BIO 235
Plants & People
Evolution &
Domestication
of Crops

Lecture 8
Revolution or Evolution? The tempo of domestication and the evolution of agriculture

- domestication and the rapid evolution of plant genomes
- how fast was domestication?
- how quickly did agriculture evolve?
- selection coefficients under domestication
- de-domestication
- geotemporal patterns of crop origins and the development of agricultural societies
- the Fertile Crescent; Mesoamerica; China

Colin Hughes
Institute of Systematic Botany
colin.hughes@systbot.uzh.ch

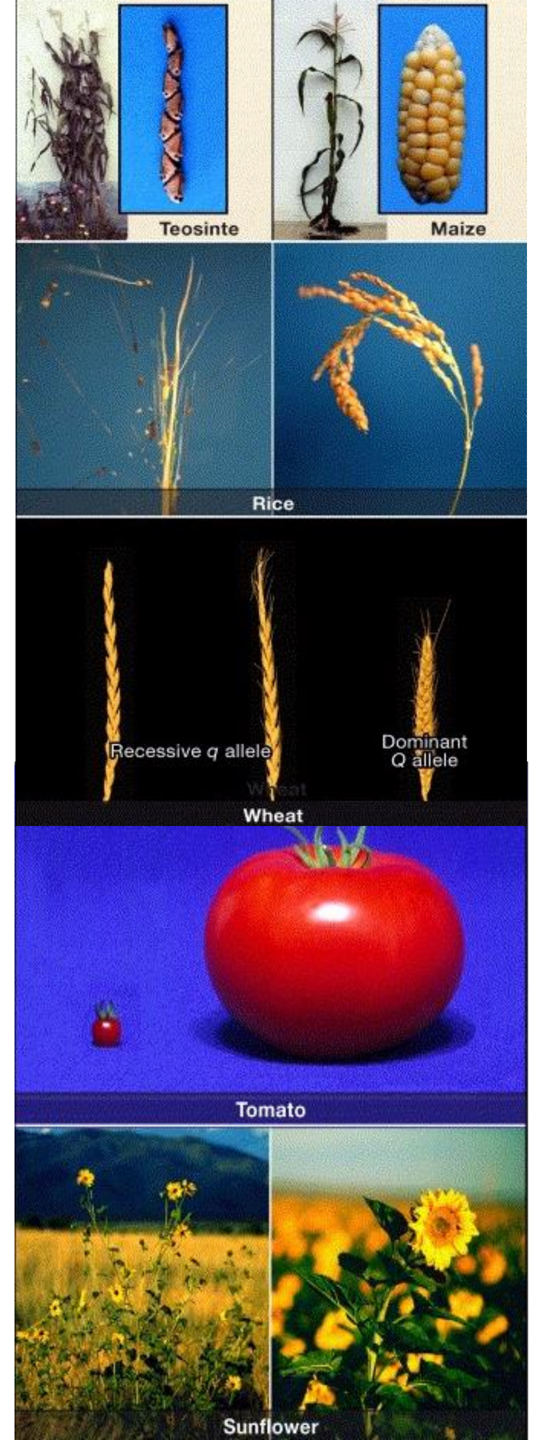
Genes & Domestication – Conclusions

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 regulation of transcription factors has played a central role in domestication, as found more widely in plant developmental genetics.

Changes often involve just single or a few amino acids



Revolution vs Evolution

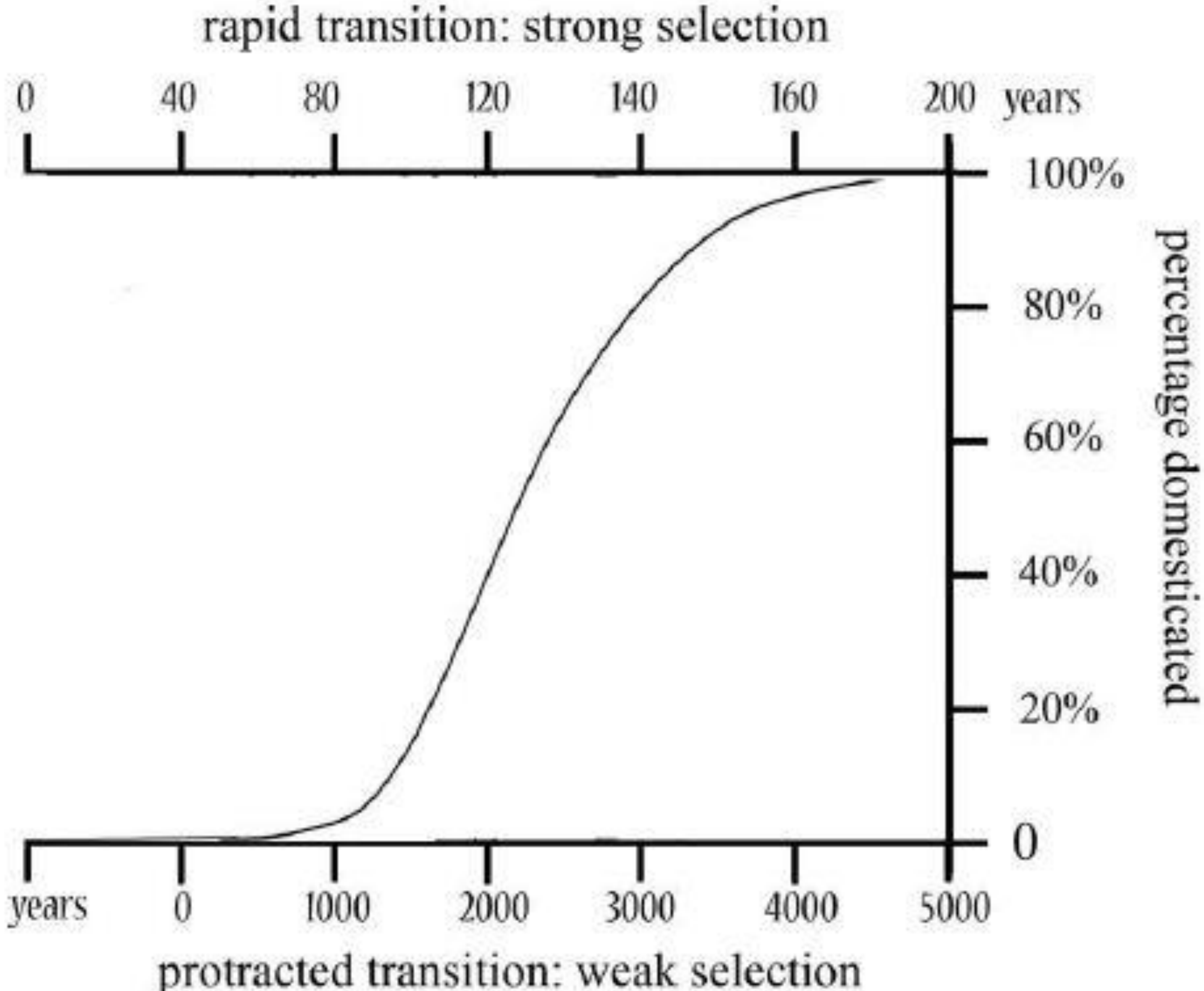
<u>Idea of rapid species evolution in domesticated taxa</u>

- cultivation exerts selection pressures for recurrent adaptations
- presumption that selection under domestication is strong
- rapid or very rapid evolution of cultivated species
- timespan of domestication of a few 100 years

<u>Domestication as a form of animal / plant coevolution</u>

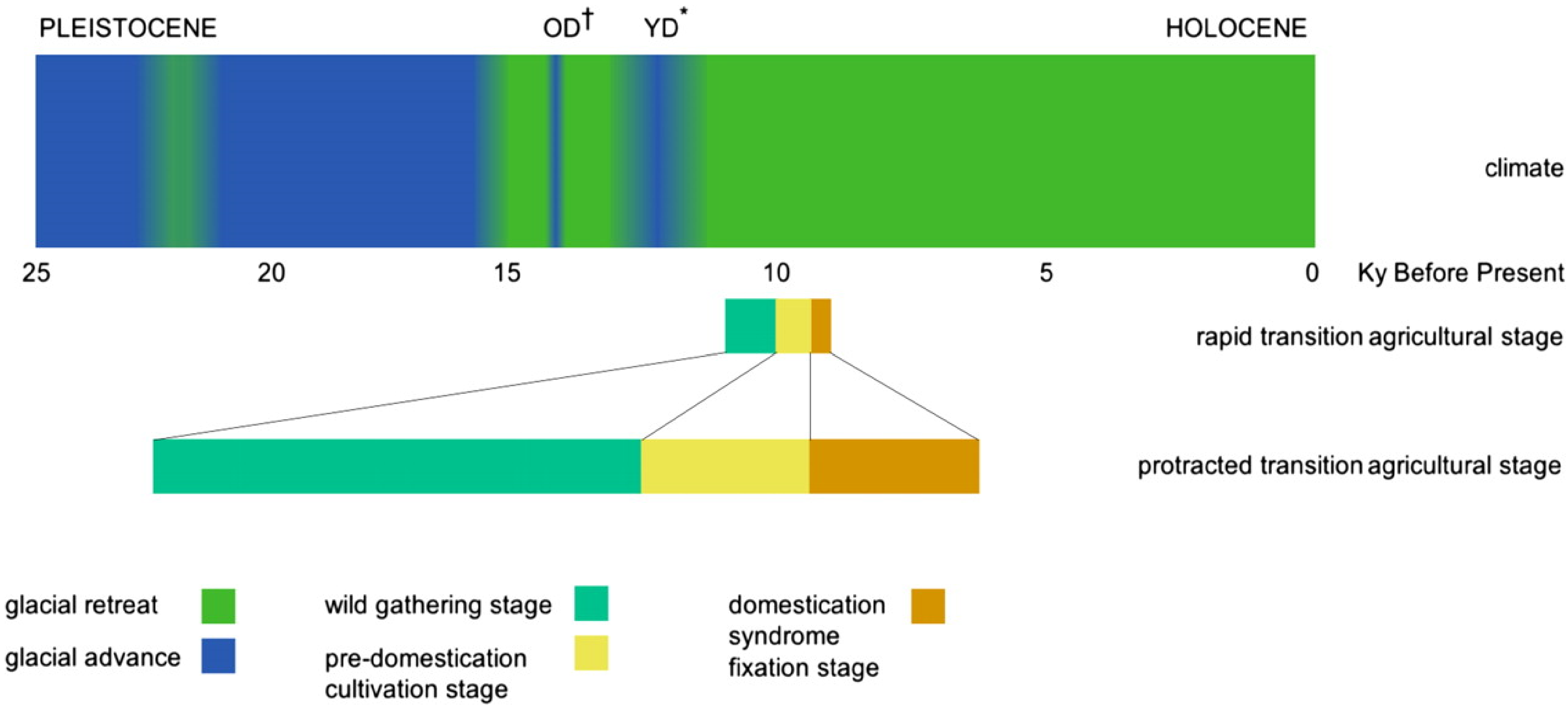
- conceptually similar to evolutionary diversification driven by other multispecies interactions
- similar levels and patterns of evolutionary change to those observed in wild species
- timespan of domestication several 1000 years

How fast was crop domestication?
Neolithic revolution or gradual evolution?

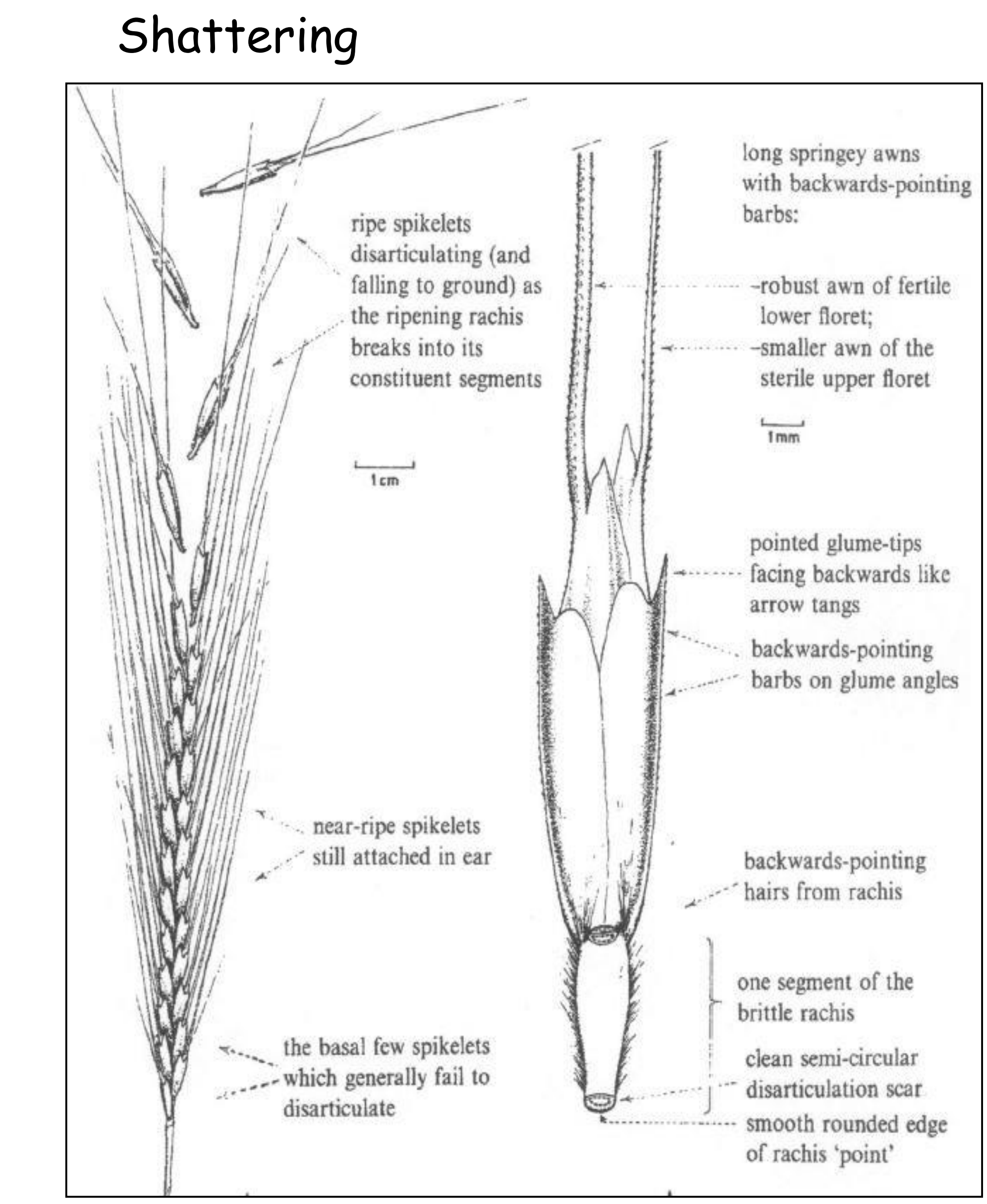


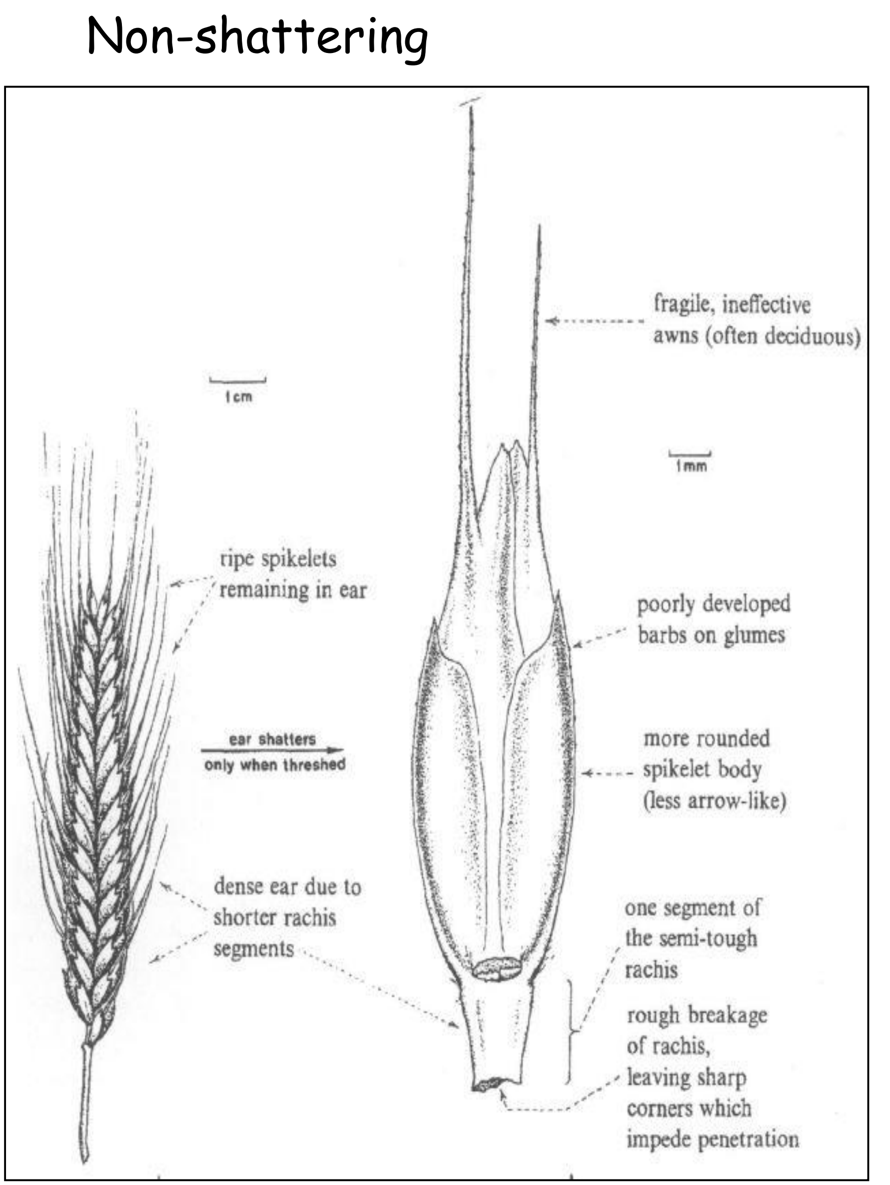
Fuller et al. (2010)

How fast was crop domestication?
Neolithic revolution or gradual evolution?



