

Phylogeny and classification of Lejeuneaceae subtribe Cheilolejeuneinae (Marchantiophyta) based on nuclear and plastid molecular markers

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Abstract – Cheilolejeuneinae is an early diverging lineage of Lejeuneaceae tribe Lejeuneae with a pantropical distribution. The current phylogeny and classification of this subtribe is based on morphological and limited-sampling molecular studies. Here we present a molecular phylogeny of Cheilolejeuneinae and related lineages based on maximum parsimony and maximum likelihood analyses, as well as Bayesian inference of two chloroplast regions (*trnL-F*, *trnG*) and the nuclear ribosomal ITS1-5.8S-ITS2 region, to test the monophyly of this subtribe, and to re-evaluate the infrageneric classification of *Cheilolejeunea*. The results confirm the monophyly of Cheilolejeuneinae, which consists of one single genus, *Cheilolejeunea*. *Aureolejeunea* and *Omphalanthus* are nested in *Cheilolejeunea* and, consequently, all species (11) and varieties (2) accepted in these two genera are transferred to *Cheilolejeunea*. Based on morphological and molecular evidence a new infrageneric classification of *Cheilolejeunea* into nine sections is proposed: sect. *Anomalolejeunea*, sect. *Cheilolejeunea*, sect. *Cyrtolejeunea*, sect. *Euosmolejeunea*, sect. *Leucolejeunea*, sect. *Paroicae*, sect. *Omphalanthus*, sect. *Strepsilejeunea* and sect. *Xenolejeunea*. *Cheilolejeunea decurviloba* is resolved in a sister relationship to *Pycnolejeunea densistipula* and *C. gaoi* constitutes a separate lineage remote from Cheilolejeuneinae.

***Aureolejeunea* / *Cheilolejeunea* / *Cheilolejeunea gaoi* / infrageneric classification /
Lejeuneae / *Omphalanthus* / *Pycnolejeunea decurviloba***

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INTRODUCTION

Molecular phylogenetic investigations have substantially altered our understanding of the systematic relationships among liverworts, an early-diverging land plant lineage (e.g., Heinrichs *et al.*, 2005, 2007; Forrest *et al.*, 2006; He-Nygrén *et al.*, 2006; Shaw *et al.*, 2015). As a result, intuitive arrangements based on morphological similarity have been replaced by phylogenetic classifications integrating morphological data and molecular evidence (Frey & Stech, 2005, 2008, 2009; Crandall-Stotler *et al.*, 2009a, b).

This paper focuses on Lejeuneaceae, the largest family of the liverworts with more than a thousand species in some 68 genera (Gradstein, 2013b; Wang *et al.*, 2014). The species abound in humid tropical forests where they occupy different epiphytic niches, ranging from large tree trunks to tiny twigs and surfaces of living leaves (Gradstein, 1994). Recent molecular studies have provided a phylogenetic backbone of the family and have supported a subdivision into subfamilies, tribes and subtribes (e.g., Wilson *et al.*, 2007; Sukkharak *et al.*, 2011; Dong *et al.*, 2012, 2013; Heinrichs *et al.*, 2012a, 2012b, 2013, 2014a, 2014b; Gradstein, 2013b; Ye *et al.*, 2013a; Yu *et al.*, 2013).

In spite of these efforts, the phylogenetic relationships within the suprageneric groups of Lejeuneaceae remain incompletely known. This holds especially for Lejeuneae, the largest and most diverse tribe with 40 genera in 12 subtribes (Gradstein, 2013b; Heinrichs *et al.*, 2014b; Schäfer-Verwimp *et al.*, 2014). Here, we focus on the subtribe Cheilolejeuneinae Gradst., a basal lineage of Lejeuneae containing three or four genera, *Aureolejeunea* R.M. Schust., *Cheilolejeunea* (Spruce) Steph. and *Omphalanthus* Lindenb. *et* Nees. A further putative member of this subtribe, *Leiolejeunea* A. Evans, was recently excluded from Cheilolejeuneinae and placed in its own subtribe Leiolejeuneinae Schäfer-Verw. *et* Heinrichs (Schäfer-Verwimp *et al.*, 2014). Characteristic features of Cheilolejeuneinae are the distal hyaline papilla on leaf lobules, usually large, coarsely segmented oil bodies, the spores ornamented by numerous rosettes (> 10), the presence of striatene-type sesquiterpenes and the scarcity of flavonoids (Gradstein *et al.*, 1988, 2003; Gradstein, 2013b). In a global molecular phylogenetic study of Lejeuneaceae, Cheilolejeuneinae were recovered as monophyletic (Wilson *et al.*, 2007); moreover, it was suggested that *Cheilolejeunea*, *Omphalanthus* and *Aureolejeunea* might be congeneric. Since *Omphalanthus* is the oldest generic name in this group but *Cheilolejeunea* has by far the largest number of species, the latter name has been proposed for conservation (Ye *et al.*, 2011).

Cheilolejeunea contains an estimated 80-100 species and is pantropical in distribution (Thiers, 1997; Ye *et al.*, 2010). The genus is traditionally recognized by creeping to ascending growth, pale green color, thin stems with a 2(-4) cells wide ventral merophyte and enlarged epidermis cells, leaf lobules with 1(-2) teeth and a hyaline papilla usually at the distal side of the second tooth, leaf cells with 1-3(-5) large, coarsely granular (rarely finely granular) oil bodies, bifid (rarely undivided) underleaves, gynoecea without or with 1-2 lejeuneoid or pycnolejeuneoid innovations and an inflated perianth with 3-5 smooth keels, rarely pluriplicate or without keels (Thiers, 1997; Gradstein *et al.*, 2001; Zhu & So, 2001; Renner, 2012). A subgeneric classification was proposed by Schuster (1963, 1980), who recognized seven subgenera mainly derived from leaf and underleaf characters (Table 1). In recent years the circumscription of the genus has become expanded by the transfer of *Cyrtolejeunea* A. Evans, *Cystolejeunea* A. Evans, *Trachylejeunea* (Spruce) Schiffn.

Table 1. Infrageneric classification systems for the genus *Cheilolejeunea*. Subgenera of Schuster sampled in this study are marked by an asterisk.

<i>Schuster (1963, 1980)</i>	<i>Ye et al. (proposed here)</i>
*Subg. <i>Cheilolejeunea</i> (Spruce) Steph.	Sect. <i>Anomalolejeunea</i>
*Subg. <i>Euosmolejeunea</i> (Spruce) R.M. Schust.	Sect. <i>Cheilolejeunea</i>
Subg. <i>Renilejeunea</i> R.M. Schust.	Sect. <i>Cyrtolejeunea</i>
*Subg. <i>Strepsilejeunea</i> (Spruce) R.M. Schust.	Sect. <i>Euosmolejeunea</i>
Subg. <i>Tegulilejeunea</i> R.M. Schust.	Sect. <i>Leucolejeunea</i>
*Subg. <i>Xenolejeunea</i> Kachroo & R.M. Schust.	Sect. <i>Paroicae</i>
*Subg. <i>Anomalolejeunea</i> (Spruce) R.M. Schust.	Sect. <i>Omphalanthus</i>
	Sect. <i>Strepsilejeunea</i>
	Sect. <i>Xenolejeunea</i>

and *Leucolejeunea* A. Evans to *Cheilolejeunea* (Grolle *et al.*, 2002; Wilson *et al.*, 2004, 2007; Gradstein & Ilkiu-Borges, 2009; Malombe, 2009; Ye & Zhu, 2010). A recent molecular phylogenetic study on Lejeuneaceae subtribes provided evidence for *Cystolejeunea*, *Cyrtolejeunea*, and *Leucolejeunea* in early diverging lineages of Cheilolejeuneinae, allowing them to be considered as independent genera (Heinrichs *et al.*, 2014a). However, a follow-up study (Schäfer-Verwimp *et al.*, 2014) demonstrated the presence of the generic type of *Cheilolejeunea* in the *Cystolejeunea* lineage. To avoid nomenclatural confusion, the latter authors proposed a wide genus concept for *Cheilolejeunea* including *Aureolejeunea*, *Cyrtolejeunea*, *Cystolejeunea*, *Evansiolejeunea*, *Leucolejeunea*, and *Omphalanthus*.

