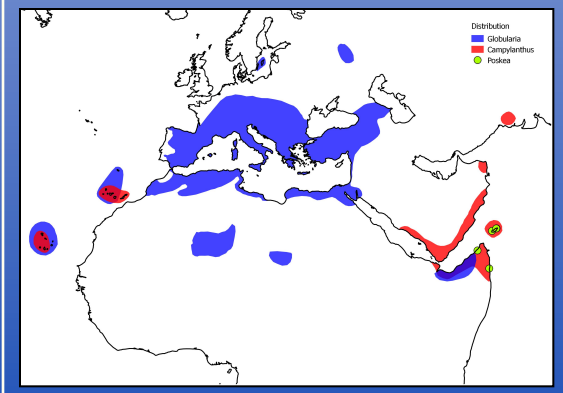
Parallel bursts of recent and rapid radiation in the Mediterranean and Eritreo-Arabian biodiversity hotspots as revealed by *Globularia* and *Campylanthus* (Plantaginaceae)



XV OPTIMA Meeting
June, 6-11 2016
MONTPELLIER

Hans Peter Comes
& Matthias Affenzeller
Dept. of Ecology & Evolution
Salzburg University
Austria

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Mediterranean Basin & Macaronesia (MED)

- Global floristic hotspot (Mittermeier et al., 2005)
- Hotspot of recent and rapid radiations, where (net) species diversification rates are sometimes very high (> 1 spp. myr^{-1}) and exceptionally fast – also globally *
- Most of these radiations are most likely ‚adaptive', excepting a few (e.g. Aegean *Nigella*).

* (e.g. *Cistus*: 1.46–2.44 spp. myr^{-1}, Guzmán *et al.*, 2009; *Dianthus*: 2.2–7.6 spp. myr^{-1}, Valente *et al.* 2010; *Centaurea*: 1.95 spp. myr^{-1}, Bell *et al.*, 2012). Reviewed in Valente & Vargas (2013).

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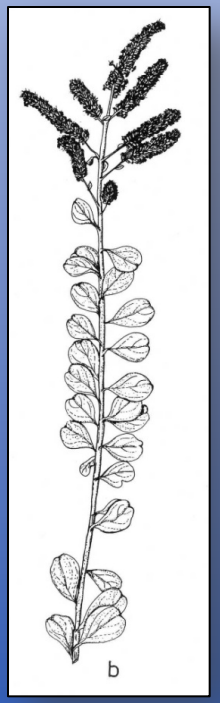
Eritreo-Arabian/Horn of Africa Region (EAR)

- One of only two global biodiversity hotspots that are **entirely arid** (Mittermeier et al., 2005)
- Vascular plant richness: **5,000 spp.**, (1/5th of the MED); **c. 50% endemic** (Conservation International, 2008)
- Dry-evergreen shrubland, semi-desert grassland, and low-growing dune and rock vegetation
- ***e.g. Dracaena, Commiphora, Boswellia, Poskea socotrana, Campylanthus…***

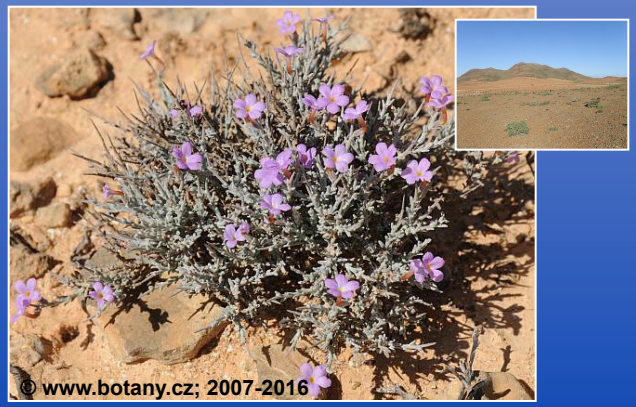
Campylanthus **(c. 18 spp.) crown age: *c.* 4.68 (2.00–8.07) Ma based on nuclear (ITS) sequence data ***

* Thiv et al. (2010) *Mol. Phyl. Evol.*, 54, 607–616.

Dracaena cinnabari (Socotra)



Poskea socotrana



Campylanthus spinosus (Jemen)

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Eritreo-Arabian/Horn of Africa Region (EAR)

Campylanthus sp.
Collected by Dr. Jacqueline Henrot
in the Eastern Hajar Mountains on 20 April 2007
Filed in triplicate at the Oman National Herbarium under JH/232

c. 15 spp. in EAR

Campylanthus hajarensis spec. nov. (Oman)

Hjertson et al. (2008) *Nordic J. Botany*, 26, 35–37.

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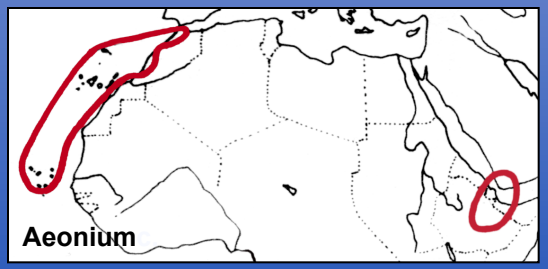
Eritreo-Arabian/Horn of Africa Region (EAR) – Macaronesia

- One of only two global biodiversity hotspots that are **entirely arid** (Mittermeier et al., 2005)
- Vascular plant richness: **5,000 spp., c. 50% endemic** (Conservation International, 2008)
- Dry-evergreen shrubland, semi-desert grassland, and low-growing dune and rock vegetation
- *E.g. Dracaena, Poskea socotrana, Campylanthus* spp. (c. 18 spp.)

***Campylanthus* has two disjunct species in Macaronesia: 'Rand Flora'**



- Dracaena
- Euphorbia spp.
- Smilax aspera
- Etc.

Campylanthus glaber (Cape Verde Islands)

C. salsoloides (2n=14) (Canary Islands)

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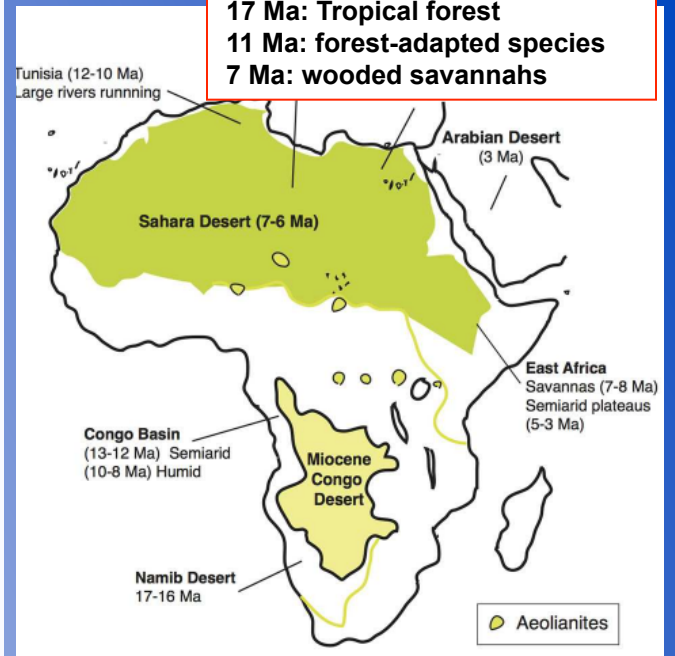
Living on the edge: timing of Rand Flora disjunctions congruent with ongoing aridification in Africa

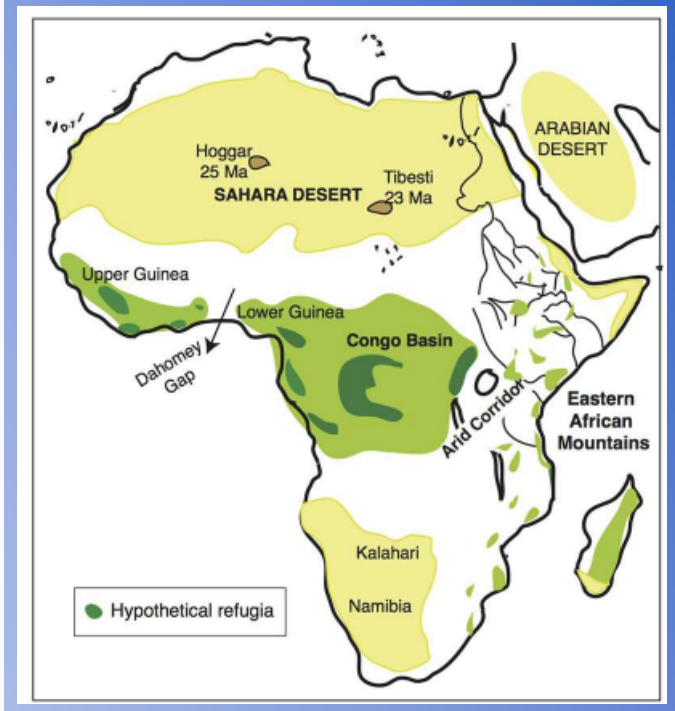
frontiers in Genetics
ORIGINAL RESEARCH
published: 01 May 2015
doi: 10.3389/fgene.2015.00154

Lisa Pokorny[1], Ricarda Riina[1], Mario Mairal[1], Andrea S. Meseguer[2], Victoria Culshaw[1], Jon Cendoya[1], Miguel Serrano[3], Rodrigo Carbajal[3], Santiago Ortiz[3], Myriam Heuertz[4,5,6] and Isabel Sanmartín[1]**

Pokorny et al. (2015)

17 Ma: Tropical forest
11 Ma: forest-adapted species
7 Ma: wooded savannahs





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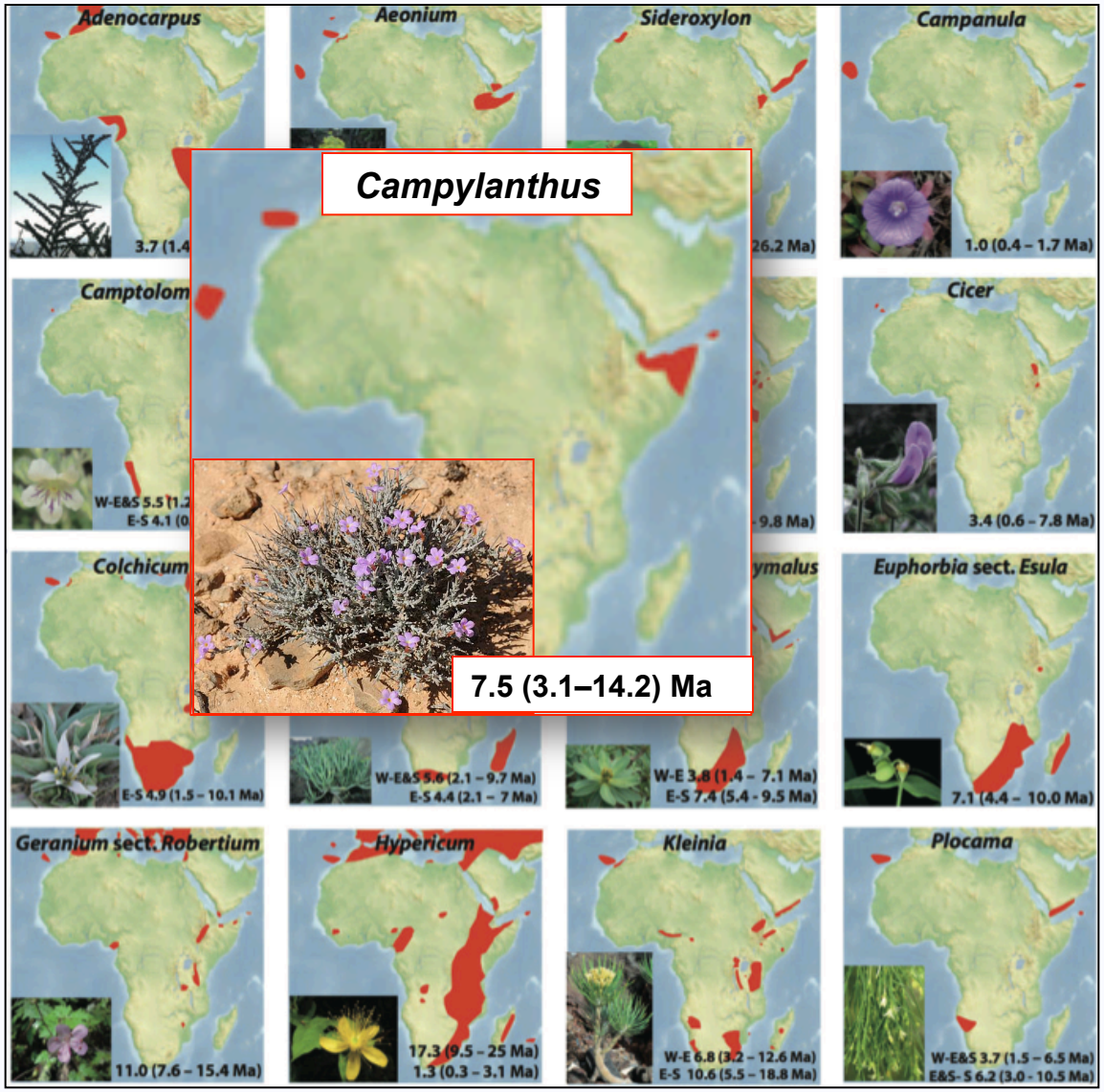

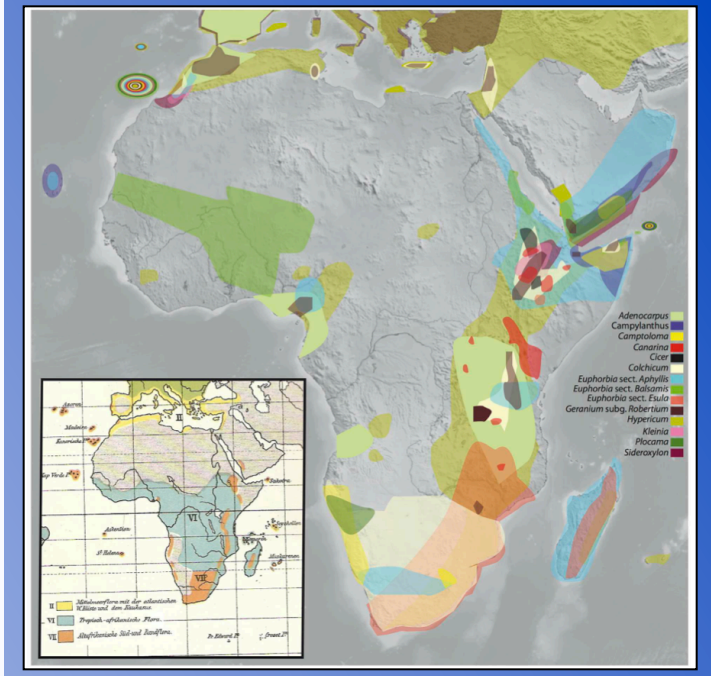

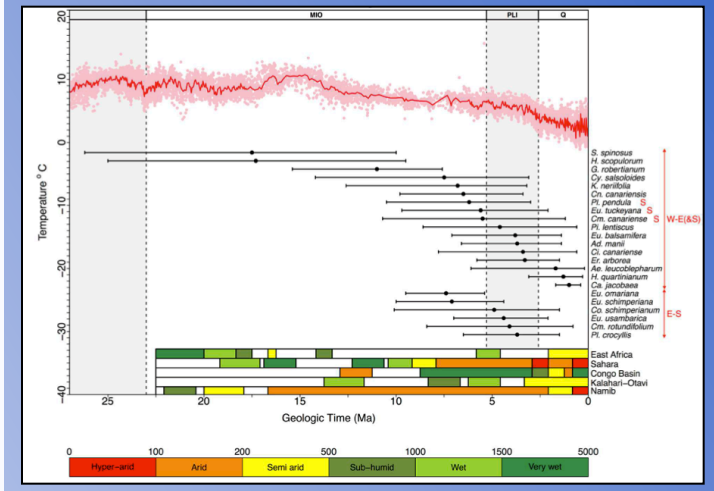

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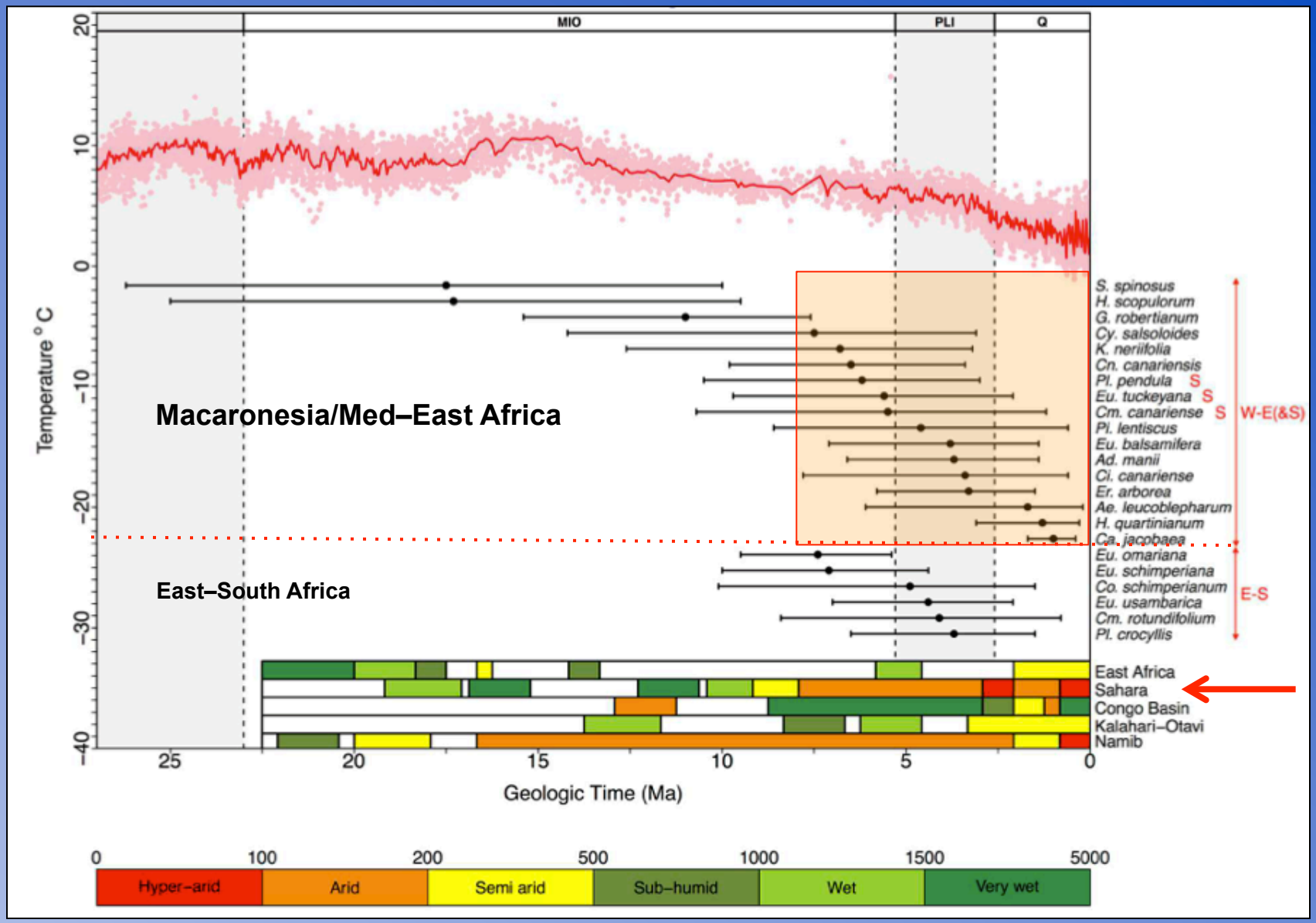
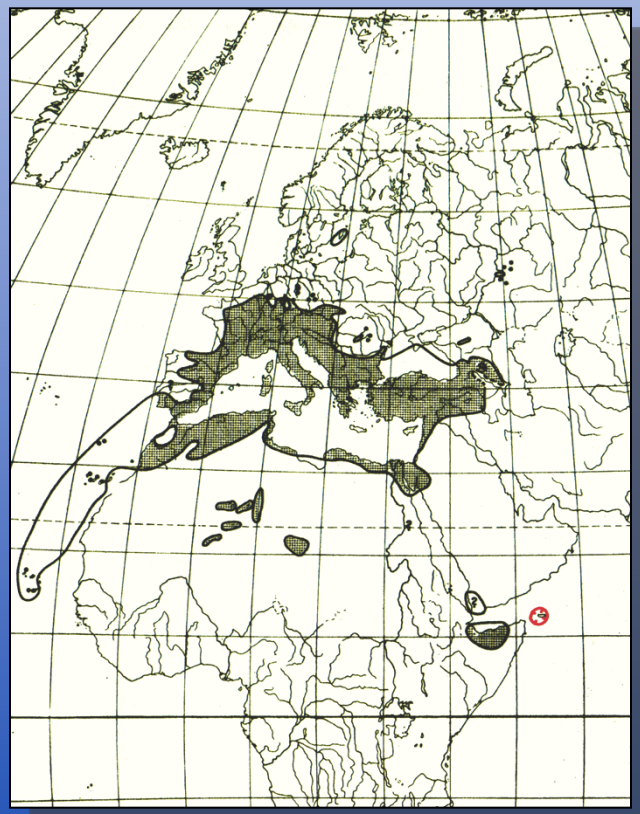


