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Type studies on *Frullania* subgenus *Meteoriopsis* (Hepaticae). I. The lectotypification of the genus *Frullania*, *F.* subgen. *Thyopsiella* and *F.* subgen. *Meteoriopsis*, and some species transferred from subgen. *Meteoriopsis* to subgen. *Thyopsiella*

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Abstract – A type revision of the species assigned to *Frullania* subgen. *Meteoriopsis* revealed that *F. aculeata* Taylor, *F. atrata* (Sw.) Nees, *F. capilliformis* Steph. (= *F. brasiliensis* Raddi), *F. caracensis* Steph. (= *F. brasiliensis*), *F. crinoidea* Spruce ex Steph. (= *F. atrata*), *F. effusa* Steph. (= *F. brasiliensis*), *F. goebeliana* Steph. (= *F. brasiliensis*), *F. hastatistipula* Steph. (= *F. brasiliensis*), *F. involuta* Hampe ex Steph., *F. lechleri* Steph.(= *F. atrata*), *F. leiboldiana* Steph. (= *F. atrata*), *F. liebmaniana* Lindenb. & Gottsche (= *F. atrata*), *F. lindeniana* Steph. (= *F. atrata*), *F. mucronata* (Lehm. & Lindenb.) Lehm. & Lindenb. (= *F. brasiliensis*), *F. subaculeata* Spruce (= *F. atrata*), *F. tenuis* Hampe ex Lehm. (= *F. brasiliensis*) and *F. uleana* Steph. (= *F. involuta*) were erroneously included in this subgenus and are members of subgen. *Thyopsiella*. In order to maintain subgen. *Meteoriopsis* in its original sense, *F. atrata* is rejected as the lectotype and *F. peruviana* Gottsche is proposed as the new lectotype. It is also pointed out that the lectotype of the genus *Frullania* is *Frullania dilatata* (L.) Dumort., not *F. tamarisci* (L.) Dumort. For this reason, the name *F.* subgen. *Trachycolea* Spruce is replaced by *F.* subgen. *Frullania* and the name *F.* subgen. *Thyopsiella* Spruce (lectotype: *F. tamarisci* (L.) Dumort., here designated) is maintained.

Frullania subgenus Frullania / Frullania subgenus Meteoriopsis / Frullania subgenus Thyopsiella / Hepaticae / lectotypification / Neotropics / nomenclature / taxonomic revision

Resumen – La revisión de los especimenes tipo de las especies asignadas a *Frullania* subgénero *Meteoriopsis* reveló que *F. aculeata* Taylor, *F. atrata* (Sw.) Nees, *F. capilliformis* Steph. (= *F. brasiliensis* Raddi), *F. caracensis* Steph. (= *F. brasiliensis*), *F. crinoidea* Spruce ex Steph. (= *F. atrata*), *F. effusa* Steph. (= *F. brasiliensis*), *F. goebeliana* Steph. (= *F. brasiliensis*), *F. hastatistipula* Steph. (= *F. brasiliensis*), *F. involuta* Hampe ex Steph., *F. lechleri* Steph.(= *F. atrata*), *F. leiboldiana* Steph. (= *F. atrata*), *F. liebmaniana* Lindenb & Gottsche (= *F. atrata*), *F. lindeniana* Steph. (= *F. atrata*), *F. mucronata* (Lehm. & Lindenb.) Lehm. & Lindenb. (= *F. brasiliensis*), *F. subaculeata* Spruce (= *F. atrata*), *F. tenuis* Hampe ex Lehm. (= *F. brasiliensis*) y *F. uleana* Steph. (= *F. involuta*) fueron erróneamente incluidas en este subgénero y son miembros del subgénero *Thyopsiella*. Para mantener el subgénero

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Meteoriopsis en su sentido original, *F. atrata* se rechaza como lectótipo y se propone a *F. peruviana* Gottsche como nuevo lectótipo. También se aclara que el lectótipo del género *Frullania* es *F. dilatata* (L.) Dumort., y no *F. tamarisci* (L.) Dumort. Por esta razón, el nombre *F.* subgénero *Trachycolea* Spruce debe ser remplazado por *F.* subgénero *Frullania* y el nombre *F.* subgénero *Thyopsiella* (lectótipo (nov.): *F. tamarisci*) debe ser mantenido.

Frullania subgénero Frullania / Frullania subgénero Meteoriopsis / Frullania subgénero Thyopsiella / Hepáticas / lectotipificación / Neotrópico / nomenclatura / revisión taxonómica

INTRODUCTION

The genus *Frullania* was established by Raddi (1818) for two northern-temperate species of the genus *Jungermannia*, *J. dilatata* L. (= *F. dilatata* (L.) Dumort.) and *J. tamarisci* L. (= *F. tamarisci* (L.) Dumort.). Spruce (1884) in his epoche-making treatment of the liverworts of Amazonia and the Andes of Peru and Ecuador, described 47 species of *Frullania* and divided the genus into six subgenera: *Chonanthelia, Diastaloba, Homotropantha, Meteoriopsis, Thyopsiella,* and *Trachycolea*. These subgenera were based on branching pattern, leaf insertion, shape and insertion of the lobule, and the morphology of the perianth. Some of the subgenera described by Spruce have been the subject of critical taxonomic revisions, e.g., subgen. *Thyopsiella* (Stotler, 1969, as subgen. *Frullania*) and subgen. *Chonanthelia* (Yuzawa, 1991), while others such as subgen. *Diastaloba* and subgen. *Meteoriopsis* have not been studied in detail. This paper is the first of a series dealing with the taxonomy of *Frullania* subgen. *Meteoriopsis*.

Spruce (1884) assigned to subgen. *Meteoriopsis* plants with a pendent habit and indefinite growth, deeply cordate leaves (with two large auricles, one at the dorsal and one at the ventral leaf base) which are strongly convoluted around the stem when dry and do not spread widely when moistened, narrow cylindrical lobules, and smooth, three-keeled perianths. The latter two characters were shared with subgen. *Thyopsiella* which is the sister group of subgen. *Meteoriopsis*. *Frullania* subgen. *Thyopsiella* was separated from subgen. *Meteoriopsis* by the non-pendent habit of the plants, the spreading, semicordate leaves (with only one instead or two auricules at leaf base), and the shorter, clavate to cylindrical lobules. Four neotropical species were included in subgen. *Meteoriopsis*: *F. atrata* (Sw.) Nees, *F. atrosanguinea* Taylor, *F. peruviana* Gottsche and *F. aculeata* Taylor.

Stephani (1911), in his world-wide treatment of the genus *Frullania*, assigned 49 species to subgenus *Meteoriopsis* (including 29 new ones) based solely on the possession of a pendent habit. The species from tropical America were classified into two different sections: sect. *Acutifolia* and sect. *Obtusifolia*.

