



Notes on Early Land Plants Today. 72. Infrageneric classification and new combinations, new names, new synonyms in *Frullania* (Marchantiophyta)

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Abstract

The liverwort family Frullaniaceae is circumscribed to include the single genus, *Frullania*, and has a complex and confusing taxonomical history. An overview is provided for the infrageneric classification adopted for the forthcoming worldwide checklist based on recent morphological and molecular studies. The genus is preliminarily subdivided into eleven subgenera, *F.* subg. *Chonanthelia*, *F.* subg. *Diastaloba*, *F.* subg. *Diversitextae*, *F.* subg. *Frullania*, *F.* subg. *Homotropantha*, *F.* subg. *Mammillosae*, *F.* subg. *Meteorioopsis*, *F.* subg. *Microfrullania*, *F.* subg. *Saccophora*, *F.* subg. *Steerea*, and *F.* subg. *Thyopsiella*, as well as several sections. However, some of the subgeneric divisions are only doubtfully recognized because there is still insufficient knowledge to arrive at a decision regarding their systematic status and placement. The taxa may be either originally not well described, not restudied recently or molecular analyses point to a more complex internal structure of the respective group. Fourteen new synonyms, eight new combinations, five new names, eight lectotypifications, and one new variety are provided.

Introduction

Frullania Raddi (1818: 9) is worldwide in distribution and is one of the largest and taxonomically most complex genera of leafy liverworts with more than 2,000 published names ascribed to the genus (von Konrat *et al.* 2010).

The current contribution follows the series of Early Land Plant Today Notes and is similar in content, structure and format to Söderström *et al.* (2015) that likewise deals with *Plagiochila* (Dumortier 1831: 42) Dumortier (1835: 14). The current paper provides only an overview of the infrageneric classification adopted as part of the forthcoming worldwide checklist of liverworts (Söderström *et al.*, in press). We do not attempt here to provide a full synopsis of the over 30 sections and subsections that have been historically described. The paper also includes several new synonyms, new combinations, new names and lectotypifications. *Schusterella* Hattori *et al.* (1972: 330), *Amphijubula* Schuster (1970: 298) and *Steerea* Hattori & Kamimura (1971: 429) have been considered segregate genera of *Frullania*, but are now considered synonyms of this genus (Engel 1978, Hattori & Mizutani 1982, Stotler & Crandall-Stotler 1987, Schuster 1992, von Konrat *et al.* 2006, 2011b, Hentschel *et al.* 2009). *Neohattoria* Kamimura (1962: 218) has also historically been placed in *Frullania* (Hattori & Mizutani 1982, Stotler & Crandall-Stotler 1987). However, the authors are actively investigating recently collected material identified as *Neohattoria* using molecular tools to test this relationship. Whereas the circumscription of Frullaniaceae can be deemed sufficiently clarified, the subgeneric classification of *Frullania* is still a matter of much controversy (e.g., Hentschel *et al.* 2009, Uribe 2011).

The content of the paper is in two parts. First, an infrageneric classification is provided, including only those subgenera and sections that are recognized in the forthcoming liverwort worldwide checklist (Söderström *et al.*, in

press). The second part focuses on new synonyms or new names at the species level and below associated with miscellaneous names. Both parts have novel nomenclatural elements.

The format of this note follows Söderström *et al.* (2012). Fourteen new synonyms, eight new combinations, five new names, eight lectotypifications, and one new variety are provided.

Infrageneric structure of *Frullania*

Over the last five decades, there have been abundant changes and modifications to the subgeneric classification of *Frullania*, in part due to the establishment of supposedly allied genera, and the contractions and expansions of generic, subgeneric and sectional concepts. Consequently, this has led to a complex and confusing classification. Attempts to circumscribe subgenera and sections within the whole distributional range of the genus have been very limited (Hattori 1980b, Yuzawa 1991, Hentschel *et al.* 2009). There have been various proposals for a subdivision of *Frullania* into natural species groups (e.g., Spruce 1884, Verdoorn 1930, Vanden Berghen 1976, Hattori 1976, Stotler & Crandall-Stotler 1987, Yuzawa 1991, Schuster 1992). As a result, these authors established more than fifteen subgenera and over thirty sections and subsections based on morphology. Recently, Hentschel *et al.* (2009) presented the most comprehensive molecular phylogeny of *Frullania* to date.

According to the molecular data several robust lineages within *Frullania* could be assigned to morphologically circumscribed subgenera and provide evidence for the monophyly of a suite of currently accepted taxa. The results point to a general congruence of morphological subgeneric classifications and the molecular topologies. However, in some cases previous subgeneric assignment for a few taxa, e.g., *F.* subg. *Diastaloba* Spruce (1884: 55) and *F.* subg. *Microfrullania* (Schuster 1970: 280) Schuster (1992: 34), based on morphological evidence is not supported by the molecular data and further modifications and refinements of the morphology-based subgeneric concepts are necessary to arrive at a more comprehensible and natural subdivision. Although the analysis of Hentschel *et al.* (2009) is based on a rather large dataset in terms of the number of accessions investigated as well as the number of molecular markers utilized, the taxon sampling is still inadequate to revise all supraspecific taxa, especially the many published sections and subsections. Hentschel *et al.* (2009) have already provided strong evidence that several sections and subsections are polyphyletic, e.g., *F.* sect. *Ornithocephalae* Verdoorn (1930: 50), *F.* sect. *Integristipulae* Verdoorn (1930: 49), and *F.* subsect. *Ericoides* Schuster (1985: 371) and many are suspected synonyms, e.g., *F.* sect. *Coniferae* Schuster (1985: 372).

Due to the fact that several key taxa and type specimens, e.g., *F. ciliata* Lindenb. et Gottsche in Gottsche *et al.* (1847: 775), *F. clemensiana* Verdoorn (1932: 493), *F. diversitexta* Stephani (1897: 89), *F. errans* Verdoorn (1930: 59), *F. junghuhniana* Gottsche in Gottsche *et al.* (1845: 444), *F. mammillosa* Hattori (1977 [1978]: 424), *F. subtilissima* (Nees ex Montagne 1840: 333) Lindenb. in Gottsche *et al.* (1845: 443), *F. ternatensis* Gottsche in Gottsche *et al.* (1846: 465), and *F. vaginata* (Swartz 1781: 35) Dumortier (1835: 13), have not been studied yet, we have adopted a rather conservative approach for the circumscription of the subgenera and sections included in the forthcoming worldwide checklist of hornworts and liverworts (Söderström *et al.*, in press). The following annotated synopsis of infrageneric ranks basically reflects a consensus of an informal *Frullania* Working Group that met at the Field Museum of Natural History in Chicago in 2009 and 2012. The subgenera outlined below reflect the infrageneric classification adopted for the forthcoming worldwide checklist. Discussion is provided to support that classification, which is outside the auspices of the checklist. References to articles in the nomenclature code follows McNeill *et al.* (2012).

