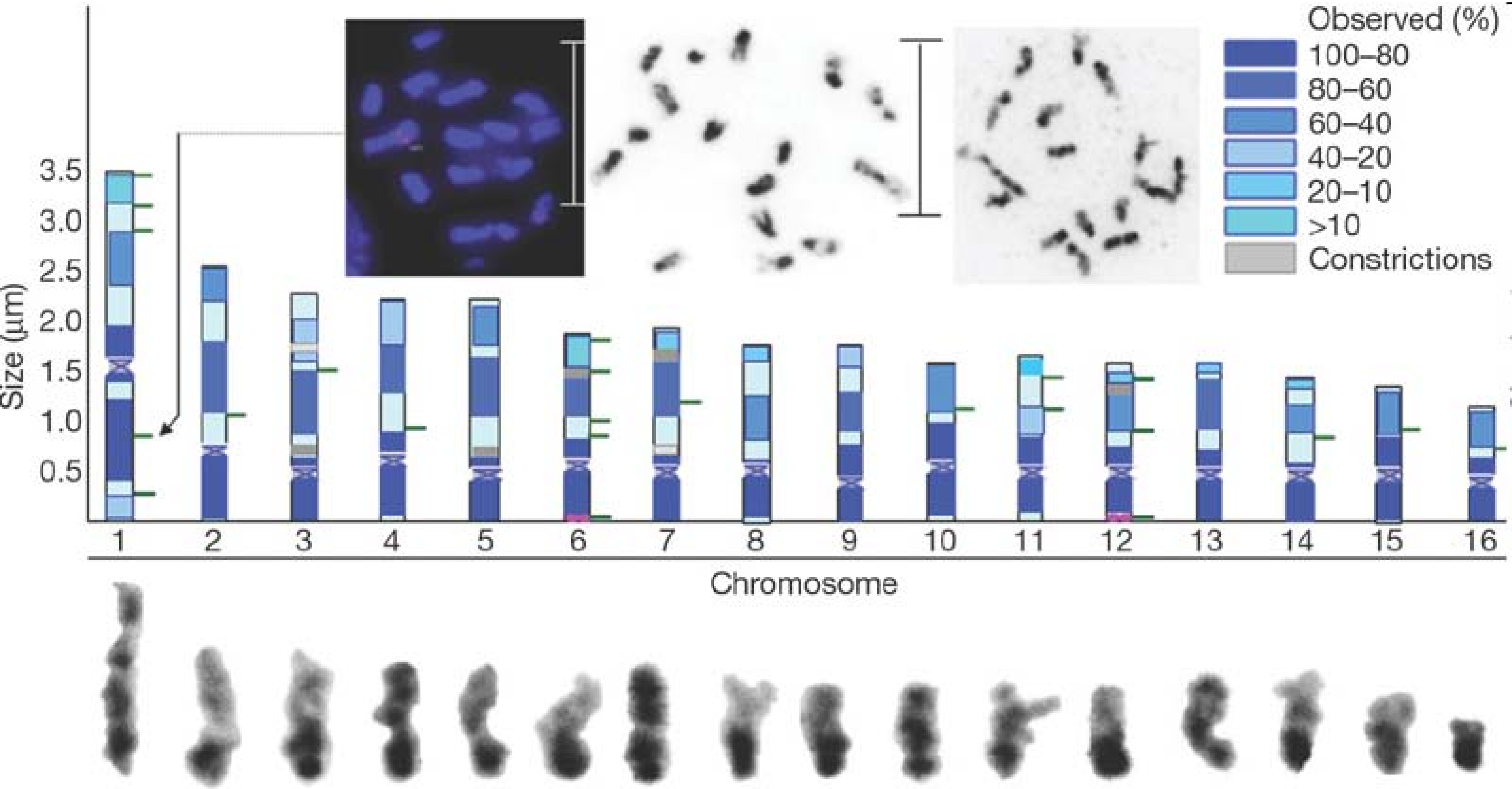
Introduction to Bee Genetics

Some Basic Bee Biology

- *Haplo-diplontic organism*
- Workers and queens: two sets of 16 chms
- Drones: one unpaired set of 16
- Eggs laid in drone cells are unfertilised


