



## 蕨类植物 *rpoC1* 内含子缺失及其分子进化速率

彭阳<sup>1</sup>, 苏应娟<sup>2, 3\*</sup>, 王艇<sup>1\*</sup>

<sup>1</sup>华南农业大学生命科学学院, 广州 510642; <sup>2</sup>中山大学生命科学学院, 广州 510275

<sup>3</sup>中山大学深圳研究院, 深圳 518057

**摘要** *rpoC1* 基因编码RNA聚合酶 $\beta'$ 亚基蛋白, 在转录过程中与DNA模板结合, 与 $\beta$ 亚基形成的 $\beta$ - $\beta'$ 亚基复合体构成RNA合成的催化中心。以*rpoC1*基因为研究对象, 在贝叶斯因子大于20的条件下, 用HyPhy软件位点模型检测到3个正选择位点和541个负选择位点; 用PAML软件位点模型检测到10个正选择位点, 其中3个位点的后验概率超过99%。此外, 基于最大似然法构建64种蕨类植物的系统发育树, 结合HyPhy软件分析*rpoC1*基因的转换率、颠换率、转换率/颠换率、同义替换率、非同义替换率以及同义替换率/非同义替换率, 探讨*rpoC1*基因内含子丢失与分子进化速率的关系。结果表明, *rpoC1*基因内含子缺失对转换率、颠换率以及非同义替换率有一定影响。

**关键词** *rpoC1*, 内含子, 正选择位点, 选择压力

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*rpoC1* (RNA polymerase beta' subunit) 基因编码RNA聚合酶 $\beta'$ 亚基, 属于遗传系统基因 (genetic system genes)。在转录过程中, RNA聚合酶 $\beta'$ 亚基与DNA模板结合, 与 $\beta$ - $\beta'$ 复合体共同构成RNA合成的催化中心。因此*rpoC1*基因在转录过程中具有重要作用。内含子在调节基因表达和可变剪接 (alternative splicing) 中扮演重要角色, 一个基因可以因此而编码多种不同的蛋白质。研究发现, 芽殖酵母 (*Saccharomyces cerevisiae*) 基因组中内含子的存在促进饥饿条件下细胞存活, 其通过抑制TORC1和PKA途径核糖体蛋白基因的营养感应来增强对饥饿的抗性 (Parenteau et al., 2019; Morgan et al., 2019)。*rpoC1* 基因内含子丢失发生在许多谱系中, 被认为是仙人掌亚科 (Cactoideae) (Wallace and Cota, 1996) 与番杏科 (Aizoaceae) 舟叶花族和弥生花族 (Thiede et al., 2007) 的一种近裔共性 (synapomorphy) 特征。

蕨类植物是维管植物的第二大类群, 现存约12 000种, 主要分布于中低海拔的热带、亚热带地区。蕨类植物起源于距今约3.59亿年的泥盆纪, 经历过3次“物种辐射” (Lovis, 1977; Rothwell, 1987)。本

研究的海金沙属 (*Lygodium*) 是海金沙科的基部类群 (Schuettpelz and Pryer, 2007)。海金沙属为陆生攀缘植物, 根状茎有毛而无鳞片, 叶呈单轴型, 叶脉通常分离, 孢子囊生于小脉顶端且形如梨状, 孢子为四面体。目前, 海金沙属包含约45种, 中国有10种 (中国科学院中国植物志编辑委员会, 1959)。最古老的海金沙化石源于侏罗纪时期 (Taylor et al., 2009)。蕨类植物*rpoC1*基因绝大部分位于叶绿体基因组大单拷贝区, 大小为2 800 bp左右。Kim等 (2014) 检测了有限的蕨类样本, 发现在蕨类植物中*rpoC1*基因内含子丢失仅发生在海金沙属中。经统计, 本研究的64种蕨类植物仅海金沙属内含子缺失。

分子进化速率最早由Zuckerkandl和Pauling (1962) 提出, 进化速率一般定义为单位时间内分子在每个位点上 (核苷酸或氨基酸) 发生的替换数。对于基因的编码区和非编码区而言, 它们具有不同的核苷酸替换模式。非编码区由于其核苷酸的替换对翻译后的氨基酸序列影响较小, 故一般直接采用总核苷酸的替换速率作为其替换速率; 编码区则将替换速率分为两种类型: 同义替换率 (synonymous substitution rate,

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\* 通讯作者。E-mail: suyj@mail.sysu.edu.cn; tingwang@scau.edu.cn

$d_S$ )和非同义替换率(nonsynonymous substitution rate,  $d_N$ )。通过比较每一个非同义位点上的非同义替换率和每一个同义位点上的同义替换率可以揭示正选择或负选择作用(positive or negative selection)。若 $d_S$ 大于 $d_N$ ,说明该DNA处于负选择作用下;若 $d_N$ 大于 $d_S$ ,说明该DNA处于正选择作用下。在核苷酸水平上,替换率包括转换率(transition rates)和颠换率(transversion rates)。一般情况下,核苷酸转换率大于颠换率。

基于构建的系统发育树和密码子替换模型可对不同支系和不同氨基酸位点的适应性进化进行极大似然法检测。由于不同氨基酸位点功能可能有所不同,故不同位点选择压力存在差异。Yang (1998)提出检测适应性进化的3种模型,即分支模型(branch model)、位点模型(site model)和分支-位点模型(branch-site model)。这3种模型均通过似然比检验(likelihood ratio test, LRT)检测不同模型之间的差异,然后进行显著性分析,从而确定选择模型。

目前,关于蕨类植物 $rpoC1$ 基因内含子丢失的研

究相对较少,其对分子进化速率的影响尚不明确。本研究通过检测 $rpoC1$ 基因的选择位点并分析 $rpoC1$ 基因的替换速率,解析 $rpoC1$ 基因内含子丢失与分子进化速率的关系。

1 材料与方法

1.1 序列数据

选取包含25个科的64种蕨类植物(表1),其序列数据来自NCBI (National Center for Biotechnology Information)的GenBank数据库(<https://www.ncbi.nlm.nih.gov/>)。除毛秆蕨(*Callistopteris apiifolia*)、*Ceratopteris richardii*和*Polypodium glycyrrhiza*叶绿体基因组数据不全外,其余61种蕨类植物均选取叶绿体基因组全序列。此外,为获得海金沙(*Lygodium japonicum*)以及南国田字草(*Marsilea crenata*)的叶绿体基因组数据,于中国科学院武汉植物园采集样本,使用DNeasy Plant Mini Kit (QIAGEN)试剂盒提取幼叶总DNA,并通过HiSeq 2000测序系统(Illumina)测

表1 植物材料名称和叶绿体基因组序列GenBank登录号

Table 1 Plant materials used in this study and GenBank accession numbers of chloroplast genome sequences

Family name	Species	GenBank accession number	Length (bp)
Aspleniaceae	<i>Asplenium pekinense</i>	KY427331	152479
	<i>As. prolongatum</i>	KY427332	151115
	<i>Hymenasplenium unilaterale</i>	KY427350	151723
Athyriaceae	<i>Athyrium anisopterum</i>	NC_035738	151284
	<i>At. opacum</i>	KY427335	150979
	<i>At. shearerii</i>	KY427330	151068
	<i>At. sinense</i>	KY427333	151319
	<i>Deparia lancea</i>	KY427338	151011
	<i>De. pycnosora</i>	KY427339	151126
	<i>De. viridifrons</i>	KY427340	150939
	<i>Diplazium bellum</i>	KY427343	151601
	<i>Di. dilatatum</i>	KY427344	151114
	<i>Di. dushanense</i>	KY427345	150179
	<i>Di. striatum</i>	KY427346	150779
	<i>Di. unilobum</i>	KY427347	127840
Blechnaceae	<i>Austroblechnum melanocaulon</i>	KY427334	150202
	<i>Woodwardia unigemmata</i>	NC_028543	153717
Cibotiaceae	<i>Cibotium barometz</i>	MH105066	166027
Cyatheaceae	<i>Alsophila podophylla</i>	MG262389	166151
	<i>Al. spinulosa</i>	NC_012818	156661
Cystopteridaceae	<i>Cystopteris chinensis</i>	KY427337	151269

表1 (续)

Table 1 (continued)

Family name	Species	GenBank accession number	Length (bp)
Dennstaedtiaceae	<i>Pteridium aquilinum</i>	NC_014348	152362
Diplaziopsidaceae	<i>Diplaziopsis cavaleriana</i>	KY427341	151934
	<i>Dip. javanica</i>	KY427342	151496
	<i>Homalosorus pycnocarpus</i>	KY427349	152159
	<i>Cyrtomium devexiscapulae</i>	NC_028542	151684
Dryopteridaceae	<i>C. falcatum</i>	NC_028705	151628
	<i>C. fortunei</i>	MG913607	151699
	<i>Dryopteris decipiens</i>	KY427348	150987
	<i>Dr. fragrans</i>	KX418656	151978
Equisetaceae	<i>Equisetum arvense</i>	NC_014699	133309
	<i>E. hyemale</i>	NC_020146	131760
Hymenophyllaceae	<i>Callistopteris apiifolia</i>	MH265125	144918
	<i>Hymenophyllum holochilum</i>	MH265124	142214
	<i>Vandenboschia speciosa</i>	NC_041000	146874
Hypodematiaceae	<i>Hypodematium crenatum</i>	KY427351	149794
Lygodiaceae	<i>Lygodium japonicum</i>	NC_022136	157260
	<i>L. microphyllum</i>	NC_039378	158891
Marattiaceae	<i>Angiopteris angustifolia</i>	NC_026300	153596
	<i>An. evecata</i>	NC_008829	153901
Marsileaceae	<i>Marsilea crenata</i>	NC_022137	151628
	<i>Pilularia americana</i>	KY863504	153076
Onocleaceae	<i>Matteuccia struthiopteris</i>	KY427353	151003
	<i>Onoclea sensibilis</i>	KY427354	148395
Ophioglossaceae	<i>Botrychium ternatum</i>	KM817789	139127
	<i>Helminthostachys zeylanica</i>	KM817788	145120
	<i>Mankyua chejuensis</i>	NC_017006	146221
	<i>Osmundastrum cinnamomeum</i>	NC_024157	142812
Polypodiaceae	<i>Lepisorus clathratus</i>	NC_035739	156998
	<i>Polypodium glycyrrhiza</i>	KP136832	129223
Psilotaceae	<i>Psilotum nudum</i>	NC_003386	138829
Pteridaceae	<i>Adiantum shastense</i>	MG432483	150414
	<i>Ceratopteris richardii</i>	KM052729	148444
	<i>Myriopteris lindheimeri</i>	NC_014592	155770
Rhachidosoraceae	<i>Rhachidosorus consimilis</i>	KY427356	152642
Schizaeaceae	<i>Schizaea elegans</i>	KX258660	156603
	<i>S. pectinata</i>	KX258661	156392
Thelypteridaceae	<i>Ampelopteris prolifera</i>	KY427329	151772
	<i>Christella appendiculata</i>	NC_035842	151571
	<i>Macrothelypteris torresiana</i>	KY427352	151130
	<i>Pseudophegopteris aurita</i>	KY427355	149917
	<i>Stegnogramma sagittifolia</i>	KY427357	151132
Woodsiaceae	<i>Woodsia macrochlaena</i>	KY427358	150987
	<i>W. polystichoides</i>	KY427359	150685

