



Early divergence of an Azorean endemic species in the moss genus *Rhynchostegiella* (Brachytheciaceae)

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Abstract

Using the moss genus *Rhynchostegiella* (Brachytheciaceae) as a model, we address the question of whether taxonomic shortcomings account for the extremely low rates of endemism reported in the Azorean bryophyte flora. Eight accessions initially assigned to three of the four previously reported species in the Azores were identified as a distinct species using the Generalized Mixed Yule Coalescent method in the context of a molecular phylogenetic analysis of the genus. *Rhynchostegiella azorica* sp. nov. is therefore described as a new species that is endemic to the Azores. Its morphological features intergrade with those observed in other species, with a seta that ranges from almost smooth to rough; a length to width ratio of the laminal cells that matches the one of the *R. curviseta* group; but a leaf apex that is typical of the *R. tenella* group. This suggests that previous reports of four *Rhynchostegiella* species from Azores are erroneous and that a single, morphologically variable species, *R. azorica*, occurs in the archipelago. *Rhynchostegiella azorica* is sister to the remainder of the species of the genus, whose most recent common ancestor was dated at 4–20 Ma. This points to a more ancient origin in comparison with other Macaronesian endemic species of the genus. The unexpected discovery of an Azorean endemic species in *Rhynchostegiella* suggests that patterns of endemism in the Azorean bryophyte flora are not well estimated from traditional taxonomic knowledge and point to the necessity of an extensive integrative taxonomic revision.

Key words: integrative taxonomy, Macaronesia, bryophyte

Introduction

Since DNA sequence data have become more widely used and accessible, traditional species concepts have been increasingly challenged (see Kadereit *et al.* 2012 for review). This might have substantial consequences for our understanding of biogeographic patterns of biodiversity. For example, studies based on the analysis of distribution data from checklists found that the flora of the Azores differs from other island floras in the exceptionally low number of radiations and the low number of single-island endemics (Carine & Schaefer 2010), which has been an area of controversial interpretations (see Carine *et al.* 2012 for review). Schaefer *et al.* (2011) attempted at further understanding the mechanisms underlying this pattern by exploring the molecular phylogeography of endemic Azorean angiosperms and found a strong geographic structure in patterns of genetic variation. If the lineages identified on a molecular basis were recognized taxonomically, the spatial pattern of endemic species distributions would be much similar to that reported in other archipelagos (Schaefer *et al.* 2011).

Taxonomic issues in describing and understanding biodiversity patterns are expected to culminate as organisms decrease in size and morphological complexity (Whittaker *et al.* 2005). In bryophytes, DNA-based investigation (e.g., Bell *et al.* 2012; Hutsemékers *et al.* 2012; Medina *et al.* 2012, 2013) increasingly helped identifying unexpected species differentiation within widely circumscribed species exhibiting trans-oceanic disjunct distribution patterns. These new species often proved to be unambiguously distinguishable morphologically (Medina *et al.* 2012, 2013), although strong morphological overlap among similar species makes it sometimes necessary to implement barcoding techniques (Buczowska & Dabert 2011; Stech *et al.* 2013). Such results might offer an explanation for one of the

most striking biogeographic features of bryophytes, that is, their extremely low rates of endemism (see Vanderpoorten *et al.* 2010 for review). In the Azores in particular, five species of mosses and three of liverworts are endemic to the archipelago, representing 1.7% and 1.8% of moss and liverwort species, respectively (Vanderpoorten *et al.* 2011). This contrasts markedly with the 35% endemism rate observed in the native angiosperm flora (Vanderpoorten *et al.* 2011). However, bryophytes exhibit high capacities for long-distance dispersal, so that their apparent failure to diversify on islands could alternatively be explained by the homogenization of their genetic structure due to intense gene flow. The finding of a strong and balanced gene flow between island and continental populations in the moss *Rhynchostegium riparioides* (Hedwig 1801: 242) Cardot in Tourret (1913: 231) supports such a hypothesis (Hutsemekers *et al.* 2011). Differences in dispersal capacities between seed plants and bryophytes could therefore explain why the bulk of Macaronesian endemic angiosperms are of Mediterranean origin (Carine *et al.* 2004), whereas an increasing body of evidence indicates that Macaronesian endemic bryophytes are recent neo-endemics originating from geographically remote ancestors (Vanderpoorten *et al.* 2011). Mounting evidence suggests, however, that patterns of genetic variation in bryophytes are highly structured at the local scale (Hutsemekers *et al.* 2010, 2013; Korpelainen *et al.* 2011, 2012; Patiño *et al.* 2013), suggesting that in situ speciation could potentially still take place.

Here, we address the question of whether taxonomic shortcomings account for the extremely low rates of endemism reported in the Azorean bryophyte flora, focusing on the moss genus *Rhynchostegiella* (Schimper 1852: 201) Limpricht (1896: 207). The genus includes species that are among the smallest within the pleurocarpous mosses. It has progressively become a convenient repository for small Brachytheciaceae members of doubtful taxonomic position, making it a prime candidate for further DNA based taxonomic investigation. Based on sampling of recent specimens encompassing the range of morphological variation of the species reported to date from the Azores, we aim to (i) revisit the taxonomic status of Azorean *Rhynchostegiella* and determine the extent to which they differ genetically and morphologically from continental populations and (ii) place them in a species-level phylogeny of the genus and identify their relationships.

Material and Methods

Taxon sampling and molecular protocols

A total of 87 accessions were sampled representing the eight species of *Rhynchostegiella* (as recircumscribed by Aigoïn *et al.* 2009a) from throughout their distribution ranges. In the Azores, *R. bourgaeana* (Mitten 1870: 309) Brotherus (1909: 1162), *R. curviseta* (Bridel 1812: 111) Limpricht (1896: 211), *R. durieui* (Montagne 1849: 319) P. Allorge & Persson (1952: 87), *R. litorea* (De Notaris 1838: 31) Limpricht (1896: 214), and *R. tenella* (Dickson 1801: 16) Limpricht (1890: 206) have been reported from the archipelago (<http://www.azoresbiportal.angra.uac.pt/pesquisa.php?lang=en&sstr=3>, Ellis *et al.* 2011). Of these, *R. durieui* was transferred into its own genus *Pseudorhynchostegiella* Ignatov & Vanderpoorten in Aigoïn *et al.* (2009a: 219). *Rhynchostegiella bourgaeana* was reported from a single locality near Ponta Delgada in São Miguel (Silvera 1937). It has not been observed since and we were unable to locate any corresponding specimen. *Rhynchostegiella curviseta* was reported from Corvo, Flores, São Jorge, and Santa Maria; *R. litorea* from Terceira (Ellis *et al.* 2011); and *R. tenella* from all islands but Flores. Eight accessions initially assigned to three of the four previously reported species from Flores, Faial, and Terceira were sampled (Table 1). Six species from other genera of Helicodontioideae, including *Aerolindigia capillacea* (Hornschuch in Martius 1840: 58) M. Menzel (1991: 322), *Clasmatodon parvulus* (Hampe 1839: 46) Sullivant (1856: 660), *Helicodontium capillare* (Hedwig 1801: 221) A. Jaeger (1878: 225), *Homalotheciella subcapillata* (Hedwig 1801: 83) Brotherus (1908: 1133), and ‘*Rhynchostegiella leptoneura* Dixon & Thériot in Dixon (1931: 168), were sampled as outgroups.

DNA was extracted using a standard CTAB protocol. Three chloroplast loci (the *trnL-F* region, the *atpB-rbcL* intergenic spacer, and the *psbT-H* region) were amplified and sequenced following the protocols of Aigoïn *et al.* (2009b). Indels were scored as missing data, resulting in a total of 1193 unambiguously aligned positions.

Phylogenetic analyses

Phylogenetic inference was performed with BEAST v1.7.5 (Drummond *et al.* 2012) in order to jointly explore the relationships of the Azorean accessions and estimate their timing of divergence. The GTR+ γ +I was selected as the best-fit substitution model based on the AIC as implemented by jModeltest 2.1.4 (Darriba *et al.* 2012). Previous attempts at dating the phylogeny of *Rhynchostegiella* and related genera employed a prior distribution of absolute

TABLE 1. Voucher information and GenBank accession numbers of the Azorean collections of *Rhynchospora* included in the phylogenetic analysis. Accessions sharing the same accession numbers are listed together and correspond to the same multilocus haplotype.

Voucher	location	habitat	<i>trnL-F</i>	<i>atpB-rbcL</i>	<i>psbI-H</i>
<i>Vanderpoorten 12/II</i> (LG)	Flores, Fajazinha, Poço das Patas, 39°N26', 31°W14'	Splash zone of a waterfall at 263 m	KF718847	KF718851	KF718855
<i>Vanderpoorten & Patiño RHY832</i> (LG)	Faial, 38°N45', 28°W45'	Dry rocks under <i>Pittosporum</i> at 168 m	KF718847	KF718851	KF718855
<i>Vanderpoorten 12/2, 12/26</i> (LG)	Flores, Fajazinha, Poço das Patas, 39°N26', 31°W14'	Dry rocks under <i>Pittosporum</i> at 255 m	KF718845	KF718849	KF718853
<i>Vanderpoorten 18/I</i> (LG)	Terceira, Aqualva, 38°N47', 27°N11'	Rocks under <i>Pittosporum</i> in a dry, shaded gorge at the sea level	KF718845	KF718849	KF718853
<i>Vanderpoorten 12/25</i> (LG)	Flores, Fajazinha, Poço das Patas, 39°N26', 31°W14'	Dry rocks under <i>Pittosporum</i> at 255	KF669711	KF718848	KF718852
<i>Vanderpoorten 14/3</i> (LG)	Flores, Faja Grande, Rocha do Rixo, 39°N29', 31°W15'	Cliff rocks under <i>Erica azorica</i> at 162 m	KF669711	KF718848	KF718852
<i>Vanderpoorten FLOR2</i> (LG)	Flores, between Mosteiro & Lajedo, 39°N24', 31°W14'	Dry rocks in disturbed <i>Erica scoparia</i> heath with <i>Pittosporum undulatum</i> , <i>Echium gardnerianum</i> , <i>Cyrtomium falcatum</i> , <i>Selaginella kraussiana</i>	KF718846	KF718850	KF718854

substitution rates across land plants (Aigoin *et al.* 2009b). Here, we used a more specific distribution derived from the analysis of the entire Moss Tree of Life (Cox *et al.* 2010) calibrated with 35 fossils (B. Laenen *et al.* 2014). This distribution had a mean of 4.453×10^{-4} and a standard deviation of 1.7727×10^{-6} substitutions per site per Myr. Four Monte Carlo Markov Chains were run simultaneously for 100,000,000 generations, with sampling every 10,000 generations under a birth-death and a Yule speciation model, respectively. The latter was selected against the former based on Bayes factors and employed in subsequent analyses. Convergence and mixing of the four chains was checked using the program TRACER 1.6 (Rambaut *et al.* 2013). One thousand trees were discarded as ‘burn-in’ and the remaining trees from each of the four runs were combined.

We used the GMYC model as implemented by the SPLITS package (Ezard *et al.* 2009) available from “<http://R-Forge.R-project.org>” to identify species on the basis of the phylogeny. This method identifies shifts in diversification rates associated with the change from reticulate evolution (a neutral coalescent model) to divergent evolution (a Yule pure birth model) (see Fujisawa & Barraclough 2013 for review). Single and multiple-threshold GMYC models were applied to the ultrametric tree obtained from the BEAST analysis.

Results

The 50% majority-rule consensus built from the trees sampled from the posterior probability distribution is shown in Fig. 1. All the Azorean accessions formed a clade supported with a posterior probability of 1.00 that is resolved as sister to all other accessions of *Rhynchostegiella* included in the analysis, and which form a clade supported with a posterior probability of 1.00. The most recent ancestor of the Azorean clade (crown age) dated back to 1.57 Ma (95% HPD: 0.06–3.21 Ma), but the stem age is 8.67 [4.24, 12.16] Ma. Using both the single and multiple threshold versions of the GMYC model, the likelihood (LGMYCsingle = 212.1064 and LGMYCmultiple = 214.1417) was marginally to significantly higher than that of the null model of uniform coalescent branching rates ($L_0 = 208.3605$; $P = 0.057$ and $P = 0.041$, respectively) and the clade including all of the Azorean accessions was recognized as a distinct species (Fig. 1).

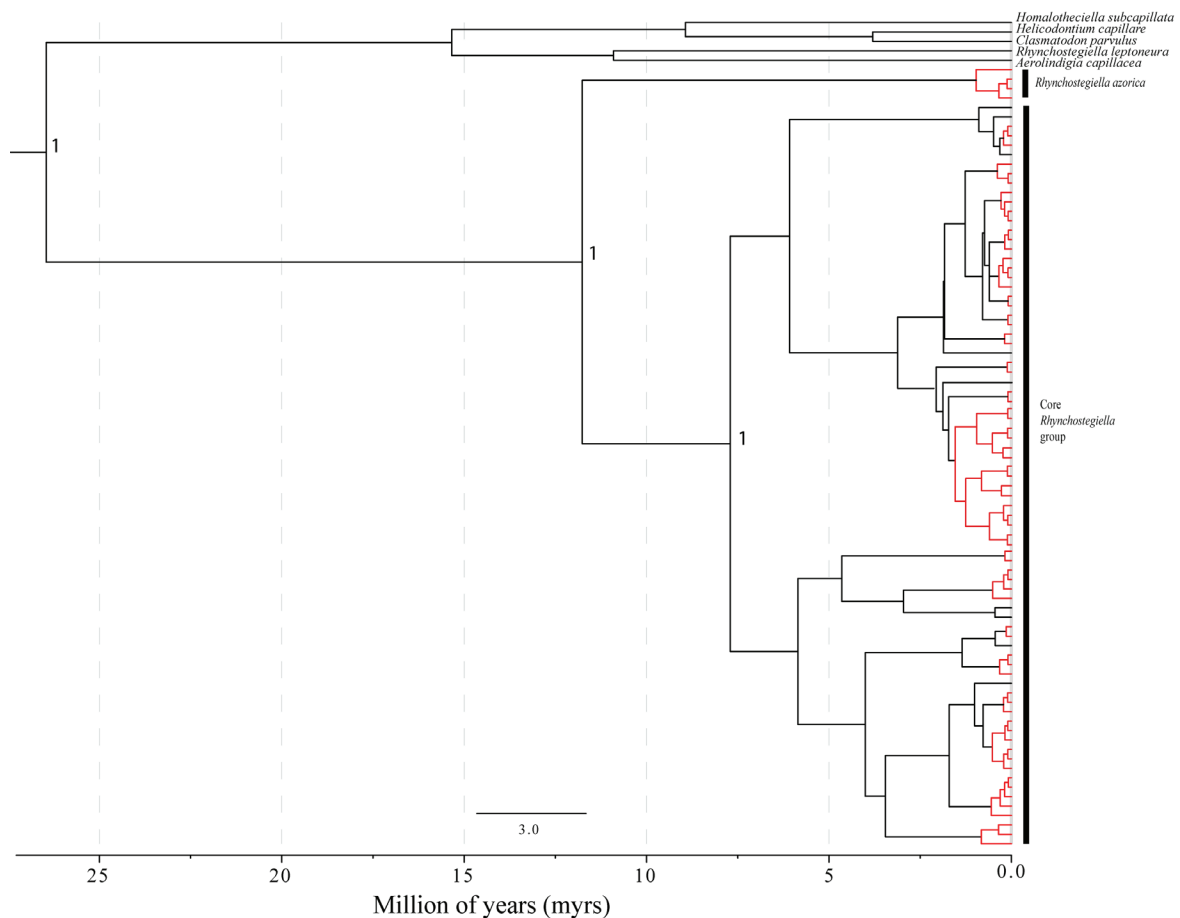


FIGURE 1. 50% majority-rule consensus from the trees sampled from the posterior probability distribution of a BEAST analysis of three chloroplast genes in the moss genus *Rhynchostegiella*. Numbers below the branches are the posterior probabilities. Clades highlighted in red correspond to the ones identified as distinct species by the GMYC model (see Material and Methods for details).

Morphologically, the specimens of the Azorean clade are quite variable in the characters that are used in the taxonomy of the genus. The seta can be either almost smooth or rough; the mid-leaf cells are 25.0–73.5 µm long, and the costa can reach 25–80% of leaf length (Table 2). The relatively narrow leaves, with a length to width ratio of 4.0–6.5 and a narrowly acuminate apex (17–27 µm wide at 100 µm and 35–55 µm at 200 µm below apex), are the feature that most clearly distinguish the Azorean specimens from *R. curviseta* and similar species with relatively broader leaves (length to width ratio 2.4–3.6) and shortly blunt at apex (27–97 µm wide at 100 µm and 44–191 µm at 200 µm below apex). The distinction between the specimens of the Azorean clade with other long-leaved species, such as *R. tenella*, mostly lies in the length of the laminal cells, 25.0–82.0(–89.0) µm in the former and 40.0–134.5 µm in the latter.

TABLE 2. Morphological differentiation between *Rhynchostegiella tenella*, *R. curviseta* and *R. azorica*.

Character	<i>R. tenella</i>	<i>R. curviseta</i>	<i>R. azorica</i>
Laminal cell length to width ratio	10–20	8–10	5–9
Stem leaf apex	Longly and narrowly acuminate	Blunt or obtuse	Longly acuminate
Width at 100 µm below apex	10.5–25.0 µm	27.5–96.5 µm	17–27 µm
Width at 200 µm below apex	17.0–38.0 µm	44.0–191.0 µm	35–55 µm
Costa	Distinctly delimited below, ending diffusely above at (40–)70% of leaf length to subpercurrent	Distinctly delimited, ending 50–65% of leaf length	Diffusely delimited, ending 25–80% way up leaf
Costa width near base	25.0–46.0 µm	27.5–54.5 µm	19.0–31.5 µm
Mid-leaf cell length	40.0–132.5 µm	27.5–86.0 µm	25.0–82.0(–89.0) µm
Seta ornamentation	Smooth or almost so	Rough	Slightly (only visible in compound microscope) to clearly rough

Discussion

The Azorean clade is interpreted as a new endemic species whose morphological characteristics are largely shared with other species of the genus, making it challenging to identify on morphological grounds. Traditionally, *Rhynchostegiella* has been divided into two groups of species, hereafter the *R. curviseta* and the *R. tenella* groups. The former is mainly characterized by rough setae; a laminal leaf cell length to width ratio <10; a leaf length to width ratio of 3–5; blunt leaf apices, and a preference for aquatic or sub-aquatic habitats. Species of the *R. tenella* group tend to occur in drier habitats. They exhibit a smooth seta (except *R. litorea*), the laminal leaf cell length to width ratio and the leaf length to width ratio are 10–20 and 6–10, respectively, and the leaf apex is long-acuminate (Dirkse & Bouman 1995). *Rhynchostegiella azorica* is variable in those features, with a seta that ranges from almost smooth to rough; a wide habitat preference, from the splash zone of waterfalls to dry forest rocks; a length to width ratio of the laminal cells that matches the one of the *R. curviseta* group; but a leaf apex that is typical of the *R. tenella* group. Since the eight accessions initially assigned to three of the four previously reported species in the Azores actually belong to *R. azorica*, this suggests that previous reports of four *Rhynchostegiella* species from Azores are erroneous and that a single, morphologically variable species, *R. azorica*, occurs in the archipelago.

Most often, new moss species revealed by molecular studies can be characterized by the combination of gametophytic and sporophytic traits (Medina *et al.* 2012, 2013). Although nobody welcomes the prospect of floods of new ‘species’ swamping the literature and herbaria and recognizable only using cytological or molecular techniques (see Kadereit *et al.* 2012 for review), the definition of species that, like *R. azorica*, are weakly characterized by their morphologies is, however likely to increase with the advance of molecular techniques. This is especially true in genera comprising aquatic species whose morphological variation can seriously mislead taxonomists due to convergence and plasticity (Olsson *et al.* 2009, Hutsemekers *et al.* 2012). In this context, molecular phylogenies offer a unique framework to revisit patterns of morphological evolution and identify the taxonomically relevant characters, and to supply taxonomists with easy, fast and cheap DNA ‘barcodes’ in those groups where strong overlap in morphological features among species render the use of such approaches necessary for a definitive identification (Stech *et al.* 2013).

Rhynchostegiella azorica is sister to the remainder of the species of the genus, whose most recent common

ancestor was dated at 4–20 Ma (myrs, Aigoïn *et al.* 2009b). This points to a more ancient origin as compared to other Macaronesian endemic species of the genus. Since *R. bourgeana* was reported from the Cadiz area (Guerra *et al.* 2014), Macaronesian endemic *Rhynchostegiella* species include *R. trichophylla* Dirkse & Bouman (1995: 110) and *R. macilenta* (Renauld & Cardot 1902: 440) Cardot (1905: 214–215), whose ancestor was dated at 2–14 and 0–1 myrs, respectively. The comparatively ancient origin of *R. azorica* raises the question of the origin of its endemism. All *Rhynchostegiella* species are bisexual and therefore, frequently fertile. Their spores are <20µm, a size that meets the critical condition for long-distance dispersal by wind (Wilkinson *et al.* 2012). The phylogenetic position of *R. azorica* renders the identification of its area of origin challenging. The sister clade of *Rhynchostegiella* is comprised of genera with a predominantly South or North American origin. This is reminiscent of the Neotropical origin of other Azorean endemic bryophytes (Vanderpoorten & Long 2006) and of striking disjunctions of species distributed in South or North America and the Azores (Rycroft 2003, Dias *et al.* 2009). One hypothesis for explaining the disjunctions with tropical areas is that (sub)tropical species exhibit a strong niche conservatism that prevent them from colonizing extra-tropical areas (Hettwer Giehl & Jarenkow 2012). Bryophyte taxa disjunct between the tropics and Macaronesia would hence not exhibit an ecological niche that would allow them to colonize continental Europe. Another hypothesis is that such disjunctions are caused by massive extinctions in Europe during the Quaternary glaciations.

While our results are inconclusive regarding the origin of the Azorean endemic *R. azorica*, they nonetheless highlight the extent to which the Azorean bryophyte flora still requires extensive taxonomic work. The unexpected discovery of new endemic species in a genus like *Rhynchostegiella* suggests that patterns of endemism in the Azorean bryophyte flora are not well estimated from traditional taxonomic knowledge. Schaefer *et al.* (2011) and Carine *et al.* (2012) highlighted that current knowledge of endemic seed plant diversity on oceanic islands may be far from complete. This certainly holds even more true in taxa with reduced morphologies like bryophytes, calling for a substantial broad-scale revision of the Azorean bryophyte flora in an ‘integrative taxonomy’ framework.

Taxonomy

Rhynchostegiella azorica Hedenäs & Vanderpoorten *sp. nov.* (Fig. 2)

Similar in leaf morphology to *R. curviseta* but differing from the latter by its long acuminate leaf apex. Characterized by one synapomorphic mutation from A to C in the *trnL* region and another from G to A in the *atpb_rbcL* spacer.

Holotype: PORTUGAL. Azores: Flores, between Mosteiro and Lajedo, 39°N24', 31°W14', on rocks within a lowland vegetation dominated by *Pittosporum undulatum*, *Erica azorica*, *Hedychium gardnerianum*, *Cyrtomium falcatum*, and *Selaginella kraussiana*, January 2009, Vanderpoorten FLOR2 (LG).

Plants tiny, rigid, wiry, green or dark green, irregularly and sometimes repeatedly branched. *Stem* without central strand, cortex of 2–3 layers of small and slightly incrassate cells, cells inside large, thin-walled or slightly incrassate; pseudoparaphyllia foliose, triangular; paraphyllia absent; rhizoids inserted below leaves, red-brown, not or weakly branched, smooth; axillary hairs 1–2 per axil, strictly axillary or inserted on stem shortly above leaf, with 1–2 upper cells, 7.5–8.5 µm wide, hyaline, basal cell short-rectangular, hyaline or pale brownish. *Stem leaves* erecto-patent to spreading, straight or somewhat homomallous, (0.20-)0.42–1.25 mm long, with a length to width ratio of 4.0–6.5, narrowly triangular, with long-acuminate apex (17–27 µm wide at 100 µm and 35–55 µm at 200 µm below apex), sometimes keeled near base, otherwise plane; costa single, ending 25–80% way up leaf, diffusely delimited, 19.0–31.5 µm wide near insertion, surface cells on both ad- and abaxial sides similar to adjoining lamina cells, smooth or occasionally ending in a spine; margin denticulate or finely and obtusely so above, entire or almost so below, plane; median lamina cells 25.0–82.0(-89.0) x 4.0–8.5 µm, linear, with a length to width ratio of 4–11 and shortly tapering ends, slightly incrassate, eporose, smooth; basal cells rectangular or elongate-rectangular, shorter and slightly wider than mid-leaf cells, incrassate or slightly so, eporose; alar cells undifferentiated from other basal cells or quadrate, shortly rectangular, or rectangular, slightly incrassate, eporose, and forming a weakly differentiated oblong group along leaf margin, extending from leaf margin 40–60% of distance to costa at insertion, not decurrent. *Branch leaves* similar to stem leaves or more strongly denticulate, proximal branch leaves triangular, acute or acuminate. *Autoicous*, or some shoots with only perichaetia. *Perigonia* laterally inserted on stem, intermixed with perichaetia; perigonial leaves from broad basal part suddenly narrowed to distinct acumen, acuminate; margin entire, bordered; paraphyses

present, thin-walled. *Perichaetia* laterally inserted on stem, inner perichaetial leaves straight and erect or upper leaf portions slightly homomalous or spreading, from narrowly triangular or oblong-triangular base gradually narrowed to narrowly acuminate apex, smooth; costa absent or single, very short and indistinct; margin irregularly finely denticulate above; paraphyses 3–5-celled, thin-walled, sparse. *Calyptra* cucullate, 2–3 stratose, cells homogeneous, smooth, naked. *Seta* 3–8 mm, red, slightly (visible in compound microscope) to clearly rough, with narrow central strand and a cortex of 2–3(–4) layers of small and incrassate cells, when dry untwisted or dextrorse. *Capsule* of *Brachythecium*-type or sometimes short-cylindrical and curved in transition to seta, not furrowed, not constricted below mouth when dry, orthogonal; lid rostrate; annulus separating, of (1-)2 rows of cells; exothecial cells 19–48 x 12–23 μm , varying around quadrate to rectangular, thin-walled, but strongly collenchymatous with superficial thickenings, below mouth 0–2 rows of small, transversely oblong to shortly rectangular cells; stomata round-pored. *Exostome* well developed, reddish orange, on lower outside cross-striolate, sometimes with minute papillae on top of striolations, above papillose, not furrowed, margin weakly dentate above, border narrow below, gradually disappearing above zone of transition in outside ornamentation, primary peristomial layer normally developed. *Endostome* basal membrane 36–46% of endostome height, endostome yellow, finely papillose above, very finely so below, cilia 1–2, when two often merged, longest ones as long as processes or almost so, nodose, processes narrow and narrowly (<3 μm) perforate. *Spores* 11.5–16.0 μm , almost smooth, mature in winter half-year.

Additional specimens seen: PORTUGAL. Azores: Flores, Fajazinha, Poço das Patas, 260m, 39°N25'15", 31°W14'08", January 2009, *Vanderpoorten* 12/2, 12/11, 12/25, 12/26 (LG); Flores: Faja Grande, 160m, 39°N29'00", 31°W15'19", January 2009, *Vanderpoorten* 14/3 (LG); Faial: 260m, 38°N45'22", 28°W45'37", 8 March 2012, *Vanderpoorten & Patino* RHY832 (LG); Terceira: Agualva, 70m, 38°N47'31", 27°W11'17", January 2009, *Vanderpoorten* 18/1 (LG); Faial, 1937, *H. Persson* sn (S-B196675); Faial, Cedros, 1000 m, 19 March 1992, *H. Greven* sn (herb. Dirkse 29583); Terceira, Santa Barbara, 24 April 1937, *H. Persson* sn, (S-B9092).

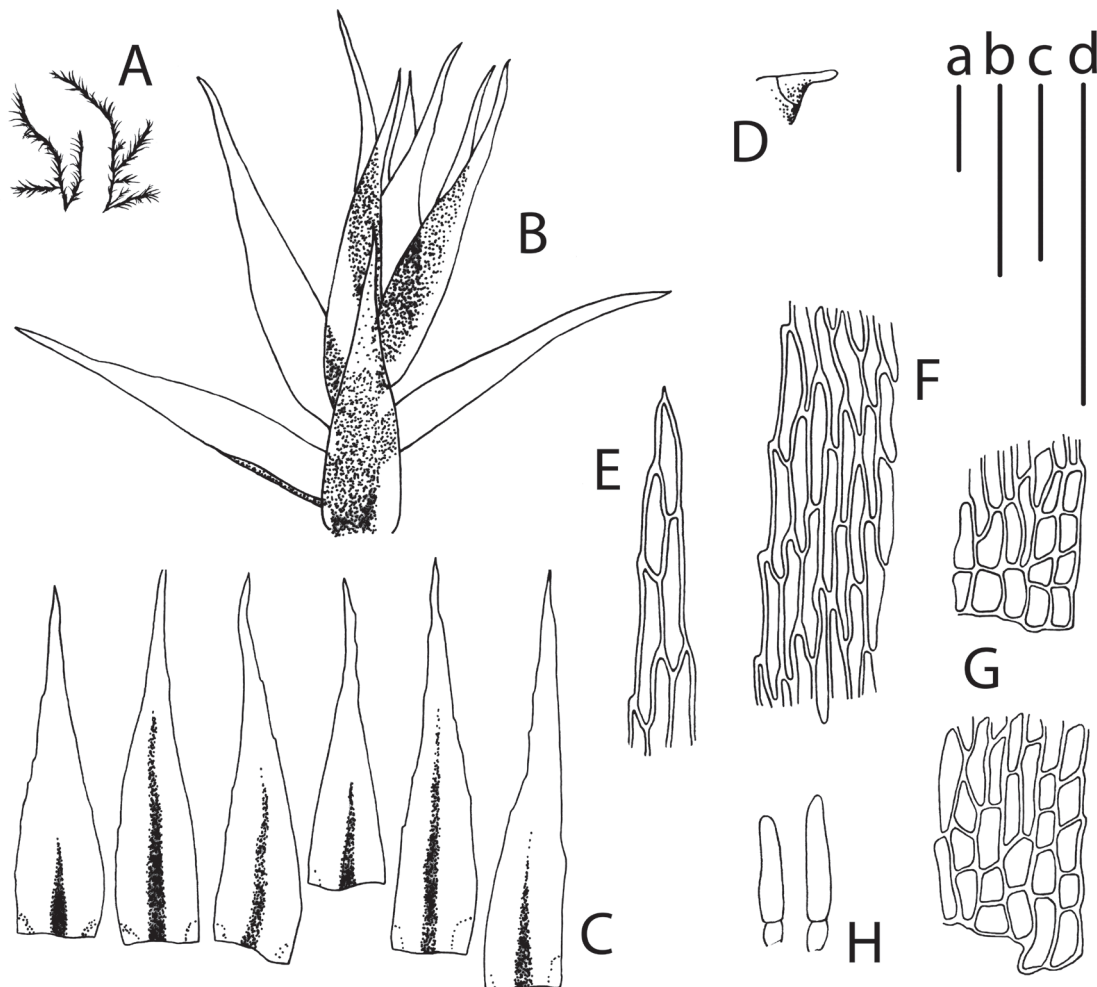


FIGURE 2. *Rhynchostegiella azorica* Hedenäs & Vanderpoorten (from *Vanderpoorten FLOR2*, holotype). A, habit; B, apex of branch; C, stem leaves; D, capsule lid; E, stem leaf apex; F, leaf lamina cells from mid-leaf; G, alar cells; H, axillary hairs. Scales: a, 2 cm (A); b, 2 mm (D); c, 100 μm (E–H); d, 450 μm (B, C).

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