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Couverture / *Cover* :
From top left, to bottom right, by line: *Riccardia vohimanensis*, *Riccardia corbieri*, *Riccardia gasparii*, *Riccardia longispica* phenotype erosa, *Riccardia fastigiata*, *Ricardia martinii*, *Riccardia angusticosta*. Blue colors are due to methylen blue coloration.

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A taxonomic revision of Aneuraceae (Marchantiophyta) from eastern Africa with an interactive identification key

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ABSTRACT
A taxonomic revision of the liverwort family Aneuraceae in eastern Africa is presented based on the results of an integrative approach. Molecular and morphological data lead to the recognition of fourteen species in eastern Africa, in three genera: eleven species in *Riccardia* Gray, two in *Aneura* Dumort. and one in *Afroriccardia* Reeb & Gradst. One further species, *R. multifida*, may be expected in eastern Africa and is included in this treatment. Keys, descriptions and illustrations are provided for the accepted species together with data on types, synonymy, geographical distribution, habitat and differentiating characters. A knowledge database was built using Xper3 and an interactive key was generated using the Xper3 platform tools. *Riccardia gasparii* sp. nov., *R. martinii* sp. nov. and *R. vohimanensis* sp. nov. are described as new to science. A comparison with other regions of the world shows that Africa has relatively few Aneuraceae taxa; only the Holarctic region, with the exception of East Asia, has fewer species. Moreover, dendroid taxa and species with cuticular ornamentation are lacking in Africa. On the other hand, Africa stands out by the presence of the endemic genus *Afroriccardia*. More collecting is needed in future to clarify the species ranges, the status of questionable taxa and the knowledge of local floras.

KEY WORDS
Africa,
Aneuraceae,
interactive key,
liverworts,
Riccardia,
new species,
new combinations,
new synonyms.

RÉSUMÉ

Une révision taxonomique des Aneuraceae de l'Afrique de l'Est, incluant une clé d'identification interactive.
Nous présentons une révision taxonomique de la famille d'hépatiques Aneuraceae pour l'Afrique de l'Est, basée sur une approche de taxonomie intégrative. Les données moléculaires et morphologiques ont conduit à la reconnaissance de quatorze espèces en Afrique de l'Est, réparties en trois genres : onze espèces de *Riccardia* Gray, deux d'*Aneura* Dumort. et une d'*Afroriccardia* Reeb & Gradst. Une autre espèce est attendue en Afrique de l'Est, *R. multifida*, incluse dans le traitement. Les clés, descriptions et illustrations sont fournies pour les espèces acceptées, accompagnées de données sur les types, la synonymie et la distribution géographique. Une base de connaissance utilisant Xper3 a été élaborée et une clé d'identification interactive a été générée. *Riccardia gasparii* sp. nov., *R. martinii* sp. nov. and *R. vohimanensis* sp. nov. sont décrites comme nouvelles pour la science. L'Afrique héberge moins d'espèces d'Aneuraceae que d'autres régions du monde et l'on n'y rencontre aucune espèce dendroïde ou avec cuticule ornementée ; d'un autre côté, le genre endémique *Afroriccardia* y a été décrit. Des collectes supplémentaires sont nécessaires afin de préciser certains taxons aux limites encore discutables, et d'enrichir les flores locales.

MOTS CLÉS
Afrique,
Aneuraceae,
clé interactive,
hépatiques,
Riccardia,
espèces nouvelles,
combinaisons nouvelles,
synonymes nouveaux.

INTRODUCTION

Species delimitation, description and name attribution are the necessary steps towards classification, one of the main goals of systematics. Species identification based on morphological characters is only possible when clear species hypotheses are available. The generation of robust species hypotheses requires an integrative approach, using all available tools from molecules to morphology, and preferably supported by various decision tools (Debortoli *et al.* 2016; Johnston *et al.* 2017).

Here we present a taxonomic revision of the liverwort family Aneuraceae in eastern Africa using the results of the species delimitation approach applied in a previous study (Reeb *et al.* 2018). Knowledge of Aneuraceae of Africa has been reviewed by Jones (1956), Perold (2001a, b, 2003), Reeb & Bardat (2014) and others. About 37 species have been described from Africa, the majority of them by Stephani (e.g. 1891, 1892, 1898-1924) and furthermore by S.W. Arnell, W. Pearson, G. Gola and others. Most of these species are now considered synonyms. The first critical taxonomic revisions were by Jones (1956), who accepted seven species in the single genus *Riccardia* Gray, and by Meenks & Pócs (1985) who recognized ten species in East Africa, two in *Aneura* (L.) Dumort. and eight in *Riccardia*. Perold (2001a, b, 2002a, b) presented detailed descriptions of selected species from southern Africa and Reeb & Bardat (2014) discussed the types of the African *Riccardia* species. A preliminary worldwide molecular analysis of Aneuraceae by Rabeau *et al.* (2017) included eight species from Africa: seven of *Riccardia* (*R. chamedryfolia* (With.) Grolle, *R. longispica* (Steph.) Pearson and five unidentified spp.) and *Aneura comosa* Steph. The latter species proved to represent a new genus, *Afroriccardia* Reeb & Gradst. The African *Riccardia* species were spread over different clades in the molecular tree, together with species from other continents.

In the present treatment fourteen species in three genera (*Afroriccardia, Aneura, Riccardia*) from eastern Africa, including the East African islands, are recognized based on the results of morphological and molecular analysis. Three species are new to science, *R. gasparii* sp. nov., *R. martinii* sp. nov. and *R. vohimanensis* sp. nov. Descriptions and illustrations are presented as well as d two identifications keys, a classical dichotomous key and an interactive online key based on formalized description using Xper3 software.

MATERIAL AND METHODS

Molecular species delimitation was conducted using tree-based and non-tree-based methods (Fontaneto *et al.* 2015; Reeb *et al.* 2018). We present a RaxML tree based on concatenated chloroplasts markers (*mat*K, *psb*A-*trn*H, *trn*L-F), synthesizing previously published first results (Rabeau *et al.* 2017; Reeb *et al.* 2018). The tree building ran on Cipres Science Gateway (Miller *et al.* 2010) using RaxML (Stamatakis 2006) with a fast bootstraping. The analysis of African Aneuraceae included 93 samples of *Riccardia,* six of *Afroriccardia comosa* and eight of *Aneura*. Vouchers used in the molecular analysis (Reeb *et al.* 2018) and (Fig. 1) are indicated in the taxonomic treatment by an asterisk (*).

Morphological species delimitation was based on examination of more than 1300 specimens from Africa, including 300+ collections made by the first author and the remaining ones from various herbaria as listed in the acknowledgments.

Interactive identification key.

An interactive knowledge database was built using Xper3 (http://www.xper3.en) and an interactive key was generated using the Xper3 platform tools (http://african-riccardia.identificationkey.org/mkey.html) (Guide line Appendix 1). The Xper system builds a species character matrix from which identification with multi-access paths is generated (Vignes-Lebbe *et al.* 2016, 2017; Klimmek & Baur 2018). It allows to use all available characters at any time during the identification process. While dichotomous keys sometimes provide only reproductive characters, thus preventing identification of sterile material, interactive identification keys enable the use

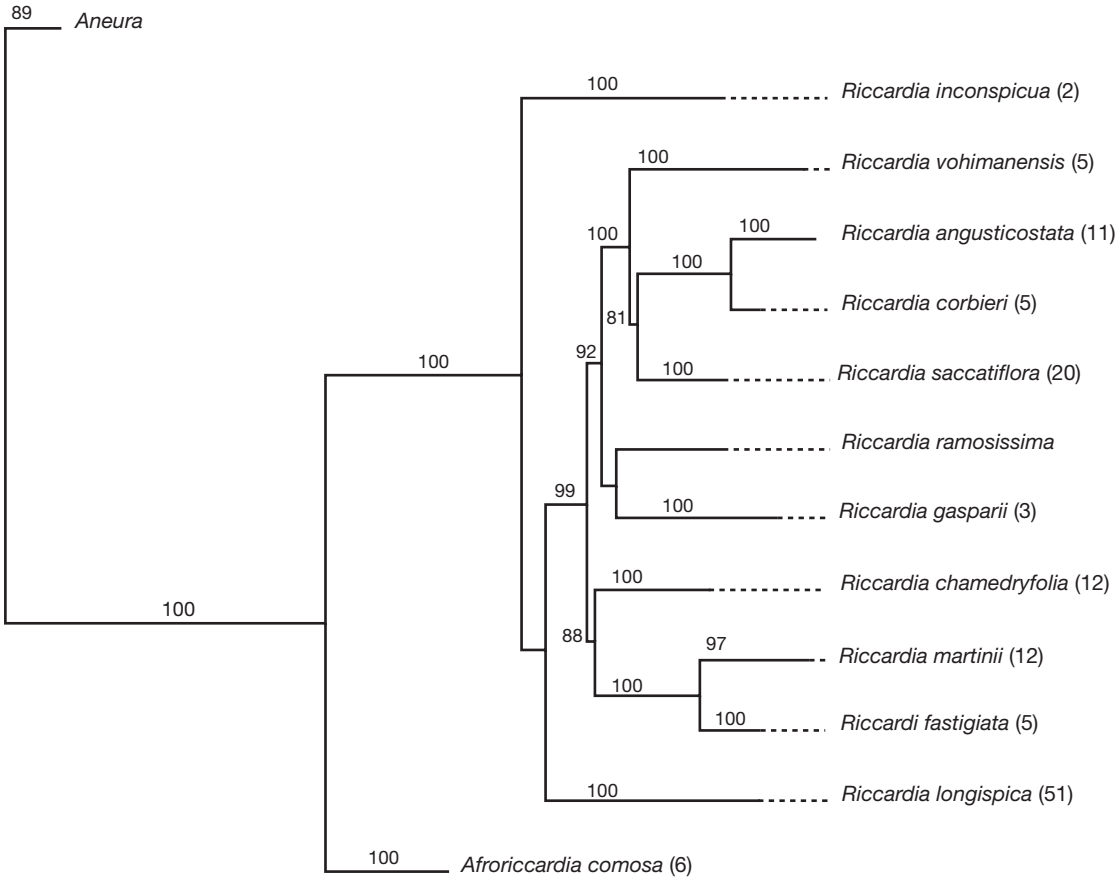

Fig. 1. — RaxML tree of Aneuraceae of eastern Africa based on concatenation of chloroplast *mat*K, *psb*A-*trn*H and *trn*L-F sequences (modified after Reeb *et al.* 2018). Numbers in brackets are number of specimens analysed, numbers on branches are bootstrap values, obtained by fast bootstrapping.

of any character. The Xper system allows integration of different types of information, including images of taxa, characters and character states, definitions and comments. Characters and taxa description are standardized and stored in the taxa / characters matrix requiring a strict and exhaustive definition of characters and characters states, including character hierarchy. Parent-children character dependences allow to describe only subcharacters when the parent character is validated. Various additional tools enhance the application of the system, such as comparisons between taxa or taxon groups and history of the identification process, etc. All the data (characters, taxa) can be immediately modified with new information.

Morphological characters

Characters used in the taxonomy of Aneuraceae are frequently unstable or age-dependent, or are absent in the material examined. Here we discuss some of the main characters used in the dichotomous key, including problematic or unclear characters. Ramification order and thallus description were reviewed in Reeb *et al.* (2018). The thallus consists of axis and branches. Branches may be considered "trees" in a graphic sense, rooted by the junction with the axis. The axis is the sum of segments of the same order (Reeb *et al.* 2018). We use here the term "ultimate branch" (= "terminal branch"; Reeb *et al.* 2018) for the youngest branches, as in Gradstein & Reeb (2018a). All characters are described and commented in the interactive key (http://african-riccardia.identificationkey.org/mkey.html).

Thallus Size

Total length of the thallus is measured as an euclidean distance, from basal point to the highest point. The thallus is considered as small if the length ≤ 1 mm, as large if the length is ≥ 1 mm.

Reiteration of the thallus

A reiteration is the growth of a new branched thallus from a parent one; the base of the regenerated thallus is cylindrical, being born from a spore. Reiteration may take place on the main or secondary axis. It was not previously used as a character but is observed only in some species.

Differentiation between creeping and erect branches

The main axis is usually prostrate in the African species, at least in young plants, and never erect like in some South American *Riccardia* species (Hässel de Menéndez 1972; Gradstein & Reeb 2018a). The primary or ultimate branches, on the other hand, may be attached or ascending from the substrate. This character can be taxonomically useful, but it is age-dependent. In young populations the distinction between creeping axis and ascending branches is usually clear but in old ones the

Key to the genera of Aneuraceae of Africa

1. Thallus less than 2 mm wide, irregularly or regularly 1-3-pinnate or palmate ..... *Riccardia* Gray
— Thallus more than 2 mm wide, unbranched or irregularly 1(-2)-pinnate 2

2. Thallus (3-)4-15 mm wide, unbranched or irregularly 1-pinnate, closely adherent to the substrate. Gynoecia in notches under the thallus margin. Archegonia not bordered by a large and dense cluster of rhizoids..... ..... *Aneura* (L.) Dumort.
— Thallus 2.5-4 mm wide, irregularly 1-(2)-pinnate, not closely adherent to the substrate. Gynoecia on up to 1 cm long lateral branches. Archegonia bordered by a large and dense cluster of rhizoids .... *Afroriccardia* Reeb & Gradst.

distinction may be obscured by regeneration of new thalli within the mat.

Axis shape

Shape of the main axis may be different at the base and in the middle of the axis. As this difference cannot be observed in broken thalli, shape of the main axis should as a rule be observed in the middle portion of the axis, between two junctions (branching points). Junctions with the branches may also be different and may be characterized by the presence of wings (in species with unwinged axes).

Cell walls thickenings

Thickened cells may occur in old populations of many species but their presence is not constant. They can be observed in thallus cross sections or in dorsal view when the epidermal cell walls are thickened. In the latter case, the cell walls are often orange or brownish colored by polyphenols.

Wings

Many species have wings, consisting of translucent, unistratose rows of cells along the thallus margin. Single protruding cells at the thallus margins are not considered wings and are described as "bulging" or "protruding" cells. Wings should preferably be observed in thallus cross section. In dorsal view, wings may be confused with a 2-3-stratose, wing-like, translucent band of cells along the thallus margin. The width of this translucent band in dorsal view can be a discriminant characters for some species (Furuki 1991).