Aureolejeunea and *Omphalanthus* are small genera with about half a dozen species each and are restricted to tropical America with exception of *A. rotalis* (Hook.f. *et* Taylor) Gradst. *et* P. Geissler from St. Helena and *O. roccatii* (Gola) R.M. Schust. from East Africa (Gradstein, 2013a). *Aureolejeunea* differs from *Cheilolejeunea* by its brown color, rigid stems with epidermis cells not larger than medullary cells, leaf cells with very large, sometimes coalesced trigones, without intermediate thickenings and with smaller oil bodies, and undivided underleaves. Most of these characters are shared with *Omphalanthus*, but the latter lacks brown pigmentation, has pendent growth and has thicker stems with a 4-12 cells wide ventral merophyte. The African *O. roccatii* stands out by the lack of gynoeceal innovations and was sometimes placed in the monospecific genus *Evansiolejeunea* Vanden Berghen (as *E. roccatii* (Gola) Vanden Berghen).

In the present paper, we reconstruct a comprehensive phylogeny of Cheilolejeuneinae using chloroplast and nuclear DNA markers. By including accessions covering almost the whole range of morphological variation within the group, we present a revised classification of the subtribe.

MATERIALS AND METHODS

Taxon sampling

We sampled 46 species and a total of 53 accessions of *Cheilolejeunea*, from throughout most of the taxonomic and geographical width of the genus, as well as 3 species of *Aureolejeunea* (3 accessions) and 4 of *Omphalanthus* (6 accessions)

including *O. roccatii* (= *Evansiolejeunea roccatii*). Samples of the monospecific subgenera *Renilejeunea* R.M. Schust. and *Tegulilejeunea* R.M. Schust. of *Cheilolejeunea* were not available for this study, and the former genus *Trachylejeunea* (now considered a synonym of *Cheilolejeunea*) was represented by only one single species. The ingroup also included representatives of Lejeuneae subtribes Echinolejeuneinae (*Anoplolejeunea* (Spruce) Schiffn.), Ceratolejeuneinae (*Ceratolejeunea* J.B. Jack *et* Steph.), Leirolejeuneinae (*Leirolejeunea* A. Evans), Lejeuneinae (*Lejeunea* Lib.), and Pycnolejeuneinae (*Pycnolejeunea* (Spruce) Schiffn.) (Gradstein, 2013b; Heinrichs *et al.*, 2014a; Schäfer-Verwimp *et al.*, 2014). Representatives of *Brachiolejeunea* (Spruce) Schiffn. (Brachiolejeuneae) and *Acrolejeunea* Schiffn. (Ptychantheae) were chosen as the outgroup based on the analyses of Wilson *et al.* (2007). Voucher information and Genbank accession numbers are listed in Appendix 1. All voucher specimens were carefully examined and original identifications were verified and corrected if necessary.

DNA extraction, amplification, sequencing and alignment

Genomic DNA was extracted from dried herbarium material or fresh material using DNeasy™ Plant Mini Kit (QIAGEN). Two chloroplast regions (*trnL-F*, *trnG*) and the nuclear ribosomal internal transcribed spacer 1 and 2 with the intervening 5.8S ribosomal subunit (ITS1-5.8S-ITS2, collectively called nrITS) were amplified by polymerase chain reaction (PCR), employing 35 cycles of 30 sec at 95°C, 45 sec at 50°C and 1 min at 72°C, preceded by an initial 1 min melting step at 95°C and followed by a final extension period of 7 min at 72°C. Amplification and sequencing primers followed those described in Shaw *et al.* (2003, *trnL-F* and *trnG*), and Hartmann *et al.* (2006, nrITS).

Phylogenetic analysis

All sequences were assembled and checked for inaccurate base calling in Sequencher v4.1 (Gene Codes Corp. 2000) or PhyDE® 0.997 (Müller *et al.*, 2010). Consensus sequences were then aligned manually in PhyDE® 0.997. Positions that were ambiguously aligned in the dataset were excluded before any phylogenetic analysis; gaps were coded as missing data.

Maximum parsimony (MP) analyses were performed with command files using the parsimony ratchet (Nixon, 1999) generated from the program PRAP2 (Müller, 2007) applying the default settings, and executed in PAUP 4.0b10 (Swofford, 2002). Heuristic bootstrap searches under parsimony were performed with 10000 replicates.

The three regions were first analyzed separately using MP to check possible incongruence in topology. Strict consensus trees from these separate analyses were compared to identify conflicting nodes supported by at least 70% (Mason-Gamer & Kellogg, 1996). They gave no evidence of incongruence. Thus the three datasets were combined into a single matrix. The Akaike information criterion implemented in MrModeltest v.2.3 (Nylander, 2004) was used to choose the best-fit substitution models for the maximum likelihood (ML) analysis and the Bayesian inference (BI) analysis. A General Time Reversible (GTR) model with gamma-distributed rate variation across sites and a proportion of invariable sites was selected for all the three regions. ML trees were generated using the program GARLI version 2.0 (Zwickl, 2006) with models implemented. GARLI 2.0 was employed for conducting

1000 bootstrap replicates. Bayesian analyses were applied to the combined data in MrBayes (Huelsenbeck & Ronquist, 2001) using selected models with four independent Markov chain Monte Carlo (MCMC) simulations runs with four chains for 1000000 generations and sampled every 1000th generation. The program Tracer v1.5 (Rambaut & Drummond, 2009) was used to confirm the burn-in point and examine the log likelihoods. The outputs from the four runs were combined for final inference of posterior probabilities (PP) of both trees and model parameters after discarding the burn-in.

RESULTS

A total of 70 new ITS, 58 new *trnG* and 62 new *trnL-F* sequences were generated for this study. The bootstrap consensus trees from the individual ITS, *trnL*, and *trnG* datasets were compared and no evidence of supported incongruent patterns was found. These three datasets were therefore combined into a single analysis. The aligned matrix contained 2519 unambiguously aligned nucleotide position characters, including 1373 in the ITS, 691 in the *trnG* and 455 in the *trnL*. Of the total character sites, 1308 were constant, 961 were parsimony-informative and 250 were variable but parsimony uninformative.

The maximum parsimony (MP) analysis resulted in 121 maximally parsimonious trees of 4833 steps, with a consistency index (CI) of 0.429 and a retention index (RI) of 0.659. A single most likely tree (lnL = -26149.7231) was found in the maximum likelihood (ML) analysis. BI analyses resulted in highly similar topologies with the most likely tree. Figure 1 shows the 50% majority-rule consensus tree from the analyses of the concatenated dataset obtained by the BI approach, with support values (> 50) from the ML and MP analyses plotted onto the Bayesian tree.

In the phylogenetic tree (Fig. 1), Cheilolejeuneinae with exclusion of *Cheilolejeunea decurviloba* (Steph.) X.L. He and *C. gaoi* R.L. Zhu, M.L. So et Grolle form a well-supported monophyletic group (MP analysis BS 97%; ML analysis BS 100%; PP 1). The Cheilolejeuneinae clade is well resolved at branch ends, with a total of 11 well-supported clades identified, but with an unresolved backbone. Five of these clades include the type species of subgenera of *Cheilolejeunea* proposed by Schuster (1963, 1980; Table 1). Three further clades correspond to *Omphalanthus* + *Aureolejeunea*, *Cyrtolejeunea* and *Leucolejeunea*, respectively. *Cystolejeunea lineata* (Lehm. et Lindenb.) A. Evans grouped together with members of subg. *Cheilolejeunea* (Spruce) Steph. and *Trachylejeunea aneogyna* (Spruce) Grolle was nested in *Cheilolejeunea* in an unresolved position. *Evansiolejeunea roccatii* was recovered in a small clade together with *Leucolejeunea turgida* (Mitt.) Verd. (= *Cheilolejeunea turgida* (Mitt.) W. Ye et R.L. Zhu) and far removed from *Omphalanthus*. *Cheilolejeunea decurviloba* formed a clade with *Pycnolejeunea densistipula*. Accessions of *Cheilolejeunea gaoi*, finally, formed a robust lineage together with *Anoplolejeunea conferta*, well separate from Cheilolejeuneinae and the remainder of the tribe Lejeuneae.

DISCUSSION

The present study is the most comprehensive molecular-phylogenetic investigation of the subtribe Cheilolejeuneinae available to date. The results confirm the monophyly of the group, proposed by Wilson *et al.* (2007) and Schäfer-Verwimp *et al.* (2014) based on relatively limited sampling, and support the inclusion of *Cyrtolejeunea*, *Cystolejeunea* and *Leucolejeunea* in *Cheilolejeunea*. The results also confirm that *Aureolejeunea*, *Evansiolejeunea* and *Omphalanthus* should be transferred to *Cheilolejeunea*. The systematic position of *Leiolejeunea* in our results is congruous with those in Schäfer-Verwimp *et al.* (2014) supporting it as a separated subtribe. As a result, the subtribe Cheilolejeuneinae as defined by Gradstein (2013b) consists of only one genus, the large pantropical *Cheilolejeunea*.