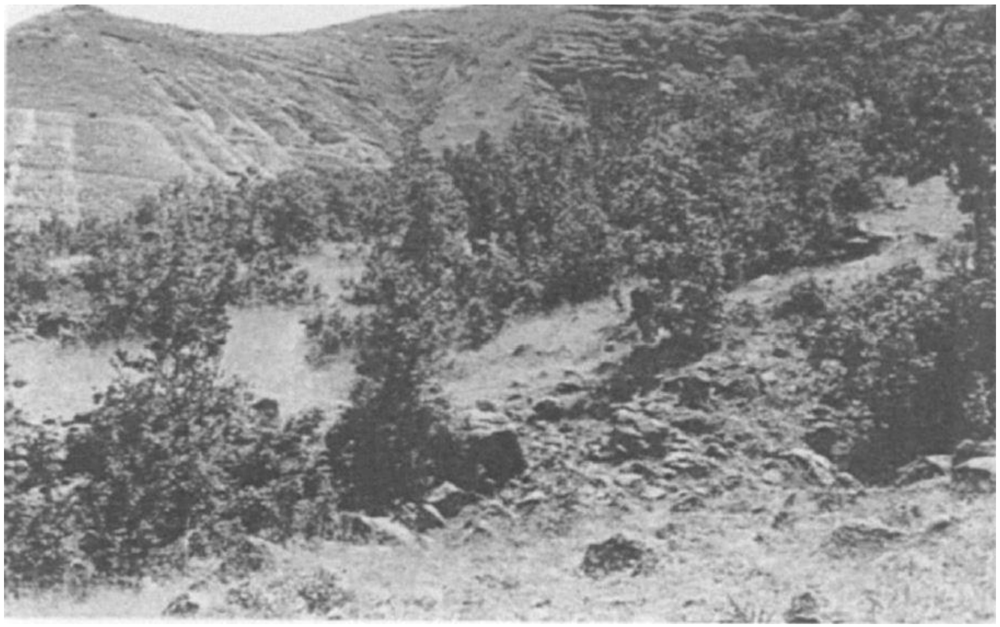
OD = Older Dryas; YD = Younger Dryas = cool, dry climatic episodes between 10,000 and 15,000 BP





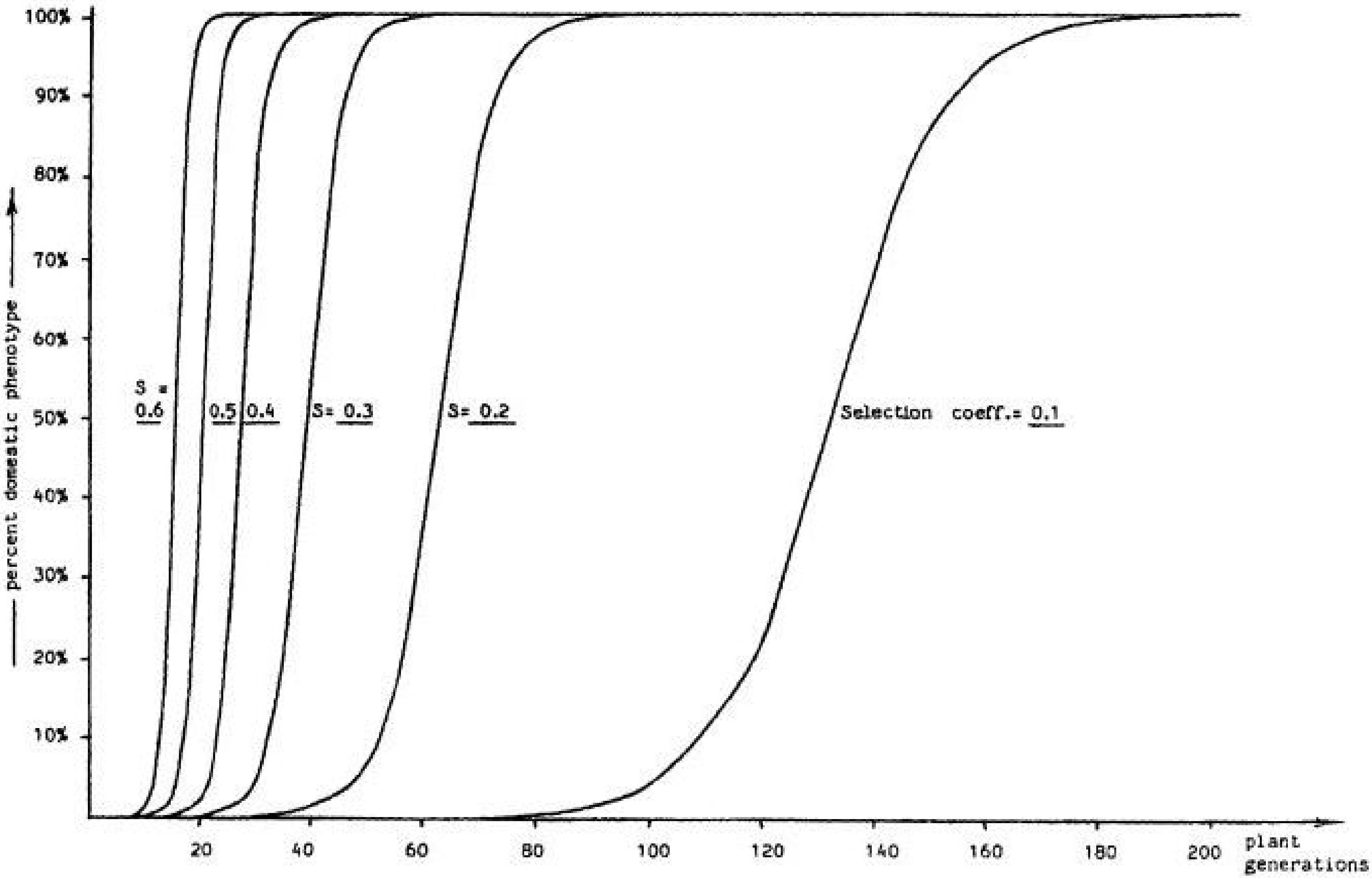
Hillman & Davies (1990)

Rates of domestication: experimental approaches



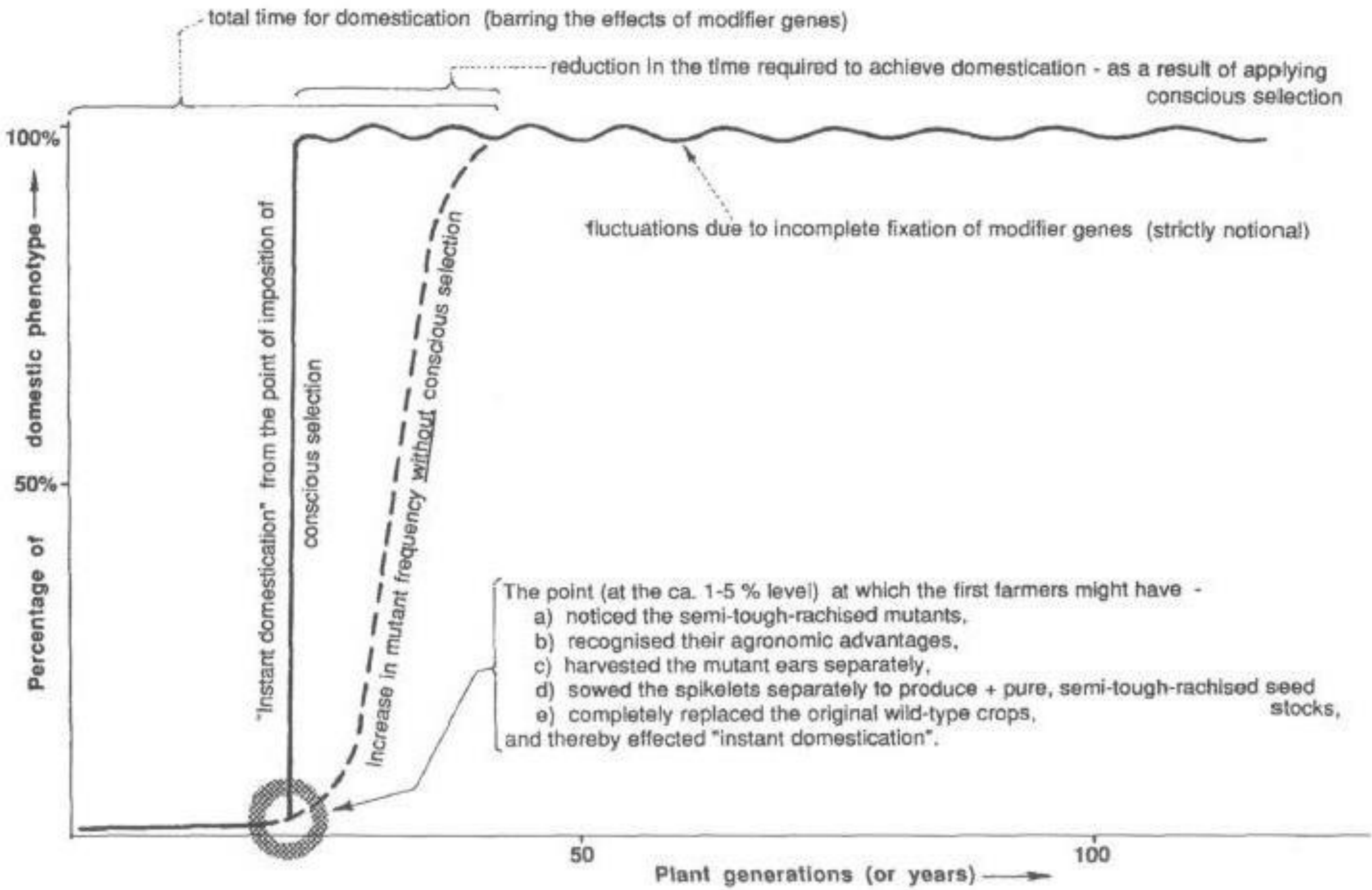
Hillman & Davies (1990)

Rates of domestication: unconscious selection for non-shattering spikelets based on: cultivation on wild shattering einkorn wheat, new ground cultivated each year, sickle harvesting of nearly ripe spikelets



Hillman & Davies (1990)

Inclusion of conscious selection



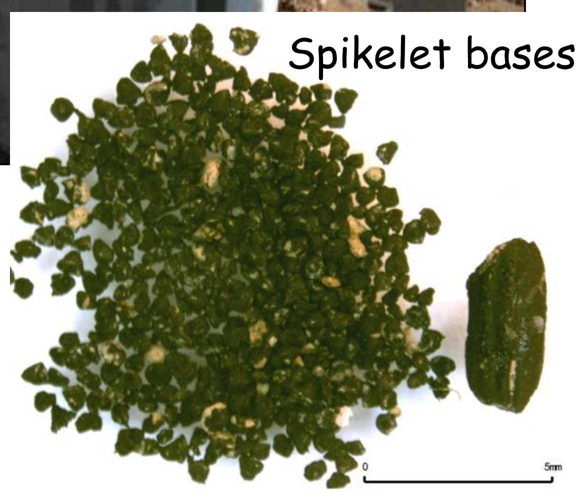
Hillman & Davies (1990)

Measuring phenotypic rates of evolution during the domestication process

Archaeology – track phenotypes through time to estimate rates of evolution and strengths of selection under domestication

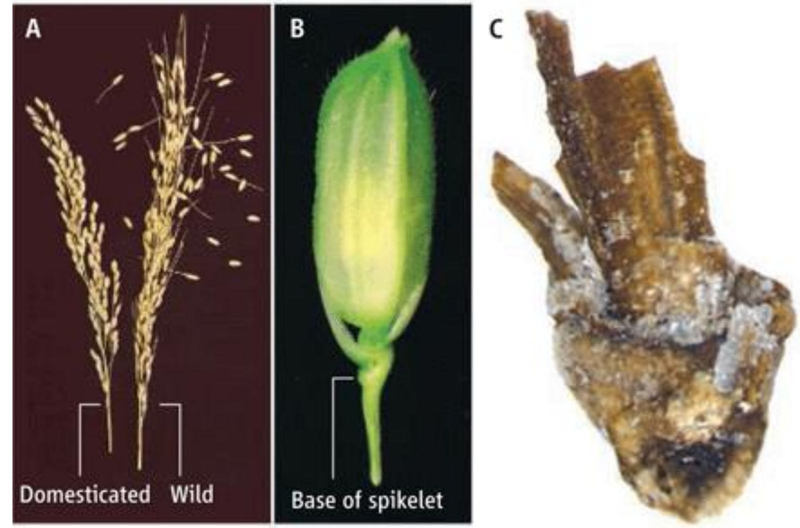
Two particular traits – rachis non-shattering in cereal crops & grain / seed size in seed crops – can provide quantitative information on phenotypic evolution during domestication

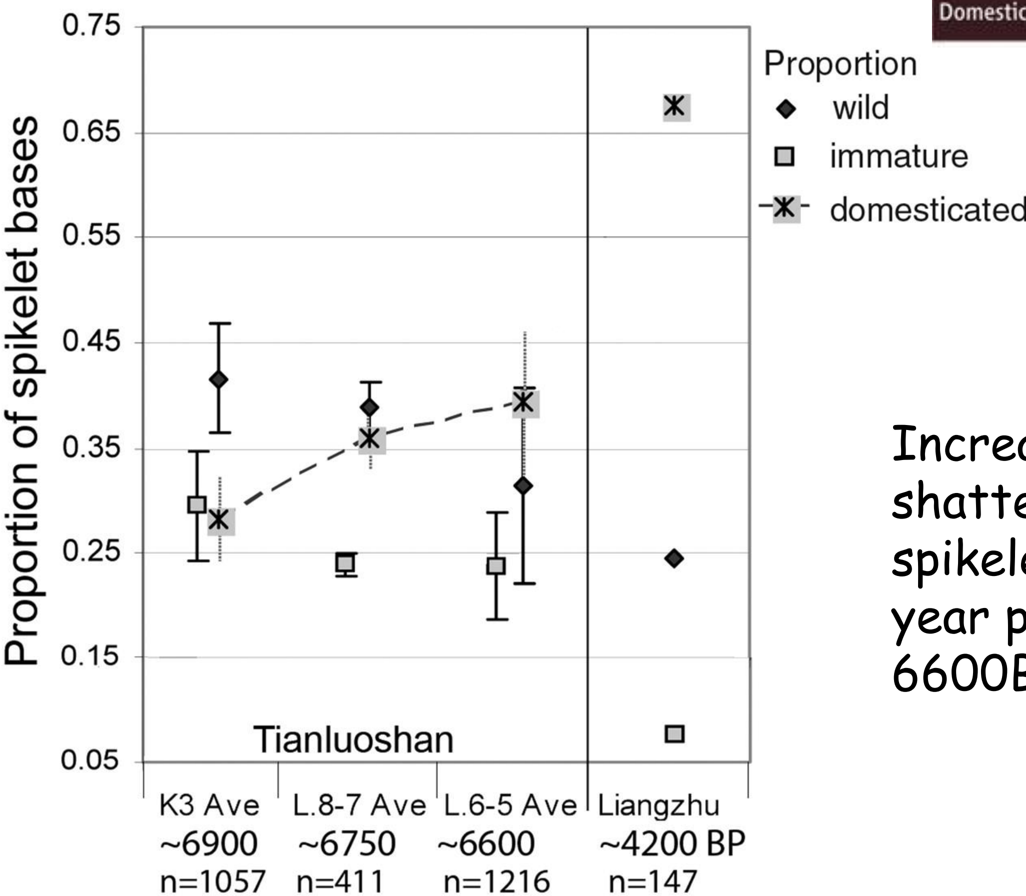
Recovery: FLOTATION of archaeological sediments for macro-remains



First flotations in USA: 1962 Iran: 1963.
Become more widespread from the 1960s.

Rice Domestication in the lower Yangtze, China

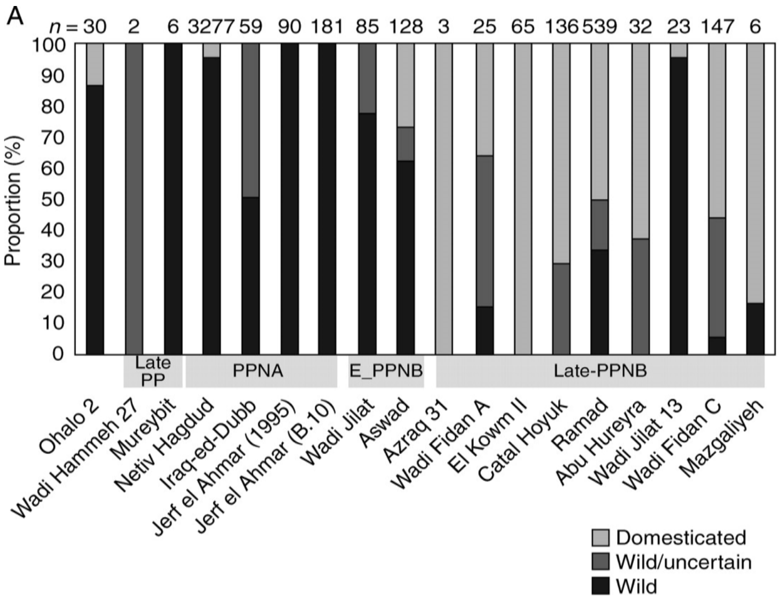




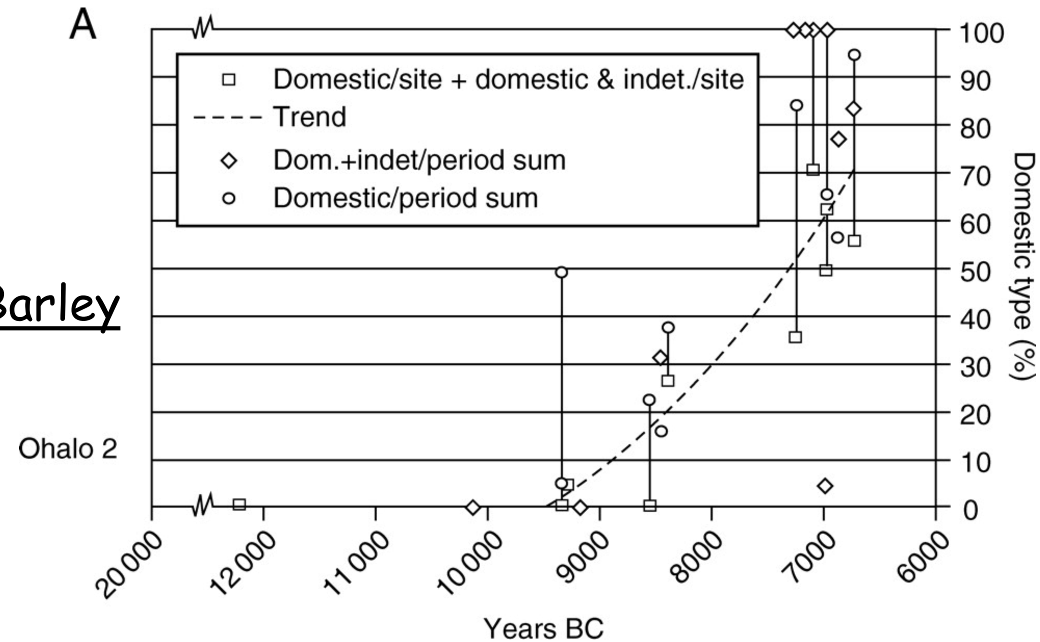
Increasing proportion of non-shattering (domesticated) rice spikelets from 27% to 39% over a 300 year period between 6,900 and 6600BP

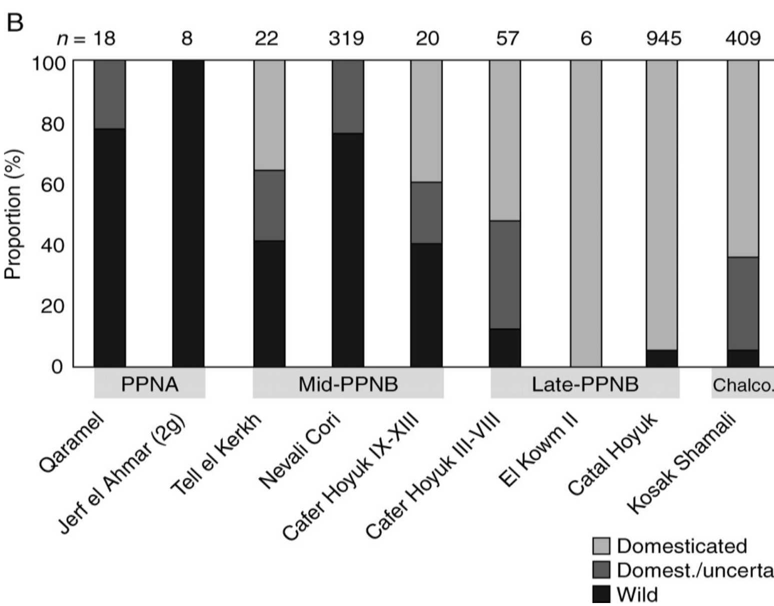
Fuller et al. (2009); Jones & Liu (2009)

