

Notes on the Plagiochilaceae, IX. A Review of the Genus
Plagiochila (DUM.) DUM. (Hepaticae) in
the Galapagos Islands*

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As already listed by WEBER (1966), eleven species of *Plagiochila* had been reported from the Galapagos Islands since ÅNGSTROM (1873). Recently, the senior author (INOUE, 1977) described four species new to science from these islands, based on the collections made by the junior author during the 1976 expedition to the Galapagos Islands led by Dr. W. A. WEBER, University of Colorado Museum (cf. WEBER *et al.*, 1977).

In the present paper we are reviewing all the species ever recorded from the islands, including the new ones. Notes on taxonomic relationships to mainland South American species are also provided. The main specimens studied were those collected during the 1976 expedition and those gathered from vegetation plots by Dr. H. H. Vander WERFF in the course of his survey of the vegetation of the islands in 1974-75 (Vander WERFF, 1978). Additional specimens were kindly provided by Dr. W. A. WEBER. We have also seen the types or vouchers for the previous records, which were received on loan from the Conservatoire et Jardin Botaniques, Geneva (G), the California Academy of Science, San Francisco (CAS), Washington University at Seattle (WTU) and the British Museum, London (BM).

We are very grateful to the curators of the herbaria listed above for their generosity in sending these specimens. The junior author is indebted to the Estación Biológica Charles Darwin (Santa Cruz) for field-work assistance and the Netherlands Foundation for the advance of Tropical Research (WOTRO) for financial support. The present work was completed at the National Science Museum and we acknowledge with thanks the support given by the Japan Society of Promotion of Science. The senior author's contributions were made possible by a Grant in Aid of Scientific Research (No. 248016) from the Ministry of Education, Science and Culture, Japan.

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Key to species

1. Surface of leaf-cells distinctly roughened with verrucose cuticle; (plants small, filiform; leaves oblong, with only two prominent teeth at apex).....(1) *P. scabrifolia* INOUE
1. Surface of leaf-cells completely smooth.....2
 2. Branches rather frequently present, mostly of the terminal and *Frullania*-type.....3
 3. Leaves usually more than 2 times as long as wide, frequently linear-oblong or sometimes oblong, often caducous; common above 400 m.s.m., especially in the pampa region.....(2) *P. bursata* (DESV.) LINDENBG.
 3. Leaves usually less than 2 times as long as wide, oblong-ovate or oblong-rectangular, never linear-oblong, always persistent.....4
 4. Leaves soft-textured; leaf-cells usually lacking trigones; teeth on leaf-margin usually ciliar, with elongated terminal cells of 3.2–3.7 times as long as wide; very rare.....(3) *P. galapagona* INOUE
 4. Leaves rigid; leaf-cells usually with distinct, large, nodulose trigones; teeth on leaf-margin small, triangular, not ciliar, with terminal cells of 2.8–3.2 times as long as wide; very common from 150 m.s.m. upwards, in shaded places.....(4) *P. guilleminiana* MONT.
 2. Branches quite few, if present exclusively lateral-intercalary.....5
 5. Leaves fragile, dropping off from middle or basal portion.....6
 6. Leaves closely imbricate, ovate, long decurrent dorsally and ventrally; stem surface almost completely hidden by leaves; leaves fragmenting from middle portion; in moist places.....(5) *P. gradsteinii* INOUE
 6. Leaves remote, oblong-rectangular, hardly decurrent dorsally and ventrally; stem surface widely exposed; leaves dropping off from very base (thus shoots often quite denuded); on rock in wet pampa region.....(6) *P. inouei* GROLLE
 5. Leaves always persistent.....7
 7. Leaves soft-textured, oblong, apex narrowly rounded; teeth on leaf-margin small, short ciliar, usually restricted to apical margin (rarely extending to middle of ventral margin); basal leaf-cells not forming vitta-area.....(7) *P. subplana* LINDENBG.
 7. Leaves rigid, oblong-ovate, apex bilobed to 1/3–1/2 the length; teeth on leaf-margin large, broad-based, triangularly acuminate, present on whole ventral margin; basal leaf-cells forming vitta-area.....(8) *P. spinifera* ÅNGSTR.

