Molecular Phylogenetics and Evolution 62 (2012) 109–116

Contents lists available at SciVerse ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Invasion of protein coding genes by green algal ribosomal group I introns

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ARTICLE INFO

Article history:
Received 7 October 2010
Revised 4 June 2011
Accepted 17 September 2011
Available online 24 October 2011

Keywords:
Chlorophyceae
Chloroplast *rbc*L gene
GIY-YIG
Group I introns
HNH
Homing endonucleases

ABSTRACT

The spread of group I introns depends on their association with intron-encoded homing endonucleases. Introns that encode functional homing endonuclease genes (HEGs) are highly invasive, whereas introns that only encode the group I ribozyme responsible for self-splicing are generally stably inherited (i.e., vertical inheritance). A number of recent case studies have provided new knowledge on the evolution of group I introns, however, there are still large gaps in understanding of their distribution on the tree of life, and how they have spread into new hosts and genic sites. During a larger phylogenetic survey of chlorophyceaen green algae, we found that 23 isolates contain at least one group I intron in the *rbc*L chloroplast gene. Structural analyses show that the introns belong to one of two intron lineages, group IA2 intron-HEG (GIY-YIG family) elements inserted after position 462 in the *rbc*L gene, and group IA1 introns inserted after position 699. The latter intron type sometimes encodes HNH homing endonucleases. The distribution of introns was analyzed on an exon phylogeny and patterns were recovered that are consistent with vertical inheritance and possible horizontal transfer. The *rbc*L 462 introns are thus far reported only within the Volvocales, Hydrodictyaceae and *Bracteacoccus*, and closely related isolates of algae differ in the presence of *rbc*L introns. Phylogenetic analysis of the intron conserved regions indicates that the *rbc*L699 and *rbc*L462 introns have distinct evolutionary origins. The *rbc*L699 introns were likely derived from ribosomal RNA L2449 introns, whereas the *rbc*L462 introns form a close relationship with *psb*A introns.

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1. Introduction

Group I introns are widely distributed in genes of various lineages throughout the tree of life (Bhattacharya et al., 1996; Haugen et al., 2005; Saldanha et al., 1993). Transcribed as part of precursor transcripts, the introns are precisely removed post-transcriptionally by a group I ribozyme encoded by the intron itself. Group I introns are therefore known as self-splicing introns. Among photosynthetic lineages, group I introns have been found in the nuclear genes of diatoms, euglenoids and red algae and in the chloroplast genes of brown algae and other chlorophyll a and c-containing algae. The nucleus, mitochondrion and chloroplast of the green algae contain group I introns and the embryophytes have group I introns in the chloroplast and mitochondrion (Bhattacharya et al., 1994, 1996; Haugen et al., 2005).

The widespread distribution of group I introns in nature is in agreement with their ability to effectively spread into homologous, but intronless DNA, by a highly efficient mechanism known as "homing" (Edgell, 2009). Mobility of introns through "homing" is promoted by highly specific intron-encoded endonucleases (i.e., homing endonucleases, or HEs) that typically recognize and cleave sequences of 15–25 bp in length. This cleavage initiates a double-stranded break and repair pathway that results in an insertion of the intron sequence into the intron-lacking allele. Conserved protein motifs found within HEs are used to distinguish among the five different families, i.e., LAGLIDADG, GIY-YIG, His-Cys box, HNH and PD-(D/E)XK (Marcaida et al., 2010). In addition to the process of "homing", phylogenetic analyses suggest that intron-HEG elements also have the ability to spread into heterologous sites (see Haugen and Bhattacharya, 2004). Movement into heterologous sites is restricted, in part, by the limited ability of homing endonucleases to recognize and cleave new DNA targets. This limitation is sometimes overcome by the insertion of the intron-HEG element into neighboring sites. One striking example of the same intron-HEG element in neighboring genic positions is found in the small (S) rRNA gene of fungi. Here, a group IC2 ribozyme with a LAGLIDADG HEG inserted into the P9 structure has spread into positions S1210, S1224 and S1247 (Haugen and Bhattacharya, 2004).

Within the green algae the majority of group I introns are found in nuclear and chloroplast genes (Haugen et al., 2005). Chloroplast group I introns have been reported from a wide variety of genes and relatively few described to occur in the *rbc*L gene, the first

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1055-7903/$ - see front matter Published by Elsevier Inc.
doi:10.1016/j.ympev.2011.09.027

reported within Volvocales (Chlorophyceae) (Nozaki et al., 1998) and the second in *Pseudendoclonium akinetum* (Ulvophyceae) (Pombert et al., 2005). The volvocalean introns are inserted at position 462 of the *rbc*L gene and some contain an open reading frame (ORF) whereas others are lacking an ORF or contain a pseudogene-like degenerate ORF (Nozaki et al., 1998). Some of these ORFs encode a homing endonuclease with a conserved motif belonging to the GIY-YIG family. In contrast, the *Pseudendoclonium* intron is inserted at nucleotide position 699 of the *rbc*L gene and contains an ORF (Pombert et al., 2005). Here we report new cases of group I introns in the *rbc*L gene of multiple isolates of the family Hydrodictyaceae and the genus *Bracteacoccus* (Chlorophyceae). These introns are inserted at the same 462 position as was described in the Volvocales (Nozaki et al., 1998, 2002), or at position 699 as reported in *Pseudendoclonium* (Pombert et al., 2005). Phylogenetic analyses of the *rbc*L exon and conserved regions of the intron are utilized to compare relationships of the host taxa and introns to assist in determining the intron inheritance patterns.