序(Gao et al., 2013)。将测序、组装和注释完成的序列上传至NCBI。

将从NCBI下载的叶绿体基因组全序列或部分序列数据导入Genious Prime 2019软件中,分别提取*rbcL*、*matK*及*rpoC1*基因序列。用BioEdit7.0.5.3软件(Hall, 1999) Accessory Application模块中的ClustalW Multiple Alignment进行序列多重比对,并手工校正(附录1)。分别建立64种蕨类植物的*rbcL*数据集、*matK*数据集、*rbcL*与*matK*的串联数据集以及*rpoC1*数据集。其中,*rpoC1*数据集包括*rpoC1*基因数据集、*rpoC1*外显子数据集和*rpoC1*氨基酸数据集。

## 1.2 系统发育树的构建

根据已有的系统发育树,对*rbcL*编码序列(coding sequence, CDS)与*matK*编码序列的串联数据集用最大似然法(maximum likelihood, ML)构建的系统发育树进行手工校正,并根据Smith等(2006)和The Pteridophyte Phylogeny Group (2016)的系统发育树对该树进行部分修改。该树将用于后续分子进化分析。

用jModelTest2.1.10软件(Darriba et al., 2012)进行核苷酸替换模型选择。根据赤池信息准则(Akaike Information Criterion, AIC)选取最佳模型(TVM+I+G)(附录2)(Akaike, 1974)。在PhyML-3.1\_win32.exe(Guindon et al., 2010)应用程序中导入已比对完成的序列文件,设置最佳模型的相关参数。其中,自展值设为1 000, C值设为6,然后运行程序。用FigTree v1.4.3软件对已构建的系统发育树进行编辑和美化。

## 1.3 分子进化速率分析

使用HyPhy2.2.4 (hypothesis testing using phylogenies)软件分析海金沙属和其它62种蕨类植物的*rpoC1*外显子的转换率(transition rate, *trst*)、颠换率(transversion rate, *trsv*)、转换率/颠换率(*trst/trsv*)、替换数(number of substitutions,  $E_s$ )、转换数(number of transition,  $E_t$ )、颠换数(number of transversion,  $E_v$ )、同义替换率(synonymous substitution rate,  $d_s$ )、非同义替换率(nonsynonymous substitution rate,  $d_N$ )以及 $d_N/d_s$ (Pond and Muse, 2005)。

转换率、颠换率以及两者比值的分析用局部参数下核苷酸HKY85替换模型;同义替换率、非同义替换

率以及 $\omega$ 值( $d_N/d_s$ )分析选用局部参数下密码子MG94×HKY85\_3×4模型。将 $d_N$ 和 $d_s$ 分别约束,分析不同约束条件下的似然比检验(LRT)所得到的 $P$ 值,探究海金沙属*rpoC1*基因的替换速率是否明显大于其它蕨类植物。使用SPSS16软件中的曼-惠特尼(Mann-Whitney)秩和检验对实验统计结果进行差异显著性分析,比较海金沙属和其它蕨类植物在替换速率方面的差异。

## 1.4 选择压力分析

使用HyPhy软件中的密码子MG94×HKY85×3\_4×2\_Rates模型,通过设定Rate Het参数以及调用类别处理器(categories processor)执行后验贝叶斯(posterior Bayes)分析。其中贝叶斯因子(后验概率与先验概率的比值)设定为大于20,检测不同位点经受的选择压力。

## 1.5 适应性进化分析

采用基于机理式模型的PAML4.9软件中的codeml程序分析海金沙属*rpoC1*基因的适应性进化(Yang, 1997, 2007)。分析时采用分支间可变 $\omega$ 模型、位点间可变 $\omega$ 模型和分支-位点模型。

分支间可变 $\omega$ 模型(Yang, 1998)允许在不同支系上 $\omega$ 值不同。其中,单一比率(one-ratio, M0)模型假定系统发育树上的各支系 $\omega$ 相同;二比率(two-ratio, MT)模型设定前景支和背景支,前景支和背景支分别具有不同的 $\omega$ 值;自由比率(free-ratio, MF)模型假定系统发育树上各支系 $\omega$ 值不同。

位点间可变 $\omega$ 模型(Nielsen and Yang, 1998; Yang et al., 2000)允许不同位点上 $\omega$ 值不同,包含7种密码子替换模型,分别为M0(单一比率)、M1a(近中性)、M2a(选择)、M3(离散)、M7(beta)、M8(beta &  $\omega$ )和M8a(beta &  $\omega_s=1$ )。这7种密码子模型可分为4套嵌套模型,即M2a和其零假设模型M1a(筛选正选择位点)、M3和其零假设模型M0(检测各位点 $\omega$ 是否一致)、M8和其零假设模型M7(筛选正选择位点,易产生假阳性)以及M8和其零假设模型M8a(有助于降低假阳性)。分别对4套嵌套模型进行LRT运算,比较不同模型间的差异显著性。在PAML软件中运行2种贝叶斯方法鉴定正选择位点:NEB(native empirical Bayes)(Nielsen and Yang, 1998; Yang et al.,

2000) 和 BEB (Bayes empirical Bayes) (Yang, 2005)。前者使用极大似然估计(maximum likelihood estimates, MLEs)参数(如比例 $p$ 和比率 $\omega$ )来检验位点后验概率, 未考虑取样误差, 产生的假阳性高; 后者可以通过引用贝叶斯检验处理取样误差, 故在筛选正选择位点时使用后者, 但BEB只可在M2a和M8下运行(Yang, 1998; Yang and Neilson, 2002; Zhang et al., 2005)。

分支-位点模型(Zhang et al., 2005)将系统发育树分为前景支和背景支, 不仅位点间 $\omega$ 值变化, 同时支系间 $\omega$ 值也变化。该模型主要用于检测前景支中正选择作用对部分位点的影响, 仅允许前景支中出现正选择位点。本研究采用该模型下的MA (model A)中检验2 (Model=2, NSsites=2)筛选正选择位点。设置以海金沙属分支为前景支的Ma0, 其 $\omega$ 值固定为1; 设置以海金沙属分支为前景支的Ma1, 其 $\omega$ 为估计值。MA与位点模型中M1a进行差异显著性比较。若差异显著, 说明前景支在进化进程中受到正选择作用或受到的选择约束较宽松。

筛选出来的正选择位点根据SWISS-MODEL (<https://www.swissmodel.expasy.org/>)数据库比对结果, 绘制正选择位点的空间位置图。

## 2 结果与讨论

### 2.1 64种蕨类植物系统发育树

参考Smith等(2006)的蕨类植物分类系统和The Pteridophyte Phylogeny Group (2016)的系统发育树, 选取*rbcl*编码序列(CDS)与*matK*编码序列的串联数据集, 在PhyML软件下用最大似然法(ML)构建系统发育树。

由于*matK*和*rbcl*编码序列串联构建的系统发育树与目前认可的蕨类系统树存在细微差异, 为保证构建的系统发育树与目前认可的蕨类系统树基本一致, 在手工校正过程中, 改变了部分物种的系统发育位置, 使其拓扑结构发生了一定改变; 且本系统发育树并非用于系统发育分析, 其作用主要是为后续分子进化分析提供树文件。构建的系统发育树如图1所示。

### 2.2 *rpoC1*基因的进化速率

使用HyPhy软件局部参数下核苷酸HKY85替换模型

和密码子MG94×HKY85\_3×4模型计算海金沙属和其它蕨类*rpoC1*外显子的进化速率(附录3), 大部分蕨类 $d_N$ 值小于 $d_S$ ,  $trsv$ 值小于 $trst$ 。用似然比检验判断海金沙属和其它蕨类的替换速率是否存在显著差异。似然比检验的 $P$ 值及Mann-Whitney检验值如表2所示。其中, 海金沙属*rpoC1* CDS的 $trst$ 均值和 $trsv/trst$ 均值大于其它蕨类植物。在似然比检验中, 仅有 $trst$ 、 $trsv$ 以及 $d_N$ 的 $P$ 值小于0.05, 说明海金沙属*rpoC1* CDS在转换率、颠换率以及非同义替换上与其它蕨类植物有显著差异。Mann-Whitney秩和检验值均无显著差异, 与似然比检验结果相差较大, 推测原因是海金沙属样本量少(仅2个), 秩和检验误差大。

### 2.3 *rpoC1*基因的选择压力分析

用HyPhy软件Rate Het参数下密码子MG94×HKY85×3\_4×2\_Rates模型进行正选择位点和负选择位点筛选。在贝叶斯因子大于20的条件下, 筛选出正选择位点3个, 负选择位点541个(表3)。3个正选择位点的贝叶斯因子均在35–50之间(图2A); 541个负选择位点的贝叶斯因子最大超过 $2.4 \times 10^{12}$  (图2B), 说明筛选出来的位点均受到了较强的选择作用。结合64种蕨类植物 $\omega$ 值, 发现除大囊岩蕨(*Woodsia macrochl-aena*)、*Schizaea elegans*、尖裂荚果蕨(*Matteuccia struthiopteris*)和毛柄双盖蕨(*Diplazium dilatatum*)外, 其余蕨类植物 $\omega$ 值均小于0.5。因此, 相较于正选择作用, *rpoC1*基因所受到的负选择压力更大。由此表明, *RPOC1*蛋白在长期的进化过程中比较保守。

