Phylogenetic and population structure of the *nod*-free but nodulating *Bradyrhizobium* phylogroup

Lu Ling[1,2^], Alicia Camuel[3,4^], Sishuo Wang[1], Xiaojun Wang[2], Xinqin Lin[2], Nico Nouwen[3,4], Eric Giraud[3,4*], Haiwei Luo[1,5*]

[1]Simon F. S. Li Marine Science Laboratory, School of Life Sciences and State Key Laboratory of Agrobiotechnology, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, China

[2]Shenzhen Research Institute, The Chinese University of Hong Kong, Shenzhen, China

[3]IRD, Laboratoire des Symbioses Tropicales et Méditerranéennes (LSTM), UMR IRD/ SupAgro/INRA/ Université de Montpellier /CIRAD, TA-A82/J– Campus de Baillarguet 34398 Montpellier cedex 5, France

[4]PHIM Plant Health Institute, Université Montpellier, IRD, CIRAD, INRAE, Institut Agro, Montpellier, France

[5]Institute of Environment, Energy and Sustainability, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, China

[^]**These are co-first authors**: Lu Ling, Alicia Camuel

[*]**These are co-corresponding authors:** Eric Giraud (eric.giraud@ird.fr), Haiwei Luo (haiweiluo@cuhk.edu.hk)

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Abstract

Bradyrhizobium is a main rhizobial lineage of which the majority of its members nodulate legume plants using Nod factors (NFs) encoded by the *nod* genes. However, the "photosynthetic" phylogroup within *Bradyrhizobium* (PB) does not contain *nod* genes but are still capable of establishing a nitrogen-fixing symbiosis with some tropical legumes of the *Aeschynomene* genus. Furthermore, members of this phylogroup colonize rice roots and promote plant growth. Despite this unique combination of ecological features, genomes of only 13 PB members are sequenced, and almost all are isolated from *Aeschynomene* spp. nodules. Here, we sequenced 208 new PB members predominantly associated with rice. The extended PB phylogroup comprises three main clades: a basal clade with significant expansion of its diversity, followed by the diversification of a singleton clade from a new clade exclusively represented by our strains. Although the PB strains universally lack the canonical *nod* genes, all 27 assayed strains representing the broad diversity of these clades induced nodules on *Aeschynomene indica*. Interestingly, significant differences in the efficiency of symbiosis between the main clades were observed and the singleton clade showed an intermediate symbiotic phenotype aligning well with its intermediate phylogenetic position. Our strain collection expands the phylogenetic and ecological diversity of the *nod*-free but nodulating *Bradyrhizobium* and shows that the NF-independent nodulation of *Aeschynomene* is a common trait of this phylogroup, in contrast to the photosynthetic trait originally thought as its unifying feature.

Introduction

Bradyrhizobium is one of the largest and most diverse rhizobial genera and the primary symbiont of a wide range of legumes [1, 2]. The genus *Bradyrhizobium* encompasses seven phylogenetic supergroups (phylogroups) [3, 4], among which the "photosynthetic" *Bradyrhizobium* (PB) supergroup is one of the most special. First, these bacteria are photosynthetic which is a very rare property in rhizobia [3]. Second, members belonging to this supergroup can form nitrogen-fixing nodules not only on roots but also on stems of some tropical semi-aquatic species of the *Aeschynomene* genus [5]. Finally, the most original feature of the PB strains is the fact that these nodulating bacteria lack the canonical *nodABC* genes encoding the enzymes that synthesize the core structure of the nodulation factors (NF).

The available evidence indicates that the PB phylogroup takes a novel symbiotic strategy that differs from the traditional universal NF-based pathway [6, 7]. Although several attempts have been made to identify the symbiotic determinants of PB strains by mutagenesis, the mechanism has not yet been discovered [8]. This mystery has become more intriguing since the recent discovery of another NF-independent symbiotic process present in a wide variety of non-photosynthetic *Bradyrhizobium* strains [9]. This last process relies on a Type III secretion system (T3SS) which secretes, into the plant cells, effectors (T3Es) able of triggering nodulation [10-12]. The absence of T3SS in most PB strains indicates that they use a distinct symbiotic mechanism that was shown specific to this phylogroup [12].

