



รายงานวิจัยฉบับสมบูรณ์

รหัสแถบดีเอ็นเอและอนุกรมวิธานของไลเคนกลุ่ม Thelotremoid *Graphidaceae*
(Ascomycota: Ostropales) ในประเทศไทย

(DNA Barcoding and Systematics on Lichens of Thelotremoid
Graphidaceae (Ascomycota: Ostropales) in Thailand)

ผู้ช่วยศาสตราจารย์ ดร.ขวัญเรือน พาป้อง

กรกฎาคม 2558

สัญญาเลขที่ RSA5580045

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มหาวิทยาลัยมหาสารคาม

สนับสนุนโดยสำนักงานกองทุนสนับสนุนการวิจัยและมหาวิทยาลัยมหาสารคาม

(ความเห็นในรายงานนี้เป็นของผู้วิจัย สกว. และมหาวิทยาลัยมหาสารคามไม่จำเป็นต้องเห็นด้วยเสมอไป)

กิตติกรรมประกาศ

โครงการวิจัยนี้ได้รับทุนสนับสนุนการวิจัยจากสำนักงานกองทุนสนับสนุนการวิจัย (สกว.) และมหาวิทยาลัยมหาสารคาม ภายใต้ทุนพัฒนานักวิจัย (เมธีวิจัย สกว.) ปี พ.ศ. 2555-2558 (3 ปี)

ขอขอบคุณภาควิชาชีววิทยาและฟิสิกส์และพืชพันธุ์เห็ดที่มีฤทธิ์ทางยา คณะวิทยาศาสตร์ มหาวิทยาลัยมหาสารคาม ให้ความอนุเคราะห์สถานที่ปฏิบัติการวิจัยและเวลาในการดำเนินการวิจัย

ขอบพระคุณ รองศาสตราจารย์ ดร.กัณธรีย์ บุญประกอบ หน่วยวิจัยไลเคน มหาวิทยาลัยรามคำแหง ให้คำแนะนำในการดำเนินการวิจัย ขอขอบคุณ Dr.H. Thorsten Lumbsch (Director, Integrative Research Center, MacArthur Associate Curator Science & Education, The Field Museum, Chicago USA) ขอขอบคุณ Dr.Robert Lücking (Collection manager) และเจ้าหน้าที่ในห้องปฏิบัติการ the Pritzker Laboratory for Molecular Systematics at The Field Museum สำหรับงานด้านชีวโมเลกุลเพื่อจัดทำดีเอ็นเอบาร์โค้ดของไลเคนในโครงการวิจัยนี้

บทคัดย่อ

รหัสโครงการ: RSA5580045

ชื่อโครงการ: รหัสแถบดีเอ็นเอและอนุกรมวิธานของไลเคนกลุ่ม Thelotrema *Graphidaceae* (Ascomycota: Ostropales) ในประเทศไทย

ชื่อนักวิจัย: ผู้ช่วยศาสตราจารย์ ดร.ขวัญเรือน พาป้อง

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ระยะเวลาโครงการ: 3 ปี (2555-2558)

ไลเคนกลุ่ม Thelotrema เป็นสมาชิกกลุ่มใหญ่ในวงศ์ Graphidaceae วงศ์ย่อย Graphidoideae การศึกษครั้งนี้เฉพาะไลเคนในกลุ่ม Thelotrema ประกอบด้วย 2 เผ่า ได้แก่ เผ่า Ocellularieae และ Thelotremateae ส่วนใหญ่พบแพร่กระจายในเขตร้อนชื้นในประเทศไทย ศึกษาอนุกรมวิธานและจัดทำรหัสแถบดีเอ็นเอหรือดีเอ็นเอบาร์โค้ดเพื่อการจำแนกได้อย่างถูกต้องและแม่นยำในอนาคตโดยศึกษาลักษณะทางฟีโนไทป์ที่ใช้ในการจัดจำแนกระดับสกุลและชนิด ได้แก่ ลักษณะทัลลัส พบสาหร่ายสีเขียวกลุ่ม Trentepohlioid การมีแอโพธีเซียหลายแบบและอยู่แบบเดี่ยวๆ แอโพธีเซียมีและไม่มีคอลิเวมล่า พบพาราไฟซิสด้านข้าง แอสโคสปอร์ทำปฏิกิริยากับไอโอดีนหรือไม่ รวมทั้งพบสารไลเคนกลุ่ม depsidones ไลเคนกลุ่ม Thelotrema ในประเทศไทยพบทั้งหมด 81 ชนิด 16 สกุล ได้แก่ *Astrochapsa astroidea*, *A. calathiformis*, *A. pseudophlyctis*, *A. pulvereodiscus*, *Chapsa discoidea*, *C. laemensis*, *C. indica*, *C. leprocarpoides*, *C. patens*, *Chroodiscus argillaceus*, *Ch. australiensis*, *Ch. defectus*, *Ch. homchantarae*, *Ch. khaolungensis*, *Ch. kaosokensis*, *Compositrema thailandicum*, *Cruentotrema kurandense*, *Cr. cruentatum*, *Glaucotrema glaucophaenum*, *Leucodecton anamalaiense*, *L. compunctellum*, *L. confusum*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. cf. classicum*, *My. polytrema*, *Nitidochapsa leprieurii*, *N. aggregata*, *Ocellularia albocincta*, *O. allosporoides*, *O. ascidioidea*, *O. brunneospora*, *O. cavata*, *O. cerebriformis*, *O. croceoisidiata*, *O. diacida*, *O. diospyrosis*, *O. dolichotata*, *O. exigua*, *O. flavescens*, *O. flavoperforata*, *O. fumosa*, *O. inthanonensis*, *O. interponenda*, *O. khuntanensis*, *O. kohangangensis*, *O. krathingensis*, *O. laeviusculoides*, *O. massalongoi*, *O. microstoma*, *O. neoleucina*, *O. orthomastia*, *O. papillata*, *O. perforata*, *O. pluriporoides*, *O. pluripora*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. salazinic*, *O. subdolichotata*, *O. subgranulosa*, *O. subleucina*, *O. thelotremoides*, *O. violacea*, *O. wolseleyana*, *Pseudochapsa albomaculata*, *P. phlyctidioides*, *Pseudotopeliopsis longispora*, *Rhabdodiscus crassus*, *R. subcavatus*, *R. subemersus*, *Stegobolus berkeleyanus*, *Thelotrema adjectum*, *T. bicinctulum*, *T. defossum*, *T. porinoides*, *T. rugatulum*, *T. subadjectum*, *T. triseptatum* และ *T. patwardhanii* ข้อมูลที่ได้จากโครงการวิจัยนี้ค้นพบไลเคนชนิดใหม่ของโลก 10 ชนิด และชนิดที่พบในประเทศไทยเป็นครั้งแรก 15 ชนิด นอกจากนี้ข้อมูลจากผลงานวิจัยนี้ยังช่วยเพิ่มเติมข้อมูลด้านชีวโมเลกุลที่ศึกษาไลเคนกลุ่มนี้ทั่วโลกสามารถใช้เป็นฐานข้อมูลได้ในอนาคต

คำหลัก: รหัสแถบดีเอ็นเอ, ไลเคน, อนุกรมวิธาน, Thelotrema *Graphidaceae*

Abstract

Project Code: RSA5580045

Project Title: DNA Barcoding and Systematics on Lichens of Thelotremoid *Graphidaceae*

(Ascomycota: Ostropales) in Thailand

Investigator: KHWANRUAN PAPONG

E-mail Address: khwanruan.p@staff.msu.ac.th

Project Period: 3 years (2012-2015)

Thelotremoid lichen is large group of family Graphidaceae, subfamily Graphidoideae. This propose focused on tribe Ocellularieae and Thelotremateae, both can distributed in tropical rainforest in Thailand. Various phenotype characters have been used for classification at the genus and species levels, including thallus, trentepohlioid photobiont, apothecioid, solitary ascomata lacking both a columella and lateral paraphyses, and having non-amyloid ascospores as well as secondary chemistry with depsidones group. Thelotremoid lichen in Thailand were found 81 species and 16 genera such as *Astrochapsa astroidea*, *A. calathiformis*, *A. pseudophlyctis*, *A. pulvereodiscus*, *Chapsa discoides*, *C. laemensis*, *C. indica*, *C. leprocarpoides*, *C. patens*, *Chroodiscus argillaceus*, *Ch. australiensis*, *Ch. defectus*, *Ch. homchantarae*, *Ch. khaolungensis*, *Ch. kaosokensis*, *Compositrema thailandicum*, *Cruentotrema kurandense*, *Cr. cruentatum*, *Glaucotrema glaucophaenum*, *Leucodecton anamalaiense*, *L. compunctellum*, *L. confusum*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. cf. classicum*, *My. polytrema*, *Nitidochapsa leprieurii*, *N. aggregata*, *Ocellularia albocincta*, *O. allosporoides*, *O. ascidioides*, *O. brunneospora*, *O. cavata*, *O. cerebriformis*, *O. croceoisidiata*, *O. diacida*, *O. diospyrosis*, *O. dolichotata*, *O. exigua*, *O. flavescens*, *O. flavoperforata*, *O. fumosa*, *O. inthanonensis*, *O. interponenda*, *O. khuntanensis*, *O. kohangangensis*, *O. krathingensis*, *O. laeviusculoides*, *O. massalongoi*, *O. microstoma*, *O. neoleucina*, *O. orthomastia*, *O. papillata*, *O. perforata*, *O. pluriporoides*, *O. pluripora*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. salazinica*, *O. subdolichotata*, *O. subgranulosa*, *O. subleucina*, *O. thelotremoides*, *O. violacea*, *O. wolseleyana*, *Pseudochapsa albomaculata*, *P. phlyctidioides*, *Pseudotopeliopsis longispora*, *Rhabdodiscus crassus*, *R. subcavatus*, *R. subemersus*, *Stegobolus berkeleyanus*, *Thelotrema adjectum*, *T. bicinctulum*, *T. defossum*, *T. porinoides*, *T. rugatulum*, *T. subadjectum*, *T. triseptatum* และ *T. patwardhanii*. This project was investigated 10 new species and 15 new records from Thailand. The molecular studies in this project was help to fill gaps in the molecular data set from a previous project as well as the database can be used for the future.

Keywords: DNA Barcode, Lichens, Systematics, Thelotremoid *Graphidaceae*

Output จากโครงการวิจัยที่ได้รับทุนจาก สกว. และ มมส.

1. ผลงานตีพิมพ์ในวารสารวิชาการนานาชาติ (ระบุชื่อผู้แต่ง ชื่อเรื่อง ชื่อวารสาร ปี เล่มที่ เลขที่ และหน้า) พร้อมแจ้งสถานะของการตีพิมพ์ เช่น submitted, accepted, in press, published
 - 1.1 **Papong, K.B.**, Mangold, A., Lücking, R. & Lumbsch, H.T. (2014) New species and new records of thelotremoid Graphidaceae (Ascomycota: Ostropales) from Thailand. *Phytotaxa*; 189(1): 232-244. Impact factor = 1.376. (Published)
 - 1.2 **Papong, K.**, Lücking, R. & Lumbsch, H.T. (2015) New species of genus *Ocellularia*, thelotremoid Graphidaceae (Ascomycota: Ostropales) from Thailand. *Lichenologist* (submitted)
 - 1.3 **Papong, K.**, Lücking, R. & Lumbsch, H.T. (2015) The Monograph of *thelotremoid Graphidaceae* (Ascomycota: Ostropales) in Thailand. *Phytotaxa* (in prepare)
 - 1.4 Lumbsch, H.T., Parnmen, S., Kraichak, E., **Papong, K.B.** & Lücking, R. (2014) Evolution of morphological, anatomical and chemical characters in Graphidaceae focusing on subfamily Graphidoideae (Ascomycota: Ostropales). *Systematics and Biodiversity*; 1-21. Impact factor = 2.153. (Published)
 - 1.5 Lücking, R., Aptroot, A., Boonpragob, K., Caceres, M.E.S., Ertz, D., Harris, R.C., Jia, Ze-F., Kalb, K., Kraichak, E., Landemer, J.C., Mangold, A., Manoch, L., Mercado-Diaz, J., Moncada, B., Mongkolsuk, P., **Papong, K.B.**, Parnmen, S., Pelaez, R., Poengsungnoen, V., Plata Rivas, E., Saipunkaew, W., Sipman, H.J.M., Sutjaritturakan, J., Broeck Vanden, D., Von Konrat, M., Weerakoon, G. & Lumbsch, H.T. (2014) One hundred and eleven new species of Graphidaceae: closing the gap or a drop in the bucket? *Phytotaxa*; 189(1): 007-038. Impact factor = 1.376. (Published)
 - 1.6 Kraichak, E., Parnmen, S., Lücking, R., Rivas Plata, E., Aptroot, A., Caceres, M. E. S., Ertz, D., Mangold, A., Mercado-Diaz, J. A., **Papong, K.B.**, Van Den Broeck, D., Weerakoon, G. & Lumbsch, H.T. (2014) Revisiting the phylogeny of Ocellularieae, the second largest tribe within Graphidaceae (lichenized Ascomycota: Ostropales). *Phytotaxa*; 189(1): 052-081. Impact factor = 1.376. (Published)
 - 1.7 **Papong, K.B.**, Lücking, R., Kraichak, E., Parnmen, S. Von Konrat, M. & Lumbsch, H.T. (2014) Twenty-three new species in the lichen family Graphidaceae from New Caledonia (Ostropales, Ascomycota). *Phytotaxa*; 189(1): 204-231. Impact factor = 1.376. (Published)

Note: There publication was productivity of collaboration with the researcher from The Field Museum, Chicago USA (the project was financial supported by NSF)

2. การนำผลงานวิจัยไปใช้ประโยชน์

- เชิงวิชาการ (มีการพัฒนาการเรียนการสอน/สร้างนักวิจัยใหม่)

2.1 ข้อมูลจากผลการวิจัยที่ได้จากโครงการวิจัยนี้ผู้วิจัยได้นำไปพัฒนาเอกสารประกอบการเรียนการสอนในรายวิชา 0203368 วิทยาไลเคนส์ (Lichenology) สำหรับนิสิตปริญญาตรี ภาควิชาชีววิทยา คณะวิทยาศาสตร์ มหาวิทยาลัยมหาสารคาม

2.2 พัฒนาคำราสำหรับการสอนรายวิชา 0203514 นิเวศวิทยาและอนุกรมวิธานของไลเคนส์ (Ecology and Taxonomy of Lichens) สำหรับนิสิตปริญญาโทและเอก ภาควิชาชีววิทยา คณะวิทยาศาสตร์ มหาวิทยาลัยมหาสารคาม

2.3 โครงการวิจัยนี้สร้างนักวิจัยรุ่นใหม่ด้านอนุกรมวิธานไลเคนจำนวน 1 คน สำเร็จการศึกษาระดับปริญญาโท นางสาวรัตนา เพ็งเพระ ปัจจุบันทำงานเป็นอาจารย์และนักวิจัย ณ คณะวิทยาศาสตร์ ราชภัฏบุรีรัมย์

3. อื่นๆ (เช่น ผลงานตีพิมพ์ในวารสารวิชาการในประเทศ การเสนอผลงานในที่ประชุมวิชาการ หนังสือ การจดสิทธิบัตร)

3.1 **Papong, K.B.** Pengproh, P. Thelotreroid Graphidaceae lichen in Ko Pha-ngun, Suratthani province. THAI JOURNAL OF BOTANY 5 (Special Issue): 49-62. (in Thai) (Proceeding)

3.2 นำเสนอผลงานเรื่อง “ไลเคนกลุ่ม Thelotreroid Graphidaceae ในเกาะพัง จังหวัดสุราษฎร์ธานี (Thelotreroid Graphidaceae Lichen at Ko Pha-ngun, Suratthani Province)” ในงานประชุมวิชาการพฤกษศาสตร์แห่งประเทศไทย ครั้งที่ 7 ณ หอประชุมพ่อขุนรามคำแหงมหาราช มหาวิทยาลัยรามคำแหง (หัวหมาก) กรุงเทพมหานคร วันที่ 3 -5 เมษายน 2556

3.2 นำเสนอผลงานแบบบรรยายเรื่อง “การศึกษาอนุกรมวิธานของไลเคนกลุ่ม Thelotreroid Graphidaceae (เผ่า Ocellularieae และ Thelotremateae) โดยลักษณะทางสัณฐานวิทยา โครงสร้างภายในและสารไลเคนในประเทศไทย” ในงานประชุมวิชาการ อนุกรมวิธานและซิสเทมาติกส์ในประเทศไทย ครั้งที่ 4 ณ คณะวิทยาศาสตร์ มหาวิทยาลัยนเรศวร วันที่ 23 -25 พฤษภาคม 2557

3.3 นำเสนอผลงานแบบโปสเตอร์เรื่อง “Biodiversity of lichenized fungi tribe Ocellularieae, subfamily Graphidoideae in Thailand” ในงานประชุมวิชาการ การบริหารจัดการความหลากหลายทางชีวภาพแห่งชาติ ครั้งที่ 2 ณ โรงแรมธรรมรินทร์ ธนา จังหวัดตรัง ระหว่างวันที่ 10-12 มิถุนายน 2558

3.4 **Khwanruan Bustatorn Papong**, H. Thorsten Lumbsch, Robert Lücking. (2013) *Lichens, Graphidaceae - Ocellularia. Rapid Color Guide #544* version 1 10/2013 (printed and online). (Online publication)

http://fieldguides.fieldmuseum.org/guides?region=All&country=Thailand&type=Fungi+and+lichens&subject=All&items_per_page=25&=Filter

3.5 **Khwanruan Bustatorn Papong**, H. Thorsten Lumbsch, Robert Lücking. (2013) *Lichens, Graphidaceae - Astrochapsa, Chapsa, Compositrema, Nitidochapsa, Pseudochapsa, Pseudotopeliopsis. Rapid Color Guide #545* version 1 10/2013 (printed and online). (Online publication)

http://fieldguides.fieldmuseum.org/guides?region=All&country=Thailand&type=Fungi+and+lichens&subject=All&items_per_page=25&=Filter

3.6 **Khwanruan Bustatorn Papong**, H. Thorsten Lumbsch, Robert Lücking. (2013) *Lichens, Graphidaceae - Glaucotrema, Leucodecton, Melanotrema, Myriotrema, Thelotrema*. **Rapid Color Guide #546** version 1 10/2013 (printed and online).

(Online publication)

http://fieldguides.fieldmuseum.org/guides?region=All&country=Thailand&type=Fungi+and+lichens&subject=All&items_per_page=25&=Filter

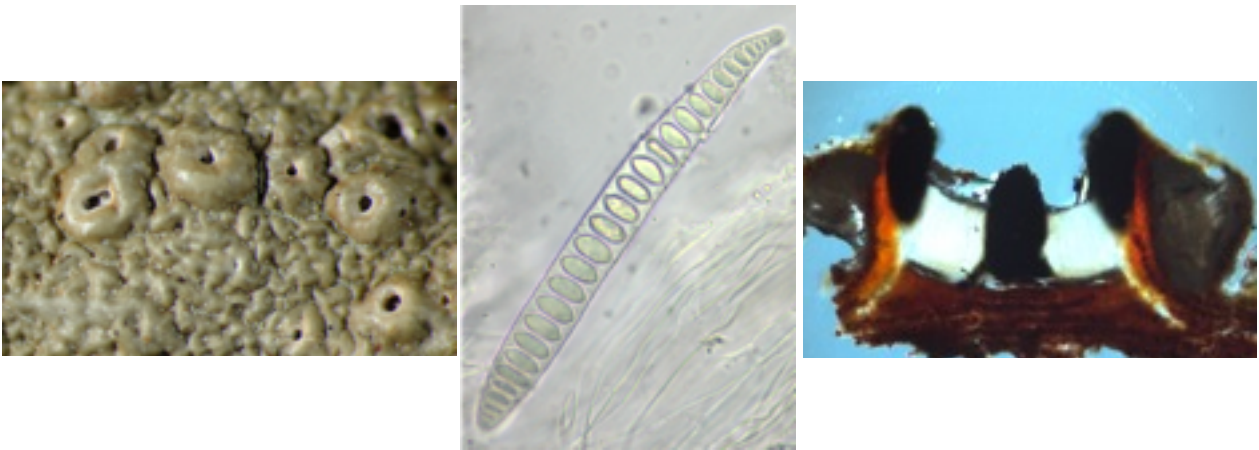
3.7 **Khwanruan Bustatorn Papong**, H. Thorsten Lumbsch, Robert Lücking. (2013) *Lichens, Graphidaceae - Rhabdodiscus, Stegobolus*. **Rapid Color Guide #547** version 1 10/2013 (printed and online).

(Online publication)

http://fieldguides.fieldmuseum.org/guides?region=All&country=Thailand&type=Fungi+and+lichens&subject=All&items_per_page=25&=Filter

DNA barcoding and Systematics of Thelotremaoid *Graphidaceae* (Ascomycota: Ostropales) in Thailand

Financial supported: Thailand Research Fund (TRF) and Mahasarakham University
2012-2015



CHAPTER 1

Introduction

Systematics of Thelotremoid *Graphidaceae*

Thelotremoid *Graphidaceae* is large group of lichens within the family *Graphidaceae*, with more than 1,000 species described based on morphological and molecular data (Frisch *et al.* 2006; Hale 1981; Mangold *et al.* 2008b, 2009; Rivas Plata *et al.* 2010a, 2010b, Lumbsch *et al.* 2010). Morphologically the taxa can be recognized by having immersed-erumpent, rounded ascomata (thelotremoid lichens). Twenty one genera are currently accepted: *Acanthotrema*, *Chapsa*, *Chroodiscus*, *Diploschistes*, *Fibrillithecis*, *Gyotrema*, *Ingvariella*, *Leptotrema*, *Leucodecton*, *Melanotrema*, *Melanotopelia*, *Myriotrema*, *Nadvornikia*, *Ocellularia*, *Pseudoramonia*, *Redingeria*, *Reimnitzia*, *Schizotrema*, *Thelotrema*, *Topeliopsis*, *Wirthiotrema* (Mangold *et al.* 2008b; Mangold *et al.* 2009; Rivas Plata *et al.* 2010a, 2010b; Lumbsch *et al.* 2010).

The genera of Thelotremoid *Graphidaceae* (*Thelotremataceae*) were traditionally separated by ascospore characters (Redinger 1936; Salisbury 1972; Hale 1973, 1974a, 1974b, 1978a, 1978b): [1] transversely septate and hyaline ascospores (*Ocellularia*), [2] transversely septate and brown (*Phaeotrema*), [3] muriform and hyaline (*Thelotrema*) and [4] muriform and brown (*Leptotrema*). Salisbury (1971, 1972, 1978) and Hale (1980, 1981) used excipular characters to distinguish groups: uncarbonized with lateral paraphyses (*Thelotrema*), non-carbonized and lacking lateral paraphyses (*Myriotrema*), and carbonized and lacking lateral paraphyses (*Ocellularia*). A combination of characters was then used by Kalb (2004) and Frisch *et al.* (2006) to circumscribe genera, including vegetative, ascomatal, and chemical characters (*Chapsa*, *Leucodecton*, *Stegobolus*, *Acanthotrema*, *Ampliotrema*, *Fibrillithecis*, *Gyotrema*, *Melanotrema*, *Redingeria* and *Reimnitzia*). Further contributions added three further genera, *Melanotopelia* and *Schizotrema* (Mangold *et al.* 2008b; Mangold *et al.* 2009). *Wirthiotrema* is characterized combination with myriotremoid thalli, apothecia and secondary chemistry (Rivas Plata *et al.* 2010a).

There is a large diversity of ascoma-morphology in the group, which was classified by Rivas Plata *et al.* (2010b) into a number of morphological groups [1] Aulaxinoid: apothecia immersed-erumpent with black, carbonized thalline margin (*Thelotrema*), Chroodiscoid: apothecia immersed-erumpent and open by regularly triangular marginal lobules or become recurved (*Chroodiscus* and *Chapsa astroidea*), [2] Fissurinoid: apothecia immersed-erumpent and open by irregular cracks in thallus (*Acanthotrema*, *Chapsa dissuta* and *Reimnitzia*), [3] Leprocarpoid: apothecia immersed-erumpent and open by irregular marginal lobes (*Chapsa indica*), [4] Platycarpoid: apothecia immersed-erumpent and open by irregular marginal lobes but with a free excipulum and forming a distinct double margin (*Chapsa platycarpa*), [5] Lamelloid: apothecia erumpent to prominent, concentric rows of lobulate excipula (*Chapsa lamellifera*), [6] Glauculentoid: apothecia immersed-erumpent and open by irregular marginal lobes but tend to have a free excipulum and irregular split between excipulum and thalline margin (*Leucodecton*), [7] Scabioid: apothecia immersed-erumpent and open by irregular marginal lobes but with regenerating hy-

menia that produce concentrically layered excipula with eventually cover the disc (*Chapsa aggregata*), [8] Schizotremoid: apothecia immersed-erumpent narrow pore from the beginning and excipula are more or less carbonized (*Schizotrema*), [9] Lepadinoid: apothecia immersed-erumpent to more typically prominent and feature a free excipulum and distinct double margin, excipulum prominent and undulate-lobulate (*Fibrillithecis*, *Leucodecton*, *Myriotrema* and *Thelotrema*), [10] Topeliopsidoid: apothecia prominent to sessile and open with numerous, the margins often exfoliate (*Chapsa meridensis* and *Topeliopsis*), [11] Melanotopelioid: apothecia prominent to sessile and open with numerous, thallus margins is reduced (*Melanotopelia*), [12] Pseudoramonioid: apothecia prominent to sessile and open with numerous with distinct stipe, [13] Urceolarioid: apothecia prominent to sessile and have a narrow pore with entire margin (*Thelotrema*), [14] Gyrotremoid: apothecia immersed-erumpent and open by regularly triangular marginal lobules, shallow rings of old excipula (*Gyrotrema*), [15] Cruentodiscoid: apothecia erumpent but are covered by thalline tissue, carbonized excipulum ("*Ocellularia*" *cruentata*), Ocellularioid: apothecia erumpent to prominent with a thick thalline margin, entire pore (*Fibrillithecis* and *Thelotrema*), [16] Glaucophaenoid: apothecia erumpent to prominent with thin thalline margin (*Fibrillithecis insignis*, *Myriothea glaucophaenum*, *Wirthiotrema santessonii*), [17] Myriotremoid: apothecia immersed and open with narrow, entire pore (*Leptotrema*, *Leucodecton*, *Myriotrema*, *Wirthiotrema*), [18] Porinoid: apothecia erumpent to prominent with very narrow entire pore resembling an ostiolum of a genuine perithecium (*Leucodecton bisporum*).

Generic Concepts in Thelotremoid *Graphidaceae*

Thelotremoid *Graphidaceae* is characterized by ±rounded, immersed to emergent ascomata, simple to sparingly branched paraphyses and predominantly distoseptate ascospores. Ascomata type are show a remarkable variability openings, including perithecioid, urceolate and apothecioid structures (Mangold *et al.* 2009).

In traditional classification, following Müller Argoviensis (1887), Redinger (1936) and Zahlbruckner (1923), a typological concept has been applied to the core of the family *Thelotremataceae* (now Thelotremoid *Graphidaceae*), using ascospore septation (transversal *versus* muriform) and pigmentation (hyaline *versus* brown) to distinguish between *Ocellularia*, *Phaeotrema*, *Thelotrema*, and *Leptotrema*. Many workers have recognized this concept as artificial, but no attempts towards a critical revision were made. Salisbury (1971, 1972, 1978) proposed to merge all species into a single genus *Thelotrema*, with several subgenera. Based on Salisbury (1978), Hale (1980) proposed a generic concept that relied on schematic use of excipular characters: [1] *Thelotrema*, with hyaline excipulum having periphysoids (columella absent), [2] *Myriotrema*, with hyaline excipulum lacking periphysoids (columella partly present), and [3] *Ocellularia*, with carbonized excipulum lacking periphysoids (columella partly present). Pycnidial features partly confirmed this concept (Matsumoto & Deguchi 1999), but many species could not be placed unambiguously within either genus, and smaller lineages are not properly recognized.

Frisch *et al.* (2006) described five new genera and resurrected four older names, using a combination of ascomata characters such as the exciple structure and pigmentation and the occurrence and structure of the columella and lateral paraphyses. In 2008b Mangold *et al.* described the new genus *Melanotopelia* distinguished by having regenerating ascomata with a distinctly layered margin, dark-pigmented to carbonized marginal proper exciple and non-amyloid ascospores. Following the year Mangold *et al.* (2009) described new genus *Schizotrema* is characterized by erumpent, regenerating, perithecioid or apothecioid ascomata with a ±distinctly layered margin, an apically free proper exciple dark brown to carbonized at the margin, hyaline, non-amyloid or amyloid ascospores. The molecular data show two taxa including in *Ampliotrema* and *Stegobolus* were nested within *Ocellularia*, and *Stegobolus* was polyphyletic. Consequently, *Ampliotrema* and *Stegobolus* were reduced to synonymy with *Ocellularia* (Mangold *et al.* 2009). Recently, Rivas Plata *et al.* (2010b) described the new genus *Wirthiotrema* that is characterized by a combination of myriotrema-like thalli and apothecia with paraplectenchymatous excipulum, l-ascospores, and stictic acid as secondary compound.

Secondary chemistry is another important character complex in Thelotremoid *Graphidaceae* (Hale 1973, 1974a, 1974b, 1975, 1978a, 1978b; Frisch *et al.* 2006; Hale 1981; Staiger 2002; Staiger *et al.* 2006; Kalb *et al.* 2004; Frisch *et al.* 2006; Mangold *et al.* 2008b, 2009; Rivas Plata *et al.* 2010a, 2010b, Lumbsch *et al.* 2010). The core of the thelotremoid lichens has beta-orcinol depsidones (such as psoromic, stictic, and protocetraric acids) and rarely lichexanthone and anthraquinones, while depsides and mono-aromatic compounds are characteristic of *Diploschistes* (Guderley & Lumbsch 1996). Data available of Thelotremoid *Graphidaceae* indicate that secondary chemistry is important for alpha-taxonomic purposes but mostly does not indicate higher-level relationships.

Diversity of Thelotremoid *Graphidaceae*

The diversity of Thelotremoid *Graphidaceae* is generally poorly known in SE Asia especially in Thailand. Most of reports are from Europe, the Neotropics, and Australia (Purvis *et al.* 1995; Aptoot 2010; James 1977; Hale 1974b, Hale 1978b, Lucking 1999; Redinger 1936; Lumbsch & Elix 2003, Lumbsch *et al.* 2008, 2010; Mangold *et al.* 2007a, 2007b, 2008a, 2008b, 2009; Galloway 2001; Messuti *et al.* 2010; Rivas *et al.* 2010a, 2010b) (Table 1). Thelotremoid lichens are one of the most important components of tropical ecosystems (Santesson 1952; Sipman & Harris 1989) and their diversity is currently vastly underestimated, especially in rainforest habitats. Data of this project will be filling the gaps in our knowledge of SE Asian taxa of Thelotremoid *Graphidaceae*. Except for Hale's detailed contributions (Hale 1974b, 1978b, 1981), critical revisions and keys are rarely provided. A key to microlichens from India (Awasthi 1991) includes *Thelotremataceae*, and Lumbsch & Elix (2003) assembled a key to genera in Australia. A multi-entry key to all known *Diploschistes* spp. has been published by Lumbsch & Guderley in the LIAS system (www.lias.net). Mangold *et al.* (2009) provided the keys and description species of *Thelotremataceae* occur in Australia. Recently, Keys of Thelotremoid *Graphidaceae* provided by Rivas Plata *et al.* (2010a) a

world-wide key to thelotremoid *Graphidaceae* and Lumbsch *et al.* (2010) key to the species of *Thelotremataceae* in subantarctic regions.

Table 1.1 List of geographical regions from which thelotremoid *Graphidaceae* have been reported.

Region	References
Europe	Purvis <i>et al.</i> 1995; Aptoot 2010; James 1977
North America	Lendemer & Harris 2014
South Africa	Guderley & Lumbsch 1996; Guderley <i>et al.</i> 1997
Tropical Africa	Lücking 2014; Van Den Broeck <i>et al.</i> 2014
Australia	Lumbsch & Elix 2003, Lumbsch <i>et al.</i> 2008, 2010; Mangold <i>et al.</i> 2007a, 2007b, 2008a, 2008b, 2008c, 2009, 2014; Galloway 2001
Tasmania	Kantvilas 2000
India and Nepal	Pant & Upreti 1993; Nagarkar <i>et al.</i> 1988; Patwardhan & Kulkarni 1977
Aldabra, Indian Ocean	Sipman, 2010
Sri Lanka	Hale 1981; Weerakoon <i>et al.</i> 2014
Thailand	Homchantara 1999; Homchantara & Coppins, 2002; Papong <i>et al.</i> 2010, 2014; Poengsungnoen 2014a, 2014b; Sutjaritturakan <i>et al.</i> 2014
China	Kalb & Jia 2014
Philippines	Rivas Plata <i>et al.</i> 2014
Neotropics and SE Asia	Sipman 2014
Andaman Islands	Singh, 1970
Africa	Frisch <i>et al.</i> 2006

Region	References
Argentina	Messuti <i>et al.</i> 2010; Ferraro <i>et al.</i> 2014
Brazil	Redinger 1936; Caceres <i>et al.</i> 2014
Costa Rica	Lücking 1999; Rivas <i>et al.</i> 2010a, 2010b
Puerto Rico	Mercado-Diaz <i>et al.</i> 2014
Dominica	Hale 1974b
Panama	Hale 1978b
Colombia	Pelaez <i>et al.</i> 2014
New Caledonia	Papong <i>et al.</i> 2014

Molecular phylogeny and DNA barcode of Thelotremoid *Graphidaceae*

DNA Barcoding and molecular studies on lichens are becoming increasingly popular to enhance our understanding of the evolution of these unique symbiotic organisms. Current molecular data of Thelotremoid *Graphidaceae* reported are largely based on collections made in Australia and the Neotropics (Lumbsch & Elix 2003, Lumbsch *et al.* 2008; Mangold *et al.* 2007a, 2007b, 2008a, 2008b, 2008c, 2009). The knowledge of the diversity and phylogeny of East Asian Thelotremoid *Graphidaceae* is currently poor and largely based on early research by Homchantara. She firstly reported a number of new species of *Thelotremataceae* from Thailand (Homchantara & Coppins 2002), based on morphological and chemical studies. In a subsequent study, however, we identified some problems with the species concept used in that paper and given the increased knowledge of the diversity in the family, reduce some of those to synonymy with previously described taxa (Papong *et al.* 2010). Further, workshop on *Thelotremataceae* in Thailand in 2008, financially supported by a NSF grant to The Field Museum, Chicago (PI-Dr.Lumbsch), a higher diversity of Thelotremoid lichens was found on a field trip to Khao Yai National Park, indicating that the diversity of the family is much higher than assumed.

Graphidaceae is most diverse tropical lichen family and thelotremoid taxa are an important element of the diversity of the family. Hence this group plays a key role in our understanding of the importance of lichens for SE Asia tropical ecosystems, especially in the diversity of forest types in Thailand, such as lower montane rainforest, tropical rainforest, dry evergreen forest, mangrove forest, and dry dipterocarp forest.

In traditional taxonomy the two families *Graphidaceae* and *Thelotre mataceae* were separated. *Thelotre mataceae* was a large family of predominantly tropical and subtropical crustose lichen-forming fungi, with more than 1,000 described species (Hale 1981; Frisch *et al.* 2006). *Graphidaceae* has also been a large family with high diversity in tropical to subtropical region, with more than 1,000 described species (Staiger 2002; Staiger *et al.* 2006). Species of *Thelotre mataceae* were characterized by a predominantly lichenized life-style, crustose thallus growth form with trentepohlioid photobiont (except in *Diploschistes*), immersed to sessile, rounded to rarely elongate-lirellate ascomata with unbranched paraphyses, and mostly distoseptate ascospores. While species of *Graphidaceae*, sharing almost all characters with *Thelotre mataceae*, but distinguished by having lirelliform ascomata, which, however, are rarely rounded to ellipsoid, such as *Acanthothecis hololeuroides*, *Diorygma confluen*, *Glyphis scyphulifera*, *Graphis muscicola*, *Leiorreuma hypomelaenum*, and *Phaeographis lobata* (Staiger 2002; Kalb *et al.* 2004). The distinction of both families was based on ascoma shape and development. However, the presence of intermediate forms, for example roundish ascomata in some *Graphidaceae*, lobate to almost lirelliform ascomata in some *Thelotre mataceae* (Mangold *et al.* 2008a) made the distinction questionable, despite the fact that some of the typical species of each family are easily recognized.

Mangold *et al.* (2008a) provided evidence using molecular data that strongly suggest both families *Graphidaceae* and *Thelotre mataceae* cannot be separated and, consequently, *Thelotre mataceae* was placed into synonymy with *Graphidaceae* (Figure 1). Figure 1 shows a phylogenetic tree based on molecular data of both families (*Graphidaceae* and *Thelotre mataceae*), in which it is clear that both families are not monophyletic. Further, the results further indicate that some of the clades need re-evaluation. For example *Thelotrema* taxa are spread over several clades within Thelotremoid *Graphidaceae*.

Several studies focused on the phylogeny and taxonomy of certain clades within *Thelotre mataceae* (Thelotremoid *Graphidaceae*) and were helpful for understanding that morphological complex group of lichens (Mangold *et al.* 2006, 2007a, 2007b, 2008a; Lumbsch & Mangold 2007; Lumbsch *et al.* 2007). Molecular studies on Thelotremoid *Graphidaceae* used genes coding for mitochondrial small subunit (mtSSU) and nuclear large (nuLSU) rDNA sequences (Grube *et al.* 2004; Lücking *et al.* 2004; Mangold *et al.* 2008a) and ITS was used by Martin *et al.* (2003). The genus *Nadvornikia* (*Thelotre mataceae*) was found being monophyletic, but nested within a paraphyletic *Graphidaceae* (Grube *et al.* 2004; Lumbsch *et al.* 2004). This was shown previously with smaller sampling (Frisch *et al.* 2006; Staiger *et al.* 2006; Miadlikowska *et al.* 2006; Grube *et al.* 2004; Lücking *et al.* 2004; Mangold *et al.* 2008a; Lumbsch *et al.* 2004).

In this project we focus on molecular phylogenetic studies and systematics of Thelotremoid *Graphidaceae*, one of the large groups within the family *Graphidaceae*. Since the group of lichen is an important element of undisturbed rainforests, its species have great potential as indicators of ecological continuity, and at the same time, they are endangered by ongoing destruction of their natural environments. In addition, molecular studies included in this project will help to fill gaps in the molecular data set used by Mangold *et al.* (2008a). This project will attract future students to

this fascinating group of organisms, provide widely accessible, easy-to-use interactive identification tools and databases, set up a framework for a taxonomic and systematic outline of Thelotremaid *Graphidaceae*, help to understand the evolution and ecosystems habitat in Thailand and SE Asia, and contribute to the understanding and application of species concepts in Thelotremaid *Graphidaceae*. From previous studies, a number of tools, such as keys, materials, and molecular data are at hand for our research on Thelotremaid *Graphidaceae* in Thailand (Lumbsch & Elix 2003, Lumbsch *et al.* 2008; Mangold *et al.* 2007a, 2007b, 2008a, 2008b, 2009; Hale 1981; Frisch *et al.* 2006; Staiger 2002; Staiger *et al.* 2006; Kalb *et al.* 2004; Rivas Plata *et al.* 2010a, 2010b; Lumbsch *et al.* 2010).



Fig. 1. Phylogeny of Graphidaceae and Thelotremataceae as inferred from a two gene-partition analysis. This is a 50% majority-rule consensus tree based on 30,000 trees from a BMC-MC tree sampling procedure. Branches with posterior probabilities equal or above 0.96 and MP bootstrap support values above 70% are indicated in bold. Type species of in-group genera indicated by an asterisk. Graphidaceae taxa indicated by black bars, grey bars representing Thelotremataceae taxa. Groups mentioned in the text are marked by letters.

CHAPTER 2

Methodology

2.1 Specimen sampling

Specimens were collected to obtain fresh material, all over the country and in all ecological habitats (Fig. 2.2). Collections and type specimens will be deposited in the herbarium MSUT, with duplicates in RAMK and F. Ecological data to characterized the ecosystems will be collected on the field trips, such as forest types (Fig. 2.3), altitude record by GPS, microhabitat, and substrate will identified with scientific name.

List of collections locality for Thelotreroid Graphidaceae in Thailand. (Fig. 2.1)

1. Chiang Mai Province: Doi Sutep - Pui National Park, Tatmok Waterfall, 18°57' N, 89°51' E, 535 m, mixed deciduous forest.
2. Chiang Mai Province: Doi Inthanon National Park, Huai Sai Lueang Waterfall, 18°31' N, 98°27' E, 1,062 m, montane forest.
3. Chiang Mai Province: At roadside on road to Tambon Thap Sadet, 18°56' N, 99°23' E, 1,439 m, montane forest.
4. Me Hong Son Province: Huai Nam Dang National Park, Helicopter Pad Site, 19°18' N, 98°36' E, 1,670 m, montane forest.
5. Me Hong Son Province: Huai Nam Dang National Park, Outlook at roadside, 19°17' N, 98°35' E, 1,443 m, free-standing trees.
6. Me Hong Son Province: Pha Sai - Tham Pla National Park, Pha Sua Waterfall, 19°25' N, 97°55' E, 275 m, dry dipterocarp forest.
7. Me Hong Son Province: Mae Surin National Park, Mae Surin Waterfall, 18°56' N, 98°04' E, 1,193 m, montane forest.
8. Me Hong Son Province: Mae Yom Laung Forest Park, Mae Yom Laung Waterfall, 18°49' N, 98°02' E, 936 m, montane forest.
9. Lam Pang Province: Chaeson National Park, Chae son Waterfall, 18°50' N, 99°28' E, 462 m, tropical rainforest.
10. Chiang Rai Province: Khun Chae National Park, Gurgling Trail, 19°04' N, 99°24' E, 875 m, tropical rainforest.
11. Chiang Rai Province: Doi Laung National Park, Champathong Waterfall, 19°13' N, 99°44' E, 512 m, tropical rainforest.
12. Chiang Rai Province: Doi Laung National Park, Pugang Waterfall, 19°26' N, 99°41' E, 600 m, tropical rainforest.
13. Chiang Rai Province: Doi Laung National Park, Wang Kaew waterfall, 19°19' N, 99°40' E, 600 m, tropical rainforest.
14. Uttaradit Province: Phu Soi Daow National Park, natural trail to top of mountain; Alt. 800 m.

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- 15.Pitsanulok Province: Phu Hin Rong Kla National Park, Rumklao Paradon waterfall, 16° 59' 871" N, 101° 00' 925" E, Alt. 1,170 m., tropical rainforest.
 - 16.Pitsanulok Province: Phu Hin Rong Kla National Park, The communist stronghold, 16° 59' 156" N, 100° 59' 871" E, Alt. 1,341 m., tropical rainforest.
 - 17.Pitsanulok Province: Phu Hin Rong Kla National Park, Political School, 16° 59' 560" N, 101° 00' 710" E, Alt. 1,287 m., tropical rainforest.
 - 18.Pitsanulok Province: Phu Hin Rong Kla National Park, Water wheel, 16° 59' 560" N, 101° 00' 710" E, Alt. 1,287 m., tropical rainforest.
 - 19.Pitsanulok Province: Phu Hin Rong Kla National Park, Lan Hin Tae, 17° 00' 212" N, 100° 59' 490" E, Alt. 1,641 m., lower montain rainforest.
 - 20.Petchaboon Province: Phu Hin Rong Kla National Park, Trail to Mhun Dang waterfall, 16° 55' 861" N, 101° 03' 081" E, Alt. 1,640 m., lower montain rainforest.
 - 21.Muk Dahan Province: Wat Tham Chao Pha, Phu Pha Kud, trail from temple to top of mountain; 16°46'N, 104°43'E, Alt. 285 m; dry dipterocarp forest.
 - 22.Muk Dahan Province: Nhung Sung district, Phu Pha Kam conservation area, 16°43'N, 104°43'E, Alt. 290 m, dry evergreen forest.
 - 23.Ubon Ratchathani Province: Phu Joung Na yoy National Park, Hui Lung Waterfall, 14° 26' 213" N, 105° 16' 372" E, 365 m, dry evergreen forest.
 - 24.Ubon Ratchathani Province: Phu Joung Na yoy National Park, Kaeng Ka Lao, 14° 26' 213" N, 105° 16' 372" E, 365 m, dry evergreen forest.
 - 25.Ubon Ratchathani Province: Kaeng Ta Na National Park, cross the brigde to forest, 15° 17' 814" N, 105° 28' 325" E, 119 m, dry evergreen forest.
 - 26.Ubon Ratchathani Province: Pha Tam National Park, trail to Huai Sanom, 15° 27' 620" N, 105° 34' 615" E, 245 m, dry evergreen forest.
 - 27.Ubon Ratchathani Province: Pha Tam National Park, Sang Chan waterfall, 15° 30' 945" N, 105° 35' 392" E, 124 m, dry evergreen forest.
 - 28.Sakon Nakhon Province: Phu Pan National Park, Kham hom waterfall; Alt. 500 m.
 - 29.Nakorn Ratchasima Province: Wang Nam Khaew District, Sakaerat Environmental Research, Sakaerat Biosphere Reserves, Natural trail between fire buffer zone 5-6, 14° 30' 32" N, 101° 55' 63" E, Alt. 417 m, Dry evergreen forest.
 - 30.Loei Province: Phu Ruea District, Phu Ruea National Park, trail from Hin Sam Chan waterfall to Huai Phai waterfall, 17° 29' 98" N, 101° 20' 17" E, Alt. 1,163 m, Lower montane rainforest.
 - 31.Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, along creek near impounding reservoir; Alt. 450 m; remnants of rainforest along creek.
 - 32.Surat Thani Province: Ko Phangang, Northern Island, Chaloklam area, E of Chaloklam Rd.; 9° 76' N, 100° 03' E, Alt. 450 m.

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- 33.Surat Thani Province: Koh Phangang , Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, Alt. 400 m; secondary rainforest.
- 34.Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra; 9°76'N, 100°03'E, Alt 400 m.
- 35.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Phetra National Park, Ko Lidee, natural trail to Maphaow bay, 6° 46' 76" N, 99° 45' 69" E, Alt. 12 m, Dry evergreen forest.
- 36.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Phetra National Park, Ko Lidee, natural trail from Ko Wa to Lamvahn view point, 6° 47' N, 99° 46' E, Alt. 2 m, Mangrove forest.
- 37.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Phetra National Park, Natural trail from haed quarter to view point, 6° 50' N, 99° 45' E, Alt. 10 m, Dry evergreen forest.
- 38.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Tarutao National Park, Roadsite on trail to Ao Talo wow, 6° 41' N, 99° 39' E, Alt. 100 m, Dry evergreen forest.
- 39.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Tarutao National Park, Lu Du waterfall, 6° 39' N, 99° 37' E, Alt. 30 m, Tropical rainforest.
- 40.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Tarutao National Park, Ao Son bay, 6° 39' N, 99° 37' E, Alt. 30 m; Beach forest.
- 41.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Tarutao National Park, Ao Thalo Wow, natural trail, 6° 37' N, 99° 41' E, Alt. 5 m; Tropical rainforest.
- 42.Satun Province: La-Ngu district, Islands of Andaman sea, Mu Ko Tarutao National Park, Ao Thalo Wow, road side 3 km from the beach, Tropical rainforest.
- 43.Satun Province: Kun Doon district, Thale Ban National Park, Thale Ban National Park, Rane waterfall, 6° 43' N, 100° 10' E, Alt. 100 m; Tropical rainforest.
- 44.Satun Province: Kun Doon district, Thale Ban National Park, Rayon waterfall, 6° 45' N, 100° 9' E. Alt. 100 m; Tropical rainforest.
- 45.Satun Province: Kun Doon district, Thale Ban National Park, Natural trail behide the bangalow, 6° 45' N, 100° 9' E, Alt. 100 m; Tropical rainforest.
- 46.Songkla Province: Muang district, Tone Nga Chan Wildlife Sanctuary, Tone Nga Chan waterfall, 6° 57' N, 100° 14' E, Alt. 123 m; Tropical rainforest.



Fig. 2.2 Forest types for collecting samples. A. Dry evergreen forest, B-C. Lower montane rainforest, D. Tropical rainforest, E. Dry dipterocarp, F-G. Secondary forest and H. Beach forest.



Fig. 2.3 Collecting equipment for lichens and herbarium collection.

2.2 Morphological, Anatomical and Chemical Data (Phenotype Data)

2.2.1 The morphology and anatomy of thallus, ascomata and conidiomata will be studied for about 50 characters. Most of the characters defined for these groups can be applied to the data matrix for Thelotrema *Graphidaceae*. Morphological and anatomical data will be obtained by microscopic study of fresh and herbarium material. We will use epifluorescence techniques (Grube & Lücking 2001, 2002) to infer fine structures of tissues, hyphae, and ascospores. Additional anatomical characters will be studied, such as mode of spore septation (Lumbsch *et al.* 1997), ascospore ornamentation, and amyloidity of ascoma parts. (Fig. 2.4 and 2.5)

2.2.3 Secondary chemistry data will be studied according to standard methods (Santesson 1967; Culberson 1972; Culberson & Johnson 1976; Elix *et al.* 1988; Mietzsch *et al.* 1993; Feige *et al.* 1993; Huneck *et al.* 1994; Egan 2001; Lumbsch 2002) by both thin layer chromatography (TLC) and high-performance liquid chromatography (HPLC). (Fig. 2.6)

2.3 Molecular Data (Genotype Data)

DNA extraction and sequencing

The SIGMA REDEExtract-N-Amp Plant PCR Kit will be used to isolate DNA, following the manufacturer's instructions, except only 10 µl of extraction buffer and 10 µl dilution buffer are used following Avis *et al.* (2003). Dilutions of these extractions (rather than the stock DNA solution) were found to work best for PCR, and a 20x DNA dilution will then be used in subsequent PCR reactions. Samples will be PCR amplified and/or sequenced using the mrSSU1, mrSSU2, mrSSU2r and mrSSU3r primers (Zoller *et al.* 1999) for the mitochondrial small subunit (mtSSU), primers for the nuclear ribosomal large subunit rDNA (nuLSU), the ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) for ITS. The 10 µl PCR reactions consist of 5 µM of each PCR primer, 3 mM of each dNTP, 2 µl of 10 mg/mL 100X BSA (NEW ENGLAND BIOLABS), 1.5 µl 10X PCR buffer (ROCHE APPLIED SCIENCE) 0.5 µl Taq, approximately 2 µl diluted DNA, and 2 µl water. The PCR cycling conditions are as follows: 95° C for 5 minutes, followed by 35 cycles of 95° C for 1 minute, a locus-specific annealing temperature for 1 minute, and 72° C for 1 minute, followed by a single 72° C final extension for 7 minutes. An annealing temperature of 53° C will be used for mtSSU, while 57° C is used for nuLSU and variable settings for ITS. Samples are visualized on a 1% ethidium bromide-stained agarose gel under UV light and bands are gel extracted, heated at 70° C for 5 minutes, cooled to 45° C for 10 minutes, treated with 1 µl GELase (EPICENTRE BIOTECHNOLOGIES) and incubated at 45° C for at least 24 hours. The 10 µl cycle sequencing reactions consist of 1-1.5 µl of BIG DYE version 3.1, 2.5-3 µl of Big Dye buffer, 6 µM primer, 0.75-2 µl GELased PCR product and water. The cycle sequencing conditions are as follows: 96° C for 1 minute, followed by 25 cycles of 96° C for 10 seconds, 50° C for 5 seconds and 60° C for 4 minutes. Samples will be precipitated and sequenced in an APPLIED BIOSYSTEMS 3730 DNA Analyzer and sequences assembled in SEQUENCHER 4.9. This protocol, with minor variations, has worked well for samples of Thelotrema *Graphidaceae* in our experience. (Fig. 2.8 and 2.9)

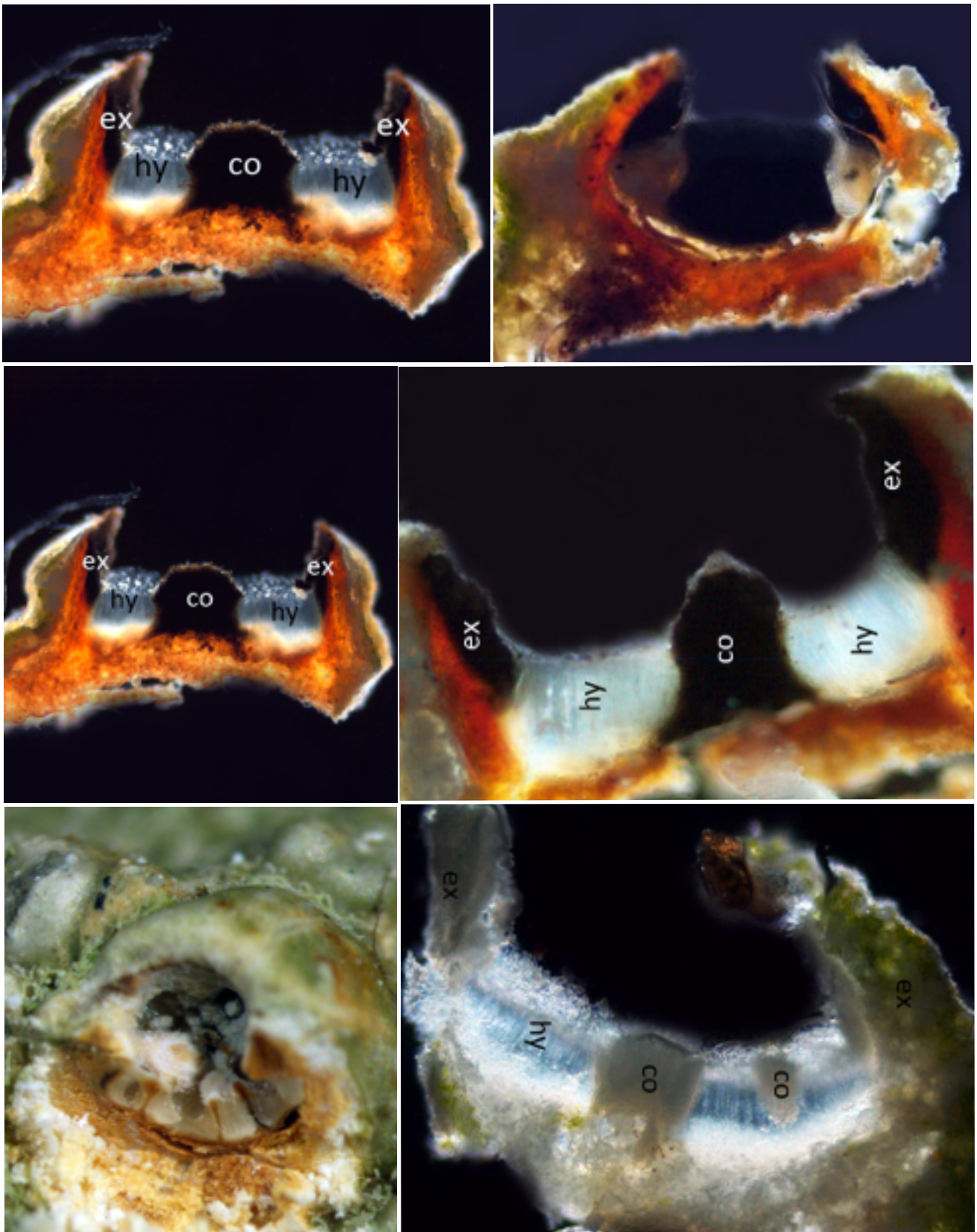


Fig. 2.4 Anatomical of apothecia, hy = hymenium, ex = excipulum, co = columella.

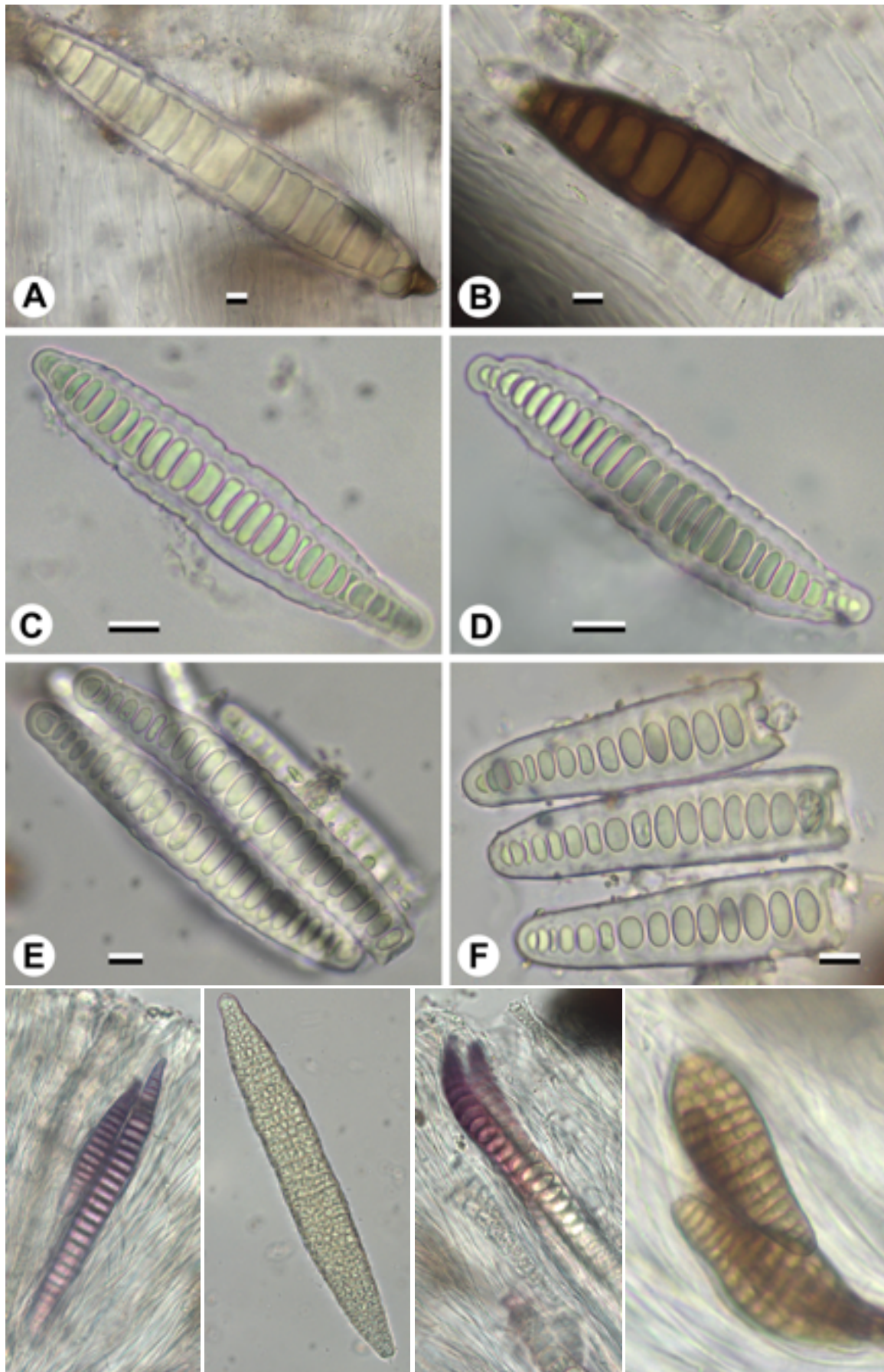


Fig. 2.5 Ascospores and asci of Thelotrema Graphidaceae.



Fig. 2.6 Thin Layer Chromatography (TLC) for determined secondary metabolites.

2.4 Data Analyses

Phylogenetic analysis

Phylogenetic trees will be deriving by maximum parsimony, maximum likelihood, and Bayesian approaches. Different datasets (genes, phenotype data) will first be analyzed independently and trees will be tested for supported conflict using COMPATPY (Kauff & Lutzoni 2002). We also use a Bayesian approach to examine heterogeneity in phylogenetic signal among data partitions (Buckley *et al.* 2002). For single genes and combined analyses, topologies reaching 0.95 posterior probabilities will be estimated. The combined analysis topology will be compared for conflict with the 0.95 posterior intervals of single gene analyses. Molecular datasets will be combined if no supported conflict is detected in the relationships between clades; in case of conflict, the conflicting sequence will be inspected for possible errors and if no apparent error is detected, the corresponding OTU will be removed from the combined dataset and the conflict will be documented based on the individual datasets. Conflict in the terminal positions of individual OTUs will be neglected as long as the genus or species group disposition of the OTU remains unchanged. Combined total and non-conflictive datasets will be used for total evidence analysis, excluding and including phenotype data. Since mtSSU and ITS contain highly variable parts difficult to align, in addition to standard alignment programs such as CLUSTALW2 (Thompson *et al.* 1994), we use an iterative procedure in which ambiguous regions are aligned with Muscle 3.6 (Edgar 2004) through MESQUITE 2.71; the alignment will be manually refined and other portions realigned with Muscle. Regions that cannot be aligned with statistical confidence will be delimited as ambiguous regions. Ambiguous regions will be pairwise aligned using log-affine gap cost scores implemented in NGILA 1.2.1 (Cartwright 2007) and the cost matrix will be compared to the mean character distance matrix derived from the non-ambiguous alignment portion under a Jukes-Cantor model, using the Spearman rank correlation coefficient. If the coefficient is 0.3 or higher, it can be expected that the ambiguous region contains substantial phylogenetic signal supporting both major and terminal clades. In that case, the ambiguous region will be coded using PICS-Ord, a novel method developed by us which used Principal Component Analysis ordination to transform the log-affine gap cost score matrix computed in NGILA into integer codes derived from the ordination axes. This method allows for ambiguous region coding of large datasets and the codes can be analysed under MP and as separate partition under Bayesian approaches (Huelsenbeck & Ronquist 2001) and ML in RAxML 7.2.4 (Stamatakis 2006).

Phylogenetic analyses will be performed using PAUP* 4.0b10 (Swofford 2003), MrBAYES (Huelsenbeck & Ronquist 2001), RAxML 7.2.4 (Stamatakis 2006) and GARLI 0.96 (Zwickl 2006). Since choice of oversimplifying substitution models can yield incorrect phylogenetic estimates (Bruno & Halpern 1999), prior to model based searches a model will be calculated using a likelihood ratio test as implemented in MODELTEST 3.7 (Posada & Crandall 1998). Branch supports are calculated using non-parametric bootstrapping (Felsenstein 1985) for MP and ML searches and posterior probabilities from MCMC samplings. To evaluate the possibility of alternative tree topologies, parametric bootstrapping will be used following Goldman *et al.* (2000). Phylogenetic null hypothe-

ses agreeing with hypotheses formulated previously will be tested using additional MCMC tree sampling procedures performed as described above. The probability of the null hypothesis being correct is calculated by counting the presence of the topology in the MCMC sample (Lewis 2001). Character evolution will be studied using a combined Bayesian/likelihood (Pagel 1994, 1999) and a fully Bayesian (Huelsenbeck *et al.* 2003) approach, using ancestral character state reconstruction as implemented in MESQUITE 2.71.

2.5 Database

2.5.1 Images

Specimen images are created using a NIKON Coolpix 5400 digital camera in combination with a LEICA MS5 stereomicroscope equipped with a ZEISS W-PI 10x/23 ocular, as well as a JENOPTIC ProgRes CT3 digital camera, allowing precise photographs of morphological details. For images in the field, a NIKON D90X camera is used. Anatomical details from microscopical sections are imaged using a ZEISS Axioscope compound microscope connected to a JENOPTIC ProgRes CT5 digital camera. Images are stored in high-resolution and high quality JPG format (15 × 11.25 cm, 300 dpi) for publications and mid-resolution JPG format (800 × 600 pixels, 72 dpi) for web use, which will also be available through our database. The images database will be access public on website.

2.5.2 Type specimens

Information on type specimens, including label and specimen images, is stored in our database in Database/lichens/ThaiTheloproject, will be display on website.

Literature reference data are sampled in EXCEL and will be stored in a central database accessible to all participants. (Fig. 2.3)

2.5.4 Rapid Lichen Guides

The Field Museum's Environment, Culture & Conservation Program has a successful program of Rapid Color Guides, including fungi and lichens. The guides consist of laminated 8.5" × 11" sheets with color images. Such guides have proven popular and useful for students, park rangers, and ecotourists, and are available for download from the Field Museum website (fm2.fmnh.org/plantguides) and Natural Medicinal Mushroom Museum website. (Fig. 2.10 and appendix)

1. DNA extraction



2. PCR – amplification



3. Electrophoresis - visualization



4. Sequencing



5. Alignment



Fig. 2.7 Molecular method, DNA extraction and sequencing.



Fig. 2.8 The Pritzker Laboratory for Molecular Systematics at The Field Museum, Chicago USA

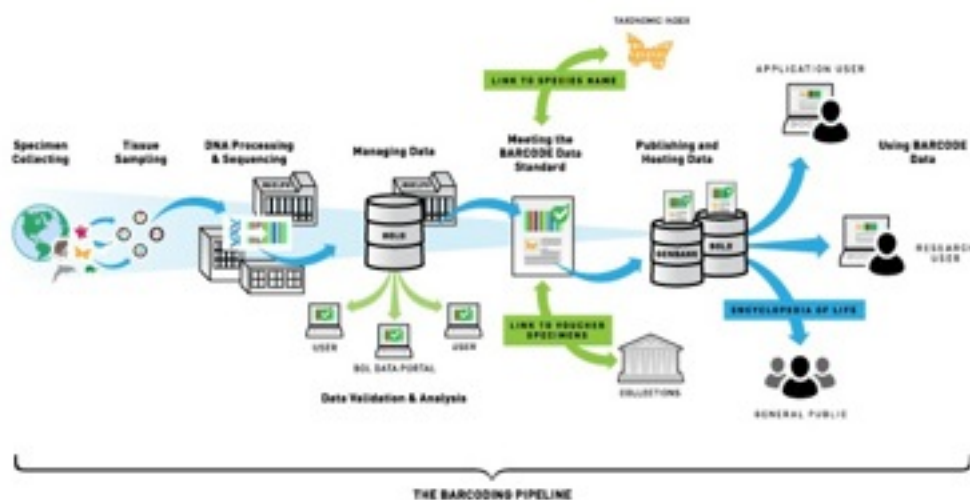


Fig. 2.9 DNA barcoding submit to BOLD.

CHAPTER 3

Results

Thelotremoid lichen is large group of family Graphidaceae, subfamily Graphidoideae. This propose focused on tribe Ocellularieae and Thelotremateae, both can distributed in tropical rainforest in Thailand. Various phenotype characters have been used for classification at the genus and species levels, including thallus, trentepohlioid photobiont, apothecioid, solitary ascomata lacking both a columella and lateral paraphyses, and having non-amyloid ascospores as well as secondary chemistry with depsidones group. Thelotremoid lichen in Thailand were found 81 species and 16 genera; *Astrochapsa* (4 species), *Chapsa* (5 species), *Chroodiscus* (6 species), *Compositrema* (1 species), *Cruentotrema* (2 species), *Glaucotrema* (1 species), *Leucodecton* (3 species), *Melanotrema* (2 species), *Myriotrema* (3 species), *Nitidochapsa* (2 species), *Ocellularia* (37 species), *Pseudochapsa* (2 species), *Pseudotopeliopsis* (1 species), *Rhabdodiscus* (1 species), *Stegobolus* (1 species) and *Thelotrema* (8 species) show in Table 3.1.

Table 3.1 List of genera and species of Thelotremoid Graphidaceae in Thailand

Genera	Species
<i>Astrochapsa</i> Parnmen, Lücking & Lumbsch	<i>A. astroidea</i> (Berk. & Broome) Parnmen, Lücking & Lumbsch <i>A. calathiformis</i> (Vain.) Parnmen, Lucking & Lumbsch <i>A. pseudophlyctis</i> (Nyl.) Parnmen, Lucking & Lumbsch <i>A. pulvereodiscus</i> (Hale) Parnmen, Lucking & Lumbsch
<i>Chapsa</i> Massal.	<i>C. discoides</i> (Stirt.) Lücking <i>C. laemensis</i> (Homchant. & Coppins) Lumbsch & Papong <i>C. indica</i> Massal. <i>C. leprocarpoides</i> (Hale) M. Cáceres & Lücking <i>C. patens</i> (Nyl.) A. Frisch

Genera	Species
<i>Chroodiscus</i> Müll. Arg.	<i>Ch. argillaceus</i> (Müll. Arg.) Lücking & Papong <i>Ch. australiensis</i> Vezda & Lumbsch <i>Ch. defectus</i> Papong & Lücking <i>Ch. homchantarae</i> Papong & Lücking <i>Ch. khaolungensis</i> Papong & Lücking <i>Ch. khaosokensis</i> Papong & Lücking
<i>Compositrema</i> Rivas Plata, Lücking & Lumbsch	<i>Co. thailandicum</i> Rivas Plata, Papong & Lumbsch
<i>Cruentotrema</i> Rivas Plata, Papong, Lumbsch & Lücking	<i>Cr. kurandense</i> (Mangold) Rivas Plata, Lumbsch & Lücking <i>Cr. cruentatum</i> (Mont.) Rivas Plata, Lumbsch & Lücking
<i>Glaucotrema</i> Rivas Plata & Lumbsch	<i>G. glaucophaenum</i> (Kremp.) Rivas Plata & Lumbsch
<i>Leucodecton</i> A. Massal.	<i>L. anamalaiense</i> (Patw. & C. R. Kulk.) Rivas Plata & Lücking <i>L. compunctellum</i> (Nyl.) Frisch, in Frisch, Kalb & Grube <i>L. confusum</i> Papong, Lumbsch & Lücking
<i>Melanotrema</i> Frisch	<i>M. melanophthalmum</i> (Homchant. & Coppins) Papong & Lumbsch <i>M. platystomum</i> (Mont.) Frisch
<i>Myriotrema</i> Fée	

Genera	Species
	<i>My. clandestinum</i> (Fée) Hale
	<i>My. cf. classicum</i> Lücking
	<i>My. polytrema</i> Hale
<i>Nitidochapsa</i> Parnmen, Lücking & Lumbsch	
	<i>N. lepreurii</i> (Mont.) Parnmen, Lücking & Lumbsch
	<i>N. aggregata</i> (Hale) Poengsungnoen, Lücking & Lumbsch
<i>Ocellularia</i> G. Mey.	
	<i>O. albocincta</i> (Hale) Divakar & Mangold
	<i>O. allosporoides</i> (Nyl.) Patw. & C. Kulk.
	<i>O. ascidioidea</i> Hale
	<i>O. brunneospora</i> Homchantara & Coppins
	<i>O. cavata</i> (Ach.) Müll. Arg.
	<i>O. cerebriformis</i> Papong, Lücking & Lumbsch
	<i>O. croceosidiata</i> Sipman
	<i>O. diacida</i> Hale
	<i>O. diospyrosis</i> Homchantara & Coppins
	<i>O. dolichotata</i> (Nyl.) Zahlbr.
	<i>O. exigua</i> Müll. Arg.
	<i>O. flavescens</i> Homchantara & Coppins
	<i>O. flavoperforata</i> Lücking
	<i>O. fumosa</i> (Ach.) Müller
	<i>O. inthanonensis</i> Homchantara & Coppins
	<i>O. interponenda</i> (Nyl.) Hale
	<i>O. khuntanensis</i> (Homchantara & Coppins) Lumbsch & Papong

Genera	Species
	<i>O. kohangangensis</i> Papong, Mangold & Lücking
	<i>O. krathingensis</i> Homchantara & Coppins
	<i>O. laeviusculoides</i> Sipman & Lücking
	<i>O. massalongoi</i> (Mont.) Hale
	<i>O. microstoma</i> (Müll. Arg.) Hale
	<i>O. neoleucina</i> Homchantara & Coppins
	<i>O. orthomastia</i> (Kremp.) Zahlbr.
	<i>O. papillata</i> (Leight) Zahlbr.
	<i>O. perforata</i> (Leight.) Müll. Arg.
	<i>O. pluriporoides</i> Homchantara & Coppins
	<i>O. pluripora</i> Hale
	<i>O. pseudopapillata</i> Papong, Mangold & Lücking
	<i>O. rhicnoporoides</i> Homchantara & Coppins
	<i>O. salazinica</i> Papong, Mangold & Lücking
	<i>O. subdolichotata</i> Papong, Mangold & Lumbsch
	<i>O. subgranulosa</i> (Homchantara & Coppins) Lumbsch & Papong
	<i>O. subleucina</i> Homchantara & Coppins
	<i>O. thelotremoides</i> (Leight.) Zahlbr.
	<i>O. violacea</i> Räsänen
	<i>O. wolseleyana</i> Homchantara & Coppin
<i>Pseudochapsa</i> Parnmen, Lucking & Lumbsch	
	<i>P. albomaculata</i> (Sipman) Parnmen, Lucking & Lumbsch
	<i>P. phlyctidioides</i> (Mull. Arg.) Parnmen, Lucking & Lumbsch

Genera	Species
<i>Pseudotopeliopsis</i> Parmen, Lücking & Lumbsch	<i>Ps. longispora</i> Papong, Lücking & Parmen
<i>Rhabdodiscus</i> Vain.	<i>R. crassus</i> (Müll. Arg.) Rivas Plata, Lücking & Lumbsch <i>R. subcavatus</i> (Nyl.) Rivas Plata & Lumbsch <i>R. subemersus</i> (Müll. Arg.) Rivas Plata, Lücking & Lumbsch
<i>Stegobolus</i> Mont.	<i>S. berkeleyanus</i> Mont
<i>Thelotrema</i> Ach.	<i>T. adjectum</i> Nyl. <i>T. bicinctulum</i> Nyl. <i>T. defossum</i> (Müll. Arg.) Mangold <i>T. porinoides</i> Mont. & Bosch <i>T. rugatulum</i> Nyl. <i>T. subadjectum</i> Mangold <i>T. triseptatum</i> Mangold <i>T. patwardhanii</i> (Hale) Rivas Plata & Mangold

Taxonomic Treatments

1. *Astrochapsa* Parnmen, Lücking & Lumbsch

[MycoBank MB 801540]

Type species: *Astrochapsa astroidea* (Berk. & Broome) Parnmen, Lücking & Lumbsch.

Differing from *Chapsa* s.str. in the more frequently densely corticate thallus, the mostly recurved apothecial margin, and the almost exclusively subdistoseptate, non-amyloid ascospores.

Thallus usually with dense cortex, rarely with loose cortex or ecorticate. Apothecia erumpent, rounded to irregular in outline; disc exposed; margin lobulate to usually recurved. Excipulum usually brown. Ascospores septate to muriform, fusiform-ellipsoid to oblong-cylindrical, with slightly thickened septa and angular lumina (subdistoseptate), colorless or rarely brown, almost exclusively 1-. Secondary chemistry: no substances or frequently stictic acid and relatives; apothecial disc sometimes pigmented.

Etymology: Derived from “astro” (Greek, starry) because of the star-like morphology of the ascomata and the genus name *Chapsa*.

1.1 *Astrochapsa astroidea* (Berk. & Broome) Parnmen, Lücking & Lumbsch

[MycoBank MB 801502]

Bas.: *Platygrapha astroidea* Berk. & Broome, J. Linn. Soc., Bot. 14: 109 (1873);

=*Chapsa astroidea* (Berk. & Broome) Caceres & Lücking in Caceres, Libri Botanici 22: 51 (2007).

Thallus: crustose, immersed, continuous, diffuse, effuse, smooth, plane; upper surface: brownish green (olivaceous, olive green), greenish brown (olive brown), yellowish brown; marginal and upper surface: absent, photobiont: *Trentepohlia* sp. Ascoma: apothecial, apothecioid – hymenial, immersed, innate, 2-3 mm diam.; disc greyish, with dense pruinose, subhymenial layers brownish to blackish brown; paraphyses present; epithecium hyaline; asci unitunicate, tholus amyloidity (iodine reaction) absent, ascospores fusiform, transversely septate 2-7 septate, hyaline, 9-20 x 3-5 µm.

Secondary chemistry: no substances detected by TLC.

1.2 *Astrochapsa calathiformis* (Vain.) Parnmen, Lücking & Lumbsch

[MycoBank MB 801503]

Bas.: *Thelotrema calathiforme* Vain., Hedwigia 46: 174 (1907);

=*Chapsa calathiformis* (Vain.) Lumbsch & Papong in Papong et al., Lichenologist, 42: 136 (2010).

=*Thelotrema phluense* Homchantara & Coppins

Thallus: crustose, continuous, diffuse, effuse, cracked, fissured, fractured, rimose, smooth, plane; upper surface greenish grey, marginal and upper surface: absent, photobiont: *Trentepohlia* sp. Ascoma: apothecial, apothecioid – hymenial, immersed, innate, 0.03-1.2 mm diam. disc greyish, with fine pruinose, paraphyses present, asci unitunicate, tholus amyloidity (iodine reaction) absent, ascospores muriform, hyaline to pale brown, 22.5-30 x 8-10 µm.

Secondary chemistry: constictic acid and stictic acid.

Notes: This species is readily identified by its shiny, greenish grey, continuous thallus, 8-spored asci and muriform ascospores that become brown when mature. The species is distinctive and difficult to confuse with any other taxon.

1.3 *Astrochapsa pseudophlyctis* (Nyl.) Parnmen, Lucking & Lumbsch

[MycoBank MB 801511]

Bas.: *Graphis pseudophlyctis* Nyl. in Hue, Nouv. Arch. Mus. Nat. Hist., Sér. 3, 3: 163 (1891); =*Chapsa pseudophlyctis* (Nyl.) Frisch, Biblioth. Lichenol. 92: 120 (2006).

Thallus crustose, continuous, diffuse, effuse, upper surface brownish to greenish grey, upper surface epruinose, smooth, plane, uneven, undulate, trentepohlioid, apothecial, apothecioid – hymenial, immersed, innate, 0.2-0.35 mm diam., brownish with dense pruinose, paraphyses present, unbranched, epithecium hyaline, tholus non-amyloid, ascospores submuriform to muriform, hyaline, 12-20 x 2-6 µm.

Secondary chemistry: no substances detected by TLC.

Notes: The species is characterized by its white to whitish, whitish-grey to pale-grey thallus lacking secondary compounds, round to angular apothecia with jagged, often eroded margins having a white crystalline inner surface, 1-6-spored asci, and hyaline muriform ascospores.

1.4 *Astrochapsa pulvereodiscus* (Hale) Parnmen, Lucking & Lumbsch

[MycoBank MB 801512]

Bas.: *Thelotrema pulvereodiscum* Hale, Bull. Br. Mus. Nat. Hist., Bot. 8(3): 268 (1981);

=*Chapsa pulvereodiscus* (Hale) Rivas Plata & Mangold in Rivas Plata et al., Lichenologist 42: 183 (2010).

Thallus corticolous, whitish gray, 8-10 cm broad, thin, dull, fissuring with age; cortex very thin, 5-7 µm; algal layer continuous, 10-15 µm; medulla 10 µm or less, mostly hypophloeodal; apothecia dispersed. chroodiscoid, round to irregularly elongate, 0.8-1.2 mm thalline rim low, suberect, becoming sorediate at tips and on the inner side, exciple free, thick, partially filling the disc, periphysoids present; disc blackish or white pruinose; hymenium 60-100 µm; spores brown, muriform, 4-5 x 9-10 µm, 1-2 x 3-4 loculate, shrivelling at maturity, l-.

Secondary chemistry: Stictic and constictic acids.

2. *Chapsa* Massal.

Species type: *Chapsa indica* Massal.

Thallus: Corticolous, continuous, fissured or rarely fissured-areolate, endophloeodal or epiphloeodal (up to c. 0.2 mm thick), white, greenish-grey, fawn, dark olive-grey or brown-olive, decorticate or corticate, smooth, verrucose or rarely strongly warty, with a matt to glossy, mealy, compact or cartilaginous surface. Prothallus line thin, brownish. Photobiont layer c. 20-160 µm thick, often

within the substrate, with scattered to numerous photobiont cells and usually few to numerous calcium oxalate crystals. A distinct layer of calcium oxalate crystals (crystallostratum) is sometimes developed basal to the photobiont layer. Medulla thin, indistinct or absent, endophloeodal. Phenocortex: Most species are decorticate. The corticate species differ in the type of the phenocortex. Apothecia: *Chroodiscus*-type, disc c. 0.25-2.3 mm in diam., rounded, angular, reniform and occasionally elongated or slightly branched, level with the surface of the thallus or slightly emergent. Margin fissured to lobed, usually strongly raised, rim-like to recurved or reflexed, with a thick, compact or felty, white, pale brown or fawn inner surface. Periderm layer present, often indistinct. Proper exciple fused or (rarely) free from the thalline margin. Columella structures always lacking. Disc pale brown, brown or blackish, usually with a thin to thick, fine, coarse or slightly felty, white or bluish-white pruina. Proper exciple: *Thelotrema*-type, cupular, up to 30(130) µm thick, periphysate, hyaline or pale brown, comprising a thick walled, conglutinated prosoplectenchyma. Rarely almost paraplectenchymatic and formed from thin-walled, angular cells with a dense cytoplasm. The hypothecium is 3-30 µm deep, hyaline to pale brown and formed from conglutinated prosoplectenchymatic hyphae. Perithysoids: Always free, perpendicular to the proper exciple or inclined towards the epihymenium, up to 50 µm long and c. 1.5-2.5 µm wide, with rectangular to long rectangular cells, not being constricted at the septa. The variability in the structure of the periphysoids is rather great. This variation often correlates with the hypothetical phylogenetic relationship of the species:

- In species of the *C. indica*-group (*C. indica*, *C. leprieurii*, *C. leprocarpa*, *C. patens* and *C. pseudophlyctis*) the apices of the periphysoids are typically moniliform (sometimes indistinct) and show a dense coating of greyish to brownish granules.
- The periphysoids of the other species have simple tips. These are often adspersed by greyish to brownish granules, but a dense granular coating similar to that of the former species is not developed. The periphysoids of this type and of the former are usually more or less inclined towards the epihymenium.
- The periphysoids of *C. platycarpa* are short (up to 15 µm long), densely arranged and perpendicular to the proper exciple. They are fused above the hymenium, where the cell walls often assume a pale brown or greenish-brown pigmentation.

Hymenium: 55-210 µm high, clear, I-.

Epihymenium: 5-15 µm high, hyaline or with a pale brown pigmentation in the hymenial gelatine. In most species the epihymenium is slightly granular by the incorporation of small calcium oxalate crystals and fine greyish to brownish granules adspersed to the tips of the paraphyses.

Paraphyses: 1.5-2.5 µm in diam., rigid, strongly conglutinated, rather widely spaced in the hymenial gelatine.

- The paraphyses of the *C. indica*-group (*C. indica*, *C. leprieurii*, *C. leprocarpa*, *C. patens* and *C. pseudophlyctis*) have moniliform tips which are formed from up to five quadratic to short rectangular cells with slightly constricted septa (=Chapsa-type). A dense granular coating of grey-

ish to brownish crystals extends far into the hymenium. This granular coating is transformed into a dark-brown to black pigmentation of the apical cell walls in some specimens.

- The moniliform tips of the paraphyses are reduced to a single slightly thickened cell in most other species of the genus. They are sparsely adspersed by small greyish to brownish granules, but a dense granular coating is lacking.
- A slight to moderate dendroid branching characterises *C. alborosella*, *C. cinchonara* and *C. diploschistoides*. The densely branched paraphyses-tips of *C. zahlbruckneri* form a loose epithecium. As in the former species, the tips of the paraphyses are sparsely adspersed by small greyish to brownish granules, but a dense granular coating is lacking.

Ascus: Narrowly to broadly clavate, 45-200 x 7-40 µm, of the *Thelotrema*-type, I-.

Ascospores: 1-8/ascus, small to large, hyaline or brown, transversely septate, submuriform to densely muriform, 12-160 x 3.5-40 µm, with a weak to strong endospore development, I- or I+ purplish-blue, halonate or not.

Chemistry: Most species lack lichen compounds. Stictic acid, and rested compounds in the stictic acid chemosyndrome are established for *C. platycarpa* and *C. zahlbruckneri*. Protocetraric acid is known from *C. eitenii*.

Notes: The corticolous *Thelotremoid-Graphidaceae* with chroodiscoid apothecia and ascospores of the thick-walled type were recently classified in *Thelotrema* (Salisbury 1972b, Hale 1980, 1981; Matsumoto 2000). However, they were already recognised as distinct from the central *Thelotrema lepadinum*-group, which led to their segregation as a separate species group or at sub-generic level. In both classifications it was referred to *Asteristion* Leight.

