Reconstructing Evolution in the Metzgeriales Schljakov subord. Pallaviciniineae R.M. Schust.,
the “Vascularized” Liverworts

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Introduction:
Recent multigene analyses of the simple thalid liverworts (Forrest & Crandall-Stotler 2005, Crandall-Stotler et al. 2009) resolve the Pallaviciniinae Mag. and Hymenophylophytaeae R. M. Schust., as sister taxa in a strongly supported monophyletic clade, subtended by Phyllothallia E. A. Hodgs. This clade is generally characterized by elongate capsules that often open by slits, antheridia and archegonia protected by scales, and strands of usually thick-walled, hydrolyzed cells, i.e., a vascular strand, in the thallus midrib. Morphologically based circumscriptions of genera and subfamilies within the Pallaviciniinae are problematic since many lineages within the family are vascularized and many morphological markers of natural phylogenetic units have expanded across genera and genera. To identify morphological markers of natural phylogenetic units we have expanded taxon sampling within the Pallaviciniinae and coupled our analysis to the study of type specimens to morphological units.

Materials and Methods:
Sequences were generated for 4 chloroplast genes, namely rbcL, rps4, petA and trnL, for 62 ingroup and 12 outgroup accessions, following methods described in Forrest & Crandall-Stotler (2004). Parsimony analyses (MP) were conducted using PAUP* version 4.0b10 (Swofford 2002). Bootstrap (BS) support was calculated under an MP criterion, with 1000 BS replicates, each BS replicate consisting of an heuristic search with five random addition replicates. Voucher specimens of the accessions used in the molecular analyses were identified by comparison to type specimens. The name applied to each accession represents the closest fit to a respective type specimen, rather than currently applied nomenclature, i.e., taxonomic reductions have not been recognized.

Results:
The analyses recovered 10,000 equally parsimonious trees of length 5289. Despite the large number of trees, there is good resolution in the bootstrap consensus (Fig. 1). Three major clades, corresponding to I) the Hymenophylophytaeae, II) the Pallaviciniinae subf. Moerckieae R. M. Schust. plus Hattorianthaceae R. M. Schust., & Innoue, and III) the Pallaviciniinae minus the Moerckieae and Hattorianthaceae, have been identified (Figs. 2, 3). Within the latter, 5 well-supported lineages are resolved (Fig. 2), with 3 of these including accessions of Pallavicinia Green. Neothallus Hasek., which was formerly placed in the subf. Moerckieae, is resolved with Xonothallus R. M. Schust. and several species of Symphyogyna Nees & Mont. in a subclade of this latter genus. No one morphological character can reliably identify all of the lineages, but oil body morphology, type of shoot-sporophyte association, and spore wall architecture are predictive of some relationships, as detailed in the illustrations and discussions below (Figs. 4-7).

Acknowledgements:
We thank NSF [PEET award (DEB 9977961)] for financial support. We also would like to acknowledge S. Sipos (SIU) for sharing laboratory facilities and the following colleagues for either providing us with plant material, assisting us in the field, and/or for allowing us to incorporate one of their photos: J. Duskett, A. Flik, D. Gieradz, A. Kruse, D. Long, M. Mainz, J. Skaeth, B. Tan, and L. Zhang. Special thanks are extended to Rachel Murray for her technical assistance in assembling the poster.

Conclusions:
The taxa of the suborder Pallaviciniinae R. M. Schust. are in need of revisionary studies. There is definitely more variation in Pallavicinia in Asia than is accounted for by the species reductions of Grolle & Piippo (1986). The strongly supported relationship of P. xiphoides with Podomitrium, rather than with the other species of P. sect. Subcolita, is puzzling and mandates detailed morphological studies of this complex, as does the strongly supported dichotomy in the genus Symphyogyna. Characters traditionally used to assign taxa to ranks should be supplemented with diagnoses of spore wall architecture and oil body morphology.

Literature Cited: