

The genus *Dirina* (Roccellaceae, Arthoniales) revisited

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Abstract: *Dirina* (Roccellaceae, Arthoniales) is a monophyletic genus of crustose, saxicolous or corticolous lichenized fungi. Twenty-four species are accepted in the genus, including nine new species: *Dirina angolana*, *D. arabica*, *D. astridae*, *D. canariensis*, *D. indica*, *D. madagascariensis*, *D. pacifica*, *D. pallescens* and *D. sorocarpa*. A phylogenetic hypothesis is presented based on data from four molecular markers, β -tubulin, ITS 1 and 2, nuLSU and RPB2, including all recognized *Dirina* species worldwide. New combinations proposed include *Dirina badia* for *Roccellina badia*, *Dirina jamesii* for *Roccellina jamesii*, *Dirina candida* for *Chiodecton candidum* and *Dirina teichiodes* for *Lecidea teichiodes*. Two species are reinstated: *Dirina approximata* and *D. monothalamia* (as a new name of *Chiodecton africanum*). Asexual morphs described earlier at the rank *forma* are no longer recognized as taxonomic units viz., *Dirina catalinariae* f. *sorediata*, *D. insulana* f. *sorediata*, *D. massiliensis* f. *sorediata*, *D. paradoxa* ssp. *paradoxa* f. *sorediata* and *D. massiliensis* f. *aponina*. One species, *Dirina calcicola*, is transferred to *Fulvophyton* and two other species, *Dirina insulae-howensis* and *Dirina neozelandica*, are transferred to *Schismatomma*. *Dirina follmannii* is not accepted in *Dirina* and placed as *incertae sedis*. A key to the species of *Dirina* is provided. Vicariance through plate tectonics and continental drift versus long distance dispersal to explain biogeographical patterns is discussed.

Key words: biodiversity, cryptic species, lichenized fungi, phylogeny, taxonomy, vicariance

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Introduction

Dirina is a subtropical genus of lichenized fungi with a preference for areas with Mediterranean climates extending into adjacent temperate and tropical regions. It is predominantly distributed over the Northern Hemisphere (Tehler 1983; Tehler & Irestedt 2007). All species are mainly restricted to coastal habitats and may be very common locally. *Dirina* uses *Trentepohlia* as photobiont and the lichen life form is crustose with a white-greyish to greyish brown thallus; the cortex is composed of anticlinally or loosely anticlinally arranged hyphae and the medulla

is normally white. The fruiting bodies are apothecioid, circular but often undulating in outline, usually sessile but sometimes also immersed, up to 2.5 mm in diameter with a pruinose disc. The thalline margin is well developed; all species have a characteristically carbonaceous hypothecium, distinct from the neighbouring white medulla. The asci are thick-walled, fissitunicate and contain eight fusiform, 3-septate, hyaline spores, within the size range of 15–35 \times 4–8 μ m. The conidia are filiform and curved; most species produce soredia for vegetative dispersal, and for which usually distinctly sorediate morphs have developed. Secondary metabolites are typically erythrin, lecanoric acid and the unidentified substance C (see below) present in all species.

The history of the genus *Dirina* and more details of the morphological and chemical aspects, as well as images of the species not shown here, can be found in earlier references (Tehler 1983, 1985, 1986, 1988, 2002; Tehler *et al.* 1995).

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Much has happened in the past thirty years since the last revisionary study of the genus *Dirina* was published (Tehler 1983). At that time seven species, three subspecies, and two forms were recognized and by 2007 (Tehler & Irestedt 2007) only five species had been added to the list. In the present study, the number of *Dirina* species has risen to 24, of which nine are new to science. The primary source of the new knowledge comes from fresh material collected during numerous field trips made by two of the authors (AT and DE), to both old and new distribution areas around the world. Another major source of the new knowledge is data obtained from molecular studies.

Here, we will incorporate and analyze all new information not previously treated for the genus *Dirina* by combining data from molecular studies with new and old morphological and chemical evidence. We will also touch upon the biogeography of this exciting group in a phylogenetic context, and discuss it in relation to the recently revised sister genus *Roccella* and other genera in the family *Roccellaceae* (Tehler *et al.* 2004, 2009a, b, 2010; Tehler 2007; Tehler & Irestedt 2007; Ertz & Tehler 2011).

Materials and Methods

Terminal taxa and taxon sampling

The study is based on collections made by Anders Tehler from Angola (2009), the Azores (2000, 2010), Canary Islands (2000, 2011), Cape Verde (2009/2010), Croatia (1980), France (2008), French Antilles (1981), Galapagos Islands (2005), Germany (1977), Gibraltar (2009), Great Britain (1979), Greece (1978), Hawaii (2010), Italy (1979, 2008), Mauritius (2003), Mexico (1976, 1993, 1995, 1996, 2007), Morocco (1978), Netherland Antilles (2006), Norway (1981), Peru (1981, 2006), Poland (1977), Portugal (1979, 2010), Senegal (2011), Socotra Island (2008), Spain (1976, 1979, 2007, 2009), Sweden (1976, 1977, 1982, 1983, 1998, 2007), United States (1976, 1981, 1992, 1993, 1994, 1995, 1997, 2008, 2010); on collections made by Damien Ertz from Belgium (s.ann.), Canary Islands (2009, 2011), Cape Verde (2011), France & Corsica (2011), Madagascar (2008), Madeira (2007), Portugal (2011), Spain (2011), United States (2008); and on specimens from the herbaria: ABL, B, BG, BM, BR, C, CANB, CBFS, COLO, DUKE, E, FH, FI, G, GBG, GZU, H, L, LD, LISU, LWG, M, MEL, MSC, NY, O, PAD, PC, RO, S, TUR, U, UC, UPS, US, W, ZT.

A total of 203 *Dirina* samples were used for the molecular investigations (Appendix 1), representing all *Dirina* species recognized worldwide. We tried to achieve a sample series with large morphological variation and with a large and representative geographical distribution. DNA voucher collections were also used for the TLC investigations. Designated voucher specimens are deposited in S and BR. All material in S is searchable and all types are imaged through the database Krypto-S at <http://www.nrm.se/krypto-s>.

Amplification, sequencing and alignment

The phylogeny of *Dirina* was examined by analyzing DNA sequences obtained from four loci: the nuclear ribosomal internal transcribed spacers ITS 1 and ITS 2 (and the intermediate 5.8s region), the nuclear large subunit ribosomal RNA gene (LSU), the second largest RNA polymerase subunit (RPB2) and the β -tubulin gene. Extractions, amplifications and sequencing procedures generally follow Tehler & Irestedt (2007) and Tehler *et al.* (2009a, b, 2010).

For the β -tubulin gene several new primers were designed, based on some initial *Dirina* sequences obtained using the primers Bt3-LM and Bt-10LM (Myllys *et al.* 2001). The β -tubulin region was subsequently amplified in two partially overlapping fragments. For the first fragment the primer pair Bt3-MIa (ATC ACA ACG CGA ACA ACT GCT GA) and Bt-intR (CAC AAG TTG ATG CAC TGA AAG AGT) was primarily used. For samples that produced weak or unspecific PCR-products with the former primer combination, the primer Bt3-MIa was replaced with Bt3M-MIb (CAA AAG AAA TAT GTT CCG CGT GC). The second fragment was amplified with the primers BtintF (AAG AGT TCC CTG ACC GCA TGA T) and Bt-10LM (Myllys *et al.* 2001). The thermocycling program for both β -tubulin fragments started with initial denaturation at 95°C for 5 min, followed by two cycles of 95°C for 30 s, 54°C for 30 s, 72°C for 60 s, followed by another two cycle phase and one 36-cycle phase with identical temperatures and intervals, except that the annealing temperatures were reduced to 52°C and 50°C, respectively. The thermocycling program ended with an extension at 72°C for 5 min.

The sequence fragments were assembled to complete sequences with SeqMan II(tm) (DNASTAR Inc.). Ambiguous nucleotide positions were coded with the appropriate IUPAC codes. Alignments were carried out using the computer program ClustalX 2.0.9 (Larkin *et al.* 2007) under Multiple Alignment Mode, with all parameters set to default. Before the final phylogenetic analyses, some minor manual adjustments were made in the ITS alignments at positions where ClustalX had obviously failed to create the most parsimonious solution.

Choice of outgroup

The outgroup taxa and the rooting taxon were chosen from the fruticose genus *Roccella* which is the well-corroborated sister group to *Dirina* (Tehler 1983; Ertz & Tehler 2011 and references therein).

Phylogenetic analysis

For the phylogenetic analyses, we used the programs T.N.T. Tree Analysis Using New Technology 1.1 (Goloboff *et al.* 2008) and MrBayes 3 (Ronquist & Huelsenbeck 2003). In all analyses gaps were treated as missing data.

The parsimony analyses used the New Technology search with sectorial search, ratcheting, drifting, tree fusing and driven search options in effect, all using default settings. Resampling tree searches were done with parsimony jackknifing (Farris *et al.* 1996) under the New Tech search as implemented in T.N.T. (Goloboff *et al.* 2008); 1000 replicates submitted to TBR branch swapping were conducted. In parsimony jackknifing the data are internally resampled with a jackknifing technique to find well-supported groups. Resampling works by calculating a tree for each of a large number of subsamples (pseudoreplicates) of characters from the data, then finding a summary tree, which comprises the groups occurring in the majority of trees for subsamples. The tree for each pseudoreplicate is found by parsimony analysis, and each pseudoreplicate is formed by randomly selecting characters from the data without replacement, each character having a fixed chance $1/e$ (about 36%) of being excluded. With this resampling technique, the actual number of characters used may vary from replicate to replicate. Groups found in less than 50% of the trees for pseudoreplicates were discarded, thus eliminating unjustified (poorly supported) resolution caused by ambiguous data sets.

Bayesian inference (Huelsenbeck *et al.* 2001; Holder & Lewis 2003) was used to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion (AIC) (Akaike 1973) and the program MrModeltest 2.2 (Nylander 2005) in conjunction with PAUP* (Swofford 1998). Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes 3.2 (Ronquist & Huelsenbeck 2003). The analyses of the combined data set were performed with the models selected for the individual gene partitions, as well as with the parameter proportion of invariable sites (I) excluded for partitions with a gamma distribution included in the model. The exclusion of invariable sites could be justified since the gamma distribution already allows for sites with very low rates (Yang 2006) and as applying many model parameters in a Bayesian analyses may lead to over-optimization where model parameters have difficulties converging on the same target distribution (Nylander *et al.* 2004). All parameters in the selected models were allowed to vary among the partitions, except the topology that was constrained to be the same. All chains were run for 50 million generations, with trees sampled every 1000th generation. The trees sampled during the burn-in phase (i.e. before the chain had reached its apparent target distribution) were discarded. The Bayesian Inference analyses were run on the University of Oslo Biportal (www.biportal.uio.no). The plots of the likelihood and model parameters against

generation provided by the Biportal were used to check for convergence and to estimate when the chains had reached their apparent target distribution.

Chemistry

For routine screening of secondary chemistry, 'spot tests' on thalli and ascomata were performed with a water solution of potassium hydroxide (K), and with a commercial solution of potassium hypochlorite (C). The reaction with *p*-phenylenediamine was not performed, for health reasons and because it is known to be invariable for *Dirina* (Tehler 1983). Thin-layer chromatography (TLC) of acetone extracts was performed on 20×20 cm silica gel 60 F254 layer aluminium or glass plates using solvent systems C, EA and G. For the visualization of the spots, 10% sulphuric acid was used as a reagent (Orange *et al.* 2001). *Punctelia subrudecta* and *Trapelia glebulosa* were used as control species for the identification of lecanoric and gyrophoric acids, respectively.

Results

Loci and alignments

Altogether we analyzed β -tubulin, ITS rDNA, nuLSU rDNA and RPB2 sequences from 203 *Dirina* samples and three *Rocella* outgroup species (Appendix 1). Most sequences were newly produced for this study and have been deposited in GenBank (KC107837–KC108627). In a few cases we were not able to read the full target region and a few sequences consequently miss short fragments, mainly in the beginning or at the end of the sequences. Taking this into account, the individual gene alignments vary as follows: for the protein coding RPB2 gene, no insertion or deletions were detected and the analyzed partition consisted of 923 sites; the LSU partition consisted of 906 sites and the individual sequences varied in length between 886 bp and 891 bp; the ITS partition consisted of 824 sites and the individual sequences varied in length between 575 bp and 681 bp; the β -tubulin partition consisted of 836 sites and the individual sequences varied in length between 836–834 bp. The concatenated data set contained 3489 aligned sites, of which 1278 were variable and 1100 parsimony informative.

We were unable to sequence eight samples which were included in the data set as missing data: *Dirina madagascariensis* 13215 for

β -tubulin; *D. immersa* 9322 and *D. madagascariensis* 13086 for ITS; *D. indica* LWG-111, *D. indica* LWG-112, *D. indica* LWG-115 and *D. indica* LWG-117 for LSU; *D. fallax* 16421 for RPB2. The aligned data set contained 206 terminals and 3489 aligned sites.

Analyses of the ITS region before and after the manual adjustments also produced trees that were topologically fully congruent (only nodal support values were marginally changed), suggesting that modest adjustments in ambiguous regions in ITS only have minor effects on the topological results. Similarly, Tehler *et al.* (2009b, 2010) found that analyses of alternative ITS alignments of New and Old World *Roccella* species had minor effects on the topological results. In addition, the independent gene trees were found to have no significant topological conflicts. Based on these observations, we found it was warranted to not exclude any positions for the final analyses of the concatenated data set, as the most variable regions may be potentially important for resolving particularly terminal branches in the tree.

Phylogenetic analyses and species concepts

There were no significant conflicts between the different gene tree topologies. The parsimony jackknife (PJ) tree (not shown) and the Bayesian tree (Figs 1–4) were mutually without topological conflict as obtained from the combined analyses. The most parsimonious trees had a best score of 4459 and the strict consensus tree (not shown) was of the same general topology as that of the PJ tree.

The Bayesian tree was generally better resolved and received stronger node support than the parsimony jackknife tree. Nodes without parsimony jackknife support also had poor posterior probability (PP) values, except for the major group *Dirina angola* through *D. madagascariensis* which received full PP support but a PJ frequency below 50% (Figs 1–4).

The *a priori* selection of nucleotide substitution models suggested that the GTR+I+G model had the best fit for ITS, LSU, and RPB2, while HKY+I+G had the best fit for β -tubulin. In the Bayesian inference analyses

of the combined data set, where we strictly used these models, the likelihood value, as well as several model parameters, did not converge on the same target distribution. The posterior of the proportion of invariable site parameter in particular fluctuated considerably. In contrast, in the runs where the proportion of invariable sites parameter (I) was excluded from the models, all parameters as well as the likelihood value converge on the same target distribution. The results suggest that we have problems with over-optimization in the analyses where the posterior of the proportion of invariable sites parameter was included. However, when comparing the resulting tree topologies from the individual runs with the proportion of invariable site parameter included, as well as comparing them with the runs where the proportion of invariable site parameter was excluded, the tree topologies were found to be almost identical. The only topological differences observed were found in a few weakly supported nodes (posterior probabilities < 0.80), while all strongly supported nodes (posterior probabilities > 0.95) remained the same. Overall, the results suggest that strongly supported nodes are robust regardless of whether the proportion of invariable site (I) parameter is included or not, which makes sense since the gamma distribution also allows for sites with very low rates (Yang 2006). However, due to the convergence problem in the analyses, where the proportion of invariable site parameter was included, we here present the tree based on the analyses where the proportion of invariable site parameter was excluded (Figs 2–4). This final inference was based on a total of 100 000 samples from the posterior, after discarding the burn-in phase.

Phylogenetic species recognition similar to that of Grube & Kroken (2000) and Taylor *et al.* (2000) has been applied for the recognition of species in *Dirina*, that is, concordance of multiple gene trees to identify the smallest congruent monophyletic groups between which recombination, as expressed by incongruence between single-gene trees, normally does not occur. This type of species concept has recently been successfully applied in lichen fungal phylogeny (Tehler *et al.* 2009a,

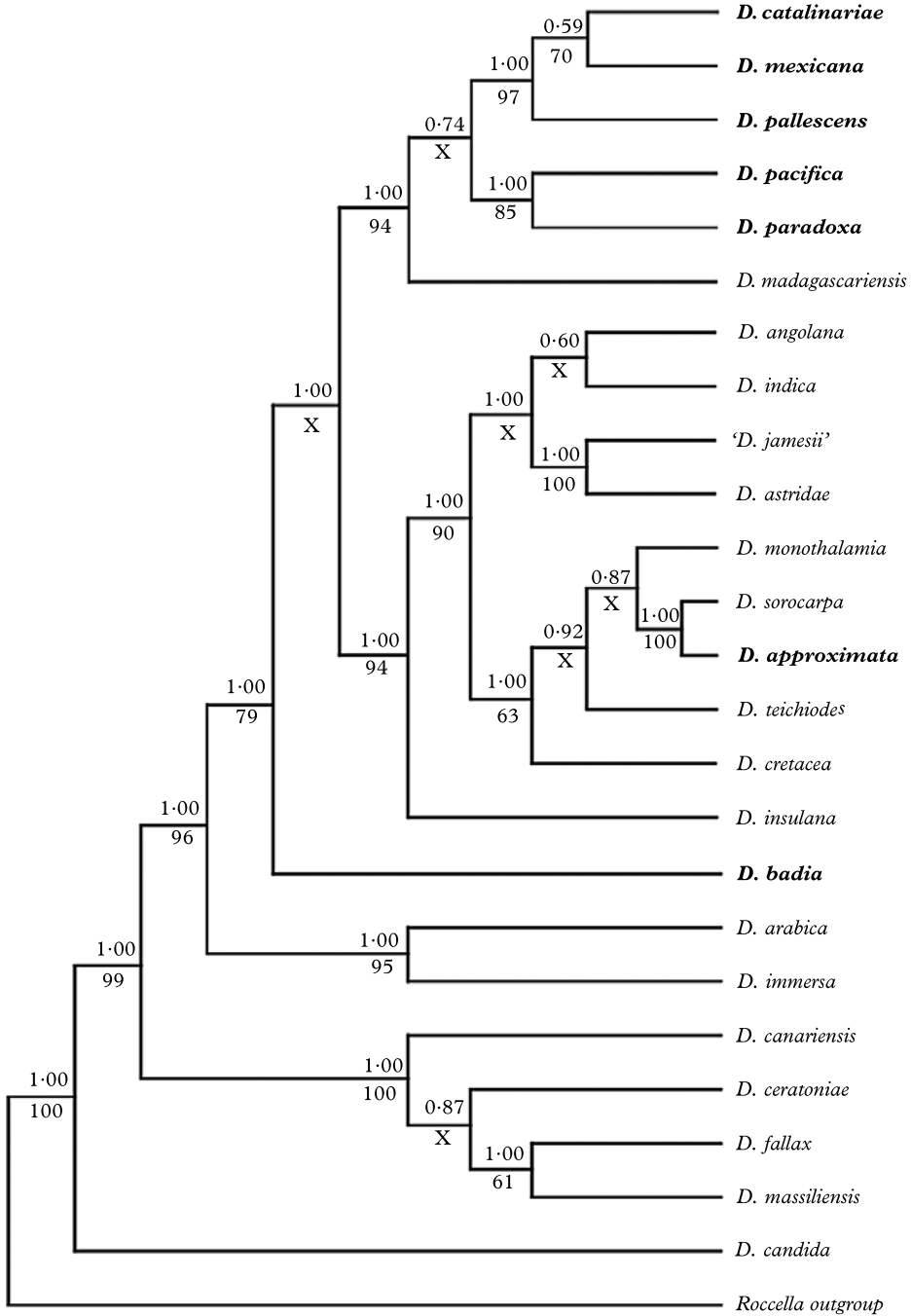


FIG. 1. Overview tree showing *Dirina* species, redrawn from the Bayesian tree (Figs 2–4). Posterior probability values shown above nodes; parsimony jackknife frequencies shown below nodes, frequencies below 50% indicated by X. New World species indicated by bold font.

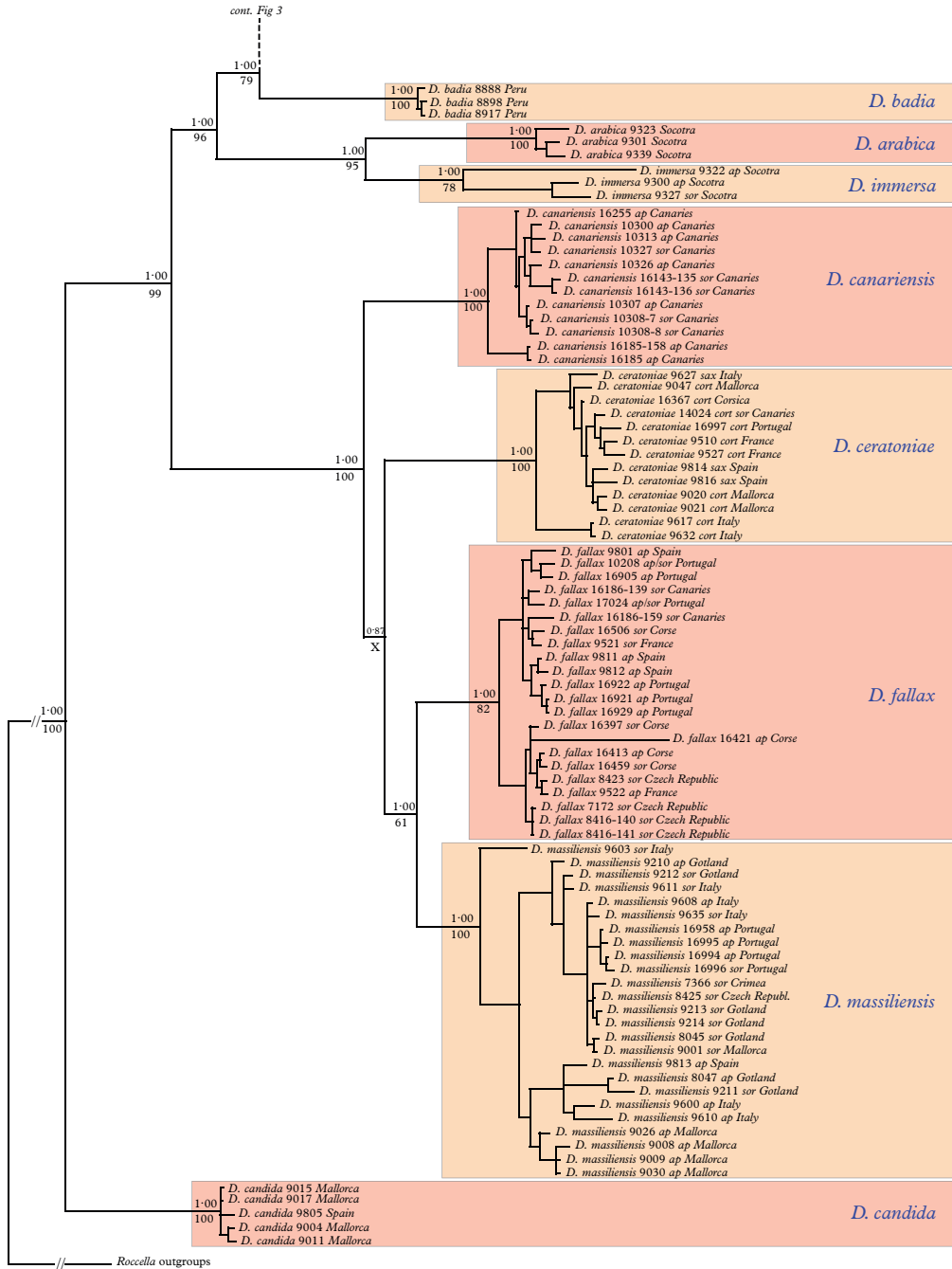


FIG. 2. Part one of tree received from Bayesian analysis with posterior probability values shown above nodes. Parsimony jackknife frequencies received from parsimony analyses using TNT, shown below nodes, frequencies below 50% indicated by X; ap = apothecial, sor = sorediate, sax = saxicolous, cort = corticolous. Support values not shown for intraspecific nodes. Specimen numbers correspond to collection number (cf. Appendix 1). Geographical origin indicated for each specimen. Boxes for readability only. Parts two and three are shown in Figs 3 and 4.

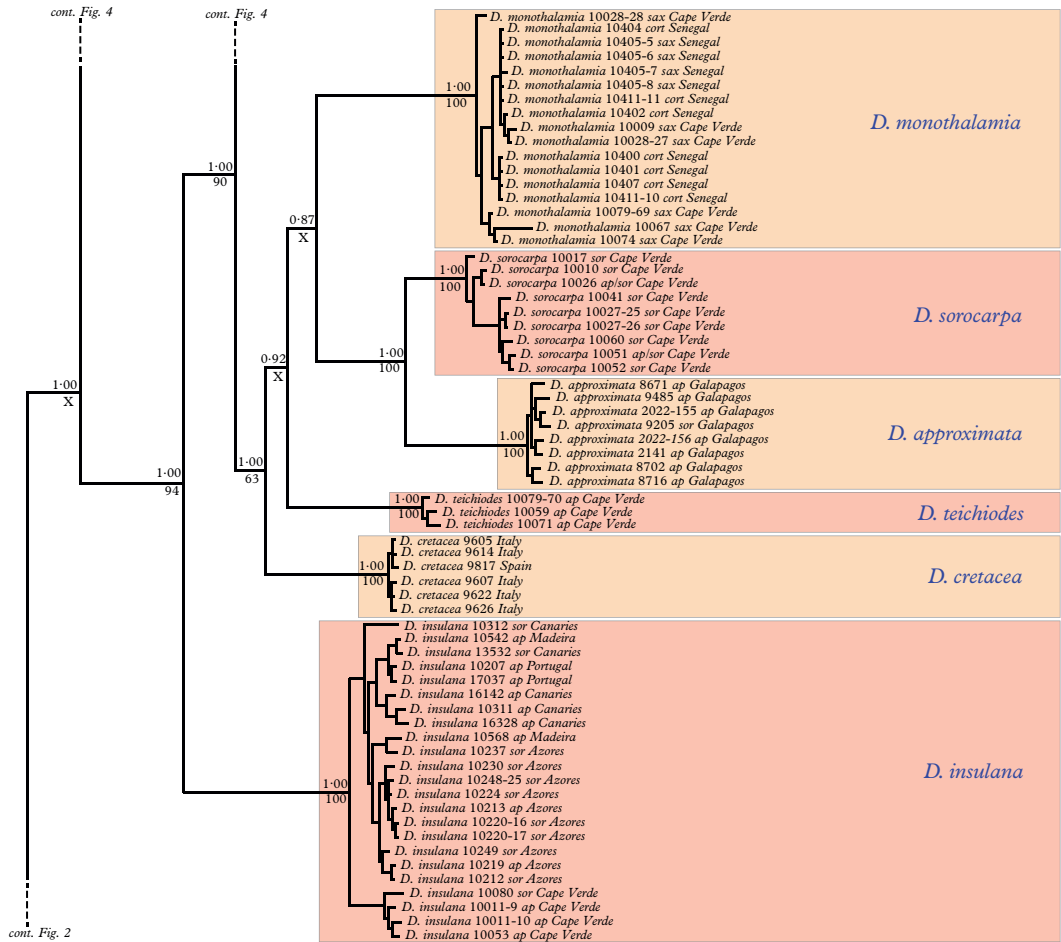


FIG. 3. Part two of tree received from Bayesian analysis with posterior probability values shown above nodes. Parsimony jackknife frequencies received from parsimony analyses using TNT, shown below nodes, frequencies below 50% indicated by X; ap = apothecial, sor = sorediate, sax = saxicolous, cort = corticolous. Support values not shown for intraspecific nodes. Specimen numbers correspond to collection number (cf. Appendix 1). Geographical origin indicated for each specimen. Boxes for readability only. Parts one and three are shown in Figs 2 and 4.

b., 2010; Wedin *et al.* 2004, 2009). The specimens examined in the combined data set of the present study (Figs 1–4) cluster into logical entities recognized as species. Each of the species entities receives significant PP and PJ support for all except one, *Dirina jamesii*, which lacks both PP and PJ support and which is recognized only in the strict consensus tree. The *Dirina jamesii* specimens will for the time being be retained as a species on the basis of the consensus tree and on the relative morphological and anatomical homogeneity, such as sessile to semi-

sessile ascomata and the pseudohypothecial extension.

The sister species to the rest of the genus *Dirina* is *D. candida*, which has immersed ascomata. Three other species also have immersed ascomata (*D. insulana*, *D. mexicana* and *D. immersa*) but they are all placed in unrelated groups in various places in the tree. The most parsimonious hypothesis is that they have reverted to the primitive character state with immersed ascomata (see Discussion below).

