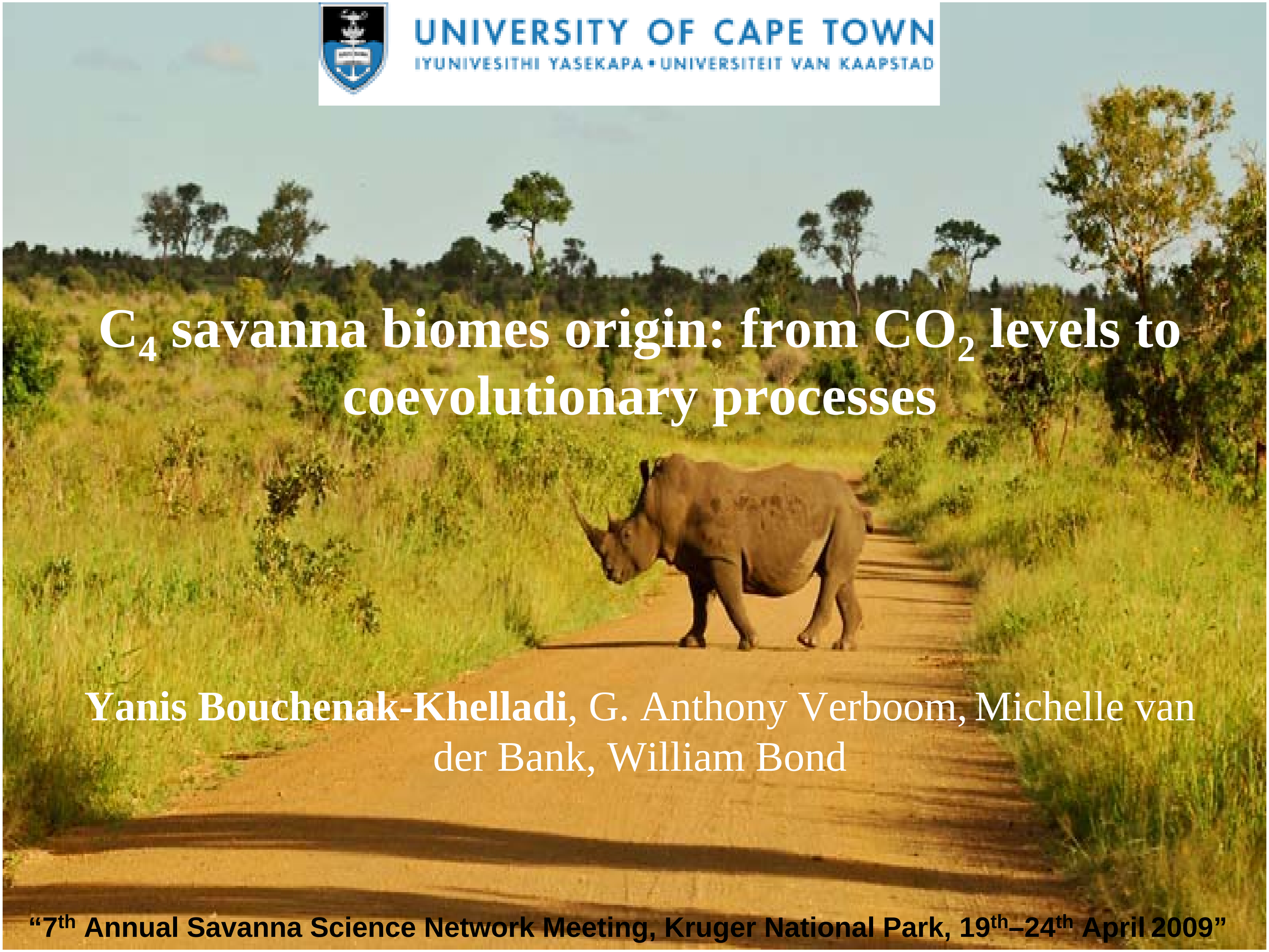

UNIVERSITY OF CAPE TOWN
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C_4 savanna biomes origin: from CO_2 levels to coevolutionary processes

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"7th Annual Savanna Science Network Meeting, Kruger National Park, 19th–24th April 2009"

Zuckerland and Pauling (1965): " […] we first have to determine to what extent the phylogenetic tree derived from molecular data in independence from the results of organismal biology coincides with the phylogeny constructed on the basis of organismal biology. If the two trees are in agreement (topology and branching events), the best available proof of the reality of macro-evolution would be furnished!"

Evolutionary processes can be identified and quantified using phylogenetic trees by:

- **comprehensive** taxon sampling
- ancestral ecology (habitat, soil/water requirements…) reconstructions
- molecular dating

When did ancestors of a lineage occur? Where?

What were the most likely ecological adaptations of such ancestors compared to present-day species?

What ecological/environmental factors could explain the evolution of such adaptations?

Importance of savannas

• Biodiversity hotspot: largest grazers diversity in Africa

• Cover a large part of Africa, Australia, India and South America

• **Present-day biome that is a "witness" of the opening of the forest cover in the Cenozoic (50-25 million years ago)**

Savannas are dominated by C_4 grasses

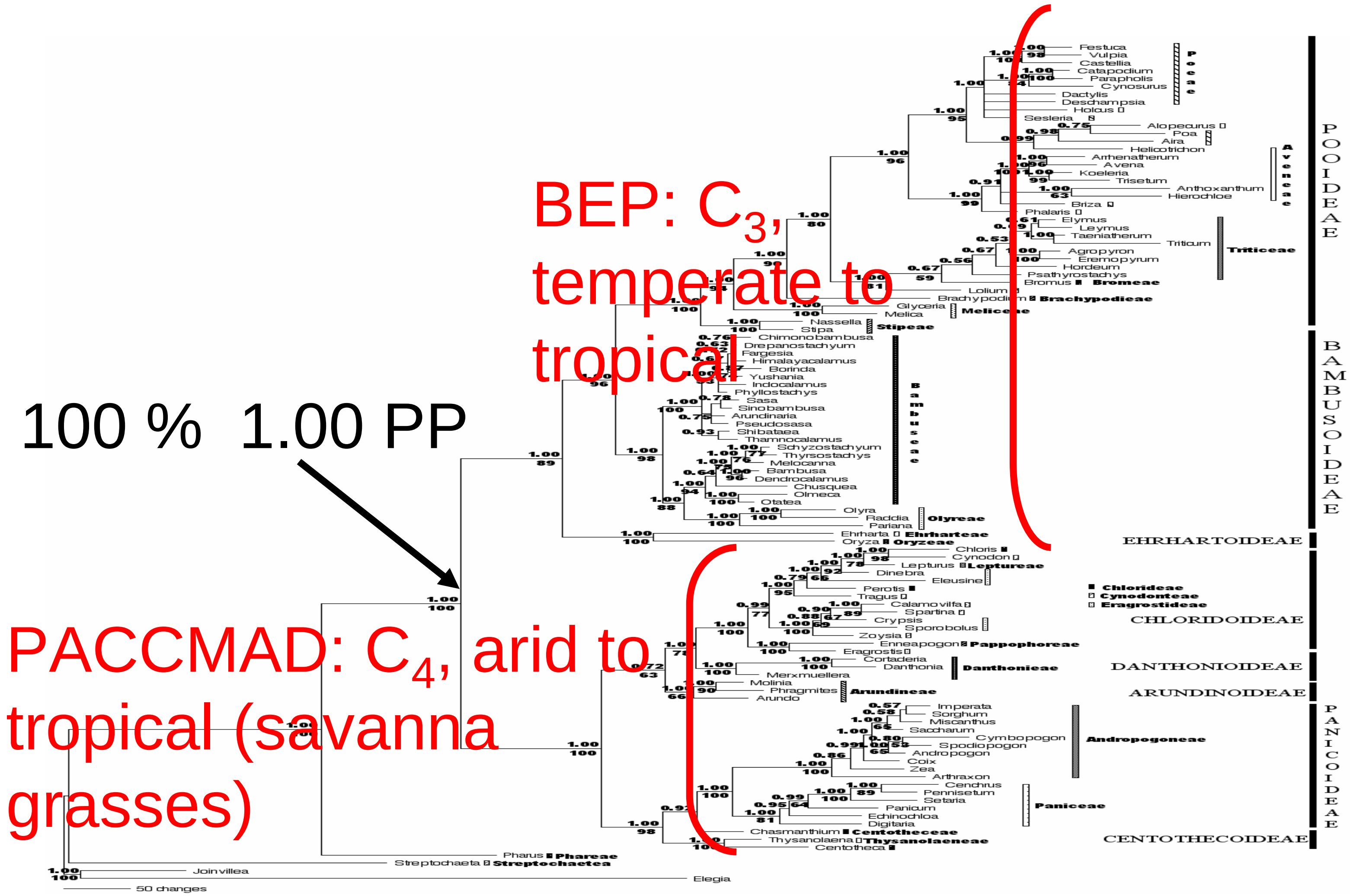
Grasses (Poaceae) account for 60% of all C_4 plants (4,500 species)

Constitute main diet of large grazers

C_4 grasslands expansion alters regional climates, reduces air quality and is likely to respond to human-induced global change

Phylogenetic trees are the basis of a powerful approach to identify and quantify evolutionary patterns and processes that shaped the present-day diversity of species in any community, biome, continent or even at a global scale

Bouchenak-Khelladi et al., 2008



Several abiotic (CO_2 levels, rainfall, fire) and biotic (herbivory, plants water use efficiency) factors drove C_4 grasses evolution

• **Fire:** C_4 grasses are well-adapted to fire (Bond et al., 2003)

• **Aridity/Rainfall**: Use of water very efficiently (less evapotranspiration/Adaptation to aridity?)

