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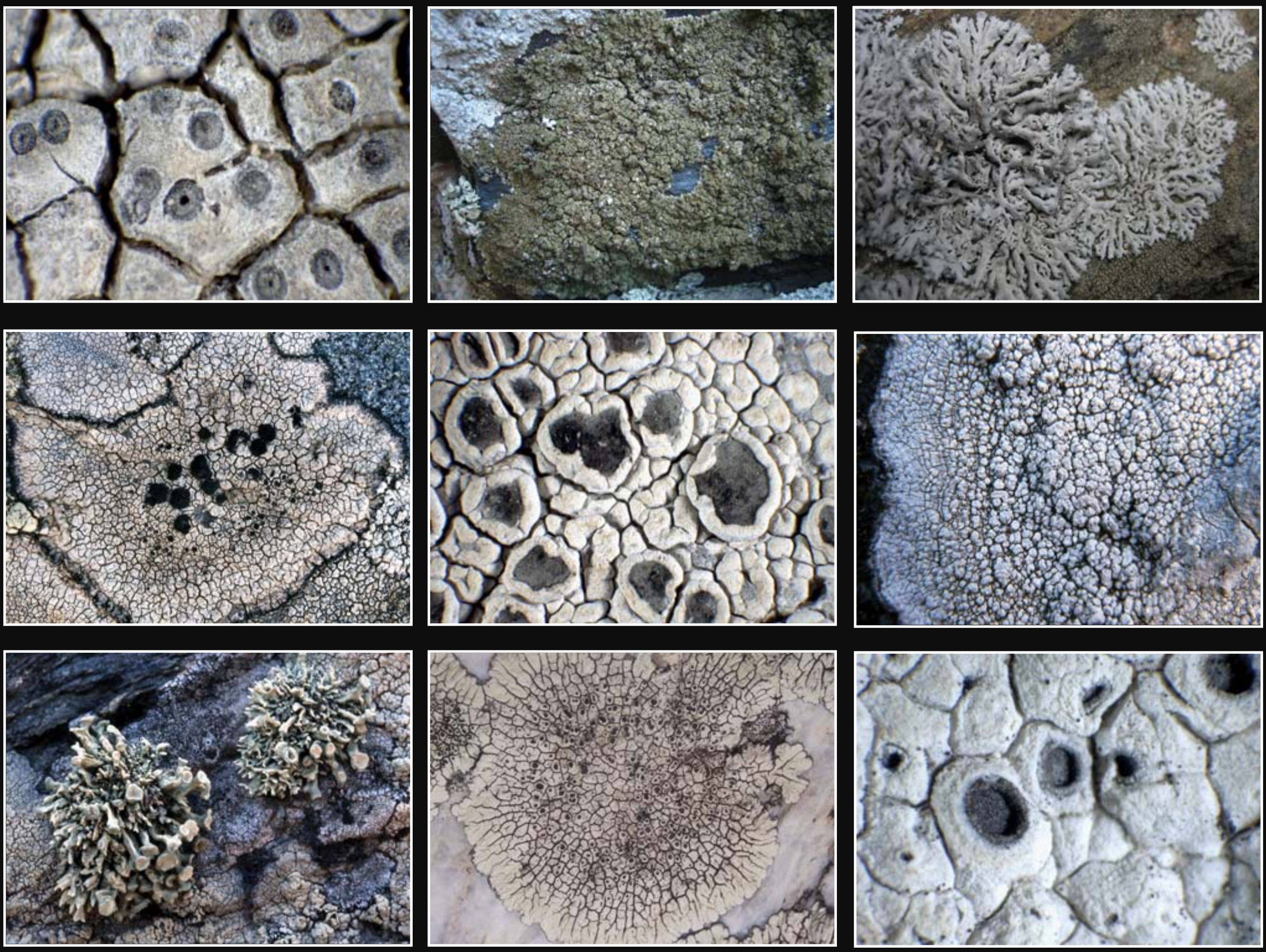
TESI DOCTORAL



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Barcelona 2012

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Memòria presentada per Samantha Fernández Brime
per optar al grau de Doctor per la Universitat de Barcelona

Programa de Doctorat de Biologia Vegetal corresponent al
bienni 2005-2007 del Departament de Biologia Vegetal
de la Facultat de Biologia de la Universitat de Barcelona

Directors: Dr. Francesc Xavier Llimona Pagès i Dra. Ester Gaya Bellés

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Samantha Fernández Brime Dr. Xavier Llimona Pagès Dra. Ester Gaya Bellés

Barcelona, Gener de 2012

Als meus pares i al meu germà.

Y a Ricardo.

Where ferns or flowers

could find no safety from the drenching showers,

there hung they brilliant lichens, and the sun

bade radiant hues dwell on them

Jessie M. E. Saxby

Agraïments

Sembla mentida que finalment ho pugui dir "He acabat la tesi!!!". Sóc molt conscient de la quantitat de persones que m'han ajudat i recolzat durant aquest viatge acadèmic, científic i personal. El meu petit homenatge, es dedicar-vos unes línies a tots i totes els que, d'alguna forma o altra, m'heu acompanyat.

En primer lloc, el meu més sincer agraïment al meus dos directors, el Dr. Xavier Llimona i la Dra. Ester Gaya. A en Xavier, perquè des de les classes de Micologia durant la carrera em vas transmetre la passió pels líquens i els fongs, i pels petits tresors que ens amaga la natura. Moltes gràcies per confiar en mi quan era estudiant i "enredar-me" en tot això, per la teva dedicació i compromís i, sobretot, per la teva inesgotable paciència i tendresa. I a l'Ester, pel gran esforç professional que has fet encabint la direcció d'aquesta tesi en la infinitat de feina que sempre estàs fent. Has estat incondicionalment sempre que t'he necessitat, tant a nivell científic com personal; fos l'hora que fos, mai has dit no. La teva capacitat de treball i la teva energia inesgotable són inspiradores, i han estat fonamentals per tirar endavant.

Gràcies a tot l'equip de liquenologia que m'ha acollit aquests anys. Al Néstor Hladun, t'agraeixo enormement el suport logístic, gràcies al qual he pogut disposar, entre d'altres coses, d'un laboratori de molecular a Botànica; al Pere Navarro-Rosinés, per l'ajuda i les ensenyances en l'estudi dels fongs liquenícoles; a la Mireia Giralt, per la revisió dels exemplars dels gèneres *Amandinea*, *Buellia* i *Rinodina*; a la Mercedes Barbero, per ensenyar-me a utilitzar les tècniques de cromatografia en capa fina; a l'Antonio Gómez-Bolea, per la confiança que has dipositat en mi en els projectes en els que hem treballat plegats. Un agraïment especial és per l'Esteve Llop, per les enriquidores discussions taxonòmiques i, sobretot, perquè has estat un gran company. I per últim, però no menys importants, per les liqueno-nenes, Diana i Gemma, que heu estat les meves companyes d'aventures durant aquests anys en els que hem compartit hores de despatx, excursions, congressos... us trobaré molt a faltar!!!

Estic molt agraïda a la comunitat de liquenòlegs nacional i internacional, especialment a Claude Roux, Cécile Gueidan, Thorsten Lumbsch, Andreas Frisch, Robert Lücking i Eimy Rivas Plata, per resoldre els meus dubtes taxonòmics o nomenclaturals, per enviar-me manuscrits inèdits i per compartir amb mi el seu coneixement.

Aquest ha estat un molt bon lloc de treball, gràcies sobretot a tots els companys i companyes de la unitat de Botànica, que han fet les jornades laborals molt més amenes: Núria, Berta, Montse, Aaron, Romero, Roser, Josep Maria, Estela, Oriol... Un agraïment especial al meu veí de despatx, José Manuel Blanco, per l'ajuda amb les qüestions estadístiques, a l'Albert Ferré, per l'ajuda en l'elaboració del mapa inclòs en el treball florístic i, sobretot, a la Laura Armengot, per donar-me sempre un cop de mà quan ho he necessitat.

I would like to express a huge acknowledgment to the entire François Lutzoni lab, from Duke University, which hosted me during two visits in 2008 and 2009. Thank you so much François, for letting me be part of your group, for introducing me into the phylogenetics world, and for being an example of hard work and dedication. I am also very grateful to Jolanta Miadlikovska for your infinite patience helping me with phylogenetic analyses, to Frank Kauff for answer all my emails with methodological questions, and to Katalin Molnar, Bernie Ball, Suzanne Joneson, and Tami McDonald, for your help in the lab. I have a special acknowledgment to Molly McMullen, from the Duke's Herbarium, for being the most efficient curator I have ever met, but especially, for being such a great friend. Last, but not least, thanks to Carl Rothfels, Marianna Ricca, and Maria Prieto, because you guys together with Ester, made my days in Durham, an unforgettable time.

No puc deixar de donar les gràcies als meus pares pel vostre suport (remarco) INCONDICIONAL. Perquè mai heu qüestionat què faig o perquè ho faig, senzillament sempre esteu allà. Els dos m'heu ensenyat amb el vostre exemple a ser treballadora, a lluitar i, per sobre de tot, a ser lliure i fidel a mi mateixa. I al meu germà Ignasi, sempre tan íntegre i coherent, perquè m'has ensenyat a ser valenta per defensar en el que crec, i això també m'ha ajudat a formar-me com a científica. Suposo que els tres us deureu sentir molt orgullosos de mi en aquests moment, però creieu-me si us dic que sóc jo la que se sent orgullosa de poder tenir-vos com a família.

Gràcies als meus amics, perquè sou una part de la meva vida tant important, que no puc imaginar-me sense ella. A les meves "Teresines", Mireia i Isis, perquè que des de que ens vam conèixer a la carrera, senzillament, no he deixat de riure. Gràcies per les cerveses, els viatgets, les converses a les escales i a Skype, i per ser tan bones amigues! Sou genuïnes, úniques i insubstituïbles. I a tota la colla que conforma el The-Parta, que m'heu acollit durant tot aquest temps fent-me partícip de les mil i unes propostes lúdico-festives possibles: Martuki, Luís, Guillem, Iker, Tana, Georgina, Laiuski, Rut, Diana, Cris, Rubén, Jordi, Juli. Gemma, Anabel... Sou gent meravellosa, plena d'energia i positivisme, i heu estat capaços d'animar-me sempre que ha calgut.

Gràcies a tots els amics que he tingut la sort de trobar més enllà de les parets de la Facultat de Biologia. A tota la "crew" de ballarines: Agnès, Ester, Sua, Carol, Mystik, Rebeca, Ana... per tots els bons moments durant les classes, els assajos, les actuacions i els concerts que hem gaudit juntes durant aquest anys. I perquè a més de ser les millors companyes de ball, sou encara millors amigues! I també a tota la "Chupipandi": Sonia, Ari, Alba, Gloria i Toñi. Perquè heu estat un deliciós regal aquest any, en el que m'ha fet tanta falta desconnectar de tant en tant, perquè sempre he trobat en vosaltres un lloc per oblidar-me del món mentre saltem i suem.

Gràcies a totes aquelles persones que m'estimo i que malauradament, ara no veig tant com jo voldria. A la Núria i la Dani, que sou amigues des de fa tants anys, gràcies per seguir mantenint en el vostre món un raconet per mi. I a la Verónica i la Raquel, pels moments memorables que hem passat juntes i pels que ens queden per viure. Als meus estimats Félix i Andrea, els millors companys de pis que es pot tenir, pels riures, per les converses a la cuina, per recollir-me la roba quan plovia i, sobretot, per haver-me fet un foradet en les vostres vides.

Y por último, no me olvido, gracias a ti. Cuando nos conocimos ya estaba metida en esto hasta el cuello, y te avisé, corre mientras puedas. No es fácil estar al lado de alguien que se dedica a la investigación, ya que tenemos un *tempo* propio, que a menudo no se ajusta al del resto del mundo. Pero te has quedado conmigo, y me has apoyado con tu paciencia, comprensión y cariño. Gracias, sencillamente, por estar/aguantar/sobrevivir a mi lado. Y por endulzarme la vida.

A tots vosaltres, i als que potser em deixo, **MOLTES GRÀCIES**!!!!!

Aquesta tesi ha estat possible gràcies a la concessió d'una beca predoctoral FPU (Formación del Profesorado Universitario) del Ministerio de Educación y Ciencia. La recerca, ha estat parcialment finançada pel projecte de recerca del CGL2007-66734-C03-02 (Ministerio de Educación y Ciencia), 2005SGR01047 (Departament d'Universitats, Recerca i Societat de la Informació) i pels projectes "Filogènia molecular de les Teloschistales i Ostropales. II Part" i "Líquens del Mar d'Avall" de la Secció de Ciències Biològiques de l'Institut d'Estudis Catalans.

INTRODUCCIÓ

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1. INTRODUCCIÓ AL TREBALL FLORÍSTIC

1.1. JUSTIFICACIÓ

La present tesi s'integra en una de les línies de treball del Grup de Liquenologia del Departament de Biologia Vegetal (Unitat de Botànica) de la Universitat de Barcelona. Aquesta línia, té com a objectiu obtenir un coneixement el més complet possible de la biodiversitat dels líquens i fongs liquenícoles del territori català i de la part occidental de la regió mediterrània, així com la descripció de les comunitats liquèniques d'aquesta àrea. Són diversos els resultats d'aquesta línia de treball, on trobem dades florístiques, taxonòmiques, corològiques, iconogràfiques, ecològiques i fitocenològiques.

El primer treball realitzat en aquest grup va ser l'estudi dels líquens gipsícoles de la meitat oriental de la península Ibèrica (Llimona, 1973, 1974), el qual, en l'àmbit de Catalunya, incloïa l'estudi dels afloraments de guix de la Segarra, Anoia, Conca de Barberà i Baix Llobregat. Més tard, es realitzaren altres treballs de tesi extensos, com el dedicat als líquens silicícoles de la part alta del Montseny (Hladun, 1981) – precedit d'un treball de tesina sobre els líquens de les Agudes (Hladun, 1977), – i als de la comarca del Maresme (Barbero, 1998) i als líquens calcícoles del sud-oest de Catalunya (Navarro-Rosinés, 1992), – precedit també d'una tesina sobre els líquens calcícoles d'una part de la Segarra (Navarro-Rosinés, 1985). Pel que fa als líquens epífits, es començà per un tractament extensiu d'una gran part de Catalunya (Gómez-Bolea, 1985), seguit d'un exhaustiu estudi de la flora i vegetació epifítica de la plana i les serralades litorals tarragonines (Giralt, 1991), de la part meridional de Catalunya (Boqueras, 1993) i dels alzinars en diferents graus d'estat ecològic (Longán, 2001). Aquests treballs, als quals cal afegir altres estudis florístics o amb continguts parcialment florístics producte de l'activitat del mateix grup (p. e., Navarro-Rosinés &

Hladun, 1991; Boqueras *et al.*, 1993; Llop *et al.*, 2010, en revisió); i altres treballs que s'esmenten en l'apartat 1.2.), han permès atènyer un bon coneixement de la diversitat dels líquens i fongs liquenícoles de l'àrea d'estudi i àrees properes, tot i que aquest grau de coneixement varia àmpliament d'una comarca a una altra. Malgrat la importància d'aquestes aportacions a la flora liquenològica de Catalunya [recollides al Mòdul LiqueCat del Banc de Dades de Biodiversitat de Catalunya (Hladun, 2011)], encara queden moltes àrees del territori, especialment hàbitats poc freqüents o poc extensos però amb una extraordinària heterogeneïtat de substrats i de condicions microclimàtiques, que no han estat estudiats amb deteniment, tot i la seva potencial riquesa i diversitat liquèniques.

Una d'aquestes àrees és l'actualment inclosa dins del Parc Natural de Cap de Creus, a l'extrem oriental dels Pirineus. En aquesta àrea hi trobem una extensa seqüència d'afloraments de roques àcides, com esquists, fil·lites, quarsites i gneis entre les metamòrfiques, i granits, granodiorites i pegmatites entre les intrusives. Alguns d'aquests afloraments fan accessibles roques de les més antigues de Catalunya (Folch, 1988). De forma més puntual, també s'hi troben afloraments de substrats carbonatats, com calcàries, marbres i sorres consolidades amb ciment calcari.

El clima de la zona és típicament mediterrani, amb un llarg període eixut durant l'estiu (només amb algunes tempestes intenses i breus de caràcter local, a finals d'agost) i la major part de les pluges concentrades entre setembre i desembre i al març [segons les dades climàtiques sintetitzades a Franquesa (1995)]. Sovint entren en l'àrea els vents del nord i nord-est (Tramuntana), secs i freds, que suposen un factor bioclimàtic de màxima importància, ja que accentuen l'evapotranspiració i l'assecament del sòl. Segons la classificació de Bolós (1985), la península del Cap de Creus forma part de la regió de tramuntana (territori ruscínic), caracteritzada per un clima general mediterrani marítim amb vents del nord intensos, fent que la humitat del clima sigui inferior al d'àrees properes situades al sud o a l'oest.

La vegetació de la península del Cap de Creus està influïda pels factors ambientals i també per la destacada activitat antròpica, no gaire intensa a la zona litoral, però molt perceptible a l'interior de l'àrea. En aquesta zona més alterada, hi hagueren antigament explotacions d'alzinars i suredes, i extenses rompudes i abancalaments, especialment per a plantar vinya a causa de la forta demanda generada per la crisi de la fil·loxera a França. Un cop fet l'arrabassament de la vegetació arbòria, les vinyes foren abandonades en arribar la fil·loxera a la zona al 1877, fet que va donar pas a la revegetació dels vessants en moltes àrees amb comunitats arbustives, especialment estepars d'estepa negra, bruguerars de bruc boal o espinars d'argelaga, i també algunes pinedes i pastures d'hivernada pel bestiar vacum. Aquestes comunitats vegetals, a més, han estat periòdicament afectades per incendis, en part provocats per afavorir les esmentades pastures (Folch, 1988; Franquesa, 1995). Així doncs, la major part dels afloraments de roca i dels terraprims (sòls poc profunds, pedregosos i esquelètics), en trobar-se en una àrea afectada per les activitats agrícoles (especialment en el passat) i els incendis (en el present), tenen una vegetació vascular poc densa o gairebé inexistent. Per tant, en aquests substrats, sovint només els briòfits (sobretot als indrets humits, alts i orientats al nord), poden disputar l'espai a la colonització dels líquens. El més freqüent és l'ocupació total o parcial de les roques per part de les comunitats liquèniques que, d'aquesta manera, participen de forma considerable en la conformació del paisatge amb les coloracions que presenten (Figura 1).

En l'àrea del Parc, cal destacar també l'abundància d'ecosistemes aquàtics continentals, com ara rieres i rierols de cabal fluctuant (sovint inexistent durant l'estiu, però amb tolls persistents), cadolles, impluvis i entollaments efímers, llacunes litorals i salabroses o endorreiques, fonts i degotalls. Alguns d'aquests hàbitats són únics a Catalunya, perquè tot i trobar-se a baixa altitud i propers al litoral, presenten una contaminació sovint baixa i, en diverses èpoques de l'any, acullen riques poblacions d'algues epicontinentals (Cambra, 1995). Pel que fa al medi marí, el primer catàleg d'espècies d'algues marines de la costa catalana (Ballesteros & Romero, 1982) citava uns 200 tàxons al litoral de la península del Cap de Creus, posant de manifest l'alta diversitat d'algues bentòniques en aquesta regió.

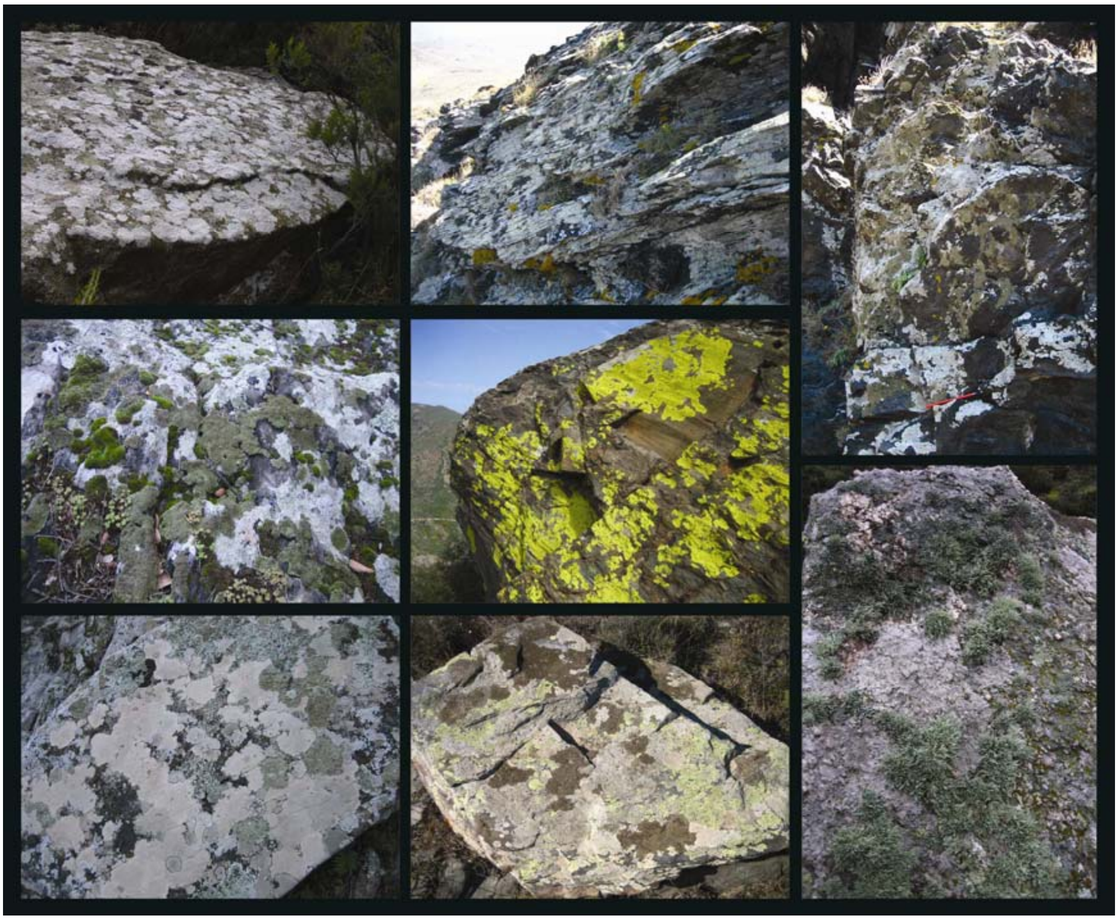

Figura 1: Exemples d'aflorament de roca silícia al Parc Natural de Cap de Creus, àmpliament colonitzats per líquens, els quals, poden compartir l'espai amb briòfits (Font: Xavier Llimona Pagès i Samantha Fernández Brime).

A mitjans de la dècada dels vuitanta, amb la finalitat d'adquirir un coneixement complet i detallat del patrimoni criptogàmic (incloent algues marines i continentals, briòfits, fongs, líquens i falgueres) de la península del Cap de Creus i de la Serra de Verdera, es va impulsar el projecte "Flora i Vegetació Criptogàmica del proposat Parc Natural del Cap de Creus", mercès al suport econòmic de la Universitat de Barcelona i la CIRIT (Cambra, 1995; Casas *et al*., 1998). Com a resultat dels estudis de recerca dels diferents grups d'investigació implicats en aquest projecte multidisciplinar, destaquen els treballs publicats sobre les algues marines (p. e., Perera, 1986, 1987; Rull, 1987; Rull & Gómez Garreta, 1990a, 1990b), les algues continentals (p. e., Cambra, 1986, 1987, 1989a, 1989b; Tomás *et al.*, 1987), les cianofícies i microalgues del sòl (Vela & Hernández-Mariné, 1987; Hernández-Mariné, 1995) i els briòfits (Casas, 1995; Casas *et al.*, 1998; treballs que s'afegeixen a un estudi previ de Casas, 1958). Els resultats sobre els pteridòfits van quedar inclosos en un extens treball sobre la vegetació del Cap de Creus (Franquesa, 1995). Els estudis referents al component liquènic d'aquesta àrea van quedar resumits en una única publicació (Llimona, 1995). Tot i ser aquest un treball de gran interès, ja que va caracteritzar per primera vegada els principals grups de líquens saxícoles i terrícoles de la zona i va citar-ne les espècies més destacades per la seva abundància o singularitat, no deixa de tractar-se d'un treball sintètic, que recull molt parcialment la riquesa real del component liquènic de la zona i no menciona les localitats del material estudiat.

En el moment d'iniciar aquesta tesi, era encara manifesta la necessitat d'estudiar de forma exhaustiva la major part dels líquens saxícoles i terrícoles del Parc Natural de Cap de Creus, així com d'examinar el component liquènic de la gran diversitat d'hàbitats, ens alguns casos únics a Catalunya, esmentats més amunt. Aquestes mancances van justificar que s'endegués un treball florístic d'abast més ampli que, recollint les dades preexistents, en completés la part florística amb una caracterització bàsica de les comunitats i que, a més, incorporés dades de caràcter ecològic, fins ara inexistents. Aquesta visió més global i integrada era essencial per a una aproximació a l'estat de conservació de la flora liquènica, i per extensió, dels hàbitats del Parc colonitzats pels líquens. La dominància del component liquènic en el Parc Natural de Cap de Creus converteix les dades a obtenir en aquest estudi, en una eina imprescindible, especialment en la tria dels indrets on el component liquènic és més ric i valuós, que s'haurien de tenir en consideració a l'hora de dissenyar polítiques de gestió i conservació en el Parc.

1.2. ANTECEDENTS HISTÒRICS

No és objecte del present apartat fer un recorregut exhaustiu a través de la història de la liquenologia a Espanya, ja que aquesta ha estat àmpliament tractada a Llimona (1973, 1985, 2009). No obstant, esmentarem els treballs que han fet referència als líquens del Cap de Creus, a més d'esmentar altres obres destacades sobre la flora saxícola i terrícola de la regió mediterrània de Catalunya i de la resta de la península Ibèrica.

Les primeres citacions de líquens recol·lectats a l'àrea inclosa dins del Parc Natural de Cap de Creus, apareixen en els treballs del botànic català Manuel Llenas i Fernández, a principis del segle XX. En el seu treball «Enumeración y distribución de los Peltigeráceos de Cataluña» (1905) i, en la que fou la seva obra més important, la seva tesi doctoral titulada «Ensaig d'una flora liquènica de Catalunya» (1909), Llenas cita recol·leccions fetes a Cadaquès, Sant Pere de Rodes i al Cap de Creus. Malauradament, durant més de 50 anys, la flora liquenològica de la península del Cap de Creus va deixar d'ésser objecte de nous estudis. A principis de la dècada dels seixanta, membres de l'escola liquenològica provençal porten a terme un exhaustiu estudi dels líquens del no gaire allunyat bosc de la Maçana, a l'Albera (Clauzade & Rondon, 1960). Aquest estudi, a més de la riquesa en espècies que va reportar (266 líquens i 4 fongs liquenícoles), va representar una valuosa aportació al coneixement de l'autoecologia de les espècies i una primera aproximació a les comunitats liquèniques. Aquest fet va convertir l'esmentat estudi en un treball de referència per a futurs estudis al Cap de Creus i altres zones dels Pirineus Orientals.

A mitjans dels anys seixanta, Xavier Llimona va reprendre les prospeccions liquenològiques al Cap de Creus. Els primers resultats de les seves observacions van ser integrats en una revisió molt general del component liquènic de Catalunya (Llimona, 1969). Més endavant, gràcies a les seves recol·leccions, observacions de camp i elaboració d'inventaris, algunes dades sobre els líquens i les comunitats liquèniques del Cap de Creus es van incloure en els treballs fitocenològics de Wirth &

Llimona (1975), Crespo *et al.* (1976) i Llimona & Egea (1985). Algunes localitats del Cap de Creus i de la Serra de Verdera van ser incloses també en treballs que abastaven una àrea d'estudi més àmplia. És el cas de la tesi doctoral de Gómez-Bolea (1985) centrada en els líquens epífits de Catalunya, en la que 6 de les 158 localitats prospectades estan incloses en l'àrea del Cap de Creus, o la tesi de Pereira (1992) sobre els líquens hidròfils de la península Ibèrica, que va incloure 5 localitats situades dins del Parc. La continuïtat de les prospeccions liquenològiques per part de Xavier Llimona i col·laboradors al llarg dels anys ha permès aplegar un nombre considerable de recol·leccions de líquens del Cap de Creus, especialment saxícoles. Alguns d'aquests espècimens han estat inclosos en els estudis de revisió dels gèneres *Rinodina* (Giralt & Barbero, 1995; Giralt & Llimona, 1997; Giralt, 2001) i *Dimelaena* (Rico *et al.*, 2003, 2006) a la península Ibèrica, en l'estudi taxonòmic de *Glyphopeltis ligustica* (Egea *et al.*, 1995) i *Protoparmelia montagnei* (Barbero *et al.*, 2006) o en la revisió taxonòmica del grup de *Caloplaca saxicola* (Gaya, 2009), per citar alguns treballs rellevants. Malgrat tot, la major part del material recol·lectat no ha estat estudiada en profunditat, i bona part de les mostres resten encara sense identificar. Només el treball anteriorment citat de Llimona (1995) en fa una síntesi, com a capítol d'un llibre més general sobre el patrimoni geològic, natural i cultural de l'àrea que més endavant hauria d'esdevenir el Parc Natural de Cap de Creus, segons la Llei 4/1998, de 12 de març (DOGC núm. 2641, 01/04/1998).

Pel que fa a la resta de Catalunya, el coneixement dels líquens saxícoles i terrícoles de les zones properes a la costa, s'ha anat ampliant amb la realització de diversos treballs, de major o menor extensió. En referència als líquens de roques àcides, entre els treballs clàssics destaca el de Llenas (1902), que cita 64 espècies dels voltants de Barcelona, entre elles nombrosos líquens saxícoles. Més recentment, les obres de Torres & Hladun (1982), Barbero *et al.* (1996) i, sobretot, Barbero (1998), recullen les dades dels líquens saxícoles del gran batòlit granític que s'estén al llarg de la comarca del Maresme. El treball florístic del massís de Cadiretes (Llop & Hladun, 2003) inclou 79 cites de líquens silicícoles. Cal destacar també els estudis de tipificació de la vegetació marina i litoral de la Costa Brava de Ballesteros (1982,

1992) que, tot i ocupar-se fonamentalment de les comunitats d'algues bentòniques, van caracteritzar en detall les comunitats de líquens silicícoles instal·lades a la zona supralitoral. Pel que fa als estudis de líquens calcícoles, destaquen els treballs realitzats sobre substrats carbonatats de les Illes Medes (Llimona *et al.*, 1984) i de la zona costanera de la Catalunya meridional (Navarro-Rosinés, 1992). Les citacions de líquens terrícoles de les zones baixes i properes a la costa de Catalunya, es recullen als treballs de Llimona (1973) i Hladun *et al.* (1994) pels sòls carbonatats i guixencs, i als de Torres & Hladun (1982) i Llop & Hladun (2003) pel que fa als sòls àcids.

Fora de Catalunya, els líquens saxícoles i terrícoles de la península Ibèrica de regions properes a la mar Mediterrània han estat objecte de nombrosos estudis. A la Comunitat Valenciana, destaquem els treballs sobre els líquens silicícoles de la Serra d'Espadà (Calatayud & Barreno, 1994) i de les Illes Columbretes (Llimona, 1980), dues àrees que posteriorment es van incloure en el treball de tesi sobre els líquens dels substrats no carbonatats de la part oriental del Sistema Ibèric i de les Illes Columbretes (Calatayud, 1998). Destaquen també els treballs sobre els líquens calcícoles del litoral alacantí (Alonso & Egea, 1989; Alonso *et al.*, 1989) i el treball de Barreno *et al.* (1989), que inclou dades sobre els líquens terrícoles del Parc Natural de la Font Roja. Pel que fa al sud-est peninsular, és la regió de la qual es compta amb més dades sobre el component liquènic, gràcies als nombrosos treballs d'Egea i col·laboradors sobre la flora i la vegetació liquènica de les roques silícies (p. e., Egea & Llimona, 1981, 1982, 1984, 1987, 1994), les roques calcàries (Egea & Torrente, 1985; Alonso & Egea, 1994, 1996) o els sòls carbonatats (Alonso & Egea, 1996). Finalment, per la seva proximitat i semblança amb algunes àrees de la nostra zona d'estudi, cal fer esment d'alguns dels treballs realitzats a les Illes Balears sobre els líquens saxícoles i terrícoles, tant sobre substrats calcaris, dominants en l'arxipèlag balear (p. e., Llimona, 1976; Breuss, 1988; Boom, 1999), com no carbonatats (p. e., Mus, 1985a, 1985b; Mus & Egea, 1989) i també sobre els dos tipus de substrats (p. e., Stolley & Kappen, 2002).

2. INTRODUCCIÓ A LA REVISIÓ TAXONÒMICA I FILOGENÈTICA DELS GÈNERES *DIPLOSCHISTES* I *INGVARIELLA*

2.1. JUSTIFICACIÓ

En el plantejament inicial d'aquesta tesi vam decidir incorporar un element addicional de caire més taxonòmic i filogenètic. Fent ús de les dades i espècimens recollits per al treball florístic, vam seleccionar aquells tàxons que resultessin conflictius o amb necessitat de ser revisats. Per aquest motiu, vam plantejar un examen més exhaustiu centrat en els gèneres *Diploschistes* i *Ingvariella*. Sabedors de la seva presència al Cap de Creus gràcies a dades prèvies publicades (Llimona, 1995) o inèdites, tots dos gèneres havien estat recol·lectats durant l'estudi florístic; el gènere *Diploschistes*, amb especial abundància. Els espècimens d'aquest darrer gènere havien dut problemes d'identificació i molts conceptes d'espècies restaven poc clars. Les incomptables col·leccions de *Diploschistes* provinents de la zona i del sud de França, acumulades per Xavier Llimona al llarg dels anys, no feien sinó reflectir la dificultat de delimitar aquests tàxons i les vacil·lacions dels autors.

Per tal de resoldre les qüestions plantejades per ambdós gèneres, vam fer ús de dos tipus de dades: caràcters emprats tradicionalment en taxonomia (p. e., morfològics, anatòmics, químics, ecològics) i caràcters provinents de diversos marcadors moleculars. Les dades esmentades estaven destinades a un posterior estudi filogenètic combinat. Aquesta investigació exigia però, no només la inclusió d'exemplars recol·lectats en el territori objecte de l'estudi florístic, sinó també exemplars d'altres àrees més o menys allunyades. En els següents apartats, s'exposa un resum de l'estat actual del coneixement d'ambdós gèneres, i quins han estat els conflictes taxonòmics que hem abordat específicament en el nostre estudi.

2.2. EL GÈNERE *DIPLOSCHISTES*

2.2.1. ANTECEDENTS HISTÒRICS

Les primeres dues espècies pertanyents a l'actual gènere *Diploschistes* van ser descrites a finals del segle XVIII sota els noms de *Lichen scruposus* (Schreber, 1771) i *L. muscorum* (Scopoli, 1772). Posteriorment, Acharius (1803) va descriure el gènere *Urceolaria*, al qual va transferir les espècies *Lichen scruposus*, *L. ocellatus* Vill. i *L. cinereocaesius* Sw., i on hi va incloure més endavant dues espècies més: *Urceolaria gypsacea* i *U. diacapsis* (Acharius, 1810). El primer problema taxonòmic sorgeix del fet que dins del gènere *Urceolaria*, Acharius hi va incloure espècies que actualment formen part d'altres gèneres, com és el cas d'*Aspicilia* A. Massal. o *Gyalecta* Ach. D'altra banda, Massalongo (1852) va proposar el gènere *Limboria* per ubicar-hi els tàxons *Urceolaria actinostoma* Pers. i la nova espècie *Limboria euganea*, reunint així en un mateix gènere les dues espècies descrites fins el moment amb apotecis de tipus peritecioide. Finalment, Norman (1853) va descriure el gènere *Diploschistes*, dins del qual va incloure únicament les espècies *D. ocellatus* i *D. scruposus*. La proposta de Norman (*op. cit.*) no va ser àmpliament acceptada i, en obres posteriors, com la de Tuckerman (1872) sobre els líquens d'Amèrica del Nord, aquestes espècies encara es tractaven dins del gènere *Urceolaria*, com a *U. ocellata* i *U. scruposa*. Entre finals del segle XIX i principis del XX, el nombre d'espècies incloses dins del gènere *Diploschistes* va augmentar progressivament, sobretot amb al treball de Zahlbruckner (1892), que hi va transferir 17 tàxons provinents del gènere *Urceolaria*.

Un cop acceptada la circumscripció del gènere *Diploschistes*, es va proposar la primera classificació al nivell de família per a aquest gènere. *Diploschistes* es va incloure, juntament amb el gènere *Conotrema* Tuck., dins de la família de les *Diploschistaceae* (Zahlbruckner, 1905). Aquesta classificació es va mantenir durant més de mig segle, i només alguns autors (Smith, 1921; Watson, 1929) van assenyalar les semblances morfològiques entre les *Diploschistaceae* i les *Thelotremataceae*, ja que únicament es diferenciaven pel tipus de fotobiont (trebuxioide i trentepolioide, respectivament). Gilenstam (1969) fou el primer en modificar la classificació proposada per Zahlbruckner (1905), ja que va transferir el gènere *Conotrema* a la família *Stictidaceae*, basant-se en les similituds amb *Stictis* Pers. pel que fa a l'estructura de l'apoteci. Finalment, Henssen & Jahns (1974) van proposar fusionar les *Diploschistaceae* dins de les *Thelotremataceae*, donades les notables semblances en l'anatomia i l'ontogènia dels apotecis que ambdues famílies presentaven, i considerant que la presència d'un fotobiont diferent no era justificació suficient per mantenir les dues famílies separades.

2.2.2. DELIMITACIÓ DEL GÈNERE *DIPLOSCHISTES*

La circumscripció genèrica més estesa dins de les *Thelotremataceae* s'ha basat en l'estructura i pigmentació de l'exciple, tal i com va establir Hale en diferents treballs (1980, 1981). Recentment, Frisch *et al.* (2006) han proposat afegir als esmentats caràcters, els lligats a la presència o absència de columel·la. Per tant, seguint les propostes de Hale (1980, 1981) i Frisch *et al.* (2006), *Diploschistes* es distingeix pel fet de tenir la següent combinació de caràcters: presència d'un exciple pseudoparenquimàtic carbonitzat i amb paràfisis laterals, i absència de columel·la. Addicionalment, el gènere es caracteritza per ser saxícola o terrícola, i per tenir tal·lus crustaci, fotobiont de tipus trebuxioide, apotecis de tipus lecanoroide, urceolat o peritecioide (vegeu apartat següent), himeni no amiloide, format per paràfisis simples i ascs de claviformes a subcilíndrics i espores de submurals a murals, hialines quan són joves, després de color bru verdós, que es tornar bru fosc en la maduresa.

Una de les espècies més conegudes i amplament distribuïdes del gènere *Diploschistes* és *D. ocellatus*. Ara bé, aquest tàxon presenta diferències notables pel que fa als trets establerts com a diagnòstics pel gènere, ja que té un exciple extraordinàriament reduït, de color bru molt clar i no presenta paràfisis laterals. En canvi, té un marge tal·lí molt ben desenvolupat, que contrasta amb la resta tàxons del gènere en els que aquest marge es troba molt reduït. A més a més, també presenta diferències químiques: *D. ocellatus* té depsidones del β-orcinol (substàncies del complex de l'àcid norstíctic), mentre la resta de membres del gènere contenen dèpsids de l'orcinol (àcids lecanòric, diplosquistèsic i orselínic) o bé, no presenten substàncies liquèniques. Aquestes diferències fenotípiques tan notables en *D. ocellatus* plantegen seriosos dubtes sobre la seva pertinença al gènere *Diploschistes*, una qüestió que ha estat objecte d'estudi en diversos treballs (Lumbsch & Tehler, 1998; Martín *et al.*, 2000, 2003; vegeu apartat 2.2.5.).

2.2.3. SUBDIVISIÓ DEL GÈNERE *DIPLOSCHISTES*

Dins del gènere *Diploschistes* s'observen tres morfologies d'apotecis molt ben diferenciades:

1. Apotecis lecanorins: caracteritzats per tenir un marge tal·lí molt ben desenvolupat, gruixut i persistent, un exciple propi molt reduït i sense paràfisis laterals. Està present únicament en *D. ocellatus*.

2. Apotecis urceolats: caracteritzats per tenir un disc netament còncau, que pràcticament no es veu quan els apotecis són joves, un marge tal·lí de prim a més o menys gruixut, immers o lleugerament prominent i un exciple molt ben desenvolupat, carbonitzat i amb paràfisis laterals.

3. Apotecis peritecioides: caracteritzats per ser molt tancats, de forma que el disc, profundament còncau i enfonsat – només s'obre a l'exterior mitjançant un porus, i per això pren una morfologia molt semblant a la d'un periteci – un marge tal·lí reduït i sempre immers i un exciple ben desenvolupat, carbonitzat i amb paràfisis laterals.

Lettau (1932) fou el primer que va considerar importants les diferències morfològiques dels apotecis, i va subdividir el gènere en dos grans grups: el grup *actinostomus*, format per les espècies d'apotecis peritecioides, i el grup *scruposus*, que comprenia les d'apotecis urceolats i lecanorins. Posteriorment, Lumbsch (1985) va afegir-hi una tercera subdivisió i va separar *D. ocellatus* en el seu propi grup *ocellatus*. Aquests grups s'han mantingut per motius pràctics, donada la utilitat de poder referirse a grups d'espècies en diversos tractaments del gènere (p. e., Lumbsch, 1989; Lumbsch & Elix, 1989). Malgrat tot, en diverses obres (Guderley *et al*., 1997; Lumbsch *et al*., 1997) s'ha assenyalat que es tracta de grups artificials, ja que fins el moment no s'ha pogut demostrar que es tractin de grups naturals monofilètics.

2.2.4. ESTUDIS TAXONÒMICS RECENTS

El treball de Lettau (1932), anteriorment citat, va representar el primer tractament taxonòmic de les espècies de *Diploschistes* que es trobaven al continent europeu, en el qual hi va incloure 12 espècies. Posteriorment, i quasi de forma simultània, van aparèixer els treballs sobre la flora liquenològica europea de Poelt (1969) i Ozenda & Clauzade (1970) centrats, sobretot, en les regions centreeuropea i mediterrània respectivament. El tractament de les espècies del gènere *Diploschistes* presents a Europa en aquestes dues obres va resultar força diferent (vegeu Taula 1). Mentre Poelt (1969) [partint de la classificació proposada per Lettau (1932)] citava 15 espècies i 4 varietats, Ozenda & Clauzade (1970) acceptaven 10 espècies i 2 varietats (Taula 1). Posteriorment, el treball de Clauzade & Roux (1985), basat en el d'Ozenda & Clauzade (1970), va reduir a 6 les espècies de *Diploschistes*, per a les quals va proposar una complexa classificació infragenèrica, amb 10 subespècies i 4 varietats (Taula 1). La publicació del treball de Lumbsch (1988), que revisava la identitat dels tàxons *D. gypsaceus* (Ach.) Zahlbr. i *D. diacapsis* (Ach.) Lumbsch, va provocar un canvi en el tractament sistemàtic proposat a Clauzade & Roux (1985) per a les espècies de *Diploschistes* amb apotecis urceolats, pruïna blanca i de substrats carbonatats; aquests canvis es van recollir en el tercer suplement de l'obra florística de Clauzade & Roux (1989). Finalment, el treball més recent i complet sobre la taxonomia d'aquest gènere és la monografia de Lumbsch (1989) sobre les espècies de *Diploschistes* de la regió holàrtica. En aquesta obra de revisió, la proposta taxonòmica de Lumbsch (*op. cit.*) per a les espècies de *Diploschistes* se situa en una posició intermèdia entre les classificacions proposades per Poelt (1969) i Clauzade & Roux (1985, 1989), ja que accepta 10 espècies a la regió europea i 14 al conjunt de la regió holàrtica (Taula 1).

Si bé és cert que la classificació i taxonomia proposada a Lumbsch (1989) ha estat àmpliament acceptada (p. e., Pant & Upreti, 1993; Lumbsch & Elix, 2003; Fletcher & Hawksworth, 2009; Mangold *et al.*, 2009), altres autors (p. e., Freire Dopazo & García Molares, 1999; Terrón *et al.*, 2000; Roux & Gueidan, 2002; Roux *et al.*, 2006) han seguit el tractament sistemàtic establert per Clauzade & Roux (1989). Les diferències més notables entre les classificacions exposades a la Taula 1, corresponen al complex format pels tàxons amb apotecis urceolats [amb l'excepció de *D. bisporus* (Bagl.) J. Steiner; vegeu apartat 2.3.]. Clauzade & Roux (*op. cit.*) distingeixen dins d'aquest grup únicament dues espècies, *D. diacapsis* i *D. scruposus* (Schreb.) Norman, les quals separen segons el número d'espores per asc, vuit i quatre respectivament. Dins de cada espècie, proposen una divisió en subespècies i varietats, que recullen les diferències en la morfologia del tal·lus (presència o absència de pruïna, coloració) i les afinitats per un tipus de substrat concret (roques àcides o bàsiques o sòl). Lumbsch (1989), en canvi, no fa la distinció a partir del número d'espores i atorga el nivell d'espècie a moltes de les subespècies proposades per Clauzade & Roux (1989). Per tant, el tractament sistemàtic d'aquest grup d'espècies difereix substancialment entre Clauzade & Roux (*op. cit.*) i Lumbsch (1989), ja que atorguen diferent importància als caràcters diagnòstics de les espècies. N'és l'exemple més clar el cas del número d'espores per asc: mentre a Clauzade & Roux (1989) es considera un caràcter fonamental per a separar tàxons al nivell d'espècie, Lumbsch (1989) el considera un tret variable al nivell infraespecífic. Com a conseqüència del valor que aquest autors donen als caràcters diagnòstics a l'hora de separar tàxons, ens trobem amb casos conflictius, com és la identitat de *D. interpediens* (Nyl.) Zahlbr. Aquest tàxon viu sobre roques àcides, té tal·lus gris verdós, sense pruïna i els ascs octosporats. Clauzade & Roux (1989) van tractar *D. interpediens* com una subespècie de *D. diacapsis*, atès que ambdós taxons tenen ascs octosporats, tot i que *D. diacapsis* es pot distingir clarament de *D. interpediens* per tenir el tal·lus de blanc a gris clar, molt pruïnós i perquè viu sobre sòls guixencs o carbonatats. Lumbsch (1989), en canvi,

Taula 1. Tractament sistemàtic de les espècies holàrtiques del gènere *Diploschistes* segons diferents autors.

Poelt (1969)	Ozenda & Clauzade (1970)	Clauzade & Roux (1985)	Clauzade & Roux (1989)	Lumbsch (1989)
D. actinostomus (Ach.) Zahlbr. var. *farinosus* (Anzi) Zahlbr.	*D. actinostomus* (Ach.) Zahlbr. var. *caesioplumbeus* (Nyl.) J. Steiner var. *farinosus* (Anzi) Zahlbr.	*D. actinostomus* (Ach.) Zahlbr. var. *caesioplumbeus* (Nyl.) J. Steiner var. *farinosus* (Anzi) Zahlbr.	*D. actinostomus* (Ach.) Zahlbr. var. *caesioplumbeus* (Nyl.) J. Steiner var. *farinosus* (Anzi) Zahlbr.	*D. actinostomus* (Ach.) Zahlbr.
D. albescens Lettau	*D. albescens* Lettau	*D. bisporus* (Bagl.) J. Steiner var. *ochraceus* (Anzi) Poelt	*D. bisporus* (Bagl.) J. Steiner var. *ochraceus* (Anzi) Poelt	*D. aeneus* (Müll. Arg.) Lumbsch
D. bisporus (Bagl.) J. Steiner var. *ochraceus* (Anzi) Poelt	*D. bryophilus* (Ehrh.) Zahlbr.	*D. euganeus* (A. Massal.) Zahlbr.	*D. diacapsis* (Ach.) Lumbsch subsp. *interpediens* (Nyl.) Clauzade & Cl. Roux subsp. *neutrophila* Clauzade & Cl. Roux subsp. *siculus* (Jatta) Clauzade & Cl. Roux	*D. badius* Lumbsch & Elix
D. bryophilus (Ehrh.) Zahlbr. var. *iridatus* (A. Massal.) Poelt	*D. euganeus* (A. Massal.) Zahlbr.	*D. gypsaceus* (Ach.) Zahlbr. subsp. *interpediens* (Nyl.) Clauzade & Cl. Roux subsp. *neutrophila* Clauzade & Cl. Roux subsp. *siculus* (Jatta) Clauzade & Cl. Roux	*D. euganeus* (A. Massal.) Zahlbr.	*D. bisporus* (Bagl.) J. Steiner
D. caesioplumbeus (Nyl.) Vain.	*D. gypsaceus* (Ach.) Zahlbr.	*D. ocellatus* (Vill.) Norman	*D. ocellatus* (Vill.) Norman	*D. caesioplumbeus* (Nyl.) Vain.
D. calcareus (Müll. Arg.) J. Steiner	*D. lichenicola* (Montl.) Vain.			*D. candidissimus* (Kremp.) Zahlbr.
D. euganeus (A. Massal.) Zahlbr.	*D. ocellatus* (Vill.) Norman			*D. diacapsis* (Ach.) Lumbsch
	D. ochraceus (Nyl.) Zahlbr.			*D. euganeus* (A. Massal.) Zahlbr.
				D. gypsaceus (Ach.) Zahlbr.

Taula 1. Continuació.

Poelt (1969)	Ozenda & Clauzade (1970)	Clauzade & Roux (1985)	Clauzade & Roux (1989)	Lumbsch (1989)
D. gypsaceus (Ach.) Zahlbr.	*D. scruposus* (Schreb.) Norman	*D. scruposus* (Schreb.) Norman	*D. scruposus* (Schreb.) Norman	*D. hypoleucus* Zahlbr.
D. interpediens (Nyl.) Zahlbr.	*D. violarius* (Nyl.) Zahlbr.	subsp. *albescens* (Lettau) Clauzade & Cl. Roux	subsp. *albescens* (Lettau) Clauzade & Cl. Roux	*D. muscorum* (Scop.) R. Sant.
D. ocellatus (Vill.) Norman		subsp. *cretaceus* (Ach.) Clauzade & Cl. Roux	subsp. *gypsaceus* (Ach.) Clauzade & Cl. Roux	*D. ocellatus* (Vill.) Norman
D. ochrophanes Lettau		subsp. *iridatus* (A. Massal.) Clauzade & Cl. Roux	subsp. *iridatus* (A. Massal.) Clauzade & Cl. Roux	*D. prominens* (Vain.) Lumbsch
D. ptychochrous Lettau		subsp. *muscorum* (Scop.) Clauzade & Cl. Roux	subsp. *muscorum* (Scop.) Clauzade & Cl. Roux	*D. scruposus* (Schreb.) Norman
D. scruposus (Schreb.) Norman		var. *parasiticus* (Sommerf.) Zahlbr.	var. *parasiticus* (Sommerf.) Zahlbr.	
var. *violarius* (Nyl.) Lettau		subsp. *ochrophanes* (Lettau) Clauzade & Cl. Roux	subsp. *violarius* (Nyl.) Clauzade & Cl. Roux	
D. siculus (Jatta) Poelt		subsp. *ptychochrous* (Lettau) Clauzade & Cl. Roux		
D. steppicus Reichert		subsp. *violarius* (Nyl.) Clauzade & Cl. Roux		

va considerar que *D. interpediens* era molt semblant a *D. scruposus* morfològicament i ecològica, i que tan sols es diferenciaven perquè el darrer presenta quatre espores per asc. Això el va portar a sinonimitzar ambdues espècies, mantenint el nom més antic, que era *D. scruposus*. Per últim, d'altres autors (p. e., Barbero, 1998; Terrón *et al.*, 2000; Burgaz *et al.*, 2007) han optat per seguir el concepte de Zahlbruckner (1892), i consideren *D. interpediens* com una espècie independent tant de *D. diacapsis* com de *D. scruposus*. En general, la taxonomia del complex d'espècies properes a *D. scruposus* (*i. e.*, *D. diacapsis*, *D. interpediens*, *D. gypsaceus* i *D. muscorum*) és encara conflictiva.

2.2.5. ESTUDIS DE FILOGÈNIA MORFOLÒGICA I MOLECULAR

El primer treball que va intentar explicar les relacions existents entre els diferents membres del gènere *Diploschistes*, va ser el publicat per Lumbsch & Tehler (1998). Aquest estudi es fonamentava en l'anàlisi cladística basada en caràcters fenotípics (morfològics, químics i ecològics). Els resultats d'aquesta anàlisi recuperaven el grup *scruposus* com a monofilètic, incloent *D. ocellatus*, mentre que el grup *actinostomus* es resolia com a parafilètic, motiu pel qual es va considerar com a un grup sense reconeixement taxonòmic. Lumbsch & Tehler (*op. cit.*) van comparar aquests resultats amb les hipòtesis proposades per Lumbsch (1986, 1989) sobre les tendències evolutives de diversos caràcters (morfològics, químics i ecològics) en el gènere *Diploschistes*. El resultats de Lumbsch & Tehler (1998) van recolzar aquestes hipòtesis pel que fa a l'evolució de l'obertura dels apotecis, segons les quals els apotecis peritecioides representarien un estat de caràcter més ancestral (plesiomòrfic), mentre els apotecis urceolats i lecanorins resultarien d'aparició més recent (apomòrfics).

Des de la dècada dels noranta, la millora de les tècniques d'extracció i amplificació de l'ADN en líquens (p. e., Armaleo & Clerc, 1995; Grube *et al.*, 1995; Martín & Winka, 2000), han permès la utilització de les dades moleculars en els estudis de tipus taxonòmic. L'estudi de Martín *et al.* (2000) va ser el primer referit al gènere *Diploschistes*, i en ell van fer ús de les dades moleculars per avaluar la variabilitat morfològica mostrada per l'espècie *D. ocellatus*. I és que dins d'aquesta espècie, Llimona (1973) havia descrit la var. *almeriensis*, per agrupar els espècimens estrictament gipsícoles i amb una morfologia del tal·lus peculiar (arèoles quasi digitades i amb pseudocifel·les grosses), i s'investigava la possibilitat que es tractés d'una espècie diferent. La reconstrucció filogenètica emprant el separador transcrit intern de l'ADN ribosòmic nuclear (nuITS), va permetre demostrar que les poblacions designades com a *D. ocellatus* var. *almeriensis* no formaven un clade separat de la resta de *D. ocellatus* i, per tant, l'anàlisi no donava suport a la seva separació com a un tàxon apart de *D. ocellatus*. A més, aquest estudi va mostrar per primera vegada la separació de *D. ocellatus* respecte de la resta del gènere, contradient els resultats de Lumbsch & Tehler (1998), que el situaven dins del grup *scruposus*.

Més endavant, Martín *et al.* (2003) presenten la primera filogènia molecular per al gènere *Diploschistes* en sentit ampli, basada novament en el nuITS. Aquest treball ampliava considerablement el nombre d'espècies de *Diploschistes* incloses respecte al de Martín *et al.* (2000). Un cop més, els resultats obtinguts es contraposaven amb els obtinguts en les anàlisis de Lumbsch & Tehler (1998). En primer lloc, el grup *actinostomus* es resolia com a monofilètic, amb un alt recolzament estadístic. En canvi, el grup *scruposus* resultava parafilètic. A més, es confirmava la relació distant de *D. ocellatus* respecte a la resta d'espècies del gènere, tal i com es mostrava a Martín *et al.* (2000). La posició de *D. ocellatus* en els arbres filogenètics resultants de l'estudi de Martín *et al.* (2003) indicava l'existència d'una considerable variabilitat genètica, la qual va ser també avaluada amb el càlcul de les distàncies genètiques. Els valors d'aquestes distàncies genètiques entre *D. ocellatus* i la resta d'espècies del gènere van resultar ser superiors als valors establerts per a membres d'un mateix gènere, segons s'indicava a Lumbsch (2002). Davant aquests resultats, Martín *et al.* (2003) no van treure conclusions ni van acabar d'aclarir si era preferible tractar *D. ocellatus* com un membre de *Diploschistes* allunyat de la resta d'espècies del gènere, o bé com un llinatge independent dins de la família *Thelotremataceae*. Malgrat tot, els resultats de Martín *et al.* (*op. cit.*) van suposar un important avenç per entendre les relacions filogenètiques entre els diferents tàxons de *Diploschistes* i, alhora, va deixar obertes interessants qüestions com ara quina és la delimitació natural del gènere o l'existència de grups filogenètics que es corresponguessin a la morfologia dels apotecis.

Un dels primers treballs que va incloure un nombre considerable de tàxons pertanyents a les *Thelotremataceae* va ser l'estudi de Lumbsch *et al.* (2004). Tot i que l'objectiu principal d'aquest estudi era investigar la posició filogenètica dels gèneres de fongs liquenitzats amb mazedi *Pyrgillus* i *Nadvornikia*, la filogènia obtinguda aportava dades interessants sobre les relacions de diversos gèneres inclosos dins de les *Thelotremataceae*. Pel que fa als resultats referents a *Diploschistes*, el gènere es resolia com a monofilètic sense incloure *D. ocellatus*, que restava sense resoldre's dins de la família. Altres treballs filogenètics centrats en la delimitació dels gèneres i en aclarir les seves relacions dins de les *Thelotremataceae* (p. e., Frisch *et al.*, 2006; Lumbsch *et al.*, 2008), van incloure també espècimens de *Diploschistes* en les seves anàlisis, però tampoc van poder resoldre la seva posició dins de la família.

El treball filogenètic de Mangold *et al.* (2008), va ser el primer en revelar que les famílies *Thelotremataceae* i *Graphidaceae*, que s'havien mantingut tradicionalment separades per la forma dels apotecis (arrodonits en la primera i lirel·liformes en la segona), formen part d'un mateix clade. Baloch *et al.* (2010) i Rivas Plata *et al.* (2011) han confirmat recentment els resultats de Mangold *et al.* (2008). En conseqüència, s'han sinonimitzat ambdues famílies, mantenint el nom de *Graphidaceae* ja que és el més antic. Aquest ha estat el concepte de família que nosaltres hem seguit al llarg d'aquesta tesi. Malgrat tot, en algunes ocasions encara ens referirem a les *Thelotremataceae* quan ens referim al concepte que es tenia d'aquesta família en els treballs previs als resultats de Mangold *et al.* (*op. cit.*).

2.3. EL GÈNERE *INGVARIELLA*

2.3.1. ANTECEDENTS HISTÒRICS I TAXONOMIA DEL GÈNERE

La única espècie del gènere monotípic *Ingvariella* Guderley & Lumbsch, es va descriure originalment com a *Urceolaria bispora* per Baglietto (1871). En la diagnosi de l'espècie, Baglietto (*op. cit.*) esmenta la presència d'un marge tal·lí gruixut i un marge propi prim i poc visible. Posteriorment, *U. bispora* va ser transferida al gènere *Diploschistes* (Steiner, 1893), combinació que es va mantenir durant més d'un segle, de forma que aquest tàxon va ésser tractat com a *D. bisporus* en diverses obres florístiques europees (p. e., Poelt, 1969; Clauzade & Roux, 1985, 1989; Nimis, 1993). També Lumbsch (1989) inclou aquesta espècie en la monografia del gènere *Diploschistes*, per a la qual indica la presència d'un exciple pseudoparenquimàtic, carbonitzat i gruixut, amb paràfisis laterals, sense esmentar la presència de cap marge tal·lí. Un estudi anatòmic més detallat de *D. bisporus* per part de Guderley *et al.* (1997), va revelar que aquesta espècie té el marge dels apotecis format per elements provinents de l'himeni (paràfisis i ascs), que es troben col·lapsats i fortament pigmentats. També van observar que aquests elements himenials es podien agrupar dins els apotecis, formant estructures semblants a les columel·les. D'aquesta manera, basant-se en la manca d'un exciple propi veritable i de paràfisis laterals, i en la presència d'una estructura semblant a una columel·la, Guderley *et al.* (*op. cit.*) van segregar aquest tàxon de *Diploschistes*, i van proposar el nou gènere *Ingvariella* per a reubicar-lo.

2.3.2. POSICIÓ SISTEMÀTICA DE *INGVARIELLA* EN LES *OSTROPALES*

En l'estudi de Guderley *et al.* (*op. cit.*), el nou gènere *Ingvariella* es va mantenir dins de la família de les *Thelotremataceae*. Els autors van considerar que era proper al gènere *Diploschistes* en ser l'un i l'altre els únics membres de la família que presenten fotobionts trebuxioides i una distribució semblant en zones àrides i subàrides dels dos hemisferis. No es va descartar tampoc, una relació propera amb altres gèneres com

Myriotrema, per l'absència de paràfisis laterals, o bé amb *Ocellularia*, que presenta formació de columel·la.

El conflicte principal però, no rau en quins són els gèneres dins de les *Thelotremataceae* als quals *Ingvariella* és més proper, sinó en si la inclusió d'*Ingvariella* en aquesta família és correcta o no. Tradicionalment, les *Thelotremataceae* s'han definit per reunir els següents trets: apotecis amb desenvolupament hemiangiocàrpic, exciple pseudoparenquimàtic, paràfisis laterals absents o presents, paràfisis simples, ascs unitunicats, hamateci i ascs no amiloides i espores de transversalment septades a muriformes, amiloides o no (Hale, 1980, 1981; Poelt, 1973; Henssen & Jahns, 1974). El gènere *Ingvariella* però, presenta notables diferències respecte els caràcters propis de la família *Thelotremataceae* ja que no presenta un exciple pseudoparenquimàtic i, a més, el seu himeni reacciona positiu al lugol (primer groc, després vermell) i els ascs tenen parets amiloides.

D'altra banda, cal destacar les afinitats morfològiques que presenta *Ingvariella* amb *Sagiolechia atlantica* descrita per Henssen (1995). Aquesta espècie [que ocupa una posició incerta dins de la família de les *Gomphillaceae* (Lumbsch & Huhndorf, 2010)] també presenta elements himenials col·lapsats (que han perdut la seva forma, coloració i funció original) formant part del marge dels apotecis. La diferència fonamental és que en el cas de *S. atlantica*, aquests elements himenials es troben organitzats sobre un exciple molt ben desenvolupat (Henssen, 1995), que no s'observa a *Ingvariella*. També considerem destacables les semblances entre els caràcters himenials d'*Ingvariella* i els d'altres famílies dins de les *Ostropales* com les *Stictidaceae* o les *Phlyctidaceae*. Es per aquest motiu, que en aquest estudi hem considerat que el gènere *Ingvariella*, amb una estructura del marge dels apotecis força única dins de les *Ostropales*, demanava una revisió més acurada de les seves afinitats dins d'aquest ordre.

3. ESTRUCTURA DE LA TESI DOCTORAL

La següent tesi s'organitza en quatre capítols. El format de cada un d'aquests capítols es correspon al d'un manuscrit científic. Per tant, qualsevol pot ser llegit independentment dels altres. Tots han estat escrits en anglès, que és la llengua vehicular més utilitzada en les publicacions científiques. Els capítols 1 i 3 es troben en diferents fases de preparació per a la seva publicació i ja presenten el format exigit per les revistes a les quals seran enviats. Els capítols 2 i 4 s'han publicat en les revistes indexades *The Lichenologist* i *Mycologia* respectivament.

El capítol 1 recull el treball florístic realitzat sobre els líquens saxícoles i terrícoles al Parc Natural de Cap de Creus. Les espècies que s'hi tracten han estat estudiades, sobretot, a partir del material obtingut en les recol·leccions realitzades durant aquest treball de tesi, i complementat amb el material recol·lectat prèviament pel nostre grup d'investigació. El mostreig s'ha realitzat en 34 localitats, que suposen una representació raonable dels diversos ambients que es troben a l'àrea d'estudi, tant pel que fa a la diversitat de substrats com de condicions ecològiques i climàtiques locals. El gruix del treball correspon al catàleg, integrat per 294 espècies, acompanyat dels comentaris sobre l'autoecologia de cadascuna d'elles. Quan una espècie ho requereix, hi ha també un comentari i discussió de tipus taxonòmic. A continuació, les espècies s'han agrupat per afinitats ecològiques, relacionant-les amb els tipus de comunitats o associacions liquèniques conegudes. En tercer lloc, la seva agrupació segons el tipus de distribució permet una primera aproximació a l'anàlisi fitogeogràfica de la flora de l'àrea d'estudi. En l'Apèndix 1, aportem un llistat de tot el material estudiat, que ha quedat dipositat a l'herbari del Centre de Documentació de Biodiversitat Vegetal (CeDocBiv, Herbari BCN-Lich.).

El capítol 2 està dedicat al primer resultat taxonòmic derivat de l'estudi florístic inclòs al capítol 1, en el que es descriu una nova espècie de fong liquenícola, *Lichenostigma rupicolae* Fdez.-Brime & Nav.-Ros., dins del subgenère *Lichenogramma*.

El capítol 3 és un exhaustiu treball de revisió centrat en el gènere *Diploschistes*, que pretén establir la circumscripció del gènere i la seva sistemàtica, ja que estudis taxonòmics i filogenètics previs, tot i ésser altament meritoris i rigorosos, no han pogut resoldre-la satisfactòriament. El treball consta de dues parts. La primera, és un estudi de tipus filogenètic, per investigar la monofília i la delimitació de *Diploschistes*, i per inferir les seves relacions amb altres gèneres de la família. Els marcadors moleculars emprats han estat la subunitat 28S de l'ADN ribosòmic nuclear (nuLSU) i la subunitat 16S de l'ADN ribosòmic mitocondrial (mtSSU). Aquest marcadors van ser triats atenent a la utilitat que han demostrat per delimitar gèneres i inferir relacions intergenèriques en diferents famílies de líquens (p. e., Mangold *et al*., 2008; Papong *et al*., 2009; Nordin *et al*., 2010). Les dues regions s'analitzen de forma combinada, mitjançant els mètodes de màxima parsimònia, màxima versemblança i inferència bayesiana.

La segona part consisteix en un estudi filogenètic i taxonòmic centrat únicament en el gènere *Diploschistes*. L'anàlisi filogenètica tracta d'inferir la història evolutiva del gènere, que faci possible aclarir la circumscripció i relacions dels grups prèviament establerts segons la morfologia dels apotecis, i posar a prova si aquest tret morfològic és sinapomòrfic per a cadascun dels grups. Alhora, aquestes anàlisis són emprades per examinar la taxonomia d'una selecció d'espècies, amb especial èmfasi en *D. diacapsis*, *D. gypsaceus*, *D. interpediens*, *D. muscorum* i *D. scruposus*. En les anàlisis filogenètiques basades en dades moleculars, s'han emprat els marcadors moleculars nuITS i mtSSU, que ja han demostrat una alta eficiència per a resoldre la filogènia infragenèrica en diversos grups de líquens (p. e., Crespo *et al*., 2001; Blanco *et al*., 2004; Crewe *et al*., 2006; Divakar *et al*., 2006; Wedin *et al*., 2006). També hem fet una selecció de caràcters morfològics i químics i els hem analitzat filogenèticament, combinats i sense combinar amb les dades moleculars. La decisió d'analitzar filogenèticament els caràcters morfològics, en lloc mapar-los directament sobre les filogènies moleculars, respon a diversos motius. En primer lloc, en aquest estudi es vol examinar el grau de resolució i recolzament estadístic que s'assoleix amb la filogènia morfològica, en comparació amb els resultats que s'obtenen amb la filogènia molecular, quan els dos tipus de dades s'analitzen separadament. En segon lloc, es pretén explorar la contribució dels caràcters morfològics a la filogènia quan s'analitzen conjuntament amb els caràcters moleculars. Totes les matrius de dades, moleculars o morfològiques, independentment o de forma combinada, s'analitzen amb màxima parsimònia i, addicionalment, algunes matrius moleculars també s'examinen amb mètodes de màxima versemblança i d'inferència bayesiana. Paral·lelament a les anàlisis filogenètiques, s'estudien 127 plecs de *Diploschistes*, que figuren a l'Apèndix 2, per tal d'explorar, revisar i seleccionar aquells caràcters morfològics i anatòmics tradicionalment emprats en aquest gènere per a delimitar espècies i grups d'espècies i valorar-ne la seva utilitat i potencialitat com a caràcters sinapomòrfics d'aquestes espècies i grups.

El capítol 4 està dedicat a l'estudi de la circumscripció del gènere *Ingvariella*, que pretén confirmar la seva identitat com a gènere independent de *Diploschistes*. Partint de la base de les nostres observacions de les característiques anatòmiques de l'apoteci, es posa en dubte la inclusió d'*Ingvariella* en l'antiga família *Thelotremataceae* i es considera la seva possible afinitat amb altres famílies dins de les *Ostropales*. Per tal de resoldre aquestes qüestions i explorar la posició filogenètica d'*Ingvariella* dins l'ordre, hem analitzat filogenèticament una matriu de dades que inclou exemplars pertanyents a diferents famílies de les *Ostropales*. Els marcadors moleculars nuLSU i mtSSU són analitzats de forma combinada amb els mètodes de màxima parsimònia, màxima versemblança i inferència bayesiana. Com en el cas de l'estudi filogenètic endegat pel gènere *Diploschistes*, hem revisat 17 mostres (incloses en el suplement "ONLINE DATA SUPPLEMENT 2", inclòs al final del mateix capítol), amb la intenció d'estudiar més detalladament l'estructura del marge de l'apoteci d'*Ingvariella*.

OBJECTIUS

OBJECTIUS

A continuació, presentem els objectius generals d'aquesta tesi, pel que fa al treball florístic (objectius 1 al 5) i a la revisió taxonòmica i filogenètica dels gèneres *Diploschistes* (objectius 6 i 7) i *Ingvariella* (objectiu 8).

1. Elaborar un catàleg florístic dels líquens saxícoles i terrícoles, i dels seus fongs paràsits, de l'àrea inclosa dins del Parc Natural de Cap de Creus, des de la zona litoral fins a les localitats situades a la part culminal de la Serra de Verdera, que ens proporcioni una aproximació el més exhaustiva possible al coneixement de la riquesa florística del territori.

2. Elaborar un herbari dels tàxons recol·lectats i estudiats, per dipositar-los en les col·leccions de referència del Centre de Documentació de Biodiversitat Vegetal de la Universitat de Barcelona (CeDocBiV, Herbari BCN-Lich), com a material testimoni de les citacions d'aquesta tesi.

3. Examinar les diferències morfològiques, anatòmiques o ecològiques que trobem en els tàxons estudiats respecte a les dades procedents de la bibliografia de que disposem, a fi i efecte de contribuir al coneixement de llur variabilitat.

4. Caracteritzar les preferències ecològiques de les espècies incloses en el catàleg florístic, sobre la base de les observacions de camp, per tal de conèixer millor la seva autoecologia i fer propostes de conservació del territori.

5. Realitzar una caracterització preliminar de les comunitats liquèniques observades en l'àrea d'estudi, a partir de les dades recopilades sobre l'ecologia del material recol·lectat.

6. Investigar la monofília i la delimitació del gènere *Diploschistes*, i estimar les relacions filogenètiques amb altres gèneres de la família *Graphidaceae*, mitjançant l'ús de dades moleculars.

7. Reconstruir la filogènia morfològica i molecular del gènere *Diploschistes*, cercant la resposta a respondre dues qüestions: 1) quines són les relacions existents entre els tàxons inclosos actualment dins del gènere, i quina és la correspondència amb els grups morfològics proposats per Lettau (1932) i Lumbsch (1985); 2) fins on arriba la concordança entre la filogènia i la delimitació basada en dades únicament morfològiques de les espècies, amb especial èmfasi en el conjunt d'espècies format per *D. diacapsis*, *D. gypsaceus*, *D. interpediens*, *D. muscorum* i *D. scruposus*.

8. Confirmar la independència del gènere *Ingvariella* respecte del gènere *Diploschistes* i investigar la seva posició sistemàtica dins de l'ordre *Ostropales*.

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Informe dels directors de la Tesi Doctoral referent al factor d'impacte i a la contribució de la doctoranda a cadascun dels articles publicats.

El Dr. Xavier Llimona i Pagès, Professor Emèrit de la Universitat de Barcelona, i la Dra. Ester Gaya Bellés, investigadora de la Universitat de Duke, com a directors de la Tesi Doctoral elaborada per Samantha Fernández Brime, amb el títol "Els líquens saxícoles i terrícoles del Parc Natural de Cap de Creus, amb un estudi filogenètic aplicat a la sistemàtica dels gèneres *Diploschistes* i *Ingvariella*",

INFORMEN

Que els treballs de recerca duts a terme per Samantha Fernández Brime com a part de la seva formació predoctoral i inclosos a la seva Tesi Doctoral han donat lloc a la preparació de 4 manuscrits (2 ja publicats i 2 més pendents d'enviar a revisió en el moment del dipòsit de la tesi). A continuació es detalla la llista d'articles així com els índexs d'impacte (segons el SCI del ISI Web of Knowledge) de les corresponents revistes.

1- Fernández-Brime, S., Llop, E., Gaya, E., and Llimona, X. (In prep.). “**Saxicolous and terricolous lichens, and their lichenicolous fungi, from the Cap de Creus Natural Park (Northeast Spain)**”.

Es preveu enviar aquest treball a la revista *Nova Hedwigia* que té un índex d’impacte de 0.913 (ISI Journal Citation Report 2010). Tenint en compte aquest índex d’impacte, *Nova Hedwigia* ocupa el 106è lloc de 188 revistes en la seva categoria (“Plant Sciences”), amb un índex d’impacte mitjà de 1.102.

2- Fernández-Brime, S., Llimona, X., and Navarro-Rosinés, P. 2010. ***Lichenostigma rupicolae*** **(Lichenotheliaceae), a new lichenicolous species growing on** ***Pertusaria rupicola***. *The Lichenologist* 42(3): 241–247.

L’índex d’impacte de la revista *The Lichenologist* és en l’actualitat de 1.231 (ISI Journal Citation Report 2010). Aquesta revista està inclosa a les categories “Plant Sciences” i “Mycology”. En la primera categoria, *The Lichenologist* ocupa el lloc 90è de 188 revistes, amb un índex d’impacte mitjà de 1.102. A la segona categoria, aquesta revista ocupa la posició 15ena de 23 revistes, amb un índex d’impacte mitjà de 1.626.

3- Fernández-Brime, S., Gaya, E., Llimona, X., and Lutzoni, F. (In prep.). **Phylogenetic study of** ***Diploschistes*** **(Graphidaceae, Ostropales, lichen-forming Ascomycota), based on morphological, chemical, and molecular data.**

Es preveu enviar aquest article a la revista *Taxon*. L’índex d’impacte de la revista *Taxon* és en l’actualitat de 2.364 (ISI Journal Citation Report 2010). Aquesta revista està inclosa a les categories “Plant Sciences” i “Evolutionary Biology”. En la primera categoria, *Taxon* ocupa la posició 46ena de 188 revistes, amb un índex d’impacte mitjà de 1.102. En la segona categoria, *Taxon* ocupa el lloc 28è de 45 revistes, amb un índex d’impacte mitjà de 2.674.

4- Fernández-Brime, S., Llimona, X., Molnar, K., Stenroos, S., Högnabba, F., Björk, C., Lutzoni, F., and Gaya, E. 2011. **Expansion of the Stictidaceae by the addition of the saxicolous lichen-forming genus *Ingvariella***. *Mycologia* 103(4): 755–763.

L'índex d'impacte de la revista *Mycologia* és en l'actualitat de 1.641 (ISI Journal Citation Report 2010). Aquesta revista està inclosa a la categoria "Mycology". Tenint en compte aquest índex, *Mycologia* ocupa l'11è lloc de la seva categoria, que inclou 23 revistes, amb un índex d'impacte mitjà de 1.626.

A més, CERTIFIQUEN:

Que Samantha Fernández Brime ha participat activament i ha estat la responsable principal en el desenvolupament del treball de recerca associat a cadascun dels articles, així com en la seva redacció. La seva participació ha involucrat tots els passos del procés d'elaboració d'aquests treballs, i en concret la seva contribució a cadascuna de les tasques ha estat la següent:

- Plantejament inicial dels objectius de cadascun dels treballs.
- Disseny experimental i treball de camp, incloent la recol·lecció dels espècimens i selecció del material d'herbari destinats a identificació i seqüenciació.
- Classificació i identificació de tot el material recol·lectat.
- Anàlisis químiques de les mostres (TLC).
- Codificació dels caràcters fenotípics per a posterior anàlisi.

- Extracció i seqüenciació de l'ADN.

- Compilació de dades, realització de totes les anàlisis filogenètiques i interpretació de resultats.

- Redacció dels articles, incloent figures i taules, i seguiment del procés de revisió.

Finalment, certifiquem que cap dels coautors dels manuscrits detallats més amunt ha utilitzat, ni pretén utilitzar, implícitament o explícita, la informació produïda i presentada amb l'objectiu d'elaborar una altra Tesi Doctoral.

Atentament,

Ester Gaya Bellés   Xavier Llimona Pagès

Barcelona, 05 de Gener de 2012

COMPENDI DE PUBLICACIONS

CAPÍTOL 1: Líquens saxícoles i terrícoles, i els seus fongs liquenícoles, del Parc Natural de Cap de Creus (nord-est d'Espanya)

CAPÍTOL 1

Saxicolous and terricolous lichens, and their lichenicolous fungi, from the Cap de Creus Natural Park (Northeast Spain)

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Es preveu enviar aquest article a la revista *Nova Hedwigia*

RESUM

El següent treball està centrat en l'estudi de la flora formada pels líquens saxícoles i terrícoles del Parc Natural de Cap de Creus (NE de la península Ibèrica). Com a resultat d'aquest treball, s'ha elaborat un catàleg florístic en el què se citen 263 espècies de líquens i 31 de fongs liquenícoles per a l'àrea d'estudi. Del total de tàxons citats, 9 són primeres cites per a la península Ibèrica: *Arthonia lecanorina*, *Caloplaca arcis*, *C. austrocitrina*, *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon simplicatum*, *Endococcus buelliae*, *Micarea melaenida*, *Polyccocum rinodinae* i *P. teresum*. L'estudi inclou també la caracterització de les comunitats liquèniques més notables de la zona estudiada. Els resultats de l'anàlisi fitogeogràfic dels líquens ens ha permès determinar que la flora liquènica està formada per tres grups de distribució principals: espècies mediterrànies, temperades-mediterrànies i espècies d'àmplia distribució. Addicionalment, la flora es veu enriquida amb espècies de distribució atlàntica, que apareixen en els enclavaments més humits, i fins i tot espècies de distribució centreuropea o àrtico-boreal, que tot i ser poc nombroses, han trobat en la zona microhàbitats adients per al seu creixement.

Saxicolous and terricolous lichens, and their lichenicolous fungi, from the Cap de Creus Natural Park (Northeast Spain)

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ABSTRACT

The saxicolous and terricolous lichen flora from the Cap de Creus Natural Park (NE Iberian Peninsula) was investigated. The present study reports 263 lichen taxa and 31 lichenicolous fungi from the study area, of which nine are new for the Iberian Peninsula: *Arthonia lecanorina*, *Caloplaca arcis*, *C. austrocitrina*, *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon simplicatum*, *Endococcus buelliae*, *Micarea melaenida*, *Polycoccum rinodinae*, and *P. teresum*. From a phytogeographical point of view, the flora is mainly composed of Mediterranean temperate species and Mediterranean lichens in a broad sense, enriched with a considerable number of Atlantic species in the most humid sites of the Park. The large number of different microclimatic conditions in the area, combined with frequent extensions of rock outcrops, makes the Cap de Creus Natural Park an extraordinary region for the diversity of saxicolous and terricolous lichens.

KEYWORDS

Lichen flora, Iberian Peninsula, lichen diversity, Mediterranean lichens.

INTRODUCTION

The Natural Park of Cap de Creus is located in the most northeastern corner of the Iberian Peninsula, and comprises 13,843 hectares, of which 10,780 comprise the Cap de Creus peninsula and 3,064 belong to the surrounding marine area. This Park represents an area of interest due to its geological characteristics, with outcrops of pre-hercynian materials, exhibiting a wide variety of rock types, and even including unique features, such as visible pegmatite intrusions within metamorphic schists. With a surface area of almost 140 km^2 and a maximum elevation of 670 m, the area has a markedly abrupt relief, with steeply sloped areas, numerous gullies, and cliffs near the Mediterranean Sea up to 50 m high. Although the climate is typically Mediterranean, the area is strongly influenced by cold and dry northern winds and by the formation of local fog banks. The combination of this special lithology (with predominantly siliceous substrates, but also with some calcareous areas), orography, and local climatic conditions, leads to a high number of different microhabitats, suitable for a rich saxicolous and terricolous lichen flora. Since 1965, the senior author (X.L.) has surveyed and studied the lichens of several areas of the Natural Park of Cap de Creus. However, except for a short synthetic work (Llimona, 1995) and a few data included in scattered studies (e.g., Wirth & Llimona, 1975; Crespo et al., 1976; Llimona & Egea, 1985), the saxicolous and terricolous lichen flora of this area remains undescribed. Therefore, this work represents the first attempt to carry out a broad survey of the saxicolous and terricolous lichen flora of the Cap de Creus peninsula and its Natural Park.

Geomorphology, geology and soil

The study area is part of the easternmost extreme of the Eastern Pyrenees, with the mountain range ‘Serra de Verdera’ holding the highest elevations of the peninsula (i.e., Sant Salvador de sa Verdera, 670 m). From this peak, the mountain range branches off in different directions forming hills of lower elevations, being the most important Puig de Queralbs (621 m), Pení (606 m), Muntanya Negra (433 m), and Puig Vaquer (413 m). The topography of the Cap de Creus peninsula is conditioned by its tectonic structures and by its special lithological composition, whereas its polygonal shape is linked by the dominant shear strain directions (Carreras & Druget, 1995). In fact, the Cap de Creus peninsula constitutes an eastern outcrop of the Hercynian basement of the Pyrenaic Axial Zone (Druget, 1997). This Axial Zone was originally deep-seated, but the old rocks of the Hercynian basement posteriorly emerged in the Cap de Creus, as a result of the erosion that followed the raising of the Pyrenees. Most of the peninsula consists of a sequence of sedimentary rocks, originating before the Upper Ordovician, which experienced repeated events of folding and metamorphism (Carreras & Druget, 1995). As a consequence, metamorphic schists formed, which are currently predominant in the lithology of the study area. Additionally, pre-hercyniane intrusive igneous rocks in the metasedimentary sequence also experienced hercynian deformation and metamorphism, giving rise to gneisses in Port de la Selva, metabasites in Muntanya Negra, and pegmatite dykes along the northern part of the peninsula (Carreras & Druget, 1995; Druget, 1997). Due to the fusion and crystallization processes of sediments from deeper levels, two intrusive granodioritic batholiths were formed: the most massive located in the Serra de Verdera, and the second, between the locality of Roses and Punta Falconera (Carreras & Druget, 1995). In Cap Norfeu, there is a remarkable outcrop of sedimentary rocks (limestone) from the Lower Palaeozoic that gave rise to one of the few calcareous areas in the whole Cap de Creus peninsula. Finally, materials from the Hercynian basement are sporadically covered by quaternary deposits, as is the case of the eolianites located at Les Cavorques. These deposits are formed by siliceous grains (mainly coming from the northern area of the Cap de Creus peninsula) carried by the wind, which later became loosely cemented with carbonates. These types of deposits are named as ‘climbing dunes’, and it will be the term we will use to refer to this special type of substrate.

The abrupt topographical relief and the predominantly schistose substrates have led to the formation of shallow, cobbly, and poorly developed soils over most of the study area. Only on horizontal or on gently sloping areas, with colluvial deposits, and under the protection of the forest canopy, soils are more structured.

Climate

In accord with its geographic location, the climate of the study area is typically Mediterranean. Winters are mild, January being the coldest month with a mean temperature of 9ºC, and only occasionally reaching freezing point. In summer, the warmest month is July with a mean temperature of 24.9ºC. The mean annual precipitation in the study area barely reaches 541 mm. Most of the precipitation falls between September and December, while summer is the driest period, with only local storms (Fig. 1). The Tramuntana wind is one of the most remarkable climatic traits of the area. This wind blows from north-northwest, with high frequency and intensity (it can reach up to 120 km/h), with the consequence of considerable drying of the soil and vegetation, and a decrease in temperatures. The final climatic feature is the occurrence of fog banks when the Tramuntana does not blow. Then, the humid winds of Gregal (NE) and Llevant (E) form persistent fog banks along the shady side of the Serra de Verdera mountain range, and the Garbí wind (SW) forms local fog banks at the crests and peaks of Pení and Sant Salvador. Although this contribution of water is not quantified as precipitation, it is very significant for the activation of the lichen.

Vegetation

The abrupt topographical relief and the Mediterranean climatic conditions, in addition to the effect of the cold and dry northern wind, define the vegetation of this area. An exhaustive study of the vegetation of the Cap de Creus peninsula by Franquesa (1995) distinguished two main vegetation units. The first unit comprises the vegetation that extends along the littoral, which is organized in three different parallel belts. The first vegetation belt appears near the sea, where it receives the influence of saltwater splashes, and is characterized by communities of *Armeria ruscinonensis* Girard. The second vegetation strip, is not directly sprayed by the sea, but is affected by the strong wind and the deposition of marine aerosols. This vegetation range shows sparse shrubland communities of *Astragalus massiliensis* Lam. (cushion-shaped thorny growth form), accompanied by littoral creeping forms of *Cistus salvifolius* L. and *Lavandula stoechas* L. Above the second vegetation belt, where the conditions are less severe, is the coastal maquis. Within this third belt, on the northern coast of the peninsula, wind-exposed areas are characterized by the presence of *Juniperus macrocarpa* Sibth. & Sm., while in sheltered and lower areas, which are more humid and have deeper soils, the maquis of *Myrtus communis* L. find their habitat. On the southern coast, which is markedly warmer than the northern one, there are sporadic shrublands with *Euphorbia dendroides* L., *Cneorum tricoccon* Gueld. ex M. Bieb. (rare), and *Olea europaea* L. var. s*ylvestris* (Miller) Lehr., or even poorly developed mosaics of *Pinus halepensis* Mill.

The second vegetation unit described in Franquesa (1995) represents the inland vegetation, strongly determined by climatic factors, especially droughts, and by a long story of human activities that have triggered important changes in the territory. One of the main effects of human activity has been the high frequency of wildfires, which has favoured the post-fire establishment of siliceous shrublands, especially *Cistus* and *Erica* heath (*Cisto-Sarothamnetum catalaunici*). According to vegetation maps of the area (Carreras et al., 2004), the acidic substrates combined with the Mediterranean climatic conditions, allow the development of sclerophyllous forests of *Quercus suber* L. and *Q. ilex* L., mainly at the top of hills or bottom of valleys. Only in scarce, isolated sites of the shady side of Serra de Verdera, where humidity is higher, there are small formations of chestnut mixed deciduous thickets (*Carici-Quercetum pubescentis*). Finally, patches of plantations of *Pinus halepensis* and *P. pinea* L., usually coming from old afforestations, can be found in the lowlands.

MATERIAL & METHODS

The main scope of this study included saxicolous lichens, epiphytic lichens (only if sporadically growing on rocks), terricolous lichens, and their lichenicolous fungi. For this purpose, we studied specimens from collections of S.F.B. and X.L. from 34 localities, as well as from X.L. personal herbarium from the same localities. The whole set of examined collections have been deposited in the BCN-Lich. In order to survey a wide range of habitats, localities were selected based on substrate type, degree and orientation of slopes, and microenvironmental conditions.

Macroscopic characters were examined using an Olympus VMZ dissecting microscope (x40). Hand-cut or freezing microtome sections and squash preparations were used to examine microscopic characters with an Olympus CH-2 light microscope (x100, oil immersion). Initial observations and measurements were performed with sections mounted in water. To detect amyloidity of the thallus medulla and/or hymenium, sections were stained with 0.4% Lugol's iodine solution (IKI). To detect and observe amyloid structures of lecanorean asci, sections were first pre-treated with 10% aqueous solution of potassium before applying IKI.

Spot test reactions were performed on the cortex and/or medulla using the following test solutions: 10% aqueous solution of potassium hydroxide (K), aqueous calcium hypochlorite (C), and para-phenylenediamine dissolved in 96% ethyl alcohol (P). To analyze the secondary substances in specimens belonging to the genera *Buellia*, *Cladonia*, *Flavoparmelia*, *Lepraria*, *Parmotrema*, *Pertusaria*, *Punctelia*, *Ramalina*, *Rinodina*, and *Xanthoparmelia*, we performed Thin-Layer Chromatographies (TLC) of acetone extracts according to standardized procedures (Elix & Ernt-Russell, 1993).

Selected specimens were photographed using a Pixera Pro 150 ES camera attached to a stereomicroscope Olympus SZ60. For each selected specimen, multiple images in different focal planes were taken, and subsequently assembled into a final unique picture using the software Helicon Focus 5.2.

For taxa identifications, we followed the general flora literature of Clauzade & Roux (1985, 1989), Nimis (1993), Nash III et al. (2002, 2004, 2007), Nimis & Martellos (2004), Purvis et al. (1992), and Smith et al. (2009), as well as more specific taxonomic studies for some groups (e.g., Torrente & Egea, 1989; Burgaz & Ahti, 2009; Giralt, 2001, 2010; Gaya, 2009; Prieto et al., 2010a, 2010b).

List of localities

The following list indicates the collection sites included in this study, arranged from the most northwesterly site to the most southeasterly one (Fig. 2). For each locality, the following information is provided: local place name (according to toponymy accepted by the Institut Cartogràfic de Catalunya, http://www.icc.es/), type of the most representative substrate sampled, geographic coordinates, and altitudinal range.