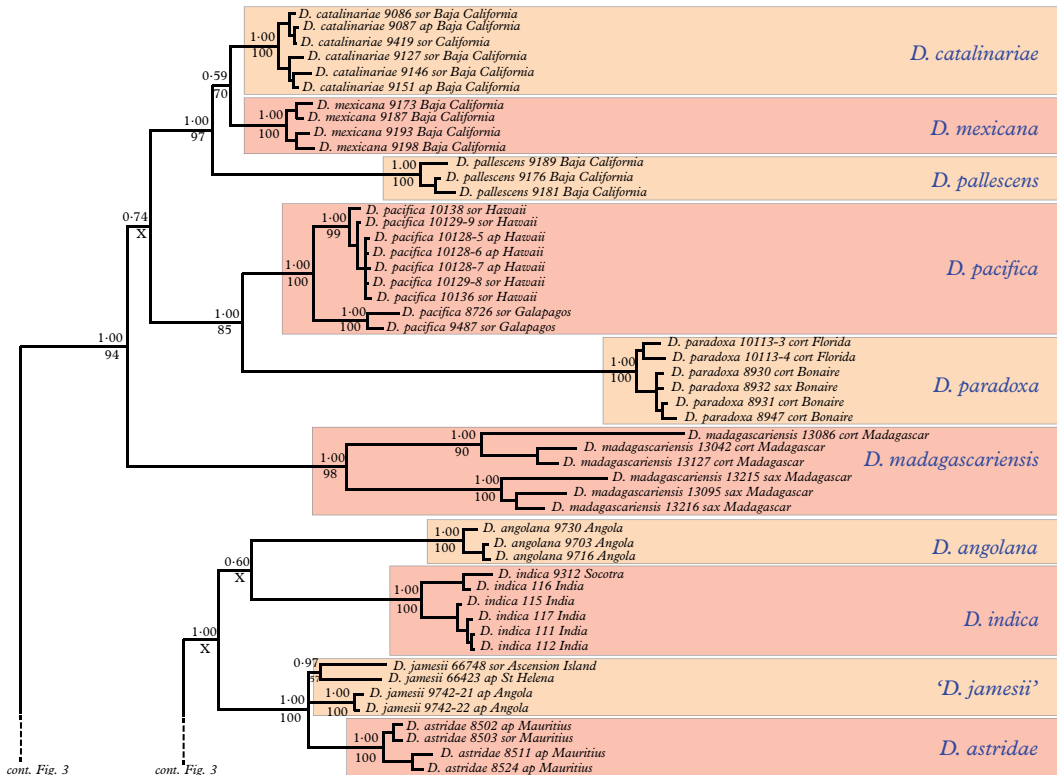


FIG. 4. Part three of tree received from Bayesian analysis with posterior probability values shown above nodes. Parsimony jackknife frequencies received from parsimony analyses using TNT, shown below nodes, frequencies below 50% indicated by X; ap = apothecial, sor = sorediate, sax = saxicolous, cort = corticolous. Support values not shown for intraspecific nodes. Specimen numbers correspond to collection number (cf. Table 1). Geographical origin indicated for each specimen. Boxes for readability only. Parts one and two are shown in Figs 2 and 3.

The greatest species diversity is found in the Mediterranean and Macaronesian region, with 10 species: *Dirina candida*, *D. massiliensis*, *D. ceratoniae*, *D. fallax*, *D. canariensis*, *D. monothalamia*, *D. sorocarpa*, *D. teichiodes*, *D. cretacea* and *D. insulana* (Figs 1–4).

On basis of the phylogenetic tree, the general distribution patterns in *Dirina* are best explained by vicariance, although several events involving long distance dispersal must be postulated to account for the distribution of some species.

Morphology

Thallus. All species are crustose and little variation is seen in thallus morphology. Species growing on calciferous rock are generally more whitish and have a thicker, more chalk-like consistency of the thallus and medullary

texture. Species growing on acidic or volcanic rock are usually darker, thinner and have a less chalk-like thallus and medullary texture.

Medulla. Corticolous species have a medulla with a more or less observable hyphal texture, particularly near the substratum. Saxicolous species generally have a medulla of chalk-like texture, in which the hyphae are less prominent and hardly discernible but sometimes loose hyphae may develop in contact with the substratum. To observe these hyphae, use a stereomicroscope and gently lift off small pieces of the thallus from the substratum with a sharp knife or razor. Some species have a C+ red reaction, both in the medulla and the cortex layer, whereas most species have a C+ red reaction only in the cortex layer. To observe the medulla C reaction, make a perpendicular cut in the

thallus, preferably at the edge of the piece of rock on which the specimen was collected. Apply the C solution exclusively to the medulla by using a sharp needle or knife.

Ascomata. Nearly all species of *Dirina* have pluricarpocentral discothecia-type ascomata. One species, *Dirina cretacea*, has stromatoid-like pluricarpocentral synascomata. A few species have immersed, monocarpocentral, solitary ascomata [see Tehler (1990) for a discussion on ascoma development in *Arthoniales*]. The discothecia-type of ascomata are usually sessile with a clearly constricted base. Sessile or semi-sessile ascomata with an unconstricted base may be present in some species.

Disc. The pruinose surface of the disc is in many species smooth and even or only finely rimose with very intricate cracks, such as in *Dirina canariensis* (Fig. 5E). In other species the disc surface is more or less rimose, that is marked with numerous cracks running in all directions along the disc surface as in *Dirina fallax* (Fig. 6A). This feature may be difficult to evaluate. The distinction between an even surface and a surface with subtle rimulae may be hard to make. In some cases it may even be transitional, and variation between ascomata within single specimens may range from a completely even surface to one with a very intricately cracked surface. In these cases majority rule should be applied when the feature is studied, and at least ten ascomata and disc surfaces should be observed in high magnification under stereomicroscope before an opinion can be reached.

Chemistry

We found erythrin, lecanoric acid and eleven unidentified substances in the genus *Dirina* in c. 140 specimens investigated by TLC (Table 1). Erythrin and the unidentified substance C (UV+ bluish before heating) were present in all species. Lecanoric acid was present in all species, with the exception of *D. mexicana*.

Traces of lecanoric acid have previously been detected by HPLC in *Dirina mexicana* (Tehler et al. 1995). The substance is probably present in small amounts in *D. mexicana* and thus difficult to detect by TLC. This

might also explain its absence in a few samples in some other species. Interestingly, several substances are more or less apomorphic to various groups and support the species circumscription for those clades. For instance, the very characteristic substance F (greyish with very low Rf value) is present only in *Dirina mexicana*, *D. pacifica* and sometimes in *D. catalinariae*, three neotropical species. It is absent in *Dirina pallescens*, the sister species of the clade *D. catalinariae* + *D. mexicana*, and in *D. paradoxa*, the sister species of *D. pacifica*. Substance J is autapomorphic for *Dirina madagascariensis* and substance A is autapomorphic for *D. angolana*. Substance B is always present in *Dirina angolana*, *D. catalinariae*, *D. pallescens* and *D. sorocarpa*.

Taxonomy

Dirina Fr.

Fries 1825: 244.—*Dirina* Fr. sect. *Eudirina* Redinger 1936:126. nom. illeg.; type: *Dirina repanda* Fr. = *Dirina ceratoniae* (Ach) Fr.

Dirinopsis De Not. 1846: 187; type: *Dirinopsis massiliensis* De Not. = *Dirina massiliensis* Durieu et Mont.

Thallus crustose, effuse, smooth, surface becoming cracked, often slightly verruculose or areolate, sometimes bullate, usually creamy white to white-grey or white-green, sometimes dark grey or grey-brown or white-yellow, usually pruinose sometimes subglabrous, prothallus brown or sometimes nearly white, loose, but when contiguous crust-like and black. *Soralia* when present punctiform, rimiform, globose or maculiform, usually of paler colour than the surrounding thallus. **Cortex** with the hyphae mainly anticlinally arranged; the separate hyphae are hyaline or nearly so in a hyaline or pale yellow-brown gelatinous substance; numerous crystals often incorporated in the cortex layer making the separate hyphae hard to distinguish. **Medulla** usually white and chalk-like, but near the substratum often composed of loose hyphae. **Photobiont** *Trentepohlia*.

Ascomata apothecioid or stromatoid, lecanorine, nearly always present and numerous (except in sorediate forms), solitary or aggregated, usually sessile with constricted base, sometimes immersed or sub-immersed, rarely

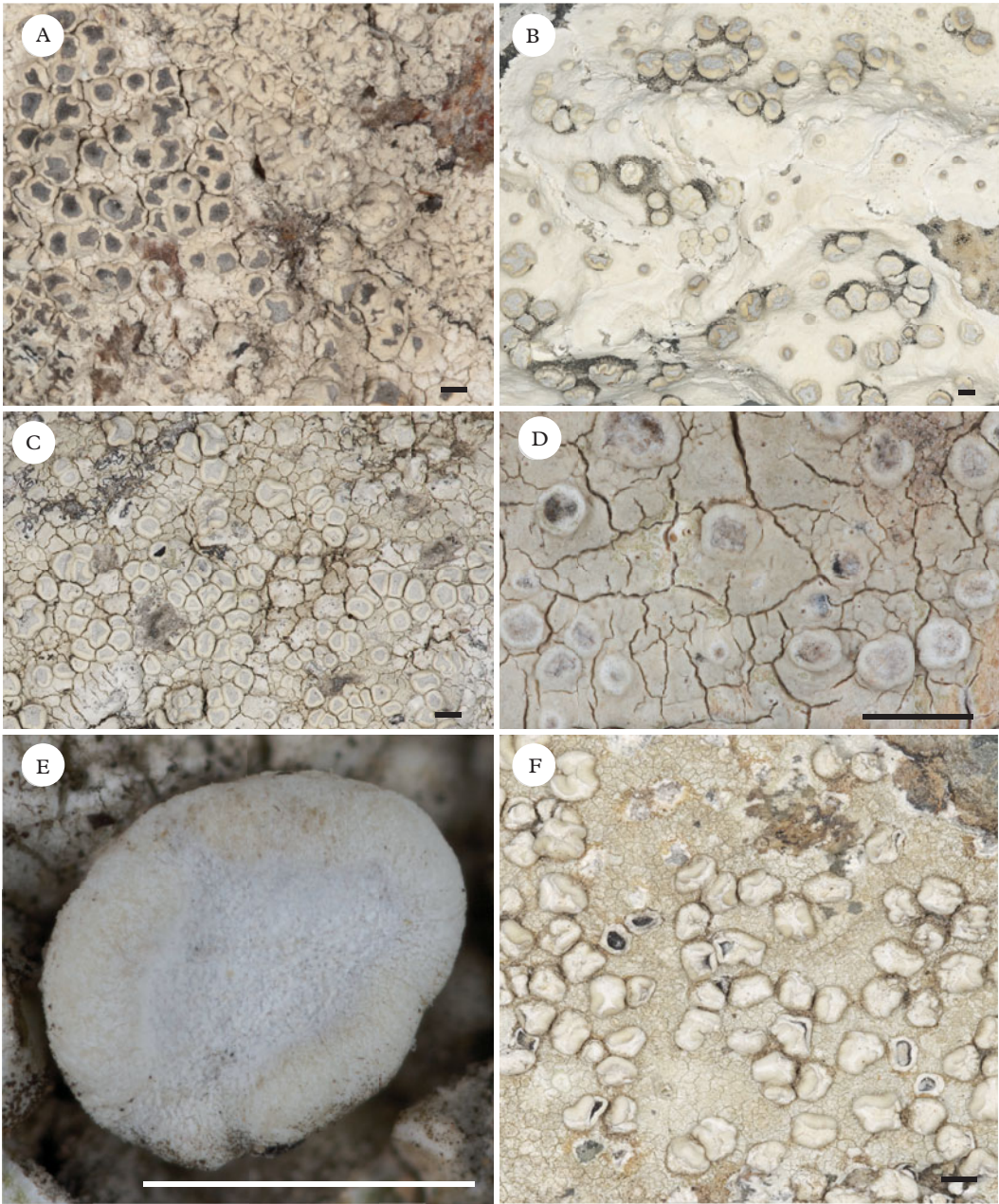


FIG. 5. *Dirina* species, habitus. A, *D. angolana*, holotype [Angola, 2009, *Tehler* 9730 (S-F210729)]; B, *D. arabica*, holotype [Socotra Island, 2008, *Tehler* 9301 (S-F210762)]; C, *D. astridae*, holotype [Mauritius, 2003, *Tehler* 8502 (S-L55012)]; D, *D. indica*, isotype [India, Gujarat, 2008, *Rawal* 09-011280 (S-F218410)]; E, *D. canariensis*, ascomata close up, holotype [Canary Islands, 2011, *Tehler* 10300 (S-F210768)]; F, *D. canariensis*, holotype [Canary Islands, *Tehler* 10300 (S-F210768)]. Scales: A–F = 1 mm. Photographs Emma Hultén. In colour online.

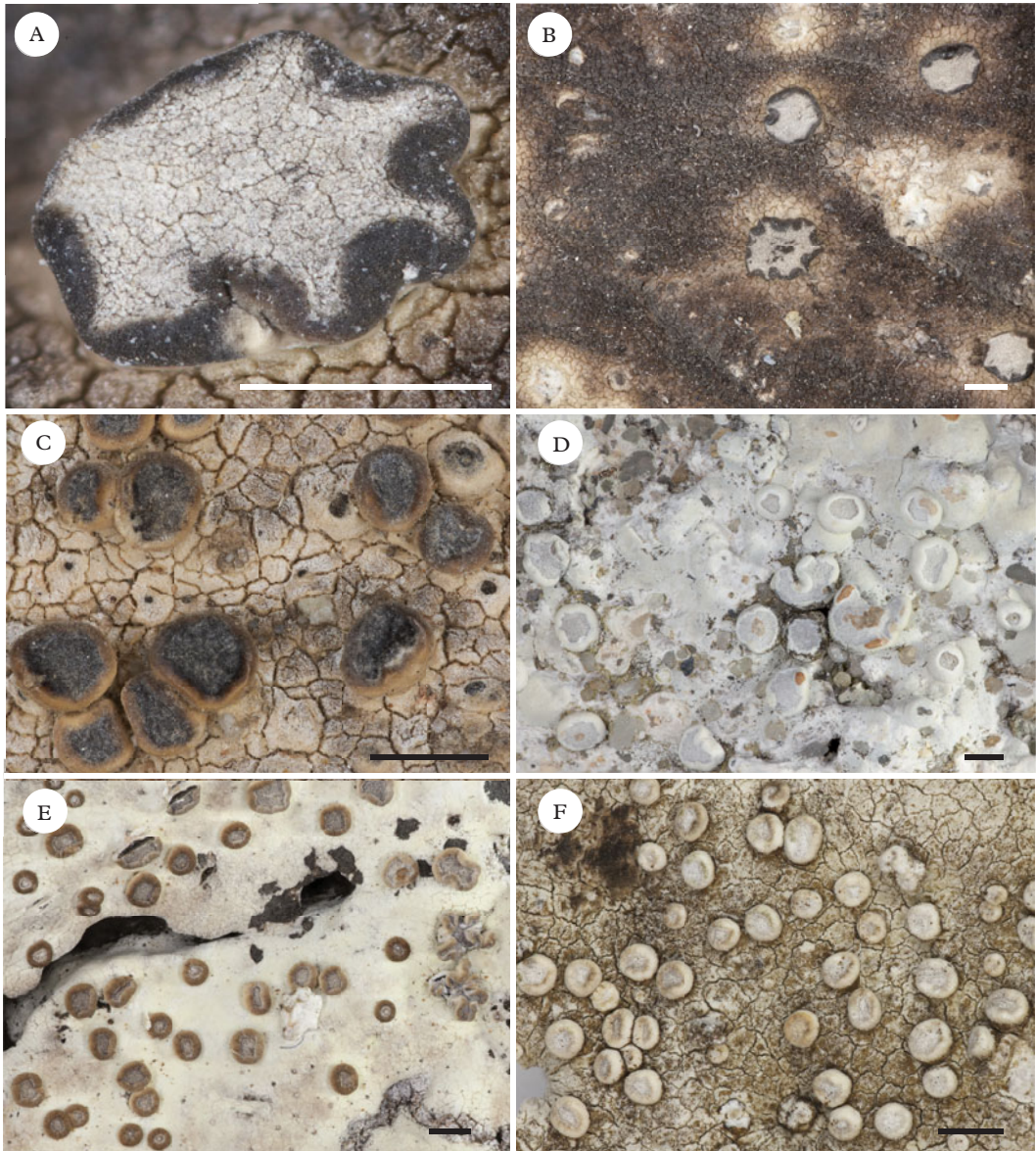


FIG. 6. *Dirina* species, habitus. A & B, *D. fallax*, neotype [Sardinia, 1987, *Ahti* 47193 (S-F184389)], ascomata close up (A) and overview (B); C, *D. fallax*, [lectotype of *Dirina repanda* var. *schistosa* Bagl., Sardinia, s. ann., *Gennari* s. n. (S-F184363)]; D, *D. madagascariensis*, isotype [Madagascar, 2008, *Ertz* 13216 (S-F213217)]; E & F, *D. pacifica*, holotype [Hawaii, 2010, *Tehler* 10128 (S-F210836)], variation in thallus and thalline margin colour. Scales: A–F = 1 mm. Photographs Ramona Ubral Hedenberg. In colour online.

substipitate, evenly dispersed over thallus surface but not near the margins; *disc* pruinose, white-grey to dark grey; *thalline margin* when young entire, when old undulating or strongly

undulating; *proper exciple* (parathecium) thin or inconspicuous. *Hypothecium* carbonaceous or dark brown, usually sharply defined towards the white medulla. *Hymenium* hyaline,

TABLE 1. *Lichen substances detected by TLC in the species of Dirina.*

Species	Secondary substance												
	erythrin	lecanoric	A	B	C	D	E	F	G	H	I	J	K
Rf in solvent C*			5	8	18	42	46	1	35	21	36	40	43
Rf in solvent G*			20	28	58	55	70	9	51	56	51	56	57
<i>Dirina angolana</i>	+	+	+	+	+								
<i>D. approximata</i>	+	+			+								
<i>D. arabica</i>	+	+			+								
<i>D. astridae</i>	+	+			+	+				(+)	(+)		(+)
<i>D. badia</i>	+	+			+							+	
<i>D. canariensis</i>	+	+			+					(+)			
<i>D. candida</i>	+	+			(+)								
<i>D. catalinariae</i>	+	+		+	+			(+)					
<i>D. ceratoniae</i>	+	+			+								
<i>D. cretacea</i>	+	(+)			+								
<i>D. fallax</i>	+	+			+					(+)			
<i>D. immersa</i>	+	+			+								
<i>D. indica</i>	+	+			+								
<i>D. insulana</i>	+	+			+								
<i>D. jamesii</i>	+	+			+								
<i>D. madagascariensis</i>	+	+			+								+
<i>D. massiliensis</i>	+	+			+	(+)	(+)			(+)			
<i>D. mexicana</i>	+				+				+	(+)			
<i>D. monothalamia</i>	+	+			+								
<i>D. pacifica</i>	+	+			+				+	(+)			
<i>D. pallescens</i>	+	+		+	+								
<i>D. paradoxa</i>	+	+			+								
<i>D. sorocarpa</i>	+	(+)		+	+								
<i>D. teichiodes</i>	+	(+)			+								

* Rf values in solvents C and G are the 'Relative Rf values' as defined by Orange *et al.* (2001, p. 64) and calculated with reference to norstictic acid selected as standard.

+ substance nearly always present; (+) substance sometimes or rarely present.

50–140 μm thick; *paraphysoids* unbranched or sparsely branched, 1–2 μm diam.; hymenial strands thin or inconspicuous. *Epithecium* brownish, 35–80 μm thick; paraphysoids continued from the hymenium, branched and intertwined, with smooth or slightly ornamented tips, 1–3 μm diam.; incorporated crystals often make the separate hyphae hard to distinguish. *Asci* hyaline, clavate, bitunicate, constantly 8-spored, fissi- or semi-fissitunicate, 70–120 \times 12–18 μm . *Ascospores* hyaline and smooth, when old sometimes brownish, fusiform or obtusely fusiform, usually curved but also straight, often with one end tapering more than the other, 3-septate; gelatinous sheath missing or inconspicuous.

Pycnidia numerous, few or absent, evenly dispersed over the thallus surface, often with a preference for the margins or the immediate margin, immersed or slightly elevated like black or dark brown dots. *Conidia*, only microconidia seen, thread-like and sickle-shaped, 12–16 \times 1 μm .

Chemistry. Erythrin, lecanoric acid, and the unidentified substances A–K. Spot tests: thallus surface C+ red, K–, KC+ red, PD–; medulla C– or sometimes C+ red, K–, sometimes KC+ red, PD–; hymenium itself I+ red-brown but, depending on iodine concentration, a slightly I+ blue reaction may occur in the transition zones epithecium/

hymenium and hypothecium/hymenium and in the hymenial strands, K/I+ blue; hypothecium K+ dark olive green.

Distribution and habitat. Except for a few species, the genus is confined to the Northern Hemisphere. All species grow on high vertical cliffs and rocks and/or on trees and shrubs along arid and mainly subtropical

coasts around the world. Habitats are on the immediate coastline, usually not ranging more than a couple of km inland. The species grow with a northerly or southerly exposure depending on hemisphere, well above the littoral and away from direct sea-spray, usually at altitudes between 10–200 m depending on exposure to the sea.

Key to *Dirina* species

Many, or even most, *Dirina* species are very similar in habit. Discrete characters are few and determination may be difficult since indiscrete, more or less overlapping characters will also have to be used in the key. Most species are endemic or have restricted distributions and the likelihood of a correct species determination can be correlated to its geographical distribution with great accuracy. However, some very similar sympatric species, such as *Dirina monothalamia* and *D. teichiodes*, cannot be reliably distinguished from one another except by examining their DNA-data. This is also true for sterile, sorediate morphs of *Dirina fallax* and *D. canariensis* (see Discussion). Furthermore, the character with C– or C+ red medulla is very difficult to examine in specimens with thin thalli which is often the case with sterile morphs. In such cases, *Dirina insulana*, which is also present in its sterile form in the Canary Islands, may be indistinguishable from *D. fallax* and *D. canariensis*. Another difficult and variable character is the medulla with loose hyphae near the substratum. Saxicolous *Dirina ceratoniae* is very hard to distinguish from *D. massiliensis*, but in *D. ceratoniae* the medullary hyphae near the substratum are usually more or less loose or byssoid. However, in some specimens, particularly those with thin thalli, this character may fail or be very difficult to see.

1	Specimens mainly fertile, ascomata present	2
	Specimens mainly sterile, soralia present	31
2(1)	Saxicolous	3
	Corticolous.	23

Saxicolous species

3(2)	Growing on calciferous rock.	4
	Growing on acidic rock	11
4(3)	Ascomata sessile with constricted base.	5
	Ascomata immersed or semi-sessile with unconstricted base	9
5(4)	Medulla chalk-like, but with loose hyphae near the substratum	6
	Medulla chalk-like, also near the substratum	7
6(5)	Disc pruina with rimose surface (Europe, usually corticolous sp.)	D. ceratoniae
	Disc pruina with even surface (Caribbean, usually corticolous sp.)	D. paradoxa
7(5)	Ascospores 25–35 µm long [mean value 30 µm]	D. madagascariensis
	Ascospores 17–26 µm long [mean value 22 µm or less]	8
8(7)	Medulla C+ red (Socotra Island)	D. arabica
	Medulla C–	D. massiliensis

- 9(4) Ascomata pluricarpocentral, stromatoid **D. cretacea**
 Ascomata monocarpocentral, non-stromatoid 10
- 10(9) Disc faintly C+ red (Socotra Island) **D. immersa**
 Disc C- (Mediterranean) **D. candida**
- 11(3) Ascomata immersed 12
 Ascomata sessile or semi-sessile 13
- 12(11) Medulla C+ red **D. insulana**
 Medulla C- **D. mexicana**
- 13(11) Disc pruina with rimose surface (cf. Fig. 6A) 14
 Disc pruina with even or only finely rimose surface (cf. Fig. 5E) 17
- 14(13) Medulla C+ red **D. catalinariae**
 Medulla C- 15
- 15(14) Ascospores 27–33 [mean length 30 μm] (Peru) **D. badia**
 Ascospores [mean length 24 μm] 16
- 16(15) Thallus surface faintly red, ascospore width mean 5.5 μm (Europe and Macaronesia)
 **D. fallax**
 Thallus surface red, ascospore width mean 4.5 μm (Hawaii and Galapagos)
 **D. pacifica**
- 17(13) Disc C- or faintly C+ red, only sometimes C+ red 18
 Disc C+ red 20
- 18(17) Medulla chalk-like also near the substratum (Ascension, St Helena, Angola)
 **D. jamesii**
 Medulla chalk-like but with loose hyphae near the substratum 19
- 19(18) Ascomata common, usually in the absence of soralia (Caribbean) **D. paradoxa**
 Ascomata uncommon, always in the presence of soralia (Cape Verde) **D. sorocarpa**
- 20(17) Ascospore mean width 5.5 μm (Mascarenes) **D. astridae**
 Ascospore mean width 4.5 μm 21
- 21(20) Disc pruina with even surface, ascomata slightly smaller > 1.5 mm diam.
 (Canaries) **D. canariensis**
 Disc pruina with finely rimose surface, ascomata slightly larger > 2 mm diam.
 (Cape Verde) 22
- 22(21) Thalline margin usually slightly undulating, thallus surface plane (cf. Fig. 7D)
 **D. teichiodes**
 Thalline margin usually undulating to strongly undulating, thallus surface plane to
 slightly rugose-verruculose (cf. Fig. 7A) **D. monothalamia**

Corticolous species

- 23(2) Ascospores longer, mean length 29–31 μm 24
 Ascospores shorter, mean length 23–26 μm 28
- 24(23) Disc C- or faintly C+ red 25
 Disc C+ red 26
- 25(24) Ascomata slightly smaller, up to 2.0 mm diam. (Madagascar)
 **D. madagascariensis**
 Ascomata slightly larger, up to 2.5 mm diam. (Baja California) **D. pallescens**

- 26(24) Disc pruina with even surface (cf. Fig. 5F) **D. indica**
 Disc pruina with rimose or only finely rimose surface (cf. Fig. 6A) 27
- 27(26) Thallus creamy brown to dirty brownish **D. badia**
 Thallus creamy white to white-brownish **D. approximata**
- 28(23) Disc pruina coarsely or finely rimose 29
 Disc pruina even 30
- 29(28) Disc pruina coarsely rimose (Mediterranean) **D. ceratoniae**
 Disc pruina finely rimose (Cape Verde, Senegal) **D. monothalamia**
- 30(28) Ascomata base constricted **D. paradoxa**
 Ascomata base unconstricted or semi-constricted **D. angolana**

Sterile specimens

- 31(1) Corticolous 32
 Saxicolous 34
- 32(31) Soralia maculate to confluent, pinkish (Canaries) **D. ceratoniae**
 Soralia punctiform to maculiform, of thallus colour 33
- 33(32) Medulla white (Galapagos) **D. approximata**
 Medulla dirty white (Peru) **D. badia**
- 34(31) Growing on calciferous rock 35
 Growing on acidic rock 36
- 35(34) Medulla C+ red (Socotra) **D. immersa**
 Medulla C- (Europe) **D. massiliensis**
- 36(34) Medulla chalk-like but with loose hyphae near the substratum 37
 Medulla chalk-like also near the substratum 39
- 37(36) Medulla C+ red (California, Baja California) **D. catalinariae**
 Medulla C- 38
- 38(37) Thallus pale, usually creamy white to white-brownish (Cape Verde)
 **D. sorocarpa**
 Thallus dark, usually greyish or greenish brown **D. fallax** (mainly Europe)
 or **D. canariensis** (Canaries)
- 39(36) Medulla C+ red (Macaronesia) **D. insulana**
 Medulla C- 40
- 40(39) Medulla dirty white (Atlantic islands, Angola) **D. jamesii**
 Medulla white 41
- 41(40) Unidentified substance F present (Hawaii, Galapagos) **D. pacifica**
 Unidentified substances H or K present (Mascarenes) **D. astridae**

Dirina angolana Tehler & Ertz sp. nov.

Mycobank No.: MB 802894

Thallus obligately corticolous, epruinose. Ascomata sessile with base not constricted or semi-constricted. Disc pruina with even surface. Unidentified secondary metabolites A and B present.