• **CO_2 levels**: C_4 pathway efficiency under low CO_2 conditions:
_Triggering factor (Sage, 2001; Bouchenak-Khelladi et al., 2009)
_Driving factor (Christin et al., 2008; Vincentini et al., 2008)

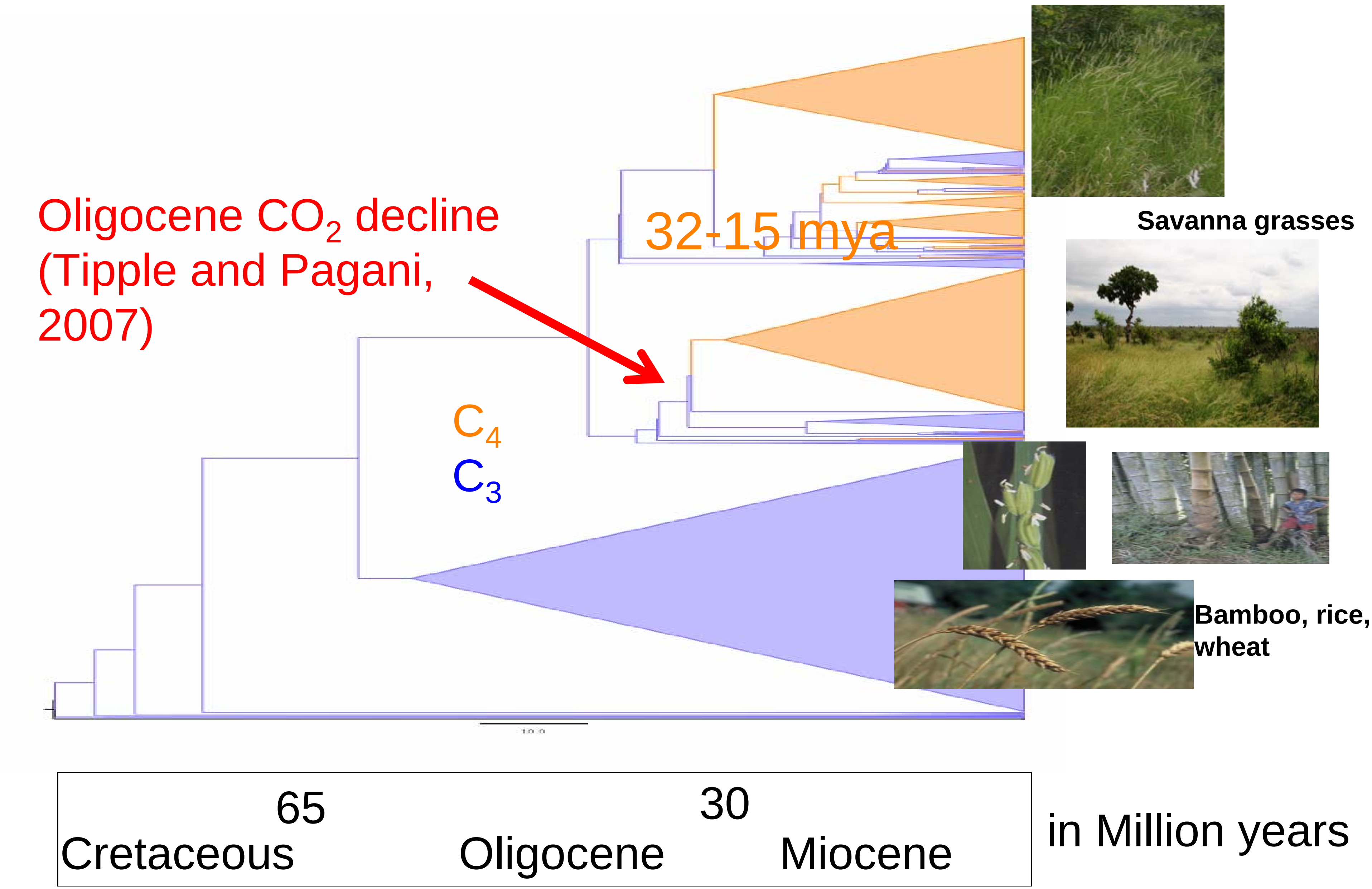
• **Herbivory:** Grazing pressure in the last 30 million years, grasses/grazers coevolution (Stebbins & Crampton, 1961; Coughenour, 1985; Chapman, 1996; Stromberg, 2006; Bouchenak-Khelladi et al., 2009)

