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Goodbye or welcome Gondwana? – insights into the phylogenetic biogeography of the leafy liverwort *Plagiochila* with a description of *Proskauera*, gen. nov. (Plagiochilaceae, Jungermanniales)

J. Heinrichs[1], **M. Lindner**[1], **H. Groth**[1], **J. Hentschel**[1], **K. Feldberg**[1], **C. Renker**[2], **J. J. Engel**[3], **M. von Konrat**[3], **D. G. Long**[4], and **H. Schneider**[1]

[1] Department of Systematic Botany, University of Göttingen, Germany
[2] Department of Soil Ecology, UFZ Centre for Environmental Research Leipzig-Halle Ltd., Germany
[3] Department of Botany, Field Museum, Chicago, USA
[4] Royal Botanic Garden Edinburgh, Scotland, UK

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Abstract. Molecular phylogenies based on chloroplast gene *rps*4 sequences and nuclear ribosomal ITS sequences have been generated to investigate relationships among species and putative segregates in *Plagiochila* (Plagiochilaceae), the largest genus of leafy liverworts. About a fourth of the ca. 450 accepted binomials of Plagiochilaceae are included in these phylogenetic analyses, several represented by multiple accessions. A clade with *Chiastocaulon*, *Pedinophyllum*, and *Plagiochilion* is placed sister to a clade with numerous accessions of *Plagiochila*. *Plagiochila pleurata* and *P. fruticella* are resolved sister to the remainder of Plagiochilaceae and transferred to the new Australasian genus *Proskauera* which differs from all other Plagiochilaceae by the occurrence of spherical leaf papillae. The historical biogeography of Plagiochilaceae is explored based on the reconstructions of the phylogeny, biogeographic patterns and diversification time estimates. The results indicate that the current distribution of Plagiochilaceae cannot be explained exclusively by Gondwanan vicariance. A more feasible explanation of the range is a combination of short distance dispersal, rare long distance dispersal events, extinction, recolonization and diversification.

Key words: Jungermanniales, Plagiochilaceae, *Plagiochila*, *Proskauera*, biogeography, divergence time estimates, phylogeny, Gondwana.

Introduction

Application of Wegener's (1915) theory of continental drift and climate reconstructions have greatly affected our understanding of diversification of plant life on earth. Over the last decades, the 160 million year history of the breakup of Gondwana (McLoughlin 2001) and its effects on extant vegetation has been a major focus but also a controversial aspect of plant biogeography (e.g. Givnish and Renner 2004, Raven and Axelrod 1974, Schuster 1979). Gondwanan disjunctions have often been explained by vicariance. In recent years, however, evidence has been provided that many putative Gondwanan disjunctions can also be attributed to long distance dispersal (e.g. Heinrichs et al. 2005b, McGlone 2005, Renner 2004a, Yuan et al. 2005) or Laurasian migration (e.g. Davis et al. 2002, Weeks et al. 2005).

The application of phylogenetic approaches using in particular DNA sequence data improved our understanding of liverwort (Marchantiophyta) phylogeny (e.g. He-Nygrén et al. 2004, Lewis et al. 1997). Complex thalloids (Marchantiopsida) as well as a few leafy liverworts (*Haplomitrium* Nees) and simple thalloids (*Treubia* K.I.Goebel, *Apotreubia* S. Hatt. & Mizut.) form the first main branches of liverworts (Crandall-Stotler et al. 2005, Heinrichs et al. 2005a). The majority of the leafy liverworts (Jungermanniidae) and the simple thalloids (Metzgeriidae) have been identified as a derived clade, with the leafy liverworts nested within thalloids (Davis 2004, Forrest and Crandall-Stotler 2005, Heinrichs et al. 2005a).

Marchantiophyta have been described as an early diverging lineage of land plants that possibly dates back to Silurian times (e.g. Graham et al. 2004, Groth-Malonek and Knoop 2005, Kenrick and Crane 1997, Qiu et al. 1998, Wellman et al. 2003). Inferring the age of liverworts as a whole and their major lineages is greatly hampered by the scarcity of the fossil record and the poor state of preservation of most older fossils (Oostendorp 1987). Thus, the age of major lineages of liverworts as well as their diversification is still unknown (Krassilov and Schuster 1984). Several extant genera of Jungermanniidae are known from Cretaceous or early Tertiary amber fossils (Grimaldi et al. 2002, Grolle and Meister 2004); extinct *Cheirorhiza brittae* Krassilov has been described from Upper Jurassic to Lower Cretaceous deposits of the Bureja Basin, Amur (Krassilov 1970, 1973). Accordingly, the Jungermanniidae lineage has a minimum age that links it to Gondwanan times.

As early as 1969, Schuster stated that "Jungermanniales are excellent subjects for phytogeographical analysis" and speculated that "many but probably not all major groups of the Jungermanniae may have originated in ... Panantarctica ("Gondwanaland")". In this context, Schuster (1979) stressed the existence of liverworts with disjunct ranges in the cool or cold Antipodes. Based on comparisons of recent distributions of putatively old families, he favoured an explanation of their ranges by short-range dispersal before the final disassembly of Gondwana rather than relatively recent long-distance dispersal. Similar arguments were prefered in hypotheses concerning angiosperms showing disjunct distributions in the Southern Hemisphere (Raven and Axelrod 1974, Thorne 1978), but recently these ideas were challenged in studies using DNA sequence data and phylogenetic approaches (e.g. Knapp et al. 2005, Pennington and Dick 2005, Renner 2004b, Tremetsberger et al. 2005, Winkworth et al. 2002). These studies argued instead for alternative scenarios involving long distance dispersals.

Here we test Schuster's (1969, 1979) hypotheses relating to biogeographical aspects of jungermannialean liverworts by exploring the historical biogeography of *Plagiochila* (Dumort.) Dumort., a cosmopolitan genus with an extant diversity of 400 to 450 species (Gradstein et al. 2001, Heinrichs 2002, So and Grolle 2000), representing the largest genus of hepatics. *Plagiochila* is widespread throughout the tropics and the Southern Hemisphere (e.g. Hässel de Menéndez 1983, Inoue 1984, Inoue and Schuster 1971) and belongs to the most common and abundant elements of the cryptogamic flora of humid tropical forests (e.g. Gradstein et al. 1989, Parolly and Kürschner 2004, Wolf 1993).

Materials and methods

Taxon sampling, outgroup, DNA amplification, and DNA sequencing. The chloroplast gene *rps*4/nuclear ribosomal ITS data set of Heinrichs et al. (2005b) was extended with 27 accessions of *Plagiochila* to include representatives of all *Plagiochila* subgenera accepted by Inoue (1984). The ingroup was completed with the Plagiochilaceae genera *Chiastocaulon* Carl, *Pedinophyllum* (Lindb.) Lindb., and *Plagiochilion* S.Hatt. (Groth and Heinrichs 2003) as well as the Lophocoleaceae genera *Chiloscyphus* Corda and *Heteroscyphus* Schiffn. (Hentschel et al. 2006). Based on the results of Heinrichs et al. (2005a) *Herbertus sendtneri* (Nees) Lindb. (Herbertaceae) was designated as the outgroup taxon. Fifty three sequences were newly

Table 1. Geographic origins, voucher numbers, and GenBank/EMBL accession numbers of the investigated taxa. Accession numbers of new sequences in bold

Taxon and distribution	Voucher Origin	Voucher	Accession number (ITS)	Accession number (*rps*4)
Chiastocaulon dendroides (Nees) Carl	Japan	*Ohnishi 5770* (HIRO)	AY438233	AY438213
Chiloscyphus cuspidatus (Nees) J.J.Engel & R.M.Schust.	Germany	*Hentschel Bryo01411* (JE)	**AM180586**	–
Chiloscyphus cuspidatus	China	*Koponen et al. 48430* (HE)	–	AY462348
Chiloscyphus latifolius (Nees) J.J.Engel & R.M.Schust.	Germany	*Hentschel Bryo0416* (JE)	**AM180587**	–
Chiloscyphus latifolius	U.S.A.	*Davis 393* (DUKE)	–	AY608085
Chiloscyphus profundus (Nees) J.J.Engel & R.M.Schust.	Germany	*Marin s.n.* (GOET)	AJ422240	–
Chiloscyphus profundus	U.S.A.	*Sargent's culture collection 481*	–	AF231889
Herbertus sendtneri (Nees) Lindb.	Bolivia	*Groth s.n.* (GOET)	AJ413177	AY438203
Heteroscyphus aselliformis (Reinw. et al.) Schiffn.	Indonesia	*Gradstein 10240* (GOET)	**AM180588**	–
Heteroscyphus splendens (Lehm. & Lindenb.) Grolle	Malaysia	*Schäfer-Verwimp & Verwimp 18905* (GOET)	**AM180589**	–
Pedinophyllum interruptum (Nees) Kaal.	British Isles	*Rycroft 020907* (GOET)	AY438234	AY438216
P. acanthocaulis Sull. I	Argentina	*Long 31680* (GOET)	**AM180590**	**AM180486**
P. acanthocaulis II	Chile	*Holz 252* (GOET)	**AM180591**	**AM180487**
Plagiochila adiantoides (Sw.) Lindenb.	Costa Rica	*Heinrichs et al. 4314* (GOET)	AJ422027	AY438204
P. aerea Taylor	Costa Rica	*Heinrichs et al. 4321* (GOET)	AJ422028	AY438205
P. alternans Lindenb. & Gottsche	Bolivia	*Heinrichs et al. GP 16* (GOET)	AY550130	AY547691
P. andina Steph.	Bolivia	*Heinrichs & Müller 4100* (GOET)	**AM180592**	**AM180488**
P. ansata (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	Chile	*Holz 570A* (GOET)	**AM180593**	**AM180489**
P. arbuscula (Lehm. & Lindenb.) Lindenb.	Japan	*Yamaguchi 18280* (HIRO)	AY550131	AY547692
P. asplenioides (L.) Dumort.	Germany	*Heinrichs & Groth 4339* (GOET)	AJ414629	AY547693
P. austinii A.Evans	U.S.A.	*Risk 10849* (DUKE)	AJ748130	AY608099
P. banksiana Gottsche	New Zealand	*Frey & Pfeiffer 98-T121* (GOET)	AY550132	AY547694
P. bantamensis (Reinw. et al.) Mont.	Japan	*Yamaguchi 16890* (HIRO)	AY275160	AY547695
P. barteri Mitt.	Malawi	*O'Shea M7062a* (GOET)	AJ866749	AJ866764
P. bicuspidata Gottsche	Costa Rica	*Holz CR 99-787* (GOET)	AY550133	AY547696
P. bifaria (Sw.) Lindenb.	Ecuador	*Holz EC-01-416* (GOET)	AJ422010	AY438206