Observed (%)
100–80
80–60
60–40
40–20
20–10
>10
Constrictions
Size (µm)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Chromosome

- Drones – x (sometimes n), aka ‘haploid’
- Queens – 2x (or 2n), aka ‘diploid’
- Drones produce sperm (each one identical) by mitosis (normal division)
- Queens produce gametes by meoisis (a reduction division which involves recombination* of parental chromosomes)
- Such gametes are all different, unlike the sperm

* Recombination is the exchanging of segments of partner chromosomes

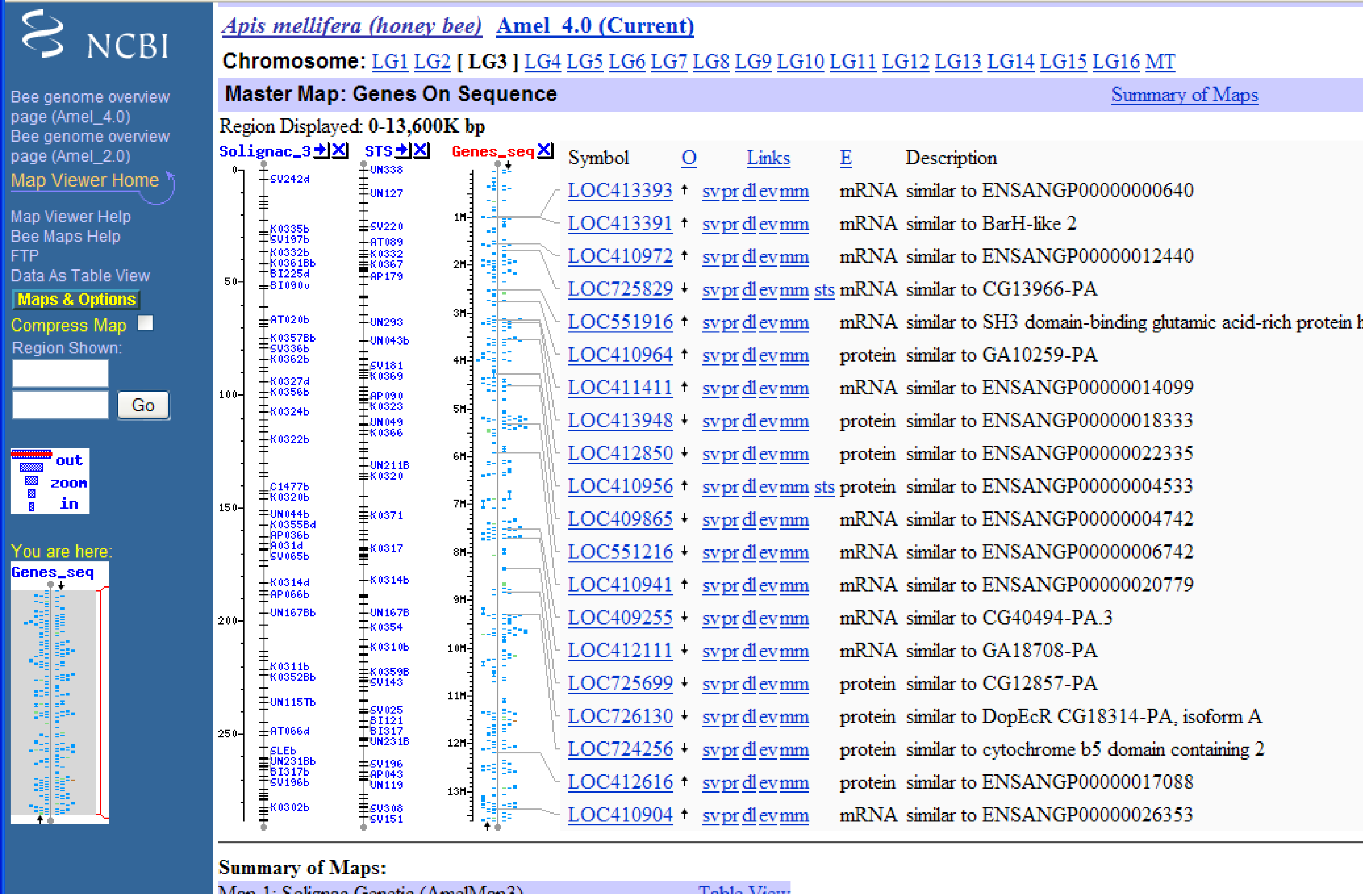
- Queens have around 10-15 mates
- Recombination rates are the highest known for any animal, 10x greater than most
- Implications are that hybrids quickly end up with very mixed chromosomes

What does this mean?

