Species and subspecies concepts in taxonomy: An introduction to the confusion

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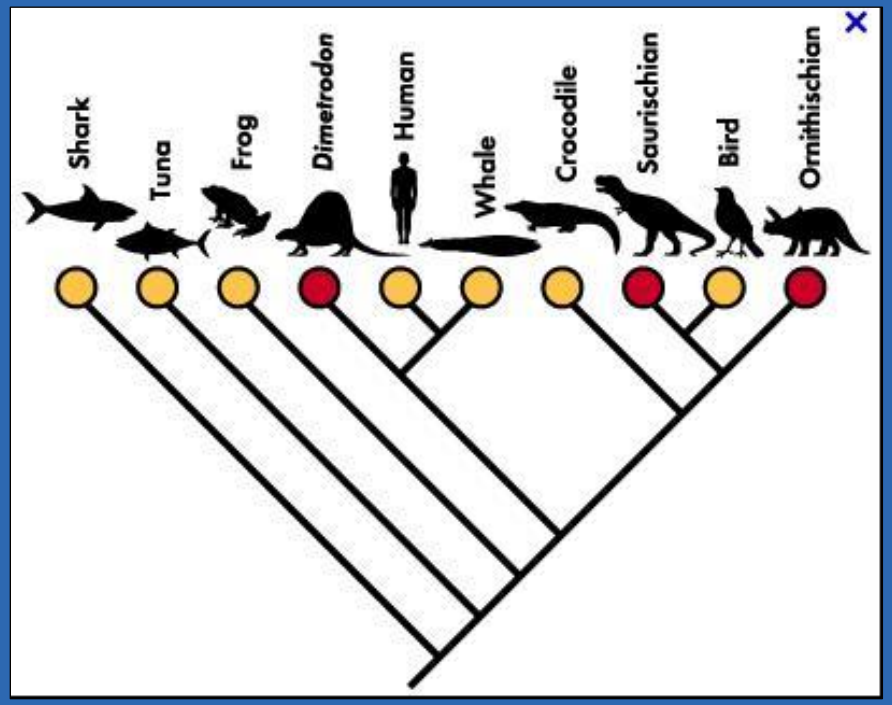
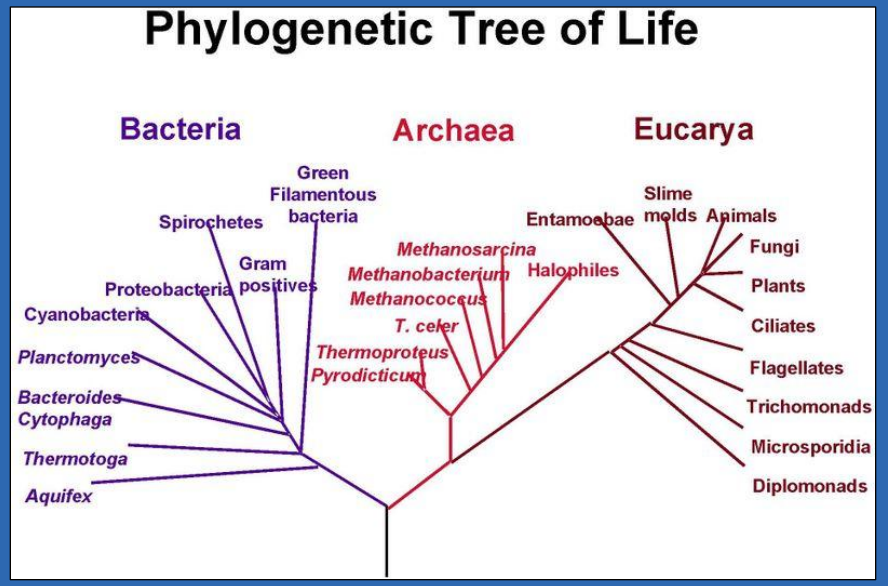
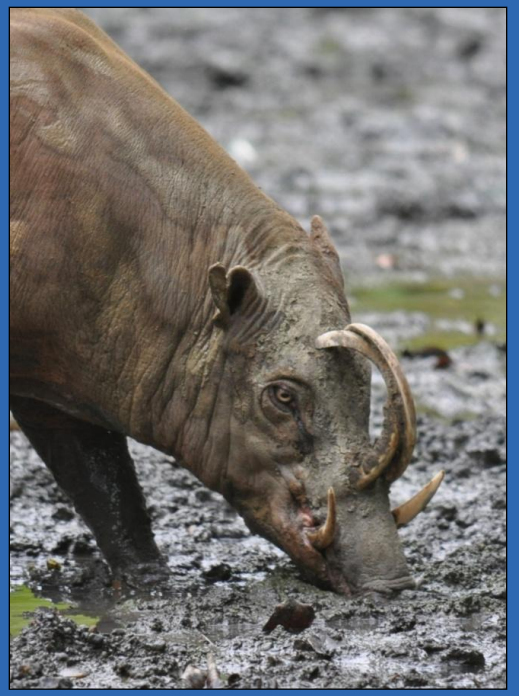