***Frullania* subg. *Chonanthelia* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 8, 1884 (Spruce 1884). Lectotype (Hattori 1982: 261):—*Frullania gibbosa* Nees in Gottsche *et al.* (1845: 411).**

Note:—*Frullania* subg. *Chonanthelia* was monographed by Yuzawa (1991), who proposed several new infrageneric entities. Besides a few exceptions, most of his categories are natural and reflected in the topologies presented by Hentschel *et al.* (2009). However, due to the placement of *F. gibbosa* in the respective analyses and the use of *F.* sect. *Chonanthelia* as a putative autonym of *F.* subg. *Chonanthelia* without formal description or combining it (e.g., Yuzawa 1991) several nomenclatural refinements are necessary. For the forthcoming worldwide checklist we adopt three sections, namely *F.* sect. *Cladocarpicae*, *F.* sect. *Chonanthelia* and *F.* sect. *Pluricarinatae*.

***Frullania* (subg. *Chonantheria*) sect. *Cladocarpicae* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 11, 1884 (Spruce 1884). Lectotype (Yuzawa 1991: 245):—*Frullania brachyclada* Spruce (1884: 11), *nom. illeg.* (ICN Art. 53.1, non Lehm. 1844) [= *Frullania tunguraguana* Clark & Frye (1952: 133)].**

= *Frullania* sect. *Acrocarpicae* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 11, 1884 (Spruce 1884), *syn. nov.* Lectotype (**here designated**):—*Frullania arecae* (Sprengel 1821: 99) Gottsche (1863: 236) [= *Frullania obscura* (Swartz 1806: 1869) Dumortier (1835: 13), *cf.* Gradstein (2012)]. Note:—This lectotypification makes the section synonymous with *F.* sect. *Cladocarpicae* (*cf.* Hentschel *et al.* 2009).

***Frullania* (subg. *Chonantheria*) sect. *Chonantheria* Yuzawa ex Hentschel et von Konrat, sect. nov.** Holotype (Hattori 1982: 161):—*Frullania gibbosa* Nees in Gottsche *et al.* (1845: 411).

Note:—Yuzawa (1991) and others have used the name *F.* sect. *Chonantheria* as a putative autonym below *F.* subg. *Chonantheria*. However, the establishment of any subdivision of a genus under a subdivision that does not include the type of the genus, does not create an autonym (*cf.* ICN Art. 22.1). We here validate the name by referring to Yuzawa's English description of *F.* sect. *Chonantheria* (Yuzawa 1991: 200) and the selection of a holotype made here.

***Frullania* (subg. *Chonantheria*) sect. *Pluricarinatae* (Yuzawa, Mues et S.Hatt.) Hentschel et von Konrat, comb. nov.** Basionym:—*Frullania* ser. *Pluricarinatae* Yuzawa, Mues et S.Hatt., *J. Hattori Bot. Lab.* 63: 428, 1987 (Yuzawa *et al.* 1987). Type (ICN Art. 22.6):—*Frullania pluricarinata* Gottsche (1864: 168).

Note:—The new section is created to host the taxa Hentschel *et al.* (2009) erroneously referred to *F.* sect. *Chonantheria* as we have not been able to find any existing sectional name that can be applied.

***Frullania* subg. *Diastaloba* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 55, 1884 (Spruce 1884). Lectotype (Hattori 1982: 235):—*Frullania subtilissima* (Nees ex Montagne 1840: 333) Lindenb. in Gottsche *et al.* (1845: 443).**

Note:—This subgenus is characterized basically by the shape, position and orientation of the leaf lobule (Spruce 1884). According to the molecular data at hand, the subgenus includes at least four genetically distinct lineages, provisionally named “*Diastaloba* I–IV” (Hentschel *et al.* 2009). Furthermore, the *Diastaloba*-like habit reoccurs in *F.* subg. *Microfrullania*, which makes the discrimination between both subgenera even more challenging (Schuster 1992). Although much progress has been made towards a refined circumscription of *F.* subg. *Microfrullania* (e.g., von Konrat *et al.* 2006, Hentschel *et al.* 2009, von Konrat *et al.* 2010, 2011a, 2012, 2013), the taxonomic problems concerning the classification of *F.* subg. *Diastaloba* have not yet been satisfactorily solved. *Frullania* subg. *Diastaloba* was typified by Hattori (1982) with *F. subtilissima*, a rare and enigmatic species from Guyana. Based on preliminary observations, including the study of relevant type specimens, a morphological characterization of the corresponding lineages seems possible. A taxonomical revision is currently underway and will lead to an extensive reclassification of this by far most complex subgenus. We hereby recognize the four informal clades that correspond to “*Diastaloba* I, II, III and IV” and have attempted to place species within these units for the forthcoming worldwide liverwort checklist (Söderström *et al.*, in press). Not all purported taxa of these groups have been investigated using molecular tools. However, attempted groupings have been made based on morphological similarity and purported relationships described by previous workers, especially the many publications by S. Hattori on the genus. Since we do not yet know in which of the four lineages the type, *F. subtilissima*, belongs, we refrain from giving them formal sectional names. Below a brief discussion of these four natural units is presented.

Diastaloba I corresponds to three well supported clades which in Hentschel *et al.* (2009) included the type species of *F.* sect. *Graciles* Verdoorn (1930: 110) [type *F. gracilis* (Reinwardt *et al.* 1824: 221) Nees in Gottsche *et al.* (1845: 452)], *F.* sect. *Serratae* Verdoorn (1930: 85) [type *F. serrata* Gottsche in Gottsche *et al.* (1845: 453)] and *F.* sect. *Inconditum* von Konrat *et al.* (2010: 480) [type *F. hodgsoniae* von Konrat *et al.* (2010: 492)] (as *Rostratae*). Although not included in any molecular study, *F.* sect. *Vaginatae* Verdoorn (1930: 141) [type *F. vaginata* (Swartz 1781: 35) Dumortier (1835: 13)], *F.* subsect. *Ternatenses* Hattori (1976: 466) [type *F. ternatensis* Gottsche in Gottsche *et al.* (1846: 465)], *F.* sect. *Sinuatae* Schuster (1985: 371) [type *F. sinuata* Sande Lacoste (1854: 424)], *F.* sect. *Pycnophyllae* Schuster (1985: 370) [type *F. pycnophylla* Hattori (1973a: 60) (= *F. curvistipula* Stephani (1911: 541))] and *F.* sect. *Curvistipulae* Schuster (1991: 144) [type *F. curvistipula*] seem to belong here.

Diastaloba II includes the type species of one section in Hentschel *et al.* (2009), *F.* sect. *Lucidae* Verdoorn (1930: 125) [type *F. repandistipula* Sande Lacoste (1854 [1855]: 422)]. Although not included in any molecular study, *F.* sect. *Ocellatae* Schuster (1985: 371) [type *F. ocellata* Hattori & Kamimura (1973: 531)] seems to belong here.

Diastaloba III comprises two species from Madagascar, *F. usambarana* Schiffn. ex Stephani (1894: 160) and *F. grossiclava* Stephani (1910: 384); neither of these represent a type of any subgeneric taxon. We were not able to find any existing name that would be possible to apply on this group.