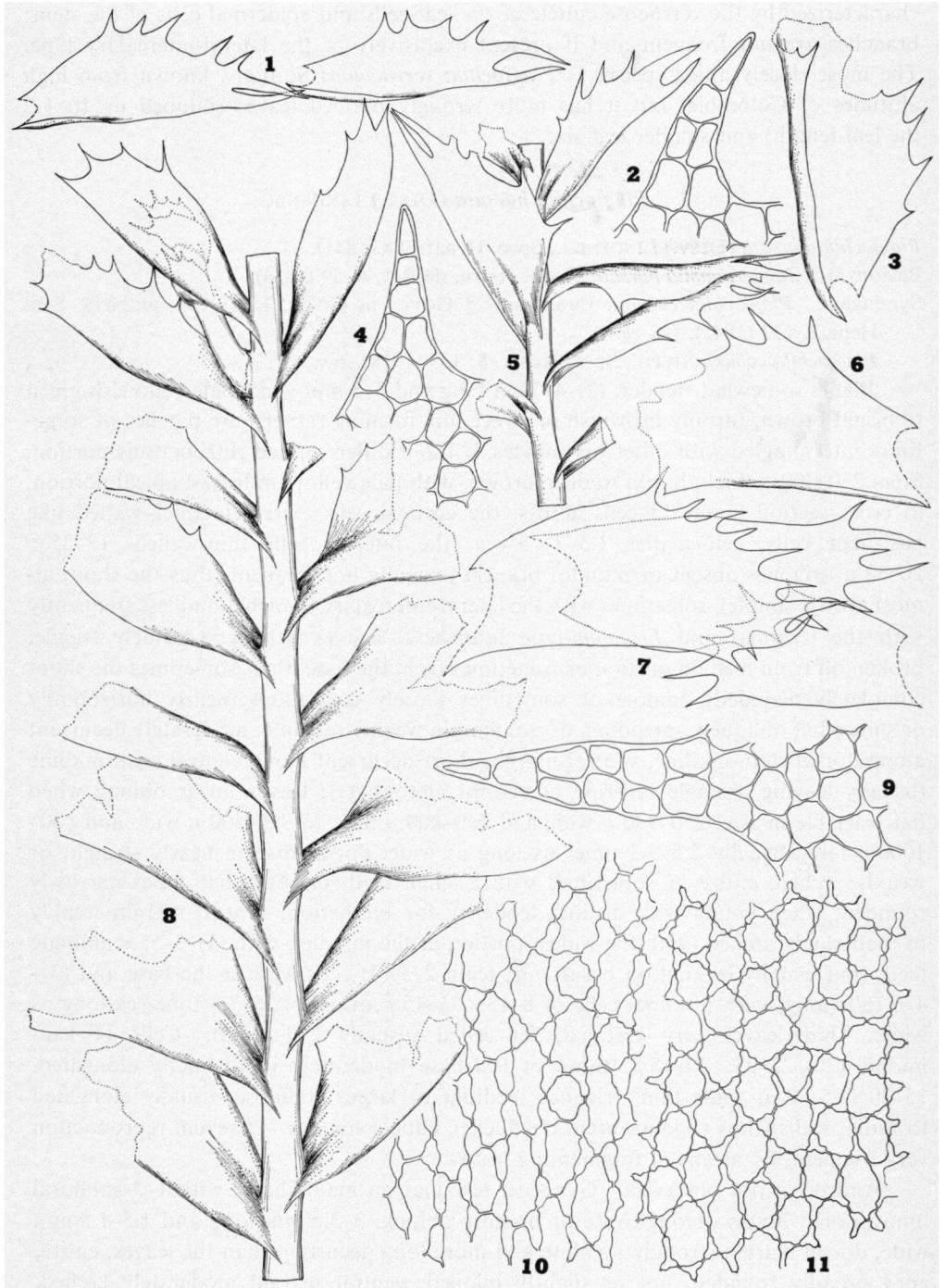
1. *Plagiochila scabrifolia* INOUE

Plagiochila scabrifolia INOUE, Bull. Nat. Sci. Mus. ser. B, 3: 53 (1977).

Type. Galapagos: *Isabela*; Vulcan Cerro Azul, S.-exposed slope in wet pampa, in rock-crevices under overhanging ferns, in deep shade, alt. 750 m., GRADSTEIN and SIPMAN H423b (TNS; isotypes in U, COLO).

Endemic and thus far only known from the type locality. This species is well

Fig. 1. *Plagiochila bursata* (DESV.) LINDENBG. 1, 3, 6, 7. Leaves, $\times 22$. 2, 4, 9. Teeth from ventral leaf-margin, $\times 230$. 5. Part of shoot, ventral view, $\times 22$. 8. Part of shoot, dorsal view, $\times 22$. 10. Cells from leaf-base, $\times 330$. 11. Cells from leaf-middle, $\times 230$. All figs. based on SIPMAN H371.



characterized by the verrucose cuticle of the leaf-cells and epidermal cells of the stem; branches are not frequent and if present exclusively of the lateral-intercalary type. The most closely allied species is *Plagiochila verruculosa* SCHUST., known from high altitudes of Colombia, but it has more strongly bilobed leaves (bilobed up to 1/2 the leaf-length) and smaller leaf-size.

2. *Plagiochila bursata* (DESV.) LINDENBG.

Plagiochila bursata (DESV.) LINDENBG., Spec. Hepat.: 88 (1841).

Basionym: *Jungermannia bursata* DESV., Journ. de Bot. 4: 59 (1824).

Synonyms: *Plagiochila cuneata* LINDENBG. et GOTT., in GOTT., LINDENBG. et NEES, Syn. Hepat.: 632 (1847), *syn. nov.*

Plagiochila cobana STEPH., Spec. Hepat. 6: 138 (1918), *syn. nov.*

Plants somewhat slender, (2)–4–7 cm long and 3–5 mm wide, pale yellowish green to bright brown, turning brownish in direct sun, forming rather pure patches or sometimes intermingled with other bryophytes, without differentiated rhizomatous portion. Stem 270–300 μ thick, bright to deep brown, with pale yellowish brown apical portion, in cross section about 13 cells across, the cortical cells extremely thick-walled like bast-fiber cells, cell-cavities 1.5–3 \times 5–8 μ , the interior cells thin-walled, 13–25 \times 20–33 μ , trigones absent or minute; branches usually not frequent (thus the shoot almost always simple), sometimes with the lateral-intercalary branches and less frequently with the terminal and *Frullania*-type branches. Leaves usually extremely fragile, broken off from median portion or sometimes from the base (thus, sometimes the shoot completely denuded), remote or sometimes loosely contiguous, nearly horizontally or somewhat obliquely spreading, dorsal margin weakly revolute, moderately decurrent along dorsal stem-midline, ventral margin short decurrent along ventral stem-midline (usually leaving a single cell-row of ventral merophyte); leaves linear oblong when flat, variable in size, 250–330 μ wide and 550–800 μ long to 320–400 μ wide and 800–1000 μ long, usually 2.5–3.3 times as long as wide, dorsal margin nearly straight or weakly arched, entire or sometimes with a small teeth on distal half, apex narrowly rounded, when young with distinct tendency for bilobation, ventral margin weakly to moderately arched (with the widest portion at the middle), with (1)–3–5, acuminate teeth (but usually lacking on basal 1/3); teeth 2–3–(4) cells wide at the base and (3)–4–6 cells long, with terminal cells of 8–13 \times 33–45 μ , usually 2.5–3.8 times as long as wide. Underleaves very vestigial, few-celled (usually 2–3-celled). Cells of leaf-middle (20)–25–33 \times 30–45 μ , those of leaf-base moderately to distinctly elongated, 15–30 \times 55–80 μ , walls thin, trigones medium to large, nodulose, usually elongated to radial walls (thus trigones often confluent), cuticle smooth. Asexual reproduction very frequent, by means of fragmenting leaves.

Androecia not observed. Gynoecia terminal on main shoot, with 1–3 subfloral innovations; bracts oblong-ovate or broadly oblong, 3–3.5 mm long and 1.5–1.8 mm wide, dorsal margin strongly revolute and more long decurrent than the leaves, entire, apex broadly rounded, not or slightly bilobed, ventral margin moderately arched,

