

Evidence for Rampant Homoplasy in the Phylogeny of the Epiphyllous Liverwort Genus *Cololejeunea* (Lejeuneaceae)

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Abstract—Rampant homoplasy can be a major challenge in the classification of land plants that have limited morphological differences and/or ecological diversity, such as liverworts and mosses. Here we present the first comprehensive molecular phylogeny of the derived liverwort genus *Cololejeunea* and its close relatives. We used three markers (*trnL-F*, *rbcL*, and nrITS) and 116 accessions representing the geographic range as well as the morphological diversity of this predominantly epiphyllous genus. The molecular data support three major lineages: *Colura*, *Myriocoleopsis*, and *Cololejeunea*. *Myriocoleopsis* species were resolved in a clade with *Cololejeunea minutissima*. *Aphanolejeunea* and *Chondriolejeunea* were both resolved as putative monophyletic groups, and nested in the *Cololejeunea* clade. *Cololejeunea angustiflora* was found to be sister to the clade comprising the remaining *Cololejeunea* species. Currently accepted subgenera of *Cololejeunea* were paraphyletic or polyphyletic. Six out of 30 species with multiple accessions were not supported as natural taxa. The current classifications of *Cololejeunea* have been influenced by frequent homoplasy of morphological characters and do not accurately reflect species relationships. A new classification for this genus is outlined. Our data did not provide evidence for ancient vicariance events where major clades and continents are associated, instead some evidence was recovered for recent intercontinental species range expansion.

Keywords—*Aphanolejeunea*, biogeography, chloroplast sequence data, *Chondriolejeunea*, molecular phylogeny, *Myriocoleopsis*.

Homoplasy caused by convergent evolution due to adaptation to similar environmental conditions and/or developmental constraints has been recovered numerous times across the tree of life (e.g. Wake 1991; Wake et al. 2011). Thus, it is not surprising that evidence of homoplasy has been found in many groups of land plants, especially in lineages associated with unique life strategies, such as the predominantly epiphytic grammitid ferns (Ranker et al. 2004) and various groups of aquatic plants (Barrett and Graham 1997; Tanaka et al. 1997). Evidence for frequent homoplasy in gametophyte morphology was documented as a major problem in the classification of derived liverwort lineages in which species richness contrasted with limited morphological complexity and conservatism of niche preferences (Heinrichs et al. 2005a; Heinrichs 2006; Heslewood and Brown 2007; Hentschel et al. 2007, 2009; Feldberg et al. 2010; Devos et al. 2011; Dong et al. 2012; Heinrichs et al. 2012a). In the present study, we tested the hypothesis of rampant homoplasy in the species-rich genus *Cololejeunea* (Spruce) Schiffn.

Cololejeunea, with more than 400 published binomials (ELPT report: <http://www.early-land-plants-today.org/Home>), is arguably among the most species-rich genera of liverworts, representing a derived lineage in Lejeuneaceae (Wilson et al. 2007a). These usually small sized liverworts grow preferably in extreme habitats, such as on the surface of living leaves [= epiphyllous], on twigs [= ramicolous], or in running water [= rheophyllous] (Gradstein et al. 2003).

The currently accepted generic concept of *Cololejeunea* is based on its incubous foliation, leaves consisting of a dorsal lobe and a ventral lobule, *Lejeunea*-type branching, lack of underleaves, and transverse section of stem comprising of 5(–8) cortical cells and 1 medullary cell (Benedix 1953; Zhu

and So 2001; Asthana and Srivastava 2003). Historically, more than twenty subgenera have been proposed for this genus, although most recent studies recognized eight subgenera: *Aphanolejeunea* (A. Evans) Benedix, *Leptocolea* (Spruce) Schiffner, *Taeniolejeunea* (Zwick.) Benedix, *Pedinolejeunea* Benedix ex Mizutani, *Cololejeunea*, *Metzgeriopsis* (K. L. Goebel) Pócs, *Chlorolejeunea* Benedix, and *Cryptolejeunea* Benedix (Benedix 1953; Mizutani 1961; Zhu and So 2001; Pócs and Piippo 2012). Some controversial arguments have been raised about the inclusion of several morphological delimited groups within *Cololejeunea* such as *Aphanolejeunea*, *Metzgeriopsis*, and *Chondriolejeunea* (Benedix) Kis & Pócs. These taxa had been treated as separate genera based on morphological distinctiveness, e.g. *Aphanolejeunea*-type branches in *Aphanolejeunea*, thalloid sterile gametophyte in *Metzgeriopsis*, and presence of underleaves in *Chondriolejeunea*. However, the independent generic status of these genera was rejected in context of their shared morphological similarity with *Cololejeunea*. Recent molecular phylogenetic studies recovered evidence to support inclusion of *Aphanolejeunea* and *Metzgeriopsis* within a wide concept of *Cololejeunea* (Ahonen 2004; Heinrichs et al. 2005b; Gradstein et al. 2006; Wilson et al. 2007a), even though few samples were included in these studies. Thus, we assumed that the ongoing debates about the status of putative segregates and the infrageneric classification may be at least partly caused by the interpretation of natural relationships based on morphology alone.

The abundance of homoplasy in morphological characters is arguably one of the main factors for problems related to the current interpretation of species relationships (Wake 1991). We hypothesized that homoplasy often occurs in the morphological characters of *Cololejeunea* given the small size of

this group and recovered frequency of parallel evolution of phenotype in extreme habitats. DNA sequence data has been shown to reveal the natural classification of lineages in which homoplasy misleads efforts based on morphology only (e.g. Endress 2002; Schneider et al. 2009). In light of previous molecular studies on Lejeuneaceae (Ahonen et al. 2003; Gradstein et al. 2003; Groth-Malonek et al. 2004; Wilson et al. 2004, 2007a, b; Hartmann et al. 2006; Heinrichs et al. 2009a, 2012b, c; Renner et al. 2011; Sukkharak et al. 2011; Dong et al. 2012), this study was designed to reconstruct the phylogeny of *Cololejeunea* by using two chloroplast genome regions (*trnL-F*, *rbcL*) and one nuclear genome region (nrITS). Our sampling was designed to represent not only the morphological variation, especially of putatively taxonomic informative characters, but also the geographic range of the genus. In addition, we sampled the representatives of all putative segregates, e.g. *Aphanolejeunea*, *Chondriolejeunea*, and *Myriocoleopsis* Schiffner as well as the putative sister genus *Colura* (Dumort.) Dumort. The recovered phylogeny was employed to address the following questions: 1) monophyly or paraphyly of previously proposed taxonomic units respectively, such as segregated genera and subgenera; 2) evidence for rampant homoplasy in the evolution of morphological characters among derived Lejeuneaceae.

MATERIALS AND METHODS

Taxon Sampling and Outgroup Taxa Selection—We sampled a total of 128 accessions representing 80 species for this study. Ingroup species were selected to represent the morphological variation, proposed classifications, and geographic distribution of *Cololejeunea* and its close relatives. The sampling of *Cololejeunea* (116 accessions representing 68 species) was constrained by the availability of material suitable for DNA studies. One species of *Drepanolejeunea*, two of *Diplasiolejeunea*, three of *Colura*, and two of *Myriocoleopsis* were included as ingroup species based on previous work by Wilson et al. (2007b). Four species of *Lejeunea* Lib. were selected as outgroup species. Major challenges to this project were the rather small size of specimens and the fact that often several taxa co-occurred on the surface of the same leaf. Thus, particular care was taken to separate gametophytes for DNA extraction from specimens. Identification of specimens was checked before and after DNA analyses.