Diastaloba IV corresponds to a group of distinctive plants that have strong microphyllous branches and long, narrow lobules oblique to the stem, e.g., *F. hypoleuca* Nees in Gottsche *et al.* (1843: 471) and *F. obcordata* (Lehmann 1834: 51) Lehm. et Lindenb. in Gottsche *et al.* (1845: 447) [= *F. caulisequa* (Nees 1833: 373) Montagne (1839: 51)]. As with the previous group, none of the taxa included by Hentschel *et al.* (2009) in this group is a type of any subgeneric taxon, and we have no existing name that we think may be applicable to it.

***Frullania* subg. *Diversitextae* (Kamim.) S.Hatt., *J. Hattori Bot. Lab.* 59: 154, 1985 (Hattori & Lin 1985). Basionym:—*Frullania* subsect. *Diversitextae* Kamim., *J. Hattori Bot. Lab.* 24: 80, 1961 (Kamimura 1961). Type (ICN Art. 22.6):—*Frullania diversitexta* Stephani (1897: 89).**

Note:—We treat *F.* subg. *Diversitextae* as circumscribed by Hattori & Lin (1985) as monotypic and including only *F. diversitexta*. Kamimura (1961) first diagnosed *F.* subg. *Diversitextae* as a subsection of subg. *F.* sect. *Diastaloba*. Hattori & Lin (1985) raised it to subgeneric rank recognizing its somewhat chimeric appearance; the combination of tuberculate perianths—a feature unique to *F.* subg. *Frullania*, and its otherwise *Diastaloba*-like habit. This species has not yet been included in a molecular study, and its phylogenetic position therefore remains unclear. Judging from a morphological point of view, especially the development of the first branch leaf and the first branch underleaf as well as the shape of the stylus, there are certain affinities with the “*Diastaloba* I”-clade of Hentschel *et al.* (2009).

***Frullania* subg. *Frullania*, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 8, 1884 (Spruce 1884). Lectotype (Evans 1918: 468):—*Frullania major* Raddi (1818: 9), *nom. illeg.* (ICN Art. 52.1; earlier name included) ≡ *Frullania dilatata* (Linnaeus 1753: 1133) Dumortier (1835: 13).**

Note:—Raddi (1818) included two species in his new genus *Frullania*, *F. major* (Raddi 1818: 9) and *F. minor* Raddi (1818: 10), both being illegitimate as they included earlier names. Raddi had Linnaeus’ (1753: 1134) synonymy confused treating the larger species [*F. tamarisci* (Linnaeus 1753) Dumortier (1835: 13)] as *F. minor* and the smaller species [*F. dilatata* (Linnaeus 1753: 1133) Dumortier (1835: 13)] as *F. major*. Evans (1918: 468) was the first to select a type. He selected *F. dilatata* which was included as a synonym of *F. major* in Raddi (1818). It is often argued that Evans used the American Code and thus that the typification was mechanical, which is not allowed by the International Code (*cf.* ICN Art. 10.5(b)). However, in this case he did not choose the species first mentioned by Raddi, but a synonym of it, and thus it cannot be a mechanical selection. Frye & Clark (1947: 736) lectotypified the genus with *F. tamarisci*. However, their synonymy included *F. major*, the only element of their synonymy possible to choose as lectotype. Thus, the lectotype of *Frullania* (and also the autonym) is *F. major* which has long been treated as a synonym of *F. tamarisci* (e.g., Frye & Clark 1947). Also, *F.* subg. *Frullania* was used for what is now *F.* subg. *Thyopsiella* while what we currently accept as *F.* subg. *Frullania* used to be named *F.* subg. *Trachycolea* Spruce (1884: 31). *Frullania* subg. *Frullania* accommodates about 250 accepted species and represents one of the most speciose subgenera of *Frullania*, especially in the extratropical regions, and includes a large number of polymorphic species (Hentschel *et al.* 2009). The further subdivision in a number of sections and subsections as well as the occurrence of many rather polymorphic species makes this subgenus taxonomically fairly difficult (Schuster 1992, Hentschel *et al.* 2009). Hence, it is not surprising that the group remains unrevised on a global scale. Yuzawa (1991) regarded species of *F.* subg. *Frullania* as being closely related to species of *F.* subg. *Chonanthelia*, but the lineage proved to be distinct based on the morphological and molecular data at hand (e.g., Schuster 1992, Hentschel *et al.* 2009). Although the analysis of Hentschel *et al.* (2009) is based on a rather large dataset, the taxon sampling is still inadequate to revise all sections and subsections, but it is obvious that the sectional and subsectional assignment for several taxa based on morphological evidence is not supported by the molecular data. Key taxa to be investigated include the missing type species of supraspecific entities, e.g., *F. errans* Verdoorn (1930: 59), *F. monocera* (Hooker & Taylor 1845: 89) Gottsche *et al.* (1845: 418) and *F. ornithocephala* (Reinwardt *et al.* 1824: 216) Nees in Gottsche *et al.* 1845: 425, and more accessions of genetically complex species, like *F. ericoides* (Nees 1833: 346) Montagne (1839: 51), *F. nepalensis* (Sprengel 1827: 324) Lehm. in Gottsche *et al.* (1845: 422), and *F. fugax* (Hooker & Taylor 1845: 87) Gottsche *et al.*

(1845: 445). Despite strong evidence that some sections and subsections likely will become synonyms (Hentschel *et al.* 2009), proposing formal synonymy now would only contribute to the already inflated sectional and subsectional classification due to some paraphyletic species such as *F. ericoides* Nees (1833: 346) Montagne (1839: 51). However, a suite of subclades can be recognized at present and are therefore adopted for the forthcoming worldwide checklist.

***Frullania* (subg. *Frullania*) sect. *Acutilobae* Verd., *Ann. Bryol., Suppl.* 1: 44, 1930 (Verdoorn 1930). Lectotype (**here designated**):—*Frullania monocera* (Hooker & Taylor 1845: 89) Gottsche *et al.* (1845: 418).**

Note:—Schuster (1992) noted that the form of gynoecial axes in this section should be investigated citing that typical members, e.g. *F. allanii* Hodgson (1949: 371), bear gynoecia on unspecialised leafy axes that again branch, in contrast to the simple gynoecial branches of *F. bonincola* Hattori (1978: 551), which is purportedly allied to the section. Kamimura (1961) noted that *F. sect. Acutilobae* is a weak taxon and that the acute rostrum of the leaf-lobules was the only significant difference between *F. sect. Acutilobae* and *F. sect. Trachycolea*. However, Hattori (1983) stated that *F. sect. Acutilobae* was unique with the long piliferous beaks of the leaf-lobules. The molecular analysis by Hentschel *et al.* (2009) supports this classification.