The molecular phylogeny of *Cheilolejeunea* reveals twenty monophyletic groups that are variously supported by bootstrap percentages and Bayesian posterior probabilities (Fig. 1). Nine of these, including 75% of the *Cheilolejeunea* species analysed, correspond to currently recognized infrageneric groups; the remaining lineages are very small and comprise 13 species. The characteristics of the nine monophyletic groups are as follows:

1. **Anomalolejeunea clade** (88% ML analysis BS, 67% MP analysis BS, PP 0.87). This clade is comprised of five paleotropical species, *Cheilolejeunea pluriplicata* (Pearson) R.M. Schust. (type of *C.* subg. *Anomalolejeunea* (Spruce) Schiffn.), *C. ecarinata* Vanden Berghen, *C. laeviuscula* (Mitt.) Steph., *C. krakakammae* (Lindenb.) R.M. Schust. and *C. pocsii* E.W. Jones. Previously, these species had been associated with the subgenera *Anomalolejeunea*, *Euosmolejeunea* (Spruce) R.M. Schust. or *Strepsilejeunea* (Spruce) R.M. Schust. (Vanden Berghen, 1984; Jones, 1988; Zhu *et al.*, 2002). Morphological characteristics of the Anomalolejeunea clade are the rounded or obtuse leaf apex, lejeuneoid innovations and two or more oil bodies per cell. The neotropical *C. laevicalyx* (J.B. Jack *et* Steph.) Grolle and the Australian *C. mimosa* (Hook. f. *et* Taylor) R.M. Schust., recovered as a separate lineage in the analysis, are morphologically rather similar to the members of the Anomalolejeunea clade but differ by acute leaf apices.

2. **Cheilolejeunea clade** (100% ML analysis BS, 98% MP analysis BS, PP 1.00). This is an early diverging lineage of *Cheilolejeunea* characterized by absence of gynoeical innovations and frequent presence of a long and thin lobule tooth. This clade comprises the neotropical *C. adnata* (Kunze *ex* Lehm.) Grolle (type of the genus *Cheilolejeunea*), the neotropical *Cystolejeunea lineata* and *Cheilolejeunea larsenii* Mizut. from tropical Asia. Further species that might belong to this group but were not yet sequenced are *C. albovirens* (Hook.f. *et* Taylor) E.A. Hodgs. (Oceania), *C. exinnovata* E.W. Jones (West Africa) and *C. verrucosa* Steph. (Asia). The Cheilolejeunea clade was recovered as sister to the *Cyrtolejeunea* clade, albeit without support. Morphologically, these two clades resemble each other by the long lobule tooth.

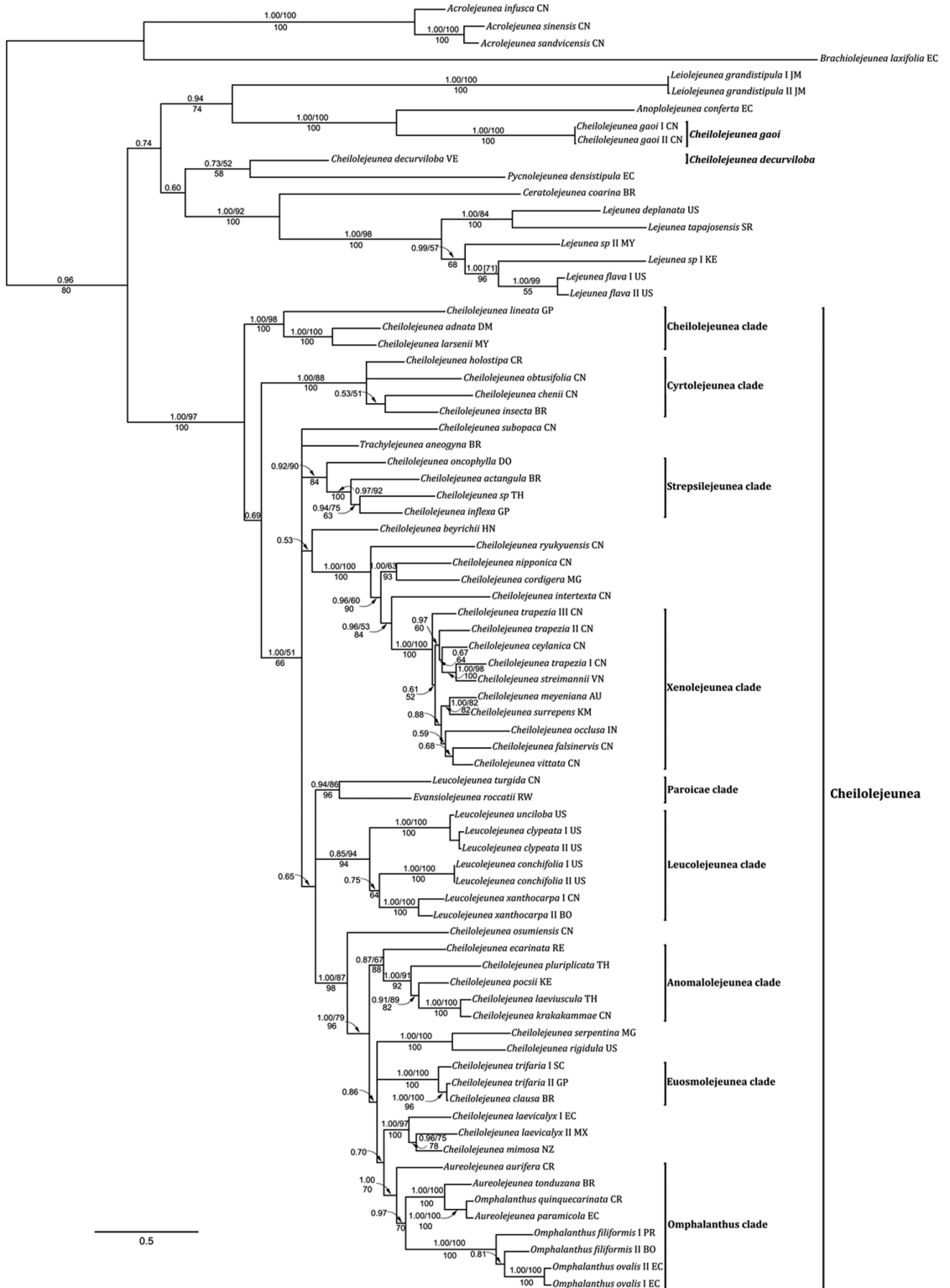
3. **Cyrtolejeunea clade** (100% ML analysis BS, 88% MP analysis BS, PP 1.00). The former genus *Cyrtolejeunea*, consisting of the neotropical *Cyrtolejeunea holostipa* (Spruce) A. Evans (type) and *Cheilolejeunea insecta* Grolle *et* Gradst. as well as *C. chenii* R.L. Zhu *et* M.L. So and *C. obtusifolia* (Steph.) S. Hatt. from eastern Asia (Grolle *et al.*, 2002), is a well-supported group within *Cheilolejeunea*. The group can be readily separated from the rest of the genus by the minute plant size, suberect leaves, finely segmented, *Jungermannia*-type oil bodies, long and sharp lobule tooth (also present in Cheilolejeunea clade), undivided or short-bifid

underleaves, and pycnolejeuneoid innovations. These delicate plants were originally believed to be close to *Microlejeunea* (Evans, 1903) but were subsequently placed near *Cheilolejeunea* due to the distal hyaline papilla (Schuster, 1963). *Cheilolejeunea ulugurica* Malombe, Eb. Fisch. et Pócs from East Africa, which has not yet been sequenced, should be a further member of this clade (Malombe *et al.*, 2010; Ye *et al.*, 2013b).

