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An integrative taxonomic revision of  
Aneuraceae H.Klinggr. (Marchantiophyta) from  
Guadeloupe and Martinique, French West Indies

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# An integrative taxonomic revision of Aneuraceae H.Klinggr. (Marchantiophyta) from Guadeloupe and Martinique, French West Indies

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## ABSTRACT

Identification of Aneuraceae H.Klinggr. from the West Indies is a challenge as a modern taxonomic treatment for the region is lacking. Here we present a revision of the species from Guadeloupe and Martinique using an integrative, morphological and molecular approach. We recognize seven species of *Riccardia* Gray (*R. chamedryfolia* (With.) Grolle, *R. fucoidea* (Sw.) C.Massal., *R. hymenophytoidea* (Spruce) Meenks, *R. innovans* (Steph.) Pagán, *R. regnellii* (Ångstr.) K.G.Hell, *R. schwaneckeii* (Steph.) Pagán, *R. stipatiflora* (Steph.) Pagán) and one species of *Aneura* Dumort. (*A. pinguis* (L.) Dumort.) based on examination of types and other collections, as well as on molecular species delimitation analysis using barcoding methods. All species are briefly discussed and illustrated, and a key to species is provided. *Riccardia diabolina* (Spruce) Pagán, *R. distans* (Spruce) Pagán, *R. grossidens* (Steph.) Pagán and *R. virgata* (Gottsche ex Steph.) Pagán are new synonyms of *R. fucoidea*, and *R. fendleri* (Steph.) Pagán, *R. planifrons* (Spruce) Pagán and *R. subsimplex* (Steph.) Pagán are new synonyms of *R. regnellii*.

## KEY WORDS

Liverworts,  
Aneuraceae,  
West Indies,  
species delimitation,  
integrative taxonomy,  
lectotypification,  
new synonyms.

## RÉSUMÉ

*Taxonomie intégrative des Aneuraceae H.Klinggr. (Marchantiophyta) de Guadeloupe et Martinique, Antilles françaises.*

L'identification des Aneuraceae H.Klinggr. des Antilles françaises est délicate car on ne dispose pas de traitement taxonomique complet pour la région. Nous présentons ici une révision des espèces de Guadeloupe et de Martinique, basée sur une approche intégrative, morphologique et moléculaire. Nous reconnaissons sept espèces de *Riccardia* Gray (*R. chamedryfolia* (With.) Grolle, *R. fucoidea* (Sw.) C.Massal., *R. hymenophytoides* (Spruce) Meenks, *R. innovans* (Steph.) Pagán, *R. regnellii* (Ångstr.) K.G.Hell, *R. schwaneckeii* (Steph.) Pagán, *R. stipatiflora* (Steph.) Pagán) et une espèce d'*Aneura* Dumort. (*A. pinguis* (L.) Dumort.), établies après l'examen des spécimens types et d'autres collections, ainsi que sur une délimitation d'espèces utilisant une approche moléculaire. Toutes les espèces sont brièvement discutées et une clé d'identification des espèces est proposée. *Riccardia diabolina* (Spruce) Pagán, *R. distans* (Spruce) Pagán, *R. grossidens* (Steph.) Pagán et *R. virgata* (Gottsche ex Steph.) Pagán sont des synonymes nouveaux de *R. fucoidea*, et *R. fendleri* (Steph.) Pagán, *R. planifrons* (Spruce) Pagán et *R. subsimplex* (Steph.) Pagán sont des synonymes nouveaux de *R. regnellii*.

**MOTS CLÉS**  
Hépatiques,  
Aneuraceae,  
Antilles françaises,  
délimitation d'espèces,  
taxonomie intégrative,  
lectotypification,  
synonymes nouveaux.

## INTRODUCTION

The Guadeloupe Archipelago and the island of Martinique are French overseas departments in the Lesser Antilles (West Indies) with a tropical moist climate. They are each characterized by the presence of an active volcano, La Soufrière (1467 m) on Guadeloupe and La Montagne Pelée (1397 m) on Martinique. Major changes in climate, soil and vegetation occur along an altitudinal gradient from the coast to the volcanic summits (Portécop 1979; Rousteau *et al.* 1996). Both islands are an integral part of the Caribbean biodiversity hotspot (Myers *et al.* 2000) and harbor a very rich bryophyte flora due, in part, to the presence of intact native rainforests.

Aneuraceae H.Klinggr. is a family of simple thalloid liverworts and notorious for expressing high variation in morphological characters and phenotypic polymorphy (e.g. Schuster 1992; Reeb & Gradstein 2020). Species from the West Indies have been reported by Husnot (1875), Spruce (1895), Stephani (1900), Duss (1904), Pagán (1939, 1942) and Meenks (1986, 1987). A first catalogue of the liverworts of Guadeloupe was published by Pagán (1942) who recorded 12 species of *Riccardia* Gray (Aneuraceae). As noted by Steere (1942: 75) in his obituary of F. M. Pagán: "Through his many collecting seasons [...] he had collected the species of *Riccardia* especially assiduously, with the plan of eventually preparing a monographic treatment of this difficult genus". The project never materialized due to the untimely death of Pagán in 1942 at the age of 45. As he had studied only little material from Guadeloupe and had not examined the type specimens, many of the *Riccardia* species recorded are now synonyms (this paper). In a recent checklist, Lavocat Bernard & Schäfer-Verwimp (2011) listed 13 species of Aneuraceae from Guadeloupe and eight from Martinique, all of them members of the genus *Riccardia*. Subsequently, four additional species of *Riccardia* as well as *Aneura pinguis* (L.) Dumort. were recorded from Guadeloupe (Lavocat Bernard & Reeb 2016) and four species of *Riccardia* from Martinique (Lavocat Bernard 2018).

Identification of Aneuraceae from the West Indies is a challenge as a modern taxonomic treatment for the region is lacking. Here we present a revision of the species from Guadeloupe and Martinique (French West Indies) using an integrative, morphological and molecular approach. We recognize seven species of *Riccardia* and one species of *Aneura* Dumort. based on examination of types and other collections, as well as on species delimitation analysis using barcoding methods (Kress & Erickson 2008; Puillandre *et al.* 2012).

## MATERIAL AND METHODS

We examined over 200 collections including type specimens from BM, G, MANCH and S and additional material from NY (leg. Duss, det. F. Pagán), PC (unidentified collections of Le Gallo) and the private herbaria of E. Lavocat Bernard (specimens ELB) and C. Reeb (specimens CR). The specimens of this study, kept in the herbarium of Elisabeth Lavocat-Bernard, will be deposited to the New York Botanical Garden (NY) with duplicates in Paris (PC). Morphological characters were defined following Reeb & Gradstein (2020). Consulted literature on Aneuraceae included Meenks & Pócs (1985), Meenks & de Jong (1985), Meenks (1987), Furuki (1991), Schuster (1992), Paton (1999), Gradstein & Costa (2003), Gradstein & Reeb (2018a, b), Reeb & Gradstein (2020), Gradstein (2021) and the unpublished treatment of Cuban Aneuraceae by J. D. L. Meenks (cited as "Meenks 1984" in Meenks 1986).

Molecular species delimitation analysis was conducted complementing the study of Rabeau *et al.* (2017). Molecular sampling included 24 specimens from the French West Indies collected by the two first authors as well as 33 specimens from other areas (South America, Europe, Africa, Asia), including four specimens of *Afroriccardia comosa* (Steph.) Reeb & Gradst. designated as outgroup in this study (Appendix 1). DNA was extracted according to the protocols described in Rabeau *et al.* (2017). Amplification of three chloroplastic

markers, *psbA-trnH*, *trnL-F* and *rps4*, was conducted and sequences were obtained by Sanger technology and/or using amplicon multiplex (Hinsinger *et al.* 2015). As the clustering results obtained for the three markers (for methods see below) were identical, they were concatenated and considered as a single locus.

Alignment of the three concatenated markers was built using MAFFT (Rozewicki *et al.* 2019) and slightly refined by hand. Ambiguous regions were removed using Gblocks (Castresana 2000), with the options “allow smaller final blocks” and “allow gaps in final blocks”, in order to include only unambiguous alignable regions in the final matrix.

*Riccardia* expresses major phenotypic plasticity, therefore morphological-taxonomic studies should preferably be combined with genetic analysis, in an integrative framework, in order to propose reliable species hypotheses (Dayrat 2005; Fontaneto *et al.* 2015; Reeb *et al.* 2018). The goal of the analysis is to partition the dataset (the samples) in a number of clusters, each of them considered as a potential species. When the partitions obtained with the different methods are not identical, a comparison is conducted using various combinatorial methods to arrive at the final species proposal (Debortoli *et al.* 2016).

Here we are using two types of partitioning methods, both using a threshold to delineate intra- and inter specific divergences (Renner *et al.* 2017): 1) distance-based methods with ABGD (Automatic Barcode Gap Discovery; Puillandre *et al.* 2012) and ASAP (Assemble Species by Automatic Partitioning; Puillandre *et al.* 2021); and 2) tree-based methods with bPTP (bayesian Poisson Tree Processes; Zhang *et al.* 2013) and GMYC (Generalized Mixed Yule Coalescent; Fujisawa & Barraclough 2013). The ABGD approach requires two user input values:  $P$ , maximum intraspecific distance, and  $X$ , a proxy for minimum gap width. Following Puillandre *et al.* (2012) the default value of  $X = 1.5$  and  $P$ -values was kept between 0.001 and 0.01, with Kimura distance chosen (identical reliable clusters were found with lower values until  $P_{max} = 0.005$ ). Results from recursive partition were retained because it gives the finest partition for a dataset (Puillandre *et al.* 2012).

ASAP is an ascending hierarchical clustering method merging sequences into “groups”, that are successively further merged until all sequences form a single group (Puillandre *et al.* 2021). From the original dataset, ASAP creates a first partition grouping sequences from ranked distances and merging them successively, building new partitions. For each new created partition, two indices are calculated: 1) the probability  $p$ -val of panmixia; and 2) a relative gap metric  $W$ . Then, the  $p$ -val (the smallest being of rank 1) and  $W$  (the largest being of rank 1) are respectively ranked, according to successive partitions; the ASAP score for a partition is the average of  $p$ -val and  $W$ . The lower the ASAP score, the more reliable is the hypothesis (for details see Puillandre *et al.* 2021). The ASAP output ranks the partitions and group sequences according a distance-based tree. We retained two ASAP scores with reasonable assumptions considering morphological species hypothesis, including 1) not excessive lumping between already well-recognized species; and 2) not excessive splitting within the dataset (see Results below and Appendix 2).