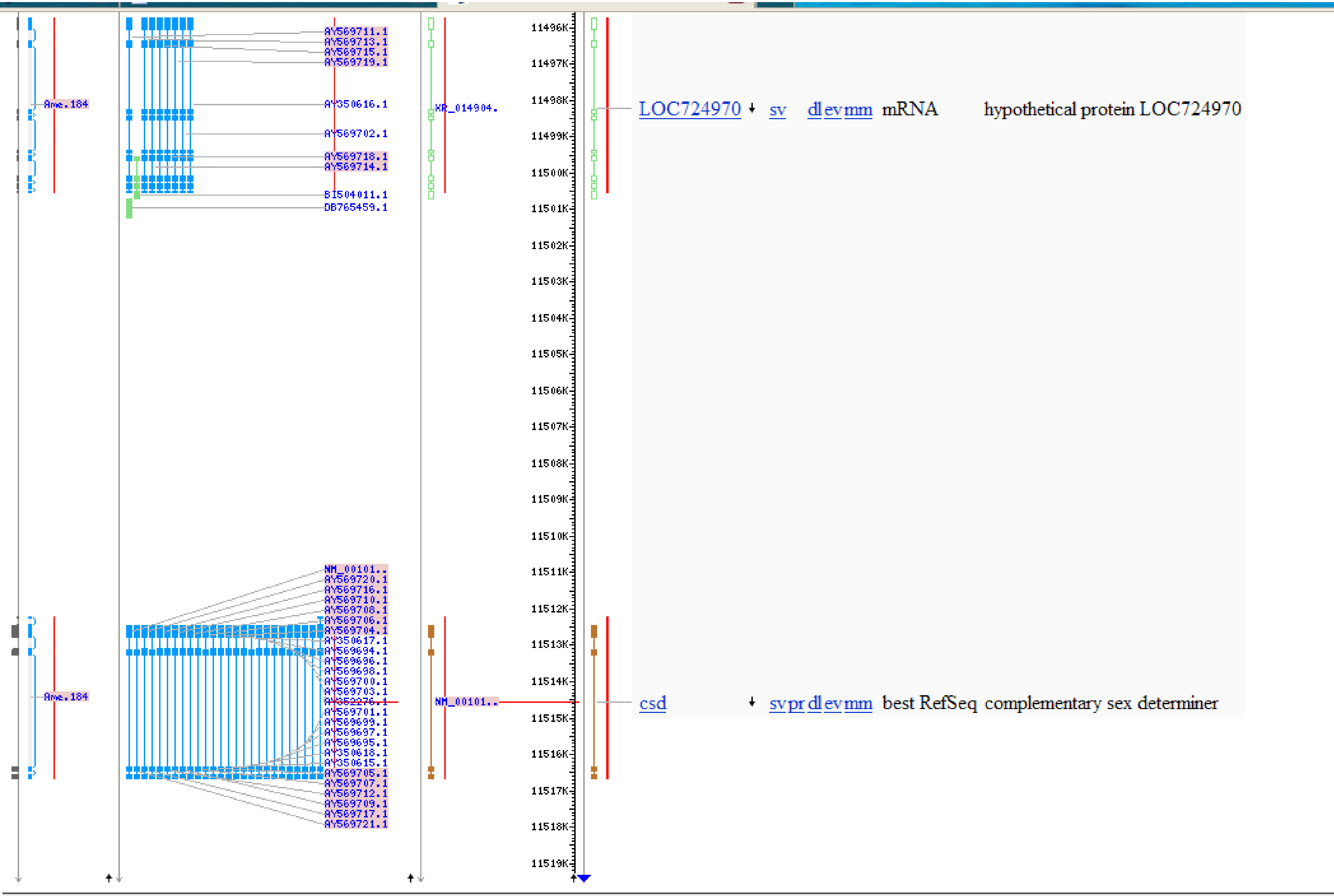
- Drones ‘filter out’ bad gene versions (a version of a gene is an ‘allele’) as there is no masking of effects with functioning versions
- Single queens can store most of the variation* found in the bees of an area
- No-one knows why recombination rate is very high