1. Vilajuïga - Quermançó castle and its vicinities, granitic batholith and calcareous mortar from the castle’s walls, 42°20' N-3°05' E, 100-120 m.
2. Vilajuïga - Valley of Coma de l’Infern, granodiorite blocks, 42°19' N-3°07' E, 110-125 m.
3. Llançà - La Valleta, granodiorite outcrops, 42°21' N-3°06' E, 90-110 m.
4. Llançà - Cau del Llop cove, schists by the sea, 42°21' N-3°09' E, 0-5 m.
5. Llançà - Puig Vaquer, sunny side, schists, 42°20' N-3°10' E, 375-400 m.
6. El Port de la Selva - Roca de Caltré, schists and quartz dikes, 42°20' N-3°10' E, 200-250 m.
7. El Port de la Selva - Above the main path to the Sant Pere de Rodes monastery and ruins of Santa Helena, granodiorite outcrops, 42°19' N-3°09' E, 515-575 m.
8. El Port de la Selva - Sant Salvador castle and its vicinities, granodiorites and schists, 42°19' N-3°10' E, 550-655 m.
9. El Port de la Selva - Crest between Sant Salvador castle and the Queralbs peak, granodiorites, 42°18' N-3°10' E, 600-615 m.
10. El Port de la Selva - Punta de s’Arenella, open siliceous soil crusts with isolated schist rocks, 42°21' N-3°10' E, 0-5 m.
11. El Port de la Selva - Trail to the Masos, above cala Tamariua, northeast-facing gneiss and schists, 42°20' N-3°12' E, 90-100 m.
12. El Port de la Selva - Les Cavorques, climbing dunes, open forest of *Pinus pinea*, 42°18' N-3°12' E, 60-80 m.
13. El Port de la Selva - Pla de Palau, schists near the Romanyac stream, 42°18' N-3°13' E, 30-35 m.
14. El Port de la Selva - At the bottom of Salt de la Gorga, schists near the Romanyac stream , 42°18' N-3°13' E, 125-130 m.
15. El Port de la Selva - At the top of Salt de la Gorga, schists, 42°18' N-3°13' E, 180-195 m.

16. El Port de la Selva - Muntanya Negra, near Puig dels Bufadors, metabasites and carbonated schists from the vestiges of an old shepherd's shelter, 42°18' N-3°15' E, 350-385 m.
17. El Port de la Selva - Coll de sa Perafita, by the trail to Mas dels Bufadors, metamorphic schists, 42°18' N-3°14' E, 270m.
18. La Selva de Mar - Above Mas de la Fàbrega, schists near trail, 42°19'N-3°11' E, 75-100 m.
19. Cadaqués - Prat d'en Pagès, siliceous shallow soil crust, 42°19' N-3°17' E, 100 m.
20. Cadaqués - Racó de sa Claveguera, schists and pegmatites, 42°19' N-3°18' E, 25-50 m.
21. Cadaqués - Rec de Cala Bona, schists, 42°18' N-3°18' E, 30-35 m.
22. Cadaqués - Cala Jonquet, schists nearby the sea, 42°18' N-3°17' E, 0-5 m.
23. Cadaqués - El Pení, between sunny side, Sant Sebastià and the Pení peak, schists, 42°16' N-3°14' E, 400-450 m.
24. Cadaqués - El Pení, shady side, near the road to the military base, 42°17' N-3°14' E, 500-525 m.
25. Cadaqués - Trail to Mas d'en Baltre, schists, 42°16' N-3°16' E, 120-140 m.
26. Cadaqués - Torrent de Sant Pius V, near the trail to Mas d'en Baltre, schists, 42°16' N-3°16' E, 165-175 m.
27. Cadaqués - Cala Nans, north-facing schistose outcrops, 42°16' N-3°17' E, 25-35 m.
28. Cadaqués - Sa Planassa, close to Punta Prima, by the sea cliffs, metamorphic schists, 42°15' N-3°17' E, 100 m.
29. Cadaqués - Mas de la Sala, quartz dike emerging among *Cistus* scrubland, 42°15' N-3°16' E, 180-200 m.
30. Roses - Cap Norfeu, northern limestone cliffs near Rec de la Calç, 42°14' N-3°15' E, 40-50 m.
31. Roses - Serrat de Can Berta, slopes of schists near the road to Cadaqués, 42°17' N-3°12' E, 150 m.

32. Roses - Mas de la Torre del Sastre, quartz and schist outcrops in *Cistus* scrubland, 42°14' N-3°12' E, 175-200 m.
33. Roses - Punta Falconera, slopes of weathered granite nearby the road to Cala Montjoi and an abandoned quarry of marble, isolated granodiorite blocks, 42°14' N-3°13' E, 25 m.
34. Roses - Above Canyelles Petites and s'Almadrava, granodiorite in sunny dry valley, 42°15' N-3°12' E, 100-130 m.

RESULTS

List of taxa

The species presented in this catalogue are arranged alphabetically. For each taxon, a brief note on ecology is provided, along with the number of the collection site. If considered necessary, a comment on morphology, distribution, or a concise taxonomical discussion is added. For those specimens analyzed with TLC, the content of lichen substances is given. Nomenclature follows mostly Roux (2011) and Nimis & Martellos (2008), and author names are abbreviated according to the most recent version of the "Authors of Fungal Names" (www.indexfungorum.org). Species of lichen and lichenicolous fungi new to the Iberian Peninsula are indicated by the symbol #, and those new to the autonomous community of Catalonia by a +.

Acarospora epithallina H. Magn.

This species forms minute, orange areoles, arranged in a more or less scattered manner on thalli of *Acarospora hilaris* (Fig. 3A). This species was collected only in one locality, and it was also observed, but not collected, in the Serrat de la Guerra mountain range (42°19' N-3°10' E). This is a characteristic species from the lichen association *Acarosporetum epithallino-hilaris* Crespo, Barreno & Follman, which has its chorological optimum in the Luso-Extremadurense vegetation province (Crespo et al., 1976). We consider that this taxon is occasionally present in our area of study, mainly represented by juvenile and sterile squamules, since it is far from the centre of its distribution in the Iberian Peninsula. Loc: 34.

Acarospora hilaris (Dufour) Hue

This taxon has a placodioid, lobed thallus, forming well-delimited rosettes, with a characteristic citrine colour (Fig. 3A). In our study area, we observed that young thalli are usually sterile. This species is locally very abundant, growing on steeply inclined to vertical surfaces (rarely wetted by rain) of very hard siliceous rocks, such as granite and schists, on sunny exposures. Loc: 5, 13, 15, 34.

Acarospora microcarpa (Nyl.) Wedd.

Lichenicolous lichen that grows on silicicolous species of *Diploschistes*. It has been previously reported on *D. actinostomus* from the study area (Llimona, 1995), and on *D. gyrophoricus* from the nearby area of Maresme (Barbero, 1998). However, the specimens collected in this study were found only on thalli of *D. euganeus*, growing on horizontal to gently sloping surfaces, sun-exposed, and slightly eutrophied. Loc: 22, 34.

+ ***Acarospora modenensis*** H. Magn.

This taxon has an extremely reduced white thallus, often visible only as a thin rim surrounding the apothecia (Fig. 3B). It has been reported from very few localities in the Iberian Peninsula (Pereira, 1992; Calatayud & Barreno, 1994; Aragón et al., 2006) and, in fact, its worldwide distribution is still poorly known (Nimis & Poelt, 1987). In this study, it was found growing on weathered granite, on subvertical, sun-exposed surfaces. Loc: 33.

Acarospora oligospora (Nyl.) Arnold

This species is easily recognizable because of its polysporous asci with 16 to 32 ascospores (Clauzade & Roux, 1985). It grows in the same locality and conditions as *A. modenensis*. Loc: 33.

Acarospora cf. ***scotica*** Hue

Two specimens were found, each with extensive thalli, formed by dull dark brown, sharp-edged areolae, with black margins. Although it has abundant, immersed apothecia, the identification of the specimens is not completely certain since no ascospores were found; *A. scotica* has been reported as usually sterile in the Sonoran Desert (Knudsen, 2007). Loc: 5, 28.

+ ***Acarospora sinopica*** (Wahlenb.) Körb.

This taxon shows thalli formed by more or less aggregated, rounded, rust-red areolae, with punctiform apothecia. This species usually occurs from the montane to the alpine belts (Wirth, 1980). It has been recorded in the Iberian Peninsula living from 800 up to 2300 m (Sancho, 1986; Terrón, 1991; Terrón et al., 2000a, 2000b; Barreno & Pérez-Ortega, 2003). Although this species clearly prefers high elevations, it seems that in the study area there are some sites that are humid and cold enough to be suitable for its growth. All previous records from the Iberian Peninsula, as well as our specimens, grow on subvertical to vertical surfaces of iron-rich schists, usually accompanied by *Tremolecia atrata*. Loc: 8, 16.

Acarospora sulphurata (Arnold) Arnold

This species is very similar to *A. hilaris*, but it has a flatter thallus with shorter and wider lobules, and globose instead of ellipsoidal ascospores. It grows on moderately inclined to subvertical, rather nutrient-enriched surfaces of schists, preferably on sunny exposures. Loc: 5, 17.

Acarospora umbilicata Bagl.

The thallus of this taxon is formed by more or less imbricate, olive green areolae, covered by disperse, white pruina, C+ and KC+ reddish. It grows on nutrient-enriched surfaces of siliceous rocks. Loc: 31, 33.

Acarospora veronensis A. Massal.

This taxon shows a remarkable variation of thallus colour in the study area, being brownish-yellow on sheltered rock faces, and becoming dark brown on sun-exposed sites. It grows from flat to vertical surfaces of hard siliceous rocks, usually in eutrophied sites. Loc: 5, 15, 16, 26, 28.

Acrocordia macrospora A. Massal.

This species has fissurate-areolate, dull greyish-brown thalli, and large (up to 0.8 mm diam.), black perithecia, with involucrellum extending towards the margins, but never covering the perithecia at the base. It prefers to grow on protected sites of siliceous rocks. Loc: 16, 31.

Agonimia opuntiella (Buschardt & Poelt) Vězda

This tiny taxon is easily recognized by its greenish-grey, squamulose thallus, with minute hyaline hairs on the surface. In the study area, it grows very abundantly on the climbing dunes mixed with terricolous mosses and on siliceous schists, always in open habitats. Loc: 12, 26.

Amandinea sp.

Several specimens belonging to the same taxon of the genus *Amandinea* were found in this study with the following characters: thallus minute, rimose, pale grey, negative to all chemical spot tests (K, KC, C, and P), apothecia lecideine, sessile, 0.2-0.4 diam., with small *Physconia*-type ascospores of size 10-12(-13) x (5-)6-7 µm, and filiform recurved pycnidiospores. Among all known saxicolous *Amandinea* species, our specimens can only be assigned to *A. punctata* (Hoffm.) Coppins & Scheid. or *A. lecideina* (H. Mayrhofer & Poelt) Scheid. & H. Mayrhofer. However, according to the literature, both taxa have larger ascospores (8-20 × 5-9 µm and 10-15 x 6.5-8.5 µm, respectively), which in *A. punctata* additionally belong to the *Buellia*-type. Loc: 22, 27.

Anaptychia runcinata (With.) J. R. Laundon

This foliose lichen was found forming big rosettes up to 20 cm diam., sometimes with big ocellate apothecia. It is locally abundant, but restricted to localities with high air humidity. It was found growing on moderately inclined schist surfaces or on terricolous mosses and other foliose lichens, generally on north exposures. Loc: 7, 15, 16.

Anema nummularium (Dufour) Nyl.

This taxon forms small, peltate, black thalli, with few lecanorine apothecia in the centre, typically on calcareous rain-track surfaces (Moreno, 1988). However, in the study area, *A. nummularium* grows on sheltered rain-track surfaces of granites and schists. This might be because, although the rocks are acid, carbonates and other salts from dust, animal excrements, etc., are dissolved in the water layer (Llimona & Egea, 1985). Loc: 13, 33.

Arthonia lecanorina (Almq.) R. Sant.

This is a lichenicolous fungus that usually grows on apothecial discs of the *Lecanora dispersa* group (Grube, 2007). In the study area, it was found growing on *L. dispersa*. Loc: 8.

+ ***Arthonia molendoi*** (Heufl. ex Frauenf.) R. Sant.

This taxon is a lichenicolous fungus that grows on *Caloplaca* and *Xanthoria* species (Grube, 2007). In our study area, it was found only on *Caloplaca aegaea*. Loc: 4.

Arthonia varians (Davies) Nyl.

This species is a lichenicolous fungus described as parasitic on apothecial discs of *Lecanora rupicola* group (Grube, 2007). The only studied sample was found however, parasiting *Lecanora polytropa*, a species that does not belong to the *L. rupicola* group. Nevertheless, the morphological characters of our specimen (pale hypothecium, 3-septate ascospores of size 15-17 x 4-5 µm) fit the description of *Arthonia varians* provided by Grube (2007). Therefore, our finding adds a new host to this lichenicolous species. Loc: 16.

Aspicilia caesiocinerea (Nyl. ex Malbr.) Arnold

We found considerable variation in the thallus morphology of this species in both colour (from white or pale grey to dark bluish-grey, sometimes dark olive green), and areolae shape (from polygonal and flat to rounded and somewhat convex). One of the morphotypes we found shows the thallus formed by white, convex areolae (Fig. 3C), which can be confused with *A*. *supertegens* Arnold. All our specimens, however, have ascospores of size 24-29 x 13-16 µm and pycnidiospores of size 7-11 x 1 µm whereas in *A*. *supertegens* ascorpores are slightly shorter (15-25 x 10-14 µm) and pycnidiospores are remarkably longer (17-40 x 1 µm). This is a widespread and ubiquitous taxon, which grows on hard siliceous rocks, from flat to subvertical surfaces, on all possible exposures. Loc: 1, 3, 6, 8, 9, 13, 15, 17, 23, 24, 25, 26.

Aspicilia calcarea (L.) Mudd

Although this is a common and widespread taxon, it was collected in the study area only once, growing on exposed surfaces of limestone near the coast. Loc: 30.

Aspicilia contorta (Hoffm.) Kremp. subsp. ***hoffmanniana*** S. Ekman & Fröberg ex R. Sant.

This species was found on carbonate-rich substrates as well as on nutrient-enriched schists, commonly in open situations. It has been previously reported from the study area as part of the lichen communities that grow on rain-tracks of siliceous rocks [Llimona & Egea, 1985, sub *A. hoffmannii* (Ach.) Flagey]. Loc: 6, 8, 12, 30.

Aspicilia cupreoglauca B. de Lesd.

This species can be distinguished from the more common taxon *A*. *intermutans* (Nyl.) Arnold, by its bright brown thallus and the presence of dark pigments in the cortex layer. It grows on hard siliceous rocks, on inclined surfaces in sunny exposures, such as top of blocks. Loc: 7, 8, 16, 22.

Aspicilia farinosa (Flörke) Flagey

This taxon is morphologically very similar to *A. calcarea* due to the presence of pruina that gives a white farinose appearance to the thallus, but *A. farinosa* has smaller ascospores and paraphyses branched and anastomosing. It grows on exposed limestone surfaces. Loc: 30.

Aspicilia inornata Arnold

This species also has a similar appearance to *A. calcarea*, because of its chalky white thallus and pruinose apothecia (Fig. 3D), but it can be distinguished by having 6-8 ascospores per ascus, and by living on siliceous rocks (Clauzade & Roux, 1985). In the study area, it grows on sheltered schistose surfaces, at an unusually low altitude, considering that this taxon has previously been reported in the Iberian Peninsula between 800 and 2650 m (Hladun, 1981; Terrón, 1991; Aragón et al., 2006; Etayo, 2010). Loc: 4, 28, 33.

Aspicilia intermutans (Nyl.) Arnold

We found some variation in the colour of the thallus of this species, from pale beige to brown. The paler specimens can be confused with *A. epyglypta* (Norrl. ex Nyl.) Hue, a maritime taxon that also has thallus K+ red. All our specimens, however, have ascospores of size 23-32 x 10-17 µm and short conidia 6-10 x 1 µm, while *A. epyglypta* have shorter ascospores (18-26 x 11-15 µm) and larger conidia (11-24 x 1 µm). This is the most abundant species of genus *Aspicilia* in the study area, similarly with previous reports from areas of the eastern Mediterranean (Calatayud & Barreno, 1994). It has a broad ecological amplitude, as it appears growing on different siliceous substrates, more or less rich in nutrients, preferably on horizontal or gently sloping surfaces, and, usually, at ground level. Loc: 3, 6, 7, 8, 9, 15, 16, 20, 21, 23, 24, 25, 26, 27, 28.

+ ***Aspicilia subdepressa*** (Nyl.) Arnold

This taxon is very similar to specimens of *A. caesiocinerea* with a dark bluish-grey thallus. In fact, *A. subdepressa* had been considered a variety of *A. caesiocinerea* by Clauzade & Roux (1985). However, Roux et al. (2011) recently reconsidered its status as an independent species since it can be distinguished from *A. caesiocinerea* by having a thallus K+ yellow, smaller ascospores and by the lack of aspicilin (Roux et al., 2011). Our records significantly widen the known distribution of this species, which was previously considered as limited to environments from the montane to the subalpine belts (Roux et al., 2011). In the Iberian Peninsula, it has been reported from Serra da Estrela (Boom & Giralt, 1999) and from the Galician coast, sub *A. caesiocinerea* var. *subdepressa* (e.g., Paz-Bermúdez, 1998; Freire Dopazo et al., 2000; Paz Bermúdez et al., 2003). Loc: 3, 6, 23, 27, 31.

Bagliettoa calciseda (DC.) Gueidan & Cl. Roux

This taxon has been recently transferred to the genus *Bagliettoa* based on its lithocortex, a type of cortex present in all the species of this genus, but absent in other species of *Verrucaria* s. l. (Gueidan & Roux, 2007). In our study, *B. calciseda* was very abundant in the climbing dunes, where it grows extensively on the calcareous cement, avoiding the siliceous grains. Several specimens were parasited by *Caloplaca polycarpa*. Loc: 12.

Bagliettoa cazzae (Zahlbr.) Vězda & Poelt

This species is recognized by its endolithic thalli and small perithecia (up to 0.2 mm diam.) with radially striated involucrellum. It is locally abundant, and grows on steep surfaces of limestone near the sea, preferably on sheltered sites. Loc: 30.

Botryolepraria lesdainii (Hue) Canals, Hern.-Mar., Gómez-Bolea & Llimona

This taxon has its thallus formed by loosely organized hyphae, with a cotton-like aspect, that hold the photobiont in their distal parts. In our area of study, it was found on sheltered surfaces on the climbing dunes. Loc: 12.

Buellia abstracta (Nyl.) H. Olivier

(= *Buellia sequax* sensu Scheidegger 1993 not *Buellia sequax* (Nyl.) Zahlbr s. str.)

In Scheidegger (1993), the species *B. abstracta* was synonymized under *B. sequax* (Nyl.) Zahlbr. A recent morphological and chemical study of the type material of these two species by Giralt et al. (2011), however, has re-established the identity of *B. sequax*, and has recovered the species *B. abstracta.* According to Giralt et al. (2011), both taxa can be easily distinguished based on the following characters: *B. sequax* has a *dispersa*-type proper exciple, a hymenium inspersed with oil droplets, *Dirinaria*-to *Physconia*-type ascospores, when young, and *Buellia*-type, when mature, and atranorin, chloroatranorin, and diploicin as major compounds, whereas *B. abstracta* has a *aethalea*-type proper exciple, a hymenium not inspersed with oil droplets, *Buellia*-type ascospores, narrower than those in *B. sequax*, and may sometimes contain norstictic acid. Almost all our specimens that were initially identified as *B. sequax* following Scheidegger (1993) and other floras (e.g., Bungartz et al., 2007; Coppins et al., 2009), were ascribed to *B. abstracta* sensu Giralt et al. (2011). In the study area, we found remarkable variation of the thallus morphology among specimens of *B. abstracta* (i.e., from endolithic to well-developed rimose thalli). This species was found on sun-exposed surfaces of different types of siliceous rocks, frequently with some soil deposition. Loc: 3, 13, 15, 19, 25, 26, 27, 28, 31, 33.

Buellia atrocinerella (Nyl.) Scheid.

This species was found only once, growing on steep, sun-exposed schists. Although this taxon seems to occur rarely in the study area, it has been recorded as more abundant in other Mediterranean areas (Egea, 1980, sub *Rinodina atrocinerella*; Calatayud & Barreno, 1994). Loc: 23.

Buellia badia (Fr.) A. Massal.

This taxon forms minute crustose, areolate to subsquamulose, brown thalli that initially grow on other lichens (in our study area, usually on *Xanthoparmelia* species), and eventually it can grow independently on siliceous substrates, on sun-exposed gently sloping surfaces. Previous studies stated that this species lacks secondary substances (e.g., Scheidegger, 1993; Coppins et al., 2009), or if present, these substances are likely to be contaminants of host lichens (Bungartz et al., 2007). However, we detected several lichen substances (e.g., norstictic acid) belonging to the thallus of *B. badia* itself, agreeing with other recent work from other regions (M. Giralt, pers. comm.). Loc: 6, 23, 25, 26, 28, 34.

Buellia caloplacivora Llimona & Egea

This species, described by Llimona & Egea (1984) from the Columbretes islands (Castelló, Spain), was treated as a synonym of *B. sequax* [sensu Scheidegger (= *B. abstracta*)] in the revision of the genus *Buellia* by Scheidegger (1993). However, in a recent study of the genus *Buellia* s. l. in the Canary Islands (Giralt & Boom, 2011) *B. caloplacivora* has been reconsidered as an independent taxon, because it can be clearly distinguished from *B. sequax* sensu Scheidegger (= *B. abstracta*) by the following characters: excipulum *aethalea*-type, epihymenium dark olivaceous to aeruginose N+ red-violet, hypothecium with oil droplets, and larger ascospores. Based on these traits, Giralt & Boom (2011) have considered that *B. caloplacivora* is more closely related to species of the *B. subalbula*-group than to *B. sequax* sensu Scheidegger (= *B. abstracta*). Additionally, Giralt & Boom (2011) describe in their study two different chemotypes for *B. caloplacivora* (one without lichen substances and the other containing norstictic acid), and two morphotypes (one with thick, rimose, chalky thalli, with apothecia often pruinose, and the other with thin, creamy to ochraceous thalli, and usually epruinose apothecia). Both chemotypes and morphotypes were found in our study area. We initially identified the specimens of *B. caloplacivora* with thick, chalky thallus and norstictic acid as *B. maritima* (A. Massal.) Bagl. following the concept for this taxon of Bungartz et al. (2007). However, *B. maritima* is an accepted and correct synonym of *B. stellulata* (M. Giralt, pers. comm.) and, therefore (and in contrast to *B. caloplacivora*) it is unrelated to the *B. subalbula*-group, contrary to what was stated by Bungartz et al. (2007). Further studies are necessary to unravel the complex taxonomy of the *B. subalbula*-group in the Northern Hemisphere [a taxonomic revision of this group from the Southern Hemisphere has already been published (Bungartz et al., 2011)]. *Buellia sequax* s. str. (see Giralt et al., 2011) is not closely related to either *B. caloplacivora* (and the other taxa of the *B. subalbula*-group) or *B. abstracta* (= *B. sequax* sensu Scheidegger). In the study area, *B. caloplacivora* was found on acidic and calcareous substrates, on moderately inclined, sun-exposed surfaces, associated with *Caloplaca* species. Loc: 7, 21, 30.

Buellia dispersa A. Massal.

This is a very polymorphic lichen species, for which three different morphotypes have been described by Bungartz et al. (2002) based on the type of thallus growth, the shape and colour of the areolae, and the presence and distribution of pruina on the surface. All the specimens from this study fit with the morphotype I described in Bungartz et al. (2002). This taxon was found frequently in the study area, on horizontal to moderately inclined schistose surfaces. Loc: 6, 13, 16, 17, 20, 22, 25, 26.

Buellia leptoclinoides (Nyl.) J. Steiner

This species can be easily distinguished from the other *Buellia* species found in the study area by its hymenium inspersed with oil droplets and the *Callispora*-type ascospores. In fact, this is the only saxicolous member of *Buellia* s. str. (= *Hafellia*) present in the study area. It grows on moderately inclined to subvertical faces of acidic rocks. Loc: 21, 27.

Buellia spuria (Schaer.) Anzi

This taxon has white, rimose-areolate thalli, a conspicuous black hypothallus, and a green to olive epihymenium, N+ violet. These morphological traits are shared with *B. stellulata* (Taylor) Mudd, but both taxa can be clearly separated based on their secondary substances: *B. spuria* contains atranorin and norstictic and connorstictic acids, while *B. stellulata* also contains atranorin, but additionally has 2'-*0*-methylperlatolic and confluentic acids (Bungartz & Nash, 2004). It was found in the study area on horizontal to subvertical acidic rocks. Loc: 3, 6, 16, 23, 25, 27, 28.

Buellia stellulata (Taylor) Mudd

This taxon has minute, white, rimose-areolate, K+ yellow thallus, with conspicuous black hypothallus, I- medullae, and cryptolecanorine apothecia. It was found very frequently in the study area, growing on siliceous rocks, mainly on sun-exposed surfaces. Loc: 6, 13, 15, 16, 20, 22, 23, 25, 26, 27, 32.

Buellia subdisciformis (Leight.) Vain.

This species is very similar to *B. leptoclinoides* as both have thick, rimose thalli, medulla I-, and adnate to sessile, large apothecia. *Buellia subdisciformis*, however, does not have a hymenium inspersed with oil droplets and its ascospores are *Physconia*-type instead of *Callispora* -type. It was found growing on different hard siliceous rocks and on various inclinations (from horizontal rocks to overhanging surfaces), although it was more frequent north-facing surfaces, avoiding direct sunlit. Loc: 6, 7, 11, 16, 20, 21, 22, 24, 25, 28, 33.

Buellia tesserata Körb.

This taxon forms a whitish to grey, areolate thallus with a conspicuous, dark, fimbriate prothallus, and markedly convex apothecia. Several specimens collected in the study area show an unusually thick thallus, formed by strongly convex areolae (Fig. 3E). Small, young thalli, with still immersed apothecia, are somewhat similar to *B. stellulata*, but can be readily distinguished since *B. tesserata* contains 3-chlorodivaricatic acid (Rico et al., 2003). An additional distinguishing character is the colour of the epihymenium, which is green-aeruginose and N+ red-violet in *B. stellutata*, and brown and N- in *B. tesserata*. Loc: 4, 21, 22, 23, 27, 28, 29, 33.

Buellia tirolensis Körb.

This species has rimose-areolate thallus, formed by bright brown areolae with a white margin (Fig. 3F). It is very closely related with *B. atrocinerella*, even considered as potentially conspecific (M. Giralt, pers. comm.). In fact, both taxa differ in the size of the marginal areolae and the ascospores, the former being more elongate and the latter slightly larger in *B. atrocinerella* than in *B. tirolensis* (Scheidegger, 1993). It grows on nutrient-enriched sun-exposed schists. Loc: 15, 23, 28.

Caloplaca aegaea Sipman

This taxon is easily distinguished from *C. thallincola* (Wedd.) Du Rietz (the other siliceous coastal species of the *C. aurantia* group, absent from the study area) by having shorter and apically non-appressed lobules, paraplectenchymatous cortex, thicker paraphyses, and rhomboidal ascospores. Additionally, they have different distributions: *C. aegaea* is mostly Mediterranean, whereas *C. thallincola* has a clearly Atlantic distribution (Gaya, 2009). In the study area, *C. aegaea* grows on granite and schists, on horizontal or gently sloping surfaces, usually at shaded and humid sites, such as sites near inland freshwater streams or in the supralittoral zone in coastal localities. Loc: 2, 4, 14, 27.

Caloplaca aetnensis B. de Lesd.

This *Caloplaca* species is characterized by having whitish thallus, orange proper margin, and a prominent, crenate thalline margin when apothecia are young. It was collected on weathered granite, on sun-exposed and heavily nutrient-rich surfaces, sometimes close to the soil surface. Loc: 32, 33.

Caloplaca alociza (A. Massal.) Mig.

This species usually has an endolithic (rarely epilithic) thallus, with immersed black apothecia. It grows on sunny exposed calcareous rocks. Loc: 30.

Caloplaca aractina (Fr.) Häyrén

This taxon is characterized by having a dark grey to black thallus, and apothecia with a thick, persistent concolor thalline margin. It grows on hard siliceous rocks from moderately inclined to vertical, mainly north-facing surfaces. Loc: 4, 7, 11, 20, 24 25, 26.

Caloplaca arcis (Poelt & Vĕzda) Arup

This taxon was collected in one site, growing on mortar, and the identity of the specimens was kindly confirmed by Ulf Arup. This species, which belongs to the *Caloplaca citrina* group, is characterized by having its thallus covered by coarse blastidia. Loc: 7.

Caloplaca arenaria (Pers.) Müll. Arg.

This taxon forms inconspicuous thalli with flat, orange apothecia, not larger than 0.6 mm in diam. It is easy to distinguish from other species of the *Caloplaca ferruginea* group by the width of the isthmus, which can reach up to 3 µm. It is very frequent in the study area, especially on enriched-nutrient sun-exposed siliceous rocks. Loc: 6, 22, 23, 25, 27, 28, 31, 33.

Caloplaca atroflava (Turner) Mong.

This species has a dark grey to black thallus with a green tinge, very similar to *C. aractina*, but the latter has a persistent concolor thalline margin while *C. atroflava* lacks this thalline margin and has a proper margin. It was found in only one locality where it was very abundant, growing on siliceous rocks at the sides of a small stream, on sites temporarily submerged when water levels increase. Loc: 13.

Caloplaca aurantia (Pers.) Hellb.

This taxon was found as quite abundant near massive limestone outcrops, on sunny nutrient-enriched surfaces. It also forms well-developed thalli on the most compacted areas of the climbing dunes. Loc: 12, 30.

Caloplaca austrocitrina Vondrák, P. Říha, Arup & Søchting

Few thalli from a taxon belonging to the *C. citrina* group were found growing on the banks of a stream. These specimens have thalli formed by areolae or small aggregated squamules, 0.5-1.5 mm wide and 175-330 µm thick, with marginal soralia when young, although soralia may cover the entire surface when thalli grow old. The morphology of these specimens fits the descriptions given for the species *C. austrocitrina*, a recently described species from the Black Sea region, included in the most recent key for the *C. citrina* group (Vondrák et al., 2009). This taxon is very similar *C. flavocitrina* (Nyl.) H. Olivier, and the main distinguishing feature is that *C. austrocitrina* has larger and thicker areolae than *C. flavocitrina* (Vondrák et al., 2009). In its original description, *C. austrocitrina* was reported growing on cement mortar near water, as was the case with our specimens, which live at the banks of a stream, and are temporarily submerged when water levels increase after rain. Loc: 13.

Caloplaca carphinea (Fr.) Jatta

This lobed *Caloplaca* species has a characteristic yellowish-green thallus, being very similar to *Dimelaena oreina*. In addition, the two species grow frequently together in the study area. *Caloplaca carphinea* has, however, the polarilocular ascospores and the apothecial disc K+ purple. This species is quite abundant on sunny quartz outcrops. Loc: 30, 32.

Caloplaca crenularia (With.) J. R. Laundon

This taxon is one of the most widespread and frequent in the study area. It shows a wide variation of the thallus morphology, from almost inconspicuous to well-developed and thick. The thallus colour can also vary from dull pale grey to dark greenish-grey, almost black. It was growing mainly on slightly nutrient-enriched surfaces of acidic rocks, from to subhorizontal to overhanging surfaces. Loc: 6, 8, 11, 18, 15, 16, 20, 21, 22, 25, 26, 27, 28.

Caloplaca diffusa Vondrák & Llimona

This taxon has been recently described within the *Caloplaca crenulatella* complex, partly based on specimens from our study area (Vondrák et al., 2011). This species is similar to *C. maritima*, but has a continuous diffuse thallus, thinner ascospore septa, and grows on coastal siliceous cliffs, around seepage crevices and at the bottom of seasonal streams (Vondrák et al., 2011). In the study area, it was collected at the edge of seasonal streams in areas that were occasionally inundated, especially during autumn and spring. Loc: 13, 14.

Caloplaca flavescens (Huds.) J. R. Laundon
Specimens with flattened and wide lobules can be confused with *C. aurantia*, but *C. flavescens* can be unequivocally recognized by its lemon-shaped to rhomboidal ascospores, and the presence of crystals in the upper cortex (Gaya, 2009). It was found growing on the mortar of the walls of the Quermançó castle, on carbonate-rich schists and limestone. Loc: 1, 16, 30.

+ ***Caloplaca flavocitrina*** (Nyl.) H. Olivier
This species is very similar to *C. citrina* (Hoffm.) Th.Fr., but it has mainly marginal soralia that do not cover the entire areolae surface (Arup, 2006). Although previous works have found that this taxon quite often has apothecia (Arup, 2006), very few of the specimens studied in this study were fertile. It was found growing on carbonate-rich rocks, as well as on siliceous rocks, usually forming small thalli. It constitutes the second record for the Iberian Peninsula, after Etayo (2010); as Etayo remarks in his work, this taxon has probably been confused with *C. citrina* in previous records for Spain and Portugal. Loc: 8, 12, 15, 33.

Caloplaca flavovirescens (Wulfen) Dalla Torre & Sarnth.
We found that *C. flavovirescens* was quite abundant in localities with limestone, forming big thalli on steep surfaces, usually exposed to the north. Loc: 30.

+ ***Caloplaca furax*** Egea & Llimona
This taxon appears growing on thalli of silicicolous *Aspicilia*. It starts its development forming a small, dark greyish-green, subsquamulose thallus, which can grow extensively until it covers almost completely the host thallus (Fig. 4A). In the study area, it was found mainly on the *A. caesiocinerea* specimens growing in sunny exposures. Loc: 6, 13, 17, 26, 32.

Caloplaca grimmiae (Nyl.) H. Olivier

Lichenicolous lichen growing on *Candelariella vitellina*, it forms minute thalli with dull reddish apothecia. Rare in the study area. Loc: 7, 34.

Caloplaca inconnexa (Nyl.) Zahlbr. var. ***nesodes*** Poelt & Nimis

This variety of *C. inconnexa* is parasitic on diverse species of silicicolous *Aspicilia* (Fig. 4B) and is apparently restricted to the Mediterranean area (Nimis & Poelt, 1987). In the study area, it was found only on thalli of *A. caesiocinerea* specimens growing on horizontal or gently sloping surfaces, usually near small streams or small ledges where water pools for a short time after rain. Loc: 3, 6, 9, 14, 26.

Caloplaca irrubescens (Nyl.) Zahlbr.

The thallus of *C. irrubescens* is very variable, from sublobate, fissurate-areolate to subsquamulose. It is frequent in steeply inclined siliceous rocks, in sunny rain-track surfaces. It usually invades other common lichens from these special ecological conditions, such as *Lichinella stipatula* or *Peltula euploca*. Loc: 1, 6, 9, 15, 17, 28, 34.

Caloplaca ligustica B. de Lesd.

This taxon grows on weathered granites on subvertical surfaces that receive direct sunlight. In the two localities where it was found it is very abundant but, surprisingly, it was absent from other sunny localities on the same substrate. Loc: 33, 34.

Caloplaca marina Wedd.

This taxon grows abundantly in maritime localities, on very exposed surfaces, sometimes on the supralittoral zone, subject to salt water spray. Loc: 4, 10, 15, 20, 27.

Caloplaca maritima (B. de Lesd.) B. de Lesd.

Arup (1997) pointed out that *C. maritima* is less restrictive in its habitat requirements than *C. marina*, and can occur from coastal areas to a few kilometres inland. However, in the study area, *C. maritima* was found in almost the same localities as *C. marina*, usually near to the coast. Loc: 4, 15, 20, 21, 22.

Caloplaca polycarpa (A. Massal.) Zahlbr.

This taxon was found growing on limestone, as well as on the thallus of *Bagliettoa calciseda*. Loc: 12.

Caloplaca rubelliana (Ach.) Lojka

This species commonly has thin, small thalli, which are easy to spot in the field for their rust-red colour, and *Aspicilia*-like apothecia (Fig. 4C). It grows on hard steeply siliceous rocks, usually near rain-tracks. Loc: 5, 6, 13, 17, 26, 28, 32, 34.

Caloplaca subochracea (Wedd.) Werner var. ***luteococcinea*** Clauzade & Cl. Roux

This variety of *C. subochracea* shows considerable variability of the thallus colour, from pale yellow to orange, depending on exposure of the thallus to the sun, as reported by Nimis & Martellos (2008). It is locally very abundant, growing on coastal limestone outcrops, from sun-exposed to sheltered sites. Loc: 30.

Caloplaca variabilis (Pers.) Müll. Arg.

This species can be confused with epilithic forms of *C. alociza*, as both have a grey thallus with epruinose black apothecia. However, the thalline margin of *C. alociza* becomes rapidly excluded, while it is persistent in *C. variabilis*. A recent molecular phylogenetic study (Muggia et al., 2008) has confirmed the separation of these taxa. Loc: 30.

Caloplaca vitellinula (Nyl.) H. Olivier

This species is very similar to *Candelariella aurella* (Hoffm.) Zahlbr. (which usually grows nearby), but can be easily distinguished by its K+ purple apothecia and polarilocular ascospores. Although it has been reported from neighbouring

Mediterranean areas (Barbero, 1998) growing on weathered granite, in our study area, it was only found on marbles. Loc: 33.

Candelariella aurella (Hoffm.) Zahlbr.

This taxon can be separated from other *Candelariella* species by having 8-spored asci and a reduced thallus. It was found on marble and on carbonate-rich schists. Loc: 4, 16, 21, 31.

Candelariella vitellina (Hoffm.) Müll. Arg.

This taxon is one of the most common lichens in the area, growing on siliceous rocks as well as on thalli of other crustose lichens. Loc: 6, 7, 8, 13, 14, 21, 24, 25, 26, 28, 34.

Catillaria atomarioides (Müll. Arg.) H. Kilias

This species is very similar to *C. chalybeia* (Borr.) A. Massal., but its apothecia are smaller, not larger than 0.4 mm in diam. It is thought to be a rather common species on siliceous substrates, but we recorded it from only two localities. It may have been overlooked at other sites, due to its small size. Loc: 8, 25.

Catillaria chalybeia (Borrer) A. Massal.

This is a ubiquitous lichen that grows on various siliceous rocks, on sheltered, nutrient-enriched surfaces, and near water seepage surfaces. It has been also found growing on other lichen thalli. Loc: 2, 7, 8, 9, 10, 13, 25, 31, 33.

Catillaria lenticularis (Ach.) Th. Fr.

This species is also similar to *C. chalybeia*, but in *C. lenticularis* apothecia are brown to dark brown rather than black, the excipulum is not carbonized, and it usually grows on calcareous substrates. Loc: 25, 30.

Cercidospora caudata Kernst.

Lichenicolous fungus growing on *Caloplaca arenaria*. It is mainly characterized by its markedly heteropolar ascospores, with the lower cell considerably longer than the upper cell and also slightly curved. Loc: 22, 28.

Cercidospora solearispora Calat., Nav.-Ros. & Hafellner

Lichenicolous fungus growing on *Aspicilia* spp., mostly on species that contain norstictic acid (Navarro-Rosinés et al., 2009a). This taxon is characterized by its markedly heteropolar ascospores (the lower cell is 1/3 of the overall length), sole-shaped. It was found growing on *A. intermutans*, and it had been previously recorded from the study area, growing on *A. cupreoglauca* (Navarro-Rosinés et al., 2009a). Loc: 25.

Cercidospora sp. 1

We found a specimen of *Cercidospora* growing on apothecia of *Caloplaca irrubescens*, which does not match any known species. It is very similar to *Cercidospora caudata*, as it has heteropolar ascospores, with the lower cell longer and slightly curved. However, our specimen has mainly tetrasporate asci, while *C. caudata* has octosporate asci and is a parasite of *Caloplaca arenaria*. Based on the characteristics of number of ascospores per ascus and the lichen host species, we consider that this specimen belongs to a potentially undescribed species. Our observations are based in one heavily infected sample of *Caloplaca arenaria* and, for this reason, more specimens are needed to revise in order to describe this putative new species. Loc: 28.

Cercidospora sp. 2

We found a specimen of *Cercidospora* growing on apothecia and thalli of *Caloplaca crenularia*, having octosporate asci and heteropolar ascospores, with the lower cell longer than the upper one, and slightly curved. These characteristics are shared with *Cercidospora caudata*, but the ascospores of our specimen are (14-)15-19.5(-24) x 4-

6.5 µm, while in *C. caudata* are (16-)18-25(-33) x 4-6(-7) µm. Based on the differences in the spore size and the lichen host species, we consider that this specimen seems to belong to a new undescribed species. Our observations are, however, based in only one sample of *Caloplaca crenularia*, which present very few parasitic perithecia of *Cercidospora* sp. 2**.** Therefore, as for the previous taxon, more specimens are needed to revise in order to describe this putative new species. Loc: 17.

Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.
Despite being a widespread taxon, in the study area it was collected only once, living on siliceous soils among rocks. The TLC revealed that the specimen only contains protocetraric and fumarprotocetraric acids, despite confumarprotocetraric and quaesitic acids have also been reported in this taxon (Burgaz & Ahti, 2009). Loc: 16.

+ ***Cladonia firma*** (Nyl.) Nyl.
This species shows a well-developed primary thallus, formed by big squamules, dark olive green in colour, P+ red, and it very rarely bears podetia (not seen in our samples). It contains atranorin and protocetraric and fumarprotocetraric acids. It was found growing on soil and on a shallow layer of soil on schists. Loc: 7.

Cladonia foliacea (Huds.) Willd.
Our specimens contain fumarprotocetraric and usnic acids. It is locally abundant, growing on sun-exposed siliceous soils in open grasslands. Loc: 3, 19.

Cladonia furcata (Huds.) Schrad.
This is a species very variable chemically, with several described chemotypes (Burgaz & Ahti, 2009). All our specimens correspond to the chemotype I containing fumarprotocetraric and protocetraric acids. Loc: 7, 19.

Cladonia homosekikaica Nuno
This taxon is morphologically very similar to *C. chlorophaea*, with its finely sorediate

podetia. TLC analyses, however, revealed some collections belong to *C. homosekikaica* because they contain homosekikaic acid, in addition to fumarprotocetraric acid, which is also present in *C. chlorophaea*. It was found growing on exposed sites on siliceous soil (in locality 30, it was collected on granitic sand near limestone outcrops). Loc: 7, 30.

Cladonia humilis (With.) J.R. Laundon

This taxon is very similar to *C. chlorophaea* and *C. homosekikaica*, as all have scyphose podetia, covered by farinose soredia, P+ red. However, *C. humilis* has smaller squamules and shorter podetia than the other two similar taxa. This species is very variable chemically, with up to three different chemotypes (Burgaz & Ahti, 2009), but our specimens all belong to chemotype I, with atranorin and fumarprotocetraric and protocetraric acids. It has been found on exposed acid soils. Loc: 8.

Cladonia mediterranea P. A. Duvign. & Abbayes

In this species, the primary thallus is evanescent, and the secondary thallus is cushion-like shape, formed by ecorticate podetia, dichotomically branched. It is similar to *C. mitis* Sandst., which usually has podetia ramified in three branches, but sometimes shows dichotomous branches. For this reason, TLC analyses are required to clearly separate these two taxa: both species have usnic acid, but in *C. mediterranea* we have detected perlatolic acid, while *C. mitis* has rangiformic acid. *Cladonia mediterranea* is a rather rare taxon with a Mediterranean-Atlantic distribution range (Nimis & Poelt, 1987). A recent monograph on the genus *Cladonia* (Burgaz & Ahti, 2009) drew attention to the alarming decline of *C. mediterranea* in Spain and Portugal, due to the perturbation of its favoured habitat (i.e., coastal forests of *Quercus suber*). We examined the decline of this lichen in our study area as well: the studied material from the locality 7 is from a collection of X. Llimona in May, 1986, and two wildfires have affected this locality since then (in July, 1986 and August, 2000). Despite a recent exhaustive survey, we did not find *C. mediterranea* in locality 7 again, probably meaning that this population is unrecoverable. Loc: 3, 7.

Cladonia pyxidata (L.) Hoffm.
All specimens analyzed contain fumarprotocetraric acid as a major compound. It is locally very abundant, growing on siliceous soils, on sites more or less covered by shrubs. Loc: 19.

Cladonia rangiformis Hoffm.
This taxon can be confused with *C. furcata* because of its morphological similarities, but it can be distinguished chemically by the presence of atranorin and rangiformic acid [all specimens analyzed belong to chemotype I sensu Burgaz & Ahti (2009)]. It grows on siliceous soil, preferably on exposed sites. Loc: 3, 25, 33.

Cladonia subcervicornis (Vain.) Kernst.
This species of *Cladonia* is easily distinguishable by its erect large squamules, with deeply lobed margins, and with a bluish-grey upper surface and a white lower surface that only becomes blackened at the base. It was found on somewhat sheltered acid soils. Loc: 7.

+ ***Cladonia subrangiformis*** L. Scriba ex Sandst.
The only collection we found belongs to the chemotype I, which contains atranorin and fumarprotocetraric acid as major compounds, and is the most frequent in the Iberian Peninsula (Burgaz & Ahti, 2009). It was collected on open siliceous soil. Loc: 19.

Collema cristatum (L.) Weber ex F. H. Wigg.
We found it only once on a limestone fissure, but it grows very abundantly on the climbing dunes, on gently sloping, well-lit surfaces. Loc: 13, 28.

Collema flaccidum (Ach.) Ach.

This is a suboceanic species (Nimis & Poelt, 1987) that is very rare in the area of study; we found it only once, growing on the climbing dunes. Loc: 12.

Collema ryssoleum (Tuck.) A. Schneider

We found this species usually growing on shaded, or scarcely sun-exposed, steep surfaces, with frequent water seepages. Loc: 7, 13, 23, 26, 33.

Collema subflaccidum Degel.

This species can be confused with *C. flaccidum*, but *C. subflaccidum* has smaller globose isidia, while *C. flaccidum* has flattened and ascending isidia. It is very rare in the study area, probably because of its oceanic to suboceanic distribution (Nimis & Poelt, 1987). We found it once on a schistose surface with water seepages. This is a species that grows typically on *Fraxinus* bark, and rarely on siliceous rocks (Gilbert et al., 2009a). Loc: 7.

Collema tenax (Sw.) Ach.

This taxon is a common and widespread species, which was collected from siliceous soils and from calcareous soils, where it was more abundant. Loc: 19, 30.

Coscinocladium gaditanum (Clemente) A. Crespo, Llimona & D. Hawksw.

This species is rather similar to *Diplocia canescens*, but thallus does not react with K, and has well-delimited punctiform soralia (Fig. 4D). It grows abundantly on the porous mortar of the Quermançó castle. Loc: 1.

Cyphelium marcianum B. de Lesd.

Lichenicolous lichen that grows on *Pertusaria pseudocorallina*, where it forms scattered, convex, lead-coloured granules. Our findings considerably increase the number of occurrences of this species in the Iberian Peninsula, from where there are very few previous records. Loc: 7, 11, 16, 22, 24.

Dactylospora parellaria (Nyl.) Arnold

Lichenicolous fungus found growing on *Ochrolechia parella*. There are a few previous reports of this taxon from the Iberian Peninsula (Sampaio, 1970a, sub *Lecidea parellaria* Nyl.; Navarro-Rosinés et al., 1994; Boom & Etayo, 2000). Loc: 8, 20, 25.

Dermatocarpon luridum (Dill. ex With.) J. R. Laundon

This is a cool-temperate to subarctic-subalpine species (Nimis & Martellos, 2008). Probably for this reason, *D. luridum* was found once, growing on north-facing schists on a long-lasting water seepage surface. Loc: 7.

Dermatocarpon miniatum (L.) W. Mann

Although this taxon usually grows on calcareous rocks, it was found on metamorphic schists and granites, on moderately sun-exposed rain-tracks and on sites temporarily submerged after rain. Loc: 1, 7, 13, 15, 23, 27.

Dimelaena oreina (Ach.) Norm.

This species is quite common in the study area, growing on hard siliceous rocks, especially quartz, on sunny and windy exposures. Despite being one of the most frequent lichen species in the alpine belts, it can also grow at much lower altitudes in warm dry sites (Nimis & Poelt, 1987) as demonstrated by its occurrence in our study area. Loc: 6, 8, 15, 23, 29, 28, 32.

Diploicia canescens (Dicks.) A. Massal.

This species shows greenish-grey lobed thalli, with coalescing soralia, and very rarely forms apothecia (none of our studied specimens was fertile). It grows on siliceous rocks, usually on subvertical surfaces or overhangings, protected against direct sunlight and from rain. Loc: 11, 16, 23, 24, 31.

Diploicia subcanescens (Werner) Hafellner & Poelt

This taxon is very similar to *D. canescens*, but its thalli and lobes are more robust, its colour is ash grey or whitish, soralia rarely break out, and apothecia are frequent. Their distributions are also different; since *D. subcanescens* is mainly a Mediterranean species, *D. canescens* lives in the Mediterranean and Atlantic regions of Europe. It is found on siliceous rocks, on sheltered surfaces, in areas with persistent dew. Loc: 16, 20, 27, 28.

Diploschistes actinostomus (Ach.) Zahlbr.

This species has perithecioid apothecia and brownish thallus, and grows on various siliceous rocks, on sun-exposed, flat or moderately sloping surfaces. Loc: 8, 11, 21, 22.

+ ***Diploschistes caesioplumbeus*** (Nyl.) Vain.

This species is similar to *D. actinostomus*, but has grey thalli and larger ascospores. It grows on nutrient-rich siliceous rocks, in sun-exposed conditions. Loc: 7, 13, 22, 24.

Diploschistes diacapsis (Ach.) Lumbsch subsp. ***neutrophilus*** (Clauzade & Cl. Roux) Clauzade & Cl. Roux

This subspecies was described to accommodate specimens of *D. diacapsis* with medulla I+ that grow on neutral clay soils instead of on carbonated or gypsum-rich soils (Clauzade & Roux, 1985, 1989). We have not observed amyloid medulla in any of our specimens. However, we did observe other morphological features that distinguish this subspecies, such as a considerable thinner thallus and its growth very adpressed to the soil, while generally the lower part of *D. diacapsis* gets detached from the substratum and arching from it as it grows old (Souza-Egipsy et al., 2002). It grows abundantly on the climbing dunes, preferring flat surfaces. Loc: 12.

Diploschistes euganeus (A. Massal.) J. Zahlbr.

This taxon is easily distinguished from the morphologically similar *D. actinostomus* by its lack of secondary substances and its broad ascospores. It grows on dry, sun-exposed siliceous rocks. Loc: 22, 25, 28, 34.

Diploschistes interpediens (Nyl.) Zahlbr.

In other works (e.g., Pant & Upreti, 1993; Fletcher & Hawksworth, 2009), this taxon has not been recognized at the species level after being synonymized with *D. scruposus* (Schreb.) Norm. by Lumbsch (1989). However, *D. interpediens* has eight ascospores per ascus, instead of four like in *D. scruposus*, and has a Mediterranean distribution, while *D. scruposus* has a broader distribution. Based on these traits, we consider that they must be treated as separate taxa. Loc: 3, 22.

Diploschistes muscorum (Scop.) R. Sant.

The species *D. muscorum* starts its development on *Cladonia* squamules, but can become independent and continue growing on mosses or on soil. Although some authors (e.g., Clauzade & Roux, 1985; Fletcher & Hawksworth, 2009) found this taxon to be restricted to calcareous soils, all our samples were collected on siliceous soils. Loc: 3, 19.

Diploschistes ocellatus (Vill.) Norm.

This species of *Diploschistes* is clearly distinguished from all other species of the genus for having lecanoroid apothecia and norstictic acid as a major compound. In the study area, this species is quite abundant locally on the climbing dunes, where it preferably colonizes horizontal to gently sloping exposed surfaces. Loc: 12.

Diploschistes scruposus (Schreb.) Norm.

This is a widespread species, found always on siliceous rocks, on moderately to very exposed sites. In locality 30, it grows on heavily weathered granite, near limestone outcrops. Loc: 6, 25, 30.

Diplotomma alboatrum (Hoffm.) Flot.

We have included under this name several specimens that were initially identified as *Buellia glaucoatra* (Nyl.) Clauzade, following Ozenda & Clauzade (1970) and Clauzade & Roux (1985). These specimens were characterized by having thick, verrucose-squamulose thalli and by living close to the sea, above the supralittoral belt (locality 20). However, we have not retained them separately as *B. glaucoatra* because the study of Nordin (2000), on the grounds of morphology and phylogenetic reconstruction based on molecular data, concluded that *B. glaucoatra* is a synonym of *Diplotomma alboatrum*. This taxon was found growing on sheltered calcareous and nutrient-enriched siliceous rocks. Loc: 9, 20, 30.

Diplotomma chlorophaeum (Hepp ex Leight.) Kr.P. Singh & S. R. Singh

This taxon was found in the study area usually forming inconspicuous thalli. It is, however, easy to recognize because of its K+ red thallus reaction (due to the presence of norstictic acid as a major compound), Pd+ yellow, and its muriform ascospores. Nordin (2000) synonymized it with *D. alboatrum*, based on morphology and phylogenetic evidences. On a later phylogenetic study by Nordin & Tibell (2005), however, the authors have reconsidered the possibility of recognizing again *D. chlorophaeum* as an independent taxon. We decided to treat *D. chlorophaeum* separately from *D. alboatrum*, based on the phylogenetic evidences showed by Nordin & Tibell (2005), and supported as well by its different chemistry and ecology (*D. chlorophaeum* is strictly saxicolous, occurring on coastal sites, while *D. alboatrum* can be both saxicolous and epiphytic and has a broad distribution) Loc: 8, 17, 23.

Diplotomma hedinii (H. Magn.) P. Clerc & Cl. Roux

This species is very similar to *D. alboatrum*, from which it has recently been separated (Clerc, 2004, sub *D.* '*hedinianum*'), based on the ascospore features: while *D. alboatrum* has mostly submuriform ascospores, *D. hedinii* has (1-)3-septate ascorpores, lacking always longitudinal septa. It has been previously reported from the Iberian Peninsula by Llop et al. (in review). In our study, it was found growing on various calcareous substrates (mortar, dunes, carbonated schists), in exposed conditions. Loc: 1, 16.

Dirina massiliensis Durieu & Mont.

We observed a variability of its thallus morphology similar to that reported by Tehler (1983): on limestone outcrops near the coast (locality 30), *D. massiliensis* grows very abundantly, forming white, thick, areolate to almost subfruticose thalli. In contrast, on siliceous substrates, this lichen behaves in a more ombrophobous and sciaphilous manner, and always has relatively thin, brownish-grey thalli. In the study area, it was usually found growing together the two forms described of this species: with apothecia (f. *massiliensis*) and with only soralia (f. *sorediata* (Müll. Arg.) Tehler). Transitional forms of *D. massiliensis* with both ascocarps and soralia are rare (Tehler, 1983), but were found in our study area as well (Fig. 4E). Tehler's sorediate form had been previously treated as the species *D. stenhammarii* (Fr.) Poelt & Follmann (Poelt & Follmann, 1968, sub. *D. stenhammarii*). Later, Nimis & Poelt (1987) uphold the identity of this species, since they considered *D. stenhammarii* to be phylogenetically distantly related from *D. massiliensis*. This was supported by the biogeographical differences between the taxa, as *D. stenhammarii* is from boreal areas and *D. massiliensis* is mainly Mediterranean. The frequent occurrence of both taxa in our study areas, however, does not support the statement of differing chorology. We consider that different reproductive characters are not sufficient to consider these two species independently because, although not frequent, transitional forms (with apothecia and soralia) exist. Therefore, we decided to follow Tehler (1983). It grows on north-facing subvertical surfaces or overhangings, and is the most common ombrophobous lichen species in the study area, on both calcareous and siliceous substrata. Loc: 21, 22, 24, 25, 30.

Endocarpon pusillum Hedw.

This species occurs very frequently on siliceous soils, but also grows on the climbing dunes, always in sun-exposed areas. Contrary to other species living in the same habitat, such as *Epiphloea terrena* and *Gyalideopsis athalloides*, this taxon is not ephemeral and does not become inconspicuous during dry periods. Loc: 10, 12, 19, 28.

Endocarpon simplicatum (Nyl.) Nyl

This taxon was found growing on sunny acid soils, coexisting with the previous taxon. It can be distinguished from *E. pusillum* because it has one large spore (42-120 x 24-35 µm) per ascus, while *E. pusillum* has 2-spored asci and the ascospores themselves are shorter (25-60 x 11-23 µm). Loc: 19, 28.

Endococcus buelliae (C. W. Dodge) Matzer

This is a lichenicolous fungus that has previously been described growing only on *Buellia* species and *Dimelaena radiata* (Matzer, 1993; Matzer et al., 1996). In this study, however, we found it growing on *D. oreina*. A closely related species to *Endoccocus buelliae* is *E. oreinae* Hafellner, which was described as parasite on *Dimelaena oreina* in the Sonoran desert (Hafellner et al., 2002). The *Endoccocus* species are characterized by having a very restricted host-specificity (Lawrey & Diederich, 2003); which suggests that, on the grounds of lichen host species, our specimens should be identified as *E. oreinae*. However, the samples we have studied have ascospores of size 12-16 x 6.5-8.5 µm, with a warty surface, which are more similar to those of *E. buelliae* (8-15 x 6-9 µm, with granulose ornamentation) than to the ascospores of *E. oreinae* (16-20 x 5-7 µm, smooth, with no perispore). In a recent work, Etayo (2010) also found a specimen of *Endococcus* growing on *Dimelaena oreina*, but with ascospores more similar to those of *Endococcus buelliae*. This specimen was named *E.* cf. *oreinae*. We concluded, however, that ascospore morphology is a more reliable trait that solely host-specificity and, consequently, our samples were finally identified as *E. buelliae*, adding a novel host to this lichenicolous taxon. Loc: 29, 32.

+ ***Endococcus fusiger*** Th. Fr. & Almq.

Lichenicolous fungus growing on species of *Rhizocarpon* with dark thalli. In the study area, it was found growing on *R. geminatum* and *R. polycarpum*. It has previously been reported in two other localities on the Iberian Peninsula (Etayo, 2010). Loc: 19, 22.

+ ***Endococcus macrosporus*** (Hepp ex Arnold) Nyl.

Lichenicolous fungus growing on species of *Rhizocarpon* with yellow thalli. Some specimens were initially misidentified as *E. exerrans* Nyl., which is also a parasite of yellow *Rhizocarpon*, but *E. macrosporus* has larger perithecia and ascospores. As with the previous taxon, it has previously been reported in only few localities on the Iberian Peninsula (Etayo, 2010), while it seems to be common in our study area. Loc: 11, 16, 21, 23, 24.

Endococcus verrucosus Hafellner

Lichenicolous fungus growing on *Aspicilia* thalli; in the study area, it was found on *A. cupreoglauca* and *A. intermutans*. It has previously been recorded twice on the Iberian Peninsula (Hafellner, 1994; Llop et al., 2010). Loc: 7, 16, 25.

+ ***Enterographa pitardii*** (B. de Lesd.) Redinger

This species has brownish thallus, formed by areoles with crenate margin, with conspicuous black hypothallus, and urceolate apothecia, punctiform or lirelliform (Fig. 4F). Following Torrente & Egea (1989), we initially identified this specimen as *Enterographa zaborskiana* (M. Choisy & Werner) Egea & Torrente, which had been previously recorded from only one locality on the Iberian Peninsula (Torrente & Egea, 1989). A later work by Sparrius (2004), synonymized *E. zaborskiana* with *E. pitardii*. *Enterographa pitardii*, itself, had previously been reported from only one locality in Portugal by Tavares (1965). Therefore, it seems that this species is very rare on the Iberian Peninsula. In the study area, it was collected on a siliceous overhanging. Loc: 7.

Epiphloea terrena (Nyl.) Trevis.

This taxon forms minute, squamulose, thalli which are very similar to soil colour (Fig.

5A), with cyanobacteria as a photobiont, and submuriform ascospores. This is an uncommon species, previously reported on the Iberian Peninsula from the area of s'Arenella (locality 10) by Llimona (1995). Here, it is reported from two new localities, both sharing the shallow argillaceous siliceous soil of the previous locality. This lichen is invisible during dry periods of the year, perhaps concealed by a clay layer, or perhaps because it is ephemeral, in the same way as *Gyalideopsis athalloides* (Nyl.) Vězda. Loc: 10, 19, 27.

Evernia prunastri (L.) Ach.
This widespread taxon is usually epiphytic, but it was found growing on siliceous rocks, but only when it also occurs nearby on bark. Loc: 8, 13.

Flavoparmelia caperata (L.) Hale
Although it is a widely distributed species, it was found only once in the study area, growing on siliceous rocks. Compared to *F. soredians* (Nyl.) Hale, this species depends more on high humidity and avoids direct sunlight. The only sample collected was analyzed by TLC, which detected fumarprotocetraric, caperatic, and usnic acids. The caperatic acid was only detected in plate B'. Its apparent absence in plates A and C is attributed to the presence of protocetraric acid, which is dragged up with caperatic acid in the TLC as Elix & Ernt-Russell (1993) reported. Therefore, protocetraric acid, with its own grey spot, obscures the white spot of the caperatic acid. Loc: 7.

Flavoparmelia soredians (Nyl.) Hale
This taxon forms foliose, yellowish-green, sorediate thalli, similar to *F. caperata*. However, they can be distinguished chemically: the TLC analyses revealed that *F. soredians* contains salazinic, consalazinic, galbinic, and usnic acids. This species is mainly epiphytic, but it was found growing abundantly on sunny siliceous rocks. In this habitat, thalli seem to be more robust and are clearly eutrophication-tolerant. Loc: 7, 8, 23.

Fulgensia fulgens (Sw.) Elenkin

This species is locally very abundant, growing on the climbing dunes, forming small yellow thalli, and rarely developing apothecia. Loc: 12.

Glyphopeltis ligustica (B. de Lesd.) Timdal

This species has been previously reported in the study area (Egea et al., 1995). It grows on siliceous rocks, on very sunny, steep surfaces, preferring rain-track sites, where it often starts its development parasiting *Peltula euploca* (Ott & Scheidegger, 1992). Loc: 13.

Gyalecta jenensis (Batsch) Zahlbr.

We found this species growing on both sheltered conglomerates and on schists. Some authors have placed specimens growing on schists in a separate taxon, *G. schisticola* Wern. Since we have not found morphological differences between the specimens collected on conglomerates and on schists, we found no reason to support its treatment as separate taxa. Loc: 7, 30.

Gyalideopsis athalloides (Nyl.) Vězda

This terricolous lichen has endosubstratic thallus, and only the apothecia can be detected, especially when wet. There are very few records of this taxon on the Iberian Peninsula, and one of them (Llimona, 1995) is from the same locality where we found it in this study. This is a typical example of an ephemeral species, visible shortly after rain on argillaceous, neutral soil. Loc: 10.

+ ***Heteroplacidium contumescens*** (Nyl.) Breuss

This taxon is a rare species, with a scattered distribution throughout the Mediterranean region (Prieto et al., 2010a). In our study area, it was found once, growing on siliceous soil crusts. Loc: 10.

Immersaria athroocarpa (Ach.) Rambold & Pietschm.

This species has a large dull brown thallus, formed by concave areoles, and large black lecideine apothecia. It grows on siliceous outcrops, preferably on horizontal to gently sloping exposed surfaces. Loc: 1, 3.

+ ***Ingaderia troglodytica*** Feige & Lumbsch

This taxon was found on fissures and cavities of siliceous rocks in maritime environments. Previous authors like Nimis & Martellos (2008) have suggested that this taxon could be an aberrant form of *Dirina massiliensis* or *Lecanographa grumulosa* (Dufour) Egea & Torrente. Molecular techniques might be necessary to clarify the identity of this taxon. Loc: 20.

Ingvariella bispora (Bagl.) Guderley & Lumbsch

This species is locally quite abundant, forming large and well-developed thalli, in flat or gently inclined, sun and rain-exposed surfaces of metamorphic schists, with some soil accumulation. In our study area, *I. bispora* grows at a remarkably low altitude, very close to the coast, in contrast to previous records for this taxon in the Iberian Peninsula, from areas at 1000-2000 m (Hladun, 1981; Barreno & Rico, 1982; Rowe, 1985; Sancho, 1986; Paz-Bermúdez et al., 2009). Loc: 25, 26.

+ ***Involucropyrenium tremniacense*** (A. Massal.) Breuss

This taxon, distributed throughout south-central Europe and the Mediterranean region, has been previously reported on the Iberian Peninsula only from two localities that are distant from the study area (Prieto et al., 2010a). It grows on exposed calcareous soils. Loc: 12.

Lecania atrynoides M. Knowles

This taxon was collected from the supralittoral zone (20-50 cm above the sea level) to less than 1 km inland, growing on subvertical and somewhat shaded surfaces of metamorphic schists. Loc: 21, 22.

+ ***Lecania inundata*** (Hepp ex Körb.) M. Mayrhofer

This *Lecania* has thick thallus, formed strongly convex areoles with warty surface. It was found growing on calcareous schists, on steep, sunny surfaces. Loc: 16.

Lecania sylvestris (Arnold) Arnold

This species is locally abundant, growing on limestone or marble, near the coast. Loc: 30, 33.

Lecania turicensis (Hepp) Müll. Arg.

Although it is not very abundant locally, it was found in different localities, growing on several types of calcareous rocks (limestone, marble, porous mortar) and occasionally on siliceous rocks. It is morphologically similar to *L. atrynoides* since both have white thallus and ascospores of size 10-15 x 4-6 µm, but *L. turicensis* has pruinose apothecia and is not a maritime species. Loc: 1, 11, 30, 33.

Lecanographa grumulosa (Dufour) Egea & Torrente

This species grows on overhanging surfaces or shallow caves, on calcareous and siliceous rocks, in coastal localities, associated with *Dirina massiliensis* and *Roccella phycopsis*. Silicicolous thalli are thinner, more brownish, and more strongly ombrophobous and sciaphilous than calcicolous thalli. Loc: 22, 30.

Lecanora albescens (Hoffm.) Branth. et Rostr.

This species was found growing on the climbing dunes and on coastal metamorphic schists. Loc: 4, 12.

Lecanora campestris (Schaer.) Hue

This common species is quite frequent on nutrient-enriched siliceous rocks, preferably on shaded surfaces, and sometimes near streams, on sites that are occasionally inundated. Loc: 6, 8, 13, 33.

Lecanora dispersa (Pers.) Röhl.

This taxon, included in the *L. albescens* group, was found only on siliceous rocks, on both exposed and sheltered surfaces, although previous studies reported it mainly growing on calcareous substrata (Edwards et al., 2009). Loc: 6, 8, 9, 33.

Lecanora gangaleoides Nyl.

This taxon forms conspicuous, whitish-grey thalli, composed of convex areolae that react K+ yellow, and apothecia with black discs. It grows on various siliceous rocks, on both sunny and shaded surfaces, usually on wind-swept ridges. Loc: 7, 8, 11, 24.

Lecanora muralis (Schreb.) Rabenh.

This widespread and common species grows on nutrient-enriched, flat or gently sloping siliceous rocks. Loc: 1, 8, 11, 24, 27.

Lecanora polytropa (Ehrh.) Rabenh.

This species occurs locally abundant on siliceous rocks, on moderately sloping to subvertical surfaces, usually exposed to the north. Loc: 7, 8, 16.

Lecanora praepostera Nyl.

This taxon, also known for a long time as *L. schistina* (Nyl.) Arnold, has a thick, white thallus, and apothecia with dark brown to black discs, and is very similar to *L. gangaleoides*. However, it can be distinguished by having flat areolae with somewhat crenate margins, and showing reaction K+ red, due to the presence of norstictic acid. It frequently occurs on north-facing inclined surfaces on hard siliceous rocks. Loc: 7, 8, 11, 16, 21, 22, 24, 26, 33.

Lecanora rupicola (L.) Zahlbr. subsp. ***sulphurata*** (Ach.) Leuckert & Poelt

Out of the infraspecific taxa within *L. rupicola* described by Leuckert & Poelt (1989), our samples all belong to the subspecies *sulphurata*, which is characterized by its yellowish thallus KC+ orange. We found it growing on mostly shaded and inclined surfaces of hard siliceous rocks. Loc: 3, 7, 8, 11, 22, 24, 25.

+ ***Lecanora salina*** H. Magn.

This taxon is very similar to *L. dispersa* since both taxa have a very reduced thallus (often visible only as thin rim surrounding the apothecia) that is K-, C- and KC-. However, *L. dispersa* is clearly differentiated by the absence of diffuse crystals in the exciple. *Lecanora salina* was found frequently in the study area, usually on nutrient-enriched siliceous rocks, sometimes in unusual ecological conditions such as near water streams (where it tolerates short immersions) and on the supralittoral belt. Although it seems to be a common species, it has been recorded only once before from the Iberian Peninsula (Martínez et al., 2001). Due to its similarity with the common *L. dispersa*, it might have been misidentified. Loc: 13, 15, 19, 20, 22, 25, 28.

Lecanora sulphurea (Hoffm.) Ach.

This taxon has a yellowish-green thallus and apothecia with green-black discs. It cannot be confused with *L. rupicola* subsp. *sulphurata* because *L. sulphurea* has a C- apothecial disc, while in *L. rupicola* subsp. *sulphurata* it is C+ yellow and lacks greenish tinges. It grows abundantly in coastal localities, mainly on exposed siliceous rocks. Loc: 11, 21, 25.

Lecidea fuscoatra (L.) Ach.

This species grows on siliceous rocks, on subhorizontal to more rarely steep surfaces, fully exposed to sunlight. Loc: 8, 33.

Lecidea sarcogynoides Körb.

In all samples of *L. sarcogynoides* that we studied, the thallus was absent. This species is mainly characterized by having an exciple that is blackish in its outer part, turning dark purple in the inner parts, and a hymenium that is reddish to pale purple. It grows on schists, nearly at ground level, on sunny exposures of more or less horizontal surfaces. Loc: 25, 28, 33.

Lecidella asema (Nyl.) Knoph & Hertel var. ***elaeochromoides*** (Nyl.) Nimis & Tretiach
This variety of *L. asema* has a yellow thallus, C+ orange, and black, convex, lecideine apothecia, with a green epihymenium that reacts N+ purple. It is very common in the study area, on siliceous rocks, on horizontal to gently sloping surfaces, fully exposed to sunlight. Loc: 3, 6, 11, 15, 18, 20, 21, 22, 24, 25, 26, 27, 28.

Lecidella scabra (Taylor) Hertel & Leuckert
This taxon forms thin, minute, grey, rimose-areolate thalli, with well-defined yellowish-green soralia. Although apothecia are known for this species (Fletcher et al., 2009a), all of our specimens were sterile. It was found on sheltered siliceous rocks. Loc: 8, 16, 28.

Lecidella stigmatea (Ach.) Hertel & Leuckert
This species was found locally abundant, on subvertical limestone cliffs. Loc: 30.

Lepraria nivalis J. R. Laundon
This species has more or less thick, cottony, white thallus, usually sublobed, medulla present, and granules of size 0.1-0.35 mm. *Lepraria nivalis* is chemically a very heterogeneous taxon; Leuckert et al. (2004) distinguished up to six chemotypes. We analyzed our specimens by TLC, and all of them contained atranorin and stictic, constictic and cryptostictic acids, corresponding to chemotype IV sensu Leuckert et al. (2004). All the specimens were collected on weathered siliceous rocks or on soil derived from siliceous rocks, on sheltered sites. Loc: 2, 18.

Leprocaulon microscopicum (Vill.) Gams
This taxon is a very common species, even though it was collected from only one

locality, probably because it was overlooked during sampling. This species was found on thin layers of soil, on a small overhangs, mixed with the thalli of *Lepraria nivalis*. Loc: 18.

Leptogium gelatinosum (With.) J. R. Laundon
This taxon was found locally very abundant, growing on open areas on the climbing dunes. Loc: 13.

Leptogium lichenoides (L.) Zahlbr.
This taxon is similar to the previous *L. gelatinosum*, but it has isidia-like extensions at the lobes margin. It grows in open areas with short and sparse vegetation, on siliceous soil. Loc: 10, 25.

Lichenostigma cosmopolites Hafellner & Calat.
Lichenicolous fungus growing on *Xanthoparmelia*. In the study area, it was only found growing on *X. tinctina*. Loc: 6, 7, 17, 26.

Lichenostigma elongata Nav.-Ros. & Hafellner
Lichenicolous fungus growing on *Aspicilia* and *Lobothallia* species. It was found on *Aspicilia caesiocinerea*, *A. contorta*, and *A. intermutans*. Loc: 12, 21, 25, 26.

Lichenostigma rugosum G. Thor
Lichenicolous fungus growing on *Diploschistes* species. It was found on *D. caesioplumbeus* and *D. interpediens*. Loc: 3, 7.

Lichenostigma rupicolae Fdez.-Brime & Nav.-Ros.
Lichenicolous fungus growing on *Pertusaria rupicola*. This taxon occurs very frequently in the study area, which is from where it was originally described. Loc: 8, 11, 15, 16, 21, 22, 25, 26.

Lichenostigma sp.

An undescribed species of *Lichenostigma* subgenus *Lichenogramma* was frequently found growing on *Pertusaria monogona*. Initially, we considered it to be *L. rupicolae* growing on a novel host, but after a detailed study, we observed several differences between our samples and typical *L. rupicolae*. The *Lichenostigma* species on *Pertusaria monogona* has larger hyphal strands, formed by a main axis with lateral ramifications, lacks macroconidia, and has stromata present all across the strands. Unfortunately, very few fertile stromata carrying spores were found in the studied specimens of *Lichenostigma* sp. Therefore, more specimens are needed to revise, study and compare ascospore features with those in *L. rupicolae*. Loc: 7.

Lichinella cribellifera (Nyl.) P. P. Moreno & Egea

This taxon was collected once, on sunny, steep, rain-tracks of weathered granite. It has been previously reported from other localities in the study area (Llimona & Egea, 1985). Loc: 1.

Lichinella stipatula Nyl.

This species grows under the same ecological conditions as the previous taxon (sun-exposed, steep surfaces with frequent water seepages after rain), but it is much more abundant in the study area. Loc: 1, 7, 13, 24, 26, 28, 34.

Lobothallia radiosa (Hoffm.) Hafellner

This is a widespread species, found on a wide variety of substrata (Nimis & Martellos, 2008). In the study area, it was found on nutrient-enriched granites, schists, and carbonate-rich siliceous rocks. Loc: 2, 6, 12, 28.

 # *Micarea melaenida* (Nyl.) Coppins

This species has effuse, whitish thalli, with minute, emarginated black apothecia. It was found only in one locality, growing on argillaceous soil. This is a rare species, which has previously been found in few, scattered, and distant localities (in France, Germany, and Hungary) (Coppins, 1983). Loc: 10.

Muellerella lichenicola (Sommerf.) D. Hawksw.

Lichenicolous fungus growing on a diverse range of lichen species. In this study, it was found growing on *Lecanora campestris*, *L. praepostera*, and *Tephromela atra*. Loc: 7, 8, 18.

Muellerella pygmaea (Körb.) D. Hawksw.

Lichenicolous fungus growing on a diverse range of mainly crustose lichen species. Its perithecia and ascospores are larger than in *M. lichenicola*. It was found growing on *Acarospora veronensis*, *Aspicilia caesiocinerea*, *A. intermutans*, and *Dimelaena oreina*. Loc: 9, 15, 16, 32.

Nephroma parile (Ach.) Ach.

This species has a mainly cool-temperate to circumboreal-montane distribution (Nimis & Martellos, 2008). It was, therefore, scarce in the study area, and it was found only once, growing on shaded fissures of compacted siliceous soil. Loc: 1.

Ochrolechia parella (L.) A. Massal.

This species is quite common in our study area, where it grows on various siliceous rocks, on horizontal to subvertical surfaces, in all exposures, but especially on north-facing surfaces. Loc: 1, 7, 8, 11, 20, 22, 24, 25.

Opegrapha calcarea Turner ex Sm.

This species is common in overhangings, preferably on hard calcareous rocks (as carbonate-rich schists and limestone), but also on nutrient-enriched siliceous rocks. Loc: 16, 30, 31.

+ ***Opegrapha cesareensis*** Nyl.

This taxon was found once, growing on overhanging schists. It has been previously recorded in the Iberian Peninsula, only from the Atlantic coast (Paz-Bermúdez & Carballal, 1999; Sánchez-Biezma et al., 1999). Loc: 7.

Opegrapha lutulenta Nyl.

This is an ombrophilous species that was found growing on vertical shaded surfaces or roofs of shallow caves, on metamorphic schists. Loc: 7, 20.

Opegrapha rupestris Pers.

This species of lichenicolous lichen grows on crustose members of the Verrucariaceae. In the study area, it was found growing on the thallus of *Bagliettoa calciseda*. Loc: 12.

Parmelia saxatilis (L.) Ach.

This taxon was found on siliceous outcrops, growing directly on the rock or on top of saxicolous mosses, in shaded and humid sites. Loc: 7.

Parmelina tiliacea (Hoffm.) Hale

This is a widespread species that can be both saxicolous and epiphytic. It was found from moderately inclined to subvertical north-facing surfaces of hard siliceous rocks, in areas with long-lasting dew. Loc: 8, 9, 16.

Parmotrema perlatum (Huds.) M. Choisy

This taxon forms foliose thalli with a grey upper surface and a dark brown lower surface, ciliate lobed margins, and marginal soralia. The identification of our specimens was confirmed by TLC: all contain atranorin, and stictic, cryptostictic, and constictic acids. It was found growing on schists and mosses, in humid sites. Loc: 7, 8.

Parmotrema reticulatum (Taylor) M. Choisy

This species is very similar to the previous one, but this has a clearly reticulate-cracked surface. It was found once, growing on saxicolous mosses on a subvertical, sheltered schistose surface. Loc: 21.

Peltigera collina (Ach.) Schrad.

This is a widespread taxon, with a markedly oceanic tendency (Burgaz & Martínez, 2003). It was found only once, growing on acidic soil, sheltered by a granodiorite block. Loc: 7.

Peltigera membranacea (Ach.) Nyl.

This species was found growing on mosses and on soil, in sheltered areas protected from direct sunlight. Loc: 2, 7.

Peltula euploca (Ach.) Poelt

This species forms peltate olive green squamules, with deep brown sorediate margins. It is very common on rain-track surfaces, usually in sunny exposures, growing along with *Lichinella stipatula*. Loc: 1, 7, 13, 17, 23, 26, 28, 33, 34.

Peltula obscurans (Nyl.) Gyeln.

This taxon has a similar ecology to *P. euploca* (it grows on sunny rain-track surfaces), but it is a more thermophilous species. Consequently, its distribution in the study area is more restricted than *P. euploca*. Loc: 17, 26, 31.

Peltula omphaliza (Nyl.) Wetmore

This species is morphologically similar to *P. euploca*, but it differs in that the margins of the squamules are never sorediate. It grows together with *P. euploca* and *P. obscurans*, but it is the least frequently occurring of the three taxa. Loc: 17, 31.

Peltula placodizans (Zahlbr.) Wetmore

This taxon can be distinguished from the three other squamulose species of *Peltula* found in the study area by its tiny, orbicular, lobate, crustose thallus, formed by minute clustered areolae. All specimens that were studied were sorediate, although fertile specimens have been reported from the north of Africa (Egea, 1989). Loc: 1, 13.

Pertusaria albescens (Huds.) M. Choisy & Werner

This species is characterized by being K-, C-, KC-, and P-. Although it usually lives on bark, it can occasionally grow on siliceous rocks (Chambers et al., 2009), like we found it in our study area. Loc: 26.

Pertusaria aspergilla (Ach.) J. R. Laundon

This species forms crustose pale grey sorediate thalli. All specimens were analyzed by TLC and contained protocetraric and fumarprotocetraric acids. It grows on hard siliceous rocks, on subvertical surfaces, usually facing north. Loc: 1, 7, 8, 9, 24, 33.

Pertusaria excludens Nyl.

This species is recognized by its yellowish-grey thallus that reacts K+ red (the presence of norstictic and connorstictic acids was revealed by TLC), and is densely covered by soralia. It is quite abundant in the study area, growing on hard siliceous rocks, on inclined and sheltered surfaces. Loc: 1, 7, 8, 9, 11, 33.

Pertusaria flavicans Lamy

This species was collected once, growing on granite, on an inclined north exposed surface. This species lives from the montane to the supramediterranean belts, in the Mediterranean and Eurosiberian areas, and when it occurs in dry areas (such as our area of study) it is heliophobous, colonizing only surfaces that are not exposed to direct sunlight (M. Boqueras, pers. comm.). Loc: 1.

Pertusaria lactea (L.) Arnold

This taxon is similar to *P. aspergilla*, having both pale grey thallus and soralia. However, *P. lactea* has a C+ red thallus, since it contains lecanoric acid. We only found it once, growing on metamorphic schists, even though it is regarded as a common species (Chambers et al., 2009). Loc: 20.

Pertusaria leucosora Nyl.

This species is also very similar to *P. aspergilla*, as both have pale grey sorediate thalli, which react K+ yellow, C-, and Pd+ red. In addition, the two species grow frequently together. The only way to identify *P. leucosora* reliably is by performing TLC, since it lacks fumarprotocetraric acid (which is present in *P. aspergilla*). It occurs frequently on siliceous rocks, on sunny or sheltered surfaces. Loc: 3, 6, 8, 11, 15, 33.

Pertusaria monogona Nyl.

This taxon is very similar to *P. excludens* with which it shares a yellowish-grey and thick thallus that reacts K+ red (norstictic and connorstictic acids were detected by TLC). However, instead of soralia, *P. monogona* has immersed apothecia, with characteristic 1-spored asci. *Pertusaria monogona* forms unusually large (up to 80 cm in diam.) and thick (up to 5 mm) thalli, and very often, the older parts of the thallus are detached from the rock. It is quite abundant locally, growing on hard siliceous rocks, on inclined and sheltered surfaces. Loc: 3, 7, 9, 11, 27.

Pertusaria pluripuncta Nyl.

The only specimen found in the study area has a yellow thallus, delimited by a blackened margin, with pycnidia in almost all of the areolae, and lacking apothecia; apparently, this taxon is rarely fertile (M. Boqueras, pers. comm.). It was found growing on sun-exposed siliceous rocks. Loc: 11.

Pertusaria pseudocorallina (Lilj.) Arnold

This species is characterized by having simple to ramified isidia, with a brown-pigmented apical part. In young specimens, isidia are scattered all over the thalli, but as the individuals grow old, isidia become concentrated, forming clearly-visible, dull brown patches. Rarely fertile, the first known specimen with apothecia was reported from the study area (locality 7) by Wirth & Llimona (1975); we also found fertile specimens at a coastal locality (locality 12) (Fig. 5B). It is one of the most common species of *Pertusaria* in the study area, growing on hard siliceous substrates, on shallowly inclined to subvertical surfaces, mainly on north orientations. Loc: 3, 1, 7, 8, 11, 15, 16, 21, 22, 24, 25.

Pertusaria rupicola (Fr.) Harm.

This is the most common species of *Pertusaria* in the study area, where it grows on hard siliceous rocks, on shallowly inclined to subvertical surfaces that face north to northeast, usually on wind-exposed sites. It is the dominant species in the *Pertusarietum rupicolae* community Wirth & Llimona (Wirth & Llimona, 1975), giving its characteristic yellowish colour. Many of the studied samples were heavily colonized by *Lichenostigma rupicolae*. Loc: 1, 7, 8, 11, 15, 16, 20, 21, 22, 24, 25, 26.

Phaeophyscia hirsuta (Mereschk.) Essl.

This species is easily recognized by the presence of hyaline cortical hairs. Initially, specimens with mostly marginal soralia were identified as *P. cernohorskyi* (Nádv.) Essl., following the key in Esslinger (1978). We finally placed, however, those specimens in *P. hirsute*, since a recent revision of the genus by Esslinger (2004) has finally considered that these two taxa belong to the same species. It was found on sun-exposed surfaces of acidic rocks, usually near rain-tracks. Loc: 1, 28, 33, 34.

Phaeophyscia orbicularis (Neck.) Moberg

This is a cosmopolitan species known from a wide variety of substrata, including bark and calcareous and siliceous rocks (Nimis, 1993). However, in the study area it was found only twice, at sun-exposed and nutrient-enriched acidic rocks. Loc: 8, 9.

Physcia adscendens (Fr.) H. Olivier

This taxon is identified by the presence of lateral fibrils at the lobe margins and by its typical helmet-shaped soralia. It is a very common species that can grow on different substrates; in our study area, it was collected on exposed nutrient-rich siliceous rocks. Loc: 7, 19, 31.

Physcia biziana (A. Massal.) Zahlbr.

This species is characterized by the absence of soralia and the presence of thick white pruina. Although this taxon lives mainly on wood, it can also rarely occur on rocks (Clauzade & Roux, 1985). It was found growing on sheltered schistose surfaces. Loc: 5.

Physcia caesia (Hoffm.) Hampe ex Fürnr.

This species is characterized by the presence of bluish-grey laminal soralia. Although it occurs on basic substrates and very rarely on siliceous rocks (Edwards & Coppins, 2009), it was found growing on metamorphic schists in our study area. Loc: 8, 22.

Physcia dubia (Hoffm.) Lettau

This species can be distinguished from *P. caesia* by the whitish soralia and the medulla K- instead of K+ yellow. It occurs frequently, growing on nutrient-enriched rocks, with a tendency to prefer sites with short-time rain-tracks. Loc: 7, 13, 15, 21, 23, 29.

Physcia tenella (Scop.) DC.

It is very similar to *P. adscendens*, but it has marginal lip-shaped soralia. It was found on siliceous rocks. Loc: 8, 9.

Physcia tribacia (Ach.) Nyl.

It can be distinguished from *P. dubia* by its paraplectenchymatous (rather than prosoplectenchymatous) lower cortex (Figueras, 2011). It grows on sun-exposed and nutrient-enriched siliceous rocks. Loc: 3, 17, 23.

Placidiopsis custnani (A. Massal.) Körb.

Although this species usually prefers calcareous soils (Prieto et al., 2010b), in this study it was collected only once, growing on compacted siliceous soil. Loc: 33.

+ ***Placidium tenellum*** (Breuss) Breuss

This taxon was found as one of the main species colonizing the climbing dunes. It also occasionally occurred on siliceous soil crusts at a coastal locality (locality 27), despite the fact that this taxon rarely grows on acid soils (Prieto et al., 2010a). Loc: 13, 27.

Placynthium tremniacum (A. Massal.) Jatta

This species was found growing abundantly on the climbing dunes where, probably due to the instability of the substrate, it is not able to form proper rosettes. It can be distinguished from the similar species *P. nigrum* (Huds.) Gray, by its inconspicuous prothallus and 1-septate ascospores, compared to the well-developed prothallus and unicellular, slightly larger ascospores of *P. nigrum* (Burgaz, 2010). Loc: 12.

Polycoccum rinodinae Van den Boom

Lichenicolous fungus growing on saxicolous *Rinodina* species; in our study area it was only found parasiting *R. beccariana*. This taxon has previously only been reported from various localities in the Canary Islands, from where it was formally described (Boom, 2010). Loc: 7, 24.

+ ***Polycoccum rubellianae*** Calat. & V. Atienza

Lichenicolous fungus growing on *Caloplaca rubelliana*. This species has been considered very selective with regard to its host species, even within the same genus (Atienza et al., 2003). However, in the material that we studied, as well as finding *Polycoccum rubellianae* growing on *Caloplaca rubelliana*, we found it growing on nearby thalli of *Aspicilia caesiocinerea*. Loc: 26.

Polycoccum teresum Halici & K. Knudsen

Lichenicolous fungus growing on *Xanthoria* species. This recently described taxon was previously known only from the type locality in western Turkey (Halici et al., 2009). Loc: 16.

Polysporina simplex (Dav.) Vězda

This species is very frequent and abundant, especially on sun-exposed, nutrient-enriched siliceous rocks. Some of the specimens we examined were terricolous, despite the fact that this taxon rarely lives on compacted soil (Hitch et al., 2009). Loc: 6, 9, 10, 13, 15, 17, 19, 22, 24, 25, 28, 31, 33.

\+ ***Porina byssophila*** (Körb. ex Hepp) Zahlbr.

This taxon was found once, forming a very small, greyish-green thallus, minute perithecia (up to 0.2 mm diam.), and 3-septate ascospores. It was growing on a sheltered limestone surface. Loc: 30.

Porina chlorotica (Ach.) Müll. Arg.

This is a very sciaphilous species, which was growing on sheltered siliceous rocks. Loc: 7, 28.

Porpidia cinereoatra (Ach.) Hertel & Knoph

This species grows on horizontal or moderately sloping surfaces of siliceous rocks, exposed to the rain, but protected from direct sunlight. It grows in places where water remains for a short time after rain. Loc: 7, 14.

\+ ***Porpidia hydrophila*** (Fr.) Hertel & A. J. Schwab

This is an even more hydrophilous species than the previous taxon, found on long-lasting water seepages on acidic rocks. Loc: 25.

Protoblastenia rupestris (Scop.) J. Steiner

This species can be confused with a *Caloplaca* species due to it has bright orange apothecia, but unlike those species, its epithecium never reacts K+ purple and the ascospores are simple. It grows on nutrient-enriched siliceous rocks, on surfaces close to the ground or to rain-tracks. Loc: 16, 31.

