

The genus *Plagiochila* (Marchantiophyta) in Colombia

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Abstract

Plagiochila is the largest genus of bryophytes of Colombia. A total of 175 species have been recorded from the country but the majority of these are synonyms. In this paper 57 species are accepted for Colombia. A key to the Colombian species of *Plagiochila* is provided and each species is briefly described, with data on types, synonyms, published illustrations, morphology, geographical distribution and habitat, as well as a brief discussion of differentiating characters and taxonomic affinity. Among the countries of tropical America, Colombia has the highest diversity of *Plagiochila* followed by Ecuador (53 species) and Costa Rica (50 species). More than half of the Colombian species are widely distributed throughout tropical America and seven of them occur also in Africa and/or Western Europe. About one fourth of the species are restricted to the northern Andes, which is the centre of diversity of *Plagiochila* in the New World. The majority of the species grow as epiphytes in humid Andean forests. Diversity peaks in the upper montane forest belt between 2000-3000 m. Sixteen species occur in the páramo belt and five are exclusive to páramo. Eighteen species occur in lowland rainforest. *Plagiochila eggersii*, recorded from lowland rainforest of the Chocó, is new to Colombia.

Key words: Andean forest, bryophytes, Colombia, elevational distribution, liverworts, páramo, *Plagiochila*, taxonomy.

El género *Plagiochila* (Marchantiophyta) en Colombia

Resumen

Plagiochila es el mayor género de briófitos de Colombia. Un total de 175 especies han sido registradas para el país, pero la mayoría de estos nombres son sinónimos. En este trabajo se aceptan 57 especies para Colombia. Se proporciona una clave para las especies colombianas de *Plagiochila* y cada especie se describe brevemente con datos sobre los tipos, sinónimos, ilustraciones publicadas, morfología, distribución y hábitat, así como un breve análisis de sus caracteres principales y afinidad taxonómica. Entre los países de la América tropical, Colombia tiene la mayor diversidad de *Plagiochila* seguido de Ecuador (53 especies) y Costa Rica (50 especies). Más de la mitad de las especies colombianas están ampliamente distribuidas en América tropical y siete de ellas se presentan también en África y / o Europa occidental. Alrededor de una cuarta parte de las especies están restringidas para los Andes del norte, que es el centro de diversidad de *Plagiochila* en el Nuevo Mundo. La mayoría de las especies crecen como epífitas en bosques húmedos andinos. La mayor diversidad se encuentra entre 2000-3000 m. Dieciséis especies se encuentran en los páramos y cinco son exclusivas de páramo. Dieciocho especies se encuentran en la selva tropical. *Plagiochila eggersii*, encontrada en la selva del Chocó, es nueva para Colombia.

Palabras claves: bosque Andino, briófitas, Colombia, distribución altitudinal, hepáticas, páramo, *Plagiochila*, taxonomía.

Introduction

Plagiochilaceae are a large family of the liverworts (Marchantiophyta) with an estimated 450 species in nine genera (Söderström, *et al.*, 2016; Gradstein, 2015a). The species grow mainly as epiphytes and are abundant in tropical montane forests where bryophyte layers are often dominated by Plagiochilaceae (e.g., Wolf, 1994). About 95% of the species of Plagiochilaceae belong to *Plagiochila* (Dumort.) Dumort., which has an almost worldwide distribution and is the only genus in the family occurring in tropical America. Gradstein, *et al.* (2001) recognized three further Neotropical genera, *Plagiochilion* S.Hatt.

with two Neotropical species and *Stereochila* Inoue and *Szweykowskia* Gradst. & E.Reiner with one species each. However, these four species are now included in *Plagiochila* and the genera *Stereochila* and *Szweykowskia* are no longer recognized (Heinrichs, 2002).

The genus *Plagiochila* is readily recognized by the rather firm, greenish or brownish plants with stiff stems - due to the presence of a thick-walled cortex - and succubous leaves with

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a recurved dorsal margin and decurrent dorsal base (Fig. 1G). The leafy shoots usually arise from a rhizome-like, creeping stem and the branches always originate from the lateral side of the leafy stem, never from the ventral side; branching is “intercalary” or “terminal” (Gradstein, *et al.*, 2001, p. 6-7). The leaves may be transverse, obliquely spreading or widely spreading. In obliquely or widely spreading leaves, the leaf surface may be horizontal or “ventrad”; in the latter case the leaf surface is tilted towards the ventral side of the stem (Fig. 1E; the two leaves shown on the right-hand side of stem are “ventrad”). The leaf margins are usually toothed, especially at the apex and along the ventral margin; occasionally they

are entire. The ventral leaf bases are often “shouldered” (basal portion of ventral margin somewhat extended parallel to the stem before curving outwards) or expanded across and beyond the stem (“ampliate”; Fig. 1H,I). When strongly “ampliate”, the ventral leaf bases are concealing the stem and may curve downwards, forming a crest. Underleaves are absent or very small and rhizoids are usually few, originating scattered from the ventral stem surface. The plants are always dioicous. Androecia are typically arranged in long and narrow spikes, which are much narrower than the vegetative shoots. Gynoecia have a laterally flattened perianth with a wide, truncate mouth, which is usually fringed by numerous long

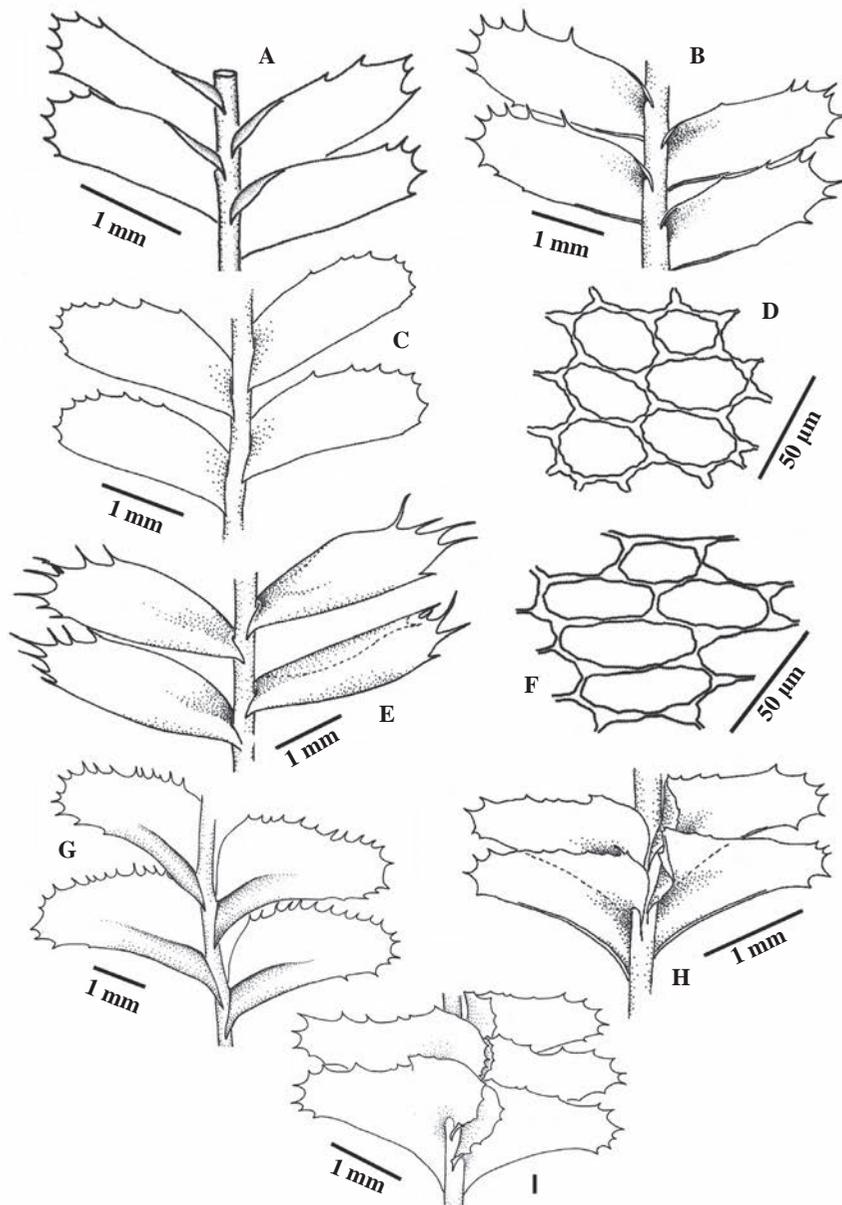


Figure 1. Selected *Plagiochila* species. A: *P. crispabilis*, portion of plant in ventral view; B: *P. subplana*, portion of plant in ventral view; C: *P. rutilans*, portion of plant in dorsal view; D: *P. rutilans*, midleaf cells; E: *P. aerea*, portion of plant in dorsal view; F: *P. aerea*, midleaf cells; G: *P. adianthoides*, portion of plant in dorsal view; H: *P. raddiana*, portion of plant in ventral view; I: *P. montagnei*, portion of plant in ventral view. All drawings by A.-L. Ilkiu-Borges.

teeth (rarely entire) (Fig. 2A). The sporophyte has a thick seta made up of numerous rows of cells and the capsule has a thick, 4-9-layered wall. Spores are unicellular or pluricellular due to endosporous germination and elaters have 1-2(-3) brown spirals. Vegetative reproduction is common, by small plantlets (propagula) originating from the ventral surface of leaves, by caducous leaves or by leaf fragmentation.

Plagiochila is the largest genus of bryophytes of Colombia, although the total number of species in the country has been exaggerated. About 175 species have been recorded (**Uribe**

& **Gradstein**, 1998) but almost two third of them are now considered synonyms or misidentifications (**Heinrichs**, 2002; **Heinrichs & Gradstein**, 2000; **Heinrichs, et al.**, 1998, 1999, 2000b, 2002a, 2002b, 2005a; **Müller, et al.**, 1999; **Gradstein & Uribe**, 2015; **Gradstein**, 2015a, this paper). In this paper 57 species are accepted for Colombia; a few further species remain doubtful taxa. Presumably the earliest *Plagiochila* record from Colombia appeared in the “Flora de la Real Expedición Botánica del Nuevo Reino de Granada” directed by José Celestino Mutis, which contains an illustration of an unidentified species of *Plagiochila* (**Aguirre & Calonge**,

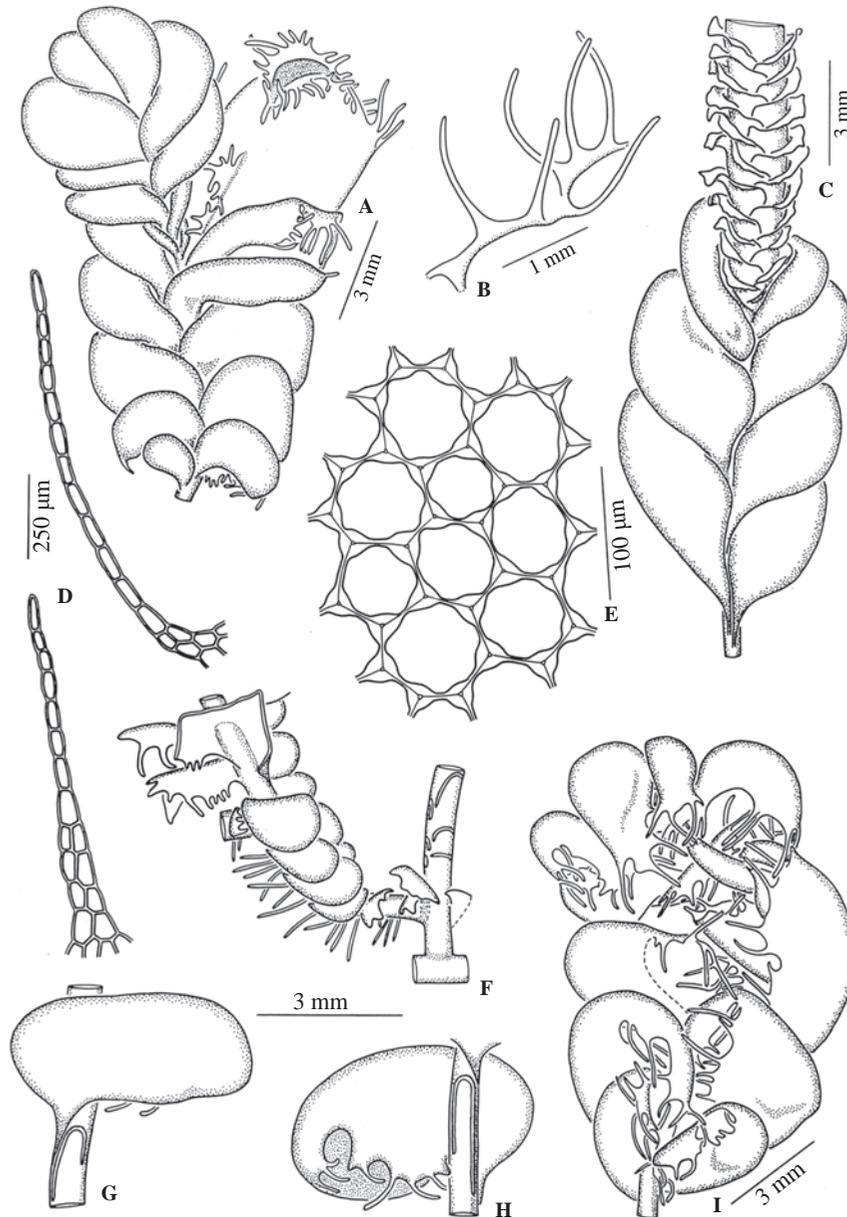


Figure 2. *Plagiochila cucullifolia* (= *Szweykowskia cucullifolia*). A: Portion of female plant in dorsal view, with mature perianth and one innovation; B: Portion of leaf margin with long-linear teeth; C: Portion of male plant in dorsal view, showing the basal part of the long male spike; D: Teeth of leaves; E: Midleaf cells; F: Base of stem showing lateral-intercalary branching (some leaves removed); G,H: Leaves in lateral view; I: Upper portion of plant in ventral view. All drawings by E.M. Reiner-Drehwald. Reproduced from *Fragmenta Floristica and Geobotanica* with permission of the copyright-holder.

1985: Lam. XII). Alexander von Humboldt and Aimée Bonpland collected *P. adianthoides* (Sw.) Lindenb. in Cauca (Kunth, 1822). The first major contribution to our knowledge of Colombian *Plagiochila* was by Gottsche (1864) who reported 25 *Plagiochila* species, many of them new to science, based on collections of Alexander Lindig and José Jerónimo Triana made mainly in Cundinamarca. Further species from Colombia were reported by Jack & Stephani (1892), Stephani (1901-1905), Herzog (1932, 1934, 1955), Robinson (1967), Winkler (1976) and others. In total, 44 species of *Plagiochila* were described as new to science based on specimens from Colombia. However, only eight of these are currently accepted (*P. amicta*, *P. cleefii*, *P. cuatrecasii*, *P. cucullifolia*, *P. grandicrista*, *P. guevarai*, *P. paraphyllina*, *P. trichostoma*), the rest are considered synonyms.

In this paper, keys and descriptions are provided for the *Plagiochila* species occurring in Colombia. It is the first modern treatment of the genus for Colombia, and the first one for any tropical Andean country. The text was written in the framework of the forthcoming “Guide to the Liverworts and Hornworts of Colombia and Ecuador” (in prep.). An important basis for this study were the recent publications on the taxonomy and phylogeny of neotropical *Plagiochila* by J. Heinrichs and his associates (e.g., Groth, et al., 2002; Heinrichs, 2002; Heinrichs & Gradstein, 2000; Heinrichs, et al., 1998, 1999, 2000a, 2000b, 2001b, 2002a, 2004a, 2004b, 2005a, 2005b; Müller, et al., 1999). For each species a brief description is provided together with data on types, synonyms (names used for Colombia), published illustrations, geographical distribution, habitat as well as a brief discussion of differentiating characters and taxonomic affinity. The descriptions are based on examination of herbarium specimens and on recent literature, while the distribution data are taken from Gradstein & Uribe (2015) with updates. For specimen citations the cited literature may be consulted. Nomenclatural changes that have occurred since the appearance of the latest checklist of *Plagiochila* of Colombia (Gradstein & Uribe, 2015) are listed in Appendix 1, <http://www.raccefyn.co/index.php/raccefyn/article/downloadSuppFile/272/1267>.

Among neotropical countries, Colombia has the largest number of *Plagiochila* species followed by Ecuador (53 species), Costa Rica (50 species) and Brazil (34 species) (Table 1). The high *Plagiochila* richness of Colombia may be explained by the enormous eodiversity of the country, viz. the large tracts of humid tropical montane forest and páramo habitats on three different Andean cordilleras reaching to well over 5000 m. The much lower diversity in Brazil, a country eight times larger than Colombia, is probably due to the lower elevation of the mountains, reaching to maximally 2994 m (Pico da Neblina).

On a global basis, China has the highest *Plagiochila* diversity (ca. 80 species), followed by Colombia (Table

Table 1. Number of *Plagiochila* species in different countries/regions of the world. Some species numbers are updated here, taking account of new synonymy.

Country/region	Number of accepted species	Reference
Colombia	57	this paper
Ecuador	53	Léon-Yanez et al. (2006)
Costa Rica	50	Dauphin (2005)
Brazil	34	Gradstein (2015b)
Guianas	20	Gradstein (1997)
Jamaica	23	Söderström et al. (2011)
Guadeloupe	20	Lavocat & Schäfer-Verwimp (2013)
Eastern North America	21	Schuster (1980)
Europe (incl. Macaronesia)	16	Schumacker & Váňa (2005)
Tropical Africa	ca. 40	Heinrichs et al. (2005c)
China	ca. 80	So (2001)
Malaysia	46	Chua-Petit (2011)
Java	31	Söderström et al. (2010)
New Zealand	25	Glenny (1998)
New Caledonia	23	Thouvenot et al. (2011)

1). Species richness generally decreases towards higher latitudes with 25 species being found in New Zealand, 21 in Eastern North America and 16 in Europe.

The distribution of the species of *Plagiochila* in Colombia is still incompletely known (Table 2). *Plagiochila adianthoides*, *P. aerea*, *P. fuscolutea* and *P. raddiana* are recorded from ten or more departments and may be considered the most common *Plagiochila* species of Colombia. In contrast, 21 species or about 35% are only known from one or two departments; these include *P. bryhnii*, *P. cleefii*, *P. cuneata*, *P. distinctifolia*, *P. eggersii*, *P. fastigiata*, *P. grandicrista*, *P. gymnocalycina*, *P. heterophylla*, *P. husnotii*, *P. lingua*, *P. loriloba*, *P. paraphyllina*, *P. patriciae*, *P. patula*, *P. revolvens*, *P. rudischusteri*, *P. stricta*, *P. subundulata*, *P. tenuis* and *P. trichostoma*. Many of these species may be more common in Colombia than is currently known. Hundreds of unidentified *Plagiochila* collections are housed in Colombian herbaria and it may be expected that specimens of these “rare” species are among them. It is hoped that the present paper will stimulate the identification of the unidentified materials, leading to further improvement of our knowledge of *Plagiochila* in Colombia.

In terms of elevation (Table 2), about 95% of the species are found in humid Andean forests of Colombia, above 1000 m. Species richness peaks in the upper montane forest belt, between 2000–3000 m, where more than two third of the species have been recorded. In contrast, only 18 species (30%) are found in lowland rainforests, below 500 m. Two

Table 2. Distribution of *Plagiochila* species of Colombia. Abbreviations: A = tropical Andes, Afr = tropical Africa, Br = Brazil, Ca = Caribbean, CA = Central America, CR = Costa Rica, Eur = Western Europe, Mac = Macaronesia, N = Neotropics, nA = northern Andes.

Species of <i>Plagiochila</i>	Occurrence in Colombia (number of departments)	Elevation (m) in Colombia	World range
<i>adanthoides</i>	10	300-3400	N
<i>aerea</i>	12	100-3300	N
<i>alternans</i>	9	2000-3300	N
<i>amicta</i>	3	1400-3100	N
<i>bifaria</i>	7	450-4000	N, Eur
<i>breuteliana</i>	9	200-2700	N
<i>bryhni</i>	2	2000-2600	A
<i>canelensis</i>	3	2500-4000	A
<i>cleefii</i>	1	3150-4300	nA
<i>crinata</i>	8	1500-2300	N
<i>cuatrecasii</i>	3	3600-4200	nA
<i>cucullifolia</i>	4	1300-3000	nA
<i>cuneata</i>	1	2600	A
<i>deflexirama</i>	5	900-2800	N
<i>dependula</i>	5	3150-4300	nA
<i>disticha</i>	6	100-2000	N
<i>distinctifolia</i>	1	100-2600	N
<i>diversifolia</i>	4	500-2600	N
<i>dominicensis</i>	3	200-2500	N
<i>eggersii</i>	1	30-400	Chocó, W Indies
<i>ensiformis</i>	8	2150-4000	nA
<i>exigua</i>	3	1800-3900	N, Afr, Eur
<i>fastigiata</i>	1	1680	CA, Colombia
<i>fuscolutea</i>	12	2200-4100	A
<i>grandicrista</i>	2	2000-2400	nA
<i>guevarai</i>	4	3300-3800	nA
<i>gymnocalycina</i>	2	300-1500	N
<i>heteromalla</i>	2	1200-3900	A
<i>heterophylla</i>	2	1150-3400	N, Eur
<i>husnotii</i>	1	30	N
<i>laetevirens</i>	4	800-3000	N
<i>lingua</i>	1	750	A, Br
<i>longispina</i>	8	2700-4050	A, Mac
<i>loriloba</i>	1	2900-3300	Colombia, CR
<i>macrostachya</i>	6	30-3000	N
<i>montagnei</i>	5	100-2600	N
<i>ovata</i>	5	3000-4000	A
<i>pachyloma</i>	6	2000-4100	nA
<i>papillifolia</i>	4	2000-3600	N, Mac

<i>paraphyllina</i>	2	3000-3700	nA
<i>patriciae</i>	1	3500	nA
<i>patula</i>	2	960-2800	N
<i>punctata</i>	4	1600-4300	N, Afr, Eur
<i>raddiana</i>	11	50-3300	N
<i>revolvens</i>	1	3150-4300	nA
<i>rudischusteri</i>	1	1500-1600	nA
<i>rutilans</i>	6	300-3200	N
<i>stricta</i>	2	100-2400	N, Afr, Mac
<i>subplana</i>	7	100-1900	N
<i>subundulata</i>	1	2040	Br, Colombia
<i>superba</i>	9	1000-3200	N
<i>tabinensis</i>	4	1500-3100	A
<i>tamariscina</i>	3	180-2000	N
<i>tenuis</i>	2	750-3500	N
<i>trichostoma</i>	2	1900-4000	A
<i>turgida</i>	3	1800-3500	nA
<i>vincentina</i>	8	80-2200	N

of these, *P. husnotii* and *P. eggersii*, are only known from the Chocó; the latter species is newly recorded here from Colombia. Sixteen species, finally, occur in the páramo belt and six of these, *P. cleefii*, *P. cuatrecasii*, *P. dependula*, *P. guevarai*, *P. paraphyllina* and *P. revolvens*, are largely exclusive to páramo.

