

SYSTEMATICS AND PHYLOGENY

Phylogeny and taxonomy of *Archilejeunea* (Marchantiophyta: Lejeuneaceae) based on molecular markers and morphology

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Abstract *Archilejeunea*, a pantropical liverwort genus of about 22 species, has not been revised worldwide and recent phylogenetic study showed that the genus is not monophyletic. We addressed phylogenetic relationships of *Archilejeunea* by using nuclear (ITS) and chloroplast (*rbcL*, *trnL-F*) DNA regions. Bayesian, likelihood and parsimony phylogenetic analyses of a broad sampling of the group resolved the species in three robust clades, which are morphologically distinct. Based on our molecular phylogenetic results, we split *Archilejeunea* into two distantly related genera, *Archilejeunea* s.str. with six species and *Dibrachiella* stat. nov. with nine species. Both groups have tropical Afro-American distributions but the range of *Archilejeunea* is much more restricted than that of *Dibrachiella*. *Archilejeunea* is sister to *Verdoornianthus* from Amazonia and *Dibrachiella* is member of a clade together with the paleotropical *Ptychanthus* and *Tuzibeanthus*, and the pantropical *Spruceanthus*. Five species previously placed in *Archilejeunea* (*A. abbreviata*, *A. amakawana*, *A. kiushiana*, *A. olivacea*, *A. planiuscula*) are resolved in *Spruceanthus*, which is morphologically very similar to *Dibrachiella*. Fifteen new combinations and one replacement name are proposed. Ancestral state reconstruction showed that morphological characters traditionally used to define genera of Ptychanthoideae are highly homoplasious. *Spruceanthus* differs from *Dibrachiella* in possessing homogeneous oil bodies.

Keywords *Dibrachiella*; Lejeuneaceae; liverworts; morphological analysis; polyphyly; *Spruceanthus*; taxonomy

Supplementary Material The Electronic Supplement (Tables S1–S2; Figs. S1–S2) is available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>. The DNA sequence alignment, independent maximum parsimony trees of chloroplast regions (*trnL-F*, *rbcL*) and the nuclear region (nrITS) with support values, and a single tree of maximum likelihood analyses (Fig. 1) are deposited on TreeBase (<http://purl.org/phylo/treebase/phyloids/study/TB2:SI7264>).

■ INTRODUCTION

Lejeuneaceae subfam. Ptychanthoideae with about 180 species in 19 genera (Söderström & al., 2015) is one of the most thoroughly studied groups of tropical liverworts. Taxonomic treatments have been published for tropical America (Gradstein, 1994), West Africa (Wigginton, 2004), tropical Asia (Mizutani, 1961, 1968; Gradstein & al., 2002; Haerida & al., 2010; Kornochalert & al., 2012) and Australia (Thiers & Gradstein, 1989), and full or partial revisions are available for all genera with the exception of *Archilejeunea* (Spruce) Steph., *Caudalejeunea* (Steph.) Schiffn. and *Spruceanthus* Verd. (e.g., Gradstein, 1975, 1994, 2012, 2015; Vanden Berghen, 1984; Mizutani, 1989; Reiner-Drehwald & Weis, 2001; Zhu & Gradstein, 2005; Pócs, 2008; Sukkharak & Gradstein, 2014; Sukkharak, 2015). Phylogenetic relationships based on morphological traits were studied by Gradstein (1994), Gradstein & al.

(2003) and Sukkharak & al. (2011), whereas Wilson & al. (2007) explored generic relationships within the subfamily using a four-marker molecular dataset of 15 genera. These studies suggested that the genera of Ptychanthoideae are monophyletic with the exception of *Archilejeunea*, and are characterized by a combination of molecular data and mostly non-exclusive morphological character states (Sukkharak & al., 2011).

Here we focus on *Archilejeunea*, one of the least known genera of Ptychanthoideae with about 22 species (Shi & al., 2015). The group is pantropical in distribution and characterized by stems without enlarged epidermis cells, isodiametric leaf cells with unpigmented walls, simple-triangular to radiate trigones, segmented oil bodies, presence of gynoeical innovations, and perianths with 4–5 smooth to weakly toothed keels (Gradstein, 1994). The species are traditionally placed in two subgenera, the neotropical *A.* subg. *Archilejeunea* (five spp.) and the pantropical *A.* subg. *Dibrachiella* (Spruce) Schiffn.

(ca. 17 spp.). The two groups are distinguished by innovation leaf sequence, which is pycnolejeunoid in subg. *Archilejeunea* (basal leafy appendage of innovation is an underleaf) and lejeuneoid in subg. *Dibrachiella* (basal leafy appendage is a lateral leaf), and by the occurrence of reduced lobules in subg. *Dibrachiella* (Gradstein & Buskes, 1985).

Recent molecular-phylogenetic studies indicated that *Archilejeunea* is not monophyletic (Wilson & al., 2007). Members of *A.* subg. *Archilejeunea* were resolved in a clade with *Caudalejeunea* and *Schiffneriolejeunea* Verd., while those of *A.* subg. *Dibrachiella* were resolved in a distant clade with species of *Spruceanthus* and *Ptychanthus* Nees. The close relationship of *A.* subg. *Dibrachiella* and *Spruceanthus*, a genus of seven species in Asia and Australasia and one in tropical America, is supported by many morphological similarities (Amakawa, 1964; Thiers & Gradstein, 1989), but the close affinity to *Ptychanthus* is not. Similarly, a close relationship between *A.* subg. *Archilejeunea*, *Caudalejeunea* and *Schiffneriolejeunea* is not evident from morphology (Gradstein, 1994). According to Gradstein (1994), *A.* subg. *Archilejeunea* is very similar to *Verdoornianthus* Gradst., a small Amazonian genus of two species characterized by lack of innovations. The phylogenetic relationship between *Verdoornianthus* and *Archilejeunea* has not yet been studied with molecular methods, however.

The study by Wilson & al. (2007) was based on very limited sampling of *Archilejeunea* and *Spruceanthus*. Moreover, *Verdoornianthus* was not included in this study. The aim of the present studies is to reconstruct the phylogeny of *Archilejeunea* based on an extensive sampling of this genus and other members of Ptychanthoideae. By using two chloroplast DNA (cpDNA) regions (*rbcL*, *trnL-F*) and the nuclear ribosomal internal transcribed spacer (nrITS) we determine the phylogenetic relationships of the species of the polyphyletic *Archilejeunea*.

■ MATERIALS AND METHODS

Taxon sampling. — For morphological delimitation and characterization of the species we studied approximately 600 specimens of *Archilejeunea* from 16 herbaria (BR, COL, E, EGR, FH, G, GOET, HIRO, HSNU, MANCH, MO, NICH, NY, PC, STR, U), including type specimens of all species currently recognized. For molecular analyses we sampled 46 species (74 accessions) of 17 genera of Ptychanthoideae (Appendix 1), representing all genera recognized in the subfamily with the exception of two rare monospecific genera (*Cephalantholejeunea* M.Reiner & G.Weis, *Cephalolejeunea* Mizut.). Our sampling included 12 species (29 accessions) of *Archilejeunea*, representing more than half of the species in the genus and covering the entire taxonomic diversity and geographical range of the group. We also included 5 species (out of 8 recognized) of *Spruceanthus* as well as the 2 species of *Verdoornianthus*, which had not been investigated by molecular methods before. All voucher specimens were carefully examined and identifications were corrected when necessary. For the outgroup we included 8 species representing 6 genera of

Lejeuneoideae tribe Brachiolejeuneae (Wilson & al., 2007). A total of 133 sequences (45 nrITS, 45 *rbcL*, 43 *trnL-F*) were newly generated for this study; 112 additional sequences were download from GenBank including 92 from Wilson & al. (2007), 11 from Hartmann & al. (2006), 6 from Wilson & al. (2004) and 3 from Wang & al. (2014b). Voucher information and Genbank accession numbers are listed in Appendix 1.

DNA extraction, PCR and sequencing. — Total genomic DNA was extracted using DNeasy plant mini kits (Qiagen, Hilden, Germany). Two chloroplast regions (*rbcL*, *trnL-F*) and nuclear ribosomal internal transcribed spacers 1 and 2 with the intervening 5.8S ribosomal subunit (nrITS) were amplified using the polymerase chain reaction (PCR). Amplification protocols and sequencing primers followed Wilson & al. (2004) and Gradstein & al. (2006) for *rbcL*, Taberlet & al. (1991) for *trnL-F* and Hartmann & al. (2006) for nrITS. Bidirectional sequencing was generated by Jie Li Biology Inc., China (<http://www.genebioseq.com>).