### 2.4 *rpoC1*基因的适应性进化

使用PAML软件codeml程序下的分支模型、位点模型和分支-位点模型分析*rpoC1*基因的适应性进化。在分支模型下进行单一比率和以海金沙属为前景支的二比率检验, 得到单一比率似然值为-33 984.018 106, 二比率似然值为-33 971.070 759 (表4)。将单一比率和二比率进行似然值检验, 得到 $P$ 值为 $3.606 \times 10^{-7}$  (表5), 表明单一比率模型和二比率模型差异显著, 海金沙属与其它蕨类植物之间 $\omega$ 值差异显著。单一比率模型和自由比率模型在自由度为125、二倍对数似然值为169.474 0下进行卡方检验,  $P$ 值为0.005, 表明不同支系间的 $\omega$ 值差异显著。

模型M8a的似然值 $\ell = -32\ 735.212\ 985$ , 与模型

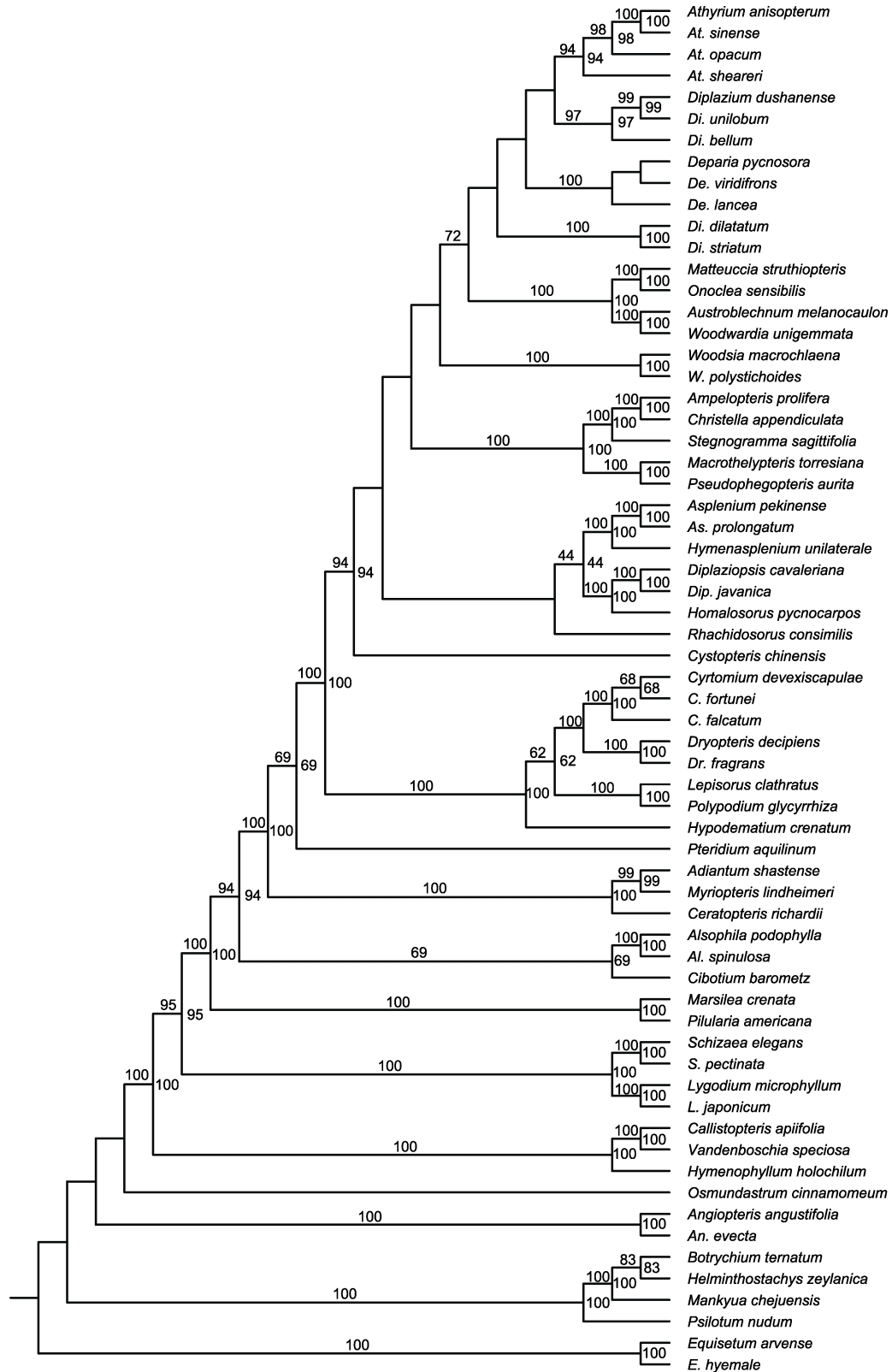


图1 64种蕨类植物的系统发育树

Figure 1 Phylogenetic tree of 64 ferns species

表2 海金沙属与其它蕨类植物*rpoC1*编码序列(CDS)进化速率检验

Table 2 Evolution rate test of *rpoC1* coding sequences (CDS) of *Lygodium* and other ferns

	$E_t$	$E_v$	$trsv/trst$	$trst$	$trsv$	$d_N$	$d_S$	$\omega$
<i>Lygodium</i>	0.014	0.004	0.118	0.579	0.007	0.022	0.147	0.144
Other ferns	0.022	0.005	0.096	0.088	0.010	0.045	0.201	0.256
<i>P</i> value	1.000	1.000	1.000	0.008	0.036	0.000	0.517	1.000
Mann-Whitney	0.834	0.778	0.362	0.834	0.778	0.502	0.923	0.316

$E_t$ : 转换数;  $E_v$ : 颠换数;  $trst$ : 转换率;  $trsv$ : 颠换率;  $d_N$ : 非同义替换率;  $d_S$ : 同义替换率;  $\omega$ :  $d_N/d_S$   
 $E_t$ : Number of transition;  $E_v$ : Number of transversion;  $trst$ : Transition rate;  $trsv$ : Transversion rate;  $d_N$ : Nonsynonymous substitution rate;  $d_S$ : Synonymous substitution rate;  $\omega$ :  $d_N/d_S$

表3 *rpoC1*基因正选择和负选择位点

Table 3 Positive and negative selection sites of *rpoC1*

Amino acid sites	
Positive selection sites	156, 184, 568
Negative selection sites	1-3, 6-12, 14-21, 23-26, 28-32, 35-37, 39-42, 44-54, 56, 58-63, 66-74, 76, 79-82, 84, 86-102, 104-107, 109-128, 130-136, 138, 139, 141-144, 147-155, 158-173, 180-181, 183, 186-191, 193-195, 197-198, 200-208, 211, 213-218, 223, 225, 228-230, 232-235, 237, 241-244, 246-247, 249-258, 260-276, 278-291, 294-296, 298-301, 303-315, 318-337, 339-344, 346-368, 370-391, 393-400, 402-411, 413-414, 416-417, 419-434, 436-437, 439-440, 442, 444-445, 447-449, 453-455, 457-480, 482-492, 494-499, 501-526, 528-538, 540-550, 553-556, 558-561, 566-567, 575, 577, 579, 582-583, 586-588, 590-591, 593, 597-600, 603-613, 620, 622, 625-626, 628, 630, 632-635, 639, 642-644, 646, 648-649, 654, 660, 663-668, 671-674, 676, 677, 679-682, 687-689, 694, 697, 710

M8相比2倍对数似然值 $2\Delta l=2\times(-32\,715.067\,141+32\,735.212\,985)=40.291\,7$ , 由 $\chi^2$ 分布(Df.=1)得出 $P=2.187\times 10^{-10}$ , 即 $P$ 值远小于0.05, 因此模型M8a被极显著地拒绝。模型M2a和M8的假定条件中均允许 $\omega$ 值大于1, PAML分析结果均显示*rpoC1*基因中存在正选择位点。与它们各自对应的零假设模型M1a和M7相比, 模型M2a比M1a多2个参数, 它们的LRT统计量 $2\Delta l=42.484\,8$ , 卡方检验 $P$ 值为 $5.950\times 10^{-10}$ 。模型M8与M7相比, 在自由度为2的条件下,  $2\Delta l=106.583\,8$ 。在95%水平上, 模型M2a鉴定出4个氨基酸位点(687P、692S、697S和700A)受到正选择, 其中687P、

692S和697S后验概率超过99%; 模型M8鉴定出10个氨基酸位点(578V、579Y、686S、687P、689T、692S、693I、696T、697S和700A)受到正选择, 其中687P、692S和697S后验概率超过99%。

2.5 RPOC1蛋白质三维结构

将海金沙RPOC1蛋白质序列导入SWISS-MODEL中, 通过与结核分枝杆菌(*Mycobacterium tuberculosis*) RNAP启动子蛋白质(SMTL ID: 6ee8.1)序列进行

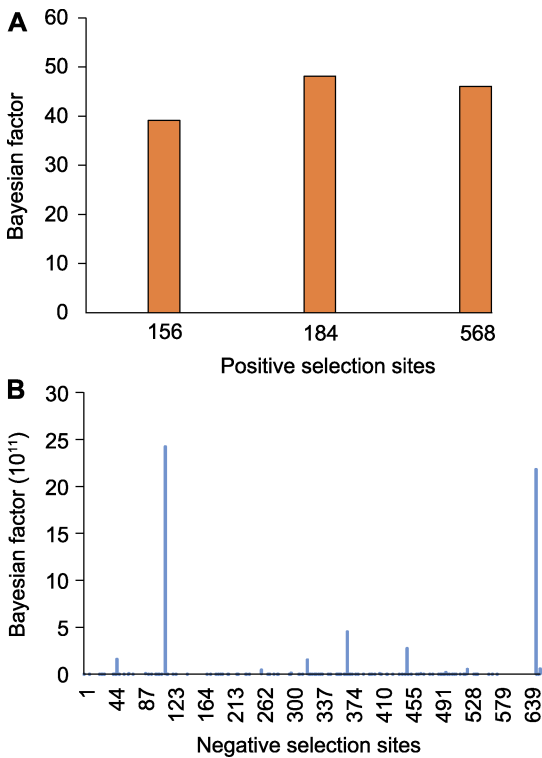


图2 *rpoC1*氨基酸残基正(A)负(B)选择位点  
Figure 2 Positive (A) and negative (B) selection sites of *rpoC1* amino acid residues

