

“Things Fall Apart”:

A mitogenomic challenge to the ***“Out of Africa”***
theory of the evolution of **Honey Bees** (*Apis mellifera* L.)



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Acknowledgement

I respectfully acknowledge the territory in which we gather as the ancestral homeland of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi'kmaq and Beothuk.

I strive for respectful relationships with all the peoples of this province as we search for collective healing and true reconciliation and honour this beautiful land together

Questions

Who you buzzin' round now Billy bee, Billy bee

Who you buzzin' round now?

Who you buzzin' round now, Billy bee

Why you buzzin' round her not me?

- The Haden Triplets





Honey gathering, ~ 8 KYA

(Araña Caves, Valencia, Spain: UNESCO World Heritage Site)



Apiculture in Egypt

(Tomb of Rekhmire, New Kingdom, mid-15th cent. BCE)



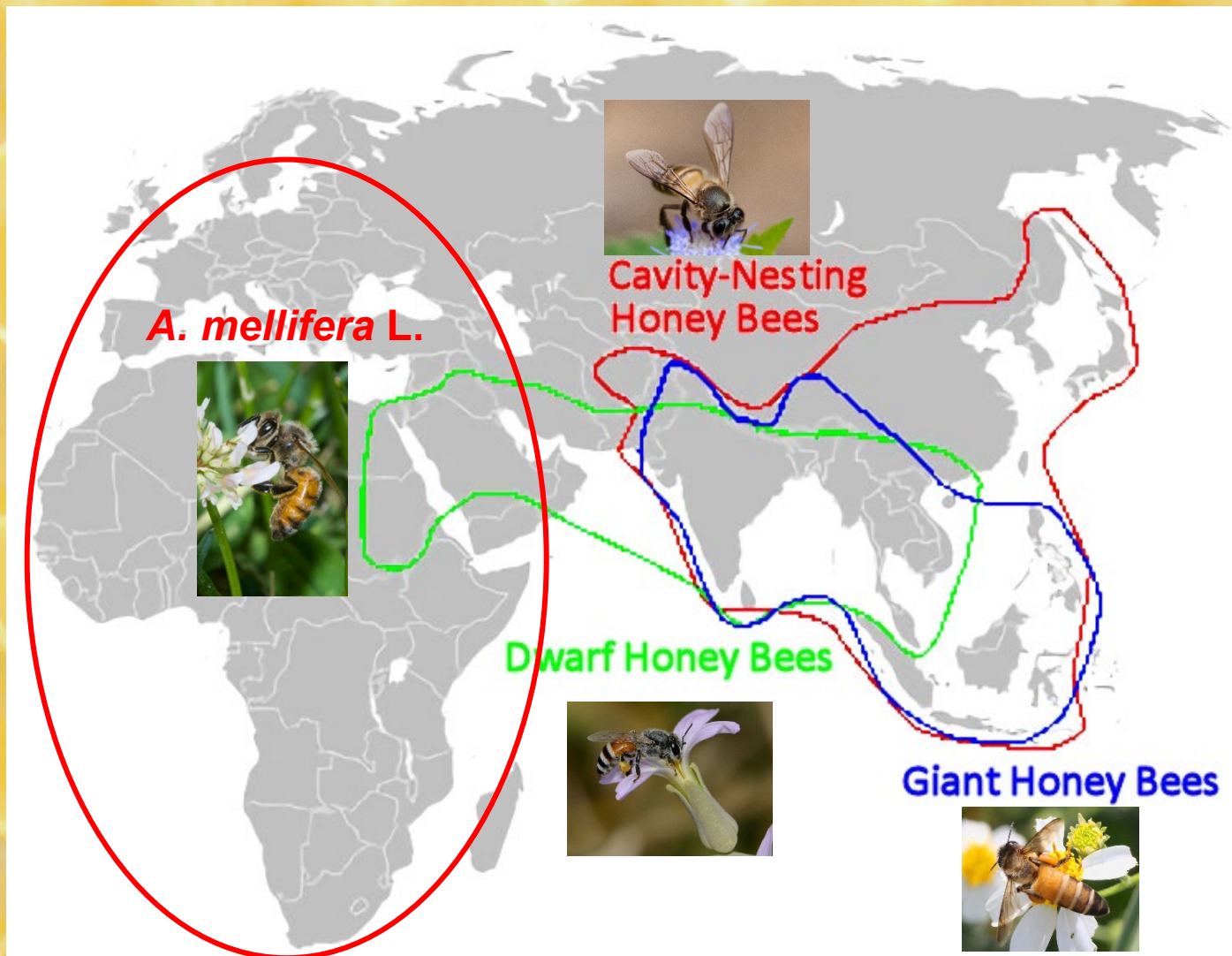
Apiculture of Honey Bees

Tagged *Queen* ♀, *Drone* ♂ & *Worker* ♀

More questions

“I don't think they play at all fairly,” Alice began, in rather a complaining tone, “and they all quarrel so dreadfully one can't hear oneself speak - and they don't seem to have any rules in particular: at least, if there are, nobody attends to them - and you've no idea how confusing it is all the things being alive....”