Phylogenetic analyses. — All sequences were assembled and aligned manually using PhyDE v.0.997 (<http://www.phyde.de/>). Ambiguous positions (103 *trnL-F*, 1167 ITS) were excluded from the alignments and lacking data were coded as missing. The DNA sequence alignments were submitted to TreeBase (<http://purl.org/phylo/treebase/phylovs/study/TB2:SI7264>).

Maximum parsimony, maximum likelihood and Bayesian inference phylogenetic methods were used to analyse the data. The chloroplast and nuclear regions were explored by visual comparison of the tree bootstraps obtained from independent maximum parsimony analyses of each region. Bootstrap values of similar nodes less than 70% were not considered as incongruent among DNA markers. As the results showed no evidence for incongruent nodes, a combined dataset was used for phylogenetic analyses.

Maximum parsimony (MP) analyses were executed in PAUP* v.4.0b10 (Swofford, 2002) with command files for the parsimony ratchet (Nixon, 1999) generated using the program PRAP2 (Wall & al., 2008). The following options were implemented: tree bisection-reconnection (TBR) branch swapping, characters treated as equally weighted and unordered, gaps treated as missing characters. Bootstrap analyses were performed with 10,000 replicates.

Maximum likelihood (ML) analyses were performed in PhyML v.3.0 (Guindon & Gascuel, 2003). jModeltest v.2.1.3 (Posada, 2008) was used to select the best-fit nucleotide substitution model for the ML analyses, based on Akaike information criterion (AIC). A general time reversible model with a proportion of invariable sites and gamma-distributed rate variation across sites (GTR+I+G) was selected. The number of random starting trees (Nst) was five and bootstrap values were obtained with 100 replicates.

Bayesian inference (BI) analyses were conducted using MrBayes v.3.2 (Ronquist & al., 2012). MrModeltest v.2.3 (Nylander, 2004) as implemented in PAUP* v.4.0b10 was used to select the optimal nucleotide substitution model for BI analyses; the GTR+I+G model was the best-fit for all three markers. Nst = 6 and rates = invgamma were used for BI analyses of the combined sequence dataset. Four simultaneous Markov chains

were run for five million generations and sampled every 1000th generation. The first 1000 samples were discarded as burn-in samples. Posterior probability (PP) confidence values were generated from trees found after the initial burn-in period.

Bayesian test of topology. — The polyphyly of *Archilejeunea* was tested following Bergsten & al. (2013) by contrasting the fit of two topology models, one where *Archilejeunea* was forced to monophyly and one where the analyses were unconstrained. The marginal likelihood of the models was calculated using the stepping-stone sampling method of Xie & al. (2011); interpretation followed Kass & Raftery (1995).

Ancestral state reconstruction. — Thirteen morphological characters traditionally used for delimitation of genera of Ptychanthoideae (Gradstein, 1975, 1994; Thiers & Gradstein, 1989; Gradstein & al., 2002; Sukkharak & Gradstein, 2014) were scored for ancestral state reconstruction (Table 1; Electr. Suppl.: Table S1), to describe the evolution and the taxonomic relevance of the characters. All characters were scored as discrete binary or multistate characters. Missing data were coded as uncertain (?) in the character matrix (Electr. Suppl.: Table S1). Character reconstruction was done by using maximum likelihood with Mesquite v.2.75 (Maddison & Maddison, 2011), applying the model “Markov k-state 1 parameter”, and characters were plotted on the ML tree (Fig. 1).

A Bayesian approach as implemented in BayesTraits v.2.0 (www.evolution.reading.ac.uk/) was used to reconstruct morphological character states at selected nodes (Fig. 1) on the trees generated by MrBayes, taking into account phylogenetic uncertainty in the reconstructions of ancestral states (Pagel & al., 2004). A maximum likelihood analysis was run to derive an empirical prior. BayesTraits uses reversible-jump Markov chain Monte Carlo (MCMC) methods to derive posterior probabilities on trait values at ancestral nodes of phylogenies (Pagel & Meade, 2006). Ancestral state reconstruction of each character was performed using the MultiState module, allowing for rapid state changes. We used a hyperprior approach

specifying an exponential prior seeded from a uniform prior in the interval 0–100 in the absence of information on rates and varied RateDev parameters until acceptance rates changed in the preferred range of 20%–40%. A total of 10 million iterations were run for each analysis with sampling every 10,000 generations and the first one million samples discarded as burn-in. The resulting posterior probability distributions were used to produce final estimates of the probabilities for ancestral state estimates (Table 2).

■ RESULTS

Of 2854 (1101 ITS, 1274 *rbcL*, 479 *trnL-F*) DNA base pairs analysed, 1705 (373 ITS, 1006 *rbcL*, 326 *trnL-F*) were constant and 1149 (728 ITS, 268 *rbcL*, 153 *trnL-F*) variable; 219 (74 ITS, 99 *rbcL*, 46 *trnL-F*) variable characters were parsimony uninformative and 930 (654 ITS, 169 *rbcL*, 107 *trnL-F*) parsimony informative.

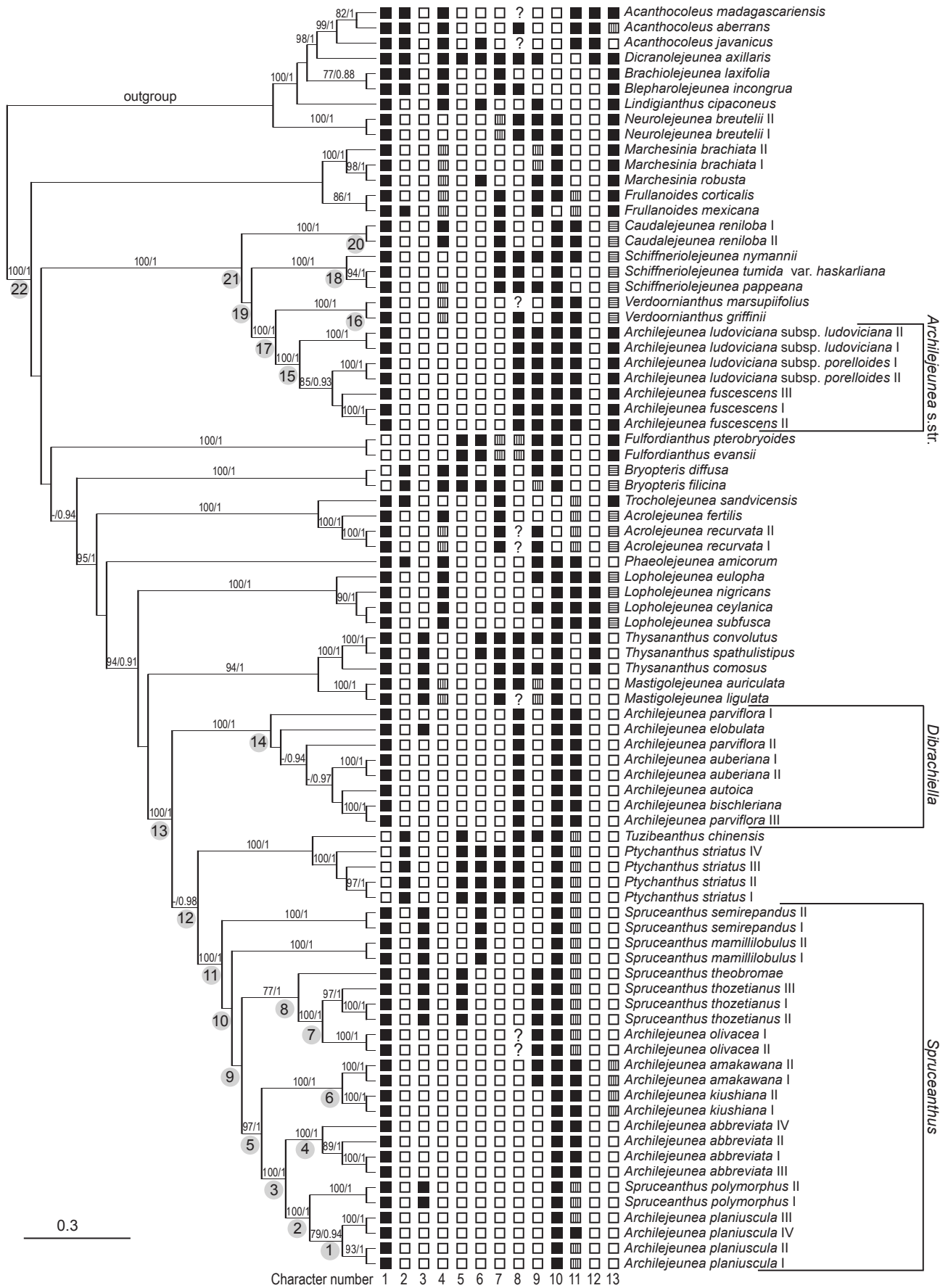
The MP analyses resulted in one most parsimonious tree of a length of 5518 steps, a consistency index (CI) of 0.359 and a retention index (RI) of 0.684 (Electr. Suppl.: Fig. S1). A single most likely tree ($-\ln L = 30,496.9582$) was found in the ML analyses (Fig. 1). The ML and BI topologies did not show any major conflict. Bayesian posterior probabilities (PP_{BI}) are indicated in the ML tree.