Chapsa is understood to include species having chroodiscoid apothecia, a periphysoids-bearing proper exciple, rather distinct and rigid paraphyses with either moniliform or branched tips (occasionally simple), and ascospores of the thick-walls type. *Chapsa* so defined shows some morphological heterogeneity and probably includes some unrelated elements. The centre of the genus is formed from the *Chapsa indica*-group (*C. indica*, *C. leprocarpa*, *Ca. patens* and *C. pseudophlyctis*) being characterised by paraphyses and periphysoids of the *Chapsa*-type, angular to elongated apothecia with a fused proper exciple, a white-felty to crystalline inner surface of the apothecial margin and a blackish disc covered by distinct white, typically more or less felty pruina, hyaline, transversely septate or muriform, I- ascospores with usually a weak endospore development (I+ pale purplish-blue in few specimens of *C. cinchonara*) and an endophloeodal, ecorticate, pale to dark olive-grey or greenish-grey thallus. *Achanthotrema* and *Chroodiscus* differ from *Chapsa* by ascospores of the thin-walled type. They appear to be not closely related to that genus. *Reinmitzia* is the only other genus of the *Thelotremoid-Graphidaceae* with chroodiscoid apothecia and ascospores of the thick-walled type. It differs mainly in the early ascospore development, which includes a prominently thick-walled stage but lacks a distinct halo. Furthermore, the mature ascospores have oblique septa and an irregular arrangement of the locules. The paraphyses are rather lax when compared to those of *Chapsa*. Also, the thick thallus is distinctive, which includes large columns of calcium oxalate crystals in the photobiont layer.

2.1 *Chapsa discoides* (Stirt.) Lücking in Sipman et al. (2012: 35)

Bas: *Graphis discoides* Stirt., *Proc. Roy. Phil. Soc. Glasgow* 13: 187 (1881).

=*Chapsa velata* (Müll. Arg.) Cáceres & Lücking, *Libri Bot.* 22: 54 (2007).

=*Thelotrema velatum* Müll. Arg., *Bull. Soc. Bot. Belgique* 32: 147 (1893).

=*Thelotrema deightonii* C. W. Dodge, *Beih. Nova Hedwigia* 12: 100 (1964).

Thallus: light grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc exposed, brown, thickly white-pruinose and therefore appearing blue-grey; margin lobulate to recurved, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 80–100 µm high, clear; periphysoids present, paraphyses unbranched, thick, apically moniliform. Ascospores 2–4(–8)/ascus, muriform, 30–60 × 12–20 µm, ellipsoid, with thin septa and rectangular lumina, colorless, I– (non-amyloid).

Secondary chemistry: no substances detected by TLC.

Notes: This species is very similar to *Chapsa pseudophlyctis* (Nyl.) Frisch, but differs in the white- grey thallus and blue-grey apothecial discs. In *C. pseudophlyctis*, the thallus is olive and the apothecial disc is pale brown with a thin white pruina. *Chapsa leprocarpoides* (Hale) Cáceres & Lücking has a free excipulum, smaller ascospores, and often aggregate apothecia. *Chapsa leprocarpa* (see above) and relatives differ in single-spored asci with larger ascospores.

2.2 *Chapsa laemensis* (Homchant. & Coppins) Lumbsch & Papong, in Papong, Boon-

pragob, Mangold, Divakar & Lumbsch, *Lichenologist*, 42(2): 136 (2010)

Bas: *Thelotrema laemense* Homchantara & Coppins.

Thallus: crustose, continuous, diffuse, effuse, smooth, plane; upper surface whiteish, greenish yellow, marginal and upper surface: absent, photobiont: *Trentepohlia* sp. Ascoma: apothecial, apotheciod – hymenial, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.5–0.7 mm diam. disc greyish, periphysoids present, paraphyses present, asci unitunicate, tholus amyloidity (iodine reaction) absent, ascospores narrowly ellipsoidal, hyaline 22.5–38 × 7–11 µm.

Secondary chemistry: constictic acid and stictic acid.

2.3 *Chapsa indica* Massal.

Thallus: corticolous, brownish-white to olive-grey, continuous, c. 0.03–0.1 mm thick, matt to slightly glossy, without compact surface, the bark substrate often showing through the thallus surface; a white medullary layer absent. Prothallus line thin, brownish, Phenocortex absent. Photobiont layer 35–100 µm thick, with inclusions of some calcium oxalate crystals, partly or completely endophloeodal. Medulla endophloeodal. Apothecia: dispersed, level with the thallus, rounded to usually angular or shortly elongated, often slightly branched, 0.25–1 mm broad and up to 1.3 mm long. Margin low, jagged to lobed, incurved to recurved, with a thick white-felty to crystalline inner

surface; proper exciple fused. Disc pale brown, usually covered by thick white-felty to crystalline pruina. Phenocortex absent. Photobiont layer 10-30(-100) μm thick. Periderm layer 15-90 μm thick, comprising a loosely organised to moderately dense, moderately brown conglutinated prosoplectenchyma, with calcium oxalate crystals and usually distinct rows of periderm cells embedded between the hyphae. Proper exciple cupular, c. 7-15 μm deep at the base, 3-12 μm wide laterally, hyaline, formed from conglutinated prosoplectenchymatic hyphae with elongated (4-8 x 1-1.5 μm) cells. Periphysoids up to 40 μm long, dense, free, perpendicular or inclined towards the epihymenium, c. 2 μm wide, with up to five rectangular to long rectangular cells; the tips strongly moniliform and intensely adspersed with fine greyish to brownish granules. Hymenium 80-165 μm high, clear. Ascospores 4-25-37 loculate, 65-125 x 8-11 μm , almost thin-walled or with moderate endospore development, with subacute ends, halonate, l-. Asci narrowly clavate, c. 80-155 x 12-24 μm . Paraphyses simple, straight, 2-2.5 μm wide; tips strongly moniliform and intensely adspersed with fine greyish to brownish granules. Epihymenium unpigmented, 10-15 μm high.

Secondary chemistry: No lichen compounds detected by TLC.

Notes: *C. indica* is readily identified by its decorticate, thin or largely endophloeodal, white to olive-grey thallus, small angular or shortly elongated apothecia with a blackish but usually densely white-felty disc, paraphyses and periphysoids of the *Chapsa*-type and large hyaline, transversely septate ascospores. Three closely related species, *C. cinchonara*, *C. leprocarpa* and *C. pseudophlytis*, are found in the African mycobiota. These differ in ascospore characters.

2.4 *Chapsa leprocarpoides* (Hale) M. Cáceres & Lücking

Bas: *Thelotrema leprocarpoides* Hale

Thallus: crustose, continuous, diffuse, effuse, smooth to uneven; upper surface whiteish, greenish yellow, marginal and upper surface: absent, photobiont: *Trentepohlia* sp. Ascoma: apothecial, apotheciod – hymenial, erumpent, 0.5-1.0 mm diam. disc whiteish, proper margin fissured: loulate, periphysoids present, paraphyses present, asci unitunicate, tholus amyloidity (iodine reaction) absent, ascospores 4-8 per ascus, narrowly ellipsoidal, hyaline, 25-40 x 8-15 μm .

Secondary chemistry: No lichen compounds detected by TLC.

2.5 *Chapsa patens* (Nyl.) A. Frisch

Bas: *Thelotrema patens* Nyl.

Thallus: corticolous, greenish-grey, continuous to slightly fissured, c. 0.07-0.15 mm thick, slightly uneven to verrucose, matt, without compact surface, the bark substrate in some specimens showing through the thallus surface; a white medullary layer absent. Prothallus line thin, brownish. Phenocortex absent. Photobiont layer 70-150 μm , with inclusions of some calcium oxalate crystals, largely endophloeodal. Medulla endophloeodal. Apothecia: dispersed, level with the thallus, rounded to slightly angular, 0.8-2 mm in diam. Margin strongly raised, deeply fissured to lobed, incurved to upright but usually not strongly recurved in the apical parts, with a thick, pale-brown to white-felty and sometimes slightly crystalline inner surface; proper exciple fused. Disc pale

brown, covered by thick white-felty to crystalline pruina. Phenocortex absent. Photobiont layer 70-110 µm thick. Periderm layer 15-70 µm thick, comprising a loosely organised and only slightly brown conglomerated prosoplectenchyma, usually with decomposed periderm cells embedded between the hyphae. Proper exciple cupular, c. 15-25 µm deep and hyaline to pale brown at the base, 60-130 µm wide laterally, hyaline, formed from strongly conglomerated, prosoplectenchymatic hyphae with short to long rectangular cells. Perphysoids up to 50 µm long, free, perpendicular to the proper exciple or inclined towards the epihymenium, c. 1.5-2 µm wide, with up to six long rectangular cells, in the apical parts indistinctly moniliform and intensely adspersed with fine greyish to brownish granules. Hymenium 170-210 µm high, clear. Ascospores 1/ascus, hyaline, densely muriform, 90-158 x 22-35 µm, almost thin-walled, with rounded ends, l-. Asci clavate, c. 105-200 x 25-40 µm. Paraphyses simple, straight, 2-2.5 µm wide; tips strongly moniliform and intensely adspersed with fine greyish to brownish granules. Epihymenium unpigmented, 10-15 µm high. Secondary chemistry: No lichen compounds detected by TLC.

3. *Chroodiscus* Müll. Arg.

Thallus smooth to uneven or distinctly verrucose, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded or lobate-lirellate; disc exposed, grey to grey-brown or scarlet-red; margin lobulate to recurved, white-grey or yellow-orange. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, ellipsoid, with thin septa and rectangular lumina, l- (non- amyloid), 1-septate to submuriform.

Secondary chemistry: stictic acid and satellites sometimes present, apothecial disc sometimes with anthraquinones.

Notes: The genus *Chroodiscus*, previously only including foliicolous taxa (Santesson 1952), had been emended to include corticolous species with chroodiscoid apothecia (Kalb 1991; V zda 1992; Kantvilas & V zda 2000). However, Frisch (2006) retained *Chroodiscus* in its traditional sense and placed most corticolous species in *Chapsa*. This has been confirmed by molecular data (Papong *et al.* 2009a).

3.1 *Chroodiscus argillaceus* (Müll. Arg.) Lücking & Papong, Bryologist 112: 154 (2009)

Bas: *Ocellularia argillacea* Müll. Arg., Flora 66: 352 (1883).

=*Ocellularia argillacea* var. *radians* Müll. Arg., Flora 66: 352 (1883).

=*Chroodiscus parvisporus* Kalb & Lücking in Lücking & Grube, Stapfia 80: 271 (2002).

Thallus light grey-green, smooth to uneven, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.6 mm diam.; disc exposed, grey; margin fused, lobulate to recurved, white-grey. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–60 µm high, clear;

paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3-septate, $8\text{--}10 \times 2.5\text{--}3.5 \mu\text{m}$, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid).

Secondary chemistry: stictic acid.

Notes: This species belongs in the early diverging group of the genus, together with the palaeotropical *C. mirificus* (Kremp.) R. Sant. and relatives (Lücking *et al.* 2008c; Papong *et al.* 2009b). It was described as *C. parvisporus* from Australia (Lücking & Grube 2002), but revision of the putative synonyms of *C. mirificus* (Santesson 1952) revealed *argillaceus* as an earlier epithet (Papong *et al.* 2009b).

3.2 *Chroodiscus australiensis* Vezda & Lumbsch, in Lumbsch & Vezda, Nova Hedwigia 50: 246 (1990) Papong *et al.*, 2007

Thallus light grey-green, smooth to uneven, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.15–0.3 mm diam.; disc exposed, scarlet-red; margin fused, lobulate to recurved, orange to scarlet-red. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–50 μm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 1-septate, $7\text{--}10 \times 2\text{--}2.5 \mu\text{m}$, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: stictic acid, apothecial disc with orange-red (K+ purple) anthraquinone.

Notes: *Chroodiscus australiensis* is the most widely distributed species of the genus (Lücking *et al.* 2008b). Its photobiont is morphologically different from that of other species of the genus (Lücking & Grube 2002) but molecular phylogenetic analyses show that photobiont morphology plays only a minor role in defining clades within the Trentepohliaceae (Nelsen *et al.* 2011).

3.3 *Chroodiscus defectus* Papong & Lücking, in Papong, Lücking, Thammathaworn & Boonpragob, Bryologist 112(1): 155 (2009)

Etymology. The epithet refers to the absence of isidia compared to *Chroodiscus mirificus*.

Thallus smooth to uneven but lacking distinct verrucae, 10–15 mm thick, greenish gray, in section with a thin, cartilaginous cortex and an irregular layer of calcium oxalate crystals; photobiont *Trentepohlia*, with angular-rounded cells in short irregular threads (type A sensu Lücking & Grube 2002). Apothecia round, 0.2–0.5 mm diam.; disc brown-gray, non-pruinose; hymenium 50–55 mm high; asci 40–50 $\times$ 12–14 mm; ascospores 8 per acus, oblong-ellipsoid, submuriform with 3–5 transverse and 0–1 longitudinal septa per segment, 10–18 $\times$ 3–5 mm. Chemistry: stictic acid detected with TLC (solvent C); thallus and apothecial sections under the microscope with K+ pale to intense yellow efflux.

Notes: This species resembles *Chroodiscus mirificus* in ascospore septation and size but persistently lacks the isidia typical of the latter. The two seem to form a species pair (but see dis-

cussion below). We have reexamined literature reports and many specimens reported from African and Southeast Asia previously identified as *Chroodiscus mirificus*.

3.4 *Chroodiscus homchantarae* Papong & Lücking, in Papong, Lücking, Thammathaworn & Boonpragob, Bryologist 112(1): 155 (2009)

Etymology. Named after the first lichenologist in Thailand, the late Prof. Natsurang Homchantara (1957–2006), who studied Thelotremaaceae in Thailand and elsewhere in Southeast Asia.

Thallus smooth to uneven but lacking distinct verrucae, 15–20 mm thick, greenish gray, in section with a thin, cartilaginous cortex and an irregular layer of calcium oxalate crystals; isidia present, disciform, 0.1–0.5 mm diam., formed from the thallus or laterally along linear, radiate thallus branches; photobiont *Trentepohlia*, with angular- rounded cells in short irregular threads (type A sensu Lücking & Grube 2002). Apothecia round, 0.15– 0.45 mm diam., disc brown-gray, non-pruinose; hymenium 40–50 mm high; asci 40–50 3 8–10 mm; ascospores 8 per acus, oblong-ellipsoid, 3-septate, 8– 14 3 3–4 mm. Chemistry: stictic acid detected with TLC (solvent C); thallus and apothecial sections under the microscope with K+ pale to intense yellow efflux.

Notes: This species is closely related to *Chroodiscus mirificus*, the two of them forming disciform isidia, but the latter differs by its submuriform ascospores. Both are to be considered sporomorphs in the sense of Wirth and Hale (1978). *Chroodiscus homchantarae* also seems to form the isidiate counterpart of *Ch. argillaceus*, but the ascospores in the latter are slightly smaller (8– 10 mm long). The collection from Malaysia cited below is a well-developed mixture of two separate taxa: one forms thalli with abundant isidia and few apothecia, the ascospores being exclusively 3-septate, whereas the other has numerous apothecia but consistently lacks isidia, and the ascospores are submuriform. Superficial examination would identify this material as a single species, *Ch. mirificus*, but critical revision revealed the presence of *Ch. homchantarae* and *Ch. defectus* instead.

3.5 *Chroodiscus khaolungensis* Papong & Lücking, in Papong, Lücking, Thammathaworn & Boonpragob, Bryologist 112(1): 156 (2009)

Etymology. Named after the type locality.

Thallus smooth to uneven but lacking distinct verrucae, 15–20 mm thick, greenish gray, in section with a thin, cartilaginous cortex and an irregular layer of calcium oxalate crystals; photobiont *Trentepohlia*, with angular-rounded cells in short irregular threads (type A sensu Lücking & Grube 2002). Apothecia round, 0.15–0.35 mm diam., disc brown-gray, non-pruinose; hymenium 40–50 mm high; asci 40–50 3 10–12 mm; ascospores 8 per acus, oblong, 3-septate, 18–24 3 3–4 mm. Chemistry: stictic acid detected with TLC (solvent C); thallus and apothecial sections under the microscope with K+ pale to intense yellow efflux.

Notes: *Chroodiscus khaolungensis* resembles *Ch. argillaceus* but has much longer ascospores (twice as long), in fact the longest in the genus (not considering the corticolous species that do not belong here).

3.6 *Chroodiscus khaosokensis* Papong & Lücking, in Papong, Lücking, Thammathaworn & Boonpragob, *Bryologist* 112(1): 156 (2009)

Etymology. Named after the type locality.

Thallus distinctly and coarsely verrucose, 15–20 mm thick, greenish gray; photobiont *Phycopeltis*, with rectangular cells in closed, radiating plates. Apothecia round, 0.3–0.6 mm diam., disc brown-gray, non-pruinose; hymenium 40–50 mm high; asci 40–50 3 8–10 mm; ascospores 8 per acus, oblong-ellipsoid, (3–)5-septate, 10–12 3 3–4 mm. Chemistry: stictic acid detected with TLC (solvent C); thallus and apothecial sections under the microscope with K+ pale to intense yellow efflux.

Notes: *Chroodiscus khaosokensis* is closely related to *Ch. verrucosus* but differs by its finally 5-septate ascospores. It thus forms a sporomorph of the latter. Transversely 5-septate ascospores are rare in the genus and so far only known from the lichenicolous *Ch. rubentiicola*. All African material of *Ch. verrucosus* is consistently 3-septate.

4. *Compositrema* Rivas Plata, Lücking & Lumbsch, *Taxon* 61 (6): 1172 (2012)

[MB#801246]

Thallus pale green-grey to olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; isidia sometimes present; photobiont layer with scattered clusters of calcium oxalate crystals between photobiont cells. Apothecia grouped into distinct pseudostromata, the latter erumpent to sessile, rounded to angular; discs pale brown, thinly white-pruinose; margins of pseudostromata and individual apothecia becoming fissured-lobulate. True columella absent. Excipulum prosoplectenchymatous, pale to dark brown, sometimes almost carbonized; periphysoids absent. Paraphyses unbranched. Ascospores 8/ascus, ellipsoid, with thick septa and lens-shaped lumina, colorless to pale brown, I+ violet-blue, 3-septate.

Secondary chemistry: psoromic acid (P+ yellow).

4.1 *Compositrema thailandicum* Rivas Plata, Papong & Lumbsch, *Taxon* 61 (6): 1174 (2012)

[MB#801248]

Thallus pale green-grey to olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Pseudostromata erumpent to prominent, angular-rounded, 0.5–1.0 mm diam., composed of 3–7 individual apothecia, each 0.1–0.3 mm diam.; margin of pseudostromata fissured-lobulate, becoming chroodiscoid, inside white-pruinose; disc of individual apothecia partially covered by margins, pale brown, thinly white-pruinose; margin of individual apothecia fissured-lobulate, white-pruinose, partially filling the pseudostromata in concentric layers. Columella absent in individual apothecia. Excipulum of individual

apothecia thin, prosoplectenchymatous, dark brown to almost carbonized; periphysoids absent. Hymenium 70–80 µm high; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 10–13 × 4.5–5.5 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue. Secondary chemistry: psoromic acid (scraped parts of thallus and apothecial pruina P+ yellow).

5. *Cruentotrema* Rivas Plata, Papong, Lumbsch & Lücking, in Rivas Plata *et al.*, Fungal Diversity 52: 119 (2011).

Type. *Cruentotrema cruentatum* (Mont.) Rivas Plata, Lumbsch & Lücking.

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer lacking clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded; disc hidden by a partially splitting thallus layer that exposes a deep red-pigmented medulla; margin formed by the outer portions of the thallus layer, lobulate to recurved, brown-black, red-pruinose. Columella absent. Excipulum prosoplectenchymatous, upper half carbonized in mature apothecia; periphysoids absent. Paraphyses unbranched. Ascospores 8/ascus, 3-septate to submuriform, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances or medulla of apothecial margin in two species with dark red isohypocrellin.

Notes: This recently established genus is another segregate from *Ocellularia* s.lat. and, as *Clandestinotrema*, is closely related to *Dyplolabia* and *Fissurina* (Rivas Plata & Lumbsch 2011a; Rivas Plata *et al.* 2012a). In fact, *Cruentotrema* and *Dyplolabia*, although quite different morphologically, are hardly distinguishable genetically. The seemingly chroodiscoid apothecia somehow resemble those of *Chroodiscus*, *Chapsa*, and *Gyrotrema*, but their anatomy and ontogeny is very different. Whereas in the latter genera, the disc is exposed by the rupturing excipular and thalline margin, in *Cruentotrema* the thalline margin splits horizontally and only the outer part opens, whereas the inner part remains largely intact and covers the disc. The deep red pruina is thus not indicating the disc but the medulla of the splitting thalline margin. As in the case of the distantly related *Clandestinotrema* and *Melanotrema*, *Cruentotrema* finds a remarkable parallel taxon in the unrelated *Acanthothecis sanguinoloba* (Redinger) Staiger & Kalb, which has the same apothecial morphology and ontogeny but differs in its amyloid ascospores of the *Graphis* type and apically spinulose paraphyses (Staiger & Kalb 1999).

5.1 *Cruentotrema kurandense* (Mangold) Rivas Plata, Lumbsch & Lücking, Fungal Diversity 52 (1): 119 (2011)

[MB#563430]

Bas: *Ocellularia kurandensis* Mangold, Flora of Australia 57: 321 (2009) [MB#540698]

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, yellowish brown, glossy, smooth, continuous to slightly verrucose, rimose. True cortex continuous, to 50 µm thick, yellowish, formed by irregular hyphae, often with substratum inclusions. Algal layer moderately well devel-

oped, continuous; calcium oxalate crystals abundant, mostly small and scattered, rarely clustered. Vegetative propagules not seen. Ascomata inconspicuous, to c. 0.4 mm diam., rounded apothecoid to indistinctly chroodiscoid in older stages, erumpent, solitary to marginally fused and somewhat clustered, immersed. Disc rarely becoming partly visible from above, whitish, epruinose. Pores formed by the thalline rim margin, to c. 0.2 mm diam., irregular, split and lobed to slightly layered, in more open ascomata the proper exciple becoming visible as a dark brown to blackish internal layer, externally pale greyish or paler than or concolorous with the thallus; thalline rim incurved, occasionally erect. Proper exciple fused, moderately thick, yellowish to yellowish brown internally, dark brown or carbonised towards the margins, with substratum inclusions, non-amyloid. Hymenium to c. 90 µm thick, not inspersed, moderately conglomerated; paraphyses straight to slightly bent, parallel to slightly interwoven, unbranched, with moderately thickened tips; columellar structures absent. Epihymenium hyaline, with greyish granules. Asci 8-spored; tholus thick. Ascospores submuriform to muriform, ellipsoidal, fusiform or somewhat clavate, with rounded to subacute ends, hyaline, non-amyloid, 15-25 x 7-10 µm, with 6-8 x 1-3 locales; locales rounded to slightly angular, mostly irregular; end cells hemispherical to conical; transversely septa distinct; ascospore wall initially thick, becoming thin, non-halonate; endospore thick. Pycnidia not seen. Secondary chemistry: No lichen compounds detected by TLC.

5.2 *Cruentotrema cruentatum* (Mont.) Rivas Plata, Lumbsch & Lücking, Fungal Diversity 52 (1): 119 (2011)

[MB#563429]

Bas.: *Stictis cruentata* Mont., Annales des Sciences Naturelles Botanique 3: 96 (1855)

=*Mellitiosporium cruentatum* (Mont.) Sacc., Sylloge Fungorum 8: 704 (1889)

=*Triblidium cruentatum* (Mont.) Sherwood, Mycotaxon 5 (1): 169 (1977)

=*Ocellularia cruentata* (Mont.) Haffellner & Magnes. in Papong et al., 2010

=*Arthothelium puniceum* Müll. Arg., Hedwigia 32 (2): 133 (1893)

=*Thelotrema rhododiscum* Homchant. & Coppins, The Lichenologist 34 (2): 135 (2002)

Thallus: crustose, continuous, diffuse, effuse, smooth, plane; upper surface brownish green (olivaceous, olive green), photobiont: *Trentepohlia* sp. Ascoma: apothecial, apothecoid – hymenial, immersed, innate, 0.5-1.2 mm diam. disc greenish brown with pruinose, paraphyses present, ephithecium brownish, asci unitunicate, tholus amyloidity (iodine reaction) absent, ascospores submuriform to muriform, ellipsoidal, oblong, oblong-obtuse, hyaline, 15-25 x 8-12 µm.

Secondary chemistry: unknown/unidentified compound(s).

6. *Glaucotrema* Rivas Plata & Lumbsch, in Rivas Plata, E., Lücking, R. & Lumbsch, H.T. Taxon 61 (6): 1174 (2012)

[MB#801245]

Thallus pale green-grey to pale olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals between photobiont cells. Apothecia erumpent to prominent, rounded to angular; disc flesh-colored to pale brown, thinly white-pruinose; margins entire to rarely fissured. True columella absent but pseudocolumella often present, usually formed by tissue strands originating from the lateral excipulum. Excipulum prosoplectenchymatous, colorless, fused or becoming free to fenestrate; periphysoids absent. Paraphyses unbranched. Ascospores 8/ascus, 3-septate, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue.

Secondary chemistry: psoromic acid (P+ yellow).

6.1 *Glaucotrema glaucophaenum* (Kremp.) Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1175)

=*Thelotrema glaucophaenum* Kremp., Nuovo Giorn. Bot. Ital. 7: 19 (1875)

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale yellowish green to olive-green, ±glossy, smooth, continuous to rugose to verrucose, occasionally sparingly rimose. True cortex ±continuous, to c. 25 µm thick, consisting of periclinal hyphae. Algal layer poorly to well developed, ±continuous; calcium oxalate crystals sparse to abundant, large and clustered; medulla usually distinct. Vegetative propagules not seen. Ascomata often conspicuous, to c. 0.8 mm diam., often larger when fused, ±rounded to irregular, apothecioid to somewhat chroodiscoid, solitary to more often fused, becoming slightly to distinctly emergent, mostly irregularly or regularly urceolate. Disc usually partly visible from above, rarely completely exposed, pale flesh-coloured, whitish-pruinose. Pores broad to gaping, to c. 0.6 mm wide, ±rounded to irregular, entire to slightly ragged; proper exciple often becoming apically visible, rarely completely visible from above, ±free, whitish, occasionally slightly shrunken, incurved to erect, rarely slightly recurved. Thalline rim margin broad to gaping, ±rounded, more commonly irregular, thick, entire, but usually split to lacerate or eroded, concolorous to whitish (due to the exposed medulla) and somewhat pruinose; thalline rim usually becoming erect to slightly recurved. Proper exciple fused to partly or entirely free, thick, hyaline internally, pale brownish or greyish marginally, occasionally including substratum material, non-amyloid. Hymenium to c. 100 µm thick, not inspersed, strongly conglutinated; paraphyses thick, irregular and often distoseptate, ±interwoven, with thickened irregular tips; lateral paraphyses and true columella absent; columella-like structures often present among fused ascomata. Epihymenium hyaline, with coarse greyish granules and fine crystals. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, occasionally with a single longitudinal septum, ±ellipsoidal to oblong, with narrowly rounded to subacute ends, hyaline, variably amyloid, but usually distinctly amyloid at maturity, 10–18 (–20) × 5–8 µm, with 2–6 (–8) × 1 (–2) locules; locules ±rounded, subglobose to lentiform or oblong; end cells hemispherical to conical; septa thin to thick, often irregular; ascospore wall thin to thick, thinly halonate; endospore thick.

Pycnidia not seen; according to Frisch *et al.* (2006) immersed in thalline warts with a brownish pore; conidia fusiform, to $6 \times 1.5 \mu\text{m}$.

Secondary chemistry: Thallus K+ yellowish, C–, P+ yellow; containing psoromic acid (major), 2'-O-demethylpsoromic acid (minor to trace), subpsoromic acid (trace).

7. *Leucodecton* A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3(5): 325 (1860).

Type species: *Leucodecton compunctum* (Ach.) A. Massal.

Thallus variously colored, smooth to uneven or minutely grainy, sometimes gall-forming, ecorticate or with loose (rarely dense) cortex; photobiont layer and medulla with (often columnar) clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded; disc usually covered by narrow pore, rarely partially exposed; margin entire to minutely lobulate, usually with split between thallus and proper margin (double margin), variously colored. Columella absent. Excipulum paraplectenchymatous, colorless to brown; periphysoids absent. Paraphyses unbranched. Ascospores 1–8/ascus, transversely septate to muriform, ellipsoid to oblong, with slightly thickened septa and rounded lumina, colorless to mostly brown, I– or young slightly I+ violet-blue (amyloid). Secondary chemistry: no substances or mostly stictic acid and satellites, rarely norstictic acid.

Notes: *Leucodecton* is an enigmatic genus as most species resemble the genus *Leptotrema* in many aspects, such as thallus morphology, apothecial type, excipulum structure, and ascospores (Frisch 2006). However, the two genera are not closely related: while *Leptotrema* and *Reimnitzia* form a clade sister to the *Ocellularia* clade, *Leucodecton* is well supported within the *Chapsa*-*Thelotrema* clade (Mangold *et al.* 2008a; Papong *et al.* 2009a; Rivas Plata & Lumbsch 2011a, b). This is surprising as it is the only lineage within this clade lacking periphysoids. On the other hand, the secondary chemistry of *Leucodecton* is well in line with *Chapsa* and *Thelotrema*, with stictic acid being the dominant component, and all three genera share the paraplectenchymatous excipulum and the often thick outer ascospore walls. Two species of *Leucodecton*, *L. glaucescens* and *L. occultum*, do resemble a minute *Chapsa* and *Thelotrema*, respectively, and both are phylogenetically at the base of the *Leucodecton* clade, suggesting that the *Leptotrema*-type morphology of other species, such as *Leucodecton phaeosporum* (Nyl.) Rivas Plata & Lücking (Rivas Plata *et al.* 2010a), is derived and evolved parallel to that of *Leptotrema* (Rivas Plata & Lumbsch 2011a).

7.1 *Leucodecton anamalaiense* (Patw. & C. R. Kulk.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 184)

Bas.: *Thelotrema anamalaiense* Patw. & C.R. Kulk., Norwegian Journal of Botany 24: 127 (1977)
=*Myriotrema anamalaiense* (Patw. & C.R. Kulk.) Hale, Mycotaxon 11 (1): 132 (1980)

Thallus pale tannish grey, c. 8 mm broad, smooth, continuous; cortex loosely organized, 10–18 μm , irregularly pored; algal layer 10–15 μm , medulla 30–50 μm with numerous crystals; apothecia immersed in the periderm, 0.3–0.5 mm diam., exciple partially free, usually visible as an inner ring

through the pore; pore round, 0.1-0.2 mm diam., depressed at maturity, white rimmed; hymenium 150-170 µm; spore colourless, muriform, 15-20 x 70-75 µm, 2-4 x 12-15 loculate, 2-4/ascus, l+ blue.

Secondary chemistry: Stictic and constrictic acids.

7.2 *Leucodecton compunctellum* (Nyl.) Frisch, in Frisch, Kalb & Grube, Biblioth. Lichenol. 92: 155 (2006)

Bas.: *Thelotrema compunctellum* Nyl., *Bull. Soc. Linn. Normandie*, sér. 2, 2: 77 (1868).

=*Leptotrema compunctellum* (Nyl.) Zahlbr., *Cat. Lich. Univ.* 2: 632 (1923).

=*Thelotrema monosporum* var. *subgemium* Nyl., *Bull. Soc. Linn. Normandie*, sér. 2, 2: 77 (1868).

=*Thelotrema subgemium* (Nyl.) Nyl., *Sert. Lich. Trop. Labuan Singapore* 5 (1891).

=*Thelotrema elachistoterum* Leight., *Trans. Linn. Soc. London* 27: 169 (1870).

=*Leptotrema elachistoterum* (Leight.) Patw. & C.Kulk., *Norweg. J. Bot.* 24: 128 (1977).

=*Myriotrema elachistoterum* (Leight.) Hale, *Mycotaxon* 11: 133 (1980).

=*Leucodecton elachistoterum* (Leight.) Frisch, in A.Frisch, K.Kalb & M.Grube, *Biblioth. Lichenol.* 92: 155 (2006).

=*Thelotrema reclusum* Kremp., in W.Nylander, *Bull. Soc. Linn. Normandie*, sér. 2, 7: 168 (1873).

=*Leptotrema reclusum* (Kremp.) Zahlbr., *Cat. Lich. Univ.* 2: 639 (1923).

=*Myriotrema reclusum* (Kremp.) Hale, *Mycotaxon* 11: 135 (1980).

=*Anthracotheceum oligosporum* Müll.Arg., *Flora* 71: 48 (1888).

=*Leptotrema oligosporum* (Müll.Arg.) Patw. & Makhija, *Bryologist* 83: 368 (1980).

=*Thelotrema microglaenoides* Vain., *J. Bot.* 34: 206 (1896).

=*Leptotrema microglaenoides* (Vain.) Zahlbr., *Cat. Lich. Univ.* 2: 637 (1923).

=*Leptotrema deceptum* Hale, *Smithsonian Contr. Bot.* 16: 39 (1974).

=*Myriotrema deceptum* (Hale) Hale, *Mycotaxon* 11: 133 (1980).

=*Myriotrema nuwarensense* Hale, *Bull. Brit. Mus. (Nat. Hist.) Bot.* 8: 289 (1981).

=*Leptotrema nuwarensense* (Hale) Nagarkar, Sethy & Patw., *Mycotaxon* 27: 74 (1986).

=*Leucodecton nuwarensense* (Hale) Frisch, in A.Frisch, K.Kalb & M.Grube, *Biblioth. Lichenol.* 92: 155 (2006).

=*Leucodecton biokense* Frisch, in A.Frisch, K.Kalb & M.Grube, *Biblioth. Lichenol.* 92: 152 (2006).

Thallus endophloeodal to epiphloeodal, to c. 500 µm thick, pale grey to greenish grey or pale yellowish brown, often with a grainy-speckled surface, dull to slightly glossy, smooth, continuous to rugose and/or minutely verruculose, rimose or not. Protocortex ±continuous, to c. 20 µm thick. Algal layer poorly to well developed, ±continuous; calcium oxalate crystals usually abundant, large, clustered, occasionally forming columns. Vegetative propagules not seen. Ascomata mostly inconspicuous, to c. 0.4 mm diam., ±rounded, perithecioid, rarely somewhat apothecioid, solitary, immersed to slightly emergent, then hemispherical with similar surface features to the thallus. Disc not visible from above. Pores usually minute, to c. 0.05 (–0.10) mm diam., ±rounded, with an entire margin; apex of proper exciple becoming visible, forming a fused or ±free inner pore margin,

incurved, bright-translucent to pale brownish, often thinning and appearing darker in older ascomata. Thalline rim margin thick, ±rounded, entire, small, incurved, concolorous with or brighter than the thallus. Proper exciple fused to apically free in older ascomata, thin to thick, hyaline to pale yellowish internally, pale orange-brown to yellowish brown or brownish marginally, non-amyloid or slightly amyloid at the base. Hymenium to c. 200 µm thick, strongly conglutinated; paraphyses ±bent to distinctly curly in apical parts, unbranched to sparingly branched towards the margins, with slightly thickened tips. Epithymenium indistinct or lacking, hyaline and without granules in perithecioid ascomata, thin and with greyish brown granules and small crystals in apothecioid ascomata. Asci 1–4-spored; tholus usually absent. Ascospores muriform, oblong to oblong-ellipsoidal, with rounded to narrowly rounded ends, becoming distinctly brown at late maturity, non-amyloid to faintly amyloid, 35–80 × 10–35 µm (in 2–4-spored asci), 60–130 × 10–35 µm (in 1-spored asci), with 10–45 × 3–12 locules; locules ±rounded to angular, mostly irregular; transverse septa thin but distinct, regular; ascospore wall thick, non-halonate; endospore thick. Pycnidia not seen.

Secondary chemistry: Thallus K⁺ yellow, C[–], P⁺ orange; containing constictic acid (major), stictic acid (major), cryptostictic acid (minor to trace), hypoconstictic acid (minor to trace), hypostictic acid (minor to trace).

7.3 *Leucodecton confusum* Papong, Lumbsch & Lücking

Mycobank # 809244

Differing from *Leucodecton expallescent* in the psoroplectenchymatous thallus cortex and smaller ascomata and ascospores.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven-verrucose, light greenish grey; prothallus absent. Thallus in section 100–150 µm thick, with prosoplectenchymatous cortex, 10–15 µm thick, and massive medulla, 80–140 µm thick, filled with large clusters of calcium oxalate crystals and numerous small, grey crystals; photobiont layer irregular, immersed in the medulla. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata, immersed-erumpent, with nearly complete thalline margin, 0.1–0.2 mm diam., 0.12–0.15 mm high; disc covered by 0.05–0.1 mm wide pore; proper margin distinct, separated from the thalline margin by a split (double margin), entire, visible as white ring within the pore; thalline margin entire, smooth, light greenish-grey to whitish. Excipulum entire, yellowish brown, 20–30 µm wide; laterally covered by algiferous, corticate thallus, 50–100 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–15 µm high, yellowish; hymenium 90–100 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 90–100 × 10–12 µm. Ascospores 8 per ascus, ellipsoid to fusiform or with distal end tapering and acute and proximal end rounded, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 10–

13 × 5–6 µm, 1.8–2.3 times as long as wide, hyaline, subdistoseptate with angular lumina, I+ violet-blue.

Secondary chemistry: Stictic, constictic, and acetylconstictic acids (medulla P+ orange-red, section with K+ persistently yellow efflux).

Etymology: The specific epithet refers to the confusing similarity with a *Thelotrema* species.

Distribution and Ecology: The new species was collected on Ko Phangan island in southern Thailand growing on bark of an unknown tree. The new species is known only from the type locality.

Notes: *Leucodecton confusum* at first glance can be mistaken for a *Thelotrema* species, but lacks the periphysoids characteristic of the latter. There are two other species of *Leucodecton* with similar ascomata and hyaline ascospores and stictic acid chemistry. *Leucodecton expallescent* (Nyl.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 184) has only a loose cortex and larger ascomata producing larger ascospores (10–13 × 5–6 µm). The recently described *L. inspersum* Rivas Plata & Lücking (2013: 24) agrees with *L. confusum* in the verrucose thallus with prosoplectenchymatous thallus, but has larger ascomata, an inspersed hymenium, and much larger ascospores (25–40 × 12–15 µm). The only similar species in *Thelotrema* is *T. myriocarpum* Fée (1825: 94) which, apart from the presence of periphysoids, can be distinguished by its smooth thallus, slightly larger ascomata, and larger ascospores.

8. *Melanotrema* Frisch

Melanotrema Frisch in Frisch & Kalb, Biblioth. Lichenol. 93: 382 (2006).

Type. *Melanotrema platystomum* (Mont.) Frisch.

Thallus light grey-olive to yellow-grey, with loose cortex or rarely ecorticate or with dense cortex. Apothecia erumpent to prominent, angular-rounded to elongate-lirellate; disc partially covered; margin entire to fissured or rarely lobulate, fused or free. Columella present, broad-stump-shaped to irregular or reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized (rarely brown); periphysoids absent. Paraphyses unbranched. Ascospores septate to submuriform, ellipsoid to oblong, with thick septa and lens-shaped lumina, colorless to mostly (dark) brown, I+ violet-blue (amyloid) in colorless or young ascospores.

Secondary chemistry: no substances or stictic acid or lichexanthone, rarely protocetraric or psoromic acid.

Notes: *Melanotrema* is one of the recent segregates of *Ocellularia* s.lat. established by Frisch & Kalb (2006). It is characterized by the usually loosely corticate thallus containing mostly stictic acid, lichexanthone, or no substances, and the irregularly chroodiscoid apothecia with broad stump-shaped to irregular-reticulate columella. Most similar are species in *Redingeria* and *Stegobolus* s.lat., such as *Redingeria glaucoglyphica* (Sipman) Frisch and *Stegobolus metaphoricus* (see below), and the morphological distinction of the three genera is not clearcut (Frisch & Kalb 2006).

Molecular data suggest that the core group of *Melanotrema*, comprising *M. meiospermum* and relatives, is genetically distinct from both *Redingeria* and *Stegobolus* s.lat. (Rivas Plata *et al.* 2012b), and morphologically intermediate species need to be sequenced to ascertain their correct phylogenetic relationships. For instance, the species described as *Leptotrema microsporum* morphologically best fits into *Melanotrema* but genetically belongs in *Redingeria*, as *R. microspora* (see below). Another genus to be easily confused with *Melanotrema* is *Clandestinotrema*, which includes species such as *C. stylothecium* (see above) that agree in thallus and apothecial morphology with *Melanotrema*, but have I-negative, tryptethelioid ascospores with diamond-shaped lumina (Rivas Plata & Lumbsch 2011a).

8.1 *Melanotrema melanophthalmum* (Homchant. & Coppins) Papong & Lumbsch, in Papong, Boonpragob, Mangold, Divakar & Lumbsch, *Lichenologist*, 42(2): 135 (2010)
= *Ocellularia melanophthalma* Homchant. & Coppins

Thallus crustose, continuous, diffuse, effuse, upper surface greenish grey, verruculose, minutely warted, verrucose, warted, apothecial, apothecioid – hymenial, immersed, innate, blackish or brownish, 0.7-1.5 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 8-12 septa, hyaline, 40-54 x 8-10 µm, I+ blue.

Secondary chemistry: protocetraric acid.

8.2 *Melanotrema platystomum* (Mont.) Frisch in Frisch & Kalb, *Biblioth. Lichenol.* 92: 397 (2006).

Bas.: *Thelotrema platystomum* Mont., *Ann. Sci. Nat. Bot., Ser. 2*, 19: 79 (1843).

= *Ocellularia platystoma* (Mont.) Zahlbr., *Cat. Lich. Univ.* 2: 598 (1923).

= *Ocellularia concolor* Meyen & Flotow, *Nova Acta Acad. Leopold.-Carol.* 19, Suppl.: 230 (1843).

Thallus light grey-olive, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1 mm diam.; disc partially covered by 0.3–0.5 mm wide pore, filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black, felty white-pruinose. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–9-septate, 16–25 x 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: no substances detected by TLC.

Notes: *Melanotrema platystomum* is identical to *M. meiospermum* in all characters except the persistently colorless ascospores. Hale (1978) reported the species from Panama as *Ocellularia concolor*.

9. *Myriotrema* Fée

Myriotrema Fée Écorc. xlix, 103 (1825); from the Greek myrios (innumerable) and trema (a hole), in reference to the numerous ascomata of some species.

Type species: *Myriotrema olivaceum* Fée.

Thallus endophloeodal to epiphloeodal, usually a shade of olive or grey, with greenish to yellowish or whitish tones. True cortex and protocortex present. Photobiont trentepohlioid. Prothallus thin to indistinct, pale to darkish brown. Ascomata $\pm$ rounded, rarely $\pm$ irregular, elongate or lirelliform, perithecioid or apothecioid, solitary to fused, rarely forming stroma-like structures. Proper exciple non-amyloid to amyloid basally, hyaline to pale yellowish, rarely orange internally, yellowish to reddish or greyish to brownish marginally, apically often darkened or covered by granules. Hymenium non-amyloid, usually not interspersed, rarely interspersed, conglutinated; paraphyses often with $\pm$ thickened apices, distinctly or irregularly septate, usually $\pm$ bent and interwoven, occasionally parallel, often $\pm$ richly branched; lateral paraphyses and true columella absent, but fused ascomata often with columella-like structures. Epihymenium hyaline, with or without granules. Asci (1–) 8-spored, clavate; wall and apex non-amyloid. Ascospores 1–2-seriate, transversely septate to submuriform or muriform, hyaline to brown, amyloid or non-amyloid, halonate or not. Conidiomata pycnidial, with fusiform or bacilliform conidia.

Secondary Chemistry: Orcinol depsidones or unknown compounds present, or secondary metabolites absent.

Notes: Recognised as a section of *Thelotrema* by Salisbury (1978), *Myriotrema* was reintroduced by Hale (1980, 1981) for taxa without lateral paraphyses and a non-carbonised proper exciple. Subsequently, Frisch et al. (2006) excluded several species on morphological grounds, partially supported by molecular data, and transferred them to other genera, e.g. *Fibrillithecis*, *Leptotrema*, *Leucodecton*, *Ocellularia* and *Stegobolus*. In its current circumscription, the genus is still considered to be heterogeneous, and further studies are required to elucidate phylogenetic relationships. *Fibrillithecis*, *Leptotrema* and *Leucodecton* are separated from *Myriotrema* principally by the structure of the proper exciple. However, the relationship with *Ocellularia* is less well understood, and the current placement of several taxa in *Ocellularia*, particularly those lacking a columella and having indistinct carbonisation, requires further study.

9.1 *Myriotrema clandestinum* (Fée) Hale

Type species: *Thelotrema clandestinum* Fée

Thallus endophloeodal to epiphloeodal, to c. 700 μ m thick, pale olive-green to yellowish olive, often with paler patches due to the discontinuous algal layer, $\pm$ glossy, smooth, continuous to rugose, non-rimose. True cortex usually continuous, slightly yellowish, to c. 50 μ m thick, formed by periclinial to somewhat irregular hyphae, rarely partly non-conglutinated and forming a protocortex. Algal layer well developed, continuous, but often partly thinning or patchily absent; calcium oxalate crystals sparse or absent, usually in scattered clusters; medulla distinct. Vegetative propagules not seen. Ascomata usually inconspicuous, to c. 0.3 mm diam., $\pm$ rounded, apothecioid, solitary or marginally fused, often clustered, forming dense aggregations, usually immersed, rarely

somewhat emergent and hemispherical. Disc often becoming partly visible from above, pale flesh-coloured, epruinose to slightly pruinose. Pores small, occasionally rather broad, to c. 0.1 (–0.2) mm diam., mostly ±rounded to somewhat irregular, entire, rarely slightly split; proper exciple not visible from above. Thalline rim margin usually ±thin, rarely thick, paler than the thallus, forming a narrow pale brownish to off-white ring, level with the thallus to somewhat raised; thalline rim incurved. Proper exciple fused, thin to thick, hyaline internally, pale yellowish to yellowish grey marginally, non-amyloid. Hymenium to c. 90 (–100) µm thick, not inspersed, strongly conglutinated; paraphyses straight to sparingly branched, distinctly septate, slightly interwoven, with faintly to markedly thickened tips; lateral paraphyses and columellar structures absent. Epihymenium hyaline, rarely with fine greyish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, sometimes with a single longitudinal septum, ellipsoidal to fusiform, mostly with narrowly rounded to subacute ends, hyaline, strongly amyloid, 10–25 (–27) × 6–8 µm, with 3–6 (–7) × 1 (–2) locules; locules ±rounded to somewhat acute, subglobose to lentiform or irregular, with similar or hemispherical to conical end cells; septa thin, sometimes slightly irregular; ascospore wall thick, occasionally with a thin halo; endospore thin to thick. Pycnidia in thalline warts, with brownish pores surrounded by a paler zone. Mature conidia not seen; according to Frisch et al. (2006) bacilliform, to c. 8 × 1.5 µm.

Secondary chemistry: Thallus K⁺ yellowish, C[–], P⁺ yellow; containing psoromic acid (major), subpsoromic acid (minor to trace). Mangold *et al.* (2009)

9.2 *Myriothema cf. classicum* Lücking

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire, fused, forming a broad yellow-white rim around the pore. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3 transverse and 0–1 longitudinal septa per segment, 15–20 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I⁺ violet-blue (amyloid).

Secondary chemistry: psoromic, subpsoromic and 2'-O-demethylpsoromic acids.

Notes: This new species differs from other species with submuriform ascospores and psoromic acid chiefly in apothecial morphology: *Myriotrema concretum* and *M. hartii* (see below) have prominent to sessile apothecia lacking a white rim and the excipulum is free in the latter species, which also produces isidia. *Myriotrema rugiferum* (Harm.) Hale shares the immersed apothecia with *M. classicum* but has a free excipulum (double margin) and also lacks the white rim characteristic of the new species. Most similar in apothecial anatomy is *M. clandestinum* (see above), which has transversely septate ascospores and also lacks a broad white rim around the

apothecial pore. The epithet was chosen because the apothecia of the new species resemble the whitewall tires of classic automobiles.

9.3 *Myriotheema polytrema* Hale, Bull. Brit. Mus. (Nat. Hist.), Bot. 8: 291 (1981)

Thallus endophloeodal to epiphloeodal, to c. 300 µm thick, pale olive to yellowish grey or greyish, occasionally with paler patches due to an uneven algal layer, glossy, smooth, continuous to slightly rugose, non-rimose. True cortex continuous, slightly yellowish, to c. 30 µm thick, consisting of periclinal to irregular hyphae. Algal layer well developed, continuous, but occasionally partly thinning or absent; calcium oxalate crystals abundant, small to large, clustered, rarely scattered; medulla sometimes distinct. Vegetative propagules not seen. Ascomata usually inconspicuous, to c. 0.35 mm diam., ±rounded, apotheciod, solitary to marginally or rarely entirely fused, often densely clustered, immersed. Disc often becoming partly visible from above, pale flesh-coloured, epruinose to slightly pruinose. Pores to c. 0.2 mm diam., ±rounded to somewhat irregular, entire, rarely slightly split; proper exciple not visible from above. Thalline rim margin thin, brighter than the thallus, forming a narrow to moderately broad fawn to off-white ring, level with the thallus to somewhat raised; thalline rim incurved. Proper exciple fused, thin, hyaline to pale yellowish internally, pale orange to yellowish brown marginally, sometimes greyish brown apically, non-amyloid. Hymenium to c. 70 µm thick, not inspersed, strongly conglutinated; paraphyses straight to slightly bent, ±irregular and distinctly septate, parallel to slightly interwoven, with thickened somewhat irregular tips; lateral paraphyses and columellar structures absent. Epihymenium hyaline, occasionally with fine greyish granules. Asci 8-spored; tholus initially thick, not visible at maturity. Ascospores transversely septate, oblong to ellipsoidal or somewhat fusiform, with ±rounded to narrowly rounded ends, hyaline, usually strongly amyloid, 10–18 (–22) × 6–8 µm, with 3 or 4 locules; locules mostly ±rounded, subglobose to oblong or slightly irregular; end cells having the same shape or hemispherical to conical; septa thin to thick, ±regular; ascospore wall thick, occasionally thinly halonate; endospore thick. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P+ yellowish to reddish; containing 2-hydroxy-hypoprotocetraric acid (major), convirensic acid (trace), 2-hydroxynornotatic acid (trace), hypoprotocetraric acid (trace).

10. *Nitidochapsa* Parnmen, Lücking & Lumbsch

Thallus dark olive green, 5–8 cm broad, shiny, continuous; cortex poorly developed to lacking; algal layer 10–15 µm, with numerous periderm and crystalline inclusions; apothecia dispersed; chroodiscoid, round to irregularly elongate, 1–2 mm wide, the thalline rim suberect, ascospore transversely septate, l–.

10.1 *Nitidochapsa leprieurii* (Mont.) Parnmen, Lücking & Lumbsch, Bryologist 116: 131 (2013)

=*Chapsa lepriurii* (Mont.) Frisch, in Frisch, Kalb & Grube, *Biblioth. Lichenol.* 92: 105 (2006)

Mangold *et al.* (2009); Parnmen *et al.* (2013a)

Thallus endophloeodal to epiphloeodal, to c. 300 µm thick, dark olive-green to olive-brown or pale yellowish brown, dull to waxy, smooth, continuous to slightly verrucose, non-rimose. True cortex ±continuous, to c. 30 µm thick, pale yellowish, consisting of periclinal to irregular hyphae. Algal layer continuous or discontinuous; calcium oxalate crystals abundant, mostly small. Vegetative propagules not seen. Ascomata conspicuous, to c. 1.7 (–2.0) mm diam., ±rounded to irregular, especially in fused ascomata, apothecioid to chroodiscoid in older ascomata, erumpent, solitary or fused, often in groups of 2–several, immersed. Disc occasionally not visible to more often partly visible from above, distinctly greyish-pruinose, sometimes covered with the same whitish cottony material as thalline rim. Proper exciple not visible from above, rarely becoming visible when partly detached, whitish; thalline rim thick, indistinctly split to entire, often appearing somewhat eroded, with a ±thick whitish cottony surface, occasionally with minute needle-like crystals, usually erect to recurved. Exciple fused to apically partly free, thin, colourless to pale yellowish internally to pale to medium orange or brownish marginally, apically densely covered with greyish granules. Hymenium to 110 µm thick, moderately conglutinated; paraphyses straight to slightly bent, parallel to slightly interwoven, the tips ±distinctly thickened, slightly irregular; lateral paraphyses conspicuous, to 35 µm long. Epihymenium hyaline, with greyish granules. Asci 8-spored; tholus initially thick, becoming thin. Ascospores transversely septate, rarely submuriform, oblong to ellipsoidal or somewhat clavate with rounded to narrowly rounded or, rarely, subacute ends, brown, distinctly amyloid, 9–25 (–28) × 6–8 (–11) µm, with 4–7 (–8) × 1 (–2) locules; locules ±rounded, subglobose to more often lentiform or oblong; end cells hemispherical, rarely conical; septa thin to thick, regular at maturity; ascospore wall thick, non-halonate; endospore thick.

Secondary chemistry: Thallus K–, C–, P–; no compounds detectable by TLC.

10.2 *Nitidochapsa aggregata* (Hale) Poengsungnoen, Lücking & Lumbsch

[Mycobank #809142]

=*Phaeotrema aggregatum* Hale, *Smithson. Contr. Bot.* 16: 29. 1974;

=*Thelotrema aggregatum* (Hale) Hale, *Mycotaxon* 11: 131. 1980;

=*Chapsa aggregata* (Hale) Sipman & Lücking in Rivas Plata *et al.*, *Lichenologist* 42: 182. 2010;

=*Pseudotopeliopsis aggregata* (Hale) Parnmen, Lücking & Lumbsch, *PLoS ONE* 7(12): e51392. 2012.

=*Thelotrema leucastrum* Tuck., *Proc. Amer. Acad. Arts* 6: 269. 1866.

Thallus smooth to uneven, oxalate crystals irregular, thallus cortex prosoplectenchymatous, ascomata aggregate, 0.5–1.0 mm diam., margin lobulate, columella colorless, excipulum colorless, periphysoid present, ascospores transversely septate, 7–9 septate, 8 per ascus, 10 × 25 µm, brown to dark brown, I+ weak or young I+ blue.

Secondary chemistry: Thallus K–, C–, P–; no compounds detectable by TLC.

11. *Ocellularia* G. Mey., Nebenst. Beschäft. Pflanzenk. 1: 327 (1825), nom. cons.; from the Latin ocellus (an eye), -ula (diminutive) and -aria (indicating possession), in reference to the appearance of the ascomata.

Type: *Ocellularia obturata* (Ach.) Spreng.

Thallus endophloeodal to epiphloeodal, usually a shade of olive or grey, with greenish to yellowish or whitish tones. True cortex or a protocortex present in epiphloeodal thalli. Photobiont trentepohlioid. Prothallus thin or indistinct, pale to rather dark brown. Ascomata $\pm$ rounded, perithecioid to apothecioid, rarely $\pm$ irregular or elongate, solitary to strongly fused, rarely forming stroma-like structures. Proper exciple non-amyloid to basally amyloid, brown to blackish brown or pale yellowish, rarely hyaline, apically often darkened or covered by granules. Hymenium non-amyloid, interspersed with oil droplets or small crystals, or clear, conglutinated; paraphyses unthickened or $\pm$ thickened at the apices, straight to $\pm$ bent, parallel or interwoven and branched; lateral paraphyses absent; columella absent or simple to complex and reticulate. Epihymenium hyaline to $\pm$ brownish, with or without granules. Asci 1–8-spored, clavate, non-amyloid. Ascospores 1–2-seriate, transversely septate to submuriform or muriform, hyaline to brown, halonate or not, amyloid or non-amyloid. Conidiomata pycnidial, with bacilliform, fusiform or oblong conidia.

Secondary chemistry: β -orcinol depsidones, orcinol depsidones or unknown compounds present, or secondary compounds absent.

Notes: Until recently, this genus was circumscribed to include thelotremataceous taxa that lacked lateral paraphyses and possessed a carbonised exciple. However, because excipular carbonisation is variable in this group, Frisch *et al.* (2006) included species with a simple columella, a proper exciple of prosoplectenchymatous cells and strongly amyloid ascospores, but also those with a hyaline exciple. Taxa lacking a columella and having an interspersed hymenium were segregated in *Ampliotrema*, while those with complex columellar structures were assigned to *Gyrotrema* Frisch, *Melanotrema*, *Redingeria* Frisch and *Stegobolus*. Molecular studies do not fully support some of the segregates (Frisch *et al.*, 2006; Mangold *et al.*, 2008). Taxa included in *Ampliotrema* and *Stegobolus* were nested within *Ocellularia*, and *Stegobolus* was also polyphyletic, suggesting that complex columellae evolved several times independently within the *Ocellularia* clade. Consequently, *Ampliotrema* and *Stegobolus* are regarded here as being synonyms of *Ocellularia*. The distinction between *Ocellularia* and *Myriotrema* is poorly understood; see the discussion under *Myriotrema*.

11.1 *Ocellularia albocincta* (Hale) Divakar & Mangold, Lichenologist 42: 135 (2010); *Myriotrema albocinctum* Hale, Bull. Brit. Mus. (Nat. Hist.), Bot., Ser. 8: 273 (1981).

Thallus light grey-olive, uneven-verrucose and often cracked, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc covered by 0.05–0.1 mm wide pore, flesh-colored; margin entire, yellow-white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 80–110 μ m high, clear; paraphyses unbranched. As-

cospores 8/ascus, 5–7-septate, 15–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, + violet (amyloid).

Secondary chemistry: no substances detected by TLC.

Notes: This is the only species of *Ocellularia* with an uncarbonized excipulum that lacks a columella and secondary substances and has small, transversely septate, colorless ascospores. In spite of the uncarbonized excipulum, the apothecial anatomy and morphology suggests close relationship with *O. papillata* and related species, rather than *Myriotrema* s.str. *Ocellularia papillata* chiefly differs in the dark brown excipulum and columella, whereas *O. barroensis* has prominent apothecia with irregular pseudocolumella. The most similar species is *O. rhicnoporoides* Homchan-tara & Coppins, which has an apically carbonized excipulum (Papong *et al.* 2010). The type material of *Myriotrema albocinctum* contains discordant pieces representing two different species, one with uncarbonized and one with apically carbonized excipulum, the latter corresponding to *O. rhicnoporoides*. We have therefore selected a piece with uncarbonized apothecia (already annotated by T. Matsumoto in 1996) as lectotype. The two collections cited below are remarkable for their ecological divergence: one is from an upper montane cloud forest at nearly 3000 m altitude, whereas the other is from lowland rain forest at sea level. Both collections agree in all important details, although *Sipman 46553* has larger, more abundant crystals in the thallus.

11.2 *Ocellularia allosporoides* (Nyl.) Patw. & C. Kulk.

Bas.: *Thelotrema allosporoides* Nyl., *Bull. Soc. Linn. Normandie*, sér. 2, 7: 167 (1873)

=*Leptotrema allosporoides* (Nyl.) Müll.Arg., *Bull. Herb. Boissier* 2, App. 1: 75 (1894).

=*Thelotrema apayoense* Vain., *Ann. Acad. Sci. Fenn., ser. A*, 15(6): 189 (1921);

=*Ocellularia apayoensis* (Vain.) Zahlbr., *Cat. Lich. Univ.* 2: 583 (1923).

=*Ocellularia groenhartii* Hale, *Mycotaxon* 3: 173 (1975)

Thallus endophloeodal to epiphloeodal, to c. 600 µm thick, pale greenish to yellowish green or pale olive, ±glossy, smooth, continuous to ±verruculose, mainly non-rimose. True cortex continuous, to c. 40 µm thick, yellowish, consisting of periclinal hyphae. Algal layer well developed, continuous; calcium oxalate crystals sparse to abundant, small and scattered, rarely clustered; distinct medulla often present at ascomatal margin. Vegetative propagules not seen. Ascomata ±conspicuous, to c. 1.5 mm diam., ±rounded, apothecioid, solitary to marginally fused, immersed, rarely strongly emergent, mostly hemispherical, occasionally somewhat flattened. Disc with the columella visible from above, distinctly pruinose, off-white to brownish, free, entire to slightly irregular, especially in older ascomata. Proper exciple not visible from above; thalline rim margin to 0.7 mm diam., ±rounded, entire, thick, concolorous with the thallus to off-white or brownish; thalline rim incurved. Proper exciple fused, moderately thin to thick, yellowish brown to pale or dark brownish, usually only indistinctly carbonised, rarely strongly carbonised, sometimes amyloid at the base. Hymenium to c. 250 µm thick, not inspersed, markedly conglutinated; paraphyses ±bent to curly, especially towards the unthickened to slightly thickened tips, parallel to slightly interwoven,

unbranched; columellar structures well-developed in mature ascomata, to c. 500 µm wide, entire, rarely complex, usually brown to slightly carbonised, rarely strongly carbonised, usually covered with a ±thick layer of greyish granules. Epihymenium hyaline, with greyish or brownish granules. Asci 4–8-spored; distinct tholus absent; lateral ascus wall rather thick in immature stages, becoming moderately thin. Ascospores transversely septate, oblong to oblong-fusiform, with ±rounded to subacute or acute ends, hyaline, strongly amyloid, 50–120 (–130) × 10–18 µm, with 8–20 (–22) locules; locules ±rounded to slightly angular, oblong to lentiform or ±irregular; end cells similar or subglobose, hemispherical to conical; septa thick, regular; ascospore wall thick, non-halonate at maturity; endospore thick. Pycnidia immersed, with a darkened pore. Conidia fusiform, to 5 × 1 µm.

Secondary chemistry: Thallus K–, C–, P–; containing norisonotatic acid (major), norsubnotatic acid (major to absent).

11.3 *Ocellularia ascidioidea* Hale, Bull. Brit. Mus. Nat. Hist., Bot. Ser., 8: 300 (1981).

Thallus light grey-olive, minutely verrucose, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–0.9 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, grey; margin entire, yellow-white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 15–20 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ brown-violet (amyloid).

Secondary chemistry: no substances detected by TLC.

Notes: This species belongs in a difficult group of taxa with small, colorless, transversely septate ascospores. It is characterized by its lack of secondary substances and the comparatively large, prominent apothecia. Most similar are *O. barroensis* and *O. landronii* (see below); the first differs in the uncarbonized excipulum and columella and the second in the black columella and proper margin and the often fissured thalline margin. Hale (1981) compared the species to *O. papillata* (see below), but that species has smaller, erumpent apothecia and a brown excipulum and columella.

11.4 *Ocellularia brunneospora* Homchantara & Coppins, Lichenologist, 34(2): 119 (2002)

Yoshimura, 1978; Homchantara & Coppins, 2002), Papong et al., 2010

Thallus crustose, continuous, diffuse, effuse, upper surface greyish, smooth, plane, apothecial, apothecioid – hymenial, isubsessile, subimmersed, adnate, semi-immersed, emergent, blackish, with pruinose, 0.65–0.7 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 3–5 septa, ellipsoidal, brown, 11–14 × 6–7 µm, I+ blue.

Secondary chemistry: norisonotatic acid, norsubnotatic acid.

Notes: This species is characterized by small, transversely septate ascospores and the presence of the norisonotatic chemosyndrome. It agrees chemically with *O. chonestoma* (Leight.) Zahlbr. but this species differs in having larger ascospores. Other *Ocellularia* spp. containing norisonotatic and norsubnotatic acids (formerly named Chonestoma unknowns) include *O. allosporoides* (Nyl.) Patw. & C. Kulk. and *O. baileyi* Müll. Arg. (Mangold *et al.* 2009). Both of these species have larger hyaline ascospores (50–130 and 18–40 µm, respectively). (Papong *et al.*, 2010)

11.5 *Ocellularia cavata* (Ach.) Müll.Arg., Flora 65: 499 (1882).

Bas.: *Ocellularia cavata* (Ach.) Müll. Arg., Flora 64: 499 (1882).

=*Thelotrema cavatum* Ach., Kongl. Vetensk. Akad. Nya Handl. 33: 92 (1812).

=*Thelotrema obturatum* Ach., Nova Acta Reg. Acad. Sci. Holmiae 33: 92 (1812).

=*Ocellularia obturata* (Ach.) Spreng., Linn. Syst. Veg., Edit. 16, 4(1): 242 (1827).

=*Thelotrema cavatum* var. *obturatum* (Ach.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1858).

=*Ocellularia cavata* var. *obturata* (Ach.) Redinger, Ark. Bot. 28A(8): 39 (1936).

=*Ascidium cinchonarum* Fée, Méth. Lichénogr. Gen.: Tab. 1, fig. 22 (1824) ('1825'); Essai Crypt. Exot.: 96 (1825).

=*Ocellularia cinchonarum* (Fée) Spreng., Linn. Syst. Veget., Edit. 16, 4(1): 242 (1827).

=*Thelotrema cinchonarum* (Fée) Vain., Étud. Lich. Brésil 2: 82 (1890).

=*Ascidium cinchonarum* f. *intermedium* Nyl., Ann. Sci. Nat., Bot., Sér. 5, 7: 319 (1867).

=*Thelotrema inscalpens* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 319 (1867). Lectotype (Mangold *et al.* 2009: 655).

=*Ocellularia lindigiana* Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 29(8): 9 (1887).

=*Thelotrema lindigianum* (Müll. Arg.) Harm., Bull. Séanc. Soc. Sci. Nancy, Sér. 3, 13: 48 (1912).

=*Ascidium xanthostromizum* Nyl., Sert. Lich. Trop. Labuan Singapore: 20 (1891).

=*Ocellularia xanthostromiza* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 604 (1923).

=*Thelotrema chrysostroma* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 187 (1921).

Thallus grey-olive, smooth to uneven, with dense, paraplectenchymatous cortex; medulla pale orange; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black columella; margin entire, black, laterally covered by often eroding thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–15-septate, 25–70 x 7–12 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: cinchonarum unknowns, medulla with pale orange (K+ red) pigment.

Notes: *Ocellularia cavata* is the generic type of *Ocellularia*. This and related species have a pigmented medulla, often in combination with cinchonarum unknown or other rare secondary substances, rather conspicuous, prominent apothecia with well-developed columella, medium-sized to large, mostly transversely septate ascospores, and a more or less paraplectenchymatous

cortex (Rivas Plata *et al.* 2012b). In many species the apothecial margin erodes to expose the pigmented medulla. Since this phenomenon is most commonly observed in this group, one might assume a functional role of exposing the pigment to potential dispersal agents such as ants. *Ocellularia cavata* has an extensive synonymy (Hale 1974, 1978; Frisch 2006; Mangold *et al.* 2009) and the circumscription of this species is somewhat unclear. The synonyms listed here are those where conspecificity with the type of *Thelotrema cavatum* has been definitely established by us.

11.6 *Ocellularia cerebriformis* Papong, Lücking & Lumbsch

Differing from *Ocellularia thelotremoides* in the folded, brain-like thallus surface and the large, prominent ascomata with thick, bulging margins, as well as the non-carbonized, complex columella.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface conspicuously folded, resembling the surface of a brain, light grey-green, with numerous minute, white papillae, medulla white; prothallus absent. Thallus in section 100–150 µm thick, with prosoplectenchymatous cortex, 10–15 µm thick, photobiont layer 30–50 µm thick, and thick medulla, 80–100 thick, with large clusters of calcium oxalate crystals; both photobiont layer and medulla also with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata rounded, erumpent to prominent, with complete thalline margin, 0.8–1.2 mm diam., 0.3–0.5 mm high; disc covered by 0.2–0.5 mm wide pore, with white-tipped, irregular columella visible but deeply immersed; proper margin distinct, entire, visible as thin, whitish to pale brown rim around the pore; thalline margin entire, smooth to uneven, bulging, light grey-green. Excipulum entire, yellowish, 30–70 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, irregular, divided into several, partially radiating, thin strands, light brown, individual strands 50–100 µm wide and 150–170 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 130–150 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 120–130 × 15–20 µm. Ascospores 8 per ascus, ellipsoid, muriform with 5 transverse and 1–2 longitudinal septa per segment, 18–25 × 9–12 µm, 1.8–2.3 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry: Protocetraric and virensic acids (medulla P+ orange-red).

Etymology: The specific epithet refers to the brain-like surface of the thallus (Latin: *cerebrum* = brain).

Distribution and Ecology: The new species was collected in north-eastern Thailand in a dry dipterocarp forest, growing on the trunks of *Shorea siamensis* in the understory. It is only known from the type locality.

Notes: The new species resembles *Ocellularia thelotremoides* (Leight.) Zahlbruckner (1924: 603), in the small, (sub-)muriform ascospores and the protocetraric acid chemistry. The lat-

ter, however, has a smooth to uneven thallus, a carbonized, finger-like columella, and longer ascospores. Anatomically most similar is the African *O. cameroonensis* Frisch in Frisch *et al.* (2006: 203), which agrees in the uncarbonized, irregular columella, but has smaller ascomata with thinner margins and transversely septate ascospores. *Ocellularia subsimilis* (Hale) Hale (1980: 38) also has (sub-)muriform ascospores and protocetratic acid, as well as uncarbonized columella and excipulum, but its thallus is verrucose, not folded, and its ascomata are much smaller (to 0.5 mm wide) with narrow pore and finger-like columella.

11. 7 *Ocellularia croceoisi* Sipman, Tropical Bryology 6: 8 (1992)

[MB#359897]

Thallus crustose, continuous, diffuse, effuse, upper surface brownish grey, smooth, plane, with isidia, apothecial, apothecioid – hymenial, sessile, subimmersed, adnate, semi-immersed, emergent, sessile, superficial, greenish, with pruinose, 0.5-1.0 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 11-15 septa, hyaline, 35-50 x 7-8 μ m, I+ blue.

Secondary chemistry: unknown/unidentified compounds.

11.8 *Ocellularia diacida* Hale, Mycotaxon 7: 378 (1978)

Thallus endophloeodal to epiphloeodal, to c. 200 μ m thick, greyish to greenish grey or pale olive, dull to glossy, smooth, continuous to verrucose or verruculose, rimose or not; verrucae near ascomata often eroded, exposing the white to yellowish or pale orange medulla. True cortex discontinuous, to c. 20 μ m thick, formed by irregular hyphae, in part not conglutinated and forming a protocortex. Algal layer well developed, continuous; calcium oxalate crystals moderately large and scattered. Vegetative propagules not seen. Ascomata $\pm$ inconspicuous, to c. 0.8 mm diam., $\pm$ rounded, but usually irregular, apothecioid when mature, solitary to marginally fused, immersed to moderately emergent, then verrucose-hemispherical to urceolate. Disc with the columella visible from above in mature ascomata, entire, free, slightly pruinose, rather dark grey. Pores formed by the thalline rim margin, to c. 0.3 mm diam., $\pm$ rounded to irregular, entire to split or evanescent, then the apex of the proper exciple becoming visible from above as a brownish line, moderately thin to moderately thick, concolorous with the thallus; thalline rim incurved. Proper exciple fused, pale to medium brown internally, dark brown to distinctly carbonised marginally and towards the tips, usually strongly amyloid at the base. Hymenium to c. 130 μ m thick, not interspersed, distinctly conglutinated; paraphyses slightly bent, $\pm$ interwoven, unbranched, with moderately thickened tips; columellar structures moderately developed, to 200 μ m wide, entire, brownish to carbonised in the upper parts, $\pm$ covered with greyish granules. Epihymenium brownish, with greyish or brownish granules. Asci 8-spored; tholus initially thick, moderately thin when mature. Ascospores transversely septate, oblong to fusiform, with $\pm$ rounded to subacute ends, hyaline, occasionally slightly brownish with age, distinctly amyloid, 15–40 x 6–9 μ m, with 4–12 locules; locules $\pm$ rounded to

slightly angular, oblong to ±lenticiform, with hemispherical to conical end cells; septa moderately thick; ascospore wall and endospore moderately thick; wall non-hyaline. Pycnidia not seen. Secondary chemistry: Thallus K⁺ orange, C⁻, P⁻; containing hirtifruictic acid (major), conhirtifruictic acid (major), the main 'cinchonarum unknown' (major to trace), and the 'cinchonarum unknown' accessory compound 'spot 1' (trace).

11.9 *Ocellularia diospyrosis* Homchantara & Coppins, Lichenologist, 34(2): 123 (2002)

(Yoshimura, 1978; Homchantara & Coppins, 2002), Papong et al., 2010

Thallus crustose, continuous, diffuse, effuse, upper surface brownish green (olivaceous, olive green), smooth, plane, apothecial, apothecioid – hymenial, immersed, innate, blackish, 0.6-0.65 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 11-22 septa, hyaline, 75-164 × 11-20 µm, I⁺ blue.

Secondary chemistry: constictic acid, stictic acid.

Notes: This species is characterized by large and hyaline, transversely septate ascospores, a simple columella and by the presence of the stictic acid chemosyndrome. It is superficially similar to *O. pyrenuloides* Zahlbr., which, however is readily distinguished by smaller ascospores with less loculi (18–24 × 6–7 µm with 5–6 loculi). The South African *O. henatomma* (Ach.) Müll. Arg. differs in having longer ascospores and the presence of the hypoprotocetraric acid chemosyndrome (Frisch et al. 2006). alfa-acetylconstictic was found as accessory substance.

11.10 *Ocellularia dolichotata* (Nyl.) Zahlbr., Catalogus Lichenum Universalis 2: 589

(1923)

[MB#395996]

Bas.: *Thelotrema dolichotatum* Nyl., Sertum Lich. Trop. Labuan Sing.: 19 (1891)

=*Thelotrema bataanum* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 188 (1921)

=*Ocellularia bataana* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 583 (1923)

=*Thelotrema siamense* Vain., Hedwigia 46: 175 (1907)

=*Ocellularia siamensis* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 600 (1923)

Thallus light grey-green-yellow, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–1.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thick thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 300–400 µm high, clear; paraphyses unbranched but laterally anastomosing. Ascospores single, 17–27-septate, 180–250 × 20–30 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I⁺ violet-blue (amyloid).

Secondary chemistry: no substances detected by TLC.

Notes: *Ocellularia dolichotata* is a unique species easily recognized by the columellate, carbonized apothecia, large multiseptate ascospores, and lack of lichen substances. Most similar is *Ocellularia allospora* (Nyl.) Zahlbr. which has brown, bicaudate ascospores.

11.11 *Ocellularia exigua* Müll. Arg., Hedwigia 31: 284 (1892)

[MB#396007]

Thallus crustose, continuous, diffuse, effuse, olivaceous, verrucose, greenish grey, apothecia immersed, with collumela emergent, 0.5-0.7 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 6-10 septa, hyaline, 26-30 x 7-8 µm, I+ blue.

Secondary chemistry: no substances detected by TLC.

11.12 *Ocellularia flavescens* Homchantara & Coppins, Lichenologist, 34(2): 123 (2002)

(Yoshimura, 1978; Homchantara & Coppins, 2002), Papong et al., 2010

Thallus crustose, continuous, diffuse, effuse, upper surface whitish grey, smooth, plane, apothecial, apothecioid – hymenial, immersed, innate, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.1-0.4 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores muriform, ellipsoidal, hyaline, 12.5-20 x 7-11 µm, I+ blue.

Secondary chemistry: lichexanthone.

Notes: This species is readily recognized by the presence of lichexanthone, which is rare in thelotremoid lichens. Similar species containing lichexanthone include *Ocellularia metaphorica* (Nyl.) Hale, *Melanotrema astro-lucens* (Sipman) A. Frisch and *M. lirelliforme* (Tuck.) A. Frisch. The first differs in having a reticulate columella and brown, ornamented ascospores (Frisch et al. 2006), while the two *Melanotrema* species are distinguished by having brown, transversely septate ascospores.

11.13 *Ocellularia flavoperforata* Lücking, in Sipman et al., Phytotaxa 55: 1-124 (2012)

MycoBank #800084

Differing from *Ocellularia perforata* in the pale yellow medullary pigment.

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; medulla pale yellow; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black columella; margin entire, red-brown, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, red-brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–25 x 6–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: hypoprotocetraric and 4-O- demethylnotatic acids (exposed medulla P– but masked by pigment reaction; section K– but masked by pigment reaction; TLC!), medulla with pale yellow (K+ red) pigment.

Notes: This new species is identical to *Ocellularia perforata* in all aspects but differs in the pale yellow medulla. This is the first pigmented species known in the *O. papillata* group.

11.14 *Ocellularia fumosa* (Ach.) Müller (1887: 7)

Bas.: *Thelotrema fumosum* Ach., Kongl. Vetensk. Acad. Nya Handl. 33: 91 (1812).

=*Ocellularia xantholeuca* Müll.Arg., Hedwigia 30: 51 (1891).

=*Ocellularia rimosa* Hale, Smithsonian Contr. Bot. 16: 27 (1974).

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale greenish grey to olive or brownish, dull to slightly glossy, smooth, rarely continuous to usually ±verrucose, often distinctly rimose. True cortex discontinuous, to c. 20 µm thick, formed by irregular hyphae, in parts not conglutinated and forming a protocortex. Algal layer well developed, continuous; calcium oxalate crystals moderately large, scattered. Vegetative propagules not seen. Ascomata ±inconspicuous, to c. 0.8 mm diam., ±rounded to more often irregular, apothecioid when mature, solitary to marginally fused, immersed to rather emergent, then verrucose-hemispherical to urceolate. Disc with the columella visible from above, entire, free, slightly pruinose, dark grey. Pores formed by the thalline rim margin, to c. 0.4 mm diam., ±irregular, mostly split or eroded, then the apex of the proper exciple becoming visible from above as a brownish to dark grey line, moderately thick, concolorous with the thallus or brighter; thalline rim incurved. Proper exciple fused, moderately thin to moderately thick, pale to medium brown internally, dark brown to carbonised marginally and towards the tips, usually distinctly amyloid at the base. Hymenium to c. 150 µm thick, densely inspersed, distinctly conglutinated; paraphyses slightly bent, ±interwoven, unbranched, with moderately thickened tips; columellar structures moderately well developed, to 200 µm wide, entire, the upper parts brownish to carbonised, ±covered with greyish granules. Epihymenium brownish, with greyish or brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, fusiform to oblong-fusiform, rarely clavate, with narrowly rounded to subacute ends, hyaline, distinctly amyloid, 25–40 × 7–10 µm, with 6–12 (–13) locules; locules ±rounded to slightly angular, ±lenticiform, with hemispherical to conical end cells; septa moderately thick, regular; ascospore wall moderately thick, non-halonate; endospore moderately thick. Pycnidia not seen.

Secondary chemistry: Strain I: Thallus K–, C–, P–; no compounds detectable by TLC. Strain II: Thallus K+ orange, C–, P–; containing hirtifructic acid (major), conhirtifructic acid (major) acid, the main ‘cinchonarum unknown’ (major to trace), the ‘cinchonarum unknown’ accessory compound ‘spot 3’ (minor to trace).

11.15 *Ocellularia inthanonensis* Homchantara & Coppins, Lichenologist, 34(2): 123 (2002)

(Yoshimura, 1978; Homchantara & Coppins, 2002), Papong et al., 2010

Thallus crustose, continuous, diffuse, effuse, cracked, fissured, fractured, rimose, upper surface whitish grey, rugose, plicate, folded, pustulate, faveolate, wrinkled, apothecial, apothecioid – hymenial, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.8-1.0 mm diam., paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores muriform, narrowly ellipsoidal, hyaline, 134-265 x 22.5-37 µm, I+ blue.

Secondary chemistry: hypoprotocetraric acid, 2-hydroxy-hypoprotocetraric acid.

Notes: This species is characterized by 1-spored asci, large, muriform, hyaline ascospores, eolumellate ascomata, and the presence of the (newly identified) 2-hydroxy-hypoprotocetraric and hypoprotocetraric acids. Similar species include *O. arecae* (Vain.) Hale and *O. eumorpha* (Stirt.) Hale. The latter has 1–2-spored asci, the ascospores turn brown when mature, and it contains conviresenic acid as a major constituent in addition to hypoprotocetraric acid. *Ocellularia arecae* differs in having a columella.

11.16 *Ocellularia interponenda* (Nyl.) Hale, Mycotaxon 11 (1): 137 (1980)

Thallus crustose, continuous, diffuse, effuse, upper surface whitish grey, smooth, plane, apothecia immersed, innate, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.5-1.4 mm diam., ostiole margin thick, pale to pale yellow, carbonized collumela, prosoplectenchymatous exipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores muriform, ellipsoidal, hyaline, 55-75 x 15-25 µm, I+ blue, 3-6/ascus.

Secondary chemistry: salazinic acid.

Notes: *O. interponenda* can be recognised by ostiole margin thick and pale to pale yellow, also with salazinic acid.

11.17 *Ocellularia khuntanensis* (Homchantara & Coppins) Lumbsch & Papong, in Pa-

pong, Boonpragob, Mangold, Divakar & Lumbsch, Lichenologist, 42(2): 132 (2010)

Bas.: *Myriotrema khuntanense* Homchantara & Coppins Yoshimura, 1978; Homchantara & Coppins, 2002), Papong et al., 2010

Thallus crustose, continuous, diffuse, effuse, upper surface whitish grey, smooth, plane, apothecia immersed, innate, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.5-1.0 mm diam., ostiole pale, with an only apically carbonized exciple, reticulate columella, prosoplectenchymatous exipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, ellipsoidal, hyaline, I+ blue, 8/ascus.

Secondary chemistry: 2'-O-demethylpsoromic and subpsoromic acids.

Notes: The size of the ascospores is similar to that of *Ocellularia auberiana* (Mont.) Hale, but this species differs by the presence of a reticulate columella. Another similar species is *O. minutula* Hale, which, however, is readily distinguished by its smaller ascospores (Hale 1978b). Accessory substances, 2'-O-demethylpsoromic and subpsoromic acids were found.

11.18 *Ocellularia kohangangensis* Papong, Mangold & Lücking, in Papong *et al.*, Phytotaxa 189(1): 232-244 (2014)

Mycobank 809246

Distinguished by the combination of partially columellate ascomata, broad, brown, submuriform ascospores, and the cinchonarum unknown chemosyndrome.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven, silvery grey and glossy, medulla white; prothallus absent. Thallus in section 80–100 µm thick, with prosoplectenchymatous cortex, 5–10 µm thick, photobiont layer 20–30 µm thick, and medulla 50–60 µm thick, with clusters of calcium oxalate crystals and numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–11 × 6–10 µm. Ascomata rounded, erumpent, with nearly complete thalline margin, 0.4–0.6 mm diam., 0.2–0.3 mm high; disc covered by 0.1–0.2 mm wide pore, sometimes filled by black-tipped columella; proper margin distinct, entire, visible as whitish to pale yellowish rim around the pore, sometimes becoming annulate; thalline margin entire, smooth to uneven, glossy silvery grey. Excipulum entire, carbonized, 30–50 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 100–150 µm thick; columella present in some ascomata, in others absent, finger-like, carbonized, up to 150 µm wide and 150–180 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 120–130 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical, 110–120 × 15–20 µm. Ascospores 8 per ascus, uniseriate, broadly oval, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 15–20 × 10–12 µm, 1.4–1.8 times as long as wide, brown when mature, distoseptate with lens-shaped to irregular lumina, I+ violet-blue when young.

Secondary chemistry: Two lower cinchonarum unknowns (medulla and section C–, K–, P–).

Etymology: The specific epithet refers to the type locality.

Distribution and Ecology: The new species was collected on an island in southern Thailand, growing on bark in the understory of a secondary forest. It is known only from the type locality.

Notes: This new species does not seem to have any close relative in the family. Currently, no species is known with this combination of ascospore type and chemistry. *Rhabdodiscus submersus* (Müll. Arg.) Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1176) agrees in chemistry and the carbonized, columellate ascomata, but its ascospores are hyaline and transversely septate, and its ascomata feature a broad, complex columella. *Ocellularia exigua* Müller (1892: 284) is superficially similar to the new species in having a narrow columella, but differs also by its hyaline, transversely septate ascospores.

11.19 *Ocellularia krathingensis* Homchantara & Coppins, Lichenologist, 34(2): 125 (2002)
Yoshimura, 1978; Homchantara & Coppins, 2002), Papong *et al.*, 2010

Thallus crustose, continuous, diffuse, effuse, upper surface greenish grey, verruculose, minutely warted, apothecia immersed, innate, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.35-0.4 mm diam., ostiole pale, with an only apically carbonised exciple, carbonised columella, prosoplectenchymatous excipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 7-10 septa, narrowly ellipsoidal, hyaline, 18.5-27 × 5.5-8.5 µm, I+ blue, 8/ascus.