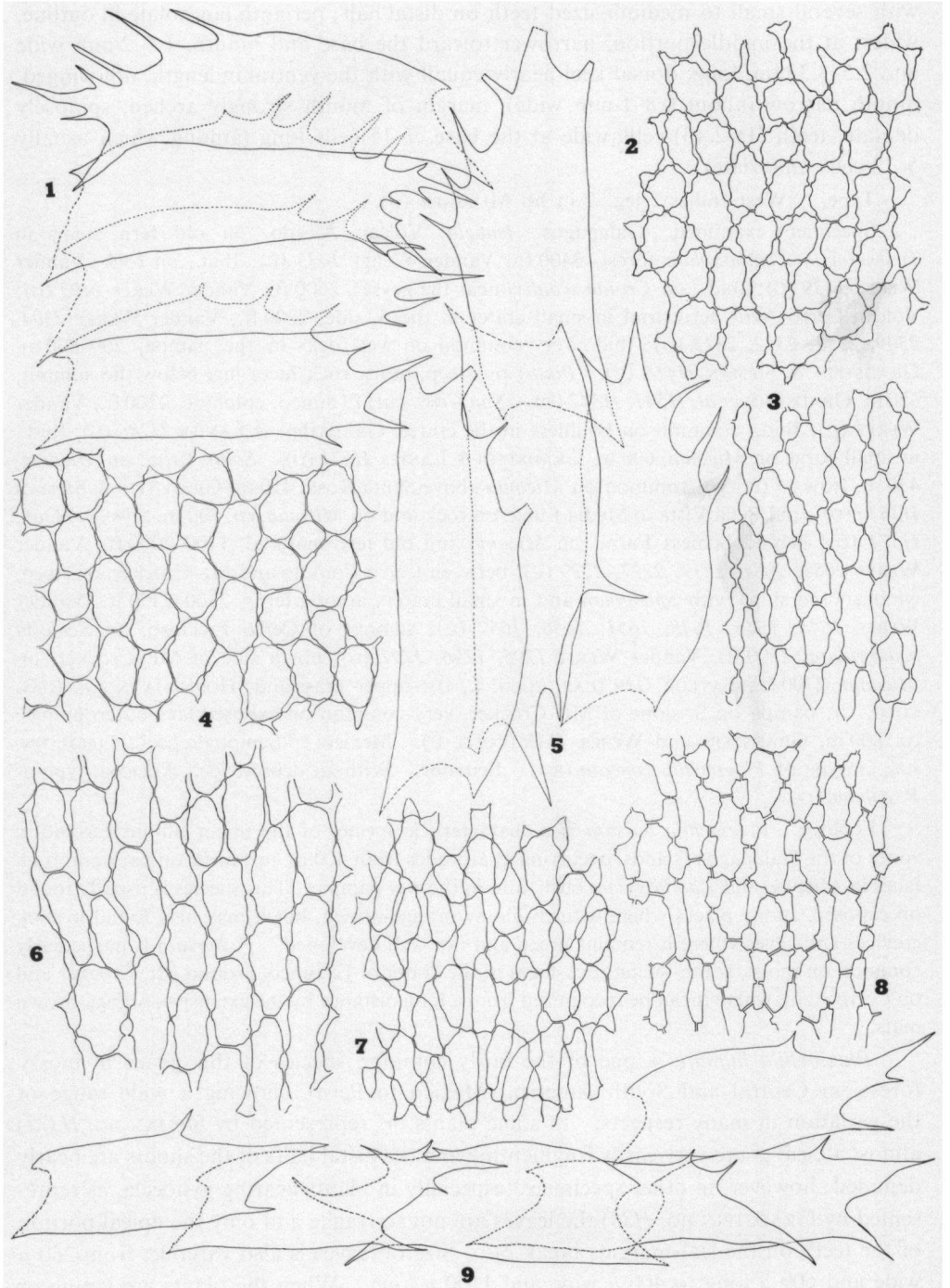
with several small to medium-sized teeth on distal half; perianth lanceolate in outline, widest at the middle portion, narrower toward the base and mouth, 1.5–2 mm wide and 2.5–3.3 mm, long, dorsal keel nearly equal with the ventral in length, not winged, mouth narrow (about 0.8–1 mm wide), margin of mouth strongly arched, spinosely dentate, teeth (1)–2–(3) cells wide at the base, 7–15 cells long (among which usually 5–12 cells uniseriate).

Type. "West Indies", leg. ? in hb MEISSNER (G).

Specimens examined. Galapagos. *Isabela*: Volcan Alcedo, on old fern stems in *Tournefortia-Zanthoxylum* forest, 3400 ft., Vander WERFF 1433 (U); Ibid., on rock, Vander WERFF 1439 (U); Ibid., on *Croton scouleri* near the geyser, 2600 ft., Vander WERFF 1493 (U); Volcan Cerro Azul, terrestrial in small crater at the S. side, 2200 ft., Vander WERFF 2304, 2309, 2311, 2312, 2313 (U); Ibid., very common on wet rocks in the pampa, 700–800 m, GRADSTEIN & SIPMAN H416 (U). *Pinta*: on steep, moist rock faces just below the summit, 650 m, GRADSTEIN *et al.* H541, H542 (U). *San Cristobal*: El Junco, epiphyte, 2200 ft., Vander WERFF (U); Ibid., common on boulders in the crater, GRADSTEIN & LANIER H286 (U); Ibid., in small gorge on *Miconia*, 600 m, GRADSTEIN & LANIER H271 (U). *Santa Cruz*: on *Miconia*, 430 m, Itow 37 (COLO); common on *Miconia* above Santa Rosa, 450 m, GRADSTEIN & SIPMAN H363a (U); trail Bella Vista to Media Luna, on rock and on *Miconia*, ca. 500 m, SIPMAN H368, H371 (U); behind Schiess Farm, on *Miconia* and old fern material, 1700–2000 ft., Vander WERFF 2083, 2081, 2217, 2227, 2229 (U); between Cerro Camote and Mt. Crocker, on steep, windexposed slope with *Sphagnum* and in small craters among ferns, 2100–2350 ft., Vander WERFF 1645, 1646, 1648, 1651, 1656, 1657 (U); summit of Cerro Precioso, on *Scalesia pedunculata*, 2500 ft., Vander WERFF 1795, 1796, 1797 (U); north side of Mt. Crocker, on *Miconia*, 2700 ft., TAYLOR G29 (CAS, COLO, K, U); upper grassland, HORNEMANN *s.n.* (CAS, COLO, U); pampa on S. slope of Mt. Crocker, very common on exposed lava outcroppings, ca. 800 m, GRADSTEIN and WEBER H36 (COLO, U). Mexico. "Sempoaltepec", LIEBMANN, *s.n.*, isotype of *Plagiochila cuneata* (BM). Ecuador. Without definite loc., ALLIONI, type of *P. cobana* (G).

Ecology. *Plagiochila bursata* is a characteristic species of the upper humid vegetation zones of the Galapagos Islands, occurring at altitudes from 400 m. upwards, on bark and rock faces in *Miconia* and *Zanthoxylum* bush, and in the wet pampa. This species is usually found on exposed, sunny places where it turns glossy orange-brown, but it may also be found in rock crevices and caves where it remains green and not well developed. *P. bursata* is particularly common on moist, south-facing rock-faces in the crater of El Junco, around Mt. Crocker and on Cerro Azul, where it can be recognized from a long distance by the extensive, orange-brown mats.

Plagiochila bursata is one of the fairly common species of this genus in mossy forests in Central and South America (Mexico to Peru), showing a wide range of the variation in many respects. In some plants (as represented by SIPMAN no. H371) almost all leaves are very easily fragmenting and the distal halves of the shoots are nearly denuded; however, in other specimens (especially in plants bearing gynoeceia, as represented by GRADSTEIN no. H36) the leaves are not so fragile and only the apical portion of the teeth on the leaf-margins break off. Size of leaves is also variable, from 260 μ wide and 600 μ long to 400 μ wide and 1100 μ long. When the plants are young or



not well developed, the young leaves are small and rather soft-textured, with distinctly bilobed apex and additional 1–(2) large teeth on the ventral margin; such a weak phenotype of this species is completely identical with the type specimen of *P. cuneata* LINDENBG. (including var. *loriloba* HERZ. = *P. loriloba* HERZ. *nom. nud.*) and *P. bicuspidata* GOTT. However, in mainland South America, when maximally developed under favorable condition, the plants are more rigid, being as large as 6 mm wide and 10 cm long, and the leaves are hardly fragmenting (especially when they have gynoecia).

Among the specimens from the Galapagos Islands cited above, we found only two specimens with gynoecia while no male plants were observed. In mainland South America, male plants were rather frequently found; they have more frequent terminal branches together with frequent lateral-intercalary branches; the androecia are on branches (of both lateral-intercalary and terminal types) and the bracts are in 4–6–(8) pairs.