* Each queen carries 2 alleles in her own cells plus the sperm from 10-15 mates

The Honeybee Genome Has Been Decoded



Freely available online, chm 3 showing all the genes present (pale blue boxes)



Part of chm 3 with a gene crucial to honeybee population genetics, *csd*.

Amino acid alignment of the hypervariable region with a variable number of (N)1–4/Y repeats that were excluded in the evolutionary sequence analysis.

```
          330                                                                        404
B2-25     EPKIIS---SLLNNTIHNN---------------NNYK-------------------KLQYYN--INYIEQPVPV
A2-8      ERKIIS---SLSNNYNYNNN-----------NYKYNYNN----------------YNKKLYYKNYIINIEQPVPV
B1-4      EPKIIS---SLSNKTIHNN-----------NNYKYNYNNNNYNNN--NYNNNYNNNCKKLYYN--IINIEQPVPV
A1-18     EPKIIS---SLSNKTIHN---------------NNNYNNY---------------NNKKLYYN--INYIEQPVPV   Type I
D1-16     EPKIIS---SLSNKTIHNN---------------NNYNNNNYNNNYNNYNNNNYNNYKKLYYN--IINIEQPVPV
S2-33     ETKIIS---SNNYNYKNY---------------NNNYNS------------------KKLYYN--IINIEQPVPV
S7-16     EPKIIS---SLSNSCNYS---------------NNYYNNN---------------NYKKLYYN--INYIEQPIPV
S7-5      EPKIIS---SLSNNTIHN---------------NN--------------------YNKKLYYN--IINIEQPVPV
D1-22     EPKIIS---SLSNNYKYSNYNNYN------NYNNNNYNN----------------YNKKLYYKNYIINIEQPVPV
D2-38     EPKIIS---SLSNNYN-----------------YNNYNN----------------NYKPLHYN--INYIEQPVPV
A-5       ESKIIS---SLSNKTIHN---------------NNNYKN----------------YNKKLYYN--IINIEQPVPV
S2-31     EPKIIS---SLSNNYN-----------------YNNYNN----------------NYKPLYYN--IINIEQPVPV
D1-18     EPKIIS---SLSNNYKYSNYNNYNNNYNNYNNYNNNYNN----------------NYKKLYYN--INYIEQPVPV
A1-28     EPKIISNNNSLSNNYN----------------YNNNYNN------------YNKHNYNKLYYN--INYIEQPIPV

B2-17     EHRIIP-----------------------------------------------------------SHYIEQPAPV   Type II
```

Hasselmann M , Beye M PNAS 2004;101:4888-4893

PNAS

Csd gene

- Controls gender
- If only one type present, functionally male
- If two different types, functionally female
- Diploids with 2 identical copies are ‘diploid drones’ from fertilised eggs laid in worker cells
- Diploid drones are usually eaten as young larvae and a drain on colony resources
- See later for population effects

The Main Races: Where From?

The genetics of different bee races

- Paper by Whitfield on ‘Thrice out of Africa’
- Perfectly matches Ruttner’s morphometric study

In North America, introductions of the subspecies *Apis mellifera mellifera* began as early as 1622. Subsequent introductions of *A. m. ligustica* (the “Italian” bee) began in 1859, followed by introductions of at least seven other subspecies from Europe, the Near East, and northern Africa (the descendants of which are collectively called “European”) (*10*). Early introductions in South America are less clear, but probably also involved