比对, 基于同源建模原理得到其蛋白质结构图(图3)。其中, HyPhy软件筛选出来的正选择位点156T、184F及568I如图3所示。异亮氨酸(isoleucine, I)和苯丙氨酸(phenylalanine, F)均为非极性R基氨基酸。156T和184F正选择位点靠近DNA结合结构域, 周围大部分氨基酸为非极性R基氨基酸(疏水氨基酸), 568I正选择位点周围大部分是不带电荷的极性R基氨基酸。

2.6 讨论

2.6.1 *rpoC1*基因内含子缺失及与进化速率的关系

目的基因的选择是分子系统学研究最关键的环节之一。由于不同基因行使的功能不同, 它们的进化速率也存在一定差异。对于不同分类阶元的系统发育和分子进化研究一般选用不同的DNA序列。目前, 对*atpB* (Korall et al., 2006)、*rps4* (Guillon, 2004)以及*rbcL* 基因(Dubuisson, 1997)已研究得较为深入, 而对*rpoC1*基因的研究较少。对于内含子缺失的研究, 由

于我们仅分析了海金沙属与其它蕨类植物的进化速率差异, 且海金沙属叶绿体基因组全序列只公布了2个物种(海金沙和小叶海金沙(*L. microphyllum*)), 因此, 在样本量以及对比分析上存在一定不足。后续研究可以增加海金沙属物种的叶绿体基因组测序分析, 扩大研究对象数目, 比较海金沙属与其它属之间的进化速率差异, 以获得更加准确的结果。*rpoC1*基因内含子缺失的属对应的分子进化速率与其它蕨类植物之间有一定的区别, 但并不能完全说明*rpoC1*基因内含子缺失事件必然对分子进化速率有影响, 其与海金沙属进化速率高可能存在关联。因此, 在后续研究中可以深入分析。*rpoC1*基因内含子缺失在植物中较为常见, 牻牛儿苗科(Geraniaceae) (Weng et al., 2014)、禾本科(Poaceae) (Katayama and Ogiwara, 1993)、西番莲科(Passifloraceae) (Hansen et al., 2006)、豆科(Fabaceae) (Downie et al., 1998)、草海桐科(Goodeniaceae) (Downie et al., 1996)、仙人掌

表4 *rpoC1*基因在不同模型下的参数估计值和对数似然值

Table 4 Parameters estimates and log-likelihood values of the *rpoC1* gene under different models

	Model	Np	ℓ	Parameter estimate	Positive selection sites
Branch model	M0	128	-33984.0181	$\omega=0.18862$	Not allowed
	MA	129	-33971.0708	$\omega_1=0.19344, \omega_2=0.07154$	Not allowed
Site model	Model 1a (M1a)	129	-33025.1095	$P_0=0.77581, \omega_0=0.09604$ $P_1=0.22419, \omega_1=1.00000$	Not allowed
	Model 2a (M2a)	131	-33003.8671	$P_0=0.77323, \omega_0=0.09782$ $P_1=0.20583, \omega_1=1.00000$ $P_2=0.02094, \omega_2=2.53148$	687P**, 697S** 692S**, 700A*
	Model 3 (M3)	132	-32770.6265	$P_0=0.45915, \omega_0=0.02383$ $P_1=0.39593, \omega_1=0.23422$ $P_2=0.14492, \omega_2=0.91531$	None
	Model 7 (M7)	129	-32768.3591	$P=0.36168, q=1.11178$	Not allowed
	Model 8 (M8)	131	-32715.0671	$P_0=0.95310, P=0.46388$ $q=2.02806, P_1=0.04690$ $\omega=1.62513$	578V*, 579Y*, 686S* 687P**, 689T*, 692S** 693I*, 696T*, 697S**, 700A*
	Model 8a (M8a)	130	-32735.2130	$P_0=0.91188, P=0.48169$ $q=2.38635, P_1=0.08812$ $\omega=1.00000$	None
	Branch-site model	Ma0	130	$P_0=0.77581, P_1=0.22419$ $P_{2a}+P_{2b}=0.00000, \omega_2=1.00000$	Not allowed
		Ma1	131	$P_0=0.77581, P_1=0.22419$ $P_{2a}+P_{2b}=0.00000, \omega_2=1.00000$	None

Np: 参数编号; \*\* 后验概率  $P>99\%$ ; \*后验概率  $P>95\%$

Np: Number of parameters; \*\* Posterior probability  $P>99\%$ ; \* Posterior probability  $P>95\%$



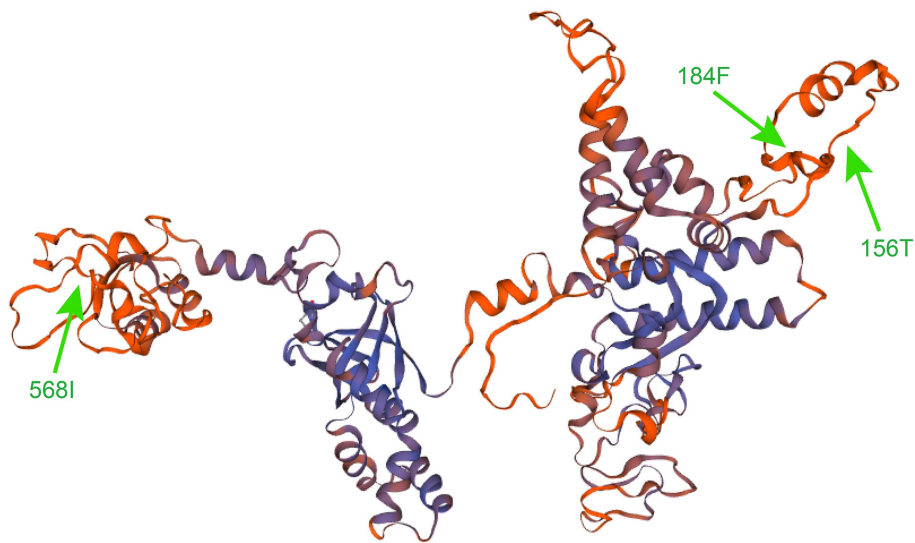


图3 海金沙RPOC1蛋白质的三维结构

Figure 3 Three-dimensional structure of RPOC1 protein in *Lygodium japonicum*

表5 PAML4.9软件中不同模型的似然比值检验统计量(2Δl)  
Table 5 Likelihood ratio test statistic (2Δl) for different models in PAML4.9

Model comparison	Df.	2Δl	P value
M0 & MA	1	25.8947	$3.606 \times 10^{-7}$
M1a & M2a	2	42.4848	$5.950 \times 10^{-10}$
M0 & M3	4	2426.7832	0
M7 & M8	2	106.5838	0
M8a & M8	1	40.2917	$2.187 \times 10^{-10}$
M0 & MF	125	169.4740	$4.998 \times 10^{-3}$

Df.: 自由度 Df.: Degree of freedom

科(Cactaceae) (Wallace and Cota, 1996)以及番杏科(Aizoaceae) (Thiede et al., 2007)中均存在该事件。*rpoC1*基因内含子存在于被子植物的共同祖先中,随后在禾本科和柱状仙人掌亚科的谱系中独立丢失(Downie et al., 1996)。而真核生物基因组中的内含子密度变化超过3个数量级,因此在进化过程中必然发生大量的内含子增加和/或损失(He et al., 2017)。Downie等(1998)研究了65种苜蓿属(*Medicago*)质体*rpoC1*内含子,结果表明有17个物种缺少内含子,而其中有3种在内含子含量方面是异质的,且*rpoC1*内含子在该群体的进化过程中独立丢失至少3次。目前,关于*rpoC1*基因内含子丢失与分子进化速率的关系研究较少,部分研究集中在*rpoC1*基因内含子丢失与系统发育关系的重建上。Hansen等(2006)发现*rpoC1*内

含子缺失对西番莲属系统发育树构建有一定的影响。在似然比检验中, *trst*、*trsv*以及 $d_N$ 的 $P$ 值小于0.05,说明海金沙属*rpoC1* CDS在转换率、颠换率以及非同义替换率上与其它蕨类有显著差异;但Mann-Whitney检验值显示无显著差异,与似然比检验结果相差较大,推测原因是海金沙属样本量少(仅2个),秩和检验误差大。此外,*rpoC1*基因的转换率、颠换率、同义替换率和非同义替换率在不同类群之间差异较大。桫欏类和合囊蕨类的分支短,进化速率相对较慢;铁角蕨类和凤尾蕨类分支长,进化速率相对较快。海金沙目中莎草蕨科*Schizaea elegans*的颠换率、非同义替换率和 $\omega$ 值非常高,其有可能正在经历正选择作用。

2.6.2 *rpoC1*正选择位点

HyPhy软件筛选出的正选择位点与PAML软件筛选出来的位点不同,可能是由于软件筛选原理和方法有差异。HyPhy要求贝叶斯因子大于20; PAML则要求后验概率大于95%或99%。此外, PAML位点模型需要所有谱系的平均 $d_N$ 大于 $d_S$ ,该谱系中的正选择位点才可被筛选到,因此正选择位点可能会由于谱系 $d_N$ 小于 $d_S$ 而无法被检测出来。*rpoC1*基因多处于负选择作用下,负选择位点更加保守,有利于维持蛋白质结构和功能的稳定(Hong et al., 2008)。由于筛选出来的正选择位

点空间结构在SWISS-MODEL构建的模型中置信度较低, 因此, 对其所处二级结构以及结构域的分析需要进一步建模。相较于中性突变, 正选择发生频率低, 一般只发生在序列的少数位点或某个短的历史时期, 尤其是正选择作用发生在进化早期且已经被固定下来(Perutz, 1983; Newcomb et al., 1997)。因此, 检测正选择位点相对困难。正选择位点对于探究该基因适应性进化和其蛋白质功能位点有重要意义。此外, 正选择位点的确定还可以用于分析蛋白质序列的适应性进化。

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## Intron Loss and Molecular Evolution Rate of *rpoC1* in Ferns

Yang Peng<sup>1</sup>, Yingjuan Su<sup>2, 3\*</sup>, Ting Wang<sup>1\*</sup>

<sup>1</sup>College of Life Sciences, South China Agricultural University, Guangzhou 510642, China; <sup>2</sup>School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China; <sup>3</sup>Research Institute of Sun Yat-sen University in Shenzhen, Shenzhen 518057, China

**Abstract** The *rpoC1* gene encodes the RNA polymerase  $\beta'$  subunit protein, which binds to the DNA template during transcription, and the  $\beta$ - $\beta'$  subunit complex formed with the  $\beta$  subunit constitutes a catalytic center for RNA synthesis. In this study, the *rpoC1* gene mutations in ferns were surveyed. With Bayes factor greater than 20, HyPhy site model detected 3 positive selection sites and 541 negative selection sites; the PAML site model detected 10 positive selection sites, three of which had posterior probabilities greater than 99%. In addition, a phylogenetic tree of 64 ferns was constructed based on the maximum likelihood method. We calculated the transition rate, transversion rate, transition rate/transversion rate, synonymous substitution rate, nonsynonymous substitution rate, and synonymous substitution rate/nonsynonymous substitution rate by HyPhy to analyze the relationship between intron loss of *rpoC1* gene and molecular evolution rates. The results indicate that intron loss of the *rpoC1* gene might play a role in its transition rate, transversion rate and nonsynonymous substitution rate in ferns.