3. *Plagiochila galapagona* INOUE

Plagiochila galapagona INOUE, Bull. Nat. Sci. Mus. ser. B, 3: 50 (1977).

Type. Calapagos: *Santa Cruz*; spring above Santa Rosa, on wet soil, 450 m. s.m GRADSTEIN H364 (TNS; isotype in U).

Endemic and only known from the type locality. This species is very close to *Plagiochila subplana* but sharply different in having the terminal, *Frullania*-type branches and more ciliar teeth of leaves, which are not restricted to the apical margin but are present on almost the whole ventral margin.

4. *Plagiochila guilleminiana* MONT. in LINDENBG.

Plagiochila guilleminiana MONT. in LINDENBG., Spec. Hepat.: 152 (1844).

Synonyms: *Plagiochila andersonii* ÅNGSTR., Kongl. Vet.-Akad. Försh. Stockholm 30: 114 (1873), *syn. nov.*

Plagiochila subsimplex STEPH., Spec. Hepat. 2: 233 (1902), *syn. nov.*

Plants somewhat robust, (3)–4–8 cm long and 5–6 mm wide, yellowish green to pale brownish, or sometimes bright brown, forming compact patches on substrata, usually with differentiated rhizomatous portion. Stem deep brown at middle to basal portion, bright to pale brown in upper portion, about 450 μ thick, in cross section about 23 cells across, the cortical cells in 4–5 layers, very thick-walled like bast-fiber cells, cell-cavities 3–5 \times 8–13 μ , the interior cells 15–25 \times 20–33 μ , moderately thick-walled, trigones distinct, nodulose; branches moderate in number, of the terminal and *Frullania*-type and less frequently of the lateral-intercalary type, branches always as vigorous as the main shoots. Leaves rigid, persistent, approximate or closely

Fig. 2. *Plagiochila bursata* (DESV.) LINDENBG. 1, 5, 9. Leaves, $\times 22$. 2, 4, 7. Cells from leaf-middle, $\times 230$. 3, 6, 8. Cells from leaf-base, $\times 230$. Figs. 1, 4, 6 based on GRADSTEIN and SIPMAN H416, figs. 2, 3, 5 based on GRADSTEIN and LANIER H271, and others on GRADSTEIN *et al.* H542.

imbricate, nearly horizontally or obliquely spreading, dorsal margin moderately (or sometimes strongly) revolute and rather narrowly recurved, long decurrent along dorsal stem-midline (covering more than half of dorsal stem-surface), ventral margin moderately to closely appressed to the opposite leaf-bases, forming weak (or sometimes distinct) keel on ventral side of shoot, moderately to long decurrent along ventral stem-midline (usually leaving ventral merophyte of 2–3 cells wide); leaves when flat ovate oblong, 1.5–2.5 mm wide and 2.5–3.4 mm long, 1.3–1.6 times as long as wide, dorsal margin nearly straight to weakly arched, entire, apex broadly rounded or narrowly truncate or rarely subobtusate, with 3–5, small triangular teeth, ventral margin nearly straight from distinctly dilated basal margin, sometimes weakly undulate (especially on middle to basal portion), with (1)–3–5, small teeth (but rarely entire), terminal cells of teeth 8–12 × 25–35 μ and 2.8–3.2 times as long as wide. Leaf-cells 17–25 × 25–35 μ at the middle, 20–25 × 35–50 μ at the base, cuticle smooth, thin-walled, trigones large, nodulose or triangularly acute, sometimes radially elongated and confluent. Underleaves usually small, oblong, 2–4 cells wide and 3–5 cells long. Asexual reproduction sometimes frequent, by means of numerous propagula on ventral surface of leaves. Gynoecea and androecea not observed.

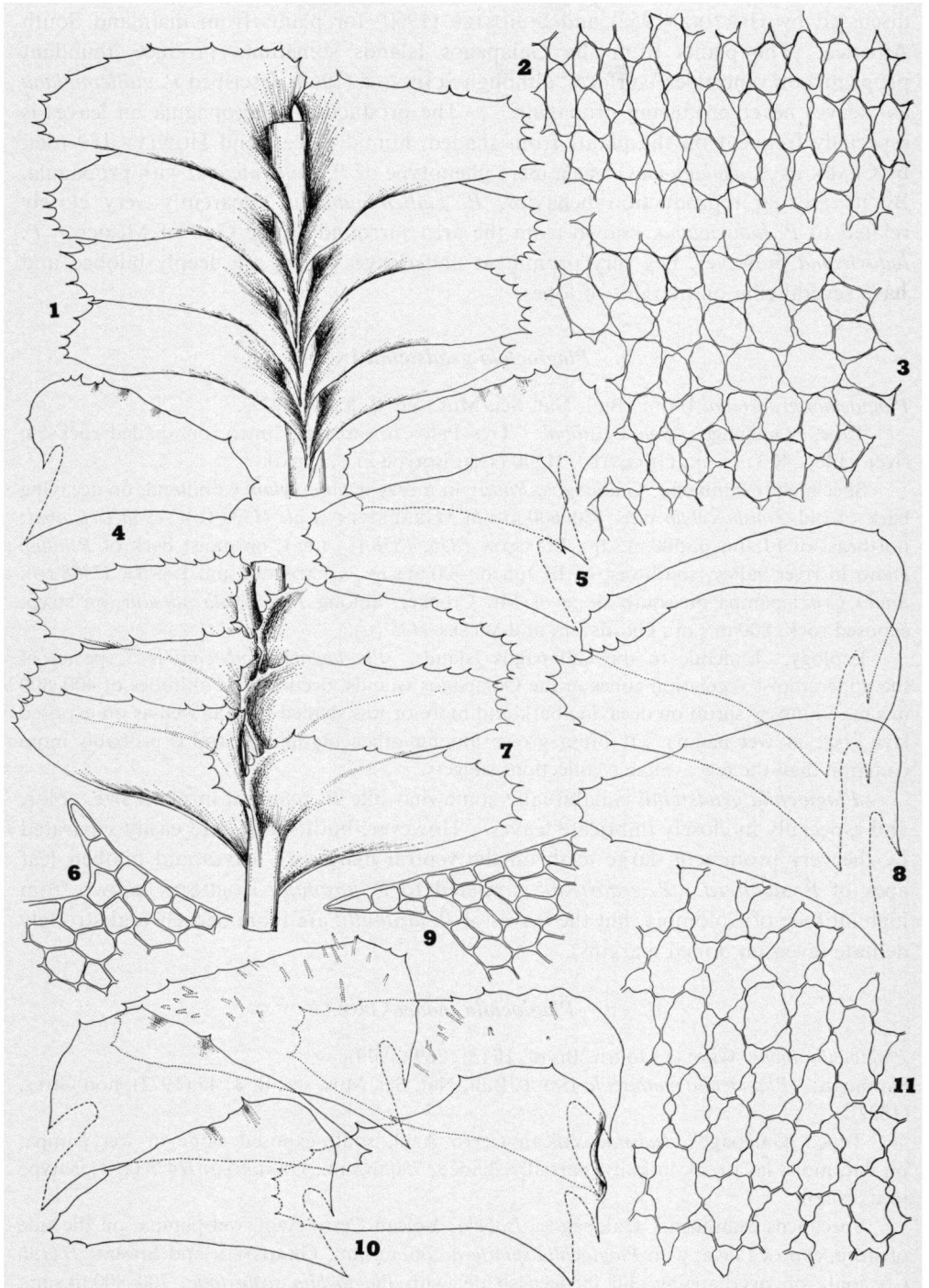
Type. Brazil; RADDI, s.n. (isotype in BM).