4. **Euosmolejeunea clade** (100% ML analysis BS, 100% MP analysis BS, PP 1.00). Although many species have been associated with the subgenus *Euosmolejeunea* (Spruce) R.M. Schust. in the past, our results found support for only two species in this group, the pantropical *C. trifaria* (Reinw., Blume *et* Nees) Mizut. (type of *C.* subg. *Cheilolejeunea*) and the neotropical *C. clausa* (Nees *et* Mont.) R.M. Schust. They are characterized by large, bifid underleaves and a short, blunt lobule tooth (Schuster, 1980). The Asiatic *C. lindenberghii* (Gottsche) Mizut. and the Pacific *C. cookiensis* (Steph.) R.M. Schust *et* Kachroo and *C. parkinsonii* (Steph.) Mizut., all with large, bifid underleaves, are probable further members of this group. Zhu *et al.* (2002) placed the subgenera *Anomalolejeunea* (Spruce) R.M. Schust. and *Strepsilejeunea* (Spruce) R.M. Schust. in subg. *Euosmolejeunea* but this is not supported by our results.

5. **Leucolejeunea clade** (94% ML analysis BS, 94% MP analysis BS, PP 0.85). This clade comprises four species formerly placed in *Leucolejeunea* sect. *Leucolejeunea*: *L. clypeata* (Schwein.) A. Evans (type; southeastern U.S.A.), *L. conchifolia* (A. Evans) A. Evans (neotropical), *L. uncioloba* (Lindenb.) A. Evans (Afro-American) and *L. xanthocarpa* (Lehm. *et* Lindenb.) A. Evans (pantropical) (Grolle & Piippo, 1990). Characteristics of this group are undivided underleaves, robust stems without hyalodermis and (2-) 4-8 cells wide ventral merophyte, pycnolejeuneoid innovations, cells with one very large and very coarsely granular oil body, and monoicy (Schuster, 1987, 2006). *Leucolejeunea japonica* (Horik.) Verd. (endemic to Japan), which also has a single large oil body per cell, should be a further member of this group. Species of the former genus *Leucolejeunea* with more than one oil body per cell were recovered in Paroicae clade (see below) or are still unstudied (*L. caducifolia* Gradst. *et* Schäf.-Verw., *L. gradsteinii* Grolle *et* Piippo, *L. suprema* Grolle *et* Piippo). Similarly, the small Asiatic sect. *Omphalanthopsis* (R.M. Schust.) Grolle *et* Piippo (*L. decurrens* (Steph.) Mizut., *L. loriana* (Steph.) Mizut.) could not be sampled in this study.

6. **Omphalanthus clade** (70% ML analysis BS, PP 1.00). The mainly neotropical genera *Aureolejeunea* and *Omphalanthus* (one species, *A. rotalis* (Hook.f. *et* Taylor) Gradst. *et* P. Geissler, on St. Helena) were recovered as members of *Cheilolejeunea* in this study, in a single, well-supported clade. The group shares robust stems and undivided underleaves with the *Leucolejeunea* and *Paroicae* clades but differs from the latter by ascending to pendent growth, sometimes dark-brownish color (*Aureolejeunea*), leaf cells with very large trigones, no intermediate thickenings, 3-5 smaller and less coarsely granular oil bodies, and by lejeuneoid innovations. The spores ornamented by more than ten rosettes and the absence of flavonoids may be further characters of this clade (Gradstein, 2013b). Within the *Omphalanthus* clade, *O. filiformis* (Sw.) Nees and *O. ovalis* (Lindenb. *et* Gottsche) Gradst. form a monophyletic group sister to *Aureolejeunea* species except for the type species, *A. aurifera* R.M. Schust., whose position in this clade remains unresolved. Two species of *Aureolejeunea* (*A. lumae* (Herzog) Slageren, *A. rotalis*) and three of *Omphalanthus* (*O. baracoensis* Mustelier, M.E. Reiner *et* Gradst., *O. huanucensis* (Gottsche) Gradst., *O. jackii* (Steph.) Gradst.) could not be sampled in this study. The African *Evansiolejeunea roccatii*, formerly associated with *Omphalanthus*



(Schuster, 1963; Gradstein, 2013a), was recovered as a member of the next clade, far removed from the *Omphalanthus* clade.

7. **Paroicae clade** (96% ML analysis BS, 86% MP analysis BS, PP 0.94). Schuster's placement of the Asiatic *Leucolejeunea paroica* N. Kitag. and *L. turgida* in a separate taxonomic group, *L. sect. Paroicae* R.M. Schust. (Schuster, 2006), is supported in this study. The Paroicae clade is morphologically similar to the *Leucolejeunea* clade except for the presence of more than one oil body (2-3) per cell. The enigmatic *Evansiolejeunea roccatii* from East Africa, sometimes placed in *Omphalanthus* (as *O. roccatii* (Gola) R.M. Schust.), proved to be a further member of this clade. The position of the latter species in this clade is supported by its robust, holostipous habit, in spite of the absence of gynoecial innovations. *Evansiolejeunea roccatii* has 3-4 very coarsely granular oil bodies per cell (Fischer, 2013: p. 382, fig. 298).

8. **Strepsilejeunea clade** (84% ML analysis BS, 90% MP analysis BS, PP 0.92). Three species from tropical America (*C. acutangula* (Nees) Grolle, *C. oncophylla* (Ångstr.) Grolle et M.E. Reiner, and *C. inflexa* (Hampe ex Lehm.) Grolle, the type species of *Strepsilejeunea*) and *C. sp.* from Asia (Thailand) constitute the *Strepsilejeunea* clade. The group is recognized by convex leaves with pointed apices, leaf cells frequently mamillate or papillose and pycnolejeuneoid innovations. Our results indicate that *Strepsilejeunea* differs from *Euosmolejeunea* and is worthy of taxonomic recognition, as previously advocated by Jones (1988), Schuster (1963, 1980) and others. *Cheilolejeunea krakakammae* (Lindenb.) R.M. Schust. and *C. pluriplicata*, which were formerly associated with *Strepsilejeunea* (Jones, 1988) but differ by lejeuneoid innovations, are not members of this clade and belong in the *Anomalolejeunea* clade.

9. **Xenolejeunea clade** (100% ML analysis BS, 100% MP analysis BS, PP 1). Members of the paleotropical subgenus *Xenolejeunea* Kachroo et R.M. Schust., as emended by Thiers (1992), formed a strongly supported clade in all analyses. The group is morphologically characterized by rectangular lobules more than 1/2 × lobe length, pycnolejeuneoid innovations and occasional presence of an ocellate vitta in leaf lobes (e.g., *C. falsinervis* (Sande Lac.) Kachroo et R.M. Schust.). Eight species of *Xenolejeunea* were included in the analysis; four further species (*C. incisa* (Gottsche) R.M. Schust. et Kachroo, *C. gardneri* (Mitt.) Mizut., *C. gigantea* (Steph.) R.M. Schust. et Kachroo, *C. longidens* (Steph.) R.M. Schust. et Kachroo) should belong here but were not yet investigated.

The clades recognized here deviate from Schuster's (1980) infrageneric classification system of *Cheilolejeunea* (Table 1) in several important respects: (1) The circumscription of the genus has become considerably broadened by the inclusion of *Aureolejeunea* (*Omphalanthus* clade), *Cystolejeunea* (*Cheilolejeunea* clade), *Cyrtolejeunea* (*Cyrtolejeunea* clade), *Evansiolejeunea* (*Paroicae* clade), *Leucolejeunea* (*Leucolejeunea* and *Paroicae* clades), *Omphalanthus* (*Omphalanthus* clade) and *Trachylejeunea* (clade unclear; see below). (2) Subgenus *Anomalolejeunea* is expanded to include various former members of subg. *Euosmolejeunea* and species with lejeuneoid innovations formerly placed in subg. *Strepsilejeunea* (3) Subgenus *Euosmolejeunea* is limited to *C. clausa* (tropical America) and *C. trifaria* (pantropical)

◀ Fig. 1. A 50% majority-rule phylogram from the BI of the combined ITS, *trnG* and *trnL-F* dataset is illustrated with posterior probability values above 0.5 indicated left above the branch and bootstrap percentages of MP above 50% right above the branch, bootstrap percentages of ML above 50% below the branch. Origin of taxa sampled are annotated by a two-letter country code according to the "ISO 3166-1 alpha-2" (http://www.iso.org/iso/english_country_names_and_code_elements).

but presumably contains further species from tropical Asia and the Pacific region. The common neotropical *C. rigidula* (Mont.) R.M. Schust. is not a member of this group. (4) Subgenus *Strepsilejeunea* is limited to acute-leaved species with pycnolejeuneoid innovations; those with lejeuneoid innovations are transferred to subg. *Anomalolejeunea*.