– Alice's Adventures in Wonderland



Distribution of *Apis* subgenera

Micrapis, *Megapis*, & *Apis*

A. florea in Africa; *A. mellifera* in Europe, Near East, & Africa

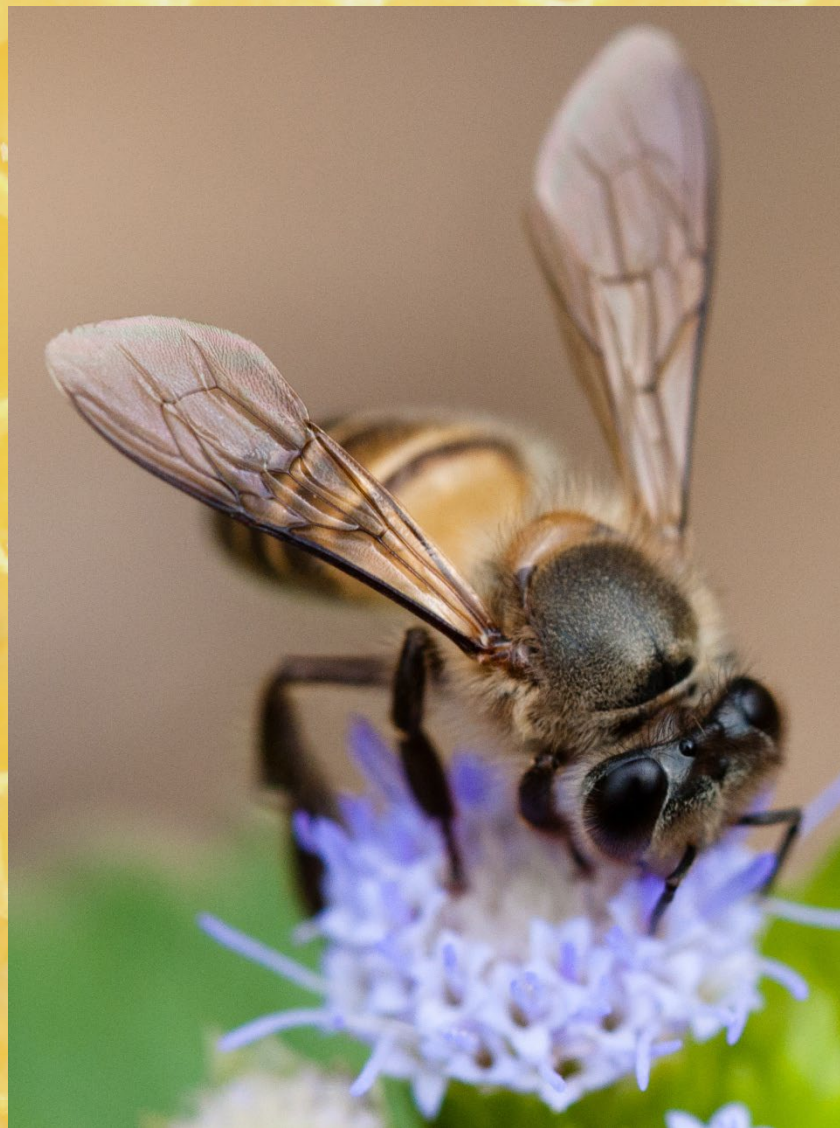


Dwarf Honey Bee (*Apis florea*)
(7 ~ 10 mm)



Giant Honey Bee (*Apis dorsata*)

(17 ~ 20 mm)



Cavity-Nesting Bee (*Apis cerana*)

(10 ~ 12 mm)



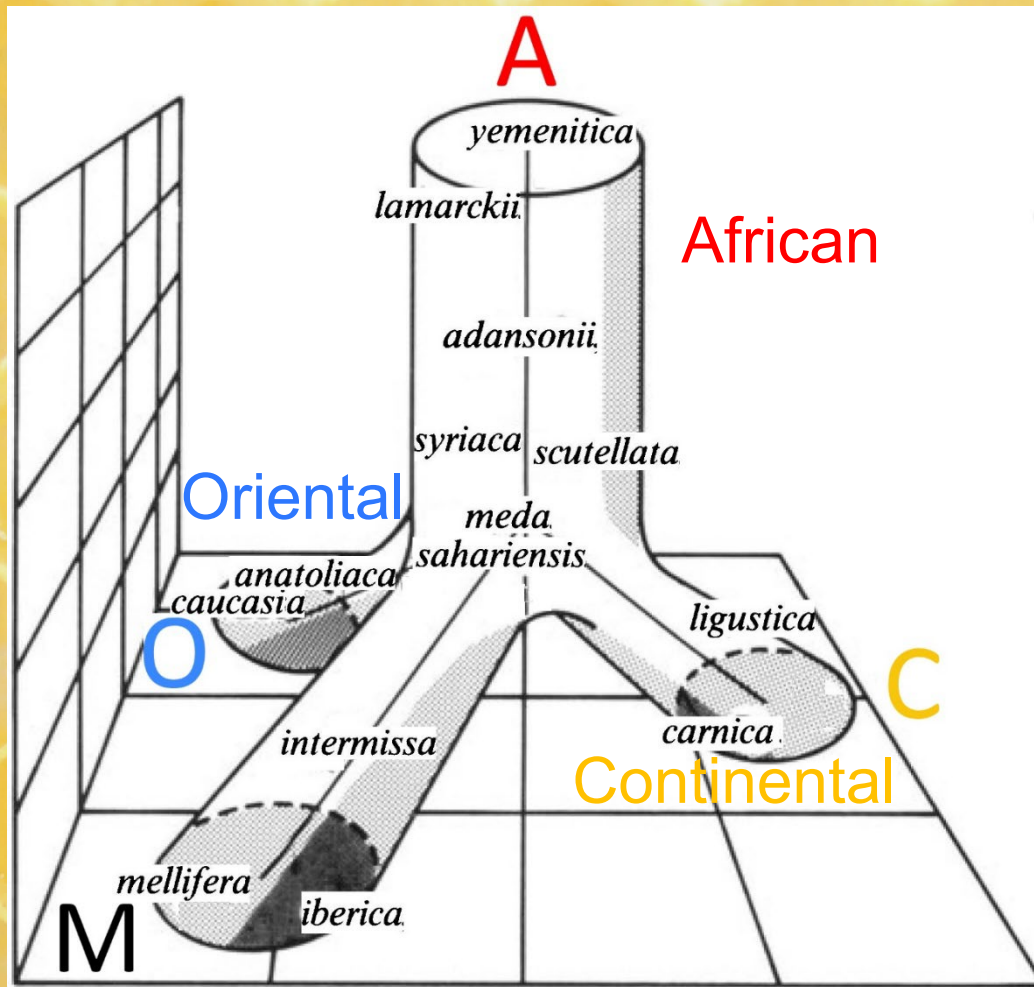
Western (European) Honey Bee

Apis m. mellifera L. (10 ~ 12 mm)