Secondary chemistry: no substance detected by TLC.

Notes: *Ocellularia krathingensis* can be recognized by the combination of ascomata with an only apically carbonized exciple and a complex, carbonized columella, 8-spored asci with hyaline, amyloid, transversely septate ascospores and the lack of secondary metabolites.

11.20 *Ocellularia laeviusculoides* Sipman & Lücking, The Lichenologist 34 (2): 125 (2002) [MB#475970]

Differing from *Ocellularia papillata* in the pale brown excipulum.

Thallus light green-grey, smooth, with dense, prosoplectenchymatous cortex without internal splitting; photobiont layer and medulla with scattered clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded, 0.3–0.6 mm diam.; disc covered by 0.2–0.4 mm wide pore, partially filled by brown-black, white-pruinose columella; margin entire, white to pale brown, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous (pale) brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–9-septate, 20–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ dark violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Notes: *Ocellularia laeviusculoides* is here segregated from *O. papillata* s.str., with which it shares the absence of lichen substances, presence of a carbonized columella and small, colorless, amyloid ascospores. It differs by the uncarbonized excipulum, which shows in abraded margins as a pale brown rather than dark brown ring, the ascocarps remaining mostly immersed, and the smoother thallus. The species is reminiscent of *Myriotrema laeviusculum*, but that taxon has protocetraric acid, an uncarbonized pseudocolumella, brown, muriform ascospores, and columnar crystals in the thallus.

11.21 *Ocellularia massalongoi* (Mont.) Hale, Mycotaxon 11: 137 (1980)

Bas.: *Ascidium massalongoi* Mont., Ann. Sci. Nat., Bot., sér. 4, 14: 174 (1860).

=*Thelotrema massalongoi* (Mont.) Zahlbr., Cat. Lich. Univ. 2: 624 (1923).

=*Ascidium pachystomum* Leight., Trans. Linn. Soc. London 27: 171 (1869)

=*Thelotrema pachystomum* (Leight.) Müll.Arg., Flora 74: 112 (1891)

=*Thelotrema monobactrium* var. *endoleuca* Vain., Ann. Acad. Sci. Fenn., ser. A, 15(6): 178 (1921).

=*Thelotrema monobactrium* var. *endorhoda* Vain., Ann. Acad. Sci. Fenn., ser. A, 15(6): 178 (1921).

=*Thelotrema monobactrium* var. *geminipara* Vain., Ann. Acad. Sci. Fenn., ser. A, 15(6): 178 (1921).

Thallus endophloeodal to epiphloeodal, to c. 100 µm thick, olive to pale brownish green, sometimes with reddish spots, glossy, smooth, continuous to slightly verrucose, non-rimose. True cortex hyaline to slightly yellowish, to c. 30 µm thick, consisting of periclinal hyphae. Algal layer well developed, continuous; calcium oxalate crystals large and clustered. Vegetative propagules not seen. Ascomata conspicuous, to c. 1.8 mm diam., ±rounded to slightly irregular, perithecioid, solitary, rarely marginally fused, distinctly emergent, occasionally slightly verrucose, hemispherical to urceolate. Disc not visible from above, in older stages the pores filled with the columella tip, ±pruinose, off-white to pale brownish, free, entire. Proper exciple not visible from above; thalline rim margin small to moderately broad, opening late, to c. 0.3 mm diam., ±rounded, entire to slightly eroded, ±raised and funnel-shaped to annulate, off-white to pale brownish, often slightly pruinose internally; thalline rim incurved. Proper exciple fused, moderately thin to moderately thick, dark brown to carbonised, non-amyloid. Hymenium to c. 500 µm thick, not interspersed, strongly conglutinated; paraphyses thin, bent to slightly curly distally, slightly interwoven, unbranched to sparingly branched towards the margins and columella, with moderately thickened tips; columellar structures well developed, to c. 250 µm wide, entire, conical, with a narrowly rounded tip, carbonised, covered with greyish or brownish granules. Epihymenium hyaline, with greyish or brownish granules. Asci 1 (–2)-spored; tholus initially thick, thin when mature. Ascospores muriform, oblong-ellipsoidal, often slightly irregular, with ±rounded to narrowly rounded ends, hyaline, distinctly amyloid, 170–250 × 35–45 µm, with numerous locules; locules ±rounded to ±angular, subglobose to irregular; transverse septa indistinct and irregular; ascospore wall and endospore initially thick, becoming thin; wall non-halonate. Pycnidia not seen.

Secondary chemistry: Thallus K⁺ yellow → red, C[–], P⁺ orange; containing salazinic acid (major).

11.22 *Ocellularia microstoma* (Müll. Arg.) Hale, in Mangold, Elix & Lumbsch, Flora of Australia (Melbourne) 57: 653–659 (2009)

Bas.: *Thelotrema microstomum* Müll.Arg., Flora 74: 113 (1891).

=*Myriotrema microstomum* Müll. Arg.

=*Ocellularia kansriae* Homchantara & Coppins, Homchantara & Coppins, 2002

=*Ocellularia peremergens* Homchantara & Coppins, Homchantara & Coppins, 2002

Thallus endophloeodal to epiphloeodal, to c. 600 µm thick, pale greenish grey to yellowish grey or olive, ±glossy, smooth, continuous to ±verrucose, rimose or not; verrucae near ascomata often eroded, exposing the white medulla. True cortex ±continuous, to c. 30 µm thick, formed by irregular to periclinal hyphae. Algal layer well developed, continuous; calcium oxalate crystals large and clustered. Vegetative propagules not seen. Ascomata conspicuous, to c. 1.5 mm diam., ±rounded to irregular, perithecioid to indistinctly apothecioid, solitary to marginally fused, ±emergent, often verrucose, usually depressed-urceolate. Disc not visible from above. Pores formed by the thalline rim margin, to c. 0.1 mm diam., ±rounded, moderately thick, depressed to distinctly annulate, en-

tire or eroded, then the apex of the proper exciple becoming visible as a brownish line; thalline rim incurved. Proper exciple fused, moderately thin to moderately thick above, yellowish brown to brownish internally and in the lower parts, usually dark brown or, rarely, carbonised marginally and distally, distinctly prosoplectenchymatous, occasionally amyloid at the base. Hymenium to c. 500 μm thick, not inspersed, moderately conglutinated; paraphyses $\pm$ bent to curly towards the tips, parallel to slightly interwoven, unbranched, with slightly thickened tips; columellar structures absent. Epihymenium hyaline, without granules. Asci 1-spored; tholus absent; lateral walls initially thick, becoming thin. Ascospores muriform, oblong-ellipsoidal to oblong-fusiform, often $\pm$ irregular, with $\pm$ rounded to subacute ends, hyaline to yellowish or becoming pale greyish brown, strongly amyloid, 150–300 (–330) $\times$ 30–60 μm , with numerous locules; locules $\pm$ angular, subglobose to irregular; transverse septa thin, distinct and regular; ascospore wall initially thick, non-halonate; endospore initially thick. Pycnidia not seen.

Secondary chemistry: Thallus K+ yellowish brown, C–, P+ orange-red; containing protocetraric acid (major), fumarprotocetraric acid (major to trace), conprotocetraric acid (minor to trace), virensic acid (trace).

Notes: This species is characterized by ecolumellate, emergent, perithecioid ascomata, 1-spored asci with large, hyaline, muriform ascospores and the presence of the protocetraric acid chemosyndrome (Mangold *et al.* 2009). Conprotocetraric and virensic acids were found as accessory substances.

11.23 *Ocellularia neoleucina* Homchantara & Coppins, Lichenologist, 34(2): 126 (2002)

Thallus crustose, continuous, diffuse, effuse, upper surface brownish green (olivaceous, olive green), smooth, plane, apothecial, apothecioid–hymenial, immersed, innate, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.3–0.4 mm diam., ostiole pale, with an only apically carbonised exciple, carbonised columella, prosoplectenchymatous exipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 3–5 septa, ellipsoidal, hyaline, 11–18.5 $\times$ 4–7 μm , I+ blue, 8/ascus.

Secondary chemistry: constictic acid, stictic acid.

Notes: This taxon is characterized by hyaline, submuriform ascospores, a reticulate columella and the presence of the stictic acid chemosyndrome. *Ocellularia leucina* (Müll. Arg.) Hale and *O. subleucina* are similar species. The latter differs by having larger ascospores and lacking secondary metabolites, while the former taxon contains psoromic acid. Constictic acid was found as accessory substance.

11.24 *Ocellularia orthomastia* (Kremp.) Zahlbr., Cat. Lich. Univ. 2: 597 (1923)

Bas.: *Ascidium orthomastium* Kremp., Nuovo Giorn. Bot. Ital. 7: 60 (1875).

Thallus epiphloeodal, to c. 200 μm thick, pale greenish grey to pale olive, dull to slightly glossy, smooth, continuous to verrucose or verruculose, rimose. True cortex $\pm$ discontinuous, to c. 30 μm

thick, formed by periclinal hyphae. Algal layer well developed, continuous; calcium oxalate crystals abundant, small to moderately large, scattered. Vegetative propagules not seen. Ascomata ±conspicuous, to c. 0.8 mm diam., ±rounded to slightly irregular, apothecioid at maturity, solitary to marginally fused, moderately to distinctly emergent, often verrucose and hemispherical to urceolate. Disc with the columella visible in older stages, epruinose to slightly pruinose, off-white to brownish or dark grey, free to fused with the thalline rim, entire. Pores formed by the thalline rim margin, to c. 0.4 mm diam., ±rounded to irregular, sometimes depressed, entire to split or eroded to evanescent, then the apex of the proper exciple becoming visible from above as a brownish to dark grey line, thin to thick, concolorous with the thallus or brighter; thalline rim incurved. Proper exciple fused, thin to thick, yellowish brown to brownish internally, dark brown to carbonised marginally and above, often amyloid at the base. Hymenium to c. 180 µm thick, not inspersed, conglutinated; paraphyses straight to slightly bent, parallel to slightly interwoven, unbranched, with scarcely thickened tips; columellar structures well-developed, to c. 500 µm wide, entire, carbonised, sometimes covered with greyish granules. Epihymenium hyaline, with brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, mostly fusiform to oblong-fusiform, with acute to subacute ends, hyaline, amyloid, 40–70 × 7–13 µm, with 12–17 locules; locules ±rounded to slightly angular in younger stages, then ±lenticiform to oblong or rectangular, with hemispherical to conical end cells; septa moderately thick, regular; ascospore wall and endospore moderately thick; wall halonate at the apices. Pycnidia not seen. Secondary chemistry: Thallus K–, C–, P–; no compounds detectable by TLC.

11.25 *Ocellularia papillata* (Leight) Zahlbr., Zahlbr., Catr. Lich. Univ. 2: 597(1923)

Bas.: *Thelotrema papillatum* Leight., *Trans. Linn. Soc. London* 27: 169 (1869).

=*Myriotrema rongklaense* Homchantara & Coppins

=*Ocellularia viridipallens* Müll.Arg., *Flora* 70: 397 (1887)

=*Thelotrema collativum* Kremp., *Nuovo Giorn. Bot. Ital.* 7: 20 (1875)

=*Thelotrema zamboangense* Vain., *Ann. Acad. Sci. Fenn., ser. A*, 15(6): 192 (1921)

=*Ocellularia zamboangensis* (Vain.) Zahlbr., *Cat. Lich. Univ.* 2: 604 (1923).

=*Ocellularia ascidioidea* Hale, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 8: 300 (1981).

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale greenish grey to olive or brownish, dull to glossy, smooth, continuous to verrucose or verruculose, rimose or not. True cortex ±continuous, to c. 50 µm thick, formed by irregular hyphae. Algal layer well developed, continuous; calcium oxalate crystals small to moderately large, scattered or clustered. Ascomata ±conspicuous, apothecioid at maturity, to c. 0.8 mm diam., ±rounded to irregular, solitary to fused, immersed to moderately emergent, often verrucose, hemispherical to urceolate. Disc with the columella visible in mature ascomata, ±distinctly pruinose, off-white to brownish or dark grey, often fused with the thalline rim, entire. Pores formed by the thalline rim margin, c. 0.4 mm diam., ±rounded to irregular, thin to thick, occasionally depressed, entire to split and/or evanescent,

brownish to dark grey due to the protuberant proper exciple, otherwise concolorous with the thallus; thalline rim incurved. Proper exciple fused, thin, yellowish brown to brownish internally, dark brown or carbonised marginally and distally, often amyloid at the base. Hymenium to c. 150 µm thick, not inspersed, distinctly conglutinated; paraphyses straight to bent, slightly interwoven, unbranched, with slightly thickened tips; columellar structures well developed in older ascomata, to 300 µm wide, entire, brownish to carbonised, with or without a ±thick covering layer of greyish granules. Epihymenium hyaline, sometimes with greyish or brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, oblong to fusiform or ellipsoidal, with ±rounded to narrowly rounded or rarely subacute ends, hyaline, distinctly amyloid, 10–35 (–45) × 6–10 µm, with 4–10 locules; locules initially ±rounded to slightly angular, then ±lenticiform to oblong or rectangular, with hemispherical to conical end cells; septa moderately thick, regular; ascospore wall and endospore moderately thick; wall non-halonate. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P–; no compounds detectable by TLC.

Notes: *Ocellularia papillata* forms the center of a group of species that also includes *O. perforata*, *O. terebrata*, and *O. thelotremoides* (see below), characterized by a thallus with proso-plectenchymatous cortex with internal splitting, small, immersed-erumpent apothecia, small ascospores, and variable chemistry but usually psoromic or protocetraric acid. Excipular and columella carbonization varies greatly in this group and often one can find specimens with pale excipulum but carbonized columella or viceversa. This variation has usually been accepted at the species level, and forms with different levels of carbonization have been included within *O. papillata*, for example. However, such variation is not known from other groups within the *Ocellularia-Myriotrema* clade and thus we postulate that these forms are specifically distinct and sometimes not even closely related. This is supported by molecular data (Rivas Plata *et al.* 2012b). Therefore, *O. papillata* is here accepted to include specimens with (dark) brown but not distinctly carbonized excipulum and columella. The white papillae on the thallus correspond to accumulations of calcium oxalate crystals. They may be flat or slightly raised, and are found similarly in *O. perforata*. The species was already reported from Costa Rica by Breuss (2001).

11.26 *Ocellularia perforata* (Leight.) Müll. Arg., Nova Hedwigia 31: 284 (1892)

Bas.: *Thelotrema perforatum* Leight., Trans. Linn. Soc. London 25: 477 (1866).

=*Thelotrema gymnocarpum* Nyl., Ann. Sci. Nat., Bot., sér. 5, 7: 317 (1867)

=*Ocellularia gymnocarpa* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 592 (1923).

=*Thelotrema terebratum* var. *abbreviatum* Vain., Étud. Class. Lich. Brésil 2: 83 (1890)

=*Ocellularia terebrata* var. *abbreviata* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 602 (1923).

=*Ocellularia violacea* Räsänen, Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat 3: 184 (1949)

=*Ocellularia violacea* var. *glauca* Räsänen, Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat 3: 185 (1949)

=*Ocellularia subterebrata* Vězda, Lich. Sel. Exs. [748] (1969)

=*Ocellularia thryptica* Hale, Phytologia 26: 415 (1973).

=*Thelotrema perforatum* var. *pauciseptatum* Purvis & P. James, Biblioth. Lichenol. 58: 350 (1995).

=*Myriotrema khaoyaiantum* Homchantara & Coppins Homchantara & Coppins, (2002)

Thallus endophloeodal to epiphloeodal, to c. 600 µm thick, pale greenish grey to yellowish grey or pale olive, dull to glossy, smooth, continuous to verrucose or verruculose, rimose or not. True cortex ±continuous, to c. 40 µm thick, formed by irregular hyphae. Algal layer well developed, continuous; calcium oxalate crystals small to moderately large, scattered or clustered. Vegetative propagules not seen. Ascomata conspicuous at maturity, to c. 0.6 mm diam., ±rounded to irregular, becoming apothecioid, solitary to fused, immersed to somewhat emergent, rarely strongly emergent, often verrucose, hemispherical to urceolate. Disc with the columella visible at maturity, epruinose to ±distinctly pruinose, off-white to brownish or dark grey, free, entire. Pores formed by the thalline rim margin, to c. 0.4 mm diam., ±rounded to irregular, moderately thin to thick, occasionally depressed, entire to split and/or evanescent, brownish to dark grey due to the protuberant proper exciple, otherwise concolorous with the thallus or brighter; thalline rim incurved. Proper exciple fused, moderately thin to thick, yellowish brown to brownish internally, dark brown, rarely carbonised marginally and above, often amyloid at the base. Hymenium to c. 120 (–150) µm thick, not inspersed, distinctly conglutinated; paraphyses straight to slightly bent, interwoven, unbranched, with slightly thickened tips; columellar structures well developed at maturity, to 300 µm wide, entire, brownish to carbonised, with or without a ±thick layer of greyish granules. Epihymenium hyaline, sometimes with greyish or brownish granules. Asci 8-spored; tholus initially thick, becoming thin. Ascospores transversely septate, rarely with a single longitudinal septum, oblong to fusiform or ellipsoidal, with ±rounded to narrowly rounded or subacute ends, hyaline, amyloid, 15–35 (–40) × 7–10 (–12) µm, with 4–10 (–12) locules; locules initially ±rounded to slightly angular, then ±lenticiform to oblong or rectangular, with hemispherical to conical end cells; septa thick, regular; ascospore wall and endospore moderately thick; wall non-halonate. Pycnidia not seen. Secondary chemistry: Thallus K+ yellowish brown, C–, P+ orange-red; containing protocetraric acid (major), conprotocetraric acid (trace), fumarprotocetraric acid (trace), virensic acid (trace).

Notes: *Ocellularia perforata* is like the closely related *O. papillata* (see above) a species complex, comprising forms with variable excipular and columella carbonization. We have accepted under *O. perforata* s.str. specimens with (dark) brown excipulum and columella, thus similar to *O. papillata*, but differing in the presence of the protocetraric acid chemosyndrome. Specimens with distinctly carbonized excipulum and/or columella have to be studied further, as they possibly represent separate taxa. Preliminary molecular data suggest that some of these forms are not even closely related (Rivas Plata *et al.* 2012b). The reported variation in ascospore size (with up to 50 µm) also suggests that there are several taxa involved, one now being separated as *O. cryptica* (see above).

11.27 *Ocellularia pluriporoides* Homchantara & Coppins, Lichenologist, 34(2): 127 (2002)

Thallus grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.6–0.9 mm diam.; disc covered by narrow, 0.05–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, pale brown, laterally covered by thalline layer. Columella present, simple to reticulate, apically carbonized. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–13-septate, 30–50 × 7–10 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: psoromic, subpsoromic and 2'-O-demethylpsoromic acids.

Notes: *Ocellularia pluriporoides* resembles *O. terebrata* but has a reticulate columella, an uncarbonized excipulum, and larger ascospores with more numerous septa. The Costa Rican material matches the type well. Also similar are *O. minutula* and *O. pluripora* Hale, both with simple columella (uncarbonized in the first) and smaller ascospores. *Ocellularia psorbarroensis* (see below) also has an irregular but uncarbonized columella and smaller ascospores than *O. pluriporoides*. The most similar species of *Stegobolus*, *S. anamorphus*, has larger, prominent to sessile apothecia and distinctly smaller ascospores.

11.28 *Ocellularia pluripora* Hale, Bulletin of the British Museum for Natural History 8 (3): 319 (1981)

[MB#112490]

Thallus dull greenish grey, 5–12 cm broad, shiny continuous; cortex dense 10–12 µm, with aculeate hyphae, splitting internally; algae layer 15 µm, interrupted by crystals; medulla to 130 µm with remnants of cortical layer and large crystals; apothecia numerous, semi-emergent, solitary or fused with 2 or more pores in the same wart, 0.6–1.0 mm diam., the exciple weakly carbonised; columella 90–130 µm; pore round, 0.05–0.1 mm diam., white rimmed; hymenium 90–120 µm; ascospores hyaline, transversely septate, 5–7 loculate, 14–21 × 5–8 µm, I+ blue.

Secondary chemistry: Psoromic and norpsoromic acids.

11.29 *Ocellularia pseudopapillata* Papong, Mangold & Lücking, in Papong *et al.*, Phytotaxa 189(1): 232–244 (2014)

Mycobank 809247

Differing from *Ocellularia papillata* in the uneven-verrucose thallus, the thin, indistinctly fissured proper margin of the ascomata, and the carbonized columella.

Thallus corticolous on branches, epiperidermal, up to c. 5 cm diam., continuous; surface uneven-verrucose, light yellowish green, medulla white; prothallus absent. Thallus in section 30–50 µm thick, with prosoplectenchymatous cortex, 5–10 µm thick, photobiont layer 15–20 µm thick, and medulla 20–30 µm thick, with scattered clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, green, 7–12 × 6–9 µm. As-

comata rounded, erumpent, with complete thalline margin, 0.3–0.4 mm diam., 0.12–0.15 mm high; disc covered by 0.05–0.1 mm wide pore more or less filled with black-tipped columella but columella often immersed; proper margin indistinct, entire to slightly fissured, visible as whitish rim around the pore; thalline margin entire to slightly fissured, smooth, light yellowish green. Excipulum entire, prosoplectenchymatous, brown to dark brown, 15–20 µm wide, fused with thalline margin and difficult to separate from the bordering periderm; laterally covered by algiferous, corticate thallus containing periderm layers; columella present, finger-like, carbonized, up to 100 µm broad and 120–150 µm high; hypothecium prosoplectenchymatous, 5–10 µm high, hyaline; hymenium 90–100 µm high, hyaline, clear; epithecium indistinct, 5–10 µm high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, 90–100 × 12–15 µm. Ascospores 8 per ascus, ellipsoid, 5–7-septate, 20–25 × 7–8 µm, 2.5–3.5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry: No substances detected by TLC.

Etymology: The specific epithet refers to the superficial similarity with *Ocellularia papillata*.

Distribution and Ecology: The new species was collected on an island in southern Thailand, growing on bark in the understory of a rainforest remnant. It is known only from the type locality.

Notes: This new species belongs in a larger complex of taxa sharing small, columellate ascomata and small, hyaline, transversely septate ascospores, in combination with lack of secondary substances. Traditionally, all such material was identified as *Ocellularia papillata* (Leight.) Zahlbruckner (1923: 597). However, molecular phylogenetic studies (Rivas Plata *et al.* 2012, 2013) show that variations in thallus and ascoma morphology, excipulum and columella carbonization, as well as ascospore size, represent distinct species that are not even closely related in some cases. Typical *O. papillata* is characterized by a smooth thallus and erumpent ascomata with rather broad, brown proper margin and dark brown (not carbonized) excipulum and irregular columella. Most of the material traditionally identified with that name does not belong to this species. Material with uneven-verrucose thallus and ascomata with thin, entire, whitish proper margin and (apically) carbonized excipulum and columella bears the name *O. viridipallens* (see below). A recently described species from Costa Rica, *O. subpyrenuloides* Lücking in Sipman *et al.* (2012: 150) is characterized by blackened ascomata with a carbonized columella but dark brown (not carbonized) excipulum. The new species described here, *O. pseudopapillata*, agrees in excipulum and columella with the latter, but has ascomata that are light yellowish green (not blackened) and the margin is often fissured.

11.30 *Ocellularia rhicnoporoides* Homchantara & Coppins, Lichenologist, 34(2): 128 (2002)

Thallus crustose, continuous, diffuse, effuse, upper surface yellowish green, smooth, plane, apothecial, apothecioid–hymenial, immersed, innate, sessile, subimmersed, adnate, semi-immersed, emergent, 0.3–0.5 mm diam., ostiole pale, carbonised exciple, carbonised columella,

prosoplectenchymatous excipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 5-7 septa, ellipsoidal, hyaline, 14-25 x 5.5-8.5 µm, I+ blue, 8/ascus.

Secondary chemistry: no substance detected by TLC.

Notes: This taxon is characterized by immersed, perithecioid, ecolumellate ascomata, an apically carbonized exciple, 8-spored asci with hyaline, transversely septate ascospores and by the lack of secondary metabolites.

11.31 *Ocellularia salazinica* Papong, Mangold & Lücking, in Papong *et al.*, Phytotaxa 189(1): 232-244 (2014)

Mycobank #809248

Differing from *Ocellularia interponenda* in the ascomata with broad pore and broad, white-tipped columella becoming irregular and rhabdodiscoid.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven-verrucose, light grey-green; prothallus absent. Thallus in section 80–100 µm thick, with paraplectenchymatous cortex, 10–20 µm thick, photobiont layer 20–30 µm thick, and medulla 40–60 thick, with scattered clusters of calcium oxalate crystals; both photobiont layer and medulla also with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 x 6–10 µm. Ascomata rounded to irregular in outline, erumpent to prominent, with nearly complete thalline margin, 0.8–1.5 mm diam., 0.4–0.6 mm high; disc covered by 0.3–0.6 mm wide pore, more or less filled by white-tipped, broad to irregularly dissected columella; proper margin distinct, entire, visible as broad, whitish rim around the pore; thalline margin entire, smooth to uneven, light grey-green. Excipulum entire, partially carbonized, partially orange, 30–70 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, broad to irregularly dissected and then forming irregular teeth, carbonized, up to 300 µm wide and 300–350 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 200–250 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 200–230 x 25–30 µm. Ascospores 2–4 per ascus, oblong, richly muriform, 80–100 x 15–22 µm, 4–5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry: Salazinic acid (medulla P+ orange-red, in section with K+ yellow efflux forming small, red crystals).

Etymology: The specific epithet refers to the unusual chemistry.

Distribution and Ecology: The new species was collected on an island in southern Thailand, growing on bark in the understory of a secondary forest. It is known only from the type locality.

Notes: Salazinic acid is a rare substance in Graphidaceae, only known from a handful of species in *Melanotopelia* Lumbsch & Mangold in Mangold *et al.* (2008b: 43) (1), *Ocellularia* Meyen

(1825: 327) (2), and *Thelotrema* Acharius (1803: 43) (2). Within *Ocellularia*, two closely related species, *O. massalongoi* (Mont.) Hale (1980: 137) and *O. interponenda* (Nyl.) Hale (1980: 137), produce this substance. Both agree with the new species in the muriform ascospores and carbonized excipulum and columella, and all three species appear to be closely related, but they differ in the narrow-pored ascomata with finger-like columella (Fig. 3E–F). Indeed, the new species externally resembles a species of *Rhabdiscus* Vainio (1921: 184), but that genus is anatomically and chemically distinct, in having small ascospores and psoromic acid as main secondary compound (Rivas Plata *et al.* 2012).

11.32 *Ocellularia subdolichotata* Papong, Mangold & Lumbsch in Papong *et al.*, *Phytotaxa* 189(1): 232–244 (2014)

Mycobank #809249

Differing from *Ocellularia dolichotata* in the smooth, white thallus and 2–4-spored asci with smaller ascospores.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface smooth, white; prothallus absent. Thallus in section 80–120 µm thick, with paraplectenchymatous cortex, 10–20 µm thick, photobiont layer 20–40 µm thick, and medulla 40–70 µm thick, with large clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–10 µm. Ascomata round, prominent, with complete thalline margin, 0.8–1.2 mm diam., 0.4–0.6 mm high; disc completely covered by 0.1 mm wide pore, filled by white-tipped columella; proper margin thin, entire, visible as narrow, brownish rim around the pore; thalline margin entire, smooth, white. Excipulum entire, carbonized, 20–30 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, finger-like, 100–150 µm wide and 300–400 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 250–300 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 220–250 × 25–30 µm. Ascospores 2–4 per ascus, oblong to cylindrical, 25–35-septate, 150–180 × 15–18 µm, 9–11 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry: No substances detected by TLC.

Etymology: The specific epithet refers to the close relationship with *Ocellularia dolichotata*.

Distribution and Ecology: The new species was collected on an island in the gulf of Thailand in the south of the country. It is known only from the type locality.

Notes: *Ocellularia subdolichotata* closely resembles *O. dolichotata* (Nyl.) Zahlbruckner (1924: 589) in the prominent, columellate and carbonized ascomata, large, transversely septate ascospores, and lack of secondary substances. The latter, however, differs consistently in the finely verrucose, pale yellowish brown thallus and the larger ascospores (180–250 × 20–30 µm; Fig. 4D). A third, similar species that is usually included as synonym of *O. dolichotata* is *O. siamense*

(Vain.) Zahlbruckner (1923: 600). It is similar to *O. dolichotata* in morphology, but its ascospores are even smaller than in *O. subdolichotata* (70–120 × 11–15 µm). Typical specimens of *O. dolichotata* were also identified in the same collection and are cited.

11.33 *Ocellularia subgranulosa* (Homchantara & Coppins) Lumbsch & Papong, in Papong, Boonpragob, Mangold, Divakar & Lumbsch, *Lichenologist*, 42(2): 133 (2010)

Bas.: *Myriotrema subgranulosum* Homchantara & Coppins, Homchantara & Coppins, (2002)

Thallus ashy whitish to tannish mineral grey; 8–15 cm broad, shiny, continuous; cortex weakly developed and irregularly pored, up to 8 µm thick with some aculeate hyphae; algal layer 10 µm, medulla mostly hypophloeodal, embedded between periderm layers; apothecia numerous and conspicuous, strongly emergent and in part basally constricted, 0.8–1.5 mm diam., the amphitheci-um with a thick medulla easily abraded and exposed, exciple carbonised; columella well developed, 90–130 µm diam., pore round, 0.2–0.5 mm diam., hymenium 90–140 µm; ascospores hyaline, transversely septate, 6–8 loculate, 18–25 × 5–6 µm, 1–2/ascus.

Notes: The taxon is characterized by perithecioid ascomata, 1–2-spored asci with hyaline, amyloid, transversely septate ascospores and by the presence of the norisonotatic and norsubnotatic acids (formerly named *Chonestoma* unknowns). Similar species include *O. chonestoma* (Leighton) Zahlbr. and *O. nylanderiana* Hale; the former species being readily distinguished by its smaller ascospores, while the latter has longer and thinner ascospores with up to 18 loculi (Hale 1981).

11.34 *Ocellularia subleucina* Homchantara & Coppins, *Lichenologist*, 34(2): 129 (2002)

[MB#475977]

Thallus crustose, continuous, diffuse, effuse, cracked, fissured, fractured, rimose, upper surface greyish green, smooth, plane, rugulose, finely wrinkled, apothecial, apothecioid–hymenial, subsessile, subimmersed, adnate, semi-immersed, emergent, with pruinose, 0.3–0.5 mm diam., ostiole pale, carbonised exciple, carbonised columella, prosoplectenchymatous exipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores muriform, ellipsoidal, hyaline, 20–25 × 5.5–7 µm, I+ blue, 8/ascus.

Secondary chemistry: no substance detected by TLC.

Notes: This taxon is characterized by perithecioid ascomata with a simple columella, 8-spored asci with hyaline, amyloid, submuriform ascospores and by the lack of secondary metabolites. A similar species is *Ocellularia subcalvescens* (Nyl.) Divakar & Mangold [Basionym: *Thelotrema subcalvescens* Nyl., *Bull. Soc. Linn. Normand.* III 7: 168, (1873); type: India, Andaman Islands, Kurz, 1867 (H-NYL 22726—holotype)]. It is distinguished by faintly amyloid ascospores that do not exceed 21µm in length.

11.35 *Ocellularia thelotremoides* (Leight.) Zahlbr., 11(1): 138 (1925)

Bas.: *Ascidium thelotremoides* Leight., *Trans. Linn. Soc. London* 27: 170 (1869).
 =*Thelotrema albidopallens* Nyl., *Bull. Soc. Linn. Normandie*, sér. 2, 7: 168 (1873).
 =*Thelotrema australiense* Müll.Arg., *Flora* 70: 61 (1887).
 =*Ocellularia psathyroloma* Müll.Arg., *Hedwigia* 30: 183 (1891).
 =*Thelotrema microphthalmum* Müll.Arg., *Bull. Herb. Boissier* 3: 314 (1895).
 =*Thelotrema secernendum* Harm., *Bull. Soc. Sci. Nancy* 13: 40 (1912).
 =*Thelotrema leucocheilum* Vain., *Ann. Acad. Sci. Fenn.*, ser. A, 15(6): 182 (1921).
 =*Thelotrema subsimile* Hale, *Phytologia* 27: 497 (1974); *Ocellularia subsimilis* (Hale) Hale, *Mycotaxon* 11: 138 (1980).
 =*Myriotrema viride* Nagarkar & Hale, *Mycotaxon* 35: 440 (1989).
 =*Myriotrema thailandicum* Homchantara & Coppins, Homchantara & Coppins, (2002)

Thallus endophloeodal to epiphloeodal, to c. 500 µm thick, pale greenish grey to yellowish grey or olive, dull to glossy, smooth, continuous to verrucose, non-rimose. True cortex discontinuous, to c. 50 µm thick, consisting of irregular hyphae. Algal layer well developed, continuous; calcium oxalate crystals ±small and scattered. Vegetative propagules not seen. Ascomata conspicuous in older stages, to c. 0.6 mm diam., ±rounded to irregular, apothecioid at maturity, solitary to fused, immersed to moderately emergent, rarely strongly emergent, often verrucose, hemispherical to urceolate. Disc with the columella visible in mature ascomata, epruinose to ±pruinose, off-white to brownish or dark grey, free or fused with the thalline rim, entire. Pores formed by the thalline rim margin, to c. 0.3 mm diam., ±rounded to irregular, moderately thin to thick, entire to slightly split or evanescent and brownish due to the protuberant proper exciple, otherwise concolorous with the thallus or brighter; thalline rim incurved. Proper exciple fused, moderately thin to thick, yellowish brown to brownish internally, dark brown or, rarely, carbonised marginally and above, often amyloid at the base. Hymenium to c. 180 µm thick, not inspersed, conglutinated; paraphyses straight to slightly bent and interwoven, unbranched, with slightly thickened tips; columellar structures ±well developed in older stages, to 200 µm wide, entire, brownish to carbonised, with or without a ±thick layer of greyish granules. Epihymenium hyaline, occasionally with greyish or brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores muriform, ellipsoidal to fusiform, often medially constricted, with ±rounded to narrowly rounded ends, hyaline, distinctly amyloid, 15–35 (–40) × 7–13 µm, with 6–8 (–10) × 1–4 locules; locules initially ±rounded to slightly angular, becoming oblong to subglobose or ±irregular; transverse septa moderately thin, regular; ascospore wall thick, non-halonate; endospore thick. Pycnidia not seen. Secondary chemistry: Thallus K+ yellowish brown, C–, P+ orange-red; containing protocetraric acid (major to trace), fumarprotocetraric acid (major to trace), conprotocetraric acid (minor to trace), confumarprotocetraric acid (minor to trace), virensic acid (trace).

11.36 *Ocellularia violacea* Räsänen, *Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat* (Arch. Soc. Zool. Bot. Fenn. Vanamo) 3: 184 (1949).

Thallus grey-olive, verrucose, with dense, paraplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.8 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–25 × 7–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: protocetraric and virensic acids.

Notes: This taxon was considered a synonym of *Ocellularia perforata* (Mangold *et al.* 2009) but is here kept separate due to the unusual combination of pale excipulum and distinctly carbonized columella. Like *O. papillata*, *O. perforata* is considered a variable species with regard to carbonization (Mangold *et al.* 2009; Papong *et al.* 2010), but this seems to reflect an ad-hoc concept rather than thorough analysis of the available material. *Ocellularia violacea* was commonly found at mid elevations in very humid rain forests.

11.37 *Ocellularia wolseleyana* Homchantara & Coppin, Lichenologist 34 (2):133-140 (2002).

Thallus crustose, cracked, fissured, fractured, rimose, upper surface greyish to greyish green, smooth, plane, rugulose, finely wrinkled, apothecial, apothecioid–hymenial, immersed, innate, 0.3–0.5 mm diam., ostiole pale, exciple colourless, prosoplectenchymatous excipulum, carbonized, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores muriform, narrowly ellipsoidal, brownish to yellowish brown, 94–177 × 22.5–46.5 µm, I+ blue, 8/ascus.

Secondary chemistry: 2'-O-demethylpsoromic acid, psoromic acid.

Notes: This species is characterized by perithecioid ascomata lacking a columella, hyaline, muriform ascospores and the presence of psoromic acid. Morphologically it resembles *O. profunda* (Stirt.) Mangold, Elix & Lumbsch, which, however, is readily distinguished by its brown ascospores at late maturity, a cone-shaped columella, and larger ascospores (Mangold *et al.* 2007b). 2'-O-demethylpsoromic was found as accessory substance.

12. *Pseudochapsa* Parnmen, Lucking & Lumbsch, in Parnmen S, Lucking R, Lumbsch HT. PLoS ONE 7(12): e51392. (2012)

[MycoBank MB 801542].

Type species: *Pseudochapsa dilatata* (Mull. Arg.) Parnmen, Lucking & Lumbsch.

Differing from *Chapsa* s.str. in the usually brown excipulum and the almost exclusively distoseptate, amyloid ascospores.

Thallus usually with loose cortex or ecorticate, very rarely with dense cortex. Apothecia erumpent, rounded to irregular in outline; disc exposed; margin usually fissured to lobulate, rarely recurved.

Excipulum usually brown. Ascospores septate to muriform, fusiform-ellipsoid to oblong-cylindrical, mostly with thickened septa and lens-shaped to rounded lumina (distoseptate), colorless or very rarely brown, almost exclusively I+ violet-blue (amyloid). Secondary chemistry: no substances or frequently stictic acid and relatives; apothecial disc rarely pigmented.

Etymology: Derived from “pseudo” (Greek, false) and the genus name *Chapsa*.

12.1 *Pseudochapsa albomaculata* (Sipman) Parnmen, Lucking & Lumbsch, n Parnmen

S, Lucking R, Lumbsch HT. PLoS ONE 7(12): e51392. (2012)

[MycoBank MB 801519]

Bas.: *Thelotrema albomaculatum* Sipman, Trop. Bryol. 5: 89 (1992)

=*Chapsa albomaculata* (Sipman) Sipman & Lucking in Lichenologist, 42: 183 (2010).

Thallus crustose, continuous, diffuse, effuse, upper surface greenish grey, rugulose, finely wrinkled, epruinose, apothecial, apothecioid–hymenial, subsessile, subimmersed, adnate, semi-immersed, emergent, 0.3-0.6 mm diam., greyish to brownish, ostiole pale, exciple colourless, prosoplectenchymatous excipulum, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 5-9 septa, hyaline, 12-20 x 4-5 µm, I+ blue, 8/ascus.

Secondary chemistry: unknown/unidentified compounds.

12.2 *Pseudochapsa phlyctidioides* (Mull. Arg.) Parnmen, Lucking & Lumbsch, in Parn-

men S, Lucking R, Lumbsch HT. PLoS ONE 7(12): e51392. (2012)

[MycoBank MB 801528]

Bas.: *Ocellularia phlyctidioides* Mull. Arg., Hedwigia 32: 130 (1893);

=*Chapsa phlyctidioides* (Mull. Arg.) Mangold, Aust. Syst. Bot. 21: 221 (2008).

=*Thelotrema phlyctidioides* (Müll.Arg.) Hale, Mycotaxon 11: 132 (1980).

Thallus endophloeodal to epiphloeodal, to c. 150 µm thick, pale grey to greenish grey, dull, smooth to slightly uneven, continuous to verrucose or verruculose, often rimose. True cortex absent; pseudocortex indistinct, discontinuous, to c. 10 µm thick. Algal layer ±continuous, poorly developed; calcium oxalate crystals sparse to abundant, small to large, solitary or clustered. Vegetative propagules not seen. Ascomata conspicuous, to c. 0.8 mm diam., ±rounded to slightly irregular, often appearing a little branched or irregular in fused ascomata, apothecioid to indistinctly chroodiscoid, erumpent, solitary or fused, regenerating, immersed to slightly emergent. Disc partly visible from above, pale flesh-coloured, pruinose. Proper exciple not visible from above; thalline rim margin variable, split, ragged or lobed, ±concolorous with the thallus or brighter, incurved to erect when young, becoming layered, splitting and opening irregularly, breaking away in some parts, the remaining portions finally forming the new inner thalline rim, whitish-pruinose, incurved to erect, slightly recurved only in the outer layers. Proper exciple fused, thin to evanescent, hyaline internally to pale yellowish and strongly amyloid marginally. Hymenium to c. 80 µm thick, in post-mature ascomata occasionally with crystal inclusions, moderately conglutinated; paraphyses

slightly bent, parallel to interwoven, the tips slightly thickened, somewhat irregular; lateral paraphyses inconspicuous, to c. 20 µm long. Epihymenium hyaline, with yellowish grey granules and crystals. Asci 8-spored; tholus initially thick, not visible at maturity. Ascospores transversely septate, very rarely with a single longitudinal septum, ellipsoidal to fusiform or clavate, the ends ±rounded to subacute, hyaline, non-amyloid to faintly amyloid, 15–24 × 5–7 µm, with 4–8 × 1 (–2) locules; locules ±rounded to slightly angular, subglobose to more often lentiform or acutelen-tiform, with hemispherical to conical end cells; septa thin to thick, regular; ascospore wall thick, non-halonate; endospore thick.

Secondary chemistry: Thallus K+ yellowish to brown, C–, P+ orange; containing stictic acid (major), constictic acid (major to minor), hypostictic acid (major to minor), cryptostictic acid (trace), a-acetylhyposstictic acid (trace).

13. *Pseudotopeliopsis* Parnmen, Lucking & Lumbsch, in Parnmen S, Lucking R, Lumbsch HT. PLoS ONE 7(12): e51392. (2012)

[MycoBank MB 801543]

Type species: *Pseudotopeliopsis laceratula* (Hale) Parnmen, Lucking & Lumbsch.

Differing from *Chapsa* s.str. in the densely corticate thallus and the *Topeliopsis*-like apothecia with striate excipulum filling the disc. Thallus usually with dense cortex, rarely with loose cortex. Apothecia erumpent, rounded to irregular in outline; disc pore- like; margin fissured lobulate, in concentric layers covering the disc. Excipulum hyaline to brown. Ascospores septate to muri- form, fusiform-ellipsoid to oblong-cylindrical, with slightly thick- ened septa and angular lumina (subdis- toseptate), colorless to brown, I–.

Secondary chemistry: no substances.

Etymology: Derived from “pseudo” (Greek, false) and the genus name *Topeliopsis*.

13.1 *Pseudotopediopsis longispora* Papong, Lücking & Parnmen in Papong *et al.* Phyto- taxa 189(1): 232–244 (2014)

Mycobank # 807504

Differing from other species of *Pseudotopeliopsis* in the long, transversely septate ascospores.

Thallus corticolous, partially endoperidermal, up to 5 cm diam., continuous; surface uneven, fol- lowing the contours of the bark, olive-green; prothallus absent. Thallus in with dense, proso- plectenchymatous cortex, 10–20 µm thick, irregular photobiont layer immersed in the periderm, 20–30 µm thick, and irregular medulla immersed in the periderm, 30–50 µm thick, encrusted with clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata angular-rounded, immersed to erumpent, with lateral thalline margin, 0.3–0.5 mm diam., 0.2–0.25 mm high; disc more or less covered by narrow pore, flesh-colored, white-pruinose; proper margin more or less erect, lobulate, white, with split towards thalline margin, distinctly layered; thalline margin indistinct. Excipulum

colorless to pale yellowish, 30–50 µm wide, paraplectenchymatous; laterally covered by grey crystals; columella absent; hypothecium prosoplectenchymatous, 10–15 µm high, colorless to pale yellowish; hymenium 150–170 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, granular. Paraphyses unbranched, apically thin, smooth; periphysoids present, short (10–15 µm); asci fusiform, 140–160 × 40–50 µm. Ascospores 4–8 per ascus, oblong, 21–29-septate, 100–150 × 15–18 µm, 6–8 times as long as wide, hyaline, distoseptate with thickened septa and lens-shaped lumina and thick outer wall, I+ violet-blue.

Secondary chemistry: No substances detected by TLC.

Distribution and ecology: This taxon was collected in a relict montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes: *Pseudotopeliopsis longispora* is externally similar to the other known species of the genus in having a corticate thallus and small, immersed-erumpent, chroodiscoid ascomata with layered margins. However, it differs from all other currently known *Pseudotopeliopsis* Parnmen *et al.* (2012: e51392) species in having long, transversely septate ascospores. The other similar species have quite different ascospores: large and muriform in *P. laceratula* (Müll. Arg.) Parnmen *et al.* (2012: e51392) and *P. scabiomarginata* (Hale) Parnmen *et al.* (2012: e51392), and small and transversely septate in *P. scabiocarpa* (Hale) Parnmen *et al.* (2012: e51392).

14. *Rhabdodiscus* Vain., Annales Academiae Scientiarum Fennicae 15 (6): 184 (1921) [MB#4682]

14.1 *Rhabdodiscus crassus* (Müll. Arg.) Rivas Plata, Lücking & Lumbsch, Taxon 61 (6): 1175 (2012) [MB#801255]

Bas.: *Leptotrema crassum* Müll. Arg., Flora (Regensburg) 65 (21): 332 (1882)

=*Ocellularia crassa* (Müll. Arg.) Hale, Mycotaxon 11 (1): 136 (1980)

=*Stegobolus crassus* (Müll. Arg.) Frisch, Bibliotheca Lichenologica 92: 448 (2006)

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 1–2.5 mm diam.; disc partially covered by 0.5–1.5 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, white-pruinose. Columella present, broad-stump-shaped to lobate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 12–19 6–8 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-O-demethylpsoromic acids.

Notes: The concept of *Stegobolus crassus*, which belongs to the core of the *S. auerianus* group (*Rhabdodiscus*), is confusing in the literature. At some point, all forms with complex columella, submuriform brown ascospores, and psoromic acid were subsumed under this epithet, including *S. fissus* and other similar taxa (Mangold *et al.* 2009). However, close examination

showed that species within this complex can be distinguished by the development and shape of their columellae, and hence we do not only agree with Frisch & Kalb (2006) that *S. fissus* should be kept separate but also further species must be distinguished: *Thelotrema cubanum* Tuck., with broad-stump-shaped, entire columella that completely fills the disc to the margin, *Stegobolus crassus* with lobate columella with broad-stump-shaped center, *Thelotrema epitrypum* Nyl., with similar columella as in *S. crassus* but producing isidia, *Leptotrema integrum* Müll. Arg., with fissured columella, *Ocellularia marivelensis*, with fissured columella and grainy thallus surface due to columnar clusters of calcium oxalate crystals, *Trypethelium schizostomum* Leight., with reticulate columella with narrow center, *Thelotrema inalbescens* Nyl., with reticulate columella and white thallus, and *Stegobolus fissus* with radiate columella similar to that of *S. radians*.

14.2 *Rhabdodiscus subcavatus* (Nyl.) Rivas Plata & Lumbsch in Rivas Plata *et al.* Taxon 61 (6): 1176 (2012)

[MB#801269]

Bas.: *Thelotrema subcavatum* Nyl., Acta Societatis Scientiarum Fennicae 7: 449 (1876)

=*Ocellularia subcavata* (Nyl.) Zahlbr., Catalogus Lichenum Universalis 2: 601 (1923)

=*Stegobolus subcavatus* (Nyl.) Frisch, Bibliotheca Lichenologica 92: 491 (2006)

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale greenish to pale yellowish grey or olive, ±glossy, smooth, continuous to verrucose, ±rimose. True cortex continuous or discontinuous, to c. 30 µm thick, formed by periclinal hyphae. Algal layer well developed, usually continuous, occasionally discontinuous due to crystal inclusions; calcium oxalate crystals abundant, large, scattered or clustered. Vegetative propagules not seen. Ascomata ±conspicuous, to c. 1.5 mm diam., ±rounded to irregular (especially fused ascomata), apothecioid, solitary to fused, emergent, hemispherical to urceolate or subglobose. Disc with the columella visible from above, markedly pruinose, off-white to pale reddish, free or fused with the thalline rim, entire. Pores formed by the thalline rim margin, to c. 0.4 mm diam., ±rounded to irregular, sometimes annulate, moderately thin to thick, entire to split or evanescent, then the proper exciple becoming visible from above as a brownish line, otherwise paler than the thallus or off-white; thalline rim incurved. Proper exciple fused, moderately thin to thick, brownish to carbonised, sometimes amyloid at the base. Hymenium to c. 130 µm thick, not interspersed, distinctly conglutinated; paraphyses straight to slightly bent, parallel to interwoven, unbranched, with slightly thickened tips; columellar structures well developed, c. 800 µm wide, replacing much of the hymenium, entire, carbonised, covered with a thick layer of whitish or greyish granules. Epihymenium hyaline to brownish, with greyish or brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores transversely septate, oblong to ellipsoidal or clavate, with ±rounded to subacute ends, hyaline, distinctly amyloid, 10–25 × 5–8 (–10) µm, with 4–8 (–10) locules; locules ±rounded, oblong to lentiform, with hemispherical to conical end cells; septa thick, regular; ascospore wall thick, non-halonate; endospore thick.

Pycnidia not seen; *vide* Frisch *et al.* (2006) emergent with a pale or rather dark pore; conidia bacilli-form, to $8 \times 1.5 \mu\text{m}$.

Secondary chemistry: Thallus K+ yellowish, C–, P+ yellow; containing psoromic acid (major), 2'-O-demethylpsoromic acid (minor to trace), subpsoromic acid (minor to trace).

14.3 *Rhabdodiscus subemersus* (Müll. Arg.) Rivas Plata, Lücking & Lumbsch, Taxon 61 (6): 1176 (2012)

[MB#801270]

Bas.: *Ocellularia subemersa* Müll. Arg. (1886)

=*Stegobolus subemersus* (Müll. Arg.) Frisch, Bibliotheca Lichenologica 92: 492 (2006)

Thallus crustose (crustaceous) – endosubstratal, inconspicuous, immersed, crustose (crustaceous) – episubstratal – unspecified, cracked, fissured, fractured, rimose, upper surface brownish (if pale: fawn, tan; if mid: cinnamon), greenish grey, brownish green (olivaceous, olive green), smooth, plane, verrucose, warted, rugulose, finely wrinkled, epruinose, apothecial, apothecioid-hymenial, subsessile, subimmersed, adnate, semi-immersed, emergent, sessile, superficial, 0.5-1.8 mm diam., brownish with pruinose scarce, sparse, fine, ephithecium brownish, periphysoid absent, paraphyses present, unbranched, ascus unitunicate, tholus non-amyloid, ascospores transversely septate, 3-5 septa, hyaline, $11-20 \times 4.5-6 \mu\text{m}$, I+ blue, 8/ascus.

Secondary chemistry: unknown/unidentified compounds.

15. *Stegobolus* Mont. Hooker's London J. Bot. 4(3): 4 (1845).

Type. *Stegobolus berkeleyanus* Mont.

Thallus usually grey-olive, smooth to uneven or verrucose, usually with dense, prosoplectenchymatous cortex; photobiont layer and medulla (if developed) with clusters of calcium oxalate crystals. Apothecia prominent to sessile, angular-rounded to elongate-lirellate; disc partially covered to exposed, usually filled by columella; margin entire to fissured-lobulate, laterally covered by thalline layer. Columella present, broad- stump-shaped to lobate-reticulate or radiate, pale brown to carbonized, usually white-pruinose. Excipulum prosoplectenchymatous, brown to carbonized; periphysoids absent. Paraphyses unbranched. Ascospores transversely septate to muriform, small, ellipsoid-fusiform to oblong, with thick septa and lens-shaped lumina, colorless or brown, I+ violet-blue (amyloid) at least when young.

Secondary chemistry: variable, frequently psoromic acid and satellite substances.

Notes: The genus *Stegobolus* was resurrected by Frisch & Kalb (2006) for a group of species with complex columella previously placed in *Ocellularia* and *Myriotrema* (Hale 1980). The morphological distinction between *Stegobolus* and two further genera with complex columella, *Melanotrema* and *Redingeria* (Frisch & Kalb 2006), proved difficult. Molecular phylogenetic analysis, however, showed that the genera are well separated phylogenetically and also that *Stegobolus* sensu Frisch & Kalb (2006) forms two separate lineages which are not closely related, *Stegobolus* s.str. and *Rhabdodiscus* (Rivas Plata *et al.* 2012b), the latter corresponding to the *S. auerianus*

group as defined by Frisch & Kalb (2006). Since it is yet unclear to which lineage the unsequenced species belong, we are here treating *Stegobolus* in a wide sense, including also the species belonging in *Rhabdodiscus*. Species of *Stegobolus* s.str. appear to have apothecia with mostly uncarbonized excipulum, whereas in species of *Rhabdodiscus*, the excipulum is generally carbonized.

15.1 *Stegobolus berkeleyanus* Mont, in Hook., London J. Bot. 4: 4 (1845);

Ocellularia berkeleyana (Mont.) Zahlbr., Cat. Lich. Univ. 2: 584 (1923).

Byssophytum album Groenh., Nederlandsch. Kruidkundig Archief 46: 783 (1936).

Thelotrema leucotylum Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 7: 166 (1874).

Ocellularia leucotyla (Nyl.) Müll. Arg., Bull. Soc. Roy. Bot. Belgique 30: 51 (1891).

Thallus grey-olive, smooth to uneven, producing schizidia, with dense, prosoplectenchymatous cortex; schizidia prominent, 0.5-1 mm diam.; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded, 0.5–2 mm diam.; disc exposed, flesh-colored, partly filled by white-pruinose columella; margin fissured to lobulate, pale brown, felty white-pruinose. Columella present, reticulate, pale brown. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 12–22 × 5–7 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid).

Secondary chemistry: psoromic, subpsoromic and 2'-O-demethylpsoromic acids.

Notes: The type species of *Stegobolus* is characterized by apothecia and ascospores similar to those of *S. anamorphus* (see above), but differs from the latter in the formation of schizidia on the thallus. The species is often sterile and may then be confused with other species of the family producing schizidia. However, most of these have a different chemistry: stictic acid and in part lichexanthone in *Chapsa calathiformis* (Vain.) Lumbsch & Papong and *Myriotrema frondosolucens* (see above), hypoprotocetraric acid in *Myriotrema neofrondosum* and *Stegobolus actinotus*, and cinchonarum unknown in '*Stegobolus montagnei* Frisch & Emmerer' (ined.; Frisch & Kalb 2006). The only other known species with schizidia and psoromic acid is *Myriotrema frondosum* Hale, which has a different type of apothecia and in sterile condition can be separated from *Stegobolus berkeleyanus* by the different ontogeny of the schizidia, which are not prominent as in the latter.

16. *Thelotrema* Ach., Methodus 130 (1803)

from the Greek thele (a nipple) and trema (an opening or hole), in reference to the morphology of the ascomata in the type species.

Type: *T. lepadinum* (Ach.) Ach.

Thallus immersed to superficial, greyish to greenish or olive, with yellow, brown or white tones. Thallus ecorticate, or with a protocortex or a true cortex. Photobiont trentepohlioid. Prothallus thin to indistinct, brown. Ascomata ±rounded, rarely slightly irregular, perithecioid or apothecioid, rarely becoming ±indistinctly chroodiscoid. Proper exciple ±free, rarely fused. Hymenium non-amy-

loid; paraphyses parallel to $\pm$ distinctly interwoven, usually unbranched, rarely sparingly branched; tips slightly to distinctly thickened; lateral paraphyses present; true columella absent; columella-like structures rarely present in fused ascomata. Epihymenium usually hyaline, occasionally greyish or brownish, rarely yellowish, egranulose or granulose. Asci 1–8-spored, clavate, non-amyloid. Ascospores 1–3-seriate, transversely septate to muriform, hyaline to yellowish or brown, non-amyloid to distinctly amyloid; ascospore wall thin to thick, smooth or occasionally crenate, non-halonate to $\pm$ distinctly halonate. Conidiomata pycnidial, with ellipsoidal to oblong conidia (not seen in Australian species).

Secondary chemistry: β -Orcinol depsidones present or absent.

The original circumscription of *Thelotrema* has been modified to accommodate species with non-carbonised ascomata and lateral paraphyses. Meanwhile, other species have been transferred to genera such as *Topeliopsis*, *Reimnitzia* and *Chapsa*. *Thelotrema* s. str. is characterised by perithecioid to apothecioid ascomata, with a $\pm$ free proper exciple and lateral paraphyses.

Notes: The genus *Thelotrema* was first circumscribed in a modern sense by Frisch (2006); it is rather well-characterized by having apothecia with a double margin and periphysoids. *Thelotrema* has been shown to be monophyletic (Lumbsch *et al.* 2008; Mangold *et al.* 2008; Papong *et al.* 2009a; Rivas Plata & Lumbsch 2011a, b), with the exception of a few species with *Thelotrema*-like apothecia that fall outside the genus, such as *Chapsa platycarpa* (see above) and *Thelotrema bicinctulum* Nyl. (Rivas Plata & Lumbsch 2011a). Species of *Thelotrema* are mostly found at higher elevations and in (semi-)exposed situations and several species, including the type species, *T. lepadinum*, have close to cosmopolitan distribution ranges.

16.1 *Thelotrema adjectum* Nyl., Flora 49: 290 (1866)

Thallus predominantly endophloeodal, to c. 70 μ m thick, greyish green to pale olive, dull to slightly glossy, smooth to somewhat uneven, continuous to slightly verrucose, rimose or not. Prothecortex discontinuous, to c. 10 (–25) μ m thick, or the thallus ecorticate. Algal layer well developed, continuous; calcium oxalate crystals abundant, small to large, often clustered. Vegetative propagules not seen. Ascomata inconspicuous, to c. 0.4 mm diam., $\pm$ rounded, apothecioid, solitary, rarely marginally fused, immersed to slightly emergent, then $\pm$ hemispherical. Disc partly visible from above, pale greyish to pale flesh-coloured, epruinose. Proper exciple not visible from above to apically visible, off-white, incurved. Pores small, to c. 0.2 mm diam., $\pm$ rounded to irregular, entire to more often split. Thalline rim margin thick, $\pm$ rounded to irregular, entire to split to somewhat eroded, slightly layered, inner part off-white to pale brown, outer parts concolorous with the thallus to pale brown (occasionally reddish) due to the protuberant substratum, incurved to erect. Proper exciple fused to apically free, thin to thick, hyaline internally, pale yellowish to pale orange marginally, occasionally incorporating substratum particles, often amyloid at the base. Hymenium to c. 200 μ m thick, not inspersed, moderately conglutinated; paraphyses parallel to slightly interwoven, unbranched, the tips unthickened to slightly thickened; lateral paraphyses conspicuous or not, to c. 20 μ m long; columellar structures absent. Epihymenium hyaline, lacking

granules and crystals, or with fine greyish granules. Asci 4–8-spored; tholus initially thick, thin when mature. Ascospores muriform, mostly fusiform, rarely somewhat clavate, most with narrowly rounded ends, non-amyloid to faintly amyloid, 40–80 × 8–25 µm, with 12–18 × 1–6 locules; locules ±rounded to slightly angular, especially in younger ascospores, subglobular to oblong to somewhat irregular; transverse septa thin, regular to slightly irregular; ascospore wall thick, often thinly halonate; endospore thin. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P–; no secondary substances detectable by TLC.

16.2 *Thelotrema bicinctulum* Nyl., Ann. Sci. Nat., Bot., sér. 4, 15: 46 (1861)

Bas.: *Thelotrema terebrans* Nyl., Bull. Soc. Linn. Normandie, sér. 2, 7: 166 (1873)

=*Ocellularia terebrans* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 602 (1923)

=*Myriotrema terebrans* (Nyl.) Hale, Mycotaxon 11: 138 (1980).

=*Ocellularia demersa* Müll.Arg., Mém. Soc. Phys. Genève 29(8): 9 (1887)

=*Thelotrema albidulum* Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1857)

=*Thelotrema demersum* (Müll.Arg.) G.Salisb., Nova Hedwigia 29: 408 (1978).

=*Ascidium octolocularis* C.Knight, in F.M.Bailey, Proc. Roy. Soc. Queensland 1: 152 (1884).

=*Ocellularia octolocularis* (C.Knight) Shirley, Proc. Roy. Soc. Queensland 6: 188 (1889).

=*Porina octolocularis* (C.Knight) C.Knight, in J.Shirley, Proc. Roy. Soc. Queensland 6: 183 (1889).

Thallus endophloeodal to epiphloeodal, to 500 (–800) µm thick, pale greyish green to pale yellowish grey or olive, dull to glossy, smooth to occasionally partly porous-uneven, continuous to verrucose, rimose or not, the upper thalline layers often partly flaking away and exposing the whitish medulla. True cortex continuous, occasionally discontinuous or lacking in large parts, to c. 35 µm thick, consisting of irregular to periclinal hyphae. Algal layer mostly ±well developed, continuous, sometimes becoming discontinuous due to large crystal inclusions; calcium oxalate crystals abundant, often almost occupying the lower levels of the thallus, variable in size, scattered or clustered; medulla whitish. Vegetative propagules not seen. Ascomata ±inconspicuous, to c. 0.4 mm diam., ±rounded, apothecioid, mostly solitary, rarely slightly fused, predominantly ±immersed. Disc often becoming partly visible from above, greyish, coarsely pruinose. Pores small, to c. 0.12 mm diam., ±rounded to somewhat irregular, the apex or upper levels of the proper exciple visible from above, free, entire to slightly split, occasionally ±jagged, off-white, mostly incurved, rarely somewhat erect, occasionally ±distinctly shrunk. Thalline rim margin thin, ±rounded to slightly irregular, entire to slightly split, concolorous with the thallus or paler, often somewhat raised; thalline rim incurved, concolorous with the thallus. Proper exciple free in the upper parts, thin and hyaline internally to pale yellowish to dark yellowish brown marginally, apically often covered by greyish granules, non-amyloid, occasionally amyloid at the base. Hymenium to c. 100 µm thick, not interspersed, moderately conglutinated; paraphyses straight to slightly bent, slightly interwoven, unbranched, the tips slightly thickened; lateral paraphyses often inconspicuous, to c. 25 µm long; columellar structures absent. Epihymenium hyaline, with greyish granules. Asci 8-

spored; tholus initially thick, thinning or not visible at maturity. Ascospores transversely septate, narrowly ellipsoidal to fusiform or clavate, with ±rounded to subacute ends, hyaline, non-amyloid to faintly amyloid, 20–35 × 5–7 µm, with 8–11 locules; locules ±rounded to angular, predominantly oblong to lentiform or rectangular, with hemispherical to conical end cells; septa thin, regular; ascospore wall thin to thick, usually thinly halonate. Pycnidia not seen.

Secondary chemistry: Thallus K+ yellowish to brown, C–, P+ orange; containing stictic acid (major), constictic acid (minor to trace), hypostictic acid (minor to trace), a-acetylconstictic acid (trace), hypoconstictic acid (trace), cryptostictic acid (trace), a-acetylhypoconstictic acid (trace).

16.3 *Thelotrema defossum* (Müll. Arg.) Mangold in H.T.Lumbsch, A.Mangold, M.P.Martín & J.A.Elix, *Austral. Syst. Bot.* 21: 221 (2008)

Bas.: *Ocellularia defossa* Müll.Arg., *Bot. Jahrb.* 5: 138 (1884).

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale yellowish grey to pale olive, dull to slightly glossy, smooth, continuous to distinctly verrucose and rimose. Protocortex discontinuous, to 10 µm thick. Algal layer well developed, continuous or discontinuous due to crystal inclusions; calcium oxalate crystals sparse to abundant, small to large, scattered or clustered. Vegetative propagules not seen. Ascomata inconspicuous, to c. 0.3 mm diam., usually ±rounded, occasionally slightly elongate, apothecioid, solitary or fused, mostly immersed, sometimes becoming somewhat raised in strongly verrucose thalli. Disc not visible or becoming partly visible from above, greyish, predominantly epruinose. Pores to c. 0.2 mm diam., usually ±rounded, occasionally slightly elongate or somewhat irregular, entire to slightly split, apex of the proper exciple visible from above, occasionally somewhat shrunken, off-white, pale brownish towards the base, predominantly incurved. Thalline rim margin thin to thick, broad, entire to slightly split, ±rounded to irregular or elongate, rarely slightly layered, largely incurved, rarely somewhat erect, concolorous with the thallus or slightly paler. Proper exciple becoming partly free above, thin, hyaline internally, pale to dark brown marginally, apically often dark brown to slightly carbonised, often amyloid at the base. Hymenium to c. 80 µm thick, not inspersed, conglutinated; paraphyses moderately interwoven, unbranched, the tips ±thickened; lateral paraphyses inconspicuous, to c. 15 µm long; columellar structures absent. Epihymenium hyaline, rarely with sparse greyish granules. Asci 4–8-spored; tholus initially thin to thick, thin when mature. Ascospores transversely septate, mostly clavate, occasionally oblong to fusiform, with ±rounded to subacute ends, hyaline, initially non-amyloid, becoming weakly amyloid, 10–30 (–40) × 5–8 µm, with 4–11 (–12) locules; locules ±rounded to ±angular, lentiform to depressed-cuboidal; end cells hemispherical to conical; septa becoming thick, regular; ascospore wall mostly thin, with an often thick smooth to irregular halo. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P–; no secondary compounds detectable by TLC.

16.4 *Thelotrema porinoides* Mont. & Bosch, Enum. Pl. Ins. Java Sumatra Detexit 484 (1855)

=*Thelotrema cavatum* var. *porinoides* (Mont. & Bosch) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 118 (1858).

=*Ocellularia porinoides* (Mont. & Bosch) Zahlbr., *Cat. Lich. Univ.* 2: 599 (1923).

=*Thelotrema albidiforme* Leight., *Trans. Linn. Soc. London* 27: 170 (1869).

=*Ocellularia albidiformis* (Leight.) Zahlbr., *Ann. Mycol.* 14: 50 (1916).

=*Thelotrema exanthismocarpum* Leight., *Trans. Linn. Soc. London* 27: 169 (1869).

=*Ocellularia exanthismo-carpa* (Leight.) Zahlbr., *Cat. Lich. Univ.* 2: 590 (1923).

=*Thelotrema obovatum* Stirt., *Trans. Glasgow Soc. Field Nat.* 1: 21 (1873).

=*Ocellularia obovata* (Stirt.) Müll.Arg., *Bull. Herb. Boissier* 2, App. 1: 74 (1894).

=*Ocellularia platyklamys* Müll.Arg., *Bull. Herb. Boissier* 3: 313 (1895).

=*Thelotrema homothecium* Vain., *Ann. Acad. Sci. Fenn.*, ser. A, 15(6): 190 (1921).

=*Ocellularia homothecia* (Vain.) Zahlbr., *Cat. Lich. Univ.* 2: 593 (1923).

Thallus predominantly endophloeodal, epiphloeodal and up to c. 30 µm thick near ascomata, greyish green, dull to slightly glossy, smooth to uneven (due to the protuberant substratum), continuous to slightly verruculose, non-rimose. Protocortex continuous or discontinuous, to c. 30 µm thick. Algal layer well developed, continuous or discontinuous; calcium oxalate crystals usually common, small to large, often clustered. Vegetative propagules not seen. Ascomata ±conspicuous, to c. 0.9 mm diam., ±rounded, apothecioid, sessile, solitary, occasionally fused, usually emergent, rarely subglobose with a constricted base, usually hemispherical to broadly cylindrical or conical with a depressed apex. Disc usually not visible from above, pale greyish, distinctly pruinose. Pores small to moderately wide, to c. 0.3 mm diam., ±rounded, entire to split, the proper exciple completely to apically visible from above, free, apically pale, darker towards the base, incurved to slightly erect, occasionally slightly shrunken. Thalline rim margin thick, ±rounded, entire to split, lacerate or eroded, often slightly to distinctly layered, incurved to erect, mostly whitish or paler than the thallus, occasionally slightly pruinose; thalline rim surface often irregular-verruculose to verruculose. Proper exciple free, ±thin, hyaline internally, greyish brown marginally, often covered with greyish granules, non-amyloid to faintly amyloid at the base. Hymenium to c. 220 µm thick, not inspersed, moderately conglutinated; paraphyses interwoven, unbranched, the tips slightly thickened; lateral paraphyses conspicuous, to c. 40 µm long; columellar structures absent. Epihymenium hyaline, with greyish or brownish granules and small crystals. Asci 8-spored; tholus initially thick, not visible at maturity. Ascospores transversely septate, oblong-fusiform to, occasionally, oblong-clavate, the ends usually narrowly rounded, rarely subacute, hyaline, strongly amyloid, 40–150 (–170) × 15–22 µm, with 14–26 (–28) locules; locules ±rounded to slightly angular in younger stages, later subglobose to mostly lentiform; end cells ±conical; septa thin to thick, regular; ascospore wall very thick, thinly halonate. Pycnidia not seen.

Secondary chemistry: Thallus K+ yellowish to brown, C–, P+ orange; containing constictic acid (major), stictic acid (major), hypostictic acid (minor), hypoconstictic acid (trace), cryptostictic acid (trace), a-acetylhypoconstictic acid (trace).

16.5 *Thelotrema rugatum* Nyl., Bull. Soc. Linn. Normandie, sér. 2, 7: 168 (1873).

=*Tremotylium australiense* Müll.Arg., *Flora* 65: 500 (1882).

=*Phanotylium australiense* (Müll.Arg.) Clem., *Gen. Fungi* 81 (1909).

=*Tremotylium nitidulum* Müll.Arg., *Hedwigia* 32: 132 (1893).

Thallus endophloeodal to epiphloeodal, to c. 200 µm thick, pale yellowish grey to pale greyish green, dull to slightly glossy, usually smooth, occasionally becoming partly eroded, then uneven to porous, rarely continuous, usually rugose and verrucose, ±rimose to areolate. Protocortex ±discontinuous, to 25 µm thick, occasionally becoming conglutinated and forming a true cortex of periclinal hyphae. Algal layer usually well developed, continuous or discontinuous; calcium oxalate crystals abundant, small to large, clustered. Vegetative propagules not seen. Ascomata conspicuous or not, to c. 1 mm diam., ±rounded, perithecioid to apothecioid, erumpent to sessile, solitary to rarely marginally slightly fused, immersed, rarely emergent, usually verrucose-hemispherical, rarely urceolate. Disc not visible from above, rarely becoming partly visible, greyish, pruinose. Pores variable, small to gaping, to c. 0.3 (–0.8) mm diam., ±rounded to irregular, the proper exciple apically to completely visible from above, usually free only in the upper parts, off-white, often somewhat shrunken, usually entire to slightly split, in apothecioid ascomata split, occasionally layered, incurved. Thalline rim margin ±rounded, small to gaping, entire to slightly split, sometimes eroded, thin to thick, incurved, concolorous with the thallus. Proper exciple apically free, rarely completely free, thin to thick, with a thick hyaline part internally, pale yellowish to yellowish brown marginally, apically sometimes covered with greyish to dark grey granules, occasionally amyloid. Hymenium to c. 250 µm thick, not inspersed, moderately conglutinated; paraphyses parallel or slightly interwoven, unbranched, the tips slightly thickened; lateral paraphyses often inconspicuous, to c. 25 µm long; columellar structures absent. Epihymenium hyaline and without granules, occasionally thin with small greyish granules and small crystals. Asci 1 (–2)-spored; tholus initially thin to thick, not visible at maturity. Ascospores muriform, cylindrical to oblong-ellipsoidal or broadly fusiform, with ±rounded to narrowly rounded ends, hyaline, occasionally pale yellowish when old or decayed, faintly to rarely strongly amyloid, 80–220 × 15–45 µm, with numerous locules; locules ±rounded to angular, subglobular to irregular; transverse septa thin, distinct, usually regular; ascospore wall and endospore thin; wall often with a thin to thick halo. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P–; no secondary compounds detectable by TLC.

16.6 *Thelotrema subadjectum* Mangold in Mangold, Elix & Lumbsch, *Fl. Australia* 57: 658 (2009).

Thallus endophloeodal to epiphloeodal, to c. 100 µm thick, pale greyish to pale greyish green, dull to somewhat glossy, slightly pruinose to uneven, continuous, sparingly rimose or not, ecorticate. Algal layer poorly to well developed, ±continuous; calcium oxalate crystals often lacking, or sparse, then small and frequently clustered. Vegetative propagules not seen. Ascomata inconspicuous, to c. 0.6 mm diam., ±rounded, apothecioid, usually solitary, rarely marginally fused, usually immersed. Disc usually not visible from above, pale greyish to whitish, pruinose. Pores small, to c. 0.15 mm diam., ±rounded to irregular, entire to slightly split, the apex of the proper exciple visible from above, whitish, incurved, rarely shrunken. Thalline rim margin thick, ±rounded, entire to slightly split, occasionally ±funnel-shaped, concolorous with the thallus to whitish. Proper exciple becoming free, thick, hyaline internally, pale brownish to greyish marginally, often incorporating substratum material, apically often covered by greyish granules, usually amyloid at the base and at the margin of the subhymenium. Hymenium to c. 120 µm thick, not inspersed, conglutinated; paraphyses parallel to slightly interwoven, unbranched, the tips slightly thickened; lateral paraphyses conspicuous, to c. 25 µm long; columellar structures absent. Epihymenium hyaline, with fine to coarse greyish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores submuriform to muriform, mostly oblong to somewhat fusiform or clavate, with ±rounded to narrowly rounded ends, hyaline, faintly amyloid, 25–35 × 8–10 µm, with 10–14 × 1–4 locules; locules ±rounded to slightly angular, subglobose or irregular to more often ±oblong; immature ascospores with large, conical end cells, otherwise hemispherical; transverse septa thick, regular; ascospore wall thick, distinctly halonate; endospore thick. Pycnidia not seen.

Secondary chemistry: Thallus K–, C–, P–; no secondary compounds detectable by TLC.

16.7 *Thelotrema triseptatum* Mangold, in Mangold, Elix & Lumbsch, Fl. Australia 57: 658 (2009).

Thallus endophloeodal to epiphloeodal, to 50 µm thick, greyish, dull to glossy, smooth to slightly uneven, continuous, sparingly rimose or non-rimose. Protocortex discontinuous, to 25 µm thick. Algal layer poorly developed, ±continuous; calcium oxalate crystals sparse, small to large. Vegetative propagules not seen. Ascomata inconspicuous, to 0.3 mm diam., ±rounded, apothecioid, solitary to marginally fused, immersed. Disc not visible from above, rarely partly visible, pale flesh-coloured, epruinose. Pores to c. 0.1 mm diam., ±rounded to slightly irregular, the upper parts of the proper exciple visible from above, free, entire to slightly split, off-white, incurved. Thalline rim margin thick, entire to obscurely split, ±rounded, often slightly sunken, concolorous with the thallus. Proper exciple free in the upper parts, thin, hyaline internally, yellowish orange at the margin, often incorporating bark layers, faintly amyloid. Hymenium to c. 80 µm thick, not inspersed, distinctly conglutinated; paraphyses ±bent, interwoven, unbranched, the tips thickened; lateral paraphyses inconspicuous, to c. 10 µm long; columellar structures absent. Epihymenium indistinct, hyaline, lacking granules but with fine crystals. Asci 8-spored; tholus initially thick, thin to thick at maturity. Ascospores transversely septate, fusiform to clavate, the ends ±rounded to subacute,

hyaline, amyloid, $15\text{--}20 \times 6\text{--}7 \mu\text{m}$, with 4 locules; locules $\pm$ rounded to $\pm$ angular, predominantly rounded-cuboid; end cells conical; septa thick, regular; ascospore wall thick, non-halonate. Pycnidia not seen.

CHEMISTRY: Thallus K+ yellowish to brown, C–, P+ orange; containing stictic acid (major), hypostictic acid (trace).

16.8 *Thelotrema patwardhanii* (Hale) Rivas Plata & Mangold, in Rivas Plata, Lücking, Sipman, Mangold, Kalb & Lumbsch, *Lichenologist* 42(2): 184 (2010)

=*Myriotrema grandisporum* Homchantara & Coppins

The types of the *Myriothema grandisporum* and *Thelotrema patwardhanii* agree well in containing norstictic acid and having large, transversely septate ascospores that turn brown at maturity and inconspicuous lateral paraphyses. The hymenia of both species include numerous brown ascospores. The ascospore size in the protologue of *T. patwardhanii* is given as $150\text{--}210 \times 21\text{--}25 \mu\text{m}$ with 20–30 transverse septa. However, we have also found up to 46 transverse septa in the type material and also ascospores up to $230 \mu\text{m}$. These measurements fall within the variability recorded by Homchantara & Coppins (2002) for *M. grandisporum* ($169.5\text{--}271.0 \times 17.0\text{--}28.5 \mu\text{m}$ and 45–49 transverse septa). In addition, we found the transverse septation of ascospores in the type of *M. grandisporum* to be more variable (35–49). Accessory connorstictic acid was found in addition to norstictic acid.

Secondary substances of Thelotremoid *Graphidaceae* in Thailand

Secondary chemistry is another important character complex in Thelotremoid *Graphidaceae* (Hale 1973, 1974a, 1974b, 1975, 1978a, 1978b; Frisch *et al.* 2006; Hale 1981; Staiger 2002; Staiger *et al.* 2006; Kalb *et al.* 2004; Frisch *et al.* 2006; Mangold *et al.* 2008b, 2009; Rivas Plata *et al.* 2010a, 2010b, Lumbsch *et al.* 2010). The core of the thelotremoid lichens has beta-orcinol depsidones (such as psoromic, stictic, and protocetraric acids) and rarely lichexanthone and anthraquinones, while depsides and mono-aromatic compounds are characteristic of *Diploschistes* (Guderley & Lumbsch 1996). Data available of Thelotremoid *Graphidaceae* indicate that secondary chemistry is important for alpha-taxonomic purposes but mostly does not indicate higher-level relationships. Secondary chemistry data of this project was studied according to standard methods (Santesson 1967; Culberson 1972; Culberson & Johnson 1976; Elix *et al.* 1988; Mietzsch *et al.* 1993; Feige *et al.* 1993; Huneck *et al.* 1994; Egan 2001; Lumbsch 2002) by both thin layer chromatography (TLC). (Table 3.2)

Table 3.2 Secondary substances of Thelotremoid *Graphidaceae* in Thailand

Species	Secondary substances
<i>Astrochapsa astroidea</i>	no lichen substances
<i>A. calathiformis</i>	constictic and stictic acids
<i>A. pseudophlyctis</i>	no lichen substances
<i>A. pulvereodiscus</i>	constictic and stictic acids
<i>Chapsa discoidea</i>	no lichen substances
<i>C. laemensis</i>	constictic and stictic acids
<i>C. indica</i>	no lichen substances
<i>C. leprocarpoides</i>	no lichen substances
<i>C. patens</i>	no lichen substances
<i>Chroodiscus argillaceus</i>	stictic acid
<i>Ch. australiensis</i>	stictic acid, anthraquinone
<i>Ch. defectus</i>	stictic acid
<i>Ch. homchantarae</i>	stictic acid
<i>Ch. khaolungensis</i>	stictic acid

Species	Secondary substances
<i>Ch. khaosokensis</i>	stictic acid
<i>Compositrema thailandicum</i>	psoromic acid
<i>Cruentotrema kurandense</i>	no lichen substances
<i>Cr. cruentatum</i>	unknown compound
<i>Glaucotrema glaucophaenum</i>	psoromic acid, 2'-O-demethylpsoromic acid and subpsoromic acid
<i>Leucodecton anamalaiense</i>	constictic and stictic acids
<i>L. compunctellum</i>	constictic acid, stictic acid, cryptostictic acid, hypoconstictic acid and hypostictic acid
<i>L. confusum</i>	stictic, constictic, and acetylconstictic acids
<i>Melanotrema melanophthalmum</i>	protocetraric acid
<i>M. platystomum</i>	no lichen substances
<i>Myriotrema clandestinum</i>	psoromic acid and subpsoromic acid
<i>My. cf. classicum</i>	psoromic, subpsoromic and 2'-O-demethylpsoromic acids
<i>My. polytrema</i>	2-hydroxy-hypoprotocetraric acid, convirensic acid, 2-hydroxynornotatic acid and hypoprotocetraric acid
<i>Nitidochapsa leprieurii</i>	no lichen substances
<i>N. aggregata</i>	no lichen substances
<i>Ocellularia albocincta</i>	no lichen substances
<i>O. allosporoides</i>	norisonotatic acid and norsubnotatic acid
<i>O. ascidioidea</i>	no lichen substances
<i>O. brunneospora</i>	norisonotatic acid and norsubnotatic acid.
<i>O. cavata</i>	cinchonarum unknowns
<i>O. cerebriformis</i>	protocetraric and virensic acids
<i>O. croceoisidiata</i>	unknown compound

Species	Secondary substances
<i>O. diacida</i>	hirtifructic acid, conhirtifructic acid and cinchonarum unknown
<i>O. diospyrosis</i>	constictic acid, stictic acid
<i>O. dolichotata</i>	no lichen substances
<i>O. exigua</i>	no lichen substances
<i>O. flavescens</i>	lichexanthone
<i>O. flavoperforata</i>	hypoprotocetraric and 4-O-demethylnotatic acids
<i>O. fumosa</i>	no lichen substances
<i>O. inthanonensis</i>	hypoprotocetraric acid, 2-hydroxy-hypoprotocetraric acid
<i>O. interponenda</i>	salazinic acid
<i>O. khuntanensis</i>	2'-O-demethylpsoromic and subpsoromic acids
<i>O. kohangangensis</i>	cinchonarum unknowns
<i>O. krathingensis</i>	no lichen substances
<i>O. laeviusculoides</i>	no lichen substances
<i>O. massalongoi</i>	salazinic acid
<i>O. microstoma</i>	protocetraric acid, fumarprotocetraric acid, conprotocetraric acid and virensic acid
<i>O. neoleucina</i>	constictic acid, stictic acid
<i>O. orthomastia</i>	no lichen substances
<i>O. papillata</i>	no lichen substances
<i>O. perforata</i>	protocetraric acid, conprotocetraric acid, fumarprotocetraric acid and virensic acid
<i>O. pluriporoides</i>	psoromic, subpsoromic and 2'-O-demethylpsoromic acids
<i>O. pluripora</i>	psoromic and norpsoromic acids
<i>O. pseudopapillata</i>	no lichen substances
<i>O. rhicnoporoides</i>	no lichen substances
<i>O. salazinica</i>	salazinic acid

Species	Secondary substances
<i>O. subdolichotata</i>	no lichen substances
<i>O. subgranulosa</i>	norisonotatic and norsubnotatic acids (formerly named Chonestoma unknowns)
<i>O. subleucina</i>	no lichen substances
<i>O. thelotremoides</i>	protocetraric acid, fumarprotocetraric acid, conprotocetraric acid, confumarprotocetraric acid and virensic acid
<i>O. violacea</i>	protocetraric and virensic acids
<i>O. wolseleyana</i>	2'-O-demethylpsoromic acid, psoromic acid
<i>Pseudochapsa albomaculata</i>	unknown compound
<i>P. phlyctidioides</i>	stictic acid, constictic acid, hypostictic acid, cryptostictic acid and a-acetyl hypoconstictic acid
<i>Pseudotopeliopsis longispora</i>	no lichen substances
<i>Rhabdodiscus crassus</i>	psoromic, subpsoromic and 2'-O-demethylpsoromic acids
<i>R. subcavatus</i>	psoromic, subpsoromic and 2'-O-demethylpsoromic acids
<i>R. subemersus</i>	unknown compound
<i>Stegobolus berkeleyanus</i>	psoromic, subpsoromic and 2'-O-demethylpsoromic acids
<i>Thelotrema adjectum</i>	no lichen substances
<i>T. bicinctulum</i>	stictic acid, constictic acid, hypostictic acid, a-acetylconstictic acid, hypoconstictic acid, cryptostictic acid and a-acetyl hypoconstictic acid
<i>T. defossum</i>	no lichen substances
<i>T. porinoides</i>	constictic acid, stictic acid, hypostictic acid, hypoconstictic acid, cryptostictic acid and a-acetyl hypoconstictic acid
<i>T. rugatulum</i>	no lichen substances
<i>T. subadjectum</i>	no lichen substances
<i>T. triseptatum</i>	stictic acid and hypoconstictic acid
<i>T. patwardhanii</i>	connorstictic acid and norstictic acid

Phylogenetic and DNA barcode of Thelotremoid *Graphidaceae* in Thailand

Several previous studies focused on the phylogeny and taxonomy of certain clades within *Thelotremataceae* (Thelotremoid *Graphidaceae*) and were helpful for understanding that morphological complex group of lichens (Mangold *et al.* 2006, 2007a, 2007b, 2008a; Lumbsch & Mangold 2007; Lumbsch *et al.* 2007). Molecular studies on Thelotremoid *Graphidaceae* used genes coding for mitochondrial small subunit (mtSSU) and nuclear large (nuLSU) rDNA sequences (Grube *et al.* 2004; Lücking *et al.* 2004; Mangold *et al.* 2008a) and ITS was used by Martin *et al.* (2003). This project focused on the tribe Ocellularieae and Thelotremateae both belong to subfamily Graphidoideae (Table 3.3).