Table 1. (continued)

Taxon and distribution	Voucher Origin	Voucher	Accession number (ITS)	Accession number (*rps*4)
P. boryana Steph.	Bolivia	*Heinrichs et al. 4182* (GOET)	AJ866753	AJ866768
P. britannica Paton	British Isles	*Rycroft 00015* (GOET)	AY275162	AY438207
P. buchtiniana Steph.	Bolivia	*Groth s.n.* (GOET)	AJ413306	AY438208
P. carringtonii ssp. *lobuchensis* Grolle	Bhutan	*Long 28857* (GOET)	AJ414631	AY438209
P. chonotica Taylor I	Chile	*Holz & Franzaring CH-00-108* (GOET)	AY550134	AY547697
P. chonotica II	Chile	*Holz 631* (GOET)	**AM180594**	**AM180490**
P. circinalis (Lehm. & Lindenb.) Lindenb.	New Zealand	*Pfeiffer 98-T166* (GOET)	**AM180595**	**AM180491**
P. colorans Steph.	Rwanda	*Buchbender & Fischer 1115* (GOET)	AJ866751	AJ866765
P. cristata (Sw.) Lindenb.	Costa Rica	*Heinrichs et al. 4192* (GOET)	AJ422015	AY438210
P. crozetensis Kaal.	Marion Islands	*Gremmen 94-57* (JE)	**AM180596**	**AM180492**
P. cucullifolia var. *anomala* Heinrichs & Gradst.	Ecuador	*Holz EC-01-558* (GOET)	AY330711	AY438211
P. deflexa Mont. & Gottsche	Costa Rica	*Heinrichs et al. 4160* (GOET)	AJ416083	AY569439
P. deflexirama Taylor	Costa Rica	*Heinrichs et al. 11* (GOET)	AY550135	AY547698
P. deltoidea Lindenb.	New Zealand	*Frey 98-T116* (GOET)	AY550136	AY547699
P. dependula Taylor	Ecuador	*Heinrichs et al. 4442* (GOET)	**AM180597**	**AM180493**
P. disticha (Lehm. & Lindenb.) Lindenb.	Ecuador	*Holz EC-01-436* (GOET)	AJ422014	AY438214
P. cf. *divergens* Steph.	Kenya	*Solga & Fischer s.n.* (GOET)	AJ866736	AJ866756
P. diversifolia Lindenb. & Gottsche	Ecuador	*Holz EC-01-17* (GOET)	AJ413308	AY438215
P. dura De Not.	Chile	*Drehwald 3190* (GOET)	AY550137	AY547700
P. dusenii Steph.	Chile	*Holz & Franzaring* CH 00-146 (GOET)	**AM180598**	**AM180494**
P. elegans Mitt.	China	*Long 33675* (GOET)	**AM180599**	**AM180495**
P. ensiformis Taylor	Ecuador	*Sauer & Gradstein* MS-E 115 (GOET)	AY275163	AY547701
P. equitans Gottsche	Chile	*Holz 625* (GOET)	**AM180600**	**AM180496**
P. exigua (Taylor) Taylor	Ireland	*Hakelier s.n.* (GOET)	AF539461	AY547702
P. fasciculata Lindenb.	Australia	*Renker 18.2-1* (GOET)	**AM180601**	**AM180497**
P. flexuosa Mitt.	Japan	*Kurita* 147 (HIRO)	AY550138	AY547703
P. frondescens (Nees) Lindenb.	Indonesia	*Schäfer-Verwimp* 20704 (GOET)	AY438237	AY438219
P. fruticosa Mitt.	India	*Long 23002* (GOET)	AY438235	AY438217
P. fusca Sande Lac.	Indonesia	*Gradstein 10259* (GOET)	**AM180602**	**AM180498**
P. fuscobrunnea Steph.	Chile	*Dierßen "2002-51"* (GOET)	**AM180603**	–

P. fuscolutea Taylor	Costa Rica	*Heinrichs et al. 4400* (GOET)	AJ416086	AY547704
P. fusifera Taylor	Seychelles	*Pócs 9342/B* (GOET)	AJ866746	AJ866760
P. gigantea Lindenb.	New Zealand	*Engel & von Konrat 23911* (GOET)	**AM180604**	**AM180499**
P. gymnocalycina (Lehm. & Lindenb.) Mont.	Bolivia	*Drehwald & Reiner-Drehwald 4729* (GOET)	AY390531	AY438218
P. hakkodensis Steph.	Japan	*Yamaguchi 12271* (HIRO)	AY275164	AY547705
P. heterophylla Lehm.	British Isles	*Rycroft et al. 97006* (GOET)	AY275165	AY547706
P. heterostipa Steph.	Malawi	*O'Shea M7070a* (GOET)	AJ866735	AJ866757
P. hookeriana (Hook. f. & Taylor) Gottsche et al.	Chile	*Holz 560* (GOET)	**AM180605**	**AM180500**
P. incerta Gottsche	Madagascar	*Pócs 9447/L* (GOET)	AJ866737	AJ866761
P. integerrima Steph.	Malawi	*O'Shea M7552a* (GOET)	AY275166	AY547707
P. korthalsiana Molk.	Indonesia	*Gradstein 10258* (GOET)	**AM180606**	**AM180501**
P. lastii Mitt.	Comoros	*Pócs et al. 9273/U* (GOET)	AY550139	AY547708
P. longiramea Steph.	Bolivia	*Heinrichs et al. 4071* (GOET)	AF539463	AY547709
P. macrostachya Lindenb.	Ecuador	*Holz EC-01-80* (GOET)	AJ422016	AY547710
P. magna Inoue	Japan	*Kurita 258* (HIRO)	AY275167	AY438221
P. cf. *neesiana* Lindenb.	Chile	*Holz 808* (GOET)	**AM180607**	–
P. nobilis Gottsche	Indonesia	*Gradstein 10253* (GOET)	**AM180608**	AM180502
P. obcuneata Steph.	Chile	*Holz 676* (GOET)	**AM180609**	–
P. obovata Step. I	Chile	*Holz 385* (GOET)	**AM180610**	AM180503
P. obovata II	Chile	*Holz 583* (GOET)	**AM180611**	**AM180504**
P. orbicularis (S.Hatt.) S.Hatt.	Japan	*Kurita 32* (HIRO)	AY275168	AY438222
P. ovalifolia Mitt.	Japan	*Ohnishi 5723* (HIRO)	AY275169	AY547711
P. ovata Lindenb. & Gottsche	Costa Rica	*Heinrichs et al. 4158* (GOET)	AJ422017	AY547712
P. patentissima Lindenb.	Brazil	*Gradstein 3703* (GOET)	AY550140	AY547713
P. patriciae Heinrichs & H.Anton	Costa Rica	*Holz CR-00-176* (GOET)	AY275170	AY547714
P. pectinata Lindenb.	D.R. Congo	*Pócs 91148/A* (GOET)	AJ866754	–
P. peculiaris Schiffn.	Bhutan	*Long 28832* (GOET)	AY550141	AY547716
P. poeltii Inoue & Grolle	India	*Long 22802* (GOET)	AY550142	AY547717
P. porelloides (Nees) Lindenb. I	Germany	*Heinrichs & Groth 4340* (GOET)	AJ414633	AY547718
P. porelloides *II*	Japan	*Ohnishi 5720* (HIRO)	AY550144	AY547723
P. pulcherrima Horik.	Japan	*Ohnishi 5771 (HIRO)*	AY438239	AY438223
P. punctata (Taylor) Taylor I	British Isles	*Rycroft 01013* (GOET)	AJ413174	AY547719
P. punctata II	Ecuador	*Holz EC-01-389* (GOET)	AJ422018	AY547715
P. raddiana Lindenb.	Ecuador	*Holz EC-01-45* (GOET)	AJ422020	AY438225
P. renitens (Nees) Lindenb.	Malaysia	*Schäfer-Verwimp 18736/A* (GOET)	AY569440	AY569441

