# 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?


2 cm






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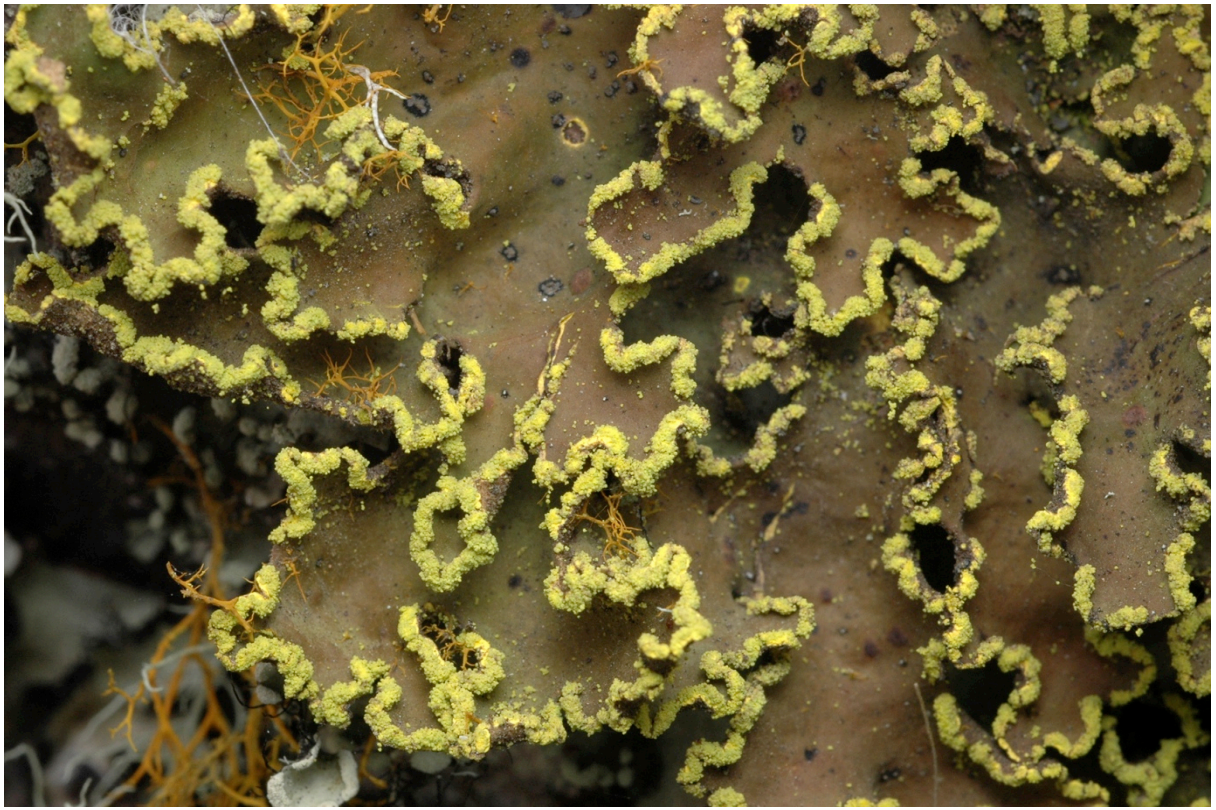









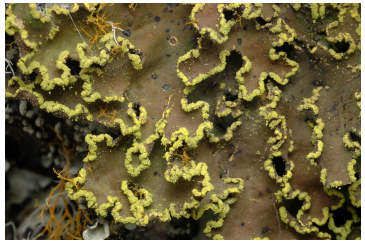







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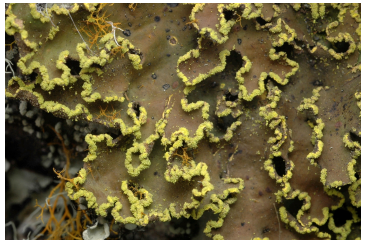








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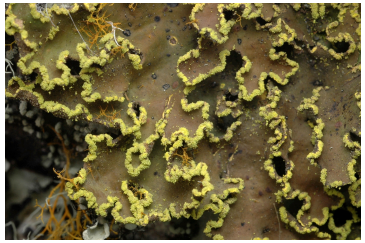


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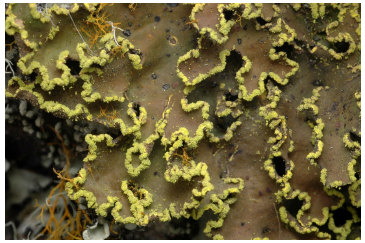


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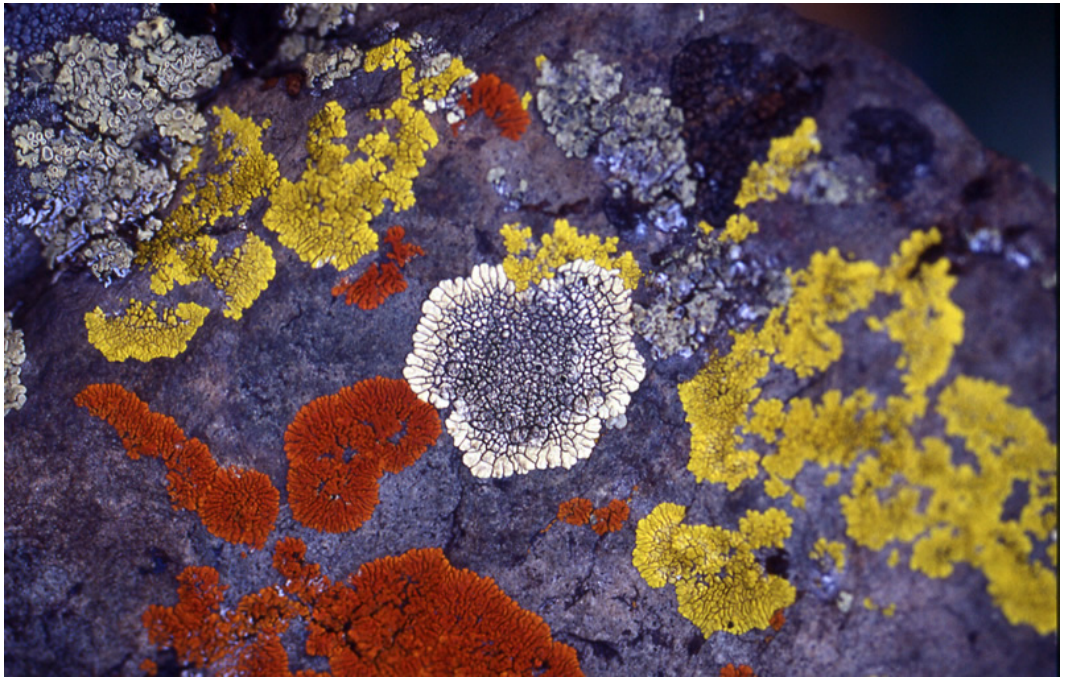

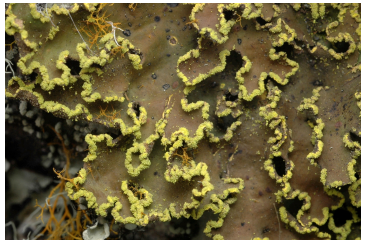


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# What is a lichen?

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

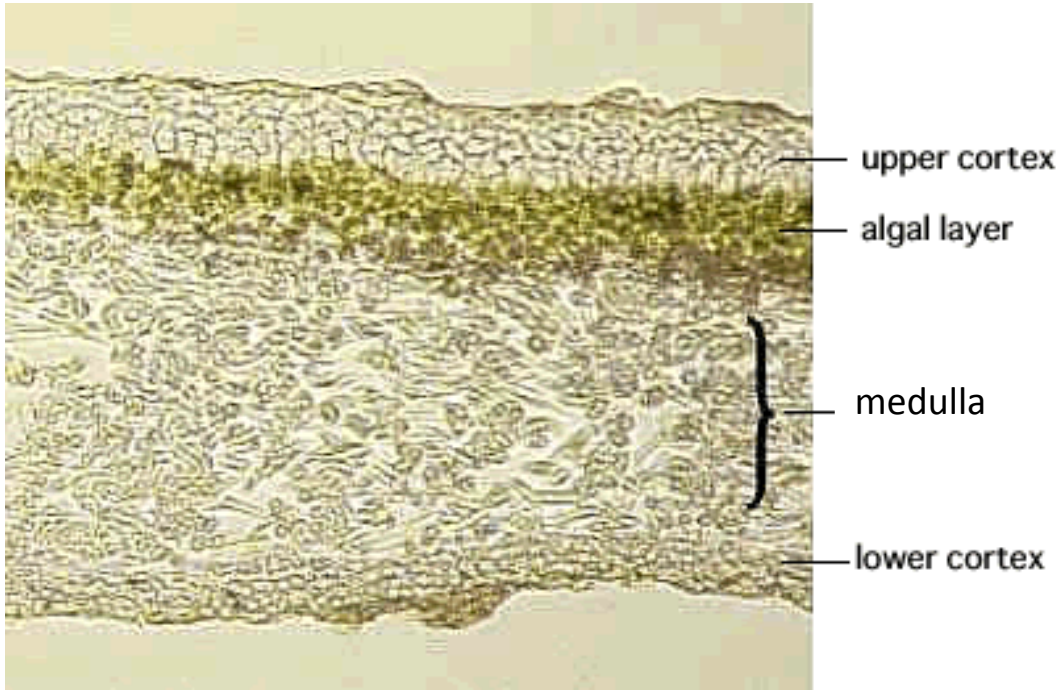

# What is a lichen?

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

A single morphological entity

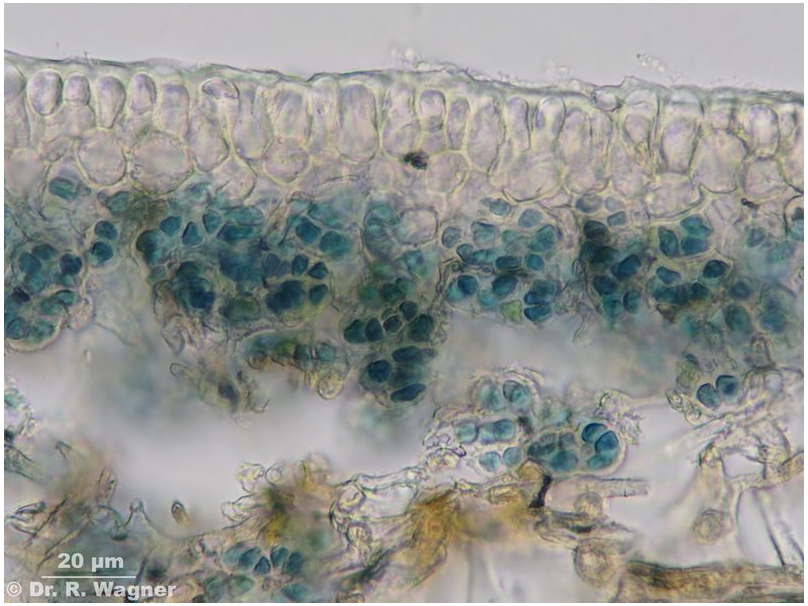
# What is a lichen?

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

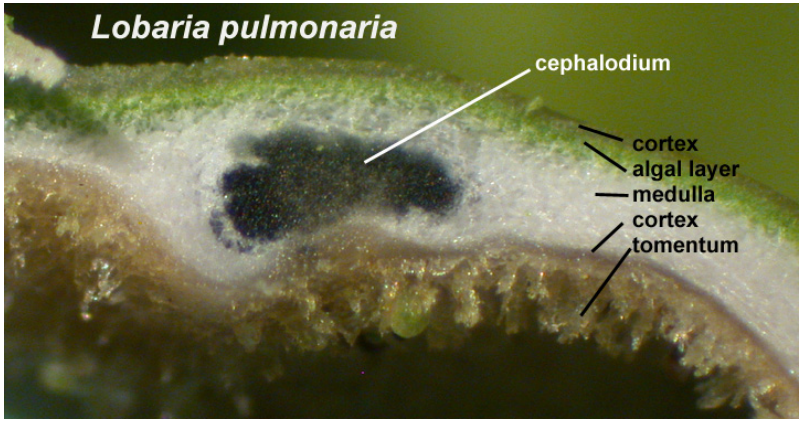
# What is a lichen?

It is a symbiosis between **a fungus** and
a green alga**, a cyanobacteria (cyanolichen)**



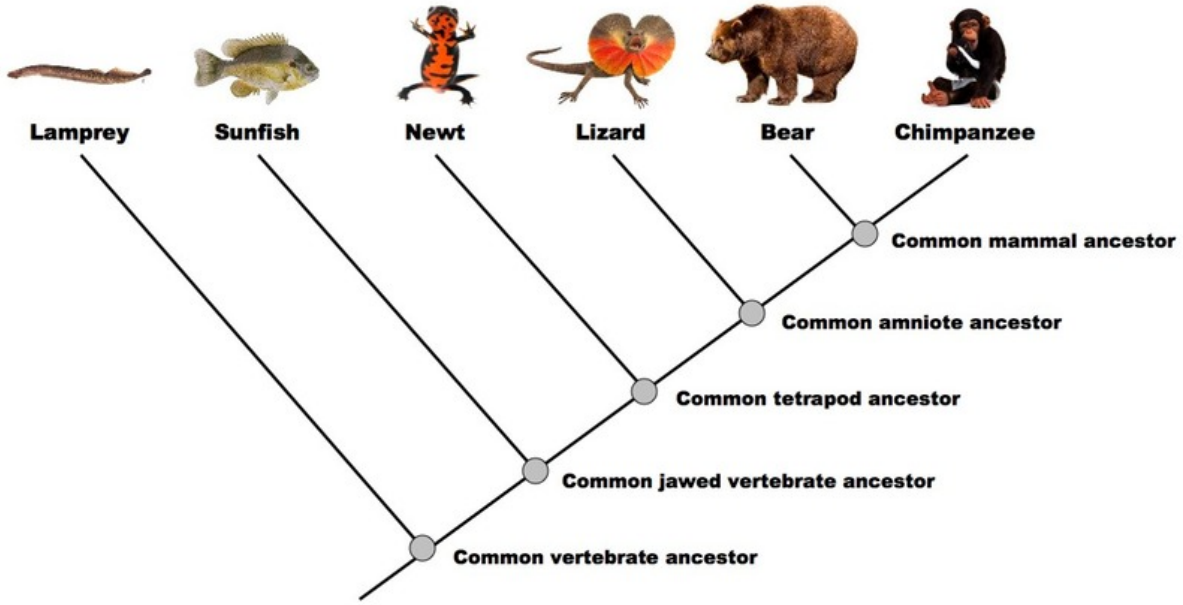
# What is a lichen?

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



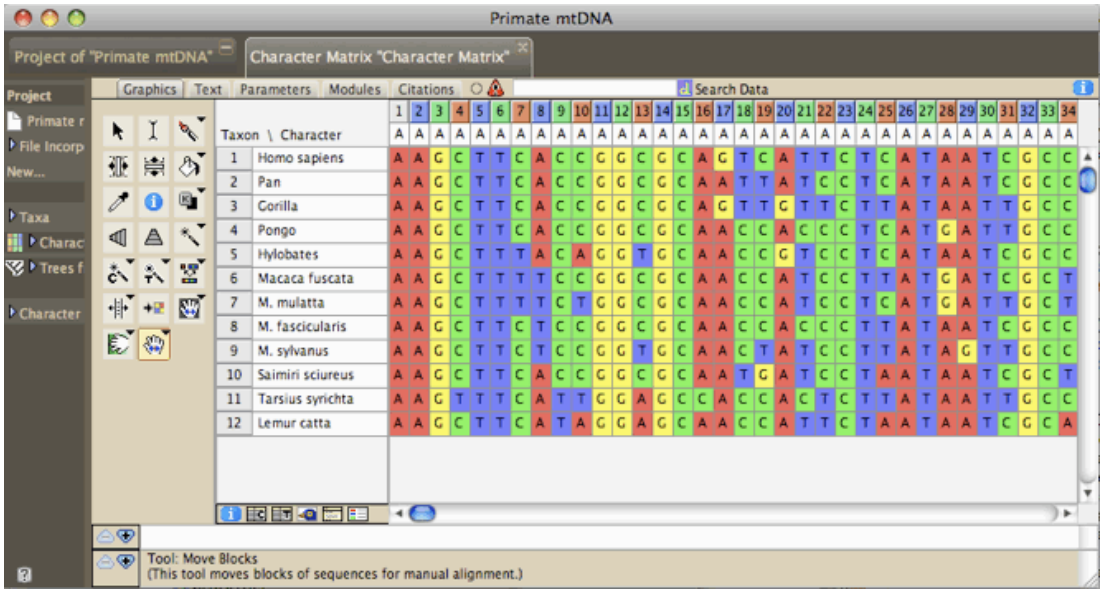
# Phylogenetics and the study of evolution

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



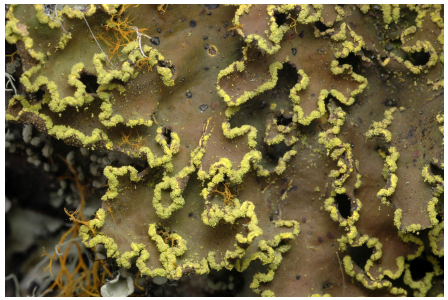

Uses: classification; reconstruction of ancestral states; study of adaptation; evolution of genes; diversification rates; key innovations; dates of divergence; biogeography; coevolution and cospeciation; assessment of biodiversity; epidemiology …

# Molecular phylogeny


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

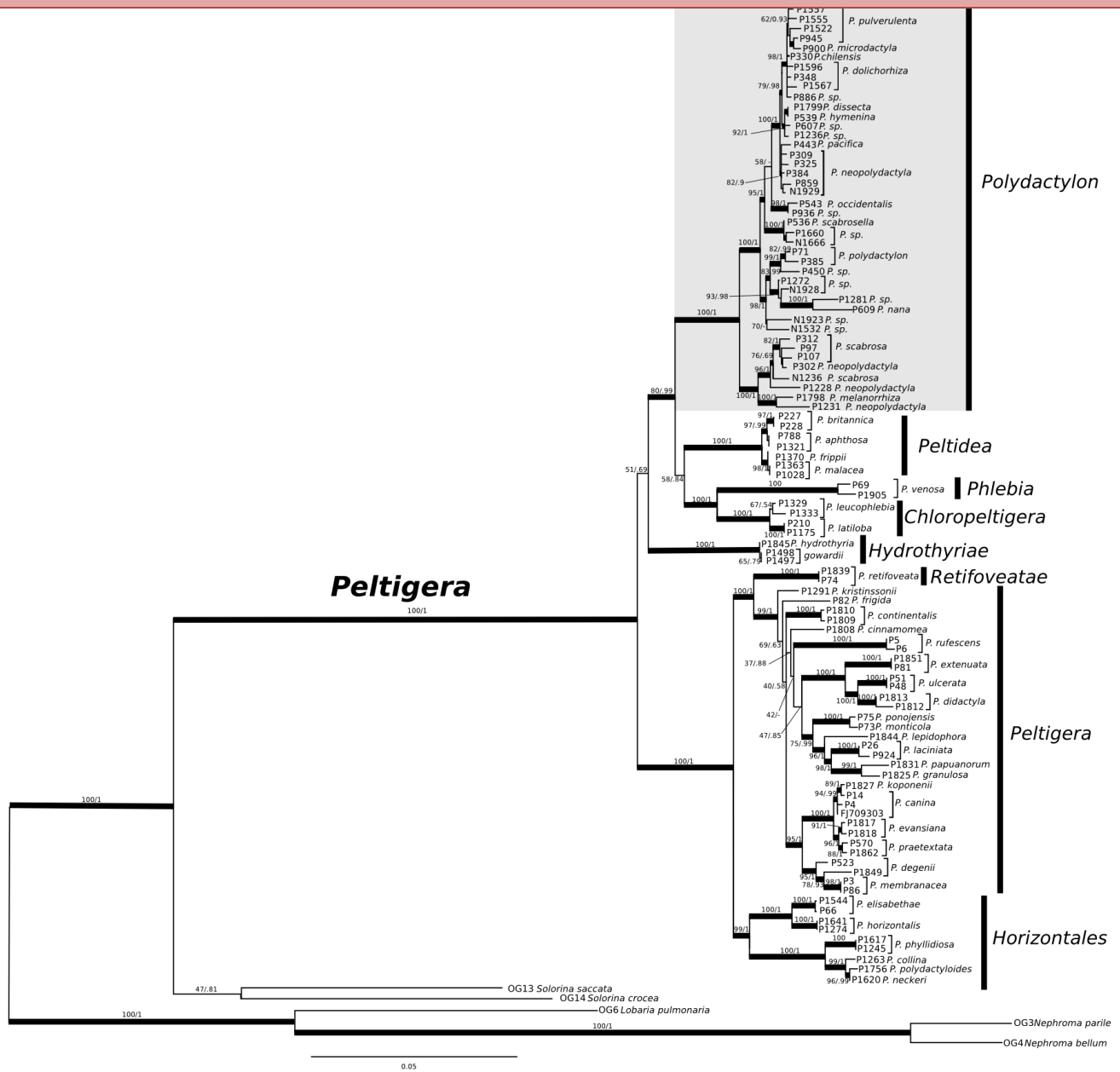
# The genus *Peltigera*

- 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*



# 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…)

*Consider these results in light of various hypotheses of evolution of mutualism

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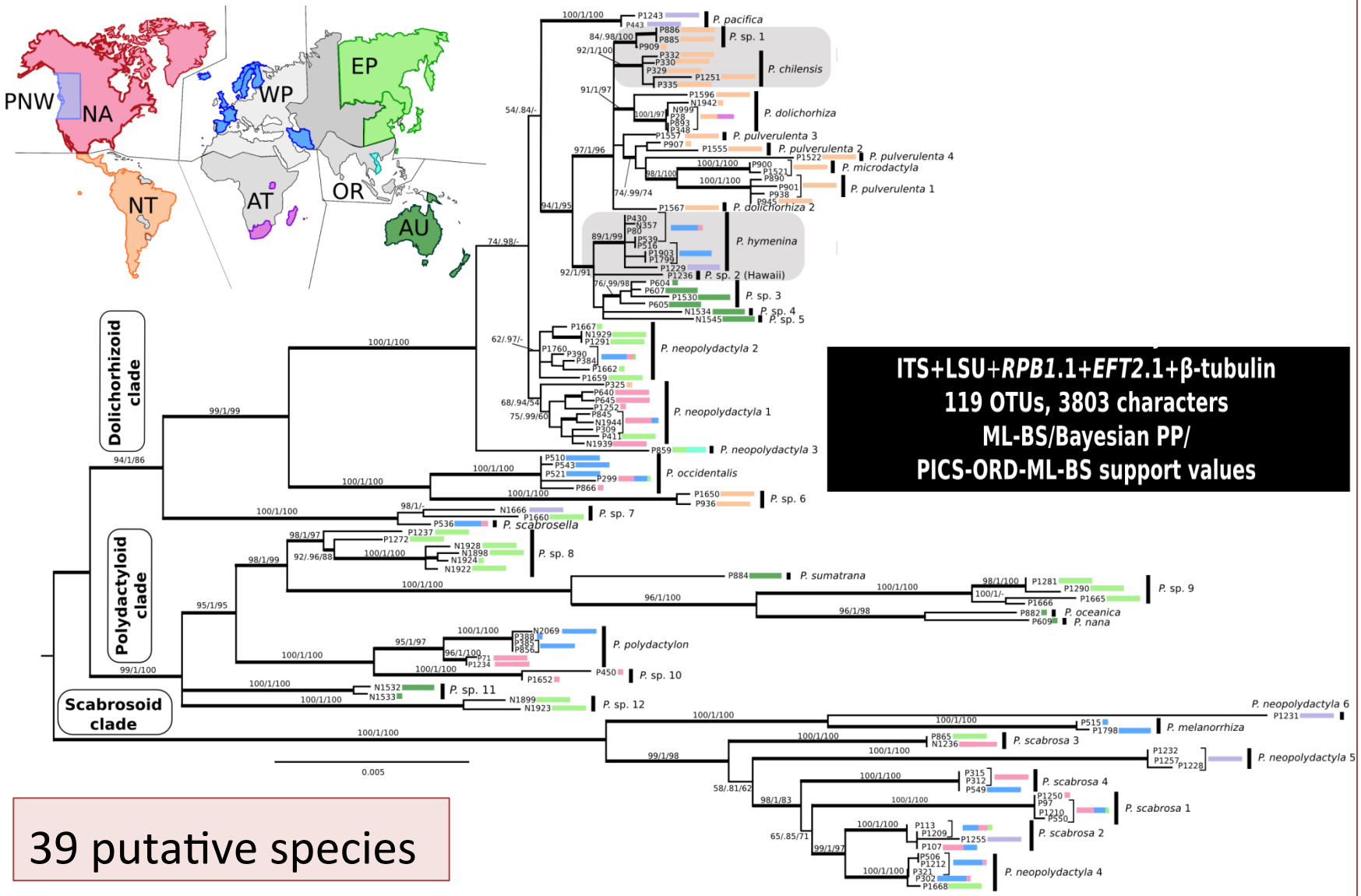


**ITS+LSU+*RPB1*.1+*EFT2*.1+β-tubulin**
**119 OTUs, 3803 characters**
**ML-BS/Bayesian PP/**
**PICS-ORD-ML-BS support values**

39 putative species

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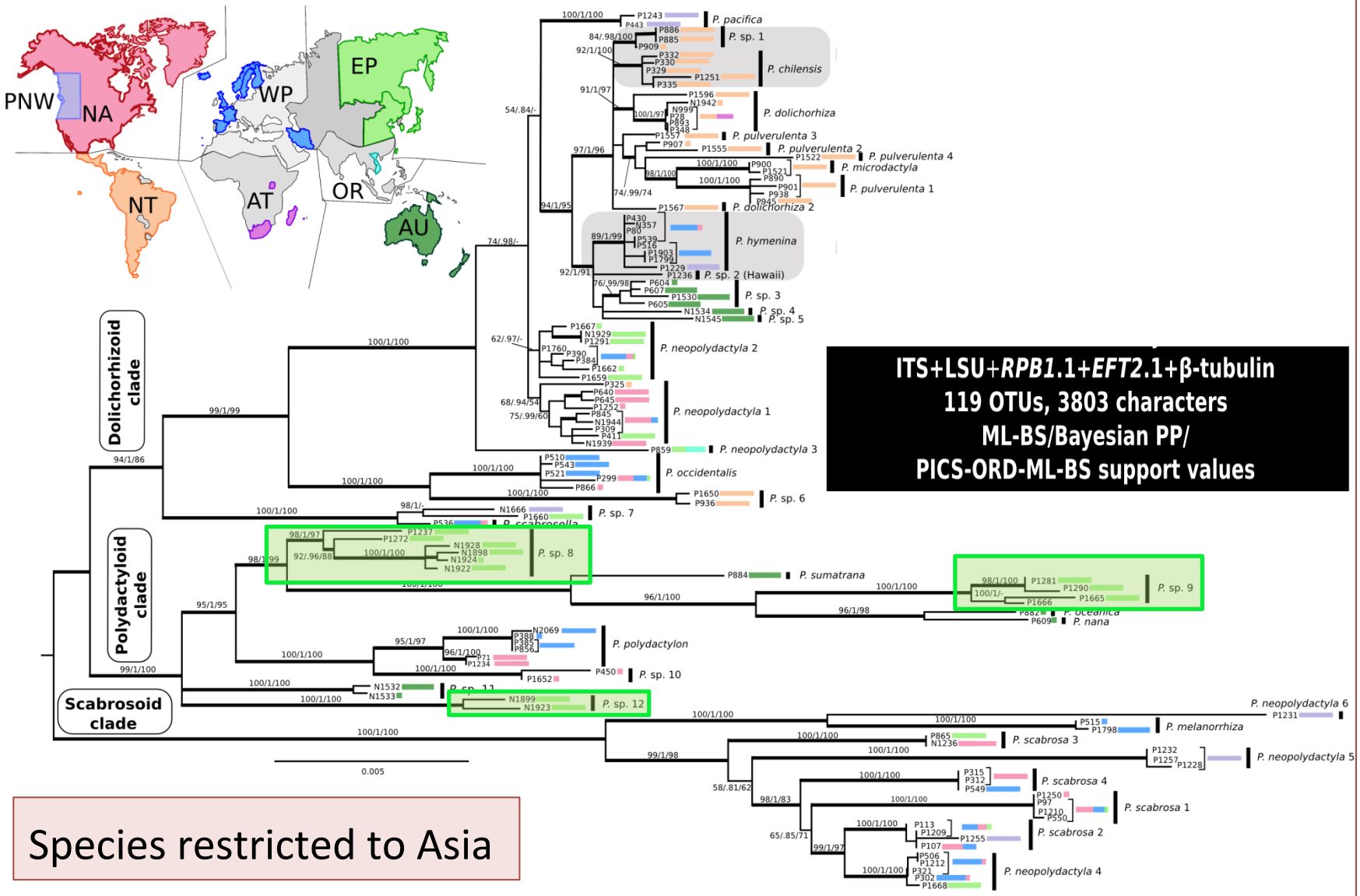


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Species restricted to Asia

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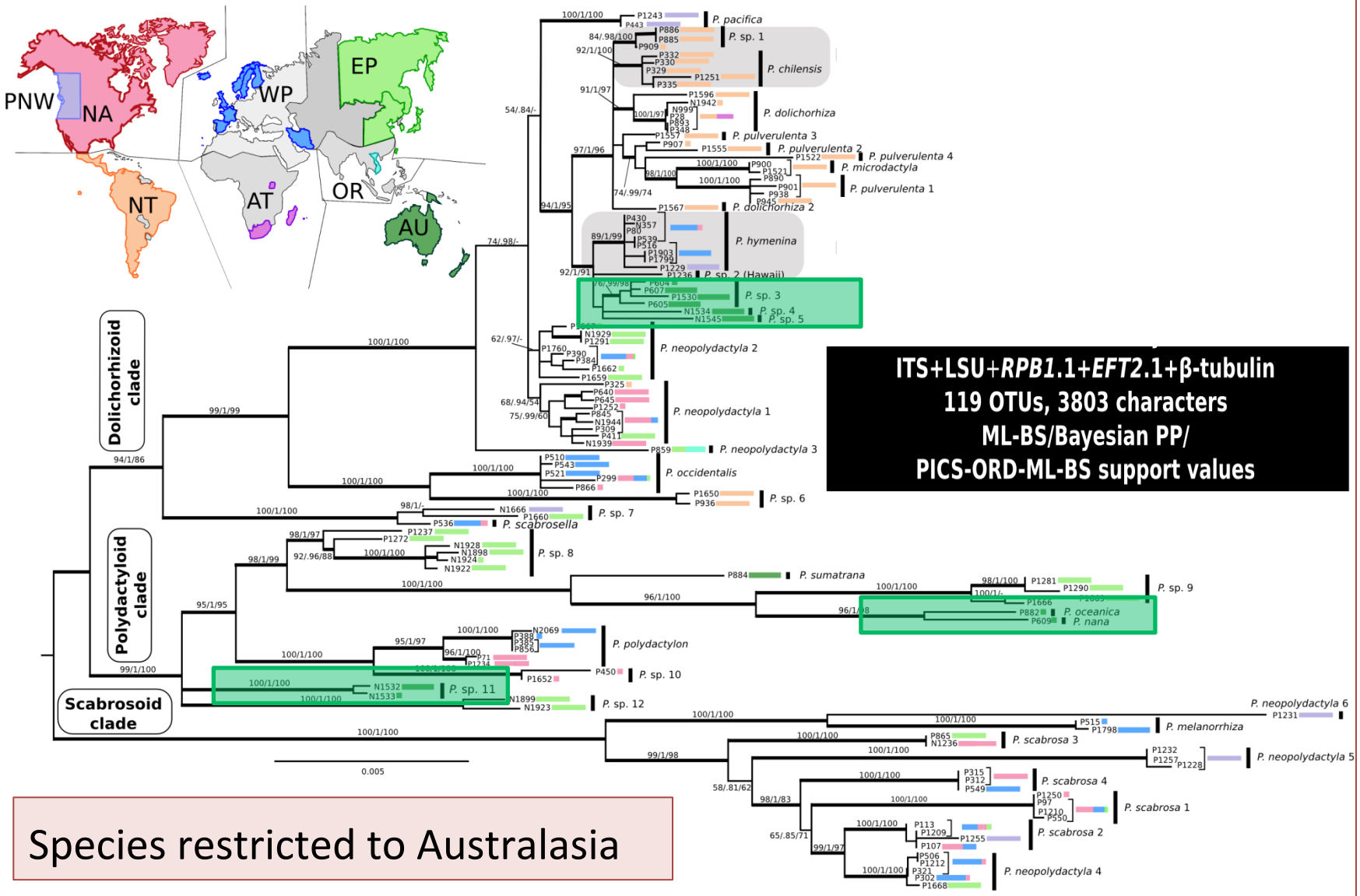


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Species restricted to Australasia

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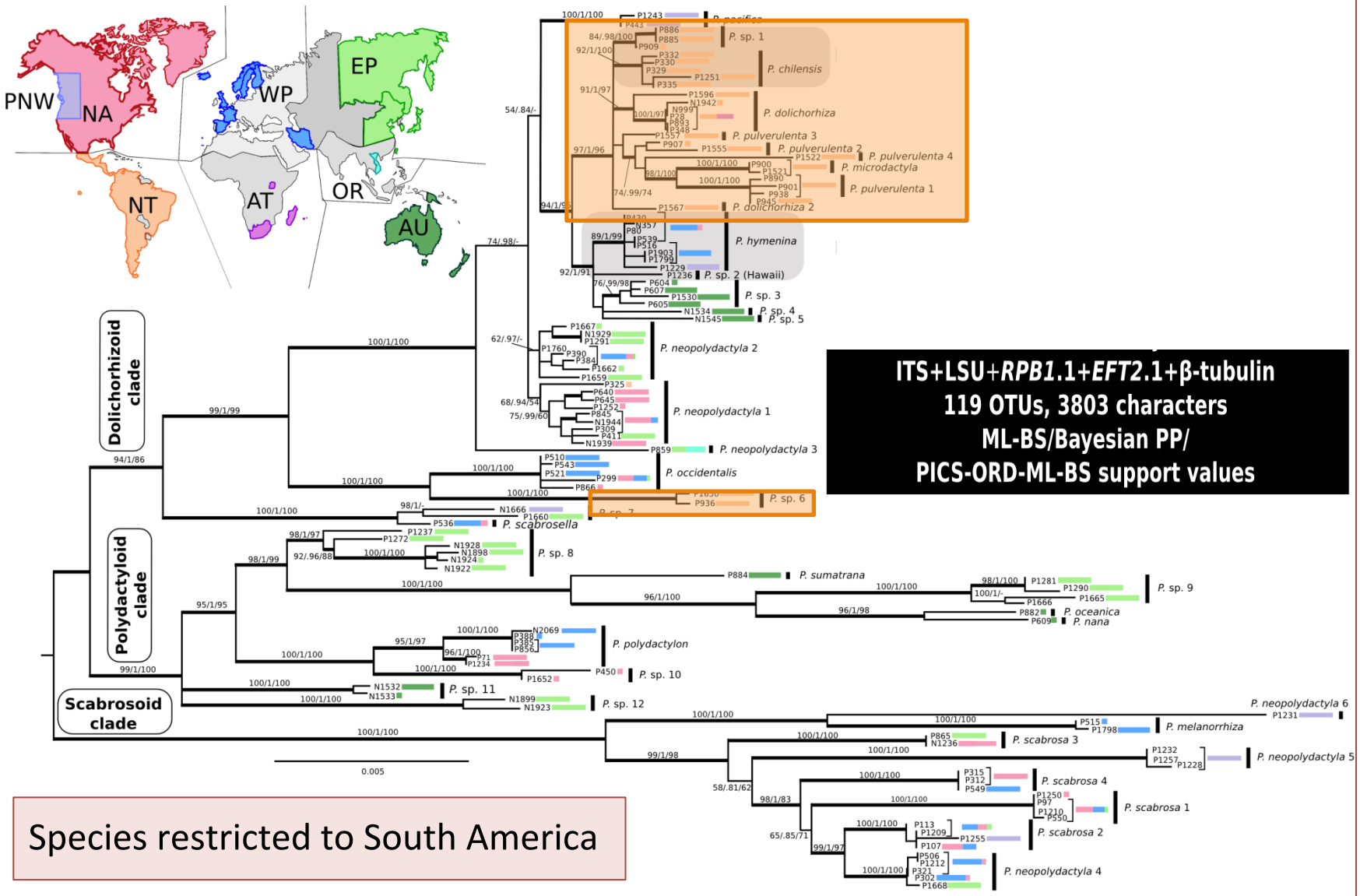


