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Towards a monophyletic classification of Lejeuneaceae V: the systematic position of *Pictolejeunea*

JULIA BECHTELER[1], GAIK EE LEE[1,2], ALFONS SCHÄFER-VERWIMP[3], MATT A. M. RENNER[4], DENILSON F. PERALTA[5] & JOCHEN HEINRICHS[1]

[1] *Department of Biology I and GeoBio-Center, Ludwig Maximilian University, Menzinger Str. 67, 80638 Munich, Germany; e-mail: julia.bechteler@campus.lmu.de; jheinrichs@lmu.de*
[2] *School of Marine and Environmental Sciences, University of Malaysia Terengganu, Mengabang Telipot, 21030 Kuala Terengganu, Terengganu, Malaysia; gaik.ee@umt.edu.my*
[3] *Mittlere Letten 11, 88634 Herdwangen-Schönach, Germany; e-mail: moos.alfons@kabelbw.de*
[4] *Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia; e-mail: Matt.Renner@rbgsyd.nsw.gov.au*
[5] *Instituto de Botânica, Caixa Postal 68041, 04045-972 São Paulo, SP, Brazil; e-mail: denilsonfperalta@gmail.com*

Abstract

With more than 1,000 species in some 70 genera, Lejeuneaceae represent the largest family of liverworts. Although much progress has been made in recent years, the supraspecific classification of Lejeuneaceae has not yet been satisfactorily solved. Maximum likelihood and Bayesian analyses of a three marker dataset (nrITS, cp DNA *rbc*L and *trn*L-*trn*F) derived from 85 accessions of Lejeuneeae and 13 outgroup species revealed *Pictolejeunea picta* in a sister relationship to the remainder of Lejeuneeae, the most speciose tribe of Lejeuneaceae. Based on the outcome of the phylogenetic analyses, we establish subtribe Pictolejeuneinae *subtr. nov.*

Key words: classification, Lejeuneeae, Pictolejeuneinae, Porellales, liverwort, molecular phylogeny

Introduction

With more than 1,000 species (He & Zhu 2011), Lejeuneaceae are the largest family of the liverworts (Söderström *et al.* 2016). They are morphologically well circumscribed by lateral branches of the *Lejeunea*- or *Frullania*-type, fascicled rhizoids from underleaf base, 2-3-lobed leaves with the ventral lobule broadly attached to the dorsal lobe along a keel, gynoecia with a single archegonium and a single series of bracts and bracteoles, beaked perianths, sporophytes enclosed by a stalked calyptra, 2-stratose capsule walls, elaters adherent to the capsule valves, and spores with rosette markings in the exine (Crandall-Stotler *et al.* 2009). Centres of diversity are the humid tropics where Lejeuneaceae constitute a considerable portion of the epiphytic, especially epiphyllic diversity (Lücking 1995; Pócs 1996; Gradstein 1997; Gradstein *et al.* 2001). Lejeuneaceae are notorious for their complicated supraspecific classification and some 90 genera were accepted at the beginning of the millennium (Gradstein *et al.* 2003). Since then, molecular phylogenetic studies resolved several genera nested in others, e.g. *Chondriolejeunea* (Benedix 1953: 75) Kis & Pócs (2001: 293) and *Metzgeriopsis* Goebel (1888: 54) in *Cololejeunea* (Spruce 1884: 291) Schiffner (1893: 121) (Gradstein *et al.* 2006; Yu *et al.* 2013), *Myriocolea* Spruce (1884: 305) in *Colura* (Dumortier 1831: 32) Dumortier (1835: 12) (Heinrichs *et al.* 2011), and *Oryzolejeunea* (Schuster 1970: 338) Schuster (1992: 249), *Sphaerolejeunea* Herzog (1938: 88) and *Taxilejeunea* (Spruce 1884: 212) Schiffner (1893: 125) in *Lejeunea* Libert (1820: 372) (Wilson *et al.* 2007; Heinrichs *et al.* 2012, 2013; Ye *et al.* 2013). A revised classification of Lejeuneaceae thus accepted only 68 genera in two subfamilies, three tribes and eight subtribes, however several genera had not, at that stage, been included in molecular phylogenies and were thus not assignable to subtribes (Gradstein 2013). Subsequently, several changes to the classification of Gradstein (2013) were introduced including the reinstatement of *Allorgella* Tixier (1980: 612) (Bechteler *et al.* 2016), description of *Gradsteinianthus* R.L.Zhu & Jian Wang in Wang *et al.* (2016: 29) and the synonymy of *Aureolejeunea* Schuster (1978: 428), *Cyrtolejeunea* Evans (1903: 553), *Cystolejeunea* Evans (1906: 16), *Evansiolejeunea* Vanden Berghen (1948: 86), *Omphalanthus* Lindenberg & Nees in Gottsche *et al.* (1845: 303) and *Leucolejeunea* Evans (1907: 225) with *Cheilolejeunea* (Spruce 1884: 251) Stephani (1890: 284) (Schäfer-Verwimp

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et al. 2014; Ye *et al.* 2015). Several genera were moved from one subtribe to another, e.g. *Vitalianthus* Schuster & Giancotti (1993: 447) from Drepanolejeuneinae to Lepidolejeuneinae (Bechteler *et al.* 2016), *Otolejeunea* Grolle & Tixier in Tixier (1980: 609) from Cyclolejeuneinae to Lepidolejeuneinae (Heinrichs *et al.* 2014b) and *Bromeliophila* Schuster (1994: 226) from Lejeuneinae to Cyclolejeuneinae (Heinrichs *et al.* 2014a). In addition, the classification of Lejeuneeae was further completed by introduction of the subtribes Leptolejeuneinae (Heinrichs *et al.* 2014c), Leiolejeuneinae (Schäfer-Verwimp *et al.* 2014), Pycnolejeuneinae and Xylolejeuneinae (Heinrichs *et al.* 2014b).