In the Bayesian test of topology, marginal likelihood was $-30,600.47$ for the unconstrained hypothesis and $-31,194.79$ for the constrained hypothesis (Table 2). The unconstrained hypothesis (polyphyly of *Archilejeunea* s.l.) was very strongly supported ($2 \times \log_e BF$ [Bayes Factor] > 10).

In the phylogenetic trees (Fig. 1; Electr. Suppl.: Fig. S1) accessions of *Archilejeunea* are resolved in three robust clades: the *Archilejeunea* s.str. clade (node 15; $BS_{MP} = 100$, $BS_{ML} = 100$, $PP_{BI} = 1$), the *Dibrachiella* clade (node 14; $BS_{MP} = 100$, $BS_{ML} = 100$, $PP_{BI} = 1$) and the *Spruceanthus* clade (node 11; $BS_{MP} = 100$,

Table 1. Morphological-anatomical characters scored for phylogenetic analysis of 83 specimens of Lejeuneaceae subfam. Ptychanthoideae.

No.	Characters	Character states
1	Growth habit	0) dendroid; 1) not dendroid
2	Branching type	0) exclusively or mainly <i>Lejeunea</i> -type; 1) exclusively or mainly <i>Frullania</i> -type
3	Flagellae	0) absent; 1) present
4	Size of epidermis cells	0) not (or scarcely) larger than medullary cells; 1) distinctly larger than medullary cells; 2) dorsally larger, ventrally not larger than medullary cells
5	Subepidermis	0) absent; 1) present
6	Leaf margin	0) entire or slightly toothed; 1) distinctly toothed
7	Trigones in leaf lobes	0) not cordate; 1) cordate; 2) absent
8	Oil bodies	0) homogenous; 1) segmented; 2) absent
9	Sexual condition	0) monoicous; 1) dioicous; 2) monoicous and dioicous
10	Lobules of male bracts	0) epistatic; 1) hypostatic
11	Number of perianth keels	0) 0–3; 1) 4–5; 2) usually more than 5
12	Perianth keel margin	0) smooth or slightly toothed; 1) distinctly toothed
13	Subfloral innovations	0) lejeuneoid; 1) pycnolejeuneoid; 2) lejeuneoid and pycnolejeuneoid; 3) absent



BS_{ML} = 100, PP_{BI} = 1). The remaining genera of the ingroup with multiple accessions were monophyletic with strong support.

The *Archilejeunea* s.str. clade contained the two sampled species of *A.* subg. *Archilejeunea* (*A. fuscescens* (Lehm. & Lindenb.) Fulford, *A. ludoviciana* (Lehm.) P.Geissler & Gradst.) and was sister to the *Verdoornianthus* clade with strong support (BS_{MP} = 100, BS_{ML} = 100, PP_{BI} = 1). The *Archilejeunea*-*Verdoornianthus* clade formed a robust clade together with *Schiffneriolejeunea* and *Caudalejeunea* (BS_{MP} = 100, BS_{ML} = 100, PP_{BI} = 1).

The *Dibrachiella* clade consisted of five species of *Archilejeunea* subg. *Dibrachiella*, three from tropical America (*A. auberiana* (Nees) Steph., *A. bischleriana* Gradst., *A. parviflora* (Nees) Steph.) and two from Africa (*A. autoica* Vanden Berghen, *A. elobulata* Steph.). *Archilejeunea parviflora* (3 accessions) was not monophyletic.

The *Spruceanthus* clade contained five species of *Archilejeunea* subg. *Dibrachiella* (*A. abbreviata* (Mitt.) Vanden Berghen, *A. amakawana* Inoue, *A. kiushiana* (Horik.) Verd., *A. olivacea* (Hook.f. & Taylor) Steph., *A. planiuscula* (Mitt.) Steph.) and all sampled species of *Spruceanthus* (*S. mamillolobulus* (Herzog) Verd., *S. polymorphus* (Sande Lac.) Verd., *S. semirepandus* (Nees) Verd., *S. theobromae* (Spruce) Gradst., *S. thozetianus* (Gottsche & F.Muell.) B.M.Thiers & Gradst.). The species of this group formed several strongly to weakly supported clades, including the *A. planiuscula*-*S. polymorphus*-*A. abbreviata* clade (BS_{MP} = 99, BS_{ML} = 100, PP_{BI} = 1), the *A. amakawana*-*A. kiushiana* clade (BS_{MP} = 100, BS_{ML} = 100, PP_{BI} = 1), and the *A. olivacea*-*S. thozetianus*-*S. theobromae* clade (BS_{MP} < 70, BS_{ML} = 77, PP_{BI} = 1).

Ancestral state reconstruction of morphological characters showed that many characters traditionally used to classify genera of Ptychanthoideae are homoplastic; most character states changed more than twice (Electr. Suppl.: Fig. S2). In the *Archilejeunea*-*Verdoornianthus*-*Schiffneriolejeunea*-*Caudalejeunea* clade, single state changes occurred for trigone shape (cordate to non-cordate), oil bodies (homogenous to segmented), number of perianth keels (5 to 0–3) and subfloral innovations (absent to present), and in the *Spruceanthus*-*Tuzibeanthus*-*Ptychanthus*-*Dibrachiella* clade for growth habit (not dendroid to dendroid), branching type (*Lejeunea*-type to *Frullania*-type), trigone shape (not cordate to cordate) and subfloral innovations (lejeuneoid to lejeuneoid and pycnolejeuneoid).

In the BayesTraits analysis of the *Archilejeunea* s.str., *Dibrachiella* and *Spruceanthus* clades (Fig. 1: nodes 15, 14 and 11, resp.), projecting growth habit, *Lejeunea*-type branching, absence of subepidermis, non-cordate trigones in leaf lobes, hypostatic lobules of male bracts and smooth margin of

Table 2. Estimations of marginal likelihood using four independent stepping-stone sampling runs (SS) of the unconstrained and constrained hypotheses.

SS runs	Marginal log likelihood unconstrained	Marginal log likelihood constrained	2 × log _e BF unconstrained versus constrained
1	-30,610.39	-31,194.23	
2	-30,613.42	-31,193.99	
3	-30,613.27	-31,218.90	
4	-30,599.09	-31,197.87	
Mean	-30,600.47	-31,194.79	1188.64

In the constrained hypothesis *Archilejeunea* s.l. (= *Archilejeunea* s.str. clade + *Dibrachiella* clade + several species in the *Spruceanthus* clade) was forced to monophyly, in the unconstrained hypothesis *Archilejeunea* s.l. was not forced to monophyly.

perianth keels were recovered as ancestral character states for all three clades with maximal support (PP = 1), while epidermis cells not larger than medullary cells received a support of PP > 0.95. In addition, absence of flagellae was inferred as ancestral character state for the *Archilejeunea* s.str. clade (PP = 0.98), entire leaf margin, segmented oil bodies and perianth with 4–5 keels for the *Archilejeunea* s.str. and *Dibrachiella* clades (PP = 0.98, 1, 0.99 and 0.9, 1, 1, resp.), and lejeuneoid innovations and monoicy for the *Dibrachiella* and *Spruceanthus* clades (PP = 1, 0.98 and 0.99, 0.91, resp.). Homogeneous oil bodies, >5 perianth keels and toothed leaf margins, finally, were ancestral character states for the *Spruceanthus* clade (PP = 1, 1, 0.93, resp.) and dioicy for the *Archilejeunea* s.str. clade (PP = 0.98).

The *Spruceanthus* clade, finally, stood out by the occurrence of several character shifts, for example to absence of flagellae (node 5; PP = 0.94), entire leaf margin (node 10; PP = 0.6) and presence of both lejeuneoid and pycnolejeuneoid innovations in the *A. amakawana*-*A. kiushiana* subclade (node 6; PP = 1); to presence of subepidermis (PP = 0.95) in the *A. olivacea*-*S. thozetianus*-*S. theobromae* clade (node 8), and again to absence of subepidermis in the *A. amakawana*-*A. kiushiana*-*A. abbreviata*-*S. polymorphus*-*A. planiuscula* clade (node 5; PP = 1).

