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Multiple transoceanic dispersals and geographical structure in the pantropical leafy liverwort *Ceratolejeunea* (Lejeuneaceae, Porellales)

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ABSTRACT

Aim How disjunct distributions arise and why organisms differ in diversification patterns remain some of the most compelling fundamental questions in biogeography. We carry out phylogeographical analyses of the pantropical liverwort genus *Ceratolejeunea* to identify its geographical origin and the dispersal routes by which it gained its Neotropical-African disjunction. Furthermore, we investigate whether there is geographical structure in *Ceratolejeunea* on islands and whether island diversity is a result of radiations or recurrent migration.

Location America, Africa and Australasia.

Methods Sequences of two chloroplast regions (*trnL-F*, *rbcL*) and the nuclear ribosomal ITS region were obtained for 55 accessions of 20 species to explore the phylogeny, divergence times and ancestral areas of *Ceratolejeunea*. The phylogeny was reconstructed using maximum likelihood and Bayesian inference approaches, and divergence times were estimated with a Bayesian relaxed clock method and fossil and secondary calibrations. Ancestral areas were estimated using BioGeoBEARS.

Results *Ceratolejeunea* likely originated in the Neotropics during the Palaeogene (42.2 Ma, 95% HPD: 22.2–64.8) and the initial diversification of its crown group took place between the Eocene and Miocene (25.5 Ma, 95% HPD: 16.6–35.8). Although boreotropical migration and subsequent extinction in northern regions cannot be rejected, the observed disjunctions are best explained by four transoceanic dispersal events from the Neotropics to Africa during the late Oligocene to Pleistocene. Geographical structure is prevalent on islands, particularly in the *C. cornuta* complex. Three species and the subgenus *Ceratolejeunea* are recovered as paraphyletic.

Main conclusions Widespread paraphyly and sister group relationships between disjunct taxa indicate an important role of cryptic speciation and transoceanic dispersal with subsequent genetic differentiation in the evolution of *Ceratolejeunea*. On islands, recurrent migration, rather than radiation, has shaped bryophyte diversity.

Keywords

ancestral area estimation, bryophyte, divergence time estimation, Jungermanniopsida, long-distance dispersal, phylogeny, tropics

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INTRODUCTION

Transoceanic disjunctions are common in plants, particularly between tropical America and tropical Africa (Thorne, 1972; Raven & Axelrod, 1974). In the last few decades, evidence

pointing to long-distance dispersal (LDD), rather than vicariance, as the mechanism behind many of these disjunctions has mounted (Renner, 2004; de Queiroz, 2005; Christenhusz & Chase, 2013). The underlying dispersal routes and diversification patterns across space and time, however, are less well

understood (Renner, 2004; Cook & Crisp, 2005; Sanmartín *et al.*, 2007; Winkworth *et al.*, 2015). Although, for instance, the importance of asymmetrical west to east dispersal caused by the West Wind Drift in the Southern Hemisphere has been demonstrated (Sanmartín & Ronquist, 2004; Sanmartín *et al.*, 2007), clear general patterns for the directionality of dispersal have yet to be found. Furthermore, studies have shown that diversification rates differ between angiosperms and other major plant groups (e.g., Laenen *et al.*, 2014) and that a major cause may be dispersal capacity and associated gene flow (Vanderpoorten *et al.*, 2011). However, case studies of colonization and diversification in individual groups are needed to clarify underlying factors.

Bryophytes (mosses, liverworts and hornworts) often exhibit transoceanic disjunctions at the species level and higher (Schofield & Crum, 1972; Delgadillo, 1993; Gradstein, 2013). As in many vascular plants, divergence time estimates have placed the origin of numerous disjunct taxa after continental break-ups, meaning many bryophytes are too recent for their distributions to be explained by Gondwanan vicariance rather than LDD (Heinrichs *et al.*, 2009; Villarreal & Renner, 2014). An important factor likely promoting the widespread LDD patterns in bryophytes, which are mainly wind dispersed, is their high dispersal capacity (Van Zanten & Gradstein, 1988). In accordance with the findings of Renner (2004) for angiosperms, studies in bryophytes have found evidence of eastward dispersal from tropical America to Atlantic islands and tropical Africa and Asia (Heinrichs *et al.*, 2005, 2013; Patiño *et al.*, 2015). Despite these proven dispersal abilities, net diversification is generally lower in bryophytes than in angiosperms (Laenen *et al.*, 2014). On islands, angiosperms often diversify *in situ* after colonization (Emerson, 2002; Price & Wagner, 2004), while bryophytes do so much more rarely (Vanderpoorten *et al.*, 2010). Although this may in part be due to the morphological similarity between genetically distinct bryophytes, a phenomenon known as ‘cryptic speciation’ (Shaw, 2001), some disjunct species have been shown to exhibit genetic variation unrelated to geographical patterns (Korpelainen *et al.*, 2005; Grundmann *et al.*, 2007; Vanderpoorten *et al.*, 2008). This has led to the hypothesis that large Mediterranean islands act as mainland to bryophytes (Grundmann *et al.*, 2007). However, when island speciation does occur, it often does not result in radiation but in genera represented only by a single endemic island species, a process termed ‘anagenetic speciation’ (Patiño *et al.*, 2014).