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Species restricted to South America

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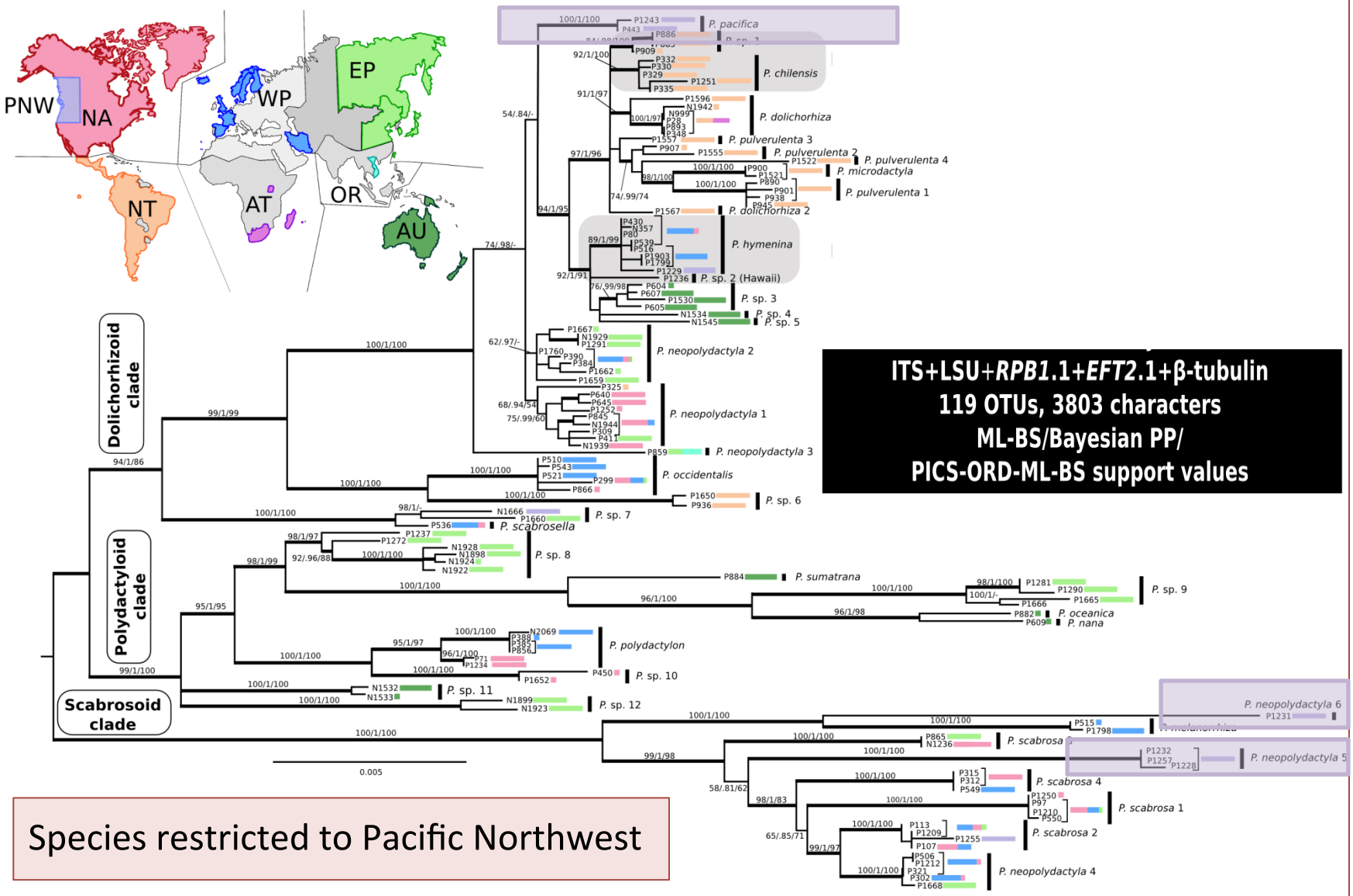


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Species restricted to Pacific Northwest

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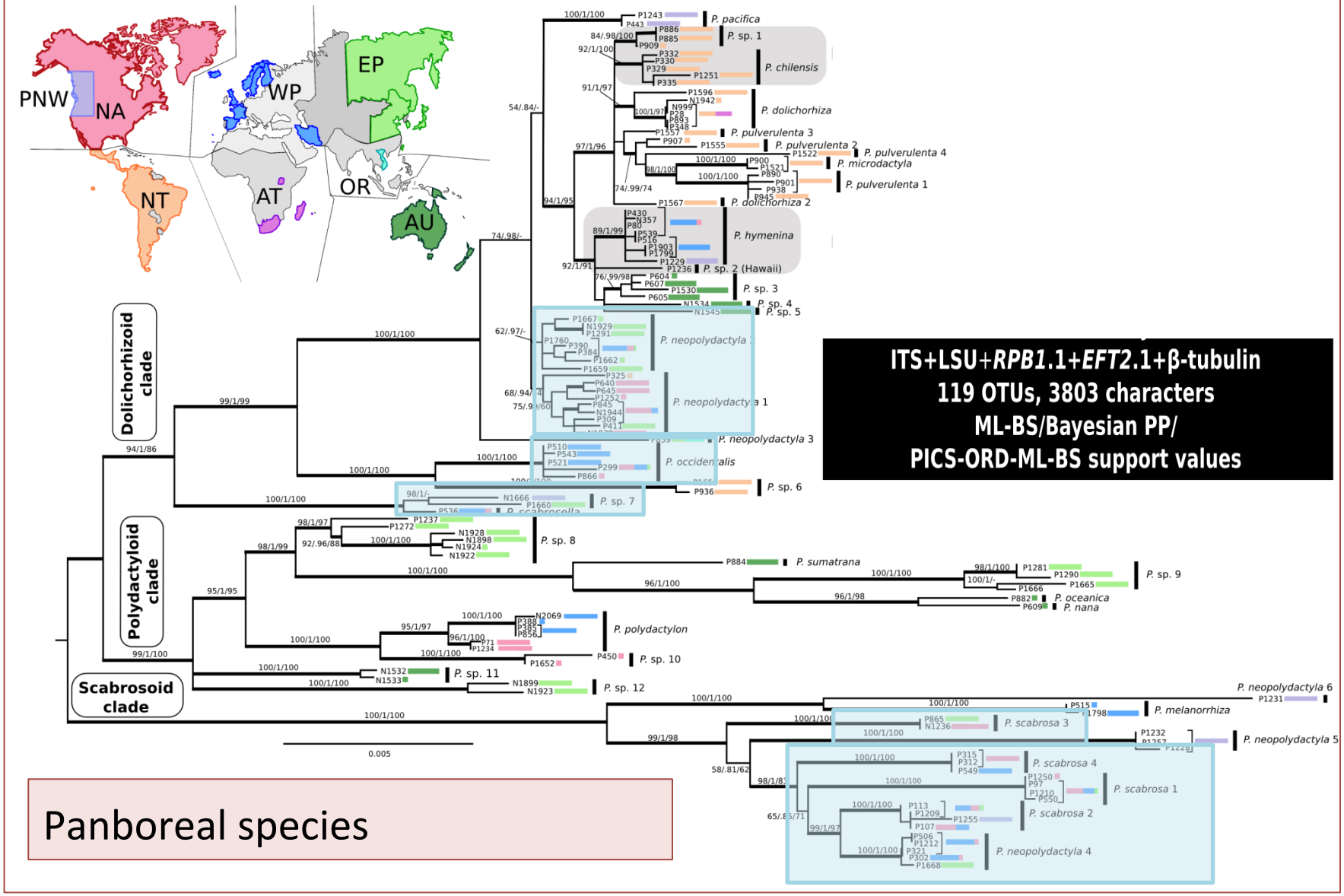


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Panboreal species

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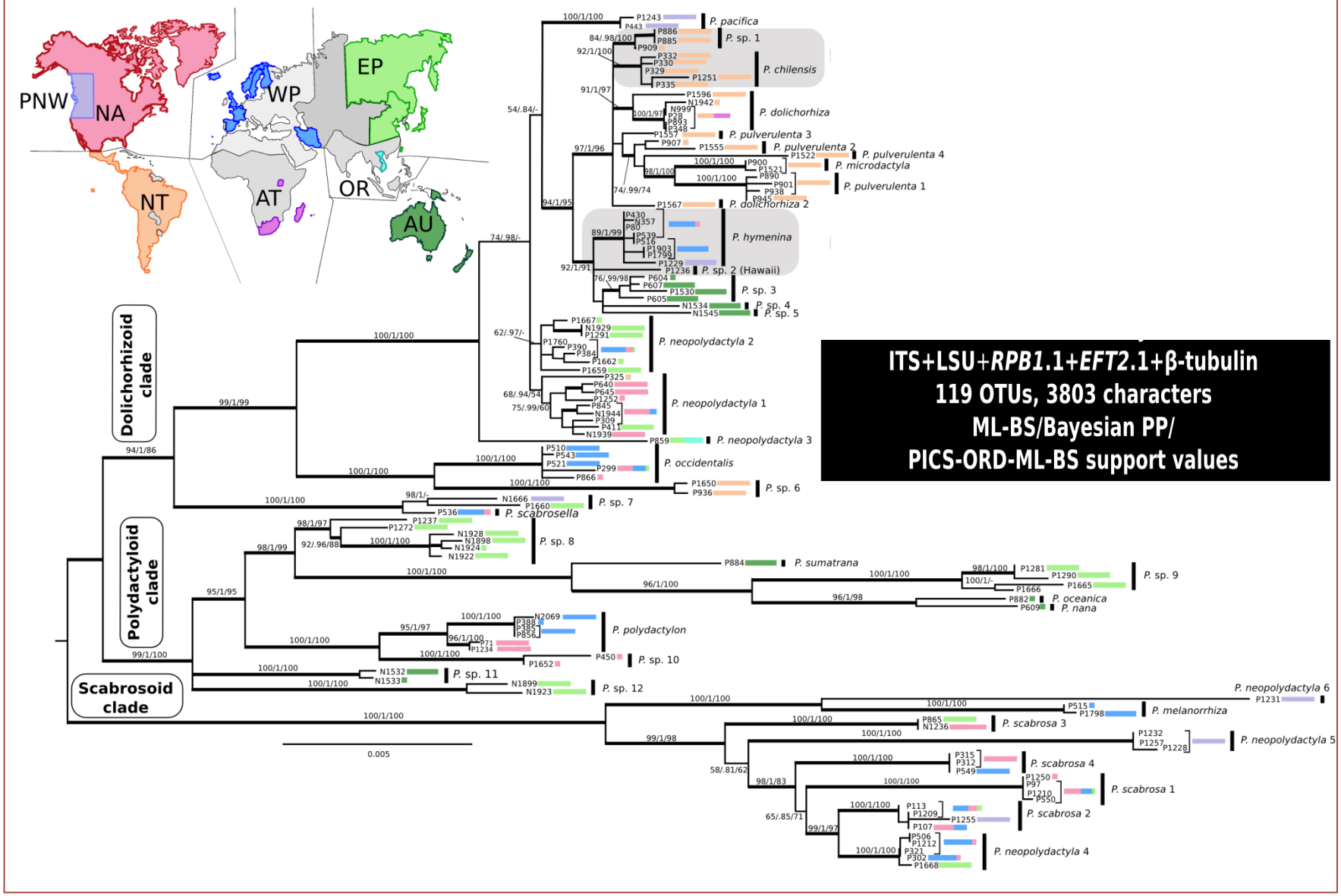

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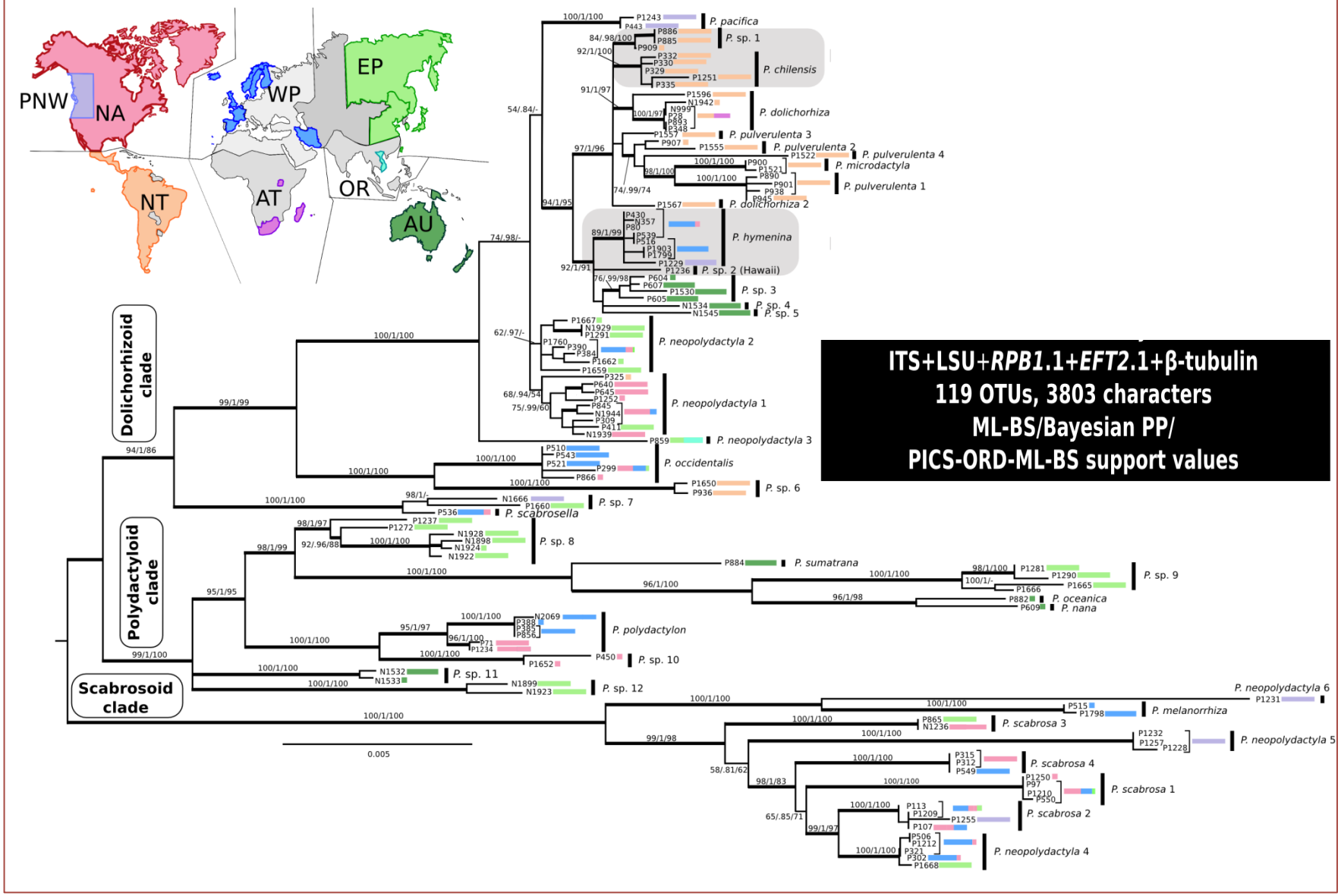

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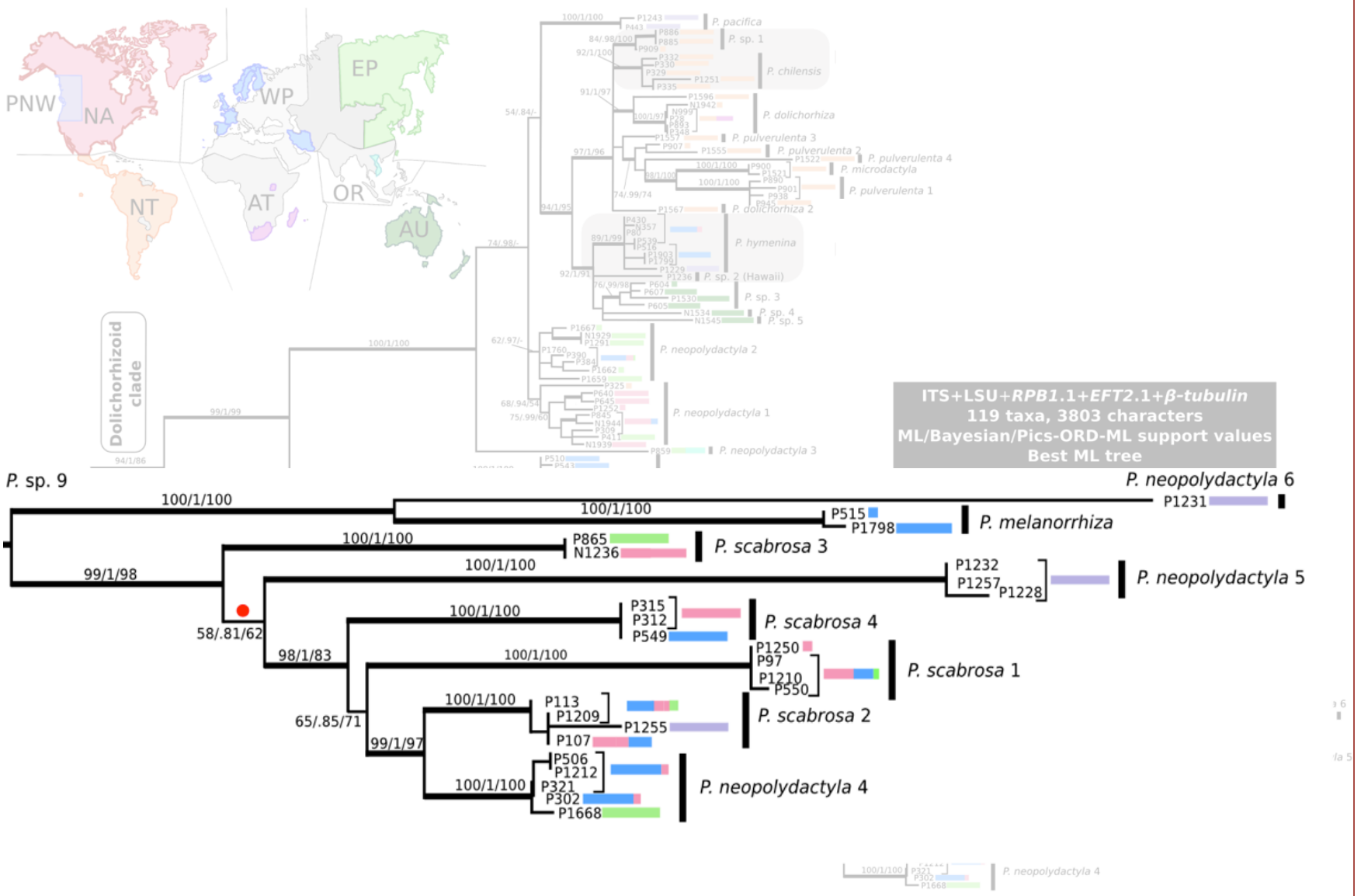

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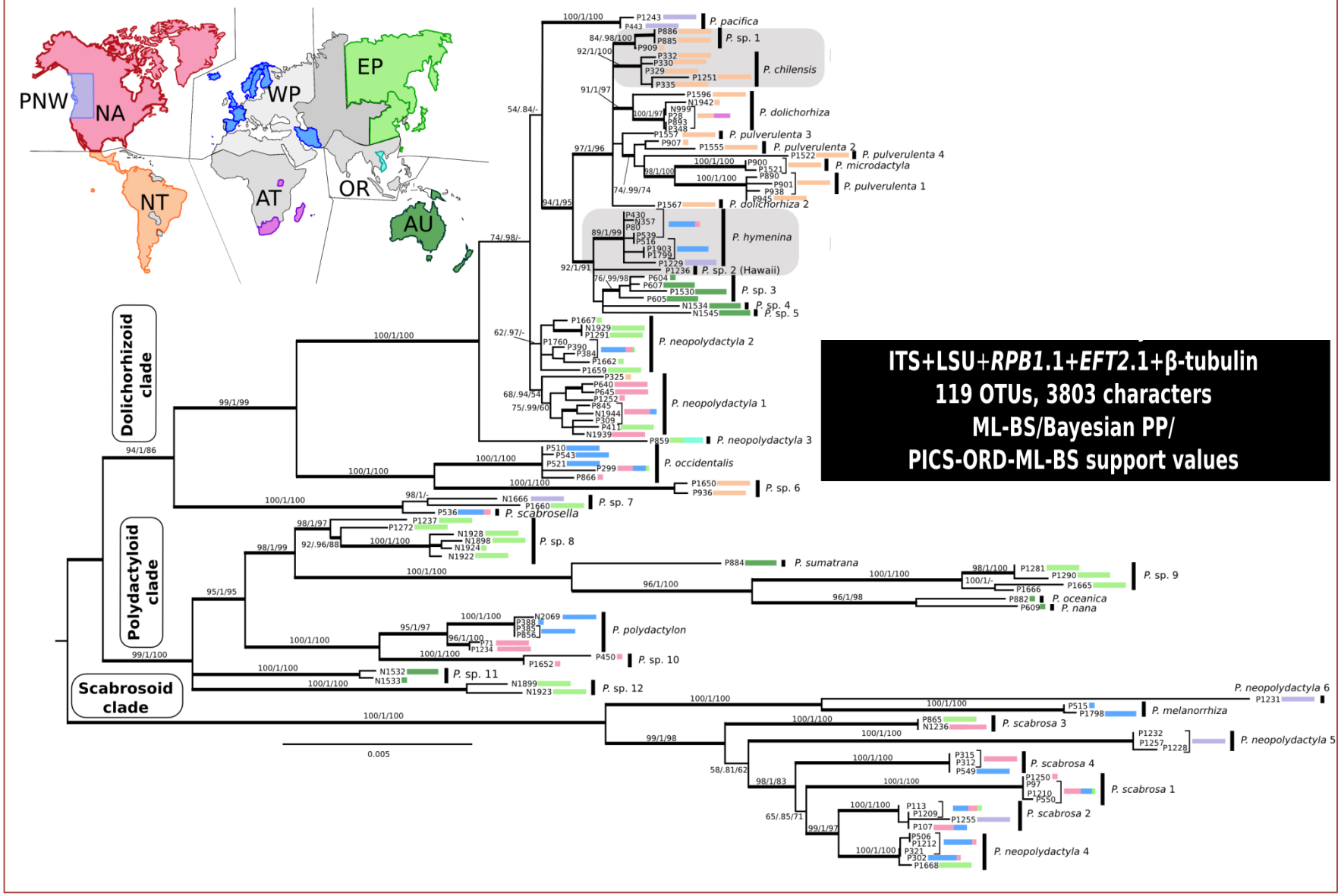

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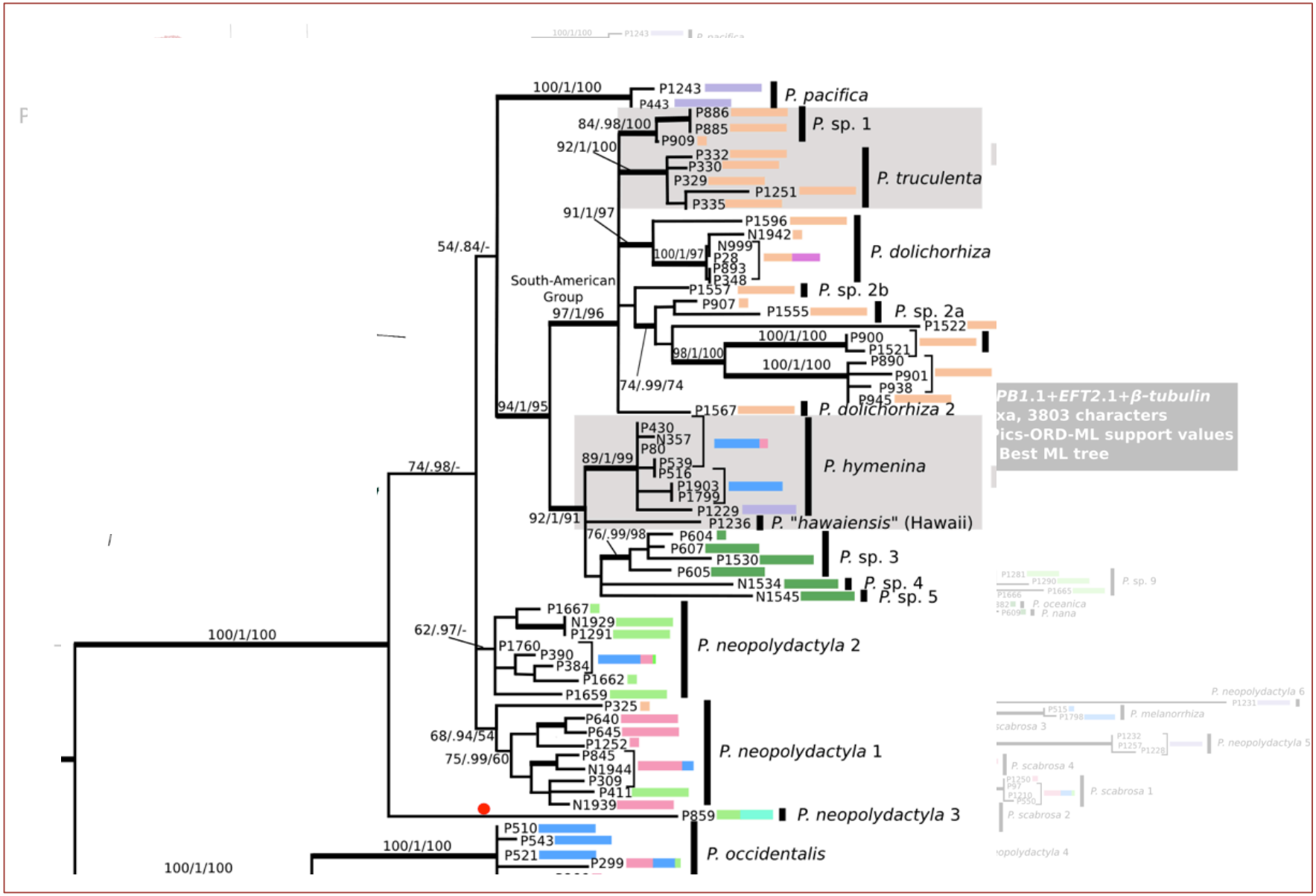
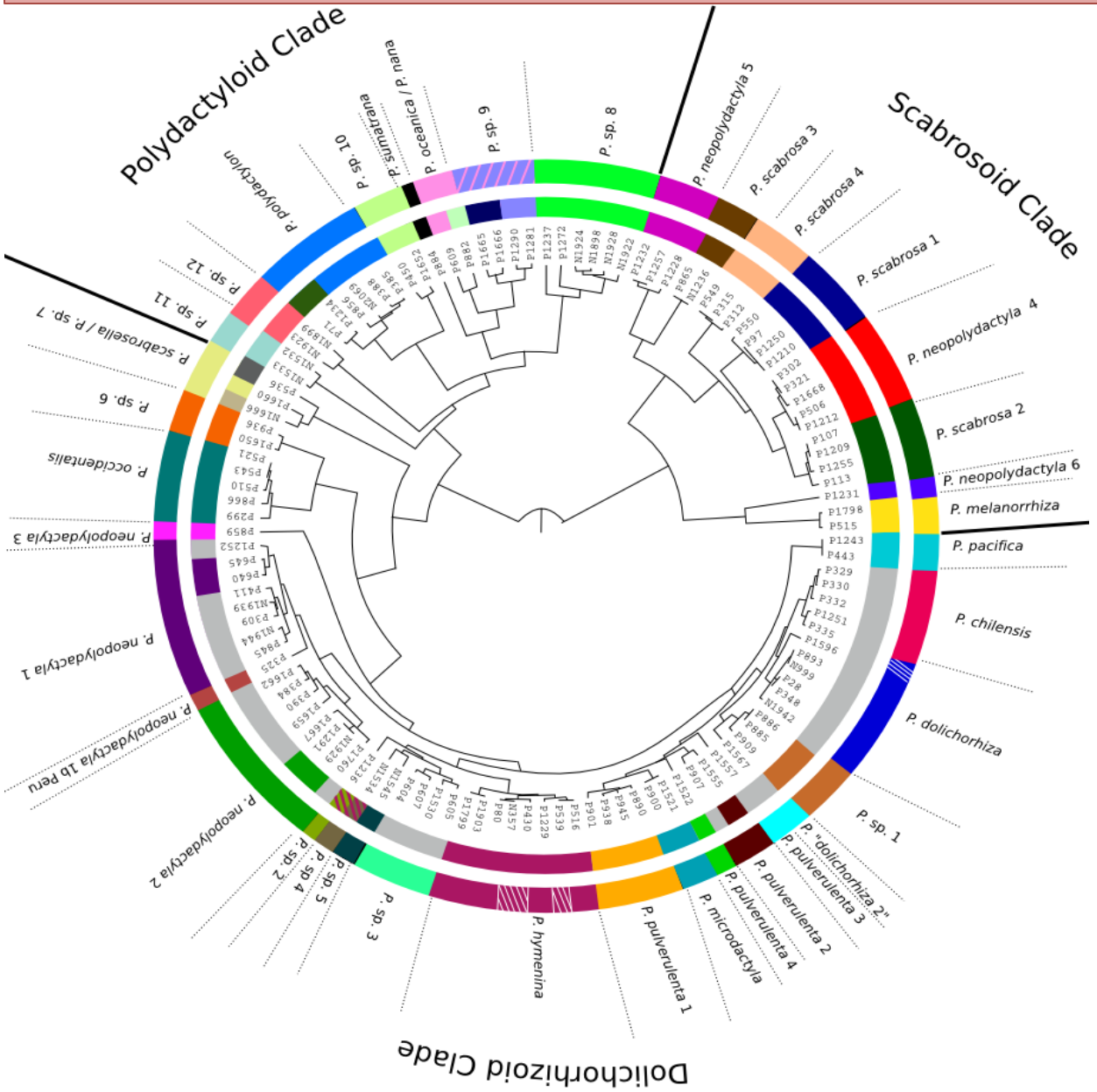
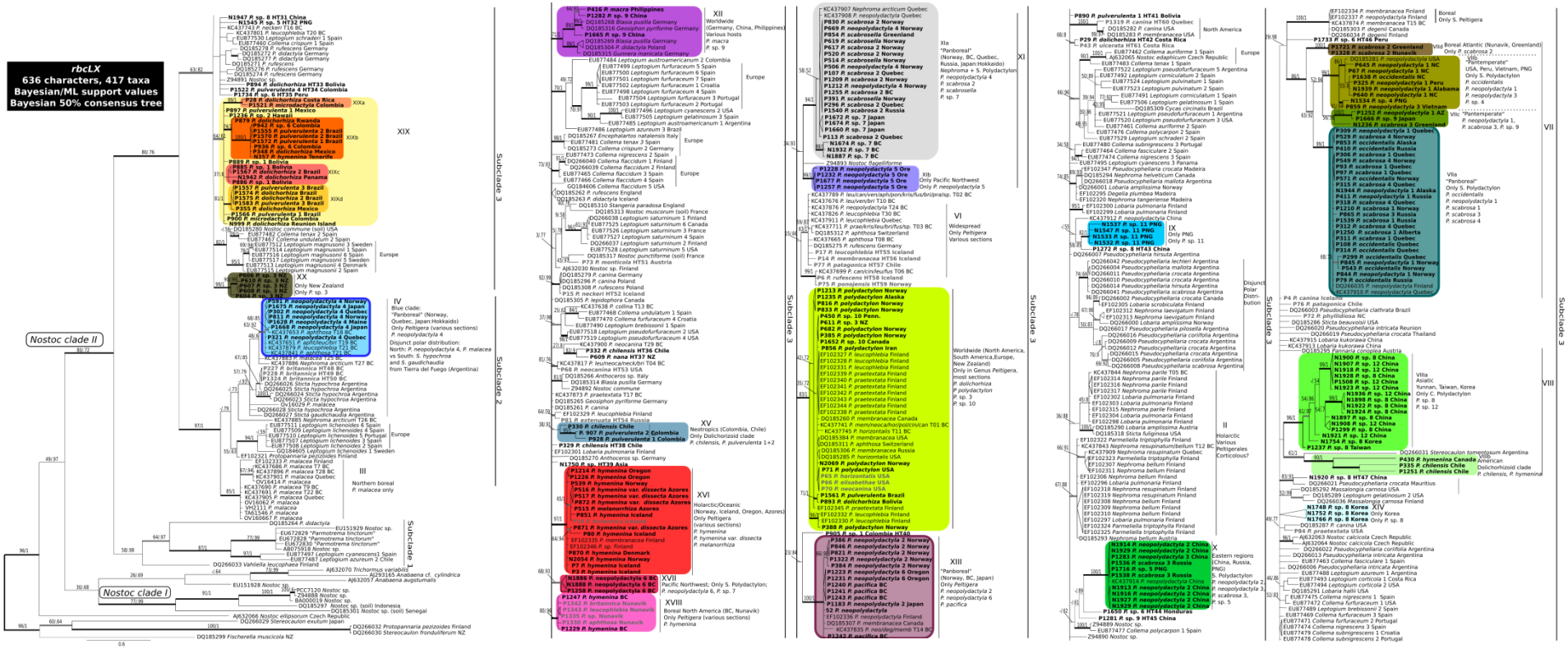


# 2a. Species delimitation (discovery)



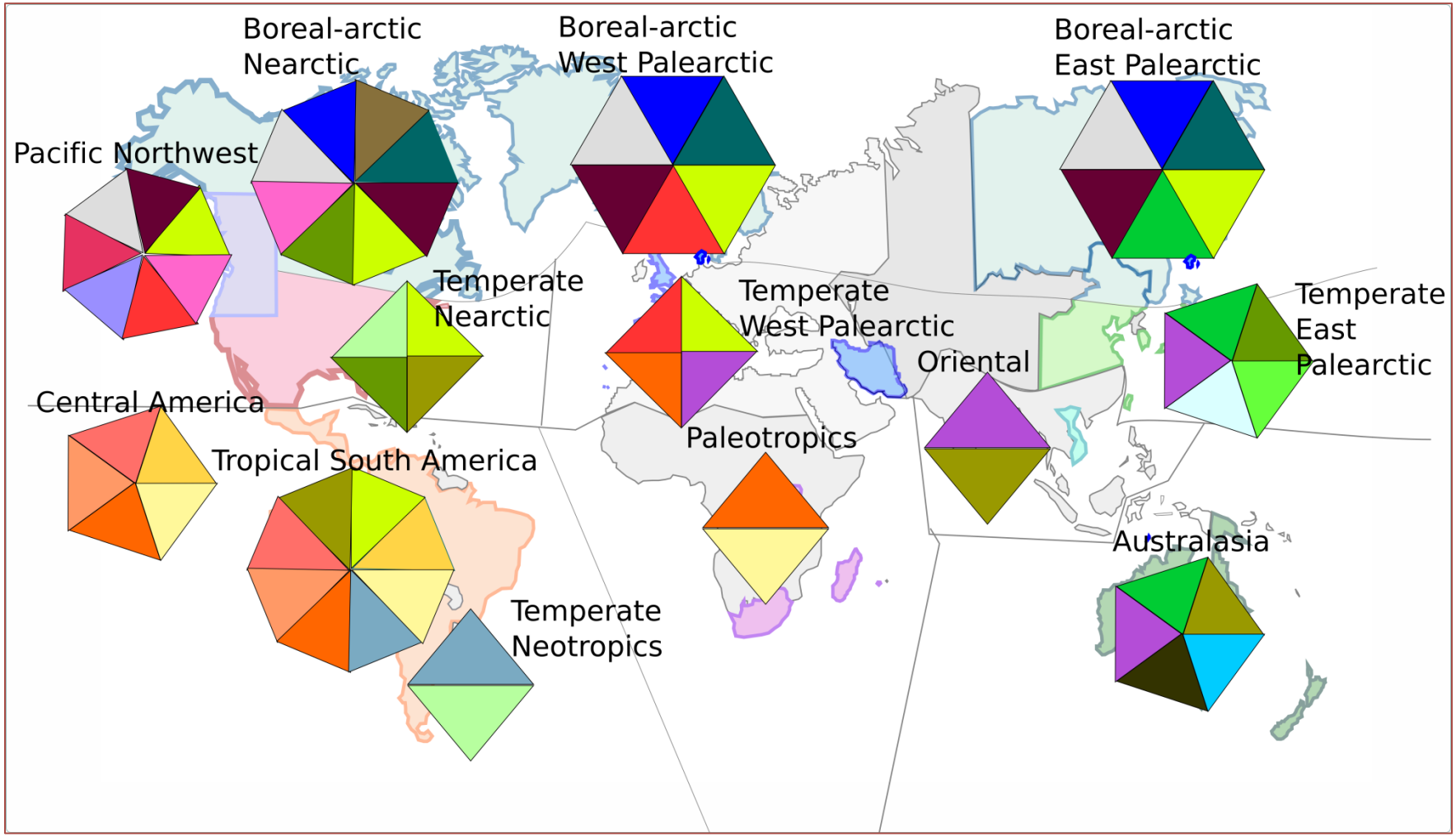

- 2 methods: Structurama (all loci) and bGMYC (ITS)
- Attribute « provisional species » to the samples used in the analyses