Pictolejeunea Grolle (1977: 248) is a small Neotropical-Asian genus with six currently accepted species (Söderström *et al.* 2016) whose exact systematic position is unknown (Gradstein 2013). Ilkiu-Borges (2005) found the genus in a polytomy with several other lejeuneoid genera using a cp DNA *trn*L-*trn*F alignment, and rightly considered this marker alone insufficient to resolve the phylogeny of Lejeuneeae. Here, we include nrITS, *rbc*L and *trn*L-*trn*F sequence data of *Pictolejeunea* in an alignment of Lejeuneaceae and investigate its phylogenetic position. We demonstrate its sister relationship with the remainder of Lejeuneeae, and introduce the new subtribe Pictolejeuneinae.

Materials & Methods

Taxon sampling, DNA extraction, PCR amplification, sequencing and alignment

Dried specimens of the generitype *Pictolejeunea picta* (Gottsche ex Stephani 1913a: 223) Grolle (1977: 252) from the herbarium SP were used to isolate gametophytical tissue (Table 1). DNA extraction, PCR amplification and sequencing were carried out as described in Bechteler *et al*. (2016). Three markers were amplified: the chloroplast *rbc*L gene and *trn*L-*trn*F region and the nuclear ITS region (ITS1-5.8S-ITS2). In a first step the newly obtained sequences were compared with GenBank sequences using the nucleotide BLAST search (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch; Altschul *et al.* 1990), and then added to the Lejeuneaceae alignment of Wilson *et al.* (2007) to test the hypothesis that *Pictolejeunea picta* belongs to the Lejeuneeae (Gradstein 2013). Since this hypothesis was confirmed (results not shown here) the newly obtained sequences were aligned with sequences of 83 Lejeuneeae specimens downloaded from GenBank (http://www.ncbi.nlm.nih.gov/genbank/). The outgroup consisted of 13 Ptychanthoideae and Brachiolejeuneeae according to the phylogenetic hypotheses presented in Wilson *et al.* (2007). Sequences were aligned manually in PhyDE v.0.9971 (http://www.phyde.de/index.html) and ambiguous positions were excluded for phylogenetic analyses.

TABLE 1. Taxa used in the present study, including information about the origin of the studied material, voucher information, as well as GenBank accession numbers.

Taxon	Voucher	*rbc*L	*trn*L-F	nrITS
Acrolejeunea fertilis (Reinw. *et al.*) Schiffn.	Bali, Schäfer-Verwimp & Verwimp 17009 (GOET)	AY684929	DQ987391	DQ987281
Allorgella semperiana (Steph.) Bechteler *et al.*	Australia, Streimann 57955 (EGR)	KT626926	KT626942	KT626909
Allorgella semperiana	Indonesia, Schäfer-Verwimp & Verwimp 24836/C (M)	KT626927	---------	KT626910
Anoplolejeunea conferta (C.F.W.Meissn. ex Spreng.) A.Evans	Ecuador, Schäfer-Verwimp & Nebel 33081/B (M)	KJ408336	KJ408359	KJ408310
Anoplolejeunea conferta	Venezuela, Pócs *et al.* 9712/BA (M)	KJ408337	KJ408360	KJ408311
Anoplolejeunea conferta	Costa Rica, Schäfer-Verwimp & Holz 154 (M)	KJ408335	KJ408358	KJ408309
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	Costa Rica, Bernecker 97-53 (GOET)	DQ983655	DQ987384	DQ987267
Bromeliophila natans (Steph.) R.M.Schust.	Brazil, Santa Catarina, Gehrig s.n. (GOET)	KF039849	KF039879	KF039812
Bryopteris diffusa (Sw.) Nees	Bolivia, Acebey & Villavicencio 855 (GOET)	AY548085	AM237147	AM237095
Ceratolejeunea cubensis (Mont.) Schiffn.	Guadeloupe, Schäfer-Verwimp & Verwimp 22279/B (M)	KF606946	KF606941	KF606936
Ceratolejeunea laetefusca (Austin) R.M. Schust.	Brazil, Schäfer-Verwimp 33995 (M)	KF606947	KF606942	KF606937

...continued on the next page

TABLE 1. (Continued)

