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Functional PTB phosphate transporters are present in streptophyte algae and early diverging land plants

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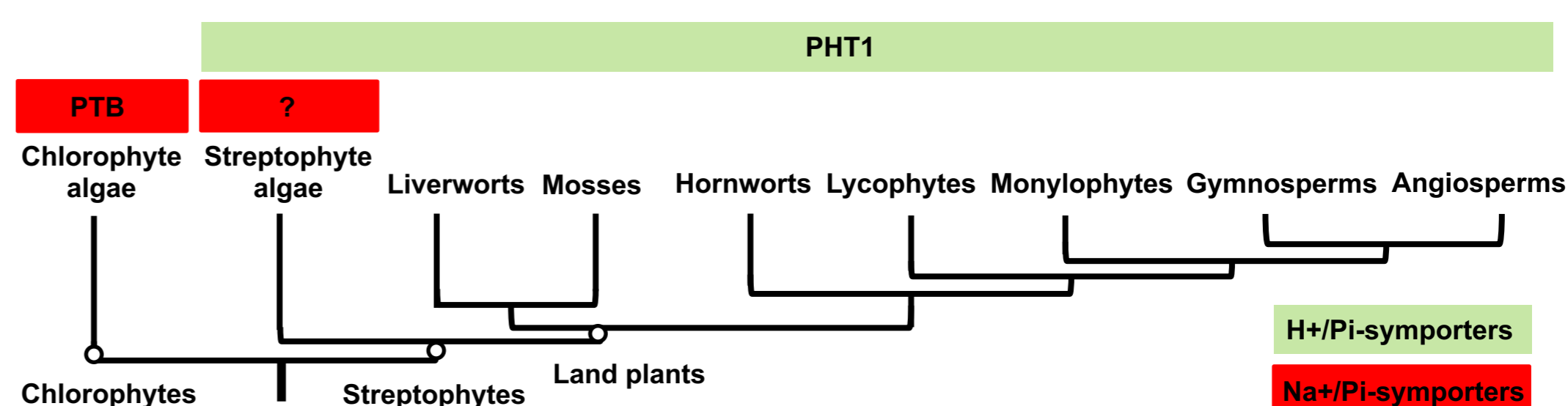
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Introduction

- Green plants – streptophytes and chlorophytes – use plasma membrane Pi-transporters to absorb phosphate (Pi) from the environment.
- In angiosperms, the most diverged group of land plants, H⁺/Pi-symporters (PHT1) are responsible for Pi-uptake from the environment, while Na⁺/Pi-symporters (PTB) are hypothesised to carry-out Pi-uptake in chlorophytes.
- PHT1 sequences are present in early diverging land plant and streptophyte algae but Na⁺-uptake is required for Pi-uptake in streptophyte algae implying that both H⁺/Pi-symporters and Na⁺/Pi-symporters are active in streptophytes.

To understand the evolution of Pi-uptake during land adaptation we set out to determine if Na⁺/Pi-symporters were present in streptophyte lineages.