Verdoorn (1930) in his study on the species of *Frullania* from the Indo-Malayan archipelago adopted Stephani's definition of the subgen. *Meteoriopsis* and included all species with a pendent habit in the subgenus. In total, 11 Asiatic species of subgen. *Meteoriopsis* in two sections (sect. *Vaginatae* and sect. *Orientales*) were recognized.

Kamimura (1961) treated the genus *Frullania* for Japan and assigned one species, *F. tenuicaulis* Mitt., to subgen. *Meteoriopsis*. Moreover, he proposed *Frullania atrata* (Sw.) Nees, the first species decribed by Spruce in subgen. *Meteoriopsis*, as the lectotype of the subgenus.

Hattori (1972) observed the existence of intermediate forms between subgen. *Meteoriopsis* and subgen. *Thyopsiella* (the latter as subgenus "*Frullania*") and suggested that pendent growth, even though being a striking character of the plants in the field, had little taxonomic relevance. In his series of papers on the genus *Frullania* from Asia published between 1972 and 1986, he initially treated subgen. *Meteoriopsis* as a section of subgen. *Thyopsiella* (Hattori, 1972, as subgen. *Frullania*), but later he considered it a separate subgenus (Hattori, 1977). On the other hand, he treated *Frullania* sect. *Orientalis* Verdoorn as a separate subgenus in 1976 (Hattori, 1976) but returned it to sectional level within subgen. *Meteoriopsis* in 1977, as originally proposed by Verdoorn (1930). Schuster (1992) also included the subgen. *Orientalis* in subgen. *Meteoriopsis* (note that the name *Meteoriopsis* is consistently misspelled "*Meteoropsis*" in the latter publication).

In the framework of a monograph of the subgen. *Meteoriopsis* undertaken by the first author, we have examined the types of all species previously assigned to subgen. *Meteoriopsis* and found that several species do not fit the original diagnosis of this subgenus as defined by Spruce (1884). Specifically, we noted that the pendent habit, considered the main character of subgen. *Meteoriopsis* by most previous authors, is not exclusive to this subgenus. Although all species of subgen. *Meteoriopsis* have pendent growth, not all pendent species of *Frullania* belong to subgen. *Meteoriopsis*. As will be shown in this and following papers, the species assigned to subgen. *Meteoriopsis* belong to at least four different subgenera. Moreover, the current lectotypifications of the genus *Frullania* and *F.* subgenus *Meteoriopsis* are erroneous and must be changed.

RESULTS

The lectotypification of *Frullania* Raddi, *F.* subgen. *Thyopsiella* Spruce and *F.* subgen. *Meteoriopsis* Spruce

According to Frey & Clark (1947), Stotler (1968) and others, *Frullania tamarisci* (L.) Dumort. is the lectotype of the genus *Frullania* (see also Farr *et al.*, 1979). However, as pointed out to us by Dr. R. Grolle (pers. comm.), these authors have overlooked the earlier lectotypification by Evans (1918, 1920), who chose *F. dilatata* (L.) Dumort. as the lectotype of *Frullania*. Since *F. dilatata* (typification see Grolle, 1970, 1976) is a genuine member of the genus *Frullania* and fits the protologue of the genus, the lectotypification by Evans, being the earliest one, must be followed according to Art. 10.5, ICBN (Greuter et al., 2000). As a consequence, the name *Frullania* subgen. *Trachycolea* Spruce (Type: *F. dilatata*; Spruce, 1884: 32) becomes a synonym of *F.* subgen. *Frullania* and the name *F.* subgen. *Thyopsiella* Spruce (Lectotype: *F. tamarisci* (L.) Dumort., **new, here designated**) should be retained. As the subgen. *Thyopsiella* has never been lectotypified, we designate *F. tamarisci* as the lectotype, being the oldest, best known and most widespread species of this subgenus and perfectly fitting the original description of this group. Although Spruce (1884) did not provide a formal description of *Frullania tamarisci* in his treatment of the subgen. *Thyopsiella*, the species was mentioned several times in the discussion (Spruce, 1884, p. 42-43). From the protologue it is clear that Spruce considered *F. tamarisci* (L.) Dumort. a typical element of subgen. *Thyopsiella*.

As mentioned in the introduction, *F. atrata* was designated as the lectotype of subgen. *Meteoriopsis* (Kamimura, 1961), being the first species out of four described by Spruce (1884) in his original publication. Our study of the holotype of *Frullania atrata* (Sw.) Nees in the Swartz herbarium in Stockholm has revealed that the type specimen of *F. atrata* has semicordate leaf bases with only one auricle (at the dorsal base) instead of two and does not have strongly convoluted leaves, hence is clearly a member of the subgen. *Thyopsiella* (see also Gradstein & Pinheiro da Costa, 2003). If the lectotypification proposed by Kamimura (1961) would be accepted, *Frullania* subgen. *Meteoriopsis* would become a synonym of *Frullania* subgen. *Thyopsiella* (or vice versa). In order to maintain subgen. *Meteoriopsis* in its original sense (Art. 10.5, ICBN; Greuter *et al.*, 2000), it is necessary to reject the lectotypification by Kamimura and to select a new lectotype. We propose here *Frullania peruviana* Gottsche, one of the four species originally assigned by Spruce and a genuine member of subgen. *Meteoriopsis* (as defined by him), as the new lectotype.

Frullania subgenus ***Meteoriopsis*** Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 37. 1884. **Lectotype** (**new, here designated**): *Frullania peruviana* Gottsche (non Kamimura, 1961).

A complete description and illustration of *Frullania peruviana* Gottsche will appear in the forthcoming monograph of the subgen. *Meteoriopsis*.

Species transferred from subgen. *Meteoriopsis* to subgen. *Thyopsiella*

Study of the type materials revealed that the following species were erroneously included in subgen. *Meteoriopsis* and are instead members of subgen. *Frullania*: *F. aculeata* Taylor, *F. atrata* (Sw.) Nees, *F. capilliformis* Steph. (= *F. brasiliensis* Raddi), *F. caracensis* Steph. (= *F. brasiliensis*), *F. crinoidea* Spruce ex Steph. (= *F. atrata*), *F. effusa* Steph. (= *F. brasiliensis*), *F. goebelliana* Steph (= *F. brasiliensis*), *F. hastatistipula* Steph (= *F. brasiliensis*), *F. involuta* Hampe ex Steph., *F. lechleri* Steph. (= *F. atrata*), *F. leiboldiana* Steph. (= *F. atrata*), *F. liebmaniana* Lindenb & Gottsche (= *F. atrata*), *F. lindeniana* Steph. (= *F. atrata*), *F. mucronata* (Lehm. & Lindenb.) Lehm. & Lindenb. (= *F. brasiliensis*), *F. subaculeata* Spruce (= *F. atrata*), *F. tenuis* Hampe ex Lehm. (= *F. brasiliensis*) and *F. uleana* Steph. (= *F. involuta*). The accepted species, together with their new synonyms, are described and illustrated below.