***Frullania* (subg. *Frullania*) sect. *Australes* Verd., *Ann. Bryol., Suppl.* 1: 58, 1930 (Verdoorn 1930). Lectotype (Hattori 1976: 463):—*Frullania errans* Verdoorn (1930: 59).**

Note:—Verdoorn (1930) first established *F. sect. Australes* as a section within *F. subg. Frullania* (as *F. subg. Trachycolea*). Later Hattori (1976) made a new combination raising the rank of *F. sect. Australes* to subgenus. Hentschel *et al.* (2009) showed molecular evidence that *F. subg. Australes* forms a robust subclade and is nested within a polytomous topology with several sections of *F. subg. Frullania*. We therefore prefer Verdoorn's (1930) treatment of *F. sect. Australes* as a section of *F. subg. Frullania*. The majority of species of this lineage is distributed in Eastern Asia and Australasia, but according to the Hentschel *et al.* (2009) phylogeny the neotropical *F. glomerata* and African *F. obscurifolia* Mitten (1879: 400) also belong here.

***Frullania* (subg. *Frullania*) sect. *Frullania*, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 11, 1884 (Spruce 1884).**

***Frullania* (subg. *Frullania*) sect. *Irregulares* E.A.Hodgs. ex S.Hatt., *J. Hattori Bot. Lab.* 54: 143, 1983 (Hattori 1983). Holotype (Hattori 1983:143):—*Frullania deplanata* Mitten (1855: 161).**

Note:—This section was originally proposed by Hodgson (1949), but was invalid because a Latin diagnosis was omitted. Later, Hattori (1983: 143) validated the section. Hodgson (1949) included only a single species, *F. deplanata*. *Frullania* sect. *Irregulares* as currently circumscribed includes solely species from New Zealand (Hentschel *et al.* 2009).

***Frullania* (subg. *Frullania*) sect. *Planae* R.M.Schust., *Phytologia* 57: 372, 1985 (Schuster 1985). Type (ICN Art. 22.6):—*Frullania plana* Sullivant (1849: 175).**

Note:—This section is seemingly monotypic (Schuster 1985, 1992). Schuster (1992) provided a detailed analysis comparing and distinguishing it from *F. sect. Frullania* (as *F. sect. Trachycolea*).

***Frullania* subg. *Homotropantha* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 35, 1884 (Spruce 1884). Lectotype (Kamimura 1961: 57):—*Frullania replicata* (Nees 1833: 369) Montagne (1840: 333) [= *Frullania nodulosa* (Reinwardt *et al.* 1824: 217) Nees in Gottsche *et al.* (1845: 433), *cf.* Kamimura 1961].**

Note:—This subgenus was thoroughly revised by Hattori (1980b) and is here circumscribed to include three sections, *F. sect. Remotilobae*, *F. sect. Fallaces* and *F. sect. Nodulosae*. The latter two were incorporated in the molecular study of Hentschel *et al.* (2009) and resolved as monophyletic in a well supported sister relationship.

***Frullania* (subg. *Homotropantha*) sect. *Fallaces* Verd., *Rev. Bryol. Lichénol.* 1: 112, 1928 (Verdoorn 1928a). Type (ICN Art. 22.6):—*Frullania fallax* Gottsche in Gottsche *et al.* (1845: 432).**

Note:—The integrity of *F. sect. Fallaces* seems to be supported by both the morphological evidence described by

(Hattori 1980b) as well as the molecular analysis presented by Hentschel *et al.* (2009), although the type species has not yet been included in any molecular systematic study. *Frullania fallax* is regarded as most closely related to *F. intermedia* which is well known for its pronounced morphological plasticity (Hattori 1980b) and is possibly represented by a species complex.

***Frullania* (subg. *Homotropantha*) sect. *Nodulosae* Verd., *Rev. Bryol. Lichénol.* 1: 116, 1928 (Verdoorn 1928a). Type (ICN Art. 22.6):—*Frullania nodulosa* (Reinwardt *et al.* 1824: 217) Nees in Gottsche *et al.* (1845: 433).**

Note:—Hattori (1980b) has used the name *F.* sect. *Homotropantha* as a putative autonym of *F.* subg. *Homotropantha* and included *F.* sect. *Nodulosae* in its synonymy. However, the establishment of any subdivision of a genus under a subdivision that does not include the type of the genus, does not create an autonym (*cf.* ICN Art. 22.1). Thus the oldest available name must be used.

***Frullania* (subg. *Homotropantha*) sect. *Remotilobae* Verd., *Rev. Bryol. Lichénol.* 1: 119, 1928 (Verdoorn 1928a). Type (ICN Art. 22.6):—*Frullania remotiloba* Stephani (1894: 152).**

Note:—This section was established by Verdoorn (1928a) to accommodate *F. remotiloba*. Later Verdoorn (1930) added *F. heteromorpha* Schiffner (1890: 38). Some doubts were expressed by Hattori (1980b) regarding the sectional placement of *F. heteromorpha*, because the species shows some similarities with members of *F.* sect. *Fallaces*. According to Hattori (1980b, 1982) *F. remotiloba* may be considered as an ancestral species of *F.* subg. *Homotropantha* closely related to *F.* subg. *Diastaloba*. None of the respective species have been available for a molecular phylogenetic analysis yet.

***Frullania* subg. *Mammillosae* S.Hatt., *J. Hattori Bot. Lab.* 60: 226, 1986 (Hattori 1986a). Type (ICN Art. 22.6):—*Frullania mammillosa* Hattori (1977 [1978]: 424).**

Note:—Representatives of this subgenus exhibit a *Diastaloba*-like habit, but are otherwise characterized by the development of stem-leaves with apiculate or pilose apices (Hattori 1986a). The phylogenetic affiliation of this subgenus remains unclear, because a taxonomic revision of *F.* subg. *Diastaloba* is still lacking. Until now, no species currently placed in *F.* subg. *Mammillosae* have been investigated by molecular methods.

***Frullania* subg. *Meteoriopsis* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 37, 1884 (Spruce 1884). Lectotype (Uribe & Gradstein 2003):—*Frullania peruviana* Gottsche in Gottsche *et al.* (1846: 465).**

Note:—The taxonomic history of this subgenus is fairly complicated and its current circumscription is strongly influenced by recent taxonomical efforts in *F.* subg. *Diastaloba* and *F.* subg. *Thyopsiella*. Spruce (1884) established *F.* subg. *Thyopsiella* to accommodate species with a prostrate to ascending habit while species with a pendent growth were assigned to *F.* subg. *Meteoriopsis* Spruce. Hattori (1972a) doubted the taxonomic relevance of the habit and synonymized *F.* subg. *Meteoriopsis* with *F.* subg. *Thyopsiella* (using the name *F.* subg. *Frullania*, *cf.* above). Spruce's (1884) treatment is supported by both the morphological evidence presented by Uribe (2008) as well as the molecular study by Hentschel *et al.* (2009) where the types of the two subgenera, *F. peruviana* and *F. tamarisci*, are located in different clades. In the present circumscription *F.* subg. *Meteoriopsis* includes species with a pendent (*F.* sects. *Intumescentes* and *Meteoriopsis*), and a prostrate growth form (*F.* sect. *Obtusilobae*). Ongoing taxonomic studies have revealed that several taxa formerly assigned to *F.* subg. *Meteoriopsis* as circumscribed here, are indeed members of the specious “*Diastaloba* I”-clade of Hentschel *et al.* (2009) and closely related to *F. apiculata* (Reinwardt *et al.* 1824: 222) Nees in Gottsche *et al.* (1845: 452), *F. serrata* Gottsche in Gottsche *et al.* (1845: 453) and *F. subdentata* Stephani (1911: 545). Currently no extra-neotropical member of *F.* sects. *Intumescentes* and *Meteoriopsis* is known because most of the Asiatic species formerly placed in *F.* subg. *Meteoriopsis* exclusive of *F.* sect. *Obtusilobae* are presumably more closely related to *F.* subg. *Diastaloba*.

