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Plagiochila rutilans (Hepaticae): A Poorly Known Species from Tropical America

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Abstract. *The neotropical liverwort,* Plagiochila rutilans *Lindenb., is conspecific* with P. remotifolia *Hampe & Gottsche,* P. farlowii *Steph.,* P. harrisana *Steph, and* P. organensis *Herzog.* Plagiochila standleyi *Carl is reduced to a variety of* P. rutilans. Plagiochila gymnocalycina *(Lehm. & Lindenb.) Mont. and* P. portoricensis *Hampe & Gottsche (=* P. simplex *(Sw.) Lindenb.) are excluded from the synonymy of* P. rutilans. Plagiochila rutilans *var.* liebmanniana *Gottsche is a synonym of* P. crispabilis *Lindenb.;* P. rutilans *var.* laxa *Lindenb. and var.* angustifolia *Herzog are conspecific with* P. gymnocalycina. *Sporophytes of* P. rutilans *are described for the first time. Fresh material of* P. rutilans *exhibits a distinct odor of peppermint caused by the presence of several menthane monoterpenoids, principally pulegone. NMR (nuclear magnetic resonance) fingerprints and GC-MS data indicate that the lipophilic secondary metabolite profiles are distinct for the two varieties accepted in this study.*

Lindenberg (1839–1844), in his excellent treatment of the genus *Plagiochila,* described *Plagiochila rutilans* Lindenb. as a new species based on a single gathering from Brazil and accepted a single variety, *P. rutilans* var. *laxa* Lindenb., originating from Jamaica. Later authors (Gottsche 1863–1867; Herzog 1932, 1955; Spruce 1884–1885) published further varieties and forms from various parts of the Neotropics.

Stephani (1901–1906) proposed a synonymy of *P. rutilans* 1840 with *P. gymnocalycina* (Lehm. & Lindenb.) Mont. 1839 (Bas. *Jungermannia gymnocalycina* Lehm. & Lindenb. 1833), *P. portoricensis* Hampe & Gottsche 1853, and *P. remotifolia* Hampe & Gottsche 1853 and erroneously accepted the name *P. rutilans* instead of the older *P. gymnocalycina.* Although Schiffner and Arnell (1964) doubted the conspecificity of the taxa, Stephani's synonymy was widely accepted in herbaria and by recent authors (e.g., Fulford 1987).

Species of *Plagiochila* produce many secondary metabolites that may be taxonomically significant (e.g., Anton et al. 2000; Heinrichs et al. 2000; Rycroft et al. 2001). The only previous work on the chemistry of *P. rutilans* (Huneck et al. 1984) concerned a single collection from Cuba. A phenolic compound was isolated and assigned the structure 3-methoxy-5-prenylbenzene-1,2-diol (**1**; chemical compounds and structures are identified by numerals printed in bold in Fig. 1), as well as an oil with a peppermint-like odor that was not investigated further. During field work in various parts of the Neotropics (Bolivia, Brazil, and Costa Rica) we were able to study several stands of *P. rutilans* and regularly recognized a distinct odor of peppermint in the species. In contrast, a similar odor could not be recognized in fresh *P. gymnocalycina.* These observations, in the context of our ongoing work on the systematics of the genus *Plagiochila* in tropical America (e.g., Heinrichs et al. 2000; Müller et al. 1999), prompted us to undertake a detailed taxonomic investigation of *P. rutilans* and the synonyms proposed by Stephani (1901–1906), using morphological and phytochemical evidence gathered from examination of herbarium specimens and fresh material.

MATERIALS AND METHODS

Phytochemistry.—Using NMR and GC-MS fingerprinting (Rycroft 1996, 1998), we have determined the lipophilic secondary metabolites of the eleven specimens of *P. rutilans* shown in Table 1. Details of extraction, analyses, revision of the structure of compound **1** (to **2**), and

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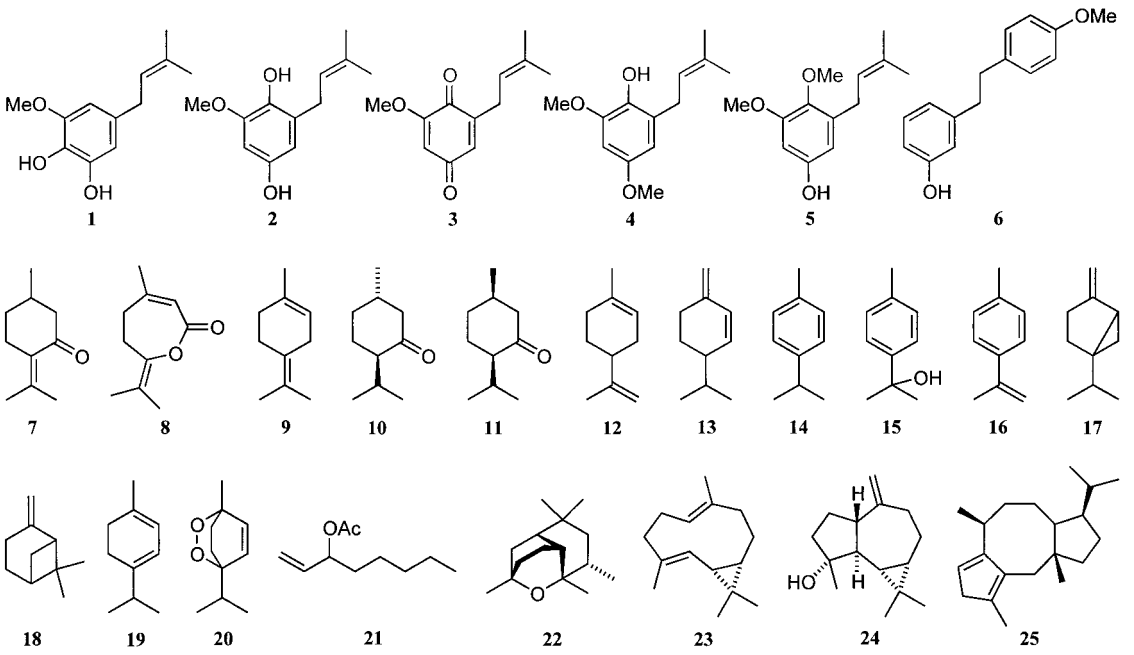

FIGURE 1. Chemical structures, numbered to coincide with the numbers printed in bold used in the text and Table 2 (where the names of the compounds are to be found).

structural elucidation of the new compounds **3**–**5** and **8** are presented elsewhere (Rycroft & Cole 2001). The results are summarized in Table 2. Specimens (i)–(viii) are recent (post 1997) and gave good extracts, six of which, (i)–(vi), were related in composition. Specimens (vii) and (viii) clearly belong to a different chemical race. Although chemical differences were considered independently of morphology, it became apparent that the two chemical races are congruent with taxa that could be defined morphologically, namely *P. rutilans* var. *rutilans* and var. *standleyi* (see below). Specimens (ix)–(xi) are older, but were nevertheless included in the study because (ix) is a voucher from the work of Huneck et al. (1984). They gave meagre extracts and are not included in Table 2, but from the compounds identified it was evident that all three belong to var. *rutilans.*

TAXONOMIC TREATMENT

PLAGIOCHILA RUTILANS Lindenb., Spec. Hepat. (fasc. 2–4): 47. 1840. TYPE: BRAZIL. *Raddi 57* (holotype, W hb. Lindenb. 583 [ster.]; isotype, W ''583'' [female, only bracts]).