The highly disjunct, epiphytic liverwort genus *Ceratolejeunea* is particularly well suited to investigate biogeography, as it contains pantropical species, regional endemics and many species occurring on islands. *Ceratolejeunea* comprises c. 40 species, with a centre of diversity in South America (c. 26 species), but also occurring in sub-Saharan Africa (c. 11 species) and in tropical Asia and Oceania (about seven species) (see Table S1.1 for references and further information). Previous dating analyses have ruled out vicariance as the cause for this distribution (Feldberg *et al.*, 2014). Of par-

ticular interest is the pantropical *C. cornuta*, which has been alternatively interpreted as a morphologically variable species (Pócs & Chantanaorrapint, 2015) or a complex of local endemics including species restricted to African islands (Wigginton, 2004).

In this study, we aim to answer the following questions. First, what is the geographical origin of *Ceratolejeunea* and by which dispersal routes did the genus gain its disjunction between the Neotropics and Africa? Second, is there evidence of geographical structure in *Ceratolejeunea*, particularly on islands? And finally, if *Ceratolejeunea* accumulated local diversity on islands, was this achieved via radiations or recurrent migration? Based on the studies underlining the paucity of radiations and the importance of anagenetic speciation in bryophytes, we expect potential diversity to have accrued on islands via multiple migration events.

MATERIALS AND METHODS

Taxon sampling, DNA sequencing and alignment

Twenty *Ceratolejeunea* species were sampled based on availability and to represent the distribution range and morphological diversity of the genus. Asian accessions could not be sampled due to lack of available material, Australasia is appropriately represented with one species (of two), and no samples from the rest of Oceania were available. Phylogenetic trees were rooted on *Luteolejeunea herzogii*, the sole species of the sister genus of *Ceratolejeunea* (Piippo, 1986; Wilson *et al.*, 2007a). Voucher details of the plant material are given in Table S1.2.

Plant tissue was isolated from herbarium material and used to extract genomic DNA with the Invisorb Spin Plant Mini Kit (Invitex, Berlin, Germany). Polymerase chain reaction (PCR) was conducted for the nuclear ribosomal internal transcribed spacer region nrITS1–5.8S–ITS2 (ITS) and the plastid regions *rbcL* and *trnL-F*. PCR and sequencing protocols followed Hartmann *et al.* (2006) for the ITS region and Gradstein *et al.* (2006) for *trnL-F* and *rbcL*. Sequencing was carried out on an ABI 3730 capillary sequencer using the BigDye Terminator Cycle Sequencing 3.1 Kit (PE Applied Biosystems, Foster City, CA, USA). A total of 148 sequences were newly generated. Alignment was done separately for the nuclear and plastid sequences using the MUSCLE online version (<http://www.ebi.ac.uk/Tools/msa/muscle/>) with default settings. The aligned sequences were then inspected by eye in BioEDIT 7.0.5.3 (Hall, 1999) and manually adjusted to conserve sequence homology when necessary. Ambiguous sites were excluded.

The total dataset comprised 54 sequences of ITS, 51 of *trnL-F* and 48 of *rbcL*, not including all three markers available from the outgroup *Luteolejeunea*. Total missing data amounted to 12%, mainly due to repeated failure to sequence *rbcL* in seven accessions (Table S1.2). Clades with bootstrap values (BP) 70–94 were defined as moderately supported and those with BP ≥ 95 as strongly supported

(following Erixon *et al.*, 2003). Because there was no supported topological contradiction between the single genes and between the partitions, the nuclear and plastid data matrices were concatenated, resulting in an alignment of 2424 nucleotides.

Phylogenetic analysis

Maximum-likelihood (ML) inference was carried out using RAxML 8.0.0 (Stamatakis *et al.*, 2008) with the extended majority rule bootstrapping criterion (Pattengale *et al.*, 2010) and the analysis partitioned into a nuclear and a plastid region. The best-fit models of evolution selected in jMODELTEST 2 (Darriba *et al.*, 2012) under the Akaike information criterion (AIC; Akaike, 1973), TVM+ Γ +I and TrN+ Γ +I, were not available in RAxML. Because of this, the best-fitting overparameterized available model, GTR+ Γ +I in both cases, was employed. This approach follows the suggestion given by Posada (2008).