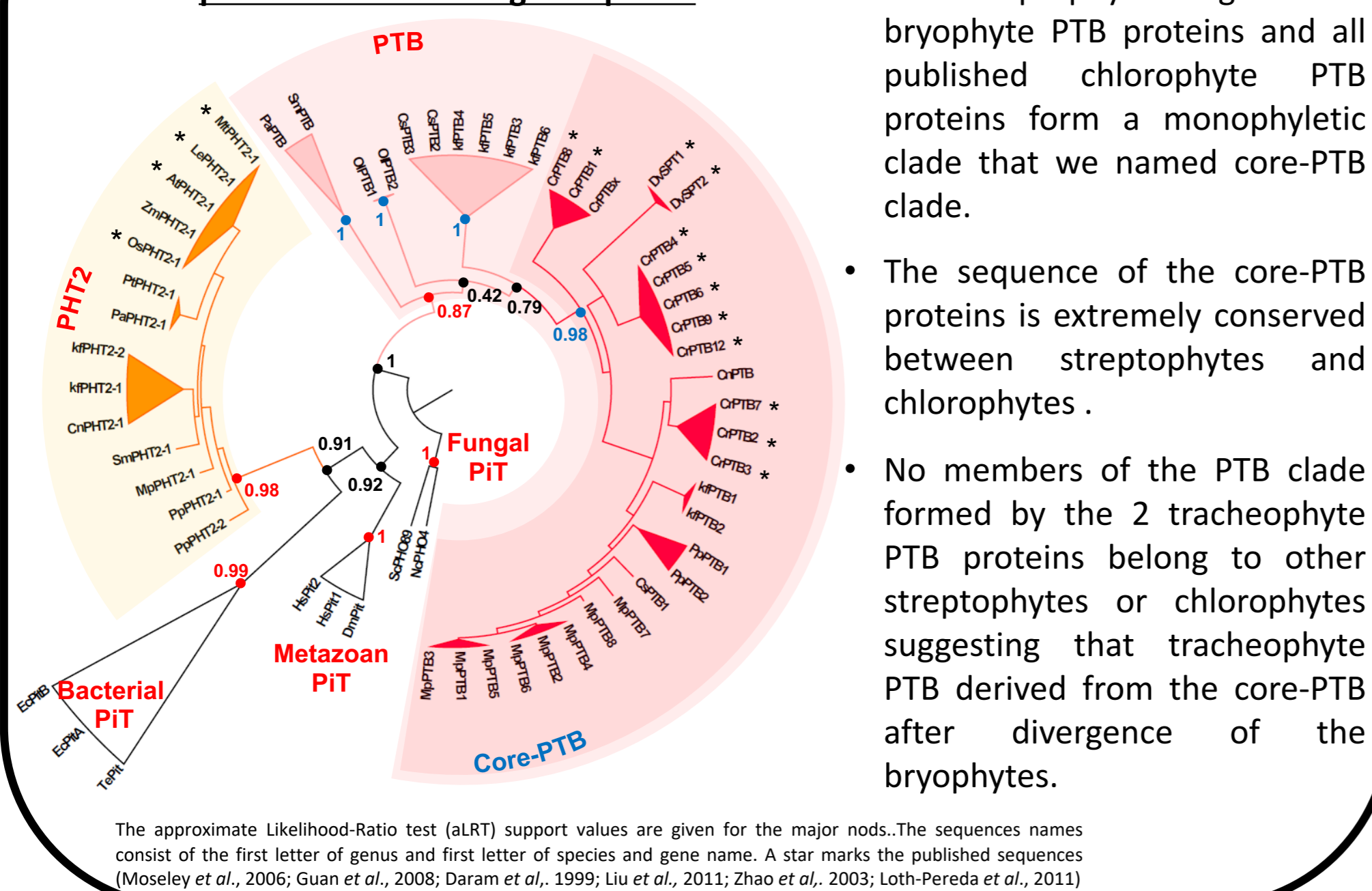
Pi-uptake mechanisms and Pi-symporters in the streptophyte phylogeny



After Wickett et al., 2014; Moseley et al., 2006; Li et al., 2005; Nussaume et al., 2011; Delaux et al., 2015