Sexual branches

The sexual branches can be sessile or pedunculate by a short stalk, developed by vegetative growth of the sexual branch.

Number of antheridial or archegonial pairs

Their number depends on the age of the branch and is highly variable for antheridial pairs. Therefore, median and maximal number of antheridial pairs is given in the descriptions.

Axis and wing of sexual branches

Male and female branches are constituted of a basal portion or axis in which the gametangial chambers are buried, in two rows. The chambers are open on the dorsal side. The sexual branches are often winged (wing scaly, or constituted of cilia); in wingless sexual branches the margin is bordered by a single row of cells. The width of the wing relative to the axis of the sexual branch is a relevant taxonomic character in several species.

Mycorrhiza-like fungi

Basidiomycetes of the order Tulasnellales, identified as members of the genus *Sebacina* Tul. & C.Tul., are exclusively associated with the Aneuraceae family (Krause *et al.* 2011; Bidartondo & Duckett 2009; Pressel *et al.* 2010). They may be observed in cross section, with or without a blue coloration (coton blue, methylene blue) as intracellular packs (the plasmic membrane being kept intact).

SYSTEMATICS

Family Aneuraceae

A family of five genera worldwide (Preußing *et al.* 2010; Rabeau *et al.* 2017), including three in Africa: *Riccardia* Gray, *Aneura* Dumort. and *Afroriccardia* Reeb & Gradst. The principal characteristics of Aneuraceae are: 1) thallus pinnate or unbranched; 2) midrib usually indistinct; 3) gametoecia at thallus margins or on short lateral branches; 4) sporophyte in a fleshy calyptra; and 5) elaters attached to the tips of the valves.

Genus *Afroriccardia* Reeb & Gradst.

Remarks

A monospecific African genus. For characters of *Afroriccardia* see under the species.

Afroriccardia comosa (Steph.) Reeb & Gradst.

Aneura comosa Steph., *Botanical Gazette* 15: 281 (1890). (*Riccardia comosa* [Steph.] E.W.Jones nom. inval.). — Type: Réunion, 1889, *Rodriguez s.n.* (holo-, G[G00045027]!; iso-, PC[PC0103522]!).

Further specimens examined. — **Madagascar**. Angavokely Forest, 18°55'16"S 47°44'30"E, 1600 m, 2.II.2011 *Reeb CR11188** (PC0763877, TAN); Zahamena National Park, 17°38'19"S, 48°36'46"E, 1156 m, 28.XII.2013, *Reeb* & *Andriamanantena 13Z28** (PC0763872, TAN), *13Z32** (PC0763873, TAN). Zahamena National Park, on seeping rocks, highest part of the river

KEY TO THE SPECIES OF *ANEURA* OF EASTERN AFRICA

1. Thallus 9-20 cells thick in the middle (cross section). Male branches short, with 2-5 pairs of antheridial chambers along its length ..... *A. pinguis* (L.) Dumort.
— Thallus 5-8(-9) cells thick in the middle. Male branches 6–25 antheridial chambers long, frequently branched *A. latissima* Spruce

crossing the camp, 17°38'22.7"S, 48°38'45.3"E, 1294 m, 30.XII 2013, *Reeb* & *Andriamanantena 13Z55** (PC0763874, TAN).
Réunion. Source pétrifiante de Hell-Bourge, *G. de l'Isle 220* (PC0716023); below Piton de la Fournaise, Mare Longue reserve, 21°20'30"S, 55°44'30"E, 175-300 m, 05.IX.1997, *Vojko 9432AB** (EGR); *de Lisle 570bis* (PC0716024, G00264057); *Rodriguez s.n.* (G00264058); plaine des palmistes, without collector (PC0716026).
Mauritius. *Rodriguez s.n.* (PC0716025).
Uganda. Bwindi National Park, Rukungiri, Kitahurira bridge, 1480 m, 30.I.1996, *Wigginton U5039A** (E00430553).

DISTRIBUTION. — *Afroriccardia comosa* is a rare species that was long known only from a few 19th century collections from Réunion and Mauritius. Recently, it was additionally recorded from Madagascar and Uganda (Rabeau *et al.* 2017).

HABITAT. — On damp rock surfaces in shaded places close to water beds (shaded rivers, entrances of caves with water), in humid evergreen forest at mid-montane elevations in Uganda and Madagascar (1100-1600 m) and at lower elevation in Réunion (175-300 m).

DESCRIPTION
Dioicous (? androecia not seen).

Thallus
Green, to 7 cm long, main axes 2.5-4.0 mm wide, creeping, ± regularly (2-)pinnate, with 1-2 reiterations, branches alternate to subopposite, stolons not observed.

Rhizoids
Developing over the whole width of the ventral surface of the thallus.

Main axis
Plano-convex to biconvex, 6-8(-10) cells thick, margin entire, acute, unwinged, epidermis cells in cross section 1.5-2.0× smaller than medullary cells, all cells thin-walled.

Ultimate branches
To 8 mm long, 0.8-2.0 mm wide, 4-5 cells thick, with a conspicuous, 3-4(-6) cells wide wing, branch margins parallel, crenulate, thallus surface cells becoming smaller to the margin, not or slightly bulging; branch apex rounded to truncate and usually narrowly incised (to 130 µm deep).

Mucilage papillae
On branches *c.* 20, present below the apex and in four rows on the ventral branch surface.

Female branches
Solitary or grouped on main axes and primary branches, 0.5-1.0 mm long, archegonia (only unfertilized ones seen) in pairs, covered by a dense cluster of rhizoids originating from beneath the apex of the female branches, rhizoids to 0.7 mm long, with strongly thick-walled tips.

Multicellular paraphyses
Lacking.

Male branches and sporophyte
Not seen.

Vegetative reproduction
Not observed.

COMMENT
The species was tentatively placed in the synonymy of *Lobatiriccardia coronopus* (De Not.) Furuki by Reeb & Bardat (2014) but subsequent molecular and morphological study showed that it constitutes a separate, monospecific genus (Rabeau *et al.* 2017). *Afroriccardia comosa* resembles *Lobaticcardia* Furuki in the broad, pinnately branched thallus and the wide expansion of rhizoids on ventral thallus surface, but differs in the long female branches (to 1 cm long) with one pair of archegonia. The presence of female branches is shared with *Riccardia* but the broad thallus and the large cluster of rhizoids covering the archegonia distinguish *Afroriccardia* from *Riccardia*. In the molecular tree *Afroriccardia* was sister to *Riccardia* and *Lobatiriccardia* (Rabeau *et al.* 2017).

Genus *Aneura* Dumort.

REMARKS
About 20 species worldwide (Söderström *et al.* 2016); two species in Africa. *Aneura* is recognized by the rather broad and fleshy, glossy green, scarcely branched, dioicous thallus with entire to somewhat crisped margins and without midrib.

Aneura latissima Spruce

Riccardia latissima (Spruce) Schiffn., *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 67: 177 (1898) — Type: Brazil, Amazonas, Rio Negro, on rotten logs, *Spruce s.n.* (syn-, MANCH!).

Aneura pseudopinguis (Herzog) Pócs, *Acta Botanica Hungarica* 29: 133 (1983) (*Riccardia pinguis* Herzog). — Type: Brazil, St. Catarina, Jaraguá, 3.X.1937, *Carl s.n.* (holo-, JE n.v.), syn. fide Gradstein (2013).

SPECIMENS EXAMINED. — **Madagascar**. Alaotra-Mangoro, Vohimana Reserve 18°55'09.9"S, 49°30'49.4"E, 827 m, 15.IV.2010, *Reeb, Andriamanantena & Bidault CRAE142,*(PC0724341A, TAN) ; Mar-

omizaha Reserve 18°58'34.4"S, 48°27'54.5"E, 1095 m, 05.VII.2012, *Reeb MTM1280* (PC, TAN); Sava, Makirovana, 14°10'29.3"S, 49°57'07.7"E, 695 m, 06.V.2010, *Reeb CR282* (PC0763839).

Distribution. — Tropical South America and tropical Africa (Gradstein *et al.* 1983; Meenks & Pócs 1985). Widespread in tropical Africa, recorded from Angola, Bioko, Congo, Ethiopia, Gabon, Ghana, Ivory Coast, Mauritius, Madagascar, Malawi, Nigeria, Reunion, Rwanda, São Tomé and Principe, Seychelles, Sierra Leone, Tanzania, Uganda and Zimbabwe (Wigginton 2018). Records of *A. latissima* from South Africa are referred to *A. pinguis* (Perold 2001a).

Habitat. — On rotten wood and bark, rock and muddy banks in humid submontane and montane forests (Meenks & Pócs 1985).

Description

Meenks & Pócs (1985), Wigginton (2004). Mycorrhiza-like fungi may be observed in thallus cross-section, but they do not seem to be constantly present in African *Aneura*.

Comment

Jones (1956) treated *A. latissima* as a synonym of the widespread *A. pinguis* but Meenks & Pócs (1985 as *A. pseudopinguis*) showed that it differs from *A. pinguis* by the thinner thallus and the longer and often branched male branches (see key). As noted by Perold (2001a) and Jones (in Wigginton 2004), some overlap is noted in these characters, especially in the morphology of the male branches. Meenks & Pócs (1985) furthermore mentioned that the spores in *A. latissima* are smaller than those of *A. pinguis*. We have studied a few *Aneura* specimens from Madagascar and found that all had thalli less than nine cells thick, hence we consider them to belong to *A. latissima*. As we have seen only little African material, without sporophytes, the *Aneura* treatment of Meenks & Pócs (1985) and Wigginton (2004) is followed here.

Riccardia submarginata S.W.Arnell from South Africa was placed in the synonymy of *A. latissima* by Meenks & Pócs (1985 as *A. pseudopinguis*) but according to Perold (2001a) the thallus in this species is up to 13 cells thick (15 cells thick according to Arnell 1963) and therefore better fits *A. pinguis*.

Aneura pinguis (L.) Dumort.

Jungermannia pinguis L., *Species Plantarum* 1: 1136 (1753). — *Riccardia pinguis* (L.) Gray, *A Natural Arrangement of British Plants* 1: 684 (1821). — Type: Europa (Grolle 1976).

Description

Perold (2001a).

Comment

Aneura pinguis is known from South Africa and has also been reported from tropical Africa (e.g. Tanzania) where it seems to be rare (Meenks & Pócs 1985). According to the latter authors, most tropical African records of *A. pinguis* belong to *A. latissima*. We have not studied *A. pinguis* and refer to the excellent treatment for Africa by Perold (2001a). The species is genetically highly diversified and shows much cryptic speciation (Bączewics *et al.* 2017). The complexity of *A. pinguis* was already noted by Proskauer (1971) who stated (quotation from Perold 2001a: 172): "*Riccardia pinguis*, a species which we have long known to present a nightmarish problem[…] probably requiring more than a single lifetime of research for a minimum of understanding".

Genus *Riccardia* Gray

Remarks

About 100 species worldwide (Söderström *et al.* 2016). Based on the results of species delimitation analysis (Reeb *et al.* 2018), 12 species are recognized in Africa. Eleven of these occur in eastern Africa (Fig. 1) and three are new to science: *R. gasparii* sp. nov., *R. martinii* sp. nov. and *R. vohimanensis* sp. nov. In addition, *Riccardia multifida*, a species known from South Africa, may be expected to occur in eastern Africa and is therefore included in this treatment. The genus *Riccardia* is characterized by the 1-3-pinnately or palmately branched thalli with a narrow, 0.3-1.5(-2) mm wide axis and short sexual branches. The archegonia and antheridia are developed in two straight rows on separate branches. The genus is closely related to *Aneura* and *Afroriccardia* but the latter two genera have broader, less branched axes (more than 2 mm wide). In early literature, *Riccardia* was part of *Aneura* (e.g. Stephani 1898-1924).

Riccardia angusticosta (Steph.) Grolle

(Fig. 2A-E)

Aneura angusticosta Steph., *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 88: 724 (1913). — Type: Tanzania, Usambara, 1909, *Brunnthaler s.n.* (G[G0067547]!).

Aneura congoana Steph., *Species Hepaticarum* 6: 23 (1917). — Type: Zaire (Reeb & Bardat 2014).

Aneura stephanii Besch. ex Steph., *Revue Bryologique* 20: 60 (1893). (*Riccardia stephanii* [Besch. ex Steph.] E.W.Jones nom. illeg.). — Type: Congo (Jones 1956 as *R. stephanii*).

Aneura travisiana Pearson, *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 65: 1 (1921). — Type: Cameroon (Jones 1956 as *R. stephanii*).

Riccardia amazonica auct., (e.g. Meenks & Pócs 1985; Wigginton 2004; Reeb & Bardat 2014), non typus.

Riccardia capensis S.W.Arnell, see *Index Hepaticarum* — Type: South Africa (Reeb & Bardat 2014).

Further specimens examined. — **Gabon**. Ougoué-Invido, réserve intégrale d'Ipassa, 00°30'N, 12°48'E, 510 m, 18.IV.2006, *Vanderpoorten GAB1695** (LG).
Ghana. West Region, Aiyinasi, 13.II.1971, *Jones 1364C* (E00018737), *1361C* (G00264220).
Madagascar. Alaotra-Mangoro, Vohibola reserve, 18°34'53.4"S, 49°14'32.2"E, 5 m, 18.IV.2010, *Reeb, Andriamanantena & Bidault CRAE176* (PC0764349A); Sava, Makirovana, 14°10'29.3"S, 49°57'07.7"E, 695 m, 06.V.2010, *Reeb CR275* (PC0763840A),

Key to the species of *Riccardia* of eastern Africa

1. Thallus margins with numerous small, simple or branched papillae. Thallus very small, 2-10 mm long..... *R. inconspicua* (Steph.) Reeb & Bardat
— Thallus margins without papillae. Thallus small or large 2

2. Ultimate branches not winged (but sometimes bordered by a 1-cell wide hyaline band consisting of protruding cells, one in cross section) 3
— Ultimate branches winged, the wings (1-)2-6 cells wide, ± unistratose..... 7

3. Margins of dried thalli white. Walls of dorsal epidermis cells thickened, often orange-colored..... *R. martinii* sp. nov.
— Margins of dried thalli not white. Walls of dorsal epidermis cells thin or thickened, not orange-colored..... 4

4. Main axis in cross section circular to ellipsoid, stoloniform, without mycorrhizal fungi..... 5
— Main axis in cross section plano-convex to concave-convex, not stoloniform, with mycorrhizal fungi in the ventral half 6

5. Branching corymbose. Ultimate branches linear, inner cell walls often thickened ..... *R. ramosissima* (Steph.) Grolle
— Branching not corymbose. Ultimate branches tong-like to triangular, all cells thin-walled ..... *R. gasparii* sp. nov.