Representative specimens examined. Galapagos. *Floreana* (Charles Isl.): ANDERSSON, s.n., type of *Plagiochila anderssonii* (s), ANDERSSON, s.n., type of *P. subsimplex* (g), HOWELL 189, as *P. asplenioides* (WTU), 560 m.s.m., ITOW 9 (COLO), RODRIGUEZ s.n. and ORTIZ s.n. (COLO), 300–350 m.s.m., GRADSTEIN H158, H187 (U). *Isabela*: Volcan Alcedo, 2800–3400 ft., Vander WERFF 1434, 1470, 1545 (U), GRADSTEIN and WEBER H242 (U); Volcan Cerro Azul, 2200–2600 ft., Vander WERFF 2298, 2311 (U), GRADSTEIN and SIPMAN H400 (U). *Pinzon*: on bark and rock near summit, 350–460 m.s.m., GRADSTEIN and SIPMAN H475 (U), Vander WERFF 2358, 2366 (U). *Pinta*: 400–450 m.s.m., GRADSTEIN et al., H513 (U), Vander WERFF 2358, 2366 (U). *San Cristobal*: near Progreso, 250–300 m.s.m., BALASZ 12E (EGR, U), 350–650 m.s.m., GRADSTEIN and LANIER, 5 colls. (U). *Santa Cruz*: HOWELL 269, as *Plagiochila martiana* (WTU), 230–400 m.s.m., ITOW 12, 18, 42 (COLO), WEBER 31, 72, 78, 79, 103 (COLO), BALAZS 13 (EGR, U), 150–700 m.s.m., Vander WERFF, 40 colls. (U), 200–750 m.s.m., GRADSTEIN et al., 4 colls. (U). *Santiago*: STEWART 3404, as *Plagiochila martiana* (WTU), 680 m.s.m., PIKE 21 (COLO).

Ecology. With *Frullania brasiliensis* this is probably the most common and widespread liverwort in the Galapagos Islands. It is found throughout the moist zone and also in the more mesic upper transition zone from 150 m.s.m. upwards, on bark and rock and occasionally also on leaves (Bella Vista, El Progreso) and on alluvial soil (El Junco). The species is particularly common in moist woodlands where it can be found on almost every kind of tree or shrub. *Plagiochila guilleminiana* prefers rather shaded conditions and is consequently rarer in the pampas, where it is replaced by the common *P. bursata*.

Plagiochila guilleminiana shows a rather wide range of variation, as already

Fig. 3. *Plagiochila guilleminiana* MONT. 1. Part of shoot, dorsal view, ×14. 2, 3. Cells from leaf-middle, ×230. 4, 5, 8, 10. Leaves, ×14. 6, 9. Teeth from leaf-apex, ×230. 7. Part of shoot, ventral view, ×14. 11. Cells from leaf-base, ×230. Figs. 1, 2, 4, 5, 7 based on GRADSTEIN H158, figs. 3, 8, 11 on GRADSTEIN H285, and others on GRADSTEIN H187.



discussed by HERZOG (1952) and SCHUSTER (1960) for plants from mainland South America. The plants from the Galapagos Islands sometimes produce abundant propagula on ventral leaf-surfaces, although SCHUSTER (1960) described *P. guilleminiana* as "leaves never producing propagula". The production of propagula on leaves is especially frequent on the plants from shaded, humid places, and HOWLLE 189 (det. by CLARK as *P. asplenioides*) was a mere phenotype of *P. guilleminiana* with propagula. By its asexual reproduction behavior, *P. guilleminiana* is apparently very closely related to *P. ludoviciana*, known from the area surrounding the Gulf of Mexico. *P. ludoviciana*, however, has very prominent underleaves which are deeply bilobed and have several cilia on margins of lobes.

5. *Plagiochila gradsteinii* INOUE

Plagiochila gradsteinii INOUE, Bull. Nat. Sci. Mus. ser. B, 3: 47 (1977).

Type. Galapagos. *San Cristobal*: Tres Palos towards El Junco, on shaded rocks in river valley, 400 m.s.m., GRADSTEIN H300 (TNS; isotype in U, COLO).

Specimens examined. Galapagos. *Pinta*: in mossy *Zanthoxylum* woodland, on decaying bark of old *Zanthoxylum* tree, 550–600 m.s.m., GRADSTEIN *et al.* H533 (U). *San Cristobal*: northeast of El Junco, 500 m.s.m., ELIASSON 1856, 1858 (U, UPP); on moist bark of *Psidium guava* in river valley, southwest of El Junco, 500 m.s.m., GRADSTEIN and LANIER H308 (U). *Santa Cruz*: pampa on south slope of Mt. Crocker, among *Plagiochila bursata*, on steep, exposed rock, 800 m.s.m., GRADSTEIN and WEBER H35 (U).

Ecology. Endemic to the Galapagos Islands. *Plagiochila gradsteinii* is a species of the upper, moist vegetation zones of the Galapagos Islands, occurring at altitudes of 400–800 m.s.m., in mossy shrub on decaying bark and more or less shaded rock as well as on exposed lava rock in wet pampa. It often grows among other bryophytes and is probably more common than the few available collections suggest.

Plagiochila gradsteinii is habitually somewhat like *P. spinifera* in plant size, color, and especially in closely imbricate leaves. However, both species are easily separated by the very prominent, large teeth on the ventral margin of leaves and bilobed leaf apex of *P. spinifera*. *P. gradsteinii* is related to *P. jaramillii* ROBINSON known from high altitude of Colombia, but the leaves of *P. jaramillii* are more densely and strongly dentate (even on dorsal margins).

6. *Plagiochila inouei* GROLLE

Plagiochila inouei GROLLE, Journ. Bryol. 10 (3): 269 (1979).

Synonym: *Plagiochila nudiuscula* INOUE, Bull. Nat. Sci. Mus. ser. B, 3: 45 (1977), non GOTT. (1882).

Type. Galapagos. *Isabela*: Volcan Cerro Azul, south-exposed slope in wet pampa, on flat, moist lava rock in gully, partially shaded, 750 m.s.m., GRADSTEIN H426 (TNS; isotype in U, COLO).

Specimens examined. Galapagos. *Isabela*: Volcan Cerro Azul, wet pampa, on the side of steep, exposed lava, with *Plagiochila spinifera*, 740 m.s.m., GRADSTEIN and SIPMAN H413b (U); *ibid.*, on overhanging cliff in deep shade, with *Plagiochila scabrifolia*, 700–800 m.s.m.,

GRADSTEIN and SIPMAN *H423a* (v). *Santa Cruz*: pampa on south slope of Mt. Crocker, on steep cliff, 800 m.s.m., GRADSTEIN and WEBER *H37* (COLO, v).