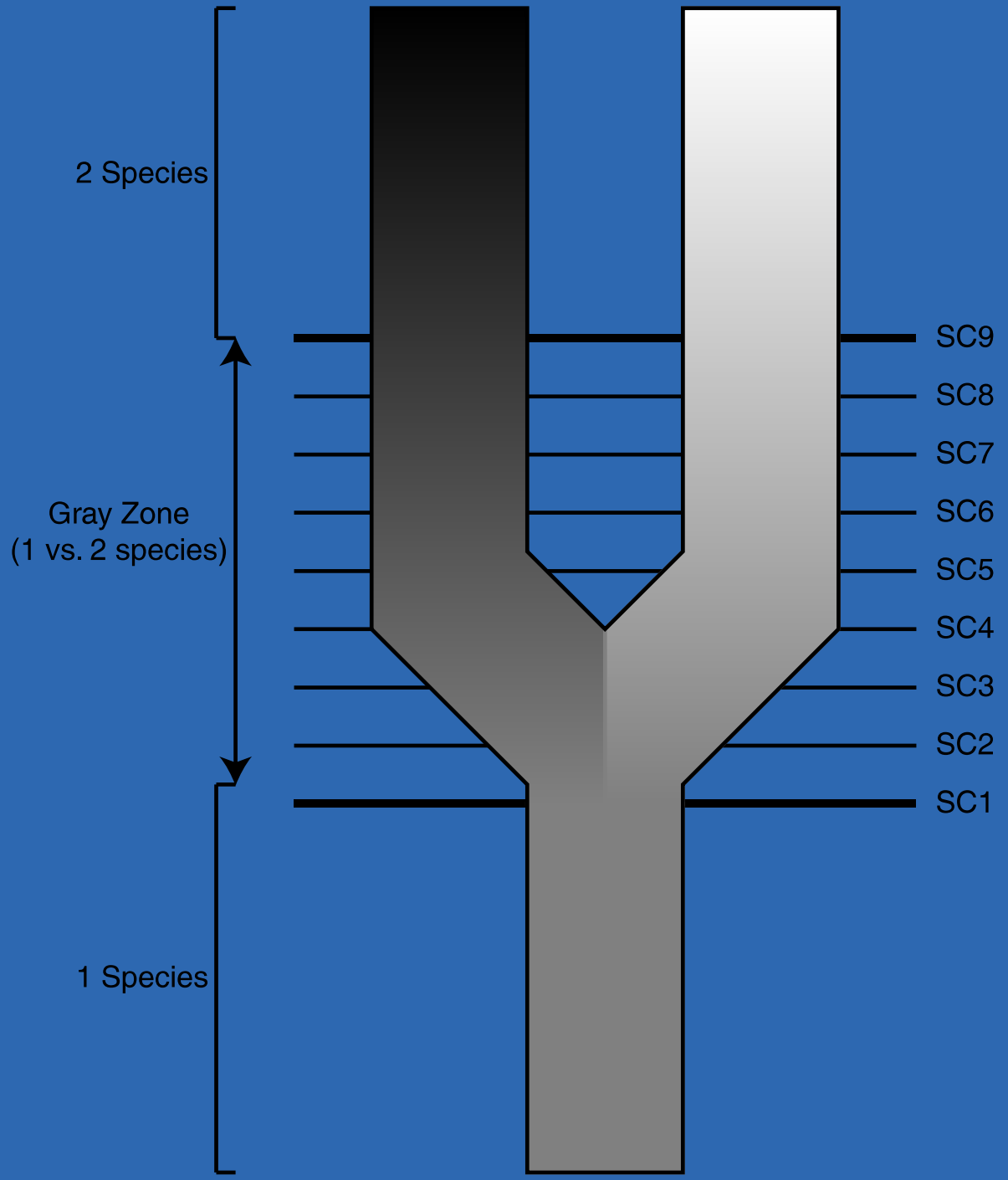
This stuff is really technical and boring to some of us, why should we care?