Type: Angola, Luanda prov., 35 km S Luanda, 1 km N of Palmeirinhas, 2009, Anders Tehler 9730 (S-F210729—holotype; BR—isotype).

(Fig. 5A)

Thallus obligately corticolous, surface plane to slightly rugose-verruculose, epruinose,

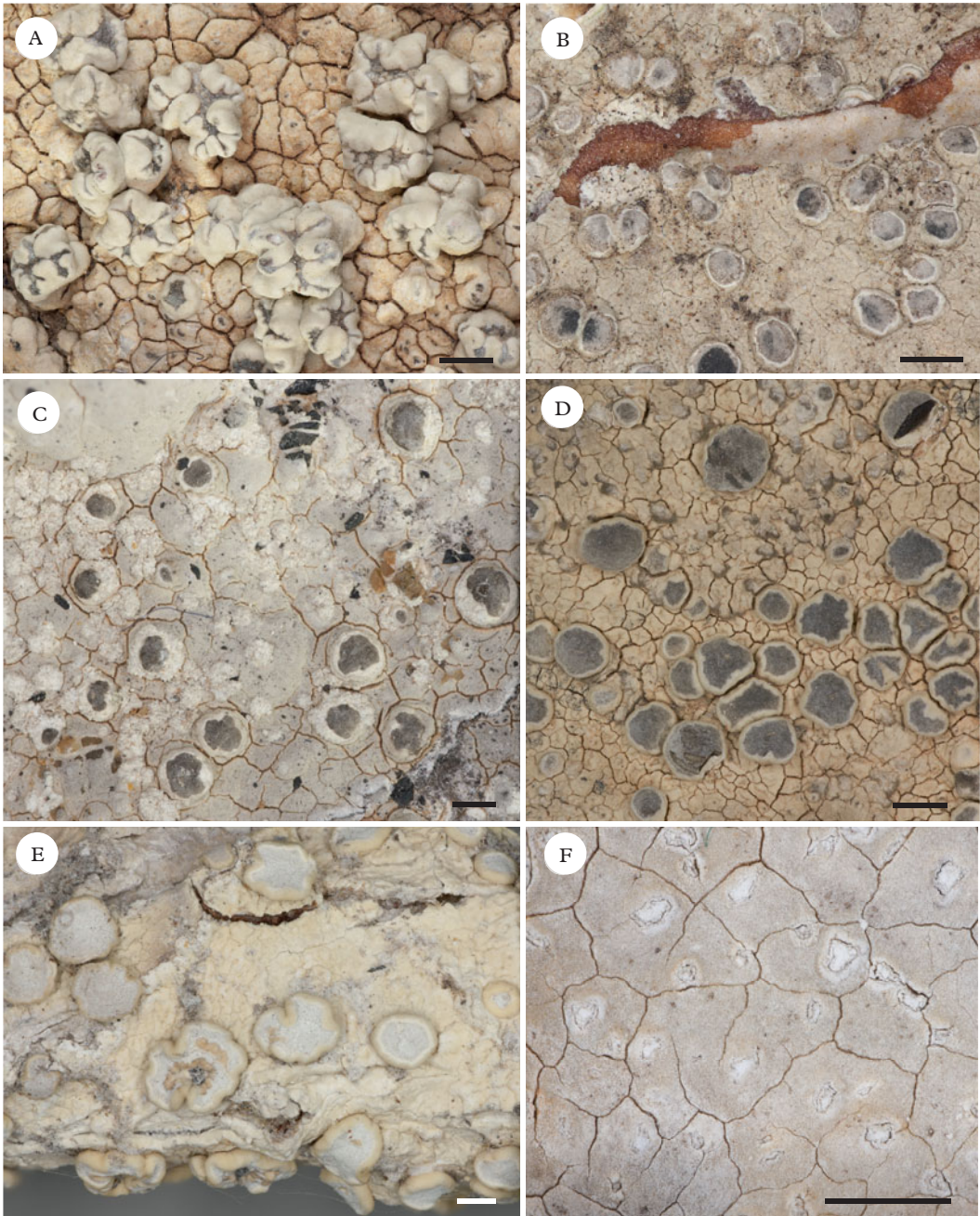


FIG. 7. *Dirina* species, habitus. A, *D. monothalamia* [Cape Verde, 2010, *Tehler* 10074 (S-F210827)], saxicolous specimen with strongly undulating thalline margins; B, *D. monothalamia*, lectotype [Senegal, s. ann., *Perrottet* 4 (G-291546)], corticolous specimen; C, *D. sorocarpa*, holotype [Cape Verde, 2010, *Tehler* 10026 (S-F210855)]; D, *D. teichiodes*, epitype [Cape Verde, 2010, *Tehler* 10071 (S-F210861)]; E, *D. pallescens*, holotype [Baja California Sur, 2007, *Tehler* 9181 (S-F210843)]; F, *D. immersa* [Socotra, 2008, *Tehler* 9300 (S-F210796)], DNA voucher specimen. Scales: A–F = 1 mm. Photographs Ramona Ubral Hedenberg. In colour online.

creamy white, 0.1–0.7 mm thick; *cortex* 25–45 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base not constricted or semi-constricted, >1.5 mm diam.; *disc pruina* with even surface, white-grey; *thalline margin* present, entire sometimes undulating; *ascospores* 23–30 × 4–5 µm, mean length 26.1 µm, mean width 4.7 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ faintly red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances A, B, C.

Etymology. The name refers to the geographical region of Angola.

Distribution and habitat. *Dirina angolana* has been collected only in Angola. It grows preferably on the trunks of *Adansonia* trees near the sea, but sometimes several km from the coast in the provinces of Luanda and Bengo, Angola.

Remarks. *Dirina angolana* is characterized by its epruinose thallus and sessile ascomata with unconstricted base, but most distinctly by its chemistry and the presence of the unidentified substance A which is autapomorphic for the species.

Additional material examined. **Angola**: Bengo: 2–3 km S of Barra do Dande, along the Hwy, 8°29′03″S 13°22′32″E, 2009, Tehler 9716 (S-F210728). Luanda: just N of Luanda, c. 5 km N of Cacucaco, 8°4′70″S 13°26′35″E, 2009, Tehler 9703 (S-F210727).

Dirina approximata Zahlbr.

Ann. Mycol. **29**: 78 (1931).—*Dirina paradoxa* ssp. *approximata* (Zahlbr.) Tehler, *Lichenologist* **18**: 296 (1986); type: Ecuador, Galapagos Islands: I. Seymour (South Seymour Island), 1929, Albert W.C.T. Herre s. n. [W—lectotype sel. by Tehler (1983); B, BM, G, GBG, H, KASSEL, L, LD, M, NY, S-L6, UC, UPS—isolectotypes].

Dirina herrei Zahlbr., *Ann. Mycol.* **29**: 78 (1931); type: Galapagos, I. Santa Maria (Charles Isl.) Post Office Bay, 1929, Albert W.C.T. Herre s. n. [LD—lectotype sel. by Tehler (1983); UPS—isolectotype and as Zahlbr. *Lich. Rar. Exs.* n. 269 in B, W].

(Figs – see Tehler 1983)

Thallus obligately corticolous, surface plane to slightly rugose-verruculose, slightly pruinose, creamy white to white-brownish, 0.1–0.7 mm thick; *cortex* 10–50 µm thick; *medulla* chalk-like, but with loose hyphae near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.0 mm diam.; *disc pruina* with finely rimose surface, white-grey; *thalline margin* present, entire; *ascospores* 28–33 × 4–5 µm, mean length 30.8 µm, mean width 4.2 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Distribution and habitat. *Dirina approximata* is endemic to the Galapagos Islands. It is a strictly corticolous species growing on the bark of various trees and shrubs.

Remarks. *Dirina approximata* was earlier regarded as one of three subspecies under *D. paradoxa* Tehler (Tehler 1983, 1986). On the basis of the present molecular data, *Dirina approximata* was placed with high support in a sister species relationship to one of its former subspecies, *D. sorocarpa* (earlier *D. paradoxa* ssp. *africana*), endemic to the Cape Verde Islands. It was not closely related to the former main species *D. paradoxa*. On the basis of this evidence, *Dirina approximata* is now raised from subspecies to species level. The disjunction with the sister pair species distributed in the Galapagos and Cape Verde (Figs 1 & 2) is bewildering, and can only be explained by an ancient long distance dispersal event (see Biogeography below).

Additional material examined. **Ecuador**: Galapagos Islands: Daphne Major on the SW side, 00° 25′789″S 090° 22′498″W, 2005, Tehler 8716 (S-F96203); Floreana, lava flow behind beach at SE side of Punta Cormorán (“White Beach”), c. 100 m inland, permanent plot 40, alt. 4 m, 1°13′44.5″S 90°25′27.7″W, 2011, A. Yáñez 2141 (S-F210742); c. 150 m inland, alt. 6 m, 1°13′45.6″S 90°25′28.7″W, 2011, Bungartz 9485 (S-F210737); Floreana, trail going to Post Office Bay off

the dirt road between highlands and Puerto Velasco Ibarra, lower slope of Cerro Post Office, alt. 73 m, 1°14'33"S 90°26'43.5"W, 2010, *A. Yáñez* 2022 (S-F210738); on smooth bark of *Bursera* between the Post-Office and cinder cone, 1971, *Weber* (S-L60672); Islote Gardner por Española, SW-part of the island, walking up to the top, alt. 21 m, 1°20'41.5"S 89°38'49.2"W, 2010, *Bungartz* 9205 (S-F210735); Rábida, NE point, 00°24.965'S 090°42.105'W, 2005, *Tehler* 8762 (S-F96211); small point on the SE side, (Jervis) 0°25.720'S 90°42.628'W, 2005, *Tehler* 8702 (S-F96192); Santa Cruz, NE coast between Punta Carrión and Cerro Colorado, 0°33.519'S 90°11.968'W, 2005, *Tehler* 8671 (S-L72898); Santa Maria (Charles Isl.), Post Office Bay, 1929, *Herre* s. n. (LD, UPS); South Seymour, 1929, *Herre* s. n. (GBG, S-L6); s. ann., *Herre* s. n. (W).

Dirina arabica Tehler & Ertz sp. nov.

Mycobank No.: MB 802895

Thallus obligately saxicolous on calciferous rock. Medulla C+ red. Soralia absent. Ascomata numerous, sessile, circular in outline, base constricted, >2.0 mm in diam. Disc pruina with even or finely rimose surface.

Type: Yemen, Socotra Island, Homill near the village, in the eastern part of the island, alt. 350 m, 2008, *Anders Tehler* 9301 (S-F210762—holotype; BR—istotype).

(Fig. 5B)

Thallus obligately saxicolous on calciferous rock, surface plane, slightly pruinose, creamy white, 0.1–0.5 mm thick; *cortex* 20–40 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.0 mm diam.; *disc pruina* with even surface or finely rimose surface, white-grey; *thalline margin* present, entire to undulating; *ascospores* 17–26 × 4–7 µm, mean length value 21.77 µm, mean width value 5.35 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C+ red; disc C+ faintly red or nearly negative. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Etymology. The name refers to the geographical region Arabia.

Distribution and habitat. *Dirina arabica* is endemic to Socotra Island. It grows on the Eocene limestone rocks.

Remarks. *Dirina arabica* is the sister species to *D. immersa*. They are sympatric and grow in the same localities, but are easily distinguished by the appearance of the ascomata, which are sessile in *Dirina arabica* but immersed in *D. immersa*. *Dirina arabica* is habitually and morphologically very similar to *D. massiliensis* but differs by its C+ red medulla, a feature shared only by four other species, *D. immersa*, *D. candida*, *D. insulana* and *D. catalinae*.

Additional material examined. **Yemen**: Socotra Island: in the southern part of the island along the road where it leads up into the mountains from the south, alt. 300 m, 12°35.581'N 54°18.298'E, 2008, *Tehler* 9323 (S-F210763); Mumi plateau, Ant Kashara, eocene limestone blocks, 1994, *Mies & Printzen* 236a2 (S-F60885); Sefflah, the ridge just S of the village on S coast at the E most part of the island, alt. 400–600 m, 12°30.723'N 54°26.037'E, 2008, *Tehler* 9339 (S-F210764); s. loc., 1881, *Balfour* s. n. (G).

Dirina astridae Tehler sp. nov.

Mycobank No.: MB 802896

Thallus obligately saxicolous on acidic rock. Soralia present (usually in the absence of ascomata). Ascomata present (usually in the absence of soralia), sessile, with base constricted. Disc pruina with even surface or finely rimose surface. Unidentified secondary metabolites D, H, I and K present or sometimes present.

Type: Mauritius, Port Louis Distr., Port Louis, Mt. Signal, on the peak c. 200 m east of the tele station, 2003, *Anders Tehler* 8502 (S-L55012—holotype; BR—istotype).

(Fig. 5C)

Thallus obligately saxicolous on acidic rock, surface plane to slightly rugose-verruculose, slightly pruinose, creamy white to white-grey, 0.1–1.0 mm thick; *cortex* 35–45 µm thick; *medulla* chalk-like also near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of soralia), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >1.5 mm diam.; *disc pruina* with even surface or finely rimose surface, white; *thalline margin* present, entire to undulating and often strongly undulating; *ascospores* 22–30 × 5–6 µm, mean length 25.41 µm, mean width 5.31 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C−; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, D, H, K occasional and I rare.

Etymology. The name refers to the first author's daughter Astrid, who led the way to this species on a joint field trip to Mauritius.

Distribution and habitat. *Dirina astridae* is endemic to the Mascarene Islands and has only been collected on Mauritius. It is strictly saxicolous, growing on acidic or volcanic rock.

Remarks. *Dirina astridae* has its closest relative, *Dirina jamesii*, on the African West Coast in Angola and the Atlantic islands of St. Helena and Ascension Island. The topology suggests some level of incomplete sorting of two recently split lineages, thus the sample group including *Dirina astridae* and *D. jamesii* should not be considered conspecific (Fig. 4). No other *Dirina* species exhibits such a conspicuous species disjunction and, furthermore, *Dirina astridae* differs in some important aspects such as clearly sessile ascomata, thicker spores and a complex chemistry with substances D, H, I and K, none of which are present in *D. jamesii*.

Additional material examined. **Mauritius:** *Black River:* Mt St. Pierre, the eastern peak near Bambous, c. 7 km E Quatre Bornes, fertile specimen, 20°16'2'S 57°25'5'E, 2003, Tehler 8524 (S-L55029); sorediate specimen, Tehler 8525 (S-L55030). *Port Louis:* Mt. Signal, on the peak c. 200 m east of the tele station, 20°11'S 57°30'E, 2003, Tehler 8503 (S-L55013). *Savanne:* Maconde on the south coast, c. 500 m W of Baie du Cap, fertile specimen, 20°29'700'S 57°22'648'E, 2003, Tehler 8511 (S-L55022); sorediate specimen, Tehler 8510 (S-L55021).

***Dirina badia* (Tehler) Tehler & Ertz comb. nov.**

Mycobank No.: MB 802897

Roccellina badia Tehler, *Opera Bot.* 70: 67 (1983); type: Peru, Dept. Lambayeque, Prov. Chiclayo, Cerro de Reque, c. 12 km SE of Chiclayo, alt. 200–500 m, 1981, Rolf Santesson & Anders Tehler P132:8 (S-L7934—iso-type; B, BM, C, FH, G, H, LD, LIL, MSC, NY, O, R, TNS, UPS, US, W—iso-types).

Dirina approximata ssp. *hioramii* f. *sorediata* Tehler, *Opera Bot.* 70: 38 (1983).—*Dirina paradoxa* ssp. *paradoxa* f. *sorediata* (Tehler) Tehler, *Lichenologist* 18: 296 (1986); type: Peru, Dept. Tumbes, 14 km (road dis-

tance) NE of Puerto Pizarro, alt. <50 m, 1981, Rolf Santesson & Anders Tehler P123:3 (S-L1—holotype; BM, R, S-L12, UPS—iso-types).

(Figs – see Tehler 1983)

Thallus facultatively saxicolous/corticulous on acidic rock, surface plane, rugose-verruculose to nearly squamulose or suffruticose, slightly pruinose, creamy brown to brown, 0.3–1.5 µm thick; *cortex* 20–40 µm thick; *medulla* chalk-like, but with loose hyphae near substratum, white to white-brown, rarely white rusty red; *soralia* present (usually in the absence of ascomata), punctiform.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.5–2.0 mm diam.; *disc pruina* with rimose surface, white; *thalline margin* present, entire to undulating; *ascospores* 27–33 × 4–5 µm, mean length 29.9 µm, mean width 4.8 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C−; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, I.

Distribution and habitat. *Dirina badia* is restricted to northern Peru where it is common on the small desert mountains near the sea, several kilometres inland. It is usually saxicolous growing on acidic rock but it occurs also on twigs, branches and the bark of small trees and shrubs.

Remarks. *Dirina badia* was earlier referred to the genus *Roccellina*, primarily on the basis of its apparent hypothecial extension (Tehler 1983). However, as a result of the molecular analysis in combination with a reciprocal illumination (Hennig 1966) of specimens in *Dirina badia*, it was evident that the extensions developed were pseudo-hypothecial and analogous to the true hypothecial extensions found in *Roccellina*. The latter are prolongations that originate from the same carbonaceous tissue as that of the hypothecium. The pseudo-hypothecial extension in *Dirina badia* originates and develops from the dirty brownish medullary tissue. This is indicated by the KOH reaction in which the dark brown true hypothecial extension turns

olive-green like the hypothecium, whereas the pseudo-hypothecial extension remains dirty brownish. The cortex tissue is made up of bifurcate, intertwined hyphae but still they are mainly anticlinally arranged as with the cortex type in *Dirina*.

At the same localities where *Dirina badia* was present, we also collected corticolous specimens that are very similar to *D. badia* in most respects except for their corticolous habitat. No corticolous specimens were available for molecular study and thus we cannot verify that these specimens belong to the same species as *D. badia*, but they have the same type of pseudo-hypothecial extension and contain the unidentified substance I as in *Dirina badia*. No saxicolous specimens of *Dirina badia* have been found with soredia. Thus, the sorediate *Dirina* specimens in Peru that were earlier placed under *D. paradoxa* f. *sorediata* are only tentatively placed under *D. badia* since these specimens might belong to *D. approximata*. Future molecular studies will reveal their accurate position.

The similar and sympatric species *Roccellina nigrocincta* is readily distinguished by its shorter ascospores, different secondary metabolites, the C– disc and the thallus surface which is C– or only faintly C+ red.

Additional material examined. **Peru:** *Lambayeque:* Chiclayo, el Cerro la Guitarra [saxicolous], 6°58'37.9"S 79°26'38"W, 2006, *Tehler* 8898 (S-F210766); Cerro de Reque, [saxicolous], 6°52'57.5"S 79°46'41.1"W, 2006, *Tehler* 8917 (S-F210767); c. 12 km SE of Chiclayo, [corticolous], 6°52'57.5"S 79°46'41.1"W, 1981, *Santesson & Tehler* P132:3 (S-F90334). *Libertad:* Pacasmayo, Cerro Chilco, c. 8 km SE of San Pedro de Lloc, [saxicolous], 7°28'16"S 79°26'38"W, 2006, *Tehler* 8888 (S-F210765); [corticolous], 1981, *Santesson & Tehler* P127:1 (S-F90354). *Piura:* Piura, Desierto Sechura, [corticolous], 6°5'5' S 81°55'W, 1981, *Santesson & Tehler* P114:22 (S-F90346); Paita, Cerro Chocán, [corticolous], 5°9'S 80°58'W, 1981, *Santesson & Tehler* P115:11 (S-F171196). *Tumbes:* NE of Puerto Pizarro, [corticolous], 3°28'S 80°23'W, 1981, *Santesson & Tehler* P123:1 (S-L7936).

***Dirina canariensis* Tehler & Ertz sp. nov.**

Mycobank No.: MB 802909

Thallus obligately saxicolous on acidic rock. Soralia present (usually in the absence of ascomata). Ascomata present (usually in the absence of soralia). Disc pruina

with even surface, C+ red. Ascospores mean width value 4.83 µm

Type: Spain, Canary Islands, Gran Canaria, Playa de Tasarte c. 6 km N Puerto de Mogán, in slope S of the playa, alt. 130–250 m, 2011, *Anders Tehler* 10300 (S-F210768, holotype; BR—isotype).

(Fig. 5E & F)

Thallus obligately saxicolous on acidic rock, surface plane, epruinose or slightly pruinose, creamy white to white-brownish, 0.1–0.7 mm thick; *cortex* 25–35 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >1.5 mm diam.; *disc pruina* with even surface, white-grey; *thalline margin* present, entire to undulating; ascospores 20–25 × 4–5 µm, mean length 25.02 µm, mean width 4.83 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, H occasional.

Etymology. The name refers to the geographical region of the Canary Islands.

Distribution and habitat. *Dirina canariensis* is endemic to the Canary Islands. It grows on vertical rocks and cliffs, often several km inland.

Remarks. *Dirina canariensis* belongs to the European monophyletic group with *D. cerasotoniae*, *D. massiliensis* and *D. fallax*, and is placed as the sister species to these three species (Figs 1 & 2). *Dirina canariensis* also appears in a sterile, sorediate form. Sorediate specimens of *Dirina canariensis* are morphologically indistinguishable from sorediate specimens of the partly sympatric species *D. fallax*, and very hard to distinguish from sorediate specimens of *D. insulana*. The latter has a C+ red medulla but this character may be very difficult to examine as thalli are often very thin.

Additional material examined. Spain: Canary Islands: Gran Canaria, Jardín Canario, 27°3,912'N 15°27,777'W, 2011, *Tehler* 10313 (S-F210771); Gran Canaria, Mirador de Tasartico, 27°56.216'N 15°45.845'W, [fertile specimen], 2011, *Tehler* 10326 (S-F210772); [sorediate specimen], *Tehler* 10327 (S-F210773); Montañeta Redonda, just S of el Mirador de Fataga, 27°46'15"N 15°37'1"W, 2011, [fertile specimen], *Tehler* 10307 (S-F210769); [sorediate specimen], *Tehler* 10308 (S-F210770); La Gomera, Arure, trail N of Mirador Ermita del Santo, 28°07'55"N 17°19'23"W, 2011, *Ertz* 16255 (BR); San Sebastián de la Gomera, Roque de Berruga, 28°05'34"N 17°11'17"W, 2011, *Ertz* 16185 (BR); N of road to Hermigua, La Gerode, path to Casas de Jaragán and Montaña Ismael, 28°07'45"N 17°08'50"W, 2011, *Ertz* 16143 (BR); Tenerife, Anaga Peninsula, Pico del Ingles, 1978, *Sipman* 9540 (U); Ladera de Guimar, Lomo Marrero near Mirador Don Martín, 1978, *Walker* 103 (BM); near La Laguna, 1977, *Straka & Pichler* 2236 (GZU); NW part S of Los Silos, 1976, *Santesson* 26652 (UPS).

***Dirina candida* (Müll. Arg.) Tehler & Ertz comb. nov.**

Mycobank No.: MB 802910

Chiodecton candidum Müll. Arg., *Rev. Mycol. (Toulouse)* 6: 19 (1884); type: Egypt, Alexandria, 1879, *Ascherson* s. n. [G-66241—lectotype sel. by Tehler (1983)].

(Figs – see Tehler 1983)

Thallus obligately saxicolous on calciferous rock, surface plane, pruinose, white to white-grey, 0.2–2.0 mm thick; *cortex* 30–50 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, monocarpocentral, numerous, immersed, circular or linear in outline, 0.1–0.8 mm diam.; *disc pruina* with rimose surface, white to white-grey; *thalline margin* absent or sometimes with a thin margin; *ascospores* 18–20 × 5–7 µm, mean length 18.75 µm, mean width 5.75 µm.

Chemistry. Spot tests: thallus surface C+ red, but often faint or negative if the uppermost layer is not scraped or cut away; *medulla* C+ red; *disc* C–. Secondary metabolites: erythrin; lecanoric acid occasional, weak or absent; unidentified substances C sometimes absent.

Distribution and habitat. *Dirina candida* is distributed in the southern part of the Mediterranean region, from Andalusia in Spain,

east to Libya and Egypt. It is restricted to calciferous rocks near the sea.

Remarks. *Dirina candida* was earlier referred to as *D. immersa* (Tehler 1983), a species described by Müller Argoviensis on material collected by Balfour from Socotra Island. It has the same morphology, anatomy and chemistry as *Dirina candida* and, in the lack of distinguishing characters, the two taxa were considered conspecific by Tehler (1983). In this new study, the molecular data from four phylogenetic markers indisputably indicate that *Dirina candida* and *D. immersa* should be acknowledged as two distinct and unrelated species.

Dirina candida has not been found sorediate, in contrast to the otherwise virtually identical *D. immersa*. Fortunately, their distribution areas are not sympatric.

Additional material examined. Libya: Cyrenaica: Wadi Derna, 25 km SW of Derna, 1982, *Anderberg* 1051 (S-F63434).—**Gibraltar:** along the Mediterranean Steps, 2009, *Tehler* 9805 (S-F210774).—**Spain: Alicante:** Javea, Cap de Sant Antoni, 38°48'15"N, 0°11'47"E, 2011, *Ertz* 17120, 17129 (BR). **Almería:** Carboneras, Punta de los Muertos, 1975, *Tehler* 1208 (S-F63433). **Cádiz:** Parque Natural de la Breña y Marismas de Barbate, Torre del Tajo at Mirador Acontilado, 36°10.734'N 5°58.372'W, 2009, *Tehler* 9818 (S-F210775). **Mallorca:** Cala Figuera, 5 km SE of Santanyi, 39°19'49.9"N 003°10'03.0"E, 2007, *Tehler* 9015 (S-F66049); Torre d'eu Beu, 39°19'41.1"N 003°10'40.0"E, 2007, *Tehler* 9017 (S-F66051); Cala Santanyi at Caló de N'Estrany, 1979, *Tehler* 4673 (S-F60758); Formentor 25 m before the tunnel, 1979, *Tehler* 4705 (S-L3479); N-part, Punta la Nao, 1978, *Thor* 628 (S-F60759); Playa de Cala Santanyi, 39°19'36.2"N 003°08'51.5"E, 2007, *Tehler* 9004 (S-F66088); 4 km SE of Santanyi, 300 m north of the inlet, 39°19'35.5"N 003°09'09.0"E, 2007, *Tehler* 9011 (S-F66077). **Murcia:** Mazarron, 30 km W of Cartagena, 1976, *Tehler* 1245 (S-F63432).

***Dirina catalinariae* Hasse**

Bryologist 14: 102 (1911); type: USA, California, Los Angeles Co., St. Catalina Isl., on beach boulders near Avalon, 1911, *H. E. Hasse* 3020 [FH—lectotype sel. by Tehler (1983)].

Dirina catalinariae f. *sorediata* Tehler, *Opera Bot.* 70: 36 (1983); type: Mexico, Baja California, Punta Banda just by La Bufadora, 1976, *Anders Tehler* 1665 (S-L3—holotype; BM, COLO, E, H, L, LD, M, NY, RO, U, UC, UPS, US, W, ZT—isoatypes).

(Figs – see Tehler 1983)

Thallus obligately saxicolous on acidic rock, surface plane, rugose-verruculose to nearly squamulose or subfruticose, slightly pruinose, creamy white to white-greyish, 0.2–1.1 mm thick; *cortex* 35–65 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* and *ascomata* often present side by side, punctiform, maculiform, flat or often capitate.

Ascomata present, often side by side with *soralia*, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.5–2.0 mm diam.; *disc pruina* with rimose surface, white-grey; *thalline margin* present, entire to undulating, strongly undulating or even so strongly undulating as to become stromatoid; *ascospores* 23–29 × 5–6 µm, mean length 26.1 µm, mean width 5.4 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C+ red; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances B, C, F occasional.

Distribution and habitat. *Dirina catalinariae* grows on rocks and cliffs along the coast from Monterey Co. in California (USA) to Laguna Manuela, Baja California (Mexico).

Remarks. *Dirina catalinariae* is the only *Dirina* species in which vegetative and sexual reproduction are not separated into two distinctively either fertile or sterile, sorediate morphs. *Ascomata* and *soralia* are frequently found side by side on the same thallus.

Dirina catalinariae f. *sorediata* was earlier treated as a separate taxon (Tehler 1983), but is now included under the nominal species *Dirina catalinariae*.