Rates of crop domestication

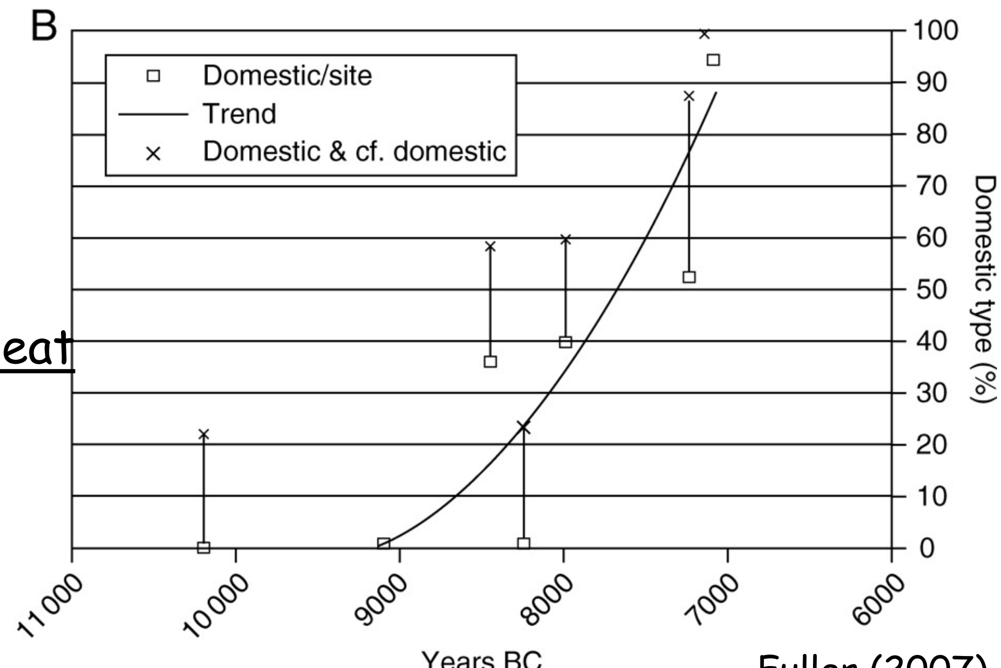


Barley



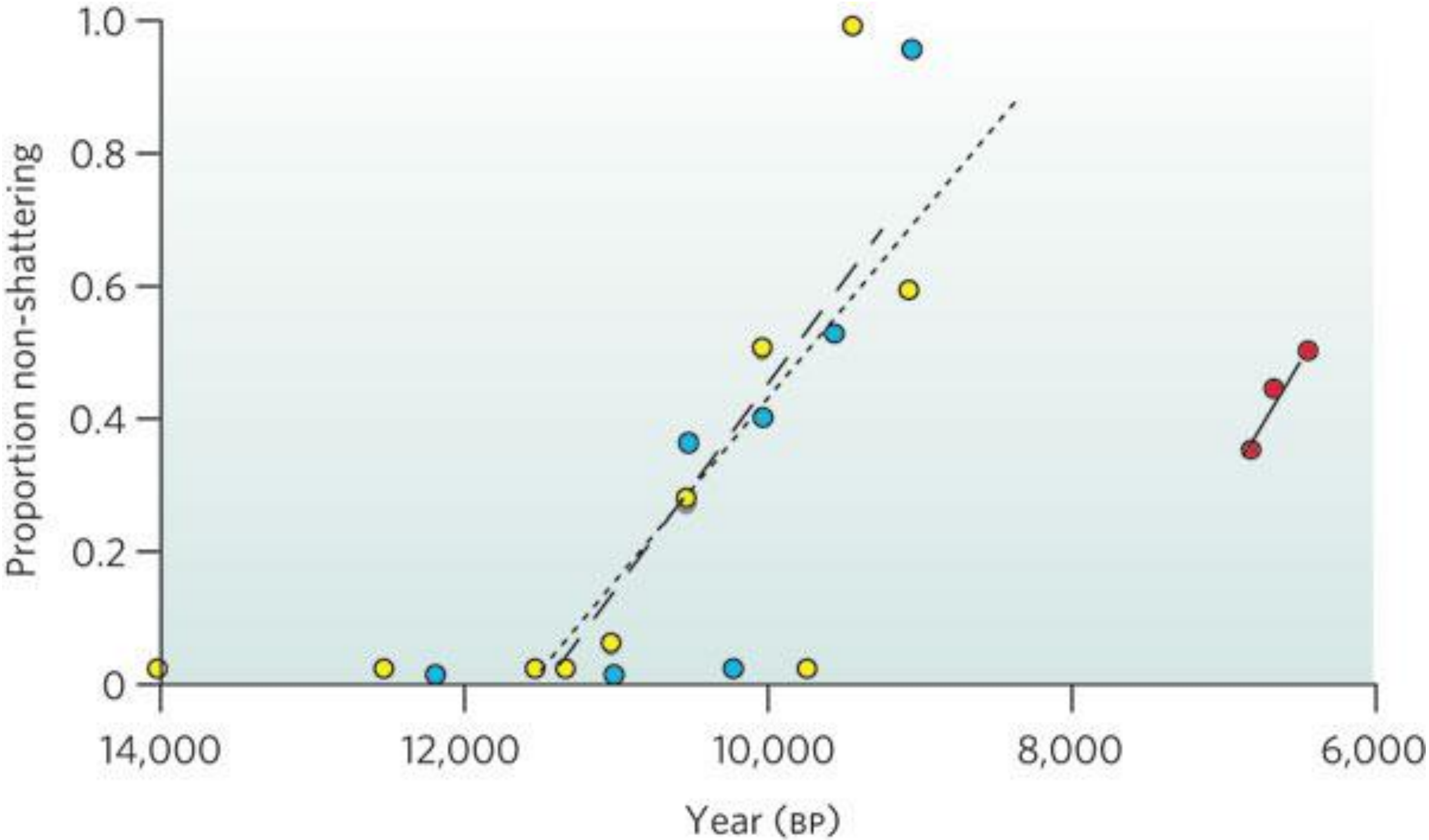


Wheat

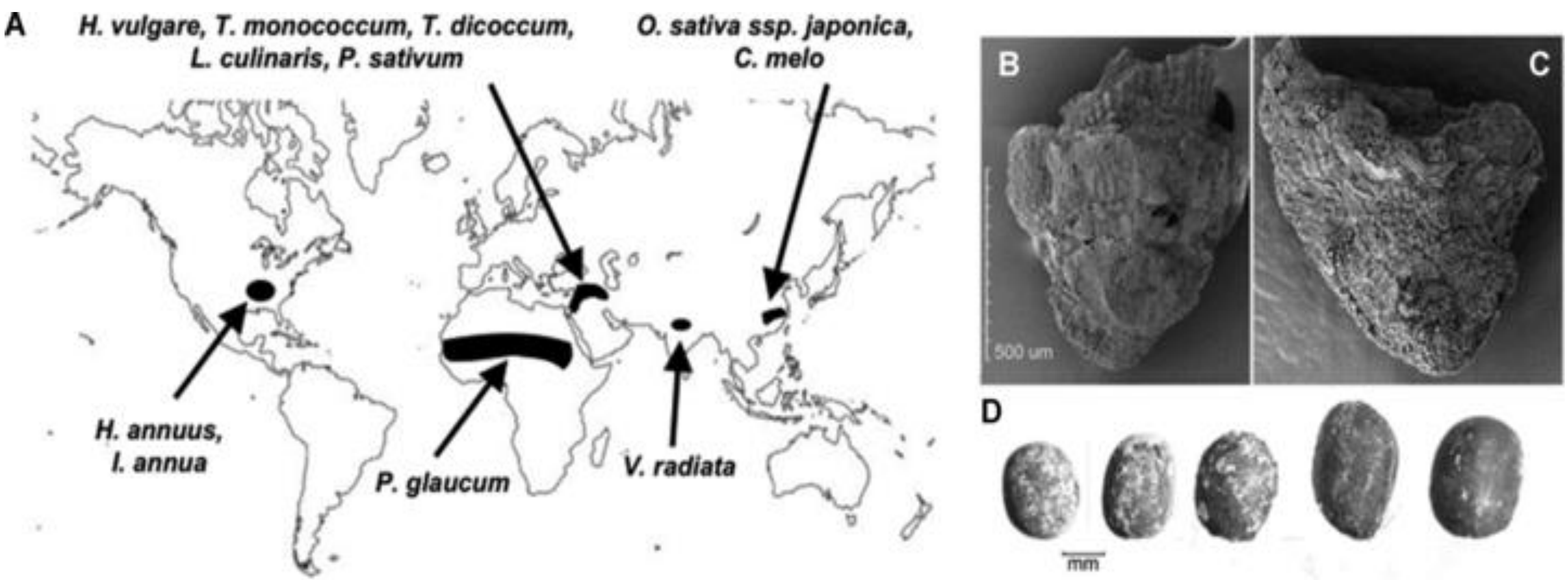


Fuller (2007)

Frequency of non-shattering, domesticated forms of barley, wheat and rice in the archaeological record



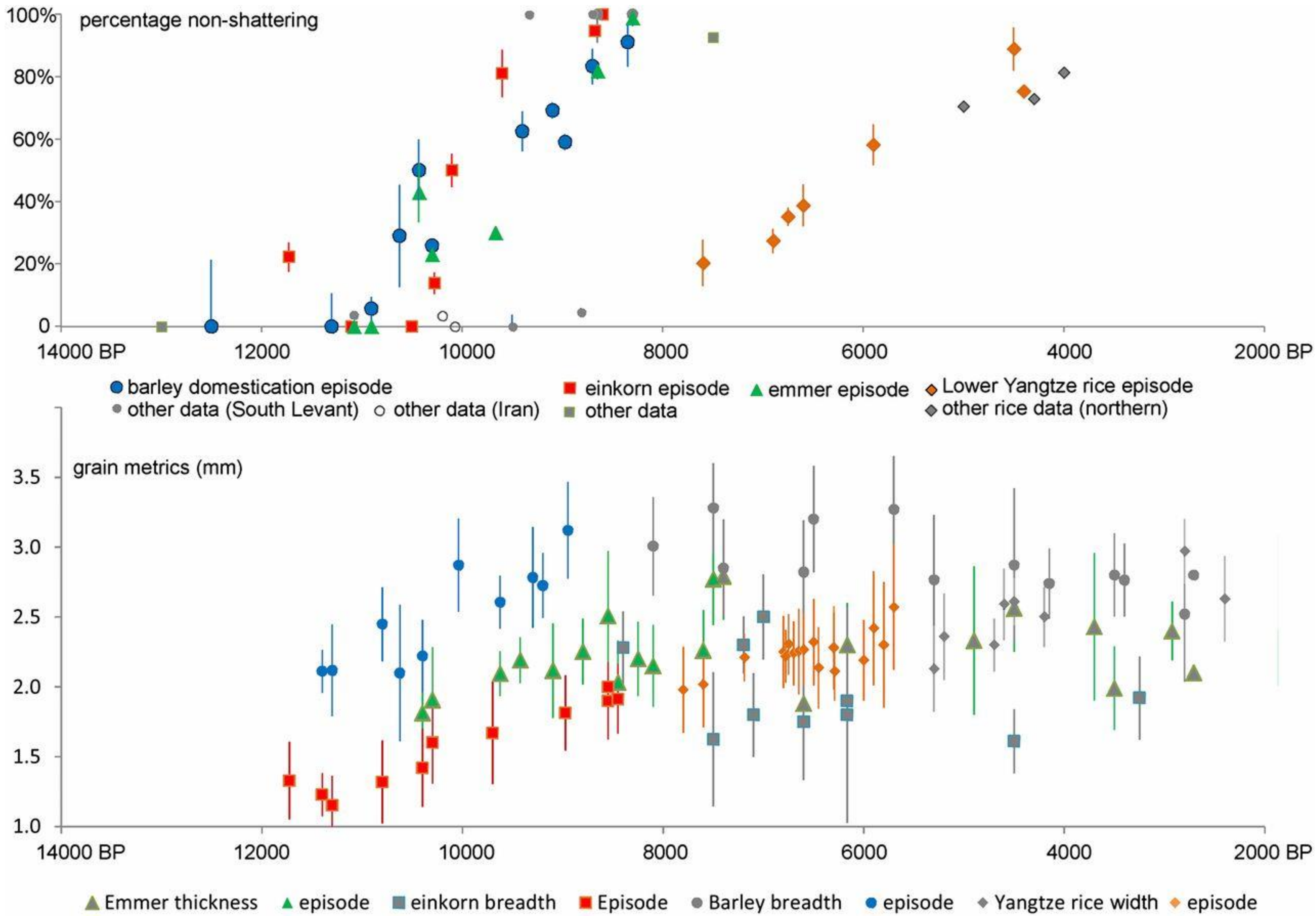
Purugganan & Fuller (2009)



Non-shattering & grain/seed size
60 archaeological sites in five regions that date from the Neolithic (12,000BP) to historical times (800BP)
11 crop species: 5 cereals – *Hordeum vulgare*, barley; *Triticum monococcum*, einkorn wheat; *Triticum dicoccum*, emmer wheat; *Pennisetum glaucum*, pearl millet; *Oryza sativa*, rice; 3 legumes – *Vigna radiata*, mung bean; *Pisum sativa*, pea; *Lens culinaris*, lentil; plus *Cucmis melo*, melon; *Helianthus annuus*, sunflower; *Iva annua*, sumpweed, a relic crop from eastern North America.

Purugganan & Fuller (2010)

Evidence for protracted domestication episodes in Old World cereals



Fuller et al. (2014)

Non-shattering & Grain/Seed Size

8189 spiklets from 12 sites

- Einkorn wheat - > 3,000 years to go from 22% at 11,725BP to 95% by 8675BP

- Rice: increase in % non-shattering from 27% to 39% between 6,900BP & 6,660BP, giveing a fixation time span of >2,500 years

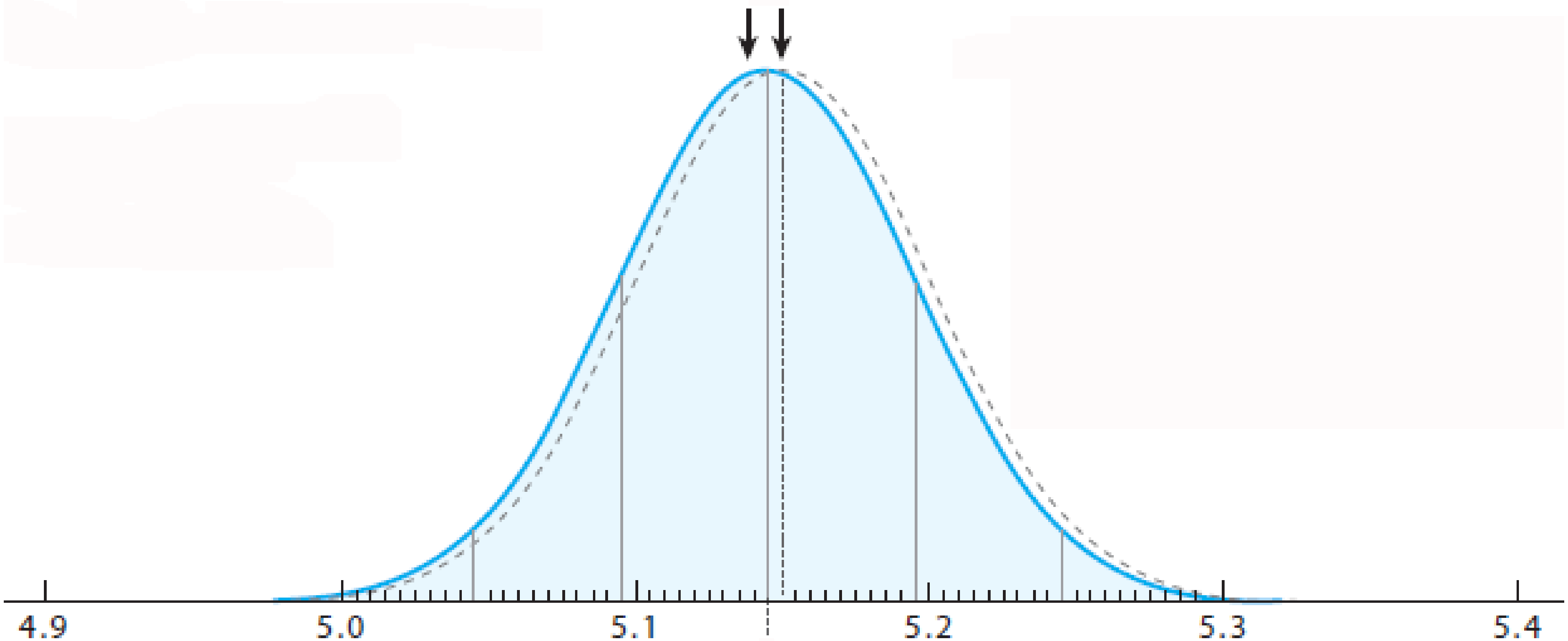
- Barley: <4% at 11,075BP to >90% by 8350BP

Indicates that non-shattering, and hence domestication, did not occur rapidly, but may have taken several 1000 years to rise to fixation in these crop species

Changes in size happened prior to non-shattering in grasses; seed size increase in pulses slower – different selective thresholds in different plant groups

Purugganan & Fuller (2010)

Comparing rates of change: *haldanes* (change of standard deviation across generations)



Gingerich, P. D. (2009) Rates of Evolution. *Annual Rev. Evol. Ecol. Syst.*

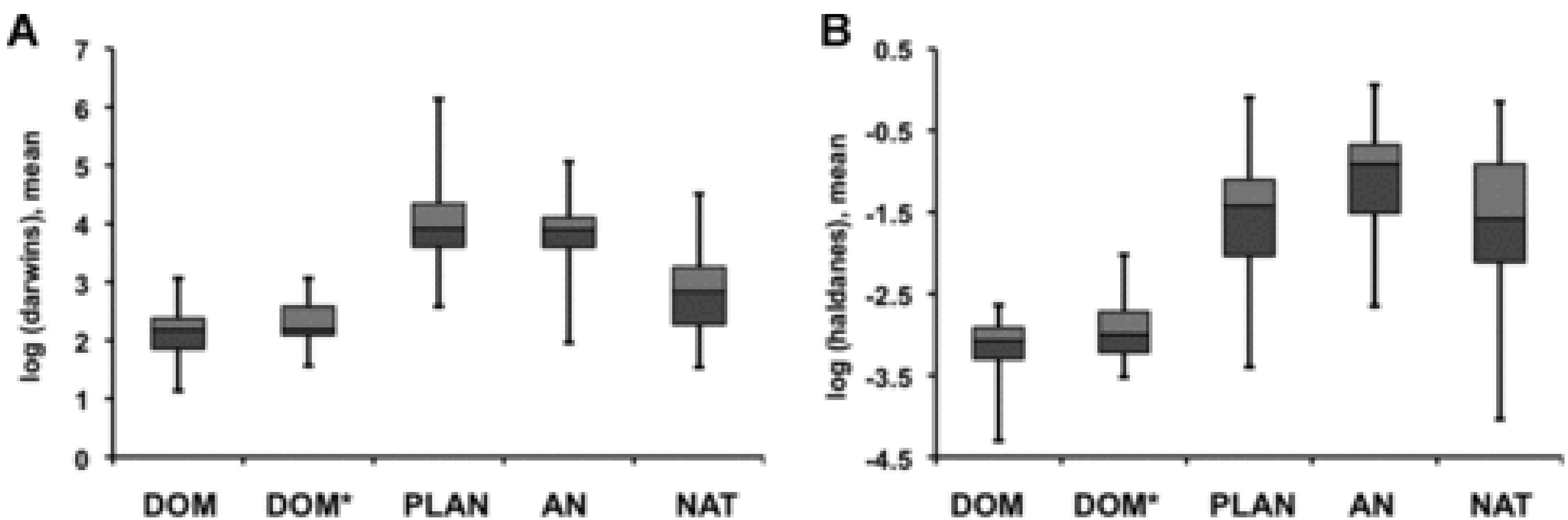
Darwin = one logarithmic increase in phenotypic value of a trait per million yrs

Appllied to archaeobotany: Purugganan and Fuller (2011) *Evolution*, Fuller, Asouti and Purugganan (2012) *Vegetation History and Archaeobotany*

Comparison of evolutionary rate estimates

The ‘darwin‘ = one logarithmic increase in the phenotypic value of a trait for each million years of evolution

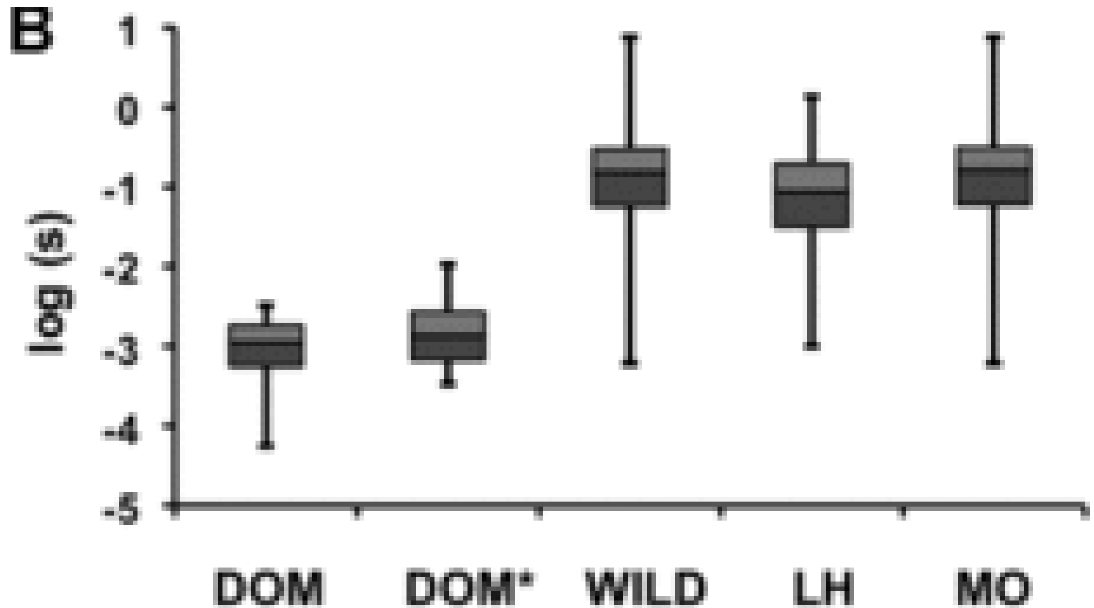
The ‘haldane‘ = the change of one standard deviation of a trait value per generation
A- in darwins; B – in haldanes
DOM = domestication; DOM* = domestication under a shortened (2,000 yr) domestication period
Wild PLAN = plants; AN = animals anthopogenic; NAT = animals natural