**Key words** *rpoC1*, intron, positive selection site, selection pressure

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\* Authors for correspondence. E-mail: suyj@mail.sysu.edu.cn; tingwang@scau.edu.cn

(责任编辑: 白羽红)

**附录1** 64种蕨类植物经手工校正后*rpoC1* CDS序列

**Appendix 1** The *rpoC1* CDS sequence of 64 ferns after manual correction

**附录2** jModelTest2.1.10基于AIC得到的*matK*和*rbcL*串联集核苷酸模型参数

**Appendix 2** Nucleotide model parameters of *matK* and *rbcL* tandem set based on AIC of jModelTest2.1.10

**附录3** *rpoC1* 基因分子进化速率

**Appendix 3** Molecular evolution rate of *rpoC1* gene

<http://www.chinbullbotany.com/fileup/1674-3466/PDF/t19-105.pdf>

附录1 64种蕨类经手工校正后 *rpoC1* CDS序列

Appendix 1 The *rpoC1* CDS sequence of 64 ferns after manual correction

>*Adiantum shastense*

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>*Alsophila podophylla*

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>*Alsophila spinulosa*

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>*Ampelopteris prolifera*

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>*Angiopteris angustifolia*

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>*Angiopteris evecta*

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>*Asplenium pekinense*

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>*Asplenium prolongatum*

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>*Athyrium anisopterum*

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>*Athyrium opacum*

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>*Athyrium shearerii*

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>*Athyrium sinense*

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>*Austroblechnum melanocaulon*

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>*Botrychium ternatum*

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>*Callistopteris apiifolia*

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>*Ceratopteris richardii*

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>*Christella appendiculata*

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>*Cibotium barometz*

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>*Cyrtomium devexiscapulae*

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> *Cyrtomium falcatum*

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>*Cyrtomium fortunei*

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>*Cystopteris chinensis*

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>*Deperia lancea*

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>*Deparia pycnosora*

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>*Deparia viridifrons*

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>*Diplaziopsis cavaleriana*

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>*Diplaziopsis javanica*

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>*Diplazium dushanense*

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>*Diplazium striatum*

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>*Diplazium unilobum*

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>*Dryopteris decipiens*

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>*Dryopteris fragrans*

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>*Equisetum arvense*

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>*Equisetum hyemale*

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>*Helminthostachys zeylanica*

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>*Homalosorus pycnocarpus*

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>*Hymenasplenium unilaterale*

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>*Hymenophyllum holochilum*

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>*Hypodematium crenatum*

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>*Lepisorus clathratus*

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>*Lygodium japonicum*

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>*Lygodium microphyllum*

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> *Macrothelypteris torresiana*

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> *Mankyua chejuensis*

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> *Marsilea crenata*

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>*Matteuccia struthiopteris*

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>*Myriopteris lindheimeri*

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>*Onoclea sensibilis*

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> *Osmundastrum cinnamomeum*

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>*Pilularia americana*

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>*Polypodium glycyrrhiza*

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>*Pseudophegopteris aurita*

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>*Psilotum nudum*

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>*Pteridium aquilinum*

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>*Rhachidosorus consimilis*

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>*Schizaea elegans*

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> *Schizaea pectinata*

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CAATACTCTTATTGAATTTTTATCCGGAAGTGAATTCACCCCTGAGGGGCTTATA  
GTTTGTCAAAAGAGACTTGTCCAGGAAGCTGTGGATGCCCCCATCGATAACAG  
CATACGCGGACAACCAATGAGAGGTGTCAGTGACAGACCCTACAAGTCTTTCT  
CGGAAGTGATTGAAGGAAAAGAGGGGCGATTCCGCGGGAATCTGCTTGGGAA  
GCGGGTGCATTATCCAGGTCGTTTCGTTATCGTCGTGGGTCCATCGCTTCTACT  
ACACCAATGTGGATTACCTAGAGAATCGTCGATAGAACTTCTTCAAGCATTTGT  
GATTCTGTGACCCAATTGGGCGACATCTCGCTCGCAACTTGCGAGCTGCTAGAA  
ACATGATTCTGTAGAAAAGAACCCATTATTTGGAAAGTTCCTCGAGAAGTCATGC  
AAGGTCATCCCATATTGCTGAATCGAGCACCTACGCTACATAGATCAGGTATTC  
AAGCGTTCCAACCTATTTTATGTCAGGGGCGAGCCATTTGCCTACATCCATTGG  
TTTGTGGGGGGTTCAATGCAGATTCCGACGGAGATCAAATGGCTGTCCATGTC  
CCTCTTTCTTTAGAAGCTCAGACTGAGGCTCGTTCTCCAATGTCTTCACACACTA  
ATCTCCTATCTCCCGCCACGGGGGATCCCGTTCTTGTACCAACCCAAGATATGC  
TTCTTGGTATTCACGCACTAACTATTGGTAATAGAAAAGGAATTTATGAAAGC---  
AGATATCCATCTGCCGGA-----GATTGTCACCTCTCAC-----TTCAAAATACG  
GTATTTTGCAAGTCGCAGCGACGTTCTCAGGGCCAAACAACCTGGAACAAATTGA  
CTCTCACAGTTCTCTGTGGCTTCGGTGAATACTGAGCCATATTTGATTGGTCC  
AAAGACTCGTGAATTTCTGTGCAATCCCAATATGAATCTTCGGGAACCTCCTTT  
CACTTCTACGGCGATTACCACATGAGGAGGTGCAGAGGGGGTAGCAAGCTCAG  
TACTCACATCCTTACAACAGCCGGTTCGCATCTTGTCCAACCAGCAGCTCAGAGA  
GGCGATACAGGGGATTTGAGAATCTCTTTCAGGTCGTAATGGTCAGGTCAGAG  
CAACAATTAAA-----

> *Stegnogramma sagittifolia*

ATGATTCATCGAACTAATTATCAACAGCTTCGGGTTGGACTGGCTTCCCCGAGCAG  
ATCCGCAGCTGGGCTGAGAGGAAGTTACCCAATGGAGACGTCTGCGGGCAAG  
TCGATCAACCTTACACGTTGCATCACAAGACTCATAAACCAGAGAGAGATGGCT  
CATTTCTGTGAAAAGATACTCGGGCCCGTAAAAAGCGGCGTCTGCGCGTGTGGA  
AACTATCGATCTGTGATAACGGAGAGGAGTATTCCAATTTCTGCAACATTGC  
GGAGTTGAGTTTATCGACTCCCGGGTTCGAAGATACCGAATGGGATACATTA  
CTTGCGTGTCCGGTAACCCACGTGTGGTTCTCAAAACGAATCCCTAGTTATATT

GCAAATCCACTTGCCAAACCTCTTAAGGAATCAGAAAGCCCGGTATATTGCGAT  
ACC---TATCCCAATCTTTCTCTTGCTAGGCCCGTGGCCGAAAGGCCCAACCTAT  
TAAGATTGCGAGGTTTGTTCATTATGAAGAC-----CGATCCTGGAGAAAC  
ATGCTTCCCATTTTTTCTCCACTCGAAATTATGAAACACTTCAAGGGAACGAAA  
TCGCCACTGGGGGAGATGCCGTCAAAAAAGGATTAAGTGTGATCTGCGA  
AGTGTTCATGGATCGTGCACATTTGGAGTGGCAGGCGCCGACAAAGCAAAGGCC  
TGTTGGGAATGAATGGGAAGATCGAACAATTCAAAGGAGGAAAGATCTTTTGGT  
TAGACGGATGAAATTAGCCAAGGATTTCTTACGGACGAACCTAAAAGCGGAATG  
GATGGTTTTAGATCTCTCGCCGTTCTGCCACCAGAATTGAGACCAATAGTTGA  
ATCGTATGAAGGCGAATTAGTTACTTCCGACCTTAACGAGCTTTACAGAAAGGT  
GATTCATCGAAAT---ACTCTTGCCGAATTCTTATCGGGGAGTGAC---ACGCCGGA  
GGGATTAATTGTTTGTGAGAAGAGACTTATTCAAGAAGCCGTAGACGCCCCCAT  
TGATAATGGTATACGTGGGCAACCAATGAGGGATATCAATAACAGACCCTACAA  
ATCATTTTCGGAGGTTATTGAGGGCAAAGAAGGACGATTTCTGTGAGAATTTGCT  
TGGAAAACGGGTTGACTACCCGGGCGGTTTCGTTATTGTCGTAGGCCCGTCTC  
TTTCATTACATCAATGTGGATTACCCCGAGAAATGTCAATTGAACCTTTCCAAGT  
ATTTGTAATTCGTAACCTTGATCGGACGACATCTCGCTTGTAATCTACGATCGGCT  
AAAAGTATGATACGAAAAGAAGATCCCGTTATATGGGAAGTTCTTCGGGAAGTT  
ATGCGGGGTACCCCATACTGCTGAATCGAGCACCTACTTTGCATAGGCTGGG  
TATACAGGCATTTCAACCCATTTTGGTGGGAAGGACGTGCCATTCTGTTTACATCC  
GTTGGTTTGTGGGGGGTTTAACGCAGATCTCGACGGAGATCAGATGGCCGTTT  
ATGTGCCCTATCTCTCGAAGCTCAGATTGAAGCTCGTCTTCCAATGTTTTCAC  
ACATAAATTTGTTATCCCCCGCTACGGGCGATTCTGTATCTGTCCCGAGTCAAG  
ACATGCTTCTCGGTCTTTATGTACTAACAATTGAGAATAAGCAAGGAATCTATGG  
AAAC---AGACATTCCGTTTTCTGTGAGA-----GGAAATGATGTCCACCCCGCCCC  
TACCGGAATACCCCGTTTTGGTAGTTACTACGACATACTCAGGGCCAAGGAATC  
AAATCAAATTGATTTCTGTAGTTTCTTGTGGCTTCGATGGGAAACTAATTTGGAA  
ATGATTGGTTTGAAGATTCGTGAATTACCTGTTGAATCCCAACATGAATCCTTGG  
GAACATCTCTTACCCTTATGATAATTACCAGATTAGAAAGTGTAGGAAGGGAT  
CTATCTCAAGTATATATGTACTTACCACGGCTGGTCGCGTTTTGTTTAACCAACA  
ACTTAGGGAAGCGATGCAGGGTGTATCAAAAGCCTCT---TCGTGTGCTACTTCG  
TCCGTACCGGATATGGCGACGCGAGACAAAATGTCCATATCCAACCGCAAAAA  
TGAAGAA