= *Plagiochila remotifolia* Hampe & Gottsche, Linnaea 25: 340. 1853 (''1851''). Syn. *fide* Stephani (1901–1906: 250) and here confirmed. TYPE: PUERTO RICO. *Schwanecke s.n.* (lectotype, here designated, G 024070 [*c. per. unico*]).

= *Plagiochila farlowii* Steph. in Herzog, Biblioth. Bot. 87(2): 198. 1916. TYPE: BOLIVIA. COCHABAMBA. Tablas, 1800 m, *Herzog 4633* (holotype, G [*c. per.*, scanty]).

TABLE 1. Specimens of *Plagiochila rutilans* used for the chemical analyses.

No.	Source	Date of collection	Date of extraction	Weight (mg) extracted
(i)	BOLIVIA. Chapare: *Heinrichs et al. 4181* (GOET)	24.X.1997	3.V.2000	45
(ii)	BOLIVIA. Cotapata: *Groth 101* (GOET)	24.IX.2000	20.X.2000	6
(iii)	BRAZIL. Itatiaia: *Costa & Gradstein 3868* (GOET)	10.V.2000	9.VI.2000	34
(iv)	BRAZIL. Itatiaia: *Costa & Gradstein 3776* (GOET)	IV.2000	2.V.2000	51
(v)	COSTA RICA. Tapanti: *Heinrichs et al. 4195* (GOET)	9.X.1999	13.VI.2000	17
(vi)	COSTA RICA. San Gerardo de Dota: *Holz CR 00-0654* (GOET)	14.III.2000	2.X.2000	17
(vii)	COSTA RICA. Zurqui: *Heinrichs et al. 4191* (GOET)	8.X.1999	3.V.2000	35
(viii)	COSTA RICA. Zurqui: *Heinrichs et al. 4302* (GOET)	8.X.1999	20.X.2000	17
(ix)	CUBA. Sierra Maestra: *Pócs & Reyes 9046/E* (U)	10.XI.1978	19.VI.2000	20
(x)	CUBA. Sierra Maestra: *Pócs 9200/M* (JE hb. Huneck)	31.X.1980	6.VII.2000	28
(xi)	ECUADOR. Tinalandia: *Arts Ec. 18/036* (GOET)	18.VII.1991	7.VII.2000	20

TABLE 2. Terpenoids and lipohilic aromatic compounds in *Plagiochila rutilans* var. *rutilans* and var. *standleyi*. The compound numbers correspond with Figure 1, the specimen numbers with Table 1. The absolute amounts of compounds extracted from the specimens were determined from the NMR spectra wherever possible and estimated by comparison with the GC-MS TIC integration in the other cases. The absolute amounts were converted to % w/w of the specimens and the maximum amounts found are indicated as follows: "–": not detected; "(+)": <0.01% "+": 0.01–0.1% "++": 0.2–0.6% "+++": 1–3% "++++": 5%. The compounds shown as present were present in all the specimens in each column, except for α-terpinene (**19**), that was not detected in specimen (v).

Compound number	Name	Specimen numbers			
		Plagiochila rutilans var. *rutilans*			var. *standleyi*
		(ii)–(v)	(i)	(vi)	(vii), (viii)
2	2-methoxy-6-prenylhydroquinone	+++	–	++	–
3	2-methoxy-6-prenyl-1,4-benzoquinone	+	(+)	+	–
4	2-methoxy-4-*O*-methyl-6-prenylhydroquinone	+	(+)	(+)	–
5	2-methoxy-1-*O*-methyl-6-prenylhydroquinone	–	+	–	–
6	3-hydroxy-4′-methoxybibenzyl	(+)	(+)	–	++++
7	pulegone	+++	+	–	–
8	3,7-dimethyl-2,6-octadien-1,6-olide	–	–	++	–
9	terpinolene	+++	–	+	–
10	menthone	++	(+)	–	–
11	isomenthone	+	(+)	–	–
12	limonene	++	+	+	+++
13	β-phellandrene	+	+	–	++
14	*p*-cymene	+	(+)	–	+
15	8-*p*-cymenol	+	+	+	–
16	*p*-isopropenyltoluene	(+)	(+)	–	–
17	sabinene	+	(+)	+	–
18	β-pinene	+	–	(+)	–
19	α-terpinene	(+)	–	–	++
20	ascaridole	–	–	–	++
21	1-octen-3-yl acetate	+	+	+	+
22	peculiaroxide	++	+	++	–
23	bicyclogermacrene	++	–	+	+
24	spathulenol	+	+	(+)	–
25	fusicoccadiene	+	(+)	+	–

= *Plagiochila harrisana* Steph., Spec. Hep. 6: 165. 1918. TYPE: JAMAICA. Greenhill Wood, 4000 ft, *Harris 11089* (holotype, G 025833 [male]).

= *Plagiochila organensis* Herzog, Repert. Spec. Nov. Regni Veg. 21: 23. 1925. TYPE: BRAZIL. RIO DE JANEIRO. Serra dos Orgãos, Morro Açu, 2200 m, *v. Lützelburg 6350a* (holotype, JE [ster.]).

= *Plagiochila distinctifolia* Lindenb. fo. *linearifolia* Herzog, Rev. Bryol. Lichénol. 11: 15, *nom. inval.* [art. 32.1(c)]. ORIGINAL MATERIAL: COSTA RICA. HEREDIA. Cerro de Las Lajas N of San Isidro, 2000–2400 m, 07.03.1926, *Standley & Valerio 51512* (JE [*c. per.*]).

