Volume 18: 325–369 Publication date: 22 September 2015 dx.doi.org/10.7751/telopea8895





plantnet.rbgsyd.nsw.gov.au/Telopea • escholarship.usyd.edu.au/journals/index.php/TEL • ISSN 0312-9764 (Print) • ISSN 2200-4025 (Online)

Endemism in the genus Pertusaria (Pertusariales, lichenized Ascomycota) from the Galapagos Islands

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Abstract

This revision of *Pertusaria* in the Galapagos Islands documents twenty-four species, twenty-two being new to the archipelago. Secondary chemistry correlates well with morphology and anatomy and is particularly useful in distinguishing these taxa. Eight species are described as new to science, and seven are known only from the Galapagos: *Pertusaria albineoides*, *P. cerroazulensis*, *P. darwiniana*, *P. medullamarilla*, *P. stictica*, *P. thioisidiata* and *P. xanthoisidiata*. *Pertusaria lueckingii* is new, but it also occurs in Central America (El Salvador). Three new endemic varieties are described based on their chemistry: *Pertusaria thioisidiata* var. *isidiogyrophorica*, *P. tejocotensis* var. *stictica* and *P. xantholeucoides* var. *thamnolica*. In contrast with previous studies on other genera where rates of endemism of 8–10% were observed, in *Pertusaria* 30–37% of all species and 41–46% of all taxa are considered endemic.

Introduction

With a recent world-wide key to the species, *Pertusaria* appears to be one of the better known and more extensively studied lichen genera (Archer and Elix 2011). Nevertheless, since this key first went online, new species continue to be discovered. For the Galapagos, Weber (1986) cited only three species, and although all were described as endemic, he considered that *P. bispora* (Farl.) Linder, could possibly be a synonym of the widely distributed *P. pustulata* (Ach.) Duby, and that the type of *P. colobina* Tuck., was likely mislabelled and did not actually originate from the Islands. Subsequent updates of the checklist (*e.g.*, Elix and McCarthy 1998, Weber 1993) do not include any additional species of *Pertusaria*. For the archipelago this essentially left only one confirmed record of this highly diverse genus, a genus that is otherwise well represented throughout the tropics, common in dry forests like the Galapagos lowlands, and highly diverse in cloud forests, a vegetation type well represented in the humid Galapagos highlands.

It would appear obvious that these few records from almost thirty years ago seriously underestimated the natural diversity of this genus in the archipelago. In order to assess the species diversity of Galapagos *Pertusaria* for the 2005-2015 Galapagos Lichen Inventory (Bungartz *et al.* 2011), we examined both historic collections and specimens collected more recently. The results presented here report many records of species previously

overlooked as well as a large number of new taxa (species and varieties), all but one of which are unknown from continental America (or elsewhere), and may be endemic to the archipelago.

Materials and Methods

The Galapagos Archipelago comprises more than 123 islands in the eastern Pacific Ocean: islands, islets and large rocks that emerged from the sea as a result of volcanic hot spot activity; fourteen islands are somewhat arbitrarily recognized because of their size as the principal islands (Snell *et al.* 1995, 1996). The Galapagos climate is unusually dry, with a hot and cool season and prevailing winds from the south and south-east (Trueman and d'Ozouville 2010). Five principal vegetation zones can be distinguished: coastal, dry, transition, humid and high altitude dry zone (Bungartz *et al.* 2009, Tye *et al.* 2002, Tye and Francisco-Ortega 2011).

As part of the Galapagos Lichen Inventory the following islands have been visited and vegetation zones surveyed: Isabela (Volcán Sierra Negra, Volcán Alcedo, Volcán Darwin, Volcán Cerro Azul), Santiago (incl. Rábida, Bartolomé), Santa Cruz (incl. Santa Fé, Plaza Sur, Plaza Norte, Roca Gordon, Pinzón), Pinta, Española, Floreana and San Cristóbal.

Herbarium collections of the inventory are deposited at CDS; specimens from historic collections have also been examined (B, COLO, CAS, FH, H, OSC, S). Detailed collection information of Galapagos specimens used in this study can be downloaded from the CDF Collections Database (http://www.darwinfoundation. org/datazone/collections/).

All specimens were examined with a Zeiss Stemi DV4 dissecting microscope and a Zeiss Imager A1 compound microscope equipped with differential interference contrast. Macrophotographs were taken with a Nikon D300 and/or D7000, 62 mm Nikkor Micro Lens and R1C1 macro flash directly in the field, or using a Novoflex macro-table to take images of herbarium specimens; for photographic magnifications higher than 1:1 an extension tube or Novoflex bellows was used. For microphotographs the compound microscope was equipped with a Nikon DSLR phototube. Photographs in the laboratory were taken with Control My Nikon 5.2 (http://www.controlmynikon.com/); all photos were databased with the program IDimager 5 using the Darwin Core XML schema to embed collection and identification information as XMP metadata (http://owl.phy.queensu.ca/~phil/exiftool/TagNames/DarwinCore.html). Photographs were further processed with Adobe Photoshop CS6 software.

For spore measurements the Zeiss Imager A1 compound microscope was equipped with an ocular micrometre. Where possible, ascospores of at least three different specimens were measured, typically more than 10 ascospores per specimen. However, for some species insufficient material resulted in fewer measurements. In the descriptions these numbers are presented as:

(minimum length–)average length minus SD – average length plus SD(–maximum length) μm long,

(*minimum width–*)*average width minus* SD–*average width plus* SD(–*maximum width*) μ m wide (*n* = *total number of spores measured*). Note: 'SD' = standard deviation; *n* = number of samples.

For the identification key to species (see below), the extreme values were considered less useful for identification purposes and so were not included. When conidia were observed, measurements are given as minimum and maximum of length and width; the total number of measurements (n) is included. Generally, less conidia were measured than ascospores and in several species we did not observe pycnidia. Therefore, measurements are presented as rounded to the nearest micrometer. Macroscopic thallus characteristics (e.g., diam. of soralia, apothecia, etc.) were measured using an ocular micrometer of the Zeiss Stemi DV4, calibrated at highest magnification ($32\times$) with the smallest scale unit measuring 0.1429 mm. The typical range of measurements is presented as minimum and maximum, sometimes extreme values that lie outside the normal range are also included.

Secondary metabolites were examined from a selection of specimens using standardized thin-layer chromatography, routinely using solvent C, for selected specimens also solvent B' or solvent A (Orange *et al.* 2001, 2010), and to better resolve xanthones solvent F was used (Elix *et al.* 1991, Elix and Crook 1992). Instead of the conventional upright TLC tanks, a horizontal HPTLC developmental chamber was used (Arup *et al.* 1993). A protocol first suggested by Egan (2001) to document and conserve TLC results was modified here as follows: TLC plates were photographed with a *Nikon D7000* digital camera. Photographs were taken immediately after running the solvent, in long wave (λ 365 nm) and short wave (λ 254 nm) UV light, before applying 10% H₂SO₄. After the H₂SO₄ treatment and charring in a laboratory oven for approx. 8 min at 110°C, a second set of photographs in visible light and short-wave UV (λ 254 nm) were taken. Standard spot tests with reagents P, K and C were routinely carried out using methods described in Bungartz (2002). UV-fluorescence of thalli was studied under long wave UV light (λ 365 nm). Lugol's iodine was used to study asci following a routine protocol outlined in Bungartz (2002).

Results

This revision of *Pertusaria* from the Galapagos confirms the occurrence of the previously reported endemic, *P. albinea*. In addition, records of *P. bispora* are reduced to synonymy with the widely distributed *P. thiospoda*. Records of *Coccotrema* (*Pertusaria*) colobinum have been excluded from the Galapagos checklist.

Twenty-two species of *Pertusaria* are reported for the first time, eight are described as new to science, and seven of these are considered endemic. New chemotypes of two other taxa are described here as new varieties, while one of the newly described species occurs as two chemically distinct varieties.

Key to Pertusaria species of the Galapagos

1	Thallus lacking apothecia
1:	Thallus with verruciform apothecia 11
2	Thallus isidiate
2:	Thallus sorediate 4
3	Thallus corticolous; thiophaninic acid absent; medulla white throughout; isidia granulose to dactyliform, neither branched nor pycnidiate
3:	Thallus saxicolous; thiophaninic acid present; medulla white or pale lemon-yellow in part; isidia cylindrical or sparsely branched, apically often pycnidiate
4	Thallus containing thamnolic or haemathamnolic acid; soredia coarsely granular, KC+ bright lemon- yellow, C+ bright lemon-yellow
4:	Thallus lacking thamnolic and haemathamnolic acids; soredia farinose to moderately granular, KC-, C 7
5	Thallus saxicolous, distinctly areolate; individual areoles dispersed; containing thamnolic acid only <i>P. xantholeucoides</i> var. <i>thamnolica</i>
5:	Thallus corticolous, rimose-areolate, forming a contiguous crust with secondary fissures; containing haemathamnolic acid with ±traces of thamnolic acid or thamnolic acid only
6	Thallus containing haemathamnolic and ±traces of thamnolic acid P. commutata
6:	Thallus containing thamnolic acid; haemathamnolic acid absent P. leucosorodes
7	Stictic and norstictic acids absent; medulla and soredia K-; soralia ill defined, very irregular, coarsely granular and ±coralloid
7:	Stictic or norstictic acid present; medulla and soredia K+ yellow or K+ orange-red (crystals); soralia well delimited, rarely confluent, farinose to moderately granular, but not coralloid
8	Thallus with norstictic acid, medulla and soredia K+ orange-red (crystals) P. erythrella
8:	Thallus with stictic acid, medulla and soredia K+ yellow
9	Thallus containing lichexanthone, UV+ bright yellow; soredia well defined, but not delimited by a thalline margin or membrane
9:	Thallus containing 4,5-dichlorolichexanthone or xanthones absent, UV– or UV \pm pale yellow or dull orange (not bright); soredia delimited by a thalline margin or at least a thin thalline membrane 10
10	4,5-dichlorolichexanthone present; thallus moderately thin, contiguous to rimose, with a distinctly corticate, smooth surface; soredia typically delimited by a distinct thalline margin, rarely by a thin membrane
10:	Xanthones absent; thallus very thin, not fissured, but ±discontinuous in part (the substrate shining through); soredia delimited by a thin thalline membrane <i>P. stictica</i>
11	Thallus saxicolous 12
11:	Thallus corticolous
12	Inner ascospore wall distinctly laminated; medulla white throughout, KC-, C P. tejocotensis var. stictica
12:	Inner ascospore wall smooth, not laminated; medulla pale to deep lemon-yellow in part, KC+ orange, C+ orange

13	Lichexanthone present; isidia present, but occasionally scarce, particularly when verruciform apothecia are well developed; lemon-yellow medullary pigmentation sparse or absent <i>P. thioisidiata</i>
	Gyrophoric acid absentvar. <i>thioisidiata</i>
	Gyrophoric acid presentvar. <i>isidiogyrophorica</i>
13:	Lichexanthone absent; isidia absent, verruciform apothecia typically abundant; lemon-yellow medullary pigmentation abundant
14	Stictic or norstictic acid present; medulla K± yellow (reaction sometimes restricted to parts of the medulla only) or K+ orange-red (crystals)
14:	Stictic and norstictic acids absent; medulla K
15	Thallus lacking xanthones, surface UV–; medulla with norstictic acid, K+ orange-red (crystals)
15:	Thallus with xanthones, surface UV+ pale to bright yellow or deep orange; medulla with stictic acid, K± pale to deep yellow, norstictic acid absent (no crystals)
16	Thallus C+ orange, KC+ orange (thiophaninic acid present); surface at least with a pale yellow tinge, often distinctly lemon-yellow or deep yellow
16:	Thallus C-, KC- (thiophaninic acid absent); surface whitish to mineral grey-brown to greenish grey or ivory to beige
17	Inner ascospore wall persistently smooth; ostioles darkened, often papillate and usually encircled by a strong yellow pigmentation <i>P. texana</i>
17:	Inner ascospore wall becoming distinctly grooved with age; ostioles pale, not papillate, not encircled by a pigmentation deeper than the thallus surface
18	Ostioles punctiform, not expanding, indistinct; medulla K+ deep yellow throughout; thallus surface smooth; asci 2(-4)-spored <i>P. xanthodes</i>
18:	Ostioles punctiform to dilating, distinct; medulla K± weakly yellow (reaction often confined to parts of the lower medulla; most pronounced along the inner apothecial wall); thallus surface rugose; asci (1- or) 2-spored
19	Thallus with lichexanthone, UV+ bright yellow; surface at least in parts conspicuously papillate-verrucose; most apothecia polycarpic and several typically fused into \pm gnarled and contorted clusters, rarely single; ostioles typically expanding into a small brownish disc delimited by an inconspicuous margin; asci with $(4-)6-8$ ascospores
19:	Thallus lacking lichexanthone (or present only in traces), UV+ pale or deep yellow orange (not bright); surface coarsely wrinkled (rugose to \pm plicate), but not papillate-verrucose; some apothecia polycarpic, but typically single, rarely fused; ostioles inconspicuous, punctiform, grey, often with a translucent rim; asci with $2-4(-6)$ ascospores
20	Inner ascospore wall conspicuously spirally grooved; punctiform ostioles typically forming where the apex of the hemispherical apothecia burst open and the smooth cortex has torn apart <i>P. tetrathalamia</i>
20:	Inner ascospore wall smooth, not grooved; punctiform ostioles forming at the apex of hemispherical apothecia, sometimes in a slight depression, but cortex apically not torn apart
21	Thallus surface UV+ bright orange, distinctly lemon-yellow, rarely pale, but yellow pigmentation then always more pronounced around the ostioles
21:	Thallus surface UV– or UV±pale yellow (dull, not bright), not yellow, pale mineral grey to pale olive or greyish white to pale beige, often darker around the ostioles, but not yellow
22	Asci with 1 or 2 ascospores; inner spore initially smooth, but becoming finely to strongly incised with age (net-like ornamentation) <i>P. thiospoda</i>
22:	Asci with more than 4, typically 6 or 8 ascospores; inner spore wall remaining smooth, not becoming incised
23	As cospores broadly oblong to narrowly ellipsoid, (44–)60–79 (–88) μm long; as ci with (4–)6(–8) spores .
23:	Ascospores broadly ellipsoid to ±citriform, (37–)45–59(–68) µm long; asci with (6–)8 spores P. flavens

24	Asci with (2–)4 spores; thallus C+/KC+ orange; thiophaninic and perlatolic acids present; apothecia typically fusing, rarely single, disc-shaped to subglobose, apically distinctly flattened, constricted at their base; with (1–)2–4(–6) ostioles
24:	Asci with 8 spores; thallus C–/KC–; thiophaninic and perlatolic acids absent; apothecia wart-shaped to hemispherical, apically not flattened, not constricted at their base; with $1-3(-4)$ ostioles 25
25	Ascospores broadly ellipsoid, $31-55 \mu m \log$, $18-27 \mu m wide$, much thickened apically (to $10 \mu m$); found in the dry and lower transition zone

25: Ascospores narrowly ellipsoid; $51-68 \mu m \log_{2} 17-25 \mu m$ wide, barely thickened apically (to 4 μm); found

Pertusaria albinea Tuck., Proceedings of the American Academy of Arts and Sciences 12: 177 (1877)

Type: ECUADOR. GALAPAGOS: specific locality unknown, anno 1872, Willey s.n. (Holo: FH-Tuck60330, Tuckerman herbarium sheet no. 2223, n.v.); iso: US69128!

Taxonomic comment: Tuckerman (1877) described this species based on material collected in the Galapagos Islands by H. Willey during the Hassler Expedition of 1872. Consequently, the name has priority over Pertusaria albinea Müll.Arg. (Bulletin de l'Herbier Boissier 3: 639, 1895).

Figs 1a-d

Thallus corticolous, crustose, continuous to rimose; surface greyish white to pale beige, dull to ±shiny, smooth, epruinose, scarcely verrucose, lacking soredia and isidia; medulla white; margin not distinctly zonate, typically delimited by a thin, compact, black prothallus (especially where adjoining other thalli). Apothecia verruciform, wart-shaped to hemispherical, 0.5–1.2(–1.5) mm diam., single, typically not fusing, not constricted at their base, concolorous with the thallus, mono- to polycarpic, with 1-3(-4) brownish black, punctiform *ostioles*, delimited by a thin, ±translucent rim; *thalline exciple* dull brown outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K); *epihymenium* pale olive, K- or K± violet (reaction often very pale); proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly astomosing hyphae, ±loosely intertwined around asci; asci cylindrical, 8-spored; ascospores hyaline, citriform to broadly ellipsoid, $(24-)30-55(-73) \mu m \log_2(15-)18-28(-41) \mu m wide (n = 70); spore wall$ 2-layered; inner wall 3-4 µm wide, smooth (not grooved or laminated), apically much thickened ('trimmed'; up to 10 µm), outer wall 3–5 µm thick, with conspicuous microrugulate ornamentation; pycnidia not seen.

Chemistry: Cortex P-, K± yellowish, C-, KC-; medulla P-, K± yellowish, C-, KC-, UV± pale yellow; 2,4,5-trichlorolichexanthone, $\pm 2,5$ -dichlorolichexanthone, $\pm 4,5$ -dichlorolichexanthone.

Distribution and ecology: Endemic to the Galapagos Islands, in the dry and lower transition zone, most commonly growing on Bursera graveolens.

Notes: Pertusaria albinea is one of four fertile species with a pale greyish white to ivory thallus. It is superficially very similar to P. albineoides, P. tetrathalamia and P. cerroazulensis. Pertusaria albineoides is distinguished here by its different ecology (see below) and its longer, narrowly ellipsoid, thin-walled spores that are apically barely trimmed. Pertusaria tetrathalamia and P. cerroazulensis can look similar, but they contain stictic acid and have larger, more convex, hemispherical to subglobose apothecia; those of *P. albinea* are ±conical, wart-shaped and it lacks stictic acid. Pertusaria albinea consistently has 8, small, broadly ellipsoid spores per ascus (31-55 µm long), P. cerroazulensis typically 6–8, larger, narrowly ellipsoid, spores (45–77 µm long). Asci of P. tetrathalamia are usually 4-spored, and the spores are fusiform, conspicuously internally grooved and 83-108 µm long; it is the only corticolous species treated with a pale thallus and erumpent verruciform apothecia (*i.e.*, the cortex apically typically tears apart).

The ecology of these species also differs: P. albinea is the only species characteristic of the dry zone, P. tetrathalamia is more common in the transition zone, and both P. albineoides and P. cerroazulensis are restricted to the humid zone.

Holotype material of P. albinea in FH was analyzed in 2004 with thin-layer chromatography by U. Lange, University of Regensburg, who suggested the material did not contain secondary metabolites (plate no. 29; anal.-no. 489: 'nil'). This appears unlikely, yet the specimen in FH is now so fragmentary that no further material could be sacrificed for chemical analysis (M. Schmull, pers. comm.). We were able to locate isotype material in US and obtained permission to analyze a small fragment. This fragment (Willey s.n., US69128) contained 2,4,5-trichlorolichexanthone and 4,5-dichlorolichexanthone. Only one recently collected specimen from the Galapagos (Aptroot 65075, CDS31657) contains exactly the same xanthones, whereas other specimens examined contained 2,4,5-trichlorolichexanthone and 2,5-dichlorolichexanthone

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(the chemistry also observed in *P. albineoides*). However, this is not unusual. When present as a major component 2,4,5-trichlorolichexanthone often co-occurs with minor quantities of 4,5-dichlorolichexanthone, 2,5-dichlorolichexanthone and 2-chlorolichexanthone; the latter compounds often occur in variable concentrations and have little or no taxonomic significance.

Additional specimens examined: ECUADOR. GALAPAGOS: Isabela Island, Volcán Darwin, southwestern foothills, above Tagus Cove, 0°14'50"S, 91°21'29.89"W, 67 m alt., dry zone, trunk of *Bursera graveolens*, 11 Nov 2007, *Ertz 11748* (CDS37107); *loc. id., Bungartz 7379* (CDS37866). Santa Cruz Island, vicinity of Academy Bay, on bark of *Bursera*, 15 Feb 1964, *Weber 164* (COLO188868; L40346). Santiago Island, along the trail from Bucanero to Jaboncillos, c. 3 km SE of Bucanero, 0°10'52"S, 90°48'33"W, 362 m alt., transition zone, on bark of *Bursera*, 22 Mar 2006, *Aptroot 65389* (CDS31975).

Pertusaria albineoides Bungartz, A.W.Archer, Yánez-Ayabaca & Elix, sp. nov.

MycoBank No.: MB 814346

Similar to P. albinea, but with longer, narrowly ellipsoid ascospores with thinner apical walls.

Type: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Alcedo**, outer SE-exposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, disturbed by former grazing of goats, therefore with scattered trees (*Tournefortia rufo-sericea, Zanthoxylum fagara*), on semi-shaded, wind- and rain-exposed trunk of *Scalesia microcephala* (c. 5–15 cm diam.), 5 Mar 2006, *Bungartz* 4066 (CDS27996, holotype).

Figs 1e-f

Thallus corticolous, crustose, continuous to rimose; *surface* greyish white to pale beige, dull to ±shiny, smooth, epruinose, scarcely verrucose, lacking soredia or isidia; *medulla* white; *margin* not distinctly zonate, typically delimited by a thin, compact, black *prothallus* (especially where adjoining other thalli). *Apothecia* verruciform, wart-shaped to hemispherical, 0.3–0.7(–1) mm diam., single, typically not fusing, not constricted at their base (ampliariate), concolorous with the thallus, mono- to polycarpic, with 1(or 2) brownish black, punctiform *ostioles*, delimited by a thin, ±translucent rim; *thalline exciple* dull brown outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K); *epihymenium* pale olive, K– or K± violet (reaction often very pale); *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, 8-spored; *ascospores* hyaline, narrowly ellipsoid, (39–)51–67(–78) µm long, (16–)19–27(–31) µm wide (n = 25); *spore wall* 2-layered, *inner wall* 3–4 µm wide, smooth (not grooved or laminated), apically barely thickened (to 4 µm), *outer wall* 2–3 µm thick, with faint microrugulate ornamentation; *pycnidia* not seen.

Chemistry: Cortex P–, K± yellowish, C–, KC–; medulla P–, K± yellowish, C–, KC–, UV± pale yellow; containing 2,4,5-trichlorolichexanthone, 2,5-dichlorolichexanthone.

Etymology: Similar to 'albinea'.

Distribution and ecology: Endemic to the Galapagos Islands; known only from the humid zone of Volcán Alcedo, on *Croton scouleri* and *Scalesia microcephala*.

Notes: See discussion under P. albinea.

