

# **Integrating photobiont phylogenetic and geographical data in macroevolutionary studies of lichens: case studies in Peltigerales**

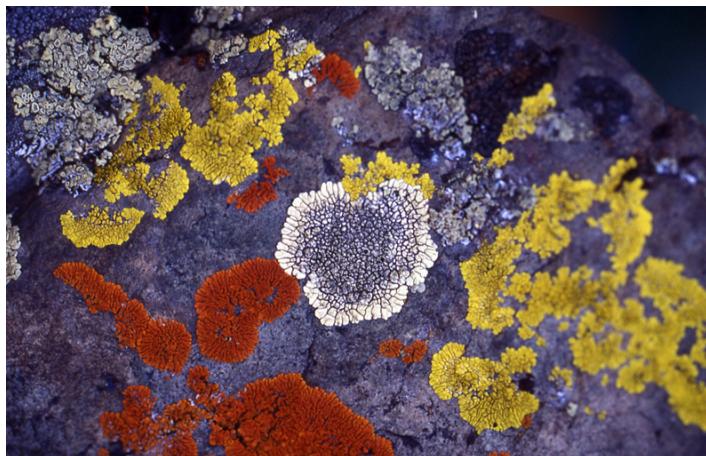
Oral defense of the doctoral thesis of Nicolas Magain



Liège, November 13 2014

# What is a lichen?





# What is a lichen?

It is a symbiosis

Symbiosis : close, prolonged association between two or more different organisms of different species that may, but does not necessarily, benefit each member



# What is a lichen?

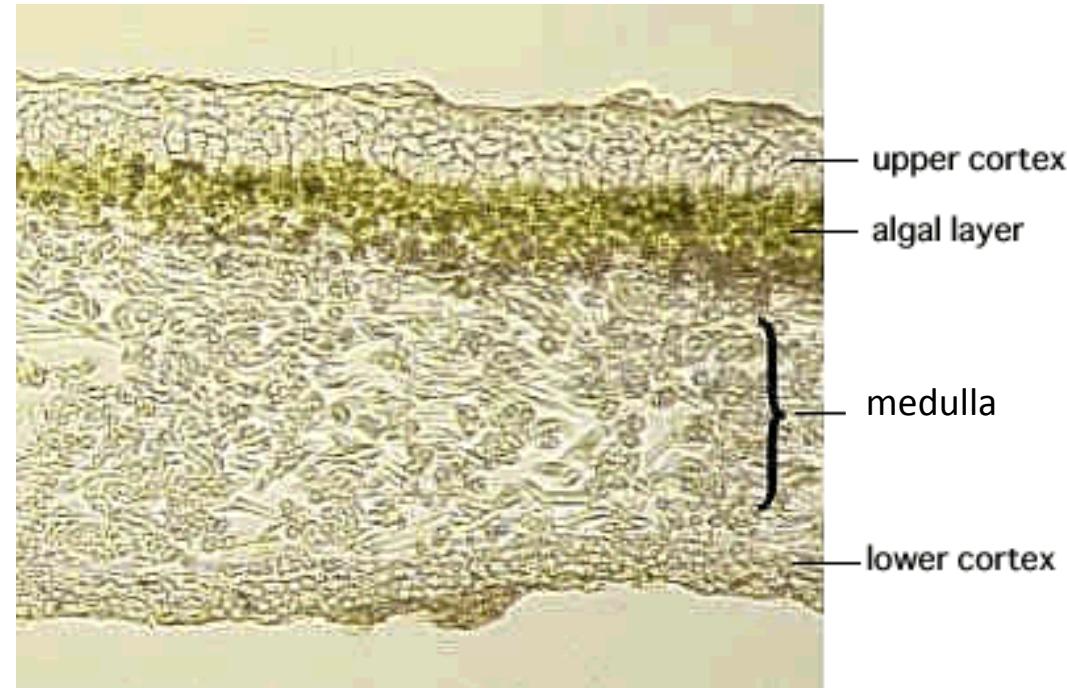
It is a symbiosis between a fungus (**mycobiont**)  
a photosynthetic partner (**photobiont**)

A single morphological entity



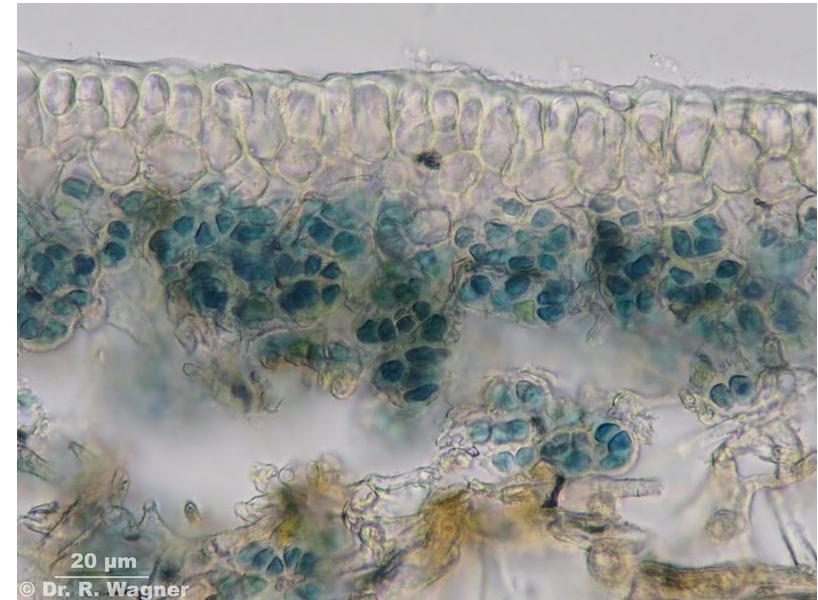
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It is a symbiosis between a **fungus** and  
**a green alga (chlorolichen)**



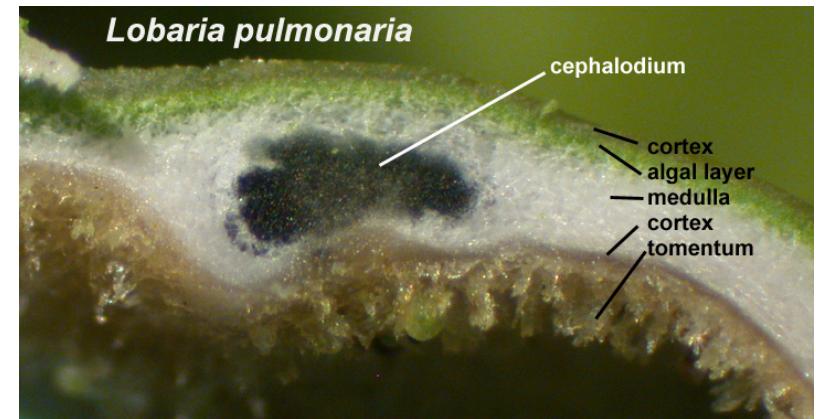
# What is a lichen?

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a green alga, a **cyanobacteria (cyanolichen)**



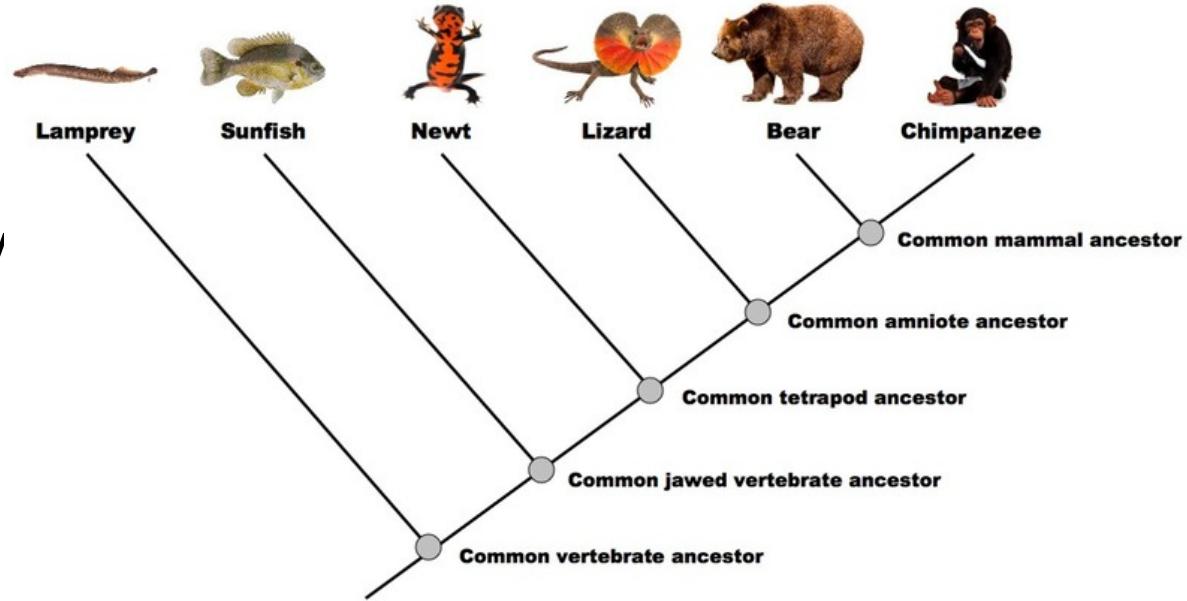
# What is a lichen?

It is a symbiosis between a **fungus** and a green alga, a cyanobacteria or **both (tripartite)**



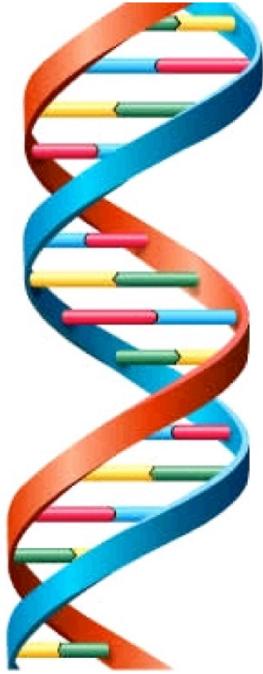
# Phylogenetics and the study of evolution

- Reconstruct the origin and evolutionary history of organisms
- Understand their relationships



Uses: classification; reconstruction of ancestral states; study of adaptation; evolution of genes; diversification rates; key innovations; dates of divergence; biogeography; coevolution and cospeciation; assessment of biodiversity; epidemiology ...

# Molecular phylogeny



A  
T  
C  
G

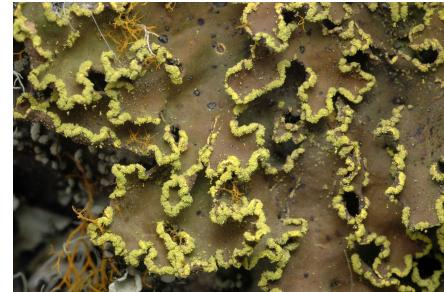
Primate mtDNA

Project of "Primate mtDNA" - Character Matrix "Character Matrix"

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
1 Homo sapiens	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A			
2 Pan	A	A	G	C	T	T	C	A	C	C	G	G	G	G	G	C	A	T	T	A	T	C	C	T	T	A	T	A	A	T	G	C			
3 Gorilla	A	A	G	C	T	T	C	A	C	C	G	G	G	G	G	G	C	A	G	T	T	G	T	T	T	A	T	A	A	T	T	G	C		
4 Pongo	A	A	G	C	T	T	C	A	C	C	G	G	G	G	G	G	C	A	A	C	C	C	T	C	T	C	A	T	G	A	T	T	G	C	
5 Hylobates	A	A	G	C	T	T	T	A	C	G	G	T	G	C	C	C	A	C	C	G	T	C	C	T	C	A	T	A	A	T	T	G	C		
6 Macaca fuscata	A	A	G	C	T	T	T	T	C	C	G	G	G	G	G	G	C	A	A	C	C	A	T	C	T	T	A	T	G	A	T	T	G	C	
7 M. mulatta	A	A	G	C	T	T	T	T	C	T	G	G	G	G	G	G	C	A	A	C	C	A	T	C	T	C	C	A	T	G	A	T	T	G	C
8 M. fascicularis	A	A	G	C	T	T	T	C	T	C	C	G	G	G	G	G	C	A	A	C	C	C	T	T	T	A	A	T	A	T	T	G	C		
9 M. sylvanus	A	A	G	C	T	T	C	T	C	C	G	G	G	G	G	G	C	A	A	C	C	C	T	T	T	A	A	T	A	G	T	T	G	C	
10 Saimiri sciureus	A	A	G	C	T	T	C	A	C	C	G	G	G	G	G	G	C	A	A	T	G	A	T	C	T	T	A	A	T	A	T	C	G	C	
11 Tarsius syrichta	A	A	G	T	T	C	A	T	T	G	G	G	G	G	G	G	C	A	A	C	C	A	T	C	T	T	A	A	T	T	G	C			
12 Lemur catta	A	A	G	C	T	T	C	A	T	A	G	G	G	G	G	G	C	A	A	C	C	A	T	T	C	T	A	A	T	A	T	C	G	C	

Sequence DNA loci (gene or non-coding region) from organisms, align sequences in matrices, model them to generate phylogenetic trees

# The order Peltigerales



- Ascomycota, Lecanoromycetes
- 9 families
- Mostly cyanolichens associating with *Nostoc* (but also tripartites or chlorolichens)
- Contains most cyanolichens



# The genus *Peltigera*

- Order Peltigerales  
(Lecanoromycetes)
- Bipartite (w. *Nostoc*) and tripartite thalli (*Nostoc* and green algae)
- Widespread, especially in boreal forests



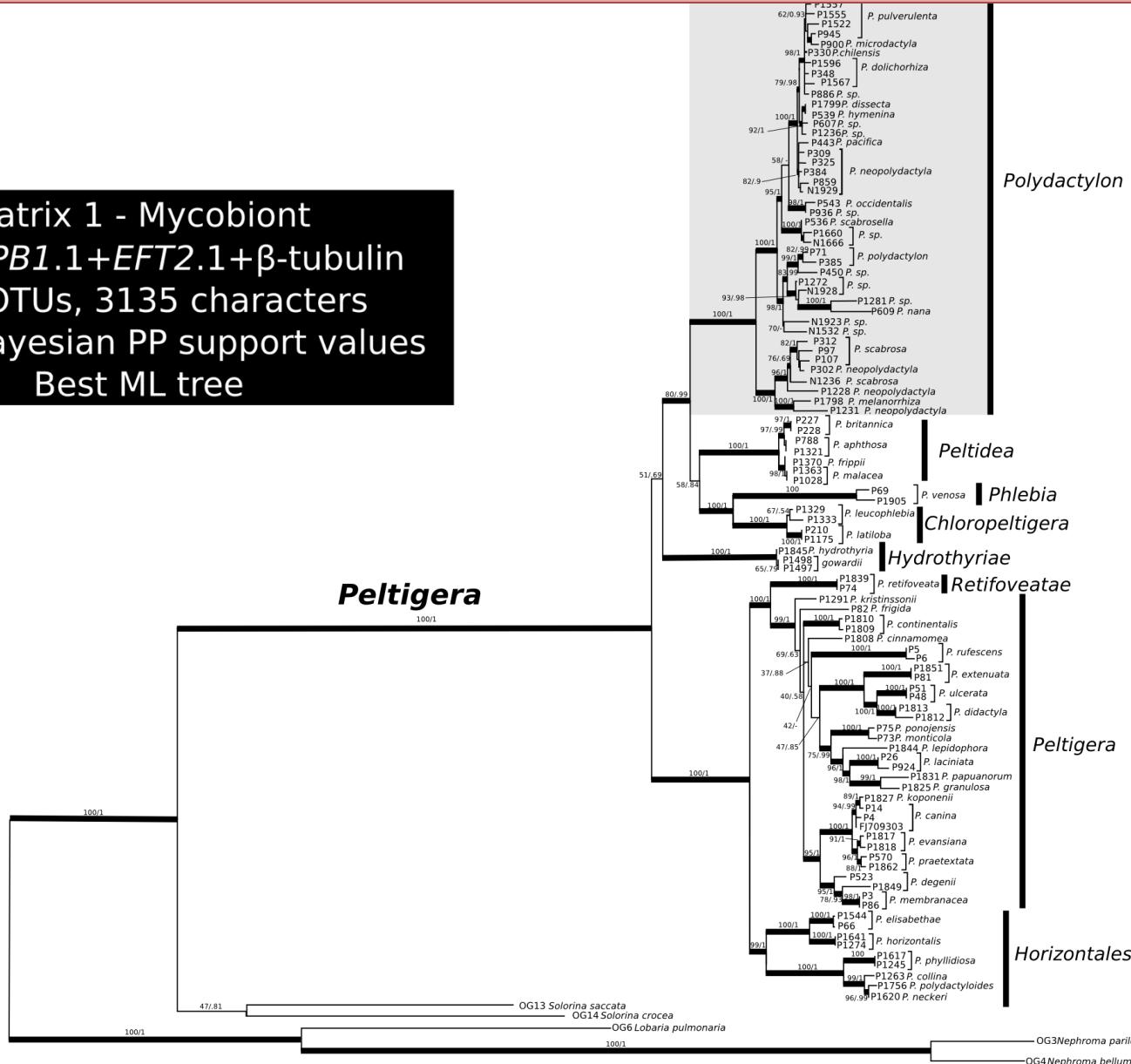
# *Peltigera* section *Polydactylon*

- Monophyletic group of species
- Only bipartite thalli (w. *Nostoc*)
- Group comprising species with different ecology and distributions (cosmopolitan, boreal, tropical, endemics...)
- Suspected presence of unrecognized or cryptic species



# Phylogeny of the genus *Peltigera*

Matrix 1 - Mycobiont  
 LSU+*RPB1.1+EFT2.1+β-tubulin*  
 106 OTUs, 3135 characters  
 ML-BS/Bayesian PP support values  
 Best ML tree



# Specificity in *Peltigera* section *Polydactylon*: aims of the study

- 1) Infer the phylogenetic relationships of both partners
- 2) Assess the specificity of both symbionts
- 3) Identify factors associated with specificity (geographic range, speciation rates, time, genetic diversity...)