Bayesian inference was undertaken with MRBAYES 3.2.5 (Ronquist & Huelsenbeck, 2003) based on the same partitions and models as the ML analysis. Two Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses, including three hot chains and one cold chain, were run for 40,000,000 generations and sampled every 1000 generations, with a random starting tree. Stationarity and convergence of runs and estimation of burnin were checked using TRACER 1.6 (available from <http://tree.bio.ed.ac.uk/software/tracer/>). Bayesian posterior probabilities (BPP) were calculated for the majority consensus tree of all sampled trees after confirming that the average SD of split frequency estimations was below 0.01 and discarding trees sampled within the burnin phase (four million generations). Values were regarded as significant when BPP \geq 0.95 (Larget & Simon, 1999). The results were visualized using FIGTREE 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Divergence time analysis

Twenty-four accessions from the combined matrix described above, representing 15 *Ceratolejeunea* species and eight distinct intraspecific populations as well as the outgroup, were used to estimate divergence times. Distinct populations were selected based on our prior knowledge of the population locality and the phylogeny. Five species were not included because they lacked an entire plastid marker. When multiple highly similar accessions were available, one was included at random to prevent erroneous results caused by short branches (Janssen *et al.*, 2008). Dating was executed using BEAST 1.8.2 (Drummond *et al.*, 2012) and the TrN+ Γ +I substitution model for the ITS partition and the TVM+ Γ +I substitution model for the plastid partition, as selected by jMODELTEST under the AIC criterion. All parameters were estimated in BEAST. Birth-death and pure-birth (Yule) tree models were compared using Bayes factors calculated based on path/stepping-stone sampling (Baele *et al.*, 2012). According to the criteria of Kass & Raftery (1995), the models did

not differ significantly (ln Bayes factor = 0.47), and thus the less complex Yule model was used. Three independent runs of the MCMC analysis were performed for 120 million generations, sampling every 6000 generations. Convergence was determined by examining the three independent log files in TRACER to confirm that separate analyses converged on the same result. ESS values $>$ 200 were regarded as good support, indicating that the parameter space had been sampled sufficiently for valid parameter estimation. Runs converged around 100 million generations. To find the appropriate clock model, a likelihood ratio test (Felsenstein, 1988) was carried out in PAUP* 4.0a146 (Swofford, 2002). A strict clock was rejected ($*P < 0.05$), and thus an uncorrelated lognormal relaxed clock model was employed (Drummond *et al.*, 2006).

For the relaxed clock approach, node age information was incorporated from a previous fossil-calibrated dating study based on the *rbcL* gene of 303 species of liverworts representing the diversity of the two orders Porellales and Jungermanniales (Feldberg *et al.*, 2014). The amber fossil *Ceratolejeunea sublaetefusca* (Heinrichs *et al.*, 2015b) was used as a further constraint. This Miocene Mexican amber fossil is coeval with Dominican amber fossils (Solórzano Kraemer, 2007) and can therefore be dated to 15–20 Ma (Iturralde-Vinent & MacPhee, 1996). Because the fossil is almost indistinguishable from the extant *C. laetefusca*, it was used to constrain the age of the major clade containing this species. Such a relatively conservative assignment is necessary, because liverworts are morphologically homoplastic and fossil assignments can thus be misleading (Renner, 2015). Because the analyses of Wilson *et al.* (2007b) and Feldberg *et al.* (2014) indicate an older age of the fossil constrained clade than that estimated for the amber, a lognormal distribution was used (offset: 14.5, mean: 1, SD: 1; 95% interval: 15–28.6 Ma). Based on the BEAST analysis of Feldberg *et al.* (2014), the split between *Luteolejeunea* and *Ceratolejeunea* was constrained at 36 Ma (SD: \pm 5) with a normal distribution on the prior. A confidence interval was not reported by Feldberg *et al.* (2014); thus, the SD was selected to include the node age identified by the study by Wilson *et al.* (2007b) and to reflect the average age of liverwort genera (Laenen *et al.*, 2014). All other priors were left as the default values. The initial 10% of trees were discarded as burnin and a maximum clade credibility tree with mean node heights constructed from the remaining trees with TREEANNOTATOR 1.8.2 (part of the BEAST package) and visualized as above with FIGTREE. The analysis was run from an empty alignment to test the influence of the priors on the posterior distribution.

Ancestral area estimation

To infer routes of dispersal or vicariance events, the distribution range of *Ceratolejeunea* was divided into three major areas: (A) the Neotropics, (B) Africa including Madagascar and further neighbouring islands and (C) Australasia.

Although Asia is part of the range of *Ceratolejeunea*, it was excluded due to a lack of samples from this area. Species distributions were obtained from the literature (Table S1.1). The Neotropical *Ceratolejeunea cornuta* and *C. diversicornua* have been considered pantropical because several African species have been synonymized with them based on morphology (Dauphin, 2003; Gradstein, 2013; Pócs & Chantanaorrapint, 2015). However, preliminary sequencing for this study did not support these synonymizations, and thus the two species were not assigned pantropical ranges.