Additional specimens examined: ECUADOR. GALAPAGOS ISLANDS: Isabela Island, Volcán Alcedo, outer SEexposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, on *Croton*, 5 Mar 2006, *Aptroot* 65073 (CDS31655); *loc. id.*, *Aptroot* 65075 (CDS31657).

Pertusaria cerroazulensis Bungartz, A.W.Archer, Yánez-Ayabaca & Elix, sp. nov.

MycoBank No.: MB 814347

Similar to P. albineoides, but containing stictic acid and lacking 2,4,5-trichlorolichexanthone.

Type: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Cerro Azul**, steep outer slopes of the volcano above Cerro Verde, 0°57'28.5"S, 91°24'29.1"W, 1238 m alt., humid zone, small, shaded woodland of *Tournefortia rufo-sericea*, *Cordia leucophlyctis* and *Psidium galapageium*, on wooden, semi-shaded twigs of Guayabillo, 7 May 2012, *Spielmann 10594* (CDS51961, holotype).



Fig. 1. a–**d** *Pertusaria albinea* (*Willey, H.* s.n., US 69128, isotype); **a** herbarium packet with specimen (photo courtesy US, scale 3 cm); **b** thallus aspect (photo courtesy US, scale 1 mm); **c** section of verruciform apothecium (scale 40 μ m); **d** broadly ellipsoid, conspicuously trimmed ascospores (scale 25 μ m); **e**, **f** *P. albineoides* (*Bungartz 4066*, CDS27996, holotype); **e** thallus aspect (scale 3 mm); **f** narrowly ellipsoid, barely trimmed ascospores (microrugulate ornamentation of outer spore wall particularly visible; scale 20 μ m).

Figs 2a-c

Thallus corticolous, crustose, continuous to rimose; *surface* ivory or creamy white to pale beige, dull to ±shiny, smooth, epruinose, ±wrinkled (rugose), lacking soredia and isidia; *medulla* white; *margin* not distinctly zonate, typically delimited by a thin, compact, black *prothallus* (especially where adjoining other thalli). *Apothecia* verruciform, hemispherical, 0.7-1.2(-1.8) mm diam., single or rarely fusing, moderately to distinctly constricted at their base, concolorous with the thallus, apically ±flattened, (mono- to) polycarpic, with (1-)2-3(-4) greyish to blackish, punctiform to ±papillate *ostioles; thalline exciple* hyaline, with few large crystals (persistent in K) and abundant minute crystals (dissolving to form a yellow solution in K, ?stictic acid), cortex lacking crystals; *epihymenium* pale olive, K-; *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, (4–)6–8-spored; *ascospores* hyaline, narrowly ellipsoid, (29–)55–77(–88) µm long, (17–)23–36(–63) µm wide (n = 46); *spore wall* 2-layered, *inner wall* 2–3 µm wide, smooth to ±irregular (not distinctly grooved or channelled), apically ±thickened (c. 4–6 µm), *outer wall* 2–4(–6) µm thick, smooth to very faintly ornamented; *pycnidia* not seen.

Chemistry: Cortex P-, K-, C-, KC-; medulla P+ orange, K+ deep yellow, C-, KC-, UV+ reddish orange; containing lichexanthone (trace), 2-chlorolichexanthone, 2,4-dichlorolichexanthone, stictic acid, cryptostictic acid, constictic acid.

Etymology: Growing on Volcán Cerro Azul.

Distribution and ecology: This rare endemic is currently only known from several collections from a small remnant woodland of Guyabillo (*Psidium galapageium*) at Volcán Cerro Azul, on Isabela Island. The southern slopes of Cerro Azul generally receive the highest rainfall in the archipelago; throughout the year they are typically enshrouded in clouds. Feral pigs and cattle roam freely and the vegetation is very heavily grazed. On the upper slopes only scarce catclaw trees (*Zanthoxylon fagara*) and *Tournefortia rufo-sericea* shrubs survive, but on the lower slopes forests of introduced Guava (*Psidium guajava*) are abundant. Trees of endemic Guyabillo only survive on the steepest, inaccessible slopes.

Notes: The species is superficially similar to both *P. albinea* and *P. tetrathalamia* (for a discussion see comments under *P. albinea*).

Additional specimens examined: ECUADOR. GALAPAGOS: Isabela Island, Volcán Cerro Azul, wide, open ditch between two lava ridges to the West above Cerro Verde, 0°57'9.40"S, 91°24'31.5"W, 1436 m alt., humid zone, on branches and twigs of *Psidium galapageium*, 6 May 2012, *Spielmann 10572* (CDS51941), *10571* (CDS51940); *Bungartz 10388* (CDS52358); on branches and trunk of *Croton*, 6 May 2012, *Spielmann 10554* (CDS51912).

Pertusaria commutata Müll.Arg., Flora 67: 269 (1884)

Figs 2a-c

Thallus corticolous or lignicolous, crustose, continuous to rimose or rimose-areolate; *surface* vivid white to pale whitish, lead-grey, greenish or olive-grey, often with a pale pinkish tinge, rarely ±beige, ±shiny, smooth, epruinose, coarsely wrinkled (rugose to ±plicate), along the margin with sparse, punctiform, often ±papillate pseudocyphellae; *soralia* 0.3–0.8(–1) mm diam., concolorous with the thallus or, more commonly, vivid white, sometimes with a pale pinkish tinge, sparse to abundant, mostly single and dispersed, very rarely ±confluent when crowded, strongly convex, hemispherical to subglobose, eventually apically ±flattened, circular in outline, distinctly pustulate, *i.e.*, forming from pseudocyphellate papillae into verrucae that break open apically to release coarse, corticate *granules* that transition into ±pseudocorticate blastidia and compact, ecorticate *soredia*; *medulla* white; *margin* not distinctly zonate, but rarely inconspicuously banded by one or several lines of a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* not observed among Galapagos specimens. *Pycnidia* not seen.

Chemistry: Cortex P± pale yellow, K+ bright lemon-yellow, C-, KC-; medulla P+ deep yellow-orange, K+ deep yellow-orange, C-, KC-; soralia K+ deep yellow-orange, C+ yellow, KC+ yellow; UV± dull yellow-orange; containing lichexanthone, 2-O-methylisohyperlatolic acid, haemathamnolic acid, cryptothamnolic acid, \pm thamnolic acid (trace).

Distribution and ecology: Widespread, circumtropical (Archer and Elix 2011); the most common sorediate species in the Galapagos, present throughout all vegetation zones, but most common in the transition zone and lower humid zone, on wide range of endemic, native and introduced trees and shrubs.



Fig. 2. a-**c** *Pertusaria cerroazulensis*; **a** section of verruciform apothecium (scale 200 μm); **b**, **c** ascospore (scale 15 μm); **b** outer wall faintly ornamented; **c** inner wall smooth, not grooved, apically trimmed. **d**, **e** *Pertusaria commutata* (scale bars 3 mm); **d** thallus with black, inconspicuously banded prothallus (*Bungartz 3695*, CDS27513); **e** thallus with blastidiate-granular soralia (*Bungartz 9940*, CDS47309); **f**, **g** *Pertusaria darwiniana* (scale bars 3 mm); **f** well-developed thallus with soredia surrounded by a thick thalline margin (*Bungartz 7712*, CDS38214, holotype); **g** poorly developed thallus with soredia surrounded by thin, membranaceous layer (*Bungartz 9648*, CDS46967).

Notes: Only the sorediate form of *P. commutata* has been found in the Galapagos. The pustulate ontogeny of its hemispherical to subglobose soredia is very distinctive, especially in well-developed thalli. Soralia begin along the thallus margin as punctiform pseudocyphellae that first become ±papillate towards the centre, then soon develop into coarse verrucae. These verrucae eventually become irregularly erumpent at the centre of their apex, first releasing corticate granules, then pseudocorticate blastidia and ultimately extruding an abundance of coarse, compact, ecorticate soredia. The margin of these pustulate soralia remains intact and typically develops into a distinct, often quite broad thalline rim that eventually becomes obscured below a mass or coarse soredia.

Two other species in Galapagos have structurally very similar soralia and possibly share much of this ontogeny, although these species are not distinctly pseudocyphellate. *Pertusaria leucosorodes* is corticolous like *P. commutata* but it is characterized by the presence of thamnolic rather than haemathamnolic acid. *Pertusaria xantholeucoides* var. *thamnolica* also contains thamnolic acid but it is a saxicolous species.

Specimens examined: ECUADOR. GALAPAGOS: Floreana Island, S of Cerro Asilo de la Paz, edge of Pampa Larga, 1°19'38.20"S, 90°27'9.59"W, 249 m alt., transition zone, on twigs and branches of dead shrub, 13 Jan 2011, Bungartz 9503 (CDS46785); trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, 1°17'58.70"S, 90°26'51.10"W, 342 m alt., transition zone, on S-exposed side of fence post, 14 Jan 2011, Bungartz 9563 (CDS46842); caldera of Cerro Pajas, trail at the end of road leading up to crater rim, 1°17'47"S, 90°27'23.19"W, humid zone, on branch of Zanthoxylon fagara, 02 Jan 2010, Hillmann GAL-34 (CDS44798); Cerro Pajas, inside the crater, 1°17'49.29"S, 90°27'23"W, 379 m alt., humid zone, on S-exposed trunk of Croton scouleri, 12 Jan 2011, Bungartz 9302 (CDS46528); Yánez-Ayabaca 1746 (CDS48024); entrance to Primavera Farm from main dirt road, 1°18'22.10"S, 90°26'29.69"W, 371 m alt., humid zone, on E-exposed trunk of Cedrella odorata, 22 Jan 2011, Bungartz 10073 (CDS47468); trail from La Primavera Farm to La Corona and Arco de la Reina, southeastern part of the island, 1°19'21.60"S, 90°24'45.89"W, 219 m alt., transition zone, on branch of Clerodendrum molle, 24 Jan 2011, Yánez-Ayabaca 2094 (CDS48440); Bungartz 10128 (CDS47523); Asilo de la Paz, Cerro Wittmer, trail in between cliffs, 1°18'50"S, 90°27'13.80"W, humid zone, on tree trunk, 3 Jan 2010, Hillmann GAL-125 (CDS44884); on W-slope of Cerro Alieri, 1°17'24.10"S, 90°27'8.90"W, 347 m alt., transition zone, on twigs of Croton scouleri, 12 Jan 2011, Bungartz 9339 (CDS46626), 9340 (CDS46627), 9346 (CDS46633), 9335 (CDS46622); inside the crater of Cerro Laguna at E-side of island, on W-exposed slope, 1°16'11.80"S, 90°23'17"W, 245 m alt., transition zone, on branches of Bursera graveolens, 20 Jan 2011, Bungartz 9940 (CDS47309), 9949 (CDS47318); SE-part of island, between Lechosos and Cerro Pajaros, slope opposite Cerro Pajaros, 1°18'26.10"S, 90°24'21.39"W, 278 m alt., transition zone, on twigs of Macraea laricifolia, 15 Jan 2011, Bungartz 9626 (CDS46905); plain between the two hills Cerro de los Chanchos and Cerro de los Burros, 1°16'40.29"S, 90°24'12.4"W, 311 m alt., transition zone, on twigs of Castela galapageia, 21 Jan 2011, Bungartz 10012 (CDS47381). Isabela Island, Volcán Alcedo, outer SE-exposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, on trunk of Tournefortia rufo-sericea; 5 Mar 2006, Bungartz 4048 (CDS27978); plain at the base of the outer E-exposed slope, along the trail going up to the rim, 0°24'47"S, 91°4'12"W,768 m alt., transition zone, on trunk of Psidium galapageium, 8 Mar 2006, Bungartz 4328 (CDS28402); on top of the crater rim, 0°27'33"S, 91°6'49"W, 1051 m alt., humid zone, on trunk of Zanthoxylum fagara, 5 Mar 2006, Bungartz 4104 (CDS28072); outer SE-exposed slope, c. 2 km below the crater rim, 0°26'16"S, 91°4'36"W, 798 m alt., transition zone, on trunk of Psidium galapageium, 7 Mar 2006, Bungartz 4225 (CDS28267); Volcán Darwin, southwestern crater rim, 0°12'11.5"S, 91°18'41.29"W, 1286 m alt., high altitude dry zone, on stem of Croton scouleri, 13 Nov 2007, Bungartz 7502 (CDS37993); c. 200 m from the southwestern crater rim, 0°12'17.19"S, 91°18'45.20"W, 1304 m alt., high altitude dry zone, on trunk of Zanthoxylum fagara, 13 Nov 2007, Bungartz 7530 (CDS38021); c. 1 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1276 m alt., high altitude dry zone, on bark of Scalesia microcephala, 13 Nov 2007, Ertz 11864 (CDS37223); Bungartz 7561 (CDS38055); southwestern slope, above Tagus Cove, 0°13'11.4"S, 91°19'14.1"W, 955 m alt., transition zone, on branches and twigs of Dodonaea viscosa, 14 Nov 2007, Bungartz 7637 (CDS38139); Volcán Sierra Negra, around the mirador El Mango, 0°53'2.20"S, 91°0'51.20"W, 174 m alt., transition zone, on branches of Cedrela odorata, 15 Aug 2008, Herrera-Campos 10673 (CDS40410). Pinta Island, along the trail up to the summit from the S-coast, 0°34'22"N, 90°45'3"W, 329 m alt., transition zone, underside of Pisonia floribunda branch, 27 Feb 2007, Bungartz 5878 (CDS33554). Pinzón Island, along the trail going up from Playa Escondida, 0°36'10"S, 90°40'1"W, 254 m alt., dry zone, on dead branches lying on the ground, 16 Feb 2006, Bungartz 3641 (CDS27459). Santiago Island, c. 200 m S of Cerro Gavilan, W-exposed slope, 0°12'30"S, 90°47'6"W, 832 m alt., humid zone, on trunk of Iochroma ellipticum, 24 Mar 2006, Bungartz 4828 (CDS28995); c. 5 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°16'52"S, 90°37'17"W, 175 m alt., dry zone, on trunk of Bursera graveolens, 16 Jul 2006, Bungartz 5032 A (CDS29245); along the trail from Bucanero to Jaboncillos, c. 5 km SE of Bucanero, 0°11'19"S, 90°47'48"W, 562 m alt., transition zone, on trunk of Bursera graveolens, 22 Mar 2006, Bungartz 4656 (CDS28743); c. 1 km below the summit, Cerro Gavilan, 0°11'45"S, 90°47'20"W, 680 m alt., transition zone, on Zanthoxylum fagara, 22 Mar 2006, Aptroot 65457 (CDS32045). San Cristóbal Island, trail to Cerro Mundo

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from the border of the National Park, NE of Puerto Baguerizo Moreno, 0°53'33.39"S, 89°34'42.5"W, 157 m alt., transition zone, on N-exposed trunk of Bursera graveolens, 25 Aug 2008, Bungartz 8671 (CDS41317). Santa Cruz Island, along the road from Bellavista to El Garrapatero, c. 4 km W from the campsite of the National Park, 0°40'38"S, 90°14'54"W, 159 m alt., dry zone, on trunk of Bursera graveolens, 14 Feb 2006, Bungartz 3574 (CDS27373); abandoned farm along the northern part of the loop road from Bellavista to Garrapatero, 0°40'58"S, 90°18'31"W, 255 m alt., humid zone, on fallen tree trunk, 19 Feb 2006, Bungartz 3695 (CDS27513); farm along the southern part of the loop road from Bellavista to Garrapatero, 0°41'12"S, 90°18'22"W, 214 m alt., humid zone, on Erythrina, 19 Feb 2006, Aptroot 64233 (CDS30800); on the North side of the island, along the dirt road to the ash quarry Mina Granillo Rojo, 0°36'56"S, 90°22'3"W, 570 m alt., transition zone, branches of Bursera graveolens, 23 Feb 2006, Bungartz 3911 (CDS27793); Aptroot 64555 (CDS31127); Steve Divine's Farm at the end of Tortoise Road, off the main road to Baltra, Tortoise Territory, 0°40'8"S, 90°24'17"W, 364 m alt., humid zone, on the side of a wooden fencepost, 23 Feb 2006, Bungartz 3958 (CDS27840); off the dirt road to Mina Granillo Rojo, on the N-side of the island, 0°37'2"S, 90°22'6"W, 294 m alt., transition zone, trunk of Bursera graveolens, 21 Jun 2006, Bungartz 4944 (CDS29157); along the trail from Puerto Ayora to Bahía Tortuga, 0°44'48"S, 90°19'14"W, 28 m alt., dry zone, on trunk of Bursera graveolens, 5 Jan 2006, Bungartz 3329 (CDS26996); at the craters of Los Gemelos, on the E-side of the road to the channel, 0°37'33"S, 90°23'5.5"W, 587 m alt., humid zone, on top of wooden banister, 21 Oct 2007, Bungartz 7098 (CDS37583); along the dirt road to Mina Granillo Rojo, off the main road to the channel, on the N-side of the island, 0°36'56.60"S, 90°22'2.70"W, 583 m alt., transition zone, on trunk lying on top of outcrop, 21 Oct 2007, Bungartz 7110 (CDS37595); Camote, finca de René Valle, lindero del Parque Nacional Galápagos, al borde, 0°38'20.69"S, 90°17'50.79"W, 473 m alt., zona húmeda, on Erythrina smithiana, 11 Jan 2007, Nugra 290 (CDS33206); cerca de la mina de granillo rojo, vía a Baltra, 0°37'2"S, 90°22'6"W, 290 m alt., zona de transición, Psidium galapageium, altura al pecho, sobre corteza, 21 Jun 2006, Nugra 6 (CDS32659); vicinity of Academy Bay, ecological zone unknown, on Bursera, 15 Feb 1964, Weber s.n. (COLO; L-40353). Santiago Island, E of salt lake at James Bay, 0°14'25"S, 90°48'50"W, 170 m alt., transition zone, on Bursera, 30 Apr 1971, Pike ID16-2 B (OSC101523), 2713 (OSC101518); easternmost crater in the highlands, 0°14'15"S, 90°42'0"W, 410 m alt., transition zone, on Bursera, 10 May 1971, Pike ID37-24 (OSC101528); near Los Gemelos craters, 0°36'31"S, 90°22'4"W, 350 m alt., humid zone, on Scalesia pedunculata, 31 May 2005, Aptroot 63401 (CDS30154); Puerto Ayora, near begin of road to Baltra, 0°44'34"S, 90°18'45"W, 25 m alt., dry zone, on Bursera graveolens 26 May 2005, Aptroot 63097 (CDS29827); Academy Bay, ecological zone unknown, 11 Jan 1929, Herre 32 (CASDS508103), 32 (CAS508103).

Pertusaria darwiniana Yánez-Ayabaca & Bungartz, sp. nov.

MycoBank No.: MB 814348

Chemically similar to *Pertusaria expolita*, but forming soralia with a distinct thalline margin (or at least a thalline membrane).

Type: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Darwin**, south-western slope, above Tagus Cove, 0°13'27.6"S, 91°19'21.2"W, 860 m, transition zone, open scrubland of *Dodonaea viscosa*, *Croton scouleri*, *Macraea laricifolia*, *Scalesia microcephala*, few *Opuntia insularis* and dry grasses in the understory, on sunny, wind- and rain-exposed twigs of *Croton scouleri*, 15 Nov 2007, *Bungartz* 7712 (CDS38214, holotype).

Figs 2f-g

Thallus corticolous or lignicolous, crustose, continuous (thin thalli often barely fissured) to rimose; *surface* greenish white to greenish grey, dull to \pm shiny, smooth, epruinose, plane; *soralia* 0.1–0.7 mm diam., greyish white, often with a distinctly yellowish to pale pinkish tinge (possibly caused by xanthones), sparse to abundant, single and dispersed, not confluent, flattened to barely excavate, circular in outline and distinctly delimited by a broad thalline margin c. 0.1 mm wide; in thin, poorly developed specimens this margin may be thin and \pm membranaceous; *soredia* farinose to \pm granular; *medulla* white; *margin* not distinctly zonate, delimited by a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* and *pycnidia* unknown.

Chemistry: Cortex P-, K-, C-, KC-; medulla P+ orange, K+ yellow, C-, KC- (reactions slow, difficult to test on the thin medulla), soralia P+ orange, K+ yellow, C-, KC-; UV± pale yellow orange; containing 4,5-dichlorolichexanthone, ±2,4,5-trichlorolichexanthone, ±stictic acid, ±constictic acid.

Etymology: Named in honour of Charles Darwin and the Charles Darwin Foundation in the Galapagos.

Distribution and ecology: A common sorediate species endemic to the Galapagos, most frequently found in the dry and transition zones, but present also in the humid and high altitude dry zones; on stems, trunks, branches and twigs of native and endemic trees and shrubs (*Pisonia floribunda*, *Bursera graveolens*, *Zanthoxylon fagara*, *Croton scouleri*, *Clerodendrum molle*, etc.).

Notes: The thalli of *P. darwiniana* are superficially very similar to *P. erythrella*, which has the same smooth, greenish white to greenish grey, rimose surface. *Pertusaria erythrella*, however, has much larger soralia that lack a well-defined thalline margin; it also lacks xanthones and contains norstictic acid. *Pertusaria oahuensis* is quite distinct from both species because of its rugose thallus surface and distinct pale yellowish colour (*q.v.*). *Pertusaria stictica* also has well-delimited soredia, but its thalli are extremely thin and contain only stictic acid.

Pertusaria darwiniana was initially believed to be conspecific with *P. expolita* R.C. Harris from the south eastern United States because of their identical chemistries. Although the type of *P. expolita* was not seen by the authors, the soredia are not remotely similar to those of the Galapagos specimens according to Richard Harris (pers. comm.). He also mentioned that *P. expolita* has a "shinier thinly corticate thallus with just the \pm fragile cortex cracked", not deeply fissured like the holotype of *P. darwiniana*.