Campylanthus Is sister to

Globularia + Poskea (= *Globularieae*)

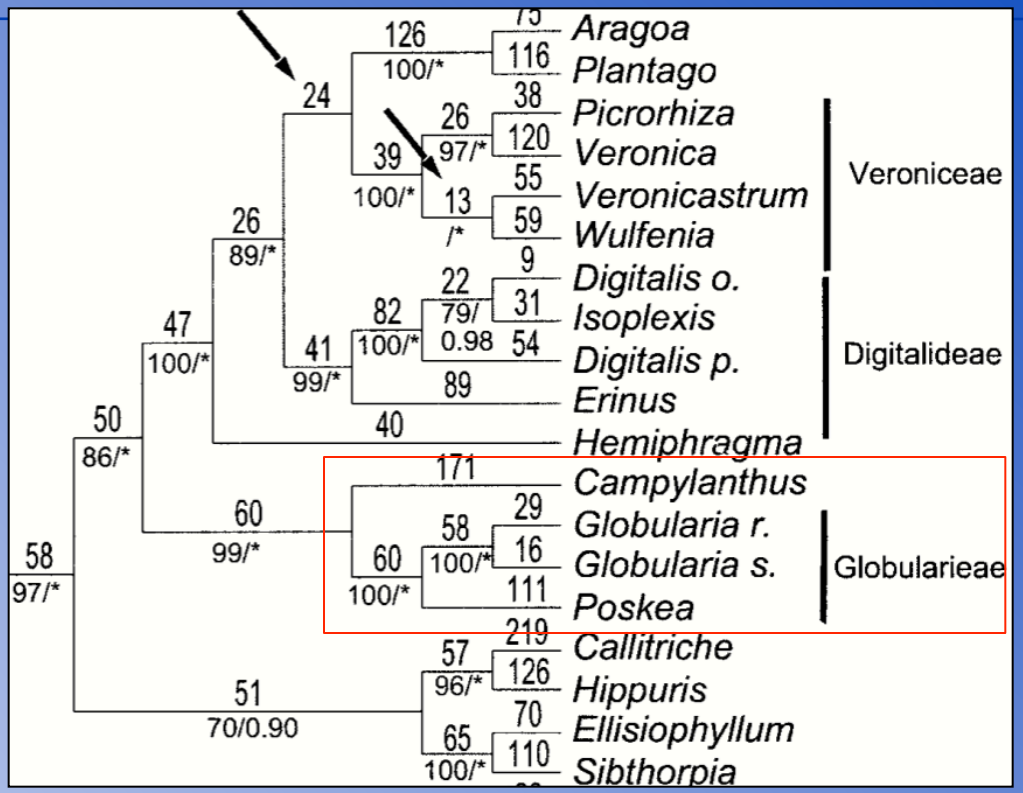


Globularia L.
Poskea socotrana BALF. fil.

American Journal of Botany 92(2): 297–315. 2005.

PIECING TOGETHER THE "NEW" PLANTAGINACEAE[1]

D. C. ALBACH,[2,5] H. M. MEUDT,[3] AND B. OXELMAN[4]



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Globularia

(Plantaginaceae)

27 Species

19 Mediterranean (incl. 4 Macaronesian)
8 Montane/alpine

Affenzeller et al., unpubl.

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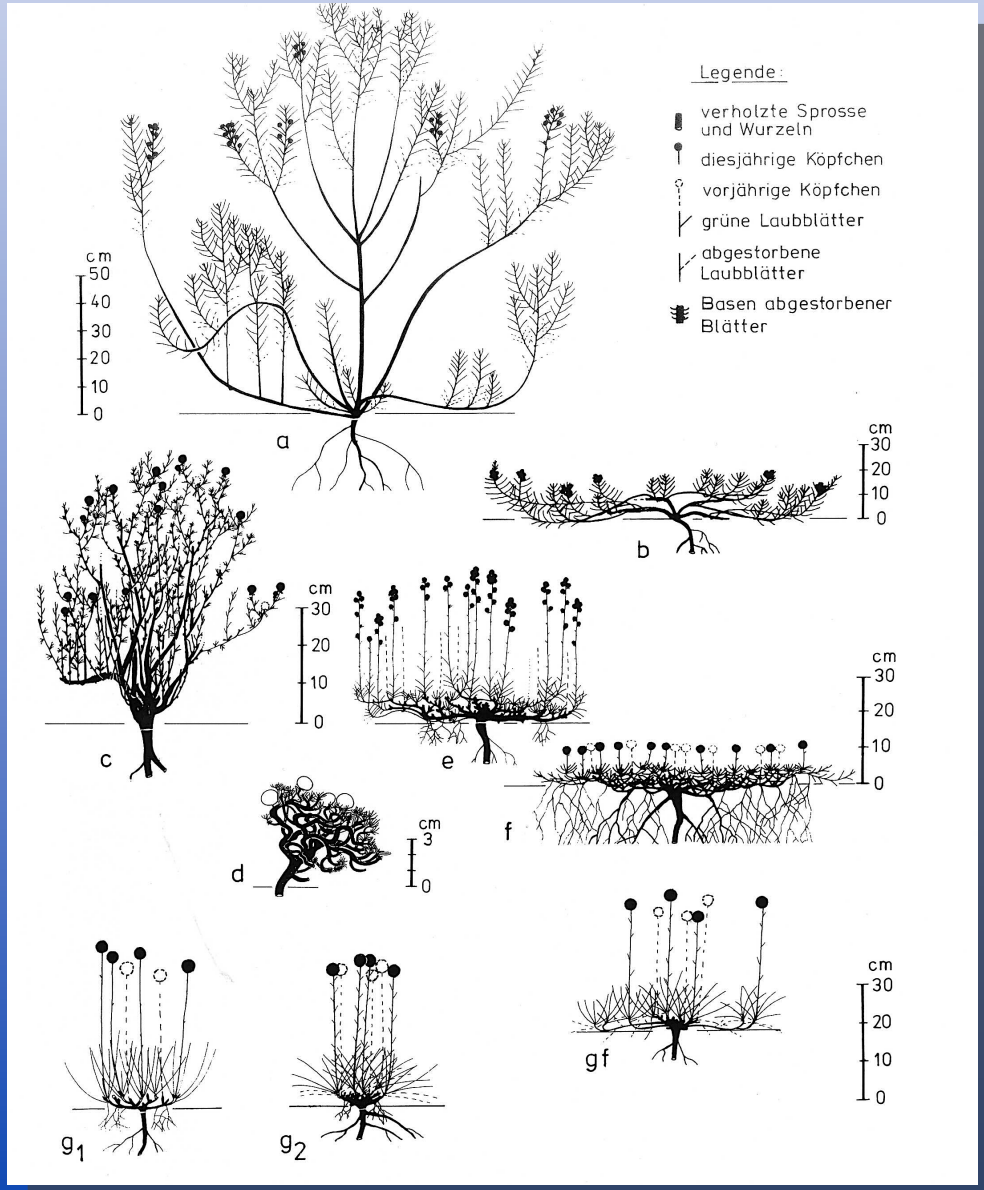
Globularia – growth forms



Source: Holländer & Jäger (1994) *Flora* 189: 223–254.

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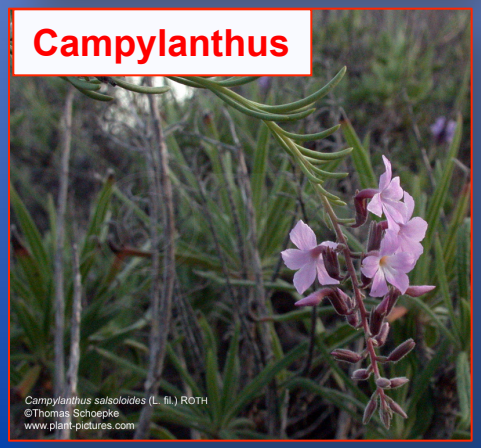
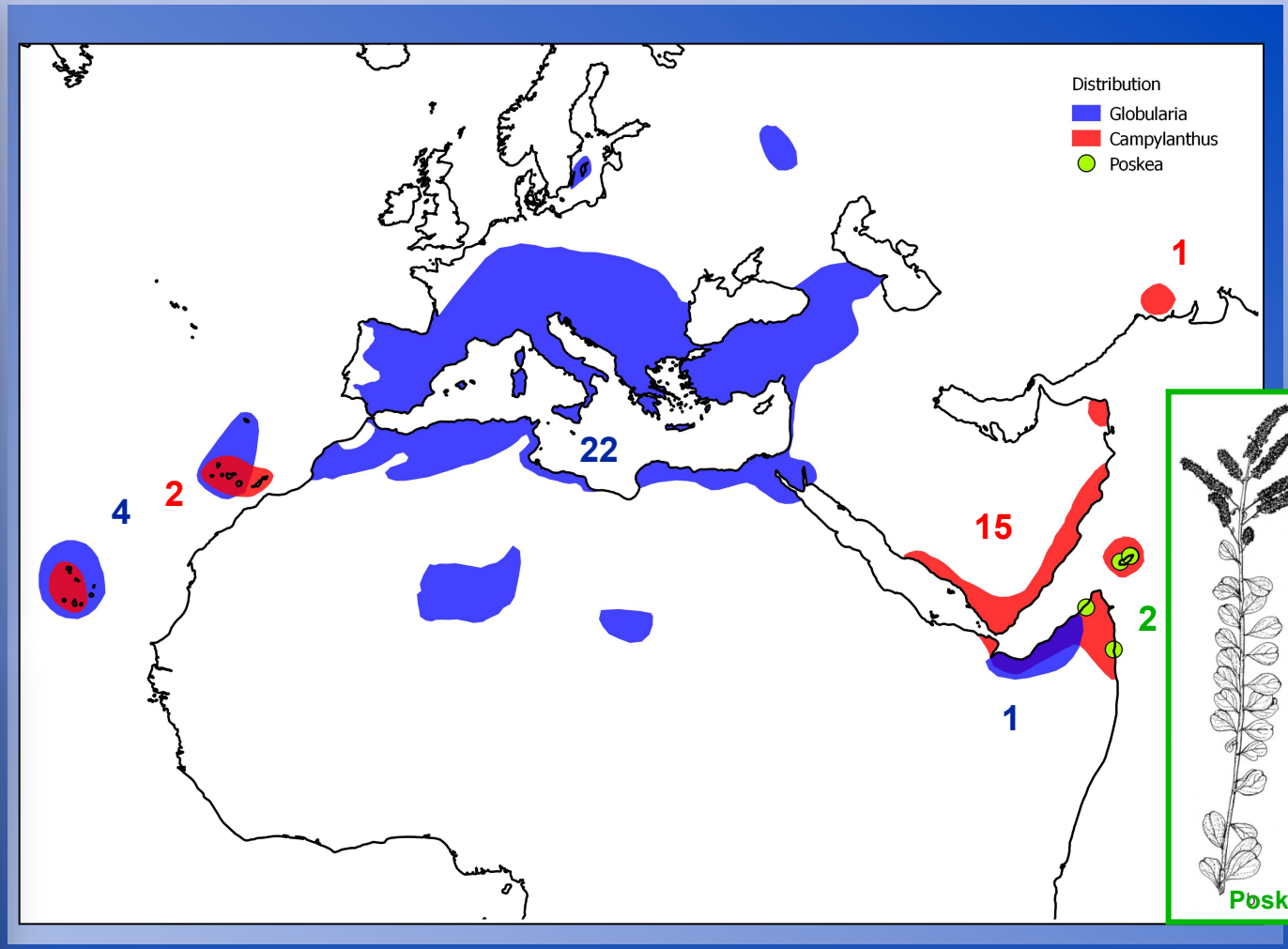
Globularia (27 spp.), *Campylanthus* (18), Poskea (2)

Globularia

Campylanthus





Affenzeller et al., unpubl.

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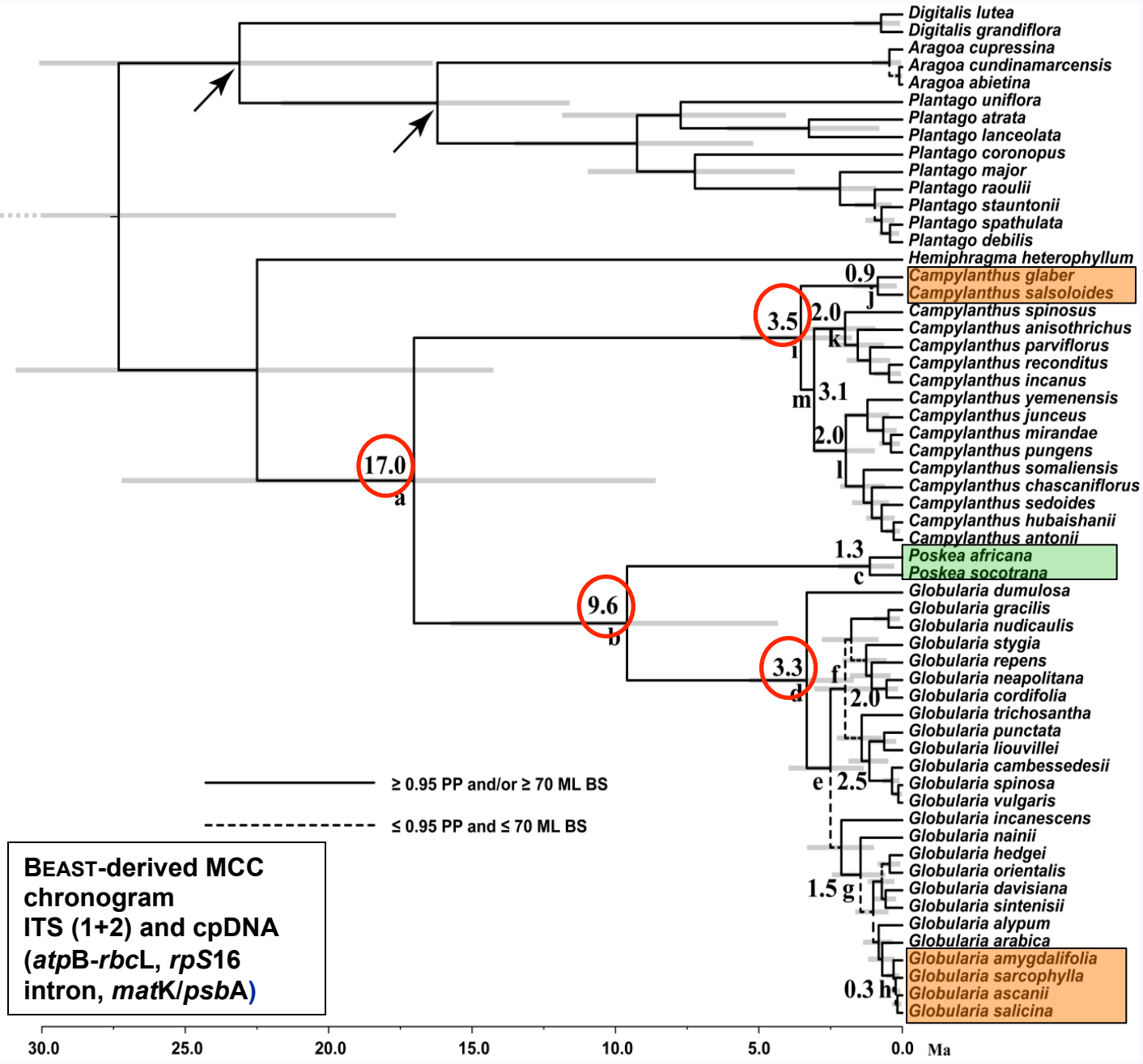
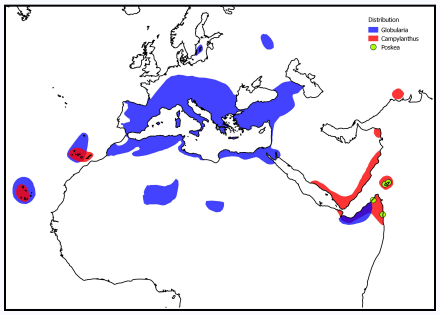


BEAST-derived MCC chronogram ITS (1+2) and cpDNA (*atp*B-*rbc*L, *rpS*16 intron, *mat*K/*psb*A)



Campylanthus

Poskea

Globularia

Affenzeller et al., unpubl.

Macaronesian species

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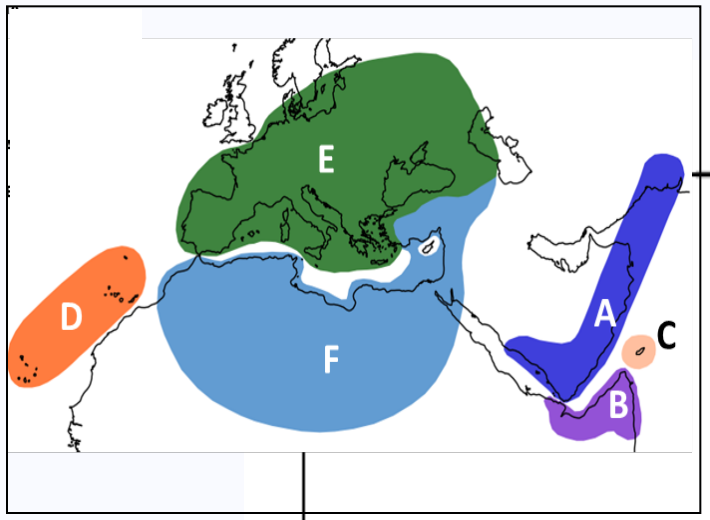

Macaronesia

Somalo-Ethiopia

South Arabia

MED-North

MED-South incl. Anatolia

Macaronesia

Campylanthus

Globularia

Affenzeller et al., unpubl.