Additional material examined. **Mexico:** *Baja California:* Ensenada, Cabo Punta Banda by La Bufadora, 31°44'30"N 116°43'30"W, 1976, *Tehler* 1657 (S-F97389); Cabo Punta Banda, 31°44'38.2"N 116°44'15.8"W, 2007, *Tehler* 9086, 9087 (S-F210776, S-F148386); Cabo Punta Banda, 31°44'34.1"N 116°44'34.4"W, 2007, *Tehler* 9091 (S-F210777); Cabo Punta Banda, below Pico Banda, 31°44'50"N 116°44'30"W, 1996, *Tehler* 7689, 7690, 7691 (S-L1767, S-L1768, S-L1769); Cabo Punta Banda, W of La Bufadora blowhole, 31°44'30"N 116°43'30"W, 1995, *Tehler* 7580, 7581, 7582, 7584, 7585, 7586 (S-L4004, S-L4010, S-L4005, S-L4006, S-L4008, S-L4009); Cabo Punta Banda, Los Arbolitos, 1977,

Tibell 7795 (S-L11737); Guadalupe Island, 28°57'30"N 118°15'W, 1996, *Tehler* 7669, 7670, 7671, 7676, 7677, 7678 (S-L1234, S-L1239, S-L1250, S-L1723, S-L1724, S-L1725); Guadalupe Island, at Fondeadero del Oeste, 28°58'50"N 118°18'50"W, 1996, *Tehler* 7656, 7657, 7658, 7659 (S-L1172, S-L1173, S-L1174, S-L1175); at Melpomene Cove, 1963, *Weber & McCoy* s. n. (S-F97386); Laguna Manuela, 28°15'N 114°07'W, 1993, *Tehler* 7238 (S-L3394); 28°14'12.5"N 114°05'57.6"W, 2007, *Tehler* 9127 (S-F210778); La Mision, N Ensenada, 1976, *Tehler* 1587, 1595 (S-F97408, S-F97387); Punta Santa Rosallita, 28°39'20"N 114°14'56"W, 1997, *Nash* 40206 (S-L10071); Punta Santo Tomás, NE Puerto Santo Tomás, 1995, *Tehler* 7603, 7604, 7605 (S-L4024, S-L4025, S-L4026); Punta Santo Tomas, between Punta Santo Tomas and Punta Rif, 31°33'20"N 116°41'20"W, 1995, *Tehler* 7631 (S-L205); San Quintin, Cerro Kenton 1995, *Tehler* 7589, 7590 (S-L4012, S-L4013); Cerro Kenton by Oyster Plant, 1995, *Tehler* 7594, 7595, 7596 (S-L4017, S-L4018, S-L4019); Cerro Kenton at Chapalta, 1995, *Tehler* 7600, 7601 (S-L4023, S-L4027); 40 km north of El Rosario, 1976, *Tehler* 1607 (S-F97404). *Baja California Sur:* Vizcaíno peninsula, Punta Eugenia, 27°51'05.1"N 115°04'16.7"W, 2007, *Tehler* 9143, 9146 (S-F210779, S-F210780); Punta Eugenia, 27°50'46.1"N 115°03'09.3"W, 2007, *Tehler* 9151 (S-F210781); 3.5 km along road to Punta Abreojos from Highway 1-27°15'N 113°10'W, 1993, *Tehler* 7228 (S-L3385).—**USA:** *California:* Los Angeles Co., Santa Catalina Island, 1976, *Tehler* 1416 (S-F97417); Avalon, 1976, *Tehler* 1419 (S-F97420); between Cactus Bay and Starlight beach, 120–170 m, 33°28'45"N 118°30'30"W, 1993, *Tehler* 7320 (S-L3159); Catalina Harbor, between Ballast Point and Lobster Point, 33°25'45"N 118°30'45"W, 1993, *Tehler* 7335, 7336 (S-L3481, S-L3174); Big Fisherman's Cove, 33°26'30"N 118°29'W, 1993, *Tehler* 7301 (S-L3141); Catalina Harbor, Pin Rock, 1976, *Tehler* 1441, 1451 (S-F97394, S-F97402); Catalina Harbor, Wells beach, 1976, *Tehler* 1426, 1428 (S-F97395, S-F97410); Monterey Co., Seventeen Mile Drive, between Bird Rock and Point Joe, 1992, *Tehler* 7072 (S-L23169); Seventeen Mile Drive, Pescadero Point, 1997, *Tehler* 7838 (S-L4045); between Monterey and Morro Bay, 2 km N of Willow Creek, 1997, *Tehler* 7859 (S-L4065); Point Lobos State Reserve, Punta de los Lobos Marinos, 1997, *Tehler* 7856 (S-L4062); Point Lobos State Reserve, Punta de los Lobos Marinos, 36°31'120"N 121°57'154"W, 2008, *Tehler* 9419 (S-F210782); S of Asilomar, China Rock, 36°36'N 121°57'W, 2008, *Ertz* 12476 (BR); Santa Barbara Co., Santa Rosa Island, Cañada Lobos, 34°01'15"N 120°05'30"W, 1994, *Tehler* 7426 (S-L3264); Santa Rosa Island, Black Mountain, 33°58'45"N 120°04'30"W, 1994, *Tehler* 7340 (S-L3177); Santa Rosa Island, NW Bee Canyon, 33°58'15"N 120°12'W, 1994, *Tehler* 7350 (S-L3189); Santa Rosa Island, East Point, 33°56'30"N 119°59'30"W, 1994, *Tehler* 7364 (S-L3202); Santa Rosa Island, Old Ranch Canyon, 33°58'15"N 119°59'30"W, 1994, *Tehler* 7366 (S-L3204); Santa Cruz Island, Prisoner's Harbor, 34°01'15"N 119°41'15"W, 1994, *Tehler* 7377 (S-L3217); Santa Cruz Island, NE of Frazer point,

34°03'45"N 119°54'45"W, 1994, Tehler 7388 (S-L3228); Santa Cruz Island, Willows Anchorage, 1976, Tehler 1485 (S-L23162); Santa Cruz Island, Coches Prietos Anchorage, 1976, Tehler 1548, 1554 (S-L23163, S-F97391); Santa Cruz Island, west of Coches Prietos beach, 1990, Bratt & Schmitt 6450 (S-L23168); Santa Cruz Island, N Frazer point, 1976, Tehler 1524, 1547 (S-F97390, S-F97399); San Luis Obispo Co., Diablo Canyon Nuclear Facility, Diablo Canyon, 1995, Tehler 7530 (S-L3133); Crowbar Canyon, 1995, Tehler 7531, 7534, 7535, 7536, (S-L3134, S-L3137, S-L3138, S-L3139); across from Lion Rock N Diablo Canyon, 35°14'N 120°52'W, alt. 10 m, 35°14'N 120°52'W, 1995, Nash & Bratt 36981 (GBG); Coon Creek Canyon, Montana de Oro State Park, 1989, Riefner 89-46 (S-L23170).

Dirina ceratoniae (Ach.) Fr.

Lichenogr. Eur. Reform. 194 (1831).—*Lecanora ceratoniae* Ach., *Lichenogr. Universalis* 361 (1810).—*Parmelia ceratoniae* (Ach.) Spreng., *Syst. Veg.* (ed. 16) [Sprengel] 4(1): 299 (1827).—*Patellaria repanda* var. *ceratoniae* (Ach.) Hepp, *Flechten Eur. Fasc.* 1–4: n. 408 (1853).—*Lecania ceratoniae* (Ach.) Stizenb., *Ber. Tätigk. St. Gallischen Naturwiss. Ges.* 1861–1862: 170 (1862).—*Lecanora repanda* f. *corticola* Harm., *Lich. France* 5: 1092; nom. illeg (1913); type: Spain, s. ann., *Lagasca* s. n. [H—lectotype sel. by Tehler (1983); UPS-L00636—isolectotype].

Dirina repanda Fr., *Systema orbis vegetabilis*: 285 (1825); type: "Eur. Austr." *corticola*, s. ann., s. coll. s. n. (name rejected by the author).

Lecanora repanda f. *lignicola* Harm., *Lichens de France. Catalogie systematique et descriptif* 5: 1092; nom. nud. (1913).—*Dirina repanda* f. *lignicola* (Harm.) Zahlbr., *Cat. Lich. Univ.* 2: 509 (1924); type: France, s. ann., *Sahel* s. n. (not retrieved).

(Figs – see Tehler 1983)

Thallus facultatively corticolous/saxicolous, on calciferous rock when saxicolous, surface plane to slightly rugose-verruculose, epruinose or slightly pruinose, creamy white to white-greenish, 0.1–1.0 mm thick; *cortex* 40–60 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* present (usually in the absence of ascomata), maculate to confluent.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.5–3.0 mm diam.; *disc pruina* with rimose surface, white-grey to dark grey; *thalline margin* present, entire to undulating; *ascospores* 21–26 × 4–5 µm, mean length 23.6 µm, mean width 4.7 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ faintly red or negative. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Distribution and habitat. *Dirina ceratoniae* occurs mainly along the coasts and islands of the Mediterranean Sea, extending to the Atlantic coasts of S Portugal and N Morocco. It appears to be more common in the western part of its distribution area. *Dirina ceratoniae* prefers open, dry habitats, natural or cultural landscape with a long continuity, near the sea. It commonly grows on trunks, old branches and twigs of various trees and shrubs such as *Ficus carica*, *Ceratonia siliqua*, *Rosmarinus officinalis*, *Juniperus phoenicea*, *Pinus halepensis*, *P. pinea*, *Pistacia lentiscus* and others. It is usually corticolous but it may also occur on calciferous rocks.

Two specimens of *Dirina ceratoniae* have been collected on the Canary Islands (Tenerife), one of which is the single specimen of *D. ceratoniae* found with soredia. With the exception of these two specimens, *Dirina ceratoniae* is otherwise not known from Tenerife and records from other Canary Islands are very rare. Interestingly, the sorediate and fertile forms were found in the Botanical Garden of Puerto de la Cruz, and the sorediate form also in the Taoro Park within the same city. Our impression is that the specimens are unhealthy, as if the habitat conditions were not right and possibly, because of these improper habitat conditions, some developed soredia. We believe that *Dirina ceratoniae* was, on some occasion, introduced to the city in connection with importing plants to the Botanic Garden or other parks (possibly including those of hotels).

Remarks. Specimens growing on rock are confusingly similar to *Dirina massiliensis*, but in *D. ceratoniae* the medullary hyphae near the substratum are usually more or less loose or nearly byssoid. However, in some specimens, particularly those with thin thalli, this character may fail or be very difficult to see. *Dirina ceratoniae* can also be distinguished from *D. massiliensis* by its more greenish, less pruinose thallus surface and its longer ascospores.

Additional material examined. **Algeria:** Alger, s. ann., *Paguy* s. n. (S-F63566); Palestro bai Alger, 1879, *Lahm* s. n. (S-F63565).—**Cyprus:** *Polis:* Akamas peninsula, 40 km N of Paphos, 1980, *Tehler* 5048b (S-F63462).—**France:** *Corse:* An der Rinde von Cerat. siliqua u Junip. Lycea, s. ann., s. coll. s. n. (S-F63455); Bonifacio, 1989, *Puntillo* s. n. (S-F63560); Sud d'Ajaccio, presqu'île du Capu di Muru, 41°44'58"N 8°40'35"E, 2011, *Ertz* 16367 (BR); Bonifacio, Saint-Julien, 41°23'28"N 9°11'31"E, 2011, *Ertz* 16527 (BR). *Var:* Isles d'Hyères, Isle de Port-Cros, Mont Vinaigre, 43°0'43"N 6°22'77"E, 2008, *Tehler* 9503 (S-F210783); Pointe du Cognet, 42°59'96"N 6°22'716"E, 2008, *Tehler* 9510 (S-F210784); Gien peninsula, La Madrague 43°2'410"N 6°5'732"E, 2008, *Tehler* 9527 (S-F210785).—**Israel:** *Mt. Carmel:* SE the Binyanaina Zikron-Yaakov R, 1964, *Galem* 4(2) (S-F63568).—**Italy:** *Isole Egadi:* Favignana, 1979, *Tehler* 4500 (S-F97443). *Isole Pelagie:* Lampedusa, M. Imbricola, 1979, *Tehler* 4560, 4561, 4562, 4563, 4565, 4569, 4570 (S-F63444, S-F63445, S-F63446, S-F63447, S-F63464, S-F63451, S-F63456); Linosa, 1979, *Tehler* 4540, 4545, 4579 (S-F63448, S-F63450, S-F63457). *Puglia:* Lecce Distr., Diso (Comune), Marina di Marittimo 39°59'483"N 18°24'869"E, 2008, *Tehler* 9616, 9617 (S-F176052, S-F176053); Dolmen Li Scusi 40°5'695"N 18°25'945"E, 2008, *Tehler* 9618 (S-F176054); Galabone (Comune), La Reggia 1 km N of Lido Conchiglie 40°6'871"N 18°0'220"E, 2008, *Tehler* 9627 (S-F176058); Otranto (Comune), 40°8'731"N 18°29'316"E, 2008, *Tehler* 9631, 9632, 9633 (S-F176065, S-F176066, S-F176067). *Sardinia:* Alberi nei dintorni di Cagliari, 1865, *Canepa* s. n. (S-F63453); Tortoli, 1866, *Marcucci* s. n. (S-F63555); Cagliari, prope oppidum Villasimi, 1987, *Vezda* s. n. (S-F63562). *Sicily:* ai Gorghi Tonoli (Mazara okl Vallo, TP), 1994, *Otonello* 18219 (S-L56062); Siracusa distr., N of Pachino, Pant. Roveta, 1979, *Tehler* 4582 (S-F63452); Prope Florentinam l. Biasols, s. ann., s. coll. 125 (S-F63454).—**Morocco:** *Rabat:* Ad cult Olea prope Rabat, 1933, *Werner* s. n. (S-F63563).—**Portugal:** *Algarve:* Lagos, 1.5 km W of Ponta de Piedade, 1979, *Tehler* 4606 (S-F63449); NW of Sagres, Cabo de Sao Vicente, 37°01'36"N 8°59'06"W, 2011, *Ertz* 16997 (BR).—**Spain:** *Almeria:* Carboneras, Punta de los Muertos, 1975, *Tehler* 1210b, 1237 (S-F63463, S-F135199); Punta de los Muertos, Torre Artillada de Mesa Roldán, 36°56'502"N 1°54'550"W, 2009, *Tehler* 9814 (S-F210786). *Cádiz:* Parque Natural de la Breña y Marismas de Barbate, Torre del Tajo at Mirador Acantilado, 36°10'734"N 5°58'372"W, 2009, *Tehler* 9816 (S-F210787). *Canary Islands:* Tenerife, Puerto de la Cruz, Botanical Garden, 2000, *Tehler* 8252 (S-L14018); Puerto de la Cruz, Taoro Park, 2009, *Ertz* 14024 (BR). *Mallorca:* Cabo Blanco, 1969, *Wall* s. n. (GBG); Costa de los Pinos, between Playa d'es Rivell and Port Vey, 1979, *Tehler* 4662, 4663 (S-F60739, S-F60740); Cabo Salinas, 1979, *Tehler* 4670, 4698 (S-F60741, S-F60743); Cala Santanyi, Calóde N'Estrany, 1979, *Tehler* 4693 (S-F60744); Cala Marsal, 1972, *Santesson* 24092a (S-F63458); Deia, 39°44'58'3"N 002°37'50'1"E, 2007, *Tehler* 9038 (S-F66045); Playa de la Rapita, 1979, *Tehler* 4653, 4667 (S-F60749, S-F60746); Playa de Cala

Santanyi, 39°19'36'2"N 003°08'51'5"E, 2007, *Tehler* 9003 9012, 9013 (S-F66039, S-F66040, S-F66041); s'Amarodor, Parc Natural de Mondragó, 39°20'44'4"N 003°11'21'2"E, 2007, *Tehler* 9020, 9021 (S-F66043, S-F66044); Salines de Llevant 39°20'33'1"N 003°00'05'6"E, 2007, *Tehler* 9040 (S-F66046); Ses Covetes 39°21'16'3"NE 002°58'11'9", 2007, *Tehler* 9046, 9047 (S-F66047, S-F66048). *Murcia:* 5 km N of La Azohia, 1976, *Tehler* 1260 (S-F63461); Los Belones, 1976, *Tehler* 1277, 1282 (S-F135175, S-F63460); Mazarron, 1976, *Tehler* 1252 (S-L3477). *Tarragona:* Tarragona, prope Cunit, 1964, *Culberson & Culberson* 12831 (S-F63459).—**Tunisia:** *Sidi Bou Saïd:* NE of Tunis, 1988, *Svane* 88 SS 7385-1 (S-F63569).

***Dirina cretacea* (Zahlbr.) Tehler**

Opera Bot. 70: 44 (1983).—*Chiodecton cretaceum* Zahlbr., *Österr. Bot. Z.* 69: 245 (1899); type: Croatia (Jugoslavia), Pula, ad saxa calcaria, 1899, *K. Stockert* s. n. (W—holotype; NY, PAD, W—isotypes).

(Figs – see Tehler 1983)

Thallus obligately saxicolous on calciferous rock, surface plane to slightly rugose-verruculose, pruinose, white-grey, 0.3–1.0 mm thick; *cortex* 40–60 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, pseudomonocarpocentral (stromatoid), numerous, sessile, circular in outline, base not constricted, > 3.8 mm diam.; *disc pruina* with even surface, white-grey; *thalline margin* present, entire; *ascospores* 19–23 × 5–6 µm, mean length 21.5 µm, mean width 5.8 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C–. Secondary metabolites: erythrin; lecanoric acid sometimes absent.

Distribution and habitat. *Dirina cretacea* is mainly distributed in the eastern Mediterranean region in Cyprus and along the coasts of the Adriatic, Ionian, and Aegean Seas. One outpost locality is known from Andalusia in Spain.

Remarks. *Dirina cretacea* is the only species with stromatoid, pseudomonocarpocentral ascomata and it is easily recognized by that feature. *Dirina cretacea* is the sister species to a group of four species (Figs 1 & 2), two from Cape Verde (*D. teichiodes* and *D. sorocarpa*),

one from both Cape Verde and Senegal (*D. monothalamia*), and one from the Galapagos (*D. approximata*).

Additional material examined. **Croatia:** *Dalmatia:* Cres, s. ann., *Baumgartner* s. n. (S-F63527); Cres, Osor, 1980, *Tehler* 5107, 5108, 5109 (S-F63531, S-F63532, S-F63544); Korcula, Vela Luka, 1980, *Tehler* 5077 (S-F63538); Korcula, Brna, 1980, *Tehler* 5063 (S-F63542); Losinj, Veli Losinj, 1980, *Tehler* 5110 (S-F63541); Pag, Borovici, 1980, *Tehler* 5094 (S-F63534); Pag, 3 km NW of Pag, 1980, *Tehler* 5085 (S-F63537); Pag, Gradac, 1980, *Tehler* 5097 (S-F63540); Peljesac peninsula, Zuljana, 1979, *Vezda* s. n. (S-F63528); Peljesac, Rat by Sreser, 1980, *Tehler* 5062 (S-F63539); Siano, 30 km N of Dubrovnik, 1980, *Tehler* 5060 (S-F63543). *Istria:* Istria, 40 km S of Rijeka, 1980, *Tehler* 5103 (S-F63535); Pula, on walls of Arena amphitheatre, 1980, *Tehler* 5117 (S-F63533); Pula, Premantura, 1980, *Tehler* 5130 (S-F63536). *Primorje-Gorski:* Krk, 1980, *Tehler* 5101 (S-L3478).—**Cyprus:** Cape Greco, 20 km S of Famagusta, 1980, *Tehler* 4999 (S-F63548); Cape Pyla, 25 km E of Larnaca, 1980, *Tehler* 5049 (S-F63545); Paphos, Tombs of the Kings, 1980, *Tehler* 5028 (S-F63551); Polis, Akamas peninsula 1980, *Tehler* 5036 (S-F63549).—**Greece:** *Crete:* 1 km W of Chora Sphakion, 1976, *Brävander* 4301 (S-F63530). *Peloponnesos:* Akhaia, Akr. Araxos, 1978, *Tehler* 4000 (S-F63529).—**Italy:** *Puglia:* Lecce Distr., Diso (Comune), Marina di Marittimo 39°59'483"N 18°24'869'E, 2008, *Tehler* 9614 (S-F176051); Galabone (Comune), Rivabella 40°5'904'N 18°1'347'E, 2008, *Tehler* 9625 (S-F176060); Galabone (Comune), La Reggia, 40°6'871'N 18°0'220'E, 2008, *Tehler* 9626 (S-F176057); Otranto (Comune), Torre San Emiliano, 40°5'444'N 18°29'781'E, 2008, *Tehler* 9606, 9607 (S-F176072, S-F176075); Santa Maria di Léuca (Comune), Capo Santa Maria di Léuca, 39°48'551'N 18°22'677'E, 2008, *Tehler* 9622 (S-F176096); Punta Ristola, 39°47'499'N 18°20'670'E, 2008, *Tehler* 9623 (S-F176097); S. Cesarea Terme (Comune), Torre Minervino, 40°3'978'N 18°28'754'E, 2008, *Tehler* 9605 (S-F176095); Porto Badisco, alt 50 m, 40°4'125'N 18°28'832'E, 2008, *Tehler* 9609 (S-F176092); S. Cesarea Terme, 1996, *Nimis & Tretiach* s. n. (S-F63525).—**Libya:** *Cyrenaica:* Wadi Derna, 25 km SW of Derna, 1982, *Anderberg* 1000 (S-F63553).—**Montenegro:** *Budva:* Tršteno, 1967, *Vezda* s. n. (S-F63526).—**Spain:** *Cadiz:* Parque Natural de la Breña y Marismas de Barbate, Torre del Tajo at Mirador Acantilado, 36°10'734'N 5°58'372'W, 2009, *Tehler* 9817 (S-F210788).

Dirina fallax De Not.

Giorn. Bot. Ital. 2(1): 189 (1846); type: Italy, Sardinia, s. ann., s. coll. s. n. (not retrieved); type: Italy, Sardinia, Prov. Sassari: Nurra, Capo (Punta) Falcone, Monte della Crocetta, near sea, alt. c. 50 m, Macchia on schistose (silicious) rocks, 1987, *Teuvo Ahti* 47193 (S-F184389—neotype sel. here; H—isoneotype).

Dirina repanda v. *schistosa* Bagl., *Comment. Soc. Crittog. Ital.* 1(5): 438 (1863).—*Dirina repanda* ssp. *schistosa* (Bagl.) Nyl., *Bull. Soc. Linn. Normandie* 6: 308 (1872).—*Dirina schistosa* (Bagl.) Nyl. in Hue, *Rev. Bot. Bull. Mens.* 5: 73 (1886).—*Lecanora repanda* var. *schistosa* (Bagl.) Harm., *Lich. France* 5: 1093 (1913); type: in rupibus schistosa ad promontorium di Carbonara in Sardinia meridionali, s. ann., *Patrizio Gemari* s. n. (S-F184363—lectotype sel. here).

Dirina repanda v. *stipitata* Nyl., *Bull. Soc. Linn. Normandie* 6: 309 (1872).—*Lecanora repanda* var. *stipitata* (Nyl.) Harm., *Lich. France* 5: 1092 (1913); type: Pyrénées Orientales, Port Vendres, Cap Béarn, 1872, *William Nylander* s. n. [H-NYL-23890—lectotype sel. by Tehler (1983)].

Lecidea praerimata Nyl., *Flora* 59(15): 235 (1876); type: Jersey, St John's, 1873, *Larbaestier* s. n. [H-NYL-10684—lectotype sel. by Tehler (1983)].

Dirina repanda v. *basaltica* Jatta, *Nuovo Giorn. Bot. Ital.* 18: 98 (1886); type: Italy, s. ann., s. coll. s. n. (not retrieved).

Dirina repanda f. *lecidaina* Oliv., *Bull. Acad. Int. Geogr. Bot.* 11(3): 55 (1902); type: France, Port Vendres, s. ann., *Goulard* s. n. (not retrieved).

Dirina schistosa f. *pedicellata* Oliv., *Bull. Acad. Int. Geogr. Bot.* 11(3): 55 (1902).—*Dirina repanda* f. *pedicellata* (Oliv.) Zahlbr., *Cat. Lich. Univ.* 2: 509 (1924); type: France, Port Vendres, s. ann., *Goulard* s. n. (not retrieved).

Dirina repanda v. *crassa* Mahue & Gillet, *Bull. Soc. Bot. France* 68(21): 285 (1921); type: Morocco, Rabat, s. ann., *Mahue & Gillet* s. n. [UPS—lectotype sel. by Tehler (1983)].

Dirina repanda f. *isidiosa* Werner, *Bull. Soc. Sci. Nat. Maroc* 14(4–6): 148 (1934); type: Morocco, Rabat, plage de Temara, 1934, *Werner* s. n. [UPS—lectotype sel. by Tehler (1983)].

Dirina repanda f. *sorediata* Werner, (1975); type: Morocco, Rabat, 1931, R. G. *Werner* s. n. (not retrieved).

(Fig. 6A–C)

Thallus obligately saxicolous on acidic rock, surface plane to slightly rugose-verruculose, epruinose, grey-brown creamy, 0.1–1.5 mm thick; *cortex* 30–60 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* (usually in the absence of ascospores), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.1–2.0 mm diam.; *disc pruina* with finely rimose surface, white-grey; *thalline margin* present, entire to undulating and often strongly undulating; *ascospores* 18–24 × 5–6 µm, mean length 21.24 µm, mean width 5.41 µm.

Chemistry. Spot tests: thallus surface C+ faintly red; medulla C–; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, G occasional.

Distribution and habitat. *Dirina fallax* has its main distribution in the western part of the Mediterranean Region and the Atlantic coasts of Europe and Africa, north from Scotland and south to Morocco, with an outpost locality in the Canary Islands. In its sorediate form, it is also present in the Czech Republic in Central Europe. It is strictly confined to siliceous and acidic rocks.

Remarks. The type of *Dirina fallax* has been searched for unsuccessfully in all relevant Italian herbaria in Florence, Genoa, Modena, Padua, Pisa, Rome, Turin and Verona. Possibly the type is lost and therefore we chose to appoint a neotype for the name *D. fallax*. We chose a specimen from Sardinia, which was mentioned with no further specifications as the type locality by De Notaris (1846).

Dirina fallax is similar to *D. massiliensis* and is also closely related to that species. *Dirina fallax* has a thinner and usually a more grey-brownish thallus compared to the thicker, whitish and chalk-like thallus of *D. massiliensis*. However, *Dirina fallax* varies considerably in colour of the thallus and thalline margin, from dark brown to greyish to creamy white. *Dirina fallax* is strictly confined to acidic rock, in contrast to its sister species *D. massiliensis*, which is strictly confined to calciferous rocks. Sorediate specimens of *Dirina fallax* are morphologically indistinguishable from sorediate specimens of the partly sympatric species *D. canariensis*. They are also very difficult to distinguish from sorediate specimens of *D. insulana*. The latter has a C+ red medulla but this character may be very difficult to examine in the often very thin thalli.