Despite these unique features, the research on photosynthetic *Bradyrhizobium* has been very limited. Currently, there are only 13 PB strains that have their genomes sequenced, largely limiting comparative genomics analysis on this important *Bradyrhizobium* phylogroup. Although most PB strains were isolated from *Aeschynomene* spp. nodules, the PB phylogroup was also

detected in paddy soil, rice roots as well as in lake water [13-16], suggesting that its members have much wider ecological niches than previously thought. Here, we cultured and sequenced the genomes of 208 isolates (Fig. 1) predominantly associated with three niches of rice (within root, rhizosphere, bulk soil). We then conducted genomic analyses and physiological assays to reveal the phylogenetic and population structure of the photosynthetic *Bradyrhizobium* supergroup.

Results and discussion

The new genomes expand the phylogenetic diversity of the photosynthetic supergroup of *Bradyrhizobium*

With the 208 newly isolated members (see Supplementary Text for photosynthetic *Bradyrhizobium* isolation), the phylogeny of the PB supergroup is split into three deep-branching clades (see Fig. S1 for their phylogenetic position in the species tree of the entire *Bradyrhizobium* genus). Clade 1 represents the evolutionarily basal lineage. It initially comprised only 12 strains, but it now has its diversity expanded by having 68 new strains representing several new lineages delineated as distinct genetically isolated populations (Fig. 1, Datasets S1 and S2; also discussed in the next section). Clade 2 is a singleton clade with only one strain (*Bradyrhizobium* sp. STM3843) available and represents a phylogenetic intermediate among the three clades. Clade 3 is new and consists exclusively of 140 new strains. The evolutionary branching order of the three clades is verified with two outgroup-independent methods (Fig. 1, Fig. S7A) and the outgroup-dependent method (Fig. S1). Collectively, our new strains appreciably increase the existing phylogenetic diversity of the PB supergroup. Comparative genomic analysis shows that except for *Bradyrhizobium* sp. ORS285, which is known to have

nod genes and use both a *nod*-dependent and -independent strategy for nodulation [17, 18], all PB supergroup members lack the *nod* genes.

Fine-scale population structure of the photosynthetic supergroup of *Bradyrhizobium*

Apart from the broad diversity of the PB supergroup, we further asked whether fine-scale phylogenetic differentiation correlates with the ecological niches where the PB supergroup members were found. Of the 208 new PB supergroup strains, 205 were collected from three rice plants located in the same rice field with each plant 5-10 m apart from the others. The remaining three strains were isolated from grassland and forest. Bacterial isolation was performed from within the root, rhizosphere, and bulk soil for each plant, collectively giving rise to 145, 23 and 40 PB strains, respectively (Dataset S1). To facilitate the correlative analysis between fine-scale phylogenetic groups and the niches, we applied the population genomics software PopCOGenT [19], which defines the boundaries of populations (reported as "main cluster" or MC) between which gene flow is limited, distinguishes recent gene flow from historical events, and detects subpopulations (reported as 'subclusters') under ongoing differentiation within a population.

Using this approach, we showed that all strains in Clade 3 share the membership of a single population (MC1), whereas strains from Clade 1 fall into many populations. In Clade 1, MC2, MC3, MC4, MC5 and MC6 are each exclusively comprised of the new strains, whereas MC7 and the remaining unassigned isolates are from published resources. In Clade 1, the within- and between-population similarity was above and below 95% ANI (Fig. S2), respectively, consistent with the operational species threshold of 95% ANI [20], whereas the 16S rRNA gene shows little divergence with the between-population similarity generally above 99% (Fig. S2, Dataset S3). Based on the available samples, intra-population subdivision occurred within MC1,

MC2 and MC4. We found that each population and subpopulation have members sampled from different plants and niches (Fig. 1), suggesting that the PB populations sampled from the rice field are not separated or subdivided according to the physical separation between plant individuals and the three typical niches (root, rhizosphere, and bulk soil).

Rather, we found an interesting association between important metabolic pathways and population identity. Remarkably, although the photosynthetic supergroup was named by the presence of the photosynthesis genes [3], these genes are exclusively and universally found in MC2, MC3, MC6 and MC7 but completely missing from MC1, MC4 and MC5 (Figure 1, dataset S4) as well as STM3843 as previously reported [21, 22]. Our result indicates that photosynthesis is far from being a common characteristic trait that defines the PB phylogroup.

