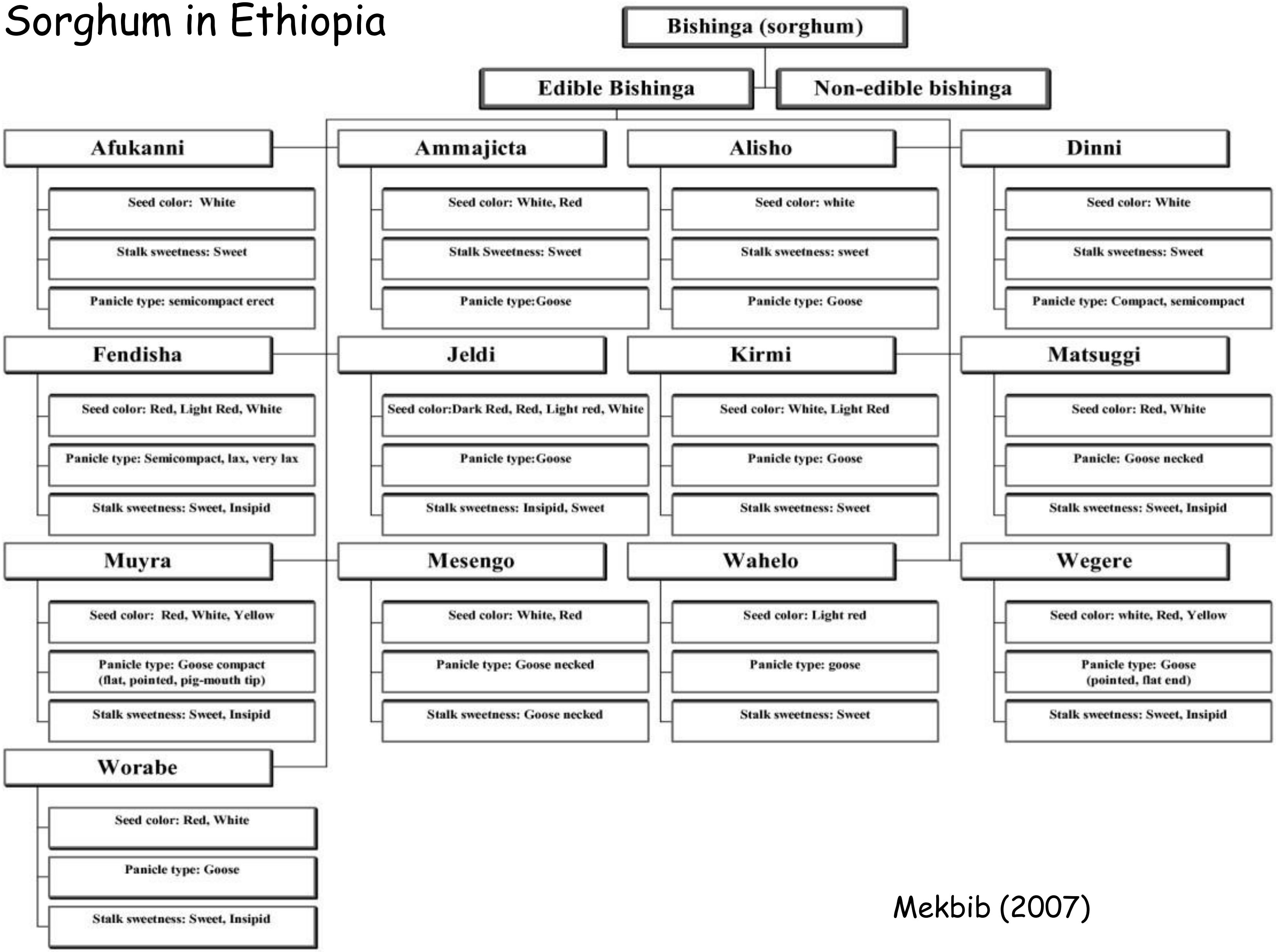


Shapiro et al. (2013); Shapiro & Domyan (2013)



Selection
- Intentional (methodical)
- Unintentional (unconscious)

Infraspecific folk taxonomy of Sorghum in Ethiopia



Mekbib (2007)

How were these changes brought about?

People were 'messing around with plants for a very long time. They had very sophisticated plant knowledge systems derived from centuries of foraging – Neolithic genetic tinkering that involved a series of steps:

- manipulation of natural vegetation
- protection of favoured species and prized individuals, culling of others
- accidental sowing – middens, camp followers
- pre-domestication cultivation, backyards, dump-heaps
- unwitting and deliberate selection
- initial domestication followed by a long period of low-level food production with continued hunting and gathering
- cultivation that included a mix of wild and domesticated species with wild varieties only gradually replaced by domesticated species
- wild and domesticated plants frequently intermixed with opportunities for geneflow
- initial domesticates still not like modern ones
- crops added sequentially over several millennia, not all at once.