Illustrations.—Heinrichs et al. (1998: figs. 4 & 5 [as *P. harrisana*]; Herzog (1925: plate IX, fig. 5 [as *P. organensis*]); Lindenberg (1839–1844: plate IX [as *P. rutilans*]; Schiffner & Arnell (1964: plate VI, figs. 56 & 57 [as *P. rutilans*]); Stephani (1985: figs. 11,120 & 11,647 [as *P. harrisana*], 11,465 [as *P. farlowii*]); this paper: figs. 2, 3, 4 (A–D), 5.

For the status of further synonyms proposed by Stephani (1901–1906) and several varieties and forms see EXCLUDENDA.

Gametophyte.—Plants with odor of peppermint (fresh materials and herbarium specimens up to ca 4 yr old), medium sized, (2.5–)3.01–8.01(–16.0) cm long and (3.5–)4.0–7.0 mm broad, green to olivaceous green, in diffuse patches, with creeping stoloniform shoots giving rise to leafy aerial stems. Stems brown, in upper parts often brownish green or greenish, widely exposed both dorsally and ventrally, stems dorsiventrally flattened, ca 180–350 × 270–450 μm thick near base, 1.2–1.6 times as wide as high, in transverse section ca 13–19 × 15–22(–26) cells, cortical cells in 2–4 layers, distinctly thick-walled, ca 10–20 × 15–30 μm, medullary cells thin walled to slightly thick-walled, ca 10–23 × 15–31 μm, trigone-like thickenings lacking or minute, triangular. Branches lacking or moderate in number, of the lateral-intercalary type. Leaves remote to moderately imbricate with rounded, truncate or acute apex, on stronger shoots ca 2.0–3.7 × 0.8–1.5 mm (flattened) and 1.8–3.7 times as long as wide, widely spreading or weakly bent to the ventral side, oblong rectangular, not ampliate, ventrally hardly to moderately decurrent with narrow, acute strip, not extending to stem midline, dorsally (hardly to) moderately, occasionally longly decurrent, extending to dorsal stem midline, ventral margin often recurved near base, at least in larger leaves, dorsal margin flat or recurved. Apex and proximal parts of leaf margin with triangular to elongate triangular teeth or teeth restricted to apical part of leaf, teeth straight or curved, those of apex pointing in various directions,

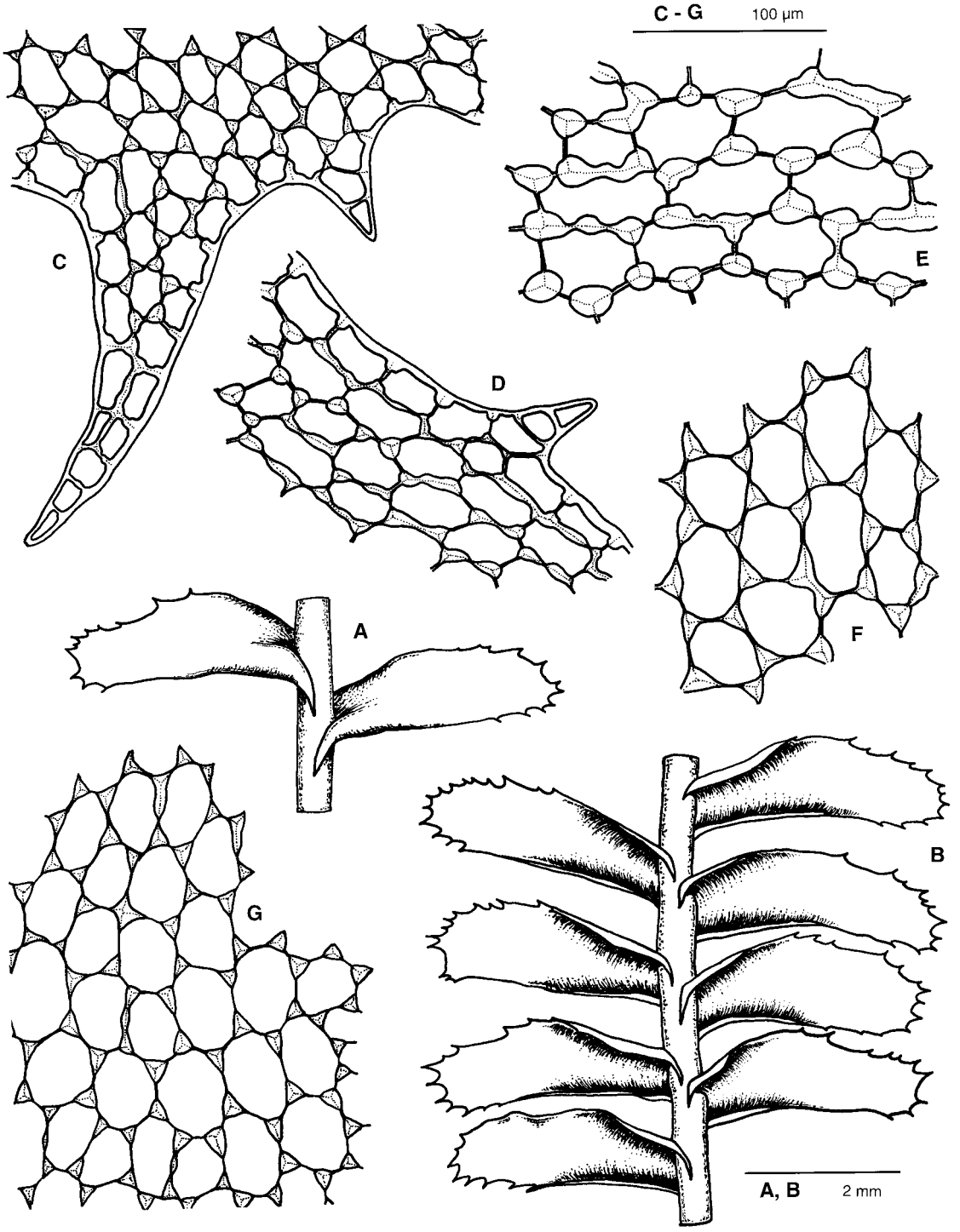

FIGURE 2. *Plagiochila rutilans* Lindenb. var. *rutilans*.—A. Part of shoot, dorsal view. — B. Part of shoot, ventral view. — C. Teeth of leaf apex. — D. Tooth of ventral leaf margin. — E,F. Cells from leaf base. — G. Median leaf cells. (All from holotype).