Aims of this talk

- Date appearance of C_4 pathway in grasses as a proxy for the origin of savannas
- Date appearance of adaptation to savanna-type habitat of ungulates
- Infer historical biogeography and ecology of grasses
- Identify and correlate herbivory trait with C_4 grasses evolution
- Further studies to identify other major ecological factors driving C_4 grasses evolution as a proxy for understanding African savanna diversity_Preliminary results from Kruger National Park

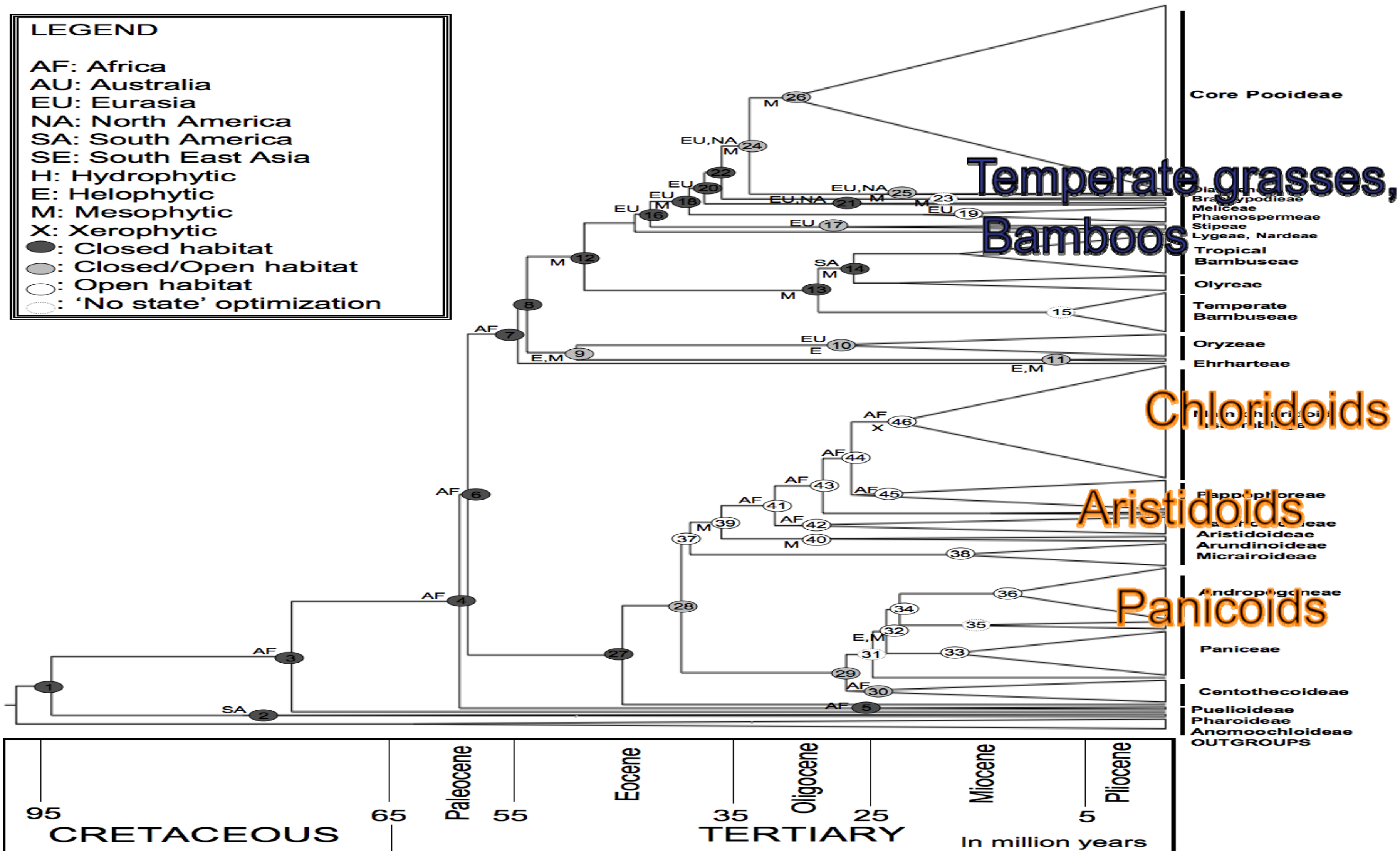
- Parsimony analysis
- 5,060 DNA characters (backbone topology)
- 470 morphological characters

