

DOES MACARONESIA EXIST? CONFLICTING SIGNAL IN THE BRYOPHYTE AND PTERIDOPHYTE FLORAS¹

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Macaronesia, which includes five mid-Atlantic archipelagos (Azores, Madeira, Selvagens, Canaries, and Cape Verdes), has been traditionally recognized as a distinct biogeographic unit whose circumscription has been intimately associated with the hypothesis that the flora is a relict of a formerly broadly distributed subtropical Tertiary flora. The concept of Macaronesia is revisited here using parsimony and Bayesian analyses of floristic data sets for the moss, liverwort, and pteridophyte floras. All analyses reject the monophyly of Macaronesia s.l., resolving the Cape Verdes with tropical Africa. Of the other Macaronesian archipelagos, the liverwort and pteridophyte analyses support, or could not reject, an Azorean-Madeiran-Canarian clade (hereafter Macaronesia s.s.), but the moss analysis resolves the Canary Islands as sister to North Africa, thus rejecting the concept of Macaronesia s.s. for this group. Dynamic interchange of taxa with neighboring continental areas rather than relictualism best explains the relationships of the Cape Verde cryptogamic flora and the Canary Island moss flora. In contrast, relictualism is consistent with a monophyletic Macaronesia s.s. for liverworts and pteridophytes. However, from the limited information available on relationships of endemic cryptogams, this explanation alone may be unsatisfactory. Spatially congruent patterns may, in fact, conceal a complex mixture of relictual distributions and more recent speciation and dispersal events.

Key words: biogeography; dispersal; Macaronesia; parsimony analysis of endemism; refugia; relictualism.

Oceanic islands have been intimately associated with the study of evolution since Darwin's theory of evolution by natural selection in Galapagos finches (Emerson and Kolm, 2005). Islands indeed represent discrete geographical entities isolated by oceanic barriers that reduce genetic interchanges with continental areas. Islands are furthermore often characterized by rapid and dramatic ecological changes resulting from a geological dynamic associated with historical and contemporary volcanic and erosional activity. Altogether, these factors have promoted fast rates of endemic speciation, making islands ideal natural laboratories for the study of evolution (Emerson, 2002; Emerson and Kolm, 2005). Typical examples of island model systems include the Galapagos, Hawaii, and Macaronesia, an array of mid-Atlantic volcanic islands including the Azores, Madeira, Selvagens, Canaries, and Cape Verdes situated in the North Atlantic Ocean between 15° and 40° N (e.g., Hansen and Sunding, 1993) (Fig. 1).

Several early authors alluded to the fact that the floras of the Macaronesian archipelagos differ from those of nearby continental areas (e.g., Webb and Berthelot, 1836–1850; see Lobin, 1982 for a review), but Engler (1879) was the first to use the term Macaronesia and was also the first to recognize a distinct biogeographic unit comprising the Azores, Madeira, and the Canaries. Later authors expanded the circumscription of the region to include also the Cape Verdes (e.g., Dansereau, 1961; Takhtajan, 1969; Bramwell, 1972, 1976) and, in some cases, continental enclave areas in North Africa and Iberia, where species with Macaronesian affinities occur (Sunding, 1979).

The delimitation of Macaronesia by Engler (1879) and

subsequent authors (e.g., Dansereau, 1961; Takhtajan, 1969; Bramwell, 1972, 1976; Sunding, 1979) placed particular emphasis on the endemic element of the vascular flora. This element constitutes approximately 20% of vascular plant species overall (Humphries, 1979) and accounts for almost two-thirds of the native Canarian (González Martín and González Artilles, 2001) and Azorean (Schäfer, 2003) floras, respectively. Endemic taxa considered characteristic of the region include several Lauraceae species (e.g., *Laurus azorica*, *Apollonias barbujana*, *Persea indica*, and *Ocotea foetens*), other taxa that are widespread within the region (e.g., *Dracaena draco* subsp. *draco*), and distinctive Macaronesian endemic groups that have undergone extensive intraregional radiation, such as the endemic genus *Argyranthemum* and Macaronesian *Echium* (e.g., Takhtajan, 1969). Engler (1879) proposed that this distinctive endemic element of the Macaronesian flora was, for the most part, a relict of a formerly widespread subtropical flora that covered southern Europe and North Africa during the Tertiary (hereafter the Engler refugium model). This hypothesis was later supported by Takhtajan (1969), Bramwell (1972, 1985), and Sunding (1979) among others; i.e., those authors who also promoted the concept of the Macaronesian region. Despite considerable variation in age (ranging from 0.04 Myr [Azores] to 24–27 Myr [Selvagens]), in altitude (from 154 m [Selvagens] to 3718 m [Canaries; Fernández-Palacios and Dias, 2001]), climate, ecology, and floristic composition across the archipelagos (see Fernández-Palacios and Dias, 2001), the Macaronesian concept has been generally widely accepted and the region is recognized as an important floristic area for conservation within the European-Mediterranean climate region (Médail and Quézel, 1997).

Several recent authors addressing the relationships of the Macaronesian archipelago floras have, however, implicitly challenged the concept of Macaronesia by classifying the floras of the different archipelagos in different biogeographic regions. For example, Rivas-Martinez et al. (2004) included the Azores

¹ Manuscript received 16 June 2006; revision accepted 26 February 2007.

This research was initiated at the Natural History Museum in the context of the EEC Synthesis exchange program. Many thanks are due to R. Schumacker and two anonymous referees for their constructive comments on a first draft of this paper. A.V. acknowledges financial support from the Belgian Funds for Scientific Research.

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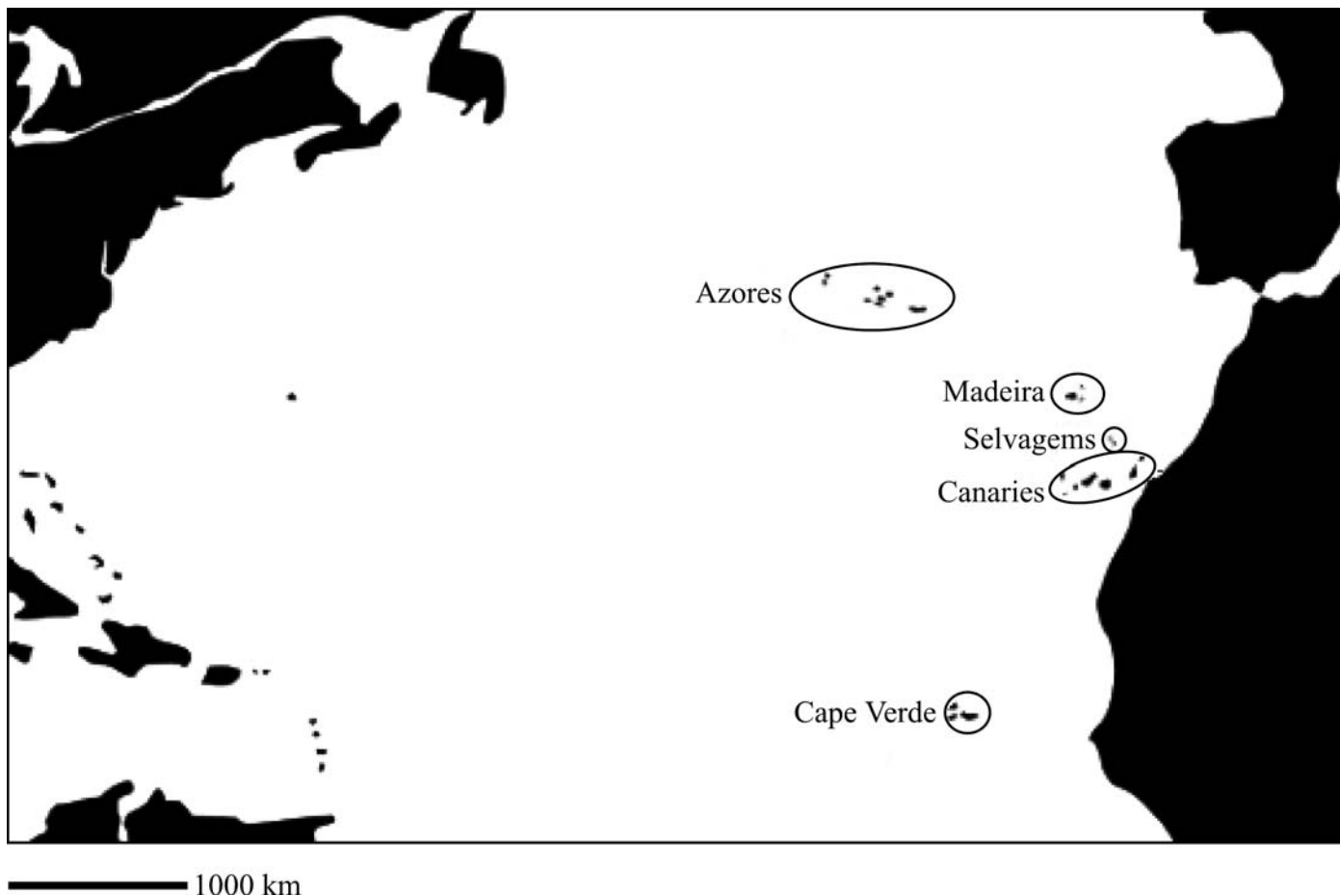


Fig. 1. Map of the north Atlantic showing the positions of the Macaronesian archipelagos.

within the Euro-Siberian region, and Madeira and the Canaries within the Mediterranean region (the Cape Verdes were not considered). Lobin (1982) placed the Azores within the submediterranean subregion, the Canaries and Madeira with western Morocco within a Canarian-Mediterranean subregion, and the Cape Verdes within the "Saharo-sindian" region. Lobin's classification utilized both the endemic and the native, non-endemic elements of the flora, an approach that is in marked contrast to the exclusive emphasis on the endemic element by Engler and other proponents of the Macaronesian concept. Indeed, it is more closely related to dispersalist island biogeographic models, emphasizing the interchange of species between continental and island areas that were first developed by Wallace (1881) for the Macaronesian archipelagos. Hereafter, we refer to this concept as the dynamic interchange model.

Paleogeographical and paleontological data do not provide irrefutable evidence for the Engler refugium model. Terrestrial plant fossils dated at 13 myr BP have been recorded from Gran Canaria, and fossils of several plant taxa that are currently restricted to or have distributions centered on Macaronesia have been discovered in continental Europe (Sunding, 1979; Frahm, 2004). These would certainly support a previously more widespread distribution for the taxa concerned, thus supporting the relict theory. In many instances, however, the identification of such fossil material is inconclusive (García-

Talavera et al., 1995). Recent dating studies have shown that some of the 20 large volcanic sea mounts located between the Canary Islands, Madeira, Selvagens, and the continent, several of which are presently less than 100 m below sea level, are at least 68 myr old (Geldmacher et al., 2001). It is conceivable that they may once have formed aerial islands, facilitating the migration of species from the continent to the islands during favorable periods and prior to continental extinction events (García-Talavera, 1997).

Recent molecular phylogenetic evidence further suggests that the patterns of relationship and evolution of the Macaronesian endemic vascular flora are much more complex than the Engler refugium model would predict (see Emerson, 2002; Carine et al., 2004; and Carine, 2005 for a review). In light of such changing views on the evolutionary history of the region's flora and because the circumscription of the region (a pattern) and the Engler refugium model (an explanatory hypothesis) have been so intimately linked, a critical re-evaluation of the concept of Macaronesia is necessary.

To date, and despite considerable debate concerning the relationships of the Macaronesian archipelago floras, consideration of the Macaronesian concept has lacked an explicit analytical framework. de Nicolás et al. (1989) presented a phenetic study of relationships of the vascular floras within the Macaronesian region and highlighted the similarities between the Canarian and Madeiran floras and the distinctiveness of

both the Azorean and Cape Verdean floras. However, no continental areas were included in the analysis, and it was consequently not possible to explicitly test the circumscription of the Macaronesian region. Furthermore, a large number of non-native taxa (estimated at between 41–49% of the Canarian flora; González Martín and González Artilles, 2001) were included in the analysis. This element of the flora introduces a substantial bias into the analysis, obscuring the signal from the native flora.