1. *Frullania atrata* (Sw.) Nees, *in* Gottsche, Lindenberg & Nees, *Syn. Hepat.*: 463. 1845. *Jungermannia atrata* Sw., *Prodr. Nov. Gen. Spec.*: 144. 1788. *Frullania atrata* (Sw.) Dumort., *Recueil Observ. Jungerm.*: 13. 1835, *nom. inval.* (Art. 32.1 (c) ICBN). **Type**. Jamaica, *Swartz s.n.* (holotype, S-B24877). **Figs 1-2**

Frullania liebmaniana Lindenb & Gottsche, *in* Gottsche, Lindenberg & Nees, *Syn. Hepat.*: 784. 1847. **Type**: México, Mirador, Aguas Santas, *Liebman s.n.* (lectotype, here designated, W 7572), **syn. nov.**

Frullania subaculeata Spruce, *Bull. Soc. Bot. France* 36 (Congrès de Botanique, Paris 1889) : CCII. 1890[1]. **Type**: Perú, *Lechler 2550* (holotype, MANCH 17176), **syn. nov.**

Frullania lechleri Steph., *Hedwigia* 33: 153. 1894. **Type**: Perú, *Lechler, 2550* (holotype, MANCH 17176), **syn. nov.**

[1] The proceedings of the Congrès International de Botanique were published in three parts, 1890-1891. The part 2 including the Spruce's article was published in August 1890 (Leussink, 1986: 258).

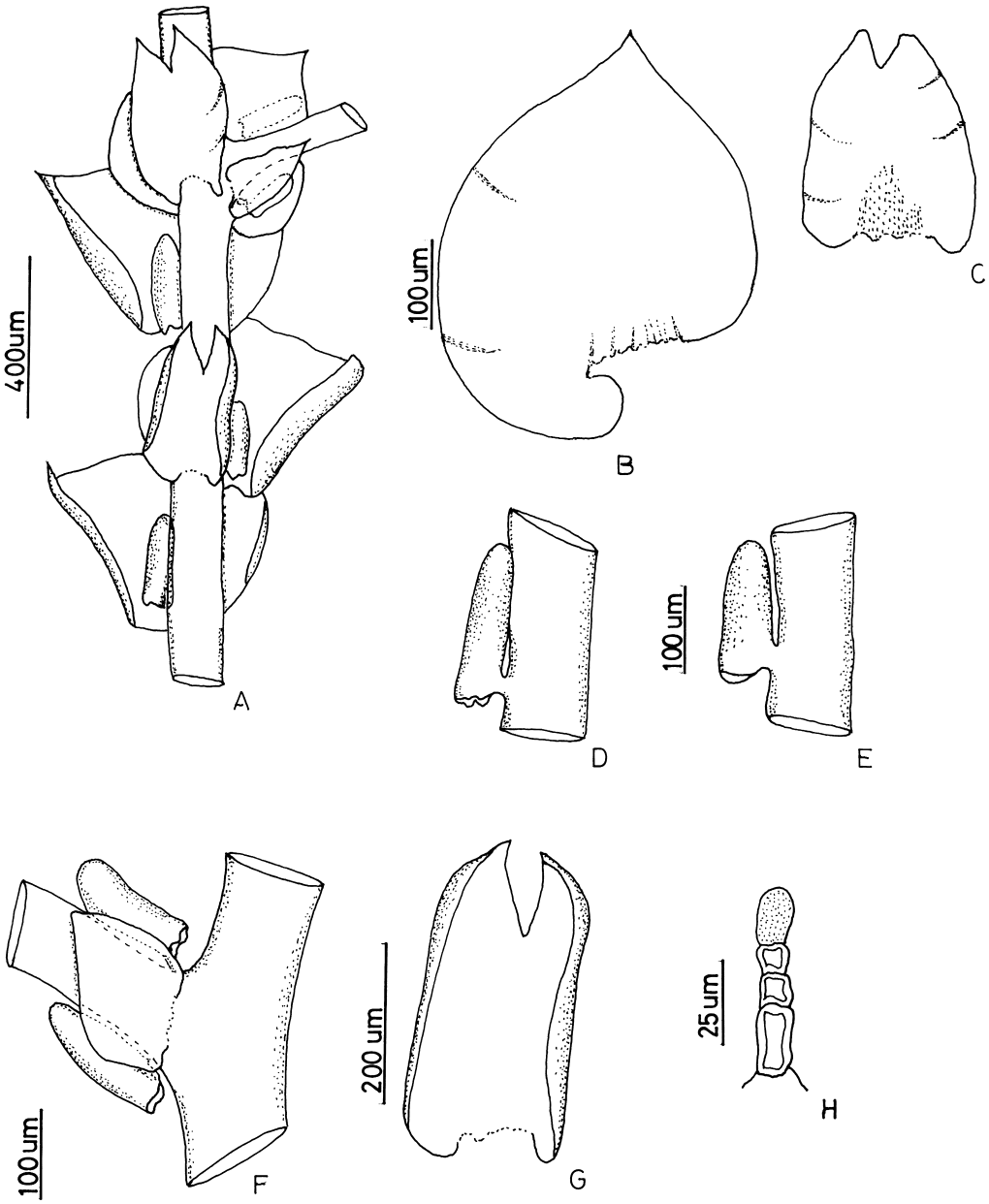

Fig. 1. *Frullania atrata* (Sw.) Nees – **A**. Part of shoot, ventral view, note the distant underleaves; **B**. Leaf of stem with dorsal base not auriculate; **C**. Underleaf; **D, E**. Ventral lobules, (D: long-cylindrical, E: cylindrical); **F**. Initial branching appendages; **G**. Underleaf; **H**. Stylus. (All from the holotype).