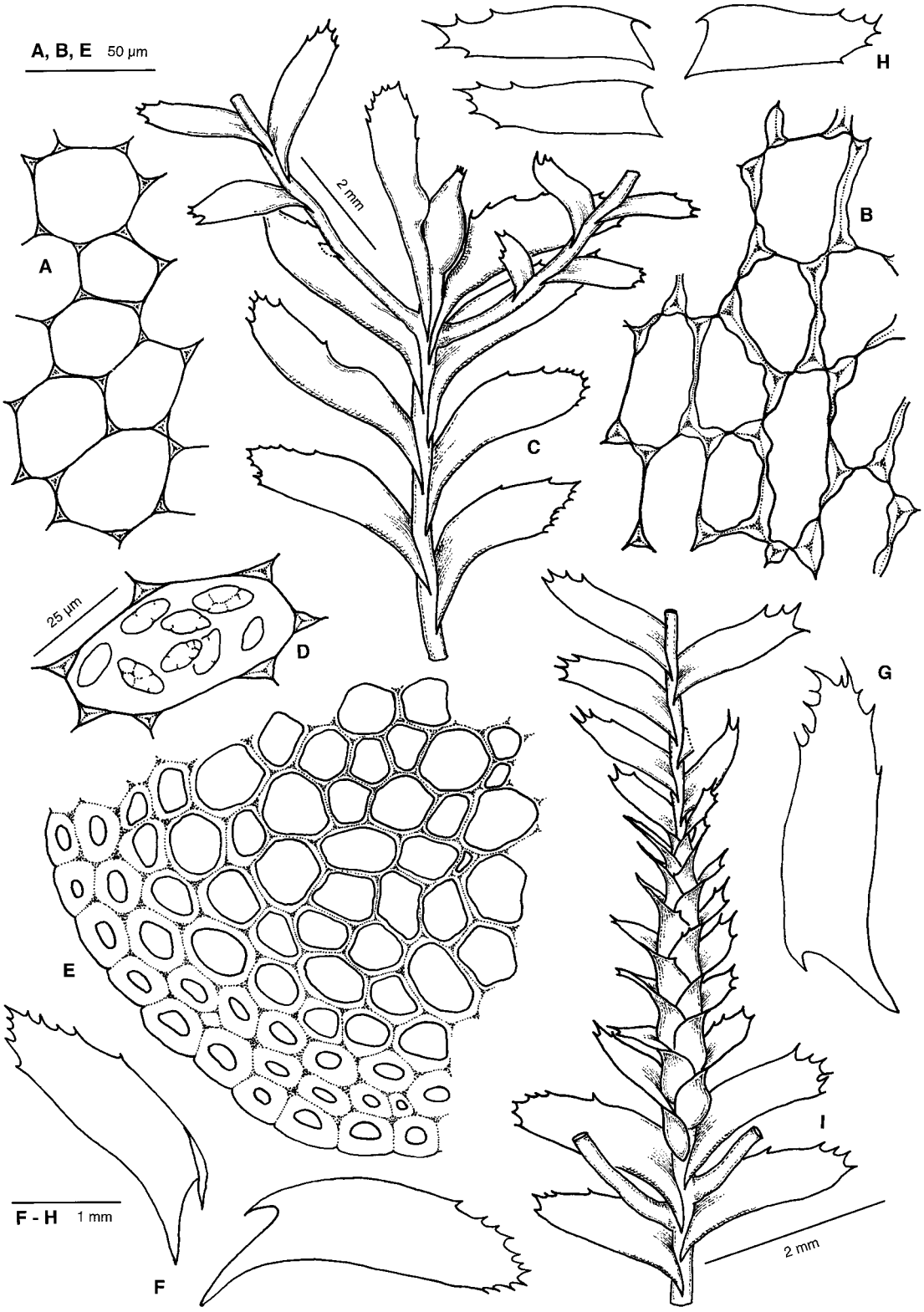

FIGURE 3. *Plagiochila rutilans* Lindenb. var. *rutilans.* — A,B. Cells from center of upper leaf half. — C. Female plant, dorsal view. — D. Leaf cell with oil bodies. — E. Transverse section of stem. — F,G,H. Leaves. — I. Male plant, dorsal view. (A–F from *Heinrichs et al. 4181* [GOET]; G from *Groth 101* [GOET]; H, I from *Heinrichs et al. 4195* [GOET]).