Also interesting is the prevalence of a unique Type III secretion system (T3SS) in MC2, MC4 and MC5 but completely missing in other populations (Fig. 1, Fig. S3B and S3C, Dataset S4). It is one of the six T3SS subtypes identified from known *Bradyrhizobium* phylotypes [23]. It was previously identified only in the PB strain *Bradyrhizobium oligotrophicum* S58 (thus named 'S58-T3SS' subtype) and its function remains unknown [23]. Since the main function of T3SS in rhizobia is to translocate effector proteins into host cells that modulate the host immune response or trigger nodulation [24], it cannot be excluded that this T3SS type specifically identified in PB members plays a role during their interaction with their host plants (*Aeschynomene* spp. and rice).

We also found that *mxa* gene sets participating in methanol metabolism were specific to MC1 (Dataset S4), which suggests that these MC1 strains may form intimate associations with plants considering that methanol is a waste product formed during plant-cell wall degradation [25]. Our methanol metabolism experiment showed that MC1 strains could not use methanol as a

sole C source (Fig. S4), hinting that the expression of *mxa* genes in these MC1 strains might be under regulation of unknown mechanisms.

The ability to nodulate *Aeschynomene indica* is a conserved trait shared by all PBs but differs between the three major PB clades

Since the new PB strains were isolated from non-legume environments, we thought that it would be very interesting to investigate (i) whether they are capable of performing nitrogen fixation under free-living and symbiotic states, (ii) whether they are capable of nodulating *Aeschynomene indica*, the typical host plant of the previously isolated PB strains, and (iii) whether there is a difference in nodulation ability across the clades and the populations. The detailed assay procedures can be seen in Supplementary Text.

All PB supergroup members have a *nif* gene cluster necessary for nitrogenase fixation. Interestingly, duplication of the *nifH* gene which encodes one of the structural proteins of the nitrogenase enzyme complex was observed in all PB strains (Fig. S3A), although the functional consequence is not known. Across the PB supergroup members, an important difference was observed regarding how the *nif* genes are structured. In most populations, all *nif* genes are co-located, along with other genes potentially involved in nitrogen fixation. This is not the case for a few members such as some basal lineages (e.g., *Bradyrhizobium* sp LMG 8443) and some members assigned to several populations (e.g., SZCCHNR1015 in MC3 and *Bradyrhizobium* sp. 83002 in MC7), where the *nif* genes were found in two contigs. This is likely due to structural rearrangement, but a DNA assembly artefact cannot be ruled out.

Another original feature observed of the PB *nif* cluster is the universal presence of the *nifV* gene encoding for a homocitrate synthase that is involved in the biosynthesis of the

nitrogenase cofactor (FeMo-Co), and which is absent in most other rhizobial lineages [26, 27]. An acetylene reduction assay on 27 representative PB strains covering all three major clades, all newly identified populations (MC1 to MC6) within Clade 1 and Clade 3, and most of the identified subpopulations within each population, confirmed their ability to fix nitrogen under free-living conditions (Fig. S5A), a trait absent in most rhizobia [27].

The plant inoculation experiments showed that all 27 representative strains were also able to induce nodules on *A. indica* (Fig. 2B, 2C). However, a significant difference in symbiosis efficiency was observed between the major clades. Clade 1 strains had the same symbiotic properties as the model strain ORS278, inducing a large number of nitrogen-fixing nodules that stimulated the growth of the plants (Fig. 2A, 2B, Fig. S5B and Fig. S6A). In contrast, Clade 3 strains formed a much smaller number of nodules compared to Clade 1 strains and the measured nitrogenase enzyme activity was lower under the symbiotic condition (Fig. 2B, Fig. S5B). Microscopic analysis showed that the nodules elicited by Clade 3 strains displayed multiple altered phenotypes: i) some nodules contained necrotic areas, ii) in others the central tissue was completely digested, and finally, iii) the nodules that displayed less drastic symptoms contained mainly dead bacteria (Fig. 2C and 2F). These observations indicate that besides inducing fewer nodules, Clade 3 strains are unable to maintain an effective chronic infection, which explains why they have no beneficial effect on plant growth (Fig. 2A, 2C and 2F). Interestingly, the singleton Clade 2 represented by strain STM3843 which is phylogenetically positioned between Clade 1 and Clade 3, showed an intermediate phenotype. The number and phenotype of the nodules is comparable to those of Clade 1 strains but stimulation of plant growth is less (Fig. 2A, 2B and 2E).