The current study shows that the classification system of Schuster (1980), as shown in Table 1, must be modified to reflect the clades shown in Fig. 1. These clades are formalized here as sections to enhance further sampling and future study of the taxonomic diversity within the genus *Cheilolejeunea*. Future study may also clarify the phylogenetic positions of the species that were not recovered in one of these clades. This includes members of the genus *Trachylejeunea* as redefined by He & Grolle (2001), a small neotropical group of 3-4 species characterized by twinned lobule teeth, and recently transferred to *Cheilolejeunea* (Gradstein & Ilkiu-Borges, 2009). Although we could not study the type, *T. acanthina* (Spruce) Schiffn., we were able to analyse the widespread Amazonian *T. aneogyna* (Spruce) Grolle, which was recovered in an unresolved systematic position within the *Cheilolejeunea* clade. Since *T. acanthina* and *T. aneogyna* are considered congeneric (He, 2003), our results seem to corroborate the transfer of *Trachylejeunea* to *Cheilolejeunea*. Further study including analysis of *T. acanthina* is necessary to determine the phylogenetic position of this group within *Cheilolejeunea*.

The systematic position of *Cheilolejeunea decurviloba*

Cheilolejeunea decurviloba (Steph.) X.L. He was recovered in a small lineage together with *Pycnolejeunea densistipula* (Lehm. et Lindenb.) Steph., outside the genus *Cheilolejeunea*. This species has a rather confusing history. It was originally described as a member of *Pycnolejeunea* (as *P. decurviloba* Steph.), but was transferred to *Cheilolejeunea* by He (1996) on account of the absence of ocelli and the avowed presence of a distal hyaline papilla. However, in her illustration of the lobule apex of *C. decurviloba*, He (1996: Fig. 2c) showed a small, one-celled and somewhat curved first lobule tooth and an indistinct second tooth, with the hyaline papilla being situated on the inside lobule surface proximal to the first tooth. A few years later, He (in Gradstein & Costa, 2003) admitted the presence of a proximal hyaline papilla in *C. decurviloba* but rather than returning the species to *Pycnolejeunea* she transferred it to *Trachylejeunea*, as *T. decurviloba* (Steph.) X.L. He. *Trachylejeunea* was subsequently placed into the synonymy of *Cheilolejeunea* by Gradstein & Ilkiu-Borges (2009) but *Trachylejeunea decurviloba* was not included in this transfer because of the presence of a proximal hyaline papilla and the absence of twinned lobule teeth, characteristic of *Trachylejeunea*, in this species. The present study confirms that *C. decurviloba* is a genuine member of *Pycnolejeunea* in spite of the absence of ocelli. The results also confirm that the number of ocelli in the leaves in *Pycnolejeunea* is variable, ranging from 0-5 (He, 1999). As shown by He (1999: Fig. 14c, d), ocelli may occasionally be absent as well typically present in the leaves of *P. contigua* (Nees) Grolle, the type of *Pycnolejeunea*. Although the presence of ocelli in the leaf lobes is considered to be an important generic character in several genera such as *Microlejeunea* (Spruce) Steph. (Dong *et al.*, 2013; Wei & Zhu, 2013), in *Cheilolejeunea* ocelli are present only in a few species, e.g. *C. falsinervis* (Sande Lac.) Kachroo et R.M. Schust., *C. insignis* Ast et Tixier, and *C. urubuensis* (Zartman et I.L. Ackerman) R.L. Zhu et Y.M. Wei (Wei *et al.*, 2013), and only occasionally in *C. aneogyna* (Spruce) A. Evans (Bastos, 2012).

The systematic position of *Cheilolejeunea gaoi*

Cheilolejeunea gaoi R.L. Zhu, M.L. So *et* Grolle is a narrowly endemic species known only from type locality in Shangsi Co., Guangxi, China (Zhu *et al.*, 2000; Zhu & So, 2003; He & Zhu, 2011). The local populations are small and threatened by human activities, and the species was therefore red-listed as an endangered bryophyte (Cao *et al.*, 2006; Zhu & So, 2003). It is characterized by an unusual combination of characters that sets it well apart from other members of the genus, as follows: (1) presence of *Allorgella*-type denticulations on leaf and underleaf margins, formed by two adjacent cells, (2) small, ovate leaf lobules without distinct teeth, (3) ental hyaline papilla, (4) finely segmented oil bodies, and (5) absence of gynoeical innovations (Zhu *et al.*, 2000; Zhu & So, 2003). Zhu *et al.* (2000) suggested an affinity to members of the genus *Pictolejeunea* Grolle (Zhu *et al.*, 2000), a small genus with six species, five of which are in tropical America and one in Borneo. However, *Pictolejeunea* clearly differs by numerous deeply pigmented ocelli in leaves, underleaves, bracts and perianths (e.g., Grolle & Reiner-Drehwald, 2005).

In our analyses *C. gaoi* was resolved in a monophyletic clade with *Anoplolejeunea* (subtribe Echinolejeuneinae), far outside the genus *Cheilolejeunea*. The monospecific, neotropical *Anoplolejeunea* is recognized by its highly inflated lobule with the free margin strongly rolled inward to the sac (Gradstein *et al.*, 2001). Despite the presence of finely segmented oil bodies, *Anoplolejeunea* clearly differs from *C. gaoi* in having gynoeical innovations, undivided underleaves and a distal hyaline papilla. The systematic position of *C. gaoi* will be addressed in a future paper.

TAXONOMIC CONCLUSIONS

The present study shows that the subtribe Cheilolejeuneinae consists of one single genus, the large pantropical *Cheilolejeunea*. Based on the above results, a first global classification system of the genus *Cheilolejeunea* based on morphological and molecular evidence is presented and formalized with circumscription below. The sections corresponds to the clades described in the previous chapter and are based on three quarter of the *Cheilolejeunea* species included in the molecular analysis. Thirteen species studied in this paper remain unclassified and should be the subject of future investigation. Two monospecific subgenera described by Schuster (1980), subg. *Renilejeunea* R.M. Schust. (type: *C. montagnei* (Gottsche) R.M. Schust.) from East Africa and subg. *Tegulilejeunea* R.M. Schust. (Type: *C. excisula* (Steph.) Mizut. = *C. incisa* (Gottsche) R.M. Schust. *et* Kachroo) from Asia, have not yet been analysed and are also omitted here.

Cheilolejeunea* sect. *Anomalolejeunea* (Schiffn.) W. Ye, Gradst. *et* R.L. Zhu, *stat. nov.

≡ *Lejeunea* subg. *Anomalolejeunea* Spruce, *Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl.* 9: 5. 1887. ≡ *Anomalolejeunea* (Spruce) Schiffn. in Engler *et* Prantl, *Nat. Pflanzenfam.* 1, 3: 127. 1893 – **Type:** *Anomalolejeunea pluriplicata* (Pearson) Schiffn. (≡ *Lejeunea pluriplicata* Pearson).

Stem with hyalodermis. Leaf apex rounded to obtuse. Lobule tooth short, blunt. Oil bodies two or more per cell. Underleaves bifid. Innovations lejeuneoid.

Distribution: paleotropical.

Cheilolejeunea* sect. *Cheilolejeunea

Type: *Cheilolejeunea decidua* (Spruce) A. Evans (\equiv *Lejeunea decidua* Spruce) (\equiv *C. adnata* (Kunze ex Lehm.) Grolle).

Stem with hyalodermis. Leaf apex rounded. Lobule tooth long. Oil bodies several per cell, coarsely granular. Underleaves bifid. Innovations absent.

Distribution: pantropical.

Cheilolejeunea* sect. *Cyrtolejeunea (A. Evans) W. Ye, Gradst. *et* R.L. Zhu, *stat. nov.*
 \equiv *Cyrtolejeunea* A. Evans, *Bull. Torrey Bot. Club* 30: 553. 1903 – **Type:** *Cyrtolejeunea holostipa* (Spruce) A. Evans (\equiv *Lejeunea holostipa* Spruce).

Plants very small and with suberect leaves. Stem with hyalodermis. Leaf apex rounded. Lobule tooth very long and sharp. Oil bodies several per cell, finely granular. Underleaves undivided to short-bifid. Innovations pycnolejeuneoid.

Distribution: tropical America, East Africa, continental East Asia.

Cheilolejeunea* sect. *Euosmolejeunea (Spruce) W. Ye, Gradst. *et* R.L. Zhu, *stat. nov.*
 \equiv *Lejeunea* subg. *Euosmolejeunea* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 241. 1884 – **Type:** *Cheilolejeunea trifaria* (Reinw., Blume *et* Nees) Mizut. (\equiv *Jungermannia trifaria* Reinw., Blume *et* Nees).