Table 3.3 List of taxa with their collection data and GenBank accession numbers for the sequences of Thelotremoid *Graphidaceae* in Thailand

Species	Tribe	Collection data	mtSSU	nuLSU	<i>RPB1</i>	<i>RPB2</i>
<i>Astrochapsa astroidea</i>	Thelotremateae	Lücking 24006 (F)	JX420977	JX421443	KF875452	JX420943
<i>Astrochapsa astroidea</i>	Thelotremateae	Lumbsch 19750a (F)	JX420974	JX421441	-	JX420859
<i>Astrochapsa astroidea</i>	Thelotremateae	Lücking 24011 (F)	JX465278	JX421445	-	JX420947
<i>Astrochapsa astroidea</i>	Thelotremateae	Lücking 24008 (F)	JX420978	JX421444	-	JX420945
<i>Astrochapsa astroidea</i>	Thelotremateae	Papong 6004 (F)	JX420975	JX421442	-	JX420865
<i>Astrochapsa pseudophlyctis</i>	Thelotremateae	Lumbsch 19750b (F)	JX421008	JX465303	KF875458	JX420858
<i>Astrochapsa zahlbruckneri</i>	Thelotremateae	Papong 6516 (F)	KF875551	JX421467	-	-
<i>Chapsa</i> aff. <i>laceratula</i>	Thelotremateae	Lücking 24007 (F)	JX420969	JX421436	KF875484	JX420944
<i>Chapsa</i> aff. <i>laceratula</i>	Thelotremateae	Lücking 24009 (F)	JX420970	JX421437	-	JX420946
<i>Chapsa indica</i>	Thelotremateae	Parnmen 18486 (RAMK)	JX465280	JX465295	KF688525	JX465322

Species	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Chapsa leprocarpa</i>	Thelotremateae	Lücking 24004 (F)	JX420995	JX421455	KF688523	JX420942
<i>Chapsa leprocarpa</i>	Thelotremateae	Lumbsch 19750c (F)	JX420993	JX421452	-	X420857
<i>Chapsa leprocarpa</i>	Thelotremateae	Kalb 38794 (hb. Kalb)	JX420994	JX421453	-	JX420928
<i>Chapsa patens</i>	Thelotremateae	Lücking 24003 (F)	JX421003	JX421459	KF688522	JX420941
<i>Chapsa</i> sp. nova 1	Thelotremateae	Parnmen 18483 (RAMK)	JX465281	JX465304	-	JX465332
<i>Chroodiscus defectus</i>	Thelotremateae	Papong 6069b (F)	JX465285	JX421469	-	JX420863
<i>Chroodiscus khaolungensis</i>	Thelotremateae	Papong 6069a (F)	FJ708495	JX421469	-	-
<i>Chroodiscus parvisporus</i>	Thelotremateae	Papong 6069c (F)	JX465285	JX421469	-	JX420863
<i>Chroodiscus verrucosus</i>	Thelotremateae	Papong 6070 (F)	JX465286	JX465307	-	-
<i>Compositrema thailandicum</i>	Ocellularieae	Lumbsch 19756o (F)	JX421019	JX421473	-	-
<i>Cruentotrema thailandicum</i>	Ocellularieae	Lumbsch 19955d1 (F)	JF828960	JF828975	-	-
<i>Glaucotrema glaucophaenum</i>	Ocellularieae	Lumbsch 19751g	-	JX421502	-	-
<i>Glaucotrema</i> sp. nov.	Ocellularieae	Papong 8560	-	KJ435152	-	-
<i>Leucodecton compunctellum</i>	Ocellularieae	Lumbsch 20205b (F)	JX421081	JX421514	-	-
<i>Myriotrema</i> aff. <i>myriotremoides</i>	Ocellularieae	Kalb 39044	-	KJ435110	-	KJ435258
<i>Myriotrema oliveum</i>	Ocellularieae	Kalb 39107	KJ435181	KJ435111	-	-
<i>Nitidochapsa leprieurii</i>	Thelotremateae	Kalb 38882	JX420991	JX421451	-	JX420930

Species	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Ocellularia albocincta</i>	Ocellularieae	Kalb 38891 (Herb. Kalb)	JX421114	-	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Lumbsch 19756w (F)	JX421102	JX421534	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Lumbsch 19756c	-	JX421535	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Lumbsch 19756e	-	JX421536	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Papong 8478	KJ435248	KJ435153	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Papong 8479	KJ435246	-	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Papong 8483	KJ435241	-	-	-
<i>Ocellularia</i> aff. <i>allosporoides</i>	Ocellularieae	Papong 8496	KJ435232	KJ435143	-	-
<i>Ocellularia</i> aff. <i>fumosa</i>	Ocellularieae	Papong 8576	KJ435231	-	-	-
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Ocellularieae	Lumbsch 20200j (F)	JX421106	JX421540	-	-
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Ocellularieae	Lumbsch 20206a (F)	JX421107	JX421541	-	-
<i>Ocellularia allosporoides</i>	Ocellularieae	Kalb 38813 (Herb. Kalb)	JX421118	JX421544	KF875454	JX420925
<i>Ocellularia allosporoides</i>	Ocellularieae	Lücking 24110	JX421116	-	-	-
<i>Ocellularia allosporoides</i>	Ocellularieae	Lücking 24130	JX421117	-	-	-
<i>Ocellularia allosporoides</i>	Ocellularieae	Lumbsch 20204a (F)	-	JX421545	-	-
<i>Ocellularia allosporoides</i>	Ocellularieae	Lumbsch 20200a (F)	JX421119	JX421546		

Species	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Ocellularia dolichotata</i>	Ocellularieae	Kalb 38892 (F)	JX421146	JX421554	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20202b (F)	-	JX421556	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20202b (F)	-	JX421557	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20200f (F)	JX421147	-	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20200k (F)	JX421148	JX421555	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20202d (F)	JX421149	JX421558	-	-
<i>Ocellularia dolichotata</i>	Ocellularieae	Lumbsch 20203d (F)	JX421150	JX421559	-	-
<i>Ocellularia exigua</i>	Ocellularieae	Papong 8434	KJ435244	-	-	-
<i>Ocellularia fumosa</i>	Ocellularieae	Lumbsch 19756h (F)	-	JX421538	-	-
<i>Ocellularia fumosa</i>	Ocellularieae	Lumbsch 19756n (F)	-	JX421539	-	-
<i>Ocellularia interposita</i>	Ocellularieae	Lumbsch 20202b (F)	JX421163	-	-	-
<i>Ocellularia interposita</i>	Ocellularieae	Lumbsch 20201c (F)	JX421164	JX421565	-	-
<i>Ocellularia</i> aff. <i>interposita</i>	Ocellularieae	Lumbsch 20203b (F)	JX421165	JX421566	-	-
<i>Ocellularia rhicnoporoides</i>	Ocellularieae	Lumbsch 19750e (F)	JX421208	JX421592	-	-
<i>Ocellularia rimosa</i>	Ocellularieae	Kalb 38767 (Herb. Kalb)	JX421211	-	-	JX420927

Species	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Ocellularia viridipallens</i>	Ocellularieae	Lücking 24131	JX421227	-	-	-
<i>Ocellularia xanthostromiza</i>	Ocellularieae	Papong 8559 (MSUT)	KJ435243	-	-	-
<i>Ocellularia</i> aff. <i>zamboangensis</i>	Ocellularieae	Kalb 39106 (Herb. Kalb)	KJ435183	KJ435112	-	-
<i>Ocellularia</i> sp. nov. 3	Ocellularieae	Lücking 24129	JX421179	-	-	-
<i>Ocellularia</i> sp. nov. 4	Ocellularieae	Lumbsch 20202e (F)	JX421186	-	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8541 (MSUT)	KJ435239	KJ435150	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8542 (MSUT)	KJ435249	KJ435154	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8552 (MSUT)	KJ435236	KJ435147	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8557 (MSUT)	KJ435238	KJ435149	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8564 (MSUT)	KJ435240	KJ435151	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8566 (MSUT)	KJ435233	KJ435144	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8567 (MSUT)	KJ435245	-	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8568 (MSUT)	KJ435237	KJ435148	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8570 (MSUT)	KJ435250	KJ435155	-	-
<i>Ocellularia</i> sp. nov. 6	Ocellularieae	Papong 8573 (MSUT)	KJ435251	KJ435156	-	-
<i>Ocellularia</i> sp. nov. 7	Ocellularieae	Papong 8574 (MSUT)	KJ435252	-	-	-

Species	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Ocellularia</i> sp. nov. 8	Ocellarieae	Papong 8439 (MSUT)	KJ435235	KJ435146	-	-
<i>Ocellularia</i> sp. nov. 8	Ocellarieae	Papong 8458 (MSUT)	KJ435247	-	-	-
<i>Rhabdodiscus mariv- elensis</i>	Ocellarieae	Lücking 24115	JX421304	-	-	-
<i>Stegobolus berke- leyanus</i>	Ocellarieae	Lumbsch 20200d (F)	-	JX421637	-	-
<i>Stegobolus berke- leyanus</i>	Ocellarieae	Lumbsch 20203e (F)	JX421333	JX421638	-	-
<i>Stegobolus berke- leyanus</i>	Ocellarieae	Papong 8444 (MSUT)	KJ435242	-	-	-
<i>Thelotrema adjec- tum</i>	Thelotremate ae	Lumbsch 20200b (F)	JX421347	JX421645	-	JX465350
<i>Thelotrema adjec- tum</i>	Thelotremate ae	Lumbsch 19756u (F)	JX465289	JX421644	-	JX420853
<i>Thelotrema verru- ciferum</i>	Thelotremate ae	Lumbsch 19751f (F)	JX421408	JX421673	-	JX420854

CHAPTER 4

Conclusion and Discussion

Systematics of Thelotremoid *Graphidaceae*

The Thelotremoid lichens belong to family Graphidaceae, subfamily Graphidoideae with two tribe are Ocellularieae and Thelotremateae. While the Graphidaceae contains four subfamilies, Fissurinoideae, Gomphilloideae, Graphidoideae, and Redonographoideae (Rivas Plata *et al.* 2012a; Lücking *et al.* 2013). Within that subfamily, seven large tribes are currently recognized, besides several smaller clades: Acanthothecieae, Diploschisteae, Graphideae, Leptotremateae, Ocellularieae, Thelotremateae and *Wirthiotremateae* (Rivas Plata *et al.* 2012a, b; Lumbsch *et al.* 2014) (Fig. 4.1).

Thelotremoid *Graphidaceae* are characterized by ±rounded, immersed to emergent ascomata, simple to sparingly branched paraphyses and predominantly distoseptate ascospores. Ascomata type are show a remarkable variability openings, including perithecioid, urceolate and apothecioid structures (Mangold *et al.* 2009).

Thelotremoid lichen in Thailand were found 81 species and 16 genera such as *Astrochapsa astroidea*, *A. calathiformis*, *A. pseudophlyctis*, *A. pulvereodiscus*, *Chapsa discoides*, *C. laemensis*, *C. indica*, *C. leprocarpoides*, *C. patens*, *Chroodiscus argillaceus*, *Ch. australiensis*, *Ch. defectus*, *Ch. homchantarae*, *Ch. khaolungensis*, *Ch. khaosokensis*, *Compositrema thailandicum*, *Cruentotrema kurandense*, *Cr. cruentatum*, *Glaucotrema glaucophaenum*, *Leucodecton anamalaiense*, *L. compunctellum*, *L. confusum*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. cf. classicum*, *My. polytrema*, *Nitidochapsa leprieurii*, *N. aggregata*, *Ocellularia albocincta*, *O. allosporoides*, *O. ascidioidea*, *O. brunneospora*, *O. cavata*, *O. cerebriformis*, *O. croceoisiadiata*, *O. diacida*, *O. diospyrosis*, *O. dolichotata*, *O. exigua*, *O. flavescens*, *O. flavoperforata*, *O. fumosa*, *O. inthanonensis*, *O. interponenda*, *O. khuntanensis*, *O. kohangangensis*, *O. krathingensis*, *O. laeviusculoides*, *O. massalongoi*, *O. microstoma*, *O. neoleucina*, *O. orthomastia*, *O. papillata*, *O. perforata*, *O. pluriporoides*, *O. pluripora*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. salaziniica*, *O. subdolichotata*, *O. subgranulosa*, *O. subleucina*, *O. thelotremoides*, *O. violacea*, *O. wolseleyana*, *Pseudochapsa albomaculata*, *P. phlyctidioides*, *Pseudotopeliopsis longispora*, *Rhabdodiscus crassus*, *R. subcavatus*, *R. subemersus*, *Stegobolus berkeleyanus*, *Thelotrema adjectum*, *T. bicinctulum*, *T. defossum*, *T. porinoides*, *T. rugatulum*, *T. subadjectum*, *T. triseptatum* และ *T. patwardhanii*. This project was investigated 10 new species and 15 new records from Thailand (Papong *et al.* 2014; 2015). The molecular studies in this project was help to fill gaps in the molecular data set from a previous project as well as the database can be used for the future (Lumbsch *et al.* 2014; Kraichak *et al.* 2014). (Fig. 4.2-4.5)

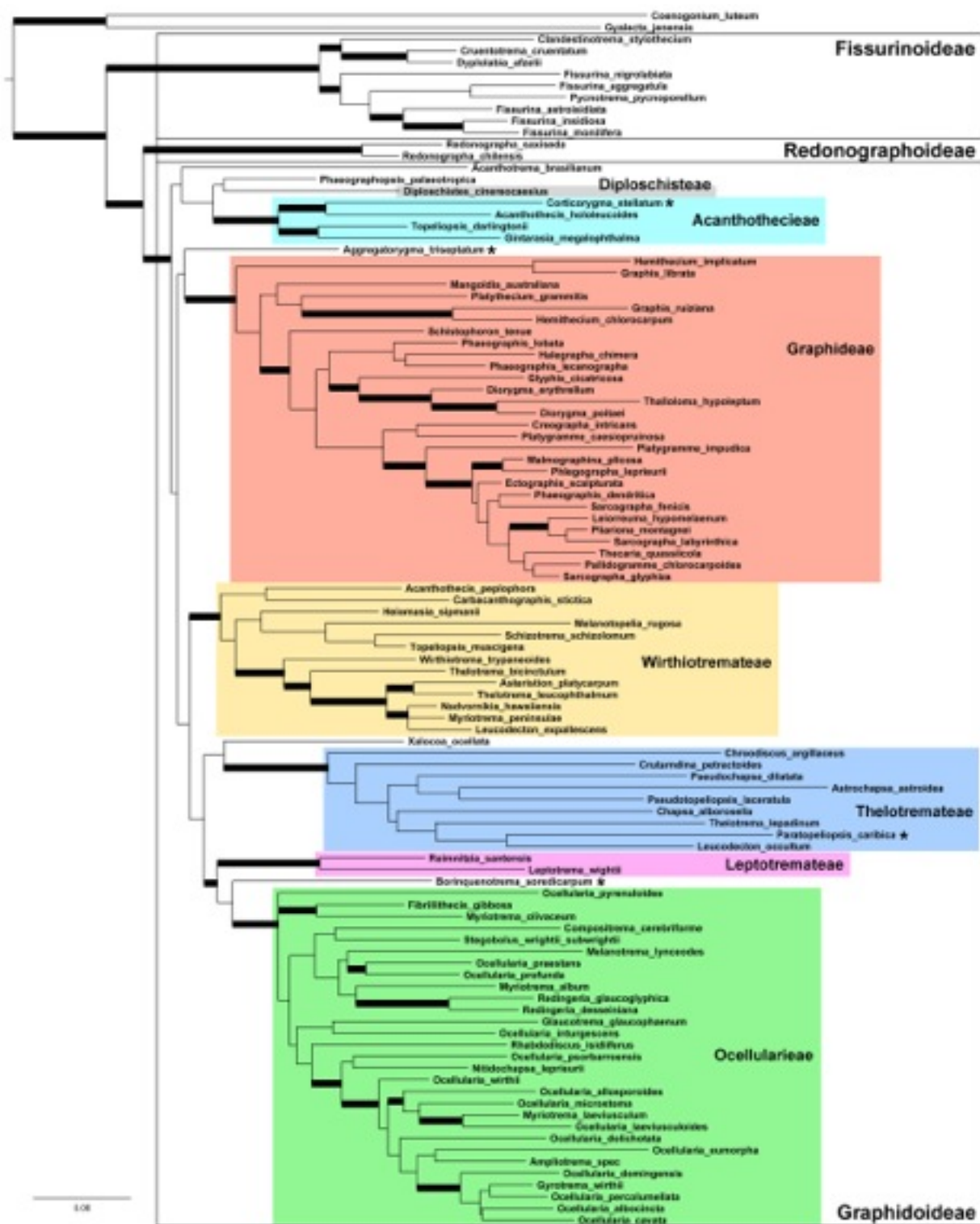


Fig. 4.1 Best-scoring maximum-likelihood tree based on a three-gene skeleton dataset of the core Graphidaceae. Thick branches indicate bootstrap support 70% or higher and/or posterior probabilities 95% or higher. Major lineages are highlighted. Novel genus lineages are marked with an asterisk. (Lumbsch *et al.* 2014)

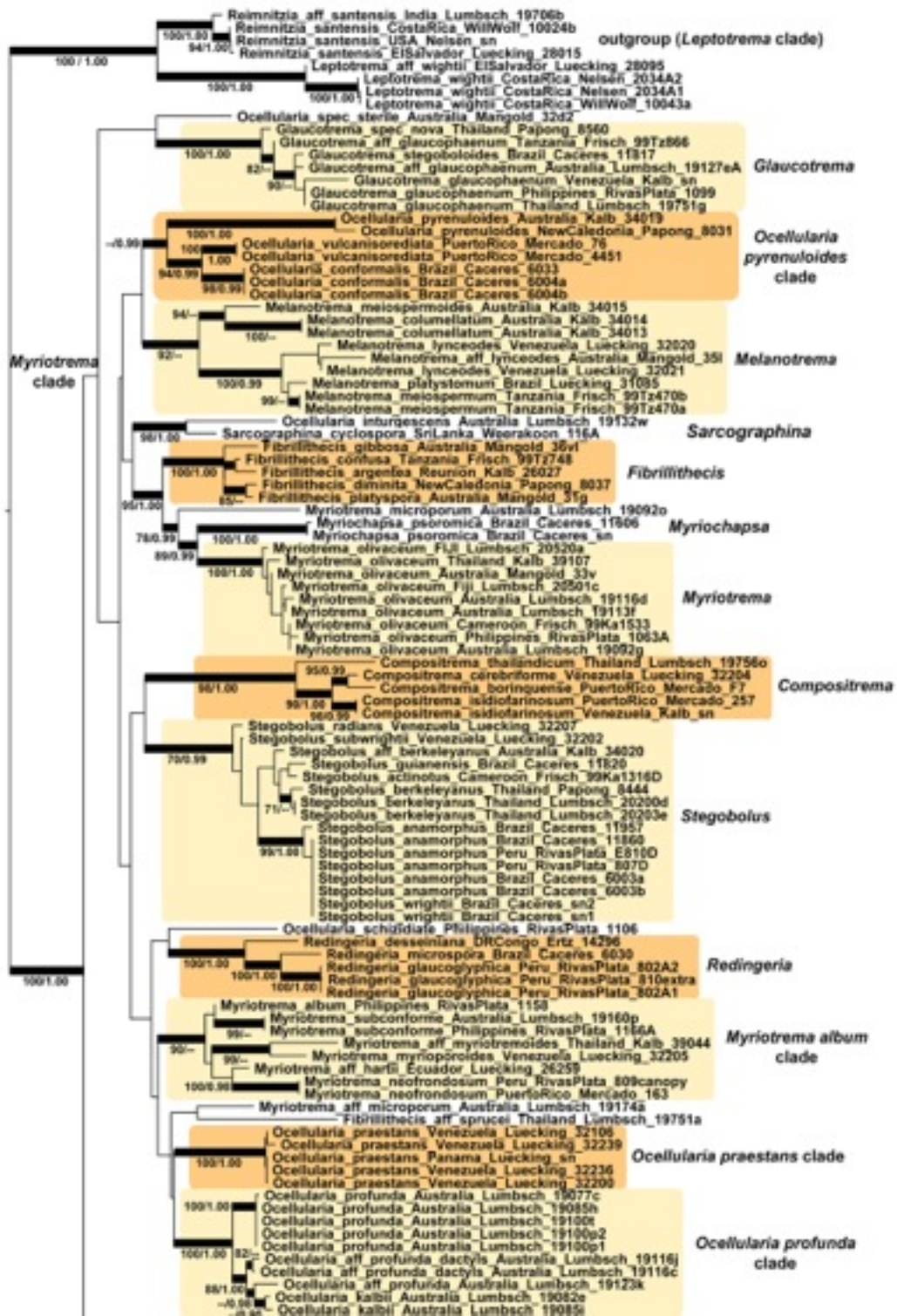


Fig. 4.2 Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Myriotrema* clade. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given. (Kraichak *et al.* 2014)



Fig. 4.3 Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Rhabdodiscus* clade and the basal portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given. (Kraichak *et al.* 2014)

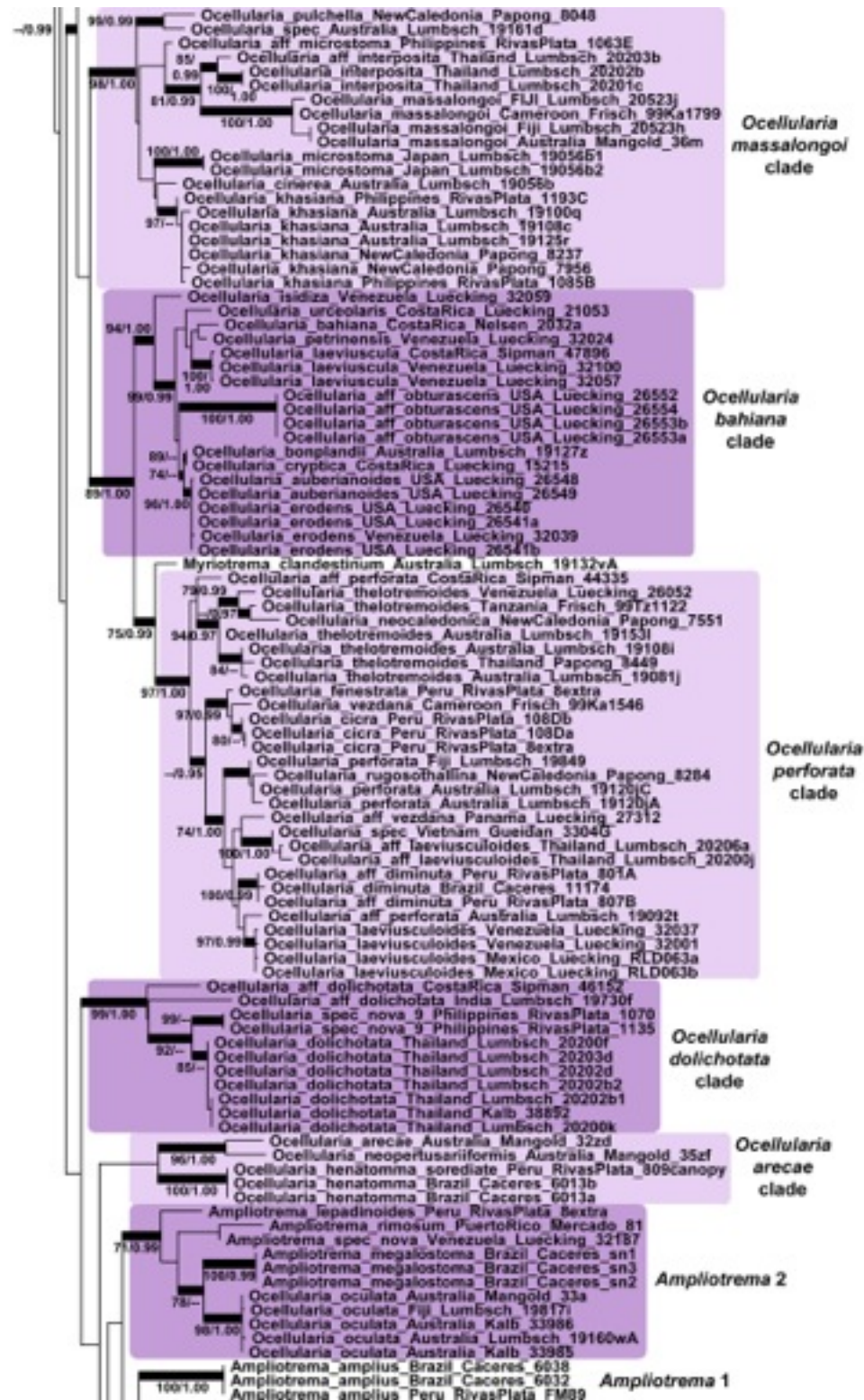


Fig. 4.4 Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the central portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given. (Kraichak *et al.* 2014)

This project was provided the Master student or young researcher who has the knowledge and understanding of Thelotrema *Graphidaceae* in Thailand. Also provide widely accessible, easy-to-use interactive identification tools and databases, set up a framework for a taxonomic and systematic outline of Thelotrema *Graphidaceae*, help to understand the evolution and ecosystems habitat in Thailand and SE Asia, and contribute to the understanding and application of species concepts in Thelotrema *Graphidaceae* by colour rapid guide (see appendix) and online publication.

http://fieldguides.fieldmuseum.org/guides?region=All&country=Thailand&type=Fungi+and+lichens&subject=All&items_per_page=25&=Filter

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APPENDIX



New species and new records of thelotremoid Graphidaceae (Ascomycota: Ostropales) from Thailand

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Abstract

Six new species of thelotremoid Graphidaceae are described from Thailand. *Leucodecton confusum* Papong, Mangold & Lücking has a densely corticate thallus and small, lepadinoid ascomata with double margin producing small, hyaline, submuriform ascospores. *Ocellularia cerebriformis* Papong, Lücking & Lumbsch is characterized by a brain-like, folded thallus surface, in combination with small, (sub-)muriform ascospores and protocetraric acid chemistry. *Ocellularia kohphangangensis* Papong, Mangold & Lücking features an unusual combination of small, brown, submuriform ascospores and the cinchonarum unknown chemistry. *Ocellularia pseudopapillata* Papong, Mangold & Lücking differs from *O. papillata* in the uneven-verrucose thallus, the thin, indistinctly fissured proper margin of the ascomata, and the carbonized columella. *Ocellularia salazinica* Papong, Mangold & Lücking is characterized by the presence of salazinic acid (a rare substance in Graphidaceae), in combination with ascomata resembling those of *Rhabdodiscus*, and comparatively large, muriform ascospores. A further species of *Ocellularia*, *O. subdolichotata* Papong, Mangold & Lumbsch, has a smooth, white thallus, prominent, columellate and carbonized ascomata, large, transversely septate ascospores (smaller than in *O. dolichotata*), and lacks secondary substances. The following 11 species are new records for Thailand: *Chapsa discoidea* (Stirt.) Lücking, *Glaucotrema glaucophaenum* (Kremp.) Rivas Plata & Lumbsch, *Leucodecton anamalaiense* (Patw. & C. R. Kulk.) Rivas Plata & Lücking, *Ocellularia fumosa* (Ach.) Müll. Arg., *O. granulifera* (Kremp.) Müll. Arg., *O. violacea* Räsänen, *O. viridipallens* Müll. Arg., *Rhabdodiscus subcavatus* (Nyl.) Rivas Plata & Lumbsch, *Stegobolus berkeleyanus* Mont., *Thelotrema defossum* (Müll. Arg.) Mangold, and *T. subadjectum* Mangold.

Key words: Diversity, south-east Asia, Thelotremataceae

Introduction

In its current, revised classification (Mangold *et al.* 2008a; Rivas Plata *et al.* 2012a; Rivas Plata & Lumbsch 2011), Graphidaceae constitutes the largest family of crustose tropical lichens with about 1800 accepted species. However, the diversity of the family is poorly known and many tropical regions are understudied. Hence new species are continuously being discovered, suggesting that the diversity is closer to 2000 or even more species. In general lichen diversity is high in the tropics, especially in microlichens (Aptroot 2001; Lücking *et al.* 2009; Sipman & Aptroot 2001; Sipman & Harris 1989). Recent surveys focusing on the Neotropics have unveiled a large number of new species of microlichens, while the Paleotropics are less well known. Especially tropical forests harbour high diversity of Graphidaceae (Lücking *et al.* 2008; Lücking *et al.* 2009; Rivas Plata *et al.* 2008; Rivas Plata *et al.* 2010; Weerakoon *et al.* 2012a; Weerakoon *et al.* 2012b).

Recently, the first author started a project on the diversity of thelotremoid Graphidaceae, which were previously placed in their own family Thelotremataceae (Frisch *et al.* 2006; Hale 1980; Mangold *et al.* 2009).

Thelotreroid Graphidaceae have rounded ascomata, in contrast to species with lirellate ascomata. The group is still relatively poorly known in Thailand and generally in south-east Asia, but preliminary studies have provided important baseline data for the distribution of species and have indicated that numerous additional species can be expected (Homchantara & Coppins 2002; Papong *et al.* 2010). Our recent studies revealed the presence of several undescribed species and additional records of species that have not previously been reported from Thailand in the recent web checklist (Aptroot & Sparrius 2013), in the previous printed checklist (Wolseley *et al.* 2002) or in other publications (Boonpragob & Polyiam 2007). This paper includes the description of five species new to science and 11 new records for Thailand.

Materials and Methods

This study is mainly based on new collections made by the first two authors deposited in F and MSUT. Sections of thalli and apothecia were cut using a razor blade and examined in water, a solution of KOH, and Lugol's solutions using a ZEISS Axioscope 2 plus compound microscope. HPTLC was performed with solvent systems A and C (Arup *et al.* 1993; Culberson 1972).

Taxonomic Treatment

Leucodecton confusum Papong, Lumbsch & Lücking, *sp. nov.* (Fig. 1A)

Mycobank 809244

Differing from *Leucodecton expallescens* in the psoroplectenchymatous thallus cortex and smaller ascomata and ascospores.

Type:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, along creek near impounding reservoir; 450 m; remnants of rainforest along creek, on bark; 15 October 2010, A. Mangold 103g (holotype MSUT!; isotype F!).

Thallus corticolous, epidermal, up to 10 cm diam., continuous; surface uneven-verrucose, light greenish grey; prothallus absent. Thallus in section 100–150 µm thick, with prosoplectenchymatous cortex, 10–15 µm thick, and massive medulla, 80–140 µm thick, filled with large clusters of calcium oxalate crystals and numerous small, grey crystals; photobiont layer irregular, immersed in the medulla. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata, immersed-erumpent, with nearly complete thalline margin, 0.1–0.2 mm diam., 0.12–0.15 mm high; disc covered by 0.05–0.1 mm wide pore; proper margin distinct, separated from the thalline margin by a split (double margin), entire, visible as white ring within the pore; thalline margin entire, smooth, light greenish-grey to whitish. Excipulum entire, yellowish brown, 20–30 µm wide; laterally covered by algiferous, corticate thallus, 50–100 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–15 µm high, yellowish; hymenium 90–100 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 90–100 × 10–12 µm. Ascospores 8 per ascus, ellipsoid to fusiform or with distal end tapering and acute and proximal end rounded, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 10–13 × 5–6 µm, 1.8–2.3 times as long as wide, hyaline, subdistoseptate with angular lumina, I+ violet-blue.

Secondary chemistry:—Stictic, constictic, and acetylconstictic acids (medulla P+ orange-red, section with K+ persistently yellow efflux).

Etymology:—The specific epithet refers to the confusing similarity with a *Thelotrema* species.

Distribution and Ecology:—The new species was collected on Ko Phangang island in southern Thailand growing on bark of an unknown tree. The new species is known only from the type locality.

Remarks:—*Leucodecton confusum* at first glance can be mistaken for a *Thelotrema* species, but lacks the periphysoids characteristic of the latter. There are two other species of *Leucodecton* with similar ascomata and hyaline ascospores and stictic acid chemistry. *Leucodecton expallescens* (Nyl.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 184) has only a loose cortex and larger ascomata producing larger ascospores (10–13 × 5–6 µm). The recently described *L. inspersum* Rivas Plata & Lücking (2013: 24) agrees with *L. confusum* in the verrucose thallus with prosoplectenchymatous thallus, but has larger ascomata, an inspersed hymenium, and much larger

ascospores ($25\text{--}40 \times 12\text{--}15\ \mu\text{m}$). The only similar species in *Thelotrema* is *T. myriocarpum* Fée (1825: 94) which, apart from the presence of periphysoids, can be distinguished by its smooth thallus, slightly larger ascomata, and larger ascospores.

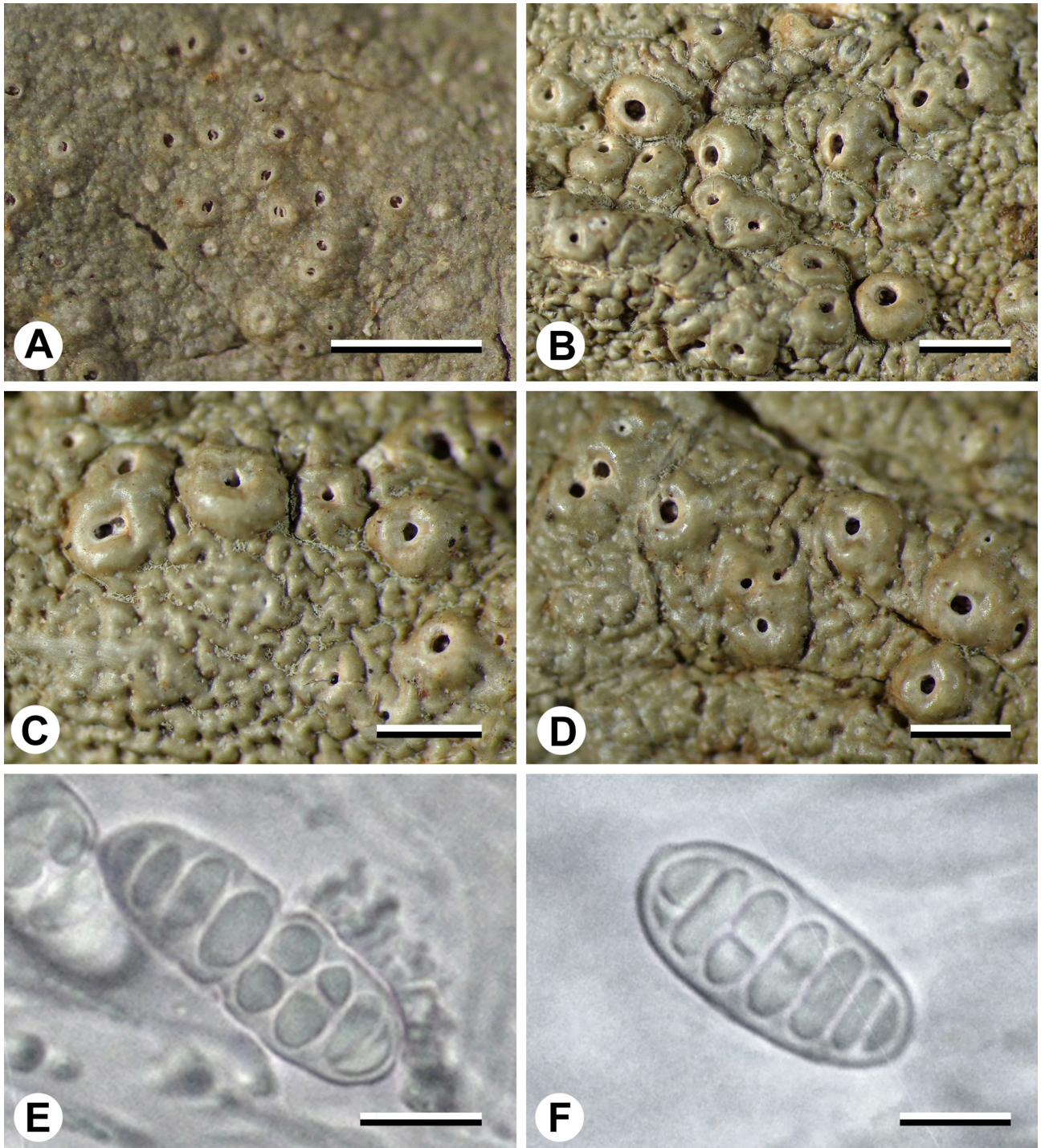


FIGURE 1. A. *Leucodecton confusum*, thallus with ascomata (holotype). B–F. *Ocellularia cerebriformis* (holotype). B–D. Thallus with ascomata. E–F. Ascospores. Scale = 1 mm, in E–F = 10 μm .

***Ocellularia cerebriformis* Papong, Lücking & Lumbsch, sp. nov.** (Fig. 1B–F)

Mycobank 809245

Differing from *Ocellularia thelotremoides* in the folded, brain-like thallus surface and the large, prominent ascomata with thick, bulging margins, as well as the non-carbonized, complex columella.

Type:—THAILAND. Muk Dahan Province: Wat Tham Chao Pha, Phu Pha Kud, trail from temple to top of mountain; 16°46'N, 104°43'E, 285 m; dry dipterocarp forest, on *Shorea siamensis*; 20 June 2009, K. Papong 6721 (holotype MSUT!; isotype F!).

Thallus corticolous, epidermal, up to 10 cm diam., continuous; surface conspicuously folded, resembling the surface of a brain, light grey-green, with numerous minute, white papillae, medulla white; prothallus absent. Thallus in section 100–150 µm thick, with prosoplectenchymatous cortex, 10–15 µm thick, photobiont layer 30–50 µm thick, and thick medulla, 80–100 µm thick, with large clusters of calcium oxalate crystals; both photobiont layer and medulla also with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata rounded, erumpent to prominent, with complete thalline margin, 0.8–1.2 mm diam., 0.3–0.5 mm high; disc covered by 0.2–0.5 mm wide pore, with white-tipped, irregular columella visible but deeply immersed; proper margin distinct, entire, visible as thin, whitish to pale brown rim around the pore; thalline margin entire, smooth to uneven, bulging, light grey-green. Excipulum entire, yellowish, 30–70 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, irregular, divided into several, partially radiating, thin strands, light brown, individual strands 50–100 µm wide and 150–170 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 130–150 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 120–130 × 15–20 µm. Ascospores 8 per ascus, ellipsoid, muriform with 5 transverse and 1–2 longitudinal septa per segment, 18–25 × 9–12 µm, 1.8–2.3 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Protocetraric and virensic acids (medulla P+ orange-red).

Etymology:—The specific epithet refers to the brain-like surface of the thallus (Latin: *cerebrum* = brain).

Distribution and Ecology:—The new species was collected in north-eastern Thailand in a dry dipterocarp forest, growing on the trunks of *Shorea siamensis* in the understory. It is only known from the type locality.

Remarks:—The new species resembles *Ocellularia thelotremoides* (Leight.) Zahlbruckner (1924: 603), in the small, (sub-)muriform ascospores and the protocetraric acid chemistry. The latter, however, has a smooth to uneven thallus, a carbonized, finger-like columella, and longer ascospores. Anatomically most similar is the African *O. cameroonensis* Frisch in Frisch *et al.* (2006: 203), which agrees in the uncarbonized, irregular columella, but has smaller ascomata with thinner margins and transversely septate ascospores. *Ocellularia subsimilis* (Hale) Hale (1980: 38) also has (sub-)muriform ascospores and protocetraric acid, as well as uncarbonized columella and excipulum, but its thallus is verrucose, not folded, and its ascomata are much smaller (to 0.5 mm wide) with narrow pore and finger-like columella.

***Ocellularia kohphangangensis* Papong, Mangold & Lücking, *sp. nov.* (Fig. 2A–B)**

Mycobank 809246

Distinguished by the combination of partially columellate ascomata, broad, brown, submuriform ascospores, and the cinchonarum unknown chemosyndrome.

Type:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; secondary rainforest, on bark; 15 October 2010, A. Mangold 102q (holotype F!).

Thallus corticolous, epidermal, up to 10 cm diam., continuous; surface uneven, silvery grey and glossy, medulla white; prothallus absent. Thallus in section 80–100 µm thick, with prosoplectenchymatous cortex, 5–10 µm thick, photobiont layer 20–30 µm thick, and medulla 50–60 µm thick, with clusters of calcium oxalate crystals and numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–11 × 6–10 µm. Ascomata rounded, erumpent, with nearly complete thalline margin, 0.4–0.6 mm diam., 0.2–0.3 mm high; disc covered by 0.1–0.2 mm wide pore, sometimes filled by black-tipped columella; proper margin distinct, entire, visible as whitish to pale yellowish rim around the pore, sometimes becoming annulate; thalline margin entire, smooth to uneven, glossy silvery grey. Excipulum entire, carbonized, 30–50 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 100–150 µm thick; columella present in some ascomata, in others absent, finger-like, carbonized, up to 150 µm

wide and 150–180 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 120–130 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical, 110–120 × 15–20 µm. Ascospores 8 per ascus, uniseriate, broadly oval, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 15–20 × 10–12 µm, 1.4–1.8 times as long as wide, brown when mature, distoseptate with lens-shaped to irregular lumina, I+ violet-blue when young.

Secondary chemistry:—Two lower cinchonarum unknowns (medulla and section C–, K–, P–).

Etymology:—The specific epithet refers to the type locality.

Distribution and Ecology:—The new species was collected on an island in southern Thailand, growing on bark in the understory of a secondary forest. It is known only from the type locality.

Remarks:—This new species does not seem to have any close relative in the family. Currently, no species is known with this combination of ascospore type and chemistry. *Rhabdodiscus subemersus* (Müll. Arg.) Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1176) agrees in chemistry and the carbonized, columellate ascomata, but its ascospores are hyaline and transversely septate, and its ascomata feature a broad, complex columella. *Ocellularia exigua* Müller (1892: 284) is superficially similar to the new species in having a narrow columella, but differs also by its hyaline, transversely septate ascospores.

***Ocellularia pseudopapillata* Papong, Mangold & Lücking, *sp. nov.* (Fig. 2C–E)**

Mycobank 809247

Differing from *Ocellularia papillata* in the uneven-verrucose thallus, the thin, indistinctly fissured proper margin of the ascomata, and the carbonized columella.

Type:—THAILAND. Surat Thani Province: Koh Phangang, Northern Island, Chaloklam area, E of Chaloklam Rd.; 9°76'N, 100°03'E, 450 m; remnant of rainforest along creek, on bark; 15 October 2010, *A. Mangold 100c* (holotype F!).

Thallus corticolous on branches, epiperidermal, up to c. 5 cm diam., continuous; surface uneven-verrucose, light yellowish green, medulla white; prothallus absent. Thallus in section 30–50 µm thick, with prosoplectenchymatous cortex, 5–10 µm thick, photobiont layer 15–20 µm thick, and medulla 20–30 µm thick, with scattered clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, green, 7–12 × 6–9 µm. Ascomata rounded, erumpent, with complete thalline margin, 0.3–0.4 mm diam., 0.12–0.15 mm high; disc covered by 0.05–0.1 mm wide pore more or less filled with black-tipped columella but columella often immersed; proper margin indistinct, entire to slightly fissured, visible as whitish rim around the pore; thalline margin entire to slightly fissured, smooth, light yellowish green. Excipulum entire, prosoplectenchymatous, brown to dark brown, 15–20 µm wide, fused with thalline margin and difficult to separate from the bordering periderm; laterally covered by algiferous, corticate thallus containing periderm layers; columella present, finger-like, carbonized, up to 100 µm broad and 120–150 µm high; hypothecium prosoplectenchymatous, 5–10 µm high, hyaline; hymenium 90–100 µm high, hyaline, clear; epithecium indistinct, 5–10 µm high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, 90–100 × 12–15 µm. Ascospores 8 per ascus, ellipsoid, 5–7-septate, 20–25 × 7–8 µm, 2.5–3.5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Etymology:—The specific epithet refers to the superficial similarity with *Ocellularia papillata*.

Distribution and Ecology:—The new species was collected on an island in southern Thailand, growing on bark in the understory of a rainforest remnant. It is known only from the type locality.

Remarks:—This new species belongs in a larger complex of taxa sharing small, columellate ascomata and small, hyaline, transversely septate ascospores, in combination with lack of secondary substances. Traditionally, all such material was identified as *Ocellularia papillata* (Leight.) Zahlbruckner (1923: 597). However, molecular phylogenetic studies (Rivas Plata *et al.* 2012, 2013) show that variations in thallus and ascoma morphology, excipulum and columella carbonization, as well as ascospore size, represent distinct species that are not even closely related in some cases. Typical *O. papillata* is characterized by a smooth thallus and erumpent ascomata with rather broad, brown proper margin and dark brown (not carbonized) excipulum and irregular columella (Fig. 2F). Most of the material traditionally identified with that name does not belong to this species. Material with

uneven-verrucose thallus and ascomata with thin, entire, whitish proper margin and (apically) carbonized excipulum and columella bears the name *O. viridipallens* (see below). A recently described species from Costa Rica, *O. subpyrenuloides* Lücking in Sipman *et al.* (2012: 150) is characterized by blackened ascomata with a carbonized columella but dark brown (not carbonized) excipulum. The new species described here, *O. pseudopapillata*, agrees in excipulum and columella with the latter, but has ascomata that are light yellowish green (not blackened) and the margin is often fissured.

Additional specimen examined:—THAILAND. Surat Thani Province: Ko Phangang, Northern Island, Chaloklam area, E of Chaloklam Rd.; 9°76'N, 100°03'E, 450 m; 15 October 2010, *A. Mangold 100a* (F).

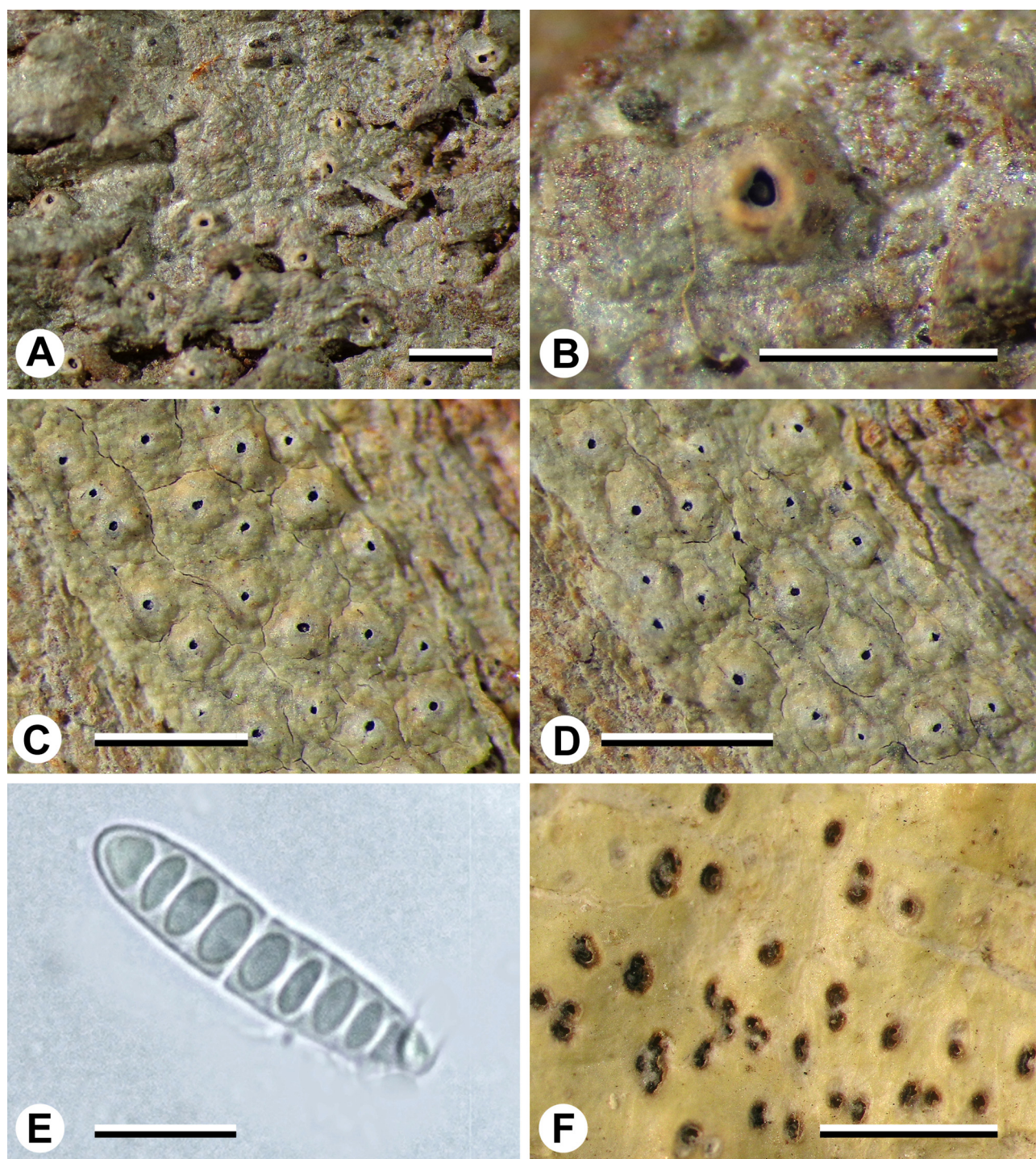


FIGURE 2. A–B. *Ocellularia kohangangensis*, thallus with ascomata (holotype). C–E. *Ocellularia pseudopapillata*, (holotype). C–D. Thallus with ascomata. E. Ascospore. F. *Ocellularia papillata*, thallus with ascomata (lectotype). Scale = 1 mm, in E = 10 μ m.

Ocellularia salazinica Papong, Mangold & Lücking, *sp. nov.* (Fig. 3A–D)

Mycobank 809248

Differing from *Ocellularia interponenda* in the ascomata with broad pore and broad, white-tipped columella becoming irregular and rhabdodiscoid.

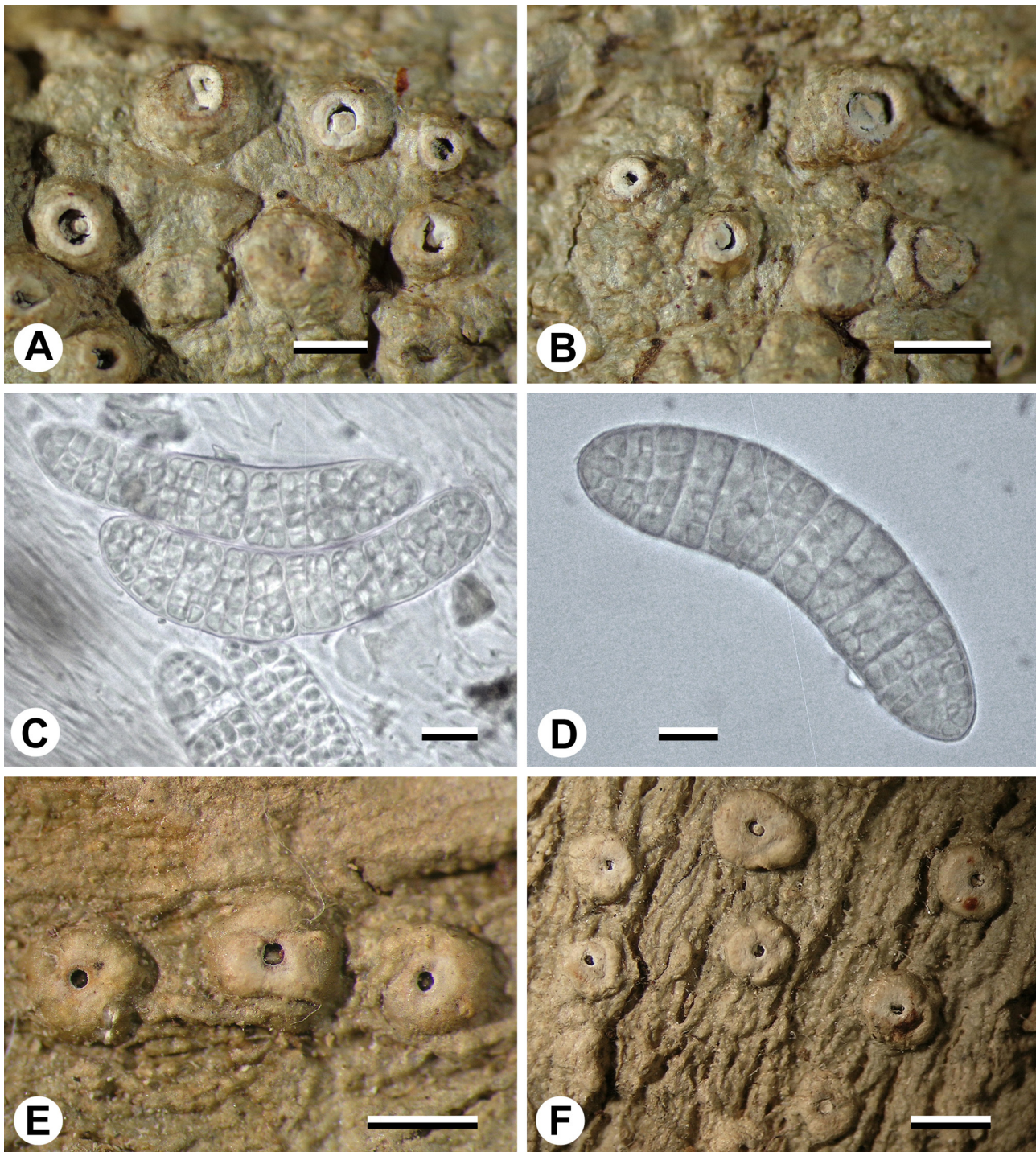


FIGURE 3. A–D. *Ocellularia salazinica* (holotype). A–B. Thallus with ascomata. C–D. Ascospores. E–F. *Ocellularia interponenda*, thallus with ascomata (E, lectotype; F, isotype). Scale = 1 mm, in C–D = 10 µm.

Type:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; secondary rainforest, on bark; 15 October 2010, *A. Mangold 102s* (holotype MSUT!; isotype F!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven-verrucose, light grey-green; prothallus absent. Thallus in section 80–100 µm thick, with paraplectenchymatous cortex, 10–20 µm thick,

photobiont layer 20–30 µm thick, and medulla 40–60 thick, with scattered clusters of calcium oxalate crystals; both photobiont layer and medulla also with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded to irregular in outline, erumpent to prominent, with nearly complete thalline margin, 0.8–1.5 mm diam., 0.4–0.6 mm high; disc covered by 0.3–0.6 mm wide pore, more or less filled by white-tipped, broad to irregularly dissected columella; proper margin distinct, entire, visible as broad, whitish rim around the pore; thalline margin entire, smooth to uneven, light grey-green. Excipulum entire, partially carbonized, partially orange, 30–70 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, broad to irregularly dissected and then forming irregular teeth, carbonized, up to 300 µm wide and 300–350 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 200–250 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 200–230 × 25–30 µm. Ascospores 2–4 per ascus, oblong, richly muriform, 80–100 × 15–22 µm, 4–5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Salazinic acid (medulla P+ orange-red, in section with K+ yellow efflux forming small, red crystals).

Etymology:—The specific epithet refers to the unusual chemistry.

Distribution and Ecology:—The new species was collected on an island in southern Thailand, growing on bark in the understory of a secondary forest. It is known only from the type locality.

Remarks:—Salazinic acid is a rare substance in Graphidaceae, only known from a handful of species in *Melanotopelia* Lumbsch & Mangold in Mangold *et al.* (2008b: 43) (1), *Ocellularia* Meyen (1825: 327) (2), and *Thelotrema* Acharius (1803: 43) (2). Within *Ocellularia*, two closely related species, *O. massalongoi* (Mont.) Hale (1980: 137) and *O. interponenda* (Nyl.) Hale (1980: 137), produce this substance. Both agree with the new species in the muriform ascospores and carbonized excipulum and columella, and all three species appear to be closely related, but they differ in the narrow-pored ascomata with finger-like columella (Fig. 3E–F). Indeed, the new species externally resembles a species of *Rhabdiscus* Vainio (1921: 184), but that genus is anatomically and chemically distinct, in having small ascospores and psoromic acid as main secondary compound (Rivas Plata *et al.* 2012).

Additional specimens examined:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold 102i* (F); *ibid.*, on trail to Khao Ra; 9°76'N, 100°03'E, 450 m; 15 October 2010, *A. Mangold 103k* (F).

***Ocellularia subdolichotata* Papong, Mangold & Lumbsch, *sp. nov.* (Fig. 4A–B)**

Mycobank 809249

Differing from *Ocellularia dolichotata* in the smooth, white thallus and 2–4-spored asci with smaller ascospores.

Type:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; secondary rainforest, on bark; 15 October 2010, *A. Mangold 102x* (holotype MSUT!; isotype F!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface smooth, white; prothallus absent. Thallus in section 80–120 µm thick, with paraplectenchymatous cortex, 10–20 µm thick, photobiont layer 20–40 µm thick, and medulla 40–70 thick, with large clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–10 µm. Ascomata round, prominent, with complete thalline margin, 0.8–1.2 mm diam., 0.4–0.6 mm high; disc completely covered by 0.1 mm wide pore, filled by white-tipped columella; proper margin thin, entire, visible as narrow, brownish rim around the pore; thalline margin entire, smooth, white. Excipulum entire, carbonized, 20–30 µm wide; laterally covered by algiferous, corticate thallus containing amorphous, orange-brown periderm layers, 200–300 µm thick; columella present, finger-like, 100–150 µm wide and 300–400 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 250–300 µm high, colorless, clear; epithecium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 220–250 × 25–30 µm. Ascospores 2–4 per ascus, oblong to cylindrical, 25–35-septate, 150–180 × 15–18 µm, 9–11 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Etymology:—The specific epithet refers to the close relationship with *Ocellularia dolichotata*.

Distribution and Ecology:—The new species was collected on an island in the gulf of Thailand in the south of the country. It is known only from the type locality.

Remarks:—*Ocellularia subdolichotata* closely resembles *O. dolichotata* (Nyl.) Zahlbruckner (1924: 589) in the prominent, columellate and carbonized ascomata, large, transversely septate ascospores, and lack of secondary substances. The latter, however, differs consistently in the finely verrucose, pale yellowish brown thallus (Fig. 4C) and the larger ascospores ($180\text{--}250 \times 20\text{--}30 \mu\text{m}$; Fig. 4D). A third, similar species that is usually included as synonym of *O. dolichotata* is *O. siamense* (Vain.) Zahlbruckner (1923: 600). It is similar to *O. dolichotata* in morphology, but its ascospores are even smaller than in *O. subdolichotata* ($70\text{--}120 \times 11\text{--}15 \mu\text{m}$). Typical specimens of *O. dolichotata* were also identified in the same collection and are cited below.

Specimens of *Ocellularia dolichotata* from the same area examined for comparison:—THAILAND. Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; $9^{\circ}76'N$, $100^{\circ}03'E$, 400 m; 15 October 2010, *A. Mangold* 102c, 102f, 102t, 102y (F); *ibid.*, on trail to Khao Ra; $9^{\circ}76'N$, $100^{\circ}03'E$, 450 m; 15 October 2010, *A. Mangold* 103e, 103n (F).

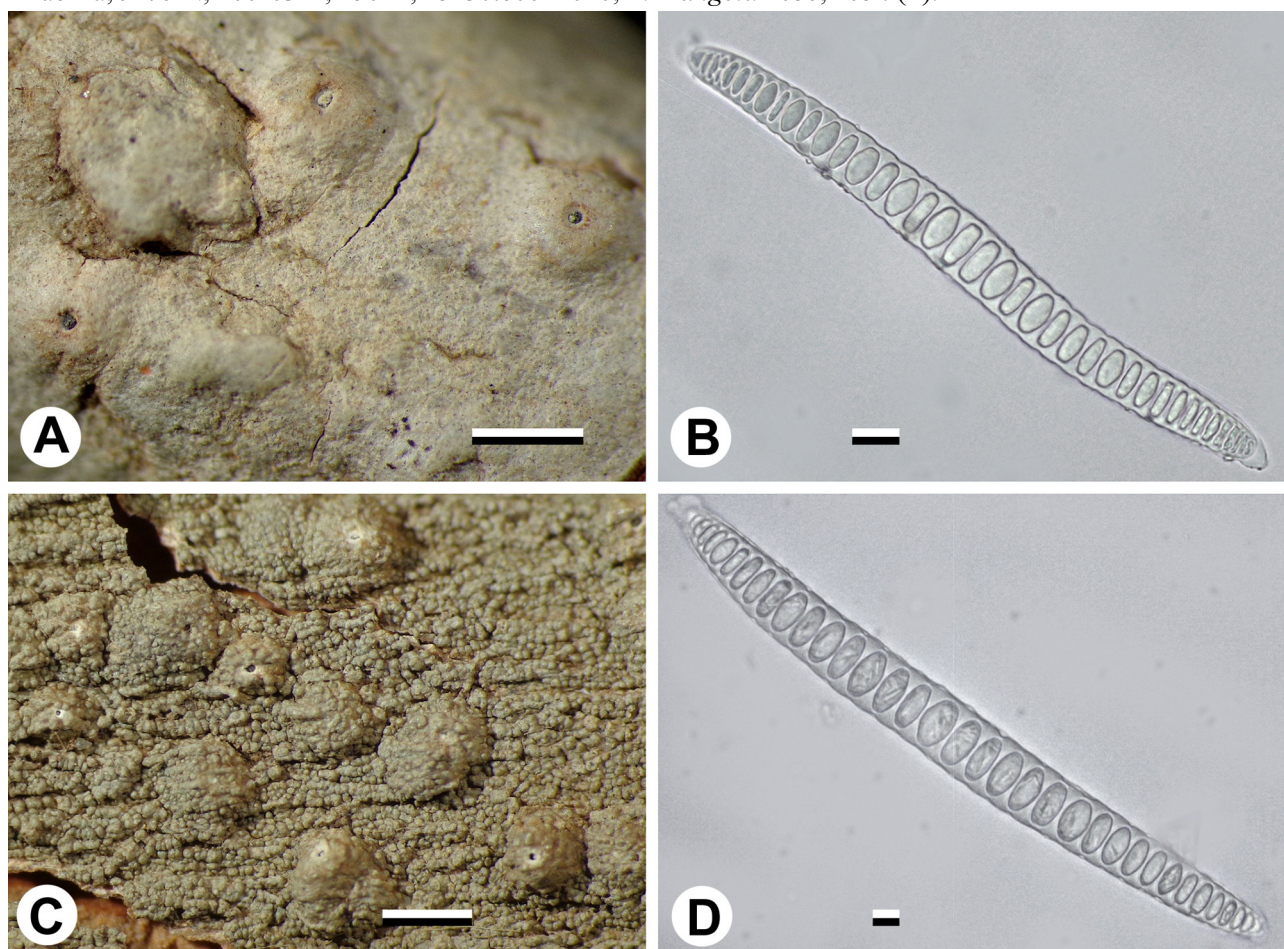


FIGURE 4. A–B. *Ocellularia subdolichotata* (holotype). A. Thallus with ascomata. B. Ascospore. C–D. *Ocellularia dolichotata* (*Mangold* 102t). C. Thallus with ascomata. D. Ascospore (*Mangold* 102t). Scale = 1 mm, in B and D = 10 μm .

New records for Thailand

Chapsa discoides (Stirt.) Lücking in Sipman *et al.* (2012: 35)

Specimen examined:—THAILAND. Uttaradit Province: Phu Soi Daow National Park, natural trail to top of mountain; 800 m; 27 February 2009, *K. Papong* 7004 (MSUT); Phu Pan National Park, Kham hom waterfall; 500 m; 23 February 2009, *K. Papong* 6521 (MSUT).

***Glaucotrema glaucophaenum* (Kremp.) Rivas Plata & Lumbsch** in Rivas Plata *et al.* (2012b: 1175)

Specimen examined:—THAILAND. Muk Dahan Province: Wat Tham Chao Pha, Phu Pha Kud, trail from temple to top of mountain; 16°46'N, 104°43'E, 285 m; 20 June 2009, *K. Papong* 6720 (MSUT).

***Leucodecton anamalaiense* (Patw. & C. R. Kulk.) Rivas Plata & Lücking** in Rivas Plata *et al.* (2010: 184)

Specimens examined:—THAILAND: Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 103i (F).

***Ocellularia fumosa* (Ach.) Müller** (1887: 7)

Specimen examined:—THAILAND. Muk Dahan Province: Wat Tham Chao Pha, Phu Pha Kud, trail from temple to top of mountain; 16°46'N, 104°43'E, 285 m; 20 June 2009, *K. Papong* 6719, 6722 (MSUT).

***Ocellularia granulifera* (Kremp.) Müller** (1892: 284) (Fig. 5B)

Specimen examined:—THAILAND: Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 102n-2 (MSUT).

***Ocellularia violacea* Räsänen** (1949: 184)

Specimen examined:—THAILAND: Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 102n (F).

***Ocellularia viridipallens* Müller** (1887: 397)

Specimen examined:—THAILAND. Surat Thani Province: Koh Phangang, Northern Island, Chaloklam area, E of Chaloklam Rd.; 9°76'N, 100°03'E, 450 m; 15 October 2010, *A. Mangold* 100b (F). Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 103c (F).

***Rhabdodiscus subcavatus* (Nyl.) Rivas Plata & Lumbsch** in Rivas Plata *et al.* (2012b: 1176) (Fig. 5C)

Specimens examined:—THAILAND: Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 102n-2 (F); *ibid.*, on trail to Khao Ra; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 103b (F).

***Stegobolus berkeleyanus* Montagne** (1845: 4)

Specimens examined:—THAILAND: Surat Thani Province: Koh Phangang, Central Island, E of Chaloklam Rd., on trail to Khao Ra, near "Khao Ra Bungalows"; 9°76'N, 100°03'E, 400 m; 15 October 2010, *A. Mangold* 102h, 102m (F).

***Thelotrema defossum* (Müll. Arg.) Mangold** in Lumbsch *et al.* (2008: 221)

Specimen examined:—THAILAND. Surat Thani Province: Koh Phangang, Northern Island, Chaloklam area, E of Chaloklam Rd.; 9°76'N, 100°03'E, 450 m; 15 October 2010, *A. Mangold* 100e, 100h (F).

***Thelotrema subadjectum* Mangold** (2009: 658) (Fig. 5D)

Specimen examined:—THAILAND. Muk Dahan Province: Wat Tham Chao Pha, Phu Pha Kud, trail from temple to top of mountain; 16°46'N, 104°43'E, 285 m; 20 June 2009, *K. Papong* & *A. Butsathron* 6716 (F, MSUT).

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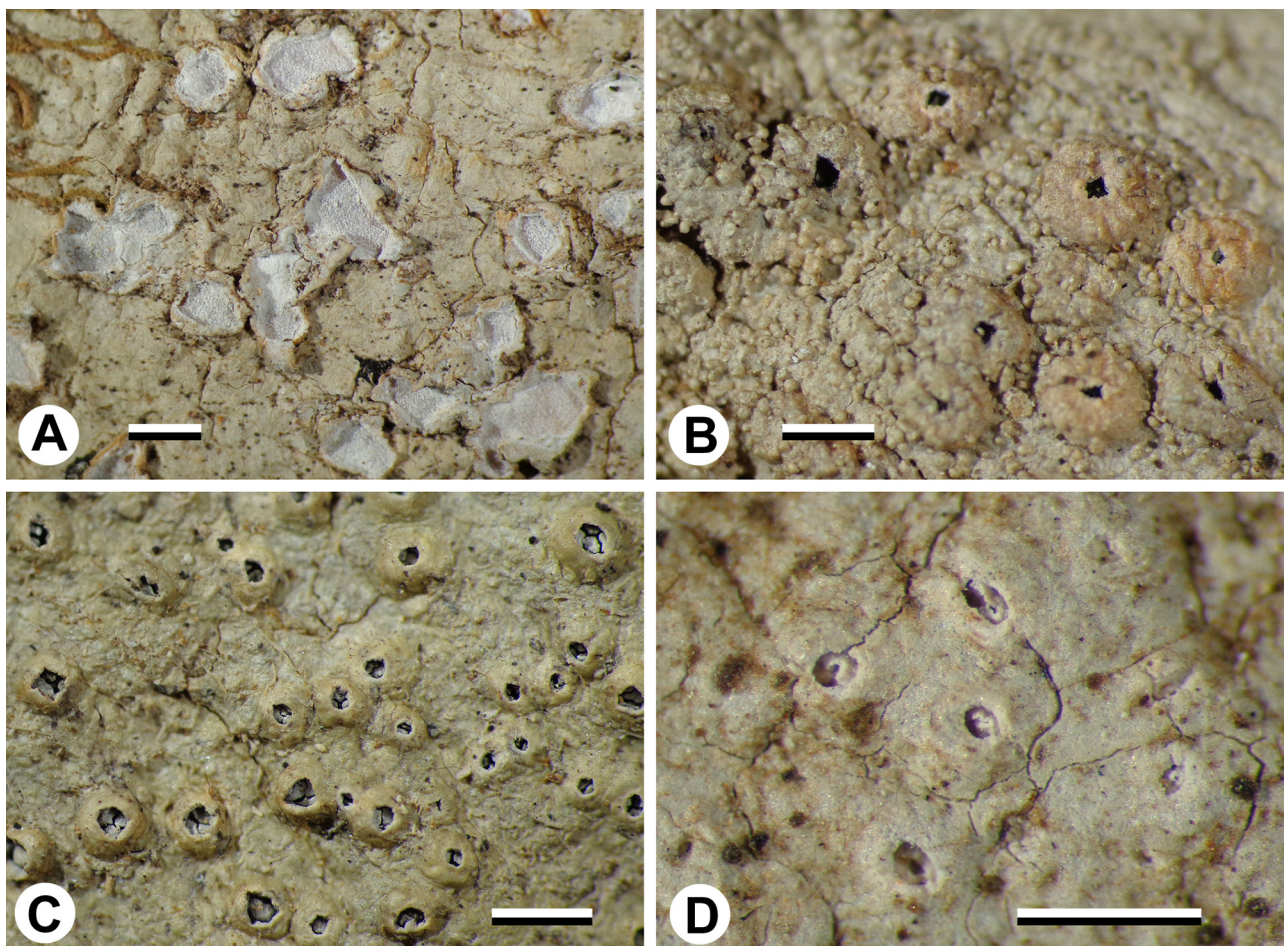


FIGURE 5. A. *Chapsa patens*, thallus with ascomata (Mangold 103m). B. *Ocellularia granulifera*, thallus with ascomata (Mangold 102n-2). C. *Rhabdodiscus subcavatus*, thallus with ascomata (Mangold 103b). D. *Thelotrema subadjectum*, thallus with ascomata (Papong & Butsathron 6716). Scale = 1 mm.

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ไลเคนกลุ่ม Thelotremoid Graphidaceae ในเกาะพงัน จังหวัดสุราษฎร์ธานี

Thelotremoid Graphidaceae lichens in Ko Pha-ngun, Suratthani province

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บทคัดย่อ. สำรวจไลเคนกลุ่ม Thelotremoid Graphidaceae ในเกาะพงัน จังหวัดสุราษฎร์ธานี โดยเก็บจากป่าดิบชื้นและป่าดิบชื้นรุ่มสอง พบว่ามีความหลากหลายชนิดของไลเคนกลุ่ม Thelotremoid Graphidaceae สูงอีกพื้นที่หนึ่งในประเทศไทย พบไลเคนทั้งหมดจำนวน 23 ชนิด 10 สกุล ได้แก่ *Astrochapsa* (1 ชนิด) *Chapsa* (2 ชนิด) *Leucodecton* (2 ชนิด) *Melanotrema* (1 ชนิด) *Myriotrema* (1 ชนิด) *Ocellularia* (9 ชนิด) *Pseudotopliopsis* (1 ชนิด) *Rhabdodiscus* (2 ชนิด) *Stegobolus* (1 ชนิด) และ *Thelotrema* (3 ชนิด)

ABSTRACT. Thelotremoid Graphidaceae lichens in Ko Pha-ngun, Suratthani province were investigated. All samples were collected in tropical rainforest and secondary forest. Ko Pha-ngun was found high species diversity of Thelotremoid Graphidaceae in Thailand. Twenty-three species, 10 genera were found; *Astrochapsa* (1 species), *Chapsa* (2 species), *Leucodecton* (2 species), *Melanotrema* (1 species), *Myriotrema* (1 species), *Ocellularia* (9 species), *Pseudotopliopsis* (1 species), *Rhabdodiscus* (2 species), *Stegobolus* (1 species) and *Thelotrema* (3 species).

คำสำคัญ: ไลเคน, Thelotremoid Graphidaceae, เกาะพงัน

KEYWORDS: lichen, Thelotremoid Graphidaceae, Ko Pha-ngun

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บทนำ

ปัจจุบันไลเคนวงศ์ Graphidaceae มีจำนวนสมาชิกมากกว่า 2,000 ชนิด เนื่องจากมีข้อมูลสนับสนุนจากการศึกษาด้านชีวโมเลกุล (DNA sequences) และความสัมพันธ์ด้านวิวัฒนาการ (phylogeny) ได้ทำการรวมไลเคน 5 วงศ์ ได้แก่ Graphidaceae, Thelotremaaceae, Asterothyriaceae, Gomphillaceae และ Solorinellaceae อยู่ในวงศ์ Graphidaceae เพียงวงศ์เดียว และแยกออกเป็น 3 วงศ์ย่อย (subfamily) ได้แก่ Fissurinoideae, Gomphilloideae และ Graphidoideae เฉพาะวงศ์ย่อย Graphidoideae แบ่งเป็น 3 tribes ได้แก่ Graphideae, Thelotremateae และ Ocellularieae ซึ่งทำให้ปัจจุบันไลเคนวงศ์ Graphidaceae มีจำนวนสมาชิกมากที่สุดในกลุ่มราที่ก่อให้เกิดไลเคน (lichenized fungi) นอกเหนือจากไลเคนวงศ์ Parmeliaceae ซึ่งพบว่ามีจำนวนสมาชิกจำนวนมากเช่นเดียวกัน (Sipman *et al.*, 2012)

ไลเคนกลุ่ม Thelotremoid Graphidaceae มีการจัดจำแนกออกเป็น 5 เคลด (clades) ได้ดังนี้ (1) **Fissurina clade** ได้แก่ สกุล *Clandestinotrema*, *Cruentotrema* และ *Pycnotrema* (2) **Topeliopsis clade** ได้แก่ สกุล *Melanotopelia*, *Nadvornikia*, *Schizotrema*, *Topeliopsis* และ *Wirthiotrema* (3) **Diploschistes clade** ได้แก่ สกุล *Acanthotrema* และ *Diploschistes* (4) **Thelotrema clade** ได้แก่ สกุล *Arthochasa*, *Chapsa*, *Chroodiscus*, *Leucodecton* และ *Thelotrema* และ (5) **Ocellularia clade** ได้แก่ สกุล *Ampliotrema*, *Fibrillithecis*, *Gyrostomum*, *Leptotrema*, *Melanotrema*, *Myriotrema*, *Ocellularia*, *Redingeria*, *Reimnitzia*, *Rhabdodiscus* และ *Stegobolus* (Rivas Plata *et al.*, 2012; Parnmen *et al.*, 2012)

ไลเคนกลุ่ม Thelotremoid Graphidaceae ในประเทศไทย มีรายงานการค้นพบตั้งแต่ปี พ.ศ. 2542 ถึง พ.ศ. 2550 พบทั้งหมด 104 ชนิด (Homchantara, 1999; Homchantara & Coppins, 2002; Wolseley *et al.*, 2002; Aptroot *et al.*, 2007) ต่อมาปี พ.ศ. 2553 Papong *et al.* (2010) ได้ศึกษาทบทวนตัวอย่างไลเคนกลุ่ม Thelothemoid Graphidaceae ที่รายงานในประเทศไทยเมื่อปี พ.ศ. 2545 พบว่าหลายชนิดเป็นชื่อพ้อง (synonym) ต่อมา รัตนา เฟื่องเพราะ และคณะ (2555) ศึกษาอนุกรมวิธานของไลเคนสกุล *Ocellularia* (Thelotremataceae) ในประเทศไทยพบทั้งหมด 45 ชนิด และได้รายงานการแพร่กระจายของไลเคนสกุลดังกล่าวเพิ่มเติมจากที่เคยมีรายงานในประเทศไทยมาแล้ว อย่างไรก็ตาม ไลเคนกลุ่ม Thelotremoid Graphidaceae ยังไม่เคยมีรายงานการเก็บตัวอย่างจากเกาะพังนัง จังหวัดสุราษฎร์ธานีมาก่อน ซึ่งในการศึกษารั้งนี้ทำให้ทราบข้อมูลเกี่ยวกับการแพร่กระจายของไลเคนในกลุ่มนี้มากขึ้นในป่าธรรมชาติของประเทศไทย และเพื่อใช้เป็นฐานข้อมูลความหลากหลายทางชีวภาพเพื่อการจัดการสิ่งแวดล้อมได้ในอนาคต

วิธีการวิจัย

เก็บตัวอย่างไลเคนกลุ่ม Thelotremoid Graphidaceae จากป่าดิบชื้นและป่าดิบชื้นรุ่มสองในเกาะพังนัง จังหวัดสุราษฎร์ธานี ที่ละติจูด 09° 78' 60" N และ 100° 01' 80" E มีความสูงจากระดับน้ำทะเล 200-450 เมตร ศึกษาลักษณะพื้นฐานวิทยาจากตัวอย่างไลเคนด้วยกล้องจุลทรรศน์กำลังขยายต่ำ ศึกษาลักษณะโครงสร้างภายในโดยการตัดตัวอย่างไลเคนด้วยมือ (free hand section) และศึกษาภายใต้กล้องจุลทรรศน์แบบใช้แสง ส่วนการศึกษาด้านสารจากไลเคน (lichen substance) ด้วยการทำรงคเลขผิวบางด้วยเครื่อง Horizontal

Developing Chamber For TLC/HPTLC 10x10 cm plate โดยใช้แผ่น HPTLC Silica gel 60 F₂₅₄ ใช้ตัวทำละลายระบบ C และใช้วิธีมาตรฐานของ Arup *et al.* (1993) โดยตัวอย่างไลเคนเก็บรักษาไว้ที่ Field Museum of Natural History (F) เมืองชิคาโก รัฐอิลลินอยด์ ประเทศสหรัฐอเมริกา และพิพิธภัณฑ์ให้ดที่มีฤทธิ์ทางยา (MSUT: Natural Medicinal Mushroom Museum) มหาวิทยาลัยมหาสารคาม

ผลการวิจัย

พบไลเคนกลุ่ม Thelotremoid Graphidaceae จำนวน 23 ชนิด 10 สกุล (ตารางที่ 1) สกุลที่พบมากที่สุด 9 ชนิด คือ *Ocellularia* รองลงมาคือสกุล *Thelotrema* พบ 3 ชนิด สกุล *Chapsa*, *Leucodecton* และ *Rhabdodiscus* พบ 2 ชนิด และสกุล *Arthochapsa*, *Melanotrema*, *Myriotrema*, *Pseudotopliopsis* และ *Stegobolus* พบเพียง 1 ชนิด ตามลำดับ (ภาพที่ 1-3)

ไลเคนกลุ่ม Thelotremoid Graphidaceae ที่สำรวจพบ 23 ชนิด มีลักษณะดังต่อไปนี้

1. *Astrochapsa astroidea* (Berk. & Broome) Parmen, Lücking & Lumbsch, PLoS ONE 7 (12): e51392 (2012)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังในแทลลัสครั้งหนึ่ง (erumpent) แบบโครโอติสคอยด์ (chroodiscoid) ขอบของแอโพธิ์เซียแตกคล้ายโลบและโค้งงอ ไม่สร้างคอลิวเมลล่า (columella) เอ็กซิพุลัมแบบพาราเพลคเทนไคมาทัส (excipulum paraplectenchymatous) สร้างเพอริไฟซอยด์ (periphysoid) แอสโคสปอร์แบบมีผนังกันตามขวาง 5-6 ผนัง (transversely septate) รูปร่างขอบขนาน (oblong) ขนาด 17.5-20 x 2.5-3 ไมครอน ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: *A. astroidea* มีแอโพธิ์เซียแบบโครโอติสคอยด์ ขอบของแอโพธิ์เซียแตกคล้ายโลบและโค้งงอคล้ายกลีบดอกไม้ หน้าจานของแอโพธิ์เซียมีสีขาวค่อนข้างเทา สังเกตง่ายในแหล่งอาศัย และมีแอสโคสปอร์แบบมีผนังกันตามขวาง 5-6 ผนัง

การแพร่กระจาย: คอสตาริกา ออสเตรเลีย บราซิล และไทย

2. *Chapsa patens* (Nyl.) A. Frisch, Bibliotheca Lichenologica 92: 111 (2006)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังในแทลลัสครั้งหนึ่ง แบบโครโอติสคอยด์ ขอบของแอโพธิ์เซียแตกคล้ายโลบและโค้งงอ ไม่สร้างคอลิวเมลล่า เอ็กซิพุลัมแบบพาราเพลคเทนไคมาทัส สร้างเพอริไฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาว (muriform) รูปร่างขอบขนาน ขนาด 55-117.5 x 17.5-27.5 ไมครอน ไม่มีสี 1 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: ลักษณะของแอโพธิ์เซียคล้ายกับ *A. astroidea* แต่แตกต่างกันที่ *C. patens* มีแอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาว ส่วน *A. astroidea* แอสโคสปอร์แบบมีผนังกันตามขวาง 5-6 ผนัง

การแพร่กระจาย: อินเดีย ศรีลังกา ญี่ปุ่น แอฟริกา บราซิล และไทย

3. *Chapsa soorediata* Kalb, Herzogia 22: 17-42 (2009)

ลักษณะที่สำคัญ: บนแทลลัสสร้างซอเรียเดีย (soredia) กระจายทั่วทั้งแทลลัส ไม่สร้างแอโพธิ์เซียบนแทลลัส

สารไลเคน: stictic acid

ข้อสังเกต: *Ch. soorediata* ลักษณะสำคัญ ไม่สร้างแอโพธิ์เซียบนแทลลัส สร้างเฉพาะซอเรียเดีย และสร้างสารไลเคนชนิด stictic acid

การแพร่กระจาย: อินเดียและไทย

4. *Leucodecton anamalaiense* (Patw.

& C.R. Kulk.) Rivas Plata & Lücking, Rivas Plata *et al.*, Lichenologist 42(2): 139-185 (2010)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครึ่งหนึ่ง รูปร่างกลม มีรูเล็ก (ostiole) ด้านบน ไม่สร้างคอลลิวเมลล่า เอ็กซิพุลัมแบบพาราเพลคเทน ไคมาทัส ไม่สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาว รูปทรงรี (ellipsoid) ขนาด 62.5-75 x 17.5-18 ไมครอน ไม่มีสี 1 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: stictic acid, constictic acid, acetyl constictic acid

ข้อสังเกต: *L. anamalaiense* ลักษณะของแอโพธิ์เซียสังเกตเห็นเพียงรูเล็กด้านบนเท่านั้น แอโพธิ์เซียส่วนใหญ่ฝังในแทลลัส

การแพร่กระจาย: ฟิลิปปินส์และไทย

5. *Leucodecton compunctellum* (Nyl.)

Frisch, Bibliotheca Lichenologica 92: 155 (2006)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครึ่งหนึ่ง รูปร่างกลม มีรูเล็กด้านบน ไม่สร้างคอลลิวเมลล่า เอ็กซิพุลัมแบบพาราเพลคเทน ไคมาทัส ไม่สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาว รูปรี ขนาด 75-100 x 17.5-30 ไมครอน สีน้ำตาล 1 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: stictic acid, constictic acid, acetyl constictic acid (ตัวอย่างจาก คอสตาริกา สร้างสารไลเคนชนิด hypostictic acid และ hypoconstictic acid)

ข้อสังเกต: *L. compunctellum* ลักษณะแอโพธิ์เซียคล้ายกับ *L. anamalaiense* แต่แตกต่างกันที่ *L. compunctellum* แอสโคสปอร์มีสีน้ำตาล ส่วน *L. anamalaiense* แอสโคสปอร์ไม่มีสี

การแพร่กระจาย: ออสเตรเลีย คอสตาริกา สิงคโปร์ ศรีลังกา อินเดีย (หมู่เกาะอันดามัน) โดมินีกา และไทย

6. *Melanotrema platystomum* (Mont.)