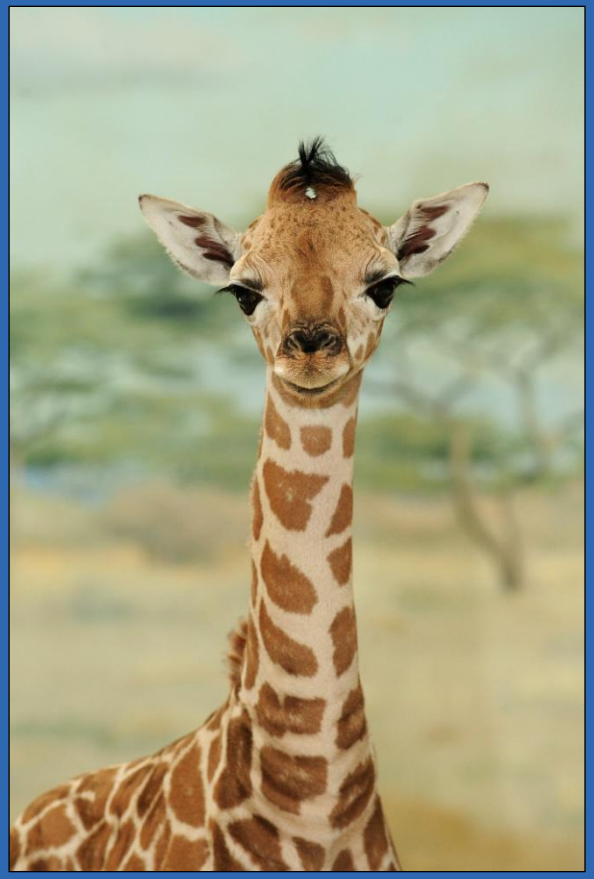
- We should want to preserve biodiversity, even biodiversity we aren't aware of, which could include hidden genetic diversity
- Our resources (time, funds, space, energy) for conserving biodiversity are desperately limited
- So we need a reliable, scientifically-sound system for identifying diversity of evolutionary significance
- And coupled with this, we will need a unified framework or at least some guiding principles to help us make decisions about wise use of resources



Species Concepts in Taxonomy

- There are over 20 species concepts in the literature
- It has also been argued that species concepts are really not definitions of species (as entities – what does it mean to be one) but rather tools for distinguishing them
- There is rampant disagreement over species concepts and how to distinguish species among people who really understand this well
  - Lots of new data are available
  - Some "facts" are being overturned (e.g. some 'species' hybridize and produce fertile offspring, speciation can occur despite ongoing hybridization, DNA can move between species)
- It has a philosophical layer to it





after de Quieroz 2007

Well-Known Species Concepts

- Biological Species Concept (the one many of us learned in school)
- Groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups
- Problems: reproductive barriers are semi-permeable, species can differentiate despite ongoing interbreeding, not easily applied to uniparental organisms, difficult to test explicitly

Well-Known Species Concepts

- Phylogenetic Species Concept
- A species is the smallest population or aggregation of populations which has fixed heritable differences from other such populations or aggregations and within which there is a pattern of descent
- Problems: high resolution could lead to oversplitting, uniparental issues, sampling errors, character choice issues, risky in fragmented populations

Well-Known Species Concepts

- Differential Fitness Species Concept
- Groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact are different species
- Problems: possibly difficult to test explicitly