Stem with hyalodermis. Leaf apex rounded. Lobule tooth blunt. Oil bodies several per cell, coarsely granular. Underleaves bifid (or undivided?). Innovations lejeuneoid.

Distribution: pantropical.

Cheilolejeunea* sect. *Leucolejeunea (A. Evans) W. Ye, Gradst. *et* R.L. Zhu, *stat. nov.*
 \equiv *Leucolejeunea* A. Evans, *Torreya* 7: 225. 1907 – **Type:** *Cheilolejeunea clypeata* (Schwein.) W. Ye *et* R.L. Zhu (\equiv *Jungermannia clypeata* Schwein.).

Stem without hyalodermis. Leaf apex rounded. Lobule tooth short or long. Oil bodies one per cell, very coarsely granular. Underleaves undivided. Innovations pycnolejeuneoid.

Distribution: pantropical.

Cheilolejeunea* sect. *Omphalanthus (Lindenb. *et* Nees) W. Ye, Gradst. *et* R.L. Zhu, *stat. nov.*

\equiv *Omphalanthus* Lindenb. *et* Nees in Gottsche *et al.*, *Syn. Hepat.*: 303. 1845 – **Type:** *Omphalanthus filiformis* (Sw.) Nees (\equiv *Jungermannia filiformis* Sw.).

= *Aureolejeunea* R.M. Schust., *Phytologia* 39: 428. 1978, **syn. nov.** – **Type:** *Aureolejeunea aurifera* R.M. Schust.

Plants ascending to pendent. Stem without hyalodermis. Leaf apex rounded to acute. Lobule tooth short. Leaf cells with large trigones, intermediate thickenings absent. Oil bodies several per cell, coarsely granular. Underleaves undivided to short-bifid. Innovations lejeuneoid.

Although species of *Omphalanthus s.str.* form a monophyletic group sister to *Aureolejeunea* species, the two groups are placed in a single section due to the unresolved position of the type of *Aureolejeunea* and because of major morphological similarities between the two groups. For example, the common *A. tonduzana* may confusingly resemble *Omphalanthus* by its green to pale brown color (instead of

dark brown). Also, the perianth in *A. tonduzana* varies from 5-keeled to terete, like in *Omphalanthus filiformis*. On the other hand, certain phenotypes of *O. filiformis* may be loosely creeping rather than pendent, like in *Aureolejeunea*, instead of being pendent. Such forms of *O. filiformis* can only be distinguished from *Aureolejeunea* by the slightly shorter lobules and dioicy. For the time being, we will put *Omphalanthus* and *Aureolejeunea* together in one separate section, including *A. aurifera*, *A. lumae*, *A. paramicola* (Herzog) R.M. Schust., *A. quinquecarinata* R.M. Schust., *A. rotalis* (= *Cheilolejeunea rotalis*), *A. tonduzana* (Steph.) Gradst., *O. filiformis*, *O. jackii* (Prantl) Gradst. and *O. ovalis*. Future work that features a wider sampling may show us more implications on the relationships among the section.

Distribution: tropical America, St. Helena.

Cheilolejeunea aurifera (R.M. Schust.) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Aureolejeunea aurifera* R.M. Schust., *Phytologia* 39: 429. 1978.

Cheilolejeunea baracoensis (Mustelier, M.E. Reiner *et* Gradst.) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Omphalanthus baracoensis* Mustelier, M.E. Reiner *et* Gradst., *J. Bryol.* 29: 95. 2007.

Cheilolejeunea filiformis (Sw.) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Jungermannia filiformis* Sw., *Prodr.*: 144. 1788 ≡ *Omphalanthus filiformis* (Sw.) Nees in Gottsche *et al.*, *Syn. Hepat.*: 304. 1845.

Cheilolejeunea filiformis var. ***platycoleus*** (Herzog) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Omphalanthus filiformis* var. *platycoleus* (Herzog) Gradst., *Phytotaxa* 76: 46. 2013
 ≡ *Omphalanthus platycoleus* Herzog, *Feddes Repert. Spec. Nov. Regni Veget.* 57: 171. 1955.

Cheilolejeunea filiformis var. ***wallisii*** (Prantl) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Lejeunea wallisii* Prantl, *Hedwigia* 31: xvii, 1892 ≡ *Peltolejeunea wallisii* (Prantl) J.B. Jack *et* Steph. in Stephani, *Sp. Hepat.* 4: 699. 1911 ≡ *Omphalanthus wallisii* (Prantl) Gradst., *J. Hattori Bot. Lab.* 45: 123. 1979 ≡ *Omphalanthus filiformis* var. *wallisii* (Prantl) Gradst., *Phytotaxa* 76: 46. 2013. The author citation “Prantl” for *Lejeunea wallisii* follows the recommendation of Söderström *et al.* (2015).

Cheilolejeunea huanucensis (Gottsche) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Lejeunea huanucensis* Gottsche in Gottsche *et al.*, *Syn. Hepat.* 3: 335. 1845
 ≡ *Omphalanthus huanucensis* (Gottsche) Gradst., *Beih. Nova Hedwigia* 80: 109. 1985.

Cheilolejeunea jackii (Prantl) W. Ye, R.L. Zhu *et* Gradst., **comb. nov.**

≡ *Lejeunea jackii* Prantl, *Hedwigia* 31: xvii. 1892 ≡ *Omphalanthus jackii* (Prantl) Gradst., *Proc. Kon. Ned. Akad. Wetensch.*, C 80: 410. 1977. The author citation “Prantl” for *Lejeunea jackii* follows the recommendation of Söderström *et al.* (2015).

Cheilolejeunea lumae (Herzog) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Brachiolejeunea lumae* Herzog, *Beih. Bot. Centralbl., Abt. 2*, 60: 15. 1939

≡ *Aureolejeunea lumae* (Herzog) van Slageren, *Meded. Bot. Mus. Herb. Rijksuniv. Utrecht* 544: 121. 1985.

Cheilolejeunea ovalis (Lindenb. *et* Gottsche) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Lejeunea ovalis* Lindenb. *et* Gottsche in Gottsche *et al.*, *Syn. Hepat.*: 754. 1847

≡ *Peltolejeunea ovalis* (Lindenb. *et* Gottsche) Schiffn., in Engler & Prantl, *Nat. Pflanzenfam.* 1, 3: 131. 1893 ≡ *Omphalanthus ovalis* (Lindenb. *et* Gottsche) Gradst., *Lindbergia* 23: 77. 1977.

Cheilolejeunea paramicola (Herzog) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Brachiolejeunea paramicola* Herzog, *Hedwigia* 74: 95. 1934 ≡ *Omphalanthus*

paramicola (Herzog) Gradst., *J. Hattori Bot. Lab.* 50: 244. 1981 ≡ *Aureolejeunea paramicola* (Herzog) R.M. Schust., *Phytologia* 61: 446. 1987.

= *Aureolejeunea paramoensis* R.M. Schust., *Phytologia* 39: 428. 1978.

Cheilolejeunea quinquecarinata (R.M. Schust.) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Aureolejeunea quinquecarinata* R.M. Schust., *Phytologia* 39: 429. 1978.

Cheilolejeunea roccatii (Gola) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Acrolejeunea roccatii* Gola, *Annal. Bot., Roma* 6: 274. 1907 ≡ *Evansiolejeunea*

roccatii (Gola) Vanden Berghen, *Bull. Soc. Roy. Bot. Belg.* 92: 117. 1960

≡ *Omphalanthus roccatii* (Gola) R.M. Schust., *Beih. Nova Hedwigia* 9: 96, 1963.

= *Evansiolejeunea renistipula* Vanden Berghen, *Rev. Byol. Lichénol.* 17: 87. 1948

≡ *Omphalanthus renistipulus* Steph., *Wiss. Ergebn. Deut. Zentr.-Afr. Exped., Bot.* 2: 123. 1911. *nom. illeg.* [non *Omphalanthus renistipulus* Lindenb. 1845].

Cheilolejeunea tonduzana (Steph.) W. Ye, R.L. Zhu *et Gradst.*, **comb. nov.**

≡ *Archilejeunea tonduzana* Steph., *Sp. Hepat.* 4: 721. 1911 ≡ *Aureolejeunea*

tonduzana (Steph.) Gradst., *Phytotaxa* 76: 46. 2013.

= *Aureolejeunea fulva* R.M. Schust., *Phytologia* 39: 429. 1978.