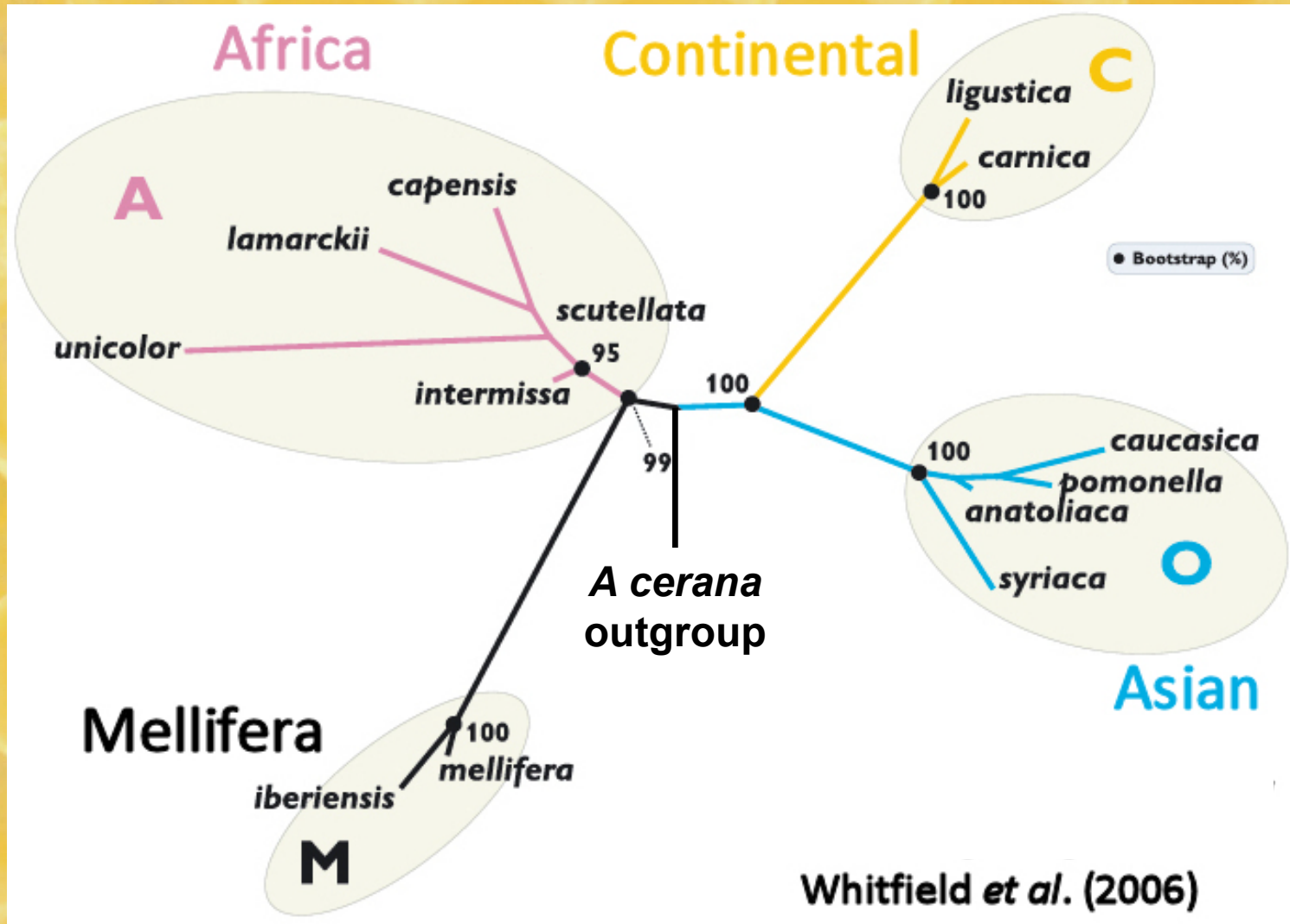
Italian Honey Bee

Apis mellifera ligustica Spinola, 1806



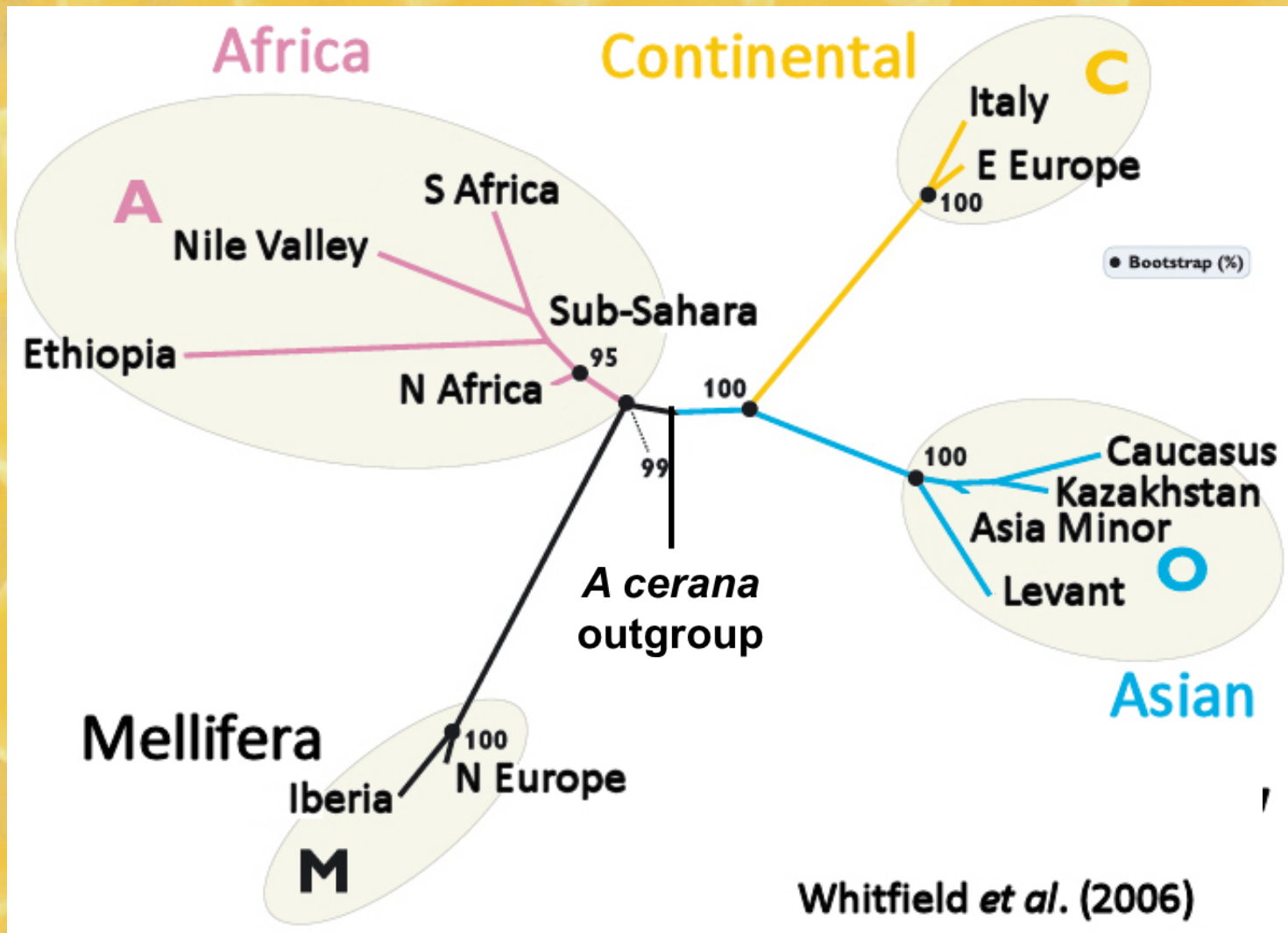
Received Wisdom:

“**A****C****M****O**” model of *A. mellifera* (Ruttner 1988)
Four subspecies groups on separate Continents



“*Out of Africa*” Hypothesis by taxon

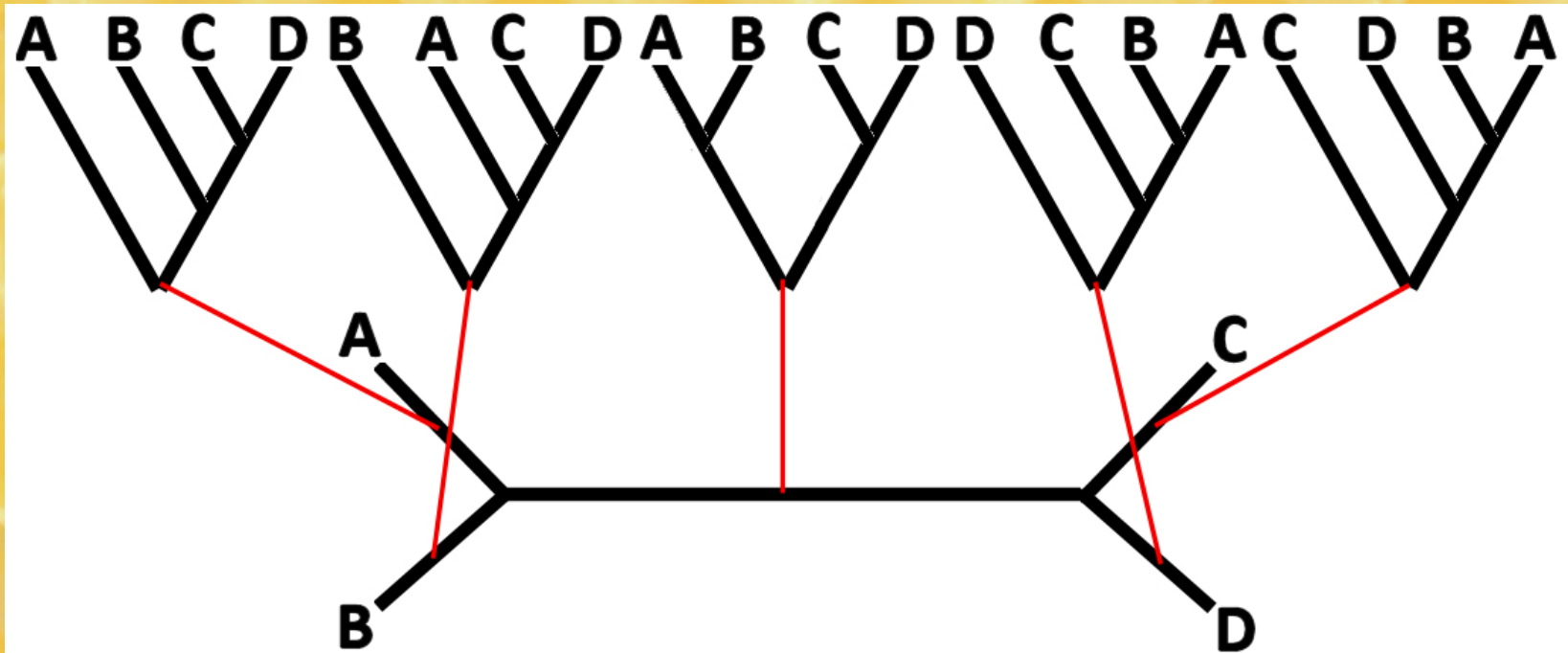
(Han et al. 2012, after Whitfield et al. 2006)



“*Out of Africa*” Hypothesis by biogeography

(Carr 2023, after Han *et al.* 2012)

On the Origin of Species



To solve a “**Four Species Problem**”:

- 1) Determine **A**'s closest *relative*: **B** or **C** or **D** ?
- 2) Suppose “**A** is more closely related to **B** than either is to **C** or **D**”
→ Unrooted **Network** with *four branches* including *one internode*
- 3) Place **root (outgroup)** on *correct branch*: **Network** → **Tree**
Rooted Tree has implications for evolutionary history