6. Main axis 8-12 cells thick (cross section). Radial walls of the epidermis cells not thickened. Immature calyptra strawberry-like, surface with numerous rounded, compact pachydermal cells ..... *R. vohimanensis* sp. nov.
— Main axis 4-6 cells thick. Radial walls of the epidermis cells thickened (Réunion) or not thickened (South Africa)..... *R. fastigiata* (Lehm.) Trevis.

7. Main axis not winged (but lateral margins sometimes with a maximally 1-cell wide hyaline band consisting of protruding cells, one in cross section)..... 8
— Main axis winged, the wings (1-)2-5 cells wide..... 10

8. Branching corymbose, not palmate. Ultimate branches only slightly and irregularly winged, the wings (0-)1(-2) cells wide. Stolons absent or rare ..... *R. ramosissima*
— Branching not corymbose, but frequently palmate. Ultimate branches distinctly winged, the wings 2-5 cells wide. Stolons common..... 9

9. Epidermis cells of the main axis more than 5× smaller than inner stem cells. Ultimate branches oblong to stocky, straight ..... *R. saccatiflora* (Steph.) S.W.Arnell
— Epidermis cells of the main axis 1-4× smaller than inner stem cells. Ultimate branches triangular to tong-like, often sinuose..... *R. corbieri* (Steph.) Reeb & Gradst.

10. Main axis in the middle of the thallus biconvex to plano-convex. Ultimate branches mostly narrowly linear, with crenulate margins. Oil bodies mostly absent in epidermis cells. South Africa (Cape Province), very rare.. ..... *R. multifida* (L.) Gray
— Main axis in the middle of the thallus plano-convex to concave-convex, never biconvex. Ultimate branches linear to oblong to tongue-shaped, margins not crenulate. Oil bodies present in epidermis cells. Widespread 11

11. Translucent area of the ultimate branches in dorsal view as wide as or wider than the midrib..... 12
— Translucent area of the ultimate branches in dorsal view narrower than the midrib 13

12. Ultimate branches narrower than the main axis. Epidermis cells on ultimate branches in oblique or straight rows ..... *R. angusticosta* (Steph.) Grolle
— Ultimate branches as wide as the main axis. Epidermis cells on ultimate branches in straight rows..... *R. longispica* (Steph.) Pearson (*erosa* phenotype)

13. Autoicous. Ultimate branches usually widened to the apex. Uncommon..... *R. chamedryfolia* (With.) Grolle
— Dioicous (rarely monoicous). Ultimate branches not widened to the apex. Very common..... *R. longispica*

ibid., 14°10'26.5"S, 49°57'26.5"E, 312 m, 05.V.2010, *Reeb CR231**, (PC0763846), *CR232** (PC0763847), *CR239** (PC0763842), *CR240** (PC0763843), *CR243** (PC0763844); Antsiranana (Sava), Manongarivo special reserve, 13°59'00"S, 18°26'00"E, 700-800 m, 02.III.1999, *Geissler 19480** (G) Tomasina (Analanjirofo), Manara Nord reserve, 16°25.8'S, 49°50.2'E, 5m, 13.VIII.1998, *Pócs & Szabó 9875AM* (EGR), ibid., road Andovoranto to Amila-Lemaitso, 18°54.2'55.4"S 49°7.3"E, 5 m, *Pócs & Szabó 9883H* *(EGR).
Malawi. Mulanje Mt., Sapitwa, 15°56'39"S, 35°34'58"E, 2800 m, 25.VI.1991, *Magombo M4312A* (E00430483), ibid., W of Minumu,

15°15'32"S, 35°38'19"E, 1980 m, *O'Shea M7124A-2* (E00430482).
Nigeria. Bénin province, 07.XII.1947, *Brenan & Jones 39* (G00264216), Ondo, Akure, 05.I.1948, *Brenan & Jones 140* (G00264218).
Tanzania. West Usumbara Mts., Mahezangulu, 1200 m, 24.I.1985, *Pócs 8520/1* (EGR).
Uganda. Kabarole, Kibale forest, 39°00'4"N, 30°23'00"E, 1410 m, 27.II.1996, *Wigginton U5291A** (E00430484).

Distribution. — Widespread in Africa; recorded from Cameroon, Congo, Ivory Coast, Gabon, Ghana, Kenya, Liberia, Madagascar, Malawi, Nigeria, Sierra Leone, South Africa, Tanzania, Uganda, Zaire, Zambia and Zimbabwe.

Habitat. — On decaying bark, humid rock or on dense bryophyte mats in humid evergreen lowland and montane forests, from sea level to 2800 m. Most collections are from 500-1000 m.

Description

Monoicous (autoicous), sometimes appearing dioicous.

Thallus

Bright green to pale green when fresh, yellowish to brown in herbarium, flaccid, translucent, in compact or loose mats, to 10(-12) mm long, main axis closely attached to the substrate, branches upright, 1-2-pinnate, not palmate, branches, alternate to subopposite, reiterations and flagelliform branches not seen, stolons rare.

Main axis

Irregularly defined, 400-800(-1200) µm wide, in cross section mostly plano-convex, sometimes concavo-convex (ellipsoid to plano-convex at the base), (3-)4(-5) cells thick, margins acute, narrowly winged, the wings 1-2(-3) cells wide, epidermis cells half smaller as inner cells to as large as inner cells, inner cells thin-walled.

Primary branches

Up to 3 mm long, rarely overlapping, variable in shape.

Ultimate branches

Tongue-shaped, oblong to linear, straight, to 1800 µm long, (300-)400-600 µm wide, in cross section plano-convex, 3-4 cells thick, broadly winged, the wings 2-3(-4) cells wide, as wide as or wider than the midrib, epidermis cells in straight or diverging rows, branch apex acute to rounded, clearly dissected, without overlapping edges, sometimes darkened by active mitosis.

Mucilage papillae

Ventral (in 2 rows) and apical, vanishing.

Sexual branches

Conspicuous, often the same size as vegetative ultimate branches and sometimes larger.

Male branches

On main axis and primary branches, sometimes grouped, with or without short stalk, straight, sometimes narrowed to apex, to 1200 µm long, margins crenate by large mamillose cells; antheridia in up to 18 pairs, the pairs separated from each other by one cell. Female branches on main axis and primary branches, not stalked, ventro-laterally inserted (ventral when young), straight, solitary, to 875 µm long, margins with straight or incurved, pluricellular hairs; archegonia in up to 20 pairs. Calyptra to 1800 µm long, straight, striate, terminating in an up to 150 µm long umbo or (when old) in loosely aggregated cells. Gemmae occasionally present, 2-celled.

Comment

The tiny autoicous plants growing tightly attached to the substrate, and the broad wings of the ultimate branches, which are as wide as or wider than the costa, are the main characteristics of *R. angusticosta*. The species was called *R. amazonica* (e.g. Meenks & Pócs 1985; Wigginton 2004; Reeb & Bardat 2014) but the latter is a Neotropical species that may not occur in Africa and is now named *R. regnellii* (Angstr.) K.G.Hell (Gradstein & Reeb 2018a). However, the species delimitation and relationships are not fully resolved between *R. regnelli* and *R. angusticosta* and more neotropical specimen must be included in further analysis. Morphologically, the African plants differ from *R. regnellii* in: 1) absence of heterothally; 2) inner cells of the main axis fully thin-walled; 3) midrib of the ultimate branches as wide as or narrower than the wings; and 4) male branches up to 18 pairs of antheridia long and with a conspicuously crenate margin. *Riccardia regnellii*, in contrast, is heterothallous with male plants smaller than female plants, the walls of the inner cells of the axis are somewhat thickened, the midrib of the ultimate branches is broader than the wings, and the male branches are up to 12 pairs of antheridia long and without crenate margin. Gradstein & Reeb (2018a) suggested that the African plants should be called *R. longispica* but further analysis of the data showed that *R. longispica* is a different species and that the correct name of the plants is *R. angusticosta*. In Reeb *et al.* (2018), *R. angusticosta* was called "*Riccardia* sp5".

Although being clearly separated from *R. longispica* in molecular analysis, *R. angusticosta* can be difficult to distinguish morphologically from the *erosa* phenotype of *R. longispica*. Differences are shown in the key.

Riccardia chamedryfolia (With.) Grolle
(Fig. 2F-I)

Jungermannia chamedryfolia With., *A Botanical Arrangement of the Vegetables of Great Britain* 2: 699 (1776). — Type: England (Grolle 1976).

Specimens examined. — **Comores**. Grandes Comores, Karthala, 1600 m, 01.V.2008, *Bardat KarP1Q2Hu1** (PC0763845).
Ethiopia. Bonga, Araba Yel forest, 37°80'77.54"N, 18°73'34"E, 1798 m, *Hylander KH5490** (ETH, PC0763857); Boka forest, 02.XI.2006, *Hylander KH5497** (ETH, PC0763862); Bale Mts., Harenna forest, 06°42'58.3"N, 39°43'32.1"E, 2380 m, 10.VIII.2011, *Reeb, Queinnec & Wégé CR11418** (ETH, PC0763898), ibid., road to Rira, 06°43'09.4"N, 39°43'11.3"E, 2392 m, 10.VIII.2011, *Reeb, Queinnec & Wégé CR11425**(ETH, PC0763893), *CR11428** (PC0763896, ETH).
Madagascar. Analamanga, Station d'Angavokely, 18°55'44.8"S,

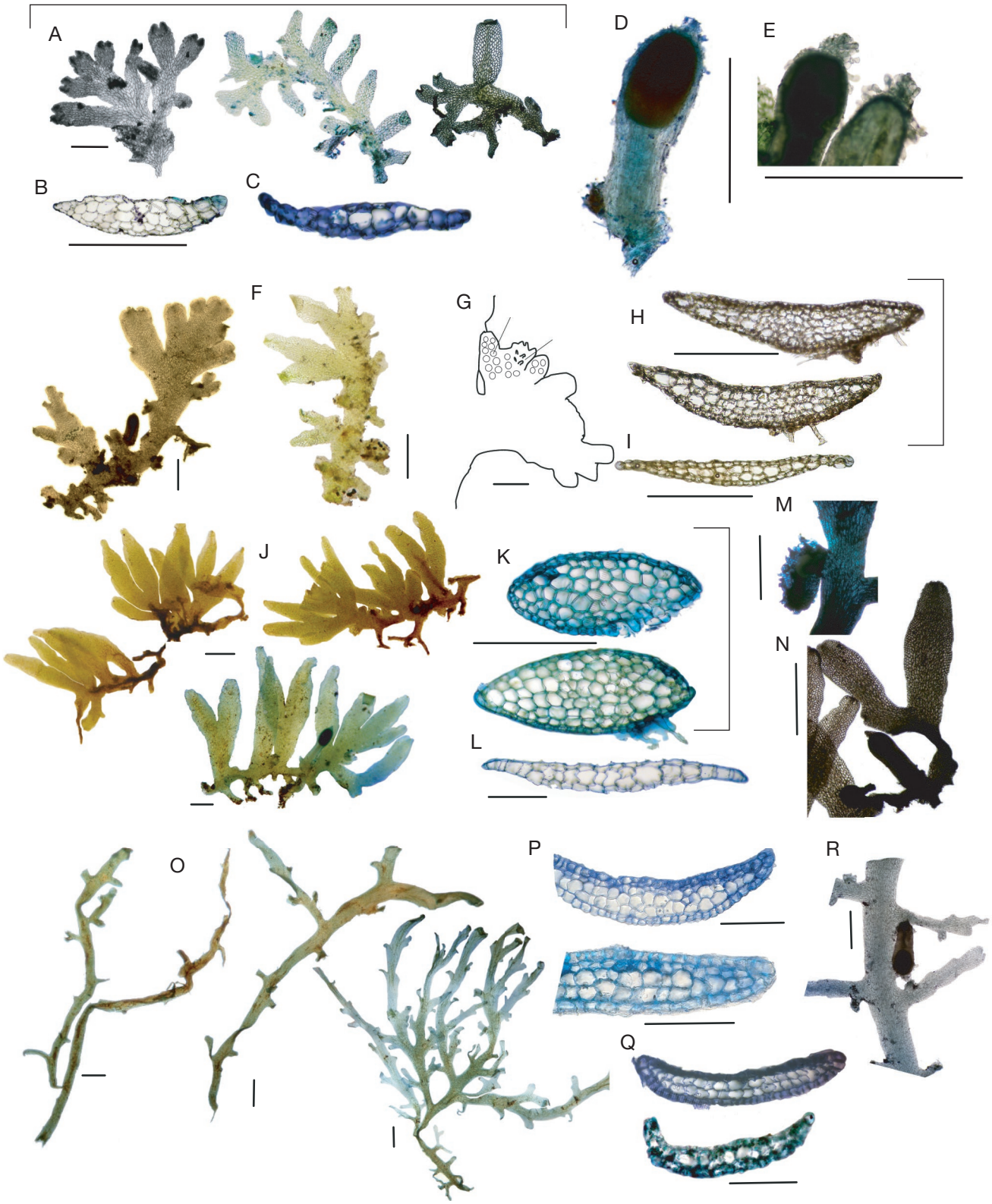

FIG. 2. — *Riccardia angusticosta* (Steph.) Grolle: **A**, thalli; **B**, main axis in cross section; **C**, ultimate branch in cross section; **D**, calyptra; **E**, upper portion of calyptra, showing umbo. From *Thollon s.n.* (*Aneura stephanii* TYPE), *Pócs 9883/H, Brenan140. Riccardia chamedryfolia* (With.) Grolle: **F**, thalli; **G**, portion of thallus showing male and female branches; **H**, main axis in cross section; **C**, ultimate branch in cross section. From *Reeb CR11156* (PC0763897), *CR11418* (PC0763898), *Hylander KH5497* (PC0763862). *Riccardia corbieri* (Steph.) Reeb & Gradst. comb. nov.: **J**, thalli; **K**, main axis in cross section; **L**, ultimate branch in cross section; **M**, portion of thallus with female branch; **N**, ultimate branches and calyptra. From *Beaver B304* (PC0763848), *Reeb CR297* (PC0763838A), *CR295* (PC0763837A). *Riccardia fastigiata* (Lehm.) Trevis.: **O**, thalli; **P**, main axis in cross section; **Q**, ultimate branches in cross section; **R**, portion of thallus with femalre branches and calyptra. From *Vojko 9422/AP, Pócs 6929/T*, *Orban 9615/CB* (PC0146833). Scale bars: A, D-F, J, M-O, R, 1 mm; B, C, G-I, K, 500 µm; L, P, Q, 200 µm.