Cheilolejeunea* sect. *Paroicae (R.M. Schust.) W. Ye, Gradst. *et* R.L. Zhu, **stat. nov.**

≡ *Leucolejeunea* sect. *Paroicae* R.M. Schust., *Hep. Anth. N. America* 4: 819. 1980 –

Type: *Cheilolejeunea kitagawae* W. Ye *et* R.L. Zhu (≡ *Leucolejeunea paroica* N. Kitag.).

Stem without hyalodermis. Leaf apex rounded. Lobule tooth short or long. Oil bodies 2-3 per cell, very coarsely granular. Underleaves undivided. Innovations pycnolejeuneoid.

Distribution: paleotropical.

Cheilolejeunea* sect. *Strepsilejeunea (Spruce) W. Ye, Gradst. *et* R.L. Zhu, **stat. nov.**

≡ *Lejeunea* sect. *Strepsilejeunea* “*Stripsilejeunea*” Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 168. 1884 –

Type: *Cheilolejeunea inflexa* (Hampe ex Lehm.) Steph. (≡ *Lejeunea inflexa* Hampe ex Lehm).

Stem with hyalodermis. Leaf apex acute. Lobule tooth short or long. Oil bodies several per cell, coarsely granular. Underleaves bifid. Innovations pycnolejeuneoid.

Distribution: Afro-American.

Cheilolejeunea sect. *Xenolejeunea* (Kachroo et R.M. Schust.) B. Thiers, *Trop. Bryol.* 5: 14. 1992.

≡ *Cheilolejeunea* subg. *Xenolejeunea* Kachroo et R.M. Schust., *J. Linn. Soc., Bot.* 56: 496. 1961 – **Type:** *Cheilolejeunea imbricata* (Nees) S. Hatt. (= *C. trapezia* (Nees) Kachroo et R.M. Schust.).

Stem with hyalodermis. Leaf apex rounded. Lobule rectangular, $> 1/2 \times$ leaf length, tooth short or long. Oil bodies several per cell, coarsely granular. Ocelli occasionally present. Underleaves bifid. Innovations pycnolejeuneoid.

Distribution: paleotropical.

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APPENDIX 1

Specimens used in this study with location, reference collection detail and GenBank accession numbers (ITS, *trnG*, *trnL-F*). Newly obtained sequences for this study are in bold face. A hyphen indicates a missing sequence.

- Acrolejeunea infusca* (Mitt.) Jian Wang bis et Gradst., China, *D.G. Long* 33574 (HSNU), **KT190894**, **KT190835**, **KT190778**.
- Acrolejeunea sandvicensis* Steph., China, *J. Wang et al.* 20090922-1 (HSNU), **KT190893**, **KT190834**, **KT190777**.
- Acrolejeunea sinensis* (Jian Wang bis, R.L. Zhu et Gradst.) Jian Wang bis et Gradst., China, *Y.M. Wei* 20100210-48 (HSNU), **KT190892**, **KT190833**, **KT190776**.
- Anoplolejeunea conferta* (C.F.W. Meissn. ex Spreng.) A. Evans, Ecuador, *R. Wilson et al.* 04-08 (GOET), DQ987335, -, DQ987438.
- Aureolejeunea aurifera* R.M. Schust., Costa Rica, *I. Holz* CR00-0812 (GOET), **KT190949**, **KT190883**, **KT190825**.
- Aureolejeunea paramicola* (Herzog) R.M. Schust., Ecuador, *A. Schäfer-Verwimp & M. Preussing* 23299/A (Herb. Schäfer-Verwimp), **KT190952**, **KT190886**, -.
- Aureolejeunea quinquecarinata* R.M. Schust., Costa Rica, *A. Schäfer-Verwimp & I. Holz* SV/H-0457/A (Herb. Schäfer-Verwimp), **KT190951**, **KT190885**, -.
- Aureolejeunea tonduzana* (Steph.) Gradst., Brazil, *D.P. Costa & S.R. Gradstein* 3725 (GOET), **KT190950**, **KT190884**, **KT190826**.
- Brachiolejeunea laxifolia* (Taylor) Schiffn., Ecuador, *J.A. Shaw* 11216E (DUKE), **KT190895**, **KT190836**, **KT190779**.
- Ceratolejeunea coarina* (Gottsche) Steph., Brazil, *Zartman* 1235.1 (DUKE), -, AY608170, AY608122.
- Cheilolejeunea acutangula* (Nees) Grolle, Brazil, *N.D. Santos et al.* 400B (RB), **KT190904**, **KT190845**, **KT190788**.
- Cheilolejeunea adnata* (Kunze ex Lehm.) Grolle, Dominica, *A. Schäfer-Verwimp & I. Verwimp* 18062 (GOET), **KT190898**, **KT190839**, **KT190782**.
- Cheilolejeunea beyrichii* (Lindenb.) M.E. Reiner, Honduras, *B. Allen* 17393 (GOET), DQ987271, -, DQ987387.
- Cheilolejeunea ceylanica* R.M. Schust. et Kachroo, China, *R.L. Zhu et al.* 20050901-6 (HSNU), **KT190914**, **KT190852**, -.
- Cheilolejeunea chenii* R.L. Zhu et M.L. So, China, *D.G. Long* 33756 (HSNU), **KT190901**, **KT190842**, **KT190785**.
- Cheilolejeunea clausa* (Nees & Mont.) R.M. Schust., Brazil, *N.D. Santos et al.* 400A (RB), **KT190940**, **KT190874**, **KT190819**.
- Cheilolejeunea cordigera* (Steph.) Grolle, Madagascar, *T. Pócs & A. Szabó* 9878/FH (EGR), **KT190910**, -, **KT190794**.
- Cheilolejeunea decurviloba* (Steph.) X.L. He, Venezuela, *T. Pócs* 00222/BB (EGR), -, -, **KT190827**.
- Cheilolejeunea ecarinata* Vanden Berghen, Réunion Island, *A. Vojtko* 9427/AS (EGR), **KT190944**, **KT190878**, -.
- Cheilolejeunea falsinervis* (Sande Lac.) Kachroo et R.M. Schust., China, *R.L. Zhu et al.* 20031202-48 (HSNU), **KT190912**, -, -.
- Cheilolejeunea gaoi* R.L. Zhu, M.L. So et Grolle I, China, *W. Ye & Y.M. Wei* 20090716-17 (HSNU), **KT190896**, **KT190837**, **KT190780**.
- Cheilolejeunea gaoi* II, China, *W. Ye & Y.M. Wei* 20090717-1 (HSNU), **KT190897**, **KT190838**, **KT190781**.
- Cheilolejeunea holostipa* (Spruce) A. Evans, Costa Rica, *A. Schäfer-Verwimp & I. Holz* SV/H-0061 (Herb. Schäfer-Verwimp), -, **KT190841**, -.
- Cheilolejeunea inflexa* (Hampe ex Lehm.) Grolle, Guadeloupe, *A. Schäfer-Verwimp & I. Verwimp* 22575 (GOET), **KT190906**, **KT190847**, **KT190790**.
- Cheilolejeunea insecta* Grolle et Gradst., Brazil, *A. Schäfer-Verwimp & I. Verwimp* 13447/A (Herb. Schäfer-Verwimp), **KT190902**, **KT190843**, **KT190786**.
- Cheilolejeunea intertexta* (Lindenb.) Steph., China, *R.L. Zhu et al.* 20050908-20