To estimate the ancestral history of *Ceratolejeunea*, we used the R package BioGEOBEARS (Matzke, 2014). This method implements the LAGRANGE DEC model (Ree & Smith, 2008), DIVA (dispersal–vicariance analysis; Ronquist, 1997) and BayArea (Landis *et al.*, 2013) within a maximum-likelihood framework. Furthermore, founder-event speciation can be added to any of these models and estimated as an additional free parameter *j*. The MCC tree from the divergence time analysis was used to infer the ancestral area probability, and all six models were compared using likelihood values and the Akaike information criterion corrected for small sample sizes (AIC_c) (Matzke, 2013, 2014). Because no species is distributed over all three defined areas, we set the maximum number of areas to two.

RESULTS

Phylogeny

The ML analysis from the combined data resolves four major clades in the genus *Ceratolejeunea* (Fig. 1), labelled as clades I–IV in the figure. Length and number of informative sites for each marker are provided in Table S1.3. Although the topology is generally well-resolved and clades I and IV show BP > 98, clades II and III show low BP of 29 and 65. Moreover, the sister relationship between clades III and IV also receives weak support (52 BP). Three sampled species occurring in Africa – *C. papuliflora*, *C. saroltae* and *C. diversicornua* – fall separately and with strong support within mainly Neotropical groupings of clades I, II and IV, respectively. Clade IV is divided into two moderately supported lineages, consisting of *C. filaria* (73 BP) and the pantropical *C. cornuta* complex (80 BP). *Ceratolejeunea diversicornua* is resolved as sister to the rest of the clade but without support. The *C. cornuta* complex shows geographically coherent patterns of genetic differentiation, being split into a paraphyletic grade of three Neotropical lineages and an African–Australasian clade. Three taxa previously considered synonymous or closely associated with *C. cornuta* are resolved within this group, a moderately supported *C. belangeriana* with clear differentiation into an African and Australasian group, a weakly resolved polyphyletic grouping of *C. calabariensis* and a moderately supported *C. mascarena* with clear genetic distinction between the Mayotte Island and the Seychelles Islands. Topologies resulting from Bayesian inference are near identical to the ML tree described (Fig. S1.1). Bayesian

posterior probabilities ≥ 0.95 all correspond to BP ≥ 70 in the ML tree, with the exception of the lower value (0.79 BPP) for *C. mascarena* and a more strongly supported sister relationship between clades III and IV (0.98 BPP). Bayesian support ≥ 0.95 BPP for three branches with BP ≥ 64 but < 70 was not considered a meaningful difference. The subgenus *Ceratolejeunea* is recovered as paraphyletic, and further taxonomic implications of the phylogeny are provided in the appendix (Comment S1.1).

Divergence time estimates and biogeography

The clock-dating matrix included 23 accessions of *Ceratolejeunea* and was calibrated with a secondary constraint and the Miocene fossil *C. sublaetefusca*. Sampling from the prior only resulted in different posterior values, indicating that our results were not strongly influenced by the prior distributions. Results of the divergence time estimates are shown in Fig. 2, while a summary including estimates and 95% higher posterior density (HPD) intervals for nodes of interest is given in Table 1. The split between the outgroup *L. herzogii* and *Ceratolejeunea* is dated from early Neogene to the Palaeogene (42.2 Ma, 95% HPD: 22.2–64.8), with the crown group diverging between the early Miocene and late Eocene (25.5 Ma, 95% HPD: 16.6–35.8). Diversification of the main clades occurred from the Miocene to Oligocene, with the Neotropical–African disjunctions occurring later in the Miocene or Pliocene. This includes the earliest disjunction with the African *C. papuliflora* in clade I. Later Neotropical–African disjunctions occur between *C. saroltae* and *C. caducifolia* (8.7 Ma, 95% HPD: 2.6–17.2) and between the Neotropical and African–Australasian *C. cornuta* group (4.3 Ma, 95% HPD: 2.3–6.6).

The best-fitting ancestral area estimation model was BAYAREALIKE+J (Table 2). The result of the ancestral area estimation is presented in combination with the BEAST tree (Fig. 2). A Neotropical origin of *Ceratolejeunea* was indicated, with four independent dispersal events from the Neotropics to Africa during the late Oligocene to Pleistocene and one later dispersal from Africa to Australasia during the Plio-Pleistocene (*c.* 2 Ma) explaining the current patterns of distribution. A Neotropical origin for *C. papuliflora*, *C. saroltae*, *C. diversicornua* and the African *C. cornuta* group was supported.