Taxon	Voucher	*rbc*L	*trn*L-F	nrITS
Cheilolejeunea asperrima (Steph.) Grolle	Costa Rica, van Melick 214551 (M)	KJ408339	KJ408362	KJ408313
Cheilolejeunea choachina (Gottsche) Gradst.	Ecuador, Schäfer-Verwimp & Nebel 33152/A (M)	KJ408341	KJ408364	KJ408315
Cheilolejeunea clausa (Nees & Mont.) Steph.	Brazil, Teixeira 39 (M)	KJ716751	KJ716776	KJ716763
Cheilolejeunea clypeata (Schwein.) W.Ye & R.L.Zhu	USA, Davis s.n. (GOET)	DQ983699	DQ987426	DQ987322
Cheilolejeunea discoidea (Lehm. & Lindenb.) R.M.Schust. & Kachroo	Panama, Schäfer-Verwimp & Verwimp 34530 (M)	KJ408343	KJ408366	KJ408317
Cheilolejeunea filiformis (Sw.) W.Ye, R.L.Zhu & Gradst.	Ecuador, Schäfer-Verwimp & Preußing 23543 (GOET)	DQ983716	DQ987393	DQ987283
Cheilolejeunea gaoi R.L.Zhu, M.L.So & Grolle	China (I), Ye & Wei 20090717-1 (HSNU)	---------	KT190781	KT190897
Cheilolejeunea gaoi	China (II), Ye & Wei 20090716-17 (HSNU)	---------	KT190780	KT190896
Cheilolejeunea holostipa (Spruce) Grolle & R.L.Zhu	Panama, Schäfer-Verwimp & Verwimp 34526 (M)	KJ408351	KJ408375	KJ408326
Cheilolejeunea insecta Grolle & Gradst.	Brazil, Schäfer-Verwimp & Verwimp 14725 (M)	KJ716749	KJ716774	KJ716761
Cheilolejeunea lineata (Lehm. & Lindenb.) Steph.	Guadeloupe, Schäfer-Verwimp & Verwimp 22183 (GOET)	AY548092	DQ987401	DQ987295
Cheilolejeunea lindenbergii (Gottsche) Mizut.	Malaysia, Pócs & Pócs 1006/AG (M)	KJ408344	KJ408367	KJ408318
Cheilolejeunea mimosa (Hook. f. & Taylor) R.M.Schust.	New Zealand, Schäfer-Verwimp & Verwimp 13745 (M)	KJ408345	KJ408368	KJ408319
Cheilolejeunea norisiae G.Dauphin & Gradst.	Panama, Schäfer-Verwimp & Verwimp 30821 (M)	KJ408346	KJ408369	KJ408320
Cheilolejeunea oncophylla (Ångstr.) Grolle & M.E.Reiner	Brazil, Peralta 11914 (M)	KJ408347	KJ408370	KJ408321
Cheilolejeunea quinquecarinata (R.M.Schust.) W.Ye, R.L.Zhu & Gradst.	Ecuador, Schäfer-Verwimp & Preußing 23299/A (GOET)	DQ983658	DQ987450	DQ987350
Cheilolejeunea revoluta (Herzog) Gradst. & Grolle	Brazil, Peralta 15116 (M)	KJ408349	KJ408372	KJ408323
Cheilolejeunea rigidula (Mont.) R.M.Schust.	Suriname, Muñoz 98-62 (GOET)	DQ983668	DQ987453	DQ987353
Cheilolejeunea rigidula	São Tomé and Príncipe, Shevock 39658 (M)	KJ716753	KJ716778	KJ716765
Cheilolejeunea unciloba (Lindenb.) Malombe	Brazil, Yano 32383 (M)	KJ716755	KJ716780	KJ716767
Cololejeunea cardiocarpa (Mont.) A.Evans	Brazil, Borhidi & Pereira BB25 (GOET)	JQ991163	JQ991278	JQ991048
Cololejeunea inflectens (Mitt.) Benedix	Malaysia, Schäfer-Verwimp & Verwimp 18861/A (GOET, as *C. peculiaris*)	AY548095	DQ238572	DQ987280
Colura cylindrica Herzog	Guadeloupe, Schäfer-Verwimp & Verwimp 22154/B (JE)	JX470969	JX470980	JX470992
Colura irrorata (Spruce) Heinrichs, Y.Yu, Schäf.-Verw. & Pócs	Ecuador, Gradstein *et al.* 10033 (GOET)	AY548073	DQ238584	DQ987279
Cyclolejeunea chitonia (Taylor) A.Evans	French Guiana, Holz FG-00-124 (GOET)	KF039844	KF039875	KF039806
Cyclolejeunea luteola (Spruce) Grolle	Dominica, Schäfer-Verwimp & Verwimp 17866 (M)	KF039823	KF039857	KF039785
Diplasiolejeunea cavifolia Steph.	Malaysia, Schäfer-Verwimp & Verwimp 19036/A (GOET)	JQ729531	JQ729641	JQ729418
Diplasiolejeunea pauckertii Steph.	Panama, De Gracia *et al.* 338 (GOET)	JQ729541	JQ729652	JQ729429

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TABLE 1. (Continued)