Frisch, Bibliotheca Lichenologica 92: 397 (2006)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครึ่งหนึ่ง รูปร่างกลมถึงมีเหลี่ยมมุม มีรูเล็กด้านบน สร้างคอลลิวเมลล่า รูปร่างคล้ายตอไม้ (broad-stump-shaped) สีดำคล้ายถ่าน (carbonized) เอ็กซิพุลัมแบบโปรโสเพลคเทน ไคมาทัส (excipulum prosoplectenchymatous) สีดำคล้ายถ่าน ไม่สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 5-9 ผนัง รูปรี ขนาด 16-25 x 6-8 ไมครอน เซลล์ภายในเป็นรูปเลนส์ (lens shaped) ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: *M. platystomum* ลักษณะแอโพธิ์เซียคล้ายไลเคนสกุล *Myriothea* แตกต่างกันที่ชนิดนี้สร้างคอลลิวเมลล่า รูปร่างคล้ายตอไม้ และสีดำคล้ายถ่าน ส่วน *Myriothea* ไม่สร้างคอลลิวเมลล่า

การแพร่กระจาย: เฟรนช์เกียนา ฟิลิปปินส์ แอฟริกา คอสตาริกา และไทย

7. *Myriotrema clandestinum* (Fée)

Hale; Mycotaxon 11(1): 133 (1980), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัส (immersed) รูปร่างกลมถึงมีเหลี่ยมมุม มีรูเล็กด้านบน ไม่สร้างคอลลิวเมลล่า เอ็กซิพุลัมแบบโปรโสเพลคเทน ไคมาทัส ไม่มีสี ไม่สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 3 ผนัง รูปรี ขนาด 10-12.5 x 5 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: psoromic acid (ตัวอย่างจากคอสตาริกา สร้างสารไลเคนชนิด subpsoromic acid และ 2'-O-demethylpsoromic acid)

ข้อสังเกต: *M. clandestinum* ลักษณะที่สังเกตง่ายแอโพธิ์เซียแบบฝังในแทลลัสมีรูเล็ก

ด้านบน สีรอบขอบรูเล็กสีครีมถึงสีเหลืองอ่อน แอสโคสปอร์แบบมีผนังกันตามขวาง 3 ผนัง และสร้างสารไลเคนชนิด psoromic acid

การแพร่กระจาย: สหรัฐอเมริกา โคลัมเบีย คอสตาริกา ออสเตรเลีย และไทย

8. *Ocellularia cavata* (Ach.) Müll. Arg.; Flora 65: 499 (1882), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เชียนูนขึ้นมาจากแทลลัส (prominent) รูปร่างกลม มีรูเล็กด้านบน ไม่สร้างคอลลิวเมลล่า สีดำคล้ายถ่านเอ็กซิพูล์มแบบโปรโสเพลคเทนโคมาทัส สีดำคล้ายถ่าน ไม่สร้างเพอร์ไฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 6-9 ผนัง รูปร่าง ขนาด 22.5-32.5 x 5-8 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 6-8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: cinchonarum unknown

ข้อสังเกต: *O. cavata* สร้างสารไลเคนชนิด cinchonarum unknowns สะสมในชั้นเมดัลล่า และให้สีค่อนข้างเหลือง ตรวจจอบอย่างง่ายโดยใช้ปลายมีดเปิดแทลลัสให้เห็นชั้นเมดัลล่าด้านในสีเหลือง

การแพร่กระจาย: โคลัมเบีย ออสเตรเลีย ศรีลังกา สิงคโปร์ บราซิล มาเลเซีย และไทย

9. *Ocellularia dolichotata* (Nyl.) Zahlbr.; Cat. Lich. Univ. 2: 589 (1923), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เชียนูนขึ้นมาจากแทลลัส รูปร่างกลม มีรูเล็กด้านบน สร้างคอลลิวเมลล่า สีดำคล้ายถ่านเอ็กซิพูล์มแบบโปรโสเพลคเทนโคมาทัส สีดำคล้ายถ่าน ไม่สร้างเพอร์ไฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 29-39 ผนัง รูปกระสวย (fusiform) ขนาด 162.5-250 x 17.5-22.5 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 2-3 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์ ตัวอย่างจากคอสตาริกามีจำนวนผนังกันตามขวางน้อยกว่า

คือ 17-27 ผนัง และพบ 1 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์ (Sipman *et al.*, 2012)

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: ไลเคนชนิดนี้ มีคอลลิวเมลล่าสีดำคล้ายถ่าน มีแอสโคสปอร์ขนาดใหญ่มีหลายผนังกันตามขวางและไม่สร้างสารไลเคน

การแพร่กระจาย: สิงคโปร์ ฟิลิปปินส์ คอสตาริกา และไทย

10. *Ocellularia interponenda* (Nyl.) Hale, Mycotaxon 11(1): 137 (1980), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เชียนูนขึ้นมาจากแทลลัส รูปร่างกลม มีรูเล็กด้านบน สร้างคอลลิวเมลล่า สีดำคล้ายถ่านเอ็กซิพูล์มแบบโปรโสเพลคเทนโคมาทัส สีดำคล้ายถ่าน ไม่สร้างเพอร์ไฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง และผนังกันตามยาว รูปกระสวย ขนาด 55-75 x 15-25 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 3-6 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: salazinic acid

ข้อสังเกต: *O. interponenda* ลักษณะแอโพธิ์เชียนูนมีรูเล็กด้านบน ขอบของรูเล็กหนามีสีครีมค่อนข้างเหลืองสังเกตง่ายและสร้างสารไลเคนชนิด salazinic acid

การแพร่กระจาย: อินเดียและไทย

11. *Ocellularia massalongoi* (Mont.) Hale, Mycotaxon 11: 137 (1980), (Homchantara, 1999)

ลักษณะที่สำคัญ: แอโพธิ์เชียนูนขึ้นมาจากแทลลัส รูปร่างกลม มีรูเล็กด้านบน สร้างคอลลิวเมลล่า สีดำคล้ายถ่านเอ็กซิพูล์มแบบโปรโสเพลคเทนโคมาทัส สีดำคล้ายถ่าน ไม่สร้างเพอร์ไฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง และผนังกันตามยาว รูปขอบขนาน ขนาด 80-125 x 17.5-25 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 4 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: salazinic acid

ข้อสังเกต: *O. massalongoi* รูปร่างทาง
สัณฐานวิทยาและสร้างสารไลเคนชนิด salazinic
acid คล้ายกับ *O. Interponenda* แตกต่างกันว่า
ไลเคนชนิดนี้มีขนาดของแอสโคสปอร์ใหญ่กว่า

การแพร่กระจาย: อินเดีย ฟิลิปปินส์
ศรีลังกา ออสเตรเลีย และไทย

12. *Ocellularia papillata* (Leighton)
Zahlbr.; Cat. Lich. Univ. 2: 597 (1923), (Mangold
et al., 2009)

ลักษณะที่สำคัญ: แอโพรีเซียขึ้นมาจาก
จากแทลลัส รูปร่างกลม มีรูเล็กด้านบน สร้างคอกลิ
เมลล่า สีน้ำตาลเข้ม เอ็กซีพุลัมแบบโพโรสเฟลคเทน
โคมาทัส สีน้ำตาลเข้ม ไม่สร้างเพอริโฟชอยด์
แอสโคสปอร์มีผนังกันตามขวาง 5-8 ผนัง รูปขอบ
ขนาน ขนาด 15-25 x 5-8 ไมครอน เซลล์ภายใน
เป็นรูปเลนส์ ไม่มีสี 6 แอสโคสปอร์/ถุงหุ้ม
แอสโคสปอร์ ตัวอย่างจากคอสตารีก้า แอสโคสปอร์
มีผนังกันตามขวาง 3-5 ผนัง 8 แอสโคสปอร์/
ถุงหุ้มแอสโคสปอร์ (Sipman *et al.*, 2012)

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: ไลเคนชนิดนี้ลักษณะทาง
สัณฐานวิทยาของแอโพรีเซียคล้ายไลเคนสกุล
Myriothea แตกต่างกันว่า *O. papillata* สร้าง
คอกลิเมลล่า สีน้ำตาลเข้ม

การแพร่กระจาย: ศรีลังกา ฟิลิปปินส์
คอสตารีก้าและไทย

13. *Ocellularia terebrata* (Ach.) Müll.
Arg., Flora 70: 398 (1887), (Homchantara,
1999)

ลักษณะที่สำคัญ: แอโพรีเซียฝังใน
แทลลัสครึ่งหนึ่ง รูปร่างกลม มีรูเล็กด้านบน
สร้างคอกลิเมลล่า สีดำคล้ายถ้ำเอ็กซีพุลัมแบบ
โพโรสเฟลคเทนโคมาทัส สีดำคล้ายถ้ำ ไม่สร้าง
เพอริโฟชอยด์ แอสโคสปอร์มีผนังกันตามขวาง

5-8 ผนัง รูปร่าง ขนาด 20-25 x 6-7.5 ไมครอน
เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 6 แอสโคสปอร์/
ถุงหุ้มแอสโคสปอร์

สารไลเคน: psoromic acid ตัวอย่าง
จากคอสตารีก้าสร้างสารไลเคน subpsoromic acid
และ 2'-O-demethylpsoromic acid (Sipman
et al., 2012)

ข้อสังเกต: *O. terebrata* ลักษณะคล้ายกับ
O. papillata แตกต่างกันว่า *O. terebrata* สร้างสาร
ไลเคนชนิด psoromic acid ส่วน *O. papillata*
ไม่สร้างสารไลเคนเลย

การแพร่กระจาย: สหรัฐอเมริกา (เกาะ
ฮาวาย) แอฟริกา อินเดีย เวเนซุเอลา บราซิล
คอสตารีก้า ออสเตรเลีย และไทย

14. *Ocellularia treloremoides* (Leighton)
Zahlbr.; Cat. Lich. Univ. 2: 603 (1923),
(Homchantara, 1999)

ลักษณะที่สำคัญ: แอโพรีเซียฝังใน
แทลลัสครึ่งหนึ่ง รูปร่างกลม มีรูเล็กด้านบน
สร้างคอกลิเมลล่า สีดำคล้ายถ้ำเอ็กซีพุลัมแบบ
โพโรสเฟลคเทนโคมาทัส สีดำคล้ายถ้ำ ไม่สร้าง
เพอริโฟชอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง
และผนังกันตามยาว รูปกระสวย ขนาด 15-30 x
7-13 ไมครอน ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้ม
แอสโคสปอร์

สารไลเคน: protocetraric acid และ
fumarprotocetraric acid

ข้อสังเกต: *O. treloremoides* มี
แอสโคสปอร์แบบมีผนังกันตามขวางและผนังกัน
ตามยาวขนาดเล็กและสร้างสารไลเคนชนิด
protocetraric acid และ fumarprotocetraric acid

การแพร่กระจาย: ศรีลังกา อินเดีย (หมู่
เกาะอันดามัน) เวียดนาม ออสเตรเลีย ฟิลิปปินส์
ทรินิแดด มาเลเซีย และไทย

15. *Ocellularia violacea* Räsänen; Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat (Arch. Soc. Zool. Bot. Fenn. Vanamo) 3: 184 (1949), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครั้งหนึ่ง รูปร่างกลม มีรูเล็กด้านบน สร้างคอลิวเมลล่า สีดำคล้ายถ่าน เอ็กซีพุลัมแบบ โพรโสเพลคเทนไคมาทัส สีน้ำตาล ไม่สร้าง เพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 5-7 ผนัง รูปรี ขนาด 15-25 x 7-8 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: protocetraric acid ตัวอย่าง จากคอสตาริก้าสร้างสารไลเคนชนิด virensic acid (Sipman *et al.*, 2012)

ข้อสังเกต: *O. violacea* แอสโคสปอร์มี ผนังกันตามขวาง 5-7 ผนัง และสร้างสารไลเคน ชนิด protocetraric acid

การแพร่กระจาย: ออสเตรเลีย คอสตาริก้า และไทย

16. *Ocellularia viridipallens* Müll. Arg.; Flora, Jena 70: 397 (1887), (Mangold *et al.*, 2009)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครั้งหนึ่ง รูปร่างกลม มีรูเล็กด้านบน สร้างคอลิวเมลล่า สีดำคล้ายถ่าน เอ็กซีพุลัมแบบ โพรโสเพลคเทนไคมาทัส สีน้ำตาล ไม่สร้าง เพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 7-8 ผนัง รูปรี ขนาด 25-30 x 7.5-8 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

การแพร่กระจาย: ออสเตรเลียและไทย

17. *Pseudotopliopsis aggregate* (Hale) Parmen, Lücking & Lumsch, PLoS ONE 7(12): e51392 (2012).

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครั้งหนึ่ง แบบโครโอติสคอยด์ ขอบของ แอโพธิ์เซียแตกคล้ายlobและโค้งงอ ไม่สร้าง คอลิวเมลล่า เอ็กซีพุลัมแบบพาราเพลคเทนไคมาทัส ไม่มีสี สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมี ผนังกันตามขวาง 4-5 ผนัง รูปรี ขนาด 17.5-25 x 5-10 ไมครอน สีน้ำตาล 8 แอสโคสปอร์/ถุงหุ้ม แอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: ไลเคนชนิดนี้มีแอโพธิ์เซีย แบบโครโอติสคอยด์ แอสโคสปอร์แบบมีผนังกัน ตามขวาง 4-5 ผนัง สีน้ำตาลและไม่สร้างสาร ไลเคน

การแพร่กระจาย: โดมินีก้า ฟิลิปปินส์ และไทย

18. *Rhabdodiscus subcavatus* (Nyl.) Rivas Plata & Lumsch, Fungal Diversity 52: 107-121 (2012)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครั้งหนึ่ง แบบโครโอติสคอยด์ ขอบของ แอโพธิ์เซียแตกคล้ายlobและโค้งงอ ไม่สร้าง คอลิวเมลล่า เอ็กซีพุลัมแบบพาราเพลคเทนไคมาทัส ไม่มีสี สร้างเพอร์โฟซอยด์ แอสโคสปอร์แบบมีผนัง กันตามขวาง 7 ผนัง รูปรี ขนาด 20-22 x 5 ไมครอน สีน้ำตาล 6 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: psoromic acid

ข้อสังเกต: *R. subcavatus* แอสโคสปอร์ แบบมีผนังกันตามขวาง 7 ผนัง สีน้ำตาลและสร้าง สารไลเคนชนิด psoromic acid

การแพร่กระจาย: ฟิลิปปินส์และไทย

19. *Rhabdodiscus submersus* (Müll. Arg.) Rivas Plata & Lumsch, Fungal Diversity 52: 107-121 (2012)

ลักษณะที่สำคัญ: แอโพธิ์เซียฝังใน แทลลัสครั้งหนึ่ง แบบโครโอติสคอยด์ ขอบของ แอโพธิ์เซียแตกคล้ายlobและโค้งงอ ไม่สร้าง

คอลลิวเมลล่า เอ็กซีพุลัมแบบพาราเพลคเทนไคมาทัส ไม่มีสี สร้างเพอร์ไฟโซยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 7 ผนัง รูปรี ขนาด 27.5-30 x 5 ไมครอน สีนํ้าตาล 6 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: cinchonarum unknowns

ข้อสังเกต: ไลเคนชนิดนี้คล้ายกับ *R. subcavatus* แตกต่างกันที่ไลเคนชนิดนี้สร้างสารไลเคนชนิด cinchonarum unknowns ส่วน *R. subcavatus* สร้างสารไลเคนชนิด psoromic acid

การแพร่กระจาย: ฟิลิปปินส์และไทย

20. *Stegobolus berkeleyanus* Mont.;

Hook., London J. Bot. 4: 4 (1845), (Rivas Plata *et al.*, 2012)

ลักษณะที่สำคัญ: แอโพธีเซียฝังในแทลลัสครึ่งหนึ่ง รูปร่างกลมคล้ายถ้วย (disc) สร้างคอลลิวเมลล่า เชื่อมกันเป็นร่างแห (reticulate) มองเห็นคอลลิวเมลล่าชัดเจนจากด้านบน สีนํ้าตาลอ่อน เอ็กซีพุลัมแบบโพโรสเพลคเทนไคมาทัส สีนํ้าตาล ไม่มีสี สร้างเพอร์ไฟโซยด์ แอสโคสปอร์แบบมีผนังกันตามขวาง 5 ผนัง รูปกระสวย ขนาด 22-25 x 5-6 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์ ตัวอย่างจากคอสตารีกามีขนาดแอสโคสปอร์เล็กกว่า (12-22 ไมครอน) 3-5 ผนังกันตามขวาง

สารไลเคน: psoromic acid ตัวอย่างจากคอสตารีกาสร้างสารไลเคนชนิด subpsoromic acid และ 2'-O-demethylpsoromic acid (Sipman *et al.*, 2012)

ข้อสังเกต: *S. berkeleyanus* สร้างคอลลิวเมลล่าเชื่อมกันเป็นร่างแห มองเห็นคอลลิวเมลล่าชัดเจนจากด้านบน สีนํ้าตาลอ่อนและสร้างสารไลเคนชนิด psoromic acid

การแพร่กระจาย: ฟิลิปปินส์ อินโดนีเซีย อินเดีย ปาปัวนิวกินี ออสเตรเลีย ปานามา คอสตารีกาและไทย

21. *Thelotrema porinoides* Mont. &

Bosch, in Miquel, Pl. Junghuhn. 4: 484 (1855), (Homchantara, 1999)

ลักษณะที่สำคัญ: แอโพธีเซียชูขึ้นมาจากแทลลัส รูปร่างกลมแบบลีพาไดโนยด์ (lepadinoid) มีรูเล็กด้านบน ไม่สร้างคอลลิวเมลล่า เอ็กซีพุลัมแบบพาราเพลคเทนไคมาทัส ไม่มีสี แอสโคสปอร์แบบมีผนังกันตามขวาง 20-23 ผนัง ผนังหนา รูปขอบขนาน ขนาด 75-87.5 x 17.5-20 ไมครอน เซลล์ภายในเป็นรูปเลนส์ ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์ ตัวอย่างจากคอสตารีกามีแอสโคสปอร์ขนาด 65-140 ไมครอน

สารไลเคน: stictic acid, constictic acid และ acetyl constictic acid ตัวอย่างจากคอสตารีกาสร้างสารไลเคนชนิด hypostictic acid

ข้อสังเกต: *T. porinoides* แอสโคสปอร์แบบมีผนังกันตามขวาง 20-23 ผนัง สร้างสารไลเคนชนิด stictic acid, constictic acid และ acetyl constictic acid

การแพร่กระจาย: มาเลเซีย อินโดนีเซีย ศรีลังกา ฟิลิปปินส์ ญี่ปุ่น ออสเตรเลีย นิวซีแลนด์ แอฟริกา สหรัฐอเมริกา (ฟลอริดา เกะฮาวาย) ปานามา โดมินีกา โซโลมอน คอสตารีกา และไทย

22. *Thelotrema rugatulum* Nyl.; Bull.

Soc. Linn. Normandie, ser. 2(7): 168 (1873), (Homchantara, 1999)

ลักษณะที่สำคัญ: แอโพธีเซียชูขึ้นมาจากแทลลัส รูปร่างกลมแบบลีพาไดโนยด์ มีรูเล็กด้านบน ไม่สร้างคอลลิวเมลล่า เอ็กซีพุลัมแบบพาราเพลคเทนไคมาทัส ไม่มีสี แอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาว รูปขอบขนาน ขนาด 90-125 x 17.5-25 ไมครอน ไม่มีสี 1 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์

สารไลเคน: ไม่สร้างสาร

ข้อสังเกต: *T. rugatulum* ลักษณะคล้ายกับ *T. porinoides* แตกต่างกันที่ไลเคนชนิดนี้

มีแอสโคสปอร์แบบมีผนังกันตามขวางและผนังกันตามยาวและไม่สร้างสารไลเคน ส่วน *T. porinoides* แอสโคสปอร์แบบมีผนังกันตามขวาง 20-23 ผนังสร้างสารไลเคนชนิด stictic acid, constictic acid และ acetyl constictic acid

การแพร่กระจาย: ออสเตรเลียและไทย

23. *Thelotrema triseptatum* Mangold, Flora of Australia 57: 658 (2009)

ลักษณะที่สำคัญ: แอโพธีเซียหนูขึ้นมาจากแทลลัส รูปร่างกลมแบบลีฟาดินอยด์ มีรูเล็กด้านบน ไม่สร้างคอลิวเมลล่า เอ็กซีพูลัมแบบพาราเพลกเทนโคมาทัส ไม่มีสี แอสโคสปอร์แบบมีผนังกันตามขวาง 3 ผนังและมีผนังกันตามขวาง 1-2 ผนัง (submuriform) ขนาด 17.5-20 x 6-7

ไมครอน ไม่มีสี 8 แอสโคสปอร์/ถุงหุ้มแอสโคสปอร์ ตัวอย่างจากออสเตรเลียแอสโคสปอร์มีผนังกันตามขวาง 3 ผนัง ขนาด 15-20 x 6-7 ไมครอน ไม่มีสี

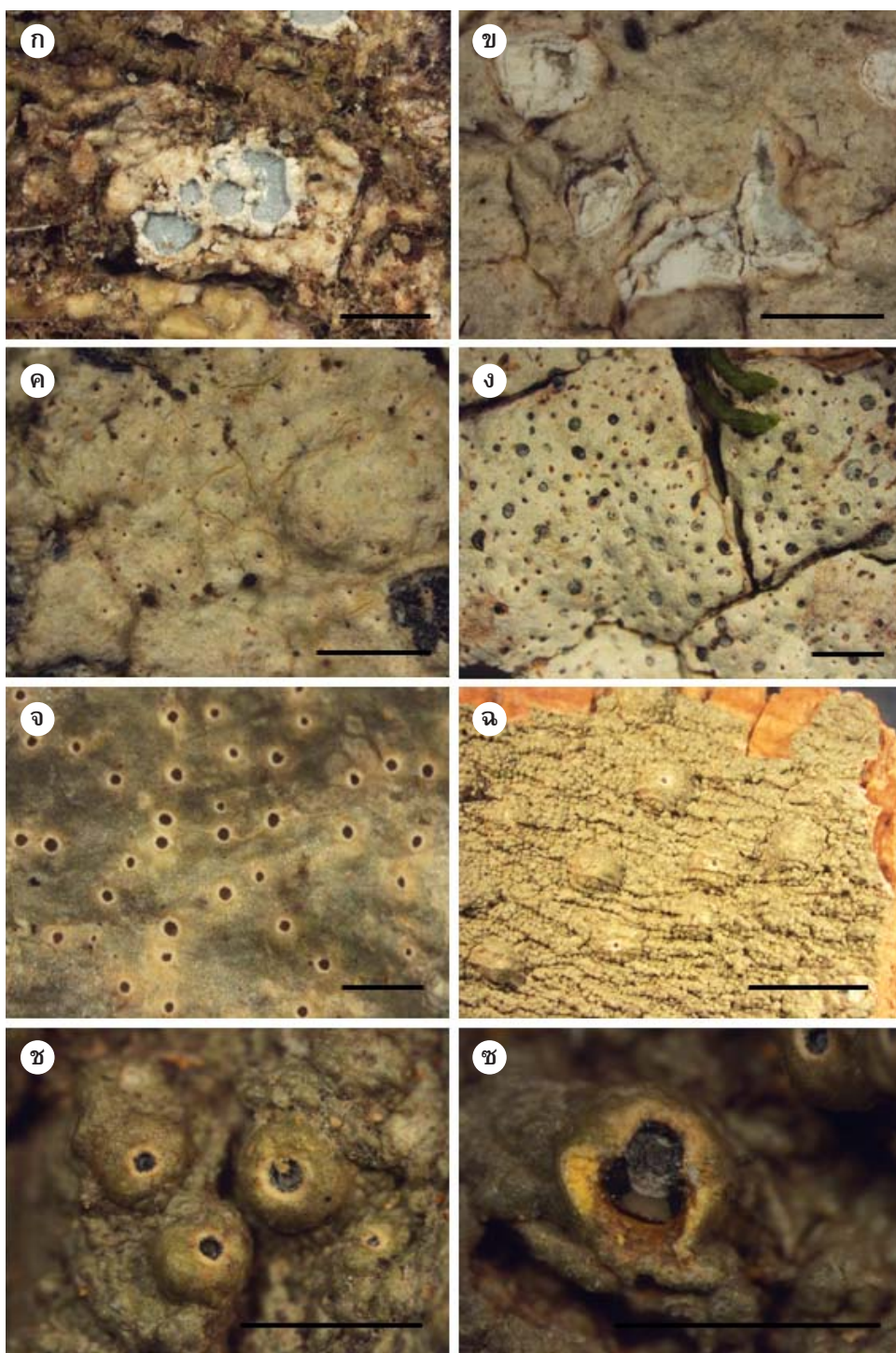
สารไลเคน: stictic acid

ข้อสังเกต: *T. triseptatum* ตัวอย่างจากออสเตรเลียแอสโคสปอร์แบบมีผนังกันตามขวาง 3 ผนัง ขนาด 15-20 x 6-7 ไมครอน ไม่มีสี ส่วนตัวอย่างจากเกาะพังแอสโคสปอร์แบบมีผนังกันตามขวาง 3 ผนังและมีผนังกันตามขวาง 1-2 ผนัง แต่ทั้งสองตัวอย่างสร้างสารไลเคนชนิดเดียวกันคือ stictic acid

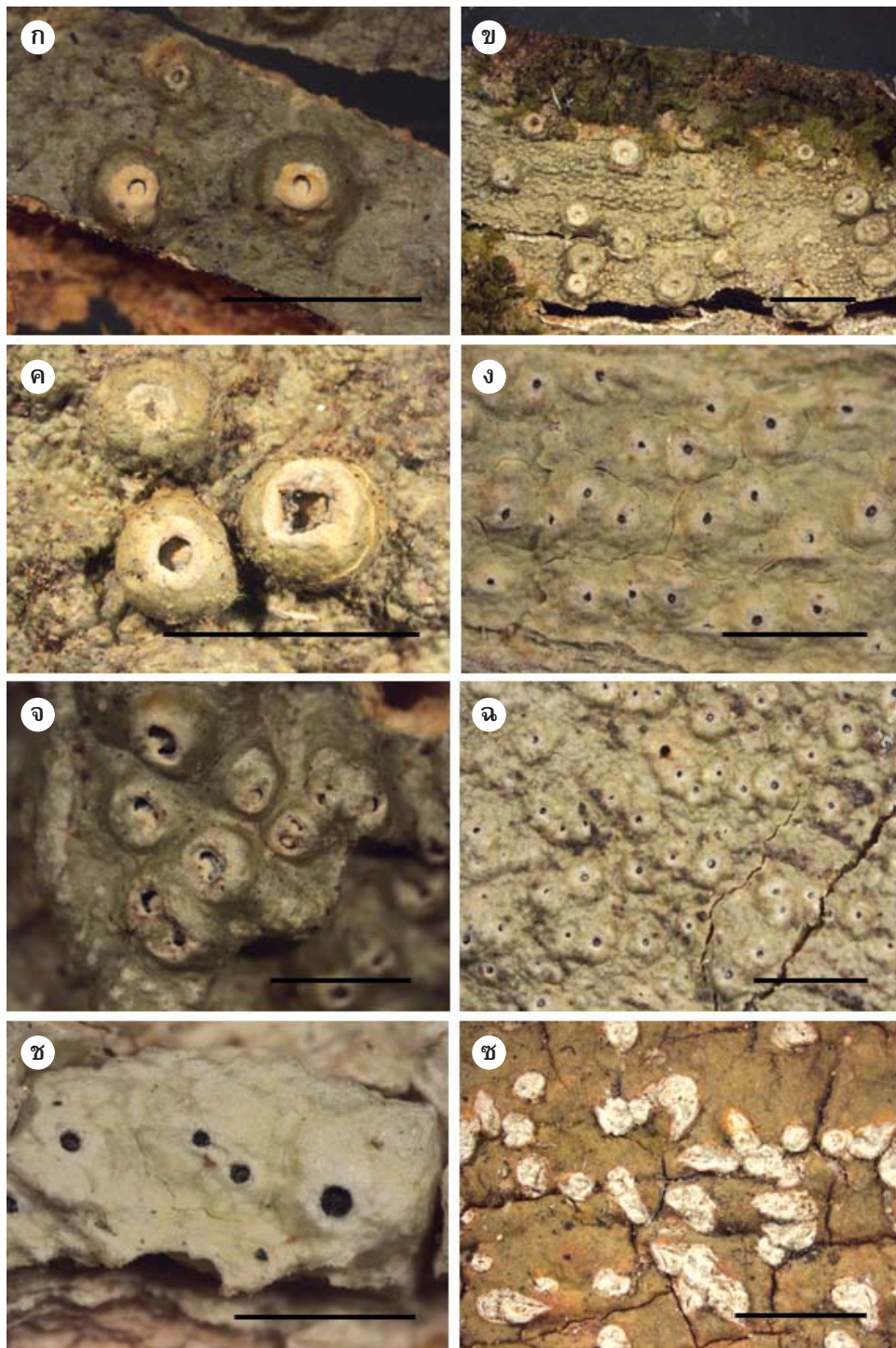
การแพร่กระจาย: ออสเตรเลีย (มีเพียงตัวอย่างต้นแบบแรก (holotype)) และไทย

ตารางที่ 1 ชนิดของไลเคนกลุ่ม Thelotremoid Graphidaceae และสารไลเคนจากเกาะพัง จังหวัดสุราษฎร์ธานี

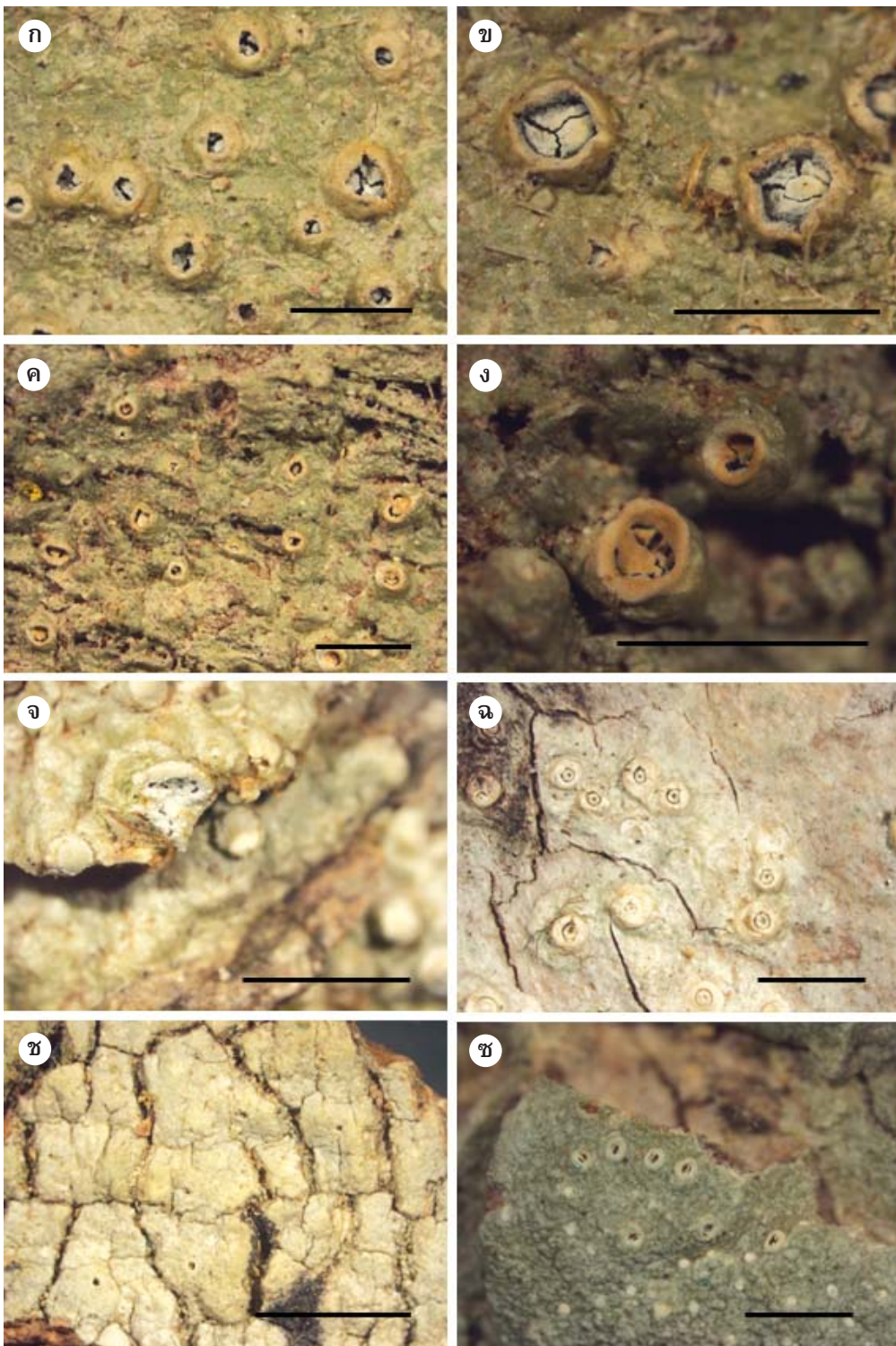
ลำดับ	ชนิด	สารไลเคนที่พบ
1	<i>Astrochapsa astroideae</i>	ไม่สร้างสารไลเคน
2	<i>Chapsa patens</i>	ไม่สร้างสารไลเคน
3	<i>C. soorediata</i>	stictic acid
4	<i>Leucodecton anamalaiense</i>	stictic acid, constictic acid, acetyl constictic acid
5	<i>L. compunctellum</i>	stictic acid, constictic acid, acetyl constictic acid
6	<i>Melanotrema platystomum</i>	ไม่สร้างสารไลเคน
7	<i>Myriotrema clandestinum</i>	psoromic acid
8	<i>Ocellularia cavata</i>	cinchonarum unknowns
9	<i>O. dolichotata</i>	ไม่สร้างสารไลเคน
10	<i>O. interponenda</i>	salazinic acid
11	<i>O. massalongoi</i>	salazinic acid
12	<i>O. papillata</i>	ไม่สร้างสารไลเคน
13	<i>O. terebrata</i>	psoromic acid
14	<i>O. trelotremoides</i>	protocetraric acid, fumarprotocetraric acid
15	<i>O. violacea</i>	protocetraric acid
16	<i>O. viridipallens</i>	ไม่สร้างสารไลเคน
17	<i>Pseudotopliopsis aggregate</i>	ไม่สร้างสารไลเคน
18	<i>Rhabdodiscus subcavatus</i>	psoromic acid
19	<i>R. subemersus</i>	cinchonarum unknowns
20	<i>Stegobolus berkeleyanus</i>	psoromic acid
21	<i>Thelotrema porinoides</i>	stictic acid, constictic acid, acetyl constictic acid
22	<i>T. rugatulum</i>	ไม่สร้างสารไลเคน
23	<i>T. triseptatum</i>	stictic acid



ภาพที่ 1 ไลเคนกลุ่ม Thelotrema Graphidaceae ก. *Astrochapsa astroidea*; ข. *Chapsa patens*; ค. *Leucodecton compunctum*; ง. *Melanotrema platystomum*; จ. *Myriotrema clandestinum*; ฉ. *Ocellularia dolichotata*; ช-ซ. *O. cavata* สเกลบาร์=1 ซม.



ภาพที่ 2 ไลเคนกลุ่ม Thelotremoid Graphidaceae ก. *Ocellularia interponenda*; ข-ค. *O. massalongoi*; ง. *O. papilata*; จ. *O. thelotremoides*; ฉ. *O. violacea*; ช. *O. viridipallens*; ซ. *Pseudotopliopsis aggregate* สเกลบาร์=1 ซม.



ภาพที่ 3 ไลเคนกลุ่ม Thelotrema Graphidaceae ก-ข. *Rhabdodiscus subcavatus*; ค-ง. *R. subemersus*; จ. *Stegololus berkeleyanus*; ฉ. *Thelotrema porinoides*; ช. *T. rugatum*; ซ. *T. triseptatum* สเกลบาร์=1 ซม.

สรุปผลการวิจัย

ไลเคนกลุ่ม Thelotremoid Graphidaceae เป็นไลเคนกลุ่มที่เจริญเติบโตได้ดีในป่าที่ไม่ถูกรบกวน เช่น ป่าดิบในเขตร้อนชื้น (tropical rainforest) ซึ่งสามารถใช้ไลเคนกลุ่มนี้เป็นดัชนีบ่งชี้ (indicator) สภาพป่าดิบชื้นได้เป็นอย่างดี (Sipman *et al.*, 2012) ซึ่งพบว่าเกาะพังมีบางส่วนของพื้นที่เกาะมีสภาพป่าเป็นป่าดิบชื้นและป่าดิบชื้นรุ่มสองหรือป่าดิบชื้นที่เคยถูกรบกวนที่ได้รับการฟื้นฟูแล้ว และพบไลเคนกลุ่ม Thelotremoid Graphidaceae ซึ่งหากเปรียบเทียบกับพื้นที่ของเกาะและพื้นที่ป่าดิบชื้นที่มีอยู่บนเกาะพบว่าไลเคนกลุ่มนี้มีความหลากหลายชนิดค่อนข้างสูง และสามารถใช้เป็นดัชนีบ่งชี้ความสมบูรณ์ของป่าบนเกาะพังได้อีกทางหนึ่ง

การศึกษาลักษณะหลากหลายทางชีวภาพและการแพร่กระจายของไลเคนกลุ่ม Thelotremoid Graphidaceae ในประเทศไทยหรือในเอเชียตะวันออกเฉียงใต้ยังมีรายงานค่อนข้างน้อย หากเปรียบเทียบกับทรัพยากรที่มีอยู่ เห็นได้จากจำนวนชนิดที่รายงานการถูกค้นพบใหม่และชนิดที่พบเป็นครั้งแรกยังมีอยู่จนถึงปัจจุบัน (ปี พ.ศ. 2556) (Homchantara, 1999; Homchantara & Coppins, 2002; Wolseley *et al.*, 2002; Aptroot *et al.*, 2007; Papong *et al.*, 2010; Papong *et al.*, 2013; รัตนา เฟื่องเพราะ และคณะ 2555) ดังนั้นหากมีการศึกษาและวิจัยด้านอนุกรมวิธานของไลเคนกลุ่ม Thelotremoid Graphidaceae ในพื้นที่อนุรักษ์อื่นๆ ของประเทศไทยคาดว่าจะพบชนิดใหม่และชนิดที่พบเป็นครั้งแรกในประเทศไทยหรือในเอเชียตะวันออกเฉียงใต้หรืออย่างน้อยได้ข้อมูลการแพร่กระจายของไลเคนกลุ่มนี้ในประเทศไทยเพิ่มมากขึ้น

กิตติกรรมประกาศ

งานวิจัยนี้ได้รับทุนสนับสนุนจากสำนักงานกองทุนสนับสนุนการวิจัยแห่งชาติ (สกว.) และมหาวิทยาลัยมหาสารคาม ทุนพัฒนานักวิจัย (เมธีวิจัย สกว.) ประจำปี 2555-2558 (ผศ.ดร.ขวัญเรือน บุตรสาทร พาบ้อง หัวหน้าโครงการ RSA-5580045) คณะผู้วิจัยขอขอบพระคุณผู้ทรงคุณวุฒิทุกท่านที่ช่วยตรวจสอบต้นฉบับในการตีพิมพ์ในครั้งนี้ ขอขอบคุณคณะวิทยาศาสตร์ที่ให้ความอนุเคราะห์ห้องปฏิบัติการสำหรับการวิจัย

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Twenty-three new species in the lichen family Graphidaceae from New Caledonia (Ostropales, Ascomycota)

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Abstract

During a field trip to Grande Terre in New Caledonia in 2012, a number of Graphidaceae were collected, among which 23 species that turned out to represent previously undescribed species: *Astrochapsa verruculosa* Papong, Lücking & Parnmen, differing from *A. megaphlyctidioides* in the thinner, verrucose thallus and smaller, distinctly chroodiscoid ascomata; *Diorygma roseopruinatum* Papong, Lücking & Parnmen, similar to *D. junghuhnii* but with pink-red pruina covering the ascomata along the slit; *Fissurina aurantiacoliellata* Papong, Lücking & Kraichak, differing from other species of *Fissurina* in the prominent to sessile ascomata with bright orange pigment; *F. fuscoalba* Papong, Lücking & Kraichak, superficially resembling *F. pseudostromaticum* but distinguished by the brown, endoperidermal thallus and the distoseptate ascospores; *F. stegoboloides* Papong, Lücking & Kraichak, with large ascomata with exposed disc resembling a species of *Stegobolus*; *Graphis leptotremoides* Papong, Lücking & Kraichak, differing from other species of *Graphis* in the gall-forming thallus, in combination with immersed, uncarbonized ascomata; *G. subelongata* Papong, Lücking & Kraichak, related to *G. neolongata* but with less branched lirellae with lateral thalline margin and with narrower, submuriform ascospores; *Leucodecton pseudostromaticum* Papong, Lücking & Lumbsch, differing from *L. expallescentes* in the pseudostromatic ascomata and larger ascospores becoming brown; *Ocellularia albocolumellata* Lücking, Lumbsch & Parnmen, similar to *O. ripleyi* but with uncarbonized excipulum and columella and broader pore of the ascomata; *O. albohallina* Lücking, Lumbsch & Parnmen, differing from *O. pluripora* in the loosely corticate, whitish thallus and ascomata with broader pore and broad columella; *O. austropacifica* Lücking, Lumbsch & Parnmen, resembling *O. dolichotata* but with green, densely corticate thallus and smaller ascospores; *O. fuscosporella* Lücking, Lumbsch & Parnmen; differing from *O. vizcayensis* in the brown ascospores; *O. inconspicua* Lücking, Lumbsch & Parnmen, akin towards *O. pseudopyrenuloides* but with ascomata with narrower pore and uncarbonized columella and with broader ascospores; *O. neocaledonica* Lücking, Lumbsch & Parnmen, differing from *O. pluripora* in the lighter thallus and lack of secondary substances; *O. pulchella* Lücking, Lumbsch & Parnmen, resembling *Ocellularia mammicula* but with green, minutely grainy thallus with columnar clusters of calcium oxalate crystals and with ascomata with narrower, non-annulate pore; *O. rugosothallina* Lücking, Lumbsch & Parnmen, differing from *O. perforata* in the carbonized excipulum and columella; *O. salmonea* Lücking, Lumbsch & Parnmen, similar to *O. baileyi* in the salmon-pink medulla but with larger ascomata with only partially carbonized excipulum and with larger ascospores; *Pseudotopeliopsis longispora* Papong, Lücking & Parnmen, differing from other species of *Pseudotopeliopsis* in the long, transversely septate ascospores; *Rhabdodiscus farinosus* Papong, Lücking & Parnmen, differing from other species of *Rhabdodiscus* in the ecorticate, finely farinose and sorediate thallus; *R. neocaledonicus* Lücking, Lumbsch & Parnmen, similar to *R. lankaensis* in the salmon-pink ascoma pigment but with submuriform, brown ascospores; *R. saxicola* Lücking, Lumbsch & Parnmen, growing saxicolous and with pseudostromatic ascomata with broad brown rim and columella contrasting with the light yellowish brown thallus; *R. thouvenotii* Lücking, Lumbsch & Parnmen, similar to *R. saxicola* but with larger, more or less solitary ascomata with narrower pore and finger-like columella; and *Thelotrema perriei* Papong, Lücking & Lumbsch, differing from *T. diplotrema* in the densely corticate, verrucose thallus and smaller ascospores. The number of new discoveries demonstrates that the South Pacific is a center of diversity of Graphidaceae. We also propose the new combinations *Ocellularia mammicula* (Hale) Lücking, *O. permaculata* (Nagarkar & Hale) Lücking and *Rhabdodiscus lankaensis* (Hale) Lücking.

Keywords: Diversity, lichens, Oceania, South Pacific, taxonomy, tropical lichens

Introduction

The remote archipelago of New Caledonia in the South Pacific is well known for its rich and distinctive flora and fauna, with a high degree of endemism and the presence of unique and phylogenetically isolated taxa (Morat *et al.* 1986, Jaffre *et al.* 1994, Cook & Crisp 2005, Murienne *et al.* 2005, Grandcolas *et al.* 2008, Espeland & Johanson 2010). Although geologically parts of New Caledonia are of Gondwanan origin, there is evidence of Palaeocene marine transgression, and hence the biota is now considered to be of more recent origin and the island has been characterized as a very old Darwinian island with colonization since 37 Ma with subsequent radiations (Grandcolas *et al.* 2008). New Caledonia has also been identified as a biodiversity hot spot based on its richness in number of species, the level of endemism, and its phylogenetic diversity (Jaffre *et al.* 1998, Myers *et al.* 2000).

The exploration of the lichen flora of New Caledonia started in the late 19th and early 20th century with studies using collections by non-lichenologists (Nylander 1868, Müller 1887a, 1893, Harmand 1914), but later on, only few studies added to our knowledge of the diversity of the archipelago. At the time when the first catalogue of lichens in the Pacific islands was prepared, 604 taxa were known from New Caledonia (Elix & McCarthy 1998). Within the last 15 years, a number of studies described new species from New Caledonia and added new records to the lichen flora of the archipelago (Marbach 2000, Ferraro *et al.* 2001, Lücking & Kalb 2001, Louwhoff & Elix 2002, Elvebakk 2007, Kalb 2008, Sérusiaux *et al.* 2008, Archer & Elix 2009, Jørgensen & Gjerde 2012). This study is based on a field trip in 2012, organized by MVK, at which KBP and HTL collected lichenized fungi. The study of the collected material adds another total of 23 new species in Graphidaceae to the lichen flora of New Caledonia, in the genera *Astrochapsa* Parnmen *et al.* (2012: e51392), *Diorygma* Eschweiler (1824: 13), *Fissurina* Fée (1824: 35), *Graphis* Adanson (1763: 11), *Leucodecton* Massalongo (1860: 325), *Ocellularia* Meyer (1825: 327), *Rhabdodiscus* Vainio (1921: 184), *Pseudotopeliopsis* Parnmen *et al.* (2012: e51392), and *Thelotrema* Acharius (1803: 130).

Material and Methods

New Caledonian specimens were collected during a field trip by KBP and HTL in September and October 2012. Anatomical studies were conducted at The Field Museum using standard light microscopy on hand-cut sections mounted in water, using a LEICA MS5 dissecting microscope and a ZEISS Axioskop 2 compound microscope. Sections were mounted in tap water, in which all measurements were taken. Secondary lichen substances were identified by high performance thin-layer chromatography (HPTLC) according to standard methods (Lumbsch 2002).

Taxonomic Treatment

Astrochapsa verruculosa* Papong, Lücking & Parnmen, *sp. nov. (Fig. 1A)

Mycobank # 807505

Differing from *Astrochapsa megaphlyctidioides* in the thinner, verrucose thallus and smaller, distinctly chroodiscoid ascomata.

Type:—NEW CALEDONIA. Province Sud: Dumbéa, Monts Dzumac, along roadside up to the mountain top; 22°02'S, 166°28'E, 920 m; relict montane forest, on bark; September 2012, *Papong & Lumbsch 7508a* (holotype IRD!; isotype F!).

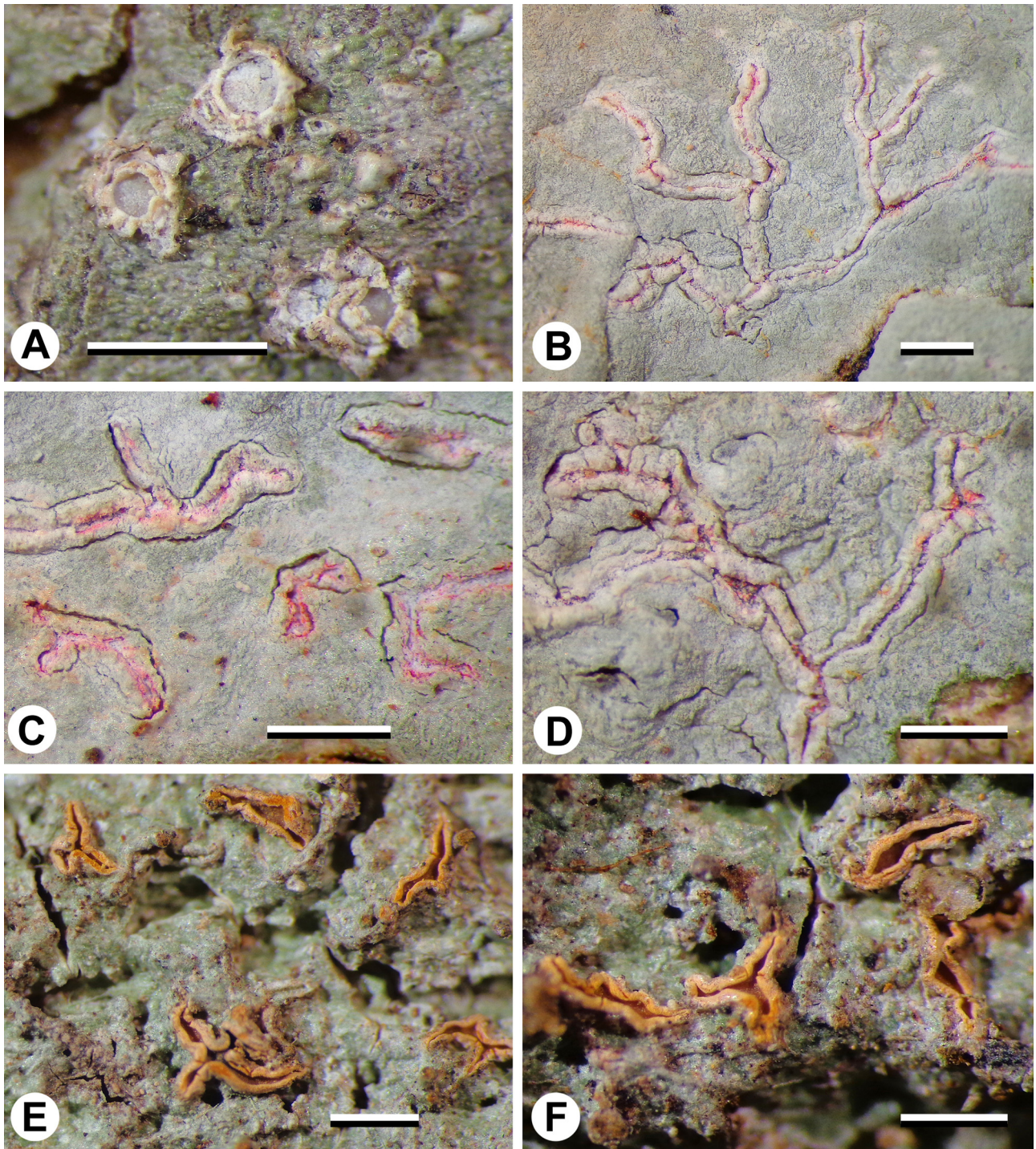


FIGURE 1. A. *Astrochapsa verruculosa*, thallus with ascomata (isotype). B–D. *Diorygma roseopruinatum*, thallus with ascomata (isotype). E–F. *Fissurina aurantiacolivellata*, thallus with ascomata (isotype). Scale = 1 mm.

Thallus corticolous, epiperidermal, up to 3 cm diam., continuous; surface minutely verrucose-rugulose, pale greyish green; prothallus absent. Thallus in section 25–50 μm thick, with thin but dense cortex, 3–5 μm thick, photobiont layer 15–25 μm thick, and medulla (developed only in verrucae) 20–30 μm thick, strongly encrusted with large clusters of calcium oxalate crystals and also (especially near ascomata) with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–11 $\times$ 6–8 μm . Ascomata dispersed to sometimes aggregate, angular-rounded, erumpent, with lateral thalline margin, 0.3–0.5 mm diam., 0.15–0.2 mm high; disc more or less exposed, flesh-colored, white-pruinose; proper margin more or less erect to slightly recurved, lobulate, white, fused with thalline margin, sometimes layered; thalline margin erect, fissured to lobulate, light greyish green. Excipulum colorless to pale yellowish, 20–30 μm wide,

paraplectenchymatous; laterally covered by thalline layer; columella absent; hypothecium prosoplectenchymatous, 7–15 µm high, colorless to pale yellowish; hymenium 60–70 µm high, colorless, clear; epihymenium granular, 5–10 µm high, brownish, dissolving in K. Paraphyses unbranched, apically slightly capitate, smooth; periphysoids present, short (10–15 µm); asci clavate to fusiform, 55–65 × 7–8 µm. Ascospores 8 per ascus, oblong-tapering, 5–7-septate, 15–20 × 4–5 µm, 3.5–4.5 times as long as wide, hyaline, subdistoseptate with very slightly thickened septa and rectangular lumina, I–.

Secondary chemistry:—Stictic acid.

Distribution and ecology:—So far the new species is only known from the type locality in the south part of Grande Terre.

Notes:—The genus *Chapsa* in both its broad and strict sense (Frisch *et al.* 2006, Parnmen *et al.* 2012) includes a number of species with small, transversely septate, non-amyloid ascospores containing stictic acid, viz. *Astrochapsa megaphlyctidioides* (Mangold) Parnmen *et al.* (2012: e51392), *Chapsa minor* (Kantvilas & Vězda) Mangold in Mangold *et al.* (2009: 654), *Pseudochapsa phlyctidioides* (Müll. Arg.) Parnmen *et al.* (2012: e51392), and *P. rhizophorae* (Kalb) Parnmen *et al.* (2012: e51392). All four differ from the new species in several morphological and/or anatomical characters. *Astrochapsa megaphlyctidioides* has a much thicker, smooth to uneven thallus and larger ascomata (up to 2 mm diam.) without distinct lobules, whereas *Chapsa minor* has larger, prominent to sessile ascomata with distinctly layered margin and larger ascospores (20–28 µm long); both species have sub-distoseptate ascospores as in the new species. *Pseudochapsa phlyctidioides* and *P. rhizophorae* differ in having distoseptate, amyloid ascospores; further, *P. rhizophorae* differs in having a loose cortex and larger ascomata and ascospores, and *P. phlyctidioides* lacks a cortex.

***Diorygma roseopruinatum* Papong, Lücking & Parnmen, sp. nov.** (Fig. 1B–D)

Mycobank # 807483

Differing from *Diorygma junghuhnii* in the pink-red pruina covering the ascomata along the slit.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Le Tipindjé, 8 km SE of Hienghène; mangrove forest, on bark; October 2012, Papong & Lumbsch 8157a (holotype IRD!; isotype F!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface minutely farinose, light grey; prothallus absent. Thallus in section 80–120 µm thick, ecorticate, with photobiont layer 40–60 µm thick, strongly encrusted with large clusters of calcium oxalate crystals, and medulla 30–60 µm thick, strongly encrusted with large clusters of calcium oxalate crystals and numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, green, 6–11 × 6–9 µm. Ascomata lirellate, irregularly to stellately branched, erumpent, with distinct labia, 3–7 mm long, 0.3–0.4 mm broad, 0.15–0.2 mm high; disc narrow, brown, white-pruinose suffused with patches of pink-red pruina; proper margin indistinct; thalline margin thick, white-pruinose. Excipulum pale yellowish in inner parts, brown in outer parts, 30–50 µm wide, prosoplectenchymatous; thalline margin 50–80 µm thick, anatomically similar to thallus; hypothecium prosoplectenchymatous, 5–10 µm high, colorless; hymenium 110–120 µm high, colorless, clear; epihymenium granular, 15–20 µm high, dark grey and suffused with bright red granules, dissolving in K giving a brief, orange-yellow efflux. Paraphyses unbranched to slightly anastomosing above and laterally, smooth; periphysoids absent; asci clavate, 100–120 × 25–35 µm. Ascospores 1 per ascus, ellipsoid to oblong, richly muriform, 60–100 × 20–30 µm, 3–4 times as long as wide, hyaline, subdistoseptate with angular lumina, I+ violet-blue.

Secondary chemistry:—Norstictic acid and unknown pink-red pigment on the ascomata; thallus P+ orange-red, microscopic section with K+ yellow efflux forming red, needle-shaped crystals; pigment K+ purple.

Distribution and ecology:—So far this taxon is only known from the type locality from a mangrove on the north side of Grande Terre.

Notes:—This new species is similar to *Diorygma junghuhnii* (Mont. & Bosch) Kalb *et al.* (2004: 157) in overall morphology, ascospore type, and chemistry. The taxon, however, differ in having a patchy, pink-red pruina developed on the ascomatal discs. At first, we mistook this feature for decomposing norstictic acid, but comparison with such specimens showed that the pigment differs from the effect of decomposing norstictic acid not only in color, but also in structure and in the K-reaction, and based on its location on in the epihymenium, where norstictic acid is not present, represents a genuine pigment of unknown chemical affinities.

***Fissurina aurantiacoliellata* Papong, Lücking & Kraichak, sp. nov.** (Fig. 1E–F)

Mycobank # 807484

Differing from other species of *Fissurina* in the prominent to sessile ascomata with bright orange pigment.

Type:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8242* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous, with scattered to dense, coarse isidioid outgrowths; surface smooth to uneven, light green, in parts minutely white-papillose; prothallus absent. Isidioid structures up to 0.7 mm high and 0.3 mm broad, cylindrical to irregular, corticate, their tips often exposing an ochraceous-brown mass of pigment granules; pigment also present in the inner and basal parts of the structure. Thallus in section 50–80 µm thick, with prosoplectenchymatous cortex, 5–10 µm thick, photobiont layer 15–20 µm thick, and medulla 30–50 µm thick, with scattered, large clusters of calcium oxalate crystals and numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 6–11 × 5–8 µm. Ascomata lirellate, unbranched to irregularly or stellately branched, prominent to sessile, with distinct, prominent labia, gaping, 0.5–1.5 mm long, 0.3–0.4 mm broad, 0.2–0.25 mm high; disc more or less exposed, orange-brown to dark salmon-colored, slightly translucent, non-pruinose or very faintly pruinose; proper margin distinct, forming orange-yellow to salmon-yellow labia; thalline margin indistinct. Excipulum orange-yellow to orange-brown, 40–60 µm wide, prosoplectenchymatous and including remnants of periderm cells, fused with thalline margin, the color caused by numerous pigment granules filling the excipular tissue; thalline margin 50–70 µm thick, anatomically similar to thallus, with scattered clusters of calcium oxalate crystals; hypothecium prosoplectenchymatous, 20–30 µm high, yellow; below the hypothecium a layer encrusted with orange-yellow granules similar to the excipulum; hymenium 60–70 µm high, yellow, clear; epihymenium granular, 5–10 µm high, orange-yellow; all (orange-)yellow parts reacting K+ violet to purple, then quickly brown and then olive-yellow. Paraphyses unbranched, smooth; periphysoids present along the inner portion of the upper excipulum, short, 5–10 µm long, minutely spinulose; asci cylindrical, 55–60 × 6–7 µm. Ascospores 8 per ascus, uniseriate, fusiform, 1-septate, 9–12 × 4.5–5.5 µm, 1.8–2.3 times as long as wide, hyaline, euseptate with more or less rectangular lumina, 1–.

Secondary chemistry:—Unknown anthraquinone present in all parts of the ascomata and the base of the isidia, K+ purple.

Distribution and ecology:—*Fissurina aurantiacoliellata* is so far only known from the type locality in the northern part of Grande Terre.

Notes:—This new species is unique within the genus in having vividly pigmented ascomata (including a yellow hymenium), which become sessile with widely gaping disc, in addition to producing isidioid outgrowths and 1-septate ascospores. Whether ascospore feature is a consistent feature is uncertain; only few ascospores were observed and it is uncertain whether they were mature.

***Fissurina fuscoalba* Papong, Lücking & Kraichak, sp. nov.** (Fig. 2A–B)

Mycobank # 807485

Differing from *Fissurina pseudostromatica* in the brown, endoperidermal thallus and distoseptate ascospores.

Type:—NEW CALEDONIA. Province Nord: Poya, Goapin, Mont Aoupinié; relict montane forest, on bark; October 2012, *Papong & Lumbsch 7725* (holotype IRD!; isotype F!).

Thallus corticolous, endoperidermal, up to 3 cm diam., continuous; surface smooth, reddish-brown; prothallus absent. Thallus in section with prosoplectenchymatous cortex, 5–10 µm thick, irregular and sparse photobiont layer immersed in the periderm, and indistinct medulla except near the ascomata, there 100–150 µm thick, formed by periderm layers encrusted with large clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata lirellate, mostly unbranched, immersed in distinct, pseudostromatic areas, lacking labia, 0.5–1 mm long, 0.1–0.2 mm broad, 0.1–0.15 mm high; disc concealed; proper margin indistinct, forming a brown line along the slit; thalline margin developed into white pseudostromata elevated above thallus level and containing 1–3 ascomata. Excipulum yellowish, apically dark

brown, 10–20 µm wide, prosoplectenchymatous, I+ light violet-blue in basal parts, fused with thalline margin; hypothecium prosoplectenchymatous, 5–10 µm high, colorless; hymenium 70–80 µm high, colorless, clear, I+ light violet-blue apically and peripherally; epihymenium indistinct. Paraphyses unbranched, smooth; periphysoids not observed; asci fusiform, 60–70 × 10–12 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, fusiform, 3-septate, 15–18 × 7–8 µm, 2–2.5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, lacking a thick outer wall, I–.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—It is so far only known from the type locality in the central part of Grande Terre.

Notes:—This new species is characterized by distinctly pseudostromatic ascomata which strongly contrast with the endoperidermal, reddish-brown thallus. No other species of *Fissurina* displays this morphology. The closest species in overall morphology, *F. pseudostromatica* Lücking & Rivas Plata in Lücking *et al.* (2011: 145) has a green, epiperidermal thallus and ascospores with thin septa. Other species with distinctly pseudostromatic ascomata, including *F. intercludens* (Nyl.) Lücking & Rivas Plata in Lücking *et al.* (2011: 144), and *F. mexicana* (Zahlbr.) Lücking & Rivas Plata in Lücking *et al.* (2011: 144), have (sub-)muriform ascospores and also differ in morphological features.

***Fissurina stegoboloides* Papong, Lücking & Kraichak, *sp. nov.* (Fig. 2C–D)**

Mycobank # 807486

Differing from *Fissurina rufula* in the large ascomata with exposed disc and the larger, amyloid ascospores.

Type:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, Papong & Lumbsch 8278 (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 15 cm diam., continuous; surface smooth, light olive-green; prothallus absent. Thallus in section 100–200 µm thick, with prosoplectenchymatous cortex with internal splitting, 10–15 µm thick, photobiont layer with internal splitting, 20–30 µm thick, and medulla 50–100 µm thick, with large clusters of calcium oxalate crystals especially in the margin of the ascomata. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata very robust, initially rounded but becoming lirellate, unbranched to irregularly or rarely stellately branched, prominent to sessile, with distinct, strongly prominent labia, gaping, 1–5 mm long, 0.7–1.2 mm broad, 0.4–0.5 mm high; disc more or less exposed, flesh-colored, slightly translucent, thinly white-pruinose; proper margin distinct, forming white labia; thalline margin developed laterally, usually not visible from above. Excipulum olive-yellow, 20–40 µm wide, prosoplectenchymatous, I+ light violet-blue in parts and at the base, fused with thalline margin; thalline margin 150–200 µm thick, anatomically similar to thallus, but massively encrusted with large clusters of calcium oxalate crystals; hypothecium prosoplectenchymatous, 10–20 µm high, pale olive-yellow; hymenium 120–150 µm high, colorless, clear, I+ light violet-blue apically and peripherally; epihymenium granular, 5–10 µm high, grey. Paraphyses unbranched, smooth; periphysoids not observed; asci fusiform, 120–130 × 15–20 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, fusiform, 3-septate, 20–25 × 10–12 µm, 1.8–2.3 times as long as wide, hyaline, distoseptate with lens-shaped to angular lumina, lacking a thick outer wall, I+ weakly but distinctly violet-blue.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—So far only known from the type locality in the northern part of Grande Terre.

Notes:—*Fissurina stegoboloides* at first glance resembles a species of *Stegobolus* Montagne (1845: 4) in having relatively short ascomata when young which feature a thick, white, prominent margin and gaping disc. However, the internal anatomy and ascospore type, with the comparatively weak amyloid reaction, identify this as a species of *Fissurina*. Within that genus, it is most similar to *F. crassilabra* Mont. & Bosch in Montagne (1856: 354) and *F. rufula* (Mont.) Staiger (2002: 160). It differs from the former by larger ascomata, which are in fact the largest known in the genus, the thick, white, rather than thin and yellowish labia, and the larger ascospores. The latter species has a concealed disc and orange-brown labia, and smaller, non-amyloid ascospores.

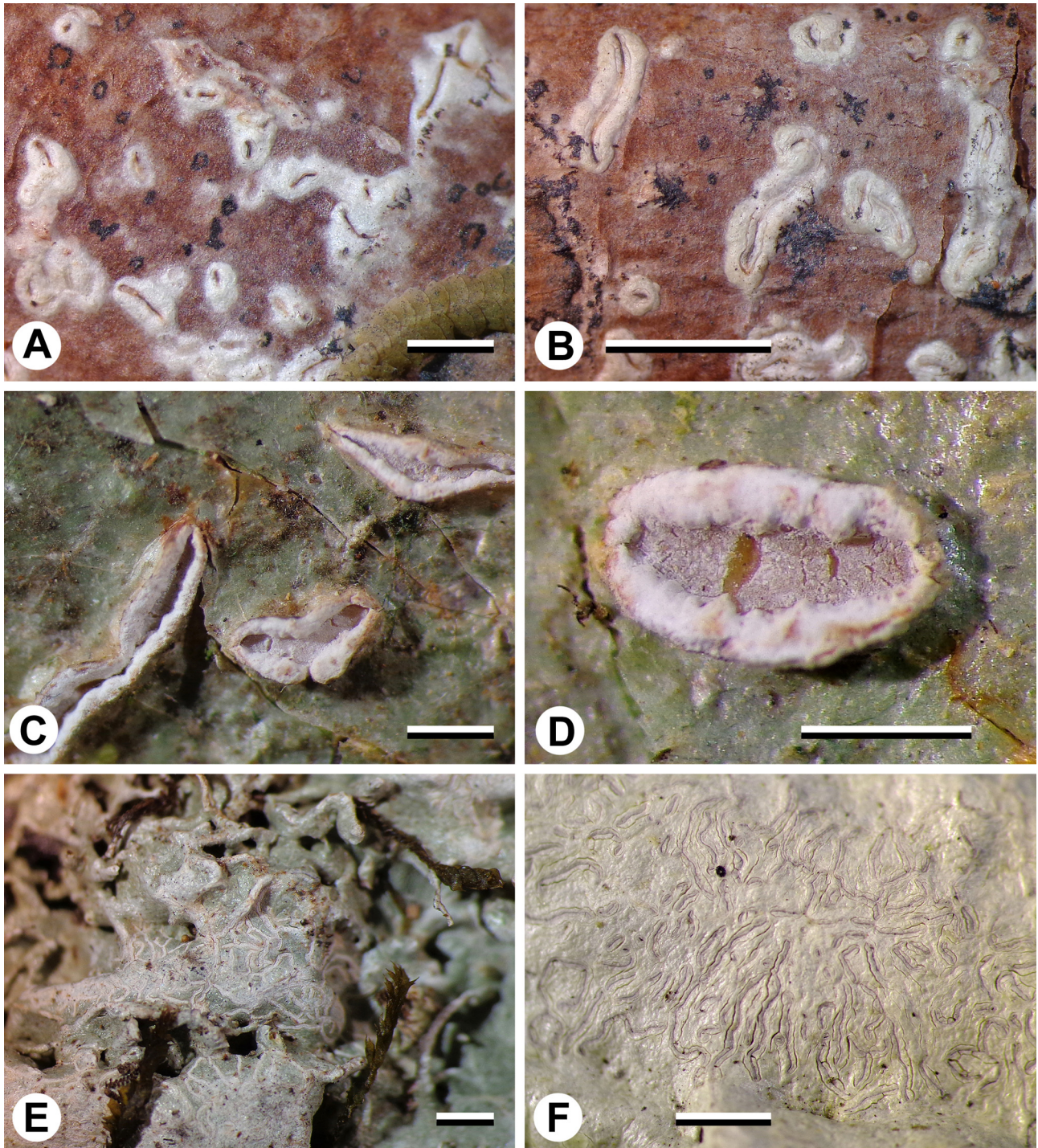


FIGURE 2. A–B. *Fissurina fuscoalba*, thallus with ascomata (isotype). C–D. *F. stegoboloides*, thallus with ascomata (isotype). E–F. *Graphis leptotremoides*, thallus with ascomata (isotype). Scale = 1 mm.

***Graphis leptotremoides* Papong, Lücking & Kraichak, *sp. nov.* (Fig. 2E–F)**

Mycobank # 807488

Differing from other species of *Graphis* in the gall-forming thallus, in combination with immersed, uncarbonized ascomata.

Type:—NEW CALEDONIA. Province Sud: Dumbéa-Yaté, Montagne des Sources, mountain top; 22°08'S, 166°36'E, 750 m; lower montane rainforest, on *Araucaria montana*; September 2012, Papong & Lumbsch 7597 (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous and muscicolous, epiperidermal, up to 10 cm diam., continuous, gall-forming with partially hollow underside; surface coarsely undulate to plicate, light grey; prothallus absent. Thallus in section 200–300 µm thick, with prosoplectenchymatous cortex 10–20 µm thick and otherwise dominated by the medulla which is massively encrusted with large clusters of calcium oxalate crystals, photobiont cells irregularly arranged in a ruptured layer deep within the medulla. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–10 µm. Ascomata dense, lirellate, much curved and irregularly branched, immersed, with lateral thalline margin, 1–5 mm long, 0.1–0.2 mm broad, 0.2–0.25 mm high; disc concealed; labia entire, thickly white-pruinose, often separated from the bordering thallus by a thin split; thalline margin formed by the bordering grey thallus. Excipulum uncarbonized, yellowish, 20–30 µm wide; hypothecium prosoplectenchymatous, 5–10 µm high, pale yellowish; hymenium 70–80 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, greyish granular. Paraphyses unbranched, smooth; periphysoids not observed; asci fusiform, 70–80 × 15–18 µm. Ascospores 8 per ascus, irregularly arranged, ellipsoid, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 15–18 × 8–10 µm, 1.7–2 times as long as wide, hyaline, distoseptate with rounded lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—This new taxon is so far only known from two collections in a montane forest in the southern part of Grande Terre.

Notes:—This new species is rather unusual in forming a thallus similar to that of *Leptotrema wightii* (Taylor) Müller (1882: 499), with which it is easily confused from the distance. The lirellate ascomata, however, readily distinguish the species. Within *Graphis*, the species is characterized by a non-carbonized excipulum, similar to species previously placed in *Hemithecium* Trevisan (1853: 11). With this combination of characters, including the small, submuriform ascospores, the species is unmistakable.

Additional specimens examined:—NEW CALEDONIA. Province Sud: Dumbéa-Yaté, Montagne des Sources, mountain top; 22°08'S, 166°36'E, 750 m; lower montane rainforest, on Rubiaceae; September 2012, Papong & Lumbsch 7604 (IRD).

***Graphis subelongata* Papong, Lücking & Kraichak, sp. nov.** (Fig. 3A–B)

Mycobank # 807487

Differing from *Graphis neoelongata* in the less branched lirellae with lateral thalline margin and the narrower, submuriform ascospores.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Koulnoué, 3 km E of Hienghène; 20°41'S, 164°59'E, 1 m; mangrove, on bark; October 2012, Papong & Lumbsch 8204b (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface smooth, white-grey; prothallus absent. Thallus in section 50–100 µm thick, with prosoplectenchymatous cortex 5–10 µm thick, photobiont layer 20–30 µm thick, and medulla 30–50 µm thick, encrusted with clusters of calcium oxalate crystals and small grey crystals; a thin layer calcium oxalate crystals and grey crystals also present between cortex and photobiont layer. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 7–10 µm. Ascomata lirellate, irregularly branched, immersed to erumpent, with distinct lateral thalline margin when young but lacking thalline margin in subsequent generations, 1–5 mm long, 0.2–0.3 mm broad, 0.15–0.2 mm high; disc concealed; labia initially entire but soon becoming densely striate, black, non-pruinose; thalline margin developed in first-generation lirellae only (with entire labia), white, in subsequent generations (with striate labia) absent. Excipulum laterally carbonized, basally discontinuous, 30–70 µm wide, apically crenulate; lateral thalline margin when present 50–100 µm thick, anatomically similar to thallus; hypothecium prosoplectenchymatous, 5–10 µm high, pale yellowish; hymenium 90–100 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, brownish granular. Paraphyses unbranched, smooth; periphysoids not observed; asci fusiform, 90–100 × 15–20 µm. Ascospores 8 per ascus, irregularly arranged, oblong-oval, submuriform with 7–11 transverse and 0–1 longitudinal septa per segment, 25–45 × 8–10 µm, 3–5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, with thick halo, I+ violet-blue.

Secondary chemistry:—norstictic acid.

Distribution and ecology:—*Graphis subelongata* is so far only known from the type collections in a mangrove in the northern part of Grande Terre.

Notes:—This new species is unique with the genus. Only few species in *Graphis* are known with a combination of striate labia, laterally carbonized excipulum, clear hymenium, and muriform ascospores. Among these, only the neotropical *G. neoelongata* Lücking in Lücking *et al.* (2009: 438) produces secondary substances (norstictic and stictic acids). That species, however, differs in having broader, eumuriform ascospores and radiately branched, immersed lirellate, lacking a distinct, prominent thalline margin except for the bordering thallus.

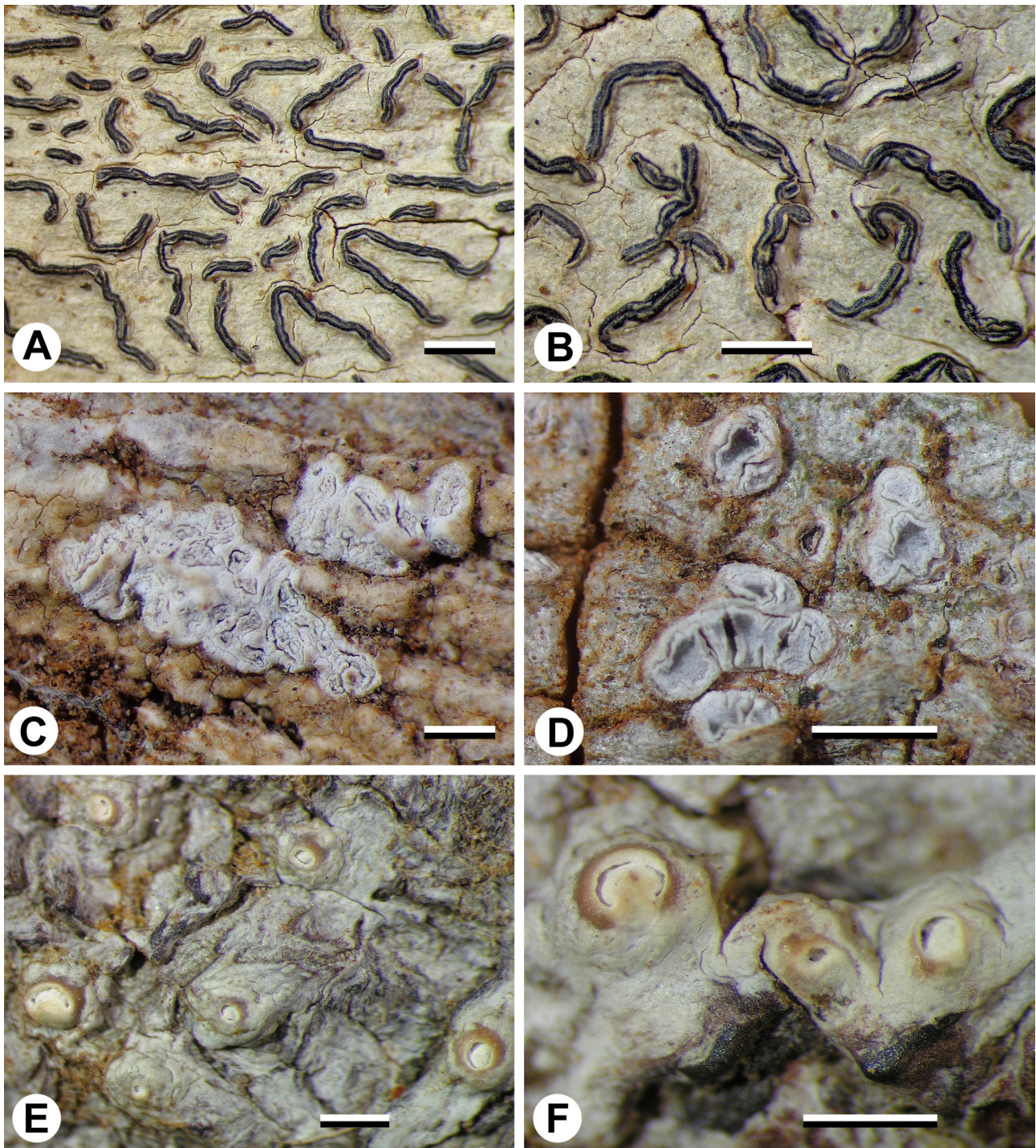


FIGURE 3. A–B. *Graphis subelongata*, thallus with ascomata (isotype). C–D. *Leucodecton pseudostromaticum*, thallus with ascomata (isotype). E–F. *Ocellularia albocolumellata*, thallus with ascomata (isotype). Scale = 1 mm.

***Leucodecton pseudostromaticum* Papong, Lücking & Lumbsch, *sp. nov.* (Fig. 3C–D)**

Mycobank # 807489

Differing from *Leucodecton expallescentis* in the pseudostromatic ascomata and larger ascospores becoming brown.

Type:—NEW CALEDONIA. Province Sud: Bouloupari, Mont Do, summit; 21°45'S, 166°00'E, 1010 m; lower montane rainforest, on bark; September 2012, *Papong & Lumbsch 7541* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, endoperidermal, up to 5 cm diam., continuous; surface uneven, following the contour of the bark, light green to pale grey-brown; prothallus absent. Thallus in section 80–120 µm thick, mostly embedded in the upper periderm, with thin, loose cortex, 3–5 µm thick, photobiont layer (embedded in periderm layers) 50–100 µm thick, and medulla 30–50 µm thick, encrusted with large clusters of calcium oxalate crystals (especially near ascomata) and also with numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata aggregate in pseudostromata, rounded to irregular or shortly elongate, immersed in the slightly elevated pseudostromata, 0.2–0.5 mm diam., 0.15–0.2 mm high; disc partially exposed, dark grey-brown, partially to completely white-pruinose; proper margin more or less erect, entire, white, with a distinct split towards the surrounding thalline tissue of the pseudostromata (double margin); pseudostromata white-pruinose, becoming pale yellowish. Excipulum yellowish, 7–15 µm wide, paraplectenchymatous; laterally covered by thalline tissue; columella absent; hypothecium prosoplectenchymatous, 20–30 µm high, pale yellowish; hymenium 70–90 µm high, colorless, clear; epihymenium granular, 10–20 µm high, dark grey, partially dissolving in K. Paraphyses unbranched, smooth; periphysoids absent; asci cylindrical to fusiform, 70–90 × 12–16 µm. Ascospores 4–8 per ascus, uniseriate to irregularly arranged, ellipsoid to almost fusiform, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 15–25 × 9–13 µm, 1.5–2 times as long as wide, becoming grey-brown, distoseptate with thick septa and wall and rounded lumina, I–.

Secondary chemistry:—Stictic acid; thallus medulla P+ orange-red, microscopic section with K+ persistently yellow efflux.

Distribution and ecology:—This new species has been collected in in lower montane to montane rainforests at different localities in Grande Terre.

Notes:—*Leucodecton* is a medium-sized genus comprising almost 30 known species (Rivas Plata *et al.* 2010). The new species fits well into this genus by having a loosely corticate thallus, containing stictic acid, having a paraplectenchymatous excipulum lacking periphysoids, and having grey-brown, muriform ascospores. The comparatively large, thelotremoid ascomata with double margin resemble those found in *L. albidulum* (Nyl.) Mangold in Mangold *et al.* (2009: 654), *L. expallescentes* (Nyl.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 184), *L. glaucescens* (Nyl.) Frisch in Frisch *et al.* (2006: 162), and *L. occultum* (Eschw.) Frisch in Frisch *et al.* (2006: 157). *Leucodecton expallescentes* is similar in gross morphology, but has solitary ascomata and smaller ascospores that remain hyaline, whereas *L. occultum* agrees in ascospore type but has solitary ascomata not aggregated in pseudostromata and produces norstictic acid. The apothecia in *L. albidulum* are typically aggregate-pseudostromatic, but are completely immersed in the thallus (pseudostromata not elevated), and the ascospores are transversely septate and about twice as long. *Leucodecton glaucescens* agrees with the new species in having densely aggregate, pseudostromatic ascomata, but forms a thick, epiperidermal thallus with columnar clusters of crystals and its ascomata have a fissured-lobulate, chroodiscoid margin.

Additional specimens examined:—NEW CALEDONIA. Province Sud: Thio, Nakaré, Mont Ningua; 21°45'S, 166°00'E, 1010 m; lower montane rainforest; September 2012, *Papong & Lumbsch 7677* (IRD); Province Nord: Ouégoa, Mont Mandjélia; 20°24'S, 164°31'E, 560 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 7980* (IRD).

***Ocellularia albocolumellata* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 3E–F)**

Mycobank # 807490

Differing from *Ocellularia ripleyi* in the uncarbonized excipulum and columella and broader pore of the ascomata.

Type:—NEW CALEDONIA. Province Nord: Ouégoa, Mont Mandjélia; 20°24'S, 164°31'E, 560 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 7986* (holotype IRD!; isotype F!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven to shallowly verrucose, white-grey; prothallus absent. Thallus in section 60–100 µm thick, with dense, paraplectenchymatous cortex, 10–20 µm thick, photobiont layer 20–30 µm thick, and medulla 30–50 µm thick, with clusters of calcium oxalate crystals and small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups,

yellowish green, 8–13 × 6–10 µm. Ascomata round, erumpent to prominent, with complete thalline margin, 0.8–1.2 mm diam., 0.3–0.5 mm high; disc covered by 0.3–0.6 mm wide pore completely filled with white-tipped columella often connected to one side of the margin; proper margin distinct, forming a thin, white rim around the pore bordered by a broader, light brown rim; thalline margin entire, smooth to uneven, whitish. Excipulum entire, uncarbonized, completely encrusted with small, grey crystals and appearing white in surface view, 50–70 µm wide; laterally covered by algiferous, corticate thallus, 100–150 µm thick, with a single, large chamber completely encrusted with a large clusters of calcium oxalate crystals; columella present, finger-like but massive and filling most of the ascoma, completely encrusted with small, grey crystals and appearing white in surface view, 200–300 µm broad and up to 400 µm high; hypothecium prosoplectenchymatous, 20–30 µm high, colorless; hymenium 200–250 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 180–220 × 20–30 µm. Ascospores 2–4 per ascus, irregularly arranged, fusiform, 19–25-septate, 100–150 × 15–20 µm, 6–8 times as long as wide, hyaline, subdistoseptate with angular to lens-shaped lumina and thick outer wall, I+ violet-blue.

Secondary chemistry:—Psoromic, subpsoromic, and 2'-*O*-demethylpsoromic acids; medulla P+ yellow, microscopic section K–.

Distribution and ecology:—This species is so far only known from the type collection in the northern part of Grande Terre, where it was collected in a relict montane forest.

Notes:—This new species is unique in the genus by having an uncarbonized excipulum and columella, in combination with large ascospores. The most similar species in terms of ascospore dimensions and chemistry is *Ocellularia ripleyi* Hale (1974a: 493) which, however, has a fully carbonized excipulum and columella, as well as a narrower pore of the ascomata.

***Ocellularia albothallina* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 4A–B)**

Mycobank # 807491

Sequence accession numbers: KJ435206 (mtSSU, holotype)

Differing from *Ocellularia pluripora* in the loosely corticate, whitish thallus and ascomata with broader pore and broad columella.