47°45'04.8"E, 1507 m, *Reeb & Andriamiarisoa CR11156** (PC0763897, TAN).
Malawi. Mulanje Mts., 15°53'32.1"S, 35°29'24"E, 2180 m, 22.VI.1991 *O'Shea M7327A-1** (E00430482), *Longton M8299A** (E00430472).
France. Réunion, Forêt de Belouve, Plateau Citrons, 21°31.5"S, 55°33.5"E, 1500 m, 18.VI.1996, *Pócs 9647A* (EGR), 1150 m, 09.IX.2013, *Bardat REU1365** (PC0146834).
Uganda. Kabala, Bwindi National Park, 10°40'S, 02°E, 2050 m, 30.I.1996, *Wiggington U5137C** (E00430554), 2070 m, 26.I.1996, *Porley U97A** (E00430540).
Zimbabwe. Melsetter District, Kasipiti, 1200 m, 28.XII.1964, *Loveridge 1289* (EGR).

Distribution. — Widespread in temperate regions of the Northern Hemisphere, also in tropical America (e.g. Gradstein & Costa 2003; Schäfer-Verwimp *et al.* 2013; Rabeau *et al.* 2017). Newly reported from Africa where the species has been found in St. Helena (Rabeau *et al.* 2017), Comores, Ethiopia, Madagascar, Malawi, Reunion and Uganda.

Habitat. — On dead wood and tree trunks in in sheltered environments in humid forests, also on humid rocks in streams and at the entrance of caves, between 900 and 2400 m.

Description
Monoicous (autoicous or paroicous).

Thallus
Green to brownish when fresh, yellow to bright brown in herbarium, flaccid, dull to glossy, to 20(-40) mm long, loosely to closely attached to the substrate with creeping to erect and sometimes recurved branches, mostly 2-3-bipinnate, sometimes palmate, branches alternate to subopposite, occasionally flagelliform, stolons rare.

Main axis
Not well-defined, variable in width, in cross section planoconvex to concave-convex, 5-6(-7) cells thick, margins acute, with narrow, 1-2 cells wide wings, epidermis cells 3-4× smaller than inner cells.

Primary branches
To 3 mm wide, 5-6(-7) cells thick, rarely overlapping, axis narrowed towards basis.

Ultimate branches
Tongue-shaped, oblong and dense, often fan-like arranged, straight and somewhat widened to the apex, to 3.5 mm long and 1.2 mm wide, in cross section concave-convex to planoconvex, winged, wings 1-4 cells wide, narrower than the midrib, apex enlarged, broad.

Mucilage papillae
Apical and in two ventral rows, persistent.

Oil bodies
Present in nearly all cells, grayish to light brown, 1-2 and rounded in epidermis cells, 1-4(-5) and fusiform in inner cells.

Sexual branches
Solitary or sometimes grouped, sessile, occurring along all the axis, laterally inserted.

Male branches
Bordered by convex cells.

Female branches
Straight, not recurved, margin with more than two cells long scales and cilia, somewhat crisped, fimbriate.

Calyptra
With scattered thick-walled cells, umbo lacking.

Gemmae
Occasionally present, 2-celled.

Comments
Riccardia chamedryfolia has not previously been recognized in Africa, probably due to confusion with the polymorphic *R. longispica*. A well-delimited cluster of *R. chamedryfolia* was recovered in the molecular analysis with new records from Guadeloupe, St. Helena and the mainland of tropical Africa, indicating a more widespread distribution of the species than was previously known (Rabeau *et al.* 2017). The species is mainly characterized by the winged, planoconvex to concave-convex axis and branches, the broad branch apices, the epidermis cells much smaller than inner thallus cells, and monoicy. Sterile plants may be confused with robust phenotypes of *R. longispica* and *R. saccatiflora* but *R. longispica* is normally dioicous whereas *R. saccatiflora* lacks an axial wing and is usually palmate, and has dark brown oil bodies.

Riccardia corbieri (Steph.) Reeb & Gradst. comb. nov.
Fig. 2J-N

Aneura corbieri Steph., *Species Hepaticarum* 6: 23, 1917. — Type: Madagascar, 1898, *Leloutre 126a* (G[G00045028]!).

Aneura nudiflora Steph., *Hedwigia* 31: 199 (1892). — *Riccardia nudiflora* (Steph.) Grolle, *Bryophytorum Bibliotheca* 48: 130 (1995). — Type: Mauritius, *Robillard s.n.* (lecto- fide Reeb & Bardat [2014], G[G0037569]!) **syn. nov.**

Further specimens examined. — **Madagascar**. Sava, Makirovana, 14°10'17.4"S, 49°57'07.5"E, 508 m, 07.V.2010, *Reeb & Pierrot CR295** (PC0763837A, TAN), *CR297** (PC0763838A, TAN).
Seychelles. Mahé, Pointe au sel, 139 m, 20.IX.2012, *Senterre & Labiche-Barreau 6310** (PC0763853, SEY), Mare aux cochons, 562 m, *Senterre & Labiche-Barreau 6258** (PC0763852, SEY), 18.II.2012, *Beaver B304** (PC0763848, SEY).

Distribution. — Madagascar, Mauritius, Seychelles.

Habitat. — On rock or dead wood in humid evergreen forests, from 100 to 560 m.

Description
Monoicous (autoicous).

Thallus
Green to olive green when fresh, yellow green to bright brown in herbarium, fleshy but not leathery, usually dull (rarely glossy), mostly flat, to 20 mm long, main axis creeping and attached to the substrate, branches ascending to erect, mostly 1-2-pinnate, not palmate, branches alternate to subopposite, flagelliform branches absent, stolons often present on the main axis, especially near the base in young plants, ultimate ascending branches wider than creeping ones.

Main axis
Very irregularly defined, in cross section ellipsoid to biconvex, 5-6(-9) cells thick, margins rounded, not winged (exceptionally margin cells bulging outwards), epidermis cells 2-4× smaller than inner cells, all cell walls thickened in mature thalli.

Primary branches
Erect, to 15 mm long, rarely overlapping.

Ultimate branches
Tongue-shaped to triangular, often sinuose, 3-5 mm long, 0.8-1.2 mm wide, cells usually in straight rows, rarely in diverging rows, in cross section plano-convex to concave-convex, with 4-5 cells wide wings, the wings narrower to as wide as the midrib, epidermis cells 2-3× smaller than inner cells, branch apex rounded to truncate to emarginate.

Mucilage papillae
In two ventral rows, persistent.

Oil bodies
Not seen.

Male branches
Along main axis and primary branches, solitary, sessile, with a narrow, one cell wide wing.

Female branches
Straight, laterally to ventro-laterally inserted, margins with up to eight cells long cilia and with broad wings as wide as or wider than the axis, the wings sometimes recurved and branch becoming cup-shaped.

Calyptra
Smooth, with a triangular umbo of aggregate cells.

Gemmae
Occasionally present, 2-celled.

Comment
Riccardia corbieri comb. nov. is mainly characterized by the main axis with rounded margins and without wings, the erect, narrowly tongue-shaped to triangular, broadly winged ultimate branches (wings 4-5 cells wide) and the calyptra with a triangular umbo. The species was considered a synonym of *R. ramosissima* by Reeb & Bardat (2014) but molecular analysis recovered these two species in different clades (Reeb *et al.* 2018; Fig. 1). Morphologically, *R. ramosissima* is separated from *R. corbieri* comb. nov. by the corymbose habit, absence of stolons, and ultimate branches with narrower, 1-3 cells wide wings.

Within the *R. corbieri* clade, two geographical subclades were found – one in Madagascar and one in the Seychelles – but no clear morphological characters were found differentiating them.

Riccardia fastigiata (Lehm.) Trevis.
(Fig. 2M-R)

Jungermannia fastigiata Lehm., *Linnaea* 4: 370 (1829). — *Aneura fastigiata* (Lehm.) Lehm. & Lindenb., *Synopsis Hepaticarum* 500 (1846). — Type: Cape Town, „Montis Teufelsberg et in vertice montis Tafelberg", *Ecklon s.n.* (lecto-, S-B104928!; isolecto-, G[G0067556]!).

? *Aneura caespitans* Steph., *Bulletin de la Société Royal de Botanique de Belgique* 30: 194 (1891) — Type: Réunion, *Rodriguez s.n.*, ex hb. Renauld (holo-, BM[BM001167936]!). **syn. nov.**

Further specimens examined. — **Réunion**. Cirque de Salazie, plaine des Merles, 21°02'50"S, 55°28'08"E, 1800 m, 24.VIII.1994, *Vojko 9422AP*, 9422V** (EGR); Forêt de Belouve, plateau des Cochons, 21°02'00"S, 55°33'00"E, 1430 m, 02.VII.1996, Orban *9615CB** (EGR, PC0146833); Piton de la Fournaise. 21°18'00"S 55°42'07"E. 1390-2100 m. 30.VI.1996. *Pócs 9613CD** (EGR). **South Africa**. Pietermaritzburg, 914 m, XII.1914, *Sim 7536*, *7538* (PRE); Knysna, 01.IV.1929, *Bottomley 3671* (PRE); eastern slope of Table Mountain, 300 m, 19.III.1995, *Arts 3318CD* (PRE).

Distribution. — South Africa, Réunion.

Habitat. — Among *Sphagnum* and on rocks in streams, between 300 and 2100 m.

Description
Monoicous (Dioicous).

Thallus
Gray green, olive to deep green when fresh, becoming darker colored in herbarium, flaccid, strap-shaped, loosely or not attached to the substrate, to 25 mm long, 1-3-pinnate, not palmate, branches alternate, flagelliform branches sometimes present, stolons not seen.

Main axis
Well-defined, to 1 mm wide, in cross section plano-convex to concave-convex, usually with mycorrhiza-like fungi in the ventral part, 4-6 cells thick, margin rounded to acute, with a translucent band of protruding cells but not clearly winged, epidermis cells *c.* 2-3× smaller than inner cells to equal in size, regularly quadrate, radial walls of the epidermis cells often thickened (in material from Réunion).

Ultimate branches
Tongue-shaped to oblong, mostly 1-2(-4) mm long and 200-400(-500) µm wide, at an angle of 60-80° with the axis, cross section similar to axis, margins with protruding cells but not

clearly winged, branch apex often broadened, rounded or cucullate, not dissected.

Mucilage papillae
In two rows, clavate.

Oil bodies
Not seen.

Male branches
Short, straight or reflexed, often shortly stalked, up to 900 µm, max. of 7-8 antheridial pairs, regularly bordered by a plane or undulate, 2-3 cells wide wing.

Female branches
Mostly solitary, laterally inserted, present along the main axis and along primary branches, sessile or shortly stalked, recurved when immature, 300-800 µm long, with wing-like scales, the scales 2-4 cells wide; archegonia in up to five pairs.

Calyptra
With an umbo of aggregated cells and pachydermal scattered cells.

Gemmae
Occasionally present, 2-celled.

COMMENTS
Riccardia fastigiata resembles *R. chamedryfolia* but the latter species is autoicous and has clearly winged branches. A noteworthy feature of the specimens of *R. fastigiata* from Réunion are the thickened radial walls of the epidermis cells. In the material from South Africa, including the type, epidermal thickenings are usually lacking. As the plants from the two regions are identical in all other respects, we treat them as conspecific. Fresh collections are needed to verify this (DNA of the South African plants could not be amplified).

Aneura caespitans Steph. is probably a synonym of *Riccardia fastigiata*. The type material (Réunion, leg. Rodriguez) is sterile and poorly developed. Reeb & Bardat (2014) did not see the type (it is lacking in G) and treated *A. caespitans* as a dubious name. They noted that the description of the species in *Species Hepaticarum* (Stephani, 1898-1924) is heterogeneous and includes characters of two different species, including the type and a specimen from Cameroon (*Dusén 251*) not mentioned in the protologue. The confusion was worsened by Stephani's illustration of *A. caespitans* in *Icones Ineditae* (Stephani 1985), which was based on the specimen from Cameroon and not on the type. We have now been able to examine both specimens (kept in BM) and found that the type belongs probably to *R. fastigiata*, as mentioned, whereas the plant from Cameroon is *R. saccatiflora*. Already E.W. Jones (in sched.) noted that the type of *A. caespitans* and the specimen from Cameroon are different taxa. Since no duplicates of the type are present in G or other herbaria, the collection in BM may be considered the holotype.

Riccardia gasparii Reeb & Gradst. sp. nov.
(Fig. 3A-E)

DIAGNOSIS. — Dioicous. Thallus very fleshy, unwinged. Axis circular to biconvex, branches with rounded margins. Male branches stalked.

TYPE. — **Madagascar**. Alaotra-Mangoro, Vohimana Reserve, Grande Cascade, 18°55'43.6"S 49°29'56.6"E, 849 m, 30.VI.2012, *Reeb MTV1246** (holo-, PC[PC0771050]; iso-, PC[PC0763876], TAN).

ETYMOLOGY. — Dedicated to Gaspard Reeb-Leurent, born 21/07/2015.

FURTHER SPECIMENS EXAMINED. — **Madagascar**. Alaotra-Mangoro, Vohimana Reserve, Grande Cascade, 18°55'43.6"S, 49°29'56.6"E, 849 m, 30.VI.2012, *Reeb MTV1257* (PC, TAN); Maromizaha Reserve, 18°58'53.02"S, 48°27'50.1"E, 1002 m, 08.VII.2012, *Reeb MTM12124** (PC, TAN), 18°58'53.10"S, 48°27'51"E, 921 m, 08.VII.2012, *Reeb MTM12127A**, *MTM12133**(PC0763885), *MTM12134** (PC0763884, TAN); Analanjirofo, Mananara Nord, E slope of Mahavoho hills, 16°27'S, 49°46.9'47.5"E, 220-300 m, 14.VIII.1998, *Pócs & Szabo 9878/W* (EGR).

DISTRIBUTION. — Alaotra-Mangoro and Analanjirofo regions of Madagascar.

HABITAT. — On rocks or boulders sometimes covered with a humus layer, in humid evergreen lowland and montane forests, between about 200 and 1000 m.