I. PTB proteins are present in streptophytes

Maximum-likelihood phylogeny of the PTB proteins across the green plants

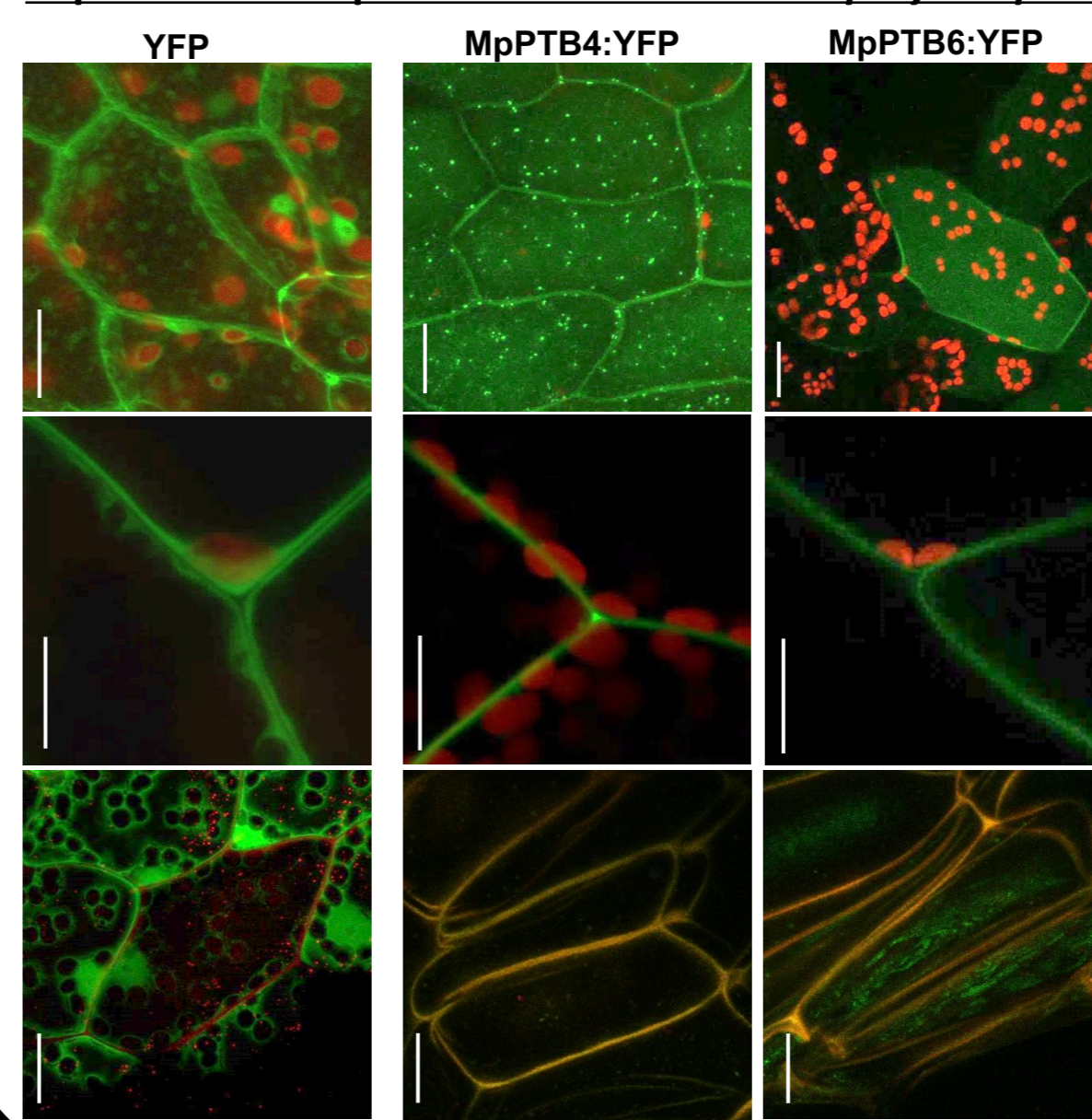


- All streptophyte algae and bryophyte PTB proteins and all published chlorophyte PTB proteins form a monophyletic clade that we named core-PTB clade.
- The sequence of the core-PTB proteins is extremely conserved between streptophytes and chlorophytes.
- No members of the PTB clade formed by the 2 tracheophyte PTB proteins belong to other streptophytes or chlorophytes suggesting that tracheophyte PTB derived from the core-PTB after divergence of the bryophytes.