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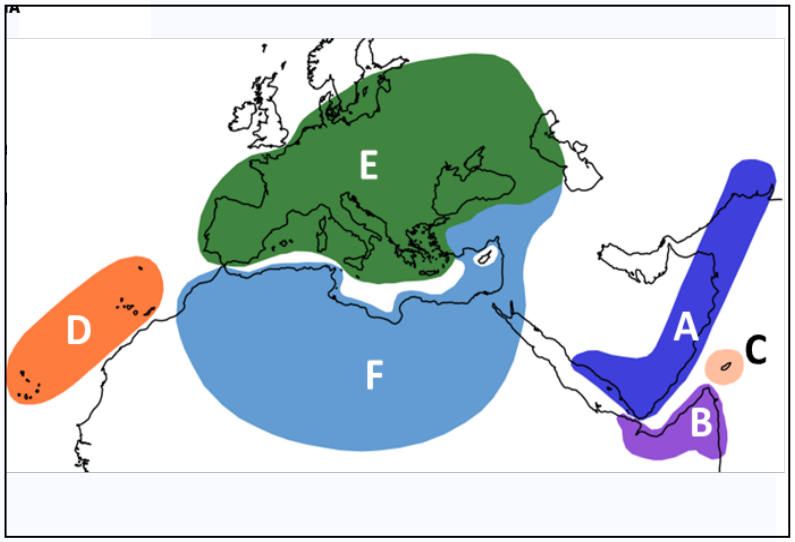
Ancestral area reconstructions on BEAST MCC tree using BBM (Bayesian Binary MCMC) in RASP (v 3.2)



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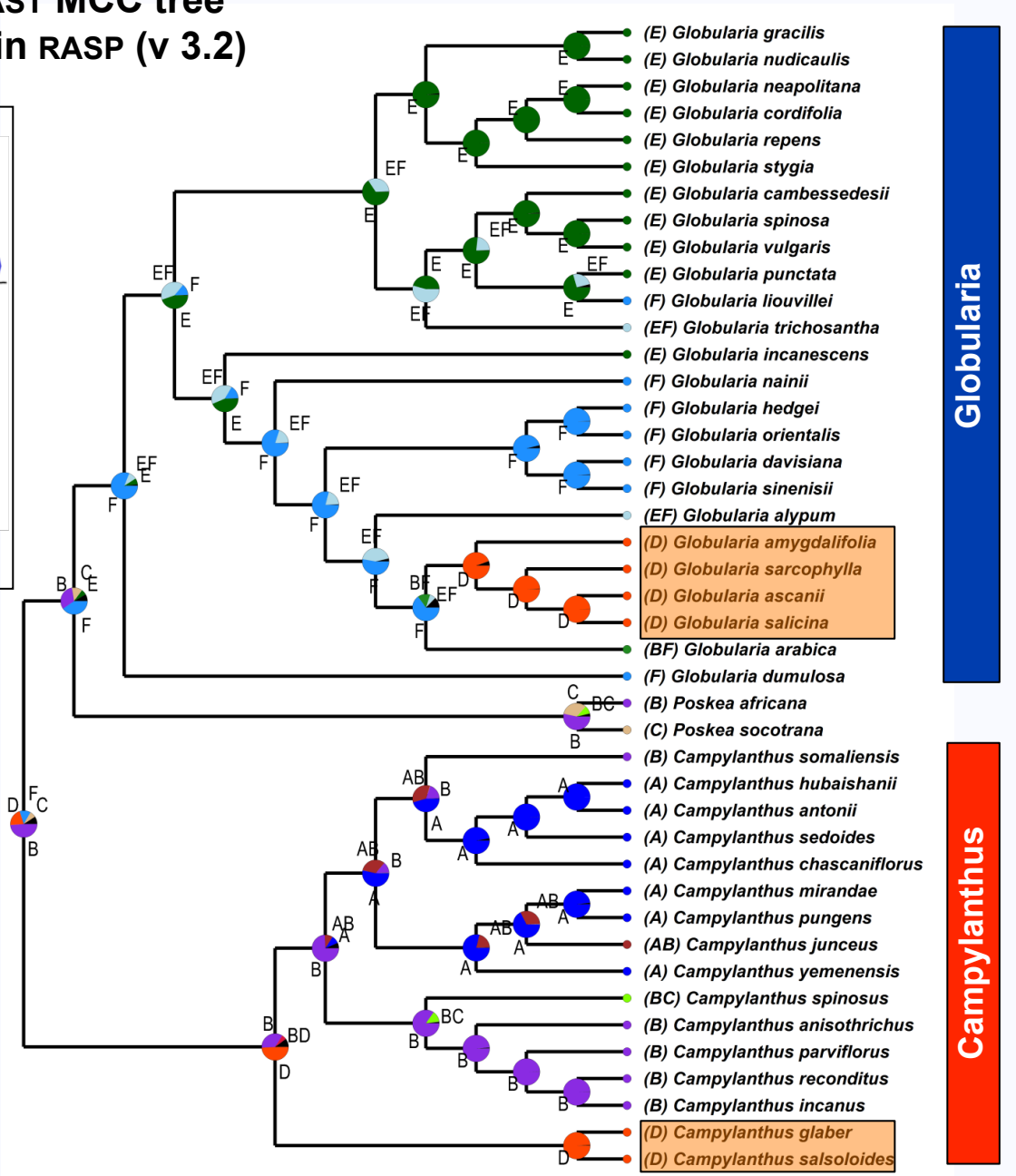

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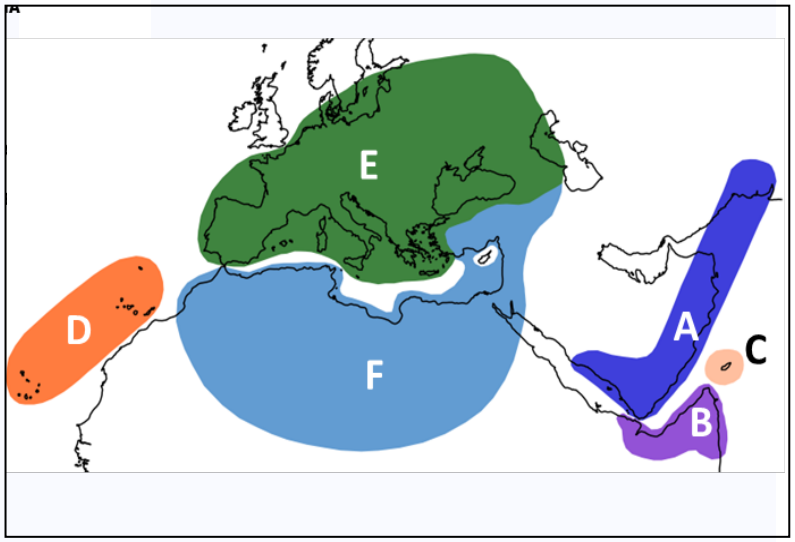

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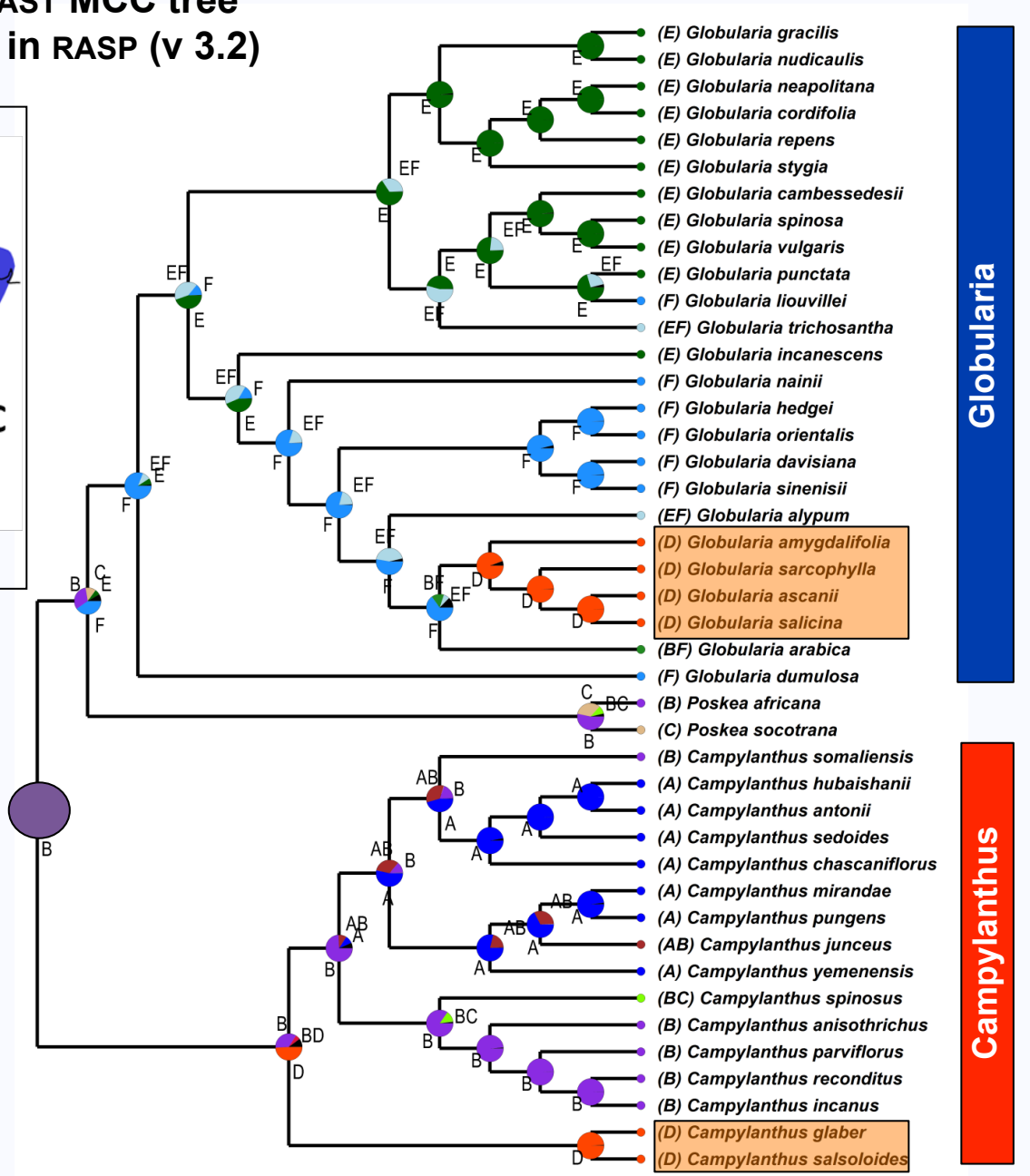

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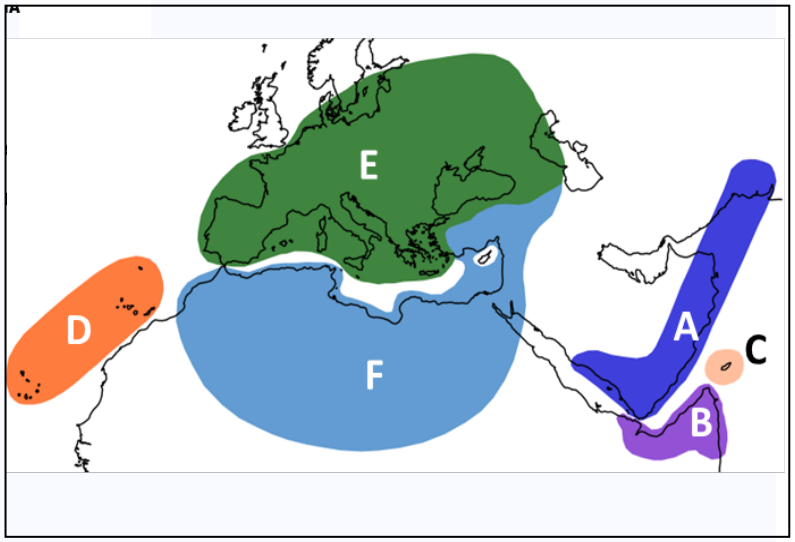

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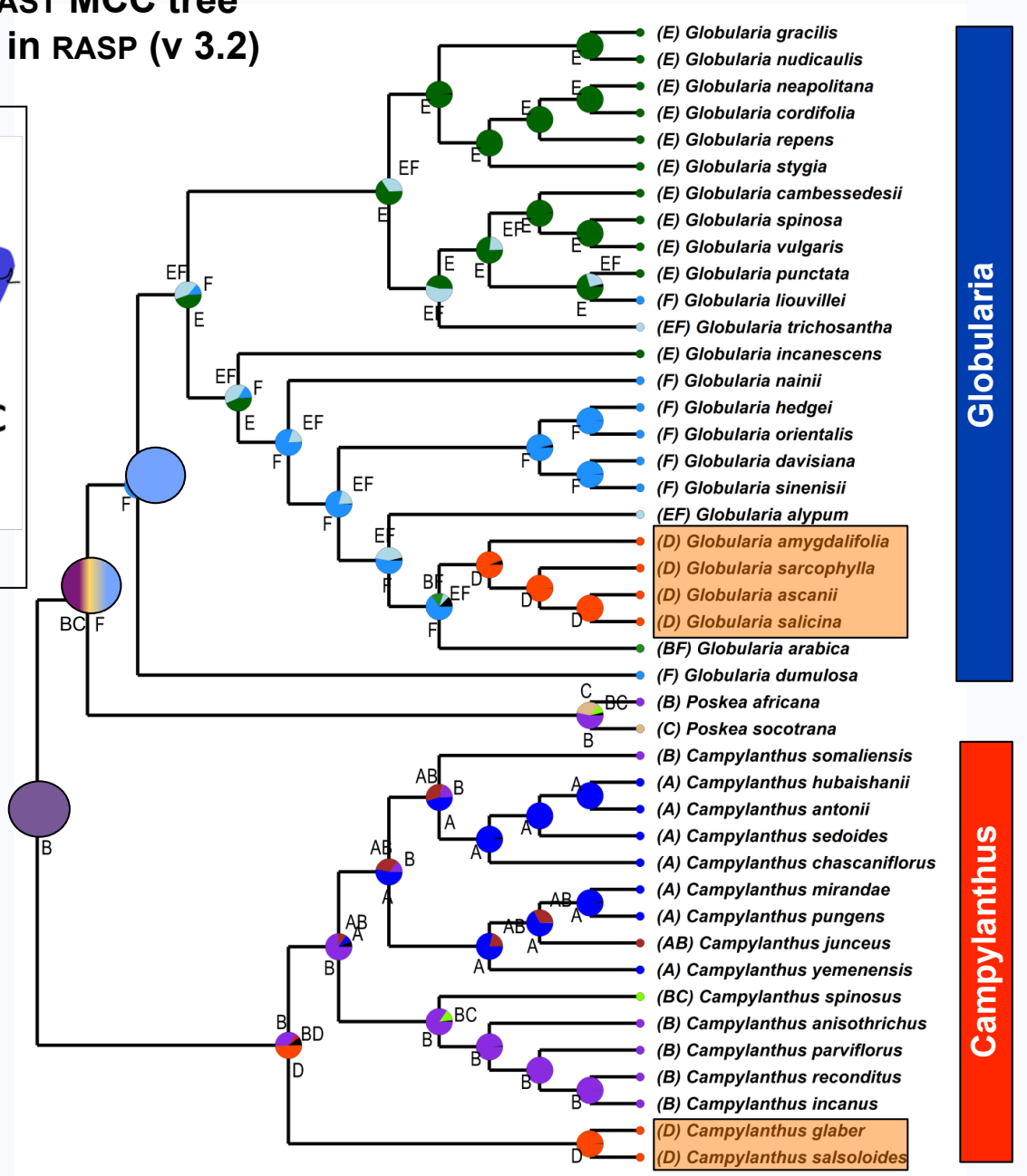

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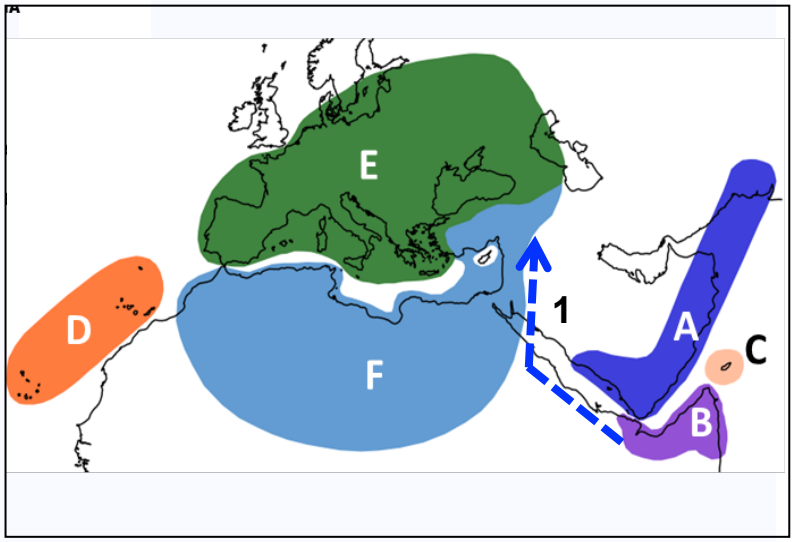

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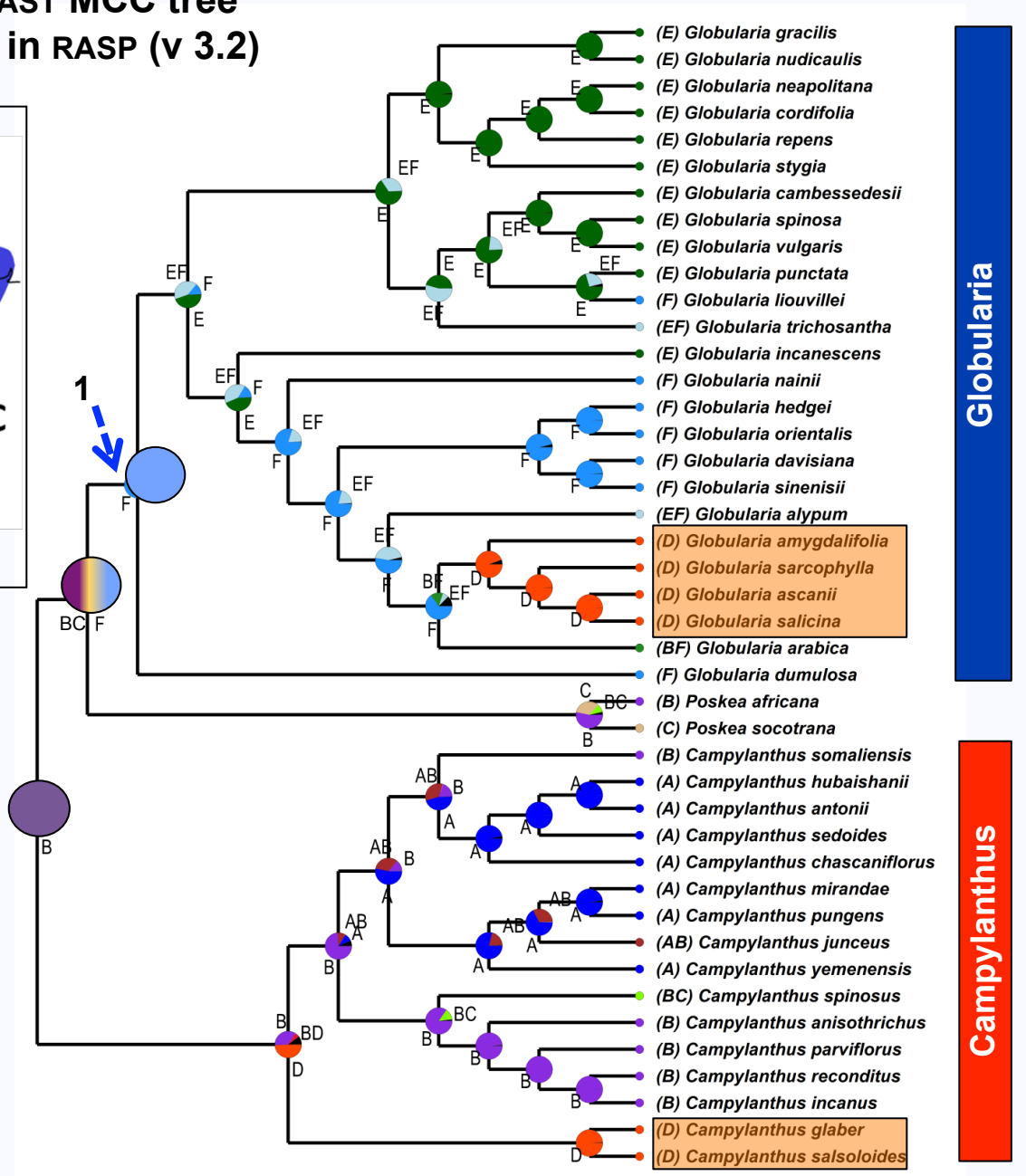