Additional material examined. **Bulgaria:** *Pontus*: Burgas, Varvara et Micurin, 1977, *Pisut & Vězda* s. n. (S-F204743).—**Czech Republic:** *Ceske Budjovice*: Stredni Povltavi, Hlbuka nad Vltavou, 49°4'31"N 14°27'8"E, 2011, *Vondrák* 8423, 8424(CBFS). *Prachatice*: Sumava Mts foothills, Husinec, 49°2'23"N 13°59'41"E, 2011, *Vondrák* 8416 (S-F184109); Sumava Mts foothills, Hu-

sinec, 49°1'59.663"N 13°59'2.735"E, 2009, *Vondrák & Merkulova* 7172 (CBFS). *Znojmo*: Podyjí National Park, Lukov, 48°50'12"N 15°53'59"E, 2011, *Vondrák* 8426 (S-F184112).—**France:** *Corse*: Ajaccio, scopulus La Parata dictus, 1969, *Lambinon, Rondon & Vězda* s. n. (S-F184388); NE de Bonifacio, 41°25'10"N 9°14'39"E, 2011, *Ertz* 16506 (BR); Cap Corse, Pino, Minerviu, 2011, *Ertz* 16459 (BR); Nord d'Ajaccio, côte sud du Golfe de Sagone, 42°01'11"N 8°43'13"E, 2011, *Ertz* 16396, 16397 (BR); Marchese (Cargèse), Punta d'Ominagna, 42°09'N 8°34'E, 2011, *Ertz* 16413, 16421 (BR). *Var*: Isles d'Hyères, Isle du Levant, 43°1.485'N 6°26.540'E, 2008, *Tehler* 9521, 9522 (S-F210789, S-F210790).—**Germany:** *Heidelberg*: Handschuhshheim, 1880, *Zwackh* s. n. (S-F204744, S-F204745); Neuenheim, 1876, *Zwackh* s. n. (S-F204747); 1880, *Zwackh* s.n. (S-F204748); s.loc., s.ann., *Bayrthoffer* s. n. (S-F204746).—**Great Britain:** *England*: **V.C. 2**, East Cornwall: Boscastle between Tintagel Head and Trevalga, 1979, *Tehler* 4626, 4629 (S-F97437, S-F204756); near Boscastle, 1939, *Lamb* 817 (S-F184235); Logan Rock, S of Penzance, 1979, *Tehler* 4638 (S-F204758); Zennor, 1979, *Tehler* 4640, 4647 (S-F97438, S-F204757).—**Greece:** *Kassandra*: 2 km SSW of Paliuro, 39°54'N 23°40'E, 39°54'N 23°40'E, 1982, *Karis* 175, 176, 178 (S-F204749, S-F204753, S-F204754).—**Italy:** *Isole Pelagie*: Linosa 1979, *Tehler* 4581 (S-F97451); Linosa, between P. Paranzello and Scoaglio dei Bovi Marini, 1979, *Tehler* 4533, 4535 (S-F97449, S-F204755); [transitions with both ascocarps and soralia] 1979, *Tehler* 4537 (S-F97450).—**Morocco:** *Grand Casablanca*: Menseouri, [some specimens with both ascocarps and soralia], 1978, *Tehler* 2158 (S-F170248).—**Portugal:** *Algarve*: SW of Aljezur, 37°17'58"N 8°52'22"W, 2011, *Ertz* 16905 (BR); SW of Aljezur, 37°18'01"N 8°52'17"W, 2011, *Ertz* 16921, 16922, 16929 (BR); Vila do Bispo, Praia do Castelejo, 1979, *Tehler* 4601 (S-F184430). *Leira*: E of Nazaré, Monte de Sao Bartolomeu, 39°35'35"N 9°03'07"W, 2011, *Ertz* 17024 (BR). *Lisbon*: Azaio just S of Cabo da Roca 38°46.138'N 9°29.871'W, 2010, *Tehler* 10208 (S-F210794).—**Spain:** *Almería*: Cabo de Gata, Punta Negra, Torre Vela Blanca, 36°43.557'N 2°10.194'W, 2009, *Tehler* 9811, 9812 (S-F210792, S-F210793). *Cádiz*: Cádiz, Punta de la Chullara, 36°18.690'N 5°16.084'W, 2009, *Tehler* 9801 (S-F210791); Lake Embalse de Celemin, 1978, *Tehler* 4300 (S-F135189); 20 km N of Tarifa, 1978, *Tehler* 2141 2145 2148 (S-F135190, S-F135193, S-F135194). *Canary Islands*: La Gomera, San Sebastián de la Gomera, Roque de Beruga, 28°05'34"N 17°11'17"W, 2011, *Ertz* 16186 (BR).

***Dirina immersa* Müll. Arg.**

Proc. Roy. Soc. Edinburgh **11**: 465 (1882); type: Socotra Island, 1881, *B. Balfour* 1322 [G-66178—lectotype sel. by Tehler (1983); G-66179—isolectotype].

Chiodecton socotranum Müll. Arg., *Proc. Roy. Soc. Edinburgh* **11**: 470 (1882); type: Socotra Island, 1881, *B. Balfour* 1346 [G-66214—lectotype sel. by Tehler (1983); G-66215—isolectotype].

Dirina immersa f. *sorediata* Müll. Arg., *Proc. Roy. Soc. Edinburgh* **11**: 466 (1882).—*Dirina massiliensis* f. *sorediata* (Müll. Arg.) Tehler, *Opera Bot.* **70**: 33 (1983); type: Socotra Island, 1881, *B. Balfour* s. n. [G-66180—lectotype sel. by Tehler (1983)].

(Fig. 7F)

Thallus obligately saxicolous on calciferous rock, surface plane, pruinose, white to white-grey, 0.2–2.0 mm thick; *cortex* 30–50 µm thick; *medulla* chalk-like also near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform.

Ascomata present (usually in the absence of *soralia*), monocarpocentral, numerous, immersed, circular or linear in outline, 0.1–0.5 mm diam.; *disc pruina* with rimose surface, white to white-grey; *thalline margin* absent; *ascospores* 16–20 × 5–7 µm, mean length 18.48 µm, mean width 5.97 µm.

Chemistry. Spot tests: thallus surface C+ red, but often faint or negative if the uppermost layer is not scraped or cut away; *medulla* C+ red; *disc* C+ faintly red. Secondary metabolites: erythrin; lecanoric acid rare; unidentified substance C.

Distribution and habitat. *Dirina immersa* is endemic to Socotra Island. It grows on calciferous rocks near the coast.

Remarks. *Dirina immersa* is the sister species to *D. arabica*. They are sympatric and grow in the same localities, but are easily distinguished from one another by the appearance of the ascomata which are immersed in *Dirina immersa* but sessile in *D. arabica*.

Dirina immersa earlier also included *D. candida*. They have similar morphology, anatomy and chemistry and, in the absence of any distinguishing characters, they were considered conspecific by Tehler (1983). In this new study, the molecular data from four phylogenetic markers indisputably indicate that *Dirina immersa* and *D. candida* should be acknowledged as two distinct and unrelated species.

Dirina immersa is also found with soredia, in contrast to the otherwise virtually identical

D. candida. Fortunately, their distributions are shown not to be sympatric.

Additional material examined. **Yemen**: Socotra Island: Homill, 12°35'16.9"N 54°18'31.2"E, 2008, Tehler 9300 (S-F210796); Mumi plateau, Ant Kashara, 1994, Mies & Printzen 244b2 (S-F159765); Sefflah, 12°30'43.4"N 54°26'02.2"E, 2008, Tehler 9340 (S-F210795); S part where the main road leads up into the mountains, 12°22'34.9"N 53°55'17.8"E, alt. 300 m, 2008, Tehler 9322, 9327 (S-F210797, S-F210798).

Dirina indica Upreti & Nayaka sp. nov.

MycoBank No.: MB 802911

Thallus obligately corticolous. *Ascomata* sessile, base not constricted or semi-constricted. *Disc pruina* with even surface, C+ red. *Ascospore* mean length value 29.11 µm.

Type: India, Gujarat, Jamnagar, Marine National Park, Pirton Island, 2008, *J. Rawal* 08-011280 (LWG—holotype; S—isotype).

(Fig. 5D)

Thallus obligately corticolous, surface plane to slightly rugose-verruculose, epruinose, creamy white to white greenish, 0.1 mm thick; *cortex* 20–30 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base not constricted or semi-constricted, >0.5 mm diam.; *disc pruina* with even surface, white; *thalline margin* present, entire; *ascospores* 23–33 × 4 µm, mean length 29.11 µm, mean width 4.46 µm.

Chemistry. Spot tests: thallus surface C+ red; *medulla* C–; *disc* C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Etymology. The name refers to the geographical region of India.

Distribution and habitat. *Dirina indica* is distributed on the west coast of India (Gujarat), the southern coast of the Arabian Peninsula in Yemen, and on Socotra Island. It is strictly corticolous, growing on various trees and shrubs such as *Avicennia*, *Adenium*, *Acacia*, *Salvadora* and *Ceriops*.

Remarks. The sister species to *Dirina indica* is *D. angolana* (Figs 1 & 2). The latter is known only in Angola and the disjunction is interesting since a similar distribution pattern was observed in the fruticose genus *Roccella*, within groups of the large but heterogenous species *R. montagnei* (Tehler *et al.* 2010).

Additional material examined. **India:** Gujarat: Jamnagar, Marine National Park, Pathapur, 2009, *Rawal* 09-011540 (LWG); Rozy Bandar, 2009, *Rawal* 09-011520 (LWG); Chaneda Island, 2008, *Rawal* 08-011556/B (LWG).—**Yemen:** *Abian Governorate:* Djebel Urays, Wadi Asurai, above Bir Asurai, 2002, *Schultz* 14239 (hb. Matthias Schultz). *Socotra Island:* Homill, in the eastern part of the island, on the ridge facing the sea, 12°35'35.2"N 54°18'25.6"E, 2008, *Tehler* 9312 (S-F210799).

Dirina insulana (Tav.) Tehler

Opera Bot. 70: 43 (1983).—*Enterographa insulana* Tav., *Portugaliae Acta Biol., Sér. B, Sist.* 3(3): 325 (1952); type: Portugal, Madeira, near Montado dos Pecegueros, on basaltic cliffs, alt. 900 m, 1951, *Tavares* 4563 (not available—not retrieved); type: Portugal, Madeira, Camara de Lobos, August 1956, *Baretto*, n. 2. hb. Tavares n. 6155 (LISU—neotype sel. by Tehler 1983).

Dirina insulana f. *sorediata* Tehler, *Opera Bot.* 70: 44 (1983); type: Portugal, Madeira, Funchal, Botanical Garden NE of the town, 1983, *Kaj Sundgren* 1 (S-LA—holotype).

(Figs – see Tehler 1983)

Thallus obligately saxicolous on acidic rock, surface plane, epruinose or slightly pruinose, grey-green or grey-brown, sometimes white-grey, 0.1–0.5 mm thick; *cortex* 20–40 µm thick; *medulla* chalk-like also near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), monocarpocentral, numerous, immersed, circular or linear in outline, 0.1–0.9 mm diam.; *disc pruina* with even surface, white-grey; *thalline margin* absent; *ascospores* 22–27 × 5–6 µm, mean length 24.7 µm, mean width 5.6 µm.

Chemistry. Spot tests: thallus surface C+ red, sometimes faintly red; medulla C+ red; disc C–. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Distribution and habitat. *Dirina insulana* is a widespread species found throughout Macaronesia in the Azores, Madeira, the Canary Islands, Cape Verde and the coast of southern Portugal. It grows on the vertical, volcanic outcrops near the sea.

Remarks. *Dirina insulana* produces both ascomata and soredia, usually in distinctly either fertile or sterile morphs. Transitional specimens with both ascomata and soralia on the same thallus are uncommon. Sorediate specimens of *Dirina insulana* are morphologically indistinguishable from sorediate specimens of the partly sympatric species *D. fallax*, *D. canariensis* and *D. sorocarpha*, but *D. insulana* is the only one of these species with a C+ red medulla. However, that character may be very difficult to observe in the often very thin thalli.

Additional material examined. **Cape Verde:** *Boa Vista:* Mt. Rochinha, N von Sal-Rei, 1987, *Mies* 559h3 (S-F151310); Mt. Vigia-massiv, Leuchtturm oberhalb Ponta do Sol, 1987, *Mies* 561f3 (S-F151312). *Brava:* Cova Rodela, 600 m, 1987, *Mies* 734,2 (S-F151295). *Fogo:* Cova Matinho, Ponta Segue-Segue, 14°56'N 24°18'W, 1988, *Mies* 1216h 2 (S-L11769). *Maio:* Mt. Batalha, 1987, *Mies* 790h2 (S-F151308). *Sal:* Monte Leão (Rabo da Junco), 16°42.030'N 22°58.929'W, 2010, *Tehler* 10080 (S-F210802). *Santiago:* N des Mt. Graciosa, N von Tarrafal, 1988, *Mies* 833g 2 (S-L11758). *Santo Antao:* Fontainhas, 17°12'N 25°06'W, 1988, *Mies* 1191i 2 (S-L11773). *Sao Nicolau:* Punta Espachim, W Ribeira Funda, 16°40'N 24°20'W, 1988, *Mies* 938c2, 941a2 (S-L11776, S-L11741); NW des Mt. Bissau, Ribeira zum Rib, Madeira Vermelha, 16°37'N 24°15'W, 1988, *Mies* 1080f 2 (S-L11770). *Sao Tiago:* between Sao Domingos and Rui Vaz, 1986, *Mies* 214m2 (S-F151307); Mt. Grande bei Milho Branco, 1986, *Mies* 331a2 (S-F151306). *Sao Vicente:* Madeiral, 16°49'N 24°56'W, 1988, *Mies* 1017c2, 1017d2 (S-L11757, S-L11740); Madeiral, 16°49.174'N 24°56.140'W, 2010, *Tehler* 10053 (S-F210801); NW of Calhau, Goa Baixo, 16°51'27"N, 24°52'42"W, 2011, *Ertz* 17279 (BR); Praia da Ceilada do Calhau, 16°51.552'N 24°52.741'W, 2009, *Tehler* 10011 (S-F210800).—**Portugal:** *Azores:* Faial, Castelo Branco, 38°31.299'N 28°42.961'W, 2000, *Tehler* 8215 (S-L12333); Horta, Conceicao, 1986, *Arvidsson* A289, A290, A291 (GBG); São Miguel, Ponta Delgada, opposite Clínica S. João de Deus in Fajã de Baixo 37°45.258'N 25°38.649'W, 2000, *Tehler* 8175b (S-L12326); 2010, *Tehler* 10224 (S-F210807); Ponta Delgada S of the airport, 37°44.454'N 25°42.381'W, 2010, *Tehler* 10212 [sorediate] (S-F210803), 10213 [fertile] (S-F210804); Ponta Delgada, Parque da Alminhas 37°45.830'N 25°44.099'W, 2010, *Tehler* 10219 [fertile]

(S-F210805), 10220 [sorediate] (S-F210806); Terceira, Angra do Heroísmo, Monte Brasil 38°38'873"N 27°13'708'W, 2010, Tehler 10237 (S-F210809); Lajos, Ponta da Serra das Lajes, by Aeroporto da Lajos, 38°47'108'N 27°6'484'W, 2010, Tehler 10248 [sorediate] (S-F210810), 10249 [fertile] (S-F210811); Praia do Vitoria, Ponta da Ma Merenda, 38°44'049'N 27°2'881'W, 2010, Tehler 10230 (S-F210808). *Lisbon*: Azaio just S of Cabo da Roca 38°46'138'N 9°29'871'W, 2010, Tehler 10207 (S-F210812); SW of Sintra, SE of Cabo da Roca, 38°45'21"N 9°28'40'W, 2011, Ertz 17037 (BR). *Madeira*: Funchal, Botanical Garden, 1982, Dahlén & Baltscheffsky 999 (S-F63436); 1983, Sundgren 2 (S-L3480); 1981, Anderberg 632 (S-F63435); Ponta de São Lourenço, 2007, Ertz 10542 (BR); Porto Santo Island, Pico do Castelo, Ertz 10568 (BR).—**South Atlantic Islands**: *Ascension Island*: Norfolk Pine track, 1976, James s. n. (S-L5079).—**Spain**: *Canary Islands*: El Hierro, Sabinosa, Punta de la Dehesa, 2009, Ertz 13532 (BR); Gran Canaria, Jardín Canario, 28°3'912'N 15°27'777'W, 2011, Tehler 10311 [fertile] (S-F210813), 10312 [sorediate] (S-F210814); La Gomera, San Sebastián, La Gerode, path to Casas de Jaragán and Montaña Ismael, 28°07'45"N 17°08'50"W, 2011, Ertz 16142, 16328 (BR).

***Dirina jamesii* (Tehler) Tehler & Ertz
comb. nov.**

Mycobank No.: MB 802912

Roccellina jamesii Tehler, *Bryologist* 88: 131 (1985); type: Ascension Island, Cricket Valley, S.W.-facing aspect, alt. 1400 ft, 1976, P. W. James s. n. (BM—holotype; S-L502—isotype).

(Figs – see Tehler 1983)

Thallus obligately saxicolous on acidic rock, surface plane, slightly pruinose, creamy white to white-brownish, 0.1–1.0 mm thick; *cortex* 40–65 µm thick; *medulla* chalk-like also near substratum, dirty white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted or unconstricted, >1.5 mm diam.; *disc pruina* with even surface or finely rimose surface, white-grey; *thalline margin* present, entire to undulating; *ascospores* 23–27 × 4–5 µm, mean length value 23.31 µm, mean width value 4.74 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red, faintly red or negative. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Distribution and habitat. *Dirina jamesii* is distributed over the two Atlantic islands, St. Helena and Ascension Island, and mainland Africa in Angola, often forming extensive mosaics on more or less dry vertical faces or underhangs of boulders and cliffs, near the sea. It is strictly saxicolous.

Remarks. During the years since *Roccellina jamesii* was described (Tehler 1985), we have had the opportunity to study and collect new material of this species. The new morphological and molecular data obtained from that material clearly indicate that *R. jamesii* should be transferred to the genus *Dirina*.

Similar to the situation with *Dirina badia*, and as a result of the molecular analysis in combination with a reciprocal illumination of the hypothecial extensions developed in *Dirina jamesii*, it was evident that the extensions developed were pseudo-hypothecial and analogous to the true hypothecial extensions found in *Roccellina*. The latter are prolongations that originate from the same carbonaceous tissue as that of the hypothecium. The pseudo-hypothecial extension in *Dirina jamesii* is more inconspicuously pale brownish (sometimes missing) and develops from the bottom layer of the dirty brownish medullary tissue. This is indicated by the KOH reaction, in which the dark brown true hypothecial extension, like the hypothecium, all turns olive-green, whereas the pseudo-hypothecial extension remains K dirty brownish. The cortex tissue is made up of bifurcate, intertwined hyphae but still they are mainly anticlinally arranged, as with the cortex type in *Dirina*.

On the basis of the newly collected material from Angola, it also became clear that the fruiting bodies range from more or less immersed over semi-sessile with unconstricted base, sometimes developing into fully sessile ascomata with a constricted base.

Dirina jamesii is treated here as a species, although it is unsupported as paraphyletic (Fig. 4). There may be more than one species involved but the sampling group and the evidence in support of describing species are simply too poor. There were only three possible collections available for molecular

investigation: one from St Helena, one from Ascension and one from Angola (two DNA samples were taken from the latter). These three collections were more or less unresolved or very poorly resolved. However, morphologically they have similarities, such as the sessile to semi-sessile ascomata, and they are grouped together in the consensus tree.

Additional material examined. **Angola:** Bengo: Caba Ledo, S of the village, 9°40.675'S 13°12.058'E, 2009, *Tehler* 9742 (S-F210815).—**South Atlantic Islands:** *St Helena:* Rupert's Valley, 15°55.547'S 5°42.436'W, 2006, *Aptroot* 66292 (ABL); above Jamestown, along track to Saddle Battery, 15°55.744'S 5°42.817'W, 2006, *Aptroot* 66423 (S-F86655). *Ascension Island:* Sisters Peak, 7°55.977'S 14°21.971'W, 2006, *Aptroot* 66748 (S-F86671); Cricket Valley, 1976, *James* s. n. (S-L5078, S-L5077); Devil's riding school, 1976, *James* s. n. (S-F196062); above Two Boats Village, 1976, *James* s. n. (S-F196068).

***Dirina madagascariensis* Tehler, Ertz, Killmann, Razafin., Sérus. & Eb. Fisch. sp. nov.**

MycoBank No.: MB 802913

Thallus facultatively saxicolous/corticolous, on calciferous rock. Medulla chalk-like also near substratum. Soralia absent. Ascomata sessile, base constricted, up to 2 mm diam. Disc C- rarely C+ red. Ascospores 25–35 × 4–5 µm, mean length value 30.6 µm. Unidentified secondary metabolite J present.

Type: Madagascar, Toalanaro (Fort Dauphin), alt. 4 m, 2008, *Damien Ertz* 13216 (BR-LICH 7484-15—holotype; S-F213217—isotype).

(Fig. 6D)

Thallus facultatively saxicolous/corticolous, on calciferous rock when saxicolous, surface plane to slightly rugose-verruculose, slightly pruinose, creamy white to white-greyish, 0.1–1.5 mm thick; *cortex* 30–50 µm thick; medulla chalk-like also near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.1–2.0 mm diam.; *disc pruina* with finely rimose surface, white; *thalline margin* present, entire to undulating; *ascospores* 25–35 × 4–5 µm, mean length value 30.6 µm, mean width value 4.74 µm.

Chemistry. Spot tests: thallus surface C+ red, sometimes upper pruina has to be re-

moved to see reaction; medulla C-; disc C- rarely C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C & J.

Etymology. The name refers to the geographical region of Madagascar.

Distribution and habitat. *Dirina madagascariensis* is endemic to, and has only been collected in, the southern part of Madagascar. It is facultatively saxicolous and corticolous, growing on calciferous rocks or on the trunks of various trees and shrubs in forests with *Didierea madagascariensis*, *Euphorbia stenoclada*, *Alluaudia comosa*, *Euphorbia laza*, *Delonix adansonoides* and *Kalanchoe grandidieri*, near the coast in the districts of Toliara and Toalanaro.

Remarks. The unidentified secondary metabolite J is characteristic for this species.

The three saxicolous and three corticolous specimens investigated are divided into two clades and may represent two species (Fig. 4). However, only the saxicolous clade receives full PP and PJ support, whereas the corticolous clade receives somewhat less PJ support (90%). We will therefore refrain from describing a corticolous and saxicolous species until a hypothesis can be tested by the analyses of more specimens. Unexpectedly, the closest relatives and the sister group to *Dirina madagascariensis* is the strictly American species group containing *D. catalinariae*, *D. mexicana*, *D. pallescens* and *D. paradoxa* (see Biogeography below). It is only distantly related to the geographically much closer species *Dirina astridae* (Mauritius), *D. arabica*/*D. immersa* (Socotra) or *D. indica* (W. India).

Additional material examined. **Madagascar:** Toliara: La Table, 23°25'09.3"S 43°47'03.1"E, 2008, *Ertz* 13095 (BR-LICH 8734-04); La Table, 23°24'40.8"S 43°47'40.0"E, 2008, *Ertz* 13127 (BR-LICH 8765-35); Ifaty, 23°07'23.1"S 43°36'34.4"E, 2008, *Ertz* 13086 (BR-LICH 8724-91); S of Ifaty, 23°10'18.6"S 43°37'09.7"E, 2008, *Ertz* 13042 (BR-LICH 7391-19). *Toalanaro:* Fort Dauphin, 25°01'37.5"S 47°00'04.9"E, 2008, *Ertz* 13215 (BR-LICH 7487-18).

***Dirina massiliensis* Durieu et Mont.**

Expl. Sci. Algeria. Cryptog. 1: 247 (1847).—*Parmelia repanda* Fr., *Lichenogr. Eur. Reform.* 177 (1831) [*Dirina repanda* auct. non Fr. (1825)].—*Parmelia massiliensis*

Dufour ex Mont., *Arch. Bot.* (Paris) 295 (1833).—*Dirinopsis massiliensis* De Not., *Giorn. Bot. Ital.* 2(1): 187 (1846).—*Urceolaria repanda* (Fr.) Schaer., *Enum. Crit. Lich. Eur.* 92 (1850).—*Secolegia repanda* (Fr.) Norman, *Nyt Mag. Naturvidensk.* 230 (1853); type: France, Marseille, Montredon, 1806, *Dufour* s. n. (UPS—lectotype sel. by Tehler 1983).

Lecanora repanda Fr. ex Duby, *Bot. Gall.* (1830); type: France, Marseille, s. ann, *Le Prevost* s. n. [UPS—lectotype sel. by Tehler (1983); M—isolectotype].

Lecidea stenhammarii Fr. ex Stenham., *Öfvers. Kongl. Vetensk.-Akad. Förh.* 4: 197 (1848); Fries, *Summa Veg. Scand.* (Fries) 155, nom. nud. 1845.—*Lecanactis stenhammarii* (Fr. ex Stenham.) Arnold, *Flora* 54: 196 (1871).—*Bilimbia stenhammarii* (Fr. ex Stenham.) Boistel, *Nouv. Fl. Lichens* 2: 33 (1903).—*Dirina stenhammarii* (Fr. ex Stenham.) Poelt & Follmann, *Herzogia* 1: 61 (1968).—*Dirina repanda* f. *stenhammarii* (Fr. ex Stenham.) Clauzade & Roux, *Bull. Mus. Hist. Nat. (Marseilles)* 35: 192 (1975); type: Sweden, Gotland, Kyllaj, Kyleiberget, “Gottlandia in grascruptio montium calcareorum, Kyleiberget, Klejven in picroccia, Sundre etc” Chr. Stenhammar scripsit, s. ann, *Christian Stenhammar* s. n. (S-L5—lectotype sel. by Tehler 1983).

Pyrenotheca aponina A. Massal., *Ric. Auton. Lich. Crost.* 151 (1852).—*Lecanactis aponina* (A. Massal.) Zahlbr., *Cat. Lich. Univ.* 2: 533 (1924).—*Dirina massiliensis* f. *aponina* (A. Massal.) Tehler, *Lichenologist* 20: 398 (1988); type: ex hb. Massalongo, [Anzi, *Lichenes rarioris Veneti* no. 85]. Ad tophum, et rupes calcareas fontium thermalium aponinarum (di Abano) in collibus Euganeis, Mass., s. ann, *A. Massalongo* s. n. (S-F177479, S-F177477, UPS).

Dirina patronii Bagl., *Mem. Reale Accad. Sci. Torino* 2(17): 397 (1857).—*Dirina repanda* f. *patronii* (Bagl.) Zahlbr., *Cat. Lich. Univ.* 2: 509 (1924); type: Italy, “Cresce su d’un vecchio muro nel villaggio Creveri presso Voltri”, s. ann, *Stefano Patrone* s. n. (not retrieved).

Dirina repanda v. *pelagosae* J. Steiner et Zahlbr., *Österr. Bot. Z.* 53(5): 177 (1903); type: Croatia (Jugoslavia), Pelagosa Isl., s. ann, *A. Ginzberger* s. n. (W—holotype).

Dirina cyclosora Poelt & Nimis, *Bull. Soc. Linn. Provence* 45: 254 (1994); type: s. ann., s. coll. s. n. [TSB—holotype (not seen); GZU—iso-type].

(Figs – see Tehler 1983)

Thallus obligately saxicolous on calciferous rock, surface plane, rugose-verruculose to nearly squamulose or suffruticose, pruinose, white-grey, 0.2–3.5 mm thick; *cortex* 40–70 µm thick; *medulla* chalk-like also near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata present (usually in the absence of *soralia*), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, 0.5–3.0 mm diam.; *disc pruina* with rimose surface, white-grey to dark grey;

thalline margin present, entire to undulating, strongly undulating or even so strongly undulating as to become stromatoid; *ascospores* 20–24 × 4–6 µm, mean length value 21.6 µm, mean width value 5.0 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ faintly red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, D, E, H rare.

Distribution and habitat. *Dirina massiliensis* is one of the most widespread species of *Dirina*. It grows on calcareous coastal outcrops along the coasts of the Mediterranean, Atlantic Ocean (from Bergen, Norway south to Morocco) and the Baltic Sea (Öland to Gotland). It also occurs on inland calcareous rocks in Central Europe, in localities with dry, open vertical cliffs and rocks resembling coastal cliffs but then only as sterile, sorediate thalli.

Remarks. *Dirina massiliensis* occurs more or less distinctly as either a fertile, ascocarpous morph or as a sterile, sorediate morph although transitional specimens with both ascomata and soralia on the same thallus occur, even if they are relatively uncommon. *Dirina massiliensis* also develops a pycnidiate morph (Tehler 1988). Both the sorediate morph and the pycnidiate morph have been treated as a separate taxa, named *Dirina stenhammarii* or *Dirina massiliensis* f. *sorediata* when sorediate and *Lecanactis aponina* or *D. massiliensis* f. *aponina* when pycnidiate. We no longer distinguish these or any other sterile morphs taxonomically, since supporting molecular data is absent. Ascomata formation is frequent in the Mediterranean region climate and rare in central and northern Europe. The northernmost localities with specimens abundantly forming ascomata are the southern point of Gotland and the small island Lilla Karlsö, close to Gotland in the Baltic Sea. The only ascoma-forming specimen on an inland locality originates from the Ardennes in southern Belgium (but no other fertile specimen has been seen since then in this country).

In Tehler (1983), *Dirina massiliensis* on calciferous rock and *D. fallax* on acidic rock were treated as conspecific, but new data

from the present investigation clearly indicate that they should each be treated at species level.

Dirina massiliensis is similar to *D. fallax* and is also closely related to that species. *Dirina massiliensis* has a thicker, whitish and chalk-like thallus compared to the thinner and more grey-brownish thallus of *D. fallax*. Furthermore, *D. massiliensis* is strictly confined to calciferous rocks whereas *Dirina fallax* is strictly confined to acidic rock.

Dirina massiliensis is confusingly similar to saxicolous *D. ceratoniae*, but the medullary hyphae in *D. massiliensis* are chalk-like throughout and never loose or byssoid near the substratum which is normally the case in *D. ceratoniae*. However, in some specimens of the latter species, particularly those with thin thalli, this character may fail or be very difficult to see. *Dirina ceratoniae* can also be distinguished from *D. massiliensis* by its more greenish, less pruinose thallus surface and its longer ascospores.