Meta-Analysis of existing data

Carr (2023). *Nature Scientific Reports*, 13:9386

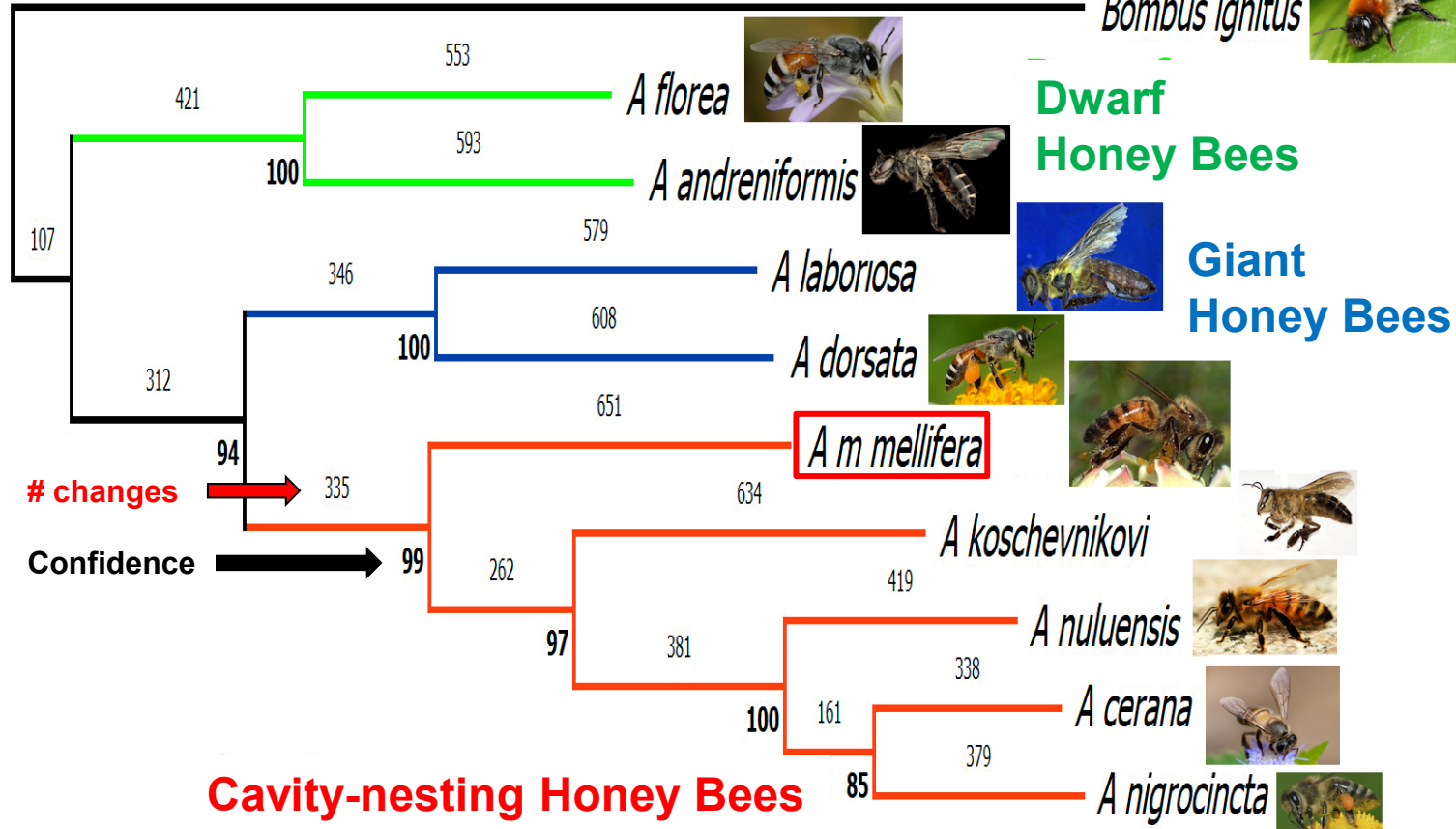
- **GenBank** whole **mtDNA** genomes
 - **mtDNA Protein Coding Genes (PCGs)** only
 - 9 heavy strand, 4 *light strand*: **11,006 bp**
 - **Outgroup *Bombus ignitus*** (Bombini): **Bumblebee**
 - ***Apis* species** (Apini: Apidae) (n = 9)
 - ***Apis mellifera* L. : Western Honey Bee**
 - n = 22 subspecies
 - n = 78 individuals (multiple reps from eight subspecies)
- **Alpha Taxonomy** issues: Accuracy of **GenBank DNA** curation
- **Phylogenetic methods**
 - **Maximum Parsimony (MP)** [minimum # **SNP** changes]
 - **Neighbor Joining (NJ)** [Shortest genetic **Distance**]
 - **Maximum Likelihood (ML)** [Model-based **Bayes**]
 - **Bootstrap** confidence: 3,000 random re-samplings
 - **Molecular Clock** from **Linearized ML**: 0.0115 subs/ site/ Myr

Bumblebees

1938

Bumble bees

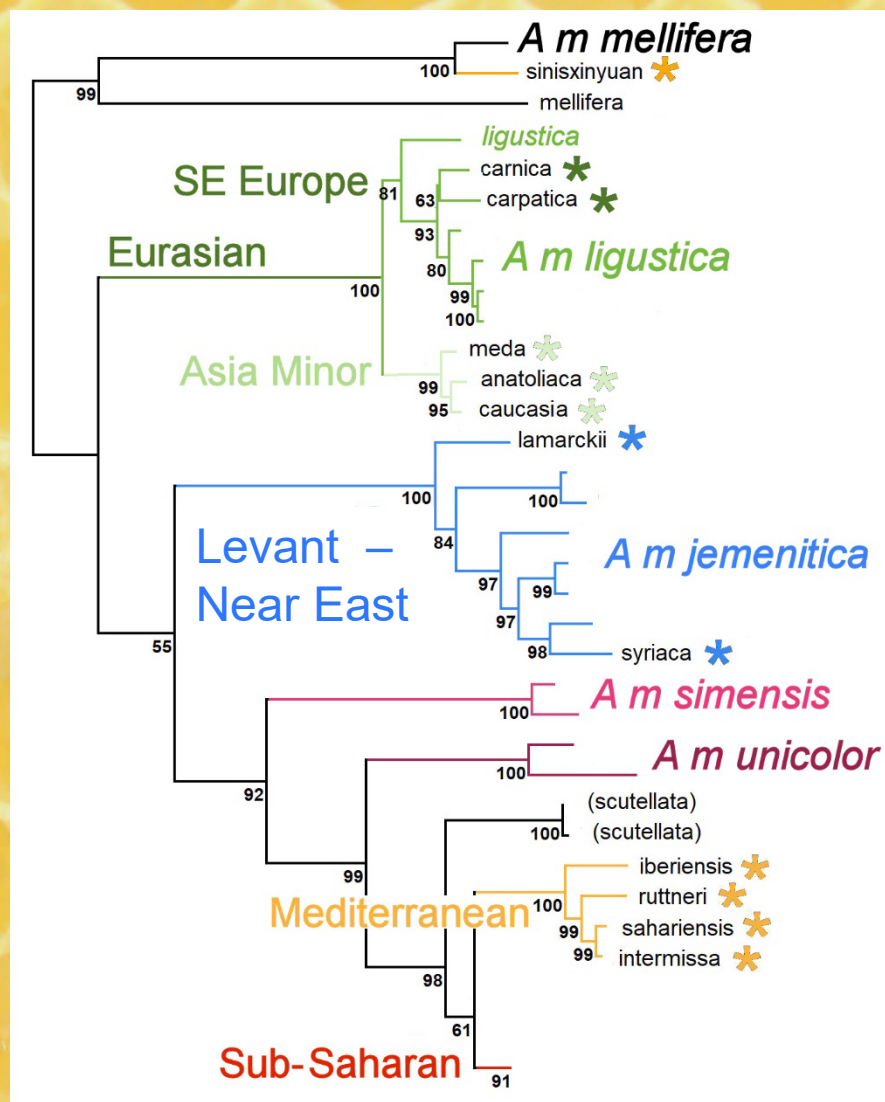
Bombus ignitus



Dwarf, Giant, & Cavity-nesting clades in *Apis*:

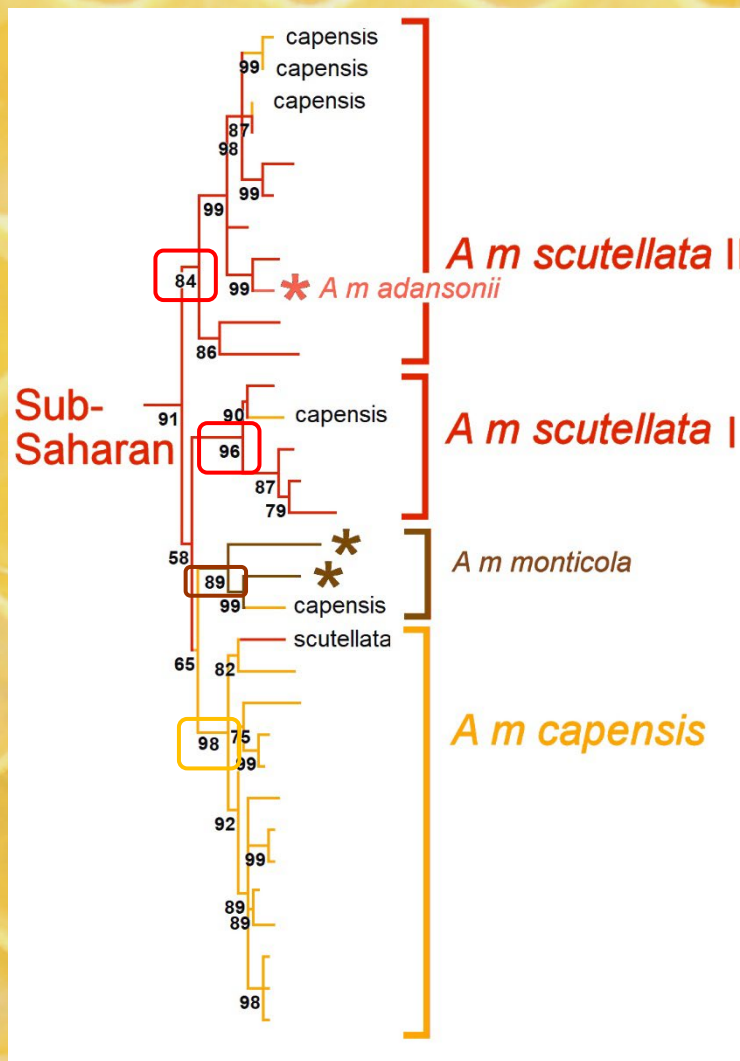
Bumblebee (*Bombus*: Bombini) outgroup

=> ***A. mellifera*** basal to cavity-nesters



Phylogeny of 18 EurAsian - AfroAsian subspecies

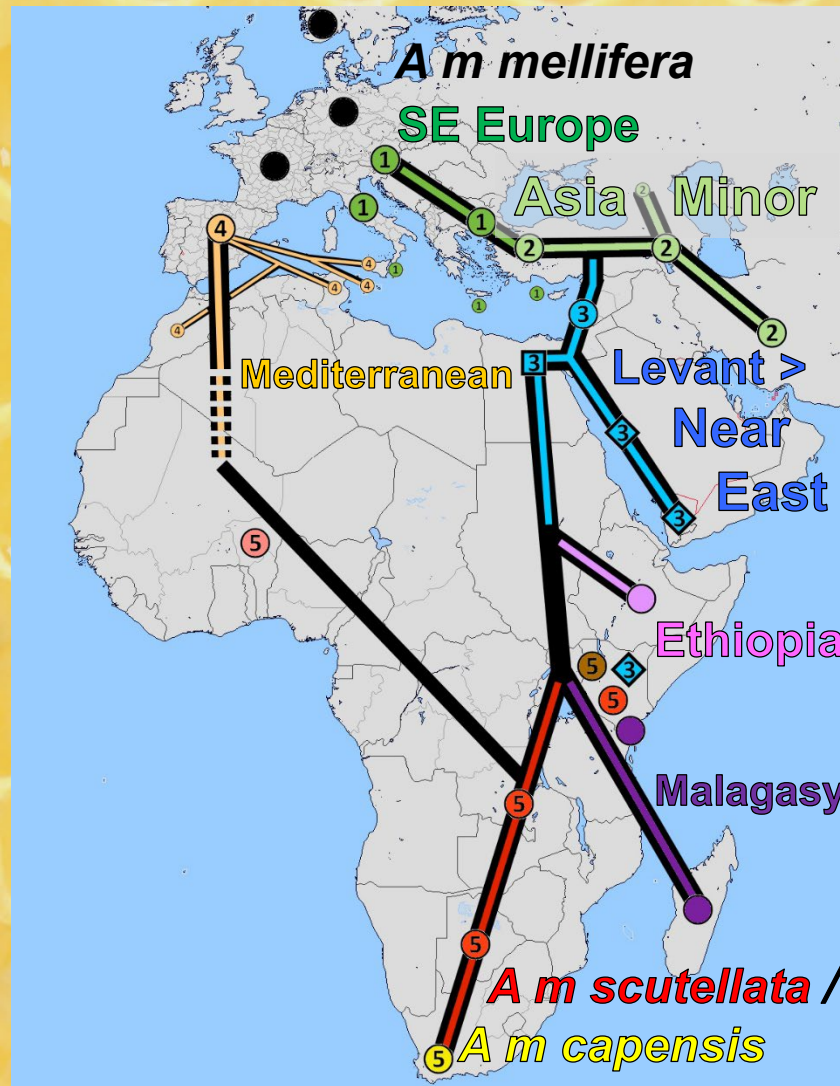
Five multi-sample (n = 22) + Thirteen singletons *