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




- 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

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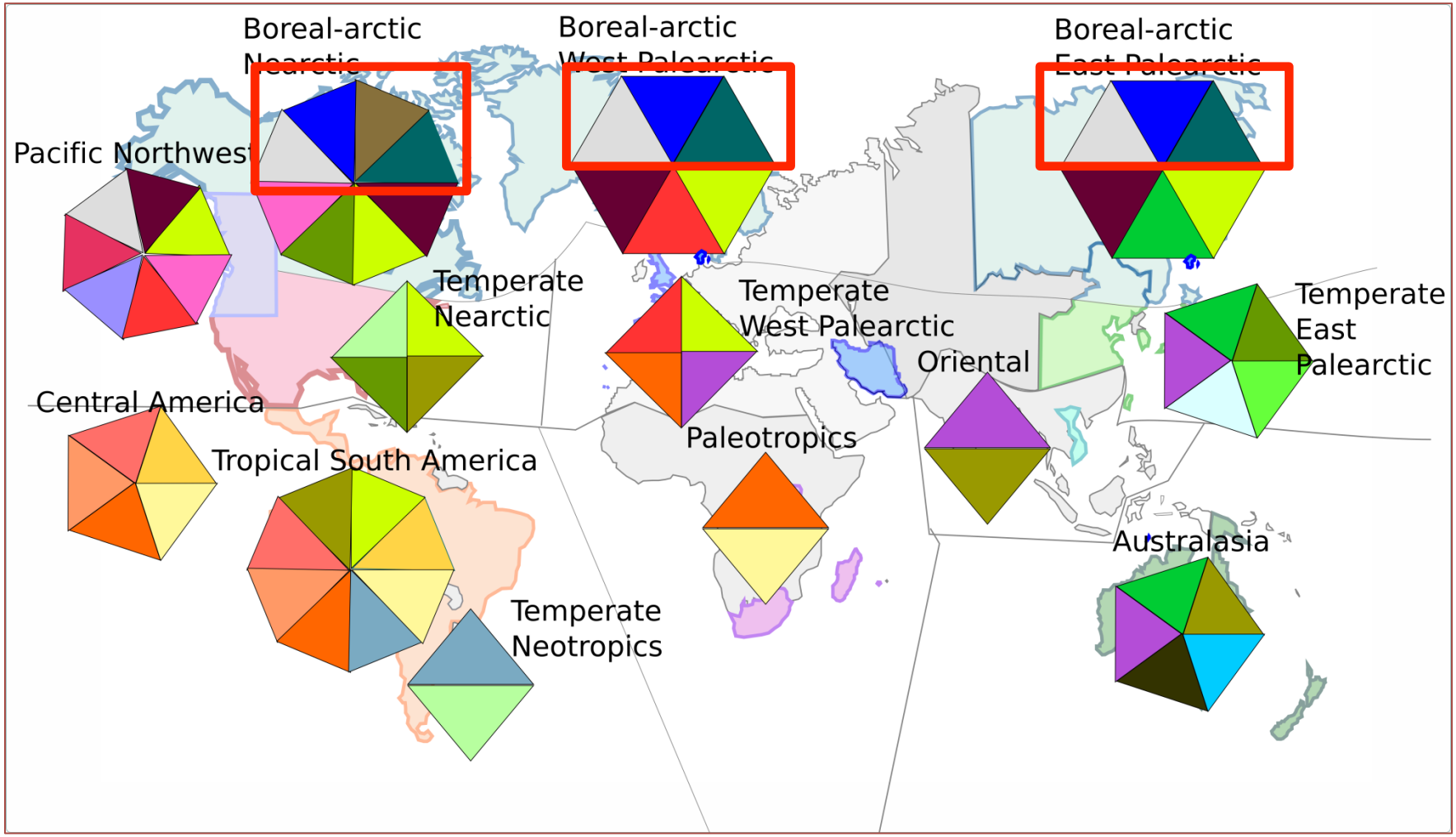


Boreal phylogroups

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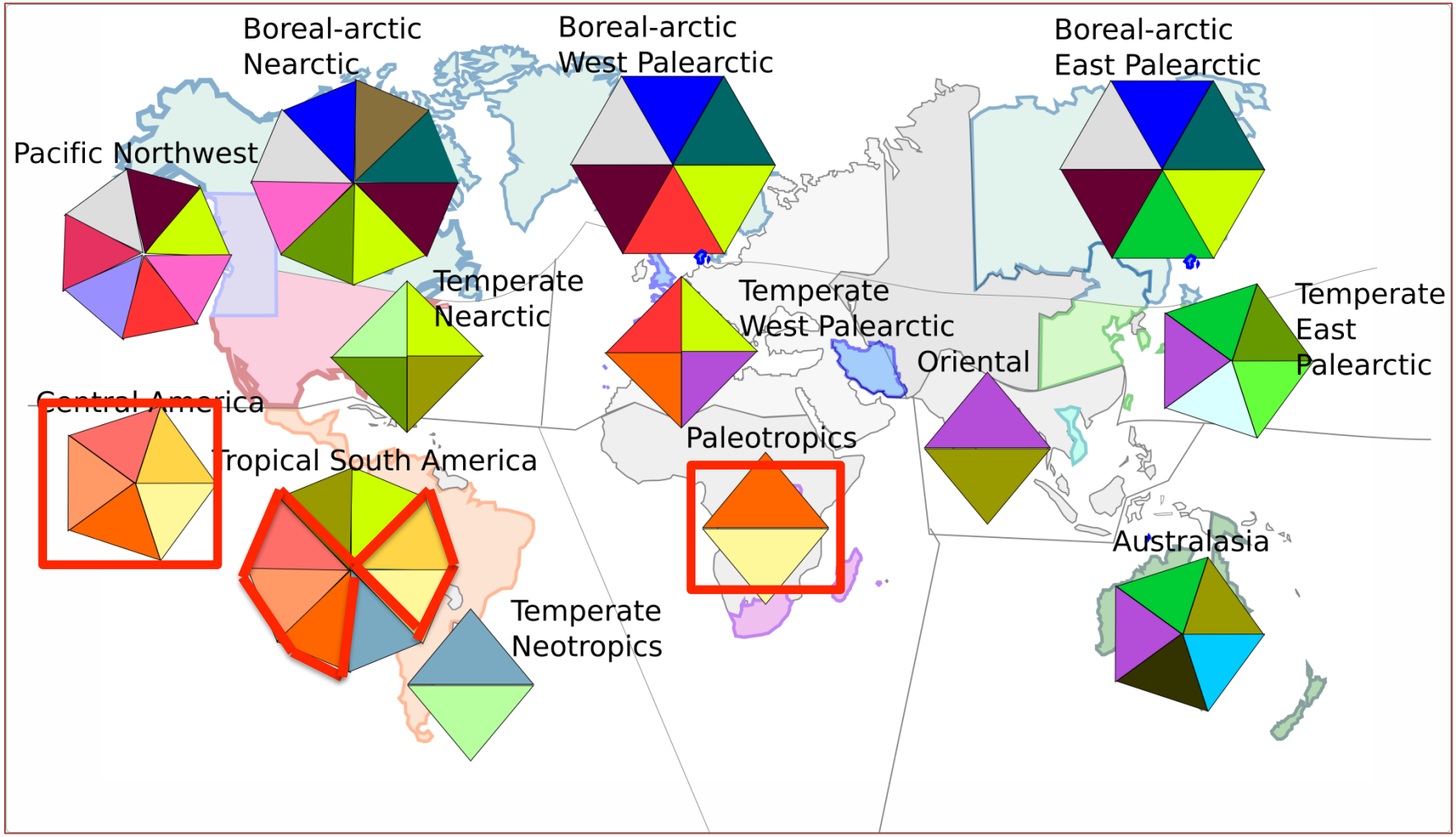


Tropical phylogroups

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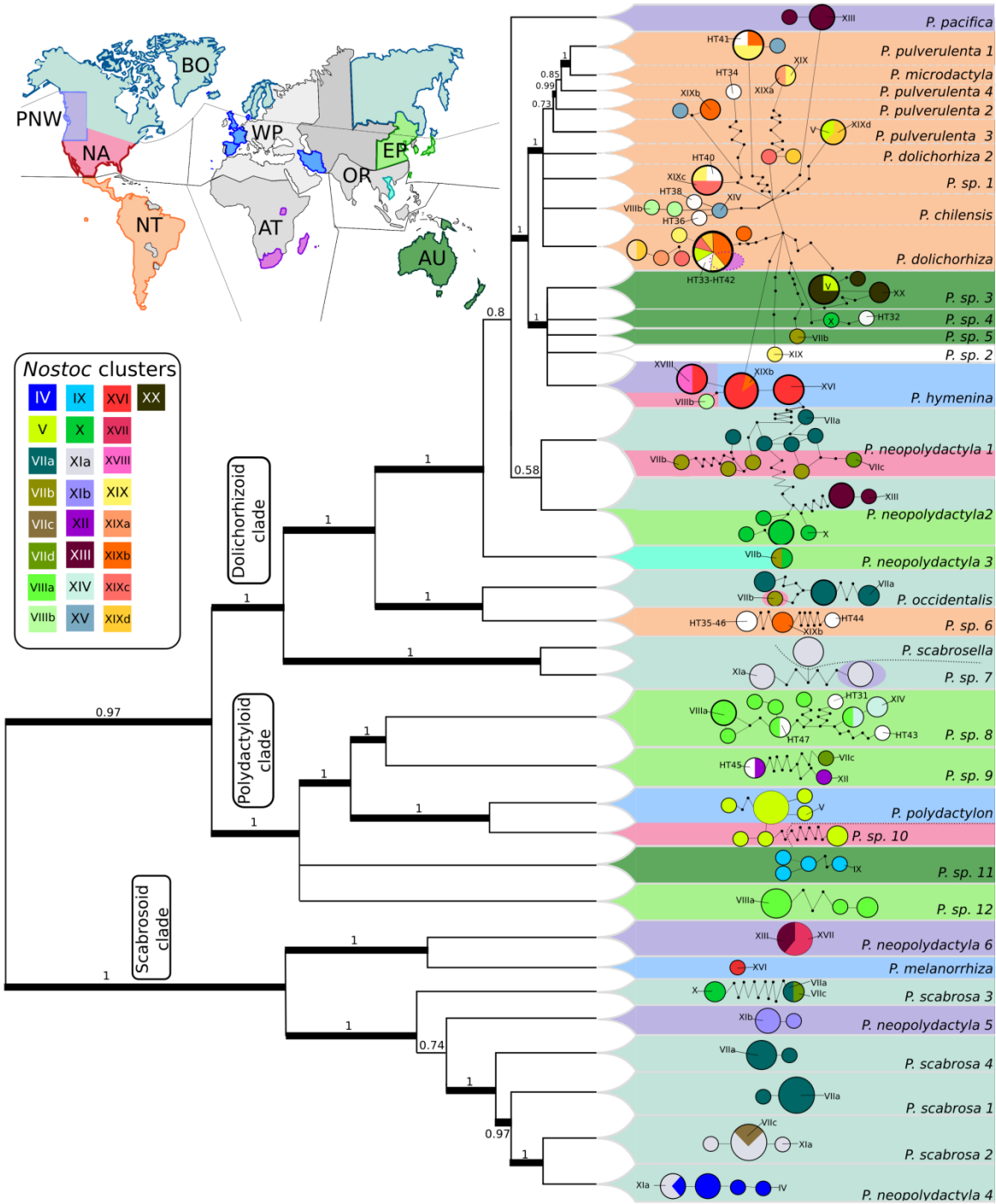
*Consider these results in light of various hypotheses of evolution of mutualism

# 2a. Specificity of the symbionts

- 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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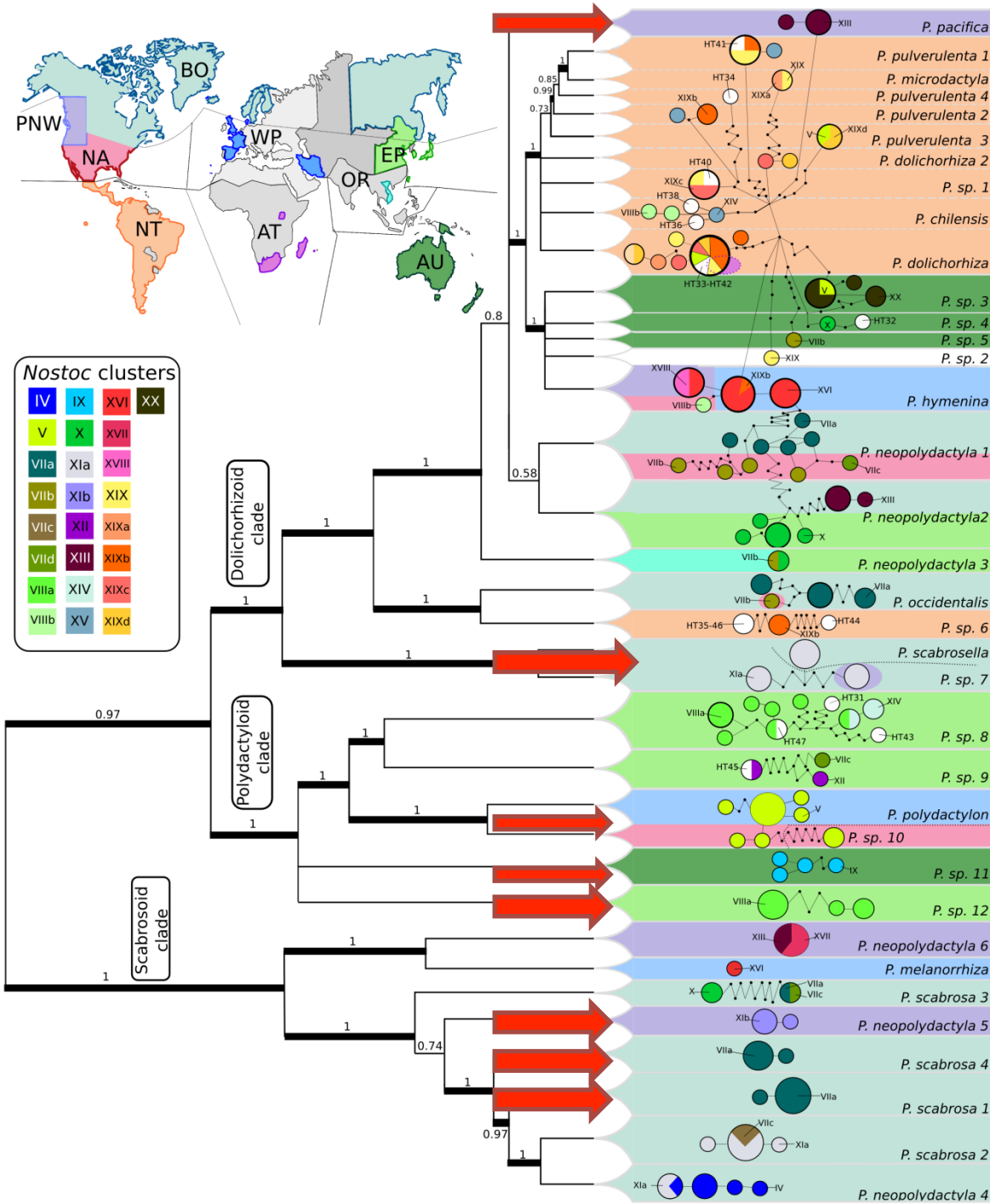

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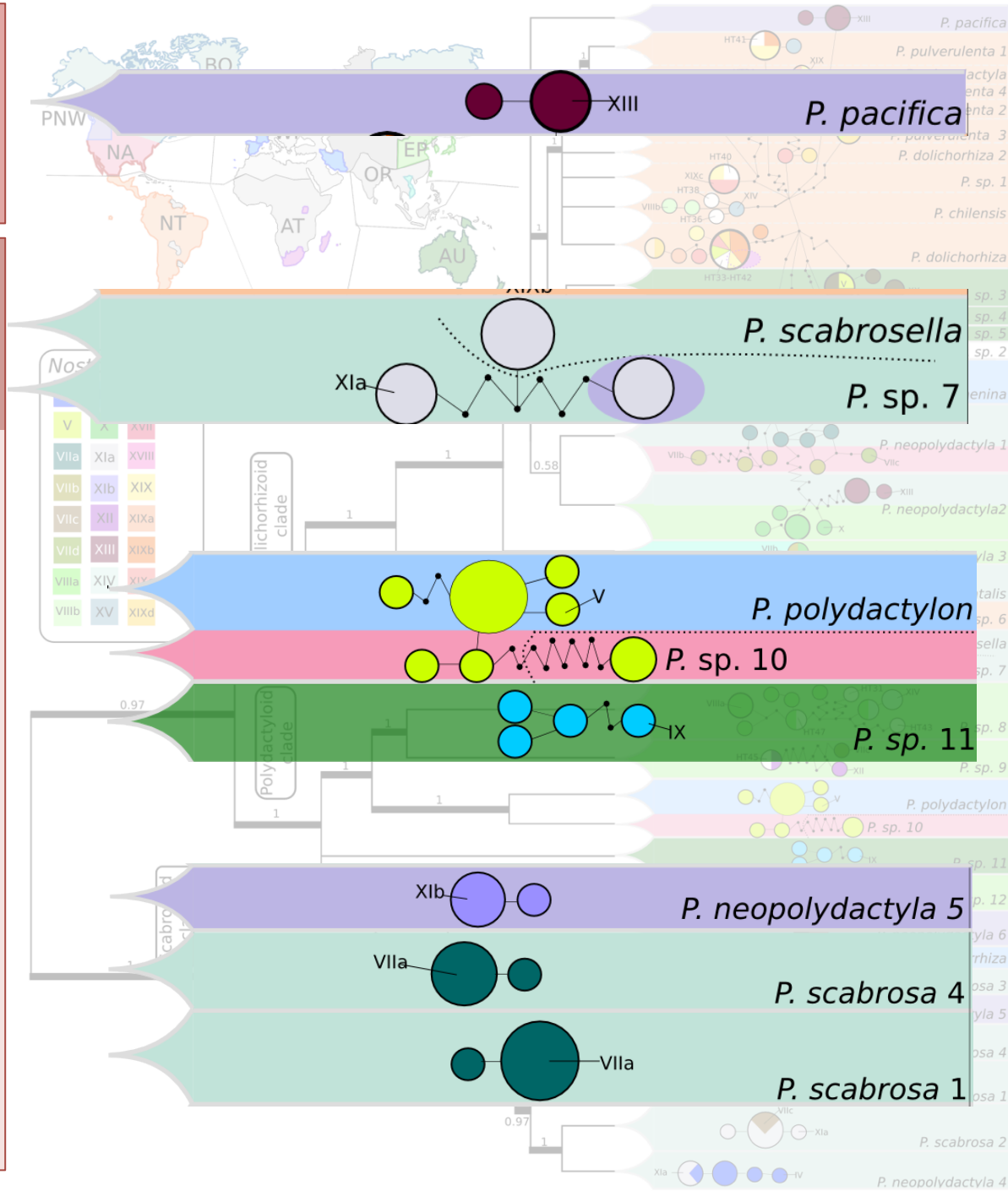

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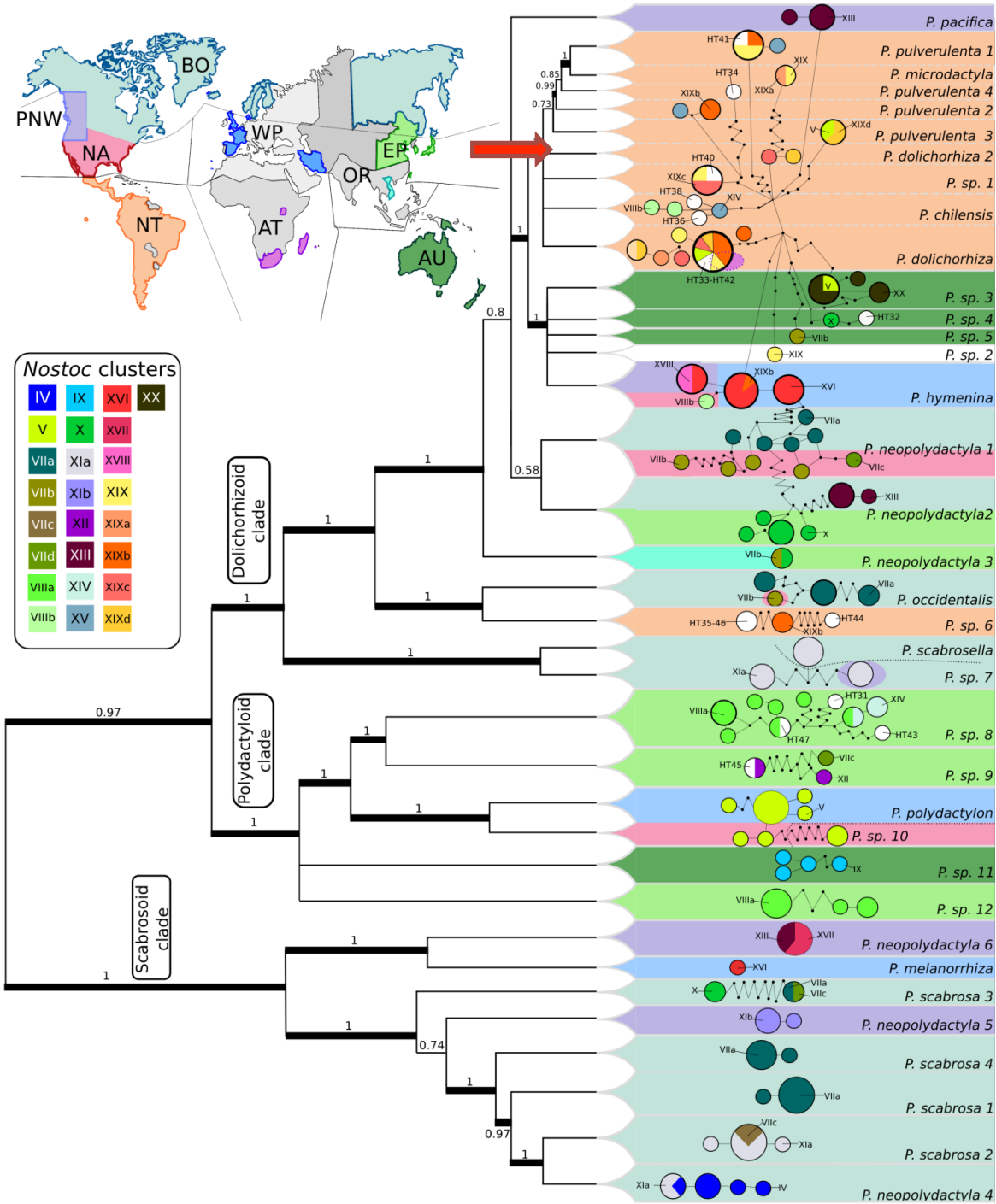

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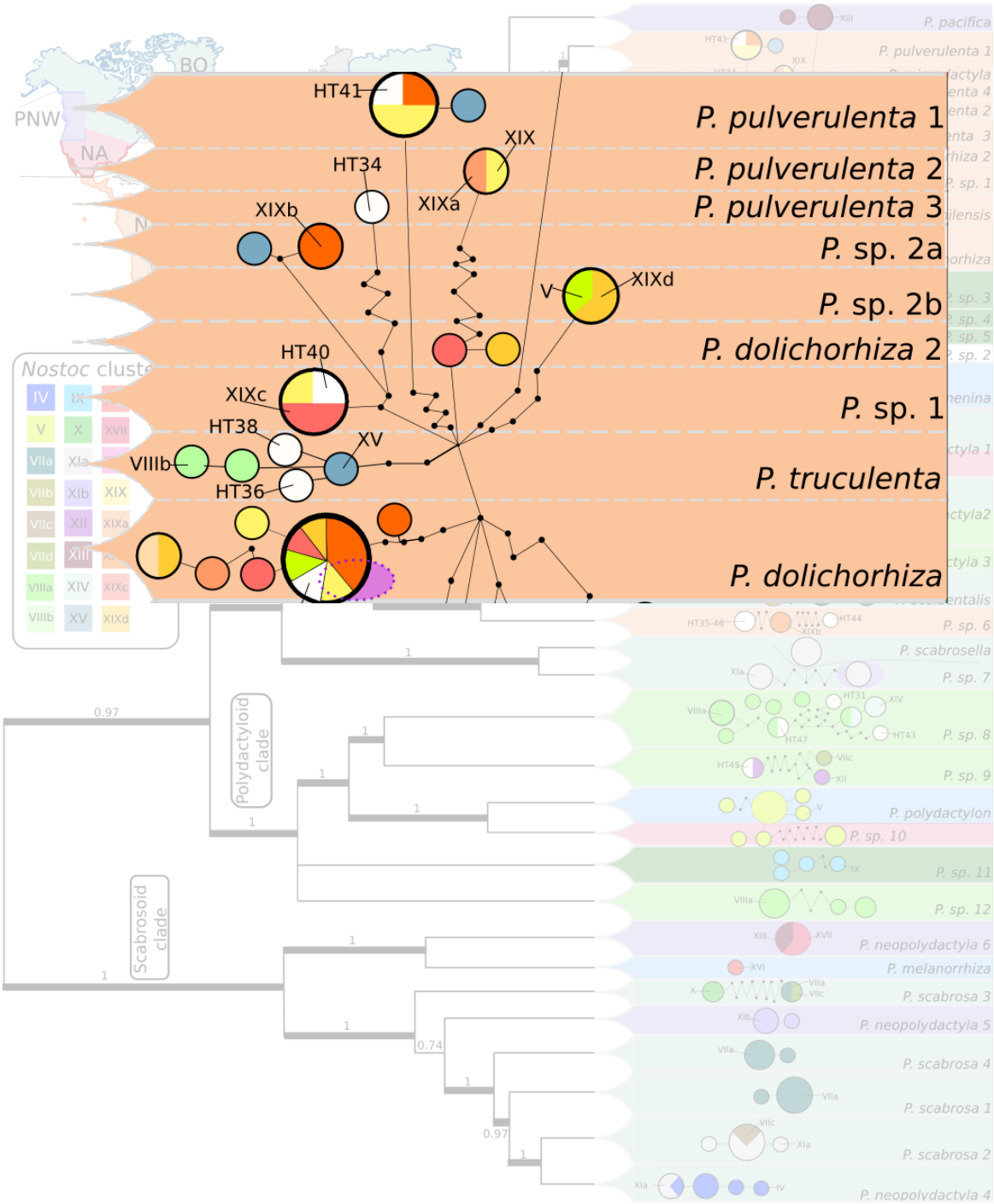

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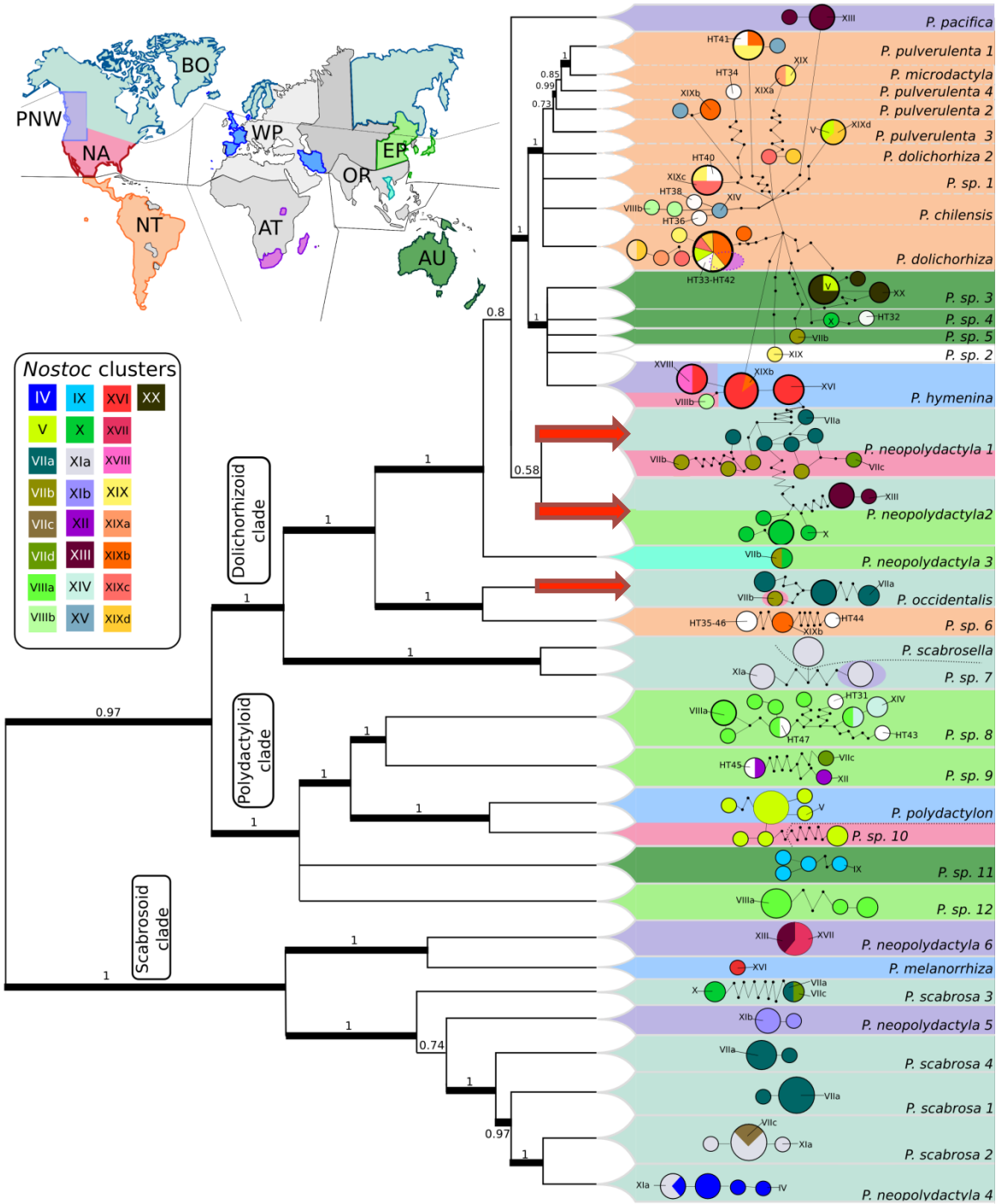

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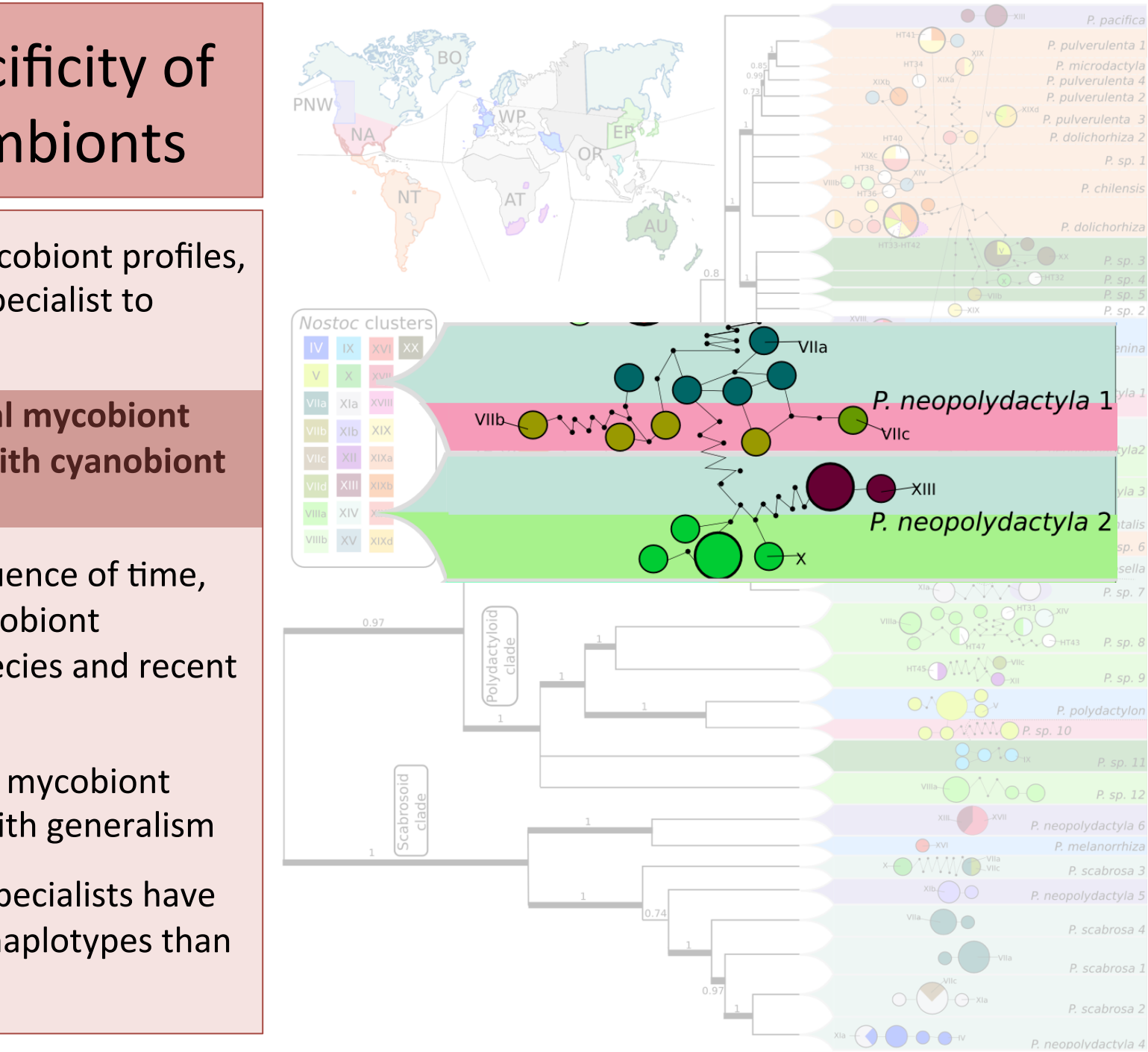
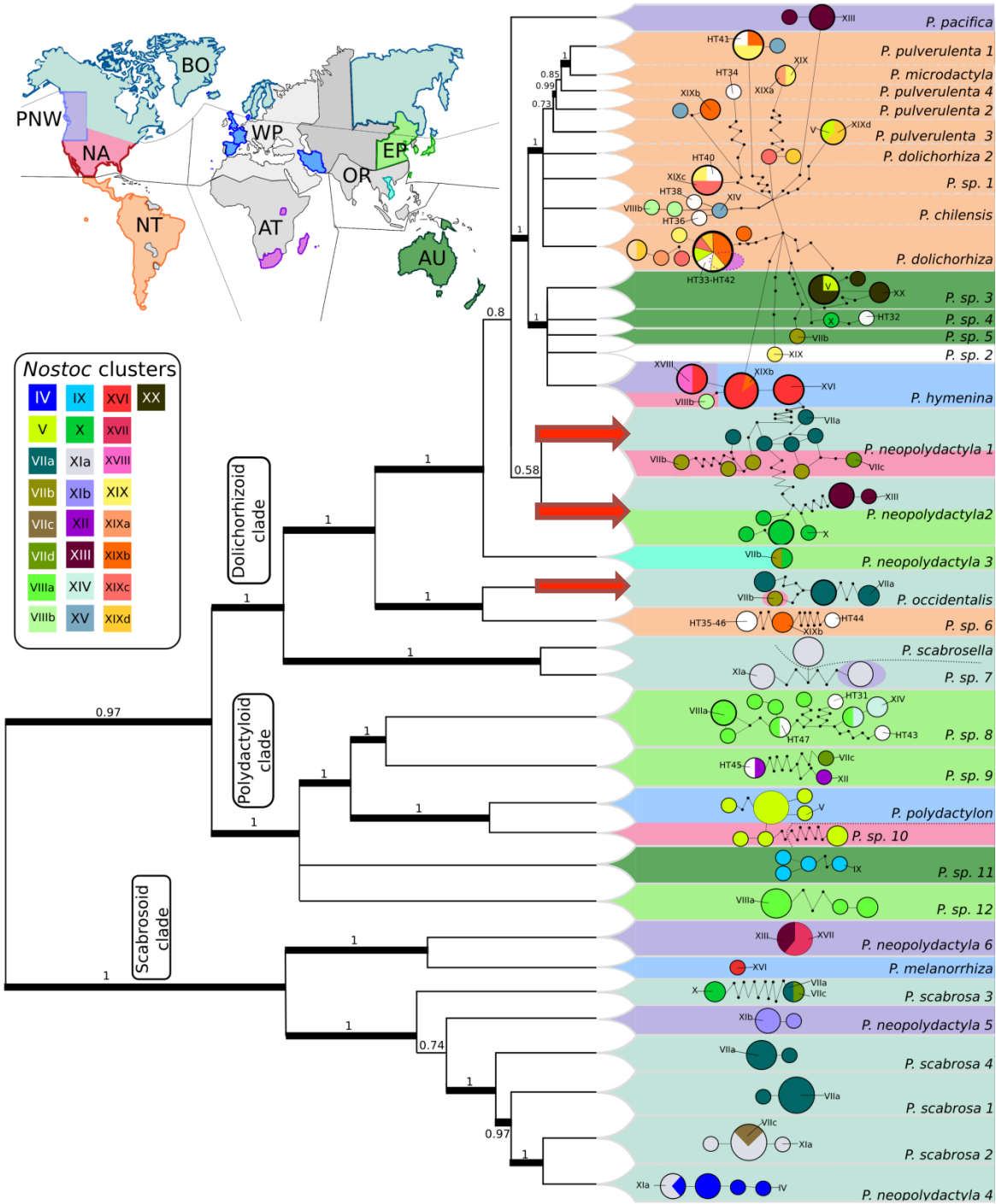