Taxon	Voucher	*rbc*L	*trn*L-F	nrITS
Drepanolejeunea anoplantha (Spruce) Steph.	Dominican Republic, Schäfer-Verwimp & Verwimp 27059 (JE)	KC313120	KC313159	KC313080
Drepanolejeunea granatensis (J.B.Jack & Steph.) Bischl.	Ecuador, Schäfer-Verwimp *et al.* 24383/B (JE)	KC313121	KC313160	KC313081
Drepanolejeunea navicularis Steph.	Ecuador, Schäfer-Verwimp & Nebel 31772/A (JE)	KC313124	KC313163	KC313085
Echinolejeunea papillata (Mitt.) R.M.Schust. Ex Hamlin	New Zealand, Schäfer-Verwimp & Verwimp 14195/A (JE)	KC313135	KC313175	KC313097
Frullanoides corticalis (Lehm. & Lindenb.) van Slageren	French Guiana, Hartmann 04-080 (GOET)	DQ983681	AM237196	AM237143
Fulfordianthus evansii (Fulford) Gradst.	Costa Rica, Dauphin s.n. (GOET)	DQ983683	AM237197	AM237144
Haplolejeunea cucullata (Steph.) Grolle	Brazil (I), Peralta *et al.* 16390 (SP)	KT626925	KT626939	KT626906
Haplolejeunea cucullata	Brazil (II), Schäfer-Verwimp & Verwimp 14560 (M)	--------	KT626940	KT626907
Haplolejeunea sticta Grolle	Reunion Island, Kis & Gyarmati 9604/G (EGR)	--------	KT626941	KT626908
Harpalejeunea grandistipula R.M.Schust.	Ecuador, Schäfer-Verwimp *et al.* 24163/B (JE)	KC313145	KC313185	KC313107
Harpalejeunea marginalis (Hook. f & Taylor) Steph.	Chile, Schäfer-Verwimp & Verwimp 8082 (JE)	KC313147	KC313187	KC313109
Harpalejeunea molleri (Steph.) Grolle	Portugal, Schäfer-Verwimp & Verwimp 29334 (GOET)	KC313148	KC313188	KC313110
Leiolejeunea grandiflora A.Evans	Jamaica (I), Schäfer-Verwimp 35394 (M)	KJ716757	KJ716782	KJ716769
Leiolejeunea grandiflora	Jamaica (II), Schäfer-Verwimp 35422 (M)	KJ716756	KJ716781	KJ716768
Lejeunea cavifolia (Ehrh.) Lindb.	Germany, Heinrichs 3695 (GOET)	AY548102	DQ238581	DQ987259
Lejeunea *flava* (Sw.) Nees	Brazil, Gradstein s.n. (GOET)	DQ983692	DQ987413	DQ987309
Lejeunea mimula Hürl.	Indonesia, Schäfer-Verwimp 20930 (GOET)	AY548104	DQ238580	DQ987261
Lejeunea pterigonia (Lehm. & Lindenb.) Mont.	Ecuador, Nöske 164 (GOET)	KF5 56549	KF556328	KF556081
Lepidolejeunea cuspidata (Gottsche) Heinrichs & Schäf.-Verw.	Guadeloupe, Schäfer-Verwimp & Verwimp 22193 (M)	KP635323	KP635348	KP635295
Lepidolejeunea delessertii (Nees & Mont.) Grolle	Réunion, Schäfer-Verwimp & Verwimp 20355/B (M)	KF039819	KF039853	KF039781
Lepidolejeunea integristipula (Jack & Steph.) R.M.Schust.	Fiji, Pócs 03307/AC (GOET)	DQ983697	DQ987417	DQ987313
Lepidolejeunea involuta (Gottsche) Grolle	Dominica, Schäfer-Verwimp & Verwimp 17855 (JE)	KP635314	KP635339	KP635285
Leptolejeunea convexistipa Bischl.	Panama, Schäfer-Verwimp & Verwimp 30861 (JE)	KF954161	KF954151	KF954154
Leptolejeunea vitrea (Nees) Schiffn.	Malaysia, Dürhammer D148 (JE)	KF954164	KF954152	KF954157
Lopholejeunea eulopha (Taylor) Schiffn.	Australia, Pócs & Streimann 9987/H1 (GOET)	AY548067	DQ987381	DQ987262
Luteolejeunea herzogii (Buchloh) Piippo	Costa Rica, Schäfer-Verwimp & Holz 0294/B (GOET)	DQ983706	DQ987467	DQ987368
Marchesinia robusta (Mitt.) Schiffn.	Ecuador, Wilson *et al.* 04-05 (GOET)	DQ983710	DQ987436	DQ987332
Mastigolejeunea auriculata (Wilson & W.J. Hooker) Schiffn.	Bolivia, Churchill 21275 (GOET)	AY548070	DQ987385	DQ987268
Metalejeunea crassitexta (J.B.Jack & Steph.) Pócs	Fiji (I), Pócs & Pócs 03303/R (EGR)	KT626918	KT626934	KT626899
Metalejeunea cucullata (Reinw., Blume & Nees) Grolle	Fiji (II), Pócs & Pócs 03305/Q (EGR)	KT626913	KT626929	KT626894

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TABLE 1. (Continued)