Ecology. Endemic to the Galapagos Islands and restricted to wet pampa on southern exposed slopes at altitude of about 700–800 m.s.m. It grows exclusively on lava rock, with a preference for steep cliffs.

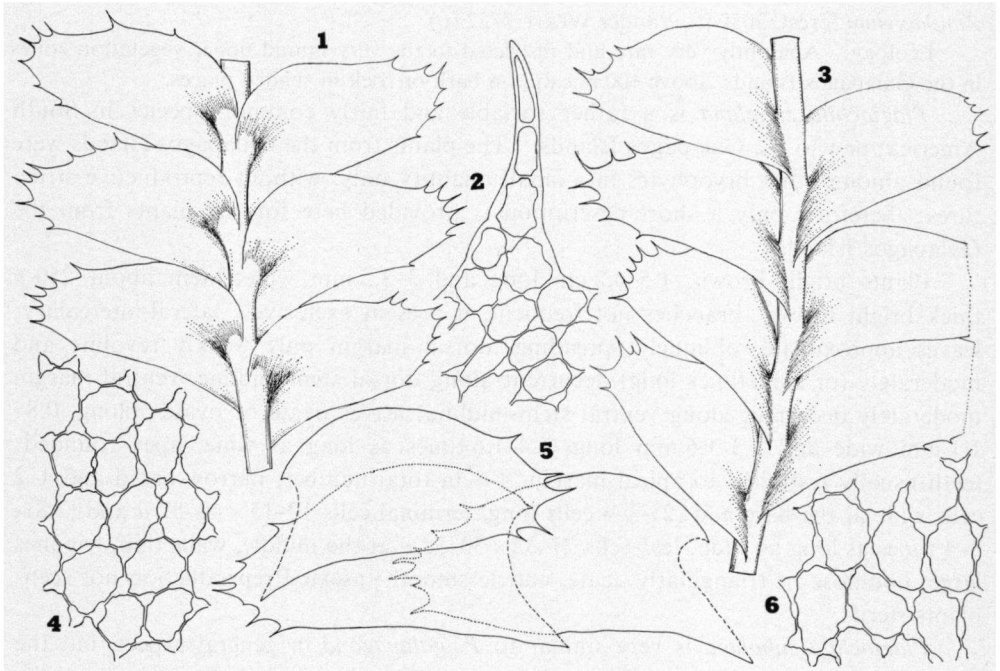


Fig. 4. *Plagiochila subplana* LINDENBG. 1. Part of shoot, ventral view, $\times 16$. 2. Tooth on leaf-margin, $\times 230$. 3. Part of shoot, dorsal view, $\times 16$. 4. Cells from leaf-middle, $\times 230$. 5. Leaves, $\times 23$. 6. Cells from leaf-base, $\times 230$. All figs. based on GRADSTEIN and SIPMAN *H428*.

Plagiochila inouei is somewhat similar to *P. scabrifolia* in habit (by similar size of plant, color and bilobed or bidentate leaf-apex, and similarly linear shape of leaves); but in *P. scabrifolia* the leaves are not fragile and the cuticle of leaf-cells is distinctly verrucose. The leaves of *P. inouei* are very easily fragmenting from the very base and quite often the shoots are represented by completely denuded, wiry stems.

The most characteristic feature of *P. inouei* is seen in the cross section of stem; the outermost layer of the cortex is somewhat thin-walled (especially the outer wall), tending to become a hyalodermis. By this feature, *P. inouei* is sharply separated from the related *P. corniculata* from mainland South America. The leaves of *P. inouei* are more elongated than those of *P. corniculata* and usually 1.75–2.3 times as long as wide.

7. *Plagiochila subplana* LINDENBG.

Plagiochila subplana LINDENBG., Spec. Hepat.: 73 (1841).

Type. Brazil: Rio de Janeiro, MARTIUS *s.n.* (G).

Specimens examined. Galapagos. *Isabela*: Vulcan Cerro Azul, pampa on south exposed slope, under ferns in wet crater, with *Plagiochila bursata*, 700–800 m.s.m., GRADSTEIN and SIPMAN H428 (U). *Santa Cruz*: Cerro Precioso, epiphyte on *Antrophyum lineatum* in *Zanthoxylum* forest, 2050 ft., Vander WERFF 1752 (U).

Ecology. Apparently very rare and restricted to the very humid upper vegetation zones in the Galapagos Islands, above 600 m.s.m., on bark or rock in shaded places.

Plagiochila subplana is a rather variable and fairly common species in South America; new to the Galapagos Islands. The plants from the Galapagos Islands were found among other bryophytes in a small quantity only, without reproductive structures; therefore, only a short description is provided here for the plants from the Galapagos Islands.

Plants bright brown, 1.5–3.2 cm long and 3–3.5 mm wide; stem about 250 μ thick bright brown; branches not frequent, if present exclusively lateral-intercalary; leaves approximate, obliquely spreading, dorsal margin only weakly revolute and moderately (or sometimes long) decurrent along dorsal stem-midline, ventral margin moderately decurrent along ventral stem-midline; leaves ovate or ovate-oblong, 0.8–1.1 mm wide and 1.3–1.6 mm long, 1.4–1.6 times as long as wide, apex rounded; teeth usually restricted to apical margin, 4–8 in total number, narrow-based and 1–2 cells wide at the base and (2)–3–4 cells long, terminal cells 10–15 \times 40–52 μ and (2.8)–3–4 times as long as wide; leaf-cells 27–32 \times 30–38 μ at the middle, walls thin, trigones large, nodulose or triangularly acute, cuticle smooth; asexual reproduction not seen; plants sterile.

Plagiochila subplana is very similar to *P. galapagona* in general aspect, but the branches of *P. galapagona* are almost always of the terminal and *Frullania*-type and the leaves are oblong-rectangular or broadly oblong; the teeth of the leaf-margin of *P. galapagona* are present on almost the whole ventral margin and never restricted to the apical margin. Furthermore, the trigones of the leaf-cells are almost absent or sometimes only minute in *P. galapagona*.