The debate concerning the Macaronesian concept has also focussed principally on the flowering plant flora. The cryptogamic, and particularly the bryophyte floras, have received much less attention, even though in terms of numbers and biomass they contribute a significant component to these insular ecosystems. The existence of a number of cryptogamic taxa of African (Manton et al., 1986) and American (Britton and Brunton, 1996; Schäfer, 2001) origin has long been acknowledged, but hypotheses to explain the origins of the Macaronesian cryptogamic flora have typically followed the Engler relictualism model, with the flora of the region considered a relict species pool from the European Tertiary flora (Gibby, 1979; Manton et al., 1986; Frahm, 2005). Examples of putative Macaronesian relicts include the fern *Woodwardia radicans*, which is presently disjunctly distributed in Macaronesia, the Iberian peninsula, Corsica, Italy, and Crete, but which is also known from Pliocene deposits in France (Gibby, 1979; Manton et al., 1986), and the moss genus *Echinodium*, currently known only from Macaronesia and Australasia but also known from Baltic and Saxon amber fossils (Eocene, 37–57 Myr BP) (Frahm, 2004). As with angiosperms, however, the generality of this explanatory model has been challenged both by recent re-interpretation of phytogeographic patterns (Schumacker, 2001) and by molecular phylogenetic evidence that, although still extremely limited (Rycroft et al., 2004; Vanderpoorten and Long, 2006), suggests that at least some elements of the Macaronesian cryptogamic flora are of much more recent origin than previously thought.

In this paper, we analyze relationships of the Macaronesian bryophyte (moss and liverwort) and pteridophyte floras in a worldwide context. Two methods were used to provide an explicit analytic framework for this study: parsimony analysis of species assemblages (PASA, Trejo-Torres and Ackerman, 2002), broadly comparable to the parsimony analysis of endemicity approach (PAE) of Morrone (1994), and a maximum likelihood (ML) model of species gains and losses (Lewis, 2001) implemented within a Bayesian context.

As opposed to more traditional clustering techniques such as UPGMA, which examine overall extant floristic relationships among areas without taking similarities due to common ancestry into account, cladistic methods attempt at grouping areas into “monocladic” groups, which can be attributed to a common hypothetical factor and which are characterized by shared species (Trejo-Torres and Ackerman, 2002). The power of PAE (and thus related approaches including PASA) to recover the history of colonization has, however, been questioned because important information on the history of biota contained in the cladistic relationships among taxa is not taken into account (Humphries, 2000; Brooks and van Veller, 2003; Santos, 2005). While it has been suggested that the parsimony criterion may implicitly favor certain mechanisms as a possible explanation for the resulting biogeographic patterns (Santos, 2005), cladistic approaches nonetheless

remain a potentially useful tool for identifying areas designated by species with congruent distributions (García-Barros et al., 2002) and have a series of attractive features for ecological studies of composition patterns. PASA is arguably a more unified tool when compared to the numerous clustering algorithms, which can return conflicting results, and also appears as a more conservative approach. While clustering techniques produce fully resolved dendrograms, cladistic analyses can indeed result in unresolved relationships when, for example, conflicting patterns are found in equally parsimonious trees (Trejo-Torres and Ackerman, 2001, 2002). In addition, the robustness of the conclusions drawn from a cladistic analysis can be easily assessed through statistics such as the bootstrap or the jackknife. Although it is possible to use these procedures in distance-based methods, they are rarely utilized for ecological studies and are actually not implemented in most ecological analysis softwares. Finally, and perhaps most importantly in the context of the present study, the significance of competing explanatory hypotheses can be statistically evaluated when model-based approaches are utilized. Specifically, these techniques are used here to determine which of the Engler relictualism model (consistent with a monophyletic Macaronesia) and dynamic interchange model (consistent with a polyphyletic Macaronesia with each archipelago most closely related to the near continent) provides a better representation of the observed floristic patterns for the three studied groups.

MATERIALS AND METHODS

Distribution data—Among bryophytes, only the mosses and liverworts were analyzed; the six species of hornwort recorded from the Macaronesian region were not included in the analyses. Indeed, the hornworts represent an independent group (Shaw and Renzaglia, 2004), which, for consistency, should be analyzed separately. However, the number of species did not warrant a separate analysis.

Distributions of mosses, liverworts, and pteridophytes were analyzed for each Macaronesian archipelago, i.e., the Azores (Az), Madeira (Mad), Canaries (Can), and Cape Verdes (CV), with the exception of the Selvagens. The cryptogamic flora of the Selvagens has not been well researched, although, with a total surface area of ca. 4 km², a strong marine influence, and little habitat diversity, the very low species diversity recorded is probably an accurate reflection of the flora. This depauperate assemblage is of predominantly widespread saline-tolerant taxa, which reveal little with regard to the biogeographic issues being tested.

Extra-Macaronesian distributions for all taxa were recorded following the floristic regions recognized by Hollis and Brummitt (1992), namely Europe (EUR), northern Africa (AF1), continental sub-Saharan Africa (AF2), Mascarene Islands (AF3), southern Africa (AF4), northern Asia (AS1), central Asia (AS2), southern Asia (AS3), southwestern Asia (AS4), western Asia (AS5), North America (AM1), Central America (AM2), Caribbean islands (AM3), northern South America (AM4), Brazil (AM5), southern South America (AM6), Australia (AU1), New Zealand (AU2), Antarctica (ANT), and Oceania (OC).

The sources for all the distribution data are listed in Appendix S1 (see Supplemental Data accompanying online version of this article). Twenty pteridophyte taxa, introduced, or thought to be introduced, into the archipelagos were excluded. The majority of these are cultivated ornamentals, many of which have become widely naturalized. For the Australasian or Asian taxa, it is easier to conclude an origin through garden sources as more plausible than wide disjunctions, but arguably some neotropical taxa, e.g., *Adiantum raddianum*, or more broadly distributed pantropical weedy taxa that were excluded, could be natural colonists. Judgement on these is, by necessity, subjective, but a restriction to disturbed areas close to habitation and the recent discovery dates were considered grounds for their exclusion. Some taxa previously considered to be introduced, e.g., *Selaginella kraussiana*, have now been shown from

palynological studies to have been present prior to human settlement (H. Schäfer, University of Munich, personal communication).

Nomenclature follows Grolle and Long (2000) for liverworts and Hill et al. (2006) for mosses except in *Leucobryum*, as Hill et al.'s treatment has important phylogeographic consequences that are at odds with recent molecular and morphological evidence (Vanderpoorten et al., 2003). For pteridophytes, nomenclature follows Tutin et al. (1993), Lobin et al. (1998), and Press and Short (1994), with the exception of the treatment of the *Asplenium ceterach* complex, more recently elucidated by Van den Heede et al. (2004), and *Polypodium*. The taxonomy of the latter is controversial and, as yet, unresolved. Some authors recognize the Azorean plants as a species distinct from the Madeiran/Canarian taxon (e.g., Schäfer, 2001), and regard both as distinct at specific level from the European *P. cambricum*, whereas others sink all of the island plants into *P. cambricum* but as a distinct subspecies (e.g., Neuroth, 1996). On the balance of available information, we have chosen to adopt an approach between these extremes.

Data analysis—Parsimony—Under MP, a cladistic analysis of the species × areas data matrix was conducted to find the most parsimonious classifications for each group. All analyses included an all-zero outgroup to allow topologies to be rooted (Morrone, 1994; Trejo-Torres and Ackerman, 2002). Parsimony analyses were performed using PAUP* beta version 4.0b5 (Swofford, 2002). Each data set was analyzed using a heuristic search comprising 1000 random replicate searches with ACCTRAN, MULPARS, and tree-bisection-reconnection (TBR) options. The equally parsimonious trees from each analysis were summarized into a strict consensus tree that was used to examine the relationship of each archipelago. Support for clades was assessed by computing decay values (BS; Bremer, 1988).

Maximum likelihood—The model of Lewis (2001), which employs equal forward and backward transition rates that can be interpreted in terms of immigration and extinction rates in the present context, was implemented within a Bayesian context to sample phylogenies and model parameters according to their posterior probabilities. Three Markov Chain Monte Carlo (MCMC) of 5 000 000 iterations each were run in MrBayes 3.0 (Huelsenbeck and Ronquist, 2003), and trees were sampled every 10 000 generations to ensure independence of successive trees. The number of generations needed to reach stationarity in the Markov Chain Monte Carlo algorithm was estimated by visual inspection of the plot of the ML score at each sampling point. The trees of the “burnin” for each run were excluded from the tree set, and the remaining trees from each run were combined to form the full sample of trees assumed to be representative of the posterior probability distribution. A 50% majority-rule consensus tree was constructed in PAUP* and rooted using an all-zero outgroup.

Constraint analyses were performed to test whether the data rejected a monophyletic concept of Macaronesia in a broad sense, i.e., including the Cape Verdes, Madeira, Canaries, and Azores (hereafter, Macaronesia s.l.), or in a narrower sense, i.e., with the Cape Verdes excluded (hereafter, Macaronesia s.s.). Significant departure of alternative topologies involving a monophyletic Macaronesian concept from the optimal topologies was tested by constraining the Macaronesian archipelagos to monophyly. Under MP, usual tests such as Kishino and Hasegawa (KH; 1989) were shown to be strongly biased when the trees compared are not derived independently of the data sets used for testing (Goldman et al., 2000). The results returned by an incorrectly applied KH test only hold if the associated *p* value is greater than twice the value required to indicate no rejection of the null hypothesis. If the *p* value is less than this, it is impossible to determine from the KH test what the result would be for any test making proper allowance for a posteriori selection of hypotheses (Goldman et al., 2000). Modified tests, such as that of Shimodaira and Hasagawa (1999), are presently only implemented under the ML criterion. Therefore, competing hypotheses regarding the monophyly of Macaronesia were only tested under ML within a Bayesian framework. For that purpose, the Bayesian analyses described were re-run under the constraint of a monophyletic Macaronesia (both sensu lato and sensu stricto). Differences in average ln *L* returned by the constrained and unconstrained analyses were compared using a *z* test.

Taxon optimizations—To identify taxa (or the shared absence of taxa) supporting groupings in each of the analyses, we used the MP criterion to reconstruct ancestral states (i.e., presence or absence of taxa) onto the strict consensus tree of the MP analysis. Both uppass and downpass optimizations (Cunningham et al., 1998) were determined for nodes of interest on the strict consensus tree using Mesquite 1.06 (Maddison and Maddison, 2005). When the

two optimizations returned conflicting states at a node, the state was termed as ambiguous. Only species with non-ambiguous reconstructions of ancestral distributions at the node of interest were considered.

Support for the reconstructions was assessed by calculating the relative probabilities of presence and absence of a species at each internal node using the ML optimization across the Bayesian sample of trees. The use of an ML model of species gains and losses for reconstructing ancestral distribution areas is complementary to the more traditional MP optimization because it provides an estimate of the confidence in the reconstructions at each node within a tree (Cunningham, 1999). We implemented the model of Lewis (2001), which assumes identical forward and backward transition rates, to find the rate value that maximizes the probability of the data given the model. The rate parameter was then fixed and the set of ancestral state probabilities derived for each internal node. These settings correspond to the “global” approach as described by Schluter et al. (1997), Pagel (1999), and Mooers (2004). If the difference in log-likelihood of the two states at a node was >2, the state with the lower likelihood was rejected. Otherwise, the reconstruction was considered as ambiguous at the node. This was performed for each tree including the node of interest to take phylogenetic uncertainty into account. The results of all trees were then combined to form the full range of probabilities of ancestral character states at a node across trees, as implemented by Mesquite. This technique provides an approximation, in a statistical sense, of the probability distribution of states at a node. Reconstruction can be considered well supported if they appear in >95% of the sampled trees. Hereafter, we use the term BaSP value (Bayesian sample proportion) to refer to the percentage of trees in the Bayesian sample, for which a reconstruction was significantly supported.

RESULTS

Pteridophytes—The pteridophyte data matrix (Appendix S1 and S2; see Supplemental Data accompanying online version of this article) comprises 102 taxa. One thousand four hundred eighty trees were sampled during the Bayesian procedure after convergence of the three independent Markov chains. Macaronesia in a broad sense is not monophyletic (Fig. 2). The Azores and Madeira are resolved as sisters within a clade with a 99% posterior probability. The Canaries are resolved as sister to the Azores + Madeira clade to form a Macaronesian s.s. clade that appears in 65% of the sampled trees. Macaronesia s.s. is sister to Europe, with which it forms a clade present in all sampled trees. This clade is included within a larger, nesting clade (posterior probability = 100%), which also includes northern Africa (AF1) and western Asia (AS5) and is hereafter termed the EurAsAf clade. The Cape Verdes belong to a distinct and distantly related sub-Saharan African clade with posterior probability of 98%, within which the archipelago is resolved as sister to continental tropical Africa (AF2; posterior probability = 71%). Constraining the Markov chains to only sample trees that fit with a monophyletic Macaronesian concept resulted in topologies that displayed significantly lower average ln *L* values (*P* < 0.001). Therefore, a broad Macaronesian concept that would include the Cape Verdes, Canaries, Azores, and Madeira, can be rejected.

The parsimony analysis, which included 82 informative characters, resulted in 38 most parsimonious trees of length 228 steps (CI = 0.443; RI = 0.673). The topology of the strict consensus tree is similar to that derived from the Bayesian analysis, albeit somewhat less resolved. The Azores and Madeira are resolved as sister taxa (BS = 3), within a trichotomy that also includes the Canary Islands and Europe (BS > 5). North Africa is resolved as sister to this clade (BS > 5). The Cape Verde Islands are resolved in a trichotomy with sub-Saharan Africa (BS = 2).

Taxa unambiguously optimized onto nodes of interest in the parsimony strict consensus tree under the MP criterion,

together with support for the reconstructions under the ML criterion across the Bayesian tree sample, are listed in Table 1.

The inclusion of the Cape Verdes within a sub-Saharan clade is supported by 21 synapomorphic species occurrences, nine of which have BaSP values significant at the 95% level under the ML criterion and four of which are restricted to sub-Saharan Africa. The shared absence of *Botrychium lunaria* (BaSP = 99%) is also characteristic for the sub-Saharan African clade.

Within the sub-Saharan Africa clade, the Cape Verdes lack any endemic pteridophyte species but are characterized by homoplastic species occurrences that correspond to disjunct distribution patterns. *Asplenium aethiopicum* subsp. *braithwaitii* and *Dryopteris oligodonta* have a homoplastic distribution that spans the Azores-Madeira clade and/or the Canaries and the Cape Verdes and are the only two elements that can be regarded as endemic to Macaronesia s.l. Four taxa found in the Cape Verdes (*Pteridium aquilinum* subsp. *aquilinum*, *Asplenium hemionitis*, *Diplazium caudatum*, and *Davallia canariensis*) are also distributed in the EurAsf clade but are not found elsewhere within sub-Saharan Africa.

Under the MP criterion, the inclusion of Macaronesia s.s. within EurAsAf and its two nested clades [the first excluding western Asia (AS5) and the second excluding northern Africa (AF1)] is characterized by the shared occurrences of 16 species endemic to the clade. The shared presence of another 15 non-endemic species further characterizes EurAsAf and its nested clades. Seventeen of the 31 taxa supporting this clade under the MP criterion are also supported by BaSP values of >95% under ML.

Macaronesia s.s., which is resolved in the Bayesian analyses and in 50% of the MP trees, is supported by the endemic *Asplenium anceps* and three further non-endemic species. The latter represent homoplastic occurrences of sub-Saharan African (*Selaginella kraussiana* and *Adiantum reniforme*) and pantropical (*Asplenium monanthes*) species. Two synapomorphic absences further characterize the Macaronesia s.s. clade. None of the taxa supporting this clade have BaSP values of >95% under the ML criterion.

Within Macaronesia s.s., the Canaries, which are sister to the clade formed by the Azores and Madeira, are characterized by the autapomorphic occurrence of four endemic species (Table 4) and the homoplastic presence of *Grammitis querennda*, a sub-Saharan African species that is nowhere else present within EurAsAf. The sistership of the Azores and Madeira is significantly supported under ML by the synapomorphic presence of four endemic and four other synapomorphic presences of non-endemic species. All have BaSp values of <95%. The clade comprising Madeira and the Azores is also characterized by the synapomorphic absence of eight species under MP, all of which have BaSp values of <95% under ML.

The Azores and Madeira each have a suite of specific autapomorphic endemic species that are listed in Table 4. The Azores are furthermore characterized by the homoplastic occurrence of four taxa, namely *Ceradenia jungermannioides*, *Grammitis marginella*, *Pityrogramma calomelanos* var. *calomelanos*, and *P. ebenea*, which have an otherwise American distribution.

Mosses—The moss data matrix (Appendix S1 and S3; see Supplemental Data accompanying online version of this article) comprises 479 taxa. In keeping with the pteridophyte analysis, the Macaronesian archipelagos do not form a monophyletic group in the 50% majority-rule consensus tree of the 1279 trees

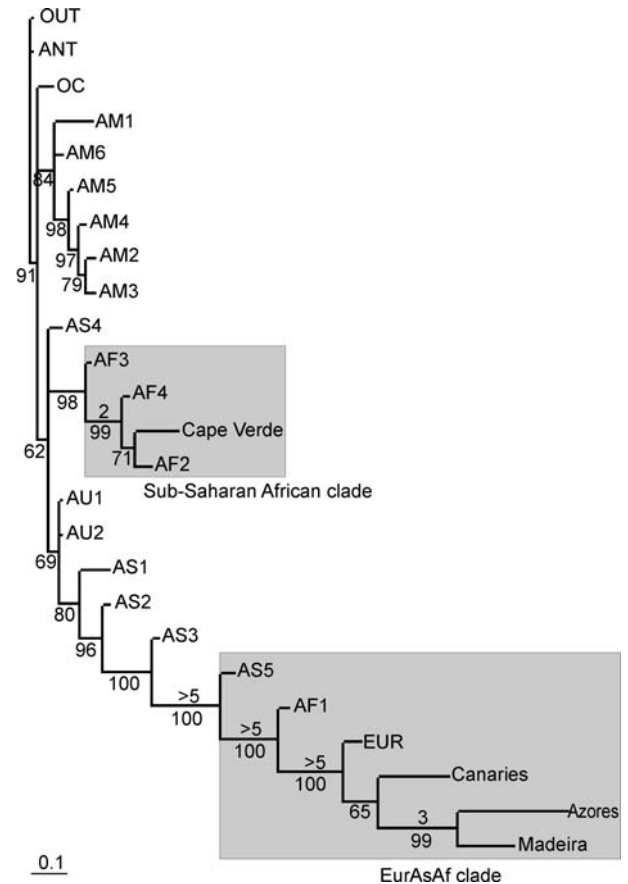


Fig. 2. Phylogeographic affinities of the Macaronesian pteridophyte flora inferred from a 50% majority-rule consensus of 1480 trees sampled after convergence of three independent Markov chains implementing a model of equal transition rates. Branch lengths were averaged over the 1480 trees. Numbers below the branches correspond to their posterior probabilities. Shaded clades correspond to the EurAsAf clade and the sub-Saharan African clade discussed in the text. Numbers above the branches of those clades are the Bremer supports. Area codes are as follows: Az, Azores; Mad, Madeira; Can, Canaries; CV, Cape Verdes. Area codes outside Macaronesia follow Hollis and Brummitt (1992): Eur, Europe; AF1, northern Africa; AF2, continental sub-Saharan Africa; AF3, Mascarene Islands; AF4, southern Africa; AS1, northern Asia; AS2, central Asia; AS3, southern Asia; AS4, southwestern Asia; AS5, western Asia; AM1, North America; AM2, Central America; AM3, Caribbean islands; AM4, northern South America; AM5, Brazil; AM6, southern South America; ANT, Antarctica; OC, Oceania; AU1, Australia; AU2, New Zealand.

sampled during the Bayesian procedure (Fig. 3). The Cape Verdes are included within a sub-Saharan African clade (posterior probability = 84%) and within this clade are resolved as sister to the Mascarene Islands (AF3) (posterior probability = 72%). The remaining Macaronesian archipelagos of the Canaries, Azores, and Madeira are included within the EurAsAf clade (posterior probability = 100%). Within the latter, the Azores and Madeira are resolved as sister areas (posterior probability = 99%), and this clade is resolved as sister area to Europe (posterior probability = 83%). The Canaries are resolved in a different subclade clade within EurAsAf that also includes northern Africa and western Asia (posterior probability = 91%). Within this subclade, the

TABLE 1. Synapomorphic pteridophyte species gains and losses of Macaronesian archipelagos and nesting clades. All reconstructions are based on a maximum parsimony (MP) optimization onto the strict consensus of the MP analysis. Asterisks indicate that the reconstruction was significant under maximum likelihood (ML) in >95% of the trees from the Bayesian sample. Endemic synapomorphic transitions are in boldface.

Clade	Synapomorphies
Cape Verdes+sub-Saharan Africa	Gains: <i>Actinopteris radiata</i> *, <i>Adiantum capillus-veneris</i> , <i>A. incisum</i> *, <i>A. philippense</i> *, <i>A. reniforme</i> , <i>Asplenium adiantum-nigrum</i> , <i>A. monanthes</i> , <i>A. trichomanes</i> subsp. <i>quadrivalens</i> , <i>Cosentinia vellaea</i> subsp. <i>vellaea</i> , <i>Cystopteris diaphana</i> , <i>Dryopteris pentheri</i> *, <i>Equisetum ramosissimum</i> , <i>Hypodematium crenatum</i> *, <i>Marsilea coromandeliana</i> *, <i>Nephrolepis undulata</i> *, <i>Ophioglossum lancifolium</i> *, <i>O. polyphyllum</i> , <i>O. reticulatum</i> , <i>Pellaea viridis</i> *, <i>Selaginella kraussiana</i> , <i>Stegnogramma pozoi</i> . Losses: <i>Botrychium lunaria</i> *.
EurAsAf, (Madeira-Azores-Canaries-EUR-AF1), and (Madeira-Azores-Canaries-EUR)	Gains: <i>Asplenium adiantum-nigrum</i> , <i>A. hemionitis</i> *, <i>A. obovatum</i> subsp. <i>lanceolatum</i> *, <i>A. onopteris</i> *, <i>A. scolopendrium</i> *, <i>Blechnum spicant</i> *, <i>Cheilanthes guanchica</i> *, <i>C. tinaei</i> , <i>Christella dentata</i> , <i>Culcita macrocarpa</i> *, <i>Davallia canariensis</i> , <i>Diplazium caudatum</i> , <i>Dryopteris affinis</i> subsp. <i>affinis</i> *, <i>D. guanchica</i> , <i>Equisetum ramosissimum</i> , <i>E. telmateia</i> *, <i>Hymenophyllum tunbrigense</i> , <i>H. wilsonii</i> *, <i>Lycopodiella inundata</i> , <i>Marsilea quadrifolia</i> , <i>Ophioglossum azoricum</i> *, <i>Oreopteris limbosperma</i> , <i>Pellaea viridis</i> *, <i>Psilotum nudum</i> , <i>Pteridium aquilinum</i> subsp. <i>aquilinum</i> *, <i>Pteris incompleta</i> *, <i>Selaginella denticulata</i> *, <i>S. selaginoides</i> , <i>Stegnogramma pozoi</i> , <i>Trichomanes speciosum</i> *, <i>Woodwardia radicans</i> *. Losses: <i>Actinopteris radiata</i> , <i>Adiantum incisum</i> *, <i>Hypodematium crenatum</i> , <i>Marsilea coromandeliana</i> . Gains: <i>Selaginella kraussiana</i> , <i>Adiantum reniforme</i> , <i>Asplenium anceps</i> , <i>A. monanthes</i> . Losses: <i>Lycopodiella inundata</i> , <i>Psilotum nudum</i> .
Madeira+Azores+Canaries ^a	Gains: <i>Asplenium reniforme</i> , <i>A. lolegnamense</i> , <i>Diphasiastrum madeirense</i> , <i>Elaphoglossum semicylindricum</i> , <i>Huperzia dentata</i> , <i>H. suberecta</i> , <i>Notholaena marantae</i> , <i>Pityrogramma calomelanos</i> var. <i>aureoflava</i> . Losses: <i>Asplenium ceterach</i> subsp. <i>ceterach</i> , <i>Cystopteris dickieana</i> , <i>Dryopteris guanchica</i> , <i>Marsilea quadrifolia</i> , <i>Ophioglossum polyphyllum</i> , <i>Polystichum aculeatum</i> , <i>Salvinia natans</i> , <i>Selaginella selaginoides</i> .
Madeira+Azores	Gains: <i>Asplenium reniforme</i> , <i>A. lolegnamense</i> , <i>Diphasiastrum madeirense</i> , <i>Elaphoglossum semicylindricum</i> , <i>Huperzia dentata</i> , <i>H. suberecta</i> , <i>Notholaena marantae</i> , <i>Pityrogramma calomelanos</i> var. <i>aureoflava</i> . Losses: <i>Asplenium ceterach</i> subsp. <i>ceterach</i> , <i>Cystopteris dickieana</i> , <i>Dryopteris guanchica</i> , <i>Marsilea quadrifolia</i> , <i>Ophioglossum polyphyllum</i> , <i>Polystichum aculeatum</i> , <i>Salvinia natans</i> , <i>Selaginella selaginoides</i> .

^a Clade collapsed on the strict consensus in the MP analyses and reconstructions only based on the Bayesian sample of trees under the ML criterion.

Canaries are resolved as sister to northern Africa (posterior probability = 81%).

Constraining the Markov chains to only sample trees that include a monophyletic group comprising either all four Macaronesian archipelagos or Macaronesia s.s. (i.e., Canaries, Azores, and Madeira) resulted in topologies that displayed significantly lower $\ln L$ values ($P < 0.001$ in both cases). Therefore, both a broad and narrow Macaronesian concept can be rejected.

Analysis of the 446 informative characters under the MP criterion resulted in eight equally parsimonious trees of length 1616 steps (CI = 0.297; RI = 0.596). The strict consensus showed broadly the same relations as the Bayesian analysis, except that the Cape Verdes are resolved as sister to continental sub-Saharan Africa (AF2) with a BS of 5. The grouping of the Azores and Madeira (BS > 5) and the Canaries-North Africa (BS = 4) were well supported.

Taxa unambiguously optimized onto nodes of interest are listed in Table 2. Under the MP criterion, the inclusion of the Cape Verde Islands within a sub-Saharan African clade is supported by 37 synapomorphic presences, nine of which are endemic. Of these, 11 receive BaSP values under ML >95%. This clade is also supported by the shared absence of 14 taxa, of which one has a BaSP value >95% under ML. Within sub-Saharan Africa, the Cape Verdes are characterized by the autapomorphic presence of the endemic genus *Perssonia* and five other endemic species (Table 5), as well as the homoplastic presence of 23 species that do not occur elsewhere in sub-Saharan Africa. Seven of those homoplastic occurrences, namely *Neckera intermedia*, *Plasteurhynchium meridionale*, *Philonotis rigida*, *Ptychomitrium nigrescens*, *Rhynchostegium megapolitanum*, *Tortula solmsii*, and *Trichostomum contortum*, are shared with the EurAsAf clade. *Cryptolepton longisetus* is the only species that could be considered a Macaronesian

element in the Cape Verde flora as this species has a homoplastic distribution spanning the Cape Verdes, Madeira, and the Canaries.

No less than 93 synapomorphic presences, 22 of which are endemic to the EurAsAf clade, characterize the inclusion of Macaronesia s.s. within the EurAsAf clade. Forty-five of the transitions from absent to present are also supported under ML by BaSP values >95%. The shared absences of three species also support this clade although the “absent” state at the EurAsAf internal node is supported in each case by BaSP values <95%.

Within the EurAsAf clade, a subclade comprising western Asia, North Africa, and the Canaries, is characterized by the synapomorphic occurrence of the mostly pantropical *Gymnostomiella vernicosa*, albeit with a BaSP value <95%, and the absence of 30 species, for which state “absent” is supported under ML by BaSp values <95%. The strong similarities of the North African and Canarian floras are further emphasized by the synapomorphic presence of *Fissidens sublimbatus* and by the shared absence of 22 additional species (BaSP < 95% in all cases). Within the Canarian-North African-western Asian clade, the Canaries are characterized by the autapomorphic presence of nine endemic species (Table 5) and the homoplastic occurrence of 17 species that have not been reported elsewhere within this clade. Among those species, noteworthy range disjunctions include *Tortula bogosica*, a sub-Saharan element; *Acaulon fontiquerianum*, *Fissidens polyphyllus*, *Gonomitrium seroi*, and *Isothecium algarvicum*, that are otherwise distributed in Europe; and *Amphidium tortuosum*, *Echinodium spinosum*, *Funaria fritzei*, *Pelekium atlanticum*, and *Rhynchostegiella macilenta*, that are shared with Madeira.

Madeira and the Azores form a clade with Europe that is, in turn, sister to the clade formed by western Asia, North Africa, and the Canaries. The grouping of Madeira, the Azores, and

TABLE 2. Synapomorphic moss species gains and losses of Macaronesian archipelagos and nesting clades. All reconstructions are based on a maximum parsimony (MP) optimization onto the strict consensus of the MP analysis. Asterisks indicate that the reconstruction was significant under maximum likelihood (ML) in >95% of the trees from the Bayesian sample. Endemic synapomorphic transitions are in boldface.

Clade	Synapomorphies
EurAsAf	<p>Losses: <i>Barbula indica</i>, <i>Philonotis uncinata</i>, <i>Syntrichia amphidiacea</i>.</p> <p>Gains: <i>Acaulon triquetrum</i>, <i>Aloina brevirostris</i>, <i>Anacolia webbii</i>, <i>Braunia alopecura</i>, <i>Bryum donianum</i>*, <i>B. funckii</i>, <i>B. mildeanum</i>*, <i>B. rubens</i>, <i>B. sauteri</i>, <i>Campylopus brevipilus</i>, <i>Campylostelium pitardii</i>, <i>C. strictum</i>, <i>Cheilothela chloropus</i>*, <i>Cinclidotus fontinaloides</i>*, <i>Cirriphyllum crassinervium</i>*, <i>Crossidium geheebii</i>*, <i>Cryphaea heteromalla</i>, <i>Cyclodictyon laetevirens</i>, <i>Cynodontium bruntonii</i>, <i>Dialytrichia mucronata</i>*, <i>Dicranella howei</i>*, <i>Encalypta streptocarpa</i>, <i>Entosthodon durieui</i>, <i>E. fascicularis</i>, <i>E. obtusus</i>, <i>E. schimperi</i>, <i>Eurhynchium striatum</i>*, <i>Fissidens crassipes</i>, <i>F. curvatus</i>*, <i>F. ovatifolius</i>, <i>F. rivularis</i>*, <i>F. serrulatus</i>*, <i>Funariella curviseta</i>*, <i>Gigaspermum mouretii</i>, <i>Grimmia crinita</i>, <i>G. decipiens</i>*, <i>G. nutans</i>, <i>G. tergestina</i>, <i>Gymnostomum viridulum</i>*, <i>Habrodon perpusillus</i>*, <i>Homalia lusitanica</i>*, <i>H. webbiana</i>*, <i>Homalothecium aureum</i>*, <i>Hycomium armoricum</i>*, <i>Hypnum cupressiforme</i> var. <i>resupinatum</i>, <i>H. jutlandicum</i>*, <i>Leptobarbula berica</i>*, <i>Leptodon smithii</i>, <i>Leucobryum glaucum</i>, <i>Mnium hornum</i>, <i>Neckera complanata</i>, <i>Neckera crispa</i>*, <i>N. pumila</i>, <i>Orthotrichum patens</i>, <i>Oxyrrhynchium pumilum</i>*, <i>O. schleicheri</i>*, <i>O. speciosum</i>*, <i>Palustriella commutata</i>, <i>Philonotis rigida</i>*, <i>Plagiomnium affine</i>*, <i>P. undulatum</i>*, <i>Plasteurhynchium meridionale</i>*, <i>P. striatulum</i>, <i>Pogonatum aloides</i>*, <i>P. nanum</i>*, <i>Pottia viridifolia</i>, <i>Rhabdoweisia fugax</i>, <i>Rhynchostegiella curviseta</i>*, <i>R. durieui</i>, <i>R. teneriffae</i>*, <i>R. tenella</i>*, <i>Rhynchostegium confertum</i>*, <i>R. megapolitanum</i>*, <i>Scorpiurium circinatum</i>*, <i>S. deflexifolium</i>, <i>Sematophyllum substrumulosum</i>, <i>Sphagnum subnitens</i>, <i>Thamnobryum alopecurum</i>*, <i>T. maderense</i>, <i>Timmiella barbuloidea</i>*, <i>Tortella inflexa</i>, <i>T. nitida</i>*, <i>Tortula canescens</i>*, <i>T. cuneifolia</i>*, <i>T. marginata</i>*, <i>T. pallida</i>, <i>T. revolvens</i>, <i>T. solmsii</i>*, <i>T. vahliana</i>, <i>Trichostomum triumphans</i>, <i>Weissia condensa</i>, <i>W. longifolia</i>, <i>Zygodon forsteri</i>.</p>
Madeira+Azores+EUR	<p>Gains: <i>Andreaea heinemannii</i>, <i>Campylopus shawii</i>, <i>Fissidens polyphyllus</i>, <i>Glyphomitium daviesii</i>, <i>Grimmia arenaria</i>, <i>Hypnum uncinulatum</i>, <i>Isothecium algarvicum</i>, <i>Myurium hochstetteri</i>, <i>Neckera intermedia</i>, <i>Pseudotaxiphyllum laetevirens</i>*, <i>Ptychomitrium nigrescens</i>, <i>P. polyphyllum</i>, <i>Rhampidium purpuratum</i>, <i>Tetrastichium fontanum</i>, <i>T. virescens</i>, <i>Ulota calvescens</i>.</p>
Madeira+Azores	<p>Losses: <i>Acaulon muticum</i>, <i>Aloina brevirostris</i>, <i>Amphidium lapponicum</i>, <i>Anomodon viticulosus</i>, <i>Aulacomium androgynum</i>, <i>Bryum cellulare</i>, <i>B. funckii</i>, <i>B. gemmiferum</i>, <i>B. gemmilucens</i>, <i>B. pallens</i>, <i>B. pallescens</i>, <i>Campylostelium pitardii</i>, <i>Crossidium aberrans</i>, <i>C. squamiferum</i>, <i>Didymodon australasiae</i>, <i>Ditrichum pusillum</i>, <i>Encalypta streptocarpa</i>, <i>Entosthodon durieui</i>, <i>E. fascicularis</i>, <i>E. schimperi</i>, <i>Fissidens exilis</i>, <i>Gigaspermum mouretii</i>, <i>Grimmia anodon</i>, <i>G. crinita</i>, <i>G. nutans</i>, <i>G. tergestina</i>, <i>Hyophila involuta</i>, <i>Lescurea mutabilis</i>, <i>Neckera menziesii</i>, <i>N. pennata</i>, <i>Orthotrichum acuminatum</i>, <i>O. patens</i>, <i>O. pumilum</i>, <i>O. striatum</i>, <i>Philonotis caespitosa</i>, <i>Plasteurhynchium striatulum</i>, <i>Pleuridium subulatum</i>, <i>Pohlia andalusica</i>, <i>P. cruda</i>, <i>P. wahlenbergii</i>, <i>Pottia viridifolia</i>, <i>Protobryum bryoides</i>, <i>Pterygoneuron subsessile</i>, <i>Pylaisia polyantha</i>, <i>Pyramidula tetragona</i>, <i>Racomitrium ellipticum</i>, <i>Santonina uncinata</i>, <i>Schistidium flaccidum</i>, <i>Scleropodium cespitans</i>, <i>Sphagnum affine</i>, <i>S. palustre</i>, <i>S. papillosum</i>, <i>S. pylaesii</i>, <i>Syntrichia fragilis</i>, <i>S. montana</i>, <i>S. papillosa</i>, <i>S. virescens</i>, <i>Thuidium delictatum</i>, <i>Timiella anomala</i>, <i>T. flexiseta</i>, <i>Tortella fragilis</i>, <i>T. inflexa</i>, <i>Tortula bolanderi</i>, <i>T. pallida</i>, <i>Trichodon cylindricus</i>, <i>Trichostomum tenuirostris</i>, <i>Weissia condensa</i>, <i>W. longifolia</i>.</p> <p>Gains: <i>Alophosia azorica</i>, <i>Andoa berthelotiana</i>, <i>Brachymenium notarisii</i>, <i>Campylopus incrassatus</i>, <i>Daltonia stenophylla</i>, <i>Echinodium prolixum</i>, <i>Fissidens coacervatus</i>, <i>F. luisieri</i>, <i>F. sublinaefolius</i>, <i>Leucodon canariensis</i>, <i>Neckera cephalonica</i>, <i>Philonotis hastata</i>.</p>
Canaries+AS5+ AF1	<p>Gains: <i>Gymnostomiella vernicosa</i>.</p> <p>Losses: <i>Andreaea alpestris</i>, <i>A. rothii</i>, <i>Bryoerythrophyllum inaequifolium</i>, <i>Bryum gemmiferum</i>, <i>B. tenuisetum</i>, <i>Campylopus brevipilus</i>, <i>Cyclodictyon laetevirens</i>, <i>Dicranella schreberiana</i>, <i>Dicranum scottianum</i>, <i>Fissidens asplenioides</i>, <i>F. bryoides</i> var. <i>caespitans</i>, <i>Grimmia ramondii</i>, <i>G. torquata</i>, <i>Hyophila involuta</i>, <i>Isopterygium tenerum</i>, <i>Kiaeria blyttii</i>, <i>Leucobryum albidum</i>, <i>Orthodontium pellucens</i>, <i>Pohlia prolifera</i>, <i>Racomitrium fasciculare</i>, <i>Rhabdoweisia fugax</i>, <i>Rhytidadelphus loreus</i>, <i>Sphagnum affine</i>, <i>S. magellanicum</i>, <i>S. papillosum</i>, <i>S. pylaesii</i>, <i>S. rubellum</i>, <i>Splachnobryum obtusum</i>, <i>Timmiella flexiseta</i>, <i>Zygodon forsteri</i>.</p>
Canaries+AF1	<p>Gains: <i>Fissidens sublimbatus</i>.</p> <p>Losses: <i>Andreaea rupestris</i>, <i>Atrichum tenellum</i>, <i>Blindia acuta</i>, <i>Brachythecium mildeanum</i>, <i>Bryoerythrophyllum ferruginascens</i>, <i>Bryum subapiculatum</i>, <i>Campylopus subulatus</i>, <i>Dicranella rufescens</i>, <i>Dicranum majus</i>, <i>Diphyscium foliosum</i>, <i>Hygrohypnum luridum</i>, <i>Hypnum cupressiforme</i> var. <i>resupinatum</i>, <i>Paraleucobryum longifolium</i>, <i>Orthodontium gracile</i>, <i>Pohlia bulbifera</i>, <i>P. longicolla</i>, <i>Racomitrium elongatum</i>, <i>Rhytidadelphus squarrosus</i>, <i>R. subpinnatus</i>, <i>Sphagnum girgensohnii</i>, <i>S. squarrosum</i>, <i>Thuidium delictatum</i>.</p>
Cape Verdes+sub-Saharan Africa (AF3 and/or AF2 and/or AF4)	<p>Losses: <i>Amblystegium serpens</i>, <i>Fissidens bryoides</i>*, <i>F. taxifolius</i>, <i>Hymenostylium recurvirostrum</i>, <i>Orthotrichum rupestre</i>, <i>Pohlia cruda</i>, <i>P. nutans</i>, <i>P. wahlenbergii</i>, <i>Sanionia uncinata</i>, <i>Sphagnum magellanicum</i>, <i>Syntrichia laevipila</i>, <i>S. papillosa</i>, <i>Tortella fragilis</i>, <i>Tortula atrovirens</i>.</p> <p>Gains: <i>Barbula bolleana</i>*, <i>Brachymenium acuminatum</i>, <i>B. exile</i>*, <i>B. notarisii</i>, <i>B. philonotula</i>, <i>Bryoerythrophyllum campylocarpum</i>*, <i>Bryum apiculatum</i>, <i>B. cellulare</i>, <i>Campylopus flaccidus</i>, <i>Crossidium squamiferum</i>, <i>Cyclodictyon laetevirens</i>, <i>Didymodon maschalogenae</i>, <i>D. rigidulus</i>, <i>Ditrichum pallidum</i>, <i>Fabronia leikipiae</i>, <i>Fissidens androgynus</i>*, <i>F. bogosicus</i>*, <i>F. sciophyllum</i>*, <i>F. usambaricus</i>, <i>Groutiella laxotorquata</i>, <i>Gymnostomiella vernicosa</i>, <i>Herpentineuron toccoeae</i>*, <i>Leptodon smithii</i>, <i>Leptophascum leptophyllum</i>, <i>Grimmia laevigata</i>, <i>Hedwigia ciliata</i> s.l., <i>Palamocladium leskeoides</i>*, <i>Pleuridium acuminatum</i>, <i>Pseudephemerum nitidum</i>, <i>Pseudoleskea pseudoattenuata</i>*, <i>Pterogonium gracile</i>*, <i>Ptychomitrium subcrispatum</i>*, <i>Splachnobryum obtusum</i>, <i>Syntrichia amphidiacea</i>, <i>Tortula bogosica</i>, <i>Trichostomum crispulum</i>, <i>T. tenuirostris</i>.</p>

Europe is characterized by 16 synapomorphic species presences (15 BaSP < 95%), four of which are endemic. Within this clade, the Madeira + Azores grouping is supported by 12 synapomorphic species, four of which are strictly endemic. The non-endemic transitions, supported under ML by BaSP values

all <95%, represent disjunct distributions patterns: *Andoa berthelotiana*, *Fissidens coacervatus*, *Leucodon canariensis*, and *Neckera cephalonica* are shared with the Canaries; *Daltonia stenophylla* with tropical America; *Brachymenium notarisii* and *Campylopus incrassatus* with sub-Saharan Africa;

TABLE 3. Synapomorphic liverwort species gains and losses of Macaronesian archipelagos and nesting clades. All reconstructions are based on maximum parsimony (MP) optimization onto the 50% majority-rule consensus of the Bayesian sample of trees. Asterisks indicate that the reconstruction was significant under maximum likelihood (ML) in >95% of the trees from the Bayesian sample. Endemic synapomorphic transitions are in boldface.

Clade	Synapomorphies
EurAsAf and Europe+AF1+Madeira+Canaries+Azores	Gains: <i>Asterella africana</i> , <i>Athalamya spathysii</i> , <i>Cephaloziella baumgartneri</i> *, <i>C. calyculata</i> , <i>Exormotheca pustulosa</i> *, <i>Fossombronina angulosa</i> *, <i>F. caespitififormis</i> , <i>F. echinata</i> , <i>F. husnotii</i> *, <i>Frullania tamarisci</i> *, <i>F. teneriffae</i> , <i>Gongylanthus ericetorum</i> , <i>Jubula hutchinsiae</i> , <i>Lejeunea eckloniana</i> *, <i>Lophocolea fragrans</i> *, <i>Lophozia turbinata</i> , <i>Mannia androgyna</i> , <i>Porella arboris-vitae</i> , <i>P. canariensis</i> , <i>Riccia bicarinata</i> , <i>R. ciliata</i> , <i>R. ciliifera</i> *, <i>R. huebeneriana</i> , <i>R. ligula</i> , <i>R. papillosa</i> , <i>R. subbijurca</i> , <i>R. trabutiana</i> , <i>R. warnstorffii</i> , <i>Riella cossoniana</i> , <i>Scapania gracilis</i> , <i>Southbya nigrella</i> , <i>S. tophacea</i> *. Losses: <i>Cephalozia catenulata</i> , <i>Cladopodiella francisci</i> , <i>Herbertus sendtneri</i> , <i>Hygrobriella laxifolia</i> , <i>Marsupella sprucei</i> , <i>Metzgeria leptoneura</i> , <i>M. temperata</i> , <i>Plagiochila exigua</i> .
Europe+Madeira+Canaries+Azores	Gains: <i>Acrobolbus wilsonii</i> *, <i>Adelanthus decipiens</i> *, <i>Aphanolejeunea microscopica</i> *, <i>Cephalozia catenulata</i> , <i>C. crassifolia</i> *, <i>Cephaloziella dentata</i> *, <i>Cladopodiella francisci</i> *, <i>Cololejeunea minutissima</i> *, <i>Colura calyptrifolia</i> , <i>Drepanolejeunea hamatifolia</i> *, <i>Frullania azorica</i> *, <i>F. microphylla</i> *, <i>Harpalejeunea molleri</i> *, <i>Herbertus sendtneri</i> , <i>Hygrobriella laxifolia</i> *, <i>Kurzia pauciflora</i> *, <i>Lejeunea flava</i> *, <i>L. hibernica</i> *, <i>L. lamacerina</i> *, <i>L. mandonii</i> , <i>Lepidozia cupressina</i> *, <i>L. pearsonii</i> , <i>Leptoscyphus cuneifolius</i> *, <i>Marchesinia mackai</i> , <i>Marsupella adusta</i> *, <i>M. profunda</i> *, <i>M. sparsifolia</i> , <i>M. sprucei</i> , <i>Metzgeria fruticulosa</i> , <i>M. leptoneura</i> *, <i>M. temperata</i> , <i>Plagiochila bifaria</i> *, <i>P. exigua</i> , <i>P. punctata</i> *, <i>P. spinulosa</i> , <i>Radula aquilegia</i> *, <i>R. carringtonii</i> *, <i>R. holtii</i> *, <i>Riccia beyrichiana</i> , <i>Saccogyna viticulosa</i> *, <i>Telaranea europaea</i> *. Losses: <i>Athalamya spathysii</i> *, <i>Frullania ericoides</i> *.
Madeira+Canaries+Azores	Gains: <i>Acanthocoleus aberrans</i> , <i>Aphanolejeunea azorica</i> , <i>A. sintenesii</i> , <i>Heteroscyphus denticulatus</i> , <i>Jungermannia callithrix</i> , <i>Odontoschisma prostratum</i> , <i>Plagiochila retrorsa</i> , <i>Radula nudicaulis</i> , <i>R. wichurae</i> . Losses: <i>Porella arboris-vitae</i> , <i>Riccia atromarginata</i> , <i>R. frostii</i> , <i>Riella affinis</i> , <i>R. cossoniana</i> , <i>Southbya nigrella</i> , <i>Sphaerocarpos michelii</i> .
Madeira+Canaries	Gains: <i>Cololejeunea schaefferi</i> , <i>Frullania polysticta</i> , <i>Lejeunea canariensis</i> , <i>Plagiochila stricta</i> , <i>P. virginica</i> , <i>Radula jonesii</i> . Losses: <i>Anastrophyllum minutum</i> , <i>Barbilophozia attenuata</i> , <i>Blepharostoma trichophyllum</i> , <i>Calypogeia integrispula</i> , <i>C. neesiana</i> , <i>Fossombronina wondraczekii</i> , <i>Herbertus sendtneri</i> , <i>Lepidozia pearsonii</i> , <i>Lophozia excisa</i> , <i>L. incisa</i> , <i>L. longiflora</i> , <i>L. turbinata</i> , <i>L. ventricosa</i> , <i>Marsupella sparsifolia</i> , <i>M. sphacelata</i> , <i>Riccia beyrichiana</i> , <i>R. huebeneriana</i> , <i>Scapania scandica</i> , <i>Trichocolea tomentella</i> .
Cape Verdes+sub-Saharan Africa	Gains: <i>Acrolejeunea emergens</i> , <i>Cololejeunea minutissima</i> , <i>Cyatodium cavernarum</i> , <i>Exormotheca pustulosa</i> , <i>Frullania socotrana</i> , <i>F. spongiosa</i> *, <i>Lejeunea caespitosa</i> *, <i>L. eckloniana</i> , <i>L. flava</i> , <i>Marchantia paleacea</i> , <i>M. pappeana</i> *, <i>Plagiochasma eximium</i> *.

and *Philonotis hastata* is a widespread tropical species. Support for the Madeira + Azores grouping is also provided by the synapomorphic absence of 68 species from the archipelagos (BaSP values <95%).

The Madeiran flora is characterized by the endemic genus *Nobregaea*, eight endemic species, and one endemic variety (Table 5), as well as the homoplastic occurrence of species elsewhere absent in the (Europe + Azores + Madeira) clade. These include five species shared with the Canaries (discussed earlier), the sub-Saharan *Brachymenium philonotula*, the neotropical *Syntrichia bogotensis*, and several species, namely *Dicranella campylophylla*, *Ditrichum difficile*, and *D. punctulatum*, whose distributions span several continents.

The Azores are characterized by the autapomorphic presence of six endemic species (Table 5) and the homoplastic

occurrence of the sub-Saharan *Campylopus flaccidus* and *Tortula bogosica*, the neotropical *Campylopus cygnaeus*, and two species, *Fissidens serratus* and *Philonotis uncinata*, with less specific distributions that span several continents.

Liverworts—The liverwort data matrix (Appendix S1 and S3; see Supplemental Data accompanying online version of this article) comprises 217 taxa. As with both pteridophyte and moss analyses, Macaronesia s.l. is not resolved as a clade in the 50% majority-rule consensus of the 1364 trees sampled during the Bayesian procedure (Fig. 4). The Cape Verdes are sister to the three regions of sub-Saharan Africa (AF2–AF4; posterior probability = 100%) whereas the Canaries, Azores, and Madeira are again included within the EurAsAf clade (posterior probability = 100%). Constraining the Markov chains to only sample trees that fit with a monophyletic Macaronesian concept resulted in topologies that displayed significantly lower ln L values ($P < 0.001$), and a monophyletic Macaronesia s.l. concept is thus rejected.

Within the EurAsAf clade, a monophyletic Macaronesia s.s. is resolved and supported by a posterior probability of 72%. Within this clade, the Canaries and Madeira form a monophyletic group with a 95% posterior probability. Macaronesia s.s. is sister to Europe, a relationship that is well supported (posterior probability = 99%).

The single most parsimonious tree of length 685 steps (CI = 0.317; RI = 0.623) resulting from the analyses of the 207 informative characters suggests at first sight a somewhat different scenario (data not shown). The Cape Verdes are again included within a sub-Saharan clade (BS = 5) and as sister area to AF2 (BS

TABLE 4. Autapomorphic, endemic pteridophyte taxa of each Macaronesian archipelago.

Archipelago	Endemics
Cape Verde	—
Azores	<i>Polypodium macaronesicum</i> subsp. <i>azoricum</i> , <i>Asplenium aethiopicum</i> subsp. nov.?, <i>Dryopteris azorica</i> , <i>D. crispifolia</i> , <i>Isoetes azorica</i> , <i>Marsilea azorica</i> .
Madeira	<i>Hymenophyllum maderense</i> , <i>Arachniodes webbiana</i> subsp. <i>webbiana</i> , <i>Dryopteris aitoniana</i> , <i>D. maderensis</i> , <i>Polystichum drepanum</i> , <i>P. falcinellum</i> .
Canaries	<i>Cheilanthes pulchella</i> , <i>Asplenium filare</i> subsp. <i>canariense</i> , <i>A. octoploideum</i> , <i>Dryopteris oligodonta</i> .

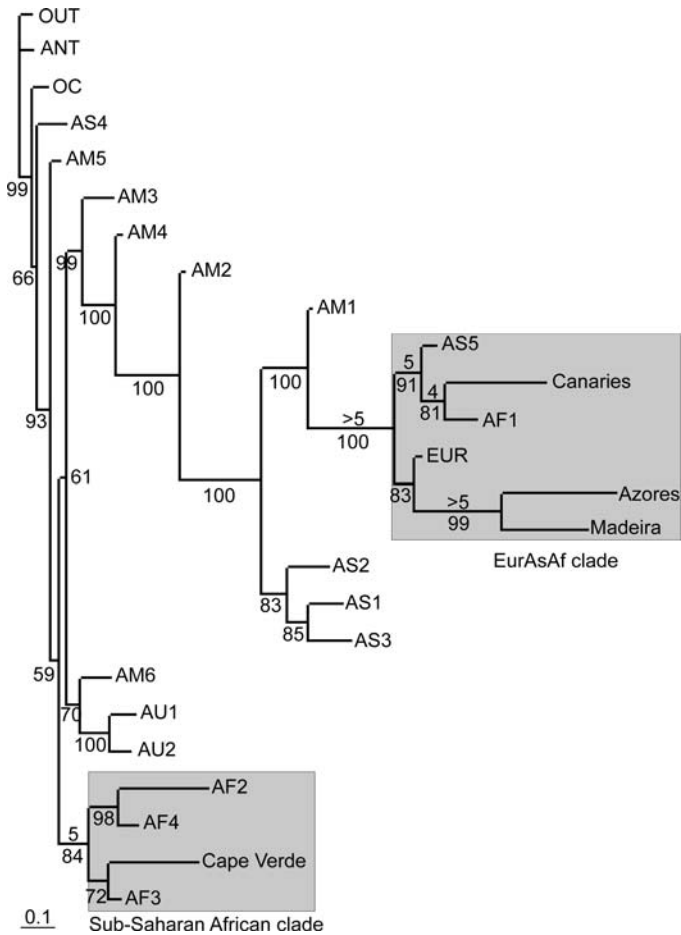


Fig. 3. Phylogeographic affinities of the Macaronesian moss flora inferred from a 50% majority-rule consensus of 1279 trees sampled after convergence of three independent Markov chains implementing a model of equal transition rates. See Fig. 2 for definitions of abbreviations.

= 5), while the three other archipelagos are included within the EurAsAf clade. Within the latter, however, the Azores + Madeira (BS = 1) form a clade that is sister to Europe (BS = 3), while the Canary Islands are resolved as sister to northern Africa (BS = 1).

TABLE 5. Autapomorphic, endemic moss taxa of each Macaronesian archipelago. Endemic genera are in boldface.

Archipelago	Endemics
Cape Verde	<i>Bryum anomodon</i> , <i>Entodon pseudoseductrix</i> , <i>Fissidens allorgei</i> , <i>Funaria chevalieri</i> , <i>Perssonia sanguinea</i> , <i>Pseudoleskea bollei</i> .
Azores	<i>Breutelia azorica</i> , <i>Echinodium renauldii</i> , <i>Fissidens azoricus</i> , <i>Sphagnum nitidulum</i> , <i>Thamnobryum rudolphianum</i> , <i>Trematodon perssonorum</i> .
Madeira	<i>Brachythecium percurrens</i> , <i>Bryoxyphium madeirense</i> , <i>Echinodium setigerum</i> , <i>Fissidens microstictus</i> , <i>F. nobreganus</i> , <i>Nobregaea latinervis</i> , <i>Plagiomnium undulatum</i> var. <i>madeirense</i> , <i>Pohlia luisieri</i> , <i>P. maderensis</i> , <i>Thamnobryum fernandesii</i> .
Canaries	<i>Aloina humilis</i> , <i>Entosthodon krausei</i> , <i>Grimmia curviseta</i> , <i>Orthotrichum handiense</i> , <i>Platyhypnidium torrenticola</i> , <i>Rhynchostegiella bourgeana</i> , <i>R. trichophylla</i> , <i>Tortella limbata</i> , <i>Tortula ampliretis</i> .

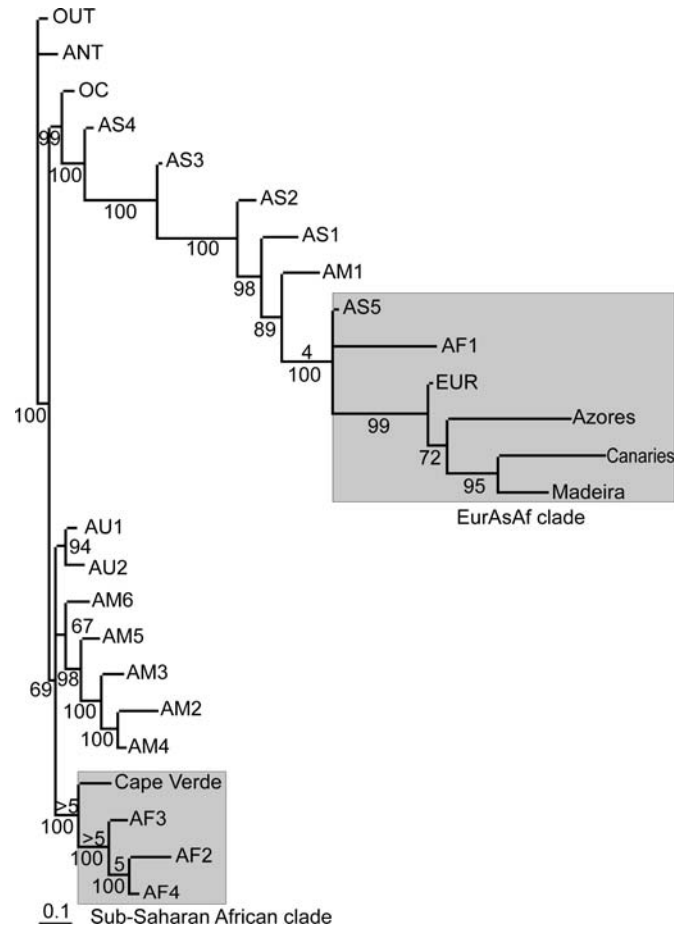


Fig. 4. Phylogeographic affinities of the Macaronesian liverwort flora inferred from a 50% majority-rule consensus of 1364 trees sampled after convergence of three independent Markov chains implementing a model of equal transition rates. See Fig. 2 for definitions of abbreviations.

Within a parsimony framework, constraining Macaronesia s.s. to monophyly resulted in a topology only three steps longer than the optimal topology. The value of $p/2$ of the associated KH test was 0.36, suggesting that the data do not significantly support the rejection of a monophyletic Macaronesia s.s. Given that the results from the Bayesian analysis are consistent with a monophyletic interpretation of Macaronesia s.s. and because Macaronesia s.s. cannot be significantly rejected based upon the MP analyses, the optimal MP topology, wherein the Canaries, the Azores, and Madeira appear in different (and weakly supported) clades, was not used to investigate species optimizations. Rather, these were investigated on the 50% majority-rule consensus tree from the Bayesian sample.

The inclusion of the Cape Verdes within sub-Saharan Africa is supported by the synapomorphic presence of 12 species, six of which are endemic (Table 3). The Cape Verdes lack any endemic species but are characterized by the presence of *Fossombronia angulosa*, *Frullania tamarisci*, *Lejeunea lamacerina*, and *Marchesinia mackai*, which do not occur anywhere else in sub-Saharan Africa and are shared with the EurAsAf clade.

The inclusion of the Azores, Madeira, and the Canaries within the EurAsAf clade is supported by 32 synapomorphic

TABLE 6. Autapomorphic, endemic liverwort taxa of each Macaronesian archipelago.