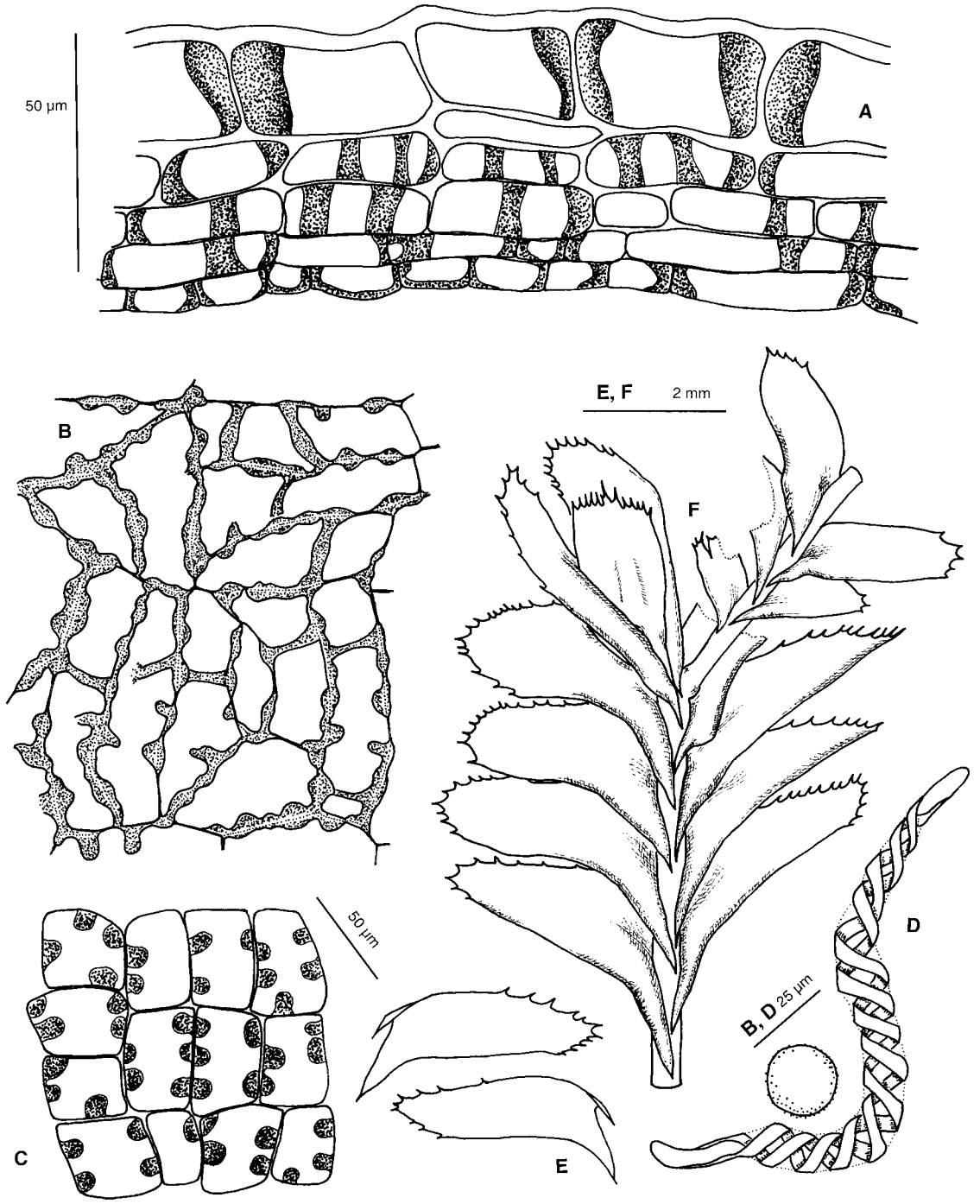

FIGURE 4. *Plagiochila rutilans* Lindenb. var. *rutilans* (A–D) and var. *standleyi* (E–F). — A. Transverse section of capsule wall. — B. Innermost layer of capsule wall, surface view. — C. Capsule wall epidermis, surface view. — D. Spore and elater. — E. Leaves. — F. Part of female plant, dorsal view. (A–D from *Groth 101* [GOET]; E from *Heinrichs et al. 4191* [GOET]; F from lectotype of *P. standleyi* [JE]).

others usually pointing forwards. Teeth 1–4 cells wide at base and (1–)3–7(–9) cells long, at apex occasionally 1(–2) somewhat broader, lobe-like teeth; leaf margin in all with (2–)4–17(–24) teeth. Leaf cell pattern regular to irregular, cells in upper third of leaf 25–55(–63) × 15–40(–46) µm and (0.9–)1.0–1.9(–2.7) times as long as wide, cells in the leaf center 25–75 × 20–40 µm and 1.0–2.5(–2.7) times

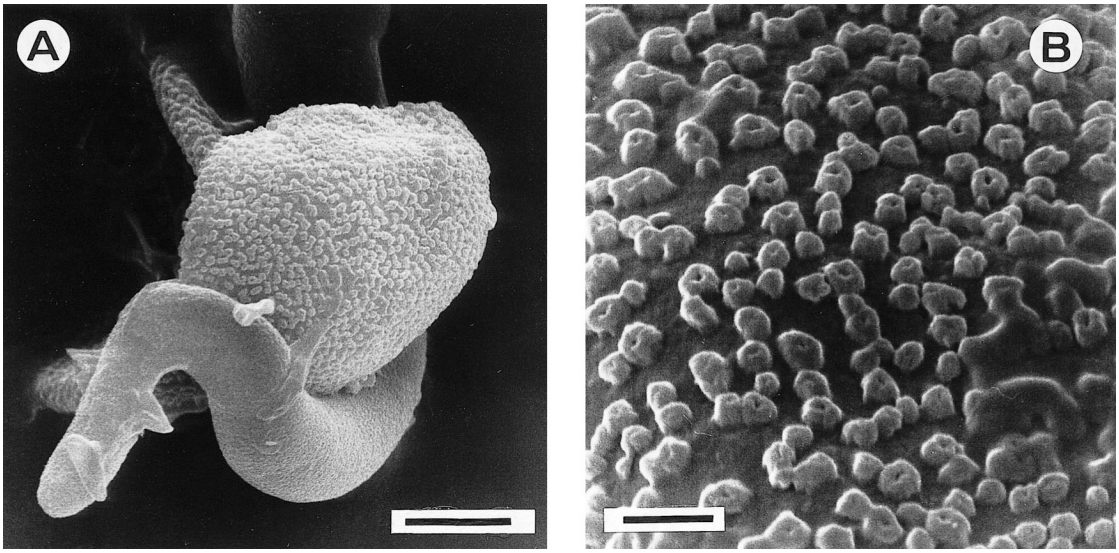

FIGURE 5. *Plagiochila rutilans* var. *rutilans.* — A. Spore and top of elater. — B. Sporoderm, close up. (A,B from Bolivian material, *Groth 101* [GOET]; direct mounting from dry capsule, SEM viewing with Zeiss DSM 960; scales: A = 5 μm, B = 1 μm).

as long as wide, basal leaf cells 25–105 μm × 20–40 μm and 1.0–5.5 times as long as wide; walls thin except those of leaf margin, trigones small to medium sized (occasionally large), triangular to subnodulose, when more strongly developed often subconfluent to confluent on long walls, intermediate thickenings ± frequent on long walls of stronger elongate cells; cuticle smooth. Oil bodies ca 6–10 per median leaf cell, colorless, ellipsoidal to fusiform, homogeneous to indistinctly coarse-segmented, ca 8–13 × 4.0–5.5 μm. Underleaves vestigial, built by several cilia often terminated by slime papillae, ca 80–150 μm broad and 80–450 μm long. Asexual reproduction occasionally by caducous leaves. Male plants as large as female plants. Androecia regularly becoming intercalary, simple, bracts in (4–)5–12(–14) pairs, imbricate, basal ones sometimes remote, opposite ones overlapping on dorsal side of shoots, basal part strongly inflated, built by cells containing somewhat less chlorophyll than those of leaves, occasionally areas present with ± hyaline and weakly inflated cells; distal part of bracts obliquely to horizontally spreading, in basal bracts more elongate and leaflike than in upper bracts (giving the androecia an elongate triangular shape), composed of cells similar to those of leaves, margin with 4–18 triangular to elongate triangular teeth, teeth ± restricted to apex or reaching inflated part of bracts. Antherida 1–2(–3) per bract, globose to broadly ellipsoidal, ca 190–230 μm long and 170–210 μm broad, with a rather short stalk, two cells wide. Gynoecia terminal on main shoots and on branches, innovations frequent, usually 1–2 in number; bracts ± leaflike but dorsal margin strongly recurved and up to 39 marginal teeth present, ± complete margin with teeth or teeth lacking on dorsal margin and/or proximal half of ventral margin. Perianths ± elliptic in dorsal view, elliptic to obdeltoid in lateral view, ca 1.7–2.4 × 1.2–1.7 mm and 1.3–1.5 times as long as wide, covered by bracts or bracts inserted slightly below the perianth, unwinged or dorsal keel with a low, smooth arch; dorsal perianth keel slightly longer than ventral one or both keels of the same length; perianth mouth weakly arched upwards or truncate, densely toothed with elongate triangular teeth, occasionally some additional slender, filiform teeth present, length of teeth variable, up to 14(–20) cells long, terminal cell blunt or acute; cells of perianth similar to leaf cells.