DNA Extraction and PCR—Genomic DNA was extracted either from silica gel dried gametophytes or herbarium specimens that were collected within the last 20 yr. Two extraction methods were applied. The DNA of the majority of specimens was extracted using a modified CTAB protocol (Doyle and Doyle 1987), while DNeasy plant mini kits (Qiagen, Hilden, Germany) was employed for a few specimens. Two regions of the chloroplast genome, the *rbcL* gene and the non-coding *trnL-F* region, and one region of the nuclear genome, the ribosomal nrITS region, were amplified separately using the following primers: *rbcL* (Wilson et al. 2004; Gradstein et al. 2006), *trnL-F* (Taberlet et al. 1991), and nrITS (Hartmann et al. 2006). The PCR was performed in a total of 25 µl reaction, containing one unit Taq-DNA-polymerase (Bioline, London, U. K.), 2.5 µl Taq Polymerase reaction buffer, 1.5 µl MgCl₂ (50 mM) (Bioline), 0.5 µl dNTPs (10 mM) (Bioline), 1 µl each of 10 µM forward and reverse primer, and 1 µl template DNA (10–25 µg). The PCR amplification was carried out using the following program: 4:00 mins initial denaturation at 94°C; followed by 30 cycles of 1:00 min denaturation at 94°C, 50 sec annealing at 50–56°C, 1:30 mins elongation at 72°C; and a final extension step at 72°C for 7 mins. Bidirectional sequences were generated on an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, California) using the BigDye biochemistry and the manufacturer's suggested protocols. All three markers were obtained for the 128 accessions investigated in this study. Voucher details and GenBank accession numbers are listed in Appendix 1. Additional samples with one or two regions were included in the initial analyses, but were excluded from the final analyses to avoid ambiguity introduced by incomplete datasets.

Phylogenetic Analysis—All sequence data were edited and assembled in Sequencher 4.8 (GeneCodes, Ann Arbor, Michigan), and manually aligned using Bioedit 7.1.3.0 (available from <http://www.mbio.ncsu.edu/bioedit/bioedit.html>) and MacClade 4.0 (available from [\[macclade.org\]\(http://macclade.org\)\). Ambiguous positions were identified visually and excluded from alignments used in subsequent analyses.](http://</p>
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Evidence for congruent signals among the three marker regions was explored by visually comparing two bootstrap consensus trees that were generated by independent maximum parsimony analyses of chloroplast regions (*trnL-F*, *rbcL*) and the nuclear region (nrITS). Finally, a combined dataset of 128 accessions was employed for phylogenetic investigations as no evidence for topological heterogeneity was recovered.

Maximum parsimony analyses (MP) were conducted with PAUP* 4.0 (Swofford 2002) using the following methods: heuristic search mode, 1,000 random-addition-sequence replicates (RAS), tree bisection-reconnection (TBR) branch swapping, with ten trees held at each step. All characters were treated as equally weighted and unordered. Gaps were treated as missing characters. Trees were summarized as a strict consensus tree if more than one MP tree was found. Bootstrap values (MP-BS) were generated using heuristic searches with 1,000 simple stepwise addition replicates and TBR branch swapping, each with ten RAS.

Models for parameters based phylogenetic analyses were selected using MrMtgui 1.01 (available from <http://www.genedrift.org/mtgui.php>) which is a cross-platform interface for Modeltest 3.7 (Posada and Crandall 1998) and PAUP* 4.0. The appropriate DNA substitution model and parameters were selected using the hierarchical likelihood ratio test (hLRT) and Akaike Information Criterion (AIC) as implemented in Modeltest. Maximum likelihood analyses (ML) were performed in PhyML 3.0 (Guindon and Gascuel 2003) as implemented via a plugin into Geneious 5.5.6 (available from <http://www.geneious.com>) with the substitution model and number of parameters (GTR + gamma + invariable sites) selected but with parameter values inferred simultaneously with the tree searches. Bootstrap values (ML-BS) for ML analyses were obtained via 200 bootstrap replicates in PhyML using the same model and parameters as in the optimal tree search.

Bayesian inference of phylogeny (BI) was performed using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). Two kinds of BI were performed: one with a single model for the combined alignment and a second one with a partitioning into chloroplast regions (*trnL-F*, *rbcL*) and nuclear region (nrITS). Each Bayesian search was carried out with the GTR model implemented, parameter values inferred simultaneously with tree searcher, runs starting with a random tree, unlinked rates, and four simultaneous Markov chains for ten million generations with sampling every 1,000th generation. The convergence of runs and estimation of burn-in phase were checked using Tracer v1.4.1 (available from <http://beast.bio.ed.ac.uk/Tracer>). Bayesian posterior probabilities (PP) were calculated for the majority consensus tree of all sampled trees after discarding the trees sampled within the burn-in phase. PP is given as PP-UP for the non-partitioned analyses and PP-PA for the partitioned analyses.

Inference of Morphological Characters—The phylogeny was used to evaluate published inter- and infrageneric classifications (Benedix 1953; Mizutani 1961). In particular, the criteria of monophyly and paraphyly were applied (Page and Holms 1998). In addition, eight morphological characters were plotted onto the obtained phylogenetic hypotheses using MP character reconstruction as implemented in Mesquite 2.74 (available from <http://mesquiteproject.org>; Table 1). The morphological characters were selected based on previous usage in classifications and completeness. These eight characters are: underleaves, branching type, vitta (a longitudinal stripe composed of elongate, often thick walled cells in the liverwort leaf), dorsal prostriction of leaf lobe cells (papillae and mammillae), hyaline cells of free leaf margin, sigmoid cells of free leaf margin, stem size, and position of hyaline papillae (tiny, thin-walled, secretory cells associated with leaf initial cells in liverworts). Information about these characters was obtained by the careful study of herbarium specimens and consideration of the literature (Benedix 1953; Mizutani 1961; Tixier 1979; 1985; Zhu and So 2001; Asthana and Srivastava 2003; Pócs 2012). These observations were used to obtain preliminary homology assessments that were articulated in character scoring schemes: either binary or multi-character states and with or without the order of character states. Phylogenetic uncertainty was taken into account by reconstructing ancestral states of each character over 100 trees. Homoplasy of these eight characters was inferred by calculating the homoplasy index (HI) and retention index (RI) for each character (Table 1). The preliminary homology assessments were critically evaluated in consideration of the phylogenetic results as well as discussion of these characters in previous studies (e.g. Gradstein et al. 2003).

RESULTS

Of a total 2,682 DNA base pairs, 1,547 were constant and 922 were parsimony informative. The MP analysis resulted in

TABLE 1. Character states, homoplasy, and retention index of each character calculated across the recovered tree topology. These characters were considered to be of taxonomic significance for the *Cololejeunea* classification according to Benedix (1953), Mizutani (1961), Tixier (1985), and Zhu and So (2001).

Character	Character states	Homoplasy index	Retention index
Underleaves	(0) lacking, (1) = present	0.00	1.0
Branching type	(0) <i>Lejeunea</i> -type, (1) exclusively or partly <i>Aphanolejeunea</i> -type	0.500	0.875
Vitta	(0) lacking, (1) = present	0.667	0.714
Dorsal protrusions	(0) lacking, (1) = present	0.900	0.757
Hyaline cells of free leaf margin	(0) lacking, (1) = present	0.837	0.808
Sigmoid cells of free leaf margin	(0) lacking, (1) = present	0.750	0.00
Stem size	(0) 5–8 cortical cells, (1) 9–20 cortical cells	0.500	0.00
Position of hyaline papillae	(0) distal or at peak of the apical tooth, (1) on the interior surface of the lobule (ental or displace), (2) proximal of apical tooth	0.913	0.677

1,212 equally parsimonious trees of a length of 5,693 steps (Fig. 1). A single most likely tree ($-\ln L = 36,701.166$) was found in the ML analysis (Fig. 1). BI analyses based on 9,001 trees obtained phylogenetic hypotheses with a mean likelihood of $-\ln L = 33,070.732$ for the un-partitioned and $-\ln L = 32,685.455$ for the partitioned model and identical topologies for both trees. Only one of them is shown (Fig. 2). The MP, ML, and BI analyses shared largely similar topologies (Figs. 1, 2).