# Geographic mosaic of coevolution theory (Thompson)

- 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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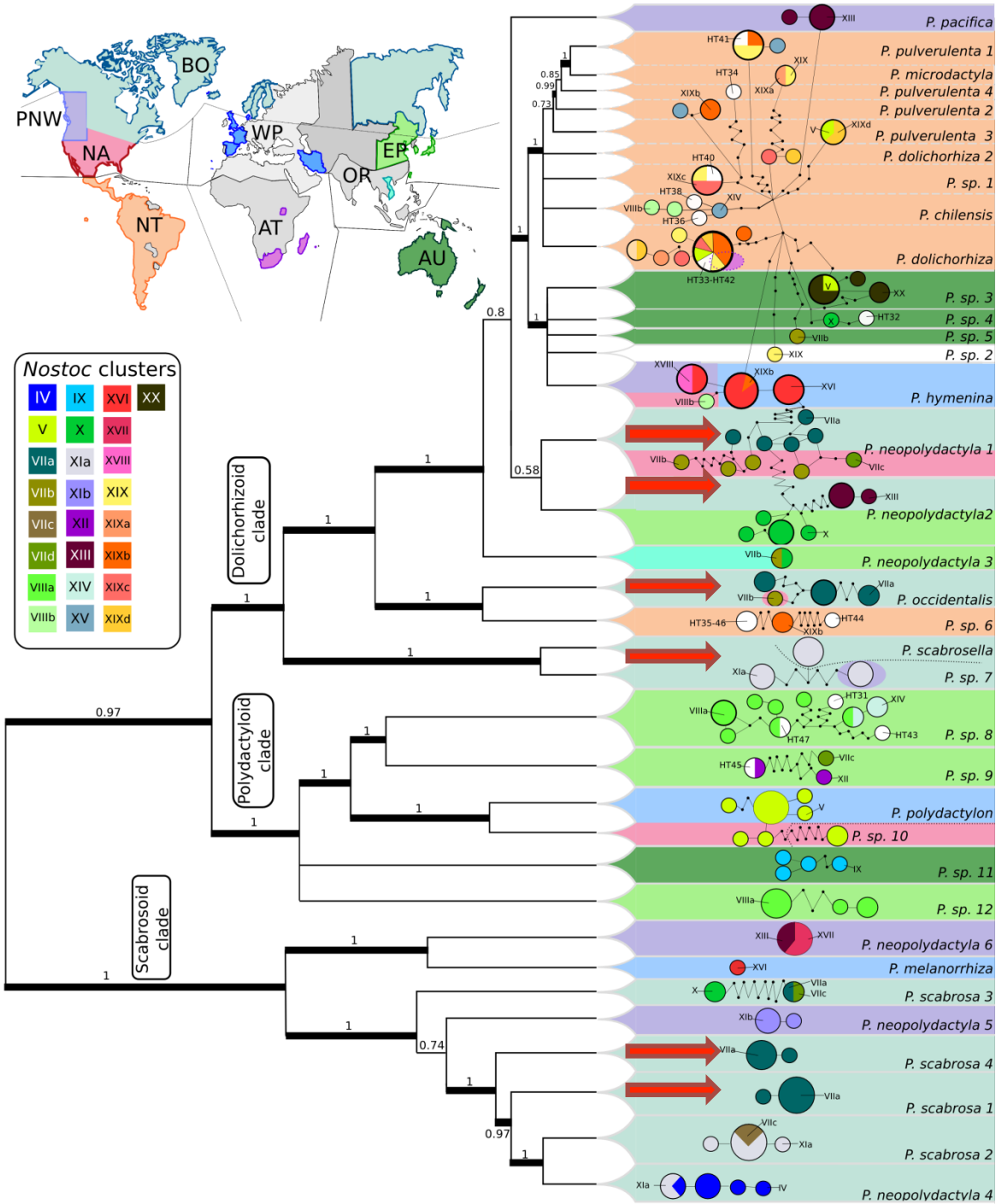

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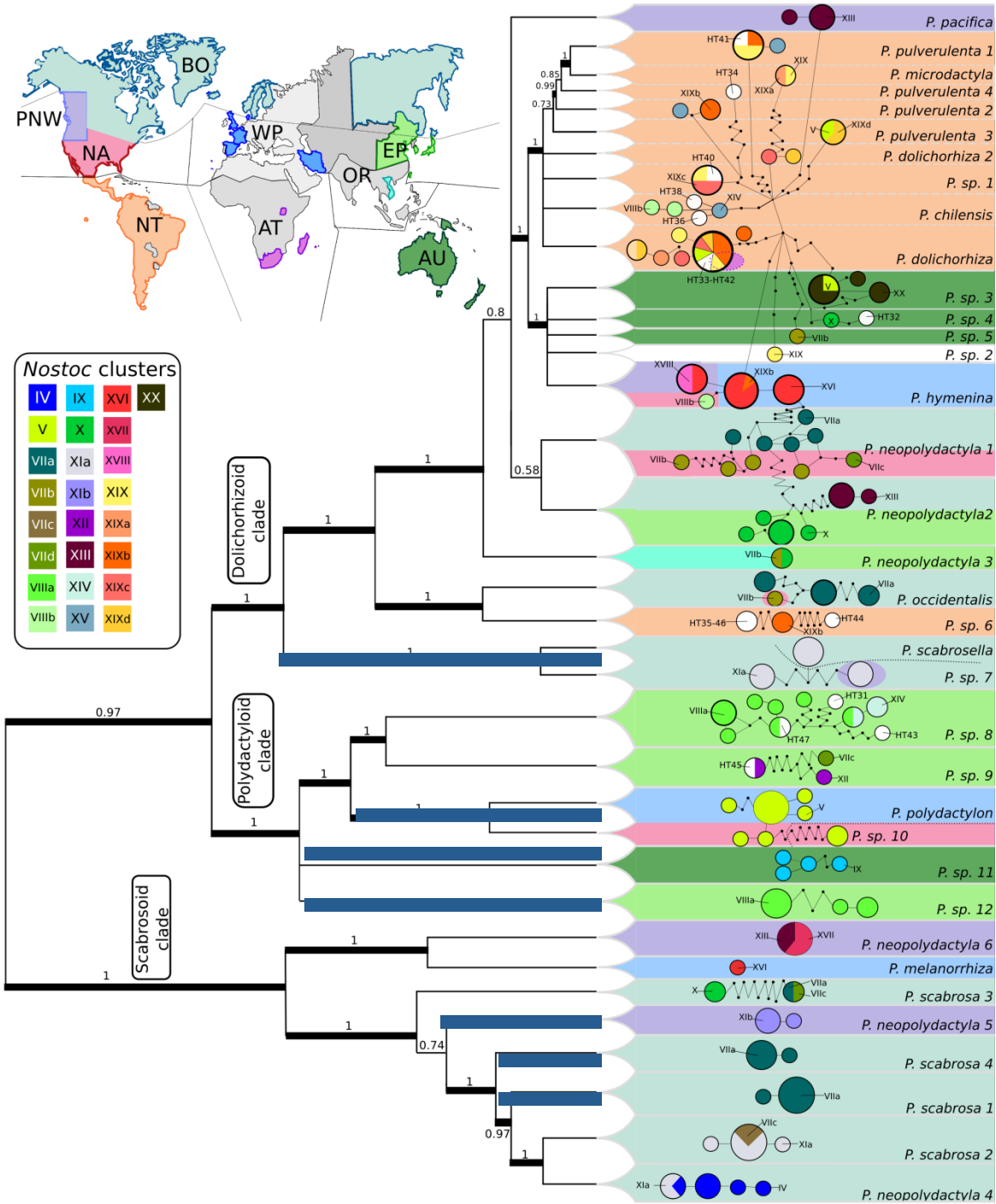

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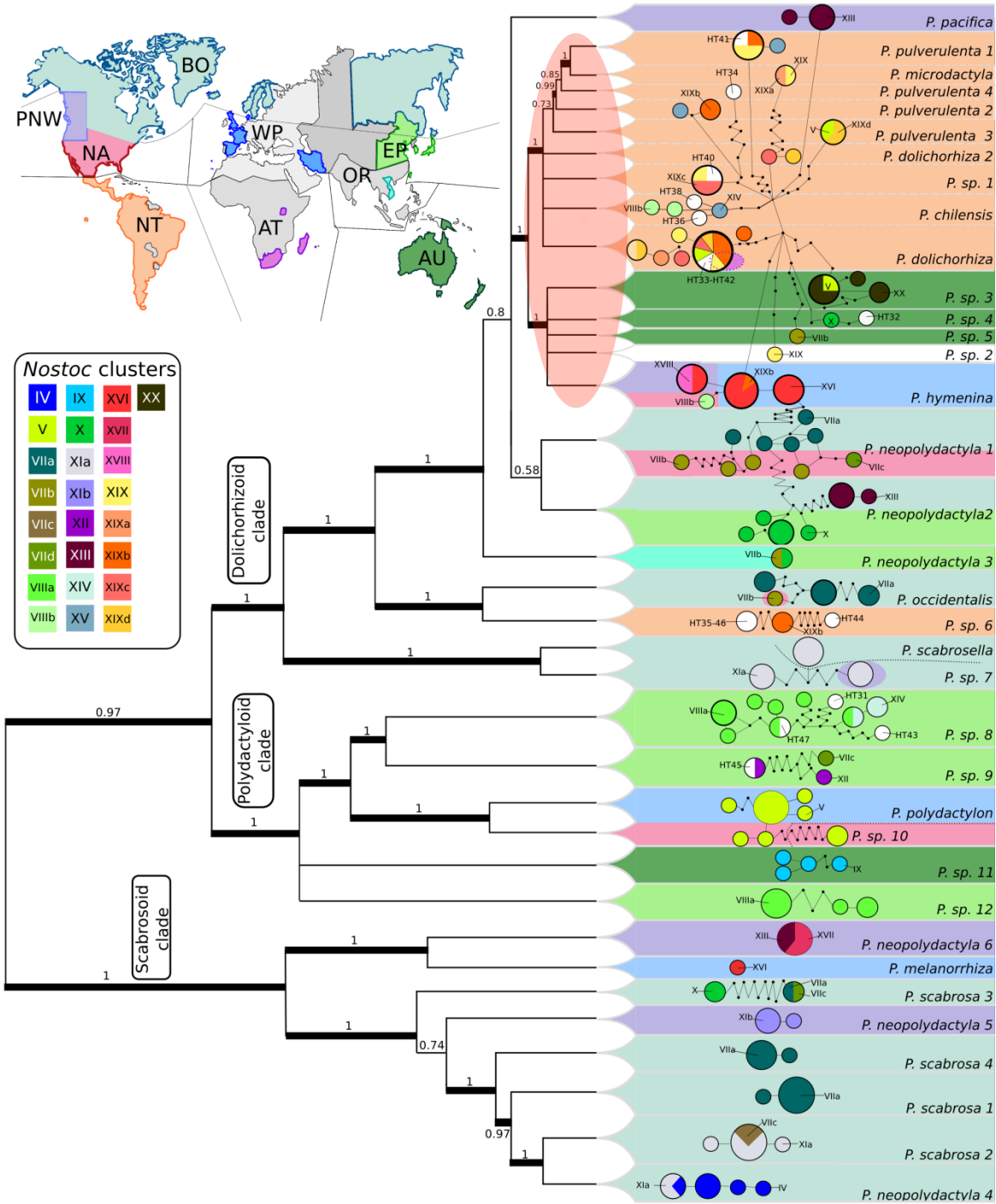

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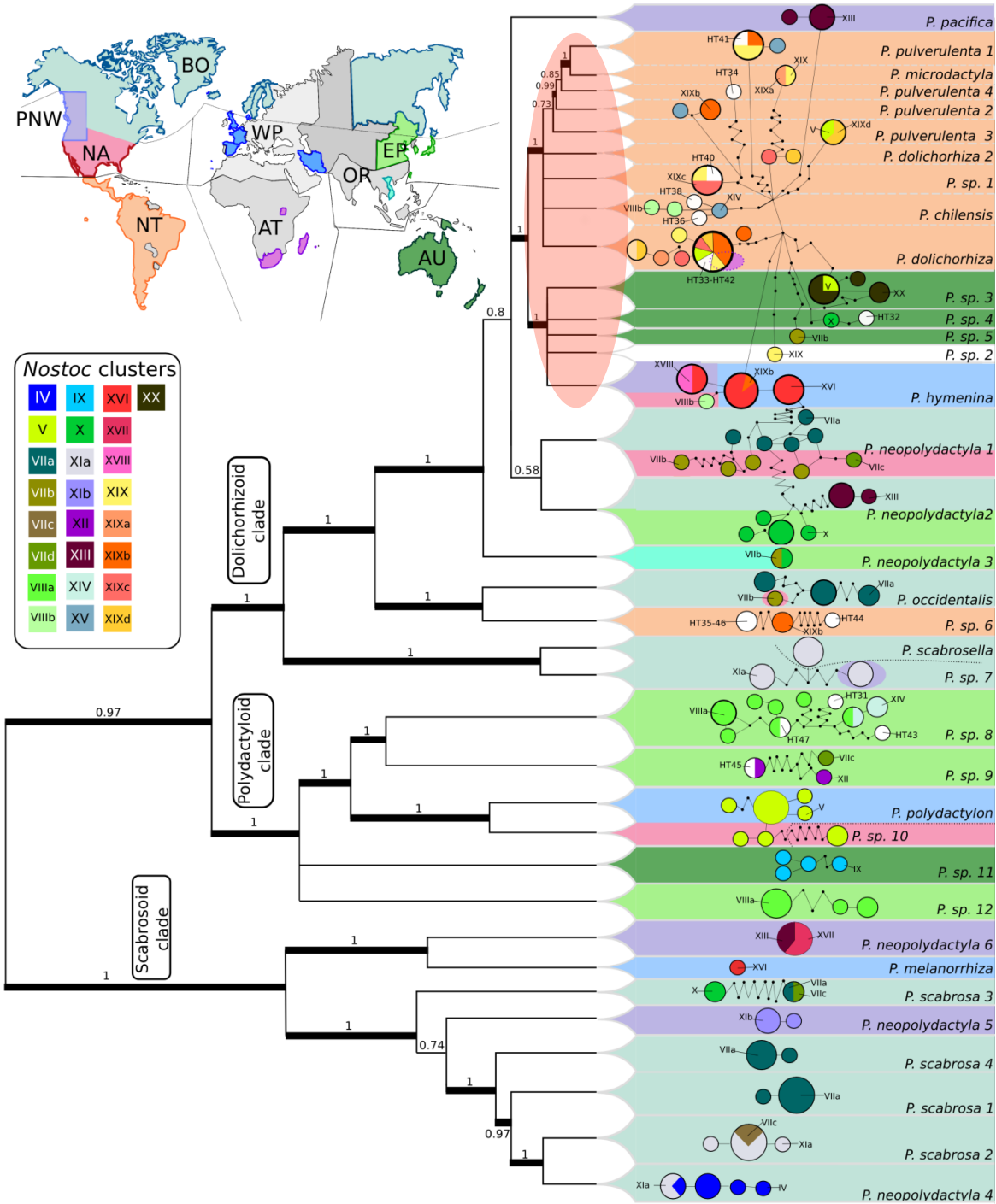
- Mycobiont specialists have usually less haplotypes than generalists



# 2a. Specificity of the symbionts

- 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
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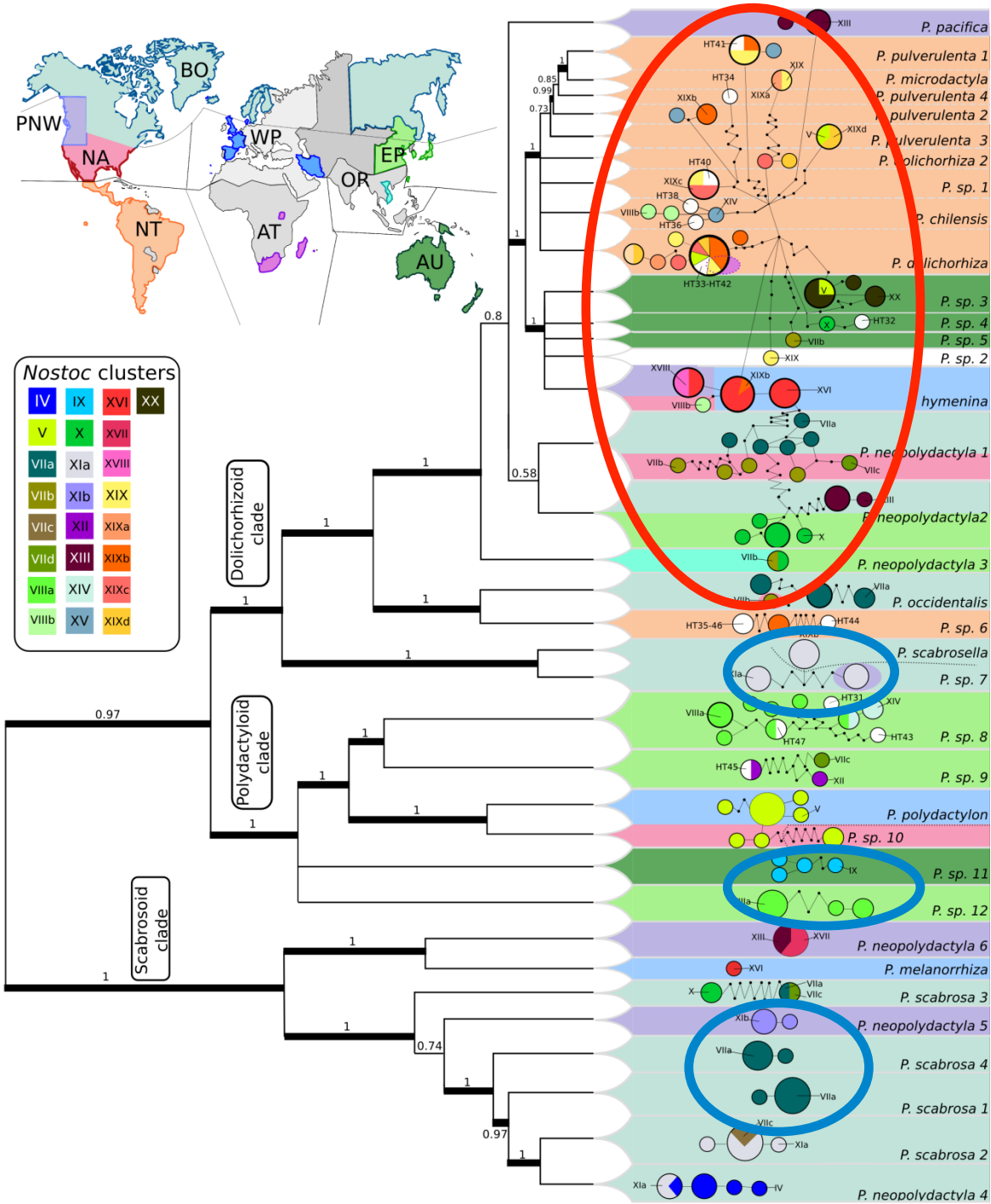
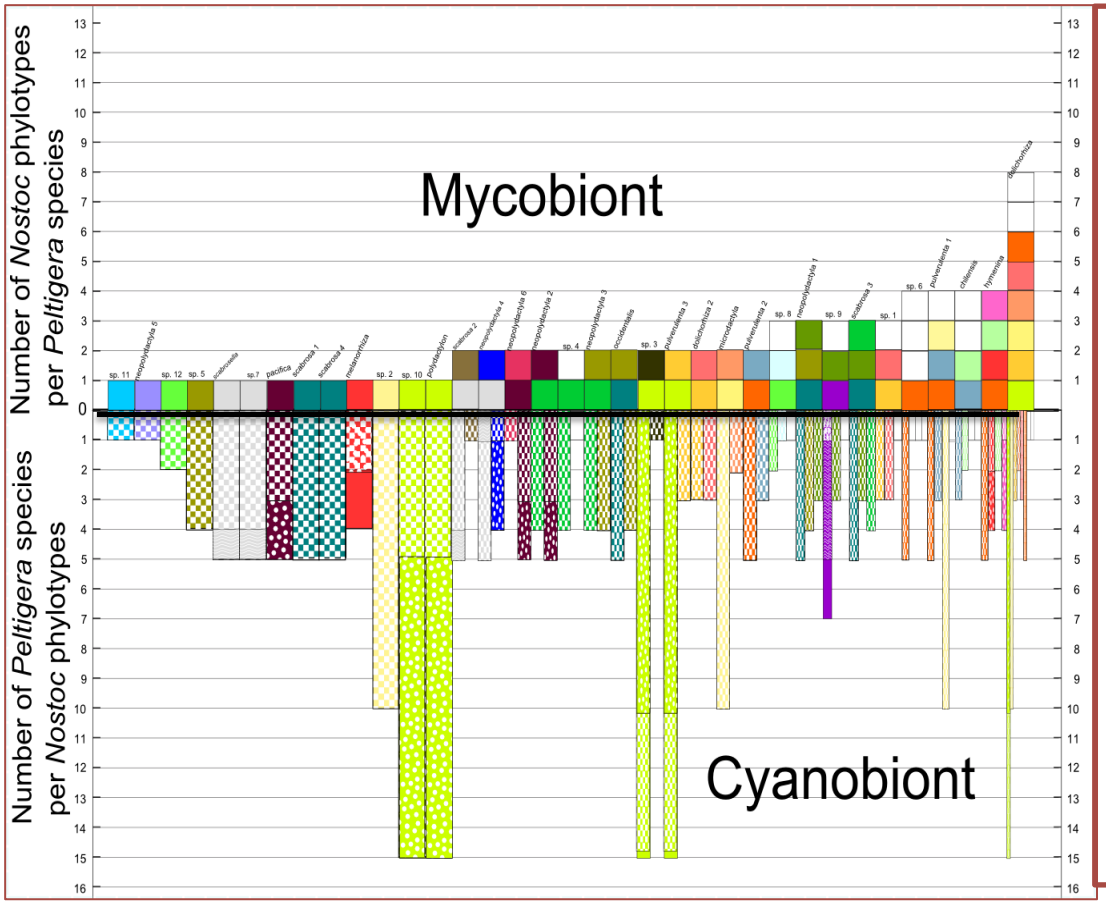
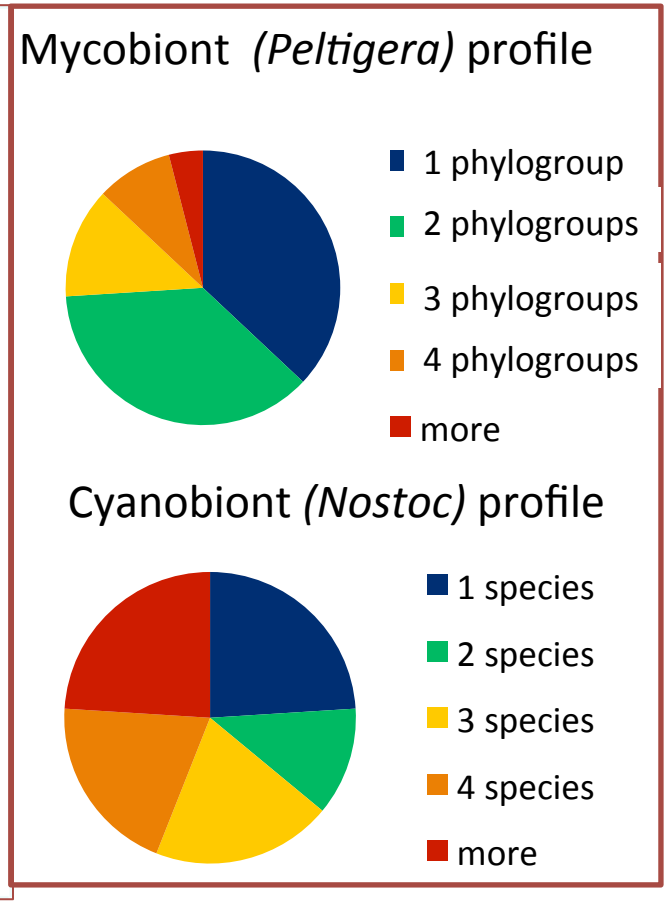


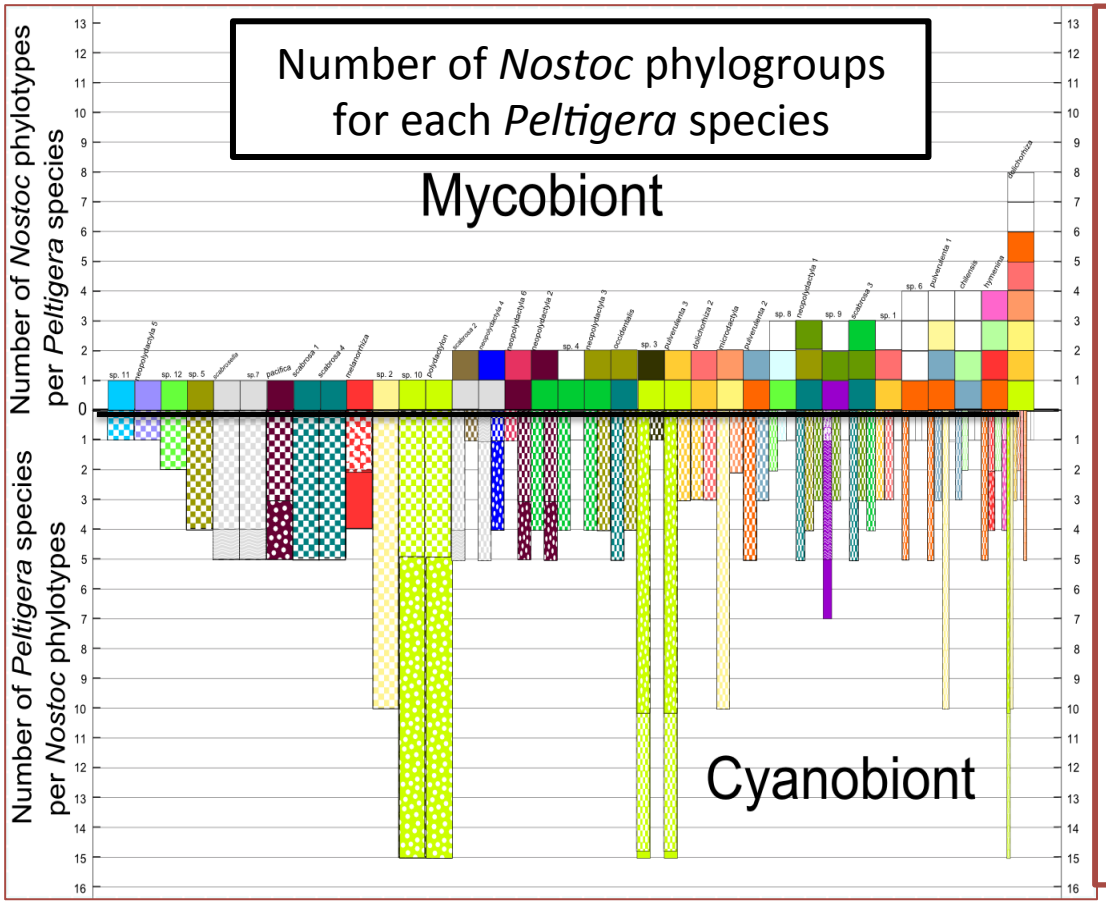
# 2b. Specificity of the symbionts

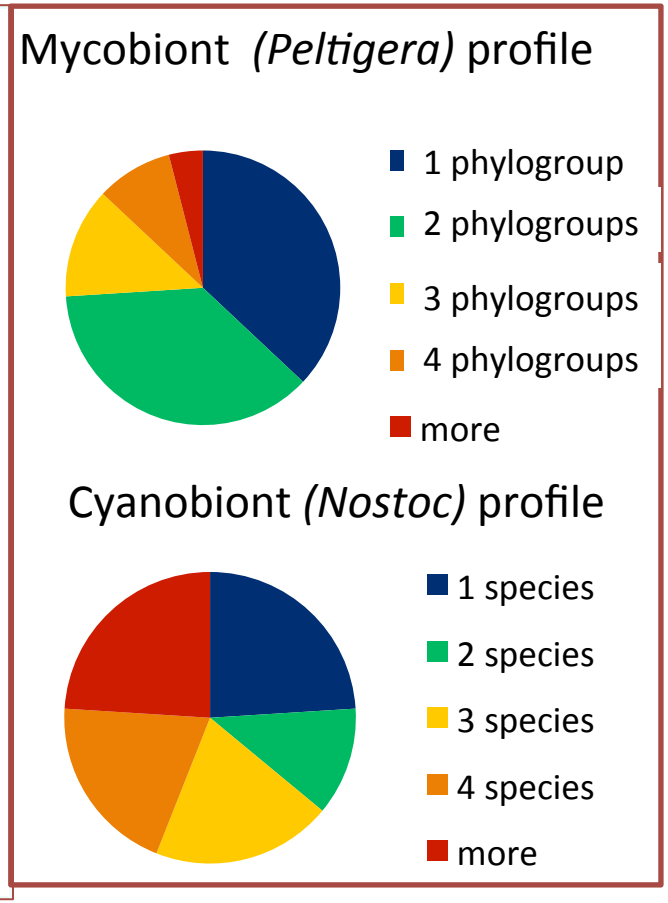



- In average, 2 phylogroups per *Peltigera* species, 3.4 species (of *Peltigera*) per *Nostoc* phylogroup.
- **The mycobiont is more specialized than the cyanobiont.**

# 2b. Specificity of the symbionts

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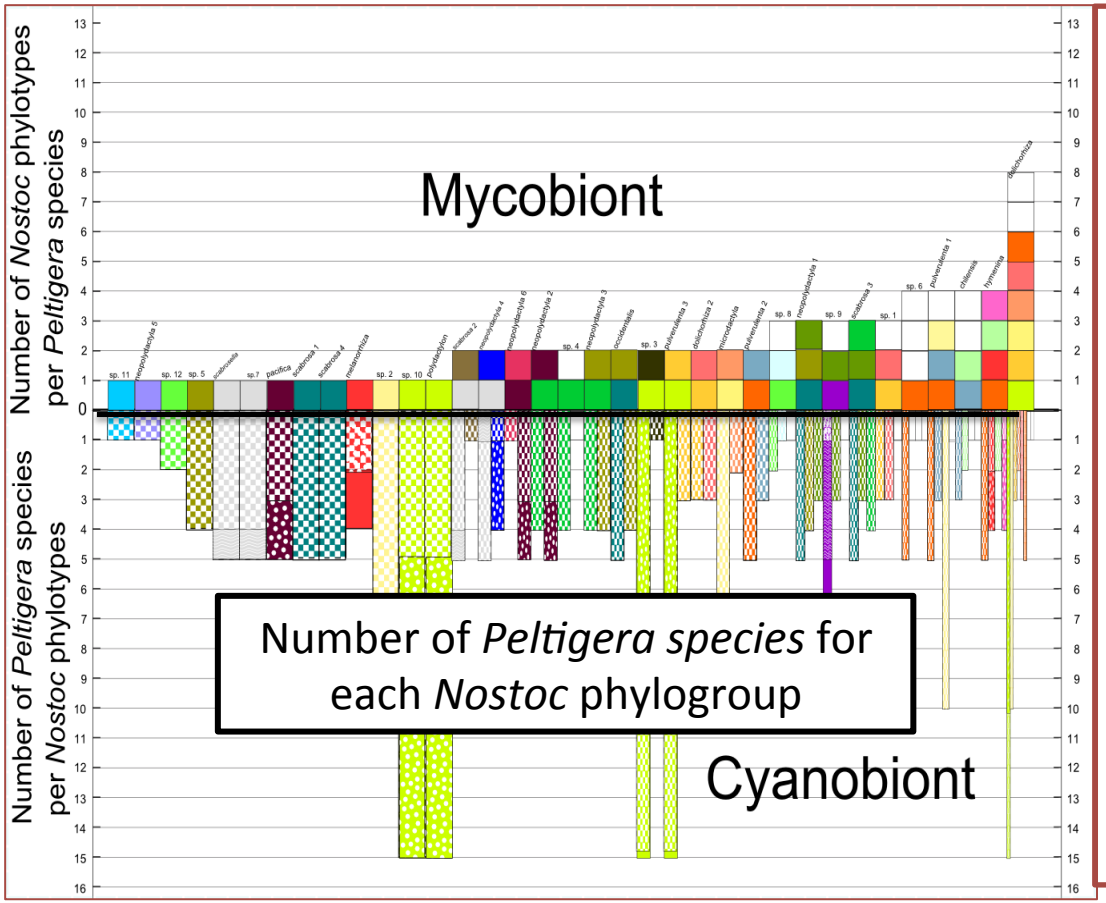