- (HSNU), **KT190908**, **KT190849**, **KT190792**.
- Cheilolejeunea krakammae* (Lindenb.) R.M. Schust., China, *R.L. Zhu* 20070319-7 (HSNU), **KT190935**, **KT190869**, **KT190814**.
- Cheilolejeunea laevicalyx* (J.B. Jack *et* Steph.) Grolle I, Ecuador, *S.R. Gradstein* 10104 (GOET), **KT190941**, **KT190875**, **KT190820**.
- Cheilolejeunea laevicalyx* II, Mexico, *S.R. Gradstein & A. Velasquez s.n.* (GOET), **KT190942**, **KT190876**, -.
- Cheilolejeunea laeviuscula* (Mitt.) Steph., Thailand, *A. Schäfer-Verwimp & I. Verwimp* 23802A (HSNU), **KT190934**, **KT190868**, **KT190813**.
- Cheilolejeunea larsenii* Mizut., Malaysia, *M.S. Chuah & K.T. Yong* 09/002/39 (HSNU), **KT190899**, **KT190840**, **KT190783**.
- Cheilolejeunea meyeniana* (Gottsche, Lindenb. *et* Nees) R.M. Schust. *et* Kachroo, Australia, *E.A. Brown & A. Leishman* 2000/45 a (EGR), **KT190915**, **KT190853**, **KT190796**.
- Cheilolejeunea mimosa* (Hook. f. *et* Taylor) R.M. Schust., New Zealand, *A. Schäfer-Verwimp & I. Verwimp* 13664 (GOET), **KT190943**, **KT190877**, **KT190821**.
- Cheilolejeunea nipponica* (S. Hatt.) S. Hatt., China, *J. Wang et al.* 20090801-5 (HSNU), **KT190909**, **KT190850**, **KT190793**.
- Cheilolejeunea obtusifolia* (Steph.) S. Hatt., China, *R.L. Zhu* 20090626-15 (HSNU), **KT190900**, -, **KT190784**.
- Cheilolejeunea oclusa* (Herzog) T. Kodama *et* N. Kitag., Indonesia, *F.I. Windadri* 3876b (IBSC), **KT190911**, -, -.
- Cheilolejeunea oncophylla* (Ångstr.) Grolle *et* M.E. Reiner, Dominican Republic, *A. Schäfer-Verwimp & I. Verwimp* 26881/A (GOET), **KT190903**, **KT190844**, **KT190787**.
- Cheilolejeunea osumiensis* (S. Hatt.) Mizut., China, *R.L. Zhu* 20090220-25B (HSNU), **KT190931**, **KT190866**, **KT190810**.
- Cheilolejeunea pluriplicata* (Pearson) R.M. Schust., Thailand, *A. Schäfer-Verwimp & I. Verwimp* 23883B (HSNU), **KT190932**, **KT190867**, **KT190811**.
- Cheilolejeunea pocsii* E.W. Jones, Kenya, *T. Pócs et al.* 04011/AW (EGR), **KT190933**, -, **KT190812**.
- Cheilolejeunea rigidula* (Mont.) R.M. Schust., U.S.A., *R. Seman* 28 (DUKE), **KT190937**, **KT190871**, **KT190816**.
- Cheilolejeunea ryukyuensis* Mizut., China, *W. Ye & Y.M. Wei* 20090715-4 (HSNU), **KT190907**, **KT190848**, **KT190791**.
- Cheilolejeunea serpentina* (Mitt.) Mizut., Madagascar, *T. Pócs et al.* 90100/AM (EGR), **KT190936**, **KT190870**, **KT190815**.
- Cheilolejeunea* sp., Thailand, *A. Schäfer-Verwimp & I. Verwimp* 24032 (HSNU), **KT190905**, **KT190846**, **KT190789**.
- Cheilolejeunea streimannii* Pócs *et* T.N. Ninh, Vietnam, *H. Schneider* V-2011-H-25-C (HSNU), **KT190920**, -, -.
- Cheilolejeunea subopaca* (Mitt.) Mizut., China, *J. Wang & T. Peng* 20111018-48 (HSNU), **KT190921**, -, -.
- Cheilolejeunea surrepens* (Mitt.) E.W. Jones, Comoro Islands, *T. Pócs* 9150/W (EGR), **KT190916**, **KT190854**, **KT190797**.
- Cheilolejeunea trapezia* (Nees) Kachroo *et* R.M. Schust. I, China, *W. Ye & Y.M. Wei* 20090715-66 (HSNU), **KT190913**, **KT190851**, **KT190795**.
- Cheilolejeunea trapezia* II, China, *R.L. Zhu et al.* 20090630-18 (HSNU), **KT190918**, **KT190856**, **KT190799**.
- Cheilolejeunea trapezia* III, Indonesia, *S.R. Gradstein* 12057 (GOET), **KT190919**, **KT190857**, **KT190800**.
- Cheilolejeunea trifaria* (Reinw., Blume *et* Nees) Mizut. I, Guadeloupe, *A. Schäfer-Verwimp & I. Verwimp* 22434 (GOET), **KT190938**, **KT190872**, **KT190817**.
- Cheilolejeunea trifaria* II, Seychelles, *M.R.D. Seaward* 111222 (EGR), **KT190939**, **KT190873**, **KT190818**.
- Cheilolejeunea vittata* (Steph. *ex* G. Hoffm.) R.M. Schust. *et* Kachroo, China, *R.L. Zhu et al.* 20050907-32 (HSNU), **KT190917**, **KT190855**, **KT190798**.
- Cystolejeunea lineata* (Lehm. *et* Lindenb.) A. Evans, Guadeloupe, *A. Schäfer-Verwimp* 22183 (GOET), DQ987295, -, DQ987401.
- Evansiolejeunea roccatii* (Gola) Vanden Berghen, Rwanda, *E. Fischer* X-RWA-1120 (Herb. Schäfer-Verwimp), **KT190923**, **KT190858**, **KT190802**.

- Leiolejeunea grandistipula* A. Evans I, Jamaica, *A. Schäfer-Verwimp* 35422 (M), KJ716768, -, KJ716781.
- Leiolejeunea grandistipula* II, Jamaica, *A. Schäfer-Verwimp* 35394 (M), KJ716769, -, KJ716782.
- Lejeunea deplanata* Nees, U.S.A., *B. Shaw* 6090 (DUKE), **KT190957**, -, **KT190832**.
- Lejeunea flava* (Sw.) Nees I, U.S.A., *P. Majestyk* 5000 (DUKE), **KT190954**, **KT190887**, **KT190829**.
- Lejeunea flava* II, U.S.A., *J.A. Shaw* 9292 (DUKE), **KT190955**, **KT190888**, **KT190830**.
- Lejeunea* sp. I, Kenya, *T. Pócs & A. Szabó* 9218/FC (EGR), **KT190953**, -, **KT190828**.
- Lejeunea* sp. II, Malaysia, *S.R. Gradstein* 10369 (GOET), **KT190956**, **KT190889**, **KT190831**.
- Lejeunea tapajosensis* Spruce, Suriname, *J. Muñoz* 98-53 (GOET), **KT190958**, **KT190890**, -.
- Leucolejeunea clypeata* (Schwein.) A. Evans I, U.S.A., *B. Shaw* 4714 (DUKE), **KT190928**, **KT190863**, **KT190807**.
- Leucolejeunea clypeata* II, U.S.A., *B.R. Speer* 896 (DUKE), **KT190929**, **KT190864**, **KT190808**.
- Leucolejeunea conchifolia* (A. Evans) A. Evans I, U.S.A., *B. Shaw* 4315 (DUKE), **KT190924**, **KT190859**, **KT190803**.
- Leucolejeunea conchifolia* II, U.S.A., *P. Majestyk* 4927 (DUKE), **KT190925**, **KT190860**, **KT190804**.
- Leucolejeunea turgida* (Mitt.) Verd., China, *W. Ye & Y.M. Wei* 20090720-20 (HSNU), **KT190922**, -, **KT190801**.
- Leucolejeunea uncioba* (Lindenb.) A. Evans, U.S.A., *P. Majestyk* 7114 (DUKE), **KT190930**, **KT190865**, **KT190809**.
- Leucolejeunea xanthocarpa* (Lehm. et Lindenb.) A. Evans I, China, *R.L. Zhu et al.* 20090630-21 (HSNU), **KT190926**, **KT190861**, **KT190805**.
- Leucolejeunea xanthocarpa* II, Bolivia, *S. Churchill* 22273 (GOET), **KT190927**, **KT190862**, **KT190806**.
- Omphalanthus filiformis* (Sw.) Nees I, Puerto Rico, *K.M. Pryer* 974 (DUKE), **KT190945**, **KT190879**, -.
- Omphalanthus filiformis* II, Bolivia, *S. Churchill et al.* 23653 (GOET), **KT190946**, **KT190880**, **KT190822**.
- Omphalanthus ovalis* (Lindenb. et Gottsche) Gradst. I, Ecuador, *A. Schäfer-Verwimp et al.* 24524 (Herb. Schäfer-Verwimp), **KT190947**, **KT190881**, **KT190823**.
- Omphalanthus ovalis* II, Ecuador, *A. Schäfer-Verwimp et al.* 24324 (GOET), **KT190948**, **KT190882**, **KT190824**.
- Pycnolejeunea densistipula* (Lehm. et Lindenb.) Steph., Ecuador, *A. Schäfer-Verwimp* 23368 (GOET), DQ987294, -, DQ987400.
- Trachylejeunea aneogyna* (Spruce) Grolle, Brazil, *A. Schäfer-Verwimp* 9751 (Herb. Schäfer-Verwimp), -, **KT190891**, -.