DISCUSSION

Phylogenetic relationships and generic circumscriptions.

— The topology obtained in this study (Fig. 1, Electr. Suppl.: Fig. S1) corresponds well with the phylogenetic hypothesis of Wilson & al. (2007), which was based on the same molecular markers and similar sets of taxa but with a much more limited sampling of *Archilejeunea* and *Spruceanthus* and without *Verdoornianthus*. The ITS alignment contained a high number of ambiguous positions (1167; 52%). Such a high percentage is not uncommon in bryophytes and has also been reported in *Lejeuneaceae* by Groth-Maloney & al. (2004) and Sukkharak & al. (2011). Our results confirm that *Archilejeunea* is not monophyletic and show that the species of this genus are distributed in three different clades. The polyphyly of *Archilejeunea* was

Fig. 1. Single most likely phylogram resulting from maximum likelihood analyses of the combined molecular datasets with indication of ML bootstrap (BS) values and Bayesian posterior probabilities (PP). Support values BS < 70 and PP < 0.9 are not reported. Morphological character states (Table 1) were plotted on the tree. Character states 0, 1, 2, 3 are indicated by □ ■ ▨ ▩, respectively. Numbers on the nodes refer to nodes analyzed in BayesTraits.

strongly supported by the Bayesian topology test (Table 2). The three groups of species are only distantly related (Fig. 1; Electr. Suppl.: Fig. S1) and belong to morphologically distinct genera. The studied species of *A.* subg. *Archilejeunea* represent the genus *Archilejeunea* while those of *A.* subg. *Dibrachiella* belong to *Spruceanthus* and *Dibrachiella* gen. nov., respectively.

(1) *Archilejeunea*. — The genus *Archilejeunea* as defined here contains the five neotropical species previously assigned to *A.* subg. *Archilejeunea*. The group is largely restricted to the rain forests of southern Central America and northern South America, ranging from Costa Rica to Ecuador and eastern Brazil. A further, undescribed species occurs in West Africa (Shi & Zhu, 2015). *Archilejeunea* is well defined by (1) glossy brown plant color, (2) isodiametric cells with distinct trigones which are usually triradiate and sometimes confluent, (3) segmented oil bodies, (4) large leaf lobules which are never reduced and have a truncate apex without or with one tooth, (5) large imbricate underleaves, (6) dioicy (paroicy in *A. badia* (Spruce) Steph.), and (7) gynoecea with 1(2) repeatedly fertile pycnolejeuneoid innovations and large bract lobules. *Archilejeunea* is resolved as sister to the Amazonian *Verdoornianthus* with strong support. The two genera are very similar in leaf morphology, stem structure and perianth but *Verdoornianthus* stands apart by dull brown plant color, lack of innovations, large lobules of leaves and female bracts, swollen, usually tristratose rhizoid discs, and autoicy (Gradstein, 1977). The close relationship of the two genera is supported by a morphological-cladistic analysis (Gradstein, 1994; Gradstein & al., 2003). The latter study also resolved a sister relationship between *Verdoornianthus* and *Cephalantholejeunea*, a rare Amazonian genus with a single species, *C. temnanthoides* (R.M.Schust.) R.M.Schust. This relationship needs further testing with molecular markers. *Archilejeunea* and *Verdoornianthus* are members of a robust clade together with *Schiffneriolejeunea* and *Caudalejeunea*. *Archilejeunea* is readily separated from these genera by the truncate lobular apex without or with one tooth, isodiametric cells with radiate trigones, and pycnolejeuneoid innovations (Fig. 1).

(2) *Dibrachiella*. — Five species of *A.* subg. *Dibrachiella*, including the three neotropical species (*A. auberiana*, *A. bischleriana*, *A. parviflora*) and two African members (*A. autoica*, *A. elobulata*) of this group, are resolved in the new genus *Dibrachiella*. Diagnostic characters of *Dibrachiella* are (1) entire leaves and bracts, (2) isodiametric cells with small, usually simple-triangular trigones, (3) segmented oil bodies (Gradstein, 1975: 144; Gradstein, 1994), (4) often reduced leaf lobules, (5) rather small, distant to subimbricate underleaves, (6) autoicy, (7) gynoecea with single or paired lejeuneoid innovations, and (8) perianths with 4–5 smooth or weakly toothed keels. Based on morphology, several further *Archilejeunea* species described from Africa should be transferred to *Dibrachiella* (see Taxonomic Implications). *Dibrachiella* is only distantly related to *Archilejeunea* and is resolved as sister to *Ptychanthus*, *Tuzibeanthus* S.Hatt. and *Spruceanthus* ($BS_{MP} = 79$, $BS_{ML} = 100$, $PP_{BI} = 1$). *Ptychanthus* is a small genus of 1–2 species with a wide distribution in the

Old World tropics. The plants are quite different from *Dibrachiella* by their dendroid habit, robust stems with a brown subepidermis, *Frullania*-type branching, frequently toothed leaves and bracts, elongate leaf cells with cordate trigones and numerous intermediate thickenings, and pluriplicate perianths. *Tuzibeanthus* is a monospecific genus restricted to East Asia. It is similar to *Ptychanthus* in growth habit, branching type, oil bodies and perianths, but can be readily recognized by its rounded or obtuse leaf apex, entired underleaves, female bracts and bracteoles (Fig. 1; Electr. Suppl.: Fig. S1). *Spruceanthus*, on the other hand, is morphologically very similar to *Dibrachiella* and several species previously assigned to *A.* subg. *Dibrachiella* were resolved as members of *Spruceanthus* in this study. The relationships between the two groups are discussed below.

Archilejeunea parviflora seems to be a polyphyletic species (Fig. 1; Electr. Suppl.: Fig. S1). This should be investigated further with more accessions and a better geographic coverage of the species, as well as by morphological analysis of herbarium material including the synonyms of *A. parviflora* (see Gradstein, 1994). Polyphyletic species are frequently detected in bryophytes and molecular analyses are an important tool to reveal the existence of cryptic or morphologically distinct species that would otherwise have remained hidden (e.g., Heinrichs & al., 2009, 2013; Sukkharak & al., 2011; Hutsemékers & al., 2012; Medina & al., 2012; Dong & al., 2012; Yu & al., 2013; Aranda & al., 2014; Hedenäs & al., 2014).

(3) *Spruceanthus*. — This is a small amphi-Pacific tropical genus of eight extant species, seven from Asia and Australia and one from Ecuador (Gradstein & al., 2014; Wang & al., 2014a, 2015). A fossil species, *S. polonicus* Grolle, has been described from Baltic amber of Central Europe (Grolle, 1985). The genus is characterized by (1) robust stems with a weakly enlarged epidermis and occasional presence of a subepidermis, (2) microphyllous branches at stem bases, (3) isodiametric or elongate leaf cells with simple-triangular to triradiate trigones, (4) homogeneous oil bodies (observed in *S. mamillilobulus*, *S. polymorphus*, *S. semirepandus*, *S. theobromae* and *S. thozetianus*), (5) lejeuneoid innovations, and (6) perianths with 5–12 smooth keels (Gradstein, 1994; Zhu & So, 2001; Wang & al., 2015). In our analyses, *Spruceanthus* is sister to *Ptychanthus*, *Tuzibeanthus* and *Dibrachiella*; this relationship was also found by Wilson & al. (2007).

Surprisingly, our results revealed that five species traditionally assigned to *Archilejeunea* (subg. *Dibrachiella*) are nested in *Spruceanthus*, including three from Asia (*A. amakawana*, *A. kiushiana*, *A. planiuscula*), one from New Zealand (*A. olivacea*) and one from Africa and south India (*A. abbreviata*; Manju & al., 2012). None of these species had previously been associated with *Spruceanthus* with the exception of *A. kiushiana* (Gradstein, 1975: 145) and *A. planiuscula* (= *S. marianus* Mizut.). The latter species is confusingly similar to the polymorphic *S. polymorphus* (Sande Lac.) Verd. (= *Archilejeunea polymorpha* (Sande Lac.) B.Thiers & Gradst.) from Asia and Australia (Thiers & Gradstein, 1989). By the placement of *A. abbreviata* in *Spruceanthus*, the genus becomes pantropical in distribution.