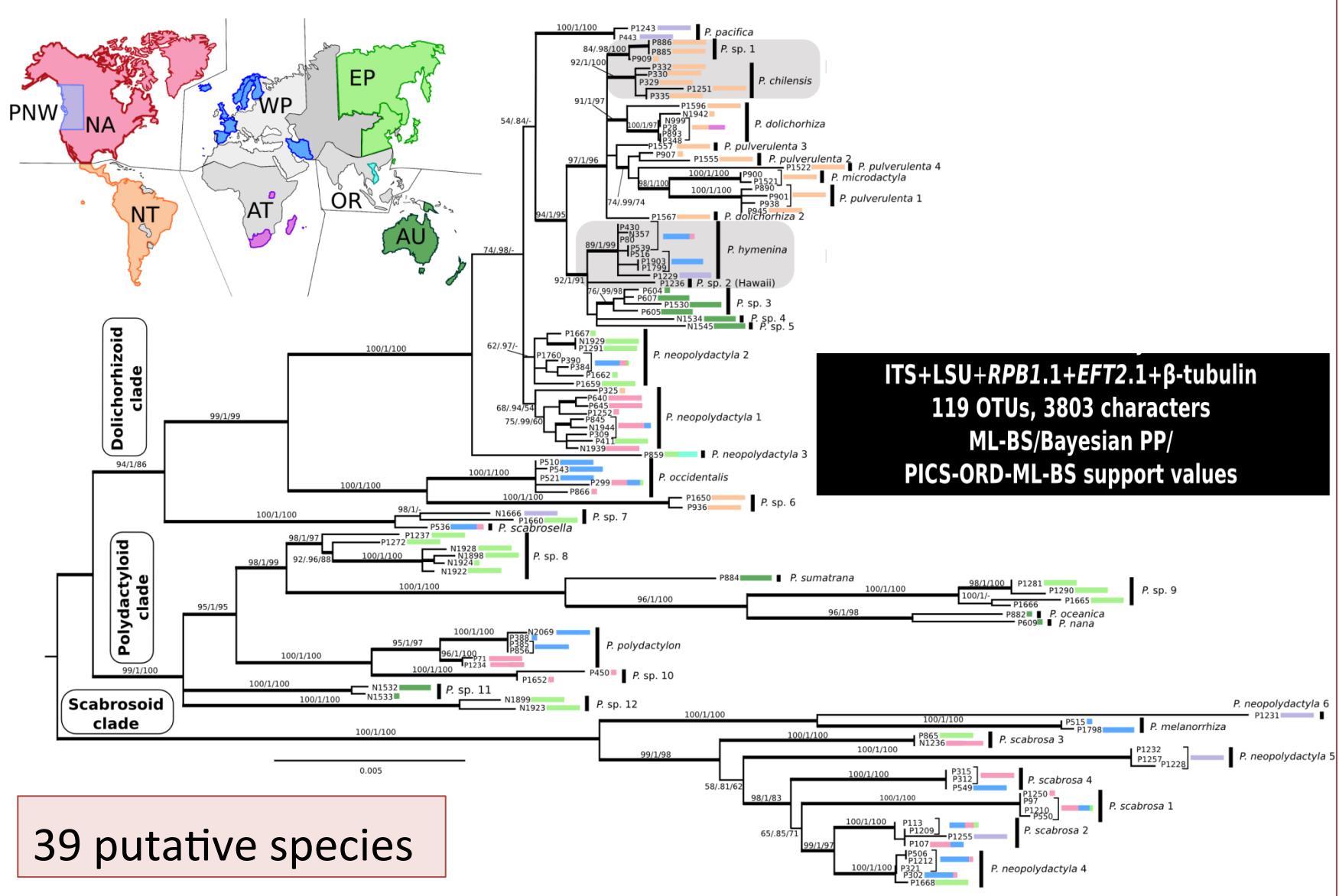
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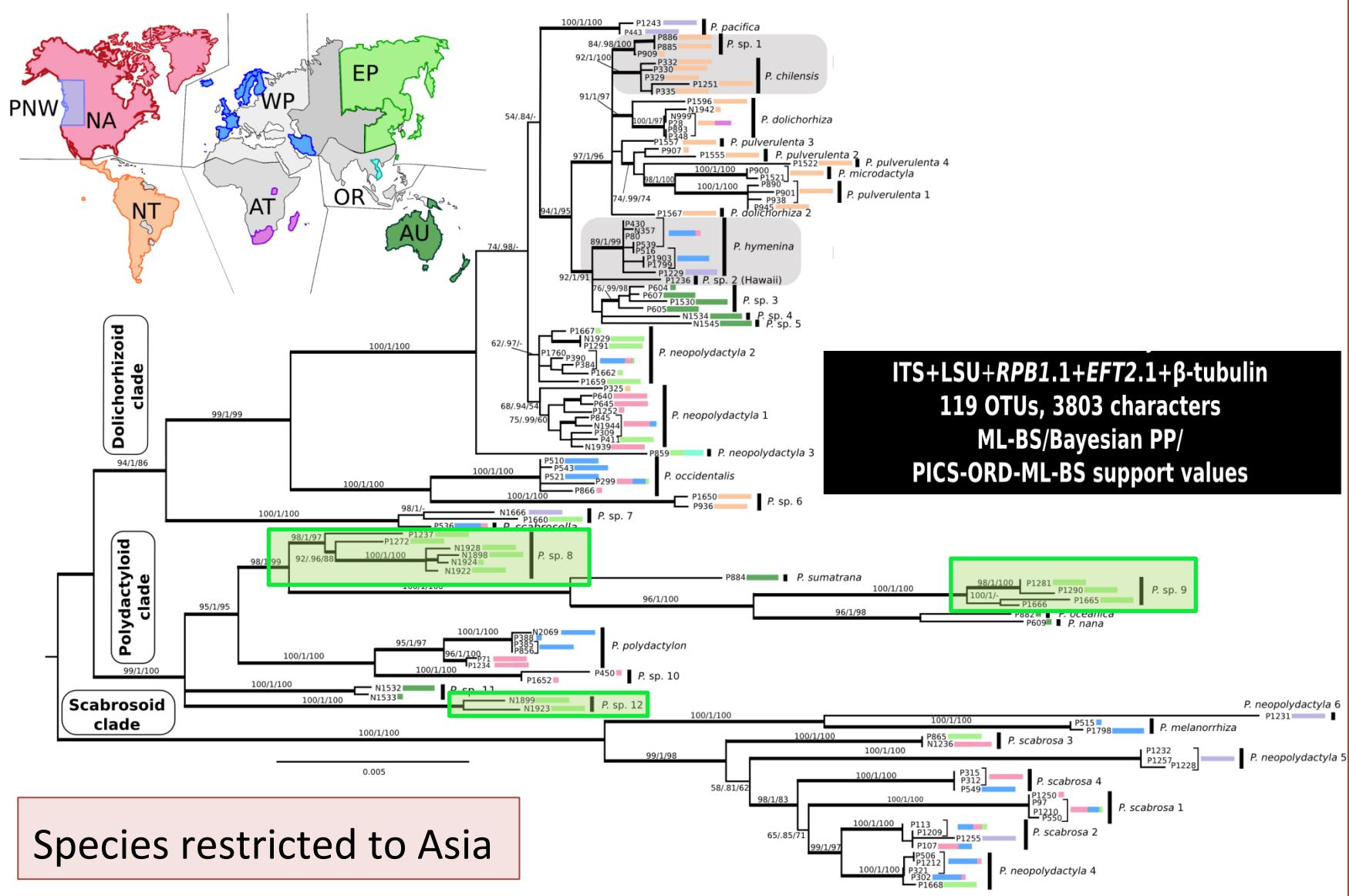
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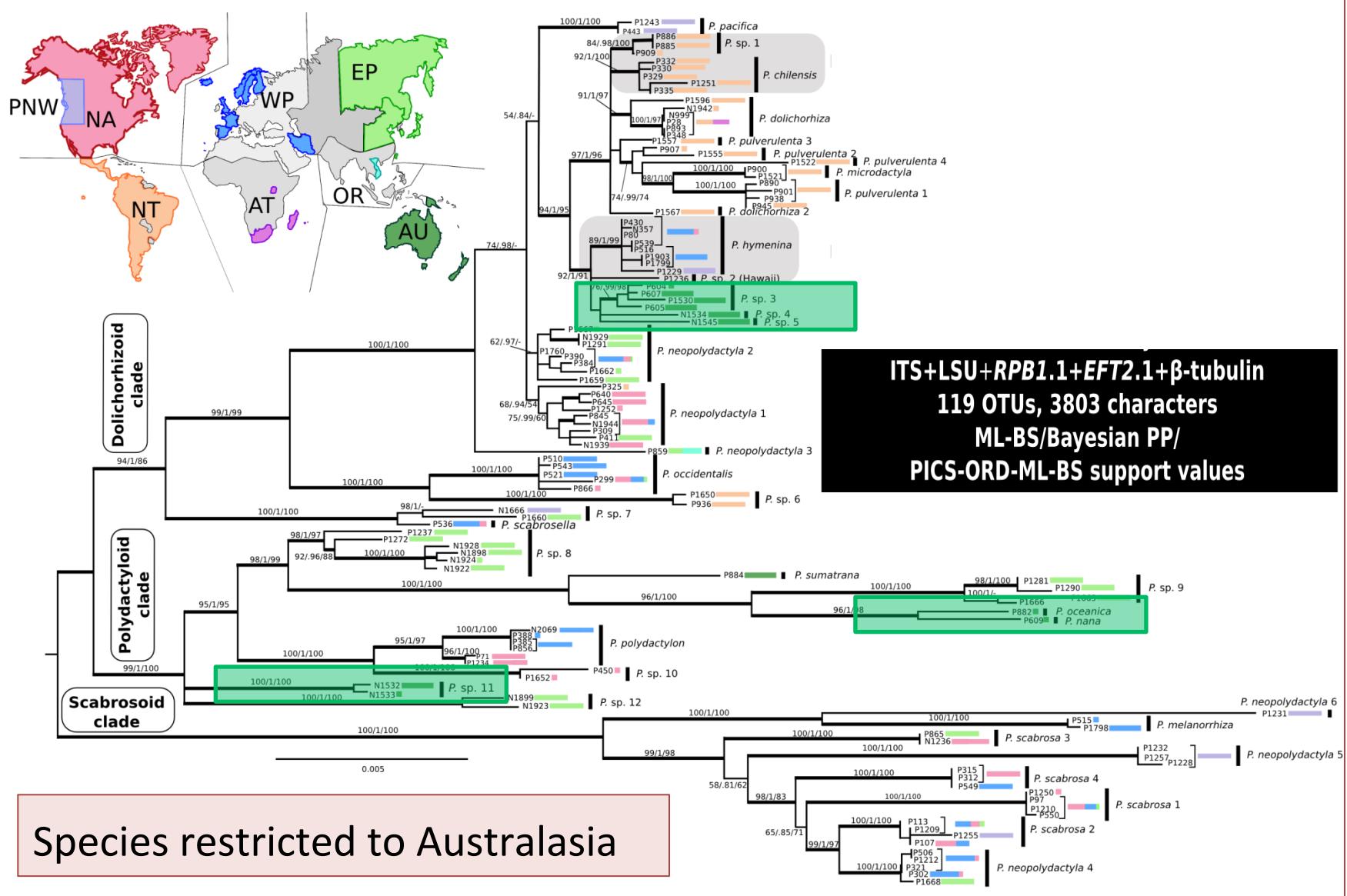
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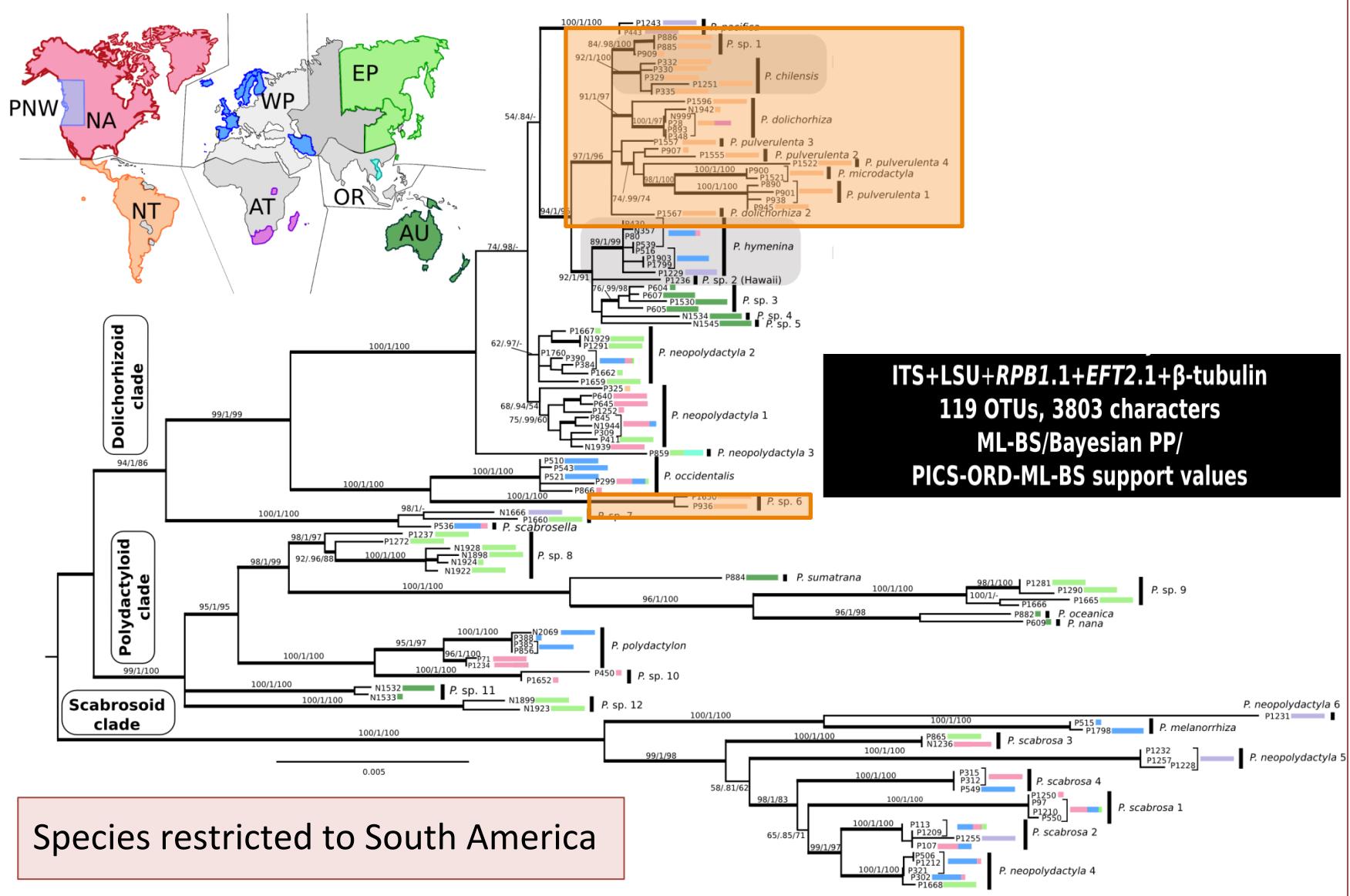
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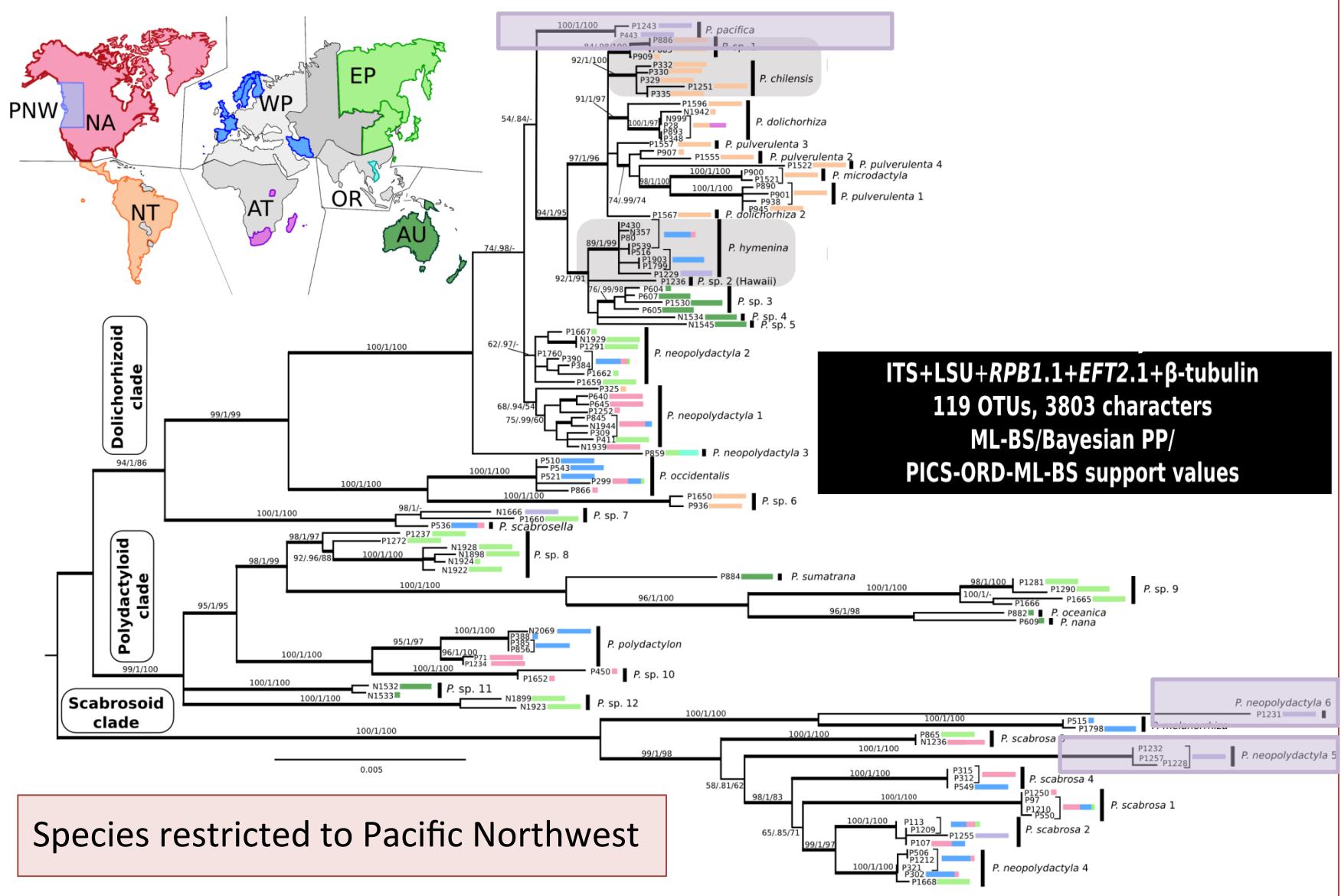
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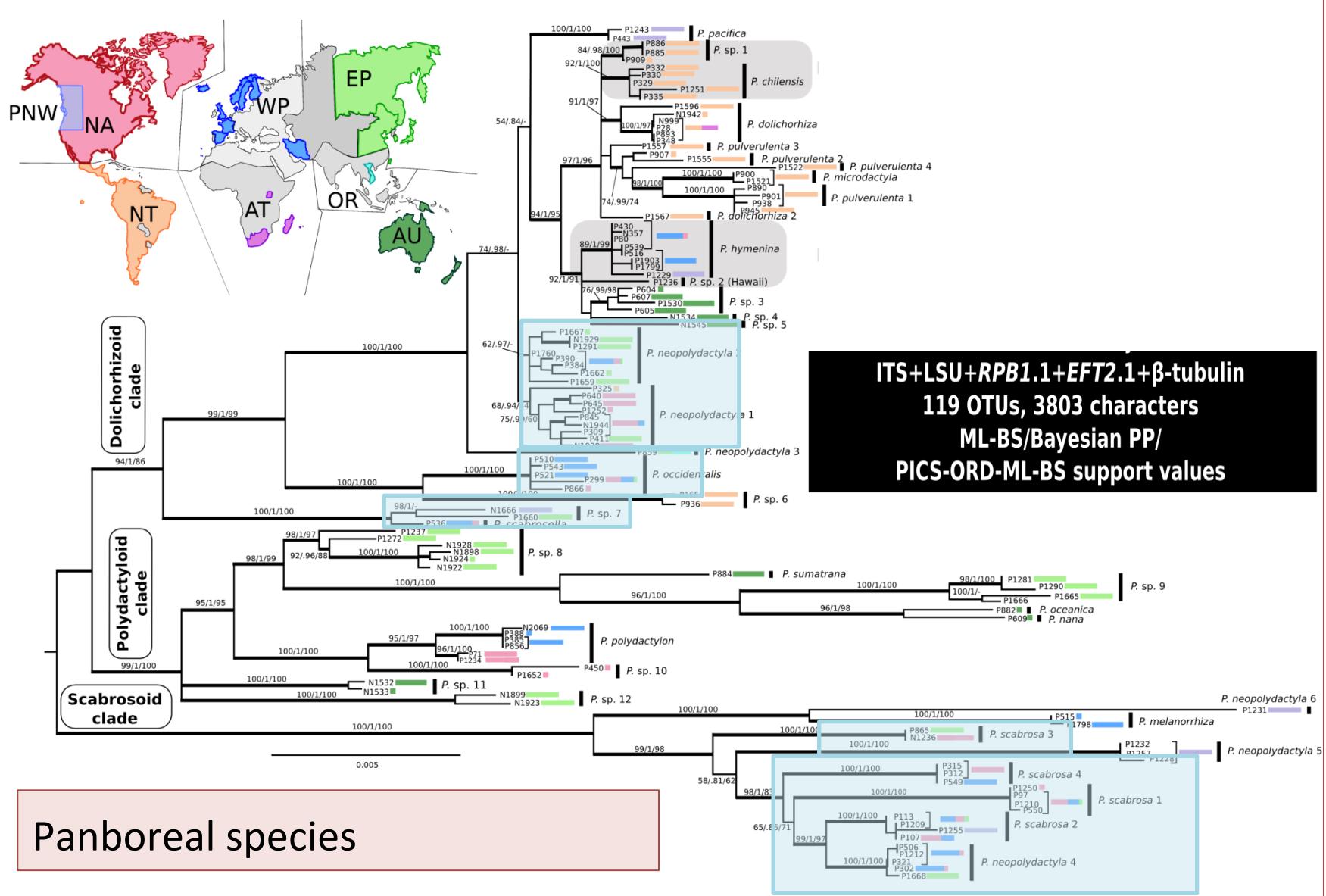
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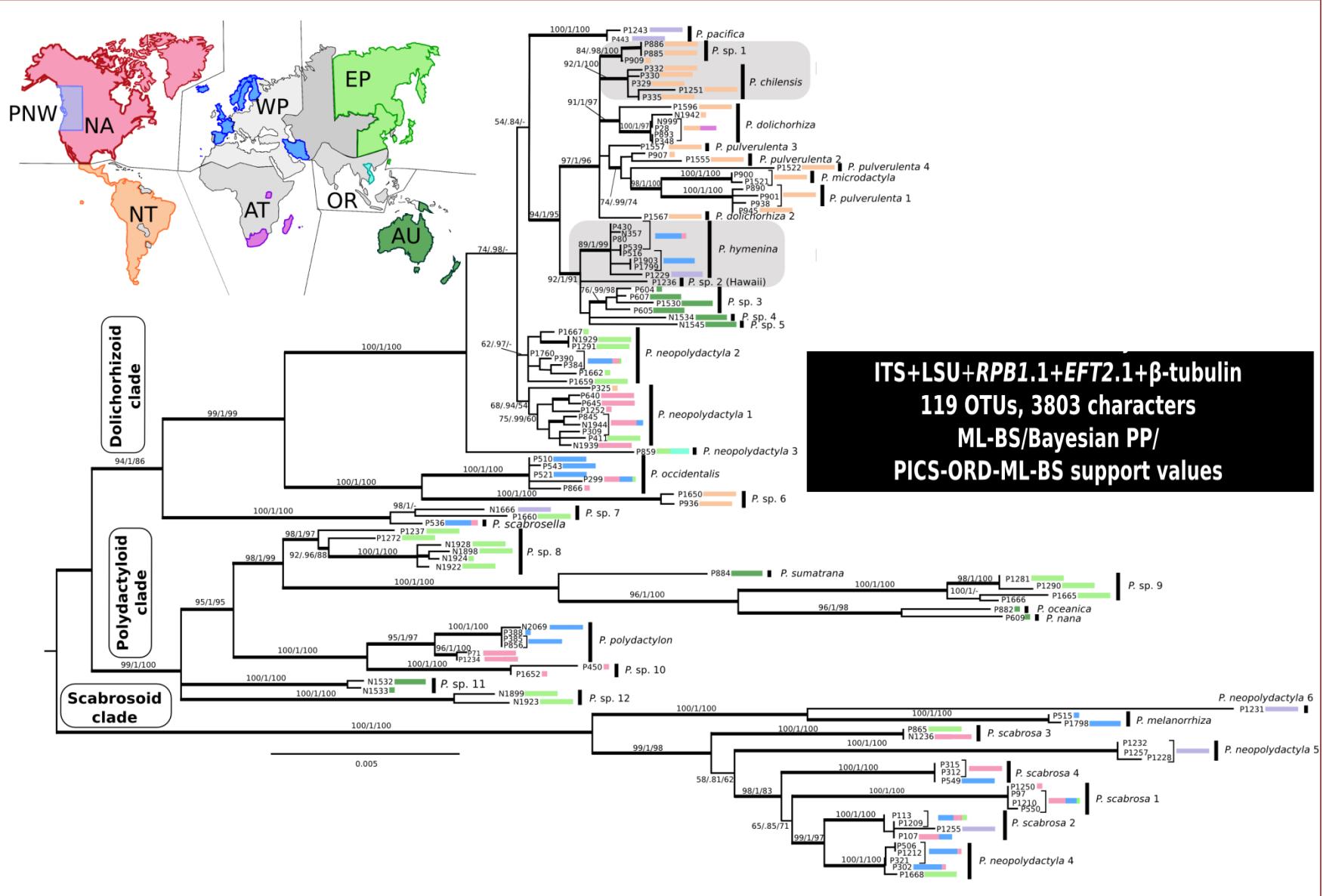
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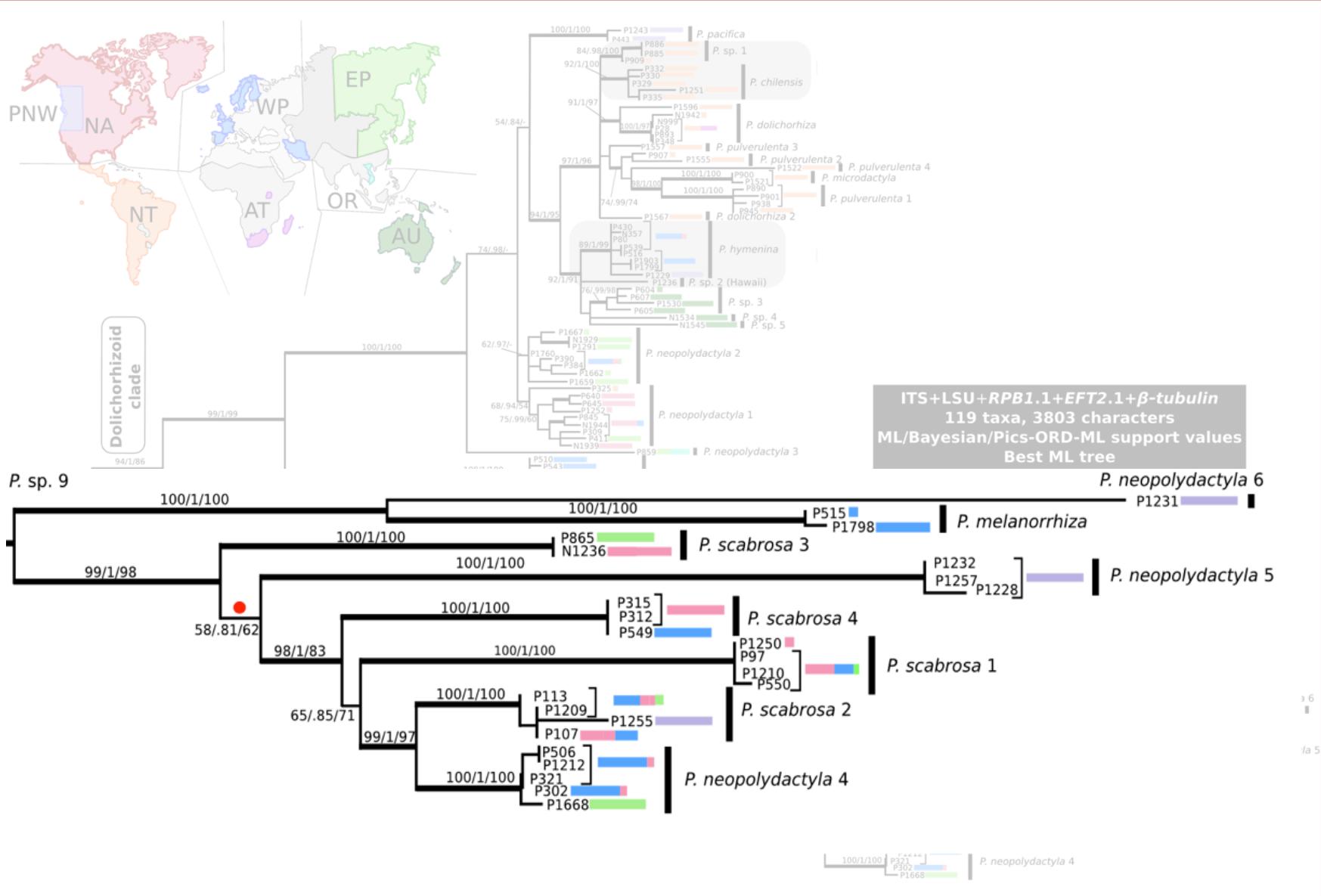
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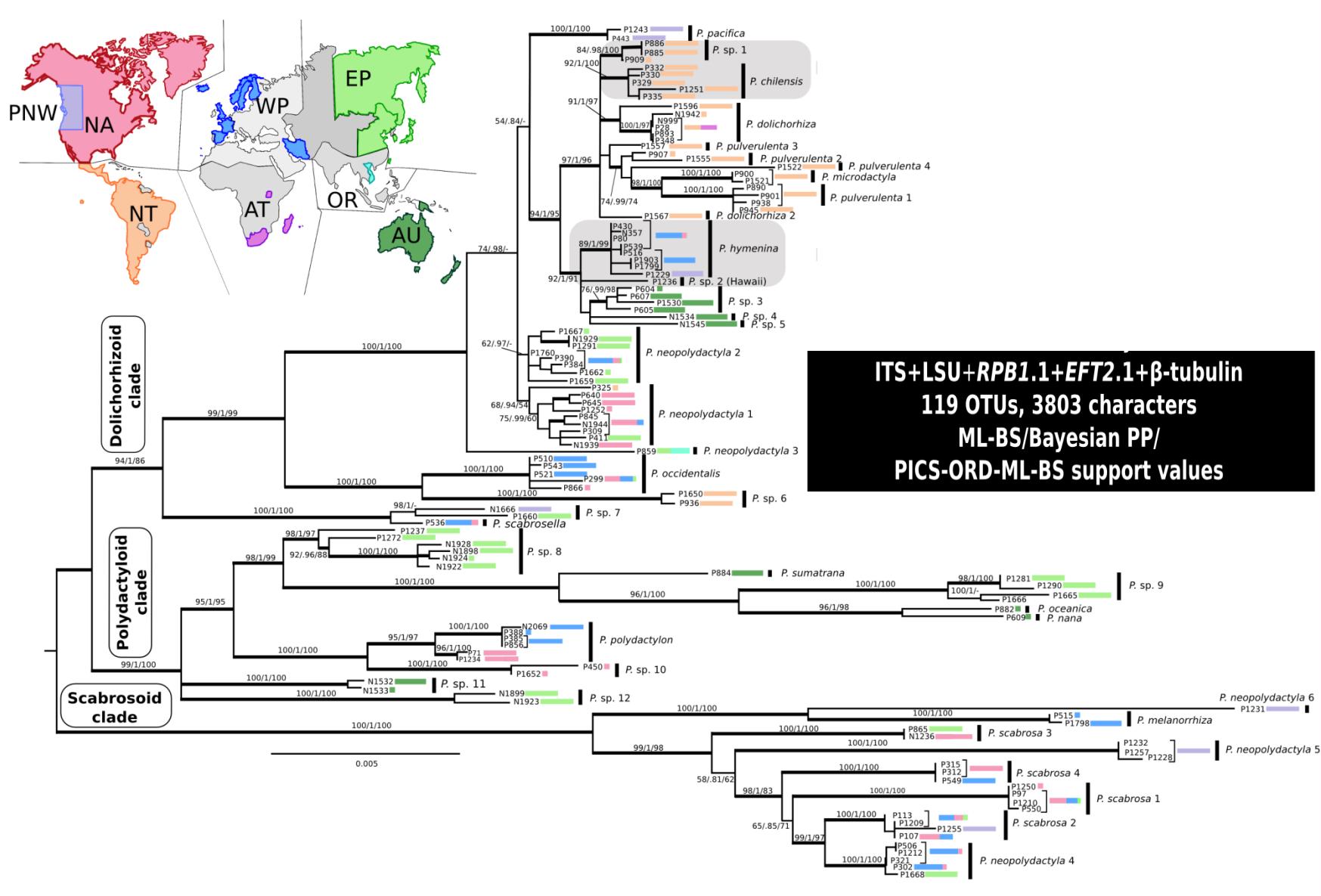
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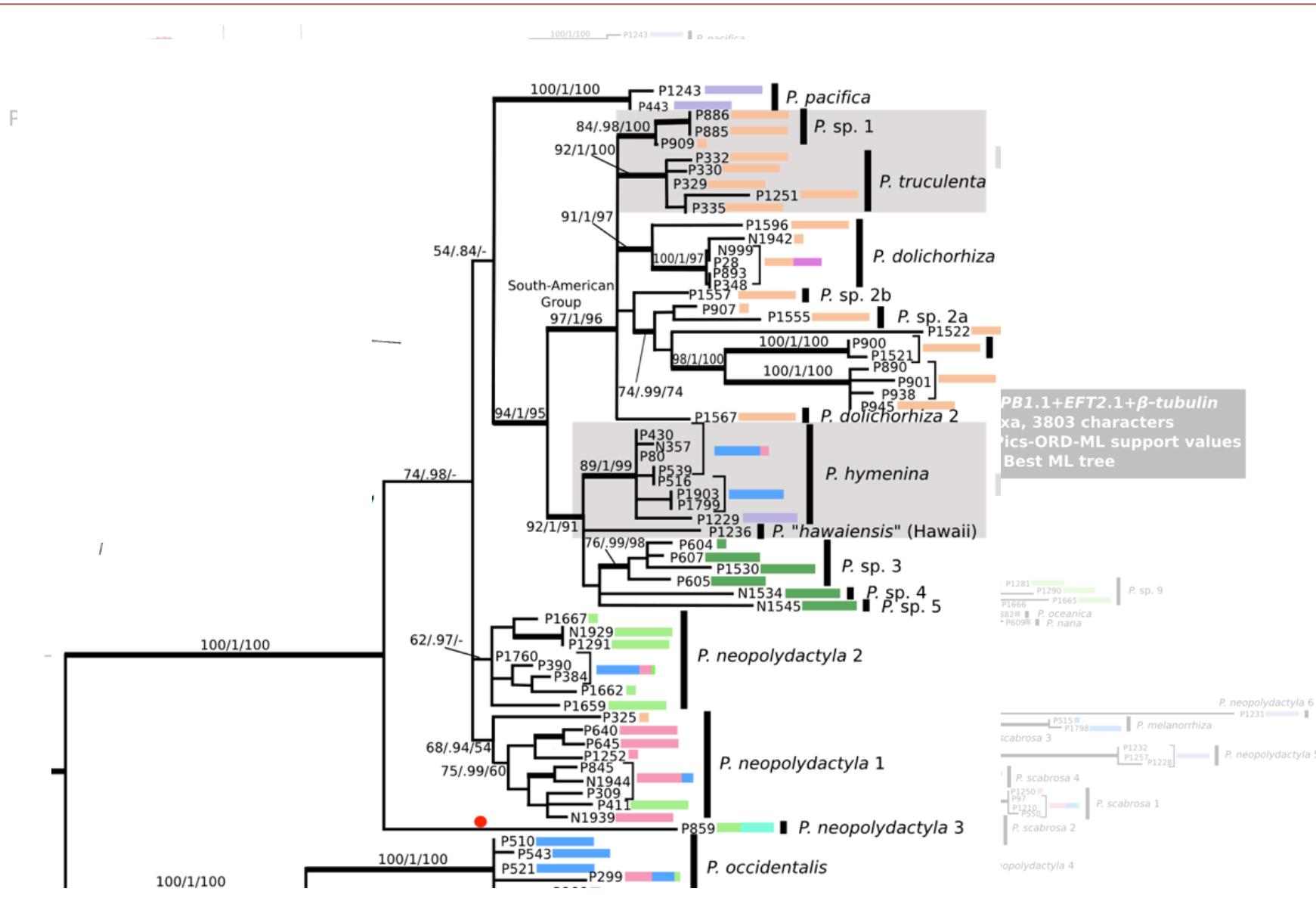
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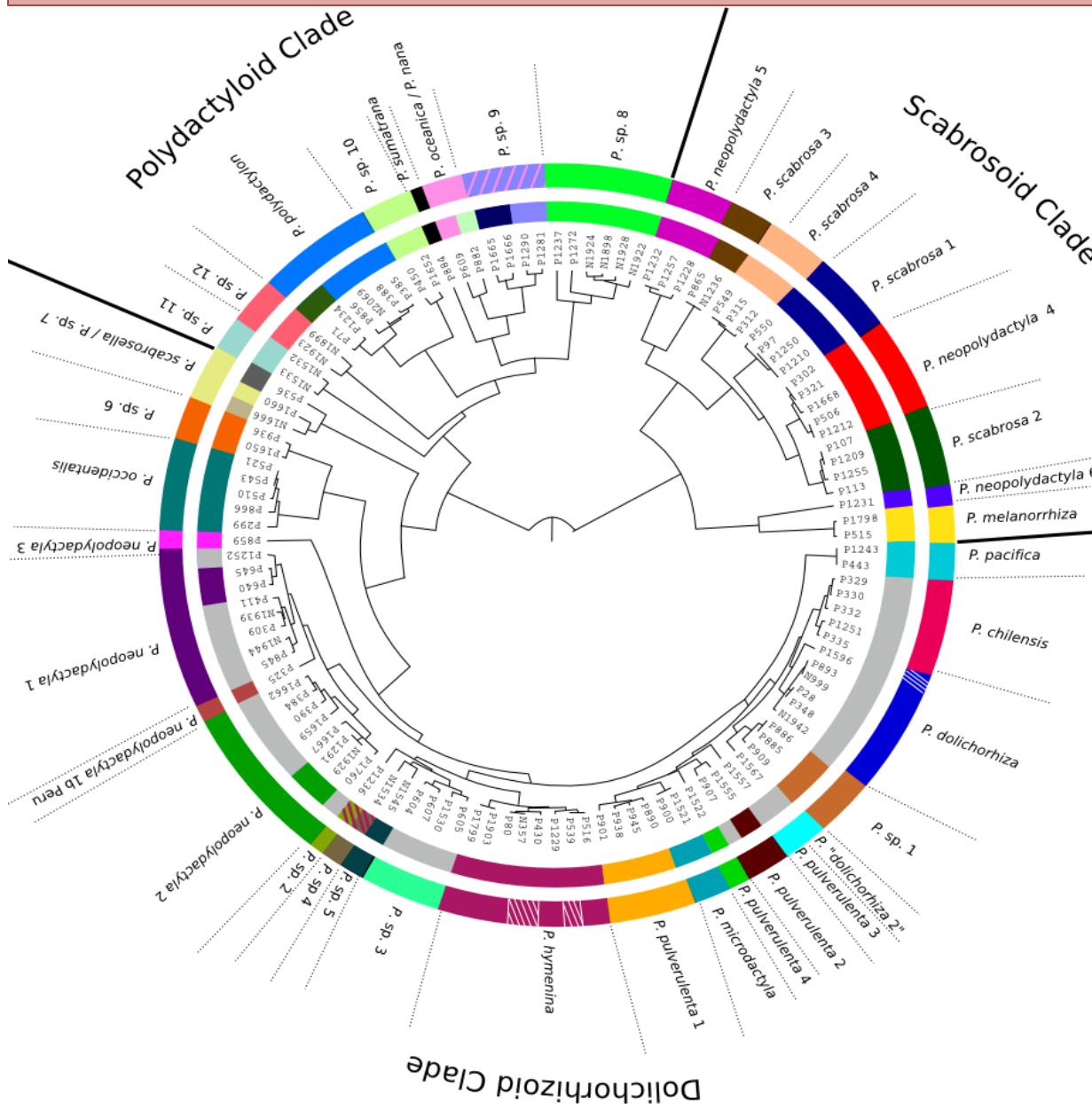
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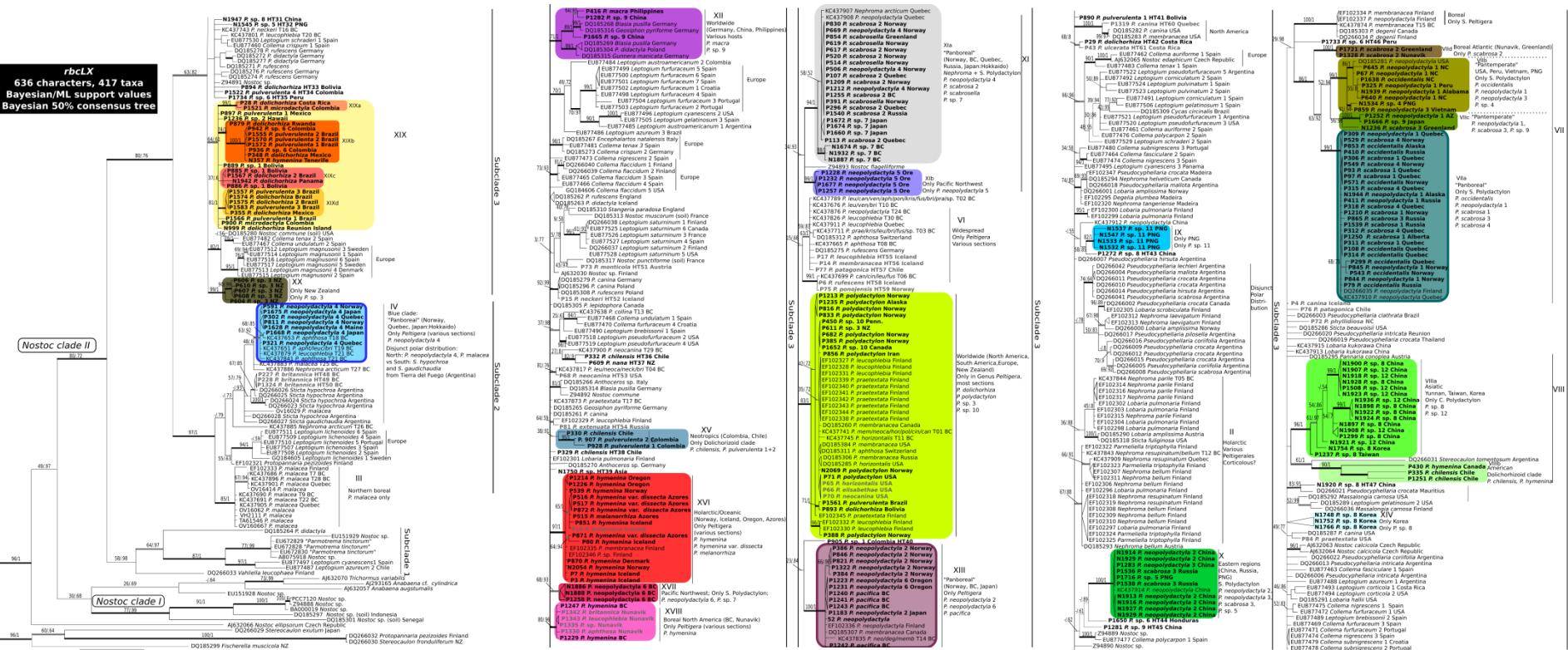
## 2a. Species delimitation (discovery)



- 2 methods:  
Structurama  
(haplotypes, all  
loci) and bGMYC  
(coalescent, ITS  
tree)
- Attribute  
« provisional  
species » to the  
samples used in  
the analyses

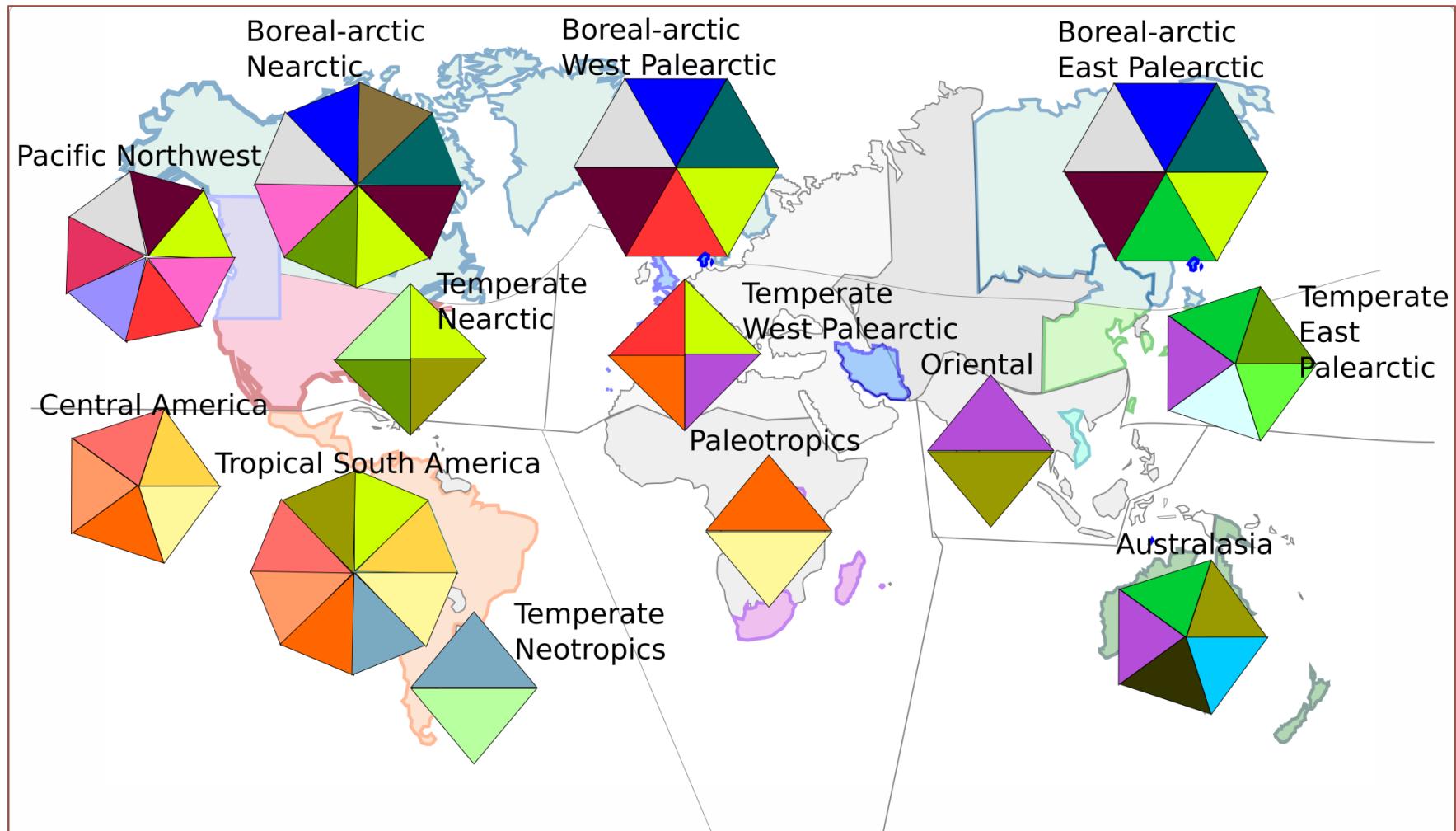
# 1b. Global *rbcLX* phylogeny of *Nostoc*

*rbcLX*  
636 characters, 417 taxa  
Bayesian/ML support values  
Bayesian 50% consensus tree



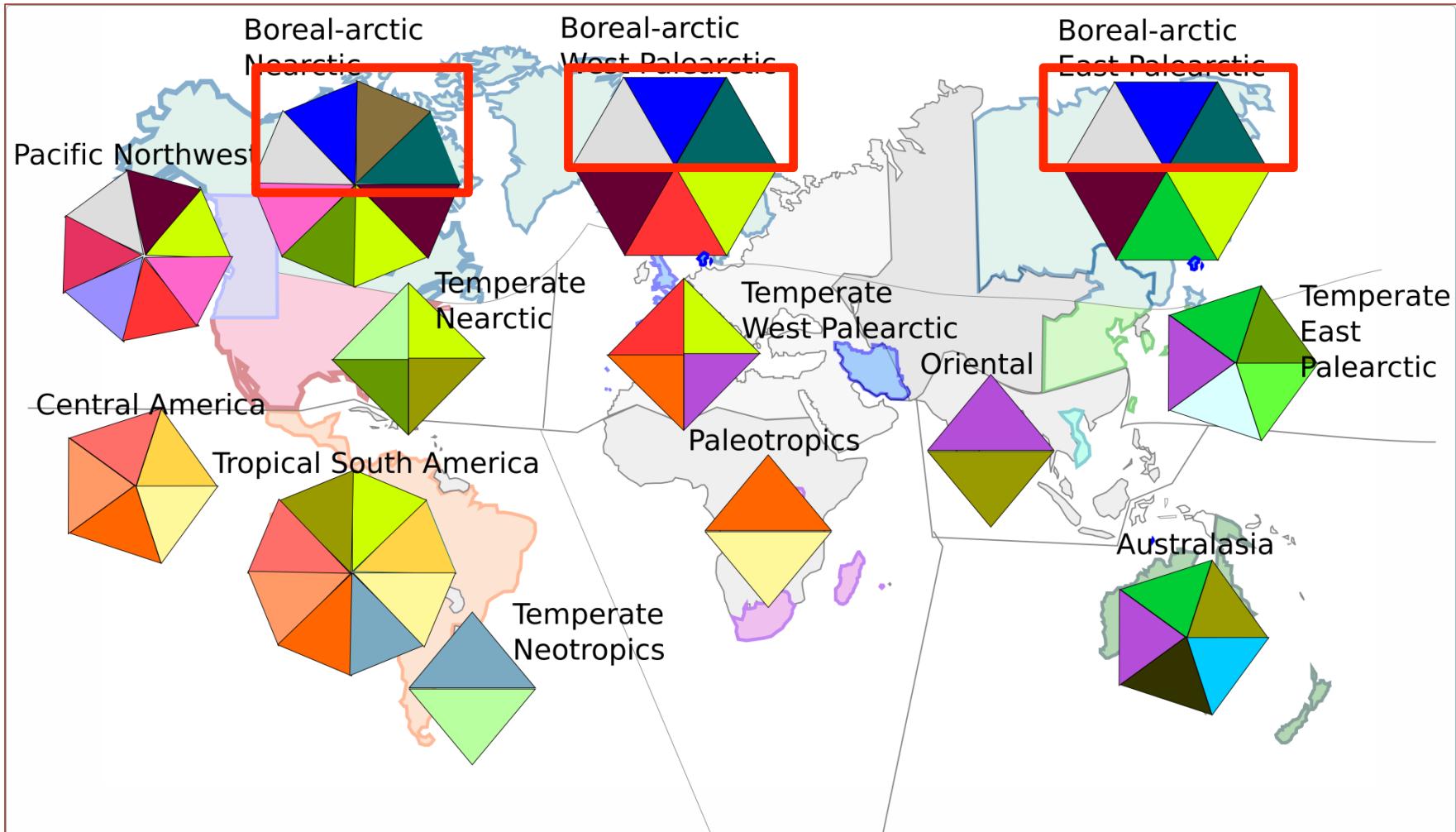
- Delimitation of 25 phylogroups based on well-supported monophyletic groups of closely related *Nostoc*
- 18 associated only with section *Polydactylon*, 22 only with *Peltigera* => specificity