DISCUSSION

The phylogeny of *Ceratolejeunea* resolves four main clades, three of which include sister group relationships between Neotropical and Palaeotropical species or clades. The ancestral area estimation supports four eastward transoceanic range expansions from the Neotropics to Africa and one from Africa to Australasia. Ancestral area estimation places the origin of the *Ceratolejeunea* crown group (node 2; Fig. 2) in the Neotropics. This result may have been influenced by the comparatively few Palaeotropical species sampled. Nonetheless, a Neotropical origin is supported by the purely Neotropical occurrence of the sister genus and the next most

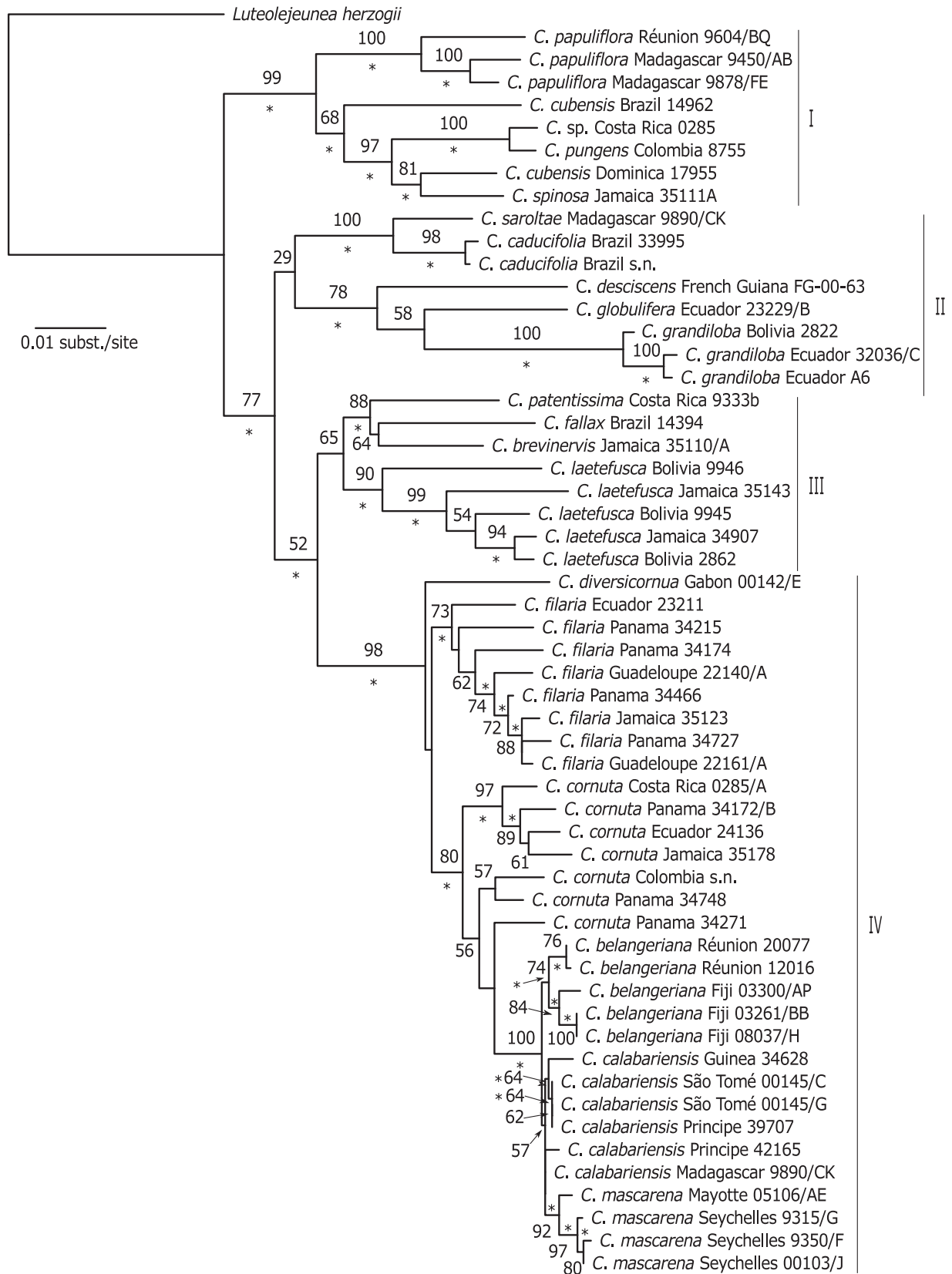


Figure 1 Maximum-likelihood (ML) phylogeny of *Ceratolejeunea* based on three markers from nuclear and plastid DNA. ML bootstrap probabilities > 50 are shown at branches (one lower value discussed in the text is also shown); a star indicates a Bayesian posterior probability ≥ 0.95 . The four major clades are labelled I to IV. [Correction added on 28 May 2016, after first online publication: Figures 1 and 2 replacement]