Species Concepts and Conservation

- Everyone agrees that proper “identification of species” is critical for conservation
- “Species” status has been used as leverage for conservation
- Frankham et al 2012, Biological Conservation + responses: an analysis of how different species concepts can impact conservation
- “the ideal species concept for conservation would minimize potential harm and maximize potential benefits, as measured by reproductive fitness and sustaining adaptive evolutionary processes”
- Trade-off: overlumping might result in outbreeding depression whereas oversplitting might result in inbreeding depression and other risks of small population size and limits ability to do genetic rescue

Frankham et al.'s Recommendations

- Substantial, demonstrated reproductive isolation should be used to define species for conservation so that genetic rescue attempts are not thwarted and outbreeding depression is minimized.
- In this way the Differential Fitness Species concept seems most appropriate, Biological Species concept is mostly appropriate
- In overlapping/adjacent populations with lack of shared alleles at >1 loci, you've got >1 species
- In fragmented populations with some diagnosable differences, apply DFSC and look for outbreeding depression or fixed chromosomal differences.

Other critiques are focused on ungulate taxonomy

- Groves & Grubb, 2011 used the phylogenetic species concept to nearly double the number of bovid species. Critiques have focused on:
  - choice of characters, lack of systematic approach, vague concepts, arbitrariness, poor sampling and sample sizes, EQUATING DIAGNOSABILITY WITH SPECIES STATUS
- Critiques: Zachos (2014), Zachos et al (2013), Heller et al (2013, 2014)

The arguments boil down to:

- What a species is vs. how we can recognize and delimit them
- All species are lineages but are all lineages species? Not necessarily…

- Is diagnosability even a phylogenetic concept or is it just a tool? Is it what makes a species?
- Can we accept grey areas in taxonomy?
- How to use taxonomy for conservation?
- All species concepts have flaws or exceptions to the rule

So what do we do now? My 2 cents from reading

- Look for what species concept is being used when “new species” or “unique populations” are being identified
- In genetics-only studies, look for nuclear DNA AND mtDNA results. mtDNA seems to be more attackable.
- Look for integration of genetic, anatomical, behavioral, and ecological data
- Look for robust sampling in #s of animals and # traits used (and make sure the traits make sense- continuous traits like length of bones are probably not useful for resolving differences)
- And then depending on how critical the situation is, take a leap of faith – but let’s ask some real experts

What is a subspecies?

- A collection of populations occupying a distinct breeding range and diagnosably distinct from other such breeding populations;
- Important features: no reproductive isolation from other subspecies, the defining features have a genetic/developmental basis, has a unique breeding range separate from others, diagnosably distinct
- Not all subspecies are future species, they can stay as they are or revert back to be undistinguishable

Complications

- Subspecies could look different due to many reasons: natural selection, sexual selection, or genetic drift+ possible impact of environment
- Many analyses of subspecies have actually found no genetic differences
- How much differentiation is enough? There is an old “75% rule”
  - The rule is frequently mis-applied and many subspecies were named before it even existed.
  - Which and how many traits should be considered?
- Smooth variation along a cline is not a proper basis for subspecies designation; instead we must look to characters that exhibit ‘breaks’ between populations
- Most subspecies have not been evaluated with modern statistical techniques
- The people I’ve talked to who do this for a living really don’t even use this concept anymore.

Przewalski's Horse

- 2004 Master Plan
- Population MK: .2503
- Inbreeding: .2426
- Genetic Diversity: 75%

- 2014 Master Plan
- Population MK: .2100
- Inbreeding: .1997
- Genetic Diversity: 78.43