To conduct the GMYC analysis, an ultrametric tree was built from the concatenate alignment of *psbA-trnH*, *trnL-F*, *rps4* using BEAST2 software bundle (BEAUti, LogCombiner, TreeAnnotator, BEAST2) (Bouckaert *et al.* 2019) and Tracer. With BEAUti, three partitions corresponding to the three genes were defined; a GTR substitution model with six gamma categories and estimate I was chosen. A Yule speciation prior distribution was chosen for tree branch lengths (every lineage can speciate at the same rate, no extinction allowed) with a normal distribution. The tree was time-calibrated according the site mutation rate already used for bryophytes of 0.0005 mutations/sites/million year with a standard deviation of 0.000153 (Villarreal *et al.* 2014; Renner *et al.* 2017). Each MCMC was run for 30 millions generations with BEAST2. Three runs were conducted and their convergence was checked with Tracer1.7.2 (Rambaut *et al.* 2018). For this purpose, the three runs were combined with LogCombiner and synthesized in a maximum clade credibility tree with Treeannotator.

The same workflow was conducted under two clock models, strict and relaxedclock. As we could not reach convergence with relaxed clock, even after increasing to 50 millions MCMC generations, only the strict clock results with all effective sample sizes (ESS) > 200 were kept.

The GMYC analysis was conducted with RStudio with R4, R Core Team (2017) using the package splits (Ezard *et al.* 2012) and its dependances ape (Paradis & Schliep 2019), MASS (Venables & Ripley 2002) and paran (Dinno 2018) with the maximum credibility clade tree as input. Single (Pons *et al.* 2006) and multi threshold (Monaghan *et al.* 2009) GMYC analysis were conducted.

The molecular dataset was subsequently analyzed by bPTP (bayesian Poisson Tree processes; Zhang *et al.* 2013) through the bPTP species delimitation server (<https://species.h-its.org/>) with 500 000 generations; a RaxML tree obtained from the same data, using CIPRES was given as the input tree and the defaults parameters were kept. Convergence was verified by eyes, using the .pdf output of the bPTP server as specified by Zhang *et al.* (2013).

A conspecificity matrix was built from the partitions obtained by the four methods (ABGD, ASPAP, GMYC, PTP) and plotted with COMA (Spöri & Flot 2020), which allows the attribution of a weight to each partition. We used the same weight  $w = 10$  in each method, but if  $n$  partitions were kept for one method (such as the two best scores in ASAP) we attributed  $w/n$  weight for each partition, e.g. five for ASAP1 partition and five for ASAP2 partition. We also ran COMA without differentiated weights, but this yielded essentially the same clusters. Finally, the molecular species hypotheses were compared with morphologically-defined species, the partitions were plotted on the bayesian maximum credibility tree obtained by GMYC analysis, and final species hypotheses were proposed.

The proposed species hypotheses are presented in the taxonomic treatment. Additional species recorded from Guadeloupe and/or Martinique by Pagán (1942) that could not be confirmed in the present study are listed under “Further record” and “Excluded records”.

KEY TO THE GENERA OF ANEURACEAE H.KLINGGR. FROM GUADELOUPE AND MARTINIQUE

1. Thallus 3-8 mm wide, simple or scarcely branched, margins undulate to plicate. Gynoecia at the thallus margin, not on branches. Male branches with antheridia in 2-3(-6) rows ..... *Aneura* Dumort.
- Thallus less than 1.5 mm wide, regularly or irregularly pinnately branched, margins plane or somewhat undulate. Gynoecia on short lateral branches. Male branches with antheridia strictly in 2 rows ..... *Riccardia* Gray

KEY TO THE ACCEPTED SPECIES OF *RICCARDIA* GRAY FROM GUADELOUPE AND MARTINIQUE

1. Whole thallus with a conspicuous, whitish border of enlarged, hyaline cells ..... *R. schwaneckei* (Steph.) Pagán
- Whole thallus not bordered by enlarged, hyaline cells ..... 2
2. Main axis winged (plants prostrate, delicate. Axis 4-7 cells thick. Branch wings narrower than the costa, margins entire. Surface cells on branches often arranged in oblique rows. Dioicous, rarely paroicous) ..... *R. regnellii* (Ångstr.) K.G.Hell
- Main axis not winged ..... 3
3. Ultimate branches winged. Plants with or without basal stolons ..... 4
- Ultimate branches not or scarcely winged, often curved (when in doubt try both leads). Plants with basal stolons ..... *R. stipatiflora* (Steph.) Pagán
4. Branch wings as wide as or wider than the midrib, wing cells regularly arranged in a grid-like pattern ..... 5
- Branch wings narrower than the midrib, wings cells not regularly arranged in a grid-like pattern ..... 6
5. Plants robust, to 8-10 cm long, main axis erect or ascending and with a subepidermis, not stolon-like, 2-4-pinnately branched. Wing cells 35-50 µm wide ..... *R. fucoidea* (Sw.) C.Massal.
- Plants smaller, to 1-2 cm long, main axis prostrate and without subepidermis, stolon-like, palmately branched. Wing cells smaller, 15-30(-35) µm wide ..... *R. hymenophytoides* (Spruce) Meenks
6. Branch wings 2-5 cells wide, surface cells on branches often arranged in oblique rows. Branches often tongue-shaped ..... *R. regnellii* (Ångstr.) K.G.Hell
- Branch wings 1-2(-3) cells wide (lacking in older parts of the thallus), surface cells on branches in straight rows. Branches mostly linear ..... 7
7. Axis biconvex, very narrow, 0.15-0.25 mm wide, hardly wider than the branches. Dioicous ..... *R. innovans* (Steph.) Pagán
- Axis plano-convex, broader, 0.3-0.7 mm wide, distinctly wider than the branches. Epidemis cells not or scarcely narrower than medullary cells. Monoicous ..... *R. chamedryfolia* (With.) Grolle

RESULTS AND DISCUSSION

The original concatenated alignment was 1270 pb long, the final alignment after Gblocks treatment was 1050 pb long with 42.46% of the sites being parsimony-informative. The partition matrix (Appendix 3) shows the raw results of the partitioning based on the four methods employed. The number of species of *Riccardia* varied from 9 (ASAP1) to 27 (GMYC single threshold) (Fig. 1)

The recursive partition of ABGD yielded 14 species (Fig. 1). With ASAP, the first (2) and third best (= lower) scores (4.5) yielded, nine and 10 species, respectively (Appendix 2); the second and the fourth best scores, however, merged several morphologically very distinct species (*R. palmata* (Hedw.) Carruth., *R. gasparii* Reeb & Gradst., *R. crenulata* Schiffn., *R. multifida* (L.) Gray). As the subsequent ASAP scores (≥ fifth ranked) splitted the dataset in an unreasonably high number of species (> 38), we did not retain them.

With bPTP, 17 species hypotheses for *Riccardia* were obtained. However, the cluster of *R. stipatiflora* (Steph.) Pagán and *R. schwaneckei* (Steph.) Pagán was not recognized and each specimen was considered a different species. GMYC pro-

posed 18 to 27 species, respectively, for single and multiple thresholds and the cluster of *R. regnellii* (Ångstr.) K.G.Hell was split into several groups (Fig. 1).

The plotting of the conspecificity matrix with COMA, finally, yielded six species for Guadeloupe and Martinique (Figs 1; 2): *Riccardia schwaneckei*, *R. chamedryfolia* (With.) Grolle, *R. stipatiflora*, *R. regnellii*, *R. fucoidea* (Sw.) C.Massal. and *R. hymenophytoides* (Spruce) Meenks.

None of them were recovered by all four methods, however. With GMYC a few specimens that morphologically belonged to *R. stipatiflora* or *R. schwaneckei* were resolved into separate lineages, due possibly to missing or ambiguous data in the raw sequences of these specimens. COMA, however, unambiguously assigned them to these two species.

*Riccardia hymenophytoides* was detected as a separate lineage with ABGD, bPTP and GMYC, but not with ASAP, which resolved the species within the *R. fucoidea* clade. In the phylogenetic tree the two species appear as sister clades. Both stand out by having broad, transparent branch wings, with cells arranged in a grid-like pattern. The two species are clearly separated, however, by habit, axial anatomy, branching pattern and wing cells size, *R. fucoidea* having an erect axis



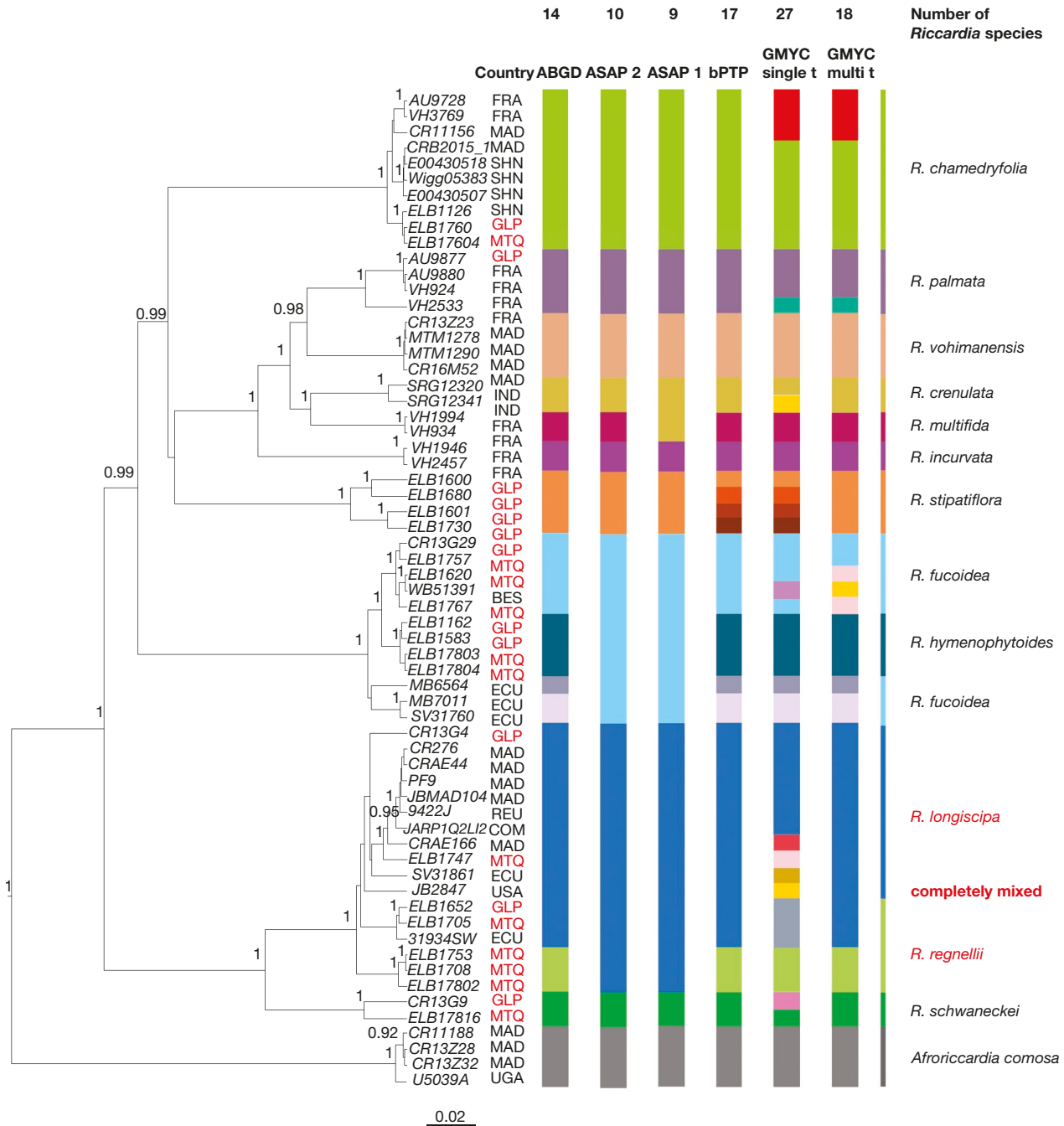


FIG. 1. — Species delimitation results plotted in regards of the Bayesian tree obtained with Beast for the GMYC analysis. Posterior probabilities > 0.9 were kept. The number for species proposed by each method is given in the highest line. Final species hypothesis are plotted on the right. Specimens from West Indies are colored in red. Abbreviations: ECU, Ecuador; REU, La Réunion; FRA, France; MAD, Madagascar; GLP, Guadeloupe; SHN, Saint Helena; MTQ, Martinique; USA, United States; COM, Comoros; IDN, Indonesia; UGA, Uganda; BES, Saba.

with a subepidermis and few stolons at the base only, pinnate branching and very large wing cells, while *R. hymenophytoides* has a prostrate axis without subepidermis and with numerous stolons, palmate branching and smaller wing cells. Moreover, they were distinct with COMA.