Table 1. (continued)

Taxon and distribution	Voucher Origin	Voucher	Accession number (ITS)	Accession number (*rps*4)
P. retrorsa Gottsche	Costa Rica	*Heinrichs et al. 4154* (GOET)	AJ422021	AY547720
P. retrospectans (Spreng.) Lindenb.	New Zealand	*Frey & Pfeiffer 98-T88* (GOET)	AY550143	AY547721
P. rubescens	Chile	*Rycroft 020723-6* (GOET)	AJ781752	AJ866767
P. rutilans (Lehm. & Lindenb.) Lindenb.	Bolivia	*Groth 101* (GOET)	AJ416081	AY438226
P. rutilans var. *moritziana* (Hampe) Heinrichs	Ecuador	*Holz EC-01-404* (GOET)	AJ416080	AY547722
P. sandei Sande Lac.	Indonesia	*Gradstein 9970* (GOET)	AJ414634	AY438227
P. sciophila Lindenb.	Japan	*Ohnishi 5400* (HIRO)	AY275171	AY547724
P. semidecurrens (Lehm. & Lindenb.) Lindenb.	Nepal	*Long 21348* (GOET)	AY275173	AY438228
P. spinulosa (Dicks.) Dumort.	Belgium	*Dauphin et al. 3811* (GOET)	AY275173	AY547725
P. squamulosa Mitt.	Kenya	*Chuah 0310/AB* (GOET)	AJ744796	AJ866758
P. streimannii Inoue	Indonesia	*Gradstein 10309* (GOET)	AJ866744	AJ866763
P. stricta Lindenb.	Costa Rica	*Heinrichs et al. 4401* (GOET)	AJ416646	AY438229
P. stricta	Madagascar	*Pócs et al. 9868/AF* (GOET)	AJ633128	AJ866766
P. strictifolia Steph.	Malawi	*Hodgetts M2490a*	AJ866734	AJ866759
P. subplana Lindenb.	French Guiana	*Holz FG-00-32* (GOET)	AY275174	AY438224
P. subtropica Steph.	Nepal	*Long 17359* (GOET)	AY550145	AY547726
P. superba (Spreng.) Mont. & Nees	Costa Rica	*Heinrichs et al. 4175* (GOET)	AJ416084	AY438230
P. tabinensis Steph.	Costa Rica	*Heinrichs et al. 4156* (GOET)	AJ422026	AY438231
P. teysmannii Sande Lac.	Indonesia	*Gradstein 10308* (GOET)	AJ866745	AJ866762
P. trabeculata Steph.	Japan	*Kurita 257* (HIRO)	AY550146	AY547727
P. trichostoma Gottsche	Costa Rica	*Heinrichs et al. 4324* (GOET)	AJ416082	AY547728
P. turgida Herzog	Ecuador	*Holz EC-70* (GOET)	AJ422024	AY547729
P. validissima Steph.	Bolivia	*Heinrichs et al. 4058* (GOET)	**AM180612**	**AM180505**
Plagiochilion mayebarae S.Hatt.	Japan	*Ohnishi 5588* (HIRO)	AY438238	AY438220
Proskauera fruticella (Hook.f. & Taylor) Heinrichs & J.J.Engel	New Zealand	*Engel & von Konrat 23943* (GOET)	**AM180613**	**AM180506**
Proskauera pleurata (Hook.f. & Taylor) Heinrichs & J.J.Engel I	New Zealand	*Schäfer-Verwimp & Verwimp 14071* (GOET)	**AM180614**	**AM180507**
Proskauera pleurata II	New Zealand	*Schäfer-Verwimp & Verwimp 13777* (GOET)	**AM180615**	**AM180508**

generated for this study (Table 1). PCR amplification, and sequencing followed the protocols described in Heinrichs et al. (2002) or Groth and Heinrichs (2003). The ITS and *rps*4 sequences of *Chiloscyphus cuspidatus* (Nees) J.J.Engel & R.M.Schust. and *C. latifolius* (Nees) J.J.Engel & R.M.Schust. come from different accessions, *Heteroscyphus* is represented by ITS sequences only.

Phylogenetic analyses. The ITS1–5.8S-ITS2 and the *rps*4 sequences were aligned manually in BioEdit version 5.09 (Hall 1999). Ambiguously aligned sites, the often incomplete end of the ITS2 sequences as well as primer regions of the *rps*4 sequences were excluded, resulting in an ITS alignment including 692 putatively homologous sites and an *rps*4 alignment with 564 sites (alignments available upon request).

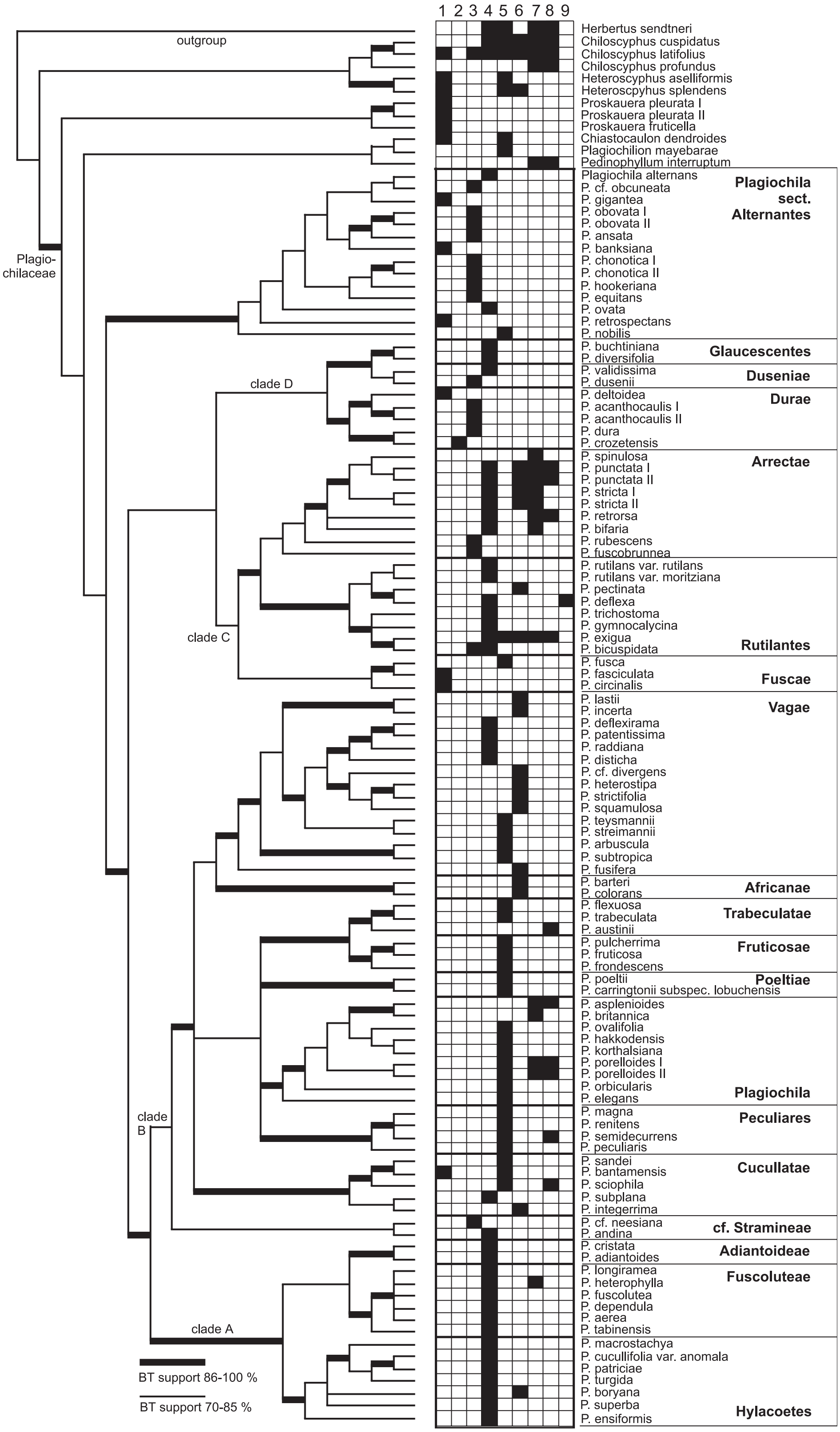
Phylogenetic trees were inferred using maximum parsimony (MP) and maximum likelihood (ML) criteria as implemented in PAUP* version 4.0b10 (Swofford 2000).

The maximum parsimony analyses were performed with the following options implemented: heuristic search mode with 20 random-addition-sequence replicates, tree bisection-reconnection branch swapping (TBR), MULTrees option on, and collapse zero-length branches off. All characters were treated as equally weighted and unordered. The confidence of branching was assessed using 1000 non-parametric bootstrap resamplings (Felsenstein 1985) with 10 random-addition-sequence replicates, TBR swapping and allowing for 10 million rearrangements. First the ITS and the *rps*4 datasets were analysed separately (trees not depticted). Congruence between the trees was inferred by inspecting bootstrap scores above 70% (Mason-Gamer and Kellogg 1996). The trees gave no evidence of incongruence. Hence the datasets were combined.