# 1c. Distribution of cyanobiont (*Nostoc*) phylogroups



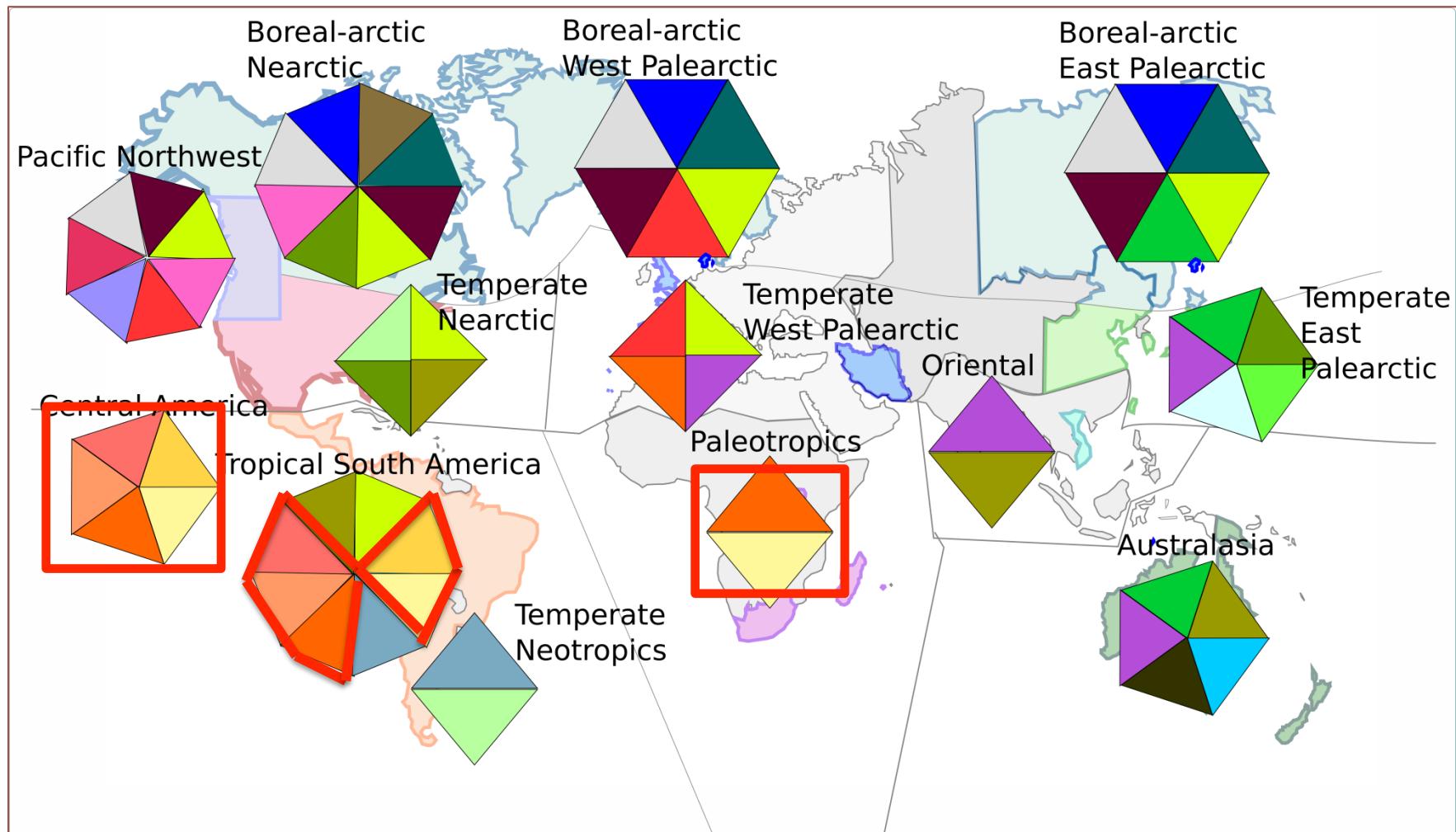
Very strong climatic and geographic patterns in the *Nostoc* distribution

# 1c. Distribution of cyanobiont (*Nostoc*) phylogroups



Boreal phylogroups

# 1c. Distribution of cyanobiont (*Nostoc*) phylogroups



Tropical phylogroups

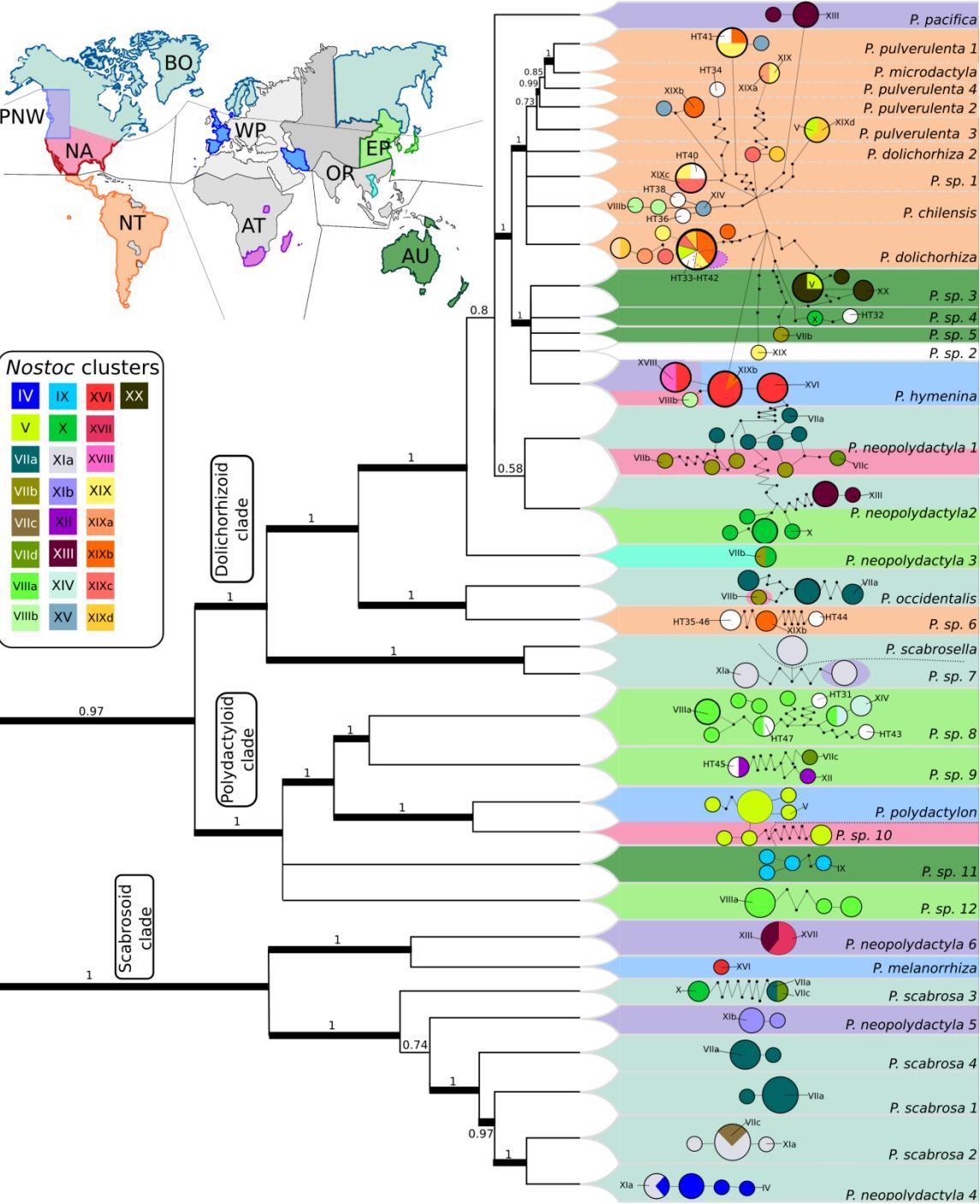
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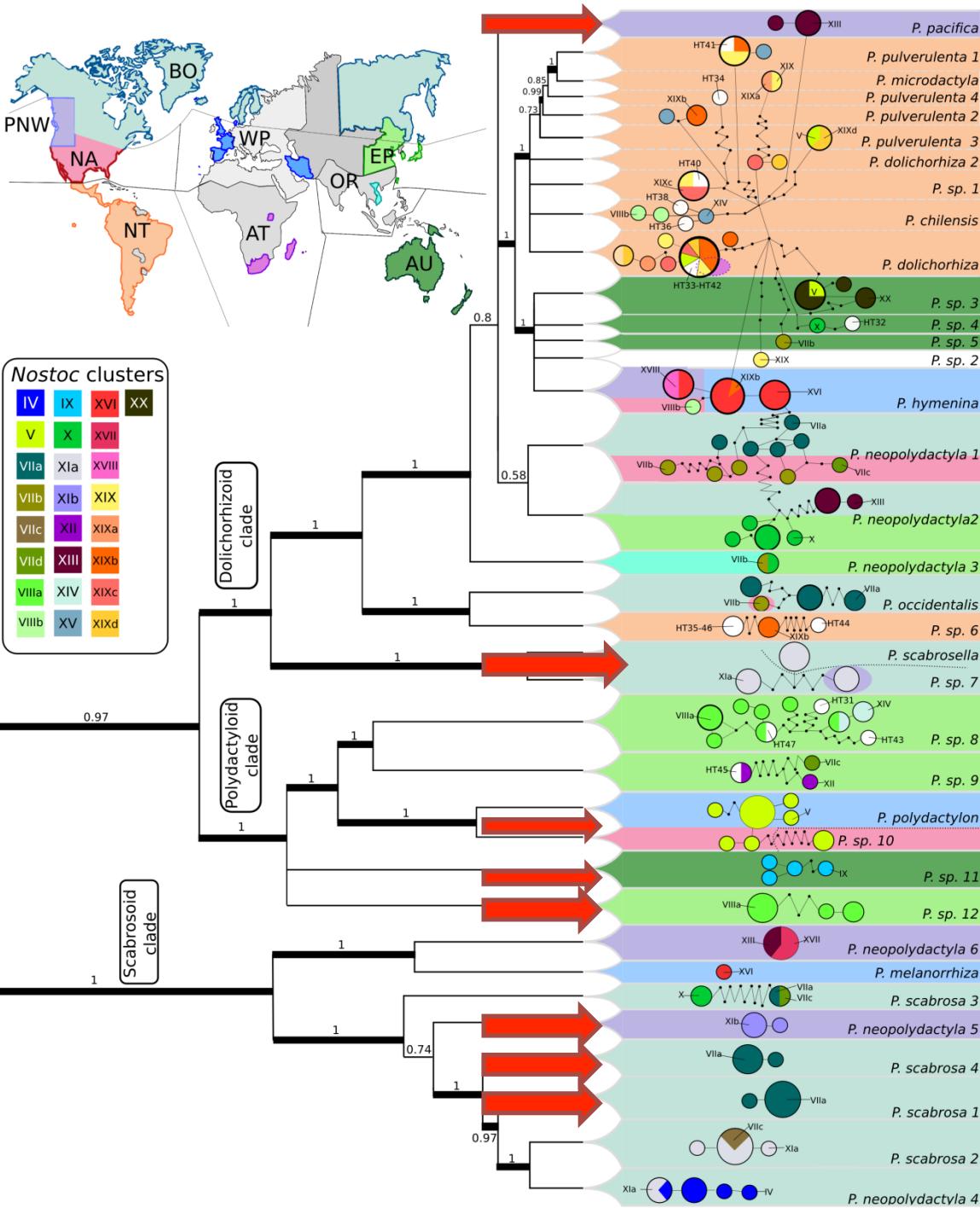
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- Different mycobiont profiles, from strict specialist to generalist
- Cases of local mycobiont specialists with cyanobiont switches
- Possible influence of time, with old mycobiont specialist species and recent generalists
- Radiation of mycobiont correlated with generalism
- Mycobiont specialists have usually less haplotypes than generalists



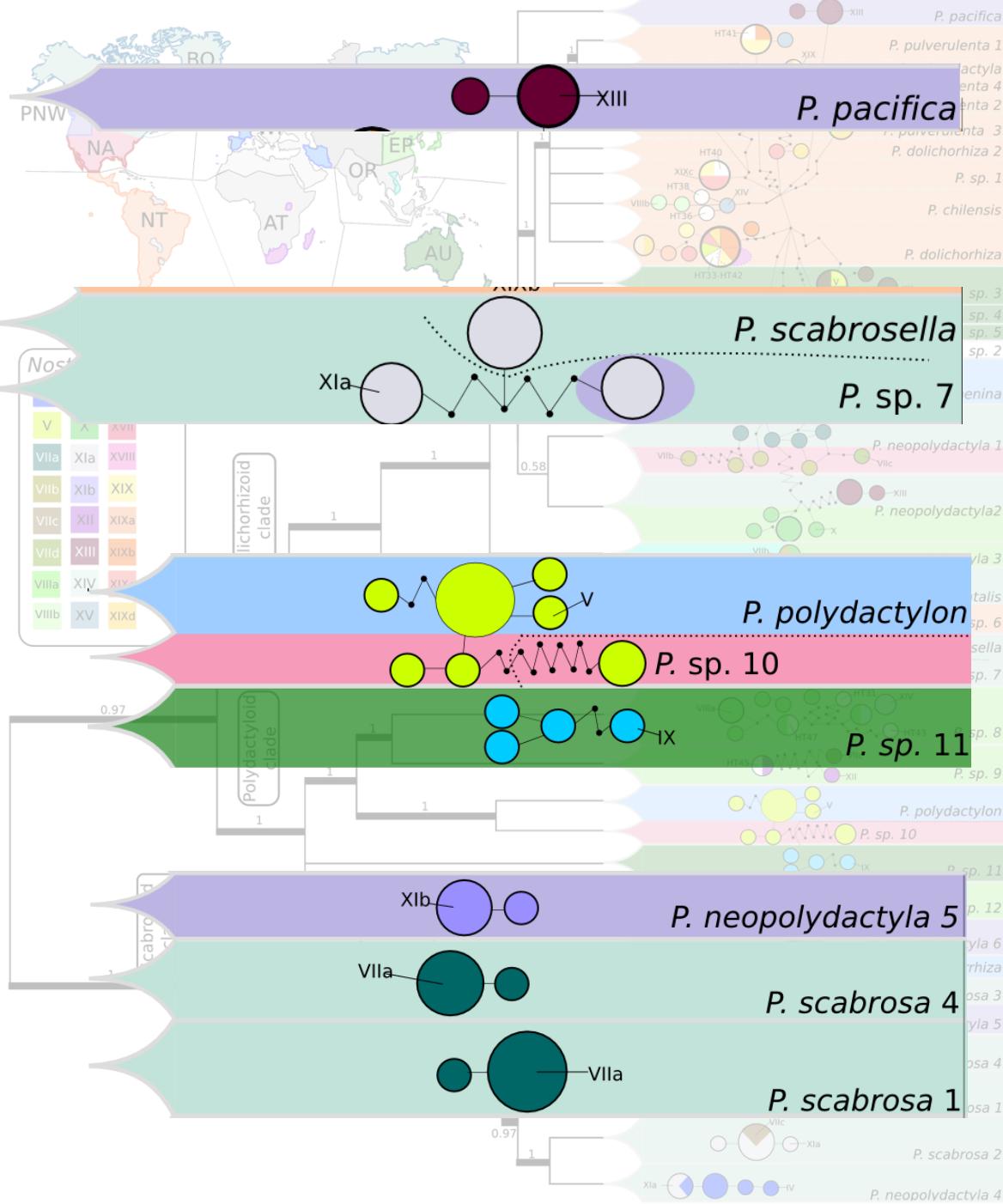
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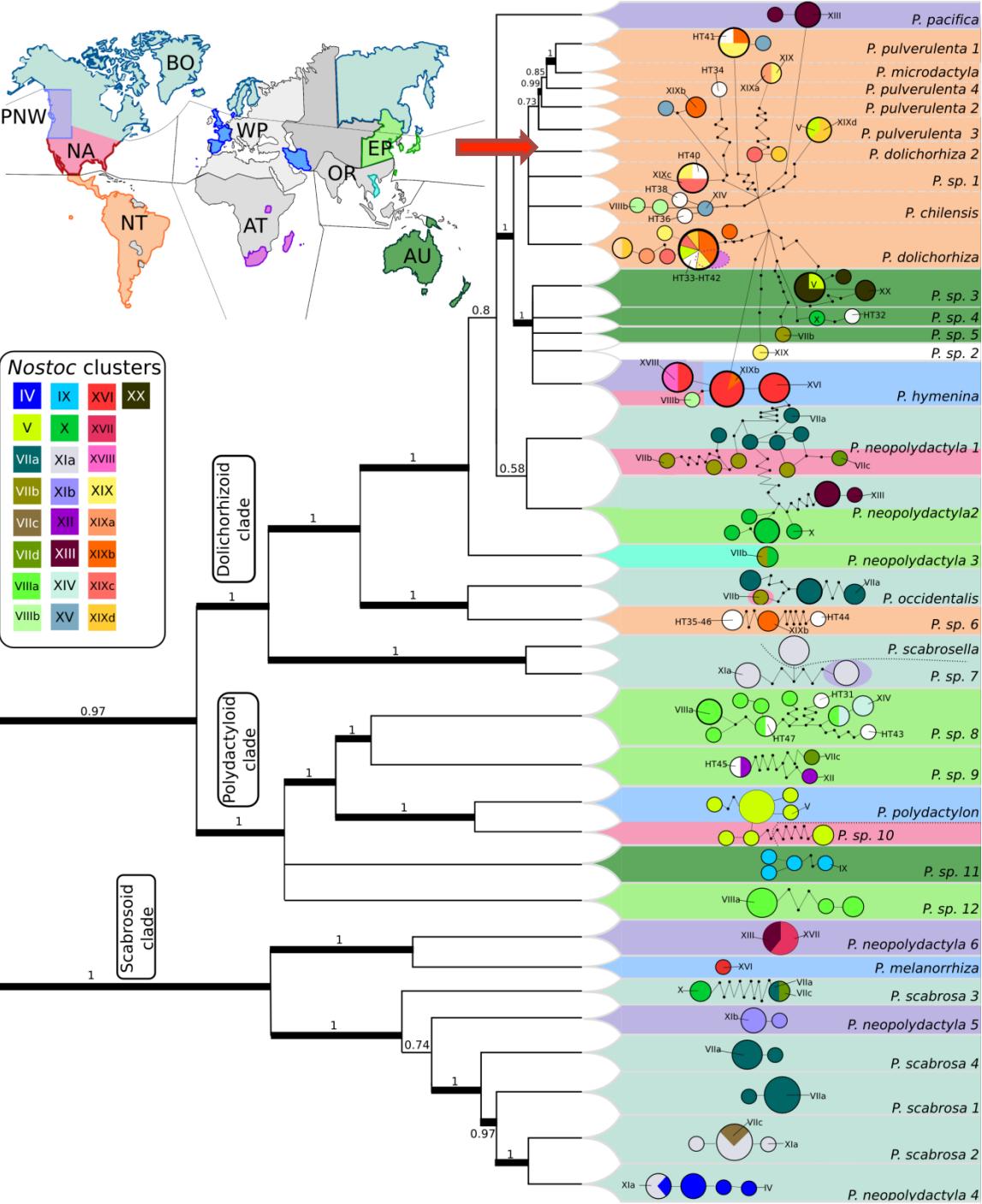
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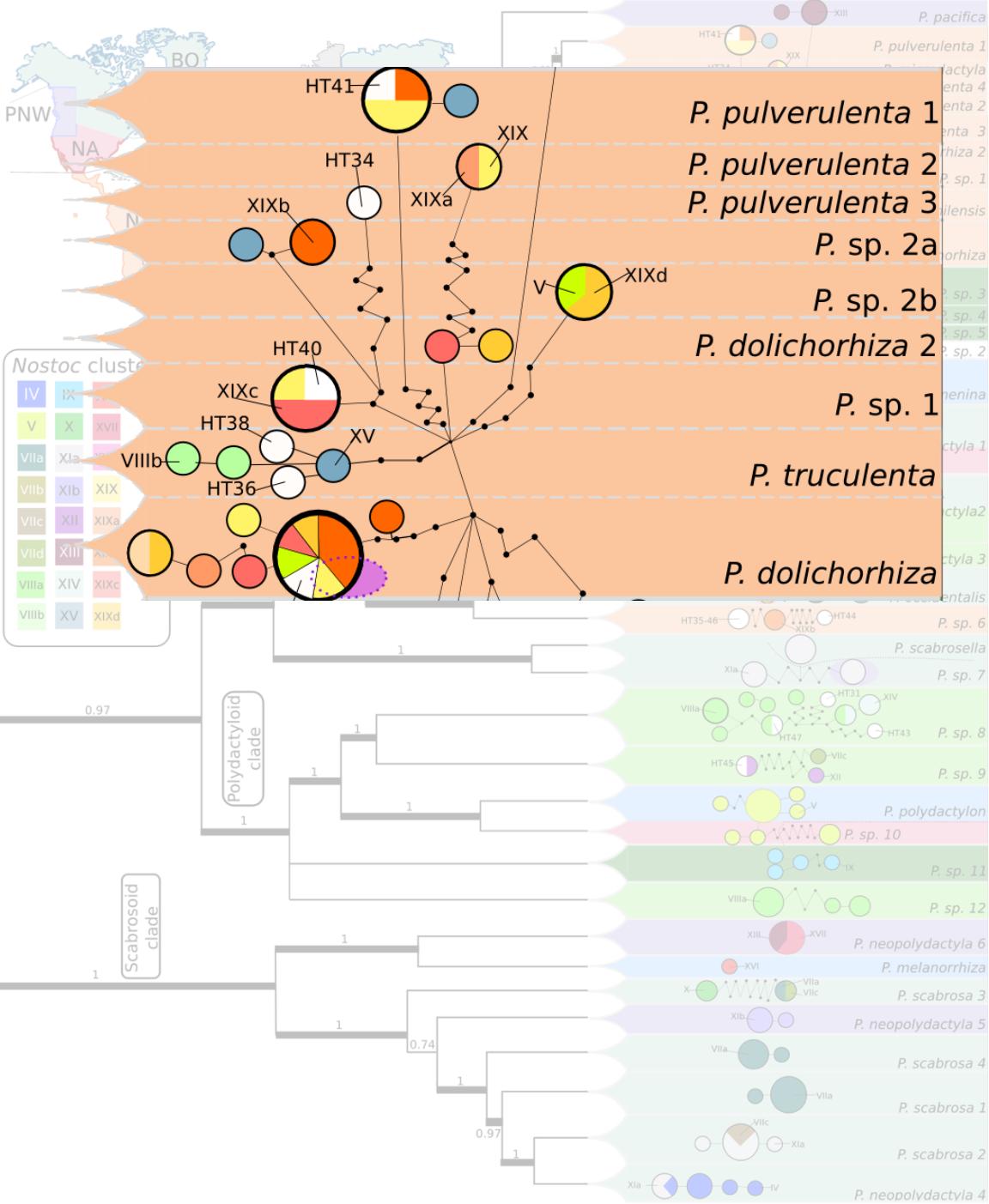
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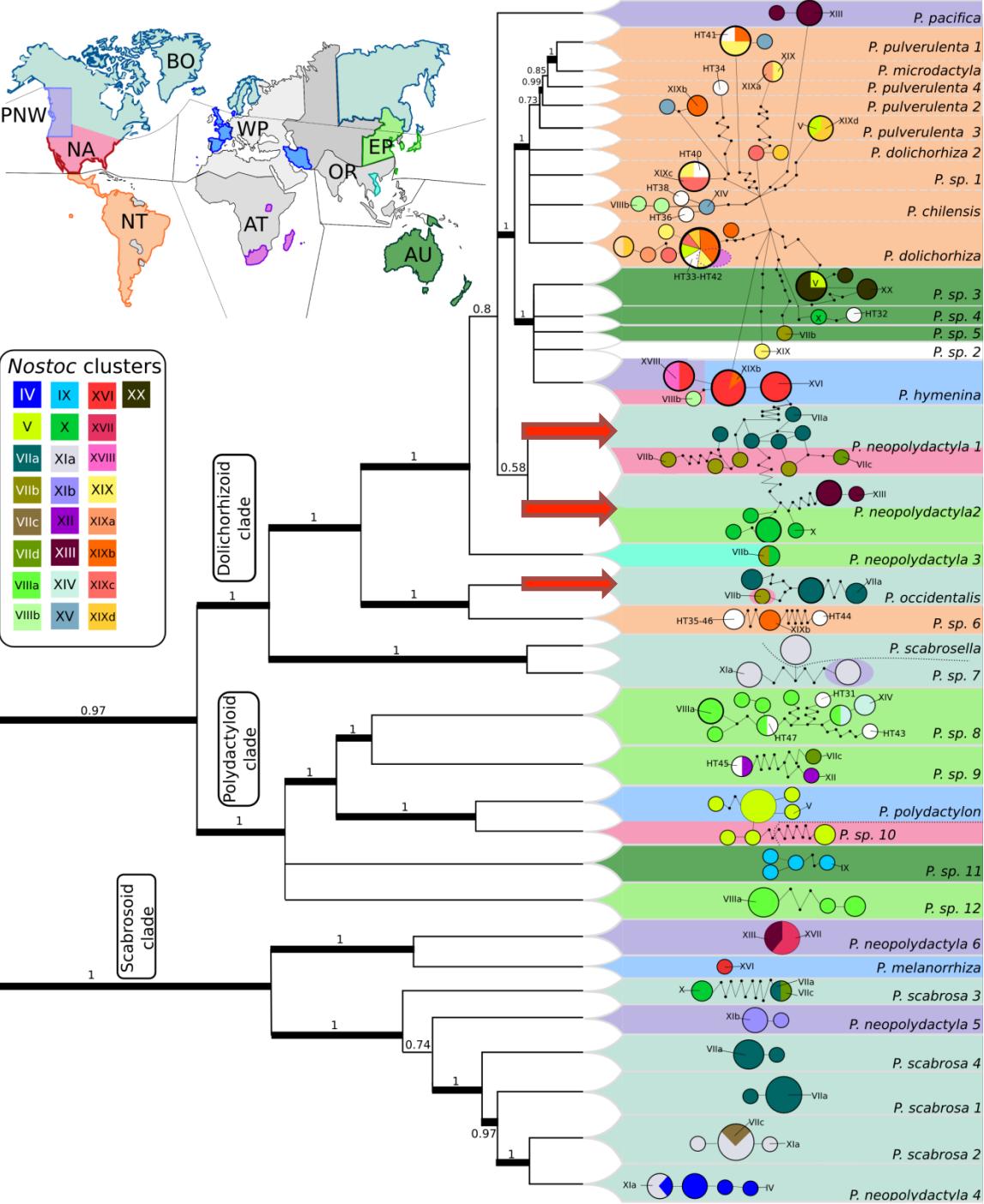
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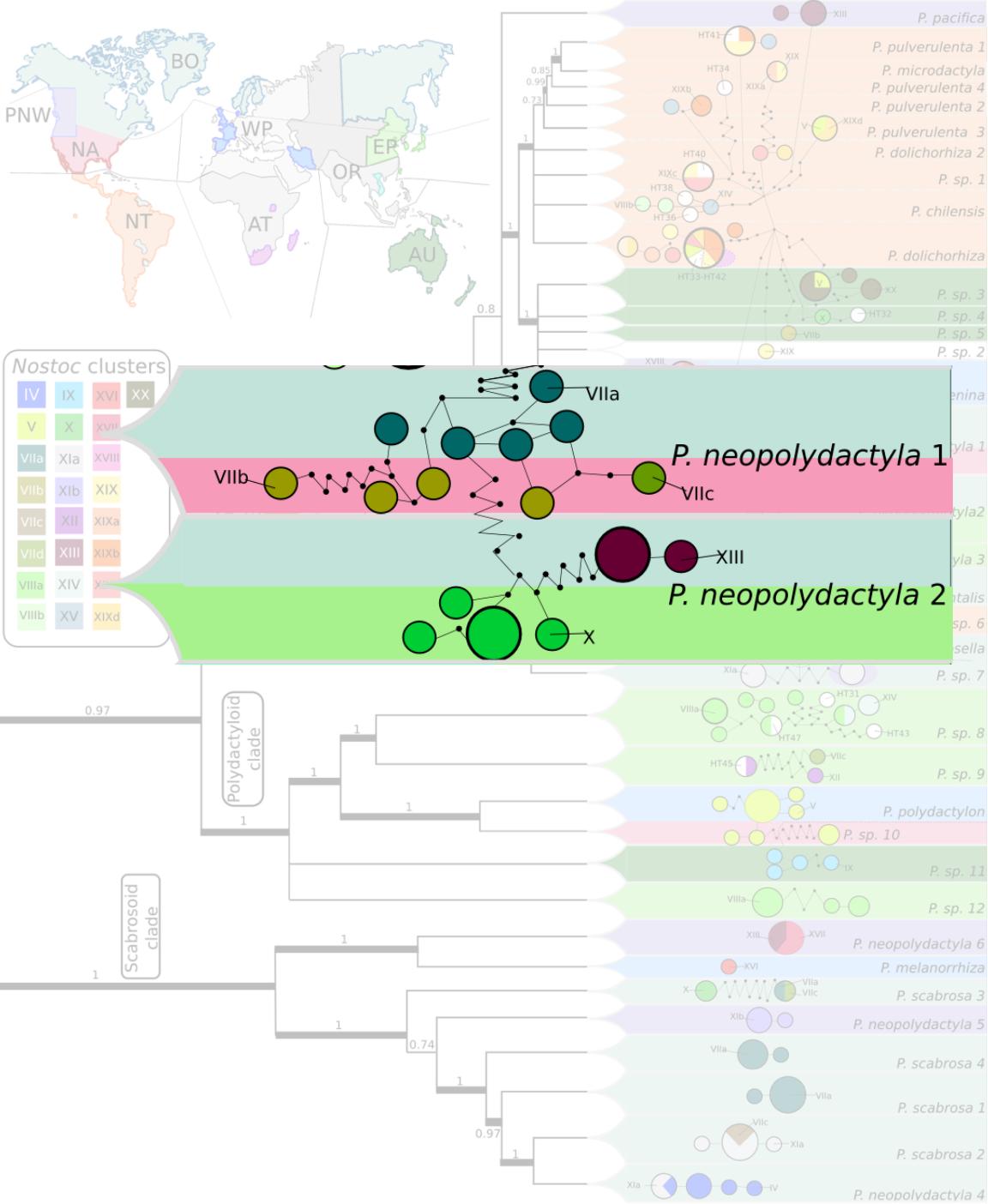
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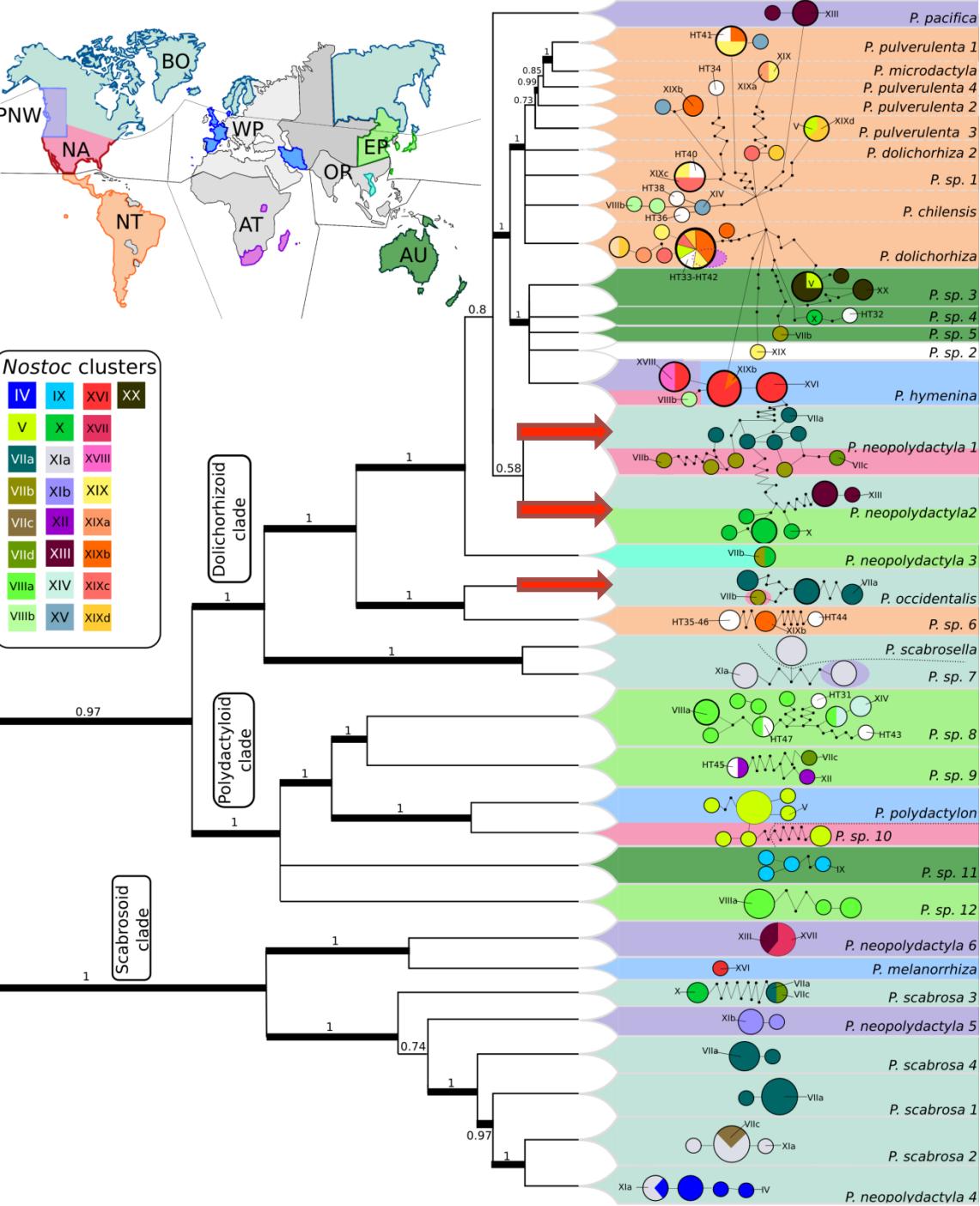
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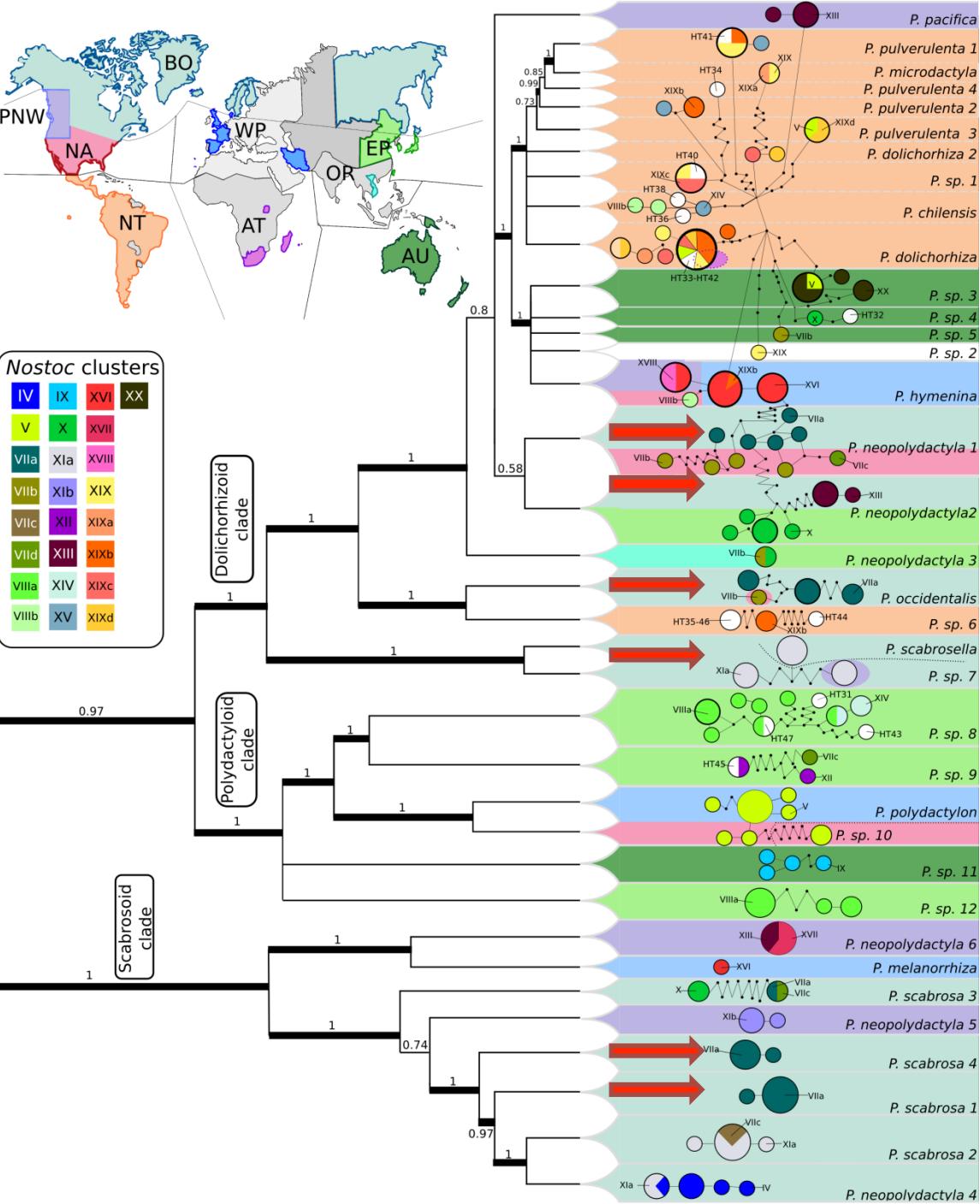
# Geographic mosaic of coevolution theory (Thompson)