A only → A and B separate

↓

Limited Mixed Line
1988

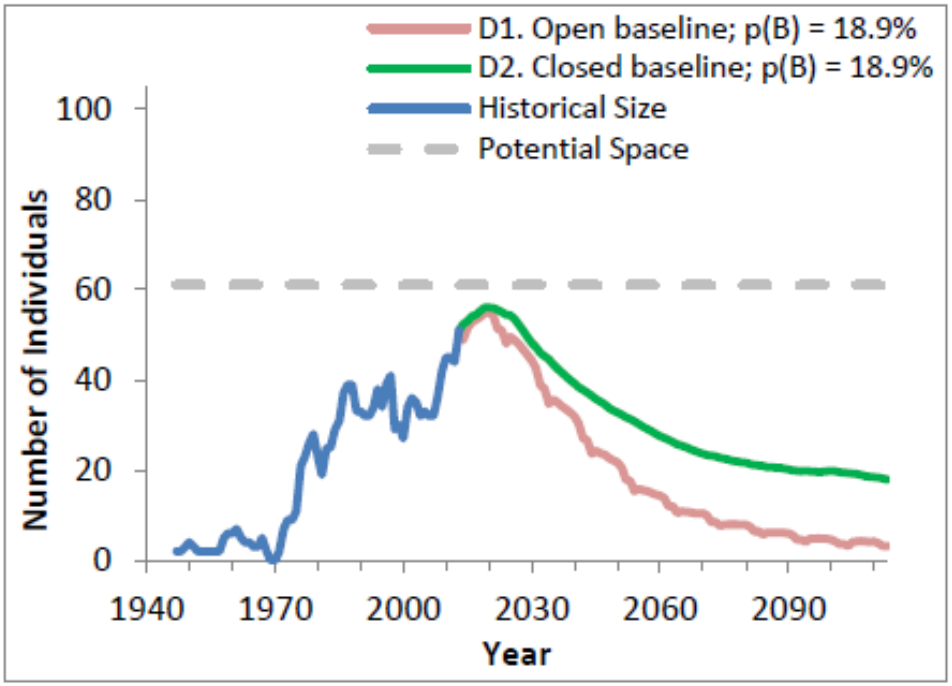
↓

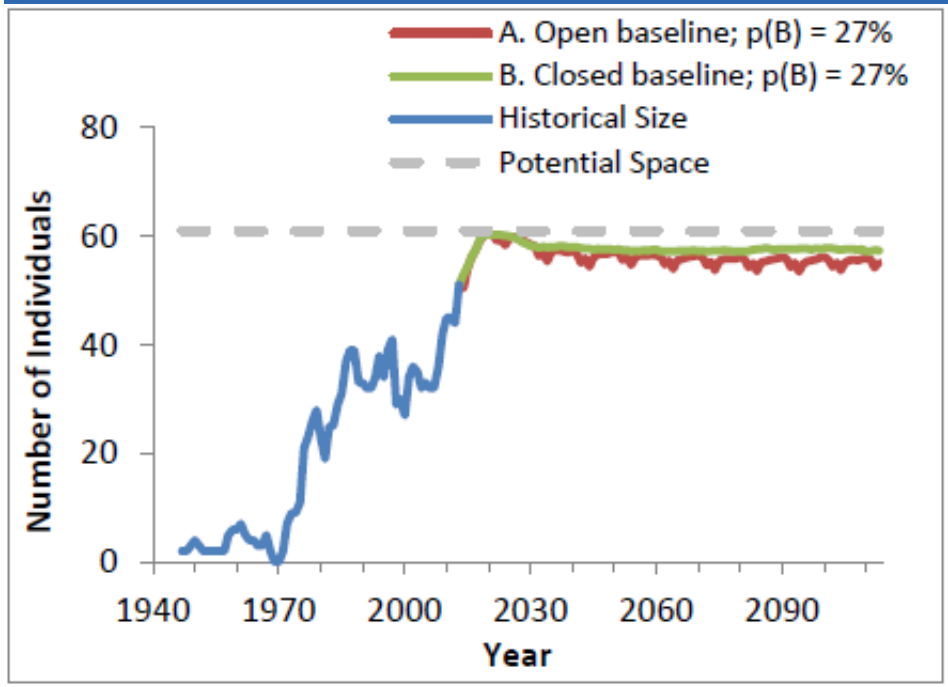
Return to A line preference
A stallions bred to B mares
2000

New genetic analyses identify genetic mixing between P horses and the domestic horse ancestor AFTER the two species diverged but BEFORE horse domestication.