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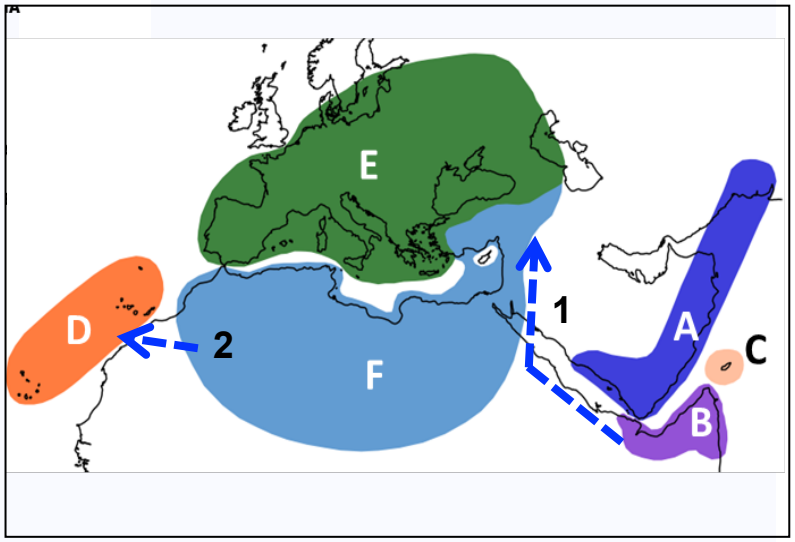

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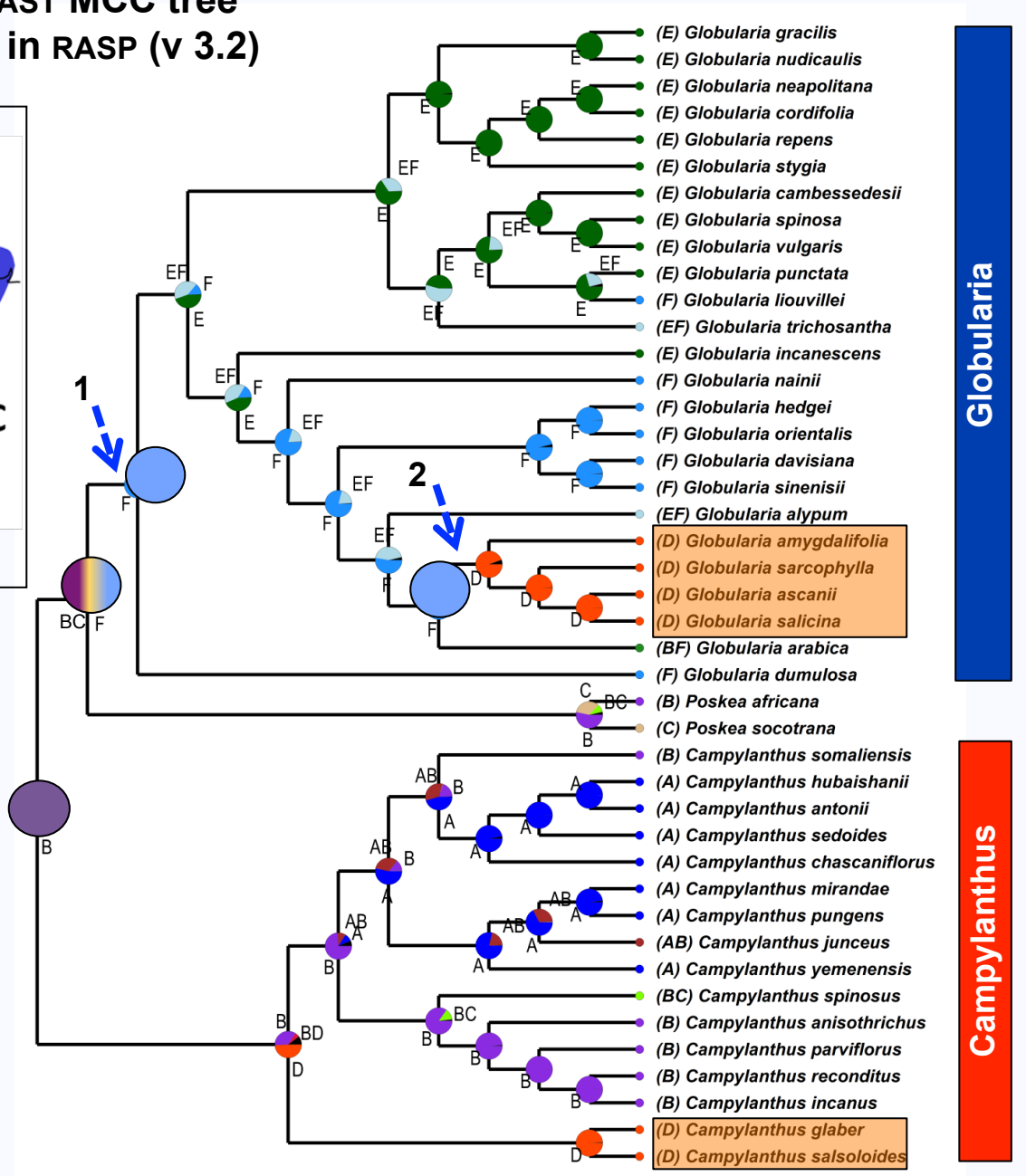

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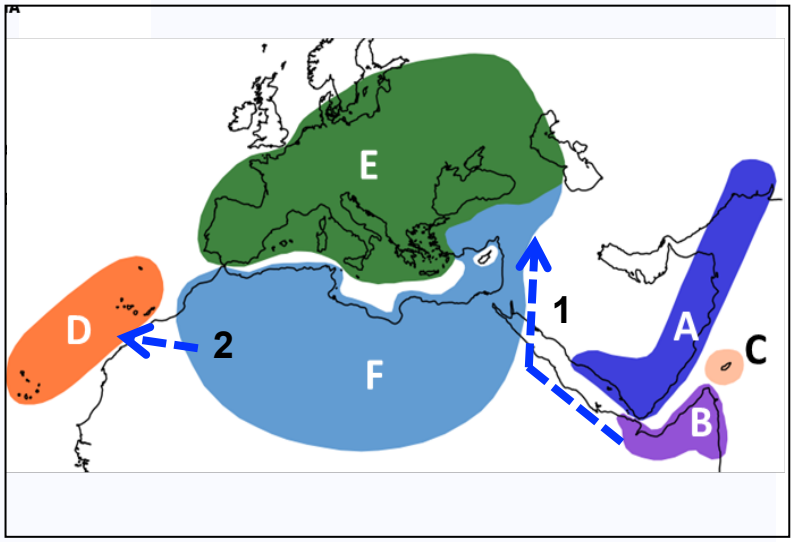

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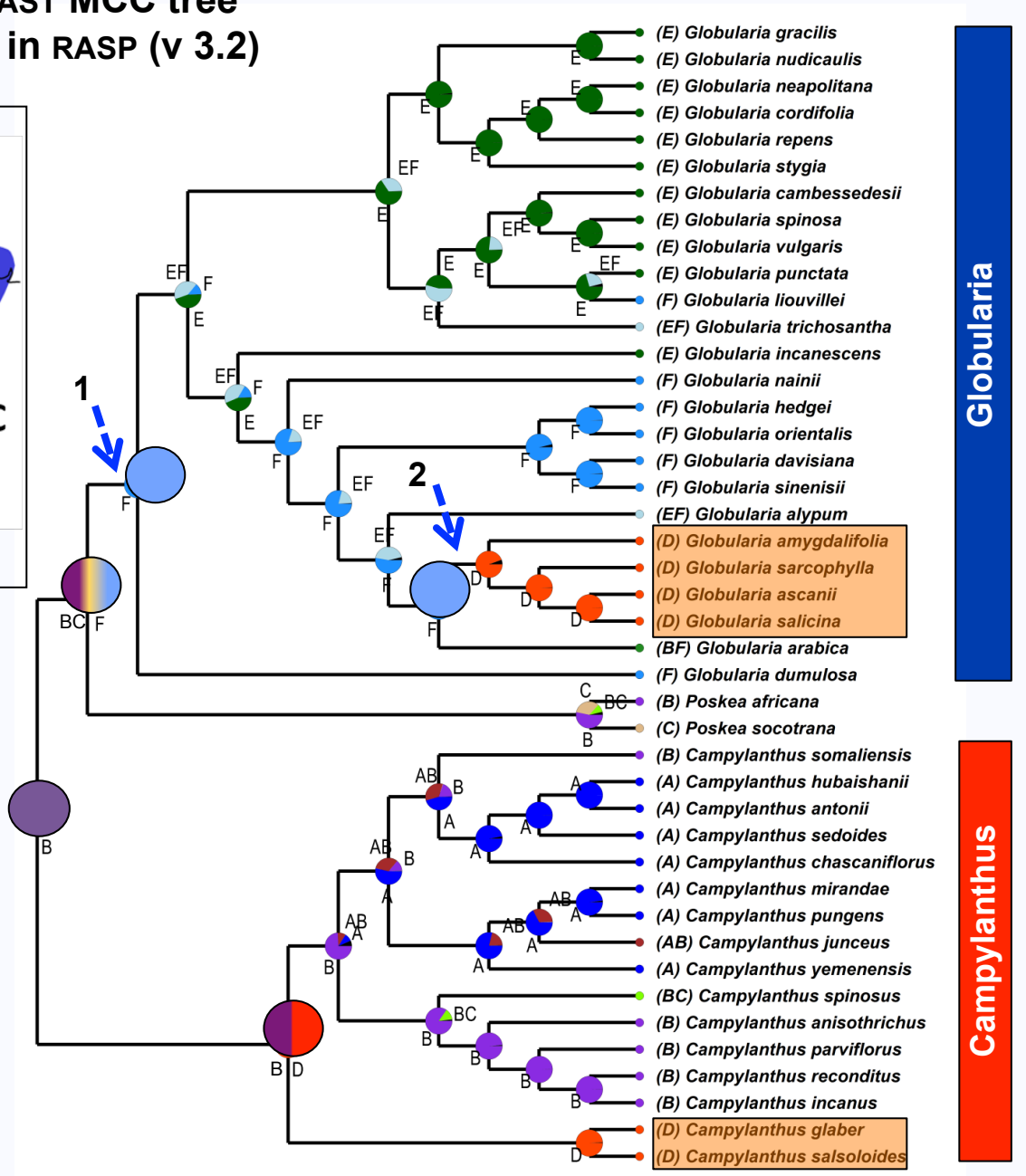

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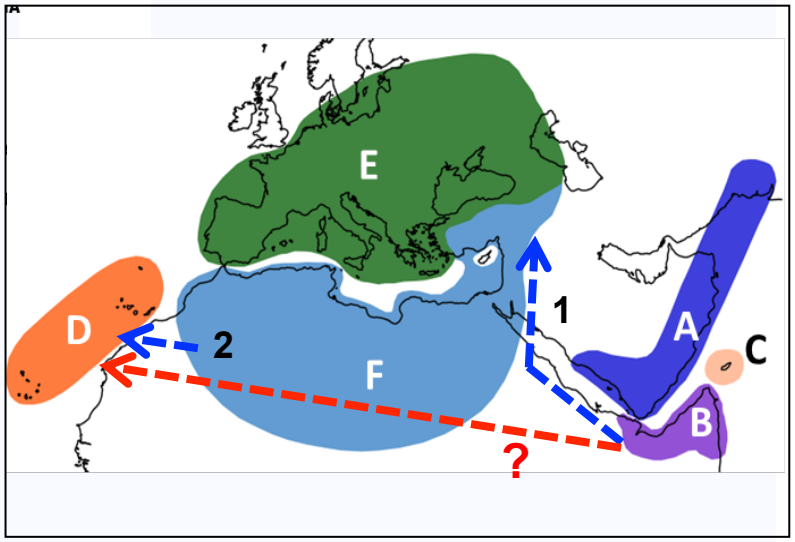

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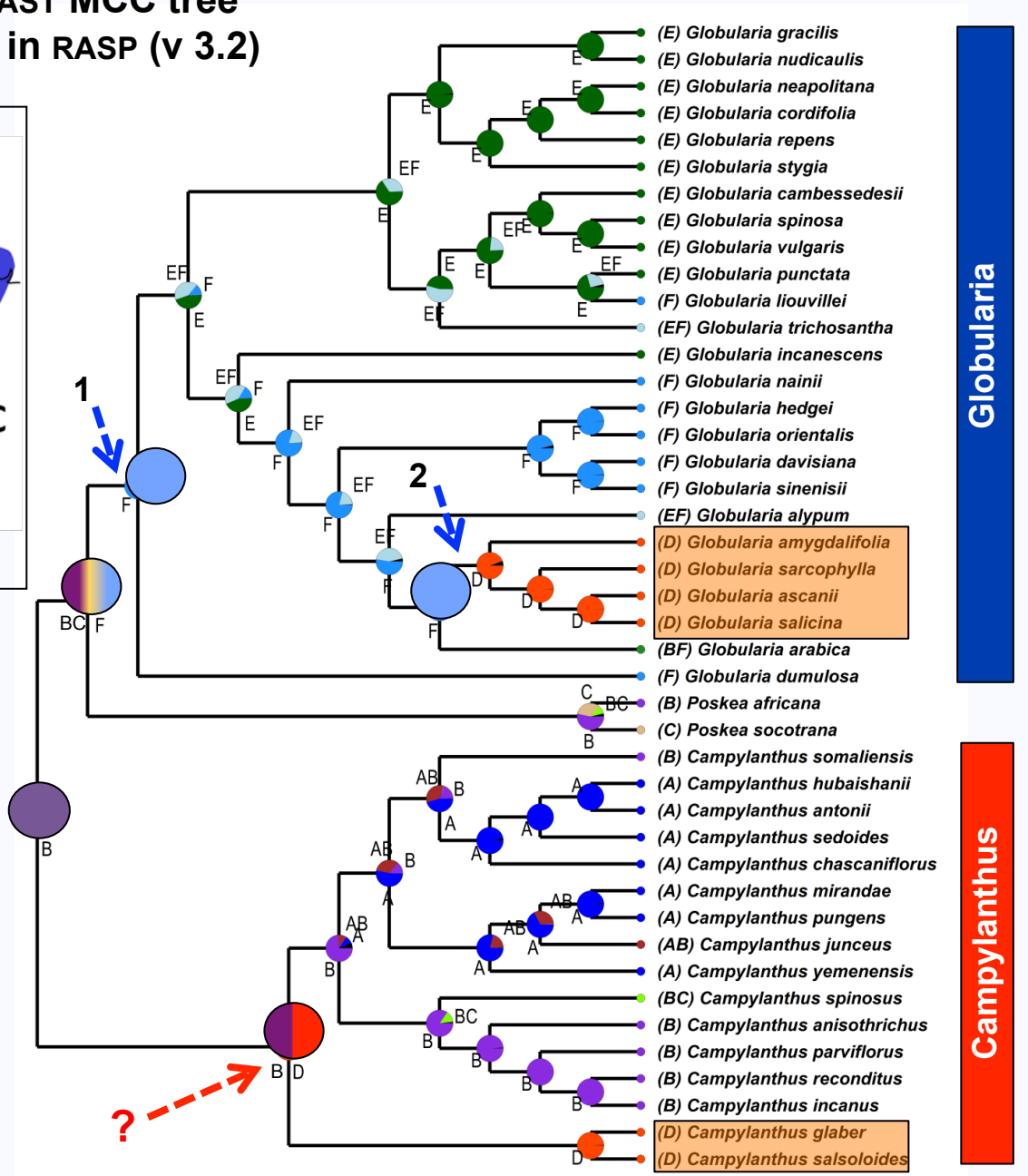

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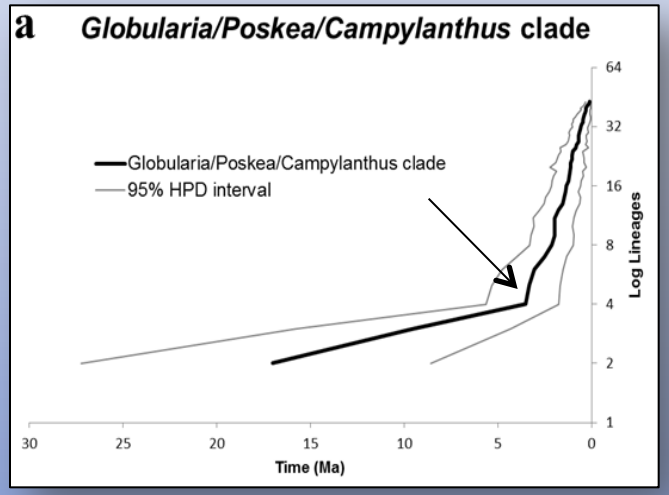
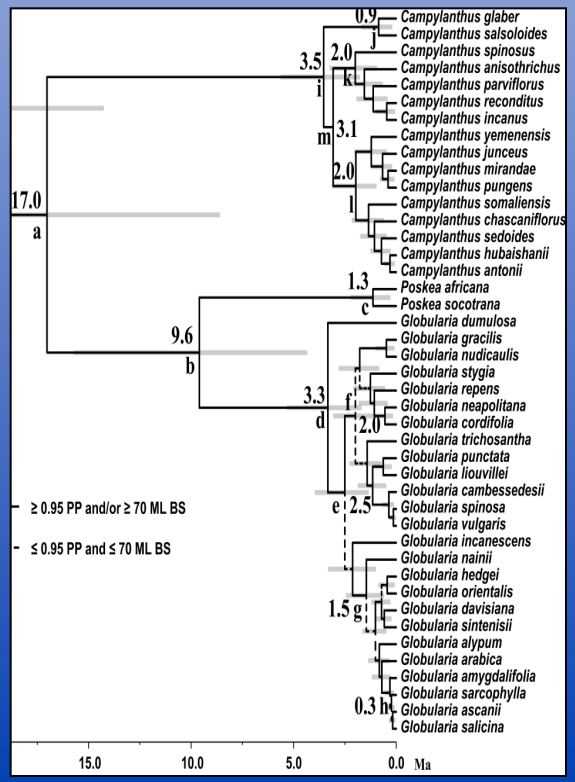
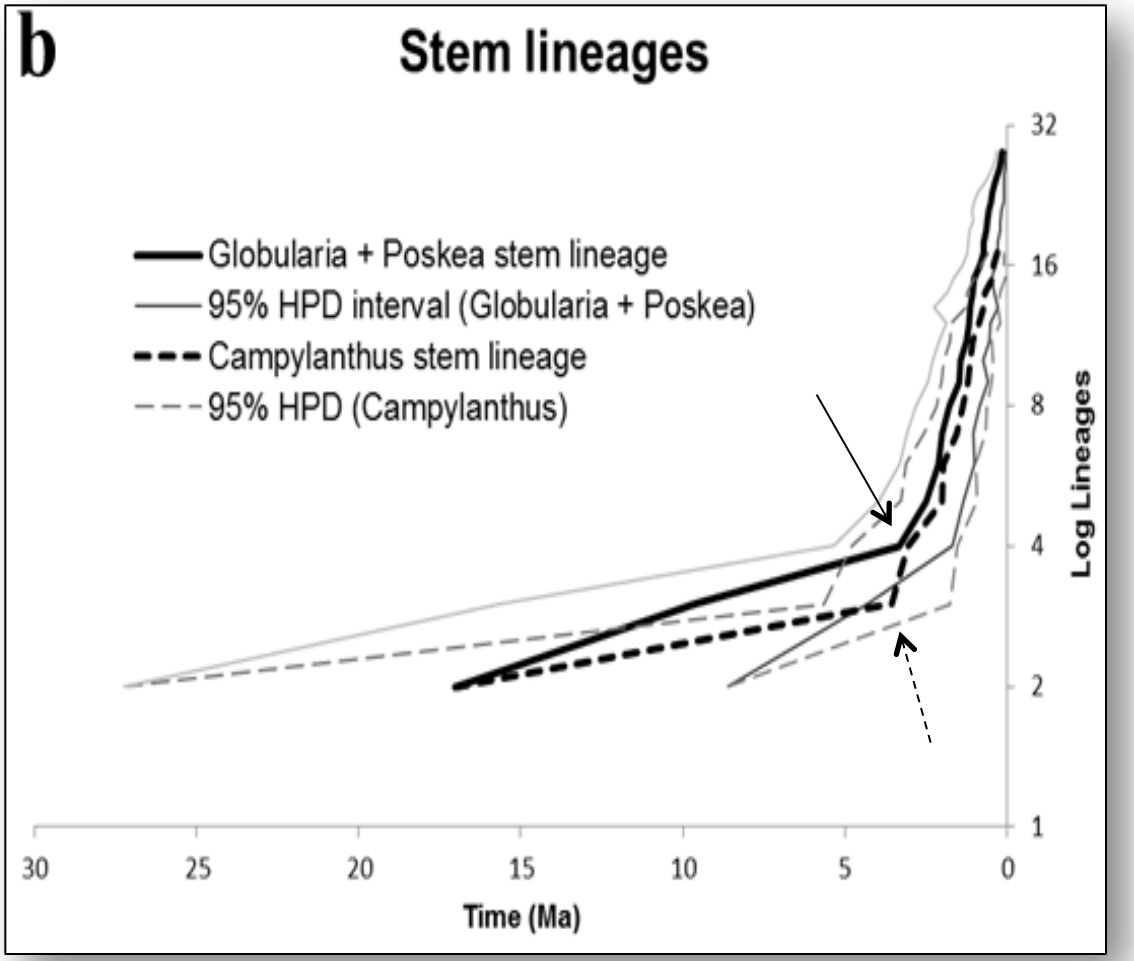




Affenzeller et al., unpubl.