Type:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8294* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven to coarsely verrucose-rugose, yellowish white; prothallus absent. Thallus in section 100–200 µm thick, with loose cortex, 5–10 µm thick, and massive medulla dominating the thallus, strongly encrusted with large clusters of calcium oxalate crystals and with small, grey crystals, photobiont layer not well-developed, immersed in the medulla and forming interrupted patches. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded, prominent, with complete thalline margin, 0.6–1 mm diam., 0.3–0.4 mm high; disc covered by 0.2–0.3 mm wide pore and completely filled by black columella; proper margin indistinct; thalline margin entire, rough to uneven, of the same color as the surrounding thallus. Excipulum entire, uncarbonized, yellow-brown, 70–100 µm wide, hardly distinguishable from amorphous remnants of periderm; laterally covered by algiferous, corticate thallus, 100–200 µm thick, massively encrusted with clusters of calcium oxalate crystals; columella present, stump-shaped, completely carbonized, 250–300 µm wide and 100–120 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 90–100 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 90–110 × 12–15 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, oblong, 5–7-septate, 20–25 × 6–7 µm, 3–4 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Psoromic, subpsoromic, and 2'-*O*-demethylpsoromic acids; medulla P+ yellow, microscopic section K–.

Distribution and ecology:—The species has been collected in a relict montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes:—This is another new species with a combination of carbonized columella and uncarbonized, brown excipulum. Two other species share these features and also produce the psoromic acid chemosyndrome.

Ocellularia pluripora Hale (1981: 319) differs in its olive-green, densely corticate thallus with smooth surface and its narrow apothecial pore and narrow, finger-like columella. *Ocellularia pluriporoides* Homchantara & Coppins (2002: 127) is distinguished by having apically a carbonized, reticulate columella and larger ascospores. The new species agrees with the neotropical *O. antillensis* Hale (1974b: 17) in gross morphology, particularly the whitish thallus and broad, black columella filling the pore of the apothecia, but that species has a strongly carbonized excipulum.

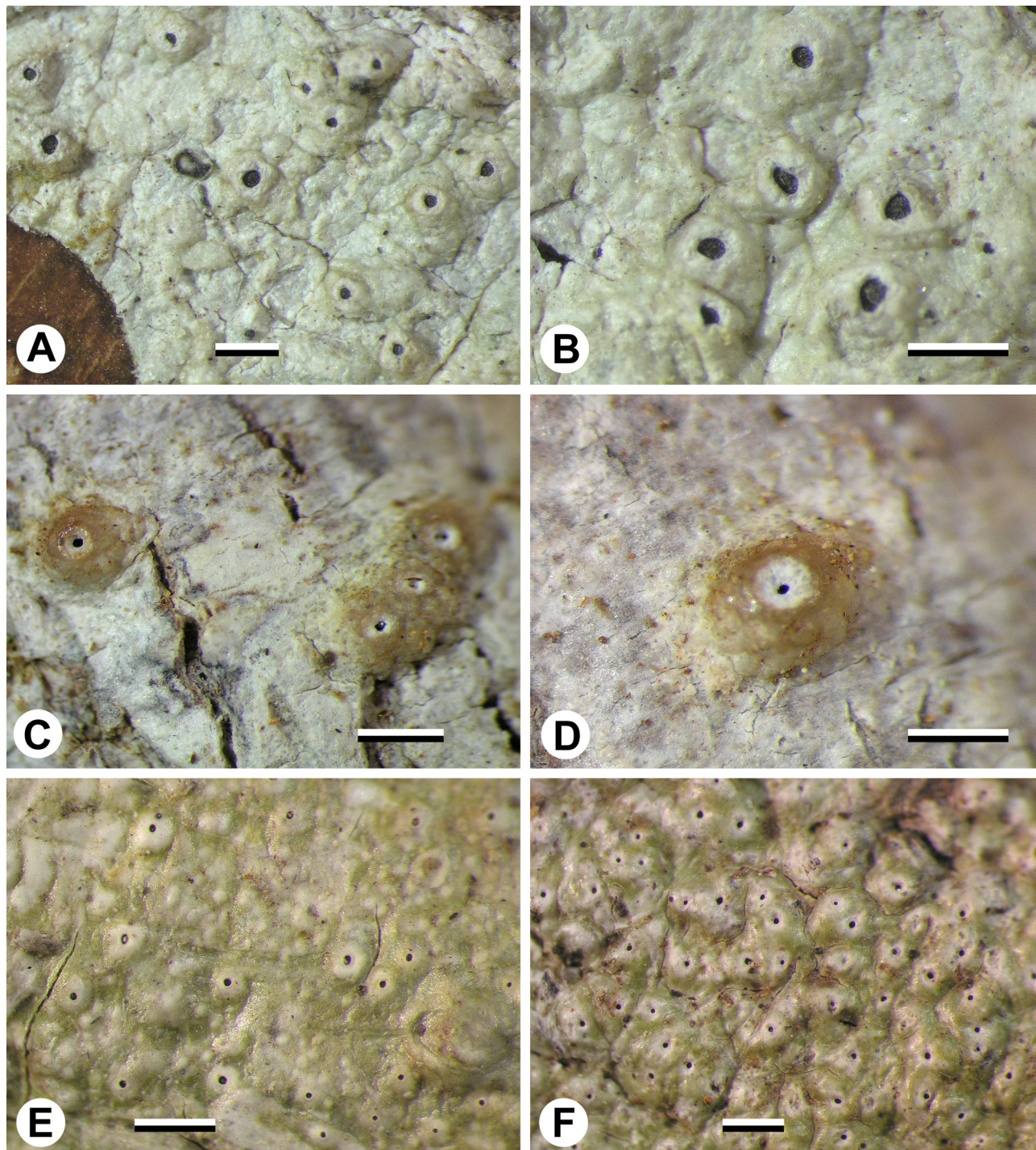


FIGURE 4. A–B. *Ocellularia albohallina*, thallus with ascomata (isotype). C–D. *O. fuscosporella*, thallus with ascomata (isotype). E. *O. inconspicua*, thallus with ascomata (isotype). F. *O. neocaledonica*, thallus with ascomata (isotype). Scale = 1 mm.

***Ocellularia austropacifica* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 7C–D)

Mycobank # 807512

Sequence accession numbers: KJ435189 (mtSSU, holotype), KJ435116 (nuLSU, holotype); KJ435190 (mtSSU, paratype), KJ435117 (nuLSU, paratype)

Differing from *Ocellularia dolichotata* in the green, densely corticate thallus and smaller ascospores.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8064* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface distinctly and densely verrucose, light olive-green, verrucae papilliform, 0.15–0.25 mm diam., tips paler; prothallus absent. Thallus in section 100–150 µm thick, with dense, prosoplectenchymatous cortex, 20–30 µm thick, photobiont layer 15–25 µm thick, and medulla 50–100 µm thick, strongly encrusted with clusters of calcium oxalate crystals and numerous small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–9 µm. Ascomata rounded, erumpent to prominent, with complete thalline margin, 0.8–1.5 mm diam., 0.3–0.5 mm high; disc covered by 0.1–0.3 mm wide pore filled with grey-tipped columella; proper margin thin, forming a pale yellowish rim around the pore; thalline margin entire, verrucose, light olive-green. Excipulum mostly uncarbonized, yellow, 50–100 µm thick, apically with thin strands of carbonization, covered by amorphous periderm layer, orange-brown, 50–100 µm thick; laterally covered by algiferous thallus, 100–150 µm thick; columella present, finger-like, carbonized, 150–200 µm broad and up to 300 µm high; hypothecium prosoplectenchymatous, 15–20 µm high, colorless; hymenium 200–250 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched to basally and apically anastomosing in lateral parts of the hymenium, apically smooth; periphysoids absent; asci fusiform, 180–220 × 25–35 µm. Ascospores 4–8 per ascus, oblong to fusiform, 11–15-septate, 80–130 × 15–20 µm, 6–7 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—The new taxon has been collected in a relict montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes:—The combination of olive-green, distinctly verrucose thallus, columellate ascomata with mostly uncarbonized excipulum, large, transversely septate ascospores, and lack of secondary substances, make this species unmistakable within *Ocellularia*. Most similar are *O. dolichotata* (Nyl.) Zahlbruckner (1924: 589) and *O. orthomastia* (Kremp.) Zahlbruckner (1924: 597), which, however, differ in the whitish thallus and fully carbonized excipulum, and larger ascospores in the case of *O. dolichotata* and smaller in the case of *O. orthomastia*. Other morphologically similar species have small ascospores not exceeding 50 µm in length.

Additional specimen examined:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall, 20°31'S, 47°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8074* (IRD).

***Ocellularia fuscosporella* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 4C–D, 5A–B)

Mycobank # 807492

Sequence accession numbers: KJ435192 (mtSSU, holotype), KJ435119 (nuLSU, holotype)

Differing from *Ocellularia vizcayensis* in the brown ascospores.

Type:—NEW CALEDONIA. Province Nord: Poya, Goapin, Mont Aoupinié; relict montane forest, on bark; October 2012, *Papong & Lumbsch 7757* (holotype IRD!; isotype F!).

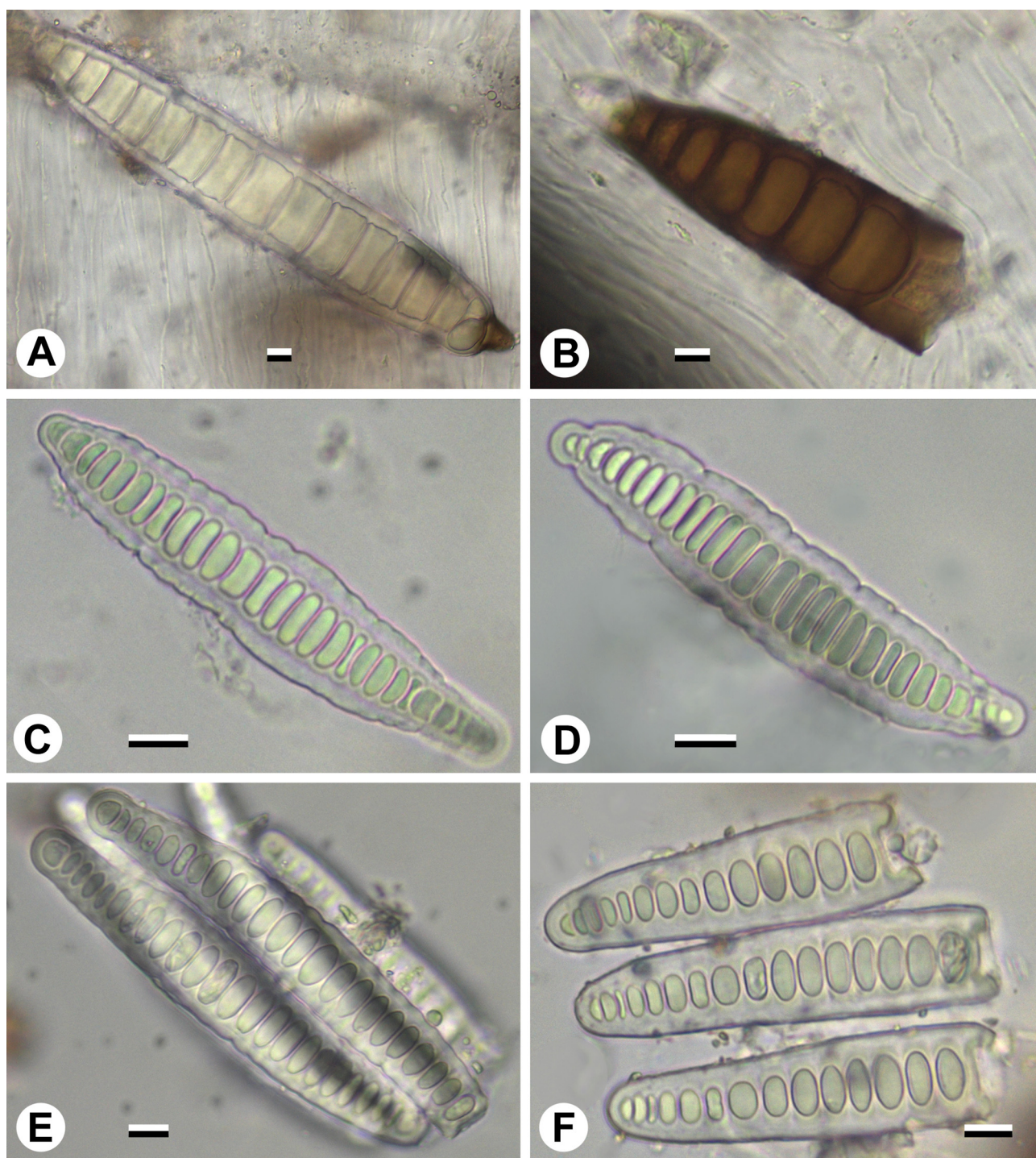


FIGURE 5. A–B. *Ocellularia fuscosporella*, mature ascospores remaining hyaline at first and then becoming dark brown (isotype). C–F. *Pseudotopeliopsis longispora*, young and mature ascospores (isotype). Scale = 10 µm.

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven, white; prothallus absent. Thallus in section 60–80 µm thick in thin parts and up to 130 µm thick in the thicker parts, with loose cortex, 5–10 µm thick, photobiont layer 20–30 µm thick, and medulla 30–50 µm thick and up to 100 µm thick in the thicker parts, with clusters of calcium oxalate crystals in the thin parts and single, massive clusters filling the thicker parts. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–9 µm. Ascomata round, strongly prominent, with complete thalline margin, 1–1.5 mm diam., 0.5–0.7 mm high; disc covered by 0.1–0.2 mm wide pore; proper margin distinct, forming a rough, white rim around the pore; thalline margin entire, smooth to uneven, light brown to orange-brown. Excipulum entire, carbonized, 40–60 µm wide;

laterally covered by algiferous, corticate thallus, 50–80 µm thick, encrusted with clusters of calcium oxalate crystals; columella absent; hypothecium prosoplectenchymatous, 20–30 µm high, colorless; hymenium 400–500 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 300–400 × 40–60 µm. Ascospores 1–2 per ascus, uniseriate to irregularly arranged, fusiform, 15–19-septate, 200–300 × 30–40 µm, 6–7 times as long as wide, hyaline but eventually becoming dark brown, subdistoseptate with angular lumina and thick outer wall, I+ violet-blue when hyaline.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—This new taxon is so far only known from the type collection in the northern part Grande Terre, where it was collected in a montane forest.

Notes:—*Ocellularia fuscosporella* produces one of the most spectacular ascospores in the genus. Large, transversely septate, distinctly brown ascospores are rare in the genus and so far only known from *Ocellularia allospora* (Nyl.) Zahlbruckner (1924: 582), which differs in having a carbonized columella. Another similar species is *O. vizcayensis* Rivas Plata, Duya & Lücking in Lumbsch *et al.* (2011: 88) from the Philippines, which agrees in morphology but has persistently hyaline ascospores. Comparison of the types confirmed the difference in ascospore pigmentation in mature ascospores.

***Ocellularia inconspicua* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 4E)**

Mycobank # 807493

Sequence accession numbers: KJ435194 (mtSSU, holotype), KJ435120 (nuLSU, holotype)

Differing from *Ocellularia pseudopyrenuloides* in the ascomata with narrower pore and uncarbonized columella as well as broader ascospores.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tendo, waterfall near the village; 20°92'S, 164°49'E, 280 m; relict montane forest, on bark; October 2012, Papong & Lumbsch 8090 (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epidermal, up to 10 cm diam., continuous; surface uneven to shallowly verrucose, light green to whitish; prothallus absent. Thallus in section 80–100 µm thick, with dense, prosoplectenchymatous cortex, 5–10 µm thick, with internal splitting, photobiont layer 30–50 µm thick, and medulla 50–60 µm thick, with scattered clusters of calcium oxalate crystals and small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–13 × 6–10 µm. Ascomata round, erumpent, with complete thalline margin, 0.3–0.5 mm diam., 0.15 mm high; disc covered by 0.05–0.1 mm wide pore; proper margin indistinct; thalline margin entire, smooth, whitish. Excipulum entire, uncarbonized, yellow-grey, 30–50 µm wide; laterally covered by algiferous, corticate thallus, 50–100 µm thick, encrusted with clusters of calcium oxalate crystals; columella present but often indistinct or developed above the hymenium only, finger-like, uncarbonized, yellow-grey, 70–100 µm wide and 120–150 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 100–120 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 100–110 × 15–20 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, oblong-ellipsoid, 3–5-septate, 15–20 × 7–10 µm, 1.8–2.3 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Psoromic, subpsoromic, and 2'-O-demethylpsoromic acids; medulla P+ yellow, microscopic section K–.

Distribution and ecology:—The new species is so far only known from the type collection in the northern part of Grande Terre, where it occurs in a relict montane forest.

Notes:—This new species is easily confused with a species of *Myriotrema* Fée (1825: xlix, 103) due to its small ascomata, but belongs to the *O. papillata* clade, as evidenced by the presence of a columella. Several species in *Ocellularia* have a combination of uncarbonized excipulum and columella, small, transversely septate ascospores, and psoromic acid chemistry. The most similar is the recently described *O. pseudopyrenuloides* Lücking in Sipman *et al.* (2012: 144) from Costa Rica, which differs in having a wider pore filled with a distinct, white-tipped columella and narrower ascospores. *Ocellularia minutula* Hale (1978: 24) differs in having smaller ascomata with apically dark brown columella and longer, narrower ascospores.

***Ocellularia neocaledonica* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 4F)

Mycobank # 807494

Sequence accession numbers: KJ435207 (mtSSU, holotype), KJ435130 (nuLSU, holotype)

Differing from *Ocellularia pluripora* in the lighter thallus and lack of secondary substances.

Type:—NEW CALEDONIA. Province Sud: Bouloupari, Mont Do, summit; 21°45'S, 166°00'E, 1010 m; montane rainforest, on bark; September 2012, *Papong & Lumbsch 7551* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 5 cm diam., continuous; surface uneven, light green to whitish green; prothallus absent. Thallus in section 50–80 µm thick, with prosoplectenchymatous cortex, 10–20 µm thick, photobiont layer 20–30 µm thick, and medulla 30–50 µm thick, with scattered clusters of calcium oxalate crystals and massively encrusted with such clusters in the ascoma margin. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata round, erumpent to prominent, with complete thalline margin, 0.6–1 mm diam., 0.25–0.3 mm high; disc covered by 0.1–0.15 mm wide pore; proper margin indistinct; thalline margin entire, smooth, forming a broad white rim slightly contrasting with the surrounding thallus. Excipulum entire, uncarbonized, orange-brown, 60–80 µm wide, not distinguishable from amorphous remnants of periderm; laterally covered by algiferous, corticate thallus, 100–200 µm thick, massively encrusted with clusters of calcium oxalate crystals; columella present, finger-like, completely carbonized, 60–80 µm wide and 100–120 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 90–100 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 90–100 × 10–12 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, oblong, 5-septate, 15–20 × 5–6 µm, 3–4 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—So far this new species is only known from the type collection in the southern part Grande Terre, where it was collected in a montane rainforest.

Notes:—The new species shares with a number of other species the combination of a carbonized columella and an uncarbonized, brown excipulum. Among these, *Ocellularia laeviusculoides* Sipman & Lücking in Sipman *et al.* (2012: 133) and *O. subpyrenuloides* Lücking in Sipman *et al.* (2012: 150) produce small, transversely septate ascospores and lack secondary substances. The latter differs by its smaller, erumpent ascomata with blackish rim around the pore, whereas the former has completely immersed ascomata with white-tipped columella filling the pore. Also *Ocellularia pluripora* Hale (1981: 319) is morphologically similar to the new species, but produces psoromic acid and its thallus and ascomata are darker.

***Ocellularia pulchella* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 6A–D)

Mycobank # 807495

Sequence accession numbers: KJ435195 (mtSSU, holotype), KJ435121 (nuLSU, holotype)

Differing from *Ocellularia mammicula* in the green, minutely grainy thallus with columnar clusters of calcium oxalate crystals and the narrower, non-annulate pore of the ascomata.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8048* (holotype IRD!; isotype F!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface uneven and minutely grainy, light green; prothallus absent. Thallus in section 100–200 µm thick, with dense, prosoplectenchymatous cortex, 10–20 µm thick, and massive medulla dominating the thallus, strongly encrusted with columnar clusters of calcium oxalate crystals and with small, grey crystals, photobiont layer developed mostly in the spaces between the clusters, slightly immersed in the medulla and forming interrupted patches. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–10 µm. Ascomata rounded, strongly prominent with tapering top, with complete thalline margin, 0.7–1.2 mm diam., 0.5–0.6 mm high; disc covered by 0.1–0.2 mm wide pore; proper margin thin, forming a pale yellowish rim around the pore; thalline margin entire, minutely grainy, of the same color as the surrounding thallus. Excipulum entire, uncarbonized, inner parts yellowish, outer

parts orange-brown, 70–100 μm wide, hardly distinguishable from amorphous remnants of periderm; laterally covered by algiferous, corticate thallus, 150–250 μm thick, massively encrusted with columnar clusters of calcium oxalate crystals; columella absent; hypothecium prosoplectenchymatous, 30–50 μm high, pale yellowish; hymenium 150–200 μm high, colorless, clear; epihymenium indistinct, 5–10 μm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, 130–160 $\times$ 25–30 μm . Ascospores 8 per ascus, uniseriate, broadly ellipsoid, muriform with irregularly arranged lumina, 20–25 $\times$ 12–15 μm , 1.5–2 times as long as wide, brown, distoseptate with rounded to irregular lumina, I–, when immature passing through a 3-septate and subsequently submuriform phase with thin septa and thick outer wall, hyaline and I+ dark violet-blue.

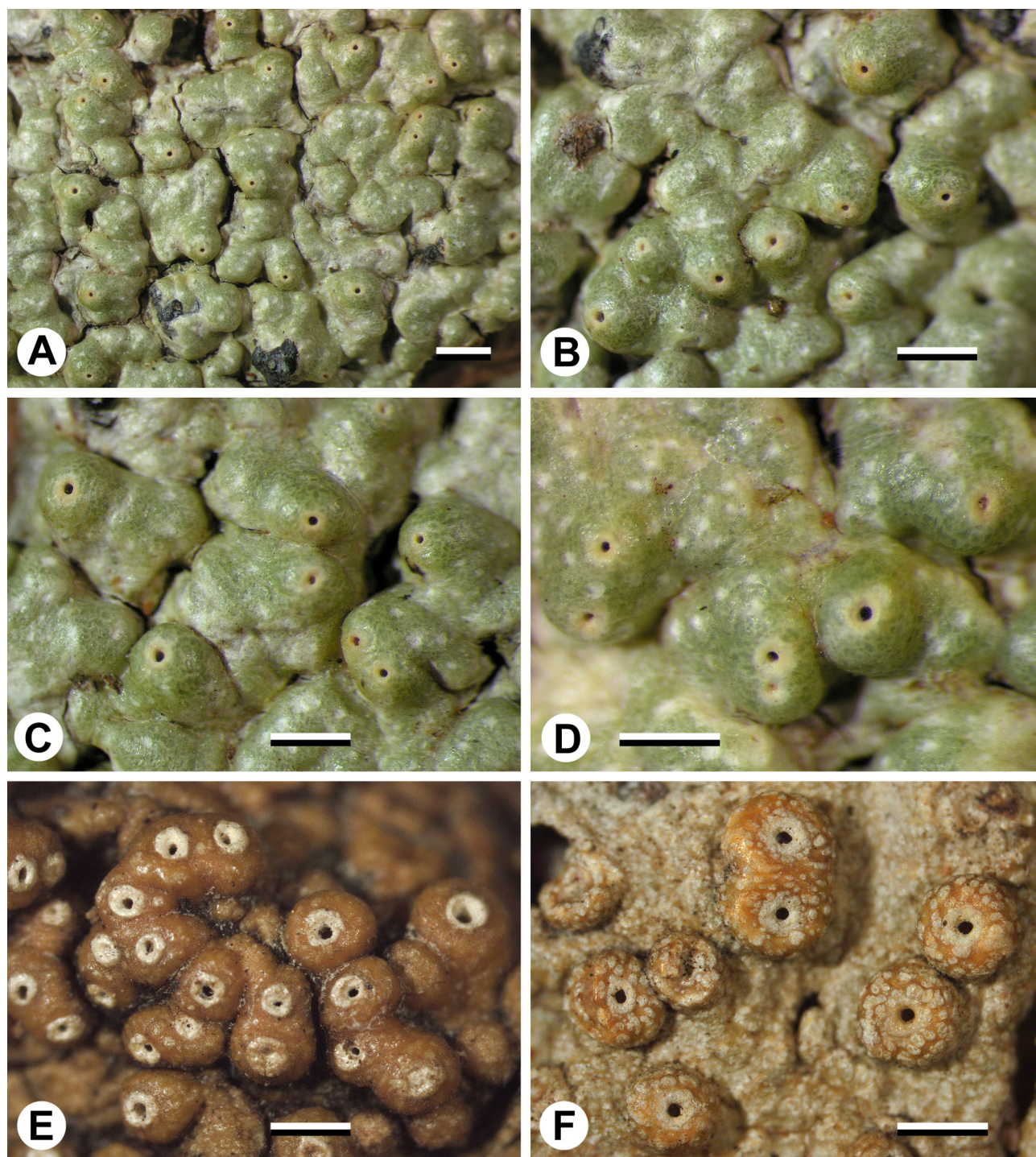


FIGURE 6. A–D. *Ocellularia pulchella*, thallus with ascomata (isotype). E. *O. mammicula*, thallus with ascomata (holotype). F. *O. permaculata*, thallus with ascomata (holotype). Scale = 1 mm.

Secondary chemistry:—Protocetraric and virensic acids (medulla P+ orange-red).

Distribution and ecology:—*Ocellularia pulchella* is so far only known from the type locality in the northern part of Grande Terre, where it occurs in a relict montane forest.

Notes:—The minutely grainy thallus surface, small, brown, muriform ascospores, and the presence of the protocetraric acid chemosyndrome suggest affinities of this new species with the *Ocellularia bahiana*-group. Molecular sequence data, however, place it in a different clade close to *O. interposita* (Nyl.) Hale (1980: 137). Three other species agree in forming prominent ascomata and lacking a columella. *Ocellularia petrinensis* David in David & Hawksworth (1995: 99), described from Mauritius, has less prominent apothecia with a flattened top, and its ascospores are weakly ornamented and amyloid, even in the pigmented stage. ***Ocellularia mammicula* (Hale) Lücking, comb. nov.** [Mycobank #807629; *Leptotrema mammiculum* Hale, *Mycotaxon* 7: 382. 1978; *Myriotrema mammiculum* (Hale) Hale, *Mycotaxon* 11: 134. 1980] (Fig. 6E) and ***O. permaculata* (Nagarkar & Hale) Lücking, comb. nov.** [Mycobank #807630; *Myriotrema permaculatum* Nagarkar & Hale, *Mycotaxon* 35: 439. 1989] (Fig. 6F), which also belong in the *Ocellularia bahiana* group, both have brown, verrucose-papillose thalli with large but not columnar clusters of calcium oxalate crystals; also their ascomata are broader with flattened top, with an annulate pore in *M. mammiculum*, whereas the thalline margin of the ascomata in *M. permaculatum* is distinctly white-papillose.

***Ocellularia rugosothallina* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 7A)

Mycobank # 807496

Sequence accession numbers: KJ435202 (mtSSU, holotype), KJ435126 (nuLSU, holotype)

Differing from *Ocellularia perforata* in the carbonized excipulum and columella.

Type:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8284* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 5 cm diam., continuous; surface distinctly ridged, light green, the ridges pale yellowish; prothallus absent. Thallus in section 60–90 µm thick, along the ridges up to 150 µm thick, with dense, prosoplectenchymatous cortex, 20–30 µm thick, photobiont layer 20–30 µm thick, and medulla 20–30 µm thick, with clusters of calcium oxalate crystals and small, grey crystals; ridges completely filled with grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded to irregular in outline, erumpent, with complete thalline margin, 0.4–0.6 mm diam., 0.15–0.2 mm high; disc covered by 0.1–0.15 mm wide pore filled with the black-tipped columella; proper margin indistinct; thalline margin entire, smooth, whitish to pale yellowish. Excipulum entire, apically carbonized, otherwise orange-brown, 20–30 µm wide, covered by amorphous periderm layer, orange-brown, 50–70 µm thick; laterally covered by algiferous, corticate thallus, 30–50 µm thick, encrusted with clusters of calcium oxalate crystals; columella present, finger-like to stump-shaped, carbonized, 100–150 µm wide and 90–100 µm high; hypothecium prosoplectenchymatous, 10–15 µm high, colorless; hymenium 75–80 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 70–80 × 10–12 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, oblong-ellipsoid, 5-septate, 15–20 × 5–6 µm, 2.8–3.5 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Protocetraric and virensic acids (medulla P+ orange-red).

Distribution and ecology:—This new taxon has been collected in a montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes:—*Ocellularia rugosothallina* shares the small, columellate ascomata, small, transversely septate ascospores, and presence of the protocetraric acid chemosyndrome with a number of other species in the genus. *Ocellularia subperforata* Nagarkar *et al.* (1988: 36) also has a verrucose to ridged thallus, but the ridges are thicker and more prominent, and the species has a fully carbonized excipulum, giving the apothecia a distinct black rim around the pore, and also a broad-stump-shaped columella. *Ocellularia violacea* Räsänen (1949: 184) has a smooth to uneven thallus and an uncarbonized excipulum, whereas in *O. thryptica* Hale (1973: 415), both the excipulum and columella are apically carbonized and the thallus is also smooth, lacking ridges; furthermore, its ascospores are about twice as large. *Ocellularia perforata* (Leight.) Müller (1892: 284) shares with the new species the verrucose-ridged thallus, but is distinguished by its dark brown excipulum and columella, and larger ascospores.

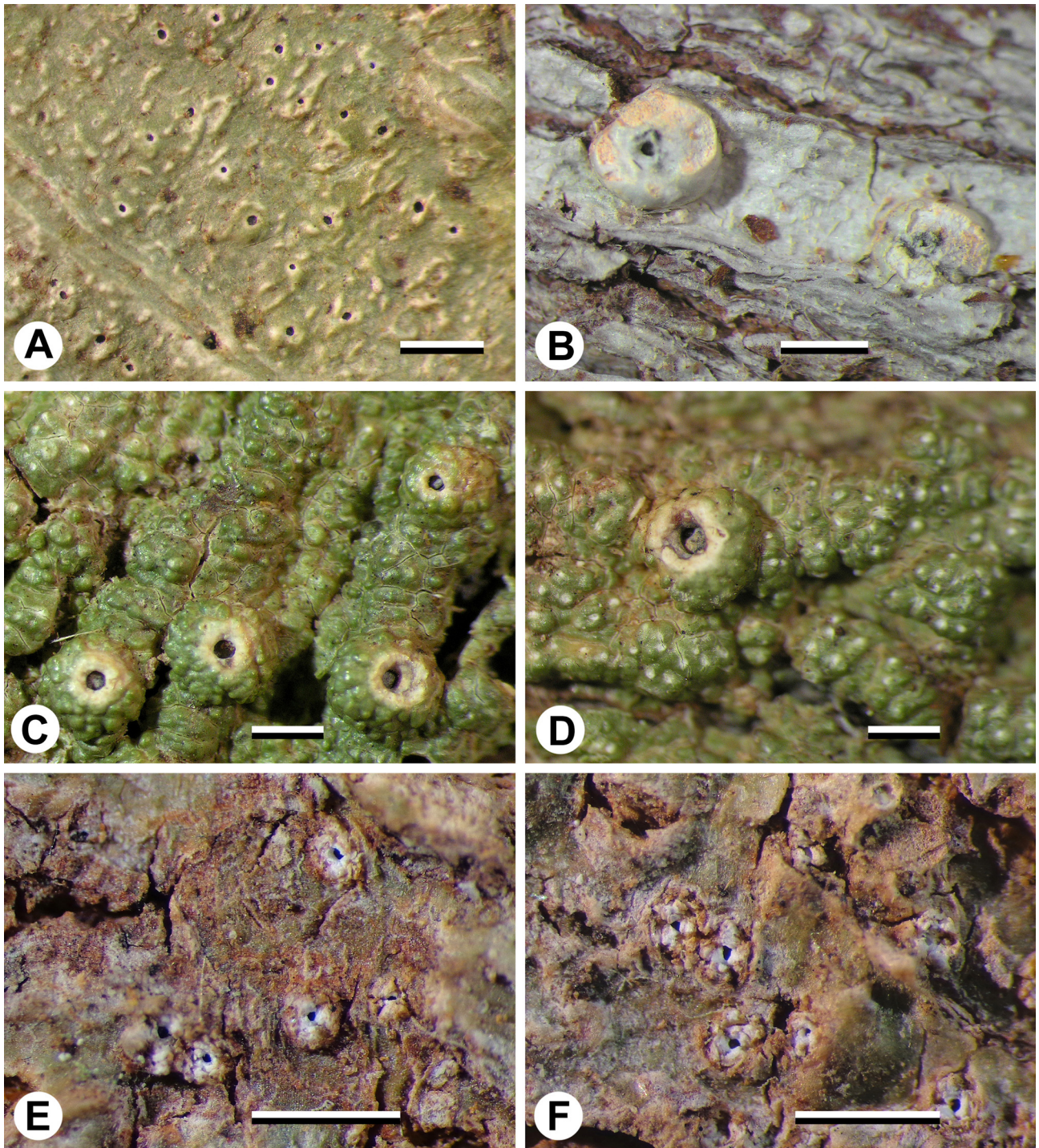


FIGURE 7. A. *Ocellularia rugosothallina*, thallus with ascomata (isotype). B. *O. salmonea*, thallus with ascomata (isotype). C–D. *O. austropacifica*, thallus with ascomata (isotype). E–F. *Pseudotopeliopsis longispora*, thallus with ascomata (isotype). Scale = 1 mm.

***Ocellularia salmonea* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 7B)**

Mycobank # 807497

Sequence accession numbers: KJ435191 (mtSSU, holotype), KJ435118 (nuLSU, holotype)

Differing from *Ocellularia baileyi* in the larger ascomata with only partially carbonized excipulum and the larger ascospores.

Type:—NEW CALEDONIA. Province Nord: Ouégoa, Mont Mandjélia; 20°24'S, 164°32'E, 780 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 7954* (holotype IRD!; isotype F!).

Thallus corticolous, epidermal, up to 10 cm diam., continuous; surface uneven to shallowly verrucose, white-grey; prothallus absent. Thallus in section 70–100 µm thick, with loose cortex, 5–10 µm thick, photobiont layer 10–20 µm thick, and medulla 50–70 µm thick, strongly encrusted with clusters of calcium oxalate crystals and numerous small, grey crystals, in surface view pale salmon-colored (best seen in thallus covering the ascomata). Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded, prominent, with complete thalline margin, 1–1.5 mm diam., 0.5–0.6 mm high; disc covered by 0.15–0.25 mm wide pore filled with white-tipped columella; proper margin thin, forming a thin, black, in inner parts white-pruinose rim around the pore; thalline margin entire, smooth, pale pinkish white. Excipulum entire, mostly uncarbonized, yellow, 30–50 µm thick, apically strongly carbonized, jet-black, up to 150 µm thick, covered by amorphous periderm layer, orange-brown, 50–100 µm thick; laterally covered by algiferous thallus, 100–150 µm thick; columella present, plug-shaped in the upper portion of the hymenium, carbonized, 250–300 µm broad and up to 300 µm high; hypothecium prosoplectenchymatous, 20–30 µm high, colorless; hymenium 400–500 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform, 350–450 × 30–40 µm. Ascospores 1(–2) per ascus, fusiform, 17–25-septate, 200–250 × 25–35 µm, 7–9 times as long as wide, hyaline, subdistoseptate with angular to lens-shaped lumina and thick outer wall, I+ violet-blue.

Secondary chemistry:—Norisonotatic and norsubnotatic acids and unknown, pale salmon-colored pigment.

Distribution and ecology:—So far only known from the type collection in the northern part of Grande Terre, where it was collected in a relict montane forest.

Notes:—The norisonotatic acid chemosyndrome ("chonestoma unknowns") is uncommon in *Ocellularia*, previously known from eight species. Among these, only *O. baileyi* Müller (1891: 51) also produces a pink medullary pigment. It is, however, readily distinguished by having smaller ascospores and ascomata with a completely carbonized excipulum. There are several *Ocellularia* species with large, transversely septate ascospores and medullary pigments, but these differ in secondary chemistry and anatomical details. For example, the North American *O. americana* Hale (1973: 413) contains gyrophoric acid and has a fully carbonized excipulum. Another species with pink medulla, *O. supergracilis* Kalb & Lücking in Sipman *et al.* (2012: 150), produces the cinchonarum unknown chemosyndrome and also has a fully carbonized excipulum, in addition to a wider pore with massive, black-tipped columella.

***Pseudotopeliopsis longispora* Papong, Lücking & Parnmen, *sp. nov.* (Fig. 5C–F, 7E–F)**

Mycobank # 807504

Differing from other species of *Pseudotopeliopsis* in the long, transversely septate ascospores.

Type:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8240* (holotype IRD!; isotype F!).

Thallus corticolous, partially endoperidermal, up to 5 cm diam., continuous; surface uneven, following the contours of the bark, olive-green; prothallus absent. Thallus in with dense, prosoplectenchymatous cortex, 10–20 µm thick, irregular photobiont layer immersed in the periderm, 20–30 µm thick, and irregular medulla immersed in the periderm, 30–50 µm thick, encrusted with clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata angular-rounded, immersed to erumpent, with lateral thalline margin, 0.3–0.5 mm diam., 0.2–0.25 mm high; disc more or less covered by narrow pore, flesh-colored, white-pruinose; proper margin more or less erect, lobulate, white, with split towards thalline margin, distinctly layered; thalline margin indistinct. Excipulum colorless to pale yellowish, 30–50 µm wide, paraplectenchymatous; laterally covered by grey crystals; columella absent; hypothecium prosoplectenchymatous, 10–15 µm high, colorless to pale yellowish; hymenium 150–170 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, granular. Paraphyses unbranched, apically thin, smooth; periphysoids present, short (10–15 µm); asci fusiform, 140–160 × 40–50 µm. Ascospores 4–8 per ascus, oblong, 21–29-septate, 100–150 × 15–18 µm, 6–8 times as long as wide, hyaline, distoseptate with thickened septa and lens-shaped lumina and thick outer wall, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—This taxon was collected in a relict montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes:—*Pseudotopeliopsis longispora* is externally similar to the other known species of the genus in having a corticate thallus and small, immersed-erumpent, chroodiscoid ascomata with layered margins. However, it differs from all other currently known *Pseudotopeliopsis* Parnmen *et al.* (2012: e51392) species in having long, transversely septate ascospores. The other similar species have quite different ascospores: large and muriform in *P. laceratula* (Müll. Arg.) Parnmen *et al.* (2012: e51392) and *P. scabiomarginata* (Hale) Parnmen *et al.* (2012: e51392), and small and transversely septate in *P. scabiocarpa* (Hale) Parnmen *et al.* (2012: e51392).

***Rhabdodiscus farinosus* Papong, Lücking & Parnmen, sp. nov.** (Fig. 8A–B)

Mycobank # 807498

Differing from other species of *Rhabdodiscus* in the ecorticate, finely farinose and sorediate thallus.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, Papong & Lumbsch 8040 (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous, sorediate; surface farinose, white-grey; prothallus absent. Soralia first visible as pale yellowish, low verrucae 0.3–0.5 mm diam., eventually breaking up and covered with tiny grey granules representing soredia; individual soredia 10–12 µm diam., with a single algal cell wrapped in a sheath of fungal hyphae with slightly projecting tips, hyphae at first hyaline but soon becoming grey-brown. Thallus in section 50–100 µm thick, ecorticate, with indistinctly separated photobiont layer and medulla, completely filled with numerous small, grey crystals and also with scattered clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata angular to elongate, erumpent, with lateral thalline margin, 1–1.5 mm diam. or up to 2 mm long, 0.2–0.25 mm high; disc more or less exposed but mostly filled by irregular, thickly white-pruinose columella; proper margin well-developed, thick, fissured, thickly white-pruinose; thalline margin indistinct. Excipulum entire, carbonized, 30–50 µm wide; laterally covered thallus layer filled with grey crystals, 50–80 µm thick; columella present, irregular to radiate, divided into numerous strands, completely carbonized, individual strands 100–150 µm wide and 100–150 µm high; hypothecium prosoplectenchymatous, 10–20 µm high, colorless; hymenium 70–80 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 70–80 × 8–10 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, oblong, 5-septate, 15–20 × 5–6 µm, 3–4 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—Psoromic, subpsoromic, and 2'-O-demethylpsoromic acids; medulla P+ yellow, microscopic section K–.

Distribution and ecology:—*Rhabdodiscus farinosus* has been collected in montane forests in the northern part of Grande Terre.

Notes:—The new species is a unique within *Rhabdodiscus* Vainio (1921: 184), characterized by a farinose, sorediate thallus and conspicuous, large, irregular ascomata with complex columella. No other species in the family is known to produce dark-pigmented soredia. The only remotely similar species is *Ocellularia discoidea* Müller (1887b: 8), which agrees in producing ascomata with fissured margins and soralia and containing psoromic acid, but differs by having a loosely corticate thallus, broad-stump-shaped columella, and ascospores twice as large.

Additional specimen examined:—NEW CALEDONIA. Province Nord: Touho, Tiwaé, Massif des Lèvres; relict montane forest, on bark; October 2012, Papong & Lumbsch 8257 (F, IRD, MSUT).

***Rhabdodiscus neocaledonicus* Lücking, Lumbsch & Parnmen, sp. nov.** (Fig. 8C)

Mycobank # 807499

Sequence accession numbers: KJ435204 (mtSSU, holotype), KJ435128 (nuLSU, holotype)

Differing from *Rhabdodiscus lankaensis* in the submuriform, brown ascospores.

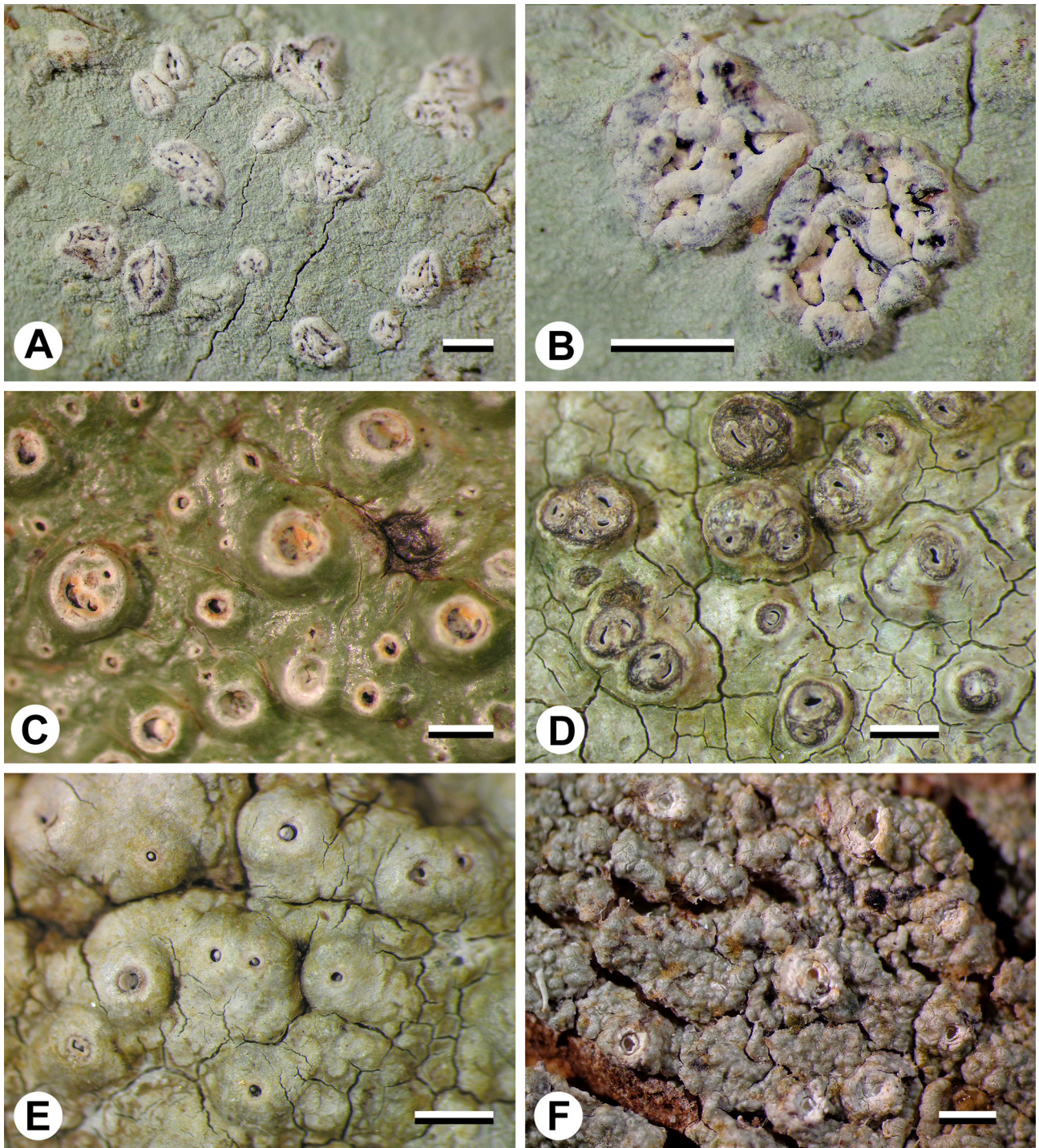


FIGURE 8. A–B. *Rhabdodiscus farinosus*, thallus with ascomata (isotype). C. *R. neocaledonicus*, thallus with ascomata (isotype). D. *R. saxicola*, thallus with ascomata (isotype). E. *R. thouvenotii*, thallus with ascomata (isotype). F. *Thelotrema perriei*, thallus with ascomata (isotype). Scale = 1 mm.

Type:—NEW CALEDONIA. Province Sud: Yaté, Montagne des Sources, right hand site along the road, 22°09'S, 166°35'E, 400 m, rainforest, on bark; September 2012, *Papong & Lumbsch* 7630 (holotype IRD!; isotype F!).

Thallus corticolous, epidermal, up to 7 cm diam., continuous; surface smooth to uneven, light olive-green to green-grey; prothallus absent. Thallus in section 150–200 µm thick, with dense, prosoplectenchymatous cortex, 20–30 µm thick, photobiont layer 20–30 µm thick, and medulla 100–150 µm thick, encrusted with clusters of calcium oxalate crystals and small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded, erumpent to prominent, with nearly

complete thalline margin, 0.8–1.5 mm diam., 0.4–0.5 mm high; disc covered by 0.3–0.6 mm wide pore and completely filled by irregular columella covered by pale salmon-yellow pigment; proper margin distinct, forming a white to pale salmon-yellow rim around the pore; thalline margin entire, smooth, olive-green to green-grey. Excipulum entire, carbonized, 50–90 µm wide, covered by an amorphous layer of periderm cells, orange-brown, 50–100 µm thick; laterally covered by algiferous, corticate thallus, 70–100 µm thick, encrusted with clusters of calcium oxalate crystals; columella present, initially stump-shaped but becoming irregular with lateral, radiating bridges, completely carbonized, 100–200 µm wide and 120–130 µm high; hypothecium prosoplectenchymatous, 10–15 µm high, colorless; hymenium 80–90 µm high, colorless, clear; epihymenium indistinct, 5–10 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci fusiform to clavate, 80–90 × 12–15 µm. Ascospores 8 per ascus, uniseriate to irregularly arranged, ellipsoid, submuriform with 3 transverse septa and 0–1 longitudinal septa per segment, 12–15 × 8–10 µm, 1.3–1.7 times as long as wide, brown, distoseptate with lens-shaped lumina, I+ violet-blue when young.

Secondary chemistry:—Psoromic, subpsoromic, and 2'-O-demethylpsoromic acids; medulla P+ yellow, microscopic section K–; unknown pale pigment in ascomata, K+ dark red.

Distribution and ecology:—The new taxon is so far only known from the type collection in the northern part of Grande Terre, where it was collected in a rain forest.

Notes:—This new species is closely related to *Rhabdodiscus lankaensis* (Hale) Lücking, *comb. nov.* [Mycobank #807631; *Ocellularia lankaensis* Hale, *Bull. Br. Mus. Nat. Hist., Bot.* 8(3): 309. 1981]. Both share the same ascoma morphology but *R. lankaensis* has transversely septate, hyaline ascospores. Molecular sequence data place the new species in *Rhabdodiscus* (Kraichak *et al.* 2014), and hence the combination of *Ocellularia lankaensis* from Sri Lanka (Hale 1981) into that genus is also proposed.

***Rhabdodiscus saxicola* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 8D)**

Mycobank # 807500

Sequence accession numbers: KJ435197 (mtSSU, holotype), KJ435123 (nuLSU, holotype)

Differing from *Rhabdodiscus crassus* in the saxicolous habit and the pseudostromatic ascomata with broad brown rim and columella contrasting with the light yellowish brown thallus.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8042* (holotype IRD!; isotype F!).

Thallus saxicolous, up to 5 cm diam., continuous; surface cracked, light yellowish brown; prothallus absent. Thallus in section 100–150 µm thick, with dense, paraplectenchymatous cortex, 20–30 µm thick, photobiont layer 40–60 µm thick, and medulla 50–70 µm thick, strongly encrusted with clusters of calcium oxalate crystals and small, grey crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–12 × 6–10 µm. Ascomata rounded, erumpent to prominent, with nearly complete thalline margin, solitary or often aggregated in pseudostromatic thallus warts, 0.6–1 mm diam., 0.3–0.4 mm high, pseudostromatic warts up to 2 mm diam.; disc covered by 0.1–0.3 mm wide pore filled with white-tipped, often irregular columella usually connected laterally to the excipulum; proper margin distinct, forming a broad brownish rim around the pore; thalline margin smooth, light yellowish brown. Excipulum very dark brown to carbonized, 80–120 µm thick; laterally covered by algiferous thallus, 100–150 µm thick; columella present, broad-stump-shaped to irregular, very dark brown to carbonized, 300–400 µm broad and up to 200 µm high; hypothecium prosoplectenchymatous, 15–25 µm high, pale brownish; hymenium 120–130 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical, 110–120 × 15–20 µm. Ascospores 8 per ascus, uniseriate, broadly ellipsoid to oval, muriform with 3 transverse and 1–2 longitudinal septa per segment, 17–25 × 12–15 µm, 1.3–1.7 times as long as wide, for a long time hyaline but eventually becoming pale brown, distoseptate with lens-shaped lumina, I+ violet-blue when hyaline.

Secondary chemistry:—No substances detected by TLC.

Distribution and ecology:—This new species is so far only known from the type collection in the northern part of Grande Terre, where it occurs in a relict montane forest.

Notes:—This is a rather unique species, both in terms of morphology and substrate ecology. At first glance it resembles a species of *Ocellularia*. However, few species in *Ocellularia* have small, (sub-)muriform ascospores

becoming brown, the most similar being *O. albomaculata* Hale (Hale 1981): 300). That species is corticolous and its columella does not become irregular. Also, the ascospores are longer and narrower. Very similar in ascoma morphology is *O. wandoorensis* Nagarkar, Sethy & Patw. (Nagarkar *et al.* 1986): 78), which, however, differs in having smaller, transversely septate and hyaline ascospores. Surprisingly, molecular sequence data place the new species in the genus *Rhabdodiscus* (Kraichak *et al.* 2014), where it is ecologically and morphologically quite unique (Rivas Plata *et al.* 2012).

***Rhabdodiscus thouvenotii* Lücking, Lumbsch & Parnmen, *sp. nov.* (Fig. 8E)**

Mycobank # 807501

Sequence accession numbers: KJ435196 (mtSSU, holotype), KJ435122 (nuLSU, holotype)

Differing from *Rhabdodiscus saxicola* in the larger, more or less solitary ascomata with narrower pore and finger-like columella.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8049* (holotype IRD!; isotype F!).

Thallus saxicolous, up to 10 cm diam., continuous; surface cracked, yellowish white; prothallus absent. Thallus in section 150–200 µm thick, with dense, paraplectenchymatous cortex, 15–20 µm thick, medulla 130–180 µm thick, strongly encrusted with clusters of calcium oxalate crystals and small, grey crystals, and irregular photobiont layer immersed within the medulla. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 8–11 × 6–10 µm. Ascomata round, erumpent to prominent, with complete thalline margin, 1–1.5 mm diam., 0.4–0.5 mm high; disc covered by 0.2–0.4 mm wide pore filled with white-tipped columella; proper margin thin, forming white rim around the pore bordered by a thin, brownish rim; thalline margin smooth, yellowish white. Excipulum carbonized in upper part, otherwise orange-brown, 80–100 µm thick; laterally covered by algiferous thallus, 100–150 µm thick; columella present, finger-like, carbonized, 100–150 µm broad and up to 200 µm high; hypothecium prosoplectenchymatous, 20–30 µm high, pale brownish; hymenium 120–130 µm high, colorless, clear; epihymenium indistinct, 10–20 µm high, colorless. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical, 110–120 × 15–20 µm. Ascospores 8 per ascus, uniseriate, broadly ellipsoid to oval, muriform with 5 transverse and 1–2 longitudinal septa per segment, 20–25 × 12–15 µm, 1.5–1.7 times as long as wide, brown, distoseptate with lens-shaped lumina, I+ violet-blue when young.

Secondary chemistry:—No substances detected by TLC.

Etymology:—This new species is named after the French Botanist Louis Thouvenot (France), who is a specialist in the flora of New Caledonia and guided us perfectly in the field and worked tirelessly to organize the field trip.

Distribution and ecology:—The new taxon has been collected in a relict montane forest in the northern part of Grande Terre and is so far only known from the type locality.

Notes:—This species is similar to *Rhabdodiscus saxicola*, with which it shares the substrate ecology, columellate ascomata, and ascospore type. However, both molecular sequence data (Kraichak *et al.* 2014) and morphological differences indicate that it is distinct from the former: the ascomata are larger and never aggregated in pseudostromatic thallus warts, the proper margin is much thinner, the excipulum is carbonized in upper parts only, and the columella always remains finger-like.

***Thelotrema perriei* Papong, Lücking & Lumbsch, *sp. nov.* (Fig. 8F)**

Mycobank # 807513

Differing from *Thelotrema diplotrema* in the densely corticate, verrucose thallus and smaller ascospores.

Type:—NEW CALEDONIA. Province Nord: Hienghène, Tao waterfall; 20°33'S, 164°47'E, 440 m; relict montane forest, on bark; October 2012, *Papong & Lumbsch 8069* (holotype IRD!; isotypes F!, MSUT!).

Thallus corticolous, epiperidermal, up to 10 cm diam., continuous; surface distinctly verrucose, light greyish green; prothallus absent. Thallus in section 100–150 µm thick, with dense, paraplectenchymatous cortex, 20–30

µm thick, photobiont layer 50–70 µm thick, and medulla 30–60 µm thick, encrusted with clusters of calcium oxalate crystals. Photobiont *Trentepohlia*; cells rounded to irregular in outline, in irregular groups, yellowish green, 7–12 × 6–9 µm. Ascomata angular-rounded, erumpent, with lateral thalline margin, 0.7–1.2 mm diam., 0.3–0.4 mm high; disc more or less covered by 0.3–0.5 mm wide pore, flesh-colored to yellowish, thinly white-pruinose; proper margin more or less erect, entire, undulate, white, separated from thalline margin by a split (double margin); thalline margin erect, entire to fissured, uneven to verrucose, light greyish green. Excipulum yellowish to orange in outer parts, 30–50 µm wide, paraplectenchymatous; laterally covered by massive thalline layer including an inner layer of clusters of calcium oxalate crystals, 50–100 µm thick, and distinct layers of periderm, 100–150 µm thick; columella absent; hypothecium prosoplectenchymatous, 10–20 µm high, yellowish; hymenium 110–120 µm high, colorless, clear; epihymenium granular, 5–10 µm high, greyish. Paraphyses unbranched, apically thin, smooth; periphysoids present, distinct (20–30 µm); asci fusiform, 110–120 × 20–25 µm. Ascospores 4–8 per ascus, oblong-tapering, 11–15-septate, 50–60 × 6–8 µm, 7–8 times as long as wide, hyaline, distoseptate with thickened septa and lens-shaped lumina, I+ violet-blue.

Secondary chemistry:—No substances detected by TLC.

Etymology:—The new species is named after the pteridologist Leon Perrie (New Zealand), who is a specialist in the flora of the South Pacific and systematics of ferns. Leon was a great companion on the field trip to New Caledonia and previous trips to Fiji.

Distribution and ecology:—*Thelotrema perriei* is so far only known from the type collection in the northern part of Grande Terre, where it was found in a relict montane forest.

Notes:—This new species is characterized by having a corticate, verrucose thallus and mid-sized ascospores. Similar ascospores are known from *Thelotrema diplotrema* Nylander (1859: 258), which differs by having a loosely corticate, smooth to uneven thallus and larger ascospores. Another similar species is *Thelotrema jugale* (Müll. Arg.) Lücking in Sipman et al. (2012: 195), which differs in its white, smooth to uneven thallus with loose cortex and the smaller, immersed ascomata.

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Revisiting the phylogeny of Ocellularieae, the second largest tribe within Graphidaceae (lichenized Ascomycota: Ostropales)

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Abstract

We present an updated 3-locus molecular phylogeny of tribe Ocellularieae, the second largest tribe within subfamily Graphidoideae in the Graphidaceae. Adding 165 newly generated sequences from the mitochondrial small subunit rDNA (mtSSU), the nuclear large subunit rDNA (nuLSU), and the second largest subunit of the DNA-directed RNA polymerase II (*RPB2*), we currently distinguish 218 species among the sequenced material, including the outgroup. This corresponds to almost half the species at this point recognized within this tribe. The newly generated sequences include 23 newly described species and one newly described genus published elsewhere in this volume. For the first time, *Sarcographina cyclospora* Müll. Arg., in spite of its distinctly lirellate ascomata, is shown to belong in tribe Ocellularieae, as strongly supported sister to *Ocellularia inturgescens* (Müll. Arg.) Mangold. The following six new combinations are proposed: *Melanotrema lynceodes* (Nyl.) Rivas Plata, Lücking & Lumbsch, *Ocellularia curranii* (Vain.) Kraichak, Lücking & Lumbsch, *O. khasiana* (Patw. & Nagarkar) Kraichak, Lücking & Lumbsch, *O. cinerea* (Müll. Arg.) Kraichak, Lücking & Lumbsch, *O. erodens* (R. C. Harris) Kraichak, Lücking & Lumbsch, and *O. laeviuscula* (Nyl) Kraichak, Lücking & Lumbsch. Further, the new name *Ocellularia hernandeziana* Kraichak, Lücking & Lumbsch is introduced for *Myriotrema ecorticatum*. The nomenclatural status of the name *Ocellularia microstoma* is clarified.

Key words: *Ampliotrema*, *Glaucotrema*, phylogenetic resolution, *Redingeria*, *Reimnitzia*, *Rhabdodiscus*, *Sarcographina*, *Stegobolus*, supermatrix

Introduction

The two largest families of lichenized ascomycetes are the crustose Graphidaceae and the predominantly foliose and fruticose Parmeliaceae. With a recent increase in species discovery, mainly in tropical regions, Graphidaceae

has surpassed Parmeliaceae in terms of global species richness, with over 2,500 species currently known and approximately 4,300 species predicted (Lücking *et al.* 2014). Graphidaceae contains four subfamilies, Fissurinoideae, Gomphilloideae, Graphidoideae, and Redonographoideae (Rivas Plata *et al.* 2012a; Lücking *et al.* 2013), among which Graphidoideae contains probably more than 75% of the species. Within that subfamily, three large tribes are currently recognized, besides several smaller clades: Graphideae, Ocellularieae, and Thelotremateae (Rivas Plata *et al.* 2012a, b).

Graphideae, containing the large genus *Graphis* Adanson (1763: 11) and otherwise the bulk of species formerly classified in Graphidaceae s.str., is the largest tribe, but recent new species discoveries, especially in the megadiverse genus *Ocellularia* Meyer (1825: 327) s.lat., have increased the known species richness in tribe Ocellularieae to the point that it now approaches the size of Graphideae. This is probably due to the fact that Ocellularieae predominantly contains species confined to undisturbed rain forests (Hale 1974, 1978, 1981; Rivas Plata *et al.* 2008), whereas Graphideae and Thelotremateae are more frequently found in semi-exposed situations in montane forests, making them more readily available for collection and decreasing the possibility for additional new species to be discovered. Hence, increased efforts to sample the diversity of Graphidaceae in undisturbed, often remote rain forest areas will mostly result in novel taxa in the genus *Ocellularia* s.lat. and its relatives. This is also shown by the contribution in this volume, where 67 of the 170 newly described species correspond to tribe Ocellularieae and only 41 to tribe Graphideae.

Tribe Ocellularieae as circumscribed by Rivas Plata *et al.* (2012b), when excluding the *Leptotrema* Mont. & Bosch in Miquel (1855: 483) clade (Lücking *et al.* 2013) principally corresponds to the genera *Myriotrema* Fée (1825: 34) s.lat. and *Ocellularia* s.lat. as circumscribed by Hale (1980). A few species previously ascribed to these genera are now included in *Clandestinotrema* Rivas Plata *et al.* (2012a: 116), *Cruentotrema* Rivas Plata *et al.* (2012a: 119), and *Pycnotrema* Rivas Plata *et al.* (2012a: 120), classified in subfamily Fissurinoideae (Rivas Plata *et al.* 2012a). The very wide traditional generic concept (*Myriotrema* and *Ocellularia*) for taxa now placed within tribe Ocellularieae (Hale 1980) was first challenged by Frisch *et al.* (2006), who reinstated or newly described the genera *Ampliotrema* Kalb ex Kalb in Frisch *et al.* (2006: 81), *Fibrillithecis* Frisch in Frisch *et al.* (2006: 135), *Gyrotrema* Frisch in Frisch *et al.* (2006: 379), *Melanotrema* Frisch in Frisch *et al.* (2006: 382), *Redingeria* Frisch in Frisch *et al.* (2006: 402), and *Stegobolus* Montagne (1845: 4), for morphologically and, in part, genetically distinct segregates of *Myriotrema* s.lat. and *Ocellularia* s.lat. This concept was further expanded based on a broad phylogeny of this group, introducing the additional genera *Compositrema* Rivas Plata *et al.* (2012b: 1172), *Glaucotrema* Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1174), and *Rhabdodiscus* Vainio (1921: 184) (Rivas Plata *et al.* 2012b). It was also recognized that tribe Ocellularieae contains further, unnamed genus-level lineages, whereas the two genera *Ampliotrema* and *Gyrotrema* do not form monophyletic groups that are distinct from *Ocellularia* s.str (Rivas Plata *et al.* 2012b).

In this contribution, we present an updated molecular phylogeny of tribe Ocellularieae, including an additional 131 OTUs and distinguishing 80 further species compared to our previous study (Rivas Plata *et al.* 2012b). We discuss the individual clades in detail and highlight the phylogenetic position of 23 new taxa described elsewhere in this volume (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Papong *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014; Weerakoon *et al.* 2014).

Material and Methods

A total of 165 new sequences of the mtSSU rDNA (94), nuLSU rDNA (56) and the *RPB2* gene (15) were obtained from 131 ingroup OTUs representing 75 species in tribe Ocellularieae. In addition, 432 sequences were used from our previous analyses, including the same outgroup, representing an additional 143 species after taxonomic revision, five more than distinguished previously (Rivas Plata *et al.* 2012b, 2013; Table 1).

New sequences were generated for this study using the Sigma REExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, USA) for DNA isolation following the manufacturer's instructions, except that 40 µL of extraction buffer and 40 µL dilution buffer were used. DNA dilutions (10x) were used in PCR reactions of the genes coding for the nuLSU, mtSSU and *RPB2*. Primers for amplification were: (a) for nuLSU: AL2R (Mangold *et al.* 2008a), and nu-

LSU-1125-3' (= LR6) (Vilgalys & Hester 1990), (b) for mtSSU: mr-SSU1 and Mr-SSU3R (Zoller *et al.* 1999), and (c) for *RPB2*: fRPB2-7cF and fRPB2-11aR (Liu *et al.* 1999). PCR reactions contained 4.5 µL R4775 Sigma REDExtract-N-Amp™ PCR ReadyMix, 0.5 µL of each primer (10 µM), 2 µL genomic DNA extract and 2 µL distilled water for a total of 10 µL. Thermal cycling parameters were: (1) for nuLSU: initial denaturation for 5 min at 94°C, followed by 35 cycles of 30 s at 95°C, 30 s at 58°C, 1 min at 72°C, and a final elongation for 10 min at 72°C; (2) for mtSSU: initial denaturation for 5 min at 95°C, followed by 35 cycles of 45 s at 94°C, 1 min at 50°C, 1 min 30 s at 72°C, and a final elongation for 10 min at 72°C; and (3) for *RPB2*: initial denaturation for 3 min at 95°C, then 1 min at 95°C, and 37 cycles of 1 min at 57°C, 1 min at 58°C, 1 min at 59°C, 1 min at 60°C, 1 min at 61°C, 1 min at 62°C, 1 min at 63°C, 1 min at 64°C and 1.5 min at 72°C, and a final elongation for 10 min at 72°C. Samples were visualized on a 1% ethidium bromide-stained agarose gel under UV light and bands were gel extracted, heated at 70° C for 10 minutes, cooled to 45° C for 5 minutes, treated with 1 µL GELase (Epicentre Biotechnologies, Madison, WI, USA) and incubated at 45° C for at least 24 hours. The 10–µl cycle sequencing reactions consisted of 1–1.5 µl of Big Dye version 3.1 (Applied Biosystems, Foster City, California, U.S.A.), 2.5–3 µl of Big Dye buffer, 6 µM primer, 0.75–2 µl gelaed PCR product and water. Samples were sequenced with PCR primers. The cycle sequencing conditions were as follows: 96° C for 1 minute, followed by 25 cycles of 96° C for 10 seconds, 50° C for 5 seconds and 60° C for 4 minutes. Samples were precipitated and sequenced using Applied Biosystems 3730 DNA Analyzer (Foster City, California, U.S.A.), sequences were assembled in SeqMan 4.03 (DNASTAR) and submitted to GenBank (Table 1).

TABLE 1. Genbank numbers and voucher information of specimens used in this study. For author names see *Index Fungorum* (<http://www.indexfungorum.org>).

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ampliotrema amplius</i>	Brazil	Cáceres	6032	JX420961	[—]	[—]
<i>Ampliotrema amplius</i>	Brazil	Cáceres	6038	JX420962	[—]	[—]
<i>Ampliotrema amplius</i>	Peru	Rivas Plata	FM89	JF828958	JF828973	[—]
<i>Ampliotrema lepadinoides</i>	Peru	Rivas Plata	8extra	[—]	JX421433	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420964	[—]	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420965	[—]	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420966	[—]	[—]
<i>Ampliotrema rimosum</i>	Puerto Rico	Mercado	81	KJ435164	[—]	[—]
<i>Ampliotrema sp. nov.</i>	Venezuela	Lücking	32187	JX420963	JX421432	JX420900
<i>Compositrema borinquense</i>	Puerto Rico	Mercado	F7	KJ435180	[—]	[—]
<i>Compositrema cerebriforme</i>	Venezuela	Lücking	32204	JX421017	JX421471	JX420901
<i>Compositrema isidiofarinosum</i>	Venezuela	Kalb	sn	JX421018	JX421472	JX420909
<i>Compositrema isidiofarinosum</i>	Puerto Rico	Mercado	257	KJ435175	[—]	[—]
<i>Compositrema thailandicum</i>	Thailand	Lumbsch	19756o	JX421019	JX421473	[—]
<i>Fibrillithecis argentea</i>	Reunion	Kalb	26027	DQ384901	[—]	[—]
<i>Fibrillithecis confusa</i>	Tanzania	Frisch	99Tz748	DQ384902	[—]	[—]
<i>Fibrillithecis platyspora</i>	New Caledonia	Papong	8037	KJ435199	[—]	[—]
<i>Fibrillithecis gibbosa</i>	Australia	Mangold	36vI	[—]	JX421485	[—]
<i>Fibrillithecis gibbosa</i>	Australia	Mangold	31g	EU075573	EU075621	[—]
<i>Fibrillithecis thailandica</i>	Thailand	Lumbsch	19751a	[—]	JX421486	[—]
<i>Glaucotrema emergens</i>	Philippines	Rivas Plata	1099	JX421061	JX421501	JX420862
<i>Glaucotrema glaucophaenum</i>	Venezuela	Kalb	sn	[—]	[—]	JX420902
<i>Glaucotrema glaucophaenum</i>	Thailand	Lumbsch	19751g	[—]	JX421502	[—]
<i>Glaucotrema glaucophaenum</i>	Australia	Lumbsch	19127eA	JX421060	[—]	[—]

.....continued on the next page

TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Glaucotrema</i> sp. nov.	Thailand	Papong	8560	[—]	KJ435152	[—]
<i>Glaucotrema stegoboloides</i>	Brazil	Cáceres	11817	KJ435228	[—]	[—]
<i>Glaucotrema subcostaricense</i>	Tanzania	Frisch	99Tz866	DQ384899	[—]	[—]
<i>Gyrotrema album</i>	Brazil	Cáceres	11349	KJ435209	[—]	[—]
<i>Gyrotrema flavum</i>	Brazil	Cáceres	11417	KJ435212	[—]	[—]
<i>Gyrotrema wirthii</i>	Costa Rica	Lücking	16301	HQ639591	[—]	[—]
<i>Gyrotrema wirthii</i>	Costa Rica	Lücking	16252	JX421071	[—]	[—]
<i>Leptotrema</i> aff. <i>wightii</i>	El Salvador	Lücking	28095	[—]	JF828977	JF828948
<i>Leptotrema wightii</i>	Costa Rica	Nelsen	2034A	EU075574	[—]	[—]
<i>Leptotrema wightii</i>	Costa Rica	Nelsen	2034A	JX421074	EU075622	[—]
<i>Leptotrema wightii</i>	Costa Rica	Will Wolf	10043a	[—]	AY605079	[—]
<i>Melanotrema columellatum</i>	Australia	Kalb	34014	DQ384894	[—]	[—]
<i>Melanotrema columellatum</i>	Australia	Kalb	34013	DQ384895	[—]	[—]
<i>Melanotrema lynceodes</i>	Venezuela	Lücking	32020	[—]	[—]	JX420915
<i>Melanotrema lynceodes</i>	Venezuela	Lücking	32021	JX421088	JX421520	JX420907
<i>Melanotrema lynceodes</i>	Australia	Mangold	351	JX421087	[—]	[—]
<i>Melanotrema meiospermoides</i>	Australia	Kalb	34015	DQ384893	[—]	[—]
<i>Melanotrema meiospermum</i>	Tanzania	Frisch	99Tz470a	DQ384890	[—]	[—]
<i>Melanotrema meiospermum</i>	Tanzania	Frisch	99Tz470b	DQ384891	[—]	[—]
<i>Melanotrema platystomum</i>	Brazil	Lücking	31085	DQ384892	[—]	JX420887
<i>Myriochapsa psoromica</i>	Brazil	Cáceres	11606	KJ435211	[—]	[—]
<i>Myriochapsa psoromica</i>	Brazil	Cáceres	sn	JX421009	JX421461	JX420884
<i>Myriotrema</i> aff. <i>hartii</i>	Ecuador	Lücking	26259	JX421089	[—]	[—]
<i>Myriotrema</i> aff. <i>microporum</i>	Australia	Lumbsch	19174a	[—]	JX421521	[—]
<i>Myriotrema</i> aff. <i>myriotremoides</i>	Thailand	Kalb	39044	[—]	KJ435110	KJ435258
<i>Myriotrema album</i>	Philippines	Rivas Plata	1158	JX421090	[—]	[—]
<i>Myriotrema clandestinum</i>	Australia	Lumbsch	19132vA	JF828963	[—]	[—]
<i>Myriotrema ecorticatum</i>	Venezuela	Lücking	32113	JX421091	JX421522	JX420914
<i>Myriotrema erodens</i>	USA	Lücking	26540	[—]	JX421523	[—]
<i>Myriotrema erodens</i>	USA	Lücking	26541a	[—]	JX421524	[—]
<i>Myriotrema erodens</i>	USA	Lücking	26541b	[—]	JX421525	[—]
<i>Myriotrema erodens</i>	Venezuela	Lücking	32039	JX421092	JX421526	JX420897
<i>Myriotrema laeviusculum</i>	Venezuela	Lücking	32057	JX421093	JX421527	JX420893
<i>Myriotrema laeviusculum</i>	Venezuela	Lücking	32100	JX421094	JX421528	JX420920
<i>Myriotrema laeviusculum</i>	Costa Rica	Sipman	47896	[—]	AY605070	[—]
<i>Myriotrema microporum</i>	Australia	Lumbsch	19092o	EU075578	EU075626	[—]
<i>Myriotrema myrioporoides</i>	Venezuela	Lücking	32205	[—]	JX421529	JX420895
<i>Myriotrema neofrondosum</i>	Puerto Rico	Mercado	163	KJ435166	[—]	[—]
<i>Myriotrema neofrondosum</i>	Peru	Rivas Plata	809canopy	JX421099	[—]	JX420880
<i>Myriotrema olivaceum</i>	Cameroon	Frisch	99Ka1533	DQ384900	[—]	[—]
<i>Myriotrema olivaceum</i>	Thailand	Kalb	39107	KJ435181	KJ435111	[—]
<i>Myriotrema olivaceum</i>	Fiji	Lumbsch	20520a	[—]	JX421531	[—]
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19113f	EU075579	EU075627	[—]
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19092g	JX421095	EU126645	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19116d	JX421096	[—]	[—]
<i>Myriotrema olivaceum</i>	Fiji	Lumbsch	20501c	JX421097	[—]	[—]
<i>Myriotrema olivaceum</i>	Australia	Mangold	33v	[—]	JX421530	[—]
<i>Myriotrema olivaceum</i>	Philippines	Rivas Plata	1063A	JX421098	[—]	[—]
<i>Myriotrema subconforme</i>	Australia	Lumbsch	19160p	JX421100	[—]	[—]
<i>Myriotrema subconforme</i>	Philippines	Rivas Plata	1166A	JX421101	[—]	[—]
<i>Nitidochapsa leprieurii</i>	Thailand	Kalb	38882	JX420991	JX421451	JX420930
<i>Nitidochapsa leprieurii</i>	Australia	Mangold	38l	[—]	JX421450	[—]
<i>Ocellularia</i> aff. <i>albobincta</i>	Peru	Rivas Plata	801D	JX421113	JX421543	JX420873
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Kalb	38813	JX421118	JX421544	JX420925
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Lumbsch	19756c	[—]	JX421535	[—]
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Lumbsch	19756e	[—]	JX421536	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8478	KJ435248	KJ435153	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8479	KJ435246	[—]	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8483	KJ435241	[—]	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8496	KJ435232	KJ435143	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Lumbsch	19105a	JX421127	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Lumbsch	19110p	JX421128	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Mangold	29aa	JX421129	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Mangold	39m	JX421130	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	New Caledonia	Papong	7982	KJ435188	KJ435115	KJ435264
<i>Ocellularia</i> aff. <i>cavata</i>	Australia	Mangold	34zc	JX421103	[—]	[—]
<i>Ocellularia</i> aff. <i>cavata</i>	New Caledonia	Papong	8257	KJ435205	KJ435129	[—]
<i>Ocellularia</i> aff. <i>crocea</i>	Puerto Rico	Mercado	218	KJ435168	[—]	[—]
<i>Ocellularia</i> aff. <i>crocea</i>	Puerto Rico	Mercado	F16	KJ435169	KJ435107	KJ435253
<i>Ocellularia</i> aff. <i>diacida</i>	Australia	Mangold	34i	[—]	JX421553	[—]
<i>Ocellularia</i> aff. <i>diminuta</i>	Peru	Rivas Plata	801A	JX421157	JX421563	JX420872
<i>Ocellularia</i> aff. <i>diminuta</i>	Peru	Rivas Plata	807B	JX421158	[—]	[—]
<i>Ocellularia</i> aff. <i>dolichotata</i>	India	Lumbsch	19730f	[—]	KJ435105	JX420852
<i>Ocellularia</i> aff. <i>dolichotata</i>	Costa Rica	Sipman	46152	[—]	KJ435104	[—]
<i>Ocellularia</i> aff. <i>domingensis</i>	Tanzania	Frisch	99Tz1145	DQ384881	[—]	[—]
<i>Ocellularia</i> aff. <i>domingensis</i>	Australia	Mangold	19j	JX421104	[—]	[—]
<i>Ocellularia</i> aff. <i>fumosa</i>	Thailand	Papong	8576	KJ435231	[—]	[—]
<i>Ocellularia</i> aff. <i>fumosa</i>	Peru	Rivas Plata	809canopy	JX421105	[—]	JX420879
<i>Ocellularia</i> aff. <i>interposita</i>	Thailand	Lumbsch	20203b	JX421165	JX421566	[—]
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Thailand	Lumbsch	20200j	JX421106	JX421540	[—]
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Thailand	Lumbsch	20206a	JX421107	JX421541	[—]
<i>Ocellularia</i> aff. <i>minutula</i>	Australia	Lumbsch	19125g	[—]	JX421542	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26553b	[—]	JX421579	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26553a	JF828967	JF828979	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26554	JX421177	[—]	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26552	JX421178	[—]	[—]
<i>Ocellularia</i> aff. <i>perforata</i>	Australia	Lumbsch	19092t	[—]	AY605073	[—]
<i>Ocellularia</i> aff. <i>perforata</i>	Costa Rica	Sipman	44335	[—]	AY605081	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia</i> aff. <i>profunda</i>	Australia	Lumbsch	19123k	EU075590	EU075636	[—]
<i>Ocellularia</i> aff. <i>profundadactyls</i>	Australia	Lumbsch	19116j	[—]	JX421586	[—]
<i>Ocellularia</i> aff. <i>profundadactyls</i>	Australia	Lumbsch	19116c	EU075588	EU075635	[—]
<i>Ocellularia</i> aff. <i>pseudochapsa</i>	Brazil	Cáceres	11726	[—]	KJ435135	[—]
<i>Ocellularia</i> aff. <i>pseudochapsa</i>	Brazil	Cáceres	11980	[—]	KJ435133	[—]
<i>Ocellularia</i> aff. <i>vezdana</i>	Panama	Lücking	27312	JX421111	[—]	[—]
<i>Ocellularia</i> aff. <i>zamboangensis</i>	Thailand	Kalb	39106	KJ435183	KJ435112	[—]
<i>Ocellularia albocincta</i>	Thailand	Kalb	38891	JX421114	[—]	[—]
<i>Ocellularia albocincta</i>	Australia	Mangold	43o	EU075585	EU075633	[—]
<i>Ocellularia albocincta</i>	Australia	Mangold	34a	JX421112	[—]	[—]
<i>Ocellularia albohallina</i>	New Caledonia	Papong	8294	KJ435206	[—]	[—]
<i>Ocellularia albula</i>	Peru	Rivas Plata	1canopy	JX421115	[—]	[—]
<i>Ocellularia allosporoides</i>	Vietnam	Gueidan	3076G	KJ435157	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lücking	24110	JX421116	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lücking	24130	JX421117	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lumbsch	20200a	[—]	JX421545	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lumbsch	20204a	JX421119	JX421546	[—]
<i>Ocellularia arecae</i>	Australia	Mangold	32zd	JX421121	JX421547	[—]
<i>Ocellularia ascidioidea</i>	New Caledonia	Papong	7511	KJ435201	KJ435125	KJ435267
<i>Ocellularia ascidioidea</i>	New Caledonia	Papong	7512	KJ435200	KJ435124	KJ435266
<i>Ocellularia auberianoides</i>	USA	Lücking	26549	JX421122	JX421548	[—]
<i>Ocellularia auberianoides</i>	USA	Lücking	26548	JX421123	JX421549	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19151u	EU075595	EU075641	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19133g	JX421124	[—]	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19151l	JX421125	[—]	[—]
<i>Ocellularia australiana</i>	Australia	Mangold	25f	JX421126	JX421550	[—]
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8064	KJ435189	KJ435116	KJ435265
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8066	KJ435187	KJ435114	KJ435263
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8074	KJ435190	KJ435117	[—]
<i>Ocellularia bahiana</i>	Costa Rica	Nelsen	2032a	[—]	AY605067	[—]
<i>Ocellularia barroensis</i>	Brazil	Cáceres	11269	KJ435221	[—]	[—]
<i>Ocellularia bonplandii</i>	Australia	Lumbsch	19127z	JX421131	EU126646	[—]
<i>Ocellularia carassensis</i>	Panama	Lücking	27015a	JX421132	[—]	[—]
<i>Ocellularia cavata</i>	Cameroon	Frisch	99Ka392	DQ384878	[—]	[—]
<i>Ocellularia cavata</i>	Cameroon	Frisch	99Ka403	DQ384879	DQ431935	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lücking	30232	JX421133	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lücking	30221a	JX421134	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lücking	30242	JX421135	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lücking	30232	JX421136	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Venezuela	Lücking	26098	JX421137	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Australia	Mangold	18d	EU075582	EU075629	[—]
<i>Ocellularia chonestoma</i>	New Caledonia	Papong	7988	KJ435208	[—]	[—]
<i>Ocellularia cicra</i>	Peru	Rivas Plata	108Db	[—]	JX421552	[—]
<i>Ocellularia cicra</i>	Peru	Rivas Plata	8extra	JX421138	[—]	JX420869