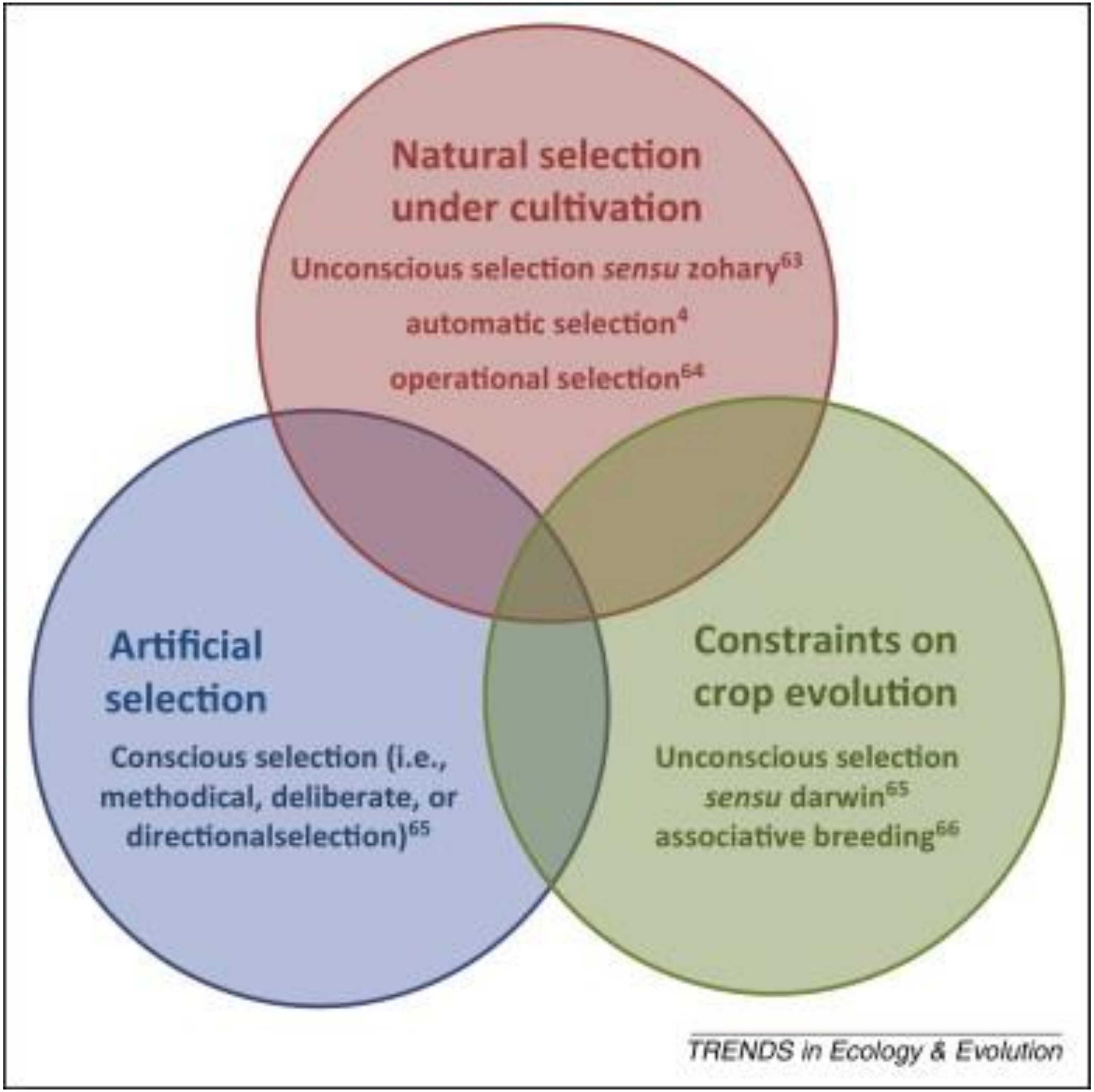
Selection

Natural selection

Artificial selection

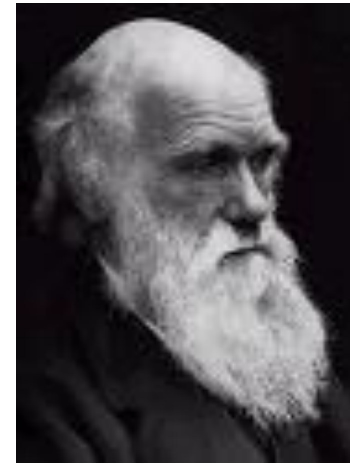
Conscious (methodical,
deliberate, directional)
e.g. colour, palatability

Unconscious (unintentional, automatic)
by-product of planting, harvesting &
cultivation conditions



Milla et al. (2015)

Darwin & 19th Century Gooseberry Fairs



'This increase is probably due in part to improved methods of cultivation...., but no doubt is in the main part due to continued selection of seedlings which have been found to be more capable of yielding such extraordinary fruit'

Ribes uva-crispa

Wild 7g $\xrightarrow{10X}$ 1852 70g

Unconscious Selection

Crop traits associated with inadvertent selection due to broadcasting and harvesting of grain crops
– "*automatic*" changes that occurred because they increase the likelihood of the seed of a genotype being collected and planted (Harlan et al. 1973).

Selection Pressure	Response	Adaptation
Harvesting spikelets	Increase in % seed recovered	Non-shattering
	Increase in seed production	> determinate growth Increased seed set Larger inflorescence > inflorescences
Seedling competition	Increase in seedling vigour	Increased seed size
	> rapid germination	Loss of or reduction in germination inhibitors Reduction in glumes or other inhibitors

Domestication as an "entangled process of behavioural and genetic innovation, response, and further response" (Fuller et al., 2010)

Plant Domestication Traits (in seed crops)

Selected by harvesting,
With subsequent resowing

Or

Selected by highly disturbed environments (tilled), through seedling competition

Also, with subsequent harvest and resowing

=unconscious selection

Gordon Hillman's experimental domestication: (Hillman and Davies 1990)

No domestication

Domestication

Fast estimates: 20-100 years
Assuming strong selection with sickles
[But this does NOT fit the archaeological evidence anymore!]

The Role of Sickles in Rachis Selection

Sickles pre-date domestication (?cereal exploitation) in both northern and southern Levant. ??If used for cereals?