Protoparmelia montagnei (Fr.) Poelt & Nimis

This taxon has an extremely high variability with regard to its morphology, and also to its chemistry, since four different chemotypes have been described (Barbero et al., 2006). A previous study of the sampled area found specimens with chemotype II and, more commonly, chemotype IV (Barbero et al., 2006). In addition, in this study, we found chemotype I (which contains lobaric and gyrophoric acids). *Protoparmelia montagnei* grows on diverse hard siliceous rocks (even iron-rich rocks), on subvertical to vertical surfaces, mainly facing north. Loc: 1, 8, 11, 16, 20, 24.

Psora gresinonis B. de Lesd.

This species is recognized by its greenish-brown squamules, whitish below, and the apothecia attached laminally to submarginally, with the proper margin becoming excluded rapidly (Fig. 5C). It is a rare taxon on the Iberian Peninsula, which has previously been recorded only twice (Llimona, 1995; Boom & Giralt, 1996), one of those records (Llimona 1995) being from our study area (locality 33). It was locally abundant, found on exposed sites, on sandy or clayey soils. Loc: 19, 33.

\+ ***Psora vallesiaca*** (Schaer.) Timdal

This *Psora* species is characterized by having brown squamules with a prominent white margin (Fig. 5D), and a medulla that reacts K+ yellow, changing to deep orange, and P+ yellow. It was collected on exposed sites, on the climbing dunes. Loc: 12.

Psorotichia vermiculata (Nyl.) Forssell

This taxon can be easily distinguished from other species of *Psorotichia* reported in the Iberian Peninsula by having longer ascospores, of length 16-20 µm (P.P. Moreno, pers. comm.). *Psorotichia vermiculata* has been actually recorded from very few localities in the Iberian Peninsula (Sampaio, 1970b; Pereira, 1992). It was found in this study on metamorphic schists, near water seepages. Loc: 4.

Punctelia subrudecta (Nyl.) Krog

This species can resemble *P. borreri* (Sm.) Krog, as both taxa have foliose thalli, a pale grey upper surface, K+ yellow, a medulla that reacts C+ red, and punctiform pseudocyphellae. They are, however, chemically different: using TLC, we detected atranorin and lecanoric acid in our specimens of *P. subrudecta*, while *P. borreri* contains atranorin, chloratranorin, gyrophoric acid and traces of fatty acids. Despite these differences in chemistry, several authors (e.g., Clauzade & Roux, 1985; Wirth, 1987) did not treat these two species as independent taxa. Later, Crespo et al. (2004) confirmed, using a molecular phylogeny, that *P. borreri* and *P. subrudecta* are indeed two different species. *Punctelia subrudecta* was found in this study on siliceous rocks or on terricolous mosses. Loc: 7, 8, 23, 33.

Ramalina breviuscula Nyl.

We found a wide range of variability in morphology in this species, from minute thalli, formed by crowded sterile laciniae (the *breviuscula* morphotype), to thalli composed of loosely attached, broader branches, with lateral apothecia (the *mediterranea* morphotype, which corresponds to the former species *R. mediterranea* H. Magn., now synonymized under *R. breviuscula*). All specimens analyzed by TLC contained usnic acid. It is the most common and widespread species of *Ramalina* in the study area, growing on steeply inclined surfaces, usually at the top of blocks, on hard siliceous rocks. This is a mainly Mediterranean species (Nimis & Martellos, 2008). Loc: 2, 7, 11, 15, 16, 20, 21, 22, 24, 29, 32, 33.

Ramalina polymorpha (Lilj.) Ach.

Specimens from the only population that we found fit within the description of *R.*

polymorpha s. str., since they have laminar soralia originated from pseudocyphellae (Arroyo et al., 1991). This species was found growing at the top of an isolated block of schists, on a nutrient-enriched site. This species has been commonly recorded at high altitudes, and its presence in the study area was restricted to a wind-exposed and humid site. Loc: 7.

Ramalina requienii (De Not.) Jatta
This species is characterized by having isidioid outgrowths at the margins of the laciniae. It can be confused with juvenile thalli of *R. breviuscula*, but they are chemically different: both taxa have usnic acid, but *R. requienii* also contains stenosporic acid, while *R. breviuscula* does not. Like *R. breviuscula*, it is classified as a Mediterranean species (Nimis & Martellos, 2008) but, in the study area, *R. requienii* is much less common, and it grows only in localities near the coast. Loc: 20, 21, 22.

Ramalina subfarinacea (Nyl. ex Cromb.) Nyl.
In the study area, it always grows in localities above 350 m high, on siliceous rocks, usually at the top or on northern exposures of blocks. Loc: 7, 8, 16.

Rhizocarpon epispilum (Nyl.) Zahlbr.
Lichenicolous lichen growing on *Pertusaria* species. In the study area, it has been found on *P. rupicola*, where it forms minute dull brown thalli (Fig. 5E). Loc: 11, 16.

Rhizocarpon geminatum Körb.
This taxon is easily recognizable by its brown thallus, 2-spored asci and muriform ascospores. It was found once, growing on very shallowly inclined, north-facing surfaces of schists near water seepages. Loc: 7.

Rhizocarpon geographicum (L.) DC.
This species is one of the most common taxa in the study area. Besides its frequent occurrence, it is also remarkable for the variability of its thallus morphology. For

example, some specimens have areolae that are 0.2-0.8 mm wide, while others have much larger areolae, up to 2.5 mm wide. A significant number of samples that potentially belongs to this species were not possible to identify with certainty because of the lack of apothecia. It was found on moderately inclined to subvertical, north to northeast-facing surfaces, on different types of siliceous rocks. Loc: 1, 6, 7, 8, 11, 15, 16, 21, 22, 23, 24, 29.

Rhizocarpon polycarpum (Hepp) Th. Fr.

This taxon is characterised by having dark brown thalli, I+ blue medulla, and 1-septate ascospores that are persistently colourless, becoming pale only when old. It is common in the study area, on hard siliceous rocks, in both coastal localities and more inland areas. Loc: 16, 21, 22, 23, 24, 25, 29.

+ *Rhizocarpon viridiatrum* (Wulfen) Körb.

This parasitic species was found once, growing on *Aspicilia caesiocinerea*, forming small thalli composed of contiguous, strongly convex, greenish-yellow areolae (Fig. 5F). Although it is initially parasitic on other crustose lichens, it can live independently as it grows older (Fletcher et al., 2009b). Loc: 6.

Rinodina alba Metzler ex Arnold

This species has a whitish, rimose-areolate thallus, which reacts K+ yellow and C+ red, a conspicuous black prothallus, and *Pachysporaria*-type ascospores. It has been found on very hard siliceous rocks (mainly schists and quartz), on steep surfaces that face north or northwest. When found in the coast (locality 22), it was living even in the supralittoral Loc: 16, 21, 22, 29, 32.

Rinodina aspersa (Borrer) J. R. Laundon

This taxon has thalli formed by slightly scattered areoles, whitish-grey, K+ yellow and C+, and delimited by a conspicuous black prothallus (Fig. 6A). The morphology and the spot test reactions of the thallus are similar to those in *R. alba*, but, conversely to the latter, *R. aspersa* is sorediate and rarely has apothecia (Giralt, 2010). It was found once, growing on sun-exposed, subhorizontal schists. Loc: 3.

+ ***Rinodina atrocinerea*** (Hook.) Körb.
This species is similar to *R. alba* as well, since both have *Pachysporaria*-type ascospores and contain atranorin and gyrophoric acid as major compounds, among other lichen substances (Giralt & Barbero, 1995). However, they can be distinguished because *R. alba* has I+ blue medulla and shorter ascospores. *Rinodina atrocinerea* is an oceanic taxon, mainly found in the Atlantic region, west Mediterranean, and Macaronesia (Giralt, 2010); in the study area, it was found only once, on a sheltered schistose surface, near a stream. Loc: 16.

Rinodina beccariana Bagl.
This taxon is very common in the study area, where it lives on hard siliceous rocks, on steeply inclined to overhanging surfaces; in coastal localities it was also found growing on the supralittoral belt. Loc: 1, 7, 8, 16, 21, 22, 24, 25, 26, 28.

Rinodina cana (Arnold) Arnold
This taxon is recognized by its areolate grey thallus, its cryptolecanorine apothecia, and its lack of secondary substances. It is only known from few localities in the Mediterranean area (dry-warm areas of the Alps, eastern Pyrenees, and few sites in Spain and Portugal) (Nimis, 1993; Giralt, 2010). In the study area, it was found once, growing on a subvertical schistose rock, facing east. Loc: 9.

Rinodina gennarii Bagl.
This taxon can be easily separated from the rest of the Iberian *Rinodina* species by its *Dirinaria*-type ascospores (Giralt, 2010). It was found on schists and granites, on subvertical surfaces facing north or northeast. Loc: 4, 8, 15.

Rinodina obnascens (Nyl.) H. Olivier

Lichenicolous lichen growing on *Aspicilia* species, where it forms small dark patches on the host thallus. Although this is regarded as a common species (Giralt, 2010), in the study area, it was recorded only twice, both times growing on *A. intermutans*. Loc: 9, 26.

+ ***Rinodina sicula*** H. Mayrhofer & Poelt

This species is characterized by its whitish-grey, areolate thallus, C+ faintly red, and ascospores *Physconia*-type. It is a rare species, which has been previously reported only once from the Iberian Peninsula, growing on siliceous rocks at rather high altitude (1300 m) (Giralt & Llimona, 1997). In the study area, it also grows on siliceous rocks (specifically, on schists) on a subvertical sun-exposed surface, at over 600 m. Loc: 9.

Rinodina teichophila (Nyl.) Arnold

This taxon forms well-developed, thick, areolate to somewhat subsquamulose, dark grey thalli (Fig. 6B), with negative reaction for all performed spot tests (K-, C-, KC-, P-), and *Mischoblastia*-type ascospores. It was found growing on more or less sheltered schists, near a stream, in areas subject to temporary inundation. Loc: 13.

Rinodina vezdae H. Mayrhofer

This taxon is characterized by its areolate, thick, pale grey, K+ faintly yellow thallus, and its *Mischoblastia*-type ascospores. This taxon belongs to the *R. oxydata* group; and it is distinguished from *R. trachytica* (A. Massal.) Bagl. & Car., by the lack of 2’-0-methylperlatolic, and from *R. oxydata* (A. Massal.) A. Massal., by its larger ascospores (Giralt, 2010). However, some authors consider that *R. vezdae* could fit within the concept of *R. oxydata* (Giralt, 2001) and that further taxonomical studies are needed to clarify the taxonomy of this group of species (Giralt, 2001, 2010). In the study area, it was found once, on a sun-exposed horizontal schistose surface, with some soil deposition. Loc: 31.

Roccella phycopsis Ach.

Although it has been reported from a wide variety of rocks, including man-made materials, such as brick walls, or even on trees (Nimis & Martellos, 2008; Benfield & Purvis, 2009), in the study area, it only grows on metamorphic schists, in the vicinity of the sea, mainly on sheltered, vertical or overhanging rock faces. Loc: 20, 22.

+ ***Roselliniella atlantica*** Matzer & Hafellner

This lichenicolous fungus was described growing on *Xanthoparmelia mougeotii* and *X. verruculifera* (Matzer & Hafellner, 1990), but it has been recorded as well growing on other parmelioid species (e.g., Sérusiaux et al., 2003; Hawksworth et al., 2010). In the Iberian Peninsula, it has been reported in very few instances (Calatayud et al., 1995; Etayo, 2002). In the study area, it was found growing on *X. loxodes*. Loc: 7.

Sarcogyne privigna (Ach.) A. Massal.

Although it is considered a cool-temperate to arctic-alpine species (Nimis & Martellos, 2008), it also grows at low altitudes in our area of study, on sheltered schistose surfaces and weathered granites. Loc: 27, 33, 34.

Sarcogyne regularis Körb.

This is a widespread species (Nimis & Martellos, 2008) that, in the study area, was found on limestone and marbles. Loc: 30, 33.

Sarcopyrenia cylindrospora (P. Crouan & H. Crouan) M. B. Aguirre

Lichenicolous fungus, which was found growing on an unidentified crustose lichen, most likely an *Aspicilia* sp., since it is the most frequent lichen host genus (Navarro-Rosinés et al., 2009b), but was also found free-living on weathered granite. Loc: 6, 33.

Scoliciosporum umbrinum (Ach.) Arnold

This taxon presented a high variety of thallus morphologies, from granular to crustose fissurate, and with coloration from green to dark brown. It is unequivocally recognized by its acicular ascospores, arranged helicoidally within the asci. It is very common on sheltered, nutrient-enriched siliceous rocks, usually near rain-tracks. It was also found growing on other crustose lichens. Loc: 1, 8, 11, 16, 24, 25, 28.

Solenopsora cesatii (A. Massal.) Zahlbr.

This taxon forms small lobed thalli, whitish, and heavily pruinose. It grows on carbonate-rich rocks, in protected sites. Loc: 33.

Solenopsora holophaea (Mont.) Samp.

This species forms small thalli, composed of more or less overlapping squamules, colour dull reddish-brown, becoming olive green when wet, and lobed, undulated margins (Fig. 6C). It was found living within sheltered fissures, on soil or soft rocks. Loc: 18, 20.

\+ ***Solenopsora vulturiensis*** A. Massal.

This species can be confused with *S. cesatii*, but *S. vulturiensis* has a thallus formed by sublobed greyish-green areolae, with light pruina, and sorediate margins. Although it has usually been found in a sterile state (Clauzade & Roux, 1985; Gilbert et al., 2009b), almost all our specimens have apothecia. It is locally abundant, growing on siliceous rocks, usually where there is some soil deposition. Loc: 2, 3, 6, 7.

Sphinctrina leucopoda Nyl.

Lichenicolous fungus growing on *Pertusaria* spp. (mainly *P. pertusa*) and *Lecanora* spp. (Muñiz & Hladun, 2011). It was found once, growing on *Lecanora rupicola* subsp. s*ulphurata*, where all apothecia of *Sphinctrina leucopoda* were clustered in the younger part of the thallus. Apparently, this species tends to grow out following the cracks or fissures of the host thallus (D. Muñiz, pers. comm.). Loc: 7.

Sphinctrina tubiformis A. Massal

Lichenicolous fungus growing on *Pertusaria pseudocorallina*. This taxon is easily recognizable by its almond-shaped ascospores. Loc: 1, 22.

Sphinctrina turbinata (Pers. Fr.) De Not

Like the previous taxon, it is a lichenicolous fungus growing on *Pertusaria pseudocorallina*. Following recommendations from Muñiz & Hladun (2011), we confirmed the identification of this species with a spot test, K+ (colour red-violet) in the section of the exciple. This test was necessary because *Sphinctrina turbinata* usually has sessile apothecia, but when it has stalked apothecia it can be confused with *S. leucopoda*. Loc: 21.

Squamarina concrescens (Müll. Arg.) Poelt

This species is characterized by the presence of friable isidia at the margin of the squamules. It was found growing on clay soil. Loc: 19.

Squamarina lentigera (Weber) Poelt

This species was found growing abundantly on sand consolidated by carbonate, especially in dry, open areas. Loc: 12.

+ *Stigmidium hageniae* (Rehm) Hafellner

Lichenicolous fungus growing on *Anaptychia runcinata*. The pale brown mycelium forms an extended net on the surface of the host thallus, causing a progressive bleaching in it. It has previously been reported once in the Iberian Peninsula, growing on *A. ciliaris* (Etayo, 2010). Loc: 7.

Stigmidium tabacinae (Arnold) Triebel

Lichenicolous fungus growing on *Toninia* species. In the study area, it is locally very abundant, growing on squamules of *T. physaroides* and *T. sedifolia*. Loc: 12.

Teloschistes chrysophthalmus (L.) Beltr.

Although this taxon is mainly epiphytic, we found it occasionally growing on siliceous rocks. Loc: 32.

Tephromela atra (Huds.) Hafellner

This species resembles *Lecanora gangaleoides* due to its whitish thallus that reacts K+ yellow, and apothecia with black discs. *Tephromela atra*, however, has a purple hymenium, while in *Lecanora gangaleoides* it is hyaline. It is a very widespread taxon, occurring mainly on north-exposed siliceous rocks. Loc: 7, 11, 13, 15, 16, 18, 20, 21, 22.

+***Thelenella muscorum*** (Th. Fr.) Vain. var. ***octospora*** (Nyl.) Coppins & Fryday

This variety differs morphologically from var. *muscorum* in its 8-spored asci (instead of 2- or 4-spored asci) and its smaller ascospores. Furthermore, it occurs considerably less frequently than var. *muscorum* (Mayrhofer & Poelt, 1985; Mayrhofer, 1987). Only one specimen was found, growing on consolidated clay soil. The only previous record of *T. muscorum* var. *octospora* in the Iberian Peninsula is from beech woods in the very humid montane belt of northern Navarra (Etayo, 1990), which is a considerably different habitat to the locality where we found it. Loc: 30.

Thelopsis isiaca Stizenb.

This taxon is a Mediterranean-Macaronesian species that is normally abundant in coastal environments (Nimis & Martellos, 2004). However, in the study area, it was found only once, but not epiphytic nor calcicolous, as it is usual for this species, but silicicolous. Loc: 22.

+ ***Thrombium epigaeum*** (Pers.) Wallr.

This ephemeral species forms very thin, greyish-green, crustose thalli with small, immersed black perithecia. It is very difficult to detect in the field, because the colour of the thallus is very similar to that of the soil. Loc: 33.

Toninia aromatica (Turner) A. Massal.

This eutrophilous taxon was found once, growing on the mortar of the Quermançó Castle. Loc: 1.

Toninia cinereovirens (Schaer.) A. Massal.

This taxon is formed by greyish-brown imbricate squamules with a dark grey margin. This taxon has been found on sunny, steep rain-track surfaces on siliceous rocks, where it is initially parasitic, using *Lichinella stipatula* as a host. Loc: 26, 28, 34.

Toninia physaroides (Opiz) Zahlbr.

This species is characterized by having columnariform squamules; sometimes even a bit branched, and usually does not have apothecia. It is one of the most abundant species growing on the climbing dunes. Loc: 12.

Toninia sedifolia (Scop.) Timdal

Sterile specimens of *T. sedifolia* might be confused with *T. physaroides*, but they are distinguished by the shape of the squamules, bullate in *T. sedifolia* and more cylindrical in *T. physaroides*; and by the absence of pseudocyphellae in *T. sedifolia* (Timdal, 1991). It was found on calcareous soil and on sand compacted by carbonates. Loc: 12, 30.

Toninia squalida (Ach.) A. Massal.

The thallus of this taxon is composed of dark brown and epruinose squamules; very similar to *T. aromatica*. However, they can be distinguished by their apothecial characters: *T. squalida* has a pale brown hypothecium and acicular ascospores, 3- to 7-septate, while *T. aromatica* has a dark reddish hypothecium and ellipsoidal-cylindrical ascospores, (1-)3-septate. It was found once, growing on a rain-track surface of siliceous rock, with cyanolichen species, such as *Lichinella stipatula*, and saxicolous mosses. Loc: 7.

Toninia tristis (Th. Fr.) Th. Fr. subsp. ***pseudotabacina*** Timdal

There are 11 subspecies recognized within *T. tristis* that can be distinguished by spore size and septation, type of pigments, terpenoid content and ecological preferences (Timdal, 1991, 2002). In the study area, we found only *T. tristis* subsp. *pseudotabacina*, growing on the climbing dunes. Loc: 12.

Trapelia coarctata (Turner ex Sm.) M. Choisy

Although it is a very polymorphic species, it can be recognized by its crustose whitish-green thallus that reacts C+ red, and its lecanorine apothecia with pinkish discs (Fig. 6D). It is a pioneer lichen that occurs frequently on siliceous rocks, near the ground, or also on consolidated soil, always on well-illuminated sites. Loc: 2, 6, 7, 24, 25, 28, 29, 33.

Trapelia involuta (Taylor) Hertel.

We found it sometimes growing near the previous taxon, but it can be easily distinguished by thallus morphology, because *T. involuta* has a thallus formed by whitish, rounded, convex areoles (Fig. 6D). It grows on nutrient-enriched surfaces, usually near the ground. Loc: 1, 6, 12, 13, 17.

+ ***Trapelia placodioides*** Coppins & P. James

This species of *Trapelia* forms a white rimose thallus, with small (0.3 mm diam. maximum) green soralia. It grows on siliceous rocks with some accumulations of soil. Loc: 3, 8.

Trapeliopsis flexuosa (Fr.) Coppins & P. James

This taxon has thallus formed by more or less agglutinated granular areoles, of a pale grey colour, with farinose soralia. It was found only once, on a sheltered vertical schist surface. Loc: 8.

Trapeliopsis wallrothii (Spreng.) Hertel & Gotth. Schneid.

Although several authors described its main reproductive strategy as sexual and do not mention asexual structures (e.g., Clauzade & Roux, 1985; Brodo et al., 2001) none of the specimens we examined was fertile and almost all presented laminar isidia (Fig. 6E), a morphology more similar to the one provided by Nimis & Martellos (2004). Locally very abundant, it grows on exposed siliceous soil crusts, usually mixed with cyanobacterial colonies. Loc: 10, 19, 22, 28.

Tremolecia atrata (Ach.) Hertel

This species is easily recognizable by its rust-coloured thallus and its black, angulose, lecideine apothecia. It was found on subvertical, sheltered surfaces of iron-rich siliceous rocks. Loc: 7 (not collected), 16.

Verrucaria amphibia Clemente

This species colonizes the coastal metamorphic schists in the supralittoral zone, where it forms almost a continuous black band, only absent on the most sun-exposed surfaces. Loc: 22.

Verrucaria dolosa Hepp

This species grows on various siliceous rocks, always in shaded conditions, and sometimes on rain-tracks. Loc: 7, 8, 28.

Verrucaria fuscella (Turner) Winch

Although we only found very small thalli of this species, it is easily recognized by its angulose, grey areolae with black margins. It was found on nutrient-enriched schists as well as growing on the thallus of *V. fusconigrescens* Loc: 13.

Verrucaria fusconigrescens Nyl.

This species occurs locally abundant, growing on siliceous rocks in exposed situations, even near small streams that are subject to temporary inundation. Loc: 3, 8, 13.

Verrucaria hochstetteri Fr.

This species is quite abundant on limestone outcrops, growing on north-facing subvertical or overhanging rock faces. Loc: 30.

Verrucaria lecideoides (A. Massal.) Trevis.

This *Verrucaria* species is easily recognizable by its immersed and flattened perithecia, which are very similar to lecideoid apothecia. It was found few times, on limestone outcrops, in sheltered situations. Loc: 30.

Verrucaria macrostoma Dufour ex DC.

This species can resemble *V. nigrescens* Pers. given that both have a dark brown thallus and grow on calcareous substrates, but *V. macrostoma* has more prominent perithecia and slightly larger ascospores (Orange et al., 2009). Loc: 30.

Verrucaria murina Leight.

This taxon has thin, green to dark brown thallus, with its surface covered by goniocysts. It is rare in the study area, found only once, growing on the climbing dunes. Loc: 12.

Verrucaria nigrescens Pers.

This species is very similar to *V. fusconigrescens*, as both have brown thalli and similar ascospores size. However, *V. fusconigrescens* has a black conspicuous prothallus, prominent perithecia, and it is mainly siliceous, while *V. nigrescens* lacks a prothallus, has immersed perithecia and occurs on calcareous rocks (Orange et al., 2009). This taxon was found in the study area growing on sun-exposed limestone surfaces and on porous mortar. Loc: 1, 30.

Verrucaria praetermissa (Trevis.) Anzi

This species was found growing abundantly on schists near a stream, on sites where is temporarily submerged when water levels increase. Loc: 13.

Verrucaria viridula (Schrad.) Ach.

This species can be easily distinguished from other *Verrucaria* taxa found in the study area by its large ascospores (29-33 x 14.5-17.5 µm). It grows on nutrient-enriched siliceous rocks. Loc: 8.

Verrucula maritimaria Nav.-Ros. & Cl. Roux

Lichenicolous lichen growing on *Caloplaca maritima*. A closely related species to *Verrucula maritimaria* is *V. hladuniana* (Nav.-Ros. & Cl. Roux) Nav.-Ros. & Cl. Roux, which has smaller size of the areoles and grows on *Caloplaca marina*. Loc: 4.

Verruculopsis flavescentaria Gueidan, Nav.-Ros. & Cl. Roux

Lichenicolous lichen growing on *Caloplaca flavescens*. This is a mainly Mediterranean taxon, even though it has also been reported from coastal areas of Ireland and Sweden (Navarro-Rosinés et al., 2007). Loc: 16.

Xanthoparmelia conspersa (Ehrh. ex Ach.) Hale

This species was found on sun-exposed, nutrient-enriched horizontal or gently sloping siliceous rocks. Loc: 6, 7, 19, 26.

Xanthoparmelia glabrans (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

Initially, these specimens were identified as *X. pulla*. The results of the TLC, however, revealed the presence of alectoronic acid as the major compound, accompanied by gyrophoric and α-collatolic acids as minor compounds. This chemistry is characteristic of *X. glabrans*. It grows on sun-exposed siliceous rocks. Loc: 17, 28, 26, 28.

Xanthoparmelia loxodes (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

This foliose taxon has a brownish-black upper surface with short coarse erupting isidia, defined as ‘pustular isidia’ by Esslinger (1977), although some authors do not consider them as true isidia (Giordiani et al., 2003). The presence of glomellic, glomelliferic, and perlatolic acids was detected by TLC. It was found on wind- and sun-exposed siliceous rocks. Loc: 7, 8.

+ ***Xanthoparmelia mougeotii*** (Schaer.) Hale
This species is easy to distinguish from other green *Xanthoparmelia* growing on the study area because its thalli form small rosettes, with narrow radiating lobes that grow closely appressed to the substrate, and its laminal, rounded soralia. Although this taxon rarely has apothecia, some of our specimens were fertile (Fig. 6F). It grows on siliceous rocks, especially on quartz, very often near the ground. Although it is not rare in the Iberian Peninsula, there are no previous records from the Iberian Mediterranean region, apart from our citations. Loc: 3, 7, 16, 24, 32.

Xanthoparmelia pulla (Ach.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch
This species can be confused with *X. glabrans*, but all specimens identified here as *X. pulla*, and analyzed by TLC, contained divaricatic and stenosporic acids as major compounds. It is very common on sun-exposed nutrient-enriched siliceous rocks. Loc: 6, 13, 15, 16, 23.

Xanthoparmelia tinctina (Maheu & Gillet) Hale
This is the *Xanthoparmelia* species more common in the study area, where it grows on gentle sloping siliceous rocks, mainly on sunny expositions. Loc: 3, 7, 15, 16, 17, 26, 28.

Xanthoparmelia verruculifera (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch
This species is very similar to *X. loxodes*, with which it shares brown isidiate thallus, but in *X. verruculifera*, isidia are longer, cylindrical, and a bit ramified. Furthermore, both species can be distinguished by their secondary compounds: the specimens belonging to *X. verruculifera* (analyzed here by TLC) contained divaricatic,

nordivaricatic, and subdivaricatic acids, while *X. loxodes* contains glomellic, glomelliferic, and perlatolic acids. Loc: 7, 8.

Xanthoria aureola (Ach.) Erichsen

This species has been frequently confused with *X. parietina* (L.) Beltr., but *X. aureola* has, among other characters, a layer of crystals in the upper surface and strap-shaped lobes, while *X. parietina* has smooth surface and spathulate lobes (Lindblom & Ekman, 2005). It grows on coastal siliceous rocks. Loc: 4, 19, 20, 21, 22, 28, 30, 32.

Xanthoria calcicola Oxner

This species can be distinguished from the previous one by its wider lobes and the presence of laminar isidia-like projections (Lindblom & Ekman, 2005). It grows on carbonated schists, as well as on nutrient-enriched acidic rocks. Loc: 16, 23, 28, 31.

+ ***Zwackhiomyces lecanorae*** (Stein.) Nik. Hoffm. & Hafellner

Lichenicolous fungus growing on species from the *Lecanora dispersa* group. In our study area, it was found on *L. salina*. It has been recently reported for the first time from the Iberian Peninsula (Etayo, 2010). Loc: 13.

Zwackhiomyces sp.

In one locality, a specimen belonging to the genus *Zwackhiomyces* was found growing abundantly on squamules of *Endocarpon pusillum*. This taxon has perithecia 0.15-0.3 mm in diam., 1-septate ascospores, constricted at the septum, (14)16-19(19.5) x (6.5)7-8(8.5) µm, and with verruciform ornamentation. This combination of traits does not fit any known species of this genus. Additionally, M. Grube communicated us (in litt., 2011) his finding of an undescribed *Zwackhiomyces* growing on *Endocarpon pusillum*, which potentially belongs to the same species as our specimens. We are waiting to receive the samples provided by M. Grube, to compare them with our specimens and check if they belong to the same putative new species. Loc: 10.

DISCUSSION

General remarks

This study of the saxicolous and terricolous lichens of the Cap de Creus Natural Park generated a catalogue of 294 taxa, of which 263 are lichens and 31 are lichenicolous fungi. A total of five taxa in the catalog could not be assigned to any known species: *Amandinea* sp., *Cercidospora* sp.1, *Cercidospora* sp. 2, *Lichenostigma* sp., and *Zwackhiomyces* sp. It will be necessary to study more material in order to clarify the identity of these taxa, and to describe them formally if they turn out to be new species.

According to the Checklist of the Lichens and Lichenicolous Fungi of the Iberian Peninsula and Balearic Islands (Hladun & Llimona, 2002-2007), together with other recent studies (Burgaz et al., 2007; Paz-Bermúdez et al., 2009; Etayo, 2010; Llop et al., 2010, in review) these are the most remarkable novelties in the catalog:

- A total of five lichens (*Caloplaca arcis*, *C. austrocitrina*, *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon simplicatum*, *Micarea melaenida*) and four lichenicolous fungi (*Arthonia lecanorina*, *Endococcus buelliae*, *Polycoccum rinodinae*, *P. teresum*) are new records for the Iberian Peninsula. Our collections of *P. rinodinae* is the first record for Europe, and the finding of *P. teresum* represents the second worldwide record of this taxon, previously known only from the type locality in western Turkey (Halici et al., 2009).
- There are ten lichens that represent second records for the Iberian Peninsula: *Arthonia molendoi*, *Caloplaca flavocitrina*, *Diplotomma hedinii*, *Endococcus fusiger*, *E. macrosporus*, *Lecanora salina*, *Rinodina sicula*, *Stigmidium hageniae*, *Thelenella muscorum* var. *octospora*, and *Zwackhiomyces lecanorae*.
- Finally, we emphasize the following taxa, given their rarity in the Iberian territory: *Acarospora modenensis*, *A. oligospora*, *A. sinopica*, *A. sulphurata*, *Aspicilia inornata*, *Buellia tirolensis*, *Enterographa pitardii*, *Epiphloea terrena*, *Gyalideopsis athalloides*, *Involucropyrenium tremniacense*, *Psora gresinonis*, *Psorotichia vermiculata*, *Rinodina aspersa*, *R. sicula*, *R. teichophila*, *R. vezdae*, and *Thrombium epigaeum*.

Crustose lichens are the most common biotype, representing 67% of the total (176 ssp.), and include the genera with the highest number of species: *Caloplaca* (27), *Verrucaria* (11), and *Buellia* (11). They are also the most widespread biotype of lichens, found on all types of rocks and in all possible inclinations and orientations, and also living on soil. The next most common biotype, foliose lichens, represent 15% (39 spp.) of the total, only around a quarter as many species as the crustose lichens. Of the foliose lichens, a large majority are parmelioid lichens, and are usually on sheltered and humid sites. Fruticose lichens represent only 3% (9 spp.), and grow only where the humidity is high (e.g., coastal localities or sites with frequent fog banks). The squamulose biotype is the third most important at 10% (25 spp.), followed by the species with dimorphic thalli that represent 4% (11 spp.). Both are the main type among the terricolous lichens. Finally, leprarioid lichens represent only 1% (3 spp.).

Lichens with trebouxioid photobionts clearly dominate, constituting 87% (229 ssp.) of the total. Lichens with cyanobacteria (8%, 20 ssp.) are almost restricted to rain-track surfaces (where, however, they are the most numerous type of lichen). Finally, species with trentepohlioid algae (5%, 14 spp.) are the less numerous in the area. It is remarkable that in coastal localities, these lichens (mainly the species *Dirina massiliensis*) cover large areas of vertical rock surfaces and cave walls and ceilings. They become, however, less abundant inland, where they scarcely occur, always on overhanging surfaces.

Lichen vegetation

Below, we characterize the main lichen communities occurring on rocks and soil in the study area. Our information about the ecology of the lichens and their habitual occurrence associated with other species is based on accurate field observations taken during collections.

1. Communities of saxicolous lichens

The presence of saxicolous lichens depends on the rock type, its hardness, mineral composition, and porosity. Other important ecological factors that can influence (perhaps even more heavily) the occurrence of the saxicolous lichens include exposition to the rain (ombrophobous versus ombrophilous species), the degree of sloping and orientation of the surfaces, altitude, the level of eutrophication, the presence and duration of water seepages and mineralizations (for example, iron-rich compounds). Based on these factors, we have characterized the following different groups of communities of saxicolous lichens found in the study area.

1.1. Silicicolous lichens and their major habitats

Silicicolous lichens are the most abundant in the study area, since acidic rocks represent the most widespread substrate, represented by metamorphic schists (predominant), granodiorites, quartz, and pegmatites, and therefore it was also the main type of substrate we surveyed.

1.1.1. Ombrophobous communities

These communities are composed by lichens growing on sheltered vertical surfaces (overhangings and walls and ceilings of open caves) that are not wetted by the rain, and receive very low sunlight. In the coastal area, these surfaces are frequently covered by the crustose species *Dirina massiliensis*, with the fertile and the sorediate forms occurring with the same frequency, and represented by its silicicolous morphotype that gives to this community its characteristic greyish-brown colour. This species is frequently accompanied by other, less abundant, crustose ombrophobous species, such as *Lecanographa grumulosa* and *Opegrapha lutulenta*. On sheltered sites near the sea, with some accumulation of soil, the community is enriched with the presence of *Thelopsis isiaca* (locality 22) or *Ingaderia troglodytica* and *Solenopsora holophaea*, with these latter two growing inside crevices (locality 20). Also at coastal sites, mostly occupying the ceiling of open caves and rain-exposed subvertical sites, the fruticose lichen *Roccella phycopsis* (also showing a greyish-brown morphotype) grows abundantly. When these vertical surfaces become more exposed to direct sunlit, *R. phycopsis* is replaced progressively by two species of *Ramalina*: *R. breviuscula* and *R. requienii*.

Even far from the coastal localities, *Dirina massiliensis* is still present on overhanging surfaces, although it does not grow as massively as near the sea. *Lecanographa grumulosa*, however, disappears away from the coast. In its place other species appear such as *Diploicia subcanescens*, *Buellia subdisciformis*, *Caloplaca crenularia*, and, occasionally, unusual species as *Enterographa pitardii* and *Opegrapha cesareensis*.

1.1.2. Subvertical to steep Southerly-oriented surfaces

On subvertical to vertical surfaces facing south, the conditions are markedly warm, since they receive daily long periods of direct sunlight, and very dry, due to the very rapid evaporation of nocturnal dewfall. The vertical south-facing surfaces of acidic rocks, especially hard ones (e.g., schist, granodiorite) are colonized by *Acarospora hilaris*, which grows very extensively in some localities, giving to these surfaces a characteristic bright citrine colouration, visible even from a distance. Occasionally, we found *A. epithallina* growing on the thalli of *A. hilaris*; the presence of this parasite is a sign of the optimal development of *A. hilaris* (Egea & Llimona, 1987). There are other photophilous species accompanying the *Acarospora* species, such as *Buellia stellulata*, *B. tesserata*, *B. spuria*, *Dimelaena oreina*, *Caloplaca arenaria*, and *Candelariella vitellina*. When these surfaces of hard rock are not vertical, but still very inclined, *A. hilaris* almost disappears and the rest of photophilous species mentioned above, become even more predominant in the community.

Previous studies (e.g., Crespo et al., 1976; Egea & Llimona, 1987, 1991) of the *Acarospora hilaris* communities of central and southern areas of the Iberian Peninsula emphasized the elevated biomass of *Caloplaca carphinea* in these communities. In our study area, however, *C. carphinea* does not appear together with *Acarospora hilaris*, but grows abundantly on various inclined sun-exposed surfaces of quartz, together with *Dimelaena oreina*, *Rinodina alba*, and *Buellia stellulata* (locality 30).

On weathered granite (a type of substrate very abundant above Punta Falconera, locality 33), the south-facing surfaces are colonized by lichens poorly recorded in the Iberian Peninsula, such as *Acarospora modenensis*, *A. oligospora*, *Caloplaca aetnensis*, and *C. ligustica*, accompanied by more common species as *Polysporina simplex*, *Phaeophyscia hirsuta*, and *Sarcogyne privigna*.

1.1.3. Subvertical to steep Northerly-oriented surfaces

Steeply inclined north-facing surfaces are well illuminated but not exposed to direct sunlight and, consequently, the evaporation of water from dewfall or fog is slower than in the south-facing surfaces. The most common community established on the north-facing rock surfaces in the study area, especially above 100 m, is the lichen community dominated by *Pertusaria rupicola*. This species provides the highest amount of lichenic biomass to the community, and gives it a characteristic dull yellow colour. *Pertusaria rupicola* grows along with other species of *Pertusaria*, such as *P. pseudocorallina*, *P. aspergilla*, and *P. leucosora*, as well as with *Rhizocarpon geographicum*, *Tephromela atra*, *Lecanora praepostera*, *L. gangaleoides*, *L. rupicola* subsp. *sulphurata*, *Buellia subdisciformis*, *Protoparmelia montagnei*, *Ochrolechia parella*, and, more sporadically, *Aspicilia cupreoglauca*, *Lecanora polytropa*, *L. muralis*, and *Scoliciosporum umbrinum*. In this community, we also found the lichenicolous lichens *Cyphelium marcianum* (on *Pertusaria pseudocorallina*) and *Rhizocarpon epispilum* (on *Pertusaria rupicola*). The specific composition and relative abundance of these species suggest that this community belongs to the association *Pertusarietum rupicolae*, described by Wirth & Llimona (1975).

The shady side of the Serra de Verdera (localities 1, 7, 9), the top of Muntanya Negra (locality 16), and sheltered areas along the northern coast (locality 11), are frequently covered by fog banks and, consequently, air humidity is especially high. In these sites, the community of *Pertusaria rupicola* is highly enriched by the presence of *P. monogona*, which forms very large and thick thalli, and aerohygrophilous species such as *Anaptychia runcinata*, *Parmelia saxatilis*, *Parmelina tiliacea*, *Ramalina breviuscula* and *R. polymorpha*, the latter growing on rocks that are frequently used as perches or roosting sites by birds. In these highly humid habitats, if rocks have iron mineralizations (localities 7, 8, 16), two ferricolous species appear, *Acarospora sinopica* and *Tremolecia atrata*, and tend to form specialized populations.

On steeply north-facing surfaces in localities below the 100 m and towards the coast, *Pertusaria rupicola* and the other *Pertusaria* species are still present, but they are considerably less abundant. The following taxa become more predominant in the community: *Lecanora sulphurea*, *L. rupicola* subsp. *sulphurata*, *Protoparmelia montagnei*, and even *Rhizocarpon geographicum*, which is still present in our study area in localities close to sea level.

1.1.4. Gently sloping or horizontal rock surfaces

The horizontal and slightly sloping surfaces of hard rocks are mainly covered by photophilous species of *Aspicilia*, *A. caesiocinerea* and *A. intermutans* being the most common species, and usually forming large thalli. Of note is the large number of samples of *Aspicilia* from these surfaces that were not successfully identified because of the absence of apothecia and pycnidia, similar to the already mentioned in Boom & Jansen (2002). Accompanying *A. caesiocinerea* and *A. intermutans* are *A. subdepressa*, *Caloplaca furax*, *C. rubelliana*, *Diploschistes actinostomus*, *D. euganeus*, *Trapelia involuta*, *Xanthoparmelia loxodes*, and *X. verruculifera*.

The dominant lithology in locality 23 is large outcrops of phyllites. Their horizontal and subhorizontal surfaces (completely exposed to sunlight and rain, and slightly nutrient-enriched by soil generated by weathering of the soft schistose rock), are highly covered by thalli of *Ingvariella bispora*, which grows in this locality at a lower altitude than reported elsewhere in the Iberian Peninsula. *Ingvariella bispora* is accompanied by other more or less photophilous lichens, such as *Lecidella asema* var. *elaeochromoides*, *Buellia abstracta*, *B. stellulata*, *Catillaria chalybeia*, *Aspicilia intermutans*, *Lecanora rupicola* subsp. *sulphurata*, *Caloplaca arenaria*, and *Lecidea sarcogynoides*.

On top of the rock outcrops, very near to the ground, horizontal surfaces are sun-exposed and strongly nutrient-enriched, mostly due to cattle dung. Here we found photophilous and eutrophication-tolerant species, such as *Xanthoparmelia pulla*, *X. glabrans*, *X. tinctina*, *X. conspersa*, *Buellia badia*, *Candelariella vitellina*, *Caloplaca crenularia*, and *Lecidea fuscoatra*. The surfaces of small quartz pebbles, very near to, or at the same level as the soil, are almost all covered by *Xanthoparmelia mougeotii*.

1.1.5. Rain-track surfaces

Rain, or condensation of morning dew, can cause a thin layer of water circulating on some steep rock surfaces for brief or, occasionally, longer periods of time. This special microenvironment has more water availability than the neighbouring areas of rock surface that are more distant from the water-layer, even without water seepages. It is also more nutrient-enriched, because of salts dissolved in the water layer. These rain-tracks can be easily detected, because the rock surface is blackened due to the growth of free-living cyanobacteria and of cyanolichens.

On sunny rain-track surfaces, we found a significant number of cyanolichens growing, *Lichinella stipatula* and *Peltula euploca* being the most common and abundant species. They are accompanied by less frequent taxa, such as *Anema nummularium*, *Peltula obscurans*, *P. omphaliza*, *P. placodizans*, *Glyphopeltis ligustica*, and *Lichinella cribellifera*, most of them thermophilous species. Along with these cyanolichens *Caloplaca irrubescens* is very common in these conditions; *Toninia cinereovirens* is found less commonly, growing on *Lichinella stipatula* and free cyanobacteria. Although *Aspicilia contorta* subsp. *hoffmanniana* has been reported as occurring relatively frequently on other silicicolous lichen communities of rain-tracks (Llimona & Egea, 1985), in our study it was rarely recorded in this environment. Finally, we found other species living more or less constantly in the vicinities of the rain-track surfaces, including *Caloplaca rubelliana* and *Catillaria chalybeia*.

When rain-tracks occur on northern-exposed inclined surfaces, *Lichinella stipatula* and *Peltula euploca* are usually present. However, the other species of cyanolichens, which are more photophilous and thermophilous, are replaced by species such as *Collema ryssoleum*, *Dermatocarpon miniatum* and, less frequently, *D. luridum*, which is more demanding of wet conditions than *D. miniatum*.

1.1.6. Surfaces near streams

We have surveyed some outcrops of schists near small streams in two localities (localities 13, 14), where lichens are usually dry, but undergo temporarily flooding when river flow increases. The most common species growing on these conditions are *Caloplaca atroflava*, *C. diffusa*, *Catillaria chalybeia*, *Aspicilia caesiocinerea*, *Lecanora campestris*, *L. salina*, *Verrucaria praetermissa*, and *V. fusconigrescens*, and more occasionally, *Caloplaca austrocitrina*, *Rinodina teichophila*, and *Verrucaria fuscella*. Of note is the presence of *Caloplaca inconnexa* var. *nesodes* on most of the *Aspicilia caesiocinerea* thalli. A previous study (Pereira, 1992) also recorded two rare hydrophyle lichens in these localities, *Pterygiopsis coracodiza* (Nyl.) Henssen and *Psorotichia suffugiens* (Nyl.) Forss. We did not find these species in our survey, however.

1.1.7. Rocky shores

A previous study by Llimona (1995) characterized the different lichen communities that are arranged vertically along rocky shores. Based on this previous characterization, and complemented by our new collections, we distinguish the following communities:

- The midlittoral zone is frequently submerged by the sea, and the only lichen growing on these conditions (although not collected in this study) is *Pyrenocollema halodytes* (Nyl.) R. C. Harris, which grows on the shells of *Chthamalus* and *Patella* species.
- The supralittoral zone, which is regularly splashed but not often submerged by the sea, is almost completely covered by the black thalli of *Verrucaria amphibia*, which occupies a band from a few centimetres to 3 m (depending of the width of the splash zone), and is only absent in the most sun-exposed sites.
- Above the supralittoral zone, the area is frequently exposed to saltwater splashes and, more rarely, to temporary inundation by seawater. Here, the lichen community is mainly formed by the species *Caloplaca marina*, *C. maritima*, *C. aegaea*, and *Lecania atrynoides*, which extend from 3 to 5 m.
- Finally, above the community dominated by the maritime species of *Caloplaca*, the lichen community receives occasional water splashes and is affected by marine breezes transporting minute salt crystals. In this zone, grow lichens that are tolerant to marine influence, such as *Xanthoria aureola*, *Rinodina alba*, *R. beccariana*, *Buellia tesserata*, and *Lecanora praepostera*. Further still above sea level, where this maritime influence becomes more moderate, the community is enriched with *Protoparmelia montagnei*, *Ramalina breviuscula*, and *R. requienii*.

1.2. Calcicolous lichens and their major habitats

The main example of calcareous substrates in the area are the limestone outcrops of Cap Norfeu (locality 30). On highly sun-exposed, horizontal to steep surfaces of limestone we found *Caloplaca aurantia*, *C. flavescens*, *Verrucaria macrostoma* and *V. nigrescens* growing very abundantly. At more sheltered sites, however, the composition of the species shifts and is dominated by *Caloplaca subochracea* var. *luteococcinea* (which gives the rock a characteristic yellowish tinge), mixed with *Verrucaria hochstetteri*, *V. lecideoides*, *Bagliettoa cazzae*, *Opegrapha calcarea*, *Porina byssophila*, and *Lecidella stigmatea*. On vertical surfaces, overhangings, and cave ceilings of this locality, we found an ombrophobous community, which covers almost all the northern cliffs of Cap Norfeu. It is mainly composed by the white calcareous morphotype of *Dirina massiliensis*, which is remarkably thicker than the silicicolous morphotype and gives the characteristic colour to this community, and accompanied by *Lecanographa grumulosa*.

Other calcareous substrates, such as the marble outcrops in Punta Falconera (locality 33) and the calcareous schists in the remains of an old shepherd's shelter (locality 16), are considerably smaller, but contribute to the richness of calcicolous lichens. Growing on these substrates, on horizontal to inclined surfaces and, mainly on sun-exposed situations, we found species such as *Caloplaca vitellinula*, *Candelariella aurella*, *Diplotomma hedinii*, *Lecania inundata*, *L. sylvestris*, and *Sarcogyne regularis*. Finally, the sporadical presence of manufactured calcareous substrates in the area, usually porous mortar, allows the growth of species such as *Caloplaca arcis* or *Coscinocladium gaditanum*.

2. Communities of terricolous lichens

2.1. The climbing dunes

The climbing dunes of les Cavorques (locality 12) are formed by siliceous grains (mainly coming from the northern coast), deposited by the wind and more or less cemented by carbonates. On this special substrate, markedly calcicolous terricolous lichens, such as *Diploschistes ocellatus*, *Involucropyrenium tremniacense*, *Placidium tenellum*, *Toninia physaroides*, and *T. tristis* subsp. *pseudotabacina*, coexist with more neutrophilous species, like *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon pusillum*, and *Psora vallesiaca*. The species *Thermutis velutina* (Ach.) Flot. and *Toninia verrucosa* (A. Missal.) Flagey were reported from the dunes in Llimona (1995), but they have not been found in recent surveys. Most part of the dunes is considerably sun-exposed, and only in the most shaded small overhangings there is enough shelter for *Botryolepraria lesdainii* to grow. In areas where the dunes are flat or gently sloping, erosion is less strong, and therefore, the dunes are much more compact. Here, saxicolous lichens such as *Caloplaca aurantia*, *Collema cristatum*, *Lobothallia radiosa*, and *Placynthium tremniacum* grow. *Bagliettoa calciseda* shows an atypical growth in this locality, spreading massively, but growing exclusively on the calcareous mortar, and clearly avoiding the siliceous grains.

2.2. The shallow soils

A very different community of terricolous lichens grows on several localities near the coast with shallow, somewhat cobbly, clay soil, which often forms a compacted crust (localities 10, 19, 28, 33). On this substrate, vascular plants are relatively infrequent because of the low capacity of the soil to retain water, and the availability of open areas allow certain terricolous lichen communities to form. Some of the most common species found on these exposed sites are *Cladonia foliacea*, *C. pyxidata*, *Endocarpon pusillum*, *Leptogium lichenoides*, *Squamarina concrescens*, *Trapeliopsis wallrothii*, and semi vagrant forms of *Xanthoria aureola*. In addition, we found on these soils, several lichens rarely reported in the Iberian Peninsula such as *Psora gresinonis*, *Endocarpon simplicatum*, and *Micarea melaenida*. Shortly after rain, or in conditions of unusually high atmospheric humidity, it is also possible to detect the presence of rare ephemeral lichens like *Epiphloea terrena*, *Gyalideopsis athalloides*, and *Thrombium epigaeum*.

A phytogeographical analysis

We have elaborated a phytogeographical analysis of the lichen-forming species of the area, excluding taxa identified as cf. and aff. or undescribed. Based on the distribution data of Nimis (1993) and Clauzade & Roux (1985), and complemented with data of Calatayud (1998), we subdivided the species into the following groups: widespread, Mediterranean, Mediterranean-Atlantic, Atlantic, Mediterranean temperate, temperate, and Artic-alpine to boreal-montane (See Table 1).

Widespread distributed species represent 19.5% of the total (51 spp.). Some of them, such as *Candelariella vitellina*, *C. aurella*, *Lecanora albescens*, *L. campestris*, *L. dispersa*, *Physcia adscendens*, *P. caesia*, and *Polysporina simplex*, correspond to eutrophilous species that grow on nutrient-enriched habitats, a common and widespread habitat type. Within this group of widespread lichens, are also species widely distributed from the coldest areas to the temperate and Mediterranean regions. These include *Cladonia pyxidata*, *Dimelaena oreina*, *Diploschistes muscorum*, *Rhizocarpon geographicum*, and *Scoliciosporum umbrinum*.

Mediterranean lichens represent 30% (78 ssp.) of the total number of species recorded in the study area. The categorization of lichens into a 'Mediterranean' group has been a debated topic (Barreno, 1991, 1994; Nimis, 1993) as, in fact, lichens have been placed in it that have a much wider distribution, far outside the Mediterranean floristic region (Calatayud & Barreno, 1994). The concept of the category 'Mediterranean' stated by Nimis (1993) includes three types of distribution. The first comprises taxa whose hitherto known distribution is restricted to the Mediterranean region; from our study area: *Acarospora modenensis*, *Bagliettoa cazzae*, *Caloplaca aegaea*, *C. furax*, *Diploschistes interpediens*, *Endocarpon simplicatum*, *Epiphloea terrena*, *Heteroplacidium contumescens*, and *Psora gresinonis* fit within this group. The second type of distribution refers to taxa whose range also includes parts of the world beyond the Mediterranean, but which nevertheless have a Mediterranean type of climate. For example: *Acarospora hilaris*, *Buellia dispersa*, *B. tesserata*, and *Lichinella stipatula* are also present in southwest North America (Calatayud, 1998), while *Glyphopeltis ligustica* and *Opegrapha lutulenta* have been found in South Africa (Egea & Alonso, 1996). The final type of distribution comprises species with a Mediterranean-Macaronesian range, which in our study area are very well represented: *Aspicilia intermutans*, *Caloplaca aetnensis*, *C. carphinea*, *C. ligustica*, *Lecanora praepostera*, *Protoparmelia montagnei*, *Ramalina requienii*, or *Rinodina alba*. Nimis (1993) categorized species as 'Submediterranean' when the centre of their distribution was in the Mediterranean region, but extended to other areas with special microclimatic conditions (such as the dry valleys of the Alps and isolated areas of south Scandinavia and the Eurosiberian region). However, following Calatayud (1998), we used a less restrictive concept of Mediterranean, which includes also Submediterranean taxa, such as *Acarospora sulphurata*, *Buellia tirolensis*, *Caloplaca aractina*, *C. irrubescens*, *C.*

rubelliana, *Diploschistes euganeus*, *Ingvariella bispora*, and *Peltula euploca*. Finally, it should be remarked that in the driest and warmer enclaves of the Mediterranean Region, live species that are also present in the arid and sub-arid areas of both hemispheres. These species belong to the xerothermic Pangaean element sensu Frey & Kürschner (1988), and include *Diploschistes ocellatus*, *Peltula obscurans*, *P. omphaliza*, and *P. placodizans*.

13.5% of the recorded species (35 spp.) in the catalog are distributed throughout both Mediterranean and Atlantic Europe areas. Among these species are rather hygrophytic taxa, such as *Anaptychia runcinata*, *Lecanora gangaleoides*, and *Ramalina subfarinacea*, which grow mainly along the coast in the Atlantic region. However, in our study area we usually found these three species growing inland, in localities with high levels of air humidity (mainly due to the frequent presence of fog banks). Within the Mediterranean-Atlantic species, some taxa are restricted to coastal areas that are exposed to humid sea-winds. This includes *Caloplaca marina*, *Coscinocladium gaditanum*, *Diploicia canescens*, *Dirina massiliensis*, *Lecania atrynoides*, *Lecanographa grumulosa*, *Roccella phycopsis*, and *Thelopsis isiaca*.

Only 2% (5 spp.) of the species in the catalog have a principally Atlantic distribution, while being rarely present in the most humid parts of the Mediterranean area. These are *Cladonia subcervicornis*, *Collema subflaccidum*, *Lecidella scabra*, and *Verrucaria praetermissa*.

29.5% (77 spp.) correspond to Mediterranean temperate species, taxa that mainly grow in Central Europe, while penetrating into the Mediterranean mountains. In our study area, some of the species with this distribution include *Caloplaca aurantia*, *Diplotomma alboatrum*, *Lecania inundata*, *L. turicensis*, *Psora vallesiaca*, *Squamarina lentigera*, *Toninia physaroides*, *Verrucaria dolosa*, and *V. lecideoides*. Within this group of Mediterranean temperate species is a contingent of species with a notable presence along the Atlantic coast from Norway to Portugal, such as *Parmotrema reticulatum*, *Peltigera collina*, and *Pertusaria pseudocorallina*.

The temperate element represents 4.5% (12 spp.) and comprises species that are widely distributed in Central Europe, extending to the Eurosiberian and the south of

Scandinavia (Calatayud, 1998). This is the case for species like *Nephroma parile*, *Ramalina polymorpha*, or *Thelenella muscorum* var. *octospora*.

Finally, three species (representing a 1% of the total) have an Arctic-alpine to boreal-montane distribution: *Acarospora sinopica*, *Dermatocarpon luridum*, and *Tremolecia atrata*. All of them have been found in localities with the highest altitudes (400-670 m), where they occur uncommonly while forming small, disperse thalli.

ACKNOWLEDGMENTS

The authors thank Mireia Giralt for the revision of the specimens of *Amandinea*, *Buellia* and *Rinodina*; Robert Lachlan for the English revision and proofreading of the manuscript; Albert Ferré for help editing Figure 1; Néstor Hladun for help with image editing. This work was carried out within the projects: CGL2007-66734-C03-02 (Ministerio de Educación y Ciencia, Spain), 2005SGR01047 (Departament d'Universitats i Recerca i Societat de la Informació, Spain), and 'Líquens del Mar d'Avall' (Institut d'Estudis Catalans, Secció de Ciències Biològiques).

6. REFERENCES

ARAGÓN, G., GARCÍA, A. & R. LÓPEZ (2006): Aportación al conocimiento de los líquenes rupícolas que colonizan las pedrizas del Parque Nacional de Cabañeros. – Bot. Complutensis **30**: 53–59.

ARROYO, R., SERIÑÁ, E & E. MANRIQUE (1991): Estudio químico y morfológico de *Ramalina polymorpha* Grex en España. – Acta Bot. Malacit. **16**: 165–174.

ARUP, U. (1997): *Caloplaca maritima*, a misunderstood species in Western Europe. – Lichenologist **29**: 503–512.

ARUP, U. (2006): A new taxonomy of the *Caloplaca citrina* group in the Nordic countries, except Iceland. – Lichenologist **38**: 1–20.

ATIENZA, V., CALATAYUD, V. & D.L. HAWKSWORTH (2003): Notes on the genus *Polycoccum* (Ascomycota, Dacampiaceae) in Spain, with a key to the species. – Lichenologist **35**: 125–135.

BARBERO, M. (1998): Estudio florístico y quimiotaxonómico de los líquenes silicícolas del Maresme. PhD Thesis, Universitat de Barcelona.

BARBERO, M., GIRALT, M., ELIX, J.A., GÓMEZ-BOLEA, A. & X. LLIMONA (2006): A taxonomic study of *Protoparmelia montagnei* (syn. *P. psarophana*) centered in the Eastern Iberian Peninsula. – Mycotaxon **97**: 299–320.

BARRENO, E. (1991): Phytogeography of terricolous lichens in the Iberian Peninsula and the Canary Islands. – Bot. Chron. (Patras) **10**: 199–210.

BARRENO, E. (1994): Análisis fitogeográfico del elemento Mediterráneo en líquenes. – Stud. Bot. **13**: 129–137.

BARRENO E. & S. PÉREZ-ORTEGA (2003): Líquenes de la Reserva Natural Integral de Muniellos, Asturias. Cuadernos de Medio Ambiente. Serie Naturaleza 5. – Consejería de Medio Ambiente y Ordenación del Territorio & KRK Ediciones, Oviedo.

BARRENO, E. & V.J. RICO (1982): Líquenes interesantes de los pisos oro- y crioromediterráneos del Pico del Lobo (Ayllon, Segovia, España). – Collect. Bot. **13**: 265–277.

BENFIELD, B. & O.W. PURVIS (2009): *Roccella*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 825–826. The British Lichen Society, London.

BOOM, VAN DEN P.P.G. (2010): New or interesting lichens and lichenicolous fungi of Gran Canaria (Canary Islands, Spain). – Willdenowia **40**: 359–367.

BOOM, VAN DEN P.P.G. & J. ETAYO (2000): Contribution to the knowledge of lichenicolous fungi and lichens from Portugal and Spain. – Österreichische Zeitschrift für Pilzkunde **9**: 151–162

BOOM, VAN DEN P.P.G. & M. GIRALT (1996): Contribution to the flora of Portugal, lichens and lichenicolous fungi I. – Nova Hedwigia **63**: 145–172.

BOOM, VAN DEN P.P.G. & M. GIRALT (1999): Contribution to the flora of Portugal, lichens and lichenicolous fungi II. – Nova Hedwigia **68**: 183–195.

BOOM, VAN DEN P.P.G. & J. JANSEN (2002): Lichens in the upper belt of the Serra da Estrela. – Österreichische Zeitschrift für Pilzkunde **11**: 1–28.

BRODO, I.M., DURAN SHARNOFF, S. & S. SHARNOFF (2001): Lichens of North America. – Yale University Press, New Haven & London.

BUNGARTZ, F., GRUBE, U., ELIX, J.A., HEININGER, C. & H. MAYRHOFER (2011): A taxonomic revision of the *Buellia subalbula*-group in the Southern Hemisphere using fluorescence microscopy. – Biblioth. Lichenol. **106**: 21–39.

BUNGARTZ, F. & T.H. NASH III (2004): The *Buellia aethalea*-group in the Greater Sonoran Desert Region with reference to similar species in North America. – The Bryologist **107**: 441–458.

BUNGARTZ, F., NORDIN, A. & M. GRUBE (2007): *Buellia.* - In: NASH III, T.H., GRIES, C. & F. BUNGARTZ (eds.): Lichen Flora of the Greater Sonoran Desert Region. Volume 3: 113–179. Lichens Unlimited, Arizona State University, Tempe.

BUNGARTZ, F., SCHEIDEGGER, C. & T.H. NASH III (2002): *Buellia dispersa* A. Massal., a variable lichen species from semi-arid to arid environments of North America and Europe. – Biblioth. Lichenol. **82**: 19–35.

BURGAZ, A.R. (2010): Nuevos datos sobre el género *Placynthium* en la Península Ibérica. – Bot. Complutensis **34**: 5–19.

BURGAZ, A.R. & T. AHTI (2009): Flora Liquenológica Ibérica. Volumen 4. Cladoniaceae. – Sociedad Española de Liquenología, Madrid.

BURGAZ A.R., ARGÜELLO, A., ATIENZA, V., FERNÁNDEZ-BRIME, S., FERNÁNDEZ-SALEGUI, A.B., FIGUERAS, G., GARCÍA OTÁLORA, M., GÓMEZ-BOLEA, A., HAWKSWORTH, D.L., HLADUN, N.L., LLIMONA, X., LLOP, E., MARCOS-LASO, B., MUÑIZ, D., PÉREZ-ORTEGA, S., DEL PRADO, R., RODRIGUES, S.A. & A. TERRÓN 2007: Lichens and lichenicolous fungi of Sierra de San Lorenzo (La Rioja Community, Spain). – Cryptog. Mycol. **28**: 133–153.

BURGAZ A.R. & I. MARTÍNEZ (2010): Flora Liquenológica Ibérica. Peltigerales: Lobariaceae, Nephromataceae, Peltigeraceae. – Sociedad Española de Liquenología, Murcia.

CALATAYUD, V. (1998): Líquenes y hongos liquenícolas de rocas no carbonatadas en el Sistema Ibérico Oriental e Islas Columbretes. PhD Thesis, Universitat de València.

CALATAYUD, V., ATIENZA, V. & E. BARRENO (1995): Lichenicolous fungi from the Iberian Peninsula and the Canary Islands. – Mycotaxon **55**: 363–382.

CALATAYUD, V. & E. BARRENO (1994): Contribution to the lichen floristics of eastern Spain - I. Silicicolous lichens and their lichenicolous fungi of Serra d'Espadà (Castelló). – Cryptog. Bryol. Lichenol. **15**: 23–41.

CARRERAS, J., CARRILLO, E., FERRÉ, A., FONT, J., GESTI, J., QUADRADA, R.V., VIGO, J. & L. VILAR (2004): Mapa de vegetació de Catalunya 1:50.000, Figueres (258, 39-11) i Roses (259, 40-11). – Institut d'Estudis Catalans, Barcelona.

CARRERAS J. & E. DRUGUET (1995): El Cap de Creus: aspectes geològics. - In: MASDEVALL, J.M., MIQUEL, A. & S. MUSQUERA (eds.): La Península del Cap de Creus i la Serra de Verdera. Actes de les IV Jornades de la Institució Catalana d'Història Natural: 17–25. Institut d'Estudis Empordanesos, Figueres.

CHAMBERS, S.P., GILBERT, O.L., JAMES, P.W., APTROOT, A. & O.W. PURVIS (2009): *Pertusaria*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 673–687. The British Lichen Society, London.

CLAUZADE, G. & C. ROUX (1985): Likenoj de Okcidenta Europo. Ilustrita determinlibro. – Bull. Soc. Bot. Centre-Ouest, Nouv. Sér. **7**: 1–893.

CLAUZADE, G. & C. ROUX (1989): Likenoj de okcidenta Europo. Suplemento 3a. – Bull. Soc. Linn. Provence **40**: 73–110.

CLERC, P. (2004): Les champignons lichénisés de Suisse. Catalogue bibliographique complété par des données sur la distribution et l'écologie des espèces. – Cryptog. Helv. **19**: 1–320.

CRESPO, A., BARRENO, E. & G. FOLLMANN (1976): Sobre las comunidades liquénicas rupícolas de *Acarospora hilaris* (Duf.) Hue en la Península Ibérica. – Anales Inst. Bot. Cavanilles **33**: 189–205.

CRESPO, A., DIVAKAR, P.K., ARGÜELLO, A., GASCA, C. & D.L. HAWKSWORTH (2004): Molecular studies on *Punctelia* species in the Iberian Peninsula, with an emphasis on specimens newly colonizing Madrid. – Lichenologist **36**: 299–308.

COPPINS, B.J. (1983): A taxonomic study of the lichen genus *Micarea* in Europe. – Bull. Brit. Mus. (Nat. Hist.), Bot. **11**: 17–214.

COPPINS, B.J., SCHEIDEGGER, C. & A. APTROOT (2009): *Buellia*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 228–238. The British Lichen Society, London.

DRUGUET, E. (1997): The structure of the NE Cap de Creus peninsula relationships with metamorphism and magmatism. PhD Thesis, Universitat de Barcelona.

EDWARDS, B., APTROOT, A., HAWKSWORTH, D.L. & P.W. JAMES (2009): *Lecanora*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 465–502. The British Lichen Society, London.

EDWARDS, B.W. & B.J. COPPINS: (2009): *Physcia*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 698–703. The British Lichen Society, London.

EGEA, J.M. (1980): Flora y vegetación de los líquenes de rocas silíceas no volcánicas de SE de España. PhD Thesis, Universidad de Murcia.

EGEA, J.M. (1989): Los géneros *Heppia* y *Peltula* (Líquenes) en Europa Occidental y Norte de África. – Biblioth. Lichenol. **31**: 1–122.

EGEA, J.M. & F.L. ALONSO (1996): Patrones de distribución en la flora liquénica xerófila del sureste de España. – Acta Bot. Malacit. **21**: 35–47.

EGEA, J.M & X. LLIMONA (1987): Las comunidades de líquenes de las rocas silíceas no volcánicas del SE de España. – Acta Bot. Barcinon. **36**: 1–123.

EGEA, J.M & X. LLIMONA (1991): Phytogeography of silicicolous lichens in Mediterranean Europe and NW Africa. – Bot. Chron. (Patras) **10**: 179–198.

EGEA, J.M., LLIMONA, X. & E. MANRIQUE (1995): Nuevos datos sobre *Glyphopeltis ligustica* (Psoraceae, Lecanorales) y su área de distribución. - In: DANIËLS, F.J.A., SCHULZ, M. & J. PEINE (eds.): Flechten Follmann. Contributions to lichenology in Honour of Gerhard Follmann: 183–192. Botanical Institute, University of Cologne, Cologne.

ELIX, J.A. & K.D. ERNT-RUSSEL (1993): A catalogue of standarized thin layer chromatographic data and biosynthetic relationships for lichen substances. 2nd edn. – Australian National University, Canberra.

ESSLINGER, T.L. (1977): A chemosystematic revision of the brown Parmeliae. – J. Hattori Bot. Lab. **42**: 1–211.

ESSLINGER, T.L. (1978): Studies in the lichen family Physciaceae. II. The genus *Phaeophyscia* in North America. – Mycotaxon **7**: 283–320.

ESSLINGER, T.L. (2004): *Phaeophyscia*. - In: NASH III, T.H., RYAN, B.D. DIEDERICH, P., GRIES, C. & F. BUNGARTZ (eds.): Lichen Flora of the Greater Sonoran Desert Region, Volume 2: 403–414. Lichens Unlimited, Arizona State University, Tempe.

ETAYO, J. (1990): Ensayo de la vegetación liquénica epifítica del Norte de Navarra. – Principe de Viana (Suplemento de Ciencias) **10**: 39–72.

ETAYO, J. (2002): Catálogo de líquenes y hongos liquenícolas del Parque Natural de Bértiz (Navarra, España). – Bull. Soc. Linn. Provence **53**: 155–170.

ETAYO, J. (2010): Líquenes y hongos liquenícolas de Aragón. – Guineana **16**: 1–501.

FIGUERAS, G. (2011): Taxonomical studies of the non-crustose genera of the Physciaceae family in the Iberian Peninsula. PhD Thesis, Universitat de Barcelona.

FLETCHER, A., GILBERT, O.L., CLAYDEN, S. & A.M. FRIDAY (2009b): *Rhizocarpon*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 792–808. The British Lichen Society, London.

FLETCHER, A. & D.L. HAWKSWORTH (2009): *Diploschistes*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 378–380. The British Lichen Society, London.

FLETCHER, A., PURVIS, O.W. & P.W. JAMES (2009a): *Lecidella*.- In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 519–525. The British Lichen Society, London.

FRANQUESA, T. (1995): El paisatge vegetal de la península del cap de Creus. – Institut d'Estudis Catalans, Barcelona.

FREIRE DOPAZO, M., MARTÍNEZ PIÑEIRO, J. & A. GARCÍA MOLARES (2000): Fragmenta chorologica occidentalia (Lichenes), 7306-7331. – Anales Jard. Bot. Madrid **57**: 386–387.

FREY, W. & H. KURSCHNER (1988): Bryophytes of the Arabian Peninsula and Socotra. Floristics, phytogeography and definition of the xerothermic Pangaean element. Studies in Arabian Bryophytes 12. – Nova Hedwigia **46**: 37–120.

GAYA, E. (2009): Taxonomical revision of the *Caloplaca saxicola* group (Teloschistaceae, Lichen-forming Ascomycota). – Biblioth. Lichenol. **101**: 1–191.

GILBERT, O.L., JAMES, P.W. & O.W. PURVIS (2009a): *Collema*. – In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 345–357. The British Lichen Society, London.

GILBERT, O.L., PURVIS, O.W. & P.W. JAMES (2009b): *Solenopsora*. – In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 842–844. The British Lichen Society, London.

GIORDANI, P., BENESPERI, R., RELLINI, I., FRATI, L., BRUNIALTI, G., PAOLI, L., ISOCRONO, D. & J.A. ELIX (2003): The lichen genus *Neofuscelia* (Ascomycota, Parmeliaceae) in Italy. – Lichenologist **35**: 377–385.

GIRALT, M. (2001): The Lichen genera *Rinodina* and *Rinodinella* (lichenized Ascomycetes, Physciaceae) in the Iberian Peninsula. – Biblioth. Lichenol. **79**: 1–160.

GIRALT, M. (2010): Flora Liquenológica Ibérica. Volumen 5. Physciaceae I: *Endohyalina*, *Rinodina* y *Rinodinella*. – Sociedad Española de Liquenología, Barcelona.

GIRALT, M. & M. BARBERO (1995): The saxicolous species of the genus *Rinodina* in the Iberian Peninsula containing atranorin, pannarin or gyrophoric acid. – Mycotaxon **56**: 45–80.

GIRALT, M. & P.P.G. VAN DEN BOOM (2011): The genus *Buellia* s. l. and some additional crustose genera of Physciaceae in the Canary Islands. – Nova Hedwigia **92**: 29–55.

GIRALT, M., BUNGARTZ, F. & J.A. ELIX (2011): The identity of *Buellia sequax*. – Mycol. Progress **10**: 115–119.

GIRALT, M. & X. LLIMONA (1997): The saxicolous species of the genera *Rinodina* and *Rinodinella* lacking spot test reactions in the Iberian Peninsula. – Mycotaxon **62**: 175–224.

GRUBE, M. (2007): *Arthonia*. – In: NASH III, T.H., GRIES, C. & F. BUNGARTZ (eds.): Lichen Flora of the Greater Sonoran Desert Region. Volume 3: 39–61. Lichens Unlimited, Arizona State University, Tempe.

GUEIDAN, C. & C. ROUX (2007). Néotypification et description de *Verrucaria calciseda* DC. – Bull. Soc. Linn. Provence **58**: 181–194.

HAFELLNER, J. (1994): Beiträge zu einem Prodromus der lichenicolen Pilze Österreichs und angrenzender Gebiete. I. Einige neue oder seltene. – Herzogia **10**: 1–28.

HAFELLNER, J., TRIEBEL, D., RYAN, B.D. & T.H. NASH III (2002): On lichenicolous fungi from North America II. – Mycotaxon **84**: 293–329.

HALICI, M.G., KNUDSEN, K., CANDAN, M. & A. TÜRK (2009): A new species of *Polycoccum* (Dothideales, Dacampiaceae) from Turkey. – Nova Hedwigia **89**: 431–436.

HAWKSWORTH, D.L., MILLANES, A.M. & M. WEDIN (2010): *Roselliniella* revealed as an overlooked genus of Hypocreales, with the description of a second species on parmelioid lichens. – Persoonia **24**: 12–17.

HITCH, C.J.B, GALLOWAY, D.J. & B.J. COPPINS (2009): *Polysporina*. – In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 728–729. The British Lichen Society, London.

HLADUN, N. (1981): Aportación a la flora, morfología y vegetación de los líquenes silicícolas de la parte alta del Montseny (Catalunya). PhD Thesis, Universitat de Barcelona.

HLADUN, N. & X. LLIMONA (2002-2007): Checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands. http://botanica.bio.ub.es/checklist/checklist.htm.

KNUDSEN, K. (2007): *Acarospora*. – In: NASH III, T.H., GRIES, C. & F. BUNGARTZ (eds.): Lichen Flora of the Greater Sonoran Desert Region. Volume 3: 1–38. Lichens Unlimited, Arizona State University, Tempe.

LAWREY, J.D. & P. DIEDERICH (2003): Lichenicolous fungi: interactions, evolution, and biodiversity. – Bryologist **106**: 81–120.

LEUCKERT, C. & J. POELT (1989): Studien uber die *Lecanora rupicola*-Gruppe in Europa (Lecanoraceae). – Nova Hedwigia **49**: 121–167.

LEUCKERT, C., WIRTH, V., KÜMMERLING, H. & M. HEKLAU (2004): Chemical lichen analyses XIV. *Lepraria nivalis* J. R. Laundon and *Lepraria flavescens* Cl. Roux & Tonsberg. – Biblioth. Lichenol. **88**: 393–407.

LINDBLOM, L & S. EKMAN (2005): Molecular evidence supports the distinction between *Xanthoria parietina* and *X. aureola* (Teloschistaceae, lichenized Ascomycota). – Mycol. Res. **109**: 187–199.

LLIMONA, X. (1995): Contribució a l'estudi de la biodiversitat de la península del Cap de Creus i serra de Verdera. I. Els fongs. II. Els líquens. - In: MASDEVALL, J.M., MIQUEL, A. & S. MUSQUERA (eds.): La Península del Cap de Creus i la Serra de Verdera. Actes de les IV Jornades de la Institució Catalana d'Història Natural: 73–86. Institut d'Estudis Empordanesos, Figueres.

LLIMONA, X. & J.M. EGEA (1984): La vegetación liquénica saxícola de los volcanes del Mar Menor (Murcia, SE de España). – Butl. Soc. Cat. Hist. Nat. **51**: 77–99.

LLIMONA, X. & J.M. EGEA (1985): Las comunidades liquénicas de las superficies de escorrentía de las rocas silíceas mediterráneas. – Anales Jard. Bot. Madrid **41**: 429–444.

LLOP, E., BARBERO, M., CHESA, M.J., FERNÁNDEZ-BRIME, S., FIGUERAS, G., GÓMEZ-BOLEA, A., HLADUN, N.L., MUÑIZ, D. & P. NAVARRO-ROSINÉS (2010): Els líquens i els fongs liquenícoles de les Planes de Son i la mata de València. - In: GERMAIN I OTZET, J. (ed.): Treballs de la Institució Catalana d'Història Natural 16: 189–227. Limpergraf, Barcelona.

LLOP, E., FERNÁNDEZ-BRIME, S., FIGUERAS, G., MUÑIZ, D. & X. LLIMONA: Aproximació al coneixement de la flora liquènica i dels fongs liquenícoles dels altiplans i conques centrals de Catalunya: el sector Segàrric. – Butll. Inst. Catalana Hist. Nat. (In review).

LUMBSCH, H.T. (1989): Die holarktischen Vertreter der Flechtengattung *Diploschistes* (Thelotremataceae). – J. Hattori Bot. Lab. **66**: 133–196.

MARTÍNEZ, I., ARAGÓN, G. & A.R. BURGAZ (2001): Propuesta de áreas de conservación en el Sistema Ibérico Central (España) utilizando la diversidad liquénica. – Bot. Complutensis **25**: 129–140.

MATZER, M. (1993): Beitrag zur Kenntnis der Ascomycetengattungen *Globosphaeria*, *Roselliniopsis* und *Synaptospora*. – Cryptog. Mycol. **14**: 11–19.

MATZER, M. & J. HAFELLNER (1990): Eine Revision der lichenicolen Arten der Sammelgattung *Rosellinia* (Ascomycetes). – Biblioth. Lichenol. **37**:1–138.

MATZER, M., MAYRHOFER, H., WIPPEL, A. & J.A. ELIX (1996): *Dimelaena radiata* (Physciaceae, Lecanorales) and its lichenicolous fungus *Endococcus buelliae* (Verrucariales). – Bryologist **99**: 450–456.

MAYRHOFER, H. (1987): Monographie der Flechtengattung *Thelenella*. – Biblioth. Lichenol. **26**: 1–106.

MAYRHOFER, H. & J. POELT (1985): Die Flechtengattung *Microglaena* sensu Zahlbruckner in Europa. – Herzogia **7**: 13–79.

MORENO, P.P. (1988): Estudio de la familia Lichinaceae en el sureste de la Península Ibérica y norte de África. PhD Thesis, Universidad de Murcia.

MUGGIA, L., GRUBE, M. & M. TRETIACH (2008): A combined molecular and morphological approach to species delimitation in black-fruited, endolithic *Caloplaca*: high genetic and low morphological diversity. – Mycol. Res. **112**: 36–49.

MUÑIZ, D. & N. HLADUN (2011): Flora Liquenológica Ibérica. Volumen 7. Calicioides. – Sociedad Española de Liquenología, Barcelona.

NASH III, T.H., GRIES, C. & F. BUNGARTZ (eds.) (2007): Lichen Flora of the Greater Sonoran Desert Region. Volume 3. – Lichens Unlimited, Arizona State University, Tempe.

NASH III, T.H., RYAN, B.D., GRIES, C. & F. BUNGARTZ (eds.) (2002): Lichen Flora of the Greater Sonoran Desert Region. Volume. 1. – Lichens Unlimited, Arizona State University, Tempe.

NASH III, T.H., RYAN, B.D., DIEDERICH, P., GRIES, C. & F. BUNGARTZ (eds.) (2004): Lichen Flora of the Greater Sonoran Desert Region. Volume 2. – Lichens Unlimited, Arizona State University, Tempe.

NAVARRO-ROSINÉS, P., BOQUERAS, M. & X. LLIMONA (1994): Primer catàleg dels fongs liquenícoles de Catalunya i zones pròximes (NE de la Península Ibèrica). – Butlletí Soc. Catalana Micol. **16-17**: 165–204.

NAVARRO-ROSINÉS, P., CALATAYUD, V. & J. HAFELLNER. (2009a): Contributions to a revision of the genus *Cercidospora* (Dothideales), 1: Introduction and species on Megasporaceae. – Mycotaxon **110**: 5–25.

NAVARRO-ROSINÉS, P., GUEIDAN, C., HLADUN, N.L. & C. ROUX (2009b): Sinopsi del género *Sarcopyrenia* (Ascomycota, hongos liquenícolas), con la aportación de tres especies nuevas. – Rev. Cat. Micol. **31**: 49–69.

NAVARRO-ROSINÉS, P., ROUX C. & C. GUEIDAN (2007): La generoj *Verrucula* kaj *Verruculopsis* (Verrucariaceae, Verrucariales). – Bull. Soc. Linn. Provence **58**: 133–180.

NIMIS, P.L. (1993): The Lichens of Italy. – Museo Regionale di Scienze Naturali, Torino.

NIMIS, P.L. & S. MARTELLOS (2004): Keys to the Lichens of Italy. I. Terricolous species. Le Guide di Dryades 1 - Serie Licheni I (L-I). – Edizioni Goliardiche, Trieste.

NIMIS, P.L. & S. MARTELLOS (2008): P.L. Nimis - Checklist of the Italian Lichens 4.0 –The Information System on Italian Lichens. http://dbiodbs.univ.trieste.it.

NIMIS, P.L. & J. POELT (1987): The lichens and lichenicolous fungi of Sardinia (Italy): an annotated list. – Stud. Geobot. **7 (Supplement 1)**: 1–269.

NORDIN, A. (2000): Taxonomy and phylogeny of *Buellia* species with pluriseptate spores (Lecanorales, Ascomycotina). – Symb. Bot. Upsal. **33**: 1–117.

NORDIN, A. & L. TIBELL (2005): Additional species in *Tetramelas*. – Lichenologist **37**: 491–498.

ORANGE, A., HAWKSWORTH, D.L., MCCARTHY, P.M. & A. FLETCHER (2009): *Verrucaria*. - In: SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.): The lichens of Great Britain and Ireland: 931–957. The British Lichen Society, London.

OTT, S. & C. SCHEIDEGGER (1992): The role of parasitism in the co-development and colonization of *Peltula euploca* and *Glyphopeltis ligustica*. – Symbiosis **12**: 159–172.

OZENDA, P. & G. CLAUZADE (1970): Les Lichens. Etude Biologique et Flore Illustree. – Masson & Cie, Editeurs, Paris.

PANT, G. & D.K. UPRETI (1993): The lichen genus *Diploschistes* in India and Nepal. – Lichenologist **25**: 33–50.

PAZ-BERMÚDEZ. G. (1998): Liques saxícolas e fungos liquenícolas da costa de Galicia. PhD Thesis, Universidad de Santiago de Compostela.

PAZ-BERMÚDEZ, G. & R. CARBALLAL (1999): Fragmenta chorologica occidentalia (Lichenes), 7083-7129. – Anales Jard. Bot. Madrid **57**:151–154.

PAZ-BERMÚDEZ G., CARBALLAL R. & M.E. LÓPEZ DE SILANES (2003): Líquenes saxícolas y arenícolas del Parque Nacional de las Islas Atlánticas (Galicia, NW España). – Cryptog. Mycol. **24**: 385–397.

PAZ-BERMÚDEZ, G., LÓPEZ DE SILANES, M.E., TERRÓN, A., ARROYO, R., ATIENZA, V., FERNÁNDEZ-BRIME, S., BURGAZ A.R., CARVALHO, P., FIGUERAS, G., LLOP, E., MARCOS, B., PINO-BODAS, R., PRIETO, M., RICO. V.J., FERNÁNDEZ-SALEGUI, A.B. & E. SERIÑÁ (2009): Lichens and lichenicolous fungi in the Montesinho Natural Park, the Serra da Nogueira and the Río Sabor Valley (Portugal). – Cryptog. Mycol. **30**: 279–303.

PEREIRA, I. (1992): Flora, vegetación y ecología de los líquenes acuáticos de España. PhD Thesis, Universitat de Barcelona.

POELT, J. & G. FOLLMANN (1968): *Lecanactis stenhammari* ein mitteleuropäischer Vertreter der Roccellaceen. – Herzogia **1**: 61-65.

PRIETO, M., ARAGÓN, G. & I. MARTÍNEZ (2010a): The genus *Catapyrenium* s. lat. (Verrucariaceae) in the Iberian Peninsula and the Balearic Islands. – Lichenologist **42**: 637–684.

PRIETO, M., MARTÍNEZ, I. & G. ARAGÓN (2010b): The genus *Placidiopsis* in the Iberian Peninsula and the Balearic Islands. – Mycotaxon **114**: 463–472.

PURVIS, O.W., COPPINS, B.J., HAWKSWORTH, D.L., JAMES, P.W. & D.M. MOORE (eds.) (1992): The Lichen Flora of Great Britain and Ireland. – Natural History Museum Publications & British Lichen Society, London.

RICO, V.J., CALATAYUD, V. & M. GIRALT (2003): *Buellia tesserata* and *Dimelaena radiata*, two closely related species. – Lichenologist **35**: 117–124.

ROUX, C. (2011): Liste des lichens et champignons lichénicoles non lichénisés de France. http://lichenologue.org/fr/

ROUX, C., NORDIN, A., TIBELL, L. & M. SOHRABI (2011): Quelques espèces d'*Aspicilia* peu connues ou nouvelles des Pyrénées-Orientales (France). – Bull. Soc. Linn. Provence n. spéc. **14**: 177–227.

ROWE, J. (1985): Flora y vegetación de los líquenes silicícolas del SW de España. PhD Thesis, Universidad de Murcia.

SAMPAIO, G. (1970b): Contribuições para o estudio dos líquenes portugueses. – Publ. Inst. Bot. "Dr. Goncalo Sampaio" **3ª série 20**: 89–107.

SAMPAIO, G. (1970a): Líquenes novos para a flora portuguesa (3ª série) – Publ. Inst. Bot. "Dr. Goncalo Sampaio" **3ª série 20**: 47–65.

SÁNCHEZ-BIEZMA, M.J., PAZ-BERMÚDEZ, G. & R. CARBALLAL (1999): Líquenes saxícolas sobre sustratos básicos de la Sierra de A Capelada (A Coruña). – Nova Acta Científica Compostelana **9**: 47–63.

SANCHO, L.G. (1986): Flora y vegetación liquénica saxícola de los pisos oro- y crioromediterráneo del Sistema Central español. PhD Thesis, Universidad Complutense de Madrid.

SCHEIDEGGER, C. (1993): A revision of European saxicolous species of the genus *Buellia* de Not. and formerly included genera. – Lichenologist **25**: 315–364.

SÉRUSIAUX, E., DIEDERICH, P., ERTZ, D. & P.P.G. VAN DEN BOOM (2003): New or interesting lichens and lichenicolous fungi from Belgium and Luxembourg. IX. – Lejeunia **173**: 1–48.

SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.L., JAMES, P.W. & P.A. WOLSELEY (eds.) (2009): The lichens of Great Britain and Ireland. – The British Lichen Society, London.

SOUZA-EGIPSY, V., ASCASO, C. & J. WIERZCHOS (2002): Ultrastructural and Biogeochemical Features of Microbiotic Soil Crusts and their Implications in a Semi-Arid Habitat. – Geomicrobiology Journal **19**: 567–580.

SPARRIUS, L.B. (2004): A monograph of *Enterographa* and *Sclerophyton*. – Biblioth. Lichenol. **89**: 1–141.

TAVARES, C.N. (1965): *Lichenes Lusitaniae Selecti Exsiccati*. – Inst. Bot. Univ. Olisiponensis **9**: 1–4.

TEHLER, A. (1983): The genera *Dirina* and *Roccellina*. – Opera Bot. **70**: 1–86.

TERRÓN, A. (1991): Flora liquénica saxícola acidófila del Macizo de el Teleno (León; NW de España). PhD Thesis, Universidad de León.

TERRÓN, A., ALVAREZ-ANDRÉS, J & J. MARTÍNEZ PIÑEIRO (2000a): Líquenes saxícolas, terrícolas y muscícolas de la Sierra de Ancares (León-Lugo, NW España). – Cryptog. Mycol. **21**: 119–129.

TERRÓN, A., BURGAZ, A.R. & J. ALVAREZ-ANDRÉS (2000b): Líquenes de la provincia de Zamora (España). – Bot. Complutensis **24**: 9–43.

TIMDAL, E. (1991): A monograph of the genus *Toninia* (Lecideaceae, Ascomycetes). – Opera Bot. **110**: 1–137.

TIMDAL, E. (2002): *Toninia*. - In: NASH III, T.H., RYAN, GRIES, B.D. & F. BUNGARTZ (eds.) Lichen Flora of the Greater Sonoran Desert Region. Volume 1: 488–501. Lichens Unlimited, Arizona State University, Tempe.

TORRENTE, P. & J.M. EGEA (1989): La Familia Opegraphaceae en el área Mediterránea de la Península Ibérica y Norte de África. – Biblioth. Lichenol. **32**: 1–282.

VONDRÁK, J., ŘÍHA, P., ARUP, U. & U. SØCHTING (2009): The taxonomy of the *Caloplaca citrina* group (Teloschistaceae) in the Black Sea region; with contributions to the cryptic species concept in lichenology. – Lichenologist **41**: 571–604.

VONDRÁK, J., ŘÍHA, P., REDCHENKO, O., VONDRÁKOVÁ, O., HROUZEK P. & A. KHODOSOVTSEV (2011): The *Caloplaca crenulatella* species complex; its intricate taxonomy and description of a new species. – Lichenologist **43**: 467–481.

WIRTH, V. (1980): Flechtenflora. Ökologische Kennzeichnung und Bestimmung der Flechten Südwestdeutschlands und angrenzender. – Verlag Eugen Ulmer, Stuttgart.

WIRTH, V. (1987): Die Flechten Baden-Wurttembergs. – Eugen Ulmer, GmbH & Co., Stuttgart.

WIRTH, V. & X. LLIMONA (1975): Das *Pertusarietum rupicolae* un. nova, eine Silikatflechten-Gesellschaft im Mittelmeerraum, mit Bemerkungen zur Taxonomie des *Pertusaria pseudocorallina*-Formenkreises. – Herzogia **3**: 335–345.

FIGURE LEGENDS

Fig. 1. Climate diagram based on data from the weather station located near the Park (Roses, 42°16' N-3°10' E), for a 16-year-period (from 1996-2011). Solid line indicates mean precipitations and dotted line indicates mean temperatures.

Fig. 2. Map of the studied area showing the locations of the 34 collection sites.

Fig. 3. Thallus of A) *Acarospora epithallina* growing on *A. hilaris*; B) *A. modenensis*; C) *Aspicilia caesiocinerea*; D) *A. inornata*; E) *Buellia tesserata*; F) *B. tirolensis* [scale bars = 1 mm].

Fig. 4. Thallus of A) *Caloplaca furax*; B) *C. inconnexa* var. *nesodes* growing on *Aspicilia caesiocinerea*; C) *Caloplaca rubelliana*; D) *Coscinocladium gaditanum*; E) *Dirina massiliensis*; F) *Enterographa pitardii* [scale bars = 1 mm].

Fig. 5. Thallus of A) *Epiphloea terrena*; B) *Pertusaria pseudocorallina*; C) *Psora gresinonis*; D) *P. vallesiaca*; E) *Rhizocarpon epispilum*; F) *R. viridiatrum* [scale bars = 1 mm].