> *Vandenboschia speciosa*

ATGATTCATCAAAATAGCTATCAACAACCTTCGAATTGAATTGGCCTCGCCTGAACAG  
ATTCGTAGTTGGTCCGAAAGACAACCTACCTAATGGAGAAATCGTTGGACAAGTA  
ACTCAACCTTATACATTGCATTATAAACTCATAAACCAGAGAGAGATGGTTTGT  
TCTGTGAAAGAATATCTGGGCGCGTAGAGAGTGGAGTCTGTGCTTGTGGAAAC  
TATCGATCTTTTGATAATAGAGAAGAGTATTCAAATTTTCGTAAACATTGTGGCG  
TCGAATTCACCGATTCCCGAGTTCGGAGACATCGAATGGGATATATAAGATTAG  
CATGTCCAGTAGCTCATGTATGGTTTTTAAACGACTTCCTAGTTACATTGAAA  
TCTTCTTGCTAGACCTGTTAAAGAATTAGAAAGCCTAGTATATTGCGATGCC---T  
ATCCCAATCTCTTTCTTGCTAGGCCTGTAGCTGAGAAACCCACCCTATTACGAT  
TGCGAGGTTTGTTCGATTACGAAGAA-----CAATCATGGAAGAATATTCTT  
CCAATCTTTTTTCTACTCGAAGCTTTGAGACTCTTCAAGGAAGAGAAATTGCTA  
CTGGAGGGGATGCTATTAAAGAATGCTTAGCTAGCTTGAATCTACAAGATATTA  
TAGATTGTGCATATTCGGAATGGCAAATATTATCAAAGCAAGGATCGACAGAAA  
ATGAATGGGAAGATCAGGCAATTCAAAGAAGAAAAAATCTTTTAGTGAGACGAA  
TAAGATTAGCTAAAAATTTCTACGGACAAACATAAGACCAGAATGGATGGTCC  
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AAGGTGAATTGATCACTTCTGATTTTAATGAACTCTATAGAAGAATAATTTACCG  
GAATAATACCCTGATTGACTTTTCGATCGAGAAGTGAGTTTACACCAGAAGGGCT  
GATTGTCTGCCAAAAGAGACTTATTCAAGAAGCTGTAGATGCCCTTATTGATAAT  
GGGATACGTGGACAGCCAATACGAGATATTAATAACAGACCCTACAAATCTTTC  
TCCGAAGTTATTGAAGGAAAAGAAGGACGATTCGGTGAGAATCTGCTTGGAAAG  
CGGGTTGATTATTCAGGTCGTTCCGTTATCGTAGTAGGTCCATCTCTCTCATTA  
CATCAATGTGGATTACCTCGCGAATTGTGCGATGGAGCTTTTCCAAGCTTTTGT

ATTCATGACTTAATTGGACGCCATATCGCTCGTAATTTACGAACTGCTAAGAATA  
TGATTCAAAAGAAAGAACCGATCATATGGAAAGTTCTTTTCGGAAGTTATGCAAG  
GTCACCCCGTATTGCTGAATCGAGCACCTACATTACACAGATTAGGTATACAAG  
CATTTCAACCGATTCTAATAGAAGGACGAGCTATTTCGGTTGCATCCATTGGTCT  
GTGGGGGGTTTAATGCCGATTTTGATGGAGATCAGATGGCGGTTTCATATACCG  
TTATCTCTAGAAGCTCAGACTGAAGCCCGTTTCCCAATGTTTTCCCATACAAACC  
TATTATCTCCTGCTACAGGAGATCCCGTCTCTGTACCAACCCAGGACATGCTTC  
TTGGTCTCTATATATTAACATATGGATAATAAGCAAGGGATTATGGAAAC---AGAT  
ACTCTTCTTGATAGATATTCGAGAGACAGGAGTTCTATTCCC-----CATCCGAAGA  
TACCTTATTTTGTAGTTATCATGACGTGCTTAGGGCTAAACGATTGAAACAGAT  
TGATCTTTATAGCTGTTTATGGCTTCGATGGAAGAGTGATTCACACATGATCAGT  
TCCAGGAATCGTGAATTACCTATTGAGTTTCAATATGAATCTTCGGGGATCTCTT  
TTCAGTTCTATGCTAGTTATCAGATTAGAAGGGATAGAGAAAATAATGCAATTGG  
CTTGATATTCTTACAACCTGCTGGTCGTATTCTATTCAATCAACAAATAGTAGAA  
GCAATACAAGGCATTTCAAAAACGTCTTGGGATTGGACTCCT-----

> *Woodsia macrochlaena*

ATGATTCATCGAGCTAATTATCAACAGCTTCGGGTTGGACTGGCTTCCCCGAACAG  
ATTCGCGGTTGGGCTGAGAGGGAGTTACCCAATGGAGATGTCGTCGGGCAAGT  
CGATCAACCTTACACGTTGCATCACAAGACTCACAAACCAGAGAGAGATGGCTC  
ATTTCTGTAAGGATACTCGGGCCCATAAAAAGCGGTGTCTGCGCGTGTGGAA  
ACTATCGATCTGTCGATAATGGAGAGGAGTATTCCAATTTTTCGAAACATTGCG  
GAGTCGAGTTTACCGATTCCCGGGTTCGAAGATACCGAATGGGATACATTAAAC  
TCGCGTGTCCGGTAACCCATGTGTGGTTTTCAAAAAGAATCCCTAGTTATATTG  
CAAATCCACTTGCCAAACCTCTTAAAGAACTAGAAAGCCCAGTATATTGCGATA  
CC---TATCCCAATCTTTTTCTTGCTAGGCCCGTGGCCAAAAGGCCCAACCTATTA  
AGATTGCGGGGTTTGTTCATTACGAAGAC-----CGATCCTGGAGAAACAT  
GCTTCCCCTATTCTTCTCCACTCGAAATTATGAAACGCTTCAAAGGAACGAAATC  
GCCACTGGGGGAGATGCCGTCAAAAAGGGATTAAGTATTTGGATCTGAAAAG  
TGTTATGGATCACGCACATTTGGAGTGGCAGGCGCCGGCGAAGCAAAGGCCT  
GTTGGGAATGAATGGGAAGACCGAACAATTCAAAGAAGGAAAGATCTTCTGGT  
CAGACGGATGAAATTAGCCAAGGATTTCTTACGGACGAATCTAAACCGGAATG  
GATGGTTCTAGACTTCCCGCCAGTTCTACCACCTGAATTGAGACCGATAGTTGA  
ATCGTATGAAGGCGAATTAGTTACTTCCGACCTTAACGAGCTCTACAGAAAGGT  
AATTCATCGAAATAATACTCTTGTGCAATTCTTATCGGGGAGTGAATTCACGCC  
GGAGGGATTAATCGTTTGTGAGAAAAGACTTATTCAAGAAGCTGTAGACGCTCC  
CATTGATAATGGTATACGTGGGCAACCAATGAGGGATATCAATAACAGACCCTA  
CAAGTCATTTTCAGAGGTTATTGAGGGCAAAGAGGGGCGATTTCTGTGAGAATTT  
GCTCGGAAAACGGGTTGACTACTCGGGTCGTTTCGTTATTGTCGTAGGCCCAT  
CTCTTTCATTACATCAATGTGGATTACCCCGAGAAATGTCAATCGAACTTTTCCA  
AGTATTTGTAATTCGTAACCTTGATCGGGCGACATCTCGCTTGTAATCTACGAGC  
GGCTAAAAGTATGATACGAAAAGGAGATCCCATTATATGGGAAATTCTTCGGGA  
AGTTATGCGTGGTCACCCCATATTGCTGAATCGGGCACCTACTTTGCATAGGTT  
GGGTATACAGGCATTTCAACCCATTTTAATAGAAGGACGTGCTATTTCGCTTGCA  
TCCATTGGTTCTGTGGGGGGTTTAACGCAGATCTCGACGGAGATCAGATGGCCG  
TTCATGTGCCCTATCTCTCGAAGCTCAGATTGAAGCTCGTCTCCCGATGTTTT  
CGCACATAAATTTGTTATCCCCCGCTACGGGCGATTCTATATGTATCCCGAGTC  
AAGACATGCTTCTCGGTCTCTATGTACTAACAATTGAAAATAAGCAAGGAATCTA  
CGGAAAC---AGACATTCCGTTTTCTGTGAGA-----GGGGGTGATTTCCAC-----CC  
TGCCAGAATACCCTGTTTCGGTAGTTACCACGACATACTCAGGGCCAAGGAATC  
AAATCAAATTGATTTTTGTAGTTTCTTGTGGCTTCGGTGGGAAACTAATTTGGAA  
ATGATTAGTTCAAAAATTCGTGAATTACCTGTTGAATCTCAATATGAATCATTGG  
GAACCTCTCTTCACTCTTATGATAATTACCAGATTAGAAAGTGTAGGAAGGGATA  
TATCTCAGGTATATATGTACTTACCACGGCTGGTCGCATCTTGTTTAATCAACAA  
TTGAAGGAAGCGATACAGGGTGTATCAAAAGCCTCT---TTGTGTGCTACTTCGT  
CCGTACCAGATATGGTAACACAAGACGAAATGCCTACATCTAGCCGCAAAAATG  
AAGAA