Sickles post-date domestication episode of rice in the Yangtze River c. 3300 cal. BC

Plant domestication through an ecological lens

Unconscious Selection via altered ecological processes.

Humans have modulated almost every ecological process occurring in the habitats where populations of early domesticates thrived.

These changes included
- supplying nutrients and water
- protecting crops from herbivory and weed competition
- regularly harvesting biomass

Thereby affecting
- soil fertility
- mode, frequency and intensity of disturbances
- presence, abundance, and dynamics of organisms other than crops.

Milla et al. (2015)

Genes and Domestication

DNA analysis and manipulation combined with crop genome research (genome maps, QTL analysis, fine resolution gene mapping, genome sequencing, candidate gene analysis, gene cloning) is revolutionising our understanding the underlying genetic control of phenotypic traits.

Cloning and evolutionary analysis of domestication-related genes to unravel the molecular basis of domestication-related changes – such as loss of seed shattering, increase in organ size, branchy to erect habit.

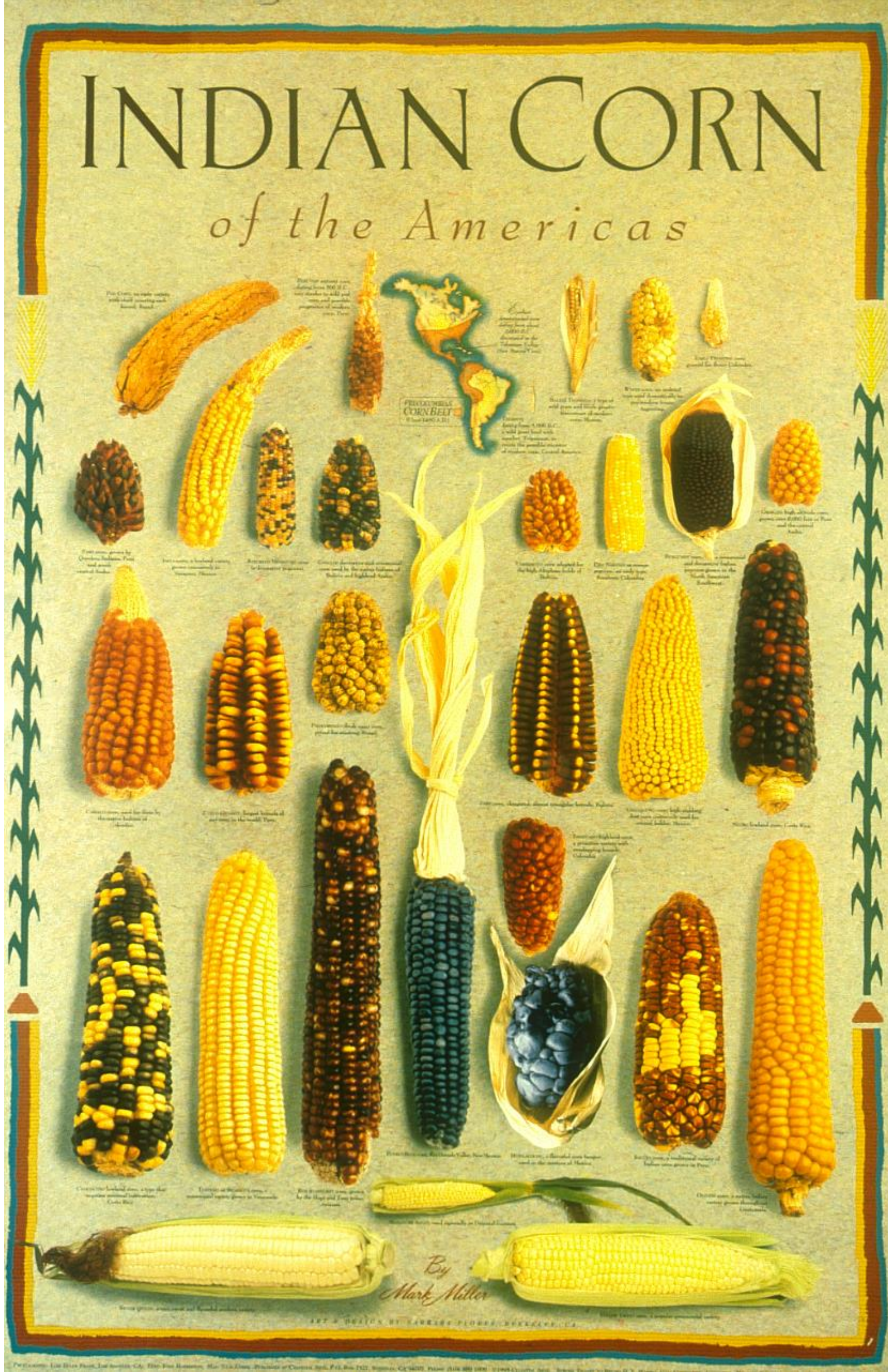
Relevant also to transferring genes between species and how to control the expression of the genes once they are transferred.

Genes & Domestication – Maize *sugary1*

- One gene one enzyme hypothesis – each gene controls a single enzyme, governing a single step in a metabolic pathway

- *Sugary1* in maize is one of the genes that produces sweet corn, encodes an enzyme converting sugar to the amylopectin fraction of starch. If this gene is inactivated, sugar accumulates in the kernels.