- A species may adapt and become specialized to another species differently in separate regions
- Long-term dynamics of coevolution may occur over large geographic ranges rather than within local populations



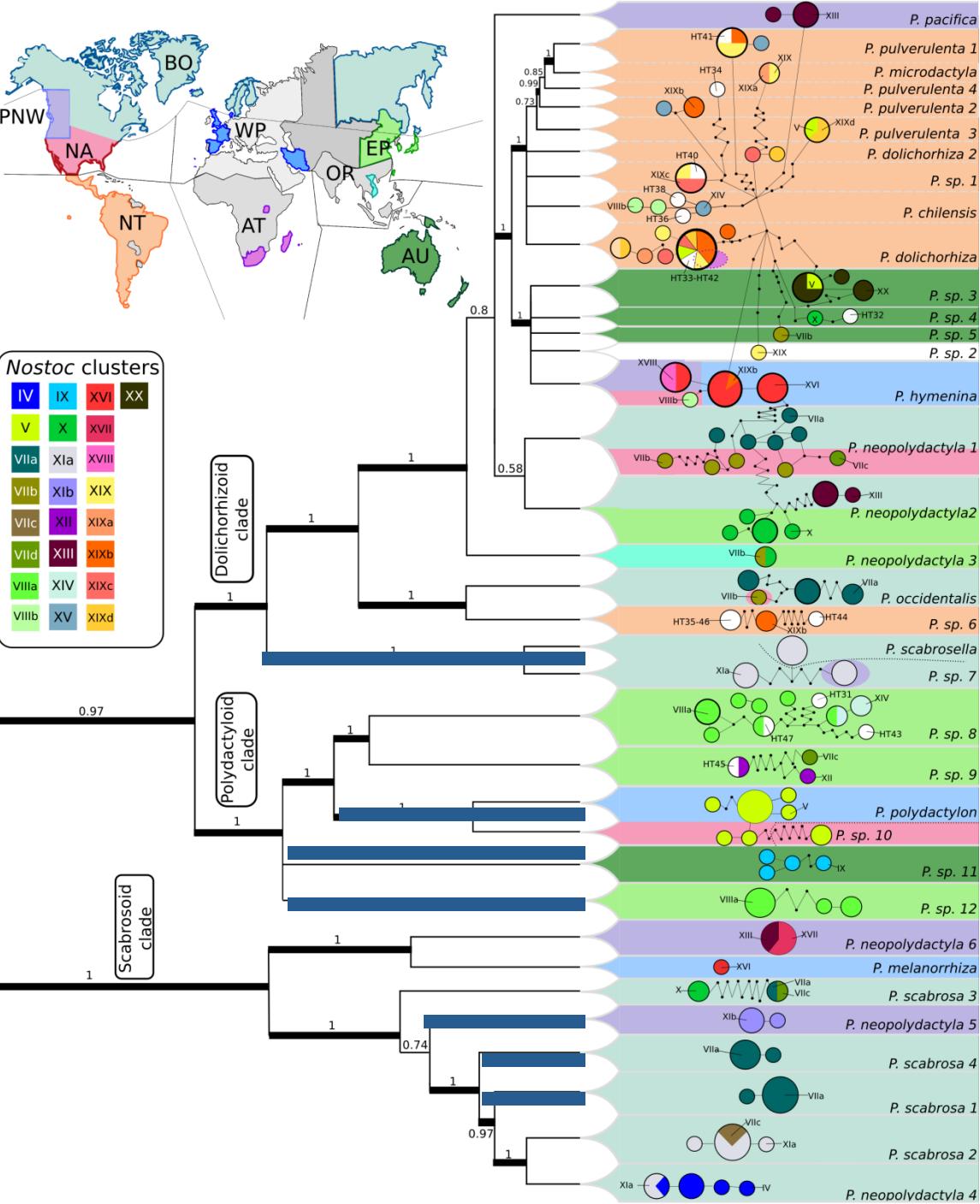
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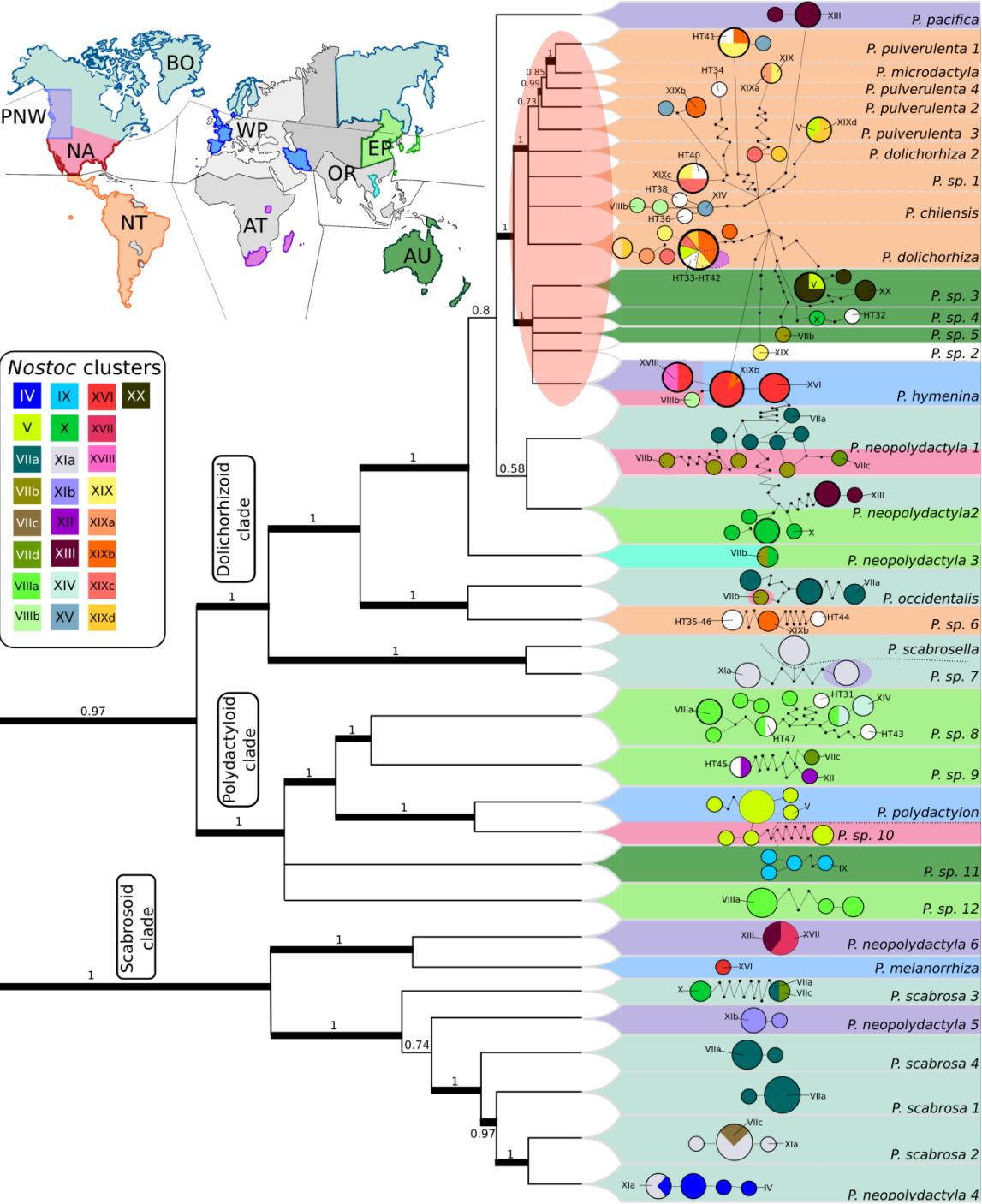
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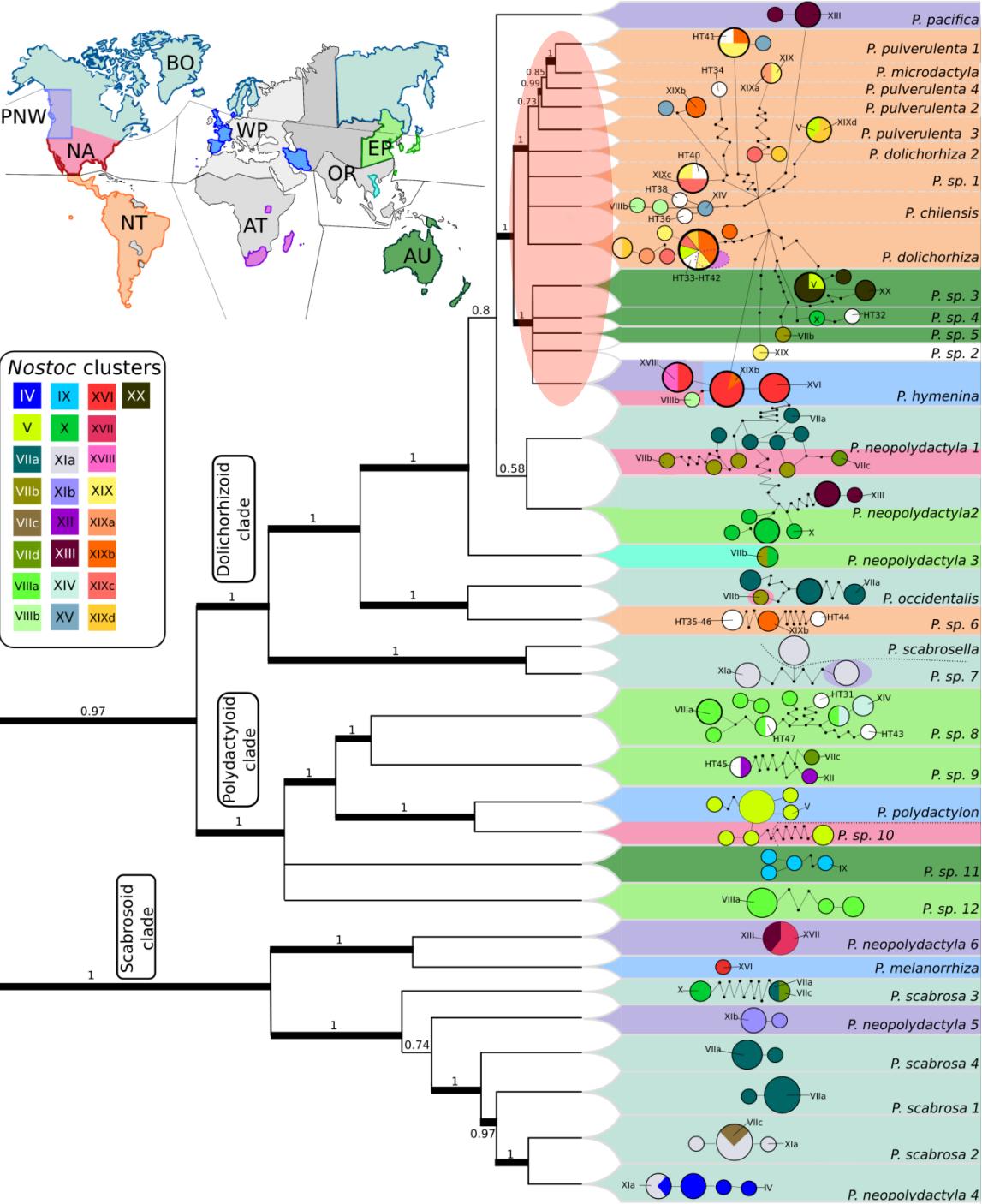
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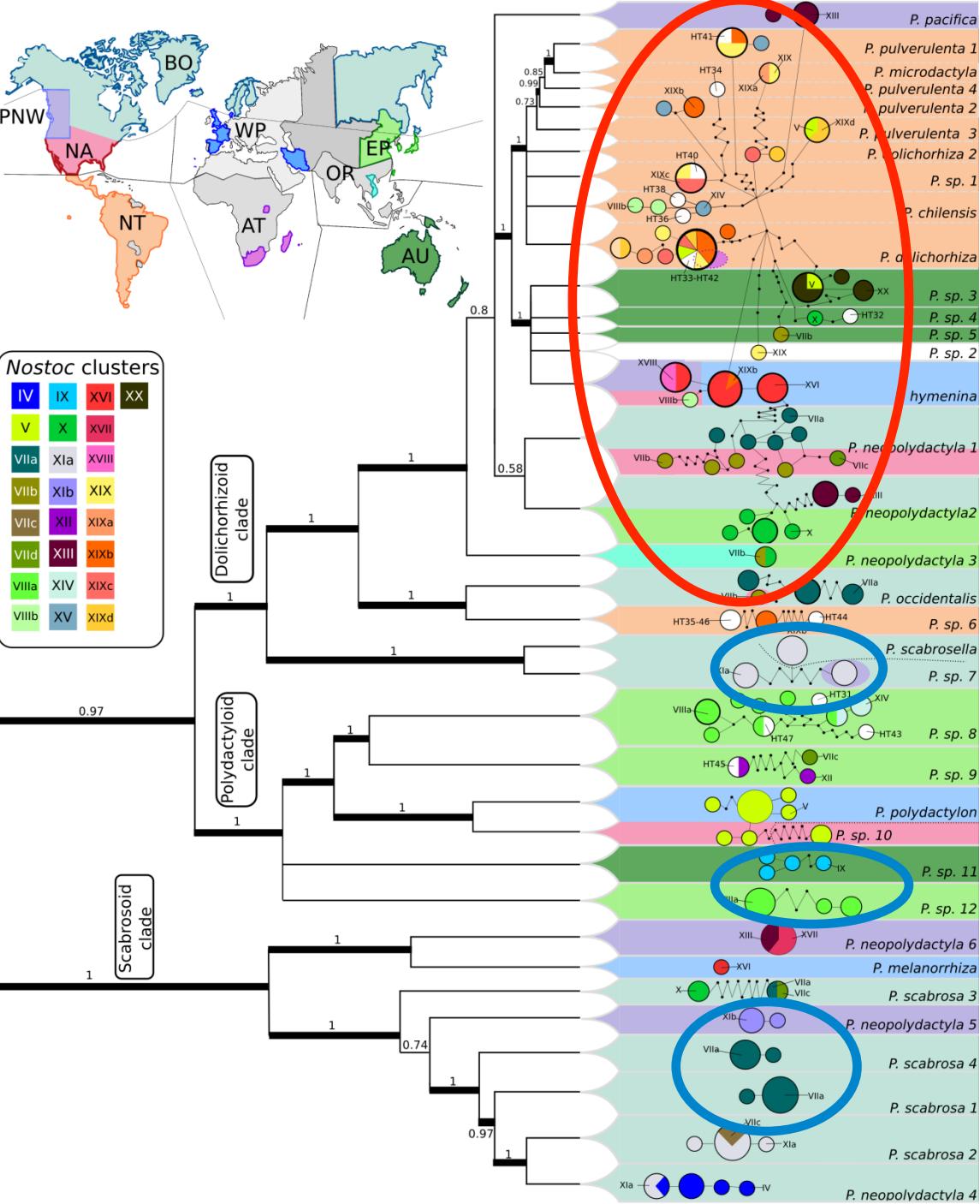
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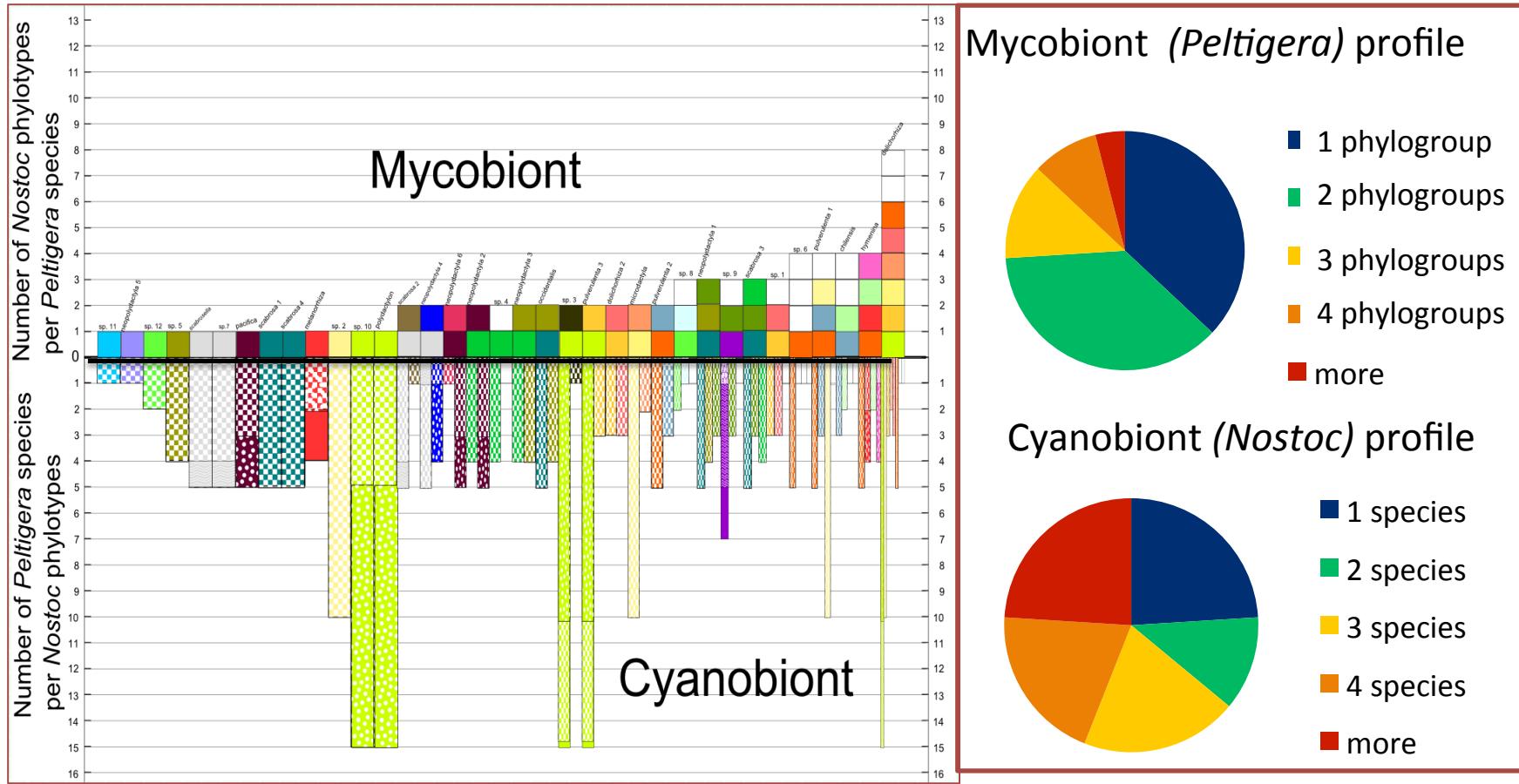


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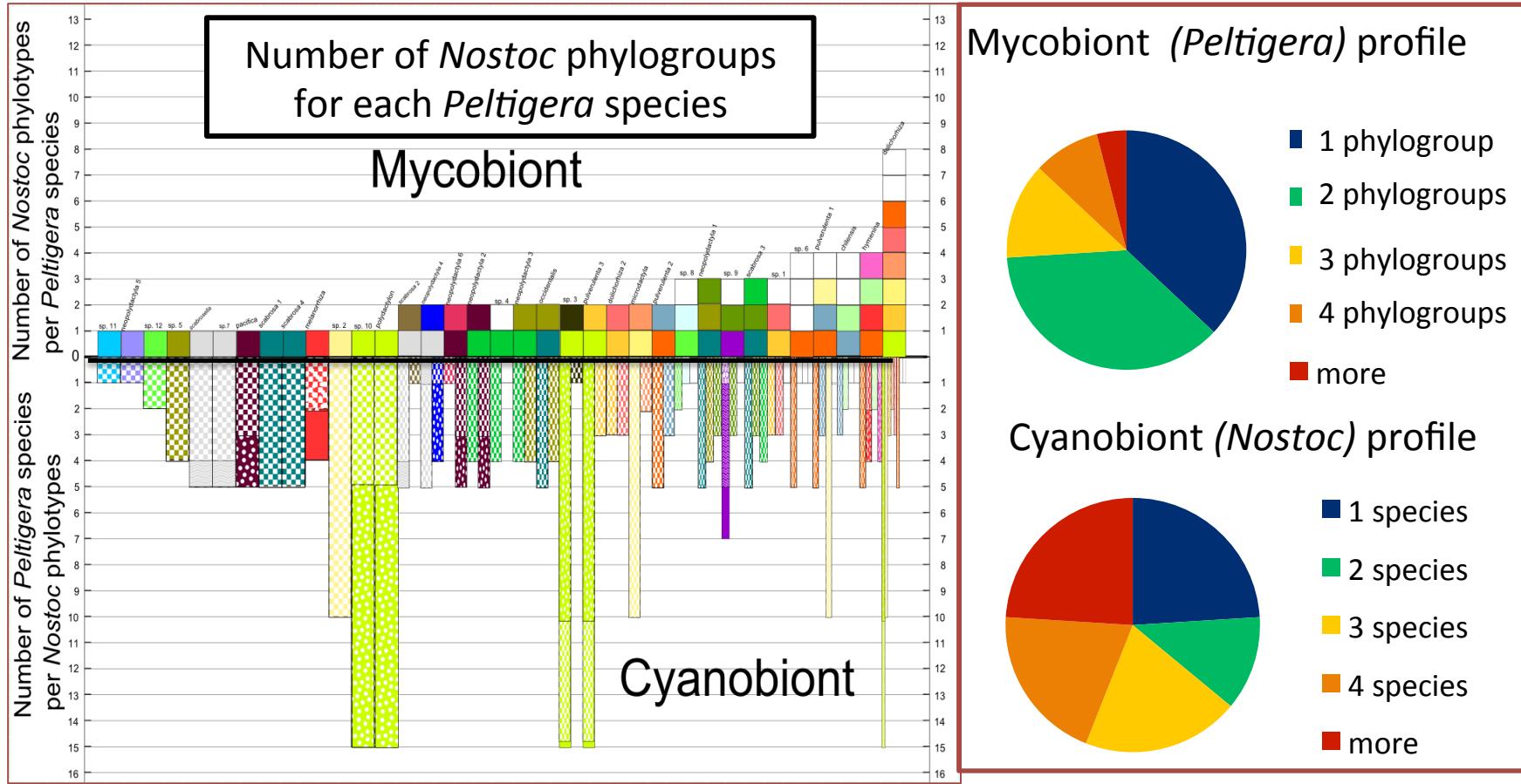


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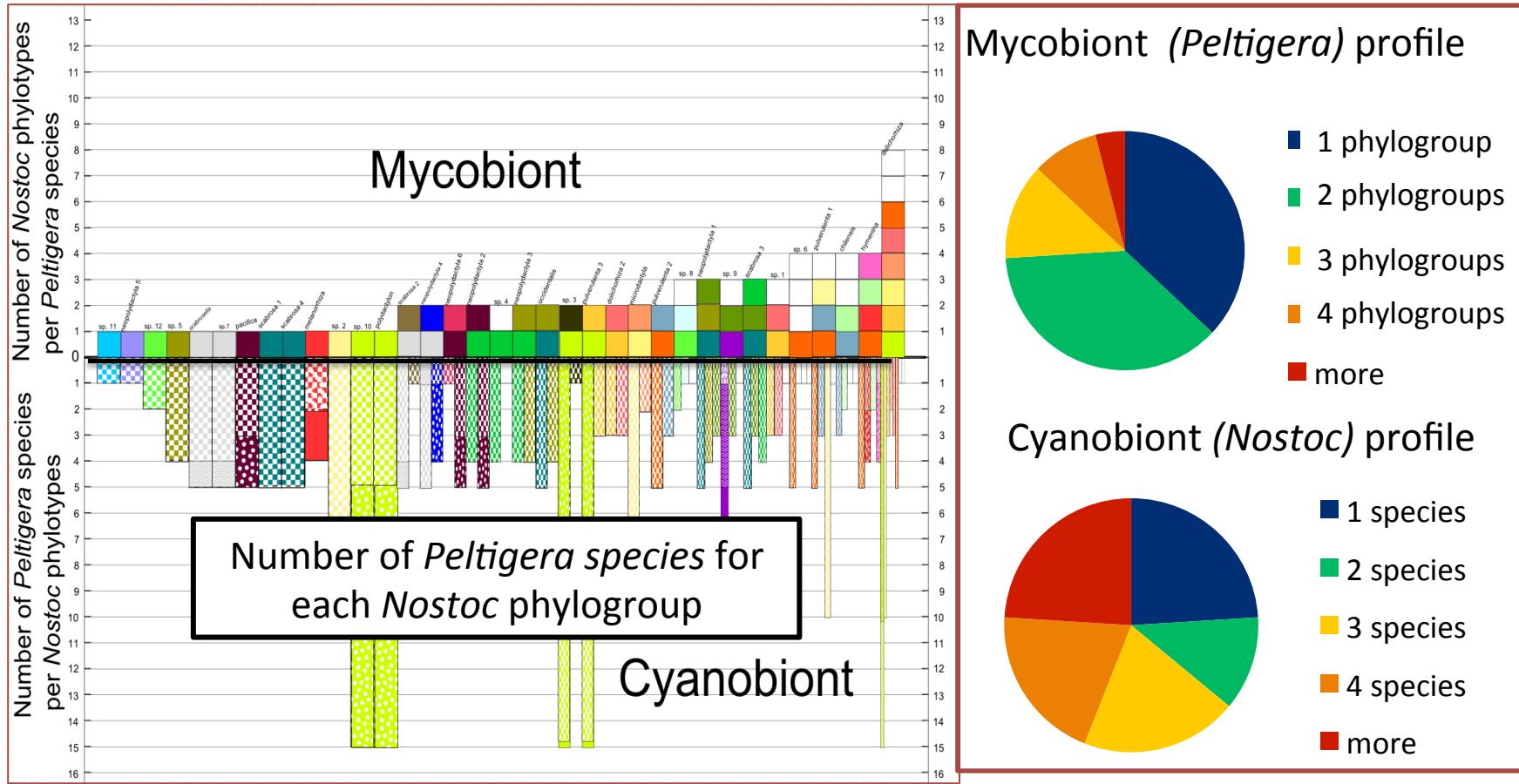
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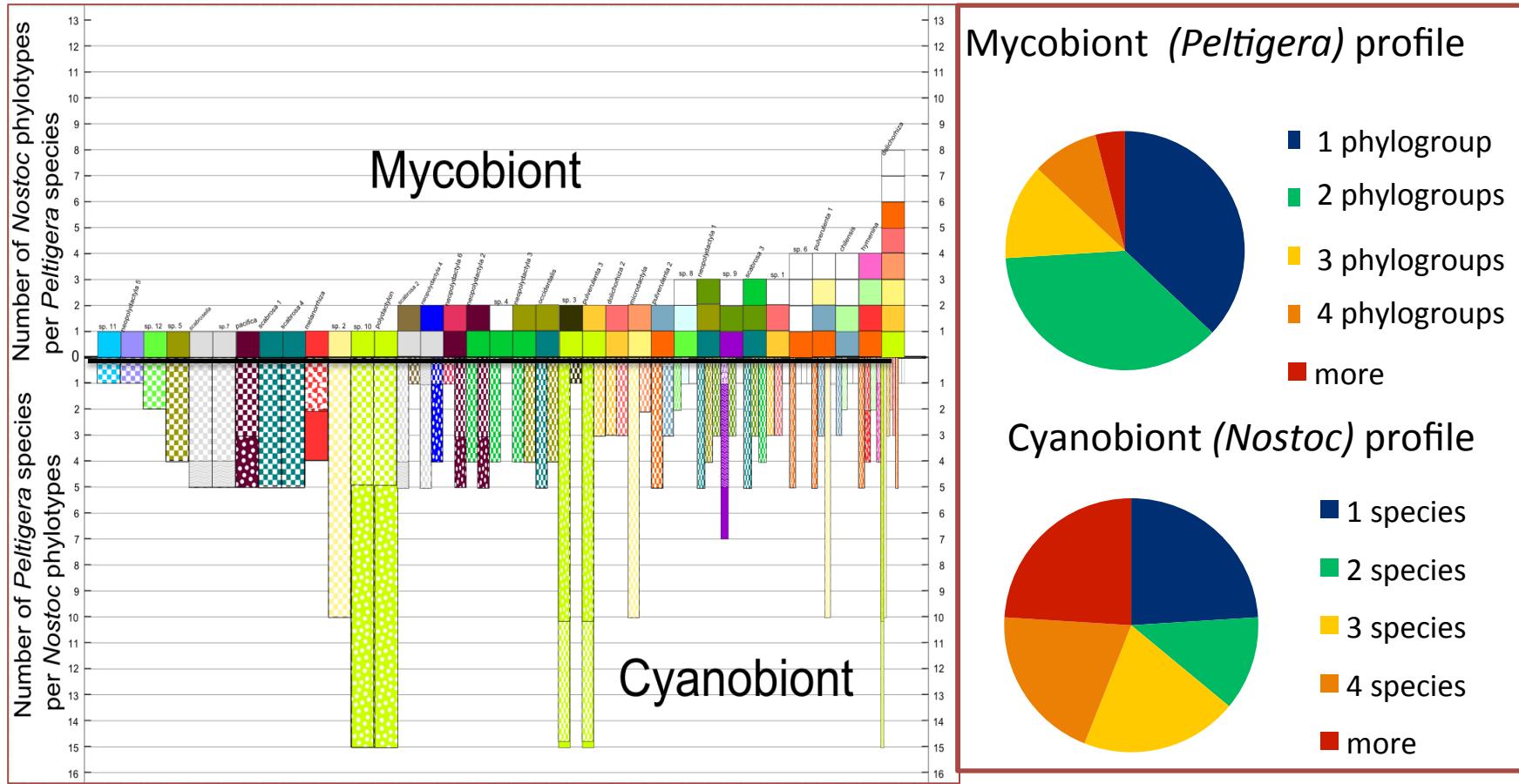
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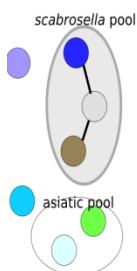
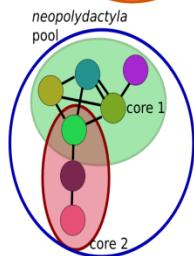
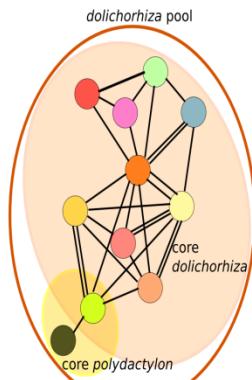
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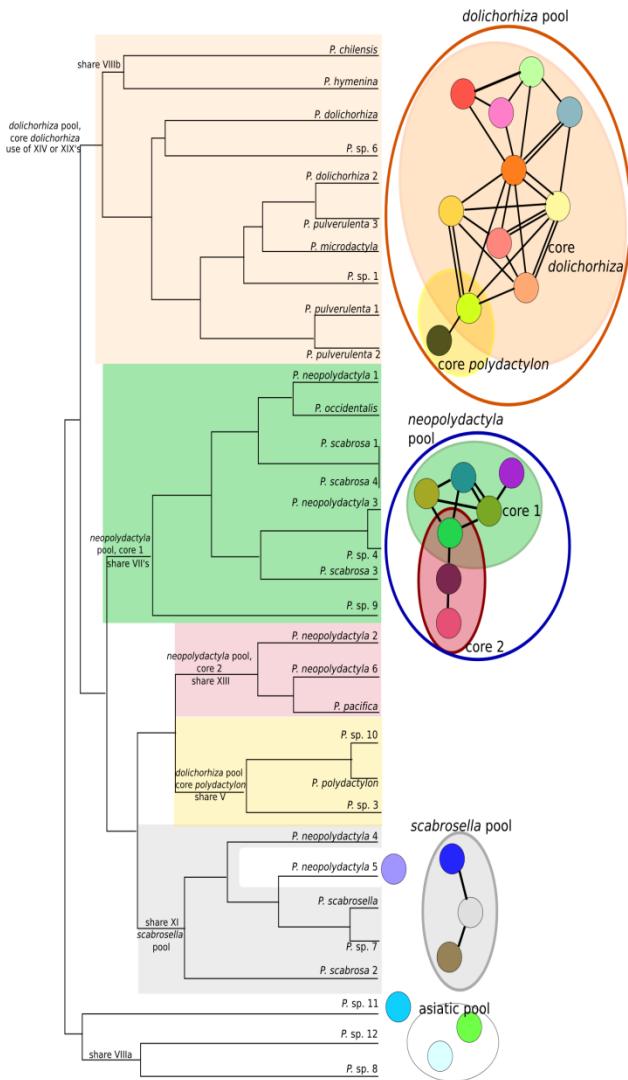
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## 3a. Factors associated with specificity