- **Recent upturn** due to strikingly similar crown ages (*Camp*: **3.5 Ma**; *Glob*: **3.3 Ma**)

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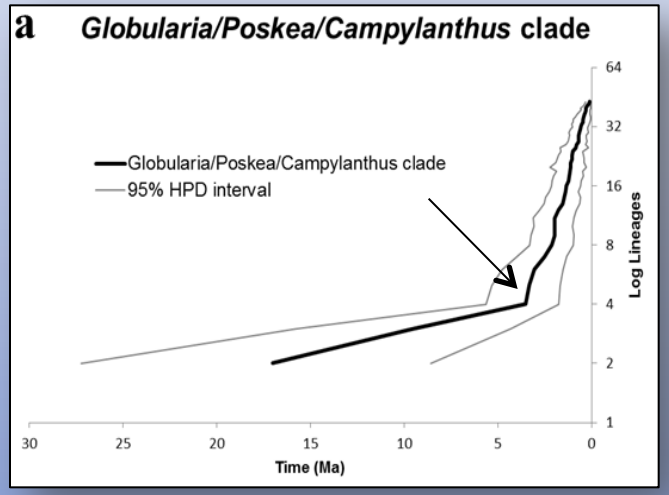
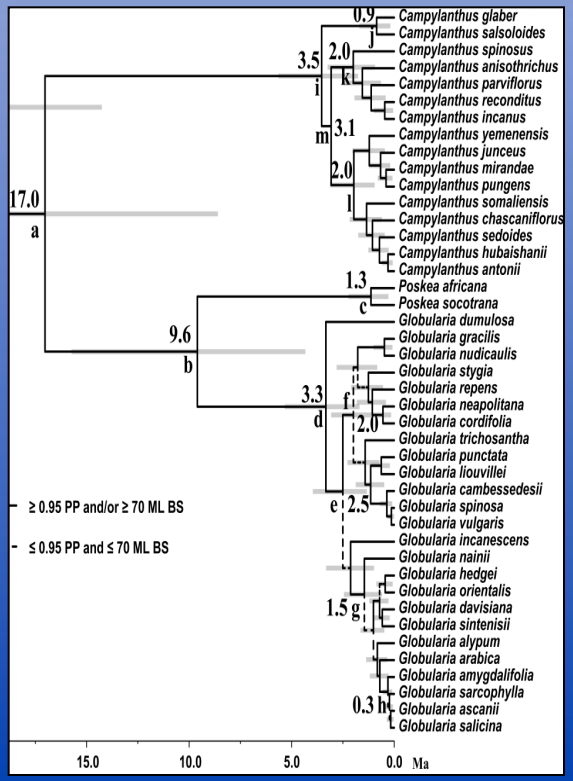
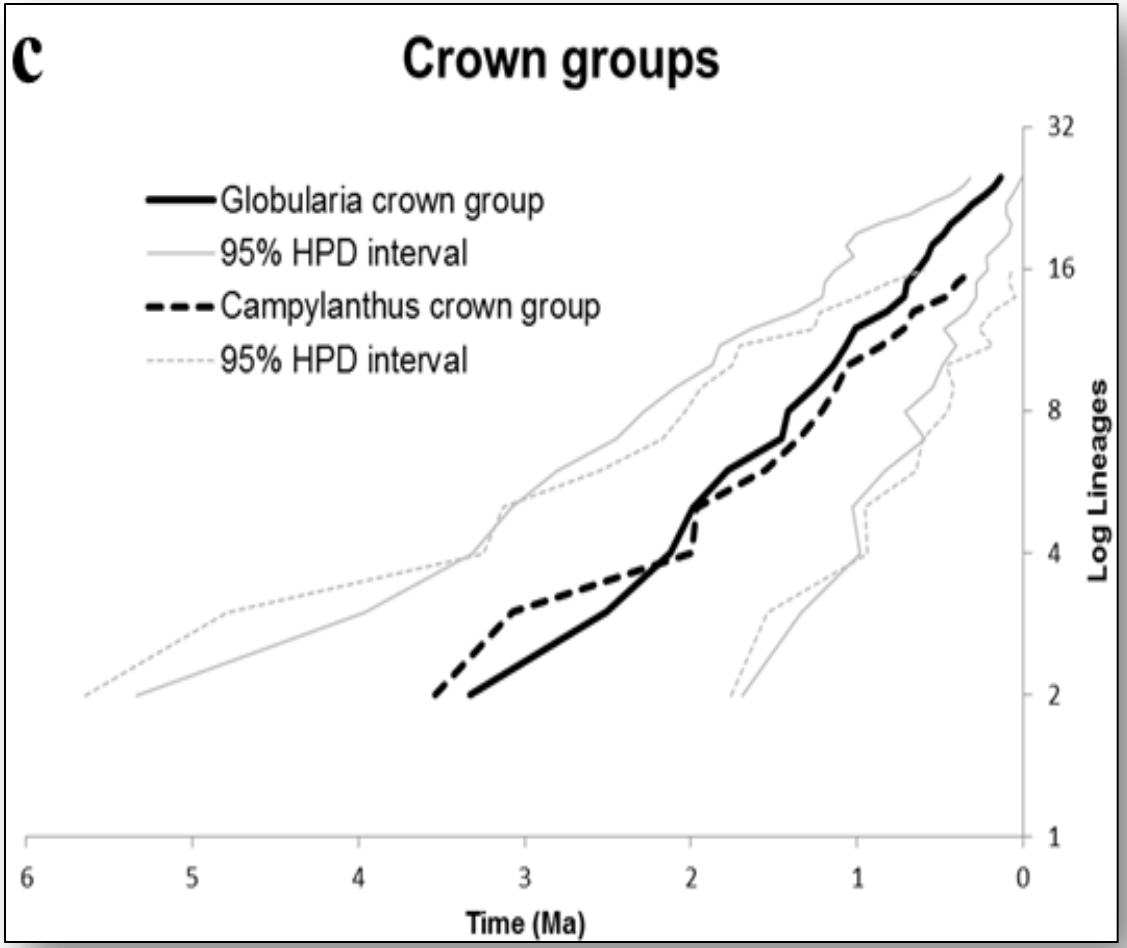




Affenzeller et al., unpubl.



- **Recent upturn** due to strikingly similar crown ages (*Camp*: **3.5 Ma**; *Glob*: **3.3 Ma**)
- **Gradual lineage accumulation in both genera … without apparent extinction**

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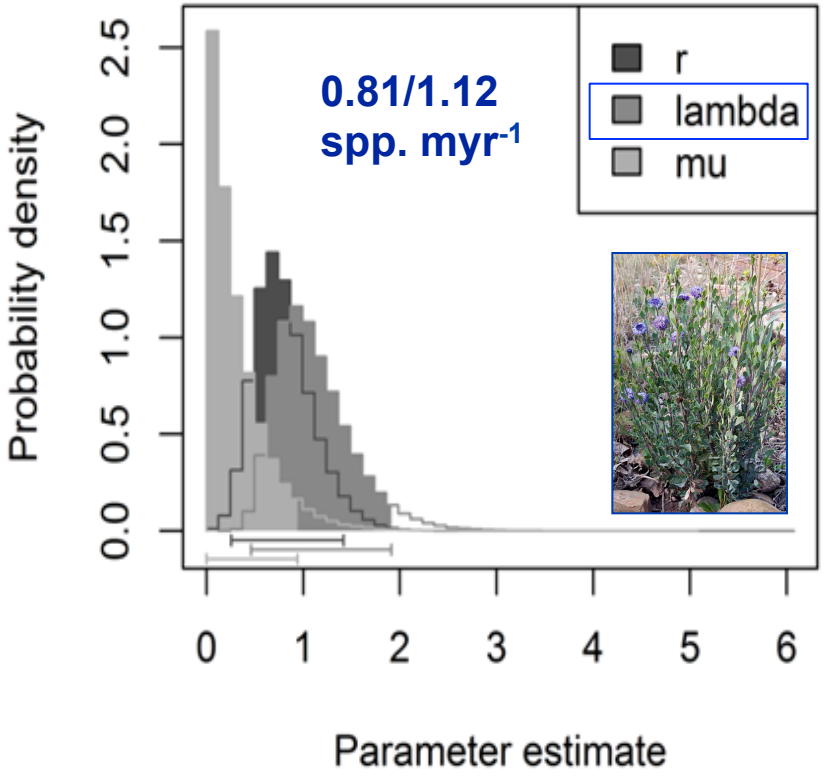
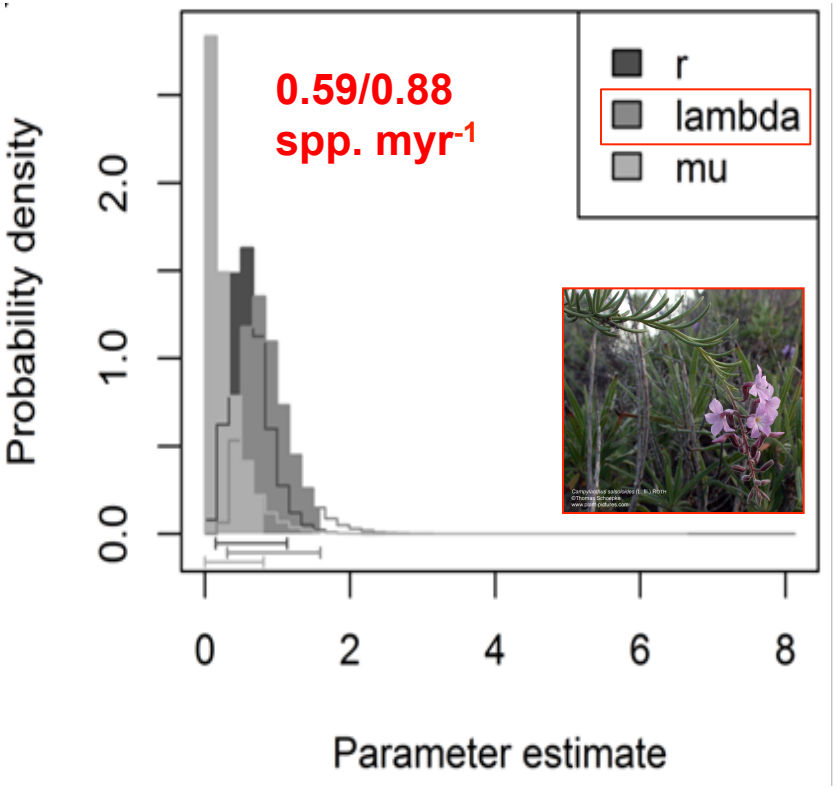
Globularia crown



Campylanthus crown*



r = diversification rate; lambda = speciation rate; mu = extinction rate

LASER (v2.3; Rabosky, 2006) / BAYESRATE (v1.6.3; Silvestro *et al.*, 2011)

* **Excluding Macaronesian species: 0.63/0.97 spp. myr^{-1}**

Affenzeller et al., unpubl.

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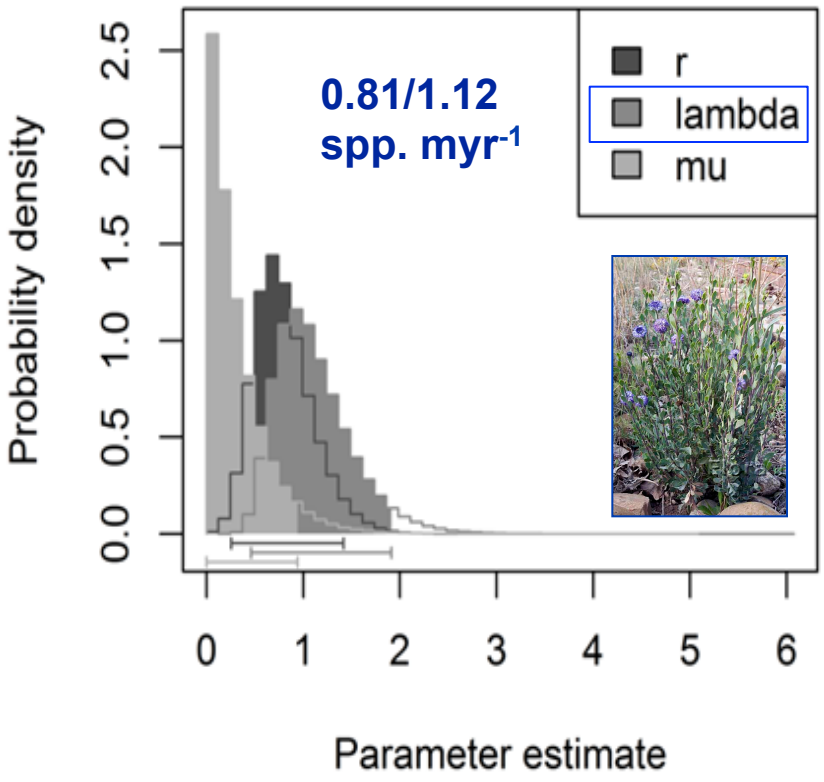
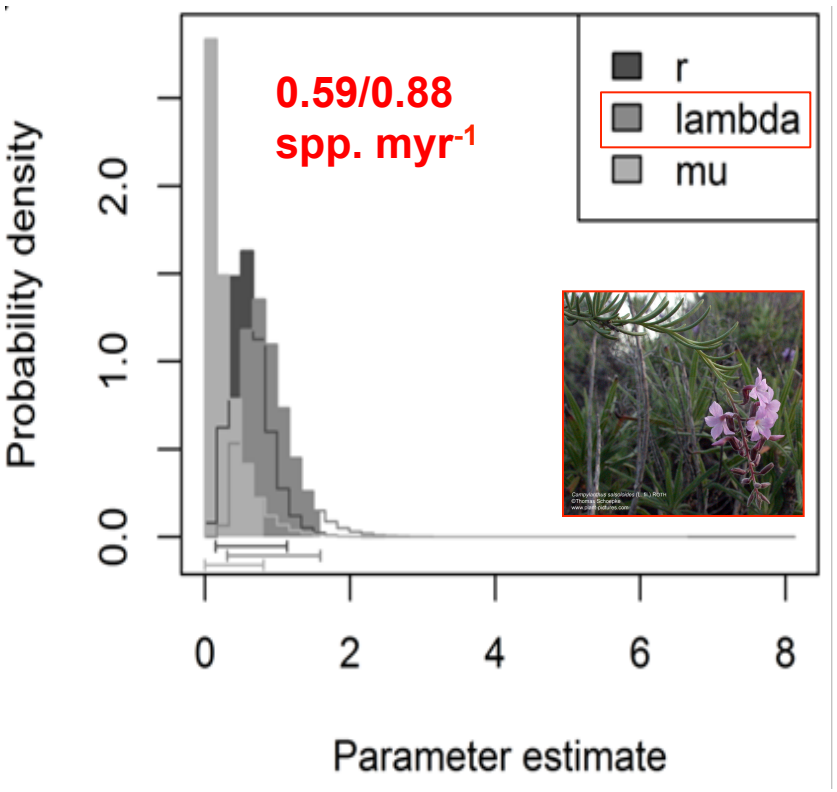
Globularia crown



Campylanthus crown



- **More 'time-for-speciation' (= older clade age) is NOT a factor for the larger clade size of *Globularia* (27 spp.) vs. *Campylanthus* (18 spp.)**

Affenzeller et al., unpubl.

r = diversification rate; lambda = speciation rate; mu = extinction rate (LASER/BAYESRATE)

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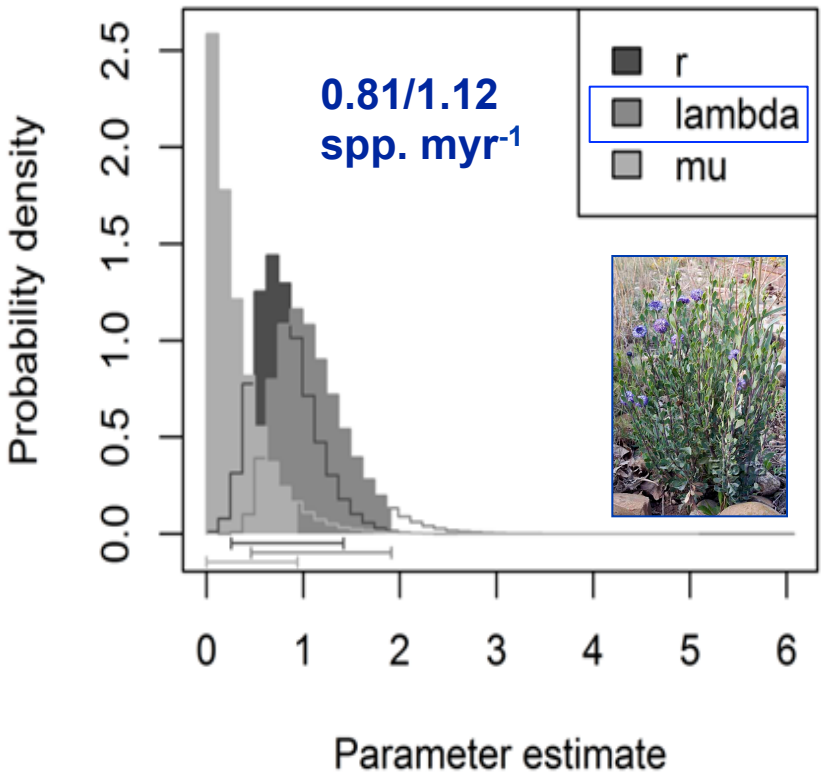
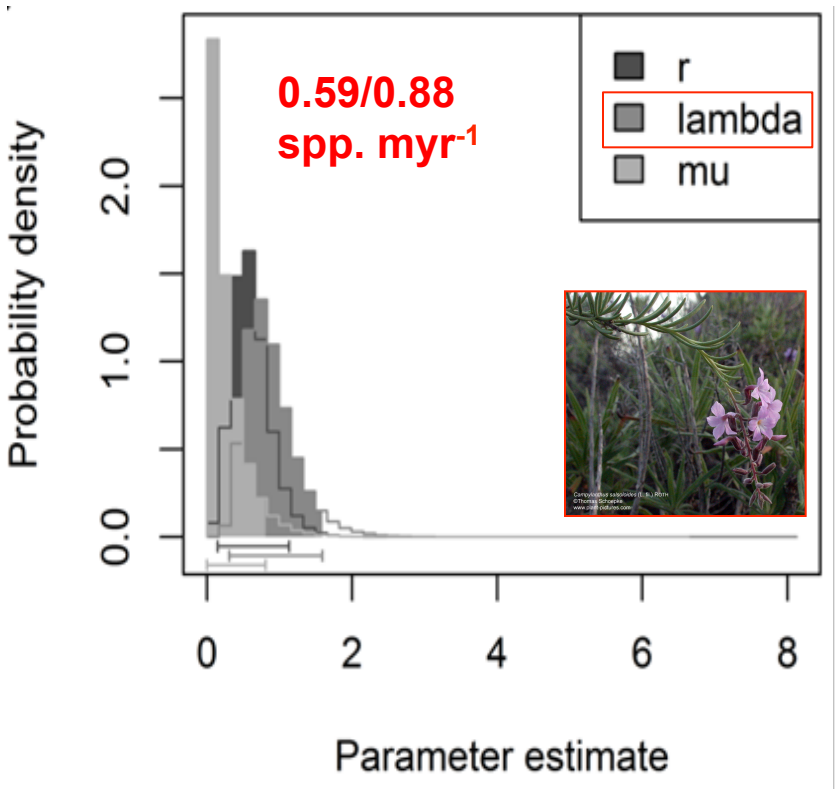
Globularia crown