Cololejeunea was resolved in a clade together with four other groups, *Aphanolejeunea*, *Chondriolejeunea*, *Colura*, and *Myriocoleopsis* (MP-BS = 99%, ML-BS = 100%, PP-UP = 1.0, PP-PA = 1.0). Within this clade, all phylogenetic analyses consistently identified three clades, defined as the *Colura* (CU), *Myriocoleopsis* (MY), and *Cololejeunea* (CO) clades. These clades were well supported in MP, ML, and BI analyses with the exception of the CO clade where ML-BS was less than 95% (Fig. 1). *Myriocoleopsis* was nested in a clade (MY) together with *Cololejeunea minutissima* (Sm.) Schiffn. The CU (*Colura*) clade was either sister to MY in BI analysis (PP-UP = 1.0, PP-PA = 1.0), or sister to the clade comprising MY and CO in ML analysis, or sister to both CO and MY in MP analysis (Fig. 1). We recognized several smaller clades in the CO clade, defined as A, B, C, and D clades. The first split of the CO clade resulted in two sister clades: one comprising three accessions of *Cololejeunea angustiflora* (Steph.) Mizut. (clade A), and the other one consisting of the remaining species of *Cololejeunea* (clades B–D). In ML and BI analyses, the clades B, C, and D formed a robust clade, sister to A although the relationships among clades B, C, and D were not fully resolved in MP and ML analyses (Fig. 1). The two segregates *Chondriolejeunea* and *Aphanolejeunea* were each resolved as monophyletic within clade D. Six sub-clades defined in D were recovered in all phylogenetic analyses and were labeled as clades D1–D6. In BI, each of the six clades received good support with the exception of D4 (Fig. 2). In MP, D1, D3, D4, and D5 were strongly supported (MP-BS \geq 95%; Fig. 1), while in ML analyses, bootstrap support above 95% was obtained for D1, D2, D4, and D5 (Fig. 1). Twenty-four out of thirty species with multiple accessions were supported as monophyletic.

The levels of homoplasy were detected by calculating the HI and RI of eight selected morphological characters across the recovered phylogeny (Table 1). Among these eight characters, the position of hyaline papillae, dorsal protrusions of leaf lobe cells, and leaf margin bordered by hyaline cells each exhibited high levels of homoplasy (HI = 0.917, RI = 0.662;

HI = 0.900, RI = 0.771; HI = 0.837, RI = 0.792, respectively) (Table 1), whereas the status of vitta and leaf margin bordered by sigmoid cells showed moderate values (HI = 0.667, RI = 0.714; HI = 0.750, RI = 0.200, respectively).

DISCUSSION

Implications for Genus Classification and Previously Segregate Genera—The results of this study provide new evidence concerning the generic and subgeneric classification of *Cololejeuneoid* liverworts such as the rejection of the generic status of *Aphanolejeunea* and *Chondriolejeunea*, as these are both nested within *Cololejeunea*. The recovered phylogeny is inconsistent with their treatment as independent genera as suggested by some authors based on the interpretation of morphological characters (Evans 1911; Thiers 1982; Kis and Pócs 2001). Conflicting arguments about the status of *Aphanolejeunea* focused on the interpretation of its *Aphanolejeunea*-type branching and dimorphic leaves that were used by some authors to distinguish the taxon from *Cololejeunea* (Evans 1938; Thiers 1982; Zhu and So 2001). However, variation of these characters across species assigned to *Aphanolejeunea* and the occurrence of transitional forms provided insufficient support for recognition of the genus (Benedix 1953; Tixier 1979; Asthana and Srivastava 2003; Pócs and Bernecker 2009). *Aphanolejeunea*-type branching also occurs in several species of *Cololejeunea* that were not considered to belong to *Aphanolejeunea* (Pócs and Piippo 2012). Several representatives of *Aphanolejeunea* have been included in recent molecular phylogenetic studies (Ahonen 2004; Heinrichs et al. 2005b; Gradstein et al. 2006; Wilson et al. 2007b) as well as in our present study. All phylogenetic studies are consistent with the inclusion of *Aphanolejeunea* within *Cololejeunea* (Pócs and Bernecker 2009) and the alternative hypothesis of recognition at the genus level is rejected to avoid the introduction of a paraphyletic *Cololejeunea*. Although all accessions of *Aphanolejeunea* sampled in this study were resolved in an exclusive clade nested in the CO clade (Fig. 1), we are not certain that *Aphanolejeunea* is monophyletic because of limited sampling. Incorporation of several critical taxa assigned to *Aphanolejeunea* in future studies, e.g. *A. diaphana* A. Evans, might provide more insight into the genetic divergence of this group and the developmental evolution of *Aphanolejeunea*-type branching. Given the trend of frequent homoplasy, multiple origins of the *Aphanolejeunea*-type branching are expected, as confirmed already with the occasional occurrence of this type of

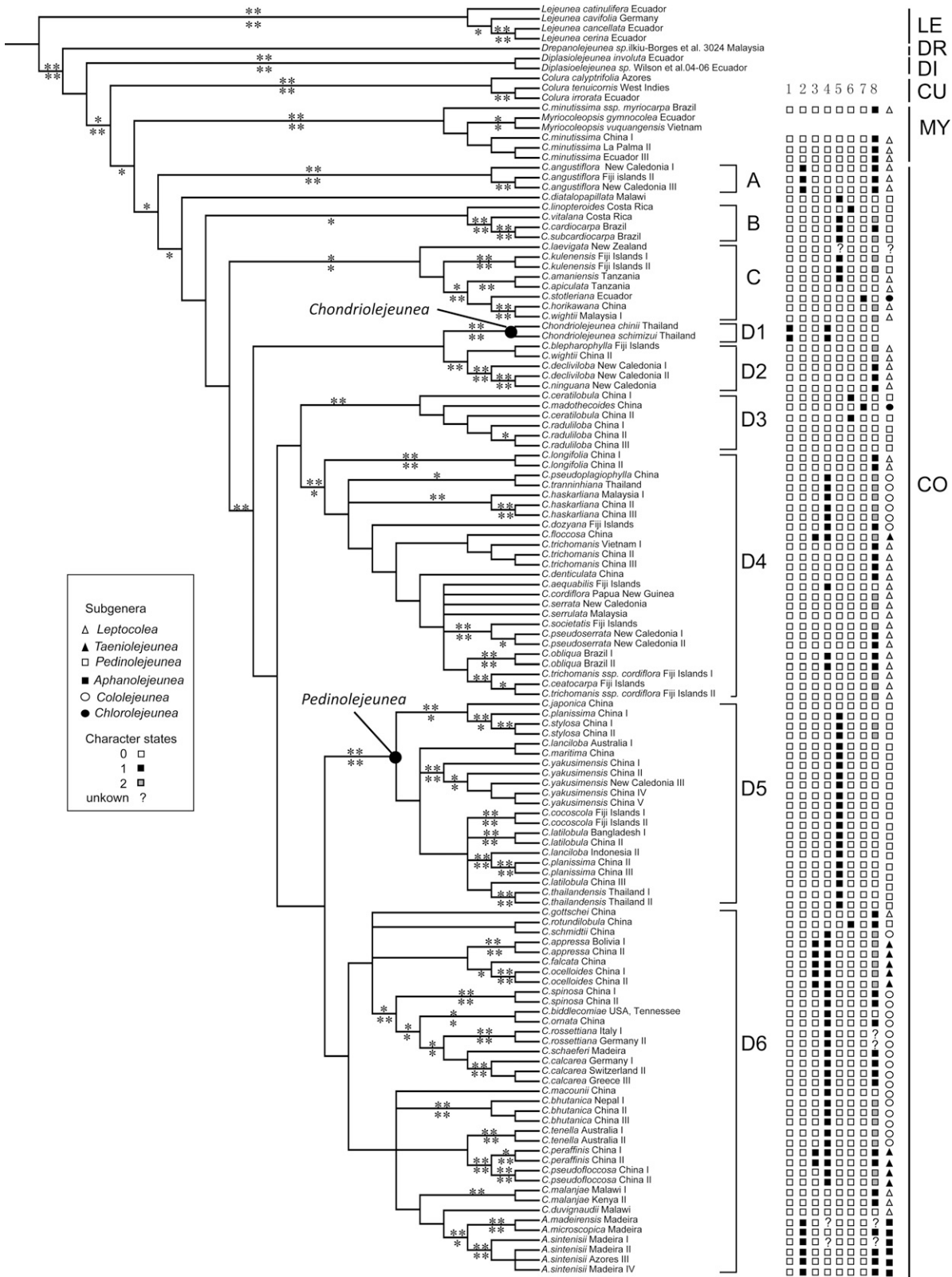


FIG. 1. Strict consensus of 1,212 equally parsimonious trees obtained by a maximum parsimony analysis of the combined dataset. Only bootstrap values $\geq 95\%$ (** = 100%, * = 95–99%) are plotted on the strict consensus tree: above branches = bootstrap values obtained by maximum parsimony analyses; below branches = bootstrap values obtained by maximum likelihood analyses. Columns to right (from left to right): clades recognized within *Cololejeunea*, abbreviations as given in the text; characters 1–8 as described below and in the text, open squares = 0, black squares = 1, ? = unknown; subgenera assignments as in the classification of *Cololejeunea* (names given in text box on the lower left corner of the figure); current genus classification abbreviated as follows: LE = *Lejeunea*, DR = *Drepanolejeunea*, DI = *Diplasiolejeunea*, CU = *Colura*, MY = *Myriocoleopsis*, CO = *Cololejeunea*. Subgenera of each taxon were assigned according to Benedix (1953) and Mizutani (1961). Characters are: 1: underleaves; 2: branching-type; 3: vita; 4: dorsal prostruction of leaf lobe cells; 5: hyaline cells of free leaf margin; 6: sigmoid cells of free leaf margin; 7: stem size; 8: postion of hyaline papillae. Character states are shown in Table 1. Subgeneric assignments for two clades with black dots on nodes, *Pedinolejeunea* and *Chondriolejeunea* are indicated in phylogeny.