Spruceanthus differs from *Archilejeunea* and *Dibrachiella* by larger plant size and more robust stems, frequent presence of microphyllous branches, perianths usually pluriplicate, and, especially, homogeneous oil bodies (Gradstein, 1994). Oil body structure (homogeneous vs. segmented) is an important taxonomic feature in Lejeuneaceae (Schuster, 1992) that is usually stable at the generic level and has been used to classify the genera of Ptychanthoideae into tribes (Gradstein, 1994). Nevertheless, the use of oil body characters in taxonomy is marred with problems. As noted by many authors, these organelles are unstable and their morphology may change rapidly (within days or even hours) after collection of the plants. It has been observed that homogeneous oil bodies may become segmented upon drying whereas segmented ones become almost homogeneous before falling apart (Gradstein & al., 1977). Since oil bodies are usually vanished in dried herbarium material they should be studied using fresh material and data obtained from dried material are unreliable (Schuster, 1992).

We examined oil bodies in fresh material of *A. amakawana*, *A. kiushiana*, *A. planiuscula*, *S. mamillilobulus*, *S. polymorphus* and *S. semirepandus*, and confirm that the oil bodies of these species are homogeneous. Furthermore, homogeneous oil bodies occur in *A. abbreviata* (E.W. Jones, in sched.). Gradstein (1975: 144) reported segmented oil bodies in the latter species based on observations of the late Dr. E.W. Jones. However, labels of Dr. Jones's specimens of *A. abbreviata* in the herbarium of Edinburgh (*Jones 6381*, E-00638903; *Jones s.n.*, E-00638896) indicate the presence of "simple" (= homogeneous) oil bodies in this species. In *A. olivacea* from New Zealand, on the other hand, Schuster (1963, 1992) noted that "oil-bodies are quite small and may be few-segmented" and Gradstein & Buskes (1985) observed coarsely segmented oil bodies in fresh material of this species. In thus appears that the oil bodies of *A. olivacea* need further observation.

Systematic significance of morphological characters.

— Ancestral state analysis shows that morphological characters traditionally used to define genera of Ptychanthoideae are highly homoplasious, in agreement with the findings of Sukkharak & al. (2011). Within the *Archilejeunea*-*Verdoornianthus*-*Schiffneriolejeunea*-*Caudalejeunea* clade, seven characters (projecting growth, *Lejeunea*-type branching, absence of flagella, absence of subepidermis, entire leaf margins, epistatic lobules of male bracts, \pm smooth perianth keels) are constant, nevertheless all of them also occur in other clades. The four genera of this clade are essentially separated by a combination of morphological traits, including presence/absence of subfloral innovations, innovation type, size of epidermis cells relative to the inner stem cells, and trigone shape (Fig. 1). *Archilejeunea* stands out by presence of pycnolejeunoid innovations, although this feature also occurs in *Frullanoides* Raddi, *Fulfordianthus* Gradst. and *Marchesinia* Gray (Fig. 1).

Within the *Spruceanthus*-*Tuzibeanthus*-*Ptychanthus*-*Dibrachiella* clade, *Ptychanthus* and *Tuzibeanthus* are readily separated from the other two genera of this clade by dendroid growth and predominance of *Frullania*-type branching (Mizutani, 1961; Fig. 1). *Spruceanthus* and *Dibrachiella* share

many similarities, e.g., *Lejeunea*-type branching, reduced leaf lobules, subisodiametric leaf cells, non-cordate trigones and lejeuneoid innovations. In addition, character analysis shows that two traits used to separate the two groups, viz. number of perianth keels and width of ventral merophyte (Thiers & Gradstein, 1989), are unstable. Thus, 5-keeled perianths characteristic of *Dibrachiella* may occur in *S. polymorphus* and *S. semirepandus*, whereas 4–6 cells wide ventral merophytes characteristic of *Dibrachiella* are also seen in *A. kiushiana* (= *S. kiushianus*), *A. planiuscula* (= *S. planiusculus*) and *S. polymorphus* (Electr. Suppl.: Fig. S2K).

Presence of flagellae on older stem portions, considered a specialized means of attachment (Gradstein, 1994), is characteristic of robust members of *Spruceanthus*, including *S. mamillilobulus*, *S. polymorphus*, *S. semirepandus*, *S. theobromae* and *S. thozetianus*. In addition, this feature occurs in *Mastigolejeunea* (Spruce) Steph. and *Thysananthus* Lindenb. (Sukkharak & al., 2011). In the present study we observed flagellae for the first time in *Archilejeunea linguifolia* Steph. (= *Archilejeunea elobulata*, Shi & al., 2015). The former species grows as a rheophyte on rocks and logs in rivers and waterfalls, where it often is fully submerged (Vanden Berghen, 1951). We suggest that the flagellae in this species may play a role in attaching the plants to the substrate in the swiftly flowing river waters (Electr. Suppl.: Fig. S2C).

Toothed leaf apices, subepidermis, dioicy and presence of both lejeunoid and pycnolejeunoid innovations are further morphological features seen in *Spruceanthus*, but these characters vary at species level and do not serve for separation of *Spruceanthus* and *Dibrachiella*. As shown earlier, oil body type appears to be the main diagnostic morphological character distinguishing these two genera.

TAXONOMIC IMPLICATIONS

The present study shows that *Archilejeunea* as traditionally conceived is polyphyletic and that species currently accepted in this genus belong in three different genera, *Archilejeunea* s.str., *Dibrachiella* (stat. nov.) and *Spruceanthus*. For each genus we provide types, synonymy, a brief description, geographical distribution and a list of included species. New combinations are made for species transferred to *Dibrachiella* or *Spruceanthus*.

Key to *Archilejeunea*, *Dibrachiella* and *Spruceanthus*

1. Gynoecial innovations pycnolejeunoid; leaf lobules never reduced *Archilejeunea*
1. Gynoecial innovations lejeuneoid (both pycnolejeunoid and lejeuneoid in *S. falcatus* and *S. kiushianus*); leaf lobules often reduced 2
2. Oil bodies segmented; perianth 4–5-keeled; ventral merophyte 4–6 cells wide *Dibrachiella*
2. Oil bodies homogenous; perianths 5–12-keeled; ventral merophyte 4–16 cells wide *Spruceanthus*

Archilejeunea (Spruce) Steph. in Hedwigia 27: 113. 1888¹ ≡ *Lejeunea* subg. *Archilejeunea* Spruce in Trans. & Proc. Bot. Soc. Edinburgh 15: 88. 1884 ≡ *Lejeunea* sect. *Monotropella* Spruce in Trans. & Proc. Bot. Soc. Edinburgh 15: 89. 1884 ≡ *Archilejeunea* subg. *Monotropella* (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130. 1893 – Type: *Archilejeunea ludoviciana* subsp. *porelloides* (Spruce) Gradst. (≡ *Lejeunea porelloides* Spruce).

Diagnostic characters. – Plants glossy yellowish-brown or dark brown, 1–3 mm wide. Stems slender, ventral merophyte 4–6(–8) cells wide; epidermis cells similar to medullary cells; subepidermis absent. Microphyllous branches absent. Leaf margins entire; midleaf cells isodiametrical, trigones rather thick, radiate and sometimes confluent; oil bodies segmented. Lobules never reduced, short rectangular with truncate apex and 0–1 tooth. Underleaves imbricate, rarely distant, 3–6 times as wide as stem. Dioicous, rarely parioicous (*A. badia*). Androecia terminal or intercalary on elongated branches, bracts in (1–)4–11 pairs. Gynoecia usually with a single, repeatedly fertile pycnolejeuneoid innovation, bracts and bracteoles entire; bracts as large as vegetative leaves or larger, lobe apex rounded to apiculate, lobules usually lanceolate-acuminate and 2/3 of lobe length, never reduced; bracteoles ovate-oblong, apex entire to shortly bifid. Perianths (2–)4–5-keeled, keels smooth or slightly toothed, the ventral keels sometimes reduced in *A. fuscescens*.

Distribution. – Southern Central America and northern South America, ranging from Costa Rica to southern Ecuador and eastern Brazil, in lowland rainforests, up to 1075 m (Schäfer-Verwimp & al., 2013). A new species, *A. gradsteinii* X.Q.Shi & R.L.Zhu, occurs in West Africa (Shi & Zhu, 2015).

Included species. – *Archilejeunea badia*, *A. crispistipula* (Spruce) Steph., *A. fuscescens*, *A. gradsteinii*, *A. ludoviciana* (Lehm.) P.Geissler & Gradst. subsp. *ludoviciana*, *A. ludoviciana* subsp. *porelloides* (Spruce) Gradst., *A. nebeliana* Gradst. & Schäf.-Verw.