Archipelago	Endemics
Cape Verde	—
Azores	<i>Bazzania azorica</i> , <i>Cheilolejeunea cedercreutzii</i> , <i>Leptoscyphus azoricus</i> , <i>Tylimanthus azoricus</i> .
Madeira	<i>Frullania sergiae</i> , <i>Plagiochila maderensis</i> , <i>Porella inaequalis</i> , <i>Riccia atlantica</i> , <i>Tylimanthus madeirensis</i> .
Canaries	<i>Riccia teneriffae</i> .

species presences, nine of which are well supported with high (>95%) BaSP values, and nine of which are endemic, and by the absence of a further eight species (Table 3). Within the EurAsAf clade, the sister group relationship between Macaronesia s.s. and Europe is supported by 41 synapomorphic presences, 29 of which have BaSP values >95% and 10 of which are endemic, and two are synapomorphic losses.

Macaronesia s.s. is characterized by two endemic species whose distribution spans across all archipelagos, namely, *Heteroscyphus denticulatus* and *Radula wichurae*, and seven disjunctly distributed taxa that occur nowhere else within the EurAsAf clade and are of neotropical (*Aphanolejeunea azorica*, *A. sintenesii*, *Jungermannia callithrix*, *Odontoschisma prostratum*, *Plagiochila retrorsa* and *Radula nudicaulis*) and pantropical (*Acanthocoleus aberrans*) origin (Table 6). A monophyletic interpretation of Macaronesia s.s. is further supported by the synapomorphic absence of seven species, all of which, however, have BaSP values of <95%. Within Macaronesia s.s., the Azores are characterized by four endemic species (Table 6) and the homoplastic occurrence of *Jamesionella rubricaulis*, *Plagiochila longispina*, *P. papillifolia*, (all predominantly neotropical), and the sub-Saharan *Lepidozia stuhlmannii*. The sister-group relationship between the Canaries and Madeira is supported by the endemics *Cololejeunea schaefferi*, *Frullania polysticta*, *Lejeunea canariensis*, and *Radula jonesii*, all of which have BaSp values <95%. A suite of 19 synapomorphic absences, albeit with low support under ML (Table 6), further characterizes this clade. In addition, the New World species *Plagiochila stricta* and *P. virginica* are shared by the Canaries and Madeira, but occur nowhere else within EurAsAf. Their presence at the internal node joining the two archipelagos is, however, supported by low BaSP values <95%.

Within the Madeiran-Canarian clade, Madeira is characterized by a suite of five endemic species (Table 6) and the homoplastic presence of the Neotropical *Cephaloziella granatensis*. The Canaries possess one endemic, *Riccia teneriffae*, and are further characterized by the homoplastic presence of the sub-Saharan *Frullania obscurifolia*.

DISCUSSION

Relationships of the Cape Verde cryptogamic flora—The results presented in this paper suggest that the Macaronesian region, comprising the Cape Verdes together with the Azores, Madeira, and Canaries, does not represent a natural floristic unit for bryophyte and pteridophyte groups when all native taxa are included. All three analyses are therefore consistent with the view of Lobin (1982) that the flora of the Cape Verdes is more closely related to the flora of sub-Saharan Africa than

to the other Macaronesian archipelagos. The well-supported Cape Verde-tropical African sister group relationship for each cryptogamic group and the non-monophyly of the Macaronesian region challenge the Engler refugium model to explain the origin of the Macaronesian flora s.l. The large number of taxa shared by the Cape Verdes and the near-continent rather suggests that the dynamic interchange model best explains the present day flora of the Cape Verdes.

Among the bryophytes distributed on the Cape Verdes, *Cryptoleptodon longisetus* is the only species that could be considered a "Macaronesian element." The distribution of this species spans three of the four archipelagos, namely, the Cape Verdes, Canaries, and Madeira, and its occurrence in moist, protected habitats in natural forests (Hedenäs, 1992) may indeed indicate a relictual origin for this species. Among pteridophytes, four taxa have a homoplastic, but exclusively Macaronesian distribution, that encompasses the Cape Verdes and other Macaronesian archipelagos. *Notholeana marantae* subsp. *subcordata* and another somewhat xerophytic rock fern, the dodecaploid *Asplenium aethiopicum* subsp. *braithwaitii* (a local variant of a widely distributed polyploid complex with its center of diversity in southern Africa), are both exclusively distributed in Madeira, the Canaries, and Cape Verdes. The claim of these taxa to be relictual is perhaps weakened by their high ploidy level (Vogel et al., 1999) and their restriction to xerophytic habitats. *Dryopteris oligodonta*, however, is thought to have its closest relatives in Madagascar (Lobin et al., 1998) and is unique to the Cape Verdes and Canaries, where it is abundant in humid laurisilva habitats in the latter. The distribution of this species may be relictual in nature. The fourth fern species within the homoplastic floristic element common to the Cape Verdes and Madeira-Canaries is *Adiantum reniforme* s.l. This species complex is also present in tropical East Africa. Such a disjunct distribution would also be consistent with the Engler refugium model. However, although inseparable by gross morphology, the Canarian and Madeiran plants are cytologically distinct (Manton et al., 1986), the former tetraploid, the latter decaploid. Unfortunately, the cytology of the disjunct Cape Verdean, African, Mascarene and Asian examples, which have collectively been referred to *A. reniforme* s.l., is unknown. The possible relictual status of the Macaronesian taxa will thus remain uncertain until their origin and relationships are established.

Relationships of the Azores, Madeira, and Canary Islands floras—All three analyses resolve the Azores, Madeira, and the Canary Islands in a clade with Europe, North Africa, and southwest Asia.

The moss and pteridophyte data sets are also consistent in resolving Madeira and the Azores as sister areas, a clade that is supported by four and four endemic synapomorphies, the synapomorphic presence of a further four and eight non-endemic species, and the synapomorphic absence of eight and 68 species in the pteridophyte and moss analyses, respectively.

The dynamic interchange model offers a possible explanation for the shared absence of taxa from the Azores and Madeira. In some instances, absences may reflect the stochastic nature of the interchange between continental and island areas with the incomplete colonization of the islands from continental source areas. In others, this pattern probably reflects the lack of suitable niches on the archipelagos. For example, a conspicuous calcicolous element comprising the mosses *Acaulon muticum*, *Aloina brevirostris*, *Amphidium lapponi-*

cum, *Anomodon viticulosus*, *Crossidium aberrans*, *C. squamiferum*, *Encalypta streptocarpa*, *Entosthodon fascicularis*, *Grimmia crinita*, *G. tergestina*, *Lescurea mutabilis*, *Neckera menziesii*, *N. pennata*, *Plasteurhynchium striatulum*, *Protobryum bryoides*, *Pterygoneuron subsessile*, *Tortella inflexa*, *Weissia condensa*, and *W. longifolia* is absent from the Azores and Madeira.

While the four pteridophyte and four moss species that are endemic to the Azores-Madeira clade could be considered evidence for the presence of traces of Tertiary relictualism in the cryptogamic flora, there is at least some evidence to suggest that these taxa are more likely to have evolved in situ by isolation following long-distance dispersal from the New World. Among the endemic pteridophytes, *Huperzia dentata* is the only Old World representative of the otherwise exclusively New World section *Reflexa*. As a hexaploid (I. Manton [deceased], unpublished data), this species is likely to be a derived representative of this distinct lineage and not basal to it. Colonization of Macaronesia from the new World best explains the observed distribution and known relationships of this taxon. The relationships of *Diphasiastrum madeirense* remain to be resolved, but some aspects of its growth form suggest closer affinities to the North American *D. digitatum* than to Eurasian taxa. *Elaphoglossum semicylindricum*, described from Madeira, was regarded as conspecific with material from Jamaica (Proctor, 1985). Proctor (1985, p. 506), however, noted that “members of this complex also occur in South America and through the paleotropics, but they may be recognizable as distinct species.” In Davidse et al. (1995), it is clear that several distinct entities have been treated under *E. paleaceum*, a synonym of *E. semicylindricum*. Further work is clearly needed to establish whether the Macaronesian material is distinct, but its affinities to the New World are incontrovertible. A further New World link is provided by the Azorean endemic aquatic *Isoetes azorica*, which has been shown to be most closely related to the North American *I. tuckermannii* (Britton and Brunton, 1996).

Among bryophytes, the very limited molecular phylogenetic evidence for the origin of Macaronesian endemics suggests that the liverworts *Leptoscyphus azoricus* and *Plagiochila maderensis* are of recent neotropical origin (Rycroft et al., 2004; Vanderpoorten and Long, 2006). Other Macaronesian endemic liverworts, such as *Tylimanthus azoricus*, are also suspected to be of recent neotropical origin (Schumacker, 2001).

In addition to a New World link for the endemic taxa supporting the Azores + Madeira clade, there is also a substantial New World element in the non-endemic pteridophyte and moss flora of the archipelagos that supports this grouping. The pteridophytes *Ceradenia jungermannioides* and *Grammitis marginella* are disjunct in the Azores and Madeira but have their main distribution area on the American continent. Similarly, five of the nine species of the moss genus *Campylopus* present in the Azores have a distribution range that spans Macaronesia and the Caribbean islands (Frahm, 1999). In the liverwort genus *Plagiochila*, more than 50% of the species found on Madeira also occur in the neotropics (Sim-Sim et al., 2005). A complete extinction of all these taxa from Europe, western Asia, and northern Africa during the Ice Ages cannot be completely ruled out. Indeed, such an explanation may be necessary for the moss genus *Echinodium*, which is currently restricted to the Macaronesian archipelagos within the EurAsAf clade, but is known from European Eocene fossils (Frahm, 2004). However, the

predominant pattern evident from both bryophyte and pteridophyte analyses is consistent with the view that the Madeiran and Azorean archipelagos have served as stepping stones for the eastward spread (and occasional isolation in the case of endemics) of American taxa (Sim-Sim et al., 2005). Muñoz et al. (2004) demonstrated that wind connectivity rather than geographic proximity is the main force driving current bryophyte distributions. Frequent depressions moving rapidly eastward at relatively low altitude (3000 m) from the American coasts and tropical cyclones of west Caribbean origin that can carry even large propagules may have provided a mechanism for colonization of these archipelagos from the New World (Schäfer, 2003).

In the liverwort and pteridophyte ML analyses, Macaronesia s.s. is resolved as a monophyletic group that is sister to Europe in the 50% majority-rule consensus of the trees sampled during the Bayesian procedure. This relationship is also recovered in 50% of MP trees from the parsimony analysis of the pteridophyte data. In liverworts, MP recovers a different set of relationships. However, a monophyletic Macaronesia s.s. is only three steps longer and under the MP criterion cannot be rejected.

Macaronesia s.s. corresponds to the circumscription of the region first proposed by Engler (1879) and before subsequent authors expanded the concept to include the Cape Verdes (e.g., Dansereau, 1961; Takhtajan, 1969; Bramwell, 1972, 1976) and, in some cases, continental enclave areas (Sunding, 1979). The recognition of Macaronesia s.s. is in marked contrast to more recent classifications that have not recognized a Macaronesian s.s. region (e.g., Lobin, 1982; Rivas-Martinez et al., 2004).