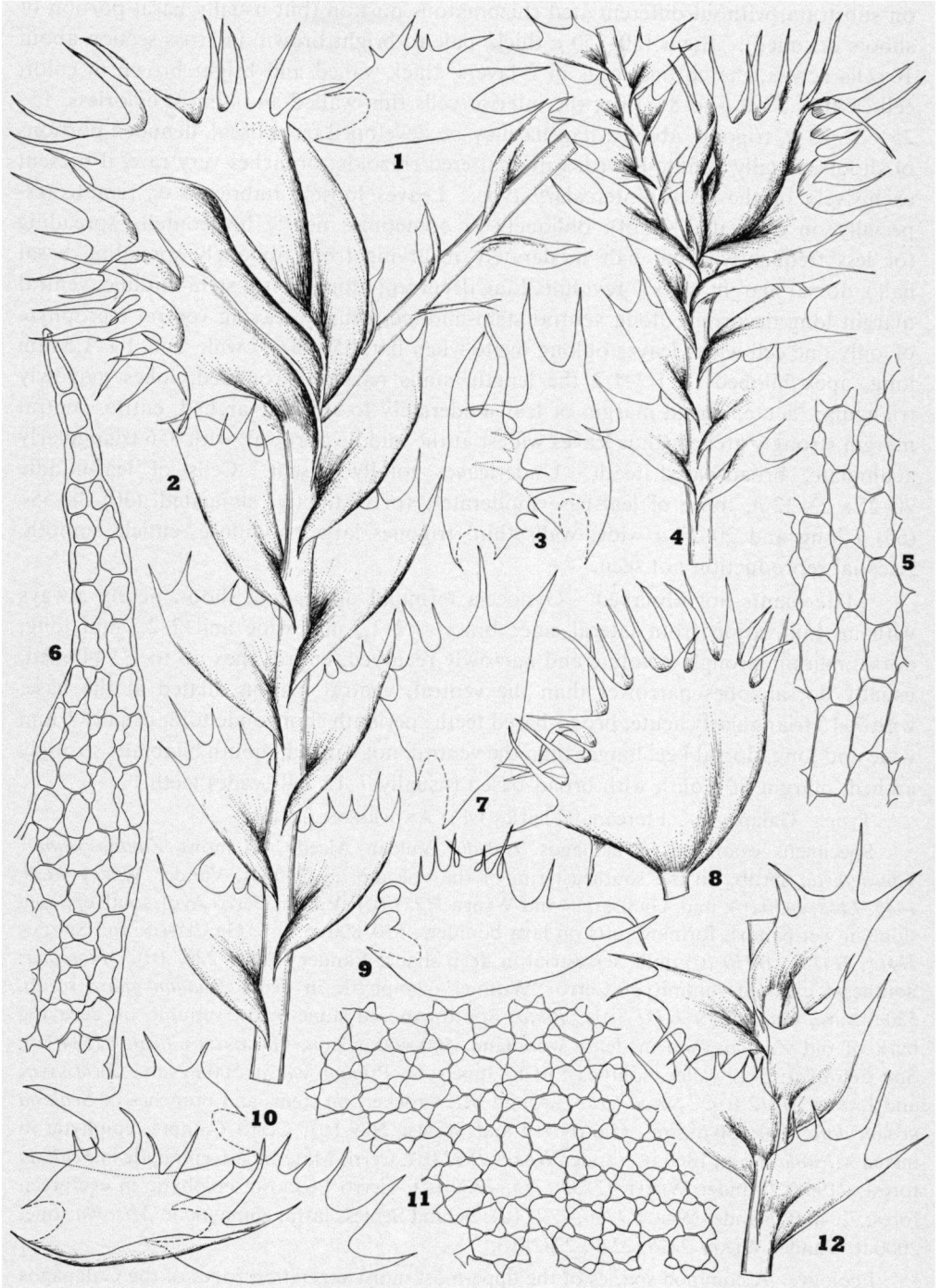
8. *Plagiochila spinifera* ÅNGSTR.

Plagiochila spinifera ÅNGSTR., Kongl. Vet.-Akad. Förh. Stockholm 30 (5): 113 (1873).

Synonym: *Plagiochila trifida* STEPH., Spec. Hepat. 6: 232 (1921), *syn. nov.*

Plants somewhat slender, small, 2–4 cm long (or sometimes up to 10 cm long), 1.7–2 mm wide, plae brownish green to bright green, usually forming compact patches

Fig. 5. *Plagiochila spinifera* ÅNGSTR. 1, 3, 7, 10. Leaves, \times 18. 2, 4. Parts of shoots, with gynoecia, dorsal view, \times 18. 5. Cells from leaf-base, \times 230. 6. Tooth from leaf-apex, \times 230. 8. Perianth, \times 15. 9. Bract, \times 15. 11. Cells from leaf-middle, \times 230. 12. Part of shoot, ventral view, \times 18. Figs. 1, 3, 7 based on GRADSTEIN and SIPMAN H402, and others on GRADSTEIN and SIPMAN H413a.



on substrata, without differentiated rhizomatous portion (but usually basal portion of shoots denuded). Stem 180–250 μ thick, pale to bright brown, in cross section about 10 cells across, the cortical cells in 2 layers, thick-walled and bright brown in color, cell-cavities $5 \times 8 \mu$ to $8 \times 13 \mu$, the interior cells thin-walled and almost colorless, $15\text{--}25 \times 22\text{--}23 \mu$, trigones absent; flagella may be developed from basal, denuded portions of shoots, usually minute-leaved, with scattered rhizoids; branches very rare, if present exclusively of the lateral-intercalary type. Leaves loosely imbricate or remote (especially on elongated shoot), obliquely or sometimes nearly horizontally spreading (or less frequently distal half moderately recurving from obliquely spreading basal half), dorsal margin weakly revolute, long decurrent along dorsal stem-midline, ventral margin long decurrent along ventral stem-midline, usually leaving ventral merophyte of only one cell wide; leaves oblong ovate when flat, 550–800 μ wide and 1.1–1.5 mm long, apex bilobed to $1/3\text{--}1/2$ the length, sinus narrowly rounded, lobes narrowly triangular, acute, dorsal margin of leaf moderately to strongly arched, entire, ventral margin strongly arched (thus leaves widest at the middle portion), with 3–6 triangularly acuminate, broad-based teeth. Underleaves totally absent. Cells of leaf-middle $20\text{--}25 \times 23\text{--}32 \mu$, those of leaf-base moderately (or distinctly) elongated, (30)–38–55–(63) μ long and 20–27 μ wide, walls thin, trigones large, nodulose, cuticle smooth. Asexual reproduction not seen.

Male plants not observed. Gynoecea terminal on leading shoot, nearly always with an innovation from lateral side; bracts 1.2–1.5 mm wide and 2–2.3 mm long, dorsal margin strongly revolute and narrowly recurved, entire, apex up to $1/3$ bilobed, usually dorsal lobes narrower than the ventral, ventral margin dilated at the base, with 7–15 triangularly acute, broad-based teeth; perianth short obdeltoid, usually 1 mm wide and long, dorsal keel longer than the ventral, not winged, mouth bilabiate, strongly arched, margin of mouth with broad-based (usually 7–15 cells wide) teeth.

Type. Galapagos. Floreana (Charles Isl.); ANDERSSON *s.n.* (s).