Additional material examined. **Belgium:** Ardennes, s. ann., s. coll., s. n. (FH); Wulveringem (Veurne), Beauvoorde, 2008, Ertz 12403 (BR).—**Croatia:** Dalmatia: Korcula, Brna, 1980, Tehler 5070, 5075 (S-F97436, S-F204729); Vela Luca, 1980, Tehler 5078, 5080 (S-F170255, S-F204730); Dubrovnik (Ragusa), s. ann., Micheletti s. n. (S-F184127); Primorje, Rab, 1926, Baumgartner 65 (S-F204702); Losinj, Veli Losinj, 1980, Tehler 5116 (S-F204704); Rab, Kampor, 1980, Tehler 5099 (S-F204705); Drvenik, 80 km SE of Split, 1980, Tehler 5061 (S-F204726); Risan, 50 km S of Dubrovnik, 1980, Tehler 5059 (S-F204727); Karlobag, 80 km N of Zadar, 1980, Tehler 5093 (S-F204728); Krk, Pinenzioi SW Fuska, 1980, Tehler 5102 (S-F204731); Pag, Gradac, 1980, Tehler 5098 (S-F204732); Pag, 3 km NW of Pag, 1980, Tehler 5091 (S-F204733); Sibenik, 1980, Tehler 5082 (S-F204734). **Istria:** Pula, on walls of the Arena amphitheatre, 1980, Tehler 5122, 5123, 5129 (S-F97432, S-F97444, S-F204707); Premantura, [transitional, apothecia-soredial], 1980, Tehler 5132, 5135, [transitional apothecia-soredial], 5140, (S-F97435, S-F97433, S-F204710); Rijeka, 1980, Tehler 5105 (S-F204706); Rovinj, 35 km NE of Pula, 1980, Tehler 5144 (S-F204712).—**Cyprus:** Cape Greco: 20 km S of Famagusta, 1980, Tehler 5010, 5015 (S-F204697, S-F97445). **Cape Pyla:** 25 km E of Larnaca, 1980, Tehler 5056, 5057 (S-F97448, S-F204719). **Paphos:** Tombs of the Kings, just outside Paphos, 1980, Tehler 5027, 5034 (S-F204720, S-F97446). **Polis:** Akamas peninsula 40 km N of Paphos, 1980, Tehler 5042, 5044 (S-F97447, S-F204696).—**Czech Republic:** Horazd'ovice: Sumava Mts, Zichovice, 49°16'28.93"N 13°35'30.59"E, 2007, Vondrák 5125 (CBFS). **Znojmo:** Podyjí National Park,

Lukov, 48°50'17"N 15°54'25"E, 2011, Vondrák 8425 (CBFS).—**France:** Antibes: s. loc., 1866, Metzler s. n. (S-F184362). **Bouches-du Rhône:** Châteauneuf-les-Martiques, 1965, Marcucci s. n. (S-F184218). **Sarthe:** Brulon calcaire de Pissegrère, 1906, Monguillon s. n. (S-F204701).—**Germany:** Bavaria: Eichstätt, 1876, Arnold s. n. (S-F204698); 1873, Arnold 560 (S-F204699); 1876, Arnold s. n. (S-F204700); 1977, Tehler 4212 (S-F204695). **Württemberg:** s. loc., 1895, Zieber s. n. (GBG).—**Gibraltar:** along the Mediterranean Steps, 2009, Tehler 9803 [fertile], 9804 [sorediate] (S-F210816, S-F210817).—**Greece:** Peloponnesos: Akhaia, Akr. Araxos, 35 km W of Patras, 1978, Tehler 4014 (S-F204722).—**Hungary:** Bükk Mts, Bükk National Park, Borsod-Abauj-Zemplen, Malyinka, 48°08'00.1"N 20°30'03.1"E, 2008, Vondrák & Khodosovtsev 6379 (CBFS); s. loc., s. ann., Lojka s. n. (S-F184415).—**Italy:** **Isole Egadi:** Favignana, 1979, Tehler 4510, 4517 (S-F97442, S-F204725). **Isole Pelagie:** Lampedusa, 1979, Tehler 4547, 4553, 4580 (S-F97441, S-F204724, S-F97440). **Puglia:** Lecce, Otranto, 1996, Nimis & Treliach s. n. (S-F97431); Otranto, 2008, Tehler 9600, 9603, 9604, 9608, 9635, 9636 (S-F176070, S-F176063, S-F176064, S-F176073, S-F176062, S-F176068); S. Cesarea Terme, 40°4.125'N 18°28.832'E, 2008, Tehler 9610, 9611 (S-F176093, S-F176091); Diso, 39°59.483'N 18°24.869'E, 2008, Tehler 9612, 9613 (S-F176049, S-F176050); Santa Maria di Léuca, 39°47.499'N 18°20.670'E, 2008, Tehler 9624 (S-F176098); Foggia, Isola Tremiti, 1997, Nimis s. n. (S-L3972). **Sardinia:** Carolim, s. ann., Canepa s. n. (GBG, S-F184125, S-F184230); Cagliari, s. ann., Canepa s. n. (S-F184183, S-F184361); Capo St. Elia, 1866, Marcucci s. n. (S-F184205, S-F184234).—**Libya:** Cyrenaica: 32 km WSW of Derna, 13 km ESE of Lamudah, 1982, Thor 2926 (S-F127872).—**Morocco:** Agadir: Cap Rhir unweit Tamri, 1967, Follmann & Follmann-Schrag s. n. (GBG). **Casablanca:** Mensouri, c. 50 km N of Casablanca, 1978, Tehler 2159 (S-F204737). **El Jadida:** Mazagan, 1932, s. coll. s. n. (S-F184126).—**Norway:** **Hordaland:** Austevoll, Litlalkaløy, 1981, Skjolddal 5802 (S-F204666). **Rogaland:** Tysvaer, Kårstø, 1981, Skjolddal 5801 (S-F204667). **Sund:** Store Sotra by Golta, 1981, Tehler 5803 (S-F204668).—**Poland:** **Karpaty:** Beskidy Zachodnie Mts., 1977, Tehler 4202 (S-F204721). **Nowy Targ:** Pieniny, Wawoz Sobczanski, 1957, Tobolewski s. n. (S-F204723).—**Portugal:** **Algarve:** Bordeira, 37°11'47"N 8°55'00"W, 2011, Ertz 16952, 16958 (BR); Cabo de Sao Vicente, 2011, Ertz 16994, 16995, 16996 (BR); 1979, Tehler 4584, 4600 (S-F184426, S-F184427); Beliche, 1944, Palhinha 3675 (S-F204703); 1951, Tavares s. n. (S-F184237). **Lisbon:** Praia da Adraga, circa Colares, 1951, Tavares s. n. (S-F184226).—**Spain:** **Almeria:** Carboneras, Punta de los Muertos, 1975, Tehler 1206, 1209 (S-F135200, S-F135201); 2009, Tehler 9813 (S-F210818). **Mallorca:** Cala Marsal and Cala Brafí, 1972, Santesson 24086a (S-F184124); Cala Santanyi, 1979, Tehler 4680, 4684, 4686 (S-F60779, S-F60767, S-F60768); Formentor, 1979, Tehler 4673, 4681, 4683 (S-F60770, S-F60772, S-F60777); Formentor, 2007, Tehler 9026, 9030 (S-F66008, S-F66010); Playa de Cala Santanyi, 2007, Tehler

9001, 9002, 9008, 9009 (S-F66003, S-F66005, S-F66006, S-F66007); Punta la Nao, 1978, *Thor* 629 (S-F60764). **Murcia:** La Azohia, 1976, *Tehler* 1255, 1256 (S-F135188, S-F135186); Los Belones, 1976, *Tehler* 1272, 1273 (S-F135176, S-F135177); Mazarron, 1976, *Tehler* 1244, 1247 (S-F135170, S-F135168).—**Sweden:** **Gotland:** Hellvi, Kyllaj, 1982, *Tehler* 5950 (S-F204645); 2007, *Tehler* 9213 (S-F96537); Lilla Karlsö, 1977, *Thor* 253, 253a(1), 253a(2), 253b (S-F204661, S-F97426, S-F97429, S-F204662); Rute, Furilden, 57°45'17.3"N 18°56'52.5"E, 2007, *Tehler* 9214 (S-F96544); Stenkyrka, Stenkyrka huk, 1980, *Anderberg* 603 (S-F204664); Sundre, Gullstajnen, 1977, *Tehler* 3015 (S-F204665); Hoburgen, 1977, *Thor* 55 (S-F204659); 1980, *Anderberg* 602 (S-F204663); 1983, *Tehler* 6000 (S-L193); 1998, *Tehler* 8044, 8045, 8046, 8047 (S-L5649, S-L5650, S-L5651, S-L5652); 2007, *Tehler* 9210, 9211, 9212 (S-F96531, S-F96534, S-F96536); Klejven, s. ann., *Stenhammar* s. n. (S-L197, S-F204649, S-F204658); Visby, Galgberget, 1982, *Thor* 2706 (S-F204646); Snäckgårdsbaden, 1977, *Thor* 252 (S-F204660); s. loc., s. ann., *Stenhammar* s. n. (S-F204647). **Öland:** Borgholm, 1860, *Hellbom* s. n. (GBG); 1871, *Molér* s. n. (GBG, S-F204642); Köping, Köpings branter, 1867, *Zetterstedt* s. n. (S-F204643); 1976, *Tehler* 2113 (S-F204641).—**Switzerland:** **Basel-land:** Liestal, Kant, s. ann., *Hepp* 757 (S-F204685).—**Ukraine:** **Crimean Peninsula:** Sevastopol, Balakalava, 44°29'42"N 33°36'4"E, 2009, *Vondrák, Merkulova & Khodosovtsev* 7366 (CBFS).

Dirina mexicana Tehler

Lichenologist 27: 256 (1995); type: Mexico, Estado de Sinaloa, 3 km NNE of Higuera de Zaragoza, hill surrounded by agricultural fields, on vertical rocks, alt. 50 m, 1993, *Anders Tehler* 7175 (S-L7—holotype; AZU, BM, ESS, H, M, NY, US, UPS—isoatypes).

(Figs – see Tehler *et al.* 1995)

Thallus obligately saxicolous on acidic rock, surface plane to slightly rugose-verruculose, slightly pruinose, white-grey to white-yellowish, 0.2–0.5 mm thick; *cortex* 20–40 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, monocarpocentral, numerous, immersed, circular or linear in outline, 0.4–0.8 mm diam.; *disc pruina* with rimose surface, white; *thalline margin* absent; *ascospores* 21–27 × 5–6 µm, mean length 24.3 µm, mean width 5.7 µm.

Chemistry. Spot tests: thallus surface C+ red in rimulae only, otherwise faintly red or C–; medulla C–; disc C–. Secondary metabolites: erythrin; unidentified substances C, F, occasional G (lecanoric acid absent but

perhaps present in very low amount, see Chemistry).

Distribution and habitat. *Dirina mexicana* has been found in coastal areas of Mexico, from Laguna Manuela in Baja California south to Cabo San Lucas, and including near Higuera de Zaragoza in Sinaloa. It grows on vertical or overhanging rocks and cliffs. Occasionally it may be abundant with individuals forming large mosaic patterns.

Remarks. *Dirina mexicana* has immersed ascomata similar to the non-related species *D. insulana*, *D. immersa* and *D. candida*. *Dirina mexicana* is partly sympatric with its sister species *D. catalinariae* and to the closely related *D. pallescens*. However, both *Dirina catalinariae* and *D. pallescens* are easily distinguished from *D. mexicana* by their conspicuously sessile ascomata with constricted base. *Dirina pallescens* is furthermore strictly corticolous whereas *D. mexicana* and *D. catalinariae* are strictly saxicolous. *Dirina mexicana* is also characterized by the combined presence of the two unidentified substances F and G, a combination that it shares only with *Dirina pacifica*.

Additional material examined. **Mexico:** **Baja California Sur:** Isla Santa Margarita, 24°24'N 111°43'W, 1993, *Tehler* 7215 (S-L10); La Palma, NW of Cabo San Lucas, 23°00'38.3"N 110°05'49.3"W, 2007, *Tehler* 9193 (S-F210821); Laguna Manuela, 28°15'N 114°07'W, 1993, *Tehler* 7236 (S-L8); Migriño, NW of Cabo San Lucas, 23°04'55.0"N 110°06'41.8"W, 2007, *Tehler* 9196 (S-F210822); Playa Punta Lobos S of Todos Santos, 23°28'N 106°50'W, 1993, *Tehler* 7156 (S-L11); S of the beach, 23°24'31.5"N 110°14'05.0"W, 2007, *Tehler* 9173 (S-F210819); 1991, *Nash* 29741 (S-F69910); Playa San Pedro, S of Todos Santos, 23°23'02.1"N 110°12'45.0"W, 2007, *Tehler* 9187 (S-F210820); Punta Gaspareno, N of Cabo San Lucas, 23°15'27.3"N 110°09'43.1"W, 2007, *Tehler* 9198 (S-F210823); 3.5 km along road to Punta Abreojos from Highway 1.27°15'N 113°10'W, 1993, *Tehler* 7229 (S-L9); W of San Ignacio at junction of road to Punta Abreojos, 1989, *Wetmore* 63893 (S-F69911). **Sinaloa:** 3 km NNE of Higuera de Zaragoza, 26°01'N 109°16'W, 1993, *Tehler* 7175 (S-L7).

Dirina monothalamia Tehler & Ertz nom. nov.

Mycobank No.: MB 802914

Chiodecton africanum Fée, *Essai Crypt. Écorc. Suppl.* 53 (1837) [non *Dirina africana* Kremp.].—*Schismatomma*

africanum (Fée) C. W. Dodge, *Beih. Nova Hedwigia* 12: 91 (1964).—*Dirina approximata* ssp. *africana* (Fée) Tehler, *Opera Bot.* 70: 39 (1983).—*Dirina paradoxa* ssp. *africana* (Fée) Tehler *Lichenologist* 18: 296 (1986); type: In Senegambia, presqu'île du cap vert (afrique) sur un vieux figuier près de Kounoun, Caramano sur les pierres, s. ann., *Perrotet* 4 [G-291546—lectotype sel. by Tehler (1983); G-291545, G-291548, H-NYL-23882, M—isolectotypes].

(Fig. 6A & B)

Thallus facultatively saxicolous/corticolous, on acidic rock when saxicolous, surface plane to slightly rugose-verruculose, slightly pruinose, creamy white to white-brownish sometimes brown to nearly dark brown, 0.1–0.7 mm thick; *cortex* 10–50 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.0 mm diam.; *disc pruina* with even surface or finely rimose surface, white; *thalline margin* present, entire to undulating to often strongly undulating; *ascospores* 23–28 × 4–5 µm, mean length 26.13 µm, mean width 4.66 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red. Secondary metabolites: erythrin; lecanoric acid rarely absent; unidentified substance C.

Etymology. The epithet '*monothalamium*' was first written by Fée on the sheet containing the type material *Chiodecton africanum*. He later crossed out '*monothalamium*' and replaced it with '*africanum*'. Therefore we will select and use *monothalamium*, the first, original epithet made by Fée.

Distribution and habitat. *Dirina monothalamia* is known from Cape Verde and the nearby African mainland in Senegal. It grows on coastal outcrops or the bark of various trees, and often on *Adansonia digitata* in Senegal.

Remarks. *Dirina monothalamia* is morphologically nearly identical to *D. teichiodes* but differs from the latter by having a slightly more rugose thallus with convex areoles, a thalline margin which in saxicolous specimens is more undulating to strongly undulating (Fig. 7A), and a slightly higher mean value of ascospore length. However, none of

these characters are discrete and they all overlap with the corresponding characters in *Dirina teichiodes*. As a result, it seems these two species can only be accurately determined with reference to each other by the analyses of molecular characters.

Corticolous specimens do not develop such undulating thalline margins as saxicolous specimens, in which they are usually not only undulating but also often strongly so.

Dirina monothalamia is also very similar to *D. sorocarpa*, but the latter is readily distinguished by the presence of soralia. *Dirina monothalamia* has never been found sorediate.

The species *Dirina africana*, currently referred to as *Diploschistes africanus* (Kremp.) Zahlbr., was described by Krempelhuber (1877) from Somaliland. Thus the epithet *africana* cannot be used for this taxon.

Additional material examined. **Cape Verde**: *Boa Vista*: Mt. Vigia, 1987, *Mies* 560a3 (S-F151297); Mt. Vigiamassiv, Ponta do Sol, 1987, *Mies* 561g3 (S-F151299). *Brava*: Sorno, 14°53'N 24°44'W, 1988, *Kalmns* 1275a2 (S-L11751); Vinagre, 14°52'N, 24°41'W, 1988, *Kalmns* 1273a2, 1274a2 (S-L11755, S-L11756, S-L11753); Furna, 1987, *Mies* 743a3 (S-F151290); S von Furna, 150 m, 1987, *Mies* 752a3, 747d3 (S-F151291, S-F151293). *Maio*: Mt. Batalha, 1987, *Mies* 790g2 (S-F151301). *Sal*: Mt. Grande, NW-Grat, 16°49'N, 22°54'W, 1988, *Mies* 1067i2, 1067j2 (S-L11747, S-L11754); Algudeiro, N Santa Maria, 16°37'N 22°56'W, 1988, *Mies* 1040a2 (S-L11752); Monte Grande, 16°49'700'N 22°56'249'W, 2010, *Tehler* 10067 (S-F210826); Buracona, 16°48'802'N 22°59'294'W, 2010, *Tehler* 10074 (S-F210827); Monte Leão (Rabo da Junco), 16°42'030'N 22°58'929'W, 2010, *Tehler* 10079-69 (S-F210828). *Santo Antao*: Fontainhas, 17°12'N 25°06'W, 1988, *Mies* 1191h2 (S-L11750). *Sao Nicolau*: W Estancia Bras nach Ribeira Funda, 16°40'N 24°20'W, 1988, *Mies* 932d 2 (S-L11748). *Sao Tiago*: Serra da Antonia, 1987, *Mies* 225f2 (S-F151304); Mt. Graciosa, 1987, *Mies* 636h3 (S-F151303). *Sao Vicente*: Punta Santo Antonio, 16°53'N 24°56'W, 1988, *Mies* 1212a2 (S-L11749); Praia da Ceilada do Calhau, 16°51'552'N 24°52'741'W, 2009, *Tehler* 10009 (S-F210824); Praia Grande 16°51'549'N 24°53'195'W, 2010, *Tehler* 10028 (S-F210825); between Baia das Gates and Calhau, NE of Monte Verde, 16°52'29'N, 24°54'46'W, 2011, *Ertz* 17246 (BR).—**Senegal**: *Dakar*: Senegal, Dakar, Bot. Garten, 1972, *Pittoni* s. n. (GZU); between Flygplatz Dakaar-Yoff und N'Gor, 1972, *Pittoni* s. n. (GZU); N'Gor, 1972, *Pittoni* s. n. (GZU); Goree, 1972, *Pittoni* s. n. (GZU); Nofaye between Sangalkam and Bambilor, 14°47'194'N 17°12'579'W, 2011, *Tehler* 10400 (S-F210829); W of Sangalkam, 10 km NE of Rufisque, 14°46'516'N 17°14'765'W, 2011, *Tehler* 10401 (S-F210830); Deni Biram Ndao, 14°50'634'N

17°11.918'W, 2011, *Tehler* 10402 (S-F210831); 5 km N Sebikhoutane, 14°43.149'N 17°09.827'W, 2011, *Tehler* 10404 (S-F210832); Ile de Gorée, 14°39.958'N 17°23.922'W, 2011, *Tehler* 10407 (S-F210834); Yoff, E of the airport S of Mbenguène, 14°44.850'N 17°17.587'W, 2011, *Tehler* 10411 (S-F210835). *Thiès*: Popenguine N of Mbour, 14°32.484'N 17°6.282'W, 2011, *Tehler* 10405 (S-F210833).

Dirina pacifica Tehler & Ertz sp. nov.

Mycobank No.: MB 802915

Thallus obligately saxicolous on acidic rock. Soralia present (usually in the absence of ascromata). Medulla C-. Ascromata present (usually in the absence of soralia), sessile. Disc pruina with rimose surface. Ascospore mean length 23.82 µm and width mean value 4.47 µm. Unidentified secondary metabolite F present and G occasional.

Type: USA, Hawaii, Oahu, Koolaupoko Distr., Makapuu Point W of the lighthouse, 2010, *Anders Tehler* 10128 (S-F210836—holotype; BR—istotype).

(Fig. 6E & F)

Thallus obligately saxicolous on acidic rock, surface plane, epruinose, creamy white to greyish or brownish, 0.1–0.3 mm thick; *cortex* 25–35 µm thick; *medulla* chalk-like also near substratum, white; *soralia* present (usually in the absence of ascromata), punctiform to maculate.

Ascromata present (usually in the absence of soralia), pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >1.5 mm diam.; *disc pruina* with rimose surface, white-grey; *thalline margin* present raising above disc, entire to undulating; *ascospores* 19–27 × 4–5 µm, mean length value 23.82 µm, mean width value 4.47 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C-; disc C+ red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances C, F, G occasional.

Etymology. The name refers to the geographical region of the Pacific Ocean.

Distribution and habitat. *Dirina pacifica* is known from the Galapagos Islands and Hawaii. It grows on coastal outcrops.

Remarks. The *Dirina pacifica* specimens from Hawaii are closely related to the specimens from the Galapagos (Figs 1–4). The

sister species to *Dirina pacifica* is *D. paradoxa*, originating from the Caribbean. *Dirina pacifica* also commonly appears in a sterile, sorediate form.

The thallus and the thalline margin vary considerably in colour from dark brown to greyish to creamy white and nearly white-yellowish (Fig. 6E & F).

The great distance between Hawaii and the Galapagos, and the fact that the Galapagos and Hawaiian specimens in all nodes form a 100% sister pair relationship, indicate that two distinct species may actually have evolved. However, there are no obvious morphological or chemical features to distinguish them. Furthermore, we have only two specimens sampled from the Galapagos. We will therefore refrain from describing two species until such a hypothesis can be tested by the analyses of more specimens.

Additional material examined. **USA: Hawaii:** Hawaii, South Kohala Distr., Waimea 20°1.400'N 155°39.950'W, 2010, *Tehler* 10138 (S-F210839); W.M. Keck Observatory Headquarters, 20°1.401'N 155°39.945'W, 2010, *Tehler* 10136 (S-F210838); Oahu, Koolaupoko Distr., Makapuu Point 21°18.539'N 157°39.432'W, 2010, *Tehler* 10129 (S-F210837); Makapuu cliffs, 1994, *Smith* 7537 (S-L5071); Makapuu cliffs, Tomtom Trail, 1981, *Smith & James* 7520 (S-L68959); 1996, *Smith & Wetmore* 7697, 7698a, 7698b, 7698c (S-L8703, S-L8700, S-L8701, S-L8702).—**Ecuador: Galapagos Islands:** Floreana, N of village 1°16'9.9"S 90°29'20.2"W, 2011, *Bungartz* 9487 (S-F210840); Floreana, Punta Luz del Dia, 01°14.181'S 090°28.501'W, 2005, *Tehler* 8693 (S-L68244); trail from Black Beach, 1976, *Weber & Lanier* L-82896 (COLO-294625); Pinzón, N coast, 00°35.851'S 090°41.221'W, 2005, *Tehler* 8748 (S-F96209); small point on the W side, 00°36.480'S 090°41.558'W, 2005, *Tehler* 8694 (S-F96088); Rábida, NE point, 00°24.852'S 090°42.205'W, 2005, *Tehler* 8778 (S-F96215); Santa Cruz, trail from Puerta Ayora to Bella Vista, 1976, *Weber & Lanier* L-82854 (COLO-294667); E of Puerto Ayora near CDRS, 00°44'45"S 90°17'39"W, 2005, *Aptroot* 63294 (hb. Aptroot); Puerto Ayora, CDRS, 0°44.869'S 90°18.408'W, 2005, *Tehler* 8600 (S-L61608); vicinity of Academy Bay, s. ann., *Weber* L-40824a L-40824b L-40824c (COLO-190270, COLO-190269, COLO-190330); Santa Fé 0°49'11"S 90°5'24"W, 2005, *Tehler* 8726 (S-L72897).

Dirina pallescens Tehler & Ertz sp. nov.

Mycobank No.: MB 802916

Thallus obligately corticolous. Soralia absent. Ascromata up to 2.5 mm diam. Disc faintly C+ red. Ascospores mean length 29.4 µm. Unidentified secondary metabolite B present.

Type: Mexico, Baja California Sur, Todos Santos, c. 5 km S of town along Highway 19, 2007, *Anders Tehler* 9181 (S-F210843—holotype; BR—isotype).

(Fig. 7E)

Thallus obligately corticolous, surface plane to rugose-verruculose, epruinose, creamy white to white-brownish, 0.1–0.5 mm thick; *cortex* 30–40 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.5 mm diam.; *disc pruina* with rimose or slightly rimose surface, white-grey; *thalline margin* present, entire to undulating; *ascospores* 27–30 × 4–5 µm, mean length value 29.4 µm, mean width value 4.4 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red, sometimes faintly red. Secondary metabolites: erythrin; lecanoric acid; unidentified substances B & C.

Etymology. The name refers to the often pale colour of the thallus.

Distribution and habitat. *Dirina pallescens* is distributed in Mexico and restricted to Baja California Sur, Sonora (Los Medanos) and Oaxaca (Puerto Angel). It grows near the sea on various trees and shrubs, such as *Bursera* and mangrove.

Remarks. *Dirina pallescens* is the corticolous sister species to *D. catalinariae* and *D. mexicana*; both are saxicolous. In addition to its corticolous habit, it can be distinguished from *D. catalinariae* by its longer and more slender ascospores. It shares the unidentified substance B with *Dirina catalinariae* but not with *D. mexicana*. Unidentified substance B is also present in the more distantly related species *D. angolana*, endemic to Angola, and *D. sorocarpa*, endemic to Cape Verde.

Additional material examined. **Mexico**: Baja California Sur: Cabo San Lucas, 22°58' 16.3"N 110°02' 42.1"W, 2007, *Tehler* 9189 (S-F210844); Todos Santos, 23°28'N 110°09'W, 1993, *Tehler* 7165 (S-L3327); Punta Lobos beach S of Todos Santos, 23°28'N 106°50'W, 1993, *Tehler* 7154 (S-L8216); just S of beach, 23°24'31.5"N 110°14'05"W, 2007, *Tehler* 9164

(S-F210841); on the ridge just south of beach, 23°24'31.5"N 110°14'05"W, 2007, *Tehler* 9176 (S-F210842); 23°28'N 106°50'W, 1993, *Tehler* 7154 (S-L8216); 1993, *Nash* 33740 (GBG, S-F69917). **Oaxaca**: Puerto Angel, 1910, *Oreutt*, 4973 (FH, L). **Sonora**: Los Médanos, 27°09'N 110°08'W, 1993, *Tehler* 7130 (S-L3296); W of Ciudad Obregon, 1993, *Wetmore*, 71824 (S-F69919).

Dirina paradoxa (Fée) Tehler

Lichenologist **18**: 296 (1986).—*Chiodecton paradoxum* Fée, *Essai Crypt. Écorc.* 64 (1824).—*Platygrapha dirinea* Nyl. (excl. *Dirina multififormis* Mont. & Bosch), *Mém. Soc. Imp. Sci. Nat. Cherbourg* **5**: 131 (1857).—*Schismatomma paradoxum* (Fée) Zahlbr., *Cat. Lich. Univ.* **2**: 563 (1924).—*Schismatomma dirineum* (Nyl.) Räsänen, *Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo"* **21**, *Not. Bot.* **16**: 6, nom. illeg. (1946); type: ad corticem crotoni *Cascarillae* et *Cinch. laccifera*, *Cassia lignea*, s. ann., *Ruiz & Pavon* 126 (G-291552—holotype; G-291551—isotype).

Platygrapha psaroleucoides Stirt., *Rep. Trans. Glasgow Soc. Field Naturalists* **4**: 166 (1876).—*Schismatomma psaroleucoides* (Sturton) Zahlbr., *Cat. Lich. Univ.* **2**: 564 (1924); type: Trinidad, Port of Spain, 1875, *Brodie* s. n. [BM—lectotype sel. by Tehler (1986)].