The symbiotic differences observed between the major clades may result from an

inability of the Clade 3 strains to cope with the plant's immune response, and/or an over-induction of the plant's defense mechanisms due to the absence or not properly recognized symbiotic signals. However, it is remarkable that all strains from the PB phylogroup, which come from different origins and geographical locations, are capable of nodulating *A. indica*.

Concluding remarks

The present study greatly expands the phylogenetic and ecological diversity of the "photosynthetic" *Bradyrhizobium* supergroup. The photosynthetic trait, which was thought to be a unifying character of these bacteria, in fact displays a patchy distribution within the supergroup. In contrast, the ability to develop a NF-independent symbiosis with *Aeschynomene* spp., despite varying in nodulation efficiency between major clades, appears to be a universal trait of the phylogroup. We therefore propose to rename this phylogroup as "*nod*-free but nodulating *Bradyrhizobium*".

The conservation of the nodulation character in such an ecologically diverse phylogroup and the fact that these strains were mainly isolated from the rice environment lacking selective pressure from legumes suggest that the symbiotic determinants governing the NF-independent, T3SS-independent symbiosis may be also essential to their life. This could explain the failures so far to identify these symbiotic determinants using loss-of-function approaches. Although it is beyond our goal to reveal these symbiotic determinants in the present study, the resulting new knowledge leads us to consider tackling this difficult problem using other methods (e.g., gain-of-function approaches). Furthermore, these data lay the ground for a new evolutionary concept of an alternative symbiotic process between rhizobia and legumes in which key symbiotic genes can be inherited vertically rather than transferred horizontally as described for *nod* genes.

In addition to their ability to use a unique symbiotic process with legumes, PB strains may also have the original function of colonizing rice roots and improving plant growth [17, 18, 28]. This new wealth of genomic sequences of strains isolated from rice could therefore be of great value in the future to improve our understanding of this plant growth stimulating effect.

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Data availability

The genomic sequences and raw reads of the 208 newly sequenced *Bradyrhizobium* isolates are in the process of uploading to NCBI (Project ID: PRJNA983111) and will be released in the next version of the manuscript.

Competing interests

The authors declare no competing interests in relation to this work.