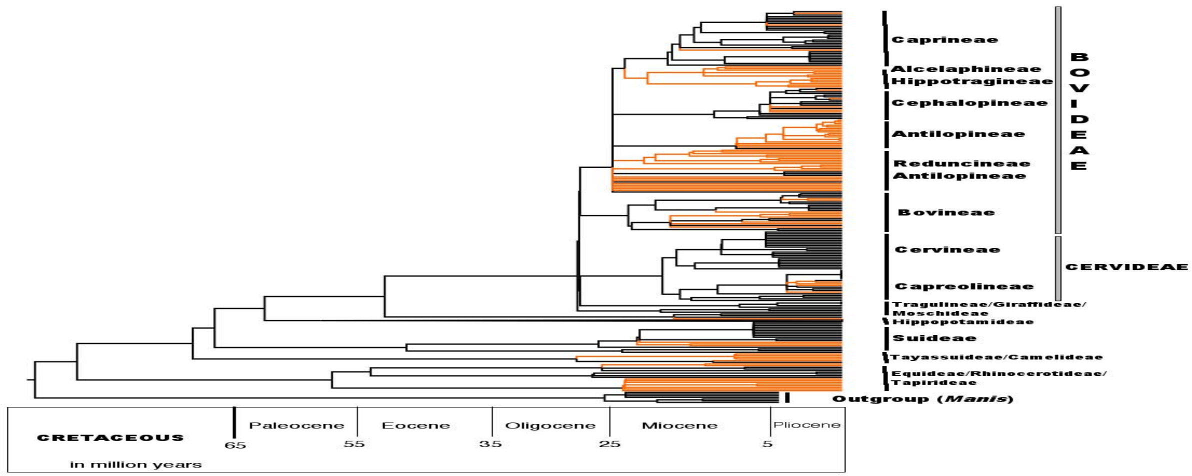
- •Bayesian molecular dating
- •C_3 vs. C_4 optimization
- •ALL 800 GRASS GENERA



Grasses ancestral habitats in Africa

Likelihood method (all grass genera)
Vegetation type + Habitat moisture
Bouchenak-Khelladi et al. (submitted), Evolution.





Bininda-Emonds et al. (2007), Nature

Animal Diversity Website

Adaptation to savanna habitats

- Appearance of savanna-adapted ungulates: 26-1 mya

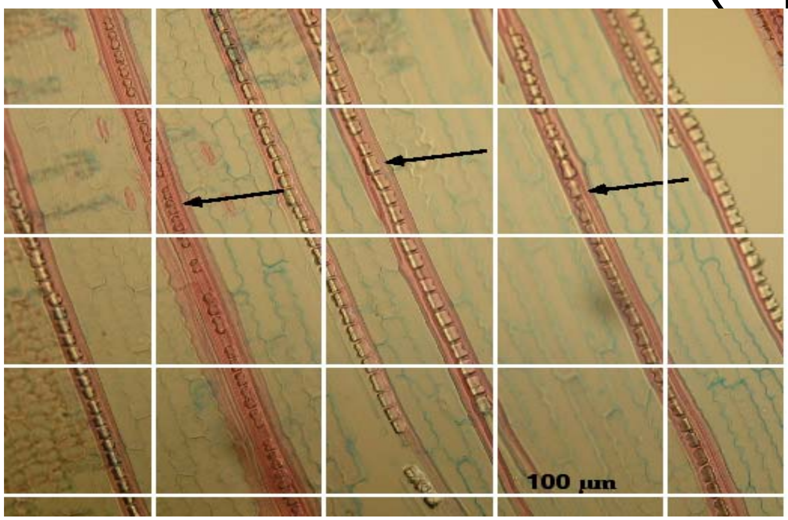
  _Migration to Africa of Ruminantia (Antilopineae, Bovineae) and Perissodactyla between 38 and 10 mya

  _African origin of C_4 major clades: Chloridoideae and Panicoideae at 25 and 30 mya, respectively

  _Today, Africa counts for 75% of C_4 grass species diversity

Which grass functional trait may be related to herbivory??

- Phytoliths (silica bodies in grass epidermal cells) are substances capable of inducing morphological changes to animal mouthparts (Piperno, 2006)



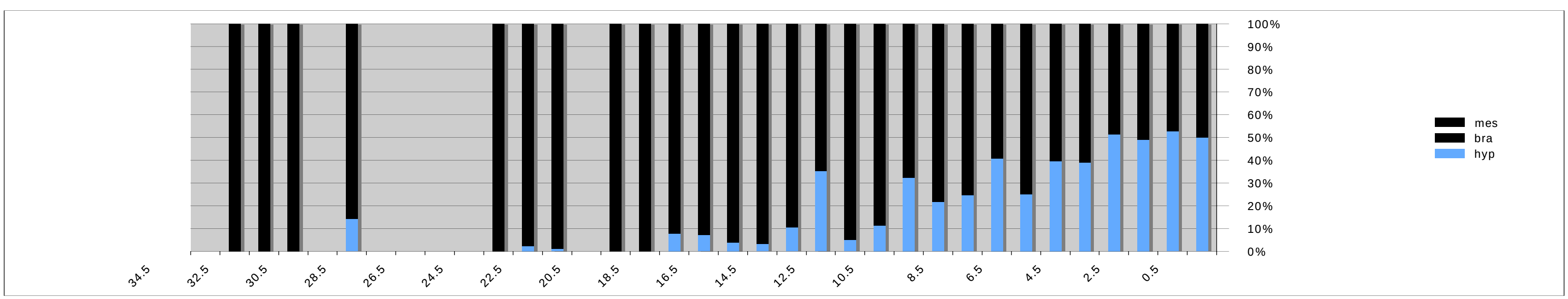
*<u>SILICA DENSITY INDEX</u>: (n*a) / A*