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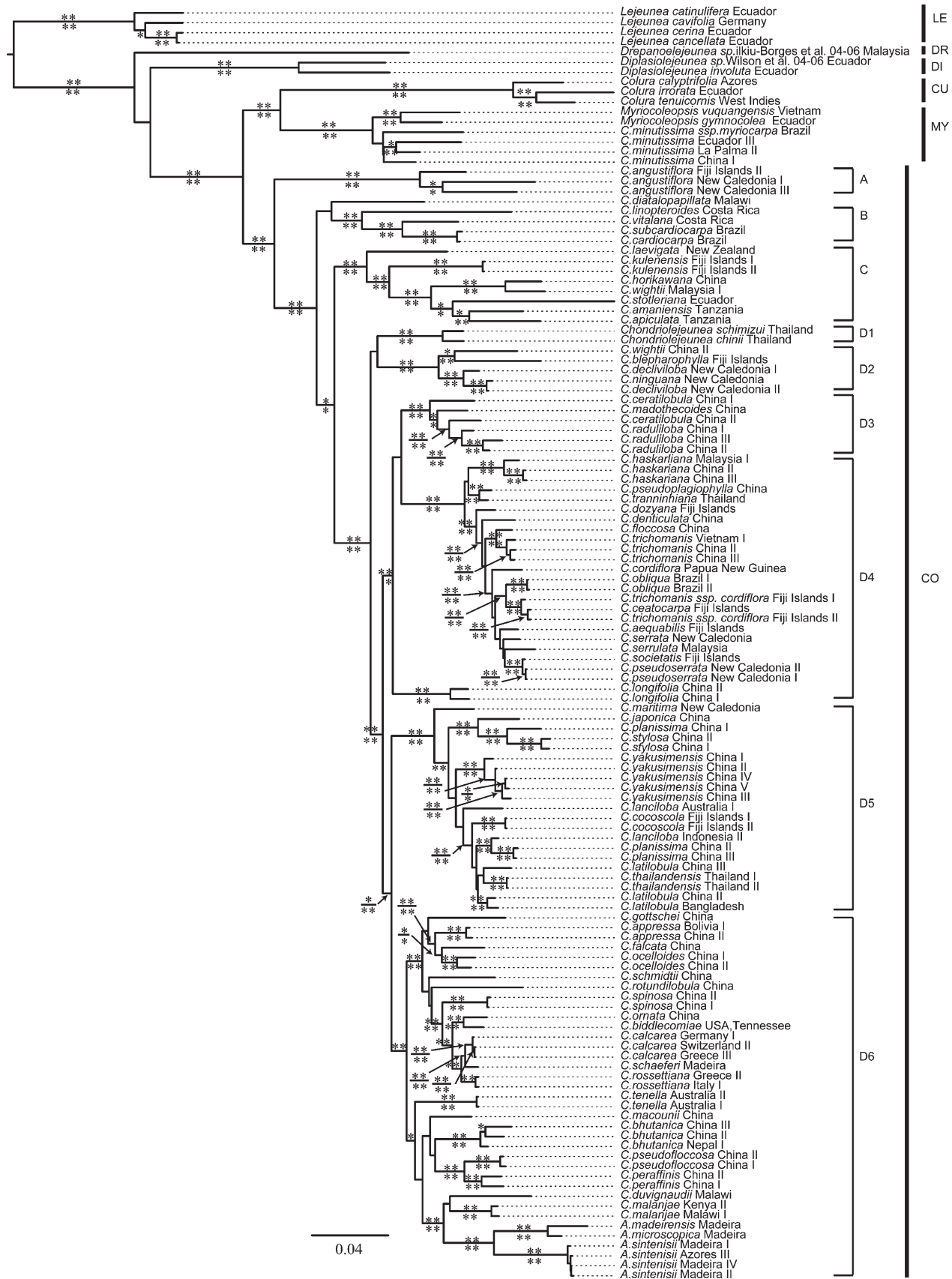


FIG. 2. Bayesian majority consensus tree calculated from the results of a Bayesian analyses of the combined dataset with a partition of cpDNA and nrDNA. The consensus tree is based on the trees recovered in 9,000,000 generations that were assembled from the results of MrBayes analyses with exclusion of the burn-in phase determined as 1,000,000 generations. Posterior Support values (PS) ≥ 0.95 are indicated by ** = 1.00 and by * = 0.95–0.99. PS generated with separated models for cpDNA and nrDNA partitions are given above branches and single model for all regions below branches. Abbreviations: LE = *Lejeunea*, DR = *Drepanolejeunea*, DI = *Diplasiolejeunea*, CU = *Colura*, MY = *Myriocoleopsis*, CO = *Cololejeunea*.

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branching in several species, such as *Cololejeunea erostrata* (Herzog) Bernecker & Pócs, *C. koponenii* (Pócs) Pócs, and *C. angustiflora* (Steph.) Mizut. The above case illustrates the problem of defining groups based on morphological distinctiveness without consideration of the morphology of related taxa.

Recently, *Chondriolejeunea* was segregated as a genus distinct from *Cololejeunea* based on an anatomical study (Kis and Pócs 2001), which provided arguments interpreting gametophytic appendages as homologous to underleaves rather than to lobule appendages called styli. However, this treatment for *Chondriolejeunea* was not supported by molecular data, as *Chondriolejeunea* species were nested in the *Cololejeunea* clade (Fig. 1). Thus, we suggested that the evolution of the stylus in *Chondriolejeunea* requires additional study to determine if the absence of underleaves is a key feature of *Cololejeunea* as is currently hypothesized. Evolutionary reversals or the invention of new unusual structures can create conflicting arguments concerning the interpretation of natural relationships based on morphology (e.g. Endress 2002; Schneider et al. 2009).

In contrast to the two previously discussed putative segregates, we found evidence to confirm the status of *Myriocoleopsis* as an independent genus. The rheophilic genus *Myriocoleopsis* was originally erected by Schiffner (1944) for *M. puigarrii* Schiffn. Currently, three species are recognized in *Myriocoleopsis* (Reiner-Drehwald and Gradstein 1997; Kis and Pócs 2001). *Myriocoleopsis* was established based on the occurrence of erect leafy axes in the gametophyte, gynoecea arranged in compound cymes, and long androecial spikes. However, the status of *Myriocoleopsis* as an independent genus was questioned in context of similarities in oil-bodies and sporophyte morphology with *Cololejeunea* (Gradstein and Vital 1975; Reiner-Drehwald and Gradstein 1995). The affinity of *Myriocoleopsis* and *Cololejeunea* was first proposed based on a molecular systematic study by Wilson et al. (2007b), in which *Myriocoleopsis* together with one *Cololejeunea* species formed a robust clade outside *Cololejeunea*. This species, *C. vuquangensis* Pócs & Ninh, was subsequently transferred to *Myriocoleopsis* (Pócs 2010) based on observed morphological similarities and phylogenetic evidence. In this study, accessions of another *Cololejeunea* species, *C. minutissima* (including both the typical subspecies and *C. m.* subsp. *myriocarpa*), were resolved outside of the CO clade and instead in a robust clade with *Myriocoleopsis* (Fig. 1). The affinities of these taxa are also supported by morphological similarities, such as lobe and lobule form, stem anatomy, and the presence of inflated 5-keeled perianths (Reiner-Drehwald and Gradstein 1995). However, there are differences between *C. minutissima* and *Myriocoleopsis* as the former has shorter androecial spikes, gynoecea with only a single innovation (rarely two), and creeping growth, a character considered an adaptation to its epiphytic habitat. A new recognition of the biological unit *C. minutissima* is required.