DESCRIPTION
Dioicous.

Thallus
Dull olive green to green when fresh, green to yellow brown in herbarium, very fleshy, rigid but not leathery (easily breaking when manipulated), to 2 cm long, 1-3-pinnate, not palmate, branches alternate to subopposite, reiterations sometimes present, stolons common, branches mostly wider than the main axis.

Main axis
Irregularly defined to well-defined in mature thalli, width variable, in cross section circular to ellipsoid at the base, circular to biconvex in the middle, 7-9(-16) cells thick, margins obtuse to rounded, not winged, epidermis cells 3-4× smaller than inner cells.

Primary branches
To 7 mm long, often overlapping.

Ultimate branches
Tongue-shaped to oblong, often sinuose (horizontally curved), to 6 mm long and 1.8 mm wide, in cross section plano-convex, 5-6(-7) cells thick, margins obtuse, not winged, epidermis cells 2-3× smaller than inner cells, branch apex rounded.

Mucilage papillae
Apical, not persistent.

Oil bodies
Not seen.

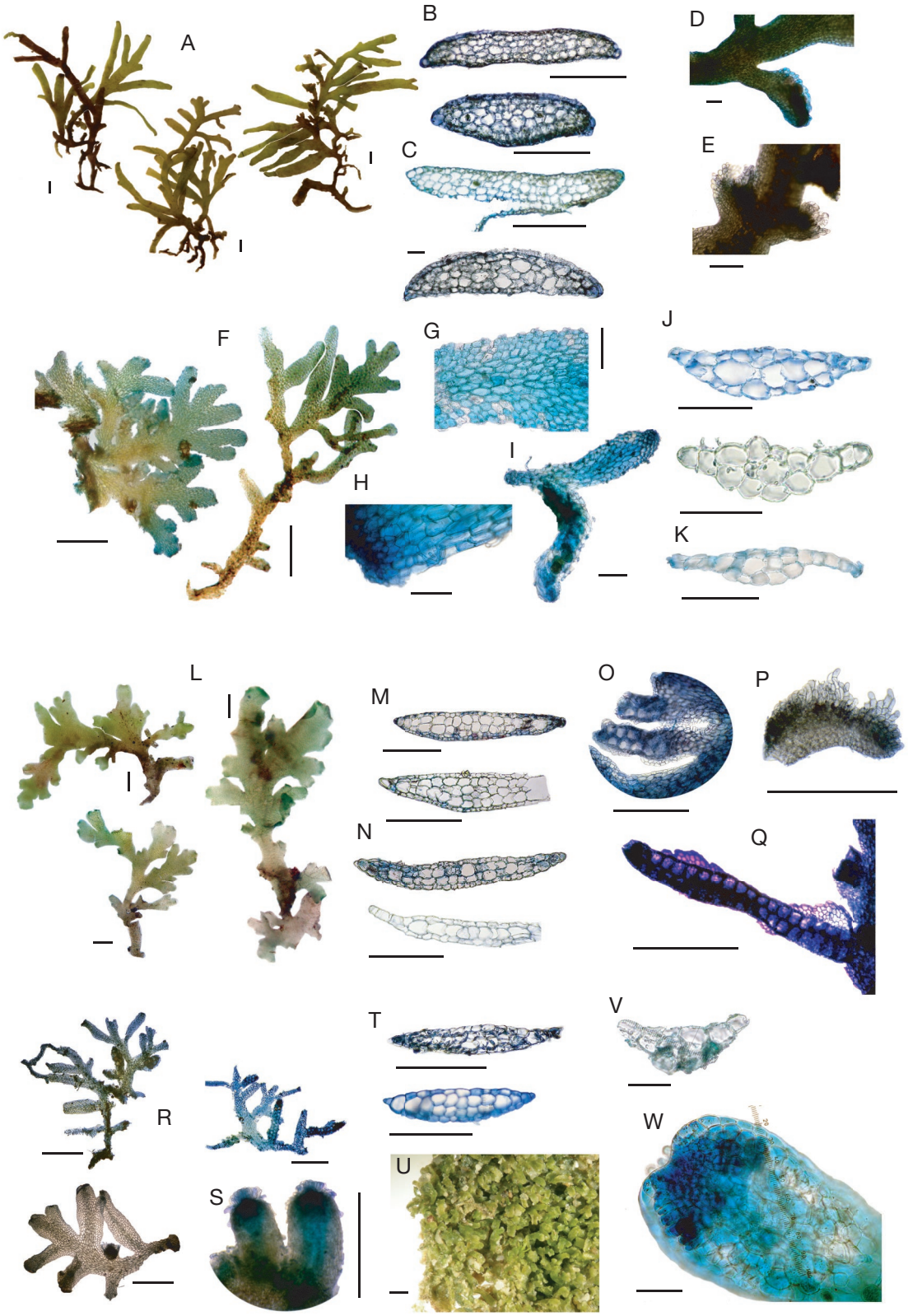

FIG. 3. — *Riccardia gasparii* Reeb & Gradst. sp. nov.: **A**, thalli; **B**, main axis in cross section; **C**, ultimate branches in cross section; **D**, male branch; **E**, female branches. From *Reeb MTV1246 (*PC0771050*), MTM12134* (PC0763884). *Riccardia inconspicua* (Steph) Reeb & Bardat: **F**, thalli; **G**, portion of ultimate branch with papillae; **H**, branched papilla (arrow); **I**, ultimate branch and male branch with papillae; **J**, main axis in cross section; **K**, ultimate branch in cross section. From *Reeb MTM1295* (PC0763882), *Pócs & Mwanjabe 6464/BP, Gardiner s.n.* (Type of Aneura exigua), *Jungner s.n.* (Type of *Aneura inconspicua*). *Riccardia longispica* (Steph.) Pearson: **L**, thalli; **M**, main axis in cross section; **N**, ultimate branches in cross section; **O**, two male branches; **P**, female branch; **Q**, male branch. From *Konya 9644/D*, *Bardat PF.2* (PC0763860), *Pócs 9612/CD, De Lisle 199* (Type), *Jones 1542b*. *Riccardia longispica* (Steph.) Pearson phenotype *erosa*: **R**, thalli; **S**,two calyptra's; **T**, main axis in cross section; **U**, thallus mat showing erect, concave ultimate branches; **V**, ultimate branch in cross section; **W**, branch apex with papillae and immature gemmae. From *Porley U35b*, *Pócs 6052/CV, Reeb CRAE193* (PC0763859). Scale bars: A, F, L, R, U, 1 mm; B, C, M-P, Q, S, 500 µm; D, E, G-K, T, 200 µm; H, V, W, 100 µm.

Male branches
On the main axis, solitary, stalked, with a scale-like wing narrower than the axis, the wing crenulate by larger cells.

Female branches
Laterally inserted, straight, bordered by a ciliate, scale-like wing.

Gemmae
Occasionally present, 2-celled.

COMMENT
Riccardia gasparii sp. nov. is characterized by its fleshy texture, the circular to ellipsoid, stoloniform main axis without wing, unwinged branches with mostly rounded margins, stalked male branches and dioicy. The species was called "*Riccardia* sp6" in Reeb *et al.* (2018). *Riccardia gasparii* sp. nov. is hitherto only known from Madagascar but could be more widespread.

Riccardia inconspicua (Steph.) Reeb & Bardat (Fig. 3F-K)

Aneura inconspicua Steph., *Hedwigia* 32: 23 (1893). — Type: Cameroon, *Junger 5* (lecto-, here designated, G[G00067564]!; isolecto-, S-B20523!).

Riccardia tenuicostata Schiffn., *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 67: 166 (1898). — *Aneura tenuicostata* (Schiffn.) Steph., *Species Hepaticarum* 1: 245 (1899). — Type: Singapore (Furuki 1994).

Aneura exigua Steph., *Species Hepaticarum* 6: 25 (1917). — Type: Seychelles (Reeb & Bardat 2014).

FURTHER SPECIMENS EXAMINED. — **Cameroon**. Ekundu N'dene, 16.III.1892, *Dusén 841* (G00264075, PC0101721). Cameroon: Kumba, Banga, S. Bakundu Forest Reserve, 5°5'50"N, 9°18'35"E, 15.III.1948, *Brenan & Jones 269* (E).
Madagascar. Alaotra-Mangoro, Maromizaha Reserve, 18°58'45"S, 48°27'51.8"E, 1011 m, 06.VII.2012, *Reeb MTM1295** (PC0763882, TAN).
Seychelles. Mahé, Congo Rouge, 46°27'40.68"S 55°26'12.768"E, 820 m, 16.IV.2012 *Senterre & Lariche SEY6265** (PC, SEY).
Tanzania. Morogoro, Uluguru Mts., Kilangala, SE of Bundunki, 1750-1950 m, 21.IX.1971, *Pócs & Mwanjabe 6464BP* (EGR).

DISTRIBUTION. — Paleotropical: tropical Africa (Cameroon, Madagascar, Seychelles, Tanzania), tropical Asia, Australia (Queensland).

HABITAT. — On rotten wood in humid lowland and montane forests, between 120 and 1950 m.

DESCRIPTION
Dioicous.

Thallus
Green to pale-green when fresh, yellow to clear brown in herbarium, flaccid and fragile, glossy, mostly flat, very small, to 10 mm long, main axis creeping and attached to the substrate, branches erect, 1-2-pinnate, not palmate, branches alternate to subopposite, stolons rare, thallus margins with mucilage papillae.

Main axis
Irregularly to clearly defined, 150-300(-350) µm wide, in cross section plano-convex, (3-)4(-5) cells thick, margins acute, with a 1-2 cells wide wing.

Ultimate branches
Tongue-shaped to oblong, up to 1.5 mm long, in cross section 3-4 cells thick, lunate to concavo-convex, with 3-4 cells wide wings, the wings as wide as or wider than the midrib.

Mucilage papillae
On all branch margins (including sexual branches), especially on ultimate branches, simple to 2-3-furcate, to 100 µm long.

Oil bodies
Not seen.

Male branches
Solitary, straight to recurved, sessile or stalked, to 1.8 mm long, with up to 20 antheridial pairs, the margin with a scale-like wing equal to sometimes wider than the axis.

Female branches
Inserted laterally, straight, solitary or grouped, with up to 22 archegonial pairs, bordered by numerous, 4-5 cells long cilia, the cilia to 250 µm long, exceeding the width of the axis.

Calyptra
625-800 µm long, with an umbo of aggregate cells.

Gemmae
Abundant, present in all collections seen, 2-celled.

COMMENT
Riccardia inconspicua is the smallest African *Riccardia* and is readily recognized by the numerous, simple or branched mucilage papillae on the thallus margins. Based on the marginal papillae, the species has been placed in a separate subgenus, *R.* subg. *Thornoneura* Furuki (Furuki 1991, 1994). The papillae are rather inconspicuous in wetted herbarium specimens but are clearly visible after bleach and blue coloration of the material. The species often grows mixed with other *Riccardia* species, especially *R. longispica*, and was treated as a synonym of *R. erosa* (synonym of *R. longispica*) by previous authors (e.g. Jones 1956).

Riccardia longispica (Steph.) Pearson (Fig. 3L-W)

Aneura longispica Steph., *Botanical Gazette* 15: 281 (1890). — Type: Réunion, *Boivin s.n.* (G[G00067568]!).

Aneura congoensis Steph., *Species Hepaticarum* 6: 23 (1917). — Type: Congo (Reeb & Bardat 2014).

Aneura grosselimbata Steph., *Species Hepaticarum* 6: 29 (1917). — Type: Tanzania (Reeb & Bardat 2014 as *R. limbata*).

Aneura holstii Steph., *Species Hepaticarum* 6: 31 (1917). — *Riccardia holstii* (Steph.) E.W.Jones, *Transactions of the British Bryological Society* 3: 78 (1956). — Type: Tanzania (Reeb & Bardat 2014 as *R. limbata*).

Aneura lepervanchei Steph., *Species Hepaticarum* 1: 255 (1899). — Type: Réunion (Reeb & Bardat 2014).

*Aneura limbat*a Steph., *Hedwigia* 30: 204 (1891). — *Riccardia limbata* (Steph.) E.W.Jones, *Transactions of the British Bryological Society* 3: 79 (1956). — Type: Cameroon, Lower Bomania, 1890, *Dusén 33* (lecto-, here designated, G[G00067566]!) **syn. nov**.

Aneura piliflora Steph., *Species Hepaticarum* 6: 38 (1917). — Type: Madagascar (Jones 1956).

Aneura reticulata Steph., *Hedwigia* 30: 204 (1891). — *Riccardia reticulata* (Steph.) S.W. Arnell, *Botaniska Notiser* 1952: 152 (1952). — Type: Cameroon (Jones 1956 as *R. limbata*).

Aneura erosa Steph., *Hedwigia* 30: 269 (1891). — *Riccardia erosa* (Steph.) E.W.Jones, *Transactions of the British Bryological Society* 3: 83 (1956). — Type: Sao Tomé, 1989, *Quintas 7* (G[G0067552]!) **syn. nov**.

Aneura tenera Steph., *Species Hepaticarum* 6: 43 (1917). — Type: Tanzania (Reeb & Bardat 2014) **syn. nov**.

? *Riccardia kilimanjarica* S.W.Arnell., *Svensk Botanisk Tidskrift* 53: 543 (1959). — Type: Tanzania (Reeb & Bardat 2014).