Almost half of the Colombian *Plagiochila* species (25) are widely distributed in the Neotropics and seven species occur also in Africa and/or Western Europe. Most of the remaining species are Andean taxa (23); some of these are distributed from Bolivia to Mexico but the majority (14 species) are largely restricted to the northern Andes, which is the centre of diversity of *Plagiochila* in the New World. Three northern Andean species, *P. cleefii*, *P. cuatrecasii* and *P. revolvens*, are rare páramo taxa which are only known from a few collections from Colombia and Ecuador. Two species, *P. husnotii* and *P. eggersii*, occur at low elevations in the West Indies and along the Pacific coast of Colombia and Central America. Based on the present data, none of the *Plagiochila* species accepted here are endemic to the country.

The neotropical species of *Plagiochila* have been classified into nine sections based on morphological and molecular evidence (Heinrichs, 2002; Söderström, 2015). Based on this classification, the *Plagiochila* species of Colombia may be arranged as follows:

Section Adianthoideae Lindenb.: *P. adianthoides*, *P. cristata*, *P. grandicrista*.

Section Arrectae Carl: *P. bifaria*, *P. cleefii*, *P. cuatrecasii*, *P. eggersii*, *P. pachyloma*, *P. papillifolia*, *P. punctata*, *P. revolvens*, *P. stricta*, *P. subundulata*, *P. tenuis*.

Section Cucullatae Schiffn.: *P. subplana*.

Section Denticulatae Schiffn. (= section *Alternantes* Carl; fide Söderström, 2015): *P. alternans*, *P. ovata*.

Section Fuscoluteae Carl: *P. aerea*, *P. dependula*, *P. fuscolutea*, *P. heterophylla*, *P. paraphyllina*, *P. rudischusteri*, *P. tabinensis*.

Section Glaucescentes Carl: *P. diversifolia*, *P. longispina*.

Section Heteromallae Lindenb. (= *Plagiochila* section *Rutilantes* Carl, syn. nov.): *P. bryhnii*, *P. cuneata*, *P. exigua*, *P. gymnocalycina*, *P. heteromalla*, *P. loriloba*, *P. rutilans*, *P. trichostoma*.

Most authors use the name *Plagiochila* sect. *Rutilantes* (Type: *P. rutilans* Lindenb.) but the earliest name of this group is *Plagiochila* sect. *Heteromallae* (Type: *P. heteromalla* [Lehm. & Lindenb.] Lindenb.). This synonymy is supported by the conspecificity of *P. oreotropha* Spruce – a member of sect. *Rutilantes* (Heinrichs, 2002) – and *P. heteromalla* Lindenb. (Gradstein, 2015a).

Section Hylacoetes Carl: *P. amicta*, *P. breuteliana*, *P. canelensis*, *P. cucullifolia*, *P. dimorpha*, *P. dominicensis*, *P. ensiformis*, *P. guevarai*, *P. husnotii*, *P. macrostachya*, *P. patriciae*, *P. superba*, *P. turgida*, *P. vincentina*.

Section Vagae Lindenb.: *P. deflexirama*, *P. disticha*, *P. distinctifolia*, *P. fastigiata*, *P. laetevirens*, *P. lingua* Steph. (?), *P. montagnei*, *P. patula*, *P. raddiana*, *P. tamariscina*,

Taxonomic revisions have been carried out of the neotropical members of the sections *Adianthoideae*, *Cucullatae*, *Denticulatae*, *Fuscoluteae*, *Glaucescentes* and *Hylacoetes* (Heinrichs, 2002; Heinrichs, et al. 1999, 2002b; Müller, et al., 1999); the remaining sections are less studied and need more work. It is recommended that future taxonomic work should focus on the less well-known groups.

Key to species of *Plagiochila* from Colombia

A few species not known from Colombia but recorded from neighbouring areas have also been included in the key. Note: leaf characters should be examined on mature, vegetative stem leaves, not on branch leaves or on leaves near the gynoeceum. Branching type should not be studied on innovations (= branches originating below the perianth). Juvenile plants cannot be identified with certainty with this key.

- 1. Leaves modified into a swollen sac (Fig. 2). *P. cucullifolia*
- 1. Leaves not modified into a swollen sac. 2
- 2. Stem apex with conspicuous, yellowish-green clusters of flagelliform branchlets (resembling miniature cauliflower), producing numerous minute lanceolate caducous leaves. Ecuador and Costa Rica, not yet known from Colombia [*P. ecuadorica* (Inoue) L.Söderstr.]

- 2. Stem apex without yellowish-green clusters of flagelliform branchlets. 3
- 3. Ventral leaf margin strongly undulate to at least the middle of the leaf *P. fastigiata*
- 3. Ventral leaf margin not undulate or slightly undulate at the base only 4
- 4. Stems with many leaf fragments (except near apex), upper half of leaves usually broken off 5
- 4. Stems not with many leaf fragments 8
- 5. Plants robust, 5-7 mm wide. Branches predominantly terminal. Ventral leaf bases ampliate. Bolivia, Peru and Ecuador, not yet known from Colombia [*P. buchtiniana* Steph.]
- 5. Plants less than 5 mm wide. Branches intercalary or lacking. Ventral leaf bases not ampliate 6
- 6. Leaves ± transverse, widest in the lower half, margins with 5-20 teeth. Leaf base with a vitta. Cells with large trigones ... *P. bifaria*
- 6. Leaves obliquely to widely spreading, widest in the upper half, deeply 2-4-lobed, margins ± entire. Leaf base without vitta. Cells with small trigones 7
- 7. Leaves distant, 2-3-lobed. Leaf cells 20-32 µm wide in midleaf *P. cuneata*
- 7. Leaves imbricate, deeply 3-4-lobed. Leaf cells 25-43 µm wide in midleaf *P. loriloba*
- 8. Leaf margin with a brownish border of larger, thicker-walled cells and with numerous sharp, linear teeth. Leaves transverse, vitta present. Leaf cells small (except for the border and vitta cells), 15-25 µm, subisodiametric *P. pachyloma*
- 8. Leaf margin with brownish border of larger, thicker-walled cells. Plants different 9
- 9. Stems bluish near stem apex. (Leaves with long-ciliate teeth all around the margins) *P. longispina*
- 9. Stems green or brownish near apex, not bluish 10
- 10. Stem leaves of mature plants with 0-3 teeth 11
- 10. Stem leaves of mature plants mostly with more than 3 teeth 31
- 11. Stem leaves linear-lanceolate, 5-10× longer than wide *P. rudischusteri*
- 11. Stem leaves not linear-lanceolate, less than 5× longer than wide 12
- 12. Cuticle papillose 13
- 12. Cuticle smooth 15

13. Plants robust, stems 4-25 cm long. Leaves entire, transverse, wider than long *P. dependula*

13. Plants small, stems 1-2 cm long. Leaves bifid, obliquely to widely spreading, longer than wide 14

14. Leaves narrowly oblong, ca. 2× longer than wide, bifid ...
..... *P. tenuis*

14. Leaves ovate to ovate-oblong, 1-1.5(-1.7) × longer than wide, bifid and usually with a few additional small teeth
..... *P. papillifolia*

15. Leaves transverse to obliquely spreading. Leaf base with a vitta. In páramo 16

15. Leaves obliquely to widely spreading. Leaf base with or without vitta. In forests and páramo 17

16. Margin of leaf apex revolute. Leaves wider than long
..... *P. revolvens*

16. Margin of leaf apex ± plane. Leaves longer than wide
..... *P. cleefii*

17. Ventral leaf bases ampliate, usually forming a high crest. Leaves ovate-triangular. Plants robust, 5-10 mm wide 18

17. Ventral leaf bases not ampliate. Leaves ovate-oblong or lingulate. Plants smaller, 0.5-5(-6) mm wide 21

18. Leaf cells 20-35 µm wide in midleaf. Dorsal leaf bases very longly decurrent, concealing the stem 19

18. Leaf cells larger, 35-60 µm wide in midleaf. Dorsal leaf bases shortly or longly decurrent 20

19. Dorsal surface of stem with small, toothed paraphyllia near the dorsal leaf base *P. paraphyllina*

19. Dorsal surface of stem without paraphyllia
..... *P. fuscolutea*

20. Ventral leaf base shortly and narrowly decurrent, the decurrent part 1 cell wide *P. ensiformis*

20. Ventral leaf base longly and broadly decurrent, the decurrent part several cells wide *P. guevarai*

21. Plants 3-6 mm wide, leaves oblong 22

21. Plants smaller, 0.5-2(-2.5) mm wide, leaves ovate to oblong 25

22. Midleaf cells distinctly elongate, many cells at least 2× as long as wide. Leaf apex with 2-3 large teeth 75

22. Midleaf cells shorter, 1-1.7× as long as wide. Leaf apex entire or with a few small teeth, occasionally bifid 23

23. Branching intercalary. Leaf apex bifid *P. heterophylla*

23. Branching terminal. Leaf apex entire or with a few small teeth, not bifid 24

24. Leaves ovate-lingulate, horizontally spreading. Leaf bases longly decurrent. Ventral leaf base with a shoulder
..... *P. patula*

24. Leaves narrowly oblong, ventrad. Leaf bases shortly decurrent. Ventral leaf base without shoulder. Ecuador; not yet known from Colombia [*P. macrifolia* Taylor]

25. Leaf apex entire 26

25. Leaf apex bifid or trifid 27

26. Plants very small, less than 1 mm wide. Leaves ovate-orbicular or subquadrate. Leaf bases hardly decurrent. In páramo, above 3000 m *P. cuatrecasii*

26. Plants larger. Leaves ovate-oblong. Leaf bases distinctly decurrent. At low elevations (below 1500 m) *P. lingua*

27. Cuticle finely papillose. Leaves narrowly oblong, about 2× longer than wide *P. tenuis*

27. Cuticle smooth. Leaves ovate to obtuse to oblong ...
..... 28

28. Leaves fragmenting, part of the leaf lamina and/or teeth broken off *P. cuneata*

28. Leaves caducous or not caducous, but never fragmenting 29

29. Leaves ovate, 1-1.5× longer than wide. Leaf bases ± not decurrent *P. exigua*

29. Leaves more elongate, 1.5-2.5× longer than wide. Leaf bases decurrent 30

30. Leaves caducous, apex bifid and ventral margin with one or more teeth. Leaf cells conspicuously elongate, many cells ca. 2× longer than wide Small form of *P. aerea*

30. Leaves not caducous, apex bifid and ventral margin entire. Leaf cells not or slightly elongate, 1-1.5× longer than wide. Central America and Venezuela, not yet known from Colombia [*P. bicuspidata* Gottsche]

31. Dorsal leaf margin toothed near the base (to be observed on vegetative leaves, not on leaves near the gynoecea). Plants robust 32

31. Dorsal leaf margin not toothed near the base. Plants small or robust 42

32. Leaves orbicular, with 100-250 small teeth all around ...
..... *P. ovata*

32. Leaves not orbicular, with less than 100 teeth 33

33. Branching mostly terminal. Teeth very long, to 15 cells long. Underleaves present *P. longispina*

33. Branching intercalary. Teeth short or long. Underleaves ± lacking 34

34. Dorsal surface of stem with small, toothed paraphyllia (sometimes only few) *P. paraphyllina*

34. Dorsal surface of stem completely smooth, without paraphyllia 35

35. Leaves 1-1.4× longer than wide 36

35. Leaves 1.4-2× longer than wide	36	47. Leaves 1.5-2.5× longer than wide, not fragmented. Underleaves absent or present. Common in lowland and montane rainforest areas (up to 3300 m)	<i>P. raddiana</i>
36. Leaves subopposite. Dorsal and ventral leaf bases shortly decurrent	<i>P. turgida</i>	48. Leaf apex bifid by 2 large teeth. Leaves elongate triangular, strongly toothed, with 15-60 teeth	<i>P. cristata</i>
36. Leaves alternate. Dorsal and ventral leaf bases longly decurrent	<i>P. patriciae</i>	48. Leaf apex not bifid. Leaves ovate-lingulate, with 10-30 teeth	49
37. Ventral leaf base toothed	38	49. Teeth on ventral leaf base linear (1 cell wide except at base). Underleaves conspicuous, 0.5-1.5 mm long, with many cilia	<i>P. disticha</i>
37. Ventral leaf base entire	40	49. Teeth on ventral leaf base at least in part triangular (more than 1 cell wide). Underleaves absent or vestigial, to 0.6 mm long, with few cilia	<i>P. montagnei</i>
38. Ventral leaf base longly decurrent	39	50. Ventral leaf base distinctly toothed, teeth linear	<i>P. disticha</i>
38. Ventral leaf base shortly decurrent	<i>P. husnotii</i>	50. Ventral leaf base entire	51
39. Leaf base with vitta	<i>P. breuteliana</i>	51. Leaves mostly 1–1.5× longer than wide, horizontally spreading	52
39. Leaf base without vitta	<i>P. vincentina</i>	51. Leaves mostly 1.5–2.5× longer than wide, horizontally spreading or ventrad [when in doubt try both leads]	53
40. Ventral leaf base ampliate	<i>P. canelensis</i>	52. Ventral leaf base with a shoulder (basal portion of ventral margin somewhat extended parallel to the stem before curving outwards). Underleaves absent. Stems not turning blackish-brown. Leaves ovate. Leaf cells with distinct trigones. Oil bodies colorless	<i>P. laetevirens</i>
40. Ventral leaf base not ampliate	41	52. Ventral leaf base without shoulder. Underleaves usually present (small, to 1 mm long). Stems turning blackish-brown. Leaves ovate-oblong. Leaf cells without or with very small trigones. Oil bodies brown	<i>P. diversifolia</i>
41. Leaves asymmetrical, elongate ovate-triangular. Androecia terminal, in a cluster of several male branches. Montane forests	<i>P. dominicensis</i>	53. Leaves ampliate or with a shoulder at the ventral base (basal portion of ventral margin somewhat extended parallel to the stem before curving outwards). Leaf bases ± longly decurrent. Plants rather robust, more than 4 mm wide	54
41. Leaves ± symmetrical, ovate-oblong to rectangular. Androecia terminal or intercalary, singly, not in a cluster. Lowland and submontane rainforests	<i>P. subplana</i>	53. Leaves not ampliate, without shoulder. Leaf bases shortly decurrent. Plants more delicate, 3-4(-5) mm wide	55
42. Branching predominantly terminal, especially in the upper parts of the plants (a few intercalary branches may be present in the lower parts of the plant). Asexual reproduction by small propagula from ventral leaf surfaces or absent (rarely by caducous leaves: couplet 52)	43	54. Midleaf cells large, 35–55 μm wide. Teeth on leaf margins long-linear, to 10 cells long	<i>P. superba</i>
42. Branching predominantly intercalary, or branches lacking. Asexual reproduction by caducous leaves, by leaf fragmentation, or absent	58	54. Midleaf cells smaller. Teeth on leaf margins shorter, triangular	<i>P. patula</i>
43. Plants pinnately branched	44	55. Leaves horizontally spreading, rectangular, margins conspicuously parallel (dorsal and ventral margins almost straight). Common in Eastern Brazil, not yet known from Colombia	[<i>P. crispabilis</i> Lindenb.]
43. Plants dichotomously branched	45	55. Leaves ± ventrad, narrowly oblong, margins not conspicuously parallel (dorsal margin ± straight, ventral margin curved)	56
44. Leaves subimbricate to imbricate, 1.1-1.8× longer than wide, widest near the base (below 1/3 of leaf length). Ventral leaf base weakly to strongly ampliate	<i>P. deflexirama</i>		
44. Leaves distant, 1.8-2.5× longer than wide, widest at 1/3-1/2 of leaf length (not near the base). Ventral leaf base not ampliate	<i>P. tamariscina</i>		
45. Ventral leaf bases distinctly ampliate, ± concealing the stem	46		
45. Ventral leaf bases not or weakly ampliate, not concealing the stem	50		
46. Ventral leaf base ± entire, longly decurrent	47		
46. Ventral leaf base toothed, shortly decurrent	48		
47. Leaves 1-1.4× longer than wide, often fragmented. Underleaves present. Rare species from high Andean forest and páramo (above 3000 m). Bolivia, Peru and Ecuador, not yet known from Colombia	[<i>P. buchtiniana</i> Steph.]		

56. Leaf margin bordered by thicker-walled cells. Asexual reproduction by propagula from ventral leaf surfaces *P. distinctifolia*

56. Leaf margin not bordered by thicker-walled cells. Asexual reproduction by caducous leaves 57

57. Leaves with 2 large teeth at apex and smaller teeth on the ventral margin. Midleaf cells about 2× as long as wide. Very common and variable species *P. aerea*

57. Leaves with a few small teeth near apex, ventral margin entire. Midleaf cells shorter, 1-1.7× as long as wide. Rare species, known from Ecuador [*P. macrifolia*]

58. Leaves (sub)opposite 59

58. Leaves alternate 61

59. Plants delicate, 2-3 mm wide. Ventral leaf base not ampliate. Leaf bases distinctly connate *P. bryhnii*

59. Plants more robust, 4-10 mm wide. Ventral leaf base ampliate. Leaf bases approximate but not distinctly connate 60

60. Midleaf cells 35–55 μm wide. Leaves distinctly longer than wide. Leaf margin not bordered by thicker-walled cells. Androecia in a cluster of 2–8 male branches *P. macrostachya*

60. Midleaf cells smaller, 25–35 μm wide. Leaves about as long as wide. Leaf margin frequently bordered by thicker-walled cells. Androecia not in a cluster *P. heteromalla*

61. Ventral leaf base ampliate, at least on older, mature leaves. Plants large, (3-)5-10 mm wide 62

61. Ventral leaf base not ampliate. Plants small or large 73

62. Midleaf cells large, ca. 35-55 μm wide. Androecia usually in a cluster of 2-8 male branches 63

62. Midleaf cells smaller, 15-35 μm wide. Androecia not in a cluster 67

63. Leaves with less than 7 teeth 20

63. Leaves usually with more than 7 teeth 64

64. Ventral leaf base longly decurrent *P. patriciae*

64. Ventral leaf base shortly decurrent 65

65. Leaves about as long as wide (0.9-1.2× longer than wide) *P. canelensis*

65. Leaves distinctly longer than wide (1.2-1.8× longer than wide) 66

66. Teeth on leaf margin narrowly triangular, mostly more than 1 cell wide. Leaves ovate-oblong, with a broad apex ... *P. amicta*

66. Teeth on leaf margin linear, mostly 1 cell wide (except at the base). Leaves usually ovate-triangular with a narrow

apex, rarely ovate-oblong with a broad apex (in *P. superba* var. *macrotricha*) *P. superba*

67. Leaves about as long as wide (1-1.2 : 1), ventrad. Leaf base with a vitta. *P. trichostoma*

67. Leaves distinctly longer than wide (1.2-2.5 : 1). Leaf base without vitta (vitta present in *P. deflexa*: couplet 71) 68

68. Leaves ovate-oblong, with a broad apex. Leaf margin with a yellowish border of thicker-walled cells. *P. adianthoides*

68. Leaves mostly ovate-triangular, with a rather narrow apex. Leaf margin without border of thicker-walled cells 69

69. Mature stem leaves 1.8–2.5× longer than wide, ventral leaf base toothed or entire 70

69. Mature stem leaves 1.2-1.8× longer than wide, ventral leaf base entire 71

70. Ventral leaf base toothed, scarcely decurrent. Leaf apex usually with 1-2 conspicuously larger teeth *P. cristata*

70. Ventral leaf base entire, longly decurrent. Leaf apex not with 1-2 conspicuously larger teeth (phenotype of *P. raddiana* with intercalary branching) *P. raddiana*

71. Ventral leaf bases weakly ampliate, not forming a crest. Leaf base with a vitta. Leaves contiguous or subimbricate, ventrad. Central America and Ecuador, not yet known from Colombia [*P. deflexa* Mitt.]