Dirina hioramii B. de Lesd., *Rev. Bryol. Lichenol.* **7**: 60 (1934).—*Dirina approximata* ssp. *hioramii* (B. de Lesd.) Tehler, *Opera Bot.* **70**: 37 (1983); type: Cuba, Cuba oriente, Guantanamo, Boca del Jaibo, arboricola, 1921, *B. Hioram* 5552a [originally in KASSEL later probably moved to KÖLN and now donated to B—lectotype sel. by Tehler (1983)].

(Figs – see Tehler 1983)

Thallus facultatively saxicolous/corticolous, on calciferous or acidic rock when saxicolous, surface plane to slightly rugose-verruculose, when saxicolous more or less bullate slightly pruinose, creamy white to white-greenish or white-brownish, 0.05–0.70 mm thick; *cortex* 10–50 µm thick; *medulla* chalk-like but with loose hyphae near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.0 mm diam.; *disc pruina* with even surface, white; *thalline margin* present, entire to undulating; *ascospores* 21–30 × 4–5 µm, mean length value 25.49 µm, mean width value 4.72 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C– or sometimes faintly red. Secondary metabolites: erythrin; lecanoric acid; unidentified substance C.

Distribution and habitat. *Dirina paradoxa* is distributed in the Caribbean region, in the Bahamas, Florida Keys, Lesser Antilles, Netherland Antilles, Venezuela and Trinidad. It grows near the coast on the bark of various trees and shrubs or on rock, both calciferous and acidic.

Remarks. *Dirina paradoxa* was earlier (Tehler 1983, 1986) regarded as a species with three subspecies. The present analysis of molecular data clearly shows that *Dirina paradoxa* is the sister species to the geographically distant *D. madagascariensis*, and not to any of its former subspecies, here referred to as *D. approximata*, *D. teichiodes* and *D. monothalamia*, which all belong to another group of species. The specimens earlier determined as *Dirina paradoxa* from Peru, both fertile and sorediate, have been transferred to *D. badia*.

This is the only *Dirina* species growing on both calciferous and acidic rocks. We have had sequences only from calciferous specimens, and so further studies including more specimens growing on both types of substrata may reveal that two species are involved, similar to the situation that was found in *Dirina massiliensis*–*D. fallax*. But, for the time being, the calciferous and acidic growing specimens will be treated as conspecific under *Dirina paradoxa*.

Additional material examined. **Bahamas:** Eleuthera: 1907, Britton & Millspaugh 5640 (FH, NY). Great Exuma: 1905, Britton & Millspaugh 3033, 3052 (FH, NY). Long Key: 1905, Brace 4149 (FH, NY). Little San Salvador: 1907, Britton & Millspaugh 5688 (FH, NY). Nassau: 1905, Wight s. n. (FH). New Providence: 1904, Britton 855 (FH, NY); 1918, Brace 9398, 9504 (FH, NY); 1918, Brace 9446 (NY). Watling Island: 1907, Britton & Millspaugh 6162 (FH, NY).—**Cuba:** Guantánamo: Puerto Escondido, Finca Ocuja, 1933, Hioram s. n. (KASSEL).—**France:** French Antilles: St. Barthelemy, N of the airport, 1981, Tehler 5545 (S-L68953).—**Netherland Antilles:** Bonaire: 1977, Slagereen 8374, 8388 (U); Seru Largu, 12°11'21.7"N 68°16'35.7"W, 2006, Tehler 8930, 8931, 8932 (S-F210845, S-F210846, S-F210847); Montana Mtn. in the Karpata region, 12°13'44.7"N 68°22'01.7"W, 2006, Tehler 8938, 8939 (S-F210848, S-F210849); Washington-Slagbaai National Park, Juwa Pass, 12°16'00"N 68°24'00"W, 2006, Tehler 8947 (S-F210850). *St. Eustatius:* SE-coast, White Wall, 1980, Sipman 14996 (S-L68954, U). *Curaçao:* 1977, Slagereen 8221, 8239 (U). *Saba:* 1980, Sipman 15233 (U).—**USA:** *Florida:* The Lower Keys, Sugarloaf Key, S of the

highway, 1981, Tehler 5595 (S-L3550); Pumpkin Key, 1921, Kelly s. n. (S-F69923 US); Sugar Loaf Blvd c. 50 m S Cayman Dr., 24°37.535'N 81°32.588'W, 2010, Tehler 10113 (S-F210851); Middle Cape, 1916, Small s. n. (US).—**Venezuela:** *Estado Falcon:* Peninsula de Paraganá, El Balsamal, 1979, Figueiras 21246, 21247 (S-L7673, S-L7674); Cerro de Santa Ana, 1979, Lopez-Figueiras & Wingfield 21750-A, 21750-B (S-L7675, S-L7676); Cuara, via Encrucijada-Santa Ana, 1979, Lopez-Figueiras 19229 (S-L7677); Santa Ana, al sur del cerro frente a Santa Ana, 1979, Lopez-Figueiras & Wingfield 21830 (S-L7678); Monte Cano, 1979, Lopez-Figueiras 21255 (S-L7679); Cerro Colorado, cercanías de Santa Ana, 1979, Lopez-Figueiras 21318 (S-L7680); Punta Prudention, Tacuato, 1979, Lopez-Figueiras & Wingfield 32492 (S-F90366).

***Dirina sorocarpa* Tehler & Ertz sp. nov.**

MycoBank No.: MB 802917

Thallus obligately saxicolous on acidic rock. Medulla with loose hyphae near the substratum, C-. Soralia present (usually in the absence of ascomata), punctiform to maculiform. Ascomata rarely present and then always together with soralia. Disc pruina with even or only finely rimose surface, C- or faintly red. Unidentified secondary metabolite B present.

Type: Cape Verde, Sao Vicente, Praia Grande on NE facing ridge above the beach, alt. 100–200 m, 2010, Anders Tehler 10026 (S-F210855—holotype; BR—iso-type).

(Fig. 7C)

Thallus obligately saxicolous on acidic rock, surface plane to slightly rugose-verruculose, slightly pruinose, creamy white to white-brownish, 0.1–0.5 mm thick; *cortex* 25–40 µm thick; *medulla* chalk-like but sometimes with slightly loose hyphae near substratum, white; *soralia* present (usually in the absence of ascomata), punctiform to maculate.

Ascomata rarely present and then always together with soralia, pluricarpocentral, discothecia, few, sessile, circular in outline, base unconstricted or constricted, > 1.8 mm diam.; *disc pruina* with even surface or finely rimose surface, white-grey to dark grey; *thalline margin* present, entire to undulating; *ascospores* 21–30 × 4–5 µm, mean length value 24.77 µm, mean width value 4.67 µm.

Chemistry. Spot tests: thallus surface C+ red; *medulla* C-; disc C- or faintly red. Secondary metabolites: erythrin; lecanoric acid sometimes absent; unidentified substances B & C.

Etymology. The epithet *sorocarpa* refers to the feature of the ascomata (ascocarps), if present, being often partly sorediate, or under all circumstances produced together with soralia elsewhere on the thallus.

Distribution and habitat. *Dirina sorocarpa* is endemic to Cape Verde and hitherto known from the islands of Sao Vicente and Sal.

Remarks. *Dirina sorocarpa* is the sister species to *D. approximata* from the Galapagos Islands. It is easily distinguished from that species by its shorter spores and its saxicolous habitat. *Dirina sorocarpa* is morphologically very similar to the closely related species *D. monothalamia* and *D. teichiodes*, but differs from those two species by the presence of soralia and by the presence of the unidentified substance B. Fully sorediate specimens of *Dirina sorocarpa* are very difficult to distinguish from sterile, sorediate specimens of the distantly related *D. insulana*. Thin thalli of the latter are very hard to examine for the C+ red medulla reaction which is otherwise a characteristic feature of that species.

Additional material examined. Cape Verde: Sao Vicente: Baia das Gatas, 16°53.420'N 24°55.605'W, 2009, *Tehler* 10017 (S-F210853); between Baia das Gatas and Calhau, 16°52'29"N, 24°54'46"W, 2011, *Ertz* 17248 (BR); Madeiral, 16°49.174'N 24°56.140'W, 2010, *Tehler* 10052 (S-F210858); Mato Inglês, 16°51.640'N 24°55.847'W, 2010, *Tehler* 10041 (S-F210856); Mato Inglês, 16°51.57'N 24°55.52'W, 2010, *Tehler* 10051 (S-F210857); Praia da Ceilada do Calhau, 16°51.552'N 24°52.741'W, 2009, *Tehler* 10010 (S-F210852); Praia Grande 16°51.549'N 24°53.195'W, 2010, *Tehler* 10027 [fully sorediate] (S-F210854). *Sal:* Ponta trás do Cagaral 16°46.590'N 22°53.335'W, 2010, *Tehler* 10060 (S-F210859).

***Dirina teichiodes* (Stirt.) Tehler & Ertz comb. nov.**

Mycobank No.: MB 802918

Lecidea teichiodes Stirt., *J. Linn. Soc., Bot.* 14: 368 (1874); type: Cape Verde, Challenger Expedition 1873, 1873, *Moseley* s. n. [H-NYL-23903—lectotype sel. by Tehler (1983); H—isolectotype]. Epitype: Cape Verde, Sal, Monte Grande at the N foot of the mountain c. 1 km from the summit, alt. 50 m, 2010, *Anders Tehler* 10071 (S-F210861—epitype sel. here; BR—isoepitype).

(Fig. 7D)

Thallus obligately saxicolous on acidic rock, surface plane, slightly pruinose, creamy white,

0.1–0.5 mm thick; *cortex* 25–40 µm thick; *medulla* chalk-like also near substratum, white; *soralia* absent.

Ascomata present, pluricarpocentral, discothecia, numerous, sessile, circular in outline, base constricted, >2.0 mm diam.; *disc pruina* with even surface or finely rimose surface, white; *thalline margin* present, entire to slightly undulating; *ascospores* 20–29 × 4–5 µm, mean length 23.13 µm, mean width 4.62 µm.

Chemistry. Spot tests: thallus surface C+ red; medulla C–; disc C+ red. Secondary metabolites: erythrin; lecanoric acid sometimes absent; unidentified substance C.

Distribution and habitat. *Dirina teichiodes* is endemic to Cape Verde. It is strictly saxicolous and known only from three localities on Sal Island (the type specimen lacks locality details).

Remarks. *Dirina teichiodes* is morphologically very similar to *D. monothalamia*. *Dirina teichiodes* has a more even and finely rimose thallus with flat areoles, a thalline margin which is usually entire or only slightly undulating, and the mean value of ascospore length is slightly shorter. However, none of these characters are decisive and they all overlap with the corresponding characters in *D. monothalamia*. As a result, it seems these two species can only be accurately determined with reference to each other by the analysis of molecular characters.

Dirina teichiodes is also very similar to *D. sorocarpa* but the latter is readily distinguished by the presence of soralia.

Additional material examined. Cape Verde: Sal: Monte Leão (Rabo da Junco), 16°42.030'N 22°58.929'W, 2010, *Tehler* 10079-70 (S-F210862); Ponta trás do Cagaral c. 2 km N of Pedra Lume, 16°46.590'N 22°53.335'W, 2010, *Tehler* 10059 (S-F210860).

Excluded taxa

***Fulvophyton calcicola* (Sparrius) Tehler & Ertz comb. nov.**

Mycobank No.: MB 802919

Dirina calcicola Sparrius, *Bryologist* 107: 522 (2004); type: USA, Florida, Key West, 1898, *Thaxter* 415 (NY—holotype).

Remarks. On the basis of the shared features of pale brownish thallus, immersed ascomata and hyaline ascospores with a distinct gelatinous sheath (perispore), we believe this species is better placed in *Fulvo-phyton* (Ertz & Tehler 2011).

Schismatomma insulae-howense (Sparrius) Tehler & Ertz comb. nov.

Mycobank No.: MB 802920

Dirina insulae-howensis Sparrius *Biblioth. Lichenol.* **89**: 87 (2004); type: Australia, New South Wales, Lord Howe Island, Intermediate Hill via track to North Hummock, 1995, *Elix* 42042 (CANB CBG-9703492—holotype).

Remarks. We have no sequences from this species but the morphological and chemical evidence, long slender ascospores and absence of secondary substances indicate that it is better placed in *Schismatomma*.

Schismatomma neozelandicum (Redinger) Tehler & Ertz comb. nov.

Mycobank No.: MB 802921

Enterographa neozelandica var. *ochracea* Redinger, *Feddes Repert. Spec. Nov. Regni Veg.* **43**: 72 (1938).—*Dirina neozelandica* (Redinger) Sparrius, *Biblioth. Lichenol.* **89**: 89 (2004); type: New Zealand, Pahia Point, Foveaux Strait, s. l., coastal rock, 1935, *Thomson* A116 [W—lectotype sel. by Sparrius (2004)].

Enterographa neozelandica var. *murina* Redinger, *Feddes Repert. Spec. Nov. Regni Veg.* **43**: 72 (1938); type: New Zealand, South Island, Bluff, 1933, *Thomson* s. n. [not in W—lectotype sel. by Galloway (2004)].

Placidopsis novozelandica C. W. Dodge, *Nova Hedwigia* **19**: 453 (1971); type: New Zealand, Stewart Island, Mutton Bird Islets, Big Stage Island, 1965, *Fineran* 912 (CANU—holotype).

Remarks. We have no sequences from this species but the morphological and chemical evidence, long slender ascospores and absence of secondary substances indicate that it is better placed in *Schismatomma*.

Incertae sedis

***Dirina follmannii* (C. W. Dodge) Sparrius**

Biblioth. Lichenol. **89**: 88 (2004).—*Enterographa follmannii* C. W. Dodge [as *E. follmanni*], *Nova Hedwigia* **12**: 324 (1966); type: Los Molles, costa (prov. Aconcagua), 1960, *Follmann* 14660-D (FH-302903—holotype).

Remarks. The holotype specimen of *Dirina follmannii* is poorly developed. We have sequences from similar specimens to the holotype, collected by Tehler in Chile, but molecular results are inconclusive since they place it with either *Pentagenella* or *Minksia*. More material is needed before the position of this species can be finally settled.

Discussion

Phylogeny

Dirina candida is the sister species and sister group to all other *Dirina* species (Figs 1–4). Following the next node in the phylogenetic tree, *Dirina* is divided into two basal groups. One has four species distributed in Macaronesia, the Mediterranean and Europe; *Dirina canariensis* constitutes the sister group to the other species in that group. The second basal group contains the rest of the species with the species pair *Dirina arabica* and *D. immersa* as the sister group to the rest of the species in that group.

Surprisingly, the characteristic feature of monocarpocentral, solitary ascomata (Tehler 1990), [referred to below as *immersed ascomata* since they are always immersed (Fig. 7F)] seems to have evolved independently several times in *Dirina* as it is found in the unrelated species *D. candida*, *D. immersa*, *D. insulana* and *D. mexicana* (Fig. 1). The evolution involving immersed ascomata in *Dirina* has obviously, on several occasions, been subjected to either gains or losses. All species in *Roccella*, the sister genus to *Dirina*, have pluricarpocentral discothecia; thus, by definition, immersed ascomata are derived, and the most parsimonious hypothesis is that they have evolved on four separate occasions. However, taking the broader view including the whole order *Arthoniales* (Ertz & Tehler 2011), it is more reasonable to suggest that the discothecium is a derived feature that evolved once at the node following *Enterographa* (Ertz & Tehler 2011), which is the sister group to the rest of *Roccellaceae* and a genus with immersed ascomata. The overwhelming majority of the species in *Roccellaceae* have

ascomata of the discothecium type, including *Sigridea*, *Roccella*, *Dirina*, *Lecanactis*, *Roccellina* and *Dendrographa*. One genus, *Syncesia*, has pluricarpocentral synascomata. Immersed ascomata are more commonly seen outside *Roccellaceae*, in other families of *Arthoniales* such as *Opographaceae*, *Roccellographaceae* and *Lecanographaceae*. Thus, a more parsimonious and plausible hypothesis is that the immersed ascomata seen in *Dirina* are all reversals to a plesiomorphic state.

Asexual morphs earlier described at the rank *forma* are no longer recognized as taxonomic units: *Dirina catalinariae* f. *sorediata*, *D. insulana* f. *sorediata*, *D. massiliensis* f. *sorediata*, *D. paradoxa* ssp. *paradoxa* f. *sorediata* and *D. massiliensis* f. *aponina*. None of these taxa constitute monophyletic, evolutionary units but are rather considered conspecific expressions of dispersal strategies since they are inclusive and nested in sexual lineages. Examples of such polymorphic lineages have been repeatedly investigated, described and exhaustively discussed in earlier papers and will not be further discussed here. We now take the final consequence of these results and cease to recognize any polymorphic sorediate taxa (Tehler 1982) included in the so-called species pair concept (Poelt 1970, 1972), unless they can be shown to have evolved into distinct monophyletic lineages.

The *Dirina pacifica* specimens from Hawaii are closely related to the specimens from the Galapagos, and the two sample groups form a sister pair. The great distance between Hawaii and the Galapagos, and the fact that the two sequenced specimens from the Galapagos form a significantly supported sister pair relationship to a likewise significantly supported sister group of specimens from Hawaii, would make a reasonable argument to recognize the two as distinct species. The specimens from Hawaii contain the unknown secondary product H, but we have not been able to confirm whether this product is also present in the Galapagos specimens since we have too little material available for TLC analyses. However, there are no morphological characters to distinguish the sample specimens and furthermore the DNA sampling from the Galapagos is too scanty,

with only two specimens to support a two-species hypothesis. For the time being we will consider them conspecific.

The sister species to *Dirina pacifica* is *D. paradoxa*, originating from the Caribbean. Interestingly, the related genus *Syncesia* (*Roccellaceae*) contains two species, *S. hawaiiensis* and *S. farinacea*, which show a similar pattern to that of *D. pacifica* and *D. paradoxa*. We have sequences from RPB2 and LSU of *Syncesia hawaiiensis*, as well as a *Syncesia* specimen collected in the Galapagos, which show that the Hawaiian specimens and the Galapagos specimen form a supported sister pair (A. Tehler, D. Ertz & M. Irestedt, unpublished data). *Syncesia farinacea* is mainly distributed in the Caribbean and the South American mainland. Geographically, we seem to have two similar but independent distribution patterns to indicate a Caribbean-Galapagos-Hawaii connection: firstly, the two *Dirina* populations in Hawaii-Galapagos and their sister species *D. paradoxa* in the Caribbean; and secondly the *Syncesia hawaiiensis* and the specimen from the Galapagos, and their sister species *S. farinacea* in the Caribbean. Unfortunately, we have no sequenced specimens from the Caribbean *Syncesia farinacea* population to corroborate that hypothesis.

The three saxicolous and three corticolous specimens of *Dirina madagascariensis* were divided into two clades and may thus actually represent two species. However, as with *D. pacifica*, we believe that three investigated specimens each are too few upon which to set up a two-species hypothesis. Furthermore, only the saxicolous clade receives full statistical PP and PJ support, whereas the corticolous clade receives somewhat less PJ support of 90%. Thus, for the time being, we refrain from describing separate corticolous and saxicolous species until such a hypothesis can be tested by the analysis of more specimens.

Most *Dirina* species are endemic or have restricted distributions but some very similar species are sympatric, most notably *Dirina monothalamia* and *D. teichiodes*. When saxicolous, these two species contain no discrete morphological characters on which they can be reliably distinguished from one another,

and we have found no way to safely differentiate between them other than by examining DNA-data. Another example is the sterile, sorediate morph of *Dirina fallax* which has been collected a few times in the Canary Islands, where it is morphologically and chemically indistinguishable from sterile, sorediate specimens of *D. canariensis*. Other recent phylogenetic studies on lichen species complexes also showed that morphological and chemical data might be insufficient to delimit species boundaries in several genera, suggesting that species diversity has in many cases been underestimated in the past (Divakar et al. 2010; del Prado et al. 2011; Leavitt et al. 2011; Lumbsch & Leavitt 2011; Molina et al. 2011; Núñez-Zapata et al. 2011; Orange 2012; Pino-Bodas et al. 2012).

Biogeography

The main geographical pattern suggests that vicariance has played an important role in the distribution and radiation of the species in *Dirina*. For this to be the case, we have to assume that *Dirina* is very old and that speciation is generally slow. Twelve species from the Old World are distributed in Southern and Central Europe, Macaronesia including the Atlantic islands Ascension and St. Helena, and mainland Africa in Angola; five species are distributed in the region of the Indian Ocean, Socotra, northern India, Mauritius and Madagascar; and finally there is a monophyletic group of five species present in the Americas and islands of the Pacific Ocean (Figs 1–4).

The most basal species in *Dirina* is *D. candida*, which is present in the south-west Mediterranean region, and the most basal species in *Roccella* is *R. allorgei* from the northern Macaronesian region including southern Portugal, indicating that this region is the centre of origin and the distribution area of the ancestor to the clade including both *Dirina* and *Roccella*. The general distribution pattern for *Dirina* is similar to that in *Roccella*, with a paraphyletic group of Old World species and a monophyletic group of American species derived from one of the Old World groups, notably a group that includes many Macaronesian species. In

Roccella, vicariance was proposed to explain its American–Macaronesian distribution (Tehler et al. 2009b). The ancestor to the monophyletic genus *Roccella* was suggested to have been distributed over an ancient geographical region that successively broke up into the New and Old World areas. The American and Macaronesian populations became more and more isolated from one another during the late Jurassic period, 160–145 mya, and finally, in the late Cretaceous period, 100–65 mya, they became fully separated through the formation of the South Atlantic Ocean. Successively *Roccella* established itself and radiated into the present species in the two current distribution areas.

The pattern in *Dirina* is very interesting since it is not only the sister group to *Roccella*, but it reveals a similar American–Macaronesian distribution pattern to *Roccella*, clearly indicating that both genera have independent but similar evolutionary histories. Similar to *Roccella*, *Dirina* also contains a significantly supported monophyletic group with five American species, *D. catalinariae* through *D. paradoxa*, in a sister group relationship with a likewise significantly supported monophyletic group including Old World and mainly Macaronesian species. Hence, two independently evolved genera, *Dirina* and *Roccella*, support the same vicariance pattern.

The vicariance hypothesis determined by plate tectonics anticipates the group including *Dirina* and *Roccella*, altogether 48 species, to be extraordinarily old. The precursors to the genera must have evolved or had already evolved along the coasts of the western Tethys Sea, and they must have had an established distribution at the opening of the Atlantic Ocean when Pangaea broke up into Laurasia and Gondwana in the Mesozoic period over 200 million years ago, making them older than the first angiosperms. On the one hand, this implies a very slow evolutionary rate compared with many other organisms, and furthermore that the easy cosmopolitan dispersal in lichens is not always the rule. On the other hand, as a reflection of the fact that the hot-spot islands of the Galapagos never connected to the mainland and despite the fact that conservative evolution would have prevailed for these organisms over time, it is still likely that

dispersal and adaptive radiation also played a role in the evolution of some species groups, as for example the rapid evolution of the *Roccella galapagoensis*-complex (Tehler *et al.* 2009a) once the ancestor succeeded in spreading to the islands.

Interestingly, and also in support of the hypothesis of vicariance, neither *Dirina* nor *Roccella* have in any successful way succeeded in dispersing and establishing distribution areas much outside what can be considered the fragments of the ancient region of the Tethys Sea, now mainly present in the Northern Hemisphere. Remarkably, very few species are found south of the equator, and for no obvious reason *Dirina*, as well as *Roccella*, are both absent from areas outside the ancient region of the former Tethys Sea that otherwise would obviously provide perfect growing conditions with respect to both climate and habitat, such as the areas on the South American West Coast south of the equator, South Africa and the west and south coasts of Australia. The only real exception to this pattern is the widespread species *R. montagnei*, which has evidently succeeded in dispersing into South Africa and a few localities on the north-west coast of Australia (Tehler *et al.* 2010). In *Dirina*, only four species occur in the Southern Hemisphere at any notable distance south of the equator, each endemic to its particular locality: *D. jamesii* (the South Atlantic Islands of St. Helena and Ascension), *D. angolana* (Angola), *D. astridae* (Mauritius) and *D. madagascariensis* (Madagascar).

However, there are some important exceptions and differences between *Dirina* and *Roccella*. Firstly, *Dirina* includes several instances with long distance dispersal not seen in *Roccella*. Most notably, two dispersal events towards America must have occurred, of which one must have been prior to the evolution of the monophyletic American group, namely that of *Dirina badia* to Peru, possibly from an ancient region now split up into the Mediterranean and Socotra Island. The other, and probably much more recent American dispersal event, is that of *D. approximata* in the Galapagos originating from a group of species now present in southern

Macaronesia. In addition, a long distance dispersal event must be proposed for *Dirina madagascariensis* going in the other direction back to the Old World, probably some time during the successive break into the New and Old World distribution areas. That scenario is indicated by the fact that *D. madagascariensis* is included with significant support in the monophyletic American group, but unresolved or only poorly supported as sister species to the rest of the American species within that group. Dispersal has obviously also occurred among the Old World *Dirina* species, most notably species in a poorly supported group containing *D. angolana* through *D. astridae* within the sister group to the American species otherwise containing Macaronesian species. However, two of the species in that group, *D. angolana* and *D. jamesii*, which are distributed in Angola and the Atlantic islands respectively, may simply be the result of a natural extension of the Macaronesian region into these areas during the opening of the South Atlantic Ocean. A parallel is seen in *Roccella* and the otherwise mainly Macaronesian species *R. tinctoria*, which has an out-post locality in Angola.

Recent dating studies (Lücking *et al.* 2009; Berbee & Taylor 2010; Amo de Paz *et al.* 2011), which would probably estimate the *Roccellaceae* at around 100 mya, do not agree with the assumption that vicariance through plate tectonics is responsible for the similar distribution pattern in the two independently evolved lineages, *Dirina* and *Roccella*. These dating studies extrapolated to the genera *Roccella* and *Dirina* would estimate that clade to be at the most 50 mya and, as a consequence, the *Dirina* and *Roccella* nodes would be considerably younger, perhaps in the range of 25 mya. Thus, even if molecular dating studies have been questioned and should be treated cautiously (Ayala 1999; Schwartz & Maresca 2006), such dating analyses contradict, and differ from, the proposition of plate tectonics explaining the American vs Old World distribution pattern that we see in *Dirina* and *Roccella* by a range of nearly two hundred million years. Assuming that the correct dating of *Dirina* and *Roccella* is in the range 20–30 mya, then molecular dating

analyses clearly suggest long distance dispersal to explain the cross Atlantic distribution of these two genera.

Even though most of the species in both *Dirina* and *Roccella* have developed means of both sexual dispersal (ascospores) and vegetative dispersal (soredia), they usually have very narrow distribution areas, clearly indicating a restricted mobility which in turn may indicate antiquity. The high number of endemic species in *Dirina* and *Roccella* may come as a result of this immobility. The majority of the species in both *Dirina* and *Roccella* are endemics, or even point endemics, for example *D. astridae* and *R. boryi* (Mauritius), *D. arabica* and *R. phycopsioides* (Socotra), *D. mexicana* and *R. bajasurensis* (Baja California), the latter distributed in only a 100 km western coast stretch in the most southern tip of Baja California.

Nonetheless, a few species in *Dirina* have obviously had the capability to move over oceanic distances in more recent times, thus long distance dispersal with subsequent regional species radiation is certainly plausible. In a dispersal scenario, to explain the transatlantic distribution, two ancestral species in *Dirina* and *Roccella* would independently from one another make the jump across the Atlantic Ocean, which by that time had opened to a considerable extent. Subsequently both of these species radiated into the five American *Dirina* species and nine American *Roccella* species that we see today. A similar scenario has been proposed for the *Xanthoparmelia pulla* group on the basis of a molecular dating study (Amo de Paz *et al.* 2012).

The distribution patterns in *Dirina* and *Roccella* need to be studied in more detail. All species in both *Dirina* and *Roccella* are mainly restricted to maritime coastal habitats and are often found endemic to islands such as the Galapagos Islands, the Canary Islands, the Azores, Socotra and Mauritius. For these islands, the geological age can be reasonably well determined and thus could serve as exact calibration points for the nodes in a phylogenetic tree. A molecular dating analysis is currently prepared for the *Arthoniales-*

Roccellaceae and will be presented in a forthcoming publication (A. Tehler & M. Irested, unpublished data).

