



Horsetails are the sister group to all other monilophytes and Marattiales are sister to leptosporangiate ferns [☆]



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ARTICLE INFO

Article history:

Received 4 March 2015

Revised 9 May 2015

Accepted 11 May 2015

Available online 18 May 2015

Keywords:

Ferns
Monilophyte phylogeny
Equisetales
Mitochondrial DNA
Chloroplast DNA
Group II introns

ABSTRACT

The “Monilophyte” clade comprising ferns, horsetails and whisk ferns receives unequivocal support from molecular data as the sister clade to seed plants. However, the branching order of its earliest emerging lineages, the Equisetales (horsetails), the Marattiales, the Ophioglossales/Psilotales and the large group of leptosporangiate ferns has remained dubious. We investigated the mitochondrial *nad2* and *rpl2* genes as two new, intron-containing loci for a wide sampling of taxa. We found that both group II introns – *nad2i542g2* and *rpl2i846g2* – are universally present among monilophytes. Both introns have orthologues in seed plants where *nad2i542g2* has evolved into a *trans*-arrangement. In contrast and despite substantial size extensions to more than 5 kb in *Psilotum*, *nad2i542g2* remains *cis*-arranged in the monilophytes. For phylogenetic analyses, we filled taxonomic gaps in previously investigated mitochondrial (*atp1*, *nad5*) and chloroplast (*atpA*, *atpB*, *matK*, *rbcl*, *rps4*) loci and created a 9-gene matrix that also included the new mitochondrial *nad2* and *rpl2* loci. We extended the taxon sampling with two taxa each for all land plant outgroups (liverworts, mosses, hornworts, lycophytes and seed plants) to minimize the risk of phylogenetic artefacts. We ultimately obtained a well-supported molecular phylogeny placing Marattiales as sister to leptosporangiate ferns and horsetails as sister to all remaining monilophytes. In addition, an indel in an exon of the here introduced *rpl2* locus independently supports the placement of horsetails. We conclude that under dense taxon sampling, phylogenetic information from a prudent choice of loci is currently superior to character-rich phylogenomic approaches at low taxon sampling. As here shown the selective choice of loci and taxa enabled us to resolve the long-enigmatic diversifications of the earliest monilophyte lineages.

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1. Introduction

Ferns, “fern allies”, and seed plants are vascular plants (tracheophytes) that share the ability to transport water and nutrients over long distances within the plant body. This evolutionary innovation gave rise to one of the most dramatic changes of life on earth. The classic term “fern allies” describes taxa representing the most ancient lineages of tracheophytes that have puzzled plant biologists for long owing to their unique, unorthodox anatomies: the whisk ferns (Psilotales), the horsetails (Equisetales) and the lycophytes (the latter comprising quillworts, club mosses and spike

mosses). The common names of the lycophyte groups are particularly misleading. Club mosses (Lycopodiales) and spike mosses (Selaginellales) are not mosses, but true vascular plants.

Molecular data have ultimately helped to resolve many of the phylogenetic enigmas. A first key insight set the lycophytes apart from all other vascular plants, which share a characteristic chloroplast genome inversion (Raubeson and Jansen, 1992). A second significant insight came from molecular phylogenetic analyses clearly confirming the previously suggested clade of monilophytes (“Moniliformopses”, Kenrick and Crane, 1997) to include the whisk ferns (Psilotales) and the horsetails (Equisetales) together with all eusporangiate and leptosporangiate ferns (Pryer et al., 2001). Moreover, a sister group relationship of the Psilotales and the Ophioglossales (adders’ tongues and moonworts, respectively) was early identified based on molecular data (Pryer et al., 2001; Vangerow et al., 1999; Wolf et al., 1998) suggesting the suspicious lack of elaborate fronds to be a secondary morphological reduction in the former. Accordingly, recent taxonomic treatments have suggested to classify Ophioglossales and Psilotales jointly on higher

[☆] This paper has been recommended for acceptance by Elizabeth Zimmer.

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taxonomic ranks, for example as a class Psilotopsida (Smith et al., 2006) or a subclass Ophioglossidae (Christenhusz and Chase, 2014), respectively.

Monilophytes are the sister clade of seed plants and together these two large vascular plant clades make up the clade of “Euphyllophytes” separating them from the microphyllous lycophytes. These insights have been confirmed with independent molecular studies on the backbone phylogeny of land plants (e.g. Qiu et al., 2006). However, the radiation of the early monilophyte lineages has remained unclear and left the branching order of the four prime monilophyte lineages Psilotopsida (or Ophioglossidae), Equisetales, Marattiales and the clade of leptosporangiate ferns as an unresolved polytomy. Obviously, we need further and more informative molecular data sets to resolve this crucial issue in understanding the diversification of the most ancient lineages of extant euphyllophytes.