Phylogeny of four **Sub-Saharan** subspecies

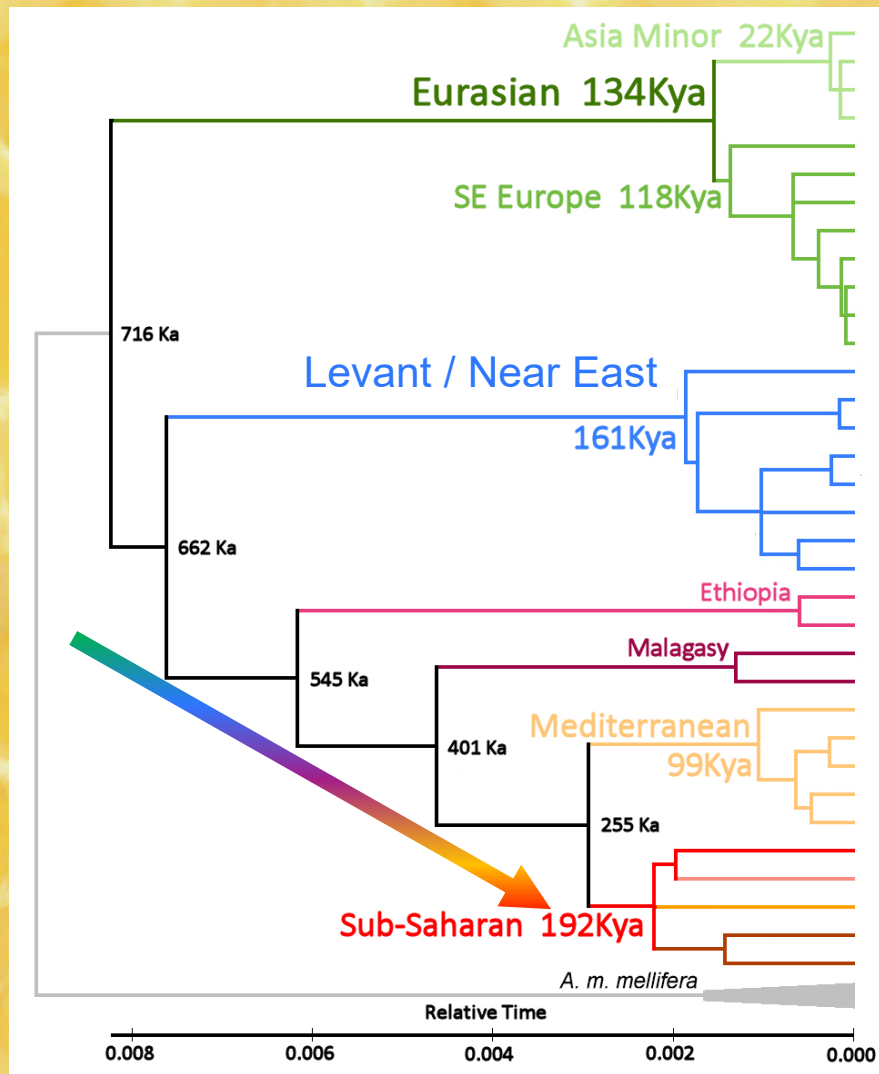
A m scutellata I & II (inc *A m adansonii*) vs *A m capensis* & *A m monticola*

Diversity ~ 200 Kya



Phylogeographic evolution of Honey Bees

“The Scramble for Africa” ?



Molecular Clock of *Apis*

A. mellifera origin ~ 800 Kya: Eurasian spread ~720 Kya
 Near Eastern presence ~ 660 Kya; African presence ~ 540 Kya

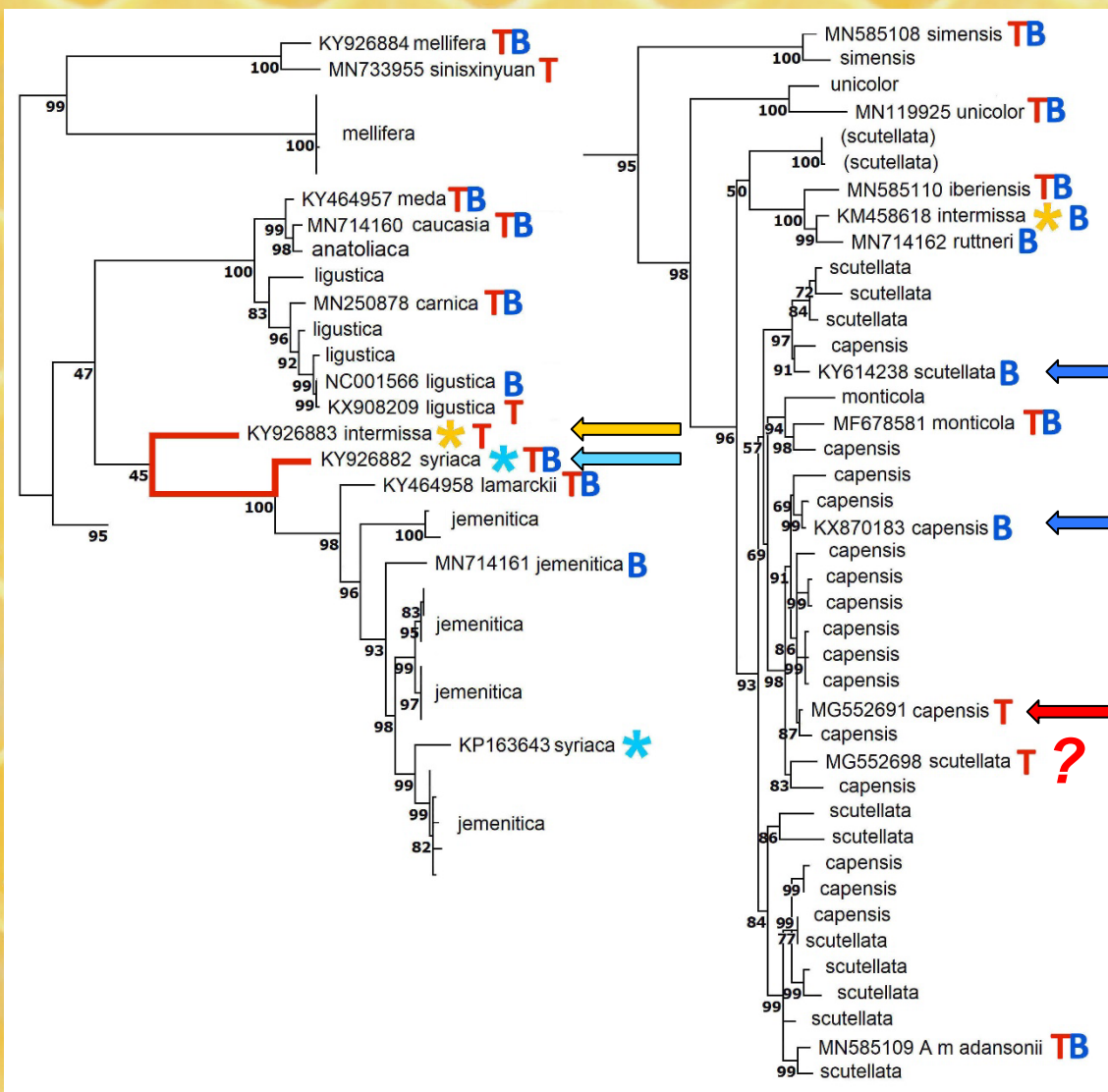
Discussion

*“I have just been thinking,
and I have come to a very important decision.*



These are the wrong sort of bees.”