Fig. 6. Thallus of A) *Rinodina aspersa*; B) *R. teichophila*; C) *Solenopsora holophaea*; D) *Trapelia coarctata* (left) and *T. involuta* (right); E) *Trapeliopsis wallrothii*; F) *Xanthoparmelia mougeotii* [scale bars = 1 mm].

Table 1. List of species with the following distributions: widespread, Mediterranean, Mediterranean-Atlantic, Atlantic, Mediterranean temperate, temperate, and Artic-alpine to boreal-montane.

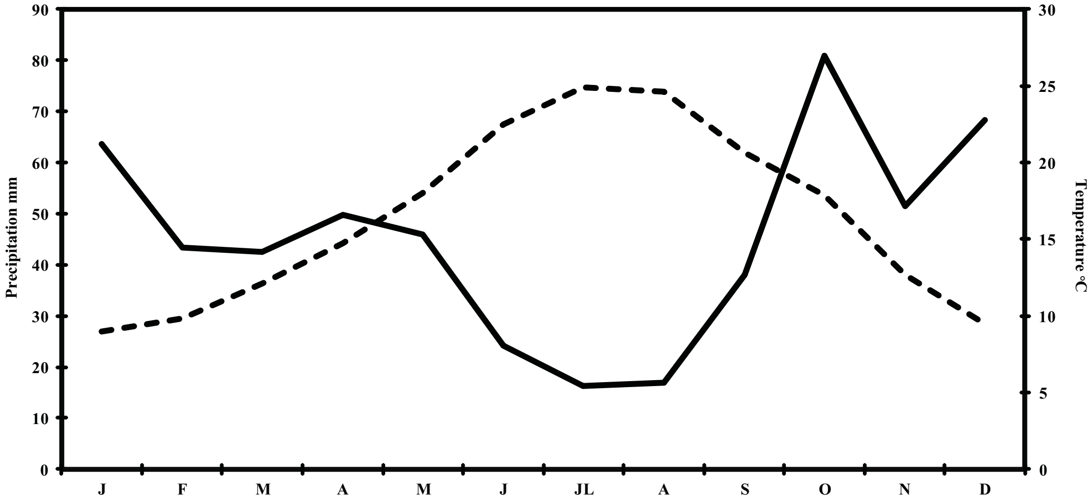
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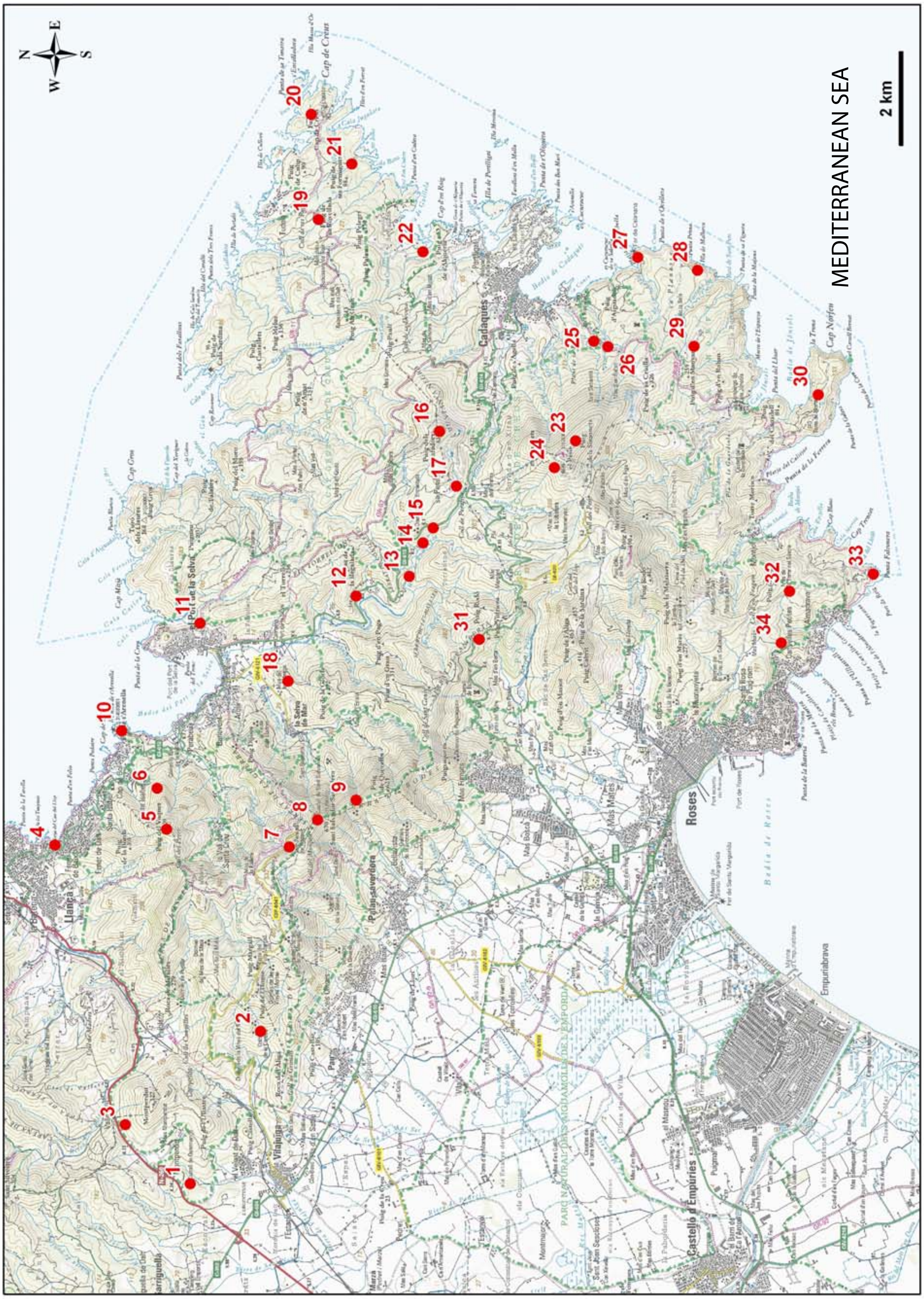
Fig. 1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Roses
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Vilajuïga
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Palau-saverdera
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Fig. 2

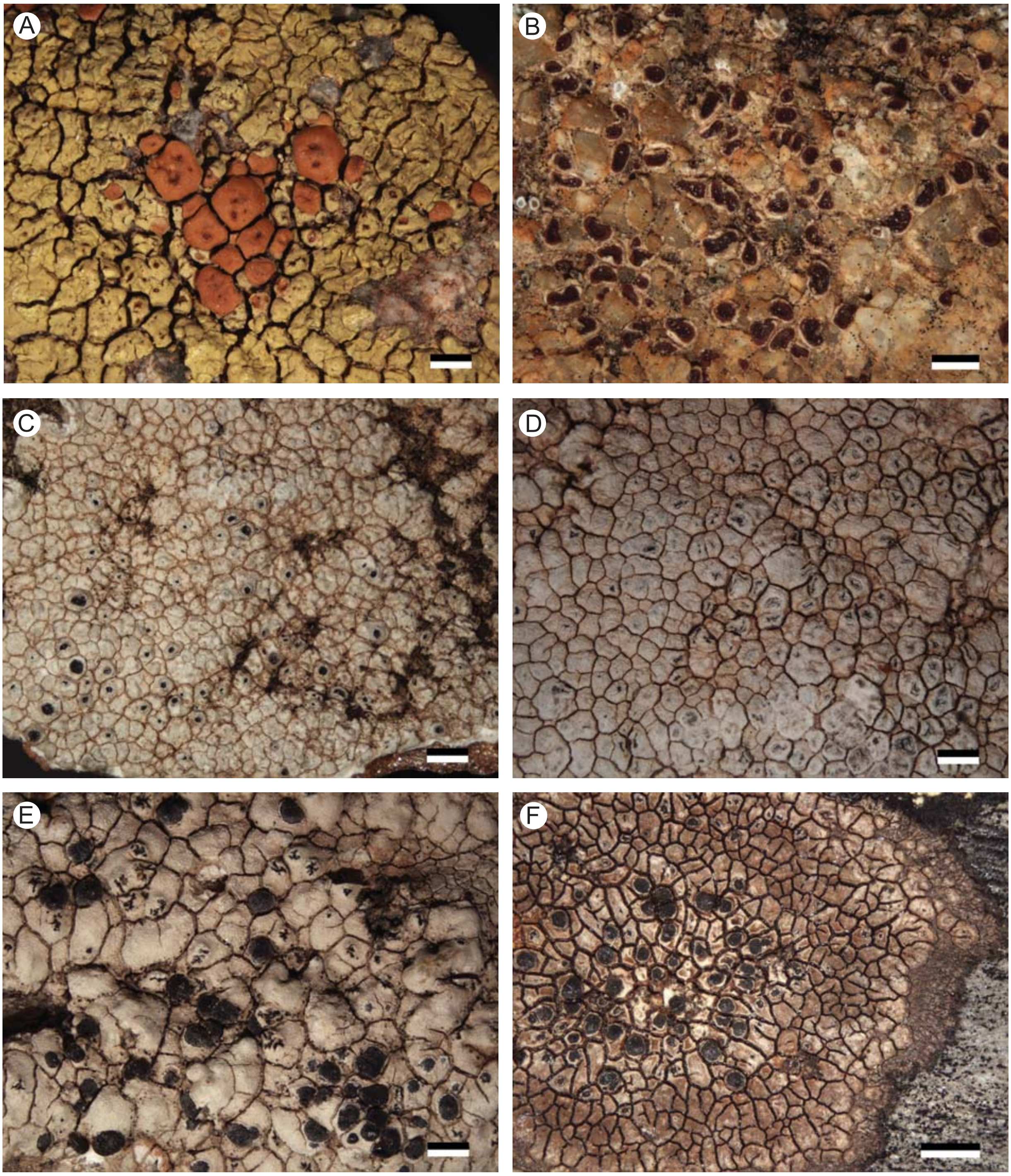

Fig. 3

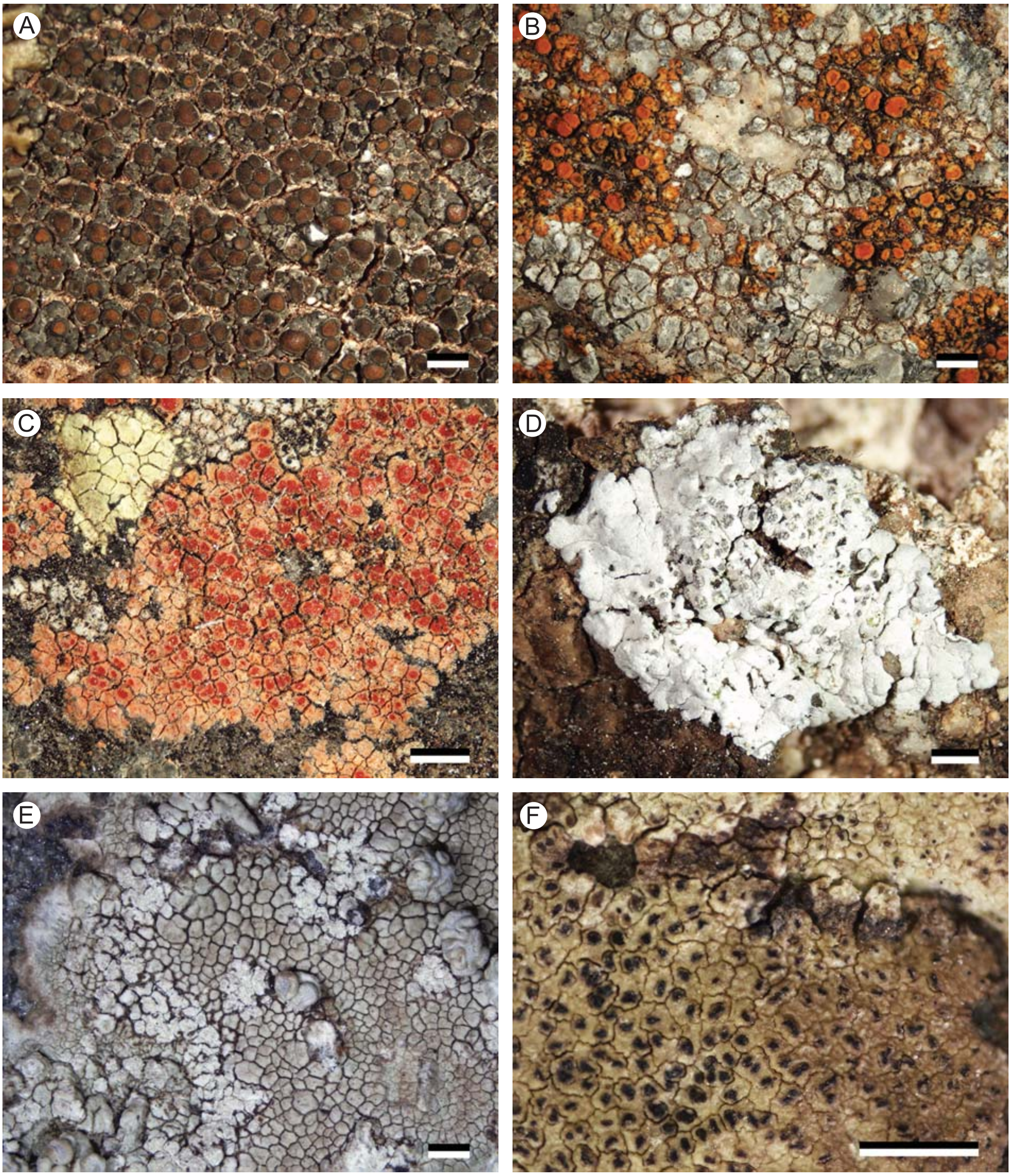

Fig. 4

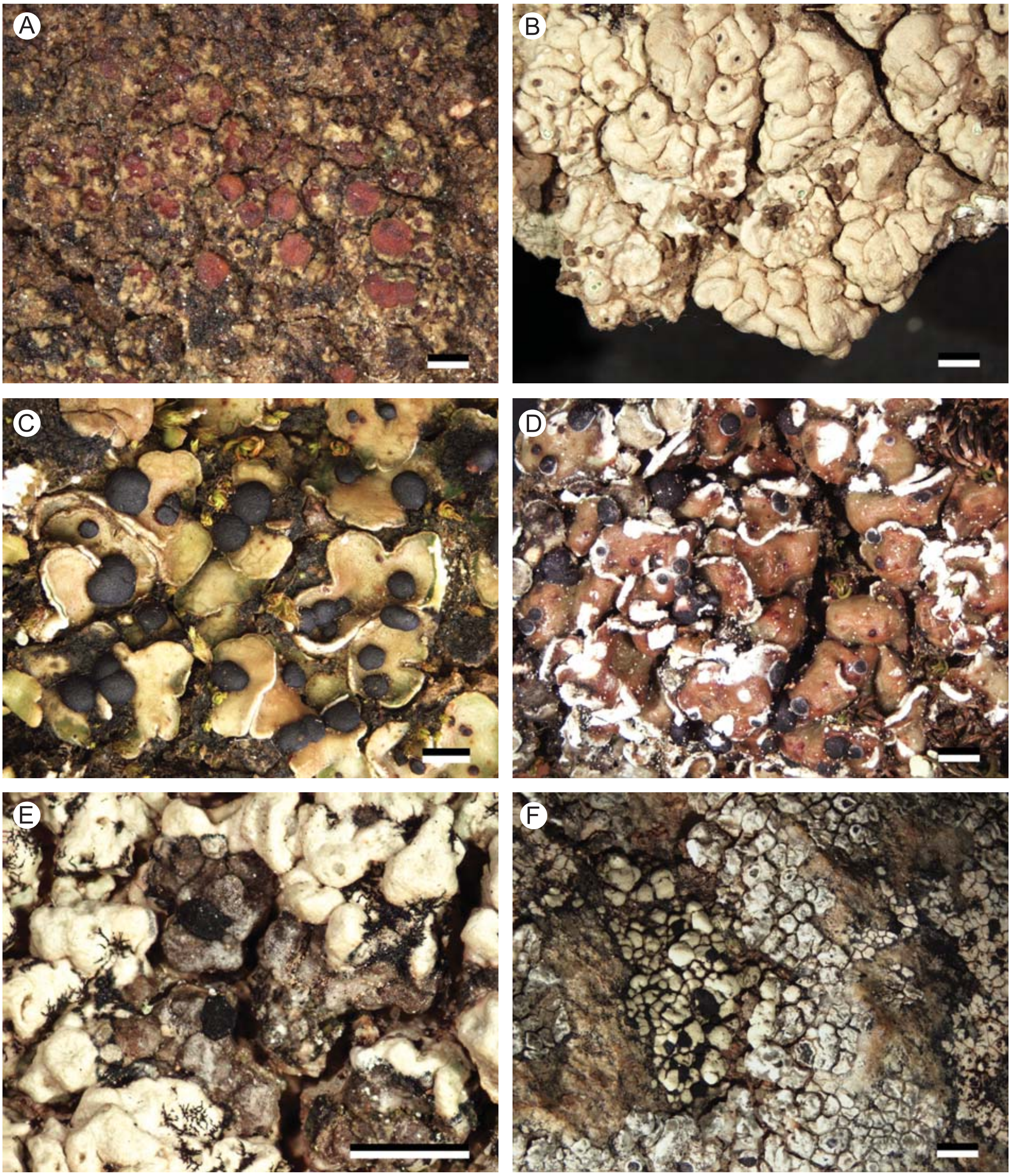

Fig. 5

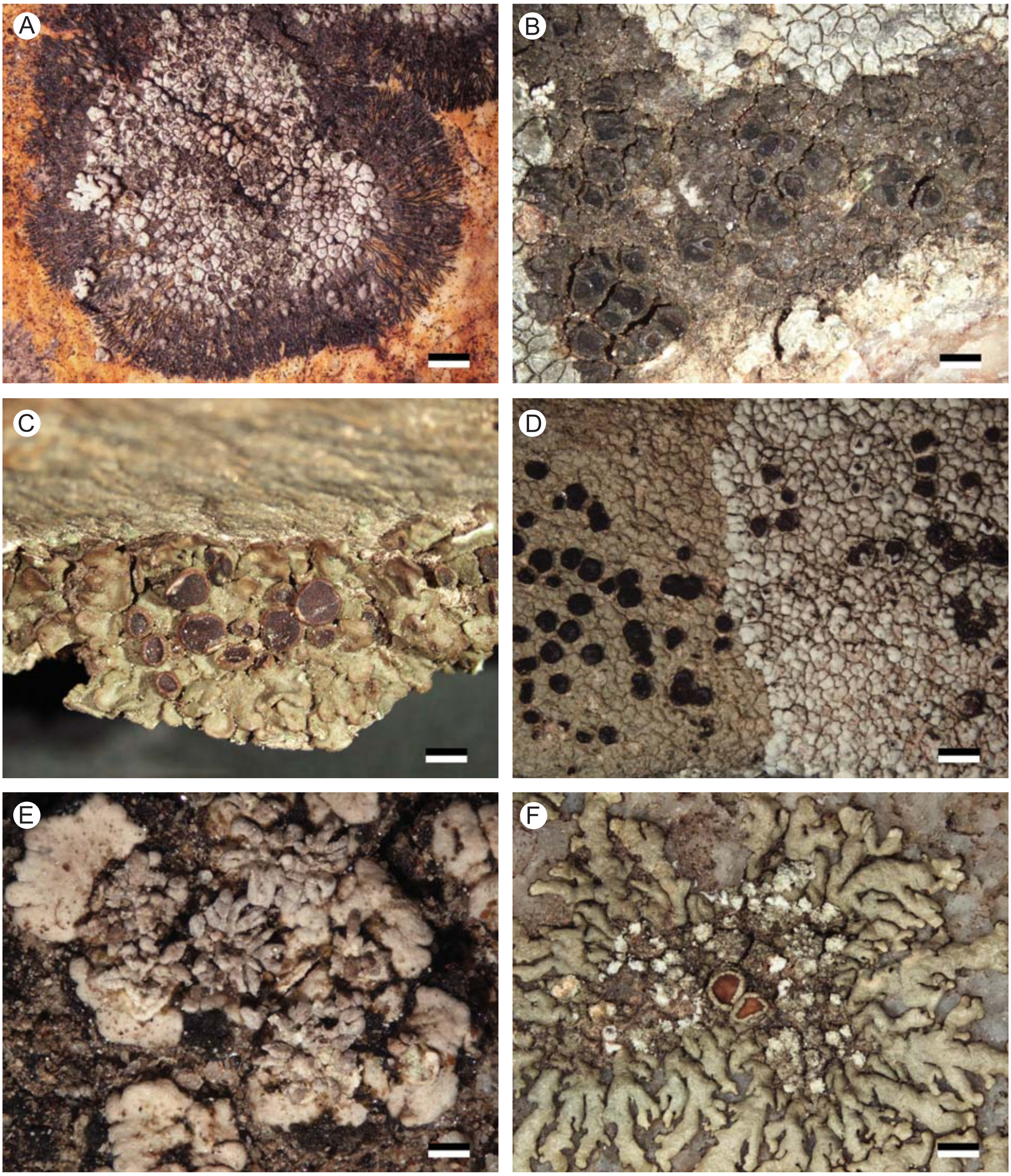

Fig. 6

Table 1. List of the lichen-forming species occurring in the Cap de Creus, grouped after their distribution.

WIDESPREAD

Acarospora veronensis
Aspicilia caesiocinerea
Buellia badia
Caloplaca arenaria
Caloplaca flavescens
Caloplaca flavovirescens
Caloplaca vitellinula
Candelariella aurella
Candelariella vitellina
Catillaria chalybeia
Cladonia chlorophaea
Cladonia furcata
Cladonia homosekikaica
Cladonia pyxidata
Collema cristatum
Collema flaccidum
Collema tenax
Dermatocarpon miniatum
Dimelaena oreina
Diploschistes muscorum
Diploschistes scruposus
Endocarpon pusillum
Lecanora albescens
Lecanora campestris
Lecanora dispersa
Lecanora muralis
Lecanora polytropa
Lecidea fuscoatra
Lecidella stigmatea
Leptogium gelatinosum
Leptogium lichenoides
Lobothallia radiosa
Opegrapha rupestris
Phaeophyscia orbicularis
Physcia adscendens
Physcia caesia
Physcia dubia
Physcia tenella
Polysporina simplex
Porina chlorotica
Protoblastenia rupestris
Rhizocarpon geographicum
Sarcogyne regularis
Scoliciosporum umbrinum
Tephromela atra
Thrombium epigaeum
Toninia sedifolia
Trapelia coarctata
Verrucaria fuscella
Verrucaria nigrescens
Xanthoparmelia pulla

MEDITERRANEAN

Acarospora epithallina
Acarospora hilaris
Acarospora microcarpa
Acarospora sulphurata
Acarospora modenensis
Anema nummularium
Aspicilia cupreoglauca
Aspicilia farinosa
Aspicilia intermutans
Bagliettoa cazzae
Buellia abstracta
Buellia atrocinerella
Buellia caloplacivora
Buellia dispersa
Buellia spuria
Buellia stellulata
Buellia tesserata
Buellia tirolensis
Caloplaca aegaea
Caloplaca aetnensis

Caloplaca aractina

Caloplaca carphinea

Caloplaca diffusa

Caloplaca furax

Caloplaca inconnexa var. *nesodes*

Caloplaca irrubescens

Caloplaca ligustica

Caloplaca polycarpa

Caloplaca rubelliana

Collema ryssoleum

Diploicia subcanescens

Diploschistes diacapsis subsp. *neutrophilus*

Diploschistes euganeus

Diploschistes interpediens

Diploschistes ocellatus

Endocarpon simplicatum

Enterographa pitardii

Epiphloea terrena

Flavoparmelia soredians

Glyphopeltis ligustica

Heteroplacidium contumescens

Ingaderia troglodytica

Ingvariella bispora

Lecanora praepostera

Lecanora rupicola subsp. *sulphurata*

Lecidella asema var. *elaeochromoides*

Leprocaulon microscopicum

Lichinella cribellifera

Lichinella stipatula

Opegrapha calcarea

Opegrapha lutulenta

Peltula euploca

Peltula obscurans

Peltula omphaliza

Peltula placodizans

Pertusaria leucosora

Pertusaria monogona

Pertusaria pluripuncta

Pertusaria rupicola

Physcia biziana

Physcia tribacia

Placidiopsis custnani

Placidium tenellum

Protoparmelia montagnei

Psora gresinonis

Psorotichia vermiculata

Ramalina breviuscula

Ramalina requienii

Rhizocarpon epispilum

Rinodina alba

Rinodina beccariana

Rinodina cana

Rinodina sicula

Solenopsora cesatii

Squamarina concrescens

Toninia cinereovirens

Xanthoparmelia glabrans

Xanthoparmelia tinctina

MEDITERRANEAN-ATLANTIC

Acarospora umbilicata

Anaptychia runcinata

Buellia leptoclinoides

Buellia subdisciformis

Caloplaca arcis

Caloplaca atroflava

Caloplaca marina

Caloplaca maritima

Caloplaca subochracea

Cladonia firma

Cladonia foliacea

Cladonia mediterranea

Coscinocladium gaditanum

Cyphelium marcianum

Diploicia canescens

Diploschistes caesioplumbeus

Diplotomma chlorophaeum

Dirina massiliensis

Lecania atrynoides

Lecanographa grumulosa

Lecanora gangaleoides
Opegrapha cesareensis
Pertusaria excludens
Ramalina subfarinacea
Rinodina aspersa
Rinodina obnascens
Roccella phycopsis
Solenopsora holophaea
Solenopsora vulturiensis
Thelopsis isiaca
Trapelia involuta
Trapeliopsis wallrothii
Verrucaria amphibia
Verrucula maritimaria
Xanthoria aureola

ATLANTIC

Acrocordia macrospora
Cladonia subcervicornis
Collema subflaccidum
Lecidella scabra
Verrucaria praetermissa

TEMPERATE-MEDITERRANEAN

Acarospora oligospora
Agonimia opuntiella
Aspicilia calcarea
Aspicilia contorta subsp. *hoffmanniana*
Aspicilia inornata
Aspicilia subdepressa
Bagliettoa calciseda
Botryolepraria lesdainii
Caloplaca alociza
Caloplaca aurantia
Caloplaca austrocitrina
Caloplaca crenularia
Caloplaca flavocitrina
Caloplaca grimmiae
Caloplaca variabilis
Catillaria atomarioides
Catillaria lenticularis
Cladonia rangiformis
Cladonia subrangiformis
Diploschistes actinostomus
Diplotomma alboatrum
Diplotomma hedinii
Evernia prunastri
Flavoparmelia caperata
Fulgensia fulgens
Gyalideopsis athalloides
Involucropyrenium tremniacense
Lecania inundata
Lecania sylvestris
Lecania turicensis
Lecanora salina
Lecanora sulphurea
Lecidea sarcogynoides
Lepraria nivalis
Micarea melaenida
Ochrolechia parella
Parmelina tiliacea
Parmotrema perlatum
Parmotrema reticulatum
Peltigera collina
Peltigera membranacea
Pertusaria albescens
Pertusaria aspergilla
Pertusaria flavicans
Pertusaria lactea
Pertusaria pseudocorallina
Phaeophyscia hirsuta
Placynthium tremniacum
Porina byssophila
Porpidia cinereoatra
Psora vallesiaca
Rhizocarpon polycarpum
Rhizocarpon viridiatrum
Rinodina atrocinerea
Rinodina gennarii
Rinodina teichophila

Rinodina vezdaea
Sarcogyne privigna
Squamarina lentigera
Teloschistes chrysophthalmus
Toninia aromatica
Toninia physaroides
Toninia tristis subsp. *peudotabacina*
Trapelia placodioides
Trapeliopsis flexuosa
Verrucaria dolosa
Verrucaria fusconigrescens
Verrucaria hochstetteri
Verrucaria lecideoides
Verrucaria macrostoma
Verrucaria murina
Verrucaria viridula
Verruculopsis flavescentaria
Xanthoparmelia conspersa
Xanthoparmelia loxodes
Xanthoparmelia verruculifera
Xanthoria calcicola

TEMPERATE

Cladonia humilis
Gyalecta jenensis
Immersaria athroocarpa
Nephroma parile
Parmelia saxatilis
Porpidia hydrophila
Punctelia subrudecta
Ramalina polymorpha
Rhizocarpon geminatum
Thelenella muscorum var. *octospora*
Toninia squalida
Xanthoparmelia mougeotii

ARTIC-BOREAL

Acarospora sinopica
Dermatocarpon luridum
Tremolecia atrata

CAPÍTOL 2: *Lichenostigma rupicolae* (*Lichenotheliaceae*), una nova espècie de fong liquenícola, creixent sobre *Pertusaria rupicola*

CAPÍTOL 2

Lichenostigma rupicolae (*Lichenotheliaceae*), a new lichenicolous species growing on *Pertusaria rupicola*

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Article publicat a la revista *The Lichenologist* (2010) 42(3): 241–247

RESUM

En el present estudi, es descriu l'espècie de fong liquenícola *Lichenostigma rupicolae* Fdez.-Brime & Nav.-Ros., descoberta en el decurs del treball florístic dedicat als líquens saxícoles i terrícoles del Parc Natural de Cap de Creus. A més d'estar present a Espanya, s'ha trobat també en material recol·lectat a França i Turquia. Aquest espècie creix abundantment sobre els tal·lus i apotecis del liquen *Pertusaria rupicola*, a sobre del qual forma taques negres constituïdes pels cordons micel·liars plurihifals que es disposen radialment i interconnectant els estromes reproductors situats en la zona central. L'estudi inclou una detallada descripció morfològica i anatòmica del nou taxon, acompanyada dels comentaris taxonòmics pertinents en relació a les espècies morfològicament més properes. Finalment, s'inclou una clau dicotòmica de totes les espècies descrites del gènere *Lichenostigma* subgènere *Lichenogramma*.

The Lichenologist **42**(3): 241–247 (2010) © British Lichen Society, 2010
doi:10.1017/S0024282909990727

Lichenostigma rupicolae (*Lichenotheliaceae*), a new lichenicolous species growing on *Pertusaria rupicola*

Samantha FERNÁNDEZ-BRIME, Xavier LLIMONA and Pere NAVARRO-ROSINÉS

Abstract: The lichenicolous fungus *Lichenostigma rupicolae* Fdez.-Brime & Nav.-Ros., collected in France, Spain and Turkey, is described as new to science. It is found growing on the surface of the thalli and apothecia of *Pertusaria rupicola*, where it forms black patches of radiating plurihyphal strands connecting the fertile stromata. An updated key of the species of subgenus *Lichenogramma* is included.

Key words: Dothideomycetes, France, lichen, lichenicolous fungi, Spain, Turkey

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Introduction

Hafellner (1982) described *Lichenostigma*, a genus of lichenicolous fungi, based on the description of *L. maureri*. Currently, it comprises 22 taxa, characterized by having ascomata without hamathecia, evanescent asci surrounded by paraplectenchymatous stromatic tissue and hyaline to brown spores with one or more septa. Within *Lichenostigma*, two subgenera have been recognized: the subgenus *Lichenostigma*, with visible rounded, cushion-like ascomata only, and the subgenus *Lichenogramma* Nav.-Ros. & Hafellner, with simple or plurihyphal dark vegetative strands interconnecting elongated to irregular-shaped ascomata (Navarro-Rosinés & Hafellner 1996).

During recent fieldwork in north-east Catalonia (Spain), SF-B and XL collected several specimens of a lichenicolous fungus growing on *Pertusaria rupicola* (Fr.) Harm. that proved to belong to the subgenus *Lichenogramma*. The exhaustive morphological study detailed here shows that the material examined differs from any described species of *Lichenostigma* and is described as a new species, *Lichenostigma rupicolae*, and compared to closely related taxa.

Material and Methods

Macroscopical characters were examined using a dissecting microscope (×40). Anatomical characters were studied in hand-cut sections and squash preparations mounted in water and Lugol's 0·4% iodine solution (I; pre- treatment with 10% KOH applied before Lugol's application is indicated as K/I) and lactophenol cotton blue (LPCB), and examined under a conventional light microscope (×100, oil immersion). The figures were prepared with the aid of a drawing tube (×1·25) fitted to the microscope. All microscopic measurements were made on material mounted in water. For the ascospore measurements, the average value is indicated in italics between the extreme values, after rejecting 10% of the highest and the lowest values. The highest and lowest absolute values are given in parentheses and the total number of ascospores measured (*n*) is also given.

The Species

Lichenostigma rupicolae Fdez.-Brime & Nav.-Ros. sp. nov.

Filamenta vegetativa nigra, superficialia, reptantia, leviter prominentia, 150–350(–400) × 15–42·5(–49) µm, pluriseriata (a 4–5 seriis cellularum composita; cellulae 5–7 µm diam.), radiale disposita. Ascomata stromatica, irregulariter rotundata, prominentia, (45–)55–90(–120) µm diam., aggregata vel prope centrum subdispersa. Hamathecium pauce evolutum, a cellulis elongatis compositus. Ascosporae (11–)11·5–14·5(–16) × (5·5–)6·5–8·5(–9·5) µm (*n* = 136), leviter obovatae vel late

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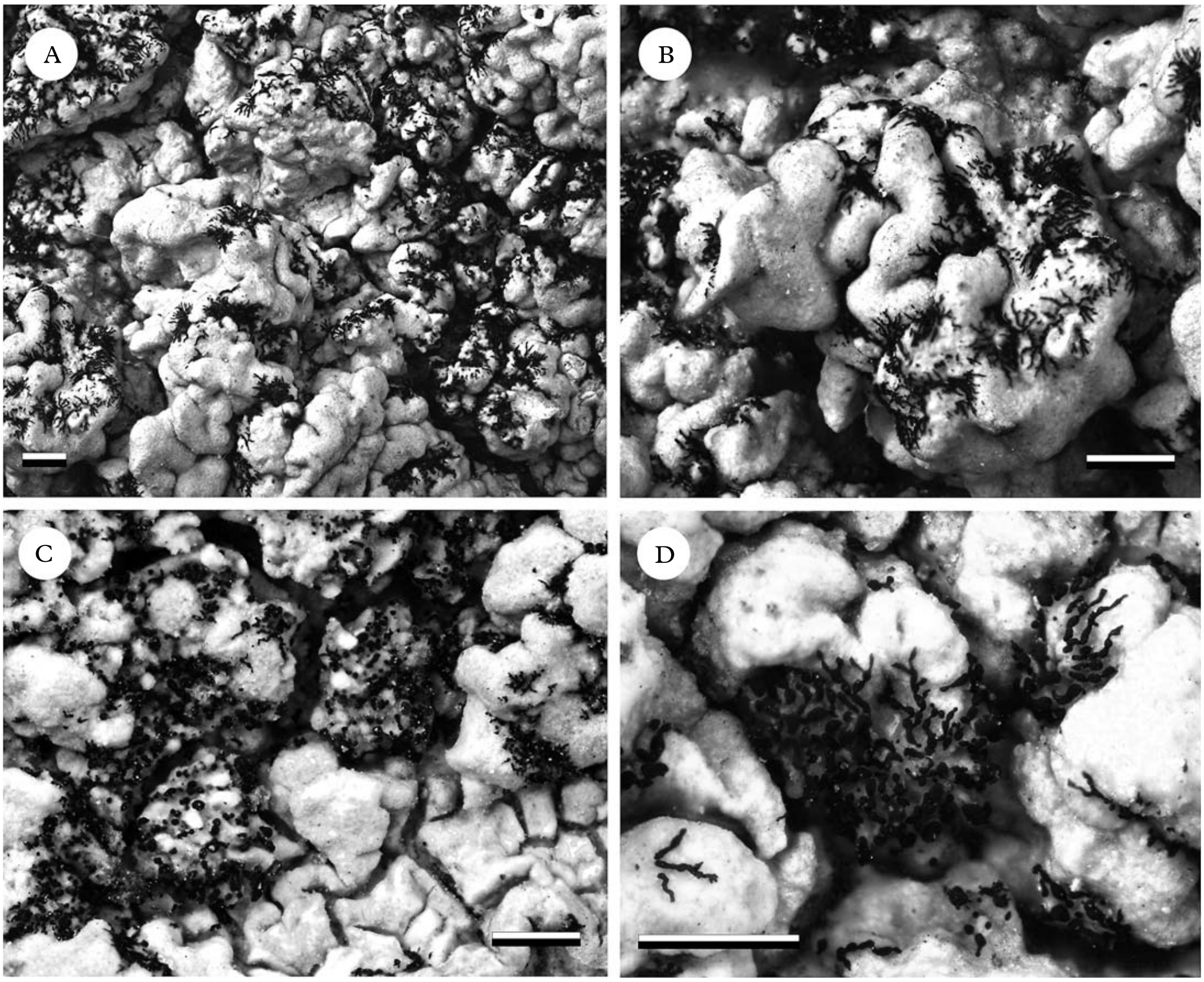

FIG. 1. *Lichenostigma rupicolae* (holotype). A, heavily infected thallus of *Pertusaria rupicola*; B, detail showing the radiate disposition of the hyphal strands; C, group of isolated ascomata; D, group of ascomata with few surrounding hyphal strands. Scales. A–D = 0·5 mm.

ellipsoideae; apices rotundati; a 1–2(–3) transseptis, interdum 1 longisepto, instructae; a maturitate dense brunneae et a parvis granulis ornamentatae. Macroconidia pluricellularia, ellipsoidalia, nigra, 9·5–17(–18·5) × (7·5–)8·5–13(–14·5) µm, super vegetativis filamentis evoluta. A *Pertusaria rupestris* parasymbiotice crescit.

Typus: Spain, Catalonia, Girona, Cadaqués, Muntanya Negra, near Puig dels Bufadors, UTM 31TG2083, on *Pertusaria rupicola*, on acidic rocks, 350 m, 19 September 2006, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16975—holotypus).

(Figs 1 & 2)

Vegetative hyphal strands superficial, forming black groups scattered over the host thallus and apothecial discs, loosely adpressed, simple or with few ramifications, about 150–350(–400) µm long and 15–42·5(–49) µm thick, consisting of 4–6 rows of isodiametric cells 5–7 µm diam. Young single infections forming dense groups of strands arranged radially, with swellings that gradually mature to become fertile stromata. In the final stage, the hyphal strands frequently lose their radial arrangement, and the ascomatic stromata remain isolated in a central position.

Ascomata stromatic, black, superficial, irregularly rounded or slightly elongate, (45–) 55–90(–120) µm long and 35–55(–60) µm thick, densely aggregated or scattered. Internal structure formed by paraplectenchymatous tissue; outer layer strongly pigmented dark brown, with lateral densely compacted cells and basal subglobose cells 6–8·5 µm; inner tissue hyaline to pale brown, composed

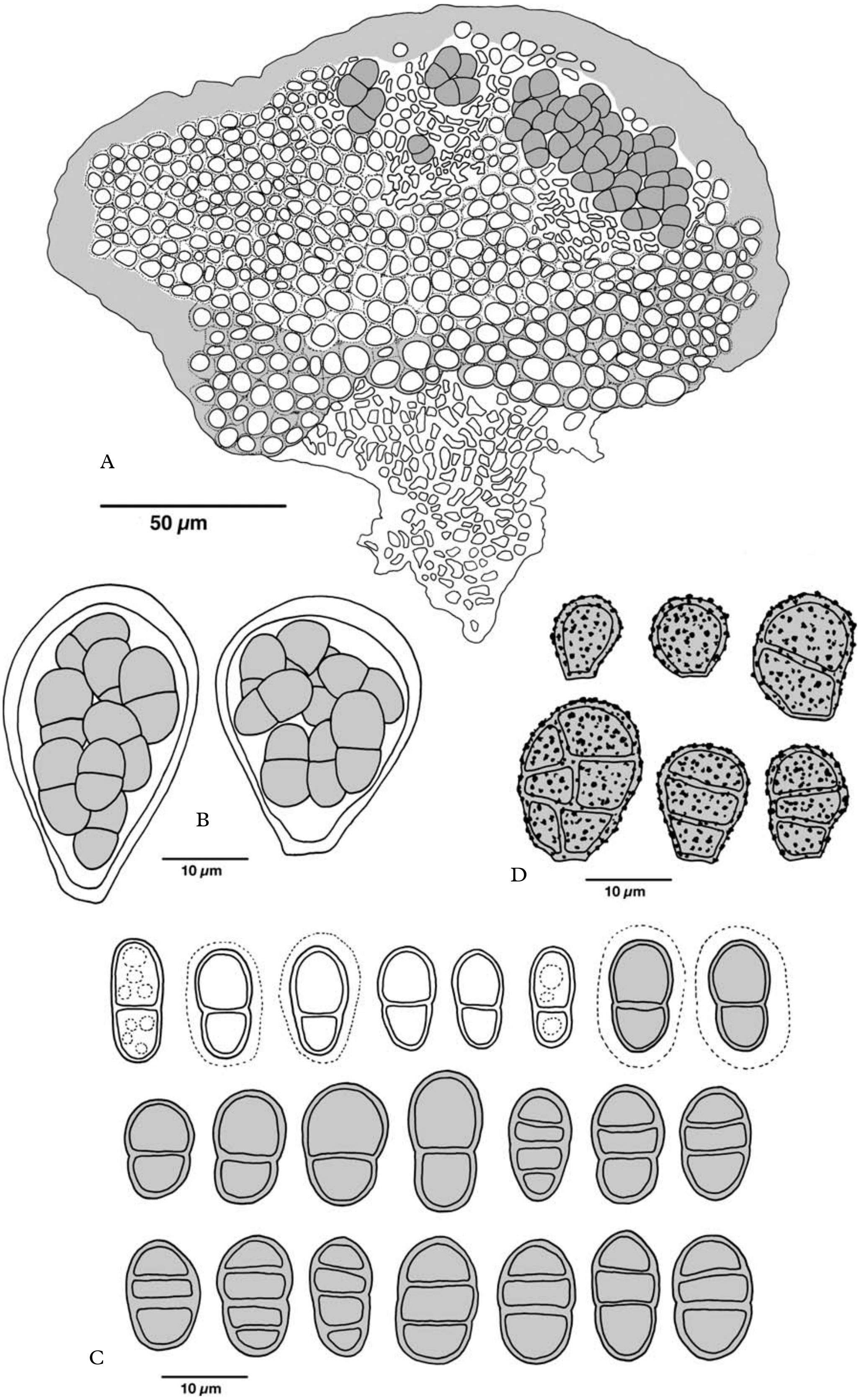

FIG. 2. *Lichenostigma rupicolae*. A, section of an ascoma packed with spores; B, young asci with 8 spores; C, ascospore outlines showing the different stages of maturation, and the variation in septation; D, macroconidia in different developmental stages. Scales. A = 50 μm; B–D = 10 μm.

of spherical hyphal cells 5–7(–9) µm diam. The cells surrounding the asci differ by their irregularly elongated shape, 3·5–6·5 × 1·5–2·5 µm, forming an incipient hamathecium. Ascomatal tissue K/I− and I−, except for the irregularly-shaped cells around the asci that are I+ blue. *Asci* arising in locules, subglobose, bitunicate, 8-spored, K/I− and I−, evanescent; young asci 28–35 × 20–24 µm; after wall disintegration, the spores remain packed in groups of eight. *Ascospores* obovoid to broadly ellipsoidal, with rounded apices, constricted at the central septum, (11–)11·5–*13*–14·5(–16) × (5·5–)6·5–*7*–8·5(–9·5) µm, with length/breadth ratio of (1·5–)1·6–*1·9*–2·1(–2·5) (*n* = 136), 1–2(–3) transverse septa, rarely with a longitudinal septum, present in one or two cells, pale brown and with a perispore hyaline when young; at maturity, they turn dark brown, with a reduced perisporal sheath and a superficial fine granular ornamentation.

Macroconidia globose to ellipsoidal 9·5–17(–18·5) × (7·5–)8·5–13(–14·5) µm, produced directly on the surface of the hyphal strands and the ascomata, erect, multicellular.

Etymology. The epithet refers to the host species, *Pertusaria rupicola*.

Distribution and habitat. *Lichenostigma rupicolae* is currently known only from the localities in France, Spain and Turkey listed in this study. It grows on the thallus and apothecial discs of *Pertusaria rupicola* and does not seem to cause any major damage to the host, as its development is mainly superficial.

Pertusaria rupicola is a saxicolous lichen that grows on north-exposed acidic rock surfaces. It is one of the species that characterizes the association *Pertusarietum rupicolae* (Wirth & Llimona 1975), in which other species of the genus *Pertusaria* are associated with *P. rupicola*, namely, *P. excludens* Nyl., *P. leucosora* Nyl., *P. monogona* Nyl., and *P. pseudocorallina* (Lilj.) Arnold. Based on our observations, we have found that *L. rupicolae* is highly selective of its host. It does not appear on any of the species mentioned above, even when their thalli are growing adjacent to the thalli of *P. rupicola*. In the type locality, *L. rupicolae* is quite abundant, and is widespread over the host thalli. Upon examination of the *P. rupicola* specimens in the BCN herbarium, *L. rupicolae* was also discovered on specimens from France and Turkey, as well as on collections from different localities within Catalonia (NE Spain). Based on our field observations, we can conclude that, although *L. rupicolae* is fairly abundant, it has been previously overlooked.

Remarks. Only one other species of *Lichenostigma* is known on *Pertusaria*: *L. epirupestris* Pérez-Ortega & Calat. (2009). This species grows on *Pertusaria pertusa* var. *rupestris* (DC.) Dalla Torre & Sarnth., and it differs from *L. rupicolae* by the absence of vegetative strands and by its larger cushion-like ascomata (up to 270 µm diam.).

Three other species of *Lichenostigma* on hosts other than *Pertusaria* form similar markedly radiating vegetative strands. These species are *L. ampla* Calat., Nav.-Ros. & Hafellner, *L. gracilis* Calat., Nav.-Ros. & Hafellner, and *L. subradians* Hafellner, Calat. & Nav.-Ros.. *Lichenostigma ampla* is characterized by having mainly submuriform ascospores, growing on *Buellia* species (Calatayud *et al.* 2004). *Lichenostigma gracilis* and *L. subradians* share 1-septate ascospores, smaller than the ascospores of *L. rupicolae*. Furthermore, *L. gracilis* has paler golden brown hyphal strands, and grows on *Acarospora fuscata* (Nyl.) Arnold (Calatayud *et al.* 2002). *Lichenostigma subradians* is characterized by its hyphal strands with few ramifications, more or less perpendicular to the central strand and by growing on yellow *Acarospora* species (Calatayud *et al.* 2002).

The ascospores of *Lichenostigma rupicolae* are similar in size to those of *L. svandae* Vondrák & Šoun, with 1–2 septate ascospores, (11–)11·5–*12·5*–13·5(–15) × (6–)6·5–*7·5*–8·5(–10) µm. However, *L. svandae* has non-radiating hyphal strands, and forms root-like hyphae growing out and downwards, penetrating the cortical layer of the host, and occurs on thalli and apothecia of *Acarospora cervina* (Ach.) A. Massal. (Vondrák & Šoun 2007).

Lichenostigma rupicolae produces macroconidia, similar to those characteristic of the genus *Lichenothelia* D. Hawksw. (Henssen 1987). These peculiar propagules are also present in other species of *Lichenostigma*, such as *L. supertegentis* Ihlen & R. Sant. (Ihlen 2004). On account of its habitat (parasitic on lichens), and the combination of the morphological characters (paraplectenchymatous ascomata and pale brown to dark brown septate spores with a thick perispore when young), *L. rupicolae* must be placed within the genus *Lichenostigma*. As it has been suggested by previous authors, molecular studies are needed to clarify the circumscription of *Lichenostigma* and its relationship to *Lichenothelia* (Ihlen 2004; Pérez-Ortega & Calatayud 2009).

Additional specimens examined (all on *Pertusaria rupicola*). **France:** Var, Six-Fours-les-Plages, Cap Sicié, Notre Dame de Mai, 350 m, 16 v 1964, on schists, *Y. Rondon* (BCN-lich 23).—**Spain:** *Barcelona*: Dosrius, Turó de Séllecs, UTM 31TDG4400, 530 m, on granitic rocks, 23 i 2009, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16974). *Girona*: Cadaqués, Mas de Rabassers de Baix, near water reservoir, 110 m, UTM 31TEG2385, on acidic schists, 22 i 1995, *X. Llimona* (BCN-lich. 16973); el Port de la Selva, Camí dels Masos, path over Cala Tamariua, 20 m, UTM 31TEG1788, on acidic schists, 15 vi 1985, *X. Llimona* (BCN-lich. 16972); *ibid.*, 24 v 2007, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16971); el Port de la Selva, Serra Carbonera, 15 v 1988, *X. Llimona* (BCN-lich. 16970); el Port de la Selva, Serra de Verdera, 550 m, UTM 31TEG1286, on granitic rocks, 19 ix 2006, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16969); Palau-Saverdera, Les Torroelles, 0–100m, UTM 31TEG1082, on granitic vertical wall, 10 x 1986, *N. L. Hladun & A. Gómez-Bolea* (BCN-lich. 8605); *ibid.*, 20 iv 2007, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16968); Vilajuïga, Castell de Quermançó, 100 m, UTM 31TEG0787, 07 iii 1992, *P. Navarro-Rosinés, Cl. Roux, X. Llimona, A. Gómez-Bolea & I. Pereira* (BCN-lich. 16967). *Tarragona*: Vimbodí, Serra de Prades, Ermita de l'Abellera, 1020 m, UTM 31TCF3374, 13 vii 1997, on red sandstone, *M. Boqueras* (BCN-lich. 16938); Vimbodí, Vall de Castellfollit, under Roca de l'Àliga, 880 m, UTM 31TCF3978, on granitic rocks, 19 ix 2006, *X. Llimona & S. Fernández-Brime* (BCN-lich. 16966).—**Turkey:** *Muğla*: Beşparmakdağ, near the pass between Narhisar and Cukurköy, 800 m, 37°28′N 27°42′E, on siliceous rocks of gneis, 17 iv 1992, *V. John* (V. John: Lichenes Anatolici Exsiccati 101).

Additional comparative material examined. ***Lichenostigma epirupestris***. **Spain:** *Tarragona*, Arnes, Serra dels Ports, Barranc del Grevolar, 800–900 m, UTM 31TBF7125, on *Pertusaria pertusa*, on *Juniperus phoenicea*, 20 x 1990, *M. Boqueras, A. Farnós & A. Gómez-Bolea* (BCN, Herb. M. Boqueras d172).

Key to the species of *Lichenostigma* subgen. *Lichenogramma*

Based on the key in Calatayud *et al.* (2002), updated with the addition of new species described since the publication of this work (Calatayud *et al.* 2004; van den Boom & Etayo 2006; Vondrák & Šoun 2007). For the remaining *Lichenostigma* subgen. *Lichenostigma*, a newly revised key is currently available (Pérez-Ortega & Calatayud 2009).

1 Vegetative strands mostly formed by a single row of cells; ascomata usually subglobose or scarcely elongated 2
Vegetative strands plurihyphal (stromatic); ascomata irregularly rounded or elongated 5

2(1) Mature ascospores brown 3
Mature ascospores mostly hyaline 4

3(2) Macroconidia over the hyphal strands, black, submural, 10–20(–26) × 7–10(–15) µm; ascomata rare; ascospores 9–10 × 4·5–5 µm; on *Lecanora sulphurella* . . . . **L. episulphurella Etayo & van den Boom**
Macroconidia absent; ascomata frequent; ascospores 10–12(–13) × 5·5–7(–8) µm; on *Diplotomma hedinii* (*hedinianum*) (= *D. epipolium* auct.) . . . . **L. epipolina Nav.-Ros., Calat. & Hafellner**

4(2) Vegetative hyphae sunken in fissures of the host thallus, ascospores 7–9(–10) × 4–5 µm; centrum I– or slightly reddish; on species of the *Buellia epigaea* group . . . . **L. semiimmersa Hafellner**

Vegetative hyphae developed on smooth thallus surface, prominent; ascospores 8–10(–11) × 3–4(–5) µm; centrum usually I+ orange-red; on *Xanthoparmelia* spp. . . . . **L. cosmopolites Hafellner & Calat.**

5(1) Strands of vegetative hyphae, at least in young infections, markedly radiating . . 6

Strands of vegetative hyphae not markedly radiating 10

6(5) Ascospores 1-septate, on *Acarospora* species 7

Ascospores with more than 1 septum, not on *Acarospora* species 8

7(6) Strands of vegetative hyphae loosely adpressed and distinctly prominent over the thallus surface; each strand formed by a main axis with few short lateral rectangular ramifications; ascospores (8–)9–10(–11) × (4–)5–6(–7) µm; mostly on yellow *Acarospora* species . . . . **L. subradians Hafellner, Calat. & Nav.-Ros.**

Strands of vegetative hyphae tightly adpressed and hardly prominent over the thallus surface; each strand with several lateral ramifications deviating at an acute angle; ascospores (8–)9–12(–13) × (4–)5–6(–7)µm; on *Acarospora fuscata* . . . . **L. gracilis Calat., Nav.-Ros. & Hafellner**

8(6) Mature ascospores 1–2(–3) septa; with abundant macroconidia; ascospores 11–14·5(–16) × (5·5–)6·5–8·5(–8·5) µm; on *Pertusaria rupicola* . . . . **L. rupicolae Fdez.-Brime & Nav.-Ros.**

Mature ascospores submuriform, 2–7 celled; no macroconidia observed 9

9(8) Vegetative strands about (50–)100–250(–400) µm long and about (9–)10–16(–20) µm wide, formed by (1–)2–5 rows of cells; ascospores (9–)10–13(–15) × 6–9(–10) µm; on *Diploicia subcanescens* . . **L. diploiciae Calat., Nav.-Ros. & Hafellner**

Vegetative strands about 60–90 µm long and about 25–55 µm wide, formed by 8–30 rows of cells; ascospores 11–16 × 7–10 µm; on *Buellia* species . . . . **L. ampla Calat., Nav.-Ros. & Hafellner**

10(5) Hyphal strands either plurihyphal or 1-cell wide; ascospores 8–9·5 × 5–6 µm; on *Caloplaca bolacina* . . . . **L. bolacinae Nav.-Ros., Calat. & Hafellner**

Hyphal strands all plurihyphal; ascospores larger 11

11(10) Ascospores 1-septate, (9–)10–13 × 6–8·5 µm; on *Aspicilia* and *Lobothallia* species . . . . **L. elongata Nav.-Ros. & Hafellner**

Ascospores with 1 or more septa 12

12(11) Hyphal strands 9·5–19·5(–25) µm thick and up to 500 µm long; 1–2 ascomata per strand; ascospores 1–2-septate, (11–)12·5–13·5(–15) × (6–)6·5–8·5(–10) µm; on *Acarospora cervina* . . . . **L. svandae Vondrák & Šoun**

Hyphal strands 8–13(–16) µm thick and up to 1000(–1500) µm long; 2–3 ascomata per strand; ascospores 1–3-septate, 10–13·5(–15·5) × 5·5–7(–8) µm; on *Squamarina* species . . . . **L. rouxii Nav.-Ros., Calat. & Hafellner**

The authors thank Dr. E. Gaya for her valuable comments on the manuscript, the curators of the Herbarium of BCN for providing material used in this work, Néstor Hladun for the help obtaining digital photographs, and Molly McMullen for the English revision. This work was carried out within the projects: CGL2007-66734-C03-02 (CICYT, Ministerio de Educación y Ciencia, Spain) and 2005SGR01047 (Departament d'Universitats, Recerca i Societat de la Informació, Generalitat de Catalunya, Spain). We gratefully acknowledge support from a PhD scholarship (FPU-Formación del Profesorado Universitario,Ministerio de Educación).

REFERENCES

Calatayud, V., Hafellner, J. & Navarro-Rosinés, P. (2004) Lichenostigma. In *Lichen Flora of the Greater Sonoran Desert Region. Volume I.* (T. H. Nash, B. D. Ryan, C. Gries & F. Bungartz, eds.): 664–669. Tempe: Lichens Unlimited. Arizona State University.

Calatayud, V., Navarro-Rosinés, P. & Hafellner, J. (2002) A synopsis of *Lichenostigma* subgen. *Lichenogramma* (*Arthoniales*), with a key to the species. *Mycological Research* **106:** 1230–1242.

Hafellner, J. (1982) Studien über lichenicole Pilze und Flechten II. *Lichenostigma maureri* gen. et spec. nov., ein in den Ostalpen häufiger lichenicoler Pilz (Ascomycetes, Arthoniales). *Herzogia* **6:** 299–308.

Henssen, A. (1987) *Lichenothelia*, a genus of microfungi in rocks. *Bibliotheca Lichenologica* **25:** 257–293.

Ihlen, G. P. (2004) A new species of *Lichenostigma* (*Lichenotheliaceae*, *Arthoniales*) from Scandinavia. *Lichenologist* **36:** 183–189.

Navarro-Rosinés, P. & Hafellner, J. (1996) *Lichenostigma elongata* sp. nov. (Dothideales), a lichenicolous ascomycete on *Lobothallia* and *Aspicilia* species. *Mycotaxon* **62:** 211–225.

Pérez-Ortega, S. & Calatayud, V. (2009) *Lichenostigma epirupestre*, a new lichenicolous species on *Pertusaria* from Spain. *Mycotaxon* **107:** 189–195.

van den Boom, P. P. G. & Etayo, J. (2006) New records of lichens and lichenicolous fungi from Fuerteventura (Canary Islands), with descriptions of some new species. *Cryptogamie, Mycologie* **27:** 341–374.

Vondrák, J. & Šoun, J. (2007) *Lichenostigma svandae*, a new lichenicolous fungus on *Acarospora cervina*. *Lichenologist* **39:** 211–216.

Wirth, W. & Llimona, X. (1975) Das *Pertusarietum rupicolae* un. nova, eine Silikatflechten-gesellschaft in Mittelmeerraum, mit Bemerkungen zur Taxonomie des *Pertusaria pseudocorallina*-formenkreises. *Herzogia* **3:** 335–346.

Accepted for publication 27 *November* 2009

CAPÍTOL 3: Estudi filogenètic del gènere *Diploschistes* (*Graphidaceae*, *Ostropales*, Ascomycota), basat en dades morfològiques, químiques i moleculars

CAPÍTOL 3

Phylogenetic study of *Diploschistes* (Graphidaceae, Ostropales, lichen-forming Ascomycota), based on morphological, chemical, and molecular data

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Es preveu enviar aquest article a la revista *Taxon*

RESUM

El gènere *Diploschistes* es caracteritza per tenir un exciple carbonitzat amb paràfisis laterals i per contenir depsidones de l'orcinol. Excepcionalment, l'espècie *D. ocellatus* presenta un exciple molt reduït i no carbonitzat, no té paràfisis laterals i conté depsidones del β-orcinol, caràcters pels quals, la seva inclusió dins de *Diploschistes* s'ha considerat dubtosa. El primer objectiu del present estudi, ha estat comprovar si *Diploschistes* és realment monofilètic segons el concepte actual que es té del gènere (*i. e.*, incloent *D. ocellatus*). Amb aquest objectiu, s'ha construït una filogènia basada en els mtSSU i nuLSU de diverses espècies de *Diploschistes* i d'altres gèneres de *Graphidaceae*. Els resultats confirmen que *Diploschistes* és monofilètic i que *D. ocellatus* dóna lloc a una primera divergència dins del gènere. Tradicionalment, dins del gènere *Diploschistes* s'han distingit tres grups d'espècies basats en la morfologia dels apotecis: grup *actinostomus* (peritecioides), grup *scruposus* (urceolats) i grup *ocellatus* (lecanorins). No s'ha demostrat encara que aquests grups, emprats àmpliament en monografies o claus, siguin entitats naturals i que, per tant, incloguin espècies amb un ancestre comú més recent. Amb l'objectiu de revisar la validesa taxonòmica i sistemàtica de la morfologia dels apotecis, en aquest estudi també s'ha construït una filogènia basada en dades morfològiques, químiques i moleculars (nuITS i mtSSU). Els nostres resultats indiquen, per primera vegada, que els tres grups morfològics considerats dins de *Diploschistes* són monofilètics i, com a conseqüència, se'n proposa una classificació infragenèrica. A més del tipus d'apotecis, aquests grups també presenten diferències notables en l'estructura de la part superior del tal·lus. Les anàlisis filogenètiques revelen novetats en algunes espècies: l'existència d'un clade dins de *D. ocellatus*, corresponent a espècimens sense apotecis que només tenen picnidis, i la presència d'un clade que agrupa tots els espècimens de la subespècie *D. diacapsis* subsp. *neutrophilus*, que es troba en una posició distant al clade que inclou a la resta de *D. diacapsis.* Per altra banda, el nostre estudi demostra que una espècie coneguda i àmpliament distribuïda com és *D. scruposus*, presenta una variabilitat molecular que no es correspon amb trets morfològics ni químics.

Phylogenetic study of *Diploschistes* (Graphidaceae, Ostropales, lichen-forming Ascomycota), based on morphological, chemical, and molecular data.

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The genus *Diploschistes* includes crustose lichen-forming fungi with a carbonized proper excipulum with lateral paraphyses, and a chemistry dominated by orcinol depsides. However, the taxon *D. ocellatus* lacks these excipular characters and has β-orcinol depsidones, being doubtful its inclusion within the genus. With the use of a two-locus dataset of mtSSU and nuLSU sequences, we confirm that the genus *Diploschistes* is monophyletic including *D. ocellatus*. Within *Diploschistes*, three different groups have been distinguished based on different ascomatal morphology: *actinostomus* (perithecioid), *scruposus* (urceolate) and *ocellatus* (lecanoroid). These groups have been widely used in monographic studies and keys, but their taxonomic value has not been confirmed yet. Phylogenetic relationships within *Diploschistes* were reconstructed using a combined dataset of morphological, chemical, nuITS, and mtSSU data in order to investigate those species groups; and to explore the monophyly of phenotypically-based species, with special emphasis on the *D. scruposus* complex, where different species concepts have been given among authors. Based on our results, a new subgeneric treatment for *Diploschistes* is proposed, and the taxonomical value of fruiting body types is confirmed. The clade corresponding to *D. ocellatus* is formed by two well-supported clades, one of them grouping specimens without ascomata, having only pycnidia. It is also remarkable that the clade containing specimens of *D. diacapsis* subsp. *neutrophilus* appears distant and unrelated to the clade with all other specimens of *D. diacapsis*. Well-known taxa such as *D. scruposus* revealed a molecular diversity not associated to morphological nor chemical traits.

KEYWORDS: ascoma morphology, phenotypically based species, morphological phylogeny, molecular phylogeny, nuITS, mtSSU, INAASE.

INTRODUCTION

Currently, the lichen-forming genus *Diploschistes* (Lecanoromycetes, Ostropales, Graphidaceae) includes 43 crustose species (Kirk & al., 2008), which grow on rocks, soil or over mosses and other lichens. *Diploschistes* is widely distributed in arid and semiarid regions of Africa, America, Australia, and Europe (Poelt, 1969; Clauzade & Roux, 1985, 1989; Lumbsch, 1989, 1993; Lumbsch & Elix, 1985, 1989, 2003; Lumbsch & al., 1993; Guderley & Lumbsch 1996; Elix & Lumbsch, 2005; Lumbsch & Mangold, 2007; Mangold & al., 2009). Although this genus has primarily a temperate distribution, a few species extend into tropical areas (Lumbsch, 1993; Lumbsch & Aptroot, 1993; Pant & Upreti, 1993; Breuss & Brunnbauer, 1997; Umaña & Sipman, 2002).

Traditionally, *Diploschistes* has been characterized by having a carbonized pseudoparenchymatous excipulum with lateral paraphyses and *Trebouxia* as a photobiont, and by the absence of a columella (Lumbsch, 1989). Three different ascomatal morphologies are present within the genus: perithecioid (ascoma enclosed by a wall and opened only by a small pore, disc not visible from above, similar to a perithecium, and well-developed carbonized excipulum), urceolate (ascoma with an exposed deeply concave disc and well-developed carbonized excipulum), and lecanoroid (ascoma with an exposed flat to moderately concave disc, and reduced hyaline excipulum). Lettau (1932) first proposed the distinction between the *actinostomus* group, with perithecioid ascomata, and the *scruposus* group, with urceolate to lecanoroid ascomata. Later on, Lumbsch (1985) introduced a third subdivision, the *ocellatus* group, to encompass a single species, *D. ocellatus*, characterized by lecanoroid ascomata, an extremely reduced pale excipulum, and lack of lateral paraphyses.

Hale (1980, 1981) had proposed a circumscription of genera within the family Thelotremataceae – now synonymized with the Graphidaceae after Mangold & al. (2008) – based on excipular characters. Following Hale's classification, *Diploschistes* was then characterized by having a well-developed carbonized pseudoparenchymatous excipulum with lateral paraphyses. However, the species *D. ocellatus* did not fit in this genus circumscription. Subsequently, Lumbsch & Tehler (1998) questioned this delimitation since *Diploschistes* shares these excipular traits with other genera of the family (e.g., *Thelotrema* has lateral paraphyses and *Ocellularia* carbonized excipulum). For this reason, Lumbsch & Tehler (1998) suggested as alternative diagnostic characters for *Diploschistes*: the presence of *Trebouxia* and the absence of the stictic acid complex. Again, *Diploschistes ocellatus* would not fit in this circumscription since it contains β-orcinol depsidones belonging to the norstictic acid chemosyndrome (substances included into the stictic acid complex), by other taxa of thelotremoid Graphidaceae (e.g., *Chapsa*, *Leptotrema*, *Thelotrema*).

Two phylogenetic studies on *Diploschistes* have been published up to date (Lumbsch & Tehler, 1998; Martín & al., 2003). Both studies were mainly aimed to determine whether *D. ocellatus* does belong to the genus and to investigate the taxonomic value of the ascoma morphology in the delimitation of monophyletic entities. In their morphology-based study, Lumbsch & Tehler (1998) showed the *scruposus* group, including *D. ocellatus*, as monophyletic, and the *actinostomus* group as paraphyletic. Conversely, in a nuITS based phylogeny, Martín & al. (2003)

recovered the *actinostomus* group as monophyletic, whereas the *scruposus* group was paraphyletic, with *D. ocellatus* as a first split of the genus. Martín & al. (2003) assessed the placement of *D. ocellatus* calculating the genetic distance between this species and the rest of the genus. The results exceeded the intergeneric distances for euascomycetes, as established in Lumbsch (2002), and Martín & al. (2003) concluded that *D. ocellatus* could be a distant early diverging member of the genus or even a different lineage within the family. However, they did not propose any taxonomical changes for this taxon in await of more comprehensive phylogenetic analyses. None of these studies drew conclusions with regard to the value of the morphology of the ascoma as a synapomorphic character to define monophyletic groups within the genus.

Delimitation problems also occur at the species level, as morphological characters used to define species have resulted on taxonomical conflicts among authors. One example is the taxonomical value deemed to the number of ascospores per asci. Poelt (1969) distinguished *D. scruposus*, with 4 spores per ascus, from *D. interpediens*, with octosporous asci. Clauzade & Roux (1985) also considered them as independent taxa, but treated *D. interpediens*, first as a subspecies of *D. gypsaceus*, and later on as a subspecies of *D. diacapsis* (Clauzade & Roux, 1989). Finally, Lumbsch (1989) merged *D. interpediens* within *D. scruposus* regardless of the differences in ascospore numbers. Another example of taxonomical conflict is the species *D. muscorum*, a parasitic species on *Cladonia* during the first stages of its development. Although broadly accepted, Clauzade & Roux (1985) treated this species as a lichenicolous subspecies of *D. scruposu*s, from which is barely distinguishable once becomes independent from *Cladonia*.

Currently, the taxonomical status of the phenotypically distinct *D. ocellatus*, as an early diverging lineage of *Diploschistes*, remains to be ascertained. Also, the value of the ascomatal morphology to delimit natural groups at the infrageneric level is still untested, and several taxonomical problems, especially within the *D. scruposus* complex, are pending to be solved. For this reason, our main goals in this study were to: (1) test the monophyly of the genus *Diploschistes* and determine its placement within the Graphidaceae; (2) to investigate the taxonomic value of the ascoma morphology within *Diploschistes*; and (3) to assess the circumscription of conflictive taxa within the *D. scruposus* complex.

MATERIAL AND METHODS

Taxon sampling. --- To test the monophyly of the genus *Diploschistes*, we conducted a set of analyses based on a combined alignment of the small subunit of the mitochondrial rDNA (mtSSU) and the large subunit of the nuclear rDNA (nuLSU) for 73 selected specimens from the Ostropales s.l. Eleven specimens of *Diploschistes* and a broad sampling within the Graphidaceae were included as part of the ingroup. To root the phylogeny, 11 species of Ostropales not belonging to the Graphidaceae were included. In total, 146 sequences were used in the concatenated alignment, of which nine were generated for the first author, and the rest were downloaded from GenBank and the AFTOL database (AFTOL.org).

To further explore the relationships within the genus *Diploschistes*, we analyzed a combined alignment of morphological and molecular data (nuITS and mtSSU). Fresh material collected in different areas of Spain and Portugal was complemented by selected material from various herbaria (BCN, DUKE, LEB, and SANT).

For the phylogenetic analyses based on morphological and chemical characters, we included 54 specimens of *Diploschistes*. The sampling was focused on the *scruposus* group and, when possible, we included individuals encompassing the whole morphological and ecological variation ascribed to each taxon. For the *actinostomus* group, we included at least two specimens of each species, except for *D. euganeus* that we only added a single specimen. Two species from the genus *Thelotrema* (*T. lepadinum* and *T. suecicum*) were used as outgroup for a total of 56 specimens included in the analyses.

For the molecular phylogenetic analyses, two matrices based on nuITS and mtSSU loci were prepared for the same specimens as in the morphological and chemical phylogeny. All sequences were newly generated for these analyses, except for five sequences of *Diploschistes* and four *Thelotrema* that were downloaded from GenBank and the AFTOL database. Voucher information and accession numbers for newly generated sequences, and ID numbers for downloaded sequences, are listed in Appendix 1.

Morphological and chemical character selection. --- A total of 33 morphological, anatomical, and chemical characters, derived from specimen-based examinations conducted by SFB, and considered potentially useful, were scored for the 54 selected specimens of *Diploschistes*. One ecological character referring to type of substrate was also included for a total of 34 characters, as it has been traditionally considered of taxonomical value (e.g., Poelt, 1969; Clauzade & Roux, 1985; Lumbsch, 1989). For the taxa of *Thelotrema* used as outgroup, there was no available material. For this reason, the scores were drawn from the literature (Culberson & al., 1977; James & Hawksworth, 2009; Mangold & al., 2009), and represent morphologic features at a species, rather than at specimen level.

From the 34 selected characters, 20 were discrete and 14 continuous. All discrete characters were scored and included directly into the data matrix using Mesquite 2.6 (Maddison & Maddison, 2009). The continuous characters were converted into discrete characters before they were incorporated into the data matrix (Figure S1) following the method described in Lutzoni & Brodo (1995), also applied by McDonald & al. (2003). The analyses were performed using the program R 2.10.1 (R Development Core Team, 2009).

Two characters were eliminated because they were invariant among taxa according to an analysis of the variance. When the null hypothesis (H_0 = no significant differences among means) was rejected, we performed a Tukey's Honest Significant Difference test for pairwise comparisons of means. Test statistic probabilities were used to determine the character state for each taxon. Pairwise comparisons having P-values ≤ 0.05 were used to assign a character state to each group; the rest of comparisons, starting with the ones with highest P-values, were used to verify the character state assigned to each remaining taxon. Following McDonald & al. (2003), when intermediate P-values were found ($P \leq 0.8$ and $P > 0.05$), the character was considered polymorphic and two states were given. The final selected characters and their character states are listed in Table S1.

Molecular data. --- Total DNA was extracted from fresh material and herbarium specimens, and isolated using a phenol-chloroform-isoamyl alcohol extraction protocol based on Lee & al. (1988). Isolated DNA was resuspended in sterile water and stored at -20 C.

Primer combinations for the three loci used in this study were: ITS1F (Gardes & Bruns, 1993) and ITS2, ITS3, and ITS4 (White & al., 1990) for the ≈ 0.6 kb nuITS; mrSSU1, mrSSU2, mrSSU2R, and mrSSU3R (Zoller & al., 1999) for the ≈ 0.8 kb of mtSSU; and LIC24R (Miadlikowska & Lutzoni, 2000), LR3, LR3R, and LR7 (Vilgalys & Hester, 1990) for the ≈ 1.4 kb at the 5’ end of nuLSU. Symmetric PCR amplifications were prepared for a 25 µl final volume as in Gueidan & al. (2007), and were carried out in a Peltier thermal cycler (Perkin Elmer, GeneAmp PCR System 2400) using the programs specified in Zoller & al. (1999) for nuITS and mtSSU, and in Gueidan & al. (2007) for nuLSU. After examination with gel electrophoresis, amplification products were purified using ExoSAP-IT (USB Corporation, Cleveland, OH) and Speedtools PCR Clean-Up Kit (Biotools, Madrid) following manufacturer’s instructions. Sequencing reactions were prepared in a 10 µl final volume using the same amplification primers, and Big Dye Terminator Cycle sequencing kit v3.1 (ABI PRISM; Perkin-Elmer, Applied Biosystems, Foster City, CA) following manufacturer’s instructions. Sequencing products were subjected to electrophoresis with an ABI 3730xl DNA analyzer (PE Applied Biosystems, Foster City, CA).

Sequence alignments. --- Sequence fragments were subjected to BLAST searches for a first verification of their identities. They were assembled and edited using Bioedit 7.0 (Hall, 1999), and aligned manually in Mesquite 2.6. Following Kjer

(1995), the nuLSU locus was aligned with the help of the secondary structure of this RNA molecule from *Saccharomyces cerevisiae*, as reported by Cannone & al. (2002). Introns and ambiguously aligned regions (sensu Lutzoni & al., 2000) were delimited manually and excluded from the analyses. Alignments were submitted to TREEBASE (http://www.treebase.org; ID number XXXX).

Phylogenetic analyses to assess the monophyly of the genus *Diploschistes* within the Graphidaceae. --- The mtSSU and nuLSU datasets for 73 specimens were analyzed separately using maximum likelihood (ML) as the optimization criterion with GARLI 0.96 (Zwickl, 2006). Models of molecular evolution were estimated for each genomic region using the Akaike Information Criterion (AIC; Akaike, 1973) implemented in jModeltest 0.1.1 (Guindon & Gascuel, 2003; Posada, 2008). The selected models were TVM+I+G (Posada, 2003) for mtSSU, and GTR+I+G (Tavaré, 1986) for nuLSU. We used GARLI 0.96, to estimate the values of base frequencies, substitution rates, proportion of invariable sites, and the shape parameter of the gamma distribution. We performed searches setting the program to stop after 10,000 generations if no improvement of the Ln likelihood ≤ 0.01 was detected, with a maximum of 500,000 generations. Before combining the two loci, topological incongruence between both datasets was examined using 1,000 replicates of ML bootstrapping under the same models described above, on each locus separately (Mason-Gamer & Kellog, 1996). Because there were no conflicts detected, the two alignments were concatenated.

Phylogenetic relationships and confidence were inferred on the combined dataset using maximum likelihood (ML1), a Bayesian approach (MB1), and weighted maximum parsimony (MP1). For ML1, the same settings were used as in the separate analyses using GARLI 0.96, with the same estimated models specified for each partition, for both ML and ML bootstrap (ML1BS) analyses. In MB1, two parallel runs with four independent chains were conducted for 5 million generations using MrBayes 3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), with trees sampled at intervals of 100 generations. The AIC in MrModeltest 2.3 (Nylander, 2004) was used to estimate the model of evolution, and GTR+I+G was selected for both partitions. The log-likelihood scores were graphically explored by plotting them against generation time with Tracer v1.4.1 (Rambaut & Drummond, 2007; http://beast.bio.ed.ac.uk/Tracer) and set stationarity when log-likelihood values reached a stable equilibrium value (Huelsenbeck & Ronquist, 2001). A burn-in sample of the first 5,000 trees was discarded for each run and the remaining 90,000 (45,000 from each run) were used to estimate branch lengths and Posterior Probabilities (MB1PP) with MrBayes 3.1.1. Finally, MP1 was performed with PAUP* 4.0b10 (Swofford, 2002). Constant sites were removed from all maximum parsimony analyses, gaps were treated as a fifth character state, and symmetric step matrices were created for unambiguous regions of the two loci separately, using STMatrix 3.0 (François Lutzoni & Stefan Zoller, Dept. of Biology, Duke University), as outlined in Gaya & al. (2003). Phylogenetic signal from ambiguously aligned regions was integrated into the analyses with the programs INAASE 2.3b (Lutzoni & al., 2000) and ARC 1.5 (Kauff & al., 2003), as in Gaya & al. (2008). Heuristic searches were performed with 1,000 random addition sequences (RAS), TBR (tree bisection-reconnection) branch swapping, MULTREES in effect, and collapsing branches with maximum branch length equal to zero. Branch support (MP1BS) was assessed with 1,000 bootstrap replicates (Felsenstein, 1985) with full heuristic searches, 36 RAS per bootstrap replicate and the same parameters as for MP1. The number of RAS per bootstrap replicate was calculated taking into consideration the number of times the shortest tree was found during the heuristic search using the original dataset.

Phylogenetic analysis within the genus *Diploschistes*. --- Analyses were performed for 56 taxa, using maximum parsimony (MP) as the optimization criterion, on the following datasets: 1) morphological-chemical dataset (MP2); 2) nuITS dataset (MP3); 3) mtSSU dataset (MP4); 4) nuITS and mtSSU combined datasets (MP5); 5) morphological-chemical and molecular combined datasets (MP6). For the morphological-chemical dataset analyses, all changes among character states were equally weighted, and to simultaneously accommodate taxa with multiple character states resulting from polymorphy, the Variable option in PAUP* was used. In MP3, MP4, MP5, and MP6 analyses, gaps were treated as a fifth character state, constant sites were removed, unambiguous portions were subjected to symmetric step matrices (ITS1, 5.8S, and ITS2 were treated separately), and ambiguously aligned regions were recovered using INAASE 2.3b.

All heuristic searches were performed as in MP1. However, in MP2 and MP4, the high number of equally most parsimonious trees filled the memory before completing the search. For this reason, we executed successive searches progressively incrementing the number of trees saved per RAS. In the first round, we saved only one tree per replicate, in the second we saved 10, in the third we saved 100, and in the fourth and fifth rounds, 1,000 and 10,000 trees were saved per replicate respectively.

With this search strategy, we could detect that, even though incrementing the number of trees saved per RAS, the topology of the majority-rule consensus tree remained the same.

Branch support was assessed by bootstrap analyses with full heuristic searches. For MP2, MP4, and MP6, we performed 10,000 bootstrap replicates, using two (in MP2 and MP6) and 10 (in MP4) RAS per bootstrap replicate and saving no more than 10 trees per RAS. For MP3 and MP5, we performed 1,000 bootstrap replicates, using five (in MP3) and two (in MP5) RAS per bootstrap replicate and saving all trees per RAS. In all bootstrap analyses, we used the same parameters as in the original maximum parsimony search.

Before combining datasets for MP5 and MP6 searches, we assessed for topological congruence among partitions as described above. Since no conflicts were detected, datasets were subsequently combined.

Additionally, we analyzed the nuITS and mtSSU combined dataset with maximum likelihood (ML2) and a Bayesian approach (MB2). For ML2, the estimated models with the AIC in jModeltest 0.1.1 were TIM2ef+G (Posada, 2008) for nuITS, and TIM1+G (Posada, 2008) for mtSSU. The settings for the maximum likelihood analysis and bootstrap searches were the same as for ML1. In MB2, the substitution models selected with the AIC in MrModeltest 2.3 were SYM+G (Zharkikh, 1994) for nuITS and GTR+G for mtSSU. Bayesian analyses were run as in MB1. Most phylogenetic analyses performed in this study were carried out on the Duke Shared Cluster Resource (DSCR).

RESULTS

Alignments and phylogenetic relationships within the Graphidaceae (MB1; ML1; MP1). --- The combined dataset for 73 specimens comprised 5526 sites (representing 1276 and 4250 sites for mtSSU and nuLSU, respectively), leaving 1229 sites after exclusion of 4297 sites corresponding to ambiguous regions and introns. In ML1 and MB1, from the included 1229 sites, 709 were constant and 520 were variable. In MP1, the 709 constant sites were excluded and ambiguously aligned regions were incorporated into the analyses as 29 INAASE characters (13 from mtSSU and 16 from nuLSU) and 437 ARC down-weighted characters (161 from mtSSU and 276 from nuLSU), for a total of 986 variable characters, of which 840 were parsimony informative.

From the three analyses performed on the combined dataset, the majority-rule consensus tree of 90,000 sampled trees from MB1 recovered a topology with 63 resolved internodes, 37 of which were highly supported (MB1PP $\geq$ 0.95). The most likely tree from ML1 (lnL = –12,848.96) revealed a similar tree, with 62 resolved internodes, 30 of those with ML1BS $\geq$ 70%. The MP1 search yielded one most parsimonious tree of 6,842.55 steps (consistency index [CI] = 0.380, retention index [RI] = 0.560, rescaled consistency index [RC] = 0.213), which was found in one island hit 122 times out of 1,000 RAS. MP1 was the most resolved tree with 71 resolved internodes, 34 of those were significantly supported (MP1BS $\geq$ 70%). The MB1 tree, with the highest number of significantly supported internodes, it is shown in Figure 1 with the statistic support indicated for all three analyses.

In all phylogenetic analyses, *Diploschistes* was recovered as monophyletic with strong support (MB1PP = 1.00, ML1BS = 94%, MP1BS = 98%). *Diploschistes ocellatus* formed an early divergence from the rest of the genus, which formed a well-supported clade (MB1PP = 1.00, ML1BS and MP1BS = 100%) but with relationships within it mostly not significantly resolved. In MB1 and ML1, *Acantotrema frischii* appeared as the closest relative to the *Diploschistes* clade, albeit without support. In MP1 (tree not shown), the nearest group to *Diploschistes* was the clade formed by the specimens of *Wirthiotrema*, *Nadvornikia hawaiiensis*, and *Thelotrema bicinctulum*, but again without support.

In general, deeper internodes within the family Graphidaceae mainly lack resolution, although some well-supported clades can be distinguished corresponding to the genera *Chroodiscus*, *Diorygma*, *Glyphis*, *Platygramme*, *Sarcographa* (including *Leiorreuma hypomelaenum*), and *Wirthiotrema*. Conversely, *Chapsa*, *Graphis*, *Thelotrema*, *Myriotrema*, and *Ocellularia*, were not monophyletic as currently circumscribed. In our phylogeny, the *Dyplolabia afzelii-Fissurina insidiosa* clade (now subfamily Fissurinoidea sensu Rivas Plata & al., 2012) established a sister relationship (MB1PP = 1, MP1BS = 99%, MP1BS = 97%) with the other Graphidaceae.

Morphological and chemical characters within *Diploschistes*. --- From the initial 34 selected characters, 32 were finally retained as two continuous characters resulted not significantly variable among the studied specimens (Table S1). The character states obtained for all 56 OTUs are summarized in Table S2. From these 32 phenotypic characters used in MP2 and MP6 analyses, 30 were parsimony informative.

Alignments within *Diploschistes*. --- The nuITS alignment included 815 sites, from which 510 sites corresponding to 36 ambiguously aligned regions and 227 constant sites were excluded from the MP3 analysis. This high number of ambiguous regions was due to the remarkable variation in length of the sequences of *Diploschistes ocellatus*, especially in ITS1 and ITS2. The signal from 34 ambiguously aligned regions was recovered as 34 INAASE characters that were combined with 78 variable characters for a total of 112 included characters, of which 100 were parsimony informative.

The final size of the data matrix of mtSSU was 899 sites. A total of eight ambiguously aligned regions were delimited, resulting in the exclusion of 158 sites. There were also excluded from the MP4 analysis 636 constant sites. Six ambiguously aligned regions were recovered as six INAASE characters and combined to the 105 remaining characters, for a total of 111 variable characters, 97 were parsimony informative.

The combined nuITS and mtSSU data matrix comprised 1714 sites, from which 668 sites were delimited and excluded from all analyses. From the total of 1046 characters subjected to ML2 and MB2 analyses, 875 were constant and 171 variable. In MP5 and MP6, constant sites were excluded and 40 INAASE coded characters were added to the data matrices for a total of 223 variable sites, of which 197 were parsimony informative.

Phylogenetic relationships within *Diploschistes* based on morphological and chemical data (MP2). --- The MP2 search yielded 58,700 equally most parsimonious trees of 293 steps (summarized on a strict consensus tree; Figure S2), which were part of 587 islands that were hit 587 times each out of 1,000 RAS (CI = 0.901, RI = 0.910, RC = 0.820). In the resulting topology, two main strongly supported clades were recovered: one including all specimens of *Diploschistes ocellatus* (MP2BS = 100%), and the other grouping the remaining members of the genus *Diploschistes* (MP2BS = 87%). Within the larger clade, most relationships were unresolved, and only four internodes were highly supported.

Phylogenetic relationships within *Diploschistes* based on molecular data (MP3, MP4, MP5, ML2, MB2). --- Six equally most parsimonious trees of 494.58 steps resulted from the MP3 search (summarized on a strict consensus tree; Figure S3) which were part of one island, hit 604 times out of 1,000 RAS (CI = 0.874, RI = 0.945, RC = 0.827). The MP4 search resulted in 90,400 equally most parsimonious trees of 227.79 steps (Figure S4), which were part of 904 islands that were hit 1,000 times out of 1,000 RAS (CI = 0.977, RI = 0.987, RC = 0.964). The MP5 search yielded 336 equally parsimonious trees (Figure S5) of 728.37 steps, which were part of one island, hit 995 times out of 1,000 RAS (CI = 0.899, RI = 0.952, RC = 0.856).

MP3 (only nuITS; Figure S3) and MP5 (combined nuITS and mtSSU; Figure S5) revealed similar topologies due to the little increase in resolution with the addition of mtSSU (MP4, only mtSSU; Figure S4). In MP3 and MP5, specimens of *Diploschistes* appeared in three main clades that correspond to the groups defined by the ascoma morphology. In MP3, the *ocellatus* and the *actinostomus* groups were strongly supported (MP3BS ≥ 70%), whereas in MP5, all three main groups obtained high support (MP5BS ≥ 70%). In MP4, relationships within *Diploschistes* were hardly resolved. Only the species *D. ocellatus* and *D. rampoddensis* appeared monophyletic with strong support (MP4BS = 98% and 91% respectively), and the *actinostomus* and *scruposus* groups were clustered with 100% bootstrap support.

The ML2 search (Figure S6) showed a loss of resolution, with 21 resolved internodes (tree not shown) of which 10 were resolved, compared to the MP analysis of the same dataset (MP5) and no supported discrepancies. Regarding to the Bayesian inference, the topology recovered was almost identical to ML2, with 19 resolved internodes. The differences of resolution among methods are due to the addition of the INAASE characters in the maximum parsimony analyses, which cannot be included in the maximum likelihood or the Bayesian inference in their current implementations (Gaya & al., 2011).

Phylogenetic relationships within *Diploschistes* based on morphological, chemical, and molecular data (MP6). --- The final combined data matrix consisted of 1786 sites, which comprised 1714 molecular characters from the concatenated nuITS and mtSSU alignments, 40 INAASE characters, and 32 morphological and chemical characters. From the total of 255 included characters, 227 were parsimony informative. The MP6 search yielded 152 equally most parsimonious trees of 1052.38 steps (summarized on a strict consensus tree; Figure 2), which were part of one island that was hit 1,000 times out of 1,000 RAS (CI = 0.873, RI = 0.928, RC = 0.811).

With the addition of morphological and chemical characters, MP6 analysis showed a decrease in the number of equally most parsimonious trees compared to MP5 (152 vs. 336 trees). However, the recovered topology (Figure 2) is quite similar to the MP5 tree (Figure S5), with slight differences in the relationships within the *scruposus* clade, and a general increase in the number of resolved and significantly supported internodes. Within the *actinostomus* group (now subgenus *Limborina*; see discussion), all species were confidently recovered as monophyletic, except for *D. euganeus*, because with one single specimen (as a second split in the group) the monophyly for this species could not be confirmed. Regarding the *scruposus* group (now subgenus *Diploschistes*; see discussion), the first divergence was recovered by a *D. diacapsis* clade, whereas in MP5 and MP3, *D. rampoddensis* represented the first split. MP6 recovered four additional monophyletic groups (*D. gypsaceus*, *D. muscorum*, and two additional clades of *D. scruposus*). Two *D. diacapsis* clades, the species *D. gypsaceus* as well as *D. rampoddensis* were significantly supported. The specimens of *D. interpediens* were placed in two different monophyletic groups, one with strong support (MP6BS = 100%). Finally, the *ocellatus* group (now subgenus *Thorstenia*; see discussion) was revealed once more as significantly monophyletic. With five additional resolved internodes and 26 supported internodes, we consider the phylogeny derived from MP6 as our best estimate of relationships within the genus *Diploschistes*.