The generic concept of *Cololejeunea* was well resolved in our molecular phylogeny following the exclusion of *Myriocoleopsis* and inclusion of *Aphanolejeunea* and *Chondriolejeunea*, though *C. angustiflora* was not resolved in CO in the ML analysis (Figs. 1, 2). Circumscription of *C. angustiflora* was considered a challenge because of its variable morphology (Zhu and So 2002). This variability was likely responsible for the numerous nomenclatural changes of this taxon since it was introduced by Stephani in 1914 (see Benedix 1953; Mizutani 1966; Pócs 1994; Zhu and So 2001). The phylogenetic relation-

ship between *C. angustiflora* and the remaining *Cololejeunea* species recovered in the present study corresponds to the variability of morphological characters that is present in this species which displays a deviant combination of character states, such as the occurrence of both *Lejeunea*-type and *Aphanolejeunea*-type branching and obovate to cylindrical, keeled perianths (Zhu and So 2002). The segregation of *C. angustiflora* from other lineages in CO is intriguing in the context of the morphological variability and phylogeny of this taxon.

Our results solved several issues about the generic concept of *Cololejeunea*. However, they have an even bigger impact on infrageneric classification of this genus. Five currently accepted subgenera of *Cololejeunea* were resolved as paraphyletic or polyphyletic in the present study, although each was well characterized by a suite of morphological characters (Fig. 1). Comparable results have also been reported in other species-rich genera of liverworts, such as *Frullania* Raddi (Hentschel et al. 2009), *Radula* Dumort. (Devos et al. 2011), and *Scapania* (Dumort.) Dumort. (Heinrichs et al. 2012a). Rampant homoplasy resulting from convergent or parallel evolution has been identified as the main reason for such phenomena (Ranker et al. 2004). Several new subgenera should be introduced for newly detected clades, while two old subgeneric names can be conserved: *Cololejeunea* subgen. *Chondriolejeunea* Benedix for D1 and *C.* subgen. *Pedinolejeunea* Benedix ex Mizut. for D5 (Fig. 1). Future taxonomic studies, with an enhanced taxon sampling is necessary to formalize these entities and determine their morphologies.

Implication for Species Classification—Six of thirty species with multiple accessions were not recovered as monophyletic in our study, including several species with morphological variation such as *Cololejeunea planissima* (Mitt.) Abeyw. and *C. lanciloba* Steph. This general trend is consistent with other studies on leafy liverworts: a vast number of morphologically recognized species were resolved as monophyletic based on molecular data but a considerable fraction of species required redefinition (e.g. Heinrichs et al. 2009b; Renner et al. 2011). The later result was interpreted as an underestimation of species numbers caused by cryptic diversity or from overestimation caused by intra-specific morphological variation and plasticity (e.g. Feldberg et al. 2004; Heinrichs et al. 2009b, 2010, 2011). Our results support the need to carry out exhaustive investigations on species complexes exhibiting high morphological and genetic diversity for exploration of underlying evolutionary processes and obtaining robust species delineations. Examples included in this study are the *Cololejeunea serrulata* complex and the *C. lanciloba* complex that both were resolved as monophyletic groups with an uncertain number of species.

Evolution of Morphological Features—Several characters commonly used to circumscribe subgenera of *Cololejeunea* were recovered as homoplastic: vitta (HI = 0.667), dorsal protrusions of leaf lobe cells (HI = 0.900), the free lobe margin with hyaline cells (HI = 0.837) and/or sigmoid cells (HI = 0.750), and the position of hyaline papillae (HI = 0.917) (see Fig. 3). Such characters with a high level of convergent or parallel evolution provide little evidence to resolve the natural relationships of a given group (Hennig 1966; Wake 1991; Kleunen and Fischer 2005). The relatively low level of homoplasy in branching type and stem size (number of cells composing the stem) may reflect our limited taxonomic sampling and may change when further species are added to the

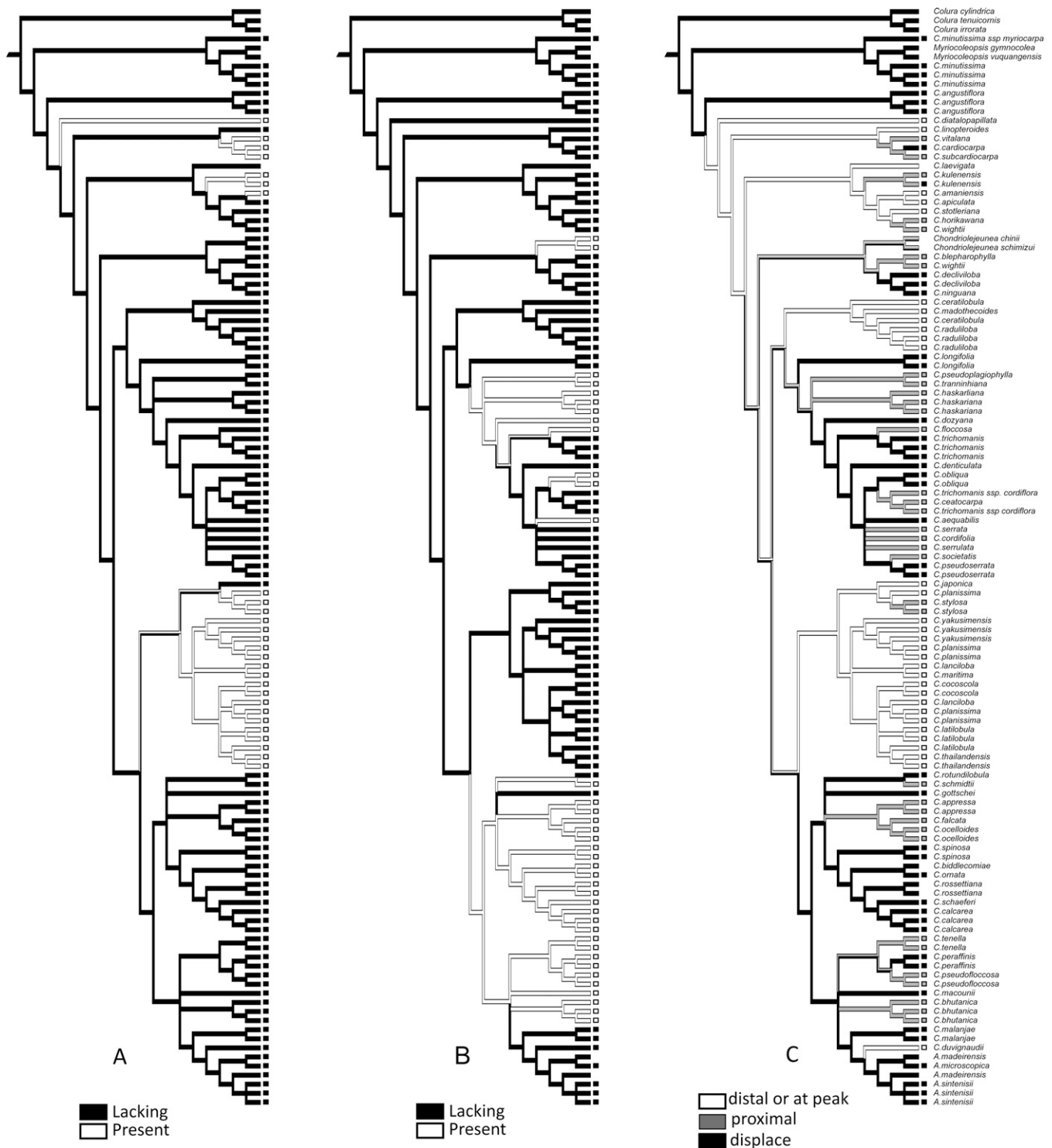


FIG. 3. Examples of characters exhibiting high level of homoplasy ($HI > 0.85$) mapped onto the strict consensus tree resulting from the heuristic maximum parsimony analysis of the combined one nuclear (nrITS) and two chloroplast regions (*trnL-F* and *rbcl*) excluding LE, DR, and DI clades. A = hyaline cells; B = dorsal protrusion; C = position of hyaline papillae.

dataset. The trend towards rampant homoplasy ($HI = 0.827$ for all characters) in *Cololejeunea* may be the result of the combination of limited developmental options in these rather small plants and/or ecological constraints such as the adaptation to extreme conditions such as epiphyllous or rheophilic habitats (Gradstein et al. 2003, 2011). A good example for ecological selection is derived from rheophilic liverworts, e.g. *C. madothecoides* (Steph.) Benedix, *C. stotteriana* Gradst. et al. as

well as those of *Myriocoleopsis* and *Myriocolea* Spruce—a former segregate of *Colura* (Heinrichs et al. 2012c), that often exhibit a rather unusual morphology consisting of creeping rhizomes, thick stems, and fertility as adaptations to habitats (Gradstein and Vital 1975; Gradstein et al. 2011).