71. Ventral leaf bases strongly ampliate, forming a high crest. Leaf base without vitta. Leaves densely imbricate, horizontally spreading, not ventrad. 72

72. Dorsal leaf bases very longly decurrent, completely concealing the stem. Leaf apex bifid. Plants very robust, 5-11 mm wide. Common species of upper montane forest and páramo, 2500-4100 m *P. fuscolutea*

72. Dorsal leaf bases not very longly decurrent, not concealing the stem. Leaf apex not bifid. Plants less robust, 2.5-5 mm wide. Rare species of montane forest, usually below 2500 m *P. grandicrista*

73. Mature stem leaves conspicuously elongate, mostly more than 2× as long as wide 74

73. Mature stem leaves mostly less than 2× as long as wide [when in doubt try both leads] 78

74. Midleaf cells conspicuously elongate, many cells at least 2× longer than wide 75

74. Midleaf cells shorter, 1–1.5(–2)× as long as wide [when in doubt try both leads]. 76

75. Leaves widest at the base. Leaf apex deeply split into 2-4 long, ± linear teeth with a broad base, teeth 1/3-2/3 of leaf length, fragile. *P. tabinensis*

- 75. Leaves widest in the middle. Leaf apex with shorter teeth, the teeth not fragile *P. aerea*
- 76. Leaf cells finely papillose. Plants less than 2 mm wide ...
..... *P. tenuis*
- 76. Leaf cells smooth. Mature plants more than 2 mm wide ..
..... 77
- 77. Leaves horizontally spreading. Plants fresh with peppermint smell. Perianth base enveloped by bracts
..... *P. rutilans*
- 77. Leaves ventrad. Plants fresh without peppermint smell. Perianth base “naked”, not covered by bracts
..... *P. gymnocalycina*
- 78. Leaf cells finely papillose 79
- 78. Leaf cells smooth 80
- 79. Plants 0.5-2 mm wide. Leaves less than 1 mm long, bifid and with 1-5 teeth on the ventral margin *P. papillifolia*
- 79. Plants larger, more than 2 mm wide. Leaves larger, not or slightly bifid, ventral margin with 5-16 teeth *P. stricta*
- 80. Leaves transverse to obliquely spreading, orbicular to ovate-oblong. Leaf base with a vitta 81
- 80. Leaves widely spreading. Leaf base with or without vitta 83

- 81. Leaves strongly caducous, parts of stems and branches without leaves *P. punctata*
- 81. Leaves not caducous, sometimes fragmented (teeth or upper half of leaf broken off) 82
- 82. Leaf cells thin-walled, with very small trigones. Leaves with 2-7 small teeth, the teeth only 1-2(-3) cells long. Very rare species *P. subundulata*
- 82. Leaf cells with large trigones. Leaves with 2-3 large teeth at apex and 2-15 usually smaller teeth on the ventral margin, the teeth 2-10(-15) cells long. Common species
..... *P. bifaria*
- 83. Leaves ventrad, often caducous or with fragile teeth (Fig. 3). Plants small, 1.5-3(-4) mm wide 84
- 83. Leaves horizontally spreading, not caducous, teeth not fragile. Plants larger, 3-10 mm wide 86
- 84. Leaves not caducous. Margins of young, apical leaves with simple to pinnately branched teeth, the teeth highly fragile, leaves below apex with broken teeth (Fig. 3). In lowland rainforest along the Pacific coast *P. eggersii*
- 84. Leaves caducous. Teeth simple, never pinnately branched, fragile or not. In montane forest 85
- 85. Leaf base with a vitta. Leaves strongly caducous, 0.9-1.2(-1.5)× longer than wide. *P. punctata*

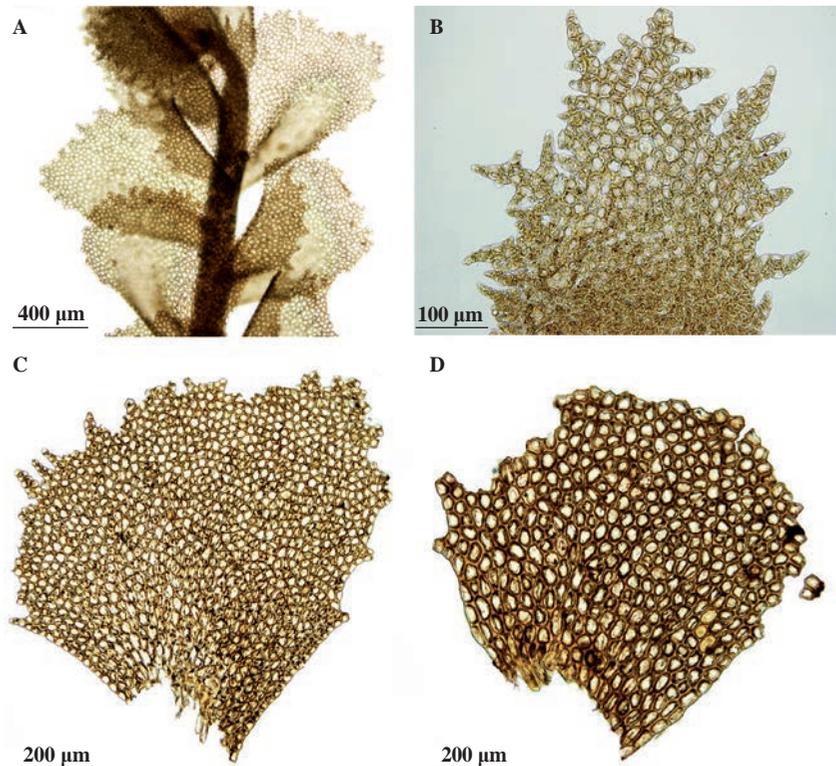


Figure 3. *Plagiochila eggersii*. A: Portion of plant in ventral view; B: Young leaf from shoot apex; C: Mature leaf from upper half of stem; D: Mature leaf from lower half of stem. Photographs by X.F. Cheng and R.L. Zhu.

85. Leaf base without vitta. Leaves caducous or not caducous, more than 1.2× as long as wide. Widespread in tropical America but not yet known with certainty from Colombia [*P. simplex* Lindenb.]
86. Leaf cells with large trigones. Leaves with 2-12 teeth, apex often bifid *P. heterophylla*
86. Leaf cells without or with very small trigones. Leaves usually with more than 12 teeth, apex not bifid 87
87. Ventral leaf base longly decurrent. Leaves ovate-oblong, with 20–100 teeth. In montane forests above 1800 m
..... *P. alternans*
87. Ventral leaf base not or shortly decurrent. Leaves rectangular to ovate-oblong, with (5–)10–40 teeth. In lowland and submontane forests, usually below 1000 m
..... *P. subplana*

Species descriptions

1. ***Plagiochila adianthoides*** (Sw.) Lindenb., Sp. Hepat. 2-4: 77. 1840; **Heinrichs** (2002). Fig. 1G

TYPE: Jamaica, leg. Browne (?) (S)

SYNONYMS: *P. esmeraldana* Steph., *P. densispina* Steph., *P. glomerulifera* Herzog, *P. keckiana* Steph., *P. procera* Lindenb.

ILLUSTRATIONS: **Heinrichs, et al.** (1998: Figs. 1-3), **Heinrichs** (2002: Plates 30-31), **Gradstein & Ilkiu-Borges** (2009: Fig. 17).

HABITAT AND DISTRIBUTION: On bark, twigs and humic soil in montane forests, (300-)1500-3400 m. Recorded from Antioquia, Boyacá, Cauca, Cundinamarca, Huila, Magdalena, Norte de Santander, Risaralda, Santander and Tolima. General distribution: widespread in tropical America but not known from Brazil.

Plants robust, 5-10 mm wide, branching scarce, intercalary. Leaves ovate-oblong with a broad apex, spreading or ± ventrad, ca. 1.2-1.8× longer than wide, shouldered or ampliate at the ventral base, margin usually with a yellowish border of elongate thicker-walled cells; with ca. 15-60 triangular to ciliate teeth along the ventral, apical and upper dorsal leaf margins, teeth to 10 cells long, not larger at apex; dorsal leaf base moderately decurrent, ventral base short decurrent. Leaf cells somewhat elongate, 15-35 µm wide in midleaf, with small to large, bluntly radiate trigones; leaf base without vitta; cuticle smooth. Androecia usually intercalary. Perianth base covered by bracts. Vegetative reproduction not observed.

Plagiochila adianthoides resembles *P. superba* and *P. amicta* but differs from the latter two species by smaller leaf cells, leaves usually with a border of thicker-walled cells and male branches not in a terminal cluster. Occasionally, the leaf border is only weakly developed or almost lacking. *Plagiochila adianthoides* may also be confused with *P. trichostoma*; for differences see under the latter species.

The epithet of *P. adianthoides* is often spelled “*adiantoides*” but the original spelling was “*adianthoides*” (**Gradstein, 2015a**).

2. ***Plagiochila aerea*** Taylor, London J. Bot. 5: 263. 1846; **Heinrichs** (2002). Fig. 1E,F

TYPE: Ecuador, leg. Jameson (E)

SYNONYMS: *P. alpina* Gottsche (incl. var. *grandis* Gottsche and var. *lindigiana* Gottsche), *P. bursata* (Desv.) Lindenb., *P. cobana* fo. *linearis* Herzog, *P. goethartii* Steph., *P. macvicarii* Steph.

ILLUSTRATIONS: **Heinrichs, et al.** (1998: Fig. 6), **Grolle & Heinrichs** (1999: Figs. 1-3), **Heinrichs** (2002: Plates 34-35), **Gradstein & Ilkiu-Borges** (2009: Fig. 17).

HABITAT AND DISTRIBUTION: on bark of trees, rock and soil in humid submontane and montane forests, also at forest margins and in scrubby vegetation, occasionally in wet lowland forest, 100-3300 m. Recorded from Amazonas, Antioquia, Arauca, Boyacá, Cauca, Chocó, Huila, Magdalena, Nariño, Quindío, Risaralda and Valle. General distribution: widespread in tropical America but not known with certainty from Brazil.

Plants small to medium-sized to rather large, (1-)3-6(-8) mm wide, pale green to brownish-green, branching usually intercalary, sometimes a few terminal branches present in the upper parts of the plant. Leaves wide-spreading, distant to imbricate, ventrad to almost horizontal, narrowly oblong, ca. 2.5-5× longer than wide, widest in the middle, apex usually with 1-2 rather long and narrow teeth, ventral margin with 0-5 smaller teeth mostly in the upper half; leaf bases shortly decurrent, ventral base not ampliate, entire. Leaf cells narrowly rectangular, (1-5-)2-2.5× longer than wide in midleaf, 30-60 x 15-30 µm, with radiate and often confluent trigones on longer walls; cuticle smooth to slightly rough by wax platelets (**Heinrichs, 2002**). Vegetative reproduction by caducous leaves.

Plagiochila aerea is a common and variable species, that is readily recognized by the narrowly oblong-rectangular, ventrad leaves with 1-2 large teeth at the apex and with several smaller teeth (sometimes only 1) on the ventral leaf margin, with elongate cells (ca. 1.5-2.5× longer than wide) and a ± smooth cuticle. The leaves are frequently caducous and the plants vary considerably size. Small, 1-2 mm wide plants with distant leaves and with only 2-3 teeth resemble *P. cuneata* but the latter species has fragmenting leaves with shorter cells. Larger plants resemble *P. distinctifolia*, *P. macrifolia* and *P. rutilans* but the latter three species have shorter leaf cells and shorter teeth at the apex. *Plagiochila aerea* is most closely related to *P. tabinensis* but the latter species is a more robust, brownish plant with leaves widest at the base and the apex more deeply split into long-linear, fragile lobe-like teeth.

3. ***Plagiochila alternans*** Lindenb. & Gottsche, in Gottsche, *et al.*, Syn. Hepat. 5: 648. 1847; **Müller, et al.** (1999).

TYPE: Mexico, leg. Liebmann (W)

SYNONYMY: *P. calomelanos* Spruce. *P. columbica* Gottsche, *P. grandifolia* Steph., *P. oblita* Steph., *P. semidentata* Steph.

ILLUSTRATION: **Robinson** (1967: Fig. 39 as *P. grandifolia*), **Müller, et al.** (1999: Figs. 3-4).

HABITAT AND DISTRIBUTION: on humic soil and moist rock in humid montane forests, 2000-3300 m. Recorded from Boyacá, Caldas, Cauca, Cundinamarca, Magdalena, Nariño, Risaralda, Santander and Tolima. General distribution: mountains of tropical America.

Plants robust, 4-10 mm wide, with intercalary branching. Leaves widely and horizontally spreading, symmetrically ovate-oblong, ca. 1.2-2× longer than wide, not ampliate at the ventral base, with numerous, 20-70(-100) teeth in the upper half and sometimes along the whole ventral margin, lower half of dorsal margin entire; dorsal and ventral leaf bases rather longly and narrowly decurrent. Leaf cells isodiametric to elongate, ca. 25-40 µm wide in midleaf, thin-walled, without or with very small trigones; cuticle smooth. Capsules narrowly cylindrical, on a long seta (**Müller, et al.**, 1999). Vegetative reproduction not observed.

Plagiochila alternans is somewhat similar to *P. subplana* but in the latter species the ventral leaf base is not or very shortly decurrent and the leaves are less densely toothed. Moreover, *P. subplana* is a lowland species, occurring usually below 1000 m. *Plagiochila alternans* is most closely related to *P. ovata* but leaves in *P. ovata* are orbicular (not ovate-oblong), distinctly ventrad and toothed all around by numerous small teeth (more than 100), and the leaf cells have large trigones. *Plagiochila ovata* occurs at somewhat higher elevation than *P. alternans*, above 3000 m.

4. ***Plagiochila amicta*** Steph., Bull. Herb. Boissier (sér. 2) 5: 895. 1905; **Heinrichs** (2002).

TYPE: Colombia, leg. Wallis (G)

SYNONYM: *P. douinii* Steph., *P. subaequalis* Steph.

ILLUSTRATION: **Heinrichs** (2002: Plate 3).

HABITAT AND DISTRIBUTION: on bark, rock or soil in montane forest and shrubby subpáramo, 1400-3100 m. Recorded from Antioquia, Cundinamarca and Magdalena. General distribution: mountains of tropical America.

Plants robust, 7-10 mm wide, branches scarce, intercalary. Leaves distant to imbricate, ovate-oblong with a broad apex, ca. 1.2-1.8× longer than wide, shouldered or ampliate at the ventral base, unbordered, with ca. 6-40 triangular teeth along the ventral, apical and upper dorsal margin, teeth rather short, to 6 cells long, more than one cell wide to near apex; dorsal leaf base moderately decurrent, ventral base shortly decurrent. Leaf cells large, ca. 35-55 µm wide

in midleaf, slightly elongate, with small radiate trigones; cuticle smooth. Androecia in a fan-shaped cluster at plant apex. Vegetative reproduction not observed.

Plagiochila amicta is very similar to *P. superba*, especially its var. *macrotricha*, but the teeth in *P. superba* are mostly linear (not triangular), of only 1 row of cells except near the base of the tooth.

5. ***Plagiochila bifaria*** (Sw.) Lindenb., Sp. Hepat. 5: 127. 1843; **Heinrichs, et al.** (1998, 2004a).

TYPE: Jamaica, leg. Swartz (S)

SYNONYMS: *P. arrecta* Gottsche, *P. centrifuga* Spruce, *P. echinella* Gottsche (?), *P. exesa* Lindenb. & Gottsche, *P. fragilis* Taylor, *P. horrida* Gottsche (*syn. nov.*), *P. increscentifolia* Spruce, *P. jaramilloi* H. Rob. (*syn. nov.*), *P. pinnatidens* Steph.

ILLUSTRATIONS: **Robinson** (1967: Figs. 56-58 as *P. "jaramillii"*), **Heinrichs, et al.** (1998: Fig. 8; 2004a: Figs. 3-5), **Gradstein & Costa** (2003: Fig. 78).

HABITAT AND DISTRIBUTION: common on bark, twigs, decaying wood, humic soil and rock in montane forests, scrub and páramo, 450-4200 m. Recorded from Amazonas, Boyacá, Cesar, Cundinamarca, Huila, Magdalena and Nariño. General distribution: mountains of tropical America, coast of Western Europe.

Plant small to medium-sized, 1-3 mm wide, stems long and almost unbranched, arising from a creeping rhizomatous base, stem apex curved, branches (when present) intercalary, sometimes flagelliform. Leaves distant to imbricate, transverse and laterally appressed to obliquely spreading, sometimes secund, asymmetrically ovate-suborbicular to ovate-oblong, 0.8-1.5× longer than wide, often fragmenting and upper part of leaf or teeth broken off, margin unbordered, dorsal margin usually recurved, ± straight and entire or with 1-2 teeth near apex, ventral margin arched and plane, ventral and apical margins with 3-20 short or long, linear to triangular to lobe-like teeth (to 10 cells long), leaf apex usually with 2-3 larger teeth; ventral and dorsal bases shortly to longly decurrent. Leaf cells subisodiametric in midleaf, ca. 15-30 µm wide, trigones conspicuous, often large; leaf base with a distinct vitta; cuticle ± smooth. Male plants smaller than female plants, male branches slender, singly or flabellate and in a fan-shaped cluster of up to ten male branches. Vegetative reproduction by leaf fragmentation.

Plagiochila bifaria is a common and highly variable species, which has been described under many different names. Characteristic are the transverse to obliquely spreading leaves with a ± entire, recurved dorsal margin, with 2-3 large apical teeth and with 2-15 linear to triangular to lobe-like teeth on the ventral margin, furthermore a distinct vitta, small cells (ca. 15-30 µm wide) with large trigones, and an almost smooth cuticle. The mature

perianth is cylindrical but immature perianths are typically shorter and broader, campanulate (**Heinrichs, et al.**, 1998). On the Galapagos Islands where only female plants occur (described as *P. spinifera* Taylor), the perianths are always campanulate.

Plagiochila bifaria resembles *P. retrorsa* Gottsche from Mexico and Central America but the leaves in *P. retrorsa* are more ovate-triangular in shape and more densely toothed, with teeth being present also along the dorsal margin (**Rycroft, et al.**, 2001). The latter species is not known from Colombia. The leaves in *P. bifaria* may be strongly fragmenting; *P. fragilis* Taylor is a phenotype of *P. bifaria* with broken leaves and *P. exesa* Lindenb. & Gottsche a phenotype with caducous teeth (**Gradstein**, 2015a).

Based on the original descriptions and illustrations, *P. horrida* Gottsche described from Mexico (**Gottsche**, 1963, p. 170, Tab. XIII) and *P. jaramilloi* H. Rob. described from Colombia (**Robinson**, 1967) are synonyms of *P. bifaria*. *Plagiochila echinella* Gottsche described from Colombia may be a further synonym of *P. bifaria*.

6. **Plagiochila breuteliana** Lindenb., Sp. Hepat. 5: 150. 1843; **Heinrichs** (2002).

TYPE: St. Kitts, leg. Breutel (W)

SYNONYMS: *P. breuteliana* var. *acutifolia* Herzog, *P. breuteliana* var. *novo-granatensis* Gottsche, *P. paucispinula* Herzog

ILLUSTRATION: **Heinrichs** (2002: Plates 6-7).

HABITAT AND DISTRIBUTION: on bark and soil in lowland and montane rainforest, 200-2700 m. Recorded from Antioquia, Boyacá, Caquetá, Chocó, Cundinamarca, Guajira, Magdalena, Risaralda and Valle. General distribution: tropical America.

Plants rather robust, 5-8 mm wide, branches scarce, intercalary. Leaves elongate-triangular to oblong with a narrow or broad apex, ca. 1.4-2× longer than wide, shouldered to ampliate at the ventral base, unbordered, with ca. 20-80 triangular to ciliate teeth, the teeth to 10 cells long, dorsal and ventral leaf bases toothed and longly decurrent. Leaf cells large, ca. 35-55 µm wide in midleaf, slightly elongate, with small radiate trigones; leaf base with a vitta; cuticle smooth. Androecia usually intercalary on long branches (not in a fan-shaped cluster). Vegetative reproduction not observed.

Plagiochila breuteliana is very similar to *P. vincentina*, both species have ampliate leaves with toothed and longly decurrent leaf bases (both dorsal and ventral). The two species differ mainly in the presence of a short vitta in the leaves of *P. breuteliana*.

7. **Plagiochila bryhnii** Steph., Biblioth. Bot. 87: 192. 1916.

TYPE: Bolivia, leg. Herzog (G)

SYNONYMS: *P. reclinata* Herzog, *Plagiochilion bryhnii* (Steph.) Inoue, *Plagiochilion reclinata* (Herzog) R.M.Schust.

ILLUSTRATION: **Herzog** (1932: Fig. 22 as *P. reclinata*), **Inoue** (1964: Fig. 6 as *Plagiochilion bryhnii*), **Gradstein, et al.** (2001: Fig. 63).

HABITAT AND DISTRIBUTION: on moist earth banks in montane forest, 2000-2600 m. Recorded from Santander and Valle. General distribution: tropical Andes.

Plants delicate, 2-3 mm wide, branches scarce, lateral-intercalary. Leaves distant, secund, opposite and with connate dorsal and ventral bases, asymmetrically ovate, ca. 1.1-1.3× longer than wide, margin unbordered, with 7-14 teeth along the ventral and apical margin, often with 1-2 larger teeth at apex; dorsal leaf base longly decurrent, ventral leaf base shortly decurrent, not shouldered and not ampliate. Leaf cells rather small, 15-30 µm wide in midleaf, walls flexuose with small to somewhat swollen trigones, leaf border lacking, leaf base without vitta; cuticle smooth. Perianth base stalked and “naked”, not covered by bracts. Vegetative reproduction by caducous leaves.

Plagiochila bryhnii is the only neotropical species of *Plagiochila* with connate leaf bases. Opposite leaves are shared with *P. macrostachya* and *P. heteromalla* but in the latter two species the leaf bases are not connate, the plants are more robust (more than 4 mm wide) and the leaves are ± imbricate with a highly shouldered or ampliate ventral base and more strongly toothed margins (more than 15 teeth per leaf). In addition, *P. heteromalla* differs by bordered leaves and *P. macrostachya* by larger leaf cells.

Because of its opposite leaves, *P. bryhnii* was placed in *Plagiochilion* S.Hatt. by **Inoue** (1964). However, the latter genus differs by ventral branching (lateral in *Plagiochila*).

8. **Plagiochila canelensis** Steph., Bull. Herb. Boissier (sér. 2) 5: 926. 1905; **Heinrichs** (2002).

TYPE: Ecuador, leg. Spruce (G)

SYNONYM: *P. axillaris* J.B.Jack & Steph.

ILLUSTRATION: **Heinrichs** (2002: Plates 8-9).

HABITAT AND DISTRIBUTION: On bark and soil in upper montane forest and páramo, 2500-4000 m. Recorded from Cauca, Chocó and Cundinamarca. General distribution: tropical Andes.

Plagiochila canelensis is similar to *P. superba* var. *superba* but differs in the leaves being hardly wider than long (ca. 1.2-1.6× longer than wide in *P. superba*). For a description of this taxon see **Heinrichs** (2002). *Plagiochila canelensis* is a rare species that has been collected a few times in upper montane forest and páramo.

9. **Plagiochila cleefii** Inoue, Stud. Cryptog. S. Peru: 95. 1987.

TYPE: Colombia, leg. Cleef (TNS)

ILLUSTRATION: **Inoue** (1987: Fig. 1).

HABITAT AND DISTRIBUTION: On soil and moist rock in humid páramo, 3200-4300 m. Recorded only from Meta (type). General distribution: northern Andes (Colombia, Ecuador).

Plants small to medium-sized, 1-2.5 mm wide, green to pale brown to dark-brown, stems long, not or little branched, apex curved, branches intercalary, creeping rhizomatous base lacking. Leaves distant to subimbricate, transverse to obliquely spreading, elongate-obovate, usually widest at or above the middle, 1.1-1.3× longer than wide, apex rounded to emarginate to short-bifid, ± plane, entire or with 1-2(-3) small teeth, dorsal and ventral margins entire, dorsal margin straight, slightly recurved, ventral margin curved, plane; dorsal base longly decurrent, ventral base shortly to longly decurrent. Leaf cells subisodiametric, 20-30 µm wide in midleaf, trigones small to large, not elongate along the cellwalls, cuticle smooth; leaf base with a short vitta. Perianth mouth finely toothed. Vegetative reproduction by caducous leaves.