- In N American sweet corn, a single nucleotide substitution in the coding region of the gene causes a single amino acid change that inactivates the enzyme



Genes & Domestication – Maize *tb1*

Wang et al (1999)
Doebley (2004)

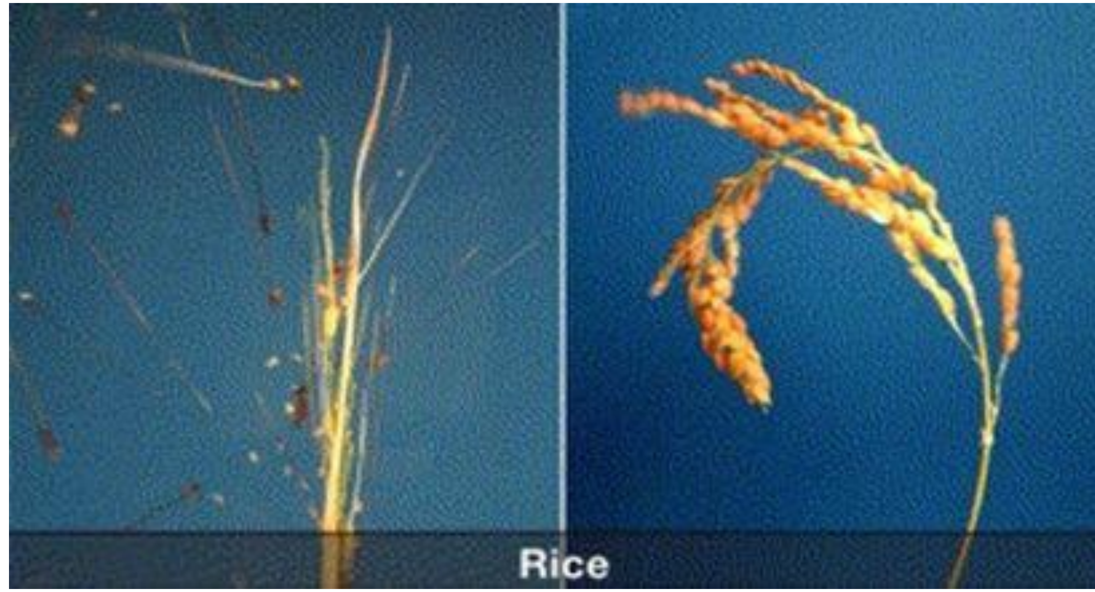
- *tb1* is a key domestication gene in maize
- It encodes a TCP protein (TCPs are growth regulators)
- It is expressed in the axillary meristems of maize but not teosinte
- Tb1 mutant has pleiotropic effects on apical dominance, length of lateral branches and development of spikelets
- Presence of maize *tb1* gene in teosinte suppresses outgrowth of axillary branches
- Lack of any fixed amino acid differences between maize and teosinte in the *tb1* protein
- Differences in tb1 expression patterns between maize and teosinte indicate that human selection was targetted at regulatory differences that produced a higher level or tb1 message in maize.
- Identical *tb1* genes in different maize accessions support single origin

Genes & Domestication – Rice shattering sh4

Sh4 is the key shattering gene that distinguishes cultivated from wild rice

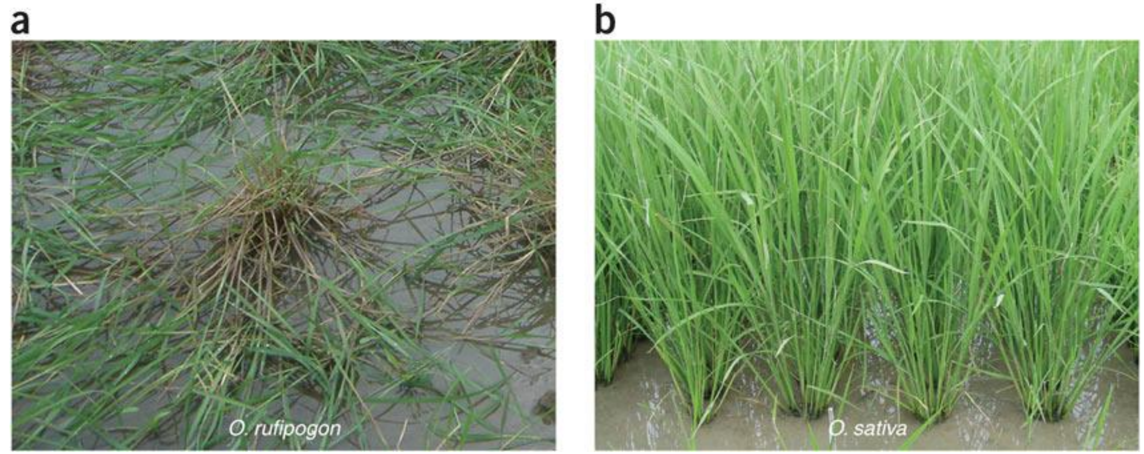
Sh4 is a transcription regulator responsible for reduced shattering via activation or not of the abscision process.

