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The lichen genus *Ramalina* on the Galapagos

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Abstract: *Ramalina* species are among the most abundant lichens on the Galapagos Isles. A total of fifteen species have been distinguished, four of which are described as new here: *Ramalina darwiniana*, *R. fragilis*, *R. furcellangulida* and *R. polyforma*. These new species are considered to be endemic to the Galapagos whereas previous reports refer to relatively common, more widely distributed species. Several other species are reported here for the first time from the Galapagos.

Key words: endemism, identification key, new species

Introduction

Lichens are generally widespread in their distribution, but there are notable exceptions. For example, endemic lichens are especially known from isolated tropical mountains, fog-induced lichen zones in coastal deserts (Namibia, N. Chile, Baja California) and some isolated Pacific and Atlantic islands (e.g., Hawaii and the Galapagos).

The lichens of oceanic islands are still generally poorly known, although the Canary, Cape Verde Isles and Madeira have been relatively well-studied (Hafellner 1995) and there is a recent checklist of Azores lichens (Rodrigues & Aptroot 2005).

The lichen flora of (sub)tropical oceanic islands is generally characterized by two main elements: (1) a pan(sub)tropical element in the humid upland regions, rarely containing endemics, and more often consisting of widely distributed lichens only; (2) a dry Mediterranean to semi-desert element, which more frequently contains endemic species usually restricted to an island group or, very rarely, to a single tiny island only.

Even where lichen endemism is relatively common, it is usually restricted to a few taxonomic groups. In the *Roccellaceae*, a family that occurs mainly in coastal regions and is abundant on islands and in coastal deserts, several genera are endemic to small areas. For example, *Combea* De Not., a genus endemic to coastal Namibia, *Ingaderia* Darb., endemic to coastal Chile and *Roccellographa* J. Steiner, endemic to Socotra. In most other lichen groups only a few, conspicuous species are known to be endemic, for example, the genus *Mobergia*, which is endemic to Southern California and Baja California.

By far the richest regional endemism has been reported from the genus *Ramalina* Ach. Of the 40 species that occur in Macaronesia (not counting 10 doubtful records), half the species are not known from outside this group of islands (Krog 1990; Krog & Østhagen 1980*a*, *b*). Some of the Macaronesian species occur on most of these Atlantic islands, others are restricted to one or a few islands of one archipelago. The most striking endemism is to be found on the small (much smaller than St Helena), mostly flat island of Porto Santo near Madeira where no fewer than six species of *Ramalina* occur on its old volcanic cones, none of which has ever been found

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elsewhere (Krog 1990; Krog & Østhagen 1980*b*). These islands with high *Ramalina* endemism share many characteristics with other isolated, volcanic islands. For example, both the Galapagos Islands and Hawaii are also strongly isolated, characterized by extensive, harsh lava fields, and their low coastal regions are semi-deserts where coastal fog or drizzle is common for at least part of the year.

The coastline of the volcanic, equatorial Galapagos Islands often comprises extensive cliffs or rugged lava flows. Once these lava flows reach a certain age, saxicolous lichens become a conspicuous element of the flora. Much earlier all shrubs and deciduous trees in these lower zones are clad in an abundance of corticolous lichens. Soil lichens are generally not common on the islands; if they can be found, they occur typically in the humid mountains. The coastal regions are relatively dry, but during the cool season receive abundant misty drizzle (called garúa), especially on the SE sides of the islands that are exposed to the cold sea current. The rock is predominantly volcanic, but varies from soft lapilli to hard basalt cliffs. Overhangs occur inside volcanic cones or at the entrances of lava caves.

The vegetation of the Galapagos is predominantly semi-arid, but there are seven higher islands that are characterized by humid zones in their highlands, and four of these, the inhabited islands of Floreana, Santa Cruz, Isabela and San Cristóbal, also have extensive areas of farmland. Five basic vegetation zones can generally be distinguished throughout the Galapagos (*sensu* Tye *et al.* 2002; modified from Wiggins & Porter 1971):

1 a *Coastal Zone* characterized by rocky lava shores, mangroves and occasional beaches;
2 a *Dry Zone* with extensive bare lava flows, scrubland or open forest dominated by *Bursera graveolens*;
3 a *Transition Zone*, often characterized by the endemic guava tree *Psidium galapageium*, and typically draped in curtains of *Ramalina usnea* (Fig. 1A);
4 a *Humid Zone* that differs from island to island and can be further subdivided into different vegetation types such as the *Zanthoxylum fagara*-forest that is typically densely covered in carpets of *Frullania* spp., the *Scalesia* forests that are dominated by endemic *Scalesia*-trees, and the extensive scrubland dominated by endemic *Miconia robertsoniana*, ferns or *Tournefortia* spp.;
5 a *High-altitude Dry Zone*, which is present only above the cloud level and restricted to two islands only, Isabela and Fernandina.

The lichen flora and vegetation of the coastal and arid regions of the Galapagos resemble at first sight those of Baja California, Southern Madagascar or Macaronesia. Yellowish *Lecanora* and *Pertusaria* species are abundant on coastal cliffs and can be recognized from afar. Furthermore, species of *Buellia*, *Caloplaca*, *Ramalina* and the *Roccellaceae* (A. Aptroot & L. B. Sparrius, unpublished) are also abundant, both in biomass and species numbers. In this coastal zone, the semi-arid lowlands, and the transition zone, species diversity of the genus *Ramalina* is highest. Only a few species are more typical of the humid, subtropical highlands.

Although the Galapagos Islands are geologically young, many plant and animal species, and even some genera, are endemic, many to single islands only. An estimated 32–43% of species of vascular plants, *c.* 50% of the invertebrates (excluding insects), 47% of the insect species, and 59% of the land vertebrate species are endemic to the Galapagos (Tye *et al.* 2002). Despite the fact that lichens are generally much more widespread than most other organisms, the coastal lichens at least also show some endemism (Weber 1986; Weber & Gradstein 1984). The dominant, yellow *Lecanora pseudopinguis* W. A. Weber, which colours coastal cliffs is endemic, as are several *Buellia* spp. (e.g. *Buellia straminea* Tuck., *Buellia galapagona* W. A. Weber, Weber 1986). Some of the *Roccella* species seem to be endemic (Follmann 2001), even after their

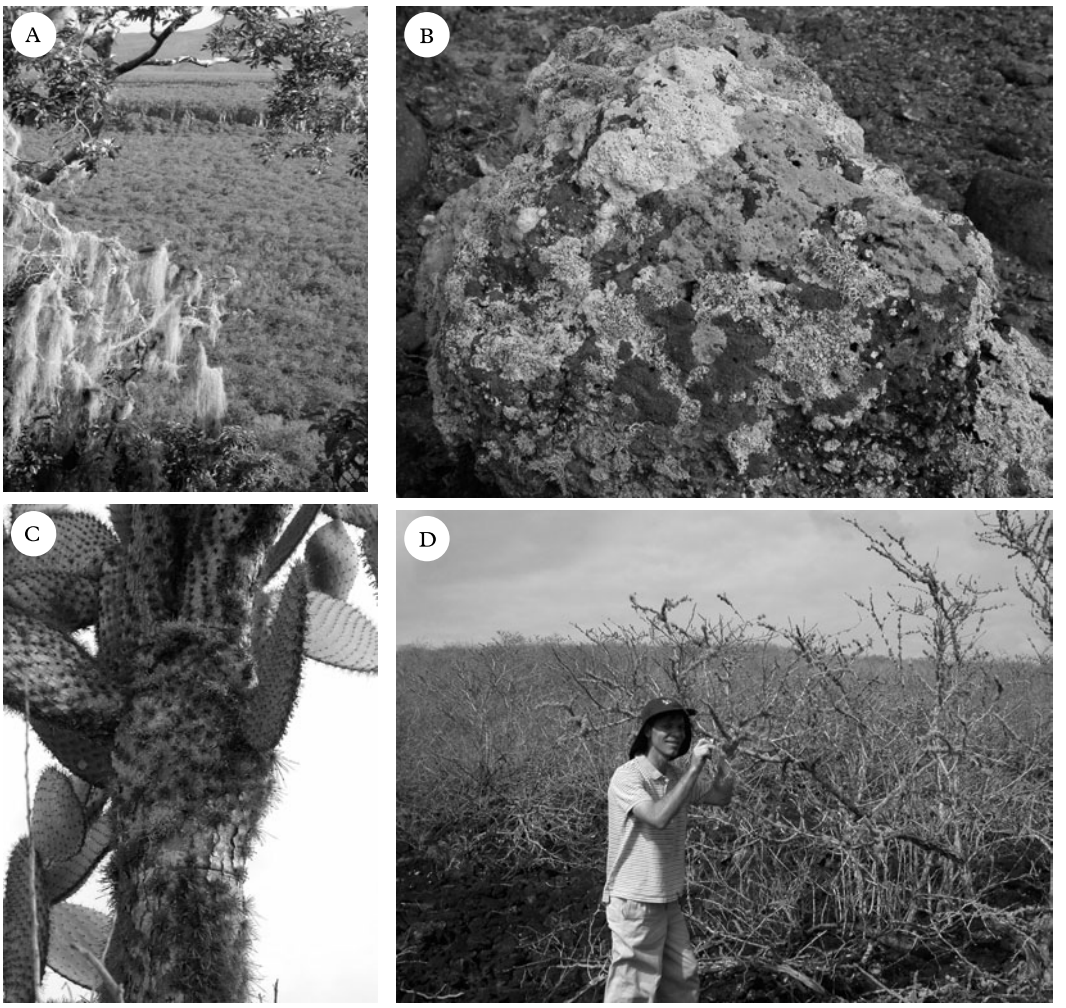

FIG. 1. Typical habitats of *Ramalina* species on the Galapagos. A, transition zone with dominant *R. usnea*, inside the crater of Volcán Alcedo on Isabela Island; B, lava bomb on South Plaza Island (near Santa Cruz), rich coastal lichen vegetation with several *Ramalina* species; C, endemic *Opuntia echios* near the Charles Darwin Research Station on Santa Cruz Island with *Ramalina* species; D, collecting *Ramalina* species on twigs on Pinzón Island.

taxonomy has been revised (Tehler 2006, 2007).

This present paper focuses on the genus *Ramalina*. Several new species are described which are characteristic of the dry and coastal zones of the Galapagos and currently believed to be endemic.

Materials and Methods

This study is based on several field trips during 2005–2007. The first author visited the Galapagos during May–June 2005, and in February–March 2006. In 2005 he visited two islands, Santa Cruz and San Cristóbal (the south-western part). In 2006 both authors visited Isabela (Volcán Alcedo), Santa Cruz, Santiago (western parts and highlands), Pinzón, Plaza Norte, Plaza Sur and Roca Gordon. In 2006 and 2007 the second author also visited Santiago (western, southern and eastern parts), Bartolomé, Rábida, Pinta and San Cristóbal (north-eastern arid areas). On all islands except Roca Gordon, extensive collections of *Ramalina* specimens were made. An effort was made to visit all major habitats, including the peaks. Specimens were studied in the herbarium of the Charles Darwin Research Station (CDS) and at ABL.

A total of 439 *Ramalina* specimens were collected, all are fully databased and deposited at CDS, with selected duplicates at ABL. A selection of specimens was analyzed at ABL for cortical and medullary chemistry using standardized thin-layer chromatography (Orange *et al.* 2001). In 2006 the second author visited the herbarium of the Californian Academy of Sciences (CAS) in San Francisco, and the Herbarium of the Colorado State University (COLO). Only a few *Ramalina* specimens are deposited at CAS (collected during the Expedition of the Californian Academy of Sciences to the Galapagos Islands 1905–1906, the Galapagos International Scientific Project 1964, and The Hopkins Galapagos Expedition 1899 by the Leland Stanford Junior University). All COLO specimens collected by W. A. Weber were on loan and thus were not available for the present study.

Results

Ramalina species are abundant on the Galapagos Islands, especially in coastal and slightly inland regions, up to *c.* 400 m altitude. The twigs and branches of shrubs and trees and the horizontal to vertical surfaces of lava cliffs are often covered with a mosaic of species (Fig. 1). In upland regions, they are accompanied and partly replaced by *Usnea*. The largest lichens are *Ramalina* species which grow on deciduous *Bursera* trees, particularly in dry areas.

A total of fifteen species of *Ramalina* could be distinguished, most of them recognizable in the field. All species are morphologically distinct but chemically rather homogenous. Even species that have a somewhat similar morphology nevertheless can be distinguished in the field when they grow side-by-side. Four species could not be identified using any of the regional taxonomic treatments (e.g. Kashiwadani & Kalb 1993; Kashiwadani & Nash 2004; Landrón 1972; Magnusson 1956; Stevens 1987) nor with the remaining scattered literature in which *Ramalina* species have been described. They are, therefore described here as new to science and are believed to be endemic to the Galapagos Islands.

The eleven remaining species are also distributed outside the Galapagos and include all seven species previously correctly reported from the archipelago (e.g., Weber 1986). These widespread species are most abundant in the interior of the islands, whereas the four new species are predominant in the coastal areas.

No distinct geographical distribution pattern was observed among the various islands within the the Galapagos archipelago. Most of the common species were found on all islands that were visited, although some species were only locally abundant. This agrees well with observations by Weber & Gradstein (1984), who suggest that no inter-island endemism can be observed among Galapagos lichens.

In the richest coastal areas, up to ten corticolous species could be found side-by-side, and up to five saxicolous species. These are partly the same species. The common species especially can be found both on lava rock, and on tree bark, branches, twigs, cacti and/or spines.

All the *Ramalina* species contain usnic acid in their cortex. In addition, atranorin was found infrequently, particularly in species with a relatively pale grey (as opposed to greenish grey) colour, but the substance was not found to be a reliable character to distinguish species (in contrast to the thallus colour itself). In general, only the main medullary substances were determined. The most common major medullary substance was salazinic acid, often accompanied by, or replaced by, sekikaic or divaricatic acid, or more rarely by boninic or norstictic acid. In some species medullary substances were consistently absent; in other species substances could be either present or absent.

An identification key and details about the habitat preference and the distribution on the Galapagos (mostly in terms of coastal vs inland locations) are given below for all species, with full descriptions for the new species only.

Key to the *Ramalina* species known from the Galapagos Islands

1 Thallus sorediate 2
Thallus not sorediate, usually with apothecia 8

2(1) Thallus lobes mostly angular to terete, not distinctly flattened throughout and not canaliculate 3
Thallus lobes distinctly flattened throughout or canaliculate 7

3(2) Thallus cortex with distinct chondroid strands, visible at the surface as striae or linear pseudocyphellae, lobe tips curled; saxicolous, coastal to lower transition zone . . . . . **R. polyforma**
Thallus cortex lacking chondroid strands, surface not distinctly striate, lacking pseudocyphellae, lobe tips not curled (no hooks) 4

4(3) Thallus small, <2 cm, coralloid; branches ± terete; surface uneven, matt, not smooth, pale greyish lemon (often with atranorin); resembling a small *Roccella*; saxicolous, coastal to lower transition zone . . . . . **R. fragilis**
Thallus generally larger, >2 cm (except most immature specimens), shrubby, terete or angular, occasionally flattened in parts; surface even, ± shiny, smooth, dull green (usnic acid only, no atranorin), not resembling a *Roccella*; saxicolous or corticolous 5

5(4) Thallus ± originating from a single holdfast (like a ''bouquet of flowers''); lobes erect, strap-like and sparsely branched, mostly angular, but somewhat flattened at the base; with usnic acid only (no other secondary metabolites found); on rock, mostly inland (humid highlands) . . . . . **R. camptospora**
Thallus not distinctly originating from a single holdfast; lobes suberect, thin, slender and richly branched, terete or angular, resembling an *Usnea*; with usnic, sekikaic and/or salazinic acid; on bark or wood, rarely on rock 6

6(5) Thallus lobes thin, angular to indistinctly flattened, apically branching into isidiate branchlets, soralia laminal, punctiform, pustulate, exuding coarsely granular soredia and isidiate branchlets; medulla K−, or K+ pinkish (sekikaic acid); on bark or wood, rarely on rock, mostly inland (humid highlands) . . . . . **R. peruviana**
Thallus lobes thin, terete, not flattened, finely branched, but not becoming isidiate; soralia laminal, subterminal and terminal, punctiform, pustulate, exuding coarsely granular soredia, often abraded and then appearing finely sorediate; medulla K+ yellow slowly turning red (salazinic, ± sekikaic acid); corticolous, mostly inland (humid highlands) . . . . . **R. sorediosa**

7(2) Thallus surface distinctly striate to reticulate from conspicuous chondroid strands; lobes flattened, not canaliculate, initially short and broad (antler-shaped), becoming elongate (strap-shaped) with age; occasionally with curled tips (hooks); soredia lateral, rarely terminal; typically on rock, rarely on wood, coastal to lower transition zone . . . . . **R. polyforma**
Thallus surface smooth, not striate, without chondroid strands; lobes ± flattened to distinctly canaliculate; elongate (strap-shaped); soredia often terminal, capitate; on bark or wood, very rarely on rock, mostly inland (humid highlands) . . . . . **R. sorediantha**

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8(1) Thallus pendulous, lobes slender, with age developing into long, *Usnea*-like strands that frequently become longitudinally contorted (drill-like); mostly corticolous, mostly inland (humid highlands) . . . . . **(R. usnea s. lat.)**9
Thallus shrubby, lobes erect, not pendulous, flattened, canaliculate, angular or irregular, but not distinctly contorted (not drill-like) 10

9(8) Medulla K−, not forming orange needle-shaped crystals (microscope!); thallus straps thin to moderately wide, often strongly contorted; common . . . . . **R. usnea s.str.**
Medulla K+ orange becoming red, forming needle-shaped crystals (often slow, microscope!); thallus straps very thin, often less contorted; rare (possibly overlooked) . . . . . **R. anceps**

10(8) Thallus lobes ± originating from a common holdfast, erect, slender, very strongly canaliculate, rolled up at the base and thus resembling terete branches, apically unfolding but remaining deeply canaliculate, lacking warts or pseudocyphellae, but lobes faintly striate; apothecia mostly laminal, the lobes slightly bent at the apothecia (geniculate), few apothecia terminal; medulla K−, UV−; mostly corticolous, rarely lignicolous, only inland (humid highlands) . . . . . **R. puiggarii**
Thallus lobes not originating from a common holdfast, erect, but soon branching, angular or flattened or moderately canaliculate, but not distinctly rolled-up; typically with warts and/or pseudocyphellae; apothecia geniculate or not, laminal or terminal; medulla K+ red, or K−; mostly corticolous, rarely saxicolous, inland or coastal 11

11(10) Thallus lobes narrow, angular in cross-section, branch-like, not canaliculate; surface smooth or irregular, gnarled or with broad warts, but not distinctly ridged or tuberculate 12
Thallus lobes moderately narrow to broadened, not branch-like, but ± flattened in cross-section, canaliculate, smooth or with parallel or reticulate ridges; typically with at least some distinctly tuberculate pseudocyphellae 13

12(11) Thallus lobes forming distinctly angular branches, not flattened; lobe tips typically curled into hooks (''croziers''); pseudocyphellae common, mostly linear, forming broad, white striations; thallus surface dull, irregularly gnarled, occasionally with flat, broad warts, but not distinctly tuberculate; apothecia often geniculate; medulla K+ orange soon red (salazinic acid); corticolous, coastal to arid zone . . . . . **R. furcellangulida**
Thallus lobes angular, but at least basally ± flattened; lobe tips pointed, not curled, pseudocyphellae rare, forming thin, white surface striations; thallus surface shiny, smooth, not gnarled or warted; apothecia laminal, but rarely geniculate; medulla K− or K+ pinkish (sekikaic acid); corticolous, coastal to arid zone . . . . . **R. montagnei**

13(11) Thallus lobes short, broadened, somewhat hollow and inflated; surface distinctly reticulate, the whole thallus wrinkled; with abundant marginal and laminal tuberculate pseudocyphellae; lower side of apothecia ± wrinkled; medulla loose, all Galapagos material K−; corticolous, coastal to arid zone . . . **R. aspera**
Thallus lobes ± elongate, narrow to moderately broadened, not hollow or inflated, surface smooth, not wrinkled, but often with parallel or reticulate ridges, pseudocyphellae punctiform and tuberculate, or abraded along ridges into

± elongate lines; lower side of apothecia smooth or wrinkled; medulla dense; all Galapagos material K+ yellow, slowly red 14

14(13) Thallus lobes distinctly flattened, not canaliculate; lobe tips typically curled into "crozier"-like hooks; surface conspicuously lined with distinct, parallel ridges; ridges abrading into broadened, linear pseudocyphellae; lower side of apothecia smooth, not tuberculate, not ridged, but occasionally with few linear or punctiform pseudocyphellae; corticolous, coastal to arid zone . . . . . **R. sideriza**

Thallus lobes irregularly flattened to distinctly canaliculate; lobe tips typically blade-like, rarely curled; surface smooth, not distinctly striate, but often warted with tuberculate pseudocyphellae (especially along the lobe margins); lower side of apothecia often distinctly reticulately ridged or with tuberculate warts 15

15(14) Thallus lobes narrow to moderately broadened, typically not strap-shaped, irregularly flattened, ± wrinkled and not distinctly canaliculate, not anastomosing, not forming holes; lobe tips tapered, blade-like, not curled backwards; surface dull, uneven, irregular and ± wrinkled, but not distinctly ridged, with abundant marginal and laminal tuberculate pseudocyphellae; tubercules rarely abrading and becoming ± elongated, but not distinctly linear; apothecia smooth to tuberculate below; mostly corticolous, coastal to arid zone . . . . . **R. complanata**

Thallus lobes narrow to moderately broadened, often elongate, becoming strap-shaped, always distinctly canaliculate, frequently anastomosing and thus occasionally forming distinct, oval holes; lobe tips occasionally curled backwards ("crozier"-like) but mostly blade-like; surface shiny, uneven, occasionally reticulately ridged; pseudocyphellae sparse or absent, if present mostly confined to few tubercules along lobe margins, rarely along surface ridges, especially on the reticulate lower side of the apothecia; mostly corticolous, coastal to arid zone . . . . . **R. darwiniana**

a Thallus lobes moderately broadened, up to 15 mm wide, broadly canaliculate to barely flattened . . . . . **R. darwiniana var. darwiniana**

b Thallus lobes narrow, up to 3 mm wide, strongly and deeply canaliculate . . . . . **R. darwiniana var. curvida**

The Species

Ramalina anceps Nyl.

Synopsis methodica lichenorum **1**(2)**:** 291 (1860).

(Fig. 2A)

A pan-American species already reported from the Galapagos by Weber (1986). The species is corticolous, typically draping branches and twigs throughout the transition zone. It has rarely been collected and is possibly overlooked because of its similarity to *R. usnea* of which this taxon may just be a chemotype. Galapagos specimens of *R. anceps* appear overall thinner and less contorted than specimens of *R. usnea*, but this variability is not a reliable diagnostic morphological character to distinguish the two taxa. Their validity as distinct species should therefore be re-assessed on the basis of material from their whole (pan-American) distribution range. Weber (1986, p. 482) already stated: ". . . the lines that separate these taxa are not clear to me . . ."

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, along the trail going up the E-slope, at the NW-side of the trail, 0°24′5″S, 91°2′36″W, alt. 420 m, arid zone, open *Bursera graveolens* stand with an occasional *Pisonia floribunda* and *Zanthoxylum fagara* and shrubs of *Macraea larici-*

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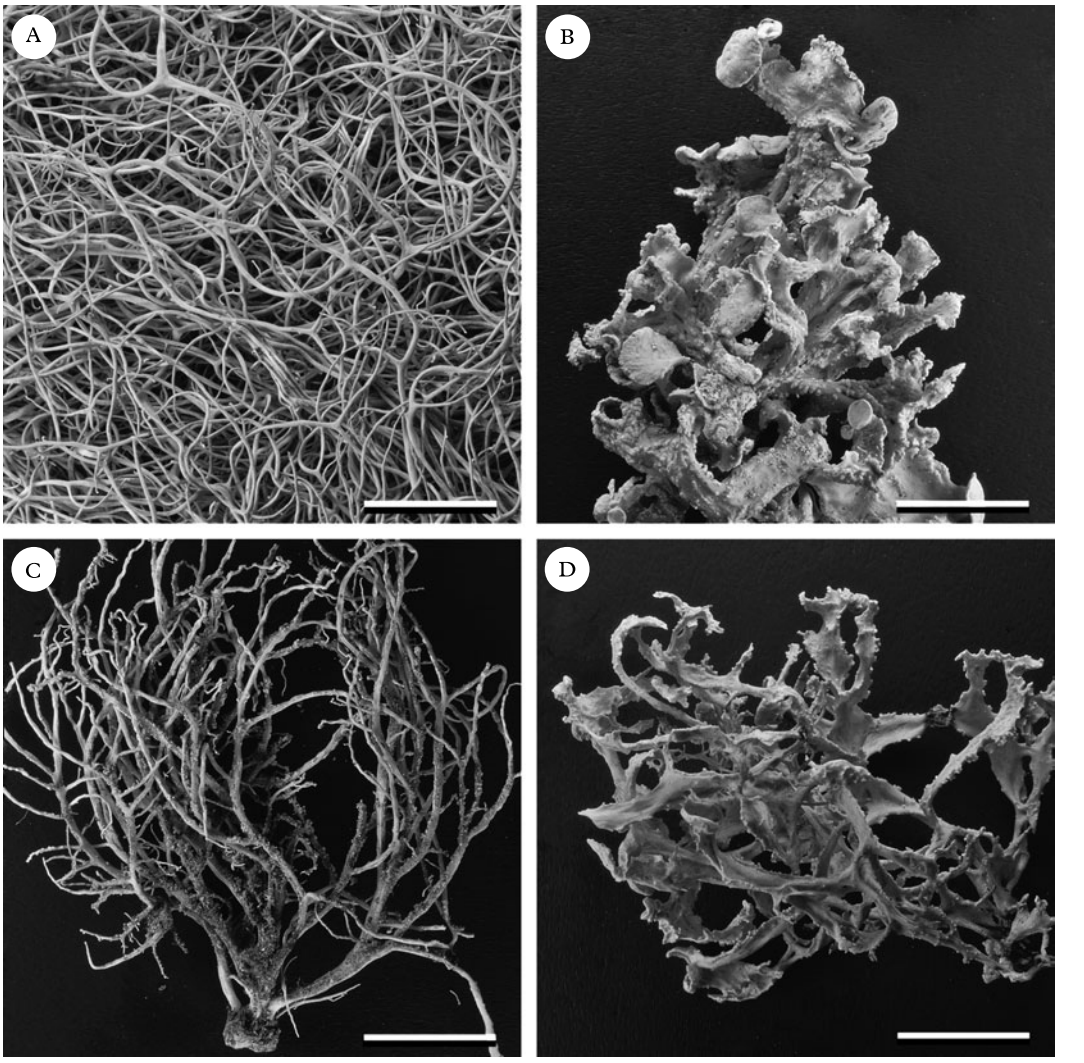

FIG. 2. Herbarium specimens of *Ramalina* species from Galapagos. A, *R. anceps* (*Aptroot* 63942, CDS *no.* 30499); B, *R. aspera* (*Bungartz* 4807, CDS *no.* 28926); C, *R. camptospora* (*Aptroot* 63208 A, CDS *no.* 29939); D, *R. complanata* (*Aptroot* 64903, CDS *no.* 31481). Scales: A=2 cm; B–D=1 cm.

folia and *Waltheria ovata*, on bark, twigs of *Zanthoxylum fagara*, semi-shaded, wind- and rain-exposed, 2006, *F. Bungartz* 4342 (CDS *no.* 28426); Pinta Island, along the trail up to the summit from the S-coast, 0°34′22″N, 90°45′3″W, alt. 329 m, transition zone, open woodland of *Zanthoxylum fagara*, *Pisonia floribunda*, and few *Trema micrantha*; grasses and *Justicia galapagana* in the understorey, on bark, twigs of *Zanthoxylum fagara*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 5856 (CDS *no.* 33532); San Cristóbal Island, Cerro Partido along trail from entrance to Cerro Pelado to Ripioso, 0°51′23″S, 89°27′37″W, alt. 376 m, transition zone, rocky SW-exposed slope of hill with *Jasminocereus thouarsii*, *Clerodendrum molle* var. *glabrescens*, *Psidium galapageium*, *Bromeliaceae* and ferns growing in rock crevices, on bark, twigs of *Psidium galapageium*, S-exposed, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6586 (CDS *no.* 34806); Santa Cruz Island, farm along the southern part of the loop road from Bellavista to Garrapatero, 0°41′12″S, 90°18′22″W, alt. 214 m, agricultural zone, coffee and *Guava* plantations, on bark, branches and trunk of recently logged *Cedrela odorata* tree on the ground, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 3733 (CDS *no.* 27593); Santiago Island, along the trail from Bucanero to Jaboncillos, *c.* 3 km SE of Bucanero,

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0°10′52″S, 90°48′33″W, alt. 362 m, transition zone, open woodland of large *Bursera graveolens* and smaller *Psidium galapageium* trees, grassland and basalt boulders in between, on bark, *Bursera*, 2006, *A. Aptroot* 65394 (CDS *no.* 31980).

Ramalina aspera Räsänen

Ann. bot. Soc. zool. bot. fenn. Vanamo **20:** 5 (1944).

(Fig. 2B)

A pan-American species new to the Galapagos; material of this taxon was reported as *R. complanata* by Weber (1986). The species is corticolous and grows, often abundantly, in the coastal and dry zone. It is frequently confused with *R. complanata*, from which it can be distinguished by its shorter, distinctly broadened and often ± hollow or inflated lobes. All Galapagos specimens are K− and do not contain salazinic acid (Kashiwadani & Kalb 1993). In contrast, *R. complanata* typically reacts K+ yellow, slowly turning red. The colour photograph of *R. complanata* in Brodo *et al.* (2001) is a good likeness of typical *R. aspera* and may be a misidentification.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, along the trail going up the E-slope, barranco to the SE-side of the trail, 0°24′2″S, 91°2′36″W, alt. 410 m, arid zone, basalt boulders and outcrops at the NW-exposed slope of the barranco, *Bursera graveolens* and *Zanthoxylum fagara* growing in between, on bark, dead twig, NE-exposed, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 4385 (CDS *no.* 28470); Pinta Island, along the trail up to the summit from the S-coast, 0°33′22″N, 90°44′34″W, alt. 88 m, arid zone, open woodland of *Bursera graveolens* and few *Opuntia galapageia* with an understorey of *Croton scouleri*, *Castela galapageia*, *Waltheria ovata*, *Lantana peduncularis* among Pahoehoe lava, on bark, twigs of dead *Castela galapageia*, sunny, wind-and rain-exposed, 2007, *F. Bungartz* 6027 (CDS *no.* 33706); Pinzón Island, along the trail going up from Playa Escondida, 0°36′5″S, 90°39′54″W, alt. 225 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64132 B (CDS *no.* 30695); San Cristóbal Island, crest of Cerro Tortuga, *c.* 4 km inland from the NW-coast, 0°44′54″S, 89°23′32″W, alt. 116 m, arid zone, open *Piscidia carthagenensis* woodland with few *Bursera graveolens* and dense understorey of *Croton scouleri*, *Cordia lutea*, and *Mentzelia aspera* on rocky SE-exposed slope of hill, on bark, twigs of *Cordia lutea*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6537 (CDS *no.* 34755); Santa Cruz Island, along the S coast of Santa Cruz, *c.* 1·5 km to the east of the CDRS, 0°44′59″S, 90°17′42″W, alt. 13 m, bare coastal lava rocks with *Cryptocarpus pyriformis*, *Jasminocereus thouarsii*, *Opuntia echios*, and *Scutia spicata* occasionally in between, on wood, 2006, *A. Aptroot* 63699 (CDS *no.* 30254); Santiago Island, along the trail from the caseta in La Central to La Bomba, halfway down to the coast, 0°12′54″S, 90°43′21″W, alt. 293 m, arid zone, open woodland of *Bursera graveolens* and *Opuntia galapageia* with shrubs of *Castela galapageia* among basalt boulders and rocks, on bark, *Castela* twigs, 2006, *A. Aptroot* 65615 (CDS *no.* 32205).

Ramalina camptospora Nyl.

Bull. Soc. Linn. Normandie, sér. 2, **4:** 120 (1870).

(Fig. 2C)

A pan-American species new to the Galapagos; found mostly inland, often on mountain peaks and outcrops (currently known from Santiago, Pinzón, and Santa Cruz Island). The sorediate *R. camptospora* possibly forms a species pair with the fertile *R. puiggarii*. Both species have thallus lobes that originate from a central holdfast, are sparingly, mostly dichotomously branched and neither contain secondary metabolites in their medulla. The lobes of *R. camptospora* are, however, basally angular and soon become flattened, whereas the lobes of *R. puiggarii* are very strongly canaliculate, rolled up and thus appear terete.

Selected specimens examined. **Ecuador:** *Galápagos*: Pinzón Island, along the trail going up from Playa Escondida, 0°36′0″S, 90°39′46″W, alt. 150 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64151 B (CDS *no.* 30715); Santa Cruz Island, near Puntudo, 0°38′41″S, 90°20′13″W, alt. 750 m, fern zone, on rock (basalt lava), 2005, *A. Aptroot* 63208 A (CDS *no.* 29939); Santiago Island, summit of Cerro Gavilan, N- and E-side of the crater, 0°12′20″S, 90°47′3″W, alt. 840 m, fern-sedge zone, N- and NE-exposed, steep basalt cliffs of crater rim with ferns growing in crevices, on rock (basalt lava), 2006, *A. Aptroot* 65739 (CDS *no.* 32331).

Ramalina complanata (Sw.) Ach.

Lichenogr. univ.: 599 (1810).—*Lichen complanatus* Sw., in. Ach., *K. Vet. Nya. Handl.* **18:** 290 (1797).

(Fig. 2D)

Previously reported from the Galapagos; corticolous, rarely saxicolous, from the coastal throughout the dry and into the transition zone, often abundant. Although no *Ramalina* specimens from COLO were available for comparison, we suspect that all material reported by Weber (1986) as *R. complanata* belongs to *R. aspera*. The two species were in the past often confused. Material of *R. complanata* s.str. in COLO was probably reported as *R. denticulata*. In comparison with *R. aspera* thallus lobes of *R. complanata* are only moderately broadened. They are never hollow or inflated and their medulla typically reacts K+ yellow, slowly turning red (salazinic acid). As in *R. aspera*, the thallus surface of *R. complanata* has abundant tuberculate pseudocyphellae. *Ramalina darwiniana* has a similar chemistry; it also reacts K+ yellow, slowly turning red (salazinic acid). The species was previously not recognized and is described below as new. In contrast to *R. complanata*, *R. darwiniana* has lobes that are shiny, and distinctly canaliculate. These lobes are occasionally anastomosing and thus forming holes; the lobe tips are typically curled backwards like shepherds' crooks. Unlike *R. aspera* or *R. complanata*, which have a densely tuberculate pseudocyphellate surface, pseudocyphellae of *R. darwiniana* are typically restricted to tubercules along the lobe margins.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Turtle Cove, on dead branches, 1906, *A. Stewart* 364 (CAS *no.* 640922); Volcán Alcedo, highest cinder cone along the trail going up the E-slope, 0°23′37″S, 91°1′31″W, alt. 250 m, arid lowlands, basalt outcrops, at the bottom scattered *Bursera graveolens* trees and shrubs of *Castela galapageia*, on bark, *Bursera*, 2006, *A. Aptroot* 65026 (CDS *no.* 31608); Gardner Island, near Española, iv 1899, *R. E. Snodgrass* s.n. (CAS *no.* 691735); Española Island, on dead bushes, 1906, *A. Stewart* 368 (CAS *no.* 640925); Floreana Island, alt. 300 m, on twigs, 1905, *A. Stewart* 366 (CAS *no.* 640923); Pinta Island, along the trail up to the summit from the S-coast, 0°34′3″N, 90°44′56″W, alt. 233 m, transition zone, open woodland with *Bursera graveolens*, *Zanthoxylum fagara*, *Pisonia floribunda*, *Croton scouleri*, and few *Opuntia galapageia* among old lava flows, on bark, stem of *Croton scouleri* (*c.* 3 cm diam.), SE-exposed, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 5966 (CDS *no.* 33644); Pinzón Island, along the trail going up from Playa Escondida, N- to W-facing cliff above a crater, 0°36′29″S, 90°40′14″W, alt. 318 m, dry transition zone with *Cordia lutea*, *Croton scouleri*, and at the bottom of the cliff also *Scalesia baurii* ssp. *baurii*, on bark, twigs, 2006, *A. Aptroot* 64057 (CDS *no.* 30618); Rábida Island, alt. 150 m, on dead twigs, 1905, *A. Stewart* 374 (CAS *no.* 637098); cerca la playa de Rábida, 0°23′58″S, 90°42′36.1″W, alt. 27 m, con vegetación de zona costera y árida, dominante *Bursera graveolens*, sobre corteza de *Bursera*, altura al pecho, 2006, *F. Nugra* 92 (CDS *no.* 32746); San Cristóbal Island, Wreck Bay, on bark, twigs and branches, 1906, *A. Stewart* 365 (CAS *no.* 640924); north-western foothills of Media Luna, inland from the NW-coast, 0°43′41″S, 89°18′44″W, alt. 75 m, arid zone, open woodland of *Cordia lutea* and *Bursera graveolens*, on bark, twigs of *Cordia lutea*, semi-shaded, wind- and rain-exposed, 2007, *F. Bungartz* 6196 (CDS *no.* 34408); Cerro Colorado, enclosure for *Calandrinia galapagosa* near the viewpoint on the top, 0°54′58″S, 89°26′5″W, alt. 350 m, transition zone, open shrubland with *Croton scouleri*, *Macraea laricifolia*, *Calandrinia galapagosa* and few trees among lava boulders on SE-exposed slope of cinder cone, on rock, SE-exposed front of soft and weathered tuff outcrop, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6710 (CDS *no.* 34954); Santa Cruz Island, at the North side of the island, along the dirt road to the ash quarry Mina Granilla Roja, 0°36′56″S, 90°22′3″W, alt. 570 m, lower transition zone, dry semi-deciduous forest with *Bursera graveolens* and *Zanthoxylum fagara*, on bark, twigs, 2006, *A. Aptroot* 64562 (CDS *no.* 31134); along the trail from Puerto Ayora to Bahía Tortuga, 0°44′48″S, 90°19′14″W, alt. 28 m, deciduous forest in arid zone, with *Bursea graveolens*, *Acacia rorundiana*, and *Opuntia echios*, over basalt, on bark, twigs of *Acacia insulae-jacobi*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 3357 (CDS *no.* 27024); Santiago Island, *c.* 7 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°17′4″S, 90°38′21″W, alt. 190 m, arid zone, shrubland of *Castela galapageia* and *Macraea laricifolia* with occasional trees of *Bursera graveolens*, on bark, twigs of *Castela galapageia*, sunny, wind-and rain-exposed, 2006, *F. Bungartz* 5071 (CDS *no.* 29284); along the trail from Bucanero to Jaboncillos, *c.* 2 km SE of Bucanero, 0°10′34″S, 90°48′55″W, alt. 225 m, arid zone, open woodland with *Bursera graveolens*, *Vallesia glabra*, *Castela galapageia*, *Cordia lutea* and grasses (e.g, *Cenchrus platyacanthus*) among basalt boulders and outcrops, on bark, *Castela* twigs, 2006, *A. Aptroot* 65365 (CDS *no.* 31951).

Ramalina darwiniana Aptroot & Bungartz sp. nov.

Ramalina corticola lignicola et saxicola, thallo laciniis canaliculatis pseudocyphellatis, verrucis marginalibus, soraliis destituto, apotheciis laminalibus cupulatis in laciniis geniculatis, acidis salazinicis ± sekikaicis ± divaricaticis continens.

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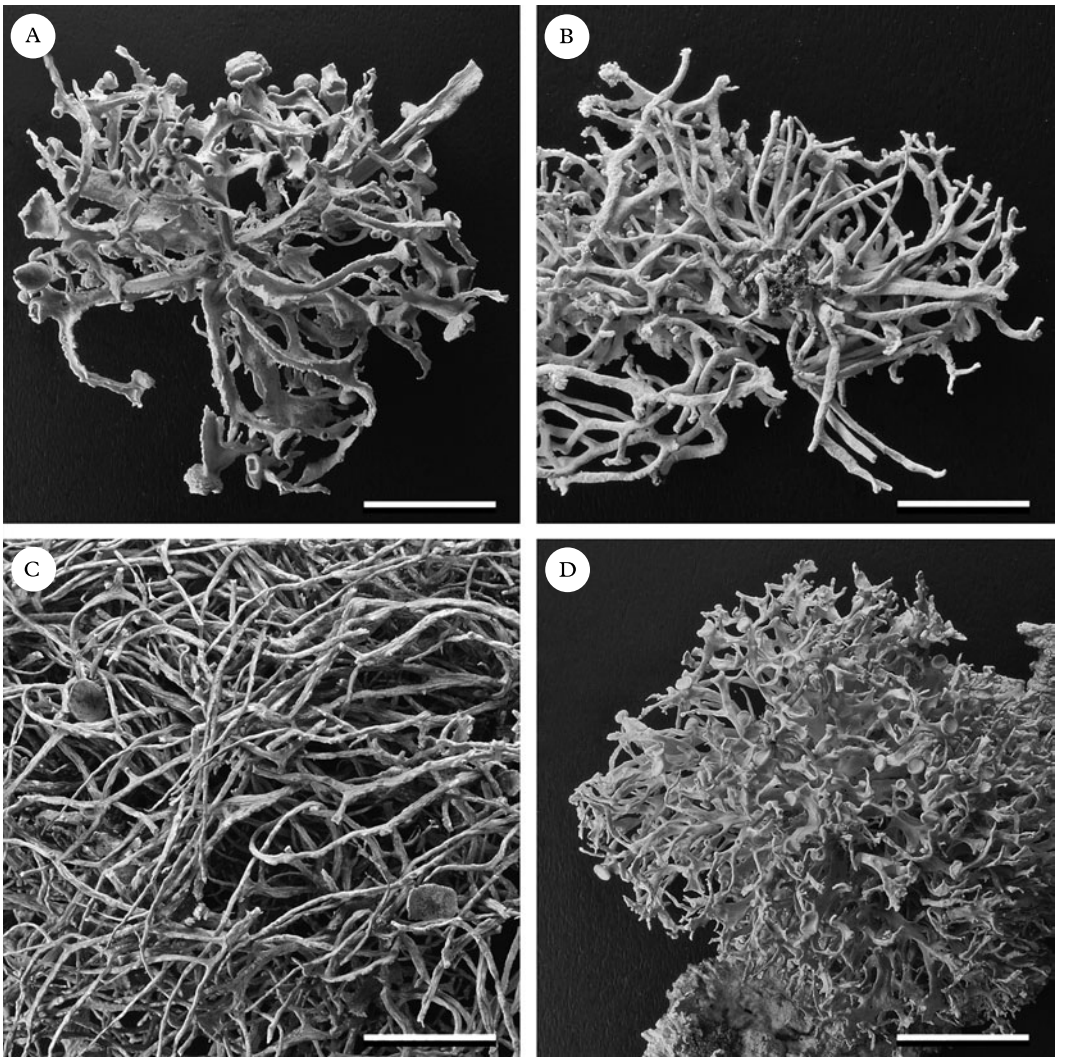

FIG. 3. Herbarium specimens of *Ramalina* from Galapagos. A, *R. darwiniana* (*Aptroot* 64433; CDS *no.* 31001—holotype); B, *R. fragilis* (*Aptroot* 64127; CDS *no.* 30174—holotype); C, *R. furcellangulida* (*Aptroot* 64128; CDS *no.* 30690); D, *R. montagnei* (*Aptroot* 64161; CDS *no.* 30725). Scales: A=1 cm; B–D=2 cm.

Type: Ecuador, Galápagos Islands, Plaza Sur Island, 0°34′59″S, 90°9′54″W, alt. 1 m, coastal zone; eastern part with scattered and low vegetation of *Sesuvium portulacastrum* & *Tiquilia galapagoa* with occasional *Opuntia*, western part also with scattered shrubs of *Grabowskia boerhaaviaefolia*, *Maytenus octogona*, and *Castela galapageia*, on wood, twig, 21 February 2006, *A. Aptroot*, 64433 (CDS *no.* 31001—holotypus; ABL—isotypus).

(Fig. 3A)

Thallus shrubby, greenish grey, decaying parts becoming red, without a distinct holdfast, relatively densely branched, up to 15 cm diam., but usually much smaller (3–7 cm); *branches* initially upright, hanging down when older, in most parts distinctly canaliculate and in section broadly crescent-shaped to ± flattened, sometimes also markedly curved in the longitudinal direction and

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frequently with curved lobe tips ('shepherds' crooks'), slender to relatively broad (up to 15 mm wide), occasionally anastomosing, leaving oval to elongated holes; *lobe margins* with rounded, irregular warts from which irregular, punctiform or sublinear pseudocyphellae develop; *soralia* absent.

Apothecia common, *c.* 2–7 mm diam., cupular, laminal to subterminal; disc yellowish to pinkish grey; branches often bent at the apothecia (geniculate), verrucose below with crateriform pseudocyphellae; *ascospores* hyaline, 1-septate, narrowly oblong, usually ± curved, 10–12 × 4–5 µm.

Pycnidia mostly marginal, hemispherical, 0·1–0·2 mm diam., ostiole pale ochre; *conidia* rod-shaped, 5–6 × 0·5–1·0 µm.

Chemistry. *Medulla* K+ orange yellow, soon red, UV+ white or UV − (salazinic ± sekikaic ± divaricatic acid); *cortex* with usnic acid, occasionally (e.g. in the type collection) also with atranorin.

Etymology. Named in honour of Charles Darwin, and to recognize the scientific accomplishments of the Charles Darwin Research Station.

Notes. This new species is corticolous or lignicolous, rarely also saxicolous, and grows throughout the coastal and arid zone, rarely higher. It is often abundant on twigs and branches in coastal shrub and dry forest. It is similar to *R. complanata*, which, however, has an irregularly flattened, not distinctly canaliculate surface and laminal tuberculate pseudocyphellae. *Ramalina sideriza* is also vaguely similar in habitus and as with *R. darwiniana* has hooked lobe tips, but it has flattened lobes with a distinctly striate, often coarsely linear pseudocyphellate surface.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, highest cinder cone along the trail going up the E-slope, 0°23′37″S, 91°1′31″W, alt. 250 m, arid lowlands, basalt outcrops, at the bottom, scattered *Bursera graveolens* trees and shrubs of *Castela galapageia*, on bark of *Bursera*, 2006, *A. Aptroot* 65030 (CDS *no.* 31612); Pinta Island, at the S-coast, a little E of Cabo Chalmers, 0°33′2″N, 90°46′3″W, alt. 10 m, coastal zone, old lava flow with scarce vegetation (*Opuntia galapageia*, *Alternathera filifolia*, *Prosopis juliflora*), on bark, dead twigs of *Bursera graveolens* lying on the ground, semi-shaded, wind- and rain-exposed, 2007, *F. Bungartz* 6077 (CDS *no.* 33756); Pinzón Island, along the trail going up from Playa Escondida, 0°35′58″S, 90°39′32″W, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64160 (CDS *no.* 30724); Plaza Sur Island, eastern part, 0°34′59″S, 90°9′54″W, alt. 1 m, coastal zone, scattered and low vegetation of *Sesuvium portulacastrum* and *Tiquilia galapagoa* with occasional *Opuntia* spp. in between, on wood of dead twigs, 2006, *A. Aptroot* 64433 (CDS *no.* 31001); Rábida Island, NW-side of Rábida, 0°23′59″S, 90°42′35″W, alt. 27 m, on top of coastal cinder cliff above the beach; N-exposed slope with lava boulders, rocks and young *Bursera graveolens* trees (max. 3 m in height), on bark, twigs of *Bursera graveolens*; sunny, wind- and rain-exposed, 2006, *F. Bungartz* 5351 (CDS *no.* 29567); San Cristóbal Island, near Rosa Blanca, inland from the SE-coast of the island, 0°49′13″S, 89°21′38″W, alt. 16 m, arid zone, open *Bursera graveolens* woodland with *Scutia spicata* in the understorey on top of lava flow, on bark, twigs of *Bursera graveolens*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6412 (CDS *no.* 34627); Santa Cruz Island, Puerto Ayora, near CDRS, 0°44′32″S, 90°18′10″W, alt. 1 m, on rock (basalt lava), 2005, *A. Aptroot* 63074 (CDS *no.* 29802); Charles Darwin Research Station, path near shoreline west of library, growing on *Maytenus octogona*, 1982, *P. Bentley* 17 (CDS *no.* 10881); E of Puerto Ayora, near Charles Darwin Research Station, on lava blocks of wall around tortoise pens, 1 m alt., 2006, *A. Aptroot* 64172 (CDS 30735); near Los Gemelos craters, 0°36′31″S, 90°22′4″W, alt. 350 m, on wood, 2005, *A. Aptroot* 63397 C (CDS *no.* 30150); along the trail from Puerto Ayora to Bahía Tortuga, above the dunes, 0°45′36″S, 90°19′55″W, alt. 16 m, coastal zone with *Cryptocarpus pyriformis* & *Prosopis juliflora*, on bark, dead twigs of *Prosopis juliflora* lying on open ground, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 3396 (CDS *no.* 27063); Santiago Island, *c.* 7 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°17′4″S, 90°38′21″W, alt. 190 m, arid zone; shrubland of *Castela galapageia* and *Macraea laricifolia* with occasional trees of *Bursera graveolens*, *Zanthoxylum fagara* and *Psidium galapageium* on NE-exposed slope, on bark, trunk of *Acacia rorudiana* (*c.* 20 cm diam.), W-exposed, shaded, wind- and rain-sheltered, 2006, *F. Bungartz* 5124 (CDS *no.* 29337).

Ramalina darwiniana var. curvida Aptroot var. nov.

Ramalina darwiniana var. typica differt thallo laciniis canaliculatis curvatis, 2–3 mm diam. max.

Typus: Ecuador, Galápagos Islands, Santa Cruz Island, Puerto Ayora, near the Charles Darwin Research Station, 0°44′32″S, 90°18′10″W, alt. 5 m, on twigs of coastal shrubs, 24 May 2005, *A. Aptroot* 63029 (CDS *no.* 29757—holotypus; ABL—isotypus).

Notes. *Ramalina darwiniana* var. *curvida* is described here to accommodate specimens that have consistently narrow, more strongly and deeply canaliculate lobes. In the field the two varieties can often be distinguished when growing side by side. Molecular studies may help to elucidate if the two varieties should be distinguished at species level.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, highest cinder cone along the trail going up the E-slope, 0°23′37″S, 91°1′31″W, alt. 250 m, arid lowlands, basalt outcrops, at the bottom scattered *Bursera graveolens* trees and shrubs of *Castela galapageia*, on bark, *Bursera*, 2006, *A. Aptroot* 65025 (CDS *no*. 31607); Plaza Sur Island, 0°34′59″S, 90°9′54″W, alt. 1 m, coastal zone, eastern part with scattered and low vegetation of *Sesuvium portulacastrum* and *Tiquilia galapagoa*, on wood, twig, 2006, *A. Aptroot* 64434 (CDS *no*. 31002); Pinzoń Island along the trail going up from Playa Escondida, 0°35′58″S, 90°39′32″W, alt. 20–100 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark of twigs, 2006, *A. Aptroot* 64164 (CDS *no*. 30728); Santa Cruz, Puerto Ayora, CDRS area, 0°44′32″S, 90°18′10″W, alt. 1 m, on lava rock, 2006, *A. Aptroot* 64170 (CDS *no*. 30733); Santiago Island, along the trail from Bucanero to Jaboncillos, *c*. 2 km SE of Bucanero, 0°10′34″S, 90°48′55″W, alt. 225 m, arid zone, open woodland with *Bursera graveolens*, *Vallesia glabra*, *Castela galapageia*, *Cordia lutea* and grasses, among basalt boulders and outcrops, on bark, *Erythrina*, 2006, *A. Aptroot* 65362 (CDS *no*. 31948).

Ramalina fragilis Aptroot & Bungartz sp. nov.

Ramalina saxicola, thallo laciniis teretis fragilissimis, soraliis capitatis albis, apotheciis ignotis, acido ± sekikaico continens.

Typus: Ecuador, Galápagos Islands, San Cristóbal, near Tortugueria Cerro Colorado, on lava cliff, 130 m alt., 2 June 2005, *A. Aptroot* 63419 (CDS 30174—holotypus; ABL—isotypus).

(Fig. 3B)

Thallus dull, shrubby, up to 3 cm diam., upright or irregularly spreading, fragile, with very few branches, rather pale grey and resembling a small *Roccella*; *branches* terete, up to *c*. 1 mm diam., but usually much thinner; *soralia* discrete, capitate, whitish, up to *c*. 1 mm diam.

Apothecia and *pycnidia* unknown.

Chemistry. Medulla K−, UV− (no substances) or K+ pinkish, UV− (sekikaic acid); cortex with usnic acid and often atranorin.

Etymology. The small branches are relatively fragile and easily break off at the base.

Notes. Because of its similarity to *Roccella*, the small, pale thalli with terete, fragile branches can hardly be confused with any other *Ramalina* species in the Galapagos. Although it is very distinct, this small species may easily be overlooked.

Selected specimens examined. **Ecuador:** *Galápagos*: Pinzón Island, along the trail going up from Playa Escondida, 0°36′10″S, 90°40′1″W, alt. 254 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on rock, basalt, 2006, *A. Aptroot* 64127 (CDS *no*. 30689); San Cristóbal Island, near Tortugueria Cerro Colorada, 0°54′56″S, 89°26′18″W, alt. 130 m, on rock (basalt lava), 2005, *A. Aptroot* 63419 (CDS *no*. 30174); rim of crater to the NW of Media Luna, inland from the NW-coast, 0°43′51″S, 89°18′55″W, alt. 149 m, lower transition zone, basalt cliffs of inner and outer crater rim with scarce vegetation, on rock, S-exposed overhang of cliff on top of crater rim, shaded, wind- and rain-sheltered, 2007, *F. Bungartz* 6306 (CDS *no*. 34518).

Ramalina furcellangulida Aptroot sp. nov.

Ramalina corticola, thallo poly-angulato pseudocyphellato verrucoso, soraliis destituto, apotheciis laminalibus cupulatis in laciniis geniculatis, acidis ± salazinicis ± sekikaicis ± divaricaticis continens.

Typus: Ecuador, Galapagos Islands, Isabela, Volcán Alcedo, highest cinder cone along the trail going up the east slope, on bark of *Bursera graveolens*, 250 m alt., 10 March 2006, *A. Aptroot* 65029 (CDS 31611—holotypus; ABL—isotypus).

(Fig. 3C)

Thallus shrubby, greenish grey to pale grey, decaying parts sometimes becoming red, up to 5 cm diam. but usually much smaller (1–3 cm), relatively densely branched, without a distinct holdfast; *branches* initially upright, hanging down when older, in section irregularly angular, typically not flattened, sometimes markedly curved in the longitudinal direction and frequently with curved lobe tips (‘‘shepherds’

crooks''), relatively slender (up to 2 mm wide), often with rounded, irregular, laminal warts that typically abrade into parallel, linear pseudocyphellae, rarely also with few punctiform tuberculate pseudocyphellae, or with pycnidial or apothecial warts; *soredia* absent.

Apothecia common, *c*. 1–4 mm in diam., cupular, laminal, disc yellowish grey, branches often strongly bent at the apothecia (geniculate, apothecia thus appearing ''two-stalked''); *ascospores* narrowly oblong, usually ± curved, 16–20 × 3–4 µm.

Pycnidia mostly marginal, hemispherical, 0·1–0·2 mm diam., ostiole pale ochre; *conidia* rod-shaped, 4–5 × 0·5–0·7 µm.

Chemistry. Medulla K+ orange-yellow, soon red, rarely K−, UV+ white or UV− (divaricatic or salazinic and/or sekikaic acid); cortex with usnic acid, often also with atranorin.

Etymology. From the Latin words ''*furcellatus*'' meaning forked, and ''*angulus*'' meaning angular because of its angular, forked branches.

Note. This species is mostly corticolous, rarely also saxicolous and grows throughout the coastal and arid zone, where it is often abundant.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, highest cinder cone along the trail going up the E-slope, 0°23′37″S, 91°1′31″W, alt. 250 m, arid lowlands, basalt outcrops, at the bottom scattered *Bursera graveolens* trees and shrubs of *Castela galapageia*, on bark, *Bursera*, 2006, *A. Aptroot* 65029 (CDS *no*. 31611); Pinta Island, along the trail up to the summit from the S-coast, 0°33′29″N, 90°44′37″W, alt. 108 m, arid zone, open shrubland with *Corton scouleri*, *Waltheria ovata*, *Opuntia galapageia*, and few *Bursera graveolens* among flat Pahoehoe lava, on bark, branch of *Bursera graveolens*, SE-exposed; sunny, wind- and rain-exposed, 2007, *F. Bungartz* 5997 (CDS *no*. 33675); Pinzón Island, along the trail going up from Playa Escondida, 0°36′10″S, 90°40′1″W, alt. 254 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *Aptroot*, *A*. 64128 (CDS *no*. 30690); Plaza Sur Island, 0°34′59″S, 90°9′54″W, alt. 1 m, coastal zone, eastern part with scattered and low vegetation of *Sesuvium portulacastrum* and *Tiquilia galapagoa* with occasional *Opuntia*, on rock (basalt lava), 2006, *A. Aptroot* 64456 (CDS *no*. 31025); San Cristóbal Island, crest of Cerro Tortuga, *c*. 4 km inland from the NW-coast, 0°44′54″S, 89°23′32″W, alt. 116 m, arid zone, open *Piscidia carthagenensis* woodland with few *Bursera graveolens* and dense understorey of *Croton scouleri*, *Cordia lutea*, and *Mentzelia aspera* on rocky SE-exposed slope of hill, on bark, twigs of *Cordia lutea*; sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6531 (CDS *no*. 34749); near Rosa Blanca, inland from the SE-coast of the island, 0°49′13″S, 89°21′38″W, alt. 16 m, arid zone, open *Bursera graveolens* woodland with *Scutia spicata* in the understory on top of lava flow, on bark, twigs of *Bursera graveolens*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6415 (CDS *no*. 34630); S of Punta Pit at the NE-coast of the island, 0°43′27″S, 89°15′6″W, alt. 113 m, coastal zone, on top a crater rim, open shrubland with *Cordia lutea* and abundant *Mentzelia aspera* as ground cover, on bark, twigs of dead shrub, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6115 (CDS *no*. 33794); Santa Cruz Island, along shore E of Puerto Ayora near CDRS, 0°44′45″S, 90°17′39″W, alt. 20 m, coastal zone, on rock, coastal lava, 2005, *A. Aptroot* 63276 C (CDS *no*. 30014); Santa Cruz Island, along the S coast of Santa Cruz, *c*. 1 km to the east of the CDRS, 0°44′45″S, 90°17′39″W, alt. 13 m, bare coastal lava cliffs, SW-exposed, *Cryptocarpus pyriformis* and *Jasminocereus thouarsii* occasionally in between, on bark, twigs of *Cryptocarpus pyriformis*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 3429 (CDS *no*. 27135); Santiago Island, *c*. 5 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°16′35″S, 90°37′23″W, alt. 172 m, arid zone, plateau of lava flows and boulders with scarce vegetation (*Bursera graveolens*, *Castela galapageia*, *Mentzelia aspera*), on bark, twigs of *Castela galapageia*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 5239 (CDS *no*. 29454).

Ramalina montagnei De Not.

Giorn. Bot. Ital. **1**(1)**:** 218 (1846).

(Fig. 3D)

This predominantly Central American species is reported here as new to the Galapagos. It is a typical corticolous element of the coastal and arid zone. The species is characterized by narrow lobes, which are ± angular and never canaliculate. Towards the base its branches become distinctly flattened, the lobe tips are pointed and not curled backwards. The apothecia are laminal along the side of the branches. The branches have a dense medulla, a smooth to finely

striate surface with parallel, linear pseudocyphellae; tubercules are absent. The species reacts K− or K+ pinkish (sekikaic acid). The Galapagos material does not contain stenosporic acid.

Selected specimens examined. **Ecuador:** *Galápagos*: Pinta Island, at the S-coast, a little E of Cabo Chalmers, 0°33′2″N, 90°46′3″W, alt. 10 m, coastal zone, old lava flow with scarce vegetation (*Opuntia galapageia*, *Alternathera filifolia*, *Prosopis juliflora*), on bark, dead twigs of *Bursera graveolens* lying on the ground, semi-shaded, wind- and rain-exposed, 2007, *F. Bungartz* 6076 (CDS *no.* 33755); Pinzón Island, along the trail going up from Playa Escondida, 0°36′5″S, 90°39′54″W, alt. 225 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64133 (CDS *no.* 30696); San Cristóbal Island, saddle between the two summits of Cerro Tortuga, 0°44′52″S, 89°29′27″W, alt. 140 m, arid zone, open *Piscidia carthagenensis* woodland with understorey of *Cordia lutea*, on bark, twigs of *Cordia lutea*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6556 (CDS *no.* 34774); Santa Cruz Island, at the North side of the island, along the dirt road to the ash quarry Mina Granilla Negra, 0°34′22″S, 90°19′55″W, alt. 27 m, arid zone, dry deciduous lowland forest (*Bursera graveolens*, *Heliotropium* sp., *Acacia* sp, *Zanthoxylum fagara*), on bark, twigs, 2006, *A. Aptroot* 64481 (CDS *no.* 31053); Santiago Island, along the trail from Bucanero to Jaboncillos, *c.* 2 km SE of Bucanero, 0°10′34″S, 90°48′55″W, alt. 225 m, arid zone, open woodland with *Bursera graveolens*, *Vallesia glabra*, *Castela galapageia*, *Cordia lutea* and grasses, among basalt boulders and outcrops, on bark, *Castela* twigs, 2006, *A. Aptroot* 65366 (CDS *no.* 31952).

Ramalina peruviana Ach.

Lichenogr. univ. 599 (1810).

(Fig. 4A)

A pantropical species previously reported from the Galapagos by Weber (1986); mostly corticolous, mostly inland. Because of its thin branches and a similar habitus, *R. peruviana* could be mistaken for *R. sorediosa*. Though equally thin, the branches of *R. peruviana* are, however, irregularly angular to indistinctly flattened, and never terete. Most diagnostic are the fine isidiate branchlets, that develop from the soralia and are also typically present at the tip of thallus branches, of *R. peruviana*. These branchlets cannot be observed in *R. sorediosa*.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Villamil, alt. 410 m, on dead twigs, 1905, *A. Stewart* 372 (CAS *no.* 638118); Volcán Alcedo, in the crater, 0°27′9″S, 91°6′41″W, alt. 780 m, transition zone, mostly *Bursera graveolens* and dense scrub on uneven lava, on bark, twigs, 2006, *A. Aptroot* 64750 (CDS *no.* 31325); outer SE-exposed slope and crater rim, 0°27′29″S, 91°7′19″W, alt. 1089 m, fern-sedge zone, tortoise pasture with scattered trees (*Tournefortia rufo-sericea*, *Zanthoxylum fagara*), on bark, *Tournefortia*, 2006, *A. Aptroot* 65038 (CDS *no.* 31620); Pinzón Island, along the trail going up from Playa Escondida, N- to W-facing cliff above a crater, 0°36′29″S, 90°40′14″W, alt. 318 m, dry transition zone with *Cordia lutea*, *Croton scouleri*, and at the bottom of the cliff also *Scalesia baurii* ssp. *baurii*, on bark, twigs, 2006, *A. Aptroot* 64059 (CDS *no.* 30620); San Cristóbal Island, S of Punta Pit at the NE-coast of the island, 0°43′27″S, 89°15′6″W, alt. 113 m, coastal zone, on top a crater rim, open shrubland with *Cordia lutea* and abundant *Mentzelia aspera* as ground cover, on bark, twigs of dead shrub, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6110 (CDS *no.* 33789); Santa Cruz Island, along the southern part of the loop road from Bellavista to Garrapatero, 0°41′30″S, 90°18′10″W, alt. 210 m, agricultural zone, coffee and guava plantations, on bark, *Cedrela*, 2006, *A. Aptroot* 64221 (CDS *no.* 30787); along the road from Bellavista to El Garrapatero, at the boundary of the National Park, 0°40′0″S, 90°15′46″W, alt. 252 m, transition zone with *Zanthoxylum fagara*, *Lantana camara*, *Citrus* sp, and *Croton scouleri*, on rock (basalt lava), 2006, *A. Aptroot* 63938 A (CDS *no.* 30494); Santiago Island, *c.* 5 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°16′35″S, 90°37′23″W, alt. 172 m, arid zone, plateau of lava flows and boulders with scarce vegetation (*Bursera graveolens*, *Castela galapageia*, *Mentzelia aspera*), on bark, twigs of *Castela galapageia*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 5238 (CDS *no.* 29453).

Ramalina polyforma Aptroot sp. nov.

Ramalina saxicola, thallo laciniis teretis vel applanatis, irregulariter divisis, rugulosostriatis, soraliis apicalibus confluentibus, apotheciis ignotis, acidis ± salazinicis ± sekikaicis ± divaricaticis continens.

Typus: Ecuador, Galápagos Islands, Santa Cruz, on coastal lava cliffs E of Puerto Ayora near Charles Darwin Research Station, 20 m alt., 29 May 2005, *A. Aptroot* 63412 (CDS 30176—holotypus; ABL—isotypus).

(Fig. 4B & C)

Thallus dull, shrubby, up to 3 cm diam., upright, greenish grey, somewhat fragile, very variable in branching pattern, for example, with few, short, stout and broadly flattened, antler-like branches that have

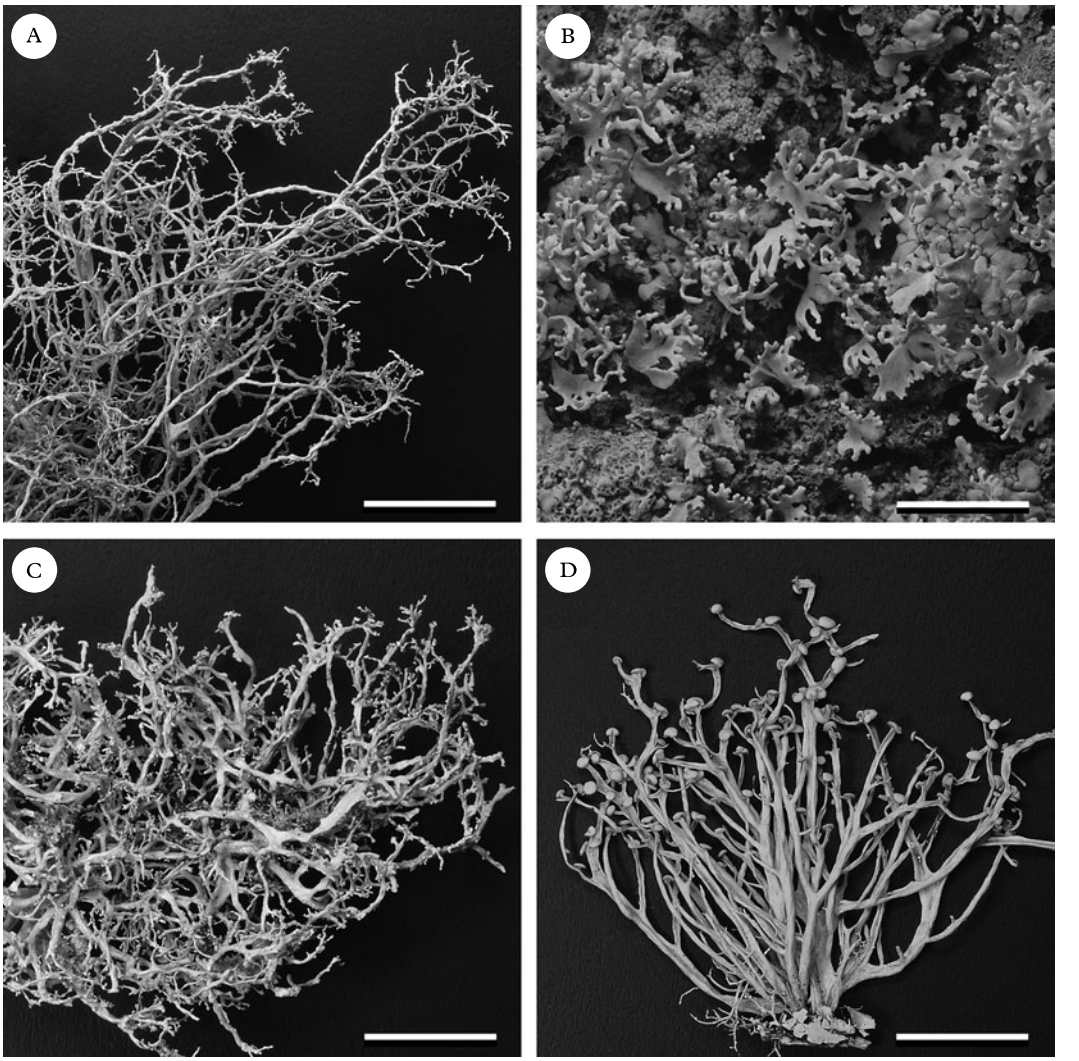

FIG. 4. Herbarium specimens of *Ramalina* species from Galapagos. A, *R. peruviana* (*Aptroot* 64221, CDS *no.* 30787); B, *R. polyforma*, antler-shaped morphotype (*Aptroot* 64371, CDS *no.* 30936); C, *R. polyforma*, irregularly branched morphotype (*Aptroot* 64019, CDS *no.* 30580); D, *R. puiggarii* (*Aptroot* 65496; CDS *no.* 32085). Scales: A=2 cm; B=0·7 mm; C–D=1 cm.

curled tips (Fig. 4B), or with densely ramified, irregularly angular branches that apically become terete (Fig. 4C), occasionally with curled tips (hooks), up to *c.* 3 mm diam., but usually much thinner; *surface* wrinkled, irregularly striate from cartilaginous cortical strands; *soredia* rather discrete but occasionally confluent, capitate or irregular, but mostly terminal, yellowish, up to *c.* 1 mm diam.

Apothecia and *pycnidia* unknown.

Chemistry. Medulla K+ orange-yellow, soon red, rarely K−, UV+ white or UV− (salazinic ± sekikaic ± divaricatic acid or nil); cortex with usnic acid.

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Etymology. The species has a very variable morphology.

Notes. This species is the most common (often the dominant) saxicolous *Ramalina* on the Galapagos. It has been found in all vegetation zones on moderately exposed to sheltered rocks. It appears to be more common along the coast, throughout the arid zone and the lower transition zone, only one specimen is known from higher altitudes. The species is unusually variable with two morphological extremes that nevertheless intergrade.

Selected specimens examined. **Ecuador:** *Galápagos*: Bartolomé Island, N-side of island, near Pinnacle Rock, 0°17′2″S, 90°33′15″W, alt. 10 m, W-exposed steep slope of lava flow (basalt) with scarce low vegetation, on rock, small protrusions of *aa*-lava rock, W-exposed, sunny, wind- and rain-sheltered, 2006, *F. Bungartz* 5325 (CDS *no.* 29541); Isabela Island, Volcán Alcedo, cinder cone *c.* 100 m from the shore and a little N of Islote Cowley, 0°22′54″S, 91°0′4″W, alt. 17 m, coastal zone, basalt outcrops (*aa*-lava) bare of vegetation, on rock, SE-exposed front of basalt outcrop, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 4503 (CDS *no.* 28589); Isabela Island, Volcán Alcedo, highest cinder cone along the trail going up the E-slope, 0°23′37″S, 91°1′31″W, alt. 250 m, arid lowlands, basalt outcrops, at the bottom scattered *Bursera graveolens* trees and shrubs of *Castela galapageia*, on rock (basalt lava), 2006, *A. Aptroot* 65004 (CDS *no.* 31584); Pinzón Island, along the trail going up from Playa Escondida, N- to W-facing cliff above a crater, 0°36′29″S, 90°40′14″W, alt. 318 m, dry transition zone with *Cordia lutea*, *Croton scouleri*, and at the bottom of the cliff also *Scalesia baurii* ssp. *baurii*, on rock (basalt lava), 2006, *A. Aptroot* 64019 (CDS *no.* 30580, Fig. 4C); Plaza Norte Island, 0°34′47″S, 90°9′47″W, alt. 1 m, coastal zone, vertical, S-exposed coastal cliffs and on top of island inpenetrable thicket of *Grabowskia boerhaaviaefolia* and *Scutia spicata* with occasional *Opuntia* in between, on wood, twig, 2006, *A. Aptroot* 64380 (CDS *no.* 30945); Plaza Sur Island, 0°34′59″S, 90°9′54″W, alt. 1 m, coastal zone, eastern part with scattered and low vegetation of *Sesuvium portulacastrum* and *Tiquilia galapagoa* with occasional *Opuntia* sp., on rock (basalt lava), 2006, *A. Aptroot* 64458 (CDS *no.* 31027); San Cristóbal Island, from Punta Tortuga *c.* 3 km inland close to Cerro Tortuga, 0°44′39″S, 89°23′32″W, alt. 79 m, arid zone, young basalt lava flow of bare *aa*-lava, on rock, NW-exposed cavity in small basalt outcrop, shaded, wind- and rain-sheltered, 2007, *F. Bungartz* 6506 (CDS *no.* 34723); Santa Cruz Island, Puerto Ayora, near CDRS, 0°44′32″S, 90°18′10″W, alt. 1 m, on rock (basalt lava), 2006, *A. Aptroot* 63680 (CDS *no.* 30236); Santa Cruz Island, at the east coast of the island, *c.* 400 m N of Cerro Colorado, on top of the coastal cliff; E-exposed, 0°34′47″S, 90°10′21″W, alt. 21 m, arid zone, scattered scrubs of *Castela galapageia*, *Acacia rorudiana*, and *Opuntia echios* among basaltic rocks, a rare *Bursera graveolens* in between, on rock, lava, 2006, *Aptroot, A.* 64371 (CDS *no.* 30936, Fig. 4B); Santiago Island, summit of Cerro Gavilan, N- and E-side of the crater, 0°12′20″S, 90°47′3″W, alt. 840 m, fern-sedge zone, N- and NE-exposed, steep basalt cliffs of crater rim with ferns growing in crevices, on rock (basalt lava), 2006, *A. Aptroot* 65656 (CDS *no.* 32247).

Ramalina puiggarii Müll. Arg.

Flora, Jena **64:** 83 (1881).

(Fig. 4D)

A pan-American species previously reported from the Galapagos by Dodge (1936). This report was refuted by Weber (1986) who instead used the name *R. linearis* (Sw.) Ach., based on a New Zealand type, for this taxon. It grows only inland from the lower transition zone into the humid highlands, on bark or wood, rarely on rock. The species can very easily be recognized by its strongly canaliculate upright lobes that are rolled up and thus appear terete. They are sparsely branched and grow from a common holdfast like a ''bouquet of flowers''.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, outer E-exposed slope just below the crater rim, 0°25′17″S, 91°5′8″W, alt. 1077 m, fern-sedge zone, basalt outcrops, SE-exposed slope with scattered shrubs of *Tournefortia rufo-sericea*, *Opuntia insularis*, *Lantana peduncularis* and occasional trees of *Zanthoxylum fagara* among basalt rubble, on rock (basalt lava), 2006, *A. Aptroot* 65146 (CDS *no.* 31729); San Cristóbal Island, Cerro Partido along trail from entrance to Cerro Pelado to Ripioso, 0°51′23″S, 89°27′37″W, alt. 376 m, transition zone, rocky SW-exposed slope of hill with *Jasminocereus thouarsii*, *Clerodendrum molle* var. *glabrescens*, *Psidium galapageium*, *Bromeliaceae* and ferns growing in rock crevices, on wood, twigs of dead tree, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6617 (CDS *no.* 34837); Santa Cruz Island, near Los Gemelos craters, 0°36′31″S, 90°22′4″W, alt. 350 m, on wood, 2005, *A. Aptroot* 63397 B (CDS *no.* 30149); Santa Cruz Island, along the road from Los Gemelos towards the N-coast of the island, *c.* 1 km N of Los Gemelos, 0°37′7″S, 90°22′35″W, alt. 584 m, transition zone with open dry forest, *Scalesia pedunculata*, on bark, twigs, 2006, *A. Aptroot* 63773 (CDS *no.* 30333); Santiago Island, summit of Cerro Gavilan, outer

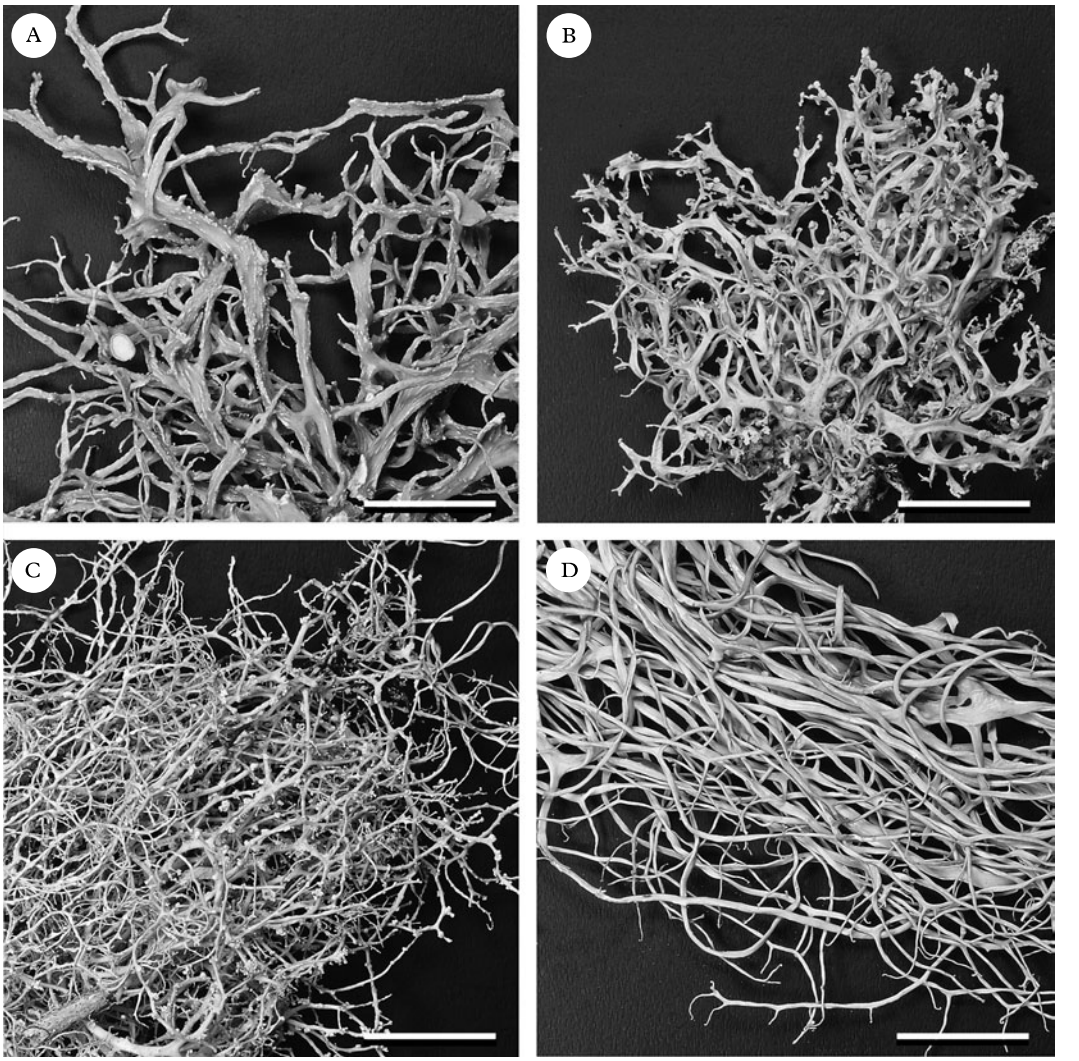

FIG. 5. Herbarium specimens of *Ramalina* species from Galapagos. A, *R. sideriza* (*Aptroot* 65302, CDS *no.* 31888); B, *R. sorediantha* (*Bungartz* 4576; CDS *no.* 28663); C, *R. sorediosa* (*Aptroot* 63944; CDS *no.* 30501); D, *R. usnea* (lobes 1 mm; *Bungartz* 5170; CDS *no.* 29383). Scales: A–B=1 cm; C=2 cm; D=1 cm.