DISCUSSION

Generic circumscription of *Diploschistes*. --- Our phylogenetic analysis of the family Graphidaceae, based on mtSSU-nuLSU (Figure 1), confirms the monophyly of the genus *Diploschistes* including the species *D. ocellatus*. These results are consistent with the molecular phylogeny presented by Martín & al. (2003). Apart from the morphological and chemical differences between *D. ocellatus* and the remaining members of the genus, remarkable molecular differences are also present, as shown by the long branches on the MB1 and ML2 trees (Figure 1 and S6 respectively). Due to this molecular variation, Martín & al. (2003) considered that *D. ocellatus* could be potentially considered as a different genus apart from *Diploschistes*. In the present study, with a considerably increased taxon sampling for the family Graphidaceae, the species *D. ocellatus* has resulted to be nested again with *Diploschistes* in all analyses. Based on these results, we cannot reject the hypothesis of monophyly for this genus including the group *D. ocellatus*. Therefore, we consider here that *Diploschistes* can be recognized as a monophyletic genus in it is current circumscription

A recent study of Rivas Plata & Lumbsch (2011) revealed the existence of similar morphotypes (referring to thallus, ascoma, and ascospore morphology) in distantly related lineages within the Graphidaceae due to the occurrence of parallel evolution. These results have important consequences for the classification of this group of lichens, since the combination of ascomatal characters (i.e., excipulum structure and pigmentation, occurrence of lateral paraphyses), which have been traditionally used for generic circumscription of thelotremoid Graphidaceae (Hale, 1980, 1981), cannot be considered reliable. Frisch & al. (2006) introduced the use of the character 'formation of columella' (which in the case of *Diploschistes*, is lacking) to be added to the excipular characters proposed by Hale (1980, 1981) to delimit genera within the Thelotremataceae. However, the presence of a columella has been revealed as highly homoplasic character in a recent study of Rivas Plata & Lumbsch (2011). Therefore, the only synapomorphy available to circumscribe the genus *Diploschistes* is the type of photobiont. Interestingly, *Diploschistes* is the only genus within the Graphidaceae – after transferring *Ingvariella* to the Stictidaceae (Fernández-Brime & al., 2011) – with trebouxioid photobionts and a distribution across both hemispheres, mainly in arid and semiarid regions. All other taxa within this family have trentepohlioid algae and they mainly occur in tropical and subtropical areas. In order to study the evolution on photobiont and habitat switches among these taxa, first we need a stable phylogenetic framework for this family. In this study, we could not assess with confidence the sister relationships of *Diploschistes* with other members of the Graphidaceae. The inclusion of more informative loci, such as protein coding genes (e.g., Rivas Plata & Lumbsch, 2011), will be necessary to assess deep relationships within this family that we could not resolve here with nuclear and mitochondrial ribosomal RNA-coding loci.

Relative contribution of morphological, chemical, and molecular characters to the *Diploschistes* phylogeny. --- In this study (MP2; Figure S2**),** morphological, anatomical, and chemical traits traditionally used in the taxonomy of *Diploschistes* have shown to be useful to delimit several species (i.e., *D. actinostomus*, *D. candidissimus*, *D. diploschistoides*, *D. gypsaceus*, *D. muscorum*, and *D. ocellatus*). However, they failed in delimiting phenotypically similar species, such as *D. interpediens, D. rampoddensis*, and *D. scruposus,* or to group the specimens of *D. diacapsis*.

The topology of the combined molecular datasets (nuITS+mtSSU) has revealed to be very similar to the nuITS topology. However, it was necessary the combination of both loci to confidently recover the *actinostomus*, *scruposus*, and *ocellatus* groups (proposed as subgenera in this study). The addition of morphological and chemical data to the molecular combined dataset recovered for the first time *D. gypsaceus* and *D. muscorum* as monophyletic, and significantly supported the species *D.*

candidissimus, and both clades of *D. diacapsis*. This is not the first time that the inclusion of phylogenies based on phenotypic characters provide an additional source of information to corroborate molecular-based phylogenies (Lutzoni & Vilgalys 1995; Miadlikowska & Lutzoni, 2000; McDonald & al., 2003; Gaya & al., 2011).

Infrageneric classification within *Diploschistes*. --- Since Lettau (1932) and Lumbsch (1989) established the grouping of *Diploschistes* species based on the opening of the ascomata, these groups have been broadly used in taxonomic treatments of the genus for practical reasons. However, none of these groups has ever been formally recognized, since previous phylogenetic works (i.e., Lumbsch & Tehler, 1998; Martín & al., 2003) did not recover them as monophyletic entities. Our results, derived from concatenated datasets (Figure 2), reveal for the first time these three morphological groups as significantly supported monophyletic entities. Consequently, a new subgeneric treatment for this genus is proposed.

Based on molecular data and morphological evidence, we propose here to consider the *actinostomus* group as a new subgenus, *Diploschistes* subg. *Limborina* (see Taxonomic conclusions). In this group, all taxa have ascomatal perithecioid, share a mainly continuous to rimose-areolate thallus (Figure 3A), and the presence of a more or less differentiated protocortex, formed by loosely organized hyphae anticlinally arranged (Figure 3B). Additionally, in all examined thallus cross-sections, we detected a dark pigment incrusted in the hyphae walls from the distal part of this protocortex (Figure 3C).

For the *scruposus* group, we propose the creation of the new subgenus, *Diploschistes* subg. *Diploschistes* (see Taxonomic conclusions). In this clade all specimens have ascomata urceolate and mainly verrucose thalli (Figure 3D). There is no distinguishable cortex or protocortex, and only an epinecral layer can be observed with some remnants of hyphae (Figure 3E), with granules of fuliginous pigmentation (Figure 3F).

Finally, we consider that the taxon *Diploschistes ocellatus* must be placed on the monotypic subgenus *Diploschistes* subg. *Thorstenia* (see Taxonomic conclusions). This species is unique for having ascomata lecanoroid, thallus formed by strongly convex areolae (Figure 3G), and a well developed prosoplectenchymatous cortex formed by dense, anticlinally organized hyphae (Figure 3H). Dark pigmentation granules are disposed in a thin layer on top of this cortex, but never associated to the hyphae walls (Figure 3I). These traits can be added to the above-mentioned characters (i.e., lack of a distinguished carbonized excipulum with lateral paraphyses, and presence of β-orcinol depsidones belonging to the norstictic acid chemosyndrome instead of orcinol depsides), which already separated *D. ocellatus* from the rest of the genus.

Species delimitation in *Diploschistes*. --- Within the species *Diploschistes ocellatus* (subgenus *Thorstenia*), we observed two morphotypes, which correspond to two well-supported groups (Figure 2). One of them contains exclusively fertile specimens, with ascomata and pycnidia (specimens 1, 2, and 5), whereas the other group consists of specimens with only pycnidia (specimens 3 and 4). These grouping might represent an example of lichen 'species pair' (Poelt, 1970) and the clade formed by specimens 3 and 4 would be a sister taxon to *D. ocellatus* that reproduces only vegetatively through the pycnidiospores. However, in recent species pair studies based on molecular data (e.g., Articus & al., 2002; Cubero & al., 2004; Buschbom & Mueller, 2006) members of species pairs form a single monophyletic group without distinction. With the present results, and based on our very limited sampling, we cannot conclude if the specimens that do not form ascomata represent an independent taxon. For this reason, we propose to create the variety *D. ocellatus* var. *tenuis* (see Taxonomic conclusions).

Within the subgenus *Diploschistes*, the taxon *D. scruposus* is a cosmopolitan species that occurs in numerous zonobiomes, especially in the Northern Hemisphere, and it is actually one of the most broadly sampled taxa in the genus. This species shows a wide range of morphological variation, which has resulted in the description of numerous varieties and subspecies (see Lumbsch, 1989). Two chemical races have also been described: one of them has lecanoric acid as a major compound and orsellinic acid as a minor compound, and a second one has lecanoric and diploschistesic acids as major compounds and orsellinic acid as a minor compound. However, no morphological characters have been found related to these two chemotypes (Lumbsch, 1989). In our study, we attempted to cover the broadest morphological and ecological variation, including specimens of *D. scruposus* from different climatic areas, as well as from various siliceous substrates (weathered granite, schists, quartz). The combined phylogeny (Figure 2) recovered this species as polyphyletic within the subgenus *Diploschistes*. Despite the phenotypical variability mentioned above, we have found neither obvious morphological or chemical differences nor a biogeographical pattern that correlate with the placement of the specimens of *D. scruposus* in three different clades. Therefore, until further studies resolve this species complex, we propose to provisionally treat this taxon as *D. scruposus* agg. following Grube & Kroken (2000).

In the monographic study of *Diploschistes* from the Holartic region, Lumbsch (1989) included within *D. scruposus* the species *D. interpediens*, which typically has eight spores per ascus instead of four. With this synonymyzation, *D. scruposus* became characterized by having four to eight spores, a concept followed by later authors (e.g., Pant & Upreti, 1993; Mangold & al., 2009). In our study, however, we treated them *a priori* as two different taxa. Since none of the samples identified as *D. interpediens* appear nested within the *D. scruposus* clades in our analyses, we consider that they should be treated as separate taxa, distinguishable by the number of ascospores. Furthermore, *D. interpediens* is restricted to the Mediterranean region, while *D. scruposus* presents a wide distribution across the Northern Hemisphere. However, as it happens for *D. scruposus*, specimens of *D. interpediens* do not share a most recent common ancestor, being recovered in two independent groups. These results are not reflecting different populations geographically isolated, since specimens 5 and 9 of *D. interpediens* are placed in two different clades, but were collected in the same locality. As we have not found so far phenotypical traits that could justify these two separate origins, we propose to treat this taxon for the time being as *D. interpediens* agg.

Diploschistes rampoddensis shows morphological similarities with *D. interpediens*, as both are saxicolous, have urceolate ascomatal, and octosporous asci. However, *D. rampoddensis* has thinner and friable thallus, and lacks diploschistesic acid. In our phylogeny (Figure 2), *D. rampoddensis* is confidently recovered as monophyletic, separate from closely related taxa.

Diploschistes gypsaceus is a species well defined morphologically (heavily whitish-pruinose thallus), chemically (lack of diploschistesic acid), and ecologically (lives on vertical, sheltered surfaces of carbonated rocks), which has been recognized by many authors (e.g., Poelt, 1969; Lumbsch, 1989; Sérusiaux & al., 1999). However, in Clauzade and Roux's classification (1989), *D. gypsaceus* was treated as a subspecies of *D. scruposus*. Based on our results (Figure 2), the combined phenotypical and molecular data support the recognition of this taxon at the species level.

Diploschistes muscorum is one of the most easily recognizable and collected species from the genus. This species initiates its development as a parasite on *Cladonia* and then becomes independent and able to grow over other substrates (e.g., soil, mosses). The morphology of the thallus changes during the different phases of the life cycle of *D. muscorum*; as a consequence, a large number of infraspecific taxa have been described (Lumbsch, 1989). In our study, we included individuals in different developmental stages to cover this morphological variation. The species was recovered as monophyletic with high support only in the morphological-chemical phylogeny (Figure S2). When the phenotypical and molecular data were combined, *D. muscorum* was still monophyletic, but with low support.

The specimens identified as *Diploschistes diacapsis* are recovered in two distantly related monophyletic clades in our topology (Figure 2). During the morphological survey, we found differences in thallus morphology and ecology among the examined specimens, which subsequently correlated with the two different origins in our phylogenetic analyses. Specimens 1, 2, and 3 have thick thallus, which becomes convex and very loosely attached to the substratum, and show a preference for gypsiferous soils and for highly calcareous soils from inland continental areas. These specimens fit with the morphology and ecology of the type material used to describe *D. diacapsis* (H-ACH-isolectotype, 936a, not seen). Specimens 4, 5, and 6 have a thinner thallus, which becomes very flat, as it always grows completely attached to the substratum, on moderately calcareous to decarbonated soils, in coastal areas. These individuals have the same morphology and ecology as the subspecies described by Clauzade & Roux (1989) as *D. diacapsis* subsp. *neutrophilus* (Herbarium C. Roux 99, holotypus, seen). Our morphological and molecular results strongly support that taxa referred to as *D. diacapsis* subsp. *neutrophilus* has to be recognized at the species level (see Taxonomic conclusions).

Apart from the lack of phylogenetic signal to clearly circumscribe several taxa, relationships within the subgenus *Diploschistes* remain also mainly unresolved, even when combined morphological, chemical, and molecular data were analyzed. These results may be explained under a recent or incomplete lineage sorting scenario, but it would be necessary the use of faster evolving molecular markers and carry on an exhaustive sampling among different populations to test this hypothesis and to perform analyses under coalescence models.

Taxa from the subgenus *Limborina* were revealed as highly supported monophyletic entities, except for *D. euganeus* with just a single specimen, and well-established relationships. However, very few samples were included from this group and we cannot discard the possibility of more complex relationships among taxa from this subgenus, as it has been shown for the subgenus *Diploschistes*. Therefore, further studies will need a larger sampling for the *Diploschistes* with perithecioid ascomata.

TAXONOMIC CONCLUSIONS

Genus *Diploschistes* Norman

Diploschistes subg. ***Limborina*** – Fdez.-Brime, Gaya, Llimona & Lutzoni ***subg. nov. ad int.*** – Type: *Diploschistes actinostomus* (Ach.) Zahlbr.

Mycobank no. XXXXX

Diagnosis: thallus rimose-areolate, sometimes verrucose-areolate; poorly developed protocortex, with dark parietal pigments on hyphae walls, and an upper thin translucent epinecral layer; ascomata perithecioid, immersed, not subdivided, with disc not visible from above, opened only by a small pore; thalline margin thin, immersed; proper excipulum well developed, radially striated, carbonized in section (dark brown to blackish), with lateral paraphyses.

Etymology: the name recalls the ancient genus *Limboria nom. conf.*, used by Massalongo (1852) to combine *D. actinostomus* and *D. euganeus*.

Diploschistes subg. ***Diploschistes*** – Fdez.-Brime, Gaya, Llimona & Lutzoni ***subg. nov. ad int.*** – Type: *Diploschistes scruposus* (Schreb.) Norman

Mycobank no. XXXXX

Diagnosis: thallus verrucose-areolate; without cortex or protocortex, with well-developed epinecral layer, generally opaque due to the presence of dark granules; ascomata urceolate, immersed to sessile, sometimes secondarily subdivided, with deeply concave disc visible from above; thalline rime margin thin, occasionally thick, immersed; proper excipulum well developed, radially striated, carbonized in section (dark brown to blackish), with lateral paraphyses.

Diploschistes subg. ***Thorstenia*** – Fdez.-Brime, Gaya, Llimona & Lutzoni ***subg. nov. ad int.*** – Type: *Diploschistes ocellatus* (Fr.) Norman

Mycobank no. XXXXX

Diagnosis: thallus formed by deeply convex areolae; well-developed prosoplectenchymatous cortex with accumulation of dark granules of pigment on its upper part, not associated to the hyphal walls; ascomata lecanoroid, sessile, with broadly open disc, flat or slightly concave; thalline rime thick and prominent; proper excipulum very reduced, not carbonized in section (pale brown), without lateral paraphyses.

Etymology: the subgenus is named after H. Thorsten Lumbsch, an expert on the group, who has made major contributions to the knowledge of *Diploschistes.*

Diploschistes ocellatus (Vill.) Norm. var. ***tenuis var. nov. ad int.***

Typus: Spain, Catalonia, Lleida, La Segarra, Torà, Font de Can Porta, by the road to Solsona, 31TCG6830, 550-600 m, 13/06/2008, *Llimona* & *Fdez.-Brime*, (BCN-Lich 19341, Holotype)

Mycobank no. XXXXX

Similar to *Diploschistes ocellatus* (Vill.) Norm. var. *ocellatus* but having thinner thallus and lacking always ascomata.

Diploschistes neutrophilus (Clauzade & Cl. Roux) Fdez.-Brime & Llimona ***comb. nov. ad int.***

Mycobank no. XXXXX

Basionym: *Diploschistes gypsaceus* subsp. *neutrophila* Clauzade & Cl. Roux in Bull. Soc. bot. Centre-Ouest, Nouv. sér., num. spec. 7: 823 (1985)

Synonym: *Diploschistes diacapsis* subsp. *neutrophila* (Clauzade & Cl. Roux) Clauzade & Cl. Roux in Bull. Soc. linn. Provence 40: 110 (1989)

ACKNOWLEDGMENTS

The authors thank the curators of the herbaria of BCN, DUKE, LEB, and SANT, in addition to Claude Roux, for providing material used in this study. Thorsten Lumbsch and Claude Roux are kindly thanked to share with us their extent knowledge about the genus *Diploschistes*. We also thank Jolanta Miadlikowska and Frank Kauff for help with the phylogenetic analyses; José Manuel Blanco for the R scripts; Molly McMullen for the English revision and proofreading; Néstor Hladun for help obtaining digital photos. This study was carried out within the project CGL2007-66734-C03-02 (Spanish government), and the project 'Filogènia molecular de les Teloschistales i Ostropales Phases I and II' (Institut d'Estudis Catalans - Secció Ciències Biològiques), a PhD scholarship (FPU–Formación del Profesorado Universitario, Ministerio de Educación) to SFB, and the Assembling the Fungal Tree of Life (AFTOL) project, supported by NSF Assembling the Tree of Life (ATOL) award DEB-0228668 to FL.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in: Petrov, B.N. & Csaki, F. (eds.), *Proceedings of the 2nd International Symposium on Information Theory.* Budapest: Akademiai Kiado.

Articus, K., Mattsson, J.E., Tibell, L., Grube, M. & Wedin, M. 2002. Ribosomal DNA and β-tubulin data do not support the separation of the lichens *Usnea florida* and *U. subfloridana* as distinct species. *Mycol. Res.* 106: 412–418.

Breuss, O. & Brunnbauer, W. 1997. Flechten aus Sri Lanka. *Ann. Naturhist. Mus. Wien, B* 99: 727–735.

Buschbom, J. & Mueller, G. 2006. Testing “species pair” hypotheses: evolutionary processes in the lichen-forming species complex *Porpidia flavocoerulescens* and *Porpidia melinodes*. *Mol. Biol. Evol.* 23: 574–586.

Cannone, J.J., Subramanian, S., Schnare, M.N., Collett, J.R., D’Souza, L.M., Du, Y., Feng, B., Lin, N., Madabusi, L.V., Muller, K.M., Pande, N., Shang, Z., Yu, N. & Gutell, R.R. 2002. The comparative RNA Website (CRW): an online database of comparative sequence and structure information for ribosomal, intron, and other RNA. *BMC Bioinformatics* 3: 2–15.

Clauzade, G. & Roux, C. 1985. Likenoj de Okcidenta Eŭropo. Ilustrita Determinlibro. *Bull. Soc. Bot. Centre-Ouest*, *Numéro Special* 7: 1–893.

Clauzade, G. & Roux, C. 1989. Likenoj de Okcidenta Eŭropo. Suplemento 3a. *Bull. Soc. Bot. Linn. Provence* 40: 73–110.

Cubero, O., Esslinger, T.L., Crespo, A. & Lumbsch, H.T. 2004. Molecular phylogeny of the lichen genus *Physconia* (Ascomycota, Lecanorales) inferred from a Bayesian analysis of nuclear ITS rDNA. *Mycol. Res.* 108: 489–498.

Culberson, C.F., Culberson, W.L. & Johnson, A. 1977. *Second supplement to Chemical and Botanical Guide to Lichen Products*. St. Louis: American Bryological and Lichenologial Society.

Elix, J.A. & Lumbsch, H.T. 2005. Additional lichen records from Australia 55, *Diploschistes conceptionis. Australas. Lichenol.* 56: 8–9.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

Fernández-Brime, S., Llimona, X., Molnar, K., Stenroos, S., Högnabba, F., Björk, C., Lutzoni, F. & Gaya, E. 2011. Expansion of the Stictidaceae by the addition of the saxicolous lichen-forming genus *Ingvariella*. *Mycologia* 103: 755–763.

Frisch, A., Kalb, K. & Grube, M. 2006. Contributions towards a new systematics of the lichen family Thelotremataceae. *Biblioth. Lichenol.* 92: 1–556.

Gardes, M. & Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes: application to the identification of mycorrhizae and rusts. *Mol. Ecol.* 2: 113–118.

Gaya, E., Lutzoni, F., Zoller, S. & Navarro-Rosinés, P. 2003. Phylogenetic study of *Fulgensia* and allied *Caloplaca* and *Xanthoria* species (Teloschistaceae, lichen-forming ascomycota). *Am. J. Bot.* 90:1095–1103.

Gaya, E., Navarro-Rosinés, P., Llimona, X., Hladun, N. & Lutzoni, F. 2008. Phylogenetic reassessment of the Teloschistaceae (lichen-forming Ascomycota, Lecanoromycetes). *Mycol. Res.* 112: 528–546.

Gaya, E., Redelings, B.D., Navarro-Rosinés, P., Llimona, X., De Cáceres, M. & Lutzoni, F. 2011. Align, or not to align? Resolving species complexes within the *Caloplaca saxicola* group as a case study. *Mycologia* 103: 361–378.

Grube, M. & Kroken, S. 2000. Molecular approaches and the concept of species and species complexes in lichenized fungi. *Mycol. Res.* 104: 1284–1294.

Guderley, R. & Lumbsch, H.T. 1996. The lichen genus *Diploschistes* in South Africa (Thelotremataceae). *Mycotaxon* 58: 269–292.

Gueidan, C., Roux, C. & Lutzoni, F. 2007. Using a multigene phylogenetic analysis to assess generic delineation and character evolution in Verrucariaceae (Eurotiomycetes, Ascomycota). *Mycol. Res.* 111: 1145–1168.

Guindon, S. & Gascuel, O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst. Biol.* 52: 696–704.

Hale, M.E. 1980. Generic delimitation in the lichen family Thelotremataceae. *Mycotaxon* 11: 130–138.

Hale, M.E. 1981. A revision of the lichen family Thelotremataceae in Sri Lanka. *Bull. Br. Mus. (Nat. Hist.) Bot.* 8: 227–332.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/*NT. Nucleic Acids Symp. Ser.* 41: 95–98.

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.

James, P.W. & Hawksworth, D.L. 2009. *Thelotrema*. Pp. 891–893 in: Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. (eds.). *The Lichens of Great Britain and Ireland*. London: British Lichen Society.

Kauff, F., Miadlikowska, J. & Lutzoni, F. 2003. Arc – a program for ambiguous region coding. v.1.5. Duke University, Durham.

Kirk, P.M., Cannon, P.F., David, J.C. & Stalpers, J.A. (eds.). 2008. *Ainsworth & Bisby's Dictionary of the Fungi*, 10th ed. Wallingford: CAB International.

Kjer, K.M. 1995. Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from frogs. *Mol. Phylogenet. Evol.* 4: 314–330.

Kornerup, A. & Wanscher, J.H. 1981. *Taschenlexikon der Farben* 3rd ed. Göttingen: Muster-Schmidt Verlag.

Lee, S.B., Milgroom, M.G. & Taylor, J.W. 1988. A rapid, high yield mini-prep method for isolation of total genomic DNA from fungi. *Fungal. Genet. Newsl.* 35: 23–24.

Lettau, G. (1932–1937). Monographische Bearbeitung einiger Flechtenfamilien. Beihefte, *Repertorium Speciei Novi Regni Vegetale* 135: 5–194.

Lumbsch, H.T. 1985. The lichen genus *Diploschistes* in the southern Hemisphere. *DSIR Bot. Div. Newsl., Suppl.* 2: 9–10.

Lumbsch, H.T. 1989. Die holarktischen Vertreter der Flechtengattung *Diploschistes* (Thelotremataceae). *J. Hattori Bot. Lab.* 66: 133–196.

Lumbsch, H.T. 1993. Studien über die Flechtengattung *Diploschistes* I. *Nova Hedwigia* 56: 227–236.

Lumbsch, H.T. 2002. How objective are genera in euascomycetes? *Perspectives in Plant Ecology, Evolution and Systematics* 5: 91–101.

Lumbsch, H.T. & Aptroot, A. 1993. Studien über die Flechtengattung *Diploschistes* II. *Nova Hedwigia* 56: 237–239.

Lumbsch, H.T. & Elix, J.A. 1985. A new species of the lichen genus *Diploschistes* from Australia. *Pl. Syst. Evol.* 150: 237–239.

Lumbsch, H.T. & Elix, J.A. 1989. Taxonomy of some *Diploschistes* spp. (lichenized ascomycetes, Thelotremataceae) containing gyrophoric acid. *Pl. Syst. Evol.* 167: 195–199.

Lumbsch, H.T. & Elix, J.A. 2003. The lichen genus *Diploschistes* (Thelotremataceae) in Australia. *Biblioth. Lichenol.* 86: 119–128.

Lumbsch, H.T., Feige, G.B. & Egea, J.M. 1993. Two lichens new to Europe. *Lichenologist* 25: 303–306.

Lumbsch, H.T. & Mangold, A. 2007. *Diploschistes elixii* (Ostropales: Thelotremataceae), an overlooked terricolous species from Western Australia. *Lichenologist* 39: 459–462.

Lumbsch, H.T. & Tehler, A. 1998. A cladistic study of the genus *Diploschistes* (Ascomycotina, Thelotremataceae). *Bryologist* 101: 398–403.

Lutzoni, F. & Brodo, I.M. 1995. A Generic Redelimitation of the *Ionaspis*-*Hymenelia* Complex (Lichenized Ascomycotina). *Syst. Bot.* 20: 224–258.

Lutzoni, F. & Vilgalys, R. 1995. Integration of morphological and molecular datasets in estimating fungal phylogenies. *Canad. J. Bot.* 73 (Suppl. 1): S649–S659.

Lutzoni, F., Wagner, P., Reeb, V. & Zoller, S. 2000. Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. *Syst. Biol.* 49: 628–651.

Maddison, W.P. & Maddison, D.R. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.6. http://mesquiteproject.org.

Mangold, A., Elix J.A. & Lumbsch, H.T. 2009. Thelotremataceae. Pp. 195–420 in: McCarthy, P.M. (ed.), *Flora of Australia*. Canberra and Melbourne: ABSR and CSIRO Publishing.

Mangold, A., Martín, M.P., Lücking, R. & Lumbsch, H.T. 2008. Molecular phylogeny suggests synonymy of Thelotremataceae within Graphidaceae (Ascomycota: Ostropales). *Taxon* 57: 476–486.

Martín, M.P., LaGreca, S. & Lumbsch, H.T. 2003. Molecular phylogeny of *Diploschistes* inferred from ITS sequence data. *Lichenologist* 35: 27–32.

Mason-Gamer, R.J. & Kellogg, E.A. 1996. Testing for phylogenetic conflict among molecular datasets in the tribe Triticiae (Gramineae). *Syst. Biol.* 45: 524–545.

Massalongo, A.B. 1852. *Ricerche sull'autonomia dei licheni crostosi.* Verona: A. Friziero.

McDonald, T., Miadlikowska, J. & Lutzoni, F. 2003. The lichen genus *Sticta* in the Great Smoky Mountains: a phylogenetic study of morphological, chemical, and molecular data. *Bryologist* 106: 61–79.

Miadlikowska, J. & Lutzoni, F. 2000. Phylogenetic revision of the genus *Peltigera* (lichen-forming ascomycetes) based on morphological, chemical and large subunit nuclear ribosomal DNA data. *Int. J. Pl. Sci.* 161: 925–958.

Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Pant, G. & Upreti, D.K. 1993. The lichen genus *Diploschistes* in India and Nepal. *Lichenologist* 25: 33–50.

Poelt, J. 1969. Bestimmungsschlüssel europäischer flechten. Lehre: J. Cramer.

Poelt, J. 1970. Das Konzept der Artenpaare bei den Flechten. *Vorträge aus dem Gesamtgebiet der Botanik, Neue Folge* **4**: 187–198.

Posada, D. 2003. Using Modeltest and PAUP* to select a model of nucleotide substitution. Pp. 6.5.1–6.5.14 in; Baxevanis, A.D., Davison, D.B., Page, R.D.M., Petsko, G.A., Stein, L.D. & Stormo, G.D. (eds.), *Current Protocols in Bioinformatics*. New York: John Wiley & Sons, Inc.

Posada, D. 2008. jModelTest: phylogenetic model averaging. *Molec. Biol. Evol.* 25: 1253–1256.

Rambaut, A. & Drummond, A.J. 2007. Tracer v1.4.1 Available from http://beast.bio.ed.ac.uk/Tracer

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R–project.org

Rivas Plata, E., Lücking, R. & Lumbsch, H.T. 2012. A new classification for the family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). *Fung. Diversity.*

Rivas Plata, E. & Lumbsch, H.T. 2011. Parallel evolution and phenotypic divergence in lichenized fungi: A case study in the lichen-forming fungal family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). *Mol. Phylogenet. Evol.* 61: 99–107.

Ronquist, F. & Huelsenbeck, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Sérusiaux, E., Diederich, P., Brand, A.M. & van den Boom, P.P.G. 1999. New or interesting lichens and lichenicolous fungi from Belgium and Luxembourg, VIII. *Lejeunia* 162: 1–95.

Swofford, D.L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony* (** and other methods*). Version 4.0b10. Sunderland, Massachusetts: Sinauer Associates.

Tavaré, S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. Pp 57–86 in: Miura, R.M. (ed.), *Some mathematical questions in biology - DNA sequence analysis*. Providence: Amer. Math. Soc.

Umaña, L. & Sipman, H. 2002. *Líquenes de Costa Rica*. Santo Domingo de Heredia: Edit. INBio.

Vilgalys, R. & Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J. Bacteriol.* 172: 4238–4246.

White, T.J., Bruns, T., Lee, S. & Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J., & White, T.J. (eds.), *PCR protocols: a guide to methods and applications*. New York: Academic Press, Inc.

Zharkikh, A. 1994. Estimation of evolutionary distances between nucleotide sequences. *J. Molec. Evol.* 39: 315–329.

Zoller, S., Scheidegger, C. & Sperisen, C. 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming Ascomycetes. *Lichenologist* 31: 511–516.

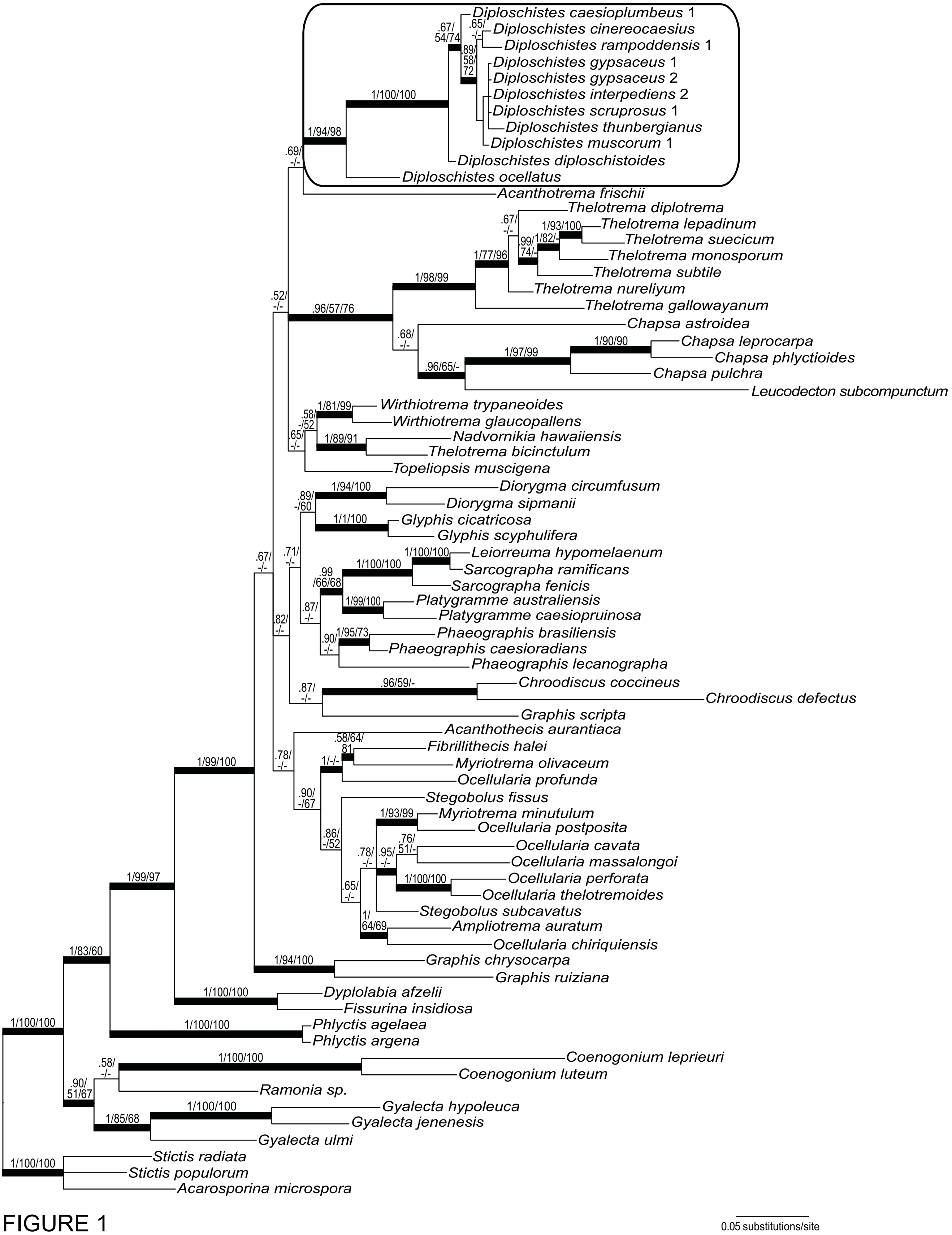
Zwickl, D.J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin.

Figure legends

Figure 1. Bayesian inference resulting from a 50% majority-rule consensus of 90,000 sampled trees based on combined mtSSU and nuLSU sequences, depicting phylogenetic relationships among 61 taxa from the Graphidaceae, and 11 species from the Ostropales (i.e., Coenogoniaceae, Gyalectaceae, Phlyctidaceae, Stictidaceae) used as outgroup taxa. Support values above branches are indicated as MB1PP/ML1BS/MP1BS. Thicker internodes show significant support for at least one statistical method ($PP \geq 0.95$, MLBS and $MPBS \geq 70\%$).

Figure 2. Strict consensus tree of 152 equally most parsimonious trees based on combined nuITS, mtSSU, and morphological-chemical data of *Diploschistes* taxa. Parsimony bootstrap percentages (BS) greater than 50% are shown above branches. Highly supported branches ($BS \geq 70\%$) are indicated by bold lines.

Figure 3. Morphological and anatomical characters of the thallus of *Diploschistes candidissimus* (subgenus *Limborina*), *D. scruposus* (subgenus *Diploschistes*), and *D. ocellatus* (subgenus *Thorstenia*). **A-C**, *Diploschistes candidissimus* (BCN-Lich 19340): **A**, habit; **B**, protocortex formed by loosely organized hyphae (arrows); **C**, dark granules incrusted in the hyphae walls (arrows); **D-F**, *Diploschistes scruposus* (BCN-Lich 19328): **D**, habit; **E**, epinecral layer containing remnants of hyphae (arrows); **F**, dark pigmentation distributed on the epinecral layer (arrows); **G-I**, *Diploschistes ocellatus* (BCN-Lich 19341): **G**, habit; **H**, cortex formed by dense, anticlinally organized hyphae (arrows); **I**, dark pigmentation located on top of the protocortex, not embedded on the hyphal walls (arrows). EL: epinecral layer; PL: photobiont layer.



Diploschistes caesioplumbeus 1
.65/ -/-
Diploschistes cinereocaesius
.67/ 54/74
Diploschistes rampoddensis 1
.89/ 58/ 72
Diploschistes gypsaceus 1
Diploschistes gypsaceus 2
1/100/100
Diploschistes interpediens 2
Diploschistes scruprosus 1
Diploschistes thunbergianus
1/94/98
Diploschistes muscorum 1
.69/ -/-
Diploschistes diploschistoides
Diploschistes ocellatus
Acanthotrema frischii
Thelotrema diplotrema
.67/ -/-
1/93/100
Thelotrema lepadinum
.99/ 74/-
1/82/-
Thelotrema suecicum
Thelotrema monosporum
1/77/96
Thelotrema subtile
1/98/99
Thelotrema nureliyum
.52/ -/-
.96/57/76
Thelotrema gallowayanum
Chapsa astroidea
.68/ -/-
1/90/90
Chapsa leprocarpa
1/97/99
Chapsa phlyctioides
.96/65/-
Chapsa pulchra
Leucodecton subcompunctum
1/81/99
Wirthiotrema trypaneoides
.58/ -/52
Wirthiotrema glaucopallens
.65/ -/-
1/89/91
Nadvornikia hawaiiensis
Thelotrema bicinctulum
Topeliopsis muscigena
1/94/100
Diorygma circumfusum
.89/ -/60
Diorygma sipmanii
1/1/100
Glyphis cicatricosa
Glyphis scyphulifera
.71/ -/-
1/100/100
Leiorreuma hypomelaenum
1/100/100
Sarcographa ramificans
.67/ -/-
.99 /66/68
Sarcographa fenicis
1/99/100
Platygramme australiensis
.87/ -/-
Platygramme caesiopruinosa
.82/ -/-
1/95/73
Phaeographis brasiliensis
.90/ -/-
Phaeographis caesioradians
Phaeographis lecanographa
.87/ -/-
.96/59/-
Chroodiscus coccineus
Chroodiscus defectus
Graphis scripta
Acanthothecis aurantiaca
.58/64/ 81
Fibrillithecis halei
1/99/100
.78/ -/-
1/-/-
Myriotrema olivaceum
Ocellularia profunda
.90/ -/67
Stegobolus fissus
1/93/99
Myriotrema minutulum
.86/ -/52
Ocellularia postposita
.76/ 51/-
Ocellularia cavata
.78/ -/-
.95/ -/-
Ocellularia massalongoi
1/99/97
1/100/100
Ocellularia perforata
.65/ -/-
Ocellularia thelotremoides
Stegobolus subcavatus
1/ 64/69
Ampliotrema auratum
Ocellularia chiriquiensis
1/83/60
1/94/100
Graphis chrysocarpa
Graphis ruiziana
1/100/100
Dyplolabia afzelii
Fissurina insidiosa
1/100/100
1/100/100
Phlyctis agelaea
Phlyctis argena
.58/ -/-
1/100/100
Coenogonium leprieuri
Coenogonium luteum
.90/ 51/67
Ramonia sp.
1/100/100
Gyalecta hypoleuca
1/85/68
Gyalecta jenenesis
Gyalecta ulmi
1/100/100
Stictis radiata
Stictis populorum
Acarosporina microspora
0.05 substitutions/site

FIGURE 1

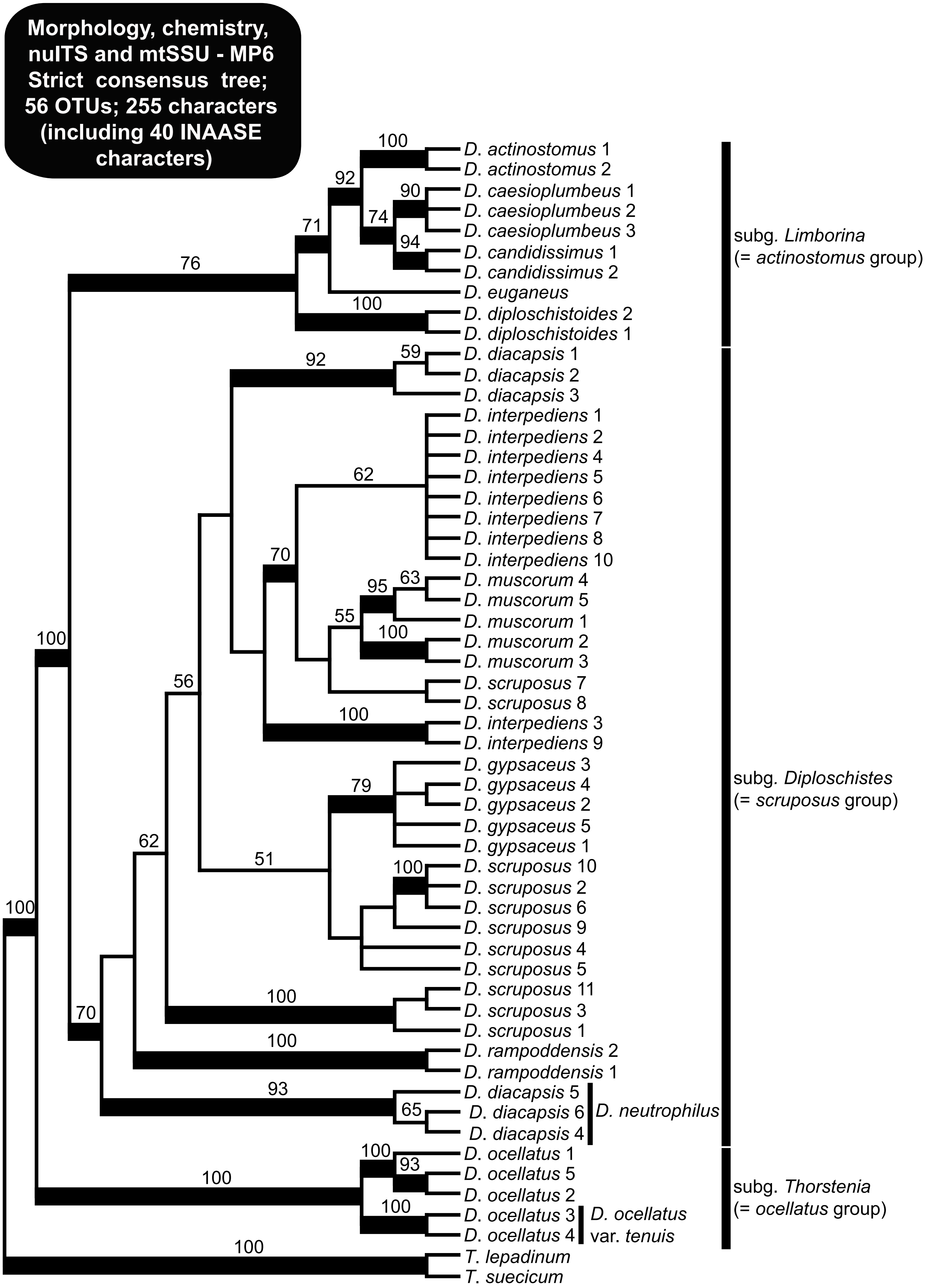
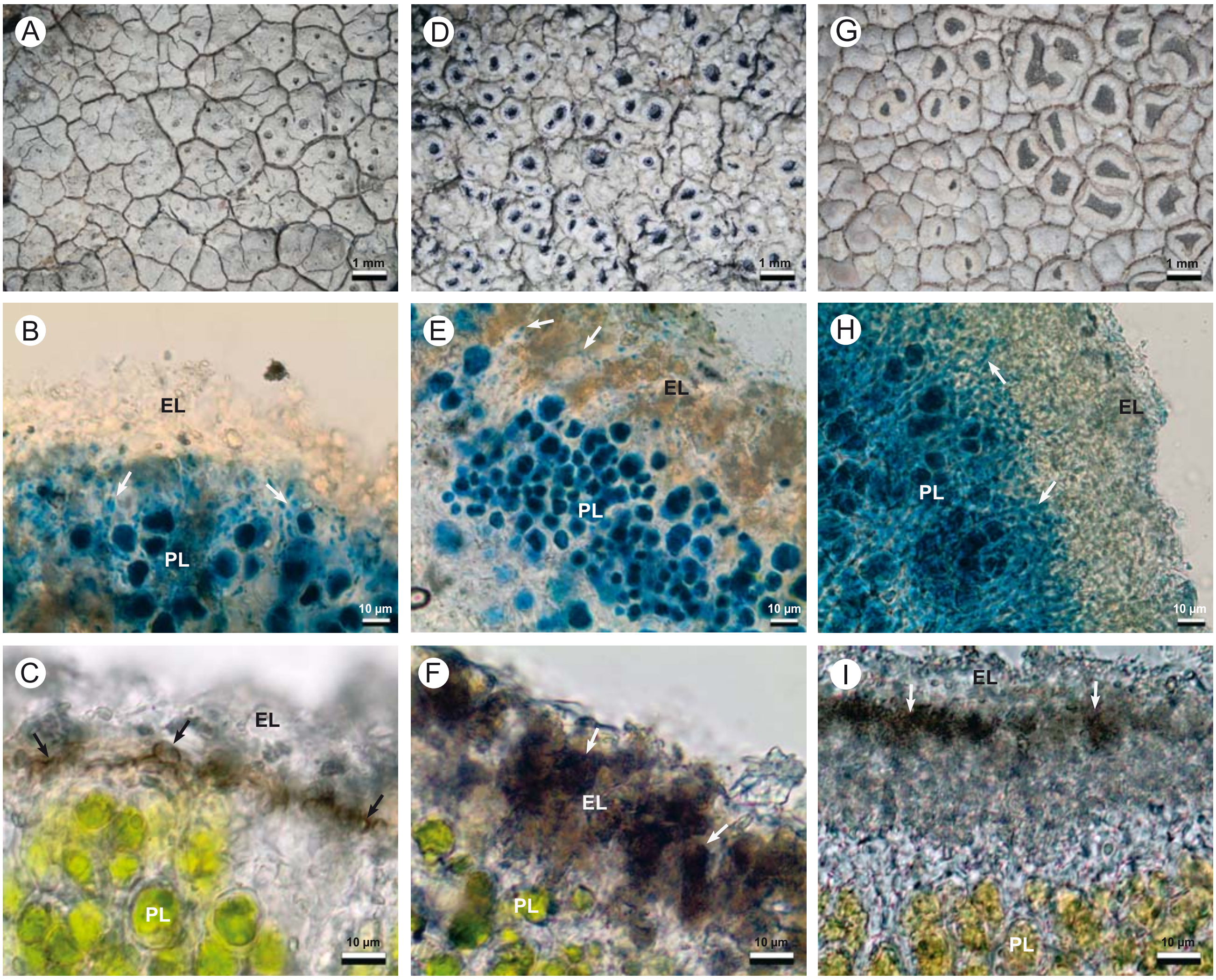

Morphology, chemistry, nuITS and mtSSU - MP6 Strict consensus tree; 56 OTUs; 255 characters (including 40 INAASE characters)
100
92
71
76
90
74
94
100
D. actinostomus 1
D. actinostomus 2
D. caesioplumbeus 1
D. caesioplumbeus 2
D. caesioplumbeus 3
D. candidissimus 1
D. candidissimus 2
D. euganeus
D. diploschistoides 2
D. diploschistoides 1
subg. *Limborina* (= *actinostomus* group)
92
59
D. diacapsis 1
D. diacapsis 2
D. diacapsis 3
62
D. interpediens 1
D. interpediens 2
D. interpediens 4
D. interpediens 5
D. interpediens 6
D. interpediens 7
D. interpediens 8
D. interpediens 10
70
95
63
55
100
D. muscorum 4
D. muscorum 5
D. muscorum 1
D. muscorum 2
D. muscorum 3
D. scruposus 7
D. scruposus 8
100
D. interpediens 3
D. interpediens 9
100
56
79
D. gypsaceus 3
D. gypsaceus 4
D. gypsaceus 2
D. gypsaceus 5
D. gypsaceus 1
51
100
D. scruposus 10
D. scruposus 2
D. scruposus 6
D. scruposus 9
D. scruposus 4
D. scruposus 5
subg. *Diploschistes* (= *scruposus* group)
62
100
D. scruposus 11
D. scruposus 3
D. scruposus 1
70
100
D. rampoddensis 2
D. rampoddensis 1
93
65
D. diacapsis 5
D. diacapsis 6
D. diacapsis 4
D. neutrophilus
100
100
100
93
100
D. ocellatus 1
D. ocellatus 5
D. ocellatus 2
D. ocellatus 3
D. ocellatus 4
D. ocellatus var. *tenuis*
subg. *Thorstenia* (= *ocellatus* group)
100
T. lepadinum
T. suecicum

FIGURE 2


A
1 mm
D
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G
1 mm
B
EL
PL
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E
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PL
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H
EL
PL
10 µm
C
EL
PL
10 µm
F
EL
PL
10 µm
I
EL
PL
10 µm

FIGURE 3

Appendix 1. List of sequences used in the phylogenetic analyses. Voucher information and GenBank accession numbers are provided for specimens newly sequenced for this study, whereas GenBank ID numbers are provided for sequences retrieved directly from GenBank.

Species, voucher information (geographic origin, collector, herbarium), nuITS, mtSSU, nuLSU
Acanthothecis aurantiaca* (Müll. Arg.) Staiger & Kalb**: —, 90995142, 90995106; ***Acanthotrema frischii* Lücking** [as ***A. brasilianum* (Hale) A. Frisch** in GenBank]: —, 110585750, 90995105; ***Acarosporina microspora* (R.W. Davidson & R.C. Lorenz) Sherwood**: —, 46411377, 46411432; ***Ampliotrema auratum* (Tuck.) Kalb ex Kalb**: —, 156739879, 156739928; ***Chapsa astroidea* (Berk. & Broome) Cáceres & Lücking**: —, 156739881, 156739929; ***Chapsa leprocarpa* (Nyl.) Frisch**: —, 156739883, 156739930; ***Chapsa phlyctioides* (Müll. Arg.) Mangold**: —, 156739884, 156739932; ***Chapsa pulchra* (Müll. Arg.) Mangold**: —, 156739886, 156739934; ***Chroodiscus coccineus* (Leight.) Müll. Arg.**: —, 110585749, 19171976; ***Chroodiscus defectus* Papong & Lücking**: —, 224797138, 224797131; ***Coenogonium leprieurii* (Mont.) Nyl.**: —, 46411453, 19171977; ***Dimerella lutea* (Dicks.) Trevis.**: —, 46411454, 12025070; ***Diorygma circumfusum* (Stirt.) Kalb, Staiger & Elix**: —, 90995140, 55139914; ***Diorygma sipmanii* Kalb, Staiger & Elix**: —, 90995138, 55139915; ***Diploschistes actinostomus* (Ach.) Zahlbr.**: (1) USA, *Yahr 4569* (DUKE 0016461), XXX, XXX, —; (2) [as ***D. scruposus in GenBank] USA, AFTOL ID-98,

336397129, 46411447, —; ***Diploschistes caesioplumbeus* (Nyl.) Vain.**: (1) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 17182), XXX, 330369529, 330369540; (2) Spain, *Llimona & Fernández-Brime 101* (BCN-Lich 19323), XXX, XXX, —; (3) Spain, *Llimona s.n.* (BCN-Lich 19325), XXX, XXX, —; ***Diploschistes candidissimus* (Kremp.) Zahlbr.**: (1) USA, *Worthington 23741* (DUKE 0144447), XXX, XXX, —; (2) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19340), XXX, XXX, —; ***Diploschistes cinereocaesius* (Sw.) Vain.**: —, 119642420, 113958939; ***Diploschistes diacapsis* (Ach.) Lumbsch**: (1) Spain, *Yahr 2431a* (DUKE 0030912), XXX, XXX, —; (2) USA, *Nash III 44742* (DUKE 0130126), XXX, XXX, —; (3) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19347), XXX, XXX, —; ***Diploschistes diploschistoides* (Vain.) G. Salisb.**: (1) Australia, *Elix 27941 & al.* (DUKE 0144445), XXX, XXX, 47525220; (2) Australia, *Lumbsch & Guderley 11115n* (DUKE 0018863), XXX, XXX, —; ***Diploschistes euganeus* (A. Massal.) Zahlbr.**: Australia, *Lumbsch 5524b* (DUKE 01444451), XXX, XXX, —; ***Diploschistes gypsaceus* (Ach.) Zahlbr.**: (1) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 17180), XXX , 330369530, 330369541; (2) Spain, *Llimona s.n.* (BCN-Lich 19324), XXX, XXX, —; (3) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19345), XXX, XXX, —; (4) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19346), XXX, XXX, XXX; (5) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19340), XXX, XXX, —; ***Diploschistes interpediens* (Nyl.) Zahlbr.**: (1) Portugal, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19317), XXX, XXX, —; (2) Spain, *Llimona & Hladun s.n.* (BCN-Lich 19319), XXX, XXX, XXX; (3) Spain, *Llimona & Paz-Bermúdez s.n.* (BCN-Lich

18007), XXX, XXX, —; (4) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19350), XXX, XXX, —; (5) Spain, *Gómez-Bolea & Figueras s.n.* (BCN-Lich 14751), XXX, XXX, —; (6) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19355), XXX, XXX, —; (7) Spain, *Fernández-Brime s.n.* (BCN-Lich 19335), XXX, XXX, —; (8) Spain, *Paz-Bermúdez s.n.* (SANT 10820); (9) Spain, *Hladun & Muñiz s.n.* (BCN-Lich 14104); (10) France, *Llimona s.n.* (BCN-Lich 19322), XXX, XXX, —; ***Diploschistes muscorum*** **(Scop.) R. Sant.**: (1) USA, *Yahr 4500* (DUKE 0016462), XXX, XXX, XXX; (2) Italy, *Fernández-Brime s.n.* (BCN-Lich 19333), XXX, XXX, —; (3) Spain, *Hladun & Muñiz s.n.* (BCN-Lich 14435), XXX, XXX, —; (4) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19344), XXX, XXX, —; 5. Spain. *Fernández-Brime s.n.* (BCN-Lich 19334), XXX, XXX, —; ***Diploschistes ocellatus*** **(Fr.) Norman**: (1) Spain, *Yahr 2475a* (DUKE 0030907) XXX, XXX, —; (2) Australia, *Lumbsch 10734c & Curnow* (DUKE 0144450), XXX, XXX, —; (5) Spain, Terrón s.n. (LEB 6251), XXX, XXX, —; ***Diploschistes ocellatus*** **var. *tenuis* Fdez.-Brime & Llimona *ad int.***: (1) [as ***D. ocellatus*** 3] Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19341), XXX, XXX, —; (2) [as ***D***. ***ocellatus*** 4] Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 17181); XXX, 330369531, 330369542; ***D. neutrophilus*** **(Clauzade & Cl. Roux) Fdez.-Brime & Llimona *ad int.***: (1) [as ***D***. ***diacapsis*** 4] Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19329), XXX, XXX, —; (2) [as ***D***. ***diacapsis*** 5] Spain, *Llimona s.n.* (BCN-Lich 19329), XXX, XXX, —; (3) [as ***D***. ***diacapsis*** 6] Spain, *Llimona s.n.* (BCN-Lich 19338), XXX, XXX, —; ***Diploschistes rampoddensis*** **(Nyl.) Zahlbr.**: (1) —, 20334361, 8926416 (2) Spain, *Llimona*, *Hladun & Muñiz s.n.* (BCN-Lich. 18009), XXX, XXX, —; (3) Spain, *Llimona & Hladun s.n.* (BCN-Lich. 18011), XXX, XXX, —; ***Diploschistes scruposus* (Schreb.) Norman**: (1) Spain, *Llimona s.n.* (BCN-Lich 19328) XXX, XXX, XXX; (2) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19351), XXX, XXX, —; (3) Spain, *Llimona s.n.* (BCN-Lich 14227) XXX, XXX, —; (4) Spain. *Llimona & Hladun s.n.* (BCN-Lich 19326), XXX, XXX, —; (5) Spain, *Llimona s.n.* (BCN-Lich 19316), XXX, XXX, —; (6) Spain, *Llimona & Fernández-Brime 533* (BCN-Lich 19327), XXX, XXX, —; (7) Spain, *Hladun & Muñiz s.n.* (BCN-Lich 14398), XXX, XXX, —; (8) Spain, *Llimona & Fernández-Brime s.n.* (BCN-Lich 19354), XXX, XXX, —; (9) Spain, *Llimona s.n.* (BCN-Lich 19302), XXX, XXX, —; (10) *Llimona & Fernández-Brime s.n.* (BCN-Lich 19336), XXX, XXX, —; (11) *Llimona & Fernández-Brime s.n.* (BCN-Lich 19337), XXX, XXX, —; ***Diploschistes thunbergianus* (Ach.) Lumbsch & Vězda**: —, 20334362, 8926417; ***Dyplolabia afzelii* (Ach.) A. Massal.**: —, 90995126, 90995099; ***Fibrillithecis gibbosa* (H. Magn.) Rivas Plata & Lücking** [as ***Myriotrema halei* (Tuck. & Mont.) Hale**) in GenBank]: —, 156739888, 156739936; ***Fissurina insidiosa* C. Knight & Mitt.**: —, 123979266, 123979316; ***Glyphis cicatricosa* Ach.**: —,55831959, 55139920; ***Glyphis scyphulifera* (Ach.) Staiger**: —, 90995133, 55139922; ***Graphis chrysocarpa* (Raddi) Spreng.**:—, 90995164, 19171983; ***Graphis ruiziana* (Fée) A. Massal.**: —, 90995162, 90995122; ***Graphis scripta* (L.) Ach.**: —, 110585705, 62005329; ***Gyalecta hypoleuca* (Ach.) Zahlbr.**: —, 336397124, 19171988; ***Gyalecta jenensis* (Batsch) Zahlbr.**: —, 46411460, 12025074; ***Gyalecta ulmi* (Sw.) Zahlbr.**: —, 46411461, 18481692; ***Leiorreuma hypomelaenum***

(Müll. Arg.) Staiger: —, 90995148, 90995110; ***Leucodecton subcompunctum* (Nyl.) Frisch**: —, 156739890, 156739938; ***Myriotrema minutulum* (Hale) Hale**: —, AFTOL2096, AFTOL2096; ***Myriotrema olivaceum* Fée**: —, 110585734, 156739942; ***Nadvornikia hawaiiensis* (Tuck.) Tibell**: —, 156739896, 47525224; ***Ocellularia cavata* (Ach.) Müll. Arg.**: —, 110585713, 90995112; ***Ocellularia chiriquiensis* (Hale) Hale**: —, 156739897, 156739944; ***Ocellularia massalongoi* (Mont.) Hale**: —, 156739899, 156739946; ***Ocellularia perforata* (Leight.) Müll. Arg.**: —, 156739902, 156739949; ***Ocellularia postposita* (Nyl.) Frisch**: —, 110585707, 55139903; ***Ocellularia profunda* (Stirt.) Mangold, Elix & Lumbsch**: —, 156739905, 156739951; ***Ocellularia thelotremoides* (Leight.) Zahlbr.**: —, 156739907, 156739953; ***Phaeographis brasiliensis* (A. Massal.) Kalb & Matthes-Leicht**: —, 90995135, 55139917; ***Phaeographis caesioradians* (Leight.) A.W. Archer**: —, 90995145, 55139916; ***Phaeographis lecanographa* (Nyl.) Staiger**: —, 90995160, 90995120; ***Phlyctis agelaea* (Ach.) Flot.**:—, 330369535, 330369536; **Phlyctis argena (Ach.) Flot.**: —, 119514137, 119513981; ***Platygramme australiensis* Staiger**: —, 90995147, 55139919; ***Platygramme caesiopruinosa* (Fée) Fée**: —, 90995150, 55139918; ***Ramonia* sp.**: —, 32141094, 37960830; ***Sarcographa fenicis* (Vain.) Zahlbr.**: —, 90995144, 90995108; ***Sarcographa ramificans* (Kremp.) Staiger**: —, 90995158, 90995119; ***Stegobolus fissus* (Nyl.) Frisch**: —, 156739909, 156739955; ***Stegobolus subcavatus* (Nyl.) Frisch**: —, 156739910, 156739956; ***Stictis populorum* (Gilenstam) Gilenstam**: —, 34148564, 48995464; ***Stictis radiata* (L.) Pers.**: —, 46411482, 15216674; ***Thelotrema bicinctulum* Nyl.**: —, 156739913, 156739957;

***Thelotrema diplotrema* Nyl.**: —, 156739914, 156739958; ***Thelotrema gallowayanum* Mangold, Elix & Lumbsch**: —, 156739915, 156739968; ***Thelotrema glaucopallens* Nyl.**: —, 110585740, 47525213; ***Thelotrema lepadinum* (Ach.) Ach.**: (1) —, 32141089, 37960825; (2) 336397130, 123979268, —; ***Thelotrema* monosporum Nyl.**: —, 156739916, 156739961; ***Thelotrema nureliyum* Hale**: —, 156739919, 156739964; ***Thelotrema subtile* Tuck.**:—, 156739922, 156739966; ***Thelotrema suecicum* (H. Magn.) P. James**: (1) —, 32141090; 37960826; (2) 45720761, 189039350, —; ***Topeliopsis muscigena* (Stizenb.) Kalb**: —, 156739926, 156739971; ***Wirthiotrema trypaneoides* (Nyl.) Rivas Plata & Lücking** [as ***Myriotrema trypaneoides* (Nyl.) Hale** in GenBank]: —, 156739895, 156739943.

— Sequence missing

Supplementary table and figure legends

Figure S1. Conversion of continuous characters to discrete. Box plots representing 12 continuous characters included in the morphological-chemical data matrix for 12 species of *Diploschistes* and two outgroup taxa. The central line within the box is the median, the boxed areas represent 50 % of the sample and the vertical lines represent the whole sample. Species whose distribution for a given character did not differ significantly according to the Tukey's HSD test were given multiple characters states, shown in the upper side of each plot. A. Thallus thickness (Table S1; char. 6); B. Epinecral layer thickness (Table S1; char. 8); C. Ascoma diameter (Table S1; char. 11); D. Hymenium thickness (Table S1; char. 15); E. Ascus length (Table S1; char. 16); F. Ascus width (Table S1; char. 17); G. Ascospore length (Table S1; char. 19); H. Ascospore width (Table S1; char. 20); I. Ascospore shape (Length/Width ratio) (Table S1; char. 21); J. Number of transverse septa (Table 1; char. 22); K. Number of longitudinal septa (Table S1; char. 23); L. Number of locules per ascospore (Table S1; char. 24).

Table S1. List of the ecological (1), morphological (2–25), and chemical (26–32) characters selected for the phylogenetic analyses of 56 taxa and their states. Characters excluded for being uninformative are marked with an asterisk. The numbers within parenthesis following colors correspond to the codes in Kornerup & Wanscher (1981).

Table S2. Data matrix for ecological (1), morphological (2–25), and chemical (26–32) characters. Continuous characters for specimens within each taxon were scored identically. Characters and character states are described in Table S1. ? = character state unknown. For certain characters, some specimens were assigned multiple character states because they were polymorphic and were analyzed as such: A = 0&1; B = 1&2; C = 2&7. Polymorphisms were analyzed using the Variable option in PAUP*.

Figure S2. Phylogenetic relationships among 54 individuals of *Diploschistes* and two outgroup species, using maximum parsimony as the optimization criterion. Strict consensus tree of 58,700 equally most parsimonious trees based on morphological-chemical data alone (MP2). Parsimony bootstrap percentages (BS) greater than 50% are shown above branches. Highly supported internodes (MPBS ≥ 70%) are indicated by bold lines.

Figure S3. Phylogenetic relationships among 54 individuals of *Diploschistes* and two outgroup species, using maximum parsimony as the optimization criterion. Strict consensus tree of six equally most parsimonious trees based on nuITS alone (MP3). Parsimony bootstrap percentages (BS) greater than 50% are shown above branches. Highly supported internodes (MPBS ≥ 70%) are indicated by bold lines.

Figure S4. Phylogenetic relationships among 54 individuals of *Diploschistes* and two outgroup species, using maximum parsimony as the optimization criterion. Strict consensus tree of 90,400 equally most parsimonious trees based on mtSSU alone (MP4). Parsimony bootstrap percentages (BS) greater than 50% are shown above branches. Highly supported internodes (MPBS ≥ 70%) are indicated by bold lines.

Figure S5. Phylogenetic relationships among 54 individuals of *Diploschistes* and two outgroup species, using maximum parsimony as the optimization criterion. Strict consensus tree of 336 equally most parsimonious trees based on the nuITS and mtSSU combined datasets (MP5). Parsimony bootstrap percentages (BS) greater than 50% are shown above branches. Highly supported internodes (MPBS ≥ 70%) are indicated by bold lines.

Figure S6. Phylogenetic relationships among 54 individuals of *Diploschistes* and two outgroup species. using maximum likelihood as the optimization criterion. Support values above branches indicate maximum likelihood support values and posterior probabilities, ordered as ML2BS/MB2PP. Thicker internodes indicate significant support for at least one statistical method (MLBS ≥ 70%, PP ≥ 0.95).

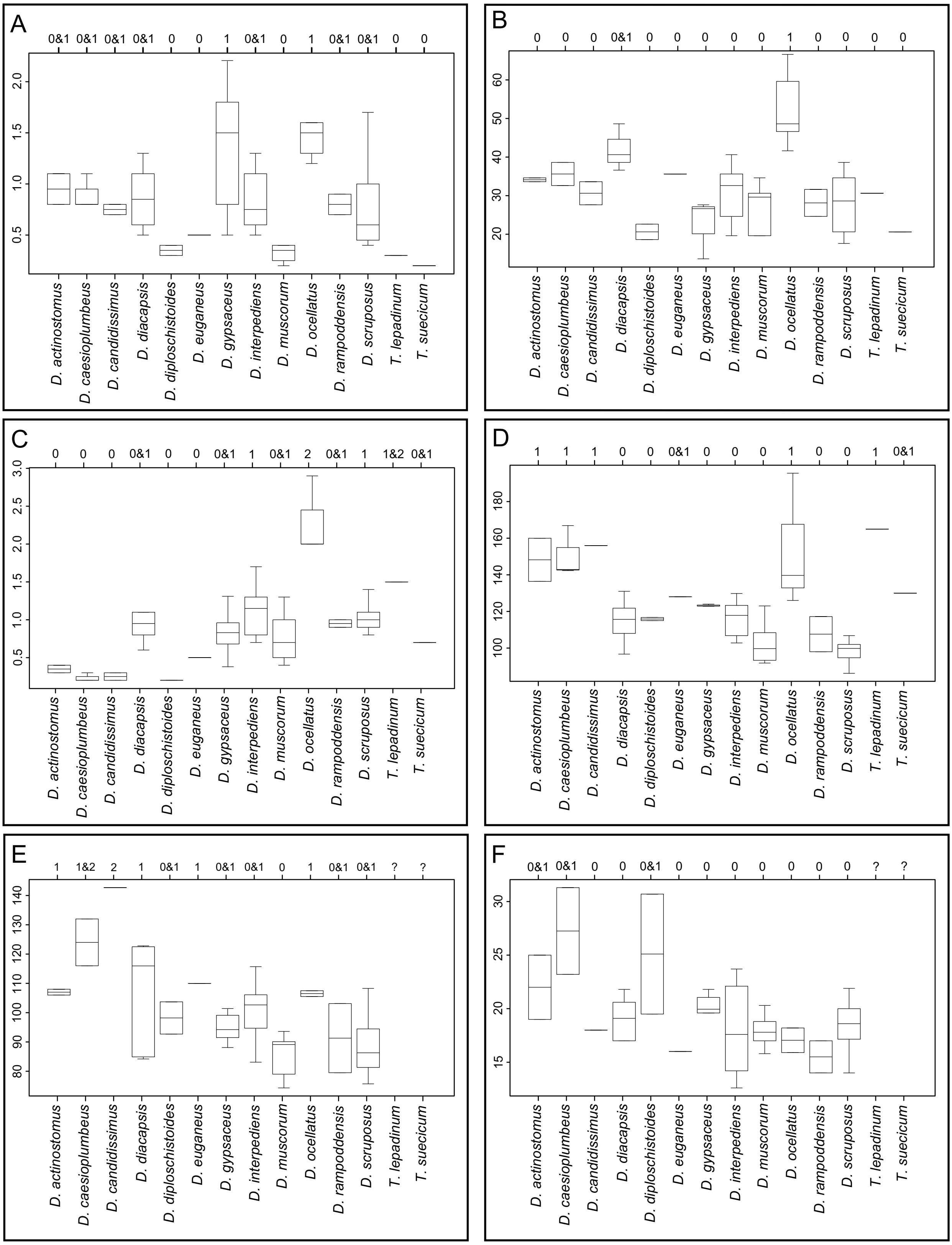
A
0&1 0&1 0&1 0&1 0 0 1 0&1 0 1 0&1 0&1 0 0
0.5 1.0 1.5 2.0
B
0 0 0 0&1 0 0 0 0 0 1 0 0 0 0
20 30 40 50 60
C
0 0 0 0&1 0 0 0&1 1 0&1 2 0&1 1 1&2 0&1
0.5 1.0 1.5 2.0 2.5 3.0
D
1 1 1 0 0 0&1 0 0 0 1 0 0 1 0&1
100 120 140 160 180
E
1 1&2 2 1 0&1 1 0&1 0&1 0 1 0&1 0&1 ? ?
80 90 100 110 120 130 140
F
0&1 0&1 0 0 0&1 0 0 0 0 0 0 0 ? ?
15 20 25 30
D. actinostomus
D. caesioplumbeus
D. candidissimus
D. diacapsis
D. diploschistoides
D. euganeus
D. gypsaceus
D. interpediens
D. muscorum
D. ocellatus
D. rampoddensis
D. scruposus
T. lepadinum
T. suecicum

FIGURE S1 A-F

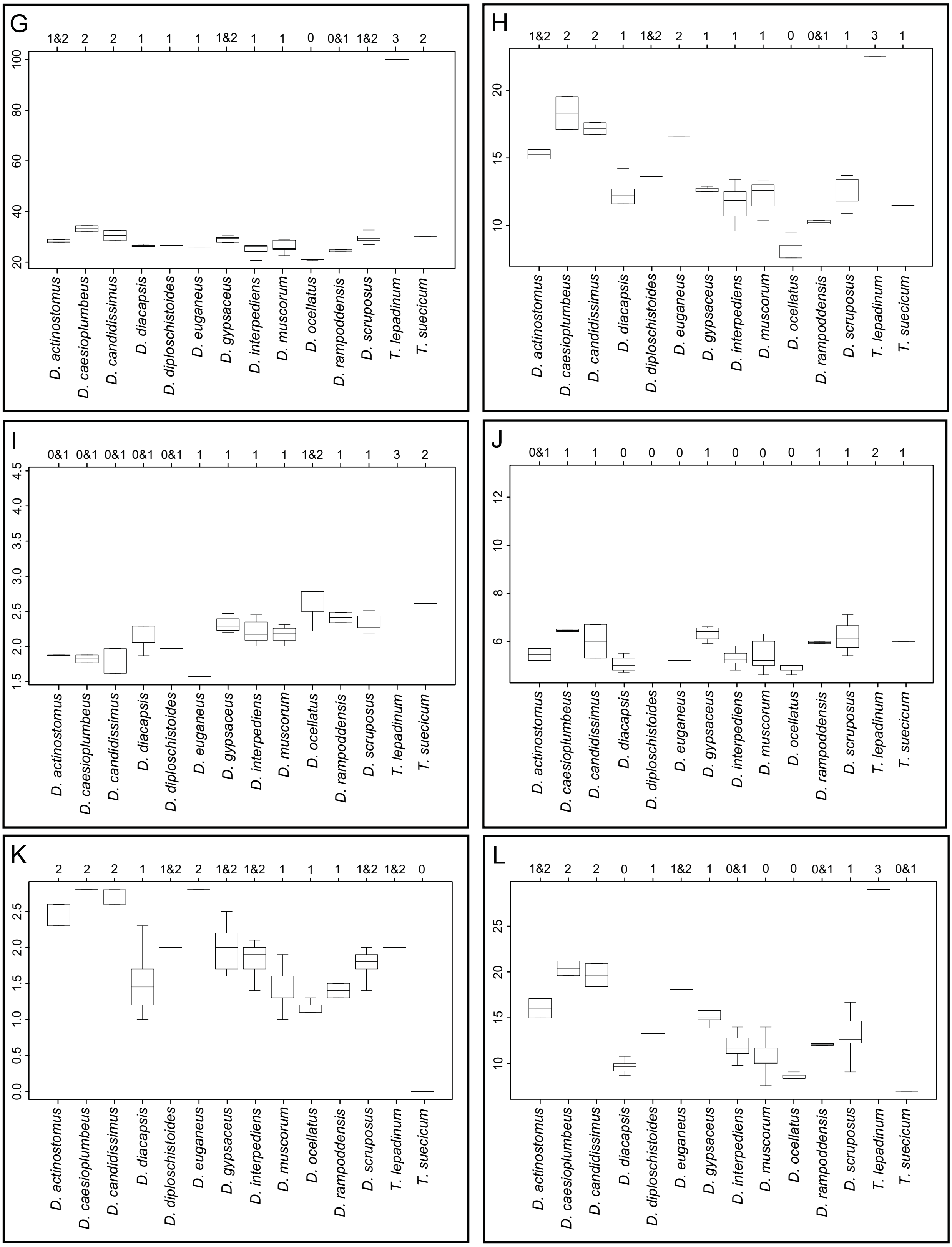
G
1&2 2 2 1 1 1 1&2 1 1 0 0&1 1&2 3 2
20 40 60 80 100
H
1&2 2 2 1 1&2 2 1 1 1 0 0&1 1 3 1
10 15 20
I
0&1 0&1 0&1 0&1 0&1 1 1 1 1 1&2 1 1 3 2
1.5 2.0 2.5 3.0 3.5 4.0 4.5
J
0&1 1 1 0 0 0 1 0 0 0 1 1 2 1
6 8 10 12
K
2 2 2 1 1&2 2 1&2 1&2 1 1 1 1&2 1&2 0
0.0 0.5 1.0 1.5 2.0 2.5
L
1&2 2 2 0 1 1&2 1 0&1 0 0 0&1 1 3 0&1
10 15 20 25
D. actinostomus
D. caesioplumbeus
D. candidissimus
D. diacapsis
D. diploschistoides
D. euganeus
D. gypsaceus
D. interpediens
D. muscorum
D. ocellatus
D. rampoddensis
D. scruposus
T. lepadinum
T. suecicum

FIGURE S1 G-L

Table S1

Character name	Character states	Character name	Character states
1. Substrate type	0: siliceous rock 1: carbonate rock 2: soil 3: lichen/moss 4: bark	16. Ascus length	0: short (75–100 µm) 1: medium (100–125 µm) 2: long (>125 µm)
2. Photobiont type	0: trebouxioid 1: trentepohlioid	17. Ascus width	0: narrow (13–23 µm) 1: wide (>23 µm)
3. Thallus color	0: white (-A1) 1: grayish white (-B1) 2: grayish yellow (2B3) 3: orange grey (5B2) 4: bluish white (22A2, 23A2) 5: bluish gray (23B2, 23D3) 6: greenish white (25A2, 26A2) 7: greenish grey (25B2, 28B2) 8: grayish brown (6D3)	18. Ascospores per ascus	0: 4 spores per ascus 1: 6–8 spores per ascus
4. Pruina on upper surface	0: absent 1: present	19. Ascospore length	0: very short (21–25 µm) 1: short (25–29 µm) 2: long (29–33 µm) 3: very long (<33 µm)
5. Thallus type	0: continuous-rimose 1: rimose-areolate 2: verrucose-areolate	20. Ascospore width	0: very narrow (8–12 µm) 1: narrow (12–16 µm) 2: wide (16–20 µm) 3: very wide (>20 µm)
6. Thallus thickness	0: thin (0.2–0.8 mm) 1: thick (>0.8 mm)	21. Ascospore shape (Length/Width ratio)	0: broadly ellipsoid (1.6–2.1) 1: ellipsoid (2.1–2.8) 2: narrow ellipsoid (2.8–3.5) 3: very narrow (>3.5)
7. Cortical layer type	0: absent 1: cortex 2: protocortex	22. Number of transverse septa	0: 4–6 septa 1: 6–8 septa 2: >8 septa
8. Epinecral layer thickness	0: thin (10–40 µm) 1: thick (>40 µm)	23. Number of longitudinal septa	0: absent 1: mainly 1 septum 2: mainly 2 or more septa
* Algal layer thickness	µm	24. Number of locules per ascospore	0: 6–12 locules 1: 12–18 locules 2: 18–24 locules 3: >24 locules
9. Ascoma presence	0: absent 1: present	25. I reaction spores	0: I- 1: I+
10. Ascoma type	0: perithecioid 1: urceolate 2: lecanoroid 3: lepadioid	26. K reaction thallus	0: K- 1: K+ yellow 2: K+ yellow turning red
11. Ascoma diameter	0: small (0.1–0.8 mm) 1: medium (0.8–1.5 mm) 2: large (>1.5 mm)	27. C reaction thallus	0: C- 1: C+ red
12. Excipulum development	0: reduced 1: well-developed	28. I reaction medulla	0: I- 1: I+ blue or purple
13. Excipulum color	0: colorless to pale brown 1: dark brown to black	29. Lecanoric acid	0: not detected 1: detected
* Excipulum thickness	µm	30. Diploschistesic acid	0: not detected 1: detected
14. Lateral paraphyses	0: absent 1: present	31. Orsellinic acid	0: not detected 1: detected
15. Hymenium thickness	0: thin (85–130 µm) 1: thick (>130 µm)	32. Stictic acid aggregates	0: not detected 1: detected

Table S2

	1. Substrate type	2. Photobiont type	3. Thallus color	4. Pruina on upper surface	5. Thallus type	6. Thallus thickness	7. Upper surface layer type	8. Upper surface layer thickness	9. Ascoma presence	10. Ascoma type	11. Ascoma diameter	12. Excipulum development	13. Excipulum color	14. Lateral paraphyses	15. Hymenium thickness	16. Ascus length
D. actinostomus 1	0	0	3	0	0	A	0	0	1	0	0	1	1	1	1	1
D. actinostomus 2	0	0	3	0	0	A	0	0	1	0	0	1	1	1	1	1
D. caesioplumbeus 1	0	0	5	0	0	A	0	0	1	0	0	1	1	1	1	B
D. caesioplumbeus 2	0	0	5	0	0	A	0	0	1	0	0	1	1	1	1	B
D. caesioplumbeus 3	0	0	5	0	0	A	0	0	1	0	0	1	1	1	1	B
D. candidissimus 1	1	0	4	1	0	A	0	0	1	0	0	1	1	1	1	2
D. candidissimus 2	1	0	4	1	0	A	0	0	1	0	0	1	1	1	1	2
D. diacapsis 1	2	0	A	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diacapsis 2	2	0	A	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diacapsis 3	2	0	A	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diacapsis 4	2	0	0	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diacapsis 5	2	0	0	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diacapsis 6	2	0	0	1	1	A	0	A	1	1	A	1	1	1	0	1
D. diploschistoides 1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	A
D. diploschistoides 2	0	0	5	0	0	0	0	0	1	0	0	1	1	1	0	A
D. euganeus	0	0	8	0	0	0	0	0	1	0	0	1	1	1	A	1
D. gypsaceus 1	1	0	4	1	1	1	0	0	1	1	A	1	1	1	0	A
D. gypsaceus 2	1	0	6	1	1	1	0	0	1	1	A	1	1	1	0	A
D. gypsaceus 3	1	0	7	1	1	1	0	0	1	1	A	1	1	1	0	A
D. gypsaceus 4	1	0	4	1	1	1	0	0	1	1	A	1	1	1	0	A
D. gypsaceus 5	1	0	7	1	1	1	0	0	1	1	A	1	1	1	0	A
D. interpediens 1	0	0	2	0	1	A	0	0	1	1	1	1	1	1	A	A
D. interpediens 2	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 3	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 4	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 5	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 6	0	0	7	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 7	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 8	0	0	7	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 9	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. interpediens 10	0	0	7	0	1	A	0	0	1	1	1	1	1	1	0	A
D. muscorum 1	3	0	7	0	1	0	0	0	1	1	A	1	1	1	0	0
D. muscorum 2	3	0	7	0	1	0	0	0	1	1	A	1	1	1	0	0
D. muscorum 3	3	0	7	0	1	0	0	0	1	1	A	1	1	1	0	0
D. muscorum 4	3	0	7	0	1	0	0	0	1	1	A	1	1	1	0	0
D. muscorum 5	3	0	7	0	1	0	0	0	1	1	A	1	1	1	0	0
D. ocellatus 1	1	0	0	1	2	1	1	1	1	2	2	0	0	0	1	1
D. ocellatus 2	2	0	0	1	2	1	1	1	1	2	2	0	0	0	1	1
D. ocellatus 3	1	0	0	1	2	1	1	1	0	?	?	?	?	?	?	?
D. ocellatus 4	1	0	0	1	2	1	1	1	0	?	?	?	?	?	?	?
D. ocellatus 5	1	0	0	1	2	1	1	1	1	2	2	0	0	0	1	1
D. rampoddensis 2	0	0	2	0	1	A	0	0	1	1	A	1	1	1	0	A
D. rampoddensis 1	0	0	2	0	1	A	0	0	1	1	A	1	1	1	0	A
D. scruposus 1	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 2	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 3	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 4	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 5	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 6	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 7	0	0	7	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 8	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 9	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 10	0	0	6	0	1	A	0	0	1	1	1	1	1	1	0	A
D. scruposus 11	0	0	2	0	1	A	0	0	1	1	1	1	1	1	0	A
T. lepadinum	4	1	C	0	A	0	B	0	1	3	B	1	0	1	1	?
T. suecicum	4	1	C	0	A	0	B	0	1	3	A	1	0	1	A	?