Arguably, the most interesting feature is the evolution of underleaves (a third row of leaves found on the ventral surface of the stem) in some liverworts lineages. Number and

presence of underleaves were considered highly important taxonomic characters in Lejeuneaceae (Gradstein et al. 2003). The majority of genera in Lejeuneaceae have one underleaf per leaf pair. *Cololejeunea* and *Myriocoleopsis* are characterized by the absence of underleaves, whereas *Colura* and *Diplasiolejeunea* possess one underleaf per leaf. In the current study, *Colura* was resolved as sister either to *Myriocoleopsis* (BI; Fig. 2) or to the clade comprising *Cololejeunea* and *Myriocoleopsis* (MP and ML; Fig. 1). Hence, one underleaf per pair leaf could be the ancestral state of the common ancestor of *Cololejeunea*, *Myriocoleopsis*, and *Colura* (including *Myriocolea*; see Heinrichs et al. 2012c), but this requires further investigation with a more comprehensive sampling of *Colura* and *Siphonolejeunea* as well as *Drepanolejeunea* and *Diplasiolejeunea*. Furthermore, the interpretation of the underleaf-like structure of *Chondriolejeunea* is in question and could be the result of an evolutionary reversal, thus homologous to underleaves, or a gain of a new structure, the stylus. The hypothesis of evolutionary reversal is intriguing, as it would add a further example rejecting Dollo's law (Gould 1970; Collin and Miglietta 2008). The alternative hypothesis of re-evolution is also intriguing because inventions of new structures are rare events in the evolutionary history of plants (Ilgic et al. 2006). However, the invention of a new structure may involve simple processes such as translocation in the early stage of shoot ontogeny, like the translocation of the collar of leaf origin in the *Lejeunea*-type branches (Crandall 1969).

Biogeography—Recent studies supported the hypothesis of the frequent occurrence of wide distributions with or without disjunct ranges in liverwort species (e.g. Heinrichs et al. 2009a, b; Fuselier et al. 2011; Dong et al. 2012). These relatively large ranges may be the result of a combination of mechanisms supporting either long-distance dispersal and/or slow rates of molecular and morphological evolution following ancient vicariance events (Shaw 2001; Vanderpoorten and Shaw 2010). The global sampling of *Cololejeunea* in the present work did not allow for an exhaustive analysis of the biogeographical history of the lineage. Given the current evidence that divergent events of epiphyllous liverworts occurred in the Tertiary (Heinrichs et al. 2007; Wilson et al. 2007a), the intercontinental ranges of some *Cololejeunea* taxa are likely caused by long distance dispersal of spores or gemmae rather than by ancient vicariance (Zanten 1978; Zanten and Pócs 1981; Zanten and Gradstein 1988; Muñoz et al. 2004). Comparable results have been reported in other genera of leafy liverworts (Heinrichs et al. 2005a, 2011, 2012a; Feldberg et al. 2007, 2010; Devos and Vanderpoorten 2009; Hentschel et al. 2009). The association of wide distribution ranges and breeding systems has been discussed in previous studies (Yeates 1908; Frahm 2008; Heinrichs et al. 2009a; Hock et al. 2009), in which spores were considered to play an important role in long distance dispersal, although the significance of asexual propagules can't be ruled out (Pohjamo et al. 2006). This hypothesis is consistent with the observation in the current study that several monoecious *Cololejeunea* species, e.g. *C. angustiflora*, possess intercontinental ranges, a distributional pattern not found in dioecious *Cololejeunea* species as a result of restricted distributions or sparse sampling.

The absence of clearly defined geographical ranges may coincide with the preference for epiphyllous growth. Adopting a high dispersal capacity may be part of the strategy required to successfully colonize these habitats. Such adaptation is expected given the short-lived nature of this

habitat and its island-like distribution (Hock et al. 2009). Both spatial and temporal distributions may result in a selection towards fast re-colonization.

Perspectives—Previous morphological studies have indicated that the unique characteristic of the *Tuyamaella-Cololejeunea* complex is the great variety of neotenic features involving heterochronic events (Gradstein et al. 2003). The primary neoteny and/or protonemal neoteny occurring in gametophytes of *Cololejeunea* taxon (including *Aphanolejeunea*, *Chondriolejeunea*, and *Metzgeriopsis*) (Gradstein et al. 2006) was presumed to be a development constraint in the ontogeny of this group, which limits morphological space and is probably the result of adaptation to ephemeral habitats. Such inherited limitations are hypothesized to increase the likelihood of homoplasy (Wake et al. 2011). This hypothesis is consistent with our conclusion that the rampant morphological homoplasy in this genus has hampered circumscription of infra-generic entities and several morphologically variable species. Thus, the recovered phylogeny will allow future studies to reconstruct the impact of ecological and developmental factors on the evolution of these liverworts especially in the context of species divergence in a highly restricted and competitive environment.

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APPENDIX 1. Names, origins, vouchers (herbarium), and GenBank accession numbers used for phylogenetic analyses in alphabetical order. GenBank accession numbers are listed in the following order: nrITS, *rbcl*, *trnL-F*. Sequences in bold were obtained from GenBank.