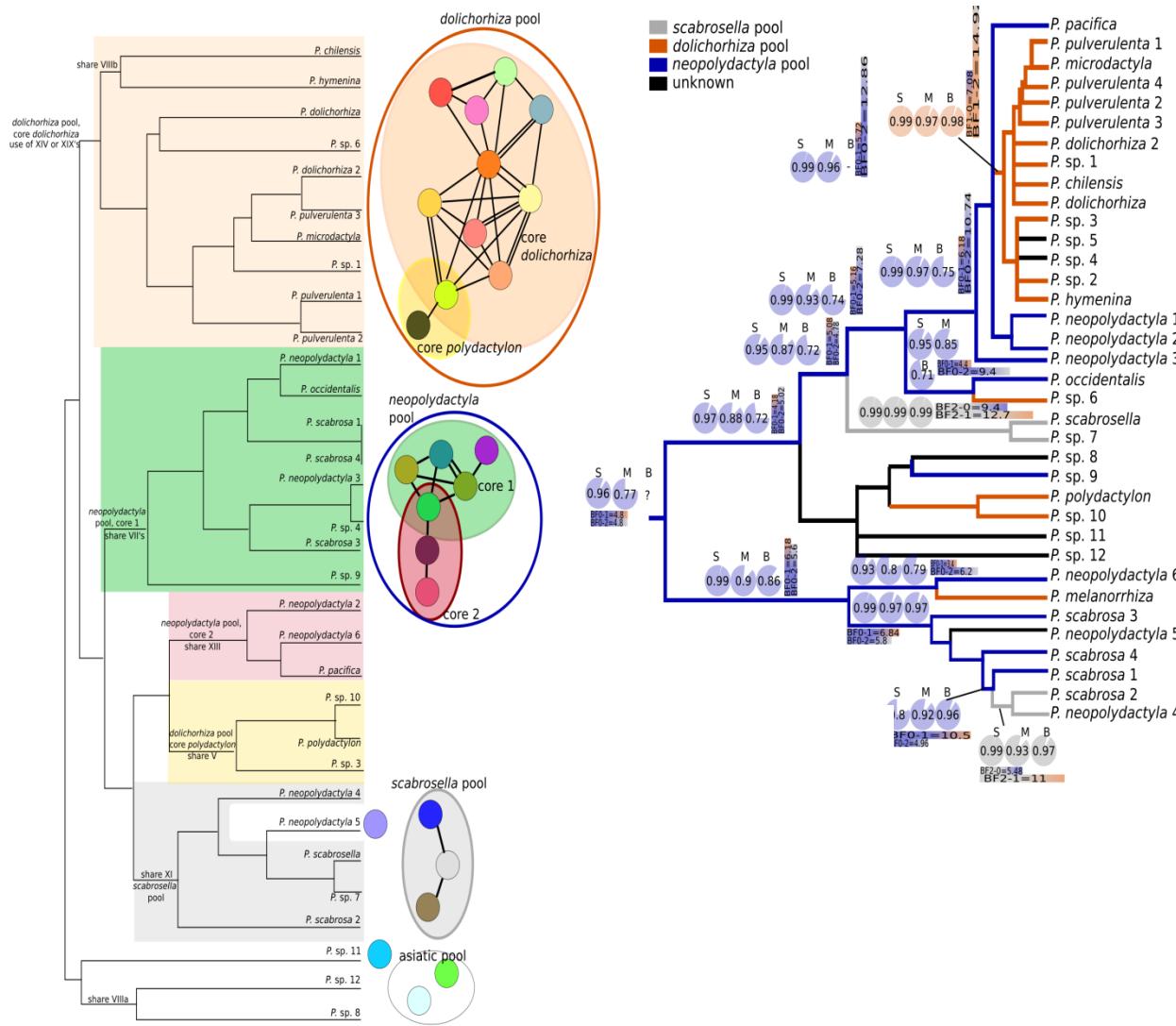
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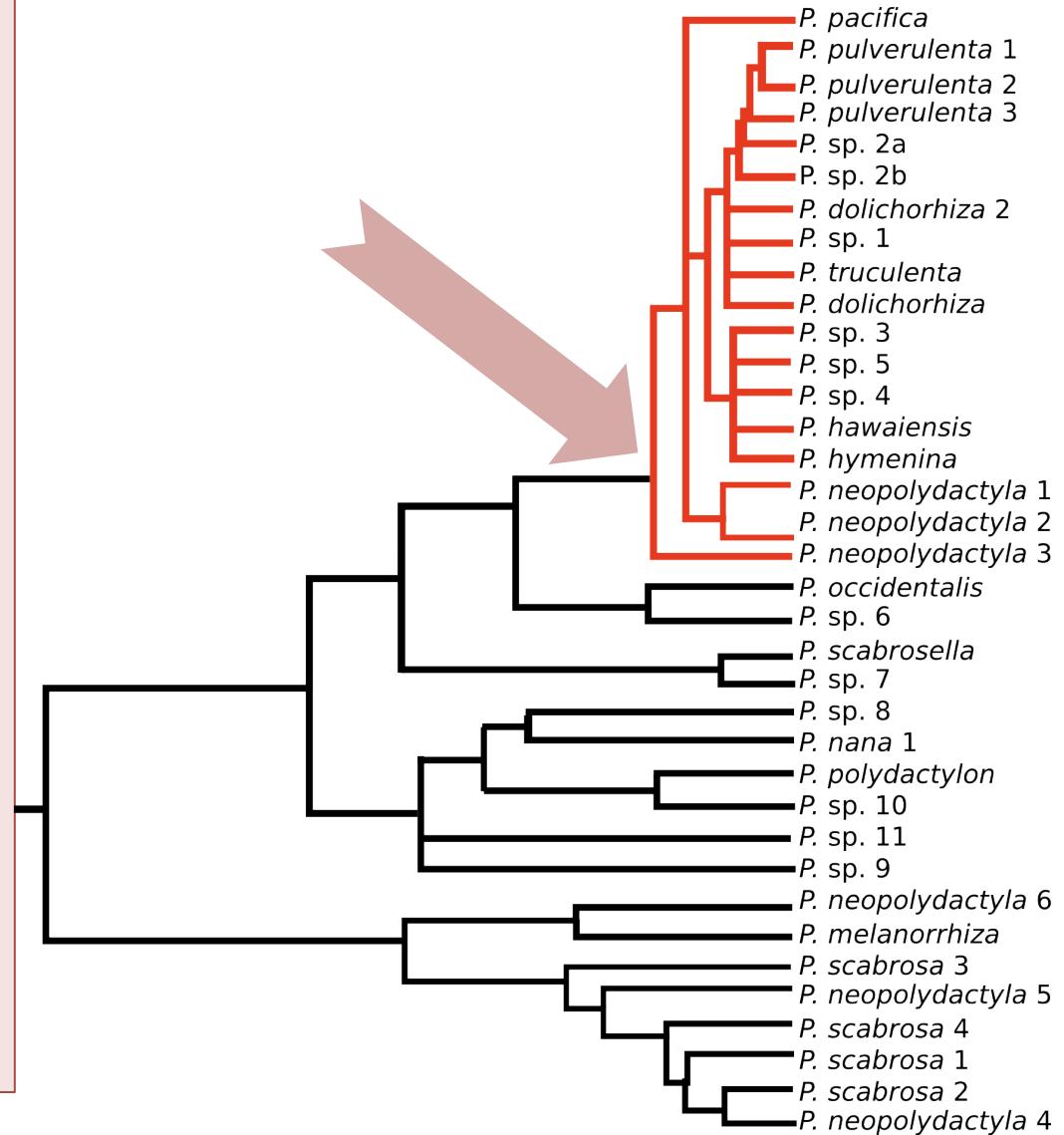
## 3b. Impact of specialization on speciation rate

- 1) BiSSE: comparing specialists (1 *Nostoc* phylogroup only) and non-specialists *Peltigera* species:
  - a) speciation rates significantly higher in generalists
  - b) switching rate generalist => specialist significantly higher than specialist => generalist

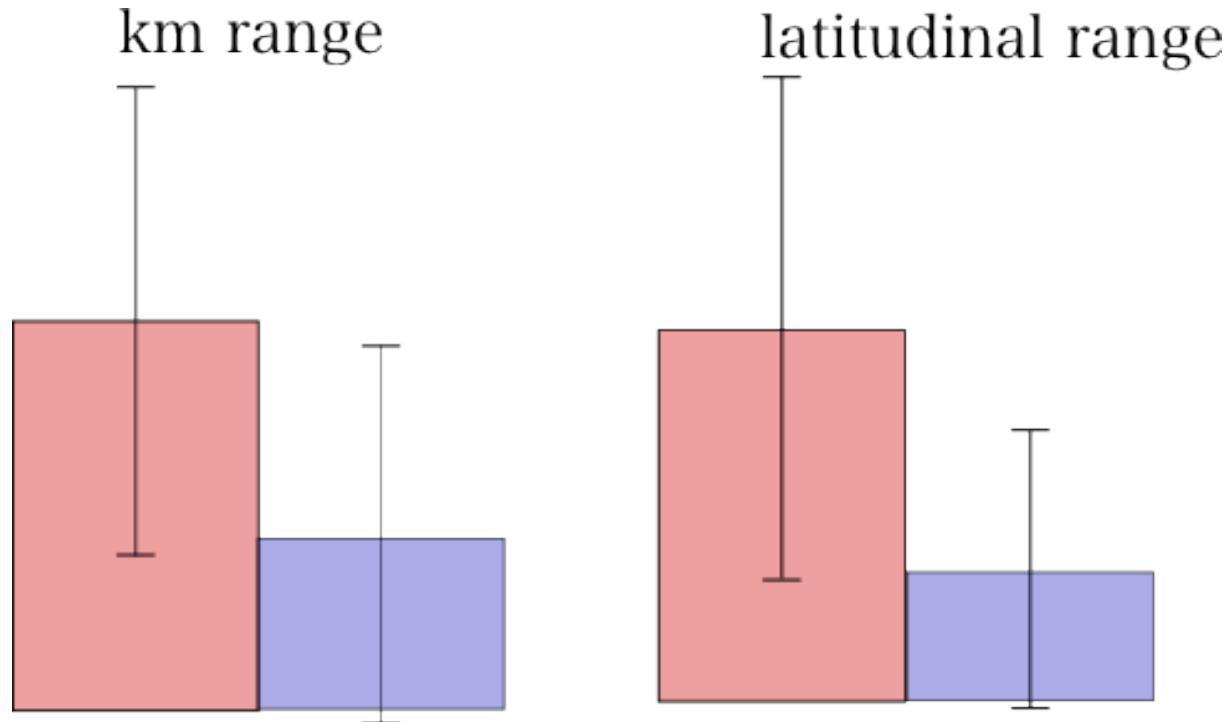
## 3b. Impact of specialization on speciation rate

2) MEDUSA, BAMM:  
significant shift in  
speciation rate at  
the base of the big  
cosmopolitan  
radiation

=> possible link with  
generalism



### 3c. Correlation between specificity and geographical range (mycobiont)

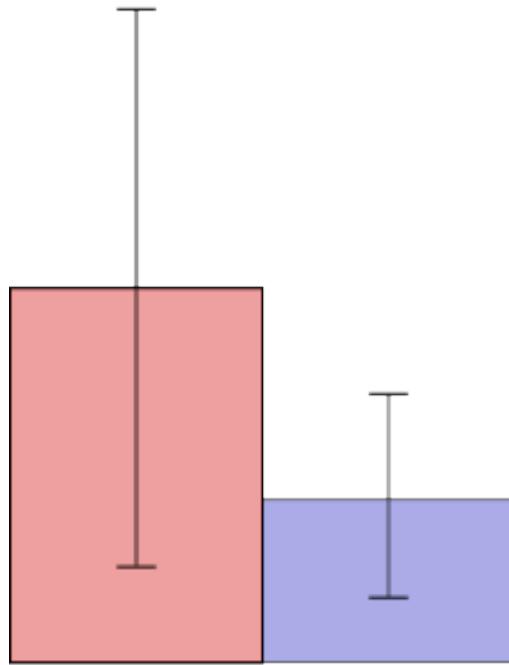


Average range of a non-specialist species: 7720 km and 27.5° of latitude

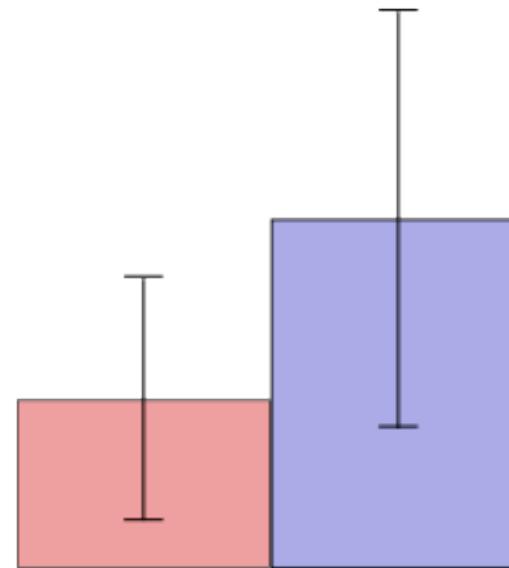
Average range of a specialist species: 3340 km and 8.5° of latitude

### 3d. Genetic diversity and evolution of specificity through time

No. haplo ITS



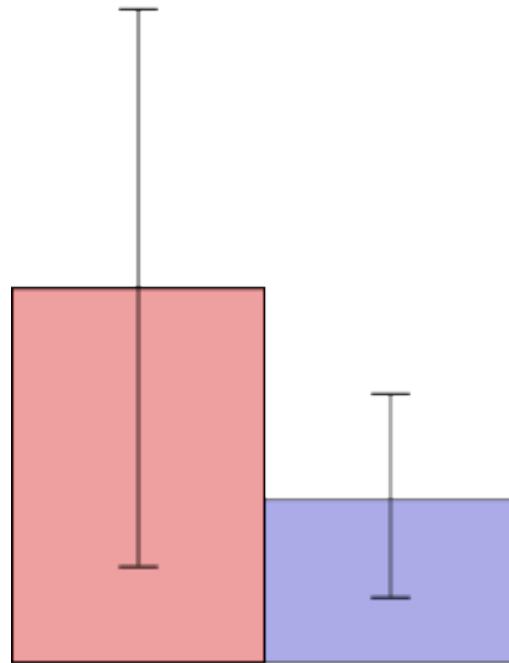
Time



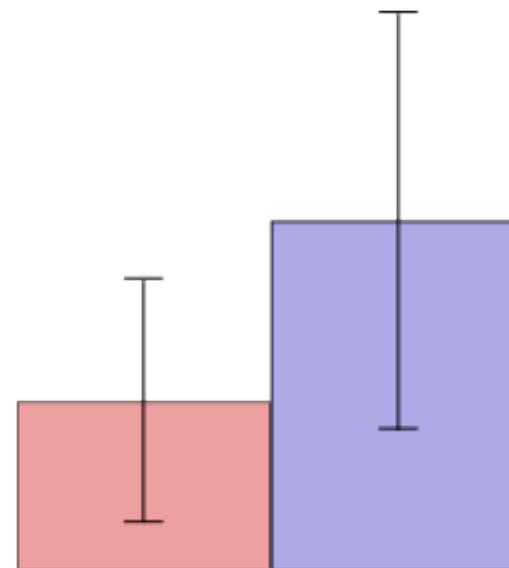
- In average, less genetic variation in specialist (3.2 haplo) vs generalist (7.4) mycobiont species
- Trend of increased specialization with time (specialists on branches in average 2.1 times longer)

# Law & Lewis Paradigm of mutualistic interactions

No. haplo ITS



Time



- Positive selection on the most widespread/best adapted symbiont haplotype
- Reduced diversity as a result of adaptation to a specific symbiont under specific environmental conditions

# Model of evolution of lichen symbiosis

- Recent generalist species can colonize more habitats and have a wider range because they can use several symbionts present in different regions or environments.
- But through time, species can specialize on certain photobionts to optimize the fitness of the symbiosis, resulting in a narrower distribution, and reducing their genetic diversity.
- Specializing on different photobionts in different places might lead to isolation, divergence and speciation.
- Expanding to new environments might restore a more generalist selection of *Nostoc*.
- Mycobiont switching to a different *Nostoc* phylogroup might expand the geographical range of the species and eventually lead to speciation.

# Species delimitation in *Peltigera* section *Polydactylon*: Aims of the study

- See if cosmopolitan units are actual species or assemblages of distinct lineages
- Test three very variable new loci: IGS1, IGS3 and IGS16
- Compare 5 methods on two very different clades: Scabrosoid and Dolichorhizoid
- See if geography and the identity of the photobiont can help identifying species

# Species concepts and phylogeny

- **General lineage species concept**

”a separately evolving metapopulation lineage” (De Queiroz 1998)

# Species concepts and phylogeny

- **General lineage species concept**
- Morphological species concept  
individuals belong to a same species if they share diagnostic morphological characters

# Species concepts and phylogeny

- **General lineage species concept**
- Morphological species concept
- Biological species concept

“groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr 1940)

# Species concepts and phylogeny

- **General lineage species concept**
- Morphological species concept
- Biological species concept
- **Phylogenetic species concept**

“a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind” (Eldredge and Cracraft 1980)

=> monophyly

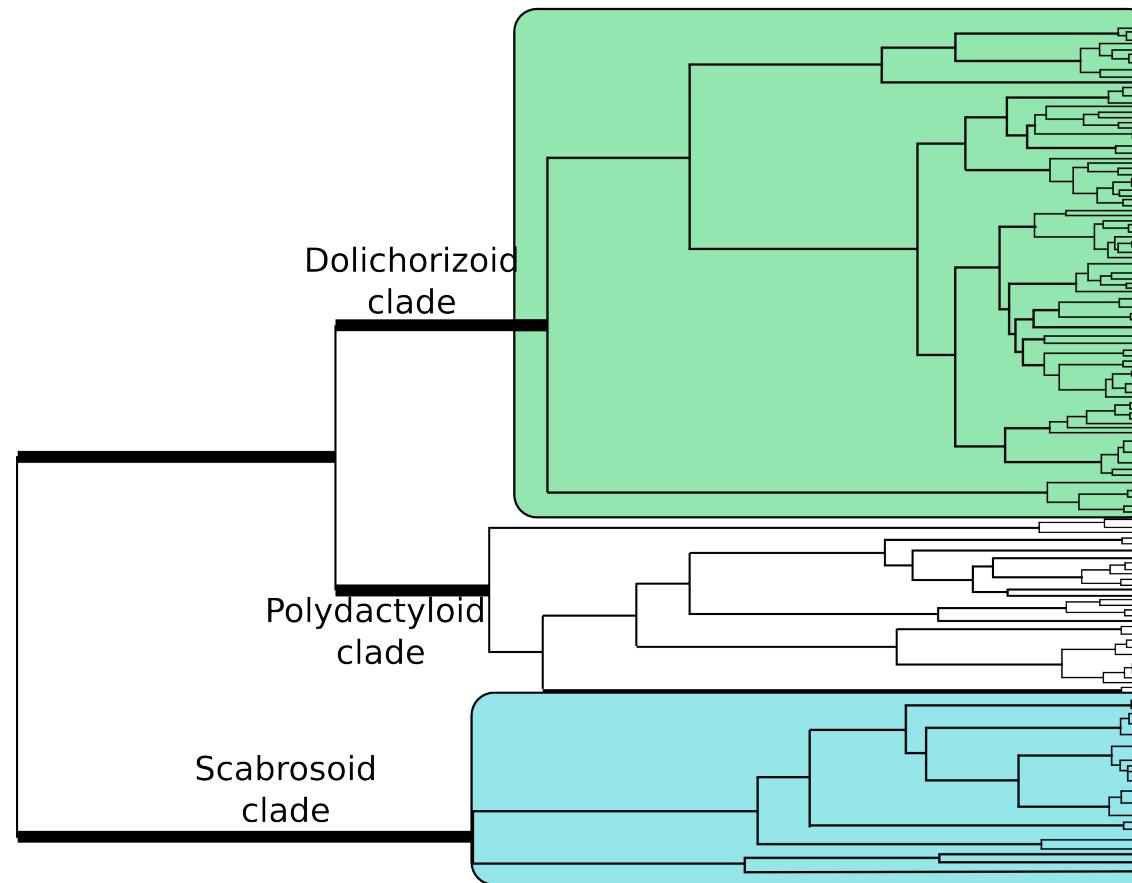
# Species concepts and phylogeny

- **General lineage species concept**
- Morphological species concept
- Biological species concept
- **Phylogenetic species concept**
- **Genealogic species concept**

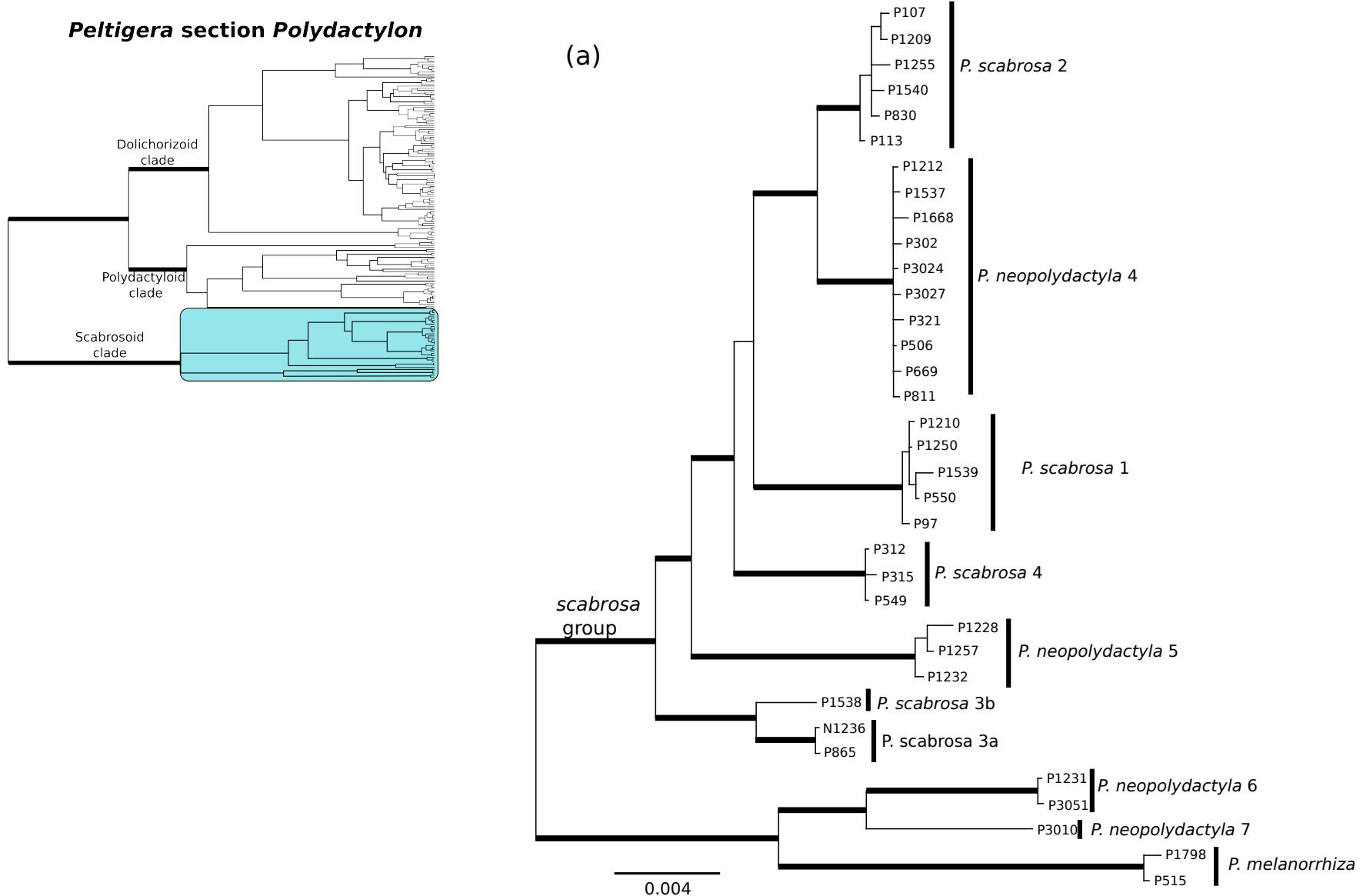
“basal group of organisms whose members are all more closely related to each other than they are to any organisms outside the group” (Hudson and Coyne 2002)

# Species delimitation in Dolichorhizoid and Scabrosoid clades

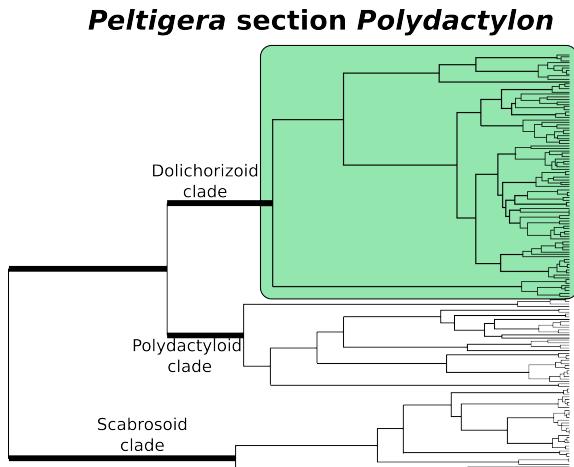
## ***Peltigera* section *Polydactylon***



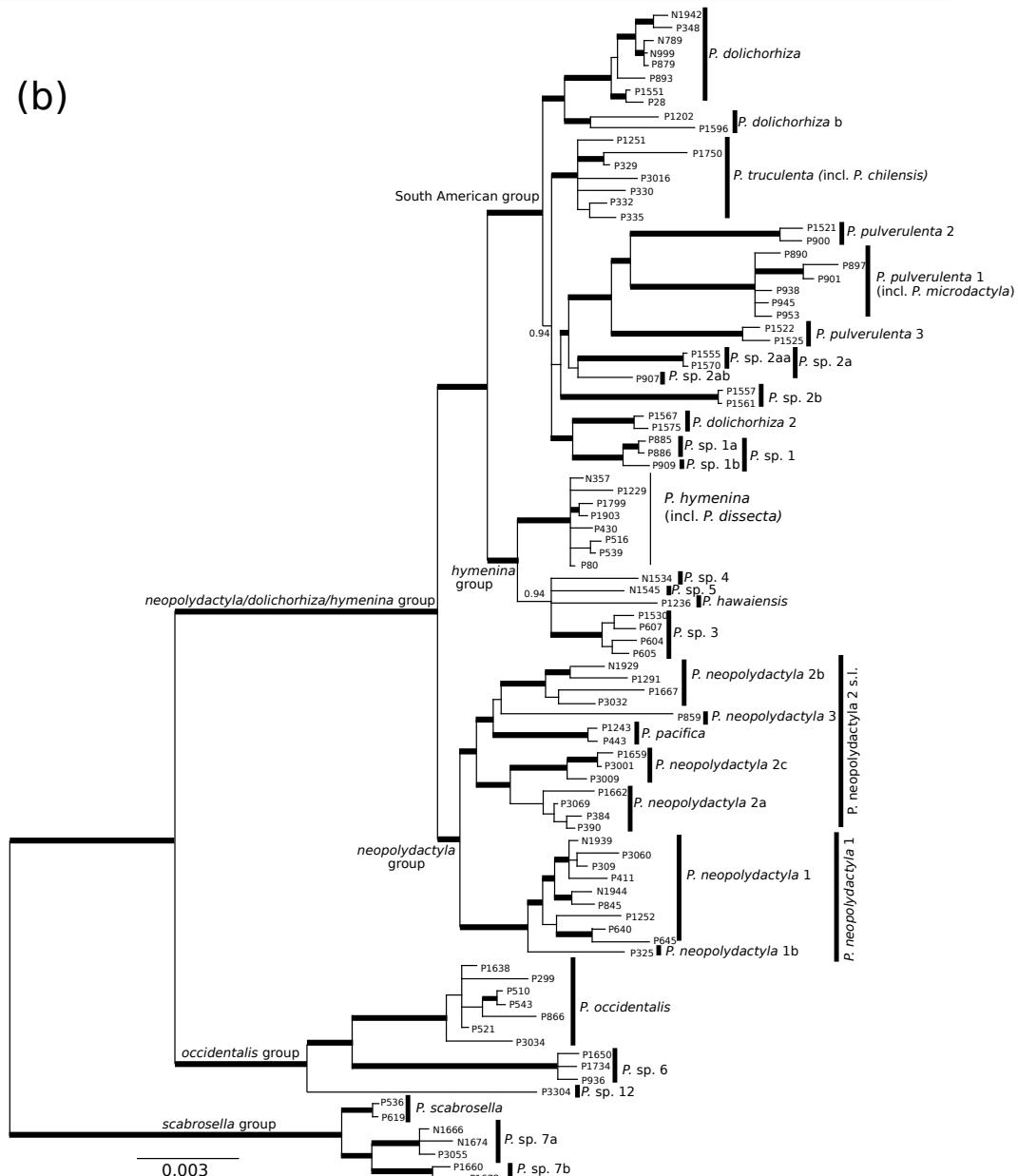
# a. Scabrosoid clade



## b. Dolichorhizoid clade



(b)



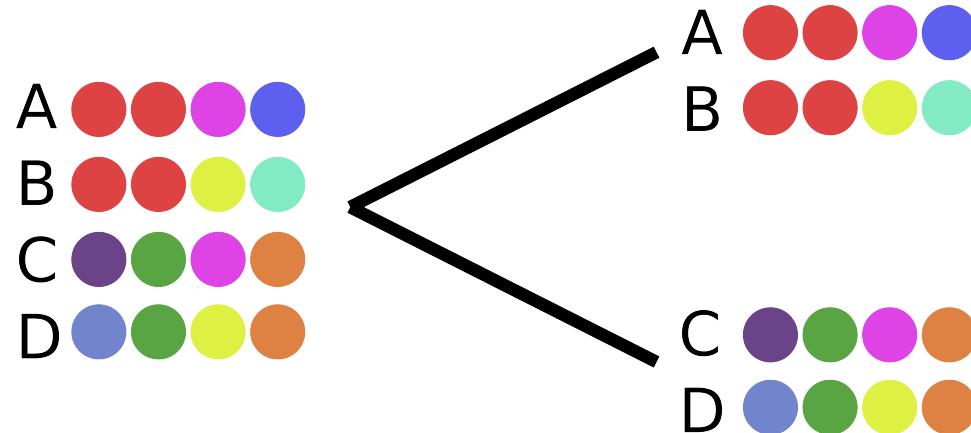
# Species delimitation methods

Allele based		
Structurama		
Tree based		
	Coalescent framework	Substitutions
Find a threshold on trees	bGMYC	bPTP
Fit data from multiple loci	spedeSTEM, BPP	

# Species delimitation methods

## a. Structurama

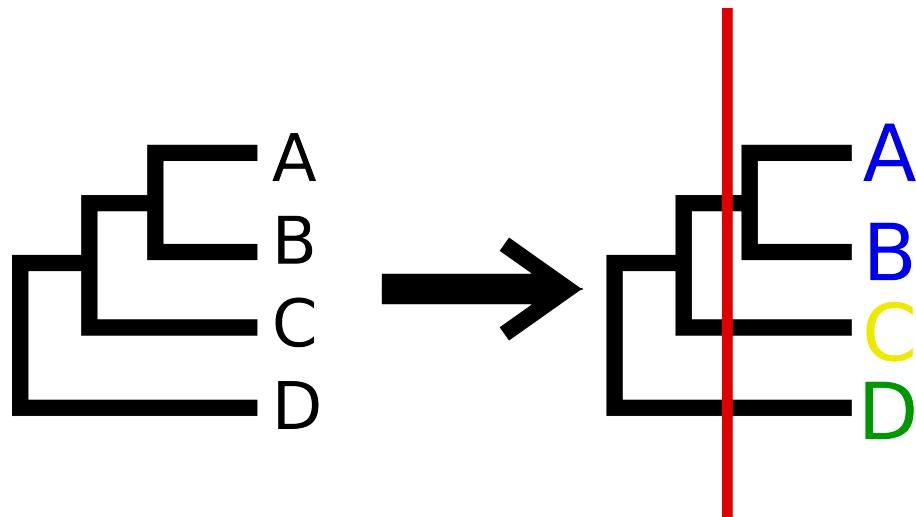
- Assigns samples to clusters to maximize H-W equilibrium and minimize linkage disequilibrium based on set of alleles
- Can estimate the number of clusters