Table S2. Continuation

	17. Ascus width	**18. Ascospores per ascus**	**19. Ascospore length**	**20. Ascospore width**	**21. Ascospore shape (length/width ratio)**	**22. Number of transverse septa**	**23. Number of longitudinal septa**	**24. Number of locules**	**25. I reaction spores**	**26. K reaction of the thallus**	**27. C reaction thallus**	**28. I reaction medulla**	**29. Lecanoric acid**	**30. Diploschistesic acid**	**31. Orsellinic acid**	**32. Stictic acid aggregates**
D. actinostomus 1	A	1	B	B	A	A	2	B	0	0	1	1	1	1	0	0
D. actinostomus 2	A	1	B	B	A	A	2	B	0	0	1	1	1	1	0	0
D. caesioplumbeus 1	A	1	2	2	A	1	2	2	0	0	1	1	1	0	0	0
D. caesioplumbeus 2	A	1	2	2	A	1	2	2	0	0	1	1	1	0	0	0
D. caesioplumbeus 3	A	1	2	2	A	1	2	2	0	0	1	1	1	0	0	0
D. candidissimus 1	0	1	2	2	A	1	2	2	0	0	1	1	1	0	0	0
D. candidissimus 2	0	1	2	2	A	1	2	2	0	0	1	1	1	0	0	0
D. diacapsis 1	0	1	1	1	A	0	1	0	0	1	1	0	?	?	?	?
D. diacapsis 2	0	1	1	1	A	0	1	0	0	1	1	0	?	?	?	?
D. diacapsis 3	0	1	1	1	A	0	1	0	0	1	1	0	1	1	0	0
D. diacapsis 4	0	1	1	1	A	0	1	0	0	1	1	0	1	1	0	0
D. diacapsis 5	0	1	1	1	A	0	1	0	0	1	1	0	1	0	0	0
D. diacapsis 6	0	1	1	1	A	0	1	0	0	1	1	0	1	1	0	0
D. diploschistoides 1	A	1	1	B	A	0	B	1	1	0	1	1	1	0	0	0
D. diploschistoides 2	A	1	1	B	A	0	B	1	1	0	1	1	1	0	0	0
D. euganeus	0	1	1	2	0	0	2	B	0	0	0	0	0	0	0	0
D. gypsaceus 1	0	0	B	1	1	1	B	1	0	1	1	0	1	0	0	0
D. gypsaceus 2	0	0	B	1	1	1	B	1	0	1	1	0	1	0	0	0
D. gypsaceus 3	0	0	B	1	1	1	B	1	0	1	1	0	1	0	0	0
D. gypsaceus 4	0	0	B	1	1	1	B	1	0	1	1	0	?	?	?	?
D. gypsaceus 5	0	0	B	1	1	1	B	1	0	1	1	0	1	0	0	0
D. interpediens 1	0	1	1	1	1	0	B	A	0	1	1	0	1	1	1	0
D. interpediens 2	0	1	1	1	1	0	B	A	0	1	1	0	1	1	1	0
D. interpediens 3	0	1	1	1	1	0	B	A	0	1	1	0	1	1	0	0
D. interpediens 4	0	1	1	1	1	0	B	A	0	1	1	0	1	1	1	0
D. interpediens 5	0	1	1	1	1	0	B	A	0	1	1	1	1	1	1	0
D. interpediens 6	0	1	1	1	1	0	B	A	0	1	1	0	1	1	0	0
D. interpediens 7	0	1	1	1	1	0	B	A	0	1	1	0	1	1	1	0
D. interpediens 8	0	1	1	1	1	0	B	A	0	1	1	1	1	1	1	0
D. interpediens 9	0	1	1	1	1	0	B	A	0	1	1	0	1	1	1	0
D. interpediens 10	0	1	1	1	1	0	B	A	0	1	1	1	1	1	1	0
D. muscorum 1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0
D. muscorum 2	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0
D. muscorum 3	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0
D. muscorum 4	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0
D. muscorum 5	0	0	1	1	1	0	1	0	0	1	1	0	?	?	?	?
D. ocellatus 1	0	1	0	0	B	0	1	0	0	2	0	0	0	0	0	1
D. ocellatus 2	0	1	0	0	B	0	1	0	0	2	0	0	0	0	0	1
D. ocellatus 3	0	?	?	?	?	?	?	?	?	2	0	0	0	0	0	1
D. ocellatus 4	0	?	?	?	?	?	?	?	?	2	0	0	0	0	0	1
D. ocellatus 5	0	1	0	0	B	0	1	0	0	2	0	0	0	0	0	1
D. rampoddensis 1	0	1	A	A	1	1	1	A	0	1	1	0	1	0	0	0
D. rampoddensis 2	0	1	A	A	1	1	1	A	0	1	1	0	1	0	0	0
D. scruposus 1	0	0	B	1	1	1	B	1	0	1	1	1	1	0	0	0
D. scruposus 2	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 3	0	0	B	1	1	1	B	1	0	1	1	1	1	1	0	0
D. scruposus 4	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 5	0	0	B	1	1	1	B	1	0	1	1	0	1	0	1	0
D. scruposus 6	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 7	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 8	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 9	0	0	B	1	1	1	B	1	0	1	1	0	1	1	0	0
D. scruposus 10	0	0	B	1	1	1	B	1	0	1	1	0	1	1	1	0
D. scruposus 11	0	0	B	1	1	1	B	1	0	1	1	1	1	1	0	0
T. lepadinum	?	A	3	3	3	2	B	3	A	0	0	?	0	0	0	0
T. suecicum	?	1	2	1	2	1	0	A	A	0	0	?	0	0	0	0

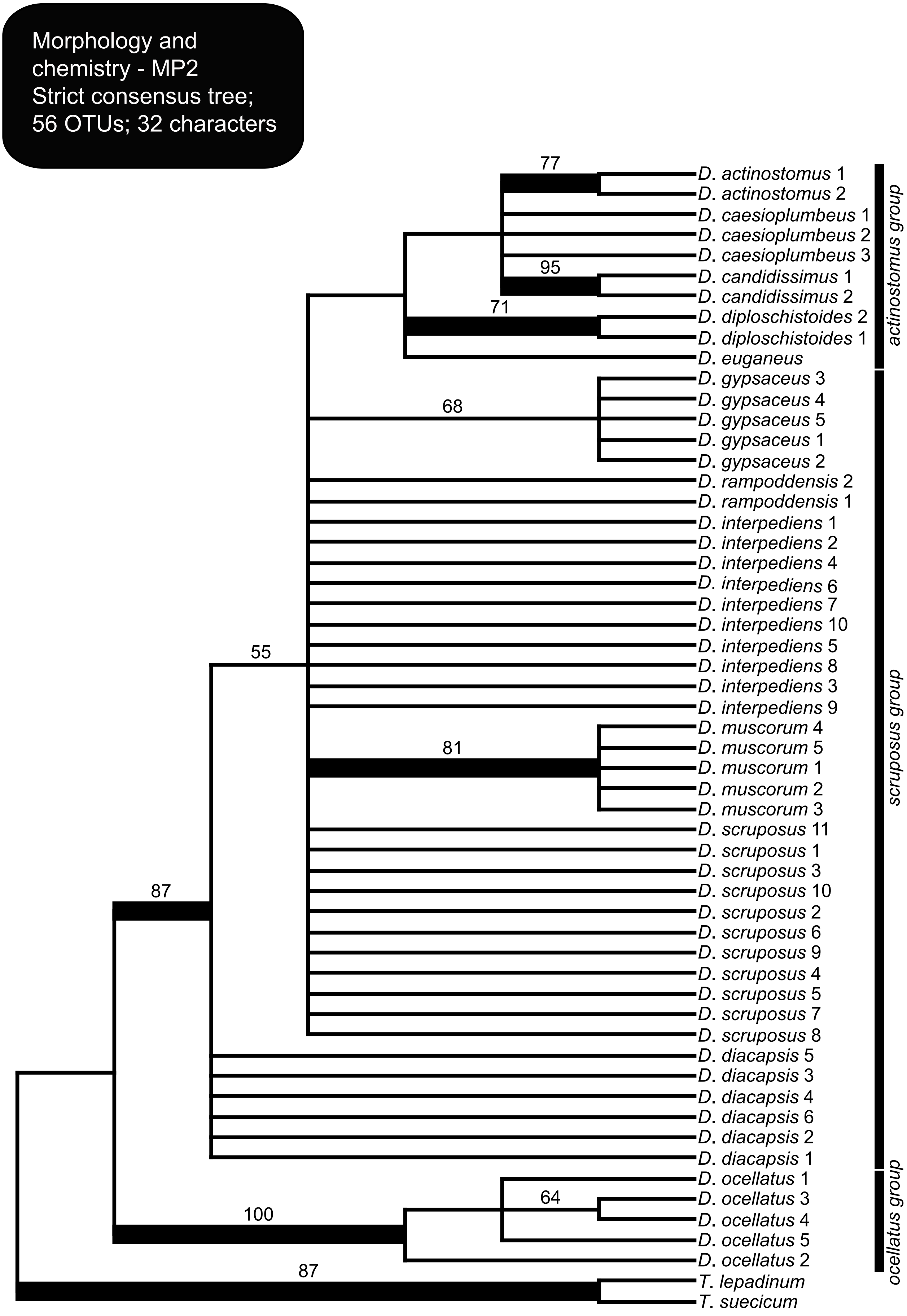
Morphology and chemistry - MP2
Strict consensus tree;
56 OTUs; 32 characters

FIGURE S2

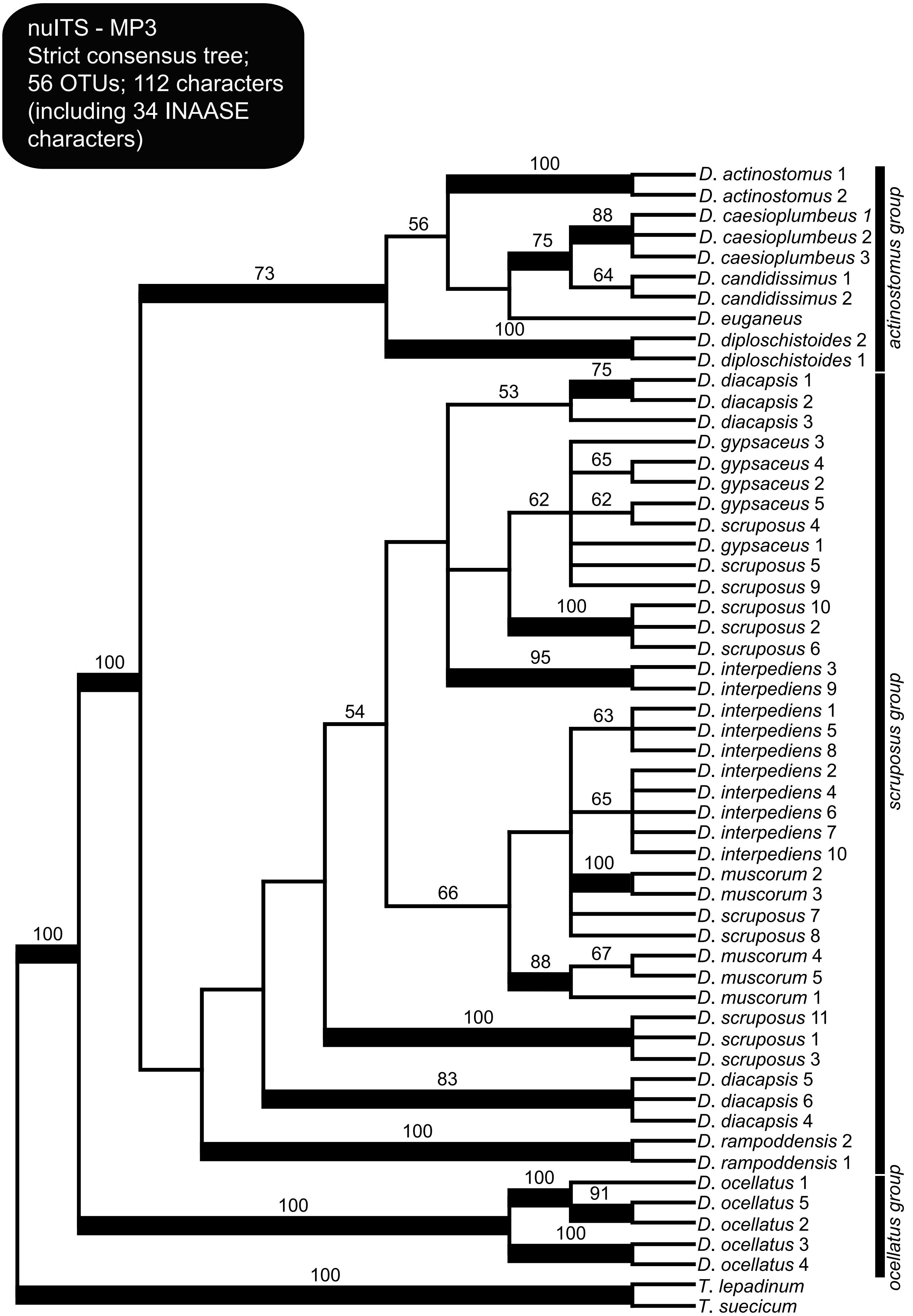
nuITS - MP3
Strict consensus tree;
56 OTUs; 112 characters
(including 34 INAASE
characters)
100
88
56
75
73
64
100
75
53
65
62
62
100
95
100
54
63
65
100
66
100
67
88
100
83
100
100
91
100
100
100
D. actinostomus 1
D. actinostomus 2
D. caesioplumbeus 1
D. caesioplumbeus 2
D. caesioplumbeus 3
D. candidissimus 1
D. candidissimus 2
D. euganeus
D. diploschistoides 2
D. diploschistoides 1
D. diacapsis 1
D. diacapsis 2
D. diacapsis 3
D. gypsaceus 3
D. gypsaceus 4
D. gypsaceus 2
D. gypsaceus 5
D. scruposus 4
D. gypsaceus 1
D. scruposus 5
D. scruposus 9
D. scruposus 10
D. scruposus 2
D. scruposus 6
D. interpediens 3
D. interpediens 9
D. interpediens 1
D. interpediens 5
D. interpediens 8
D. interpediens 2
D. interpediens 4
D. interpediens 6
D. interpediens 7
D. interpediens 10
D. muscorum 2
D. muscorum 3
D. scruposus 7
D. scruposus 8
D. muscorum 4
D. muscorum 5
D. muscorum 1
D. scruposus 11
D. scruposus 1
D. scruposus 3
D. diacapsis 5
D. diacapsis 6
D. diacapsis 4
D. rampoddensis 2
D. rampoddensis 1
D. ocellatus 1
D. ocellatus 5
D. ocellatus 2
D. ocellatus 3
D. ocellatus 4
T. lepadinum
T. suecicum
actinostomus group
scruposus group
ocellatus group

FIGURE S3

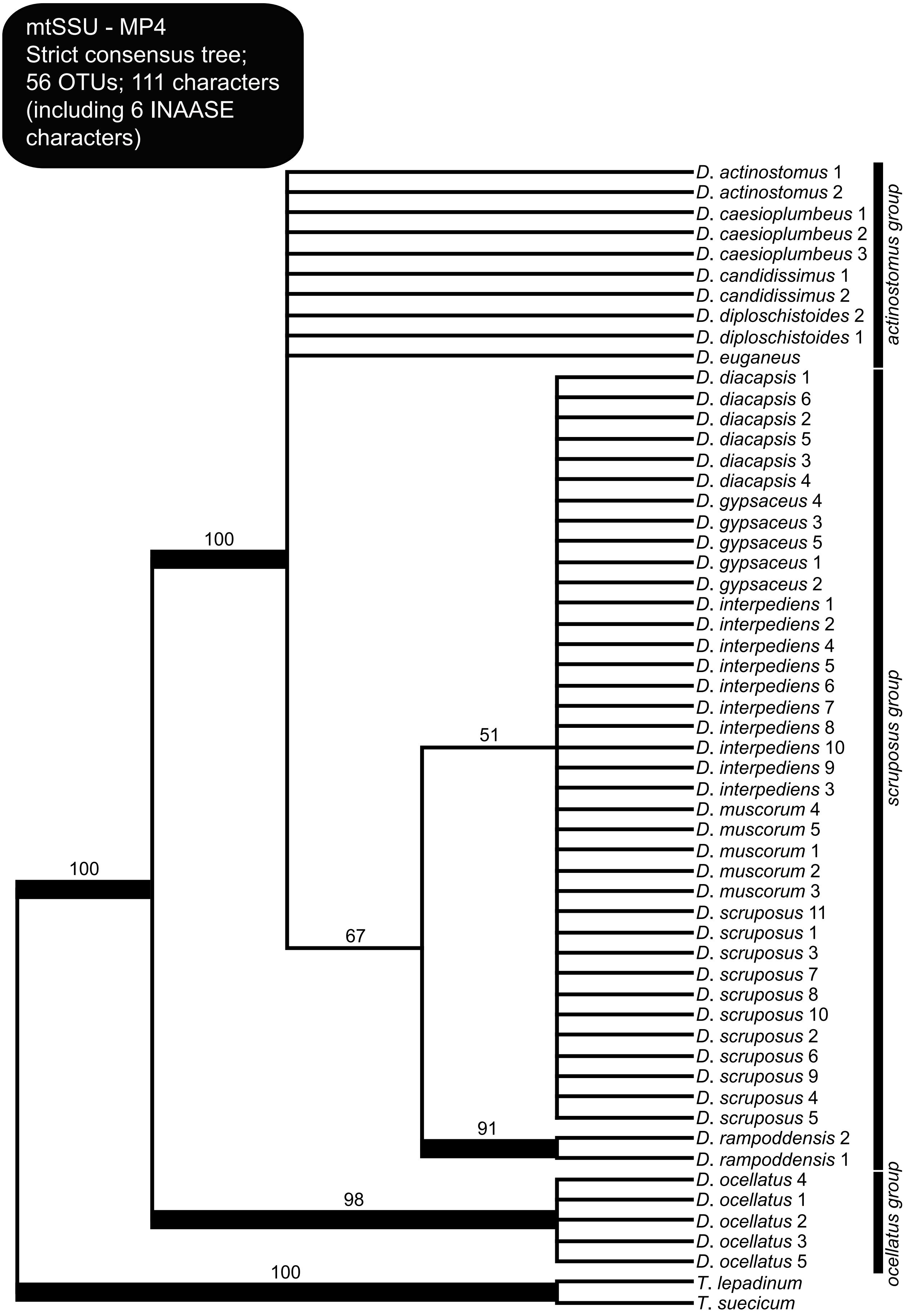
mtSSU - MP4
Strict consensus tree;
56 OTUs; 111 characters
(including 6 INAASE
characters)
100
100
51
67
91
98
100
D. actinostomus 1
D. actinostomus 2
D. caesioplumbeus 1
D. caesioplumbeus 2
D. caesioplumbeus 3
D. candidissimus 1
D. candidissimus 2
D. diploschistoides 2
D. diploschistoides 1
D. euganeus
D. diacapsis 1
D. diacapsis 6
D. diacapsis 2
D. diacapsis 5
D. diacapsis 3
D. diacapsis 4
D. gypsaceus 4
D. gypsaceus 3
D. gypsaceus 5
D. gypsaceus 1
D. gypsaceus 2
D. interpediens 1
D. interpediens 2
D. interpediens 4
D. interpediens 5
D. interpediens 6
D. interpediens 7
D. interpediens 8
D. interpediens 10
D. interpediens 9
D. interpediens 3
D. muscorum 4
D. muscorum 5
D. muscorum 1
D. muscorum 2
D. muscorum 3
D. scruposus 11
D. scruposus 1
D. scruposus 3
D. scruposus 7
D. scruposus 8
D. scruposus 10
D. scruposus 2
D. scruposus 6
D. scruposus 9
D. scruposus 4
D. scruposus 5
D. rampoddensis 2
D. rampoddensis 1
D. ocellatus 4
D. ocellatus 1
D. ocellatus 2
D. ocellatus 3
D. ocellatus 5
T. lepadinum
T. suecicum
actinostomus group
scruposus group
ocellatus group

FIGURE S4

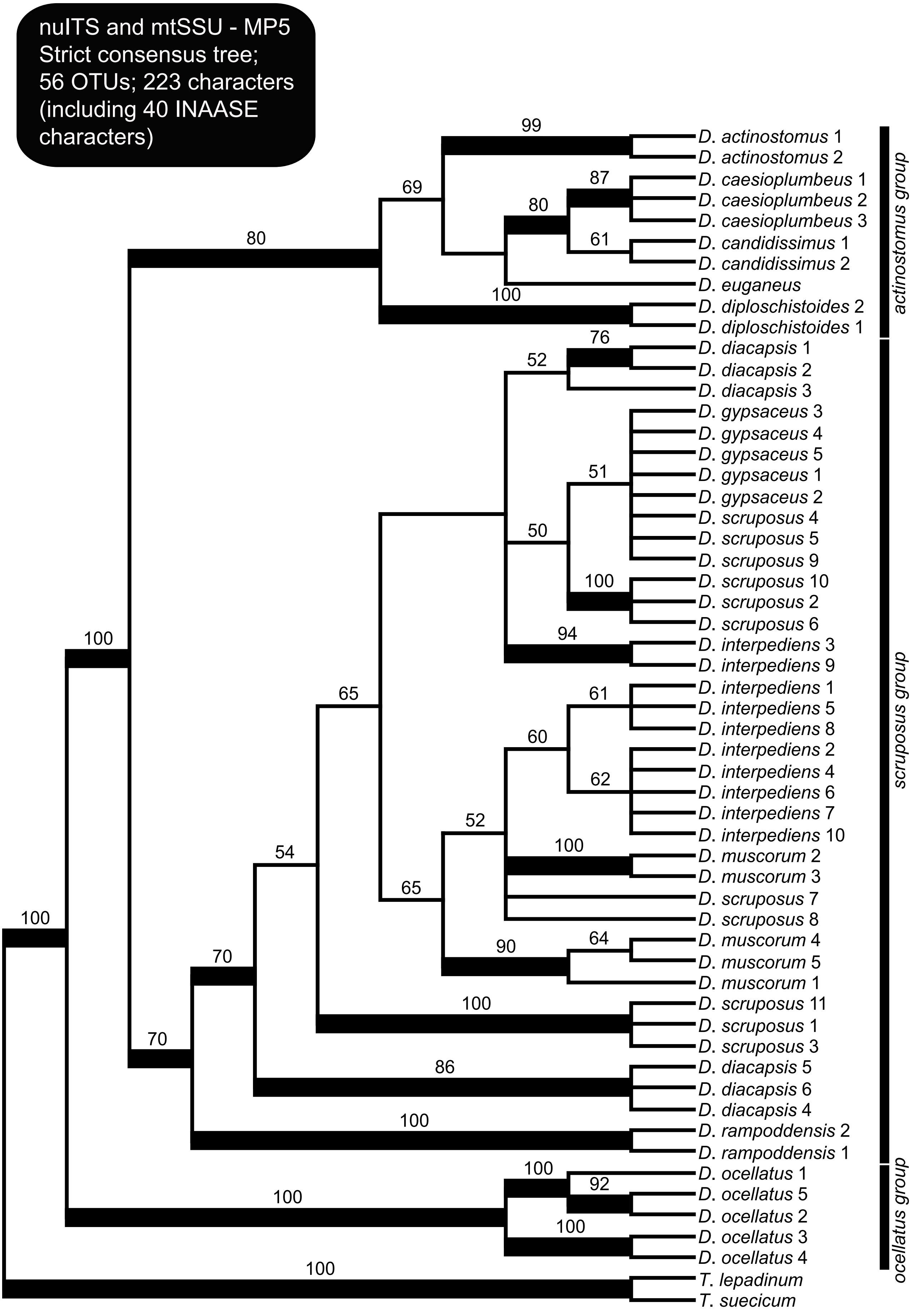
nuITS and mtSSU - MP5
Strict consensus tree;
56 OTUs; 223 characters
(including 40 INAASE
characters)
99
69
87
80
80
61
100
76
52
51
50
100
94
100
65
61
60
62
52
100
54
65
90
64
70
100
100
70
86
100
100
92
100
100
100
D. actinostomus 1
D. actinostomus 2
D. caesioplumbeus 1
D. caesioplumbeus 2
D. caesioplumbeus 3
D. candidissimus 1
D. candidissimus 2
D. euganeus
D. diploschistoides 2
D. diploschistoides 1
D. diacapsis 1
D. diacapsis 2
D. diacapsis 3
D. gypsaceus 3
D. gypsaceus 4
D. gypsaceus 5
D. gypsaceus 1
D. gypsaceus 2
D. scruposus 4
D. scruposus 5
D. scruposus 9
D. scruposus 10
D. scruposus 2
D. scruposus 6
D. interpediens 3
D. interpediens 9
D. interpediens 1
D. interpediens 5
D. interpediens 8
D. interpediens 2
D. interpediens 4
D. interpediens 6
D. interpediens 7
D. interpediens 10
D. muscorum 2
D. muscorum 3
D. scruposus 7
D. scruposus 8
D. muscorum 4
D. muscorum 5
D. muscorum 1
D. scruposus 11
D. scruposus 1
D. scruposus 3
D. diacapsis 5
D. diacapsis 6
D. diacapsis 4
D. rampoddensis 2
D. rampoddensis 1
D. ocellatus 1
D. ocellatus 5
D. ocellatus 2
D. ocellatus 3
D. ocellatus 4
T. lepadinum
T. suecicum
actinostomus group
scruposus group
ocellatus group

FIGURE S5

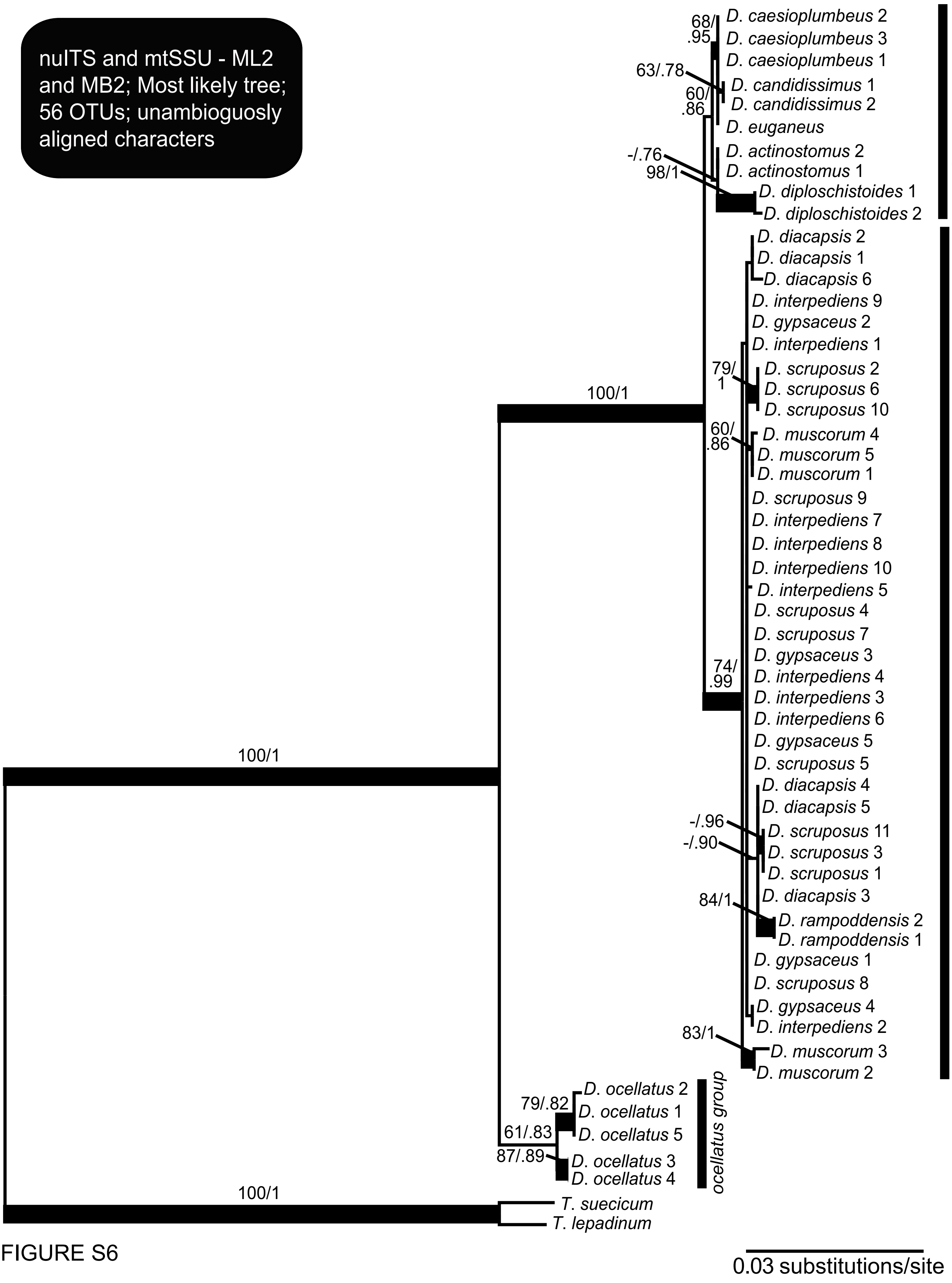
nuITS and mtSSU - ML2 and MB2; Most likely tree; 56 OTUs; unambioguosly aligned characters
68/ .95
D. caesioplumbeus 2
D. caesioplumbeus 3
D. caesioplumbeus 1
63/.78
D. candidissimus 1
60/ .86
D. candidissimus 2
D. euganeus
-/.76
D. actinostomus 2
98/1
D. actinostomus 1
D. diploschistoides 1
D. diploschistoides 2
actinostomus group
D. diacapsis 2
D. diacapsis 1
D. diacapsis 6
D. interpediens 9
D. gypsaceus 2
D. interpediens 1
79/ 1
D. scruposus 2
D. scruposus 6
100/1
D. scruposus 10
60/ .86
D. muscorum 4
D. muscorum 5
D. muscorum 1
D. scruposus 9
D. interpediens 7
D. interpediens 8
D. interpediens 10
D. interpediens 5
D. scruposus 4
D. scruposus 7
D. gypsaceus 3
74/ .99
D. interpediens 4
D. interpediens 3
D. interpediens 6
D. gypsaceus 5
100/1
D. scruposus 5
D. diacapsis 4
D. diacapsis 5
-/.96
D. scruposus 11
-/.90
D. scruposus 3
D. scruposus 1
D. diacapsis 3
84/1
D. rampoddensis 2
D. rampoddensis 1
D. gypsaceus 1
D. scruposus 8
D. gypsaceus 4
D. interpediens 2
83/1
D. muscorum 3
D. muscorum 2
scruposus group
D. ocellatus 2
79/.82
D. ocellatus 1
61/.83
D. ocellatus 5
87/.89
D. ocellatus 3
D. ocellatus 4
ocellatus group
100/1
T. suecicum
T. lepadinum
0.03 substitutions/site

FIGURE S6

CAPÍTOL 4: Expansió de les *Stictidaceae* amb la inclusió del gènere de líquens saxícola *Ingvariella*

CAPÍTOL 4

Expansion of the Stictidaceae by the addition of the saxicolous lichen-forming genus *Ingvariella*

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Article publicat a la revista *Mycologia* (2011) 103(4): 755–763.

RESUM

El gènere monotípic *Ingvariella* (fongs liquenitzats) fou originalment escindit de *Diploschistes* a partir de la morfologia de l'exciple, i mantingut dins de la família de les *Thelotremataceae* (= *Graphidaceae*) dins de l'ordre de les *Ostropales*. En aquest estudi, després de revisar en detall la morfologia d'*Ingvariella*, vam detectar l'existència d'un himeni que reaccionava positiu amb el lugol (primer groc, després vermell) i la presència d'ascs amiloides, els quals suggerien la seva afinitat amb d'altres famílies de l'ordre, apart de les *Thelotremataceae*. Per aquest motiu, els objectius d'aquest treball han estat avaluar la identitat d'*Ingvariella* com a gènere independent i investigar la seva posició sistemàtica dins de l'ordre de les *Ostropales*. Amb aquest objectiu, s'han inferit relacions filogenètiques amb una matriu de dades molecular, basada en una regió nuclear (nuLSU) i una mitocondrial (mtSSU), en la què s'han inclòs diversos espècimens de *I. bispora* i una selecció de 59 tàxons que recollien una àmplia representació de fongs de les *Ostropales*. Els resultats de les anàlisis filogenètiques revelen que el gènere *Ingvariella* és monofilètic i pertany a la família de les *Stictidaceae*. Les anàlisis també mostren com a grup germà d'*Ingvariella* el gènere *Cryptodiscus*, que inclou fonamentalment fongs sapròfits i una espècie de liquen. Amb la inclusió del primer gènere de líquens saxícoles dins d'aquesta família, s'expandeix considerablement l'àmplia diversitat ecològica de les *Stictidaceae*, dins de les quals s'han inclòs des de fongs sapròfits i líquens corticícoles de mida petita, fins a espècies que poden ésser facultativament liquenitzades. A més dels resultats esmentats, s'inclouen també noves dades sobre les relacions entre d'altres famílies pertanyents a les *Ostropales*.

Mycologia, 103(4), 2011, pp. 755–763. DOI: 10.3852/10-287

Expansion of the Stictidaceae by the addition of the saxicolous lichen-forming genus *Ingvariella*

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Abstract: The monotypic, lichen-forming genus *Ingvariella* originally was segregated from *Diploschistes* and placed within the Thelotremataceae (Ostropales) based on aspects of exciple morphology. However, the I+ hymenium and amyloid ascus wall suggest affinities to families other than the Thelotremataceae. To assess the identity of *Ingvariella* and to investigate its placement within the Ostropales, we inferred phylogenetic relationships of *I. bispora* by comparison of mtSSU rDNA and nuLSU rDNA sequences for 59 species encompassing a broad array of ostropalean fungi by means of Bayesian, maximum likelihood and weighted maximum parsimony methods. Here we report that *Ingvariella* is a member of the Stictidaceae, sister to the mainly saprotrophic genus *Cryptodiscus*. The inclusion of the first saxicolous lichen-forming fungus within this family expands the broad ecological diversity of the Stictidaceae, where saprotrophic fungi, corticicolous lichen-forming fungi and lichenized and non-lichenized conspecific taxa have been described previously. We also present new insights into the relationships among other families within the Ostropales.

Key words: *Diploschistes*, exciple morphology, *Ingvariella*, molecular phylogenetics, Ostropales, Stictidaceae

INTRODUCTION

The genus *Diploschistes* Norman (FIG. 1A) is characterized as having a carbonized pseudoparenchymatous exciple with lateral paraphyses (''periphysoids''), a trebouxioid photobiont and lacking a columella (FIG. 1C, D). In fact, this is the only genus within the Thelotremataceae not having trentepohlioid algae as a photobiont. The species initially described as *Diploschistes bisporus* (Bagl.) Steiner has almost lecideine apothecia (FIG. 1B) that exhibit a pseudoexciple formed by degenerating paraphyses and asci from the outermost part of the hymenium, sometimes with an extremely reduced exciple and no lateral paraphyses (FIG. 1E, F).

Based on these distinctive morphological characters, Guderley et al. (1997) transferred *D. bisporus* to a new monospecific genus, *Ingvariella* Guderley & Lumbsch, within the Thelotremataceae. Traditionally, the generic concepts within this family were based on ascospore septation and pigmentation (Müller 1887, Redinger 1936). Later, Salisbury (1971) used excipular structure to distinguish groups within the Thelotremataceae. This classification then was adopted mainly by Hale (1980, 1981), who modified the generic concept by adding the identity of the photobiont to the excipular characters. As a result, these genera were included: *Diploschistes*, *Myriotrema*, *Ocellularia* and *Thelotrema* (Guderley et al. 1997). However, authors argued later that the characters used to delimit these genera resulted in large and heterogeneous taxa (Frisch 2006). Furthermore, some authors (e.g. Nimis 1998) considered the use of excipular characters as insufficient to segregate *Ingvariella* from *Diploschistes* and proposed to treat *Ingvariella* as a subgenus within *Diploschistes* s. l.

Despite lacking some of the diagnostic characters of the Thelotremataceae (e.g. a true pseudoparenchymatous exciple, non-amyloid ascus wall), Guderley et al. (1997) maintained *Ingvariella* within this family and considered it to be related to *Diploschistes* because both genera are saxicolous, have trebouxioid photobionts and a similar distribution in arid and semiarid areas, whereas the rest of the family is mainly tropical and in association with trentepohlioid algae. On the other hand, they also noted that with the

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Submittted 21 Sep 2010; accepted for publication 30 Jan 2011.

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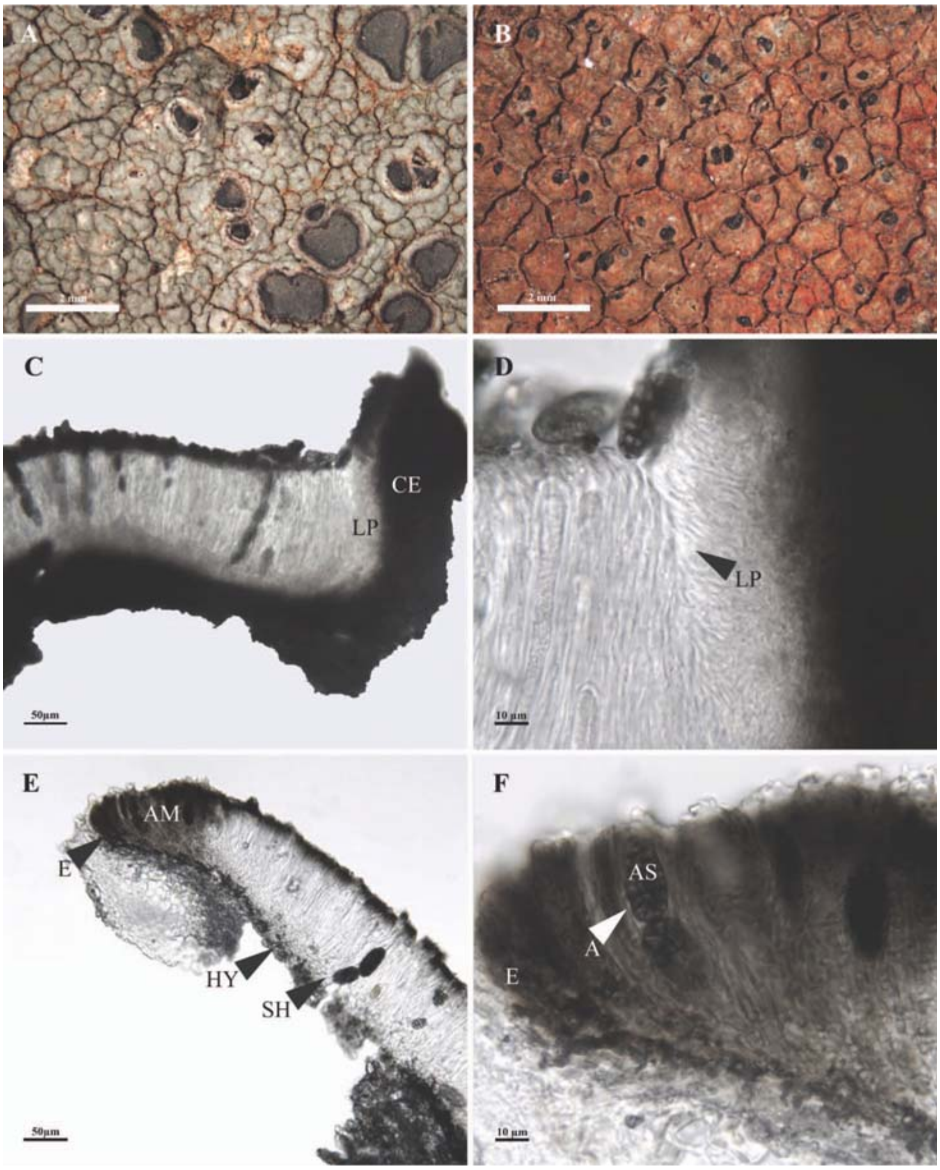

FIG. 1. Thallus morphology and ascomatal features of *Diploschistes scruposus* (A, C, D) and *Ingvariella bispora* (B, E, F). A. Fertile thallus of *Diploschistes scruposus* with well-developed urceolate apothecia. B. Fertile thallus of *Ingvariella bispora* with deeply urceolate apothecia. C. Longitudinal section of an apothecium, showing the well developed carbonized pseudoparenchymatous exciple (CE) with lateral paraphyses (LP). D. Detail of lateral paraphyses (arrow, LP). E. Longitudinal section of an apothecium with the apothecial margin (AM) formed by decaying hymenial elements. A very thin pigmented layer underneath the subhymenium (arrow, SH) can be observed representing the hypothecium/lower ascoma margin (arrow, HY). This layer extends in the outer part of the apothecial margin (arrow, E) and could be considered an extremely reduced exciple. F. Detail of the lateral margin with ascospores (AS), degenerated asci (arrow, A), and reduced exciple (E).

absence of lateral paraphyses and the presence of columella-like structures *Ingvariella* could be related to other genera within Thelotremataceae, such as *Ocellularia* and *Myriotrema*, which also have columella structures.

Ingvariella shares features with other families currently included in the Ostropales. For instance, like the mainly tropical and crustose family Gomphillaceae, *Ingvariella* has urceolate apothecia, muriform ascospores and a chloroccoid photobiont. Henssen (1995) reported that *Sagiolechia atlantica* Henssen (recently transferred to a new family Sagiolechiaceae, Baloch et al. 2010) has an apothecial margin similar to that of *Ingvariella*, in which the marginal parts of the hymenium degenerate in old fruiting bodies, even though a well formed proper exciple is present.

Alternatively, *Ingvariella* also could be ascribed to families such as the Phlyctidaceae and the Stictidaceae, both of which include some members having a chloroccoid photobiont and hymenia, which have unbranched paraphyses, KOH/I+ (blue) ascus walls and lack periphysoids. While the Phlyctidaceae have a true thalline margin and depsidones as secondary compounds, both the Stictidaceae and *Ingvariella* lack this type of margin and depsidones. These shared traits with other families suggest that the traditional placement of *Ingvariella* within the Thelotremataceae is somehow arbitrary and an alternative placement within the Ostropales cannot be completely discarded. The main goal of this study was to revisit the classification of *Ingvariella* by inferring its phylogenetic relationships within the Ostropales.

MATERIALS AND METHODS

Taxon sampling.—To infer the phylogenetic placement of *Ingvariella*, we used the mtSSU and nuLSU loci for a total of 59 species, representing most families within the Ostropales s. l. according to Kauff and Lutzoni (2002) and Lücking et al. (2004) (i.e. Coenogoniaceae, Gomphillaceae, Graphidaceae, Gyalectaceae, Odontotremataceae, Phlyctidaceae, Stictidaceae and Thelotremataceae). *Ingvariella bispora* (Bagl.) Guderley & Lumbsch is represented by three specimens in the mtSSU dataset and by two in the nuLSU. To root the phylogeny two outgroup taxa were selected from the Agyriales based on previous studies that showed its sister relationship to the Ostropales s. l. (Miadlikowska et al. 2006) for a total of 61 species.

In total, 125 sequences were used for this study (see ONLINE DATA SUPPLEMENT 1 for GenBank accession numbers), of which 11 were generated by the first author and the rest were obtained from GenBank and the AFTOL database (AFTOL.org). The concatenated alignment was deposited in TreeBASE (accession number S11040).

DNA extraction, amplification and sequencing.—Genomic DNA was isolated with a phenol-chloroform-isoamyl alcohol extraction protocol based on Lee et al. (1988). Isolated DNA was resuspended in sterile water and stored at −20 C.

We amplified and sequenced these loci: 0.8 kb mtSSU and 1.4 kb nuLSU with primers mrSSU1–mrSSU3R (Zoller et al. 1999) and LR0R (or LIC24R)–LR7 (Vilgalys and Hester 1990, Miadlikowska and Lutzoni 2000), respectively. Symmetric PCR amplifications were prepared as in Gueidan et al. (2007), and amplifications were carried out in a Peltier thermal cycler (Perkin Elmer, GeneAmp PCR System 2400) with programs specified in Zoller et al. (1999) for mtSSU and in Gueidan et al. (2007) for nuLSU. After examination by gel electrophoresis, PCR products were purified with Speedtools PCR Clean-Up Kit (Biotools, Madrid) following manufacturer instructions. Sequencing reactions were prepared in a 10 µL final volume with the same amplification primers and Big Dye Terminator Cycle sequencing kit v3.1 (ABI PRISM, Perkin-Elmer, Applied Biosystems, Foster City, California), following manufacturer instructions. Sequencing products were subjected to electrophoresis with an ABI 3730xl DNA analyzer (Applied Biosystems).

Sequence alignment.—Sequence fragments were subjected to BLAST queries for a first verification of their identities and to rule out fungal contaminants. Subsequently, they were assembled and contigs were edited with Bioedit 7.0 (Hall 1999) and aligned manually with Mesquite 2.6 (Maddison and Maddison 2010, http://mesquiteproject.org). The nuLSU locus was aligned with the help of the secondary structure of *Saccharomyces cerevisiae* as reported by Cannone et al. (2002) following Kjer (1995). Ambiguously aligned regions (sensu Lutzoni et al. 2000) and introns were delimited manually and excluded from the analyses. For the ambiguous regions, their unequivocal coding and the elaboration of symmetric step matrices for each of coded characters were generated with the program INAASE 2.3b (Lutzoni et al. 2000, http://www.lutzonilab.net/downloads).

Phylogenetic analyses.—The mtSSU and nuLSU datasets, with 62 sequences each (including two specimens of *I. bispora*), were analyzed separately with GARLI 0.96 (Zwickl 2006) using maximum likelihood (ML) as the optimization criterion. Models of molecular evolution were estimated for each separate genomic region with the Akaike information criterion (AIC) (Akaike 1973) implemented in Modeltest 3.7 (Posada and Crandall 1998). The selected model for mtSSU was TVM + I + G (Posada 2003) and for nuLSU GTR + I + G (Tavaré 1986). We used GARLI to estimate the values of base frequencies, substitution rates, proportion of invariable sites and the shape parameter of the gamma distribution. We performed searches setting the program to stop after 10 000 generations if no improvement of the Ln likelihood ≤ 0.01 was detected, with a maximum of 500 000 generations.

Topological incongruence between the two datasets was examined with 1000 replicates of ML bootstrapping (ML BS) under the same models described above on each locus separately. A conflict was assumed to be significant if two different relationships (one being monophyletic and the other being non-monophyletic) for the same set of taxa both were supported with bootstrap values $\geq 70\%$ (Mason-Gamer and Kellog 1996). Because no conflicts were detected, we concatenated the two alignments and analyzed this combined dataset phylogenetically.

Phylogenetic relationships and confidence were inferred with maximum likelihood (ML), a Bayesian approach (MB) and weighted maximum parsimony (wMP) based on a combined dataset of 63 OTUs (including an additional specimen of *I. bispora* for which we have only the mtSSU sequence). For the maximum likelihood search, the same settings were used as in the separate analyses with GARLI 0.96, and the same estimated models were specified for each partition for both ML and ML bootstrap (ML BS) analyses.

For the Bayesian analysis, two parallel runs with four independent chains were conducted 10 000 000 generations with MrBayes 3.1.1 (Ronquist and Huelsenbeck 2003), with trees sampled every 100 generations and using GTR + I + G model of nucleotide substitution for both partitions estimated with the AIC in Modeltest 3.7. We plotted the

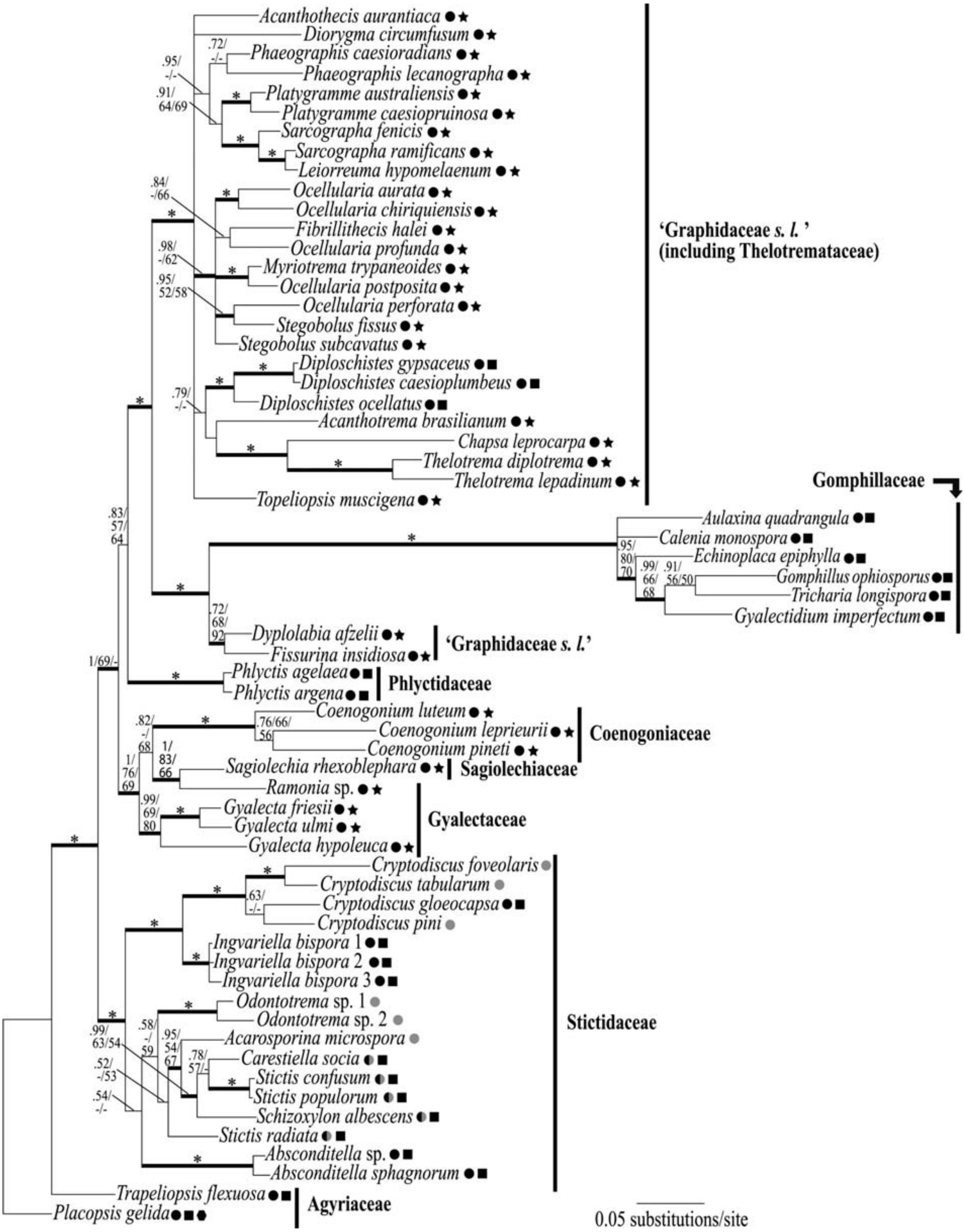

FIG. 2. Bayesian inference of phylogenetic relationships among 59 species, representing 35 genera, from the Ostropales (s. l.) based on concatenated nuLSU and mtSSU. Two genera from the Agyriales were selected as outgroup taxa. Support values above branches are ordered as PP/ML BS/wMP BS. Thicker internodes indicate significant support for at least one statistical method (PP ≥ 0.95, ML BS and wMP BS ≥ 70%). An asterisk above the internode indicates that all three measures of

log-likelihood scores against generation time with Tracer 1.4.1 (Rambaut and Drummond 2007, http://beast.bio.ed.ac.uk/Tracer) and concluded that stationarity was reached when log-likelihood values reached the same stable equilibrium value in both independent runs (Huelsenbeck and Ronquist 2001). A burn-in sample of 10 000 trees was discarded for each run, and the remaining 180 000 (90 000 from each run) were used to calculate posterior probabilities (PP) with the majority rule consensus tree command implemented in PAUP* 4.0b10 (Swofford 2002).

The wMP analysis was performed with PAUP*. Gaps were treated as a fifth character state and symmetric step matrices were created for unambiguous portions of the two loci separately with STMatrix 3.0 (Lutzoni and Zoller, Duke University, http://www.lutzonilab.net/downloads) as outlined in Gaya et al. (2011). Constant sites were removed from wMP searches and wMP bootstrap analyses (wMP BS). Phylogenetic signal from ambiguous regions was recovered without violating positional homology with INAASE 2.3b (Lutzoni et al. 2000). Heuristic searches were performed with 1000 random addition sequences (RAS), TBR (tree bisection reconnection) branch swapping, MULTREES in effect and collapsing branches with maximum branch length equal to zero. Branch support was estimated with 1000 nonparametric bootstrap replicates (Felsenstein 1985) with full heuristic searches, four RAS per bootstrap replicate and the same parameters as for the initial wMP analyses. The number of RAS per bootstrap replicate was calculated taking into account the number of times the shortest tree was hit during the heuristic search with the original dataset.

RESULTS

Alignments and phylogenetic analyses.—The final size of the combined dataset for the 63 specimens (representing 59 species of Ostropales and two outgroup taxa from Agyriales) was 6170 sites (1505 mtSSU sites and 4665 nuLSU sites), leaving 1091 sites (398 mtSSU and 693 nuLSU sites) after exclusion of 67 ambiguous regions and nine introns. Of the 1091 characters included in the ML and MB searches, 623 were constant and 468 were variable. For wMP analyses, the 623 constant sites were excluded and 45 coded INAASE characters replaced 29 and 16 ambiguously aligned regions from the mtSSU and nuLSU datasets, respectively, for a total of 513 variable characters, of which 411 were parsimony informative.

The majority rule consensus tree of 180 000 sampled trees from the Bayesian inference obtained in this study is included (FIG. 2) with branch lengths and support values. With 36 highly supported internodes (PP $\geq$ 0.95), this was the most resolved and well supported tree, including deep phylogenetic relationships, resulting from the three phylogenetic analyses. The topology of this tree was almost identical to the ML tree and was similar to the wMP majority rule consensus tree. However, the most likely tree ($-\ln$ likelihood = 11159.0312) recovered only 28 significantly supported internodes (ML BS $\geq$ 70%). The wMP analysis with 45 additional (INAASE) characters revealed three equally most parsimonious trees of 4114.59 steps, which were found in one island hit 720 times out of 1000 RAS. The number of internodes with high support (wMP BS $\geq$ 70%) was 28.

Phylogenetic relationships.—All analyses supported the monophyly of the three specimens of *I. bispora* with high confidence (1 PP, 100% ML BS and wMP BS), sister to the monophyletic *Cryptodiscus* s. str. (1 PP, 100% ML BS and wMP BS). Both genera are nested within the monophyletic family Stictidaceae (sensu Baloch et al. 2009), a result well supported by all measures of phylogenetic confidence (1 PP, 86% ML BS and 77% wMP BS). The Stictidaceae represents the first divergence from the remaining members of the Ostropales s. l. (sensu Miadlikowska et al. 2006), with the Stictidaceae s. str. clade (sensu Baloch et al. 2010) recovered as weakly supported. In our phylogeny, the placement of *Absconditella* and two undescribed taxa of the genus *Odontotrema* is uncertain within the Stictidaceae.

The Gyalectaceae is shown here to form a monophyletic group together with the Coenogoniaceae and Sagiolechiaceae (1 PP, 76% ML BS and 69% wMP BS). The Coenogoniaceae is recovered as monophyletic (1 PP, 100% ML BS and wMP BS), whereas the Gyalectaceae resulted paraphyletic. Our analyses reveal strong evidence for a shared recent common ancestor of *Ramonia* (Gyalectaceae) with *Sagiolechia* (= *Rhexophiale*) *rhexoblephara* (Sagiolechiaceae). Based on our taxon sampling, *Phlyctis* also is supported as a monophyletic group (1 PP, 100% ML BS and wMP BS) but with an uncertain placement within the Ostropales s. l.

We found a strongly supported sister relationship between the monophyletic family Gomphillaceae and two members of the Graphidaceae (1 PP, 90% ML BS and 84% wMP BS), *Fissurina insidiosa* and *Dyplolabia afzelii*. The Gomphillaceae clade showed a remarkably long branch, previously reported and tested for long-branch attraction effect by Lücking et al. (2004). As

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←
support were significant. Black circles following names of taxa indicate lichen-forming fungi; gray circles, saprotrophic fungi; and circles half black and gray, lichenized and non-lichenized conspecific taxa. Squares indicate lichen-forming taxa associated with trebouxioid or chlorococcal green algae, whereas a star refers to trentepohlioid green algae and a pentagon to cyanobacteria. Graphidaceae is indicated in quotes to highlight that in this phylogeny this family has not resulted monophyletic.

expected, members of the Thelotremataceae appeared nested within the main Graphidaceae clade (1 PP, 92% ML BS, 88% wMP BS), consistent with previously published results indicating that the Thelotremataceae should be treated as a synonym within the Graphidaceae (Kauff and Lutzoni 2002, Grube et al. 2004, Lumbsch et al. 2004, Frisch et al. 2006, Staiger et al. 2006, Mangold et al. 2008, Baloch et al. 2010). Thus, we henceforth will refer to this clade with the family name Graphidaceae. Phylogenetic placements of most taxa within the Graphidaceae s. l. could not be resolved here with high confidence.

DISCUSSION

The establishment of *Ingvariella* as a segregate taxon from *Diploschistes* is in agreement with traditional taxonomy of Guderley et al. (1997), however its placement within the Stictidaceae, as revealed, here is contrary to that of Guderley et al. (1997) who maintained *Ingvariella* within the Graphidaceae. Of interest, *Ingvariella* is the first exclusively lichenized saxicolous species known to date within the Stictidaceae. Although the Stictidaceae traditionally was recognized as a family composed of saprotrophic fungi, some authors included lichenized taxa (Gilenstam 1969, Sherwood 1977) based mainly on the morphology of the apothecial margin, the type of apical apparatus and ascus and ascospore shape. The hypothesis that the Stictidaceae included both lichenized and non-lichenized fungi was confirmed by Winka et al. (1998).

Lutzoni et al. (2001), using *Stictis radiata* to represent the Stictidaceae, concluded that the non-lichenized members of the Ostropales are derived from a lichenized ancestor. Wedin et al. (2004, 2005a, 2006) further demonstrated that specimens of *Conotrema* (lichenized) were nested within *Stictis* (saprotrophic) in different clades and showed that lichenization was present in some taxa of saprotrophic Stictidaceae. Subsequently, Wedin et al. (2004) used the term ''optional lichenization'' to describe this alternation of nutritional modes by the same species. Schoch et al. (2006) revealed the placement of the halotolerant fungus *Glomerobolus gelineus* Kohlm. & Volkm.-Kohlm. as closely related to the Stictidaceae, further expanding the ecological diversity exhibited by the Ostropales. According to Schoch et al. (2006) the ecology and nutritional mode of ostropalean saprobic taxa are best explained as being derived from loss of lichenization (Lutzoni et al. 2001, 2004; Reeb et al. 2004). Ecological and nutritional diversity is not restricted to the Ostropales. Gueidan et al. (2008) showed that rock-inhabiting and human pathogenic fungi (Chaetothyriales) shared a most recent common ancestor with lichen-forming fungi classified within the Verrucariales and Pyrenulales.

In general, relationships among the remaining members of the Stictidaceae revealed in our analyses are similar to phylogenetic results reported by Baloch et al. (2009, 2010) and Wedin et al. (2005a, 2006). Our results add support to the suggestion of Baloch et al. (2009) that *Absconditella* should be retained as a separate genus, apart from *Cryptodiscus*, based on differences in appearance of the ascoma and thickness and features of the ascomatal wall. Our data also support the placement of two undescribed taxa of genus *Odontotrema* within the Stictidaceae, as in Baloch et al. (2009, 2010).

A main feature in the circumscription of the Stictidaceae has been the structure of the ascoma margin: the presence of several wall layers, their pigmentation and the formation of crystals (Wedin et al. 2006). However, several authors have reported a wide range of variation of the apothecial margin in different genera within the family (Gilenstam 1969; Sherwood 1977; Wedin et al. 2005a, 2006) or even among individuals with different nutritional modes (saprotrophs vs. lichens) within the same species (e.g. *Schizoxylon albescens*, *Stictis confusum*, *S. mollis*, *S. populorum*; see Wedin et al. 2006). Regarding *Ingvariella*, none of the samples we examined (see ONLINE DATA SUPPLEMENT 2) or descriptions of this genus (Guderley et al. 1997; Lumbsch 1989, 2004; Mangold et al. 2009) bore any resemblance to the typical ascoma margin of the Stictidaceae, demonstrating that this structure by itself does not provide a reliable set of diagnostic characters for this family. Nor does the exciple of *Ingvariella* share similarities with members of the Graphidaceae, although the exciple structure is also variable in this family. Nevertheless, the hymenium of *Ingvariella* shares several features with some Stictidaceae: KOH/I+ (faint blue) ascus walls and numerous filiform paraphyses. When stained with IKI, the hymenium turns yellow and then brownish red, as reported (e.g. Baloch et al. 2009, Vězda and Vivant 1975) for other Stictidaceae genera (e.g. *Absconditella*, *Cryptodicus*). Conversely, the hymenium in the Graphidaceae differs from *Ingvariella* by the non-amyloid ascus walls and lack of a hymenial iodine reaction, except for a few taxa (e.g. *Glyphis*), where the reaction is blue but never yellow or reddish. In addition, *Ingvariella* has broadly ellipsoid brown muriform spores, while ascospores in the Stictidaceae are typically cylindrically elongated or filiform, colorless, thin-walled and with multiple transversal septa (Sherwood 1977). Although muriform spores occasionally occur (Gilenstam 1969, Sherwood 1977), brown spores are rare within the Stictidaceae (Sherwood 1977).

With regard to the other families in our phylogeny, the familial placement of *Sagiolechia* within the Ostropales has been questioned (Wedin et al. 2005b). Based on morphological and anatomical features, some authors have included the genus within the Graphidaceae (Vězda 1967) and others within the Gomphillaceae (Henssen 1995). A close relationship with the Gyalectaceae was reported by Wedin et al. (2005b). Recently, Baloch et al. (2010) transferred this genus to a new family, Sagiolechiaceae. In our analyses, the sister relationship of *Ramonia* and *Sagiolechia* suggests that the familial assignment of *Ramonia* should be re-evaluated in the context of this new classification.

In our results, the phylogenetic position of the clade *Fissurina insidiosa-Dyplolabia afzelii* agreed with Miadlikowska et al. (2006), where *Fissurina insidiosa* was sister to *Gyalidea hyalinascens* (Gomphillaceae), and to Baloch et al. (2010), where the *Fissurina-Dyplolabia* group was revealed sister to a monophyletic group formed by the Gomphillaceae and Solorinellaceae. These results suggested that clade *Fissurina-Dyplolabia* should be treated separately from the Graphidaceae, otherwise this family would be rendered paraphyletic.

In conclusion, our phylogenetic study based on mtSSU and nuLSU data demonstrated that *Ingvariella* must be transferred to the Stictidaceae. Based on current knowledge, we consider that some hymenium features (e.g. reaction of the hymenium when stained with IKI and amyloid ascus walls), combined with the type of photobiont (chloroccoid when lichenized), could be potential synapomorphies for the Stictidaceae, supporting the placement of *Ingvariella* within this family. However, further studies will be needed to find diagnostic morphological characters that can help in defining natural taxonomic entities within the Stictidaceae and the Ostropales in general.

ACKNOWLEDGMENTS

The authors thank the curators of herbaria B, BCN, DUKE and MAF, in addition to Geir Hestmark, for providing material used in this study. Valérie Hofstetter also is thanked for generating some of the unpublished sequences in the AFTOL database used for this study; Frank Kauff and Jolanta Miadlikowska for help with the phylogenetic analyses; Esteve Llop, Pere Navarro, Mats Wedin and Andreas Frisch for useful comments on the results; Molly McMullen for the English revision and proofreading; and Néstor Hladun for help with image editing and for providing lab facilities. This study was supported by projects (CGL2007-66734-C03-02) and Filogènia molecular de les Teloschistales i Ostropales. II Part (IEC Secció Ciències Biològiques), a doctoral scholarship (FPU-Formación del Profesorado Universitario, Ministerio de Educación) to SFB, and the Assembling the Fungal Tree of Life (AFTOL) project, supported by NSF Assembling the Tree of Life (ATOL) award DEB-0228668 to FL.

LITERATURE CITED

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, eds. Proceedings of the 2nd International Symposium on Information Theory. Budapest: Akademiai Kiado. p 267–281.

Baloch E, Gilenstam G, Wedin M. 2009. Phylogeny and classification of *Cryptodiscus*, with a taxonomic synopsis of the Swedish species. Fungal Divers 38:51–68.

———, Lücking R, Lumbsch HT, Wedin M. 2010. Major clades and phylogenetic relationships between lichenized and non-lichenized lineages in Ostropales (Ascomycota: Lecanoromycetes). Taxon 59:1483–1494.

Cannone JJ, Subramanian S, Schnare MN, Collett JR, D'Souza LM, Du Y, Feng B, Lin N, Madabusi LV, Muller KM, Pande N, Shang Z, Yu N, Gutell RR. 2002. The comparative RNA Website (CRW): an online database of comparative sequence and structure information for ribosomal, intron and other RNA. BMC Bioinformatics 3:2–15, doi:10.1186/1471-2105-3-2

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791, doi:10.2307/2408678

Frisch A. 2006. The lichen family Thelotremataceae in Africa. Bibl Lichenol 92:3–370.

———, Kalb K, Grube M. 2006. Molecular phylogeny of the Thelotremataceae. Bibl Lichenol 92:517–539.

Gaya E, Redelings BD, Navarro-Rosinés P, Llimona X, de Cáceres M, Lutzoni F. 2011. Align or not to align? Resolving species complexes within the *Caloplaca saxicola* group as a case study. Mycologia 103:361–378, doi:10.3852/10-120

Gilenstam G. 1969. Studies in the lichen genus *Conotrema*. Ark Bot 7:149–179.

Grube M, Baloch E, Lumbsch HT. 2004. The phylogeny of Porinaceae (Ostropomycetidae) suggests neotenic origin of perithecia in Lecanoromycetes. Mycol Res 108: 1111–1118, doi:10.1017/S0953756204000826

Guderley R, Lumbsch HT, Feige GB. 1997. *Ingvariella*, a new genus in the Thelotremataceae (lichenized Ascomycotina). Nova Hedwig 64:147–154.

Gueidan C, Roux C, Lutzoni F. 2007. Using a multigene phylogenetic analysis to assess generic delineation and character evolution in *Verrucariaceae* (Eurotiomycetes, Ascomycota). Mycol Res 111:1145–1168, doi:10.1016/j.mycres.2007.08.010

———, Ruibal Villaseñor C, de Hoog GS, Gorbushina AA, Untereiner WA, Lutzoni F. 2008. A rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. Stud Mycol 61:111–119, doi:10.3114/sim.2008.61.11

Hale ME. 1980. Generic delimitation in the lichen family Thelotremataceae. Mycotaxon 11:130–138.

———. 1981. A revision of the lichen family Thelotremataceae in Sri Lanka. Bull Br Mus (Nat Hist) Bot 8:227–332.

Hall TA. 1999. Bioedit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98.

Henssen A. 1995. *Sagiolechia atlantica*, eine neue Flechte von den Atlantischen Inseln (Ascomycotina, Ostropales). Bibl Lichenol 58:123–136.

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinf Appl Note 17: 754–755.

Kauff F, Lutzoni F. 2002. Phylogeny of the Gyalectales and Ostropales (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. Mol Phylogenet Evol 25:138–156, doi:10.1016/S1055-7903(02)00214-2

Kjer KM. 1995. Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from frogs. Mol Phylogenet Evol 4:314–330, doi:10.1006/mpev.1995.1028

Lee SB, Milgroom MG, Taylor JW. 1988. A rapid, high yield mini-prep method for isolation of total genomic DNA from fungi. Fungal Genet Newsl 35:23–24.

Lücking R, Stuart BL, Lumbsch HT. 2004. Phylogenetic relationships of Gomphillaceae and Asterothyriaceae: evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. Mycologia 96:283–294, doi:10.2307/3762064

Lumbsch HT. 1989. Die holarktischen Vertreter der Flechtengattung *Diploschistes* (Thelotremataceae). J Hattori Bot Lab 66:133–196.

———. 2004. *Ingvariella*. In: Nash TH III, Ryan BD, Diederich P, Gries C, Bungartz F, eds. Lichen flora of the greater Sonoran Desert region II. Lichens and Lichenicolous Fungi. Tempe: Lichens Unlimited, Arizona State Univ. p 136–137.

———, Schmitt I, Palice Z, Wiklund E, Ekman S, Wedin M. 2004. Supraordinal phylogenetic relationships of Lecanoromycetes based on a Bayesian analysis of combined nuclear and mitochondrial sequences. Mol Phylogenet Evol 3:822–832, doi:10.1016/j.ympev.2003.11.001

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim YW, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the Fungal Tree of Life: progress, classification and evolution of subcellular traits. Am J Bot 91:1446–1480, doi:10.3732/ajb.91.10.1446

———, Pagel M, Reeb V. 2001. Major fungal lineages are derived from lichen symbiotic ancestors. Nature 411: 937–940, doi:10.1038/35082053

———, Wagner P, Reeb V, Zoller S. 2000. Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. Syst Biol 49:628–651, doi:10.1080/106351500750049743

Maddison WP, Maddison DR. 2010. Mesquite: a modular system for evolutionary analysis. Version 2.73. http://mesquiteproject.org

Mangold A, Elix JA, Lumbsch HT. 2009. Thelotremataceae. In: Flora of Australia. Vol. 57, Lichens 5. Canberra and Melbourne: ABRS and CSIRO Publishing. p 242–243.

———, Martin MP, Lücking R, Lumbsch HT. 2008. Molecular phylogeny suggests synonymy of Thelotremataceae within Graphidaceae (Ascomycota: Ostropales). Taxon 57:476–486.

Mason-Gamer RJ, Kellogg EA. 1996. Testing for phylogenetic conflict among molecular datasets in the tribe Triticiae (Gramineae). Syst Biol 45:524–545, doi:10.1093/sysbio/45.4.524

Miadlikowska J, Kauff F, Hofstetter V, Fraker E, Grube M, Hafellner J, Reeb V, Hodkinson BP, Kukwa M, Lücking R, Hestmark G, García Otalora M, Rauhut A, Büdel B, Scheidegger C, Timdal E, Stenroos S, Brodo I, Perlmutter G, Ertz D, Diederich P, Lendemer JC, May P, Schoch CL, Arnold AE, Gueidan C, Tripp E, Yahr R, Robertson C, Lutzoni F. 2006. New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA- and two protein-coding genes. Mycologia 98:1088–1103, doi:10.3852/mycologia.98.6.1088

———, Lutzoni F. 2000. Phylogenetic revision of the genus *Peltigera* (lichen-forming ascomycetes) based on morphological, chemical and large subunit nuclear ribosomal DNA data. Int J Plant Sci 161:925–958, doi:10.1086/317568

Müller Argoviensis J. 1887. Graphideae Féeanae inclus. trib. affinibus nec non Graphidaea exoticae Acharii, El. Friesii et Zenkeri e novo studio speciminum originalium expositae et in novam dispositionem ordinatae. Mém Soc Phys Hist Nat Genève 29:1–80.

Nimis PL. 1998. A critical appraisal of modern generic concepts in lichenology. Lichenologist 30:427–438.

Posada D. 2003. Using Modeltest and PAUP* to select a model of nucleotide substitution. In: Baxevanis AD, Davison DB, Page RDM, Petsko GA, Stein LD, Stormo GD, eds. Current protocols in bioinformatics. John Wiley & Sons. p 6.5.1–6.5.14.

———, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818, doi:10.1093/bioinformatics/14.9.817

Redinger K. 1936. Thelotremataceae brasilienses imprimis ex herbario Regnelliano cognitae praetereaque in herbariis Krempelhuberi, Mülleri Arg., Nylanderi, Wainionis et Zahlbruckneri asservatae. Ark Bot 28A 8: 1–122.

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the Pezizomycotina (euascomycetes, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. Mol Phylogenet Evol 32:1036–1060, doi:10.1016/j.ympev.2004.04.012

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574, doi:10.1093/bioinformatics/btg180

Salisbury G. 1971. The Thelotremata of Angola and Mocambique. Rev Biol (Lisbon) 7:271–280.

Schoch CL, Kohlmeyer J, Volkmann-Kohlmeyer B, Tsui CKM, Spatafora JW. 2006. The halotolerant fungus *Glomerobolus gelineus* is a member of the Ostropales. Mycol Res 110:765–772, doi:10.1016/j.mycres.2005.10.001

Sherwood MA. 1977. The Ostropalean fungi. Mycotaxon 5: 1–277.

Staiger B, Kalb K, Grube M. 2006. Phylogeny and phenotypic variation in the lichen family Graphidaceae (Ostropomycetidae, Ascomycota). Mycol Res 110:765–772, doi:10.1016/j.mycres.2006.05.003

Swofford DL. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.

Tavaré S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. In: Miura RM, ed. Some mathematical questions in biology—DNA sequence analysis. Providence, Rhode Island: American Mathematical Society. p 57–86.

Vězda A. 1967. Flechtensystematische Studien VI. Die Gattung *Sagiolechia* Massal. Folia Geobot Phytotaxon 2:383–396.

———, Vivant J. 1975. *Absconditella pauxilla* Vězda et Vivant sp. n., un nouveau lichen des Pyrenees-Atlantiques. Folia Geobot Phytotaxon 10:205–108.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172:4238–4246.

Wedin M, Döring H, Gilenstam G. 2004. Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis-Conotrema* complex. New Phytol 164:459–465, doi:10.1111/j.1469-8137.2004.01198.x

———, ———, ———. 2006. *Stictis* s. lat. (Ostropales, Ascomycota) in northern Scandinavia, with a key and notes on morphological variation in relation to lifestyle. Mycol Res 110:773–789, doi:10.1016/j.mycres.2006.04.010

———, ———, Koenberg K, Gilenstam G. 2005a. Generic delimitations in the family Stictidaceae (Ostropales, Ascomycota): the *Stictis-Conotrema* problem. Lichenologist 37:67–75, doi:10.1017/S0024282904014653

———, Wiklund E, Crewe A, Döring H, Ekman S, Nyberg A, Schmitt I, Lumbsch HT. 2005b. Phylogenetic relationships of Lecanoromycetes (Ascomycota) as revealed by analyses of mt SSU and nLSU rDNA sequence data. Mycol Res 109:159–172, doi:10.1017/S0953756204002102

Winka K, Ahlberg C, Eriksson OE. 1998. Are there lichenized Ostropales? Lichenologist 30:455–462.

Zoller S, Scheidegger C, Sperisen C. 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming Ascomycetes. Lichenologist 31:511–516.

Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion [doctoral dissertation]. Austin: Univ Texas Press. 115 p.

ONLINE DATA SUPPLEMENT 1. Specimen voucher information and GenBank accession numbers for 63 mtSSU and 62 nuLSU sequences included in this study. Sequences in bold were generated in this study by SFB. All other sequences were retrieved from GenBank, except for unpublished sequences marked with an asterisk, which were retrieved directly from the AFToL data base.

Taxon name	**Collector and voucher information**	**GenBank accession numbers**	
		mit SSU	**nu LSU**
Absconditella sp.	Ecuador, Palice 3820 (herb. Palice)	AY300873	AY300825
Absconditella sphagnorum	Czech Republic, 17-02-2002 Palice (herb. Palice)	AY300872	AY300824
Acanthothecis aurantiaca	Australia, Kalb 33945 (herb. Kalb)	DQ431965	DQ431929
Acanthotrema brasilianum	Cameroon, Frisch 99/Ka40 Dupl. 1999	DQ384916	DQ431928
Acarosporina microspora	AFTOL-ID 78	AY584612	AY584643
Aulaxina quadrangula	Costa Rica, Lucking s.n. (F, sample No. 66)	AY341364	AY341350
Calenia monospora	Costa Rica, Lucking s.n. (F, sample No. 1a)	AY341365	AY341351
Carestiella socia	Sweden, Gilenstam 2437a (UPS)	AY661678	AY661682
Chapsa leprocarpa	Australia, Lumbsch 19125k & Mangold (F)	EU075568	EU075615
Coenogonium leprieurii	AFTOL-ID 351	AY584698	AF465442
Coenogonium luteum	AFTOL-ID 352	AY584699	AF279387
Coenogonium pineti	Germany, 24-01-2002 Palice (herb. Palice)	AY300884	AY300834
Cryptodiscus foveolaris	Sweden, Gilenstam 2603a (UPS)	AY661673	AY661683
Cryptodiscus gloeocapsa	Czech Republic, 16-02-2002 Palice (herb. Palice)	AY300880	AF465440
Cryptodiscus pini	Sweden, Wedin & Baloch 26VII07 (S)	FJ904705	FJ904683
Cryptodiscus tabularum	Sweden, Baloch SW073 (S)	FJ904710	FJ904688
Diorygma circumfusum	Australia, Kalb 33922 (herb. Kalb)	DQ431963	AY640019

Diploschistes caesioplumbeus	Spain, Llimona & Fdez.-Brime, BCNLich 17182 (BCN)	**HQ659170**	**HQ659181**
Diploschistes gypsaceus	Spain, Llimona & Fdez.-Brime, BCNLich 17180 (BCN)	**HQ659171**	**HQ659182**
Diploschistes ocellatus	Spain, Llimona & Fdez.-Brime, BCNLich 17181 (BCN)	**HQ659172**	**HQ659183**
Dyplolabia afzelii	Dominican Republic, Kalb 33153 (herb. Kalb)	DQ431949	DQ431922
Echinoplaca epiphylla	Mexico, Herrera et al. s.n. (F, sample No. M13)	AY341368	AY341354
Fibrillithecis halei	Australia, Mangold 31g (F)	EU075573	EU075621
Fissurina insidiosa	AFTOL-ID 1662	DQ972995	DQ973045
Gomphillus ophiosporus	Costa Rica, Will-Wolf 10006a (F, sample No. 101)	AY341371	AY341357
Gyalecta friesii	AFTOL-ID 4926	HQ659178*	HQ659179*
Gyalecta hypoleuca	AFTOL-ID 380	HQ659180*	AF465453
Gyalecta ulmi	Scheidegger, n. 0047589 (DUKE)	AY584706	AF465463
Gyalectidium imperfectum	Costa Rica, Lucking s.n. (F, sample No. 2)	AY341372	AY341358
Ingvariella bispora 1	Portugal, Rico 3683/1, MA Lich 15288 (MA)	**HQ659173**	**HQ659184**
Ingvariella bispora 2	Spain, Llimona s.n., BCNLich 17183 (BCN)	**HQ659174**	**HQ659185**
Ingvariella bispora 3	Italy, A.Vezda Lich. Selecti Exsicc. 2206, No. 144446 (DUKE)	**HQ659175**	**----------**
Leiorreuma hypomelaenum	Australia, Kalb 33916 (herb. Kalb)	DQ431971	DQ431933
Myriotrema trypaneoides	Australia, Lumbsch 19167v & Mangold (F)	EU075580	EU075628
Ocellularia aurata	Australia, Mangold 33a (F)	EU075564	EU075613
Ocellularia chiriquiensis	Australia, Mangold 18d (F)	EU075582	EU075629
Ocellularia perforata	Australia, Lumbsch 19120ja & Mangold (F)	EU075587	EU075634
Ocellularia postposita	Tanzania, Frisch 99/Tz1879	DQ384873	AY640008
Ocellularia profunda	Australia, Lumbsch 19123k & Mangold (F)	EU075590	EU075636
Odontotrema sp. 1	Sweden, Gilenstam 2560 (UPS)	AY661674	AY661684
Odontotrema sp. 2	Sweden, Gilenstam 2601b (UPS)	AY661675	AY661685

Phaeographis caesioradians	Australia, Kalb 33917 (herb. Kalb)	DQ431968	AY640021
Phaeographis lecanographa	Mexico, RLD 071 (herb. Kalb)	DQ431983	DQ431943
Phlyctis agelaea	AFTOL-ID 1670	HQ659176*	HQ659177*
Phlyctis argena	AFTOL-ID 1375	DQ986880	DQ986771
Placopsis gelida	Iceland, Heidmarsson 28486 (herb. Heidmarsson)	AY212859	AY212836
Platygramme australiensis	Australia, Kalb 33930 (herb. Kalb)	DQ431970	AY640024
Platygramme caesiopruinosa	Dominican Republic, Kalb 33150 (herb. Kalb)	DQ431973	AY640023
Ramonia sp.	Palice 2336 (herb. Palice)	AY300921	AY300871
Sagiolechia rhexoblephara	Sweden, 2002 Palice s.n. (herb. Palice)	AY853341	AY853391
Sarcographa fenicis	Australia, Kalb 33920 (herb. Kalb)	DQ431967	DQ431931
Sarcographa ramificans	Costa Rica, Luecking 16229g (B) (herb. Kalb)	DQ431981	DQ431942
Schizoxylon albescens	Sweden, Gilenstam 2696a (UPS)	DQ401142	DQ401144
Stegobolus fissus	Australia, Lumbsch 19108f & Mangold (F)	EU075594	EU075640
Stegobolus subcavatus	Australia, Lumbsch 19151u & Mangold (F)	EU075595	EU075641
Stictis confusum	Sweden, Wedin 7070 (UPS)	DQ401141	DQ401143
Stictis populorum	Sweden, Gilenstam 2610a (UPS)	AY527356	AY527327
Stictis radiata	Sweden, Gilenstam 2449a (UPS)	AY340532	AY527308
Trapeliopsis flexuosa	AFTOL-ID 1028	DQ986862	AF274118
Thelotrema diplotrema	Australia, Lumbsch 19127v & Mangold (F)	EU075599	EU075643
Thelotrema lepadinum	USA, Printzen 5745 (herb. Printzen)	AY300916	AY300866
Topeliopsis muscigena	Australia, Mangold 5d (F)	EU075611	EU075656
Tricharia longispora	Costa Rica, Lucking s.n. (F, sample No. 37)	AY341374	AY341360

ONLINE DATA SUPPLEMENT 2. Specimens examined of *Ingvariella bispora*, GREECE. EAST AEGEAN ISLANDS. Nomos Samos, Ikaria Island, road along antennas on Mt. Atheras, 26º 17,2' E, 37º 38,7' N, 800 m, gneiss rocks, 15 09 2002, *Sipman & Raus 48700* (B 60 0165171); 26º 16,5' E, 37º 38,1' N, 800 m, schists, 16 09 2002, *Sipman & Raus 48821* (B 60 0165170); Frandato, W of Dafni, 26º 08,34' E, 37º 36,13' N, 510 m, gneiss rocks, 24 09 2002, *Sipman & Raus 49531* (B 60 0165169); STEREA ELLAS. Periferia Protevousis, Dimos Kifisia, N Attika, Mt. Penteli, W-side, 23º 52,66' E, 38º 04,74' N, 950 m, siliceous rocks, 05 10 2005, *Sipman & Raus 54578* (B 60 0135534); WESTERN AEGEAN ISLANDS. Nomos Evvias, Ep. & Dim. Karistos, S Evvia, mountain slope above Metochi, along road to Stavros, 24º 28,29' E, 38º 01,59' N, 550 m, schists, 25 09 2005, *Sipman & Raus 53822* (B 60 0127650); summit area of Mt. Ochi, 24º 27,9' E, 38º 03,5' N, 1370 m, schists, 26 09 2005, *Sipman & Raus 54004* (B 60 0127506); Mt. Kastanolongos, W of Andia, 24º 30,4' E, 38º 02,8' N, 820 m, schists, 28 09 2005, *Sipman & Raus 54098* (B 60 0141917); PORTUGAL. TRAS-OS-MONTES. Bragança, Serra da Nogueira, to Alimonde, 29TPG789261, 1040 m, ultrabasic rocks, 06 09 2006, *Rico 3683/1* (MAF 15288), *Rico 3683/1 dupl* (MAF 15289); SPAIN. GIRONA. Cadaqués, Mas d'en Baltre, 31TEG214804, 70 m, schists, 26 01 2010 *Llimona* s.n., (BCNLich 17183); TENERIFE. Santiago de Teide, Teno Mts., along de road to Masca, Degollado de Cherpe, 1000 m, basalt, 29 11 1989, *Lumbsch 7212a & Mietzsch* (DUKE 0144864); IRAN. CHACHARMAHAL & BAKHTIYARI. S of Shahrekord, 50º 53,9' E, 32º 29,3' N, 1700 m, stone, 24 01 2007, *Valadbeigi 7062* (B 60 0175776); ITALY. SARDINIA, Monte Limbara Sud, 9º 11' E, 40º 47' N, 630 m, granite, 1999, *Nöske 419* (B 60 0123600); Cagliari, Giara di Gesturi, over Gesturi, 550 m, basalt, 14 07 1987, *Nimis, Tetriach & Vězda* (A. Vězda: Lichenes Selecti Exsiccatti 2206); TURKEY. TRABZON. Araklı distr., SE of Paskalar Yaylası, 40º 01,7' E, 40º 40,1' N, 2400 m, siliceous rocks, 17 08 2005, *Kinalioglu 1468* (B 60 0163237); N of Polot Yaylası, 2520 m, siliceous rocks, 04 08 2002, *Kinalioglu 1142* (B 60 0131767); N of Polot Yaylası, 2550 m, calcareous rocks, 06 08 2002, *Kinalioglu 1176* (B 60 0131768).

RESUM GENERAL I DISCUSSIÓ DELS RESULTATS

RESUM GENERAL I DISCUSSIÓ DELS RESULTATS

1. RESUM DE L'ESTUDI FLORÍSTIC

1.1. RESULTATS DEL CATÀLEG

Com a resultat de l'estudi dels líquens saxícoles i terrícoles, i els seus fongs liquenícoles, en l'àrea del Parc Natural de Cap de Creus, s'ha elaborat un catàleg amb totes les espècies identificades fins el moment, que inclou 294 tàxons, dels quals 263 corresponen a fongs liquenitzats i 31 a fongs liquenícoles. Amb els exemplars estudiats, s'ha constituït un herbari format per 845 plecs, el qual ha estat dipositat al Centre de Documentació de Biodiversitat Vegetal de la Universitat de Barcelona (CeDocBiV, Herbari BCN-Lich).

Des del punt de vista sistemàtic [segons la classificació proposada a Lumbsch & Huhndorf (2010)], les espècies incloses al catàleg pertanyen a 104 gèneres d'ascomicets, que es reparteixen en 44 famílies, 17 ordres i 6 classes. Els ordres amb major representació són les *Lecanorales* i les *Teloschistales*, amb 72 i 70 tàxons citats respectivament, seguit de les *Verrucariales*, amb 27 tàxons. Pel que fa a les famílies, les *Physciaceae* i *Teloschistaceae* són les més abundants en espècies, amb 39 i 31 tàxons citats i, a continuació, vindrien les *Verrucariaceae*, amb 26 tàxons. Com a gèneres més ben representats destaca *Caloplaca* (*Teloschistaceae*) amb 27 espècies, seguit de *Buellia* (*Physciaceae*), *Cladonia* (*Cladoniaceae*) i *Verrucaria* (*Verrucariaceae*) amb 11 espècies cadascuna, i *Lecanora* (*Lecanoraceae*), *Pertusaria* (*Pertusariaceae*) i *Rinodina* (*Physciaceae*) amb 10 espècies cadascuna.

A partir de les espècies identificades, podem resumir les dades referents a noves citacions de la següent manera:

- 9 tàxons són noves cites per a la península Ibèrica: *Arthonia lecanorina*, *Caloplaca arcis*, *C. austrocitrina*, *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon simplicatum*, *Endococcus buelliae*, *Micarea melaenida*, *Polycoccum rinodinae* i *P. teresum*. Cal destacar que *P. rinodinae* és també primera cita per a Europa (es coneixia únicament de les Illes Canàries, d'on va ser descrita) i que la troballa de *P. teresum* representa la segona cita d'aquest tàxon (conegut només de la localitat original, a Turquia).

- A més de les noves cites per a la península, 34 tàxons són nous a Catalunya: *Acarospora modenensis*, *A. sinopica*, *Arthonia molendoi*, *Aspicilia subdepressa*, *Caloplaca flavocitrina*, *C. furax*, *Cladonia firma*, *C. subcervicornis*, *Diploschistes caesioplumbeus*, *Endococcus fusiger*, *E. macrosporus*, *Enterographa pitardii*, *Heteroplacidium contumescens*, *Ingaderia troglodytica*, *Involucropyrenium tremniacense*, *Lecania inundata*, *Lecanora salina*, *Opegrapha cesareensis*, *Placidium tenellum*, *Polycoccum rubellianae*, *Porina byssophila*, *Porpidia hydrophila*, *Psora vallesiaca*, *Rhizocarpon viridiatrum*, *Rinodina atrocinerea*, *R. sicula*, *Roselliniella atlantica*, *Solenopsora vulturiensis*, *Stigmidium hageniae*, *Thelenella muscorum* var. *octospora*, *Thrombium epigaeum*, *Trapelia placodioides*, *Xanthoparmelia mougeotii* i *Zwackhiomyces lecanorae*.

1.2. TAXONOMIA

1.2.1. FONGS LIQUENÍCOLES

Durant la realització d'aquest treball florístic s'ha publicat una nova espècie de fong liquenícola, *Lichenostigma rupicolae* Fdez.-Brime & Nav.-Ros., que creix sobre el tal·lus i els apotecis de *Pertusaria rupicola*. En l'àrea d'estudi, *Lichenostigma rupicolae* s'ha detectat freqüentment en molts dels espècimens de *Pertusaria rupicola* estudiats. De la mateixa manera, es va trobar fàcilment en les mostres de *P. rupicola* que vam demanar en préstec a l'herbari BCN-Lich amb l'objectiu de cercar més casos de presència de l'esmentat fong liquenícola. Per aquest motiu, podem concloure que es tracta d'un paràsit força habitual en aquesta espècie de *Pertusaria*. De fet, aquest fong liquenícola no havia passat desapercebut als especialistes, els quals, fins ara, havien vist obstaculitzada la seva descripció, per manca de material fèrtil (P. Navarro-Rosinés, com. pers.).

El gènere *Lichenostigma* es caracteritza fonamentalment per formar ascocarps de tipus estromàtic, dins dels quals els ascs es desenvolupen enmig d'un teixit pseudoparenquimàtic; és a dir, no formen filaments interascals (Navarro-Rosinés & Hafellner, 1996). El gènere *Lichenothelia* és molt semblant a *Lichenostigma* perquè també fa estromes com a estructura reproductora. En canvi, a *Lichenothelia* els ascs es troben en un hamateci, o bé de tipus pseudoparenquimàtic, o bé format per cèl·lules allargades que formen pseudoparàfisis (Henssen, 1987). És un tret destacable que a *Lichenostigma rupicolae* hem observat al voltant d'alguns ascs, la presència de cèl·lules irregularment allargades, diferents de les cèl·lules esfèriques que formen la resta del compacte teixit interascal, i que hem interpretat com un hamateci incipient. Aquest teixit, no s'havia observat en cap espècie de *Lichenostigma* prèviament descrita, i mostra una certa afinitat amb el tipus d'hamateci que presenta *Lichenothelia*. A més a més, també hem observat en la nostra espècie la formació de macroconidis en la superfície dels cordons miceliars, quelcom que havia estat prèviament citat per Ihlen (2004) de l'espècie *Lichenostigma supertegentis*. La presència de macroconidis en aquestes dues espècies de *Lichenostigma* també és un fet rellevant, ja que fins que es va descriure *L. supertegentis* (Ihlen, *op. cit.*), es considerava que la formació de macroconidis era un tret que diferenciava el gènere *Lichenothelia* de *Lichenostigma*. Els caràcters esmentats serien indicatius, de la proximitat entre els gèneres *Lichenostigma* i *Lichenothelia*. Tant Ihlen (*op. cit.*), com altres autors (Pérez-Ortega & Calatayud, 2009), consideren que caldria estudiar aquests dos gèneres en un context filogenètic basat en dades moleculars, per tal d'investigar-ne la seva delimitació, ja que la circumscripció actual dels mateixos, basada en caràcters morfològics, no resulta prou clara.

A més de la nova espècie descrita, han estat trobats en aquest estudi alguns fongs liquenícoles que no han pogut ésser assignats a cap de les espècies conegudes fins el moment, tot i que han pogut ésser identificats al nivell de gènere:

- *Lichenostigma* sp. L'espècie designada com *Lichenostigma* sp. (paràsit sobre el tal·lus de *Pertusaria monogona*) presenta notables diferències amb *Lichenostigma rupicolae* pel que fa als cordons miceliars, ja que a *Lichenostigma* sp. són notablement més llargs, es ramifiquen partint d'un cordó miceliar central més gruixut i no formen macroconidis. De moment, però, el material examinat presenta pocs estromes fèrtils amb espores, i això fa necessària la revisió de més material per poder conèixer amb més detall els seus caràcters esporals.

- *Zwackhiomyces* sp. Els espècimens de *Zwackhiomyces* sp. que hem trobat creixent sobre *Endocarpon pusillum* han estat recol·lectats en una única localitat, on aquest fong paràsit era molt abundant. La disponibilitat de suficient material ens ha permès estudiar en detall aquest tàxon i comparar-lo amb les espècies descrites de *Zwackhiomyces*, fins arribar a la conclusió que es tracti d'una espècie que encara no ha estat descrita. Martin Grube ens ha esmentat (*in litt.*, 2011) la presència d'aquesta potencial espècie nova de *Zwackhiomyces* en recol·leccions d'*Endocarpon pusillum* fetes a França. Restem a l'espera de poder estudiar aquest material extrapeninsular, per tal d'incloure'l en la publicació de la descripció formal d'aquesta espècie.

- *Cercidospora* sp. Pel que fa a les espècies de fongs liquenícoles designades al catàleg com a *Cercidospora* sp. 1 (paràsit de *Caloplaca irrubescens*) i *Cercidospora* sp. 2 (paràsit de *Caloplaca crenularia*), el material de què disposem no és gaire abundant ni prou desenvolupat, motiu pel qual considerem que cal recol·lectar i estudiar més mostres si volem aclarir la identitat d'aquests dos tàxons.

1.2.2. FONGS LIQUENITZATS

Pel que fa als líquens, del conjunt d'exemplars examinats en aquest estudi, hem trobat una sèrie d'espècimens que, malgrat compartir semblances amb espècies ja descrites, no han pogut ésser atribuïts amb certesa a cap d'elles per la presència de diferències en caràcters clau per a la delimitació d'aquestes espècies o bé per absència d'estructures fèrtils. A continuació esmentem els espècimens problemàtics:

- S'han trobat dos exemplars amb un tal·lus ben desenvolupat, que han estat identificats com a *Acarospora* cf. *scotica*. La manca d'espores, que ens permetessin confirmar-ne la identificació, ens ha obligat a deixar les mostres com a cf. Serà necessari estudiar més material per assegurar la presència d'aquest tàxon en l'àrea d'estudi.

- Els exemplars trobats, caracteritzats per la presència de picnidiòspores filiformes i recorbades, i espores del tipus *Physconia*, s'han assignat provisionalment a *Amandinea* sp. Les espècies més properes a aquest tàxon són *A. punctata* i *A. lecideina*, que es diferencien d'*Amandinea* sp. per la mida més gran de les espores. El gènere *Amandinea* se separa de *Buellia*, únicament, per les picnidiòspores llargues, filiformes i corbades (Scheidegger, 1993). Segons Bungartz (2004), aquesta separació ha reunit dins del gènere *Amandinea* espècies amb notables diferències entre elles, pel que fa a l'anatomia dels apotecis, morfologia del tal·lus o contingut químic. Tant en l'anàlisi cladístic presentat per Bungartz (*op. cit.*), com en la filogènia molecular de Helms *et al.* (2003), *Amandinea* apareix agrupat dins del clade de *Buellia*. Per totes aquestes evidències morfològiques i filogenètiques, Bungartz (2004) qüestiona obertament la validesa del gènere *Amandinea*. Per això, caldrà estudiar més exemplars d'aquesta *Amandinea* sp. que hem trobat en la nostra àrea d'estudi, per poder-ne determinar correctament la identitat, sense descartar possibles afinitats amb espècies del gènere *Buellia*.

1.3. BIOTIPUS I FOTOBIONTS

En el conjunt de tàxons liquènics estudiats, hi trobem la següent representació de biotipus: 67% crustaci (176 espècies), 15% foliaci (39 espècies), 10% esquamulós (25 espècies), 4% tal·lus compost (corresponent a les 11 espècies de *Cladonia*), 3% fruticulós (9 espècies) i 1% leprarioide (3 espècies). Si els biotipus s'analitzen considerant únicament als líquens saxícoles, la proporció dels crustacis s'eleva fins el 75%, mentre la proporció d'esquamulosos i de fruticulosos disminueix fins a un 4% per a cadascun.

El biotipus crustaci domina clarament a tota l'àrea d'estudi tot i que, a mida que les condicions d'humitat augmenten, es fa més notable la presència de líquens foliacis i fruticulosos. Per exemple, la localitat 25 (vora el Mas d'en Baltre), que reuneix unes condicions ambientals generals tèrmiques i seques (com en la gran majoria de l'àrea interior del Parc, que està per sota dels 400 m) presenta 39 tàxons, dels quals un 92% són crustacis, un 5% foliacis i un 3% compostos. Si la comparem amb la localitat 22 (cala Jonquet), en la que han estat trobats 37 tàxons, continuen predominant els de biotipus crustaci, que representen un 86%. Però gràcies a les condicions d'humitat lleugerament superiors a les de la localitat 25 (per la influència dels vents marins humits), augmenta la presència de líquens fruticulosos i foliacis, que representen el 8% i el 6% respectivament.

En localitats on la humitat ambiental és considerablement més elevada (per sobre els 400 m o en vessants orientats al nord), la presència dels biotipus amb una demanda hídrica més alta es fa més evident, fet que suposa un augment en la riquesa de biotipus i també d'espècies. Per exemple, la localitat 7 (sobre el camí al monestir de Sant Pere de Rodes) es troba en un vessant nord, on amb freqüència es formen boires més o menys persistents. Aquesta localitat és molt rica en espècies, amb 62 tàxons dels quals un 52% corresponen al biotipus crustaci, un 31% al foliaci, un 6% al fruticulós, un 6% al compost i un 5% a l'esquamulós.