The taxonomic status of *R. regnellii* (synonym: *R. amazonica* (Spruce) Gradst. & Hekking), finally, was ambiguous in this study. In the phylogenetic tree some West Indian specimens (*ELB1753*, *17808*, *17802*) formed a clade corresponding to a cluster rec-

ognized by ABGD, bPTP and GMYC, but other West Indian specimens of the species (e.g. *ELB1652*, *17805*, *1747*) formed a lineage together with African material identified as *R. longispica* (Steph.) Pearson (Fig. 2). These results cast doubt on the separation of the neotropical *R. regnellii* and the African *R. longispica*. The latter species is a highly polymorphic species and very close to *R. angusticosta* Steph. from Africa, which in the past was considered conspecific with *R. regnellii* (Reeb & Gradstein 2020). The results of the present study suggest that the separation of the

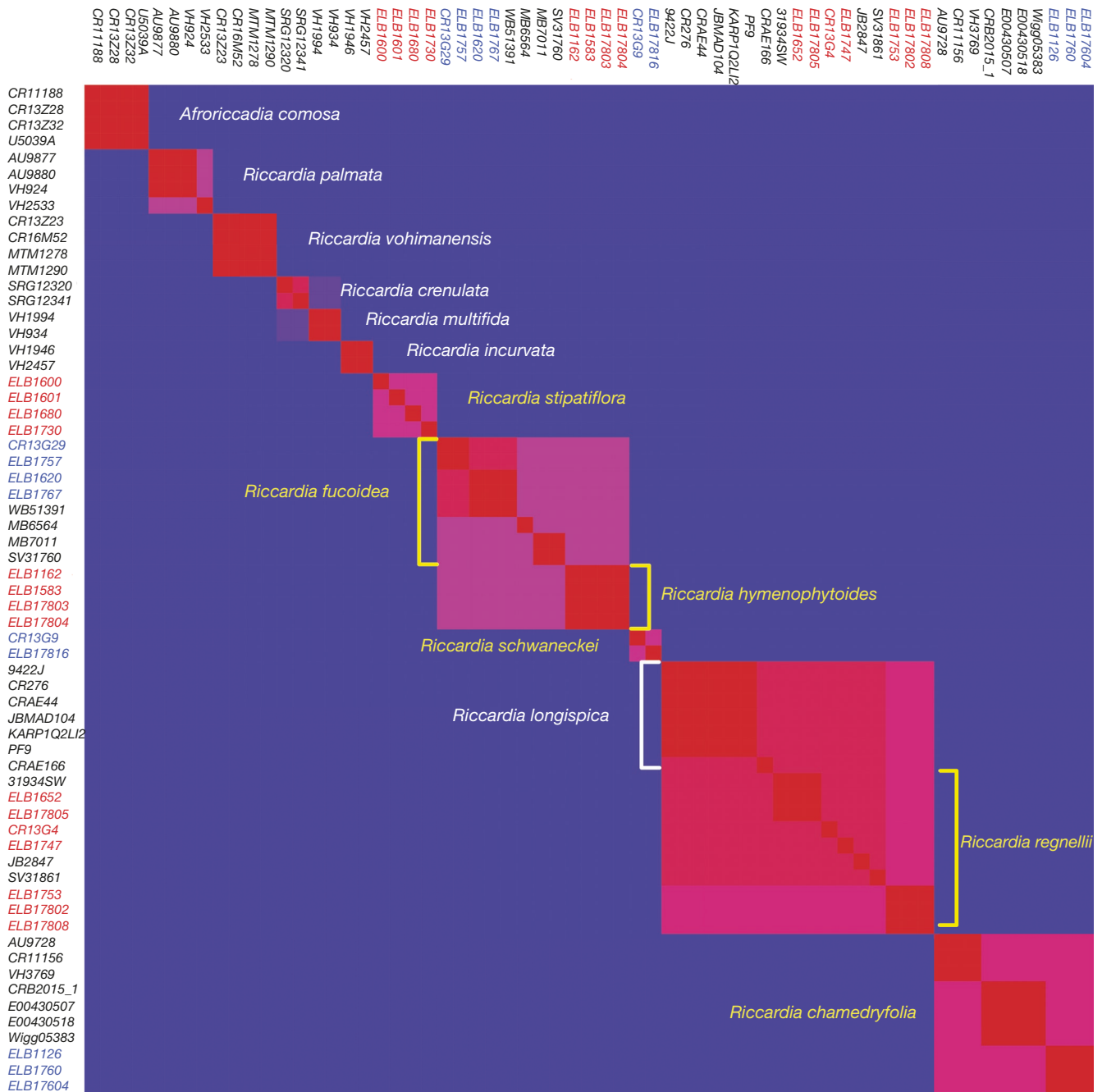


Fig. 2. — Conspecificity matrix built with COMA. Specimens from West Indies are colored in red and blue; species recorded in West Indies are colored in yellow; specimens outside of West Indies are colored in black; species not recorded in West Indies are colored in white.

neotropical and African populations of this complex into more than one species may not be warranted. If combined, the correct name of the Afro-american species would be *R. regnellii*, being the oldest name. We recommend further work on this group, using a broader, targeted sampling and additional markers.

Several species recently recorded from Guadeloupe and Martinique are missing in the molecular alignment/matrix. The rare *Riccardia innovans* (Steph.) Pagán endemic to Guadeloupe (Gradstein & Lavocat Bernard 2020), is not included because amplification of the extracted DNA failed. *Riccardia cataractarum* (Spruce) Schiffn., a South American species recorded

from Guadeloupe by Lavocat Bernard & Reeb (2016) and from Martinique by Lavocat Bernard (2018), is missing in the matrix because the sequenced material (*ELB1753*) was resolved in the *R. regnellii* cluster in the molecular analysis. Reexamination of the material showed that the material from the French West Indies was misidentified and belonged to *R. regnellii*. Based on the results of the integrative species delimitation analysis, we retain six species of Aneuraceae in the French West Indies: *Riccardia chamedryfolia*, *R. fucoidea*, *R. hymenophytoides*, *R. regnellii*, *R. schwaneckeii* and *R. stipatiflora*. In addition, *R. innovans* and *Aneura pinguis* (L.) Dumort. are recognized based on morphology.



## TAXONOMIC TREATMENT

Phylum MARCHANTIOPHYTA Stotler & Crand.-Stotl.  
Family ANEURACEAE H. Klinggr.  
Genus *Aneura* Dumort.

*Aneura pinguis* (L.) Dumort.

*Jungermannia pinguis* L., *Species Plantarum* 1: 1136 (1753). — *Aneura pinguis* (L.) Dumort., *Sylloge Jungermanniinearum Europae Indigenarum*: 86 (1831). — Type: Europe (Grolle 1976).

*Jungermannia sessilis* Spreng., in Linnaeus, *Systema Vegetabilis* (ed. 16) 4: 232 (1827). — *Aneura sessilis* (Spreng.) Gottsche, Lindenb. & Nees, *Synopsis Hepaticarum*: 495 (1845). — Type: Haiti. (“Hispaniola”), *Bertero s.n.* (n.v.); syn. *vide* Stephani (1900).

SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. — **Guadeloupe**. National Park of Guadeloupe, Carbet Falls, Capesterre Belle-Eau, 16°02'38"N, 61°38'29"W, 637 m, 28.VII.2013, *Lavocat Bernard & Reeb ELB1890*; Mamelle de Pigeon, Bouillante, 16°10'N, 61°44'W, 519 m, 08.II.2013, *Reeb & Lavocat Bernard CR13G49*.

DISTRIBUTION AND HABITAT. — Subcosmopolitan; in the West Indies reported from Cuba, Haiti, Dominican Republic, Puerto Rico, Guadeloupe, Dominica and St. Vincent (Stephani 1900; Gradstein 1989; Schäfer-Verwimp 2010; Lavocat Bernard & Reeb 2016). *Aneura pinguis* was first collected in Guadeloupe by L'Herminier (Stephani 1900) and its presence in the island was confirmed by Lavocat Bernard & Reeb (2016). In Guadeloupe the species grows on the faces (mostly top) of small boulders along paths (e.g. Mamelle de Pigeon) as well as on decaying logs.

ILLUSTRATIONS. — Schuster (1992), Paton (1999), Gradstein *et al.* (2001).

## REMARKS

*Aneura pinguis* is characterized by the fleshy, 3-8 cm wide, glossy green thallus with undulate to plicate margins, plano-convex in cross section, 9-20 cells thick. Fungal endosymbiotes are present in the ventral cells rows. The plants are dioicous; male branches have antheridia in 2-3(-6) irregular rows and are sometimes 2-3 divided; gynoecia are produced below the thallus margin, beneath the notch of a lateral branch and hidden by a small expansion of the thallus, and the archegonia are protected by shiny and scaly paraphyses.

The taxonomy of the genus *Aneura* is not clear (Wachowiak *et al.* 2007; Wawrzyniak *et al.* 2018; Reeb & Gradstein 2020), but according to current knowledge the specimens from Guadeloupe should be called *A. pinguis*. *Aneura latissima* Spruce, the other accepted species of *Aneura* in the Neotropics and known from tropical South America and also from Africa (Reeb & Gradstein 2020), differs by having a thinner (5-8 cells thick), darker green thallus.

Genus *Riccardia* Gray*Riccardia chamedryfolia* (With.) Grolle

*Jungermannia chamedryfolia* With., *A Botanical Arrangement of all the Vegetables Naturally Growing in Great Britain* 2: 699 (1776). —

*Riccardia chamedryfolia* (With.) Grolle, *Transactions of the British Bryological Society* 5 (4): 772 (1969). — Type: England (Grolle 1976).