A single amino acid substitution differentiates the shattering and non-shattering alleles



Li et al (2006)

Genes & Domestication – Rice growth habit *prog1* gene



Transition from prostrate to erect growth habit critical in rice domestication to generate improved plant architecture and increased grain yield via increased plant density and enhanced photosynthetic efficiency

Prostrate growth is controlled by a semi-dominnat gene prostrate growth (*prog1*)

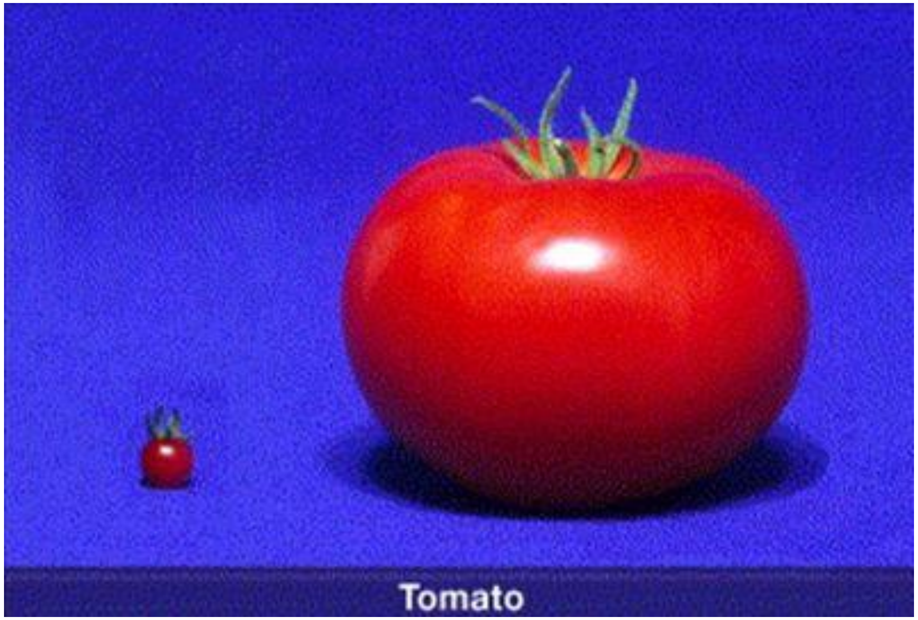
Prog1 variants in domesticated rice disrupt *prog1* function and inactivate *prog1* expression

All domesticated cultivars tested carry identical mutations in the *prog1* coding region (15SNPs and 6 indels invoking 20 amino acid changes)

Mutations in a single gene can alter and improve plant architecture and yield. This potentially the product of artificial selection against undesirable prostrate architecture

Jin et al (2008); Tan et al. (2008)

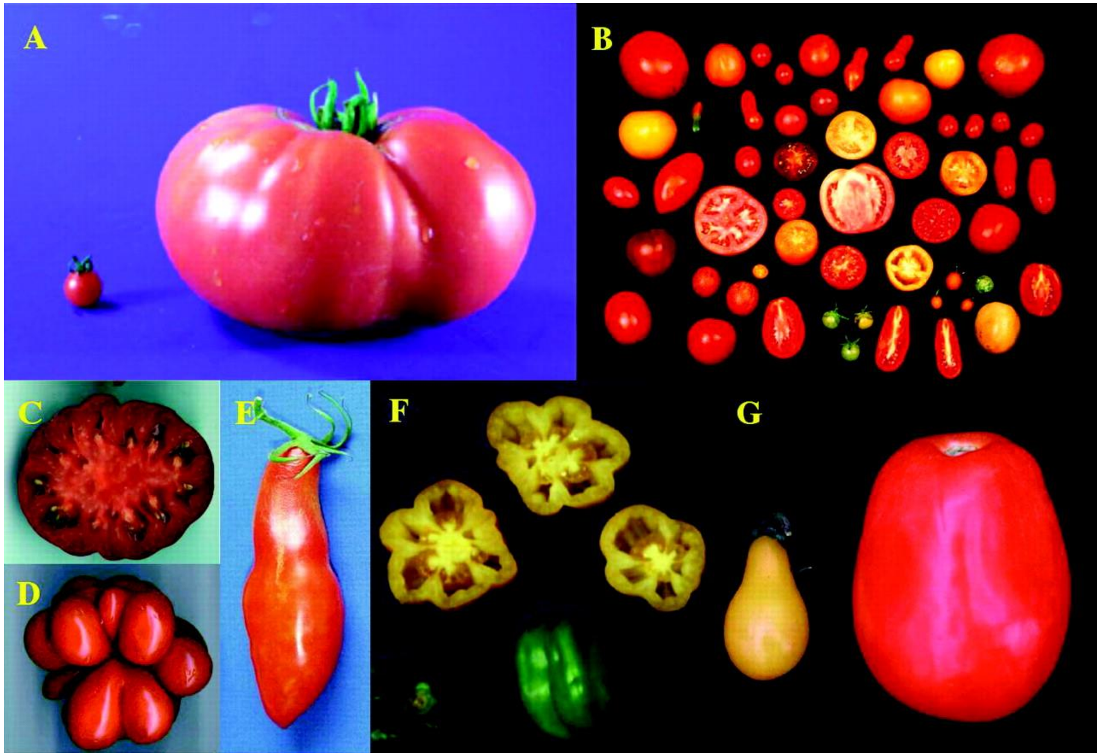
Genes & Domestication – Tomato Fruitweight 2.2



Fruitweight 2.2 (*fw2.2*) identified as a large effect QTL controlling 30% of the difference in fruit mass between wild and cultivated tomato

No differences in protein sequence between the large and small-fruited alleles

Supports the model that changes in gene regulation underlie the evolution of tomato fruit size, as controlled by *fw2.2*



Tanksley (2004)