Campylanthus crown



- **More 'time-for-speciation' (= older clade age) is NOT a factor for the larger clade size of *Globularia* (27 spp.) vs. *Campylanthus* (18 spp.)**

- **There is no (LTT) evidence for higher spatial-ecological limits in the Mediterranean/alpine regions compared to the arid Horn of Africa**

Affenzeller et al., unpubl.

r = diversification rate; lambda = speciation rate; mu = extinction rate (LASER/BAYESRATE)

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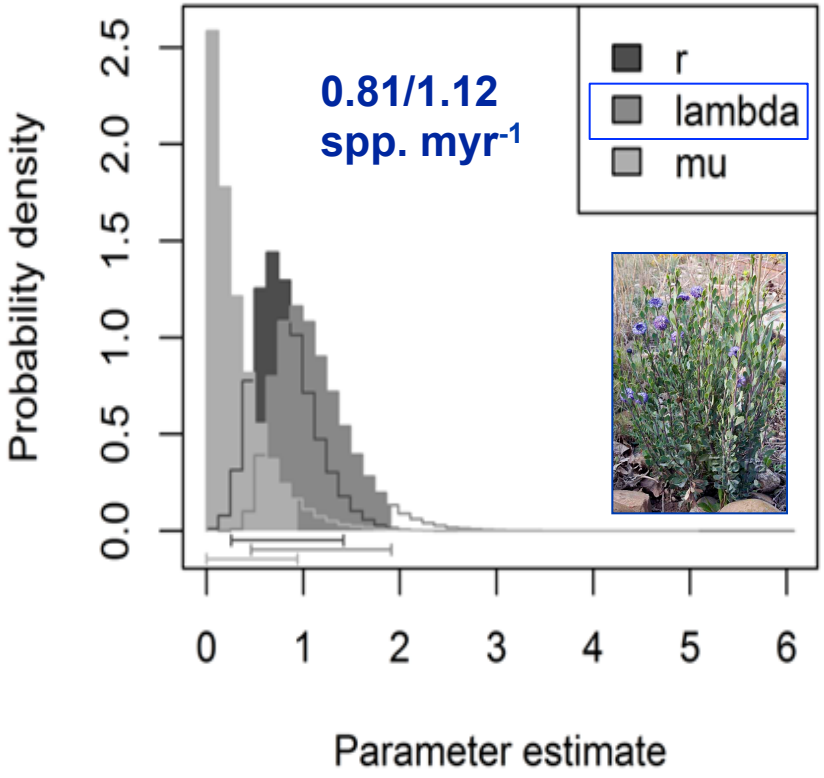
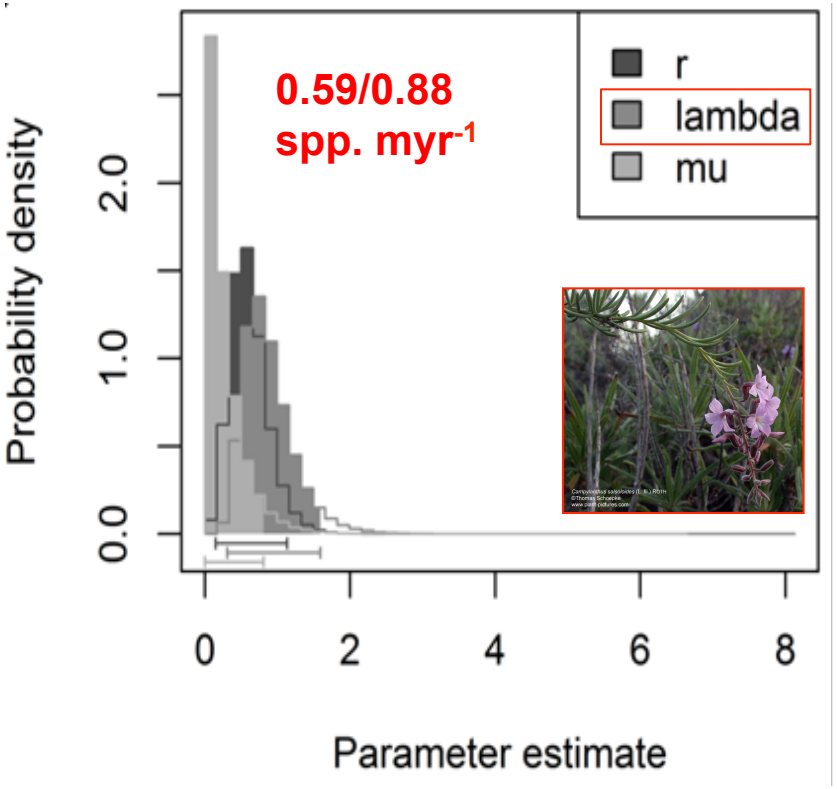
Globularia crown



Campylanthus crown



Conclusion:
Higher species richness of *Globularia* compared to *Campylanthus*
Is most likely due to a slightly increased speciation rate *per se*!

Affenzeller et al., unpubl.

r = diversification rate; lambda = speciation rate; mu = extinction rate (LASER/BAYESRATE)

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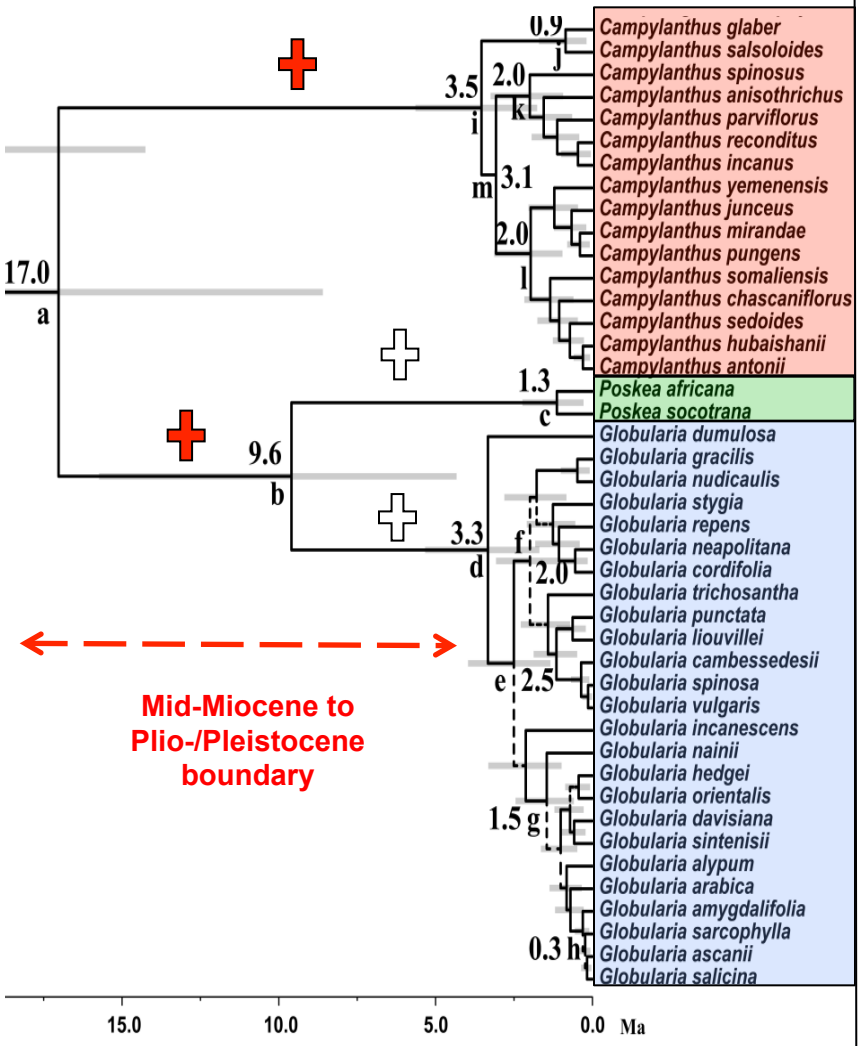
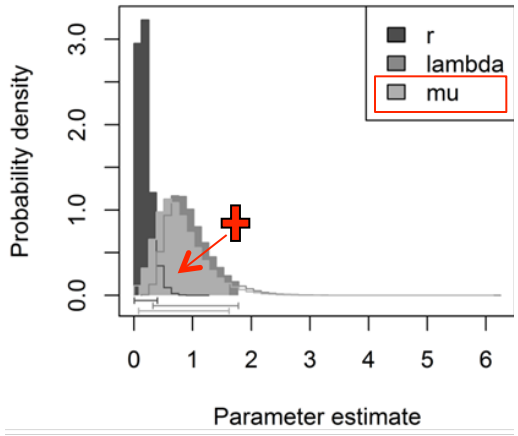
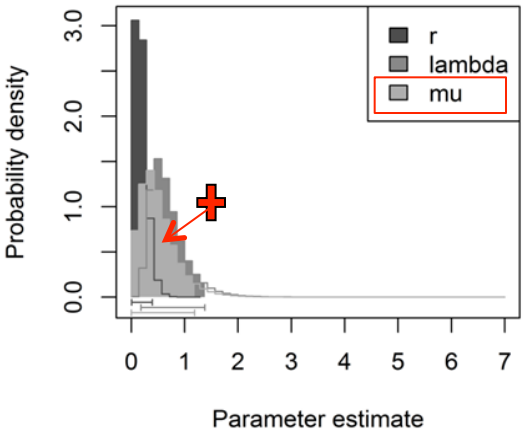


Mid-Miocene to Plio-/Pleistocene boundary

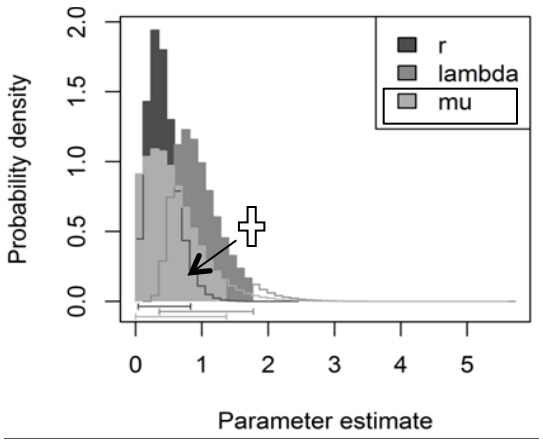
Globularia + Poskea stem



Campylanthus stem



Globularia + Poskea crown



- **Long subtending branches in phylogeny …**
- **…associated with high rates of extinction (mu)**
- **No stasis !**

Affenzeller et al., unpubl.

r = diversification rate; lambda = speciation rate; mu = extinction rate (LASER/BAYESRATE)

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Epilogue I: *Globularia* vs. *Campylanthus*

Macaronesian species of *Globularia* and *Campylanthus* are NOT vicariant relicts related to Sahara desert formation (c. 7–6 Ma)

Distribution
Globularia
Campylanthus
Poskea

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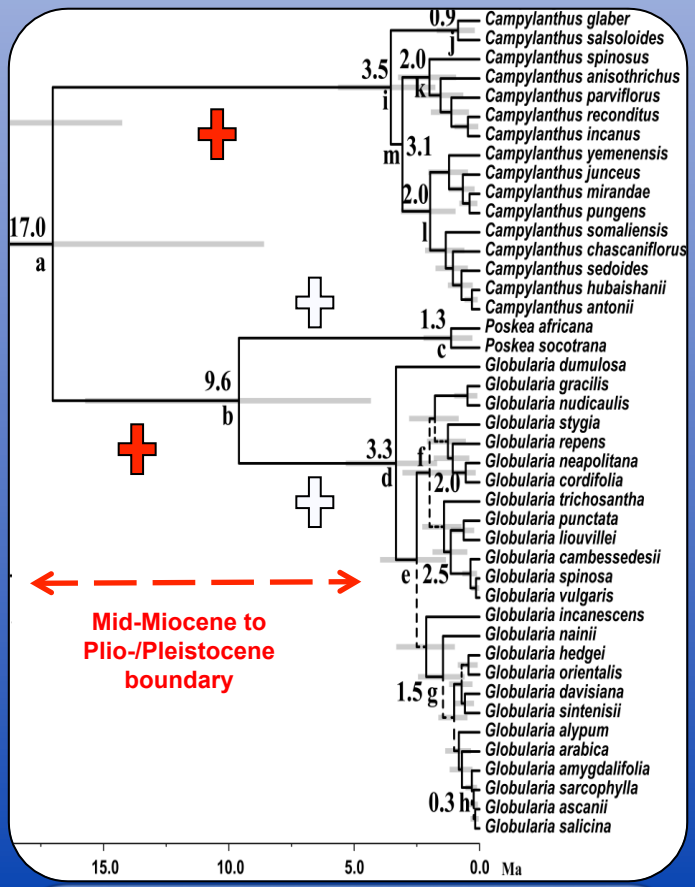
Epilogue II: *Globularia* vs. *Campylanthus*



- Signals of **extinction** in the deeper portions of phylogeny may relate to a Mid-to-Late Miocene increase of aridification in East Africa.
- If so, the **common ancestors** of *Campylanthus* and *Globularia* (+ *Poskea*) were likely **adapted to more humid conditions** and/or denser vegetation ...
- .... and may have **escaped extinction through adaptation** in response to an otherwise lethal, that is, **increasingly more arid climate**.

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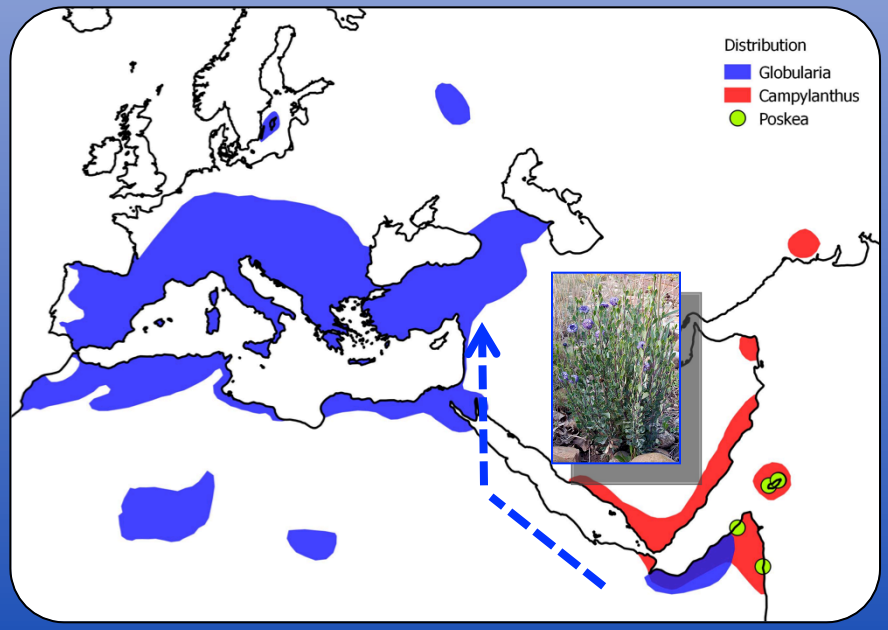
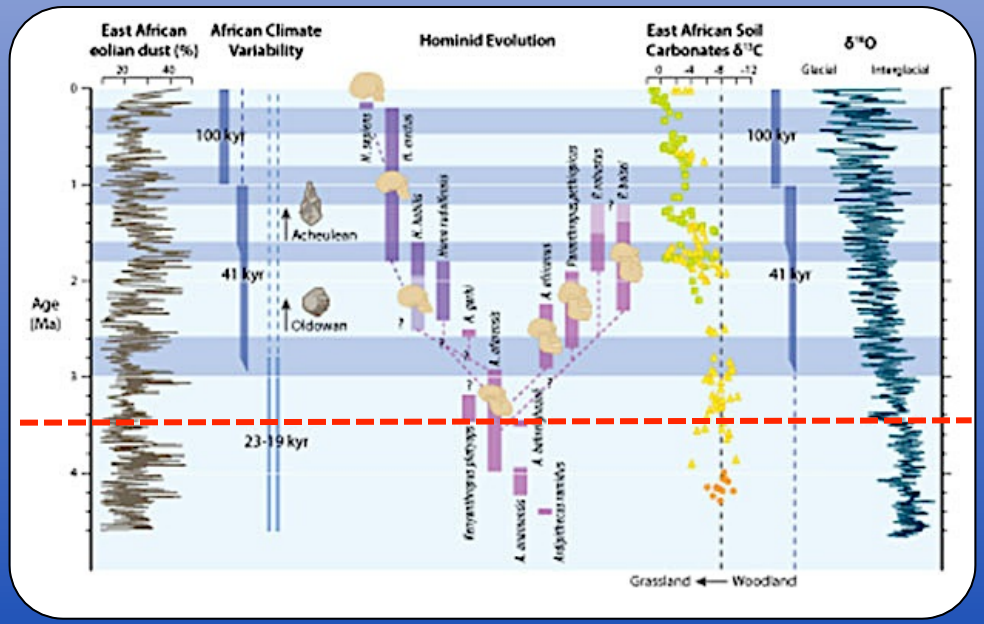
Epilogue III: *Globularia* vs. *Campylanthus*

Increased climate instability during the Late Miocene/Pliocene might have selected for greater ecological flexibility in the ancestor of *Globularia* as precondition for its northward immigration into the Mediterranean Region ('variability selection hypothesis'; Maslin *et al.*, 2014).





Source: Campisano et al. (2012) *Nature Education Knowledge* 4(3):5

Maslin et al. (2014) East African climate pulses and early human evolution. *Quaternary Science Reviews*, 101, 1–17.