Purugganan & Fuller (2010)

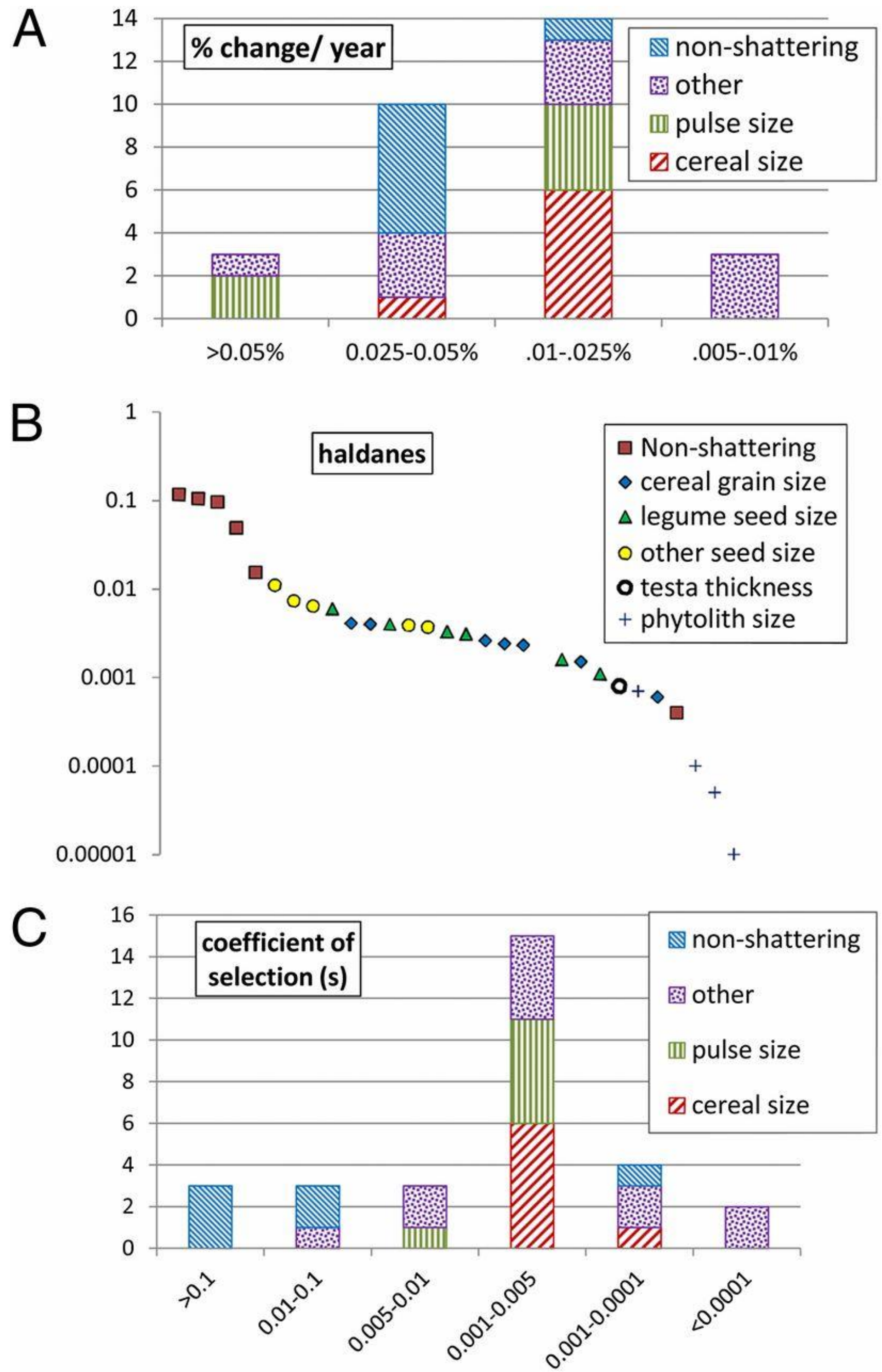
Comparison of selection coefficients

DOM = domestication; DOM* = domestication under a shortened (2,000 yr) domestication period
WILD = Wild; LH = life history traits; MO = morphological traits



Purugganan & Fuller (2010)

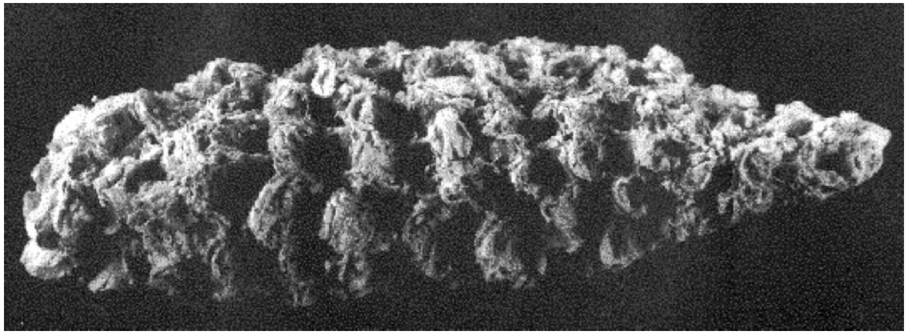
Rates of change in domestication traits

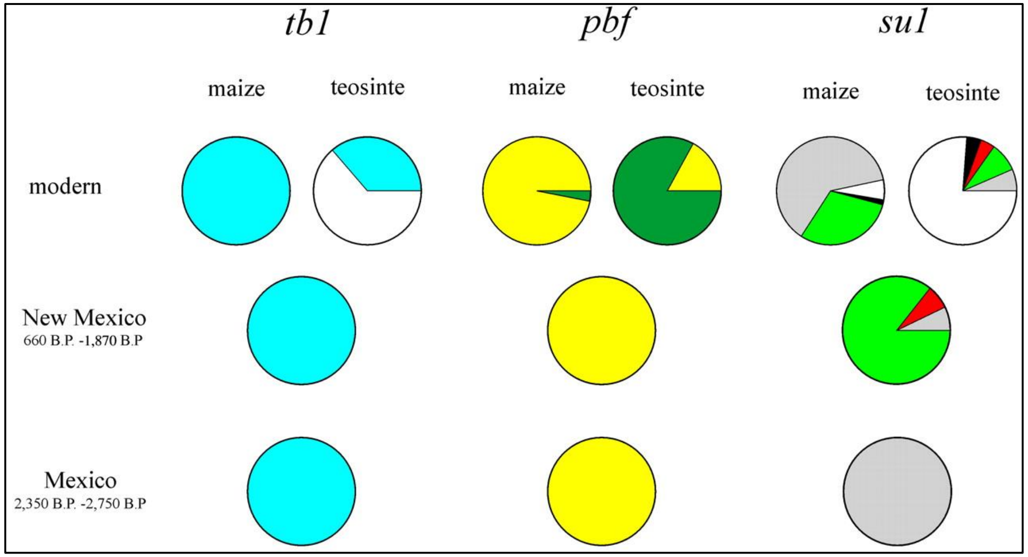


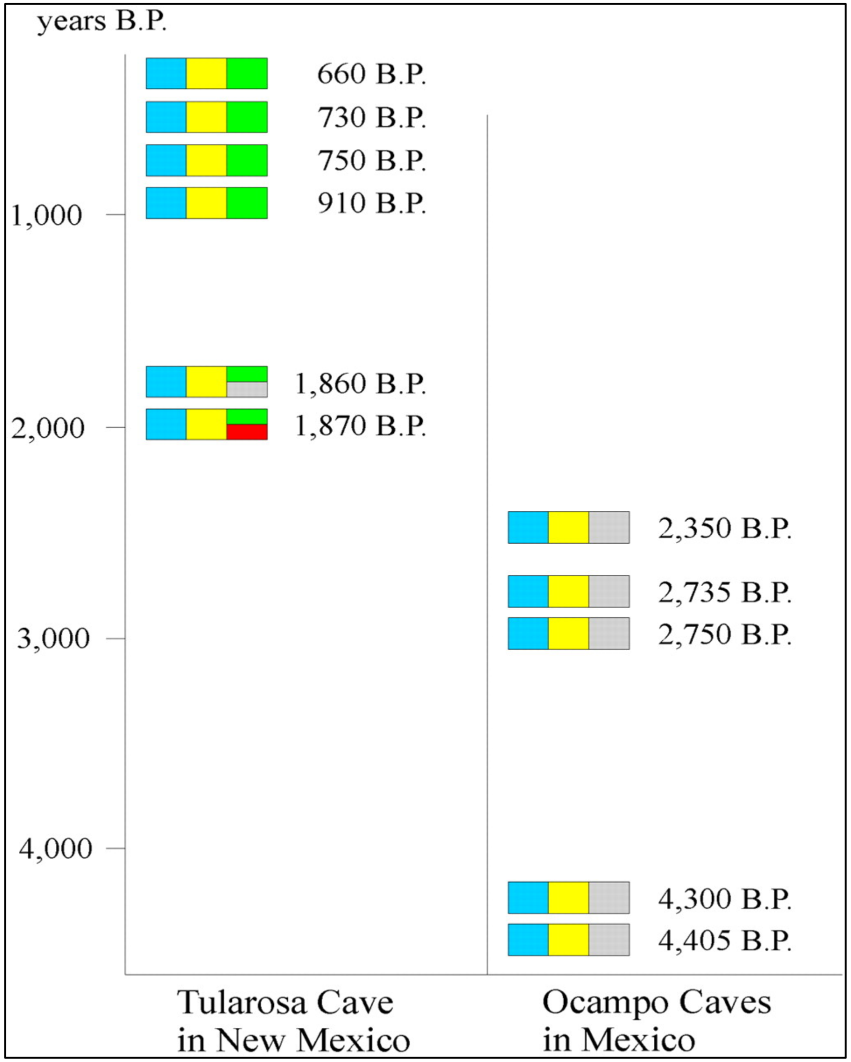
Fuller et al. (2014)

Early allelic selection in Maize as revealed by ancient DNA

-Maize domesticated at least 6,250 BP in S-C Mexico
-Three genes: plant architecture (*tb1*), storage protein synthesis (*pbf*) and starch production (*su1*) characterized from ancient DNA from archaeological maize samples
-Alleles typical of modern maize present by 4,400 BP, but even 2,000 BP ellelic selection on one gene still not complete

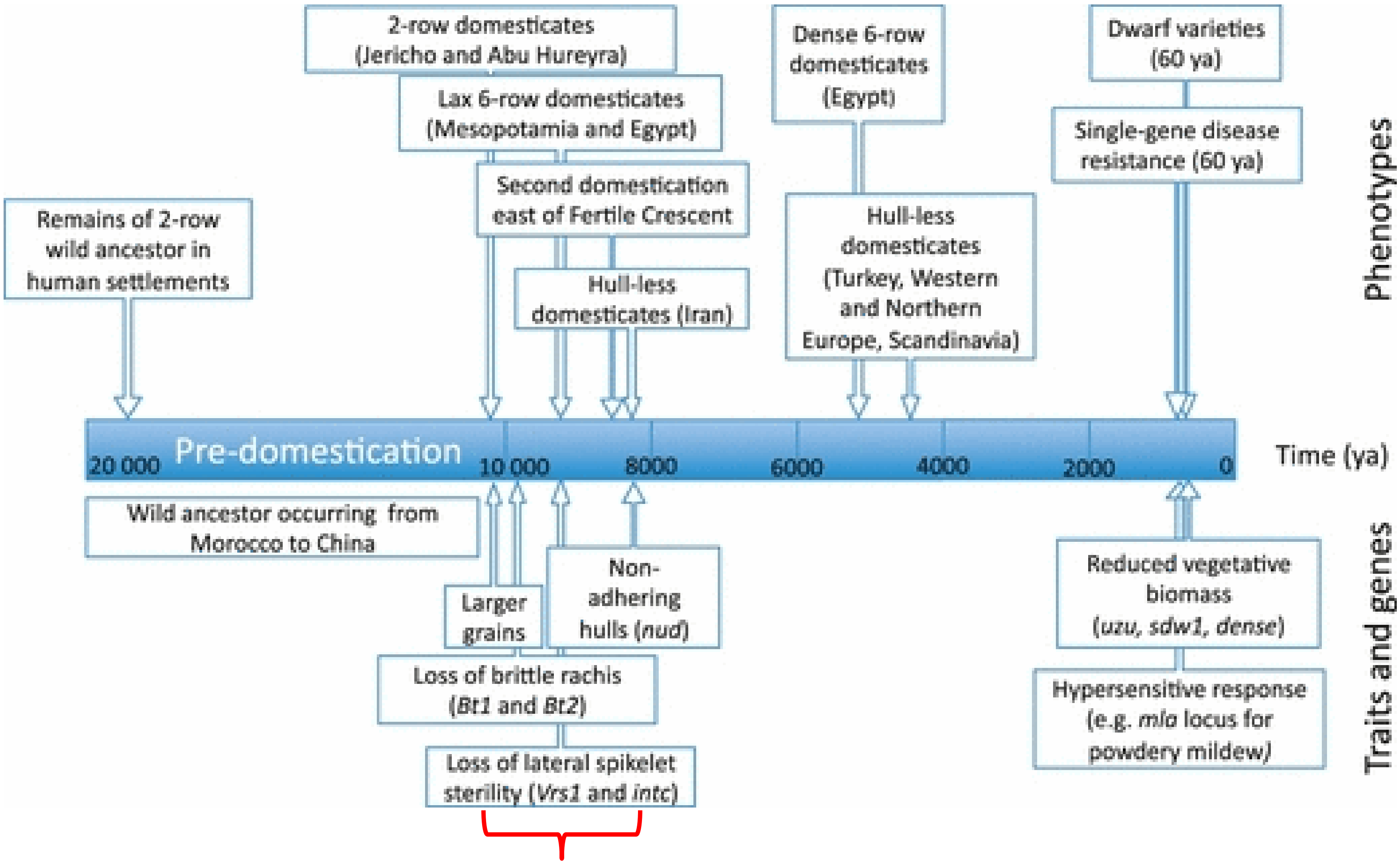






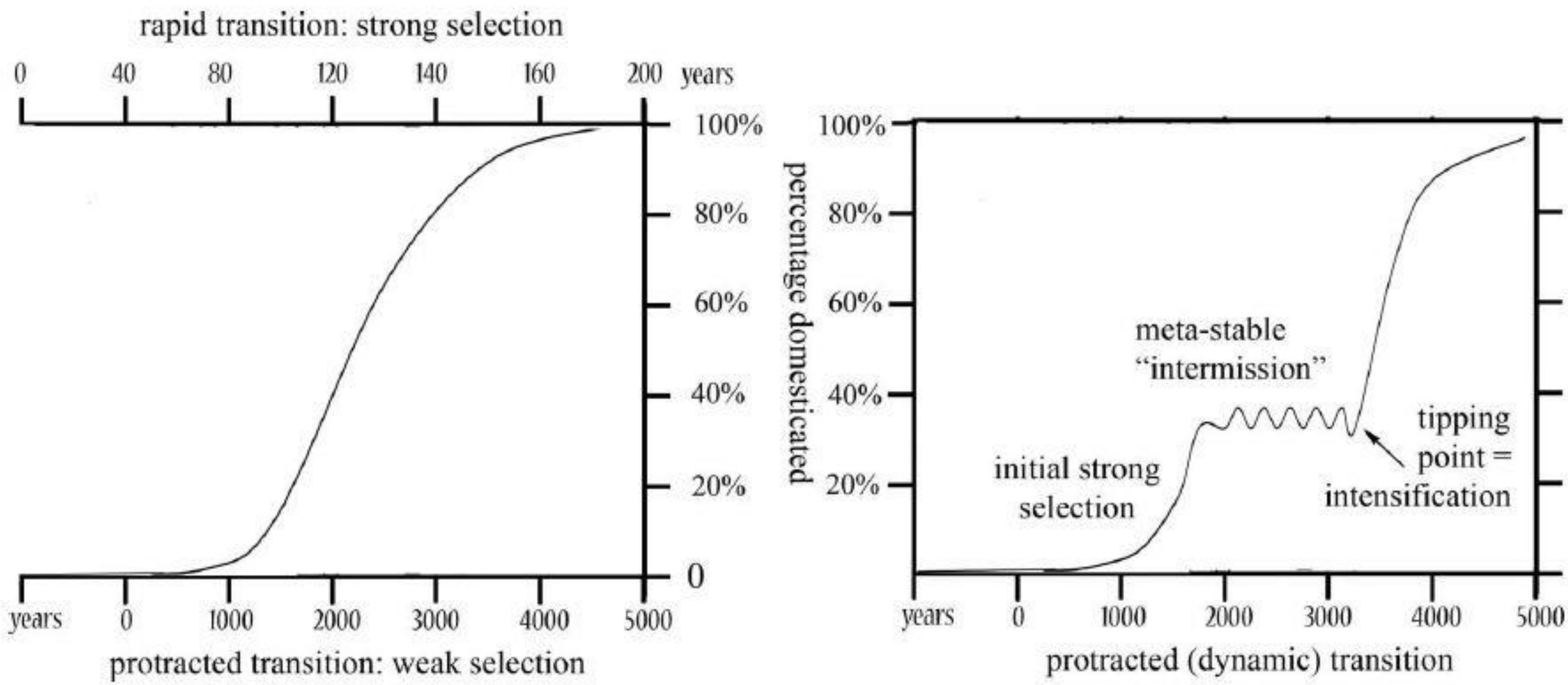
Jaenicke-Despres et al. (2003)

Temporal trajectory of barley domestication



c. 2,000 yrs for establishment of key elements of the barley domestication syndrome

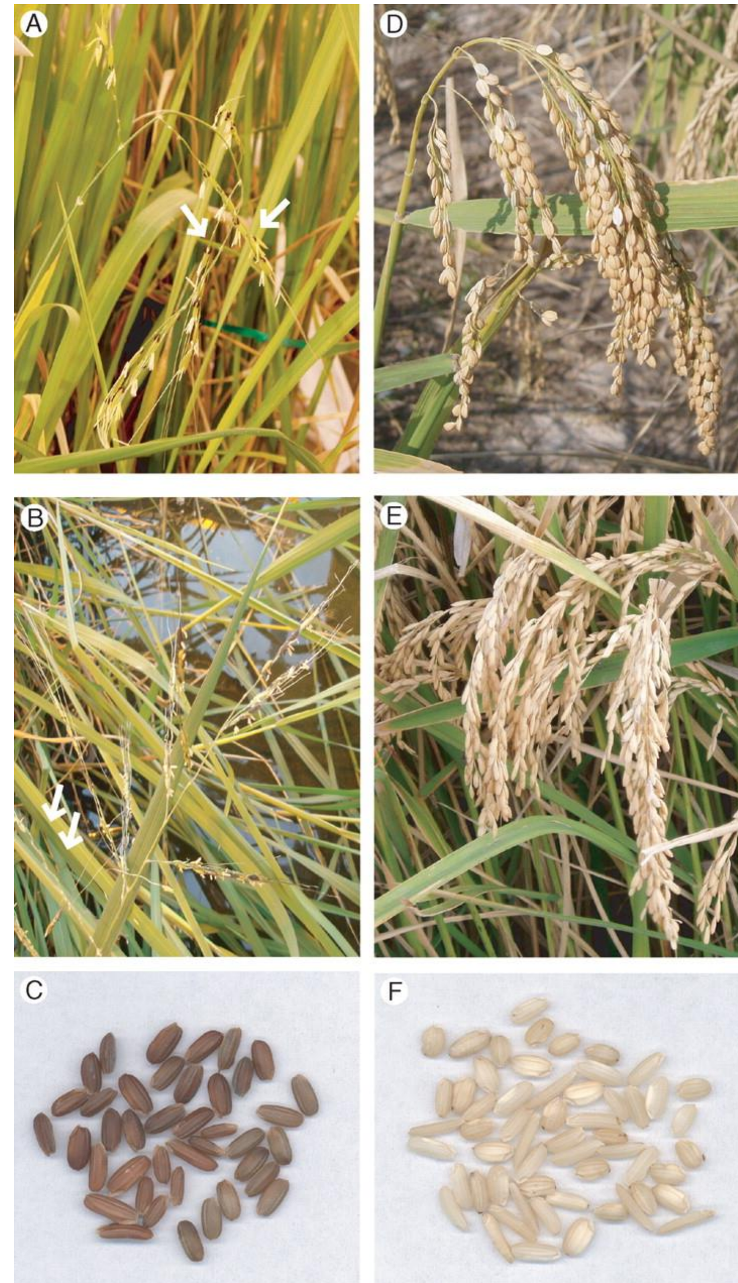
Meta-stable semi-domestication



Fuller et al. (2010)

Weed evolution by de-domestication

Crop progenitors are often weeds of disturbed, ruderal sites, pre-adapted to growing in open habitats, and hence to cultivation. *Oryza rufipogon*, the progenitor of rice is a good example



Weed evolution by de-domestication / feralisation: Rice

Crop progenitors are often weeds of disturbed, ruderal sites, pre-adapted to *growing* in open habitats, and hence to cultivation.