To decide on the nucleotide substitution model with the smallest number of parameters that best fits the data, the program Modeltest 3.06 (Posada and Crandall 1998) was used. The GTR + I + G model (General Time Reversible, Lanave et al. 1984, Tavaré 1986) selected both by the hierarchical likelihood ratio test and the Akaike Information Criterion (Akaike 1974) was used for subsequent maximum likelihood analyses. ML analyses were implemented as heuristic search with one addition sequence replicate. Branching confidence was assessed using 150 bootstrap resamplings (Felsenstein 1985) in ML analysis using a neighbor joining tree as starting tree, TBR swapping and allowing for 3000 rearrangements under the GTR + I + G model.

Estimating divergence times. A likelihood ratio test (Felsenstein 1981) rejected the presence of a molecular clock. Therefore non-parametric rate smoothing (NPRS; Sanderson 1997) as implemented in the program r8s (Sanderson 2003) was used to transform the ML phylogram into a chronogram. The NPRS analyses were performed using the Powell algorithm, different maxiter parameters (up to 500), 10 restarts, and 10 to 20 time guesses. The chronogram was calibrated with the best available fossil of Plagiochilaceae, the baltic amber fossil *Plagiochila groehnii* Grolle & Heinrichs with an age of about 50 million years (Grolle and Heinrichs 2003). The sterile unbranched fossil resembles the extant *P. sciophila* Lindenb. of sect. *Cucullatae* Schiffn. However, *Plagiochila* is well known for its extensive morphological homoplasy at section level (Groth et al. 2004b, Heinrichs 2002), making it impossible to unequivocally assign the fossil to this section. Even the generic placement is not absolutely reliable as genera of Plagiochilaceae are partly defined by branching pattern or sex distribution. Accordingly three different assignments of the fossil were performed, within *Plagiochila* sect. *Cucullatae*, at the base of *Plagiochila*, or at the base of Plagiochilaceae respectively. The above strategy was developed to explore putative scenarios in a group of land plants which is well known for its poor fossil record and to minimize the effect of incorrect assignments of fossils – either as calibration points or in the form of age constraints – as one of the major sources of errors in attempts to estimate divergence times (Magallón 2004).

Exploring the biogeography of *Plagiochila*. Areas of putative endemism were defined based on the distribution of species included in the analysis (Fig. 1) with the objective to reduce the number of polymorphisms (occurrence of a species in more than one area). In general, we follow currently accepted main areas of bryophyte distribution (Wijk et al. 1959) and recognize the following areas: Australasia, Southern South America, Subantarctics, Neotropics, Asia, Western Holarctics, Eastern Holarctics, Africa, and Hawaiian Islands. Taxa occurring in more than one of the areas were scored as polymorphic. Maximum parsimony


1 2 3 4 5 6 7 8 9
outgroup
Herbertus sendtneri
Chiloscyphus cuspidatus
Chiloscyphus latifolius
Chiloscyphus profundus
Heteroscyphus aselliformis
Heteroscpyhus splendens
Proskauera pleurata I
Proskauera pleurata II
Proskauera fruticella
Chiastocaulon dendroides
Plagiochilion mayebarae
Pedinophyllum interruptum
Plagio-chilaceae
Plagiochila alternans
P. cf. obcuneata
P. gigantea
P. obovata I
P. obovata II
P. ansata
P. banksiana
P. chonotica I
P. chonotica II
P. hookeriana
P. equitans
P. ovata
P. retrospectans
P. nobilis
Plagiochila sect. Alternantes
P. buchtiniana
P. diversifolia
Glaucescentes
P. validissima
P. dusenii
Duseniae
clade D
P. deltoidea
P. acanthocaulis I
P. acanthocaulis II
P. dura
P. crozetensis
Durae
P. spinulosa
P. punctata I
P. punctata II
P. stricta I
P. stricta II
P. retrorsa
P. bifaria
P. rubescens
P. fuscobrunnea
Arrectae
P. rutilans var. rutilans
P. rutilans var. moritziana
P. pectinata
P. deflexa
P. trichostoma
P. gymnocalycina
P. exigua
P. bicuspidata
Rutilantes
clade C
P. fusca
P. fasciculata
P. circinalis
Fuscae
P. lastii
P. incerta
P. deflexirama
P. patentissima
P. raddiana
P. disticha
P. cf. divergens
P. heterostipa
P. strictifolia
P. squamulosa
P. teysmannii
P. streimannii
P. arbuscula
P. subtropica
P. fusifera
Vagae
P. barteri
P. colorans
Africanae
P. flexuosa
P. trabeculata
P. austinii
Trabeculatae
P. pulcherrima
P. fruticosa
P. frondescens
Fruticosae
P. poeltii
P. carringtonii subspec. lobuchensis
Poeltiae
P. asplenioides
P. britannica
P. ovalifolia
P. hakkodensis
P. korthalsiana
P. porelloides I
P. porelloides II
P. orbicularis
P. elegans
Plagiochila
P. magna
P. renitens
P. semidecurrens
P. peculiaris
Peculiares
P. sandei
P. bantamensis
P. sciophila
P. subplana
P. integerrima
Cucullatae
clade B
P. cf. neesiana
P. andina
cf. Stramineae
P. cristata
P. adiantoides
Adiantoideae
P. longiramea
P. heterophylla
P. fuscolutea
P. dependula
P. aerea
P. tabinensis
Fuscoluteae
clade A
P. macrostachya
P. cucullifolia var. anomala
P. patriciae
P. turgida
P. boryana
P. superba
P. ensiformis
Hylacoetes
BT support 86-100 %
BT support 70-85 %

reconstructions were performed using MacClade version 4.05 (Maddison and Maddison 2000) by treating areas of putative endemism as unordered and equally weighted character states. Reconstruction of ancestral areas using maximum parsimony is frequently employed to explore patterns of distribution without explicit statements concerning the processes underlying the history of the observed patterns. This approach avoids biases that may lead to erroneous reconstructions of vicariance hypotheses such as pseudocongruence or pseudoincongruence (Donoghue and Moore 2003). In early attempts, we also employed Dispersal-Vicariance analysis (Ronquist 1996, 1997) as well as weighting schemes to explore hypotheses of dispersal and vicariance. However, several studies reported problems for process-oriented approaches with large and complex data sets to obtain correct estimates of biogeographical changes (Sanmartin and Ronquist 2004, Yuan et al. 2005).

Scanning electron microscopy. Air dried leaves, spores and elaters of Plagiochilaceae were observed using a scanning electron microscope ZEISS DMS 960 after fixing on double adhesive tape and sputter coating with gold.

Results

Of the 1256 investigated characters, 524 (ITS: 325, *rps*4: 199) were parsimony informative, 221 autapomorphic (ITS: 116, *rps*4: 105) and 511 (ITS: 251, *rps*4: 260) constant. The heuristic search recovered 5880 equally most parsimonious trees with a length of 3095 steps, a corrected consistency index of 0.31, a retention index of 0.67 and a rescaled consistency index of 0.24. The strict consensus of these trees is shown in Fig. 1 which also includes a scheme with the distribution of the species. Maximum likelihood analysis of the combined data set using the GTR model (parameters: base frequencies $A = 0.2794$, $C = 0.2005$, $G = 0.2632$, $T = 0.2569$, proportion of invariable sites 0.1888, gamma shape 0.6788, and molecular clock not enforced) recovered a single tree with $\ln = -18081.625$ (Fig. 2) which is largely congruent with the MP topology. Differences are found only in weakly or unsupported topologies or in support of some clades.

The well supported Plagiochilaceae are placed sister to Lophocoleaceae. The robust (ML) or weakly supported (MP) *Plagiochila* subgen. *Plagiochila* is resolved sister to a well (ML) or weakly (MP) supported clade with *Chiastocaulon dendroides* (Nees) Carl, *Plagiochilion mayebarae* S.Hatt., and *Pedinophyllum interruptum* (Nees) Kaal. *Plagiochila pleurata* (Hook.f. & Taylor) Gottsche et al. of *P.* subgen. *Pleurochila* Inoue and *P. fruticella* (Hook.f. & Taylor) Gottsche et al. form a robust monophyletic lineage. They are sister to the remainder of Plagiochilaceae albeit without support. *Plagiochila fruticella* and *P. pleurata* are the only representatives of Plagiochilaceae with a leaf lamina covered by strongly protruding, spherical papillae (a few *Plagiochila* species have low papillae, the majority of the family have a smooth leaf surface); *P. pleurata* is the only member of the family with a pluriplicate perianth. Based on the molecular topology and the morphological differences, the new genus *Proskauera* is proposed here to accommodate *P. pleurata* and *P. fruticella*:

Proskauera Heinrichs & J.J.Engel gen. nov. (Figs. 4, 5)* *Plagiochila* (Dumort.) Dumort. similis, sed differt lamina foliorum papillis sphaericis obsita. Perianthia pluriplicata (*Proskauera pleurata*) vel laevissima (*P. fruticella*).

Type: ***Proskauera pleurata*** (Hook.f. & Taylor) Heinrichs & J.J.Engel, comb. nov.

Jungermannia pleurata Hook.f. & Taylor, *London J. Bot.* 3: 372. 1844; *Plagiochila pleurata* (Hook.f. & Taylor) Taylor & Hook.f. ex Gottsche, Lindenb. & Nees, Syn. Hepat. 5: 633 (1847).

