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20,000 species and five key markers: The status of molecular bryophyte phylogenetics

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Abstract

A number of reviews have accompanied and monitored the progress of molecular phylogenetic research on bryophytes, focusing on the publication record itself, bryophyte phylogeny and systematics in the molecular era, as well as the evolution and phylogenetic utility of markers from different genomes. However, none of the recent reviews include a detailed characterization of all molecular markers used in bryophyte phylogenetics. Here we provide an overview of the history and current state of marker utilization, including coding and non-coding sequence markers from all three genomes as well as fingerprinting approaches. The molecular architecture and evolutionary peculiarities, as well as practical aspects such as amplification and sequencing strategies, are outlined for the DNA sequence markers, with a focus on the most commonly employed regions. Their phylogenetic utility and potential for solving some of the remaining, pressing questions in bryophyte phylogeny, as well as their suitability for molecular species identification by DNA barcoding, are discussed.

Key words: Bryophytes, DNA barcoding, mitochondrial DNA, molecular markers, nuclear DNA, plastid DNA, phylogenetics

Introduction

During the last two decades, analyses of molecular data have had a major impact on our understanding of plant evolution and relationships on all taxonomic levels, from the deep nodes separating the major plant groups to species and populations. Currently, molecular characters are primarily obtained from three different sources: (i) DNA sequences of specific coding or non-coding regions from one of the three plant genomes (plastid, mitochondrial, or nuclear markers), (ii) structural genomic characteristics (e.g. gene order, gain or loss of genes or non-coding regions), and (iii) genetic fingerprints. The largest numbers of publications and sequences are available for angiosperms, the most species-rich extant plant group; however, quite a large amount of molecular data has been accumulated for bryophytes as well. The first DNA sequences of bryophytes were published in the early 1980's (Katoh *et al.* 1983), but it took another decade until molecular phylogenies of bryophytes appeared. For the present overview, 382 papers, published up to the end of 2009, were compiled from different sources (PubMed, Current Contents, manual search of journal contents) that contain original datasets for bryophytes based on DNA sequences and/or DNA fingerprinting. This corresponds to an average of 35 publications per year in the last decade (1999−2009, Fig. 1). Not considered here are technical notes, studies based solely on allozymes, as well as phylogenies including (few) bryophyte representatives but mainly focusing on other plant groups. The earliest studies mainly focused on the relationships between the three major bryophyte groups and other land plants (cf. Fig. 1), an issue only recently resolved with confidence (Qiu *et al.* 2006). In the majority of publications, however, questions at

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