Chloroplast loci have been the prime choices for molecular phylogenetic studies among land plants for obvious reasons. Chloroplast genomes are highly conserved and stoichiometrically dominating in total plant DNA preparations allowing for straightforward primer design and PCR amplification approaches covering wide taxon ranges. Plant mitochondrial genomes in contrast are structurally much more variable. On the other hand, exactly this mtDNA variability may contain interesting cladistic information. The now widely accepted placement of hornworts as the sister clade to tracheophytes has been suggested early on the basis of a characteristic shared mitochondrial intron in the *nad5* gene (Groth-Maloney et al., 2005). In contrast to chloroplasts, mitochondrial intron patterns diverge strongly between early plant clades and contribute phylogenetic information (Pruchner et al., 2002, 2001; Qiu et al., 1998). Similarly, plant mitochondrial intron sequences (Volkmar and Knoop, 2010; Volkmar et al., 2012;

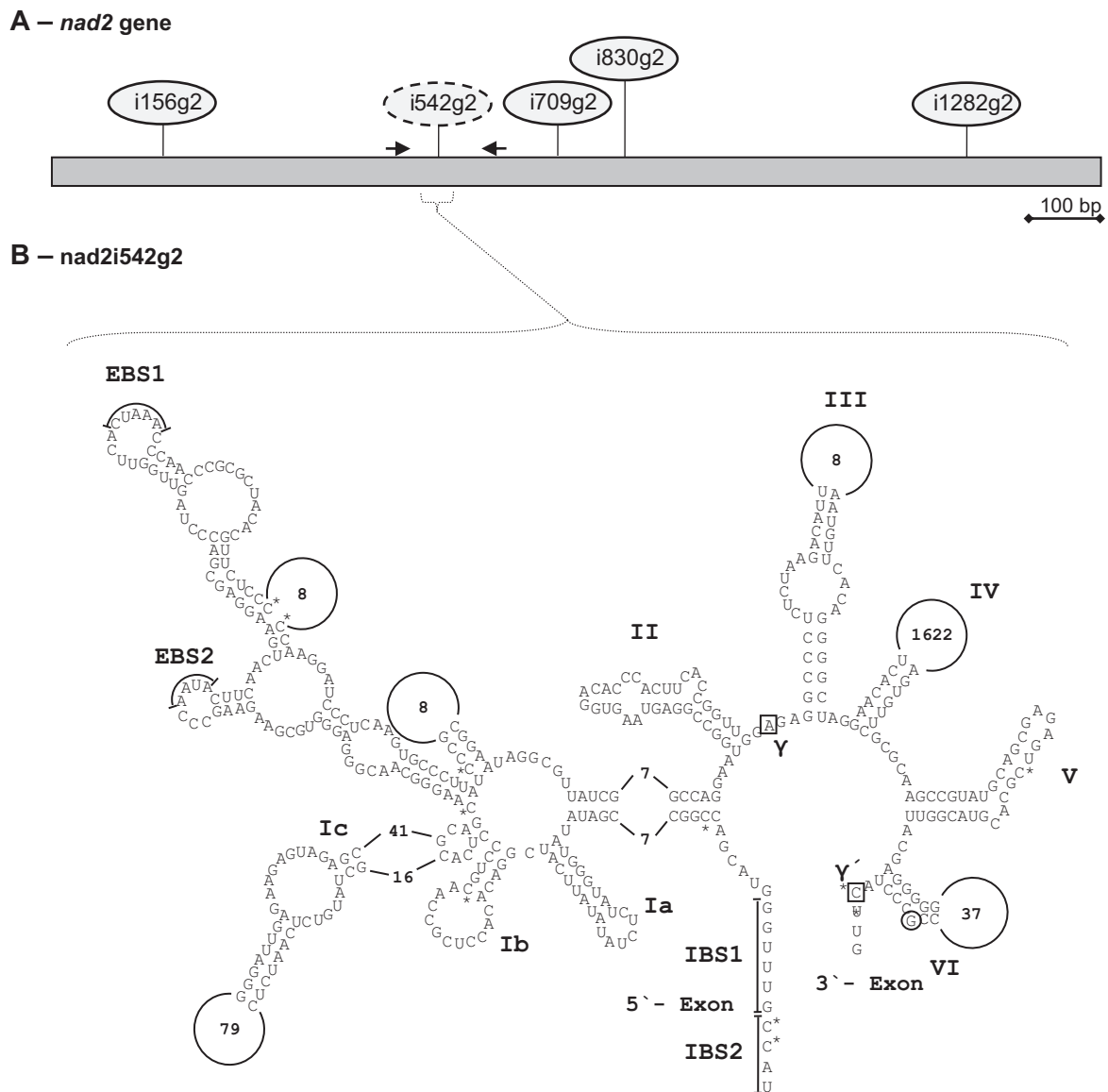


Fig. 1. (A) The mitochondrial *nad2* gene in seed plants contains four group II introns (*nad2i156g2*, *nad2i542g2*, *nad2i709g2* and *nad2i1282g2*), which are differentially conserved among bryophytes and lycophytes with the latter additionally featuring intron *nad2i830g2* (Pruchner et al., 2002). Owing to genomic disruption of intron *nad2i542g2*, *trans*-splicing is necessary for the maturation of the *nad2* mRNA in seed plants. Targeting a PCR amplicon encompassing *nad2i542g2* now identifies this intron as universally conserved in the *cis*-splicing state in monilophytes. Arrows indicate the positions of the PCR primers used in this study. The scale bar indicates 100 base pairs (bp). (B) Secondary structure modeling of the monilophyte *nad2i542g2* intron of *Gleichenia dicarpa* identifies all features typically conserved in group II introns. The six intron domains are labelled with Roman numerals (I–VI) and tertiary interaction sites are named with Greek letters (Michel and Ferat, 1995). EBS: exon binding site, IBS: intron binding site. The branch point adenosines for lariat formation is encircled. Numbers indicate unpaired nucleotides. Potential sites of RNA editing are marked with asterisks.

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