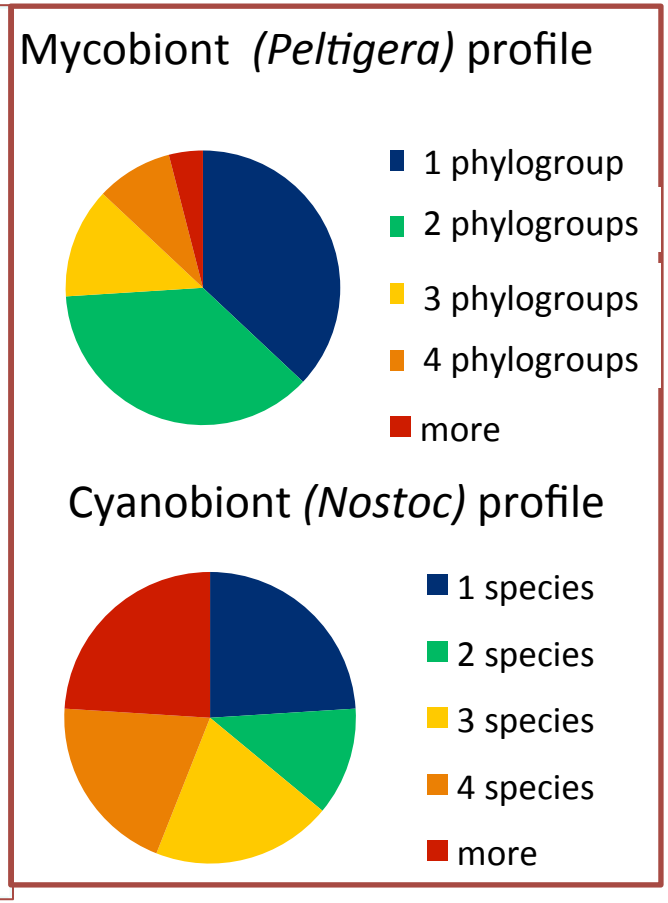


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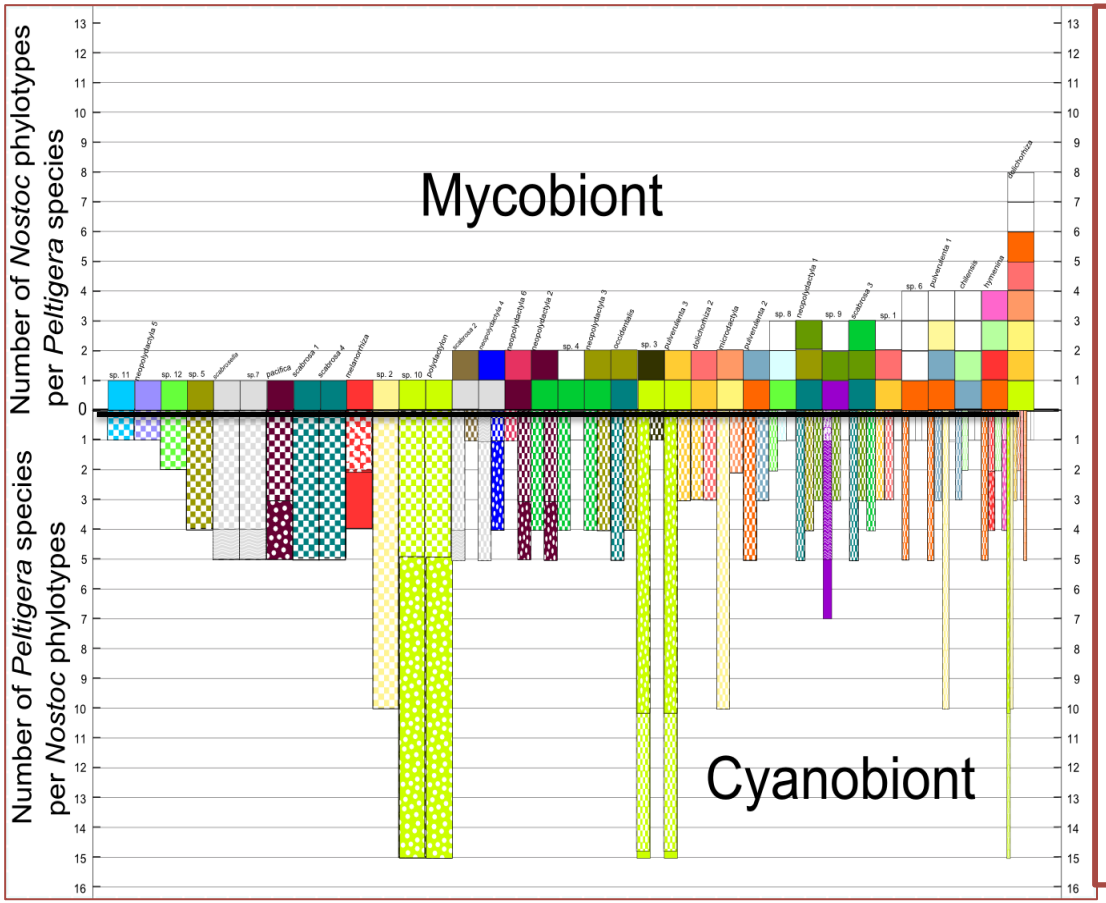


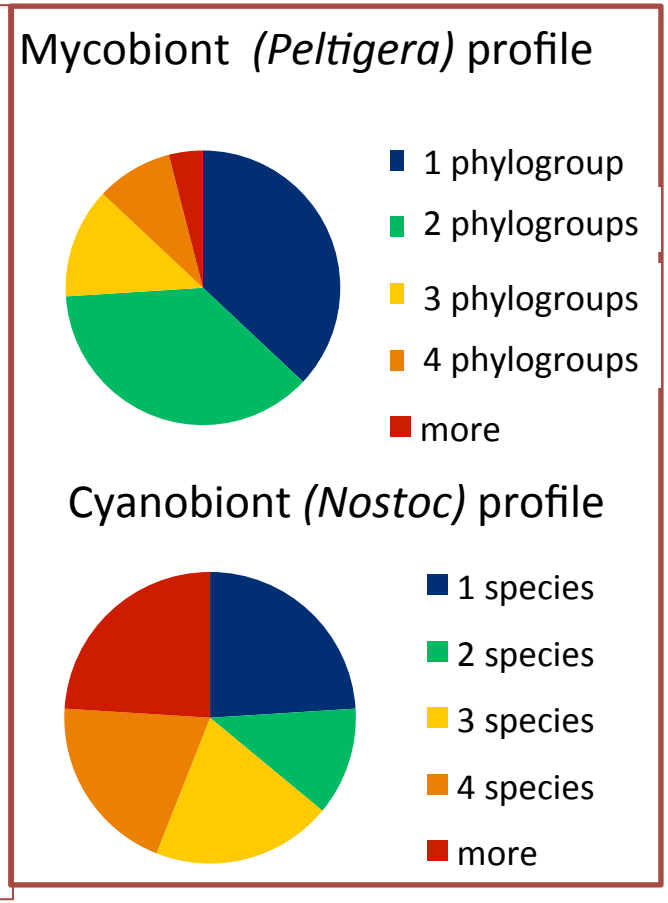


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- **The mycobiont is more specialized than the cyanobiont.**

# Aims of the study

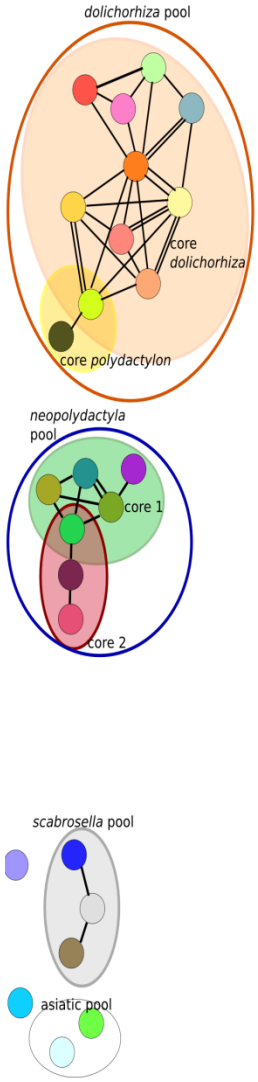
1) Infer the phylogenetic relationships of both partners

2) Assess the specificity of both symbionts

3) Identify factors associated with specificity (geographic range, speciation rates, time, genetic diversity…)

*Consider these results in light of various hypotheses of evolution of mutualism

# 3a. Factors associated with specificity




- *Nostoc* pools shared by sets of mycobiont species (Uni Frac)
- Switches of *Nostoc* pools might be correlated with mycobiont expansion to new regions/ environments and/ or driving speciation
- Geographic mosaic of coevolution

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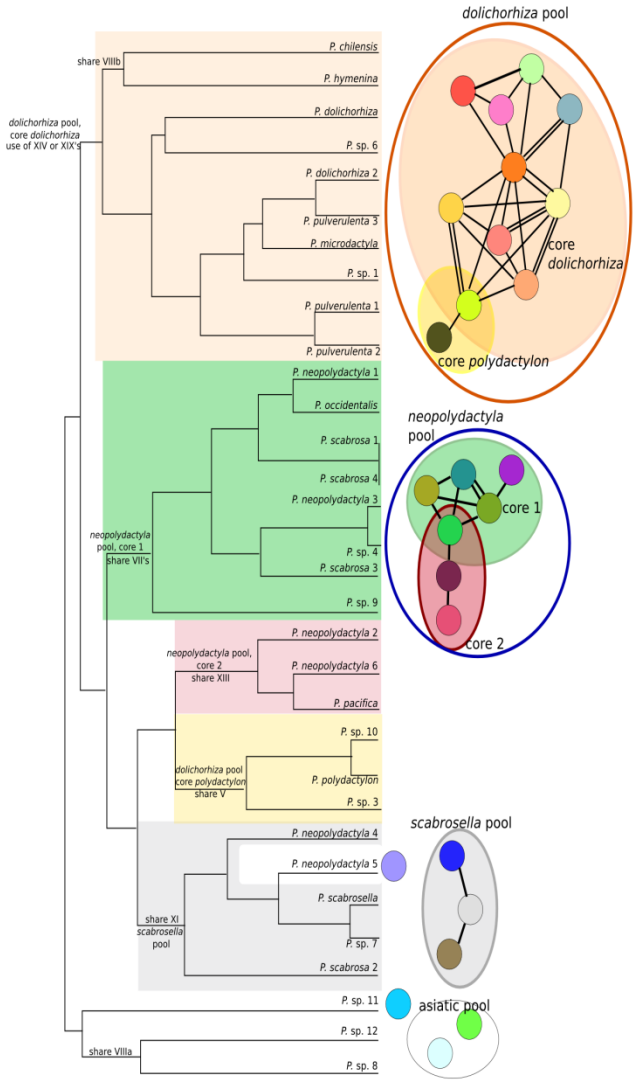


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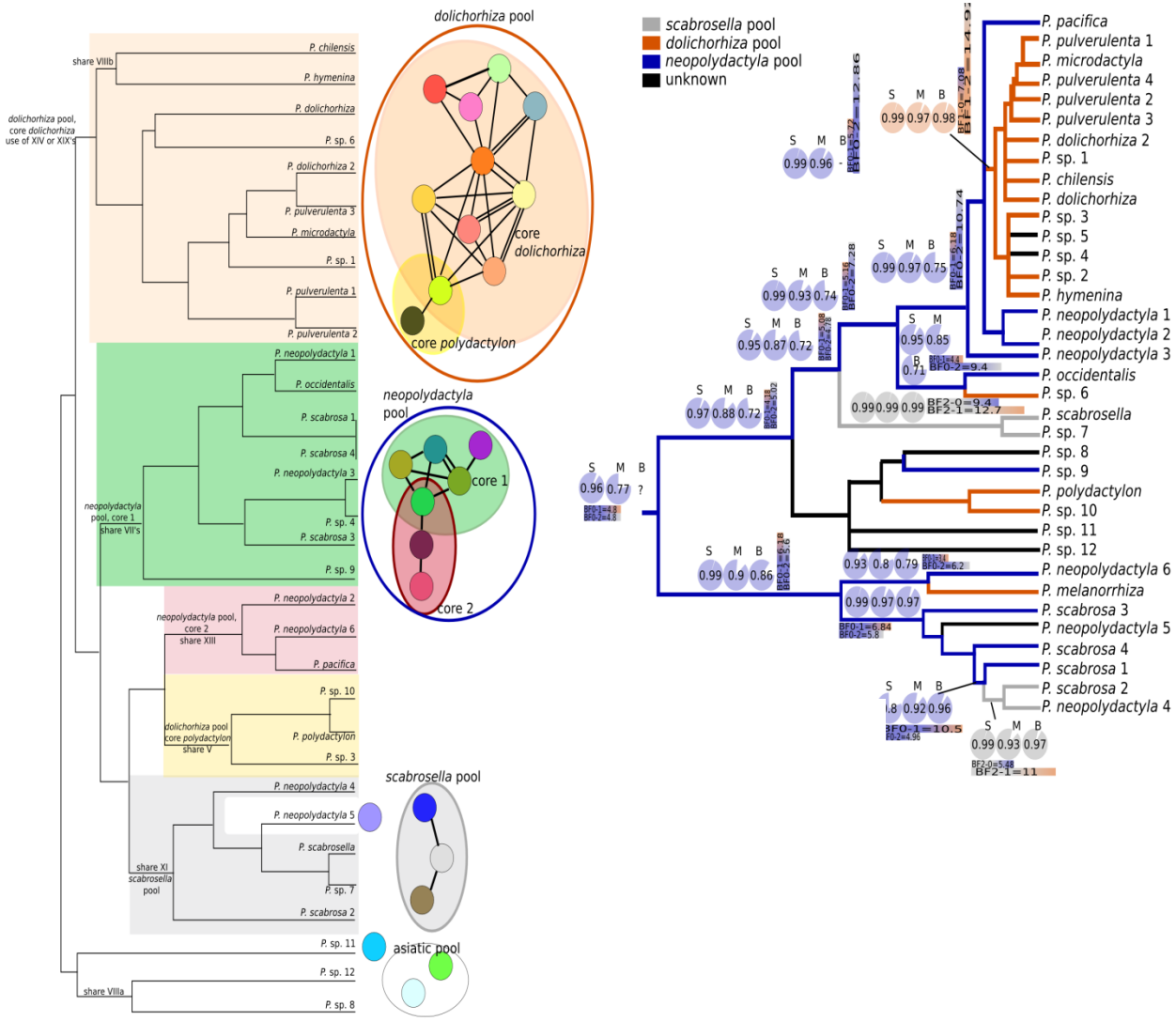


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- Switches of *Nostoc* pools might be correlated with mycobiont expansion to new regions/ environments and/ or driving speciation
- Geographic mosaic of coevolution

# 3b. Impact of specialization on speciation rate

1) BiSSE: comparing specialists (1 *Nostoc* phylogroup only) and non-specialists *Peltigera* species:

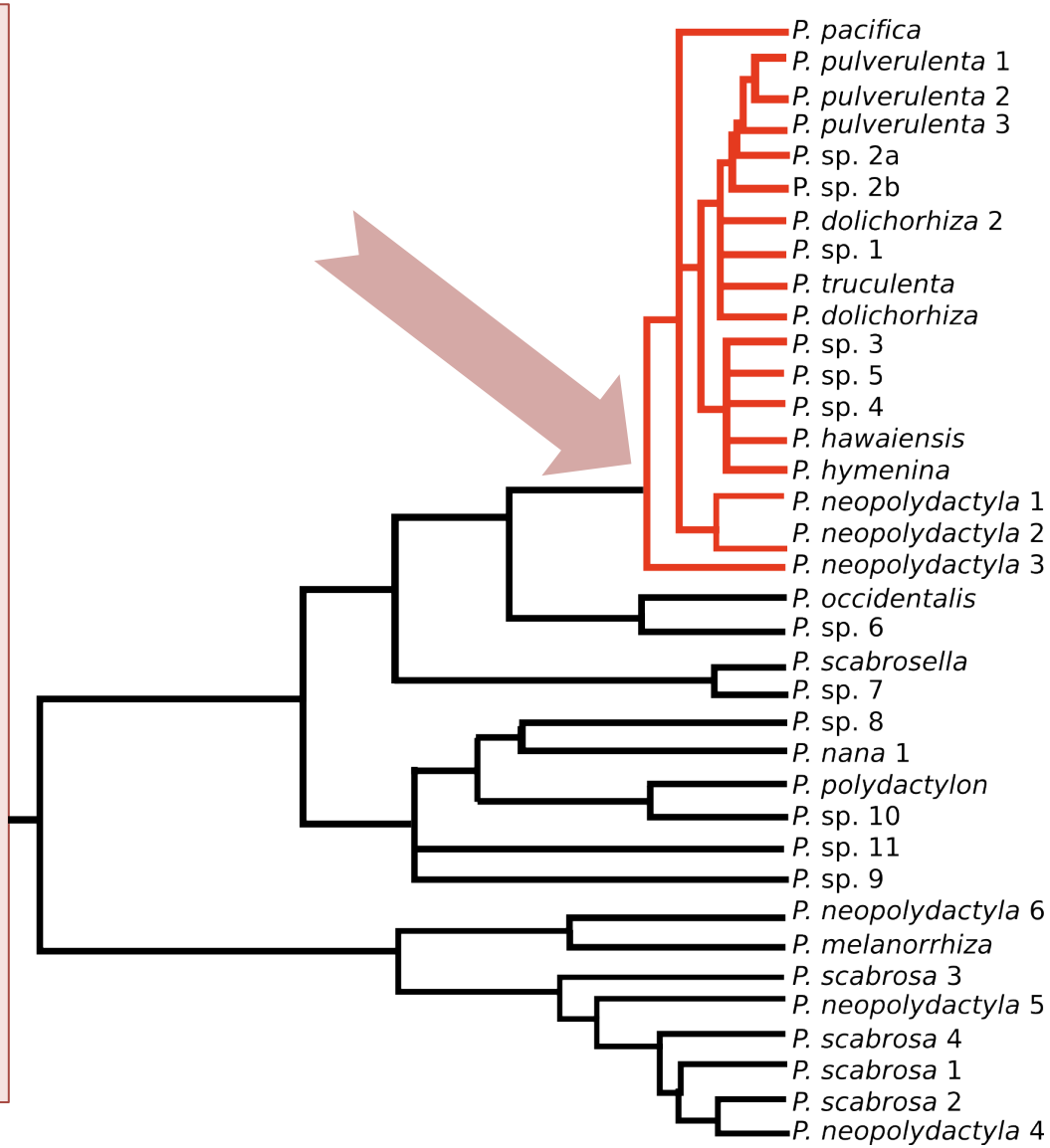
    a) speciation rates significantly higher in generalists

    b) switching rate generalist => specialist significantly higher than specialist => generalist

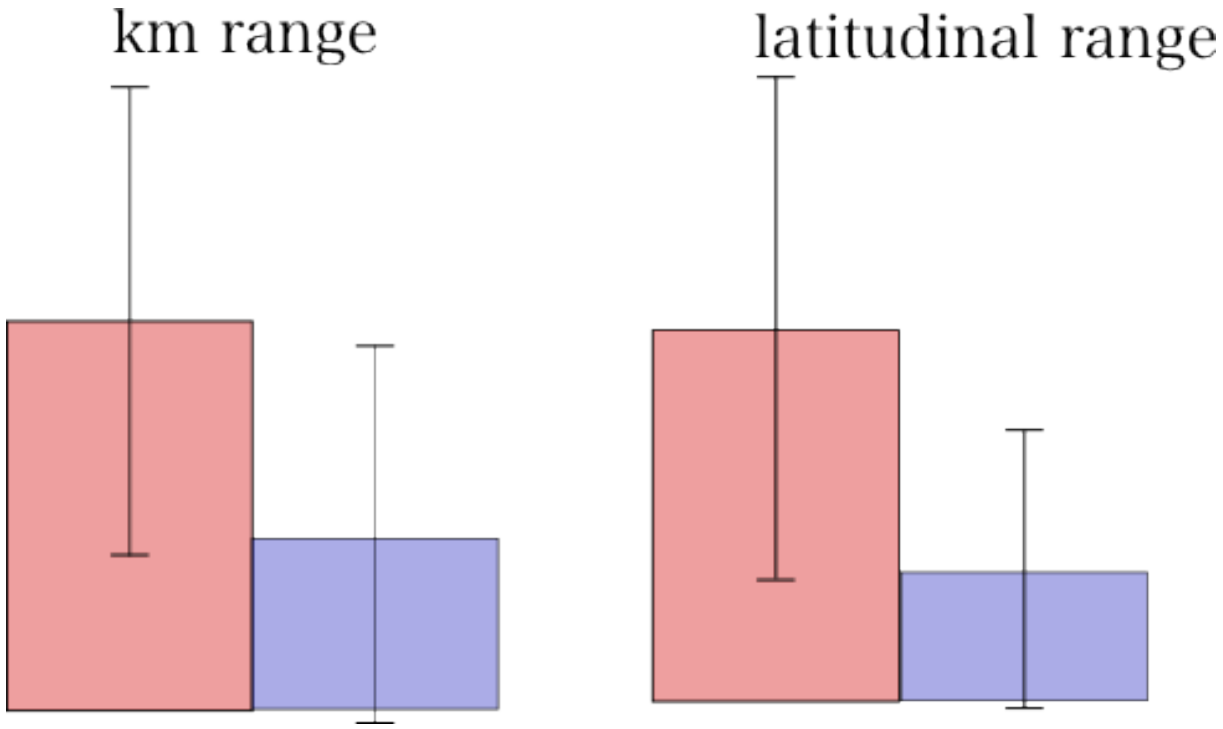
# 3b. Impact of specialization on speciation rate

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

=> possible link with generalism



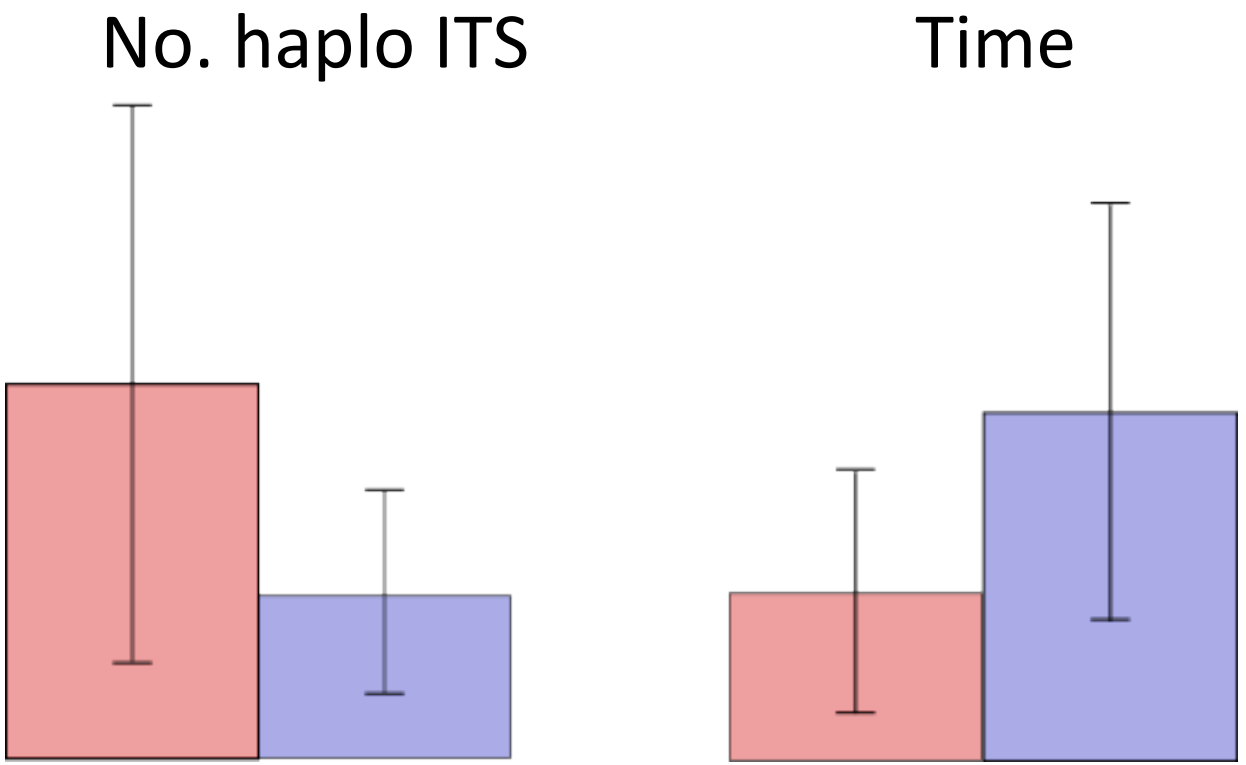
# 3c. Correlation between specificity and geographical range (mycobiont)




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

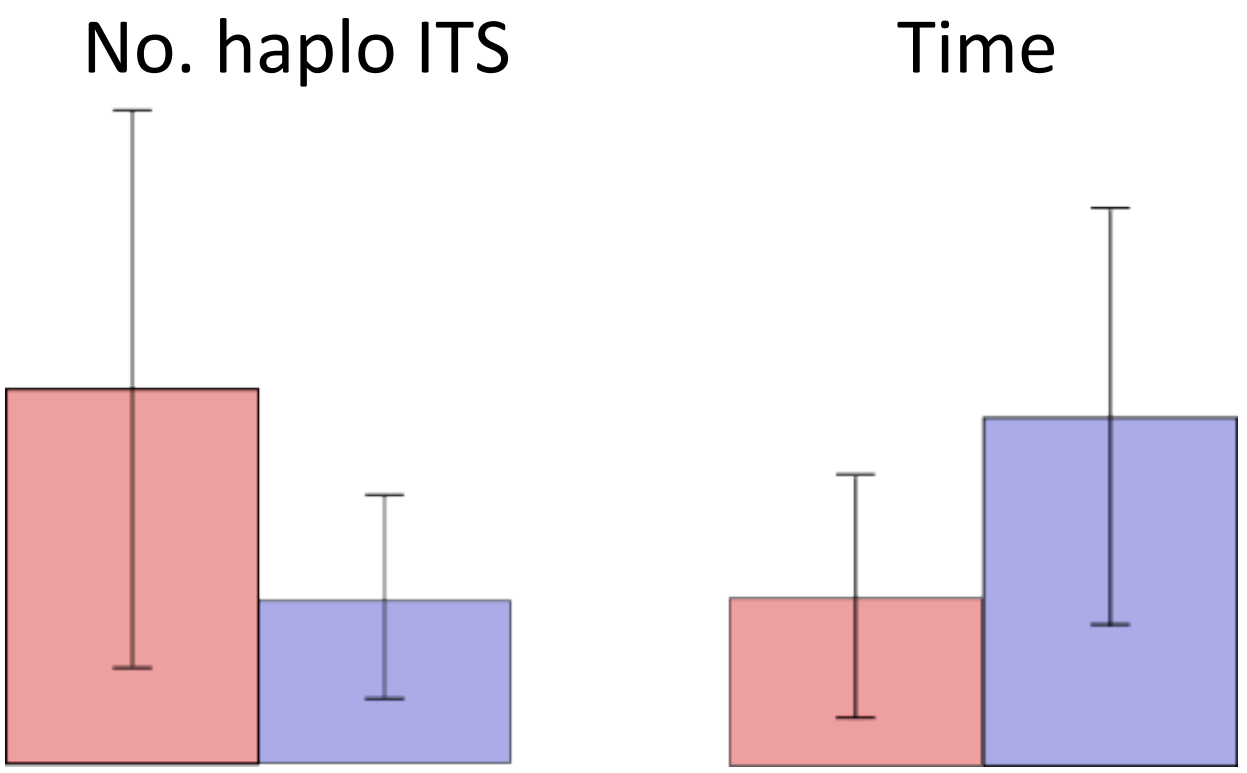
Average range of a specialist species:  3340 km and 8.5° of latitude

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




- 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




- 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)

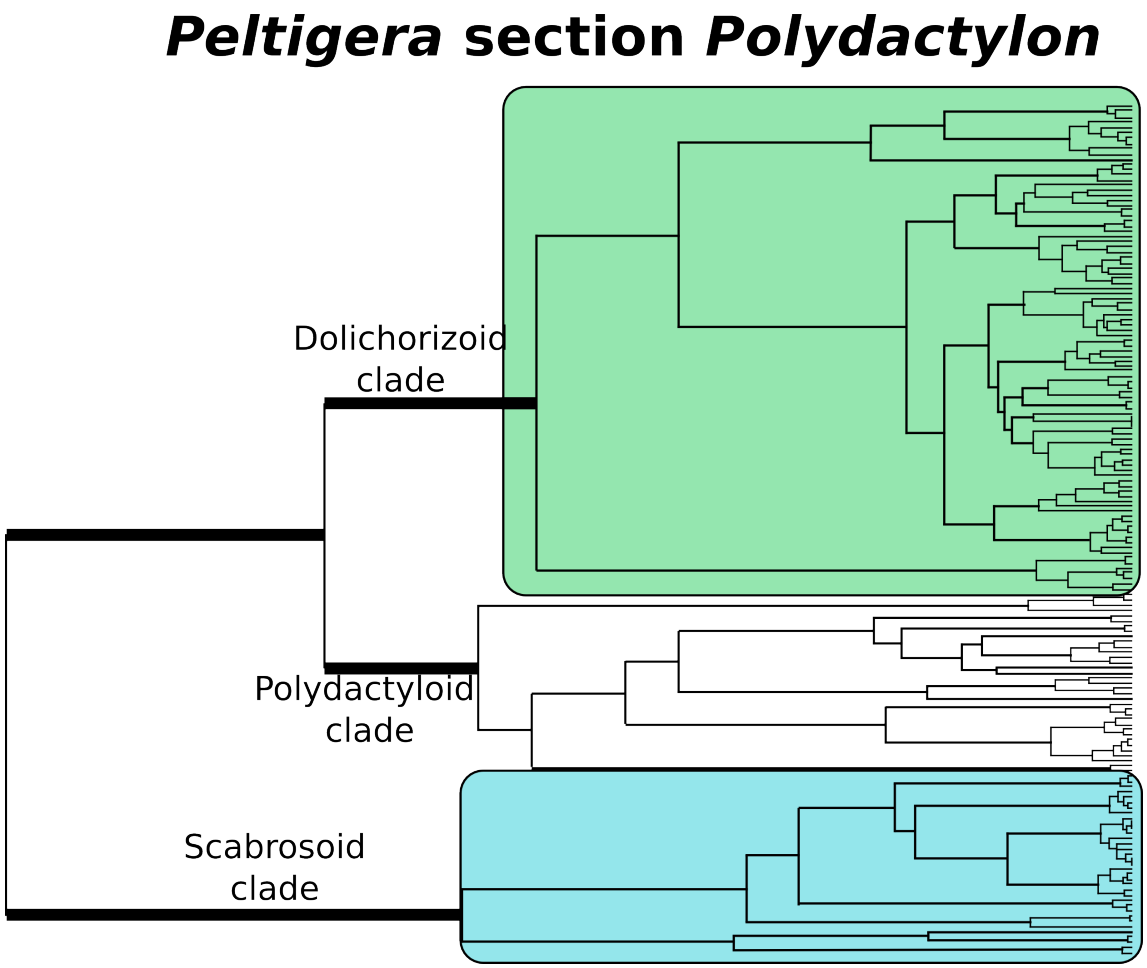
=> monophyly

# Species concepts and phylogeny

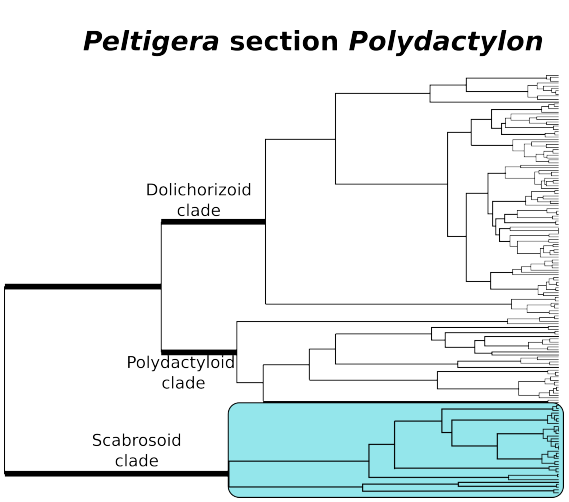
- **General lineage species concept**
- Morphological species concept
- Biological species concept
- **Phylogenetic species concept**
- **Genealogic species concept**

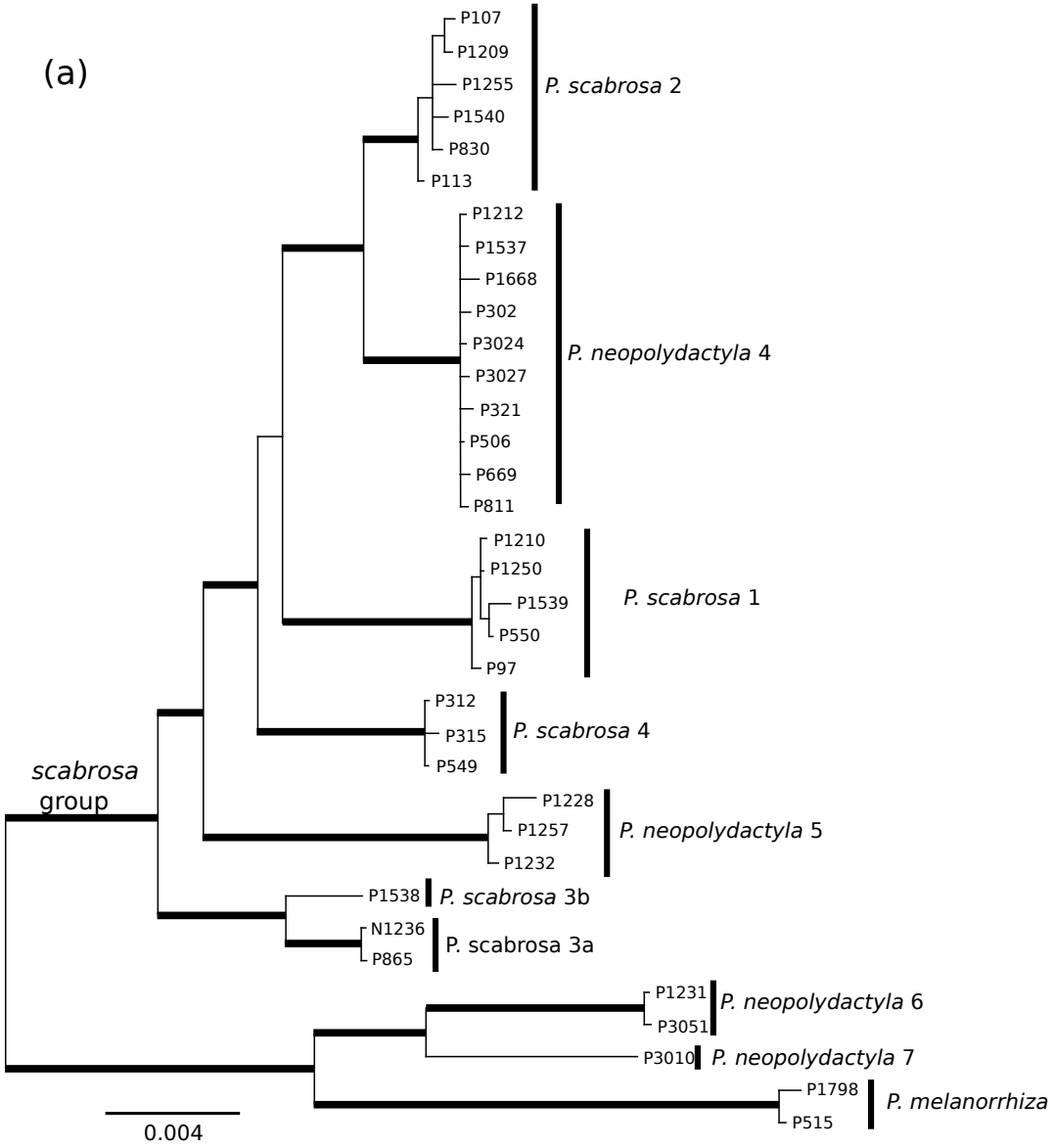
"basal group of organisms whose members are all more closely related to each other than they are to any organisms outside the group" (Hudson and Coyne 2002)