The approximate Likelihood-Ratio test (aLRT) support values are given for the major nodes. The sequence names consist of the first letter of genus and first letter of species and gene name. A star marks the published sequences (Moseley et al., 2006; Guan et al., 2008; Daram et al., 1999; Liu et al., 2011; Zhao et al., 2003; Loth-Pereda et al., 2011)

II. *M. polymorpha* PTB proteins are at the plasma membrane

Expression of MpPTB fused to YFP in *M. polymorpha*



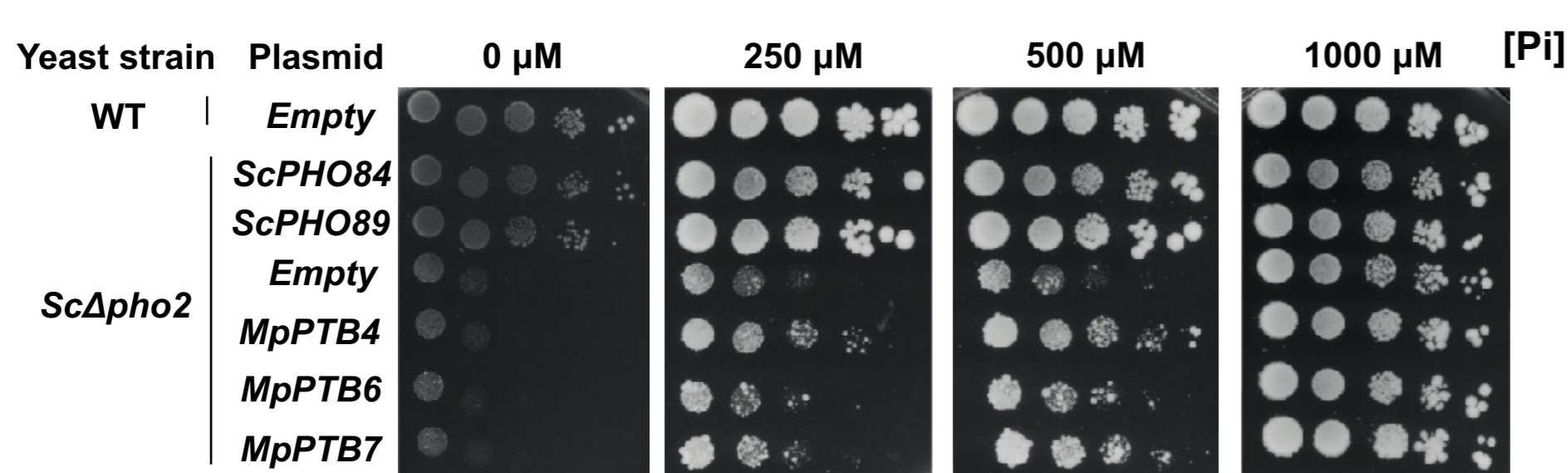
In cells expressing MpPTB:YFP but not in cells expressing YFP alone:

- The maximum projection of cells Z-scans the YFP signal (green) form a uniform layer following the boundaries of the cells.
- The details of the cell boundaries show that the YFP signal is delimited to a layer (green) and not found around chloroplasts (red).
- YFP (green) colocalize with the membrane dye FM4-64 (red).

Confocal images of YFP and chlorophyll (A) and, YFP and FM4-64 emission signals in *M. polymorpha* expressing YFP or MpPTB:YFP under the OsAct promoter.