Aphanolejeunea madeirensis (Schiffn.) Grolle. MADEIRA. *Schäfer-Verwimp & Verwimp* 25948 (JE), JQ991027, JQ991142, JQ991257. *Aphanolejeunea microscopica* (Tayl.) A. Evans. MADEIRA. *Schäfer-Verwimp & Verwimp* 25955 (GOET), JQ991028, JQ991143, JQ991258. *Aphanolejeunea sintenisii* (Steph.) Steph. MADEIRA. *Drehwald & Drehwald* 960325 (GOET), JQ991026, JQ991141, JQ991256; MADEIRA. *Schäfer-Verwimp & Verwimp* 25854 (GOET), JQ991029, JQ991144, JQ991259; AZORES. *Schäfer-Verwimp & Verwimp* 29522 (GOET), JQ991030, JQ991145, JQ991260; MADEIRA. *Schäfer-Verwimp & Verwimp* 25856/B (GOET), JQ991031, JQ991146, JQ991261. *Chondrolejeunea chinii* (Tixier) G. Kis et Pócs. THAILAND. *Chantanaorrapint KL1/1* (HSNU), JQ991137, JQ991252, JQ991367. *Chondrolejeunea schimizui* (N. Kitag.) G. Kis et Pócs. THAILAND. *Inuthai* 736 (HSNU), JQ991138, JQ991253, JQ991368. *Cololejeunea aequabilis* (Sande Lac.) Schiffn. FIJI ISLANDS. *Pócs & Pócs* 08037/Q (HSNU), JQ991032, JQ991147, JQ991262. *Cololejeunea amaniensis* Pócs. TANZANIA. *Pócs* 86203/W (E), JQ991033, JQ991148, JQ991263. *Cololejeunea angustiflora* (Steph.) Mizut. NEW CALEDONIA. *Müller NC281* (HSNU), JQ991036, JQ991151, JQ991266; FIJI ISLANDS. *Pócs & Pócs* 03279/AV (HSNU), JQ991034, JQ991149, JQ991264; NEW CALEDONIA. *Müller NC18A* (HSNU), JQ991035, JQ991150, JQ991265. *Cololejeunea apiculata* (E. W. Jones) R. M. Schust. TANZANIA. *Pócs* 6966/AA (GOET), JQ991037, JQ991152, JQ991267. *Cololejeunea appressa* (A. Evans) Benedix. BOLIVIA. *Gradstein* 7235 (GOET), JQ991038, JQ991153, JQ991268; CHINA. *Peng & Yu* 20100719–43 (HSNU), JQ991039, JQ991154, JQ991269. *Cololejeunea bhutanica* Grolle et Mizut. NEPAL. *Long* 17551 (E), JQ991041, JQ991156, JQ991271; CHINA. *Long* 34790 (E), JQ991040, JQ991155, JQ991270; CHINA. *Zhu et al.* 20100826–23B (HSNU), JQ991042, JQ991157, JQ991272. *Cololejeunea biddlecomiae* (Austin ex Pearson) A. Evans. U. S. A. Tennessee: *Davison* 1624 (GOET), JQ991043, JQ991158, JQ991273. *Cololejeunea blepharophylla* Pócs. FIJI ISLANDS. *Pócs & Pócs* 03279/AY (HSNU), JQ991044, JQ991159, JQ991274. *Cololejeunea calcarea* E. W. Jones GERMANY. *Schäfer-Verwimp* 31568 (GOET), JQ991047, JQ991162, JQ991277; GREECE. *Schäfer-Verwimp & Verwimp* 29744 (GOET), JQ991046, JQ991161, JQ991276; SWITZERLAND. *Long et al.* 38620 (E), JQ991045, JQ991160, JQ991275. *Cololejeunea cardiocarpa* (Mont.) A. Evans. BRAZIL. *Borhidi & Pereira* BB25 (GOET), JQ991048, JQ991163, JQ991278. *Cololejeunea ceatocarpa* (Ångstr.) Steph. FIJI ISLANDS. *Pócs & Pócs* 03284/L (HSNU), JQ991049, JQ991164, JQ991279. *Cololejeunea ceratilobula* (P. C. Chen) R. M. Schust. CHINA. *Wang et al.* 20090923–17D (HSNU), JQ991050, JQ991165, JQ991280; CHINA. *Peng & Wei* 20100920–8B (HSNU), JQ991051, JQ991166, JQ991281. *Cololejeunea cocoscicola* Tixier (I). FIJI ISLANDS. *Pócs & Pócs* 03283/O (HSNU), JQ991052, JQ991167, JQ991282; FIJI ISLANDS. *Pócs & Pócs* 03267/C (HSNU), JQ991053, JQ991168, JQ991283. *Cololejeunea cordifolia* (Steph.) R. M. Schust. PAPUA NEW GUINEA. *Streimann* 41383 (GOET), JQ991054, JQ991169, JQ991284. *Cololejeunea decliviloba* Steph. NEW CALEDONIA. *Müller NC17A* (HSNU), JQ991056, JQ991171, JQ991286; NEW CALEDONIA. *Müller NC1D* (HSNU), JQ991055, JQ991170, JQ991285. *Cololejeunea denticulata* (Horik.) S. Hatt. CHINA. *Long & Shevock* 37291 (E), JQ991057, JQ991172, JQ991287. *Cololejeunea distalopapillata* (E. W. Jones) R. M. Schust. MALAWI. *Hodgetts* M2403C (E), JQ991058, JQ991173, JQ991288. *Cololejeunea dozyana* (Sande Lac.) Schiffn. FIJI ISLANDS. *Long* 33920 (HSNU), JQ991059, JQ991174, JQ991289. *Cololejeunea duvignaudii* E. W. Jones. MALAWI. *Hodgetts* M2542 (E), JQ991060, JQ991175, JQ991290. *Cololejeunea falcata* (Horik.) Benedix. CHINA. *Peng & Yu* 20100720–75B (HSNU), JQ991061, JQ991176, JQ991291. *Cololejeunea floccosa* (Lehm. et Lindenb.) Schiffn. CHINA. *Peng & Yu* 20100714–6B (HSNU), JQ991062, JQ991177, JQ991292. *Cololejeunea gottschei* (Steph.) Pandé. CHINA. *Peng & Yu* 20100720–102 (HSNU), JQ991063, JQ991178, JQ991293. *Cololejeunea haskarliana* (Lehm. et Lindenb.) Schiffn. MALAYSIA. *Schäfer-Verwimp & Verwimp* 18866/A (GOET), JQ991066, JQ991181, JQ991296; CHINA. *Peng & Yu* 20100714–18 (HSNU), JQ991064, JQ991179, JQ991294; CHINA. *Peng & Yu* 20100720–59H (HSNU), JQ991065, JQ991180, JQ991295. *Cololejeunea horikawana* (S. Hatt.) Mizut. CHINA. *Zhang et al.* 20091031–67C (HSNU), JQ991067, JQ991182, JQ991297. *Cololejeunea japonica* (Schiffn.) Mizut. CHINA. *Zhu* 20100421–21 (HSNU), JQ991068, JQ991183, JQ991298. *Cololejeunea kulenensis* Tixier FIJI ISLANDS. *Pócs & Pócs* 03309/BM (HSNU), JQ991069, JQ991184, JQ991299; FIJI ISLANDS. *Pócs & Pócs* 03308/H (HSNU), JQ991070, JQ991185, JQ991300. *Cololejeunea laevigata* (Mitt.) Tilden. NEW ZEALAND. *von Konrat* 81 *Herangi* 503 (GOET), DQ987349, DQ238563, DQ238571. *Cololejeunea lanciloba* Steph. AUSTRALIA. *Pócs & Streimann* 9960/T (GOET), JQ991073, JQ991188, JQ991303; INDONESIA. *Sporn* 91 (GOET), JQ991072, JQ991187, JQ991302. *Cololejeunea latilobula*