Additional specimens examined: ECUADOR. GALAPAGOS: Floreana Island, trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, 1°17'17.30"S, 90°26'35"W, 360 m alt., transition zone, on trunk of Croton scouleri, 25 Jan 2011, Bungartz 10249 A (CDS47668); along trail from Primavera Farm to La Corona and Arco de la Reina, southeastern part of island, 1°19'20.60"S, 90°24'45.5"W, 221 m alt., transition zone, on fallen branch, 24 Jan 2011, Yánez-Ayabaca 2103 (CDS48462); at entrance to crater of Cerro Verde, 1°18'10"S, 90°25'8.19"W, 370 m alt., humid zone, on twigs of Croton scouleri, 15 Jan 2011, Bungartz 9643 (CDS46962), 9648 (CDS46967); on W-slope of Cerro Alieri, 1°17'24.10"S, 90°27'8.90"W, 347 m alt., transition zone, on twigs of Clerodendrum molle, 12 Jan 2011, Yánez-Ayabaca 1756 (CDS48034); inside the crater of Cerro Laguna at E-side of island, on W-exposed slope, 1°16'11.80"S, 90°23'17"W, 245 m alt., transition zone, on branches of Bursera graveolens, 20 Jan 2011, Bungartz 9937 (CDS47306); trail from La Primavera Farm to La Corona and Arco de la Reina, southeastern part of the island, 1°19'21.60"S, 90°24'45.89"W, 219 m alt., transition zone, on branches and twigs of Clerodendrum molle, 24 Jan 2011, Bungartz 10137 (CDS47532). Isabela Island, Volcán Alcedo, outer SE-exposed slope, c. 2.5 km below the crater rim, 0°26'9"S, 91°4'34"W, 795 m alt., transition zone, on wood lying on the ground, 7 Mar 2006, Bungartz 4268 (CDS28339); along the trail going up the E-slope, basalt rubble field to the SE-side of the trail and the barranco, 0°24'6"S, 91°2'53"W, 530 m alt., dry zone, on Bursera, 10 Mar 2006, Aptroot 64910 (CDS31489); Volcán Darwin, c. 1 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1276 m alt., high altitude dry zone, upper side of inclined Scalesia microcephala trunk, 13 Nov 2007, Bungartz 7556 (CDS38050). Pinta Island, on the western cliff, W of Las Pampas, 0°34'51.70"N, 90°46'25.89"W, 411 m alt., transition zone, twigs of dead trunk, 1 Feb 2008, Nugra 620 (CDS38998). San Cristóbal Island, Cerro Mundo, at the base of the rock cliffs on the S side close to the summit, 0°53'32.20"S, 89°34'40.5"W, 243 m alt., transition zone, on standing dead tree of Zanthoxylum fagara, 25 Aug 2008, Clerc 08-390 (CDS40244). Santa Cruz Island, along the road from Los Gemelos towards the N-coast of the island, c. 1 km N of Los Gemelos, 0°37'22"S, 90°22'47"W, 584 m alt., transition zone, on Zanthoxylum, 12 Feb 2006, Aptroot 63794 (CDS30353); Steve Divine's Farm at the end of Tortoise Road, off the main road to Baltra, Tortoise Territory, 0°40'8"S, 90°24'17"W, 364 m alt., humid zone, on wood, 23 Feb 2006, Aptroot 64528 (CDS31100).

Pertusaria endochroma Müll.Arg., Revue Mycologique 9: 79 (1887)

Figs 3a-d

Thallus corticolous, crustose, continuous to rimose or rimose-areolate; surface yellowish white, greenish yellow to pale or intense lemon-yellow, dull to ±shiny, smooth, epruinose or very rarely pruinose, plane and even to ±verrucose or conspicuously gnarled, rarely flaking off in scales, lacking soredia or isidia; medulla white; margin not distinctly zonate, delimited by an indistinct whitish prothallus. Apothecia verruciform, wart-shaped to hemispherical, rarely becoming subglobose, 0.5-1.2(-1.5) mm diam., single or fused, not or slightly constricted at the base, apically conical, rarely \pm flattened, concolorous with the thallus, mono- to polycarpic, with 1–3(–5) hyaline to dull grey, punctiform ostioles, delimited by a thin rim, often distinctly deeper lemon-yellow than the surrounding apothecial verrucae or emerging as small papillae on top of the apothecial verrucae; thalline exciple dull brown outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K, reforming as yellowish clusters of needle-shaped crystals; thiophaninic acid), cortex lacking crystals; epihymenium pale olive, K- or K± violet (reaction often very pale); proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; asci cylindrical, (4-)6-8-spored; ascospores hyaline, broadly oblong to narrowly ellipsoid, $(44-)60-79(-88) \mu m \log_2(23-)26-33(-39) \mu m wide (n = 58); spore$ wall 2-layered, inner wall 3-5 µm wide, smooth (not grooved or laminated), moderately thickened apically (to 8 μm), outer wall 3–5 μm thick, with conspicuous microrugulate ornamentation; pycnidia not seen.

Chemistry: Cortex P–, K–, C+ orange, KC+ orange; medulla P–, K–, C–, KC–; UV+ bright orange; containing thiophaninic acid (major), ±2-chloro-6-O-methylnorlichexanthone (minor or trace), ±4-chloro-6-O-methylnorlichexanthone (minor or trace).

Distribution and ecology: New to South America, and previously reported from Thailand and New Caledonia (Archer and Elix 2011); a relatively rare species in the Galapagos Islands, growing on twigs and branches of trees and shrubs (*Bursera graveolens, Cordia lutea, Chiococca alba*) in the dry and transition zones.

Notes: Four distinctly lemon-yellow, epiphytic *Pertusaria* species occur in Galapagos. Only *P. endochroma* and *P. flavens* consistently lack stictic acid; their medulla does not react with K, but it remains distinctly white throughout. These contrast with *P. texana* and *P. xanthodes* which both contain stictic acid and their medulla reacts K+ deep yellow, a vivid reaction that can hardly be overlooked. In *P. thiospoda*, however, the K reaction is much less distinct; it appears to be confined to the lower parts of the medulla and the central medullary layer of the apothecial wall.

The four species can also be distinguished by their ascospores. *Pertusaria endochroma* and *P. flavens* have spores that are similar in size and asci with (4-)6-8 spores and (6-)8 spores, respectively. However, *P. endochroma* generally has 4 larger spores per ascus. *Pertusaria thiospoda* usually produces (1-)2 ascospore(s) per ascus, the mature spores having a distinctly ornamented wall, with net-like incisions along the outside of the inner wall layer. *Pertusaria xanthodes* also has ornamented acospores, 2(-4) per ascus, but they are more deeply spirally grooved. It has indistinct, hyaline ostioles that do not dilate and a smoother thallus than the rugose *P. thiospoda*, *P. endochroma* and *P. flavens*.

Specimens examined: ECUADOR. GALAPAGOS: Fernandina Island, W-side, transition zone, on Chiococca alba, 15 Feb 1964, Cavagnaro, D. s.n., 315 (COLO193421; L-40437). Isabela Island, Volcán Cerro Azul, steep outer slopes of the volcano above Cerro Verde, 0°57'28.5"S, 91°24'29.10"W, 1238 m alt., humid zone, on twigs of Psidium galapageium, 7 May 2012, Bungartz 10402 (CDS52372); Volcán Darwin, southwestern foothills, above Tagus Cove, 0°14'50"S, 91°21'29.89"W, 67 m alt., dry zone, on trunk of Bursera graveolens, 11 Nov 2007, Ertz 11740 A (CDS38917), c. 1 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1276 m alt., high altitude dry zone, on branches of Zanthoxylum fagara, 13 Nov 2007, Bungartz 7544 A (CDS38038); southwestern slope, above Tagus Cove, 0°13'11.4"S, 91°19'14.1"W, 955 m alt., transition zone, on *Dodonaea viscosa*, 14 Nov 2007, Ertz 11905 (CDS37264); Bungartz 7650 (CDS38152); above Tagus Cove, 0°13'27.60"S, 91°19'21.19"W, 860 m alt., transition zone, on twigs of Croton scouleri, 15 Nov 2007, Bungartz 7699 C (CDS38202); above Tagus Cove, 0°13'59"S, 91°20'8"W, 597 m alt., dry zone, on SE-exposed trunk of Bursera graveolens, 16 Nov 2007, Bungartz 7843 (CDS38352). Pinzón Island, along the trail going up from Playa Escondida, SW-slope of the top, 0°36'36"S, 90°40'11"W, 310 m alt., transition zone, on trunk of Opuntia galapageia ssp. macrocarpa, 16 Feb 2006, Bungartz 3594 (CDS27407). San Cristóbal Island, El Ripioso, fenced off area, 0°50'48.70"S, 89°27'47.29"W, 128 m alt., dry zone, on bark, 16 May 2006, Jaramillo 2970 B (CDS38821); SW foothills of Media Luna, inland from the NW-coast of the island along the trail from Galapagera to Media Luna; bottom of small crater to the NW of Media Luna, 0°43'53"S, 89°18'57"W, 124 m alt., dry zone, on trunk of Bursera graveolens, 22 Apr 2007, Bungartz 6253 (CDS34465). Santa Cruz Island, Island on the North side of the island, along the dirt road to the ash quarry Mina Granillo Rojo, 0°36'56"S, 90°22'3"W, 570 m alt., transition zone, on Bursera, 23 Feb 2006, Aptroot 64577 (CDS31149).

Pertusaria endoxantha Vain., Hedwigia 37: 41 (1898)

Pertusaria norstictica A.W.Archer, Mycotaxon 41: 232 (1991)

Figs 3e-g

Thallus corticolous, crustose, rimose to rimose-areolate; surface mineral-grey or olive-grey, usually dull, rarely \pm glossy in part, smooth, epruinose, but occasionally becoming \pm whitish and eroded, lacking soredia and isidia, but conspicuously plicate to papillate-verrucose at least in part; *medulla* white; *margin* not distinctly zonate, indistinct, dull brownish or sometimes delimited by a thin, compact, black prothallus (especially where adjoining other thalli). Apothecia verruciform, hemispherical to subglobose, 0.7-1(-1.2) mm diam., typically fusing and forming ±gnarled and contorted clusters, ±constricted at their base and apically ±flattened, concolorous with the thallus, with 1-3(-6) blackish brown ostioles, rarely delimited by a paler ±indistinct rim, punctiform to barely expanding, single or ±aggregated, rarely fusing at the flattened top of the apothecium; thalline exciple hyaline, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K to form a deep orange solution, soon forming orange-red, needle-shaped crystals of norstictic acid); cortex hyaline, lacking crystals; epihymenium dull olive, K+ violet; proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; asci cylindrical, (4-)6-8-spored; ascospores hyaline, narrowly ellipsoid to broadly fusiform, uniseriate in the ascus, $(54-)57-78(-92) \mu m$ long, $(24-)28-34(-35) \mu m$ wide (n = 20); spore wall 2-layered, outer wall (4-)5-7 µm thick, smooth to very faintly ornamented, inner wall (2-)3-4 µm wide, smooth (not grooved or laminated), distinctly thickened apically (to 12 µm); pycnidia not seen.

Chemistry: Cortex P+ orange, K+ yellow, C-, KC-; medulla P+ orange, K+ yellow to orange (crystals), C-, KC-, UV- (pale); containing atranorin (trace), norstictic acid (forms crystals under the microscope on treatment with K).

Distribution and ecology: New to South America, this species was previously known from East Africa, Southeast Asia (Indonesia, Papua New Guinea) and Australia. In the Galapagos it is known only from the high altitude dry zone of Volcán Darwin on Isabela Island where it grows on bark of *Scalesia microcephala* and *Zanthoxylon fagara*.

Notes: Morphologically similar is *P. nigrata*, but the latter lacks norstictic acid, fluoresces bright yellow in UV light (due to lichexanthone), and has much larger ascospores.

Specimens examined: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Darwin**, c. 1 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1276 m alt., high altitude dry zone, on S-exposed *Scalesia microcephala* branch, 13 Nov 2007, *Bungartz 7570* (CDS38064), *7567* (CDS38061); *Ertz 11860* (CDS37219); on branches of *Zanthoxylum fagara*, 13 Nov 2007, *Bungartz 7544 B* (CDS54888).

Pertusaria erythrella Müll.Arg., Bulletin de l'Herbier Boissier 1: 41 (1893)

Pertusaria torulosa Vain., Annales Academiae Scientiarum Fennicae Ser. A 6: 31 (1915)

Fig. 4a

Thallus corticolous or lignicolous, crustose, continuous to rimose; *surface* greenish white to greenish grey, \pm shiny, smooth, epruinose, plane; *soralia* 0.3–1.5 mm diam., greyish white, often with a pinkish to pale reddish tinge (possibly caused by the deterioration of norstictic acid), sparse to abundant, mostly solitary and dispersed, very rarely \pm confluent, when crowded, broadly convex, hemispherical, apically \pm flattened, circular in outline and distinctly delimited, but lacking a thalline margin; *soredia* farinose to \pm granular; *medulla* white; *margin* not distinctly zonate, delimited by a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* and *pycnidia* unknown.

Chemistry: Cortex P–, K± yellowish, C–, KC–; medulla P+ yellow, K+ orange-red (crystals), C–, KC–; soralia P+ yellow, K+ orange (crystals), C–, KC–; UV± pale yellow; containing norstictic acid.

Distribution and ecology: Previously known only from Australia (Archer 2014); in Galapagos known from a single collection on bark of *Croton scouleri* from the high altitude dry zone of Volcán Darwin on Isabela Island.

Notes: *Pertusaria erythrella* is the only sorediate species in the Galapagos Islands that contains norstictic acid (the fertile, esorediate *P. endoxantha* also contains this substance). It lacks xanthones and is characterized by the distinct K+ orange-red reaction of its medulla and soralia, forming needle-shaped crystals under the microscope. The pustulate soralia can be mistaken for those of *P. commutata* var. *haemathamnolica*, but the latter forms coarser, more granular soredia. Furthermore, the soralia of herbarium specimens of *P. erythrella* often become reddish tinged with age (due to the deterioration of norstictic acid); those of *P. commutata* remain vivid white. Measurements of the soralia given in the literature vary. Specimens of *P. torulosa* Vain. from the West Indies are said to have soralia 0.4–2 mm diam. whereas those of *P. erythrella* s.str. are 0.5–1 mm diam. (Archer and Elix 2011). The soralia of the Galapagos Islands material are insignificantly smaller at 0.3–1.5 mm. All are considered here to belong to the same species, whereas *P. colorata* D. D.Awasthi & Preeti Srivast., described from India, may be distinct, with larger soralia (0.5–2 mm diam.).

Specimen examined: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Darwin**, c. 200 m from the southwestern crater rim, 0°12'17.19"S, 91°18'45.20"W, 1304 m alt., high altitude dry zone, on *Croton scouleri*, 13 Nov 2007, *Ertz 11856* (CDS37215).

Pertusaria flavens Nyl., Bulletin de la Société linnéenne de Normandie sér. 2, 3: 268 (1869)

Figs 4b-d

Thallus corticolous, crustose, continuous to rimose or rimose-areolate; *surface* yellowish white to greenish yellow, pale or deep lemon-yellow, dull to ±shiny, smooth, epruinose or very rarely pruinose, plane and even or ±verrucose to gnarled, rarely flaking off in scales, lacking soredia or isidia; *medulla* white; *margin* not distinctly zonate, delimited by an indistinct whitish *prothallus. Apothecia* verruciform, wart-shaped to hemispherical, rarely becoming subglobose, 0.5-1.2(-1.5) mm diam., single or rarely fusing, not or slightly constricted at their base, apically conical, rarely ±flattened, concolorous with the thallus, mono- to polycarpic, with 1-3(-5) hyaline to dull grey, punctiform *ostioles*, delimited by a thin rim, distinctly deeper lemon-yellow than the surrounding apothecial verrucae or emerging as small papillae on top of the apothecial verrucae; *thalline exciple* dull brown outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle-shaped crystals; thiophaninic acid), cortex lacking crystals; *epihymenium* pale olive, K– or K± violet (reaction often very pale); *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, (6–)8-spored; *ascospores* hyaline, broadly ellipsoid to ±citriform, (37–)45–59(–68) µm long, (20–)24–30(–38) µm wide (*n* = 35); *spore wall* 2-layered, *outer wall* 3–5 µm thick, with conspicuous microrugulate ornamentation, *inner wall* 3–5 µm wide, smooth (not grooved or laminated), markedly thickened apically (to 12 µm); *pycnidia* not seen.



Fig. 3. a–**d** *Pertusaria endochroma*; **a** thick thallus with prominent hemispherical, almost subglobose, apically flattened, basally slightly constricted apothecia with punctiform, yellow-rimmed ostiole (*D. Cavagnaro s.n., 315*, COLO193421, L-40437, scale 3 mm); **b** thin thallus with wart-shaped, conical apothecia (*Ertz 11740 A*, CDS38917, scale 3 mm); **c** cross section of apothecium (*D. Cavagnaro s.n., 315*, COLO193421, L-40437, scale 200 µm); **d** yellowish clusters of needle-shaped thiophaninic acid crystals forming in K (*Ertz 11740 A*, CDS38917, scale 30 µm); **e**–**g** *Pertusaria endoxantha*; **e** mineral grey thallus with verruciform apothecia with brownish blackened ostioles (*Bungartz 7567*, CDS38061, scale 3 mm); **f** ascus with eight ascospores (*Ertz 11860*, CDS37219, scale 60 µm); **g** ascospore with smooth to barely ornamented outer wall, smooth inner wall, apically distinctly trimmed (*Ertz 11860*, CDS37219, scale 15 µm).

Chemistry: Cortex P-, K-, C+ orange, KC+ orange; medulla P-, K-, C-, KC-; UV+ bright orange; containing thiophaninic (major), ±2-chloro-6-O-methylnorlichexanthone (minor or trace), ±4-chloro-6-O-methylnorlichexanthone (minor or trace).

Distribution and ecology: New to South America, previously known from the Caribbean (French Antilles; Archer and Elix 2011), but easily confused with *P. texana* and *P. endochroma* and thus likely under-recorded; in the Galapagos it occurs on the same substrates and in similar habitat to *P. texana*, but is much less common and only occasionally found, from the dry zone to the high altitude dry zone.

Notes: See comments about P. endochroma.

Specimens examined: ECUADOR. GALAPAGOS: Española Island, trail from Bahía Manzanillo on the N-coast of the island to the highest point, 1°22'18.69"S, 89°42'7.40"W, 125 m alt., dry zone, on twigs of Cordia lutea, 11 Nov 2010, Bungartz 9142 (CDS45960). Floreana Island, trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, 1°15'42.29"S, 90°26'31"W, 197 m alt., dry zone, S-exposed on trunk of Bursera graveolens, 14 Jan 2011, Bungartz 9620 (CDS46899). 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, 420 m alt., dry zone, on trunk of Bursera graveolens, 9 Mar 2006, Bungartz 4353 (CDS28437); Volcán Cerro Azul, wide, open ditch between two lava ridges to the West above Cerro Verde, 0°57'9.40"S, 91°24'31.5"W, 1436 m alt., humid zone, on branches of Psidium galapageium, 6 May 2012, Spielmann 10569 (CDS51938); steep outer slopes of the volcano above Cerro Verde, 0°57'28.5"S, 91°24'29.10"W, 1238 m alt., humid zone, on branches of Psidium galapageium, 7 May 2012, Bungartz 10405 (CDS52375); along the first few meters of the path from the Caseta del Parque to Caleta Iguana, 0°58'44.20"S, 91°26'46.29"W, 12 m alt., dry zone, on Bursera branches, 9 May 2012, Spielmann 10758 (CDS52162); Volcán Darwin, southwestern crater rim, 0°12'11.5"S, 91°18'41.29"W, 1286 m alt., high altitude dry zone, on sheltered face of Scalesia microcephala trunk, 13 Nov 2007, Ertz 11826 (CDS37185); inland from Tagus Cove at the W-coast of the island, 0°15'8.69"S, 91°22'23.10"W, 77 m alt., dry zone, N-exposed trunk of Bursera graveolens, 17 Nov 2007, Bungartz 7985 (CDS38495). San Cristóbal Island, SW foothills of Media Luna, inland from the NW-coast of the island along the trail from Galapagera to Media Luna; bottom of small crater to the NW of Media Luna, 0°43'53"S, 89°18'57"W, 124 m alt., dry zone, on trunk of Bursera graveolens, 22 Apr 2007, Bungartz 6258 (CDS34470); NW foothills of Media Luna, inland from the NW-coast, 0°43'41"S, 89°18'44"W, 75 m alt., dry zone, top of dead branch of Cordia lutea, 22 Apr 2007, Bungartz 6229 (CDS34441). Santa Cruz Island, along the trail from Puerto Ayora to Bahía Tortuga, 0°44'48"S, 90°19'14"W, 28 m alt., dry zone, on twigs of Acacia insulae-jacobi, 5 Jan 2006, Bungartz 3359 (CDS27026); waste deposit along road to Baltra, 0°35'0"S, 90°21'17"W, 300 m alt., transition zone, on bark of Bursera graveolens, 28 May 2005, Aptroot 63241 (CDS29976). Santiago Island, c. 500 m S of Bucanero, near the canyon at the northeastern foothills of Cerro Cowan, 0°10'21"S, 90°49'30"W, 70 m alt., dry zone, on branches of Bursera graveolens, 21 Mar 2006, Bungartz 4550 (CDS28636).

Pertusaria galapagoensis Elix, Yánez-Ayabaca, A.W.Archer & Bungartz, sp. nov.

MycoBank No.: MB 814349

Thallus containing the perlatolic acid chemosyndrome similar to *Pertusaria depressa*, but with additional thiophaninic acid. In this species, unlike *P. depressa* the inner ascospore wall is not smooth, but very finely and inconspicuously channelled.

Type: ECUADOR. GALAPAGOS: **Floreana Island**, entrance to Primavera Farm from main dirt road, 1°18'22.1"S, 90°26'29.7"W, 371 m alt., humid zone, pasture with elephant grass, some trees of *Cedrella odorata* and *Psidium guajava*, on sunny, wind- and rain-exposed bark of S-exposed trunk of *Cedrella odorata* (c. 30 cm diam.), 22 Jan 2011, *Bungartz 10070* (CDS47465, holotype).

Figs 5a-d

Thallus corticolous, crustose, continuous to rimose; *surface* pale mineral-grey to pale olive, dull to \pm shiny, smooth, plane, not distinctly wrinkled but often finely fissured, lacking soredia and isidia, epruinose; apothecial verrucae apically eroded and occasionally \pm pruinose; *medulla* white; *margin* not distinctly zonate, delimited by a compact, glossy black *prothallus*. *Apothecia* verruciform, disc-shaped to subglobose, 0.5–1.4(–2.2) mm diam., solitary or rarely fused, constricted at their base, apically distinctly flattened, concolorous with the thallus, mono- to polycarpic, with (1–)2–4(–6) blackish grey to jet black, punctiform *ostioles*, not delimited by a distinct rim, solitary or fusing and then often almost appearing \pm discoid, typically sunken within an apical depression of the apothecial verrucae, rarely plane; *thalline exciple* hyaline, with large crystals (persistent in K) and abundant minute crystals (dissolving in K); cortex lacking crystals; *epihymenium* olive, K+ violet (distinct); *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* sparsely to strongly inspersed with oil droplets, of branched and sparingly anastomosing hyphae \pm loosely intertwined

around asci; *asci* cylindrical, (2-)4-spored; *ascospores* hyaline, oblong to ellipsoid or ±broadly fusiform, (54-)65–95(–101) µm long, (26-)32-45(-53) µm wide (n = 20); *spore wall* 2-layered, *inner wall* 2–3(–5) µm wide, becoming ±spirally fine-channelled along its outside (very inconspicuous), thickened apically (to 8 µm), *outer wall* (3–)5 µm thick, smooth or faintly ±microrugulate; *pycnidia* not seen.