*Jungermannia sinuata* Dicks., *Fasciculus Plantarum Cryptogamicarum Britanniae* 2: 16 (1790), nom. illeg. — *Jungermannia multifida* var. *sinuata* Hook., *British Jungermanniae*: tab. 45 (1813). — *Riccardia sinuata* (Hook.) Trevis., *Memorie della Reale Istituto Lombardo di Scienze e Lettere Serie* 3, 4: 431 (1877). — Type: England.

SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. — **Guadeloupe**. Aire de Beausoleil, Saint-Claude, 16°01'53"N, 61°40'50"W, 750 m, 08.IV.2009, *Lavocat Bernard 1126*; Carbet Falls trail, 16°02'40"N, 61°38'31"W, 640 m, 27.VI.2017, *Lavocat Bernard 17604*; La Madeleine, Trois-Rivières, 16°00'30"N, 61°38'00"W, 640 m, 22.VIII.2016, *Lavocat Bernard 16854*; Sentier Mamelle Pigeon, 16°10'N, 61°44'W, 580 m, 08.II.2013, *CR13G53*, *CR13G56bis*.

**Martinique**. Mount Pelée, trail of Grande Savane, 14°48'36"N, 61°10'14"W, 1160 m, 09.VIII.2012, *Lavocat Bernard 1744*, 1760.

DISTRIBUTION AND HABITAT. — Widespread in temperate regions of the Northern Hemisphere, scattered in the Tropics. In the Neotropics recorded from the West Indies, Brazil and the northern Andes (Gradstein & Reeb 2018b), growing on bark and rock in humid habitats at middle to high elevation. In the West Indies the species is known from Cuba (Meenks unpubl.), Saba (*Buck 52491*, NY; det. SRGr), Jamaica (Söderström *et al.* 2011), Guadeloupe (Pagán 1942 as *R. sinuata*; Lavocat Bernard & Schäfer-Verwimp 2011), Martinique (Lavocat Bernard 2018) and possibly from further islands.

ILLUSTRATIONS. — Gradstein & Reeb (2018b), Reeb & Gradstein (2020).

## REMARKS

*Riccardia chamaedryfolia* is a rather widespread, autoicous species that is recognized by the prostrate, 0.3-0.6 mm wide and 1-2 cm long, irregularly 1(-2)-pinnate thalli without stolons, a 4-7(-8) cells thick, plano-convex to concavo-convex axis without wing, and the linear to tongue-shaped, narrowly winged branches, the wings 1-2(-3) cells wide. The epidermis cells are scarcely smaller than inner thallus cells and oil bodies are present in all epidermis cells (Gradstein & Reeb 2018b; Reeb & Gradstein 2020). The species is highly polymorphic and may be confused with *R. cataractarum*, a semi-aquatic South American species that was recently recorded from the French Antilles (Lavocat Bernard & Reeb 2016; Lavocat Bernard 2018). The latter species, however, is dioicous and has an axis that is biconvex in the lower half (plano-convex above), with long ± wingless vegetative branches and broadly winged sexual branches (Gradstein & Reeb 2018b; Gradstein 2021). When sterile, separation of the two species may be difficult although *R. chamedryfolia* has mostly plano- to concavo-convex thalli (rarely biconvex in older portions of plants from Great Britain; Paton 1999). Molecular species delimitation shows conserved sequences for the amplified markers of *R. chamedryfolia* (Rabeau *et al.* 2017). In the present study the *R. chamedryfolia* cluster is very well defined with each method used (Fig. 1).

*Riccardia fucoidea* (Sw.) C.Massal.

*Jungermannia fucoidea* Sw., *Nova genera et Species Plantarum seu Prodrromus*: 145 (1788). — *Riccardia fucoidea* (Sw.) C.Massal.,

*Nuovo Giornale Botanico Italiano* 17: 256 (= Epat. Terra del Fuoco) (1885). — Type: **Jamaica**. Swartz s.n. (holo-, S!).

*Aneura virgata* Gottsche ex Steph., *Hedwigia* 27: 277 (1888). — *Riccardia virgata* (Gottsche ex Steph.) Pagán, *The Bryologist* 42: 7 (1939). — Type: **Guadeloupe**. L'Herminier s.n. (holo-, G[G00114872]!), syn. nov.

*Aneura diabolina* Spruce, *Journal of the Linnean Society, Botany* 30: 366 (1895). — *Riccardia diabolina* (Spruce) Pagán, *The Bryologist* 45: 80 (1942). — Type: **Dominica**. Mt. Diablotín, on tree trunks, 4000 ft., X.1892, W. R. Elliott 699 (holo-, BM[BM013777342]!), syn. nov.

*Aneura distans* Spruce, *Journal of the Linnean Society, Botany* 30: 367 (1895). — *Riccardia distans* (Spruce) Pagán, *The Bryologist* 45: 80 (1942). — Type: **Dominica**. Mt. Trois Pitons, on tree trunks, 2500 ft., XI.1892, W. R. Elliott 763 (holo-, BM[BM013777341]!), syn. nov.

*Aneura grossidens* Steph., *Hedwigia* 32: 23 (1893). — *Riccardia grossidens* (Steph.) Pagán, *The Bryologist* 45: 80 (1942). — Type: **Guadeloupe**. L'Herminier s.n. (lecto-, fide Bonner [1962], G; n.v.), syn. nov.

SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. — **Guadeloupe**. Bois du Matouba de long de la rivière Rouge, 807 m, *A. Duss* 358, det. F. M. Pagán as *R. virgata* (NY[00611576]); Morne Pérou, Pointe Noire, 1903, *A. Duss* 75 (NY[04117505, 04117507]), 1160 (NY[04117508]); Chutes du Galion, Soufrière area, 16°01'50"N, 61°39'44"W, 820 m, 20.IX.2002, *Lavocat Bernard* 420; Carmichael trail, Soufrière area, 16°02'57"N, 61°39'42"W, 1300 m, 07.V.2007, *Lavocat Bernard* 717, 718; Soufrière, 16°02'36"N, 61°40'01"W, 1255 m, 24.VII.2013, *Lavocat Bernard* 1872, 1876; Carbet Falls, 16°02'38"N, 61°38'29"W, 637 m, 28.VII.2013, *Lavocat Bernard* 1891. **Martinique**. Bois du Lorrain, le long de la rivière de ce nom, 610-630 m, *A. Duss* 359 as *R. virgata* (NY[00611575]); Mount Pelée, trail of Grande Savane, 14°48'46"N, 61°10'14"W, 1150 m, 09.VIII.2012, *Lavocat Bernard* 1757, 1767; Rivière Picodo, Case L'Étang, Le Prêcheur, 14°47'46"N, 61°11'52"W, 200 m, 04.IV.2012, *Lavocat Bernard* 1620.

DISTRIBUTION AND HABITAT. — Widespread and common in the mountains of tropical America, up to about 4000 m (Gradstein & Reeb 2018b), occurring in bark, rock and humic soil. In the West Indies reported from Cuba, Jamaica, Puerto Rico, Dominica, Grenada, Guadeloupe and Martinique (Meenks 1987).

ILLUSTRATION. — Gradstein & Reeb (2018b).

#### REMARKS

*Riccardia fucoidea* is usually dioicous (very rarely autoicous) and recognized by the robust, to 8-10 cm long, ascending to erect, regularly 3-4-pinnate thalli with a thick, rounded axis without wing (rarely rudimentarily winged), with a subepidermis and with short stolons at the base. All branches are broadly winged, the wings are 3-7 cells wide, made up of large hexagonal cells in a regular, grid-like arrangement, c. 35-50 µm wide and 40-75 µm long, vanishing before the apex on ultimate branches, wing margins entire or toothed (Gradstein & Reeb 2018b). Among the new synonyms, *R. virgata* represents typical *R. fucoidea*, *R. diabolina* is a phenotype with wing cells with conspicuous trigones, and *R. distans* is a laxly pinnate phenotype of which Stephani (1900: 221) already wrote: "ob diese Pflanze nicht eine sehr laxe Form von Aneura fucoides ist". The type of *R. grossidens* (*Aneura grossidens*) is

clearly *R. fucoidea*. The material of *R. grossidens* recorded from Martinique by Lavocat Bernard (2018) belongs to *R. fucoidea*. For molecular data, see the remarks on *R. hymenophytoides*.

#### *Riccardia hymenophytoides* (Spruce) Meenks

*Aneura hymenophytoides* Spruce, *Transactions & Proceedings of the Botanical Society of Edinburgh* 15: 549 (1885). — *Riccardia hymenophytoides* (Spruce) Meenks, *Nova Hedwigia* 88: 101 (1987). — Type: **Peru**. Mt. Campana, 1200 m, *Spruce s.n.* (lecto-, designated by Gradstein & Reeb [2018b], G[G00282970]!).

*Aneura sprucei* Steph., *Buletin de l'Herbier Boissier* 5: 844 (1897). — *Riccardia sprucei* (Steph.) Meenks & C. De Jong, *Cryptogamie, Bryologie Lichénologie* 6: 22 (1985). — Type: **Venezuela**. "Río Cauapuna, Fl. Negro", *Spruce s.n.* (lecto-, designated by Meenks & de Jong [1985], MANCH[MANCH-cc1700]!); syn. fide Gradstein & Reeb (2018b).

SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. — **Guadeloupe**. Carbet Falls, 16°02'41"N, 61°38'30"W, 640 m, 28.VII.2013, *Lavocat Bernard & Reeb* 1894; Forêt des Bains Jaunes, 16°01'49"N, 61°40'45"W, 750 m, 07.IX.2009, *Lavocat Bernard* 1162; Rivière La Rose, Goyave, 16°08'25"N, 61°36'33"W, 110 m, 06.II.2012, *Lavocat Bernard* 1583; Forêt de Frèdy, Goyave, 16°06'23"N, 61°35'56"W, 158 m, 03.VII.2017, *Lavocat Bernard* 17704.

**Martinique**. Morne Tranchette, Morne Vert, 14°41'55.5"N, 61°07'19.6"W, 760 m, 08.VIII.2017, *Lavocat Bernard* 17803, 17804.

DISTRIBUTION AND HABITAT. — A widespread neotropical species, occurring on shaded, often lateritic soil banks and on rotten wood at low to mid elevations. Recorded from the tropical Andes (Venezuela to Bolivia), the Guianas, Brazil and the West Indies (Gradstein & Reeb 2018b). In the West Indies reported from Puerto Rico and the Virgin Islands (Gradstein 1989), Cuba and Haïti (Meenks 1987), the Dominican Republic (Schäfer-Verwimp & Pócs 2009) and Guadeloupe (Lavocat Bernard & Reeb 2016). New to Martinique.

ILLUSTRATIONS. — Gradstein & Ilkiu-Borges (2009 as *R. sprucei*), Gradstein & Reeb (2018b).