n: number of silica bodies in 10 quadrats

a: area of a single silica body

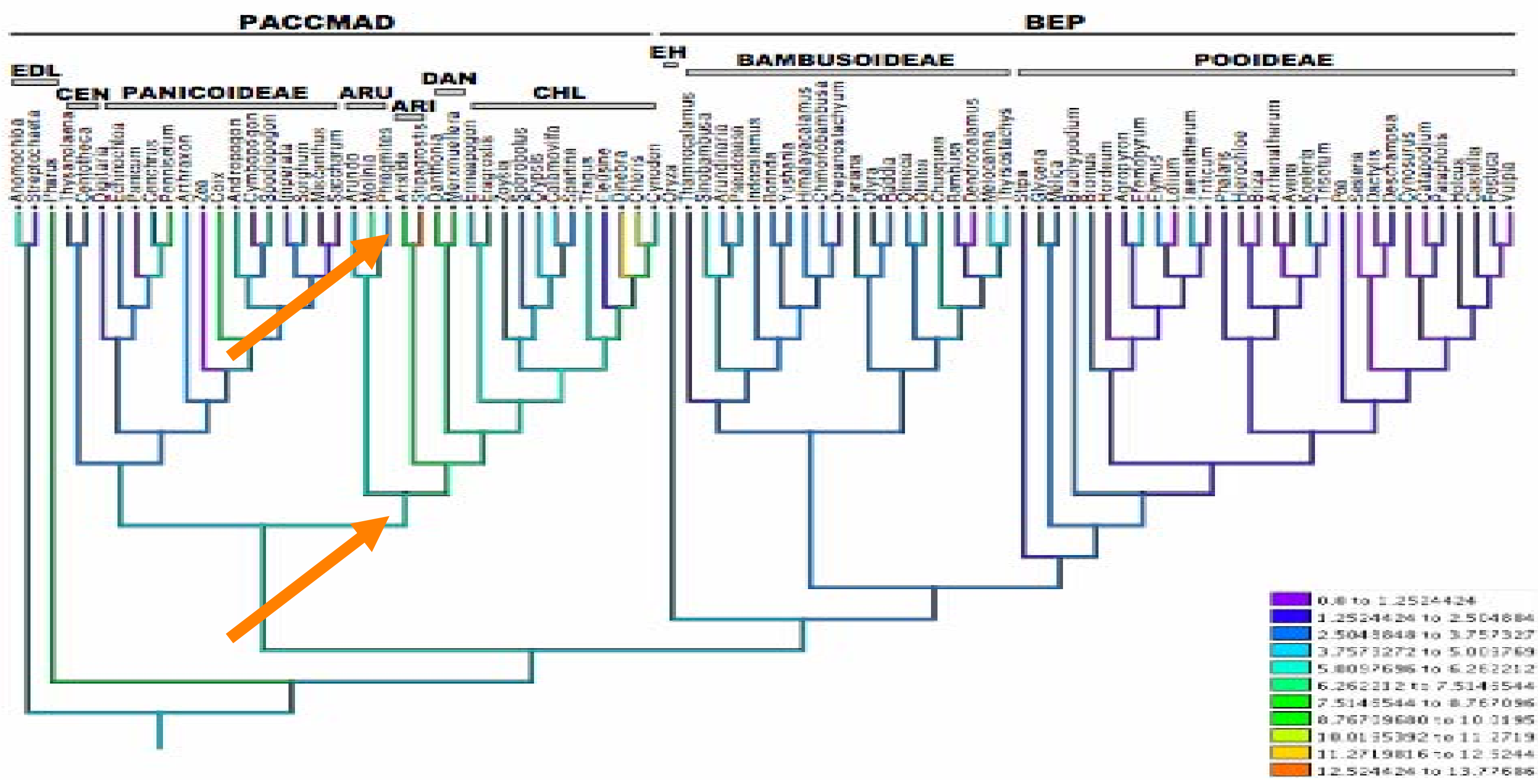
*A: area of one quadrat (100*100µm)*

- Proportion of “blue” hypsodont ungulate fossils in the Neogene record (Jernvall & Fortelius, 2002)



• GEE analysis (Paradis and Claude, 2002):

Increase in Silica Density correlated with the appearance of C_4 lineages ($p<0.05$)



Increase in silica density occurred recently (at least for Aristidoideae and Chloridoideae) between 13 and 3 million years

• Origin of **C_4 photosynthetic** pathway in grasses in the **late Oligocene-early Miocene** in **open**, **mesic and arid African** environment

• Adaptation to **savannas** by ungulates, most likely in **Africa**, from the **late Oligocene** to the early Pliocene

• **Increasing grazing** pressure in the **Miocene** may have selected for **increased C_4 grasses leaf toughness**_evolutionary arms race???