III. The expression of *M. polymorpha* PTB rescue a yeast mutant defective in Pi-uptake

Growth phenotype of yeast *Scpho2* mutant expressing MpPTB



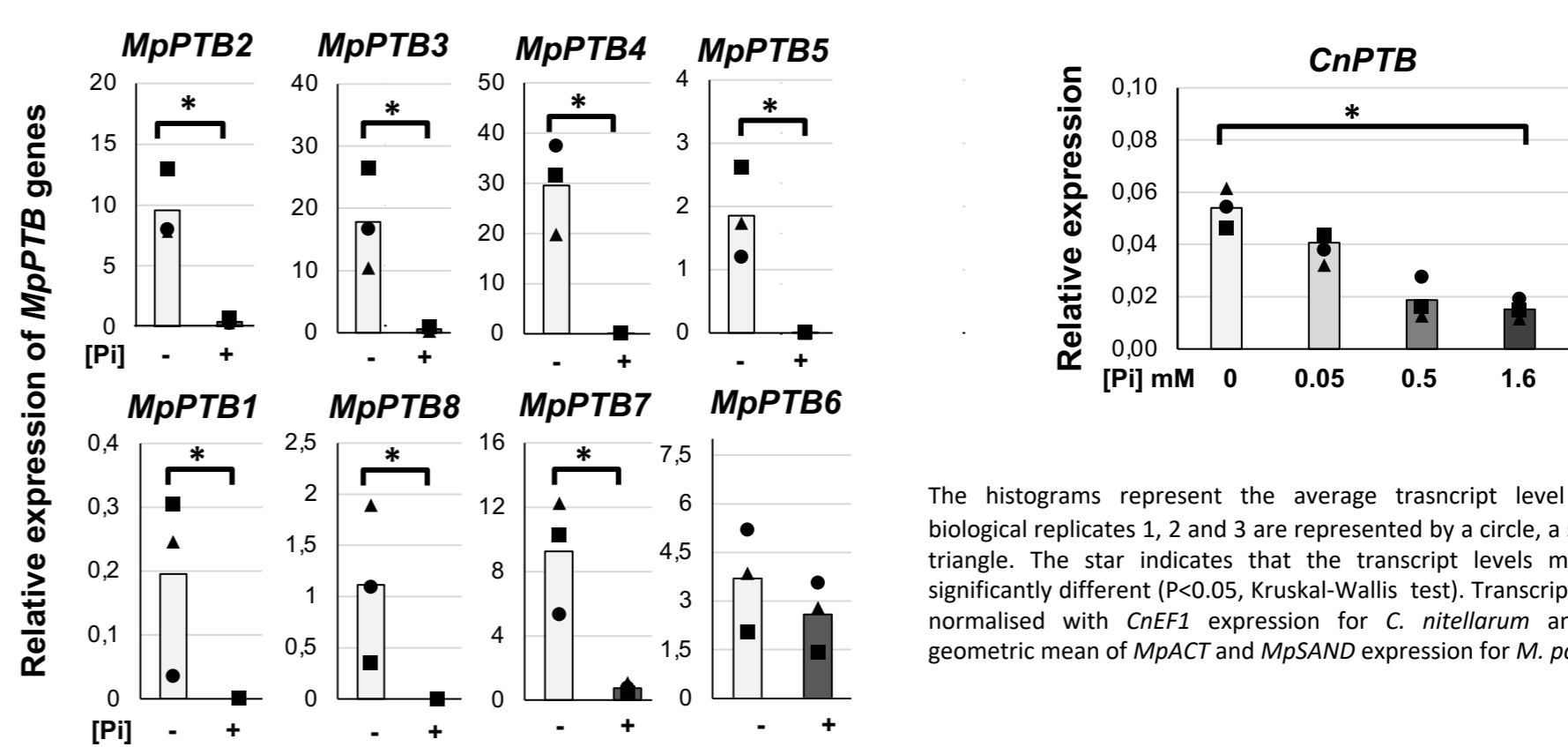
Growth phenotypes at 0, 250, 500 and 1000 μM of Pi of 10 times dilution series of WT and *ScPho2* mutant cultures transformed with the pCM189 vector without insertion (negative control) or expressing *MpPTB* genes or the yeast high-affinity Pi-symporters *ScPHO84* or *ScPHO89* (positive controls). *Scpho2* is

- ScPHO2* is a transcription factor required for the expression of the two *S. cerevisiae* high-affinity Pi-transporters: *ScPHO84* and *ScPHO89* (Pinson et al., 2004).
- The expression of MpPTB4, MpPTB6 and MpPTB7 partially rescue the growth of the *Scpho2* mutant in low-Pi conditions.