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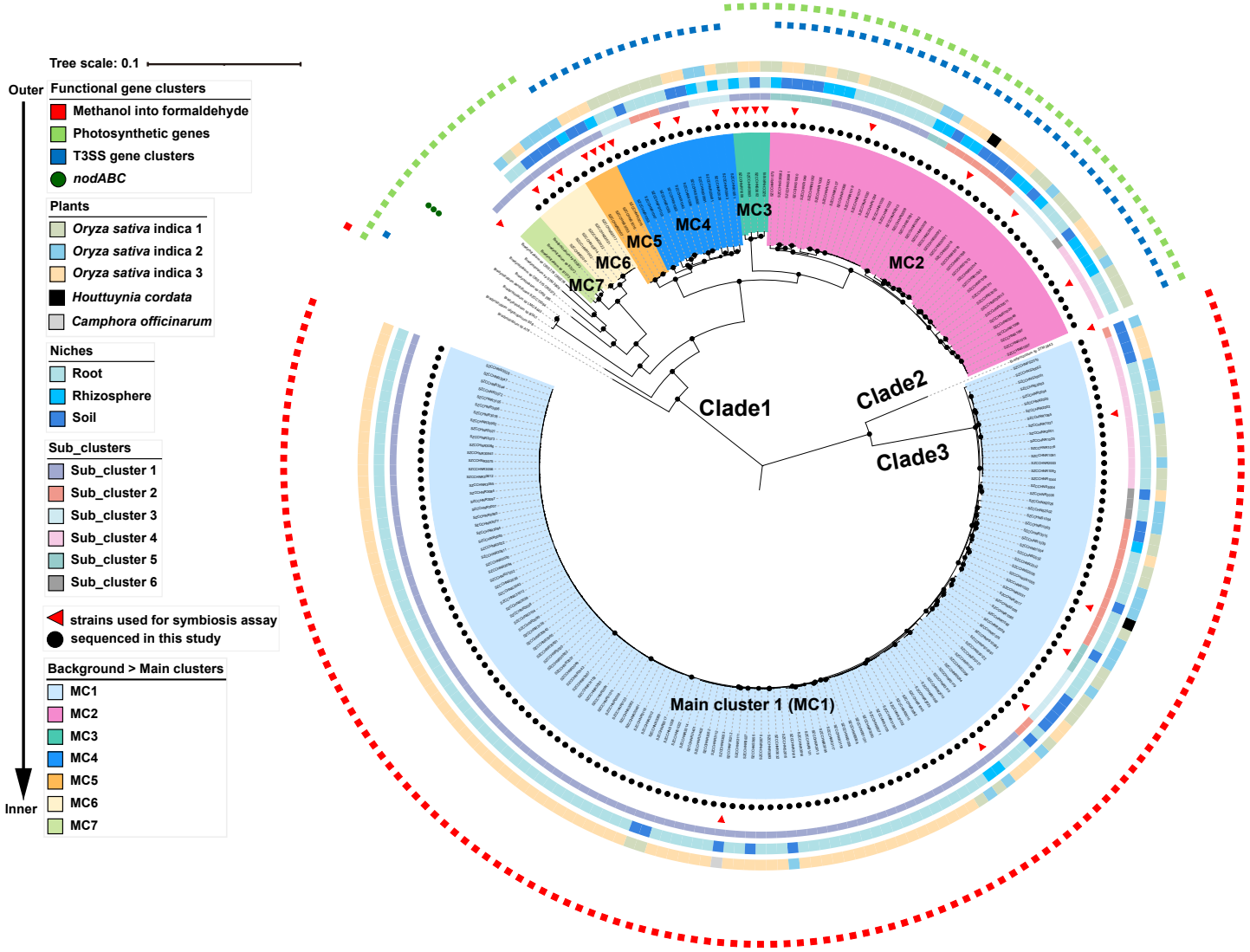
Figure legends

Figure 1. The phylogenomic tree and population delineation of the "photosynthetic" *Bradyrhizobium* (PB) supergroup. The phylogenomic tree was rooted using the minimum variance (MV) method. The 208 PB strains sequenced in the present study are indicated by black dots in the innermost layer surrounding the phylogeny. The ultrafast bootstrap values higher than or equal to 95% calculated by IQ-Tree were labeled on the nodes with black circles.

Figure 2. Symbiotic properties of several representative strains of the main populations identified in the PB supergroup. (A) Comparison of growth of the *A. indica* plants (leaf phenotype) non-inoculated (NI) or inoculated with different representative strains of PB. The six MC1 representative strains are presented in the following order: SZCCHNR1021, SZCCHNR1085, SZCCHNS30121, SZCCHNGR1005, SZCCHNRI2010 and SZCCHNF30212. For the other MCs, only one representative strain is shown: SZCCHNRI2049 (MC2), SZCCHNS3002 (MC3), SZCCHNS30592 (MC4), SZCCHNRI3016 (MC5) and SZCCHNS2021 (MC6), Photos were taken 17 days after inoculation. (B) Nodule number on *A. indica* plants induced by different representative strains of PB at 17 days after inoculation. Box plots show the results of one of the two experiments performed independently (4 plants each). (C) Symbiotic phenotypes of some representative strains tested on *A. indica*. Column 1 and 2: photo of roots and nodules. Scale bars: column 1, 0.5 cm; column 2, 0.2 cm. Column 3: Micro-sections of nodules observed using light microscopy. Scale bars: 250 μm. (D) Confocal microscopy images of micro-sections of nodules elicited by Clade 1 strains. The nodules formed by SZCCHNRI3016 from MC4 and ORS278 are shown as examples. The central nodule tissue is intracellularly infected with live spherical bacteroids stained green by SYTO9. (E) Confocal