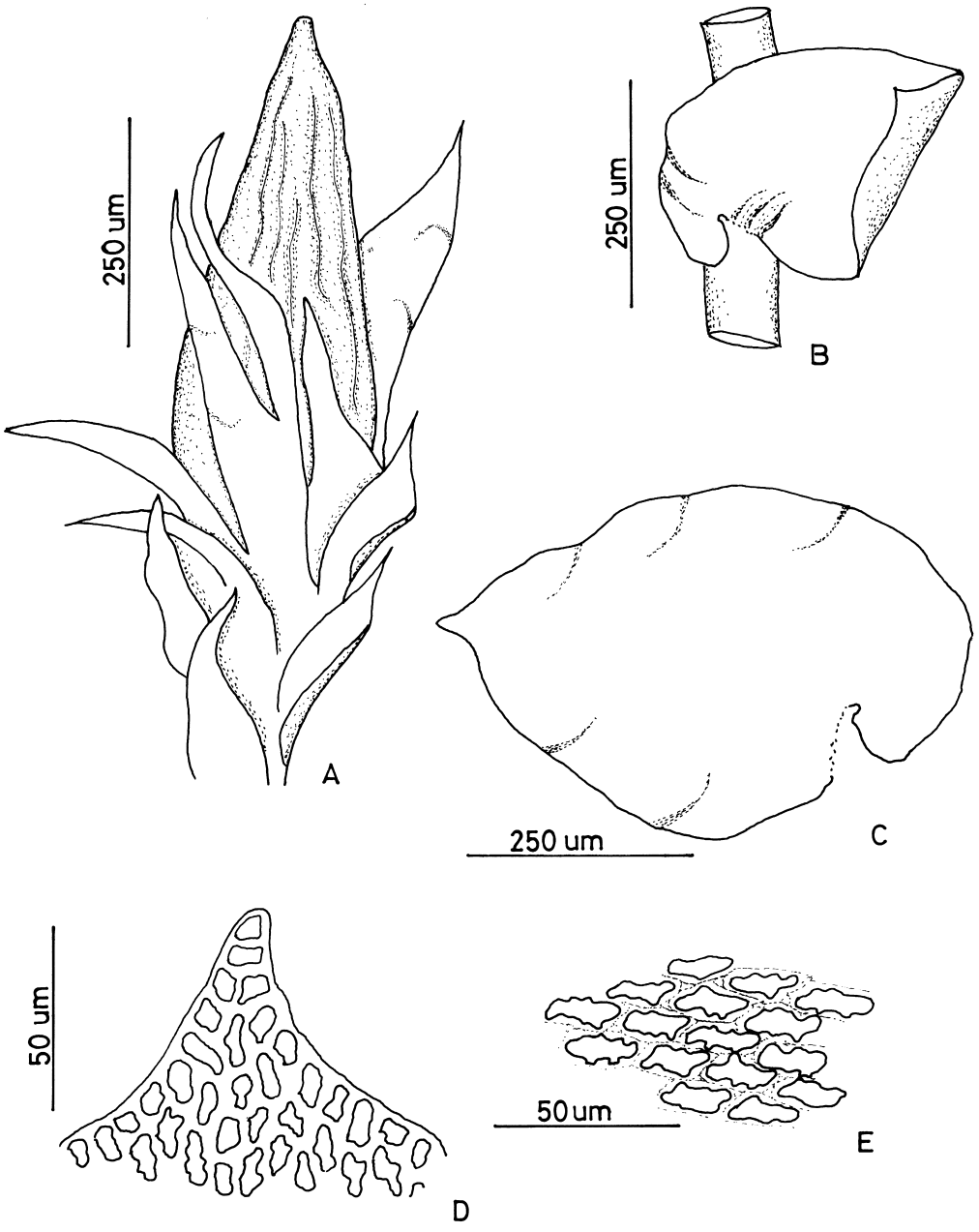

Fig. 2. *Frullania atrata* (Sw.) Nees – **A**. Perianth; **B**. Leaf, dorsal view; **C**. Leaf; **D**. Cells from apical portion of leaf; **E**. Cells from median portion of leaf. (A from the type of *F. turbata* Steph.; B, C, D, and E from the type of *F. lindeniana* Steph.).

Frullania crinoidea Spruce ex Steph. *in* Stephani, *Spec. Hepat*. 4: 604. 1911. **Type**: Peru, Mt. Guayrapurina, *Spruce s.n.* (sub *Frullania peruviana* Spruce, non Gottsche) (holotype, G 20613; isotype, MANCH 14041, 14040), **syn. nov.**

Frullania leiboldiana Steph. *Spec. Hepat*. 4: 609. 1911. **Type**: México, s.d., *Leibold s.n.*, ex hb Rabenhorst (holotype, G 20616), **syn. nov.**

Frullania lindeniana Steph., *Spec. Hepat*. 4: 603. 1911. **Type**: Cuba, *Linden 2310* (holotype, G 20617), **syn. nov.**

Frullania turbata Steph., *Spec. Hepat*. 4: 597. 1911. **Type:** Brazil, 1910, *Dusén 8461* (holotype, G 20625), syn. fide Gradstein & Pinheiro da Costa (2003).

Plants of medium to large size, up to 8 cm long and 0.8 mm wide including leves, dark reddish brown to almost black, irregularly pinnate, growing more or less pendent. Stems to 120 µm wide. **Leaves** imbricate, rounded, convolute around the stem when dry, obliquely spreading when wet except at the stem base, plane, ovate, asymmetrical, 490-650 × 390-480 µm, apex apiculate (short acuminate on branch leaves), margins entire, dorsal base auriculate, ventral base not auriculate, insertion line straight. **Leaf cells**: apical cells (20-)27-40 × (10-)19-24 µm, median cells 14-18(-20) × 5-7 µm, basal cells 14-20(-25) × 4-6 µm, all cells with thick, sinuous walls and with trigones and intermediate thickenings. **Lobules** cylindrical to clavate, 210-240 × 60-90 µm, contiguous and parallel to the stem, occasionally slightly inclined to the stem. **Stylus** filiform, erect, linear, three cells long, with a terminal, 50 µm long slime papilla. **Underlaves** ovate, distant, slightly wider than the stem, 270-560 µm × 220-360 µm, margins recurved, undulate, bifid to 1/4 the length, segments acute or obtuse, diverging, base short auriculate, insertion line straight. **Branch appendages**: first branch underleaf divided to the base into a lanceolate segment and a saccate segment, first leaf transformed into two saccate lobules. **Plants dioicous**. Gynoecia terminal on the stem, the bracts and bracteoles in three series, bracts unequally bifid, the segments acute or acuminate, entire. **Perianth** pyriform, 500 µm long, with three keels, the ventral keel narrow.

Distribution. — Probably widespread in tropical America but distribution not well known due to frequent misidentification of the species (see below). We have seen genuine collections of *F. atrata* from Cuba, Jamaica, Dominica (Morne Trois Pitons, *Elliott 491*, det. R. Spruce, MANCH 12787) and Brazil.