S-exposed crater rim, 0°12′23″S, 90°46′57″W, alt. 840 m, fern-sedge zone, S-exposed, steep basalt cliffs of crater rim with ferns growing in crevices, on bark of *Psidium*, 2006, *A. Aptroot* 65496 (CDS *no.* 32085); Santiago Island, along the trail from Bucanero to Jaboncillos, *c.* 200 m below the summit, Cerro Gavilan, 0°12′9″S, 90°47′3″W, alt. 796 m, upper part transition zone, open *Psidium galapageium* forest with *Zanthoxylum fagara*, dense understorey of *Clerodendrum molle*, *Tournefortia pubescens* and others, on bark, twigs of *C. molle*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 4729 (CDS *no.* 28840).

Ramalina sideriza Zahlbr.

Ann. K. K. Naturhist. Hofmus. **25:** 246 (1911).

(Fig. 5A)

New to Galapagos; the material collected during this study matches the specimens collected by A. Stewart in Academy Bay during the Expedition of the Californian

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Academy of Sciences to the Galapagos Islands, 1905–1906. This CAS material was annotated by H. Kashiwadani in 1999 as *R. sideriza*, a species described by Zahlbruckner from Hawaii. However, the Galapagos material differs slightly from some exsiccati collections identified as *R. sideriza* from Hawaii (Hawaii, Volcanoes Ntl. Park, 4000 ft, *Weber & Bujakiewicz*, distributed in *Weber, Lich. Exs*. no 633), which has consistently marginal apothecia and is partly geniculate. Comparison with further material of *R. sideriza* is necessary to confirm the identity of the Galapagos specimens; meanwhile they are included in this species.

The Galapagos specimens are similar to *R. complanata* and the CAS material that was annotated by Kashiwadani had previously been identified as this species. All Galapagos material can, however, be reliably distinguished from *R. complanata* by its conspicuously striate lobe surface, which soon develops into distinct parallel ridges abrading into broadened, linear pseudocyphellae. Unlike *R. complanata*, the lower surface of apothecia in *R. sideriza* is relatively smooth and not tuberculate or ridged. Furthermore, the lobe tips of *R. sideriza* are curled backwards into ''shepherds' crooks'', whereas lobes of *R. complanata* are tapered and blade-like.

The species is corticolous or lignicolous or rarely saxicolous and is a characteristic and common epiphyte throughout the coastal and arid zone.

Selected specimens examined. **Ecuador:** *Galápagos*: Tortuga Island (near Isabela Island), on bushes, 1905, *A. Stewart* 370 (CAS *no.* 640928); Española Island, v 1899, *R.E. Snodgrass* s.n. (CAS *no.* 691734); on dead branches, 1905, *A. Stewart* 367 (CAS *no.* 640926); Genovesa Island, on bushes, 1905, *A. Stewart* 369 (CAS *no.* 640927); Plaza Norte Island, 0°34′47″S, 90°9′47″W, alt. 1 m, coastal zone, vertical, impenetrable thicket of *Grabowskia boerhaaviaefolia* and *Scutia spicata* with occasional *Opuntia* in between, on wood, twig, 2006, *A. Aptroot* 64374 (CDS *no.* 30939); Santa Cruz Island, SE-side, on bushes, 1905, *A. Stewart* 371 (CAS *no.* 637096); Puerto Ayora, CDRS area, 0°44′32″S, 90°18′10″W, alt. 1 m, on rock (lava), 2006, *A. Aptroot* 64171 (CDS *no.* 30734); Santa Cruz Island, along the trail from Puerto Ayora to Bahía Tortuga, above the dunes, 0°45′36″S, 90°19′55″W, alt. 16 m, coastal zone with *Cryptocarpus pyriformis* & *Prosopis juliflora*, on bark, dead twigs of *Prosopis juliflora* lying on open ground, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 3395 (CDS *no.* 27062); San Cristóbal Island, hills S of Punta Pit at the NE-coast of the island, 0°43′16″S, 89°14′40″W, alt. 63 m, coastal zone, SSE-exposed ridge of basalt cliff, on rock at the SE-front of the cliff, semi-shaded, wind- and rain-exposed, 2007, *F. Bungartz* 6174 (CDS *no.* 34386); Santiago Island, at the W-coast of the island in Bahía Ladilla, 0°18′8″S, 90°49′56″W, alt. 10 m, S-exposed coastal lava cliff and boulders, on rock at the S-exposed cliff face, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 5394 (CDS *no.* 29610).

Ramalina sorediantha Nyl.

Bull. Soc. Linn. Normandie, sér. 2 **4:** 143 (1870).

(Fig. 5B)

A pan-American species already reported from the Galapagos by Weber (1986). It is quite abundant and widespread, mostly inland, but occasionally also coastal; mostly corticolous, rarely lignicolous. This species is not to be confused with *R. sorediosa*, which, in spite of its similar name, differs significantly in its thallus morphology. *Ramalina sorediantha* has ± flattened, in part canaliculate lobes, whereas *R. sorediosa* resembles a small *Usnea* with very thin, almost entirely terete branches that are never canaliculate.

Several specimens in CDS are currently included in *R. sorediantha* s. lat. with some reservation. These specimens have lobes that are less obviously canaliculate than *R. sorediantha* s. str. They are therefore similar to *R. pacifica*, a species previously not reported from South America. More material should be examined to clarify the identity of these specimens.

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, in the crater, 0°27′9″S, 91°6′41″W, alt. 780 m, transition zone, mostly *Bursera graveolens* and dense scrub on uneven lava, on bark, twigs, 2006, *A. Aptroot* 64751 (CDS *no.* 31326); outer SE-exposed slope and crater rim, 0°27′29″S, 91°7′19″W, alt. 1089 m, fern-sedge zone, tortoise pasture with scattered trees (*Tournefortia rufo-sericea*, *Zanthoxylum fagara*), on bark, *Zanthoxylum*, 2006, *A. Aptroot* 65046 (CDS *no.* 31628); Pinta Island, along the trail up to the summit from the S-coast, 0°34′22″N, 90°45′3″W, alt. 329 m, transition zone, open woodland of *Zanthoxylum fagara*, *Pisonia floribunda*, and few *Trema micrantha*, grasses and *Justicia*

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galapagana in the understorey, on bark, twigs of *Zanthoxylum fagara*, shaded, wind- and rain-sheltered, 2007, *F. Bungartz* 5873 (CDS *no.* 33549); Pinzón Island, along the trail going up from Playa Escondida, 0°36′5″S, 90°39′54″W, alt. 225 m, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64134 (CDS *no.* 30697); San Cristóbal Island, crest of Cerro Tortuga, *c.* 4 km inland from the NW-coast, 0°44′54″S, 89°23′32″W, alt. 116 m, arid zone, open *Piscidia carthagenensis* woodland with few *Bursera graveolens* and dense understorey of *Croton scouleri*, *Cordia lutea*, and *Mentzelia aspera* on rocky SE-exposed slope of hill, on bark, twigs of *Cordia lutea*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6536 (CDS *no.* 34754); Santa Cruz Island, along the southern part of the loop road from Bellavista to Garrapatero, 0°41′30″S, 90°18′10″W, alt. 210 m, agricultural zone, coffee and guava plantations, on bark, *Cedrela*, 2006, *A. Aptroot* 64218 (CDS *no.* 30784); abandoned farm along the northern part of the loop road from Bellavista to Garrapatero, 0°40′58″S, 90°18′31″W, alt. 255 m, agricultural zone, overgrown farm area with introduced trees such as *Cedrela odorata*, *Persea americana*, *Syzygium malaccense*, and others, small open clearing in between, on dead wood (twigs and branches) on the ground, 2006, *F. Ziemmeck* 685 (CDS *no.* 27547); Camote, finca de René Valle lindero PNG, 0°38′345″S, 90°17′846″W, alt. 473 m, Zona húmeda, sobre *Scalesia pendunculata*, corticulosos, 2006, *F. Nugra* 181 (CDS *no.* 32835); Santiago Island, along the trail from the caseta in La Central to La Bomba, halfway down to the coast, 0°12′54″S, 90°43′21″W, alt. 293 m, arid zone, open woodland of *Bursera graveolens* and *Opuntia galapageia* with shrubs of *Castela galapageia* among basalt boulders and rocks, on bark, *Castela* twigs, 2006, *A. Aptroot* 65613 (CDS *no.* 32203); outer S-exposed slope of Cerro Gavilan, 0°12′22″S, 90°47′6″W, alt. 815 m, moist upland, disturbed by former grazing of goats, artificial pampa with *Solanum americanum*, *Portulaca oleraceum*, *Senna occidentalis*, *Borreria laevis*, and grasses, basalt boulders and outcrops, on wood, standing dead tree, W-exposed, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 4806 (CDS *no.* 28961).

Ramalina sorediosa (de Lesd.) Landrón

In Kashiw. & Kalb, *Lichenologist* **25**(1)**:** 25 (1993).—*Ramalina dasypoga* var. *sorediosa* de Lesd., *Revue Bryol. et Lichénol.* **7:** 59 (1934).

(Fig. 5C)

A pan-American species previously reported from the Galapagos by Landrón (1972), repeated by Kashiwadani & Kalb (1993), but not mentioned by Weber (1986), who erroneously reported material of this species as *R. furcellata* (Mont.) Zahlbr. Abundant and widespread, especially in the humid highlands, the agricultural areas of inhabited islands as well as natural areas, more rarely also in the lowlands or along the coast; typically corticolous, rarely lignicolous, very rarely saxicolous, once also found on metal of an old car wreck. Despite its name this species should not be confused with *R. sorediantha* (see comments there).

Selected specimens examined. **Ecuador:** *Galápagos*: Isabela Island, Volcán Alcedo, outer SE-exposed slope, *c.* 2 km below the crater rim, 0°26′16″S, 91°4′36″W, alt. 798 m, transition zone, ± dense shrubby vegetation of *Tournefortia rufo-sericea* with scattered trees of *Psidium galapageium*, *Zanthoxylum fagara*, and *Solanum erianthum*, on bark, upper side of inclined *Zanthoxylum fagara* trunk, shaded, ± wind- and rain-sheltered, 2006, *F. Bungartz* 4185 (CDS *no.* 28227); on the crater rim near the hut, 0°26′33″S, 91°5′31″W, alt. 1100 m, fern-sedge zone, *Pteridium arachnoideum* and *Stachytarpheta cayennensis*, scattered low shrubs of *Tournefortia rufo-sericea* and outcrops of basalt tuff in between, on bark, *Zanthoxylum*, 2006, *A. Aptroot* 65233 (CDS *no.* 31819); Pinta Island, along the trail up to the summit from the S-coast, 0°34′22″N, 90°45′3″W, alt. 329 m, transition zone, open woodland of *Zanthoxylum fagara*, *Pisonia floribunda*, and few *Trema micrantha*; grasses and *Justicia galapagana* in the understorey, on bark, twigs of *Zanthoxylum fagara*, sunny, wind-and rain-exposed, 2007, *F. Bungartz* 5859 (CDS *no.* 33535); Pinzón Island, along the trail going up from Playa Escondida, N- to W-facing cliff above a crater, 0°36′29″S, 90°40′14″W, alt. 318 m, dry transition zone with *Cordia lutea*, *Croton scouleri*, and at the bottom of the cliff also *Scalesia baurii* ssp. *baurii*, on rock (basalt lava), 2006, *A. Aptroot* 64044 (CDS *no.* 30605); San Cristóbal Island, near Tortugueria Cerro Colorado, 0°54′56″S, 89°26′18″W, alt. 130 m, on bark, shrub, 2005, *A. Aptroot* 63431 (CDS *no.* 30186); Cerro Colorado, enclosure for *Calandrinia galapagosa* near the viewpoint on the top, 0°54′58″S, 89°26′5″W, alt. 350 m, transition zone, open shrubland of mostly *Croton scouleri*, *Waltheria ovata*, and *Macraea laricifolia* on W-exposed cinder cone, on bark, stems and branches of *Croton scouleri*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6749 (CDS *no.* 35000); Santa Cruz Island, Cerca de la mina de granillo rojo, vía a Baltra, 0°37′2″S, 90°22′6″W, alt. 290 m, Zona de transición, con árboles de *Bursera*, *Opuntia* y *Croton*, *Psidium galapageium*, *Piscidia carthagenensis*, sobre corteza, Ramas de *Cordia lutea*, corticulosos, 2006, *F. Nugra* 8 (CDS *no.* 32661); near the CDRS field-weather station below the summit of Cerro Crocker, 0°38′35″S, 90°19′42″W, alt. 830 m, fern-sedge zone, much overgrown with dead *Cinchona pubescens* trees, N-exposed slope, on wood, wooden door frame of the little weather station hut, 2005, *F. Bungartz* 3303 (CDS