***Frullania* (subg. *Meteoriopsis*) sect. *Meteoriopsis* Uribe, von Konrat et Hentschel., *sect. nov.* Type:—*Frullania peruviana* Gottsche in Gottsche *et al.* 1846: 465).**

Plants with deeply cordate leaves, with two large auricles on both sides of the base, which are strongly convoluted around the stem.

Note:—*Frullania* sect. *Meteoriopsis* was formerly used as a putative autonym below *F.* subg. *Meteoriopsis* (e.g., Kamimura 1961, Hattori 1975b, Gradstein 1999). However, the establishment of any subdivision of a genus under a subdivision that does not include the type of the genus, does not create an autonym (cf. ICN Art. 22.1). *Frullania* sect. *Vaginatae* Verdoorn (1930: 141) was placed into synonymy of *F.* sect. *Meteoriopsis* by Kamimura (1961). However, representatives of *F.* sect. *Vaginatae* are assignable to the “*Diastaloba* I”-clade of Hentschel *et al.* (2009) and therefore excluded from *F.* sect. *Meteoriopsis*. The section is circumscribed here to include solely the taxa enumerated by Uribe (2008) and the two characters used to describe the section above exclude taxa of *F.* sect. *Intumescentes* and *F.* sect. *Obtusilobae*.

***Frullania* (subg. *Meteoriopsis*) sect. *Intumescentes* R.M.Schust., *Phytologia* 57: 370, 1985 (Schuster 1985). Type (ICN Art. 22.6):—*Frullania intumescens* (Lehmann 1834: 52) Lehm. et Lindenb. in Gottsche *et al.* (1845: 460).**

***Frullania* (subg. *Meteoriopsis*) sect. *Obtusilobae* Verd., *Ann. Bryol., Suppl.* 1: 81, 1930 (Verdoorn 1930). Lectotype (Hattori 1986a: 205):—*Frullania meyeniana* Lindenb. in Gottsche *et al.* (1845: 455).**

***Frullania* subg. *Microfrullania* (R.M.Schust.) R.M.Schust., *Hepat. Anthocerotae N. Amer.* 5: 34, 1992. Basionym:—*Neohattoria* sect. *Microfrullania* R.M.Schust., *J. Hattori Bot. Lab.* 33: 280, 1970 (Schuster 1970). Type (Schuster 1970: 280):—*Neohattoria parhamii* Schuster (1963: 243) (\equiv *Frullania parhamii* (R.M.Schust.) R.M.Schust. ex von Konrat, L.Söderstr. et A.Hagborg in Söderström *et al.* (2011: 407)).**

Note:—This subgenus has been investigated by von Konrat *et al.* (e.g., 2006, 2010, 2011a, 2012, 2013). An even more comprehensive understanding might be expected when *F. neocaledonica* J.J.Engel in Engel & Smith Merrill (1999: 344) or the markedly polymorphous *F. junghuhniana* Gottsche in Gottsche *et al.* (1845: 444), and *F. rostrata* (Hooker & Taylor 1845: 87) Gottsche *et al.* (1845: 445) also are included. We recognize the three sections below as belonging to this subgenus.

***Frullania* (subg. *Microfrullania*) sect. *Amphijubula* (R.M.Schust.) von Konrat, Hentschel, Heinrichs et Braggins, *Bryologist* 114: 53, 2011 (von Konrat *et al.* 2011a). Basionym:—*Amphijubula* R.M.Schust., *J. Hattori Bot. Lab.* 33: 298 (Schuster 1970). Type (Schuster 1970):—*Amphijubula spruceana* Schuster (1970: 301) [= *Frullania microcaulis* Gola (1922 [1923]: 172), cf. von Konrat *et al.* (2011a)].**

***Frullania* (subg. *Microfrullania*) sect. *Microfrullania* (R.M.Schust.) von Konrat et Hentschel, *comb. nov.* Basionym:—*Neohattoria* sect. *Microfrullania* R.M.Schust., *J. Hattori Bot. Lab.* 33: 288, 1970 (Schuster 1970). Type:—*Neohattoria parhamii* Schuster (1963: 243) (\equiv *Frullania parhamii* (R.M.Schust. 1963: 243) R.M.Schust. ex von Konrat *et al.* in Söderström *et al.* (2011: 407)).**

Note:—Schuster (1991) used the name *F.* sect. *Microfrullania* as a putative autonym of *F.* subg. *Microfrullania*. However, the establishment of any subdivision of a genus under a subdivision that does not include the type of the genus, does not create an autonym (cf. ICN Art. 22.1). Hence, we here validate the section. Besides the type species, this section accommodates *F. chevalieri* (Schuster 1970: 289) Schuster (1992: 34), *F. microscopica* Pearson (1922: 33), and *F. neocaledonica* J.J.Engel in Engel and Smith Merrill (1999: 344).

***Frullania* (subg. *Microfrullania*) sect. *Regulares* Verd., *Ann. Bryol., Suppl.* 1: 133, 1930 (Verdoorn 1930). Lectotype (Hattori 1976):—*Frullania junghuhniana* Gottsche in Gottsche *et al.* (1845: 444).**

Note:—Verdoorn (1930) originally described *F.* sect. *Regulares* as a section of *F.* subg. *Diastaloba*. Hentschel *et al.* (2009) showed that the *F. rostrata* subclade of *F.* subg. *Microfrullania* corresponds to *F.* sect. *Regulares*. However, the type of *F.* sect. *Regulares* has not been included in any molecular analyses.

***Frullania* subg. *Saccophora* Verd., *Ann. Bryol.* 2: 121, 1928 [1929] (Verdoorn 1928b). Lectotype (Hattori 1973c):—*Frullania sublignosa* Stephani (1894: 148).**

Note:—The two subgenera, *F.* subg. *Fusiorielligerae* (Verdoorn 1930: 91) Hattori (1972b [1973]: 124) and *F.* subg. *Saccophora* (e.g., Hattori 1976, 1982, 1986b) have both been used to refer to a small group of allied taxa. However, Schuster (1992) combined both of these subgenera with reference to several shared morphological features. This treatment is adopted for the forthcoming worldwide checklist. There has been a long-lasting debate about the systematic position of this small and rather anomalous group (e.g., Stotler 1969, Hattori 1973b, 1975a, Schuster 1992, Gradstein & Costa 2003), characterized by rather small lobules, broadly inserted leaf lobes and the initial branch leaf with two saccate lobes inserted below the branch origin (cf. Schuster 1992). Although *F. gaudichaudii* (Nees & Montagne 1836: 64) Nees et Mont. in Gottsche *et al.* (1845: 435) was included in the molecular analysis by Hentschel *et al.* (2009), the study failed to resolve the systematic position of *F.* subg. *Saccophora*. Therefore, a more comprehensive study is needed.