Genes & Domestication – Conclusions

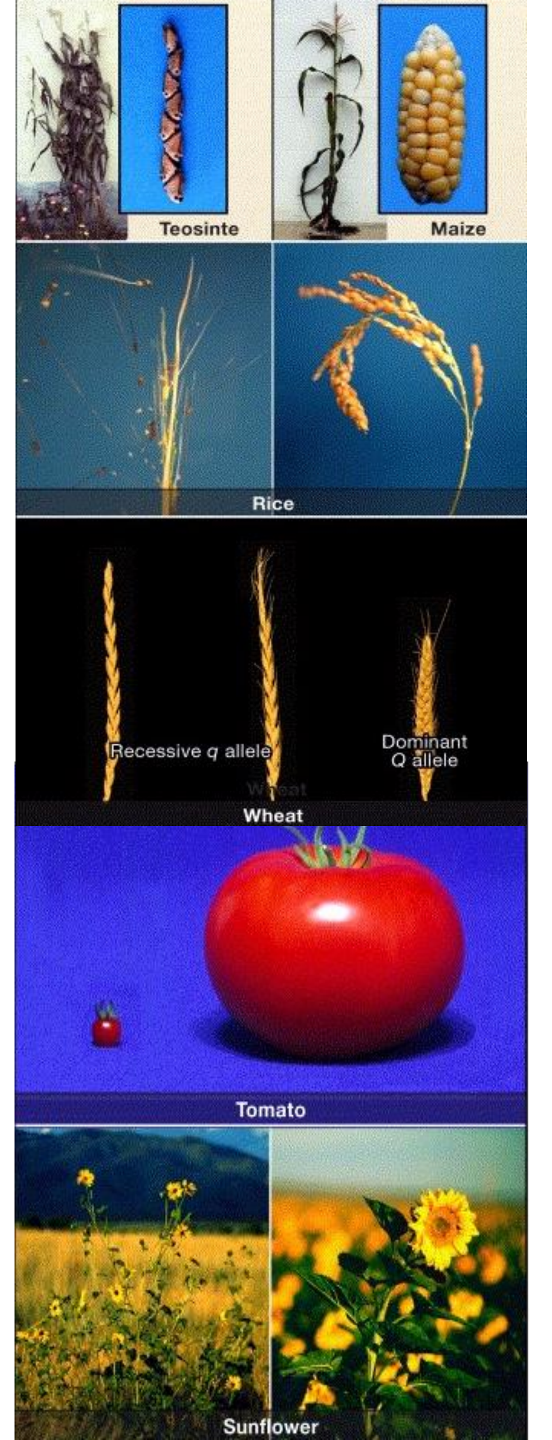
Role of human selection has been modification rather than elimination of gene function across diverse developmental pathways, reflecting the short time span of domestication.

High speed evolution represented by crop domestication the result of strong selection pressures on pre-existing variation.

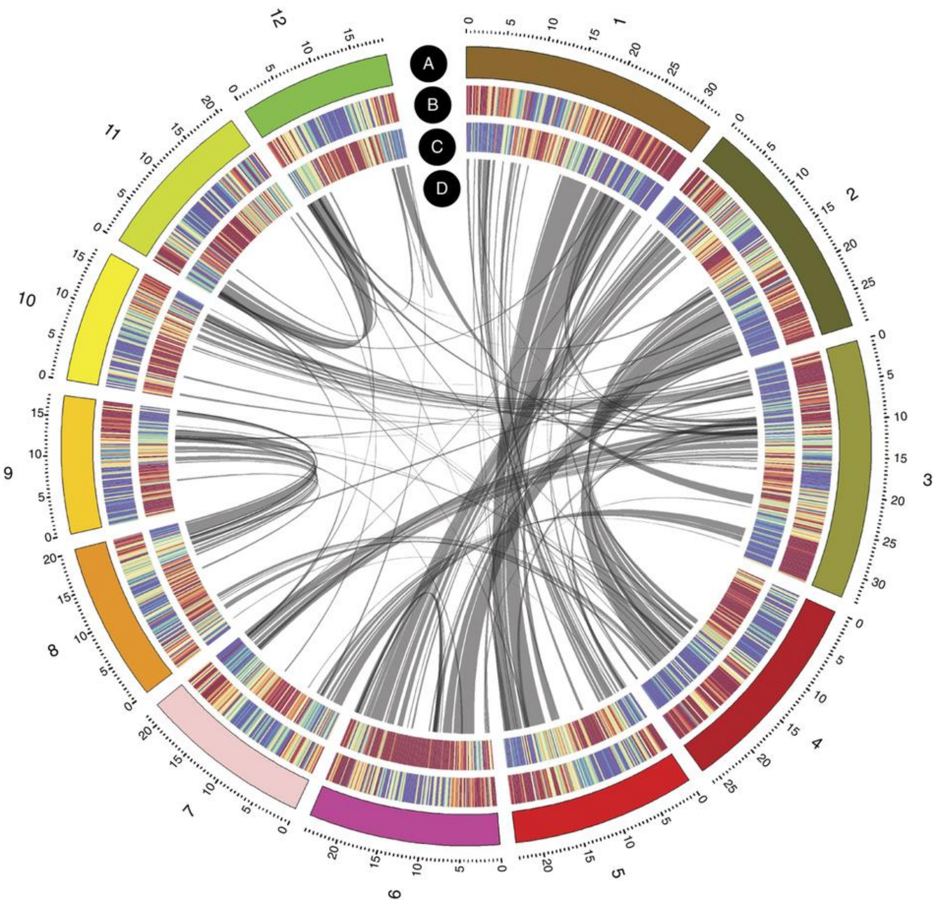
Up and down regulating of transcription factors has played a central role in domestication, as found more widely in plant developmental genetics.

Genes controlling cell division (like fw2.2) also likely to be over represented among major domestication genes.