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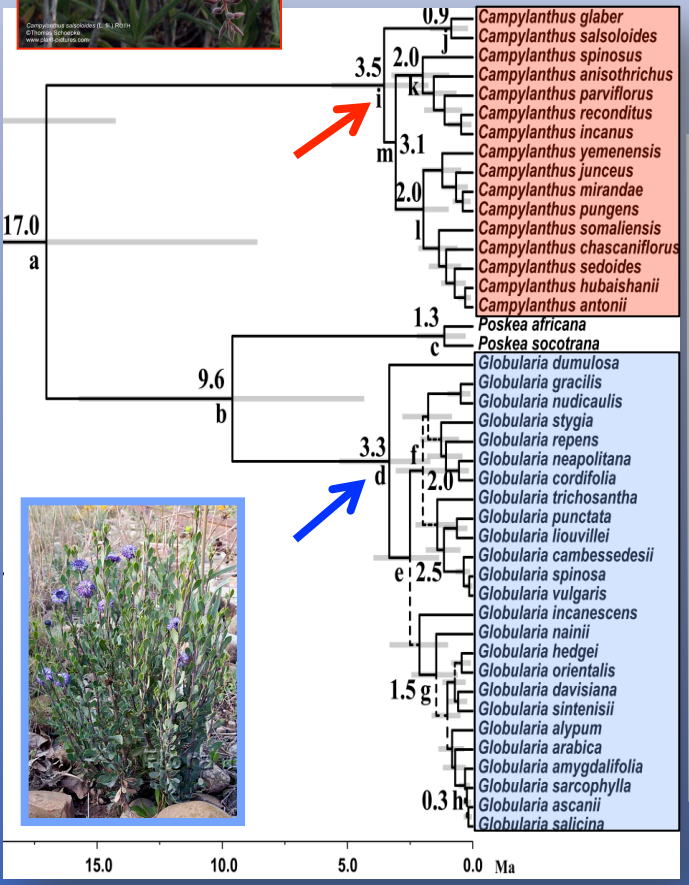
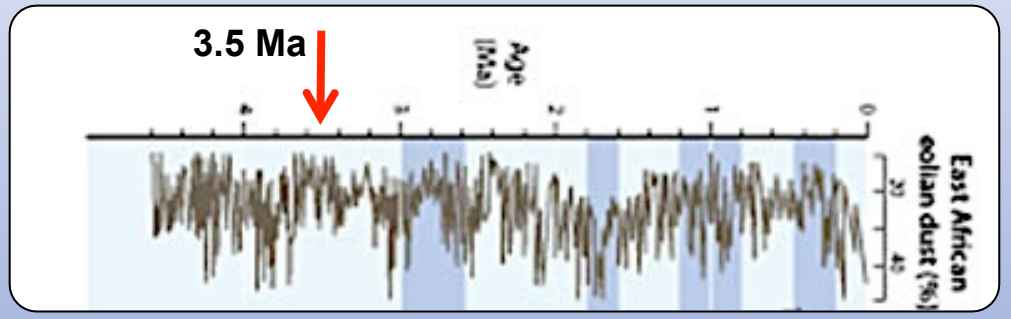
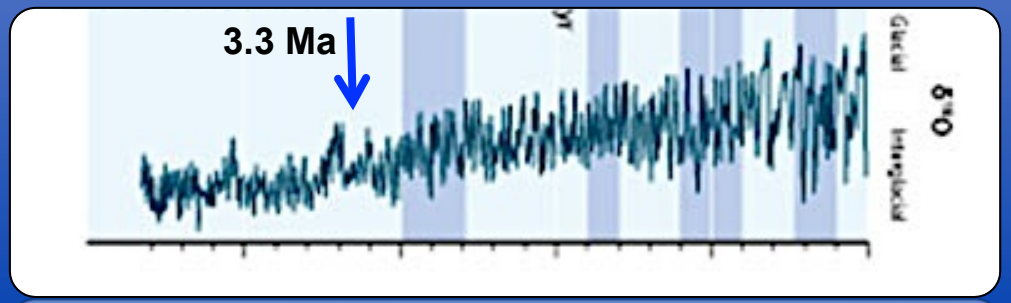




- The **parallel radiation** of ***Campylanthus*** vs. ***Globularia*** at the Plio-Pleistocene boundary (3.5 vs. 3.3 Ma) fits a scenario…
- in which the **coupling between low- and high-latitude climate shifts** has triggered a simultaneous diversification in the EAR and MED regions, respectively, …
- i.e. further **increase in aridity in E Africa** and the onset of the **Quaternary glacial cycles** further north (+ establishment of MED climate, c. 3.2 Ma)



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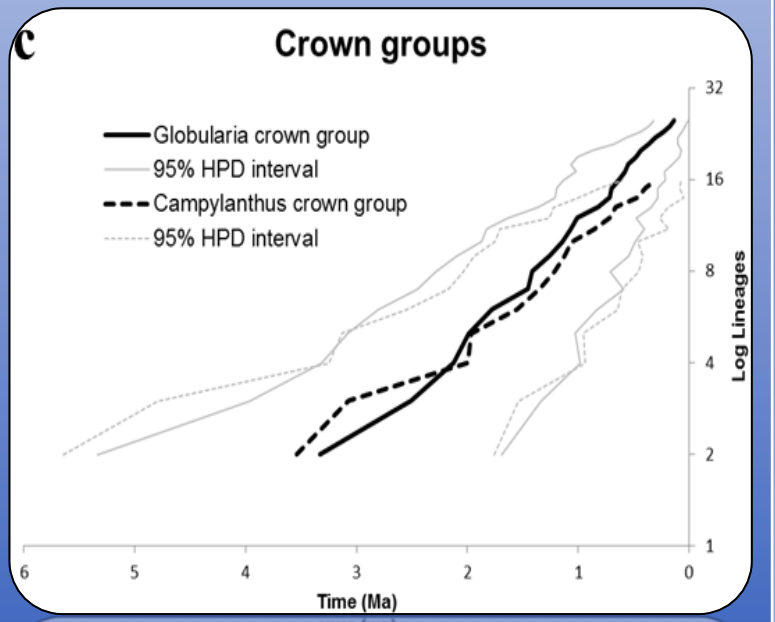

- Both genera continued diversifying **without extinction** since the Plio-/ Pleistocene.
- Larger clade size of *Globularia* due to a slightly **increased speciation** rate in MED (1.12 myr^{-1}).
- Speciation rate of *Campylanthus* remarkably high (0.88 myr^{-1}) – despite small range size in the EAR.
- Recent and rapid radiation of *Globularia* is clearly **adaptive** –
- .... that of *Campylanthus* might fit a **non-adaptive** scenario.





Acknowledgements

- **Dr. Matthias Affenzeller (Salzburg University)**
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- **Marion Kever (Mainz University)**
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- D. Bramwell, J. Carvahlo, H. Duman, J. Henrot, E. Jäger, M. & S. Kropf, M. Nydegger-Hügli, M. Thulin, P. Vargas (leaf)
- M. Thiv; RBG-Kew, Berlin-Dahlem (DNA)
- Herbaria: E, FI, M, UPS (leaf)
- Botanical Gardens: Bern, Bochum, Bordeaux, Edinburgh, Göttingen, Innsbruck, Krefeld, Marburg, Paris, Regensburg, Wien (seed)

Thank you for your attention!

G. punctata

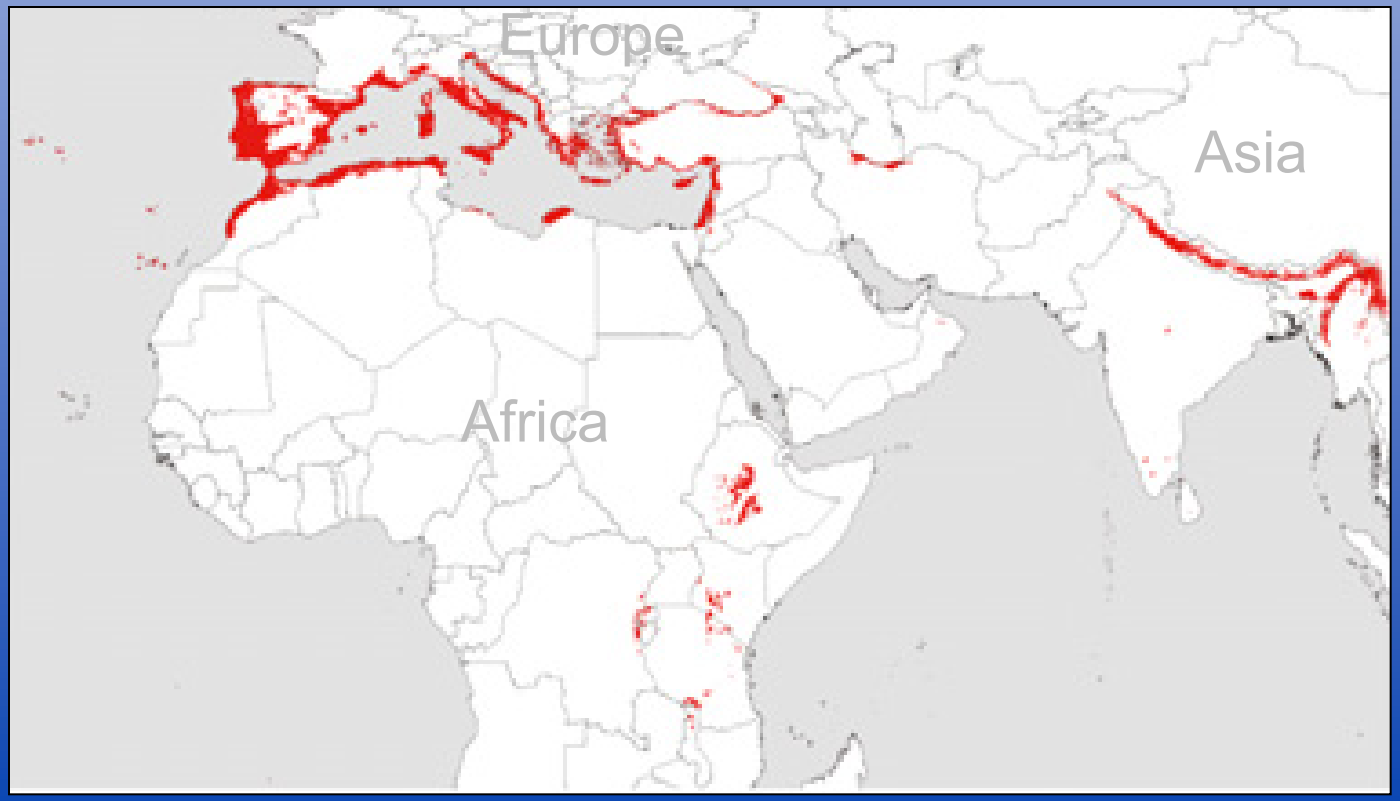
G. alypum

New Phytologist

Research

Understanding the formation of Mediterranean–African–Asian disjunctions: evidence for Miocene climate-driven vicariance and recent long-distance dispersal in the Tertiary relict *Smilax aspera* (Smilacaceae)

Chen Chen[1,2]*, Zhe-Chen Qi[1,2]*, Xi-Hui Xu[1,2]*, Hans Peter Comes[3], Marcus A. Koch[4], Xin-Jie Jin[1], Cheng-Xin Fu[1,2] and Ying-Xiong Qiu[1,2]



Chen et al. (2014) *New Phytologist*, 204, 243–255.

New Phytologist

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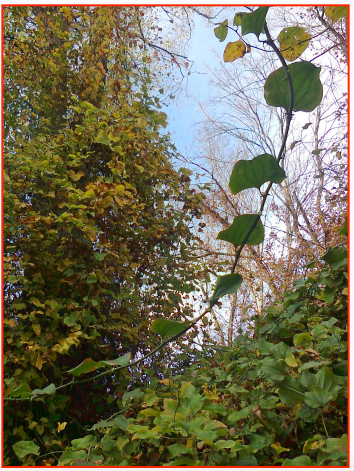

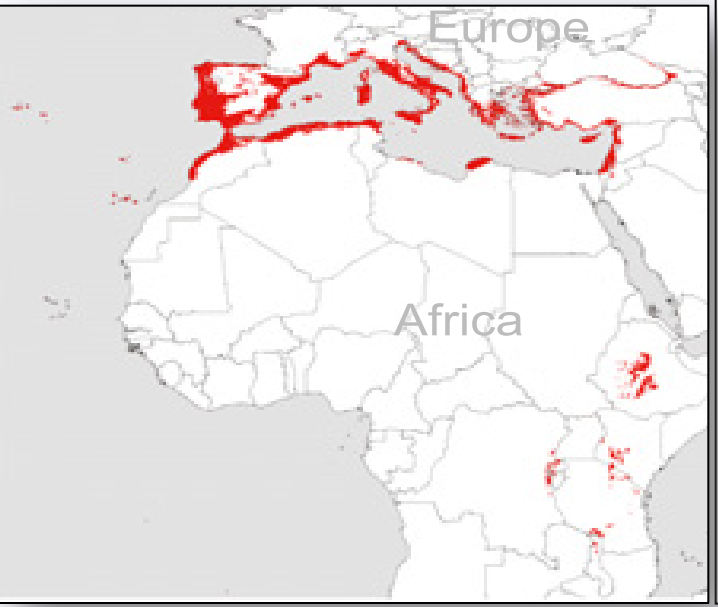

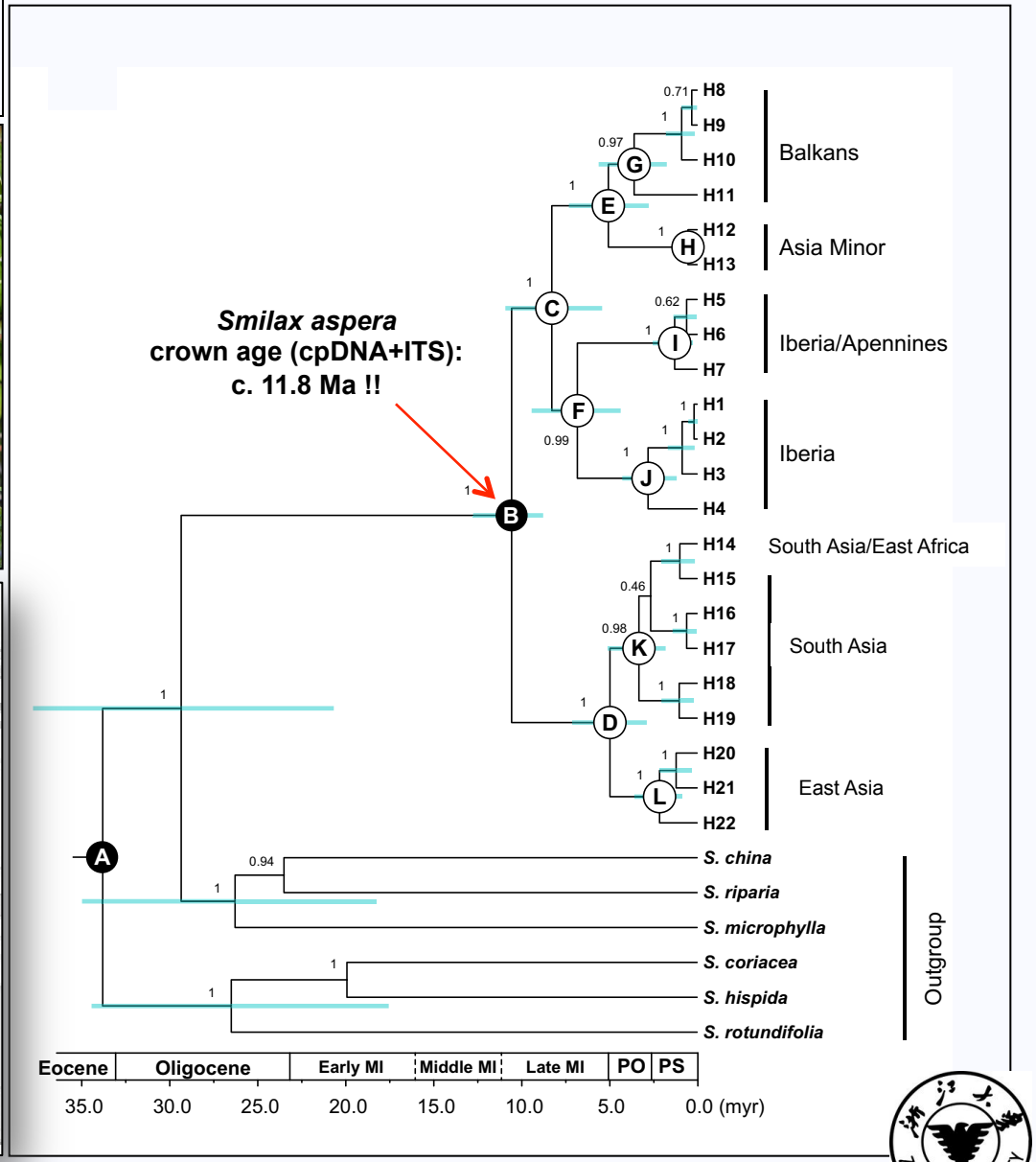

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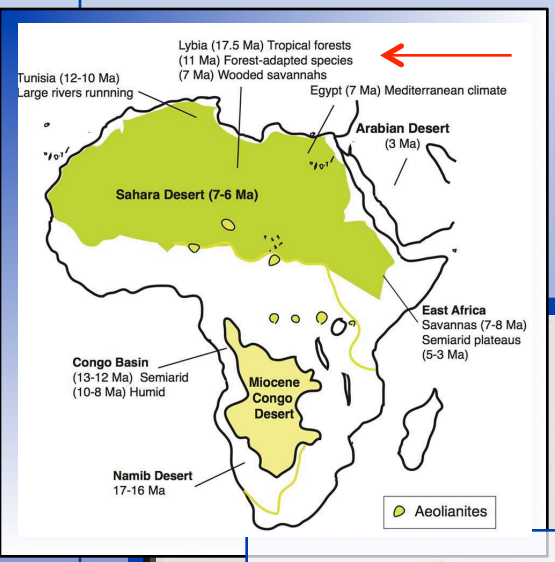
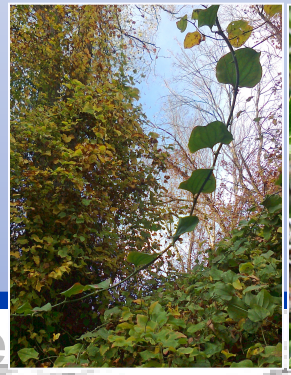
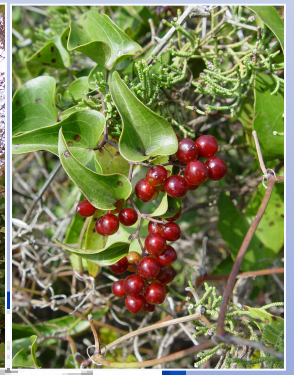


Smilax aspera





- **Timing of c. 11.8 Ma broadly fits a Late Tertiary vicariant event due to a shift from wet/sub-humid (sub)tropical forest to semi-arid wooded savannah in North Africa following the Mid-Miocene Climate Optimum (c. 17–14.5 Ma).**
- ***Smilax aspera* is of ancient origin in the Mediterranean Basin, but without having ‚radiated' there.**
- **Essentially, it is a tropical forest species but ‚preadapted' to the establishment of a dry-summer Mediterranean climate, c. 3.2 Ma (e.g. sclerophylly).**

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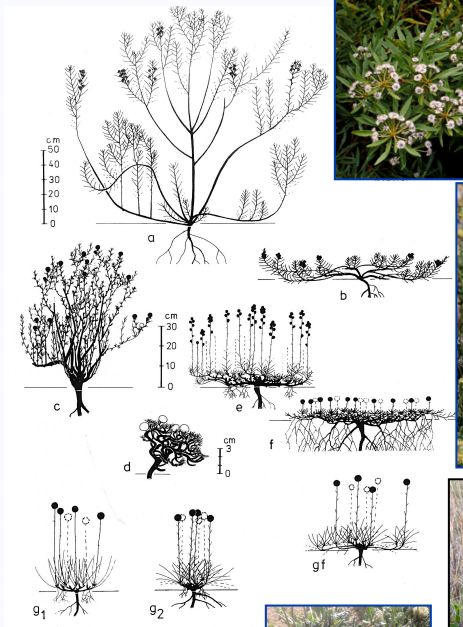
Globularia (27 spp.)

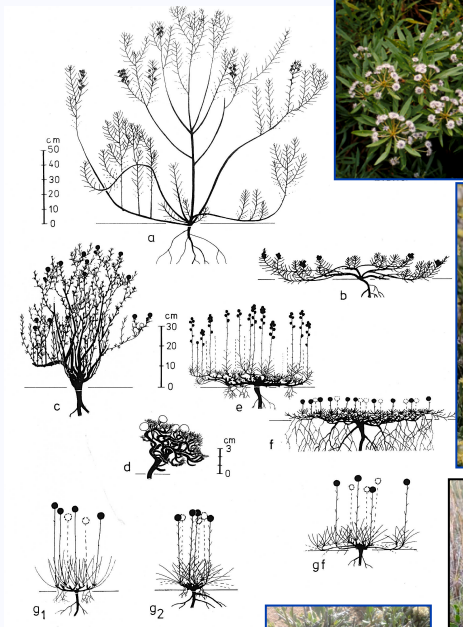


Plio-/Pleistocene: c. 3.3 Ma

Smilax aspera **crown age (cpDNA+ITS): c. 11.8 Ma !!**

Chen et al. (2014) *New Phytologist*, 204, 243–255.