Specimens examined. Galapagos. *Isabela*: Vulcan Alcedo, in moist *Zanthoxylum*—*Tournefortia* shrub, on the southeast rim of the volcano, ca. 3400 ft, Vander WERFF 1438, 1446, 1448, 1450 (v), *ibid*, GRADSTEIN and WEBER H234 (u); Vulcan Cerro Azul, south exposed slope in wet pampa, forming tufts on lava boulders, 550–800 m.s.m., GRADSTEIN and SIPMAN H411, H413a, H410 (v), *ibid*, terrestrial in deep shade, Vander WERFF 2297 (u). *Floreana*: Southeast exposed summit of Cerro “Wittmer”, epiphytic in dense *Psidium guava* scrub, 550 m.s.m., GRADSTEIN H178 (u). *Pinta*: South exposed slope below summit, on decaying bark of old *Zanthoxylum* in dense woodland, 500–600 m.s.m., GRADSTEIN *et al.*, H534 (u). *San Cristobal*: river valley, southeast of El Junco, on *Psidium guava*, 500 m.s.m., GRADSTEIN and LANIER H312 (u). *Santa Cruz*: around Mt. Crocker, on stems and branches of *Scaevola pedunculata*, 650–750 m.s.m., GRADSTEIN and WEBER H29 (u); Cerro Camote, epiphytic in mixed *Miconia* shrub, 1860 ft, Vander WERFF 1692 (u); Cerro Maternidad, epiphytic in *Scaevola* forest, 2190 ft, Vander WERFF 1773, 1775, 1779 (u); Cerro Precioso, epiphytic in evergreen forest, 2040 ft, Vander WERFF 1786, 1797 (u); behind Schiess farm, epiphytic in *Miconia* zone, 2000 ft, Vander WERFF 2228, 2229, 2232 (u).

Ecology. A common species of the uppermost moist vegetation zones of the Galapagos

Islands, occurring above 500 m.s.m. as an epiphyte in old *Zanthoxylum*, *Psidium guava* and *Miconia* bush as well as the supper edges of the *Scalesia pedunculata* forest of Santa Cruz. It always grows in moist microhabitats, shaded or exposed, and may occasionally be found on lava rock as well, e.g. in the wet pampa on the southern slope of the volcano Cerro Azul. The species is also expected to be found on Santiago.

Plagiochila spinifera seems to be an endemic species to the Galapagos Islands, with close affinities to *P. biceps* SPRUCE (known from Ecuador) and *P. bidens* GOTT. (known from West Indies); although ARNELL (1962) reported *P. spinifera* from Ecuador, we were not able to confirm his record. In *P. biceps* the leaves are more closely imbricate, with more strongly revolute dorsal margin, almost entirely covering the stem-surface (and also on ventral surface; thus no stem surface exposed); the leaf-apices are only shortly and strongly asymmetrically bilobed and the teeth on the ventral margin are much smaller (1–2 cells wide at the base and 2–5 cells long) and fewer in number (usually 2–4); the basal leaf-cells are more distinctly differentiated, forming a distinct vitta area.

Plagiochila bidens GOTT. may be more remotely related to *P. spinifera*; the leaves of *P. bidens* are more oblong and the apices of leaves are not bilobed but rounded-truncate with small, two teeth. The three species discussed above may form a natural species complex and belong to the sect. *Bidentes*.

Uncertain or Rejected Records

Plagiochila asplenioides (L.) DUM.—This species was reported by CLARK (1953) from Floreana (Charles Isl.), but proved to be *P. guilleminiana* (see p. 14).

Plagiochila breuteliana LINDENBG.—This species was reported from Santa Cruz (Indefatigable Isl.) by CLARK (1953) but proved to be *P. guilleminiana* (see p. 14).

Plagiochila martiana (NEES) NEES—This species was reported from Santa Cruz (Indefatigable Isl.) and Santiago (James Isl.); they were referred to *P. guilleminiana* (see p. 14).

Plagiochila ovata LINDENBG. et GOTT.—This species was reported by STEPHANI (1905) from the Galapagos Islands (leg. ANDERSSON), but we could not locate the specimen. As *P. ovata* is somewhat similar to *P. guilleminiana*, we think that STEPHANI's report may be based on *P. guilleminiana*.

"*Plagiochila insularis* STEPH."—This species is apparently a "nom. nud." and we could not locate the specimen from the Galapagos Islands, from where BARTRAM and ARNELL (1961) reported it.

Resumen

El género *Plagiochila* (hepatica) esta representada en las Islas Galapagos por ocho (8) especies diferentes: *P. bursata* (DESV.) LINDENBG., *P. galapagona* INOUE, *P. gradsteinii* INOUE, *P. guilleminiana* MONT., *P. inouei* GROLLE, *P. scabrifolia* INOUE, *P. spinifera* ÅNGSTR. y *P. subplana* LINDENBG.

El endemismo en este género es más alto que en otros géneros de las hepáticas, con cinco (5) especies que comienzan a conocerse solamente de los Galapagos (*P. galapagona*, *gradsteinii*, *scabrifolia*, *inouei*, y *spinifera*). Las otras tres (3) son comunes y ampliamente distribuidas a lo largo de la América tropical. La mayoría de las especies están restringidas a las zonas altas-húmedas de vegetación de las Islas Galapagos (matorrales de *Zanthoxylum*, *Miconia* y pampa) excepto *P. guilleminiana* muy común, la cual puede presentarse en la zona seca de transición de bosque. La más amplia variación de *Plagiochila* ha sido vista en Isabela (Cerro Azul), San Cristobal y Santa Cruz.

Literature Cited

- ÅNGSTROM, J., 1873. Förteckning och beskrifning öfver Mossor, samlade af Professor N. J. Andersson under Fregatten Eugenie 1851-53. *Kongl. Vet.-Akad. Förh. Stockholm*, **30**: 113-51.
- ARNELL, S., 1962. Contribution to the knowledge of the Hepaticae of Ecuador. *Sv. Bot. Tidskr.*, **58**: 334-350.
- BARTRAM, E. B. and S. ARNELL, 1961. Bryophytes of the Galapagos Islands, collected principally by Gunnar Harling in 1959. *Bryologist*, **64**: 248-250.
- CLARK, L., 1953. Some Hepaticae from the Galapagos, Cocos, and other Pacific islands. *Proc. Calif. Acad. Sci.*, **27**: 593-624.
- HERZOG, Th., 1952. Hepaticae Ecuadoriensis a Cl. Dre. Gunnar Harling annis 1946-1947 lectae. *Sv. Bot. Tidskr.*, **48**: 62-Lo8.
- INOUE, H., 1977. Notes on the Plagiochilaceae, VII. Four new species of the Genus *Plagiochila* (Dum.) Dum. from the Galapagos Isls. *Bull. Nat. Sci. Mus. ser. B*, **3** (2): 45-54.
- SCHUSTER, R. M., 1960. A monograph of the nearctic Plagiochilaceae. Part. III. Sectio Contiguae to Conclusion. *Ameri. Midl. Nat.*, **63**: 1-130.
- STEPHANI, F., 1905. *Plagiochila*. *Species Hepaticarum*, **2**: 519-595.
- WEBER, W. A., 1966. Lichenology and Bryology in the Galapagos Islands, with check lists of the lichens and bryophytes thus far reported. In R. J. BOWMAN (ed.): *The Galapagos*, pp. 190-200. Univ. California Press, Berkeley.
- , S. R. GRADSTEIN, J. LANIER and H. J. M. SIPMAN, 1977. Bryophytes and lichens of the Galápagos Islands. *Not. de Galápagos*, **28**: 7-12.
- WERFF, H. H. Vander, 1978. The vegetation of the Galapagos Islands. Thesis, University of Utrecht, The Netherlands.