Taxon	Voucher	*rbc*L	*trn*L-F	nrITS
Microlejeunea africana Steph.	São Tomé and Principe, Shevock 34576 A (GOET)	KC313150	KC313190	KC313112
Microlejeunea capillaris (Gottsche) Steph.	Costa Rica, Schäfer-Verwimp & Holz SV/H-0489/B (JE)	KC313152	KC313192	KC313114
Microlejeunea squarrosa (Steph.), Heinrichs, Schäf.-Verw., Pócs & S.Dong	Brazil, Schäfer-Verwimp 13376 (GOET)	DQ983720	DQ987446	DQ987344
Microlejeunea ulicina (Taylor) Steph.	Canary Islands, Schäfer-Verwimp & Verwimp 24666 (GOET)	KC313155	KC313195	KC313116
Myriocoleopsis gymnocolea (Steph.) M.E.Reiner & Gradst.	Ecuador, Gradstein *et al.* 10020 (GOET)	DQ238568	DQ238583	DQ987277
Neurolejeunea breutelii (Gottsche) A.Evans	Brazil, Schäfer-Verwimp 14740 (GOET)	DQ983714	DQ987405	EF011779
Otolejeunea moniliata Grolle	Madagascar (I), 9448/L (EGR)	KT626923	KT626937	KT626904
Otolejeunea moniliata	Madagascar (II), Pócs *et al.* 90113/EA (EGR)	KT626922	KT626936	KT626903
Physantholejeunea portoricensis (Hampe & Gottsche) R.M.Schust.	Guadeloupe, Schäfer-Verwimp & Verwimp 22615 (M)	DQ983719	DQ987448	DQ987346
Pictolejeunea picta (Gott. ex Steph.) Grolle	French Guiana, Holz FG00-227 (GOET)	---------	DQ207914	---------
Pictolejeunea picta	Brazil I, Lopes 202 (SP)	---------	---------	KX765484
Pictolejeunea picta	Brazil II, Lopes 192 (SP)	KX765481	KX765483	KX765483
Prionolejeunea limpida Herzog	Brazil, Schäfer-Verwimp & Verwimp 13291 (M)	KF039850	DQ207928	DQ207895
Ptychanthus striatus (Lehm. & Lindenb.) Nees	Java, Gradstein 10215 (GOET)	DQ983721	DQ987406	DQ987300
Pycnolejeunea densistipula (Lehm. & Lindenb.) Steph.	Ecuador, Schäfer-Verwimp & Preussing 23368 (M)	KJ408353	KJ408377	KJ408328
Pycnolejeunea macroloba (Nees & Mont.) Schiffn.	Brazil, Yano 32740 (M)	KJ408354	KJ408378	KJ408329
Rectolejeunea versifolia (Schiffn.) L.Söderstr. & A.Hagborg	Guadeloupe, Schäfer-Verwimp & Verwimp 22245/A (GOET)	DQ983724	DQ987444	DQ987342
Rectolejeunea flagelliformis A.Evans	Panama Schäfer-Verwimp & Verwimp 34286 (JE)	KT626924	KT626938	KT626905
Rectolejeunea truncatilobula C.J.B. Bastos	Brazil, Peralta 8083 (M)	--------	KJ408380	KJ408331
Schiffneriolejeunea nymannii (Steph.) Gradst. & Terken	Malaysia, Gradstein *et al.* 10321 (GOET)	DQ983725	DQ987424	DQ987320
Siphonolejeunea elegantissima (Steph.) Grolle	Australia, Pócs & Brown 0026/AA (E)	DQ983726	DQ987452	DQ987352
Spruceanthus thozetianus (Gottsche & F. v. Müll.) B.M.Thiers	Australia, Pócs 01107/M (GOET)	AM384877	DQ987460	DQ987362
Thysananthus spathulistipus (Reinw. *et al.*) Lindenb.	Bali, Schäfer-Verwimp & Verwimp 20790 (GOET)	DQ983739	DQ987392	DQ987282
Vitalianthus aphanellus (Spruce) Bechteler *et al.*	Brazil, Yano & Zartman 32771 (SP)	KT626920	--------	KT626900
Vitalianthus bischlerianus (K.C.Pôrto & Grolle) R.M.Schust. & Giancotti	Brazil (I), Schäfer-Verwimp & Verwimp 9505 (M)	KT626921	--------	KT626901
Vitalianthus bischlerianus	Brazil (II), Schäfer-Verwimp & Verwimp 12913 (M)	--------	--------	KT626902
Xylolejeunea crenata (Mont.) Xiao L.He & Grolle	Ecuador, Schäfer-Verwimp & Nebel 32827/A (M)	KJ408356	KJ408382	KJ408333
Xylolejeunea grolleana (Pócs) Xiao L.He & Grolle	Madagascar, Pócs & Szabó 9878/EM (EGR)	KT626911	KT626928	KT626892

Phylogenetic analyses

jModelTest2 (Darriba *et al.* 2012) was used to determine the best fit models of evolution according to the Akaike Information Criterion (Akaike 1973). This resulted in a TVM+I+G model for the *trn*L-*trn*F region and in a GTR+I+G model for *rbc*L, ITS, as well as the dataset comprising all three markers.

Maximum likelihood (ML) analyses were conducted using RAxML 8.2.4 (Stamatakis 2014). Since the three markers showed no incongruence when analysed separately, the single datasets were combined. Clades with bootstrap values (BP) of 70-94 % were regarded as moderately supported and those with BP ≥ 95 % as strongly supported (Erixon *et al.* 2003). For the final run the dataset was partitioned by markers and a GTR+G model was employed for each of them, following the recommendation given by jModelTest and Stamatakis (2016). Ten thorough ML searches in combination with the multi-parametric bootstrapping using the autoMRE function (Pattengale *et al.* 2010) were executed.

MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003) was used for Bayesian Inference (BI). Again the dataset was partitioned by markers and the GTR+I+G model as suggested by jModelTest was used for each partition. Two Metropolis-coupled Markov Chain Monte Carlo (MCMC) analyses, including three heated chains and one cold chain, were run for 10 million generations, sampled every 1000 generations. TRACER 1.6 (http://tree.bio.ed.ac.uk/software/tracer/) was used to check for convergence and stationarity and an average standard deviation of split frequency below 0.01 indicated a sufficiently long run. The initial 25 % of sampled trees were discarded as burn-in. The remainder was summarized with TreeAnnotator 1.8.2 (Drummond *et al.* 2012). The resulting maximum clade credibility (MCC) tree was visualized using FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). Bayesian Posterior Probability (PP) values were regarded as significant when PP ≥ 0.95 (Larget & Simon 1999).

Morphology

The DNA vouchers of *Pictolejeunea picta* were studied under a Carl Zeiss AxioScope A1 compound microscope equipped with a Canon 60D digital camera. The images printed in Fig. 2 are digitally stacked photomicrographic composites of up to 12 individual focal planes obtained using the software package HeliconFocus 6.7.1.

Results

The ML and BI analyses recovered highly concordant phylogenetic hypotheses (Fig. 1). A clade with three accessions of *Pictolejeunea picta* (BP=100, PP=1.00) was placed sister to the remainder of Lejeuneeae (BP=76, PP=1.00). This remainder split into two main lineages. A lineage with BP=53 and PP=0.86 included members of Cheilolejeuneinae, Echinolejeuneinae and Leiolejeuneinae. *Cheilolejeunea gaoi* Zhu *et al.* (2000: 499) was resolved in Echinolejeuneinae rather than Cheilolejeuneinae and placed sister to *Haplolejeunea* Grolle (1975: 205) (BP=90; PP=1.00). The other lineage (BP=90, PP=1.00) included representatives of Ceratolejeuneinae, Cololejeuneinae, Cyclolejeuneinae, Drepanolejeuneinae, Lejeuneinae, Lepidolejeuneinae, Leptolejeuneinae, Pycnolejeuneinae and Xylolejeuneinae. Pycnolejeuneinae were separated from the remainder of this lineage with a BP=89 and PP=1.00. All subtribes of Lejeuneeae except Ceratolejeuneinae (BP=69, PP=0.82) achieved BP percentage values of 98-100 and PP of 1.00.

Discussion

Our sampling includes 30 genera of Lejeuneeae and thus represents the most comprehensive generic sampling of this tribe available so far. As *Pictolejeunea* was resolved sister to the remainder of Lejeuneeae it should be placed in its own subtribe (see taxonomic treatment). Members of *Pictolejeunea* were originally placed within *Prionolejeunea* Spruce (1884: 152) Schiffner (1893: 127) or *Cheilolejeunea* yet these genera differ by their lack of brownish or reddish ocelli and their marginal lobule papillae. The papillae is on the free lobule margin, not positioned inside of the lobule as in *Pictolejeunea* (Grolle 1977). Ental papillae are known from several representatives of Ptychanthoideae, however, they also occur in the lejeuneoid genera *Diplasiolejeunea* (Spruce 1884: 301) Schiffner (1893: 121) and *Tuyamaella* Hattori (1951: 60) (Grolle 1977). Brownish or reddish ocelli are also not an exclusive character of *Pictolejeunea* but also occur in *Leptolejeunea moniliata* Stephani (1913b: 371) (Gradstein & Costa 2003) and *Leptolejeunea amphiophthalma* Zwickel (1933: 117) [Yang & Lin 2008, as *Leptolejeunea picta* Herzog (1942: 430)].