> *Woodsia polystichoides*

ATGATTCATCGAGCTAATTATCAACAGCTTCGGATTGGACTGGCTTCCCCTGAACAG  
ATTCGCGGTTGGGCTGAGAGGGAGTTACCCAATGGAGATGTCGTCGGGCAAGT  
CGATCAACCTTACACGTTGCATCACAAGACTCACAAACCAGAGAGAGATGGCTC  
ATTTTCGTGAAAGGATACTCGGGCCCCATAAAAAGCGGTGTCTGCGCGTGTGGAA  
ACTATCGATCTGTCGATAACGGAGAGGAGTATTCCAATTTTTGCAAACATTGCG  
GAGTCGAATTTACCGATTCCCGGGTTCGAAGATACCGAATGGGATACATTAAAC  
TCGCGTGTCCGGTAACCCATGTGTGGTTTTCAAAAAGAATCCCTAGTTATATTG  
CAAATCCACTCGCCAAACCTCTTAAAGAACTAGAAAGCCCAGTATATTGCGATA  
CC---TATCCCAATCTTTTTCTTGCTAGGCCCGTGGCCAAAAGGCCCAACCTATTA  
AGATTGCGGGGTTTGTTCATTACGAAGAC-----CGATCCTGGAGAAACAT  
GCTTCCCCTATTCTTTTCCACTCGAAATTATGAAACGCTTCAAAGAAACGAAATC  
GCCACTGGGGGAGATGCCGTCAAAAAGGGATTAACTAGTTTGGATCTAGAAAG  
TGTTATGGATCGCGCACATTTGGAGTGGCAGGCGCCAGCGAAGCAAAGGCCT  
GTTGGGAATGAATGGGAAGACCGAACAATTCAAAGAAGGAAAGATCTTTTGGTC  
AGACGGATGAAATTAGCCAAGGATTTCTTACGGACGAATCTAAAACCAGAATGG  
ATGGTTCTAGACCTCCTGCCAGTTCTACCACCTGAATTGAGACCGATAGTTGAA  
TCGTATGAAGGCGAATTAGTTACTTCCGACCTTAACGAGCTCTACAGAAAGGTA  
ATTCATCGAAATAATACTCTTGTGCAATTCTTATCGGGGAGTGAATTCACGCCG  
GAGGGATTAATCGTTTGTGAGAAAAGACTTATTCAAGAAGCTGTAGACGCTCCC  
ATTGATAATGGTATACGCGGGGCAACCAATGAGGGATATCAATAACAGACCCTAC  
AAGTCATTTTCAGAGGTTATTGAGGGCAAAGAGGGACGATTTTCGTGAGAATTTG  
CTCGGAAAACGGGTTGACTACTCGGGCCGTTTCGTTATTGTCGTAGGCCCATC  
TCTTTCATTACATCAATGTGGATTACCCCGAGAAATGTCAATTGAACTTTTCCAA  
GTATTTGTAATTCGTAACCTTGATCGGGCGACATCTCGCTTGTAATCTACGAGCG  
GCTAAAAGTATGATACGAAAAGAAGATCCCATTATATGGGAAGTTCTTCGGGAA  
GTTATGCGTGGTCACCCCATATTGCTGAATCGGGCACCTACTTTGCATAGGTTG  
GGTATACAGGCATTTCAACCCATTTTAATAGAAGGACGTGCTATTTCGCTTGCAT  
CCATTGGTTTCGTGGGGGGTTTAACGCAGATCTCGACGGAGATCAGATGGCTGT  
TCATGTGCCCTATCTCTCGAAGCTCAGATTGAAGCTCGTCTCCTGATGTTTTC  
GCACATAAATTTGTTATCCCCCGCTACGGGCGATTCTATATGTATCCCGAGTCA  
AGACATGCTTCTCGGTCTCTATGTACTAACAATTGAAAATAAACAAGGAATCTAC  
GGAAAC---AGACATTCCGTTTTCTGTTGGA-----GGGGGTGATTTTCAC-----CCT  
GCCAGAATACCCTGTTTTGGTAGTTACCACGACATACTCAGGGCTAAGGAATCA  
AATCAAATTGATTTTTGTAGTTTCTTGTGGCTTCGGTGGGAAACTAATTTGGAAA  
TGATTAGTTCGAAAATTCTGTAATTACCTGTTGAATCTCAATATGAATCATTGGG  
AACTTCTCTTCACTCTTATGATAATTACCAGATTAGAAAGTGTAGGAAGGGATAT  
ATCTCAGGTATATATGTACTTACCACGGCTGGTCGCATCTTGTTTAATCAACAAT  
TGAAGGAAGCGATACAGGGTGTGTCAAAAGCCTCT---TTGTGTGCTACTTCTTC  
CGTACCAGATATAGTAACACAAGACGAAATGCCTAAGTCTAGTCGCAAAAATGA  
AGAA

> *Woodwardia unigemmata*

ATGACTCATCGAGCTAATTATCAACAGCTTCGGATTGGACTGGCTTCCCCGAACAG  
ATTCGCGGCTGGGCTGAAAGGGAGTTACCCAATGGAGACGTTGTCGGGCAAGT  
TGATCAACCTTATACGTTGCATCATAAAACCCATAAACCGGAGAGAGATGGCTC  
ATTTTCGTGAAAGGATACTCGGGCCTATAAAAAGCGGCGTCTGCGCGTGTGGAA  
ACTGTGATCTGTGCGTGGCGGAGGGGAGTATTCCAATTTTTGCAAACATTGC  
GGAGTTGAGTTTACCGACTCCCGGGTTCGAAGATACCAAATGGGATACATTAAA  
CTTGCGTGTCCGGTAACCCACGTGTGGTTTTCAAAAACGAATCCCTAGTTATATT  
GCAAATCCACTTGCCAAACCTCTTAAAGAACCAGAAAGCCCAGTATATTGCGAT  
ACC---TATCCCAATCTTTTTCTTGCTAGGCCCGTGGCCGAAAGGCCGAACCTAT  
TGAGACTGCGGGGCTTGTTCATTACGAAGAT-----CGATCCTGGAGAAA  
CAAGCTTCCCCTTTATTTCTCTACTCGAAATTATGAAACGCTTCAGGGGAACGA  
AATCGCCACTGGGGGAGATGCCGTCAAGAAAGGATTAACTAGTTTAGATCTGC  
AAAGTGTTATGGATCGTGCATATCTGGAGTGGCAAGCGCCGGCGAAGCAAAGG  
CCTGCTGGGAATGAATGGGAAGACCGAACAATTCAAAGAAGGAAAGATCTTTTG  
GTCAGACGGATGAAATTAGCCAAGGATTTCTTACGGACGAATCTAAAACCGGAA

TGGATGGTCTTAGATCTCTTGCCGGTTCTTCCACCTGAATTAAGACCAATAGTT  
 GAGTCGTATGAAGGCGAATTAGTAACTTCCGACCTTAATGAGCTTTACAGAAAG  
 GTAATTCATCGAAATAATACTCCTGCTGAATTTTCGTCGGGGAGTGAATTCACG  
 CCGGAGGGATTAATCGTTTGTGAGAAAAGACTTATTCAAGAAGCTGTAGACGCT  
 CCCATCGATAATGGTATACGCGGGCAACCGATGAGGGATATTAATAACAGACC  
 CTACAAGTCATTTTCAGAGGTTATTGAGGGCAAAGAAGGACGATTTTCGTGAGAA  
 TTTGCTCGGAAAACGGGTTGATTACCCAGGTCGTTTCGTTATTGTTGTAGGTCC  
 GTCCCTTTTCATTACATCAATGTGGATTACCCCGAGAAATGTCAATCGAACCTTTC  
 CAAGTATTTGTAATTCGTAACCTTGATCGGACGACATCTCGCTTGTAATCTACGAG  
 CGGCTAAAAGTATGATACGAAAAGAAGATCCCGTTATATGGGAAGTTCCTCGGG  
 AAGTTATGCGGGGTCACCCCATACTGCTGAATCGAGCACCTACTTCGCACAGG  
 CTGGGTATCCAGGCATTTCAACCCATTTTAGTAGAAGGACGTGCTACTCGTTTG  
 CATCCATTGGTTTCGTGGGGGGTTTAAACGCAGATCTCGACGGAGATCAGATGGC  
 TGTTTCATGTGCCCTATCTCTCGAAGCTCAGATTGAAGCTCGTCTTCCGACGTT  
 TTCACACATAAATTTGTTATCCCCAGCTACGGGCGATTCTGTATCTGTCCCGAG  
 TCAAGACATGCTTCTCGGTCTTTATGTACTAACAATTGAGAACAAGCAAGGAAT  
 CTATGGAAAC---AGACACTCCATTTCCGTGGGG-----GGGGGTGACGCATAC---  
 ---CCTGCCGGAATACCCTGTTTCGGTAGTTACCACGACATACTCAGGGCCAAGG  
 AATCAAATCAAATTGATTCCTTCAGTTTCTTGTTGGCTTCGATGGGAACTAATTT  
 GAAAATGATTAGTTTCGAAAATTCGTGAATTCCCCGTCGAATCTCAATATGAATCC  
 TTGGGAACCTCTCTTCACTCTTATGATAATTACCAAATTAGGAAGTGTAGGAAG  
 GGATATATCTCAAGTATATATGTACTTACCACGGCTGGTCGCATTTTGCTTAATC  
 AACAGTTAAGGGAAGCGATGCAAGGTGTGTCAAAAGCCTCT---TCATGTGCTAC  
 TTCGTCCGTACCGGATGTGGTAACACAAGACGAAATGCCTAAATCTAACTGCAA  
 AAACGAAGAG

## 附录2 jModelTest2.1.10基于AIC得到的*matK*和*rbcL*串联集核苷酸模型参数

**Appendix 2** Nucleotide model parameters of *matK* and *rbcL* tandem set based on AIC of jModelTest2.1.10

Model selected:

Model = TVM+I+G  
 partition = 012314  
 -lnL = 58974.2978  
 K = 135  
 freqA = 0.3131  
 freqC = 0.1823  
 freqG = 0.1637  
 freqT = 0.3409  
 R(a) [AC] = 1.5378  
 R(b) [AG] = 8.1389  
 R(c) [AT] = 0.3907  
 R(d) [CG] = 1.4105  
 R(e) [CT] = 8.1389  
 R(f) [GT] = 1.0000  
 p-inv = 0.2860  
 gamma shape = 1.8660