◄

Fig. 1. Rooted strict consensus of 5880 equally parsimonious trees recovered during 20 random-taxon-addition-heuristic searches of the combined ITS and *rps*4 data sets. Distribution of species is indicated at branches. 1: Australasia; 2: Subantarctics; 3: Southern South America; 4: Neotropics, 5: Asia; 6: Africa; 7: Eastern Holarctics; 8: Western Holarctics; 9: Hawaiian Islands

Fig. 2. Phylogram resulting from a maximum likelihood analysis of the ITS-*rps*4 dataset

= *Plagiochia* sect. *Fruticellae* Carl, Ann. Bryol. (suppl. 2): 142. 1931. Type: *Plajiochila fruticella*.

= *Plagiochila* subsect. *Pleuratae* Inoue & R.M.Schust., J. Hattori Bot. Lab. 34: 110. 1971. Type: *Plagiochila pleurata*.

= *Plagiochila* subgen. *Pleurochila* Inoue, The genus *Plagiochila* in Southeast Asia: 23. 1984.

Type: *Plagiochila pleurata*.

Proskauera fruticella (Hook.f. & Taylor) Heinrichs & J.J.Engel, comb. nov.
Jungermannia fruticella Hook.f. & Taylor, London J. Bot. 3: 565. 1844. *Plagiochila fruticella* (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees, Syn. Hepat. 5: 639. 1847.

Etymology: *named in honour of the bryologist Johannes Max Proskauer (1923 Göttingen – 1970 Berkeley)

The robust *Plagiochila* sect. *Alternantes* Carl are sister to a clade comprising all other representatives of this genus. Several sectional type species (see below) are placed within the *Alternantes* clade, leading to the following synonymy:

Plagiochila sect. Alternantes Carl, Ann. Bryol. Suppl. 2: 75. 1931. Type: *Plagiochila alternans* Lindenb. & Gottsche.

= *Plagiochila* sect. *Robustae* Carl, Ann. Bryol. Suppl. 2: 131. 1931, syn. nov. Type: *Plagiochila robusta* Steph. (= *P. hookeriana* Lindenb., Hässel de Menéndez 2004).

= *Plagiochila* sect. *Equitantes* Carl, Ann. Bryol. Suppl. 2: 127, syn. nov. Type: *P. equitans* Gottsche.

= *Plagiochila* sect. *Obcuneatae* Carl, Ann. Bryol. Suppl. 2: 123, syn. nov. Type: *P. obcuneata* Steph.

= *Plagiochila* sect. *Giganteae* Carl, Ann. Bryol. Suppl. 2: 143, syn. nov. Type: *P. gigantea* Lindenb.

Plagiochila sect. *Alternantes* are widespread in Australasia and southern South America, with two species occuring in the Neotropics and a single species, *Plagiochila nobilis* Gottsche, restricted to tropical Asia (Fig. 1). The robust sister lineage of *Alternantes* is subdivided into the well supported clades A, B, C and the unsupported clade D. Clade A includes the neotropical sections *Adiantoideae* Lindenb., *Fuscoluteae* Carl and *Hylacoetes* Carl in a robust sister relationship to clade B with several pantropical, Asian or holarctical sections. The Bolivian endemic *P. andina* Steph. and the southern South American *P.* cf. *neesiana* Lindenb. form the first branch of clade B. Clade C is made up of sects. *Arrectae* Carl and *Rutilantes* Carl in a robust sister relationship. Species from southern South America form a paraphyletic grade at the base of *Arrectae*. A moderately (ML) or unsupported (MP) clade assigned to sect. *Fuscae* Carl is found in a sister relationship with the *Arrectae-Rutilantes* clade. This clade includes the Australasian *P. circinalis* (Lehm. & Lindenb.) Lindenb. and *P. fasciculata* Lindenb. as well as the South East Asian *P. fusca* Sande Lac.

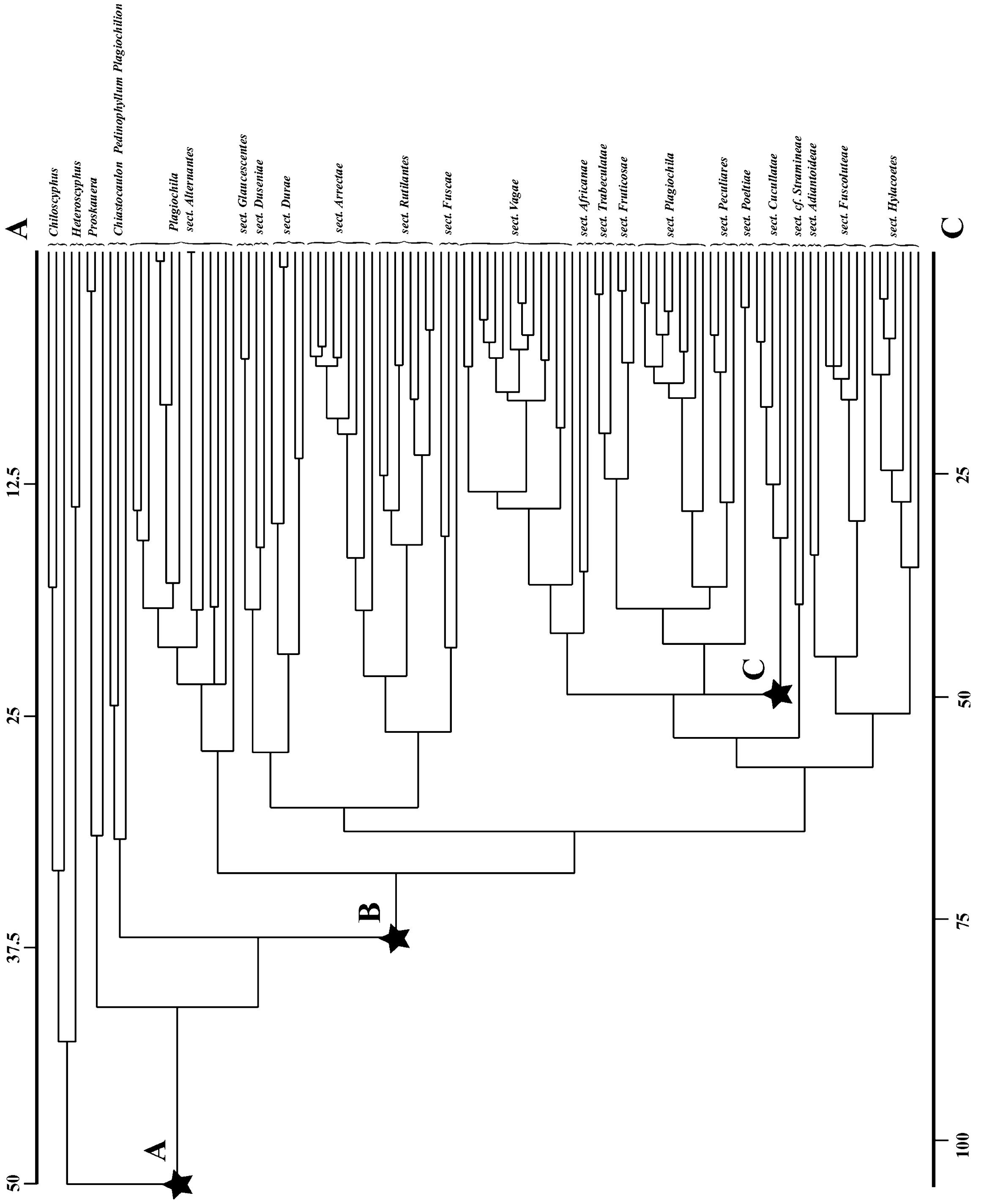
Clade D is made up of sect. *Durae* Carl which is placed sister to a clade with *P.* sects. *Duseniae* Carl and *Glaucescentes* Carl in a robust sister relationship. *Plagiochila acanthocaulis* Sull., conspecific with the type species of *P.* sect. *Hirtae* Carl, is identified as member of the *Durae*, leading to the following synonymy:

Plagiochila sect. Durae Carl, Ann. Bryol. Suppl. 2: 123. Type: *P. dura* De Not.

= *P.* sect. *Hirtae* Carl, Ann. Bryol. Suppl. 2: 122, syn. nov. Type: *P. hirta* Mitt. (syn. of *P. acanthocaulis* Sull. fide Hässel de Menéndez 1983: 89).

This section includes representatives from southern South America, the subantarctic, and Australasia.

Ancestral area reconstructions remained unresolved for the base of Plagiochilaceae and *Plagiochila*. Maximum parsimony reconstruction indicated an origin of clades A to D in the Neotropics. Clade A of *Plagiochila* shows a nearly exclusively neotropical distribution whereas clade B includes two main subclades of which one has its origin in Africa (*P.* sects. *Africanae* Heinrichs and *Vagae* Lindenb.) and the other in Asia (*P.* sects. *Peculiares* Schiffn.



to *Trabeculatae* Inoue). The chronogram (Fig. 3) indicates that the main lineages of Plagiochilaceae diversified in the same timeframe. The same holds true for most sectional clades of *Plagiochila*. *Proskauera pleurata* and *P. fruticella* as well as the species of *Plagiochila* sect. *Alternantes* have long been separated from each other.