#### REMARKS

*Riccardia hymenophytoides* is a heteroicous (autoicous or dioicous) species that is recognized by rather small, to 1-2 cm long thalli with a creeping, wingless, stolon-like, palmately branched axis without subepidermis and with ascending, flat, linear or tongue-shaped branches with broad transparent wings, the wings 4-8 cells wide, broader than the midrib, margins entire, wing cells rather small, 15-30(-35) µm wide. All thallus cells thin-walled and the epidermis cells of the axis are much smaller than medullary cells. Although the species was nested in *R. fucoidea* in the molecular analysis (Rabeau et al. 2017; this paper), it is retained as a separate taxon. The GMYC method, which highlights supposed coalescence events, shows a difference in clustering among *R. fucoidea* and *R. hymenophytoides* (Figs 1; 2). *Riccardia hymenophytoides* clearly differs from *R. fucoidea* on having a creeping axis without subepidermis and palmate branching. Moreover, the wing cells in *R. hymenophytoides* are much smaller than those in *R. fucoidea*. *Riccardia sprucei* is a rather delicate, monoicous phenotype of *R. hymenophytoides* from low elevation (Gradstein & Reeb 2018b).



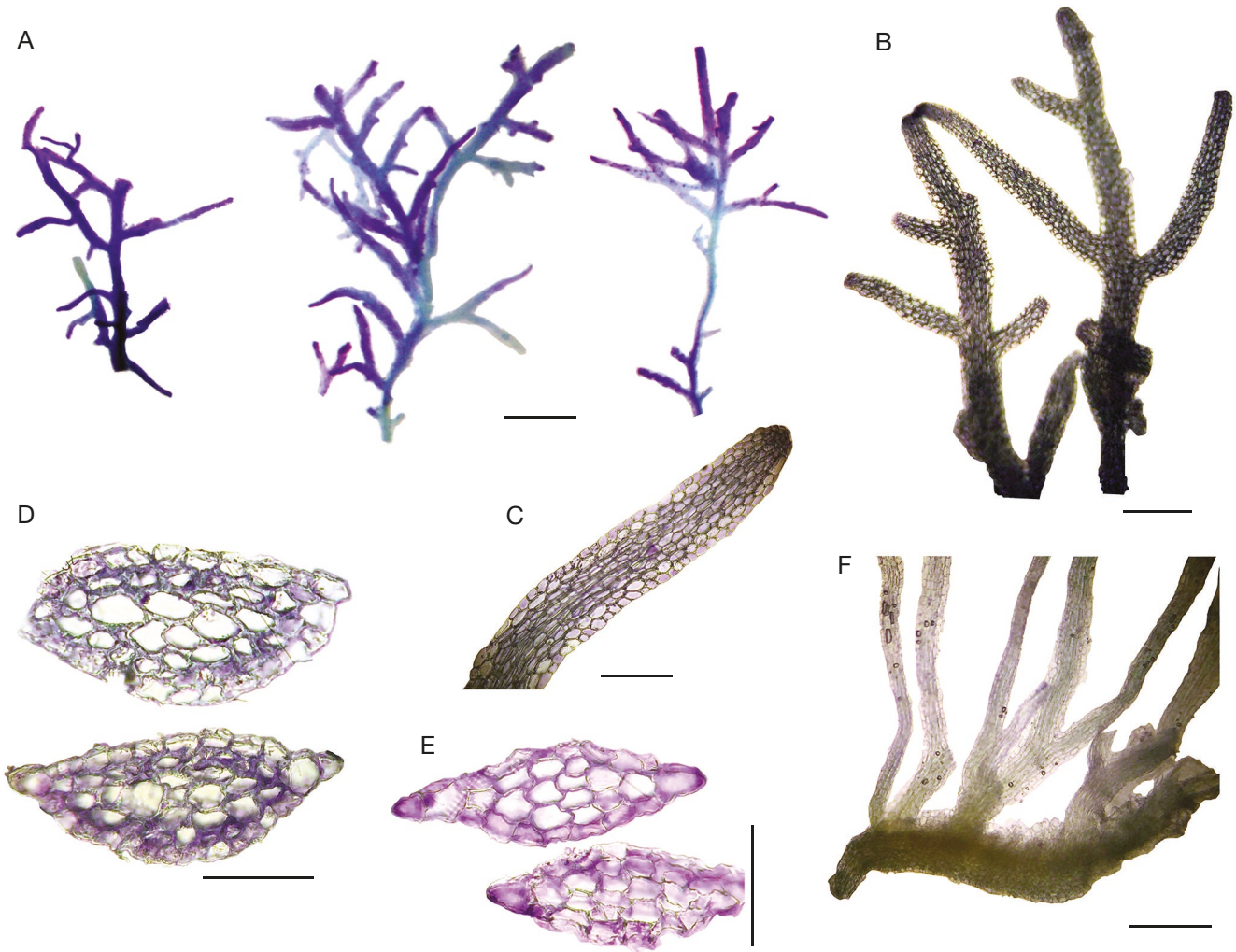


FIG. 3. — *Riccardia innovans* (Steph.) Pagán: **A**, isolated thalli (bleach + methylen blue coloration); **B**, branching patterns; **C**, ultimate branch; **D**, main axis cross section; **E**, ultimate branches cross section; **F**, vegetative innovations along female branch. All from the lectotype A. *Duss 484*. Scale bars: A, 1 mm; B, F, 500 µm; C, 250 µm; D, E, 100 µm.

*Riccardia innovans* (Steph.) Pagán  
(Fig. 3)

*Aneura innovans* Steph., in Urban, *Symbolae Antillarum* 2: 470 (1901). — *Riccardia innovans* (Steph.) Pagán, *The Bryologist* 45: 80 (1942). — Type: **Guadeloupe**. Savane-à-Mulets, “sur les arbrisseaux”, 1901, with *R. chamaedryfolia*, A. *Duss 484*, ex hb. Urban (lecto-, designated by Gradstein & Lavocat-Bernard [2020], G[G00066662]!, c.gyn.; isolecto-, NY[00611716]!).

ADDITIONAL SPECIMEN EXAMINED. — **Guadeloupe**. Carbet Falls, 16°02'45"N, 61°38'40"W, 910 m, 28.VII.2013, on humid, sloping soil, *Lavocat Bernard & Reeb 1901*.

DISTRIBUTION AND HABITAT. — Only known from Guadeloupe, growing on bark or soil.

FURTHER ILLUSTRATION. — Gradstein & Lavocat Bernard (2020).

REMARKS

*Riccardia innovans* is a very rare endemic species of Guadeloupe that is characterized by the delicate, 2-pinnate plants with a very narrow, only 0.15–0.25 mm wide, biconvex,

almost wingless axis and numerous long and narrow, linear to subulate branches. The branches are only a little narrower than the axis, plano-convex, obliquely to widely spreading, usually tapering to narrow tips, and narrowly winged by 1–2 cell wide wings. The presence of small scales on the calyptra, made up of large cells, may be a further characteristic of the species. The plants are dioicous; gemmae have not been observed. *Riccardia innovans* approaches *R. regnellii*, but the latter is a larger plant with a flat axis (not biconvex) and with broader, frequently tongue-shaped branches. In the type material, some *R. regnellii* plants are growing mixed in the dense mat of *R. innovans* and are immediately recognized by their much larger size (Gradstein & Lavocat Bernard 2020).

The isolectotype of *R. innovans* (NY) has long, thin and vegetative innovations looking as ultimate branches, all along the female branch (Fig. 3F); this could be also a retained character for the species. *Riccardia innovans* is hitherto only known from the type specimen and a single recent collection made by the first two authors in 2013. Unfortunately, the latter material could not be amplified molecularly.



*Riccardia regnellii* (Ångstr.) K.G.Hell

*Pseudoneura regnellii* Ångstr., *Öfversigt af Kongliche Vetenskaps-Akademien, Förhändlinger* 33: 90 (1876). — *Riccardia regnellii* (Ångstr.) K.G.Hell, *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Botânica* 25: 110 (1969). — Type: **Brazil**. Minas Gerais, Caldas, *Regnell s.n.* (lecto-, designated by Gradstein & Reeb [2018a], S-B260631!; isolecto-, G[G00282990]!).

*Aneura amazonica* Spruce, *Transactions & Proceedings of the Botanical Society of Edinburgh* 15: 545 (1885). — *Riccardia amazonica* (Spruce) Gradst. & Hekking, *Journal of the Hattori Botanical Laboratory* 45: 129 (1979). — Type: **Venezuela**. San Carlos del Río Negro, “in trunco putrido”, *Spruce H16* (lecto-, designated by Meenks & Pócs [1985], MANCH[MANCH-cc1680]!); syn. *vide* Gradstein & Reeb (2018a).

*Aneura fendleri* Steph., *Hedwigia* 32: 20 (1893). — *Riccardia fendleri* (Steph.) Pagán, *The Bryologist* 45: 80 (1942). — Type: **Trinidad**. *Fendler s.n.* (lecto-, designated here, G[G00066647]! autoicous). **Guadeloupe**. *Marie s.n.* (syn-, n.v.), **syn. nov.**

*Aneura subsimplex* Steph., *Hedwigia* 32: 27 (1893). — *Riccardia subsimplex* (Steph.) Pagán, *The Bryologist* 45: 81 (1942). — Type: **Cuba**. *Wright s.n.* (holo-, G[G000066692]!), **syn. nov.**

*Aneura planifrons* Spruce, *Journal of the Linnean Society, Botany* 30: 368 (1895). — *Riccardia planifrons* (Spruce) Pagán, *The Bryologist* 45: 80 (1942). — Type: **St. Vincent**. “in monte St. Andreae, ad Musarum vaginas marcescentes”, II.1892, *W. R. Elliott 145* (not found), **syn. nov.**

**SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. Guadeloupe.** Matouba, rivière Rouge, 650 m, 14.I.1961, *Le Gallo 1760*, small form from lateritic soil (PC); St. Marie, Capesterre, 22.II.1962, *Le Gallo 1292, 1269, 1298*, small forms from lateritic soil (PC); Moscou, Palmiste, 620 m, 01.III.1962, *Le Gallo 1293* (PC); “sur les arbrisseaux”, Morne Graine Verte, Matelyane, *A. Duss 71*, det. Pagán as *A. planifrons* (NY[00790036]); Rivière Quiock, 16°10'48"N, 61°41'35"W, 200 m, 10.IV.2011, *Lavocat Bernard 1436*; Carbet Falls, 16°02'48"N, 61°38'53"W, 870 m, 24.IV.2012, *Lavocat Bernard 1652*; 16°02'41"N, 61°38'30"W, 640 m, 28.VII.2013, *Lavocat Bernard 1895*.

**Martinique.** Bois du Lorrain entre la Champ Flore et du Lorrain, 650 m, *A. Duss 312* (NY[790038]), 442 (NY), 490 (NY); Mount Pelée, 14°48'36"N, 61°10'14"W, 1160 m, 9.VIII.2012, *Lavocat Bernard 1747*; 14°48'44"N, 61°09'48"W, 1205 m, 19.V.2014; 14°48'46"N, 61°09'47"W, 1245 m, 19.V.2014; Morne Tranchette, Morne Vert, 14°41'52"N, 61°07'25"W, 660 m, 8.VIII.2017, *Lavocat Bernard 17802*; Piton Lacroix, 14°41'52"N, 61°07'10"W, 800 m, 8.VIII.2017, *Lavocat Bernard 17808, 17829*.