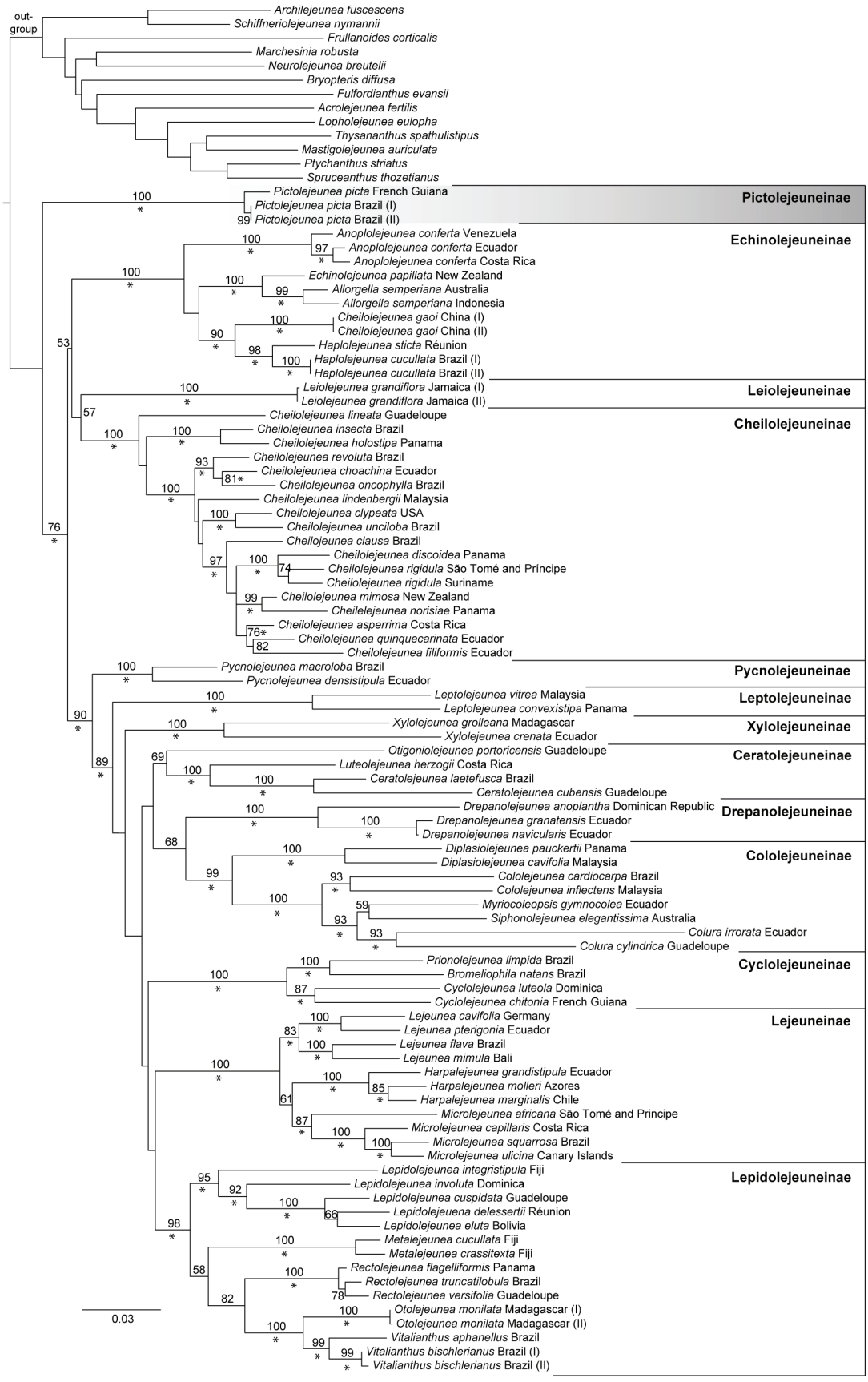

FIGURE 1 Most likely phylogram resulting from maximum likelihood analysis of the nrITS-*trn*L-*trn*F-*rbc*L dataset. Bootstrap percentage values ≥ 50 are indicated at branches. Stars indicate Bayesian Posterior Probability values ≥ 0.95.

Pictolejeunea somewhat resembles *Cheilolejeunea gaoi* "in delicate plants without secondary pigmentation, absence of gynoecial innovation, obsolete first tooth and indistinct second tooth of leaf lobule, and thin-walled cells without trigones and intermediate thickenings" (Zhu *et al.* 2000). However, according to the latter authors, *Cheilolejeunea gaoi* differs from *Pictolejeunea* in its distant, marginal hyaline papilla and the absence of ocelli in any part of the plant. According to our phylogenetic hypothesis, it is not closely related to *Pictolejeunea*. Ye *et al.* (2015) already demonstrated that *Cheilolejeunea gaoi* does not belong to *Cheilolejeunea* s.l.; however, our extended sampling indicates a close relationship with *Haplolejeunea* (Echinolejeuneinae), a genus that differs from *C. gaoi* in the presence of ocelli and pycnolejeuneoid innovations, and a lack of teeth on the free margin of the lobule (Gradstein *et al.* 2001). Considering these morphological differences, it may be appropriate to either erect a new genus to accommodate this species or alternatively to reassign this species to genus *Haplolejeunea.* However, this hypothesis should be confirmed with extended taxon sampling.