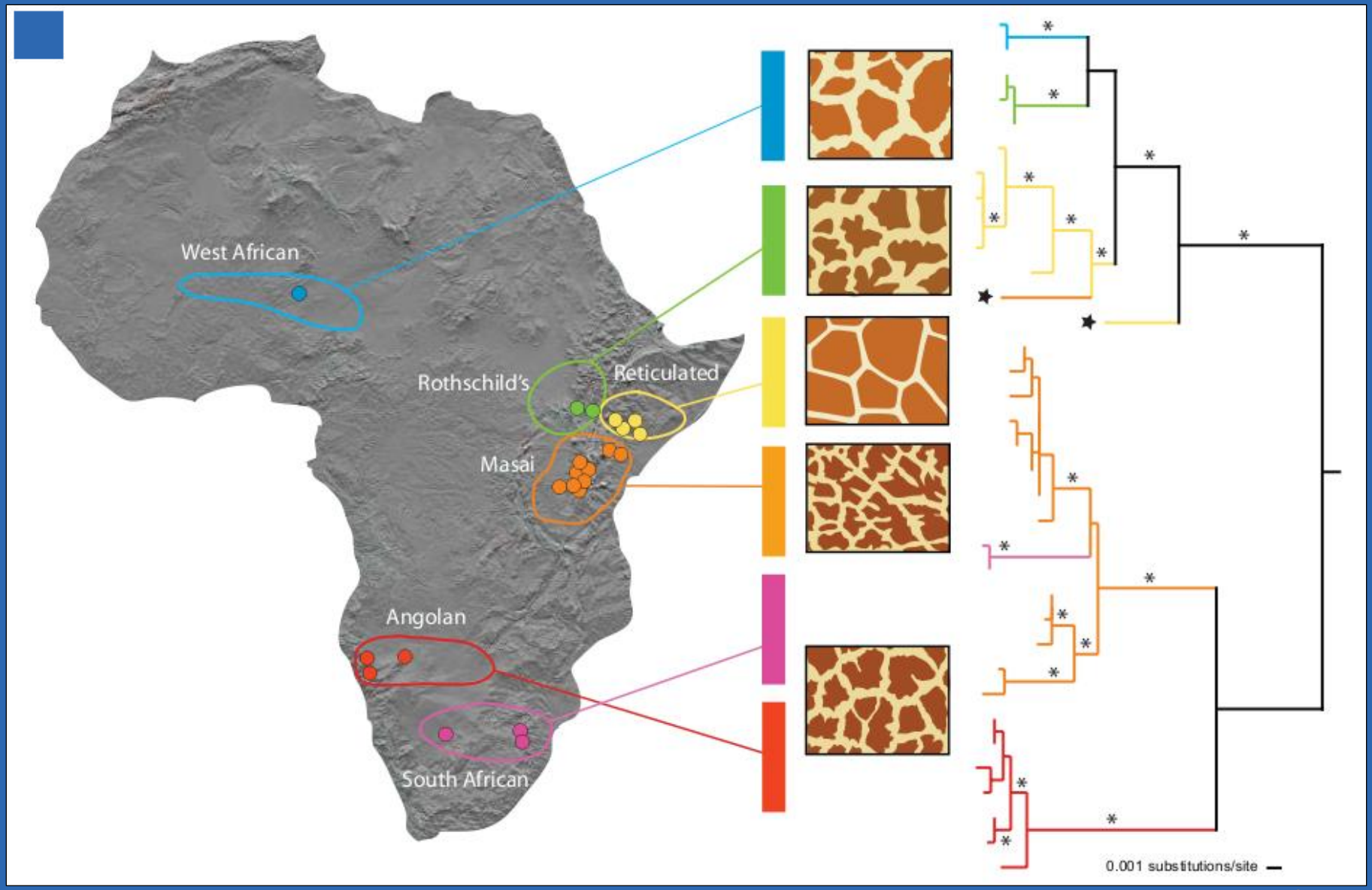
→ Neither viable
Formal adoption
of Mixed Strategy
2004

Desert Bighorn Sheep: maintaining separate subspecies leads to entire population crashing due to reduced breeding rates





Giraffes



From: Brown et al 2007

Thanks!

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- Kevin de Quieroz, National Museum of Natural History
- Photos: Julie Larsen-Maher/WCS, Brent Huffman, David Powell