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Fig. 3. Chronogram generated by applying NPRS to the ML phylogeny shown in Fig 2. Stars indicate different assignments of the Baltic amber fossil *Plagiochila groehnii*. The upper time scale A corresponds to assignment A, whereas the lower one corresponds to assignment C [scales in mill. years]. For discussion of the assignment see paragraph "Fossil record and diversification time estimates"

Discussion

Classification of Plagiochilaceae

Plagiochila is characterized by nearly exclusively lateral branching, alternating foliation with leaves usually not connected at their base, dioicy, and a laterally compressed perianth with a dorsal keel usually slightly longer than the ventral one (Heinrichs 2002, Inoue 1984, Inoue and Schuster 1971). Inoue (1984) subdivided *Plagiochila* into five subgenera. The types of the subgenera *Metaplagiochila* Inoue and *Paraplagiochila* Inoue have already been identified as members of clade "B" (Figs. 1, 2) which also includes the generitype (Groth et al. 2004b). *Plagiochila* subgen. *Chiastocaulon* (Carl) Inoue has been re-established as the monospecific genus *Chiastocaulon*, based on its position in a clade with *Plagiochilion* and *Pedinophyllum* rather than *Plagiochila*, and the frequent occurrence of ventral intercalary branches (Groth and Heinrichs 2003). The separation of *Chiastocaulon* and *Plagiochila* is corroborated in the analyses presented here. *Chiastocaulon* is resolved as sister to *Plagiochilion* in a robust sister relationship. Both genera are linked by the frequent occurrence of ventral-intercalary branches.

The remaining *Plagiochila* subgen. *Pleurochila* was erected for the only species of the Plagiochilaceae with a plicate perianth, *P. pleurata* (Fig. 4). The putative sister taxon, *P. fruticella* (Inoue 1984), has a smooth perianth and - in contrast to *P. pleurata* - frequent terminal branching. Morphologically, both species are linked by the occurrence of strongly protruding, spherical papillae (Inoue and Schuster 1971) whereas species of subgen. *Plagiochila* have a smooth cuticle or low papillae (Heinrichs 2002). *Plagiochila pleurata* and *P. fruticella* are not only morphologically well separated from the remainder of *Plagiochila* but also genetically distinct (Figs. 1, 2). Hence, they are here excluded from *Plagiochila* and transferred to the new genus *Proskauera*, representing the earliest diverging lineage of Plagiochilaceae.

Morphological circumscription of most clades of subgen. *Plagiochila* has already been discussed in previous studies (Groth et al. 2003, 2004b; Heinrichs 2002; Heinrichs et al. 2005b). Extension of the taxon sampling leads to the identification of additional clades. Molecular data now give evidence as to the systematic position of the rare Bolivian endemic *P. validissima* Steph., which was tentatively placed in sect. *Arrectae* by Heinrichs (2002), based on morphological similarities but placed near the southern South American *P. dusenii* Steph. by Anton et al. (2000), based on secondary metabolite composition. The southern South American *Plagiochila dusenii* and *P. validissima* are morphologically similar to sect. *Arrectae* in sporophyte characters, leaf shape and leaf cell pattern but differ by the occurrence of paraphyllia and papillose oil bodies. *Plagiochila acanthocaulis* also has paraphyllia but is nested within sect. *Durae*.

Exclusion of *Plagiochila* subgen. *Pleurochila* from this genus leads to an infrageneric subdivision at the section level only. Several robust multisectional lineages (i. e. *Plagiochila* clades A, B, C) are recognized within *Plagiochila*. However, we hesitate to establish new subgenera as until morphological synapomorphies are available for the corresponding lineages (see also Groth et al. 2004b).

Distribution of sectional clades of Plagiochilaceae

Several small genera of the cosmopolitan Plagiochilaceae form a grade at the base of

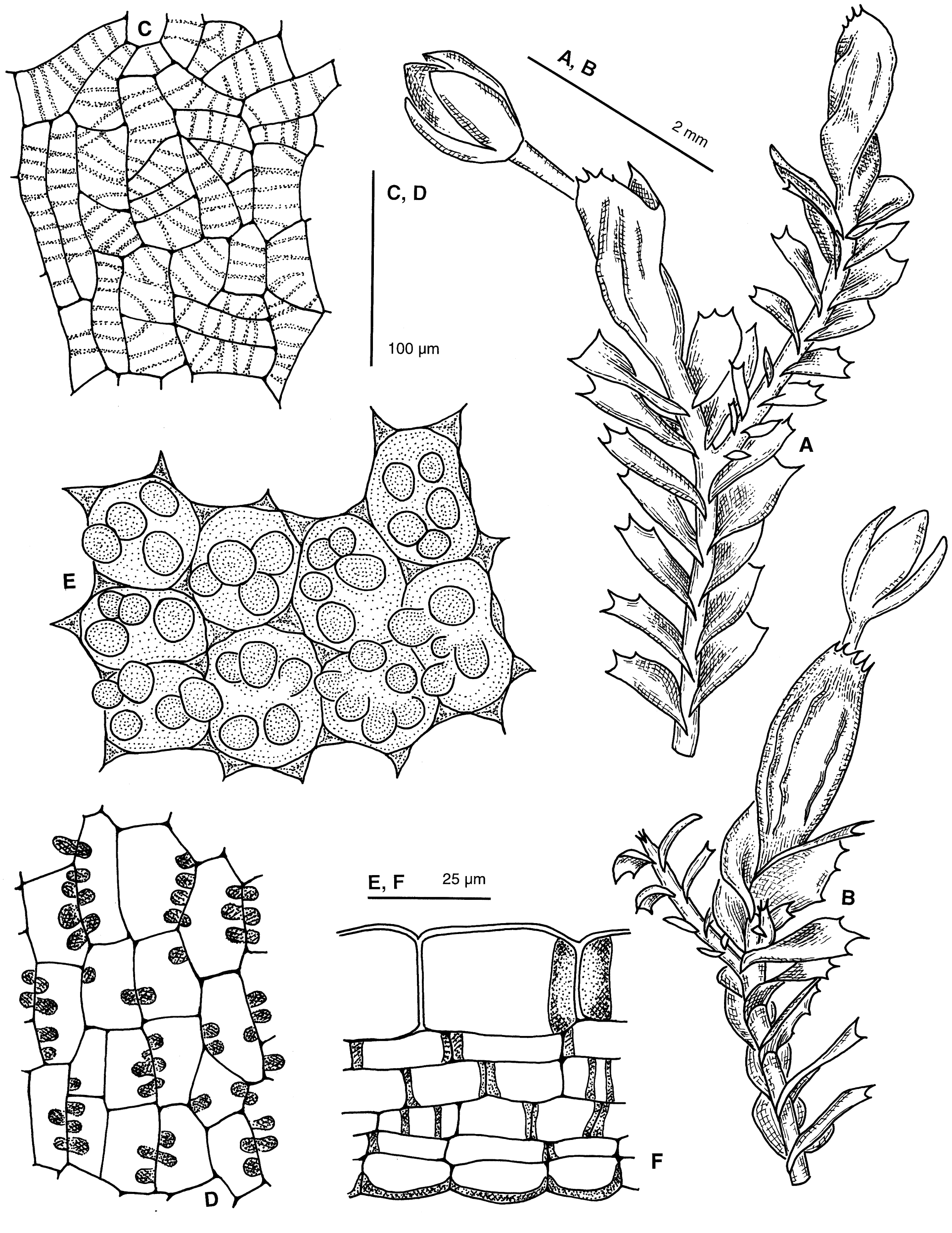

Fig. 4. *Proskauera pleurata* (Hook.f. & Taylor) Heinrichs & J.J.Engel: **A**, **B** shoots with sporophyte; **C** innermost layer of capsule wall, surface view; **D** epidermal layer of capsule wall, surface view; **E** dorsal leaf surface with papillae; **F** cross section of capsule wall [all from *Schäfer-Verwimp & Verwimp 14071* (GOET)]

the family (Figs. 1, 2). *Proskauera*, the putative sister to all other extant Plagiochilaceae, occurs in Australia and New Zealand. A second Plagiochilaceae clade includes the genera *Plagiochilion*, *Chiastocaulon*, and *Pedinophyllum* with stands in Australasia, Asia, and the holarctic (Groth and Heinrichs 2003, Heinrichs et al. 2004c). Subgeneric groups in *Plagiochila* continue to each have a restricted distribution: None of the sectional clades identified so far covers the complete range (Fig. 1). In contrast, a tendency becomes apparent that most sections have their centre of diversity in one to three main regions