Selected further specimens examined. — **Central Africa Republic**. Plateau de Kagadouba, 480 m, *Assel 729* (E00018738, EGR).
Comores. Karthala, 2010, *Bardat Karp1q2li2** (PC0763850).
Congo. Kimpese, road Lombo Fuese, 5°23'52"S, 14°28'12"E, 640 m, 13.I.2013, *Vanderpoorten 13111**.
Equatorial Guinea. Evinayong, Mt. Alen, 950 m. 25.VII.1994, *Heras VIT398/94**.
Ethiopia. Bonga, Gera Beki forest, 37°80'82.07"N, 19°96'66"E, 1881 m, 12.XII.2006, *Hylander KH5488**, *KH5491** (ETH, PC0763858).
Gabon. Ogoué-Ivindo, Réserve intégrale d'Ipassa, 00°30'N, 12°48'00"E, 510 m, 01.IV.06, *Vanderpoorten GAB1396**, 03°04'8"N, 12°46'12"E, 11.IV.06, *Vanderpoorten GAB1398**.
Ghana. Central region, Pra-Suhien Forest Reserve, 11.II.1971, *Jones 1339A* (E00018734, G00264219).
Madagascar. Alaotra-Mangoro, Vohimana Reserve, 18°55'24.2"S, 48°30'21.1"E, 860 m, 14.IV.2010, *Reeb, Andriamanantena, & Bidault CRAE74** (PC0724433B), 18°55'43.6"S, 48°29'56.6"E, 849 m, 15.IV.2010, *Reeb, Andriamanantena, & Bidault CRAE84* (PC0724365), *CRAE88** (PC0763869), 18°55'13.1"S, 48°30'57.1"E, 789 m, 29.VI.2012, *Reeb MTV1225** (PC0763889), *MTV1226* (PC), 18°55'45.7"S, 48°29'59.3"E, 918 m, 30.VI.2012, *Reeb MTV1234* (PC0763887), *MTV1237**(PC0763888), *MTV1238* (PC0763892); Alaotra-Mangoro, Maromizaha Réserve, 18°59'S, 48°28'E, 1084-1095 m, 07.VII.2012, *Reeb MTM12103** (PC0763854), *MTM12106** (PC0763855); Antsiranana, Manongarivo Special Reserve, 13°59'S, 48°26'E, 1300-1350 m, *Geissler 19708/5* (G); Sava, Parc du Marojejy, 29.XI.2009, *Bardat JBMAD104** (PC0763861), Makirovana, 14°10'29.3"S, 49°57'07"E, 695 m, 06.V.2010, Reeb CR276 (PC0763841), CR288 (PC0763836A), 14°17'10.04"S, 49°57'07.5"E, 508 m, 07.V.2010, *Reeb CR304** (PC0763833).
Malawi. Mulanje Mt., 15°53'21"S, 35°39'24"E. 2180 m, 25.VI.91, *Longton M8302A** (E), 15°55'01"S, 35°36'04"E, 2000 m, 24.VI.1991, *Kungu M3199A** (E-00430533).
Mauritius. Mt. Le Pouce, 20°13'5"S, 57°31'20"E, 750-811 m, 20.III.1995, Pócs *9537H** (EGR).
Réunion. Cirque de Salazie, 21°2'50"S, 55°28'8"E, 1899 m, 24.VIII.1994, *Szabo 9422J** (EGR); Plaine des Palmistes, 21°6'33"S, 55°39'E, 900 m, 30.VIII.1994, *Vojko 9435L** (EGR); Forêt de Belouve, 21°2'S 55°33.5'E, 1440 m, 16.VII.1996, *Konya 9644/D** (G00264189, EGR); Piton de la Fournaise, 21°18'08"S, 55°44'00"E, 1200 m, *Szabo 9609/CP** (EGR), 21°18'05"S, 55°42'05"E, 1000-1390 m, 30.VI.1996, *Pócs 9612/CD* (EGR). Plaine des fougères, 1325 m, 19.IV2011, Bardat PF.2 (PC0763860).
South Africa. Port Shepstone, Iberzana, 10 m, 23.VIII.1918, *Eyles 1407* (EGR).
Tanzania. Trail Kitoto to Meru crater, 2500 m, 11.VII.1968, *Sharp et al. P507* (E00018742, EGR); Mt. Kilimanjaro, trail Mweka to Kibo Peak, 2400-2800 m, 29.VII.1968, *Sharp et al. 7632* (E).
Uganda. Rukungiri, 1°00'00"S, 29°37'00"E, 1650 m, 07.II.1997, *Wiggington U8318C**, *U8321A*, *U8324A**.

Phenotype erosa. — **Gabon**. Province Ogououé-Ivindo, chutes de Kongou sur l'Ivindo 0°17'24"N, 12°25'18"E, 09.IV.2006, *Vanderpoorten GAB1435**.
Madagascar. Alaotra-Mangoro, Vohibola Reserve, 18°35'16.1"S, 49°14'28.8"E, 20.IV.2010, *Reeb, Andriamanantena & Bidault CRAE193* (PC0763859); Atsimo-Andrefana, massif du Makay, 21°34'05.9"S, 45°04'33.7"E, 303 m, 14.I.2011, *Reeb CR1126** (PC), 21°34'09.8"S, 45°04'35.4"E, 290 m, 16.I.2011, *Reeb CR1169** (PC0763891), 21°38'53"S, 44°59'52"E, 189 m, 23.I.2011, *Reeb CR11126** (PC0763894), *CR11127** (PC0763895).
Tanzania. Usambara Mts., Amanani, 950 m, 17.VI.1970, *Rasmussen & Esbessen B27* (EGR).
Uganda. Nyakafunjo Nat. Reserve, 24.I.1997, 1075 m, *Porley U416A* (E), 1060 m, *Hodgetts U4346A* (E); Kabale Bwindi Nat. Park, 01°23'7"S, 29°46'50"E, 2250 m, 25.I.1997, *Hodgetts U5009A** (E00430552), 2415 m, 25.I.1996, *Porley U35B** (E00430508).

Distribution. — *Riccardia longispica* is one of the most common African *Riccardia* species, recorded from almost all West and East African countries and Indian Ocean Islands (Wigginton 2018).

Habitat. — The large phenotype of *R. longispica* is mainly found on dead wood, sometimes on humid rock along streams or near waterfalls, or on dense bryophyte mats (in Réunion), between about 500 and 2500 m. The small *erosa* phenotype seems to have the same geographical distribution as the large phenotype but is mainly found on shaded lateritic soil, occasionally on rotten wood, and occurs at slightly lower elevation (200 m) on Madagascar.

Description

Dioicous, occasionally monoicous (*R. limbata*, *R. holstii*).

Thallus

Green to olive green when fresh, yellow to dark brown or green in herbarium, soft to fleshy, (10-)20-30 mm long, very variable when dry, crisped (in phenotype *erosa*) or flat, ultimate branches usually slightly recurved, main and secondary axes closely attached to the substrate from which arise the ultimate branches, branching 1-2(-3)-pinnate, sometimes palmate on young thalli, branches alternate or subopposite, reiterations sometimes present, stolons mainly seen in young thalli.

Main axis

Irregularly defined in young plants, well-defined in mature thalli, (600-)800-1200(-1400) µm wide, in cross section ellipsoid to biconvex at the base, plano-convex in the middle, 5-7(-8) cells high, margins acute, with narrow, 1-2 cells wide wings, epidermis cells at least 4-5× smaller than inner cells.

Primary branches

To 700 µm wide, occasionally overlapping.

Ultimate branches
Tongue-shaped to oblong, straight in well-developed thalli (stocky and fan-shaped in young thalli), 2.5-4.2 mm long, (0.4-)0.5-0.8(-1.0) mm wide, in cross section plano-convex to slightly concave-convex, 3-4(-5) cells thick, wings 2-4 cells wide, narrower than the midrib, epidermis cells usually in straight rows, rarely in diverging rows (obliquely to the axis), branch apex rounded to truncate with sometimes overlapping lateral edges.

Mucilage papillae
Ventral (in two rows) and apical, persistent.

Oil bodies
Present in all cells, spherical to ellipsoid to bean-shaped, finely granular, 1-2 per cell.

Male branches
Solitary, rarely grouped by two, along axis and branches, straight except when young, to 2 mm long, wing equal to narrower than the axis, scale-like, antheria in 6-12(-20) pairs.

Female branches
Ventro-laterally inserted, bordered by a scale-like, 1-2 cells wide wing, wing narrower than the axis, archegonia in 5-12 pairs.

Calyptra
To 2 mm long, terminating in a crown-like umbo and very scattered thick-walled cells armed with striations.

Gemmae
Occasionally present, especially at branch junctions, produced on deformed thallus margins, 2-celled.

Erosa phenotype (Fig. 2R-W)
Plants
Usually growing on lateritic soil.

Thallus
Very small, to 5-6 mm long only, 1-2-pinnate without reiterations, crisped when dry.

Main axis
180-320 µm wide, in cross section circular ellipsoid at the base to plano-convex in middle, 3-4 cells high, with 1-2 cells wide wings, epidermis cells 2-3× smaller than inner cells.

Ultimate branches
280-2000 µm long, 70-330 µm wide, linear to oblong, sometimes tongue-shaped, in cross section plano-convex, 3-4 cells thick, wings 3-4 cells wide, as wide as or wider than the midrib, wing cells in straight rows.

Sexual branches
Equal or longer than ultimate branches.

Male branches sessile
Or shortly stalked.

Comment
Riccardia longispica is the most difficult African species to recognize because of its large polymorphy. This variation is not correlated with genetic diversity (Rabeau *et al.* 2017; Reeb *et al.* 2018) and is presumably induced by the environment. Two phenotypes are recognized, a large phenotype (= the typical phenotype) from dead wood and humid rock, and a small phenotype (= *erosa* phenotype) from laterite soil in open areas or below vegetation, occasionally on bare, rotten wood. The small phenotype was accepted as a separate species, *R. erosa*, by Reeb & Bardat, but in a molecular analysis the species was nested in *R. ongispica* (Reeb *et al.* 2018). *Riccardia limbata* (and its synonyms; see Reeb & Bardat 2014) grouped with the large phenotype of *R. longispica* in molecular analysis and is a conspecific. The main distinction between *R. limbata* and *R. longispica* (Wigginton 2004; Meenks & Pocs 1985) was considered the presence of oblique rows of cells diverging from the midrib on ultimate branches. We found that this is a variable character that may vary even within a single thallus. The conspecificity was already suggested by Jones (1956, under *R. erosa*) and Reeb & Bardat (2014). *Riccardia longispica* phenotype *erosa* was called "*Riccardia* sp.1" and "*Riccardia* sp8" in Rabeau *et al* (2017). The identity of *Riccardia kilimanjarica* is problematic, as already discussed by previous authors (e.g. Reeb & Bardat 2014); we now believe the plant might belong to *R. longispica*.

Riccardia longispica is very close to *R. angusticosta* (= *R. amazonica* auct.) and these two species have often been confused in the past Perold 2003, especially the phenotype *erosa*. Morphological study of a large suite of material and molecular analysis (Fig. 1) showed that the two are different species, as earlier proposed by Jones (1956), Meenks & Pócs (1985) and Jones (in Wigginton 2004). Differences are shown in the key. The phenotype *erosa* is separated from *R. angusticosta* by the very narrow, 100-350 µm wide axis, the wing cells always in straight rows, and its occurrence on laterite soil. *Riccardia angusticosta*, in contrast, has a 400-1200 µm wide main axis, the wing cells on ultimate branches are in straight or oblique rows, and the plants occur mainly on rotten wood. *Riccardia longispica* may also be confused with *R. chamedryfolia* but the latter species is rare, the plants are autoicous and the ultimate branches are widened to the apex.

Riccardia martinii Reeb & Gradst. sp. nov.
(Fig. 4A-I)

Diagnosis. — Dry thallus with white margins and with an orange-colored network of thick-walled dorsal epidermis cells.

Type. — **Madagascar**. Alaotra-Mangoro, Zahamena Nat. Park, 17°38'22"S, 48°38'47"E 1247 m, 26.XII.2013, *Reeb & Andriamanantena CR13Z9** (holo-, PC[PC0763851]).