Pel que fa als fotobionts dels líquens inclosos en el catàleg, un 87% (229 espècies) presenten algues protococcoides (generalment trebuxioides), un 5% les tenen del gènere *Trentepohlia* (14 espècies) i un 8% (20 espècies) depenen de cianobacteris com a fotobiont. Per tant, els líquens amb algues protococcoides predominen en el territori, tant en número d'espècies com en recobriment. Únicament a la zona litoral, trobem una representació més notable de les espècies amb *Trentepohlia* que, tot i que són representades per un nombre reduït d'espècies, presenten un alt recobriment en les superfícies verticals o entrades de cova, on estan protegides de la insolació directa i de l'aigua de la pluja, que rarament les mulla. Els líquens amb cianobactèries estan pràcticament restringits a les superfícies d'escorrentia, quelcom íntimament lligat a la fisiologia del seu tipus de fotobiont, que exigeix de la presència d'aigua líquida per activar la fotosíntesi (Lange *et al*., 1993).

1.4. ESQUEMA DE LES COMUNITATS

Com a resultat de les observacions de camp i de les dades del catàleg florístic, hem elaborat un esquema de les comunitats del territori. Tot i que els objectius del capítol 1 s'han centrat fonamentalment en el treball florístic, en aquest apartat intentarem una aproximació les comunitats observades, dins dels esquemes sintaxonòmics ja establerts.

1.4.1. COMUNITATS SAXÍCOLES

1.4.1.1. Comunitats de líquens silicícoles

1.4.1.1.1. Comunitats ombròfiles

La majoria dels afloraments silícics es troben exposats a la pluja. Les comunitats silicícoles que estan ben adaptades a l'absorció d'aigua líquida i també de rosada, han estat tradicionalment incloses en la classe *Rhizocarpetea geographici* Mattick 1951 em. Wirth 1972.

Dels diversos ordres en què la metodologia sigmatista adaptada als líquens per Klement (1955) tipifica les comunitats silicícoles, l'ordre *Aspicilietalia gibbosae* Wirth em. Llimona et Egea 1987, correspon força bé al conjunt de les comunitats silicícoles de l'àrea estudiada (exceptuant algunes comunitats que es desenvolupen en condicions especials, que s'esmentaran a part). Hi trobem comunitats més o menys fotòfiles, però diversament tolerants a la radiació solar directa. Com a espècies més o menys característiques podem mencionar: *Aspicilia intermutans*, *A. caesiocinerea*, *A. cupreoglauca*, *Rhizocarpon geographicum*, *Candelariella vitellina*, *Xanthoparmelia pulla*, *Caloplaca crenularia* i *Lecanora campestris*.

Pel que fa a les comunitats de les superfícies assolellades, hi trobem líquens més o menys heliòfils i xeròfils, sovint nitròfils. Tradicionalment, aquestes comunitats s'inclouen en el subordre *Parmelienalia conspersae* Llimona et Egea 1987, amb *Xanthoparmelia conspersa*, *X. verruculifera*, *Caloplaca vitellinula* i *Lecidea fuscoatra* com espècies característiques.

Un cas particular en les comunitats heliòfiles, és la comunitat dominada per *Acarospora hilaris*, que s'instal·la sobre les superfícies verticals de roca molt dura. La trobem a vegades parasitada per *A. epithallina*, i acompanyada de *Dimelaena oreina* i d'espècies més o menys termòfiles com *Buellia stellulata*, *B. tesserata*, *Caloplaca arenaria i Candelariella vitellina*. Aquesta comunitat és molt propera a l'*Acarosporetum epithallino-hilaris* Crespo, Barreno et Follmann 1976, una comunitat també caracteritzada per la presència de *Caloplaca carphinea*, que en l'àrea estudiada apareix només sobre quars, i sempre associada amb *Dimelaena oreina* i *Rinodina alba*.

El granit meteoritzat, en canvi, presenta un cortegi de líquens poc aparent, encara no tipificat, on són presents espècies poc usuals com *Caloplaca ligustica*, *C. aetnensis*, *Acarospora modenensis*, *A. oligospora* i espècies més corrents, com *Polysporina simplex*, *Phaeophyscia hirsuta* i *Sarcogyne privigina*.

A baixa altitud, i més amunt de les comunitats litorals, la presència de *Diploicia subcanescens* i, molt localitzada, de *Solenopsora holophaea*, ens evoca el *Solenopsoro holophaeae-Diploicietum subcanescentis* Egea et Llimona 1987, del sud-est de la península Ibèrica.

La resta de les comunitat heliòfiles, especialment les de les superfícies poc inclinades, correspon força bé a l'aliança *Parmelion conspersae* Hadač 1984 em. Egea et Llimona 1987, amb líquens com *Caloplaca arenaria*, *Buellia atrocinerella* i *Rhizocarpon polycarpum*. És un cas especial i rar dins d'aquesta aliança, la presència ocasional d'*Acarospora sulphurata* (as. *Acarosporetum sulphuratae* Egea et Llimona 1987), que al sud-est de la península Ibèrica es desenvolupa per sobre dels 1700 m, i en la nostra àrea d'estudi es pot establir per sota dels 400 m.

Molt més freqüents sobre superfícies poc inclinades i properes al sòl (codines), són les comunitats amb *Xanthoparmelia conspersa*, *X. tinctina*, *X. pulla*, *X. glabrans*, *Buellia badia*, *Candelariella vitellina*, *Lecidea fuscoatra* i, algun cop, *Xanthoparmelia mougeotii*, una espècie força nitròfila. Aquesta comunitat recorda a la 'Comunitat de *Parmelia conspersa*' (Egea & Llimona, 1987) i al *Xanthoparmelietum tinctinae* Egea et Llimona 1987 nom. mut. (Roux *et al.*, 2011), ambdues descrites del sud-est de la península Ibèrica, tot i que en latituds més meridionals es refugia als vessants nord.

Sobre tota mena d'esquistos metamòrfics i en condicions de baixa eutròfia, trobem extenses comunitats on predomina pel seu recobriment el gènere *Aspicilia* (*A. caesiocinerea*, *A. intermutans*, *A. subdepressa*) amb *Caloplaca furax*, *C. rubelliana*, *Diploschistes actinostomus*, *D. euganeus*, *Trapelia involuta* i la penetració d'espècies menys fotòfiles, com *Lecidella asema* var. *elaeochromoides*, *Catillaria chalybeia*, *Lecanora rupicola* subsp. *sulphurata* o *Lecidea sarcogynoides*. En aquest cas, es relacionaria amb la 'Comunitat d'*Aspicilia intermutans* i *Diploschistes actinostomus*' (Egea & Llimona, 1987).

Si ens centrem ara en les superfícies poc assolellades, generalment les orientades al N o al NW, hi trobem un recobriment gairebé total de líquens crustacis, sovint de tal·lus gruixut, amb presència més ocasional i localitzada de líquens foliacis i fruticulosos. El subordre *Pertusarienalia leucosorae* Egea et Llimona 1987 inclou aquestes comunitat heliòfobes, feblement nitròfiles, que tenen el seu òptim a la regió mediterrània, però que poden penetrar en indrets especialment càlids més al nord d'aquesta regió.

La comunitat més ben definida i clàssica és el *Pertusarietum rupicolae* Wirth et Llimona 1975, caracteritzat pels colors groc pàl·lid de *Pertusaria rupicola* (sovint parasitada per *Lichenostigma rupicolae*), i acompanyada per tal·lus, sovint grans, de *P. pseudocorallina*, *P. aspergilla*, *P. leucosora*, *Lecanora gangaleoides*, *L. praepostera*, *L. rupicola* subsp. *sulphurata*, *Tephromela atra*, *Buellia subdisciformis*, *Protoparmelia montagnei* o *Ochrolechia parella*.

La part més ombrívola de la Serra de Verdera i altres punts especialment humits per la influència de les boires marines, presenten aquesta comunitat enriquida per grans i gruixuts tal·lus de *Pertusaria monogona*, diferencial del *Pertusarietum rupicolae* subass. *pertusarietosum monogonae* [pendent de tipificar, ja que la comunitat descrita sota el mateix nom per Llimona & Egea (1984) correspon a una comunitat de *Pertusaria teneriffensis*, una espècie vicariant]. Hi trobem a més, espècies aerohigròfiles com *Anaptychia runcinata* (tot i ser típica de les costes del NW de la Península i altres costes atlàntiques, aquí no és de preferències litorals), *Parmelia saxatilis*, *Parmelina tiliacea*, *Ramalina breviuscula* i, molt localitzada en cims de blocs, *R. polymorpha*, espècie relacionada amb el *Ramalinetum capitatae* Frey 1923, una comunitat oròfila aquí molt empobrida.

A baixa altitud (per sota de 100 m) i vora la costa, *Pertusaria rupicola* i altres *Pertusaria* encara hi són presents, però d'altres espècies com *Lecanora sulphurea*, *L. rupicola* subsp. *sulphurata* o *Protoparmelia montagnei*, hi predominen. Fins i tot, hi arriba *Rhizocarpon* gr. *geographicum*, representat per tal·lus estèrils. *Ramalina breviuscula* també hi és freqüent, acompanyada de *R. requienii*.

1.4.1.1.2. Comunitats ombròfobes

Especialment en localitats no gaire distants del mar, les superfícies verticals i sobreplomades, sostres, baumes i coves, són colonitzades preferentment per líquens que tenen *Trentepohlia* com a fotobiont, i presenten tolerància a la baixa il·luminació. Són termòfils i tenen capacitat per entrar en activitat gràcies a estar ben adaptats a l'absorció directa de vapor d'aigua a partir de l'atmosfera. Aquestes condicions són tan particulars, gairebé subtropicals, que els líquens que s'hi adapten apareixen tant sobre roca calcària com sobre roca silícia. Per aquesta raó, Egea (1989) va incloure el conjunt d'aquestes comunitats costaneres mediterrànies i macaronèsiques en una sola classe, *Roccelletea phycopsis* Egea 1989. Les espècies característiques predominants són les mateixes: *Dirina massiliensis*, *Lecanographa grumulosa* i *Roccella phycopsis*. Cal fer notar que a les costes silícies es presenten sempre amb una coloració gris bru, que les fa semblar diferents de les calcícoles, que són ben blanques o pàl·lides. La presència d'espècies com *Opegrapha lutulenta* i la penetració de *Diploicia subcanescens* podrien ser un reflex de l'aliança silicícola *Roccellion tinctoriae* Follmann 1976, inclosa per Egea (*op. cit.*) dins de l'ordre *Roccelletalia fuciformis* Egea 1989.

1.4.1.1.3. Comunitats dominades per factors ecològics especials

1.4.1.1.3.1. Superfícies d'escorrentia

En les superfícies d'escorrentia hi trobem un cortegi molt ben definit d'espècies, dominat per la presència de *Peltula euploca* i *Lichinella stipatula*, de l'aliança *Peltulion euplocae* Llimona et Egea 1985. La presència, molt localitzada, de líquens més termòfils com *Peltula obscurans*, *P. omphaliza*, *P. placodizans*, *Lichinella cribellifera* i *Gliphopeltis ligustica*, configuren una fàcies del *Peltuletum euplocae* Wirth 1972 em. Llimona et Egea 1984, que marca una tendència a la comunitat més termòfila del sud-est de la península Ibèrica, *Peltuletum obscuranto-euplocae* Llimona et Egea 1984. A més dels poblaments foscos de cianolíquens i cianofícies, s'hi afegeixen líquens amb fotobionts protococcoides, com *Caloplaca irrubescens*, *Physcia dubia*, *Toninia cinereovirens* (que comença essent paràsita de *Lichinella stipatula*) i, més rarament, *Aspicilia contorta* subsp. *hoffmanniana*.

Les superfícies d'escorrentia poc assolellades estan menys ben caracteritzades. Hi podem trobar *Catillaria chalybeia* i algunes *Aspicilia*, com *A. caesiocinerea*, entre els líquens crustacis. Però sovint hi destaca un cianoliquen negre i foliaci, *Collema ryssoleum*, i un d'umbilicat, *Dermatocarpon miniatum*. Aquest és un cortegi poc conegut, potser relacionat amb les *Dermatocarpetea miniati* de Wirth 1972. La presència de *Dermatocarpon luridum* entronca ja amb les comunitats hidròfiles, i indica llarga durada de la làmina d'aigua que recobreix la roca.

1.4.1.1.3.2. Superfícies temporalment inundades

L'àrea d'estudi presenta cursos d'aigua poc o gens eutrofitzada, sovint secs a l'estiu, i sobre llur llera rocosa els líquens es disposen en bandes estretes, segons la seva tolerància a la immersió. Aquestes comunitats hidrofítiques han estat ben estudiades en alguns punts de la nostra àrea d'estudi a la tesi de Pereira (1992). En aquest treball de Pereira, s'hi descriu una comunitat amb *Caloplaca atroflava*, *Verrucaria praetermissa*, *Caloplaca aegaea* (sub *C.* aff. *scopularis*) i *C. diffusa* (sub *C.* aff. *littorea*), que correspon força bé a les nostres observacions de les comunitats situades vora l'aigua, que queden cobertes només quan els rierols creixen a la primavera o a la tardor, durant períodes de pocs dies. Aquesta comunitat, anomenada *Caloplaco atroflavae-Verrucarietum praetermissae* Pereira 1992, s'inscriu en l'aliança *Verrucarietum praetermissae* Černoh. et Hadač em. Wirth 1972, pertanyent a la classe de comunitats hidròfiles *Aspicilietalia lacustris* Wirth ex Wirth 1980, dins la qual representaria l'associació més termòfila, nitròfila i de baixa altitud.

1.4.1.1.3.3. Comunitats litorals

La influència més o menys directa de la proximitat del mar, interferida sovint per l'acció eutrofitzant de les dejeccions dels ocells marins, defineix diferents bandes de comunitats litorals més o menys tolerants a la immersió per aigua de mar, que trobem ben estudiades a les Illes Britàniques i acceptablement ben caracteritzades per James *et al*. (1977). A la regió d'estudi, a la zona mediolitoral trobem *Pyrenocollema halodytes* (que resisteix llargs períodes d'immersió) instal·lat sobre closques de *Chthamalus* i *Patella*, i a la supralitoral, *Verrucaria amphibia*, formant una banda quasi contínua, de pocs centímetres a pocs metres. Aquest poblament liquènic sembla correspondre al *Verrucarietum amphibiae* Feldm. 1937 nom. mut. (Ménard, 1997), que es considera una forma vicariant de la comunitat atlàntica del *Verrucarietum maurae* DR. 1932.

Més amunt, després d'una banda sense líquens, comencen a aparèixer espècies tolerants als esquitxos i exigents en nutrients, com *Caloplaca marina*, *C. maritima* i *C. aegaea*, que acoloreixen de taronja aquesta comunitat, que representaria una variant mediterrània del *Caloplacetum marinae* DR. 1925. Més amunt, espècies com *Lecanora sulphurea*, *Diplotomma alboatrum* (ecòtipus *glaucoatrum*), ocasionalment *Thelopsis isiaca* (ecòtipus saxícola), *Rinodina alba* i, encara més amunt, *Ramalina breviuscula*, *R. requienii* i *Xanthoria aureola*, formen una comunitat que substituiria el *Ramalinetum scopularis* (DR. 1925) Klem. 1955 de les costes atlàntiques.

1.4.1.2. Comunitats de líquens calcícoles

Les comunitats de roques calcàries més o menys exposades a la pluja han estat poc explorades a l'àrea d'estudi, però al Cap Norfeu trobem, vora els penya-segats septentrionals poc insolats, extenses poblacions de *Caloplaca subochracea* var. *luteococcinea*, semblants al *Caloplacetum subochraceae* Roux 1978, on penetren líquens, preferentment endolítics, com *Verrucaria hochstetteri*, *V. lecideoides*, *Bagliettoa cazzae*, *Porina byssophila*, *Lecidella stigmatea*, relacionats amb el *Bagliettoetum cazzae* Clauzade et Roux 1975 nom. mut. (Roux *et al*., 2009)

Els penya-segats calcaris orientats al nord del Cap Norfeu, apareixen coberts per una comunitat blanca, visible de lluny i ben coneguda, el *Dirinetum massiliensis*, ben descrit per Clauzade & Roux (1975). Hi destaquem grans tal·lus amb apotecis prominents de *Dirina massiliensis* f. *massiliensis* (acompanyats de *D. massiliensis* f. *sorediata*), i tal·lus més petits de *Lecanographa grumulosa* i *Opegrapha calcarea*, sempre en posicions poc o gens mullades per la pluja.

1.4.2. COMUNITATS TERRÍCOLES

1.4.2.1. Comunitats de les dunes fòssils

A mig camí entre les condicions que troben els líquens terrícoles i els saxícoles, tenim les interessants comunitats de les dunes fòssils. És tracta d'un substrat molt peculiar, que permet que s'hi barregin espècies terrícoles marcadament calcícoles, com *Fulgensia fulgens*, *Toninia physaroides*, *T. tristis* subsp. *pseudotabacina* o *Squamarina lentigera*, amb espècies més típiques de sòls neutres o àcids, com *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon pusillum* i *Psora vallesiaca*. En les zones on les dunes estan més compactades, aleshores hi poden créixer espècies saxícoles com *Caloplaca aurantia* o *Placynthium tremniacum*. Es tracta probablement, d'una comunitat no tipificada.

1.4.2.2. Comunitats dels terraprims àcids

Grans extensions dels sòls de l'àrea d'estudi són coberts per estepars, que deixen poc espai als líquens, si exceptuem algunes gespes de *Cladonia rangiformis*. Malgrat tot, una comunitat molt característica és la que apareix en diverses localitats properes a la costa, en terraprims arenosos o llimosos (fins a formar una certa crosta). Algunes de les espècies més freqüents que es troben en els indrets més exposats són *Endocarpon pusillum*, *Cladonia foliacea*, *C. pyxidata*, *Leptogium lichenoides*, *Squamarina concrescens*, *Trapeliopsis wallrothii* i formes semi-vagrants de *Xanthoria aureola*. A més, en aquests sòls també hi trobem diversos líquens que han estat mai o rarament citats a la península Ibèrica com *Psora gresinonis*, *Endocarpon simplicatum* i *Micarea* *melaenida*. Poc després de la pluja, o en condicions d'inusual humitat atmosfèrica, també és possible detectar la presència de líquens efímers rars com *Epiphloea terrena*, *Gyalideopsis athalloides* i *Thrombium epigaeum*. Comunitats molt semblants han estat descrites de Provença per Rieux *et al.* (1977) com a variants meridionals de la comunitat *Crassuletum tilleae*.

1.5. ANÀLISI FITOGEOGRÀFICA

Els resultats de l'anàlisi fitogeogràfica dels líquens del catàleg (en la qual no hem inclòs els líquens identificats de forma incompleta, com "afinitat a" o "a confirmar"), mostren que la majoria de les espècies pertanyen a tres elements corològics principals.

El primer grup correspon a les espècies mediterrànies (30%), que es presenta com un grup heterogeni, en el qual podem distingir-hi diversos subgrups. Un primer subgrup, inclou les espècies que es distribueixen estrictament per la regió mediterrània europea (p. e., *Caloplaca aegaea*, *Epiphloea terrena*, *Psora gresinonis*). Un segon subgrup, inclou les espècies amb una distribució disjuncta, que a més d'estar presents a la regió mediterrània europea, habiten en territoris d'altres continents que gaudeixen d'un clima mediterrani (p. e., *Acarospora hilaris*, *Buellia tesserata*). Les espècies d'aquests dos subgrups apareixen en els punts més càlids del nostre territori d'estudi, com els afloraments rocosos molt exposats a la insolació directa (els orientats al sud o sud-est) o els claps exposats i secs dels terraprims silícics. Un tercer subgrup, inclou les espècies mediterrànies que estenen la seva distribució fins a les Illes Canàries (p. e., *Caloplaca aetnensis*, *Lecanora praepostera*, *Ramalina requienii*), un fet que posa de manifest l'estreta relació evolutiva i filogenètica entre ambdós territoris (Calatayud & Barreno, 1994). Finalment, un quart subgrup inclou les espècies que tenen el seu centre de distribució a la regió mediterrània, però que poden penetrar en enclavaments de clima sec i amb condicions microclimàtiques especialment tèrmiques, al nord i centre d'Europa (p. e., *Acarospora sulphurata*, *Buellia tirolensis*, *Peltula euploca*). Aquest darrer subgroup, és el que Nimis (1993) considera com l'element submediterrani, però que nosaltres hem mantingut dins del grup d'espècies mediterrànies tal i com va fer Calatayud (1998).

El segon grup, tan ben representant com l'element mediterrani, està format per les espècies de distribució temperada-mediterrània (29,5%), que es caracteritzen per tenir el seu centre de distribució al nord i centre d'Europa, i que també penetren a les muntanyes mediterrànies. Les espècies d'aquest grup es troben ben representades arreu del territori estudiat, a excepció de les contrades més càlides. Dins d'aquest grup de distribució temperada-mediterrània, algunes espècies són especialment abundants en la costa atlàntica d'Europa, i en la nostra àrea d'estudi, les hem trobat en enclavaments especialment humits com lleres de roca de rierols (p. e., *Rinodina atrocinerea*, *R. teichophila*) o sobre talussos molsosos humits (p. e., *Parmotrema reticulatum*, *Peltigera collina*).

El tercer grup inclou les espècies d'àmplia distribució (19,5%). Hi podem distingir, d'una banda, les espècies nitròfiles, que en la nostra àrea d'estudi són abundants en els hàbitats amb una certa eutròfia, i que esdevenen les espècies dominants ens els hàbitats altament nitrificats, com els marges o afloraments propers a camins molt transitats o zones de pastura. D'altra banda, hi ha les espècies que presenten una àmplia distribució mundial, amb una certa amplitud dels requeriments ecològics, des dels pols fins a les zones tèrmiques i temperades, i que en la nostra àrea d'estudi hem trobat, tant en localitats costaneres com en d'altres, situades a més altitud.

Les espècies que presenten altres tipus de distribució, tot i ésser minoritàries, enriqueixen significativament la diversitat de la flora de l'àrea. És destacable la presència d'espècies de distribució mediterràneo-atlàntica (13,5%) i atlàntica (2%), que viuen en les contrades més humides del territori estudiat, com els afloraments rocosos ombrejats vora el mar o de les obagues de les zones altes (per sobre dels 350 m), que presenten una alta humitat per l'arribada freqüent de boires. Les espècies de distribució temperada (4,5%) i distribució àrtico-boreal (1%) apareixen de forma molt escadussera, en punts on es creen unes condicions microclimàtiques prou fredes i humides per permetre el seu creixement.

Com a consideracions finals de l'anàlisi fitogeogràfica, cal destacar que les condicions climàtiques particulars de l'àrea estudiada, que inclou des de zones molt càlides i àrides, a d'altres de més fredes i humides, permeten la conjunció tant d'espècies mediterrànies (algunes de caràcter molt termòfil) com d'extramediterrànies. Per tant, el Cap de Creus representa una zona fronterera on, en poc espai, conflueixen elements florístics dispars, amb condicions fredes o càlides segons l'exposició. Per això hi trobem superfícies-refugi d'espècies termòfiles, que troben aquí alguns dels punts més septentrionals de la seva distribució (com és el cas d'*Acarospora epithallina*) i d'altres, espècies molt més resistents al fred, que poden aparèixer a escassa altitud (com *Acarospora sulphurata*, *Dimelaena oreina* o *Rhizocarpon geographicum*).

1.6. ZONES MEREIXEDORES DE MESURES DE PROTECCIÓ ESPECIAL

Finalment, considerem important destacar les localitats estudiades més interessants des del punt de vista liquenològic, tant per la seva riquesa en espècies com per la presència d'espècies singulars. Creiem que haurien d'estar considerades en els plans especials de gestió del Parc, per a la seva protecció i conservació, especialment en els plans d'àrees prioritàries de protecció en cas d'incendi:

- Localitats 7 i 8: comprenen el batòlit constituït per granodiorites i esquistos, accessible per la pista asfaltada que porta al monestir de Sant Pere de Rodes, passant pel conjunt monumental de Santa Helena, que s'estén en altitud fins al pic de Sant Salvador de Verdera. Les dues localitats són riques en espècies, amb 62 i 56 tàxons identificats respectivament, entre ells, alguns poc o mai citats a la península Ibèrica, com *Caloplaca arcis*, *Enterographa pitardii* o *Rinodina sicula*. En aquesta zona hi creix una comunitat molt ben desenvolupada, dominada per *Pertusaria monogona*, que recobreix pràcticament tots els afloraments silícics que no han estat afectats pels incendis de 1986 i de 2000. Fins a mitjans de la dècada dels 80, en aquesta comunitat els tal·lus de *P. monogona* eren en la seva majoria grans i gruixuts, de fins 80 cm de diàmetre i 5 mm de gruix (X. Llimona, com. pers.), presumiblement centenaris, i donaven al paisatge d'aquesta àrea un bell color blanc, considerat un valor paisatgístic destacable d'aquesta zona del Parc. Desafortunadament, després dels incendis esmentats, que afectaren seriosament l'obaga de la Serra de Verdera els anys 1986 i 2000, una part important d'aquesta comunitat quedà greument malmesa, com hem pogut constatar en mostrejos posteriors al segon incendi. A les superfícies rocoses afectades hi hem trobat que un alt nombre dels vells i grans tal·lus de *P. monogona* presentaven un aspecte ennegrit i parcialment desprès de la roca. També hem constatat la desaparició de *Cladonia mediterranea* d'aquesta zona de la qual tenim coneixement de la seva presència abans de l'incendi de 1986, gràcies a les recol·leccions de l'herbari personal de Xavier Llimona. Considerem escaient destacar que en aquesta àrea es troba la única població ibèrica de la umbel·lífera *Bunium bulbocastanum* L., que es troba també amenaçada pels incendis recurrents, a més de per la sobrefreqüentació del turisme (Sáez *et al*., 2010).

- Localitat 10: en la Punta de s'Arenella, el sòl silícic és poc profund, sorrenc i compactat, formant una crosta superficial. L'esparsa coberta vegetal d'aquesta localitat havia deixat àmplies àrees de sòl totalment exposades, en les què han crescut líquens terrícoles termòfils, sovint efímers (molt difícils de veure en temps sec) i molt rars a la península Ibèrica com *Epiphloea terrena*, *Gyalideopsis athalloides* i *Heteroplacidium contumescens*, a més d'altres espècies no rares, però si poc abundants, com *Psora gresinonis*. En diverses visites a aquesta localitat, hem observat una degradació progressiva d'aquest hàbitat pel seu ús com aparcament davant del recinte del far de s'Arenella, la freqüentació i l'abocament de deixalles. Però, sobretot, hem observat la presència cada vegada més extensa d'espècies del gènere *Carpobrotus*, principalment *C. edulis*, una planta invasora amplament distribuïda i molt abundant dins del Parc Natural (Guirado, 2007). Aquesta planta creix molt massivament, cobrint cada cop més àrees de sòl prèviament ocupades pel singular poblament de líquens i briòfits [aquests darrers, sobretot, representats per espècies interessants de *Riccia* (Casas *et al*., 1998)], portant a l'empobriment gradual d'aquesta comunitat de criptògames i, fins i tot, a la seva futura desaparició en aquesta localitat si no s'eradica la presència de les espècies de *Carpobrotus*.

- Localitat 13: les dunes fòssils de les Cavorques estan formades per sorres de gra silícic compactades amb ciment calcari. Aquest singular substrat, molt porós, permet la coexistència de líquens terrícoles marcadament calcícoles amb d'altres més propis de substrats àcids. En total, hem trobat 32 tàxons en aquesta zona, entre els quals destaquen *Diploschistes diacapsis* subsp. *neutrophilus*, *Involucropyrenium tremniacense*, *Psora vallesiaca*, *Toninia physaroides* o *Toninia tristis*. subsp. *pseudotabacina*. Aquest geòtop està considerat pels experts com un element únic a Catalunya i de conservació prioritària (De Andrade Meireles *et al*., 2000). El ric poblament liquènic que presenta reforçaria els arguments dels geòlegs per aplicar en aquesta àrea mesures especials de protecció.

- Localitat 19: en la comunitat de líquens terrícoles que creix en els terraprims vora el prat d'en Pagès hi hem trobat 16 tàxons, alguns dels quals són destacables per la seva raresa a la península Ibèrica com *Endocarpon simplicatum* i *Psora gresinonis*. A més, destaca la presència d'espècies saxícoles que han adoptat secundàriament formes terrícoles en aquest hàbitat, com és el cas *Polysporina simplex* i *Xanthoria aureola*. Aquesta localitat presenta una comunitat terrícola molt similar a la que es desenvolupa als sòls de la Punta de s'Arenella, i com en el cas de s'Arenella, hem trobat restes d'escombraries escampades en diferents punts de la localitat. Cal tenir present que les comunitats de líquens terrícoles silicícoles són pràcticament desconegudes a Catalunya. Les comunitats que es troben al Cap de Creus són els únics exemples de què disposem fins ara per conèixer la composició i fenologia de les espècies. Per això resulta tan important preservar al màxim aquest tipus d'hàbitats.

2. ESTUDI TAXONÒMIC I FILOGENÈTIC DE *DIPLOSCHISTES*

2.1. CIRCUMSCRIPCIÓ DEL GÈNERE *DIPLOSCHISTES*

Els resultats de les anàlisis filogenètiques basades en els marcadors mtSSU i nuLSU (anàlisis MB1, ML1, MP1, capítol 3), han confirmat la monofília de *Diploschistes* segons la circumscripció actual del gènere, que inclou l'espècie *D. ocellatus*. La filogènia obtinguda en aquest estudi, és la primera que es reconstrueix incloent un mostreig suficientment representatiu de *Diploschistes* i extens per a la família de les *Graphidaceae*. Segons s'afirmava en l'estudi de Martín *et al*. (2003), era necessari un estudi filogenètic que integrés el conjunt de les *Thelotremataceae* (família actualment inclosa en les *Graphidaceae*) per resoldre les afinitats exactes de *D. ocellatus* amb la resta de *Diploschistes* i amb altres gèneres de la família. És per això, que en el nostre estudi hem incrementat considerablement el nombre de gèneres de *Graphidaceae* inclosos respecte el treball de Martín *et al*. (*op. cit*.).

La topologia resultant de la inferència bayesiana (anàlisi MB1, Figura 1, capítol 3), ens mostra com la primera divergència separa *Diploschistes ocellatus* de la resta de membres del gènere. La longitud de branca del clade que separa de *D. ocellatus* és considerablement llarga, si es compara amb les longituds de branca que mostren les relacions filogenètiques entre la resta de membres del gènere. Això reflecteix la notable divergència molecular entre *D. ocellatus* i els altres *Diploschistes*. Aquestes evidències moleculars, conjuntament amb els caràcters morfològics i químics que presenta exclusivament *D. ocellatus*, feien dubtosa la seva pertinença a *Diploschistes*. Tot i l'augment significatiu de tàxons de les *Graphidaceae* inclosos en el grup intern, els nostres resultats demostren que tots els membres de *Diploschistes* continuen formant un únic grup, incloent *D. ocellatus*, confirmant així l'estatus monofilètic d'aquest gènere.

Els trets que tradicionalment s'han utilitzat en la delimitació del gènere són la presència d'un exciple carbonitzat i de paràfisis laterals i l'absència de columel·la

(Guderley *et al*., 1997; Mangold *et al*., 2009). Aquesta definició, evidentment, exclou a *D. ocellatus* per la seva estructura excipular i només seria vàlid per a tots *Diploschistes* el caràcter absència de columel·la. Però l'estudi recent de Rivas Plata & Lumbsch (2011) ha demostrat que la presència de columel·la en les Graphidaceae és un caràcter altament homoplàsic i per tant, no es considera un bon caràcter per a distingir gèneres. Alternativament, Lumbsch & Tehler (1998) van proposar considerar com a trets diagnòstics del gènere, la presència de *Trebouxia* com a fotobiont i l'absència del complex de l'àcid estíctic. La proposta de Lumbsch & Tehler (*op. cit.*) també presentava conflictes ja que, per una banda, *D. ocellatus* quedaria exclòs d'aquest concepte perquè conté àcids norstíctic, connorstíctic i subnorstíctic. I d'altra banda, es podria pensar que tant *Diploschistes* com *Ingvariella* tenen els dos algues trebuxioides com a fotobiont, i aleshores aquest caràcter tampoc es consideraria vàlid. Però recentment, s'ha descobert que el gènere *Ingvariella* no forma part de les *Graphidaceae* (veure més endavant, apartat 5.3.). Per tant, proposem la presència de fotobiont trebuxioide com la única sinapomorfia que comparteixen totes les espècies de *Diploschistes* en comú, i que el distingeix dels altres gènere de la família.

Malauradament, les anàlisis basades en els marcadors mtSSU i nuLSU concatenats no han pogut resoldre satisfactòriament la posició que ocupa *Diploschistes* dins de la família *Graphidaceae*. Altres estudis filogenètics basats en les mateixes regions (p. e., Mangold *et al*., 2008; Rivas Plata *et al*., 2011) tampoc no van poder resoldre les relacions intergenèriques dins de les *Graphidaceae*. En el recent treball de Rivas Plata & Lumbsch (2011) s'ha demostrat com l'ús del gen codificador per a la proteïna *RPB*2, combinat amb els mtSSU i nuLSU, augmenta el nivell de resolució i suport en els internodes més interns de les *Graphidaceae*, contribuint significativament a la reconstrucció de les relacions entre els diferents gèneres de la família. Malauradament, en el treball de Rivas Plata & Lumbsch (*op. cit.*) no es va incloure cap espècimen de *Diploschistes*, amb la qual cosa la seva posició dins de la família, encara roman per aclarir.

2.2. RESULTATS FILOGENÈTICS DEL GÈNERE *DIPLOSCHISTES*

2.2.1. FILOGÈNIA MORFOLÒGICA

La topologia generada en l'anàlisi filogenètica basada en caràcters morfològics presenta un alt nombre de politomies. Això ens indica que els caràcters morfològics i químics utilitzats no contenen prou informació per a circumscriure la majoria dels tàxons inclosos ni per a resoldre les seves relacions filogenètiques.

Malgrat la manca de resolució general dels resultats, sí podem destacar que basant-nos només en la morfologia, el gènere *Diploschistes* també se circumscriu com a monofilètic, amb un alt suport estadístic. La morfologia també permet delimitar els tàxons *D. actinostomus*, *D. candidissimus*, *D. diploschistoides* i *D. muscorum* com a quatre grups monofilètics ben suportats.

2.2.2. FILOGÈNIA MOLECULAR

Els resultats de l'anàlisi de màxima parsimònia basada en les regions nuITS i mtSSU (anàlisi MP5, Figura S5, capítol 3), mostren com el gènere *Diploschistes* es divideix en 3 clades monofilètics, tots amb un suport estadístic significatiu. Aquests llinatges, es corresponen amb els grups en què tradicionalment s'ha subdividit el gènere *Diploschistes* (els grups *actinostomus*, *scruposus* i *ocellatus*), i que fins ara s'havien considerat com a grups artificials, degut a que cap estudi havia pogut demostrar-ne el seu estatus monofilètic. Pel que fa a la delimitació dels tàxons i la reconstrucció de les relacions filogenètiques, tot i que les dades moleculars presenten una considerable millora en la resolució obtinguda respecte a l'anàlisi morfològica, no són encara prou informatives per a proporcionar delimitacions robustes en el clade del grup *actinostomus* i, sobretot, dins del clade del grup *scruposus*, que es presenta com el grup més conflictiu, ja que la majoria de relacions es troben feblement suportades, mostrant valors de *bootstrap* inferiors al 70%.

Els resultats de les anàlisis de màxima versemblança i inferència bayesiana per a la matriu concatenada del nuITS i mtSSU (anàlisis ML2 i MB2 respectivament, Figura S6, capítol 3), mostren una evident pèrdua en la resolució i confiança respecte els resultats de l'anàlisi MP5. Concretament, vuit internodes que en l'anàlisi MP5 mostren un alt suport estadístic, en les anàlisis de ML2 i MB2, o bé no es troben resolts o bé no tenen valors significatius de *bootstrap*. Destaca especialment la pèrdua de suport estadístic en els clades corresponents als grups *actinostomus* i *ocellatus* a ML2 i MB2. Les diferències entre els resultats obtinguts a les anàlisis ML2 i MB2 respecte als de MP5 s'expliquen per l'addició dels caràcters INAASE en l'anàlisi de màxima parsimònia, com s'exposa a continuació.

Entre les seqüències del nuITS de *D. ocellatus* i les de la resta d'espècimens de *Diploschistes* existeixen diferències de longitud molt notables. Aquestes diferències en la longitud de les seqüències requereixen la inserció d'espais en l'alineament que permetin mantenir l'homologia posicional (Lutzoni *et al.*, 2000), creant així, regions alineades ambiguament i que han de ser excloses de les posteriors anàlisis. En l'alineament del nuITS, amb una mida final de 815 posicions, es van delimitar 36 regions alineades ambiguament, fet que va suposar l'exclusió de 510 caràcters. En el cas del mtSSU, que ha resultat ser un marcador molecular altament conservat pel gènere *Diploschistes*, el nombre de regions ambigües delimitades va ser de vuit, suposant l'exclusió de 158 caràcters, en un alineament amb una mida final de 899 posicions. S'ha demostrat que la recuperació del senyal filogenètic d'aquestes regions alineades ambiguament pot contribuir considerablement a un augment del nivell de resolució i confiança filogenètiques (Miadlikowska *et al.*, 2003). Per aquest motiu, en totes les anàlisis de màxima parsimònia (ja fossin les anàlisis basades en els nuITS i mtSSU per separat, combinats entre ells o combinats amb la morfologia), es van integrar la majoria d'aquestes regions ambigües amb l'ajut del programa INAASE 2.3b (Lutzoni *et al.*, 2000). Aquest programa, substitueix les regions ambigües per caràcters codificats inequívocament, i calcula les *step matrices* associades a cadascun d'aquests caràcters codificats (Lutzoni *et al.*, 2000). La integració dels caràcters INAASE en les anàlisis de màxima parsimònia, permet recuperar el senyal filogenètic de les regions ambigües (que altrament es perdria, ja que són regions que s'han d'excloure) sense vulnerar l'homologia posicional (Gaya, 2006). En estudis previs (p. e., Miadlikowska & Lutzoni, 2000; Gaya *et al.*, 2003, 2008, 2011; Kawakita *et al.*, 2003) la incorporació dels caràcters INAASE en les anàlisis de màxima parsimònia va suposar un augment en el nombre d'internodes resolts i en els que tenien un alt suport estadístic, fins i tot per sobre dels que s'obtenien amb mètodes més potents com poden ser la inferència bayesiana i la màxima versemblança (Gaya *et al.*, 2003). Malauradament, els caràcters INAASE no poden ésser incorporats en les anàlisis de màxima versemblança i d'inferència bayesiana en les seves implementacions actuals (Gaya *et al.*, 2011).

2.2.3. FILOGÈNIA COMBINADA

Els resultats de l'anàlisi filogenètica combinada dels caràcters morfològics i moleculars (anàlisi MP6, Figura 2, capítol 3) són els que presenten un major nombre d'internodes resolts i recolzats en valors de *bootstrap* igual o superior al 70%, respecte a la resta de les anàlisis realitzades per a aquest estudi (*i. e.*, MP2, MP3, MP4, MP5, ML2, MB2). L'addició dels caràcters morfològics a la matriu molecular, formada per nuITS i mtSSU, ha contribuït a una reducció en el nombre d'arbres igualment més parsimoniosos en la cerca heurística, de 336 a MP5 s'ha passat a 152 a MP6. La inclusió dels caràcters morfològics ha contribuït també a la resolució dels clades de *D. candidissimus* i *D. muscorum* (tot i que el darrer amb feble suport estadístic), els quals apareixien com a grups monofilètics amb alt suport estadístic a l'anàlisi morfològica, un suport que es perdia en les anàlisis moleculars. Així mateix, aquesta addició també ha permès delimitar el clade de *D. gypsaceus*, que en cap de les anàlisis anteriors es resolia amb confiança.

La utilització de les dades morfològiques per a la reconstrucció de relacions filogenètiques, i la seva utilitat en combinar-se amb les dades moleculars, ha estat una qüestió força debatuda [per una exposició detallada d'aquesta controvèrsia veure Gaya (2006: 231−234)]. Concretament, en els estudis centrats en líquens, ha hagut un augment significatiu de treballs que han combinat els caràcters morfològics amb les dades moleculars (p. e., Lutzoni & Vilgalys, 1995; Tehler, 1995; Gaya *et al.*, 2011), i també els químics (p. e., Miadlikowska & Lutzoni, 2000; McDonald *et al.*, 2003). Els nostres resultats coincideixen amb els què s'obtenien als treballs de Miadlikowska & Lutzoni (2000) i Gaya *et al.* (2011) i que podem resumir de la següent manera: tot i que la informació filogenètica proporcionada per la morfologia, quan s'analitza independentment, no resol de les relacions dins del grup intern, sí que contribueix a augmentar la resolució i el suport de *bootstrap* en l'anàlisi combinada.

2.3. CLASSIFICACIÓ INFRAGENÈRICA DEL GÈNERE *DIPLOSCHISTES*

Basant-nos en els resultats obtinguts a l'anàlisi MP6, en aquest treball proposem una classificació per al gènere *Diploschistes*, la qual assigna als grups definits per Lettau (1932) i Lumbsch (1985) l'estatus de subgènere, i atorga al caràcter de la morfologia dels apotecis, un valor taxonòmic que fins el moment no havia pogut ésser demostrat filogenèticament.

Cal destacar que dins del gènere, estudis previs han investigat si d'altres caràcters eren útils per a recolzar-hi la classificació dels grups morfològics descrits a partir del tipus d'apoteci. Així, Lumbsch *et al.* (1997) van examinar si els dos tipus de septació de les espores descrits per Eriksson (1981), microcefàlic i macrocefàlic, eren constants en els diferent grups d'espècies de *Diploschistes*. Els resultats de Lumbsch *et al.* (1997) van mostrar que no hi havia una correlació entre el tipus de septació de les espores i el tipus d'apoteci. Per exemple, dins del grup *actinostomus* espècies com *D. aeneus* i *D. euganeus* presentaven únicament espores macrocefàliques, mentre que *D. actinostomus* i *D. autroafricanus* podien tenir espores amb els dos tipus de septació. Aquests resultats van posar en dubte el valor taxonòmic del tipus de septació de les espores a *Diploschistes* i se'n va descartar el seu ús com a caràcter discriminant.

Amb l'objectiu d'explorar altres caràcters que ens permetessin fonamentar de forma addicional la nostra proposta de classificació subgenèrica, vam realitzar una exhaustiva revisió morfològica i anatòmica dels espècimens de *Diploschistes*.

D'aquesta manera, es van estudiar tots els espècimens inclosos en les anàlisis filogenètiques, així com material addicional de les mateixes espècies (la informació referent a tots els espècimens revisats es troba llistada a l'Apèndix 2). Aquest estudi ens ha permès detectar diferències notables en l'organització del còrtex superior en els diferents grups, un caràcter que fins ara no s'havia considerat, ja que es creia que tots els *Diploschistes* formaven únicament una capa epinecral sobre la capa algal (Mangold *et al*., 2009). En primer lloc, les espècies estudiades pertanyents al grup *scruposus* són les úniques que no tenen còrtex superior, i sobre la capa algal només s'hi forma una capa epinecral gruixuda, en la què generalment es dipositen granulacions de pigment fuliginós. En els espècimens pertanyents al grup *actinostomus*, en canvi, s'ha observat una certa organització en la capa superior del tal·lus, formada per hifes verticals que s'estenen des de la regió medul·lar, i que s'organitzen molt laxament sobre la capa algal. Estrictament, aquets tipus de còrtex superior va ser descrit per Poelt (1958) sota el terme "Scheinrinde", i actualment es coneix com a pseudocòrtex (Gueidan *et al*., 2007). En la terminologia que s'ha emprat en l'estudi taxonòmic dels líquens de l'antiga família *Thelotremataceae*, per a descriure aquesta mateixa estructura d'hifes agregades, que no arriba a formar un teixit compacte sobre la capa algal, els investigadors utilitzen un altre terme, el protocòrtex (p. e., Mangold *et al*., 2009; Messuti *et al*., 2010). Per tal de ser consistents amb la terminologia emprada en la resta de treballs dels gèneres més propers a *Diploschistes*, en aquest estudi hem utilitzat aquest mateix terme. Per tant, les espècies del grup *actinostomus* presenten un protocòrtex. En la part superior d'aquestes hifes que formen el protocòrtex, es concentren pigments bruns que estan associats a les parets hifals. Per sobre del protocòrtex, acostumen a tenir una capa epinecral, generalment prima. Finalment, *Diploschistes ocellatus* presenta un còrtex superior ben constituït, de tipus prosoplectenquimàtic. En la part superior d'aquest còrtex, es distingeix una capa pigmentada bruna, sobre la qual reposa la capa epinecral. Així doncs, els caràcters del còrtex superior descrits aquí, s'afegeixen a la morfologia dels apotecis com a descriptors dels tres grups *actinostomus*, *scruposus* i *ocellatus*.

Pel que fa a la composició química del gènere, aquesta és força uniforme ja que la majoria de les espècies dels grups *scruposus* i *actinostomus* contenen àcid lecanòric, sovint acompanyat per àcid diplosquistèsic (Lumbsch & Elix, 1989). Algunes espècies tenen àcid girofòric com a compost principal, però aquestes també pertanyen a ambdós grups. Únicament *Diploschistes ocellatus* es diferencia químicament de les altres espècies del gènere per contenir àcids norstíctic, connorstíctic i subnorstíctic (Culberson & Culberon, 1971; Mangold *et al*., 2009). El nostre estudi químic, només ha pogut confirmar el coneixement que ja es tenia sobre les substàncies presents en les diferents espècies del gènere, ja que no hem trobat l'existència de compostos nous aplicant tècniques de cromatografia en capa fina. Per tant, els metabòlits secundaris no permeten fer distincions entre el gruix d'espècies que conformen aquest gènere i només separen el ja diferent morfològicament i anatòmica grup *ocellatus*.

La nova classificació del gènere *Diploschistes* que presentem en aquesta tesi, s'estableix sobre la base de la filogènia molecular i combinada, amb el suport d'evidències morfològiques, tant prèviament conegudes com inèdites. Per tant, es proposa dins de *Diploschistes* el reconeixement de tres subgèneres: *Diploschistes* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l'antic grup *scruposus*), *Limborina* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l'antic grup *actinostomus*), i *Thorstenia* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l'antic grup *ocellatus*) (veure més informació a la secció Taxonomic Conclusions, capítol 3).

2.4. RECONEIXEMENT FILOGENÈTIC DE LES ESPÈCIES TRACTADES DINS DEL GÈNERE *DIPLOSCHISTES*

Pel que fa a l'espècie *D. ocellatus*, ara inclosa en el proposat subgènere *Thorstenia*, els resultats de l'anàlisi combinada MP6 coincideixen amb la delimitació morfològica de l'espècie. En la nostra topologia, dins d'aquest subgènere, destaca la presència de dos clades monofilètics significativament suportats. Hem trobat una correlació entre l'existència d'aquests dos clades i certs trets morfològics: els espècimens 1, 2 i 5, que conformen un dels clades, desenvolupen apotecis, mentre que els espècimens 3 i 4 de l'altre clade, tot i que presenten tal·lus molt ben desenvolupats, sense signes de malaltia o d'ésser parasitats, no produeixen apotecis i només presenten picnidis com a estructures reproductores. Considerem que aquestes diferències morfològiques no són suficients per justificar l'escissió dels espècimens 3 i 4 com una espècie independent a *D. ocellatus*. Per aquest motiu, proposem conferir-los el rang de varietat *tenuis* Fdez.-Brime & Llimona *var. nova ad int.* (veure més informació a la secció Taxonomic Conclusions, capítol 3).

Dins del proposat subgènere *Limborina*, s'observa una concordança completa entre els resultats de la filogènia combinada i la delimitació morfològica de les espècies. *Diploschistes caesioplumbeus*, considerat en les classificacions de Ozenda & Clauzade (1970) i Clauzade & Roux (1985) com a subespècie de *D. actinostomus*, es reconstrueix com un tàxon filogenèticament ben delimitat, confirmant la categoria d'espècie que li conferien Poelt (1969) i Lumbsch (1989). Cal destacar però, que en la darrera versió de la *checklist* dels líquens francesos, Roux (2011) ja considera *D. caesioplumbeus* com a espècie. *Diploschistes caesioplumbeus* pot distingir-se fàcilment de *D. actinostomus* pel seu tal·lus gris plumbi i les dimensions de les espores, de (26–)30–32–35(–44) x (12–)16–18–20(–23) µm. A l'espècie *D. actinostomus*, el tal·lus és de gris clar a bru clar i les espores són relativament més petites, (21–)25–28–30(–35) x (12–)14–15–16(–19) µm. A més a més, coincidint amb estudis previs (Culberson & Culberson, 1971; Lumbsch, 1989; Mangold *et al.*, 2009), en els exemplars de *D. caesioplumbeus* hem detectat només àcid lecanòric, mentre que els de *D. actinostomus* també presentaven àcid diploquistèsic. Pel que fa a *D. candidissimus*, els dos espècimens inclosos, procedents d'Espanya i d'Amèrica del Nord, formen un grup monofilètic que es resol amb un alt suport estadístic com a grup germà de *D. caesioplumbeus*. *Diploschistes candidissimus* es diferencia de *D. caesioplumbeus* per tenir el tal·lus blanc i molt pruïnós, a més de viure sobre roques calcàries enlloc de silícies. L'únic espècimen de *D. euganeus* inclòs en les nostres anàlisis presenta una relació ben suportada amb el clade format per *D. actinostomus* + *D. caesioplumbeus* + *D. candidissimus*. Caldria l'addició de més espècimens de *D.*

euganeus per investigar si la seva delimitació filogenètica coincideix amb la seva delimitació fenotípica (es distingeix de les altres espècies amb apotecis peritecioides per les espores amplament el·lipsoïdals i l'absència de metabòlits secundaris). Finalment, els dos espècimens inclosos de *D. diploschistoides*, provinents de diferents localitats d'Austràlia, formen un grup monofilètic que ocupa una posició basal respecte a la resta de tàxons del proposat subgènere *Limborina*. L'espècimen 1 inclòs dins del clade de *D. diploschistoides* es trobava identificat com a *D. almbornii*; per tant, els nostres resultats filogenètics confirmen la decisió de Guderley & Lumbsch (1996) de considerar *D. almbornii* com a sinònim de *D. diploschistoides*. Les formes de *D. diploschistoides* amb tal·lus gris fosc es podrien confondre amb *D. caesioplumbeus*, però *D. diploschistoides* es caracteritza per tenir espores halonades, amiloides i de mida més petita, (20–)23–26–28(–34) x (10–)13–14–15(–17) µm.

El llinatge corresponent al proposat subgènere *Diploschistes* presenta la majoria de relacions filogenètiques entre tàxons sense suport estadístic o bé amb un suport feble. *Diploschistes scruposus* es revela com una espècie polifilètica, mostrant diversos orígens en l'arbre filogenètic. Tot i l'estudi detallat dels espècimens de *D. scruposus*, no hem trobat caràcters morfològics que es correlacionin amb els resultats filogenètics obtinguts; únicament els espècimens 1, 3 i 11 tenen fixat el caràcter de la medul·la amiloide. Pel que fa a la química, per aquesta espècie hi ha descrites dues races químiques: una amb àcid lecanòric com a substància principal, acompanyat d'àcid orselínic, i una amb els àcids lecanòric i diplosquistèsic com a substàncies principals, acompanyats d'àcid orselínic. En el nostre estudi, tampoc hem trobat una correlació entre aquestes races químiques i la filogènia. Per tant, els nostres resultats demostren que *D. scruposus* presenta una variabilitat molecular, que fins ara no havia estat posada de manifest, la qual no es correspon amb diferents fenotips. Davant d'aquests resultats, preferim seguir les recomanacions de Grube & Kroken (2000), els quals suggereixen que quan els resultats filogenètics revelen complexos d'espècies probablement constituïts per diversos llinatges críptics, que no poden ésser correlacionats amb caràcters fenotípics o biogeogràfics, s'ha de mantenir el nom del tàxon seguit de l'apèndix "agg.". Cal destacar que *D. scruposus* agg. és probablement el tàxon més conegut i citat dins del gènere *Diploschistes*, ja que té una distribució cosmopolita i apareix en molts zonobiomes. És molt comú a la regió temperada, però també pot créixer en el domini de la vegetació àrtico-alpina i a les parts altes de les muntanyes subtropicals (Guderley & Lumbsch, 1996; Lumbsch & Elix, 2003). Una revisió més detallada, sens dubte, requeriria la inclusió d'un mostreig geogràfic més ampli que el què s'ha utilitzat en aquest estudi. Pel que fa a la delimitació de *D. interpediens*, aquesta tampoc concorda amb la taxonomia clàssica, ja que els espècimens inclosos es troben agrupats en dos clades distants, els quals no poden ésser justificats amb caràcters de tipus morfològic, químic o biogeogràfic. De la mateixa manera que en el cas anterior, no considerem adequat proposar cap canvi taxonòmic, únicament el tractament com agregat d'espècies, fins que no quedi aclarida la filogènia d'aquestes espècies. El que sí es pot observar, és que tots els espècimens que hem assignat a *D. interpediens* pel fet de presentar vuit espores per asc apareixen agrupats, i no es troben en cap cas barrejats amb els espècimens que hem assignat com a *D. scruposus* per presentar quatre espores per asc. Considerem, doncs, que aquests resultats, tot i la manca de suport estadístic d'alguns dels internodes, corroboren la separació d'aquests dos tàxons. Recentment, Lumbsch ens ha comunicat (*in litt.*, 2010) que durant la revisió dels *Diploschistes* de la regió holàrtica, va estudiar el lectotipus de *D. interpediens* (Lusitania, Oporto, 1879, Newton, H-NYL 22181) i va observar-hi ascs octosporats. Lumbcsh (*in litt.*, 2010) també es mostra d'acord en acceptar *D. interpediens* agg. com a tàxon independent de *D. scruposus* agg., basant-se en el nombre d'espores per asc, i considerar la distribució de *D. interpediens* agg. restringida únicament a la regió mediterrània.

L'espècie *Diploschistes diacapsis* es presenta a la nostra filogènia en dos clades monofilètics: l'un (espècimens 1, 2 i 3) que inclou la forma típica de l'espècie, i l'altre (espècimens 4, 5 i 6) que inclou els espècimens que s'ajusten a la descripció de la subespècie *neutrophilus* proposada per Clauzade & Roux (1985). Hem revisat diversos exemplars, tant de la formes típiques de *D. diacapsis*, com de les formes que s'ajusten a la subespècie *neutrophilus*, inclòs l'holotipus amb el què es va descriure la subespècie (Provença, Bouches-du-Rhône, 1985, Roux, Herbari Roux 99). La revisió d'aquest material (Apèndix 2) ens permet corroborar que la subespècie *neutrophilus* es diferencia de la resta de *D. diacapsis* per presentar un tal·lus considerablement més prim, de (0.2–)0.5–0.7–0.9(–1) mm, que creix molt adherit al substrat. Les formes típiques de *D. diacapsis* revisades tenen un gruix de (0.6–)0.9–1.3–1.6(–3.2) mm, i a mida que creix el tal·lus, en lloc d'adherir-se, se separa del substrat per la zona central, arribant a elevar-se fins a 1–2 cm d'alçada (Souza-Egipsy *et al.*, 2002) A més, la subespècie *neutrophilus* ha estat recol·lectada sempre sobre sòls neutres o amb molts pocs carbonats, generalment en terraprims argilosos, i en localitats properes a la costa. En canvi, *D. diacapsis* és una espècie dominant en els sòls guixencs, tot i que pot viure també sobre sòls carbonatats, en zones amb un règim de clima àrid. Per les diferències morfològiques i ecològiques descrites, i recolzats ens els resultats filogenètics obtinguts en l'anàlisi MP6, en aquest treball proposem donar categoria d'espècie a la subespècie *neutrophilus* i, en conseqüència, designem la següent nova combinació: *Diploschistes neutrophilus* (Clauzade & Cl. Roux) Fdez.-Brime & Llimona *comb. nov. ad int.* (veure més informació a la secció Taxonomic Conclusions, capítol 3).

L'espècie *D. gypsaceus* es resol en el nostre estudi com a monofilètica, amb un alt suport estadístic. El tal·lus blanc i molt pruïnós i la seva presència en superfícies de subverticals a verticals de roques calcàries, la distingeixen clarament de tàxons propers com *D. scruposus* agg., que tot i presentar cristalls dispersos en la superfície mai no fa pruïna, i viu sempre sobre roques àcides. Pel que fa als dos espècimens inclosos de l'espècie *D. rampoddensis*, aquests també formen un clade monofilètic amb suport estadístic significatiu. *Diploschistes rampoddensis* és un taxon que es diferencia de *D. scruposus* agg. per la presència d'ascs octosporats, i de *D. interpediens* agg., per tenir un tal·lus més prim i friable, per l'absència d'àcid diplosquistèsic i per viure preferentment en roques poroses, com els gresos. De tota manera, aquestes diferències semblen no ser caràcters prou distintius, tal i com evidencia l'anàlisi filogenètica morfològica on *D. rampoddensis* no arriba a separar-se de *D. scruposus* agg. o *D. interpediens* agg. En canvi, molecularment és una espècie que divergeix clarament dels altres dos tàxons esmentats, com mostren les diferents anàlisis filogenètiques basades en el nuITS i el mtSSU. Finalment, l'espècie *D. muscorum* també apareix circumscrita a MP6 com a monofilètica, tot i que el suport estadístic és feble. El resultats confirmen la seva separació de *D. scruposus* agg. i, per tant, no recolzen la proposta de Clauzade & Roux (1985, 1989) de tractar aquest tàxon com una subespècie de *D. scruposus* agg.

Com a comentari final, voldríem destacar que un estudi filogenètic com el presentat en aquest treball, basat en dades de diferent tipus (morfològiques, químiques, moleculars) ens ha permès aclarir la llargament plantejada qüestió de si els grups morfològics en els què s'havia dividit el gènere *Diploschistes*, responien a una classificació natural o no. Aquests resultats ens permeten formular una hipòtesi alternativa a la proposada per Lumbsch (1986, 1989) sobre l'evolució del tipus d'apotecis en aquest gènere. Segon la interpretació de Lumbsch, els apotecis peritecioides serien plesiomòrfics, mentre els urceolats i lecanoroides serien apomòrfics. Els nostres resultats mostren, en canvi, que els apotecis de tipus lecanoroide són plesiomòrfics mentre els de tipus urceolat i peritecioide resulten apomòrfics. La tendència evolutiva en aquest gènere, pel que fa a l'estructura dels apotecis. Per tant, és cap a la formació d'un exciple ben constituït, carbonitzat i amb paràfisis laterals. Pel que fa a la delimitació de les espècies, la concordança entre la filogènia obtinguda i el concepte tradicional d'espècie, basat en caràcters fenotípics, ha pogut ésser confirmada en algunes d'elles. Malgrat tot, la delimitació de diversos tàxons del subgènere *Diploschistes* no s'ha pogut resoldre satisfactòriament degut a una diversitat genètica que no es troba correlacionada ni amb la morfologia ni amb l'estructura geogràfica, i que podria venir explicada per diferents escenaris (p. e., processos recents o incomplerts d'especiació, existència de flux gènic). Aquests escenaris hauran de ser investigats en propers treballs, amb la utilització de marcadors moleculars amb taxes de canvi més altes que els que hem emprat en el nostre estudi i amb la integració de models de coalescència en les anàlisis.

Les decisions taxonòmiques i nomenclaturals proposades en aquesta tesi (*i. e.*, descripció dels subgèneres per a *Diploschistes*, la creació de la varietat *tenuis* per a *D. ocellatus* i la combinació nova *D. neutrophilus*) s'han deixat com *ad int*. al capítol 3, la secció de discussió i les conclusions pel motiu següent. Durant el XVIII International

Botanical Congress a Melbourne, es va modificar el International Code of Botanical Nomenclature (a partir d'ara anomenat International Code of Nomenclature for algae, fungi, and plants). Segons el nou codi, a partir del dia 1 de gener de 2012, les novetats taxonòmiques en format electrònic es consideraran vàlides (Knapp *et al.*, 2011). Ja que el contingut d'aquesta tesi serà accessible on-line, hem preferit deixar les noves propostes nomenclaturals com a provisionals, de manera que no ens sigui incompatible la seva futura publicació vàlida.

3. DELIMITACIÓ DEL GÈNERE *INGVARIELLA* I LA SEVA POSICIÓ SISTEMÀTICA DINS DE LES *OSTROPALES*

En l'estudi del gènere *Ingvariella* basat en l'anàlisi filogenètica dels marcadors mtSSU i nuLSU concatenats, hem pogut resoldre amb confiança, en tots els mètodes d'anàlisi emprats (MB, ML, MP, capítol 4), dues qüestions principals: la monofília del gènere i la seva posició dins les *Ostropales*.

En primer lloc, es demostra que el gènere *Ingvariella* és monofilètic i independent de *Diploschistes*. La validesa de la utilització dels caràcters de l'exciple en la delimitació genèrica de l'antiga família de les *Thelotremataceae* ha estat una qüestió molt controvertida, i sovint posada en dubte (p. e., Guderley *et al.*, 1997; Mangold *et al.*, 2009). Estudis recents han demostrat que espècies filogenèticament allunyades presenten la mateixa estructura de l'exciple degut a fenòmens d'evolució paral·lela i convergència fenotípica (Rivas Plata & Lumbsch, 2011). Precisament, la crítica que va fer Nimis (1998) en el seu moment a la decisió de Guderley *et al.* (1997), era que no considerava adequat separar *Ingvariella* basant aquesta decisió únicament en caràcters excipulars, especialment si encara no es tenia clar el valor taxonòmic d'aquests caràcters dins de la família. A partir dels nostres resultats, sembla ser que en el cas concret d'*Ingvariella*, els caràcters excipulars (existència d'un marge de l'apoteci format a partir d'elements himenials degenerats) sí que demostren tenir un valor diagnòstic, i en justifiquen la seva delimitació com a gènere apart de *Diploschistes*.

Pel que fa a la situació d'*Ingvariella* dins les *Ostropales*, els nostres resultats revelen per primera vegada, la posició d'*Ingvariella* dins les *Stictidaceae*, i no pas de la família *Graphidaceae*, la pertinença a la qual no havia estat qüestionada fins al moment. Com s'exposava en la introducció d'aquesta tesi, l'estudi morfològic de diversos exemplars d'*I. bispora* ens va fer adonar de l'existència de certs caràcters (*i. e.*, reacció positiva de l'himeni a l'aplicació del lugol, tornant-se primer groc, i després vermell intens, o les parets amiloides dels ascs) que no coincidien amb les característiques donades per a la família *Graphidaceae*. Per aquest motiu, vam creure convenient estudiar si era correcta la seva posició taxonòmica dins les *Graphidaceae*, sense descartar possibles afinitats amb altres famílies de l'ordre. Pel que fa a les *Stictidaceae*, es caracteritzen pel tipus de marge dels apotecis, que està format per diverses capes, fins a 5 segons Sherwood (1977), en les quals la presència de pigments o cristalls s'han utilitzat com caràcters diagnòstic (Wedin *et al*., 2006). Si bé és cert que en certes espècies dins d'aquesta família algunes capes estan molt reduïdes o, fins i tot, han desaparegut, l'estructura del marge de les *Stictidaceae* continua essent molt diferent a la que presenta *Ingvariella*. En canvi, les *Stictidaceae* si presenten les parets dels ascs amiloides com *Ingvariella*, i, a més, membres d'aquesta família, com algunes espècies dels gèneres *Absconditella* i *Cryptodicus*, presenten les mateixes reaccions positives de l'himeni al lugol (primer groc, després vermell).

És important destacar que la nova posició sistemàtica d'*Ingvariella*, amplia considerablement el rang ecològic i el tipus de nutrició, ja de per sí força divers, en les *Stictidaceae*. Aquesta família es troba constituïda, fonamentalment, per fongs saprofítics, tot i que també se n'han descrit líquens (tots de mida molt petita i corticícoles) i, fins i tot, espècies que poden alternar formes de vida saprofítica i liquenitzada, en funció dels requeriments ecològics i ambientals (Wedin *et al*., 2004).

CONCLUSIONS

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1. Com a resultat de l'estudi florístic en 34 localitats del Parc Natural de Cap de Creus, s'ha elaborat un catàleg que inclou 294 tàxons, dels quals 263 corresponen a fongs liquenitzats i 31 a fongs liquenícoles.

2. Amb els exemplars estudiats, s'ha constituït un herbari format per 845 plecs que ha estat dipositat al Centre de Documentació de Biodiversitat Vegetal de la Universitat de Barcelona (CeDocBiV, Herbari BCN-Lich.).

3. L'espècie *Polycoccum rinodinae* és nova cita per Europa. Les espècies *Arthonia lecanorina*, *Caloplaca arcis*, *C. austrocitrina*, *Diploschistes diacapsis* subsp. *neutrophilus*, *Endocarpon simplicatum, Endococcus buelliae*, *Micarea melaenida*, *Polycoccum teresum* són noves citacions per a la península Ibèrica. El catàleg per a Catalunya es veu incrementat en 34 espècies.

4. Els gèneres millor representats en la zona d'estudi, en ordre d'abundància, són C*aloplaca*, *Buellia*, *Cladonia*, *Verrucaria, Lecanora*, *Pertusaria* i *Rinodina*, alguns dels quals inclouen espècies poc citades a la península Ibèrica.

5. S'ha descrit un espècie de fong liquenícola nova per a la ciència, *Lichenostigma rupicolae* Fdez.-Brime & Nav.-Ros., paràsit de *Pertusaria rupicola*.

6. Addicionalment, s'han trobat quatre tàxons de fongs liquenícoles potencialment nous que per ara no s'han pogut atribuir a cap espècie coneguda, i requereixen d'un estudi més detallat: *Lichenostigma* sp., *Zwackhiomyces* sp., *Cercidospora* sp. 1 i *Cercidospora* sp. 2.

7. Des del punt de vista fitogeogràfic, les condicions climàtiques particulars de l'àrea estudiada, que inclou des de zones molt càlides i seques, a d'altres de més fredes i humides, permeten la conjunció tant d'espècies mediterrànies com

d’extramediterrànies, fins i tot la presència d’algunes espècies pròpies de l’alta muntanya.

8. Destaquem les localitats situades entre Santa Helena, Sant Pere de Rodes i el pic de Sant Salvador de Verdera, la Punta de s’Arenella, les Cavorques i el Prat d’en Pagès com a zones molt valuoses pel seu component liquènic, tant per la diversitat que presenten com la singularitat dels tàxons que hi viuen. Per això, considerem que haurien d’estar considerades en els plans especials de gestió del Parc, per a la seva protecció i conservació.

9. Es confirma la monofília del gènere *Diploschistes* en la seva circumscripció actual. Dels caràcters estudiats, únicament la presència de fotobiont trebuxioide es pot considerar sinapomòrfic per a totes les espècies del gènere.

10. Es confirma la monofília dels tres grups morfològics proposats per Lettau (1932) i Lumbsch (1985) dins del gènere *Diploschistes* i, en conseqüència, se’n proposa el seu reconeixement en tres subgèneres: *Diploschistes* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l’antic grup *scruposus*), *Limborina* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l’antic grup *actinostomus*) i *Thorstenia* Fdez.-Brime, Gaya, Llimona & Lutzoni, *subg. nov. ad int.* (corresponent a l’antic grup *ocellatus*).

11. Amb el reconeixement filogenètic d’aquests subgèneres, s’atorga al caràcter de la morfologia dels apotecis, un valor taxonòmic que fins el moment no havia pogut ésser demostrat filogenèticament. Aquests subgèneres, també es diferencien pel tipus d’organització del còrtex superior, un caràcter sinapomòrfic que fins ara no havia estat considerat en la taxonomia de *Diploschistes.*

12. Els nostres resultats mostren, que els apotecis de tipus lecanoroide són plesiomòrfics mentre els de tipus urceolat i peritecioide resulten apomòrfics. En conseqüència, la tendència evolutiva en aquest gènere pel que fa a l’estructura

dels apotecis, és a formar un exciple ben constituït, carbonitzat i amb paràfisis laterals (urceolat/peritecioide).

13. En l'estudi de la filogènia morfològica, s'han pogut delimitar els tàxons *D. actinostomus*, *D. candidissimus*, *D. diploschistoides* i *D. muscorum*. Per a la resta de tàxons considerats, les dades morfològiques no han estat suficients per a poder circumscriure les espècies. A més, la posició filogenètica i les relacions entre els diferents membres de *Diploschistes* romanen en part incertes.

14. Les topologies basades en la combinació de les regions nuITS i mtSSU proporcionen suficient senyal filogenètic com per a resoldre les relacions dins del proposat subgènere *Limborina*. En canvi, en el proposat subgènere *Diploschistes*, aquestes romanen en gran part incertes.

15. En les anàlisis filogenètiques moleculars, la incorporació dels caràcters INAASE en les anàlisis de màxima parsimònia ha suposat un augment en el nombre d'internodes resolts i dels que tenen suport estadístic significatiu, fins i tot, per sobre dels que s'obtenien amb la inferència bayesiana i la màxima versemblança.

16. Les dades morfològiques i moleculars no han resultat significativament incongruents. La seva combinació proporciona una millora en la delimitació i suport d'alguns grups, però no ha permès delimitar filogenèticament la totalitat de les morfoespècies que s'han avaluat.

17. Les anàlisis filogenètiques resolen un clade dins de *D. ocellatus*, amb un bon recolzament estadístic, corresponent als espècimens amb reproducció vegetativa, sense apotecis. Per tal d'acomodar aquests espècimens es proposa la creació de la var. *tenuis* Fdez.-Brime & Llimona *var. nova ad int.*

18. Proposem donar categoria d'espècie al tàxon *D. diacapsis* subsp. *neutrophilus*, basant-nos en evidències morfològiques i ecològiques, i de recolzament

filogenètic. En conseqüència, designem la nova combinació *Diploschistes neutrophilus* (Clauzade & Cl. Roux) Fdez.-Brime & Llimona *comb. nov. ad int.*

19. En les anàlisis filogenètiques, els espècimens de *D. interpediens*, mai no han aparegut compartint un ancestre comú més recent amb els espècimens de *D. scruposus*. Aquests resultats corroboren la independència d'aquests dos tàxons, i confirmen que la diferència en el número d'espores per asc és un caràcter amb valor taxonòmic.

20. No s'ha pogut resoldre satisfactòriament la delimitació dels tàxons *Diploschistes scruposus* i *D. interpediens*, degut a que presenten una diversitat genètica que no es troba correlacionada ni amb la morfologia, la química o l'estructura geogràfica. Proposem el seu tractament com a *D. scruposus* agg. i *D. interpediens* agg. fins que se'n resolgui la seva circumscripció.

21. Es demostra que el gènere *Ingvariella*, a més d'ésser monofilètic, és un gènere independent de *Diploschistes*.

22. Els nostres resultats demostren per primera vegada, la posició d'*Ingvariella* dins la família de les *Stictidaceae*, i no pas dins la família *Graphidaceae*, com es considerava fins ara.

23. Alguns caràcters himenials, com les parets amiloides dels ascs i la reacció positiva de l'himeni amb el lugol, combinats amb el tipus de fotobiont (clorococoide) quan estan liquenitzats, podrien considerar-se sinapomorfies potencials de les *Stictidaceae*, que donarien suport a la posició d'*Ingvariella* dins de la família.

BIBLIOGRAFIA

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ACHARIUS, E. (1803): *Methodus qua omnes detectos lichenes secundum organa carpomorpha ad genera, species et varietates redigere atque observationibus illustrare tentavit Erik Acharius*. Impensis F.D.D. Ulrich, Estocolm.

ACHARIUS, E. (1810): *Lichenographia Universalis*. J.F. Danckwerts, Göttingen.

ALONSO, F.L. & EGEA, J.M. (1989): Notas sobre líquenes calcícolas del litoral de Alicante. *Folia Botanica Miscellanea* 6: 49–59.

ALONSO, F.L. & EGEA, J.M. (1994): Sobre las comunidades de líquenes calcícolas de zonas costeras del sur de la Península Ibérica y Marruecos. *Studia Geobotanica* 14: 3–25.

ALONSO, F.L. & EGEA, J.M. (1996): Contribución a los líquenes calcícolas y terrícolas de algunas localidades costeras del sur de España. *Anales de Biología* 21: 55–72.

ALONSO, F.L., EGEA, J.M. & MORENO, P.P. (1989): Flora liquénica calcícola, del litoral de la Provincia de Alicante. *Acta Botánica Malacitana* 14: 59–71.

ARMALEO, D. & CLERC, P. (1995): A rapid and inexpensive method for the purification of DNA from lichens and their symbionts. *The Lichenologist* 27: 207–213.

BAGLIETTO, F. (1871): Prospetto lichenologico della Toscana. *Nuovo Giornale Botanico Italiano* 3: 211–297.

BALLESTEROS, E. (1982): Primer intento de tipificación de la vegetación marina y litoral sobre sustrato rocoso de la Costa Brava. *Oecologia Aquatica* 6: 163–173.

BALLESTEROS, E. (1992): *Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució*. Institut d´Estudis Catalans, Barcelona.

BALLESTEROS, E. & ROMERO, J. (1982): Catálogo de las algas bentónicas (con exclusión de las diatomeas) de las costas catalanas. *Collectanea Botanica* 13: 723–765.

BALOCH, E., LÜCKING, R., LUMBSCH, H.T. & WEDIN, M. (2010): Major clades and phylogenetic relationships between lichenized and non-lichenized lineages in Ostropales (Ascomycota: Lecanoromycetes). *Taxon* 59: 1483–1494.

BARBERO, M. (1998): *Estudio florístico y quimiotaxonómico de los líquenes silicícolas del Maresme*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

BARBERO, M., GIRALT, M., ELIX, J.A., GÓMEZ-BOLEA, A. & LLIMONA, X. (2006): A taxonomic study of *Protoparmelia montagnei* (syn. *P. psarophana*) centered in the Eastern Iberian Peninsula. *Mycotaxon* 97: 299–320.

BARBERO, M., HLADUN, N. & LLIMONA, X. (1996): Líquenes de los granitos meteorizados del litoral del Maresme (Cataluña). *Folia Botanica Miscellanea* 10: 11–19.

BARRENO, E., ATIENZA, V. & SANZ, M.J. (1990): Catálogo de los líquenes epífitos y terrícolas de la Font Roja (Alicante, España). A: *Ayudas a la Investigación, 1986-1987, Instituto de Cultura "Juan Gil-Albert" Vol. 1 Ciencias Naturales* 85–99. Diputación de Alicante, Alicante.

BLANCO, O., CRESPO, A., ELIX, J.A., HAWKSWORTH, D.L. & LUMBSCH, H. T. (2004): A molecular phylogeny and a new classification of parmelioid lichen containing *Xanthoparmelia*–type lichenan (Ascomycota: Lecanorales). *Taxon* 53: 959–975.

BOOM, P.P.G. (1999): Some lichens and lichenicolous fungi from Majorca (Spain). *Linzer Biologische Beitrage* 31: 785–800.

BOQUERAS, M. (1993): *Flora i vegetació dels líquens epifítics de les terres meridionals de Catalunya*. Tesi Doctoral, Universitat de Barcelona.

BOQUERAS, M., GÓMEZ-BOLEA, A. & LLIMONA, X. (1993): Some interesting Mediterranean lichens and fungi from the Ports de Beseit range (Catalonia, Spain). *Nova Hedwigia* 57: 97–108.

BOLÒS, O. DE (1985): *Corologia de la Flora dels Països Catalans. Introducció ORCA: Notícies i comentaris, 1*. Institut d'Estudis Catalans, Barcelona.

BREUSS, O. (1988): Beitrag zur Flechtenflora Mallorcas. *Linzer Biologische Beitrage* 20: 203–215.

BUNGARTZ, F. (2004): *The lichen genus Buellia De Not. in the Greater Sonoran Desert region: saxicolous species with one-septate ascospores*. Tesi Doctoral. Arizona State University, Tempe.

BURGAZ A.R., ARGÜELLO, A., ATIENZA, V., FERNÁNDEZ BRIME, S., FERNANDEZ-SALEGUI, A.B., FIGUERAS BALAGUE, G., GARCÍA OTÁLORA, M., GÓMEZ-BOLEA, A., HAWKSWORTH, D.L., HLADUN, N.L., LLIMONA, X., LLOP, E., MARCOS-LASO, B., MUÑIZ, D., PÉREZ-ORTEGA, S., DEL PRADO, R., RODRIGUES, S.A. & TERRON, A. (2007): Lichens and lichenicolous fungi of Sierra de San Lorenzo (La Rioja Community, Spain). *Cryptogamie Mycologie* 28: 133–153.

CALATAYUD, V. (1998): *Líquenes y hongos liquenícolas de rocas no carbonatadas en el Sistema Ibérico Oriental e Islas Columbretes*. Tesi Doctoral. Universitat de València, València.

CALATAYUD, V. & BARRENO, E. (1994): Contribution to the lichen floristics of eastern Spain I. Silicicolous lichens and their lichenicolous fungi of Serra d'Espadà (Castelló). *Cryptogamie, Bryologie et Lichenologie* 15: 23–41.

CAMBRA, J. (1986): Estudi de la flora i vegetació de les algues d'aigua dolça de la península del Cap de Creus. Tesina de Llicenciatura. Universitat de Barcelona, Barcelona.

CAMBRA, J. (1987): Observaciones sobre la periodicidad de las algas filamentosas en la península del Cap de Creus (Girona). En: *Actas del VI Simpsosium Nacional de Botánica Criptogámica* 25–33. Universidad de Granada, Granada.

CAMBRA, J. (1989a): *Sphaeridiothrix compressa* and *Phaeothamnion articulatum*, two new records for the Spanish Chrysophyte flora. *Nova Hedwigia Beiheft* 95: 259–267.

CAMBRA, J. (1989b): Freshwater algae from the cape of Creus peninsula, Catalonia (NE Spain). *Nova Hedwigia* 49: 281–321.

CAMBRA, J. (1995): Aproximació a la biodiversitat algològica dels sistemes aquàtics epicontinentals del Cap de Creus. A: J.M. MASDAVALL, A. MIQUEL & S. MUSQUERA (eds.): *La península del Cap de Creus i la serra de Verdera*. Actes de les IV Jornades de la Institució Catalana d'Història Natural 61–71. Institut d'Estudis Empordanesos, Figueres.

CASAS, C. (1958): La flora briológica del Cap de Creus. *Pharmacia Mediterranea* 2: 440–459.

CASAS, C. (1995): Els briòfits del Cap de Creus. A: J.M. MASDAVALL, A. MIQUEL & S. MUSQUERA (eds.): *La península del Cap de Creus i la serra de Verdera*. Actes de les IV Jornades de la Institució Catalana d'Història Natural 87–92. Institut d'Estudis Empordanesos, Figueres.

CASAS, C., BRUGUÉS, M. & CROS, R.M. (1998): La brioflora de la península del Cap de Creus. *Acta Botanica Barcinonensia* 45: 157–172.

CLAUZADE, G. & RONDON, Y. (1960): Observations sur la vegetation lichenique de la hetraie de la Massane et de ses environs immediats, au sud d'Argeles-sur-Mer (Pyrenees-Orientales). *Vie et Milieu* 11: 437–464.

CLAUZADE, G. & ROUX, C. (1975): Stude ecologique et phytosociologique de la vegetation lichenique des roches calcaries non alterees dans les regions mediterraneenne et submediterraneenne du Sud-Est de la France. *Bulletin du Musée d'Histoire Naturelle de Marseille* 35: 153–208.

CLAUZADE, G. & ROUX, C. (1985): Likenoj de Okcidenta Eŭropo. Ilustrita Determinlibro. *Bulletin de la Société Botaniquen du Centre-Ouest Numéro Special* 7: 1–893.

CLAUZADE, G. & ROUX, C. (1989): Likenoj de okcidenta Europo. Suplemento 3a. *Bulletin de la Société Linnéenne de Provence* 40: 73–110.

CRESPO, A., BARRENO, E. & FOLLMANN, G. (1976): Sobre las comunidades liquénicas rupícolas de *Acarospora hilaris* (Duf.) Hue en la península Ibérica. *Anales del Instituto Botánico A.J. Cavanilles* 33: 189–205.

CRESPO, A., BLANCO, O. & HAWKSWORTH, D.L. (2001): The potential of the mitochondrial DNA gene for establishing phylogeny and stabilizing generic concepts in the parmelioid lichens. *Taxon* 50: 807–819.

CREWE, A.T., PURVIS, O.W. & WEDIN, M. (2006) Molecular phylogeny of Acarosporaceae (Ascomycota) with focus on the proposed genus *Polysporinopsis*. *Mycological Research* 110: 521–526.

CULBERSON, C.F. & CULBERSON, W.L. (1971): The chemistry of some species of the lichen genus *Diploschistes*. *Mycologia* 63: 422–426.

DE ANDRADE MEIRELES, J., CARRERAS, J. & DRUGUET, E. (2000): Geòtop 161. Les sorres de les Cavorques al Port de la Selva. Inventari d'espais d'interès geològic a Catalunya. Generalitat de Catalunya, Departament de Medi Ambient i Habitatge. http://www20.gencat.cat/docs/dmah/Home/Ambits%20dactuacio/Medi%20natural/Sistemes%20dinformacio/Inventari%20despais%20dinteres%20geologic/Consulta%20de%20les%20fitxes%20descriptives%20dels%20EIG/documentos/161_descrip.pdf

DIVAKAR, P.K., CRESPO, A., BLANCO, O. & LUMBSCH, H.T. (2006): Phylogenetic significance of morphological characters in the tropical *Hypotrachyna* clade of parmelioid lichens (Parmeliaceae, Ascomycota). *Molecular Phylogenetics and Evolution* 40: 448–458.

EGEA, J.M. (1989): Las comunidades liquenicas saxicolas, ombrofobas, litorales, del suroeste de Europa y norte de Africa (*Roccelletea phycopsis* classis prov.). *Studia Geobotanica* 9: 73–151.

EGEA, J.M. & LLIMONA, X. (1981): Claves analíticas de los líquenes de rocas silíceas no volcánicas del S.E. de España. *Anales de la Universidad de Murcia (Ciencias)* 37: 183–218.

EGEA, J.M. & LLIMONA, X. (1982): Los líquenes silicícolas de la Sierra del Cabo de Palos; estudio florístico fitosociológico y ecológico. *Acta Botánica Malacitana* 7: 11–38.

EGEA, J.M. & LLIMONA, X. (1984): La vegetación liquénica saxícola de los volcanes del Mar Menor (Murcia, S.E. de España). *Butlletí de la Institució Catalana d'Història Natural (Secció Botànica)* 51: 77–99.

EGEA, J.M. & LLIMONA, X. (1987): Las comunidades de líquenes de las rocas silíceas no volcánicas del S.E. de España. *Acta Botanica Barcinonensia* 36: 1–123.

EGEA, J.M. & LLIMONA, X. (1994): La flore et la végétation lichéniques des laves acides du parc naturel de la Sierra del Cabo de Gata (S.E. de l'Espagne) et des régions voisines. *Bulletin de la Société Linnéenne de Provence* 45: 263–281.

EGEA, J.M., LLIMONA, X. & MANRIQUE, E. (1995): Nuevos datos sobre *Glyphopeltis ligustica* (Psoraceae, Lecanorales) y su área de distribución. A: F.J.A. DANIËLS, M. SCHULZ & J. PEINE (eds.): *Flechten Follmann. Contributions to lichenology in Honour of Gerhard Follmann* 183–192. Botanical Institute, University of Cologne, Cologne.

EGEA, J.M. & TORRENTE, P. (1985): Aportación al conocimiento de los líquenes calcícolas del litoral del S.E. de España. *International Journal of Mycology and Lichenology* 2: 31–38.

ERIKSSON, O.E. (1981): The families of bitunicate Ascomycetes. *Opera Botanica* 60: 1–209.

FLETCHER, A. & HAWKSWORTH, D.L. (2009): *Diploschistes*. A: C.W SMITH, A. APTROOT, B.J. COPPINS, A. FLETCHER, O.L. GILBERT, P.W. JAMES & P.A. WOLSELEY (eds.): *The lichens of Great Britain and Ireland* 378–380. The British Lichen Society, London.

FOLCH, R. (1988): *Natura, ús o abús? Llibre Blanc de la Gestió de la Natura als Països Catalans*. 2a Edició ampliada 306–311. Editorial Barcino, Barcelona.

FRANQUESA, T. (1995): *El paisatge vegetal de la península del Cap de Creus*. Institut d'Estudis Catalans, Barcelona.

FREIRE DOPAZO, M. & GARCÍA MOLARES, A. (1999): Flora liquénica saxícola y arenícola de la Península de O Grove (Pontevedra, NW de España). *Acta Botánica Malacitana* 24: 13–25.

FRISCH, A., KALB, K. & GRUBE, M. (2006): Contributions towards a new systematics of the lichen family Thelotremataceae. *Bibliotheca Lichenologica* 92: 1–556.

GAYA, E. (2006): Revisió morfològica i molecular dels tàxons lobulats del gènere *Caloplaca* (*Teloschistaceae*, líquens), amb especial èmfasi en el grup de *C. saxicola*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

GAYA, E. (2009): Taxonomical revision of the *Caloplaca saxicola* group (Teloschistaceae, Lichen-forming Ascomycota). *Bibliotheca Lichenologica* 101: 1–191.

GAYA, E., LUTZONI, F., ZOLLER, S. & NAVARRO-ROSINÉS, P. (2003): Phylogenetic study of *Fulgensia* and allied *Caloplaca*, and *Xanthoria* species (Teloschistaceae, lichen-forming Ascomycota). *American Journal of Botany* 90: 1095–1103.

GAYA, E., NAVARRO-ROSINÉS, P., LLIMONA, X., HLADUN, N. & LUTZONI, F. (2008): Phylogenetic reassessment of the Teloschistaceae (lichen-forming Ascomycota, Lecanoromycetes). *Mycological Research* 112: 528–546.

GAYA, E., REDELINGS, B.D., NAVARRO-ROSINÉS, P., LLIMONA, X., DE CÁCERES, M. & LUTZONI, F. (2011): Align, or not to align? Resolving species complexes within the *Caloplaca saxicola* group as a case study. *Mycologia* 103: 361–378.

GILENSTAM, G. (1969): Studies in the lichen genus *Conotrema*. *Arkiv för Botanik* 7: 149–179.

GIRALT, M. (1991): *Flora i vegetació liquènica epifítica de la plana i serralades litorals tarragonines. Estimació de la contaminació atmosfèrica a la plana del Camp de Tarragona*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

GIRALT, M. (2001): The lichen genera *Rinodina* and *Rinodinella* (lichenized Ascomycetes, Physciaceae) in the Iberian Peninsula. *Bibliotheca Lichenologica* 79: 1–160.

GIRALT, M. & BARBERO, M. (1995): The saxicolous species of the genus *Rinodina* in the Iberian Peninsula containing atranorin, pannarin or gyrophoric acid. *Mycotaxon* 56: 45–80.

GIRALT, M. & LLIMONA, X. (1997): The saxicolous species of the genera *Rinodina* and *Rinodinella* lacking spot test reactions in the Iberian Peninsula. *Mycotaxon* 62: 175–224.

GÓMEZ-BOLEA, A. (1985): *Líquenes epífitos en Catalunya*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

GRUBE, M., DEPRIEST, P.T., GARGAS, A. & HAFELLNER, J. (1995): DNA isolation from lichen ascomata. *Mycological Research* 99: 1321–1324.

GRUBE, M. & KROKEN, S. (2000): Molecular approaches and the concept of species and species complexes in lichenized fungi. *Mycological Research* 104: 1284–1294.

GUDERLEY, R. & LUMBSCH, H.T. (1996): The lichen genus Diploschistes in South Africa (Thelotremataceae). *Mycotaxon* 58: 269–292.

GUDERLEY, R., LUMBSCH, H.T. & FEIGE, G.B. (1997): *Ingvariella*, a new genus in the Thelotremataceae (lichenized Ascomycotina). *Nova Hedwigia* 64: 147–154.

GUEIDAN, C., ROUX, C. & LUTZONI, F. (2007): Using a multigene phylogenetic analysis to assess generic delineation and character evolution in Verrucariaceae (Eurotiomycetes, Ascomycota). *Mycological Research* 111: 1145–1168.

GUIRADO I CABEZAS, M. (2007): Proposta d'assaig d'eliminació de *Carpobrotus* spp. a la Reserva Integral de Cap de Creus. Generalitat de Catalunya, Departament de Medi Ambient i Habitatge. http://www20.gencat.cat/docs/parcsnaturals/Home/Cap%20de%20Creus/Coneix-nos/Centre%20de%20Documentacio/Flora%20i%20Vegetacio/2007_Carpobrotus.pdf

HALE, M.E. (1980): Generic delimitation in the lichen family Thelotremataceae. *Mycotaxon* 11: 130–138.

HALE, M.E. (1981): A revision of the lichen family Thelotremataceae in Sri Lanka. *Bulletin of the British Museum (Botany)* 8: 227–332.

HELMS, G., FRIEDL, T. & RAMBOLD, G. (2003): Phylogenetic relationships of the Physciaceae inferred from rDNA sequence data and selected phenotypic characters. *Mycologia* 95: 1078–1099.

HENSSEN, A. (1987): *Lichenothelia*, a genus of microfungi in rocks. *Bibliotheca Lichenologica* 25: 257–293.

HENSSEN, A. (1995): *Sagiolechia atlantica*, eine neue Flechte von den Atlantischen Inseln (Ascomycotina, Ostropales). *Bibliotheca Lichenologica* 58: 123–136.

HENSSEN, A. & JAHNS, H.M. (1974): *Lichenes*. Georg Thieme Verlag, Stuttgart.