Frullania atrata is a poorly known species; the name has often been misapplied to genuine members of the subgen. *Meteoriopsis* such as *F. convoluta* Lindenb. & Gott. and *F. peruviana* Gottsche. To some extent, this confusion has been caused by Spruce (1884), who apparently confused *F. atrata* both with *F. peruviana* and *F. convoluta*. Thus, material collected by Spruce from Mt. Guayrapata, Ecuador (MANCH 12782, 12775) and described as *Frullania atrata* clearly belongs to *Frullania peruviana* Gottsche. This material was annotated as "typical" *Frullania atrata* by S. Hattori (annotation label dated 2 January 1977) and was illustrated under the name *Frullania atrata* by Stotler (1997, p. 133, 135: Figs. 15-21). Other specimens from Ecuador in the Spruce herbarium and annotated by Spruce as "*Frullania atrata* Sw. forma" (Quito, 1847, Jameson 56) or "*Frullania atrata* var.?" (Pichincha, unknown collector) belong to *Frullania convoluta*. In "Hepaticae Amazonicae et Andinae" Spruce (1884, p. 38-39) described *Frullania atrata* as having apiculate or short acuminate leaves, hence his description clearly refers to *F. peruviana*, not to *F. convoluta*. Interestingly, however, material from Dominica, *Elliott 491* (MANCH 12787) published by Spruce (1895) under the name *Frullania atrata* was correctly identified and indeed belongs to *F. atrata*.

Frullania atrata is recognized by its plane, apiculate, semicordate stem leaves, underleaves with plane to narrowly recurved margins, and a pyriform,

3-keeled perianth. The species is probably related to *F. intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb. but can be distinguished from the latter by the much more slender plants, being maximally 0.8 mm wide, the plane leaf apex (recurved in *F. intumescens*) and the almost plane, shallowly bifid underleaves.

2. *Frullania aculeata* Taylor, *London J. Bot*. 5: 407. 1846. **Type**: Ecuador, Galápagos, 1835, *Darwin s.n.* (**lectotype**, FH without number, **designated here**; isolectotypes, BM 664345, MANCH cc16072). Ecuador, Cuenca, *Jameson s.n.* (paralectotype, FH without number). **Fig. 3**

Frullania acuminata Steph., *Spec. Hepat*. 4: 606. 1911. **Type**: Peru, Tambo de la Chonta, 1876, *Wallis s.n.* (holotype, G 026717), syn. fide Gradstein & Weber (1982, p. 148).

Plants of medium to large size, to 10 cm long and 1.3 mm wide including leaves**,** dark reddish, growth projecting (not pendent). **Stems** to 100 µm wide. **Leaves** subimbricate, convolute around the stem when dry and spreading when wet, plane, triangular-ovate, 1375-1550 × 625-650 µm including the apex, apex long acuminate, acumen to 900 µm long, margins entire, strongly undulated, dorsal base auriculate, ventral base not auriculate, insertion line curved. **Leaf cells**: apical cells 25-30 × 7-12 µm, median cells (22-)25-27(-30) × 7-10(-12) µm, basal cells 27-50 × 15-30 µm, all cells with thick, sinuose walls and with trigones and intermediate thickenings. **Lobules** cylindrical to clavate, 220-260 µm × 70-83 µm, contiguous and parallel to the stem, occasionally slightly inclined to the stem, three or four times longer than broad. **Stylus** filiform, erect, linear, three cells long, 75 µm, with a terminal slime papilla. **Underleaves** oblong-lanceolate, contiguous, to two times wider than the stem, 950-1000 × 350-375 µm, margins plane or recurved, undulate, bifid to 1/3 the length, segments long acuminate, sinus wide to 550 µm, base auriculate, insertion line straight. **Branch appendages**: first branch underleaf divided to the base into a lanceolate, entire segment and a saccate segment, first branch leaf transformed into a saccate lobule. **Gametoecia** not seen.

Distribution. — Ecuador, Peru.

Frullania aculeata is easily recognized by the very long and finely acuminate leaf tip, and the species cannot be confused with any other species of the genus. The species was frequently misinterpreted by previous authors. Spruce (1884) erroneously described the leaves as being «biauriculato-cordata», whereas in the type they are clearly semicordate with only the dorsal base being auriculate. Material from Peru (*Lechler s.n.)* identified by Stephani, in 1909, as *F. aculeata* and described in full by Clark (1956) under that name belongs to *F. peruviana* Gottsche.

3. *Frullania brasiliensis* Raddi, *Mem. Mat. Fis. Soc. Ital. Modena* 19: 36. 1822. **Type**. Brazil. *Raddi s.n.* (isotype, NY). **Figs 4-5**

Frullania tenuis Hampe *ex* Lehm., *in* Lehmann, *Nov. Stirp. Pug*. 7: 13. 1838. **Type:** Ecuador, Loja, unknown collector, ex hb. Hampe (isotype, BM 6643343), **syn. nov.**

Frullania mucronata (Lehm. & Lindenb.) Lehm. & Lindenb., *in* Gottsche, Lindenberg & Nees, *Syn. Hepat*.: 461. 1845. *Jungermannia mucronata* Lehm. & Lindenb., *Nov. Stirp. Pug*. 6: 54. 1834. **Type:** Peru, unknown collector, ex hb. Kunze (isotype, G 026667), **syn. nov.**

Frullania caracensis Steph., *Spec. Hepat*. 4: 599. 1911. **Type**: Venezuela, Caracas, *A. Braun s.n.,* ex hb. Hampe (holotype, G 20610), **syn. nov.**

Frullania capilliformis Steph., *Spec. Hepat.* 6: 547. 1924 (sub *F. trichomorpha* Beauverd). **Type**: Bolivia, Comarapa, 2600 m, 1911, *Herzog 3967* (holotype, G 13669), **syn. nov.**