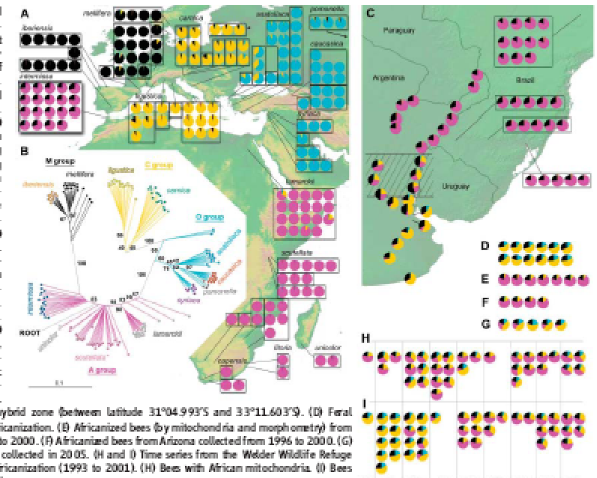
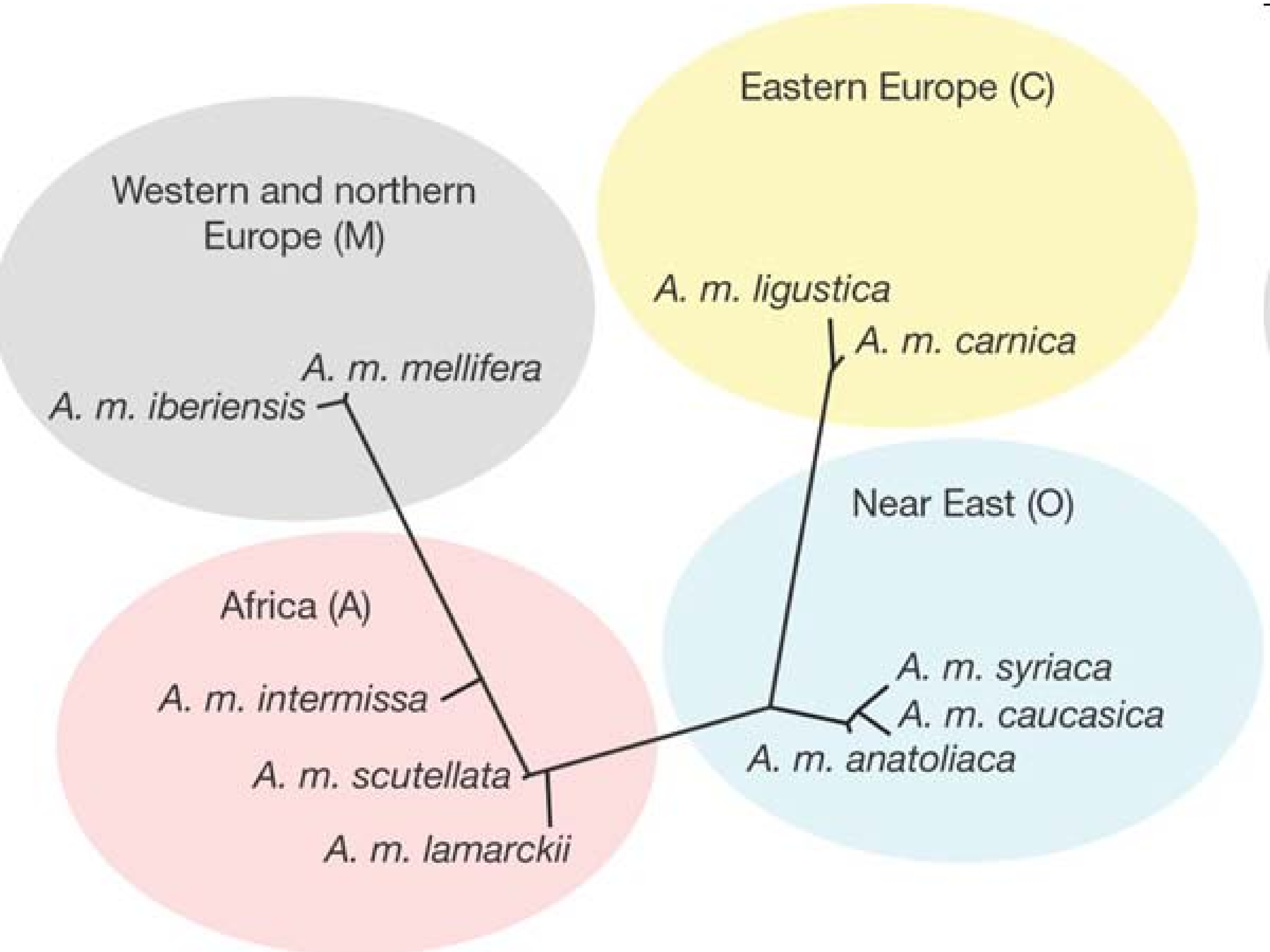