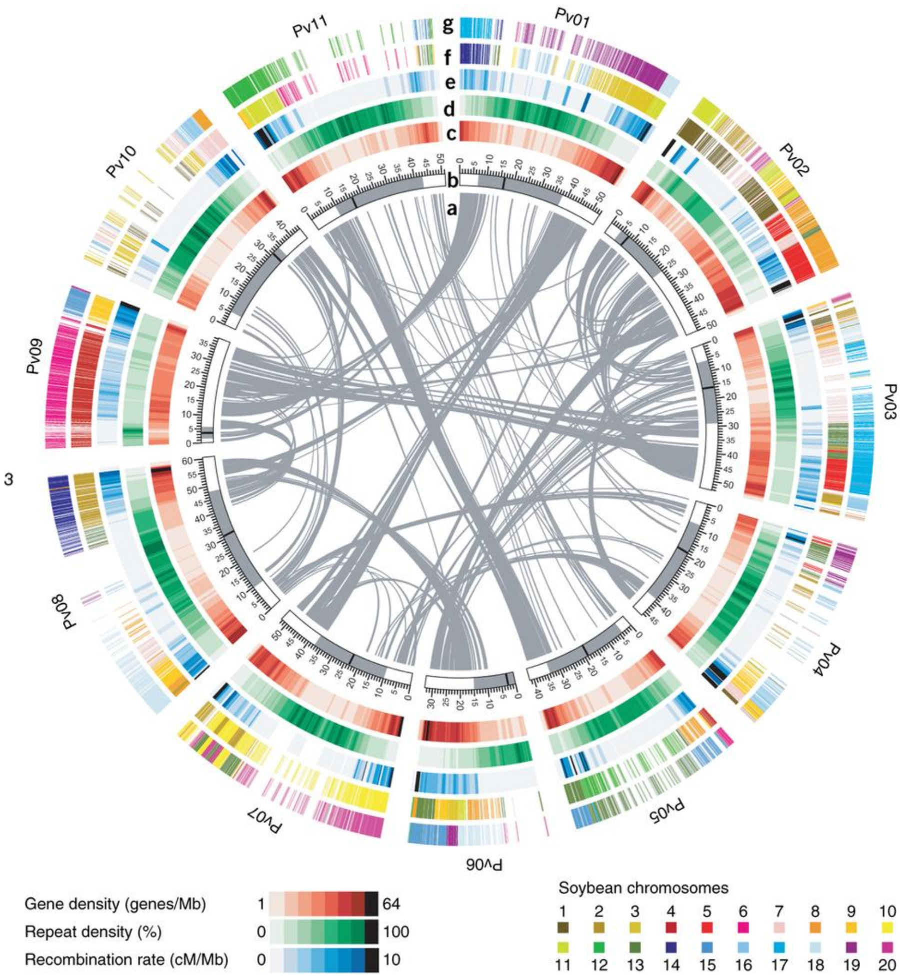
Changes often involve just single or a few amino acids



Comparative genomics of crop domestication



Asian and African rice genomes



Common bean & soya bean genomes
Andean and Mexican domesticated bean genomes

Comparative genomics of crop domestication

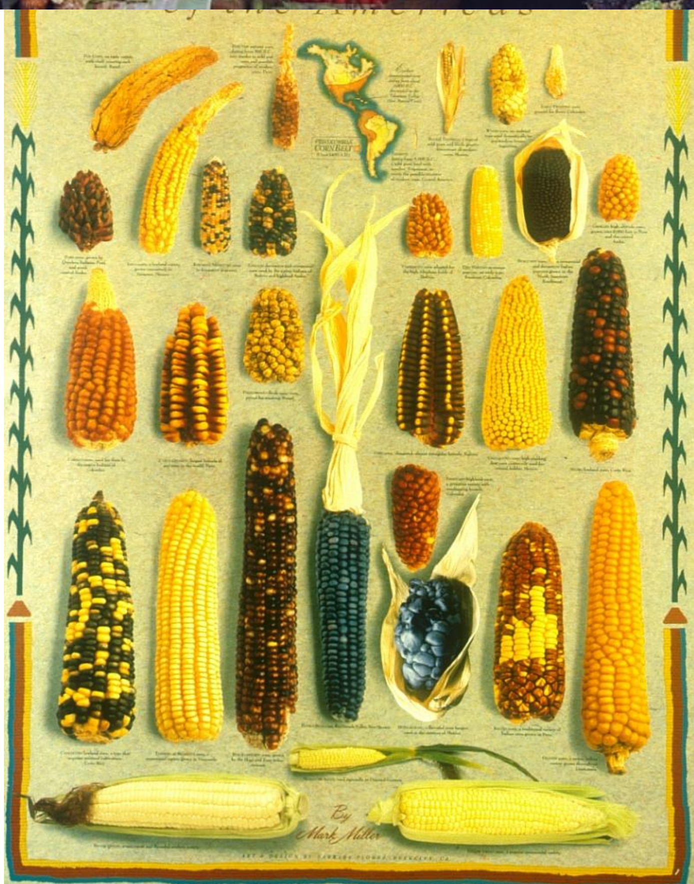
Compare gene content and conservation across genomes, e.g. 91% of Phaseolus bean genes are found in the soya bean genome.

Compare levels of genetic diversity, genetic bottlenecks and divergence, e.g. the Andean domesticated bean genome shows 4.5 times less sequence divergence than the Mesoamerican domesticated bean.