Dibrachiella (Spruce) X.Q.Shi, R.L.Zhu & Gradst., **stat. nov.** ≡ *Lejeunea* sect. *Dibrachiella* Spruce in Trans. & Proc. Bot. Soc. Edinburgh 15: 90. 1884 ≡ *Archilejeunea* subg. *Dibrachiella* (Spruce) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130. 1893 – Type: *Dibrachiella auberiana* (Mont.) X.Q.Shi, R.L.Zhu & Gradst. (≡ *Lejeunea auberiana* Mont. ≡ *Archilejeunea auberiana* (Mont.) A.Evans).

Diagnostic characters. – Plants light green to greenish-brown to black, 1–2 mm wide. Stems slender, ventral merophyte 4–6 cells wide; epidermis cells similar in size to medullary cells or slightly larger; subepidermis absent. Microphyllous branches absent. Leaf margins entire; midleaf cells isodiametrical, trigones thin, simple-triangular to short radiate, oil bodies segmented. Lobules often reduced, when well developed with 1–2 teeth. Underleaves distant or subimbricate, 2–4 times as wide as stem. Autoicous. Androecia usually terminal or intercalary on elongated branches, sometimes occupying a

specialized branch, bracts in 4–12(–15) pairs. Gynoecia with 1–2 lejeuneoid innovations, innovations usually repeatedly fertile, bracts and bracteoles entire; bracts as large as vegetative leaves or smaller, lobe apex rounded, lobules up to 2/3 of lobe length, sometimes reduced; apex of bracteoles entire to retuse. Perianths 4–5-keeled, keels smooth or slightly toothed, sometimes narrowly winged.

Distribution. – Widespread in tropical America and Africa; in lowland and lower montane rainforests, semi-deciduous forests, scrub and plantations, up to ca. 1500 m.

Included species (those marked by an asterisk are placed in *Dibrachiella* based on morphology). – **Dibrachiella africana*, **D. alata*, *D. auberiana*, *D. autoica*, *D. bischleriana*, **D. brevilobula*, *D. elobulata*, **D. jonesii*, *D. parviflora*.

New combinations and new synonyms

Dibrachiella africana (Steph.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea africana* Steph., Sp. Hepat. 4: 705. 1911 – Holotype: Equatorial Guinea. Fernando Póo, 1875, *Buchholz, s.n.* (G barcode G00045060!, sub “*Archilejeunea subinermis* Steph.”).

Dibrachiella alata (Steph.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea alata* Steph. in Bull. Soc. Roy. Bot. Belgique 32: 33. 1893 – Holotype: Africa. Mayotte, *Marie 4* (G barcode G00042853!).

Dibrachiella auberiana (Mont.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Lejeunea auberiana* Mont., Hist. Phys. Cuba, Bot., Pl. Cell.: 483. 1842 ≡ *Archilejeunea auberiana* (Mont.) Steph. in Hedwigia 29: 134. 1890 – Holotype: Cuba. *Auber s.n.* (PC [herb. Montagne]!; isotypes: W!, YU!).

Dibrachiella autoica (Vanden Berghen) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea autoica* Vanden Berghen in Rev. Bryol. Lichénol. 20: 119. 1951 – Holotype: Ivory Coast. Bouroukrou, Dec 1906, *Chevalier 17* (PC No. PC0104546!, sub “*Lopholejeunea autoica* Steph.”).

Dibrachiella bischleriana (Gradst.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea bischleriana* Gradst. in Fl. Neotrop. Monogr. 62: 62. 1994 – Holotype: Colombia. Chocó: road Quibdo–Istmina, near Certegui, 2 Aug 1992, *Gradstein 8789* (COL barcode COL000291266!; isotypes: HSNU!, U!).

Dibrachiella brevilobula (Steph.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea brevilobula* Steph., Sp. Hepat. 4: 706. 1911 – Holotype: Madagascar. 1904, *Voeltzkow s.n.* (G barcode G00045061!).

Dibrachiella elobulata (Steph.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea elobulata* Steph., Sp. Hepat. 4: 707. 1911 – Holotype: Central African Republic. 1902, *Chevalier s.n.*, hb. Corbière 59 (G barcode G00045062!).

1 The genus is usually cited as “(Spruce) Schiffn. 1893” but Söderström & al. (2015) showed that “(Spruce) Steph. 1888” is correct.

Dibrachiella jonesii (Vanden Berghen) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea jonesii* Vanden Berghen in Rev. Bryol. Lichénol. 20: 116. 1951 – Holotype: Nigeria. Benin City, Okomu forest reserve, 7 Dec 1947, *E.W. Jones 37B* (BM n.v.; isotype: E barcode E00018876!).

Dibrachiella parviflora (Nees) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Jungermannia parviflora* Nees in Martius, Fl. Bras. Enum. Pl. 1, 1: 353. 1833 ≡ *Phragmicoma parviflora* (Nees) Nees, Naturgesch. Eur. Leberm. 3: 248. 1838 ≡ *Lejeunea parviflora* (Nees) Gottsche, Lindenb. & Nees, Syn. Hepat.: 318. 1845 ≡ *Symbiezidium parviflorum* (Nees) Trevis. in Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat. 4: 402. 1877 ≡ *Archilejeunea parviflora* (Nees) Steph. in Hedwigia 29: 134. 1890 – Holotype: Brazil. “Flumen Amaz.”, *Maritus s.n.* (STR!; isotypes: G barcode G00113743!, W!).

Spruceanthus Verd. in Ann. Bryol., Suppl. 4: 151. 1934 – Type: *Spruceanthus semirepandus* (Nees) Verd.

Diagnostic characters. – Plants dull green to brown or black. Stems slender to robust, ventral merophyte (4–)6–16 cells wide; epidermis cells similar in size to medullary cells or slightly larger; brown subepidermis often present. Microphyllous branches usually present. Leaf margins entire or toothed; midleaf cells isodiametric to elongate, trigones thin or thick, usually radiate; oil bodies homogeneous. Lobules well-developed or reduced, when well-developed with 1–3 teeth. Underleaves distant or imbricate, 2.5–6 times as wide as stem. Autoicous or dioicous. Androecia terminal or intercalary on elongated branches, bracts in 4–20 pairs. Gynoecia usually with 1–2 lejeuneoid innovations, rarely with both lejeuneoid and pycnolejeuneoid innovations (*S. falcatus*, *S. kiushianus*), innovations usually repeatedly fertile, bracts and bracteoles entire or toothed; bracts as large as vegetative leaves or larger, lobe apex rounded or acute-acuminate, lobules up to 3/4 of lobe length, sometimes reduced; apex of bracteoles entire to bifid. Perianths 5–12-keeled, keels usually smooth, rarely with a few blunt teeth in *S. thozetianus*.

Distribution. – Widespread in the Paleotropics, extending from West Africa to the Pacific region, northwards to Japan (southern Honshu) and southwards to New Zealand, also in western Ecuador (*S. theobromae*); in lowland and montane rainforests and semi-deciduous forests, also in scrub and plantations, up to ca. 3000 m.

Included species (those marked by an asterisk are placed in *Spruceanthus* based on morphology). – *Spruceanthus abbreviatus*, **S. brachyanthus*, *S. falcatus*, *S. kiushianus*, **S. macrostipulus* (Steph.) Gradst., *S. mamillilobus*, *S. olivaceus*, **S. planifolius*, *S. planiusculus*, **S. pluriplicatus* (Steph.) Gradst., *S. polymorphus*, *S. semirepandus*, **S. sulcatus* (Nees) Gradst., *S. theobromae*, *S. thozetianus*.

New combinations and new synonyms

Spruceanthus abbreviatus (Mitt.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Lejeunea abbreviata* Mitt. in J. Proc. Linn.

Soc., Bot. 7: 167. 1863 (“1864”) ≡ *Archilejeunea abbreviata* (Mitt.) Vanden Berghen in Rev. Bryol. Lichénol. 20: 117. 1951 – Holotype: Cameroun. Bagroo River, 1861, *Mann s.n.* (NY barcode 00012419!)

Spruceanthus brachyanthus (J.B.Jack & Steph.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Archilejeunea brachyantha* J.B.Jack & Steph. in Bot. Centralbl. 60: 104. 1894 – Holotype: Fiji. Ovalau, *Graeffe 1646* (G barcode G00067088!).

Obs.: Reported from Papua New Guinea as “*Archilejeunea* sp.” (Gradstein & al., 2002).

Spruceanthus falcatus X.Q.Shi, R.L.Zhu & Gradst., **nom. nov.** ≡ *Archilejeunea falcata* Amakawa in J. Jap. Bot. 39: 137. 1964, nom. illeg., non Steph. in Hedwigia 34: 60. 1895 ≡ *Archilejeunea amakawana* Inoue in J. Jap. Bot. 41: 16. 1966 – Holotype: Japan. Ryukyu: Ishigaki I., Mt. Fukaiomoto, *Takara 3256* (NICH!).