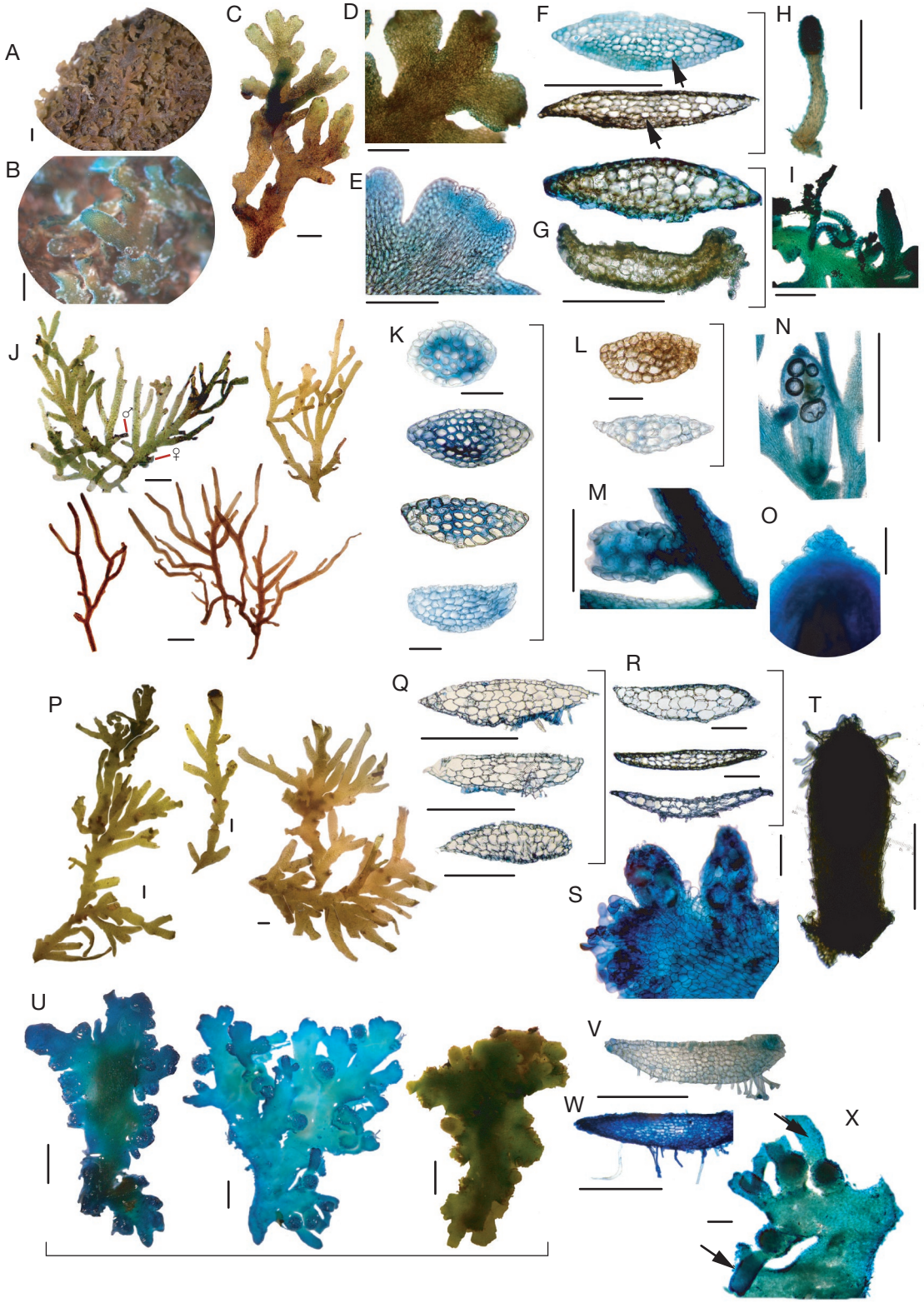

FIG. 4. — *Riccardia martinii* sp. nov.: **A**, thallus mats; **B**, dry thallus, showing white margins; **C**, moistened thallus; **D**, portion of thallus in dorsal view, showing thickened cell walls; **E**, apex of ultimate branch, showing papillae; **F**, main axis in cross section; **G**, ultimate branches in cross section; **H**, calyptra; **I**, portion of thallus with male branches. From *Sass-Gyarmati 9613/CW*, *Vojko 9660/CS*, *Pócs 9602CU, 6877/K, Bardat JBMAD78* (PC0763890), *Riccardia ramosissima* (Steph) Grolle: **J**, thalli; **K**, main axis in cross section; **L**, ultimate branches in cross section; **M**, male branch; **N**, calyptra; **O**, upper portion of calyptra, showing umbo. From *Reeb CR13Z51* (PC0763864), *Pócs 6981/A, Jelinek s.n.* (Type of *Aneura compacta*). *Riccardia saccatiflora* (Steph.) S.W.Arnell: **P**, thalli; **Q**, main axis in cross section; **R**, ultimate branches in cross section; **S**, portion of thallus with two female branch (left) and two male branches; **T**, calyptra. From *Wigginton M1758b, Reeb CR11142* (PC0763883), *Een M064, Rodriguez 182* (Type of *Aneura saccatiflora*). *Riccardia vohimanensis* Reeb & Gradst.: **U**, thalli; **V**, main axis in cross section; **W**, ultimate branch in cross section; **X**, sporophyte and calyptra with the vegetative expansion at its basis. From *Reeb MTM1278* (PC0763879), *CR13Z23* (PC0763868), *O'Shea M7327b, Een M028*. Scale bars: A-C, H-J, N, P, U, 1 mm; D-G, M, Q, T, V-X, 500 µm; K, L, R, 100 µm; O, S, 200 µm.

Further specimens examined. — **Réunion**. St Denis, 1500 m, 11.X.1962. *Een R039* (S-B12531); Piton de la Fournaise, 21°19'00"S, 55°42'00"E, 800-870 m, 23.II.1995, *Pócs 9501H** (G00264150, EGR), 21°18.5'S, 55°42'E, 800-1080 m, *Pócs 9602/CU** (G00264153, EGR), 21°18'0S, 55°42.7'E, 1800 m, 30.VI.1996, *Pócs 9612/CC, 9613/CC*, 9613/CW* (EGR); Plaine des Caffres, 21°09'S, 55°33'E, 1850 m, 22.VII.1996, *Vojko 9660/CS* (G00264121, EGR); Forêt de Bélouve, 21°4'S, 55°31.6'E, 1610-2000 m, *Pócs 9618/CU* (EGR). **Madagascar**. Alaotra-Mangoro, Zahamena Nat. Park, 17°38'22"S, 48°38'47"E 1247 m, 26.XII.2013, *Reeb & Andriamanantena CR13Z9** (PC0763856), *CR13Z25** (PC0763863); Vohimana Reserve, 18°55'43.6"S, 48°29'56.6"E, 849 m, 15.IV.2010, *Reeb, Andriamanantena & Bidault*; *CRAE106* (PC); Sava, Marojejy Nat. Park, X.2010, *Bardat JBMAD78** (PC0763890).
Tanzania. Uluguru Mts., Kinole Village, 1480-1530 m, 05.II.1973, *Pócs & Lubgwecha 6877/K* (G00264154, EGR), Kibale Forest, 1730 m, 19.X.1971, *Pócs 6477/M* (G00264161, EGR)., Bondwa, 2125 m, 13.XII.1972, *Pócs & Crosby 6947/K* (EGR), ridge and Lupanga peak, 2100-2400 m, 21.XI.1969, *Pócs & Csontos 6072/BA* (EGR).

Distribution. — Tanzania, Madagascar and Réunion.

Habitat. — On dead wood, bark on peaty soils covered a dense bryophyte layer, occurring between 400 and 4000 m but mainly found at mid elevations (800-1500 m).

Etymology. — Dedicated to Martin Reeb-Leurent, born 25/05/2011.

Description.
Monoicous (autoicous) or dioicous.

Thallus
Fleshy to leathery, rigid, green, glossy, green to dark brown or black in herbarium, to 22 mm long, when dry crisped or with recurved branches and with white margins, main axis closely attached to the substrate or to other thalli, 1-3-pinnate, sometimes palmate in young thalli, reiterations and stolons frequently present.

Main axis
Irregularly defined, 400-500 µm wide, with mycorrhiza-like fungi on the ventral side (cross section), in cross section ellipsoid to biconvex, rarely plano-convex, 7-10(-11) cells thick, with ventral subepidermis, margin acute with one bulging cell, not winged, epidermis cells more than 4-5× smaller than inner cells, radial walls of the dorsal epidermis cells usually thickened and orange-colored in dry material.

Primary branches
4-12 mm long.

Ultimate branches
Oblong, stocky to tongue-shaped, margins white or clearer, (0.2-)1.5-3 mm long, 0.3-0.4-0.7(-1.0) mm wide, in cross section lunate to concavo-convex, 4-7 cells thick, margins acute or with a 1-2 cells wide wing, epidermis cells equal or 2-4× smaller than inner cells, branch apex emarginate, dissected or retuse, without overlapping edges, young thalli with numerous multi-apical areas.

Mucilage papillae
Present, apical and in two ventral rows, 70(-100) µm long, exceeding the apex.

Male branches
Solitary or often grouped, sessile to or stalked, sometimes prolonged by vegetative growth, curved and reflexed with age, to 1 mm long, narrowly winged. the wing narrower than the axis, margins crenate by larger cells, antheridia in up to 20 pairs.

Female branches
Very short when young (seemingly immersed in the vegetative tissue), ventrally to ventro-laterally inserted, narrowly winged, the wing ornamented by short, straight cilia.

Calyptra
Rugose by scattered thick-walled, bulging cells.

Gemmae
Occasionally present.

Comment
Riccardia martinii sp. nov. stands out by the fleshy thallus bordered by white margins when dry, and by the thick-walled dorsal epidermis cells forming an orange-colored network on the dorsal thallus surface. In the analysis of African species, *R. martinii* sp. nov. is sister to *R. fastigiata* (Fig. 1). Morphologically, these two species are similar in the presence of mycorrhizal fungi and the lack of wings, but the white-colored thallus margins and the thicker, ellipsoid to biconvex axis of *R. martinii* sp. nov. readily separate this species from *R. fastigiata*. The evolutionary significance of these characters is being tested in a worldwide phylogenetic analysis of the genus *Riccardia* (Reeb, in prep.). In Rabeau *et al.* (2017), *R. martinii* sp. nov. was named "*Riccardia* sp.14" and resolved sister to *R. eriocaula* (Hook.) Besch. & C.Massal., an Australasian species (Browns & Braggins 1989). Herbarium specimens of *R. martinii* were previously named *R. longispica, R. saccatiflora* or *R. limbata.*

Riccardia multifida (L.) Gray
(Illustration: Perold 2001b)

Jungermannia multifida L., *Species Plantarum* 1: 1136 (1753). — *Aneura multifida* (L.) Dumort., *Commentationes Botanicae* 112 (1822). — Type: England (Grolle 1976).

Specimen examined. — **South Africa**. Diepwalle Forest Reserve, 07.X.2000, *Perold 4449* (PRE-P581351.0).

Distribution. — *Riccardia multifida* is widespread in temperate regions of the Northern Hemisphere; in addition, the species has been recorded from Brazil (Rio de Janeiro; Gradstein & Costa 2003) and from South Africa where it is known from several localities (Perold 2001b). The occurrence of *R. multifida* in South African was confirmed by molecular analysis (Reeb *et al.* 2018). The species is not yet known from East Africa and the Indian Ocean Islands, but may be expected there and is therefore included in this treatment.

Description
Monoicous (autoicous).

Thallus
Glossy green when fresh, green to brown in herbarium, fleshy, mostly flat, in compact layers, to 30 mm long, 1-3(-4)-pinnate, with regulary pinnate secondary branches, branches alternate to subopposite, reiterations and flagelliform branches present, stolons absent.

Main axis
Well-defined, in cross section ellipsoid, biconvex(to plano-convex) in the middle, 4-5(-8) cells thick, with a 2-3 cells wide wing, epidermis cells 2-4 × smaller than inner cells.

Primary branches
Up to 5 mm, regularly branched, branching at an angle of *c.* 45º with the axis, rarely overlapping.

Ultimate branches
Usually narrowly linear, occasionally tongue-shaped to oblong, straight, to 1.6 mm long, 0.5-0.6 mm wide, in cross section plano-convex to biconvex, 3-4 cells thick, winged, wings 3-4 cells wide, narrower than the midrib, branch apex rounded to truncate, margins crenulate by bulging cells.

Mucilage papillae
Apical and in two ventral rows, persistent.

Oil bodies
Absent or rare in epidermis cells, present in inner cells, 1(-2) per cell, spherical to ellipsoidal, light brown, finely granular.

Male branches
Along the axis, solitary to grouped, 600-750 µm long, margins crenate by larger, bulging cells.

Female branches
Laterally inserted, to 450 µm long, margins with mostly straight cilia or scales.

Calyptra
Up to 3 mm long, ornamented by loosely aggregated umbo cells and scattered thick-walled cells.

Gemmae
Not seen.

Riccardia ramosissima (Steph.) Grolle
(Fig. 4J-O)

Aneura ramosissima Steph., *Bulletin de la Societé Royal de Botanique de Belgique* 30: 196 (1891) — Type: Réunion, *Rodriguez s.n.* (G-00045033).

Aneura compacta Steph., *Hedwigia* 32: 19 (1893). — *Riccardia compacta* (Steph.) S.W.Arnell, *Botaniska Notiser* 1952: 141 (1952). — Type: South Africa, Cape province, *Jelinek s.n.* (lecto-, here designated, G[G00067549]!; isolecto-, PC[PC0101714]!, S[S-B20511]!) **syn. nov.**

Further specimen examined. — **Ethiopia**. Bale Montane, above Rira W of Aduka, 06°43'N, 39°42'E, 3320 m, 13.II.1990, *Miehe 2541* (EGR).
Madagascar. Alaotra-Mangoro, Zahamena Reserve, highest part of the river above base camp, 17°38'22.7"S, 48°38'45.3"E, 1294 m, 01.I.2014, *Reeb CR13Z51** (PC0763864).
South Africa. Mpulalanga province, Mriepskop Mt., 1550 m, 18.VI.1969, *Vorster 828B* (E-00430437); Cape province, Apollo Peak, 1219 m, 31.III.1956, *Esterhuysen & Arnell 4361* (PRE-0501890).
Tanzania. Mt. Kilimanjaro, 1972, *Pócs 6718, 6789/B* (EGR, G00264060), ibid., 1984, *Pócs 6981/A* (EGR, G00264135, G00264136).

Distribution. — Ethiopia, Tanzania, Uganda, South Africa, Madagascar, Réunion.

Habitat. — On rotten wood, moist rock and humic soil in forests and along streams, between 1200 and 3800 m.

Description
Monoicous (autoicous) or dioicous.

Thallus
Dull or glossy yellow-green to green when fresh, dark brown to black in herbarium, leathery, rigid, growing in numerous layers, to 15 mm long, 1-2(-3)-pinnate, corymbose, not palmate, branches alternate to subopposite, reiterations frequently present in mature thalli.

Main axis usually
Ill-defined due to the densely corymbose ramification, in cross section rounded to ellipsoid at the base, 5-10 cells thick, 300-400 µm wide, in the middle ellipsoid to biconvex (rarely plano-convex), 300-500 µm wide, margins obtuse by bulging cells, not winged, epidermis cells *c.* 2-4 × smaller than inner cells at least on the ventral side of the axis, occasionally equal is size.

Primary branches
And reiterations to 7 mm long.

Ultimate branches
Linear to triangular, sometimes sinuous (horizontally curved), 0.5-3(-5) mm long, 0.2-0.3 mm wide, in cross section plano-convex to biconvex, 3-6 cells thick, margins with 1-3 cells wide wings, outer margins often crenate by bulging cells, epidermis cells 2-4 × smaller than inner cells, branch apex rounded to acute, emarginate to weakly dissected.

Mucilage papillae
Apical and in two ventral rows.

Oil bodies
Ellipsoid, finely granular, 2-4 per cell.

Male branches
Solitary, along the axis, shortly stalked, sometimes prolonged by vegetative growth, straight, 400-450 µm long, with a narrow, 1 cell wide wing.

Female branches
Along the axis and primary branches, laterally inserted, to 500 µm long, margin scaly and with hair-like, straight cilia, length of cilia and scales exceeding the width of the axis.

Calyptra
To 2.5 mm long, terminating in a conical umbo of densely aggregate cells.

Gemmae
Not seen.

Comment
The main characters of *R. ramosissima* are the small, rigid thalli with corymbose ramification, the unwinged, biconvex to rounded axis, the narrowly winged branches, and monoicy. Even though only specimen could be sequenced, the species was clearly separated in the molecular analysis. *Riccardia compacta* was accepted by Reeb & Bardat (2014) but study of a large amount of material showed that it cannot be separated from *R. ramossima*. *Riccardia corbieri* comb. nov., on the other hand, was considered a synonym of *R. ramosissima* by Reeb & Bardat (2014) but molecular analysis (Reeb *et al.* 2018; Fig. 1) recovered the two species in different clades. Morphologically, *R. corbieri* is separated from *R. ramosissima* by the lack of a corymbose habit, the frequent presence of stolons, and ultimate branches with broader, 4-5 cells wide wings.

Riccardia saccatiflora (Steph.) S.W.Arnell
(Fig. 4P-T)

Aneura saccatiflora Steph., *Botanical Gazette* 15: 282 (1890). — Type: Réunion, *Rodriguez 186* (lecto-, fide Reeb & Bardat [2014], PC[PC102136]!; isolecto-, G[G00067576]!).