Plagiochila cleefii is endemic to the páramo region of the northern Andes. In Colombia the species has only been recorded from Meta but may be more widespread. It approaches *P. revolvens* but the leaves in *P. revolvens* are wider than long and the margins more strongly recurved. Plants of *P. cleefii* with caducous leaves resemble *P. punctata* but the ventral leaf margin in *P. punctata* is toothed (usually entire in *P. cleefii*).

10. **Plagiochila cristata** (Sw.) Lindenb., Sp. Hepat. 1: 33. 1840; **Heinrichs** (2002).

TYPE: Jamaica, leg. Swartz (S)

ILLUSTRATIONS: **Robinson** (1967: Fig. 28), **Heinrichs, et al.** (1998: Fig. 9), **Heinrichs** (2002: Plate 31), **Gradstein & Costa** (2003: Fig. 79).

HABITAT AND DISTRIBUTION: on bark and rock in humid montane forests, 1500-2300 m. Recorded from Antioquia, Chocó, Cundinamarca, Magdalena, Risaralda, Santander, Tolima and Valle. General distribution: mountains of tropical America.

Plants robust, 4-8 mm wide, branches scarce, intercalary, occasionally terminal. Leaves elongate-triangular to rectangular, conspicuously narrowed to a truncate and usually bifid apex, 1.8-2.5× longer than wide, ventral base strongly ampliate-cristate, forming a conspicuous crest, margin unbordered, with ca. 15-60 triangular to ciliate teeth along the ventral, apical and upper dorsal margin, teeth to 6 cells long, at apex with 1-2 or more larger teeth (to 15 cells long); dorsal leaf base moderately decurrent, ventral base not or shortly decurrent. Leaf cells ca. 18-25 µm wide in midleaf, somewhat elongate, with rather large, radiate trigones; cuticle smooth. Androecia usually intercalary. Vegetative reproduction not observed.

By its narrowly elongate-triangular leaves (more than 1.8× longer than wide) with 1-2 large, apical teeth and an ampliate ventral base, *P. cristata* is a very distinct species that can hardly be confused with any other species.

11. **P. cuatrecasii** H. Rob., The Bryologist 70: 47. 1967.

TYPE: Colombia, leg. Cuatrecasas (US)

ILLUSTRATION: **Robinson** (1967: Figs. 48-51).

HABITAT AND DISTRIBUTION: on soil in humid páramo, 3600-4200 m. Recorded from Boyacá, Meta and Risaralda. General distribution: northern Andes.

Plants very small, usually less than 1 mm wide, stems to 3 cm long, hardly branched (branching intercalary), without rhizomatous base. Leaves distant, spreading, orbicular to ovate to subquadrate, apex rounded to retuse, margins entire, plane or dorsal margin slightly recurved; leaf bases hardly decurrent. Leaf cells ca. 20-25 µm wide in midleaf, trigones large, cuticle smooth. Perianth obovate to cylindrical, perianth mouth entire or with small teeth. Vegetative reproduction not observed.

Plagiochila cuatrecasii is endemic to páramo of the northern Andes and one of the smallest species in the genus. By its entire leaves *P. cuatrecasii* approaches *P. cleefii* and *P. revolvens*, which are also confined to páramo. The latter two species, however are readily separated from *P. cuatrecasii* by their larger size (plants more than 1 mm wide) and transverse leaves with recurved dorsal margin and longly decurrent dorsal base.

Plagiochila cuatrecasii is confusingly similar to *Leptoscyphus cuneifolius* (Hook.) Mitt. which occurs in the same habitat. However, *L. cuneifolius* has underleaves (lacking in *P. cuatrecasii*).

12. **Plagiochila cucullifolia** J.B. Jack & Steph., Hedwigia 31: 24. 1892; **Heinrichs** (2002). Fig. 2

TYPE: Colombia, leg. Wallis (G)

SYNONYM: *Szweykowskia cucullifolia* (J.B. Jack & Steph.) Gradst. & M.E. Reiner

ILLUSTRATION: **Gradstein & Reiner-Drehwald** (1995: Fig. 1 as *Szweykowskia cucullifolia*), **Gradstein, et al.** (2001: Fig. 63 as *S. cucullifolia*), **Heinrichs** (2002: Plate 10).

HABITAT AND DISTRIBUTION: on bark of trees and shrubs in humid cloud forest areas and bogs, 1300-3000 m. The species usually grows in rather open habitats (exposed canopy branches, forest margins, road sides) in somewhat disturbed environments. Recorded from Antioquia, Chocó, Huila and Nariño. General distribution: northern Andes, Costa Rica.

Plants robust, 6-10 mm wide, swollen, pale yellowish-brown, ± unbranched. Leaves suborbicular, strongly convex and saccate, margins curved downwards, numerous (to 45)

long-linear teeth, the teeth 5-20 cells long and mostly 1 cell wide (except at the base). Leaf cells very large, ca. 50-80 μm wide in midleaf, cuticle smooth. Androecia terminal to intercalary, male branches not in a fan-shaped cluster. Vegetative reproduction not observed.

Plagiochila cucullifolia is a very distinct species that is immediately recognized by strongly swollen, yellowish-brown plants with leaves modified into a sac. The leaf margins bear numerous long-linear teeth and the leaf cells are very large. An unusual form with flattened leaves from southern Ecuador has been described as *P. cucullifolia* var. *anomala* Heinrichs & Gradst. (Heinrichs, et al., 2003).

13. ***Plagiochila cuneata*** Lindenb. & Gottsche, in Gottsche, et al., Syn. Hepat. 5: 632. 1847.

TYPE: Mexico, leg. Liebmann (C lectotype)

SYNONYM: *P. rara* Gottsche

ILLUSTRATION: Groth, et al. (2002: Fig. 2), Heinrichs, et al. (2004c: Fig. 1).

HABITAT AND DISTRIBUTION: on exposed or shaded bark and rock in humid montane forest vegetation, ca. 2600 m (type of *P. rara*). Recorded once from Cundinamarca (as *P. rara*). General distribution: Mexico to Bolivia.

Plants small, 1-1.5 mm wide, with a strong peppermint smell, branches scarce, intercalary. Leaves rather distant, obliquely to widely spreading, elongate obtuse to narrowly oblong, deeply bifid to trifid to 1/4-1/3 of leaf length and with or without an additional tooth near the apex, leaves usually strongly fragmenting, upper part of leaves often broken, margins entire, bases shortly decurrent. Leaf cells isodiametrical to somewhat elongate, 1-1.5 \times longer than wide, 20-32 μm wide in midleaf, thin-walled with small trigones; cuticle smooth. Vegetative reproduction by leaf fragmentation. Female bracts slightly larger than leaves and more strongly toothed. Perianth base free, not covered by bracts.

Plagiochila cuneata is only known from Colombia based on a poorly developed specimen, collected near Choachi around 1860 by Lindig and described by Gottsche (1864) as *P. rara*. The latter species was reduced to synonym under *P. cuneata* by Heinrichs, et al. (2004c). No further collections of *P. cuneata* are known from Colombia. The species is recognized by the small plants with a strong peppermint smell (fresh material) and with \pm distant, elongate obtuse leaves, which are deeply 2-3-lobed (to 1/4-1/3 of leaf length) and strongly fragmenting. The upper part of the leaves is often broken.

Plagiochila cuneata may be confused with *P. aerea* but the leaves in the latter species are caducous, not fragmenting, the cells are more elongate in midleaf (1.5-2.5 \times longer than wide), and the plants lack a peppermint smell (Grolle & Heinrichs, 1999; Groth, et al., 2002).

Plagiochila cuneata is closely related to *P. loriloba*; both species have a strong peppermint smell and strongly fragmenting leaves. However, *P. loriloba* is a more robust plant (to 2.5 mm wide) with more imbricate, deeply 3-4-lobed leaves (2-3-lobed in *P. cuneata*) and larger leaf cells, 25-43 μm wide in midleaf (Groth, et al., 2002). Small forms of *P. cuneata* resemble *P. bicuspidata* Gottsche from Central America, Venezuela and Chile, but the leaves in latter species are bifid (never trifid) and are not fragmenting (and not caducous either). *Plagiochila bicuspidata* Gottsche is not yet known from Colombia but may be expected there.

14. ***Plagiochila deflexirama*** Taylor, London J. Bot. 5: 262. 1846.

TYPE: Ecuador ("Peru"), leg. Jameson (G isotype)

SYNONYMS: *P. bryopteroides* Spruce, *P. dilatata* Steph., *P. filicina* Herzog, *subdeflexiramea* Herzog, *P. trollii* Herzog

ILLUSTRATION: Heinrichs, et al. (2002c: Fig. 1).

On bark and rotten wood in montane rainforest and cloud forest, 900-2800 m. Recorded from Antioquia, Boyacá, Casanare, Huila and Tolima. General distribution: Mexico to Bolivia.

Plants medium-sized to large, 3-5 mm wide, to 15 cm long, upper part of shoot pinnate to bipinnate by terminal branches, lower part pinnate or sparsely branched and sometimes with a few intercalary branches. Leaves (sub)imbricate, \pm ventrad, ovate to oblong, 1.1-1.8 \times as long as wide, widest near the base, conspicuously narrowed to apex, weakly to strongly ampliate, concealing the stem or not, apical and ventral margin sharply toothed, with ca. 10-25 teeth; dorsal leaf base rather longly decurrent, swollen, ventral leaf base shortly to moderately decurrent. Leaf cells isodiametric to elongate, 15-28 μm wide in midleaf, trigones conspicuous, elongate, on longer walls often subconfluent; cuticle smooth. Underleaves lacking. Vegetative reproduction by propagula from ventral leaf surfaces.

Plagiochila deflexirama is recognized by (bi)pinnate terminal branching; all other neotropical *Plagiochilas* with terminal branching are dichotomous except *P. tamariscina*. The latter species is a more delicate plant than *P. deflexirama*, with distant, more narrowly elongate leaves that are not ampliate (but sometimes shouldered). *Plagiochila bryopteroides* Spruce, *P. filicina* Herzog, *P. subdeflexiramea* Herzog and *P. trollii* Herzog are phenotypes of *P. deflexirama* with subimbricate leaves and weakly ampliate ventral leaf bases (Gradstein, 2015a).

15. ***Plagiochila dependula*** Taylor, London J. Bot. 5: 265. 1846; Heinrichs, et al. (2005a).

TYPE: Ecuador, leg. Jameson (FH)

SYNONYM: *Jamesoniella dependula* (Taylor) Steph.

ILLUSTRATION: Heinrichs, et al. (2005a: Figs. 4-5).

HABITAT AND DISTRIBUTION: on humic soil, rock and leaning trunks in very moist dwarf forests near the forest line and in wet páramo, 3150-4300 m. Recorded from Cauca, Huila, Meta, Nariño and Risaralda. General distribution: northern Andes.

Plants medium-sized to robust, stems very long (to 25 cm long), almost unbranched stems. Leaves transverse and laterally appressed, reniform, 1.5-2.5× longer wide, apex rounded, margins entire, flat. Leaf cells isodiametric to elongate, 30-40 µm wide in midleaf, trigones large and swollen, leaf base with a broad, ill-defined vitta; cuticle papillose. Perianth mouth entire. Vegetative reproduction not observed.

Plagiochila dependula is readily recognized by the transverse, reniform leaves with entire margins and rounded apex. By its leaf shape and lack of teeth, *P. dependula* was sometimes considered a member of *Jamesoniella* (Spruce) F. Lees but clearly differs from the latter genus by the flattened perianth.

16. *Plagiochila disticha* (Lehm. & Lindenb.) Lehm. & Lindenb., in Lindenberg, Sp. Hepat. 2-4: 107. 1840; **Heinrichs & Gradstein** (2000).

TYPE: Guyana, unknown collector (W)

SYNONYMS: *P. blepharobasis* Herzog, *P. falcatoserrata* Herzog, *P. juruensis* Steph., *P. serrata* (Roth) Lindenb.

ILLUSTRATIONS: **Heinrichs & Gradstein** (2000: Fig. 2), **Gradstein & Costa** (2003: Fig. 76), **Gradstein & Ilkiu-Borges** (2009: Fig. 17).

HABITAT AND DISTRIBUTION: on bark and rock in lowland and lower montane rainforests, 100-2000 m. Recorded from Amazonas, Meta, Nariño, Putumayo, Risaralda and Valle. General distribution: tropical America.

Plants medium-sized, 3-5 mm wide, dichotomous by terminal branching. Leaves widely and horizontally spreading, ovate-lingulate with a broad and longly decurrent dorsal base, 1.5-2.5× longer than wide, apex subtruncate, ventral leaf margin plane or undulate, ventral base ampliate or not ampliate, concealing the stem or not; apex and basal part of ventral leaf margin toothed, with 10-30 teeth, ventral base with few to numerous linear teeth of 1 row of cells; dorsal leaf base longly and broadly decurrent parallel to the mid-line of the stem, the decurrent part strongly swollen, ventral base shortly decurrent. Leaf cells isodiametric to elongate, 20-30 µm wide in midleaf, trigones conspicuous but not swollen, triangular to elongate, sometimes confluent on longer walls; cuticle smooth. Underleaves often conspicuous, 0.5-1.5 mm long, margins strongly ciliate. Vegetative reproduction by small plantlets (propagula) on ventral leaf surfaces.

Plagiochila disticha is very similar to *P. montagnei*, both species have terminal branching, ovate-rectangular leaves with a long-decurrent dorsal base, and toothed ventral leaf

bases. However, in *P. montagnei* the ventral leaf bases are toothed by triangular teeth or a mixture of triangular and linear teeth, whereas in *P. disticha* the teeth on ventral leaf bases are always linear, of 1 row of cells. Moreover, *P. disticha* often has conspicuous, to 1.5 mm long underleaves with numerous cilia, whereas in *P. montagnei* underleaves are absent or rudimentary, less than 0.6 mm long and with few cilia.

Plagiochila blepharobasis Herzog is a phenotype of *P. disticha* with ± undulate ventral leaf margins, strongly ampliate-ciliate ventral leaf bases and conspicuous underleaves (**Gradstein**, 2015a).

17. *Plagiochila distinctifolia* Lindenb., Sp. Hepat. 1: 17. 1839.

TYPE: Jamaica, leg. Swartz (W)

SYNONYMS: *P. diffusa* Steph., *P. lindigiana* Gottsche (*syn. nov.*), *P. miqueliana* Lehm. & Lindenb.

ILLUSTRATION: **Schuster** (1980: Figs. 608-609 as *P. diffusa*).

HABITAT AND DISTRIBUTION: on bark in moist forests, 100-2700 m. Recorded from Cundinamarca and Magdalena. General distribution: tropical America.

Plants small to medium-sized, 2-4 mm wide, dichotomous to subpinnate with few branches, branches predominantly terminal, intercalary branches few on older or broken stem portions. Leaves mostly distant (some leaves may be slightly imbricate), ± ventrad, ovate-oblong to lingulate, ca. 1.5-2.5× longer than wide, subsymmetrical, dorsal margin straight, ventral margin slightly arched, margins bordered by elongate, somewhat thicker-walled cells, toothed in the upper half with 4-15 triangular teeth, often 2-3 larger teeth present at apex (especially in young leaves); dorsal leaf base rather longly decurrent, swollen, ventral leaf base shortly decurrent, not ampliate. Leaf cells subsodiametric, 15-30 µm wide in midleaf, with rather small trigones, margin cells elongate and thicker-walled, forming a border; cuticle smooth. Vegetative reproduction by small plantlets (propagula) on ventral leaf surfaces.

Plagiochila distinctifolia is recognized by the delicate, dichotomously-branched plants with somewhat distant, ventrad, oblong leaves with a border of elongate, thicker-walled cells. The species closely resembles *P. macrifolia* but the leaves in the latter species are unbordered and much less toothed. *Plagiochila distinctifolia* may also be confused with *P. rutilans* but the latter species has intercalary branching, horizontally spreading leaves (not ventrad) without border and a strong peppermint smell (fresh plants).

Based on the description in **Heinrichs, et al.** (1999), *P. lindigiana* Gottsche should be a synonym of *P. distinctifolia*.

18. *Plagiochila diversifolia* Lindenb. & Gottsche, in Gottsche *et al.*, Syn. Hepat. 5: 640. 1847; **Heinrichs, et al.**, (2000b).

TYPE: Mexico, leg. Liebmann (W)

SYNONYMS: *P. glaucescens* Steph., *P. subdentata* Steph.

ILLUSTRATION: **Heinrichs, et al.** (2000b: Fig. 3).

HABITAT AND DISTRIBUTION: on bark of trees and shrubs, occasionally on rock or moist soil, in montane forests, (500) 1000-2600 m. Recorded from Antioquia, Cundinamarca, Magdalena and Risaralda. General distribution: mountains of Central and tropical South America.

Plants rather robust, 5-9 mm wide, green to brownish-green with dark brown stems, dichotomous in the upper half by terminal branches, older stem portions with a few intercalary branches; stems usually very dark brown in color. Leaves horizontally spreading, ovate-oblong, 1.1-1.5(-1.8)× longer than wide, apex broadly rounded, margins toothed in the upper half by about 8-30 small to large teeth, teeth sometimes extending downwards but ventral base ± entire, dorsal margin entire except in the upper half; dorsal leaf base rather longly narrowly decurrent, the decurrent part often conspicuously swollen, ventral leaf base shortly decurrent, not ampliate and without high shoulder, ventral surface of stem clearly visible. Leaf cells subisodiametrical, 20-45 µm wide in midleaf, without or with small trigones; cuticle smooth; oil bodies brown. Underleaves present, to 1 mm long, deeply bifid. Vegetative reproduction not observed.

Plagiochila diversifolia is somewhat similar to *P. laetevirens* but differs from the latter species by the more robust plants with darker brown stems, leaves more elongate, ovate-oblong, with a broadly rounded apex, longly decurrent bases and no high shoulder, leaf cells without distinct trigones and with brown oil bodies, presence of underleaves and absence of vegetative reproduction. *Plagiochila diversifolia* may also be confused with forms of *P. deflexirama* with scarcely ampliate ventral leaf bases, but branching in *P. diversifolia* is dichotomous while being pinnate in *P. deflexirama*. Moreover, *P. diversifolia* usually has small underleaves (lacking in *P. deflexirama*).

19. **Plagiochila dominicensis** Taylor, London J. Bot. 5: 270. 1846; **Heinrichs** (2002).

TYPE: Dominica, unknown collector (FH)

ILLUSTRATION: **Heinrichs** (2002: Plate 14).

HABITAT AND DISTRIBUTION: on bark and soil in humid montane forests, (200-)600-2500 m. Recorded from Chocó, Magdalena and Risaralda. General distribution: tropical America.

Plants rather robust, 5-10 mm wide, branches scarce, intercalary. Leaves asymmetrically elongate-triangular to oblong, ca. 1.5-2× longer than wide, shouldered but not ampliate at the ventral base, unbordered, with 25-65 triangular to linear teeth, the teeth to 7 cells long; dorsal leaf base usually densely toothed, rather shortly decurrent,

ventral base shortly decurrent, entire. Leaf cells large, ca. 30-55 µm wide in midleaf, elongate, with conspicuous, radiate trigones; leaf base without vitta; cuticle smooth. Androecia in a fan-shaped cluster at stem apex. Vegetative reproduction not observed.

Plagiochila dominicensis resembles *P. breuteliana*, *P. vincentina* and *P. turgida* by the toothed dorsal leaf base but the latter three species have strongly ampliate ventral leaf bases. Moreover, in *P. breuteliana* and *P. vincentina* the ventral leaf bases are toothed and longly decurrent, and the male branches are not arranged in a fan-shaped cluster at the stem apex. *Plagiochila dominicensis* may also be confused with *P. subplana* but in the latter species the leaves are rather symmetrically ovate-oblong and leaf cells are (sub) isodiametrical, without or with very small trigones.

20. **Plagiochila eggersii** Inoue, Bull. Natl. Sci. Mus. Tokyo, ser. B, 14: 138. 1988. Fig. 3

TYPE: Dominica, leg. J. Eggers (TNS)

SYNONYM: *P. pinnatispina* Gradst. in sched.

ILLUSTRATION: **Inoue** (1988: Figs. 3-5).

HABITAT AND DISTRIBUTION: on bark of living and dead trees in undisturbed and disturbed lowland rainforest, 30-400 m. New to Colombia, found in two localities in the Chocó Department: Cartegui, leg. Gradstein 8784 (COL, GOET); Nuqui, El Amargal, leg. Gradstein 8840 (COL, GOET). Also new to Panama, near the Colombian border: Cerro Pirre, leg. Salazar Allen & S. R. Gradstein 9239 as *P. exesa*, see **Gradstein & Salazar Allen** (1992) (GOET, PMA, U). General distribution: Dominica (type) and along the Pacific coast of northern South America (Colombia, Panama).

Plants delicate, leafy shoots 1-2 cm long and 1-2 mm wide, green when fresh, pale brown when dry, ascending to erect, arising from a monotropically branched, creeping rhizomatous shoot beset with rudimentary leaves, the leafy shoots flexuose and often curved when dry, sparsely and irregularly branched by intercalary branches, shoot apex curved downward to the ventral side. Stems yellowish-brown, becoming darker brown in older portions of shoot, rigid, epidermis cells in surface view narrowly elongate, thick-walled; stems 150-180 µm in diameter, 8-10 cells across, in cross section made up of 35-40 cortex cells in 2 layers and with thick, yellowish-brown walls, surrounding 16-25 slightly larger, colorless medullary cells with thin walls. Rhizoids lacking on leafy shoots, present on stoloniform shoots, scattered. Leaves distant to contiguous, obliquely to widely spreading, strongly ventrad and somewhat secund, asymmetrically ovate to obtusate, 0.4-1.2 mm long × 0.3-1.0 mm wide, 1.1-1.3× longer than wide, not ampliate, dorsal leaf margin almost straight and entire, weakly recurved, ventral leaf margin arched, recurved at the base, ventral leaf base not expanded, dorsal and ventral leaf bases shortly decurrent; leaf margins with 10-40 teeth in

the upper half of leaf or almost all around except at ventral and dorsal bases, teeth on young, apical leaves to 15 cells long and 1-2 cells wide, becoming progressively smaller towards the base of the leaf, made up of rows of subquadrate to suborbicular cells with thin walls, teeth simple or (bi) pinnately branched in two or three dimensions, with several, 2-10 cells long pinnae, margins of teeth conspicuously crenulate; teeth very fragile and soon breaking off partially (fragmenting), margins of leaves below apex and lower down the stem with broken teeth, the broken teeth 1-3(-5) cells long and 1-2 cells wide. Leaf cells slightly elongate, 35-55 μm long and 25-33 μm wide in midleaf, with rather small, radiate trigones, cells becoming more elongate and thicker-walled towards leaf base, forming an ill-defined vitta, cells at leaf margin slightly smaller, leaf border lacking; cuticle smooth; oil bodies not seen. Underleaves lacking. Androecia terminal, bracts in ca. 5 pairs, contiguous, small, opposite bracts dorsally not overlapping, distal margins of bracts with a few broken teeth, bract cells \pm similar to leaf cells; antheridia 1 per bract, antheridial stalk biserial. Gynoecia and sporophytes not seen. Vegetative reproduction by teeth fragmentation from leaf margins.