Fig. 4. a thallus of *Pertusaria erythrella* with pinkish soralia with farinose soredia (*Ertz 11856*, CDS37215, scale 3 mm); **b**–**d** *Pertusaria flavens*; **b**–**c** thallus with clusters of apothecia (*Bungartz 4353*, CDS28437); **b** general growth aspect (scale 3 mm); **c** close-up with punctiform yellow-rimmed ostioles (scale 3 mm); **d** asci with broadly ellipsoid to ±citriform ascospores with ornamented outer wall, smooth, strongly trimmed inner wall (*Bungartz 9142*, CDS45960, scale 50 μ m).

Chemistry: Cortex P–, K– (or pale yellow), C–, KC–, medulla P–, K– (or pale yellow), C± red (very faint), KC± red (very faint), UV– (dull); containing 2,4-dichlorolichexanthone, thiophaninic acid, 2-O-methylsuperlatolic acid, superplanaic acid, methyl 2-O-methylperlatolate (trace), methyl hyperplaniate (trace).

Etymology: The epithet refers to the distribution of this species.

Distribution and ecology: Endemic to the Galapagos Islands, and known from only a few collections on bark and wood in the humid zone; grows on indigenous, endemic trees (*Scalesia*) and introduced trees (*Cedrella*, *Cinchona*).

Notes: The perlatolic acid complex present in *P. galapagoensis* closely resembles that observed in *Pertusaria depressa* Mont. & Bosch from South America, a species which contains 2-chlorolichexanthone (major), hyperplanaic acid (minor), constictic acid (trace), 2-O-methylhyperlatolic acid (minor), 2-O-methylisohyperlatolic acid (minor), 2-O-methylsuperlatolic acid (major), methyl 2-O-methylperlatolate (trace), superplanaic acid (minor), methyl hyperplanaite (minor), methyl 2-O-methylperlatolate (minor). The specimens

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from the Galapagos differ because they contain thiophaninic acid and 2,4-dichlorolichexanthone and have ascospores with an ornamented inner spore wall (very inconspicuously channelled).

Additional specimens examined: ECUADOR. GALAPAGOS: Floreana Island, entrance to Primavera Farm from main dirt road, 1°18'22.10"S, 90°26'29.69"W, 371 m alt., humid zone, on E-exposed trunk of *Cedrella odorata*, 22 Jan 2011; Cerro Pajas, inside the crater, 1°17'49.29"S, 90°27'23"W, 379 m alt., humid zone, on SSE-exposed trunk of *Scalesia pedunculata*, 12 Jan 2011, *Bungartz 9281* (CDS46507). Santa Cruz Island, dirt road from Bellavista to Media Luna, 0°40'15.1"S, 90°19'21.80"W, 450 m alt., humid zone, on trunks of *Cinchona pubescens* serving as fenceposts along pastures, 10 Aug 2008, *Clerc 08-135* (CDS39989); 0°40'54"S, 90°19'26"W, 285 m alt., humid zone, on wooden pole, 28 Feb 2006, *Aptroot 64698* (CDS31272).

Pertusaria leucosorodes Nyl., Acta Societatis Scientiarum Fennicae 26 (10): 16 (1900)

Pertusaria scaberula A.W.Archer, Mycotaxon 41: 240 (1991)

Fig. 5e

Thallus corticolous or lignicolous, crustose, continuous to rimose or rimose-areolate; *surface* vivid white to pale whitish, lead-grey, greenish or olive-grey, rarely ±beige, ±shiny, smooth, epruinose, coarsely wrinkled (rugose to ±plicate), not distinctly pseudocyphellate; *soralia* 0.3–0.8(–1) mm diam., concolorous with the thallus or, more commonly, vivid white, sparse to abundant, mostly single and dispersed, very rarely ±confluent, when crowded, strongly convex, hemispherical to subglobose, eventually apically ±flattened, circular in outline, distinctly pustulate, *i.e.*, forming from verrucae that break open apically to release coarse, corticate *granules* that transition into ±pseudocorticate blastidia and compact, ecorticate *soredia*; *medulla* white; *margin* not distinctly zonate, but rarely inconspicuously banded by one or several lines of a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* unknown, most likely sorediate, *i.e.*, a hymenial layer forming within the soralia below the soredia, but *asci* and *ascospores* not observed. *Pycnidia* not seen.

Chemistry: Cortex P+ orange, K+ bright lemon-yellow, C-, KC-; medulla P+ orange, K+ bright lemon-yellow, C-, KC-; soralia P+ orange, K+ bright lemon-yellow, C+ yellow, KC+ yellow; UV+ deep orange; containing lichexanthone, 2-O-methylisohyperlatolic acid (trace), decarboxythamnolic acid, thamnolic acid.

Distribution and ecology: New to South America, previously reported from southeast Asia (Sri Lanka, Papua New Guinea), and Australia (Archer and Elix 2011); moderately common on stems, twigs and branches of native and introduced small trees and shrubs (*Clerodendrum*, *Zanthoxylon*, *Cinchona*); occurs from the upper transition zone into the humid zone.

Notes: The species is morphologically extremely similar to *P. commutata* and can only be reliably distinguished by its chemistry (thamnolic instead of haemathamnolic acid). Apothecia are unknown for both *P. leucosorodes* and the morphologically very similar, but saxicolous *P. xantholeucoides*. On sectioning pustulate soredia of the three species, a few appear to contain a hymenial layer of paraphyses below the mass of soredia, but no asci and ascospores were found in any one of the specimens examined.

Specimens examined: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Alcedo**, outer SE-exposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, at the base of *Zanthoxylum fagara*, 5 Mar 2006, *Bungartz 4069* (CDS27999); *Aptroot 65035* (CDS31617); **Volcán Darwin**, southwestern slope, above Tagus Cove, 0°13'43.29"S, 91°19'47.29"W, 724 m alt., transition zone, on stem and branches of *Jasminocereus thouarsii*, 12 Nov 2007, *Bungartz 7439* (CDS37926); **Volcán Sierra Negra**, La Cueva Sucre, abandoned farm bought by the National Park, 0°50'34.60"S, 91°1'39.10"W, 362 m alt., humid zone, on twigs in the crown of a fallen *Syzygium jambos* tree, 15 Aug 2008, *Bungartz 8265* (CDS40911). **San Cristóbal Island**, trail from Cerro Pelado to El Ripioso, S of Cerro Partido, 0°51'28.10"S, 89°27'38"W, 372 m alt., transition zone, on twigs of *Clerodendrum molle*, 23 Aug 2008, *Bungartz 8543* (CDS41189); sector of the "Gotera de agua", flat plane between the cerros Pelado and Partido, 0°51'25.60"S, 89°27'34.89"W, 377 m alt., transition zone, dead tree lying on the ground, 23 Aug 2008, *Clerc 08-325* (CDS40179). **Santa Cruz Island**, temporary *Cinchona* weather station, along the trail to El Puntudo, 0°39'6.59"S, 90°19'57.39"W, 698 m alt., humid zone, on trunk of *Cinchona pubescens*, 28 Dec 2005, *Bungartz 3287* (CDS26929). **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, 796 m alt., transition zone, on twigs of *Clerodendrum molle*, 24736 (CDS28847).

Pertusaria lueckingii Bungartz, A.W.Archer & Elix, sp. nov.

MycoBank No.: MB 814350

Thallus morphologically very similar to *P. balekensis* A.W.Archer & Elix, but containing xanthones (4,5-dichlorolichexanthone and related compounds) rather than stictic acid.

Type: ECUADOR. GALAPAGOS: **Floreana Island**, entrance to Primavera Farm from main dirt road, 1°18'22.1"S, 90°26'29.7"W, 371 m alt., humid zone, pasture with elephant grass, some trees of *Cedrella odorata* and *Psidium guajava*; on sunny, wind- and rain-exposed bark of S-exposed trunk of *Cedrella odorata* (c. 30 cm diam.), 22 Jan 2011, *Bungartz 10074* (CDS47469, holotype).

Fig. 5f

Thallus corticolous, lignicolous or saxicolous, crustose, continuous to rimose; *surface* greenish white, greenish grey or greenish brown (\pm pale olivaceous), \pm shiny, smooth, epruinose, plane; *soralia* 0.3–1.5 mm, greyish white, sparse to abundant, mostly single and dispersed, rarely \pm confluent, irregular in outline and not clearly delimited, lacking a thalline margin; *soredia* coarse, granular to \pm coralline; *medulla* white; *margin* not distinctly zonate, delimited by a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* and *pycnidia* unknown.

Chemistry: Thallus P–, K–, C–, KC–; medulla P–, K–, C–, KC–; soredia P–, K–, C–, KC–; UV± pale yellow; containing 4,5-dichlorolichexanthone (major), ±2,4,5-trichlorolichexanthone (trace), ±4,5-dichloro-3-O-methylnorlichexanthone (trace).

Etymology: Named in honour of the lichenologist Robert Lücking, who first recognized this taxon as an independent species.

Distribution and ecology: Previously reported as an undescribed species from El Salvador, Central America (Archer and Elix 2011); in the Galapagos Islands it occurs from the upper transition zone into the humid zone, in dense shaded forests, often on introduced Guava trees (*Psidium guajava*); one collection grows on shaded and sheltered lava.

Notes: Morphologically *P. lueckingii* closely resembles *P. balekensis* A.W.Archer & Elix from Australia and Papua New Guinea, but it contains xanthones (2,4,5-trichlorolichexanthone, 4,5-dichlorolichexanthone; 4,5-dichloro-3-O-methylnorlichexanthone) rather than stictic acid.

In the Galapagos Islands, *P. lueckingii* is superficially similar to other species with coarse soredia, in particular the epiphytic *P. commutata* and *P. leucosorodes*, and the saxicolous *P. xantholeucoides*, but the ontogeny and structure of their soralia are very different. In *P. lueckingii* the soralia are ill defined and the soredia appear somewhat coralloid. In the other three species with coarse soredia the soralia are well delimited, erupting from distinct verrucae. Chemically the species are also distinct, *P. commutata*, *P. leucosorodes* and *P. xantholeucoides* all contain lichexanthone accompanied either by thamnolic acid or related metabolites, both these are absent in *P. lueckingii*.

Additional specimens examined: ECUADOR. GALAPAGOS: Floreana Island, trail to Pampa Larga, going off at end of dirt road to the highlands, SSW of Cerro Asilo de la Paz, 1°19'19.10"S, 90°27'20.60"W, 265 m alt., transition zone, on SSE-exposed base of *Geoffroea spinosa*, 13 Jan 2011, *Yánez-Ayabaca 1868* (CDS48224). Isabela Island, Volcán Cerro Azul, path from the first Caseta del Parque to Caleta Iguana at the coast, approx. one third of the way, 0°59'9.5"S, 91°26'4.90"W, 224 m alt., transition zone, on trunk of *Psidium floribunda*, 7 May 2012, *Spielmann 10638* (CDS52005); path from the first Caseta del Parque to Caleta Iguana at the coast, approx. half of the way, 0°59'1.8"S, 91°26'15.4"W, 205 m alt., transition zone, on lower side of branch, 8 May 2012, *Bungartz 10445* (CDS52414); along the trail from Caleta Iguana to the first Caseta del Parque, 0°59'12.1"S, 91°25'35.79"W, 276 m alt., transition zone, on twigs and branches, 2 May 2012, *Spielmann 10369* (CDS51725). Santiago Island, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt., humid zone, lava, on rock, 23 Mar 2006, *Aptroot 65641* (CDS32231). EL SALVADOR: Ahuachapán Jujutla, La Cascada de Don Juan Ecotourism Park, about 60 km ENE of San Salvador; 13°47'N, 89°51'W, 600 m alt., disturbed remnants of tropical rain forest, Apr 2011, *Lücking 33103* (F).

Pertusaria medullamarilla Yánez-Ayabaca, Bungartz, A.W.Archer & Elix, sp. nov.

MycoBank No.: MB 814351

Thallus with a distinctly lemon-yellow medulla, overall similar to *P. endochroma*, but growing on rock; containing thiophaninic acid, 4-chloro-6-*O*-methylnorlichexanthone, 2-chloro-6-*O*-methylnorlichexanthone and 2'-*O*-methylperlatolic acid.

Type: ECUADOR. GALAPAGOS: **Pinzón Island**, in the valley on the W slope of the highest mountain, 0°36'41"S, 90°40'11"W, dry zone, open scrub with *Prosopis juliflora*, *Alternanthera filifolia*, *Maytenus octogona*, and *Croton scouleri*; on basalt; 16 Feb 2006, *Aptroot 64089* (CDS30650, holotype).



Fig. 5. a–**d** *Pertusaria galapagoensis*; **a** thallus with disc-shaped, ±fused apothecia with several deep black, punctiform ostioles (*Bungartz 10070*, CDS47465, holotype, scale 3 mm) **b**–**d** section of apothecium and ascospores (*Aptroot 64698*, CDS31272); **b** apothecial section (scale 200 μ m); **c** ascospore with outer, finely ornamented spore wall (scale 30 μ m); **d** ascospore with smooth, apically trimmed inner wall (scale 30 μ m); **e** thallus of *P. leucosorodes* with soralia with blastidiate-granular soralia (*Bungartz 8543*, CDS41189, scale 3 mm); **f** thallus of *P. lueckingii* with soralia with coarse, granular to ±coralline soredia (*Bungartz 10074*, CDS47469, scale 3 mm).

Figs 6a-d

Thallus saxicolous, crustose, rimose-areolate; *surface* pale greyish to yellowish white to pale lemon-yellow, dull to \pm shiny, smooth, epruinose, but in parts eroded, plane to barely wrinkled, lacking soredia or isidia; *medulla* conspicuously lemon-yellow; *margin* not distinctly zonate, delimited by an indistinct whitish *prothallus*. *Apothecia* verruciform, hemispherical to subglobose, 0.7-1(-1.7) mm diam., single or rarely fusing, not or slightly constricted at the base, apically conical to \pm flattened, concolorous with the thallus, mono- to polycarpic, with 1-2(-4) dark grey to black, punctiform *ostioles*, not distinctly delimited or, in part, with a pale greyish rim, most remaining punctiform, but typically some \pm expanding and even becoming \pm discoid when fusing; *thalline exciple* hyaline, with a few large crystals (persistent in K) and abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle shaped crystals; thiophaninic acid), cortex lacking crystals; *epihymenium* not inspersed, of branched and sparingly anastomosing hyphae, \pm loosely intertwined around asci; *asci* cylindrical, 2(-4)-spored; *ascospores* hyaline, oblong to ellipsoid to broadly fusiform or \pm citriform, sometimes \pm asymmetric with one slightly broader and one more narrow end, $(55-)71-108(-129) \mu m long$, $(30-)35-48(-55) \mu m$ wide (n = 33); *spore wall* 2-layered, *outer wall* $2-3(-4) \mu$ m thick, with conspicuous microrugulate ornamentation, *inner wall* $(3-)4-5 \mu m$ wide, smooth (not grooved or laminated), markedly thickened apically (to 16 μ m); *pycnidia* not known.

Chemistry: Cortex P–, K–, C+ orange, KC+ orange, medulla P–, K–, C+ orange, KC+ orange, UV+ orange; containing thiophaninic acid, 4-chloro-6-O-methylnorlichexanthone, 2-chloro-6-O-methylnorlichexanthone, 2'-O-methylperlatolic acid.

Etymology: Named for its yellow medulla (amarillo is Spanish for yellow).

Distribution and ecology: Endemic to the Galapagos; found from the dry to the humid zone, but most common in the transition zone, on semi-shaded to sunny, wind- and rain-exposed basalt boulders and cliffs.

Notes: The strictly saxicolous *P. medullamarilla* is morphologically and anatomically very similar to the corticolous *P. endochroma*, but the latter only contains thiophaninic acid. In addition to thiophaninic acid, *P. medullamarilla* also contains 4-chloro-6-*O*-methylnorlichexanthone, 2-chloro-6-*O*-methylnorlichexanthone and 2'-*O*-methylperlatolic acid. It is thus chemically distinct and not just a saxicolous form of *P. endochroma*.

Additional specimens examined: ECUADOR. GALAPAGOS: Floreana Island, trail going to Post Office Bay, off the dirt road between highlands and Puerto Velasco Ibarra, cliff at NE-side of trail (Mirador), 1°17'4.29"S, 90°26'36.60"W, 365 m alt., transition zone, on top of basalt cliff, 25 Jan 2011, *Bungartz 10213* (CDS47632). Pinzón Island (see type). San Cristóbal Island, sector of the "Gotera de agua", flat plane between the cerros Pelado and Partido, 0°51'25.60"S, 89°27'34.89"W, 377 m alt., transition zone, on basalt rocks on the ground, 23 Aug 2008, *Truong 1508* (CDS39819); Cerro Mundo, at the top of the rock cliffs on the S side close to the summit, 0°53'19.5"S, 89°34'24.30"W, 282 m alt., transition zone, on protected rock cracks on the cliff, 25 Aug 2008, *Clerc 08-393* (CDS40247). Cerro Partido, along trail from entrance to Cerro Pelado to El Ripioso, 0°51'23"S, 89°27'37"W, 376 m alt., transition zone, on E-exposed slope (80°) of basalt boulder, 28 Apr 2007, *Bungartz 6635* (CDS34855); plain between Cerro Pelado and Cerro Partido, S of El Ripioso, 0°51'27"S, 89°27'36"W, 366 m alt., transition zone, on top of small basalt rock, 28 Apr 2007, *Bungartz 6653* (CDS34889). Santiago Island, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt., humid zone, on lava rock, 23 Mar 2006, *Aptroot 65738* (CDS32330); along the trail from the caseta in La Central to La Bomba (at the coast), cliff c. 2.5 km NE of the caseta, 0°13'41"S, 90°44'10"W, 533 m alt., transition zone, horizontal ledges of SW-exposed front of basalt cliff, on rock, 25 Mar 2006, *Bungartz 4866* (CDS29065).

Pertusaria nigrata Kremp., Flora 59: 174 (1876)

Figs 6e-g

Thallus corticolous, crustose, rimose to rimose-areolate; *surface* whitish beige to mineral- or olivegrey, mostly dull, rarely \pm shiny in part, smooth, epruinose, but often becoming \pm whitish eroded in part, lacking soredia and isidia, but often conspicuously papillate-verrucose; *medulla* white; *margin* not distinctly zonate, dull brownish or sometimes delimited by a thin, compact, black *prothallus* (especially where adjoining other thalli). *Apothecia* verruciform, hemispherical to subglobose, 0.7–1(– 1.2) mm diam., rarely single, more commonly fusing into \pm gnarled and contorted clusters, \pm constricted at the base, apically \pm flattened, concolorous with the thallus, (mono- to) polycarpic, with 1–3(–5) blackish brown *ostioles*, rarely delimited by a paler \pm indistinct, slightly elevated margin, some remaining punctiform, but sometimes expanding and becoming \pm discoid, typically closely aggregated, rarely fusing at the flattened top of the apothecium; *thalline exciple* dull brownish outside, hyaline within, with abundant minute and moderately sized crystals (minute crystals dissolving, moderately sized ones persistent in K); *epihymenium*



Fig. 6. a-**d** *Pertusaria medullamarilla* (*Aptroot 64089*, CDS30650); **a** rimose areolate thallus with verruciform apothecia (scale 3 mm); **b** close-up of apothecia cut to reveal yellow medulla (scale 1 mm); **c** ascospore with outer, finely ornamented spore wall (scale 40 μm); **d** ascospore with smooth, apically strongly trimmed inner wall (scale 40 μm); **e**-**g** *Pertusaria nigrata* (*Aptroot 65034*, CDS31616); **e** papillate-verrucose thallus (scale 3 mm); **f** apothecial section (scale 200 μm); **g** ascospore with smooth, barely ornamented outer wall and smooth, apically thickened inner wall (scale 20 μm).

pale olive, K± weakly violet; *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, (4–)6–8-spored; *ascospores* hyaline, narrowly to broadly ellipsoid to broadly fusiform, or ±citriform, (73–)93–135(–148) µm long, (26–)33–56(–63) µm wide (n = 34); *spore wall* 2-layered, *outer wall* 2–3(–7) µm thick, smooth to very faintly ornamented, *inner wall* (4–)6–10 µm wide, smooth (not grooved or laminated), apically distinctly thickened ('trimmed'; up to 14 µm); pycnidia not seen.

Chemistry: Cortex P-, K-, C-, KC-; medulla P+ orange (sometimes weak), K+ yellow, C-, KC-; UV+ bright yellow; containing lichexanthone, stictic acid, constictic acid.

Distribution and ecology: Known from South America, India, Sri Lanka and Australia (Archer and Elix 2011); collected on dead wood and bark of *Scalesia* and *Zanthoxylon* in the humid zone of Volcán Alcedo, Isabela Island.

Notes: Morphologically and anatomically very similar to *P. endoxantha*, but that species has smaller ascospores, lacks xanthones and contains norstictic rather than stictic and constictic acids.

Specimens examined: ECUADOR. GALAPAGOS: **Isabela Island Volcán Alcedo**, outer SE-exposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, on twigs of *Scalesia microcephala*, 05 Mar 2006, *Bungartz 4013* (CDS27943); on *Zanthoxylum fagara*, 05 Mar 2006, *Aptroot 65034* (CDS31616); c. 100 m below the crater rim, 0°25'36"S, 91°5'12"W, 1146 m alt., humid zone, branches of dead tree, 6 Mar 2006, *Bungartz 4165* (CDS28196).

Pertusaria oahuensis H.Magn., Arkiv för botanik 31A (6): 57 (1944)

Fig. 7a

Thallus corticolous or lignicolous, crustose, rimose to rimose-areolate; surface pale yellowish to yellowish white, dull, smooth, epruinose, coarsely wrinkled (rugose to ±plicate); *soralia* 0.3–0.6 mm diam., concolorous with the thallus or slightly paler, sparse to abundant, mostly single and dispersed, very rarely ±confluent, initially ±flattened, but soon distinctly convex, hemispherical, circular in outline and distinctly delimited, but lacking a thalline margin; *soredia* farinose; medulla white; margin not distinctly zonate, delimited by a compact, shiny black prothallus (especially where adjoining other thalli). Apothecia and pycnidia not seen.

