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Systematics and morphological evolution within the moss family Bryaceae: A comparison between parsimony and Bayesian methods for reconstruction of ancestral character states

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Abstract

The Bryaceae are a large cosmopolitan moss family including genera of significant morphological and taxonomic complexity. Phylogenetic relationships within the Bryaceae were reconstructed based on DNA sequence data from all three genomic compartments. In addition, maximum parsimony and Bayesian inference were employed to reconstruct ancestral character states of 38 morphological plus four habitat characters and eight insertion/deletion events. The recovered phylogenetic patterns are generally in accord with previous phylogenies based on chloroplast DNA sequence data and three major clades are identified. The first clade comprises *Bryum bornholmense, B. rubens, B. caespiticium*, and *Plagiobryum.* This corroborates the hypothesis suggested by previous studies that several *Bryum* species are more closely related to *Plagiobryum* than to the core *Bryum* species. The second clade includes *Acidodontium, Anomobryum*, and *Haplodontium*, while the third clade contains the core *Bryum* species plus *Imbribryum.* Within the latter clade, *B. subapiculatum* and *B. tenuisetum* form the sister clade to *Imbribryum.* Reconstructions of ancestral character states under maximum parsimony and Bayesian inference suggest fourteen morphological synapomorphies for the ingroup and synapomorphies are detected for most clades within the ingroup. Maximum parsimony and Bayesian reconstructions of ancestral character states are mostly congruent although Bayesian inference shows that the posterior probability of ancestral character states may decrease dramatically when node support is taken into account. Bayesian inference also indicates that reconstructions may be ambiguous at internal nodes for highly polymorphic characters.

Keywords: Bryaceae; *Bryum*; *Plagiobryum*; Phylogeny; Evolution; Ancestral character states; Maximum parsimony; Bayesian inference; Posterior probabilities

1. Introduction

With approximately 13,000 species (Crosby et al., 1999), the mosses (Bryophyta) comprise the second largest group of land plants after the angiosperms. Unlike the angiosperms, however, mosses have two distinct alternating generations. The leafy gametophyte is the dominant generation, responsible for photosynthesis and sexual reproduction, while the sporophyte generation, which consists of an unbranched axis with a spore-producing capsule at its apex, is supported by the gametophyte throughout its lifetime. The mouth of the capsule is commonly lined with one or two concentric rows of teeth, which compose the peristome. The outer row is called the exostome and the inner the endostome. The true mosses, i.e. class Bryopsida, have an arthrodontous peristome in which the teeth consist of differentially thickened periclinal cell wall remnants. The diplolepidous peristome, usually consisting of two rows of teeth, is a form of arthrodontous peristome in which the teeth have two columns of cells up the dorsal side (Fig. 1). The diplolepidous peristome is further divided into diplolepidous-opposite and diplolepidous-alternate types. In the

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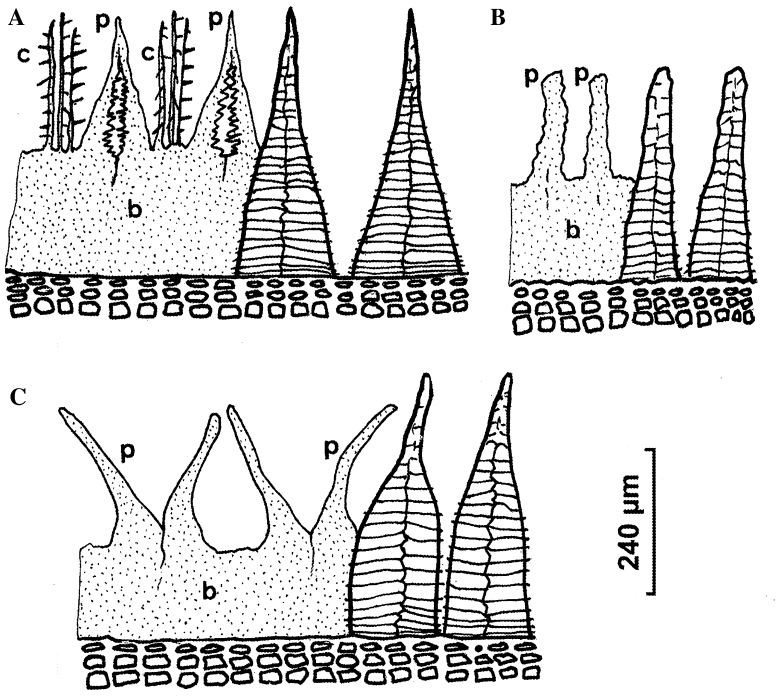