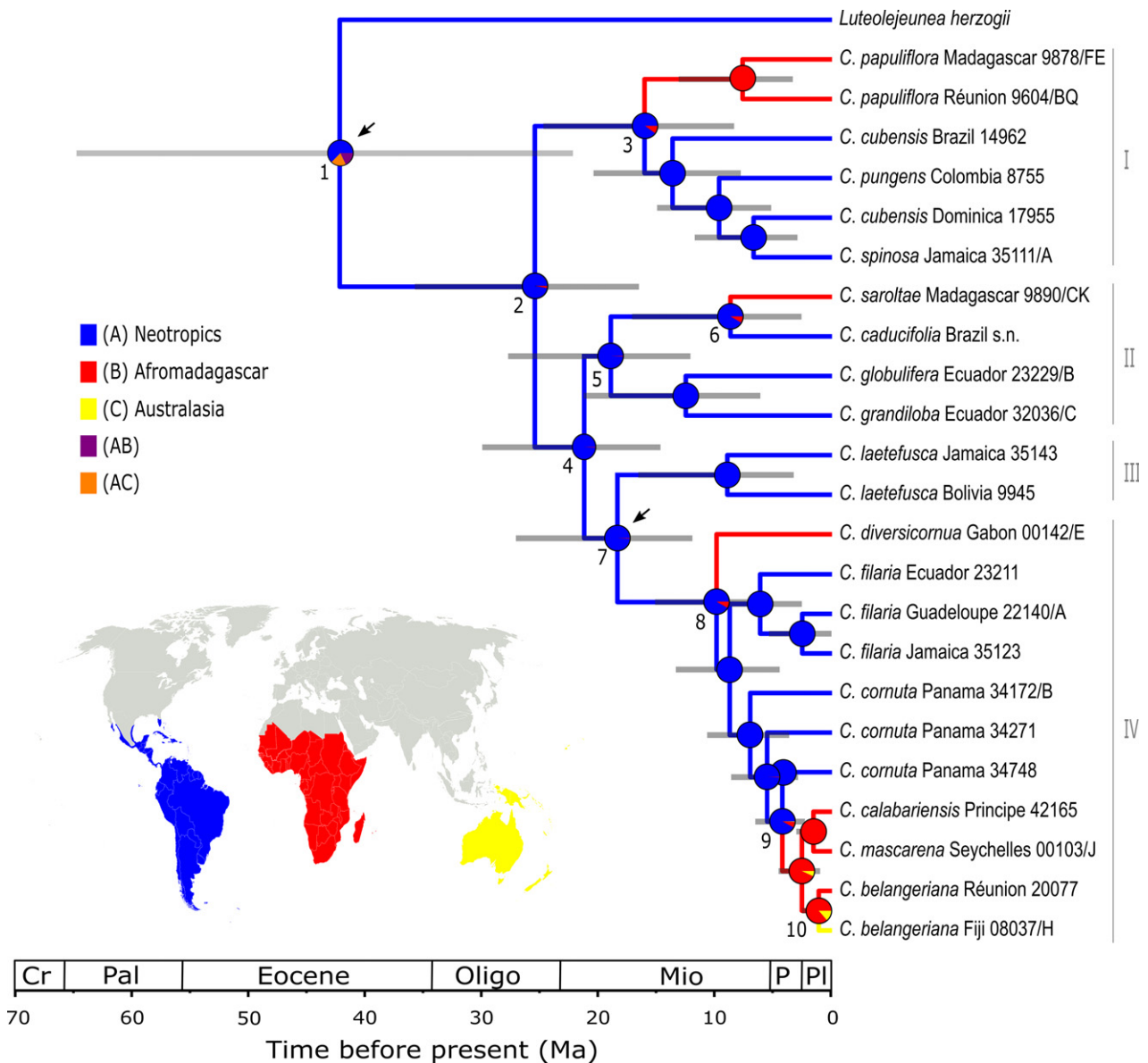


Figure 2 Time tree for *Ceratolejeunea* obtained under a relaxed clock model calibrated with a secondary age estimate and a fossil (nodes 1 and 7, respectively, marked with arrows). Blue colour-coded species are found in the Neotropics, red in Africa and yellow in Australasia. Bars at nodes indicate 95% highest posterior density (HPD) intervals around node ages. Pie charts at nodes represent probabilities for ancestral areas resulting from the BioGeoBEARS analysis with the BAYAREALIKE+J model. The four major clades also shown in Fig. 1 are labelled I to IV.

closely related genus *Otigoniolejeunea* (Wilson *et al.*, 2007b; Wei *et al.*, 2014).

Dispersal to the Palaeotropics mostly took place in the Miocene (nodes 3, 6 and 8; Fig. 2). In contrast to the other Palaeotropical species, members of the *C. cornuta* complex dispersed and diverged later, in the Plio-Pleistocene (node 9, Fig. 2). Our estimated origin of *Ceratolejeunea* between the late Eocene and early Miocene is in line with the Bayesian divergence time analysis of Feldberg *et al.* (2014) and the penalized likelihood analysis of Wilson *et al.* (2007b).