- (Herzog) Tixier BANGLADESH. *Long* 281211 (E), JQ991074, JQ991189, JQ991304; CHINA. *Peng & Wei* 20100921–39 (HSNU), JQ991075, JQ991190, JQ991305; CHINA. *Yu* 20100921–1 (HSNU), JQ991136, JQ991251, JQ991366. *Cololejeunea linopteroides* H. Rob. COSTA RICA. *Carranza-Morse s.n.* USJ46100 (GOET), JQ991076, JQ991191, JQ991306. *Cololejeunea longifolia* (Mitt.) Benedix ex Mizut. CHINA. Xizang: *Wang & Peng* 20111012–72 (HSNU), JQ991077, JQ991192, JQ991307; CHINA. *Zhu* 20100423–16 (HSNU), JQ991078, JQ991193, JQ991308. *Cololejeunea macounii* (Spruce ex Underw.) A. Evans. CHINA. *Koponen et al.* 56319 (H), AY125346, AY125942, AY144483. *Cololejeunea madothecoides* (Steph.) Benedix. CHINA. *Peng* 20100522–9A (HSNU), JQ991079, JQ991194, JQ991309. *Cololejeunea malanjae* Steph. MALAWI. *Porley* M280H (E), JQ991080, JQ991195, JQ991310; KENYA. *Pócs & Pócs* 04027/BD (JE), JQ991081, JQ991196, JQ991311. *Cololejeunea maritima* Tixier. NEW CALEDONIA. *Müller* NC131 (HSNU), JQ991082, JQ991197, JQ991312. *Cololejeunea minutissima* (Sm.) Schiffn. CHINA. *Yu* 20100922–11 (HSNU), JQ991085, JQ991200, JQ991315; CANARY ISLANDS. La Palma: *Schäfer-Verwimp & Verwimp* 24798 (GOET), JQ991083, JQ991198, JQ991313; ECUADOR. *Schäfer-Verwimp et al.* 24473 (GOET), JQ991084, JQ991199, JQ991314. *Cololejeunea minutissima* ssp. *myriocarpa* (Nees et Mont.) R. M. Schust. BRAZIL. *Gradstein* 9800 (GOET), JQ991086, JQ991201, JQ991316. *Cololejeunea ningwana* Tixier. NEW CALEDONIA. *Müller* NC2B (HSNU), JQ991087, JQ991202, JQ991317. *Cololejeunea obliqua* (Nees et Mont.) Schiffn. BRAZIL. *Schäfer-Verwimp & Verwimp* 11238 (GOET), JQ991088, JQ991203, JQ991318; BRAZIL. *Schäfer-Verwimp & Verwimp* 12006 (GOET), JQ991089, JQ991204, JQ991322. *Cololejeunea ocelloides* (Horik.) S. Hatt. CHINA. *Peng & Yu* 20100713–30 (HSNU), JQ991090, JQ991205, JQ991320; CHINA. *Peng & Yu* 20100720–75A (HSNU), JQ991091, JQ991206, JQ991321. *Cololejeunea ornata* A. Evans. CHINA. *Peng & Wei* 20100913–12A (HSNU), JQ991092, JQ991207, JQ991322. *Cololejeunea peraffinis* (Schiffn.) Schiffn. CHINA. *Zhang et al.* 20091101–48F (HSNU), JQ991094, JQ991209, JQ991324; CHINA. *Peng & Yu* 20091031–106A (HSNU), JQ991093, JQ991208, JQ991323. *Cololejeunea planissima* (Mitt.) Abeyw. CHINA. *Zhu et al.* 20100822–55 (HSNU), JQ991095, JQ991210, JQ991325; CHINA. *Peng & Wei* 20100912–7C (HSNU), JQ991098, JQ991213, JQ991328; CHINA. *Wei* 20100210–62A (HSNU), JQ991071, JQ991186, JQ991301. *Cololejeunea pseudoflocosa* (Horik.) Benedix. CHINA. *Yu* 20100922–6 (HSNU), JQ991099, JQ991214, JQ991329; CHINA. *Peng* 20100711–5A (HSNU), JQ991100, JQ991215, JQ991330. *Cololejeunea pseudoplagiophylla* P. C. Wu et J. X. Luo. CHINA. *Peng & Yu* 20100720–91 (HSNU), JQ991101, JQ991216, JQ991331. *Cololejeunea pseudoserrata* Tixier. NEW CALEDONIA. *Müller* NC9I (HSNU), JQ991102, JQ991217, JQ991332; NEW CALEDONIA. *Müller* NC6E (HSNU), JQ991103, JQ991218, JQ991333. *Cololejeunea raduliloba* Steph. CHINA. *Peng & Wei* 20100912–40A (HSNU), JQ991106, JQ991221, JQ991336; CHINA. *Peng & Wei* 20100921–33C (HSNU), JQ991104, JQ991219, JQ991334. CHINA. *Peng & Wei* 20100920–3A–4 (HSNU), JQ991105, JQ991220, JQ991335. *Cololejeunea rosettiana* (C. Massal.) Schiffn. ITALY. *Long* 35468 (E), JQ991107, JQ991222, JQ991337; GREECE. *Schäfer-Verwimp & Verwimp* 15936 (GOET), JQ991108, JQ991223, JQ991338. *Cololejeunea rotundilobula* (P. C. Wu et P. J. Lin) Piippo. CHINA. *Peng & Yu* 20100720–51 (HSNU), JQ991109, JQ991224, JQ991339. *Cololejeunea schaeferi* Grolle. MADEIRA. *Schäfer-Verwimp & Verwimp* 25642 (GOET), JQ991110, JQ991225, JQ991340. *Cololejeunea schmidtii* Steph. CHINA. *Wei* 20090221–41A (HSNU), JQ991111, JQ991226, JQ991341. *Cololejeunea serrata* (Steph.) Benedix. NEW CALEDONIA. *Müller* NC11D (HSNU), JQ991112, JQ991227, JQ991342. *Cololejeunea serrulata* Steph. MALAYSIA. *Yong* 7725 (BM), JQ991128, JQ991243, JQ991358. *Cololejeunea societatis* Tixier. FIJI ISLANDS. *Pócs & Pócs* 03289/BO (HSNU), JQ991114, JQ991229, JQ991344. *Cololejeunea spinosa* (Horik.) Pandé et R. N. Misra. CHINA. *Peng & Yu* 20100720–100 (HSNU), JQ991115, JQ991230, JQ991345; CHINA. *Peng & Yu* 20100714–7A (HSNU), JQ991116, JQ991231, JQ991346. *Cololejeunea stotleriana* Gradst., Ilkiu-Borges & Vanderpoorten. ECUADOR. *Gradstein* 12073 (BM), JQ991117, JQ991232, JQ991347. *Cololejeunea stylosa* Steph. ex Mizut. CHINA. *Peng & Yu* 20100720–47B (HSNU), JQ991118, JQ991233, JQ991348; CHINA. *Peng & Yu* 20100720–77H (HSNU), JQ991119, JQ991234, JQ991349. *Cololejeunea subcardiocalpa* Tixier. BRAZIL. *Schäfer-Verwimp & Verwimp* 9212 (GOET), JQ991120, JQ991235, JQ991350. *Cololejeunea tenella* Benedix. Austraria. *Pócs et al.* 0028/M (GOET), JQ991122, JQ991237, JQ991352. *Cololejeunea thailandensis* Tixier. THAILAND. *Schäfer-Verwimp & Verwimp* 16233 (GOET), JQ991123, JQ991238, JQ991353, THAILAND. *Schäfer-Verwimp & Verwimp* 16234/A (GOET), JQ991124, JQ991239, JQ991354. *Cololejeunea tranminhiana* Tixier. THAILAND. *Pócs & Pócs* 07014/AL (JE), JQ991125, JQ991240, JQ991355. *Cololejeunea trichomanis* (Gottsche) Steph. VIETNAM. *Pócs & Ninh* 02105/E (JE), JQ991127, JQ991242, JQ991357; CHINA. *Peng & Yu* 20100719–18A (HSNU), JQ991126, JQ991241, JQ991356; CHINA. *Peng & Yu* 20100719–16 (HSNU), JQ991113, JQ991228, JQ991343. *Cololejeunea trichomanis* ssp. *cordiflora* Pócs FIJI ISLANDS. *Pócs & Pócs* 03288/CU (HSNU), JQ991129, JQ991244, JQ991359; FIJI ISLANDS. *Pócs & Pócs* 03282/BB (HSNU), JQ991130, JQ991245, JQ991360. *Cololejeunea vitalana* Tixier. COSTA RICA. *Pócs SV/H-0473/A* (GOET), DQ987348, DQ238564, DQ238573. *Cololejeunea wightii* Steph. MALAYSIA. *Yong* 7721 (BM), JQ991132, JQ991247, JQ991362; CHINA. *Peng & Yu* 20100719–2 (HSNU), JQ991131, JQ991246, JQ991361. *Cololejeunea yakusimensis* (S. Hatt.) Mizut. CHINA. *Yu* 20100921–4 (HSNU), JQ991133, JQ991248, JQ991363; CHINA. *Long* 32613 (HSNU), JQ991134, JQ991249, JQ991364; CHINA. *Wang & Peng* 20111018–86C (HSNU), JQ991135, JQ991250, JQ991365; CHINA. *Long* 34518A (E), JQ991096, JQ991211, JQ991326. CHINA. *Long* 34521 (E), JQ991097, JQ991212, JQ991327. *Colura calyptrofolia* (Hook.) Dumort. AZORES. *Schäfer-Verwimp & Verwimp* 29196 (JE), JQ991139, JQ991254, JQ991369. *Colura irrorata* (Spruce) Heinrichs et al. ECUADOR. *Gradstein et al.* 10033 (GOET), DQ987279, AY548073, DQ238584. *Colura tenuicornis* (A. Evans) Steph. WEST INDIES. *Schäfer-Verwimp & Verwimp* 22538/A (JE), JQ991140, JQ991255, JQ991370. *Diplasiolejeunea involuta* S. Winkl. ssp. *Andicola*. ECUADOR. *Schäfer-Verwimp* 23508 (GOET), DQ987288, AY548096, DQ238582. *Diplasiolejeunea* sp., ECUADOR *Wilson et al.* 04–06 (GOET), DQ987333, DQ983676, DQ987437. *Drepanolejeunea* sp. MALAYSIA. *Ilkiu-Borges et al.* 3024 (GOET), DQ987318, DQ983678, DQ987422. *Lejeunea cancellata* Nees et Mont. ex Mont. ECUADOR. *Wilson et al.* 04–02 (GOET), DQ987329, DQ983686, DQ987433. *Lejeunea catinulifera* Spruce. ECUADOR. *Gradstein & Mandl* 10141 (GOET), DQ987307, DQ983688, DQ987411. *Lejeunea cavifolia* (Ehrh.) Lindb. GERMANY. *Heinrichs* 3695 (GOET), DQ987259, AY548102, DQ238581. *Lejeunea cerina* (Lehm. et Lindenb.) Gottsche, Lindenb. et Nees. ECUADOR. *Wilson et al.* 04–13 (GOET), DQ987339, DQ983689, DQ987441. *Myriocoleopsis gymnocolea* (Spruce) M. E. Reiner et Gradst. ECUADOR. *Gradstein et al.* 10020 (GOET), DQ987277, DQ238568, DQ238583. *Myriocoleopsis vuquangensis* (Pócs & T. N. Ninh) Pócs. VIETNAM. *Pócs* 02102/N (GOET), DQ987347, DQ983670, DQ987449.