# Species delimitation methods

## b. GMYC

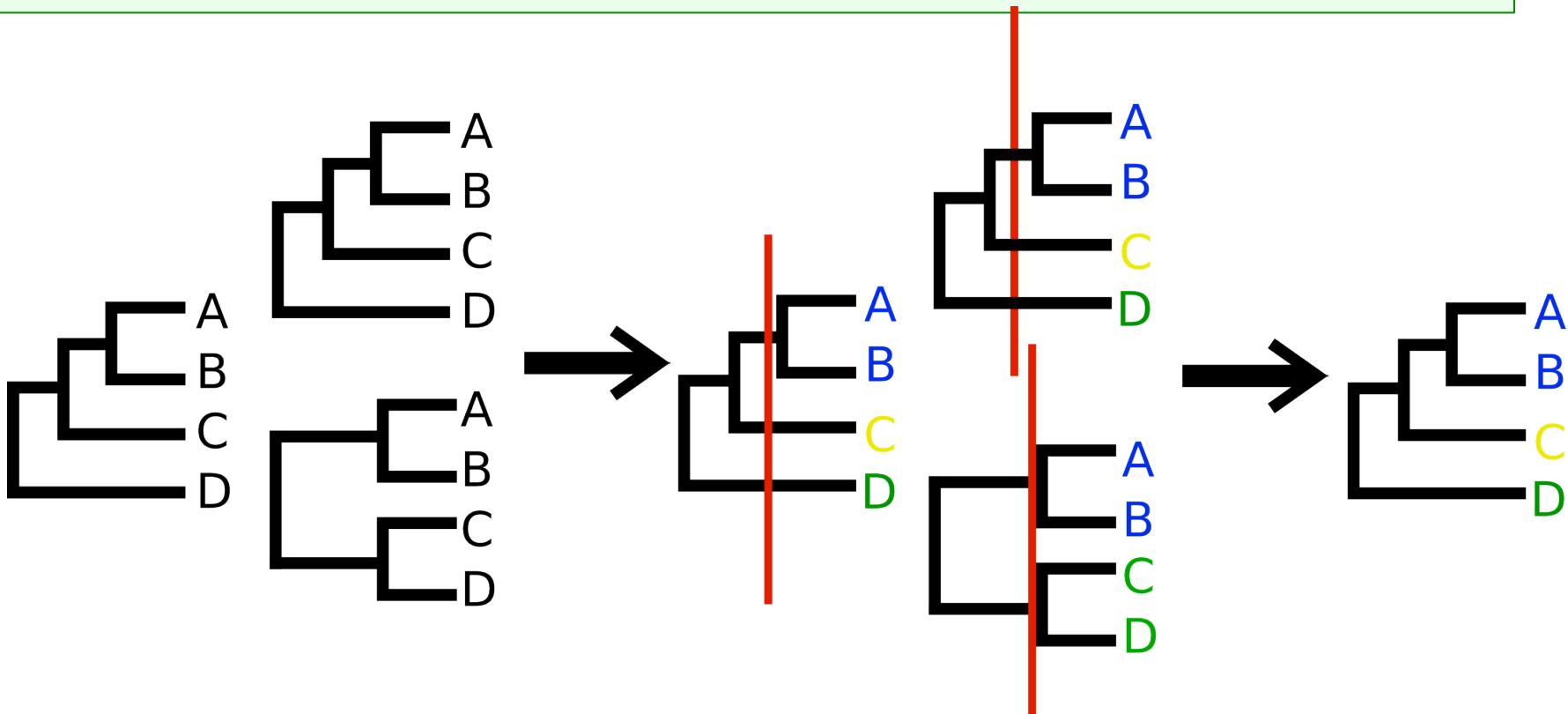
- On ultrametric trees
- Coalescence on single loci
- Searches for a threshold where branching patterns switch from interspecific to intraspecific relationships



# Species delimitation methods

## b. bGMYC

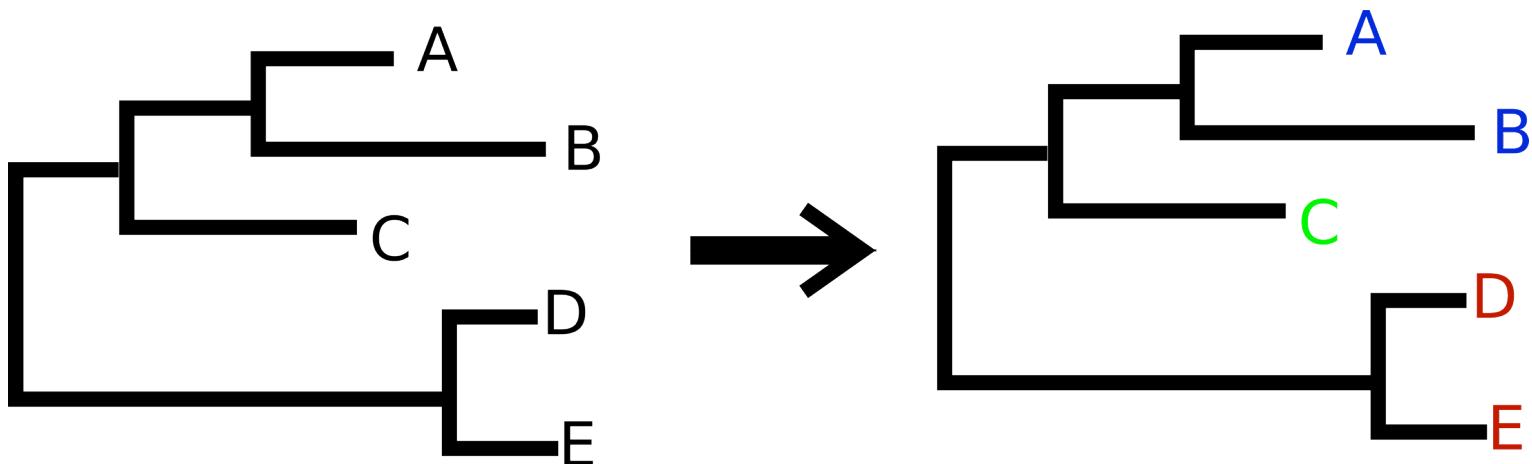
- Bayesian implementation
- Considers a set of trees, takes trees uncertainties into account



# Species delimitation methods

## c. bPTP

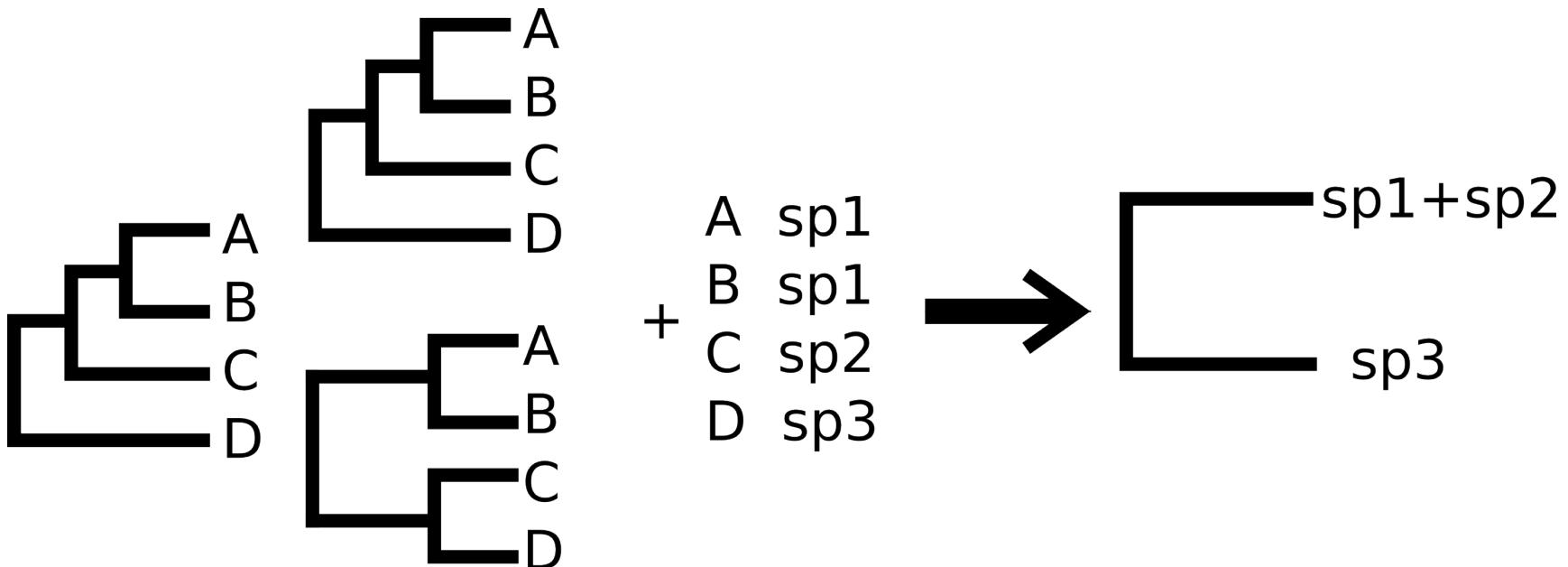
- On phylogenograms
- Based on substitutions instead of time
- Models the average number of substitutions until the next speciation event and the number of substitutions until the next within-species branching event



# Species delimitation methods

## d. spedeSTEM

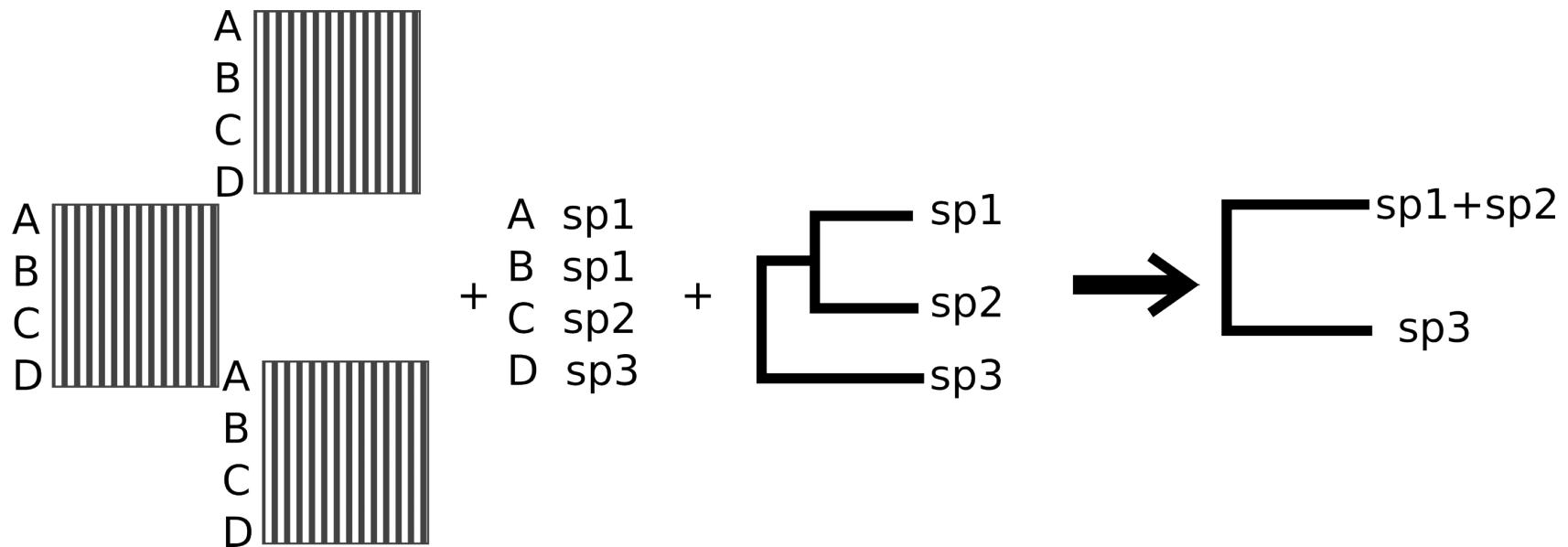
- Takes ultrametric single locus trees and species assignments
- Generate species trees
- Rearrange species to maximize the likelihood of the species tree in a coalescent framework



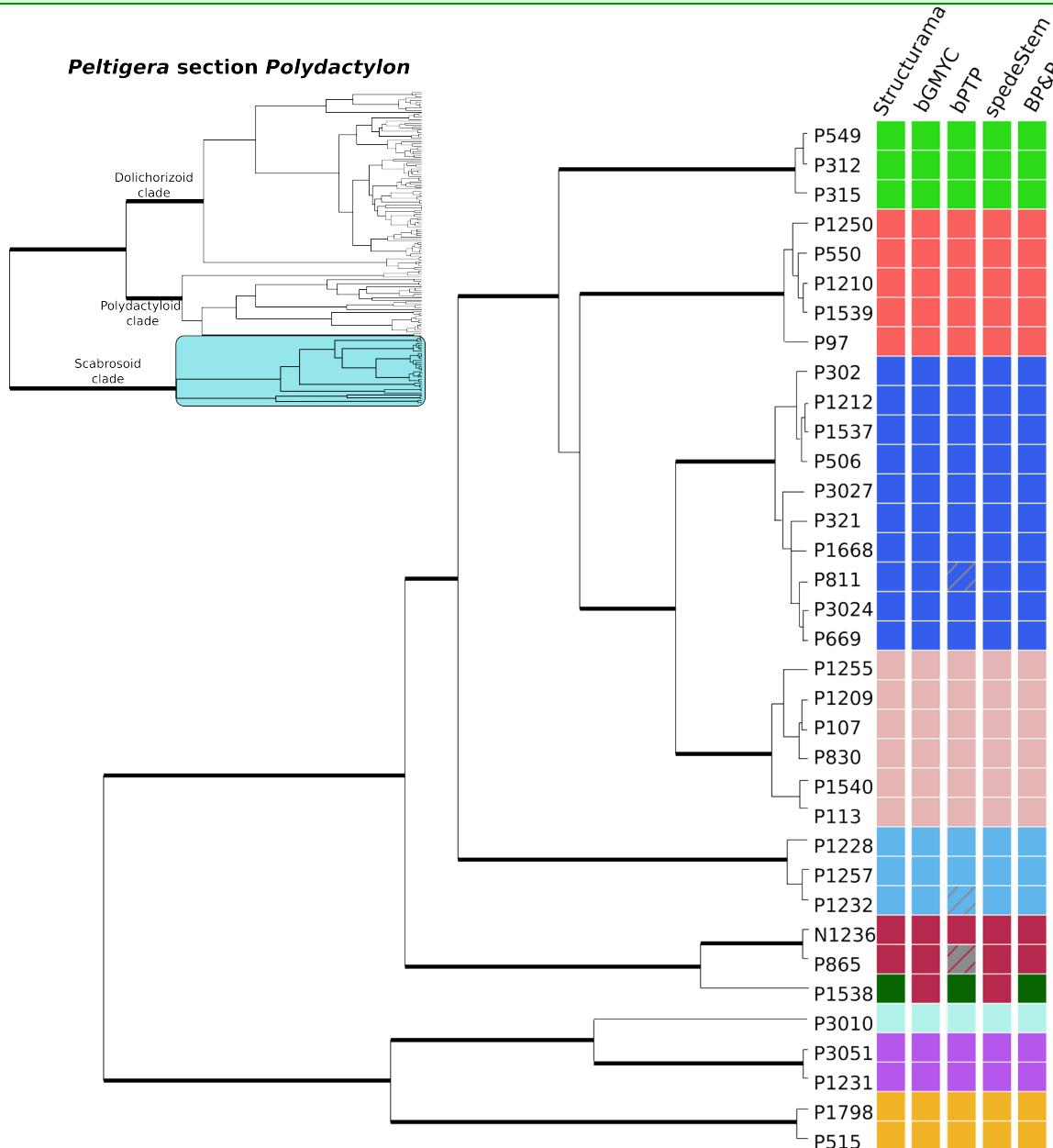
# Species delimitation methods

## e. BPP

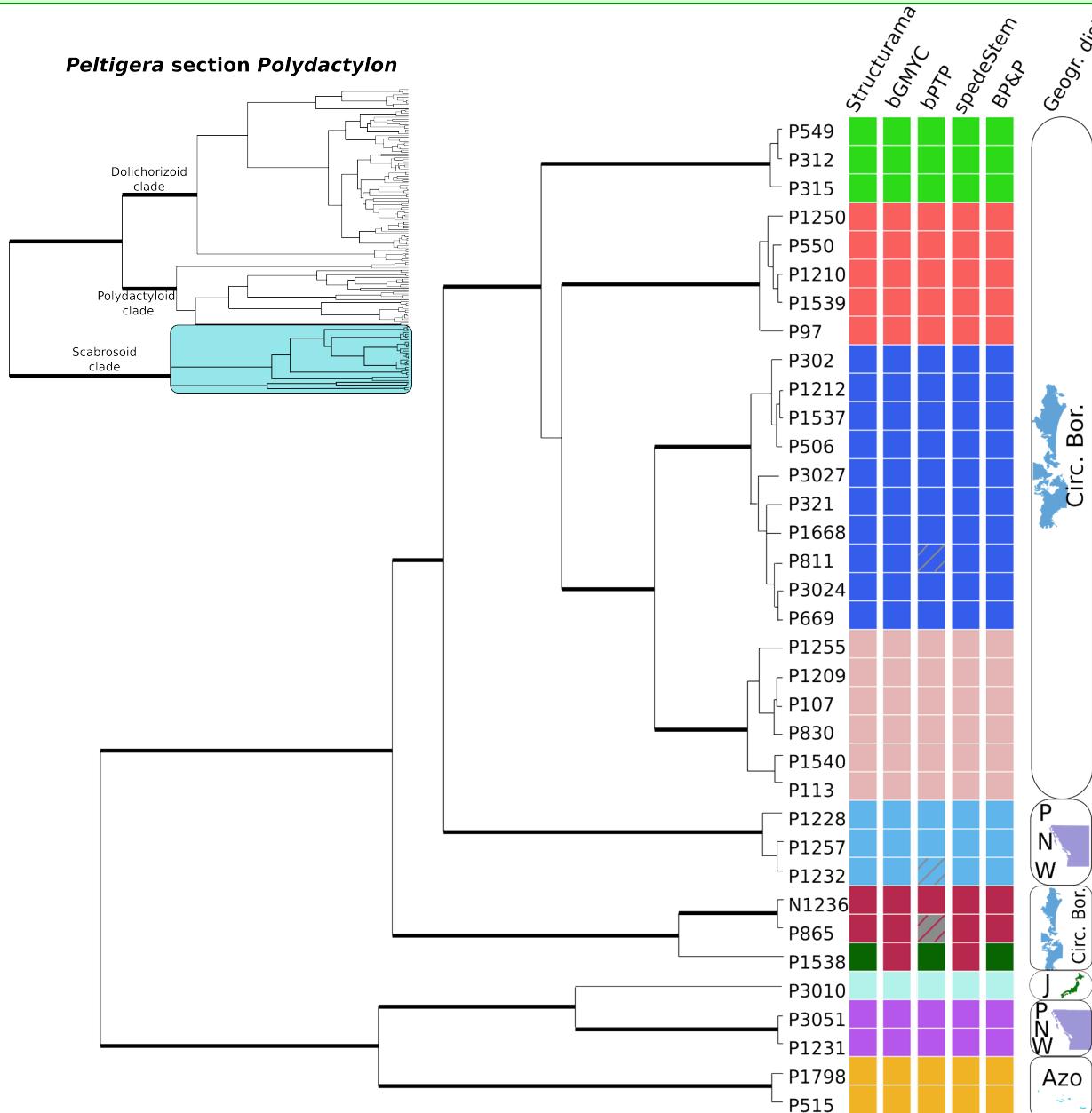
- Takes single loci matrices, species assignment and a species guide tree
- Bayesian implementation, coalescent framework
- Rearrange the species on the guide tree to best fit the data