Globularia (27 spp.)



Plio-/Pleistocene: c. 3.3 Ma

Smilax aspera
crown age (cpDNA+ITS):
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Chen et al. (2014) *New Phytologist*, 204, 243–255.

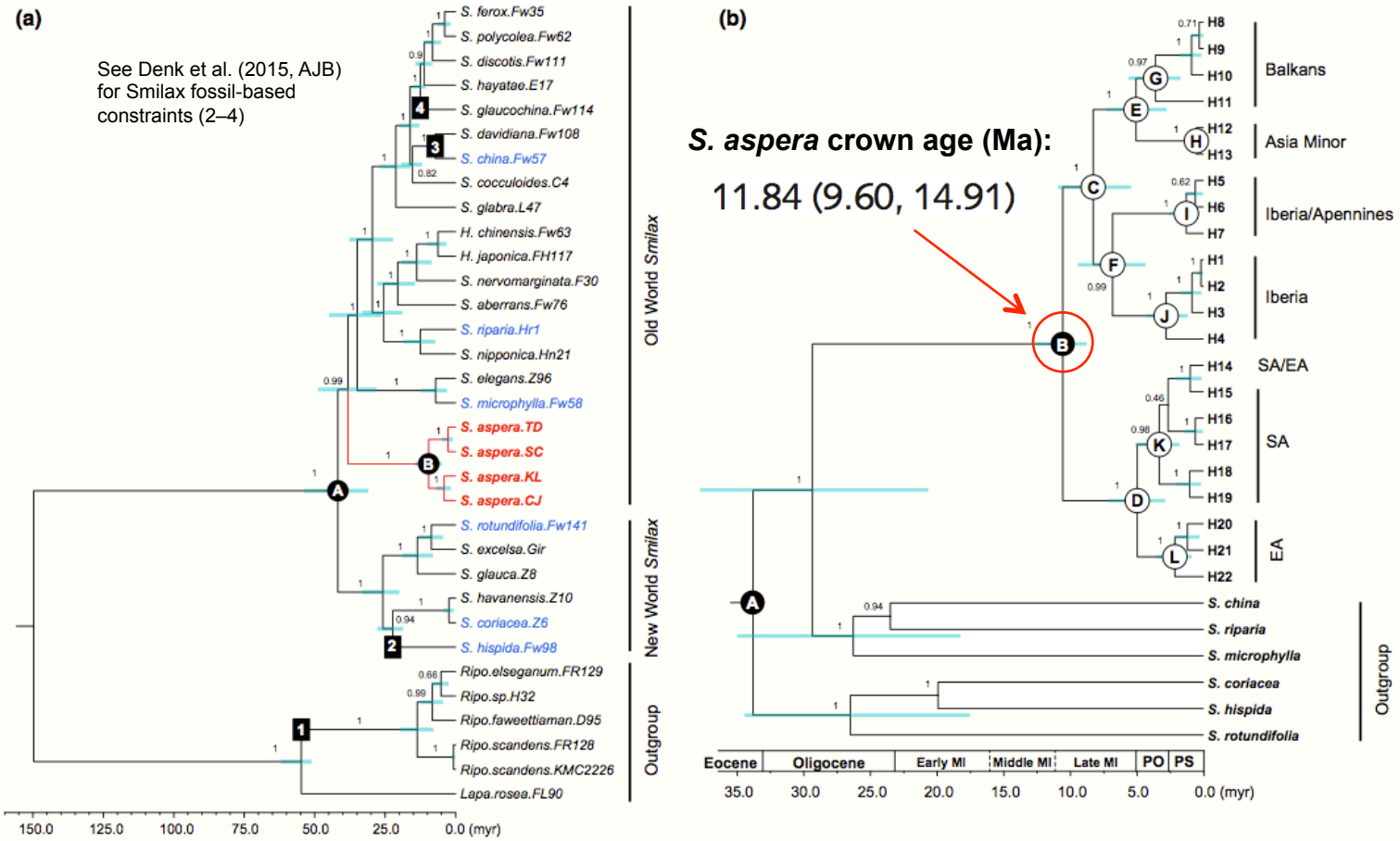
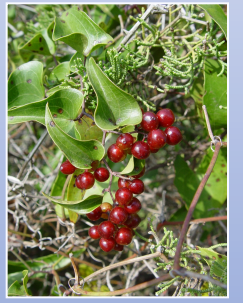
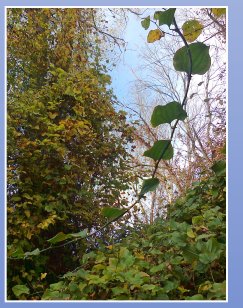


Fig. 3 BEAST-derived chronograms of: (a) Smilacaceae based on cpDNA (*ndh*A intron, *ndh*F, *mat*K, *rbc*L, *rpl*16 intron) and nrITS sequences with calibration points denoted by nodes 1–4 (Table 2; see the Materials and Methods section for further explanation); and (b) *Smilax aspera* haplotypes based on cpDNA (*atp*B–*rbc*L, *trn*C–*ycf*6, *ndh*A intron, *ndh*F, *mat*K, *rbc*L, *rpl*16 intron) and nrITS sequences, with *Smilax china*, *Smilax coriaceae*, *Smilax microphylla*, *Smilax hispida*, *Smilax riparia*, and *Smilax rotundifolia* used as outgroup. Posterior probabilities (PP > 0.50) are labelled below the branches. Grey bars on nodes indicate 95% highest posterior densities (HPDs) of time estimates (in million yr ago, Ma). Mean divergence dates and 95% HPDs for major nodes (A–L) are summarized in Table 2.





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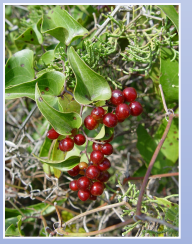
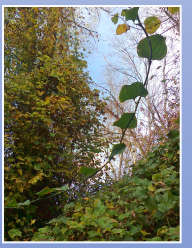




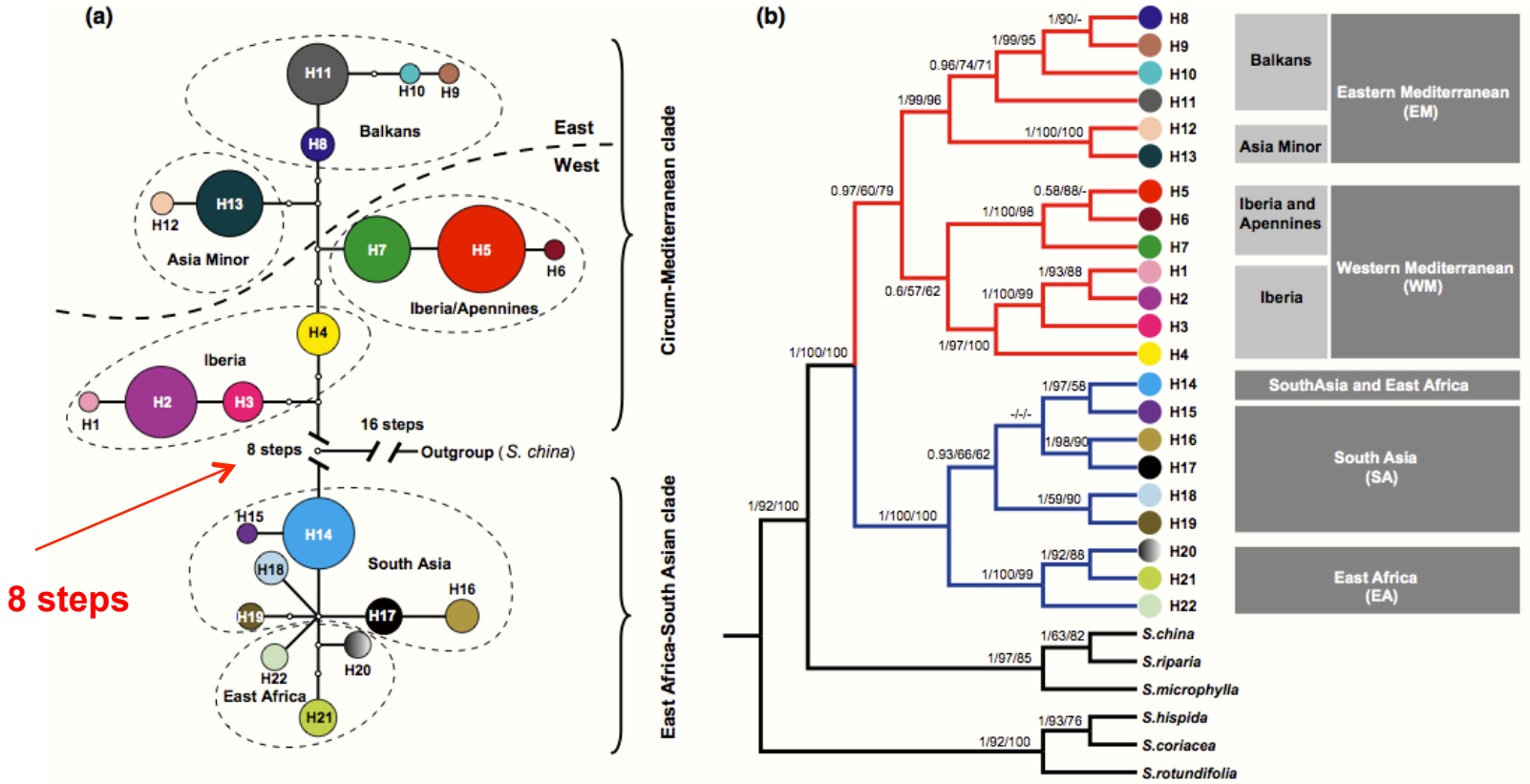


Fig. 2 (a) Ninety-five per cent statistical parsimony network of the 22 cpDNA (*atp*B–*rbc*L, *trn*C–*ycf*6, *ndh*A intron) haplotypes (H1–22) identified in *Smilax aspera*. The sequence of *Smilax china* was 23 mutations apart from the nearest haplotypes (H3, H4, H14) of *S. aspera*. The small open circles or short bars represent missing haplotypes. The size of circles corresponds to the frequency of each haplotype. (b) Bayesian inference (BI) cladograms of *S. aspera* based on cpDNA (*atp*B–*rbc*L, *trn*C–*ycf*6, *ndh*A intron, *mat*K, *ndh*F, *rbc*L, *rpl*16) and nrITS sequences. Posterior probabilities (PP > 0.50) and bootstrap values (> 50%) based on maximum likelihood (ML) and maximum parsimony (MP) analysis are sequentially indicated above the branches.

Chen et al. (2014) *New Phytologist*, 204, 243–255.

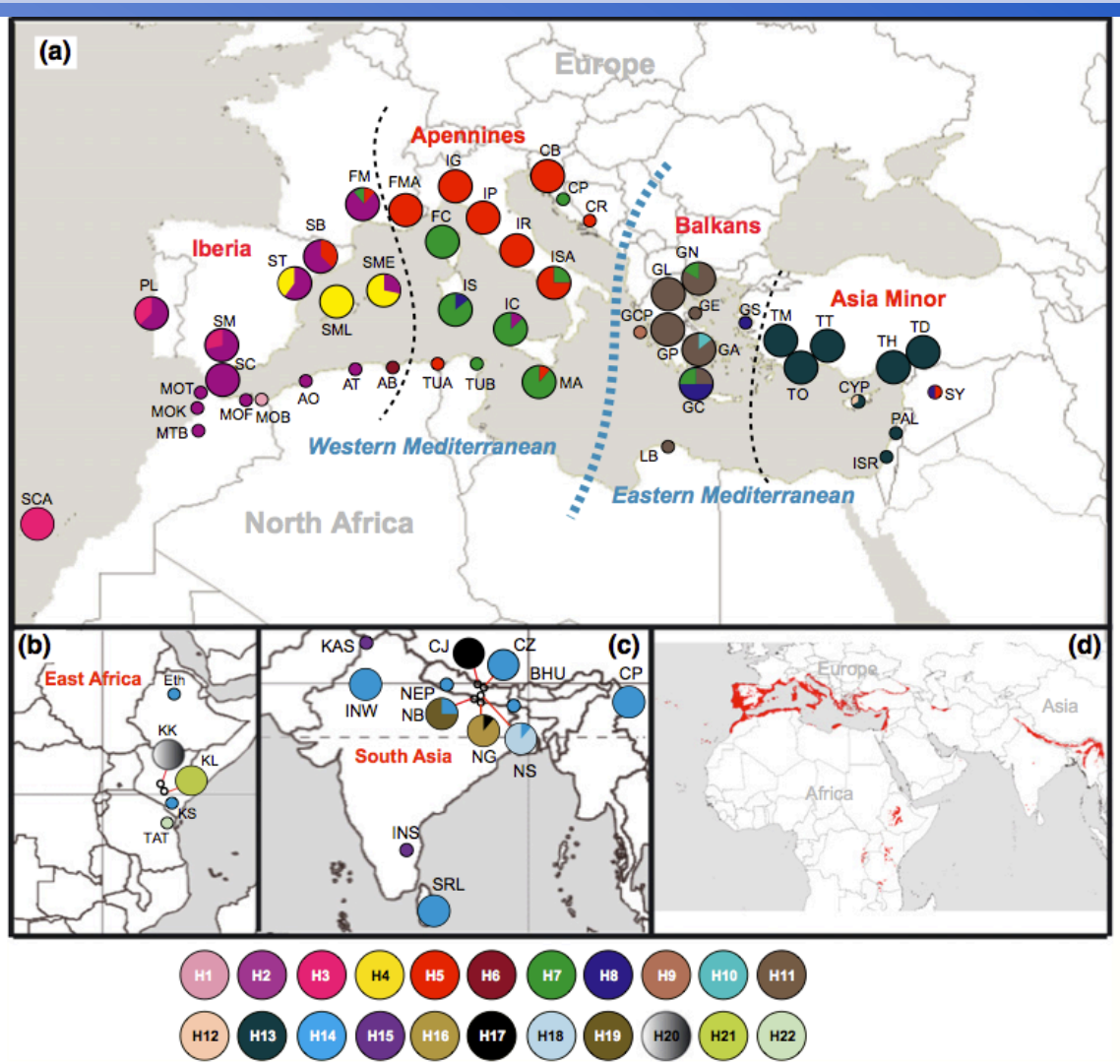


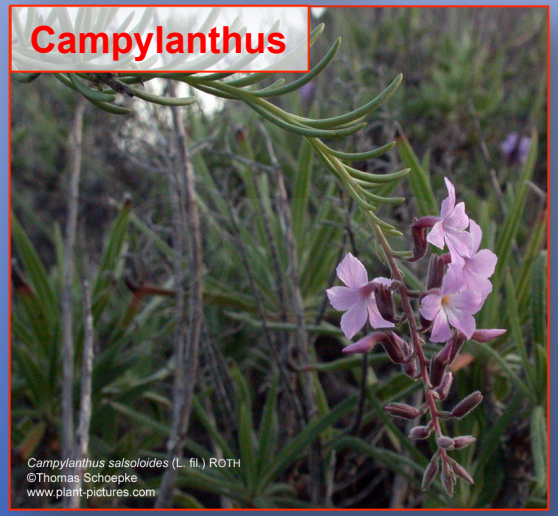
Fig. 1 (a–c) Regional distributions of cpDNA (*atp*B–*rbc*L, *trn*C–*ycf*6, *ndh*A intron) haplotypes of *Smilax aspera* in: (a) the circum-Mediterranean region (with dotted lines delimiting four biogeographical regions; Strid, 1996; Migliore *et al.*, 2012); (b) East Africa; and (c) South Asia. (d) Overall distribution range of *S. aspera* primarily based on local floras, specimen records from the Global Biodiversity Information Facility (GBIF) and herbaria (see Table S1). Large circles represent 38 populations sampled as fresh material and smaller circles represent 57 herbarium specimens (see Table S1 for locality details and the identification of population codes).

New Phytologist (2014)
www.newphytologist.com

Chen et al. (2014) *New Phytologist*, 204, 243–255.

Globularia

Campylanthus

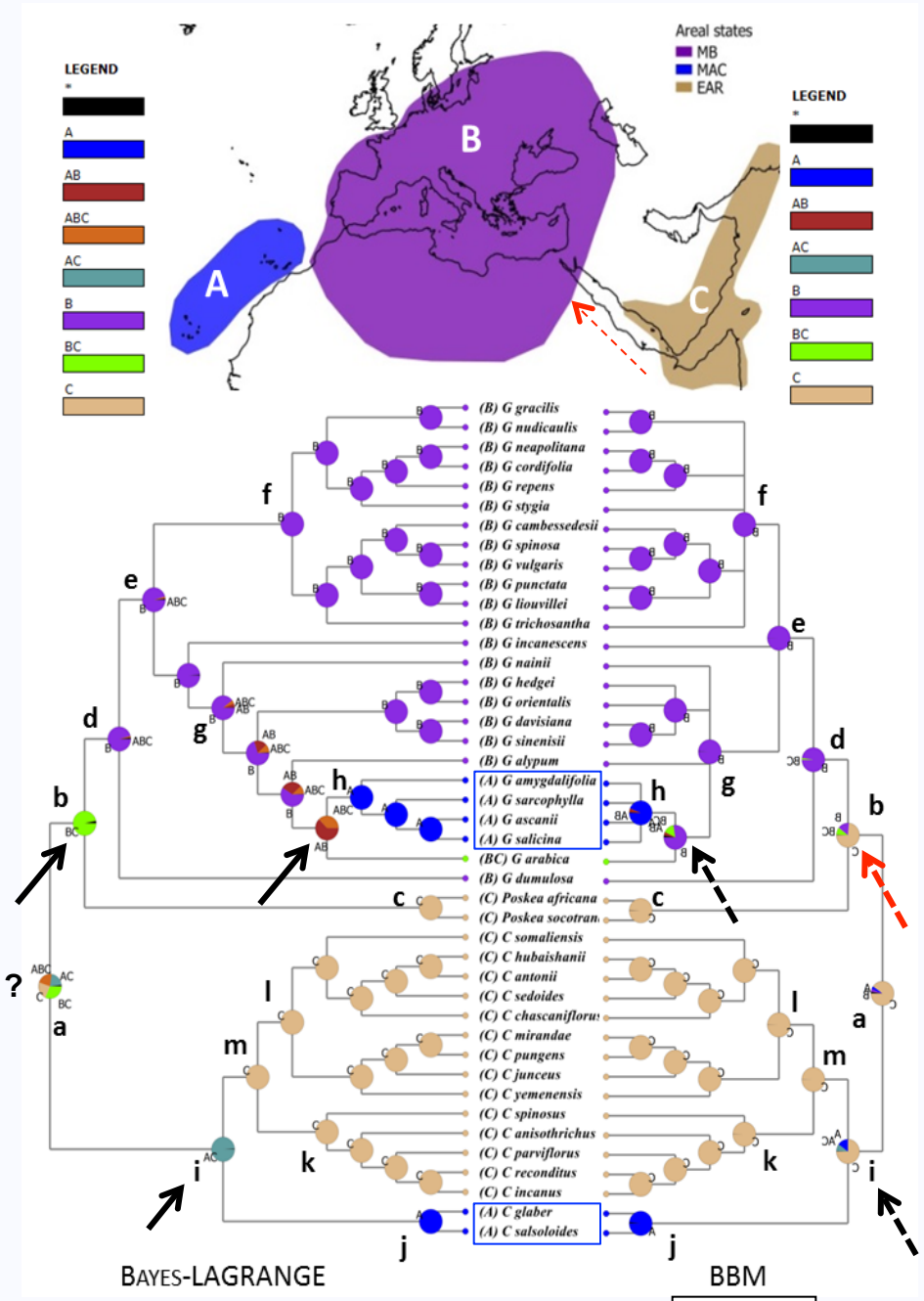


Ancestral area reconstructions using likelihood (BAYES-LAGRANGE) and Bayesian Binary MCMC (BBM; RASP) approaches plotted on the BEAST cladogram

Affenzeller et al., unpubl.

→ vicariance

⇢ dispersal



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