The recovered pattern of LDD is in accordance with the notable dispersal ability of bryophytes (reviewed in Lewis

et al., 2014). This ability has been shown, for instance, through modelling of biogeographical patterns (Vanderpoorten *et al.*, 2010) and correlations between distributions and air currents (Muñoz *et al.*, 2004). Indeed, dispersal from the Neotropics to Africa has been found in molecular studies of numerous leafy liverwort genera, including *Plagiochila* (Heinrichs *et al.*, 2005), *Bryopteris* (Hartmann *et al.*, 2006), *Lejeunea* (Heinrichs *et al.*, 2013) and *Lepidolejeunea* (Heinrichs *et al.*, 2015a). Furthermore, Patiño *et al.* (2015) hypothesized a Neotropical origin of north-eastern Atlantic bryophytes based on species distribution modelling and approximate computation analyses. An origin in the

Table 1 Relaxed clock divergence time estimates and ancestral area estimation results for nodes of interest in *Ceratolejeunea*. The 95% highest posterior density (HPD) values of the divergence time estimates are provided in square brackets. The estimated ancestral areas of each node as indicated by BioGEOBEARS using the BAYAREALIKE+J model are shown, with rounded probabilities given in per cent. When only one area is shown, the probability is 100%. Areas are abbreviated as follows: A, Neotropics; B, Africa; C, Australasia; AB, Neotropics and Africa; AC, Neotropics and Australasia. Node numbers refer to Fig. 2.

Node	Estimated divergence time in Ma with [95% HPD]	Estimated ancestral area(BAYAREALIKE+J)
1	42.2 [22.2–64.8]	A 62; AB 19; AC 18
2	25.5 [16.6–35.8]	A 97; AB 3
3	16.1 [8.4–24.8]	A 90; B 10
4	21.3 [14.7–30]	A
5	19.0 [12.2–27.8]	A 99; B 1
6	8.7 [2.6–17.2]	A 92; B 8
7	18.4 [12–27.1]	A
8	9.9 [5.4–15.2]	A 92; B 8
9	4.3 [2.3–6.6]	A 92; B 7; C 1
10	1.1 [0–2.6]	B 86; C 14

Table 2 BioGEOBEARS model comparison based on log-likelihood (lnL) and the Akaike information criterion corrected for small sample sizes (AIC_c); *n*, number of parameters; *d*, rate of dispersal; *e*, rate of extinction; *j*, relative probability of founder-event speciation. The best model is shown in bold.

	lnL	<i>n</i>	<i>d</i>	<i>e</i>	<i>j</i>	AIC _c
DEC	–20.55	2	0.023	1.65	0	45.66
DEC+J	–18.14	3	10 ^{–12}	2.7	0.078	43.49
DIVALIKE	–20.87	2	0.022	0.75	0	46.31
DIVALIKE+J	–18.47	3	10 ^{–12}	0.89	0.077	44.13
BAYAREALIKE	–21.13	2	0.024	0.78	0	46.83
BAYAREALIKE+J	–18.06	3	10^{–7}	0.92	0.074	43.31

Neotropics has also been demonstrated in pantropically distributed families of angiosperms, such as Malpighiaceae (Davis *et al.*, 2002) and Gentianaceae (Merckx *et al.*, 2013). Finally, present-day air currents over the central Atlantic provide a vector to support the inferred transoceanic dispersal (Renner, 2004). Indeed, the pattern observed in *Ceratolejeunea* is in line with evidence in favour of the Neotropics as a cradle and museum of diversity (McKenna & Farrell, 2006; Mittelbach *et al.*, 2007).

Alternatively, a boreotropical connection across the North Atlantic (Tiffney, 1985) might have enabled the colonization of the Palaeotropics, followed by extinction in large parts of North America, Europe and other northern regions as the tropical climate disappeared in the Miocene and later ages (Zachos *et al.*, 2001). The dispersal event reconstructed at the base of the *Ceratolejeunea* crown group (node 2, Fig. 2) is timed at 16.6–35.8 Ma, within the limit of boreotropical migration across the ‘North Atlantic Land Bridge’ (c. 30 Ma;

Donoghue & Smith, 2004). Molecular studies using divergence time estimates have provided evidence for plant migration along this route (Bell, 2007; Antonelli & Sanmartín, 2011). Such a migration scenario, however, is not supported by the fossil record of *Ceratolejeunea*, which is restricted to the Neotropics, although the lack of boreotropical fossils may be due to the low fossilization rate of bryophytes or the old age of Palaeotropical amber deposits containing liverwort fossils (Heinrichs *et al.*, 2015b). If we are correct in the age of the genus, the probability of finding *Ceratolejeunea* fossils in Europe or Asia is low. Thus, boreotropical dispersal cannot be formally ruled out, although the data available do not support this scenario.

The *C. cornuta* complex exhibits geographically structured genetic divergence on oceanic islands. This suggests that islands may not generally function as mainland for bryophytes as hypothesized by Grundmann *et al.* (2007) for the Mediterranean, but that dispersal between oceanic islands and mainland can be low. In agreement with this is the occurrence of typical bryophyte island syndromes, which indicate that the ocean is a barrier to gene flow (Patiño *et al.*, 2013). Important traits influencing the intensity of dispersal and thus gene flow in bryophytes may be the size, quantity and durability of spores as well as the level of asexual reproduction through vegetative propagules capable of dispersal by wind (Van Zanten & Gradstein, 1988; Van der Velde & Bijlsma, 2000, 2003; Laenen *et al.*, 2015). Although vegetative propagules are commonly implicated in short-distance dispersal (Löbel *et al.*, 2009), they can also facilitate LDD (Pohjamo *et al.*, 2006). The low frequency of asexual reproduction in *Ceratolejeunea* (Dauphin, 2003) may thus contribute to the observed low gene flow. Moreover, the *in situ* selection of phenotypes with low dispersal and rapid growth on islands may further decrease gene flow (Patiño *et al.*, 2013).