Oryza rufipogon, the progenitor of rice is often still found today as a weed in and around rice fields.

However, recent studies suggest that in many cases weedy rice is derived from domesticated crop rice, via a process of ***de-domestication***. Weedy rice shown to be more closely related to domesticated rice in fields than to common wild rice varieties.

These crop-derived weedy rices show re-aquisition of the shattering trait, but in ways where the abscission layer which leads to shattering breaks down sooner leading to earlier shattering than in wild rice – a potentially useful adaptation for beating the farmer to it and getting into the seedbank before the rice harvest.

Genetic characterization found that these weedy rices all possessed the *sh4* mutation that characterizes domesticated non-shattering rices, suggesting the acquisition of a different novel mutation in the *sh4* gene that allows shattering

Thurber et al. (2010); Zhang et al (2012)

Weed evolution by de-domestication / feralisation: Rye

Rye: bread of the poor in northern & eastern Europe

19th century immigrants introduced rye to the U.S.A. and grown widely there until the 1960s, then demand dropped and less and less rye grown

Late 1900s rye began appearing as a weed in other crops

By early 2000s weedy rye infested 1 million ha of cropland in western U.S.A.

A change in a single gene had restored seed shattering; seeds had become smaller and feral rye now phenotypically distinct and reproductively isolated (via phenological shifts) from domesticated cereal rye.

Rapid evolution away from domesticated ancestor in < 120 yr since its introduction.

Rates of crop domestication

• Available quantitative archaeobotanical data on domestication traits, and especially seed size and loss of seed dispersal mechanism, can be used to explore changes during domestication and how quickly those changes occurred.

• These data show that in domesticated grasses, changes in grain size and shape evolved prior to non-shattering ears. Initial grain size increases may have evolved during the first centuries of cultivation, within perhaps 500-1000 years. Non-shattering spikelets were much slower, becoming fixed about 1000 to 2000 years later.

• Pulses by contrast, do not show evidence for seed size increase in relation to earliest cultivation, and seed size increase may be delayed 2000 to 4000 years.

• Rates of phenotypic evolution in multiple crop species appear to be significantly slower than rates observed in wild species.

• Selection coefficients associated with domestication are at the lower end of the distribution for wild species.

• Rates are comparable for non-shattering and seed size traits and across crops and locations

• These findings require a reassessment of the nature of selection during domestication.

Purugganan & Fuller (2010); Fuller (2007)

Rates of crop domestication & the nature of selection during domestication

- The domestication process appears to have been driven largely by unconscious selection, i.e. as a byproduct of cultivating plants in agricultural environments

- Unconscious selection is similar to natural selection in novel environments established by human agriculture

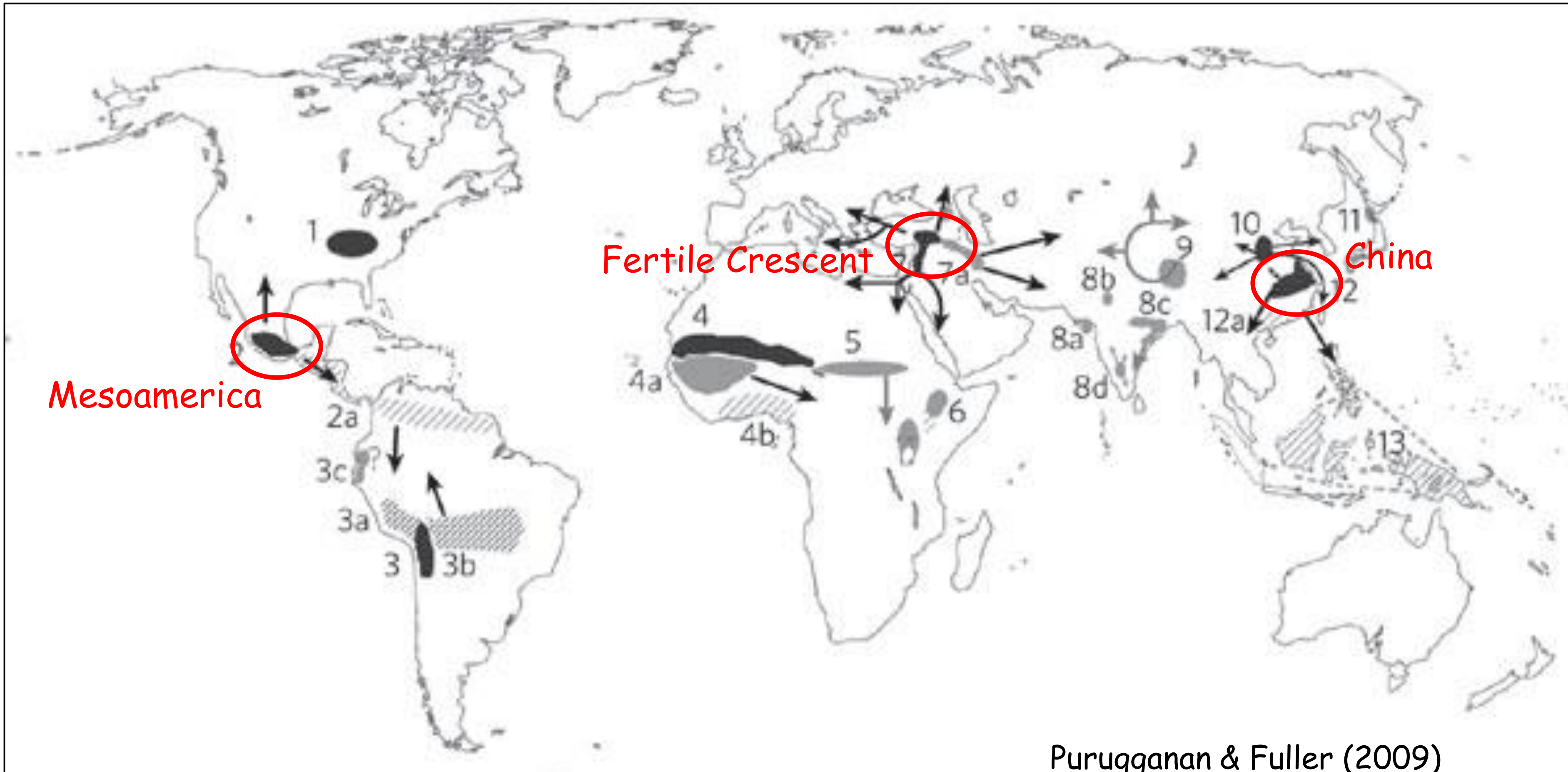
- Domestication genes may have pleiotropic effects, such that deleterious mutations may segregate at higher frequencies in population bottlenecks associated with crop origins leading to decreased selection efficiency

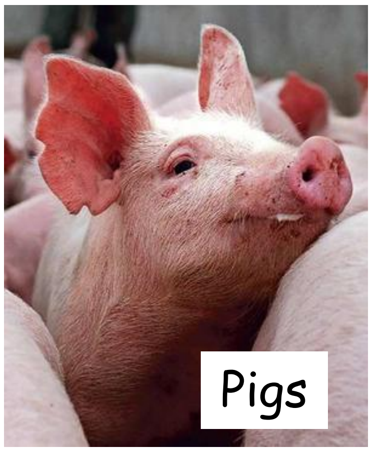
- Farmers continued to cultivate and gather wild plants alongside proto-domesticates during the initial phases of domestication, possibly resulting in gene flow that hampered fixation of selected alleles

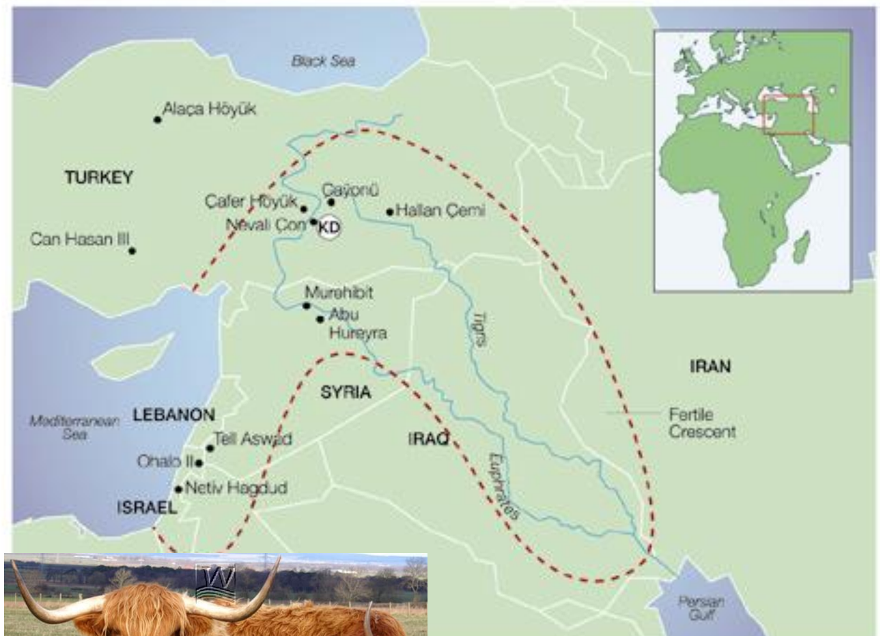
- Other domestication traits may evolve at higher rates

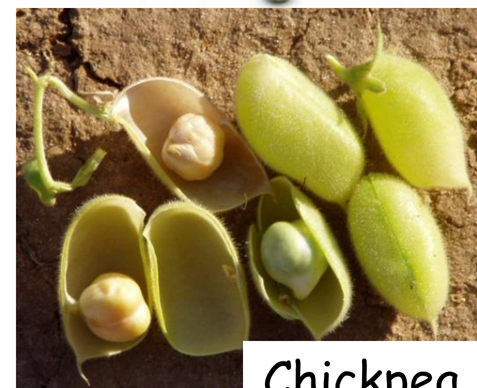
The Evolution of Agriculture
Complex regional agricultural development trajectories

– regional geotemporal patterns in the evolution of agriculture – origins, the transition from foraging to farming, and subsequent expansion and diffusion to adjacent areas



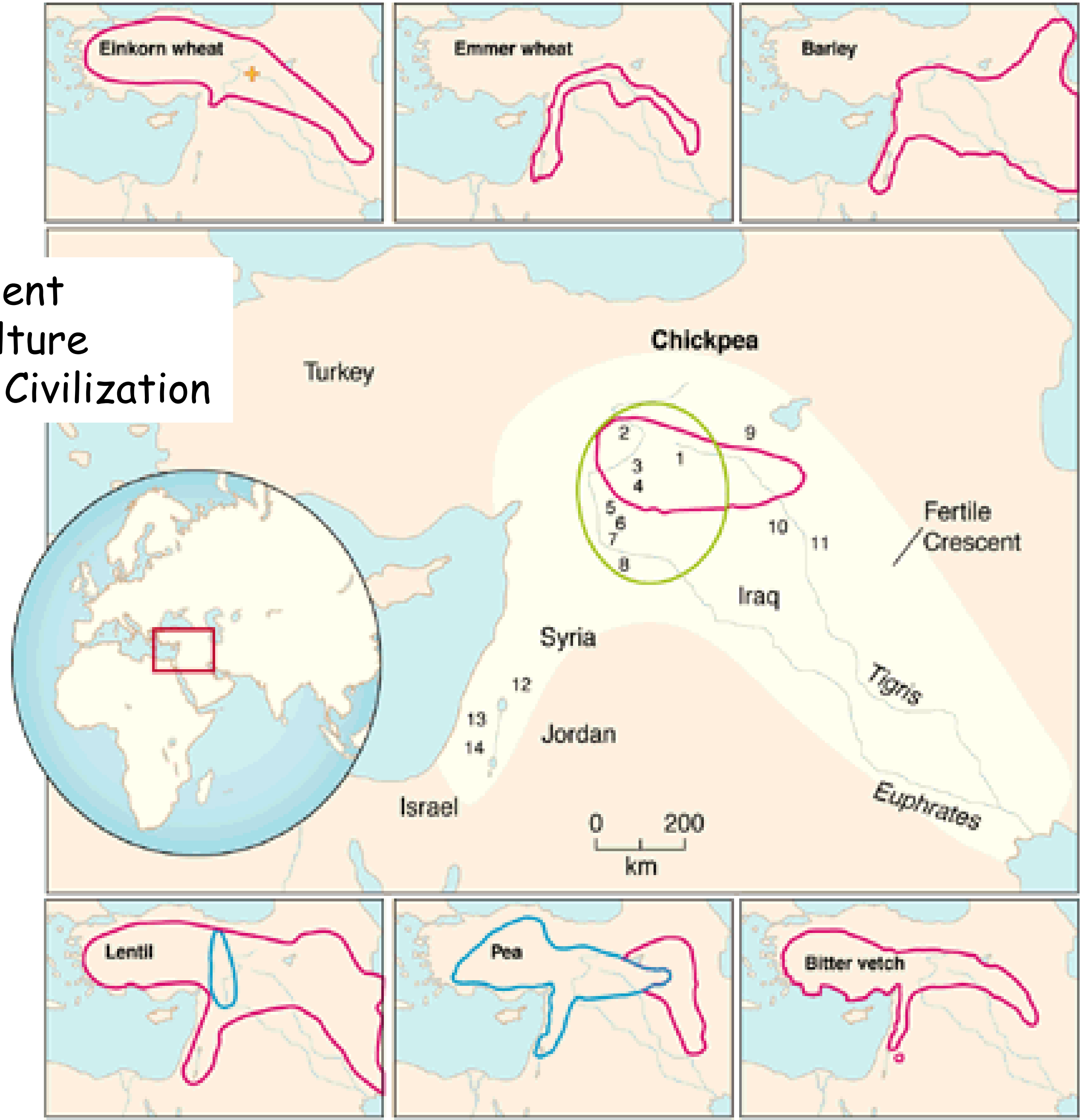






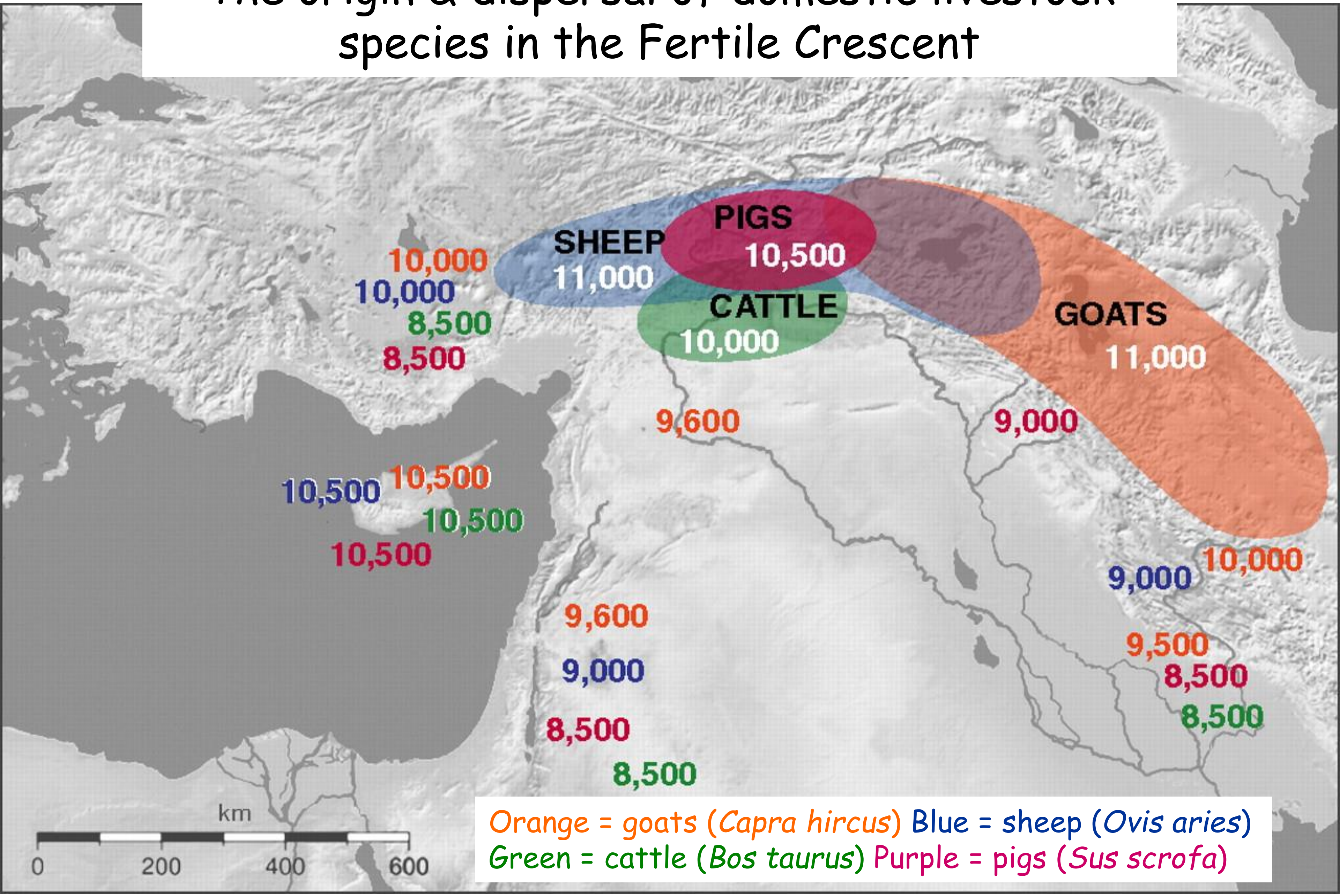
Fertile Crescent

The Core Fertile Crescent
- The Cradle of Agriculture
- The Dawn of Modern Civilization



Lev-Yadun et al (2000)

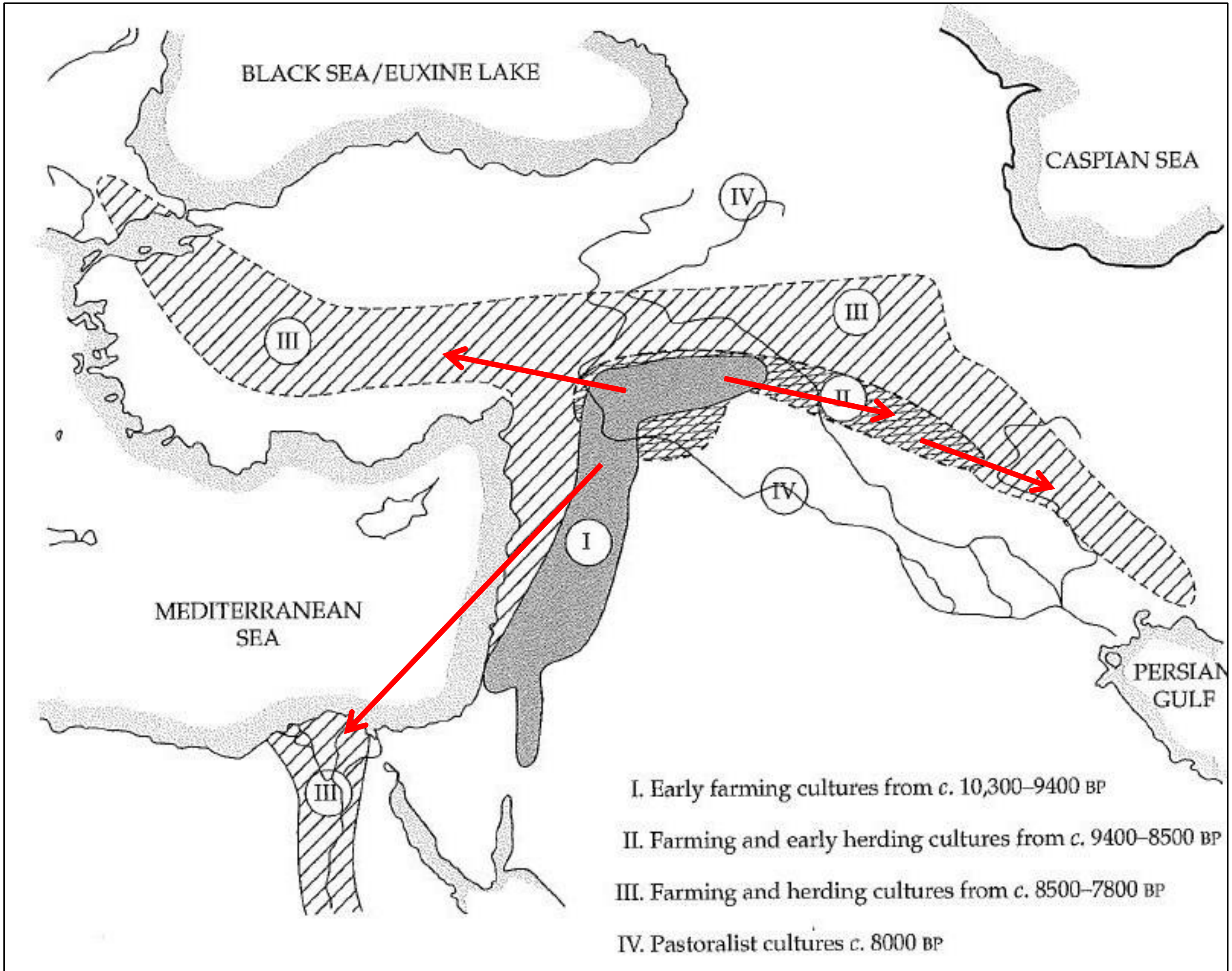
The origin & dispersal of domestic livestock species in the Fertile Crescent