Plagiochila eggersii is a rare species that was thus far only known from the type of Dominica. The plants are quite delicate and readily recognized by the strongly ventrad and somewhat secund, ovate-obcuneate leaves with numerous highly fragile teeth that are simple to pinnately branched and to 15 cells long on young leaves at the stem apex, but are broken and only 1-3 cells long on older leaves further down the stem. The peculiar, pinnately branched teeth of young leaves of *P. eggersii* set this new species well apart from other members of *Plagiochila*, which usually have simple teeth. By its ventrad, ovate-obcuneate leaves, small plant size and fragile teeth, *P. eggersii* approaches *P. cuneata* but the latter species is readily separated from *P. eggersii* by trifid leaves (with or without additional teeth) and unbranched teeth. Fragile teeth occur also in *P. bifaria* (= *P. exesa*) and *P. gymnocalycina* var. *surinamensis* (= *P. wolfii*) but the teeth in the latter two are not pinnate.

21. ***Plagiochila ensiformis*** Taylor, London J. Bot. 5: 265. 1846; **Heinrichs** (2002).

TYPE: Ecuador ("Columbia"), leg. Jameson (FH)

SYNONYM: *P. jamesonii* Taylor

ILLUSTRATION: **Heinrichs** (2002: Plate 15).

HABITAT AND DISTRIBUTION: on soil and tree bases in humid montane forest environments and páramo, 2150-4000 m. Recorded from Boyacá, Cauca, Cundinamarca, Putumayo, Risaralda, Santander, Tolima and Valle. General distribution: northern Andes.

Plants robust, 5-9 mm wide, branches scarce, intercalary. Leaves alternate (rarely subopposite), broadly ovate-triangular, 0.8-1.2 \times longer than wide, ventral base ampliate,

margin entire or with a few small teeth (1-6) at apex; dorsal and ventral leaf base shortly decurrent. Leaf cells large, ca. 35-60 μm wide in midleaf, somewhat elongate, with rather large trigones; cuticle smooth. Androecia intercalary or in a fan-shaped cluster at plant apex. Vegetative reproduction not observed.

By its broadly ovate-triangular, ampliate leaves with subentire margins *P. ensiformis* resembles *P. fuscolutea* and *P. guevarai*, but *P. fuscolutea* has smaller leaf cells and longly decurrent dorsal leaf bases while *P. guevarai* differs by very longly and broadly decurrent ventral leaf bases.

22. ***Plagiochila exigua*** (Taylor) Taylor, London J. Bot. 5: 264. 1846.

TYPE: Ireland, leg. Taylor (E isotype)

SYNONYM: *Plagiochila corniculata* auct.

ILLUSTRATIONS: **Inoue** (1980: Fig. 1 as *P. corniculata*), **Schuster** (1980: Fig. 562 as *P. corniculata*).

HABITAT AND DISTRIBUTION: on bark and soil in humid montane forests and páramo, 1800-4000 m. Recorded from Cundinamarca, Risaralda and Tolima. General distribution: mountains of tropical America and Africa, coast of Western Europe.

Plants small, 1-1.5 mm wide, branches scarce, intercalary. Leaves wide-spreading, caducous, distant to subimbricate, ventrad, ovate, 0.5-0.1 mm long, ca. 1-1.5 \times longer than wide, deeply bifid to 1/4-1/3; leaf bases not or scarcely decurrent, leaf margins entire or the ventral margin with an additional tooth. Leaf cells isodiametric to slightly elongate, 17-25 μm wide in midleaf, 1-1.5 \times longer than wide, trigones small to large, not elongate, vitta lacking; cuticle smooth. Androecia intercalary. Gynoecia very rare (not seen). Vegetative reproduction by caducous leaves.

Plagiochila exigua is readily recognized by the small plants with short-ovate, bifid leaves with entire margins or with a tooth on the ventral margin. *Plagiochila exigua* somewhat resembles *P. bicuspidata* Gottsche from Central America, Venezuela and Chile and *P. punctata*, however the latter two species have decurrent leaf bases. Moreover, the leaves in *P. bicuspidata* are not caducous while those of *P. punctata* have a vitta and more than one teeth on the ventral margin.

23. ***Plagiochila fastigiata*** Lindenb. & Gottsche, Syn. Hepat. 5: 657. 1847.

TYPE: Mexico, leg. Liebmann (W?)

HABITAT AND DISTRIBUTION: On tree trunk, 1680 m. Recorded from Cauca (**Gradstein & Feuillet Hurtado**, in press). General distribution: Mexico, Costa Rica, Colombia.

Plants medium-sized, 2-3 mm wide, leafy stems arising from a creeping stolon, unbranched or dichotomous branched in the upper portion, intercalary branches sometimes present

in lower parts. Leaves obliquely and horizontally spreading, imbricate, broadly ovate to ovate-oblong, ca. 1-1.3× longer than wide, apex rounded, with 5-13 teeth along the apical and ventral margin, ventral base entire, ventral leaf margin conspicuously undulate from the base to the middle of the leaf or beyond; dorsal base longly decurrent, the decurrent part conspicuously swollen, ventral base entire, broadly decurrent and somewhat ampliate, forming a low crest. Leaf cells isodiametric to elongate, 15-25 µm wide in midleaf, trigones conspicuous, slightly swollen; cuticle smooth. Underleaves relatively large, to 1 mm long, margins strongly ciliate. Vegetative reproduction by small plantlets (propagula) on ventral leaf surfaces.

Plagiochila fastigiata is a little known Central American species that has been recorded from one locality in Cauca. The species is readily recognized by the strongly undulate ventral leaf margin and entire ventral leaf base. The species may be confused with *P. raddiana* but in the latter species the leaves are more elongate (1.5-2.5× longer than wide) and the ventral leaf margin is not undulate or slightly undulate at the base only. *Plagiochila fastigiata* is closely related to *P. corrugata* (Nees) Mont. & Nees from Brazil and East Africa but in the latter species the ventral leaf base is toothed (Heinrichs *et al.*, 2004b).

24. ***Plagiochila fuscolutea*** Taylor, London J. Bot. 5: 263. 1846; Heinrichs (2002).

TYPE: Ecuador ("Peru"), leg. Jameson (FH)

SYNONYMS: *P. gymnostoma* J.B. Jack & Steph., *P. irmscheri* Steph. p.p. (Heinrichs 2002), *P. triangulifolia* Steph.

ILLUSTRATION: Robinson (1968: Fig. 36), Heinrichs (2002: Plates 36-38).

HABITAT AND DISTRIBUTION: on humic soil and bark in upper montane and subalpine cloud forest and in páramo, often growing in large cushions, 2200-4100 m. Recorded from Antioquia, Boyacá, Caldas, Cauca, Chocó, Cundinamarca, Magdalena, Meta, Nariño, Risaralda, Tolima and Valle. General distribution: tropical Andes.

Plants robust, 5-11 mm wide when flattened, branches scarce, intercalary. Leaves alternate, spreading or transverse and laterally appressed, broadly ovate-triangular to elongate triangular, narrowed to the apex from a very broad base, 0.7-1.5× longer than wide, apex rounded to acute to 2-3-toothed by large teeth, ventral base shouldered or ampliate-cristate, margins entire with a few teeth on the ventral margin (to 10); dorsal leaf base very longly decurrent, ventral leaf base shortly to longly decurrent. Leaf cells ca. 20-35 µm wide in midleaf, somewhat elongate, with large, swollen trigones; cuticle covered by small wax platelets, appearing smooth or weakly rough in the light microscope. Perianth mouth entire or with a few teeth. Vegetative reproduction not observed.

Plagiochila fuscolutea is a common and characteristic species of upper montane forests and páramo. By its broadly

triangular, subentire leaves *P. fuscolutea* resembles *P. ensiformis* and *P. guevarai* but the latter two species have larger leaf cells (ca. 35-55 µm wide in midleaf) and less longly decurrent dorsal leaf bases. *Plagiochila fuscolutea* is closely related to *P. paraphyllina* and but the latter species has small paraphyllia on the dorsal stem surface (lacking in *P. fuscolutea*).

25. ***Plagiochila grandicrista*** Steph., Bull. Herb. Boissier (sér. 2) 5 (2): 931. 1905; Heinrichs (2002).

TYPE: Colombia, leg. Lindig (G)

ILLUSTRATION: Heinrichs (2002: Plate 32).

HABITAT AND DISTRIBUTION: on tree trunks in humid montane forests, 2000-2400 m. Recorded from Cundinamarca and Valle. General distribution: northern Andes, Central America.

Plants medium-sized, 2.5-5 mm wide, branches scarce, intercalary. Leaves ovate-triangular, 1.3-1.8× longer than wide, apex truncate, ventral leaf bases strongly ampliate forming a high crest, margins toothed in the upper half with ca. 5-20 narrowly triangular teeth, ventral and dorsal leaf bases entire; dorsal base longly decurrent, the decurrent part swollen, ventral base shortly decurrent. Leaf cells ca. 25-35 µm wide in midleaf, somewhat elongate, with rather large, swollen trigones; cuticle smooth. Androecia usually intercalary. Vegetative reproduction not observed.

Plagiochila grandicrista is closely related to *P. adianthoides* but differs from the latter species by leaf shape (leaves ovate-triangular with a broad base and narrow apex), fewer teeth (5-20) mostly in the upper half of the leaf, and absence of a leaf border. *Plagiochila grandicrista* approaches *P. cristata* and *P. deflexa* Mitt. but *P. cristata* has much more elongate leaves (more than 1.8× longer than wide) with two large teeth at apex and a toothed ventral base, whereas *P. deflexa* (Central America and Ecuador; not yet known from Colombia) differs by leaves weakly ampliate without high ventral crest, presence of a vitta at leaf base and usual presence of two larger teeth at apex.

26. ***Plagiochila guevarai*** H. Rob. ("*guevarii*"), Bryologist 70: 48. 1967; Heinrichs (2002).

TYPE: Colombia, leg. King, Guevara & Forero (US)

ILLUSTRATION: Robinson (1968: Fig. 52 as *P. guevarii*), Heinrichs (2002: Plate 17 as *P. guevarii*).

HABITAT AND DISTRIBUTION: on bark and humic soil in páramo, 3300-3800 m. Recorded from Cundinamarca, Meta, Risaralda and Tolima. General distribution: northern Andes.

Plants robust, 5-9 mm wide, branches scarce, intercalary. Leaves alternate, ovate-triangular, narrowed to the apex from a very broad base, 0.8-1.2× longer than wide, ventral base strongly ampliate, forming a high crest, margins entire or with a few teeth (1-6) at apex; dorsal and ventral leaf bases longly decurrent. Leaf cells large, ca. 35-60 µm wide

in midleaf, somewhat elongate, with rather large, swollen trigones; cuticle smooth. Androecia usually intercalary. Vegetative reproduction not observed.

By its subentire leaves *P. guevarai* resembles *P. ensiformis* and *P. fuscolutea*; for differences see under *P. ensiformis*.

27. **Plagiochila gymnocalycina** Lindenb., in d'Orbigny, Voy. Amér. Mérid., Bot. 7: 81. 1839.

TYPE: Brazil, leg. Beyrich (W)

SYNONYMS: *P. polopolensis* Herzog, *P. wolfii* Inoue

ILLUSTRATIONS: **Heinrichs, et al.** (1998: Fig. 14), **Gradstein & Costa** (2003: Fig. 80), **Gradstein & Ilkiu-Borges** (2009: Fig. 18).

HABITAT AND DISTRIBUTION: on bark in lowland and submontane rainforest, 300-2000 m. Recorded from Caquetá, Nariño and Santander. General distribution: tropical America.

Plants medium-sized, 4-5 mm wide, branches sparse, intercalary. Leaves distant to subimbricate, ventrad, asymmetrically oblong-rectangular, widest in the middle, 2.1-3.5× longer than wide, dorsal margin straight, ventral margin curved, with 6-18 teeth in the upper half, apex occasionally with 2 larger teeth; ventral leaf base not ampliate, slightly recurved; dorsal and ventral leaf base short-decurrent. Leaf cells isodiametrical to somewhat elongate, 18-30 µm wide in midleaf, with conspicuous radiate trigones, vitta lacking; cuticle smooth. Perianth "naked", base not enveloped by bracts. Vegetative reproduction by caducous leaves common.

Plagiochila gymnocalycina is a species of relatively low elevations, in lowland and lower montane forests below 2000 m. The species is very similar to *P. simplex* and may be a synonym of the latter; for differences see under *P. simplex*. *Plagiochila gymnocalycina* has sometimes been considered a synonym of *P. rutilans* but the latter species clearly differs by horizontally spreading leaves (not ventrad), perianths covered by bracts at the base, and by the characteristic peppermint smell of fresh plants.

Plants from the Caquetá river (Morrocroy I.) with caducous teeth described as *P. wolfii* Inoue (**Inoue**, 1989) belong to *P. gymnocalycina* var. *surinamensis* (Sande Lac.) **Heinrichs & Rycroft** (**Heinrichs, et al.**, 2006).

28. **Plagiochila heteromalla** (Lehm. & Lindenb.) Lindenb., Sp. Hepat. 2-4: 83. 1840.

TYPE: Peru, leg. Kunze (PC, isotype)

SYNONYMS: *P. oresitropa* Spruce, *P. ovifolia* Steph., *Plagiochilion heteromallum* (Lehm. & Lindenb.) **Hässel**

HABITAT AND DISTRIBUTION: on bark in humid montane forests and páramo, 1200-3900 m. Recorded from Caldas, Magdalena and Risaralda. General distribution: tropical Andes, Costa Rica.

Plants medium-sized to rather robust, 4-7 mm wide, branches intercalary, rarely terminal. Leaves opposite, ventrad and secund or ± spreading, short-ovate, 1-1.2× longer than wide, shouldered to ampliate, margin frequently bordered by thicker-walled cells (by trigones and intermediate thickenings becoming confluent), toothed all around except on the lower half of the dorsal margin, with 16-44 short, narrowly triangular to ciliate teeth, the teeth to 6 cells long; dorsal and ventral leaf bases rather shortly and narrowly decurrent, opposite leaf bases approximate but not connected. Leaf cells 25-35 µm wide in midleaf, slightly elongate, with conspicuous, simple to radiate trigones and intermediate thickenings, thickenings usually larger and confluent on cells at leaf margin, forming a border, cells at leaf base more elongate, forming a short and ill-defined vitta; cuticle smooth; oil bodies homogeneous (**Heinrichs**, 2002, under *P. oresitropa*). Perianth elongate-cylindrical with a narrow stalk, perianth base covered by bracts or not. Vegetative reproduction not observed.

Plagiochila heteromalla is a little-known Andean species that is recognized by opposite and usually strongly secund leaves with leaf bases approximate (but not connate), leaf margins with a border of thicker-walled cells, and leaf bases with a short, ill-defined vitta. The species may be confused with *P. macrostachya* but the latter species has larger leaf cells and lacks a leaf border. *Plagiochila heteromalla* approaches *P. trichostoma* but the leaves in the latter species are not opposite (but sometimes almost), less strongly secund and without border.

Hässel de Menéndez (1983) transferred *P. heteromalla* to *Plagiochilion* S. Hatt. but the latter genus differs by ventral-intercalary branching.

29. **Plagiochila heterophylla** Lehm., Nov. Stirp. Pug. 10: 2. 1857; **Heinrichs** (2002).

TYPE: Costa Rica, leg. Oersted (S)

SYNONYM: *P. abscedens* Gottsche (*syn. nov.*), *P. sparsifolia* Steph.

ILLUSTRATION: **Heinrichs** (2002: Plate 39).

HABITAT AND DISTRIBUTION: on bark, rock and soil in humid montane forest areas and scrub and along rivers, 1150-3400 m. Recorded from Boyacá and Magdalena. General distribution: Mexico to Ecuador, Dominican Republic, coast of Western Europe.

Plants medium-sized, 3-6 mm wide, branches scarce, intercalary, rarely terminal. Leaves wide spreading, sometimes secund, not ventrad, ovate-oblong to ovate-triangular, ca. 1.3-2× longer than wide, not ampliate, with 2-12 teeth, apex usually bifid with two larger teeth, ventral margin with 0-10 smaller teeth in the upper half, dorsal margin usually entire; dorsal and ventral bases shortly to moderately longly decurrent. Leaf cells ca. 20-35 µm wide in midleaf,

somewhat elongate, with large, swollen trigones; leaf base without vitta; cuticle covered by small wax platelets, appearing smooth or slightly rough in the light microscope. Underleaves absent or very small and with 2-4 long-linear lobes. Vegetative reproduction not observed.

Plagiochila heterophylla has only been recorded from Boyacá and Magdalena but may be more widespread in Colombia. The species resembles *P. rutilans* but differs from the latter species by less strongly elongate leaves (usually less than 2× longer than wide), leaf apex often bifid with 2 larger teeth, and leaf cells with large, swollen trigones and with wax ornamentation on the cuticle. Fresh material is separated from *P. rutilans* by the lack of a peppermint smell.

A form with rather narrow leaves has been described as *P. heterophylla* var. *beauverdii* (Steph.) Heinrichs (= *P. sparsifolia* Steph.; fide Heinrichs, 2002). *Plagiochila abscedens* Gottsche (Type: Colombia, Tequendama, 2500 m, Aug. 1861, leg. Lindig 1710b, isotypes PC0098169, PC0098170) is a new synonym of *P. heterophylla*.

30. ***Plagiochila husnotii*** Steph., Bull. Herb. Boissier (sér. 2) 5: 178. 1905; Heinrichs (2002).

TYPE: Guadeloupe, leg. l'Herminier (G)

ILLUSTRATION: Heinrichs (2002: Plates 18, 19).

HABITAT AND DISTRIBUTION: on bark in everwet lowland rainforest along the pacific coast, 30 m. Recorded only from Chocó. General distribution: West Indies and coastal areas of northern South America.

Plants rather robust, 5-9 mm wide, branches scarce, intercalary. Leaves elongate-triangular to narrowly ovate-oblong, ca. 1.8-2.1× longer than wide, shouldered to weakly ampliate, with ca. 20-60 long triangular to linear teeth; dorsal and ventral leaf bases strongly toothed, shortly decurrent. Leaf cells large, ca. 30-55 µm wide in midleaf, slightly elongate, with small radiate trigones, leaf base without vitta; cuticle smooth. Androecia intercalary or in a fan-shaped cluster at stem apex. Vegetative reproduction not observed.

In Colombia, *Plagiochila husnotii* is a rare lowland species from rainforests of the Chocó. The species is very similar to *P. dominicensis* but the ventral leaf bases in the latter species are entire (strongly toothed in *P. husnotii*).

31. ***Plagiochila laetevirens*** Lindenb., Sp. Hepat. 2-4: 101. 1840.

TYPE: Ecuador ("Columbia"), leg. Jameson (W)

SYNONYMS: *P. bancroftii* Steph., *P. binominis* Gottsche, *P. cipaconensis* Steph., *P. contigua* Gottsche, *P. irmscheri* Steph. p.p. (Heinrichs, 2002), *P. micropteryx* Gottsche, *P. pachoenensis* Steph., *P. tocarema* Gottsche

ILLUSTRATION: Inoue (1989: Fig. 2 as *P. micropteryx*), Heinrichs, et al. (2002c: Fig. 2).

HABITAT AND DISTRIBUTION: on bark or rock in montane rainforests, usually in rather open places, also on isolated trees in meadows, 800-3000 m. Recorded from Boyacá, Cundinamarca, Risaralda and Tolima. General distribution: mountains of tropical America.

Plants soft-textured, medium-sized, 3-4 mm wide, dichotomous to irregularly pinnate, branches predominantly terminal, towards the shoot base sometimes with a few intercalary branches. Leaves obliquely to widely spreading, surface horizontal to slightly ventrad, short-ovate to ovate-oblong to ovate-triangular, 1-1.5× longer than wide, apex truncate, apical and ventral leaf margin with few to many, 5-25 coarse, triangular teeth; dorsal base shortly to longly decurrent, decurrent part swollen when long-decurrent, ventral leaf base recurved, shouldered to weakly ampliate, shortly decurrent. Leaf cells subsodiametrical, ca. 20-30 µm wide in midleaf, with rather small but conspicuous, triangular trigones; cuticle smooth. Underleaves lacking. Vegetative reproduction by numerous small plantlets (propagula) on ventral leaf surfaces.

Plagiochila laetevirens is a common and variable neotropical species that is recognized by terminal-dichotomous branching, rather short ovate-subrectangular leaves (1-1.5× longer than wide) with a shouldered ventral margin and coarsely toothed margins. The species seems to be restricted to submontane and montane environments, above 800 m. *Plagiochila laetevirens* is related to *P. distinctifolia* and *P. patula* but the latter species have more elongate leaves (more than 1.5× longer than wide). Moreover, *P. distinctifolia* is more delicate and has bordered leaves without a high shoulder. *Plagiochila laetevirens* may also be confused with *P. diversifolia* but the latter species is more robust and has larger leaf cells, brown oil bodies and small underleaves.

32. ***Plagiochila lingua*** Steph., Bull. Herb. Boissier (ser. 2) 2: 677. 1902.

TYPE: Brazil, leg. Puiggari, Icon. Steph. 11602 (G)

HABITAT AND DISTRIBUTION: on tree base along road, 750 m. Recorded from Magdalena (Gradstein, et al., 2016). General distribution: Colombia, Bolivia, southeastern Brazil.