2. Materials and methods

Table 1 lists the algal isolates that contained a group I intron in the *rbc*L gene and the corresponding GenBank accession numbers for those genes. The aquatic Hydrodictyaceae isolates were

Table 1

Sources and characteristics of the introns of green algae *rbc*L genes, organized by genic insertion site and according to the algal family (or other more inclusive taxonomic rank). Sequences that are new to this study are indicated with boldface font.

Taxon (strain[a])	Intron size (nt)	HE size (aa)	HEG location (Intron position)	Genbank accession
Intron insertion site 462				
Volvocaceae				
Pleodorina californica (UTEX 809)	1320	370	P1–P6 (3–1115)	AB006820
Pleodorina japonica (UTEX 2523)	1320	370	P1–P6 (3–1115)	AB076087
Pleodorina indica (UTEX 1990)	1324	Pseudo	P1–P6	AB076088
Volvulina compacta (NIES 582)	1217	Pseudo (exon fusion)	P1–P6	AB076089
Volvox obversus (UTEX 1865)	1320	377	P1–P6 (3 –1136)	AB076085
Volvox aureus (NIES 1157)	1387	362	P1–P6 (3–1184)	AB076086
Volvox gigas (UTEX 1895)	1318	346	P1–P6 (3–1043)	AB076084
Hydrodictyaceae				
Stauridium tetras (PL0502a)	1414	Pseudo	P1–P6	**EF078368**
Stauridium tetras (ACOI 84)	489	–	–	**EF078391**
Pseudopediastrum boryanum (AL0402MN)	1756	364	P4–P6 (267–1361)	**EF078347**
Pseudopediastrum boryanum (ML0401MN)	1662	364	P4–P6 (252–1346)	**EF078345**
Pseudopediastrum boryanum (UTEX LB470)	1756	Pseudo	P4–P6	**EF078302**
Pseudopediastrum kawraiskyi (ML0412MN)	1572	Pseudo	P2–P6	**EF078338**
Pseudopediastrum kawraiskyi (SAG 35.81)	1573	406	P2–P6 (32–1252)	**EF078316**
Astrephomenaceae				
Astrephomene gubernaculifera (UTEX 1394)	1282	Pseudo	P2–P6	AB076094, AB044170[b]
Astrephomene gubernaculifera (NIES 418)	1447	376	P2–P6 (61–1191)	AB076095, D63428 [b]
Goniaceae				
Gonium multicoccum (UTEX 2580)	549	–	–	AB006821
Gonium viridistellatum (NIES-654)	1313	362 (Exon fusion)	P1–P6 (1–1089)	AB076090
Gonium viridistellatum (NIES-289)	1287	Pseudo (exon fusion)	P1–P6	AB076091
Gonium viridistellatum (NIES-1122)	891	Pseudo (exon fusion)	P1–P6	AB07093
Chlamydomonadaceae				
Vitreochlamys aulata (NIES-1140)	1309	381	P2–P7 (17–1162)	AB076097
Intron insertion site 699				
Hydrodictyaceae				
Pseudopediastrum boryanum (FC0407WI)	628	–	–	**HM639991**
Pediastrum duplex var. *duplex* (ACOI 893)	1092	?	–	**EF078390**
Stauridium tetras (ACOI 84)	1475	168	P3–P5 (50–556)	**EF078391**
Lacunastrum gracillimum (Hg2004-1)	590	–	–	**EF078398**
Lacunastrum gracillimum (LW0201NC)	607	–	–	**HM854028**
Lacunastrum gracillimum (LN0201NC)	607	–	–	**EF078337**
Lacunastrum gracillimum (SML0401VA)	608	–	–	**EF078371**
Chlorococcaceae				
Bracteacoccus sp. (ZNP1-VF32)	833	–	–	**HM640000**
Bracteacoccus sp. (SAG 2302)	487	–	–	**HM639992**
Bracteacoccus sp. (Broady420)	1440	187	P5 (151–714)	**HM639993**
Bracteacoccus sp. (Broady668)	1048	Pseudo	P5	**HM639994**
Bracteacoccus sp. (H1-VF22)	655	–	–	**HM639995**
Bracteacoccus sp. (H1-VF16)	665	–	–	**HM639996**
Bracteacoccus sp. (EM3-VF7)				**HM746601**
Bracteacoccus sp. (UTEX EE80)	665	–	–	**HM639997**
Bracteacoccus sp. (CNP2-VF1)	763	–	–	**HM639998**
Bracteacoccus sp. (CNP2-VF7)	665	–	–	**HM639999**
Ulvophyceae				
Pseudendoclonium akinetum (UTEX 1912)	1682	246	P3–P5 (44–784)	AY835431

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[a] Isolates from public culture collections are abbreviated as UTEX (Culture Collection of Algae at the University of Texas at Austin), SAG (Sammlung von Algenkulturen in Göttingen, Germany), NIES (National Institute for Environmental Studies Microbial Culture Collection, Japan), ACOI (Culture Collection of Algae at the Department of Botany, University of Coimbra, Portugal), Hg (Culture Collection of Prof. E. Hegewald at the Institute of Chemistry and Dynamics of the Geosphere, Jülich, Germany). All other strains are held by the authors.

[b] Both accessions are needed to assemble the full *rbc*L sequence including the intron.

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