Spruceanthus kiushianus (Horik.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Lopholejeunea kiushiana* Horik. in J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 1: 129. 1932 ≡ *Archilejeunea kiushiana* (Horik.) Verd. in Ann. Bryol., Suppl. 4: 46. 1934 – Holotype: Japan. Kyushu: Hiuga Prov., Mt. Aoidake, 9 Apr 1927, *Horikawa 413* (HIRO!).

Spruceanthus olivaceus (Hook.f. & Taylor) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Jungermannia olivacea* Hook.f. & Taylor in London J. Bot. 3: 568. 1844 ≡ *Lejeunea olivacea* (Hook.f. & Tayl.) Gottsche, Lindenb. & Nees, Syn. Hepat.: 334. 1845 ≡ *Phragmicoma olivacea* (Hook.f. & Tayl.) Mitt. in Seemann, Fl. Vit.: 412. 1873 ≡ *Archilejeunea olivacea* (Hook.f. & Taylor) Steph. in Hedwigia 29: 134. 1890 – Holotype: New Zealand, *Colenso s.n.* (FH [herb. Taylor] barcode 00290563!; isotype (?): MANCH!).

Spruceanthus planifolius (Horik.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Leucolejeunea planifolia* Horik. in J. Sci. Hiroshima Univ., Ser. B., Div. 2, Bot. 1: 199. 1933 ≡ *Archilejeunea planifolia* (Horik.) Mizut. in J. Hattori Bot. Lab. 73: 175. 1993 – Holotype: Japan. Honshu: Aki Prov., Miyajima I., 20 Mar 1932, *Iwamasa 2040* (HIRO!).

Spruceanthus planiusculus (Mitt.) X.Q.Shi, R.L.Zhu & Gradst., **comb. nov.** ≡ *Lejeunea planiuscula* Mitt. in J. Proc. Linn. Soc., Bot. 5: 111. 1861 ≡ *Archilejeunea planiuscula* (Mitt.) Steph., Sp. Hepat. 4: 731. 1911 ≡ *Ptychocoleus planiuscula* (Mitt.) Verd. in Ann. Bryol., Suppl. 4: 126. 1934 – Holotype: Burma. Rangoon, *McClelland s.n.* (NY barcode 01049203!)

Species needing further study

Archilejeunea incrassata Steph. in Rev. Bryol. 35: 30. 1908 (New Caledonia).

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Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study. Voucher data is given for accessions for which DNA sequences were newly obtained, using the following format: Taxon name, country, largest political subdivision, collector and collection number (herbarium acronym), *rbcL*, *trnL-F*, nrITS GenBank accession number. Accession numbers in bold are newly generated sequences. –, missing data.