Plants rather small, ca. 2 mm wide, to 2 cm long, green, leafy stems arising from a creeping stolon, unbranched or with a few short intercalary branches in the lower half; terminal branch lacking. Stems green, becoming brown in older parts. Leaves widely and horizontally spreading, subimbricate, plane, dorsal margin flat or slightly recurved, ovate-oblong, 1.2-1.4× longer than wide, apex rounded to truncate to retuse, without teeth or with a rudimentary tooth, margins fully entire; dorsal and ventral bases rather longly decurrent, ventral base subampliate, with a low shoulder. Leaf cells subsodiametric, ca. 25-30 µm wide in midleaf, towards margin slightly smaller, hardly larger towards

base, vitta lacking; cell walls thin, trigones lacking or very small, cuticle smooth. Underleaves absent. Plants sterile. Vegetative reproduction absent.

Plagiochila lingua is a rare neotropical species that is readily distinguished by entire leaves. The leaves are widely spreading, ovate-oblong (ca. 1.2-1.4× longer than wide), with a rounded to truncate to retuse apex, entire margins and thin-walled leaf cells without or with very small trigones. Branching is sparse, intercalary. The species approaches entire-leaved forms of *P. patula* but differs from the latter species by shorter leaves (less than 1.5× longer than wide), thin-walled leaf cells without or with very small trigones, and intercalary branching.

33. **Plagiochila longispina** Lindenb. & Gottsche, in Gottsche, *et al.*, Syn. Hepat. 5: 642. 1847; **Heinrichs, et al.** (2000b).

TYPE: Mexico, leg. Liebmann (W)

ILLUSTRATION: **Robinson** (1968: Fig. 42), **Heinrichs, et al.** (2000a: Fig. 1).

HABITAT AND DISTRIBUTION: on humid rock, soil and trunk bases in very humid upper montane forest and páramo, 2700-4050 m. Recorded from Arauca, Boyacá, Caldas, Cundinamarca, Meta, Risaralda, Tolima and Valle. General distribution: tropical Andes, Costa Rica, Azores.

Plants rather robust, 5-7 mm wide, flaccid, stems in the upper part often bluish, irregularly pinnate to ± dichotomous, branching terminal and intercalary. Leaves horizontally spreading, ovate to ovate-oblong, strongly ciliate by numerous long-linear teeth (20-60) all around the leaf, the teeth to 15 cells long; dorsal leaf base rather longly and broadly decurrent, ventral leaf base not or rather longly and very narrowly decurrent, not ampliate. Leaf cells subisodiametrical, 25-40 µm wide in midleaf, with rather small, triangular trigones; cuticle smooth; oil bodies brown. Underleaves conspicuous, to 1 mm long, ciliate. Vegetative reproduction not observed.

Plagiochila longispina is a very distinct species that is readily recognized by the bluish stems (in upper part of shoot) and the strongly and longly ciliate leaves with linear teeth all around the margins. The species is related to *P. diversifolia* but in the latter species the stems are never bluish and the teeth are shorter and mainly restricted to the ventral and apical leaf margins.

34. **Plagiochila loriloba** Carl, Ann. Bryol. Suppl. 2: 47, 48. 1931.

TYPE: Colombia, leg. Killip (JE)

SYNONYM: *P. cuneata* var. *loriloba* (Carl) Herzog

ILLUSTRATION: **Herzog** (1932: Fig. 17 as *P. cuneata* var. *loriloba*), **Groth, et al.** (2002: Fig. 2).

HABITAT AND DISTRIBUTION: on branches of shrubs in the understory of upper montane forest, 2900-3300 m (**Holz,**

et al. 2001). Recorded from Cauca (Puracé). General distribution: Colombia, Costa Rica.

Plants ca. 1.5-2.5 mm wide, with a strong peppermint smell, branches scarce, intercalary. Leaves subimbricate, obliquely to widely spreading, elongate obtuse, deeply 3-4-lobed to 1/3-1/2 of leaf length, leaf lobes often diverging and frequently broken off, margins usually entire, bases shortly decurrent. Leaf cells somewhat elongate, 23-43 µm wide in midleaf, with small but distinct trigones; cuticle smooth. Vegetative reproduction by leaf fragmentation. Female bracts slightly larger than leaves and more strongly toothed. Perianth base free, not covered by bracts.

Plagiochila loriloba is a little-known species that is known in Colombia from only one collection from the Puracé (the type). The species is recognized by the strong peppermint smell (fresh material) and deeply 3-4-lobed, strongly fragmenting leaves. *Plagiochila loriloba* is closely related to *P. cuneata*; for differences see under the latter species. The new combination *Plagiochila loriloba* "(Herzog) L.Söderstr." (**Söderström, et al.**, 2015) is superfluous, this name was already validly published by **Carl** (1931).

35. **Plagiochila macrostachya** Lindenb., Sp. Hepat. 2-4: 75. 1840; **Heinrichs** (2002).

TYPE: Jamaica, unknown collector (W)

SYNONYMS: *P. contingens* Gottsche, *P. flaccida* Lindenb., *P. leptophylla* Spruce

ILLUSTRATION: **Heinrichs** (2002: Plate 20). The illustration of *P. macrostachya* in **Gradstein & Costa** (2003) shows a plant with alternate leaves and may have been based on misidentified material.

HABITAT AND DISTRIBUTION: on bark or rock in humid lowland and montane rainforest, 30-3000 m. Recorded from Antioquia, Boyacá, Casanare, Chocó, Cundinamarca and Risaralda. General distribution: tropical America.

Plants robust, 5-10 mm wide, branches scarce, purely intercalary. Leaves horizontally spreading or secund, (sub)opposite with the bases approximate, ovate-oblong or ovate-triangular, 1.2-1.6× longer than wide, margin unbordered, ventral base weakly or strongly ampliate concealing the stem or not; with 10-40 triangular to linear teeth along the ventral, apical and upper dorsal margins, teeth to 7 cells long; dorsal and ventral leaf bases ± shortly decurrent. Leaf cells large, ca. 35-55 µm wide in midleaf, slightly elongate, with small to large trigones; vitta lacking; cuticle smooth. Androecia intercalary or in fan-shaped clusters at plant apex; bracts dorsally not overlapping. Perianth base covered by bracts. Vegetative reproduction by caducous leaves.

By its opposite leaves *P. macrostachya* resembles *P. heteromalla* but the cells in the latter species are much smaller and the leaf margin is usually bordered.

36. **Plagiochila montagnei** Nees, in Nees & Montage, Ann. Sci. Nat. Bot. (sér. 2) 5: 53. 1836; Heinrichs & Gradstein (2000). Fig. 11

TYPE: French Guiana, leg. Leprieur (STR)

SYNONYMS: *P. bogotensis* Gottsche, *P. hypnoides* Lindenb.

ILLUSTRATION: **Heinrichs & Gradstein** (2000: Fig. 3), **Gradstein & Costa** (2003: Fig. 77), **Gradstein & Ilkiu-Borges** (2009: 18).

HABITAT AND DISTRIBUTION: on bark or rock in lowland and lower montane rainforests, plantations and on isolated trees, 100-2600 m. Recorded from Antioquia, Caquetá, Cundinamarca, Magdalena and Meta. General distribution: tropical America.

Plants medium-sized, 3-5 mm wide, dichotomous by terminal branching. Leaves widely and horizontally spreading, ovate-lingulate with a broad and dorsally longly decurrent base, 1.5-2.5× longer than wide, apex subtruncate, ventral leaf margin plane or undulate, ventral base strongly ampliate, forming a high crest; apex and basal part of the ventral leaf margin toothed, with 10-30 teeth, ventral base with broad, triangular teeth; dorsal leaf base longly and broadly decurrent parallel to the midline of the stem, the decurrent part strongly swollen, ventral base shortly decurrent. Leaf cells isodiametric to elongate, 20-30 µm wide in midleaf, trigones conspicuous but not swollen, triangular to elongate, sometimes confluent on longer walls; cuticle smooth. Underleaves rudimentary, to maximally 0.6 mm long. Vegetative reproduction by small plantlets (propagula) on ventral leaf surfaces.

Plagiochila montagnei is very similar to *P. disticha*; for differences see under the latter species. *Plagiochila bogotensis* Gottsche is a phenotype of *P. montagnei* with subentire ventral leaf bases (**Gradstein, 2015a**).

37. **Plagiochila ovata** Lindenb. & Gottsche, in Gottsche *et al.*, Syn. Hepat. 5: 656. 1847; **Müller, et al.** (1999).

TYPE: Mexico, leg. Liebmann (W)

SYNONYM: *P. cordillera* Steph.

ILLUSTRATION: Robinson (1968; Fig. 47 as *P. oblita*), Müller, *et al.* (1999: Fig. 6).

HABITAT AND DISTRIBUTION: on humic soil, rock and bark in upper montane and subalpine forest and in scrubby páramo, with *P. dependula*, *P. ensiformis*, *P. punctata* etc., ca. 3000-4000 m. Recorded from Boyacá, Casanare, Cundinamarca, Magdalena and Meta. General distribution: tropical Andes, Costa Rica.

Plants robust, 4.5-9 mm wide, branching intercalary. Leaves obliquely spreading, subtransverse and strongly ventrad, rounded in shape, margins with more than 100 (up to 250) small, sharp teeth all around the margin, the teeth 1-3(-4)

cells long; dorsal and ventral leaf bases rather longly and narrowly decurrent. Leaf cells isodiametric to elongate, 20-40 µm wide in midleaf, with large trigones; cuticle smooth. Capsules narrowly cylindrical, on a long seta (Müller, *et al.*, 2000). Vegetative reproduction not observed.

Plagiochila ovata is easily recognized by the rounded leaves with numerous small teeth (100-250) all around the margin. No other neotropical species of *Plagiochila* has so many teeth on the leaves. *Plagiochila ovata* is related to *P. alternans* but leaves in the latter species are longer than wide and toothed only in the upper half (> 100 teeth), and the leaf cells are thin-walled with very small trigones. Moreover, *P. alternans* occurs at lower elevation (1900-3300 m).

38. **Plagiochila pachyloma** Taylor, London J. Bot. 5: 267. 1846.

TYPE: Ecuador, leg. Jameson (G isotype)

SYNONYMS: *P. cuervina* Gottsche, *P. wallisiana* Steph.

ILLUSTRATION: **Gradstein, et al.** (2001: Fig. 62).

HABITAT AND DISTRIBUTION: on bark in upper montane forest and páramo, 2000-4100 m. Recorded from Boyacá, Magdalena, Nariño, Risaralda, Santander and Tolima. General distribution: northern Andes, Costa Rica.

Plants medium-sized, 3-5 mm wide, stems long and almost unbranched, apex curved, branches intercalary. Leaves alternate, imbricate, transverse to obliquely spreading and ventrad, suborbicular to shortly ovate-triangular, 0.9-1.2× longer than wide, ventral base ± ampliate, margins conspicuously bordered, the border usually brown, and with numerous (to 50) long and sharp, linear teeth along the ventral and apical margin, the teeth usually brown, to 8 cells long (shorter to leaf base), 1 cell wide except at the base, cell linear in long teeth; dorsal leaf base longly decurrent, ventral leaf base usually shortly decurrent. Leaf cells subsodiametric, 15-25 µm in diameter, with small or large trigones, margin cells distinctly larger and thick-walled with confluent trigones, forming a brown (rarely colorless), 1-2 cells wide border, leaf with a conspicuous vitta of larger, thinner-walled cells from base to midleaf; cuticle finely papillose or smooth. Perianth base covered by bracts. Vegetative reproduction not observed.

This strikingly beautiful Andean species is readily recognized by the transverse to obliquely spreading, rounded to ovate-triangular leaves with a brownish border of larger, thicker-walled cells and with numerous sharp, linear, brownish teeth along the ventral and apical margin. The cuticle is finely papillose or smooth. A phenotype with colorless leaf border and colorless teeth was described as *P. homochroma* Spruce. *Plagiochila pachyloma* approaches *P. bifaria* but the latter species is more delicate, the leaves are not ampliate and lack a leaf border, and the teeth are

coloreous and at least in part narrowly triangular. Moreover, the leaves in *P. bifaria* are sometimes fragmenting (not fragmenting in *P. pachyloma*).

39. **Plagiochila papillifolia** Steph., in Herzog, Biblioth. Bot. 87: 207. 1916; **Heinrichs, et al.** (2002b).

TYPE: Bolivia, leg. Herzog (G)

SYNONYMS: *P. deciduifolia* Steph., *P. verruculosa* R. M. Schust.

ILLUSTRATION: **Heinrichs, et al.** (2002b: Fig. 1).

HABITAT AND DISTRIBUTION: on bark or rock in montane cloud forest, ca. 2000-3600 m. Recorded from Antioquia, Cauca, Cundinamarca, Risaralda and Santander. General distribution: tropical America, Azores.

Plants small, ca. 0.5-2 mm wide and 1-2.5 cm long, branching scarce, intercalary. Leaves spreading, ventrad, ovate to ovate-oblong and very small, usually less than 1 mm long and 1.1-1.7× longer than wide, bifid, with 2 large teeth at the apex and a few smaller teeth (1-10) on the ventral margin; leaf bases not or hardly decurrent. Leaf cells subisodiametric, 18-25 µm wide in midleaf, leaf base without vitta; cuticle finely papillose. Vegetative reproduction by caducous leaves common.

Plagiochila papillifolia is a delicate species with a bifid leaf apex, slightly toothed ventral leaf margin, hardly decurrent leaf bases and a papillose cuticle. The species may be confused with *P. tenuis* and *P. stricta*, which also have a papillose cuticle. However, *P. tenuis* has more elongate leaves (at least 2× longer than wide) whereas *P. stricta* is a more robust plant (> 2 mm wide) with distinctly decurrent, vittate leaves (vitta lacking in *P. papillifolia*).

40. **Plagiochila paraphyllina** Herzog, Hedwigia 74: 89. 1934; **Heinrichs** (2002).

TYPE: Colombia, leg. Troll (JE)

ILLUSTRATION: **Heinrichs** (2002: Plate 42).

HABITAT AND DISTRIBUTION: on bark and soil in upper montane forest and páramo, 2500-3700 m. Recorded from Cundinamarca and Magdalena. General distribution: northern Andes.

Plagiochila paraphyllina is a rare species that resembles *P. fuscolutea* but differs from the latter by toothed dorsal leaf bases and the presence of small, toothed paraphyllia on the dorsal stem surface, near the bases of the leaves or scattered over the surface. For a full description of *P. paraphyllina* see **Heinrichs** (2002). The species is very similar to *P. longiramea* Steph. from Bolivia but in the latter species the paraphyllia and dorsal leaf bases are entire.

41. **Plagiochila patriciae** Heinrichs & H. Anton, in Heinrichs, Bryophyt. Biblioth. 58: 107. 2002.

TYPE: Costa Rica, leg. Heinrichs, et al. (GOET)

ILLUSTRATION: **Heinrichs** (2002: Plate 21).

HABITAT AND DISTRIBUTION: on bark in upper montane forest near the forest line, 3500 m. Recorded only from Antioquia. General distribution: Colombia and Costa Rica.

Plants robust, 5-7 mm wide, branches scarce, intercalary. Leaves alternate, ovate-triangular, 1-1.4× longer than wide, ventral bases strongly ampliate forming a high crest, ventral and apical margins and sometimes also the dorsal base toothed, with ca. 10-30 teeth; dorsal and ventral leaf bases longly decurrent, the decurrent ventral part toothed. Leaf cells large, ca. 30-50 µm wide in midleaf, somewhat elongate, with rather large, swollen trigones; cuticle smooth. Androecia in a fan-shaped cluster at stem apex. Vegetative reproduction not observed

Plagiochila patriciae is a rare species from high elevations in Colombia (Antioquia) and Costa Rica. By its rather short and broad, alternate leaves with longly decurrent bases the species resembles *P. guevarai*, which occurs in the same habitat. However, the leaves in *P. guevarai* have much fewer teeth (1-6) and the decurrent part of the ventral leaf base is entire.

42. **Plagiochila patula** (Sw.) Lindenb., Sp. Hepat. 1: 21. 1839; **Heinrichs, et al.** (1998).

TYPE: Jamaica, leg. Swartz (S)

SYNONYMS: *P. beskeana* Steph., *P. fallax* Lindenb. & Hampe, *P. martiana* (Nees) Lindenb.

ILLUSTRATION: **Heinrichs, et al.** (1998: Figs. 10-11), **Gradstein & Costa** (2003: Fig. 77).

HABITAT AND DISTRIBUTION: on bark and soil in lowland and montane rainforest areas, 250-2800 m. Recorded from Risaralda and Valle. General distribution: tropical America.

Plants rather robust, 4-6 mm wide, usually dichotomous by terminal branching. Leaves widely and horizontally spreading, ovate-lingulate, ca. 2-2.5× longer than wide, leaf apex broadly rounded to truncate, apical and ventral leaf margins with 0-15 teeth, ventral leaf base entire; leaf bases ± longly decurrent, ventral leaf base with a shoulder, not or slightly ampliate. Leaf cells isodiametric to elongate, 20-30 µm wide in midleaf, trigones absent or conspicuous but not swollen, triangular to elongate, sometimes confluent on longer walls; cuticle smooth. Underleaves absent or very small. Vegetative reproduction by numerous small plantlets (propagula) on ventral leaf surfaces.

Plagiochila patula resembles *P. raddiana* but differs from the latter species by the shouldered ventral leaf base which is not or only very slightly ampliate, leaving the ventral stem surface well-visible. In *P. raddiana* the ventral leaf bases are moderately to strongly ampliate, more or less concealing the ventral stem surface and often forming a crest. In both species the ventral leaf bases are entire and usually longly decurrent (exceptionally shortly decurrent).

43. **Plagiochila punctata** (Taylor) Taylor, London J. Bot. 5: 261. 1846; **Heinrichs, et al.** (2005a).

TYPE: Ireland, leg. Taylor (BM isosyntype)

SYNONYMS: *P. chinantlana* Gottsche, *P. choachina* Gottsche, *P. delapsa* Inoue (syn. nov.), *P. stolonifera* Lindenb. & Gottsche, *P. subrara* Herzog

ILLUSTRATION: **Inoue** (1988: Fig. 1 as *P. delapsa*), **Heinrichs, et al.** (2005a: Figs. 2-3).

HABITAT AND DISTRIBUTION: on soil, bark and rock in exposed montane environments and páramo, 1600-4300 m. Recorded from Cundinamarca, Magdalena, Risaralda and Tolima. General distribution: tropical America, East Africa, Western Europe.

Plants rather small, 1-3 mm wide, branching intercalary, branches and parts of stem often leafless due to caducous leaves. Leaves distant to imbricate, obliquely to widely spreading, ovate, 0.9-1.2× longer than wide, not ampliate, strongly caducous; dorsal margin almost straight and entire, plane or narrowly recurved, ventral arched and toothed, with 1-14 teeth, apex often with 2 larger teeth or lobes; dorsal and ventral leaf bases not or very shortly decurrent. Leaf cells isodiametrical to somewhat elongate, ca. 20-30 µm wide in midleaf, usually with large trigones, leaf base with a short, ill-defined vitta; cuticle smooth. Underleaves reduced. Perianth base covered by leaves. Vegetative reproduction by caducous leaves abundant.

Plagiochila punctata is readily distinguished by the small plants with shortly (ob)ovate, ventrad leaves, which are toothed at apex and along the ventral margin and are abundantly caducous, leaving part of the stem and whole branches denuded (leafless). The species resembles *P. stricta* but in the latter species the leaves are not caducous and the cuticle is papillose.

Small phenotypes of *P. punctata* from páramo with only few teeth on the ventral leaf margin were described as *P. paramicola* Herzog and *P. subrara* Herzog. These plants approach *P. cleefii*; in the latter species, however, the ventral leaf margin is usually entire. Based on the original description and illustration, *Plagiochila delapsa* Inoue from Peru is a synonym of *P. punctata*.

44. **Plagiochila raddiana** Lindenb., Sp. Hepat. 1: 9. 1839; **Heinrichs & Gradstein** (2000). Fig. 1H

TYPE: Brazil, leg. Raddi (W)

SYNONYMS: *P. connivens* Gottsche, *P. crispatodecurrrens* Herzog, *P. funckiana* Steph., *P. guilleminiana* Mont., *P. ludoviciana* Sull., *P. schlimiana* Steph., *P. silvatica* Gottsche, *P. undulifolia* Herzog

ILLUSTRATIONS: **Schuster** (1980: Fig. 599 as *P. ludoviciana*), **Inoue & Gradstein** (1980: Fig. 3 as *P. guilleminiana*), **Heinrichs & Gradstein** (2000: Fig. 4), **Gradstein & Costa** (2003: Fig. 77), **Gradstein & Ilkiu-Borges** (2009: Fig. 19).

HABITAT AND DISTRIBUTION: on bark and shaded rock (occasionally on soil or leaves) in lowland and montane rainforests, 50-3300 m. Recorded from Antioquia, Boyacá, Caquetá, Cesar, Chocó, Cundinamarca, Magdalena, Nariño, Putumayo, Risaralda and Tolima. General distribution: widespread in tropical America.

Plants medium-sized to rather robust, 4-6 mm wide, ± dichotomous by terminal branching, intercalary branches also present, especially in the lower parts of the stem. Leaves widely and horizontally spreading, ovate-oblong to ovate-lingulate with a broad and longly decurrent dorsal base, 1.5-2.5× longer than wide, apex broadly subtruncate, apical and ventral margin with ca. 4-25 teeth, ventral base entire or, very occasionally, with 1-2 small teeth, ventral leaf margin plane or slightly undulate at the base; dorsal base longly decurrent, the decurrent part conspicuously swollen, ventral base rather longly decurrent, moderately to strongly ampliate, ± concealing the stem, when strongly ampliate forming a high crest. Leaf cells isodiametric to elongate, 20-30 µm wide in midleaf, trigones conspicuous but not swollen, triangular to elongate, sometimes confluent on longer walls; cuticle smooth. Underleaves absent or present, when present very small, usually less than 1 mm long, margins ciliate. Vegetative reproduction by small plantlets (propagula) on ventral leaf surfaces.

Plagiochila raddiana is a very common and variable neotropical species that has been described under many different names. Characteristic of this species are the ventral leaf bases, which are entire, longly decurrent and usually conspicuously ampliate, concealing the stem. In some phenotypes, however, the ventral leaf base is only moderately ampliate and does not entirely conceal the stem. Such forms approach *P. patula*, which is very similar to *P. raddiana* but has not or only slightly ampliate ventral leaf bases. *Plagiochila raddiana* also approaches *P. disticha* and *P. montagnei* but in the latter species the ventral leaf bases are toothed and shortly decurrent. Branching in *P. raddiana* is normally mainly terminal but occasionally it is predominantly intercalary (e.g., Magdalena, leg. Gradstein et al. 12491, PC).