Fig. 2. Geographical and temporal patterns of diversification. (A) Assignment probabilities from *Structure* analysis (Fig. 1C, $K = 4$) of Old World individuals. *A. m. pomonella* ($N = 3$) collected from Kyrgyzstan. Three *A. m. carnica* (indicated by asterisk) were provided by a research facility. (B) Neighbor-joining tree based on allele-sharing distance. “ROOT” represents a single derived genotype consisting of 289 SNPs with one common homozygous genotype from *A. cerana* ($N = 7$) and *A. dorsata* ($N = 4$) (*32*). Branches are colored to correspond to the four groups in (A). The group labeled *scutellata** also includes *A. m. litoria* ($N = 2$) and *A. m. capensis* ($N = 3$). (C to I) *Structure* analysis (Fig. 1C, $K = 4$) of New World individuals. (C) Geographic distribution of Africanization in South America. Hatched region denotes hybrid zone (between latitude 31°04.993′S and 33°11.603′S). (D) Feral bees from Texas before Africanization. (E) Africanized bees (by mitochondria and morphometry) from Texas collected from 1996 to 2000. (F) Africanized bees from Arizona collected from 1996 to 2000. (G) Managed bees from Texas collected in 2005. (H and I) Time series from the Welder Wildlife Refuge (southern Texas) during Africanization (1993 to 2001). (H) Bees with African mitochondria. (I) Bees with European mitochondria.

Table 1. Candidate loci for selection. Subset of outlier SNPs from Fig. 3A (Set 1) and Fig. 3B (Set 2) (see table S3). The frequency of predominant *A. m. scutellata* allele is indicated. Syn, synonymous codon change. Groups for South and North America are as indicated in Fig. 2 (arranged by increasing Africanization from left to right). UTR, untranslated region; UV, ultraviolet; GTPase, guanosine triphosphatase; PKG, cGMP-dependent protein kinase.

	Old World				South America			North America							
SNP	*ligustica*	*mellifera*	*scutellata*	*caucasica*	South	Hybrid zone	North	European	1993–1995	1996–1998	1999–2001	Africanized	Near or affected gene	SNP position or effect	Gene product
							Set 1								
est6550	0.00	0.95	1.00	1.00	0.06	0.83	0.99	0.21	0.38	0.64	0.88	0.91	GB11704	5′ UTR	
ahb7495	0.00	0.94	0.97	0.00	0.13	0.42	0.97	0.08	0.29	0.50	0.46	0.91	GB10583 (*nAchRα3*)	†	Nicotinic acetylcholine receptor, α3 subunit
est8764	0.00	1.00	0.97	1.00	0.25	0.75	1.00	0.13	0.59	0.69	0.73	0.86	GB10830	S→A	
est9209*	0.03	0.98	1.00	0.36	0.19	0.75	0.97	0.21	0.54	0.62	0.79	0.91	GB10514(*Tuba1*)	Syn	Tubulin, α1 chain
est9211*	0.03	0.98	0.97	0.32	0.19	0.75	0.97	0.21	0.55	0.67	0.79	0.95	GB10514 (*Tuba1*)	Syn	Tubulin, α1 chain
							Set 2								
ahb12140	0.00	0.00	1.00	0.00	0.00	0.33	0.76	0.04	0.20	0.38	0.44	0.73	GB18171 (*UVop*)	Syn	UV-sensitive opsin
ahb11258	0.00	0.00	0.92	0.00	0.00	0.25	0.74	0.00	0.21	0.40	0.65	0.86	GB15150	Intron	GTPase activator
ahb11774	0.08	0.03	0.94	0.00	0.00	0.50	0.76	0.04	0.23	0.55	0.54	0.50	GB15050	~1500 bp 5′	
est424	0.25	0.20	0.97	0.00	0.19	0.92	0.92	0.17	0.41	0.45	0.71	0.86	GB19539	Syn	
est10185	0.00	0.00	0.91	1.00	0.06	0.50	0.81	0.13	0.32	0.57	0.58	0.45	GB18394 (*for*)	3′ UTR	*foraging*; PKG
ahb9731	0.00	0.05	0.78	0.00	0.00	0.17	0.69	0.00	0.18	0.57	0.50	0.77	GB15214	Syn	