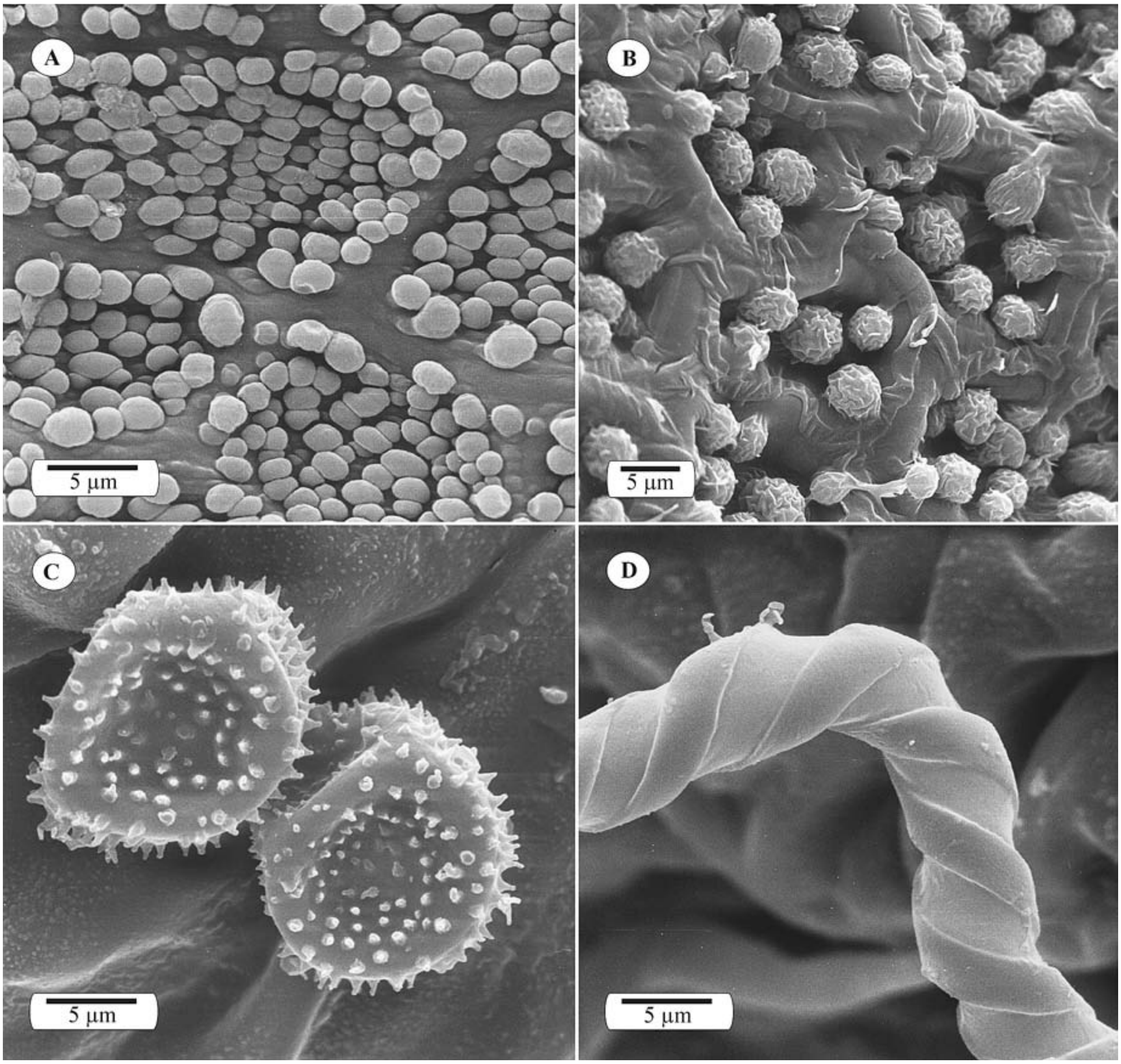

Fig. 5. SEM micrographs of *Proskauera fruticella* (Hook.f. & Taylor) Heinrichs & J.J.Engel (**A**) and *Proskauera pleurata* (Hook.f. & Taylor) Heinrichs & J.J.Engel (**B**–**D**): **A**, **B** dorsal leaf surface with spherical papillae; **C** spores; **D** part of elater [A from *Engel & von Konrat 23943* (GOET)]

populated by this genus. Early diverging lineages feature an accumulation of species with a southern distribution. Northern species are usually placed in derived clades.

Accumulation of southern species of *Plagiochila* in early diverging lineages is in accordance with Schuster's (1969, 1979) hypothesis of a Gondwanan origin. However, divergence time estimates are necessary to correlate *Plagiochila* with Gondwana.

Fossil record and diversification time estimates

Morphological homoplasy is common in spore plants and has been documented as a problem to recover natural relationships among taxa of ferns (Ranker et al. 2004), mosses (Vanderpoorten et al. 2002), and liverworts (Crandall-Stotler et al. 2005). *Plagiochila* is well known for its extensive morphological homoplasy at section level (e.g., Groth et al.

2004b, Heinrichs 2002); the homoplastic nature of most characters greatly hampers the assignment of extant species to a certain section based on morphology. Even more difficult if ever possible is the assignment of sterile gametophytic fossils to an extant lineage.

The scarce fossil record of Plagiochilaceae extends back to the early Eocene (Grolle and Heinrichs 2003). The amber fossil *Plagiochila groehnii* has recently been described as an element of the Eocene Baltic liverwort flora. This liverwort flora includes *Frullania* (subgen. *Dentatiloba*) *hamatosetacea* Grolle, *Metacalypogeia baltica* Grolle, *Nipponolejeunea subalpina* (Horik.) S.Hatt. and *Spruceanthus polonicus* Grolle (Grolle and Meister 2004) and thus shows affinities to the liverwort flora of present-day temperate Asia.

Plagiochila groehnii is morphologically similar to several members of the pantropical *P.* sect. *Cucullatae* (Grolle and Heinrichs 2003) with centre of diversity in Southeast Asia (Groth et al. 2003). The accumulation of Baltic Amber taxa with present-time centre of diversity in Asia could be taken as a further argument for a placement of the amber fossil within section *Cucullatae*. However, the sterile unbranched fragments of *P. groehnii* do not allow an unequivocal attribution to an extant taxon and could also represent atypically developed creeping shoots. Even the generic placement is not absolutely reliable as genera of Plagiochilaceae are partly defined by branching pattern or sex distribution.

Without much doubt, the Eocene fossil allows the assumption of a minimum age of Plagiochilaceae. Conservative assignment of the fossil at the base of Plagiochilaceae relates the Plagiochilaceae genera to Eocene/Oligocene times and the diversification of the majority of *Plagiochila* sections to the Miocene (Fig. 3). Assignment of the baltic amber fossil within *Plagiochila* sect. *Cucullatae* links diversification of most sectional clades of *Plagiochila* to Eocene/Oligocene times and the diversification of the genera of Plagiochilaceae to the Late Cretaceous and the Early Eocene. The latter scenario allows for a consideration of the breakup of Gondwana as the cause of some southern *Plagiochila* disjunctions. However, precise estimates of divergence times should await a dated phylogeny of Marchantiophyta which would allow definition of a maximum age of Jungermanniales and divergence time constraints for Plagiochilaceae.

Consideration of diversification scenarios

I. Out of the South. *Plagiochila* sect. *Alternantes* features an accumulation of Australasian and Andinopatagonian species, as well as a few neotropical and Southeast Asian species. Other southern taxa are placed sister to northern clades or are resolved in basal positions. The identification of predominately southern species in the *Plagiochila* sect. *Alternantes* clade is in accordance with Schuster's (1969) hypothesis of a Gondwanan origin of extant *Plagiochila*. The abundance of other Plagiochilaceae genera in Australasia (Groth et al. 2004b, Heinrichs et al. 2004c, Inoue 1986, Inoue and Schuster 1971) and southern South America (He-Nygrén and Piippo 2003) could be taken as a further argument for a southern origin of *Plagiochila*. However, several of the genera of Plagiochilaceae are also present in Asia and the holarctic. The occurrence of the tropical Asian species *P. nobilis* within *Alternantes* may also contradict a strict "out of the South" scenario.

II. Out of the North. Eocene Baltic amber fossils give unequivocal evidence for a European liverwort flora at 50 million years ago strongly differing from the recent flora (Grolle and Meister 2004). Species composition of this flora and climate reconstructions indicate that during the Eocene parts of the holarctic were covered by temperate or subtropical, humid forests (Kenrick and Davis 2004, Willis and McElwain 2002) which possibly harboured a rich liverwort flora. Cooling, especially by Pleistocene glaciations, led to massive extinction events and a subsequent extensive decline of this flora. However, it cannot be ruled out that elements of the early *Plagiochila* flora which are now present in the South once inhabited the Northern Hemisphere and disappeared there as a result of climatic changes. Presence of the Asian *Plagiochila nobilis* within the otherwise Gondwanan *P.* sect. *Alternantes* could be explained by fragmentation of an ancient cosmopolitan range. A northern origin of *Plagiochila* leads to the assumption of cosmopolitan ranges of many sections in early Tertiary times, alternatively of shifts of these sections to the South, and extensive extinction in the North.

III. More complex scenario. Tertiary climatic changes (Schuster 1979), the poor fossil record (Krassilov and Schuster 1984), and lack of a dated Jungermanniidae phylogeny hamper the reconstruction of liverwort biogeography. However, some tentative conclusions can be made with regard to Plagiochilaceae. Both experimental and molecular phylogenetic approaches indicate that many bryophytes are able to get over long distances by dispersal of spores (Feldberg et al. 2004, Heinrichs et al. 2005b, McDaniel and Shaw 2005, van Zanten 1977, van Zanten and Gradstein 1988). Even so, the majority of liverwort species including *Plagiochila* occurs in clear-cut ranges (Fig. 1) rather than showing stochastic distribution patterns. Obviously long distance dispersal is an exception and not a common occurrence in many species of bryophytes. There are several explanations for this phenomenon including low resistance of spores against drought, frost, and UV-radiation (van Zanten 1978, van Zanten and Gradstein 1988) as well as problems in establishing populations in a new environment, especially of dioicous taxa (Schuster 1979).