Plagiochila undulifolia Herzog is a phenotype of *P. raddiana* with 1-2 teeth on the ventral leaf base and *P. silvatica* Gottsche is a phenotype with subrectangular leaves (**Gradstein**, 2015a).

45. **Plagiochila revolvens** Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 358. 1851.

TYPE: Ecuador, leg. Jameson (NY)

HABITAT AND DISTRIBUTION: on moist rocky soil in superpáramo, 4000-4300 m. Recorded only from Meta. General distribution: northern Andes.

Plants medium-sized, 2-3 mm wide, green to dark-brown to blackish, stems long, ± unbranched, apex curved,

rhizomatous base lacking. Leaves imbricate, transverse, suborbicular, slightly wider than long (ca. 1.2× wider than long), apex rounded, ± recurved, margins entire, dorsal margins strongly revolute, dorsal and ventral leaf bases longly decurrent. Leaf cells subisodiametric, 20-30 µm wide in midleaf, trigones large, cuticle smooth; leaf base with a vitta. Vegetative reproduction not observed.

Plagiochila revolvens has only been recorded from superpáramo on the Nevada do Sumapaz but it may be more widespread; in Ecuador it is known from several localities. The species approaches *P. cleefii* and *P. dependula*, which also have transverse leaves with entire margins and are páramo plants. *Plagiochila dependula* differs from *P. revolvens* by the much larger plants with broadly reniform leaves, ± plane leaf margins and a papillose cuticle. *Plagiochila cleefii* is more close to *P. revolvens* but is separated from the latter by having longer than wide leaves with a plane apex and by the frequent presence of 1-2 small teeth at the leaf apex.

46. **Plagiochila rudischusteri** H. Rob., Beih. Nova Hedwigia 90: 199. 1988; **Heinrichs** (2002).

TYPE: Venezuela, leg. Steyermark (US)

ILLUSTRATION: **Robinson** (1988: Figs. 1-5), **Heinrichs** (2002: Plate 43).

HABITAT AND DISTRIBUTION: on bark of trees in coastal, lower montane rainforest, 1500-1600 m. Recorded only from Risaralda (Mistrato). General distribution: Costa Rica, Panama, Caribbean coast of Venezuela (Paria Peninsula), and the Pacific side of the Western Cordillera of Colombia.

Plants medium-sized, 3-5 mm wide, pale yellowish green to brownish, stems almost unbranched, branches intercalary. Leaves distant, transverse, linear-lanceolate, 5-10× longer than wide, the leaf margins entire or with 1-2 small teeth near apex, leaf bases not or hardly decurrent. Leaf cells narrowly elongate, 2-5× longer than wide in midleaf, 15-25 µm wide, with large, swollen trigones; cuticle smooth. Vegetative reproduction by caducous leaves.

Plagiochila rudischusteri is a very distinct species that is only known in Colombia from the Western Cordillera (Risaralda). The species is related to *P. aerea* and *P. tabinensis* but is readily separated from the latter two by the linear, transverse leaves without long teeth or lobes and leaf bases not decurrent.

47. **Plagiochila rutilans** Lindenb., Sp. Hepat. 2-4: 47. 1840; **Heinrichs, et al.** (2001b). Fig. 1C,D

TYPE: Brazil, leg. Raddi (W)

SYNONYMS: *P. cobana* Steph. (?), *P. divaricata* Lindenb., *P. harrisana* Steph., *P. perrottetiana* Mont. & Gottsche

ILLUSTRATIONS: **Heinrichs, et al.** (1998: Figs. 4-5 as *P. harrisana*), **Heinrichs, et al.** (2001b: Figs. 2-4), **Gradstein & Costa** (2003: Fig. 80), **Gradstein & Ilkiu-Borges** (2009: Fig. 19).

HABITAT AND DISTRIBUTION: on bark, rock, rotten wood and soil in lowland and montane forests and scrub, 300-3200 m. Recorded from Antioquia, Cauca, Cesar, Cundinamarca, Putumayo and Risaralda. General distribution: tropical America.

Plants medium-sized to large, 2-6 mm wide, when fresh with a strong peppermint odor, branching intercalary. Leaves distant to slightly imbricate, widely spreading horizontally, narrowly oblong-rectangular, (1.5-)2-4× longer than wide, with 5-20 teeth in the upper half, apex occasionally with 2 somewhat larger teeth; dorsal and ventral margins recurved near the leaf base, the ventral leaf base not amplified but often shouldered (with a hook-shaped curvature), shortly decurrent. Leaf cells isodiametric to somewhat elongate, 1-1.5× longer than wide in midleaf, 20-40 µm wide, with small to large trigones; cuticle smooth. Vegetative reproduction by caducous leaves.

Plagiochila rutilans is readily recognized by the horizontally spreading, narrowly oblong leaves, the subisodiametric leaf cells and the peppermint smell of fresh plants. Branching in *P. rutilans* is intercalary. In leaf shape *P. rutilans* resembles *P. aerea*, *P. distinctifolia*, *P. macrifolia* and *P. gymnocalycina* but the latter species have ventrad leaves and lack a peppermint smell. Moreover, *P. aerea* has more elongate leaf cells and *P. distinctifolia* and *P. macrifolia* have terminal branching.

Plagiochila cobana Steph. reported Cundinamarca and Valle (**Gradstein & Uribe**, 2015) resembles *P. rutilans* and may be a synonym of the latter. **Inoue & Gradstein** (1980) erroneously treated *P. cobana* as a synonym of *P. aerea* (see **Heinrichs, et al.**, 1999).

48. **Plagiochila stricta** Lindenb., Sp. Hepat. 1: 20. 1839; **Heinrichs, et al.** (1998).

TYPE: Jamaica, leg. Swartz (W)

SYNONYMS: *P. asperifolia* Steph. var. *columbica* Herzog, *P. elegantula* Herz., *P. oxyphylla* Spruce, *P. rutilans* fo. *foliicola* Herzog

ILLUSTRATIONS: **Heinrichs, et al.** (1998: Fig. 7), **Rycroft, et al.** (2002: Fig. 2).

HABITAT AND DISTRIBUTION: on bark in lowland and montane rainforest, ca. 100-2400 m. Recorded from Chocó and Cundinamarca. General distribution: tropical America, Madagascar, Macaronesia.

Plants small to medium-sized, 2-4 mm wide, branching intercalary. Leaves asymmetrically ovate to ovate-oblong, 1-2 mm long, 1.1-1.7× longer than wide, dorsal margin entire, ventral and apical margin with 5-18 teeth, the teeth ca. 2-6 cells long, often with two larger teeth at apex (to 11 cells long). Leaf cells isodiametric to somewhat elongate, 15-30(-35) µm wide in midleaf, with conspicuous trigones, leaf base with a short vitta; cuticle strongly and finely papillose. Vegetative reproduction not observed.

Plagiochila stricta is a common species that is probably more widespread in Colombia than is currently known. The species may be confused with *P. papillifolia* which shares a papillose cuticle; for differences see under the latter species.

49. **Plagiochila subplana** Lindenb., Sp. Hepat. 2-4: 73. 1840; **Heinrichs, et al.** (1999). Fig. 1B

TYPE: Brazil, leg. Martius (W)

SYNONYMS: *P. amazonica* Spruce, *P. hondurensis* Herzog, *P. kegeliana* Steph., *P. leptodictyon* Herzog

ILLUSTRATIONS: **Heinrichs, et al.** (1999: Figs. 1-2), **Gradstein & Costa** (2003: Fig. 80), **Gradstein & Ilkiu-Borges** (2009: Fig. 20).

HABITAT AND DISTRIBUTION: common on bark in shaded places in lowland and submontane rainforests and scrub, 100-1200(-1900) m. COLOMBIA: Amazonas, Boyacá, Chocó, Guanía, Magdalena, Risaralda and Valle. General distribution: widespread in tropical America.

Plants medium-sized, 2-8 mm wide, branches intercalary. Leaves ovate-oblong to rectangular, 1.3-2.5 as long as wide, horizontally spreading, with 5-40 teeth in the upper half or along the entire leaf margin; ventral leaf base not ampliate, slightly recurved, not or very shortly decurrent, dorsal leaf base shortly decurrent. Leaf cells subisodiametrical, 30-45 μm wide in midleaf, thin-walled with small, simple-triangular trigones, vitta lacking; cuticle smooth. Perianth covered by bracts. Vegetative reproduction not observed.

Plagiochila subplana is a characteristic species of low elevations, below 1200 m. The species may be confused with *P. alternans*, *P. breuteliana* and *P. simplex*. *Plagiochila breuteliana* differs by asymmetrically elongate-triangular leaves with elongate leaf cells and radiate trigones, *P. alternans* differs by the conspicuously decurrent ventral leaf bases and *P. simplex* by ventrad leaves with smaller cells, perianth base not covered by bracts and vegetative reproduction by caducous leaves.

50. **Plagiochila subundulata** Lindenb., Sp. Hepat. 5: 137. 1843.

TYPE: Brazil, leg. Beyrich (W?)

HABITAT AND DISTRIBUTION: on wet rock at the base of waterfall, 2040 m. Recorded from Magdalena (**Gradstein, et al.**, 2016). General distribution: southeastern Brazil, Colombia.

Plants rather small, 2 mm wide, to 2 cm long, bright to dark green, leafy stems upright, arising from a creeping stolon, little branched in the lower half by intercalary branching. Stems rigid, upper parts green, lower parts of stem blackish-brown. Leaves obliquely spreading, distant to contiguous, convex with recurved dorsal and ventral margins and \pm plane apex, strongly ventrad-secund, ovate to ovate-oblong

to subovate, 1.5-2 \times 1.25-1.45 mm, ca. 1.2-1.3 \times longer than wide, apex rounded, apical and upper ventral margin with 2-7 small triangular teeth, the teeth 1-2(-3) cells long, sometimes rudimentary or broken; dorsal margin recurved, dorsal base short decurrent, ventral base longly and very narrowly decurrent, not ampliate. Leaf cells isodiametric to somewhat elongate, ca. 25-40 μm wide in midleaf, towards margin smaller, quadrate to elongate, towards base elongate, forming an obscure vitta; cell walls thin, trigones minute, cuticle smooth. Underleaves absent. Plants sterile. Vegetative reproduction absent.

Plagiochila subundulata is a rare tropical South American species of wet rock in rivers and near waterfalls. Characteristic are the rather small plants with obliquely spreading and strongly ventrad, ovate to ovate-oblong leaves (ca. 1.2-1.3 \times longer than wide), slightly toothed leaf margins with 2-7 small, triangular teeth which are only 1-2(-3) cells long and sometimes broken, thin-walled leaf cells with a smooth cuticle, and a short vitta. The species seems to be related to *P. bifaria* but differs from the latter species by subentire leaves, without larger teeth at the apex, and thin-walled leaf cells.

51. **Plagiochila superba** (Spreng.) Mont. & Nees, in d'Orbigny, Voy. Amér. Mérid. 7, Bot.: 81. 1839; **Heinrichs, (2002).**

TYPE: West Indies, leg. Sieber (STR)

SYNONYMS: *P. conspicua* Taylor, *P. frontinensis* Steph., *P. pichinchensis* Taylor

ILLUSTRATION: **Heinrichs** (2002: Plates 22-26).

HABITAT AND DISTRIBUTION: on trunk bases, rotten logs, rock and humic soil in humid montane forests and scrubby páramo, ca. 1000-3200 m. Recorded from Antioquia, Cauca, Cesar, Chocó, Magdalena, Nariño, Putumayo, Risaralda and Valle. General distribution: tropical America.

Plants robust, 5-11 mm wide, branches scarce, intercalary, rarely terminal. Leaves wide-spreading, imbricate, elongate ovate-triangular and tapering to a rather narrow, truncate apex (ovate-oblong with a broad apex in var. *macrotricha*), ca. 1.2-1.6 \times longer than wide, \pm ampliate at the ventral base, unbordered; with ca. 10-40 linear teeth along the ventral, apical and upper dorsal margins, the teeth mostly one cell wide except towards the base, to 11 cells long, ventral and dorsal bases without teeth; dorsal leaf base shortly to rather longly decurrent, ventral base shortly decurrent. Leaf cells large, ca. 35-55 μm wide in midleaf, slightly elongate, with conspicuous trigones, vitta lacking; cuticle smooth. Androecia in a fan-shaped cluster at plant apex. Vegetative reproduction not observed.

Plagiochila superba is a common and variable species that is readily recognized by the robust plants with ampliate, ovate-triangular leaves with a narrow apex, margins with

numerous linear teeth (to 11 cells long, mostly one cell wide except at base, rarely wider), lower half of dorsal leaf margin entire, and large leaf cells. The species may be confused with *P. amicta* and *P. canelensis*. *Plagiochila amicta* differs by narrowly triangular teeth (not linear) and *P. canelensis* by shorter, broader leaves that are hardly longer than wide, and by the frequent occurrence of teeth on the dorsal leaf base.

Plagiochila superba var. *macrotricha* (Spruce) Heinrichs, recorded from Risaralda, Tolima and Valle, is similar to *P. amicta* in leaf shape (ovate-oblong) but the teeth in var. *macrotricha* are \pm linear as in *P. superba*.

52. ***Plagiochila tabinensis*** Steph., Bull. Herb. Boissier (sér. 2) 2: 862. 1902; **Heinrichs** (2002).

TYPE: Peru, leg. Lechler (G)

SYNONYM: *Acrobolbus laceratus* R.M.Schust.

ILLUSTRATIONS: **Schuster** (2001: Fig. 18 as *Acrobolbus laceratus*), **Heinrichs, et al.** (2001a: Figs. 1-14), **Heinrichs** (2002: Plate 45).

HABITAT AND DISTRIBUTION: on trunks and canopy branches in humid montane forest and in scrub, 1500-3100 m. Recorded from Boyacá, Cauca, Magdalena and Risaralda. General distribution: tropical Andes.

Plants robust, whitish green to brown, medium-sized to large, 4-10 mm wide, branching intercalary, occasionally terminal. Leaves contiguous to imbricate, horizontally spreading to weakly ventrad, 2-4 \times longer than wide, widest at the base, apex deeply split (to 1/3-2/3 of leaf length) into 2-4 fragile, narrowly lanceolate to linear, lobe-like teeth, ventral margin entire or with 1-3 teeth, dorsal margin \pm entire; dorsal leaf base shortly decurrent, ventral leaf base shortly decurrent (small plants) or longly decurrent (robust plants). Leaf cells distinctly elongate, (1.5-2-4 \times longer than wide, ca. 20-30 μ m wide in midleaf, with large, radiate to confluent trigones; cuticle covered by wax platelets. Vegetative reproduction by fragmenting teeth?

Plagiochila tabinensis is readily recognized by the leaf apex which is deeply split into several very long and fragile, narrowly lanceolate to linear, lobe-like teeth. *Plagiochila tabinensis* is related to *P. aerea* but the latter species is a more delicate plant with leaves widest in the middle and apical teeth usually shorter (to maximally 1/3 of leaf length) and not fragile.

53. ***Plagiochila tamariscina*** Steph., Bull. Herb. Boissier (sér. 2) 2: 685. 1902.

TYPE: Puerto Rico, leg. Sintenis (PC syntype)

HABITAT AND DISTRIBUTION: on tree trunks and rotten wood, 180-2000 m. Recorded from Boyacá, Cundinamarca, Magdalena and Valle. General distribution: tropical America.

Plants delicate, medium-sized, 2.5-5 mm wide, pale yellowish green, feather-like, (bi)pinnately branched by terminal branching. Leaves distant to subimbricate, obliquely spreading, oblong, ca. 1.8-2.5 \times longer than wide, widest in the lower third or middle, ventral and apical leaf margins sharply toothed, leaf bases shortly decurrent, ventral leaf base not expanded, with or without shoulder. Leaf cells elongate, 15-25 μ m wide in midleaf, cell walls with small trigones or \pm evenly thickened; cuticle smooth. Underleaves lacking. Vegetative reproduction by propagula from ventral leaf surfaces.

By its pinnate-terminal branching *Plagiochila tamariscina* is similar to *P. deflexirama*, but the latter species has broader, (sub)imbricate leaves that are widest near the base and weakly to strongly ampliate.

54. ***Plagiochila tenuis*** Lindenb., Sp. Hepat. 2-4: 50. 1840.

TYPE: St. Vincent, unknown collector (W)

SYNONYM: *P. bidens* Gottsche, *P. scabrifolia* Inoue

ILLUSTRATIONS: Inoue (1977: Fig. 4 as *P. scabrifolia*), **Groth, et al.** (2002: Fig. 2F,I as *P. bidens*). The illustration of *P. tenuis* in **Gradstein & Ilkiu-Borges** (2009: Fig. 20C-E) shows a plant with rather short leaves (ca. 1.5 \times longer than wide) and was presumably based on misidentified material.

HABITAT AND DISTRIBUTION: on bark and rock, 1600-3500 m, at lower elevation on Galapagos. Recorded from Magdalena and Risaralda. General distribution: tropical America.

Plants small, delicate, 1-2 mm wide, branches scarce, intercalary. Leaves narrowly oblong, 2-2.2 \times longer than wide, sometimes caducous, apex bifid to 1/5, ventral margin entire or with 1-3 small teeth. Leaf cells isodiametric to elongate, 1-2 \times longer than wide, ca. 18-28 μ m wide in midleaf, with small trigones; cuticle finely papillose. Vegetative reproduction by caducous leaves.

Plagiochila tenuis resembles *P. papillifolia* in the bifid leaves with a papillose cuticle. However, the leaves in *P. papillifolia* are shorter, less than 1.8 \times longer than wide, and more strongly toothed (up to 12 teeth). Small bifid leaves occur also in *P. aerea*, *P. cuneata*, *P. exigua* and in the Central American *P. bicuspidata*, but in the latter four species the cuticle is smooth.

55. ***Plagiochila trichostoma*** Gottsche, in Triana & Planchon, Ann. Sci. Nat., Bot. (sér. 5) 1: 113. 1864; **Heinrichs, et al.** (2002a).

TYPE: Colombia, leg. Lindig (G lectotype)

SYNONYMS: *P. granatensis* Gottsche, *P. hansmeyeri* Steph., *P. ovato-obconica* Steph., *P. permista* Spruce, *P. saltuensis* Steph.

ILLUSTRATION: **Heinrichs, et al.** (2002a: Fig. 3).

HABITAT AND DISTRIBUTION: on soil, rock, rotten logs and trunk bases in humid upper montane forest and scrubby

páramo, 1900-4000 m. Recorded from Antioquia and Cundinamarca. General distribution: tropical Andes.

Plants rather robust, 4-7 mm wide, branches intercalary. Leaves alternate to subopposite, imbricate, ventrad, shortly ovate-triangular, 0.9-1.2× longer than wide, ventral base shouldered or ampliate, margins not or slightly bordered, toothed all around except on the lower half of the dorsal margin, with 16-44 narrowly triangular to linear teeth (2-6 cells long); dorsal and ventral leaf bases rather shortly and narrowly decurrent. Leaf cells subsodiametrical, 30-40 µm wide, with large swollen trigones becoming confluent near margin; leaf base with a short vitta; cuticle smooth; oil bodies homogeneous (Heinrichs, *et al.*, 2002). Perianth base covered by bracts. Vegetative reproduction not observed.

Plagiochila trichostoma approaches *P. adianthoides* but differs by the shorter and broader leaves (maximally 1.2× longer than wide), which are distinctly ventrad or secund and lack a distinct border of thicker-walled cells, and by homogeneous oil bodies. By leaf shape and the presence of a vitta *P. trichostoma* is also similar to *P. heteromalla*, but the leaves in the latter species are opposite and bordered.

56. **Plagiochila turgida** Herzog, *Hedwigia* 72: 196. 1932; Heinrichs (2002).

TYPE: Costa Rica, leg. Standley (JE)

SYNONYM: *P. longaeva* Herzog

ILLUSTRATION: Heinrichs (2002: Plate 27).

HABITAT AND DISTRIBUTION: on bark in humid montane forests up to the páramo, 1800-3500 m. Recorded from Cauca, Huila and Risaralda. General distribution: northern Andes, Centralamerica.

Plagiochila turgida is similar to *P. macrostachya* in having subopposite leaves and large leaf cells but differs from the latter species by toothed dorsal leaf bases (entire in *P. macrostachya*) and less elongate leaves, 1-1.4× longer than wide (1.2-1.6× longer than wide in *P. macrostachya*). For a full description of *P. turgida* see Heinrichs (2002).

57. **Plagiochila vincentina** Lindenb., *Sp. Hepat.* 2-4: 39. 1840; Heinrichs (2002).

TYPE: St. Vincent, unknown collector (W)

SYNONYMS: *P. diversispina* Steph., *P. hylacoetis* Spruce, *P. variifolia* Steph.

ILLUSTRATION: Heinrichs (2002: Plates 28-29).

HABITAT AND DISTRIBUTION: on bark in lowland and montane rainforest, 50-2200 m. Recorded from Antioquia, Boyacá, Caquetá, Chocó, Cundinamarca, Magdalena, Risaralda and Valle. General distribution: tropical America.

Plants rather robust, 5-8 mm wide, branches scarce, intercalary. Leaves elongate-triangular to oblong with a narrow or broad apex, ca. 1.4-2× longer than wide, ventral

base shouldered to ampliate, margins unbordered, with ca. 20-80 triangular to linear teeth, the teeth to 10 cells long, dorsal and ventral leaf bases longly decurrent and strongly toothed. Leaf cells large, ca. 35-55 µm wide in midleaf, slightly elongate, with small radiate trigones, leaf base without vitta; cuticle smooth. Androecia usually intercalary. Vegetative reproduction not observed.

Plagiochila vincentina is very similar to *P. breuteliana*, both species have ampliate leaves with toothed and longly decurrent leaf bases. However, the leaves in *P. breuteliana* have a short vitta (vitta lacking in *P. vincentina*).