Chemistry: Cortex P–, K– (slowly turning yellow, where damaged), C–, KC–; medulla P+ orange, K+ yellow, C–, KC–; soralia P+ orange, K+ yellow, C–, KC–; UV+ bright yellow; containing lichexanthone, stictic acid, cryptostictic acid and constictic acid.

Distribution and ecology: New to South America, previously known from Hawaii and Australia (Archer and Elix 2011); the few collections from the Galapagos were all from open woodland or scattered trees in the dry and transition zone.

Notes: *Pertusaria oahuensis*, like *P. darwiniana*, contains both stictic acid and xanthones. Both species form rimose to rimose-areolate thalli but those of *P. oahuensis* typically have a more irregularly roughened surface with a distinct pale yellow tinge. Under UV-light specimens fluoresce bright orange yellow, due to the presence of lichexanthone. Thalli of *P. darwiniana* are usually greyish white, occasionally with a pale pinkish, but never distinctly yellowish tinge. These thalli are not distinctly fluorescent, but do fluoresce pale yellow under UV-light (due to 4-5 dichlorolichexanthone). While stictic acid has been found in all specimens of *P. oahuensis*, it is not always present in *P. darwiniana*, and often only in very low concentration.

The most conspicuous morphological difference between the two species is the morphology of the soralia. In *P. darwiniana* the soralia are distinctly rimmed, often by a rather broad thalline margin, rarely, if the thallus is poorly developed, only by a thin thalline membrane. If the margin is well developed, the soralia appear \pm concave and contain relatively coarse soredia that are frequently tinged distinctly pink to yellowish. *Pertusaria oahuensis* has much finer soredia, concolorous with the thallus, and formed in convex soralia that are not delimited by a distinct thalline margin. In neither species are the soralia apothecial, *i.e.*, an ascohymenial layer with asci and ascospores has not been detected below the soredia.

Specimens examined: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Sierra Negra**, Volcán Chico on the norteastern slope of Sierra Negra, 0°46'56.79"S, 91°6'4.29"W, 938 m alt., transition zone, on SW-exposed trunk of *Jasminocereus thouarsii*, 14 Aug 2008, *Bungartz 8176* (CDS40822). **Pinta Island**, along the trail up to the summit from the S-coast, 0°34'27"N, 90°45'5"W, 369 m alt., transition zone, on pad of *Opuntia galapageia*, SW-exposed, 27 Feb 2007, *Bungartz 5849* (CDS33524). **Pinzón Island**, in the valley on the W-slope of the highest mountain, 0°36'41"S, 90°40'11"W, 310 m alt., dry zone, on wood, 16 Feb 2006, *Aptroot 64082* (CDS30643). **Santiago Island**, E of salt lake at James Bay, 0°14'25"S, 90°48'50"W, 170 m alt., transition zone, on *Bursera* bark, 30 Apr 1971, *Pike ID16-2 A* (OSC101523).

Pertusaria stictica Nugra, A.W.Archer, Bungartz & Elix, sp. nov.

MycoBank No.: MB 814352

Similar to *P. albopunctata* A.W.Archer & Elix, but with a much thinner, non-fissured thallus and with excavate rather than prominent soralia.

Type: ECUADOR. GALAPAGOS: **Santa Cruz Island**, Camote, René Valles' farm, at the border of the Galapagos National Park, 0°38'15.2"S, 90°17'53.3"W, 471 m alt., humid zone, secondary forest of *Psidium galapageium* and *Scalesia pedunculata*, disturbed by restoration management from the National Park to control invasive species, growing at breast height on NE-exposed bark of *P. galapageium* [original label data: Camote, finca de René Valle, lindero del Parque Nacional Galápagos, 0°38'15.2"S, 90°17'53.3"W, 471 m alt.; zona húmeda, bosque secundario de *Psidium galapageium* y *Scalesia pedunculata*, perturbado, restaurado y Parque Nacional Galápagos intervenido por especies vegetales invasoras, sobre corteza de *P. galapageium*, altura al pecho, exposición NE]; 21 Sep 2007, *Nugra 451* (CDS36765, holotype).

Fig. 7b

Thallus corticolous or lignicolous, crustose, continuous to ±discontinuous (not fissured but the substrate in parts often shining through); *surface* greenish white to greenish grey, dull to ±shiny, smooth, epruinose, plane, not wrinkled; *soralia* 0.1–0.7 mm diam., greyish white, sparse to abundant, single and dispersed, not confluent, flattened to excavate, circular in outline and distinctly delimited by a thin and ±membranaceous layer; *soredia* farinose to ±granular; *medulla* white; *margin* not distinctly zonate, delimited by a compact, shiny black *prothallus* (especially where adjoining other thalli). *Apothecia* and *pycnidia* not seen.

Chemistry: Cortex P–, K–, C–, KC–; medulla P+ orange, K+ yellow, C–, KC–; soralia P+ orange, K+ yellow, C–, KC–; UV–; containing stictic acid (major) an constictic acid (trace).

Etymology: Named for its principal secondary metabolite, stictic acid.

Distribution and ecology: Endemic to the Galapagos; known only from two collections, both on the bark of endemic *Psidium galapageium* trees in the humid zone.

Notes: According to their chemistry (stictic acid chemosyndrome) these specimens key out as *P. albopunctata* in Archer and Elix (2011), a species considered endemic to tropical and subtropical rainforest in eastern Queensland, Australia (Archer and Elix 2009). The thalli of *P. stictica* are much thinner, in parts ±discontinuous with the substrate shining through. Unlike *P. albopunctata* s.str. they are not rimose and the soralia are not prominent, but excavate.

The clearly delimited soralia of this species with their distinct thalline rim resemble those of *P. darwiniana*. In well-developed specimens of *P. darwiniana* this rim broadens into a thick thalline margin (structurally similar to the margin of lecanorine apothecia), yet specimens with poorly developed soredia often form only a thin membranaceous layer. These species can only be reliably distinguished by their chemistry with *P. stictica* consistently lacking xanthones.

Additional specimen examined: ECUADOR. GALAPAGOS: Floreana Island, at SE-base of Cerro de los Suspiros, 1°18'5.90"S, 90°25'48.29"W, 342 m alt., humid zone, on S-exposed lower side of inclined *Psidium guajava* trunk, 22 Jan 2011, *Bungartz 10024* (CDS47393).

Pertusaria tejocotensis var. stictica A.W.Archer, Bungartz & Yánez-Ayabaca, var. nov.

MycoBank No.: MB 814353

Differs from *Pertusaria tejocotensis* var. *tejocotensis* B. de Lesd. by the presence of stictic acid and related metabolites.

Type: ECUADOR. GALAPAGOS: **Pinzón Island**, E-facing side of a valley on the W-slope of the highest mountain, 0°36'49"S, 90°40'14"W, 294 m alt., transition zone, E-facing basalt cliff and *Scalesia baurii* ssp. *baurii*; *Polypodium tridens* growing on the basalt cliff, on top and flat slope of sunny, wind- and rain-exposed basalt boulder, 16 Feb 2006, *Bungartz 3608* (CDS27426, holotype).

Figs 7c-d

Thallus saxicolous, crustose, rimose-areolate; *surface* pale to deep lemon-yellow, dull to \pm shiny, smooth, epruinose, plane to barely wrinkled, lacking soredia or isidia; *medulla* white; *margin* not distinctly zonate, not delimited by a distinct *prothallus*. *Apothecia* verruciform, hemispherical to subglobose, 0.5-0.7(-1.2) mm diam., single or rarely fusing, constricted at the base, apically not flattened, concolorous with the thallus,

mono- to polycarpic, with 1-2(-4) dark brownish to blackish grey or jet black, punctiform *ostioles*, not delimited by a distinct rim, single or rarely fusing, plane to ±sunken, or emerging as small papillae on top of the apothecial verrucae; *thalline exciple* hyaline, lacking large crystals, but with abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle shaped crystals; thiophaninic acid), cortex lacking crystals; *epihymenium* dull brown, K-; *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, (2-)4-6(-8)-spored; *ascospores* hyaline, ellipsoid to broadly fusiform or ±citriform, $(49-)54-74(-80) \mu m \log, (22-)28-37(-42) \mu m wide (<math>n = 20$); *spore wall* 2-layered, *outer wall* $2-3(-5) \mu m$ thick, with conspicuous microrugulate ornamentation, *inner wall* $(3-)4-5 \mu m$ wide, with maturity distinctly laminated, markedly thickened apically (to $12 \mu m$); *pycnidia* not seen.

Chemistry: Cortex P-, K-, C+ orange, KC+ orange; medulla P+ orange, K+ yellow, C-, KC-; UV+ orange; containing thiophaninic acid, confluentic acid, planaic acid, 2'-O-methylmicrophyllinic acid, stictic acid, constictic acid.

Etymology: Named for its distinctive chemistry.

Distribution and ecology: This is the most common taxon on rock in the Galapagos, particularly on sunny, wind- and rain-exposed boulders and cliffs in the dry and transition zones, generally found in dry habitats from the coast to the high altitude dry zone. *Pertusaria tejocotensis* var. *tejocotensis* is known from Mexico and south-western USA (Lumbsch and Nash 2002, Dibben 1980).

Notes: The stictic acid chemosyndrome is here reported for the first time from *P. tejocotensis s. lat.* It was previously considered a good diagnostic character to distinguish this species from the morphologically similar, *P. texana.* Both species contain thiophaninic acid as a major xanthone, but *P. tejocotensis* contains additional confluentic and 2'-O-methylperlatolic acid, both absent in *P. texana.* However, the two species are clearly distinguished by their substrate preferences. *P. texana* grows on bark or rarely on wood, whereas *P. tejocotensis* typically inhabits rock, rarely soil or detritus (one specimen was found to be parasitic on *Stereocaulon azulense*). In both species the number of ascospores per ascus varies, but the asci of *P. tejocotensis* most commonly contain four, rarely six to eight ascospores. In *P. texana* asci are typically 8-spored, although they occasionally may produce fewer ascospores. Both species have two-layered spore walls with the inner wall thickened apically, but in *P. tejocotensis* the inner wall appears distinctly laminated. These laminations are not observed in *P. texana.*

Additional specimens examined: ECUADOR. GALAPAGOS: Española Island, along S-coast of the island, SE of Punta Suárez, c. 500 m inland from coast, 1°22'56.60"S, 89°43'8.40"W, 133 m alt., dry zone, on top of basalt outcrop; 10 Nov 2010, Bungartz 8929 (CDS45747); trail from Bahía Manzanillo on the N-coast of the island to the highest point, 1°21'24.89"S, 89°41'57"W, 24 m alt., dry zone, on top of lava boulder, 11 Nov 2010, Yánez-Ayabaca 1657 (CDS45540), 1660 (CDS45543); 1°22'18.69"S, 89°42'7.40"W, 130 m alt., dry zone, top of basalt cliff, 11 Nov 2010, Bungartz 9111 (CDS45929). Floreana Island, trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, 1°15'42.29"S, 90°26'31"W, 197 m alt., dry zone, on top of small basalt rock, 14 Jan 2011, Bungartz 9616 (CDS46895); cliff at NE-side of trail (Mirador), 1°17'4.29"S, 90°26'36.60"W, 365 m alt., transition zone, on NE-exposed front of basalt cliff, 25 Jan 2011, Bungartz 10225 (CDS47644), 10191 (CDS47610), Yánez-Ayabaca 2137 (CDS48512); lava flow c. 200 m N of village Puerto Velasco Ibarra, at the W-coast of the island, c. 100 m inland, 1°16'10.1"S, 90°29'17.80"W, 11 m alt., coastal zone, on top of basalt boulder, 18 Jan 2011, Bungartz 9871 (CDS47209). Isabela Island, Volcán Alcedo, outer E-exposed slope just below the crater rim, 0°25'17"S, 91°5'8"W, 1077 m alt., humid zone, on lava rock, 8 Mar 2006, Aptroot 65140 (CDS31723), 65141 (CDS31724); Volcán Cerro Azul, outer, lower, densely vegetated slopes of the crater rim, 0°57'99"S, 91°24'23.19"W, 1470 m alt., high altitude transition zone, on basalt ridge, 6 May 2012, Bungartz 10381 (CDS52351); outer SE-exposed slope, c. 2.5 km below the crater rim, 0°26'20"S, 91°4'35"W, 784 m alt., transition zone, on N-exposed front of finelayered glossy basalt boulder, 7 Mar 2006, Bungartz 4288 (CDS28360), 4290 (CDS28362), 4289 (CDS28361); lava ridge to the West above Cerro Verde, 0°57'9.40"S, 91°24'32.89"W, 1442 m alt., humid zone, on lava with thin humus layer (in part parasitic on Stereocaulon azulense and thus with atranorin and norstictic acid), 6 May 2012, Bungartz 10394 (CDS52364); Volcán Darwin, southwestern slope, above Tagus Cove, 0°13'43.29"S, 91°19'47.29"W, 724 m alt., transition zone, below overhang, 12 Nov 2007, Ertz 11811 (CDS37170), 11801 A (CDS38908); 0°13'27"S, 91°19'19.5"W, 874 m alt., transition zone, SE-exposed slope of lava flow; on rock, 15 Nov 2007, Bungartz 7724 (CDS38228); c. 1.5 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1280 m alt., high altitude dry zone, slope (75°) of basalt outcrop; on rock, 14 Nov 2007, Bungartz 7613 (CDS38109); 0°13'25.60"S, 91°19'13.80"W, 900 m alt., transition zone, on horizontal rock surface on top of lava flow, 15 Nov 2007, Bungartz 7771 (CDS38279); 0°13'59"S, 91°20'8"W, 597 m alt., dry zone, top of AA-lava flow, on rock, 16 Nov 2007, Bungartz 7806 (CDS38315); Volcán Sierra Negra, Muro de las Lagrimas W of Puerto Villamil, along the stairs going up behind the wall, 0°57'52.70"S, 91°0'46.79"W, 78 m alt., dry zone, at the top of basaltic rocks at the side of the stairs (exposed), on rock, 17 Aug 2008, Truong 1279 (CDS39590), Herrera-Campos 10747 (CDS40485), Bungartz 8436 (CDS41082);

close to Volcán Chico, along the trail, 0°46'57.79"S, 91°5'59.39"W, 944 m alt., transition zone, on bare basaltic rocks, 14 Aug 2008, Truong 1242 (CDS39553), Clerc 08-147 (CDS40001); Herrera-Campos GAL-405 (CDS43295); Cerro Orchilla W of Puerto Villamil, close to the top, 0°57'45.60"S, 91°0'25.30"W, 98 m alt., dry zone, on basalt lava, 17 Aug 2008, Herrera-Campos GAL-418 (CDS43309); top of the northern crater rim, 0°48'3"S, 91°5'25.89"W, 968 m alt., humid zone, on top of basalt boulder 8 Sep 2007, Bungartz 6790 (CDS36209), 6775 (CDS36194); along dirt road from Puerto Villamil to crater of Sierra Negra, 0°55'12.4"S, 90°59'38.20"W, 30 m alt., dry zone, on S-exposed front of AA-lava, 10 Sep 2007, Bungartz 6931 (CDS36431); Las Tintoreras, small island infront of Puerto Villamil at the S-coast of Isabela, 0°58'13.6"S, 90°57'39"W, 13 m alt., coastal zone, on W-exposed front of lava rock, 10 Sep 2007, Bungartz 7012 (CDS36519), 7033 (CDS36540); southwestern slope, above Tagus Cove, 0°13'43.29"S, 91°19'47.29"W, 724 m alt., transition zone, on top of small basalt rock among lava pebbles, 12 Nov 2007, Bungartz 7417 (CDS37904). Pinta Island, N-exposed slope of highest point of the island, at crater rim, 0°35'6"N, 90°45'10"W, 620 m alt., humid zone, on SE-exposed front of basalt cliff, 26 Feb 2007, Bungartz 5750 (CDS33405); along the trail up to the summit from the S-coast, 0°34'3"N, 90°44'56"W, 233 m alt., transition zone, on top of AA-lava boulde, 28 Feb 2007, Bungartz 5970 (CDS33648); at the S-coast, a little E of Cabo Chalmers, 0°33'2"N, 90°46'3"W, 10 m alt., dry zone, on top of exposed AA-lava flow, 1 Mar 2007, Bungartz 6055 (CDS33734); SW-part of the island, along trail going up the southwestern slope to Las Pampas on the western saddle, 0°34'13.5"N, 90°45'38.20"W, 316 m alt., transition zone, on top of basalt boulder, 30 Jan 2008, Nugra 557 (CDS38935); plateau on top of the western cliff, W of Las Pampas, 0°34'52.60"N, 90°46'29.19"W, 425 m alt., transition zone, on SSW-exposed overhang/cavity of basalt boulder, 1 Feb 2008, Nugra 639 (CDS39017). 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, 318 m alt., transition zone, on lava rock, 16 Feb 2006, Aptroot 64010 (CDS30571). San Cristóbal Island, Pan de Azúcar, inland from Bahía Sardinas at the NW-coast of the island, 0°43'13"S, 89°21'14"W, 155 m alt., dry zone, on E-exposed front of cliff of consolidated tuff, 24 Apr 2007, Bungartz 6442 (CDS34657); Cerro Partido along trail from entrance to Cerro Pelado to El Ripioso, 0°51'23"S, 89°27'37"W, 376 m alt., transition zone, on S-exposed slope (20°) of basalt boulder, 28 Apr 2007, Bungartz 6611 (CDS34831); Cerro Colorado summit, around the viewpoint, 0°54'54.89"S, 89°26'1.5"W, 159 m alt., dry zone, basalt rocks, slope 15° SWW, on rock, 24 Aug 2008, Clerc 08-267 (CDS40121); Cerro Mundo, at the top of the rock cliffs on the S side close to the summit, 0°53'19.5"S, 89°34'24.30"W, 282 m alt., transition zone, in protected rock cracks of the cliff, 25 Aug 2008, Clerc 08-392 (CDS40246). Santa Cruz Island, on the North side of the island, along the dirt road to the ash quarry Mina Granillo Rojo, 0°36'56"S, 90°22'3"W, 570 m alt., transition zone, on lava rock, 23 Feb 2006, Aptroot 64550 (CDS31122). Rábida Island, E-side of the island, dry zone, 1 May 1976, Weber s.n. (COLO294662; L-62859). Santiago Island, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt., humid zone, on lava rock, 23 Mar 2006, Aptroot 65708 (CDS32300); Bungartz 4801 C (CDS43921); along the trail from the caseta in La Central to La Bomba (at the coast), cliff c. 2.5 km NE of the caseta, 0°13'41"S, 90°44'10"W, 533 m alt., transition zone, on horizontal ledges of SW-exposed front of basalt cliff, 25 Mar 2006, Bungartz 4865 (CDS29064); c. 5 km inland from the E-coast, ± at the same latitude as Bahía Sullivan, 0°16'52"S, 90°37'17"W, 175 m alt., dry zone, on S-exposed front of small basalt rock, 16 Jul 2006, Bungartz 5051 (CDS29264); 0°16'37"S, 90°37'24"W, 163 m alt., dry zone, on top of small basalt rock, 18 Jul 2006, Bungartz 5201 (CDS29414); top cinder cone, c. 1 km inland from the E-coast, at the same latitude as Isla Bartolomé, 0°17'56"S, 90°35'3"W, 222 m alt., dry zone, on NNW-exposed front of basalt rock, 20 Jul 2006, Bungartz 5313 (CDS29529); along the trail from Bucanero to Jaboncillos, c. 3 km SE of Bucanero, 0°10'52"S, 90°48'33"W, 362 m alt., transition zone, on lava rock, 22 Mar 2006, Aptroot 65397 (CDS31983); near James Bay, 0°13'45"S, 90°48'30"W, 240 m alt., dry zone, on rock, 1 May 1971, Pike 2691 (OSC101600); en el parte sureste de la isla, 0°17'54"S, 90°37'54.89"W, 163 m alt., zona seca, sobre rocas de lava basáltica, 20 Jul 2006, Nugra 117 (CDS32771); near James Bay, 0°14'0"S, 90°49'30"W, 45 m alt., dry zone, on rock, 27 Apr 1971, Pike 2613 (OSC101598).

Pertusaria tetrathalamia (Fée) Nyl., Acta Societatis Scientiarum Fennicae 7(2): 448 (1863)

Trypethelium tetrathalamium Fée, *Essai sur les cryptogames des écorces exotiques officinales*: 69 (1825) [1824]

Figs 7e-g

Thallus corticolous, crustose, continuous to rimose; *surface* ivory or creamy white to pale beige, dull to ±shiny, smooth, epruinose, coarsely wrinkled (rugose to ±plicate), lacking soredia and isidia; *medulla* white; *margin* not distinctly zonate, typically delimited by a thin, compact, black *prothallus* (especially where adjoining other thalli). *Apothecia* verruciform, subglobose, 1-2.2(-2.3) mm diam., single or rarely fusing, distinctly constricted at the base, concolorous with the thallus, the cortex apically tearing apart, (mono- to) polycarpic, with (1-)2-3(-4) blackish, punctiform *ostioles* delimited by a translucent rim, the ostioles forming where the apothecial cortex has torn apart; *thalline exciple* hyaline, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K to form a yellow solution, ?stictic acid), cortex lacking crystals; *epihymenium* pale olive, K-; *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not



Fig. 7. a rimose thallus of *Pertusaria oahuensis* with convex soralia producing farinose soredia (*Bungartz 5849*, CDS33524, scale 1.5 mm); **b** thin, ±discontinuous thallus of *P. stictica* with barely excavate soralia (*Nugra 451*, CDS36765, scale 1.5 mm); **c**, **d** *Pertusaria tejocotensis* var. *stictica*; **c** rimose areolate thallus with hemispherical to subglobose verruciform apothecia (*Bungartz 5201*, CDS29414, scale 5 mm); **d** ascospore with laminated inner spore, apically trimmed inner spore wall (*Bungartz 3608*, CDS27426, holotype of the variety, scale 20 µm); **e**-**g** *Pertusaria tetrathalamia*; **e** rimose thallus with subglobose verruciform apothecia (*Bungartz 7730*, CDS38234, scale 5 mm), **f** close-up of apothecia with cortex apically torn apart (*Bungartz 7680*, CDS38183, scale 4 mm); **g** ascospore with spirally grooved inner spore wall (*Bungartz 7680*, CDS38183, scale 20 µm).

inspersed, of branched and sparingly anastomosing hyphae, \pm loosely intertwined around asci; *asci* cylindrical, (2–)4-spored; *ascospores* hyaline, fusiform, (69–)90–115(–137) µm long, (22–)32–40(–63) µm wide (n = 72); *spore wall* 2-layered, *outer wall* 2–4(–5) µm thick, smooth to very faintly ornamented, *inner wall* 3–5 µm wide, conspicuously spirally grooved along the outside, \pm thickened apically (to 12 µm); pycnidia not seen.

Chemistry: Cortex P–, K–, C–, KC–; medulla P+ orange, K+ bright yellow, C–, KC–, UV± pale yellow; containing 4,5-dichlorolichexanthone, atranorin, stictic acid, cryptostictic acid, constictic acid.

Distribution and ecology: Throughout North and South America (Lumbsch and Nash 2002); in Galapagos common on twigs and branches of trees and shrubs (*Chiococca alba*, *Croton scouleri*, *Psidium galapageium*, *Bursera graveolens*) in the transition zone.

Notes: Most characteristic for *P. tetrathalamia* are the large, erumpent, verruciform apothecia and the few, conspicuously grooved ascospores. See also comments under *P. albinea*.

Specimens examined: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Darwin**, southwestern slope, above Tagus Cove, 0°13'27.60"S, 91°19'21.19"W, 860 m alt., transition zone, on stem of *Croton scouleri*, 15 Nov 2007, *Ertz 11926* (CDS37285); *Bungartz 7680* (CDS38183), *7699 A* (CDS54886), *7699 B* (CDS54887); 0°13'27"S, 91°19'19.5"W, 874 m alt., transition zone, on *Croton scouleri* stem, 15 Nov 2007, *Bungartz 7730* (CDS38234). **Santa Cruz Island**, dirt road to Mina Granillo Rojo, on the N-side of the island, 0°36'52.60"S, 90°22'11.80"W, 547 m alt., transition zone, on branches, 20 Aug 2008, *Clerc 08-191* (CDS40045); along the road from Los Gemelos towards the N-coast of the island, c. 1 km N of Los Gemelos, 0°37'22"S, 90°22'47"W, 584 m alt., transition zone, on thin stalks of *Chiococca alba*, 12 Feb 2006, *Bungartz 3502* (CDS27280), *Aptroot 63803* (CDS30361); on the North side of the island, along the dirt road to the ash quarry Mina Granillo Rojo, 0°36'56"S, 90°22'3"W, 570 m alt., transition zone, on *Bursera*, 23 Feb 2006, *Aptroot 64578* (CDS31150); cerca la vía sector Los Gemelos, 0°38'2.10"S, 90°23'37.89"W, 661 m alt., zona húmeda, sobre *Psidium galapageium*, 4 Jan 2007, *Nugra 278* (CDS33194); near Los Gemelos craters, 0°36'31"S, 90°22'4"W, 350 m alt., humid zone, on wood, 31 May 2005, *Aptroot 63396* (CDS30147).

Pertusaria texana Müll.Arg., Flora 67: 399 (1884)

Figs 8a-b

Thallus corticolous, crustose, continuous to rimose or rimose-areolate; surface yellowish white to pale or deep lemon-yellow, dull to ±shiny, smooth, epruinose or very rarely pruinose, often ±verrucose to gnarled, rarely flaking off in scales, lacking soredia or isidia; *medulla* white; *margin* not distinctly zonate, delimited by an indistinct whitish prothallus. Apothecia verruciform, wart-shaped to hemispherical, rarely becoming subglobose, 0.5-1.2(-1.5) mm diam., single or rarely fusing, not or slightly constricted at the base, apically conical, rarely \pm flattened, concolorous with the thallus, mono- to polycarpic, with 1–3(–5) hyaline to dull grey, punctiform ostioles, delimited by a thin rim, distinctly deeper lemon-yellow then the surrounding apothecial verrucae or emerging as small papillae on top of the apothecial verrucae; thalline exciple dull brown outside, hyaline within, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle shaped crystals; thiophaninic acid), cortex lacking crystals; epihymenium pale olive, K- or K± violet (reaction often very pale); proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; asci cylindrical, (4-)6-8-spored; ascospores hyaline, broadly oblong, broadly ellipsoid to ±citriform, $(35-)43-59(-72) \mu m \log_2(21-)26-32(-34) \mu m wide (n = 40);$ spore wall 2-layered, outer wall $3-5 \mu m$ thick, with conspicuous microrugulate ornamentation, *inner wall* $3-5 \mu m$ wide, smooth (not grooved or laminated), markedly thickened apically (to 15 µm); pycnidia not seen.

Chemistry: Cortex P-, K-, C+ orange, KC+ orange, medulla P+ orange, K+ yellow, C-, KC- UV+ deep orange; containing thiophaninic acid, 2-chloro-6-O-methylnorlichexanthone, 4-chloro-6-O-methylnorlichexanthone, stictic acid and constictic acid; a few specimens possibly with faint traces of lichexanthone or 4,5-dichlorolichexanthone.

Distribution and ecology: North and Central America (Lumbsch and Nash 2002); the most common species on bark and wood in the Galapagos, particularly in the dry and transition zone on *Bursera graveolens*, but generally found in dry habitat from the coast to the high altitude dry zone.

Notes: See comments about P. endochroma.

Specimens examined: ECUADOR. GALAPAGOS: **Española Island**, along S-coast of the island, SE of Punta Suárez, c. 500 m inland from coast, 1°22'56.60"S, 89°43'8.40"W, 133 m alt., dry zone, on twigs of *Bursera graveolens*, 10 Nov 2010, *Yánez-Ayabaca 1621* (CDS45510); along S-coast of the island, SE of Punta Suárez, c. 500 m inland from

coast, 1°22'56.60"S, 89°43'8.40"W, 133 m alt., dry zone, on twigs of Bursera graveolens, 10 Nov 2010, Bungartz 8963 (CDS45781); along S-coast of the island, SE of Punta Suárez, c. 500 m inland from coast, 1°22'56.60"S, 89°43'8.40"W, 133 m alt., dry zone, on SW-exposed trunk of Bursera graveolens, 10 Nov 2010, Bungartz 8941 (CDS45759); trail from Bahía Manzanillo on the N-coast of the island to the highest point, 1°21'24.89"S, 89°41'57"W, 24 m alt., dry zone, on twigs of Cordia lutea, 11 Nov 2010, Bungartz 9010 (CDS45828); on branches of Buresera graveolens, 11 Nov 2010, Bungartz 9028 (CDS45846); 1°21'40.60"S, 89°41'56.60"W, 48 m alt., dry zone, on W-exposed side of Bursera graveolens branch, 11 Nov 2010, Bungartz 9069 (CDS45887). Islote Gardner near Española Island, SWpart of the island, 1°20'46.39"S, 89°38'54"W, 7 m alt., coastal zone, on W-exposed trunk of Bursera graveolens, 12 Nov 2010, Bungartz 9195 (CDS46013); SW-part of the island, trail to the top, 1°20'41.5"S, 89°38'49.20"W, 21 m alt., coastal zone, on branch of Bursera graveolens, 12 Nov 2010, Yánez-Ayabaca 1721 (CDS45604). Floreana Island, 800 m above the dock, on the right side of the main road, 1°16'34.89"S, 90°29'59"W, dry zone, on branch of Bursera graveolens, 31 Dec 2009, Hillmann GAL-29 (CDS44762), at the base of Cerro Comunista, 1°17'24.5"S, 90°28'22"W, 168 m alt., dry zone, on W-exposed branch of Bursera graveolens, 16 Jan 2011, Bungartz 9765 (CDS47082); lava flow behind beach [White Beach] at SE side of Punta Cormorán, c. 150 m inland, 1°13'45.60"S, 90°25'28.69"W, 6 m alt., coastal zone, on N-side of Bursera graveolens branches, 19 Jan 2011, Bungartz 9929 (CDS47298); along trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, at Laguna Seca, 1°15'30.80"S, 90°26'26.60"W, 206 m alt., dry zone, on SW-exposed trunk/branch of Bursera graveolens, 14 Jan 2011, Bungartz 9525 (CDS46807); at the base of Cerro Comunista, 1°17'22.89"S, 90°28'22.39"W, 158 m alt., dry zone, on branch of Acacia rorudiana, 16 Jan 2011, Yánez-Ayabaca 1972 (CDS48322); c. 500 m S of La Lobería, c. 200 m inland from coast, 1°17'12.69"S, 90°29'36"W, 20 m alt., dry zone, on trunk of Bursera graveolens, 16 Jan 2011, Yánez-Ayabaca 1981 (CDS48331); Yánez-Ayabaca 1987 (CDS48337); near Flamingo lagoon E of Post Office Bay, 1°15'0"S, 90°27'0"W, 5 m alt., coastal zone, on Bursera graveolens, 15 Apr 1971, Pike 2101 (OSC101596). Isabela Island, Volcán Darwin, at the W-coast between Tagus Cove and Caleta Negra, c. 1 km inland from the coast, 0°14'50.89"S, 91°22'43.79"W, 55 m alt., dry zone, on W-exposed trunk of Bursera graveolens, 17 Nov 2007, Bungartz 7939 (CDS38449); inland from Tagus Cove at the W-coast of the island, 0°15'8.69"S, 91°22'23.10"W, 77 m alt., dry zone, on W-exposed trunk of Bursera graveolens, 17 Nov 2007, Bungartz 7978 (CDS38488); Volcán Sierra Negra, trail to Volcán Chico, along Sierra Negra crater, 0°48'53.20"S, 91°5'18.39"W, 982 m alt., humid zone, on branches of Psidium guajava, 14 Aug 2008, Clerc 08-161 (CDS40015); Velasco, 0°49'57.79"S, 91°11'11"W, 650 m alt., humid zone, on bark, 25 Jan 2006, Jaramillo 2832 (CDS38779); outer SE-exposed slope and crater rim, 0°27'29"S, 91°7'19"W, 1089 m alt., humid zone, on Croton, 05 Mar 2006, Aptroot 65074 (CDS31656); outer, lower, densely vegetated slopes of the crater rim, 0°57'99"S, 91°24'23.19"W, 1470 m alt., high altitude transition zone, on base of Psidium galapageium tree, 6 May 2012, Nugra 1077 (CDS52240); along dirt road from Puerto Villamil to crater of Sierra Negra, 0°55'12.4"S, 90°59'38.20"W, 30 m alt., dry zone, on branches and trunk of Bursera graveolens, 10 Sep 2007, Bungartz 6985 (CDS36489); southwestern foothills, above Tagus Cove, 0°14'50"S, 91°21'29.89"W, 67 malt., dry zone, on trunk of Bursera graveolens, 11 Nov 2007, Ertz 11761 (CDS37120); Bungartz 7356 (CDS37843); area around the Muro de las Lagrimas, c. 5 km W of Puerto Villamil, 0°57'54.29"S, 91°0'48.79"W, 81 m alt., dry zone, on trunk of Bursera graveolens, 17 Aug 2008, Bungartz 8395 (CDS41041); Cerro Orchilla, c. 4 km W of Puerto Villamil, 0°57'47.29"S, 91°0'27.19"W, 56 m alt., dry zone, on top of inclined branch of Bursera graveolens, 17 Aug 2008, Bungartz 8478 (CDS41124); on the crater rim near the hut, 0°26'33"S, 91°5'31"W, 1100 m alt., humid zone, on wood, 7 Mar 2006, Aptroot 65190 A (CDS31774). Pinta Island, along the trail up to the summit, c. 1 km inland from the S-coast, 0°33'8"N, 90°44'29"W, 54 m alt., dry zone, on upper side of branches of Bursera graveolens, 25 Feb 2007, Bungartz 5660 (CDS33295);, 0°33'31"N, 90°44'38"W, 107 m alt., dry zone, on trunk of Bursera graveolens, 25 Feb 2007, Bungartz 5678 (CDS33313); along the trail up to the summit from the S-coast, 0°33'22"N, 90°44'34"W, 88 m alt., dry zone, on trunk of Bursera graveolens, 28 Feb 2007, Bungartz 6025 (CDS33704); at the S-coast, a little E of Cabo Chalmers, 0°33'2"N, 90°46'3"W, 10 m alt., dry zone, on trunk of Bursera graveolens, 1 Mar 2007, Bungartz 6046 (CDS33725). Pinzón Island, along the trail going up from Playa Escondida, 0°36'10"S, 90°40'1"W, 254 m alt., dry zone, on twigs of Maytenus octogona, 16 Feb 2006, Bungartz 3621 (CDS27439). San Cristóbal Island, Cerro Colorado summit, around the viewpoint, 0°54'54.89"S, 89°26'1.5"W, 159 m alt., dry zone, on branches of Macraea laricifolia, 24 Aug 2008, Truong 1500 (CDS39811); Cerro Colorado, fenced off area., 0°54'58.39"S, 89°26'4.70"W, 132 m alt., transition zone, on Zanthoxylum fagara, 15 May 2006, Jaramillo 2821 (CDS38786); near Rosa Blanca, inland from the SE-coast of the island, 0°49'9"S, 89°21'48"W, 12 m alt., dry zone, on trunk of Bursera graveolens, 23 Apr 2007, Bungartz 6398 (CDS34613); crest of Cerro Tortuga, c. 4 km inland from the NW-coast, 0°44'54"S, 89°23'32"W, 116 m alt., dry zone, on trunk of Bursera graveolens, 25 Apr 2007, Bungartz 6523 (CDS34741); trail to Cerro Mundo from the border of the National Park, NE of Puerto Baquerizo Moreno, 0°53'33.39"S, 89°34'42.5"W, 157 m alt., transition zone, on N-exposed trunk of Bursera graveolens, 25 Aug 2008, Bungartz 8672 (CDS41318). Santa Cruz Island, trail from parking lot to El Garrapatero beach, N-side of trail, 0°41'26.69"S, 90°13'19.10"W, 6 m alt., dry zone, on Bursera graveolens, 16 Jun 2010, Rivas Plata, E. 4008 (CDS45065); along the road from Bellavista to El Garrapatero, at the boundary of the National Park, 0°40'14"S, 90°15'58"W, 252 m alt., transition zone, on trunk of Bursera graveolens, 14 Feb 2006, Bungartz 3535 (CDS27334);

along the road from Bellavista to El Garrapatero, c. 3 km from the coast, 0°40'55"S, 90°13'46"W, 45 m alt., dry zone, on Bursera, 14 Feb 2006, Aptroot 63953 (CDS30511); along the trail from Puerto Ayora to Bahía Tortuga, 0°44'48"S, 90°19'14"W, 28 m alt., dry zone, on trunk of Bursera graveolens, 5 Jan 2006, Bungartz 3326 (CDS26993), 3328 (CDS26995); along the trail from Puerto Ayora to Bahía Tortuga, 0°44'52"S, 90°19'16"W, 31 m alt., dry zone, on trunk of Zanthoxylum fagara, 5 Jan 2006, Bungartz 3371 (CDS27038); exact locality unknown, ecological zone unknown, on Bursera, Hill s.n. (FH-TUCK197159); along trail to seismic station, 20 m alt., dry zone, on Bursera *graveolens*, 18 Apr 1976, *Weber s.n.* (CDS10840); El Garrapatero, about 20 km NE of Puerto Ayora, 0°41'30"S, 90°13'39"W, m alt., dry zone, on trunks and branches, 14 Feb 2005, Tehler, A. 8645 (CDS40609); along trail to seismic station, 20 m alt., dry zone, on Bursera graveolens, 18 Apr 1976, Weber s.n. (QCA). Santa Fé Island, on top of lava flow at the N-coast of the island, 0°48'12.4"S, 90°2'34.5"W, 13 m alt., coastal zone, on upper side of inclined Bursera graveolens trunk, 25 Oct 2007, Bungartz 7201 (CDS37685), 7225 (CDS37709), 7175 (CDS37659), 7187 (CDS37671), Ertz 11626 (CDS36952); cerca la playita y el barranco en la costa norte de la isla, 0°48'12.80"S, 90°2'35.20"W, 26 m alt., zona seca, sobre corteza de Bursera graveolens, 25 Oct 2007, Nugra 460 (CDS37021). Santiago Island, c. 500 m S of Bucanero, near the canyon at the northeastern foothills of Cerro Cowan, 0°10'21"S, 90°49'30"W, 70 m alt., dry zone, on branches of *Bursera graveolens*, 21 Mar 2006, *Bungartz* 4546 (CDS28632); c. 500 m S of Bucanero, NE-rim of the canyon at the northeastern foothills of Cerro Cowan, 0°10'23"S, 90°49'30"W, 68 m alt., dry zone, on Bursera, 21 Mar 2006, Aptroot 65343 (CDS31929); along the trail from the caseta in La Central to La Bomba (at the coast), halfway down to the coast, 0°12'54"S, 90°43'21"W, 293 m alt., dry zone,on trunk of Bursera graveolens, 25 Mar 2006, Bungartz 4901 (CDS29105), 4916 (CDS29120); small hill c. 1 km inland from the E-coast, at the same latitude as Isla Bartolomé, 0°17'40"S, 90°35'10"W, 77 m alt., dry zone, on trunk of Bursera graveolens, 20 Jul 2006, Bungartz 5270 (CDS29486); along the trail from Bucanero to Jaboncillos, c. 3 km SE of Bucanero, 0°10'52"S, 90°48'33"W, 362 m alt., transition zone, on stem of Clerodendrum molle, 22 Mar 2006, Bungartz 4590 (CDS28677), 4639 (CDS28726); c. 5 km SE of Bucanero, 0°11'19"S, 90°47'48"W, 562 m alt., transition zone, on trunk of Bursera graveolens, 22 Mar 2006, Bungartz 4652 (CDS28739); SE of James Bay, 0°16'45"S, 90°50'0"W, 40 m alt., dry zone, on Bursera, 26 Apr 1971, Pike 2565 (OSC101597), 1/4 mi S of James Bay, 0°14'30"S, 90°51'30"W, 7 m alt., dry zone, on *Bursera* trunks, 25 Apr 1971, *Pike 2542* (OSC101595); en el parte sureste de la isla, 0°17'46"S, 90°35'11.4"W, 63 m alt., zona seca, sobre Bursera graveolens, 20 Jul 2006, Nugra 109 (CDS32763); 15 m alt., ecological zone unknown, on palo santo tree (Bursera graveolens), 23 Mar 1971, A. Higgins s.n. (FH197376); 5-6 km NW of Bahía Sullivan, from Cerro Inn, 0°16'42"S, 90°37'26"W, 145 m alt., dry zone, on trunk of Bursera graveolens, 15 Jul 2005, W. Simbaña 547 (CDS32383).

Pertusaria thioisidiata Yánez-Ayabaca, Bungartz, A.W.Archer & Elix, sp. nov.

MycoBank No.: MB 814354

Thallus isidiate, often fertile, superficially similar to P. subisidiosa, but containing thiophaninic acid.

Type: ECUADOR. GALAPAGOS: **Isabela Island, Volcán Alcedo**, outer SE-exposed slope, c. 100 m below the crater rim, 0°25'36"S, 91°5'12"W, 1146 m alt., humid zone, grassland disturbed by former grazing of goats, *Pteridium arachnoideum* and *Stachytarpheta cayennensis*, scattered low shrubs of *Tournefortia rufo-sericea* and outcrops of basalt tuff in between; on ±sunny, ±wind- and rain-sheltered rock, near the ground on E-exposed small basalt rock above a cliff, 6 Mar 2006, *Bungartz 4140* (CDS28171, holotype).

Figs 8c-f

Thallus saxicolous, crustose, continuous to rimose or rimose-areolate; surface faint yellowish green to distinctly pale lemon-yellow, dull to ±shiny, smooth, epruinose, plane to ±rugose, soon densely covered by short, cylindrical, simple to barely branched isidia, c. 0.1–0.3 mm diam., c. 0.4–0.7 mm tall, apically often ±inflated and frequently containing a single pycnidium with one apical ostiole; medulla white or, in parts, pale lemon-yellow; margin not distinctly zonate, not delimited by a conspicuous prothallus. Apothecia verruciform, hemispherical to subglobose, 1-2.2(-2.5) mm diam., single or rarely fusing, ±constricted at the base, concolorous with the thallus, polycarpic, with (2–)4–6(–8) blackish, punctiform ostioles, not delimited by a distinct rim; thalline exciple dull greenish olive outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle shaped crystals; thiophaninic acid); epihymenium pale olive, K+ violet; proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; asci cylindrical, (2–)4-spored; ascospores hyaline, oblong to broadly oblong or citriform, occasionally slightly asymmetric (±tear-shaped, with a more pointed and a more rounded end), $(70-)76-102(-114) \mu m \log_2(23-)34-48(-59) \mu m wide (n = 39); spore$ wall 2-layered, outer wall 3-5 µm thick, with conspicuous microrugulate ornamentation, inner wall 4-7 µm wide, apically frequently thickened ('trimmed'; up to 20 μm); *pycnidia* immersed at the tip of isidia, *conidia* acicular, 11–13 μ m long, 0.5–1 μ m wide (n = 20).



Fig. 8. a-**b** *Pertusaria texana*; **a** rimose areolate, gnarled thallus, in parts flaking off (*Bungartz 7356*, CDS37843, scale 3 mm); **b** ascospores with microrugulate outer wall and smooth, apically trimmed inner wall (*Bungartz 3326*, CDS26993, scale 25 μm); **c**, **d** *Pertusaria thioisidiata*; **c** abundantly isidiate thallus of *P. thioisidiata* var. *thioisidiata* (*Bungartz 3981*, CDS2791, scale 3 mm); **d** sparsely isidiate thallus with hemispherical to subglobose verruciform apothecia of. *P. thioisidiata* var. *isidiogyrophorica* (*Bungartz 4793*, CDS28925, holotype, scale 3 mm); **e** ascospore with outer, ornamented spore wall; **f** ascospore with smooth, apically trimmed inner wall.

Etymology: Derived from the presence of both isidia and thiophaninic acid.

Distribution and ecology: Endemic to the Galapagos, on ± sunny to shaded, ±wind- and rain-sheltered basalt outcrops and cliffs.

Notes: This new species is superficially similar to *P. subisidiosa* A.W.Archer, but the Galapagos species is saxicolous rather than corticolous and differs chemically. Two morphotypes of *P. thioisidiata* can be distinguished, one is very densely isidiate and lacks apothecia, the other one has sparse to moderately abundant isidia and often has verruciform apothecia. Both morphotypes can occur in two chemotypes, which are here distinguished as varieties: the typical and much more common variety is *P. thioisidiata* var. *thioisidiata*. It contains xanthones together with the stictic acid chemosyndrome while the less common variety *P. thioisidiata* var. *isidiogyrophorica*, contains the same suite of xanthones, but gyrophoric acid rather than stictic acid. Both always have isidia and can occasionally be fertile.

Pertusaria thioisidiata var. thioisidiata

Fig. 8c

Chemistry: Cortex P–, K± weakly yellow, C+ orange, KC + orange; medulla P–, K± weakly yellow, C+ orange, KC + orange; UV+ orange; containing lichexanthone, 2-chlorolichexanthone, thiophaninic acid, 2-chloro-6-*O*-methylnorlichexanthone, 4-chloro-6-*O*-methylnorlichexanthone (trace), 2-*O*-methylisohyperlatolic (trace) and stictic acid (trace).

Additional specimens examined: ECUADOR. GALAPAGOS: Fernandina Island, W-side, 335 m alt., transition zone, 15 Feb 1964, Cavagnaro, D. s.n. (COLO193368; L-40462). Isabela Island, Volcán Alcedo, upper NNW-exposed slope inside the crater, 0°27'27"S, 91°7'23"W, 1055 m alt., humid zone, basalt, on rock, 5 Mar 2006, Aptroot 64889 (CDS31466); outer SE-exposed slope, c. 100 m below the crater rim, 0°25'36"S, 91°5'12"W, 1146 m alt., humid zone, on conglomerated basalt tuff partially covered by soil, 6 Mar 2006, Bungartz 4143 (CDS28174); Volcán Darwin, c. 1.5 km from the southwestern crater rim, 0°12'20.5"S, 91°18'52.79"W, 1280 m alt., high altitude dry zone, on exposed rock, 14 Nov 2007, Ertz 11891 (CDS37250); southwestern slope, above Tagus Cove, 0°13'11.4"S, 91°19'14.1"W, 955 m alt., transition zone, on SE-exposed front of basalt outcrop, 14 Nov 2007, Bungartz 7619 (CDS38121); 0°13'27.60"S, 91°19'21.19"W, 860 m alt., transition zone, top of basalt boulder, 15 Nov 2007, Bungartz 7715 (CDS38217). Santa Cruz Island, along the road from Bellavista to Los Gemelos, 0°38'12"S, 90°23'46"W, 574 m alt., humid zone, on lava rock, 12 Feb 2006, Aptroot 63925 (CDS30481); on the North side of the island, along the dirt road to the ash quarry Mina Granillo Rojo, 0°36'56"S, 90°22'3"W, 570 m alt., transition zone, on lava rock, 23 Feb 2006, Aptroot 64551 (CDS31123); on the summit of El Puntudo and on adjacent E-slope, 0°38'42"S, 90°20'14"W, 780 m alt., humid zone, on exposed basalt boulders at the top of Puntudo, 28 Feb 2006, Bungartz 3981 (CDS27911); near Puntudo, 0°38'41"S, 90°20'13"W, 750 m alt., humid zone, on lava rock, 27 May 2005, Aptroot 63171 (CDS29902). Santiago Island, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt., humid zone, on lava rock, 23 Mar 2006, Aptroot 65694 (CDS32286); 4 km E of eastern summit, 0°13'15"S, 90°44'30"W, 645 m alt., transition zone, on rock, 6 May 1971, Pike 2774 (OSC101522).

Pertusaria thioisidiata var. isidiogyrophorica Yánez-Ayabaca, Bungartz, A.W.Archer & Elix, var. nov.

MycoBank No.: MB 814355

Differs from Pertusaria thioisidiata var. thioisidiata by containing gyrophoric acid rather than stictic acid.

Type: ECUADOR. GALAPAGOS: **Santiago Island**, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt.; humid zone, N- and NE-exposed, steep basalt cliffs of crater rim with ferns (*Pityrograma calomelanos* var. *calomelanos*, *Polypodium tridens*, *Doryopteris palmata*, *Adiantum concinnum*, *Blechnum polypodioides*) growing in crevices; on rock below E-exposed overhang (95° inclined) of basalt cliff; shaded, wind- and rain-sheltered; 23 Mar 2006, *Bungartz 4793* (CDS28925, holotype).

Figs 8d-f

Chemistry: Cortex P-, K± sordid yellow, C+ orange, KC+ orange; medulla P-, K+ yellow, C± faintly red (attention: easily masked by C+ orange cortex reaction), KC± faintly red (often masked by C+ orange cortex reaction); UV + orange; containing 2-chlorolichexanthone, thiophaninic acid, 2-chloro-6-O-methylnorlichexanthone, gyrophoric acid.

Etymology: Named for its isidia and distinctive chemistry.

Additional specimens examined: ECUADOR. GALAPAGOS: Santiago Island, summit of Cerro Gavilan, in crater near La Central, 0°14'7"S, 90°44'57"W, 725 m alt., humid zone, on lava rock, 25 Mar 2006, *Aptroot 65571* (CDS32159); 2.8 km E of the eastern peak, 0°13'20"S, 90°45'0"W, 740 m alt., humid zone, on rock, 6 May 1971, *Pike 2767* (OSC101521).



Fig. 9. a–**g** *Pertusaria thiospoda*; **a**, **b** recent Galapagos specimen, poorly developed (*Bungartz 9620*, CDS46899); **a** yellowish thallus with verruciform apothecia (scale 5 mm); **b** close-up of verruciform apothecia with initially greyish punctiform ostioles that dilate with age (scale 2 mm); **c** historic Galapagos specimen, well developed (*Stewart 8470*, FH00377356, neotype of *P. bispora*; scale 4 mm); **d** cross section of two closely grouped, almost fused apothecia (*Bungartz 9620*, CDS46899; scale 200 μm); **e** ascus with two ascospores (*Howell 46*, FH00471017; scale 40 μm); **f** ascospore with distinctly grooved and apically trimmed inner wall (*Archer P779*, herb. Bungartz; scale 30 μm); **g** ascospore with net-like spore ornamentation (*Stewart 8470*, FH00377356, neotype of *P. bispora*; scale 20 μm).

Pertusaria thiospoda C.Knight, Transactions of the Linnean Society of London, Botany 2: 47 (1882)

Pertusaria bispora Farlow ex Linder, Proceedings of the California Academy of Sciences ser. 4, 21: 213 (1934)

Type: ECUADOR. GALAPAGOS: **Genovesa Island** [= Tower Island; exact locality unknown; the entire island characterized by dry zone vegetation], 14 Sep 1905, *Stewart* 8407 (FH00377356, selected here as neotype of *P. bispora*).

Taxonomic Note: Linder (1934) selected a specimen of *P. bispora* collected during the Templeton Crocker Expedition of the Californian Academy of Sciences and deposited in FH as the holotype (p. 214: "...*Tower Island, on trunks and branches of Bursera graveolens, Alban Stewart, 153, type, in the Farlow Herbarium...*"). He also cited an isotype specimen from CAS (*ibid.*: "...*cotype in the Herbarium of the California Academy of Sciences, No. 119734...*"). Neither specimens could be located. We consequently select another specimen at FH, also collected by A. Stewart but with a different specimen number (*Stewart 8407;* FH00377356) as the neotype. Also mentioned in the protologue is a collection by J.T. Howell [ibnd.: "...*Revillagigedo Islands: Socorro Island, March 27, 1932 (17)...*"]. This specimen with collector number 17 could not be found. Instead two specimens deposited in FH, and apparently collected by Howell on Socorro Island during the Templeton Crocker Expedition were identified as *P. bispora* by Linder on 27 Mar 1932; both specimens are labelled with collector number 46 (*Howell 46*, FH00471017 and FH00471018).

Figs 9a-g

Thallus corticolous, crustose, continuous to rimose or rimose-areolate; surface yellowish white to greenish yellow, pale or deep lemon-yellow, dull to ±shiny, smooth, epruinose, plane and even or ±verrucose to gnarled, rarely flaking off in scales, lacking soredia or isidia; medulla white; margin not distinctly zonate, delimited by an indistinct whitish prothallus. Apothecia verruciform, wart-shaped to hemispherical, rarely becoming subglobose, 0.5-1(-1.2) mm diam., single or rarely fusing, not or slightly constricted at the base, apically conical, rarely \pm flattened, concolorous with the thallus, mono- to polycarpic, with 1–3(–5) hyaline to dull grey, punctiform to distinctly dilating ostioles, not delimited by a thin rim, deeper in colour than the surrounding apothecial verrucae, not emerging as small papillae on top of the apothecial verrucae; thalline exciple dull brown outside, hyaline inside, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K, re-forming as yellowish clusters of needle-shaped crystals; thiophaninic acid), cortex lacking crystals; epihymenium pale olive, K-; proper exciple and hypothecium hyaline to pale yellowish, not inspersed with crystals; hymenium not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; asci cylindrical, (1- or)2-spored; ascospores hyaline, broadly ellipsoid to ±citriform, $(87-)88-115(-130) \mu m \log_{10}(19-)35-39(-40) \mu m wide (n = 20); spore wall 2-layered, outer wall 3-5 \mu m$ thick, with conspicuous microrugulate ornamentation, inner wall 3-5 µm wide, initially not ornamented, but finely to strongly incised with age (forming a net-like ornamentation), only mature spores distinctly thickened apically (to 12 µm); pycnidia not seen.

Chemistry: Cortex P–, K–, C+ orange, KC+ orange; medulla P–, K± pale yellow (reaction, if present, often confined to parts of the lower medulla; most pronounced along the inner apothecial wall), C–, KC–; UV+ bright orange; containing thiophaninic acid (major), stictic acid (major), menegazziaic acid (trace), cryptostictic acid (trace), constictic acid (trace) [specimen examined, *Bungartz 9620* (CDS46899)].

Distribution and ecology: In the Galapagos this species is only known from two collections in dry open *Bursera* woodland, one from Genovesa (the type of *P. bispora*), and a second from Floreana (the only specimen collected recently). Weber (1986) cited records from Santiago and Santa Cruz, but all of his collections belong to be other species with similar, yellowish thalli (see notes below). The protologue of *P. bispora* also mentions a collection from Soccoro (Revillagigedo Islands, off the south coast of Baja California Sur, Mexico); a record confirmed here. *Pertusaria thiospoda* clearly has its centre of distribution in the western Pacific, where it is common and widely distributed in coastal Australia (including the Northern Territory), Lord Howe Island, Norfolk Island, and Vanuatu. Only one record is known as far east as the Cook Islands (Archer and Elix 2015). Reports of *P. straminella* Malme [syn. *P. megapotamica* H. Magn.] from South America most likely belong to this taxon, but there the species is reported to occur further inland. The records from Galapagos and Revillagigedo are clearly unexpected and the fact that here the species appears to be very rare may indicate that it has reached the limit of its distribution in these islands.

Notes: A unique combination of characters distinguish *P. thiospoda* from other corticolous species of *Pertusaria* present in Galapagos with a yellowish thallus. Thus the thalli do not give a distinctive reaction with K (only parts of the lower medulla and the inner apothecial wall are K+ pale yellow), the verruciform apothecia have a hyaline ostiole that dilate with age, and the asci contain only one, rarely two, thick-walled spores. In the protologue of *P. bispora* Linder (1934) describes these diagnostic traits as follows, P. 213: "...*In contrast with* P. leioplaca, *which produces from four to eight spores in an ascus, and of which the thallus, according to Hasse reacts positively to KOH, changing to yellow and then to pale violet, this species produces two spores, or*

occasionally one, in an ascus and gives but a faint yellowish reaction with KOH...."; and: Fig. 1, upper middle: "...a mature ascospore with definitely thickened lateral walls...").

Linder (1934) thus emphasized the weak K reaction in combination with one or two, thick-walled ascospores. His drawing of an ascus with two spores (Fig. 1 P. 213: "...on the left...") almost perfectly matches a similar one by Knight (1882, Plate IX no. 34) of *P. thiospoda*. Both drawings suggest that the spores are not apically thickened but have a conspicuously thickened inner spore wall, which is not distinctly ornamented. Archer (2004, P. 164) describes the ascospores of *P. thiospoda* as "smooth". However, re-examining specimens of *P. thiospoda* collected in Australia and comparing them with the neotype of *P. bispora* revealed that both have ascospores that are only smooth initially. With increasing maturity the outer part of their inner wall becomes faintly incised whereas mature to over mature ascospores are not only apically thickened, but the inner walls are distinctly ornamented! In the light microscope this ornamentation is best seen with Normanski contrast (differential interference contrast); it is easily overlooked when only young spores are examined.

The incisions on the outside of the inner wall, unlike deeper, more distinct grooves described above for other species, are not spirally twisted around the ascospores. Instead they form an irregular, net-like ornamentation. This net of incisions is best seen in mature or even over mature spores

Thalli of the Australian collections of *P. thiospoda* are paler and less distinctly yellowish than the Galapagos specimens, but nevertheless share the same chemistry, morphology, dilated ostioles, anatomy, number of acospores and spore ontogeny. Consequently we consider the two taxa to be conspecific (for superficially similar species see the discussion of *P. endochroma* and *P. xanthodes*).

Weber (1986) considered it possible that all of the yellowish *Pertusarias* in the Galapagos belong to one or several, widely distributed species. On re-examining the historic collections from FH, OSC and COLO, we established that the corticolous specimens were either *P. texana* or *P. endochroma*, and the saxicolous specimens, *P. thioisidiata* or *P. tejocotensis*, respectively. This left only the type and the specimen from Floreana cited below as confirmed Galapagos records for *P. thiospoda*. Thus *P. thiospoda* must be exceedingly rare in the archipelago, as it apparently was when Weber surveyed these islands.

Additional specimens examined: ECUADOR. GALAPAGOS: Floreana Island, trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, 1°15′42.3″S, 90°26′31″W, 197 m alt., dry zone, open forest of *Bursera graveolens* and some *Prosopis juliflora* on W-exposed slope, dry herbaceous vegetation and small boulder field, on bark of S-exposed trunk of *Bursera graveolens*, 14 Jan 2011, *Bungartz* 9620 (CDS46899).

Non-Galapagos material examined for comparison: MEXICO. REVILLAGIGEDO ISLANDS: **Soccoro Island** (exact locality and collection date unknown), *Howell 46* (FH00471017, FH00471018). AUSTRALIA. NEW SOUTH WALES: Central: Hawkesbury River, c. 47 km N of Sydney, 33°27'S, 151°08'E, near the coast, on *Avicennia marina*, 11 May 1991, *Archer P162* (herb. Bungartz); Myall River, Hawks Nest c. 30 km S of Buladelah, 32°44'S, 152°09'E, near the coast, on *Avicennia*, 15 Sep 1992, *Archer P366* (herb. Bungartz); Kattang Nature Reserve, near Perpendicular Point, 31°39'S, 152°51'E, near the coast, on dead branch, 12 Oct 1993, *Archer P601* (herb. Bungartz); track to Resolute Beach, c. 25 km N of Sydney, 33°35'S, 151°18'30"E, near the coast, on *Banksia*, 16 Dec 1995, *Archer P779* (herb. Bungartz).

Pertusaria xanthodes Müll.Arg., Flora 67: 286 (1884)

Figs 10a-b

Thallus corticolous, crustose, continuous to rimose; *surface* pale greyish white to deep lemon-yellow, dull to ±shiny, smooth, epruinose, lacking soredia and isidia, but often completely covered by densely adjoining, verruciform apothecia; *medulla* white; *margin* not distinctly zonate, not delimited by a distinct *prothallus*. *Apothecia* verruciform, hemispherical to subglobose, 0.7-1(-1.2) mm diam., single or rarely fusing, distinctly constricted at the base, concolorous with the thallus, (mono- to) polycarpic, with (1-)2-3(-4) punctiform *ostioles*, concolorous with the verruca surface and almost completely indistinct; *thalline exciple* hyaline, with few large crystals (persistent in K) and abundant minute crystals (dissolving in K into a yellow solution, ?stictic acid), cortex lacking crystals; *epihymenium* pale, K–; *proper exciple* and *hypothecium* hyaline to pale yellowish, not inspersed with crystals; *hymenium* not inspersed, of branched and sparingly anastomosing hyphae, ±loosely intertwined around asci; *asci* cylindrical, 2(-4)-spored; *ascospores* hyaline, oblong to ellipsoid, (74–)82–104(–107) µm long, (29–)34–47(–49) µm wide (n = 13); *spore wall* 2-layered, *outer wall* 2-4(-5) µm thick, smooth to faintly ornamented, *inner wall* 3-4(-5) µm wide, at maturity ±spirally grooved along its outside, ±thickened apically (to 8 µm); pycnidia not seen.

Chemistry: Cortex P–,K–,C+ orange,KC+ orange; medulla P+ orange,K+ yellow,C–,KC–; UV+ orange; containing thiophaninic acid, 4-chloro-6-O-methylnorlichexanthone (weak trace), 2-chloro-6-O-methylnorlichexanthone (weak trace), stictic acid, cryptostictic acid and constictic acid, ±various UV+ blue spots derived from the substrate.

Distribution and ecology: New to South America, previously known from North America and Bermuda (Lumbsch and Nash 2001); in the Galapagos only known from a single specimen collected on bark of *Bursera graveolens* in the dry zone of Santa Fé.

Notes: There are only three species of Pertusaria in the Galapagos that have ascospores with an inner spore wall that is distinctly grooved along its outer side, namely P. tetrathalamia, P. xanthodes, and P. thiospoda. Pertusaria tetrathalamia lacks thiophaninic acid and has a whitish to pale beige but never a distinctly yellow thallus. The single Galapagos specimen of P. xanthodes is conspicuously deep yellow. It could be mistaken for P. texana, but the ostioles are colourless and very inconspicuous, almost 'invisible' on top of the flattened hemispherical to subglobose verrucae. In contrast, P. texana has ostioles that are often grey to dark grey and usually distinctly delimited by a conspicuous deep yellow rim, a rim which is often elevated, giving the ostiole a papillate appearance. The chemistry of *P. xanthodes* is very similar to that of *P. thiospoda*, but the medulla of the latter only reacts with K in part (see above under *P. thiospoda*). Further, the thalli of *P. xanthodes* and *P. thiospoda* are dissimilar, the upper surface being shiny and smooth in P. xanthodes but becoming verrucose-rugose in P. thiospoda. In P. thiospoda the pale ostiole typically dilates with age but the hyaline, barely visible ostioles of P. xanthodes do not dilate. Pertusaria thiospoda usually produces two, rarely one ascospore(s) whereas P. xanthodes produces two or rarely four ascospores per ascus. On average the ascospores of *P. xanthodes* are slightly shorter and broader than those of *P. thiospoda*. The ornamentation of the spores in *P. xanthodes* develop rapidly, forming deep ±spirally arranged grooves around the outside of the inner spore wall (similar to that of P. tetrathalamia). In P. thiospoda the inner spore wall remains fairly smooth until with age they become finely incised along the outside, with the incisions forming a net-like pattern.

Specimens examined: ECUADOR. GALAPAGOS: Santa Fé Island, dry zone, on Bursera graveolens, 25 Oct 2007, Jonitz 28 (CDS44626).

Pertusaria xanthoisidiata A.W.Archer, Bungartz & Elix, sp. nov.

MycoBank No.: MB 814356

Thallus corticolous, coarsely isidiate, containing dichloro- and trichloroxanthones, stictic acid and related metabolites.

Type: ECUADOR. GALAPAGOS: **Pinta Island**, along the trail up to the summit from the S-coast, 0°34'31"N, 90°45'6"W, 388 m alt., transition zone, open woodland of *Zanthoxylum fagara*, and few *Trema micrantha* and *Pisonia floribunda* with understory of *Cissampelos pareira*, *Alternanthera filifolia* and *Justicia galapagana*; on SE-exposed, sunny, wind- and rain-exposed trunk of *Opuntia galapageia*, 27 Feb 2007, *Bungartz 5837* (CDS33512, holotype).

Figs 10c-d

Thallus corticolous, crustose, continuous to rimose; *surface* pale yellowish green, dull to \pm shiny, smooth, epruinose, plane, soon densely covered by short, coarse, granulose to short dactyliform, simple or sparsely branched isidia, c. 0.1–0.16 mm diam., c. 0.15–0.7 mm tall; *medulla* white throughout; *margin* not or rarely \pm concentrically zonate, delimited by a blackish brown, compact *prothallus*. *Apothecia* and *pycnidia* not seen.

Chemistry: Cortex: P–, K–, C+ orange, KC+ orange; medulla P+ deep orange, K+ yellow, C–, KC–, UV± dull orange; containing 2,5-dichlorolichexanthone, 2,4-dichlorolichexanthone 2,4,5-trichlorolichexanthone, 6-O-methylarthothelin, arthothelin (trace), stictic acid, cryptostictic acid, constictic acid.

Etymology: The name derives from the yellow isidia present in this species.

Distribution and ecology: Endemic to the Galapagos; found throughout the transition zone, in dry, open *Zanthoxylon* scrub and in woodlands of Manzanillo (*Hippomane mancinella*) along dry ephemeral streambeds.

Notes: The only other isidiate *Pertusaria* species present in the Galapagos is *P. thioisidiata*, but that species is saxicolous, contains thiophanic acid, has a medulla that is pigmented pale lemon-yellow at least in part and bears sparsely branched, cylindrical isidia which sometimes develop apical pycnidia.

Pertusaria xanthoisidiata could be confused with sterile material of *Caloplaca wrightii* (Willey) Fink, but this species has a poorly developed, effuse, pale creamy white, indistinct thallus that often remains almost entirely immersed in its substrate, causing a whitish, effuse, discoloration. By contrast, thalli of *P. xanthoisidiata* are smooth, distinctly corticate, well developed on the surface of the substrate and typically clearly delimited. The two species also differ in the formation of isidia. *Pertusaria xanthoisidiata* has much stouter, coarse, distinctly corticate isidia that are sometimes \pm eroded at their tip. *Caloplaca wrightii* has smaller, finer, granular, waxy isidia that do not erode, but break-off entirely. Due to the presence of lichexanthone, thalli of *C. wrightii* fluoresce UV+ deep to bright yellow-orange, whereas those of *P. xanthoisidiata* are UV \pm dull orange and barely show any distinct fluorescence.



Fig. 10. a-b *Pertusaria xanthodes (Jonitz 28*, CDS44626); **a** thallus with abundant, closely adjoining, verruciform apothecia with indistinct, colourless ostioles (scale 3 mm); **b** ascospore with faintly ornamented outer spore wall (scale 20 μm); **c**, **d** *Pertusaria xanthoisidiata* (scale 3 mm); **c** rimose-areolate, verrucose to sparsely isidiate thallus margin, delimited by ±zonate, blackish brown prothallus (*Bungartz 8660*, CDS41306); **d** densely isidiate thallus centre, isidia in parts eroded (*Bungartz 8657*, CDS41303); **e-f** *Pertusaria xantholeucoides* var. *thamnolica* (scale 3 mm); **e** thallus thin, radiating, discontinuous along the margin, granular-verrucose to almost plicate, developing soredia in the centre (*Bungartz 4755*, CDS28887, holotype); **f** close-up of soralia with blastidiate granular soredia (*Bungartz 7425*, CDS37912).