附录 3 *rpoC1* 基因分子进化速率表

Appendix 3 Molecular evolution rate of *rpoC1* gene

Species	$E_t$	$E_v$	$trsv/trst$	$trst$	$trsv$	$d_N$	$d_S$	$\omega$
<i>Asplenium pekinense</i>	0.019783075	0.0049432	0.122930458	0.080525608	0.00989905	0.041938484	0.179908473	0.233110112
<i>Asplenium prolongatum</i>	0.01951061	0.007575	0.191011907	0.079416558	0.015169508	0.066439699	0.140779692	0.471940929
<i>Hymenasplenium unilaterale</i>	0.034372135	0.0030222	0.043257542	0.139909343	0.006052134	0.072886809	0.237027485	0.30750362
<i>Athyrium anisopterum</i>	0.005782812	0.0004778	0.040649165	0.023538529	0.000956822	0.008718516	0.047255892	0.184495844
<i>Athyrium opacum</i>	0.011338694	0.0023935	0.103853103	0.046153352	0.004793169	0.022578427	0.094330851	0.239353583
<i>Athyrium sheareri</i>	0.011461857	0.000956	0.041035688	0.046654678	0.001914507	0.005917513	0.121367266	0.048757072
<i>Athyrium sinense</i>	0.002359254	0	0	0.009603175	0	0.004321427	0.015395068	0.280702033
<i>Diplazium bellum</i>	0.011754764	0.0014348	0.060051459	0.047846936	0.002873278	0.024596608	0.091128812	0.269910335
<i>Diplazium dilatatum</i>	0.003999262	0	0	0.016278714	0	0.011601179	0.014747756	0.786640281
<i>Diplazium dushanense</i>	0.010991797	0.0050003	0.223806346	0.044741331	0.010013394	0.029071386	0.109625606	0.265187915
<i>Deparia lancea</i>	0.009138218	0.0010203	0.054929253	0.037196469	0.002043174	0.021681688	0.058832288	0.368533819
<i>Deparia pycnosora</i>	0.004773219	0.0008921	0.091948903	0.019429051	0.00178648	0.008208174	0.043286971	0.18962228
<i>Diplazium striatum</i>	0.008033164	0	0	0.032698427	0	0.012363044	0.058766413	0.210376021
<i>Diplazium unilobum</i>	0.015655719	0.0021254	0.066789717	0.063725495	0.004256208	0.028205803	0.12315394	0.229028827
<i>Deparia viridifrons</i>	0.015073196	0.0005424	0.017702608	0.061354376	0.001086132	0.037720224	0.077988177	0.483665921
<i>Austroblechnum melanocaulon</i>	0.037311112	0.0009573	0.012622709	0.151872242	0.001917039	0.078120661	0.223227504	0.349959838
<i>Woodwardia unigemmata</i>	0.027397736	0.0023953	0.043012583	0.111520544	0.004796787	0.060140146	0.185628539	0.323981141
<i>Cibotium barometz</i>	0.016668853	0.0028129	0.083021021	0.067849387	0.005632925	0.037248159	0.126478571	0.29450174
<i>Alsophila podophylla</i>	0.01070015	0.0018735	0.086139627	0.043554202	0.003751743	0.026481972	0.075616919	0.350212265
<i>Alsophila spinulosa</i>	0.005008491	0.001043	0.102457447	0.02038671	0.00208877	0.011549569	0.038969156	0.296377192
<i>Cystopteris chinensis</i>	0.034971662	0.0052813	0.074297299	0.142349674	0.010576196	0.054664231	0.323054624	0.169210488
<i>Pteridium aquilinum</i>	0.03888016	0.0071637	0.090647624	0.158258939	0.014345797	0.067409195	0.389891048	0.17289239

<i>Diplaziopsis cavaleriana</i>	0.008794142	0	0	0.035795933	0	0.015250552	0.057932617	0.263246393
<i>Diplaziopsis javanica</i>	0.004237746	0.0004777	0.055463752	0.017249446	0.000956719	0.004349515	0.042401614	0.102578989
<i>Homalosorus pycnocarpus</i>	0.006015327	0.0014347	0.117343737	0.024484961	0.002873157	0.015413352	0.041563364	0.370839857
<i>Cyrtomium devexiscapulae</i>	0	0.0004873	null	0	0.000975908	0.002220957	0	null
<i>Cyrtomium falcatum</i>	0	0	null	0	0	0	0	null
<i>Cyrtomium fortunei</i>	0.000490155	0	0	0.001995143	0	0.002233162	0	null
<i>Dryopteris decipiens</i>	0.01274359	0.0004906	0.018939314	0.051871881	0.000982418	0.002220525	0.145647069	0.01524593
<i>Dryopteris fragrans</i>	0.010140352	0.0004899	0.023769753	0.041275586	0.00098111	0	0.117352474	0
<i>Equisetum arvense</i>	0.015235895	0.0097899	0.316121669	0.062016632	0.019604801	0.044106627	0.136862344	0.322269992
<i>Equisetum hyemale</i>	0.016518348	0.0215879	0.642968721	0.067236767	0.043231138	0.09622629	0.272658978	0.352918104
<i>Callistopteris apiifolia</i>	0.045158091	0.0133355	0.145284694	0.183812814	0.026705188	0.079605786	0.531152835	0.149873597
<i>Hymenophyllum holochilum</i>	0.037661332	0.0133724	0.174686889	0.153297787	0.026779113	0.093756884	0.350972093	0.267134869
<i>Vandenboschia speciosa</i>	0.046146451	0.0134148	0.143018075	0.187835862	0.026863923	0.086839101	0.514921742	0.16864524
<i>Hypodematium crenatum</i>	0.029251672	0.0053241	0.089544987	0.119066858	0.01066184	0.045768352	0.264932913	0.172754498
<i>Angiopteris angustifolia</i>	0.000689204	0	0	0.002805357	0	0	0.001378882	0
<i>Angiopteris evecta</i>	0.001786092	0.0004855	0.133730269	0.007270161	0.000972241	0.004469782	0.021289593	0.209951496
<i>Marsilea crenata</i>	0.040340888	0.0084126	0.102596105	0.164204728	0.016846765	0.06126126	0.399124033	0.15348928
<i>Pilularia americana</i>	0.02156959	0.0084464	0.192651996	0.087797487	0.016914361	0.034620586	0.292586284	0.118326073
<i>Matteuccia struthiopteris</i>	0.014841369	0	0	0.06041074	0	0.038763944	0.061158293	0.633829722
<i>Onoclea sensibilis</i>	0.021620692	0.0023942	0.054479552	0.088005496	0.0047945	0.052255419	0.141468139	0.369379419
<i>Botrychium ternatum</i>	0.063190702	0.0054648	0.042546993	0.257213279	0.010943652	0.129008019	0.457378093	0.282059899
<i>Helminthostachys zeylanica</i>	0.051945186	0.0114502	0.108446082	0.211439202	0.022929753	0.119067961	0.462371474	0.257515803
<i>Mankyua chejuensis</i>	0.052808832	0.0141296	0.13163468	0.214954611	0.028295481	0.123189177	0.608368417	0.202491079

<i>Osmundastrum cinnamomeum</i>	0.07184959	0.0058191	0.039845441	0.292458669	0.011653145	0.12338075	0.39243074	0.31440134
<i>Lepisorus clathratus</i>	0.024082458	0.0060763	0.124131635	0.098025941	0.01216812	0.050322459	0.226022141	0.222643934
<i>Polypodium glycyrrhiza</i>	0.017926686	0.0009777	0.026832907	0.072969307	0.001957979	0.012089808	0.181587723	0.066578332
<i>Psilotum nudum</i>	0.075707348	0.0406432	0.264116397	0.308161399	0.081390478	0.205209917	1.252844215	0.163795239
<i>Adiantum shastense</i>	0.03784276	0.0068289	0.088779522	0.154036276	0.013675267	0.085937239	0.27649272	0.31081194
<i>Ceratopteris richardii</i>	0.072506778	0.0413519	0.280584037	0.295133705	0.082809807	0.20005925	1.139486672	0.175569627
<i>Myriopteris lindheimeri</i>	0.031493677	0.003503	0.054722414	0.128192784	0.007015019	0.05501335	0.268447301	0.204931656
<i>Rhachidosorus consimilis</i>	0.029937311	0.0047991	0.078866636	0.121857706	0.009610507	0.052198262	0.251493992	0.207552718
<i>Schizaea elegans</i>	0.060306548	0.0879444	0.717446767	0.245473534	0.176114194	0.522212834	0.631003425	0.827591125
<i>Schizaea pectinata</i>	0.03476127	0.0047359	0.067026803	0.141493289	0.009483843	0.060870073	0.17574802	0.346348556
<i>Ampelopteris prolifera</i>	0.01058974	0.0014307	0.066469589	0.043104788	0.002865157	0.013082667	0.100594538	0.13005345
<i>Christella appendiculata</i>	0.018573318	0.0033446	0.088593336	0.075601377	0.006697778	0.021791594	0.192702949	0.113083865
<i>Macrothelypteris torresiana</i>	0.01964748	0.0028624	0.071674274	0.079973675	0.005732055	0.037444725	0.160021088	0.233998687
<i>Pseudophegopteris aurita</i>	0.015274778	0.0014333	0.046163102	0.062174904	0.002870186	0.026170643	0.119761501	0.218523007
<i>Stegnogramma sagittifolia</i>	0.010917477	0.0014348	0.064655907	0.044438817	0.002873232	0.026522873	0.07256113	0.365524531
<i>Woodsia macrochlaena</i>	0.006144902	0	0	0.025012389	0	0.017768852	0.023137479	0.76796837
<i>Woodsia polystichoides</i>	0.010430924	0.0009562	0.045098545	0.042458338	0.001914809	0.006563726	0.109546796	0.059917097
<i>Lygodium japonicum</i>	0.012620766	0.002184	0.085137798	0.051371935	0.004373693	0.009981026	0.139788785	0.071400766
<i>Lygodium microphyllum</i>	0.015815489	0.0048207	0.149960796	0.064375827	0.00965385	0.033587504	0.154364141	0.217586182