**DISTRIBUTION AND HABITAT.** — Widespread in tropical America, occurring on soil, shaded rock and decaying wood in lowland and montane rainforests up to the páramo belt. The species has also been recorded from Africa but the African material belongs to *R. longispica* (Steph.) Pearson (Gradstein & Reeb 2018a; Reeb & Gradstein 2020). In the West Indies reported from the Dominican Republic (Schäfer-Verwimp & Pócs 2009), Guadeloupe (Lavocat Bernard & Reeb 2016) and Martinique (Lavocat Bernard 2018).

**ILLUSTRATIONS.** — Gradstein & Ilkiu-Borges (2009), Gradstein & Reeb (2018b).

**REMARKS**

*Riccardia regnellii* is a common and very variable, heteroicous (dioicous or monoicous) neotropical species that is recognized by prostrate, irregularly 1-2-pinnate thalli (0.3-0.6 mm wide

and to 1.5 cm long) without stolons, a 3-7 cell thick, plano-convex axis without or with a narrow wing, and tongue-shaped or linear, flat, broadly winged branches. The epidermis cells are smaller than the inner cells, the branch wings are narrower than the costa and the surface cells of the branches are often arranged in oblique rows. Dioicous plants are sexually dimorphous with male thalli being slightly smaller and more elongate than female thalli; the two types of thalli may occur mixed in the same mat (Gradstein & Reeb 2018a, b).

*Riccardia fendleri* and *R. subsimplex* are an autoicous, West Indian phenotype of *R. regnellii* with winged male branches (wing 1-3 cells wide). Possibly this phenotype deserves recognition as a separate variety; this need further study.

Pagán (1942) recorded *R. subsimplex* from Guadeloupe and Martinique but the material on which these records were based (*A. Duss 182*, NY[611574]; *182a*, NY[611573]; *457*, NY) belongs to *R. stipatiflora*.

*Riccardia planifrons* was originally described from St. Vincent; we have not been able to locate the type material of the species, it is lacking in MANCH (Spruce herbarium), BM and G. A putative type specimen received on loan from BM (BM013777343) with the collection number of the holotype, “*W. R. Elliott 145*”, was from a different location, “on dead palm leaves at the foot of Souffrière Mt.”, and contained *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans and cyanobacteria, but no *Riccardia*. Based on the original description and the illustration of the type (Stephani 1985), we believe that *R. planifrons* is a synonym of *R. regnellii*. Indeed, the material recorded from Guadeloupe (*A. Duss 71*, NY[790036]) by Pagán (1942) belongs to *R. regnellii*.

In Guadeloupe *R. regnellii* varies considerably in size and plants from lateritic soil are smaller and less elongate than those growing on bark and rotten wood (observed in plants collected by Le Gallo). The small terrestrial phenotype might be described as a different form, similar to *R. longispica* (Steph.) Pearson fo. *erosa* Reeb & Gradst. from Africa (Reeb & Gradstein 2020). This needs further study based on material from throughout the range of *R. regnellii*. The molecular clustering reflects the geographic differentiation between Africa and the Neotropics, mainly due to GMYC analysis (Fig. 1) resulting in a larger cluster grouping the two species (Fig. 2).

The specimens from the French Antilles recorded as *R. cataractarum* by Lavocat Bernard & Reeb (2016) and Lavocat Bernard (2018) belong to *R. regnellii*.

*Riccardia schwanecke* (Steph.) Pagán  
(Fig. 4G-M)

*Aneura schwanecke* Steph., *Hedwigia* 27: 278 (1888). — *Riccardia schwanecke* (Steph.) Pagán, *The Bryologist* 42: 7 (1939). — Type: **Puerto Rico**. *Schwanecke 55* (holo-, G[G00066688]! c.gyn., dioicous).

**SPECIMENS EXAMINED FROM THE FRENCH ANTILLES. — Guadeloupe.** Karukéra trail, 16°02'30"N, 61°38'38"W, 700 m, 28.II.2012, *Lavocat Bernard 1599*; La Soufrière, 16°02'40"N, 61°40'02"W, 1250 m, 24.VII.2013; *Lavocat Bernard & Reeb 1863, 1864, 1874*,

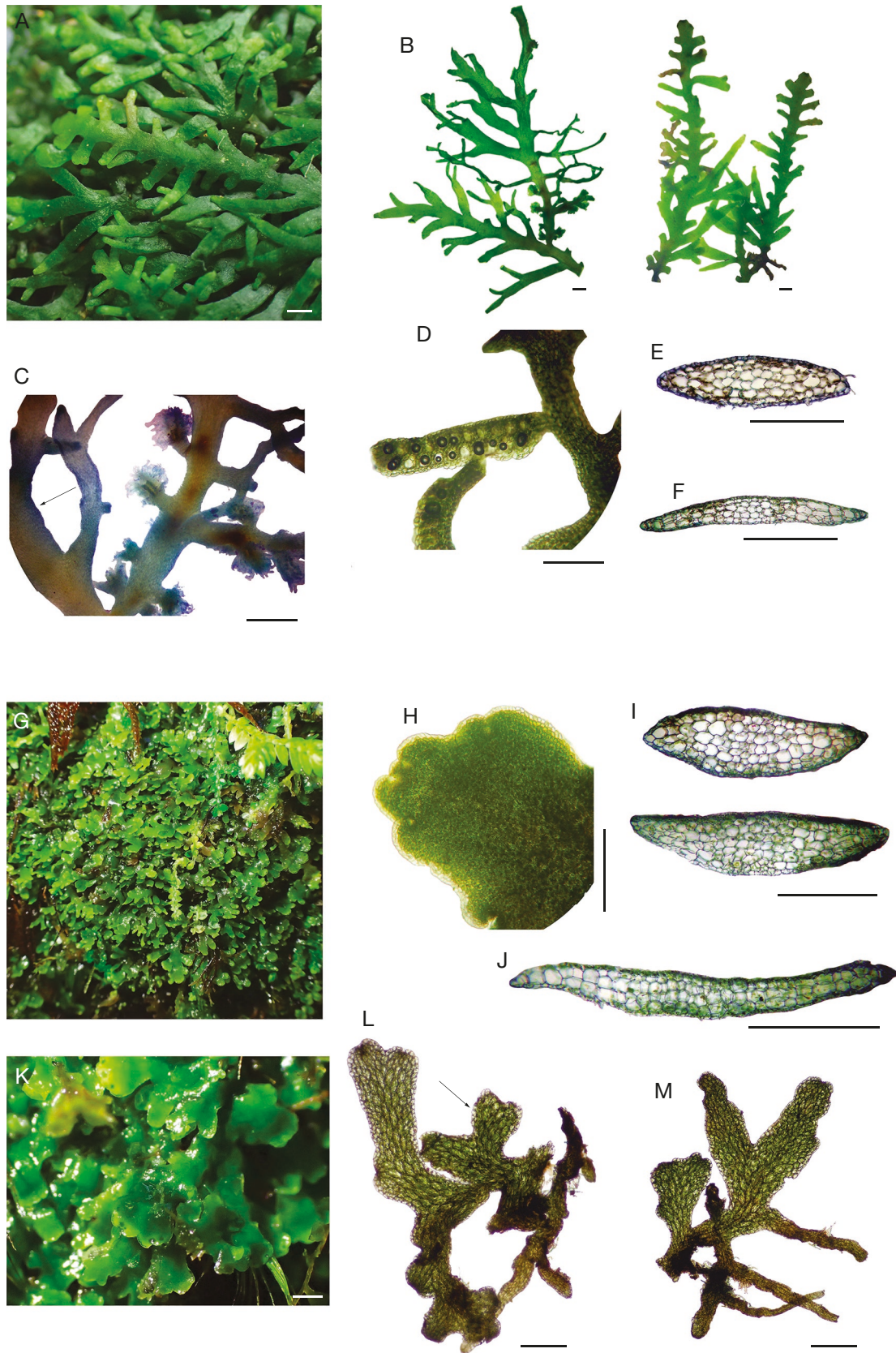


FIG. 4. — *Riccardia stipatiflora* (Steph.) Pagán: **A**, thallus mat; **B**, isolated thallus from *A. Duss 56* and *ELB17603*; **C**, female branches from *A. Duss 56*; **D**, male branch from *ELB17603*; **E**, main axis cross section from *A. Duss 56*; **F**, ultimate branch cross section from *A. Duss 56*. *Riccardia schwaneckeii* (Steph.) Pagán: **G**, **K**, thallus mats on the field; **H**, ultimate branch apex; **I**, main axis cross section; **J**, ultimate branch cross section; **L**, **M**, branching patterns from *ELB1599*. Scale bars: A-D, K-M, 1 mm; E, F, H-J, 500  $\mu$ m.



1875, CR13G9; Carbet Falls, 16°02'38"N, 61°38'29"W, 637 m, 28.VII.2013, *Lavocat Bernard & Reeb 1893, 1899*.

**Martinique.** Piton Lacroix, 14°41'54"N, 61°07'0"W, 980 m, 8.VIII.2018, *Lavocat Bernard 17816*.

**DISTRIBUTION.** — A species with a marked North-South disjunction in the Neotropics, occurring scattered in the West Indies (Cuba, Puerto Rico and the Virgin Islands, Guadeloupe, Dominica, Martinique [new], St. Vincent; e.g. Meenks [unpubl.]; Schäfer-Verwimp [2010]; Lavocat Bernard & Reeb [2016]) and again in southern Brazil (Stephani 1900; Gradstein & Costa 2003) and Uruguay (Hässel de Menendez 1964). The record from the inner, equatorial tropics (Mt. Roraima, Guyana; Gradstein & Florschütz-de Waard 1989) is probably erroneous and based on misidentified material (SRGr, pers. obs.).

#### REMARKS

*Riccardia schwaneckeii* is a dioicous species that is recognized by the rather broad, *c.* 1 mm wide, glossy green and fleshy, irregularly pinnate thalli with a notched apex, short and plump branches and a conspicuous, 1-3(-5) cells wide, hyaline wing (border) of enlarged cells with rather few chloroplast and oil bodies, the latter present in submarginal wing cells but being absent in the margin cells. Moreover, the margin cells of the wings are larger than the submarginal ones. The axis is plano-convex, *c.* 5-7 cells thick, and the epidermis cells are smaller than the medullary cells. By the rather fleshy, irregularly pinnate thallus with plump branches and a conspicuous hyaline wing of enlarged cells all around, *R. schwaneckeii* resembles *R. canaliculata* (Nees) Kuntze (subg. *Hyaloneura* R.M.Schust.) from Southeast Asia. However, *R. canaliculata* differs in having strongly enlarged ventral epidermis cells with thick walls (Furuki 1995). The putative relationship of *R. schwaneckeii* to the subg. *Hyaloneura* needs further study. The two amplified specimens belong clearly to a separate cluster (Fig. 2) but we need further analysis at a larger geographic scale to confirm our hypothesis.