microscopy images of micro-section of nodules elicited by Clade 2 strain STM3843. The nodules look normal, but a mix of live and dead bacteria (stained red by propidium iodide) can be noticed. (F) Confocal microscopy images of micro-section of nodules elicited by Clade 3 strains displaying different phenotypes: nodule containing mainly dead bacteria (SZCCHNS30121), nodule with a completely digested central tissue (SZCCHNRI2010); and nodule with a necrotic area and a digested zone (SZCCHNGR1005). Scale bars for (D), (E) and (F): column 1, 200 µm; column 2, 10 µm.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Camphora officinarum
Niches
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strains used for symbiosis assay
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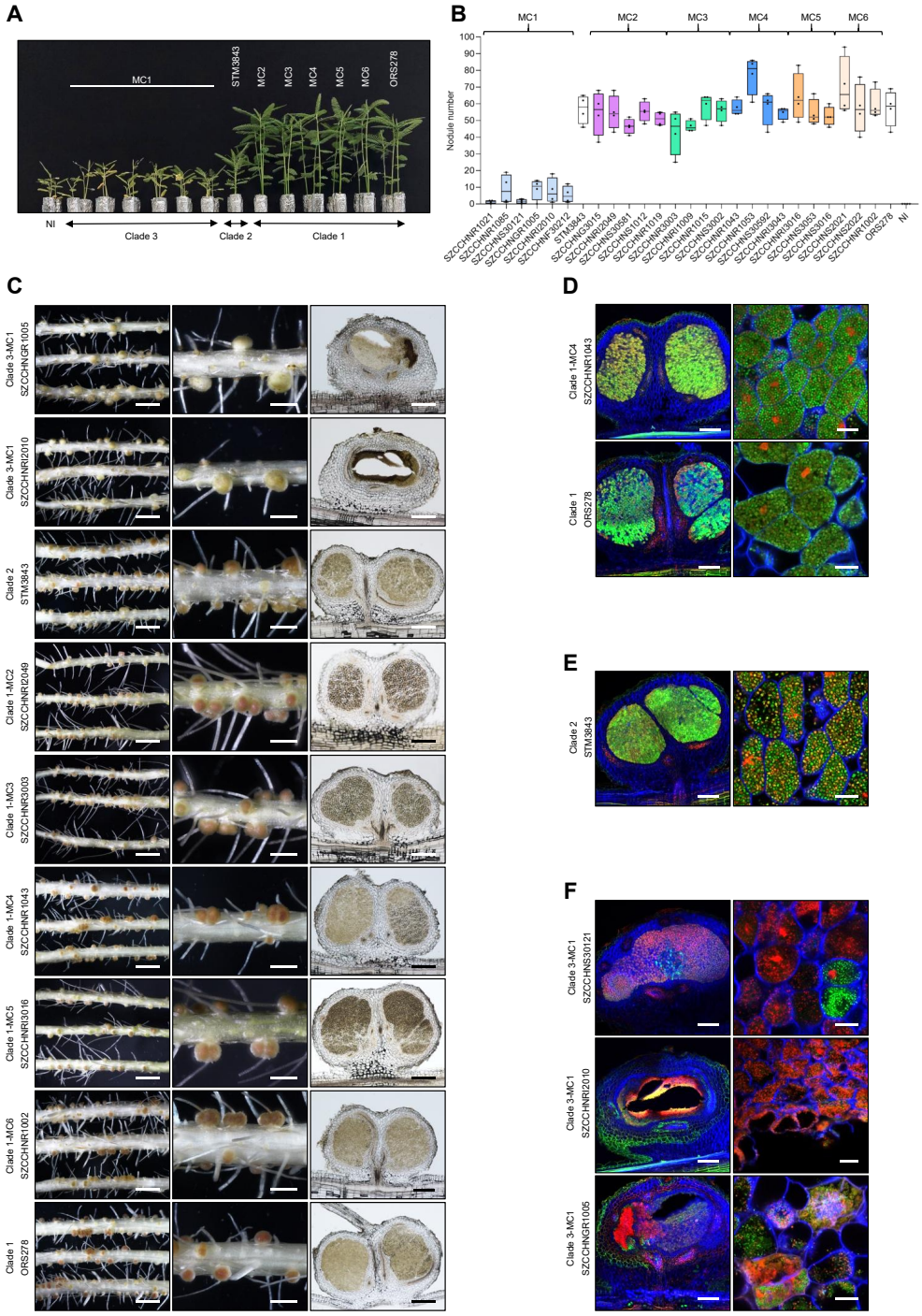
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