Sporophyte.—Capsules (description from *Groth 101*) short-exserted, exceeding the perianth ca 0.7–1.4 mm, subglobose; valves ca 1.25–1.45 mm long and 0.45–0.65 mm broad, not twisted, median epidermal cells in surface view slightly broader than long to elongate, ca 25–70 × 25–40 μm, walls slightly thickened, with 1–3 large, nodulose, brown thickenings on most long and 1–2 thickenings on many short walls, basal epidermal cells in all more elongate, with nodulose, cone-like and confluent thickenings; hypodermal cells in surface view more elongate, with small brown, ± nodulose thickenings on most walls, thickenings often confluent at their base; basal innermost cells mostly distinctly elongate, median and apical innermost cells shorter, mixed with transversely directed cells, in ± irregular pattern, short walls with few, long walls with many nodulose to cone-like thickenings often confluent at their base and partially coalesced; valves in trans-

FIGURE 6. Distribution of *Plagiochila rutilans* var. *rutilans.*

verse section ca 55–70 μm in diameter, (4–)5–6–stratose, with thickenings in all layers, epidermal cells thicker than inner cells, ca 17–30 μm thick, inner cells ca 6–14 μm thick. Spores 1(–2)–celled, globose, ca 23–28 μm in diameter, verrucate to baculate. Elaters smooth, ca 10–16 μm thick, bispiral, in the middle rarely trispiral, spirals often terminating some distance from the ends of the elater.

Phytochemistry: lipophilic compounds.—Phenolic derivatives; several abundant menthane monoterpenoids; sesquiterpenoids few and in relatively low abundance.

Ecology and distribution.—*Plagiochila rutilans* occurs in the northern and central Andes (southwards to northern Argentina) and in mountainous areas of Central America, the Greater and Lesser Antilles and southeastern Brazil (Fig. 6). The species is confined to humid, evergreen montane forest between 800 and 3,000 m e.g., Andean cloud forests and Central American oak forests. The species grows on soil, rock, and rotten logs as well as epiphytically, often near rivulets.

Plagiochila rutilans is subdivided into two varieties, *P. rutilans* var. *rutilans* and *P. rutilans* var. *standleyi* (for differentation see Table 3):

PLAGIOCHILA RUTILANS Lindenb. var. **STANDLEYI** (Herzog ex Carl) Heinrichs & D.S.Rycroft, *comb. et stat. nov.*

Plagiochila standleyi Herzog ex Carl, Ann. Bryol. 2 (suppl. 2): 80. 1931. TYPE: COSTA RICA. SAN JOSÉ. La Hondura, 1,300–1,700 m, 16.03.1924, *Standley 37881* (lectotype, designated by Herzog (1932: 232), JE [*c. per.*]); COSTA RICA. CARTAGO. Vicinity of Pejivalle, 900 m, 07./08.02.1926, *Standley & Valerio 47057* (paralectotype, JE [*c. per.*]).

Illustrations.—Herzog (1932: fig. 16 [as *P. standleyi*]); this paper: fig. 4 (E & F).

Plagiochila rutilans var. *standleyi* is known from only a few localities in the mountainous areas of Costa Rica, where it grows in similar habitats as var. *rutilans* at elevations between 900 and 1,700 m.

Representative specimens examined.—*P. rutilans* var. *rutilans*: ARGENTINA. FORMOSA. San Hilario, *Goebel s.n.* (G 025233 p.p.). BOLIVIA. COCHABAMBA. Chapare, Tiraque, road Aguirre–El Palmar, Serranía de Callejas, 3,000 m, 24.10.1997, *Heinrichs et al. 4181* (G, GOET, JE, LPB); LA PAZ. Parque Nacional Cotapata, Tunquini, 1,500 m, 24.09.2000, *Groth 101* (GOET, LPB). BRAZIL. MINAS GERAIS. Serra de Itatiaia, Brejo da Lapa, 2,100 m, 04.2000, *Costa & Gradstein 3776* (GOET, RB); RIO DE JANEIRO. Serra de Itatiaia, trail Hotel Simon-Três Picos, 1,400 m, 10.05.2000, *Costa & Gradstein 3868* (GOET, RB). COSTA RICA. CARTAGO. Tapanti, Sendero ''Natural Arboles Caídos'', 1,300 m, *Heinrichs et al. 4195* (GOET, INB); HEREDIA. Cerro de Las Lajas, N of San Isidro, 2,000–2,400 m, 07.03.1926, *Standley & Valerio 51619* (JE); SAN JOSÉ: San Gerardo de Dota, 2,900 m, 14.03.2000, *Holz CR-00-654* (GOET, INB). CUBA. SANTIAGO DE CUBA. Sierra Maestra, Gran Piedra, 1,150 m, 10.11.1978, *Pócs & Reyes 9046/E* (Inoue: *Bryophyta Selecta Exsiccata 566*, FLAS 038871, MO, U). DOMINICAN REPUBLIC. *Eggers s.n.*

TABLE 3. Differentation between *P. rutilans* var. *rutilans* and var *standleyi*

	var. *rutilans*	var. *standleyi*
color of herbarium specimens after moistening	greenish brown or brownish	at least older parts blackish
leaves	mostly remote	often imbricate
dorsal leaf base	hardly to moderately decurrent	moderately to long decurrent
dentition	leaves with up to 12(18) teeth	leaves with up to 17(24) teeth
lipophilic phenolic derivatives	2-methoxy-6-prenyl-hydroquinone and/or derivatives	3-hydroxy-4'-methoxybibenzyl abundant
monoterpenoids	pulegone and/or congeners	0-terpinene and/or ascaridole abundant

(BM). ECUADOR. PICHINCHA. Tinalandia, ca 18 km E of Sto. Domingo de Los Colorados, 830 m, 18.07.1991, *Arts Ec18/036* (GOET). GUATEMALA. ALTA VERAPAZ. (JE); Coban, *v. Türckheim 13* (JE). JAMAICA. *Swartz s.n.* (C, S hb Swartz 404). MEXICO. Cafétal, *Karsten s.n.* (BM). PANAMA. CHIRIQUI. Fortuna Hornitos, ca 1,000 m, 20.5.1988, *Salazar et al. 6201p.p.* (U). PUERTO RICO. *Sintenis s.n.* (G 025866). VENEZUELA. AMAZONAS. Atabapo, Cerro Marahuaca, 2,480–2,580 m, 1982, *Guariglia et al. 1613p.p.* (NY); NUEVA ESPARTA. La Sierra, *Bermúdez NN-0017 p.p.* (FLAS 028874). WINDWARD ISLANDS. GUADELOUPE. Basse Terre, between Saint Claude and Mulets, *De Sloover 33821* (FLAS 039928); ST. VINCENT. *Smith 1400 p.p.* (FH).