Orange = goats (*Capra hircus*) Blue = sheep (*Ovis aries*)
Green = cattle (*Bos taurus*) Purple = pigs (*Sus scrofa*)

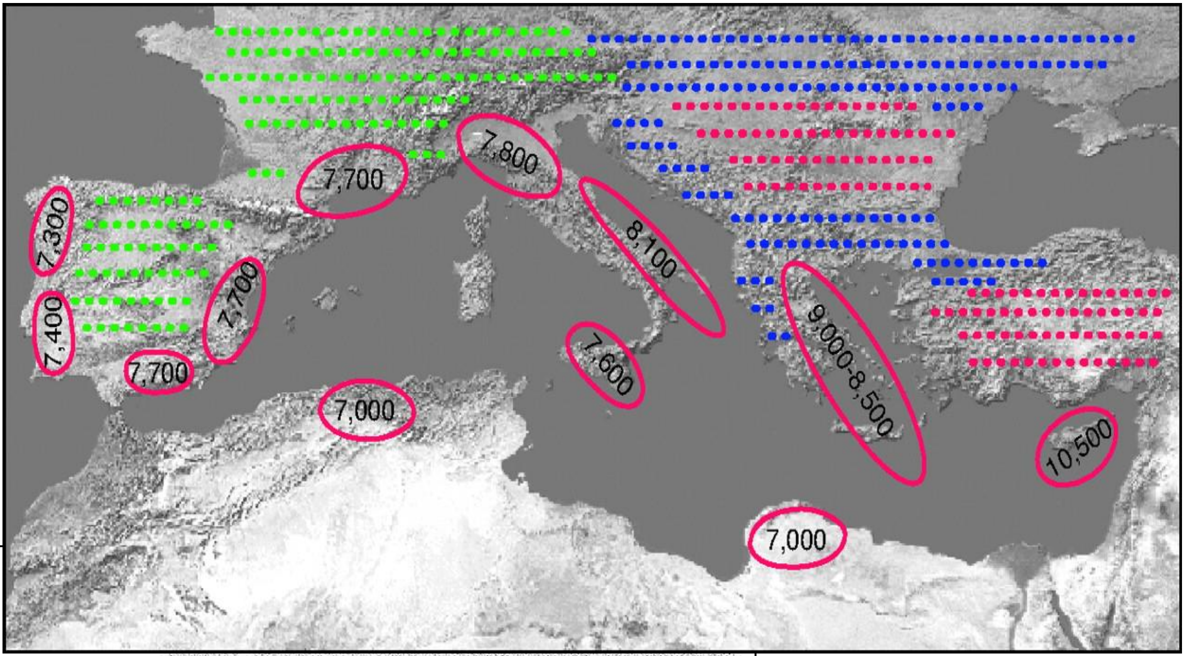
Zeder (2008)

The establishment and initial spread of agriculture in the Near East



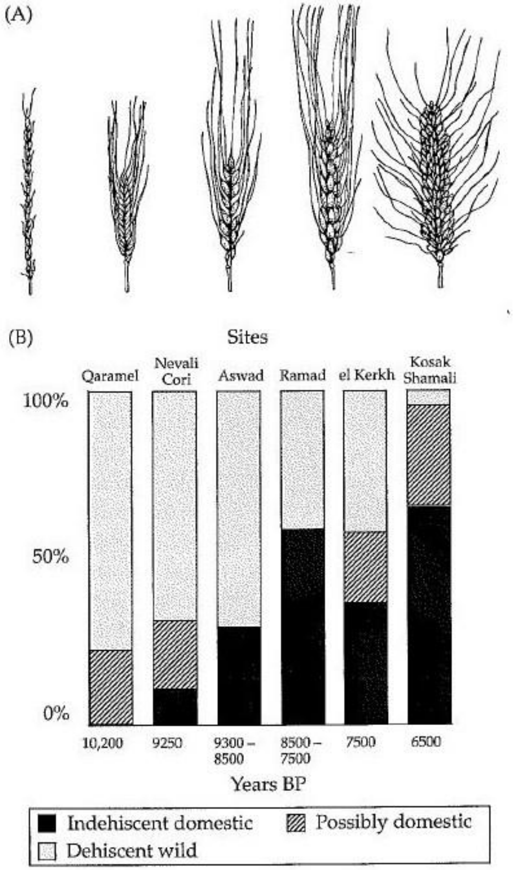
Murphy (2007)

Post-8,000 BP Agricultural expansion from the Fertile Crescent across the Mediterranean and Europe

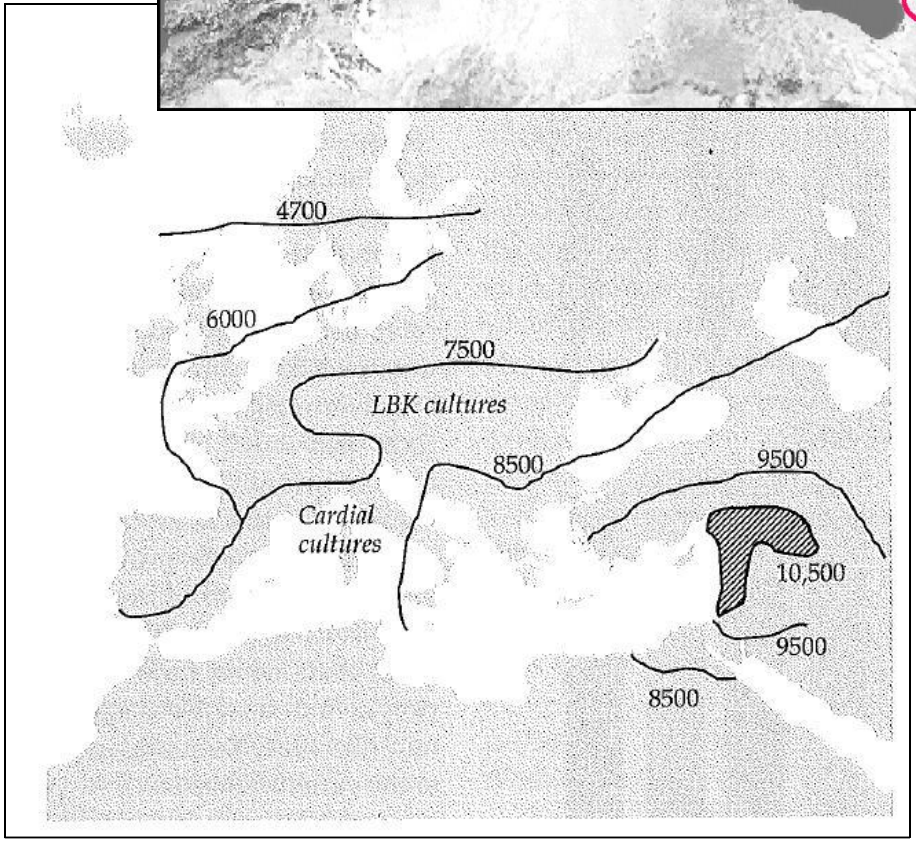


Zeder (2008)

- Settlement by colonist farmers
- Indigenous foragers adopt elements of the Neolithic farming package
- Integration of colonist farmers with indigenous forager groups

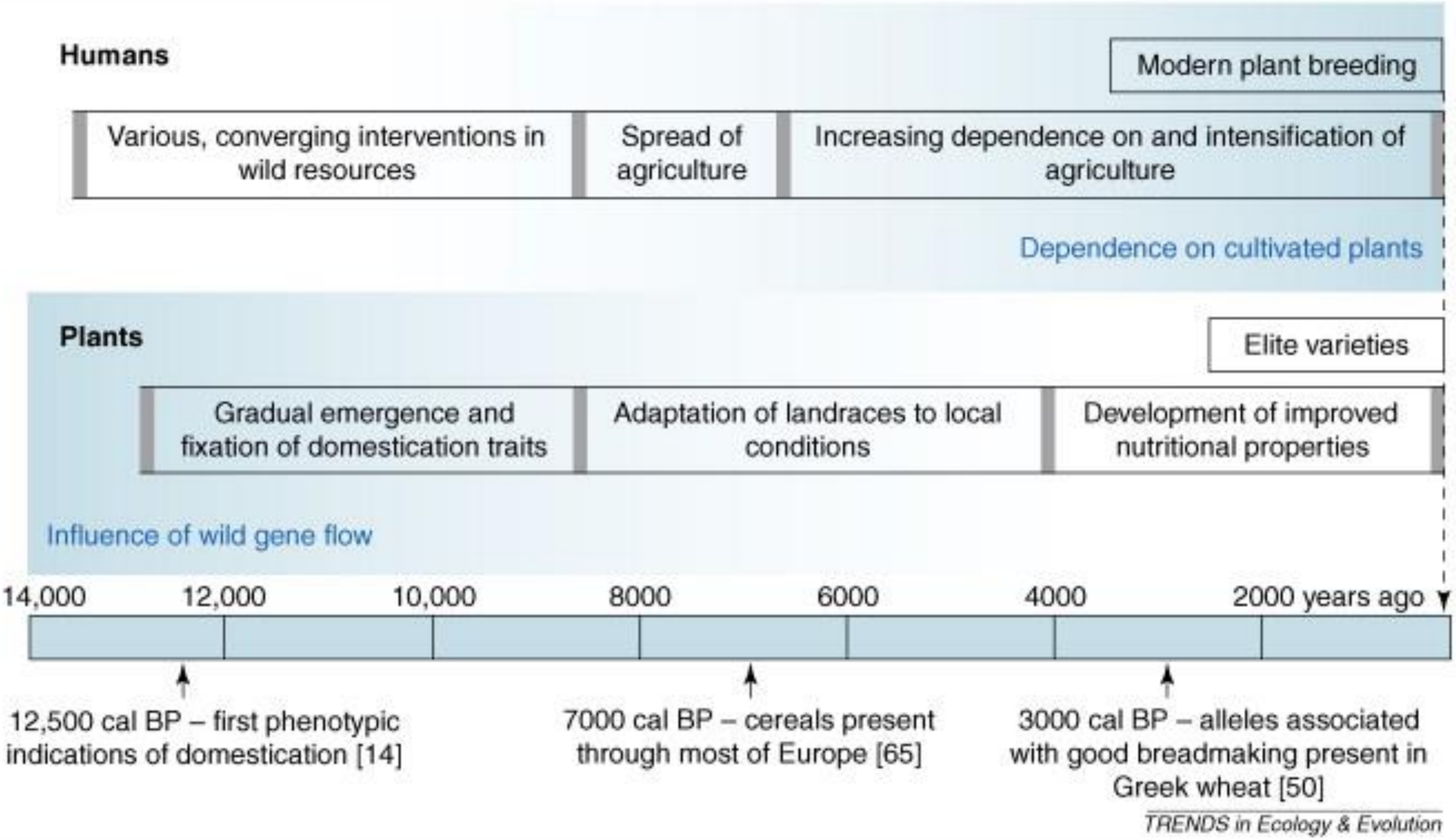


Murphy (2007)

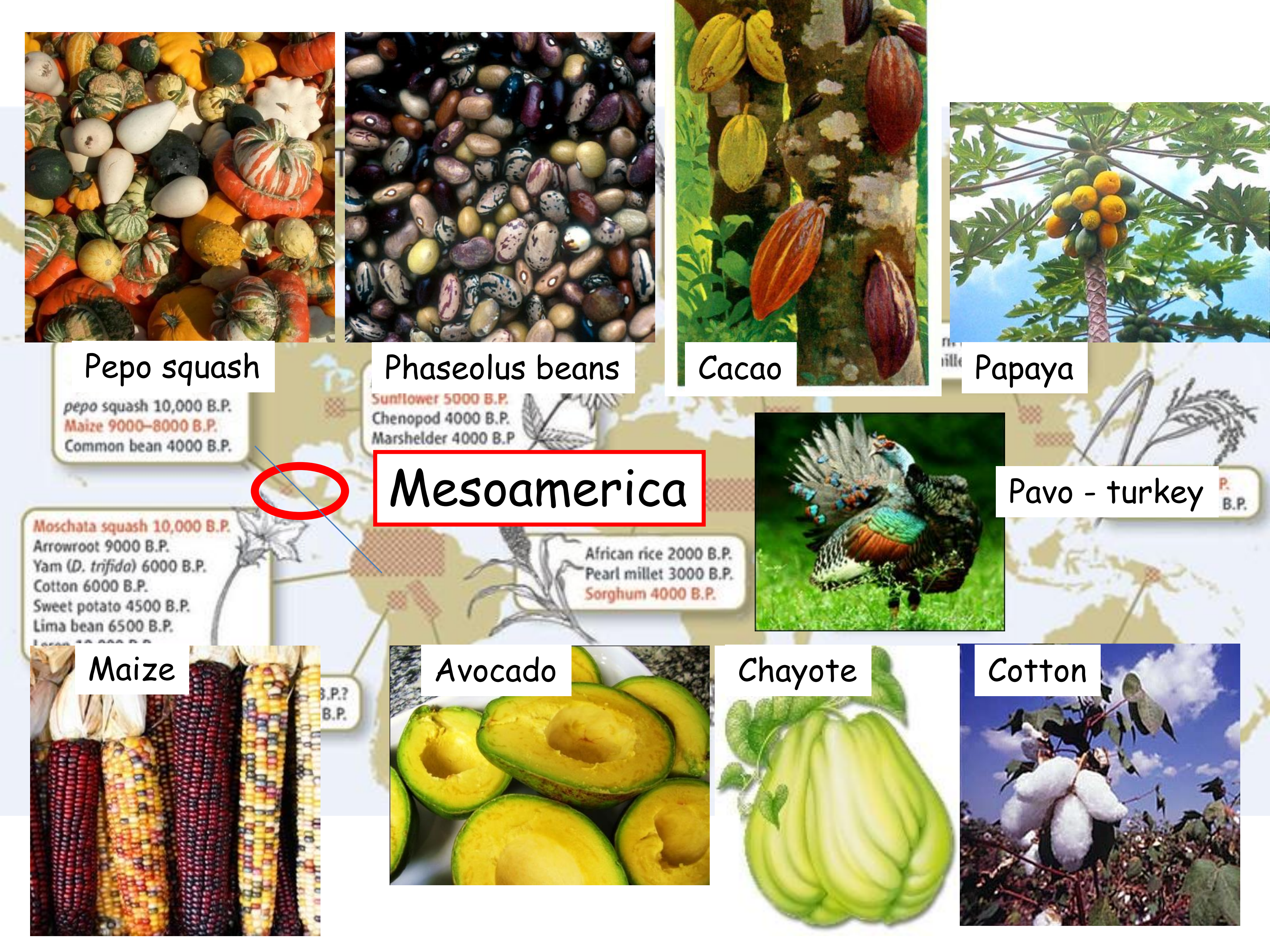


Murphy (2007)

Summary of the transition from foraging and hunting to herding and farming and the origins of agriculture in the Fertile Crescent

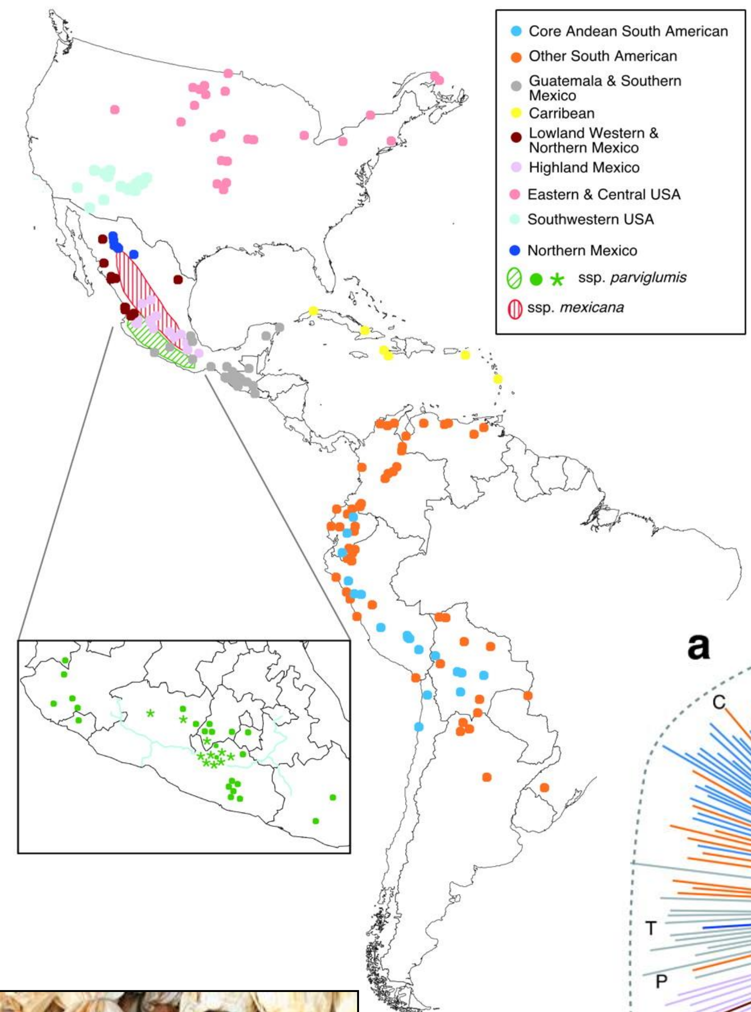


Brown *et al* (2009)



Mesoamerica
Pepo squash
Phaseolus beans
Cacao
Papaya
Pavo - turkey
Maize
Avocado
Chayote
Cotton
pepo squash 10,000 B.P.
Maize 9000–8000 B.P.
Common bean 4000 B.P.
Sunflower 5000 B.P.
Chenopod 4000 B.P.
Marshelder 4000 B.P
Moschata squash 10,000 B.P.
Arrowroot 9000 B.P.
Yam (D. trifida) 6000 B.P.
Cotton 6000 B.P.
Sweet potato 4500 B.P.
Lima bean 6500 B.P.
African rice 2000 B.P.
Pearl millet 3000 B.P.
Sorghum 4000 B.P.