# Species delimitation in Dolichorhizoid and Scabrosoid clades

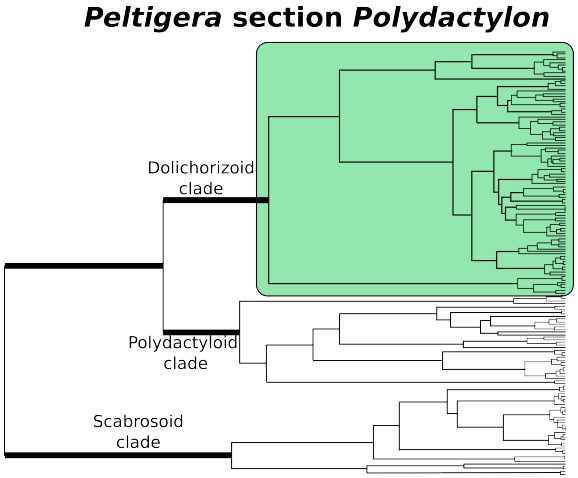


# a. Scabrosoid clade

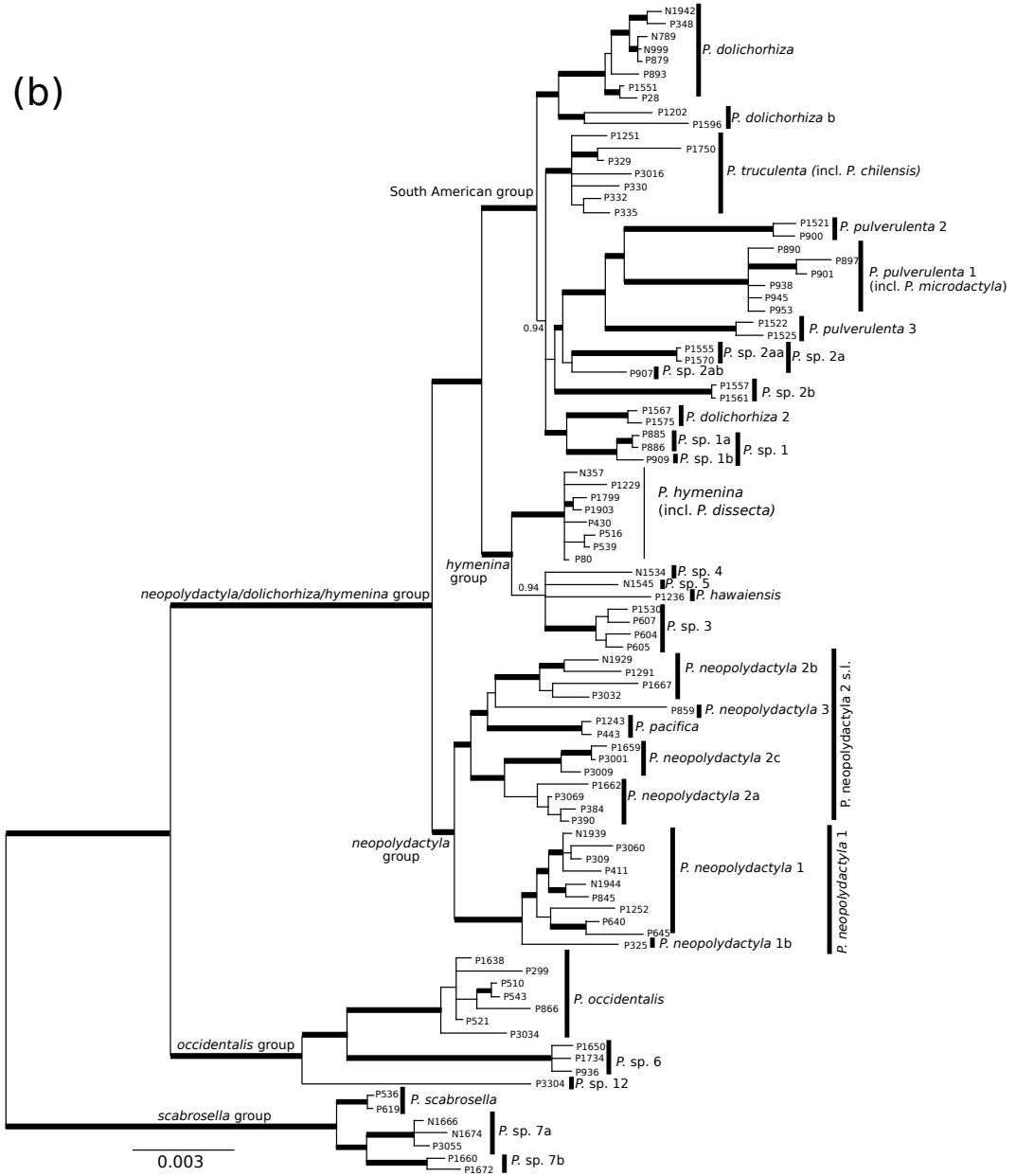


# b. Dolichorhizoid clade




(b)



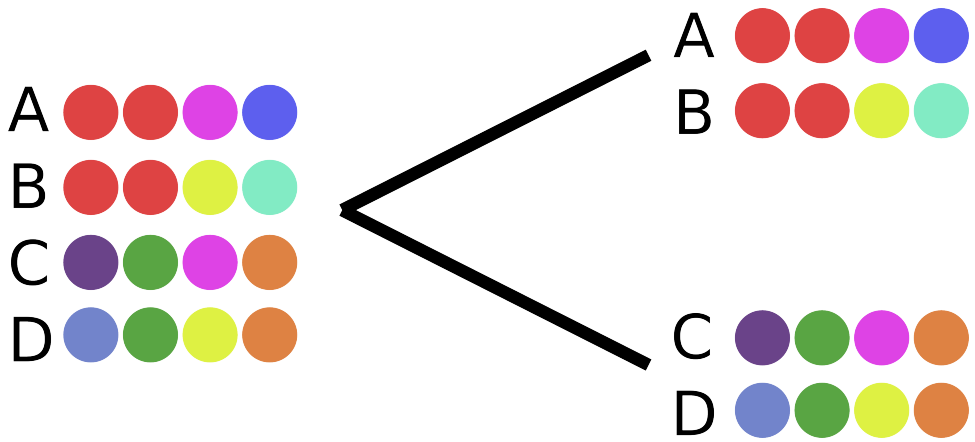
# Species delimitation methods

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

# Species delimitation methods

## a. Structurama

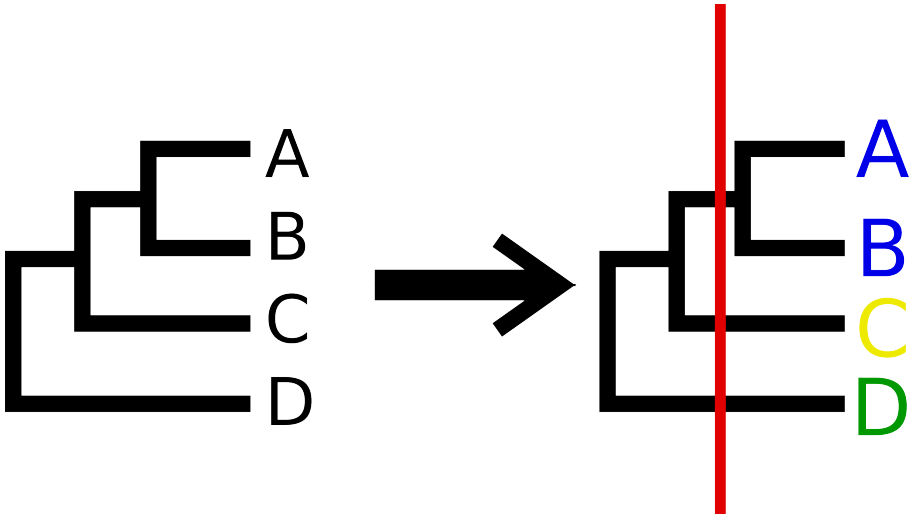
- Assigns samples to clusters to maximize H-W equilibrium and minimize linkage desequilibrium based on set of alleles
- Can estimate the number of clusters



# Species delimitation methods

## b. GMYC

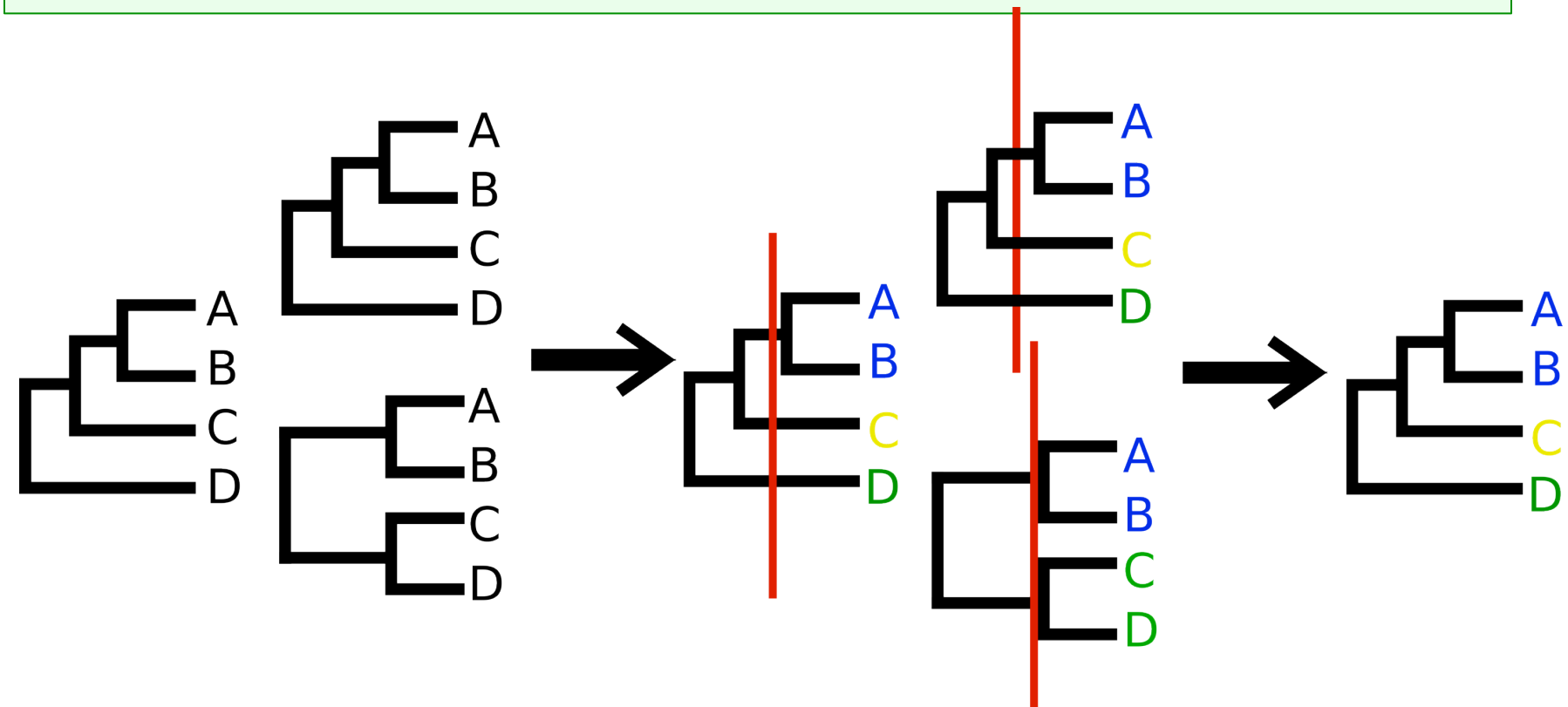
- On ultrametric trees
- Coalescence on single loci
- Searchs for a threshold where branching patterns switch from interspecific to intraspecific relationships



# Species delimitation methods

## b. bGMYC

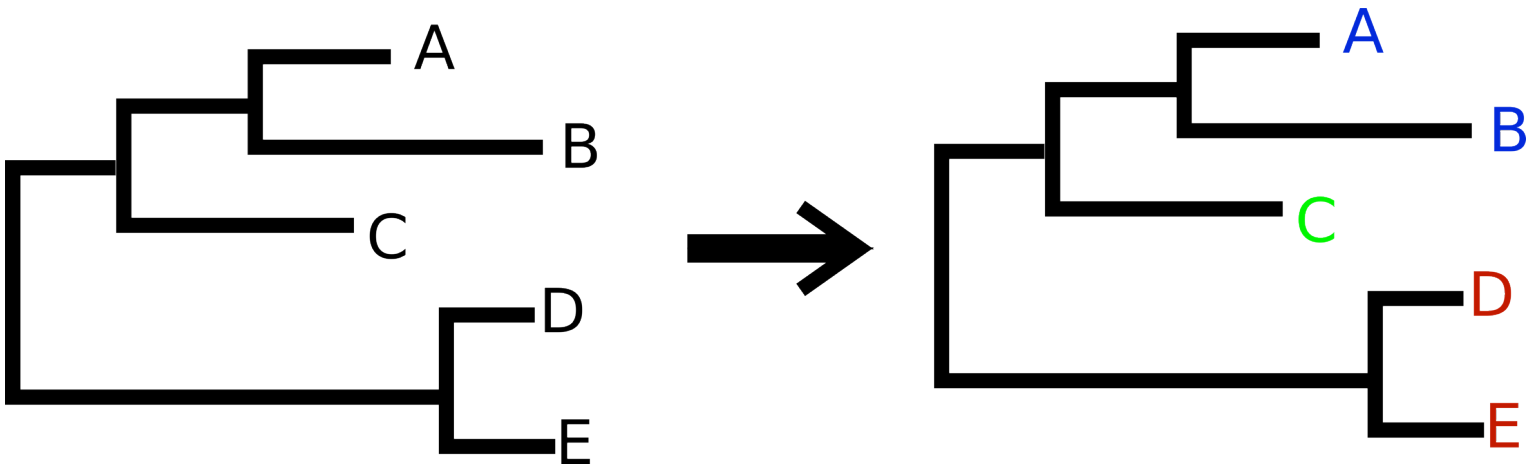
- Bayesian implementation
- Considers a set of trees, takes trees uncertainties into account



# Species delimitation methods

## c. bPTP

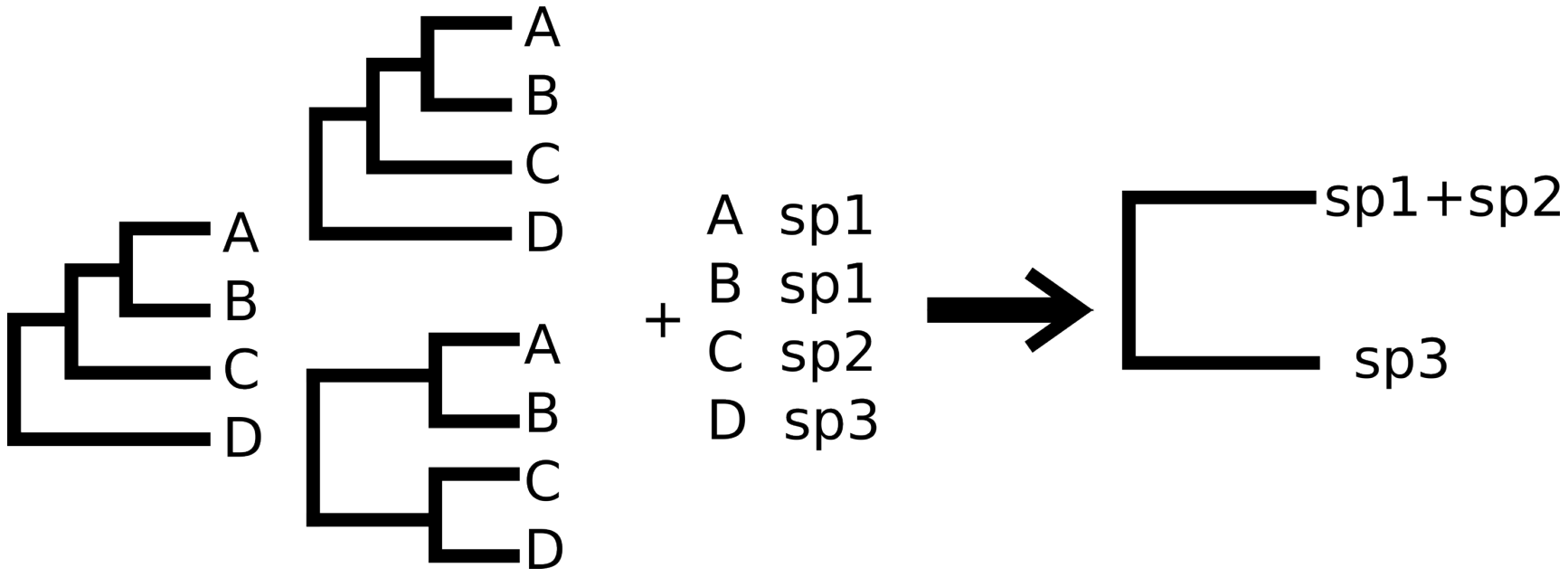
- On phylograms
- Based on substitutions instead of time
- Models a Yule process



# Species delimitation methods

## d. spedeSTEM

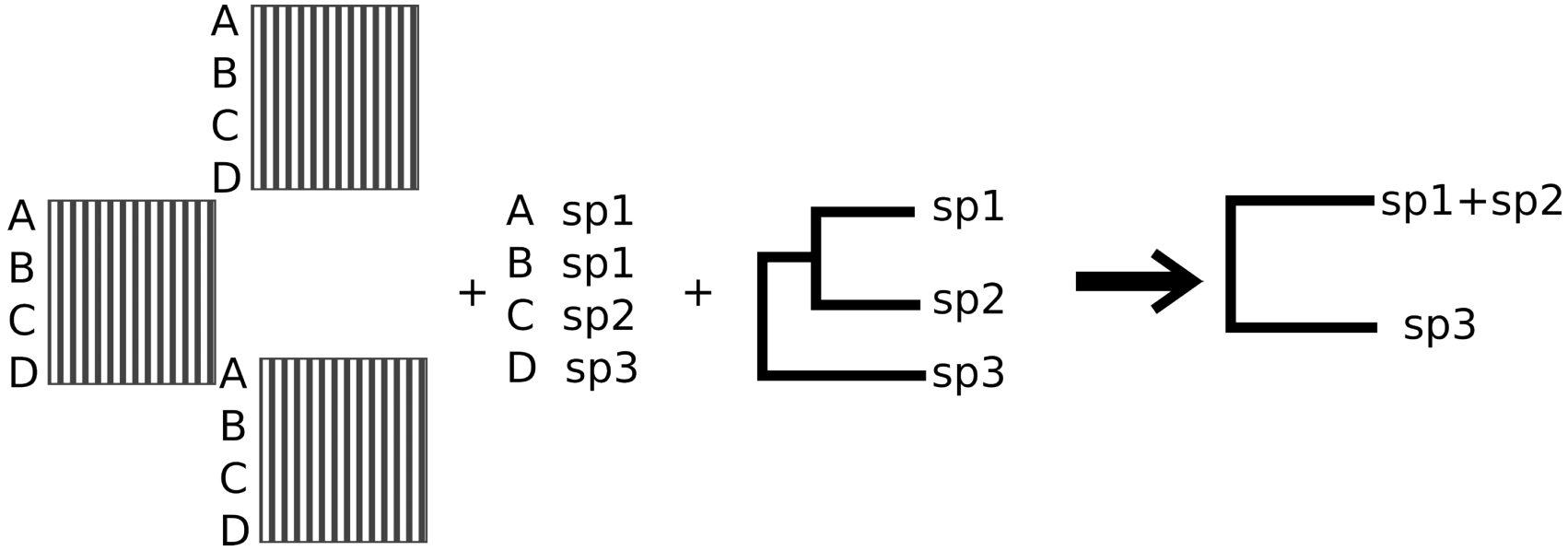
- Takes ultrametric single locus trees and species assignments
- Generate species trees
- Rearrange species to maximize the likelihood of the species tree in a coalescent framework



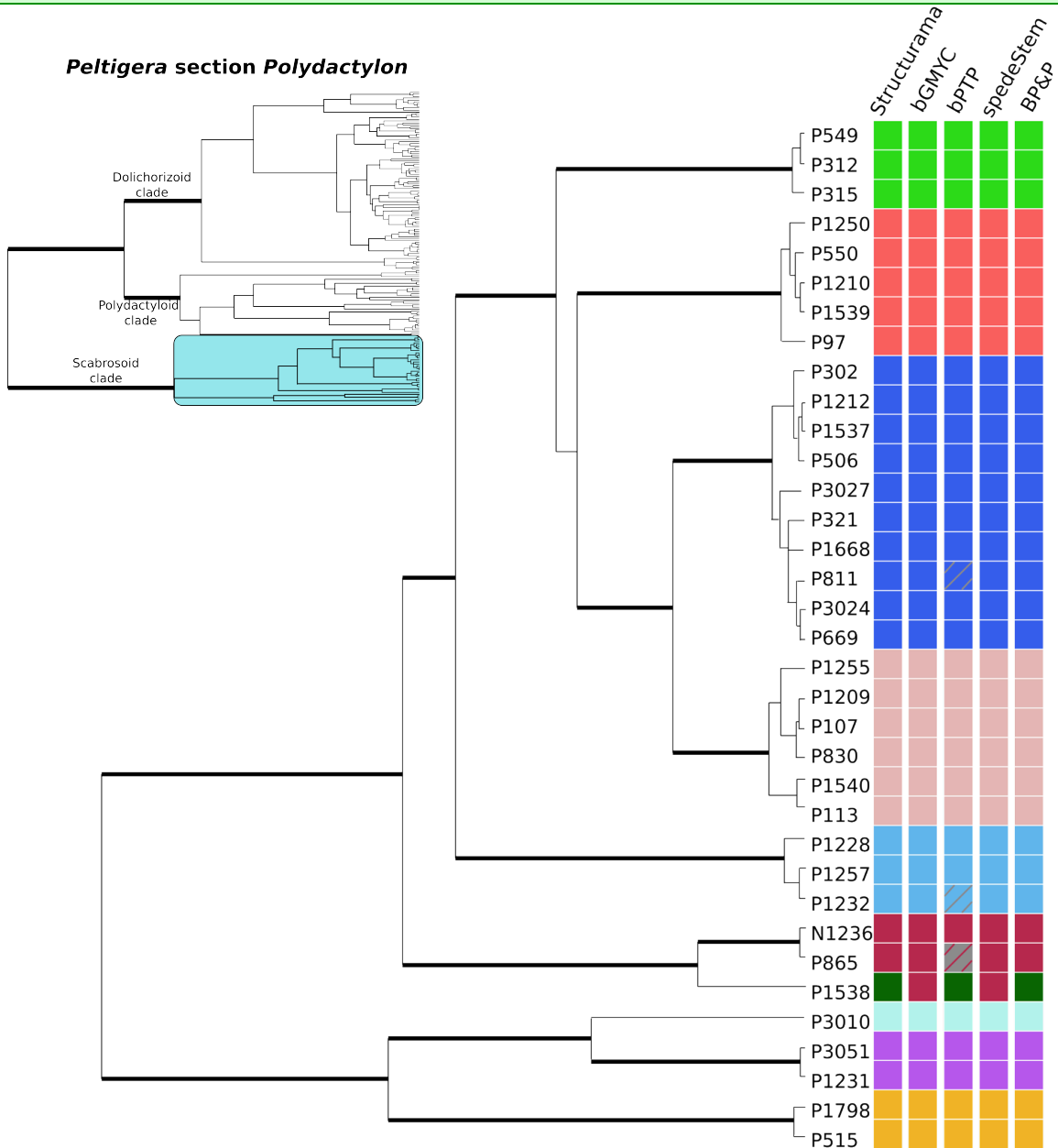
# Species delimitation methods

## e. BPP

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



# a. Scabrosoid clade



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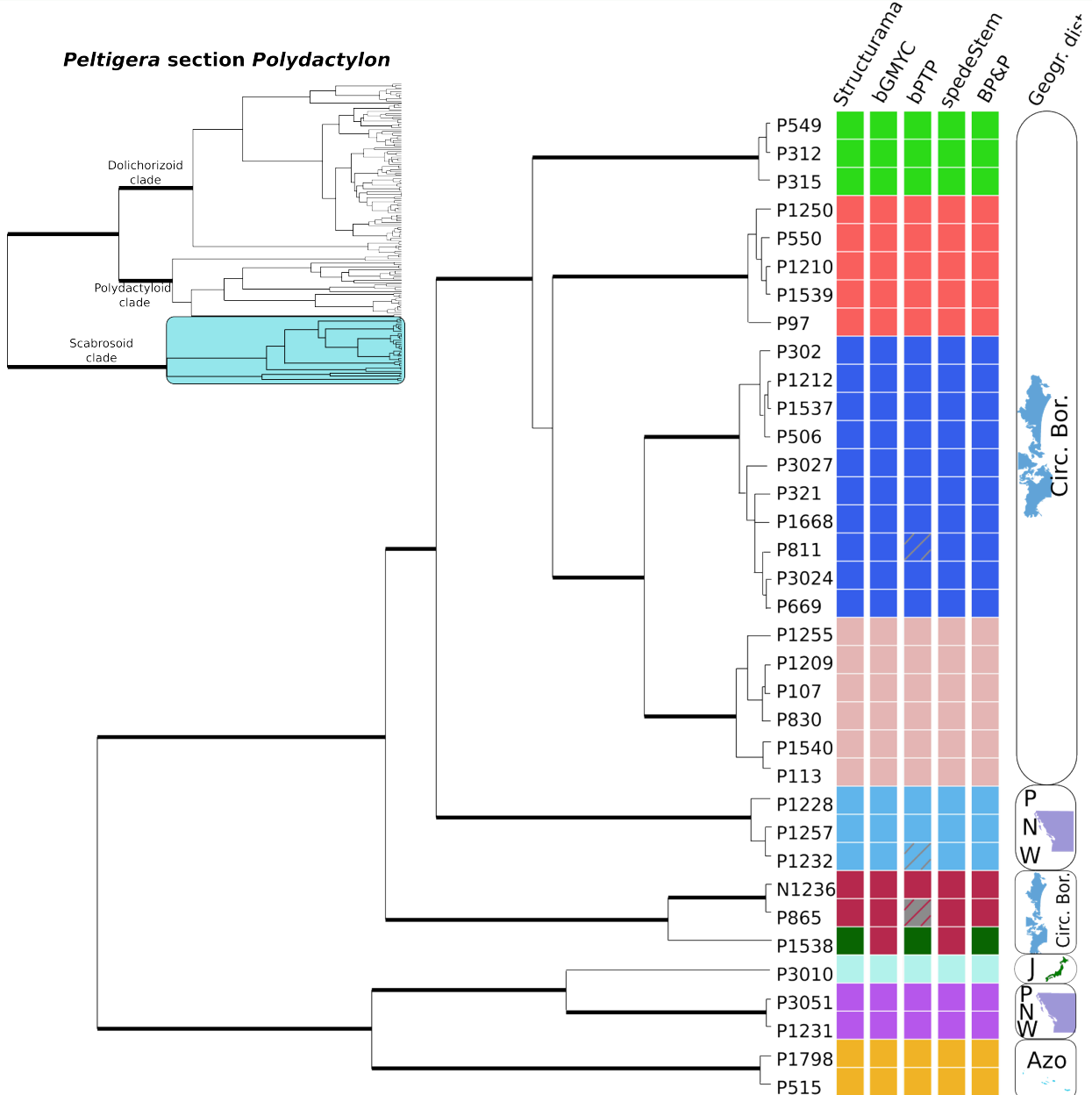

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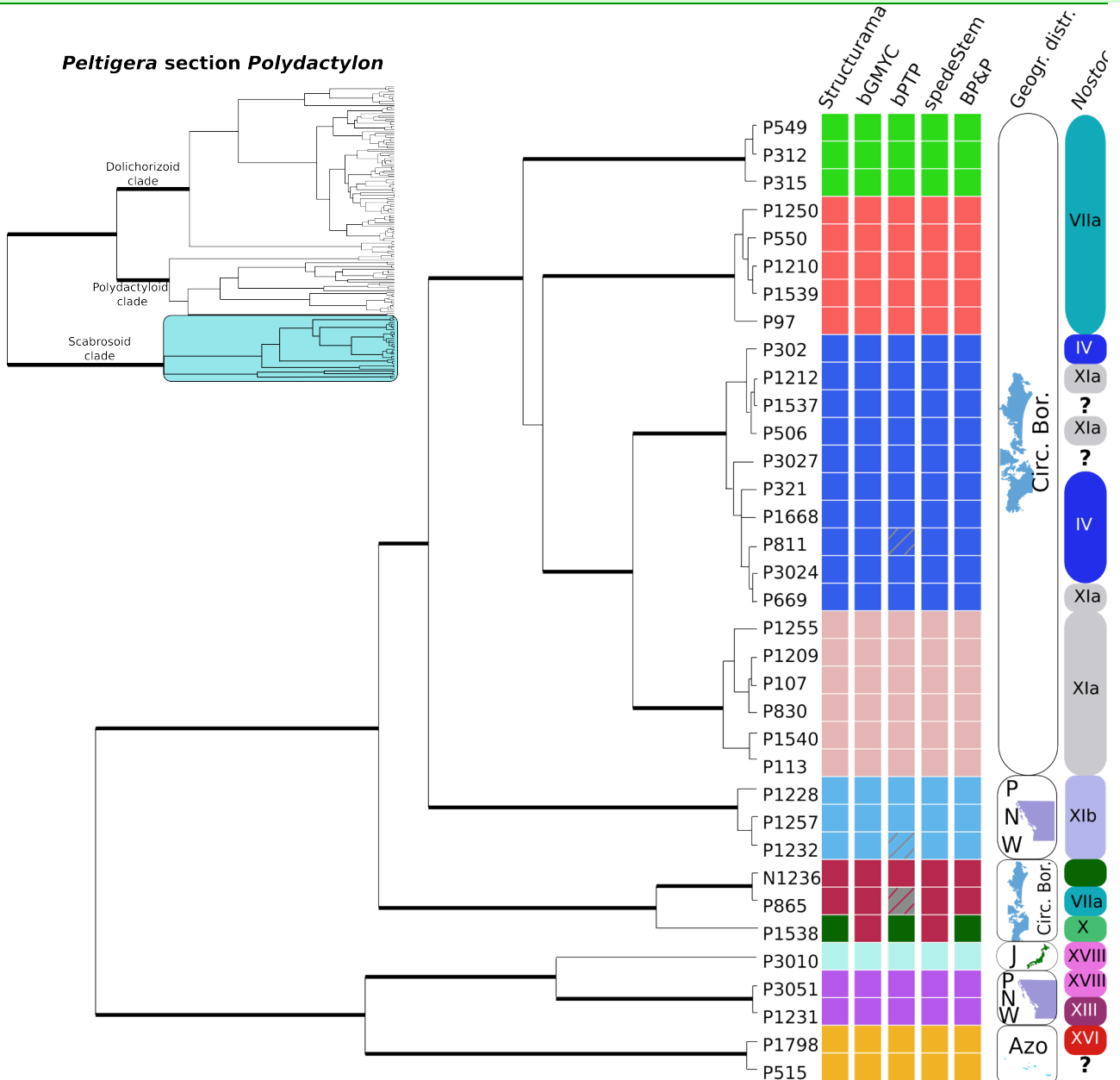