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Appendix 1. *Species and voucher information of Dirina specimens used in phylogenetic analyses. All sequences are new to this study except those with GenBank accession numbers in italics which were published previously.*

Species	Locality	Year	Collector	Collector's number	Herbarium & number	β-tub	GenBank ITS	Accession LSU	Number RPB2
<i>Dirina angolana</i>	Angola	2009	<i>A. Tehler</i>	9703	S-F210727	KC108423	KC107837	KC108230	KC108034
<i>D. angolana</i>	Angola	2009	<i>A. Tehler</i>	9716	S-F210728	KC108424	KC107838	KC108231	KC108035
<i>D. angolana</i>	Angola	2009	<i>A. Tehler</i>	9730	S-F210729	KC108425	KC107839	KC108232	KC108036
<i>D. approximata</i>	Galapagos Islands	2010	<i>A. Yáñez</i>	2022-155	S-F210738	KC108431	KC107845	KC108237	KC108041
<i>D. approximata</i>	Galapagos Islands	2010	<i>A. Yáñez</i>	2022-156	S-F210738	KC108432	KC107846	KC108238	KC108042
<i>D. approximata</i>	Galapagos Islands	2011	<i>A. Yáñez</i>	2141	S-F210742	KC108433	KC107847	KC108239	KC108043
<i>D. approximata</i>	Galapagos Islands	2005	<i>A. Tehler</i>	8671	S-L72898	KC108426	KC107840	<i>EF081388</i>	<i>DQ987631</i>
<i>D. approximata</i>	Galapagos Islands	2005	<i>A. Tehler</i>	8702	S-F96192	KC108427	KC107841	KC108233	KC108037
<i>D. approximata</i>	Galapagos Islands	2005	<i>A. Tehler</i>	8716	S-F96203	KC108428	KC107842	KC108234	KC108038
<i>D. approximata</i>	Galapagos Islands	2010	<i>F. Bungartz</i>	9205	S-F210735	KC108429	KC107843	KC108235	KC108039
<i>D. approximata</i>	Galapagos Islands	2011	<i>F. Bungartz</i>	9485	S-F210737	KC108430	KC107844	KC108236	KC108040
<i>D. arabica</i>	Socotra	2008	<i>A. Tehler</i>	9301	S-F210762	KC108434	KC107848	KC108240	KC108044
<i>D. arabica</i>	Socotra	2008	<i>A. Tehler</i>	9323	S-F210763	KC108435	KC107849	KC108241	KC108045
<i>D. arabica</i>	Socotra	2008	<i>A. Tehler</i>	9339	S-F210764	KC108436	KC107850	KC108242	KC108046
<i>D. astridae</i>	Mauritius	2003	<i>A. Tehler</i>	8502	S-L55012	KC108437	KC107851	KC108243	KC108047
<i>D. astridae</i>	Mauritius	2003	<i>A. Tehler</i>	8503	S-L55013	KC108438	KC107852	KC108244	KC108048
<i>D. astridae</i>	Mauritius	2003	<i>A. Tehler</i>	8511	S-L55022	KC108439	KC107853	KC108245	KC108049
<i>D. astridae</i>	Mauritius	2003	<i>A. Tehler</i>	8524	S-L55029	KC108440	<i>EF081375</i>	<i>EF081386</i>	<i>DQ987629</i>
<i>D. badia</i>	Peru	2006	<i>A. Tehler</i>	8888	S-F210765	KC108441	KC107854	KC108246	KC108050
<i>D. badia</i>	Peru	2006	<i>A. Tehler</i>	8898	S-F210766	KC108442	KC107855	KC108247	KC108051
<i>D. badia</i>	Peru	2006	<i>A. Tehler</i>	8917	S-F210767	KC108443	KC107856	KC108248	KC108052
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10300	S-F210768	KC108444	KC107857	KC108249	KC108053
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10307	S-F210769	KC108445	KC107858	KC108250	KC108054
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10308-7	S-F210770	KC108446	KC107859	KC108251	KC108055
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10308-8	S-F210770	KC108447	KC107860	KC108252	KC108056
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10313	S-F210771	KC108448	KC107861	KC108253	KC108057
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10326	S-F210772	KC108449	KC107862	KC108254	KC108058
<i>D. canariensis</i>	Canary Islands	2011	<i>A. Tehler</i>	10327	S-F210773	KC108450	KC107863	KC108255	KC108059
<i>D. canariensis</i>	Canary Islands	2011	<i>D. Ertz</i>	16143-135	BR-7630-73	KC108452	KC107865	KC108257	KC108061
<i>D. canariensis</i>	Canary Islands	2011	<i>D. Ertz</i>	16143-136	BR-7630-73	KC108453	KC107866	KC108258	KC108062
<i>D. canariensis</i>	Canary Islands	2011	<i>D. Ertz</i>	16185-133	BR-7639-82	KC108455	KC107864	KC108256	KC108060
<i>D. canariensis</i>	Canary Islands	2011	<i>D. Ertz</i>	16185-158	BR-7639-82	KC108451	KC107868	KC108260	KC108064
<i>D. canariensis</i>	Canary Islands	2011	<i>D. Ertz</i>	16255	BR-7774-23	KC108454	KC107867	KC108259	KC108063
<i>D. candida</i>	Spain	2007	<i>A. Tehler</i>	9004	S-F66088	KC108456	KC107869	KC108261	KC108065
<i>D. candida</i>	Spain	2007	<i>A. Tehler</i>	9011	S-F66077	KC108457	KC107870	KC108262	KC108066
<i>D. candida</i>	Spain	2007	<i>A. Tehler</i>	9015	S-F66049	KC108458	KC107871	KC108263	KC108067
<i>D. candida</i>	Spain	2007	<i>A. Tehler</i>	9017	S-F66051	KC108459	KC107872	KC108264	KC108068
<i>D. candida</i>	Gibraltar	2009	<i>A. Tehler</i>	9805	S-F210774	KC108460	KC107873	KC108265	KC108069
<i>D. catalinariae</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9086	S-F210776	KC108461	KC107874	KC108266	KC108070
<i>D. catalinariae</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9087	S-F148386	KC108462	<i>GU137787</i>	<i>GU137909</i>	<i>GU137543</i>

Appendix 1. *Continued*

Species	Locality	Year	Collector	Collector's number	Herbarium & number	β-tub	GenBank ITS	Accession LSU	Number RPB2
<i>D. catalinariae</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9127	S-F210778	KC108463	KC107875	KC108267	KC108071
<i>D. catalinariae</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9146	S-F210780	KC108464	KC107876	KC108268	KC108072
<i>D. catalinariae</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9151	S-F210781	KC108465	KC107877	KC108269	KC108073
<i>D. catalinariae</i>	USA, California	2008	<i>A. Tehler</i>	9419	S-F210782	KC108466	KC107878	KC108270	KC108074
<i>D. ceratoniae</i>	Spain	2007	<i>A. Tehler</i>	9020	S-F66043	KC108467	KC107879	KC108271	KC108075
<i>D. ceratoniae</i>	Spain	2007	<i>A. Tehler</i>	9021	S-F66044	KC108468	<i>GU137788</i>	<i>GU137910</i>	<i>GU137544</i>
<i>D. ceratoniae</i>	Spain	2007	<i>A. Tehler</i>	9047	S-F66048	KC108469	<i>Fj639084</i>	<i>Fj638966</i>	<i>Fj639025</i>
<i>D. ceratoniae</i>	France	2008	<i>A. Tehler</i>	9510	S-F210784	KC108470	KC107880	KC108272	KC108076
<i>D. ceratoniae</i>	France	2008	<i>A. Tehler</i>	9527	S-F210785	KC108471	KC107881	KC108273	KC108077
<i>D. ceratoniae</i>	Italy	2008	<i>A. Tehler</i>	9617	S-F176053	KC108472	KC107882	KC108274	KC108078
<i>D. ceratoniae</i>	Italy	2008	<i>A. Tehler</i>	9627	S-F176058	KC108473	KC107883	KC108275	KC108079
<i>D. ceratoniae</i>	Italy	2008	<i>A. Tehler</i>	9632	S-F176066	KC108474	KC107884	KC108276	KC108080
<i>D. ceratoniae</i>	Spain	2009	<i>A. Tehler</i>	9814	S-F210786	KC108475	KC107885	KC108277	KC108081
<i>D. ceratoniae</i>	Spain	2009	<i>A. Tehler</i>	9816	S-F210787	KC108476	KC107886	KC108278	KC108082
<i>D. ceratoniae</i>	Canary Islands	2009	<i>D. Ertz</i>	14024	BR-2468-52	KC108477	KC107887	KC108279	KC108083
<i>D. ceratoniae</i>	France, Corse	2011	<i>D. Ertz</i>	16367	BR-7901-53	KC108478	KC107888	KC108280	KC108084
<i>D. ceratoniae</i>	Portugal	2011	<i>D. Ertz</i>	16997	BR-9826-38	KC108479	KC107889	KC108281	KC108085
<i>D. cretacea</i>	Italy	2008	<i>A. Tehler</i>	9605	S-F176095	KC108480	KC107890	KC108282	KC108086
<i>D. cretacea</i>	Italy	2008	<i>A. Tehler</i>	9607	S-F176075	KC108481	KC107891	KC108283	KC108087
<i>D. cretacea</i>	Italy	2008	<i>A. Tehler</i>	9614	S-F176051	KC108482	KC107892	KC108284	KC108088
<i>D. cretacea</i>	Italy	2008	<i>A. Tehler</i>	9622	S-F176096	KC108483	KC107893	KC108285	KC108089
<i>D. cretacea</i>	Italy	2008	<i>A. Tehler</i>	9626	S-F176057	KC108484	KC107894	KC108286	KC108090
<i>D. cretacea</i>	Spain	2009	<i>A. Tehler</i>	9817	S-F210788	KC108485	KC107895	KC108287	KC108091
<i>D. fallax</i>	Czech Republic	2009	<i>Jan Vondrák & O. Merkulova</i>	7172	CBFS	KC108496	KC107906	KC108298	KC108102
<i>D. fallax</i>	Czech Republic	2011	<i>Jan Vondrák</i>	8416-140	S-F184109	KC108493	KC107903	KC108295	KC108099
<i>D. fallax</i>	Czech Republic	2011	<i>Jan Vondrák</i>	8416-141	S-F184109	KC108494	KC107904	KC108296	KC108100
<i>D. fallax</i>	Czech Republic	2011	<i>Jan Vondrák</i>	8423	CBFS	KC108495	KC107905	KC108297	KC108101
<i>D. fallax</i>	France	2008	<i>A. Tehler</i>	9521	S-F210789	KC108486	KC107896	KC108288	KC108092
<i>D. fallax</i>	France	2008	<i>A. Tehler</i>	9522	S-F210790	KC108487	KC107897	KC108289	KC108093
<i>D. fallax</i>	Spain	2009	<i>A. Tehler</i>	9801	S-F210791	KC108488	KC107898	KC108290	KC108094
<i>D. fallax</i>	Spain	2009	<i>A. Tehler</i>	9811	S-F210792	KC108489	KC107899	KC108291	KC108095
<i>D. fallax</i>	Spain	2009	<i>A. Tehler</i>	9812	S-F210793	KC108490	KC107900	KC108292	KC108096
<i>D. fallax</i>	Portugal	2010	<i>A. Tehler</i>	10208	S-F210794	KC108491	KC107901	KC108293	KC108097
<i>D. fallax</i>	Canary Islands	2011	<i>D. Ertz</i>	16186-139	BR-7640-83	KC108492	KC107902	KC108294	KC108098
<i>D. fallax</i>	Canary Islands	2011	<i>D. Ertz</i>	16186-159	BR-7640-83	KC108502	KC107912	KC108304	KC108107
<i>D. fallax</i>	France, Corse	2011	<i>D. Ertz</i>	16397	BR-7931-83	KC108500	KC107910	KC108302	KC108105
<i>D. fallax</i>	France, Corse	2011	<i>D. Ertz</i>	16413	BR-7938-90	KC108501	KC107911	KC108303	KC108106
<i>D. fallax</i>	France, Corse	2011	<i>D. Ertz</i>	16421	BR-7946-01	KC108497	KC107907	KC108299	
<i>D. fallax</i>	France, Corse	2011	<i>D. Ertz</i>	16459	BR-2013-91	KC108499	KC107909	KC108301	KC108104
<i>D. fallax</i>	France, Corse	2011	<i>D. Ertz</i>	16506	BR-2025-06	KC108498	KC107908	KC108300	KC108103
<i>D. fallax</i>	Portugal	2011	<i>D. Ertz</i>	16905	BR-7738-84	KC108503	KC107913	KC108305	KC108108

Appendix 1. Continued

Species	Locality	Year	Collector	Collector's number	Herbarium & number	β -tub	GenBank ITS	Accession LSU	Number RPB2
<i>D. fallax</i>	Portugal	2011	<i>D. Ertz</i>	16921	BR-7729-75	KC108504	KC107914	KC108306	KC108109
<i>D. fallax</i>	Portugal	2011	<i>D. Ertz</i>	16922	BR-7726-72	KC108505	KC107915	KC108307	KC108110
<i>D. fallax</i>	Portugal	2011	<i>D. Ertz</i>	16929	BR-7765-14	KC108506	KC107916	KC108308	KC108111
<i>D. fallax</i>	Portugal	2011	<i>D. Ertz</i>	17024	BR-9784-93	KC108507	KC107917	KC108309	KC108112
<i>D. immersa</i>	Socotra	2008	<i>A. Tehler</i>	9300	S-F210796	KC108508	KC107918	KC108310	KC108113
<i>D. immersa</i>	Socotra	2008	<i>A. Tehler</i>	9322	S-F210797	KC108509		KC108311	KC108114
<i>D. immersa</i>	Socotra	2008	<i>A. Tehler</i>	9327	S-F210798	KC108510	KC107919	KC108312	KC108115
<i>D. indica</i>	Socotra	2008	<i>A. Tehler</i>	9312	S-F210799	KC108511	KC107920	KC108313	KC108116
<i>D. indica</i>	India, Gurajat	2009	<i>J. Rawal</i>	9011520-112	S-F225426	KC108513	KC107922		KC108118
<i>D. indica</i>	India, Gurajat	2009	<i>J. Rawal</i>	9011520-116	S-F225420	KC108515	KC107924	KC108314	KC108120
<i>D. indica</i>	India, Gurajat	2009	<i>J. Rawal</i>	9011520-117	S-F225420	KC108516	KC107925		KC108121
<i>D. indica</i>	India, Gurajat	2009	<i>J. Rawal</i>	9011540-111	S-F225419	KC108512	KC107921		KC108117
<i>D. indica</i>	India, Gurajat	2009	<i>J. Rawal</i>	9011540-115	S-F225419	KC108514	KC107923		KC108119
<i>D. insulana</i>	Cape Verde	2009	<i>A. Tehler</i>	10011-9	S-F210800	KC108520	KC107929	KC108318	KC108125
<i>D. insulana</i>	Cape Verde	2009	<i>A. Tehler</i>	10011-10	S-F210800	KC108521	KC107930	KC108319	KC108126
<i>D. insulana</i>	Cape Verde	2010	<i>A. Tehler</i>	10053	S-F210801	KC108522	KC107931	KC108320	KC108127
<i>D. insulana</i>	Cape Verde	2010	<i>A. Tehler</i>	10080	S-F210802	KC108523	KC107932	KC108321	KC108128
<i>D. insulana</i>	Portugal	2010	<i>A. Tehler</i>	10207	S-F210812	KC108524	KC107933	KC108322	KC108129
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10212	S-F210803	KC108525	KC107934	KC108323	KC108130
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10213	S-F210804	KC108526	KC107935	KC108324	KC108131
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10219	S-F210805	KC108527	KC107936	KC108325	KC108132
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10220	S-F210806	KC108528	KC107937	KC108326	KC108133
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10220	S-F210806	KC108529	KC107938	KC108327	KC108134
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10224	S-F210807	KC108530	KC107939	KC108328	KC108135
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10230	S-F210808	KC108531	KC107940	KC108329	KC108136
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10237	S-F210809	KC108532	KC107941	KC108330	KC108137
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10248	S-F210810	KC108533	KC107942	KC108331	KC108138
<i>D. insulana</i>	Azores	2010	<i>A. Tehler</i>	10249	S-F210811	KC108534	KC107943	KC108332	KC108139
<i>D. insulana</i>	Canary Islands	2011	<i>A. Tehler</i>	10311	S-F210813	KC108535	KC107944	KC108333	KC108140
<i>D. insulana</i>	Canary Islands	2011	<i>A. Tehler</i>	10312	S-F210814	KC108536	KC107945	KC108334	KC108141
<i>D. insulana</i>	Madeira	2007	<i>D. Ertz</i>	10542	BR-0637-55	KC108517	KC107926	KC108315	KC108122
<i>D. insulana</i>	Madeira	2007	<i>D. Ertz</i>	10568	BR-0611-29	KC108518	KC107927	KC108316	KC108123
<i>D. insulana</i>	Canary Islands	2009	<i>D. Ertz</i>	13532	BR-8235-87	KC108519	KC107928	KC108317	KC108124
<i>D. insulana</i>	Canary Islands	2011	<i>D. Ertz</i>	16142	BR-7629-72	KC108537	KC107946	KC108335	KC108142
<i>D. insulana</i>	Canary Islands	2011	<i>D. Ertz</i>	16328	BR-7847-96	KC108538	KC107947	KC108336	KC108143
<i>D. insulana</i>	Portugal	2011	<i>D. Ertz</i>	17037	BR-9793-05	KC108539	KC107948	KC108337	KC108144
<i>D. jamesii</i>	Angola	2009	<i>A. Tehler</i>	9742-21	S-F210815	KC108542	KC107951	KC108340	KC108147
<i>D. jamesii</i>	Angola	2009	<i>A. Tehler</i>	9742-22	S-F210815	KC108543	KC107952	KC108341	KC108148
<i>D. jamesii</i>	South Atlantic Islands	2006	<i>A. Aptroot</i>	66423	S-F86655	KC108541	KC107950	KC108339	KC108146
<i>D. jamesii</i>	South Atlantic Islands	2006	<i>A. Aptroot</i>	66748	S-F86671	KC108540	KC107949	KC108338	KC108145
<i>D. madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13042	BR-7391-19	KC108544	KC107953	KC108342	KC108149

Appendix 1. *Continued*

Species	Locality	Year	Collector	Collector's number	Herbarium & number	β-tub	GenBank ITS	Accession LSU	Number RPB2
<i>D. madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13086	BR-8724-91	KC108547		KC108346	KC108153
<i>D. madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13095	BR-8734-04	KC108548	KC107957	KC108347	KC108154
<i>D. Madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13127	BR-8765-35	KC108545	KC107954	KC108343	KC108150
<i>D. madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13215	BR-7487-18		KC107955	KC108344	KC108151
<i>D. madagascariensis</i>	Madagascar	2008	<i>D. Ertz</i>	13216	S-F213217	KC108546	KC107956	KC108345	KC108152
<i>D. massiliensis</i>	Ukraine	2009	<i>Ĵ. Vondrák et al.</i>	7366	CBFS	KC108569	KC107978	KC108368	KC108175
<i>D. massiliensis</i>	Sweden	1998	<i>A. Tehler</i>	8045	S-L5650	KC108549	KC107958	KC108348	KC108155
<i>D. massiliensis</i>	Sweden	1998	<i>A. Tehler</i>	8047	S-L5651	KC108550	KC107959	KC108349	KC108156
<i>D. massiliensis</i>	Czech Republic	2011	<i>Ĵ. Vondrák</i>	8425	CBFS	KC108568	KC107977	KC108367	KC108174
<i>D. massiliensis</i>	Spain	2007	<i>A. Tehler</i>	9001	S-F66003	KC108551	KC107960	KC108350	KC108157
<i>D. massiliensis</i>	Spain	2007	<i>A. Tehler</i>	9008	S-F66006	KC108552	KC107961	KC108351	KC108158
<i>D. massiliensis</i>	Spain	2007	<i>A. Tehler</i>	9009	S-F66007	KC108553	KC107962	KC108352	KC108159
<i>D. massiliensis</i>	Spain	2007	<i>A. Tehler</i>	9026	S-F66008	KC108554	KC107963	KC108353	KC108160
<i>D. massiliensis</i>	Spain	2007	<i>A. Tehler</i>	9030	S-F66010	KC108555	KC107964	KC108354	KC108161
<i>D. massiliensis</i>	Sweden	2007	<i>A. Tehler</i>	9210	S-F96531	KC108556	KC107965	KC108355	KC108162
<i>D. massiliensis</i>	Sweden	2007	<i>A. Tehler</i>	9211	S-F96534	KC108557	KC107966	KC108356	KC108163
<i>D. massiliensis</i>	Sweden	2007	<i>A. Tehler</i>	9212	S-F96536	KC108558	KC107967	KC108357	KC108164
<i>D. massiliensis</i>	Sweden	2007	<i>A. Tehler</i>	9213	S-F96537	KC108559	KC107968	KC108358	KC108165
<i>D. massiliensis</i>	Sweden	2007	<i>A. Tehler</i>	9214	S-F96544	KC108560	KC107969	KC108359	KC108166
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9600	S-F176070	KC108561	KC107970	KC108360	KC108167
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9603	S-F176063	KC108562	KC107971	KC108361	KC108168
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9608	S-F176073	KC108563	KC107972	KC108362	KC108169
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9610	S-F176093	KC108564	KC107973	KC108363	KC108170
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9611	S-F176091	KC108565	KC107974	KC108364	KC108171
<i>D. massiliensis</i>	Italy	2008	<i>A. Tehler</i>	9635	S-F176062	KC108566	KC107975	KC108365	KC108172
<i>D. massiliensis</i>	Spain	2009	<i>A. Tehler</i>	9813	S-F210818	KC108567	KC107976	KC108366	KC108173
<i>D. massiliensis</i>	Portugal	2011	<i>D. Ertz</i>	16958	BR-7712-58	KC108570	KC107979	KC108369	KC108176
<i>D. massiliensis</i>	Portugal	2011	<i>D. Ertz</i>	16994	BR-9833-45	KC108571	KC107980	KC108370	KC108177
<i>D. massiliensis</i>	Portugal	2011	<i>D. Ertz</i>	16995	BR-9835-47	KC108572	KC107981	KC108371	KC108178
<i>D. massiliensis</i>	Portugal	2011	<i>D. Ertz</i>	16996	BR-9834-46	KC108573	KC107982	KC108372	KC108179
<i>D. mexicana</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9173	S-F210819	KC108574	KC107983	KC108373	KC108180
<i>D. mexicana</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9187	S-F210820	KC108575	KC107984	KC108374	KC108181
<i>D. mexicana</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9193	S-F210821	KC108576	KC107985	KC108375	KC108182
<i>D. mexicana</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9198	S-F210823	KC108577	KC107986	KC108376	KC108183
<i>D. monothalamia</i>	Cape Verde	2009	<i>A. Tehler</i>	10009	S-F210824	KC108578	KC107987	KC108377	KC108184
<i>D. monothalamia</i>	Cape Verde	2010	<i>A. Tehler</i>	10028-27	S-F210825	KC108579	KC107988	KC108378	KC108185
<i>D. monothalamia</i>	Cape Verde	2010	<i>A. Tehler</i>	10028-28	S-F210825	KC108580	KC107989	KC108379	KC108186
<i>D. monothalamia</i>	Cape Verde	2010	<i>A. Tehler</i>	10067	S-F210826	KC108581	KC107990	KC108380	KC108187
<i>D. monothalamia</i>	Cape Verde	2010	<i>A. Tehler</i>	10074	S-F210827	KC108582	KC107991	KC108381	KC108188
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10400	S-F210829	KC108584	KC107993	KC108383	KC108190
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10401	S-F210830	KC108585	KC107994	KC108384	KC108191
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10402	S-F210831	KC108586	KC107995	KC108385	KC108192

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Species	Locality	Year	Collector	Collector's number	Herbarium & number	β -tub	GenBank ITS	Accession LSU	Number RPB2
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10404	S-F210832	KC108593	KC108002	KC108392	KC108199
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10405-5	S-F210833	KC108587	KC107996	KC108386	KC108193
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10405-6	S-F210833	KC108588	KC107997	KC108387	KC108194
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10405-7	S-F210833	KC108589	KC107998	KC108388	KC108195
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10405-8	S-F210833	KC108590	KC107999	KC108389	KC108196
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10407-9	S-F210834	KC108594	KC108003	KC108393	KC108200
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10411-10	S-F210835	KC108591	KC108000	KC108390	KC108197
<i>D. monothalamia</i>	Senegal	2011	<i>A. Tehler</i>	10411-11	S-F210835	KC108592	KC108001	KC108391	KC108198
<i>D. monothalamia</i>	Cape Verde	2010	<i>A. Tehler</i>	10079-69	S-F210828	KC108583	KC107992	KC108382	KC108189
<i>D. pacifica</i>	Galapagos Islands	2005	<i>A. Tehler</i>	8726	S-L72897	KC108595	KC108004	<i>EF081387</i>	<i>DQ987630</i>
<i>D. pacifica</i>	Galapagos Islands	2011	<i>F. Bungartz</i>	9487	S-F210840	KC108603	KC108012	KC108401	KC108208
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10128-5	S-F210836	KC108596	KC108005	KC108394	KC108201
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10128-6	S-F210836	KC108597	KC108006	KC108395	KC108202
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10128-7	S-F210836	KC108598	KC108007	KC108396	KC108203
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10129-8	S-F210837	KC108599	KC108008	KC108397	KC108204
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10129-9	S-F210837	KC108600	KC108009	KC108398	KC108205
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10136	S-F210838	KC108602	KC108011	KC108400	KC108207
<i>D. pacifica</i>	Hawaii	2010	<i>A. Tehler</i>	10138	S-F210839	KC108601	KC108010	KC108399	KC108206
<i>D. pallescens</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9176	S-F210842	KC108604	KC108013	KC108402	KC108209
<i>D. pallescens</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9181	S-F210843	KC108605	KC108014	KC108403	KC108210
<i>D. pallescens</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9189	S-F210844	KC108606	KC108015	KC108404	KC108211
<i>D. paradoxa</i>	Lesser Antilles	2006	<i>A. Tehler</i>	8930	S-F210845	KC108607	KC108016	KC108405	KC108212
<i>D. paradoxa</i>	Lesser Antilles	2006	<i>A. Tehler</i>	8931	S-F210846	KC108608	KC108017	KC108406	KC108213
<i>D. paradoxa</i>	Lesser Antilles	2006	<i>A. Tehler</i>	8932	S-F210847	KC108609	KC108018	KC108407	KC108214
<i>D. paradoxa</i>	Lesser Antilles	2006	<i>A. Tehler</i>	8947	S-F210850	KC108610	KC108019	KC108408	KC108215
<i>D. paradoxa</i>	USA, Florida	2010	<i>A. Tehler</i>	10113-3	S-F210851	KC108611	KC108020	KC108409	KC108216
<i>D. paradoxa</i>	USA, Florida	2010	<i>A. Tehler</i>	10113-4	S-F210851	KC108612	KC108021	KC108410	KC108217
<i>D. sorocarpa</i>	Cape Verde	2009	<i>A. Tehler</i>	10010	S-F210852	KC108613	KC108022	KC108411	KC108218
<i>D. sorocarpa</i>	Cape Verde	2009	<i>A. Tehler</i>	10017	S-F210853	KC108614	KC108023	KC108412	KC108219
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10026	S-F210855	KC108615	KC108024	KC108413	KC108220
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10027-25	S-F210854	KC108616	KC108025	KC108414	KC108221
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10027-26	S-F210854	KC108617	KC108026	KC108415	KC108222
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10041	S-F210856	KC108618	KC108027	KC108416	KC108223
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10051	S-F210857	KC108619	KC108028	KC108417	KC108224
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10052	S-F210858	KC108620	KC108029	KC108418	KC108225
<i>D. sorocarpa</i>	Cape Verde	2010	<i>A. Tehler</i>	10060	S-F210859	KC108621	KC108030	KC108419	KC108226
<i>D. teichiodes</i>	Cape Verde	2010	<i>A. Tehler</i>	10059	S-F210860	KC108622	KC108031	KC108420	KC108227
<i>D. teichiodes</i>	Cape Verde	2010	<i>A. Tehler</i>	10071	S-F210861	KC108623	KC108032	KC108421	KC108228
<i>D. teichiodes</i>	Cape Verde	2010	<i>A. Tehler</i>	10079-70	S-F210862	KC108624	KC108033	KC108422	KC108229
<i>Roccella allorgeri</i>	Azores	2000	<i>A. Tehler</i>	8163	S-L12507	KC108625	<i>F7639085</i>	<i>EF081397</i>	<i>DQ987640</i>
<i>R. gracilis</i>	Mexico, Baja California	2007	<i>A. Tehler</i>	9195	S-F114045	KC108626	<i>F7639127</i>	<i>F7639009</i>	<i>F7639068</i>
<i>R. tinctoria</i>	Canary Islands	2000	<i>A. Tehler</i>	8257	S-L14796	KC108627	<i>A7634040</i>	<i>EF081428</i>	<i>DQ987671</i>