P. rutilans var. *standleyi*: COSTA RICA. SAN JOSÉ. Parque Nacional Braullio Carillo, Zurqui, Sendero ''Los Jilgueros'', Río Zurqui, 1,400 m, *Heinrichs et al. 4191, 4302* (GOET, INB).

Distinction and affinities.—*Plagiochila rutilans* is characterized by oblong-rectangular, remote to moderately imbricate leaves, exclusively lateral-intercalary branching, in surface view elongate triangular androecia with opposite bracts overlapping on the dorsal side of the stem and unfertilized perianths covered by bracts. Fresh materials and recent herbarium specimens stand out because of the peppermint odor, best noticed in moistened plants.

Plagiochila rutilans is highly polymorphic regarding leaf cell pattern and includes forms with ± isodiametric upper leaf cells as well as forms with distinctly elongate ones. Trigones of leaf cells may be small and triangular to large and subnodulose.

Most of the synonyms of *P. rutilans* proposed by Stephani (1901–1906) and the infraspecific taxa belong to other species (see EXCLUDENDA). Because of this, the herbarium materials of *P. rutilans* are very heterogeneous. Only a minority of *P. rutilans* specimens was identified correctly. *Plagiochila rutilans* may be confused with *P. aerea* Taylor (Grolle & Heinrichs 1999), but the latter may be distinguished by the long-spinosely toothed leaves and the more trabeculate leaf cell pattern. *Plagiochila rutilans* shares its leaf shape with several members of *Plagiochila* sect. *Parallelae* Carl (e.g., *P. crispabilis* Lindenb., *P. patentissima* Lindenb.); however, the frequent terminal branching of these species separates them easily from *P. rutilans.*

Chemically, *P. rutilans* is characterized by aromatic (i.e., benzenoid) compounds (prenylated hydroquinone derivatives in var. *rutilans* and a bibenzyl derivative in var. *standleyi*) as well as considerable amounts of a large number of menthane monoterpenoids. We have not conducted extensive chemical studies of the taxa with which *P. rutilans* has been confused, but we have found distinct differences that are worth recording. *Plagiochila gymnocalycina* (COSTA RICA. San Vito, 1998, *Arts CR 08/37,* hb. Heinrichs) was notable for the presence at least 1% w/w of 4-hydroxy-3′-methoxybibenzyl (an isomer of **6,** well-known in liverworts, including Plagiochilae); β-phellandrene was also present. *Plagiochila simplex* (COSTA RICA. Limón, 1998, *Arts CR 17/08,* hb. Heinrichs) contained minor amounts of 4-hydroxy-3′-methoxybibenzyl and β-phellandrene, but was distinguished by the presence of a group of calamenene derivatives, sesquiterpenoids well-known in liverworts. *Plagiochila aerea* (COSTA RICA. Tapanti, 1999, *Heinrichs et al. AHH 0283 p.p.,* GOET) gave an NMR fingerprint remarkably similar to that of the hyperoceanic European endemic *P. atlantica* F. Rose, being dominated by the 2,3-secoaromadendrane plagiochiline C but also showing a minor amount of atlanticol, an epoxybicyclogermacrenol derivative that was unique to *P. atlantica* (Rycroft & Cole 1998). An extensive chemical investigation of *P. aerea* is now in progress (by H. Anton).

PHYTOCHEMICAL COMMENTARY

Of the compounds in Table 2, 1-octen-3-yl acetate (**21**), peculiaroxide (**22**), bicyclogermacrene (**23**), (and/or spathulenol, **24**), and fusicoccadiene (**25**) were present in most of the extracts and are found frequently in Plagiochilae. The more distinctive compounds observed are considered below.

P. rutilans var. *rutilans.*—PHENOLS. We have observed four related phenolic derivatives, **2**–**5**. Compound **2** is a major feature of the NMR fingerprints of the most recent specimens, (ii)–(vi). Hydroquinones are readily oxidized to the corresponding quinones, and 2-methoxy-6-prenyl-1,4-benzoquinone (**3**) was observed as a minor component of all the extracts, even when **2** was not detected. There was very little of compound **2** remaining in specimen (ix), the voucher from the original work by Huneck et al. (1984), but rather more of the quinone **3.** The other two compounds, **4** and **5,** are an isomeric pair of methylated derivatives of **2.** Compound **4** is a minor feature of the NMR fingerprints of the recent specimens (i) and (iii)–(v), and was detected in (ii), (vi), and (x) using GC-MS, whereas compound **5** is present only in (i), but as a major feature. 3-Hydroxy-4′-methoxybibenzyl (**6**) was detected in all the specimens, except (ii) and (vi), but at levels so low that it is noted here only because of the dominance of compound **6** in var. *standleyi.*

MONOTERPENOIDS. The peppermint-like odor of the liverwort is caused by several menthane monoterpenoids, the most abundant being pulegone (**7**). The amounts present can be large: for specimen (iii), the amount of pulegone in the $CDCl_3$ extract represents 3% w/w of the dry liverwort (even though the extraction efficiency is only ca 50%). Other significant monoterpenoids are terpinolene (**9**), menthone (**10**), isomenthone (**11**), limonene

(**12**), and β-phellandrene (**13**), with *p*-cymene (**14**), 8-*p*-cymenol (**15**), *p*-isopropenyltoluene (**16**), sabinene (**17**), β-pinene (**18**), and α-terpinene (**19**) also generally present. The absolute configuration of the monoterpenoids in the extracts has not been determined.

Specimen (vi) differs significantly from the others in that pulegone was absent, but in its place was the related new lactone **8** (Rycroft & Cole 2001).

Monoterpenoids are relatively volatile, but pulegone could still be detected in the three oldest specimens, (ix)–(xi). 8-*p*-Cymenol is more noticeable in the older specimens than the recent and it is possible that the levels of the more oxidized compounds increase over time.

Many monoterpenoids have been reported from liverworts (Mues 2000), including several Plagiochilae. Their contribution to the aroma of some Plagiochilae has been described by Asakawa (1990) and the potential significance of monoterpenoids in identification of particular Plagiochilae has been noted both implicitly (Paton 1999) and explicitly (Rycroft et al. 1999). However they have not been used as characters for chemotype classification in *Plagiochila* (Asakawa 1995) or to support the establishment of taxonomic entities. Few liverworts smell of peppermint: pulegone has been reported from *Radula boryana* (Web.) Nees, but menthone and isomenthone have not been found previously in any liverwort.