Despite genetic differentiation on islands, the morphology within the *C. cornuta* complex has remained almost constant. While *C. belangeriana* can be distinguished from other members of the complex by its exerted perianth (Wigginton, 2004), *C. calabariensis* and *C. mascarena* are only morphologically characterized with difficulty by subtle differences in the dentition and shape of female involucre (Bonner, 1953). Although some liverworts are known for rapid accumulation of morphological disparity (Heinrichs *et al.*, 2003), the young age of the divergence events giving rise to these species may explain why they have accrued only few morphological characters. Nevertheless, the genetic and geographical consistency particularly of *C. belangeriana* and *C. mascarena* warrants their recognition as distinct taxa. A similar view has been taken with regard to genetically differentiated endemics with few unique morphological characters in the bryophyte *Homalothecium* (Huttunen *et al.*, 2008).

Our findings for the *C. cornuta* complex illustrate a major challenge in interpreting diversification patterns in bryophytes, namely the discrepancy between molecular and morphological data. For instance, even a prolonged period of divergence may not lead to morphological differences, as is

also illustrated by *C. laetefusca* and its putative synonym *C. caducifolia*, which are resolved in entirely different main clades despite no discernable morphological differences. In the same way, the paraphyly of *C. cornuta* and *C. cubensis* is likely owed to a taxonomy informed by misleading morphological similarities. Similar conflicts between molecular and morphological differentiation have been documented in numerous lineages of animals and plants (Foote, 1993; Mayr, 2011) and can be explained by developmental (Erwin, 2007; Wake *et al.*, 2011) and ecological (Donoghue & Ree, 2000) constraints on morphology. Thus, we assume that morphological uniformity is masking bryophyte radiations.

Hidden bryophyte radiations alone, however, are unlikely to have caused the striking differences in diversification patterns between angiosperms and bryophytes. While the *C. cornuta* complex diversified in Africa, other sampled taxa did not, reflecting a general trend of anagenesis in bryophytes (Patiño *et al.*, 2014). Common explanations for the failure of many bryophytes to radiate are strong gene flow and niche preemption (Vanderpoorten *et al.*, 2008). Although the dispersal ability of bryophytes has been implicated in intense gene flow and thus low speciation rates (Vanderpoorten *et al.*, 2011), the high levels of genetic differentiation in *Ceratolejeunea* indicate barriers to gene flow. Consequently, a good explanation for the lack of radiations on islands is niche preemption facilitated by multiple colonization events. This is illustrated by four of the islands we sampled (Guadeloupe, Jamaica, Réunion and Madagascar), which do not show monophyletic accessions of *Ceratolejeunea*. Instead, they often show accessions from entirely different major clades, as in the case of *C. papuliflora* and *C. calabariensis* on Réunion. In cases where islands appear to contain monophyletic clades, e.g., the Seychelles or Fiji, this is likely due to a lack of sampling. Other Lejeuneaceae genera occurring on these islands show similar non-monophyletic assemblages (Heinrichs *et al.*, 2015a). This pattern indicates that migration, in the form of multiple dispersal events, has played a major role in forming island diversity. On the islands, the cumulative effects of niche conservatism and niche preemption may prevent radiation. In conclusion, our findings highlight the importance of recurrent migration rather than *in situ* diversification in shaping bryophyte island diversity (Vanderpoorten *et al.*, 2008; Hutsemékers *et al.*, 2011; Laenen *et al.*, 2011). Moreover, if this reflects a general pattern as previously suggested (Vanderpoorten *et al.*, 2010, 2011; Patiño *et al.*, 2014), we expect the frequency of migration events combined with masked radiations to explain the observations of low rates of endemism in bryophytes compared to those in angiosperms.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional data and results.

BIOSKETCHES

Armin Scheben is a Master's student at the Faculty of Biology of the Ludwig Maximilian University of Munich and is interested in plant biogeography and macroevolution. This study is a result of his thesis conducted in the Heinrichs group.

The **Heinrichs group** at the Ludwig Maximilian University of Munich and collaborators are interested in the evolution of seed-free land plants, particularly liverworts.

Author contributions: J.H. conceived the study; A.S. and J.B. carried out the laboratory work; A.S. and J.H. analysed the data; A.S.-V., T.P. and G.E.L. contributed reagents/materials/morphological expertise; A.S. and J.H. led the writing and drafted the manuscript and all authors contributed to its preparation.

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