Ongoing research….

• Understanding grasses evolution can help reveal processes driving and maintaining savanna diversity and expansion

+ Species-level phylogenies

675 PACCMAD species_All African C_4 grass species (2,972)

"Phylogenetic diversification corroborates isotopic records?"

"Date the expansion of C_4 dominated biomes in Africa"

+ Localized sampling in the KNP of grass functional traits

68 KNP grass species collected in 46 10mx10m plots

Grass functional traits linked to herbivory (LDMC, leaf tensile strength)

Intraspecific variability tests

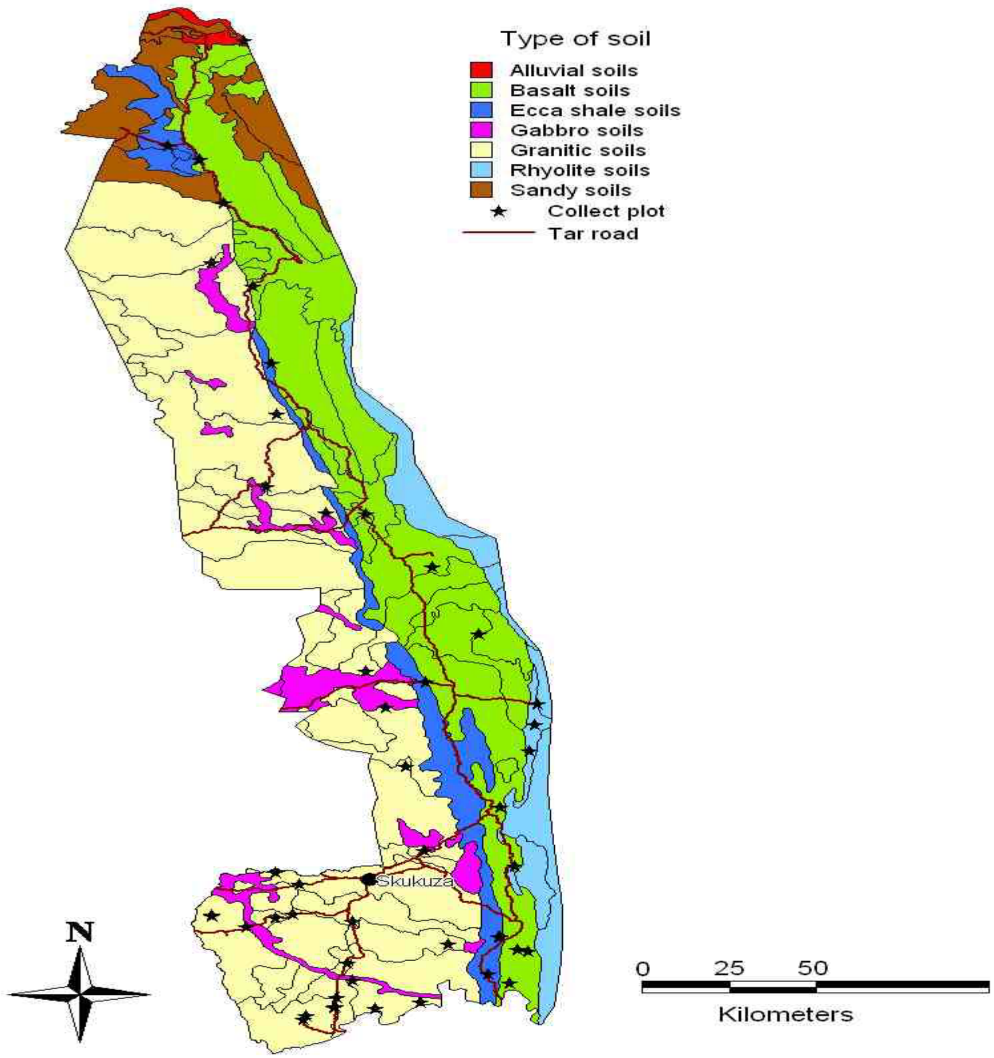
Phylogenetic clustering of traits (Traits contrasts among sampled lineages?)