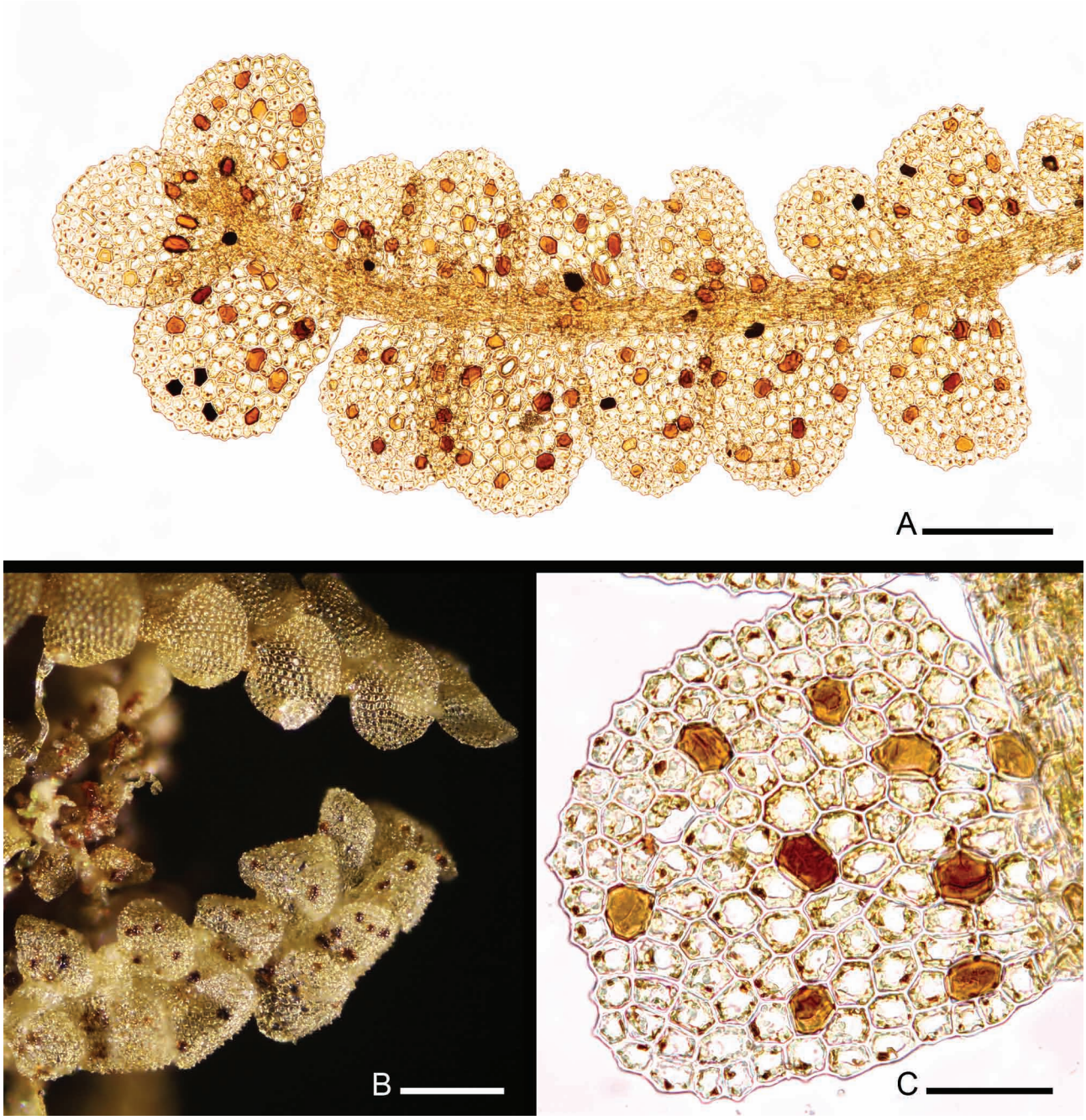

FIGURE 2 *Pictolejeunea picta* **A.** Top of shoot in ventral view. Note the reddish brown ocelli in leaves and underleaves. **B.** Portion of dried herbarium specimen. Note the ocelli and papillose leaf surface of *Pictolejeunea*. The upper plant belongs to *Lejeunea* sp. **C.** Leaf with ten scattered ocelli (A, C from DNA voucher *Lopes 202*; B from DNA voucher *Lopes 192*; scale bars A, 1.5 mm; B, 200 µm; C, 50 µm).

Perspectives

The classification of Lejeuneaceae is hampered by extensive morphological homoplasy (Gradstein *et al.* 2003, Dong *et al.* 2012, Heinrichs *et al.* 2013, Bechteler *et al.* 2016) which is also evident from the numerous taxonomical improvements since the last comprehensive supraspecific classification of the family by Gradstein (2013). Our generic sampling includes only the Neotropical type species *Pictolejeunea picta* since no material of the other five *Pictolejeunea* species was available for molecular investigation. An extension of the sampling is necessary to confirm the current genus concept of *Pictolejeunea* and its disjunct range. Of special interest are the Bornean *Pictolejeunea mizutanii* Grolle (1977: 255), the Cuban *Pictolejeunea levis* Grolle & Reiner-Drehwald (2005: 81), the only species of the genus with (lejeuneoid) innovations, and the Venezuelan *P. reginae* Ilkiu-Borges (2002: 318) which has entire underleaves and was placed in its own subgenus *Neopictolejeunea* Ilkiu-Borges (2002: 320).

Taxonomic treatment

Lejeuneaceae subtribe ***Pictolejeuneinae*** Bechteler, G.E.Lee, Schäf.-Verw., D.F.Peralta, M.A.M.Renner & Heinrichs, subtr. nov.

Typus: *Pictolejeunea* Grolle (Fig. 2)

Plants incubous with lateral branches, stem hyalodermis and ventral merophyte two cells wide; complicate-bilobed leaves with wide spreading lobes and lobules connected to lobes with a long keel; ental lobule papilla present, differentiated lobule teeth lacking, scattered pale brown to reddish ocelli in leaves, underleaves, involucres and perianths. Gynoecia usually without innovations; perianths somewhat flattened with two broad lateral keels expanded into short auricles.

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