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia cicra</i>	Peru	Rivas Plata	108Da	JX421139	JX421551	[—]
<i>Ocellularia cinerea</i>	Australia	Lumbsch	19056b	KJ435161	[—]	[—]
<i>Ocellularia confluens</i>	Australia	Lumbsch	19083	JX421141	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6004a	JX421142	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6004b	JX421143	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6033	JX421144	[—]	[—]
<i>Ocellularia conformis</i>	Panama	Lücking	sn	JX421145	[—]	[—]
<i>Ocellularia cryptica</i>	Costa Rica	Lücking	15215	[—]	AY605083	[—]
<i>Ocellularia diacida</i>	Australia	Lumbsch	19120jB	EU075583	EU075630	[—]
<i>Ocellularia diacida</i>	Australia	Lumbsch	19120jD	JF828965	[—]	[—]
<i>Ocellularia diminuta</i>	Brazil	Cáceres	11174	KJ435214	KJ435138	[—]
<i>Ocellularia dolichotata</i>	Thailand	Kalb	38892	JX421146	JX421554	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202b	[—]	JX421556	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202b	[—]	JX421557	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20200f	JX421147	[—]	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20200k	JX421148	JX421555	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202d	JX421149	JX421558	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20203d	JX421150	JX421559	[—]
<i>Ocellularia domingensis</i>	Venezuela	Lücking	32233	JX421151	JX421560	JX420918
<i>Ocellularia endomelaena</i>	Australia	Lumbsch	19136l	JX421152	[—]	[—]
<i>Ocellularia endomelaena</i>	Australia	Mangold	29a	JF828966	[—]	[—]
<i>Ocellularia endomelaena</i>	Australia	Mangold	30zt	JX421153	[—]	[—]
<i>Ocellularia eumorpha</i>	Tanzania	Frisch	99Tz1504	DQ384885	[—]	[—]
<i>Ocellularia eumorpha</i>	Australia	Lumbsch	19151zd	[—]	JX421561	[—]
<i>Ocellularia exigua</i>	Thailand	Papong	8434	KJ435244	[—]	[—]
<i>Ocellularia fecunda</i>	Panama	Lücking	27150	JX421154	[—]	[—]
<i>Ocellularia fecunda</i>	Venezuela	Lücking	32122	JX421155	JX421562	[—]
<i>Ocellularia fenestrata</i>	Peru	Rivas Plata	8extra	JX421156	[—]	[—]
<i>Ocellularia flavostroma</i>	Brazil	Cáceres	11737	[—]	KJ435141	[—]
<i>Ocellularia fumosa</i>	Cameroon	Frisch	99Ka1949	DQ384880	[—]	[—]
<i>Ocellularia fumosa</i>	Thailand	Lumbsch	19756h	[—]	JX421538	[—]
<i>Ocellularia fumosa</i>	Thailand	Lumbsch	19756n	[—]	JX421539	[—]
<i>Ocellularia fuscosporella</i>	New Caledonia	Papong	7757	KJ435192	KJ435119	[—]
<i>Ocellularia gerardii</i>	Peru	Rivas Plata	1canopy	JX421159	JX421564	[—]
<i>Ocellularia halei</i>	Brazil	Cáceres	11071	KJ435218	[—]	[—]
<i>Ocellularia henatomma</i>	Brazil	Cáceres	6013a	JX421160	[—]	[—]
<i>Ocellularia henatomma</i>	Brazil	Cáceres	6013b	JX421161	[—]	[—]
<i>Ocellularia henatommasorediate</i>	Peru	Rivas Plata	809canopy	JX421162	[—]	JX420881
<i>Ocellularia inconspicua</i>	New Caledonia	Papong	8090	KJ435194	KJ435120	[—]
<i>Ocellularia interposita</i>	Thailand	Lumbsch	20202b	JX421163	[—]	[—]
<i>Ocellularia interposita</i>	Thailand	Lumbsch	20201c	JX421164	JX421565	[—]
<i>Ocellularia inturgescens</i>	Australia	Lumbsch	19132w	EU075577	EU075625	[—]
<i>Ocellularia isidiza</i>	Venezuela	Lücking	32059	JX421166	JX421567	JX420923
<i>Ocellularia kalbii</i>	Australia	Lumbsch	19082e	EU075570	EU075618	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia kalbii</i>	Australia	Lumbsch	19085i	JX421196	[—]	[—]
<i>Ocellularia khasiana</i>	New Caledonia	Papong	7956	[—]	KJ435131	[—]
<i>Ocellularia khasiana</i>	New Caledonia	Papong	8237	[—]	KJ435132	[—]
<i>Ocellularia laeviusculoides</i>	Mexico	Lücking	RLD063b	[—]	JX421568	[—]
<i>Ocellularia laeviusculoides</i>	Mexico	Lücking	RLD063a	EU075586	EU075632	[—]
<i>Ocellularia laeviusculoides</i>	Venezuela	Lücking	32001	JX421167	JX421569	JX420896
<i>Ocellularia laeviusculoides</i>	Venezuela	Lücking	32037	JX421168	JX421570	JX420922
<i>Ocellularia landronii</i>	Brazil	Cáceres	11039	KJ435213	KJ435137	[—]
<i>Ocellularia massalongoi</i>	Cameroon	Frisch	99Ka1799	DQ384882	[—]	[—]
<i>Ocellularia massalongoi</i>	Fiji	Lumbsch	20523j	[—]	JX421571	[—]
<i>Ocellularia massalongoi</i>	Fiji	Lumbsch	20523h	JX421169	[—]	[—]
<i>Ocellularia massalongoi</i>	Australia	Mangold	36m	EU075584	EU075631	[—]
<i>Ocellularia mauritiana</i>	Peru	Rivas Plata	803D	JX421170	[—]	[—]
<i>Ocellularia microsorediata</i>	Peru	Rivas Plata	107Ca	[—]	JX421572	[—]
<i>Ocellularia microsorediata</i>	Peru	Rivas Plata	107Cb	JX421172	JX421573	[—]
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19100q	[—]	JX421574	[—]
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19108c	[—]	EU126648	[—]
<i>Ocellularia microstoma</i>	Japan	Lumbsch	19056b1	[—]	AY605074	[—]
<i>Ocellularia microstoma</i>	Japan	Lumbsch	19056b2	[—]	JX421576	JX420823
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19125r	JX421108	JX421575	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1085B	[—]	JX421577	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1063E	JX421109	[—]	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1193C	JX421110	[—]	[—]
<i>Ocellularia minutula 1</i>	Australia	Lumbsch	19167t	JX421173	JX421578	[—]
<i>Ocellularia minutula 2</i>	Australia	Lumbsch	19155d	KJ435162	[—]	[—]
<i>Ocellularia minutula 2</i>	Australia	Lumbsch	19156g	JX421174	[—]	[—]
<i>Ocellularia mordenii</i>	Puerto Rico	Mercado	238	KJ435170	[—]	[—]
<i>Ocellularia myriotrema</i>	Brazil	Cáceres	11334	KJ435224	[—]	[—]
<i>Ocellularia myriotrema</i>	Brazil	Cáceres	11576	KJ435215	[—]	[—]
<i>Ocellularia natashae</i>	Peru	Rivas Plata	1canopy	JX421175	[—]	JX420877
<i>Ocellularia neocaledonica</i>	New Caledonia	Papong	7551	KJ435207	KJ435130	[—]
<i>Ocellularia neopertusariiiformis</i>	Australia	Mangold	35zf	JX421176	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Kalb	33985	DQ384874	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Kalb	33986	DQ384875	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Lumbsch	19160wA	EU075565	EU075612	[—]
<i>Ocellularia oculata</i>	Fiji	Lumbsch	19817i	JX421377	JX421663	[—]
<i>Ocellularia oculata</i>	Australia	Mangold	33a	EU075564	EU075613	[—]
<i>Ocellularia percolumellata</i>	Brazil	Cáceres	6002a	JX421180	[—]	JX420888
<i>Ocellularia percolumellata</i>	Brazil	Cáceres	6002b	JX421181	[—]	[—]
<i>Ocellularia perforata</i>	Australia	Lumbsch	19120jA	EU075587	EU075634	[—]
<i>Ocellularia perforata</i>	Australia	Lumbsch	19120jC	JX421182	[—]	[—]
<i>Ocellularia perforata</i>	Fiji	Lumbsch	19849	JX421183	[—]	[—]
<i>Ocellularia pertusariiiformis</i>	Philippines	Rivas Plata	1074B	JX421184	[—]	[—]
<i>Ocellularia petrinensis</i>	Venezuela	Lücking	32024	JX421185	JX421532	JX420910

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia philippina</i>	Philippines	Rivas Plata	1070	JX421187	[—]	[—]
<i>Ocellularia philippina</i>	Philippines	Rivas Plata	1135	JX421188	[—]	[—]
<i>Ocellularia plicata</i>	Peru	Rivas Plata	809canopy	JX421189	[—]	[—]
<i>Ocellularia pluriporoides</i>	Brazil	Cáceres	sn	JX421190	JX421580	[—]
<i>Ocellularia polydiscus</i>	Brazil	Cáceres	11021	KJ435217	[—]	[—]
<i>Ocellularia polydiscus</i>	Tanzania	Frisch	99Tz1950	DQ384877	[—]	[—]
<i>Ocellularia polydiscus</i>	Brazil	Lücking	27966	DQ384876	[—]	[—]
<i>Ocellularia portoricensis</i>	Puerto Rico	Mercado	F19	KJ435178	[—]	KJ435256
<i>Ocellularia portoricensis</i>	Puerto Rico	Mercado	F64	KJ435179	[—]	KJ435257
<i>Ocellularia postposita</i>	Tanzania	Frisch	99TZ1879	DQ384873	[—]	[—]
<i>Ocellularia praestans</i>	Panama	Lücking	sn	JX421191	[—]	[—]
<i>Ocellularia praestans</i>	Venezuela	Lücking	32200	JX421192	JX421581	JX420892
<i>Ocellularia praestans</i>	Venezuela	Lücking	32239	JX421193	JX421582	JX420894
<i>Ocellularia praestans</i>	Venezuela	Lücking	32106	JX421194	[—]	JX420899
<i>Ocellularia praestans</i>	Venezuela	Lücking	32236	JX421195	JX421583	JX420911
<i>Ocellularia profunda</i>	Australia	Lumbsch	19077c	[—]	JX421584	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19085h	[—]	EU126647	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100p	EU075589	AY605082	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100t	JX421197	[—]	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100p	JX421198	JX421585	JX420825
<i>Ocellularia pseudochapsa</i>	Brazil	Cáceres	11719	KJ435229	[—]	[—]
<i>Ocellularia pseudochapsa</i>	Brazil	Cáceres	11790	KJ435210	KJ435134	[—]
<i>Ocellularia pseudostromatica</i>	Brazil	Cáceres	11352	KJ435223	KJ435140	[—]
<i>Ocellularia psorbarroensis</i>	Brazil	Cáceres	6007	JX421199	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	8extra	JX421200	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	108B	JX421201	JX421587	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	801D	JX421202	JX421588	JX420874
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	801D	JX421203	JX421589	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	810B	JX421204	JX421590	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	1canopy	JX421205	JX421591	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	8extra	JX421206	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	1canopy	JX421207	[—]	[—]
<i>Ocellularia pulchella</i>	New Caledonia	Papong	8048	KJ435195	KJ435121	[—]
<i>Ocellularia pyrenuloides</i>	Australia	Kalb	34019	DQ384896	[—]	[—]
<i>Ocellularia pyrenuloides</i>	New Caledonia	Papong	8031	KJ435203	KJ435127	KJ435268
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F35	KJ435171	[—]	[—]
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F75	KJ435172	KJ435108	KJ435254
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F76	KJ435176	[—]	KJ435255
<i>Ocellularia rhicnoporoides</i>	Venezuela	Lücking	32107	JX421209	JX421593	[—]
<i>Ocellularia rhicnoporoides</i>	Thailand	Lumbsch	19750e	JX421208	JX421592	[—]
<i>Ocellularia rhodostroma</i>	Costa Rica	Sipman	44335	[—]	AY605068	[—]
<i>Ocellularia rimosa</i>	Thailand	Kalb	38767	JX421211	[—]	JX420927
<i>Ocellularia rimosa</i>	Australia	Mangold	35b	JX421210	[—]	[—]
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11335	KJ435216	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11852	KJ435222	[—]	[—]
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11982	KJ435220	KJ435139	[—]
<i>Ocellularia rugosothallina</i>	New Caledonia	Papong	8284	KJ435202	KJ435126	[—]
<i>Ocellularia salmonea</i>	New Caledonia	Papong	7954	KJ435191	KJ435118	[—]
<i>Ocellularia schizidiata</i>	Philippines	Rivas Plata	1106	JX421215	[—]	[—]
<i>Ocellularia soresiate</i> 1	Peru	Rivas Plata	107C	JX421216	[—]	[—]
<i>Ocellularia soresiate</i> 2	Peru	Rivas Plata	808D	JX421217	[—]	[—]
<i>Ocellularia soresiate</i> 3	Puerto Rico	Mercado	247	KJ435177	[—]	[—]
<i>Ocellularia</i> sp. nov. 1	Venezuela	Lücking	32217	JX421120	[—]	JX420921
<i>Ocellularia</i> sp. nov. 3	Thailand	Lücking	24129	JX421179	[—]	[—]
<i>Ocellularia</i> sp. nov. 4	Thailand	Lumbsch	20202e	JX421186	[—]	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8541	KJ435239	KJ435150	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8542	KJ435249	KJ435154	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8552	KJ435236	KJ435147	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8557	KJ435238	KJ435149	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8564	KJ435240	KJ435151	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8566	KJ435233	KJ435144	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8567	KJ435245	[—]	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8568	KJ435237	KJ435148	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8570	KJ435250	KJ435155	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8573	KJ435251	KJ435156	[—]
<i>Ocellularia</i> sp. nov. 7	Thailand	Papong	8574	KJ435252	[—]	[—]
<i>Ocellularia</i> sp. nov. 8	Thailand	Papong	8439	KJ435235	KJ435146	[—]
<i>Ocellularia</i> sp. nov. 8	Thailand	Papong	8458	KJ435247	[—]	[—]
<i>Ocellularia</i> sp.	Vietnam	Gueidan	3086G	KJ435158	[—]	[—]
<i>Ocellularia</i> sp.	Vietnam	Gueidan	3304G	KJ435159	[—]	[—]
<i>Ocellularia</i> sp.	Thailand	Kalb	39042	KJ435185	[—]	KJ435261
<i>Ocellularia</i> sp.	Thailand	Kalb	39092	KJ435182	[—]	KJ435259
<i>Ocellularia</i> sp.	Thailand	Kalb	39091a	KJ435186	[—]	KJ435262
<i>Ocellularia</i> sp.	Thailand	Kalb	38839	JX421214	[—]	JX420931
<i>Ocellularia</i> sp.	Australia	Lumbsch	19161d	[—]	JX421594	[—]
<i>Ocellularia</i> sp.	Australia	Lumbsch	19082a	JX421212	[—]	[—]
<i>Ocellularia</i> sp.	Australia	Mangold	31m	JX421213	[—]	[—]
<i>Ocellularia</i> sp. soresiate 4	Australia	Lumbsch	19144a	[—]	JX421595	[—]
<i>Ocellularia</i> sp. soresiate 4	Australia	Lumbsch	19144d	EU075591	EU075637	[—]
<i>Ocellularia</i> sp. soresiate dactyls	Australia	Mangold	29b	[—]	JX421597	[—]
<i>Ocellularia</i> sp. sterile	Australia	Mangold	32d2	[—]	JX421598	[—]
<i>Ocellularia</i> sp. sterile	Australia	Mangold	35o	[—]	JX421596	[—]
<i>Ocellularia subpraestans</i>	Panama	Lücking	sn	JX421218	[—]	[—]
<i>Ocellularia terebrata</i>	Australia	Lumbsch	19132zd	JF828964	[—]	[—]
<i>Ocellularia terebrata</i>	Australia	Lumbsch	19128mA	JX421219	[—]	[—]
<i>Ocellularia terebrata</i>	New Caledonia	Papong	8256	KJ435198	[—]	[—]
<i>Ocellularia thelotremoides</i>	Tanzania	Frisch	99Tz1122	DQ384884	[—]	[—]
<i>Ocellularia thelotremoides</i>	Venezuela	Lücking	26052	JX421221	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19081j	[—]	EU126649	[—]
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19108i	EU075592	EU075638	[—]
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19153l	JX421220	[—]	[—]
<i>Ocellularia thelotremoides</i>	Thailand	Papong	8449	KJ435234	KJ435145	[—]
<i>Ocellularia thryptica</i>	Peru	Rivas Plata	103D	JX421222	[—]	[—]
<i>Ocellularia thryptica</i>	Peru	Rivas Plata	8extra	JX421223	[—]	[—]
<i>Ocellularia umbilicata</i>	Puerto Rico	Mercado	242	KJ435173	KJ435109	[—]
<i>Ocellularia urceolaris</i>	Costa Rica	Lücking	21053	JX421224	[—]	[—]
<i>Ocellularia vezdana</i>	Cameroon	Frisch	99Ka1546	DQ384883	[—]	[—]
<i>Ocellularia violacea</i>	Brazil	Cáceres	sn	JX421225	[—]	[—]
<i>Ocellularia violacea</i>	Brazil	Cáceres	sn	JX421226	[—]	[—]
<i>Ocellularia viridipallens</i>	Thailand	Lücking	24131	JX421227	[—]	[—]
<i>Ocellularia vulcanisorediata</i>	Puerto Rico	Mercado	76	KJ435174	[—]	[—]
<i>Ocellularia vulcanisorediata</i>	Puerto Rico	Mercado	4451	KJ435165	KJ435106	[—]
<i>Ocellularia wirthii</i>	Australia	Mangold	25b	JX421228	JX421599	[—]
<i>Ocellularia xanthostromiza</i>	Brazil	Cáceres	11982	KJ435219	[—]	[—]
<i>Ocellularia xanthostromiza</i>	Thailand	Papong	8559	KJ435243	[—]	[—]
<i>Ocellularia xanthostromiza</i>	Peru	Rivas Plata	809canopy	JX421171	[—]	[—]
<i>Redingeria desseiniana</i>	DR Congo	Ertz	14296	KJ145246	KJ145245	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	802A2	[—]	JX421617	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	802A1	HQ639601	JX421616	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	810extra	JX421296	JX421618	[—]
<i>Redingeria microspora</i>	Brazil	Cáceres	6030	JX421297	[—]	[—]
<i>Reimnitzia</i> aff. <i>santensis</i>	India	Lumbsch	19706b	[—]	JX421619	[—]
<i>Reimnitzia santensis</i>	El Salvador	Lücking	28015	HQ639622		JF828952
<i>Reimnitzia santensis</i>	USA	Nelsen	sn	JX443520	[—]	[—]
<i>Reimnitzia santensis</i>	Costa Rica	Will-Wolf	10024b	[—]	JX421620	[—]
<i>Rhabdodiscus</i> aff. <i>asiaticus</i>	New Caledonia	Papong	8020	KJ435193	[—]	[—]
<i>Rhabdodiscus</i> aff. <i>asiaticus</i>	Philippines	Rivas Plata	1054A	JX421298	[—]	[—]
<i>Rhabdodiscus asiaticus</i>	Australia	Kalb	sn	DQ384888	[—]	[—]
<i>Rhabdodiscus auberianus</i>	Brazil	Cáceres	11977	KJ435225	[—]	[—]
<i>Rhabdodiscus crassus</i>	Australia	Lumbsch	19108f	EU075594	EU075640	[—]
<i>Rhabdodiscus emersus</i>	Australia	Kalb	sn	DQ384889	[—]	[—]
<i>Rhabdodiscus integer</i>	Australia	Lumbsch	19108a	JX421299	[—]	[—]
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32212	JX421300	JX421621	JX420903
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32213	JX421301	JX421622	JX420904
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32201	JX421302	JX421623	JX420908
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32211	JX421303	JX421624	JX420912
<i>Rhabdodiscus marivelensis</i>	Thailand	Lücking	24115	JX421304	[—]	[—]
<i>Rhabdodiscus neocaledonicus</i>	New Caledonia	Papong	7630	KJ435204	KJ435128	[—]
<i>Rhabdodiscus saxicola</i>	New Caledonia	Papong	8042	KJ435197	KJ435123	[—]
<i>Rhabdodiscus schizostomus</i>	Philippines	Rivas Plata	1165a	JX421305	[—]	[—]
<i>Rhabdodiscus schizostomus</i>	Philippines	Rivas Plata	1165b	JX421306	[—]	[—]
<i>Rhabdodiscus</i> sp.	Vietnam	Gueidan	3039G	KJ435160	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Rhabdodiscus</i> sp.	Fiji	Lumbsch	20501j	JX421307	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	6301a	JX421308	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	6301b	JX421309	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	sn	JX421310	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	sn	JX421311	[—]	[—]
<i>Rhabdodiscus subemersus</i>	Tanzania	Frisch	99Tz388D	DQ384886	[—]	[—]
<i>Rhabdodiscus subemersus</i>	Brazil	Lücking	31665	DQ384887	[—]	[—]
<i>Rhabdodiscus thouvenotii</i>	New Caledonia	Papong	8049	KJ435196	KJ435122	[—]
<i>Sarcographina cyclospora</i>	Sri Lanka	Weerakoon	116A	KJ435230	[—]	[—]
<i>Stegobolus actinotus</i>	Cameroon	Frisch	99Ka1316D	DQ384897	[—]	[—]
<i>Stegobolus</i> aff. <i>berkeleyanus</i>	Australia	Kalb	34020	DQ384898	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	11957	[—]	KJ435142	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	11860	KJ435227	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	6003a	JX421329	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	6003b	JX421330	[—]	[—]
<i>Stegobolus anamorphus</i>	Peru	Rivas Plata	807D	JX421331	JX421634	[—]
<i>Stegobolus anamorphus</i>	Peru	Rivas Plata	E810D	JX421332	JX421635	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Lumbsch	20200d	[—]	JX421637	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Lumbsch	20203e	JX421333	JX421638	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Papong	8444	KJ435242	[—]	[—]
<i>Stegobolus guianensis</i>	Brazil	Cáceres	11820	KJ435226	[—]	[—]
<i>Stegobolus radians</i>	Venezuela	Lücking	32207	[—]	JX421639	JX420917
<i>Stegobolus subwrightii</i>	Venezuela	Lücking	32202	[—]	JX421636	JX420913
<i>Stegobolus wrightii</i>	Brazil	Cáceres	sn	JX421334	[—]	[—]
<i>Stegobolus wrightii</i>	Brazil	Cáceres	sn	JX421335	[—]	[—]

Sequences were arranged into multiple sequence alignments (MSA) for each gene using BIOEDIT 7.09 (Hall 1999) and automatically aligned with MAFFT using the -auto option (Kato & Toh 2005). The unaligned MSA for the mtSSU and nuLSU gene partitions were also submitted to the GUIDANCE web server at <http://guidance.tau.ac.il> to assess alignment confidence scores for each site (Penn *et al.* 2010a, b). GUIDANCE uses a MAFFT alignment and returns a colored MSA that allows delimiting ambiguously aligned portions of the MSA. These were then excluded from further analysis. Introns were deleted from the nuLSU gene partition because of their random occurrence but kept in the mtSSU partition if consistent within species or species groups. This resulted in alignments of 1000 sites for the mtSSU (334 OTUs), 900 sites for the nuLSU (201 OTUs), and 915 for RPB2 (63 OTUs), for a total of 2815 sites in the combined dataset and 597 out of 1203 possible individual sequences (49.6% cover). After testing for supported topological conflicts (Mason-Gamer & Kellogg 1996; Miadlikowska & Lutzoni 2000; Kauff & Lutzoni 2002), the three genes were combined into a single supermatrix. Individual datasets and the combined supermatrix were subjected to maximum likelihood search using the RAXML-HPC BlackBox 7.3.2 on the Cipres Science Gateway server (Stamatakis 2006; Stamatakis *et al.* 2005, 2008; Miller *et al.* 2010; <http://www.phylo.org/portal2/login!input.action>), with parametric bootstrapping generating 350 replicates as automatically determined by RAXML using a saturation criterion. The universal GTR-Gamma model was chosen for the analysis. For the Bayesian analysis, the data set was partitioned into three parts (one for each locus) and analyzed using MrBAYES 3.1.2 (Huelsenbeck & Ronquist 2001) on the Cipres Science Gateway server. For all loci, the GTR+I+G was chosen as the most optimal substitution model. A run with 10,000,000 generations, starting with a random tree and employing four simultaneous chains, was executed. Heating of chains was set to 0.2. Posterior probabilities were estimated by sampling trees using a variant of Markov Chain Monte Carlo (MCMC) method. Every 1000th tree was sampled to avoid autocorrelation. The first 2,500 trees

were discarded as burn in. A majority-rule consensus tree with average branch lengths was computed from the remaining trees, using the sumt option of MrBAYES. Posterior probabilities were obtained for each clade.

Results and Discussion

The overall topology for tribe Ocellularieae (Fig. 1) mirrors results obtained from earlier studies (Rivas Plata *et al.* 2012b, 2013). The well-supported tribe is divided in three main clades: (1) a large, unsupported clade containing the bulk of the genera except *Ocellularia*, here called the *Myriotrema* clade, (2) a small, strongly supported clade corresponding to the genus *Rhabdodiscus*, and (3) another large, supported clade containing *Nitidochapsa* Parmen *et al.* (2013: 128) and *Ocellularia* s.lat., here called the *Ocellularia* clade. Within the *Myriotrema* clade, the following currently accepted nine genera were recovered as monophyletic with support: *Compositrema*, *Fibrillithecis*, *Glaucotrema*, *Melanotrema*, *Myriochapsa* Parmen *et al.* (2013: 128), *Myriotrema* s.str., *Nitidochapsa*, *Redingeria*, and *Stegobolus*. In addition, the *Myriotrema* clade contains five small clades corresponding to species currently classified as *Myriotrema* or *Ocellularia*: (1) the *M. album* Fée (1825: 104) clade, (2) the *O. pyrenuloides* Zahlbr. in Magnusson & Zahlbruckner (1944: 46) clade, (3) the *O. inturgescens* (Müll. Arg.) Mangold in Mangold *et al.* (2009: 656) clade, (4) the *O. praestans* (Müll. Arg.) Hale (1980: 137) clade, and (5) the *O. profunda* (Stirt.) Mangold *et al.* (2007: 204) clade. The most striking result is the placement of *Sarcographina cyclospora* Müller (1887: 425), a species for a long time misunderstood to represent the muriform-spored counterpart of *Sarcographa* Fée (1825: xxxv, xc, 58; Zahlbruckner 1923; Staiger 2002; Archer 2009), as a lirellate representative of the *Myriotrema* clade, coming out as strongly supported sister to *Ocellularia inturgescens* (Müll. Arg.) Mangold (2009: 656). This placement is in part supported by morphology, since *Sarcographina* features a thallus anatomy composed of large, columnar clusters of calcium oxalate crystals, a feature found in several lineages within tribes Ocellularieae and Leptotremateae but unknown from *Sarcographa* and relatives. Also, the ascospores of *Sarcographina* are reminiscent of those of *Leptotrema*, *Redingeria*, and *Reimnitzia*.

The *Ocellularia* s.lat. clade, containing the bulk of *Ocellularia* species, is not supported, but within this clade, the supported *O. terebrata* (Ach.) Müller (1887: 398) clade is sister to a strongly supported clade that contains the remainder of *Ocellularia* s.lat. *Ocellularia* s.lat. contains several clades of various sizes: the *O. wirthii* Mangold *et al.* (2008b: 364) clade (strongly supported), the *O. baileyi* Müller (1891a: 51) clade (supported), the *O. massalongoi* (Mont.) Hale (1980: 137) clade (strongly supported), the *O. bahiana* (Ach.) Frisch in Frisch *et al.* (2006: 503) clade (strongly supported), the *O. perforata* (Leight.) Müller (1892: 284) clade (strongly supported), sister to *Myriotrema clandestinum* (Fée) Hale (1980: 133), the *O. dolichotata* (Nyl.) Zahlbruckner (1923: 589) clade (strongly supported), the *Ampliotrema* clade [supported but not monophyletic, since the type species, *A. amplius* (Nyl.) Kalb ex Kalb in Frisch *et al.* (2006: 81), falls outside], the *O. eumorpha* (Stirt.) Hale (1980: 136) clade (strongly supported), and *Ocellularia* s.str. (not supported), with the genus *Gyrotrema* nested near its base.

The internal topology of the outgroup (tribe Leptotremateae) suggests that both *Reimnitzia* Kalb (2001: 325) and *Leptotrema* contain an additional, unrecognized species each (Fig. 2). The specimen from India labeled *R. santensis* (Tuck.) Kalb (2001: 325) is phylogenetically distinct from the material from the Neotropics (USA, El Salvador, Costa Rica), from which the type originates. Morphologically, it differs from typical material by the smaller ascomata lacking erect to recurved marginal lobules and by the flask-shaped rather than cylindrical isidia (Fig. 3A–D). Further material from Costa Rica and Sri Lanka (Fig. 3E–F) suggests that the genus *Reimnitzia* might include a number of hitherto unrecognized species, differing chiefly in ascoma morphology. Regarding the genus *Leptotrema*, the specimen of *L. wightii* (Taylor) Müller (1882: 499) from El Salvador does not display morphological differences compared to the material from Costa Rica. Further studies will show whether these specimens warrant status as separate taxa.

In a previous phylogenetic study (Rivas Plata *et al.* 2012b), the sequenced specimens of *Glaucotrema* were considered to represent a single species, *G. glaucophaenum* (Kremp.) Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1175). In the present analysis, we added two new species, an undescribed species from Thailand and *G. stegoboloides* Cáceres *et al.* (2014) from Brazil, which differs from *G. glaucophaenum* in having larger

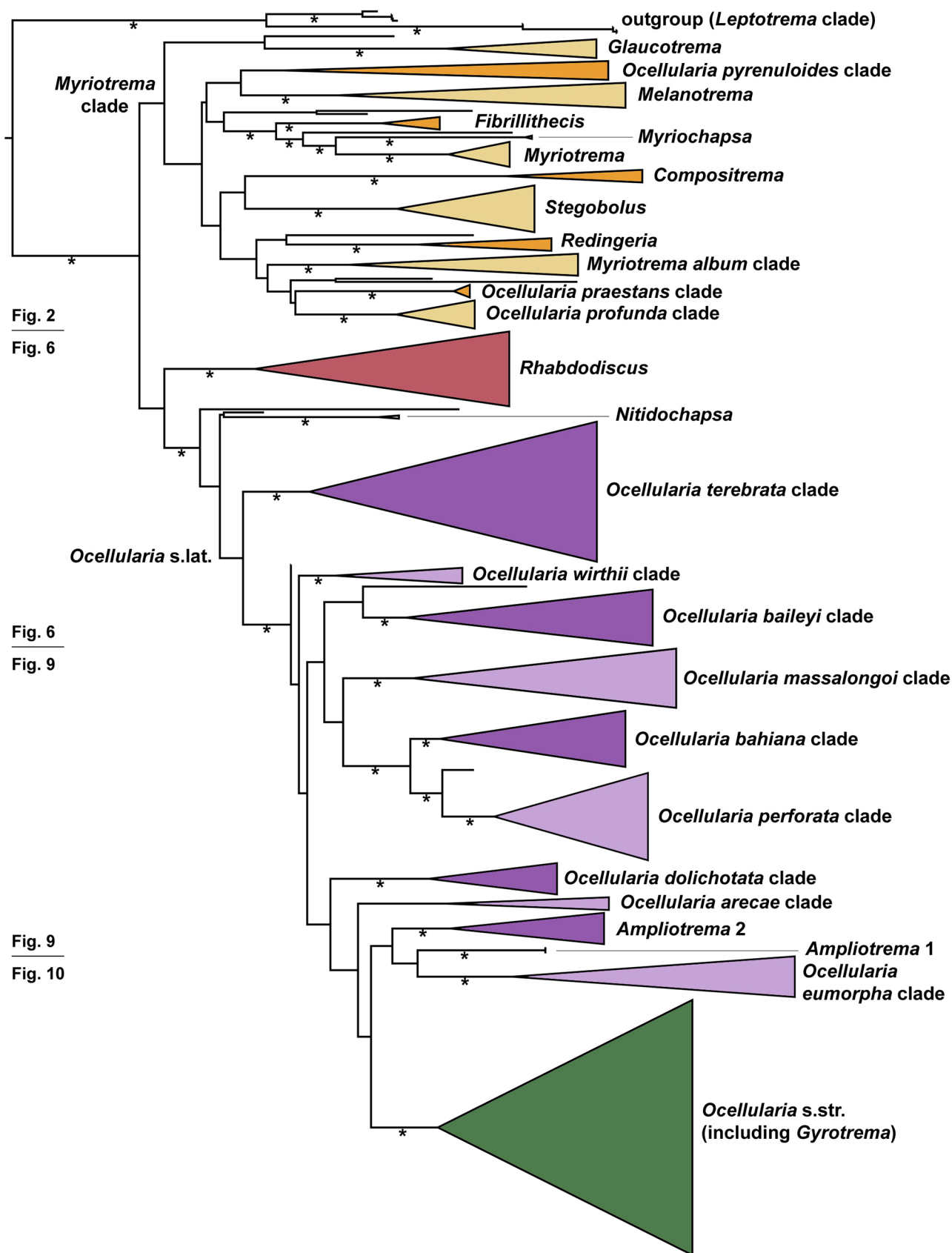


FIGURE 1. Best-scoring maximum likelihood tree of tribe Ocellarieae based on a 3-locus dataset, showing major clades. Supported clades are marked with an asterisk. Detailed phylogenies for each portion of the tree, as well as numeric support values, are depicted in Figs 2, 6, 9, 10.



FIGURE 2. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Myriotrema* clade. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

ascomata with a complex columella resembling species of the genera *Rhabdodiscus* and *Stegobolus*. The remaining material labeled *G. glaucophaenum* does not form a monophyletic clade (Fig. 2), which suggests that more than one species is involved here. This would not be surprising given that the five specimens originate from five different regions (Venezuela, Tanzania, Thailand, Philippines, Australia) and would be an example that taxa considered pantropical due to morphological similarities actually represent phylogenetically distinct clades. More samples are necessary to clarify this.

The *Ocellularia pyrenuloides* clade contains two well-supported clades (Fig. 2): *O. pyrenuloides* and a second clade including *O. conformalis* (Kremp.) M. Cáceres & Lücking in Cáceres *et al.* (2012: 809) and the newly described *O. vulcanisorediata* Mercado-Díaz *et al.* (2014). Whereas *O. pyrenuloides* is characterized by an unusual stictic acid chemistry, otherwise very rare in this tribe, *O. conformalis* produces psoromic acid and *O. vulcanisorediata* lacks substances. The latter two species have no characters that would separate them from typical species of *Ocellularia*. More sequence data of further species are needed to elucidate the composition of this clade, which either retained general plesiomorphic features within tribe Ocellularieae or evolved *Ocellularia*-like characters in parallel (Rivas Plata & Lumbsch 2011).

Within the strongly supported genus *Melanotrema* (Fig. 2), specimens identified as *M. lynceodes* (Nyl.) Rivas Plata, Lücking & Lumbsch, *comb. nov.* [Mycobank #807660; *Graphis lynceodes* Nyl., *Flora* 69: 174. 1886] from Venezuela and Australia cluster together but without support, suggesting that *Melanotrema lynceodes* as defined here might be polyphyletic. Notably, the type of *Graphis lynceodes* is from tropical Africa, so neither the Venezuelan nor the Australian material might actually represent this species phylogenetically, although they agree in morphological features.

Ocellularia inturgescens clusters with strong support with *Sarcographina cyclospora* (Fig. 2). This relationship is surprising since the two taxa have little in common in terms of morphological characters; both share a minutely grainy thallus caused by large, columnar clusters of calcium oxalate crystals, but whereas *O. inturgescens* has small, rounded, myriotremoid ascomata, those of *S. cyclospora* are lirellate and clustered in pseudostromatic areas (Fig. 4). Also, *O. inturgescens* has large, hyaline ascospores while they are small and dark brown in *S. cyclospora*. Given further the long branches leading to both taxa, it appears that this clade may represent a relict clade that included morphologically intermediate species which are now extinct (or have not yet been discovered).

The genera *Fibrillithecis*, *Myriochapsa*, and *Myriotrema* s.str. are strongly supported as monophyletic clades, sharing densely corticate thalli producing mostly psoromic acid and small, hyaline ascospores. They differ chiefly in ascomata features, with *Fibrillithecis* and *Myriochapsa* having erumpent to prominent ascomata with either fibrils (*Fibrillithecis*) or chroodiscoid lobules (*Myriochapsa*), and *Myriotrema* s.str. having small, rounded pores with double margin. The two specimens previously identified as *Fibrillithecis gibbosa* (H. Magn.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 84) do not cluster together. Revision of the material revealed that only one corresponds to *F. gibbosa* s.str., whereas the other agrees with *F. platyspora* (Harm.) Frisch in Frisch *et al.* (2006: 137). At present we are unable to explain why *Myriotrema microporum* falls outside *Myriotrema* s.str., with a supported sister group relationship to *Myriochapsa* plus *Myriotrema* s.str. *Myriotrema microporum* agrees with *M. olivaceum*, the type of *Myriotrema*, in morphology, but produces psoromic instead of olivaceic acid. There is also an additional unsupported clade formed by a specimen similar to *M. microporum* and by *Fibrillithecis* aff. *sprucei* Mangold, Lücking & Lumbsch in Lumbsch *et al.* (2011: 55). Apparently, the latter is not a genuine *Fibrillithecis* and differs from *Fibrillithecis* s.str. in the large, muriform ascospores; this taxon might also deserve separate taxonomic status.

The genera *Compositrema* and *Stegobolus* form an unsupported sister group relationship, which agrees with their general similarities in morphology (Rivas Plata *et al.* 2012b; Mercado-Díaz *et al.* 2014). In fact, two species of *Compositrema*, *C. thailandicum* Rivas Plata *et al.* (2012b: 1174) and *C. borinquense* Mercado-Díaz *et al.* (2014), strongly resemble species of *Stegobolus* and would have been placed in that genus without molecular sequence data. Within *Compositrema*, our analysis clarified the identification of a specimen from Venezuela as identical with the newly described *C. isidiofarinosum* Mercado-Díaz *et al.* (2014) from Puerto Rico. It is also interesting to note that the only paleotropical species of *Compositrema* known so far is sister to a clade containing the three neotropical species, indicating a strong geographic signal. Within *Stegobolus*, it appears that specimens identified as *S. berkeleyanus* Montagne (1845: 4) from Australia (Mangold *et al.* 2009; as *Ocellularia*) do not represent that taxon, but are phylogenetically distinct.

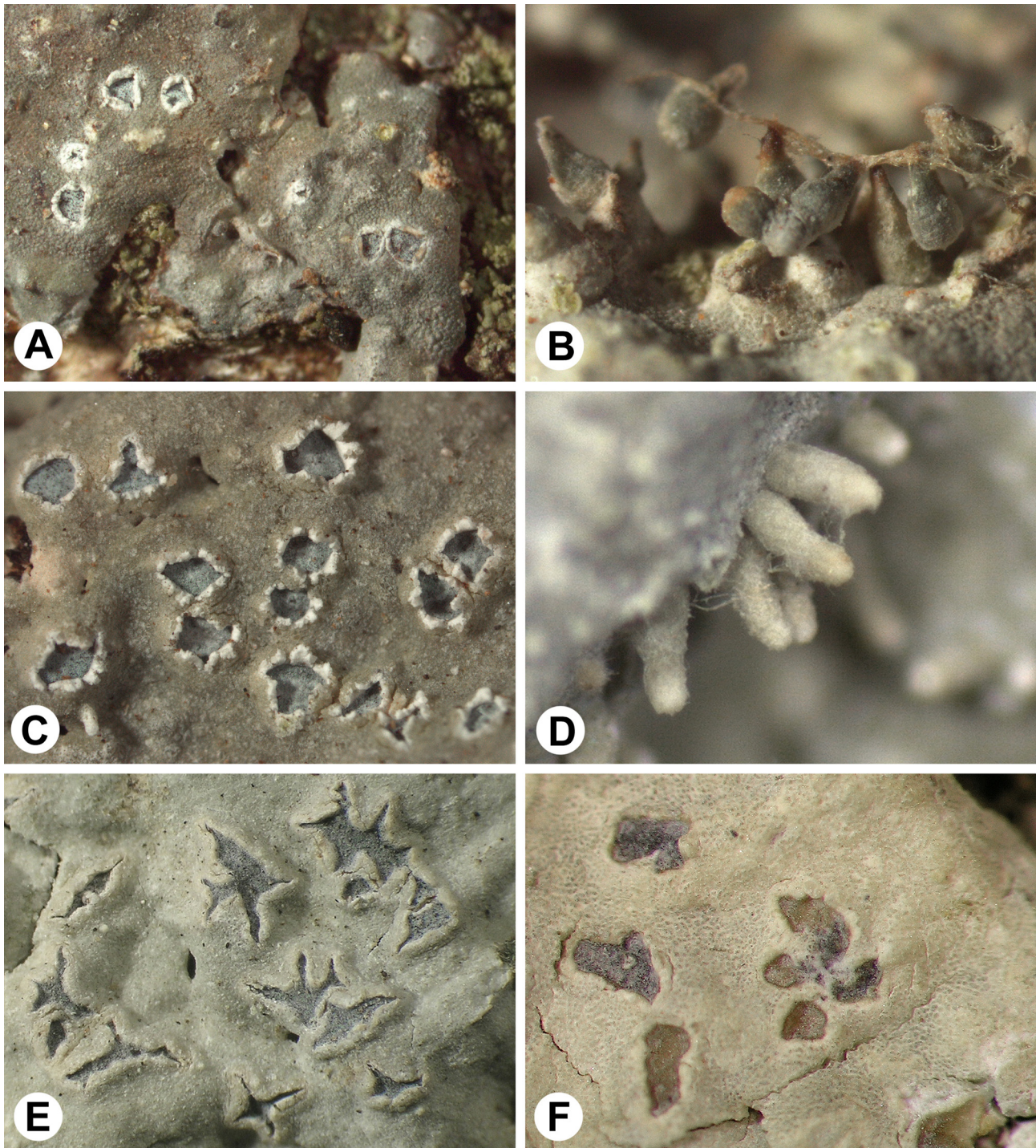


FIGURE 3. A–B. *Reimnitzia* aff. *santensis*, thallus with ascomata and isidia enlarged (India, *Lumbsch 19706b*). C. *Reimnitzia santensis*, thallus with ascomata (Florida, *Nelsen s.n.*). D. *Reimnitzia santensis*, isidia enlarged (Argentina, *Michlig et al. 106*). E. *Reimnitzia* aff. *santensis*, thallus with ascomata (Costa Rica, *Dodge 6633*). F. *Reimnitzia* aff. *santensis*, thallus with ascomata (Sri Lanka, *Weerakoon 305A*).

The genus *Redingeria* now includes three species with strong support with very different morphology. While *R. microspora* (Zahlbr.) M. Cáceres & Lücking in Cáceres *et al.* (2012: 809) features rounded ascomata, those of the newly described *R. desseiniana* Van den Broeck *et al.* (2014) and of *R. glaucoglyphica* (Sipman) Frisch in Frisch *et al.* (2006: 409) are elongate-lirellate. The inclusion of *R. desseiniana* in this genus is somewhat surprising, as this species closely resembles the genus *Phaeographopsis* Sipman in Aptroot *et al.* (1997: 129), which is not closely related (Lumbsch *et al.* 2014), in the farinose thallus, eolumellate lirellae, and dark brown, 3-septate ascospores (Fig. 5).

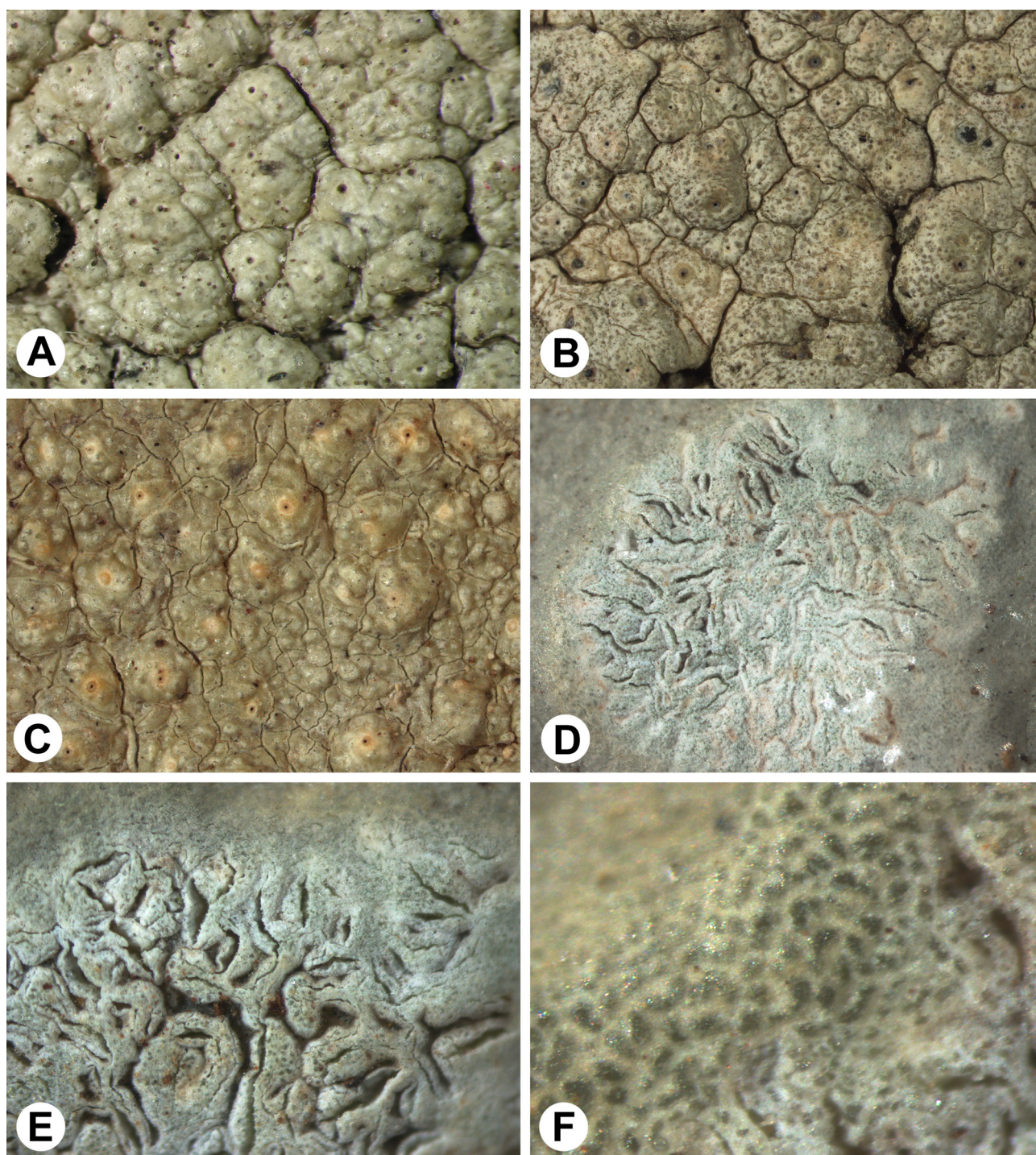


FIGURE 4. A–C. *Ocellularia inturgescens*, thallus with ascomata (A, holotype; B, Australia, Brownlie A82c; C, Australia, Tibell 12788). D–F. *Sarcographina cyclospora*, pseudostromatic ascomata and thallus surface enlarged (isotype).

Apart from *Myriotrema* s.str., there is a second clade centered around *Myriotrema album*, which is apparently not closely related. It presumably has the generic name *Ocellis* Clements (1909: 80, 175) available (Rivas Plata *et al.* 2012b). That name was introduced as new genus by Clements (1909), without giving a type but with a valid diagnosis "*Ocellularia didymospora*" (Clements 1909: 175), meaning *Ocellularia* species with 2-celled ascospores (ICN Art. 38.2). Since citing a type is only required from 1. January 1958 onwards (ICN Art. 40.1), the name *Ocellis* Clem. would be valid. However, the name coincides with a technical term (Latin: *ocellis* = dative and ablative plural of *ocellus* = eye) and hence, even if it was published before 1. January 1912, it is invalid since no species was cited in the protologue in combination with this name (ICN Art. 20.2). The citation of the type species as either *Ocellis myriopora* (Tuck.) Müll. Arg. [MB #431880] or *O. myriopora* (Tuck.) Clem. in Frisch *et al.* (2006:

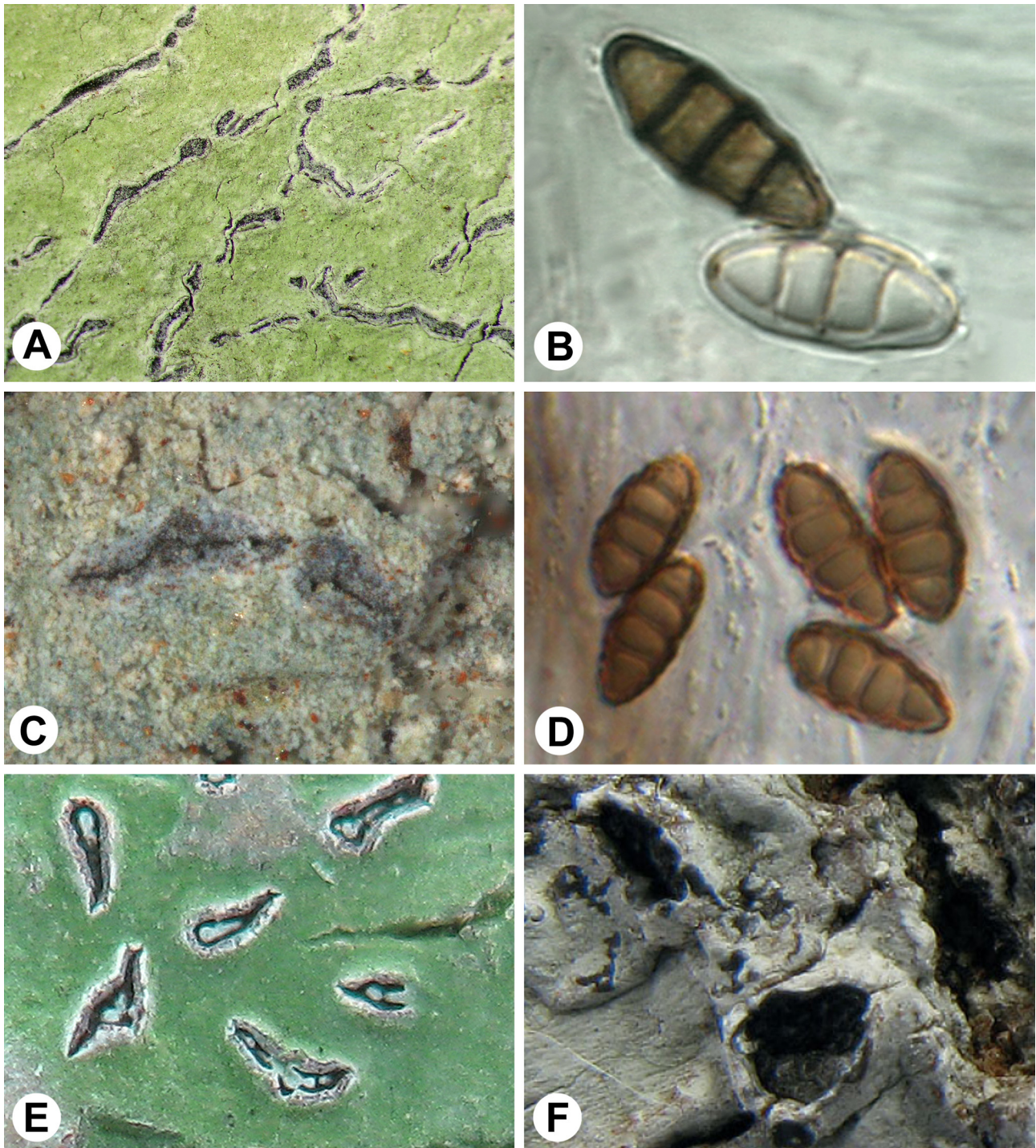


FIGURE 5. A–B. *Phaeographopsis neotropica*, thallus with ascomata and ascospores (Costa Rica, Lücking 16235a). C–D. *Redingeria desseiniiana*, ascomata and ascospores (holotype). E. *Redingeria glaucoglyphica*, thallus with ascomata (Peru, Rivas Plata 802A). F. *Redingeria microspora* (Brazil, Cáceres 6030).

166) and Mangold *et al.* (2009: 261) is incorrect, since neither Müller nor Clements made that combination and Clements (1909) did not even cite the species known at the time as *Ocellularia myriopora* (Tuck.) Müller (1888: 114). As a consequence, the *Myriotrema album* clade will eventually require the description of a new genus.

Ocellularia praestans forms an unsupported sister group relationship with *O. profunda* and relatives. We revised the taxonomy of specimens previously identified as *Ocellularia profunda* in the latter clade. The clade contains in fact four distinct taxa: *O. profunda* s.str., *O. kalbii* Mangold *et al.* (2007: 198), which differs from *O. profunda* in the lack of secondary substances, and two undescribed species, one with sorediate dactyls considered a variation of *O. profunda* (Mangold *et al.* 2009) and one with a sterile, strongly irregular thallus.



FIGURE 6. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Rhabdodiscus* clade and the basal portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

The strongly supported genus *Rhabdodiscus* comes out consistently as sister (Fig. 6) to *Nitidochapsa* plus *Ocellularia* s.lat. (Rivas Plata *et al.* 2013). Although generally with low support, *Rhabdodiscus* contains several newly described and yet unidentified species, such as *R. neocaledonicus* Papong *et al.* (2014), *R. saxicola* Papong *et al.* (2014), and *R. thouvenotii* Papong *et al.* (2014) from New Caledonia. Apparently this genus is richer in species than previously assumed and also includes species that deviate from the common pattern of olive-green, epiphytic thalli containing psoromic acid, as two of the New Caledonian species deviate in substrate (saxicolous) and chemistry.

Within the large *Ocellularia* s.lat. clade, the *O. terebrata* clade falls outside the strongly supported remainder of this group (Fig. 6), suggesting that the *O. terebrata* clade is another basal branch, next to *Rhabdodiscus*, of this species-rich lineage which contains the bulk of extant tropical species of this tribe. Our analysis suggests that specimens identified as *O. psorbarroensis* Sipman in Sipman *et al.* (2012: 145) in this clade may represent two phylogenetically distinct taxa. We also propose the new name ***Ocellularia hernandeziana* Kraichak, Lücking & Lumbsch, nom. nov.** [Mycobank #807665] for *Myriotrema ecorticatum* Lücking, J.E. Hern. & Kalb in Lücking *et al.* (2012: 4), non *O. ecorticata* Mangold in Mangold *et al.* (2009: 656)]. The non-monophyly of the newly described species *O. rondoniana* Cáceres *et al.* (2014) is due to missing data in the supermatrix on which our phylogenetic analysis was based. In this example, two of the three specimens have short mtSSU sequences whereas the third has nearly complete mtSSU and nuLSU data. The mtSSU sequences are identical in all three specimens except for different length, but since the short sequences cover a more conserved portion of the mtSSU, the analysis does not cluster all three specimens together, since mtSSU distances in this portion of the clade are generally short.

The *Ocellularia wirthii* clade was already recognized in previous analyses (Rivas Plata *et al.* 2012b, 2013) but is here recovered for the first time with strong support (Fig. 6), including besides *O. wirthii* also the newly described species *O. australiana* Mangold, Lücking & Lumbsch in Mangold *et al.* (2014) and *O. fuscosporella* Papong, Lücking & Lumbsch in Papong *et al.* (2014). Whereas *O. australiana* is similar to *O. wirthii* in most aspects, *O. fuscosporella* differs in ascoma morphology, chemistry, and especially in ascospore type. This illustrates that some of the phylogenetically defined and supported clades have few or none phenotypic synapomorphies that could be used to circumscribe the clade as a whole. On the other hand, the fact that all three species are known from a narrow area in tropical Australasia suggests regional radiations within Ocellularieae that in some cases evolved quite distinctive phenotypes, often in parallel to unrelated clades.

An unsupported clade within *Ocellularia* s.lat. includes *O. subpraestans* (Hale) Hale (1980: 138) sister to a supported clade comprising the newly described *O. austropacifica* Papong, Lücking & Lumbsch in Papong *et al.* (2014), *O. baileyi* s.lat., ***O. curranii* (Vain.) Kraichak, Lücking & Lumbsch, comb. nov.** [Mycobank #809094; *Thelotrema curranii* Vain., *Ann. Acad. Sci. Fenn., Ser. A*, 15(6): 186. 1921], and *O. allosporoides* (Nyl.) Patwardhan & Kulkarni (1977: 5) plus a close, undescribed relative of the latter lacking secondary substances (Fig. 6). This clade is of interest as it includes species with norisonotatic acid chemistry, underlining the importance of secondary chemistry in predicting phylogenetic relationships (Lumbsch *et al.* 2014). *Ocellularia austropacifica* is quite different from specimens identified as *O. baileyi* with salmon-pink medulla in both morphology and chemistry (no substances versus norisonotatic acid and pink pigment; Fig. 7). Hence, the close relationship, suggesting even possible conspecificity, comes as a surprise. Revision of the sequenced specimens labeled *O. baileyi* revealed that all of them feature a white medulla, suggesting that they might do not represent *O. baileyi* s.str. as indicated by Mangold *et al.* (2009), who accepted the latter as being variable in medulla color. The type of *O. baileyi* also has wider pores of the ascomata (Fig. 7). Due to missing sequences, the available sequence data are not sufficient to resolve the relationship between *O. austropacifica* and *O. aff. baileyi* (Fig. 8A): while mtSSU is practically identical in all specimens, nuLSU data show that *O. austropacifica* has ten synapomorphies compared to *O. aff. baileyi* (Fig. 8). However, since only one nuLSU sequence is available for that taxon, the other specimens will not be resolved correctly. This is comparable to the case of *O. allosporoides*, where specimens with norisonotatic acid (*O. allosporoides* s.str.) are not well-separated from those lacking substances (*O. aff. allosporoides*). Also here, nuLSU sequence data suggest grouping of the chemically different specimens into two clades corresponding to chemistry (Fig. 8B), but since three specimens are only represented by mtSSU data, phylogenetic analysis using a supermatrix approach does resolve this relationship.

The *Ocellularia massalongoi* clade includes *O. interposita* (Nyl.) Hale (1980: 137), *O. massalongoi* (Mont.) Hale (1980: 137), and *O. microstoma* (Müll. Arg.) Mangold *et al.* (2009: 324) and relatives (Fig. 9). All produce

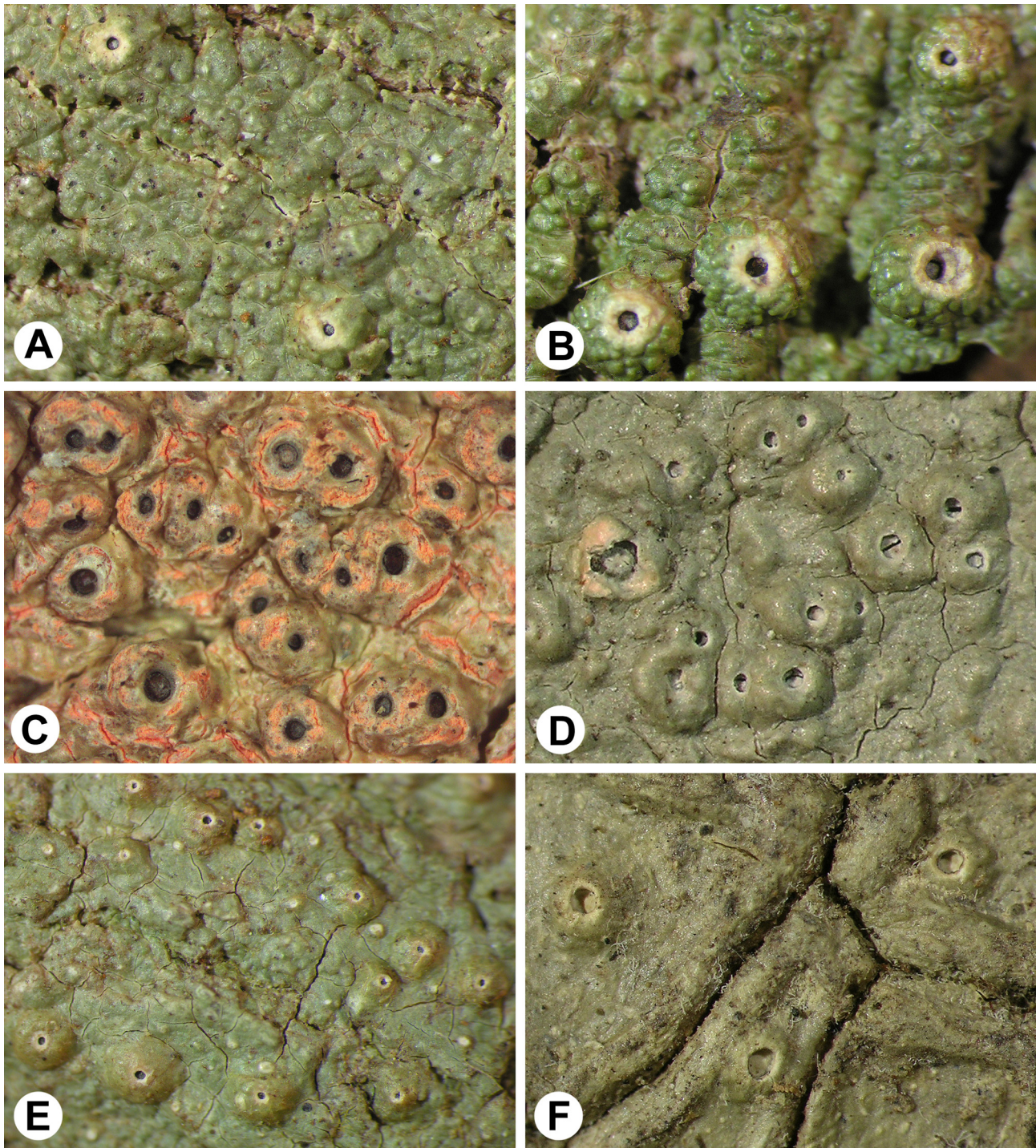


FIGURE 7. A–B. *Ocellularia austropacifica*, thallus with ascomata (A, isotype; B, paratype). C–D. *Ocellularia* cf. *baileyi*, thallus with ascomata (C, Australia, Tibell 15364; D, Australia, Kalb 34261). E. *Ocellularia* aff. *baileyi*, thallus with ascomata (New Caledonia, Papong 7982). F. *Ocellularia baileyi*, thallus with ascomata (isotype).

large, muriform ascospores but have variable chemistry including the psoromic, salazinic, and protocetraric acid chemosyndromes. Surprisingly, two species with small, dark brown ascospores are also supported in this clade, the newly described *O. pulchella* Lücking, Lumbsch & Parnmen in Papong *et al.* (2014) and a specimen from Australia previously identified as *O. bahiana* (Mangold *et al.* 2009). Both otherwise resemble species of the *O. bahiana* clade in thallus structure, ascospores, and chemistry, and would have been expected to cluster within that clade instead. Specimens hitherto identified as *Ocellularia microstoma* (Rivas Plata *et al.* 2012b, 2013) come out in three separate clades, one with specimens from Japan, one with a single specimen from the Philippines, and five

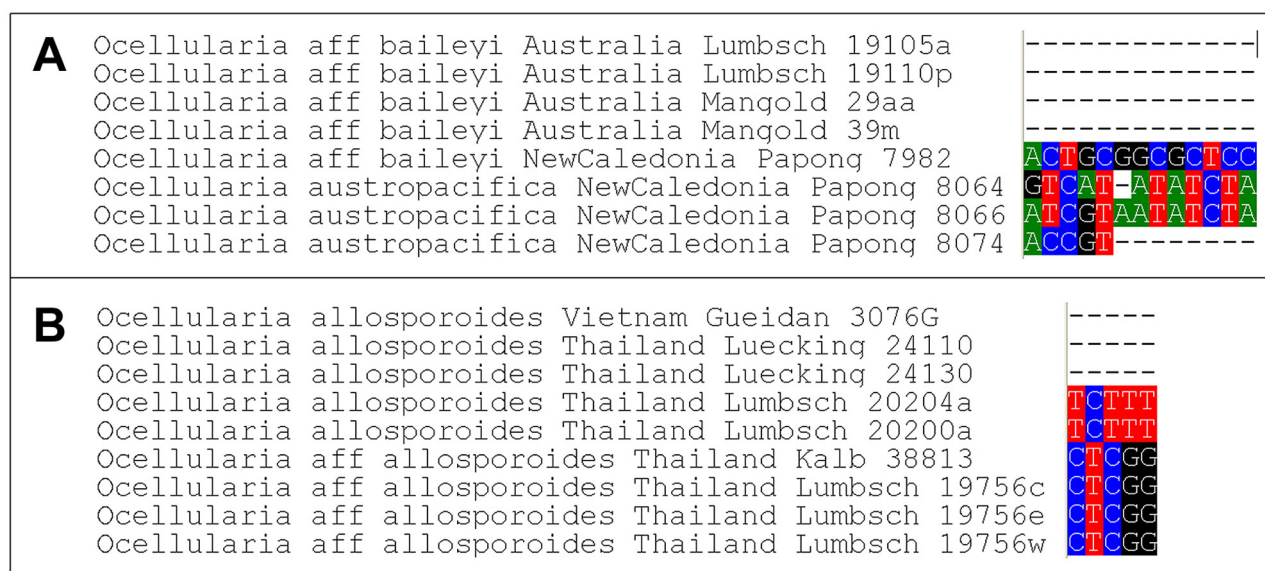


FIGURE 8. Screen shots from BIOEDIT of homologous columns of variable portions of the nuLSU for the clade containing *Ocellularia austropacifica* and *O. aff. baileyi* (above), as well as *O. allosporoides* and *O. aff. allosporoides* (below). In both cases, the species are distinguished by obvious synapomorphies in the nuLSU, but because mtSSU is practically identical between the species in each clade, specimens with mtSSU data alone cannot be resolved.

from the Philippines and Australia with two specimens from New Caledonia identified as *O. khasiana* (Patw. & Nagarkar) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807661; *Thelotrema khasianum* Patw. & Nagarkar, *Biovigyanam* 6: 8. 1980]. *Ocellularia khasiana* agrees with *O. microstoma* except for the chemistry, with protocetraric acid as main compound, whereas *O. microstoma* produces fumarprotocetraric acid, with protocetraric acid as accessory substance. Apparently, this minor chemical difference translates into phylogenetically distinct taxa. Since the type of *O. microstoma* is from Japan, we rechecked the chemistry of the Philippine and Australian specimens and found that they contain protocetraric acid as main compound. Notably, *O. cinerea* (Müll. Arg.) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807662; *Thelotrema cinereum* Müll. Arg., *Flora* 74: 112. 1891], which was included in *O. microstoma* by Mangold *et al.* (2009), is also a distinct species. It agrees with *O. microstoma* in producing fumarprotocetraric acid as main compound, but has smaller ascomata lacking a broad, flattened top and a light red-brown excipulum (dark brown in *O. microstoma*). The combination *Ocellularia microstoma* was accidentally introduced by Mangold *et al.* (2009), ascribing it to Hale (1980: 134). However, this is an erroneous citation, since Hale (1980: 134) cited the species as *Myriotrema microstomum* (Müll. Arg.) Hale. Nevertheless, the combination is valid and must be ascribed to the publication authors, viz. Mangold, Elix & Lumbsch.

No new data were obtained for the strongly supported *Ocellularia bahiana* clade (Fig. 9), except the finding that two species with phenotype features consistent with that clade fall into the *O. massalongoi* clade (see above). Two species within the *O. bahiana* clade require combination into *Ocellularia*: *O. erodens* (R. C. Harris) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807663; *Myriotrema erodens* R. C. Harris, *Some Florida Lichens*: 89. 1990] and *O. laeviuscula* (Nyl.) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807664; *Thelotrema laeviusculum* Nyl. in Triana & Planchon, *Ann. Sci. Nat. Bot., Ser. 4*, 19: 335. 1863; *Myriotrema laeviusculum* (Nyl.) Hale, *Mycotaxon* 11: 134. 1980]. *Ocellularia erodens* and *O. auberianoides* (Nyl.) Müller (1891b: 395) are closely related; both produce soralia and only differ in ascospore size. Whether the sterile, sorediate material here identified as *O. erodens* represents that species or sterile forms of *O. auberianoides* cannot be said with the data at hand, since the resolution provided by mtSSU and nuLSU sequence data might be insufficient in this case.

The strongly supported *Ocellularia perforata* clade (Fig. 9) consistently comes out as supported sister to *Myriotrema clandestinum*, seemingly providing another example of a *Myriotrema* species that requires recombination into *Ocellularia*. However, since the species with small, hyaline ascospores and psoromic acid have a very complex taxonomy and ascoma morphologies ranging from myriotremoid to ocellularioid, we prefer to

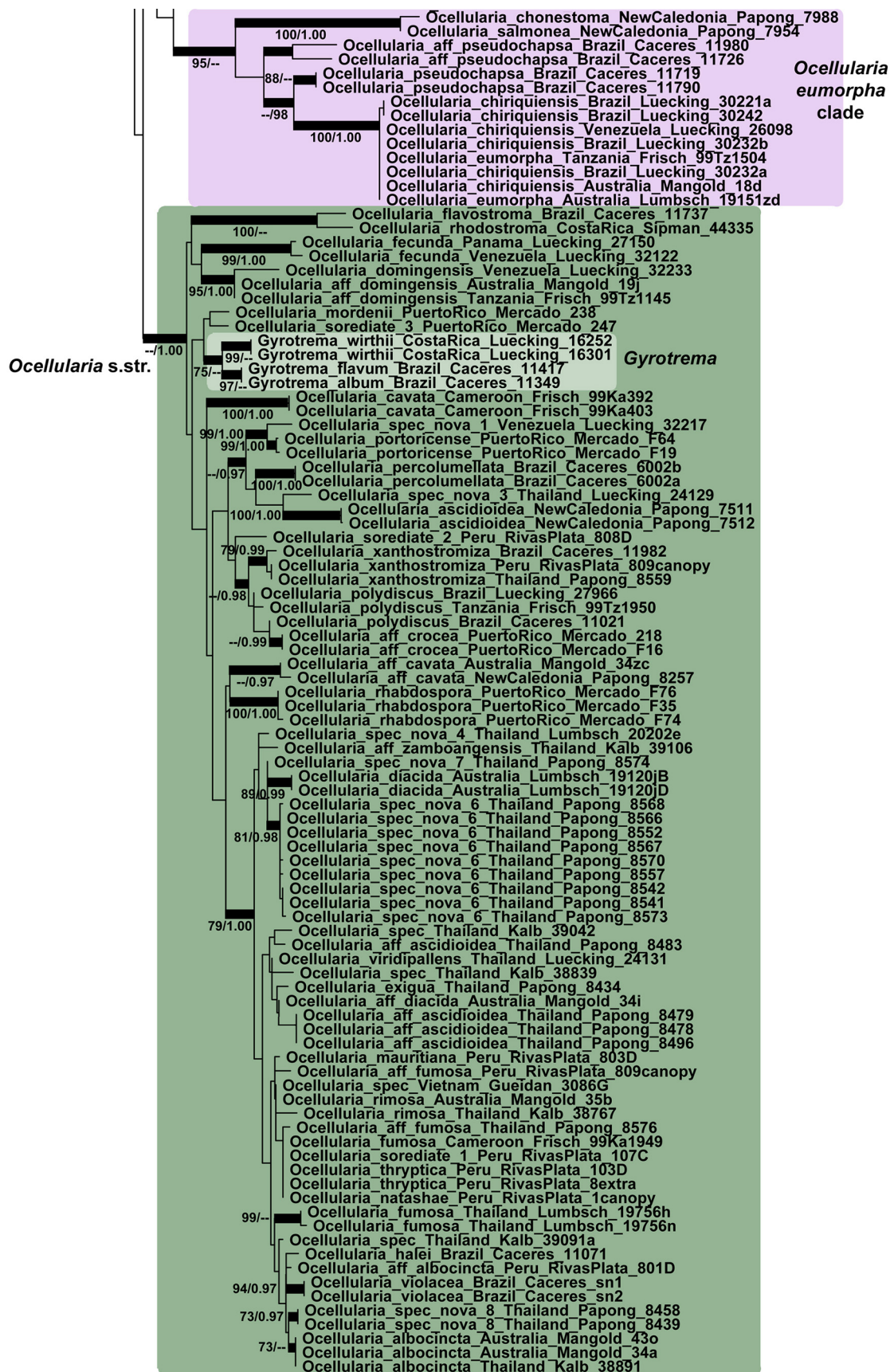


FIGURE 10. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the terminal portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

await further material of *Myriotrema clandestinum* to confirm the position of this species. It is possible that there are several, very similar taxa representing both genuine *Myriotrema* and *Ocellularia* species and hence recombining *M. clandestinum* in *Ocellularia* appears premature. Within the *O. perforata* clade, there are two further examples of unresolved, complex species-level phylogenies. Thus, the topology for material identified as *O. thelotremoides* (Leight.) Zahlbruckner (1923: 603) suggests that more than one species are involved, particularly because the newly described species *O. neocaledonica* Lücking, Lumbsch & Parnmen in Paping *et al.* (2014), is nested on a long branch within the *O. thelotremoides* complex, even if it is morphologically and chemically distinct. While *O. thelotremoides* has submuriform ascospores and protocetraric acid, *O. neocaledonica* has 5-septate, smaller ascospores and lacks secondary substances. Notably, the specimens identified as *O. thelotremoides* cluster according to their geographical distribution, further supporting the hypothesis that these represent at least three distinct taxa. Likewise, *O. rugosothallina* Lücking, Lumbsch & Parnmen in Paping *et al.* (2014) is nested on a long branch within the *O. perforata* complex. These species complexes, including also *O. papillata* (Leight.) Zahlbruckner (1923: 597) and *O. terebrata*, require further study with ample material from throughout the tropics.

The backbone of the remainder of *Ocellularia* s.lat. (Fig. 9, 10), including *Ocellularia* s.str. centered around *O. cavata* (Ach.) Müller (1882: 499), is not supported; hence this analysis does not allow any new conclusions about the position of the genera *Ampliotrema* and *Gyrotrema* (Rivas Plata *et al.* 2012b). As in our previous analysis, *Ampliotrema* forms two clades, one containing the type species, *A. amplius*, and the other comprising all other species. *Ampliotrema amplius* is unsupported sister to the *O. eumorpha* clade, which also contains *O. chonestoma* (Leight.) Zahlbruckner (1923: 586) and the newly described *O. salmonea* Lücking, Lumbsch & Parnmen in Paping *et al.* (2014) and *O. pseudochapsa* M. Cáceres, Aptroot & Lücking in Cáceres *et al.* (2014). The polyphyly of *Ampliotrema* must be studied further: the genus appears monophyletic based on mtSSU sequence data, whereas the single available nuLSU sequence for one of the three specimens of *A. amplius* clusters with *O. eumorpha* and relatives. Notably, the undescribed taxon resembling *O. pseudochapsa*, but with corticate thallus (Cáceres *et al.* 2014), also falls within this clade but represents a distinct species.

Several other newly described and undescribed species are found in this portion of the tree, particularly within the supported *Ocellularia* s.str. clade (Fig. 10), which appears to contain the largest number of species among the clades currently classified in *Ocellularia*. *Ocellularia* s.str. includes many taxa with pigmented medulla and the cinchonarum unknown chemistry, although protocetraric and hypoprotocetraric acid are also frequent. Some preliminary conclusions can be drawn about the *O. cavata* complex. Currently, this name includes all material with smooth to verrucose thallus, carbonized, columellate ascomata, small to medium-sized, transversely septate, hyaline ascospores, a pale yellow to orange medulla, and the cinchonarum unknown chemistry (Frisch *et al.* 2006; Mangold *et al.* 2009). Although very few specimens with these characters have been sequenced, they form several, only distantly related clades. Thus, *O. cavata* from tropical Africa (Cameroon) is phylogenetically distinct from specimens with similar features collected in Australia and New Caledonia. Specimens with distinctly verrucose thallus form a separate clade here identified with *O. xanthostromiza* (Nyl.) Zahlbruckner (1923: 604), previously considered a synonym of *O. cavata*. Notably, this is thus far the only confirmed case of a rain forest understory species of this tribe to have a pantropical distribution, known from Peru, Brazil, and Thailand. Other material from Thailand with comparatively small ascomata forms another clade corresponding to a yet undescribed species (spec. nova 6). Also *O. polydiscus* Redinger (1933: 61) differs from *O. cavata* in the complex columella, and *O. aff. crocea* (Kremp.) Overeem & Overeem in Overeem (1922: 118), differing from *O. cavata* in a fissured ascoma margin. These very preliminary data suggest that *Ocellularia* is one of the genera where both future inventories and an increased amount of molecular data will lead to the recognition of many more species than currently accepted.

Conclusions

The updated phylogenetic analysis of tribe Ocellularieae supported earlier findings and also exhibits consistent placements of some of the clades even with lack of support. Thus, a broader picture of the evolution and classification of this tribe is emerging. However, some clades remain undersampled, in particular those containing species currently classified in *Ocellularia* but falling outside *Ocellularia* s.lat. Species of these clades must be primary targets for gathering further sequence data, in order to better understand the phenotype features that

characterize these clades and eventually give them formal generic status. In addition, it becomes apparent that, at least in this clade, nuLSU and also *RPB2* provide a better resolution at species and species group level than mtSSU; on the other hand, the proportion of sequences routinely obtained for taxa within this clade indicates that nuLSU and particularly *RPB2* sequencing often fails. The highlighted cases suggest that especially within *Ocellularia* s.lat., additional data from these two loci may help to better resolve this clade and then either define subgenera or even additional genera.

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Research Article

High frequency of character transformations is phylogenetically structured within the lichenized fungal family Graphidaceae (Ascomycota: Ostropales)

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Graphidaceae is a large family of over 2000 predominantly tropical, lichenized fungal species encompassing a remarkable range of morphological and chemical diversity. The majority of species belongs in subfamily Graphidoideae, which also exhibits the greatest amount of variation. Various phenotype characters have traditionally been used for classification at the genus and species levels, but their correlations with phylogenetic clades are poorly known. Using a multilocus approach, we reconstructed a phylogeny for 224 taxa, representing all main genera within subfamily Graphidoideae, and employed ancestral character reconstruction and character transformation analyses to understand the evolution of morphological, anatomical and chemical characters within this group. In addition, we examined the changes of habitat and photobiont types over the phylogeny. For this purpose, we focused on 10 characters, including thallus and ascoma features and chemistry. Since previous studies have shown that results may differ depending on the reconstruction method used, both Maximum-parsimony and Maximum-likelihood approaches were employed and multistate coding of characters was used. We reconstructed the ancestral states for 64 well-supported major clades in the family and found support for the ancestor of Graphidoideae being a tropical species with a trentepohlioid photobiont, apothecioid, solitary ascomata lacking both a columella and lateral paraphyses, and having non-amyloid ascospores. The frequency of transformations of morphological and chemical characters over the phylogeny of Graphidaceae was computed, resulting in a high frequency of reversible transformations for some characters, such as secondary chemistry, whereas other characters, such as photobiont, hymenial persistence or ascoma aggregation, exhibited low frequency of transformations. However, we found that even in the character with the highest number of transformations, secondary chemistry, the shifts were highly structured phylogenetically, suggesting that the evolution of the character, rather than the character state itself, can be used to predict phylogenetic relationships with certain accuracy.

Key words: Ancestral character reconstruction, character traits, lichens, molecular phylogeny, taxonomy

Introduction

An important aspect of evolutionary biology is the understanding of the historical process of phenotypic character changes over the tree of life. In groups with poor fossil record, such as fungi in the phylum Ascomycota, including lichenized groups (Taylor *et al.*, 1995, 1997, 1999; Yuan *et al.*, 2005; Berbee & Taylor, 2007; Krings *et al.*, 2012), ancestral character reconstruction and stochastic mapping, inferred from patterns of traits in living

organisms, provide an avenue for addressing character evolution (Pagel, 1999; Lutzoni *et al.*, 2000; Huelsenbeck *et al.*, 2003; Pagel *et al.*, 2004). A growing body of studies employ these methods to better understand trait evolution in lichenized fungi (Lutzoni & Pagel, 1997; Lutzoni *et al.*, 2001; Ihlen & Ekman, 2002; Blanco *et al.*, 2006; Buschbom & Barker, 2006; Lumbsch *et al.*, 2006; Crespo *et al.*, 2007; Gueidan *et al.*, 2007; Schmitt *et al.*, 2009; Schmitt & Lumbsch, 2009; Schoch *et al.*, 2009; Baloch *et al.*, 2010; Prieto *et al.*, 2012). While powerful in assessing character evolution, limitations of these methods have also been shown (Ekman *et al.*, 2008) potentially yielding

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contradicting results, depending on taxon sampling and the employed method of phylogenetic reconstruction.

Graphidaceae, which has recently been expanded to include the previously separated families Asterothyriaceae, Gomphillaceae, Solorinellaceae and Thelotremaaceae (Mangold *et al.*, 2008b; Baloch *et al.*, 2010; Rivas Plata & Lumbsch, 2011; Rivas Plata *et al.*, 2012a, 2012b), is one of the largest families of lichen-forming fungi with over 2000 accepted species (Lücking *et al.*, 2013; Rivas Plata *et al.*, 2013). The classification within this large fungal clade has dramatically changed over the last decade. The traditional circumscription of the family and genera was largely based on ascoma (rounded vs. lirellate or pseudostromatic) and ascospore types (septation and pigmentation) (Müller, 1887; Wirth & Hale, 1963, 1978; Hale, 1974, 1978). The use of these characters was long perceived as artificial and replaced by a classification among thelotremoid taxa based on excipular structures (Salisbury, 1972a, 1972b, 1978; Hale, 1980, 1981). However, major systematic revisions only started after seminal treatments on graphidoid and thelotremoid taxa respectively by the school of Klaus Kalb (Staiger, 2002; Frisch *et al.*, 2006) with a more refined classification based on a combination of phenotypic characters. Molecular studies have further changed the classification with the identification of additional clades that are accommodated in new or resurrected genera and a revised concept at the family level (Staiger *et al.*, 2006; Mangold *et al.*, 2008a, 2008b; Nelsen *et al.*, 2010; Rivas Plata *et al.*, 2010a, 2012a, 2012b, 2013; Berger *et al.*, 2011; Lücking *et al.*, 2011, 2012, 2013; Rivas Plata & Lumbsch, 2011; Cáceres *et al.*, 2012; Parnmen *et al.*, 2012a, 2013).

Within Graphidaceae, up to four subfamilies are currently accepted (Hodkinson, 2012; Rivas Plata *et al.*, 2012a; Lücking *et al.*, 2013). Subfamily Graphidoideae constitutes by far the largest clade of this family of crustose, primarily tropical lichen-forming fungi (Rivas Plata *et al.*, 2012a). The species currently placed in this subfamily represent the core of the former families Graphidaceae and Thelotremaaceae. This apparent incongruence of traditional, morphology-based classifications and molecular phylogenies suggest that these fungi are extremely variable with regard to phenotype characters, with a high probability of characters evolving in parallel in unrelated clades, as has been shown for this family and for various other lineages in the Ascomycota (Blanco *et al.*, 2004, 2006; Crespo *et al.*, 2007; Tehler & Irestedt, 2007; Mugambi & Huhndorf, 2009; Schmitt *et al.*, 2009; Lumbsch *et al.*, 2010b; Parnmen *et al.*, 2010; Muggia *et al.*, 2011; Rivas Plata *et al.*, 2011; Rivas Plata & Lumbsch, 2011).

With the availability of molecular data, we are now able to study the evolution of phenotypic characters previously used in the classification of Graphidaceae. While most species in the family are tropical crustose lichens,

some species also occur in subtropical habitats, such as *Redonographa* (Lücking *et al.*, 2013) or have their distribution centre in non-tropical areas, such as *Diploschistes* (Lumbsch, 1989). Two main types of photobionts are found in the family, chlorococcoid and trentepohlioid, correlating with ecological features of the involved lichens (Friedl & Gärtner, 1988; Nelsen *et al.*, 2011). While numerous species have corticated thalli (Hale, 1981; Staiger, 2002; Frisch *et al.*, 2006), others lack a cortex (Lumbsch, 1989). A cortex is a distinct layer of fungal hyphae covering the upper and/or lower side of the thallus. The ascomata can be either roundish (apothecioid) or elongate (lirellate), but there is no evidence regarding the evolutionary function of ascoma shape. A few lineages form mazaedioid ascomata which consist of spore masses that accumulate on top of the ascomata. These are highly adapted to wind dispersal of the ascospores (Lumbsch *et al.*, 2004), while the majority of species in the family are characterized by ascomata with persistent hymenia. A sterile tissue within the hymenium, the so-called columella, which is often partially or totally carbonized, occurs in many tropical species; it is assumed to protect the hymenium against fungivores (Rivas Plata & Lumbsch, 2011). Sterile hyphae that grow from the margin into the central cavity of the ascoma, so-called lateral paraphyses (Henssen, 1995) or periphysoids (Hale, 1981) occur in several lineages, but their function is unknown. Ascospores in the family show different reaction to iodine, being either amyloid, hemiamyloid or non-amyloid (Baral, 1987; Rivas Plata & Lumbsch, 2011), depending on the presence and absence and chemical nature of internal wall substances.

We are now able to address questions on the possible functions of these characters in terms of ecology and adaptations of species to particular (micro-) habitats and niches. Generally, fast-evolving characters can be assumed to be ecologically modified, whereas highly conserved characters have low levels of correlation with ecological parameters, unless the clade in question is also ecologically uniform (Felsenstein, 1985; Harvey & Purvis, 1991; Coddington, 1994; Ackerly, 2003; Kraichak, 2012). In order to understand the patterns of the character evolution in this group of lichenized fungi, we assembled a dataset of four loci including 224 taxa representing all major clades of subfamily Graphidoideae, Fissurinoideae and Redonographoideae and outgroups for phylogenetic analysis. We then performed ancestral character state reconstructions of seven representative morphological and anatomical characters, secondary chemistry, the type of photobiont and the vegetation type zone. The main objectives of this study were: (1) to characterize the hypothetical ancestor of the subfamily Graphidoideae, to better understand the evolution of phenotypic and ecological characters in the core group of the family Graphidaceae; (2) to identify the number and phylogenetic signal of

character state transformations of these characters along the reconstructed phylogeny; and (3) to understand the impact of ecology on character transformations.

Materials and methods

Taxon sampling and molecular methods

The taxon sampling included the major clades of subfamilies Graphidioideae, Redonographoideae, and Fissurinoideae in Graphidaceae, plus five taxa of the genus *Gyalecta* as outgroup, based on previous molecular studies (Lumbsch *et al.*, 2010a; Parmen *et al.*, 2010). Two hundred and twenty-four species were included in the analyses (Table 1). We selected taxa for this study to represent the morphological and chemical diversity in the group and to include all major genera, except for the taxa in subfamily Gomphillioideae, from which a limited number of materials and DNA sequences were available for the current study. We included only species for which we obtained at least two of the four loci studied: nuclear LSU rDNA, mitochondrial SSU rDNA, and the protein-coding *RPB1* and *RPB2* genes. New sequences were generated for this study using the Sigma REDEExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, USA) for DNA isolation following the manufacturer's instructions, except that 40 μ L of extraction buffer and 40 μ L dilution buffer were used. DNA dilutions (5 $\times$) were used in PCR reactions of the genes coding for the nuLSU, mtSSU, *RPB1* and *RPB2*, respectively. Primers and PCR amplification condition were the same as described previously (Parmen *et al.*, 2012a, 2012b; Schmitt *et al.*, 2012; Rivas Plata *et al.*, 2013). One hundred and fifteen new sequences were generated for this study (21 mtSSU, 16 nuLSU, 54 *RPB1* and 24 *RPB2*).