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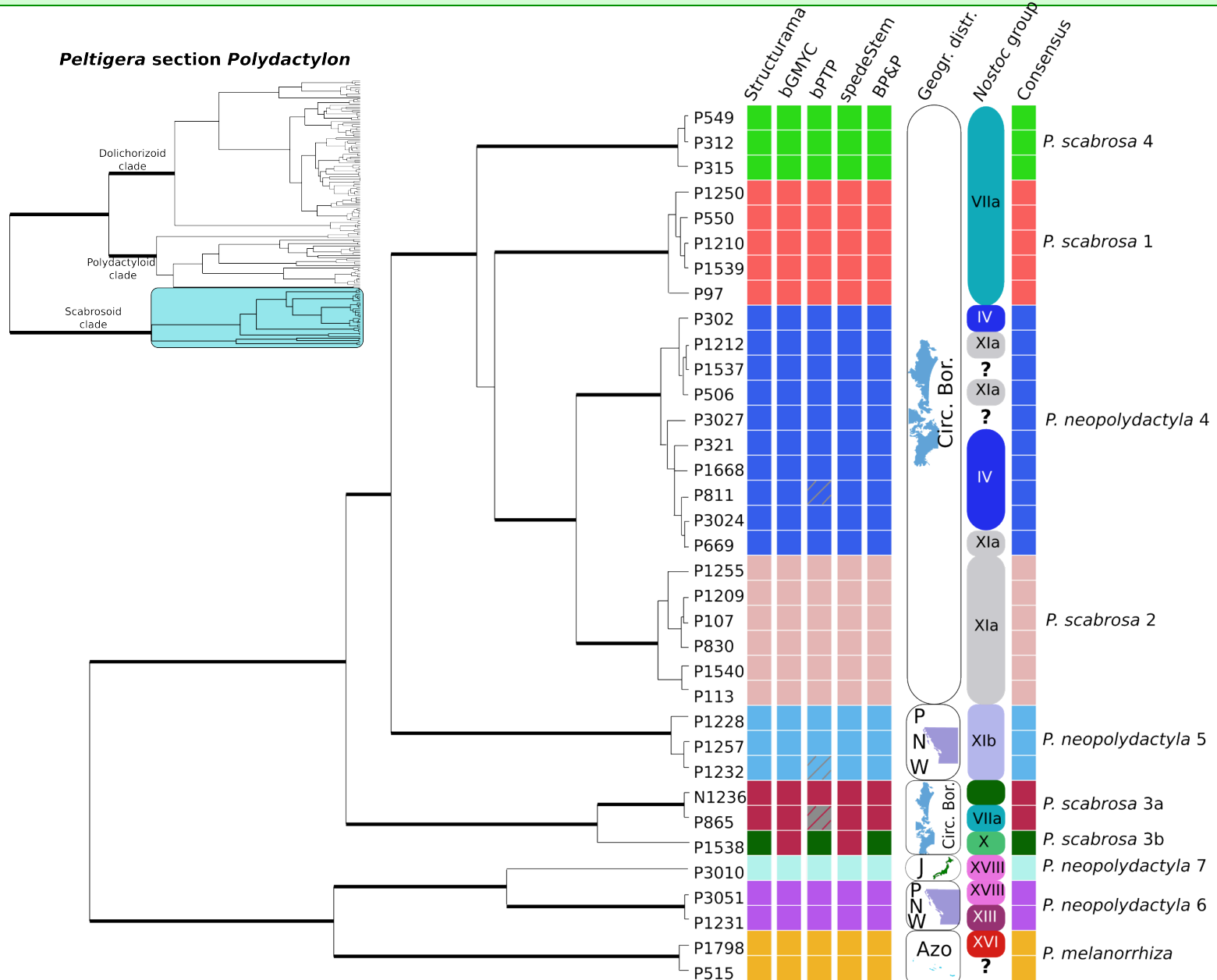
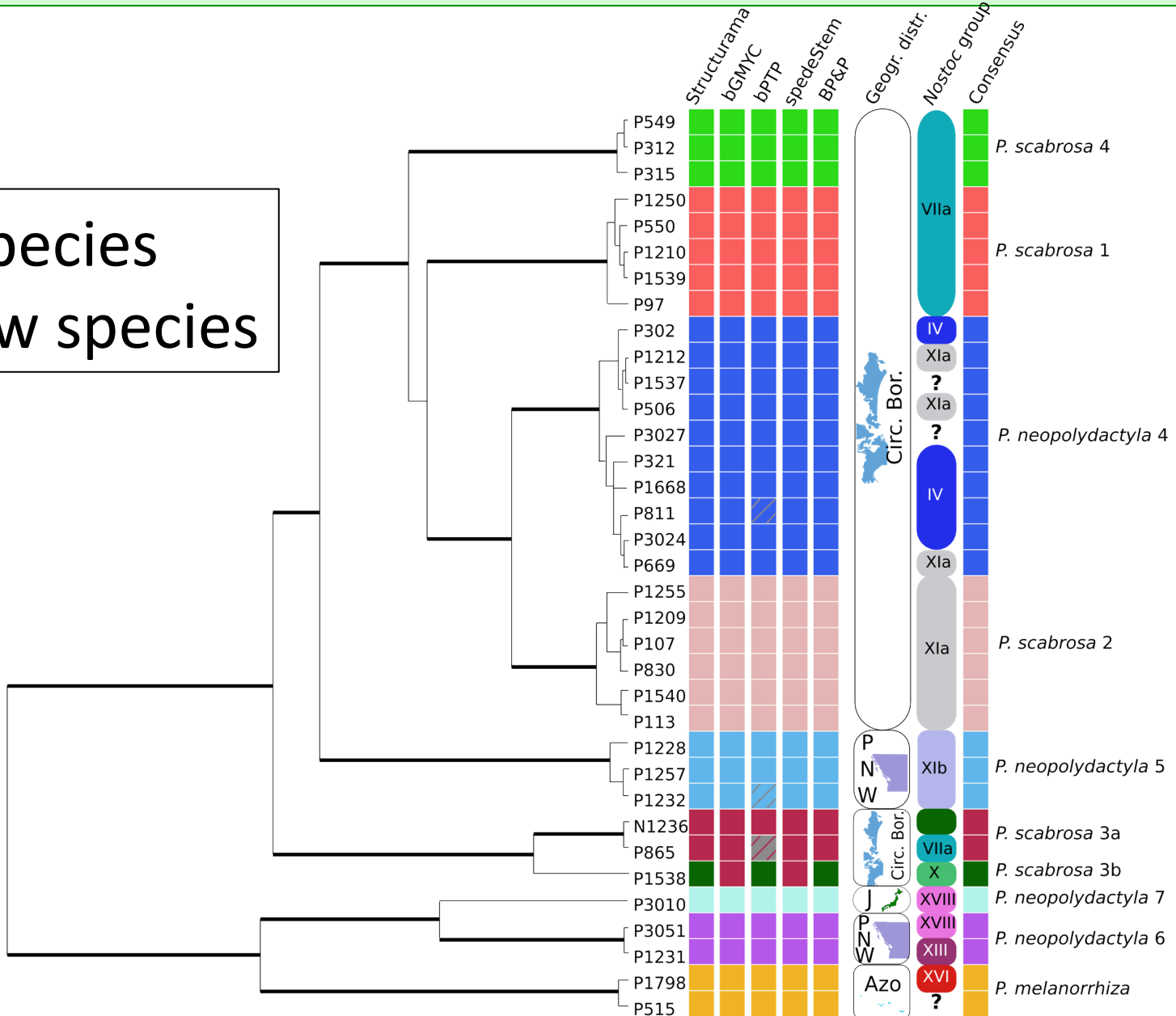
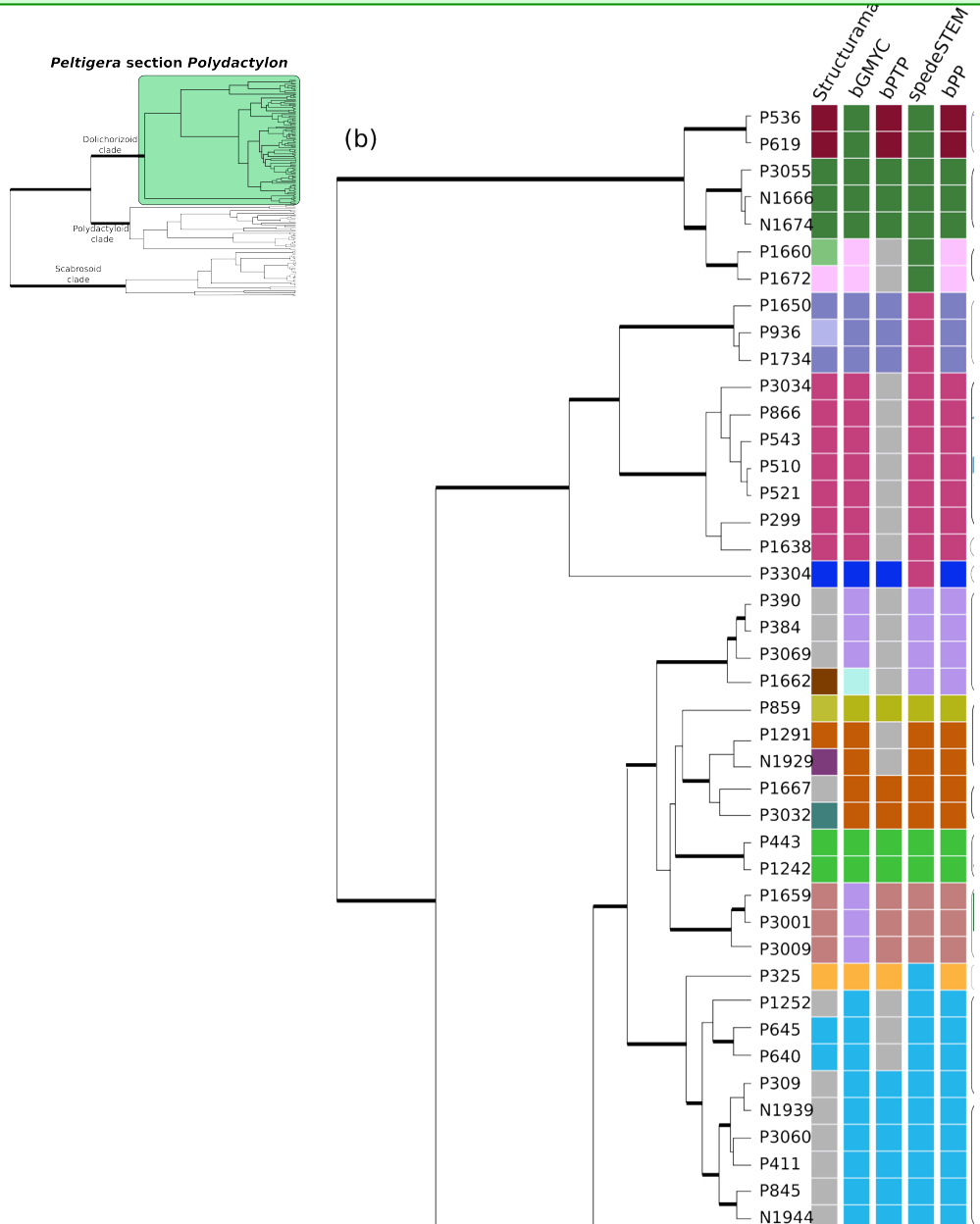


# a. Scabrosoid clade

10 species
7 new species



# b. Dolichorhizoid clade



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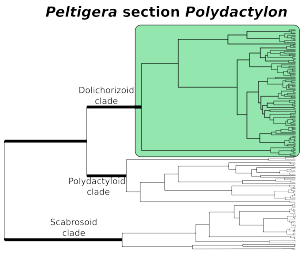


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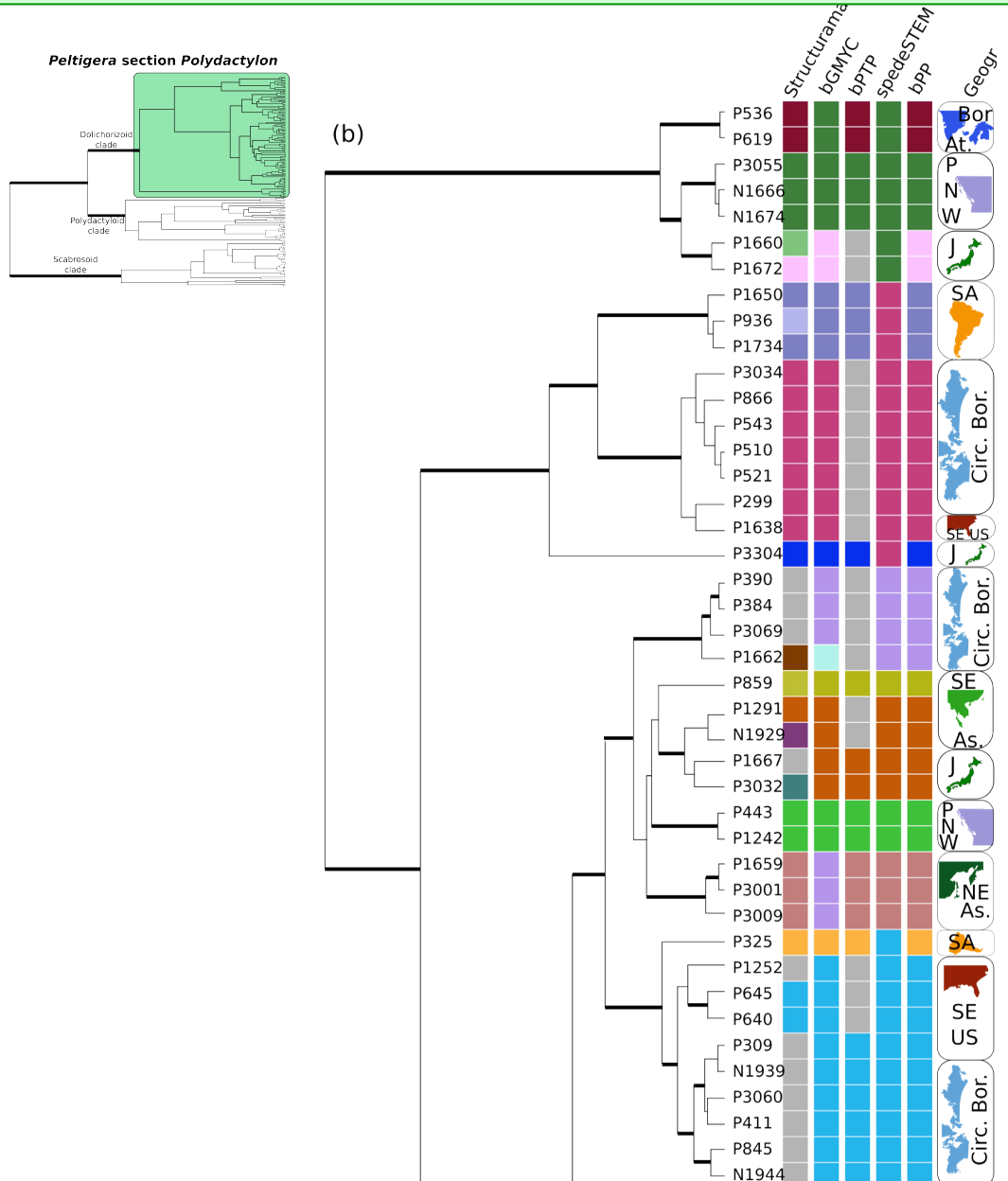

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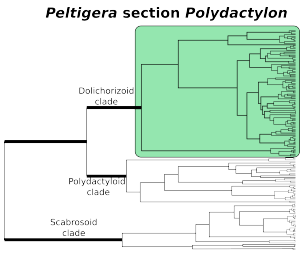


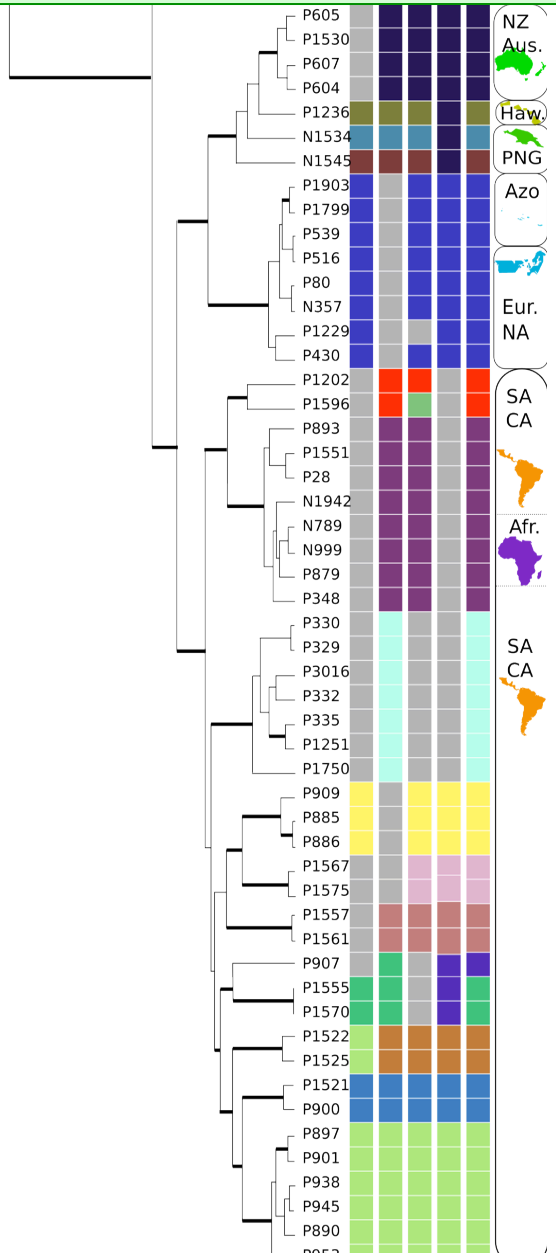

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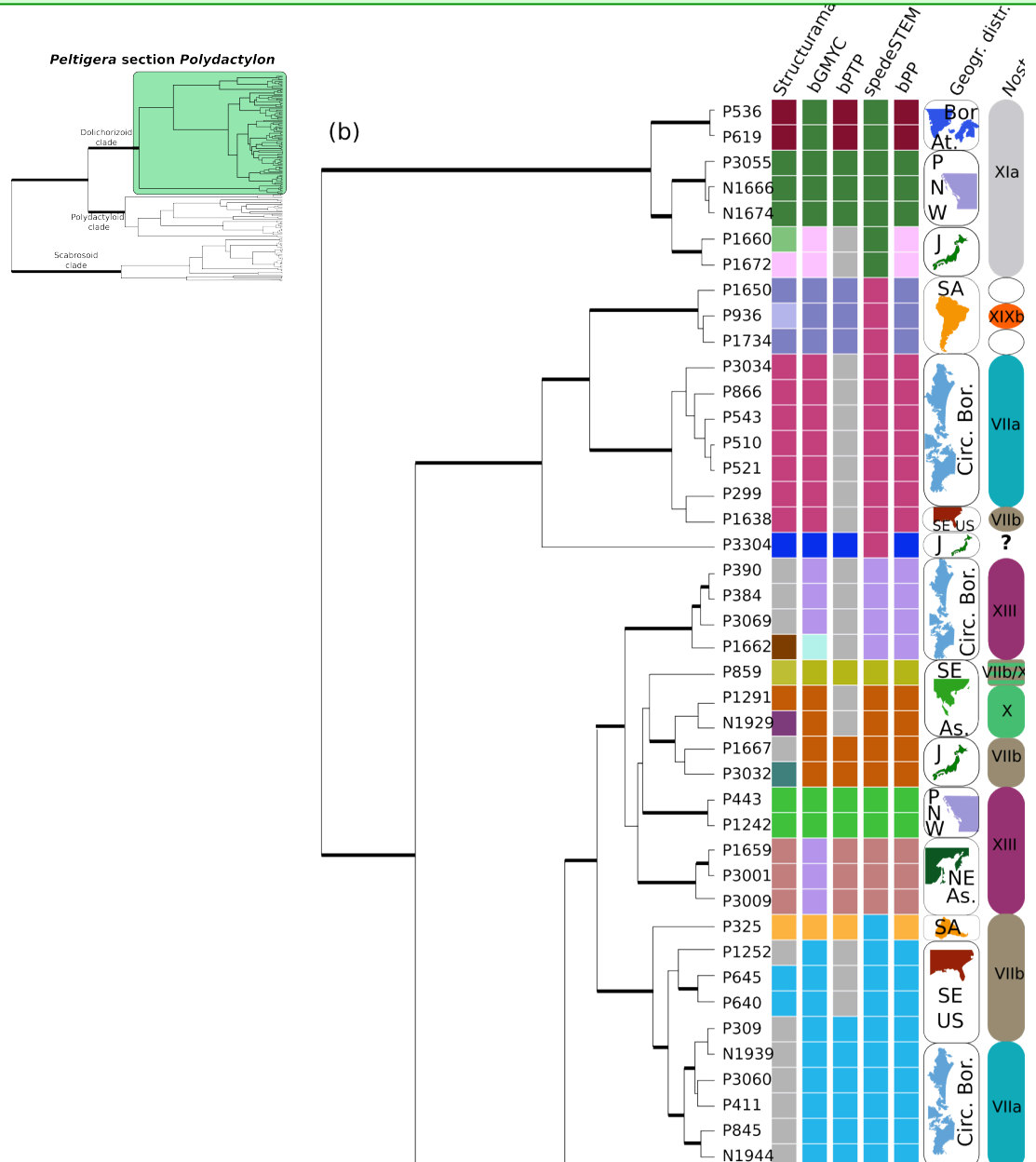

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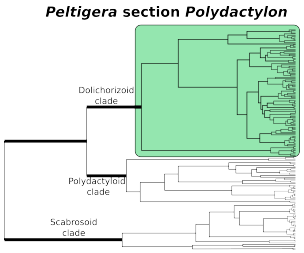


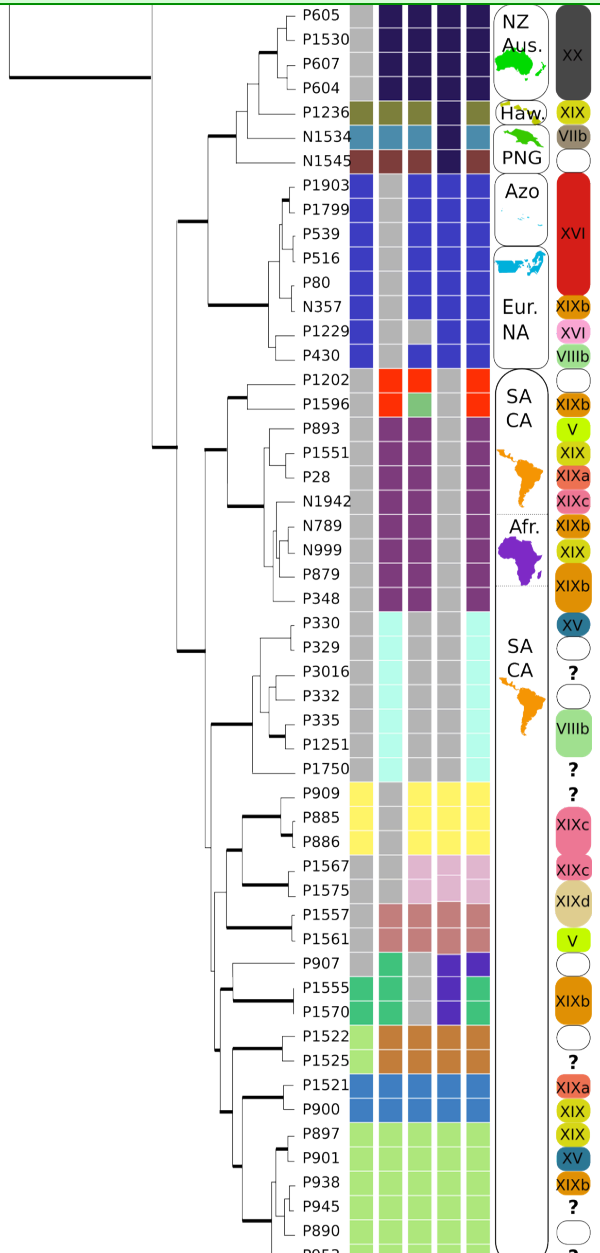

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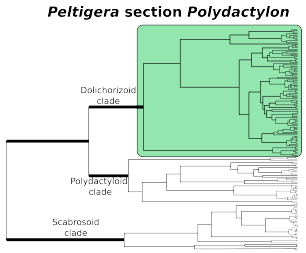


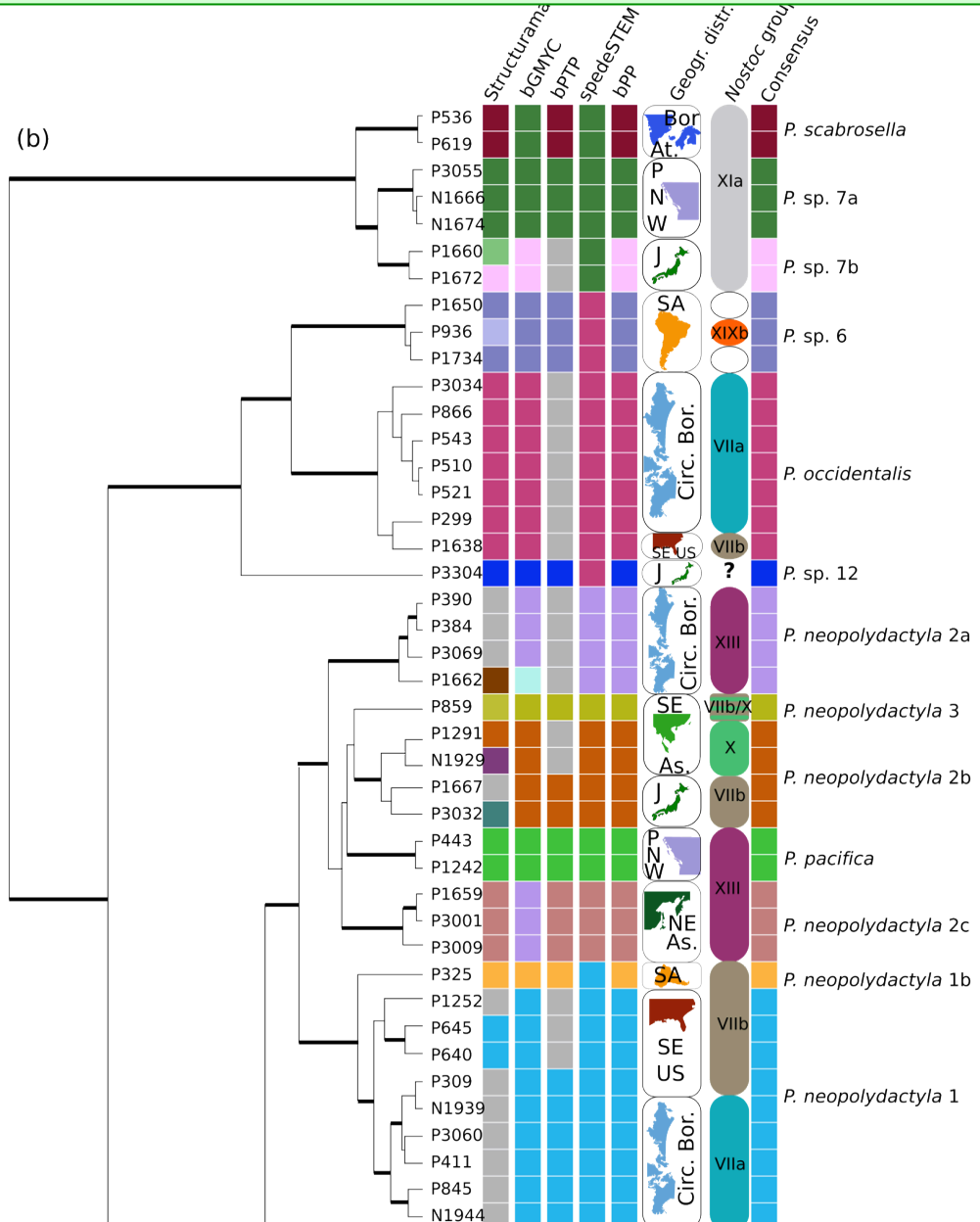

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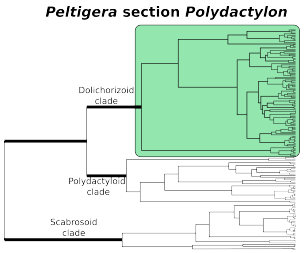
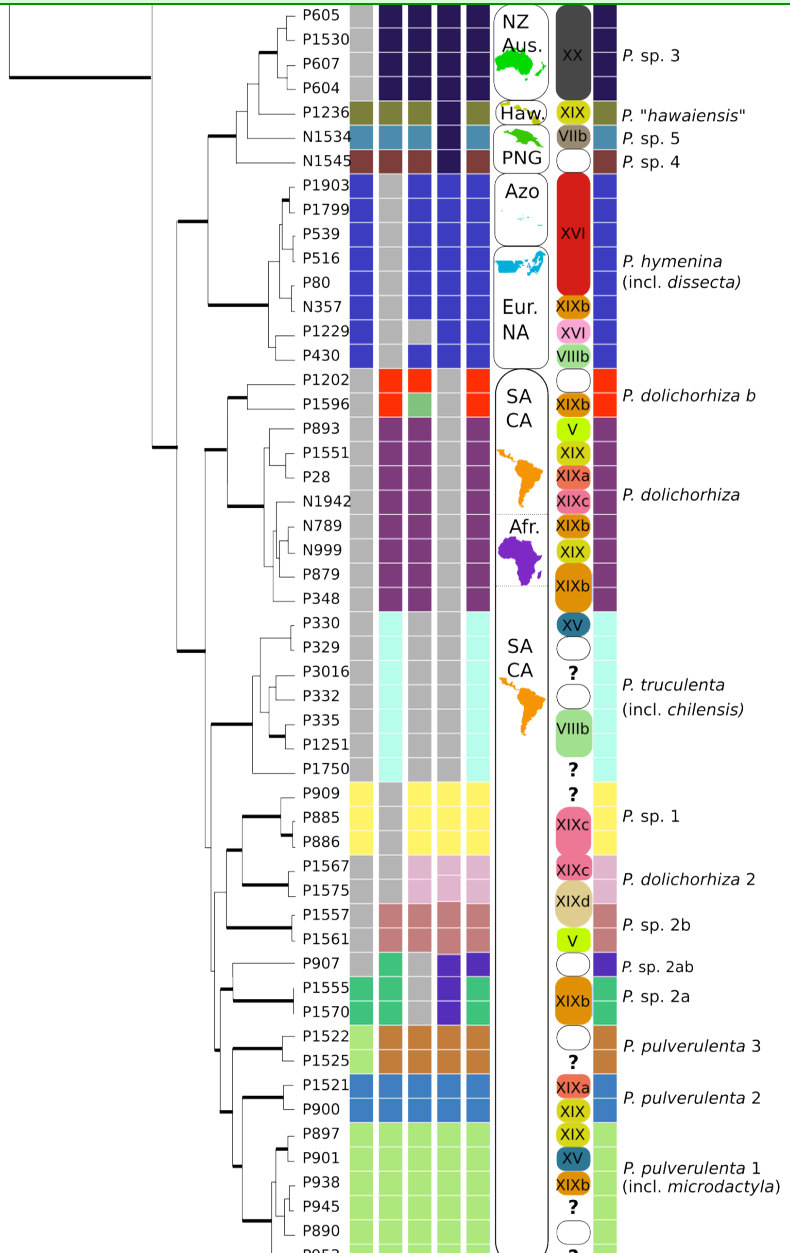
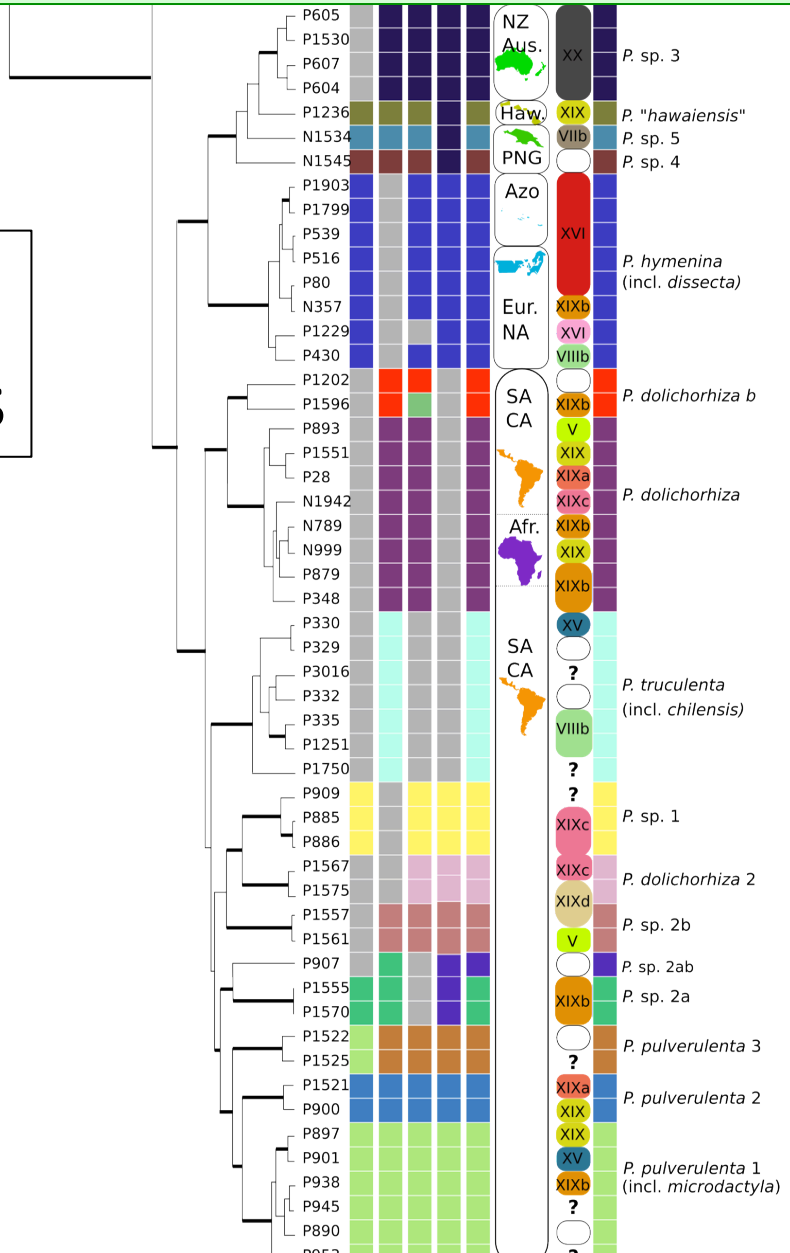


# b. Dolichorhizoid clade

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

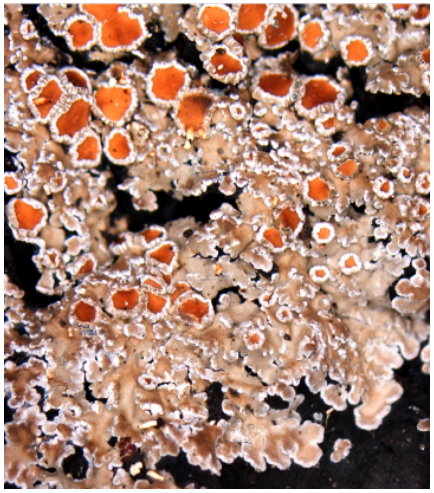
- Unlike previous assumptions, *Peltigera* species are not cosmopolitan taxa associating with a broad range of photobionts

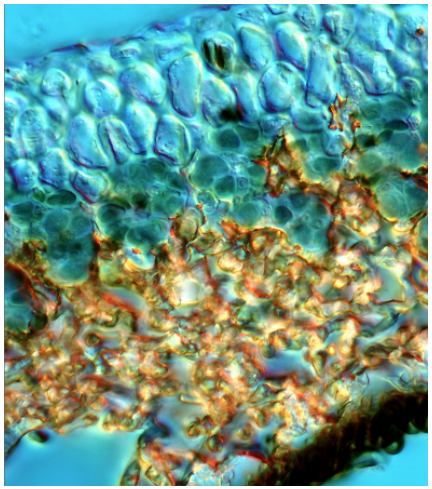
| Intitulé du projet de recherches. |
| --- |
| Français :<br>Les espèces cosmopolites sont-elles des fantômes de la Pangée ou des assemblages d'espèces cryptiques ? Le cas du champignon lichénisé Peltigera dolichorhiza.<br><br>Anglais :<br>Are cosmopolitan species ghosts from Pangea, or assemblages of cryptic species? A case study in the lichenized fungus Peltigera dolichorhiza |

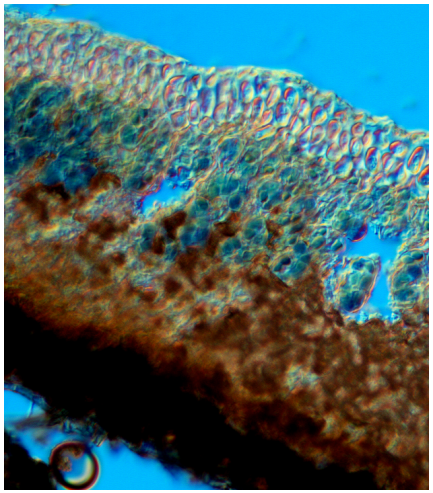
# Influence of the photobiont on the morphology and evolution of Pannariaceae