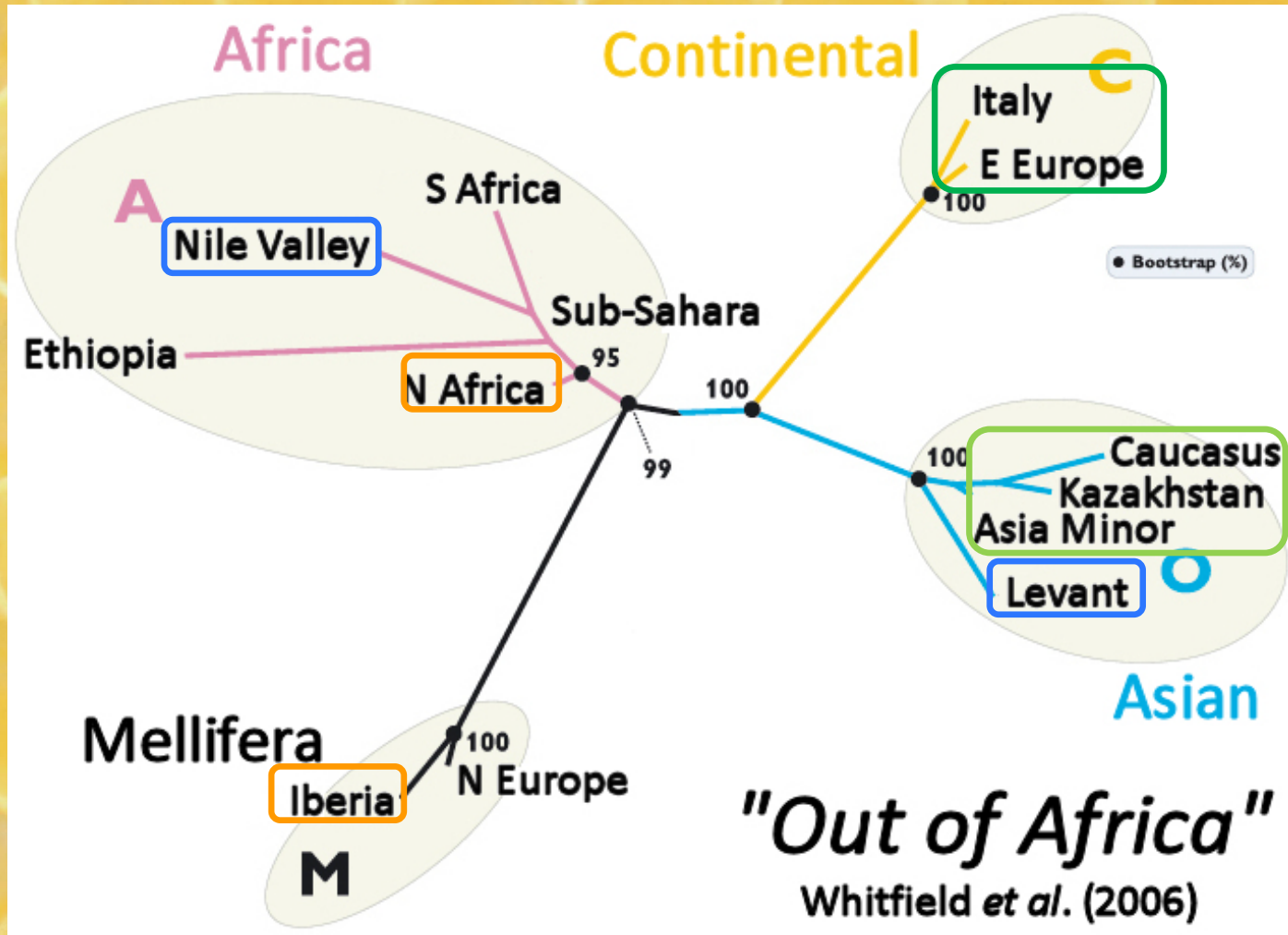
– Winnie the Pooh



The *Wrong Sort of Bees* !

[Boardman, Eimanifar *et al.* 2020 (B) vs Tihelka *et al.* 2021 (T)]

Problematic inferences from single mtDNA sequence / subspecies



"Things Fall Apart" with "Out of Africa"
 mtDNA phylogeography vs nucDNA **A****C****M****O** model

Summary:

A new phylogeography for Honey Bee evolution

(Carr SM. 2023. *Nature Scientific Reports*, 13:9386)

1. **Meta-analysis** of mtDNA of 78 individuals from 22 sub-species
2. “**Things Fall Apart**” with “**Out of Africa / Asia**” hypotheses
3. **Phylogeography** of *Apis mellifera* L.
 - Origin in Northern Europe
 - Extension to **SE Europe**
 - & Expansion into **Asia Minor**
 - Southward via **Levant / Near East** corridor
 - Into **Sub – Saharan Africa**
 - Mediterranean** lineage re-enters **Iberia**,
thence **N Africa & western islands**
4. **Sources of error** clarified by **multiple replicate sequences**
 - Paraphyly artefacts** from **mis-referral / curation** in GenBank
 - Problematic inferences** from **faulty / atypical sequences**
5. **DNA** does not lie, **but**
 - GenBank** *not* infallible
 - Curation** *sometimes* flawed
6. **Sub-species** often **weakly genetically differentiated**

Conclusions

(for non-Melittologists)

1. *“I don’t know anything about this, but I’ll tell you what I think....”*
2. Get a ***second opinion***
3. ***Don’t believe*** everything you read
4. ***Names Matter:***
“Alpha Taxonomy” still important
5. **DNA** does not lie, *but*
GenBank *not* infallible
Curation *sometimes* flawed