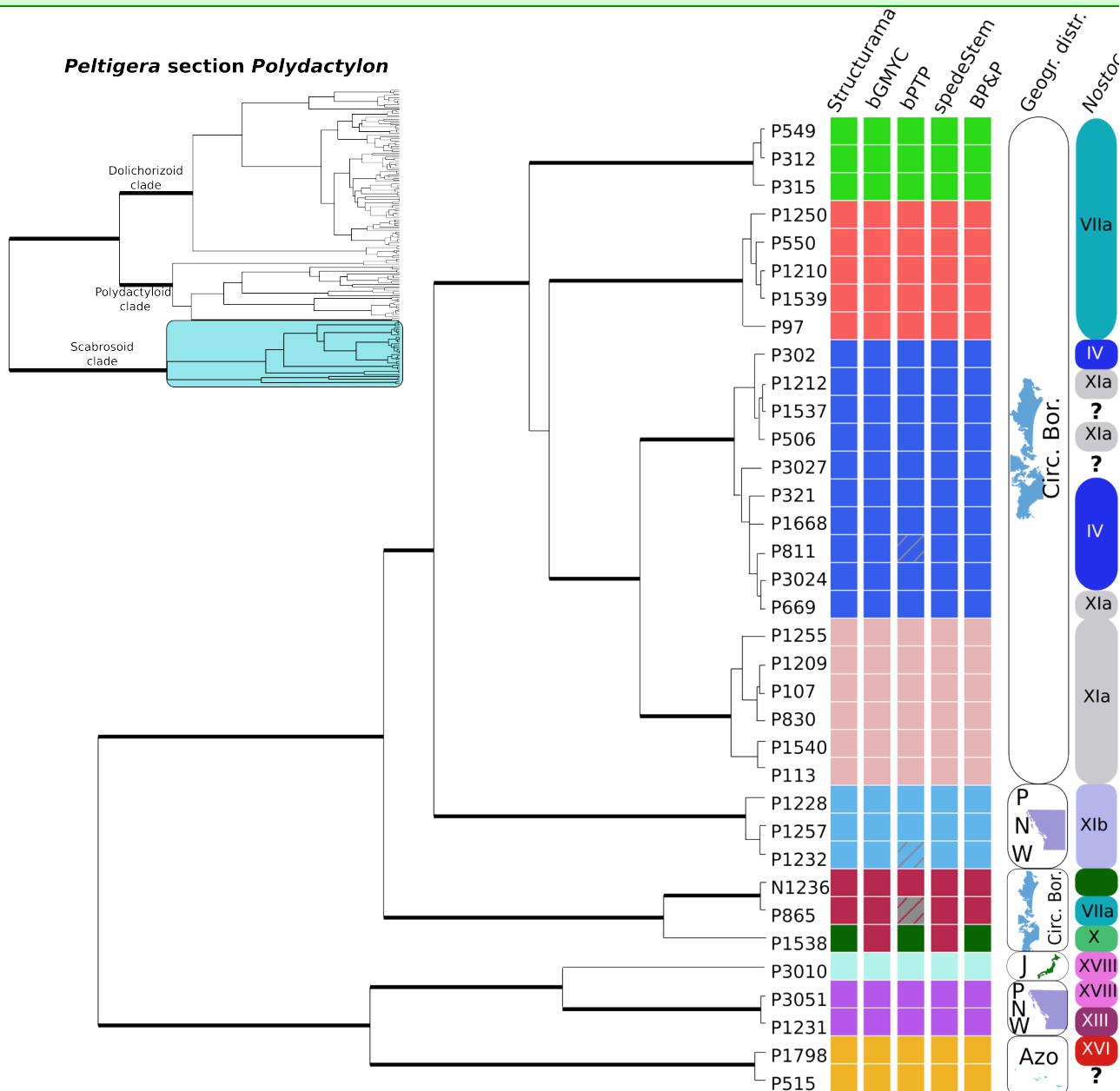
# a. Scabrosoid clade



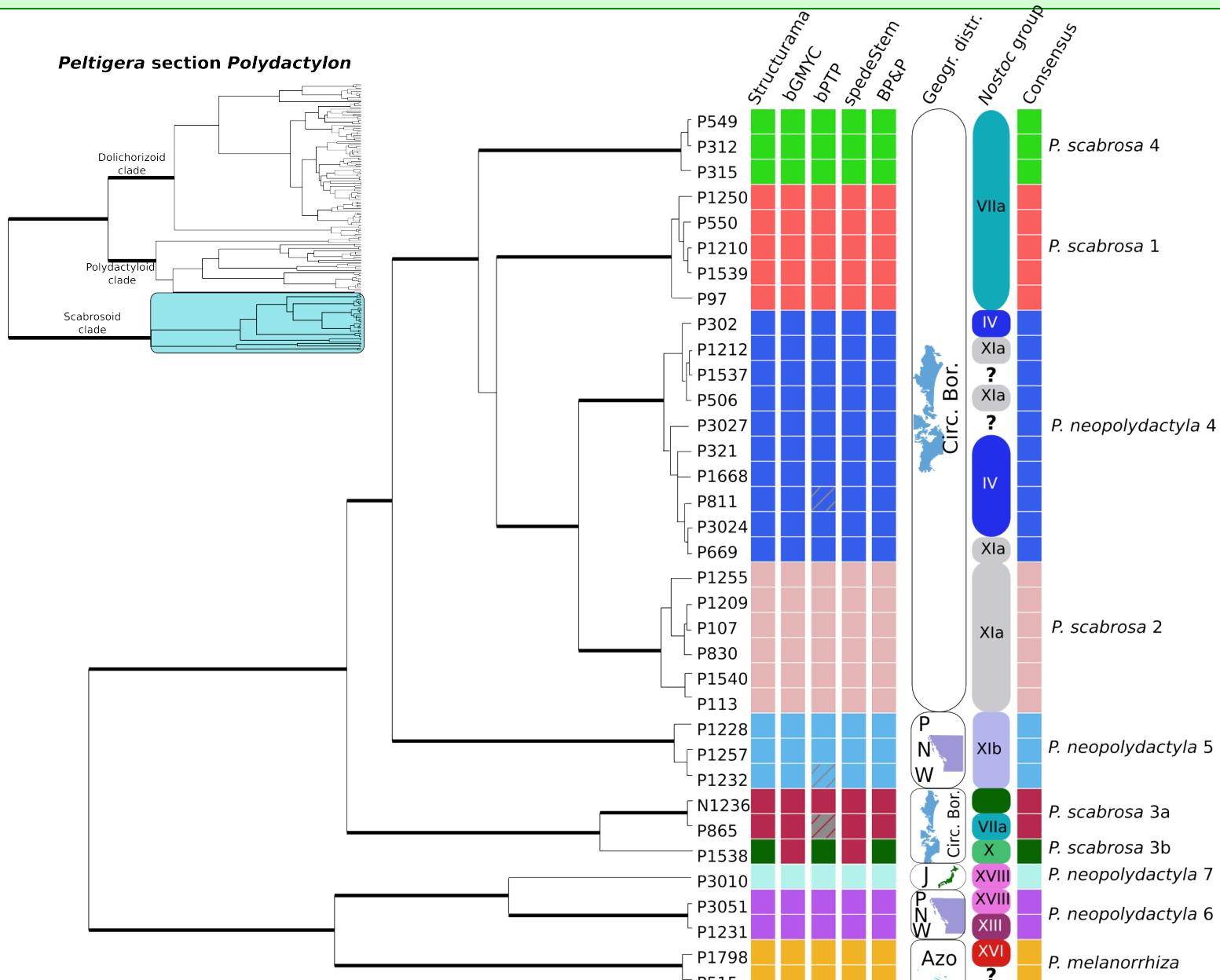
# a. Scabrosoid clade



# a. Scabrosoid clade

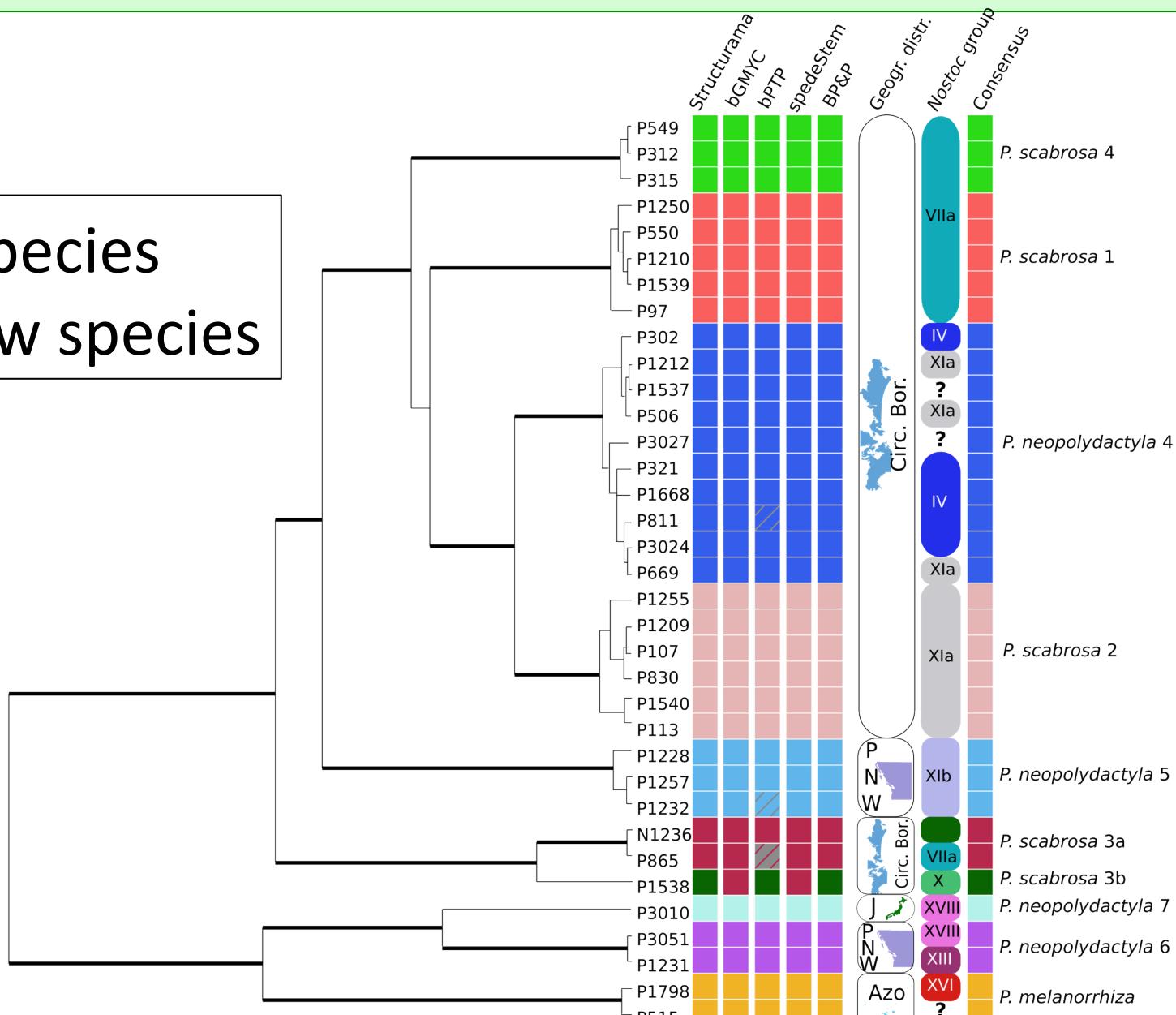


# a. Scabrosoid clade

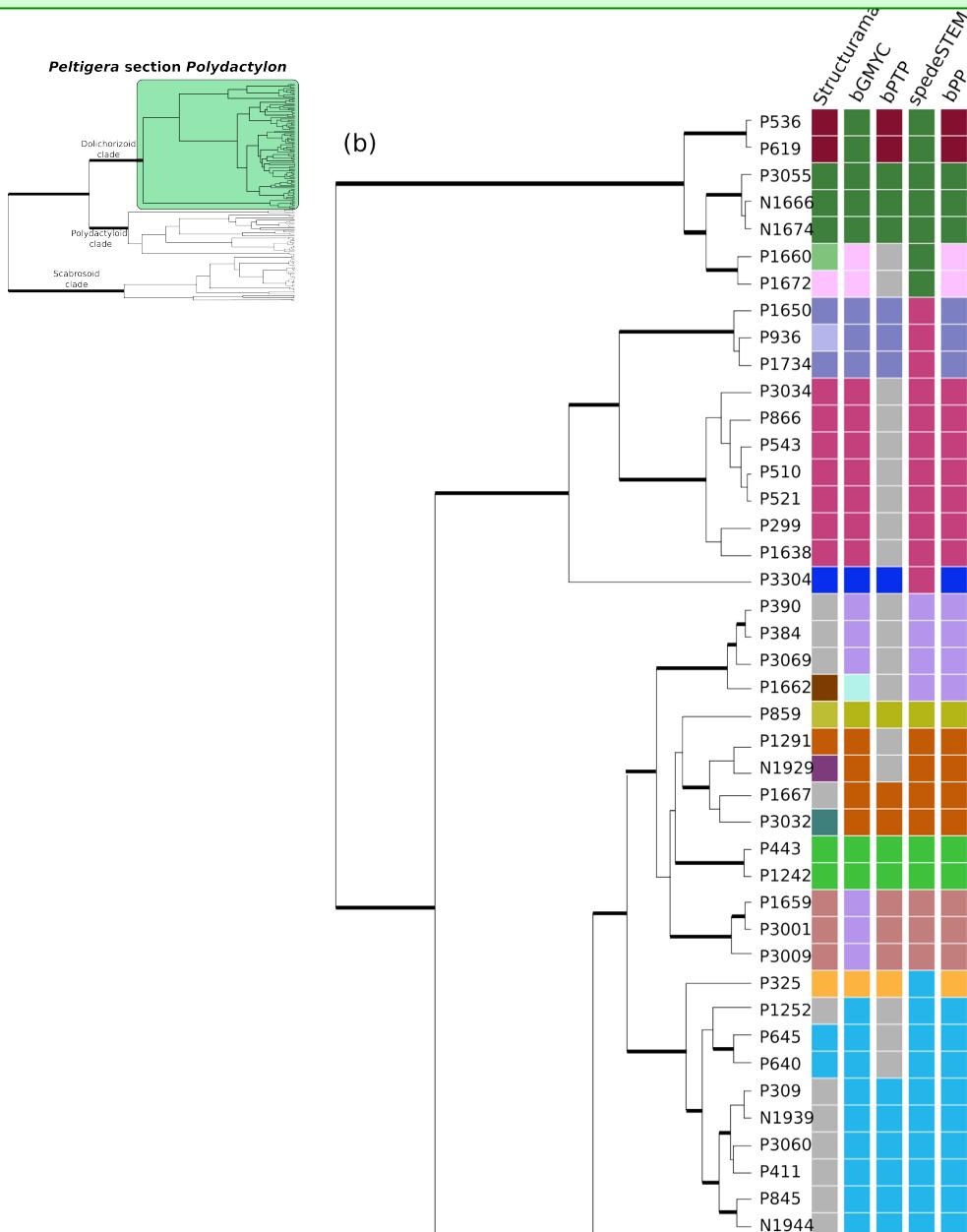


# a. Scabrosoid clade

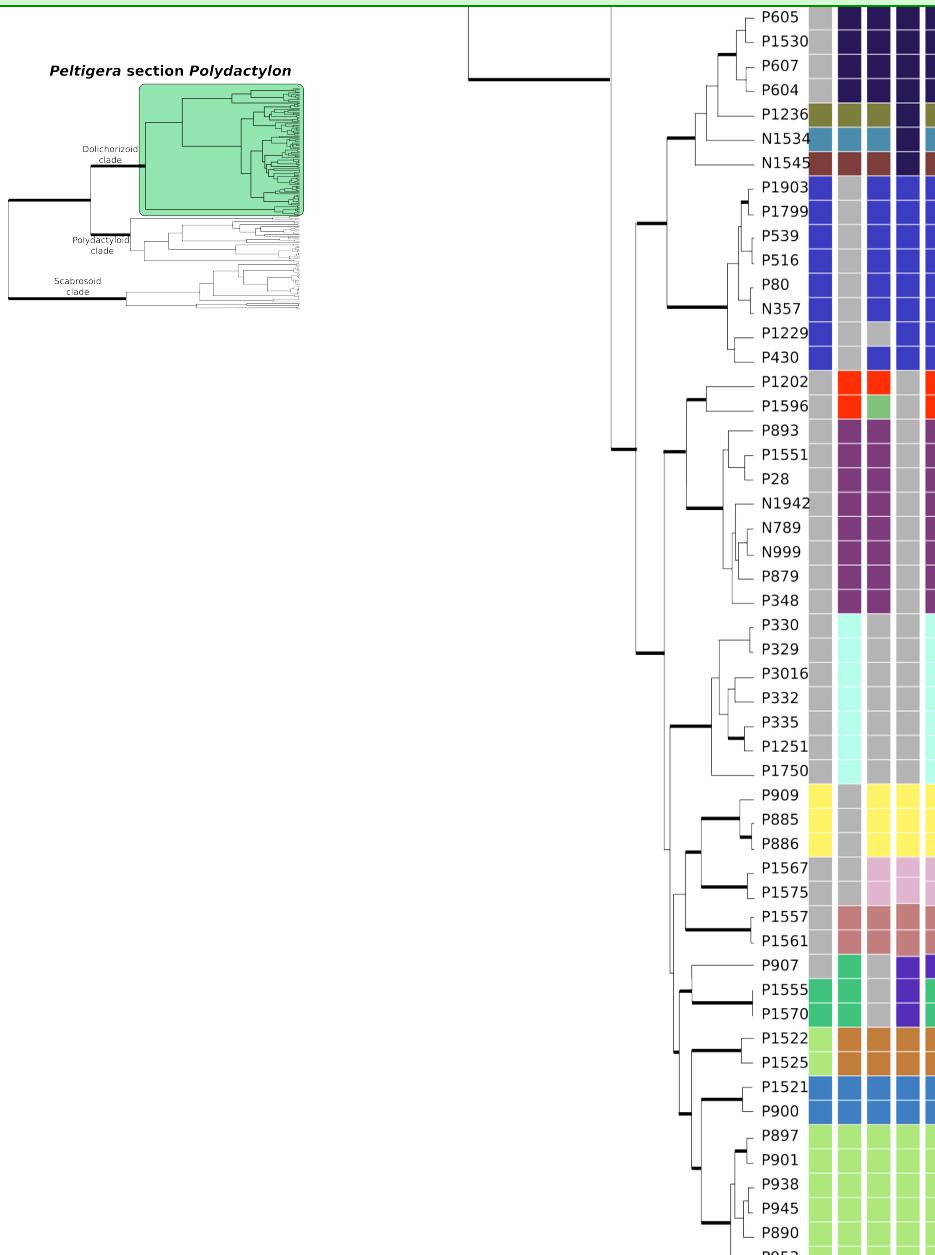
10 species  
7 new species



## b. Dolichorhizoid clade

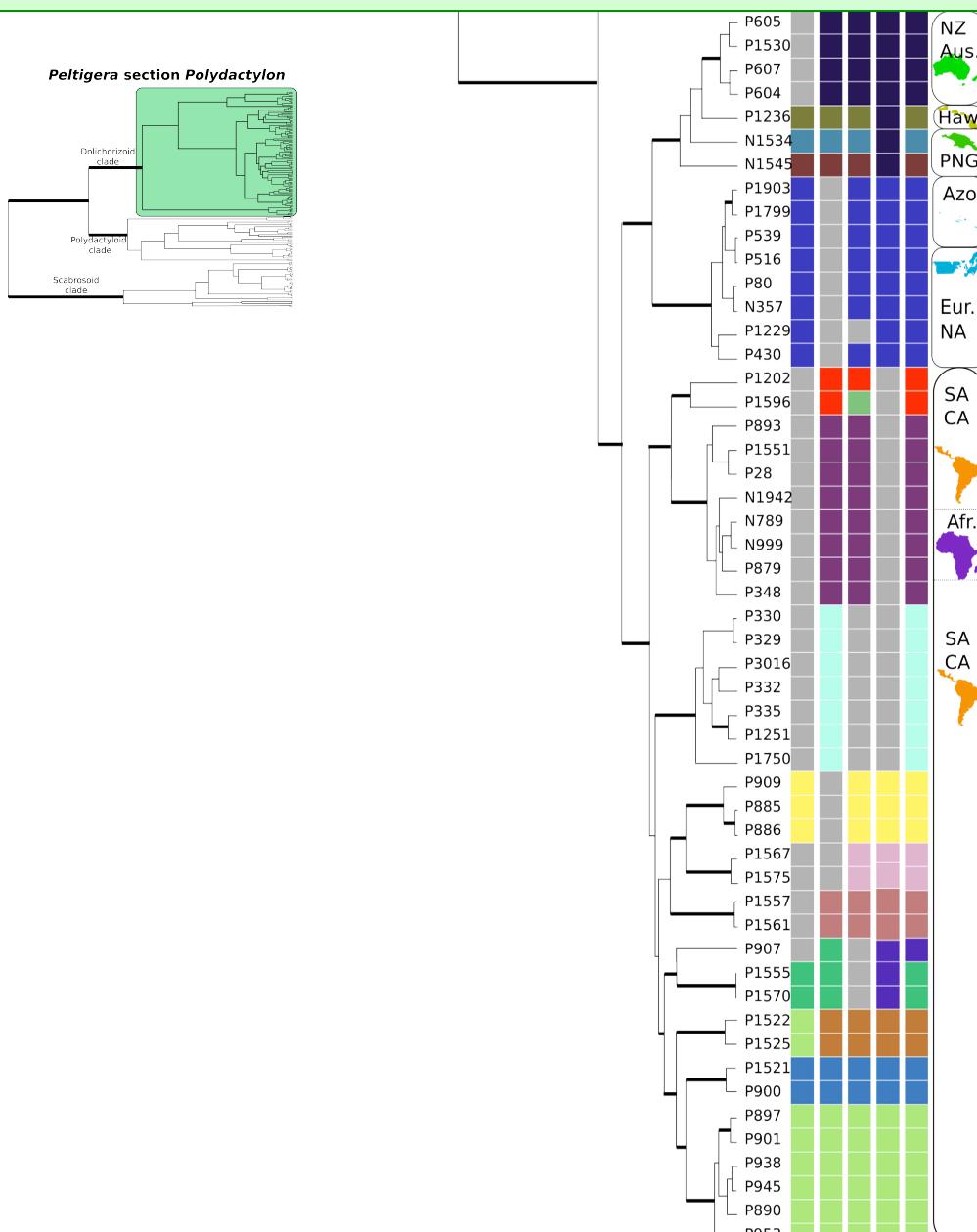


## b. Dolichorhizoid clade

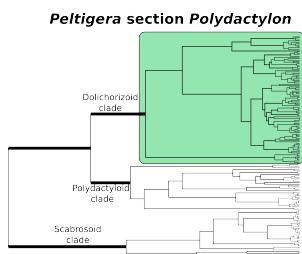




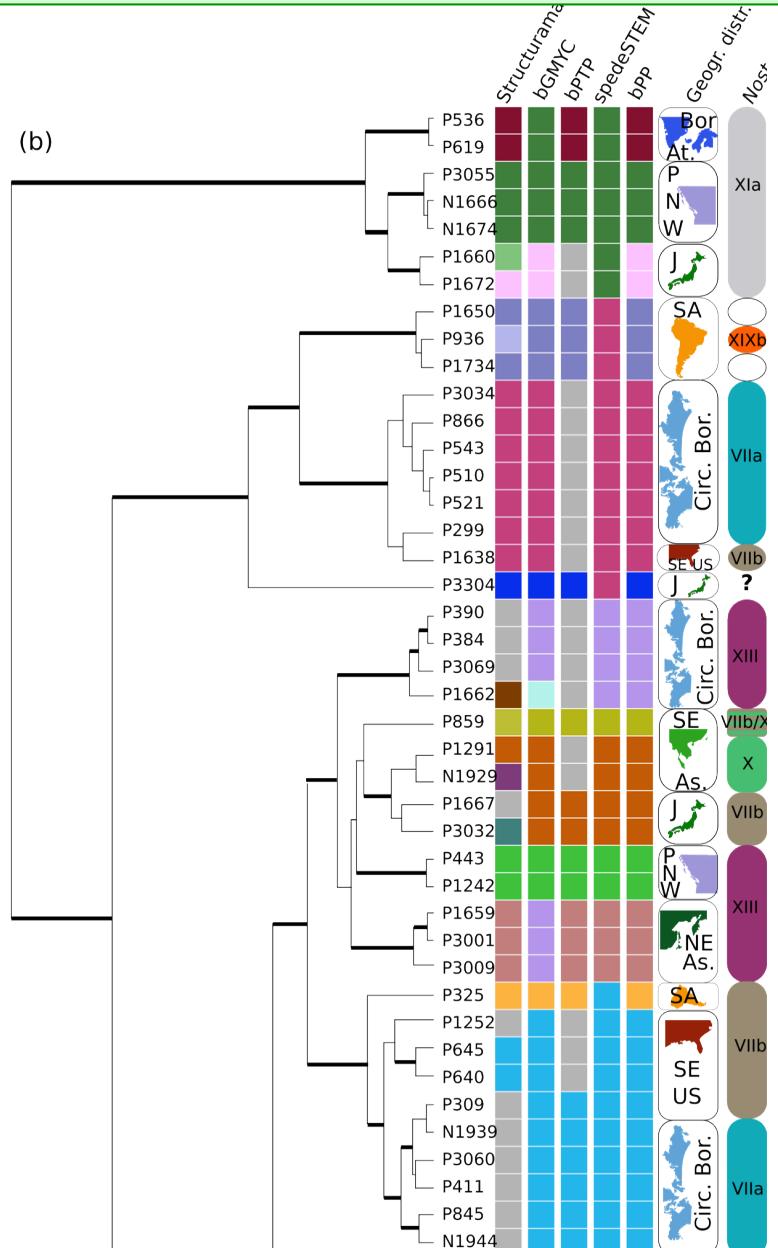
## b. Dolichorhizoid clade



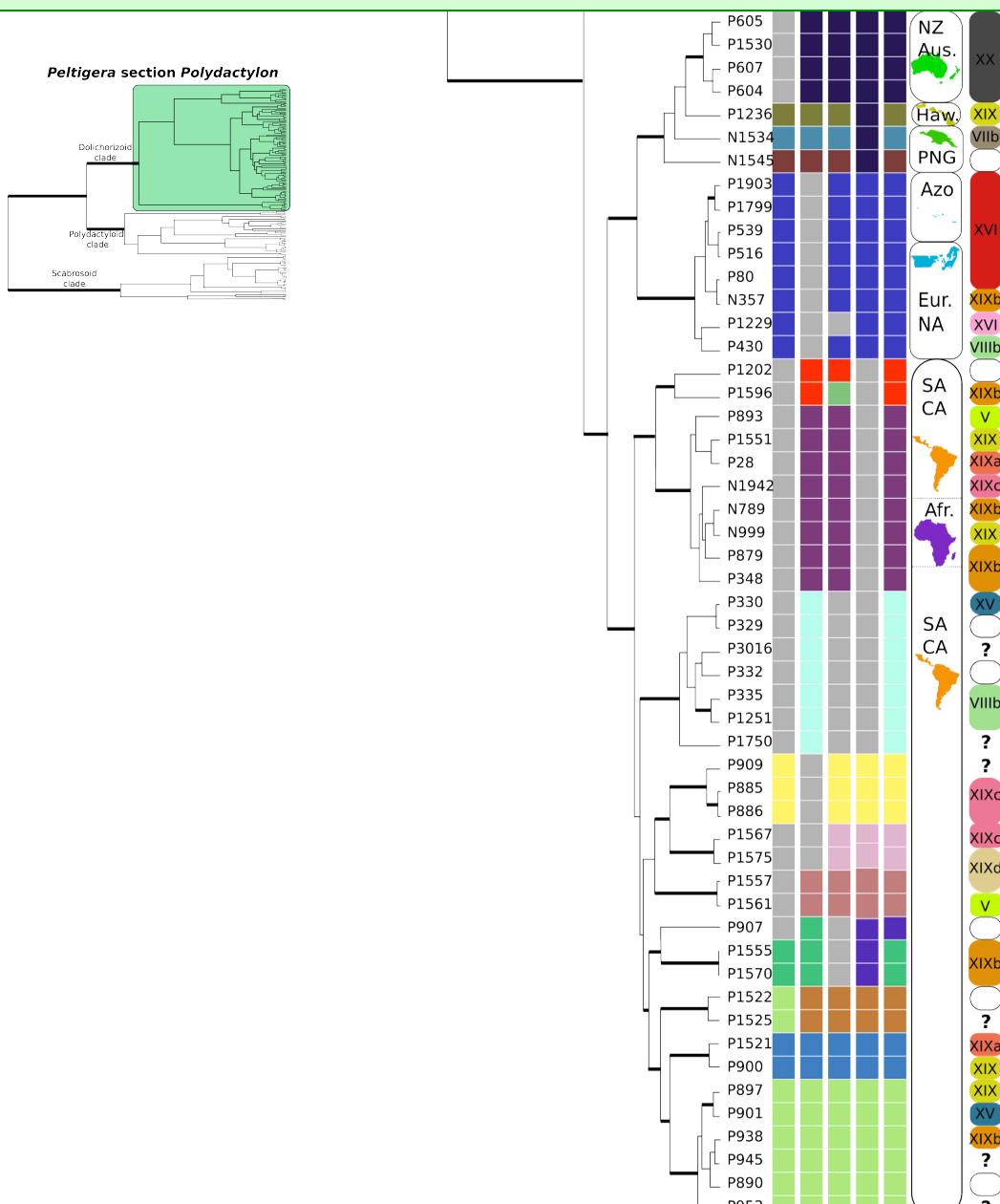
## b. Dolichorhizoid clade



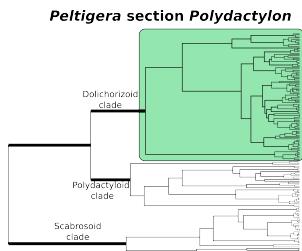
(b)



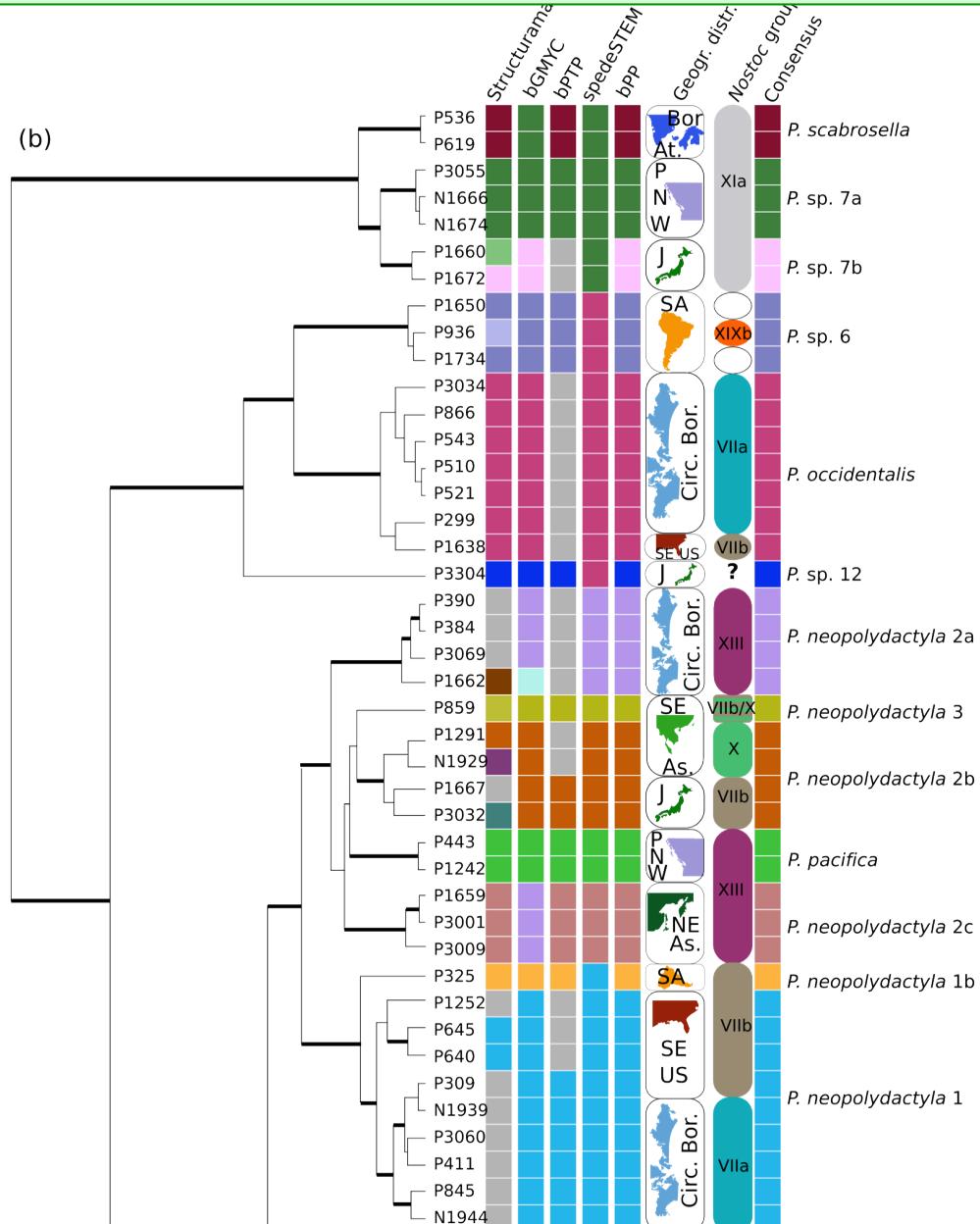
## b. Dolichorhizoid clade



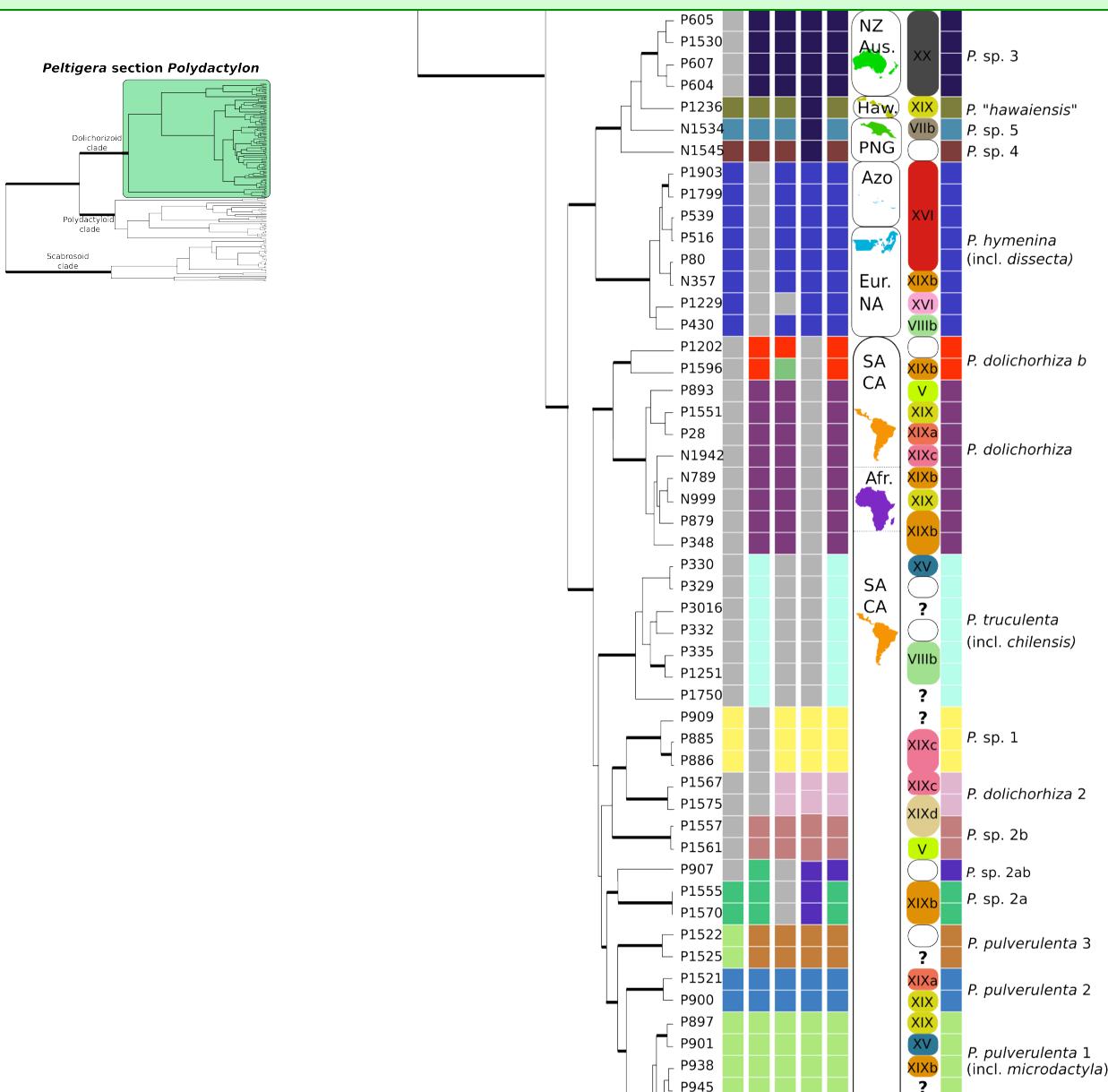
## b. Dolichorhizoid clade



(b)

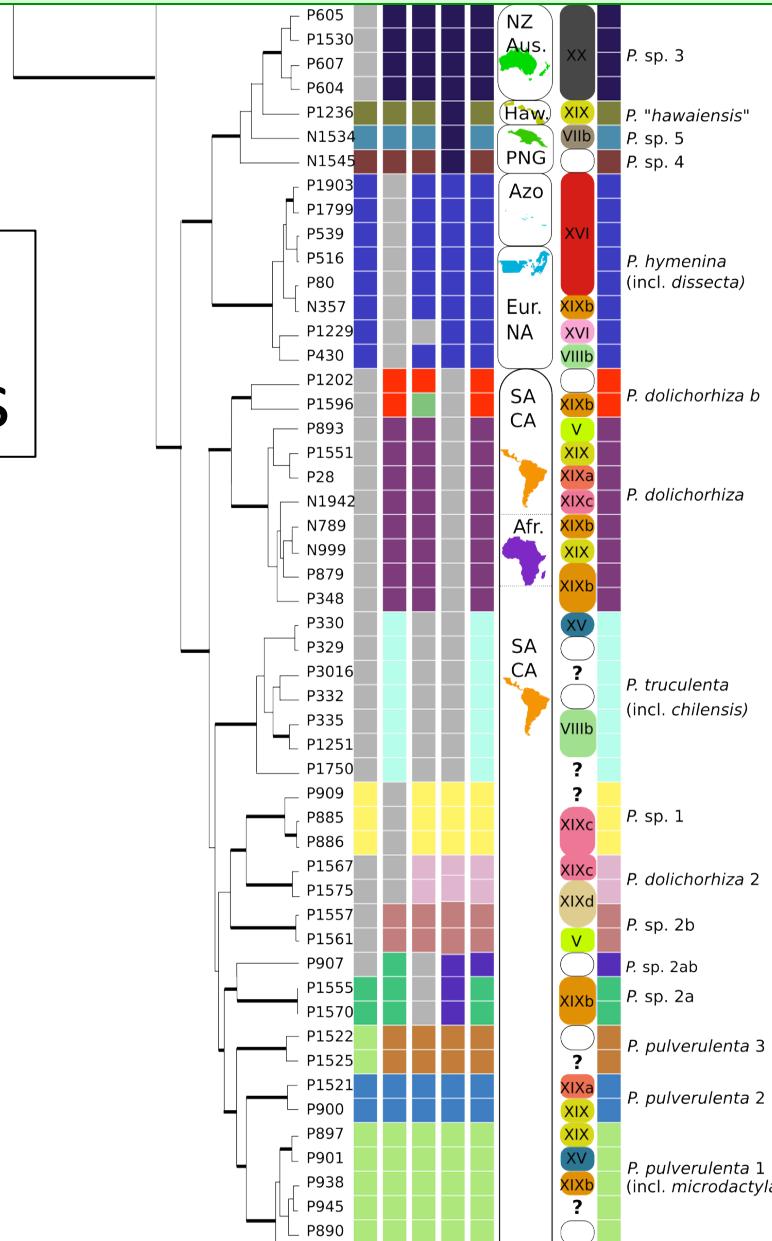


## b. Dolichorhizoid clade



## b. Dolichorhizoid clade

29 species  
22 new species



# Conclusions

- As expected, methods are more congruent in the Scabrosoid than in the Dolichorhizoid clade
- Huge amount of new, previously unrecognized species
- Once recircumscribed, some species are easily morphologically recognizable, others are not
- Same “*neopolydactyla*” morphotype appears in many instances through the tree

# Conclusions



# Conclusions

- Cosmopolitan taxa are the exception, most species are geographically well-defined  
=> Geographical data can help identifying species
- Example: *P. dolichorhiza* and *P. neopolydactyla* s. l. morphologically similar, but *P. dolichorhiza* only in South America and Africa, *P. neopolydactyla* s.l. only in Northern regions

# Conclusions

- Except in the recent radiation, most species show high specificity toward *Nostoc*  
=> *Nostoc* data can help identifying species
- Example: Phylogroup VIIa gives a specific emerald green color to the thallus when wet, in boreal regions, *P. neopolydactyla* 1 (vs *P. neopolydactyla* 2-4) and *P. scabrosa* 1 and *P. scabrosa* 4 (vs *P. scabrosa* 2) are specialized with this phylogroup

# Conclusions

With phylogroup VIIa



Classic color



# Conclusions

- Unlike previous assumptions, *Peltigera* species are not cosmopolitan taxa associating with a broad range of photobionts
- Instead, the most common scenario seems to be one *Peltigera* species associating with a certain *Nostoc* phylogroup in a certain biogeographic zone
- Similar morphotypes in different regions are in most cases distinct species

# Conclusions

- Unlike previous assumptions, *Peltigera* species are not cosmopolitan taxa associating with a broad range of photobionts

Intitulé du projet de recherches.

Français :

Les espèces cosmopolites sont-elles des fantômes de la Pangée ou des assemblages d'espèces cryptiques ? Le cas du champignon lichénisé *Peltigera dolichorhiza*.

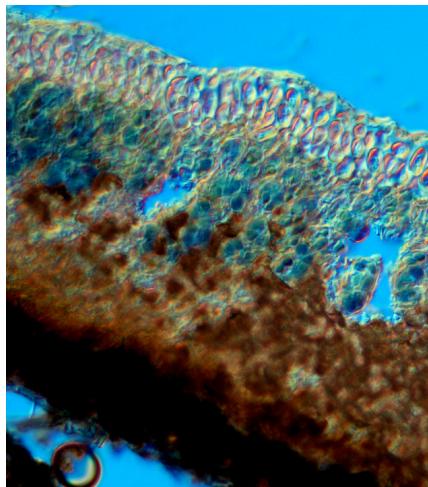
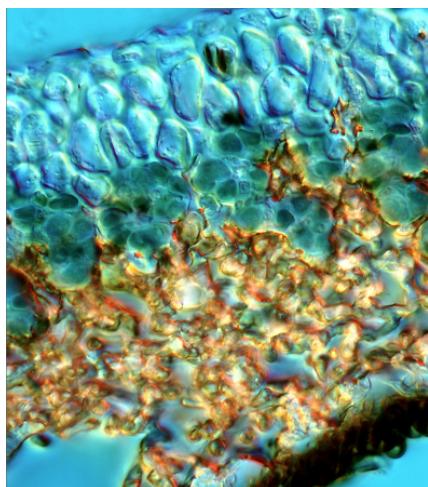
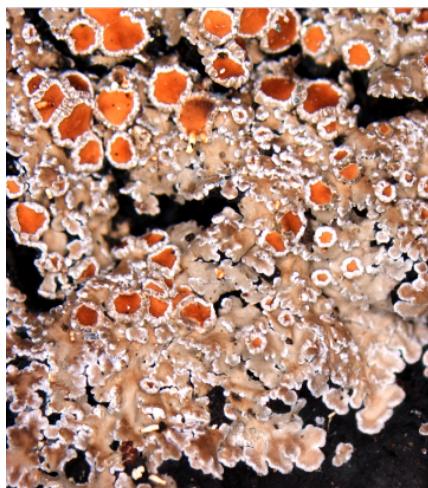
Anglais :

Are cosmopolitan species ghosts from Pangea, or assemblages of cryptic species? A case study in the lichenized fungus *Peltigera dolichorhiza*

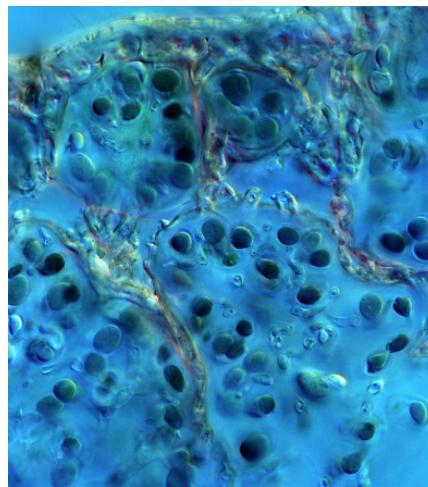
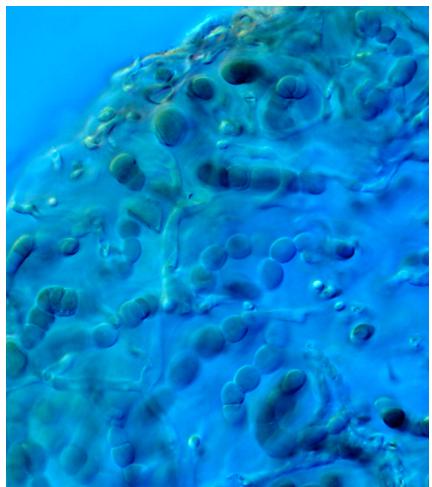
# Influence of the photobiont on the morphology and evolution of Pannariaceae

- Pannariaceae: order Peltigerales
- Molecular inferences showed higher morphological variation than expected in the family
- Three main morphological forms

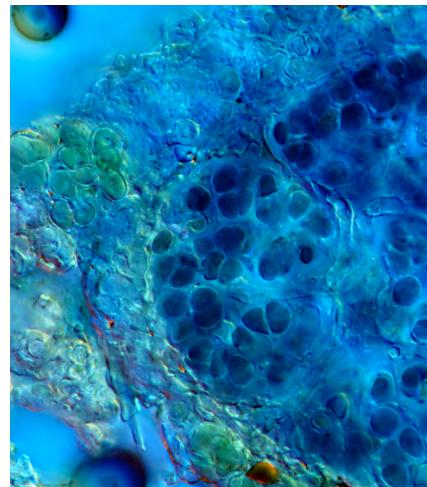
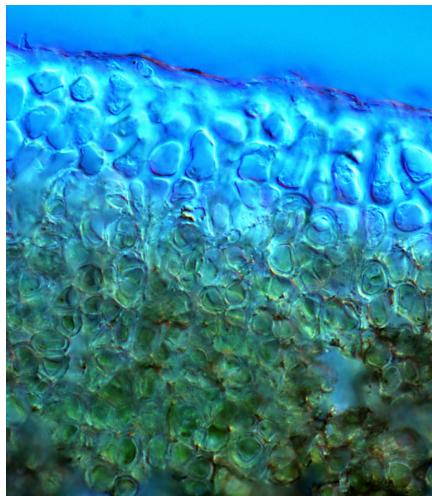
# Pannarioid thalli