Acanthocoleus aberrans (Lindenb. & Gottsche) Kruijt, Spain, Canary Islands, *Schäfer-Verwimp 4213* (GOET), DQ983647, DQ987461, DQ987365; *Acanthocoleus javanicus* (Steph.) Kruijt, Indonesia, Bali, *Schäfer-Verwimp 20817* (GOET), DQ983648, DQ987398, DQ987291; *Acanthocoleus madagascariensis* (Steph.) Kruijt, Uganda, *Pócs 97145/AA* (GOET), DQ983649, DQ987458, DQ987359; *Acrolejeunea fertilis* (Reinw. & al.) Schiffn., Malaysia, *Gradstein & al. 10358* (GOET), DQ983650, DQ987418, DQ987314; *Acrolejeunea recurvata* Gradst. I, Thailand, Songkhla, *Zhu 20111218-2* (HSNU), **KR046235**, **KR046280**, **KR046323**; *Acrolejeunea recurvata* II, Thailand, Chiang Mai, *Zhu 20111214-45* (HSNU), **KR046236**, **KR046281**, **KR046324**; *Archilejeunea abbreviata* (Mitt.) Vanden Berghen I, Guinea, Muni, *Infanta VIT 856/93* (EGR), **KR046237**, **KR046282**, **KR046325**; *Archilejeunea abbreviata* II, Gabon, Moyen-Ogooue, *Atwood 2497* (MO), **KR046238**, **KR046283**, **KR046326**; *Archilejeunea abbreviata* III, Uganda, Masindi, *Wigginton U3121a* (E), **KR046239**, **KR046284**, **KR046327**; *Archilejeunea abbreviata* IV, Malawi, Mulanje Mt., *Lonton M8657a* (E), **KR046240**, **KR046285**, **KR046328**; *Archilejeunea amakawana* Inoue I, China, Zhejiang, *Zhu 20060729-36* (HSNU), **KR046241**, **KR046286**, **KR046329**; *Archilejeunea amakawana* II, China, Zhejiang, *Zhu & Wei 20110417-11* (HSNU), **KR046242**, **KR046287**, **KR046330**; *Archilejeunea auberiana* (Mont.) A. Evans I, Bolivia, Beni, *Inturias & al. 191B* (MO), **KR046243**, **KR046288**, **KR046331**; *Archilejeunea auberiana* II, Bolivia, Santa Cruz, *Gradstein 7735* (GOET, HSNU, U), **KR046244**, **KR046289**, **KR046332**; *Archilejeunea autoica* Vanden Berghen, Guinea, Muni, *Infanta VIT942/93* (EGR), **KR046245**, –, **KR046333**; *Archilejeunea bischleriana* Gradst., Colombia, Chocó, *Gradstein 8789* (COL, HSNU, U), **KR046246**, **KR046290**, **KR046334**; *Archilejeunea elobulata* Steph., Guinea, Muni, *Infanta VIT281/94* (EGR), **KR046247**, **KR046291**, **KR046335**; *Archilejeunea fuscescens* (Lehm. & Lindenb.) Fulford I, Costa Rica, Heredia, *Bernecker 97-53* (EGR), **KR046248**, **KR046292**, **KR046336**; *Archilejeunea fuscescens* II, Costa Rica, Puntarenas, *Gradstein 9345* (GOET, HSNU), **KR046249**, **KR046293**, **KR046337**; *Archilejeunea fuscescens* III, Colombia, Campos J5-C (COL, HSNU), **KR046250**, **KR046294**, **KR046338**; *Archilejeunea kiushiana* (Horik.) Verd. I, China, Zhejiang, *Zhu & Wei 20110420-41* (HSNU), **KR046251**, **KR046295**, **KR046339**; *Archilejeunea kiushiana* II, China, Zhejiang, *Zhu & Wei 20110420-28* (HSNU), **KR046252**, **KR046296**, **KR046340**; *Archilejeunea ludoviciana* (Lehm.) P. Geissler & Gradst. subsp. *ludoviciana* I, Ecuador, Napo, *Schäfer-Verwimp ASV & MN 31733* (HSNU), **KR046253**, **KR046297**, **KR046341**; *Archilejeunea ludoviciana* subsp. *ludoviciana* II, Colombia, Chocó, *Gradstein 8870* (COL, GOET, HSNU, U), **KR046254**, **KR046298**, **KR046342**; *Archilejeunea ludoviciana* subsp. *porrelloides* (Spruce) Gradst. I, Colombia, Risaralda, *Wolf 1499* (COL, GOET), DQ983656, –, DQ987360; *Archilejeunea ludoviciana* subsp. *porrelloides* II, Colombia, Risaralda, *Wolf 1615* (COL, GOET, HSNU), **KR046255**, –, **KR046343**; *Archilejeunea olivacea* (Hook. f. & Taylor) Steph. I, New Zealand, South Island, *Beveridge JN-9* (WELT), **KR046256**, **KR046299**, **KR046344**; *Archilejeunea olivacea* II, New Zealand, North Island, *Beveridge LU-6* (WELT), **KR046257**, **KR046300**, **KR046345**; *Archilejeunea parviflora* (Nees) Schiffn. I, French Guiana, *Cremers 7598* (E), **KR046258**, **KR046301**, **KR046346**; *Archilejeunea parviflora* II, Mexico, Chiapas, *Gradstein & Equihua 7919* (EGR, GOET), **KR046259**, **KR046302**, **KR046347**; *Archilejeunea parviflora* III, Costa Rica, *Gradstein & Dauphin 9370* (GOET), DQ983657, DQ987456, DQ987356; *Archilejeunea planiuscula* (Mitt.) Steph. I, Tanzania, Muheza, *Pócs 87109/C* (EGR), **KR046260**, **KR046303**, **KR046348**; *Archilejeunea planiuscula* II, Thailand, Krabi, *Schäfer-Verwimp 16237* (GOET), **KR046261**, **KR046304**, **KR046349**; *Archilejeunea planiuscula* III, Vietnam, Hà Giang, *Zhu & al. 20131105-107* (HSNU), **KR046262**, **KR046305**, **KR046350**; *Archilejeunea planiuscula* IV, China, Guangxi, *Ye & Wei 20090715-43* (HSNU), **KR046263**, **KR046306**, **KR046351**; *Blepharolejeunea incongrua* (Lindenb. & Gottsche) van Slageren & Kruijt, Brazil, Minas Gerais, *Schäfer-Verwimp 12800* (GOET), DQ983659, DQ987397, DQ987290; *Brachiolejeunea laxifolia* (Taylor) Schiffn., Ecuador, *Wilson & al. 04-03* (GOET), DQ983660, DQ987434, DQ987330; *Bryopteris diffusa* (Sw.) Nees, Bolivia, La Paz, *Acebey & Villavicencio 855* (GOET), AY548085, AM237147, AM237095; *Bryopteris filicina* (Sw.) Nees, Bolivia, La Paz, *Drehwald 4751* (GOET), AY548087, AM237158, AM237106; *Caudalejeunea reniloba* (Gottsche) Steph. I, Malaysia, *Gradstein & al. 10378* (GOET), DQ983661, DQ987419, DQ987315; *Caudalejeunea reniloba* II, China, Yunnan, *Wang & al. 20120714-369* (HSNU), **KR046264**, **KR046307**, **KR046352**; *Dicranolejeunea axillarum* (Nees & Mont.) Schiffn., Bolivia, *Drehwald 4829* (GOET), DQ983674, DQ987377, DQ987255; *Frullanoides corticalis* (Lehm. & Lindenb.) van Slageren, French Guiana, *Hartmann 04-080* (GOET), DQ983681, AM237196, AM237143; *Frullanoides mexicana* van Slageren, Mexico, Veracruz, *Burghardt 4421a* (GOET), DQ983682, DQ987464, DQ987366; *Fulfordianthus evansii* (Fulford) Gradst., Costa Rica, *Dauphin s.n.* (GOET), DQ983683, AM237197, AM237144; *Fulfordianthus pterobryoides* (Spruce) Gradst., Costa Rica, *Dauphin 2518* (GOET), DQ983684, AM237198, AM237145; *Indigianthus cipaconeus* (Gottsche) Kruijt & Gradst., Ecuador, *Kotike & Preussing MPEO2390* (GOET), DQ983702, DQ987445, DQ987343; *Lopholejeunea ceylanica* Steph., Indonesia, Java, *Gradstein 10241* (GOET), DQ983703, DQ987469, DQ987369; *Lopholejeunea eulopha* (Taylor) Schiffn., Australia, Queensland, *Pócs & Streimann 9987/HI* (GOET), AY548067, DQ987381, DQ987262; *Lopholejeunea nigricans* (Lindenb.) Schiffn., China, Yunnan, *Wang & al. 20120714-397D* (HSNU), **KR046265**, **KR046308**, **KR046353**; *Lopholejeunea subfusca* (Nees) Schiffn., Singapore, *Zhu 20070126-19* (HSNU), **KR046266**, **KR046309**, **KR046354**; *Marchesia brachiata* (Sw.) Schiffn. I, Bolivia, *Drehwald 4501* (GOET), DQ983709, DQ987376, DQ987254; *Marchesia brachiata* II, Ecuador, *Gradstein s.n.* (GOET), DQ983708, DQ987409, DQ987303; *Marchesia robusta* (Mitt.) Schiffn., Ecuador, *Wilson & al. 04-05* (GOET), DQ983710, DQ987436, DQ987332; *Mastigolejeunea auriculata* (Wilson & W.J. Hooker) Schiffn., Indonesia, Bali, *Schäfer-Verwimp 20780* (GOET), AY548071, DQ987394, DQ987284; *Mastigolejeunea ligulata* (Lehm. & Lindenb.) Schiffn., Thailand, *Schäfer-Verwimp 16246* (GOET), DQ983711, DQ987465, –, *Neurolejeunea breutelii* (Gottsche) A. Evans I, Brazil, *Schäfer-Verwimp 14740* (GOET), DQ983714, DQ987405, DQ987299; *Neurolejeunea breutelii* II, Brazil, Rio de Janeiro, *Gradstein & Costa 3871* (GOET), DQ983713, DQ987382, DQ987264; *Phaeolejeunea amicornum* (Hürl.) Pócs, Fiji, *Pócs 03304L* (GOET), DQ983718, DQ987412, DQ987308; *Ptychanthus striatus* (Lehm. & Lindenb.) Nees I, Indonesia, Java, *Gradstein 10217* (GOET), DQ983723, DQ987403, DQ987297; *Ptychanthus striatus* II, Indonesia, Java, *Gradstein 10215* (GOET), DQ983721, DQ987406, DQ987300; *Ptychanthus striatus* III, Thailand, Chiang Mai, *Zhu 20111218-6* (HSNU), **KR046267**, **KR046310**, **KR046355**; *Ptychanthus striatus* IV, China, Yunnan, *Wang & Peng 20110520-6B* (HSNU), **KR046278**, **KR046321**, **KR046366**; *Schiffneriolejeunea nymannii* (Steph.) Gradst. & Terken, Malaysia, *Gradstein & al. 10321* (GOET), DQ983725, DQ987424, DQ987320; *Schiffneriolejeunea pappeana* (Nees) Gradst., Réunion, *Schäfer-Verwimp 20314* (GOET), AY548076, DQ238574, DQ987287; *Schiffneriolejeunea tumida* var. *haskarlina* (Gottsche) Gradst. & Terken, Indonesia, Bali, *Schäfer-Verwimp 20952* (GOET), AY548077, DQ987396, DQ987286; *Spruceanthus mamillilobulus* (Herzog) Verd. I, Vietnam, Cao Bang, *Zhu & al. 20131022-13* (HSNU), **KR046268**, **KR046311**, **KR046356**; *Spruceanthus mamillilobulus* II, China, Guangxi, *Wei & Peng 20100920-20* (HSNU), **KR046269**, **KR046312**, **KR046357**; *Spruceanthus polymorphus* (Sande Lac.) Verd. I, Vietnam, Hà Giang, *Zhu & al. 20131105-36* (HSNU), **KR046270**, **KR046313**, **KR046358**; *Spruceanthus polymorphus* II, China, Fujian, *Zhang & al. 20091029-7* (HSNU), **KR046271**, **KR046314**, **KR046359**; *Spruceanthus semirepandus* (Nees) Verd. I, Vietnam, Hà Giang, *Zhu & al. 20131102-134* (HSNU), **KR046272**, **KR046315**, **KR046360**; *Spruceanthus semirepandus* II, China, Zhejiang, *Wang 20110121-7* (HSNU), **KR046273**, **KR046316**, **KR046361**; *Spruceanthus theobromae* (Spruce) Gradst., Ecuador, Los Rios, *Andersson & Kautz AK 10* (GOET), DQ983727, DQ987407, DQ987301; *Spruceanthus thozetianus* (Gottsche & F.A. Müll.) B.M. Thiers & Gradst. I, Australia, *Pócs 01107/M* (GOET), AM384877, DQ987460, DQ987362; *Spruceanthus thozetianus* II, Australia, Queensland, *Streimann 27614* (CANB), **KR046274**, **KR046317**, **KR046362**; *Spruceanthus thozetianus* III, New Caledonia, *Müller NC728* (HSNU), **KR046275**, **KR046318**, **KR046363**; *Thysananthus comosus* (Lehm., Malaysia, *Gradstein & al. 10366* (GOET), DQ983736, DQ987425, DQ987321; *Thysananthus convolutus* (Lindenb., Indonesia, Java, *Gradstein 10205* (GOET), DQ983737, DQ987414, DQ987310; *Thysananthus spathulistipus* (Reinw. & al.) Lindenb., Indonesia, Bali, *Schäfer-Verwimp 20790* (GOET), DQ983739, DQ987392, DQ987282; *Trocholejeunea sandvicensis* Mizut., China, Guangxi, *Wei 20110214-43* (HSNU), KP182123, KP182100, KP182145; *Tuzibeanthus chinensis* (Steph.) Mizut., China, Guangxi, *Wei & Peng 20100918-9* (HSNU), **KR046279**, **KR046322**, **KR046367**; *Verdoornianthus griffinii* Gradst., Colombia, *Campos 771* (COL, HSNU), **KR046276**, **KR046319**, **KR046364**; *Verdoornianthus marsupiifolius* (Spruce) Gradst., Colombia, *Campos 769* (COL, HSNU), **KR046277**, **KR046320**, **KR046365**