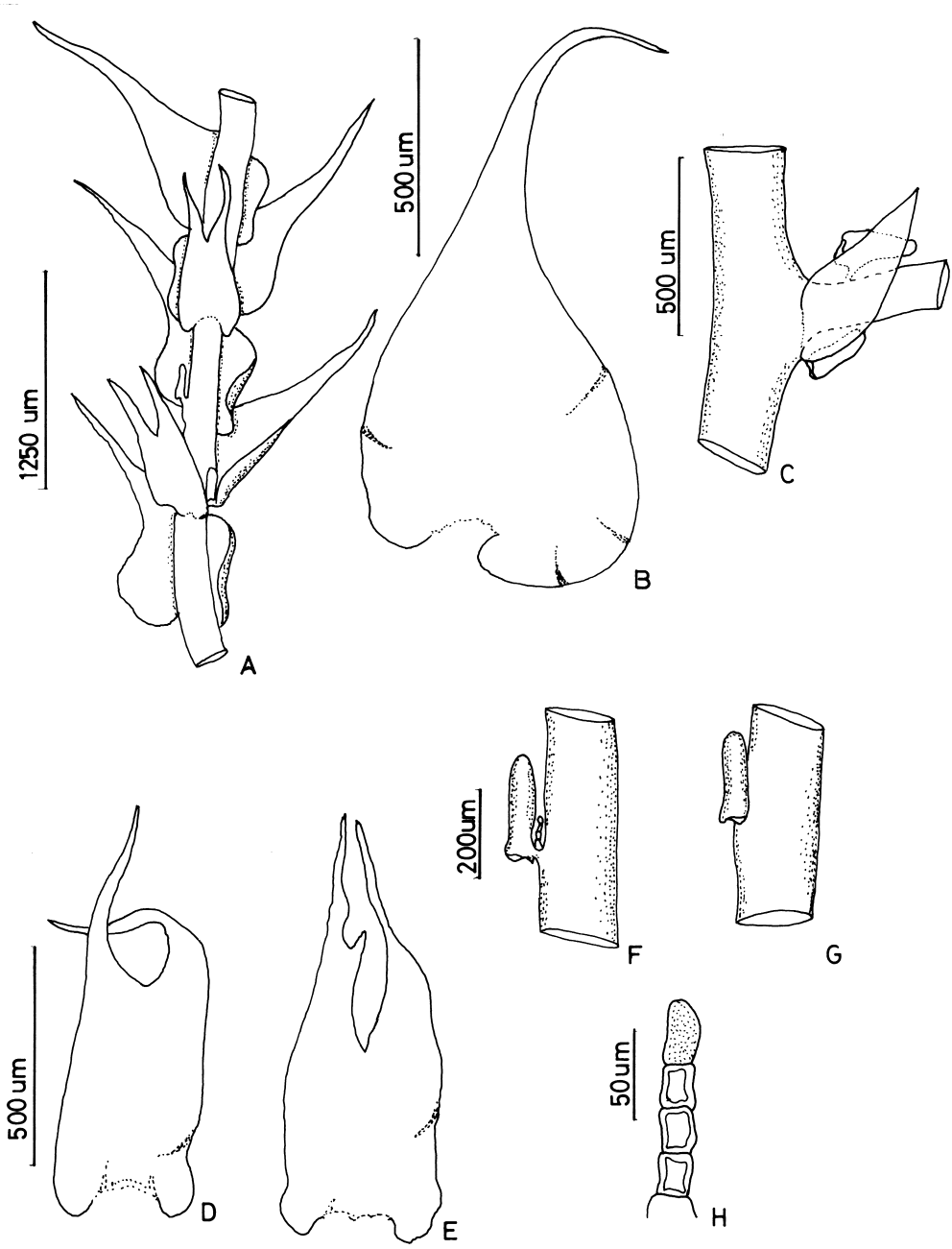

Fig. 3. *Frullania aculeata* Tayl. – **A**. Part of shoot, ventral view; **B**. Leaf; **C**. First branch underleaf and leaf; **D, E**. Underleaves; **F, G**. Ventral lobules; **H**. Stylus. (All from the type of *F. acuminata* Steph.).

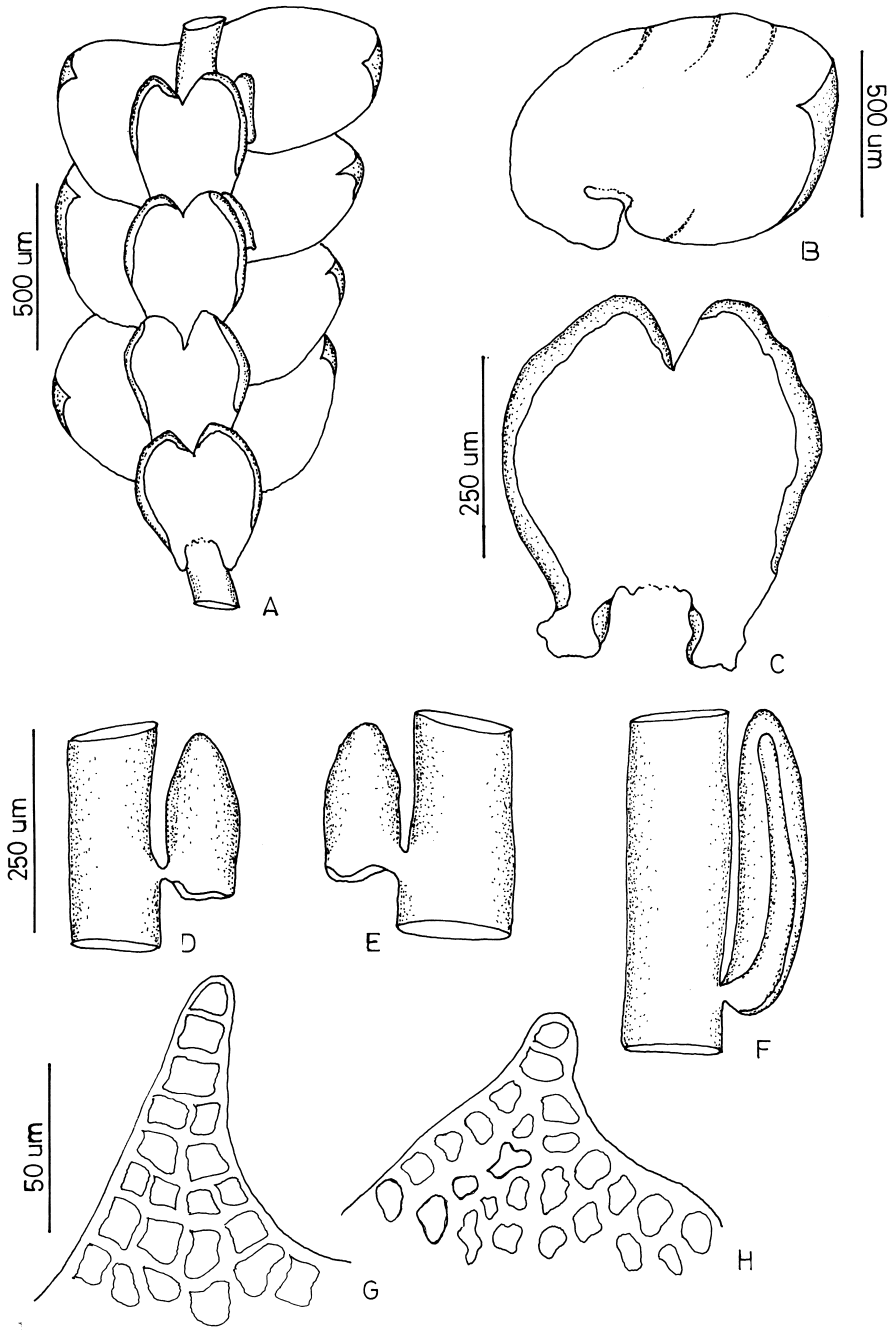

Fig. 4. *Frullania brasiliensis* Raddi – **A**. Part of shoot, ventral view; **B**. Leaf; **C**. Underleaf; **D, E**. Ventral lobules, cylindrical and clavate; **F**. Ventral lobule, canaliculate; **G, H**. Cells of apical portion (A, B, C, D, and E from the type of *F. tenuis* Hampe ex Lehm.; G from the type of *F. effusa* Steph.; H from the type of *F. goebeliana* Steph.).