Additional specimens examined: ECUADOR. GALAPAGOS: San Cristóbal Island, sector of the "Gotera de agua", trail to Cerro Pelado, 0°51'34.60"S, 89°27'35.20"W, 389 m alt., transition zone, on trunk of *Bursera graveolens*, 23 Aug 2008, *Truong 1510* (CDS39821); on trunk of *Hippomane mancinella*, 23 Aug 2008, *Clerc 08-311* (CDS40165); *Herrera-Campos GAL-485* (CDS43376); trail to Cerro Mundo, passing by the "cañadas", 0°53'32.20"S, 89°34'40.5"W, 212 m alt., transition zone, on *Hippomane mancinella*, 25 Aug 2008, *Herrera-Campos GAL-495* (CDS43386); trail from Cerro Pelado to El Ripioso, 0°51'35.29"S, 89°27'37.89"W, 384 m alt., transition zone, top of inclined *Psidium guajava* branch, 23 Aug 2008, *Bungartz 8528* (CDS41174); trail to Cerro Mundo from the border of the National Park, NE of Puerto Baquerizo Moreno, 0°53'36"S, 89°34'41.5"W, 206 m alt., transition zone, on top of *Hippomane mancinella* branch, 25 Aug 2008, *Bungartz 8660* (CDS41306); 0°53'33.39"S, 89°34'42.5"W, 157 m alt., transition zone, on N-exposed lower trunk of *Hippomane mancinella*, 25 Aug 2008, 2008, *Bungartz 8657* (CDS41303). **Santiago Island**, Guayabillos nuevo abierto, 0°14'0"S, 90°43'52"W, 625 m alt., transition zone, on wood, 25 Mar 2006, *Aptroot 65590* (CDS32179).

Pertusaria xantholeucoides Müll.Arg. var. thamnolica Bungartz & Yánez-Ayabaca, var. nov.

MycoBank No.: MB 814357

Differs from *Pertusaria xantholeucoides* var. *xantholeucoides* by containing thamnolic acid rather than haemathamnolic acid.

Type: ECUADOR. GALAPAGOS: **Santiago Island**, summit of Cerro Gavilan, inner N- and NE-exposed crater rim, 0°12'20"S, 90°47'3"W, 840 m alt., humid zone, on SW-exposed front of basalt cliff, 23 Mar 2006, *Bungartz* 4755 (CDS28887, holotype).

Figs 10e-f

Thallus saxicolous, crustose, areolate; *surface* vivid white to pale whitish to lead grey, rarely \pm pinkish beige, \pm dull, smooth, epruinose to pruinose, coarsely wrinkled granular (\pm plicate to granular-verrucose), individual areoles first developing isolated upon a thin, arachnoid, radiating prothallus; *soralia* 0.3–0.8(–1) mm diam., concolorous with the thallus or, more commonly, vivid white, sometimes with a pale pinkish tinge, sparse to abundant, mostly single and dispersed, very rarely \pm confluent, when crowded, strongly convex, hemispherical to subglobose, eventually apically \pm flattened, circular in outline, distinctly pustulate, *i.e.*, forming from verrucae that break open apically to release coarse, corticate *granules* that transition into \pm pseudocorticate blastidia and compact, ecorticate *soredia*; *medulla* white; *margin* not distinctly zonate, the individual, isolated areoles arising from a thin, radiating, arachnoid *prothallus*. *Apothecia* unknown, most likely sorediate, *i.e.*, a hymenial layer forming within the soralia below the soredia, but *asci* and *ascospores* not observed. *Pycnidia* not seen.

Chemistry: Cortex P+ orange, K+ bright lemon-yellow, C-, KC-; medulla P+ orange, K+ bright lemon yellow, C-, KC-; soralia P+ orange, K+ bright lemon yellow, C+ yellow, KC+ yellow; UV+ deep orange; containing lichexanthone, 2-O-methylisohyperlatolic acid (trace), decarboxythamnolic acid, thamnolic acid, constictic acid.

Etymology: This variety is named for its distinctive chemistry.

Distribution and ecology: This new taxon appears endemic to Galapagos, where it occurs from the transition zone into the lower humid zone, on sunny, wind- and rain-exposed boulders and cliffs. By contast, *P. xantholeucoides* var. *xantholeucoides* is known from Brazil, the Philippines (= *P. coccopoda* Vain.), and North America (= *P. moreliensis* B. de Lesd. (Archer and Elix 2011).

Notes: Morphologically specimens of *P. xantholeucoides* var. *thamnolica* closely resemble those of var. *xantholeucoides*, but they consistently contain thamnolic acid rather than haemathamnolic acid. This taxon also appears closely related to *P. leucosorodes* and *P. commutata* because of their structurally similar soralia and chemistry. The saxicolous thalli of *P. xantholeucoides* are, however, distinct insofar as they are not rimose, but distinctly areolate. Initially individual areoles develop on a thin, arachnoid, radiating prothallus and only later do they merge to form a more contiguous thallus. In contrast, the thalli of the corticolous species begin as a contiguous crust that subsequently develops fissures, *i.e.*, the thallus becomes rimose, the fissures then spread and fuse to form the rimose-areolate crust.

Specimens examined: ECUADOR. GALAPAGOS: **Isla Floreana**, trail going to Post Office Bay off the dirt road between highlands and Puerto Velasco Ibarra, cliff at NE-side of trail (Mirador), 1°17'4.29"S, 90°26'36.60"W, 365 m alt., transition zone, on S-exposed slope of basalt cliff, 25 Jan 2011, *Bungartz 10222* (CDS47641). **Isabela Island, Volcán Darwin**, southwestern slope, above Tagus Cove, 0°13'43.29"S, 91°19'47.29"W, 724 m alt., transition zone, on SW-exposed front of lava flow, 12 Nov 2007, *Bungartz 7425* (CDS37912); *Ertz 11786* (CDS37145); southwestern slope, above Tagus Cove, 0°13'27"S, 91°19'19.5"W, 874 m alt., transition zone, on top of lava flow, 15 Nov 2007, *Bungartz 7719* (CDS38223), 7725 (CDS38229); **Volcán Cerro Azul**, outer, lower,

densely vegetated slopes of the crater rim, 0°57'9.19"S, 91°24'26.39"W, 1542 m alt., high altitude transition zone, rock inside encañada, sunny, on top and slope of basaltic rock, 6 May 2012, *Spielmann 10535* (CDS51892). **San Cristóbal Island**, Cerro Partido along trail from entrance to Cerro Pelado to El Ripioso, 0°51'23"S, 89°27'37"W, 376 m alt., transition zone, on S-exposed top of ledge of basalt boulder, 28 Apr 2007, *Bungartz 6594* (CDS34814).

Coccotrema colobinum excluded from the Galapagos

Coccotrema colobinum (Tuck.) Messuti, *Flora criptogámica de tierra del fuego*. 13 (Fasc. 13): 20 (2002)

Pertusaria colobina Tuck., Proceedings of the American Academy of Arts and Sciences 12: 175 (1877)

Type: locality unknown! [most likely CHILE, almost certainly *not* GALAPAGOS; collected during the Hassler Expedition in 1872 to Chile and Galapagos; probably erroneously labelled, see below], *Hill s.n.* (FH-TUCK2223, FH00060331, lectotype selected by Messuti, in Messuti and Vobis 2002).

Figs 11a-c

The type specimen of *Pertusaria colobina* Tuck., was transferred by Messuti and Vobis (2002) and again by Messuti (2003) into *Coccotrema colobinum* (Tuck.) Messuti. It was collected by Reverend T. Hill during the Hassler Expedition to Chile and the Galapagos in 1872. The packet with the type material (FH00060331) contains five separate pieces of bark, the first three pieces on the left are labelled in black ink by the original collector T. Hill as "*Galapagos*". The second two pieces are labelled as "*Sholl Bay nr. W. entr. of Straits of Magellan*", also in Hill's handwriting. Four of these five pieces were subsequently marked in pencil as "*a, b, c,* and *d*". It is not certain, who pencilled in these letters, but the handwriting appears identical to the letters on the annotation slips added by R. Santesson, 1955. Santesson annotated specimen '*b*' as "*Most probably fr. Str. of Magellan*: Leptolichen coccophorus (*Mont.*) *Trevis.*" and specimen '*c*' and '*d*' as "*Coccotrema granulata* (Hook. f. & Taylor *nom. illegit.* He did not, however, annotate specimen '*a*'.

Messuti and Vobis (2002) and again Messuti (2003) suggested that only the two pieces of bark in the packet labelled 'a' belong to the holotype and were actually collected in the Galapagos Islands. However, it is almost certain that *all* pieces in this packet were collected at the same locality, in Sholl Bay (= Scholl Bay) near the Straits of Magellan, even though the three pieces of bark on the left (specimen 'a' and 'b') have been annotated by T. Hill as having been collected in the Galapagos. Weber (1986, P. 490) previously suggested this to be the case, citing the Santesson annotation, while Elix and McCarthy (1998) also listed *P. colobina* as doubtful following Weber's assessment.

Recently Alan Fryday (pers. comm.) re-examined the material and agreed that the *C. colobinum* thalli growing on the two pieces of bark labelled as '*a*' almost certainly belong to the same species as thalli on the piece labelled '*b*'. In fact one minute piece of this species appears broken through the middle of its thallus with one part on the bark fragment '*a*' immediately glued next to specimen fragment '*b*'.

Three other species grow on the same piece of bark labelled 'b' next to the thalli of C. colobinum: (1) the brownish pink apothecia of Lecanora sp., (2) the minute, subfruicose, coralloid white thallus of C. coccophorum, and (3) an unidentified Hypogymnia sp. Lecanora sp. grows on both pieces of bark labelled 'a' and 'b'. The coralloid thallus of C. coccophorum and the unidentified Hypogymnia sp. are only found on specimen 'b'. No species of Hypogymnia has ever been reported from the archipelago! The record of C. coccophorum would also be new to the islands. Among the more than 15,000 specimens deposited in CDS and all the other Galapagos collections examined (CAS, FH, COLO, OSC) not a single specimen was ever identified as Hypogymnia and no Galapagos specimen that we know of resembles the very distinct, coralloid thallus of C. coccophorum.

Species of *Coccotrema* (like those of *Hypogymnia*) typically inhabit cool-temperate regions, and if present in the tropics, such species would very likely be restricted to high altitudes, for example in the Andes. Messuti and Vobis (2002) and Messuti (2003) actually cite two specimens of *C. colobina* collected by Imshaug and Ohlsson (*MSC 43340, MSC 44816*) on *Nothofagus* from the Chilean coast. It therefore seems almost certain that the type of *C. colobinum*, like several other specimens collected by Reverend T. Hill during the Hassler Expedition, was mislabelled, such that *C. colobinum* never did occur in the Galapagos Islands. The record is here removed from the Galapagos checklist as it was based on an erroneously labelled specimen that is, unfortunately, the type of this species. Messuti and Vobis (2002) and Messuti (2003) considered this material a holotype, but because there are clearly several specimens inside the packet, their choice of specimen 'a' must effectively be considered a lectotypification.





Fig. 11. a–**c** collection of *Coccotrema colobinum* type material with several other species [(*Hill s.n.*, FH-TUCK2223 a, b, c, d, FH00060331, specimen "*a*" refers to the lectotype selected by Messuti and Vobis (2002) and Messuti (2003) (scale 5 cm); **a** overview of the material collected by Reverend T. Hill, on the left side three pieces of bark labelled "*a*" and "*b*", on the right two pieces labelled "*c*" and "*d*"; **b** specimen detail of the three left pieces with handwritten note by T. Hill "*Galapagos*" written below (scale 1.5 cm); **c** specimen detail of piece "*b*" on the right, closely adjoining the lower piece of "*a*" on the left, in the centre a thallus of *C. colobinum* extending across both pieces (encircled), additionally thalli of *Hypogymnia* sp. (*H.*) and *C. coccophorum* (*C.*) on piece "*b*", and thalli of *Lecanora* sp. (*L.*) on both sides (scale 3 mm).

Discussion

In the present study we found a total of 24 species of *Pertusaria* in the Galapagos Islands, 22 of which are new to the archipelago. As in other recent revisions of Galapagos lichens the diversity was much greater than reported previously (Aptroot and Bungartz 2007, Aptroot and Sparrius 2009, Aptroot *et al.* 2008, Bungartz 2008, Bungartz *et al.* 2010, Ertz *et al.* 2011, Truong et al. 2011, Yánez-Ayabaca *et al.* 2011, Bungartz *et al.* 2013, Knudsen and Bungartz 2013, 2014, Lücking *et al.* 2013). As a consequence, lichens must now be considered among the most diverse organisms of Galapagos terrestrial biodiversity.

Previous inventories clearly did not capture this diversity, Elix and McCarthy (1998) summarized lists published by Weber (Weber 1966, 1986, 1993, Weber *et al.* 1977, Weber and Gradstein 1984) and recorded 228 species with 5 varieties for the archipelago. In contrast, the current CDF Galapagos Species Checklist (Bungartz *et al.* 2011) lists a total of 579 accepted taxa. One challenge for the Galapagos lichen inventory is to determine how many lichen species are unique to this archipelago. The risk that lichens have been intentionally or accidentally introduced to the islands is very low, so most species can be considered native. However, whether they are endemic is more difficult to determine.

Yánez-Ayabaca *et al.* (2013) discussed the degree of endemism in Galapagos lichens and concluded that rates vary considerably within different species groups. For example 80% of all *Roccella* species in the Galapagos are endemic (Tehler et al. 2009) but only one species (3%) of *Cladonia* (Ahti 2000), although the taxonomy of three additional species remains poorly resolved (Yánez-Ayabaca *et al.* 2013). Among leprose and leproid lichens, Bungartz *et al.* (2013) also report very low rates of endemism. Yánez-Ayabaca *et al.* (2013) consequently assumed that the general rate of 8-10% endemism across all species groups as first proposed by Weber (1986), would not change significantly as a result of more recent investigations.

However, the genus *Pertusaria* exhibits a high degree of endemism throughout its distribution. Approximately 45% of Australian taxa are endemic (Archer 2004), 50% of New Zealand (Galloway 2007) and of all North American species (Dibben 1980), while in temperate North America approximately 75% of the species are endemic to the continent. By comparison, the degree of endemism in Galapagos *Pertusaria* could range from 30% up to 46% (if the Galapagos varieties of widely distributed species, i.e. *P. xantholeucoides* var. *thamnolica*, *P. tejocotensis* var. *stictica* are included). This relatively high rate of endemism seems quite consistent for this genus.

The apparent high degree of endemism can be discussed in context of the reproductive biology of the genus. A classic hypothesis to explain the evolution of endemic taxa on islands is the notion that species with heavier, less efficient propagules will only reach an island from an adjacent continent on rare occasions. Once established these species will remain relatively isolated from their ancestors and more likely evolve and radiate into unique species, rather than those where efficient diaspores permit regular gene exchange with their continental counterparts.

The deposition rate of particulates suspended in air is dependent upon particle size. Consequently small spores will be airborne longer and distributed farther than larger ones, and the ascospores of *Pertusaria* are generally large. The overall spore length of the Galapagos species range from 24 up to 148 µm and width from 15 to 63 µm which is unusually large by comparison with other crustose genera reported from the archipelago. In this context it is not surprising that eight of the fifteen species (57%) of Galapagos *Pertusaria* which reproduce by ascospores appear to be endemic.

One would suspect that soredia would be far more efficient propagules. Among the leprose and leproid Galapagos lichens there is only one possible endemic species, thus far reported (Bungartz *et al.* 2013). In *Pertusaria* only two of eight sorediate species are possibly endemic (25%), although both have fine, farinose soredia (viz. *P. darwiniana* and *P. stictica*). The species with coarse, presumably heavier soredia are not endemic (although *P. xantholeucoides* occurs in Galapagos as a new chemotype).

World-wide *Pertusaria* is one of few crustose lichen genera relatively well studied. A world-key by Archer and Elix (2011) treats 794 taxa, of which 482 are synonyms (or possible synonyms), this total number of accepted species is higher than previous estimates of world-wide diversity in the genus (Lumbsch and Nash 2002). Nevertheless, reviewing characters used to distinguish species in *Pertusaria*, Messuti and Archer (2009) calculate a maximum number of 3500 theoretically possible combinations, of which they consider 1550 species a realistic estimate, many times the number currently accepted.

In South America *Pertusaria* species from southern, temperate regions are best known (Archer and Messuti 1998, Dodge 1968, Fryday 2008, Lamb 1955, Messuti and Archer 2004, Messuti 2005, Osorio 1999, Osorio *et al.* 1984). The diversity in tropical parts of this continent remains poorly studied, and essentially only few, isolated reports exist (Breuss 2001, Elix *et al.* 1995, Flakus, and Kukwa 2012, Kalb 2008, Nöske and Sipman 2004, Sipman 1986).

Nevertheless, regions adjoining the Neotropics have been extensively studied. Central America and the Caribbean share some species with south-eastern USA (treated by Dibben 1980) while species from dry, subtropical regions like Baja California (north-western Mexico) were covered by Lumbsch and Nash (2002), and Schmitt *et al.* (2007).

For the Galapagos these regions, that is Central America, the Caribbean, Baja California, and even southern South America could be considered possible source areas. Weber *et al.* (1977, P. 120) and to some extent Weber and Gradstein (1984) first discussed tentative distribution patterns of Galapagos lichens, suggesting that saxicolous species along the Galapagos coast and the dry lowlands show high affinities with species from Chile. Recent studies of *Roccella* by Tehler *et al.* (2009), and of *Redonographa* by Lücking *et al.* (2013) support this hypothesis. However, among the Galapagos *Pertusaria* no species fit this pattern.

Weber *et al.* (1977) further suggested that saxicolous species from the island interior have stronger affinities with the Caribbean and Central America than with continental South America [*P. xanthodes* may be an example,

although the species also occurs in southern and Baja California (Dibben 1980)]. Finally, Weber *et al.* (1977) assumed that corticolous species, particularly of the humid highlands, were mostly widely distributed throughout the Neotropics [examples for this group may be *P. tetrathalamia*, *P. commutata*, and perhaps even *P. oahuensis*].

However, these patterns are not consistent with the known distribution of vascular plants. Only few endemic vascular plants in the Galapagos are known to have originated in Central America (12%), with most derived from ancestors that colonized the archipelago from continental South America (45%), and very few from as far as North America [5%, in particular from Baja California; for details see Tye and Francisco-Ortega (2011)]. At least for foliicolous lichens similar tendencies have been observed, where most species appear to have originated in continental South America rather than Central America (Lücking and Bungartz 2015).

Interestingly, several Galapagos species of *Pertusaria* are also known from Baja California. Two yellow corticolous species, *P. texana* and *P. xanthodes* are common there, while *P. thiospoda* occurs in nearby Revillagigedo. The yellow saxicolous *P. tejocotenis* and *P. xantholeucoides* also occur in Baja California, although the Galapagos chemotypes appear endemic varieties.

Time will tell how many Galapagos *Pertusaria* species ultimately prove to be endemic. However, a high rate of endemism is likely and we presume that most of the new species and varieties described here are restricted to these islands.

Acknowledgments

We thank Frauke Ziemmeck for managing the cryptogam collection at CDS, and assisting with collecting, data entry and curation of specimens. Diana Flores assisted with thin-layer chromatography of Pertusaria specimens. Successive Directors of Science at the Charles Darwin Foundation have supported this project: Alan Tye, Mark Gardener, Rodolfo Martinez, Ulf Härdter, and Noëmi d'Ozouville. We are further indebted to the Galapagos National Park, especially Galo Quedaza and Victor Carrión for technical support and specimen export permits. The Census of Galapagos Biodiversity and the CDF Checklist of Galapagos Species has been supported by several grants to the Charles Darwin Foundation (donors cited at http://www.darwinfoundation. org/datazone/checklists/). A checklist of Galapagos lichens is regularly updated and available at http://www. darwinfoundation.org/datazone/checklists/lichens, where contributing scientists are acknowledged. The lichen inventory received funds from The Paul and Bay Foundations, and the Erwin Warth Stiftung. In 2010 an international lichen workshop was held in Galapagos, supported by two National Science Foundation (NSF) projects (DEB 0715660 to The Field Museum; PI Robert Lücking; and DEB 0841405 to George Mason University; PI James Lawrey, subcontracted to the Charles Darwin Foundation, local coordinator F. Bungartz). Taxonomic research on Galapagos species with the goal to establish the first IUCN red list of endemic Galapagos lichens is supported by the Mohamed bin Zayed Species Conservation Fund, project 152510692. The Galapagos lichen herbarium is particularly indebted to curators of the following herbaria: COLO, CAS, FH, H, S, B. We are particular grateful to Debra Trock from the Californian Academy of Sciences, who unfortunately was not able to locate isotype material of P. bispora at CAS. Michaela Schmull from the Farlow Herbarium kindly made available specimens of P. bispora, namely the material from the Galapagos selected here as neotype, and two specimens from Socorro Island (Revillagigedo, Mexico). Michaela was extremely helpful also in locating the holotype of P. albinea at FH. Although this specimen was too fragmentary for further analysis, Michaela shared chromatographic data from a previous analysis and recommended contacting US to find isotype material. Carol Butler, Rusty Russel and Deborah Bell from the Smithsonian Institution subsequently located this material, provided high-resolution macro photographs, and sent us a minute isotype fragment for microscopic study and TLC analysis. Carolina Garcia (CDF) helped on short notice to transport this small specimen for analysis to the Galapagos. Alan Fryday (MSC) provided invaluable assistance to clarify the erroneous reports of Coccotrema ("Pertusaria") colobinum from the Galapagos; a specimen that Michaela Schmull kindly made available to us for this study. Finally, we appreciate the support by Bodo Möseler, Eberhard Fischer and Rolf Wißkirchen from the Naturhistorischer Verein der Rheinlande for facilitating specimen loans from FH to the NHV herbarium in Bonn. We are obliged to two anonymous reviewers for advice how to improve our manuscript. This publication is contribution number 2123 of the Charles Darwin Foundation for the Galapagos Islands.

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Manuscript received 4 July 2015, accepted 28 August 2015



Bungartz, Frank et al. 2015. "Endemism in the genus Pertusaria (Pertusariales, lichenized Ascomycota) from the Galapagos Islands." *Telopea: Journal of plant systematics* 18, 325–369. <u>https://doi.org/10.7751/telopea8895</u>.

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