Aneura dismieri Steph., *Species Hepaticarum* 6: 24 (1917). — Type: Madagascar (Reeb & Bardat 2014).

Aneura papulosa Steph., *Species Hepaticarum* 6: 36 (1917). nom. illeg. — Type: Seychelles (Reeb & Bardat 2014 as synonym of *R. obtusa*).

Riccardia obtusa S.W.Arnell, *Botaniska Notiser* 105: 142 (1952). — Type: Cape Province, Knysna, 28.XI.1951, *Arnell 1602* (holotype, UPS; isotypes, BOL!, S-B20192!*) **syn. nov.**

Riccardia rhodesiae S.W.Arnell., *Botaniska Notiser* 105: 150 (1952). — Type: Zimbabwe (Reeb & Bardat 2014).

Further specimens examined. — **Cameroon**. Buea, 13.VII.1891, *Dusén 251*, as *Aneura caespitans* (BM-00167935, G00067548).
Comores. Karthala, 1600 m, 01.V.2008, *Bardat KarP1Q2Li1** (PC0763849).
Madagascar. Alaotra-Mangoro, Vohimana Reserve, 18°55'15.86"S, 48°30'55.76"E, 782 m, 28.VI.2012, *Reeb MTV1211** (PC0763881A, TAN), 18°55'13.1"S, 48°30'57.1"E, 789 m, 28.VI.2012, *Reeb MTV1220* (PC0763875), *MTV1221** (PC0763880, TAN), 18°55'43.6"S, 48°29'56.6"E, 849 m, 30.VI.2012, *Reeb MTV1235** (PC0763886, TAN); Alaotra-Mangoro, Zahamena Reserve,17°38'19"S, 48°36'46.3E, 1156 m, 28.XII.2013, *Reeb CR13Z26** (PC0763870), *CR13Z27** (PC0763871), 17°38'25"S 48°38'21E, 1100 m, 29.XII.2013, *Reeb CR13Z40** (PC0763867), 17°38'22.7"S 48°38'45.3, 1294 m, 30.XII.2013, *Reeb CR13Z57** (PC0763866); Analamanga, Angavokely Reserve,18°55'12.8"S 47°44'29.3E, 1470 m, 31.I.2011, *Reeb CR11142** (PC0763883).
Malawi. Mulanje Mt., 15°56'09"S, 35°31'02"E, 980 m, 30.VI.1991, *Wigginton M1758B** (E00430531), 15°52'50"S, 35°36'36"E, 1800 m, 23.VI.1991, *O'Shea M7409A** (E00430479).
Mauritius. Black River Gorges Nat. Park, 20°24.5'S, 57°27.5'E, 540 m, 07.VIII.1996, *Pócs 9667/F** (EGR); Mt. Cocotte, 700 m, 08.X.1962, *Een M064* (S-B7132).
Réunion. 13 km W of St. Anne, 021°4'35"S, 55°37'10"E, 520-800 m, 30.VIII.1994, *Orban 9436/T** (G00264122, EGR); Cirque de Salazie, 21°03'00"S, 55°32'00"E ,1550-1800 m, 01.IX.1994, *Vojko 9438/CF** (EGR); Langevin Valley, 21°17'05"S, 55°38'05"E, 550-850 m, 20.VIII.1996, *Pócs 9686/X** (G00264118, EGR); Forêt de Tévelave, 1470 m, 27.IV.2011, *Bardat TEV.1** (PC0763865).
Tanzania. Uluguru Mts., Bondwa Peak, 1900-2000 m, VIII-X/1969 *Pócs 6011/S, 6011T; 6011/I*, 6051/AG (EGR), 1400 m, 13.XII.1970, *Jones 1210* (EGR).
Uganda. Ruwenzori Nat. Park, 2100 m, 01.II.1997, *Porley U554C** (E00430545), 22°00"S, 29°59'00"E, 2080 m, 02.II.1997, *Wigginton U8053B** (E).

Distribution. — Cameroon, East Africa, South Africa and Indian Ocean Islands.

Habitat. — Often on rock, sometimes on bark or, at highest elevations, on soil, always in humid evergreen forests and usually in or near river beds, from 540 to over 2000 m.

Description
Monoicous (autoicous or paroicous) or dioicous (*R. obtusa*).

Thallus
Fleshy, green to black green, convex with incurved branches when dry, dull to glossy, to 20 mm long, main axis closely attached to the substrate, branches arising upwards, branching 1-2-pinnate in the lower half of the thallus and palmate in the upper half, branches alternate to subopposite, reiterations present, flagelliform branches occasional, stolons frequent.

Main axis
Well-defined, 100-420 µm wide, in cross section biconvex to plano-convex at the base, 5-8 cells high, biconvex to plano-convex or concave-convex in the middle, 5-7 cells high, margins acute, of 1-2 rows of bulging cells, not clearly winged, often asymmetrical, epidermis cells more than 5× smaller than inner cells.

Primary branches
To 7 mm long, crowded and often overlapping, angles with the axis variable.

Ultimate branches
Crowded, oblong, sometimes tongue-shaped, 600-1500 µm long, 250-400(-650) µm wide, in cross-section plano-convex to concave-convex, 4-5(-7) cells thick, with 2-3(-4) cells wide wings, epidermis cells 2-4 × smaller than inner cells, margins irregularly undulate, apex widened, rounded to truncate to emarginate to dissected, without overlapping edges, with numerous multi-apical areas. Mucilage papillae apical and ventral. Oil bodies (Meenks & Pócs 1985) dark brown, present in epidermis cells.

Sexual branches
Usually grouped, lateral to ventro-laterally inserted.

Male branches
Mainly sessile, 300-500(-900 µm) long, with 2-3 cells wide scale-like wings, the wings narrowed than the axis, antheridia in 2-10 pairs.

Female branches
500-750 µm long, ventrally inserted, bordered by straight, hair-like cilia, archegonia in 2-6 pairs.

Calyptra
1.5-3 mm long, terminating in corona, surface with numerous thick-walled cells.

Gemmae
Not seen.

Comment
Riccardia saccatiflora is morphologically somewhat similar to *R. multifida* but the latter species is a larger plant (to 4 cm long) with 2-3(-4)-pinnate branching, without palmate branches, and epidermis cells usually without oil bodies (present in the epidermis in *R. saccatiflora*; Meenks & Pócs 1985). Moreover, oil bodies in *R. multifida* are light brown, while being dark brown in *R. saccatiflora*.

Riccardia obtusa (synonym of *R. papulosa*) is a dioicous phenotype of *R. saccatiflora*. For a detailed description of *R. obtusa* see Perold (2002b).

Riccardia vohimanensis Reeb & Gradst. sp. nov.
(Fig. 4U-X)

Diagnosis. — Monoicous. Thallus rigid, unwinged, with short branches. Axis plano-convex to biconvex, 8-12 cells thick, ventral side with mycorrhiza-like fungi. Immature calyptra strawberry-like.

Type. — **Madagascar**. Vohimana Reserve, 18°55'43.6S 48°29'53.6"E 849 m, 15.IV.2010, *Reeb, Andriamantena & Bidault CRAE96** (holo-, PC[PC0771053]).

Further specimens examined. — **Madagascar**. Alaotra-Mangoro, Zahamena Reserve, 17°38'22"S, 48°38'47"E, 1247 m, 27.XII.2013, *Reeb CR13Z23** (PC0763868); Maromizaha Reserve, 18°58'33.9"S 48°27'54.3"E, 1021 m, 05.VII.2012, *Reeb MTM1278** (PC0763879), 18°58'45"S, 48°27'51.8"E, 1011 m, 06.VII.2012, *Reeb MTM1290** (PC0763878); Haute Matsiatra, Andringitra Nat. Park, 22°08'4061"S, 46°53'47.4"E, 1590 m, 21.V.2016, *Reeb CR16M52* (PC).
Malawi. Mulanje Mt., 15°53'32.1"S, 35°29'24"E, 2180 m, 22.VI.1991, *O'Shea M7327A-2** (E00430480).
Mauritius. Macabé, 550 m, 03.X.1962, *Een M028** (S-B7097).

Distribution. — Malawi, Madagascar, Mauritius.

Habitat. — On dead logs (bare, smooth and very hard wood) and buttresses, rarely on humid rock, from 550 m to 2200 m.

Description
Monoicous (autoicous or paroicous).

Thallus
Leathery and rigid, green to blackish green when fresh and forming rosettes on bare substrates, dull brown to black in herbarium, closely attached to the substrate, to 22 mm long, 1-2-pinnate, not palmate, branches alternate, not flagelliform, stolons lacking.

Main axis
Well-defined, 700-1000(-1200) µm wide, in cross section plano-convex to concave-convex, with mycorrhizal fungi in the ventral part, 8-12 cells thick, margins obtuse, not winged, epidermis cells 2-4× smaller than inner cells.

Ultimate branches
Oblong and stocky, to 2 mm long and 1 mm wide, in cross section biconvex to plano-convex, 7-9 cells thick, margins acute, not winged, branch apex rounded and often widened, emarginate to weakly dissected, without overlapping edges.

Mucilage papillae
Apical and lateral.

Oil bodies
Not seen.

Sexual branches
Numerous all along axis, often close to each other.

Male branches
Mainly grouped, sessile, 300-400 µm long, not winged, with 4-8 antheridial pairs.

Female branches
Grouped, laterally inserted, 300-500 µm long, base often elongate, female branch bordered by scales or long hair-like, straight cilia, the cilia longer than the width of the axis, archegonia in 4-6 pairs.

Calyptra
Less than 1 mm long, strawberry-like when immature, densely covered by rounded, thick-walled cells.

Gemmae
Sometimes present.

Comment
Riccardia vohimanensis sp. nov. is a morphologically and molecularly well-defined species. The main characters of the species are: 1) thallus rigid, unwinged, with short branches, without stolons; 2) axis plano-convex to biconvex, 8-12 cells thick, ventral side with mycorrhizal fungi (cross section); and 3) immature calyptra strawberry-like. In Rabeau *et al.* (2017), *R. vohmanensis* sp. nov. was called "*Riccardia* sp.13" (type) and "*Riccardia* sp.12". The phylogenetic position of this new species needs confirmation.

GENERAL DISCUSSION

As a result of this study, the number of species recognized in East-Africa has been reduced from twenty-seven (Grolle 1995; Reeb & Bardat 2014) to fourteen. Sixteen species were reduced to synonymy while three species were newly described. A comparison with other African areas indicates that Eastern Africa, including the Indian Ocean Islands, is the richest area for *Riccardia* in Africa by far. Jones (1956) recognized six species in West Africa, admitting, however, the presence of an almost continuous variation among some of the species, e.g. among *R. amazonica, R. limbata* and *R. erosa* which "form a puzzling series", and among *R. limbata* and *R. longispica*: "the distinction between *R. limbata* and *R. longispica* depends chiefly on size and habits" (Jones 1956). According our treatment, only four species occur in West Africa (*R. angusticostata, R. inconspicua, R. longispica, R. saccatiflora)*, with two of them being very rare in the region and known only from Cameroon. Since West Africa has been relatively well explored (Wigginton 2004), the difference between the eastern and western part of the continent in terms of species richness of *Riccardia* may be real and not due to under-exploration.

At a wider geographic scale, a difference in terms of Aneuraceae between Africa and the other tropical regions is the lack of *Lobatiriccardia* in Africa. The latter genus is well represented in Asia and Australasia and, in addition, occurs in South America (Ecuador) (Preussing *et al.* 2010). On the other hand, Africa has one endemic genus of Aneuraceae, *Afroriccardia*, while other world regions lack endemic Aneuraceae genera with the exception of New Zealand, which harbors the genus *Verdoornia*. *Aneura* remains a puzzling genus (e.g. Bączkiewicz *et al.* 2017) and further integrative studies, including tropical and Australasian materials, are needed to resolve its taxonomy. African *Riccardia* species belong mostly to specifically African clades and only few species are in common with other continents, including *R. chamedryfolia* and *R. multifida* occurring also in the Holarctic and Neotropical regions (Rabeau *et al.* 2017) and *R. inconspicua* shared with tropical Asia.

Africa appears to be less rich in Aneuraceae than other parts of the world, with the exception of Europe, North America and large parts of Asia where only seven species occur (Grolle & Long 2000; Konstantinova *et al.* 2009; Stotler & Crandall-Stotler 2017). Patagonia is known as a biodiversity hotspot for bryophytes (Rozzi *et al.* 2008) and 45 *Riccardia* species have been described from this region and adjacent temperate areas of Chile and Argentina (Hässel de Mendendez 1972), 38 of which were retained by Söderström *et al.* (2016). In tropical America, the richest Aneuraceae flora is seen in Andes and 37 species had been recognized in this region by Meenks & Pócs (1985). However, like in the present study, a recent revision showed that many Andean species were ill-defined and that a drastic reduction in the number of accepted species (14) was necessary (Gradstein & Reeb 2018b). Southeast Asia and Australasia are also rich places for Aneuraceae; 38 species are recorded from Australia and New Guinea (Hewson 1970), 27 from New Zealand (Browns & Braggins 1989) and 21 from Japan (Furuki 1991). However, these numbers might be reduced in future when molecular studies are carried for these regions. A further striking feature of the African Aneuraceae flora is the absence of dendroid *Riccardia* species. In contrast, eight dendroid species occur in the tropical Andes (Gradstein *et al.* 2019) and several further ones are known from tropical Asia and the temperate Southern Hemisphere. Also, none of the African species have cuticular ornamentation, a feature seen in, e.g. the southern temperate *R. crassa* (Schwägr.) C.Massal. and the Andean *R. aberrans* (Steph.) Gradst.

Few species (three) of eastern African *Riccardia* have mycorrhiza-like fungi; the same number occurs in New Zealand (Hewson 1970). To estimate the evolutive value of this character a phylogeny at a world scale is needed. Likewise, biogeographical and further taxonomic studies at a world scale, including revisions of Aneuraceae floras lacking recent ones, are needed to understand the origin and evolution of Aneuraceae. Finally, further collecting efforts should be conducted in African in order to 1) clarify the species ranges and the taxonomic status of some still questionable taxa (e.g. *R. limbata*, here treated tentatively as a synonym of *R. longispica*); and 2) improve the knowledge of the floras of West Africa and several Central and East African countries.

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Appendix 1. — Xper3 Guide line for Bryology. http://sciencepress.mnhn.fr/sites/default/files/documents/fr/bryologie2020v41a2-appendice1.pdf