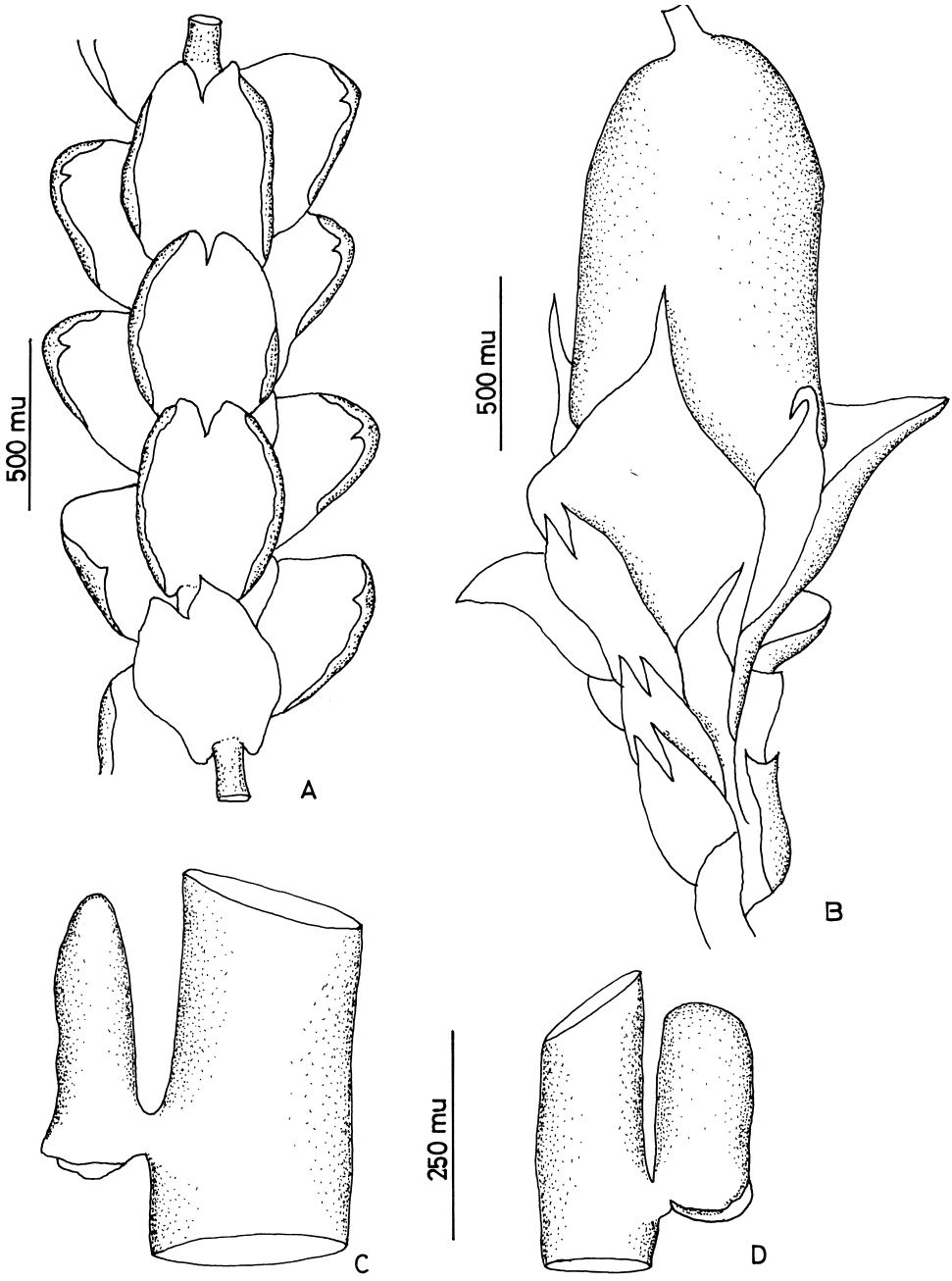

Fig. 5. *Frullania brasiliensis* Raddi – **A**. Part of shoot, ventral view; **B**. Perianth; **C**. and **D**. Ventral lobules. (All from the type of *F. caracensis* Steph.)

Frullania effusa Steph., *Spec. Hepat*. 6: 548. 1924. **Type**: Mexico, 1913, *Arsén 8001* (holotype, G 7795), **syn. nov.**

Frullania goebelliana Steph., *Spec. Hepat*. 6: 548. 1924. **Type**: Bolivia, Tablas, 3400 m, 1911, *Herzog 4569/a* (holotype, G without number), **syn. nov.**

Frullania hastatistipula Steph., *Spec. Hepat*. 6: 549. 1924. **Type**: Bolivia, Abra de San Mateo, 3000 m, 1911, *Herzog 3724* (holotype, G without number), **syn. nov.**

Plants of medium to large size, 10-11 cm long, 1.5-2 mm wide including the leaves, dark reddish brown to reddish green, growth projecting (not pendent). **Stems** 120-250 µm wide in cross section. **Branches** frequent, of the *Frullania*-type, to 1.5 cm long. **Leaves** imbricate, obliquely spreading when dry, ovate-oblong, asymmetrical, concave, (1175-)1300-1600(-1625) × (725-)825-1150(-1250) µm, apex apiculate to mucronate, recurved, margin entire, dorsal base auriculate, arching over the stem, ventral base not auriculate. **Leaf cells**: apical cells (7-)10-17 × (5-)7-12(-15) µm, median cells 17-22(-25) × 5-10(-12) µm and basal cells (25-)35-40(-47.5) × (7-)10-15(-17) µm, with walls thick, sinuous, with trigones and intermediate thickenings conspicuous. **Lobules** cylindrical to clavate, occasionally explanate or canaliculate, the cylindrical ones 220-300 × 80-110(-150) µm, contiguous to the stem and sometimes slightly inclined, the canaliculate ones to 380 × 80 µm. **Stylus** filiform, erect, three cells long, with a terminal slime papilla. **Underleaves** ovate, elliptical, imbricate to distant, 470-1050(-1175) × 400-800(-1100) µm, 5-8 times wider than the stem, margins entire, incurved or plane, bifid to 1/3 or 1/4 the length, segments acute to acuminate, base auriculate, auricles rather long, undulate, insertion line straight. **Branch appendages**: first branch underleaf divided to the base into an ovate, entire segment and a saccate segment, occasionally with a canaliculate segment; first branch leaf transformed into two saccate lobules. **Gynoecia** terminal on the stem, bracts and bracteoles in two or three series, bifid, mucronate or acute, entire. **Perianth** oblong, smooth, terete, narrowed to a long beak.