Chloridoideae vs. *Panicoideae* vs. *Aristidoideae*

Low

Rainfall

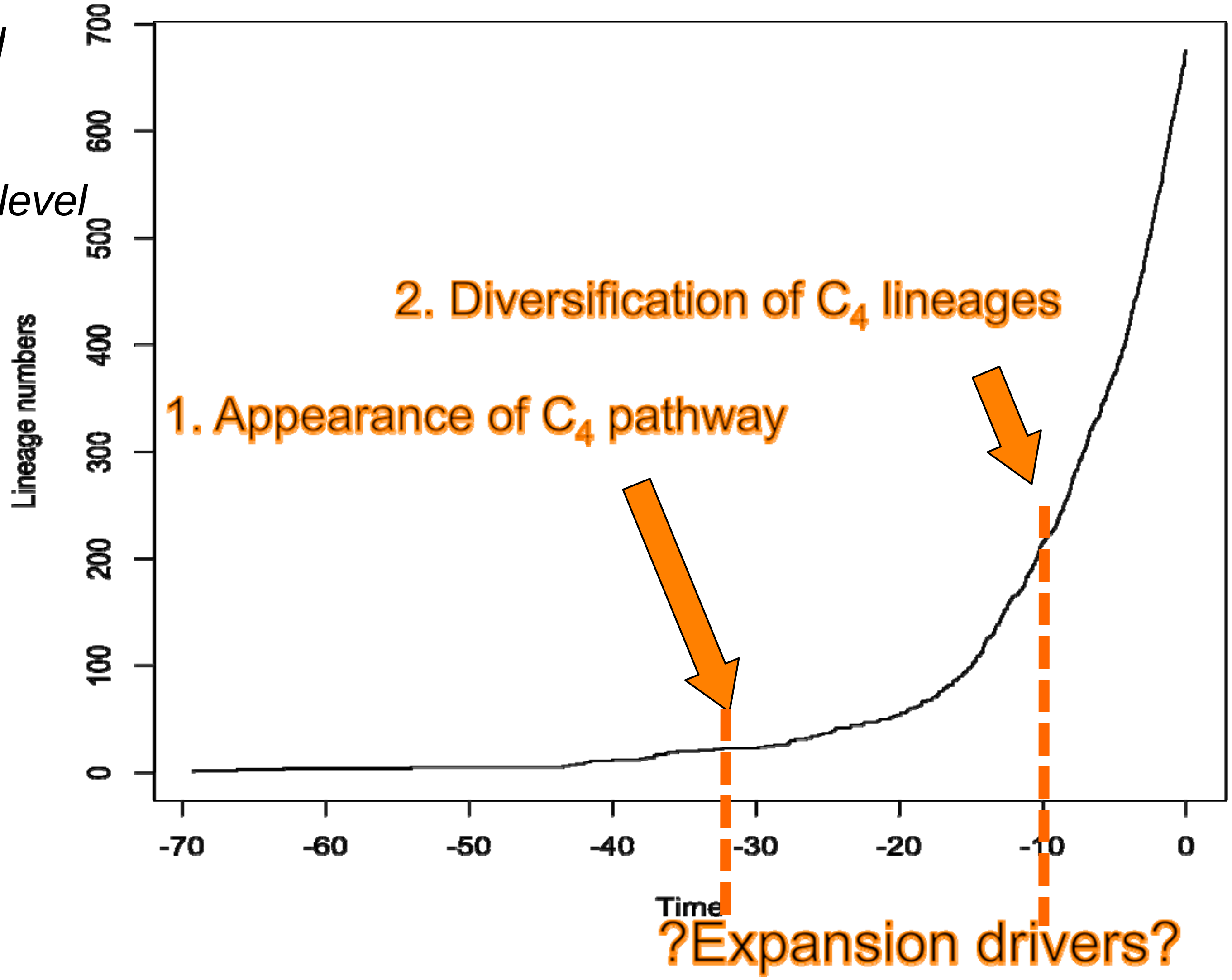
High



Granite → Basalt

Soil

• *675 sp.*
• *Nuclear and Plastid DNA regions*
• *Largest sp. level C_4 grasses phylogeny*



• **Recent diversification** of C_4 lineages suggesting that **other factors** than CO_2 decline promoted **C_4 biomes expansion in the Miocene**

- **CO_2 is not the only driver** of C_4 grass evolution and diversification: herbivory (silica bodies), seasonality/aridity (ancestral habitats of C_4), geographical dispersals (to Australia and South America) and key innovations (fire- and drought-adapted traits)

- To understand historical processes shaping savanna biomes, one needs to qualify and quantify proxies which led to C_4 grass expansion in Africa

"Did C_4 grass lineages from distantly related subfamilies(Aristidoideae, Chloridoideae and Panicoideae) adapt to similar environments? When and Where?"

"Which extrinsic factors allowed C_4 grass lineages to diversify?"

"Are grass functional traits (leaf tensile strength, LDM, silica density) evolutionary conserved?"

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