***Frullania* subg. *Steerea* (S.Hatt. et Kamim.) R.M.Schust., *Hepat. Anthocerotae N. Amer.* 5: 32, 1992 (Schuster 1992). Basionym:—*Steerea* S.Hatt. et Kamim., *J. Hattori Bot. Lab.* 34: 429, 1971 (Hattori & Kamimura 1971). Holotype:—*Steerea mastigophoroides* Hattori & Kamimura (1971: 429) [= *Frullania clemensiana* Verdoorn (1932: 493), cf. Hattori 1975d].**

Note:—With only *S. mastigophoroides* (= *F. clemensiana*) included, *Steerea* has been regarded close to but distinct from *Frullania* (e.g., Hattori & Kamimura 1971, 1976), but is now considered a synonym of this genus (Schuster 1992). The phylogenetic affiliation of this puzzling species known from the mossy forests of Mt. Kinabalu remains unclear, since it never has been investigated by molecular methods.

***Frullania* subg. *Thyopsiella* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 41, 1884 (Spruce 1884). Lectotype (Uribe & Gradstein 2003: 195):—*Frullania tamarisci* (Linnaeus 1753: 1134) Dumortier (1835: 13).**

Note:—Uribe and Gradstein (2003) lectotypified this subgenus with *F. tamarisci*, a taxon erroneously regarded as the generitype by many earlier authors. Thus, the subgenus used to be treated as *F.* subg. *Frullania* as discussed above. Whereas the circumscription of this subgenus can be deemed sufficiently clarified (Uribe & Gradstein 2003, Hentschel *et al.* 2009), the taxonomy of the highly polymorphic *F. tamarisci* is still not completely understood and currently a matter of intense investigation (e.g., Vilnet *et al.* 2014).

Nomenclatural novelties of miscellaneous *Frullania* names

Below are new synonyms, new names and new combinations for miscellaneous *Frullania* names at the rank of species and below.

***Frullania* (subg. *Meteoriopsis* sect. *Intumescentes*) *ambroonii* Steph., *Biblioth. Bot.* 87: 242, 1916 (Stephani 1916). Type:—BOLIVIA, Tablas, *Herzog 4536*, Herb. F. Stephani no. 13533 (G-00066976, lectotype **here designated**). Note:—The lectotype was annotated as type by both R. Stotler (August 1968) and Y. Yuzawa (23 November 1987), but they did not annotate the other syntype (*Herzog 4569*).**

= *Frullania harpantha* Herzog, *Beih. Bot. Centralbl., Abt. 2.* 61: 571, 1942 (Herzog 1942), **syn. nov.** Type:—COLOMBIA, Cundinamarca: Tequendama, 1929, *Troll 2140* (JE!, holotype; JE!, isotype). Note:—Raymond Stotler annotated the type as a synonym of *Frullania ambroonii* in 1969, but according to our data the synonymization has not been published yet.

***Frullania* (subg. *Thyopsiella*) *acicularis* Hentschel et von Konrat, **nom. nov. pro** *Frullania tamarisci* var. *azorica* J.-P.Frahm, *Trop. Bryol.* 27: 102, 2006 (Frahm 2006). Type:—PORTUGAL, Azores: Terceira, Serra de Santa Barbara, 22 August 2004, *Frahm Az316* (BONN, holotype; LIS, isotype). Blocking name:—*Frullania azorica* Sim-Sim, Sérgio, Mues et Kraut, *Cryptog. Bryol. Lichénol.* 16: 112, 1995 (Sim-Sim *et al.* 1995). The epithet refers to the long needle-like leaf apices.**

***Frullania* (subg. *Frullania* sect. *Frullania*) *ericoides* var. *verrucosa* (Kamim.) Hentschel et von Konrat, **comb. nov.** Basionym:—*Frullania squarrosa* var. *verrucosa* Kamim., *J. Hattori Bot. Lab.* 24: 19, 1961 (Kamimura 1961).**

Type:—JAPAN. Kochi: Tosa, 20 February 1948, *Kamimura 1321* (NICH-46849, isotype). Note:—Kamimura (1961) noted that the most diagnostic character of this variety is the verruculose cuticle of the leaf cells together with the propagules, which sometimes are seen on the ventral surface of the leaves. *Frullania ericoides* (Nees 1833: 346) Montagne (1839: 51) is a polymorphic species and Hentschel *et al.* (2009) indicated that at least two independent lineages are present. Further investigation of the complex is required.

***Frullania* (subg. *Microfrullania*) *fertilis* De Not., *Mem. Reale Accad. Sci. Torino (ser. 2)* 16: 235, 1855 (De Notaris 1857).** Type:—CHILE. Valparaiso: *Puccio* (FH).

= *Frullania magellanica* var. *diminutiva* Herzog, *Arch. Esc. Farm. Fac. Sci. Med. Cordoba* 7: 29, 1938 (Herzog & Hosseus 1938), **syn. nov.** Type:—CHILE. Valdivia: Quitaluto, *Herzog 679 ex p.* (JE!, lectotype **here designated**); Villarica: Pucón, *Herzog 204!*; Chiloé: Llanquihué, Petrohué, *Herzog 522*). Note:—Only two of the three syntypes mentioned by Herzog and Hosseus (1938) are located at JE. One of them, *Hosseus 204*, was revised by G. G. Hässel de Menéndez in 1981 as belonging to *F. fertilis*. Due to the fact that *Hosseus 679 ex p.* is fertile (c.per., c.spor, ♂) the second syntype was chosen as the lectotype. Since *F. magellanica* frequently has been confused with *F. fertilis*, Hässel de Menéndez & Rubies (2009) considered several reports of *F. magellanica* F. Weber et Nees in Gottsche *et al.* (1845: 446) and its varieties doubtful, including the records of *F. magellanica* var. *diminutiva* by Herzog & Hosseus (1938). Engel (1978), who had not seen the type specimen of *F. magellanica* cited *F. fertilis* as its synonym. A detailed account of both species is presented by Hässel de Menéndez (1983). To decide on the status of *F. magellanica* subsp. *tristaniana* (S.W. Arnell 1958: 9) Vána et J.J. Engel (2013: 59) further investigations are needed.

***Frullania* (subg. *Frullania* sect. *Australes*) *fugax* (Hook.f. et Taylor) Gottsche, Lindenb. et Nees, *Syn. Hepat.* 3: 445, 1845 (Gottsche *et al.* 1845).** Basionym:—*Jungermannia fugax* Hook.f. et Taylor, *London J. Bot.* 4: 87, 1845 (Hooker & Taylor 1845). Type:—NEW ZEALAND. On *Rimelia (Parmelia) reticulata*, 1844, *J. D. Hooker (ex herb. Lehm., S!)* (lectotype **here designated** [packet of lower right hand corner on sheet]).

= *Frullania yorkiana* Steph., *Sp. Hepat. (Stephani)* 4: 558, 1911 (Stephani 1911), **syn. nov.** Type:—AUSTRALIA. Queensland: Cape York, August 1897, *Micholitz*, Herbarium F. Stephani no. 18236 (G-00066920, lectotype designated by Hattori 1979: 152). Note:—Hattori (1979) noted the similarity with *F. fugax* and stated that it possibly is a synonym.