Distribution. — Very common throughout tropical America.

Frullania brasiliensis is an extremely variable species but can usually be recognized by the recurved, apiculate leaf apices, recurved underleaf margins and, especially, the smooth, terete perianths.

4. *Frullania involuta* Hampe ex Steph., *Spec. Hepat*. 4: 595. 1911. **Type**: Martinique, *Husnot 223* (**lectotype**, here designated, G 1298; isolectotype, BM 664353; material from «Guiana Batava» not available). **Fig. 6**

Frullania uleana Steph., *Hedwigia* 33: 155. 1894. **Type**: Brazil, Joinville, 1883, *Ule 142* (holotype, G 20626), **syn. nov.**

Plants of small or medium size, to 6 cm long and 1.5 mm wide including the leaves, reddish-yellow to reddish brown. Growing more or less pendent. **Stems** 110-130 µm wide in cross section. **Leaves** distant, convolute around the stem when dry, obliquely spreading when wet, ovate, 1175-1225 × 775-850 µm, dorsal margin toothed, ventral margin entire or occasionally with a tooth near the apex, apex acute to short acuminate, dorsal base auriculate, ventral base not auriculate**,** insertion line straight. **Leaf cells**: apical cells 12-22 × 5-7 µm, median cells 27-32 × (7)10-12 µm and the basal cells 30-37 × (7-)10-12 µm, elongated, thick walled, with trigones and intermediate thickenings coalesced. **Lobules** long-cylindrical or clavate, 170-230 × 60-90 µm contiguous and parallel to the stem. **Stylus** filiform, erect, three cell long, with a terminal slime papilla. **Underleaves** distant, more or less elliptical, 500-675 × 225-350 µm, margins entire, somewhat undulate, bifid to

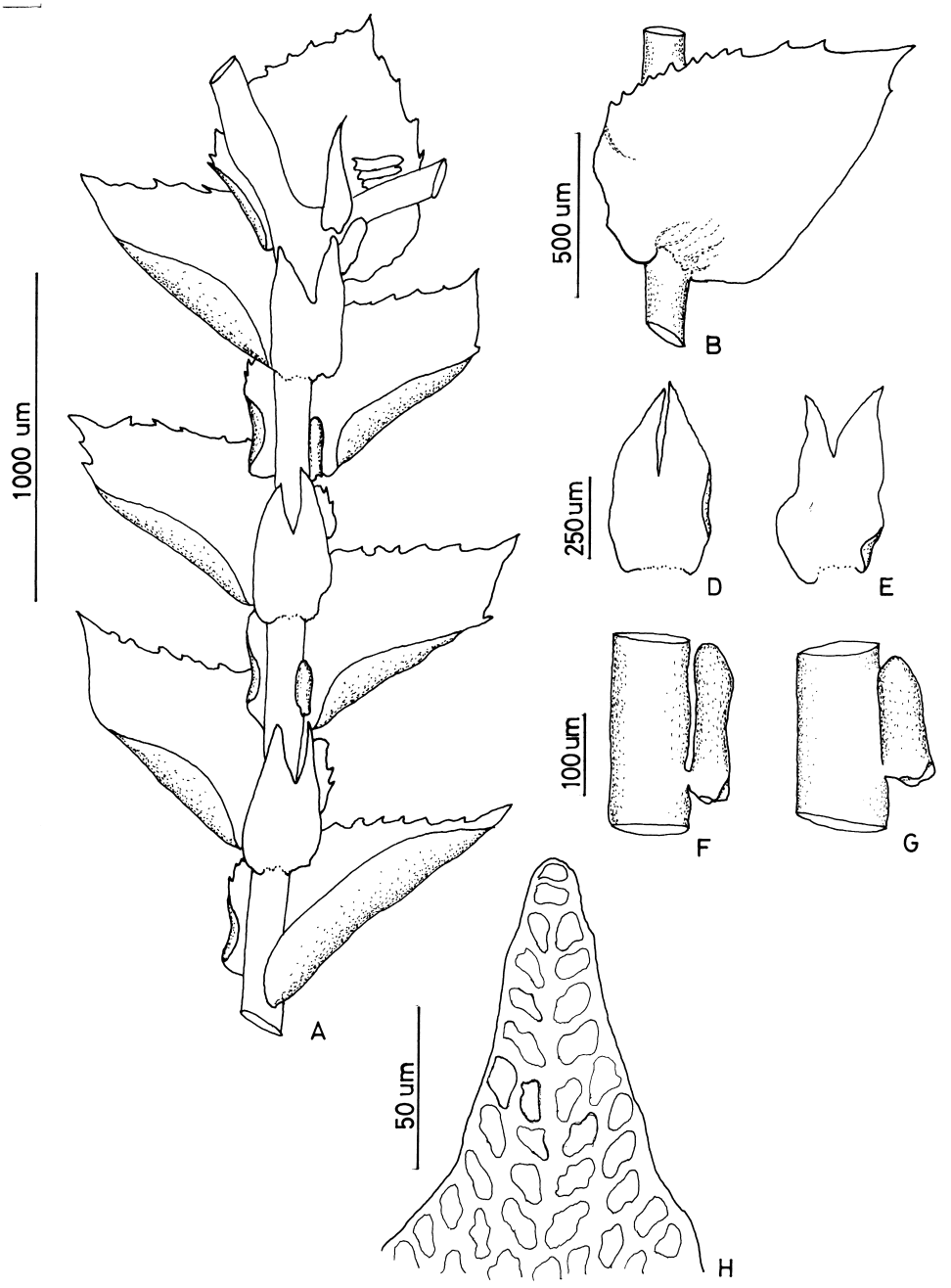

Fig. 6. *Frullania involuta* Hampe ex Steph. – **A**. Part of shoot, ventral view; **B**. Leaf; **D**. **E**. Underleaves; **F, G**. Ventral lobules; **H**. Cells of apical portion of leaf. (All from the type).

1/2 the length, segments spreading, acute, base not auriculate, insertion line straigth. **Branch appendages**: first branch underleaf divided to the base into a lanceolate, entire segment and a saccate segment, first branch leaf transformed into two saccate lobules. **Gametoecia** not seen.

Distribution. — Brazil, West Indies, Galapagos Islands.

Frullania involuta is easily recognized by the toothed dorsal margin of the leaves.

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