*These two SNPs are 939 base pairs (bp) apart. †Approximately 3000 bp 5′ of start codon for gene prediction GB10583; this gene has an alternate predicted structure (SC_Group5.240000300) (*9*) that places the SNP 30 bp upstream of the start codon.



Eastern Europe (C)
Western and northern Europe (M)
A. m. ligustica
A. m. carnica
A. m. mellifera
A. m. iberiensis
Near East (O)
Africa (A)
A. m. syriaca
A. m. intermissa
A. m. caucasica
A. m. anatoliaca
A. m. scutellata
A. m. lamarckii

Inbreeding and Outbreeding

Outbreeding:

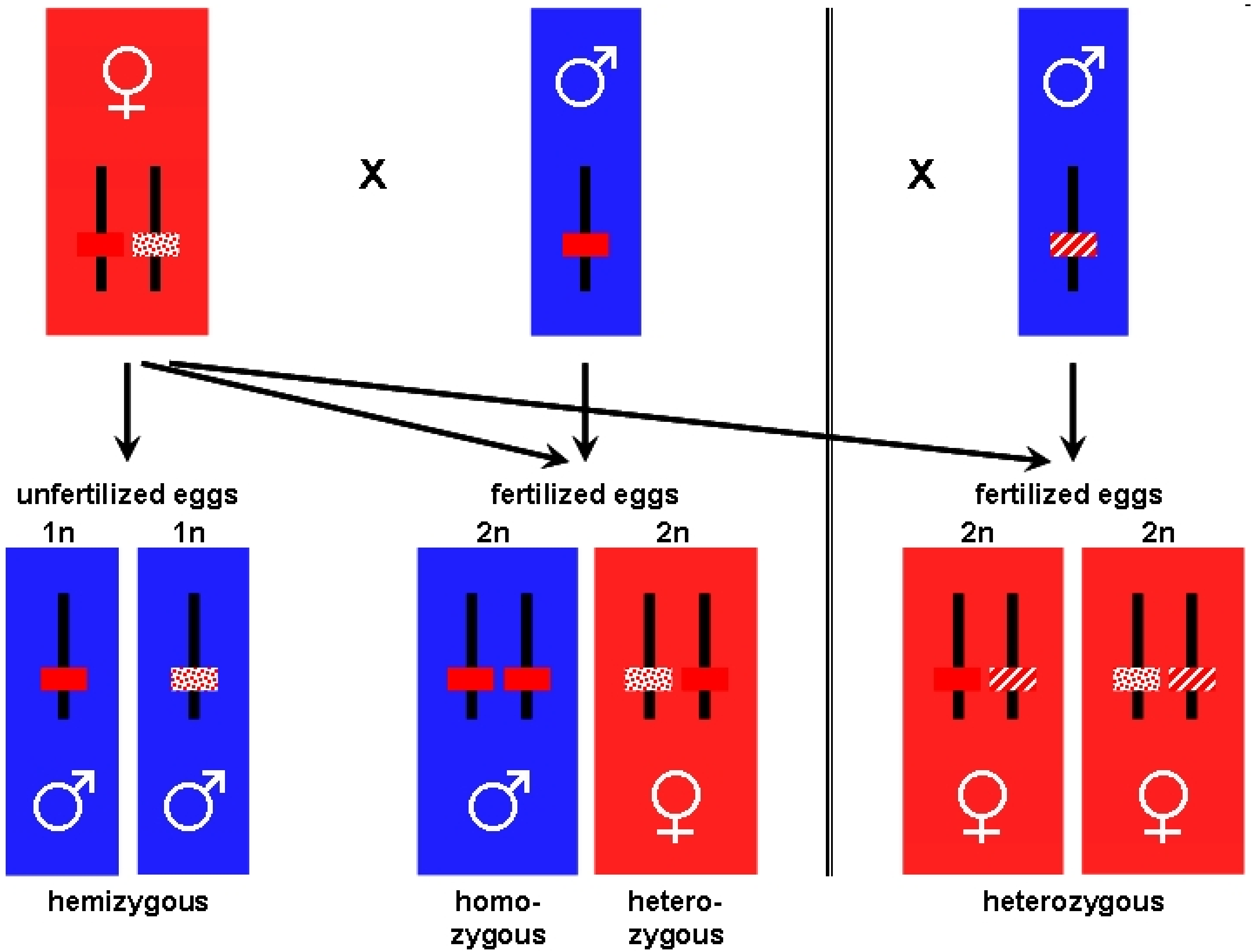
- Drones and queens fly far (10-40 miles!)
- Local mating possible, also cold flying
- DCAs are historic sites
- Controlling the drone genetics of an area is very difficult!
- Outbreeding gives general vigour
- Second and later generation crosses can be bad tempered, especially across large genetic divides