***Frullania* (subg. *Diastaloba*) *gracilis* (Reinw., Blume et Nees) Nees, *Syn. Hepat.* 3: 452, 1845 (Gottsche *et al.* 1845).** Basionym:—*Jungermannia gracilis* Reinw., Blume et Nees, *Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur.* 12(1): 221, 1824 [1825] (Reinwardt *et al.* 1824). Type:—INDONESIA. Java: s. loc. spec. (type not located; missing in STR and other searched herbaria). Note:—*Frullania gracilis* belongs to a polymorphous and taxonomically difficult species complex (e.g., Verdoorn 1929, Hattori 1974a, 1974b, 1975c) and needs further attention. Particularly, the type of *Jungermannia gracilis* has never been examined.

= *Frullania minor* var. *integribacteola* S.Hatt., *J. Hattori Bot. Lab.* 39: 293, 1975 (Hattori 1975a), **syn. nov.** Type:—INDONESIA. Sumatra, Mt. Singgalang, July 1955, *Meijer 1723* (L, holotype; NICH, isotype).

= *Frullania minor* subsp. *recurviloba* S.Hatt., *J. Hattori Bot. Lab.* 39: 293, 1975 (Hattori 1975a), **syn. nov.** Type:—INDONESIA. Sumatra, Mt. Korinchi, 29 July 1956, *Meijer B-9055* (L, holotype; NICH isotype).

***Frullania* (subg. *Frullania*) *jovetiana* von Konrat et Hentschel, **nom. nov. pro** *Frullania pseudericoides* S.Hatt., *Bull. Natl. Sci. Mus. Tokyo, B* 12: 132, 1986 (Hattori 1986c), **nom. illeg.** (ICN Art. 53.1; *hom. illeg.* [*non* S.Hatt. 1982]). Type:—INDIA. *Kurz 1409*, Herbarium F. Stephani no. 15963 (G-00115327, holotype; NICH, isotype). Blocking name:—*Frullania pseudericoides* S.Hatt., *J. Hattori Bot. Lab.* 51: 256, 1982 (Hattori 1982). Note:—The type is stored in G under the herbarium name “*Frullania jovetiana*”. It is possible that the name in Hattori (1986c) is a mistake for what was intended to be this name.**

***Frullania* (subg. *Meteoriopsis* sect. *Obtusilobae*) *kunzei* var. *maritima* R.M.Schust. ex Hentschel et von Konrat, **var. nov.** Based on:—*Frullania kunzei* var. *maritima* R.M.Schust., *J. Hattori Bot. Lab.* 70: 145, 1991 (Schuster 1991), **nom. inval.** (ICN Art. 37.7; no herbarium indicated). Type:—USA. Florida: Collier Co., Collier-Seminole State Park, *R.M.Schuster 76-390* (F!, holotype).**

Frullania* (subg. *Frullania*) *laeviperiantha* X.L.Bai et C.Gao ex Hentschel et von Konrat, *sp. nov. Based on:—*Frullania laeviperiantha* X.L.Bai et C.Gao, *Nova Hedwigia* 70: 135, 2000 (Bai & Gao 2000), *nom. inval.* (ICN Art. 37.7; no herbarium indicated). Type:—CHINA. Yunnan: Ruili, 8 July 1977, *Li Xing-jiang* 89 (HKAS, holotype; IFSBH, isotype).

***Frullania* (subg. *Meteoriopsis* sect. *Intumescentes*) *macrocephala* (Lehm.) Lehm. et Lindenb., *Syn. Hepat.* 3: 460, 1845 (Gottsche *et al.* 1845). Basionym:—*Jungermannia macrocephala* Lehm., *Nov. Stirp. Pug.* 5: 20, 1833 (Lehmann 1833). Type:—PERU. s. loc. *Kunze s. n.* (W, lectotype designated by Stotler 1969).**

= *Frullania repanda* Gottsche, *Ann. Sci. Nat. Bot. (sér. 5)* 1: 175, 1864 (Gottsche 1864), *syn. nov.* Type:—COLOMBIA. Ad Tequendamam in montibus Fusagasuganis, *Triana* 2 (COL, lectotype here designated).

***Frullania* (subg. *Frullania* sect. *Acutilobae*) *monocera* (Hook.f. et Taylor) Gottsche, Lindenb. et Nees, *Syn. Hepat.* 3: 418, 1845 (Gottsche *et al.* 1845). Basionym:—*Jungermannia monocera* Hook.f. et Taylor, *London J. Bot.* 4: 89, 1845 (Hooker & Taylor 1845). Type:—AUSTRALIA. Tasmania: Terra Van Diemen, *misit Taylor 1847 (herb. Lehmannianum)* (S-B143254!, lectotype here designated; FH!, isolectotype). Note:—*Frullania monocera* belongs to a species complex not yet fully understood (e.g., Hattori 1973a, 1979, 1980a).**

Frullania monocera* var. *acutiloba* (Mitt.) Hentschel et von Konrat, *comb. nov. Basionym:—*Frullania acutiloba* Mitt., *J. Proc. Linn. Soc. Bot.* 5: 120, 1861 (Mitten 1861). Type:—INDIA. Nilgiri Mts., *Perrottet* (NY, lectotype Hattori 1973a [see also Hattori 1975b]).

Frullania monocera* var. *subhampeana* (E.A.Hodgs.) Hentschel et von Konrat, *comb. nov. Basionym:—*Frullania subhampeana* E.A.Hodgs., *Trans. & Proc. Roy. Soc. New Zealand* 77: 370, 1949 (Hodgson 1949). Type:—NEW ZEALAND. Wairoa, Maungapoike Falls, December 1937, *E. A. Hodgson 1472* (MPN!, lectotype designated by Hattori 1979: 146). Note:—*Frullania subhampeana* has a complicated history of synonymy and recognition. Hodgson (1972: 110) regarded the taxon as a synonym of *F. novae-zelandiae* Colenso (1887: 296), a species Hattori (1979) placed in the synonymy of *F. hampeana* Nees in Gottsche *et al.* (1845: 426) which he synonymized with *F. monocera* at the same time. However, Hattori (1979, 1983) recognized *F. subhampeana* as separate from *F. monocera*, but commented that they were closely related.

Frullania monocera* var. *undulata* (Kamim.) Hentschel et von Konrat, *comb. nov. Basionym:—*Frullania undulata* Kamimura, *J. Hattori Bot. Lab.* 24: 50 (Kamimura 1961). Type:—JAPAN. Kôchi: Mt. Kajigamori, July 1950, *Hr 1385* (NICH, holotype).