no. 26958); along the road from Bellavista to Los Gemelos, 0°37′56″S, 90°23′33″W, alt. 579 m, open *Scalesia pedunculata* forest with *Rubus niveus*, *Coffea arabica*, *Zanthoxylum fagara*, and scattered lava boulders, on bark, *Scalesia*, 2006, *A. Aptroot* 63848 (CDS *no.* 30406); Santiago Island, along the trail from Bucanero to Jaboncillos, *c.* 1 km below the summit of Cerro Gavilan, 0°11′45″S, 90°47′20″W, alt. 680 m, transition zone, open *Psidium galapageium* forest with *Zanthoxylum fagara*, *Blainvillea dichotoma*, *Mentzelia aspera* and *Senna obtusifolia*, basalt boulders and outcrops in between, on wood, 2006, *A. Aptroot* 65426 (CDS *no.* 32012).

Ramalina usnea (L.) Howe

Bryologist **17:** 81, fig. 1, pl. 12, figs 1–2 (1914).

(Fig. 5D)

A pan-American species already reported from the Galapagos by Weber (1986). This is the most abundant lichen on the Galapagos, aptly named because of its similarity to long, draping, pendulous *Usnea* species. The pale green beards of this abundant lichen festoon trees throughout the transition zone, where the arid lowlands merge with the interior mountains, typically between 80–250 m alt. Occasionally, specimens may also be found at higher altitudes, where they are, however, less abundant and thus not as conspicuous. The thin, long branches are sometimes twisted, resembling drill-bits and cannot be mistaken for any other species except *Ramalina anceps*, a taxon which is possibly only a chemotype of *R. usnea* (see comments there).

Selected specimens examined. **Ecuador:** *Galápagos*: Española Island, alt. 100 m, *S. Itow* L-40694 (CAS *no.* 685185); Fernandina Island, South Fernandina, alt. 610 m, on bark of *Bursera graveolens* trees, iii 1899, *R. E. Snodgrass* s.n. (CAS *no.* 691787); Marchena Island, 20 vi 1899, *R. E. Snodgrass* s.n. (CAS *no.* 681273); Isabela Island, Villamil, alt. 150 m, on bark, trunks of trees, 1905, *A. Stewart* 376 (CAS *no.* 638140); Volcán Alcedo, in the crater, 0°27′9″S, 91°6′41″W, alt. 780 m, transition zone, mostly *Bursera graveolens* and dense scrub on uneven lava, on bark, twigs, 2006, *A. Aptroot* 64753 (CDS *no.* 31328); Marchena Island, 20 vi 1899, *R. E. Snodgrass* s.n. (CAS *no.* 681268); Pinzón Island, along the trail going up from Playa Escondida, 0°35′58″S, 90°39′32″W, arid zone with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*, on bark, twigs, 2006, *A. Aptroot* 64156 (CDS *no.* 30720); Pinta Island, along the trail up to the summit from the S-coast, 0°33′22″N, 90°44′34″W, alt. 88 m, arid zone, open woodland of *Bursera graveolens* and few *Opuntia galapageia* with an understorey of *Croton scouleri*, *Castela galapageia*, *Waltheria ovata*, *Lantana peduncularis* among Pahoehoe lava, on bark, twigs of *Bursera graveolens*, sunny, wind- and rain-exposed, 2007, *F. Bungartz* 6007 (CDS *no.* 33686); San Cristóbal Island, Westküstengebiet, alt. 120 m, im Wald, an Bäumen, 08 x 1932, *H. J. F. Schimpff* s.n. (CAS *no.* 212532); Pan de Azúcar, inland from Bahía Sardinas at the NW-coast of the island, 0°43′12″S, 89°21′14″W, alt. 143 m, arid zone, NE-exposed slope on hill of consolidated tuff with low vegetation, on bark, branches of *Bursera graveolens*, semi-shaded, wind- and rain-sheltered, 2007, *F. Bungartz* 6450 (CDS *no.* 34667); Santa Cruz Island, Academy Bay, alt. 140 m, on bark, trunks of trees, 09. xi 1905, *A. Stewart* 379 (CAS *no.* 638142); Puerto Ayora, cliff behind CDRS, 0°44′30″S, 90°18′40″W, alt. 20 m, on bark, twigs, 2006, *A. Aptroot* 64186 (CDS *no.* 30749); at base of barranco near seismic station on *Piscidia*, alt. 30 m, 11 iv 1976, *W. A. Weber* s.n (CDS *no.* 10828); off the dirt road to Mina Granilla Rojo, 0°37′2″S, 90°22′6″W, alt. 294 m, transition zone, deciduous forest of *Zanthoxylum fagara*, *Psidium galapageium*, *Pisonia floribunda*, few *Bursera graveolens* and *Cedrela odorata*, on bark, twigs of *Zanthoxylum fagara*, S-exposed; semi-shaded, wind- and rain-sheltered, 2006, *F. Bungartz* 4939 (CDS *no.* 29152); Santa Fé Island, on dead bushes, 1905, *A. Stewart* 378 (CAS *no.* 638143); Floreana Island, alt. 150 m, on bark of trees, 1905, *A. Stewart* 377 (CAS *no.* 638141); Santiago Island, *c.* 5 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°16′35″S, 90°37′23″W, alt. 172 m, arid zone, plateau of lava flows and boulders with scarce vegetation (*Bursera graveolens*, *Castela galapageia*, *Mentzelia aspera*), on bark, twigs of *Clerodendron molle*, sunny, wind- and rain-exposed, 2006, *F. Bungartz* 5235 (CDS *no.* 29450).

Discussion

The Galapagos are among the few areas in the world (including some Caribbean Islands and Macaronesia) where *Ramalina* species are so abundant that they are often the dominant epiphyte, both on native and non-native deciduous trees, along the coast and in the hills. They are also the most common group of lichens that will be easily noticed from a distance (Fig. 1). An entire vegetation zone, the Transition Zone (Fig. 1A), can be recognized by the dominance of epiphytic lichens, mostly *Ramalina usnea*, but also a few *Usnea* species, including *U. longissima*, and *Teloschistes flavicans*. The abundance of *Ramalina* has prompted

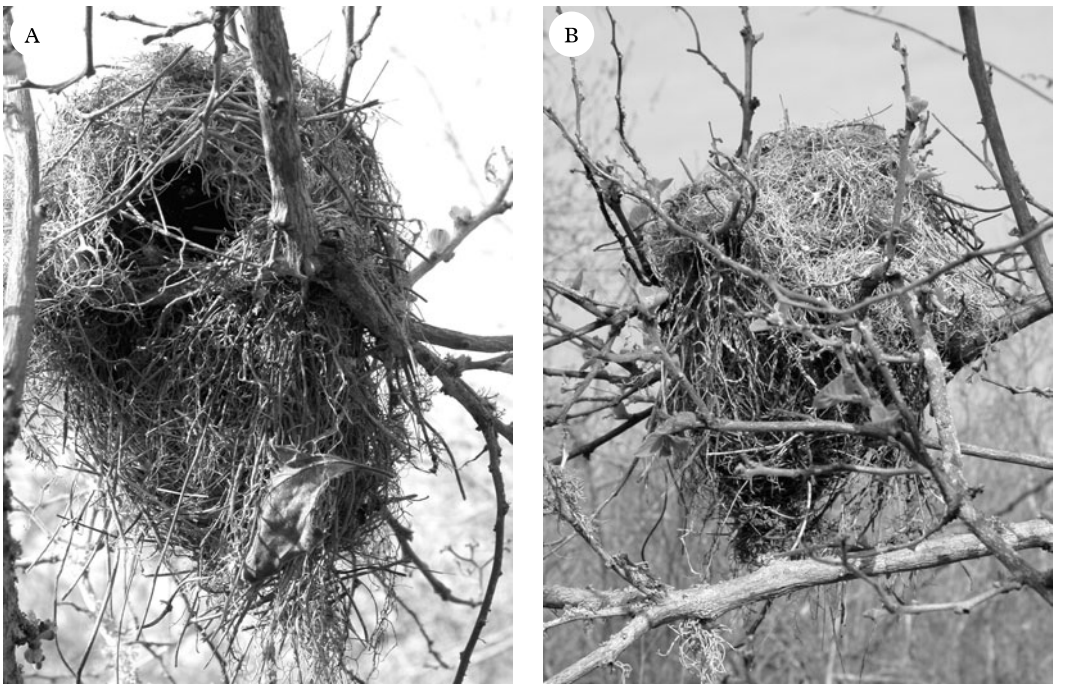

FIG. 6. *Ramalina* used in the nests of Darwin's finches on the Galapagos. A, on Santa Cruz; B, on Isabela.

at least some species of Darwin's Finches to build their nests from them (Fig. 6).

Ramalina diversity, with (for lichens) an unusually high percentage of endemism, has been reported to be high in several *ecologically similar* or *relatively nearby* areas, namely Hawaii, Baja California, Australia and the Atlantic Isles, including Macaronesia. Other floristic regions also share floristic similarities with the Galapagos, but their *Ramalina* diversity is much lower. These regions include the Chilean coast, Madagascar and Namibia; all characterized by a similar climate and flora (some of these regions even have the same lichen species in common, e.g., they share many species in the *Roccellaceae*).

Ramalina species are among the most abundant lichens on the Galapagos, and up to 11 species can be observed growing side-by-side (Fig. 1B–D). One of the richest localities is around the Charles Darwin Research Station, a collection site that all previous researchers visited. Weber (in Weber & Gradstein 1984, p. 73) already noticed that *Ramalina* species are "... in great abundance on the shrubs along the path between the Darwin Station and Puerto Ayora ..." He also reported that these populations appear unusually dynamic, observing a significant breakdown during the 1982–83 El Niño (Weber & Beck 1985). Weber's observations were mostly incidental and the recovery process was unfortunately never closely monitored. Staff at the Charles Darwin Research Station noticed that the populations began to recover only 3–4 years ago (A. Tye, personal communication). Weber (1984) suggested that the changes in population dynamics reflect a natural cycle of breakdown and recovery. Because no detailed monitoring took place, it is, however, not possible to know if populations have yet fully recovered. Obviously, drastic climatic events, such as the El Niño, strongly affect lichen populations throughout the islands. These organisms would therefore be ideal candidates to monitor long-term environmental effects on the Galapagos ecosystems caused by global climate change.

Weber (1986) reported a total of eight *Ramalina* species, all widespread and common. Several of his reports are here considered erroneous, and only five of the eight species previously recorded are accepted here. In addition, several species are now recorded for the first time and four species are described as new. These new species are all believed to be endemic.

Some of the reasons for the neglect of *Ramalina* in the Galapagos are taxonomic. In the past, species concepts in *Ramalina* have not been very stable, but there is now general agreement that species should be distinguished predominantly by their morphological characters, allowing for some chemical variation. Ideally, taxonomic concepts should be based not only on herbarium material, but also on field observations. A major controversy remains about the desirability of naming chemically deviant populations as varieties, as has been done by, for example, Stevens (1987), or whether just to number these chemical races, as done by e.g. Kashiwadani & Kalb (1993). Kashiwadani & Nash (2004) accepted relatively small morphological differences as species-specific characters, especially when co-occurring with their closest relatives.

While chemistry alone is not taken into account here as a single, diagnostic species-specific character, understanding the chemical variation among the specimens helps to characterize the different species. Most surprising is the fact that a particular chemistry appears to be prevalent in a certain region. The Galapagos *Ramalina* flora is dominated by species containing salazinic acid, often with sekikaic or divaricatic acid as an accessory or replacement substance. This can be observed to some extent in the field since salazinic acid turns red in damaged, decaying and dying parts of the lichen thalli. This can often be observed at the attachment zone, which turns red while the remaining part of the thallus remains viable. Stevens's (1987) detailed calculations demonstrate that salazinic acid occurs predominantly in *Ramalina* species generally at low latitudes in the tropics or close to the tropics. At higher latitudes this secondary metabolite is replaced by sekikaic and divaricatic acids. Further south, at even higher latitudes psoromic, boninic and cryptochlorophaeic acids become noticeable whereas at higher northern latitudes species and strains with bourgeanic, hypoprotocetraric and protocetraric acids become common. These secondary metabolites are completely absent from the Galapagos taxa.

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