The sister-group relationship between Macaronesia s.s. and Europe is supported by an Atlantic fringe element, i.e., a suite of taxa that occur only on the three archipelagos and the western seaboard of Europe. These taxa include the ferns *Ophioglossum azoricum*, *Hymenophyllum tunbrigense* (also distributed in the Americas and southwestern Asia), and *H. wilsonii*, rarely with disjunct refugia elsewhere in the case of *Dryopteris aemula* and *Trichomanes speciosum* and the liverworts *Acrobolbus wilsonii*, *Adelanthus decipiens*, *Aphanolejeunea microscopica*, *Cololejeunea minutissima*, *Colura calyptrifolia*, *Drepanolejeunea hamatifolia*, *Frullania azorica*, *F. microphylla*, *Harpalejeunea molleri*, *Herbertus sendtneri*, *Hygrobiella laxifolia*, *Lejeunea flava*, *L. hibernica*, *L. lamacerina*, *L. mandonii*, *Lepidozia cupressina*, *L. pearsonii*, *Leptoscyphus cuneifolius*, *Marchesia mackai*, *Marsupella adusta*, *M. profunda*, *M. sparsifolia*, *M. sprucei*, *Metzgeria fruticulosa*, *M. leptoneura*, *M. temperata*, *Plagiochila bifaria*, *P. exigua*, *P. punctata*, *P. spinulosa*, *Radula aquilegia*, *R. carringtonii*, *R. holtii*, *Saccogyna viticulosa*, and *Telaranea europaea*. This suite of hyper-Atlantic taxa has, at least in ferns, long been regarded as relictual of a broader Tertiary distribution range currently restricted, as in *H. tunbrigense*, to disjunct sheltered sandstone gorges refugia of Central Europe, eastward through northern Turkey and into the former USSR (Drude, 1902; Klein, 1926; Richards and Evans, 1972). The distributions of two further species that are widespread in Macaronesia and also occur in Macaronesian enclave areas on the nearby continent, also support the refugium hypothesis: *Diplazium caudatum*, which occurs throughout Macaronesia and is known from the Sierras just north of Algeciras in southernmost Spain, and *Asplenium hemionitis*, which similarly occurs on all Macaronesian archipelagos and in several

coastal enclave areas in North Africa and Portugal. In addition, a record of *Asplenium aethiopicum* from the Moroccan Anti-Atlas enclave, an area that also harbors *Dracaena draco* (Benabid and Cuzin, 1997), may prove to be of the insular subsp. *braithwaitii*, and *Polypodium macaronesticum* s.l. has been reported from the southern Spanish Macaronesian enclave north of Algeciras (Greuter et al., 1984), although this record needs confirmation. Both distributions would similarly be consistent with a broadly interpreted Engler refugium model linking the Azores-Madeira-Canarian pteridophyte flora with that of putative continental enclave areas.

Asplenium anceps is endemic to the three northern archipelagos and would also support the resolution of these three areas as a clade. Whereas this species is only known from a single collection (Lovis et al., 1977) in the Azores, it is implicated in the parentage of the Azorean endemic *A. azoricum* and its Iberian-North African counterpart *A. trichomanes* subsp. *coriaceifolium* (= *A. azomanes*), neither of which is currently sympatric (Rumsey et al., 2004). The role of *A. anceps* in the parentage of these taxa suggests that this species might once have been both more abundant on the Azores and, conceivably, present in the nearby continent. If this is the case, then the current distribution of this species would represent a contraction of its historical distribution, a scenario consistent with the Engler refugium model.

Selaginella kraussiana (otherwise confined to tropical and southern Africa) and *Asplenium monanthes* (a pantropical species), which both represent a tropical element with a northern extension into the region, also support a northern archipelago grouping, as do the Madeira-Canarian endemics *Asplenium loegnansense* and *Polypodium macaronesticum* subsp. *macaronesticum*.

In addition, the interpretation of the speciation in *Dryopteris guanchica*, currently restricted to the Canaries and along the Atlantic coast of Iberia, suggests a link between Madeira and the Canaries/Europe that is not evident from extant distribution data alone. *Dryopteris guanchica* is a polyploid derivative of a cross involving *D. maderensis*, a species endemic to Madeira, and *D. aemula*, a species present on all three northern Macaronesian archipelagos but otherwise distributed along the Atlantic coasts of Europe and in Turkey (Davis et al., 1988). At present, the parental taxon *D. maderensis* and its derivative *D. guanchica* have mutually exclusive distributions. However, for one to have arisen from the other, one or both must have been more widespread in the past. Indeed, a range of dispersal-extinction scenarios could explain the origins of *D. guanchica* and the extant distributions of these two taxa: (1) *Dryopteris guanchica* had its origins in Madeira, dispersed to the Canaries and Europe, and subsequently went extinct from Madeira, or (2) *D. maderensis* was more widespread, formerly occurring in the Canary Islands, where hybridization with *D. aemula* gave rise to *D. guanchica* before *D. maderensis* became extinct from the Canaries and *D. guanchica* dispersed to Europe; (3) as with scenario (2), but with *D. maderensis* present and giving rise to *D. guanchica* in Europe before going extinct there and *D. guanchica* colonizing the Canaries from Europe; and (4) *D. maderensis* historically present in both Europe and Canaries, independently giving rise to *D. guanchica* in these two areas and subsequently going extinct from both. Whatever the scenario involved, the speciation of *D. guanchica* requires that the species was present across several archipelagos and the southwestern coasts of Europe, a pattern that is again consistent with the Engler refugium model.

The moss analyses differ from those of the pteridophytes and liverworts with respect to the placement of the Canaries within the EurAsAf clade. For mosses, the hypothesis of a common origin of the flora of Macaronesia s.s. is rejected and the Canaries are resolved as sister area to North Africa. This placement lends further support to the dynamic interchange model by indicating a close relationship with the nearby continent rather than to a common, relictual Tertiary origin for the archipelago floras. It is notable that the relationship between the Canaries, northern Africa, and western Asia, and the sister group relationship between the Canaries and northern Africa, are supported by the shared loss of 30 and 22 species, respectively. A substantial proportion of those species, namely *Andreaea rothii*, *Blindia acuta*, *Bryoerythrophyllum ferruginascens*, *Campylopus brevipilus*, *C. subulatus*, *Diphyscium foliosum*, *Fissidens bryoides* var. *caespitans*, *Hypnum cupressiforme* var. *resupinatum*, *Leucobryum albidum*, *Orthodontium gracile*, *Rhytidiadelphus loreus*, *Sphagnum affine*, *S. papillosum*, and *S. pylaesii*, are of (sub)oceanic affinities, and this suggests that the synapomorphic absences characteristic for the Canaries and northern Africa are at least partly explained by ecological factors. The possibility that this result is an artifact due to a severe limitation in current floristic inventories seems unlikely because, while the flora of North Africa is still somewhat under-recorded, recent intensive floristic research has substantially increased our knowledge of the region's bryoflora (Ros et al., 1999). It thus appears that the Canarian and northern African flora has little floristic individuality and represents the extension of xerophytic bryofloras of the Mediterranean areas and the Middle East and of a European temperate flora in the highest mountains (Tan and Pocs, 2000).

Dispersal, relictualism, and the patterns of relationships of the archipelago floras—

The broad congruence observed between bryophyte and pteridophyte data sets with regards to the placement of the Cape Verdes serves to emphasize the remoteness of these islands from the rest of Macaronesia when contrasted with the distance between the Cape Verdes and the near continent. With respect to the northern archipelagos, the relationships suggested by the moss analyses are incongruent with a Macaronesia s.s. grouping and support the dynamic interchange model to explain the predominant floristic pattern observed. Vanderpoorten and Long (2006) recently proposed that one interpretation of the non-European and North African origin of Macaronesian endemic bryophytes and pteridophytes, which sharply contrasts with the origin of the vast majority of endemic angiosperms (Carine et al., 2004), is the existence of extensive gene flow between Macaronesian and continental populations. Endemic speciation resulting from gene-flow disruption would thus only be possible in the case of discrete long-distance dispersal events. The results of the moss analyses presented in this paper are consistent with this hypothesis. The recent development of microsatellite loci in bryophytes (Van der Velde et al., 2000; Long et al., 2006) should help to provide the necessary framework to test hypotheses of an ancient isolation vs. continuous gene flow between Macaronesian and continental populations.

In contrast to the mosses, the liverwort and pteridophyte analyses are consistent with the concept of Macaronesia s.s. and thus do not refute the Engler refugium model as an explanatory hypothesis for the relationships of the floras of these archipelagos. Differences between the mosses on one

hand and the liverworts and pteridophytes on the other may be attributable to differences in the biology of these groups.

Although the MP analyses employed in the present study are, by definition, based on the concept of synapomorphy and hence favor vicariance over long-distance dispersal as a possible explanation for the obtained biogeographical patterns (Bisconti et al., 2001; Santos, 2005), the fact, that the ML model, which does not minimize the level of homoplasy but rather maximizes the probability of the data given a model of species "gains" and "losses," returns comparable results, further suggests that the results are not biased by the optimality criterion used in the different techniques employed. The level of homoplasy present in the data, summarized by statistics such as the consistency index (CI), can actually provide a measure of the importance of long-distance dispersal. The moss data set displays the most homoplastic distribution patterns (CI = 0.297), followed by liverworts (CI = 0.317), and finally pteridophytes (CI = 0.443), and the higher levels of homoplasy in the moss data sets may reflect the greater long-distance dispersal ability of this group necessary for dynamic interchange with continental areas. Greater dispersability may involve, as emphasized, that endemic speciation in Macaronesian bryophytes rely on discrete events of long-distance dispersal rather than exchanges with nearby continents. The rarity of successful establishment following long-distance dispersal may also explain why endemic bryophytes are much less numerous than for the angiosperm flora. Macaronesian endemic bryophytes indeed represent only 9% of the archipelago floras. In the Azores, only 2% are strictly endemic to the archipelago, and this represents the lowest proportion by comparison with all the other biota (Borges et al., 2005). However, this picture based on traditional, morphological species concepts, is in urgent need of revision. The status of many of the endemic bryophytes is an area of controversy (Schumacker, 2001; Sjögren, 2001), and few molecular investigations have been undertaken to test that those supposedly endemic species are not conspecific with other, more broadly distributed taxa (Stech et al., 2001; Feldberg et al., 2004; Rycroft et al., 2004; Stech and Sim-Sim, 2006; Vanderpoorten and Long, 2006). On the other hand, actual genetic differentiation of Macaronesian endemics may have taken place without any morphological signature of the genetic divergence. Such a phenomenon, called cryptic speciation, has been increasingly documented in bryophytes (Shaw, 2001; McDaniel and Shaw, 2003; Feldberg et al., 2004).

A further point to note is that whilst a monophyletic Macaronesia s.s. for pteridophytes and liverworts is certainly consistent with the explanation provided by Engler's refugium model, the extent to which this grouping is truly explained by Engler's model remains to be ascertained. Other explanations, notably recent (postglacial) colonization of putative continental refugial areas from Macaronesia s.s. (or vice versa) are also plausible. In angiosperms, while some groups have trans- or intercontinental sister group disjunctions consistent with relictualism through large-scale continental extinction, many other groups have sister-group relationships with taxa distributed in the western Mediterranean, a pattern that may suggest a relatively recent origin for these groups (Carine et al., 2004). Furthermore, in the case of several genera, evidence suggests that the Macaronesian islands have served as a source area for continental neo-endemics. In *Convolvulus*, for example, Carine et al. (2004) demonstrated that *C. fernandesii*, a species endemic to Cabo Espichel in Portugal and thought by

Bramwell and Bramwell (2001) to be a relictual paleoendemic, is actually the result of more recent colonization from the Macaronesian region, as evidenced by its placement in a molecular phylogeny of the group and the extremely low levels of sequence divergence when compared with its close Macaronesian relatives.

Macaronesian pteridophyte and liverwort distributions that are consistent with Engler's refugium model may similarly reflect a complex mix of relictualism overlaid by more recent evolution and dispersal. The allohexaploid *Asplenium lolegnamense*, for example, is distributed in Madeira and the Canaries, but is sympatric with its putative parental taxa only in the Canaries (Van den Heede et al., 2004), a situation that may suggest northward colonization from the Canaries to Madeira rather than ancient relictualism. Similarly, within the *Adiantum reniforme* complex, the extant decaploid Madeiran plant may have been derived from the tetraploid Canarian taxon. Both cases suggest that a northward colonization, possibly in progress, rather than ancient vicariance, may explain current species distributions.

Extensive molecular research on Macaronesian taxa is necessary to determine whether or not spatially congruent distributions consistent with the Engler refugium hypothesis do indeed share a common causal explanation. The actual level of knowledge on the taxonomic status and origin of the cryptogamic endemic flora is, however, far below that achieved for angiosperms. An important and necessary task remains to better understand the evolutionary mechanisms underlying the floristic patterns described in the present paper.

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