P. rutilans var. *standleyi*.—The overwhelming feature of the NMR fingerprints of specimens (vii) and (viii) is 3-hydroxy-4′-methoxybibenzyl (**6**), at a concentration translating to 5% w/w extracted from the liverwort. Compound **6** was unknown as a natural product until it was reported recently from members of *Plagiochila* sect. *Glaucescentes* (Heinrichs et al. 2000). Compounds **2**–**5** are absent. These specimens were also notable for a peppermint-like odor, but in this case pulegone (**7**) and menthone (**10**) were absent. The monoterpenoids found were limonene (**12**), β-phellandrene (**13**), α-terpinene (**19**), and a small amount of *p*-cymene (**14**); the most distinctive one however was ascaridole (**20**), the endoperoxide derived from α-terpinene (**19**), observed at a level of ca 0.5% w/w of the dry liverwort.

EXCLUDENDA

1. PLAGIOCHILA GYMNOCALYCINA (Lehmann & Lindenb.) Mont. in D'Orbigny, Voy. Amer. Mér. 7, Bot. (2): 81. 1839.

Jungermannia gymnocalycina Lehmann & Lindenb. in Lehmann, Nov. Stirp. Pug. 5: 28. 1833. TYPE: BRAZIL. RIO DE JANEIRO, Nova Friburgo, *Beyrich s.n.* (syntypes: W hb. Lindenb. 565 [*c. per.*], JE [*c. per.*]).

Plagiochila gymnocalycina (Lindenberg 1839–1844: fig. 10; Heinrichs et al. 1998: fig. 14) differs from *P. rutilans* by oblong to oblong-ovate or elongate triangular, partly transversely directed leaves (leaves of *P. rutilans* oblong rectangular and never transversely directed), ''free'' perianths with bracts at some distance below the perianth (perianths of *P. rutilans* usually covered by bracts), and opposite male bracts usually not overlapping on the dorsal side of the stem (opposite male bracts of *P. rutilans* always overlapping). Thus, two sharply distinct species are at hand. The treatment of *P. gymnocalycina* as conspecific with *P. rutilans* by Stephani (1901–1906) is certainly erroneous.

2. PLAGIOCHILA PORTORICENSIS Hampe & Gottsche, Linnaea 25: 340. 1853 (''1852''). TYPE: PUERTO RICO. *Schwanecke s.n.* (lectotype: BM 000674172 [*c. per.* juv.]; isolectotype: BM 000674171 [*c. per.*juv.]). = *Plagiochila simplex* (Sw.) Lindenb.

The type material consists of plants with free perianths not covered by bracts and rather shortly toothed, oblong to oblong-ovate leaves, agreeing well with *P. simplex* (Sw.) Lindenb. (Heinrichs et al. 1998). The placement of *P. portoricensis* in the synonymy of *P. rutilans* by Stephani (1901–1906) is untenable.

3. PLAGIOCHILA RUTILANS Lindenb. var. ß **LAXA** Lindenb., Spec. Hepat. (fasc. 2–4): 47. 1840.

Plagiochila lambertina Gottsche, Ann. Sci. Nat., Bot. (ser. 4) 8: 329. 1857. TYPE: JAMAICA. *Lambert s.n.* (ex hb. Hooker) (holotype: W hb. Lindenb. 581 [ster.]). = *Plagiochila gymnocalycina* (Lehmann & Lindenb.) Mont.

Plagiochila rutilans var. *laxa* possesses oblong-ovate leaves that are partly directed transversely to the stem with the ventral part curved in the direction of the base of the plant. Thus, the var. *laxa* is clearly different from *P. rutilans s. str*. Leaf areolation and dentition indicate an affiliation to *P. gymnocalycina.*

4. PLAGIOCHILA RUTILANS Lindenb. var. ß **LIEBMANNIANA** Gottsche, Mexik. Leverm.: 40. 1863.

Plagiochila jovoensis Steph., Spec. Hep. 2: 224, 1902. TYPE: MEXICO. Hacienda de Jovo, *Liebmann 559a* (lectotype, here designated: W hb. Lindenb. 582 [*c. per.juv.*]). = *Plagiochila crispabilis* Lindenb., Spec. Hepat. (fasc. 1): 15. 1839.

Plagiochila rutilans var. *liebmanniana* differs from true *P. rutilans* by frequent terminal branching giving the plants a more or less pseudodichotomous habit. The oblong-rectangular leaves with recurved dorsal and ventral margins indicate a synonymy with *P. crispabilis*, a species originally de-

scribed from southeastern Brazil (Lindenberg 1839–1844).

5. PLAGIOCHILA RUTILANS Lindenb. var. **AEQUATORIALIS** Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 454, 465. 1885. Syn. of *Plagiochila aerea* Taylor *fide* Grolle & Heinrichs (1999).

6. PLAGIOCHILA RUTILANS var. **ANGUSTIFOLIA** Herzog, Hedwigia 72: 204. 1932. TYPE: BRAZIL. MINAS GERAIS. Serra do Gongo Soco e Agua Limpa, *Hoehne 155* (holotype, JE [*c. per.*, male]). = *Plagiochila gymnocalycina* (Lehmann & Lindenb.) Mont.

The type specimen of *P. rutilans* var. *angustifolia* contains female plants with cylindric, free perianths and male plants with stems plainly visible on the dorsal side of the androecia; thus it certainly belongs to *P. gymnocalycina* rather than to *P. rutilans.*

7. PLAGIOCHILA RUTILANS fo. **FOLIICOLA** Herzog, Feddes Repert. Spec. Nov. Regni Veg. 57: 163. 1955. TYPE: COLOMBIA. CAUCA. ''La Gallera'', Micay Valley, 1,400–1,500 m, *Killip 7780 p.p.* (JE).

The type of *P. rutilans* fo. *foliicola* was separated from the holotype of *P. elegantula* Herzog (JE!). Plants of *P. rutilans* fo. *foliicola* could not be traced either in the type of *P. elegantula* or in a separate specimen, and are thus probably part of the unrefurbished collection of Herzog's slide preparations. The description (''periantho longe emerso'') indicates that fo. *foliicola* has to be excluded from *P. rutilans.* We also disagree with the reassessment of *P. elegantula* as a possible variety of *P. rutilans* (Herzog 1955: 162). The type contains plants with a rough cuticle and rhizoids on the dorsal side of the stems, indicating that *P. elegantula* Herzog is conspecific with *P. stricta* Lindenb.

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