This suggests that these proteins are Pi-transporters

IV. *M. polymorpha* and *C. nitellarum* PTB genes expression is induced in low-Pi environments

Effect of the Pi-concentration of the environment on MpPTB and CnPTB genes expression



The histograms represent the average transcript level (n=3). The biological replicates 1, 2 and 3 are represented by a circle, a square and a triangle. The star indicates that the transcript levels measured are significantly different (P<0.05, Kruskal-Wallis test). Transcript levels were normalised with *CneF1* expression for *C. nitellarum* and with the geometric mean of *MpACT* and *MpSAND* expression for *M. polymorpha*.

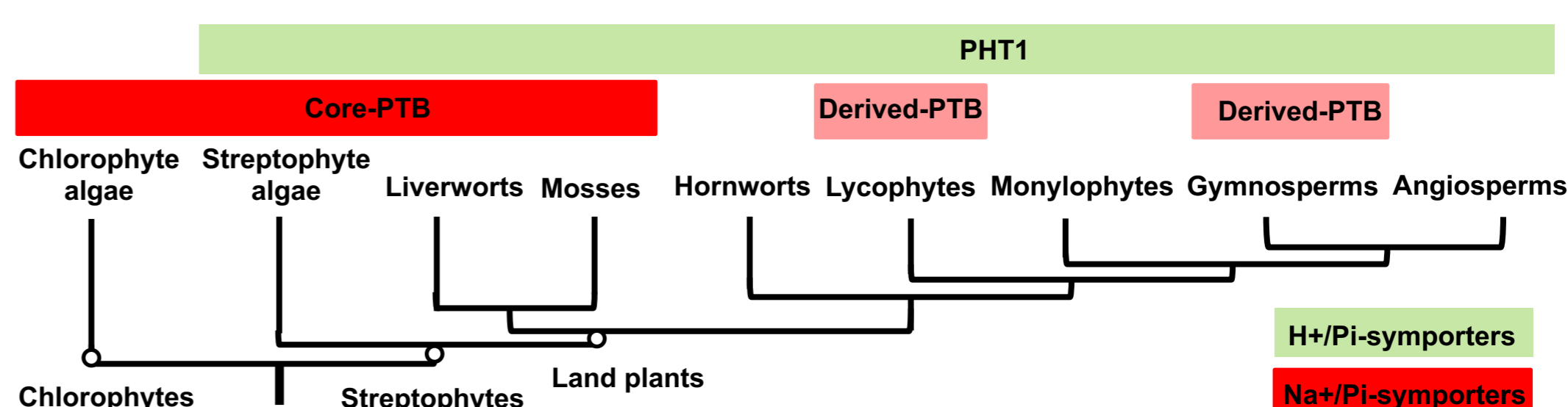
- Consistent with their role in Pi-uptake, the expression of the Pi-transporters PHT1 is up-regulated in low-Pi environments in angiosperms (Nussaume et al., 2011).
- The steady state level of the *C. nitellarum* and of 7/8 of the *M. polymorpha* PTB mRNAs is higher in plant grown in low-Pi than in replete-Pi environment.

This suggests that these proteins are involved in Pi-uptake

Conclusion and references

- PTB proteins are present in streptophytes.
- Streptophyte core-PTB proteins are functional plasma membrane Pi-transporters likely involved in Pi-uptake from the environment.
- Two Pi-uptake systems co-exist in streptophyte algae and early diverging land plants
- During their divergence from the bryophyte core-PTB, tracheophyte PTB proteins have lost the domains necessary for Pi-uptake in yeast and metazoan PTB-related proteins suggesting the loss of the Pi-uptake function.
- Na⁺/Pi symporter could be more efficient for Pi-absorption from aquatic habitat (alkaline, high Na⁺ concentration) (Moseley et al., 2006), while H⁺/Pi-symporters are efficient in soil through the creation of a H⁺ gradient (Nussaume et al., 2011).

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