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

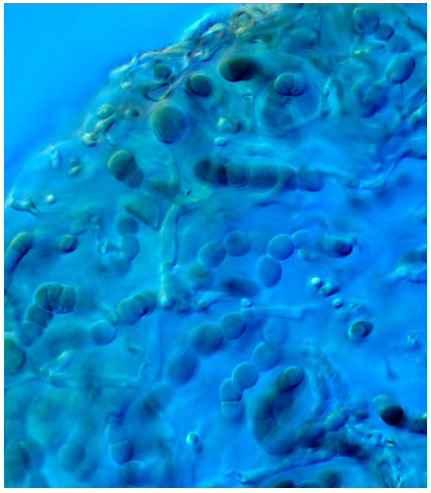
# Pannarioid thalli

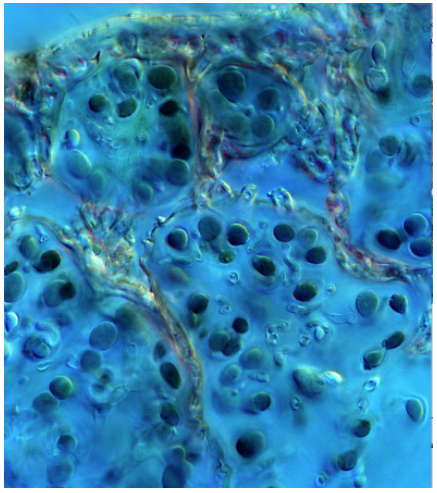


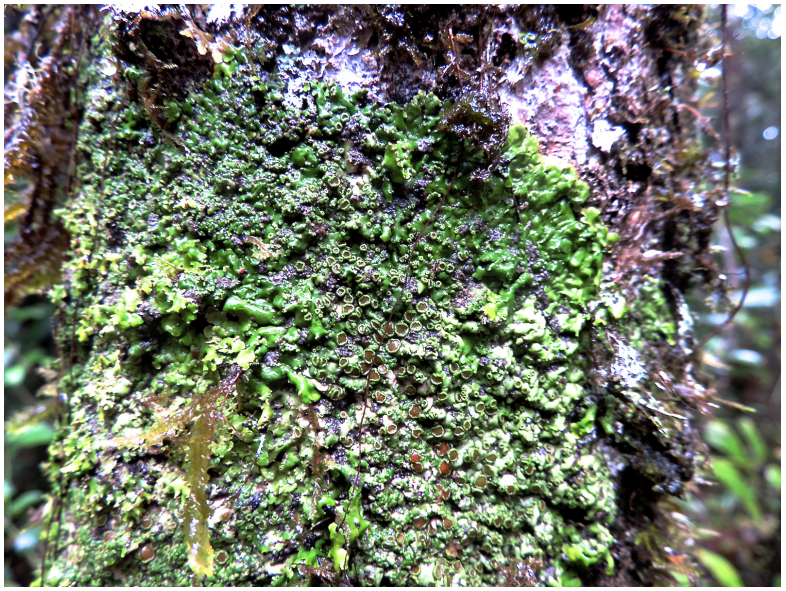


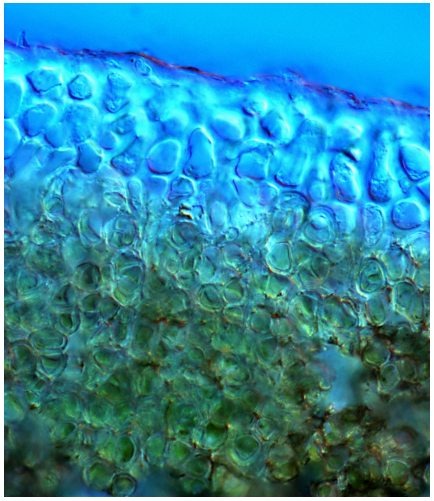
# Collematoid thalli

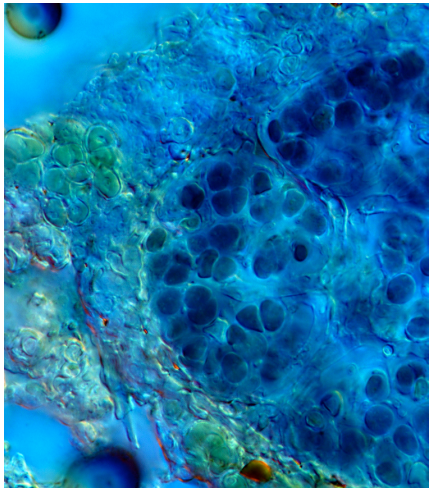




# Tripartite thalli



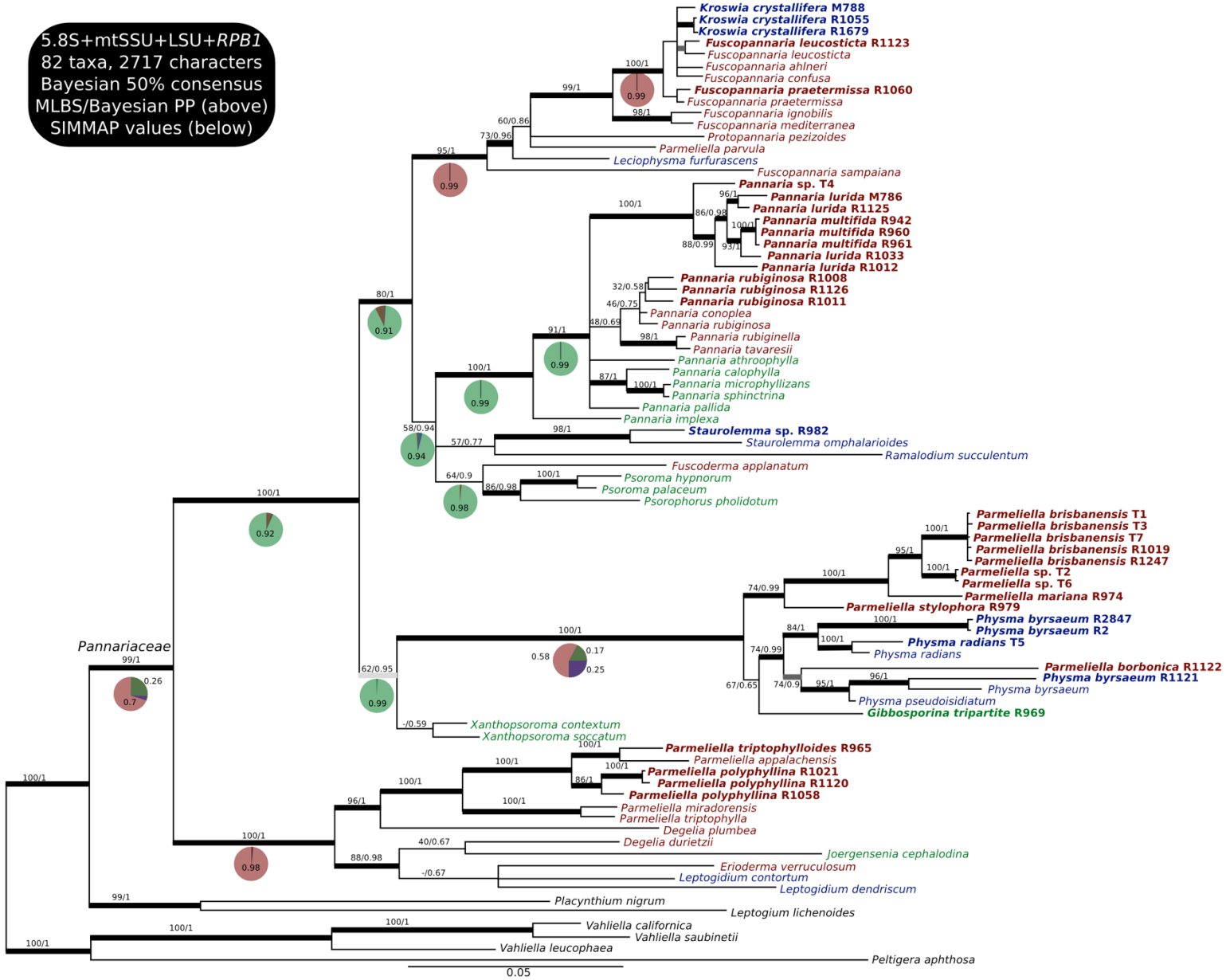




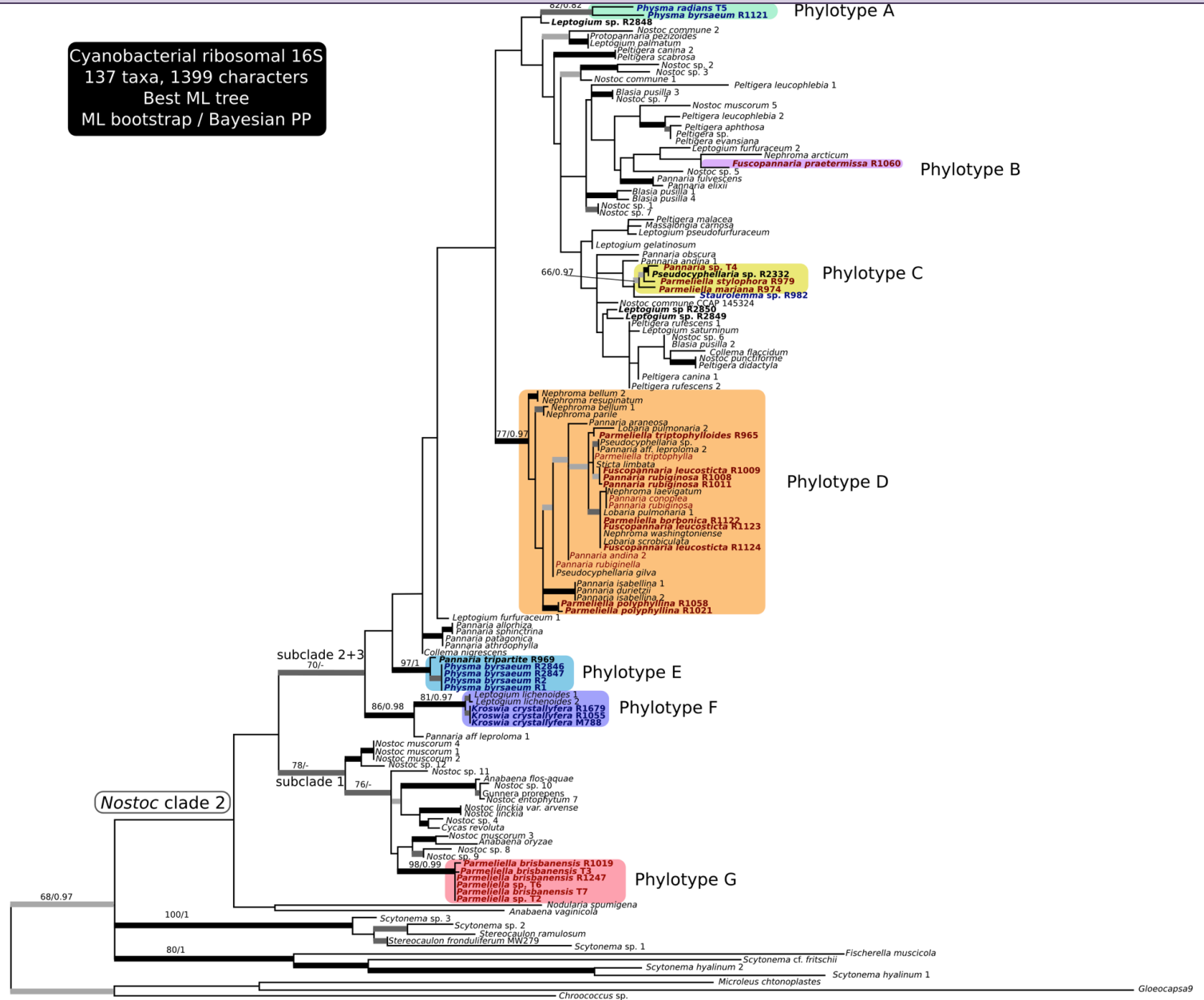
# Aims of the study

- 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

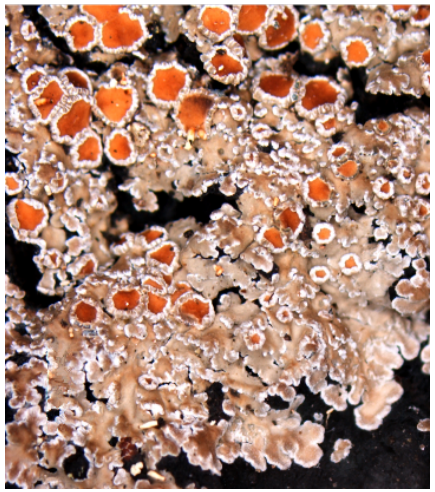
# Phylogeny of the mycobiont (fungus)



# Phylogeny of the cyanobiont (*Nostoc*)



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



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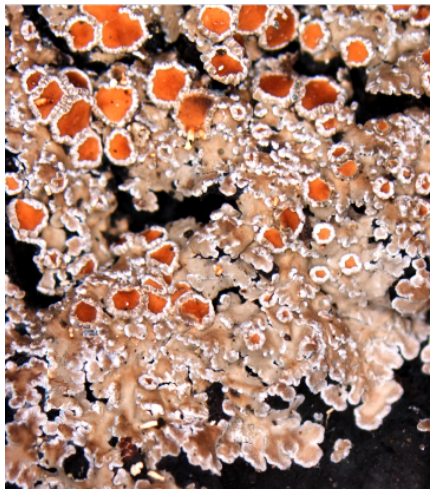

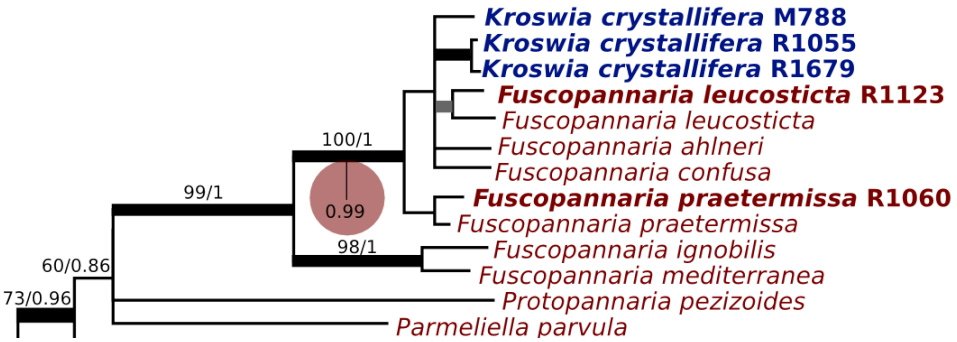


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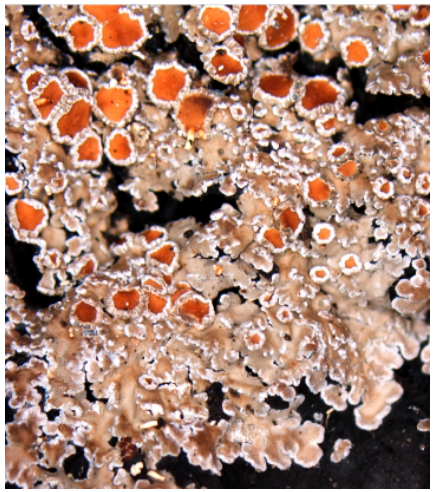

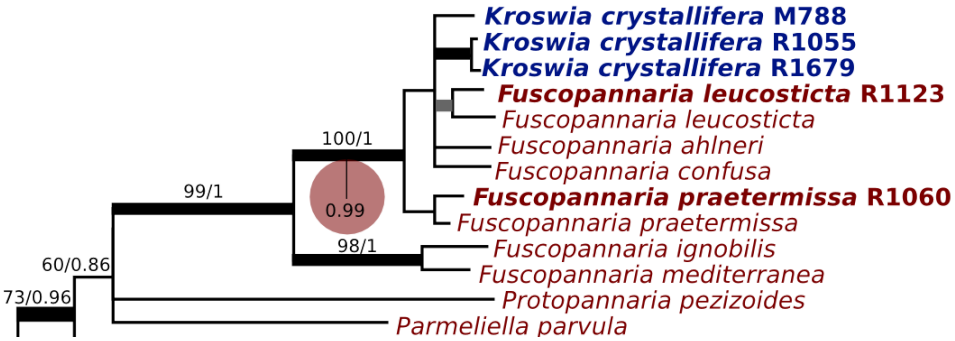


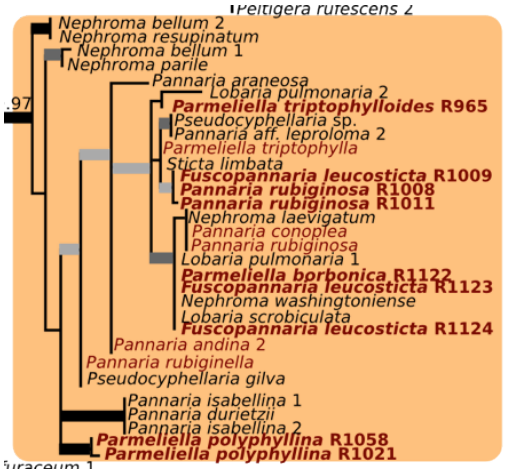

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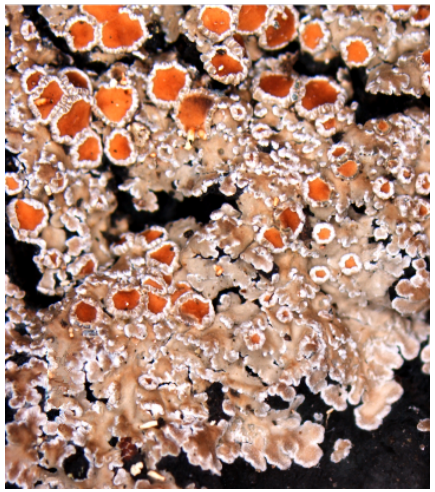

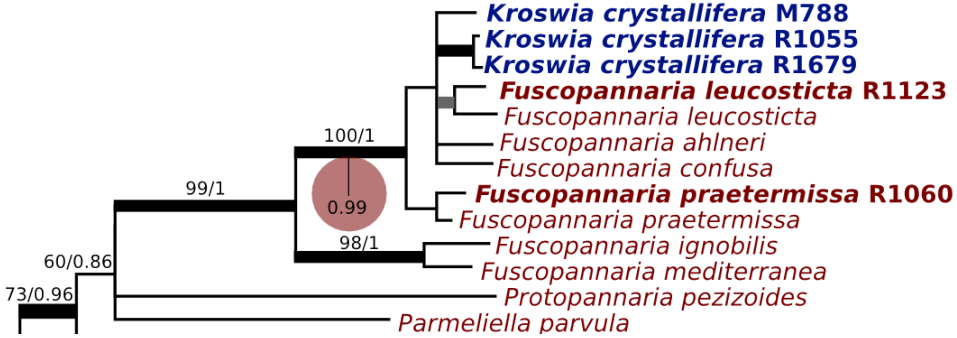


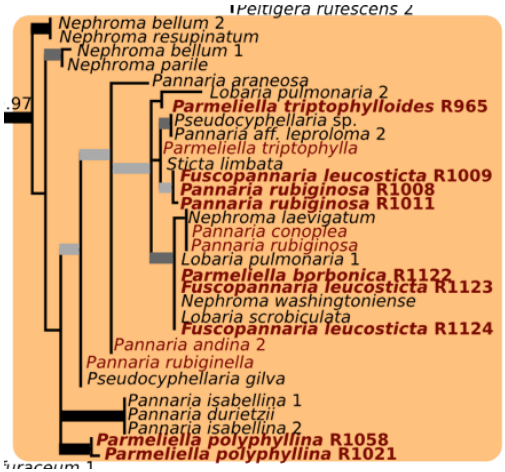


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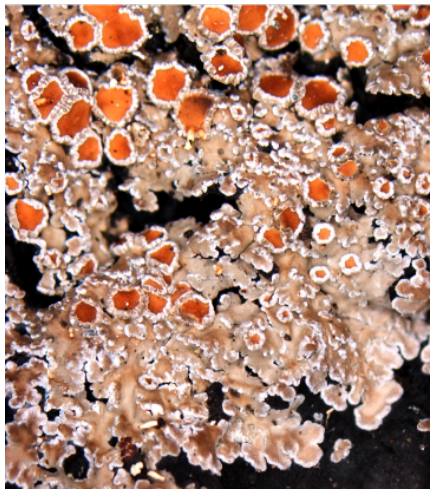

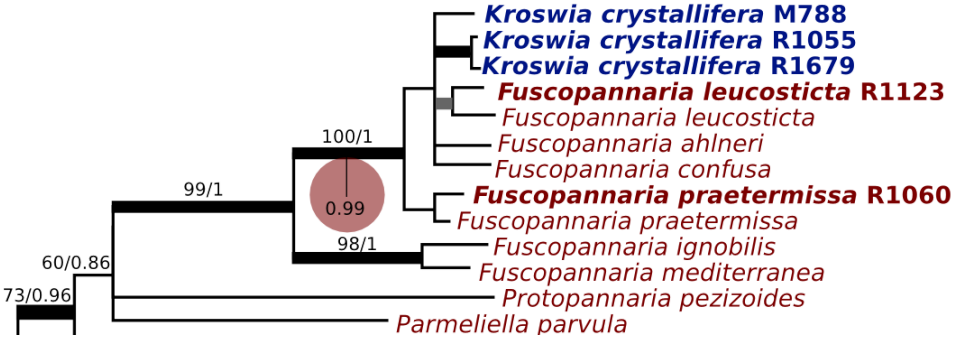


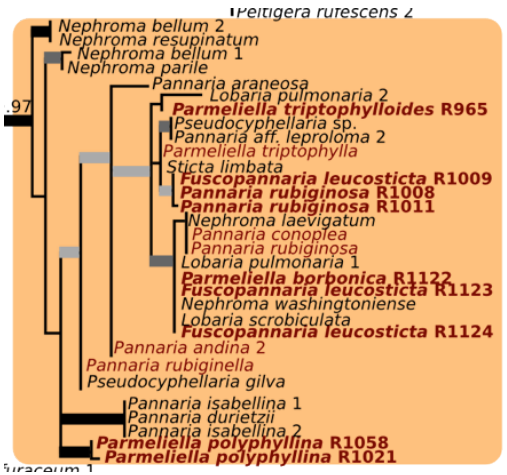



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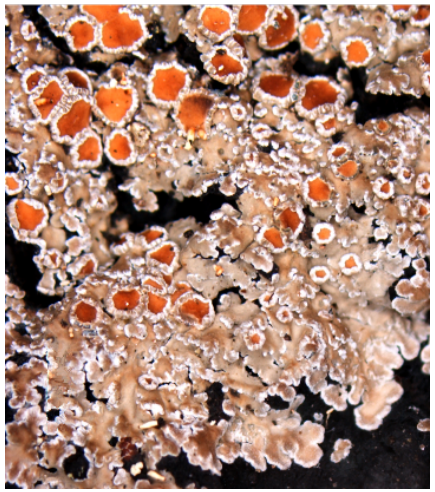

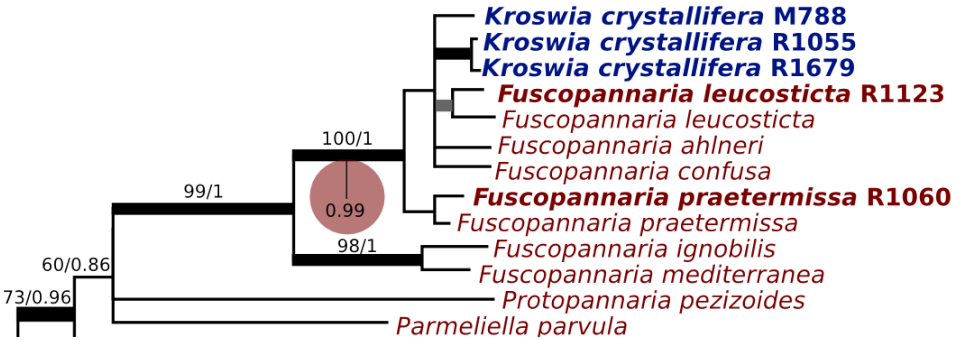


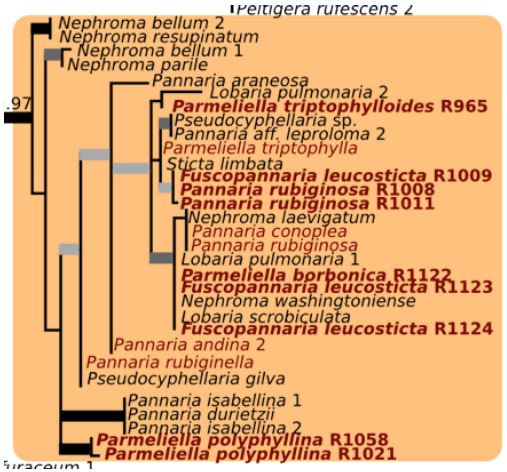



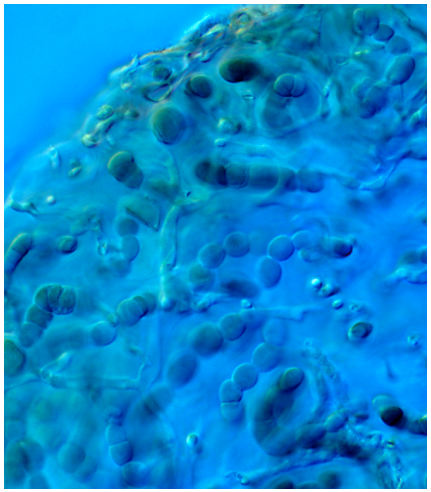

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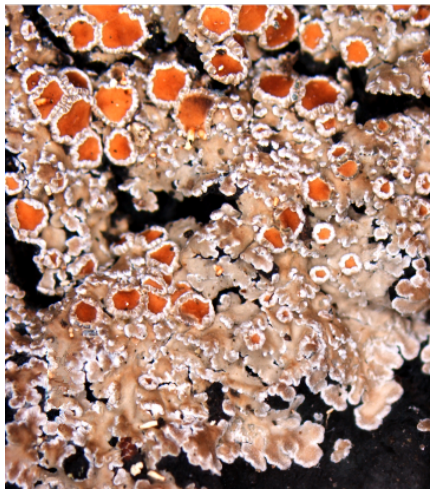

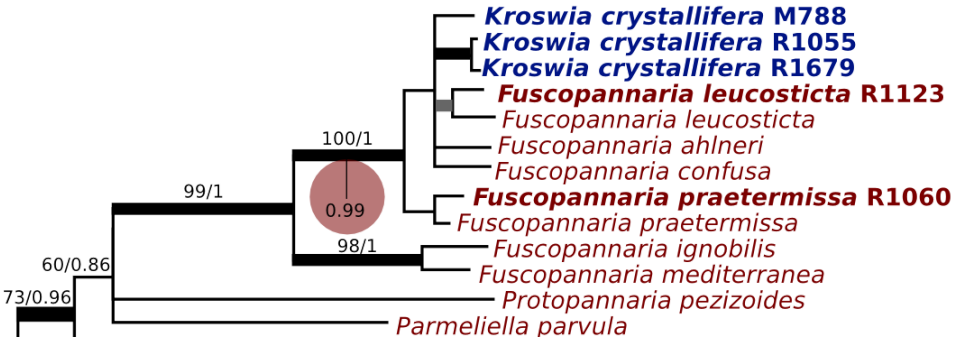


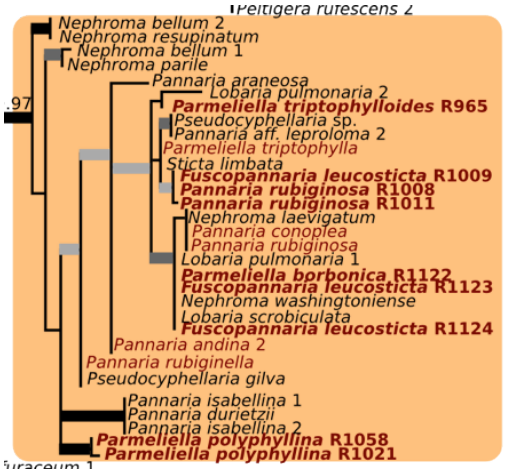



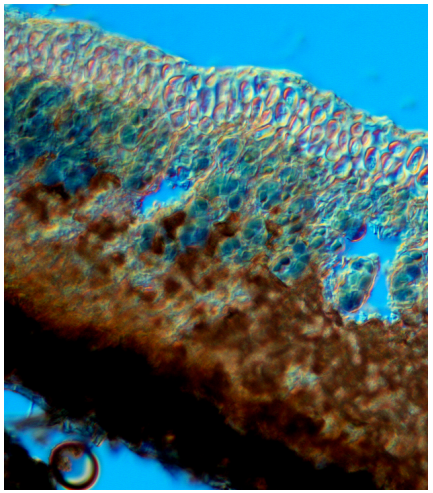

# b. The case of *Physma* and *Gibbosporina*

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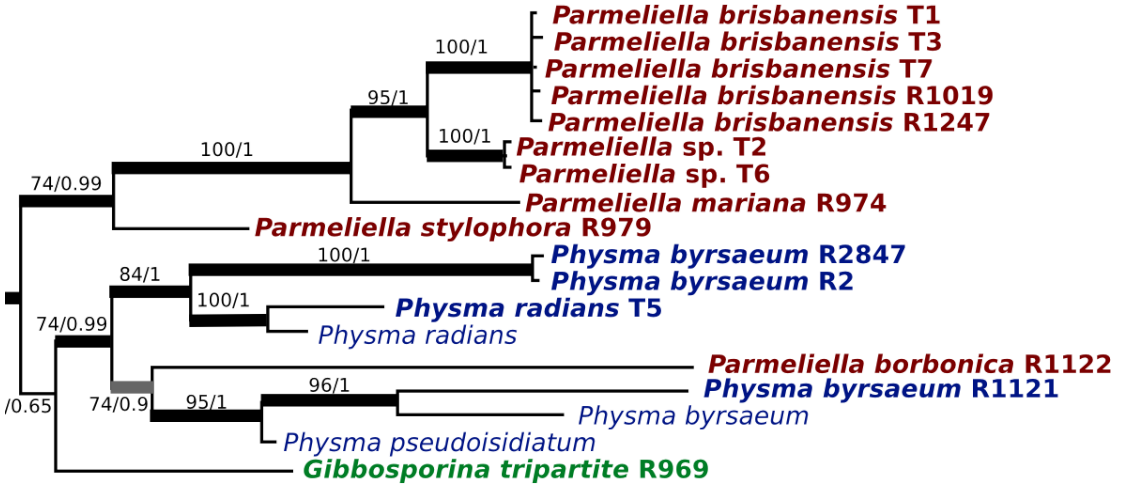


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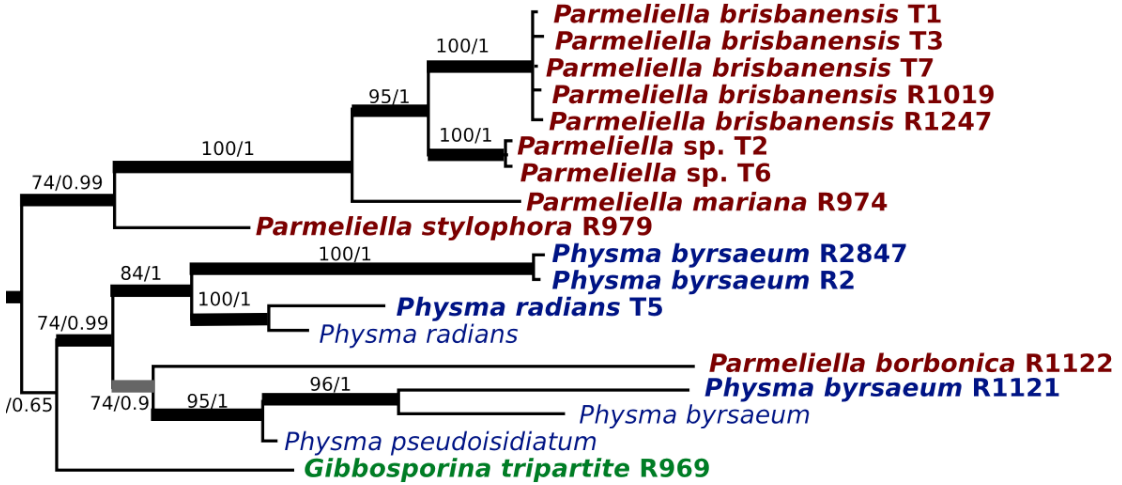


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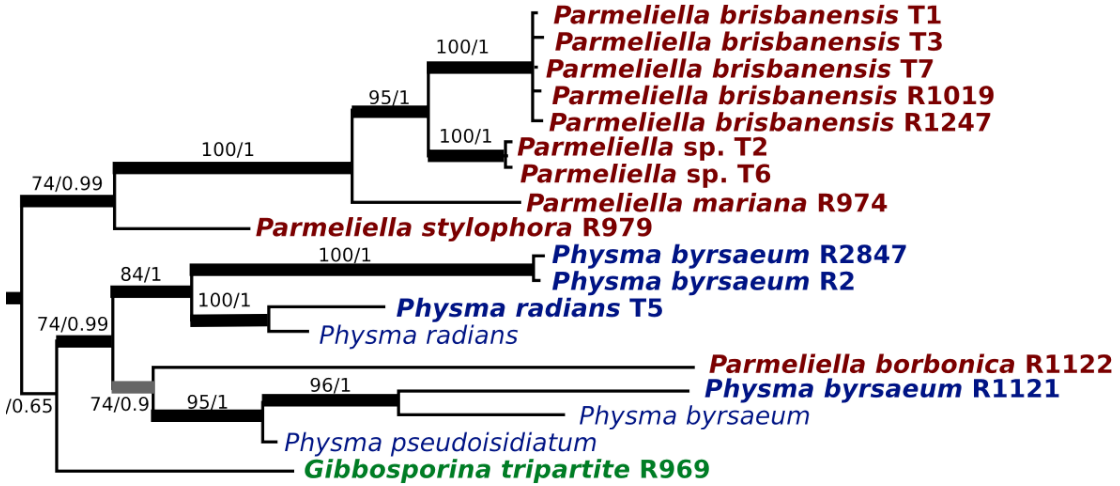
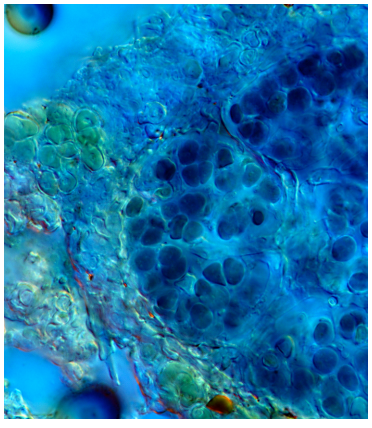
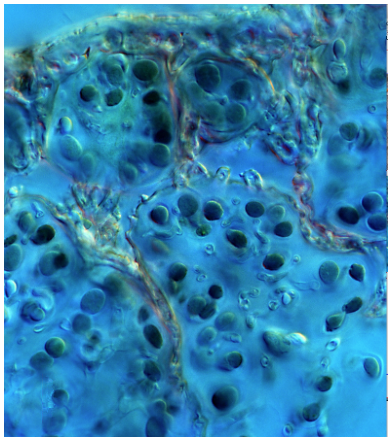
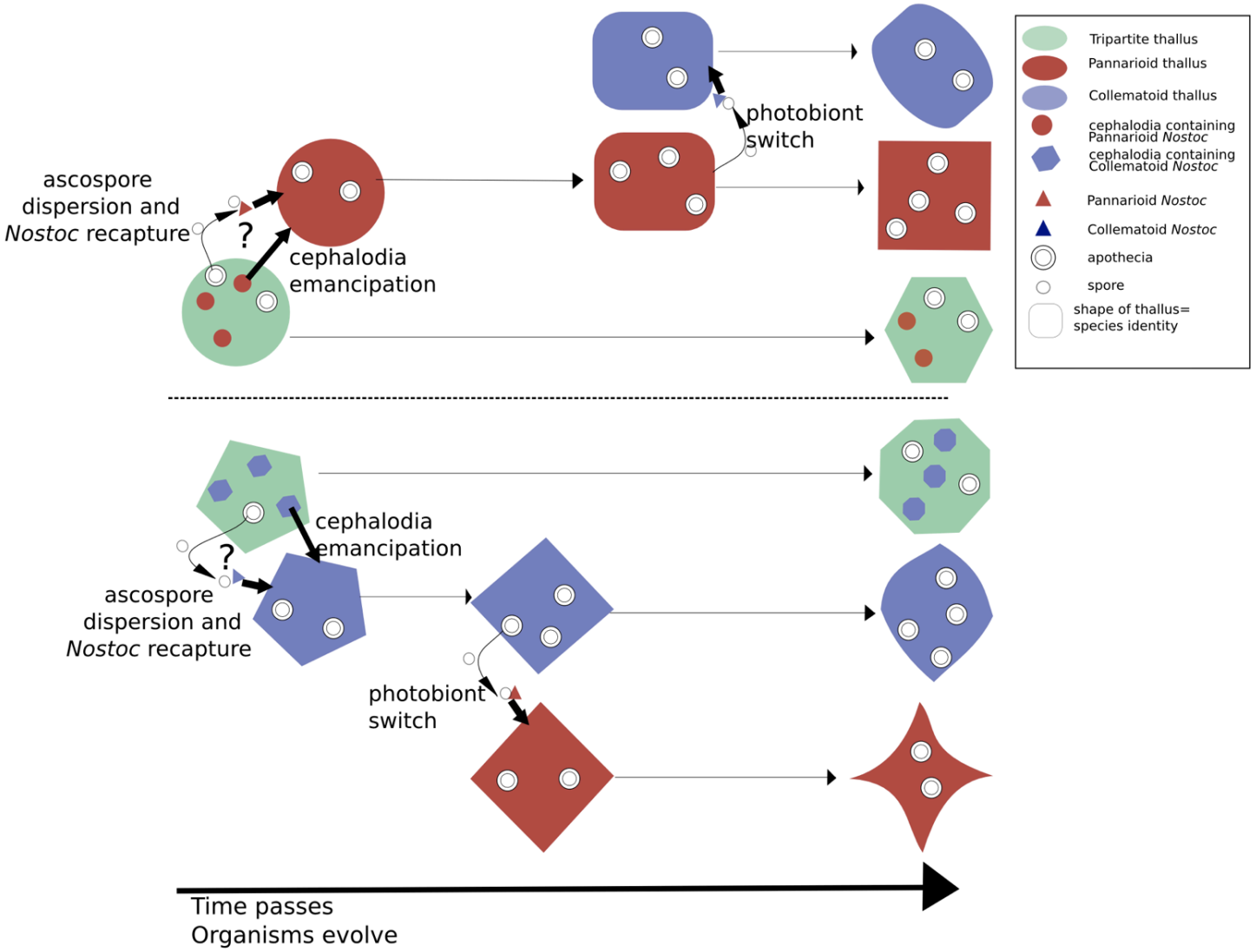








# Proposed hypothesis




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 !

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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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