HERNÁNDEZ-MARINÉ, M. (1995): Cianofícies i microalgues del sòl del Cap Norfeu. A: J.M. MASDAVALL, A. MIQUEL & S. MUSQUERA (eds.): *La península del Cap de Creus i la serra de Verdera*. Actes de les IV Jornades de la Institució Catalana d'Història Natural 53–60. Institut d'Estudis Empordanesos, Figueres.

HLADUN, N.L. (1977): *Aportación a la flora y vegetación liquénica de la región culminal de les Agudes (Montseny)*. Tesina de Llicenciatura. Universitat de Barcelona, Barcelona.

HLADUN, N.L. (1981): *Aportación a la flora, morfología y vegetación de los líquenes silicícolas de la parte alta del Montseny (Catalunya)*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

HLADUN, N.L. (2011): Mòdul LiqueCat. Banc de Dades de Biodiversitat de Catalunya. Generalitat de Catalunya i Universitat de Barcelona. http://biodiver.bio.ub.es/biocat/homepage.html

HLADUN, N.L., GÓMEZ-BOLEA, A. & LLIMONA, X. (1994): Aportació a la flora i vegetació liquènica dels aiguamolls de l'Alt Empordà. A: J. GOSÁLBEZ, J. SERRA & E. VELASCO (eds.): *Els Sistemes Naturals dels Aiguamolls de l'Empordà. Treballs de la Institució Catalana d'Història Natural* 151–166. Institució Catalana d'Història Natural, Barcelona.

IHLEN, G.P. (2004): A new species of *Lichenostigma* (Lichenotheliaceae, Arthoniales) from Scandinavia. *The Lichenologist* 36: 183–189.

JAMES, P.W., HAWKSWORTH, D.L. & ROSE, F. (1977): Lichen communities in the British Isles: a preliminary conspectus. A: M.R.D. SEAWARD (ed.): *Lichen Ecology* 295-413. Academic Press, Londres.

KAWAKITA, A., SOTA, T., ASCHER, J.S., ITO, M., TANAKA, H. & KATO, M. (2003): Evolution and Phylogenetic Utility of Alignment Gaps Within Intron Sequences of Three Nuclear Genes in Bumble Bees (*Bombus*). *Molecular Biology and Evolution* 20: 87–92.

KLEMENT, O. (1955): Prodromus der mitteleuropaischen Flechtengesellschaften. *Feddes Repert. Beih.* 135: 5–194.

KNAPP, S., MCNEILL, J. & TURLAND, N.J. (2011) Changes to publication requirements made at the XVIII International Botanical Congress in Melbourne - what does e-publication mean for you. *PhytoKeys* 6: 5–11.

LANGE O.L, BÜDEL B., MEYER, A. & KILIAN, E. (1993): Further evidence that activation of photosynthesis of lichens by dry cyanobacterial lichens requires liquid water. *The Lichenologist* 25: 175–189.

LETTAU, G. (1932–1937): Monographische Bearbeitung einiger Flechtenfamilien. Beihefte. *Repertorium Speciei Novi Regni Vegetale* 135: 5–194.

LLENAS, M. (1902): Algunos líquenes de los alrededores de Barcelona. *Boletín de la Real Sociedad Española de Historia Natural* 2: 207–211.

LLENAS, M. (1905): Enumeración y distribución de los Peltigeráceos en Cataluña. *Boletín de la Real Sociedad Española de Historia Natural* 5: 168–175.

LLENAS, M. (1909): Ensaig d'una flora liquènica de Catalunya. *Butlletí de la Institució Catalana d'Història Natural* 6: 1–39.

LLIMONA, X. (1969): Visió general dels líquens de Catalunya. *Treballs de la Societat Catalana de Biologia* 26: 58–65.

LLIMONA, X. (1973): *Las comunidades de líquenes de los yesos de España*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

LLIMONA, X. (1974): *Las comunidades de líquenes de los yesos de España*. Resum Tesi Doctoral. Universitat de Barcelona, Barcelona.

LLIMONA, X. (1976): Impressions sobre la vegetació de l'illa de Cabrera. Vegetació Liquènica. *Treballs de la Institució Catalana d'Història Natural* 7: 123–137.

LLIMONA, X. (1980): Sessions científiques: La vegetació liquénica de les illes Columbretes. *Societat Catalana de Biologia* 3–4: 146–147.

LLIMONA, X. (1985): La recerca micològica i liquenològica als Països Catalans. *Butlletí de la Institució Catalana d'Història Natural* 50: 97–114.

LLIMONA, X. (1995): Contribució a l'estudi de la biodiversitat de la península del Cap de Creus i serra de Verdera. I. Els fongs. II. Els líquens. A: J.M. MASDAVALL, A. MIQUEL & S. MUSQUERA (eds.): *La península del Cap de Creus i la serra de Verdera*. Actes de les IV Jornades de la Institució Catalana d'Història Natural 73–86. Institut d'Estudis Empordanesos, Figueres.

LLIMONA, X. (2009): La criptogàmia i la Real Acadèmia: la recerca en micologia (fongs i líquens). *Memorias de la Real Academia de Ciencias y Artes de Barcelona* 64: 119–210.

LLIMONA, X. &. EGEA, J.M (1984): La vegetación liquénica saxícola de los volcanes del Mar Menor (Murcia, SE de España). *Butlletí de la Institució Catalana d'Història Natural* 51: 77–99.

LLIMONA, X. & EGEA, J.M. (1985): Las comunidades liquénicas de las superficies de escorrentía de las rocas silíceas mediterráneas. *Anales del Jardín Botánico de Madrid* 41: 429–444.

LLIMONA, X., HLANDUN, N. & GÓMEZ-BOLEA, A. (1984): La vegetació liquènica de les Illes Medes. A: J. ROS, I. OLIVELLA & J.M. GILI (eds.): *Els Sistemes Naturals de les Illes Medes* 115–127. Institut d'Estudis Catalans, Barcelona.

LLOP, E., BARBERO, M., CHESA, M.J., FERNÁNDEZ BRIME, S., FIGUERAS, G., GÓMEZ-BOLEA, A., HLADUN, N.L., MUÑIZ, D. & NAVARRO-ROSINÉS, P. (2010): Els líquens i els fongs liquenícoles de les Planes de Son i la mata de València. A: J. GERMAIN I OTZET (ed.): *Els sistemes naturals de les Planes de Son i la mata de València* 189–227. Institució Catalana d'Història Natural, Barcelona.

LLOP, E., BARBERO, M., FERNÁNDEZ BRIME, S., FIGUERAS, G., MUÑIZ, D. & LLIMONA. X.: Aproximació al coneixement de la flora liquènica i dels fongs liquenícoles dels altiplans i conques centrals de Catalunya: el sector Segàrric. *Butlletí de la Institució Catalana d'Història Natural* (En revisió).

LLOP, E. & HLADUN, N.L. (2003): Aportació al coneixement de la flora liquènica del massís de Cadiretes (Girona, N.E. Península Ibèrica). *Butlletí de la Institució Catalana d'Història Natural* 71: 39–50.

LONGÁN, A. (2001): *Els líquens epífits com a indicadors de l'estat de conservació del bosc mediterrani. Proposta metodològica per als alzinars de Catalunya.* Tesi Doctoral. Universitat de Barcelona, Barcelona.

LUMBSCH, H.T. (1985): The lichen genus *Diploschistes* in the southern Hemisphere. *DSIR Botany Division Newsletter, Supplement* 2: 9–10.

LUMBSCH, H.T. (1986): Evolutionary trends and distribution patterns in the genus *Diploschistes*. A: *Progress and Problems in Lichenology in the Eighties*. Lecture and Poster Abstracts. Munster.

LUMBSCH, H.T. (1988): The identity of *Diploschistes gypsaceus*. *The Lichenologist* 20: 19–24.

LUMBSCH, H.T. (1989): Die holarktischen Vertreter der Flechtengattung *Diploschistes* (Thelotremataceae). *Journal of the Hattori Botanical Laboratory* 66: 133–196.

LUMBSCH, H.T. (2002): How objective are genera in euascomycetes? *Perspectives in Plant Ecology, Evolution and Systematics* 5: 91–101.

LUMBSCH, H.T. & ELIX, J.A. (1989): Taxonomy of some *Diploschistes* spp. (lichenized ascomycetes, Thelotremataceae) containing gyrophoric acid. *Plant Systematics and Evolution* 167: 195–199.

LUMBSCH, H.T. & ELIX, J.A. (2003): The lichen genus *Diploschistes* (Thelotremataceae) in Australia. *Bibliotheca Lichenologica* 86: 119–128.

LUMBSCH, H.T., GUDERLEY, R. & FEIGE, G.B. (1997): Ascospore septation in *Diploschistes* (Thelotremataceae, lichenized Ascomycota) and the taxonomic significance of macro- and microcephalic ascospore types. *Plant Systematics and Evolution* 205: 179–184.

LUMBSCH, H.T. & HUHNDORF, S.M (2010): Myconet Volume 14. *Fieldiana*, *Life and Earth Sciences* 1: 1–64.

LUMBSCH, H.T., MANGOLD, A., LÜCKING, R., GARCÍA, M.A. & MARTÍN, M.P. (2004): Phylogenetic position of the genera *Nadvornikia* and *Pyrgillus* (Ascomycota) based on molecular data. *Symbolae Botanicae Upsalienses* 34: 9–17.

LUMBSCH, H.T., MANGOLD, A., MARTÍN, M.P. & ELIX, J.A. (2008): Species recognition and phylogeny of *Thelotrema* species in Australia (Ostropales, Ascomycota). *Australian Systematic Botany* 21: 217–227.

LUMBSCH, H.T. & TEHLER, A. (1998): A cladistic study of the genus *Diploschistes* (Ascomycotina, Thelotremataceae). *The Bryologist* 101: 398–403.

LUTZONI, F. & VILGALYS, R. (1995): Integration of morphological and molecular datasets in estimating fungal phylogenies. *Canadian Journal of Botany* 73 (Suppl. 1): S649–S659.

LUTZONI, F., WAGNER, P. & REEB, V. (2000): Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. *Systematic Biology* 49: 628–651.

MANGOLD, A., ELIX, J.A. & LUMBSCH, H.T. (2009): Thelotremataceae. A: P.M MCCARTHY (ed.): *Flora of Australia* 195–420. ABSR and CSIRO Publishing, Canberra and Melbourne.

MARTÍN, M.P., LAGRECA, S. & LUMBSCH, H.T. (2003): Molecular phylogeny of *Diploschistes* inferred from ITS sequence data. *The Lichenologist* 35: 27–32.

MANGOLD, A., MARTÍN, M.P., LÜCKING, R. & LUMBSCH, H.T. (2008): Molecular phylogeny suggests synonymy of Thelotremataceae within Graphidaceae (Ascomycota, Ostropales). *Taxon* 57: 476–486.

MARTÍN, M.P. & WINKA, K. (2000): Alternative methods of extracting and amplifying DNA from lichens. *The Lichenologist* 32: 189–196.

MARTÍN, M.P., WINKA, K., LLIMONA, X. & LUMBSCH, H.T. (2000): Evaluation of morphological variation in the lichen *Diploschistes ocellatus* (Ascomycota, Ostropales): evidence from nuclear rDNA ITS sequence data. *Plant Biology* 2: 571–578.

MASSALONGO, A.B. (1852): *Ricerche sull'autonomia dei licheni crostosi e materiali pella loro naturale ordinazione*. Tipografia A. Frizierio, Verona.

MCDONALD, T., MIADLIKOWSKA, J. & LUTZONI, F. (2003): The lichen genus *Sticta* in the Great Smoky Mountains: A phylogenetic study of morphological, chemical, and molecular data. *The Bryologist* 106: 61–79.

MÉNARD, T. (1997): *Étude phytosociologique et écologique des peuplements lichéniques saxicoles calcifuges du sud-est de la France*. Tesi Doctoral. Université de Droit, d'Économie et des Science d'Aix-Marseille III.

MESSUTI, M.I., CODESAL, P.L., MANGOLD, A., LÜCKING, R. & LUMBSCH, H.T. (2010): New or interesting *Chapsa* and *Topeliopsis* species (Ascomycota: Ostropales) from Argentina. *The Lichenologist* 42: 191–195.

MIADLIKOWSKA, J. & LUTZONI, F. (2000): Phylogenetic revision of the genus *Peltigera* (lichen-forming ascomycetes) based on morphological, chemical and large subunit nuclear ribosomal DNA data. *International Journal of Plant Sciences* 161: 925–958.

MIADLIKOWSKA, J., LUTZONI, F., GOWARD, T., ZOLLER, S. & POSADA, D. (2003): New approach to an old problem: Incorporating signal from gap-rich regions of ITS and nrDNA large subunit into phylogenetic analyses to resolve the *Peltigera canina* species complex. *Mycologia* 95: 1181–1203.

MUS, M. (1985a): Líquens silicícoles de Fornalutx, Mallorca. *Bolletí de la Societat d'Història Natural de les Balears* 29: 63–73.

MUS, M. (1985b): Líquens silicícoles de l'illa de Menorca (I). *Bolletí de la Societat d'Història Natural de les Balears* 29: 109–122.

MUS, M. & EGEA, J.M. (1989): Líquenes sobre rocas no calcáreas en la Serra Nord de Mallorca, Islas Baleares (España). *Anales de Biología* 15: 115–129.

NAVARRO-ROSINÉS, P. (1985): *Flora i vegetació liquènica dels gresos calcaris de Sanaüja (La Segarra)*. Tesina de Llicenciatura. Universitat de Barcelona, Barcelona.

NAVARRO-ROSINÉS, P. (1992): *Els líquens i fongs liquenícoles dels substrats carbonatats de Catalunya meridional*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

NAVARRO-ROSINÉS, P. & HLADUN, N. (1991): Flora liquénica de las rocas carbonatadas del valle de Núria (Pirineos, Cataluña). *Monografías del Instituto Pirenaico de Ecología* 5: 75–83.

NAVARRO-ROSINÉS, P. & HAFELLNER, J. (1996): *Lichenostigma elongata* spec. nov. (Dothideales), a lichenicolous ascomycete on *Lobothallia* and *Aspicilia* species. *Mycotaxon* 57: 211–225.

NIMIS, P.L. (1993): *The Lichens of Italy*. Museo Regionale di Scienze Naturali, Torino.

NIMIS, P.L. (1998): A critical appraisal of modern generic concepts in lichenology. *The Lichenologist* 30: 427–438.

NORDIN, A., SAVIĆ, S. & TIBELL, L. (2010): Phylogeny and taxonomy of *Aspicilia* and Megasporaceae. *Mycologia* 102: 1339–1349.

NORMAN, J.M. (1853): Conatus praemissus redactionis novae generum nonnullorum Lichenum in organis fructificationes vel sporis fundatae. *Nyt Magazin for Naturvidenskaberne* 7: 213–252.

OZENDA, P. & CLAUZADE, G. (1970): *Les Lichens. Etude Biologique et Flore Illustree*. Masson & Cie. Editeurs, Paris.

PANT, G. & UPRETI, D.K. (1993): The lichen genus *Diploschistes* in India and Nepal. *The Lichenologist* 25: 33–50.

PAPONG, K., MANGOLD, A., CORUSH, J., LÜCKING, R. & LUMBSCH, H.T. (2009): Phylogenetic position of the foliicolous genus *Chroodiscus* (Ostropales, Ascomycota) inferred from nuclear and mitochondrial ribosomal DNA sequences. *Fungal Diversity* 38: 147–153.

PEREIRA, I. (1992): *Flora, vegetación y ecología de los líquenes acuáticos de España*. Tesi Doctoral. Universitat de Barcelona, Barcelona.

PERERA, M. (1986): Aproximació al coneixement florístic i ecològic de les algues bentòniques litorals del Cap de Creus. Tesina de Llicenciatura. Universitat de Barcelona, Barcelona.

PERERA, M. (1987): Resultados de un transecto de la vegetación bentónica del litoral del cabo Norfeu (Gerona). En: *Actas del VI Simpsosium Nacional de Botánica Criptogámica* 99–107. Universidad de Granada, Granada.

PÉREZ-ORTEGA, S. & CALATAYUD, V. (2009): *Lichenostigma epirupestre*, a new lichenicolous species on *Pertusaria* from Spain. *Mycotaxon* 107: 189–195.

POELT, J. (1958): Die lobaten Arten der Flechtengattung *Lecanora* Ach. sensu ampl. in der Holarktis. *Planta* 51: 288–307.

POELT, J. (1969): *Bestimmungsschlüssel europäischer flecht*en. J. Cramer, Lehre.

POELT, J. (1973): Classification. A: V. AHMADJIAN & M.E. HALE (eds.): *The Lichens* 599–632. Academic Press, New York and London.

RICO, V.J., CALATAYUD, V. & GIRALT, M. (2003): *Buellia tesserata* and *Dimelaena radiata*, two closely related species. *The Lichenologist* 35: 117–124.

RICO, V.J., CALATAYUD, V. & GIRALT, M. (2006): The lichen genus *Dimelaena* (Physciaceae, Lecanorales) in the Iberian Peninsula. *Cryptogamie, Mycologie* 27: 149–166.

RIEUX, R., RITSCHEL, G. & ROUX, C. (1977): Etude ecologique et phytosociologique de *Crassuletum tillaeae* Molinier et Tallon 1949. *Revue de Biologie et d'Ecologie Mediterraneenne* 4: 117–143.

RIVAS PLATA, E., HERNÁNDEZ, J.E., LÜCKING, R., STAIGER, B., KALB, K. & CÁCERES, M.E.S. (2011): *Graphis* is two genera. A remarkable case of parallel evolution in lichenized Ascomycota. *Taxon* 60: 99–107.

RIVAS PLATA, E. & LUMBSCH, H.T. (2011): Parallel evolution and phenotypic divergence in lichenized fungi: A case study in the lichen-forming fungal family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). *Molecular Phylogenetics and Evolution* 61: 99–107.

ROUX C. (2011): Liste des lichens et champignons lichénicoles non lichénisés de France. http://lichenologue.org/fr/

ROUX C., BÜLTMANN, H. & NAVARRO-ROSINES P. (2009): Syntaxonomie des associations de lichens saxicoles-calcicoles du sud-est de la France. 1. *Clauzadeetea immersae*, *Verrucarietea nigrescentis*, *Incertae saedis*. *Bulletin de la Société Linnéenne de Provence* 60 : 151–175.

ROUX, C., COSTE, C., BRICAUD, O. & MASSON, D. (2006): Catalogue des lichens et des champignons lichénicoles des la région Languedoc-Roussillion (France méridionale). *Bulletin de la Société Linnéenne de Provence* 57: 85–200.

ROUX, C. & GUEIDAN, C. (2002): Flore et végétation des lichens et champignons lichénicoles non lichénisés du massif de la Sainte-Baume (Var, Provence, France). *Bulletin de la Société Linnéenne de Provence* 53: 123–150.

ROUX, C., MASSON, D., BRICAUD, O., COSTE, C. & POUMARAT, S. (2011): Flore et végétation des lichens et champignons lichénicoles de quatre réserves naturelles des Pyrénées–Orientales (France). *Bulletin de la Société Linnéenne de Provence Numéro Special* 14 : 3–151.

RULL, J. (1987): Estudio de la comunidad de *Cystoseira mediterranea* en dos localidades de la península del Cap de Creus (Alt Empordà). Tesina de Llicenciatura. Universidad de Barcelona, Barcelona.

RULL, J. & GÓMEZ GARRETA, A. (1990a): Estudio de la comunidad de *Cystoseira mediterranea* en dos localidades de la península del Cap de Creus (NE de España). *Collectanea Botanica* 18: 5–19.

RULL, J. & GÓMEZ GARRETA, A. (1990b): Aportació al coneixement de la flora bentònica marina del Cap de Creus (Alt Empordà). *Folia Botanica Miscellanea* 7: 37–42.

SÁEZ, L., AYMERICH, P. & BLANCHÉ, C. (2010): *Llibre vermell de les plantes vasculars endèmiques i amenaçades de Catalunya*. Argania Editio, Barcelona.

SCHEIDEGGER, C. (1993): A revision of European saxicolous species of the genus *Buellia* de Not. and formerly included genera. *The Lichenologist* 25: 315–364.

SCHREBER, J.C.D. VON (1771): *Spicilegium florae Lipsicae*. Prostat in bibliopolio Dykiano, Leipzig.

SCOPOLI, J.A. (1772): *Flora carniolica, Editio secunda aucta et reformata*. Impensis Ioannis Pauli Krauss, Bibliopolae Vindobonensis, Viena.

SHERWOOD M.A. (1977): The ostropalean fungi. *Mycotaxon* 5: 1–277.

SMITH, A.L. (1921): *A Handbook of the British Lichens*. British Museum, London.

SOUZA-EGIPSY, V., ASCASO, C. & WIERZCHOS, J. (2002): Ultrastructural and Biogeochemical Features of Microbiotic Soil Crusts and their Implications in a Semi-Arid Habitat. *Geomicrobiology Journal* 19: 567–580.

STEINER, J. (1893): Beiträge zur Lichenenflora Griechenlands und Egyptens. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Math.-naturw. Klasse Abt. I* 102: 152–176.

STOLLEY, G. & KAPPEN, L. (2002): Contributions to the lichen flora of Menorca (Balearic Islands). *Nova Hedwigia* 75: 121–175.

TEHLER, A (1995): Morphological data, molecular data, and total evidence in phylogenetic analysis. *Canadian Journal of Botany* 73 (Suppl. 1): S667-S676.

TERRÓN, A., BURGAZ, A.R. & ÁLVAREZ, J. (2000): Líquenes de la provincia de Zamora. *Botanica Complutensis* 24: 9–43.

TOMÁS, X., CAMBRA, J. & SABATER, S. (1987): Comunidades algales del cabo de Creus (entre los 0 y los 100 m. de altitud) y su relación con el ambiente. *Limnética* 3: 111–119.

TORRES, E. & HLADUN, N.L. (1982): Aportació a la flora liquénica del Turó de Sant Mateu (Premià de Dalt - Maresme). *Collectanea Botanica* 13: 381–383.

TUCKERMAN, E. (1872): *Genera Lichenum: An arrangement of the North America lichens*. Edwin Nelson, Amherst.

VELA, A. & HERNÁNDEZ-MARINÉ, M. (1987): Algas edáficas del cabo Norfeu. En: *Actas del VI Simpsosium Nacional de Botánica Criptogámica* 185–198. Universidad de Granada, Granada.

WATSON, W. (1929): The classification of lichens I. *New Phytologist* 28: 1–36.

WEDIN, M., DÖRING, H. & GILSENSTAM, G. (2004): Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis–Conotrema* complex. *New Phytologist* 164: 459–465.

WEDIN, M., DÖRING, H. & GILSENSTAM, G. (2006): *Stictis* s. lat. (Ostropales, Ascomycotina) in northern Scandinavia, with a key and notes on morphological variation in relation to lifestyle. *Mycological Research* 110: 773–789.

WIRTH, V. & LLIMONA, X. (1975): Das *Pertusarietum rupicolae* un. nova, eine Silikatflechten-Gesellschaft im Mittelmeerraum, mit Bemerkungen zur Taxonomie des Pertusaria pseudocorallina-Formenkreises. *Herzogia* 3: 335–345.

ZAHLBRUCKNER, A. (1892): O. Kuntze's: Revisio generum plantarum, mit Bezug auf einige Flechtengattungen. *Hedwigia* 31: 34–38.

ZAHLBRUCKNER, A. (1905): Liechenes (Flechten). B. Specieller Tail. A: A. ENGLER & K. PRANTL (eds.): *Die natürlichen Pflanzenfamilien*. Teil 1, Abt. 1* 1–249. Verlag von Wilhelm Engelmann, Leipzig.

APÈNDIXS

APÈNDIX 1. Relació dels número de registre de l'herbari BCN-Lich, corresponents al material testimoni de l'estudi florístic (capítol 1).

Acarospora epithallina H. Magn.
18909
Acarospora hilaris (Dufour) Hue
18909, 18911, 18915, 18916, 18930, 19080
Acarospora microcarpa (Nyl.) Wedd.
18895, 18954, 18955
Acarospora modenensis H. Magn.
18850, 18851
Acarospora oligospora (Nyl.) Arnold
18849
Acarospora cf. ***scotica*** Hue
18912, 19072
Acarospora sinopica (Wahlenb.) Körb.
18644, 18905, 18953
Acarospora sulphurata (Arnold) Arnold
18824, 18827, 18914, 18952
Acarospora umbilicata Bagl.
18593, 18848
Acarospora veronensis A. Massal.
18629, 18631, 18632, 18636, 18641, 18643, 18910, 18960, 18975, 18980, 18985, 18988, 19138
Acrocordia macrospora A. Massal.
18594, 18597, 18598
Agonimia opuntiella (Buschardt & Poelt) Vězda
18969, 19213, 19220, 19221, 19228, 19234, 19235, 19236, 19239, 19241, 19244, 19248, 19251

Amandinea sp.

18581, 19177, 19184, 19203

Anaptychia runcinata (With.) J. R. Laundon

18468, 18497, 18724, 19129

Anema nummularium (Dufour) Nyl.

18832, 18834, 19079, 19091

Arthonia lecanorina (Almq.) R. Sant.

18755

Arthonia molendoi (Heufl. ex Frauenf.) R. Sant.

18868

Arthonia varians (Davies) Nyl.

18636

Aspicilia caesiocinerea (Nyl. ex Malbr.) Arnold

18531, 18564, 18565, 18652, 18655, 18660, 18678, 18681, 18683, 18685, 18687, 18698, 18717, 18741, 18776, 18872, 18873, 18898, 18959, 18960, 18968, 18969, 18971, 18972, 19075, 19076, 19077, 19081, 19084, 19085, 19086, 19087, 19088, 19125, 19128, 19132

Aspicilia calcarea (L.) Mudd

19270

Aspicilia contorta (Hoffm.) Kremp. subsp. ***hoffmanniana*** S. Ekman & Fröberg ex R. Sant.

18649, 19083, 19217, 19222, 19236, 19249, 19251, 19270, 19291

Aspicilia cupreoglauca B. de Lesd.

18599, 18613, 18625, 18740, 18756, 18880, 18883, 18894, 18897, 18921

Aspicilia farinosa (Flörke) Flagey

19263, 19283

Aspicilia inornata Arnold

18822, 18839, 19057

Aspicilia intermutans (Nyl.) Arnold

18469, 18550, 18562, 18563, 18579, 18617, 18623, 18657, 18658, 18659, 18661, 18666, 18667, 18674, 18682, 18706, 18717, 18725, 18747, 18749, 18750, 18881, 18897, 18961, 18962, 18970, 18976, 18985, 18989, 18997, 19021, 19024, 19031, 19033, 19038, 19039, 19040, 19041, 19043, 19044, 19045, 19047, 19051, 19052, 19056, 19064, 19070, 19130, 19142

Aspicilia subdepressa (Nyl.) Arnold

18578, 18579, 18592, 18679, 18704, 18894, 19031

Bagliettoa calciseda (DC.) Gueidan & Cl. Roux

19214, 19215, 19216, 19217, 19220, 19222, 19224, 19231, 19236, 19237, 19240, 19243, 19245, 19251

Bagliettoa cazzae (Zahlbr.) Vězda & Poelt

19275, 19277, 19285, 19293, 19294

Botryolepraria lesdainii (Hue) Canals, Hern.-Mar., Gómez-Bolea & Llimona

19246

Buellia abstracta (Nyl.) H. Olivier

18580, 18590, 18714, 18958, 18959, 18976, 18985, 19045, 19054, 19062, 19076, 19101, 19131

Buellia atrocinerella (Nyl.) Scheid.

18578

Buellia badia (Fr.) A. Massal.

18572, 18674, 18678, 18683, 18828, 18895, 18962, 18970, 18971, 18985

Buellia caloplacivora Llimona & Egea

18718, 19170, 19263

Buellia dispersa A. Massal.

18674, 18827, 18828, 18871, 18961, 18965, 18970, 18971, 19001, 19083, 19183

Buellia leptoclinoides (Nyl.) J. Steiner

18581, 19155

Buellia spuria (Schaer.) Anzi

18578, 18579, 18683, 18699, 18715, 18881, 18960, 19047, 19072

Buellia stellulata (Taylor) Mudd

18570, 18578, 18581, 18627, 18628, 18679, 18680, 18808, 18810, 18811, 18960, 18998, 19031, 19056, 19076, 19131, 19132, 19138, 19185

Buellia subdisciformis (Leight.) Vain.

18518, 18532, 18613, 18624, 18631, 18638, 18670, 18674, 18718, 18730, 18733, 18782, 18783, 18784, 18785, 18789, 18790, 18793, 18828, 18983, 18986, 18988, 18990, 19001, 19003, 19006, 19007, 19012, 19019, 19029, 19060, 19066, 19146, 19151, 19153, 19158, 19159, 19160, 19173, 19177, 19178, 19182, 19183, 19184, 19188, 19189, 19191, 19198, 19203, 19204, 19208

Buellia tesserata Körb.

18566, 18581, 18819, 18924, 18984, 18987, 18988, 19020, 19150, 19153, 19188, 19189

Buellia tirolensis Körb.

18577, 18578, 19061, 19133, 19138

Caloplaca aegaea Sipman

18491, 18492, 18582, 18816, 18821, 18868, 18869

Caloplaca aetnensis B. de Lesd.

18814, 18874

Caloplaca alociza (A.Massal.) Mig.

19268, 19285

Caloplaca aractina (Fr.) Häyrén

18532, 18533, 18763, 18818, 18820, 18883, 18959, 18968, 18994, 18996, 19001, 19023

Caloplaca arcis (Poelt & Vĕzda) Arup

18528, 18956

Caloplaca arenaria (Pers.) Müll. Arg.

18564, 18567, 18580, 18591, 18670, 18954, 18976, 18985, 19025, 19054, 19055, 19056

Caloplaca atroflava (Turner) Mong.

18898, 19077, 19081, 19084, 19085, 19086, 19090

Caloplaca aurantia (Pers.) Hellb.

19220, 19236, 19262, 19263, 19265, 19268, 19270, 19272, 19275

Caloplaca austrocitrina Vondrák, P. Říha, Arup & Søchting

18957

Caloplaca carphinea (Fr.) Jatta

18811

Caloplaca crenularia (With.) J. R. Laundon

18599, 18610, 18612, 18616, 18617, 18630, 18631, 18632, 18634, 18637, 18651, 18672, 18679, 18790, 18792, 18800, 18802, 18803, 18805, 18963, 18968, 18985, 18998, 19019, 19035, 19053, 19054, 19055, 19056, 19067, 19125, 19140, 19155, 19173, 19177, 19178, 19190, 19200, 19201, 19203, 19204, 19208, 19209

Caloplaca diffusa Vondrák & Llimona

18898, 19075, 19077, 19078, 19081, 19084, 19085, 19086, 19088, 19090, 19092, 19093, 19094, 19095

Caloplaca flavescens (Huds.) J. R. Laundon

18600, 18601, 18602, 18603, 18604, 18769, 19273, 19275, 19277, 19278, 19281, 19283, 19285, 19286, 19293, 19294

Caloplaca flavocitrina (Nyl.) H. Olivier

18652, 18812, 18816, 18882, 19224

Caloplaca flavovirescens (Wulfen) Dalla Torre & Sarnth.

19255, 19256, 19262, 19263, 19265, 19267, 19268, 19273, 19275, 19277, 19278, 19280, 19281, 19282, 19285, 19288

Caloplaca furax Egea & Llimona

18681, 18684, 18685, 18872, 18972, 19087

Caloplaca grimmiae (Nyl.) H. Olivier

18875, 18895

Caloplaca inconnexa (Nyl.) Zahlbr. var. ***nesodes*** Poelt & Nimis

18660, 18687, 18698, 18717, 18959, 18968, 19024, 19064

Caloplaca irrubescens (Nyl.) Zahlbr.

18655, 18675, 18873, 18876, 18899, 19057, 19059, 19070, 19083, 19087, 19089, 19132

Caloplaca ligustica B. de Lesd.

18814, 18878, 18879

Caloplaca marina Wedd.

18583, 18815, 18816, 18817, 18823, 19005

Caloplaca maritima (B. de Lesd.) B. de Lesd.

18815, 18816, 18817, 18821, 18823, 18868, 18869, 19127, 19140, 19141, 19170, 19186, 19193, 19196, 19202

Caloplaca polycarpa (A. Massal.) Zahlbr.

19222, 19249

Caloplaca rubelliana (Ach.) Lojka

18669, 18678, 18695, 18827, 18873, 18952, 18968, 19061, 19076

Caloplaca subochracea (Wedd.) Werner var. ***luteococcinea*** Clauzade & Cl. Roux

19269, 19271, 19272, 19281, 19283, 19286, 19293, 19294

Caloplaca variabilis (Pers.) Müll. Arg.

19257, 19261

Caloplaca vitellinula (Nyl.) H. Olivier

18831, 18838

Candelariella aurella (Hoffm.) Zahlbr.

18602, 18603, 18604, 18605, 18821, 18831, 18838

Candelariella vitellina (Hoffm.) Müll. Arg.

18472, 18473, 18654, 18680, 18738, 18746, 18756, 18875, 18894, 18895, 18943, 18961, 18962, 18965, 18970, 18985, 19031, 19055, 19056, 19058, 19062, 19081, 19084, 19167, 19170

Catillaria atomarioides (Müll. Arg.) H. Kilias

18654, 19032, 19033, 19036, 19051

Catillaria chalybeia (Borrer) A. Massal.

18498, 18662, 18726, 18728, 18755, 18858, 18859, 18860, 18894, 19031, 19035, 19056, 19081, 19083, 19084, 19085, 19086

Catillaria lenticularis (Ach.) Th. Fr.

19021, 19268, 19283

Cercidospora caudata Kernst.

18954

Cercidospora solearispora Calat., Nav.-Ros. & Hafellner

18828

Cercidospora sp. 1

19083

Cercidospora sp. 2

18827

Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.

18608

Cladonia firma (Nyl.) Nyl.

18500, 18502

Cladonia foliacea (Huds.) Willd.

18701, 19097, 19117, 19123

Cladonia furcata (Huds.) Schrad.

18499, 18501, 19109

Cladonia homosekikaica Nuno

18474, 19284

Cladonia humilis (With.) J.R. Laundon

18647

Cladonia mediterranea P. A. Duvign. & Abbayes

18920, 18925

Cladonia pyxidata (L.) Hoffm.

19096, 19100, 19102, 19105, 19108, 19114, 19116, 19118, 19122

Cladonia rangiformis Hoffm.

18526, 18700, 19049

Cladonia subcervicornis (Vain.) Kernst.

18502

Cladonia subrangiformis L. Scriba ex Sandst.

19115

Collema cristatum (L.) Weber ex F. H. Wigg.

19211, 19213, 19221, 19223, 19232, 19233, 19234, 19236, 19239, 19240, 19241, 19242, 19244, 19245, 19248, 19249, 19250, 19251, 19252, 19279

Collema flaccidum *(*Ach.) Ach.

19212

Collema ryssoleum (Tuck.) A. Schneider

18475, 18568, 18836, 18966, 19092

Collema subflaccidum Degel.

18503

Collema tenax (Sw.) Ach.

19120, 19217, 19253, 19268, 19278, 19291

Coscinocladium gaditanum (Clemente) A. Crespo, Llimona & D. Hawksw.

18767, 18771, 18772

Cyphelium marcianum B. de Lesd.

18534, 18619, 18780, 18791, 18794, 18918, 19180

Dactylospora parellaria (Nyl.) Arnold

18753, 18993, 19028

Dermatocarpon luridum (Dill. ex With.) J. R. Laundon

18476

Dermatocarpon miniatum (L.) W. Mann

18569, 18584, 18768, 18893, 19082, 19135

Dimelaena oreina (Ach.) Norm.

18570, 18676, 18680, 18740, 18808, 18810, 18989, 19010, 19018, 19137

Diploicia canescens (Dicks.) A. Massal.

18535, 18571, 18594, 18612, 18765, 18931, 18947

Diploicia subcanescens (Werner) Hafellner & Poelt

18585, 18598, 18639, 18640, 18906, 18977, 18995, 18996, 18998, 19005

Diploschistes actinostomus (Ach.) Zahlbr.

18798, 19154, 19169, 19301, 19309

Diploschistes caesioplumbeus (Nyl.) Vain.

18691, 18921, 19192, 19311, 19323, 19325

Diploschistes diacapsis (Ach.) Lumbsch subsp. ***neutrophilus*** (Clauzade & Cl. Roux) Clauzade & Cl. Roux

19218, 19223, 19312, 19329, 19330

Diploschistes euganeus (A. Massal.) J. Zahlbr.

18579, 18895, 18954, 18955, 18986, 19022, 19036, 19054

Diploschistes interpediens (Nyl.) Zahlbr.

18711, 19175

Diploschistes muscorum (Scop.) R. Sant.

18710, 18713, 19110, 19303, 19313, 19315

Diploschistes ocellatus (Vill.) Norm.

19210, 19238, 19241, 19245, 19248, 19252

Diploschistes scruposus (Schreb.) Norm.

18671, 19034, 19053, 19254, 19284, 19310, 19316, 19327

Diplotomma alboatrum (Hoffm.) Flot.

18658, 19170, 19286

Diplotomma chlorophaeum (Hepp ex Leight.) Kr.P. Singh & S. R. Singh

18604, 18651, 18755, 19056

Diplotomma hedinii (H. Magn.) P. Clerc & Cl. Roux

18601, 18602, 18603, 18604, 18605, 18766, 18771, 19218

Dirina massiliensis Durieu & Mont.

18931, 19030, 19155, 19185, 19187, 19188, 19199, 19201, 19203, 19204, 19205, 19207, 19259, 19264, 19265, 19271, 19272, 19289, 19290

Endocarpon pusillum Hedw.

18587, 18588, 18589, 18865, 18866, 18902, 18949, 18950, 18951, 18981, 18982, 19214, 19215, 19216, 19225, 19231, 19237, 19238, 19243, 19247, 19248, 19251

Endocarpon simplicatum (Nyl.) Nyl

18919, 19102, 19104, 19119

Endococcus buelliae (C. W. Dodge) Matzer

18808, 19010

Endococcus fusiger Th. Fr. & Almq.

18578, 18726, 18785

Endococcus macrosporus (Hepp ex Arnold) Nyl.

18540, 18552, 18570, 18615, 18779, 19171

Endococcus verrucosus Hafellner

18613, 18625, 18880, 18921, 19044

Enterographa pitardii (B. de Lesd.) Redinger

18735

Epiphloea terrena (Nyl.) Trevis.

18856, 18857, 18864, 18903, 18979, 19116

Evernia prunastri (L.) Ach.

18745, 18829, 18922

Flavoparmelia caperata (L.) Hale

18507

Flavoparmelia soredians (Nyl.) Hale

18509, 18510, 18511, 18573, 18751, 18751

Fulgensia fulgens (Sw.) Elenkin

19212, 19213, 19217, 19221, 19232, 19233, 19237, 19241, 19244, 19247, 19251

Glyphopeltis ligustica (B. de Lesd.) Timdal

19082, 19091

Gyalecta jenensis (Batsch) Zahlbr.

18736, 19269, 19272

Gyalideopsis athalloides (Nyl.) Vězda

15283, 15284

Heteroplacidium contumescens (Nyl.) Breuss

18854

Immersaria athroocarpa (Ach.) Rambold & Pietschm.

18705, 18770, 19287

Ingaderia troglodytica Feige & Lumbsch

18926, 18927, 19002

Ingvariella bispora (Bagl.) Guderley & Lumbsch

18962, 18963, 18964, 19026, 19027, 19031, 19036, 19037, 19038, 19040, 19051, 19052

Involucropyrenium tremniacense (A. Massal.) Breuss

19249

Lecania atrynoides M. Knowles

19170, 19186, 19193, 19196

Lecania inundata (Hepp ex Körb.) M. Mayrhofer

18601, 18602, 18605

Lecania sylvestris (Arnold) Arnold

18882, 19266, 19274, 19280, 19293

Lecania turicensis (Hepp) Müll. Arg.

18765, 18772, 18831, 18838, 19256, 19260

Lecanographa grumulosa (Dufour) Egea & Torrente

19206, 19258, 19264, 19276, 19289

Lecanora albescens (Hoffm.) Branth. et Rostr.

18823, 19220

Lecanora campestris (Schaer.) Hue

18653, 18852, 19081, 19084, 19086, 19088, 19090, 19092, 19093, 19095, 19282

Lecanora dispersa (Pers.) Röhl.

18527, 18651, 18652, 18658, 18668, 18755

Lecanora gangaleoides Nyl.

18471, 18504, 18552, 18559, 18746, 18785, 18790, 18940

Lecanora muralis (Schreb.) Rabenh.

18537, 18746, 18785, 18795

Lecanora polytropa (Ehrh.) Rabenh.

18615, 18616, 18626, 18636, 18641, 18643, 18653, 18654, 18738, 18744, 18752, 18897, 18934, 18935, 18943

Lecanora praepostera Nyl.

18518, 18534, 18540, 18541, 18613, 18616, 18620, 18622, 18635, 18637, 18730, 18731, 18735, 18736, 18739, 18783, 18786, 18796, 18937, 18940, 18941, 18945, 18974, 19150, 19151, 19155, 19160, 19168, 19171, 19178, 19189, 19190, 19197, 19198, 19200, 19204

Lecanora rupicola (L.) Zahlbr. subsp. ***sulphurata*** (Ach.) Leuckert & Poelt

18537, 18538, 18539, 18540, 18702, 18732, 18747, 18752, 18754, 18756, 18779, 18782, 18787, 18897, 18921, 18935, 19036, 19037, 19043, 19045, 19179, 19197

Lecanora salina H. Magn.

18976, 18981, 18982, 19001, 19054, 19055, 19056, 19075, 19077, 19081, 19084, 19101, 19131, 19140, 19196

Lecanora sulphurea (Hoffm.) Ach.

18779, 18782, 19043, 19158, 19161, 19165, 19167, 19170

Lecidea fuscoatra (L.) Ach.

18520, 18648, 18756, 18944

Lecidea sarcogynoides Körb.

18844, 18846, 19026, 19027, 19048

Lecidella asema (Nyl.) Knoph & Hertel var. ***elaeochromoides*** (Nyl.) Nimis & Tretiach

18543, 18579, 18680, 18703, 18892, 18894, 18933, 18960, 18962, 18964, 18973, 18975, 18980, 18983, 18986, 18988, 18989, 18990, 18995, 19024, 19025, 19031, 19038, 19040, 19042, 19043, 19044, 19045, 19047, 19048, 19051, 19130, 19150, 19151, 19153, 19167, 19180

Lecidella scabra (Taylor) Hertel & Leuckert

18525, 18654, 19057

Lecidella stigmatea (Ach.) Hertel & Leuckert

19256, 19275, 19277, 19278

Lepraria nivalis J. R. Laundon

18494, 18495, 18799, 18813, 18884, 18885

Leprocaulon microscopicum (Vill.) Gams

18885

Leptogium gelatinosum *(*With.) J. R. Laundon

19214, 19216

Leptogium lichenoides (L.) Zahlbr.

18860, 18861, 18863, 19050

Lichenostigma cosmopolites Hafellner & Calat.

18578, 18679, 18683, 18970

Lichenostigma elongata Nav.-Ros. & Hafellner

18961, 18968, 19031, 19043, 19142, 19217, 19251

Lichenostigma rugosum G. Thor

18711, 18921, 19218

Lichenostigma rupicolae Fdez.-Brime & Nav.-Ros.

18615, 18620, 18654, 18781, 18784, 18867, 18939, 18944, 18964, 19041, 19042, 19043, 19045, 19130, 19143, 19147, 19152, 19168, 19171, 19172, 19190, 19197, 19198, 19208

Lichenostigma sp.

18928, 18932, 18936

Lichinella cribellifera (Nyl.) P. P. Moreno & Egea

18876

Lichinella stipatula Nyl.

18498, 18870, 18873, 18876, 18899, 18969, 18972, 19067, 19069, 19070, 19083

Lobothallia radiosa (Hoffm.) Hafellner

18876, 18985, 19231

Micarea melaenida (Nyl.) Coppins

18907, 18908

Muellerella lichenicola (Sommerf.) D. Hawksw.

18653, 18736, 18892

Muellerella pygmaea (Körb.) D. Hawksw.

18629, 18636, 18657, 18808, 18810, 18811, 18945, 18965, 19128

Nephroma parile (Ach.) Ach.

18913

Ochrolechia parella (L.) A. Massal.

18467, 18544, 18752, 18753, 18757, 18993, 19028, 19046, 19056, 19179

Opegrapha calcarea Turner ex Sm.

18594, 18597, 19256, 19266, 19267, 19272

Opegrapha cesareensis Nyl.

18735

Opegrapha lutulenta Nyl.

18731, 18995

Opegrapha rupestris Pers.

19217, 19251

Parmelia saxatilis (L.) Ach.

18480, 18508

Parmelina tiliacea (Hoffm.) Hale

18624, 18662, 18751

Parmotrema perlatum (Huds.) M. Choisy

18483, 18512, 18646

Parmotrema reticulatum (Taylor) M. Choisy

19144

Peltigera collina (Ach.) Schrad.

18484

Peltigera membranacea (Ach.) Nyl.

18493, 18737

Peltula euploca (Ach.) Poelt

18498, 18574, 18728, 18832, 18834, 18842, 18873, 18876, 18899, 18969, 19059, 19061, 19067, 19069, 19070, 19071, 19082, 19083, 19087, 19089, 19091

Peltula obscurans (Nyl.) Gyeln.

18592, 18872, 18969

Peltula omphaliza (Nyl.) Wetmore

18592, 18873

Peltula placodizans (Zahlbr.) Wetmore

18876, 19091

Pertusaria albescens (Huds.) M. Choisy & Werner

18973

Pertusaria aspergilla (Ach.) J. R. Laundon

18523, 18549, 18659, 18749, 18757, 18778, 18833

Pertusaria excludens Nyl.

18485, 18487, 18659, 18712, 18722, 18741, 18758, 18760, 18761, 18773, 18774, 18777, 18778, 18786, 18835

Pertusaria flavicans Lamy

18775

Pertusaria lactea (L.) Arnold

19178

Pertusaria leucosora Nyl.

18522, 18686, 18688, 18690, 18692, 18708, 18744, 18754, 18778, 19134

Pertusaria monogona Nyl.

18486, 18586, 18656, 18664, 18696, 18697, 18720, 18727, 18928, 18932, 18936, 18938, 18942, 18946

Pertusaria pluripuncta Nyl.

18764

Pertusaria pseudocorallina (Lilj.) Arnold

18534, 18540, 18554, 18619, 18620, 18632, 18692, 18708, 18716, 18748, 18750, 18752, 18754, 18756, 18762, 18778, 18780, 18791, 18794, 18918, 18938, 19047,

19130, 19147, 19180, 19181

Pertusaria rupicola (Fr.) Harm.

18470, 18548, 18614, 18615, 18619, 18620, 18623, 18624, 18654, 18723, 18729, 18746, 18750, 18752, 18781, 18783, 18784, 18791, 18792, 18795, 18796, 18797, 18867, 18933, 18939, 18944, 18964, 19003, 19041, 19042, 19043, 19045, 19130, 19143, 19147, 19152, 19155, 19156, 19159, 19160, 19168, 19171, 19172, 19190, 19197, 19198, 19208

Phaeophyscia hirsuta (Mereschk.) Essl.

18767, 18841, 18842, 18899, 19059, 19067, 19070

Phaeophyscia orbicularis (Neck.) Moberg

18658, 18755

Physcia adscendens (Fr.) H. Olivier

18488, 18665, 18831, 18833, 19157, 19162

Physcia biziana (A. Massal.) Zahlbr.

18694

Physcia caesia (Hoffm.) Hampe ex Fürnr.

18693, 18743, 19183

Physcia dubia (Hoffm.) Lettau

19009, 19020, 19081, 19085, 19089, 19126, 19162

Physcia tenella (Scop.) DC.

18654, 18662

Physcia tribacia (Ach.) Nyl.

18575, 18709, 18825

Placidiopsis custnani (A. Massal.) Körb.

18516

Placidium tenellum (Breuss) Breuss

19063, 19065, 19074, 19212, 19214, 19215, 19216, 19221, 19222, 19225, 19228, 19230, 19231, 19234, 19236, 19240, 19241, 19244, 19247, 19248, 19250, 19251, 19252

Placynthium tremniacum (A. Massal.) Jatta

19214, 19215, 19216, 19217, 19221, 19222, 19223, 19225, 19231, 19232, 19236, 19237, 19244, 19247, 19248, 19249, 19251

Polycoccum rinodinae Van den Boom

18532, 18557, 18558

Polycoccum rubellianae Calat. & V. Atienza

18968

Polycoccum teresum Halıcı & K. Knudsen

18606

Polysporina simplex (Dav.) Vězda

18580, 18590, 18595, 18596, 18662, 18663, 18670, 18679, 18826, 18827, 18542, 18844, 18850, 18862, 18904, 18923, 18976, 19029, 19053, 19056, 19064, 19080, 19083, 19131, 19140, 19141, 19203, 18542

Porina byssophila (Körb. ex Hepp) Zahlbr.

19272

Porina chlorotica (Ach.) Müll. Arg.

18735, 19066

Porpidia cinereoatra (Ach.) Hertel & Knoph

18505, 18513, 18917, 18918, 19032

Porpidia hydrophila (Fr.) Hertel & A. J. Schwab

18489

Protoblastenia rupestris (Scop.) J. Steiner

18590, 18607

Protoparmelia montagnei (Fr.) Poelt & Nimis

18551, 18552, 18621, 18633, 18640, 18645, 18752, 18759, 18786, 18997

Psora gresinonis B. de Lesd.

18524, 18853, 18901, 19099, 19103, 19106, 19111, 19113, 19118, 19120

Psora vallesiaca (Schaer.) Timdal

19229, 19232, 19233

Psorotichia vermiculata (Nyl.) Forssell

18821

Punctelia subrudecta (Nyl.) Krog

18482, 18506, 18521, 18576, 18742

Ramalina breviuscula Nyl.

18490, 18514, 18553, 18611, 18624, 18631, 18788, 18809, 18835, 18993, 19000, 19013, 19016, 19020, 19136, 19149, 19163, 19194

Ramalina polymorpha (Lilj.) Ach.

18877

Ramalina requienii (De Not.) Jatta

19004, 19164, 19166, 19176

Ramalina subfarinacea (Nyl. ex Cromb.) Nyl.

18515, 18529, 18618, 18622, 18719, 18750

Rhizocarpon epispilum (Nyl.) Zahlbr.

18867

Rhizocarpon geminatum Körb.

18726

Rhizocarpon geographicum (L.) DC.

18540, 18554, 18570, 18615, 18678, 18746, 18779, 18782, 18790, 18933, 18934, 18935, 18943, 18944, 19007, 19011, 19012, 19015, 19130, 19133, 19138, 19139, 19151, 19171, 19191, 19198, 19208

Rhizocarpon. polycarpum (Hepp) Th. Fr.

18533, 18578, 18641, 18785, 19011, 19012, 19033, 19039, 19043, 19148, 19208

Rhizocarpon viridiatrum (Wulfen) Körb.

18683

Rinodina alba Metzler ex Arnold

18628, 18629, 18630, 18631, 18632, 18636, 18807, 18809, 19008, 19020, 19167, 19169, 19192

Rinodina aspersa (Borrer) J. R. Laundon

18714

Rinodina atrocinerea (Hook.) Körb.

18881

Rinodina beccariana Bagl.

18532, 18533, 18536, 18555, 18556, 18557, 18558, 18560, 18622, 18651, 18730, 18733, 18734, 18735, 18750, 18776, 18962, 18975, 18978, 18987, 19014, 19018, 19038, 19042, 19044, 19068, 19145, 19189, 19192, 19196

Rinodina cana (Arnold) Arnold

18655

Rinodina gennarii Bagl.

18651, 18658, 18755, 18823, 19075, 19141

Rinodina obnascens (Nyl.) H. Olivier

18658, 18961

Rinodina sicula H. Mayrhofer & Poelt

18654

Rinodina teichophila (Nyl.) Arnold

19081, 19086

Rinodina vezdae H. Mayrhofer

18592

Roccella phycopsis Ach.

18929, 18992, 18998, 18999, 19185, 19194, 19205

Roselliniella atlantica Matzer & Hafellner

18880, 18883

Sarcogyne privigna (Ach.) A. Massal.

18582, 18840, 18900

Sarcogyne regularis Körb.

18519, 18837, 19268

Sarcopyrenia cylindrospora (P. Crouan & H. Crouan) M. B. Aguirre

18679, 18683, 18843, 18844

Scoliciosporum umbrinum (Ach.) Arnold

18541, 18560, 18599, 18602, 18604, 18629, 18632, 18641, 18654, 18789, 18796, 18990, 19024

Solenopsora cesatii (A. Massal.) Zahlbr.

18845, 18846, 18847

Solenopsora holophaea (Mont.) Samp.

18801, 18804, 18813, 18927

Solenopsora vulturiensis A. Massal.

18494, 18495, 18669, 18670, 18703

Sphinctrina leucopoda Nyl.

18732

Sphinctrina tubiformis A. Massal

18762, 19181

Sphinctrina turbinata (Pers.:Fr.) De Not

19143

Squamarina concrescens (Müll. Arg.) Poelt

19105, 19107, 19112

Squamarina lentigera (Weber) Poelt

19227, 19238, 19239, 19240, 19252

Stigmidium hageniae (Rehm) Hafellner

18497, 18724

Stigmidium tabacinae (Arnold) Triebel

19214, 19219, 19231, 19236, 19238, 19248

Teloschistes chrysophthalmus (L.) Beltr.

18806

Tephromela atra (Huds.) Hafellner

18466, 18599, 18718, 18892, 18991, 19083, 19139, 19146, 19148, 19178, 19208

Thelenella muscorum (Th. Fr.) Vain. var. ***octospora*** (Nyl.) Coppins & Fryday

19292

Thelopsis isiaca Stizenb.

19176

Thrombium epigaeum (Pers.) Wallr.

18896

Toninia aromatica (Turner) A. Massal.

18767

Toninia cinereovirens (Schaer.) A. Massal.

18899, 18969, 19067, 19213

Toninia physaroides (Opiz) Zahlbr.

19214, 19218, 19219, 19220, 19221, 19224, 19225, 19226, 19230, 19231, 19235, 19236, 19238, 19239, 19244, 19245, 19247, 19251

Toninia sedifolia (Scop.) Timdal

19237, 19248, 19292

Toninia squalida (Ach.) A. Massal.

18870

Toninia tristis (Th. Fr.) Th. Fr. subsp. ***pseudotabacina*** Timdal

19228, 19241, 19244

Trapelia coarctata (Turner ex Sm.) M. Choisy

18496, 18513, 18517, 18561, 18668, 18673, 18677, 18886, 19017, 19073, 19074

Trapelia involuta (Taylor) Hertel.

18668, 18887, 18888, 18889, 18890, 18891

Trapelia placodioides Coppins & P. James

18651, 18668, 18703

Trapeliopsis flexuosa (Fr.) Coppins & P. James

18651

Trapeliopsis wallrothii (Spreng.) Hertel & Gotth. Schneid.

18855, 18901, 19098, 19099, 19102, 19104, 19105, 19116, 19119, 19174

Tremolecia atrata (Ach.) Hertel

18628, 18642, 18643

Verrucaria amphibia Clemente

19195

Verrucaria dolosa Hepp

18728, 18736, 18755, 18976

Verrucaria fuscella (Turner) Winch

19090, 19092

Verrucaria fusconigrescens Nyl.

18653, 18714, 19092, 19093, 19094, 19095

Verrucaria hochstetteri Fr.

19256, 19262, 19268, 19269, 19270, 19272, 19274, 19285, 19288

Verrucaria lecideoides (A. Massal.) Trevis.

19256, 19261

Verrucaria macrostoma Dufour ex DC.

19291, 19293, 19294

Verrucaria murina Leight.

19220

Verrucaria nigrescens Pers.

18771, 19270, 19274, 19275, 19277, 19280, 19281, 19283, 19285, 19291, 19293, 19294

Verrucaria praetermissa (Trevis.) Anzi

19081, 19075, 19079, 19085

Verrucaria viridula (Schrad.) Ach.

18653

Verrucula maritimaria Nav.-Ros. & Cl. Roux

18821, 18868, 18869

Verruculopsis flavescentaria Gueidan, Nav.-Ros. & Cl. Roux

18600, 18603, 18605

Xanthoparmelia conspersa (Ehrh. ex Ach.) Hale

18481, 18683, 18961, 19101

Xanthoparmelia glabrans (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

18959, 18961, 18968, 18970, 18971, 18985, 19021, 19072

Xanthoparmelia loxodes (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

18477, 18478, 18650, 18880, 18883

Xanthoparmelia mougeotii (Schaer.) Hale

18479, 18530, 18545, 18546, 18547, 18638, 18714

Xanthoparmelia pulla (Ach.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

18572, 18578, 18609, 18674, 19086, 19087, 19132

Xanthoparmelia tinctina (Maheu & Gillet) Hale

18578, 18628, 18638, 18707, 18721, 18970, 19062, 19072, 19125, 19126, 19129, 19130, 19132, 19139

Xanthoparmelia verruculifera (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch

18478, 18689, 18739

Xanthoria aureola (Ach.) Erichsen

18806, 18869, 18969, 18993, 19067, 19068, 19070, 19104, 19121, 19129, 19157, 19183, 19186, 19269, 19272, 19281, 19283, 19291

Xanthoria calcicola Oxner

18568, 18594, 18604, 18606, 18978

Zwackhiomyces lecanorae (Stein.) Nik. Hoffm. et Hafellner

19075

Zwackhiomyces sp.

18949, 18950, 18951

APÈNDIX 2. Relació de les mostres del gènere *Diploschistes* sobre les quals s'ha basat l'estudi exposat al capítol 3. Hi hem inclòs tant els exemplars recol·lectats per nosaltres com els provinents de préstecs de diversos herbaris. A les etiquetes del material d'herbari procedent de les nostres pròpies recol·leccions, hi fem constar la informació següent: país, província, localitat, quadrícula UTM, altitud en metres sobre el nivell del mar, substrat, data de recol·lecció, recol·lector i identificador, i número d'herbari (BCN-Lich). Pel que fa als plecs en préstec, hem transcrit directament la informació continguda a les etiquetes originals. Els espècimens utilitzats en les anàlisis filogenètiques del capítol 3, s'indiquen en negreta, entre claudàtors amb un * abans del nom que se'ls ha donat en les taules i els arbres filogenètics d'aquest mateix capítol.

Diploschistes actinostomus (Ach.) Zahlbr.

ESPANYA: Catalunya: prov. Girona, Parc Natural dels Aiguamolls de l'Empordà, entre Castelló d'Empúries i Torre del Vent, 31T EG1182, 30-45 m, codines darrera barraca, 20/04/2007, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 15695). − Prov. Girona, Llançà, la Valleta, 31T EG0889, 70-100 m, superfície poc inclinada de granodiorita, 09/06/1970, *leg*. i *det*. X. Llimona (BCN-Lich 19301). − Prov. Girona, el Port de la Selva, obaga del Puig Dijous, 31T EG 1586, 100 m, sobre granodiorites, 17/05/1984, *leg*. i *det*. X. Llimona (BCN-Lich 19309).

ESTATS UNITS: Missouri: Carter County, Peck Ranch Conservation Area, vicinity of Stegall Mountain fire tower and knob NW of tower, ca. 1.8 mi N of Peck Ranch Road. Stegall Mountain USGS 7.5' quad. Legal Description: E1/2 sec. 19 & W edge sec. 20 T28N R2W. 36 deg 47'N, 92 deg 43'W. Ca. 1200-1340 ft. Rhyolite glades and xeric igneous woodland on upper slopes and knobs; on rhyolite in open area. 12/Oct/1997. *Leg*. V. Reeb. *Det*. F. Lutzoni (DUKE 0047541) **[*, *D. actinostomus* 2]**, sub *D. scruposus*. − North Carolina: Pender Co., near Douglas, just N of Broxton, Broxton Rocks Nature Conservancy Preserve. 31º43'57''N, 82º51'16''W. On rock, near the Fall in rich mixed forest of *Quercus alba*, *Quercus stellata*, *Quercus marilandica*, *Hammamelis styraciflua*, and *Quercus nigra* with outcrops of Altamaha Grit boulders. 26 Jan 2003. *Leg*. R. Yahr No. 4569 (DUKE 0016461) **[*, *D. actinostomus* 1]**.

PORTUGAL: Algarve, Castro Marim, junto ao forte. Sôbre as rochas. 03/1951. *Leg*. & *Det*. C. Tav. Lichenes Lusitaniae (Herb. Carlos N. Tavares 4006).

Diploschistes caesioplumbeus (Nyl.) Vain.

ESPANYA: Catalunya: prov. Barcelona, Dosrius, camí de Can Massuet del Far a Can n'Arenes, 31T DG5407, 530 m, granit meteoritzat, 23/01/2009, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 17182) **[*, *D. caesioplumbeus* 1]**. − Prov. Girona, Cadaqués, Carena de Pení, obaga, 500-525 m, 31T EG1981, esquistos, 17/03/2006, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19323) **[*, *D. caesioplumbeus* 2]**. − Prov. Girona, el Port de la Selva, Pla de Palau, 31T EG1981, 30-35 m, esquistos vora la riera de Romanyac, 20/05/1994, *leg*. i *det*. X. Llimona (BCN-Lich 19325) **[*, *D. caesioplumbeus* 3]**. − Prov. Girona, Roses, Canyelles Grosses, 19/03/1998, *leg*. i *det*. X. Llimona (BCC-Lich 13394), sub *D*. gr. *actinostomus*. − Prov. Girona, el Port de la Selva, Sant Pere de Rodes i ruïnes de l'antic poble de Santa Helena, 31T EG1386, 515-575 m, 05/03/2004, *leg*. i *det*. X. Llimona (BCN-Lich 19311). – Prov. Tarragona, Vilanova de Prades, carretera a Albarca, 31T CF2875, 900-910 m, sobre granits, 17/04/2007, *leg*. i *det*. X. Llimona (BCN-Lich 19308). − **Galícia:** prov. A Coruña, Santiago de Compostela, Monte Pedroso, 29T NH3551, 250 m, sobre muro granítico orientación sur, 26/04/1990, *leg*. i *det*. M.E. López de Silanes i M.J. Sánchez-Biezma (SANT 7585), sub *D*. *actinostomus* var. *caesioplumbeus*.

Diploschistes candidissimus (Kremp.) Zahlbr.

ESPANYA: Catalunya: prov. Lleida, Torà, Font de Can Porta, 31T CG6830, 550-600 m, aflorament de gresos calcaris, 13/06/2008, *leg.* Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19340) **[***, ***D*. *candidissimus* 2]**. − Prov. Lleida, carretera de Torà a Solsona, 31T CG6897, 470 m, superfície horitzontal sobre gres calcari, 15/06/2009, *leg.* Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19343). − Prov. Lleida, Sanaüja, 600 m, 31T CG63. Parets rocoses assolellades, orientades al sud. 13/09/1983. *Leg.* i *det.* P. Navarro. Conf. H.T. Lumbsch 09/1984 (BCC-Lich 1895), sub *D. actinostomus* var. *farinosus*.

ESTATS UNITS: Texas: Culberson Co., Delaware Mts., 6-7 air miles SE of jct. US Hwy. 62-180 and TX Hwy. 54, ca. 31º42'28''N, 104º46'50''W, ca. 4600-5000 ft. alt. Permian sandstone outcrops at top. 08 Oct. 1994. *Leg.* R.D. Worthington 23741, Herbarium COLO (Boulder) (DUKE 0144447) **[***, ***D*. *candidissimus* 1]**.

Diploschistes diacapsis (Ach.) Lumbsch

ESPANYA: Catalunya: prov. Lleida, Alfés, Timoneda d'Alfés, 31T CG00, 230-235 m, sòl calcari, 21/10/1994, *leg.* X. Llimona, J. Vila i P. Hoyo, *det.* P. Hoyo (BCN-Lich 19331). − *Ibidem*, *leg.* X. Llimona, J. Vila i P. Hoyo, *det.* P. Hoyo (BCN-Lich 19332). − *Ibidem*, 25/10/1994, *leg.* X. Llimona, J. Vila i P. Hoyo, *det.* P. Hoyo (BCC-Lich 13393). − Prov. Lleida, Maials, carretera que porta a Almatret Km. 3-4, 31T BF8880, 350 m, sòl calcari assolellat, sobre *Cladonia* sp., 10/10/1994, *leg.* M. Barbero, M. Giralt i X. Llimona, *det.* P. Hoyo (BCN-Lich 19321). − *Ibidem*, 15/06/2009, *leg.* Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19347) **[***, ***D*. *diacapsis* 3]**. − *Ibidem*, *leg.* Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19348). − Prov. Lleida, Torà, carretera C-1412a Km. 24-25, 31T CG6729, 450 m, sòl guixenc, 15/06/2009, *leg.* Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19342). − **Madrid**: Aranjuez, 30T VK4831, 570 m, 25/06/1972, sòl guixenc, *leg*. S. Silvestre, *det*. X. Llimona (BCN-Lich 19314). − **Aragó**: prov. Saragossa, Hostel del Cierro. Km. 381-382 rd N2, Elev ca. 300 m. Behind hostel on relictual Juniperus-dominated, gypsum soil slopes. 41º29'N 00º15'W. Abundant on open soil. August 30, 2000. *Leg*. R. Yahr 2431a. *Det*. X. Llimona (DUKE 0030912) **[***, ***D***. ***diacapsis*** **1]**. − Prov. Saragossa, Pina de Ebro, Retuerta de Pina, 30T YL2294, 290 m, 03/06/2003, *leg*. i *det*. X. Llimona (BCN-Lich 19296).

ESTATS UNITS: Arizona: Mohave County, Fort Pearce Area of Critical Environmental Concern (ACEC), SE of St, George, Utah and S of Honeymoon Historic Trail, 36º59'19''N, 113º21'47'', on gypsiferous soil. 940 m, 16 May, 2006. Collected by: T.H. Nash III # 44752. Determined by: T.H. Nash III (DUKE 0130126) **[***, ***D***. ***diacapsis*** **2]**.

Diploschistes diacapsis subsp. ***neutrophilus*** (Clauzade & Cl. Roux) Clauzade & Cl. Roux

ESPANYA: Catalunya: prov. Girona, el Port de la Selva, Les Cavorques, 31T EG1785, 60-80 m, dunes fòssils, soleia, superfícies poc inclinades, 20/05/1994, *leg*. i *det*. Llimona (BCN-Lich 19312), sub *D. albescens*. − *Ibidem*, 21/10/2004, *leg*. i *det*. Llimona (BCN-Lich 19329) **[***, ***D***. ***diacapsis*** **5]**, sub *D. intepediens*. − *Ibidem*, *leg*. i *det*. Llimona (BCN-Lich 19330), sub *D. intepediens*. − Prov. Girona, massís del Montgrí, plans vora el camí a la cala Pedrosa, 31T EG1657, 90 m, sòl argilós, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19329) **[***, ***D***. ***diacapsis*** **4]**. − *Ibidem*, *leg*. D. Muñiz, *det*. S. Fdez.-Brime (BCN-Lich 20052). − Prov. Tarragona, l'Ametlla de Mar, Plana de Sant Jordi, 31T CF1633, 85-90 m, sòl argilós, 03/03/2006, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19295). − **Illes Balears:** Illa d'Eivissa, Parc Natural de Ses Salines, vora la Torre de Ses Portes, 31S CC6199, 0-5 m, sobre sòl argilós, 09/09/2008, *leg*. X. Llimona, *det*. S. Fdez.-Brime Llimona (BCN-Lich 19338) **[***, ***D***. ***diacapsis*** **6]**. − *Ibidem*, *leg*. E.

Llop, *det*. S. Fdez.-Brime (BCN-Lich 19339). − Illa de Formentera, Es Ram, 31S CC7179, 0-20 m, 11/09/2008, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 19305). − Illa de Mallorca, Llucmajor, Cap Blanc, 31S DD5870, 140 m, crosta de sòl neutre, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 19299).

FRANÇA: Languedoc, Gard, Pujaut, Plateau d'Aspre, sur argile rouge décalcifiée (à peu près non calcaire) dans une pelouse rase à *Thymus vulgaris*, graminées et mousses. Gros bloc (3 x 6 x 4 m) de grès d'Annot, au pied d'un vieil éboulì. Lat. 44,0147º N; long.; 4,7489º E. Altitudo: 85 m. Orientiĝo: ĝenerala: - ; loka: -. Deklivo: 0º. Dato: 1965/02/05. Kolektis: C. Roux. Determinis: C. Roux. Specimeno n. 178, sub *D. diacapsis* ssp. *neutrophila*. − Provença, Bouches-du-Rhône, Fos-sur-Mer, Crau, 10 km N de Fos-sur-Mer, clos de Tenque, sur grundo sabla-argila, neŭtra, en *Crassuletum tillaeae*. Altitudo : 3 m. Orientiĝo: ĝenerala: - ; loka: -. Deklivo: 90º. Dato: 1980/04/25. Kolektis: C. Roux. Determinis: C. Roux. Specimeno n. 99, sub *D. diacapsis* ssp. *neutrophila*, Holotipo. − Provence-Alpes-Côte d'Azur, Vaucluse, Gadagne, plateau de Gadagne, Volongue, garrigue à *Quercus coccifera*, sur argilo-sableaux non calcaire sur le bord d'un sentier. Lat. 44,9307º ; long.; 4,9246º E. Altitudo: 110 m. Orientiĝo: ĝenerala: - ; loka: -. Deklivo: 0º. Dato: 1978/04/07. Kolektis: C. Roux Determinis: C. Roux. Specimeno n. 178 sub *D. diacapsis* ssp. *neutrophila*.

PORTUGAL: Algarve, Próx. De Praia do Belixe Velho. Sôbre o solo. 21/12/1959, *Leg*. C. Tav. Lichenes Lusitaniae (Herb. Carlos N. Tavares 6634), sub *D. albissimus*.

Diploschistes diploschistoides (Vain.) G. Salisb.

AUSTRALIA: Queensland, 7 km E of Mount Garnet. 240 m. 17º42'S, 145º11'E. On granite; granite boulders in open woodlands dominated by *Eucalyptus* and grasses. 18 Jul 1996. H.T. Lumbsch & R. Guderley No. 11115n (DUKE 0018863) **[*, D. *diploschistoides* 2]**. – Western Australia. Gibb River Range, Gibb River Road, 38 km north-east of Gibb River Station, 16º06'S, 126º36' E. Growing on sandstone rocks in *Eucalyptus* dominated grasslands on gently sloping rocky ridge side; elevation 480 m. 13 Jul 1991. *Leg.* J.A. Elix 27941, H.T. Lumbsch & H. Streimann. *Det.* H.T. Lumbsch (DUKE 0144445) **[*, D. *diploschistoides* 1]**, sub *D. almbornii*.

Diploschistes euganeus (A. Massal.) Zahlbr.

AUSTRALIA: Western Australia, Hutt River, between Northhampton and Port Gregory. On sandstone. 28.08.1987, *Leg.* H.T. Lumbsch Nr. 5524b (DUKE 0144451) **[*, D. *euganeus*]**.

ESPANYA: Catalunya: prov. Girona, el Port de la Seva, Cala Nans, 31T EG2380, 25-35 m, esquistos orientats al Nord, amb influència marina, 17/10/2006, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 18579). − Prov. Girona, Roses, sobre pressa en la carretera de Roses a Montjoi, 31 TEG17, 100-130 m, granodiorites 20º S, 25/02/1989, *leg.* i *det.* X. Llimona (BCN-Lich 18895).

Diploschistes gypsaceus (Ach.) Zahlbr.

ESPANYA: **Catalunya**: prov. Barcelona, Collbató, camí de Sant Jeroni, 31T CG0105, 1000-1015 m, paret vertical orientada al N, 16/07/2011, *leg.* i *det.* S. Fdez.-Brime (BCN-Lich 19307). − Prov. Lleida, Montblanc, Coll de la Creu de l'Ardit, 31T CF4079, 1020-1025 m, 04/05/2006, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19297). − Prov. Lleida, Sanaüja, 31T CG6037, 450 m, aflorament de gresos, 29/12/1982, Navarro n. 10.511. − *Ibidem*, 19/05/2004, *leg.* i *det.* X. Llimona (BCN-Lich 19324) **[*, *D. gypsaceus* 2]**. − Prov. Lleida, carretera de Torà a Solsona, 31T CG6897, 470 m, superfícies subverticals de gresos, 15/06/2009, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19345) **[*, *D. gypsaceus***

3]. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19346) **[***, ***D***. ***gypsaceus*** **4]**. − Prov. Lleida, Torà, Font de Can Porta, 31T CG6830, 550-600 m, afloraments de gresos calcaris 80º E, 13/06/2008, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 17180) **[***, ***D***. ***gypsaceus*** **1]**. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19340) **[***, ***D***. ***gypsaceus*** **5]**.

Diploschistes interpediens (Nyl.) Zahlbr.

ESPANYA: Andalusia: prov. Córdoba, Villanueva de Córdoba, arroyo de Pedro Moro, 30S UH6843, 900 m, 10/04/2009, *leg*. M. Barbero, *det*. S. Fdez.-Brime (BCN-Lich 19304). − **Castella i Lleó:** prov. León, Cerro Peral, 31T QG1694, 1250 m, pizarras en contacto con el suelo, 21/06/1989, *leg*. i *det*. A. Terrón Alfonso (LEB 228), sub *D*. *scruposus*.− *Ibidem*, *leg*. A. Terrón Alfonso (LEB 229), sub *D*. *scruposus*. − **Catalunya**: prov. Barcelona, Dosrius, camí al Dolmen de ca n'Arenes, 31T DG5507, 400 m, granit meteoritzat 60º NE, 29/05/2009, *leg*. i *det*. S. Fdez.-Brime (BCN-Lich 19335) **[***, ***D***. ***interpediens*** **7]**. − Prov. Barcelona, Dosrius, carretera de Can Massuet al Far, 31T DG5228, 400 m, granit meteoritzat, 23/01/2008, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19350) **[***, ***D***. ***interpediens*** **4]**. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19352). − Prov. Barcelona, Òrrius, turó de Céllecs, 31T DG4400, 530 m, codines de superfície plana, 23/01/2009, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19355) **[***, ***D***. ***interpediens*** **6]**. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19356). − Prov. Girona, Sant Llorenç de la Muga, camí a Can Gener, 31T DG8387, 140-150 m, gresos vermells, 09/02/2007, *leg*. X. Llimona i N. Hladun, *det*. S. Fdez.-Brime (BCN-Lich 19319) **[***, ***D***. ***interpediens*** **2]**. − **Galícia**: prov. A Coruña, Puentedeume, Caaveiro, cerca de Paces, 29TNJ70, 400 m, sobre rocas graníticas, 19/04/1985, *leg*. i *det*. M.E. López de Silanes (SANT 2735), sub *D*. *scruposus*. − Prov. A Coruña, Monte Pedroso, 29T

NH3551, 400 m, granit ric en mica, 06/07/2006, *leg*. X. Llimona i G. Paz-Bermúdez, *det*, S. Fdez.-Brime (BCN-Lich 18007) **[***, ***D*. *interpediens*** **3]**. − **La Rioja**: prov. La Rioja, Anguiano, central eléctrica, 30T WM1878, 670 m, encinar, 08/09/2004, *leg*. N. Hladun i D. Muñiz, *det*. N. Hladun (BCN-Lich 14404), sub *D. muscorum* **[***, ***D*. *interpediens*** **9]**. − *Ibidem*, *leg*. N. Hladun i D. Muñiz, *det*. N. Hladun (BCN-Lich 14389), sub *D. diacapsis* subsp. *interpediens*. − Prov. La Rioja, Anguiano, encinar, 30T WM1878, saxícola, 654 m, 08/09/2004, *leg*. A. Gómez-Bolea i G. Figueras, *det*. A. Gómez-Bolea (BCN-Lich 14751), sub *D. scruposus* **[***, ***D*. *interpediens*** **5]**. − Prov. La Rioja, Anguiano-Mansilla de la Sierra, 30T WM1575, 910 m, saxícola, 08/09/2006, *leg*. i *det*. A. Terrón Alfonso (LEB 6250). − *Ibidem*, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 14537), sub *D. scruposus*. − *Ibidem*, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 14539), sub *D. scruposus*. − Prov. La Rioja, areniscas rojas al lado de la carretera, valle del Río Oja, *leg*. i *det*. G. Paz-Bermúdez (SANT 10820), sub *D. scruposus* **[***, ***D*. *interpediens*** **8]**. − *Ibidem*, *leg*. i *det*. G. Paz-Bermúdez (SANT 10821). − Prov. La Rioja, Mansilla de la Sierra, 30T WM044673, 947 m, 08/09/2004, *leg*. y *det*. A. Fernández Salegui (LEB 6230), sub *D. scruposus*.

FRANÇA: Pyrenées Orientales: Albera, carretera de Maurellans a Rinoguers, 31T DH85351, 300 m, marges granítics de la carretera, 13/06/2009, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 19322) **[***, ***D*. *interpediens*** **10]**.

PORTUGAL: Districte Algarve, Ameixial. Sôbre as rochas, 04/03/1962. Leg. C. Tav. Lichenes Lusitaniae (Herb. Carlos N. Tavares 6796), sub *D.* “*neutrophilus*”. − Districte Bragança, Valle del río Sabor, 29T PF8587, 500-520 m, granits 30º N, 05/09/2007, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19317) **[***, ***D*. *interpediens*** **1]**. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19318). – Districte Minho, Serra do Gerez-Curral do Prado. Sôbre o granito a ca. de 1000 m. 25/03/1948. *Leg*. C. Tavares Lichenes Lusitaniae (Herb. Carlos N. Tavares 2493), sub *D. scruposus*.

Diploschistes muscorum (Scop.) R. Sant.

ESPANYA: Andalusia: prov. Huelva, Santa Olalla de Cala, 29S QB4498, 500-510 m, 05/02/1984, *leg*. J. Rowe i L. Díaz, *det*. J. Rowe (SEVF 413). − **Catalunya:** prov. Barcelona, Castellolí, sobre túnel del Bruc, 31T CG9405, 580-585 m, sòl calcari assolellat, creix sobre *Squamarina* sp., 21/11/2009, *leg*. i *det*. S. Fdez.-Brime (BCN-Lich 19334) **[*, *D*. *muscorum* 5]**. − Prov. Barcelona, Castellfollit de Riubregós, 31T CG7026, 500 m, sòl guixenc sobre briòfits, 15/04/1988, *leg*. i *det*. X. Llimona (BCN-Lich 19306). − Prov. Girona, Cadaqués, prat d'en Pagès vora Mas de Rabassers, 31T EG2485, 100 m, sòl silícic assolellat, 31/03/1983, *leg*. X. Llimona i N. Hladun, *det*. X. Llimona (BCN-Lich 19315). − Prov. Girona, el Port de la Selva, Punta de s'Arenella, 31T EG1875, 0-5 m, sòl silícic assolellat, creix sobre *Cladonia* sp., 10/03/1996, *leg*. i *det*. X. Llimona (BCN-Lich 19303). − Prov. Girona, Roses, sobre Punta de la Falconera, 31T EG1875, 25 m, sòl silícic assolellat, 22/02/2001, *leg*. i *det*. X. Llimona (BCN-Lich 19313). − Prov. Lleida, Maials, carretera que porta a Almatret Km. 3-4, 31T BF8880, 350 m, sòl calcari assolellat, sobre *Cladonia* sp., 10/10/1994, *leg*. M. Barbero, M. Giralt i X. Llimona, *det*. X. Llimona (BCN-Lich 19320). − *Ibidem*, 15/06/2009, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19344) **[*, *D*. *muscorum* 4]**. − **La Rioja**: prov. La Rioja, central eléctrica, 30T WM1878. Encinar. 670 m, *leg*. N. Hladun i D. Muñiz. *det*. N. Hladun (BCN-Lich 14402). − *Ibidem*, *leg*. N. Hladun i D. Muñiz, *det*. N. Hladun (BCN-Lich 14435), sub *D. scruposus* **[*, *D*. *muscorum* 3]**. − Prov. La Rioja, Posadas, 30T VM9675, 1075 m, muscícola y terrícola, 07/09/04, *leg*. i *det*. A. Pérez Llamazares (LEB 6229). − Prov. La Rioja, Santurdejo-Pazuengos, 30T WM0689, 870 m, 09/09/2004, *leg*. i *det*. A. Terrón Alfonso (LEB 6249), sub *D. interpediens*.

ESTATS UNITS: Connecticut: Windham Co. Town of Windham. E of North Windham, W of Windham airport, SSW of Mansfield Hollow Dam. Mansfield Hollow State Park, W of bicycle path. Ca. 100 m. 41º45'N, 72º11'W. Dry gravelly area surrounded by mixed *Pinus*-*Quercus* forest. Vegetation dominated by *Cladonia* div. sp. and *Pycnothelia*. On *Cladonia* in barren. 28/07/2002. *Leg*. R. Yahr No. 4500 (DUKE 0016462) **[***, ***D*. *muscorum* 1]**. – North Carolina: Rowan Co. Tailings of abandoned Union Mine near Cabarrus County line, ca. 10 mi. NW of Asheboro in the vicinity of Gold Hill; 0.2 mi. W of CR 2352 behind cemetery, ca. 0.2 mi. S of the junction of CR 2352 and CR 2355. 35º30'N, 80º20'W. 10/05/2000. *Leg*. Rebecca Yahr No. 2378 (DUKE 0039680).

ITÀLIA: Sardenya: prov. Nuoro, Zona Archeologia di Tamuli, 32 TMK7656, 700 m, sobre molses i *Cladonia*, 23/02/2009, *leg*. i *det*. S. Fdez.-Brime (BCN-Lich 19333) **[***, ***D*. *muscorum* 2]**.

Diploschistes ocellatus (Fr.) Norman

AUSTRALIA: South Australia. Eyre Peninsula, 19 Km W of Iron Knob. Growing on soil in savannah with *Casuarina*, *Myoporum* and *Santalum* with an understorey of *Chenopodium* and *Maireana*. Elv. 250 m. 5 September, 1994. *Leg*. J.A. Elix & H.T. Lumsch 10734c. *Det*. H.T. Lumsch (DUKE 0144450) **[***, ***D*. *ocellatus* 2]**.

ESPANYA: Andalusia: prov. Granada, La Alfaguara, Fuente de la Teja, sobre rocas calcáreas, 26/04/1997, *leg*. i *det*. M. Casares (BCN-Lich 13207). − **Catalunya**: prov. Girona, el Port de la Seva, primeres dunes fòssils a la sortida del poble, lloc assolellat, *leg*. i *det*. X. Llimona, 20/05/1994 (BCC-Lich 13434). − Prov. Lleida, La Segarra, Tora-Font de Can Porta, along road to Solsona. In *Juniperus* wood above fountain with oaks and Rosmarinus and large outcrops of calcareous sandstone. Elv. 550-650m. September 1, 2000. *Leg*. R. Yahr 2475a. *Det*. R.Yahr (DUKE0030907) **[***, ***D*. *ocellatus* 1]**. − *Ibidem*, 13/06/2008, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 19341) **[***, ***D*. *ocellatus* 3]**. − *Ibidem*, *leg*. X. Llimona i S. Fdez.-Brime, *det*. S. Fdez.-Brime (BCN-Lich 17181) **[***, ***D*. *ocellatus* 4]**. − Prov. Tarragona, Alfara de Carles, Castell de Carles, 31T BF7725, 430 m, sobre lava tova basàltica 30º

S, 07/02/1999, *leg*. i *det*. X. Llimona (BCN-Lich 19298). – Prov. Tarragona, Horta de San Joan, Sant Salvador d'Horta, sobre roca calcària, 01/05/1995, *leg*. P. Hoyo & Ramírez, *det* P. Hoyo (BCN-Lich 13405). – **La Rioja**: prov. La Rioja, Anguiano, 30T WM1878, 650 m, aflorament de roca calcària, 08/09/2004, *leg*. X. Llimona *det*. S. Fdez.-Brime (BCN-Lich 19300). – Prov. La Rioja, Anguiano-Mansilla de la Sierra, 30T WM159756, 910 m, 08/09/2006, saxícola, *leg*. y *det*. A. Terrón Alfonso (LEB 6251) **[*, *D*. *ocellatus* 5]**.

OMAN: Musandam Peninsula, road Khasab-Dibba, 40R DP2171, 1576 m, on sandstone, 22/06/2009, Rothfels 2752.

Diploschistes rampoddensis (Nyl.) Zahlbr.

ESPANYA: Catalunya: prov. Girona, Sant Llorenç de la Muga, cliffs by the river la Muga, near old mine, UTM 31TDG8188, 280 m, Garumnian red beds 45º S-SW, 02/03/2007, *leg*. X. Llimona, Hladun & Muñiz, *det*. S. Fdez.-Brime (BCN-Lich 18009) **[*, *D*. *rampoddensis* 1]**. − *Ibidem*, *leg*. X. Llimona, Hladun & Muñiz, *det*. S. Fdez.-Brime (BCN-Lich 18008). − Prov. Girona, Sant Llorenç de la Muga, path to Can Gener, 31TDG8188, 150 m, Garumnian red beds, 09/02/2007, *leg*. X. Llimona & N. Hladun, *det*. S. Fdez.-Brime (BCN-Lich 18011) **[*, *D*. *rampoddensis* 2]**.

Diploschistes scruposus

CANADÀ: Ontario: Stoneleigh Rd., 250 m s.e. of hwy 117 (western junction), near Bracebridge. UTM Grid Reference: 637400 4995980 (45º06'30''N 79º15'30''W) Bracebridge Town, District of Muskoka. On exposed boulder on hill at roadside. 31/08/1999. *Leg*. & *Det*. S.R. Olszewski (DUKE 0144449).

ESPANYA: Catalunya: prov. Barcelona, Campins, carretera N, 31T DG5522, 400 m, granits meteoritzats, 05/06/2009, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19336) **[*, *D. scruposus* 10]**. − Prov. Barcelona, Dosrius, carretera de Can Massuet al Far, 31T DG5228, 400 m, granit meteoritzat, 23/01/2008, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19351) **[*, *D. scruposus* 2]**. − *Ibidem*, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19349)**]**. − *Ibidem*, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19351)**]**. − Prov. Barcelona, Òrrius, turó de Céllecs, 31T DG4400, 530 m, codines de superfície plana, 23/01/2009, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19354) **[*, *D. scruposus* 8]**. − Prov. Barcelona, Sant Celoni, carretera Km. 23-24, 31T DG 5350, 1000 m, granits meteoritzats, 05/06/2009, *leg.* X. Llimona i S. Fdez.-Brime *det.* S. Fdez.-Brime 5060951 (BCN-Lich 19337) **[*, *D. scruposus* 11]**. − Prov. Barcelona, Sant Cugat del Vallès, La Floresta, vora Can Busquets, 31T DF2287, 160-165 m, esquistos vora marge de la pista forestal, 10/03/2006, *leg.* i *det.* X. Llimona (BCN-Lich 19302) **[*, *D. scruposus* 9]**. − Prov. Girona, Selva de Mar, La Fàbrega, plaques d'esquistos fràgils situades en el marge del camí, 75-100 m, 31T EG1686, 01/11/2004, *leg.* i *det.* X. Llimona (BCN-Lich 19316) **[*, *D. scruposus* 5]**. − *Ibidem*, 21/05/2007, *leg.* X. Llimona i S. Fdez.-Brime, *det.* S. Fdez.-Brime (BCN-Lich 19327) **[*, *D. scruposus* 6]**. − Prov. Girona, Sant Llorenç de la Muga, penya-segat de la Muga, vora mina abandonada, UTM 31T DG8188, 275-280 m, bloc de gresos vermells 110º N, 02/03/2007, *leg.* X. Llimona, N.L. Hladun i D. Muñiz, *det.* S. Fdez.-Brime (BCN-Lich 19326) **[*, *D. scruposus* 4]**. − Prov. Lleida, Planes de Son, Tossal de la Cabana dels Caçadors i part superior de la Mata de València, 31T CH4221, 1850-1958 m, gresos silícics, 21/06/2007, *leg.* X. Llimona, *det.* S. Fdez.-Brime (BCN-Lich 19328) **[*, *D. scruposus* 1]**. − **La Rioja**: prov. La Rioja, Anguiano, central eléctrica. 30T WM1778. Encinar. 670 m, 08/09/2004, *leg.* N.L. Hladun & D. Muñiz, *det.* N.L. Hladun (BCN-Lich 14398), sub *D. diacapsis* subsp. *interpediens* **[*, *D. scruposus* 7]**. − Prov. La Rioja, Bobadilla,-Villaverde de Rioja, 30T WM1386, 619 m, saxícola, 09/09/2004, *leg.* i *det.* A. Terrón Alfonso (LEB 6252). − Prov. La Rioja, Ezcaray, Loc. 1., Sobre Valdezcaray. Espolón de esquistos metamórficos entre el collado (N 42º 15,061’, W 02º 58,973’, 1860 m s.m.) y 2000 m, bajo el Pico de San Lorenzo, 07/09/2004, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 14227) **[*, *D. scruposus* 3]**. − *Ibidem*, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 14228). − Prov. La Rioja, junto al río Najerilla, entre Anguiano y Mansilla de la Sierra. Melojares y cuarcitas soleadas. 910 m s.m. 30T WM15975, *leg*. X. Llimona, *det*. S. Fdez.-Brime (BCN-Lich 14544). – **Castella i Lleó:** prov. Palència, Cardaño de Abajo-Espigüeta, 30T UN55, 1600 m, sobre cuarcita, 08/07/1991, *leg*. i *det*. A. Terrón Alfonso (LEB 231).