***Frullania* (subg. *Frullania*) *multituberculata* Hentschel et von Konrat, *nom. nov. pro F. kalimantanensis* Piippo et S.Hatt., *J. Hattori Bot. Lab.* 72: 117, 1992 (Piippo & Tan 1992), *nom. illeg.* (ICN Art. 53.1; *hom. illeg.* [non S.Hatt. 1986]). Type:—PHILIPPINES. Luzon: Rizal Prov., Tanay, 1977, *Alvarez, Saprid & Guerrero 0-771187* (CAHUP, holotype; FH, H, NICH, isotypes). Blocking name:—*Frullania kalimantanensis* S.Hatt., *Bull. Natl. Sci. Mus., Tokyo*, B 12: 127, 1986 (Hattori 1986c). Note:—The epithet refers to the tuberculate perianths.**

***Frullania* (subg. *Frullania*) *nepalensis* (Spreng.) Lehm., *Nov. Stirp. Pug.* 4: 19, 1832 (Lehmann 1832). Basionym:—*Jungermannia nepalensis* Spreng., *Syst. Veg. (ed. 16) [Sprengel]* 4: 324, 1827 (Sprengel 1827). Type:—NEPAL. s. loc. spec., s. n. & s. d., *ex hb. Kunze* (S-B28164, lectotype here designated).**

= *Frullania grevilleana* var. *densa* Schiffn. ex Verd., *Ned. Kruidk. Arch. (ser. 3)* 42: 487, 1932 (Verdoorn 1932), *syn. nov.* Type:—INDIA. Sikkim: Kurseong, October 1898, *Decoly (non vidi)*, type not located; *syn. fide* description).

= *Frullania grevilleana* var. *gebaueri* Verd., *Ann. Bryol.* 5: 164, 1932 (Dixon *et al.* 1932), *syn. nov.* Type:—INDIA. Darjeeling: Kataphar, April 1915, *A. K. Gebauer* (W, herb. Verdoorn [FH?], isotypes).

Frullania* (subg. *Chonanthelia* sect. *Cladocarpicae*) *obscura* var. *spiniloba* (Steph.) Hentschel et von Konrat, *comb. nov. Basionym:—*Frullania spiniloba* Steph., *Sp. Hepat. (Stephani)* 4: 336, 1910 (Stephani 1910). Type:—ECUADOR. loc. et coll. ign., *ex hb. Müller s. n.* (G, lectotype designated by Yuzawa 1991) ≡ *Frullania arecae* var. *spiniloba* (Steph.) Yuzawa, *J. Hattori Bot. Lab.* 70: 269, 1991 (Yuzawa 1991). Note:—Gradstein (2012) showed that *F. arecae* is a synonym of *F. obscura*, but did not transfer the variety.

***Frullania* (subg. *Frullania*) *obtusangula* Hentschel et von Konrat, *nom. nov. pro Frullania formosae* Steph., *Sp. Hepat. (Stephani)* 6: 539, 1924 (Stephani 1924), *nom. illeg.* (ICN Art. 53.1; *hom. illeg.*). Type:—TAIWAN. s. loc. spec., 1903, *Faurie 44* (G, lectotype designated by Hattori & Lin 1985: 134). Blocking name:—*Frullania formosa* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 46, 1884 (Spruce 1884). Note:—Kamimura (1961) treated the species as a synonym of *F. tamsuina* Stephani (1910: 444), but he probably examined the syntype from Hawaii instead of the lectotype (*cf.* Hattori & Lin 1985). The epithet refers to the bluntly toothed underleaves.**

***Frullania* (subg. *Meteoriopsis* sect. *Intumescentes*) *paradoxa* Lehm. et Lindenb., *Syn. Hepat.* 3: 462, 1845 (Gottsche *et al.* 1845). Type:—*Jubula tamarisci* β *paradoxa*, s. loc. spec. [Tropical America] *Hampe s. n.* (W, lectotype designated by Stotler 1969: 455).**

= *Frullania flexicaulis* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 53, 1884 (Spruce 1884), *syn. nov.* Type:—ECUADOR. Mt. Mulmul, *Jameson s. n.* (MANCH, lectotype designated by Stotler 1969: 464).

***Frullania* (subg. *Frullania*) *plicata* Hentschel et von Konrat, *nom. nov. pro Frullania acutiloba* Gerola, *Lav. Bot. Ist. Bot. Univ. Padova* 12: 477, 1947 (Gerola 1947). Type:—ETHIOPIA. Socorà, 5 November 1937; Irgalem, 25 November 1937 (syntypes, *non vidi*). Blocking name:—*Frullania acutiloba* Mitt., *J. Proc. Linn. Soc., Bot.* 5: 120, 1861 (Mitten 1861).**

***Frullania* (subg. *Frullania*) *setchellii* Pearson, *Univ. Calif. Publ. Bot.* 10: 326, 1923 (Pearson 1923). Type:—NEW ZEALAND. North Island: near Waiotapu, 1904, *W. A. Setchell 159* (UC!).**

= *Frullania engelii* S.Hatt., *J. Hattori Bot. Lab.* 54: 143, 1983 (Hattori 1983), *syn. nov.* Type:—AUSTRALIA. Tasmania: Florentine River, near Gordon River Road, 5 March 1977, *J. J. Engel 15080*, (NICH!, holotype; F!, isotype). Note:—The type material of *F. engelii* and specimens from Tasmania appear morphological identical to those of *F. setchellii*.

***Frullania* (subg. *Diastaloba*) *sinuata* Sande Lac., *Ned. Kruidk. Arch.* 3: 424, 1855 (Sande Lacoste 1854 [1855]). Type (*cf.* Hattori 1986b):—INDONESIA. Java: s. loc. spec., inter *Plagiochilam abietinam*, *Junghuhn s. n. & s. d.*, *Herb. Lugd. Bat.* 910.291-442 (L).**

= *Frullania falsisinuata* S.Hatt. et Piippo, *Acta Bot. Fenn.* 133: 28, 1986 (Hattori & Piippo 1986), *syn. nov.* Type:—PAPUA NEW GUINEA. Northern Province: Isuarava, 15 January 1936, *Carr 15391* (L-HLB 937.162-27, holotype; NICH-431958, isotype). Note:—*Frullania falsisinuata* was established as a *nomen novum* for *F. sinuata* subsp. *novoguineensis* S.Hatt. (Hattori 1975a: 301).

= *Frullania falsisinuata* var. *crispidentata* S.Hatt. et Piippo, *Acta Bot. Fenn.* 133: 29, 1986 (Hattori & Piippo 1986), *syn. nov.* Type:—PAPUA NEW GUINEA. Morobe: Mt. Sarawaket Southern Range, 1981 *Koponen 31586a*. (NICH-400031, holotype; LAE, H, isotypes).

***Jubula hutchinsiae* (Hook.) Dumort., *Syll. Jungerm. Europ.*: 36, 1831 (Dumortier 1831). Basionym:—*Jungermannia hutchinsiae* Hook., *Brit. Jungerm.*: tab. 1, 1812 (Hooker 1812). Type:—IRELAND. Bantry, *Hutchins* (BM, lectotype; H-2313, isolectotype).**

= *Frullania hutchinsiae* β *compacta* Carrington, *Trans. Bot. Soc. Edinburgh* 7: 456, 1863 (Carrington 1863), *syn. nov.* Type:—IRELAND. Eagle's Nest; Cromaglan (MANCH, syntypes).

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