# Collematoid thalli



# Tripartite thalli

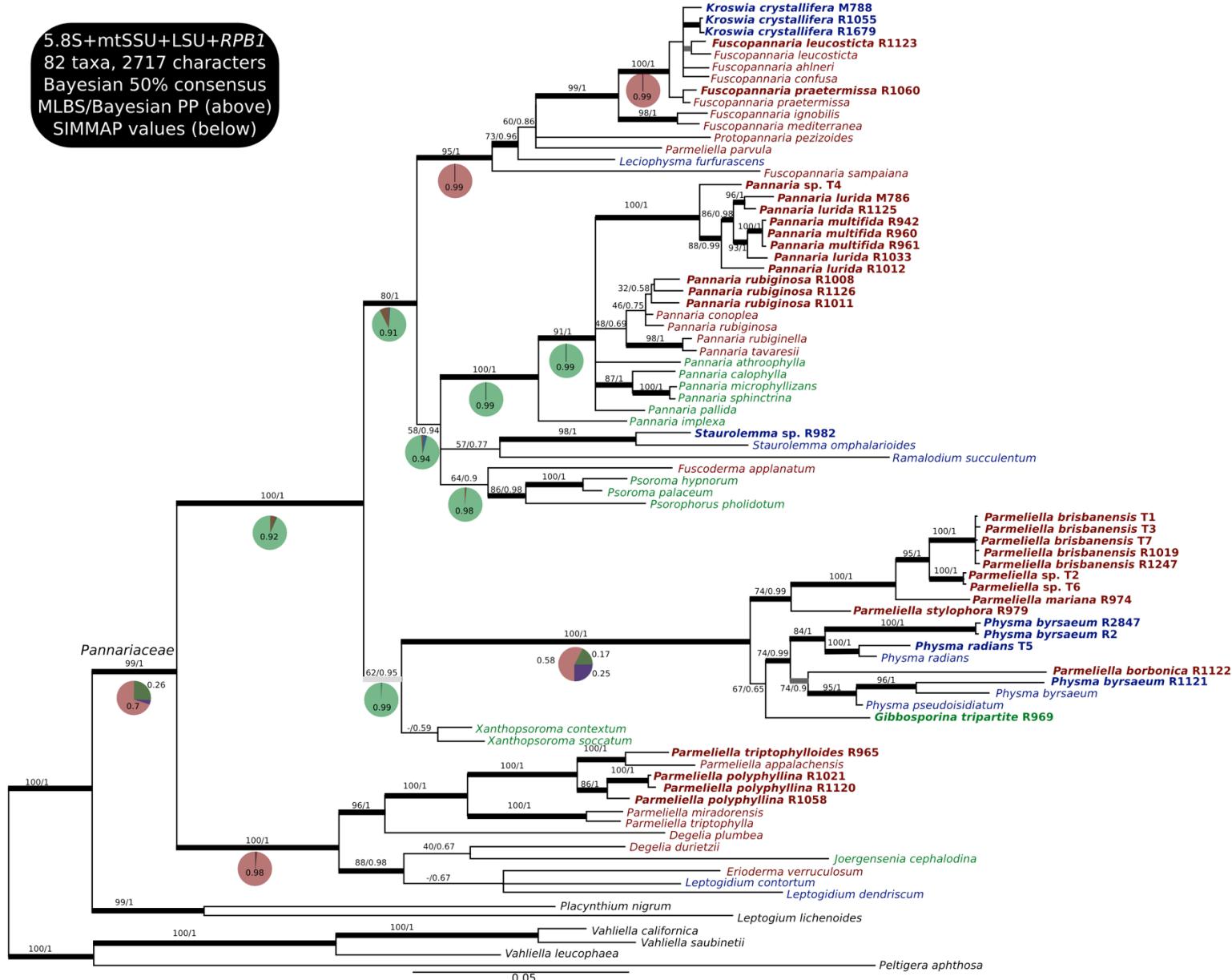


## Aims of the study

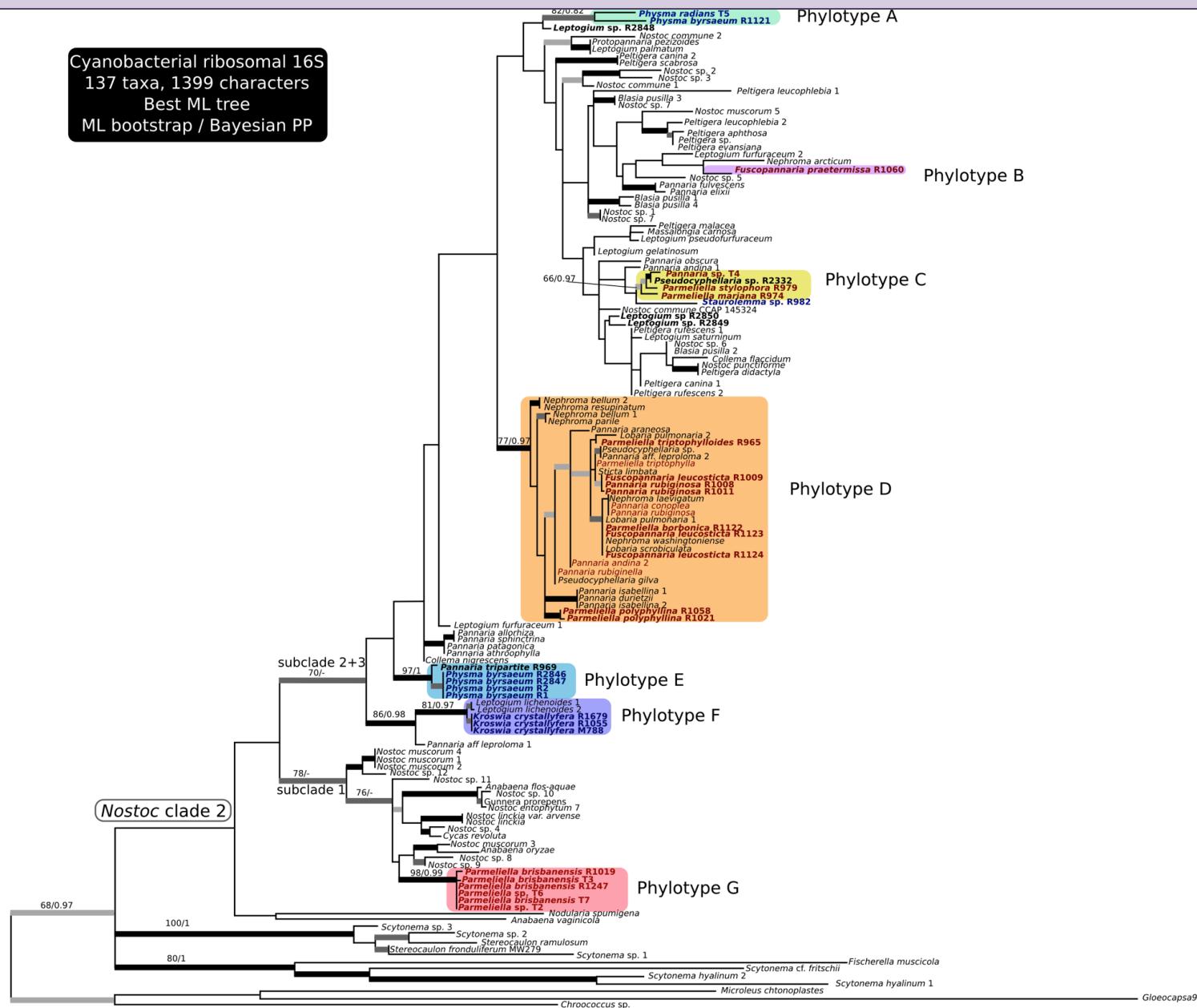
- Infer the positions of the different morphological forms throughout the family
- Consider the morphological form in light of the identity of the cyanobionts they associate with
- Propose an hypothesis for the morphological evolution in the family

# Phylogeny of the mycobiont (fungus)

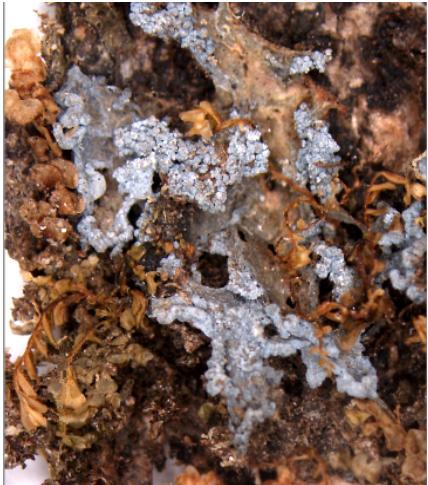
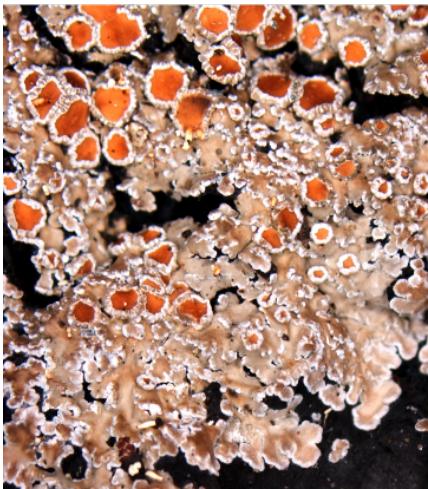
5.8S+mtSSU+LSU+RPB1  
 82 taxa, 2717 characters  
 Bayesian 50% consensus  
 MLBS/Bayesian PP (above)  
 SIMMAP values (below)



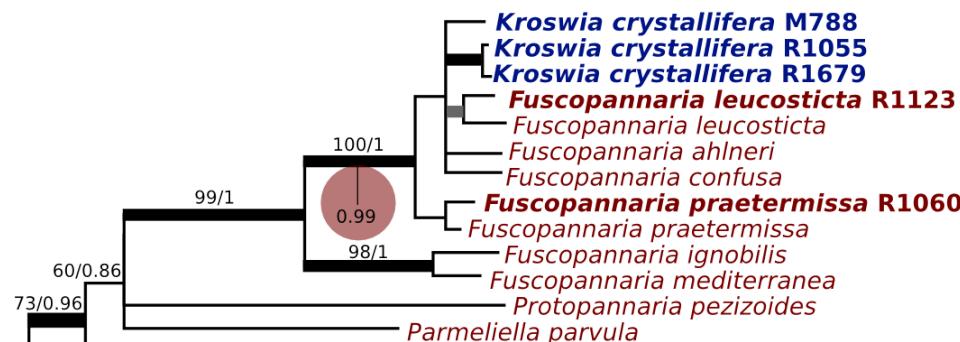
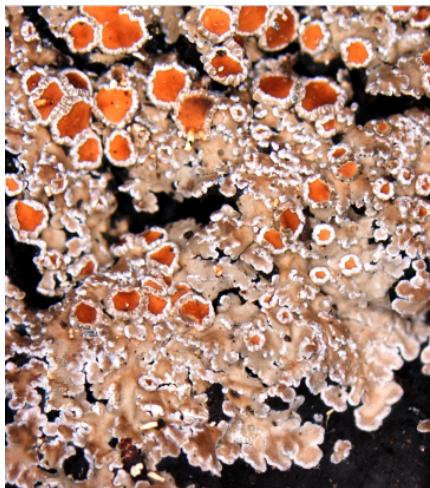
# Phylogeny of the cyanobiont (*Nostoc*)



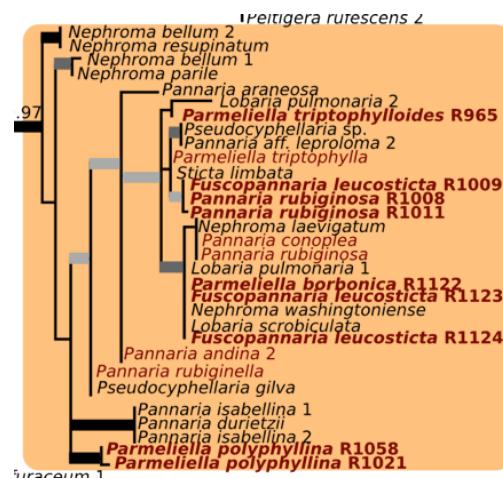
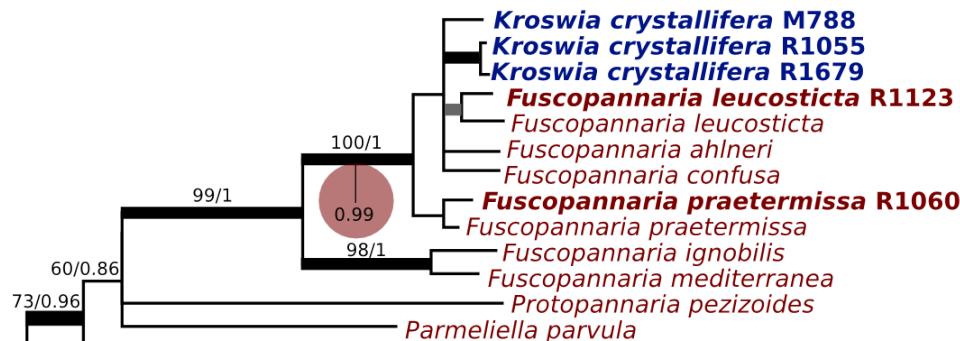
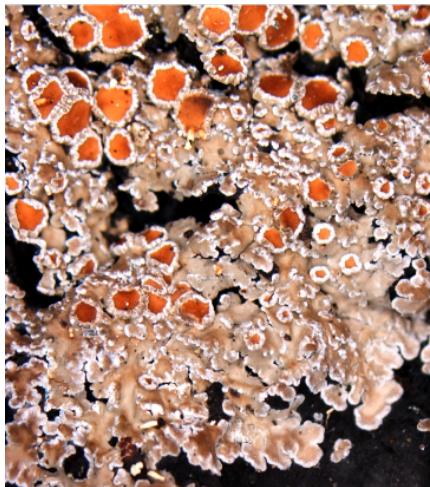
## a. The case of *Kroswia* and *Fuscopannaria*



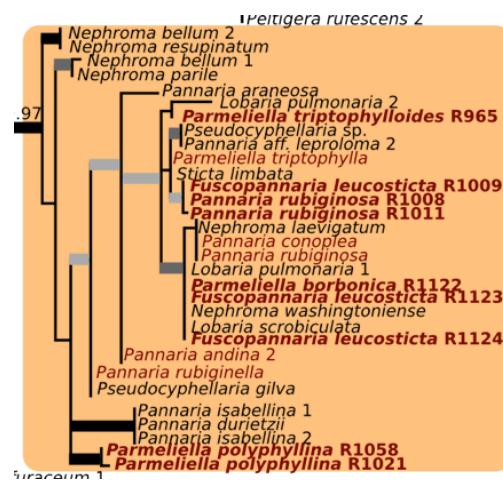
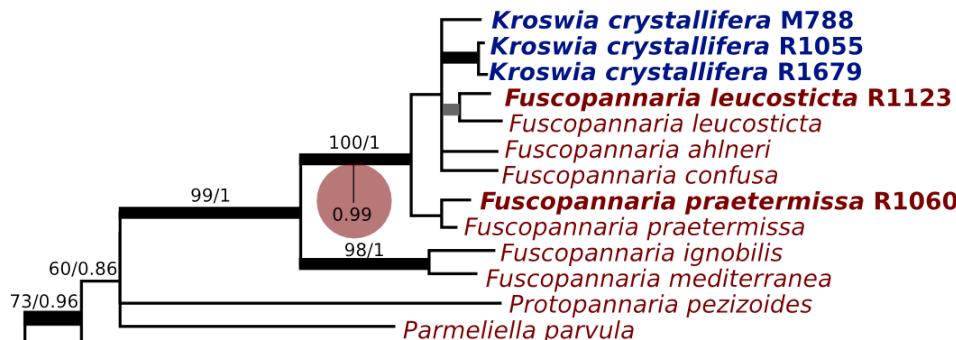
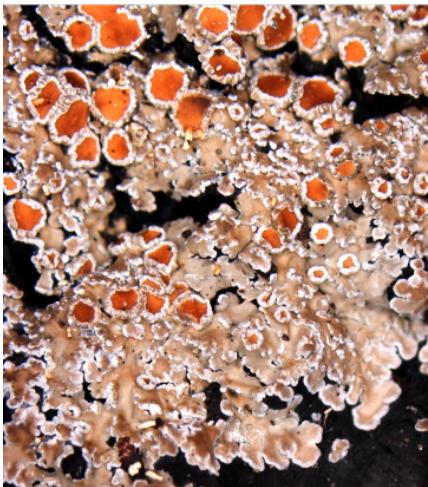
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# a. The case of *Kroswia* and *Fuscopannaria*

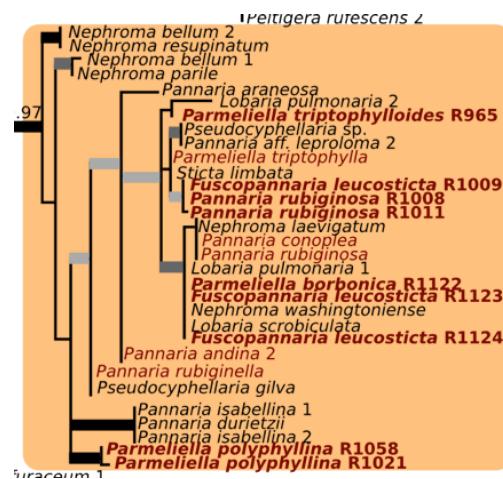
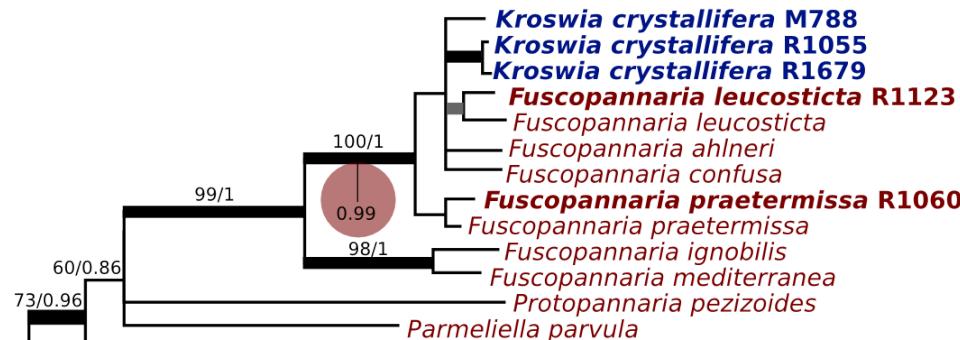
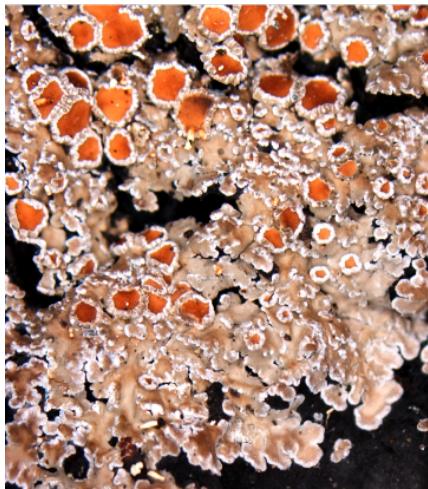


# a. The case of *Kroswia* and *Fuscopannaria*



*Leptogium lichenoides* 1  
*Leptogium lichenoides* 2  
***Kroswia crystallifera* R1679**  
***Kroswia crystallifera* R1055**  
***Kroswia crystallifera* M788**

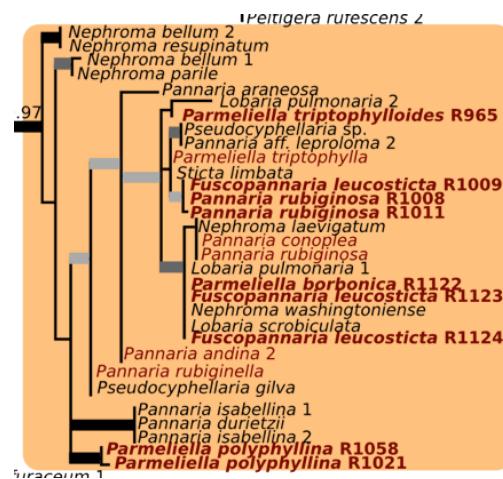
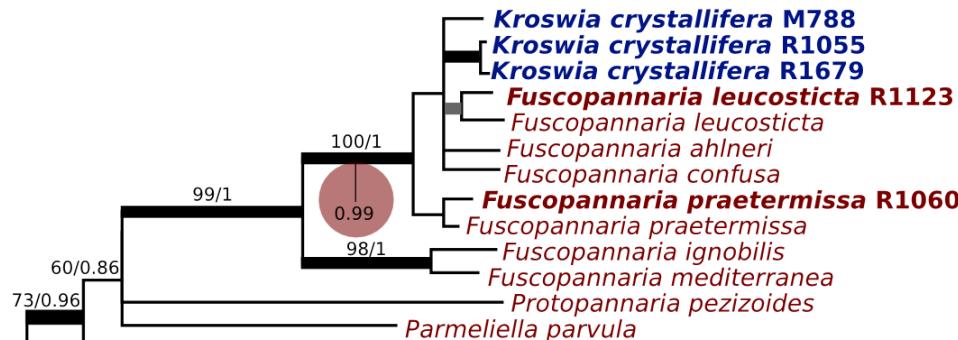
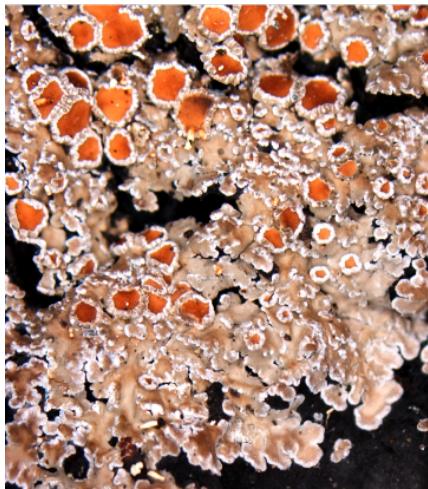
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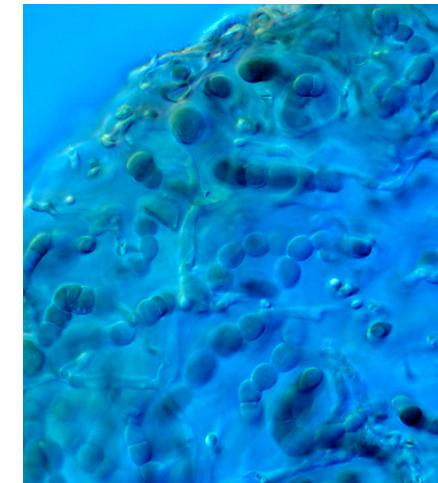
L *Leptogium lichenoides* 1  
L *Leptogium lichenoides* 2  
K *Kroswia crystallifera* R1679  
K *Kroswia crystallifera* R1055  
K *Kroswia crystallifera* M788



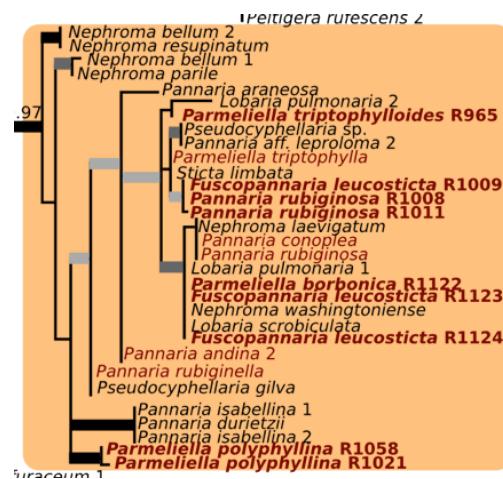
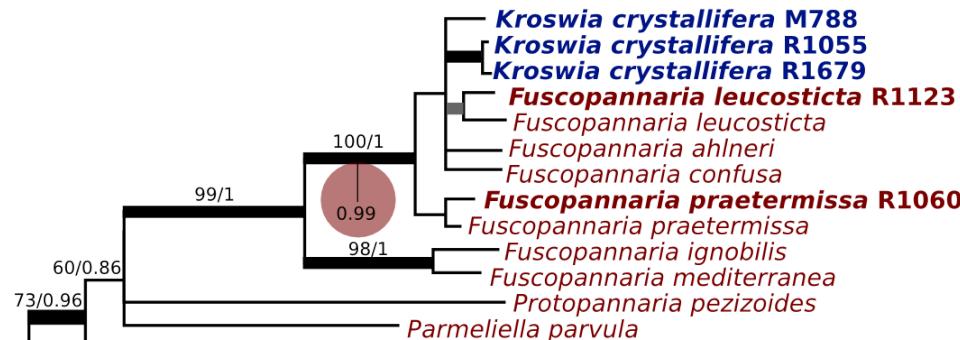
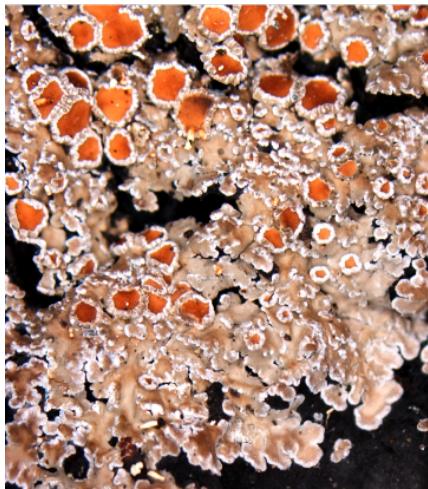
# a. The case of *Kroswia* and *Fuscopannaria*



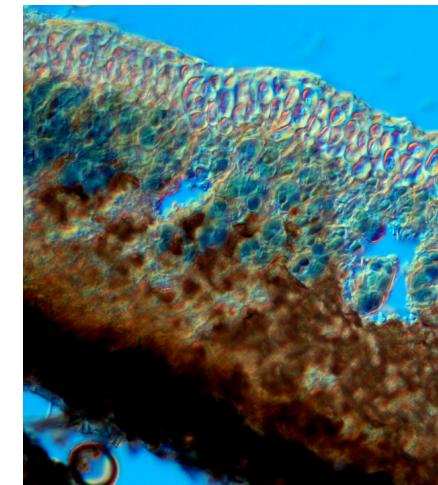
Leptogium lichenoides 1  
Leptogium lichenoides 2  
**Kroswia crystallifera R1679**  
**Kroswia crystallifera R1055**  
**Kroswia crystallifera M788**



# a. The case of *Kroswia* and *Fuscopannaria*



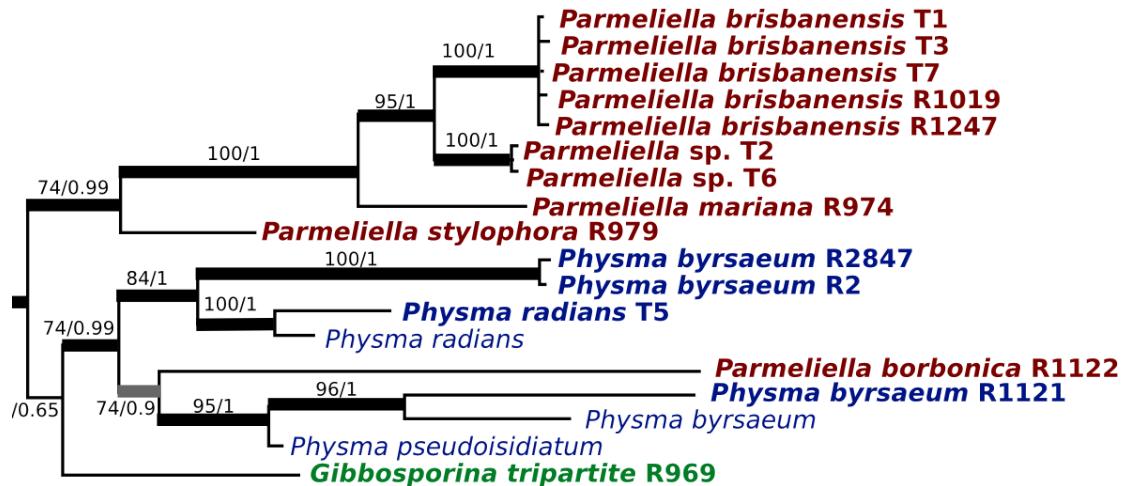
**Leptogium lichenoides 1**  
**Leptogium lichenoides 2**  
**Kroswia crystallifera R1679**  
**Kroswia crystallifera R1055**  
**Kroswia crystallifera M788**



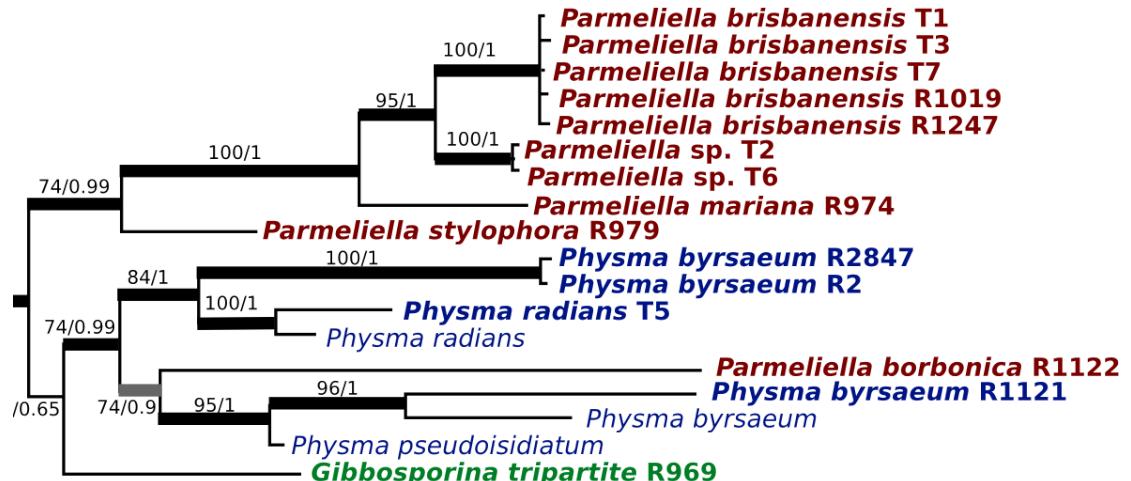
## b. The case of *Physma* and *Gibbosporina*



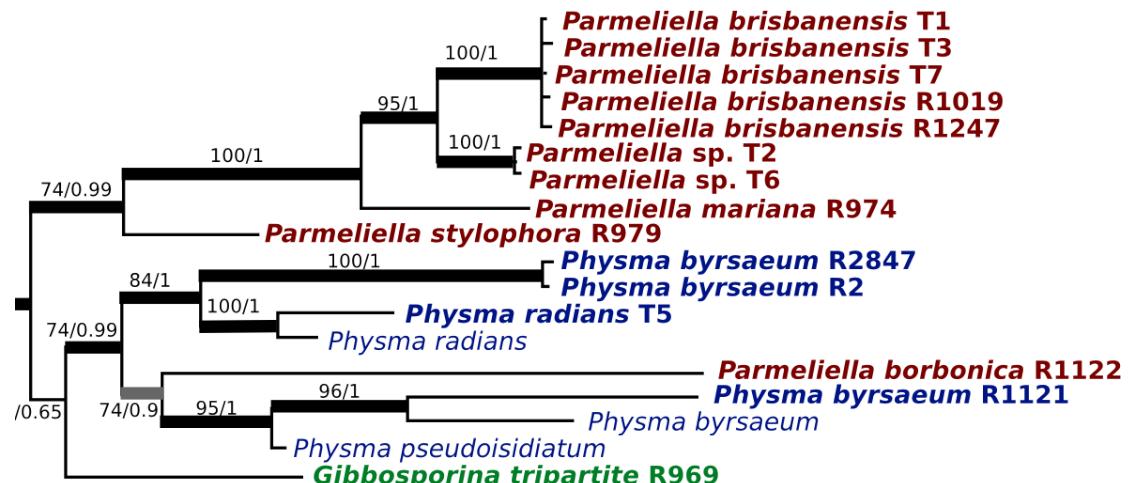
## b. The case of *Physma* and *Gibbosporina*



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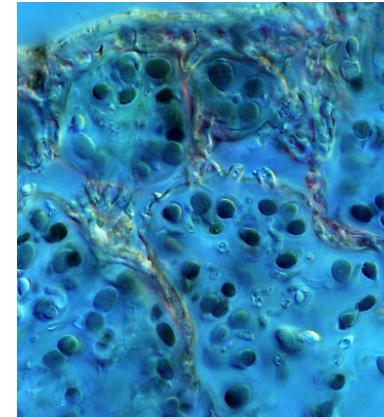
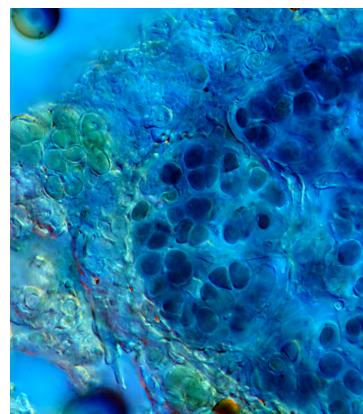


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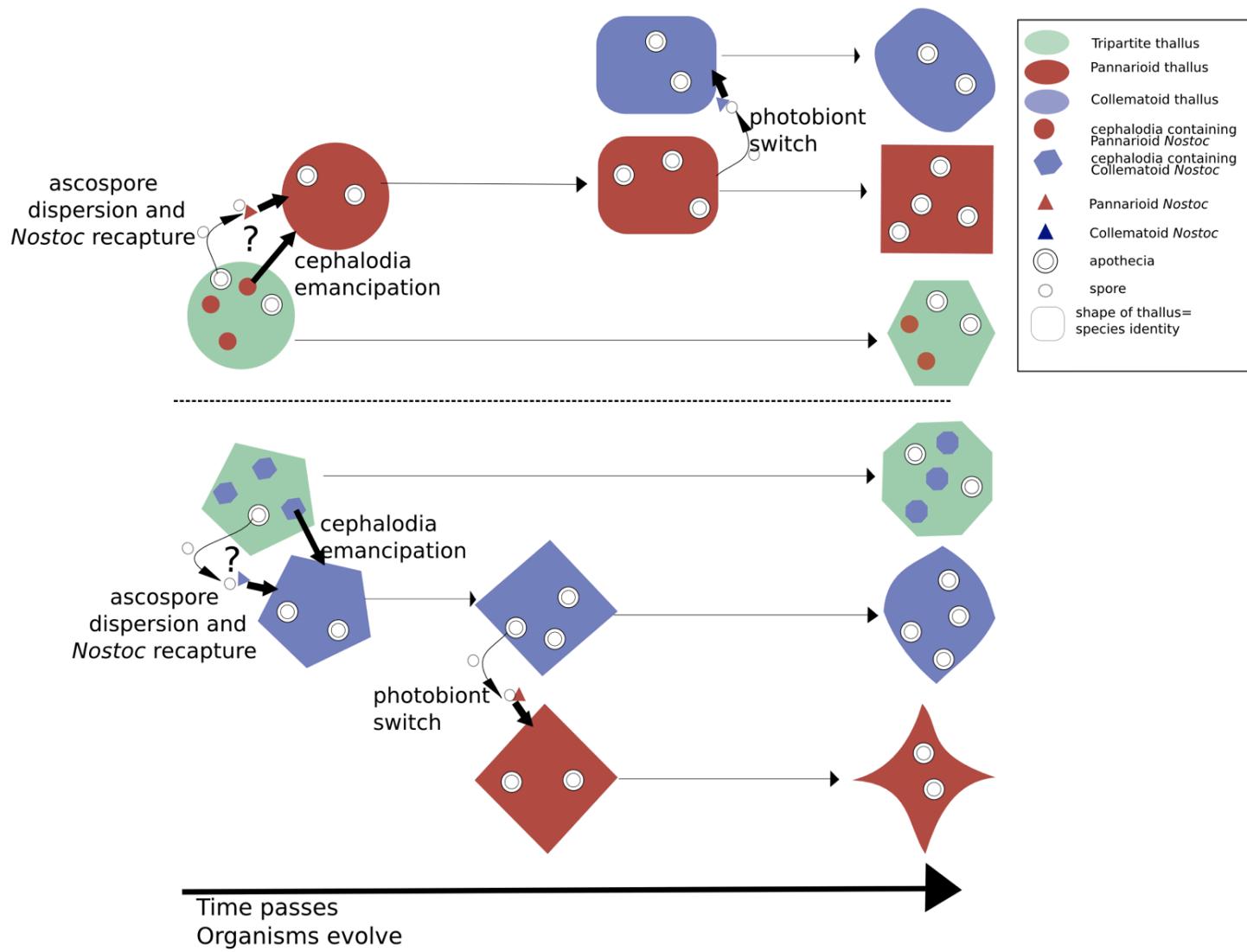


97/1

**Gibbosporina tripartite R969**  
*Physma byrsaeum* R2846  
*Physma byrsaeum* R2847  
*Physma byrsaeum* R2  
*Physma byrsaeum* R1



# Proposed hypothesis



Multiple photobiont switches and cephalodia emancipation

# Conclusions of the thesis

- The photobiont does not have an accessory role in the symbiosis
- It has an impact on macroevolution, speciation, diversification, geographic ranges, morphology...
- At different taxonomic levels
- There are clear patterns of specificity and selectivity
- Importance to study the lichen as a symbiosis and to consider the evolution of one symbiont in light of the interactions with the other symbiont

# Thank you very much for your attention !

I thank Prof. Emmanuël Sérusiaux, Laurent Gohy, Ido Cremasco at the University of Liège;



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(Ko Hsuan, Martin, Camille, Edgar, Emilie, Ryoko, Ester, Tami, Jade...)



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and my family and friends!



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