#### *Riccardia stipatiflora* (Steph.) Pagán (Fig. 4A-F)

*Aneura stipatiflora* Steph., *Hedwigia* 32: 27 (1893). — *Riccardia stipatiflora* (Steph.) Pagán, *The Bryologist* 45: 81 (1942). — Type: **Martinique.** *A. Duss 56* (lecto-, designated here, G[G00066691]! c.gyn., labeled "original"). **Martinique.** *A. Duss s.n.* (syn-?, G[G00282037]! c.andr., labeled "original").

**SPECIMENS EXAMINED FROM THE FRENCH ANTILLES.** — **Guadeloupe.** Matouba, rivière Rouge, *A. Duss 182* (NY[G11574]), 457 (NY), det. Pagán as *A. subsimplex*; Matouba, Montagne de la Madeleine, 600-900 m, 1897-1900, *A. Duss 207* (NY[G11572]), 318 (NY), 319 (NY), 398 (NY); Ravine Citerne (haut), 16°02'08"N, 61°39'31"W, 1100 m, 31.V.2003, *Lavocat Bernard 460*; Trace Karukera, 16°02'18"N, 61°38'55"W, 850 m, 28.II.2012, *Lavocat Bernard 1600, 1601*; Carbet Falls, 16°02'50"N, 61°38'49"W, 880 m, 3.VI.2012, *Lavocat Bernard 1680, 1708*; National Park of Guadeloupe, La Madeleine Trois Rivières, 16°10'N, 61°38'W, 600 m, 14.VIII.2015, *Reeb & Bernard J.F. CR15G7*; Chutes du Carbet, access path, 16°02'33"N, 61°38'26"W, 650 m, *Reeb & Lavocat Bernard CR13G22*.

**Martinique.** Rivière du Lorrain, 1899, *A. Duss 182a*, det. Pagán as *A. subsimplex* (NY[G11573]); Montagne Pelée, camp de l'Alma, Deux choux, 600-1000 m, *A. Duss 74* (NY[G11571]), 131 (NY), 140 (NY), 325 (NY); Montagne Pelée, 14°48'23.9"N, 61°09'24.7"W, 1060 m, 29.V.2016, *Lavocat Bernard 16501*.

**DISTRIBUTION.** — In the West Indies reported from Cuba (type of *R. subsimplex*), Dominica (Stephani 1900; Schäfer-Verwimp 2010) and Guadeloupe and Martinique (Lavocat Bernard & Schäfer-Verwimp 2011).

**HABITAT.** — On trees, soil and rocks in humid forests from 600 to 1100 m.

#### REMARKS

*Riccardia stipatiflora* is an autoicous species with a firm texture, a rather deep green color and a prostrate, regularly 1-2-pinnate, to 2 cm long, unwinged thallus with basal stolons and with long, linear, unwinged branches. An unusual feature of the species is that the gametocia are often produced on the stolons (hence the name "*stipatiflora*"). The main axis is biconvex in cross section and the branches biconvex to plano-convex; the ultimate branches are often curved. The male branches are bordered by a 1-2 cells wide wing and the female branches have long hairy cilia. The specimen G00066691 is chosen as the lectotype because it has gynocia, which were described in the protologue. The specimen G00282037, annotated by Stephani as "Original", is treated as a tentative syntype because the plants are male and androecia were not mentioned in the protologue. The male branches in this syntype are very long, of up to 22 pairs of antheridia, circinately curved and positioned on the stolons. Meenks (unpubl.) described the male branches as being only 1-4 pairs of androecia long based on material from Cuba. The molecular analysis shows a well defined cluster of *R. stipatiflora* (Figs 1; 2).

#### FURTHER RECORD

#### *Riccardia digitiloba* (Spruce) Pagán

*Aneura digitiloba* Spruce, *Bulletin de la Société botanique de France (Congr. Bot.)* 36: cci (1889). — *Riccardia digitiloba* (Spruce) Pagán, *The Bryologist* 42: 6 (1939). — Type: **Brazil.** Rio de Janeiro, *Glaziou 7228* (iso-, G[G00283000]!, G[G00283001]!, G[G00283002]!, G[G00283003]!).

#### REMARKS

*Riccardia digitiloba* is a dioicous, widespread neotropical species that was recorded from Guadeloupe by Pagán (1942) based on material from Bains-Jaunes (*Lefèvre & Marie s.n.*) and Petit Bourg (*Questel 1555, PC*). We have not seen these specimens and are unable to confirm the occurrence of *R. digitiloba* in the French Antilles. The species is recognized by the small-celled epidermis (epidermis cells 3-4× smaller than inner cells) and the delicate, pinnate to dichotomous thalli with linear, wingless or rudimentarily winged branches producing gemmae at the tips. The gemmiparous branches are sometimes tapering to narrow tips (Gradstein & Reeb 2018b).



## EXCLUDED RECORDS

*Riccardia cataractarum* (Spruce) Schiffn.

*Aneura cataractarum* Spruce, *Bulletin de la Société botanique de France (Congr. Bot.)* 36: cxcv (1889). — *Riccardia cataractarum* (Spruce) Schiffn., *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Denkschriften* 111: 10 (1964). — Type: Paraguay. “Roches humides de la cascade de Mobatobi”, VI.1881, *Balansa* 4245, c.gyn. (lecto-, designated by Gradstein & Reeb [2018b], MANCH!; isolecto-, G[G282999]!).

## REMARKS

*Riccardia cataractarum* is a semi-aquatic, tropical South American species that has been reported from Guadeloupe by Lavocat Bernard & Reeb (2016) and from Martinique by Lavocat Bernard (2018). The French Antillean material belongs to *R. regnellii* (see remarks under the latter species).

*Riccardia leptophylla* (Spruce) Herzog

*Aneura leptophylla* Spruce, *Transactions & Proceedings of the Botanical Society of Edinburgh* 15: 544 (1885). — *Riccardia leptophylla* (Spruce) Herzog, *Svensk Botanisk Tidskrift* 46: 65 (1952). — Type: Venezuela. San Carlos del Río Negro, *Spruce H31c* (lecto-, designated by Meenks [1987], MANCH[MANCH-cc1817], *vide* Gradstein & Reeb 2018b).

## REMARKS

*Riccardia leptophylla* is a delicate, widespread neotropical species that was recorded from Guadeloupe (“Cascade Écrevisses, De Sloover 23.544, JE) by Meenks (1987). We have not seen this material but have visited the Guadeloupean locality several times and only found *R. regnellii* there. We therefore assume that the *R. leptophylla* material from Guadeloupe belongs to *R. regnellii*.

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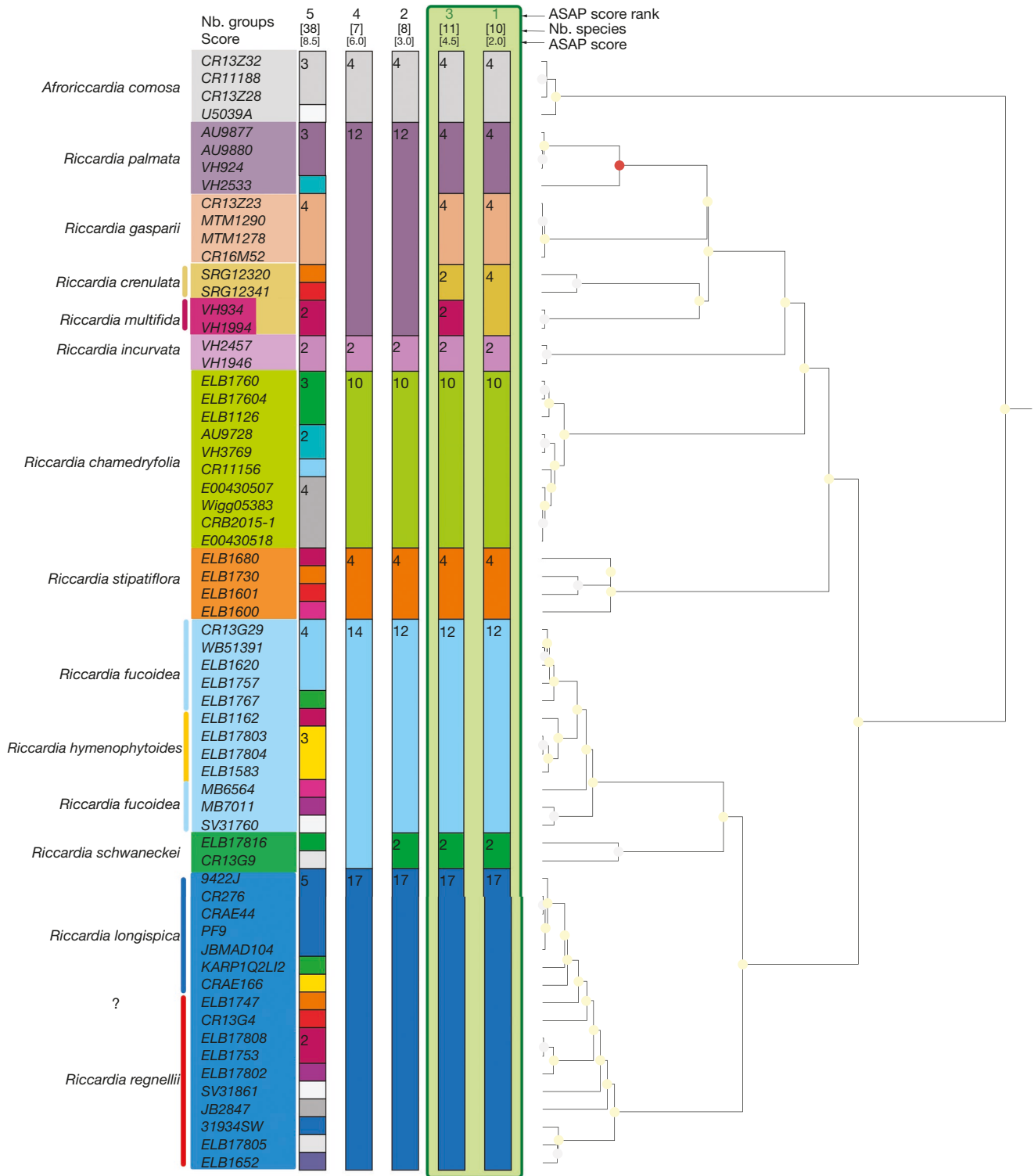
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## APPENDICES

APPENDIX 1. — Voucher information and GenBank accession numbers for Aneuraceae H.Klinggr. specimens used for molecular species delimitation. Abbreviations: **ECU**, Ecuador; **REU**, La Réunion; **FRA**, France; **MAD**, Madagascar; **GLP**, Guadeloupe; **SHN**, Saint Helena; **MTQ**, Martinique; **USA**, United States; **COM**, Comoros; **IDN**, Indonesia; **UGA**, Uganda; **BES**, Saba.