Excluded species

Plagiochila crispabilis Lindenb. (= *P. jovoensis* Steph., *P. patentissima* Lindenb.) – This Brazilian species has been erroneously recorded from Valle (Herzog, 1955) and Magdalena (Winkler, 1976); the material from Valle (leg. Killip 11652, JE) belongs to *P. tamariscina*, that from Magdalena (leg. Winkler C178, COL) is *P. punctata*. *Plagiochila crispabilis* is recognized by the wide-spreading, narrowly rectangular leaves with almost parallel margins, shortly decurrent leaf bases and a narrowly recurved ventral leaf base, which is not ampliate and lacks a high shoulder (Fig. 1A); branching is terminal and dichotomous.

Plagiochila macrifolia Taylor – This rare Andean species has been erroneously recorded from Risaralda (see Uribe & Gradstein, 1998); the specimen (leg. Wolf 1317, COL) belongs to *P. alternans*. *Plagiochila macrifolia* is distinguished by narrowly oblong, distant, ventrad leaves with entire margins and a rounded to truncate apex with 2-4 small teeth; branching is terminal-dichotomous. It closely resembles *P. distinctifolia* but the latter species usually has a leaf border of thicker-walled cells and a toothed ventral leaf margin.

Plagiochila simplex (Sw.) Lindenb. – This widespread neotropical species is surprisingly rare in the Andes and not yet known from Colombia; the record from Magdalena (Winkler, 1976) belongs to *P. tamariscina*. The species closely resembles *P. gymnocalycina* and Heinrichs, *et al.* (1998) suggested that the two species might be conspecific. They differ, however, in the shape of the leaves which are unusually more than 2× longer than wide in *P. gymnocalycina* while being less than 2× longer than wide in *P. simplex*. Material of *P. simplex* with caducous leaves may be confused with *P. punctata* but the latter species has a vitta and leaves, only 1.9-1.2× longer than wide.

Further names

The following taxa recorded from Colombia have not been studied; many of them may be synonyms or misidentifications.

Plagiochila aspleniformis R.M.Schust. – North American species; recorded from Putumayo by Robinson (1967).

Plagiochila arcta S.Winkler – Type from Magdalena, San Lorenzo, 2180 m, *Winkler C44* (ULM?). Identity unclear, original description very poor.

Plagiochila choachina Gottsche var. *phyllobola* Gottsche – Type from Cundinamarca, *Lindig s.n. Plagiochila choachina* is a synonym of *P. punctata* but this variety has not been studied.

Plagiochila discreta Gottsche – Type from Aserradero near Bogotá, *Lindig 1729c*. **Inoue** (1989) considered this species a synonym of *P. raddiana* but according to **Heinrichs & Gradstein** (2000) it is not conspecific with *P. raddiana*.

Plagiochila horrida Gottsche var. *granatensis* Gottsche – Type from Cundinamarca, *Lindig s.n. Plagiochila horrida* is a synonym of *P. bifaria* but this variety has not been studied.

Plagiochila humboldtiana Gottsche – The type of this species (“Nova Granada”, *Humboldt & Bonpland s.n.*) seems to be lost (see **Stephani**, 1901-1905).

Plagiochila interjecta Gottsche – Type from Tocarema, 2200 m, *Lindig 1705g*. **Inoue** (1989) considered this species a synonym of *P. raddiana* but according to **Heinrichs & Gradstein** (2000) it is not conspecific with *P. raddiana*.

Plagiochila laetevirens Lindenb. var. *peruviana* Spruce – Peruvian taxon; recorded from Valle by **Herzog** (1955).

Plagiochila longiramea Steph.– This Bolivian endemic was recorded from Cundinamarca by **Inoue** (in **Gradstein & Hekking**, 1979) under the name *P. apicidens* Steph., which is a synonym (**Heinrichs**, 2002). The record needs verification.

Plagiochila longitexta Steph. – Syntype from Zipacón, *Lindig s.n. Inoue* (1989) considered this species a synonym of *P. raddiana* but according to **Heinrichs & Gradstein** (2000) it is not conspecific with *P. raddiana*.

Plagiochila oblongotrigona Steph. – This African species was recorded from Cundinamarca by **Irmischer** (1914). The record is presumably erroneous.

Plagiochila perrottetiana Mont. & Gottsche var. *minor* Gottsche – Type from Cundinamarca, *Lindig s.n. Plagiochila perrottetiana* is a synonym of *P. rutilans* but this variety has not been studied.

Plagiochila relictata Steph.– Type from Pacho, *Lindig s.n.*

Plagiochila rufoviridis Spruce – Bolivian species; recorded from Colombia by **Dugas** (1929). The type of this unresolved name could not be found in MANCH (L. Loughtman, in litt.).

Plagiochila saltuensis Spruce var. *spinossissima* Herzog– Type from Valle, *Killip 11399*. *Plagiochila saltuensis* is a synonym of *P. trichostoma* but this variety has not been studied.

Plagiochila tovarina Gottsche var. *trianae* Gottsche– Type from Nova Granada (Colombia?), *Triana s.n.*

Plagiochila trianae Gottsche– Type from Zipacón, *Lindig 1796*.

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Información suplementaria

Appendix 1. Nomenclatural changes in the catalogue of *Plagiochila* of Colombia (**Gradstein & Uribe**, 2015). Synonymy based on **Gradstein** (2015a) unless otherwise stated.

Conflict of interest

The author declares that he has no conflict of interest.

Bibliography

- Aguirre, J. & Calonge, F.D. (1985).** Algas, Líquenes, Hongos, Hepáticas y Musgos. En: Flora de la Real Expedición Botánica del Nuevo Reino de Granada (1783-1816), Tomo II. Madrid: Instituto de Cultura Hispánica.
- Carl, H. (1931).** Die Artypen und die systematische Gliederung der Gattung *Plagiochila* Dum. Ann. Bryol., Suppl. **2**: 1-170.
- Chua-Petiot, M.S. (2011).** A checklist of Hepaticae and Anthocerotae of Malaysia. Polish Botanical Journal **56**: 1-44.
- Dauphin, C. (2005).** Catalogue of Costa Rican Hepaticae and Anthocerotae. Tropical Bryology **26**: 141-2018.
- Dugas, M. (1929).** Contribution à l'étude du genre «*Plagiochila*» Dum. Ann. Sci. Nat. Bot. sér. **10**, **11**: 1-199.
- Glenny, D. (1998).** A revised checklist of New Zealand liverworts and hornworts. Tuhiinga **10**: 119-149.
- Gottsche, C.M. (1863).** De Mexikanske Levermosser. Copenhagen: Bianco Lunos.
- Gottsche, C.M. (1864).** Hepaticae. [In: Triana, J.J. & Planchon, J.E. Prodromus florae novo-granatensis]. Annales des Sciences Naturelles 5, Botanique **1**: 95-198.
- Gradstein, S.R. (1997).** Hepatophyta, Anthocerophyta. In: Boggan, J., Funk, V., Kelloff, C., Hoff, M., Cremers, G. & Feuillet, C. (eds.). Checklist of the Plants of the Guianas (pp. 9–15). Washington: Smithsonian Institution.

- Gradstein S.R. (2015a).** New synonyms and new lectotypifications in Neotropical *Plagiochila* (Marchantiophyta). *Cryptogamie, Bryologie* **36**: 369-379.
- Gradstein S.R. (2015b).** Annotated key to the species of *Plagiochila* from Brazil. *Pesquisas Botanica* **67**: 23-36.
- Gradstein, S.R. & Costa, D.P. (2003).** The Liverworts and Hornworts of Brazil. *Memoirs of the New York Botanical Garden* **87**: 1-317.
- Gradstein, S.R. & Feuillet-Hurtado, C. (in press).** *Plagiochila fastigiata* Lindenb. & Gottsche. In: New national and regional bryophyte records. *Journal of Bryology*.
- Gradstein, S.R. & Hekking, W.H.A. (1979).** Studies on Colombian Cryptogams IV. A Catalogue of the Hepaticae of Colombia. *Journal of the Hattori Botanical Laboratory* **45**: 93-144.
- Gradstein, S.R. & Ilkiu-Borges, A.L. (2009).** Guide to the Plants of Central French Guiana. Part IV. Liverworts and Hornworts. *Memoirs of the New York Botanical Garden* **76, 4**: 1-140.
- Gradstein, S.R. & Reiner-Drehwald, M.E. (1995).** *Szweykowskia*, a new genus of Plagiochilaceae (Hepaticae) from tropical America. *Fragmenta Floristica et Geobotanica* **40**: 31-38.
- Gradstein, S.R. & Salazar Allen, N. (1992).** Bryophyte diversity along an altitudinal gradient in Darién National Park, Panama. *Tropical Bryology* **5**: 61-71.
- Gradstein, S.R. & Uribe, J. (2015).** Marchantiophyta. In: Bernal, R., Gradstein, S.R. & Celis, M. (eds.). *Catálogo de plantas y líquenes de Colombia*. Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia. <http://catalogoplantasdecolombia.unal.edu.co/>
- Gradstein, S.R., Churchill, S.P. & Salazar Allen, N. (2001).** Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* **86**: 1-577.
- Gradstein, S.R., Morales, C., Negritto, M.A. & Duckett, J.G. (2016).** New records of liverworts and hornworts from the Sierra Nevada de Santa Marta, Colombia. *Cryptogamie, Bryologie* **37** (in press).
- Grolle, R. & Heinrichs, J. (1999).** Redescription and synonymy of *Plagiochila aerea* Taylor 1846 (Hepaticae), first described as *Lycopodium pinnatum* by Lamarck 1792. *Nova Hedwigia* **68**: 511-525.
- Groth, H., Helms, G. & Heinrichs, J. (2002).** The systematic status of *Plagiochila* sects. *Bidentes* Carl and *Caducilobae* Inoue (Hepaticae) inferred from nrDNA ITS sequences. *Taxon* **51**: 675-684.
- Hässel de Menendez, G.G. (1983).** Informaciones nomenclaturales sobre las especies del genero *Plagiochila* (Hepaticae) de Argentina y Chile. *Boletín de la Sociedad Argentina de Botánica* **22**: 87-129.
- Heinrichs, J. (2002).** A taxonomic revision of *Plagiochila* sect. *Hylacoetes*, sect. *Adiantoideae* and sect. *Fuscoluteae* in the Neotropics with a preliminary subdivision of Neotropical Plagiochilaceae into nine lineages. *Bryophytorum Bibliotheca* **58**: 1-184.
- Heinrichs, J. & Gradstein, S.R. (1999).** On *Plagiochila longiramea* Steph. (Hepaticae), a poorly known species of Bolivia. *Candollea* **54**: 73-81.
- Heinrichs, J. & Gradstein, S.R. (2000).** A revision of *Plagiochila* sect. *Crispatae* and sect. *Hypnoides* (Hepaticae) in the Neotropics. I. *Plagiochila disticha*, *P. montagnei* and *P. raddiana*. *Nova Hedwigia* **70**: 161-184.
- Heinrichs, J., Anton, H., Holz, I. & Gradstein, S.R. (2000a).** On the blue stem colour in *Plagiochila longispina* Lindenb. & Gottsche (Plagiochilaceae). *Cryptogamie, Bryologie* **21**: 109-111.
- Heinrichs, J., Anton, H., Gradstein, S.R. & Mues, R. (2000b).** Systematics of *Plagiochila* sect. *Glaucoscentes* Carl (Hepaticae) from tropical America: a morphological and chemotaxonomical approach. *Plant Systematics and Evolution* **220**: 115-138.
- Heinrichs, J., Anton, H., Holz, I. & Grolle, R. (2001a).** The andine *Plagiochila tabinensis* Steph. and the identity of *Acrobolbus laceratus* R.M. Schust. (Hepaticae). *Nova Hedwigia* **73**: 445-452.
- Heinrichs, J., Gradstein, S.R. & Grolle, R. (1998).** A revision of the neotropical species of *Plagiochila* (Dumort.) Dumort. (Hepaticae) described by Olof Swartz. *Journal of the Hattori Botanical Laboratory* **85**: 1-32.
- Heinrichs, J., Gradstein, S.R., Groth, H. & Lindner, M. (2003).** *Plagiochila cucullifolia* var. *anomala* var. nov. from Ecuador, with notes on discordant molecular and morphological variation in bryophytes. *Plant Systematics and Evolution* **242**: 205-216.
- Heinrichs, J., Groth, H., Gradstein, S.R., Rycroft, D.S., Cole, W.J. & Anton, H. (2001b).** *Plagiochila rutilans* (Hepaticae): a poorly known species from tropical America. *The Bryologist* **104**: 350-361.
- Heinrichs, J., Groth, H., Holz, I., Rycroft, D.S., Renker, C. & Pröschold, T. (2002a).** The systematic position of *Plagiochila moritziana*, *P. trichostoma* and *P. deflexa*, based on ITS sequences of nuclear ribosomal DNA, morphology and lipophylic secondary metabolites. *The Bryologist* **105**: 189-203.
- Heinrichs, J., Groth, H., Lindner, M., Feldberg, K. & Rycroft, D.S. (2004a).** Molecular, morphological and phytochemical evidence for a broad species concept of *Plagiochila bifaria* (Sw.) Lindenb. (Hepaticae). *The Bryologist* **107**: 28-40.
- Heinrichs, J., Groth, H., Lindner, M., Renker, C., Pócs, T. & Pröschold, T. (2004b).** Intercontinental distribution of *Plagiochila corrugata* (Plagiochilaceae, Hepaticae) inferred from nrDNA ITS sequences and morphology. *Botanical Journal of the Linnean Society* **146**: 469-481.
- Heinrichs, J., Groth, M. & Sauer, M. (2004c).** New synonyms in *Plagiochila* (Hepaticae) III. *Cryptogamie, Bryologie* **25**: 35-37.
- Heinrichs, J., Lindner, M., Groth, H. & Renker, C. (2005a).** Distribution and synonymy of *Plagiochila punctata* (Taylor) Taylor, with hypotheses on the evolutionary history of *Plagiochila* sect. *Arrectae* (Plagiochilaceae, Hepaticae). *Plant Systematics and Evolution* **250**: 105-117.

- Heinrichs, J., Lindner, M., Gradstein, S.R., Groth, H., Buchbender, V., Solga, A. & Fischer, E. (2005c).** Origin and subdivision of *Plagiochila* (Jungermanniidae: Plagiochilaceae) in tropical Africa based on evidence from nuclear and chloroplast DNA sequences and morphology. *Taxon* **54**: 317-333.
- Heinrichs, J., Renker, C. & Gradstein, S.R. (1999).** A taxonomic revision of *Plagiochila subplana* Lindenb., a widespread liverwort of tropical America. *Haussknechtia Beiheft* **9**: 171-181.
- Heinrichs, J., Rycroft, D.S., Groth, H. & Cole, W.J. (2002b).** Morphological and phytochemical studies of *Plagiochila papillifolia* Steph., a neotropical liverwort new to Europe. *Journal of Bryology* **24**: 119-126.
- Heinrichs, J., Rycroft, D. S., Feldberg, K., Lindner, M. & Hartmann, F.A. (2006).** The systematic position of *Plagiochila surinamensis* inferred from nrDNA sequences, morphology and phytochemistry. *Journal of the Hattori Botanical Laboratory* **100**: 135-142.
- Heinrichs, J., Sauer, M. & Grolle, R. (2002c).** Lectotypification and synonymy of *Plagiochila* sect. *Vagae* Lindenb. (Hepaticae). *Cryptogamie, Bryologie* **23**: 5-9.
- Heinrichs, J., Wilson, R., Feldberg, K., Hentschel, J., Schäfer-Verwimp, A., León-Yáñez, S. & Yandún, S. (2005b).** The systematic position of *Plagiochila (Jamesoniella) dependula* (Jungermanniopsida) inferred from nrITS sequences and morphology, with notes on its differentiation from *Plagiochila fuscolutea*. *Journal of Bryology* **27**: 319-327.
- Herzog, T. (1932).** Beiträge zur Kenntnis der Gattung *Plagiochila* I. Neotropische Arten. *Hedwigia* **72**: 195-242.
- Herzog, T. (1934).** Die Bryophyten der Andenreisen von C. Troll (Bolivia, Columbia, Panama). *Hedwigia* **74**: 79-97.
- Herzog, T. (1955).** Hepaticae aus Colombia und Peru. *Feddes Repertorium* **57**: 156-203.
- Holz, I., Heinrichs, J., Schäfer-Verwimp, A. & Gradstein, S.R. (2001).** Additions to the hepatic flora of Costa Rica III. *Cryptogamie, Bryologie* **22**: 255-273.
- Inoue, H. (1964).** The Genus *Plagiochilon*. *Journal of the Hattori Botanical Laboratory* **27**: 52-72.
- Inoue, H. (1966).** A monograph of the hepatic genus *Szyziella* Spruce. *Journal of the Hattori Botanical Laboratory* **29**: 171-213.
- Inoue, H. (1977).** Four new species of the genus *Plagiochila* from the Galapagos Islands. *Bulletin of the National Science Museum (Tokyo) Ser. B*, **3**: 45-54.
- Inoue, H. (1987).** Notes on the Plagiochilaceae, XIV. New species of *Plagiochila* (Dum.) Dum. from Neotropics. In: Inoue, H. (ed.). *Studies on Cryptogams in Southern Peru* (pp. 95–105). Tokyo: Tokai University Press.
- Inoue, H. (1988).** Notes on the Plagiochilaceae, XV. The genus *Steereochila* Inoue and *Plagiochila eggersii*, sp. nov. *Bulletin of the National Science Museum (Tokyo) Ser. B*, **14**: 135-141.
- Inoue, H. (1989).** Notes on the Plagiochilaceae, XVI. Studies on some *Plagiochila* species in the Neotropics. *Bulletin of the National Science Museum (Tokyo) Ser. B*, **15**: 35-47.
- Inoue, H. & Gradstein, S.R. (1980).** Notes on the Plagiochilaceae, IX. A review of the genus *Plagiochila* (Dum.) Dum. in the Galapagos Islands. *Bulletin of the National Science Museum (Tokyo) Ser. B*, **6**: 7-22.
- Irmischer, E. 1914.** Beiträge zur Laubmoosflora von Kolumbien. *Mémoires de la Société des Sciences Naturelles* **5**: 994-997.
- Jack, J.B. & Stephani, F. (1892).** Hepaticae Wallisiana. *Hedwigia* **31**: 11-27.
- Kunth, C.S. (1822).** Synopsis Plantarum, quas in intere ad plagam aequinoctialem orbis novi collegerunt A. de Humboldt et Am. Bonpland. Tomus primus (pp. 40–45). Paris: Levrault.
- Lavocat Bernard, E. & Schäfer-Verwimp, A. (2011).** Checklist of the bryophytes of the Guadeloupe archipelago and Martinique (French West Indies). *Cryptogamie, Bryologie* **32**: 233-277.
- León-Yáñez, S., Gradstein, S.R. & Wegner, C. (2006).** Hepáticas y Antoceros del Ecuador. Quito: Herbario QCA.
- Mägdefrau, K. (1983).** The bryophyte vegetation of the forests and páramos of Venezuela and Colombia. *Nova Hedwigia* **38**: 1-63.
- Müller, J., Heinrichs, J. & Gradstein, S.R. (1999).** A revision of *Plagiochila* sect. *Plagiochila* in the Neotropics. *The Bryologist* **102**: 729-746.
- Robinson, H. (1967).** Preliminary studies on the bryophytes of Colombia. *The Bryologist* **70**: 1-61.
- Robinson, H. (1988).** *Plagiochila rudischusteri*, a new species from the Paria Peninsula of Venezuela. *Beiheft zur Nova Hedwigia* **90**: 199-202.
- Rycroft, D.S., Cole, W.J., Heinrichs, J., Groth, H., Renker, C. & Pröschold, T. (2002).** Phytochemical, morphological and molecular evidence for the occurrence of the neotropical liverwort *Plagiochila stricta* in the Canary Islands, new to Macaronesia. *The Bryologist* **105**: 363-372.
- Rycroft, D.S., Heinrichs, J., Cole, W.J. & Anton, H. (2001).** A phytochemical and morphological and molecular study of the liverwort *Plagiochila retrorsa* Gottsche, new to Europe. *Journal of Bryology* **23**: 23-34.
- Schumacker, R. & Váña, J. (2005).** Identification keys to the liverworts and hornworts of Europe and Macaronesia, 2nd ed. Poznań: Sorus.
- Schuster, R.M. (1980).** The Hepaticae and Anthocerotae of North America, Vol. IV. New York: Columbia University Press.
- So, M.L. (2001).** *Plagiochila* (Hepaticae, Plagiochilaceae) in China. *Systematic Botany Monographs* **60**: 1-214.
- Söderström, L. (2015).** Notes on Early Land Plants Today. 69. Circumscription of Plagiochilaceae (Marchantiophyta) with a preliminary infrageneric subdivision of *Plagiochila*. *Phytotaxa* **208**: 75-91.
- Söderström, L., Gradstein, S.R. & Hagborg, A. (2010).** A checklist of the hornworts and liverworts of Java. *Phytotaxa* **9**: 53-149.

- Söderström, L., Hagborg, A., von Konrat, M. and 38 co-authors (2016).** World checklist of hornworts and liverworts. *Phytokeys* **59**: 1-828.
- Söderström, L., Hagborg, A., Váña, J. & von Konrat, M. (2011).** Land of wood and water: A checklist of liverworts and hornworts of Jamaica. *The Bryologist* **114**: 67-91.
- Söderström, L., Pócs, T., Váña, J. & Hagborg, A. (2015).** Notes on Early Land Plants Today. 74. Validation of a few names in liverworts. *Phytotaxa* **220**: 199-200.
- Stephani, F. (1901–1905).** *Species Hepaticarum*, Vol. II. Genève: Georg & Cie.
- Stephani, F. (1916).** Hepaticae. In: Herzog, T. *Die Bryophyten meiner zweiten Reise durch Bolivia*. *Bibliotheca Botanica* **87**: 173-268.
- Thouvenot, L., Gradstein, S.R., Hagborg, A., Söderström, L. & Bardat, J. (2011).** Checklist of the liverworts and hornworts of New Caledonia. *Cryptogamic, Bryologie* **32**: 287-390.
- Uribe, J. & Gradstein, S.R. (1998).** Catalogue of the Hepaticae and Anthocerotae of Colombia. *Bryophytorum Bibliotheca* **53**: 1-99.
- Winkler, S. (1976).** Die Hepaticae der Sierra Nevada de Santa Marta, Kolumbien. I. Terrestrische, epixyle und epipetrische Arten. *Revue Bryologique et Lichénologique* **42**: 789-825.
- Wolf, J.H.D. (1994).** Epiphyte communities of tropical montane forests in the northern Andes. *Phytocoenologia* **22**: 1-103.