Inbreeding and Outbreeding

Inbreeding:

- Permits selection to be effective
- Reduces resistance to pests and disease
- Reduces colony vigour
- Colonies in many isolated areas must be exposed to a risk of inbreeding
- Main reason for problems is the *csd* gene

Complementary Sex Determiner



Effects of *csd*

- Healthy populations carry perhaps 10-15 versions of the gene
- 19 versions known
- Sustainable isolated populations below 5-10 colonies are hard to achieve, as *csd* diversity cannot be maintained
- In the long term 10-30 colonies (perhaps 50) are needed in an isolated area to maintain vigour due the *csd* effects

What does the bee breeder need to know?

- Control of outcrossing is required
- Cooperation/scale required to make progress
- Populations below 30 and certainly below 10 will suffer from inbreeding over time
- This can be countered by planned exchanges between compatible areas, or some long-distance mating
- Each colony can produce only two types of drones – you need many drone colonies

Conflicting Messages?

- A single queen can carry most of the diversity in an area
- Population sizes* below about 10 are not viable in the long term
- Why? Single queens can only produce drones with two variants of the *csd* gene.

* this assumes complete isolation

…. yet

- Many traits are heritable and so can be successfully selected for
- These include temper, productivity, hygienic behaviour, AFB resistance, chalkbrood resistance, virus resistance, *Varroa* resistance … colour, cappings colour, flying in cold, pollen storage, wing morphometry …..

notes added following the discussion ….

- Some alleles are dominant, some recessive (so effects are hidden) and some are co-dominant
- In a previous version of this document I erroneously stated that dark body colour was dominant.
- This version is updated thanks to the comments of Jon Getty on SBAi

Updated note on genetics of body colour

Body colour in honeybees is controlled by one major and several (perhaps around six) minor genes. It has been suggested that some of the minor ones have the dark form as dominant whereas the gene with the big effect has yellow as dominant over black.

The big effect gene has been called bl+ and also Y. Doesn't really matter - the effect is that a first cross between a dark (eg Amm) and a yellow bee (eg Italians or Apis mellifera ligustica) gives yellow-banded workers. This makes it easy to spot first generation hybrids between these two. First generation crosses between Amm and Carniolans are not so easy to see as the basic body colour is similar.

There are added complications such as genes that affect the sexual forms only, including genes that give dark drones in the African types. The Eastern types of Apis mellifera such as Carniolans also have gingery drones which are quite distinctive compared to dark Amm drones.

Various papers by Woyke make the genetics clear, and Laidlaw and el Banby described the dominance of yellow types earlier. The chapter in Thomas Rinderer's book on Bee Genetics and Breeding on visible mutants in honeybees by Kenneth Tucker reviews the detail of the genetics of body colour.

http://jhered.oxfordjournals.org/content/53/4/171.extract

http://jerzy_woyke.users.sggw.pl/difbocol.pdf

http://ibrastore.org.uk/index.php?main_page=product_info&products_id=99

GR 21 Nov 2011