Voucher	Collector	Species	Country	GenBank accession numbers		
				<i>psbA-trnH</i>	<i>trnLF</i>	<i>rps4</i>
31934SW	Schäfer-Verwimp	<i>Riccardia regnellii</i>	ECU	KX512110	KX512052	KX512242
9422J	Szabó, A.	<i>R. longispica</i>	REU	MG668766	MG602162	ON192968
AU9728	Unterheimer, A.	<i>R. chamedryfolia</i>	FRA	KX512178	KX512019	KX512209
AU9877	Unterheimer, A.	<i>R. palmata</i>	FRA	KX512156	KX512062	KX512252
AU9880	Unterheimer, A.	<i>R. palmata</i>	FRA	KX512155	KX512061	KX512251
CR11156	Reeb	<i>R. chamedryfolia</i>	MAD	MG668655	MG602102	ON192970
CR11188	Reeb	<i>Afroriccardia comosa</i>	MAD	KX512199	KX512009	—
CR13G29	Reeb	<i>R. regnellii</i>	GLP	KX512137	KX512081	KX512271
CR13G4	Reeb	<i>R. regnellii</i>	GLP	KX512118	KX512023	KX512295
CR13G9	Reeb	<i>R. schwaneckei</i>	GLP	KX512117	KX512050	KX512240
CR13Z23	Reeb	<i>R. vohimanensis</i>	MAD	KX512151	KX512037	KX512227
CR13Z28	Reeb	<i>A. comosa</i>	MAD	KX512200	KX512011	KX512201
CR13Z32	Reeb	<i>A. comosa</i>	MAD	MG668792	ON168487	—
CR16M52	Reeb	<i>A. comosa</i>	MAD	ON168469	ON168495	—
CR276	Reeb	<i>R. longispica</i>	MAD	ON168470	MG602152	—
CRAE166	Reeb	<i>R. longispica</i>	MAD	KX512116	KX512047	KX512237
CRAE44	Reeb	<i>R. longispica</i>	MAD	KX512108	KX512039	KX512229
CRB2015_1	Reeb	<i>R. chamedryfolia</i>	SHN	ON168471	ON168493	ON192971
E00430507	Wigginton, M.J.	<i>R. chamedryfolia</i>	SHN	KX512189	KX512097	KX512287
E00430518	Wigginton, M.J.	<i>R. chamedryfolia</i>	SHN	KX512180	KX512099	KX512289
ELB1126	Lavocat-Bernard, E.	<i>R. chamedryfolia</i>	GLP	ON168472	—	ON192972
ELB1162	Lavocat-Bernard, E.	<i>R. hymenophytoides</i>	GLP	KX512138	KX512088	KX512278
ELB1583	Lavocat-Bernard, E.	<i>R. hymenophytoides</i>	GLP	ON168473	ON168501	—
ELB1600	Lavocat-Bernard, E.	<i>R. stipatiflora</i>	GLP	KX512192	KX512070	KX512260
ELB1601	Lavocat-Bernard, E.	<i>R. stipatiflora</i>	GLP	KX512193	KX512072	KX512262
ELB1620	Lavocat-Bernard, E.	<i>R. fudoidea</i>	MTQ	KX512078	KX512268	KX512133
ELB1652	Lavocat-Bernard, E.	<i>R. regnellii</i>	GLP	—	ON168491	ON192973
ELB1680	Lavocat-Bernard, E.	<i>R. stipatiflora</i>	GLP	KX512191	KX512022	KX512212
ELB1730	Lavocat-Bernard, E.	<i>R. stipatiflora</i>	GLP	KX512194	KX512071	KX512261
ELB1747	Lavocat-Bernard, E.	<i>R. regnellii</i>	MTQ	KX512121	KX512104	KX512294
ELB1753	Lavocat-Bernard, E.	<i>R. regnellii</i>	MTQ	KX512109	KX512051	KX512241
ELB1757	Lavocat-Bernard, E.	<i>R. fucoidea</i>	MTQ	KX512139	KX512082	KX512272
ELB1760	Lavocat-Bernard, E.	<i>R. chamedryfolia</i>	MTQ	ON168474	ON168492	ON192974
ELB17604	Lavocat-Bernard, E.	<i>R. chamedryfolia</i>	GLP	—	ON168494	ON192975
ELB1767	Lavocat-Bernard, E.	<i>R. fucoidea</i>	MTQ	KX512128	KX512083	KX512273
ELB17802	Lavocat-Bernard, E.	<i>R. regnellii</i>	MTQ	ON168476	—	ON192976
ELB17803	Lavocat-Bernard, E.	<i>R. hymenophytoides</i>	MTQ	ON168477	ON168500	—
ELB17804	Lavocat-Bernard, E.	<i>R. hymenophytoides</i>	MTQ	ON168478	ON168499	ON192977
ELB17805	Lavocat-Bernard, E.	<i>R. regnellii</i>	MTQ	ON168479	ON168490	ON192978
ELB17808	Lavocat-Bernard, E.	<i>R. regnellii</i>	MTQ	ON168480	—	ON192979
ELB17816	Lavocat-Bernard, E.	<i>R. schwaneckei</i>	MTQ	ON168481	ON168488	ON192980
JB2847	Xœ	<i>R. regnellii</i>	USA	ON168482	ON168489	ON192981
JB2847	Xœ	<i>R. regnellii</i>	USA	ON168482	ON168489	ON192981
JBMAD104	Bardat, J.	<i>R. longispica</i>	MAD	MG668785	MG602153	ON192982
KARP1Q2LI2	Bardat, J.	<i>R. longispica</i>	COM	ON168483	MG602189	ON192983
MB6564	Burghardt	<i>R. fucoidea</i>	ECU	ON168484	ON168498	ON192984
MB7011	Burghardt	<i>R. fucoidea</i>	ECU	KX512136	KX512087	KX512277
MTM1278	Reeb	<i>R. vohimanensis</i>	MAD	ON168485	ON168497	ON192985
MTM1290	Reeb	<i>R. vohimanensis</i>	MAD	ON168486	ON168496	ON192986
PF9	Bardat, J.	<i>R. longispica</i>	REU	MG668732	MG602156	ON192987
SRG12320	Gradstein, R.S.	<i>R. crenulata</i>	IDN	KX512160	KX512056	KX512246
SRG12341	Gradstein, R.S.	<i>R. crenulata</i>	IDN	KX512161	KX512055	KX512245
SV31760	Schäfer-Verwimp	<i>R. fucoidea</i>	ECU	KX512142	KX512075	KX512265
SV31861	Schäfer-Verwimp	<i>R. regnellii</i>	ECU	KX512105	KX512018	KX512208
U5039A	Wigginton, M.J.	<i>A. comosa</i>	UGA	KX512127	KX512008	—
VH1946	Hugonnot, V.	<i>R. incurvata</i>	FRA	KX512195	KX512034	KX512224
VH1994	Hugonnot, V.	<i>R. multifida</i>	FRA	KX512164	KX512059	KX512249
VH2457	Hugonnot, V.	<i>R. incurvata</i>	FRA	KX512196	KX512035	KX512225
VH2533	Hugonnot, V.	<i>R. palmata</i>	FRA	KX512154	KX512064	KX512254
VH3769	Hugonnot, V.	<i>R. chamedryfolia</i>	FRA	KX512177	KX512021	KX512211
VH924	Hugonnot, V.	<i>R. palmata</i>	FRA	KX512153	KX512063	KX512253
VH934	Hugonnot, V.	<i>R. multifida</i>	FRA	KX512157	KX512060	KX512250
WB51391	Wigginton, M.J.	<i>R. fucoidea</i>	BES	KX512129	KX512080	KX512270
Wigg05383	Wigginton, M.J.	<i>R. chamedryfolia</i>	SHN	KX512184	KX512103	KX512293



APPENDIX 2. — ASAP partitions: the fifth best ASAP scores were retained. We retained the first and the third (2 and 4.5) because the partition with the second best score (3) merges three morphological very distinct species (*R. palmata* (Hedw.) Carruth., *R. gasparii* Reeb & Gradst. and *R. crenulata* Schiffr.). In the left column, the final hypothesis proposed by this study are reported, and colored bars indicate the retained species, even if the two scores we retained merged them (e.g. *R. fucoidea* (Sw.) C.Massal. and *R. hymenophytoides* (Spruce) Meenks).

APPENDIX 3. — Matrix of partition results obtained by the four methods (six analysis with two parameters for ASAP and GMYC). The numbers are randomly given by each methods for each cluster and have no correspondence between methods.

Voucher	ABGD_rec	ASAP1 (score=2)	ASAP2 (score=4,5)	bPTP 500M from RaxML	GMYC single thresh.	GMYC multithresh.
CR11188	1	1	1	16	14	7
CR13Z28	1	1	1	16	14	7
CR13Z32	1	1	1	16	14	7
U5039A	1	1	1	16	14	7
AU9877	2	2	2	11	4	10
AU9880	2	2	2	11	4	10
VH924	2	2	2	11	4	10
CR13Z23	6	3	6	7	5	1
CR16M52	6	3	6	7	5	1
MTM1278	6	3	6	7	5	1
MTM1290	6	3	6	7	5	1
SRG12320	3	4	3	8	26	2
SRG12341	3	4	3	8	27	2
VH1946	5	5	5	6	7	4
VH2457	5	5	5	6	7	4
ELB1600	8	7	8	12	18	8
ELB1601	8	7	8	13	19	8
ELB1680	8	7	8	14	20	8
ELB1730	8	7	8	15	21	8
VH1994	4	4	4	9	6	3
VH934	4	4	4	9	6	3
CR13G29	9	8	9	2	8	13
ELB1620	9	8	9	2	8	14
ELB1757	9	8	9	2	8	13
ELB1767	9	8	9	2	8	14
MB6564	13	8	9	2	25	18
MB7011	14	8	9	2	10	9
SV31760	14	8	9	2	10	9
WB51391	9	8	9	2	8	14
ELB1162	12	8	9	2	9	11
ELB1583	12	8	9	2	9	11
ELB17803	12	8	9	2	9	11
ELB17804	12	8	9	2	9	11
CR13G9	10	9	10	3	16	6
ELB17816	10	9	10	5	23	6
9422J	11	10	11	4	11	17
CR276	11	10	11	4	11	17
CRAE166	11	10	11	4	17	17
CRAE44	11	10	11	4	11	17
JBMD104	11	10	11	4	11	17
KARP1Q2LI2	11	10	11	4	11	17
PF9	11	10	11	4	11	17
31934SW	11	10	11	4	12	17
CR13G4	11	10	11	4	15	17
ELB1652	11	10	11	4	12	17
ELB1747	11	10	11	4	22	17
ELB1753	11	10	11	4	13	5
ELB17802	11	10	11	4	13	5
ELB17805	11	10	11	4	12	17
ELB17808	11	10	11	4	13	5
JB2847	11	10	11	4	24	17
SV31861	11	10	11	4	28	17
AU9728	7	6	7	1	1	15
CR11156	7	6	7	1	1	15
CRB2015_1	7	6	7	1	2	16
E00430507	7	6	7	1	2	16
E00430518	7	6	7	1	2	16
ELB1126	7	6	7	1	3	12
ELB1760	7	6	7	1	3	12
ELB17604	7	6	7	1	3	12
VH3769	7	6	7	1	1	15
Wigg05383	7	6	7	1	2	16
VH2533	2	2	2	10	29	19
Weight	10	5	5	10	5	5