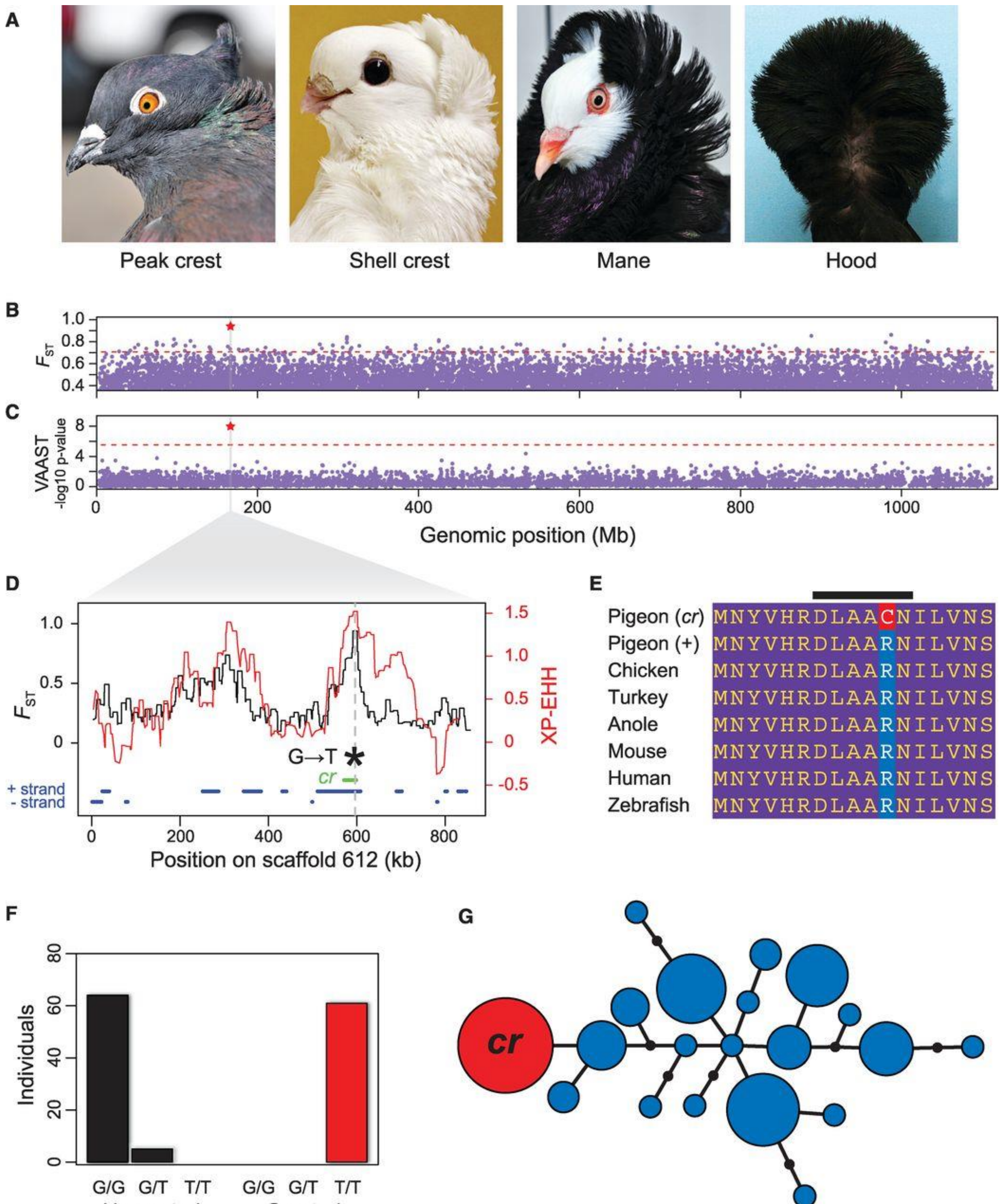
How many genes were involved in domestication, and to what extent are these shared across crops?

- the *shattering1* gene (*sh1*) which controls seed shattering in sorghum, was under parallel during the domestication of sorghum, rice and maize.
- three shattering-related genes in Asian rice, *Oryza sativa* also show changes in the domestciated African rice, *Oryza glaberrima*, but the actual changes at the DNA sequence level are different
- 59 candidate domestication genes shared between Mexican and Andean bean domesticates.

Wang et al. (2014)



Selection after domestication / crop diversification



The same mutation in the Ephrin receptor B2 gene, *EphB2*, controls the crest phenotype, an important trait in mate selection in many avian species

Shapiro et al. (2013)

BIO 235 – Plants & People – Evolution and Domestication of Crops

Course Assignment – What do we eat today?

Compile a complete list of all the plants and plant parts that you eat, drink or otherwise consume during the course of one week, i.e. over seven consecutive days. Include everything – breakfast, lunch, dinner, snacks, inhalations and ***all*** major and minor ingredients. Leave **<u>nothing</u>** out.

Annotate your list, as far as you can, in a table showing: common name / scientific name / plant family / part of the plant (seed, fruit, root, stem, leaves, etc) / region of origin (i.e. where does the plant grow naturally) / and place of production (i.e. where was the plant that supplied your food grown). For example: potato / *Solanum tuberosum* / Solanaceae / stem tuber / Andes / Switzerland. Only record each plant once on your list, even if you eat it several times.

Make an estimate of your 'food kilometers' for each plant product and for the week in total, i.e. how far in total did all the elements of your weekly food travel to reach you?

Analyse and summarize in **<u>a few pages</u>** any interesting features about the taxonomic diversity and geographic distribution of your food intake, and what it means in relation to how we use plants, and how that is changing through time. **<u>Step back and think!</u>**

Submit a **<u>hard (paper) copy</u>** of your assignment to me by 6th **<u>November</u>**, i.e. 5 weeks from today.
The assignment is worth 50% of the overall BIO235 assessment.

<u>For next week</u>:

A small snack of a few dozen wild almonds contain enough cyanide to kill humans. How did humans turn the almond into an important nut crop?