It can be expected that the spores of *Plagiochila* germinate into unisexual gametophytes (Schuster 1979). If long distance dispersal of *Plagiochila* spores takes place, the germinating single spore can only produce plants of a single sex. If at all, the arrival of another spore is purely a chance event in an indefinite time-frame. A species which is able to establish clonal populations by means of propagules or by caducous or fragmenting leaves has increasing chances of survival in a new environment. The ability to reproduce asexually increases the chance of long-term persistence of such populations and increases the likelihood of arrival nearby of a spore or asexual device of the opposite sex and the potential for sporophyte production. *Plagiochila* sects. *Arrectae*, *Rutilantes* and *Vagae* often reproduce vegetatively and include several examples of probable long distance dispersal (e.g. Groth et al. 2004a; Heinrichs et al. 2004a, b, 2005c). Long distance dispersal of *Plagiochila* species that do not have asexual reproductive devices was postulated for the Afro-American *P. boryana* (Heinrichs et al. 2005b) and the neotropical-Azorean *P. longispina* (Heinrichs et al. 2002).

In *Plagiochila*, there seems to be a correlation between disjunct species ranges and Pleistocene climate changes; species disjunctions are often observed between the Neotropics and Africa or the holarctic and between temperate or tropical Asia and the holarctic (Fig. 1). Pleistocene African vegetation has strongly been influenced by drought periods (e.g. Dupont et al. 2001, Hamilton 1982) which led to an extensive decline of humid forests. Holarctic glaciations resulted in major shifts of the local vegetation and extensive vanishing of the atlantic liverwort flora. During re-afforestation there were possibly numerous open niches that enhanced the survival chances of newcomers.

Molecular studies seem to rule out the possibility that *Plagiochila* ranges emerged exclusively by short distance dispersal. In fact these studies indicate that successful long distance dispersal occurs rarely in *Plagiochila*, especially in regions which face floral displacements as a result of climatic changes (Heinrichs et al. 2005b, Rycroft et al. 2002). In the light of these findings, a strict "out of the North" scenario with an assumption of earlier global ranges of southern clades and extensive extinction events seems rather unlikely. Possibly a modified "out of the South" scenario with extinction events in the North as the result of tertiary climate changes is better suited to explain the current section and species ranges of *Plagiochila*. This scenario also includes the postglacial recolonization of the holarctic mainly from the Neotropics and Asia (Groth et al. 2003, Heinrichs et al. 2004a, Renker et al. 2002) as a feasible explanation for many recent distribution patterns observed in *Plagiochila*. Southernmost species do not contribute to this recolonization. The centres of diversity of *Plagiochila* are mountainous regions of the humid tropics as well as temperate zones with an oceanic climate. The majority of species is obviously adapted to rather cool but nearly frost-free, humid environments and pushed back to the inner tropics in phases of aridification as was recently postulated for the fern genus *Asplenium* L. (Schneider et al. 2004).

Muñoz et al. (2004) provided evidence that southern Hemisphere disjunctions are correlated with dominating wind directions. Australasian-South American species disjunctions are unknown in Plagiochilaceae. However, the *Plagiochila* sects. *Durae* and *Alternantes* occur in both Australasia and southern South America. Although there is no evidence for rather recent long distance dispersal of Plagiochilaceae in the southernmost part of the Plagiochilaceae range, the above findings allow the possibility of ancient long distance dispersal with subsequent speciation as an explanation for the southern disjunctions at section level. An alternative explanation of the emergence of the range of southern sections would be short distance dispersal with subsequent range fragmentation and speciation (Schuster 1979). Molecular data provide growing evidence that no general patterns exist in bryophytes and scenarios differ on a case-by-case basis. McDaniel and Shaw (2003) provided evidence for a deep split between Australasian and South American *Pyrrhobryum* Mitt. whereas Quandt et al. (2001) found no sequence differences in southern South American and New Zealand *Weymouthia* Broth.

Australasia, the (sub)Antarctics and southern South America could play a critical role in the emergence of the extant *Plagiochila* diversity and harbour many putatively old elements of Plagiochilaceae (He-Nygrén and Piippo 2003, Inoue 1986, Inoue and Schuster 1971). The oldest clade identified in Plagiochilaceae to date, *Proskauera*, is restricted to New Zealand, Tasmania and one locality in Queensland (Inoue 1984, 1986; Inoue and Schuster 1971). The genetical isolation and the small size of *Proskauera* could be the result of extinction events which could be related to the glaciation of Antarctica. New Zealand was separated from Gondwana by sea-floor spreading in the late Cretaceous (McLoughlin 2001). Tertiary vegetation of New Zealand has been strongly influenced by an unstable climate and Oligocene erosion reducing the landmass to a scattered archipelago of low-lying islands (Stevens 1985). These findings lead many authors to assume that the recent flora is not a relict of Gondwanan times but at least to a great extent the result of long distance dispersal events (e.g. McGlone et al. 2001, Pole 1994, Winkworth et al. 2002). Very recently these hypotheses have been restricted to the New Zealand mountain flora (Winkworth et al. 2005). The origin of *Proskauera* predates the erosion phase and, hence, it could be a survivor of the old Gondwanan flora. Eventually the lineage disappeared from the New Zealand archipelago during phases of erosion or strong cooling but survived nearby, e.g. in Australia. The Australian flora has been strongly influenced by periods of aridification (Crisp et al. 2004) initiating in the Pliocene (Bowler 1982, Hill et al. 1999). The aridification of Australia could have caused an extensive decline of the local *Plagiochila* flora with an extant record of some 13 species (Inoue 1986), whereas New Zealand and Tasmania harbour some 26 species (Engel and Merrill 1999, Inoue and Schuster 1971). The extant Australian *Plagiochila* flora includes South East Asian elements [e.g. *P. bantamensis* (Reinw., Blume & Nees) Mont., *P. obtusa* Lindenb.] as well as New Zealand elements [e.g. *P. circinalis* (Lehm. & Lindenb.) Lindenb., *P. retrospectans* (Nees ex Sprengl.) Lindenb.]. The ranges of these species could be the result of rather recent diaspore distribution over medium distances; however, verification requires inclusion of multiple accessions from different parts of the species range.

Southern South American *Plagiochila* obviously plays a major role in the emergence of derived clades. Heinrichs et al. (2005c) proposed that *P.* sect. *Arrectae* derived from southern ancestors and diversified in the Neotropics after the rise of the Andes. Placement of the Baltic amber fossil at the base of the *Plagiochila* clade is in congruence with this scenario. If the fossil is placed within clade B, the tropical American *Arrectae* predate the last uplift event. If at some time this scenario will be identified as the more likely one, Miocene diversification of *Arrectae* in the (at that time subtropical) North and subsequent migration back to South America could become a likely scenario. A similar sequence of events has recently been proposed for the angiosperm genus *Gunnera* L. (Wanntorp and Wanntorp 2003); a northern origin of South American species has been demonstrated for, e.g. *Caltha* L. (Schuettpelz and Hoot 2004) or Burseraceae (Weeks et al. 2005).

Conclusions

Molecular data identify many southern species of Plagiochilaceae in old lineages and do not contradict the relationship between Plagiochilaceae and Gondwana. Southeast Asia represents the second phylogenetic centre of diversity of Plagiochilaceae. This region harbours a mixture of old elements and derived lineages. Southern South America and Australasia harbour many putatively old elements of *Plagiochila*.

The data related to Plagiochilaceae are in accordance with Schuster's (1969, 1979) hypotheses of a southern origin of this family. *Plagiochila*, however, could also have emerged from Southeast Asia. Molecular data provide evidence that the range of *Plagiochila* species and sections is not exclusively the result of short distance dispersal and subsequent extinction but a mixture of short distance dispersal, rare long distance dispersal events, and extinction/recolonization as a result of climate changes. Long distance dispersal of the dioecious genus *Plagiochila* occurs especially to regions subjected to climatic changes from arid or cold-arid to temperate or warm and humid.

Future prospects

Sequencing of multiple accessions of disjunct species is necessary to balance ancient versus recent long distance dispersal, especially between Australasia and Asia, two areas critical with regard to the emergence of Plagiochilaceae. Southern South America becomes highlighted as a promising region for old *Plagiochila* elements. Future studies should aim at a broader taxon sampling from this region. Resolving the diversification-time-frame of Jungermanniidae is a critical aspect of understanding the historical biogeography of derived clades such as Plagiochilaceae (Heinrichs et al. 2005a). Work to obtain these data is underway.

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Addresses of the authors: J. Heinrichs (e-mail: jheinri@uni-goettingen.de), M. Lindner, H. Groth, J. Hentschel, K. Feldberg, and H. Schneider, Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany; C. Renker, Department of Soil Ecology, UFZ Centre for Environmental Research Leipzig-Halle Ltd., Theodor-Lieser-Straße 4, 06120 Halle, Germany; J. J. Engel and M. von Konrat, Department of Botany, The Field Museum, Chicago, IL 60605-2496, USA; D. G. Long, Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, UK.