Maize + Beans



Maize – Genetic Data

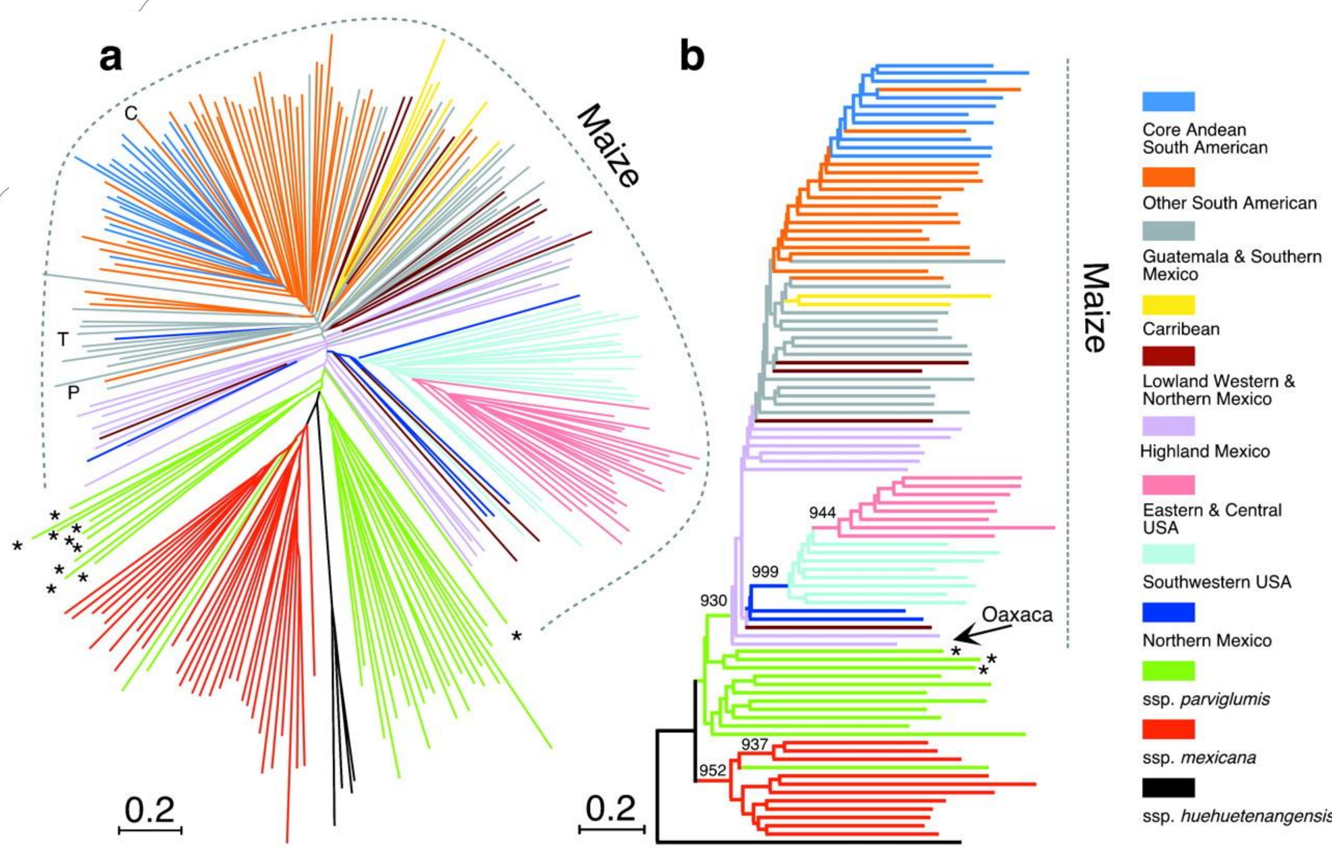
Annual teosinte – *Z. mays* ssp. *parviglumis* distributed in the Balsas Depression of southern Mexico

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

Most closely allied teosinte is in the Balsas Depression

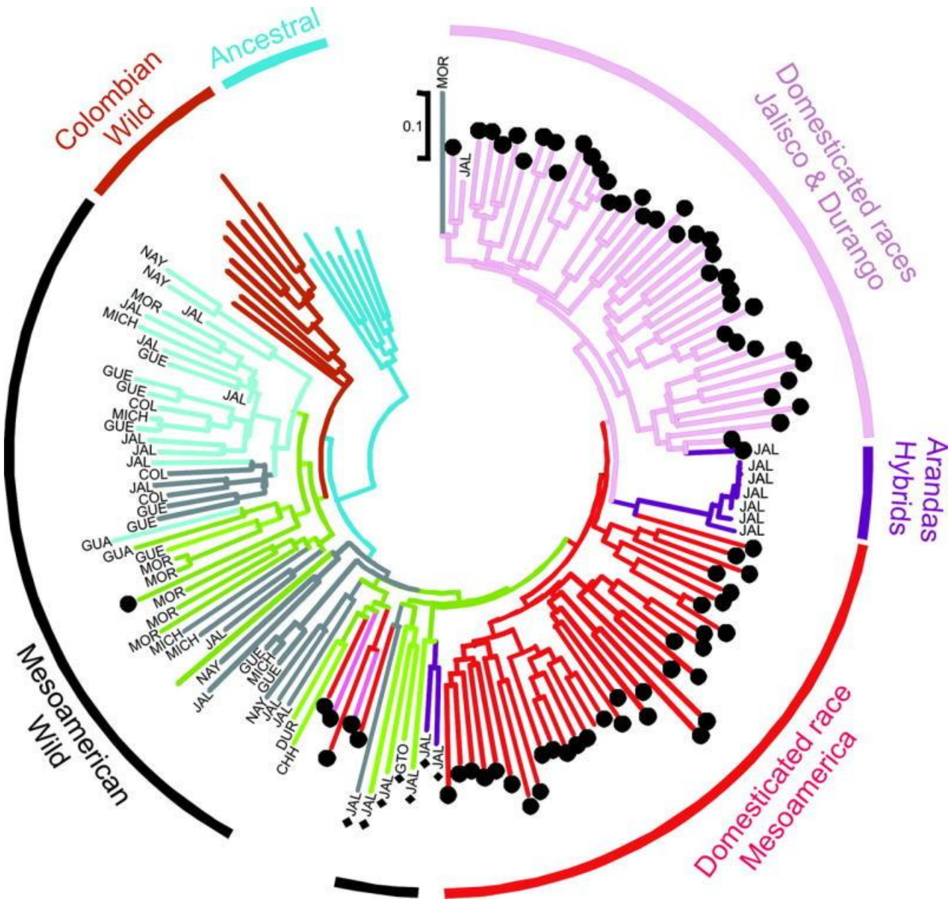
Earliest branching maize lineage from Oaxaca.

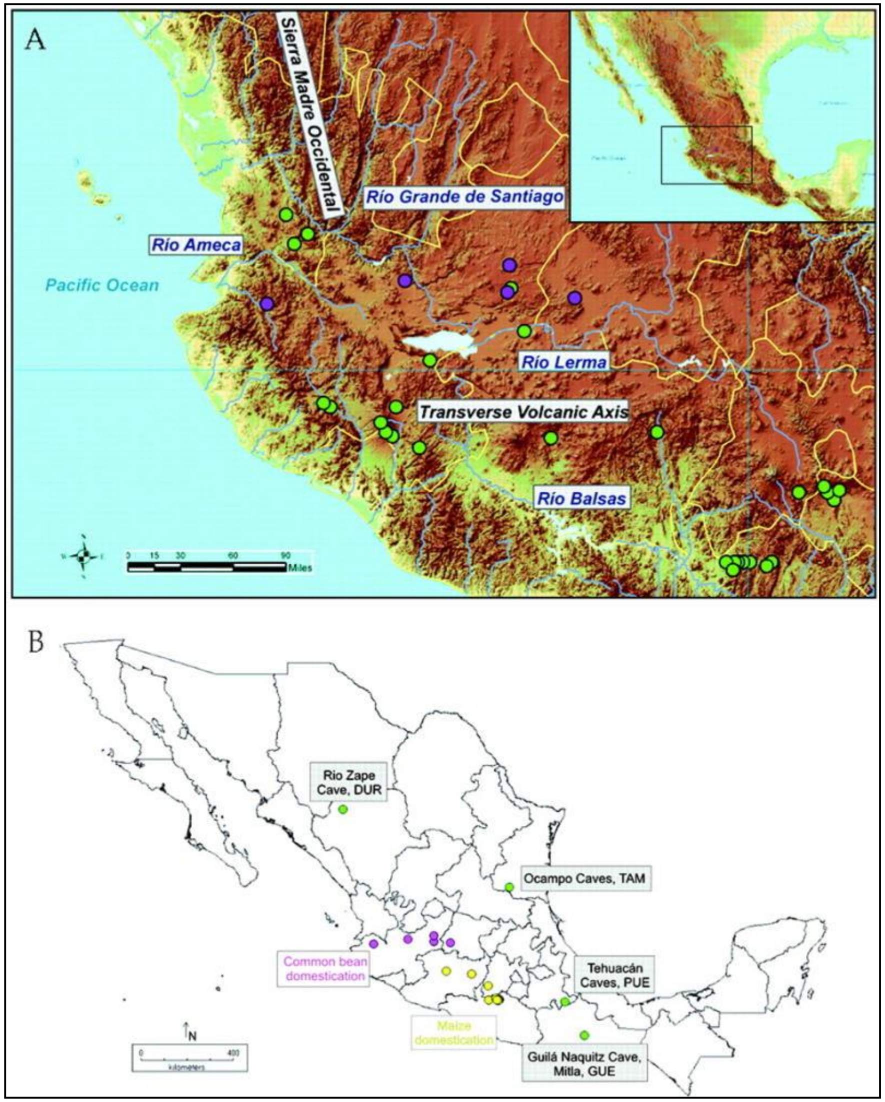
Matsuoka et al 2002 PNAS



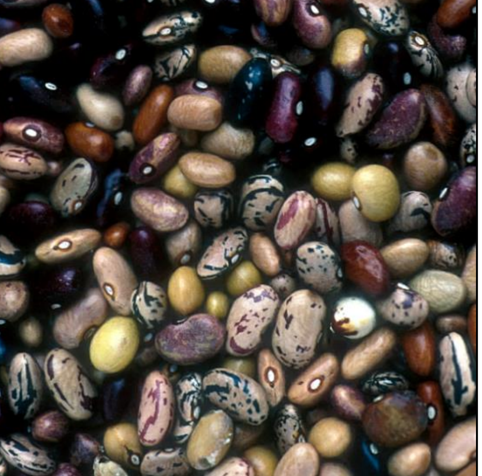
Mesoamerica

Domestication of *Phaseolus* beans in Mexico





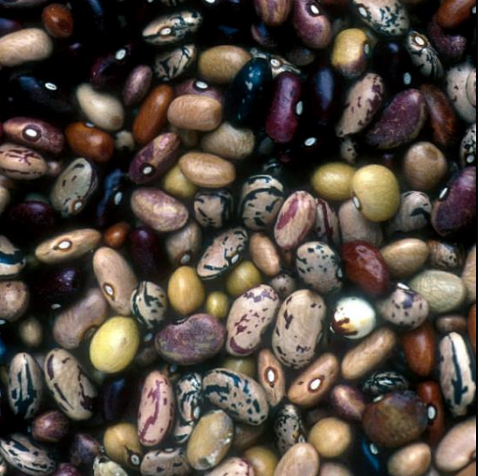
Kwak et al (2009)



Mesoamerica

	Oaxaca 17°	Tehuacán 18°30'	Tamaulipas 23°	Southwest 32°
BEAN	2100	2300	1300	2200
MAIZE	6300	5500	4300	3500
SQUASH	10,000	7,900	6300	3500

Smith (2001)



Mesoamerica

The regional geotemporal pattern of crop domestication:

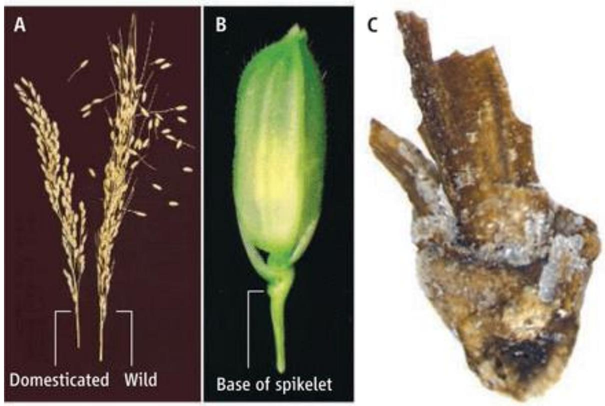
- Maize & squash first in S, then moving sequentially N
- Beans first in W, simultaneously appearing later in N & S
- Different rates of diffusion – maize fastest
- Different crops appear at different times

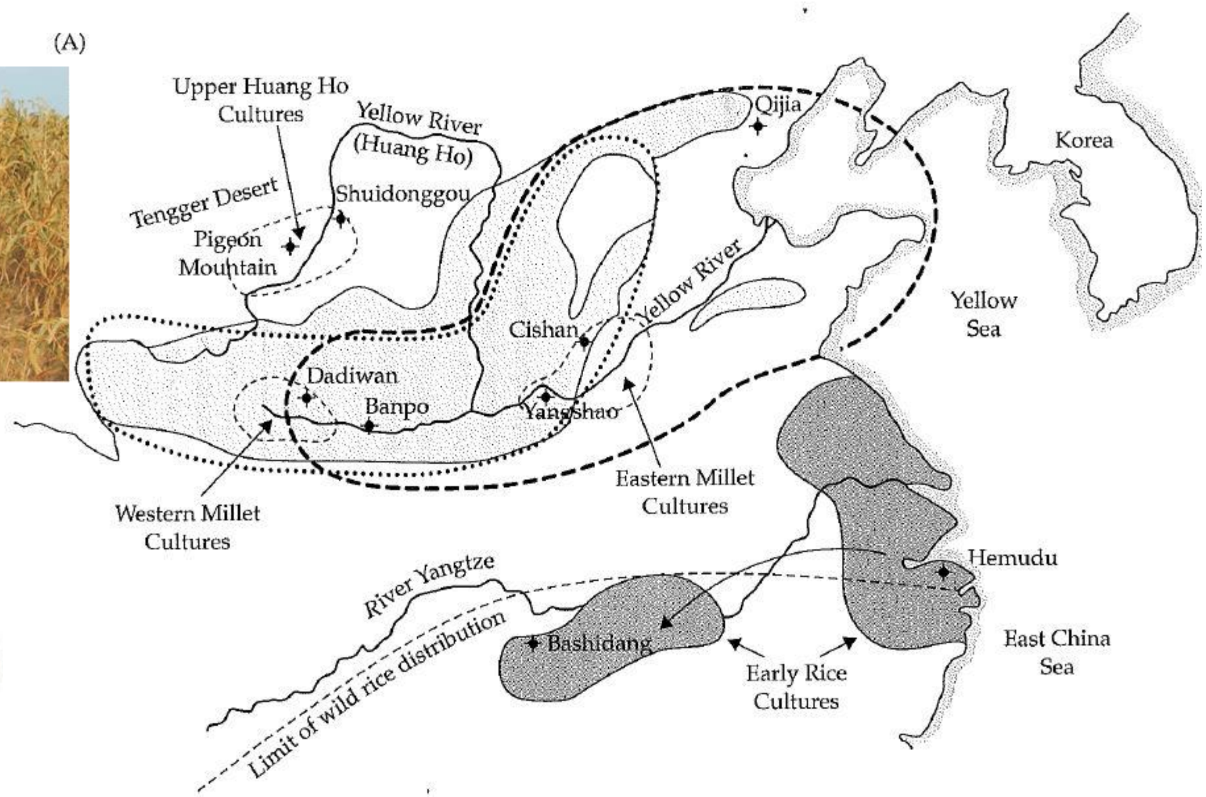
Tentative scenario for the evolution of agriculture:

- Squash 10,000 – domesticated by hunter-gatherer groups
- Maize 7,000 – domesticated by low-level food producing societies already growing squash for > 1,000 years – the *Era of Incipient Cultivation*
- 4,000 – first appearance of village-based farming societies
- Beans – 2,500 – added into already well-established farming economies

Smith (2001)

Rice & Millet in China

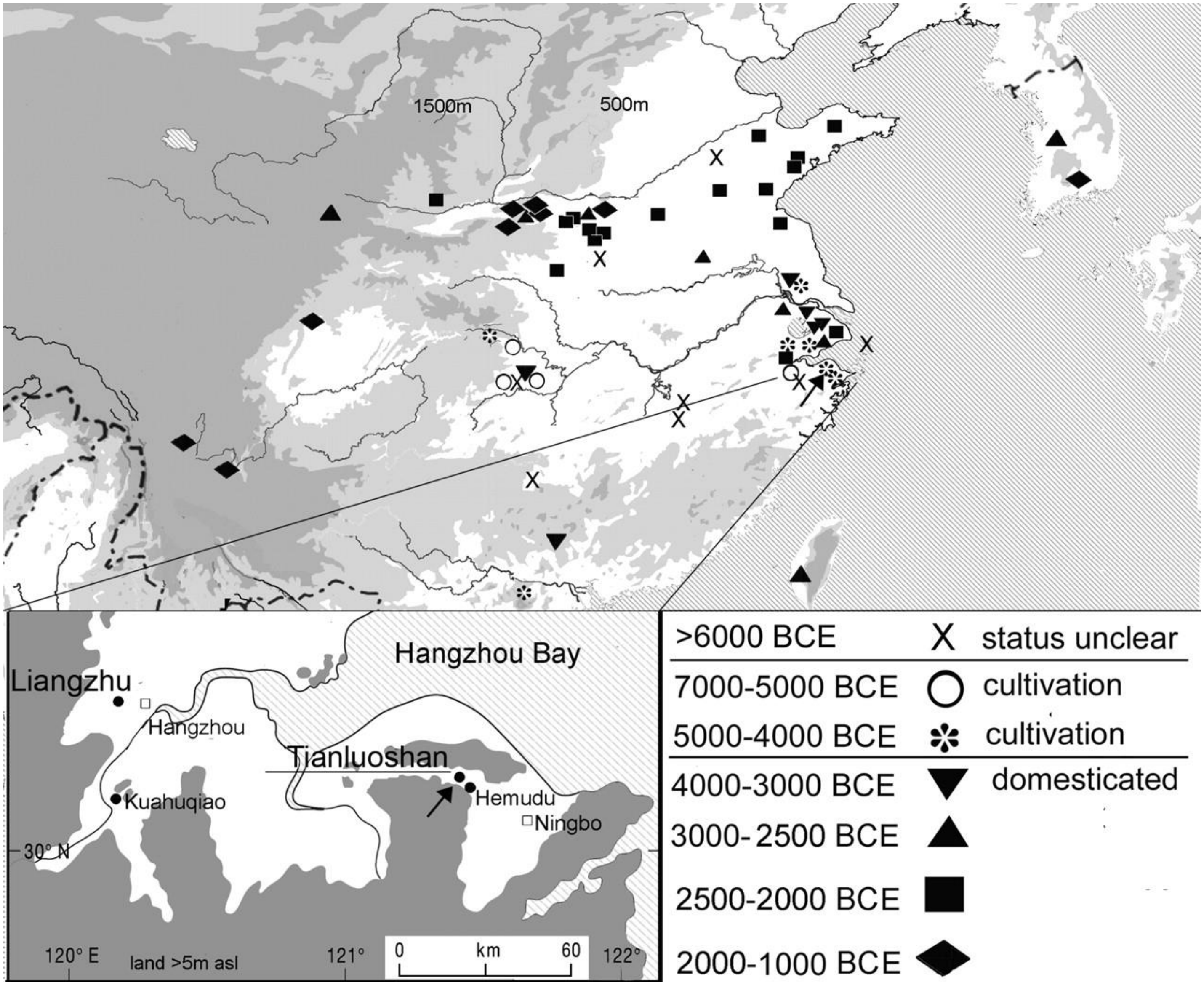




- Millet - Farming based mainly on millet (Setaria italica and Panicum miliaceum) emerged independently in at least two areas of north China c. 6,000 BP and was widely farmed across much of the Yellow River basin (grey area on map) by 5,000 BP. Rice from further south was added to farming in this area as late as 3,000 BP

- Rice - Further south in the warmer and damper climates of the Yangtse basin wetlands, rice cultivation probably started around 5,000 BP, implying a rate of domestication of the order of 1000 to 1500 years from the beginning of cultivation to full domestication, similar to the rates of grain size increase in wheat and barley.

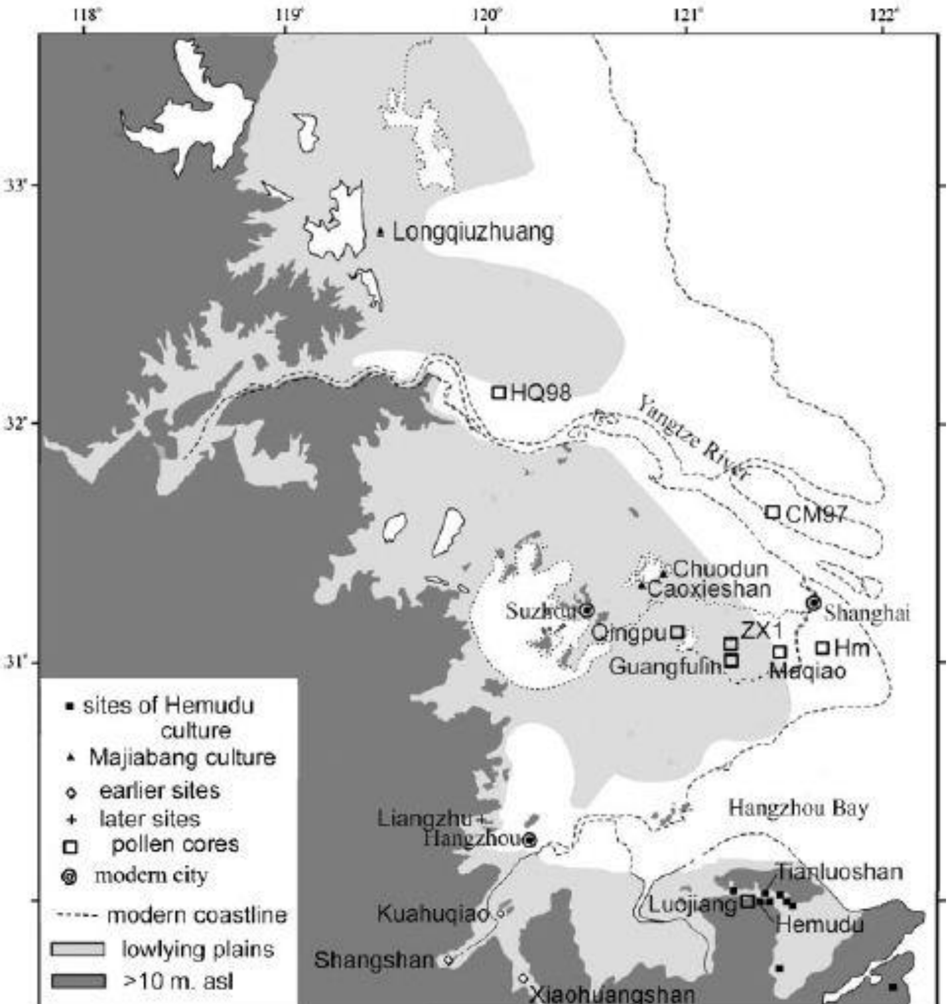
Representative early rice finds in China



Fuller et al. (2009)

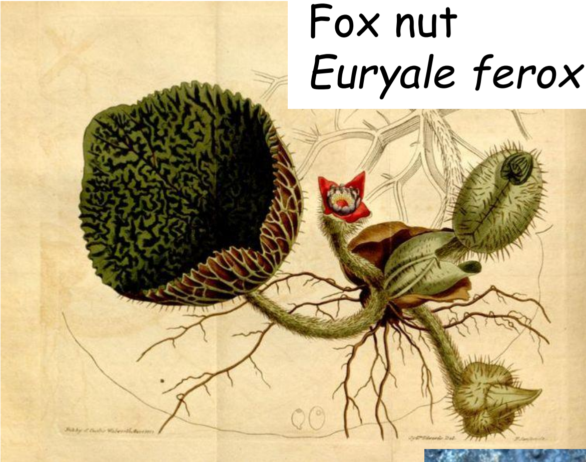
Tianluoshan

- discovered & excavated in 2004
- impressive waterlogged preservation of 24,000 plant remains, incl 2,600 rice spikelets
- Spans tipping point at which non-shattering spikelets > shattering spikelets



Fuller & Qin (2010)

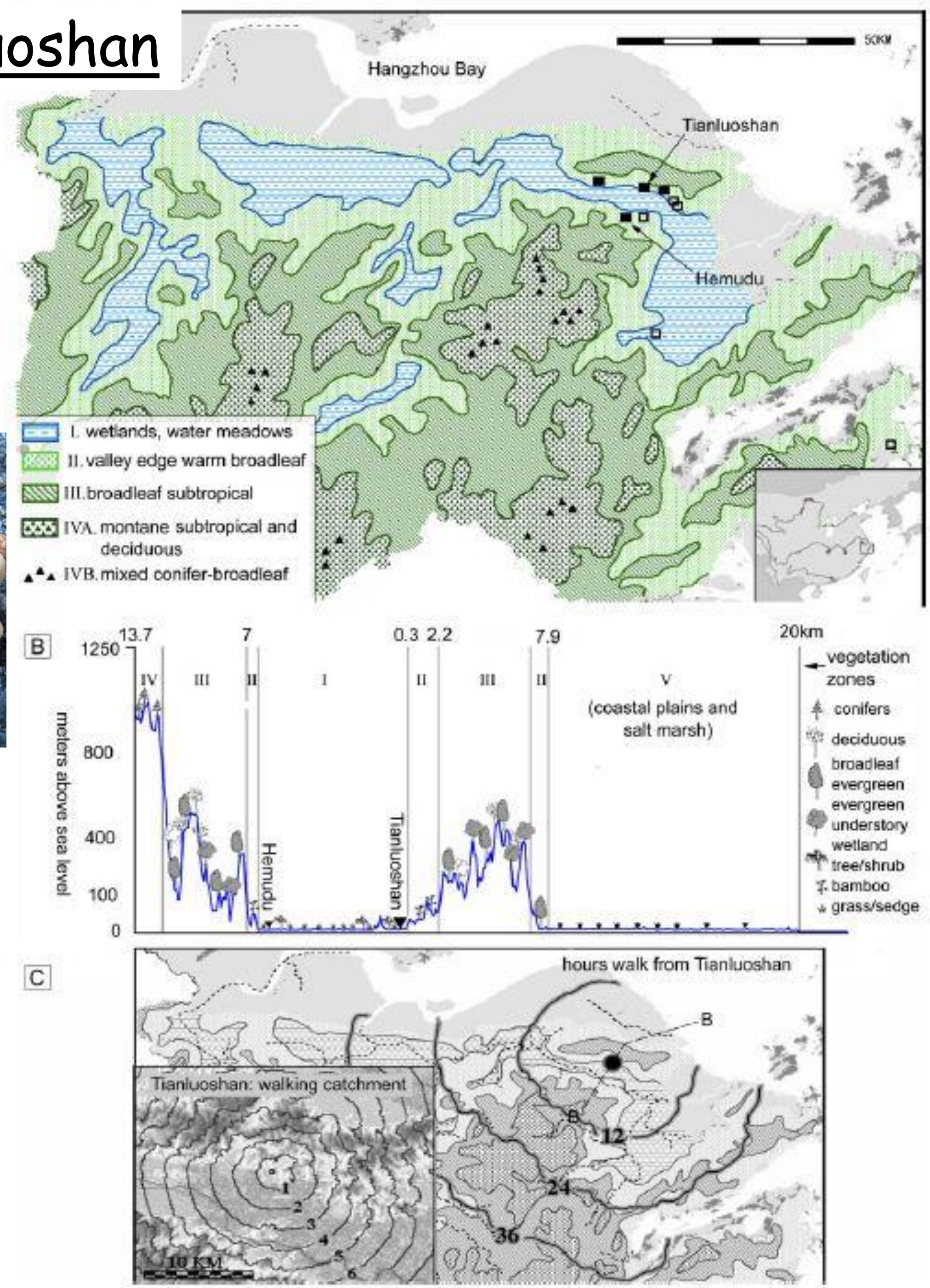
Tianluoshan



Fox nut
Euryale ferox

Acorns
Quercus spp

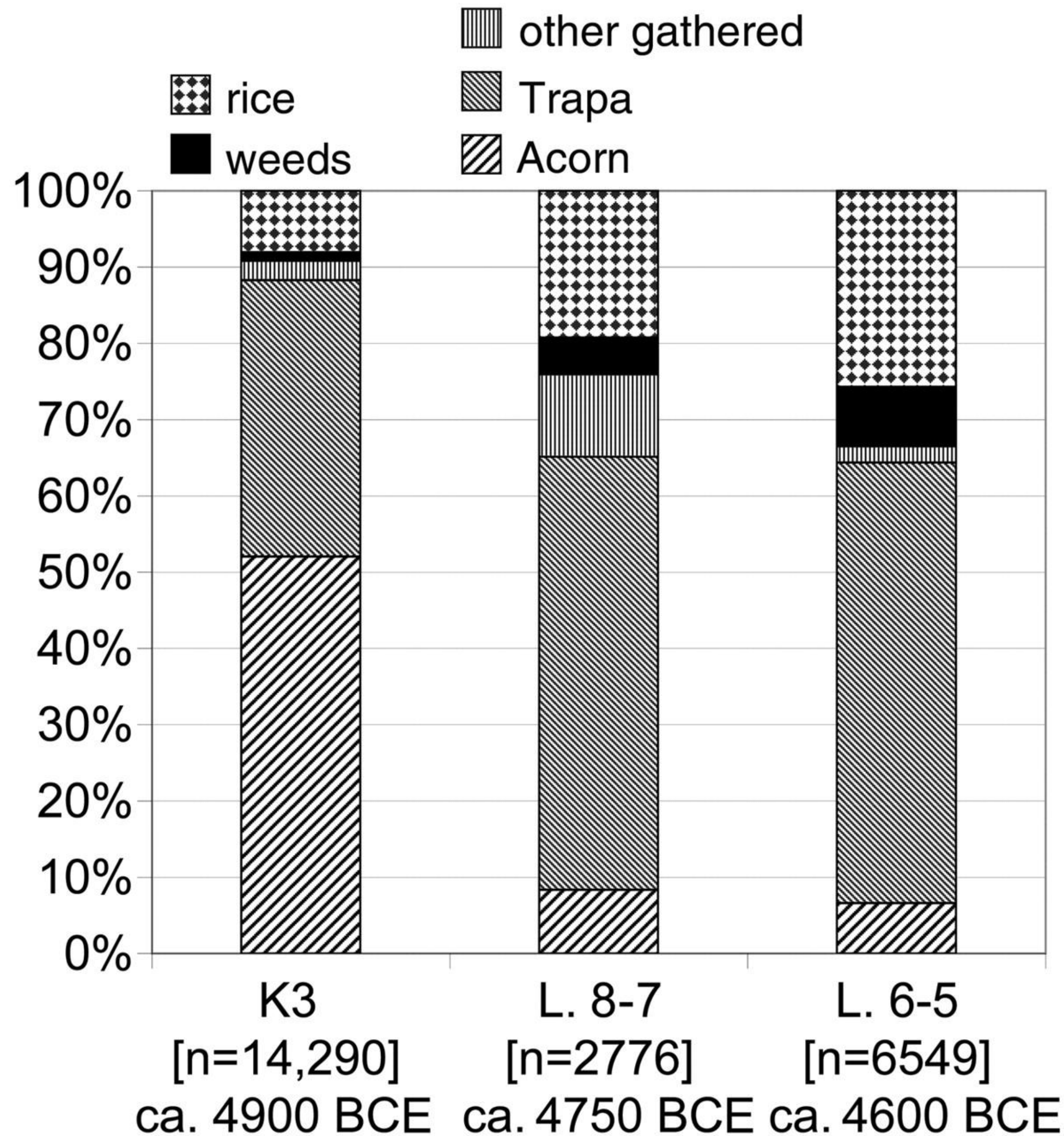
Water chestnut
Trapa natans



Tianluoshan

Increasing proportion of rice in the plant assemblage as a whole

Declining consumption of aquatic nuts and acorns



Fuller et al. (2009)

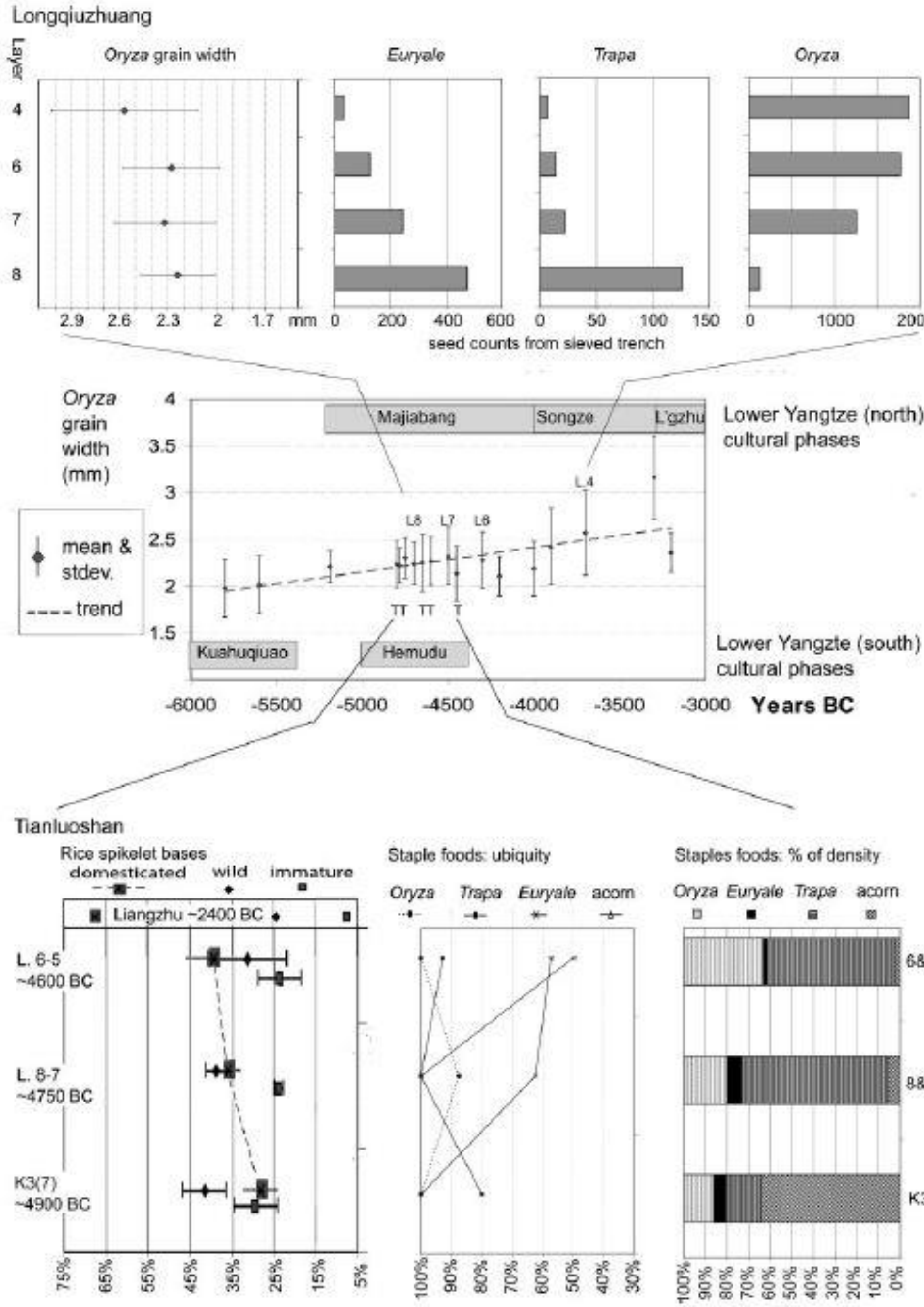
<u>Tianluoshan</u> – rice domestication indicators for the lower Yangtze

- Quantitative shifts in rice grain size and toward rice and away from wild wetland foods

- Declining oaks, increasing artistry, and cultivating rice: the environmental and social cotext of the emergence of farming in the lower Yangtze region

- Full transition from wild to domesticated rice cultivation took at least 2,000 to 3,000 years

- Rice domestication was not complete until after 6,500BP



Fuller & Qin (2010)

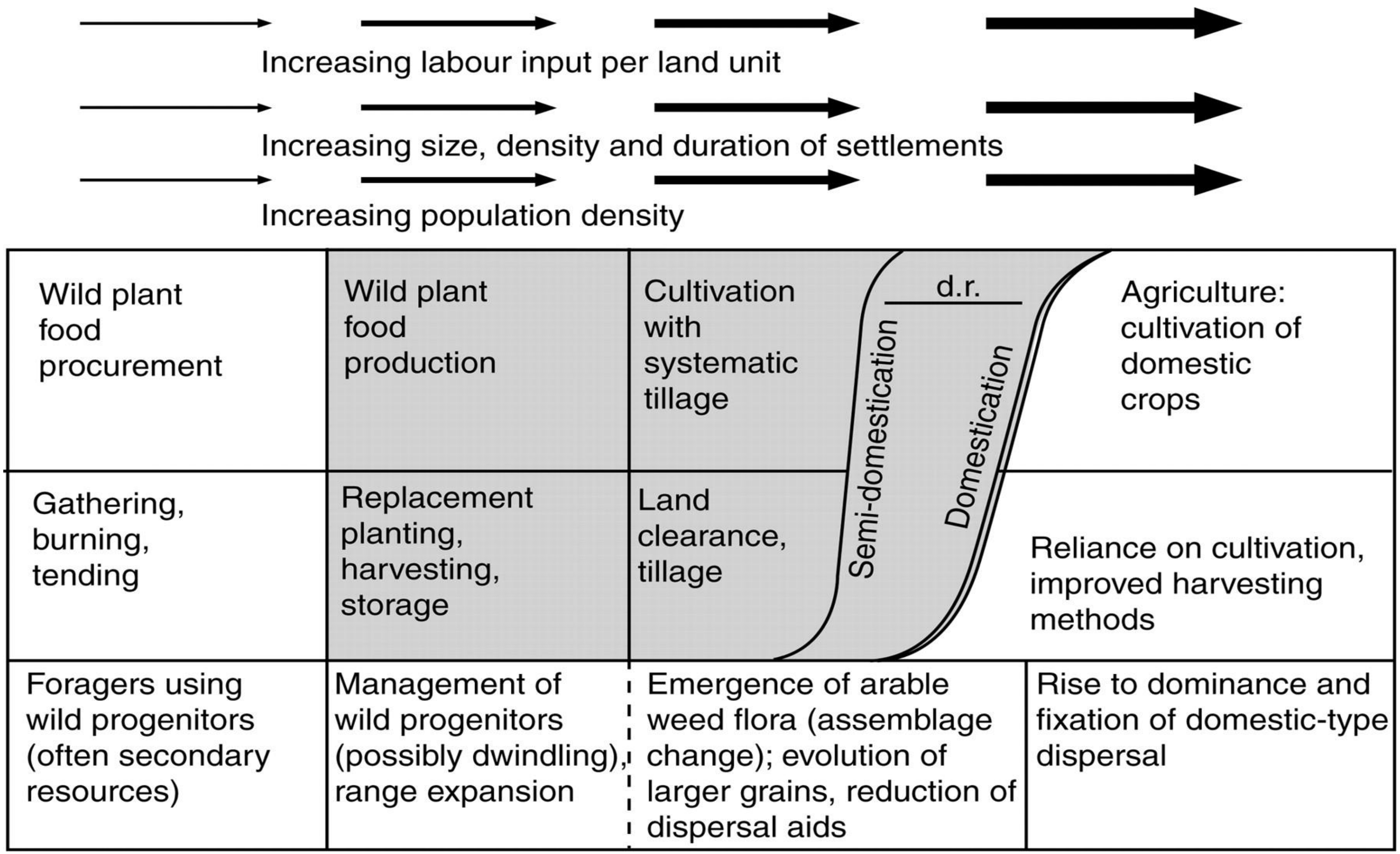
Evolution (not revolution) of Agriculture – Conclusions

Crop domestication and the origins of agriculture have been described as dubbed the *Neolithic Revolution*, but now clear that the transition from foraging to farming was a much more gradual, protracted process – spanning several millennia rather than a few centuries.

Data from all three regions – the Fertile Crescent, Mesoamerica, and China indicate that:

- Early resource management aimed at encouraging plant production and manipulation of herd structure preceded any manifestation of traditional markers of domestication by 100s if not 1000s of years.
- initial domestication and the gradual emergence of domestication traits followed by a long period of low-level food production with continued hunting and gathering, suggestive of a continuum between wild and domesticated, between foraging and farming, between hunting and herding.
- Cultivation included a mix of wild and domesticated species; wild varieties gradually replaced by domesticated species
- wild and domesticated plants frequently intermixed with opportunities for geneflow
- initial domesticates still not like modern ones, domestication as a process of gradual frequency change, with an earlier, more rapid semi-domestication, and a later, slower fixation of full domestication.
- Fixation of non-shattering (=time frame of domestication) = 1000s, not 100s of years
- crops added sequentially over several millennia, not all at once.
- domestication was a protracted, multi-stage and complex process

Co-Evolution between Plants and People – a Model for the transition from Foraging to Agriculture



d.r. = minimun estimate of domestication rate as the gap in time elapsed between semi and full domestication

Fuller (2007)

Next Week – 13 November

- Lecture 9 – Cattle, pigs, goats & sheep – similarities and differences between crop and livestock domestication

Question for next week
– how many species of animals have been domesticated?