Fig. 1. Semi-diagrammatic representation of peristomes of: (A) *Plagiobryum pseudotriquetrum* = *Bryum pseudotriquetrum* (well-developed peristome), (B) *Brachymenium pulchrum* (strongly reduced peristome), (C) *Acidodontium ramicola* (reduced peristome with endostome processes split along the keel into two lobes that have widely divergent tips). Each drawing shows about one-quarter of the peristome viewed from the exterior of the capsule mouth, with two endostome processes on left (exposed after removal of exostome teeth) and two exostome teeth on right. The endostome is stippled; it is not drawn where it passes behind the exostome teeth. On the endostome, b = basal membrane, c = cilia, p = process (partly split along keel in (A), divided into two divergent lobes in (C)).

former, the exostome and endostome teeth are opposite each other (e.g., Funariaceae), while in the latter the endostome segments alternate with the exostome teeth (e.g., Bryaceae; Fig. 1). Historically, the classification of mosses has been strongly influenced by peristomial characters (e.g., Philibert, 1884; Brotherus, 1925) and the extent of peristomial reduction has often been used to separate taxa at the generic level. Within the true mosses, two groups are traditionally recognized based on the position of the sporophyte with respect to the stem apex of the gametophyte. The first group is the pleurocarps, with extensively branched gametophytes bearing sporophytes on lateral branches, and the second group is the acrocarps, with sparsely branched gametophytes and terminal sporophytes.

1.1. Characteristics and classification of the Bryaceae

The Bryaceae are a large cosmopolitan acrocarpous moss family with a diplolepidous-alternate peristome. Traditional classifications within the family follow Brotherus (1925), who recognized three subfamilies within the Bryaceae, based mainly on capsule orientation and peristome architecture. The first subfamily, the Orthodontioideae, is characterized by erect capsules and strongly reduced endostomes. The second subfamily, the Mielichhoferioideae, accommodates genera with apparent lateral sporophyte placement and capsules without an exostome. The third subfamily, the Bryoideae, is by far the largest subfamily and includes genera of considerable morphological diversity. *Bryum* Hedw., the largest genus within the Bryoideae, is characterized by pendulous capsules with well-developed peristomes (Fig. 1A). *Anomobryum* Schimp. includes small to medium-sized mosses with julaceous gametophytes and vermicular leaf cells. *Rhodobryum* (Schimp.) Limpr. are large plants with stem leaves that are crowded in a distinct rosette at the stem apex (rosulate shoots), more than one sporophyte developed from each perichaetium (polysety), and stolons. Several genera within the Bryoideae are characterized by reduced peristomes. For instance, *Brachymenium* Schwägr., which contains many species whose gametophytes are virtually indistinguishable from certain *Bryum* species, is characterized by erect capsules with strongly reduced peristomes (Fig. 1B), while gibbous capsules with a slightly reduced exostome are characteristics for the genus *Plagiobryum* Lindb. The tropical genus *Acidodontium* Schwägr. is characterized by a peculiar endostome with processes split along the keel into two divergent lobes (Fig. 1C). To a great extent, Brotherus' system has prevailed, although some authors (e.g., Sharp et al., 1994) have suggested that the Bryoideae should be divided into the Pohlioideae, accommodating genera with long narrow cells, and a redefined Bryoideae, comprising genera with shorter, more rhombic cells.

1.2. Previous phylogenetic treatments of the Bryaceae

Phylogenetic analyses based on DNA sequence data (Cox and Hedderson, 1999; Cox et al., 2000) and morpho-