Sequences alignments and phylogenetic analyses

Alignments were done in Geneious Pro 5.5.2 (Drummond *et al.*, 2012). Ambiguously aligned portions were removed manually. The single-locus and concatenated alignments were analysed by maximum likelihood (ML) and a Bayesian approach (B/MCMC). To test for potential conflict, ML bootstrap analyses (with 2000 pseudoreplicates) were performed on the individual datasets, and resulting single-tree trees were examined for conflict, i.e. incongruences with at least 75% bootstrap support (Lutzoni *et al.*, 2004).

The ML analysis of the concatenated alignment was performed with the program RAXML-HP2 (version 7.3.1) on XSEDE (Stamatakis, 2006) using the default rapid hill-climbing algorithm. The model of nucleotide substitution chosen was GTRGAMMA, according to the results from the model selection by jModelTest2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). The

dataset was partitioned into eight parts (mtSSU, nuLSU and each codon position of *RPB1* and *RPB2*), and each gene partition was treated as independent. Introns in *RPB1* and *RPB2* sequences were removed from the analysis. Bootstrap estimates were carried out using 2000 pseudoreplicates (Stamatakis *et al.*, 2008).

The B/MCMC analysis was conducted using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), with the same substitution model as in the ML analysis. Two parallel runs with 10 000 000 generations each, starting with a random tree and employing four simultaneous chains, was executed. No molecular clock was assumed. Heating of chains was set to 0.2. Posterior probabilities were approximated by sampling trees using a variant of Markov Chain Monte Carlo (MCMC) method. To avoid autocorrelation, only every 1000th tree was sampled. The first 4000 trees were discarded as burn in. We used AWTY (Nylander *et al.*, 2007) to compare splits frequencies in the different runs and to plot cumulative split frequencies to ensure that stationarity was reached. A majority-rule consensus tree with average branch lengths was calculated from the remaining 6000 sampled trees using the sumt option of MrBayes. Posterior probabilities were obtained for each clade. Clades with bootstrap support above 70% under ML and Bayesian posterior probabilities above 0.95 were considered as strongly supported. Phylogenetic trees were visualized using the program TreeView (Page, 1996).

Ancestral character state reconstruction

Characters for the analysis including habitat, photobiont, cortex, six ascomatal characters, and secondary chemistry were analysed using multistate character coding with characters treated as unordered (Table 2 and Table S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2014.905506>). The coding was done based on our own observations of the material and recently published studies (Lücking, 2009; Lücking *et al.*, 2009, 2013; Mangold *et al.*, 2009; Lumbsch *et al.*, 2010a; Rivas Plata *et al.*, 2010b, 2012a, 2012b, 2013; Berger *et al.*, 2011; Rivas Plata & Lumbsch, 2011; Parmen *et al.*, 2012a, 2013; Sipman *et al.*, 2012;). For chemistry, instead of coding each substance separately, we coded depsidones according to the groups at positions 1 and 6, which might be either carboxyl groups (COOH), hydroxyl group (OH) or methyl group (ME). This was done to emphasize chemical relationships between substances. The three types of depsidones distinguished here include stictic acid for (1'-6'-OH) depsidones, protocetraric acid for (1'-COOH-6-ME) depsidones, and psoromic acid for (6'-COOH) depsidones.

Maximum likelihood (ML) reconstructions were carried out on each individual tree using an unrestricted

Table 1. List of taxa with their collection data and GenBank accession numbers for the sequences used in this study. Bold accession numbers indicate sequences generated for this study. Dashes (–) indicate missing data.

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Acanthothecis hololeucooides</i>	Graphidoideae	Thelotremateae	Brazil, Lücking 31303 (F)	JX420952	JX421423	–	JX420938
<i>Acanthothecis peplophora</i>	Graphidoideae	Thelotremateae	USA, Common 9126A	JX420954	JX421424	KF688524	–
<i>Acanthothecis sarcographoides</i>	Graphidoideae	Thelotremateae	Brazil, Cáceres 6785 (F)	JX420957	–	KF875493	–
<i>Acanthotrema albidiatum</i>	Graphidoideae	Thelotremateae	USA, Mercado 290 (F)	KF688506	KF688492	KF688526	KF688542
<i>Acanthotrema brasilianum</i>	Graphidoideae	Thelotremateae	Peru, Rivas Plata 0808Da (F)	JX420958	JX421429	–	JX420876
<i>Acanthotrema frischii</i>	Graphidoideae	Thelotremateae	Cameroon, Frisch 99Ka40	DQ384916	DQ431928	–	–
<i>Ampliotrema amplius</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata FM89 (F)	JF828958	JF828973	–	–
<i>Ampliotrema oculatum</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19160Wa (F)	EU075565	EU075612	–	–
<i>Asteristion leucophthalmum</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19164q (F)	JX421374	JX421658	–	JX420830
<i>Asteristion platycarpum</i>	Graphidoideae	Thelotremateae	USA, Lücking 26573 (F)	JX421007	JX421460	–	JX465328
<i>Astrochapsa astroidea</i>	Graphidoideae	Thelotremateae	Thailand, Lücking 24006 (F)	JX420977	JX421443	KF875452	JX420943
<i>Astrochapsa canaima</i>	Graphidoideae	Thelotremateae	Venezuela, Kalb 38761	JX420968	–	–	JX420948
<i>Astrochapsa mastersonii</i>	Graphidoideae	Thelotremateae	Philippines, Rivas Plata 1200 (F)	JX420999	JX465299	KF875456	JX420861
<i>Astrochapsa meridenis</i>	Graphidoideae	Thelotremateae	Costa Rica, Lücking 17770 (F)	EU075610	EU075655	–	JF828940
<i>Astrochapsa pseudophlyctis</i>	Graphidoideae	Thelotremateae	Thailand, Lumbsch 19750b (F)	JX421008	JX465303	KF875458	JX420858
<i>Astrochapsa zahlbruckneri</i>	Graphidoideae	Thelotremateae	Thailand, Papon 6516 (F)	KF875551	JX421467	–	–
<i>Austrotrema binctulum</i>	Graphidoideae	Thelotremateae	Australia, Mangold 34fa (F)	EU075598	EU075642	–	JX420839
<i>Borinquenotrema sorediicarpum</i>	Graphidoideae	Thelotremateae	USA, Mercado 266 (F)	KF875556	KF875535	KF875472	KF875514
<i>Carbacanthographis albofzelii</i>	Graphidoideae	Thelotremateae	Philippines, Rivas Plata 1059A (F)	–	JX421434	KF875470	–
<i>Carbacanthographis stictica</i>	Graphidoideae	Thelotremateae	Peru, Rivas Plata 802A (F)	JF828974	JX421435	KF875477	JX420875
<i>Chapsa aff. laceratula</i>	Graphidoideae	Thelotremateae	Thailand, Lücking 24007 (F)	JX420969	JX421436	KF875484	JX420944
<i>Chapsa alborosella</i>	Graphidoideae	Thelotremateae	Brazil, Lücking 31238a (F)	JX420972	JX421439	KF688521	JX420936
<i>Chapsa lepocarpa</i>	Graphidoideae	Thelotremateae	Thailand, Pammen 18486 (RAMK)	JX465280	JX465295	KF688525	JX465322
<i>Chapsa niveocarpa</i>	Graphidoideae	Thelotremateae	Thailand, Lücking 24004 (F)	JX420995	JX421455	KF688523	JX420942
<i>Chapsa patens</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19125k1 (F)	EU075568	EU075615	KF875492	–
<i>Chapsa pulchra</i>	Graphidoideae	Thelotremateae	Thailand, Lücking 24003 (F)	JX421003	JX421459	KF688522	JX420941
<i>Chapsa spec. nova 1</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19129t (F)	EU075571	EU075619	KC020292	JX465329
<i>Chapsa spec. nova 2</i>	Graphidoideae	Thelotremateae	Thailand, Pammen 18483 (RAMK)	JX465281	JX465304	–	JX465332
<i>Chapsa spec. nova 3</i>	Graphidoideae	Thelotremateae	Fiji, Lumbsch 19815d (F)	JX421000	JX421457	–	–
<i>Chapsa subtilacina</i>	Graphidoideae	Thelotremateae	Brazil, Lücking 31240 (F)	JX421012	JX421463	KF875494	–
<i>Chapsa thallotrema</i>	Graphidoideae	Thelotremateae	Maxico, Lücking RLD056 (F)	HQ639600	JX421466	KF688519	JX420842
<i>Chroodiscus argillaceus</i>	Graphidoideae	Thelotremateae	Venezuela, Lücking 32019 (F)	JX421013	JX467681	–	JX420905
<i>Chroodiscus australiensis</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19126a (F)	HQ639585	JX421468	–	–
<i>Chroodiscus defectus</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 5437 (F)	FJ708496	FJ708489	–	–
<i>Chroodiscus khaolungensis</i>	Graphidoideae	Thelotremateae	Thailand, Papon 6069b (F)	JX465285	JX421469	–	–
<i>Chroodiscus verrucosus</i>	Graphidoideae	Thelotremateae	Thailand, Papon 6069a (F)	FJ708495	JX421469	–	JX420863
<i>Clandestinitrema sylviothecium</i>	Fissurinoideae	Thelotremateae	Thailand, Papon 6070 (F)	JX465286	JX465307	–	–
<i>Compositrema cerebriforme</i>	Graphidoideae	Ocellulariae	Nicaragua, Lücking 28636 (F)	HQ639597	JX421470	KF875495	–
<i>Compositrema thailandicum</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32204 (F)	JX421017	JX421471	–	JX420901
<i>Cruentotrema cruentatum</i>	Fissurinoideae	Thelotremateae	Thailand, Lumbsch 19756o (F)	JX421019	JX421473	–	–
<i>Cruentotrema thailandicum</i>	Fissurinoideae	Thelotremateae	Brazil, Lücking 263 (F)	HQ639587	HQ639660	–	–
<i>Crutardina petractoides</i>	Graphidoideae	Thelotremateae	Thailand, Lumbsch 19955d1 (F)	JF828960	JF828975	–	–
			Scotland, Lumbsch 20100a (F)	JX421383	JX421664	KF875496	JX420891

(continued)

Table 1. (Continued)

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Diorygia antillarum</i>	Graphidoideae	Graphideae	USA, Nelsen 322 (F)	JX046452	JX046465	–	–
<i>Diorygia junghuhnii</i>	Graphidoideae	Graphideae	Fiji, Lumbsch 205391 (F)	JX421023	JX421474	–	–
<i>Diorygia minisporum</i>	Graphidoideae	Graphideae	Kenya, Lumbsch 19543v (F)	HQ639598	HQ639626	–	KF875520
<i>Diorygia poitaei</i>	Graphidoideae	Graphideae	Nicaragua, Lücking 28538 (F)	HQ639596	HQ639627	KF875497	JF828942
<i>Diploschistes cinereoaeusius</i>	Graphidoideae	Thelotremateae	Costa Rica, unknown 24 (F)	DQ912306	DQ883799	–	DQ883755
<i>Diploschistes diplocheistoides</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19073b (F)	KF688500	AY605076	KF688513	KF688534
<i>Diploschistes eupaneus</i>	Graphidoideae	Thelotremateae	Switzerland, Lumbsch 20605g (F)	KF688508	KF688494	KF688528	KF688544
<i>Diploschistes muscorum</i>	Graphidoideae	Thelotremateae	Ecuador, Palice 2805 (F)	AY300886	AY300836	–	–
<i>Diploschistes rampoddensis</i>	Graphidoideae	Thelotremateae	Papua New Guinea, Aptroot 39679 (F)	AF431954	AF274094	–	–
<i>Diploschistes sticticus</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19109b (F)	KF688499	JX421482	KF688512	KF688533
<i>Diploschistes thumbergianus</i>	Graphidoideae	Thelotremateae	Australia, Eldridge 3800 (F)	AY779296	AF274095	–	–
<i>Dyplolabia afzelii</i>	Fissurinoideae	Ocellularieae	USA, Lücking 26509 (F)	JX421027	JX421483	KC020294	KC020273
<i>Fibrillithecia gibbosa</i>	Graphidoideae		Australia, Mangold 31g 36vI (F)	EU075573	JX421485	KF875498	–
<i>Fissurina</i> aff. <i>dumastii</i>	Fissurinoideae		Thailand, Kalb 38899 (F)	JX421034	JX421487	–	–
<i>Fissurina</i> aff. <i>humilis</i>	Fissurinoideae		Tanzania, Frisch 99Tz2002 (M)	DQ431948	DQ431921	–	–
<i>Fissurina aggregatula</i>	Fissurinoideae		Peru, Rivas Plata 107C (F)	JX421036	JX421490	–	JX420871
<i>Fissurina astroisidiata</i>	Fissurinoideae		Mexico, Lücking RLD057a (F)	JX421040	JX421491	–	JX420843
<i>Fissurina bullata</i>	Fissurinoideae		Australia, Mangold 6f (F)	JX421041	KF875537	–	JX420838
<i>Fissurina comparimuralis</i>	Fissurinoideae		El Salvador, Lücking 28103 (F)	JX421042	JX421492	–	–
<i>Fissurina crystallifera</i>	Fissurinoideae		USA, Mercado 4462 (F)	–	KF875538	–	KF875521
<i>Fissurina insidiosa</i>	Fissurinoideae		USA, Lendemer 4793 (F)	DQ972995	DQ973045	–	DQ973083
<i>Fissurina marginata</i>	Fissurinoideae		Thailand, Lücking 24122 (F)	HQ639613	JX421493	–	–
<i>Fissurina monilicarpa</i>	Fissurinoideae		USA, Mercado 156 (F)	KF875560	KF875539	–	KF875522
<i>Fissurina nigrolabiata</i>	Fissurinoideae		Philippines, Rivas Plata 1198B (F)	JF828961	JF828976	–	JF828943
<i>Fissurina pseudostromatica</i>	Fissurinoideae		Thailand, Kalb 38827 (F)	–	JX421495	–	JX420929
<i>Fissurina rufula</i>	Fissurinoideae		Fiji, Lumbsch 205211 (F)	JX421053	JX421497	–	–
<i>Gintarasia lamellifera</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 20009b (F)	JX420990	JX421449	–	–
<i>Gintarasia megalophthalma</i>	Graphidoideae	Thelotremateae	Australia, Mangold 11s (F)	–	JX421456	KF875519	KF875519
<i>Glaucotrema glaucophaeum</i>	Graphidoideae		Philippines, Rivas Plata 1099 (F)	JX421061	JX421501	KF875499	JX420862
<i>Glyphis cicutricosa</i>	Graphidoideae	Graphideae	El Salvador, Lücking 28047 (F)	HQ639610	JX421505	KF875500	–
<i>Glyphis substriatula</i>	Graphidoideae	Graphideae	El Salvador, Lücking 28014 (F)	–	JX421506	KF875501	JF828944
<i>Graphis</i> aff. <i>caesiella</i>	Graphidoideae	Graphideae	Australia, Kalb 33919 (F)	DQ431977	DQ431938	–	–
<i>Graphis</i> aff. <i>epimelaena</i>	Graphidoideae	Graphideae	China, Sohrabi, 16579 (F)	KF875561	KF875540	KF875502	KF875523
<i>Graphis angustata</i>	Graphidoideae	Graphideae	El Salvador, Lücking 28102 (F)	HQ639612	HQ639632	–	–
<i>Graphis betulina</i>	Graphidoideae	Graphideae	China, Sohrabi 16429 (F)	KF875562	KF875541	KF875503	KF875524
<i>Graphis chlorocarpa</i>	Graphidoideae	Graphideae	Guatemala, Lücking 25522 (F)	HQ639595	–	–	JF828946
<i>Graphis gracilescens</i>	Graphidoideae	Graphideae	Australia, Kalb 33942B (F)	DQ431976	DQ431936	–	–
<i>Graphis illinata</i>	Graphidoideae	Graphideae	Mexico, Lumbsch 19639 (F)	HQ639614	JX421508	–	–
<i>Graphis implicata</i>	Graphidoideae	Graphideae	Costa Rica, Lücking 16103 (F); El Salvador, Lücking 28039 (F)	DQ431978	DQ431939	–	JF828947
<i>Graphis leptoclada</i>	Graphidoideae	Graphideae	Fiji, Lumbsch 20535b (F)	JX421068	JX421509	–	–
<i>Graphis librata</i>	Graphidoideae	Graphideae	El Salvador, Lücking 28001 (F)	HQ639621	HQ639636	–	JF828945
<i>Graphis macrocarpa</i>	Graphidoideae	Graphideae	China, Sohrabi, 16438 (F)	KF875563	KF875542	KF875504	KF875525

(continued)

Table 1. (Continued)

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Graphis oshioi</i>	Graphidoideae	Graphideae	Costa Rica, Lücking 16100c (F)	DQ431986	DQ431946	—	—
<i>Graphis pseudocineria</i>	Graphidoideae	Graphideae	USA, Lücking 26537 (F)	HQ639620	HQ639639	—	—
<i>Graphis pulverulenta</i>	Graphidoideae	Graphideae	Austria, Neuwrth 11808 (UPS)	KF875564	KF875543	—	KF875526
<i>Graphis ruiziana</i>	Graphidoideae	Graphideae	Costa Rica, Lücking 14009 (F)	DQ431985	DQ431945	—	—
<i>Graphis scripta</i>	Graphidoideae	Graphideae	Austria, Neuwrth 11834 (UPS)	KF875565	KF875544	—	KF875527
<i>Gyalecta flotowii</i>	Outgroup		Sweden, Svensson 79 (UPS)	HM244740	HM244764	KC191655	HM244794
<i>Gyalecta hypoleuca</i>	Outgroup		Austria, Hafellner 63694 (UPS)	HM244742	AF465453	KC191656	AY641060
<i>Gyalecta jenensis</i>	Outgroup		Germany, Lumbsch 21192 (F)	AF431956	AY779301	—	KF875528
<i>Gyalecta truncigena</i>	Outgroup		Sweden, Nordin 5851 (UPS)	HM244743	HM244766	KC191657	HM244796
<i>Gyalecta ulmi</i>	Outgroup		Sweden, Nordin 6408 (UPS)	AY300888	AF465463	KC191658	AY641044
<i>Kalbographia lückingii</i>	Graphidoideae	Graphideae	Dominican Republic, Kalb 33152 (Herb. Kalb)	DQ431959	DQ431926	—	—
<i>Leiorreuma hypomelaenum</i>	Graphidoideae	Graphideae	Australia, Kalb 33916 (Herb. Kalb)	DQ431971	DQ431933	—	—
<i>Leptotrema wightii</i>	Graphidoideae	Ocellulariae	El Salvador, Lücking 28095 (F)	—	EU075622	—	JF828948
<i>Leucodecton anamaliense</i>	Graphidoideae	Thelotrematae	Venezuela, Lücking 32120 (F)	JX421077	JX421512	—	—
<i>Leucodecton compunctellum</i>	Graphidoideae	Thelotrematae	Australia, Lumbsch 19161vA (F)	F1708501	F1708491	—	—
<i>Leucodecton oculum</i>	Graphidoideae	Thelotrematae	El Salvador, Lücking 28098 (F)	HQ639611	HQ639657	—	JF828949
<i>Leucodecton sordidescens</i>	Graphidoideae	Thelotrematae	USA, Mangold 50b (F)	KF875545	JX421516	—	JX420845
<i>Leucodecton subcompunctum</i>	Graphidoideae	Thelotrematae	Australia, Lumbsch 19116o (F)	EU075575	EU075623	—	—
<i>Melanotrema lyncodes</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32021 (F)	JX421088	JX421520	—	JX420907
<i>Myriochapsa psoromicia</i>	Graphidoideae	Thelotrematae	Brazil, Cáceres s.n. (F)	JX421009	JX421461	KF875451	JX420884
<i>Myriotrema ecoricatum</i>	Graphidoideae	Thelotrematae	Venezuela, Lücking 32113 (F)	JX421091	JX421522	—	JX420914
<i>Myriotrema erodens</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32039 (F)	JX421092	JX421526	—	JX420897
<i>Myriotrema laeviusculum</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32057 (F)	JX421093	JX421527	—	JX420893
<i>Myriotrema microporum</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19092o (F)	EU075578	EU075626	—	—
<i>Myriotrema myrioporoides</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32205 (F)	—	JX421529	—	JX420895
<i>Myriotrema olivaceum</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19113f (F)	EU075579	EU075627	KC020298	HM244799
<i>Myriotrema peninsulae</i>	Graphidoideae	Ocellulariae	USA, Lücking 26542 (F)	HQ639616	—	—	JF828950
<i>Nadvornikia hawaiiensis</i>	Graphidoideae	Thelotrematae	Australia, Mangold 36w (F)	EU075581	AY605080	KC020300	—
<i>Nitidochapsa lepieurii</i>	Graphidoideae	Thelotrematae	Thailand, Kalb 38882 (F)	JX420991	JX421451	—	JX420930
<i>Ocellularia</i> aff. <i>allosporoides</i>	Graphidoideae	Ocellulariae	Thailand, Lumbsch 19756w (F)	JX421102	JX421534	—	—
<i>Ocellularia</i> aff. <i>dolichotata</i>	Graphidoideae	Ocellulariae	India, Lumbsch 19730fB (F)	—	JX421537	—	JX420852
<i>Ocellularia</i> aff. <i>fumosa</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 809 (F)	JX421105	—	—	JX420879
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Graphidoideae	Ocellulariae	Thailand, Lumbsch 20200j (F)	JX421106	JX421540	—	—
<i>Ocellularia</i> aff. <i>oburascens</i>	Graphidoideae	Ocellulariae	USA, Lücking 26553a (F)	JF828967	JF828979	—	—
<i>Ocellularia</i> aff. <i>rhabdospora</i>	Graphidoideae	Ocellulariae	USA, Mercado F76 (F)	KF875546	—	KF875453	KF875505
<i>Ocellularia albocincta</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 801D (F)	JX421113	JX421543	—	JX420873
<i>Ocellularia allosporoides</i>	Graphidoideae	Ocellulariae	Thailand, Kalb 38813 (Herb. Kalb)	JX421118	JX421544	KF875454	JX420925
<i>Ocellularia annulocinnabarina</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32217 (F)	JX421120	—	—	JX420921
<i>Ocellularia auberianoides</i>	Graphidoideae	Ocellulariae	USA, Lücking 26548 (F)	JX421123	JX421549	—	—
<i>Ocellularia australiana</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19151u (F)	EU075595	EU075641	—	—
<i>Ocellularia chiriquiensis</i>	Graphidoideae	Ocellulariae	Australia, Mangold 18d (F)	EU075582	EU075629	KC020301	—
<i>Ocellularia cicra</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 108Da_8extra (F)	JX421138	JX421552	—	JX420869

(continued)

Table 1. (Continued)

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Ocellularia crocea</i>	Graphidoideae	Ocellulariae	USA, Mercado F16 (F)	KF875548	KF875529	—	KF875507
<i>Ocellularia diactida</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19120jb (F)	EU075583	EU075630	—	—
<i>Ocellularia dolichotata</i>	Graphidoideae	Ocellulariae	Thailand, Kalb 38892 (F)	JX421146	JX421554	—	—
<i>Ocellularia domingensis</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32233 (F)	JX421151	JX421560	—	JX420918
<i>Ocellularia fecunda</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32162 (F)	JX421155	JX421562	—	—
<i>Ocellularia garoana</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 801A (F)	JX421157	JX421563	KF875457	JX420872
<i>Ocellularia gerardii</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 1canopy (F)	JX421159	JX421564	—	—
<i>Ocellularia henatomma</i> ssp. <i>sorediate</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 809canopy (F)	JX421162	—	—	JX420881
<i>Ocellularia interposita</i>	Graphidoideae	Ocellulariae	Thailand, Lumbsch 20201c (F)	JX421164	JX421565	—	—
<i>Ocellularia inturgescens</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19132w (F)	EU075577	EU075625	—	—
<i>Ocellularia isidiza</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32059 (F)	JX421166	JX421567	—	JX420923
<i>Ocellularia laeviusculoides</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32037 (F)	JX421168	JX421570	—	JX420922
<i>Ocellularia massalongoi</i>	Graphidoideae	Ocellulariae	Australia, Mangold 36m (F)	EU075584	EU075631	—	—
<i>Ocellularia microascidium</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 809canopy (F)	JX421171	—	—	JX420878
<i>Ocellularia microsoedati</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 107C (F)	JX421172	JX421572	—	—
<i>Ocellularia microstoma</i>	Graphidoideae	Ocellulariae	Japan, Lumbsch 1905652 (F)	JX421140	JX421576	—	JX420823
<i>Ocellularia minutula</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19167h (F)	JX421173	JX421578	—	—
<i>Ocellularia natashae</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 1canopy (F)	JX421175	—	—	JX420877
<i>Ocellularia percollumellata</i>	Graphidoideae	Ocellulariae	Brazil, Cáceres 6002a (F)	JX421180	—	—	JX420888
<i>Ocellularia perforata</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19120ja (F)	EU075587	EU075634	—	—
<i>Ocellularia petrinensis</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32024 (F)	JX421185	JX421532	—	JX420910
<i>Ocellularia pluriporoides</i>	Graphidoideae	Ocellulariae	Brazil, Cáceres sn (F)	JX421190	JX421580	—	—
<i>Ocellularia portoricensis</i>	Graphidoideae	Ocellulariae	USA, Mercado F64 (F)	KF875547	—	KF875455	KF875506
<i>Ocellularia praestans</i>	Graphidoideae	Ocellulariae	Venezuela, Lücking 32239 (F)	JX421195	JX421583	—	JX420911
<i>Ocellularia profunda</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 19100p (F)	JX421198	JX421585	KF875459	JX420825
<i>Ocellularia psorbarroensis</i>	Graphidoideae	Ocellulariae	Peru, Rivas Plata 801D (F)	JX421202	JX421588	—	JX420874
<i>Ocellularia rhabdospora</i>	Graphidoideae	Ocellulariae	USA, Mercado F75 (F)	KF875549	KF875530	KF875460	KF875508
<i>Ocellularia rhicnoporoides</i>	Graphidoideae	Ocellulariae	Thailand, Lumbsch 19750e (F)	JX421208	JX421592	—	—
<i>Ocellularia rimosa</i>	Graphidoideae	Ocellulariae	Thailand, Kalb 38767 (Herb. Kalb)	JX421211	—	—	JX420927
<i>Ocellularia</i> spec.	Graphidoideae	Ocellulariae	USA, Mercado 4451 (F)	KF875550	KF875531	—	—
<i>Ocellularia thelotremoides</i>	Graphidoideae	Ocellulariae	Australia, Lumbsch 191081 (F)	EU075592	EU075638	—	—
<i>Pallidogramme chlorocarpoides</i>	Graphidoideae	Graphideae	Australia, Kalb 33926 (Herb. Kalb); Philippines, Rivas Plata 2008a, 2005a (F)	JX421232	DQ431932	KF875461	JF828951
<i>Phaeographis</i> aff. <i>hypoglaucoides</i>	Graphidoideae	Graphideae	Thailand, Kalb 39068 (Herb. Kalb)	KF875552	KF875532	KF875462	KF875509
<i>Phaeographis intricans</i>	Graphidoideae	Graphideae	Thailand, Kalb 38864 (Herb. Kalb)	JX421254	JX421602	KF875463	JX420924
<i>Phaeographis lecanographa</i>	Graphidoideae	Graphideae	Mexico, Lücking RLD071 (F)	DQ431983	DQ431943	—	—
<i>Phaeographis lobata</i>	Graphidoideae	Graphideae	Bermuda, Berger 19598 (F)	DQ431984	DQ431944	—	—
<i>Phaeographis platycarpa</i>	Graphidoideae	Graphideae	Australia, Mangold 30za (F)	JX421263	—	—	KF875510
<i>Phaeographis</i> spec.	Graphidoideae	Graphideae	Kenya, Lumbsch F2388 (F)	KF875553	KF875533	KF875464	KF875511
<i>Phlegographa lepreurii</i>	Graphidoideae	Graphideae	Brazil, Cáceres sn (F)	JN127363	JN127365	—	—
<i>Platygramme caestoprutinos</i>	Graphidoideae	Graphideae	Mexico, Lumbsch 19636b (F); USA, Common 9084F (F)	JX421286	JX421611	KF875465	—

(continued)

Table 1. (Continued)

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Platygramme impudica</i>	Graphidoideae	Graphideae	Philippines, Rivas Plata 1021C (F); Thailand, Kalb 38818 (Herb. Kalb)	JX421288	JX421612	–	JX420926
<i>Platygramme praestans</i>	Graphidoideae	Graphideae	USA, Lücking 9129 (F)	JX421291	–	KF875466	–
<i>Platythecium dimorphodes</i>	Graphidoideae	Graphideae	USA, Mercado F31 (F)	KF875554	–	KF875467	KF875512
<i>Pseudochapsa dilatata</i>	Graphidoideae	Thelotremataeae	Venezuela, Lücking 26143 (F)	JX420982	JX421447	–	JX420949
<i>Pseudochapsa esslingerii</i>	Graphidoideae	Thelotremataeae	Peru, Rivas Plata 809A (F)	JX420986	JX465294	KF875468	JX465321
<i>Pseudochapsa phycetoides</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19100f (F)	EU075569	–	KC020291	JX465325
<i>Pseudoramonia richiae</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19977a (F)	KF875555	KF875534	–	–
<i>Pseudotopeliopsis laceratula</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19139sa (F)	JX420988	JX421448	–	JX420831
<i>Pycnotrema pycnoporellum</i>	Fissurinoideae	Thelotremataeae	USA, Lücking 26546 (F)	JX421295	JX421615	KF875469	KF875513
<i>Redingeria glaucoglyphica</i>	Graphidoideae	Ocellulariaeae	Peru, Rivas Plata 0810extra (F)	JX421296	JX421618	–	–
<i>Redonographa chilensis</i>	Graphidoideae	Ocellulariaeae	Chile, Tehler 8407 (F)	JX890304	JX890301	–	JX890306
<i>Redonographa saxiseda</i>	Redonographoideae	Redonographoideae	Chile, Tehler 8370 (F)	–	JX890300	–	JX890305
<i>Reimnitzia santensis</i>	Graphidoideae	Ocellulariaeae	El Salvador, Lücking 28015 (F)	HQ639622	HQ639664	–	JF828952
<i>Rhabdodiscus crassus</i>	Graphidoideae	Ocellulariaeae	Australia, Lumbsch 19108f (F)	EU075594	EU075640	–	–
<i>Rhabdodiscus granulatus</i>	Graphidoideae	Ocellulariaeae	Philippines, Rivas Plata 1054A (F)	JX421298	–	KF875471	–
<i>Rhabdodiscus isidiferus</i>	Graphidoideae	Ocellulariaeae	Venezuela, Lücking 32212 (F)	JX421300	JX421621	–	JX420903
<i>Sarcographa difformis</i>	Graphidoideae	Graphideae	Fiji, Lumbsch 20501p (F)	JX421313	JX421625	–	–
<i>Sarcographa labyrinthica</i>	Graphidoideae	Graphideae	Australia, Kalb 33920 (Herb. Kalb)	DQ431967	DQ431931	–	–
<i>Sarcographa fenicis</i>	Graphidoideae	Graphideae	USA, Lücking 26559 (F)	JF828969	–	–	JF828953
<i>Sarcographa labyrinthica</i>	Graphidoideae	Graphideae	Costa Rica, Lücking 16229g (F)	DQ431981	DQ431942	–	–
<i>Sarcographa ramificans</i>	Graphidoideae	Graphideae	USA, Common 9072 (F)	JX421323	–	KF875473	–
<i>Sarcographa tricola</i>	Graphidoideae	Graphideae	Australia, Kalb 33913 (Herb. Kalb)	DQ431972	DQ431934	–	–
<i>Sarcographina glyphiza</i>	Graphidoideae	Graphideae	Ecuador, Tehler 8796 (F)	EU544933	EU544932	–	–
<i>Schizothoron tenue</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19983f (F)	JX421326	JX421631	KF875474	–
<i>Schizotrema aff. zebrinum</i>	Graphidoideae	Thelotremataeae	Australia, Mangold 24c (F)	JX421328	FJ708492	–	–
<i>Schizotrema schizoloma</i>	Graphidoideae	Thelotremataeae	Australia, Mangold 19zo (F)	EU075608	EU075652	–	–
<i>Schizotrema zebrinum</i>	Graphidoideae	Ocellulariaeae	Peru, Rivas Plata 807D (F)	JX421331	JX421634	KF875475	–
<i>Stegobolus anamorphus</i>	Graphidoideae	Ocellulariaeae	Venezuela, Lücking 32207 (F)	–	JX421639	–	JX420917
<i>Stegobolus radicans</i>	Graphidoideae	Ocellulariaeae	Venezuela, Lücking 32202 (F)	–	JX421636	–	JX420913
<i>Stegobolus subwrightii</i>	Graphidoideae	Ocellulariaeae	Philippines, Rivas Plata 2083 (F)	JX644422	HQ639666	KF875476	–
<i>Thecaria montagnei</i>	Graphidoideae	Graphideae	USA, Lücking 26567 (F)	HQ639617	HQ639667	–	–
<i>Thecaria quassitcola</i>	Graphidoideae	Graphideae	India, Lumbsch 19730i (F)	JX421344	JX421642	KF875478	JX420851
<i>Thelotrema adjectum</i>	Graphidoideae	Thelotremataeae	Australia, Mangold 27v (F)	EU075606	FJ708493	–	–
<i>Thelotrema crespoe</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19127v (F)	EU075599	JX421649	KF875479	JX420827
<i>Thelotrema diplostrema</i>	Graphidoideae	Thelotremataeae	Australia, Mangold 3j, 1d (F)	JX421357	JX421650	KF875480	JX420834
<i>Thelotrema fuscobuile</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19151k (F)	EU075600	EU075653	–	–
<i>Thelotrema gallowsyanum</i>	Graphidoideae	Thelotremataeae	Australia, Mangold 29t (F)	JX421350	JX421646	KF875481	JX420844
<i>Thelotrema inspersoprinaceum</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19100yB (F)	JX421360	–	–	JX420826
<i>Thelotrema jugale</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19997c (F)	JX421369	JX421654	KF875482	JX420867
<i>Thelotrema lepadinum</i>	Graphidoideae	Thelotremataeae	Scotland, Lumbsch 20100c (F)	JX465291	JX465313	KF875483	JX420890
<i>Thelotrema macrosporium</i>	Graphidoideae	Thelotremataeae	USA, Lendemer 6389 (F)	EU075602	EU075645	–	JX465340
<i>Thelotrema monosporoides</i>	Graphidoideae	Thelotremataeae	Australia, Lumbsch 19158w (F)	EU075601	EU075646	–	–
<i>Thelotrema monosporum</i>	Graphidoideae	Thelotremataeae					

(continued)

Table 1. (Continued)

Species	Subfamily	Tribe	Collection data	mtSSU	nuLSU	RPB1	RPB2
<i>Thelotrema nurelium</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19123j (F)	JX421376	JX421660	–	JX465341
<i>Thelotrema pachysporum</i>	Graphidoideae	Thelotremateae	Tanzania, Frisch 99Tz1051 (M); Australia, Kalb 34021 (Herb. Kalb)	DQ384918	DQ431925	–	DQ431925
<i>Thelotrema porinaceum</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19108d (F)	JX421384	AY605084	KF875485	JF828956
<i>Thelotrema porinoides</i>	Graphidoideae	Thelotremateae	Fiji, Lumbsch 20532a (F)	JX421397	JX465315	KF875486	JX465347
<i>Thelotrema subtile</i>	Graphidoideae	Thelotremateae	Japan, Ohmura 7769 (F)	JX421403	JX421668	–	JX420932
<i>Thelotrema suecicum</i>	Graphidoideae	Thelotremateae	Norway, Gaarder 4366 (F)	JX421407	JX421672	KF875487	JX420832
<i>Thelotrema verruciferum</i>	Graphidoideae	Thelotremateae	Thailand, Lumbsch 19751f (F)	JX421408	JX421673	–	JX420854
<i>Topeliopsis acutispora</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19175d (F)	KF875557	JX421675	KF875488	KF875515
<i>Topeliopsis decorticans</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19984b (F)	KF875558	JX421676	–	KF875516
<i>Topeliopsis muscigena</i>	Graphidoideae	Thelotremateae	Australia, Mangold 5d (F)	EU075611	EU075656	KF875489	JF828957
<i>Topeliopsis subdenticulata</i>	Graphidoideae	Thelotremateae	New Zealand, Knight 59967 (OTA)	KF875559	EU126656	KF875490	KF875517
<i>Wirthiotrema desquamans</i>	Graphidoideae	Thelotremateae	Australia, Lumbsch 19167v (F)	EU075580	EU075628	–	–
<i>Wirthiotrema glaucopallens</i>	Graphidoideae	Thelotremateae	Australia, Mangold 34s (F)	JX421417	KF875536	KF875491	KF875518
<i>Wirthiotrema trypaneoides</i>	Graphidoideae	Thelotremateae	Venezuela, Lücking 32003 (F)	JX421422	JX421681	–	JX420916
<i>Xalocoa ocellata</i>	Graphidoideae	Thelotremateae	Greece, Schmitt, s.n. (F)	KF688505	AY605077	DQ366252	DQ366253

Table 2. Character states of each trait analyzed in the current study and the average number of transformations in discrete morphological and chemical characters across a posterior sample of trees of lichenized fungi Graphidaceae under maximum parsimony with 95% equal-tail credible interval in parentheses.

Character	Parsimony Step	State and code
Habitat	11 (9-13)	0 = tropical 1 = subtropical 2 = non-tropical
Photobiont	2(2)	0 = trentepohlioid 1 = chlorococcoid
Cortex	22 (15-29)	0 = corticate 1 = ecorticate
Chemistry	56(28-87)	0 = nil 1 = depsidones (1'-6'-OH) 2 = depsidones (1'-COOH-6-ME) 3 = depsidones (6'-COOH) 4 = depsides
Ascoma persistence	2(2)	0 = persistent 1 = mazaedioid
Ascoma shape	14(11-17)	0 = apothecioid 1 = lirellate
Ascoma aggregation	10(10)	0 = solitary 1 = pseudostromatic
Columella	19(13-25)	0 = absent 1 = present
Lateral paraphyses	9 (8-10)	0 = absent 1 = present
Ascospore amyloidity	22 (16-28)	0 = non-amyloid 1 = amyloid 2 = hemiamyloid

(2-parameter) model of character evolution. In order to include topological uncertainty into the ancestral state reconstruction, we used the 'Trace character over trees' method of Mesquite (Maddison & Maddison, 2011). One thousand trees were randomly sampled from the post-burning of the Bayesian sampling (described above) of the concatenated dataset using the program RT (<http://www.lutzonilab.net/downloads/>), and Mesquite displayed a summary for the probability for each node and each character, indicating the probability for the different states, and also taking into account ambiguous reconstructions and the percentage of Bayesian trees in which the given node was present (Table S2, see supplemental material online).

In contrast to ML, maximum parsimony (MP) does not take into account branch lengths when reconstructing ancestral states. The reconstructions were performed over the same 1000 randomly sampled trees as in the ML analysis. We used Mesquite 2.75 (Maddison & Maddison, 2011) to carry out both ML and MP reconstructions for the character datasets.

Character state transformations

We used MP to estimate the number of character state transformations over the tree using Mesquite (Maddison & Maddison, 2011). Parsimony potentially underestimates the true amount of changes in a character over a tree (Huelsenbeck & Lander, 2003) but it gives the minimum amount of changes. To test for phylogenetic signals of the characters studied, we used two different approaches. First, we employed a randomization test (Archie, 1989) in Mesquite to calculate the number of parsimony steps from 999 randomizations of character states on the optimal ML tree. The mean number of parsimony steps and standard deviation were calculated. Then the numbers from the randomization and the observed number of parsimony steps were used to calculate the probability that the observed number of parsimony steps is higher or equal than expected from the randomization. Second, we used the fit-Discrete program in the R package ‘geiger’ (Yang, 2006) to calculate Pagel’s λ value (Pagel, 1999). For this, the likelihood values of the tree with the actual data were calculated and a tree transformed to have no phylogenetic signal ($\lambda = 0$). High phylogenetic signal of a character is indicated by $\lambda = 1$. Significant departure from lack of phylogenetic signal was calculated using a likelihood ratio test.

Results

Phylogenetic analysis

The aligned 4-gene matrix contained 3274 unambiguously aligned nucleotide positions (945 in nuLSU, 836 in mtSSU, 607 in *RPB1* and 886 in *RPB2*), with a total of 1009 constant characters. Topologies of single-locus analyses did not show conflict and hence combined analyses were performed. Since the topologies of the ML and B/MCMC analyses did not show any supported conflict, only the phylogram obtained from the ML analysis is shown with branches in bold that received strong support in Bayesian analyses (i.e. PP above 0.95 and ML bootstrap values equal or above 70% indicated at branches) (Figs S1–S3, see supplemental material online). The topology obtained from the 4-gene dataset is similar to previously published phylogenies (Lücking *et al.*, 2013; Rivas Plata *et al.*, 2013). All subfamilies, tribes and genera as previously delimited were recovered (Fig. 1).

Ancestral character state reconstructions

The characters studied and their states are listed in Table 2. Results of the ancestral character state reconstructions are listed in Tables S2–S4 (see supplemental material online), and summarized in Figs 2–7 and Figs S4–S7 (see supplemental material online). The node numbers in the

supplementary tables correspond to the clade numbers given in Fig. 1 Tables S3 and S4 (see supplemental material online), Figs 2–7 and Figs S4–S7 (see supplemental material online) only specify characters for which both MP and ML reconstructions gave strong support for the same character state.

In the ancestral character reconstruction for the character ‘habitat’ (Fig. 2), most ancestral nodes were reconstructed as being tropical, with the exception of *Redonographa*, which was reconstructed as subtropical, and the ancestral nodes of the genera *Diploschistes*, *Schizotrema* and *Topeliopsis*, which were reconstructed as being non-tropical. The reconstructions estimated a tropical habitat as ancestral for Graphidaceae and subfamily Graphidoideae. All reconstruction methods estimated a trentepohlioid photobiont as ancestral state for all nodes, with the exception of the base of the genus *Diploschistes* (Fig. S4, see supplemental material online), for which a chlorococcoid photobiont was reconstructed.

Regarding the presence or absence of cortex, the ancestral character state reconstruction for the basal nodes in Graphidaceae, with the exception of node 1 (corticated) did not yield conclusive results (Fig. 3). Within tribes Graphideae and Ocellularieae, most nodes were reconstructed as being corticate. In contrast, in tribe Thelotremaeae, most nodes were reconstructed as being ecorticate, including the basal nodes of the genera *Chapsa*, *Diploschistes*, *Leucodecton*, *Pseudochapsa* and *Thelotrema*. The ancestral state for the genera *Acanthotrema*, *Chroodiscus* and the clade including *Gintarasia* and *Pseudoramonia* were reconstructed as corticate.

Absence of secondary metabolites was reconstructed for the basal nodes in subfamily Fissurinoideae and tribe Graphideae and the base of *Acanthotrema* and *Topeliopsis* (Fig. 4). Due to the variability of presence of secondary metabolites among species, there was a higher incidence of inconclusive results compared with other characters. However, presence of (1'-6'-OH) depsidones, e.g. stictic acid and related substances, was reconstructed for the base of *Chroodiscus*, *Leucodecton*, *Phaeographis*, *Pseudochapsa*, *Redonographa*, *Wirthiotrema* and the clades including *Asteristion*, *Austrotrema*, *Nadvornikia* and *Myrtiotrema peninsulae*, as well as this group plus *Wirthiotrema*, corresponding to tribe Thelotremateae. The presence of (6'-COOH) depsidones, mainly psoromic acid, was reconstructed as ancestral trait for the base of the genera *Compositrema*, *Myrtiotrema*, *Stegobolus* and the genus *Rhabdodiscus*. For all examined nodes in *Ocellularia* s. lat. and s. str., presence of (1'-COOH-6'-ME) depsidones, such as protocetraric acid, was reconstructed as the ancestral state.

The ancestral character state for ascoma persistence for all nodes studied was reconstructed as non-mazaediate with persistent hymenium (Fig. S5, see supplemental material online), strongly suggesting that the mazaediate

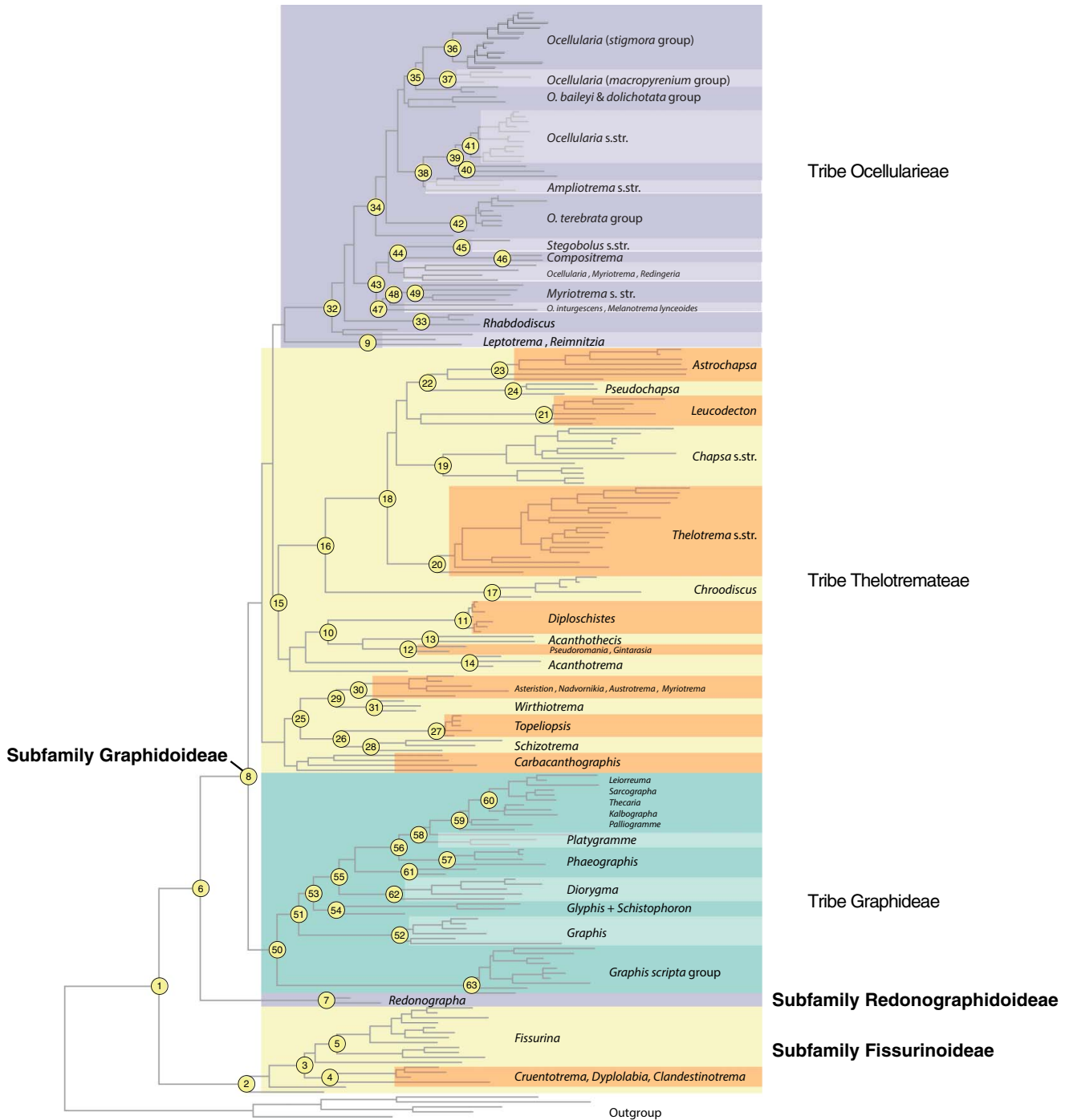
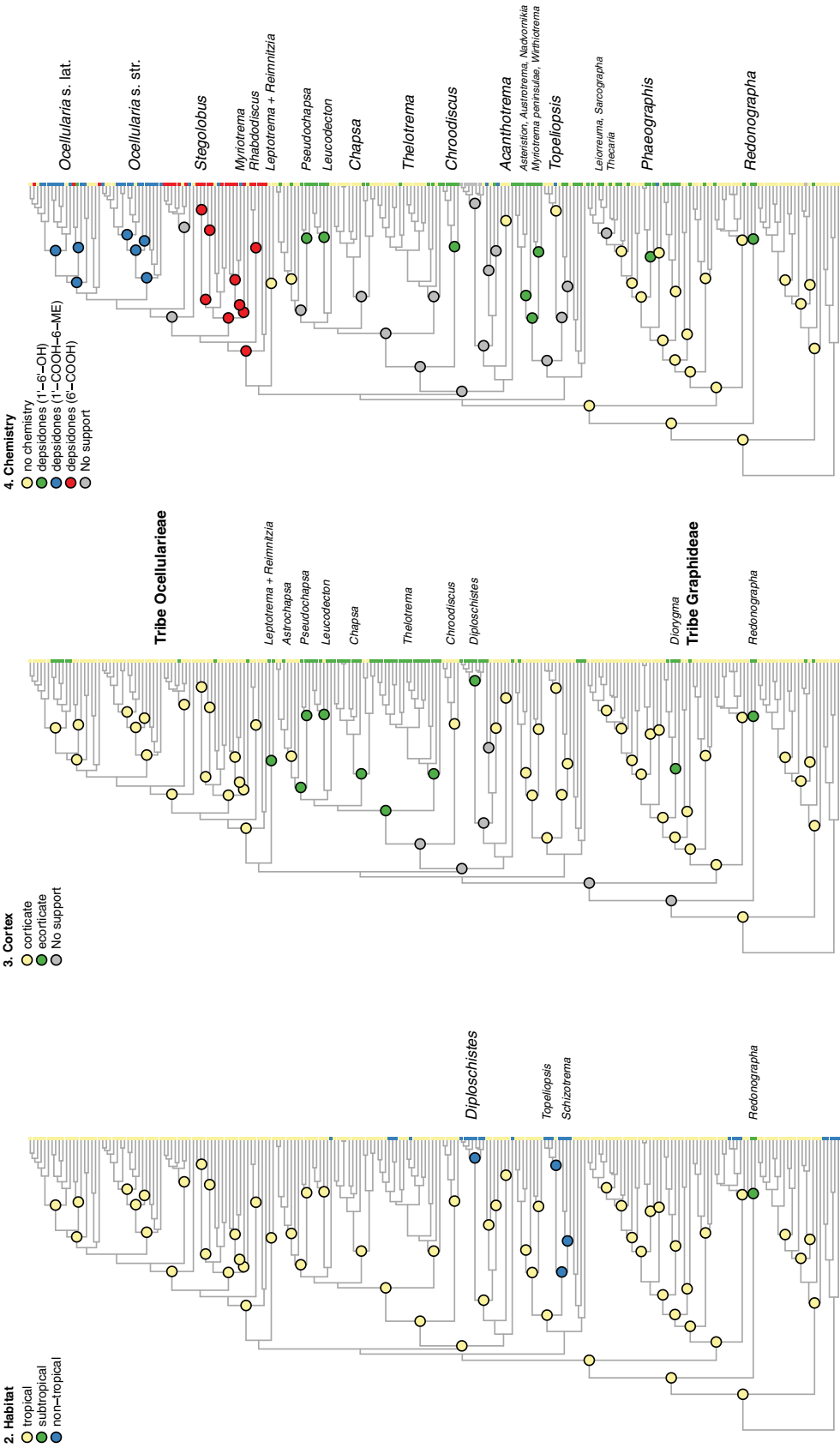


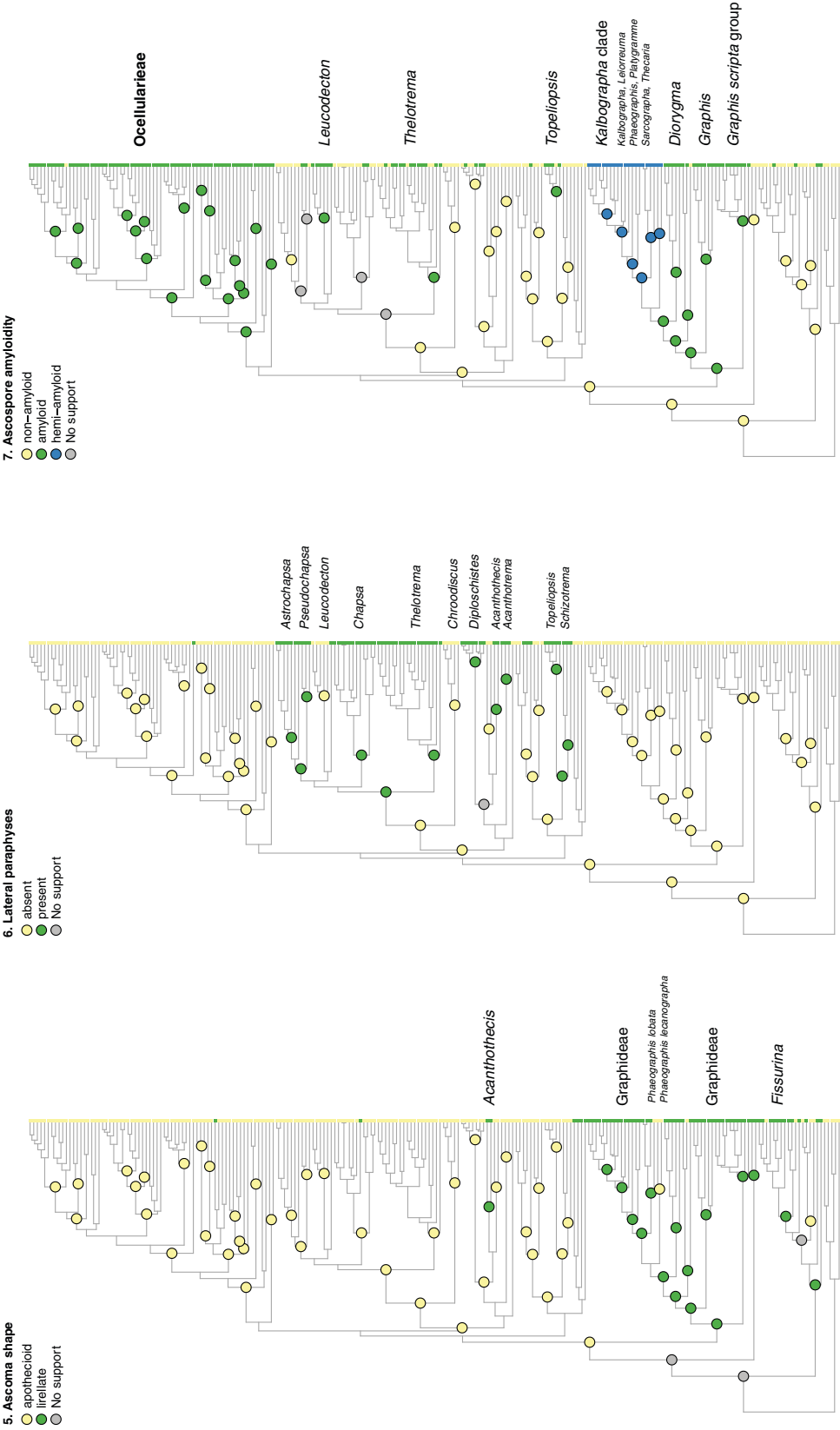
Fig. 1. Cartoon tree showing relationships of major clades in Graphidaceae. Numbers at nodes indicate well-supported nodes for which ancestral character reconstructions were performed as described in the text. Subfamily and tribe names are indicated. Tribes Graphideae, Thelotremateae and Ocellarieae are part of subfamily Graphidoideae.

ascomata found in the genera *Nadvornikia* and *Schistophoron* originated independently from ascomata with persistent hymenium. Ascoma shape for the basal node of the family and the clade including the two subfamilies Graphidoideae and Redonographidoideae was not reconstructed with certainty, whereas the base of Graphidoideae was

reconstructed as apothecioid (Fig. 5). Within Graphidoideae, most nodes in tribes Ocellarieae and Thelotremateae were reconstructed as apothecioid, except for *Acanthothecis*. In contrast, most nodes within tribe Graphideae were reconstructed as lirellate, except for the *Phaeographis lobata* + *P. spondaica* clade.



Figs. 2–4. Ancestral state reconstruction at the major nodes for (2) habitat, (3) cortex and (4) secondary chemistry of lichenized fungi family Graphidaceae. Node colours represent the reconstructed states (see legend). Inconclusive reconstructions are indicated in grey circles.



Figs. 5–7. Ancestral state reconstruction at the major nodes for (5) shape of ascoma, (6) the presence of lateral paraphyses and (7) ascospore amyloidity of lichenized fungi family Graphidaceae. Node colours represent the reconstructed states (see legend). Inconclusive reconstructions are indicated in grey circles.

Almost all reconstructions suggested solitary ascomata as ancestral state (Suppl. Fig. S6). Only for the base of *Compositrema* (tribe Ocellularieae) the analysis reconstructed pseudostromatic ascomata as the ancestral character state. For all nodes outside tribe Ocellularieae, the analyses reconstructed absence of a columella as ancestral states (Fig. S7, see supplemental material online). Within Ocellularieae, the bases of the *Macropyrenium* and *Stigmatogora* groups, *Ocellularia* s. str. and related taxa, and *Stegobolus* were reconstructed as having a columella.

The ancestral character state reconstructions for lateral paraphyses showed these to be absent at numerous basal nodes, as well as all nodes in Fissuroinoideae, Ocellularieae and Graphideae, except for *Schizotrema* and *Topeliopsis* (Fig. 6). In addition, the analysis suggests absence of lateral paraphyses at certain nodes within tribe Thelotremateae, including the clades containing the genera *Chroodiscus*, *Gintarasia*, *Leucodecton* and *Pseudoramonina*. Presence of lateral paraphyses was reconstructed for the bases of the genera *Acanthotrema*, *Acanthothecis*, *Astrochapsa*, *Chapsa*, *Diploschistes*, *Pseudochapsa*, *Schizotrema*, *Thelotrema*, *Topeliopsis* and the clade including the genera *Astrochapsa*, *Pseudochapsa* and *Pseudotopeliopsis*. In general, species with a columella lack lateral paraphyses. The ancestral state of ascospore amyloidity was reconstructed as non-amyloid for the base of Graphidaceae (Fig. 7) and several basal nodes in the family, e.g. subfam. Graphioideae and Redonographoideae. Non-amyloidity was also reconstructed as ancestral state for the base of Thelotremateae, the genera *Acanthothecis*, *Acanthotrema*, *Astrochapsa*, *Chroodiscus*, *Diploschistes*, *Gintarasia* and *Pseudoramonina*. Ascospores were reconstructed as being amyloid for the base of the genera *Diorygma*, *Graphis*, the *Graphis scripta* group in Graphideae, all nodes in Ocellularieae and two nodes in Thelotremateae (*Leucodecton* and *Thelotrema*). Within *Phaeographis* s. lat., all nodes were reconstructed as hemi-amyloid.

Character state transformations

The minimal numbers of transformations under MP are shown in Table 2. The most conserved characters were photobiont, lateral paraphyses, ascoma aggregation and persistence, and habitat, whereas by far the fastest evolving was chemistry.

Direction of these changes varies among the characters (Table 3). A few characters were reconstructed to change unidirectionally, such as the switch from trentepohlioid to chlorococcoid photobiont, from persistent to mazaediate ascomata, and solitary to pseudostromatic ascomata. In contrast, transformations from apothecioid to lirellate and vice versa were reconstructed as being almost equally common (53% vs. 46%).

We also tested whether the observed number of transformations was significantly different from expectation based on randomized data. Table 4 summarizes the results and show that for all 10 characters, both the randomization test of parsimony steps and Pagel's λ suggest high phylogenetic signal of the characters, except for ascoma persistence.

In addition, the nature of transformations was found to be highly phylogenetically structured even for the fastest evolving character, secondary chemistry. Transitions between no substances and (1' 6' OH) depsidones and vice versa were almost entirely restricted to tribes Graphideae and Thelotremateae, and the subfamily Redonographoideae, whereas transitions between no substances and (1' COOH 6' ME) and (6' COOH) and vice versa were restricted to tribe Ocellularieae in this dataset.

Discussion

Our phylogenetic study is based on a broad taxon sampling of Graphidaceae including the entire range of morphological and chemical diversity in three of the four subfamilies currently accepted, even if the species studied here represent only slightly more than 10% of the total species diversity in this lineage. The overall phylogeny is congruent with previously published analyses which are discussed elsewhere in detail (Rivas Plata *et al.*, 2013). Hence, we anticipate that including a larger number of species will not change the overall structure of the results, with the exception of possible new lineages to be discovered. Rather, we project that with increased taxon and gene sampling, higher resolution and backbone support will resolve ancestral character reconstruction for most of the presently unresolved nodes. In the current study the subfamily Gomphilloideae was not included and this might potentially influence the results on character evolution, especially the basal nodes of Graphidaceae and hence we have refrained from discussing the character states obtained for node 1 at the base of the family in detail.

We found support for the ancestor of subfamily Graphioideae to be a tropical species with a trentepohlioid photobiont, apothecioid, solitary ascomata with persistent hymenium lacking a columella and lateral paraphyses, and having non-amyloid ascospores. Among extant lineages, the taxon that comes closest to this circumscription is *Acanthotrema*. This genus indeed appears to be the relict of an ancient lineage going back almost 100 million years and usually is positioned close to the base of the subfamily (Lücking *et al.* 2013).

Reconstructions of the ancestral character state of the cortex and chemistry did not yield conclusive results for the ancestor of the subfamily. Regarding ecology, our results suggest that subtropical and non-tropical

Table 3. Proportion of changes between character states under maximum parsimony summing to 1 for ten studied characters in lichenized fungi family Graphidaceae. The second line contains maximum a posteriori value of number of transitions and 95% equal-tail credible interval in the parenthesis.

Character 1 Habitat; 0 = tropical, 1 = subtropical, 2 = non-tropical					
B	0	1	2		
0	–	0.09 1(1)	0.73 8(7-9)		
1	0.00 0(0)	–	0.00 0(0)		
2	0.18 2(1-3)	0.00 0(0)	–		
Character 2 Photobiont; 0 = trentepohlioid, 1 = chlorococcoid					
	0	1			
0	–	1.00 2(2)			
1	0.00 0(0)	–			
Character 3 Cortex; 0 = corticate, 1 = ecorticate					
	0	1			
0	–	0.68 15(11-18)			
1	0.32 7(4-11)	–			
Character 4 Chemistry; 0 = no substances, 1 = depsidones (1'-6'-OH), 2 = depsidones (1'-COOH-6'-ME), 3 = depsidones (6'-COOH), 4 = depsides					
	0	1	2	3	4
0	–	0.36 20(14-27)	0.09 5(3-8)	0.03 1.8(1-3)	0.04 2.3(1-3)
1	0.13 7.3(1-13)	–	0.00 0.19(0-1)	0.01 0.32(0-1)	0.00 0(0)
2	0.13 7(5-10)	0.02 1.3(0-2)	–	0.04 2.5(0-4)	0.00 0.1(0-1)
3	0.07 4(2-6)	0.01 0.34(0-1)	0.05 2.8(1-5)	–	0.00 0(0)
4	0.01 0.6(0-1)	0.00 0(0)	0.00 0.09(0-1)	0.00 0(0)	–
Character 5 Ascoma persistence; 0 = persistent, 1 = mazaediate					
	0	1			
0	–	1.00 2(2)			
1	0.00 0(0)	–			
Character 6 Ascoma shape; 0 = apothecioid, 1 = lirellate					
	0	1			
0	–	0.53 7.5(6-9)			
1	0.46 6.5(5-8)	–			
Character 7 Ascoma aggregation; 0 = solitary, 1 = pseudostromatic					
	0	1			
0	–	1.00 10(10)			
1	0.00 0(0)	–			
Character 8 Columella; 0 = absent, 1 = present					
	0	1			
0	–	0.63 12(9-15)			
1	0.36 7(4-10)	–			

(continued)

Character 9 Lateral paraphyses; 0 = absent, 1 = present

	0	1
0	–	0.83 7.5(7-8)
1	0.16 1.5(1-2)	–

Character 10 Ascospores amyloidity; 0 = non-amyloid, 1 = amyloid, 2 = hemiamyloid

	0	1	2
0	–	0.58 12.9(10-16)	0.00 0(0)
1	0.36 8.1(5-11)	–	0.04 1(1)
2	0.00 0(0)	0.00 0(0)	–

species in this lineage are derived from tropical taxa. However, none of these lineages re-adapted to strictly tropical rain forest vegetation, where the majority of Graphidaceae occurs. This is consistent with a previous study with a smaller taxon sampling (Lücking *et al.*, 2013).

A chlorococcoid photobiont is restricted to the non-tropical genera *Diploschistes* and *Xalocoa* (formerly *D. ocellatus*; Kraichak *et al.*, 2014). Within those clades, there was no transformation back to trentepohlioid photobionts, which are the dominant type of photosynthetic partners in this family, including other extratropical groups within the family such as *Schizotrema* and *Tope-liopsis* (Nakano, 1988; Nelsen *et al.*, 2011). Species of *Diploschistes* differ from other Graphidaceae in their peculiar ecology, being most common and diverse in subtropical, semi-arid regions in both hemispheres and growing mostly on soil and rock substrata. Other, unrelated lichenized fungi sharing these habitats almost

exclusively have chlorococcoid photobionts. Since *Diploschistes* species do not produce vegetative propagules but exclusively propagate by means of ascospores, new thalli can only be formed through resymbiosis with the appropriate photobiont, and it is highly unlikely in these habitats to encounter *Trentepohlia* algae. This is recognized by some species of *Diploschistes* being juvenile parasites on other lichen species (Hawksworth, 1982; Friedl, 1987; Friedl & Gärtner, 1988). We therefore conclude that the switch to a chlorococcoid photobiont enabled *Diploschistes* to diversify in these unusual habitats for Graphidaceae and with no reversal to a trentepohlioid photobiont in this lineage. Notably, subfamily Gomphilloideae, which was not included in this study, also is characterized by a chlorococcoid photobiont. However, this subfamily is predominantly tropical and mostly foliicolous, sharing niches with other lichens that do have trentepohlioid photobionts, so the advantage of the photobiont in this lineage is unclear.

Table 4: Observed numbers of parsimony steps of transitions and phylogenetic signals of ten studied characters in the lichenized fungal family Graphidaceae from randomization tests (Archie 1989) and Pagel's Lambda (1999). Mean_{random} and SD_{random} refer to the mean and standard deviation of the number of parsimony steps from 999 randomizations of character states. P_{random} is the probability that the observed number is higher than expected from the randomization. Thus, a low P_{random} suggests high phylogenetic signal. Lambda = 1 indicates high phylogenetic signal, and P_{LTR} is the result from the Likelihood Ratio Test when compared the likelihoods of data against the tree transformed to lambda = 0 (no signal). Therefore, a low P_{LTR} indicates a significant deviation from the model with no signal.

Character	Parsimony steps				Pagel's Lambda	
	Observed	Mean _{random}	SD _{random}	P_{random}	Lambda	P_{LTR}
Habitat	11	29.64	1.29	0.001	1	<0.001
Photobiont	2	7.93	0.31	0.001	1	<0.001
Cortex	22	59.84	3.03	0.001	1	<0.001
Chemistry	56	106.5	3.76	0.001	0.989	<0.001
Ascoma persistence	2	1.99	0.08	0.008	0	1.000
Ascoma shape	14	55.75	3.01	0.001	0.989	<0.001
Ascoma aggregation	10	14.71	0.57	0.001	0.974	0.004
Columella	19	38.97	1.89	0.001	0.825	<0.001
Lateral paraphyses	9	56.67	3.02	0.001	1	<0.001
Ascospore amyloidity	22	82.23	4.04	0.001	1	<0.001

Our study suggests that a cortex was gained twice as often as lost, and that this character has switched repeatedly over the evolution of the family (15–29 times). As discussed elsewhere (Lakatos *et al.*, 2006; Rivas Plata & Lumbsch, 2011), a dense cortex could be an adaptation to avoid oversaturation with water in understory crusts (the cortex is water-repellent) or to provide protection against high light levels and damaging UV radiation, as well as against herbivores and fungivores. However, ecorticate thalli might also be water-repellent, but respond to hydration differently (Lakatos *et al.* 2006). Given these multiple functions of the cortex and the fact that closely related lineages may show different habitat preferences, it is not surprising that a cortex has been gained or lost several times independently. Despite the fact that we coded secondary metabolites as substance classes (Huneck & Yoshimura, 1996), rather than individual substances, we reconstructed a high number of transformations. Secondary metabolites are well-known in lichenized fungi, with over 1000 substances recorded (Huneck & Yoshimura, 1996; Lumbsch, 1998; Nash, 2008) and their potential ecological importance, such as sun screens, protection against herbivores and control of carbon diffusion, has been discussed in a number of studies (Lawrey, 1983; Goljuch & Lawrey, 1988; Emmerich *et al.*, 1993; Giez *et al.*, 1994; Rikkinen, 1995; Lange *et al.*, 1997; Nybakken *et al.*, 2004, 2010; Gauslaa, 2005; McEvoy *et al.*, 2007; Solhaug *et al.*, 2009). Our study showed that the majority of the transformations (86%) are between having no substance and producing a given substance class, while transformations between different substance classes are much less common. In addition, substance classes appear to be largely conserved within major clades. Thus, basal nodes of tribe Ocellularieae (e.g. *Rhabdodiscus*, *Myriotrema*, *Stegobolus*) are reconstructed as having (6'-COOH) depsidones, i.e. psoromic acid and relatives, while the majority of clades within *Ocellularia* are reconstructed as having (1'-COOH-6'-ME) depsidones, i.e. protocetraric acid and relatives. The high level of conservation among major clades suggests that transformations between substance classes are the result of constrained evolution. The pattern of occurrence and absence of secondary metabolites within each clade suggests that there is no strong selective advantage in having medullary secondary substances, since species with and without substances often grow side by side in the same conditions, e.g. in the genera *Graphis* and *Ocellularia*.

Our analyses suggest that the transformation of ascomata with persistent hymenium to mazaediate ascomata happened at least twice in Graphidaceae and that there was no reversal from this trait back to persistent ascomata. Mazaediate ascomata are characteristic for the genera *Nadvornikia* and *Schistophoron* (Lumbsch *et al.*, 2004; Tehler *et al.*, 2009). Both genera have few species, with rather deep phylogenetic relationships, with lack of

evidence for radiation after the transformation, contrary to other mazaediate groups such as calicioid species in Physciaceae, which are very species-rich. Mazaedia are considered an adaptation to wind dispersal of ascospores, and species with such ascomata often grow in open microhabitats and particularly well on old trees with weathered bark or on wood. This is also the case with species of *Nadvornikia* and *Schistophoron*, hence representing a case of convergent evolution with unrelated lineages also producing mazaedia, such as *Heterocyphellium* and *Tylophoron* (Arthoniales), *Mazaediothecium* and *Pyrgillus* (Pyrenulales), and many of the species in Caliciales.

Ascoma shape was traditionally used to distinguish the families Graphidaceae and Thelotremaaceae, now included in a single family, as well as groups of genera within Graphidaceae. Our study confirms previous results demonstrating that ascoma shape does not constitute a synapomorphic trait characterizing monophyletic groups within Graphidaceae (Staiger *et al.*, 2006; Mangold *et al.*, 2008b; Rivas Plata *et al.*, 2013). Transformations from apothecioid to lirellate ascomata and vice versa are almost equally probable in the family. Despite the number of transformations in this character, most nodes – except the majority of basal nodes – were reconstructed with strong support as being either apothecioid or lirellate. While the character is variable at a deeper phylogenetic level, it is mostly invariable within genera and tribes (Rivas Plata *et al.*, 2012a). This suggests a high level of evolutionary plasticity at the more basal nodes but subsequent stabilization at nodes leading to major lineages. This is consistent with the observation that this character is more variable in smaller clades, such as *Acanthothecis*, which includes species with both types of ascomata (perfectly round and strongly lirellate ascomata). The reason for the observed variation and its relatively high level of conservation is unknown, but likely this character is somehow involved in protecting the hymenium and ascospores from fungivores or exposure to UV radiation. Since most species reproduce through ascospores, reproductive success depends in part on the number of ascospores produced, which is in turn a function of the hymenium surface. In lineages with rounded ascomata, the hymenium has to expand radially in order to produce a large number of ascospores, exposing a large surface area to the environment and thus making it more vulnerable. To still protect the hymenium, one solution is to maintain the ascomata relatively closed, which is observed in many lineages in tribe Ocellularieae and in the genera *Thelotrema* and *Leucodecton* (Thelotremaaceae). Another solution is to cover the hymenium with dead hyphal material and crystals for protection, as found in species with chroodiscoid ascomata in tribe Thelotremaaceae. Another alternative is to maintain the ascomata completely closed, in which case a lirellate shape is of advantage since the ascoma can grow without the necessity to expose the hymenium.

Although we found evidence for at least 10 transformations in ascoma aggregation, we found no evidence for transformations from pseudostromatic to solitary ascomata. This is consistent with results in other groups that in part produce pseudostromatic ascomata, such as Arthoniales (Ertz *et al.*, 2009).

The higher number of transformations in gaining a columella and lateral paraphyses in comparison to losing them can be interpreted as evidence for an adaptive value of these structures. A columella is a sterile tissue in ascomata that can sometimes cover large parts of the ascomata, potentially preventing fungivores from feeding on hymenial structures (Lücking & Bernecker-Lücking, 2000; Rivas Plata & Lumbsch, 2011). The adaptive value of lateral paraphyses, however, is currently not understood. The character might represent a conserved relict of the ascoma ontogeny, rather than an ecological adaptation, since the lateral paraphyses are ontogenetically a part of the generative hymenium (Henssen, 1976, 1995). It appears that in lineages forming lateral paraphyses, the hymenium originally develops throughout most of the cavity, and upon maturity and opening of the ascoma, the lateral portions of the hymenium that originally developed in the upper parts of the cavity remain vertical and sterile.

Ascospore amyloidity showed a high number of transformations (16–28), especially gains and losses of amyloidity. Similar to what we observed for secondary chemistry, in spite of the high number of transformations, this character is usually conserved at the generic and often also the tribe level, with the notable exception of tribe Thelotremateae (and subfamily Fissurinoideae). Amyloid ascospores are also found in other groups of lichen-forming and non-lichenized ascomycetes, but the ecological importance of this character is not known.

In summary, it appears that while there are a large number of transitions between phenotype character states in Graphidaceae, more than any other crustose lichen group with the exception of Arthoniales, these transitions are highly structured phylogenetically and also provide evidence to formulate hypotheses on ecological functions versus evolutionary constraints. Our results are consistent with previous studies on character evolution in the family focusing on striking cases of parallel evolution and evolutionary plasticity in closely related lineages (Rivas Plata & Lumbsch, 2011). However, our extended sampling of loci and taxa improved the confidence in the phylogenetic estimate (Rivas Plata *et al.*, 2013) and allowed for a more solid statistical approach, also demonstrating an even higher number of character transformations than previously assumed. This study hence provides an ideal base for addressing the question whether and how specific traits are correlated with ecological conditions and how these traits go along with diversification, in order to test hypotheses of adaptive radiations.

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One hundred and seventy-five new species of Graphidaceae: closing the gap or a drop in the bucket?

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Abstract

Recent studies of the global diversity of the lichenized fungal family Graphidaceae suggest that there are a large number of species remaining to be discovered. No less than 640 species have been described since 2002, including 175 new species introduced in a collaborative global effort in a single issue in this journal. These findings suggest that the largest family of tropical crustose lichens may have an even higher number of species than Parmeliaceae. To estimate whether

the discovery of 175 new species is a significant step forward in cataloguing extant diversity in this family, we employed a parametric method to predict global species richness of Graphidaceae using a GIS-based grid map approach. The model employs linear regression between observed species richness and sample score and vegetation composition per grid to predict individual grid species richness, and interpolation of species grid distributions to predict global species richness. We also applied a non-parametric species-area curve approach and non-parametric species richness estimators (Chao, Jackknife, Bootstrap) to compare the results from the different methods. Our approach resulted in a prediction of 4,330 species of Graphidaceae, including approximately 3,500 (sub-)tropical species in the core subfamilies Fissurinoideae, Graphidoideae, Redonographoideae, plus 125 species restricted to extratropical regions (outside the zone between 30° northern and 30° southern latitude) and 700 species in subfamily Gomphilloideae. Currently, nearly 2,500 species are known in the family, including species not yet formally described. Thus, our model suggests that even after describing 175 species in this issue and with another approximately 140 awaiting publication, the number of species still to be discovered and described is more than 1,800, and much work remains to be done to close this substantial gap. Based on our approach, we predict that most of this undiscovered diversity is to be found in Mexico, the northern Andean region, the eastern Amazon and central and southern Brazil, tropical West Africa, continental Southeast Asia, Indonesia, and Papua New Guinea.

Key words: Gomphillaceae, *Graphis*, *Ocellularia*, Thelotremataceae

Introduction

Graphidaceae is the largest family of tropical crustose lichens, after recent phylogenetic revisions including nearly 1,800 accepted species in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae, and another 400 in subfamily Gomphilloideae (Staiger 2002; Frisch *et al.* 2006a; Lücking 2008; Rivas Plata *et al.* 2012a, b, 2013; but see Hodgkinson 2012). While it is currently exceeded by Parmeliaceae, with more than 2,700 species (Kirk *et al.* 2008; Jaklitsch *et al.*, in prep.), as largest family of lichenized fungi overall, the amount of new species discoveries in tropical and even extratropical areas in recent years suggests that Graphidaceae might contain more species than Parmeliaceae.

Crucial to the recognition of the extraordinary diversity of Graphidaceae was the publication of two seminal monographic revisions that challenged previous classification concepts and provided a new approach to taxonomic inventories in the family (Staiger 2002; Frisch *et al.* 2006a). These works did not only provide revised keys to many of the newly recognized taxa, but stimulated the subsequent publication of further, regional to world-wide keys to large groups (Archer 2009; Lücking *et al.* 2009a; Mangold *et al.* 2009; Rivas Plata *et al.* 2010a; Gaswick & Lücking 2012), including the genera *Chapsa* Massalongo (1860: 257), *Graphis* Adanson (1763: 11), *Ocellularia* Meyer (1825: 327), and *Thelotrema* Acharius (1803: 130), providing tools to identify material that prior to these studies had been considered mostly unidentifiable. The impact of these studies is shown by the dramatic increase in publications on the family including new species discoveries, which between 2003 and 2013 amounted to no less than 140 papers by a diversity of authors, or 13 per year on average, whereas from 1950 to 2002, only 50 papers were published by few authors, or less than one per year on average. Of the nearly 1,800 species currently recognized in the three core subfamilies, more than a quarter were described or reinstated in the past ten years, compared to a more than two century long history of taxonomic contributions to the family, and further 175 are being introduced in the present issue in 18 different contributions, which represents a global effort by 30 authors from 14 countries (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Papong *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014; Weerakoon *et al.* 2014). At least 140 additional species are awaiting formal description. Adding these to the number of currently accepted species, Graphidaceae now comprises approximately 2,500 known species.

The question, however, arises whether the effort put forward in the past decade, including collaborative initiatives such as the present one, represents a substantial advance to closing the gap in the knowledge of diversity of the family Graphidaceae or whether this is merely the beginning of a trend that will hold for some time to come, adding a substantial amount of further new species not yet discovered. In other words: is the simultaneous description of 175 new species closing the gap or is it merely a drop in the bucket? How many species of Graphidaceae can we expect to exist globally?

In order to address this issue, we used a predictive model based on existing data to extrapolate the diversity of Graphidaceae at a global scale. A large number of approaches have been developed to predict species richness, with different objectives, including both the prediction of species yet unknown to science and the estimation of species richness in a given area without undertaking a complete inventory. These can be divided into roughly three categories: (1) ad-hoc methods that do not use a statistical approximation, (2) statistical methods that use non-biological, accessory data to predict species richness, and (3) statistical methods based on biological traits of the taxa in question.

Ad-hoc methods basically use taxonomic expertise in a given group to come up with predictive estimates (Gastón 1991; Colwell & Coddington 1994), but do not use any quantitative statistical approach. Predictions using non-biological traits include the analysis of publication tendencies over time (Dolphin & Quicke 2001; Costello *et al.* 2011; Joppa *et al.* 2011). These might give useful data, as shown for global lichen diversity by Sipman & Aptroot (2001), but depend on the assumption that there is an underlying correlation between overall species richness of a group in question and the rate of how species were described over time. This is not necessarily the case, since a spike in species descriptions can either indicate an exhaustive approach or the initiation of a large number of new discoveries. Thus, the number of species described over a given period of time is not a reliable predictor of true species richness, unless the pattern displays a more or less predictable behavior over time. The use of patterns of diversity correlated with taxonomic hierarchy (Mora *et al.* 2011) to predict global species richness is another approach that could be classified as non-biological in the sense that hierarchical classification of a species is not a biological trait *per se*, although biological traits do often correlate with lower taxonomic ranks such as genus. Hence, this approach has similar problems as the analysis of publication tendencies, especially since diversification rates can vary greatly between taxa of the same rank and, if using a phylogenetic approach, between sister lineages.

Parametric approaches use statistical analysis of biological traits that correlate with species richness, ranging from habitat preferences to substrate ecology, to phenotype characters. They usually have in common that they use a known data set to formulate a predictive model and then employ the model to extrapolate or interpolate towards unknown species richness in areas where the predictive parameters, such as vegetation diversity, are known. One strategy is the extrapolation from individual samples. An elegant approach to predicting global species richness in insects was put forward by the classic study of Erwin (1982). He analyzed the diversity of beetles collected through fogging from a select number of tropical trees and then categorized them as specialists (associated with a single tree species) or generalists (independent of tree species). Using the estimated number of tree species known from the tropics, he used simple extrapolation to arrive at a global predicted diversity of up to 30 million insect species. This approach was later adapted by Hawksworth (1991, 1997, 2001), using levels of host specificity of fungi, to predict at least 1.5 million fungal species.

Extrapolation from macroecological patterns is another strategy. If for a given area, species richness can be established as a function of habitat diversity and area size, species richness can be predicted for areas in which no complete species inventory has been undertaken but habitat diversity and area size are known. The model is then either direct, by computing values for species richness through correlation with environmental parameters (Radies *et al.* 2009), or indirect, by predicting species distribution ranges (MacDougall & Loo 2002; Edwards *et al.* 2006; Villaseñor *et al.* 2006; Velázquez *et al.* 2009) and subsequently calculating species richness based on these. For lichens, this approach has been proposed at a global scale focusing on tropical taxa by Lücking *et al.* (2009b). Rarefaction through interpolation is also a commonly used approach (Sanders 1968; Heck *et al.* 1975; Coleman 1981; Coleman *et al.* 1982; Foote 1992; Colwell & Coddington 1994; Magurran 2004), although it is sensitive to observed patterns of species abundances (Gotelli & Colwell 2001). In contrast, non-parametric methods use the frequency of rare species in a dataset to predict overall species richness, calculated by means of estimators such as Chao, Jackknife, and Bootstrap (Burnham & Overton 1978, 1979; Chao 1984, 1987; Smith & Van Belle 1984; Colwell & Coddington 1994; Chazdon *et al.* 1998; Hortal *et al.* 2006). The idea behind such methods is that species not yet sampled will always be rare species and hence their number can be predicted by analyzing the relative frequency of rare species already present in samples.

Related to the previous approach is the use of indicator species, which assumes that particular species or species guilds can replace habitat parameters in predicting overall species richness. This approach is particularly useful at local and regional scale for rapid inventories (Nally & Fleischman 2004) and has been used for lichens in different contexts (Rivas Plata *et al.* 2008; Aragón *et al.* 2013). However, it is not necessarily accurate for

predicting global species richness, since it requires good knowledge of relationships between species and their environment and it also assumes that these relationships do not vary with scale.

A rarely used approach is the analysis of character variation in a given group to identify potentially missing species by predicting likely character combinations that have not yet been observed in known species. For example, if a group of species displays a large number of character state combinations, such as various ascospore types with various chemical compounds in the thallus. Thereby, not all possible combinations will correspond to species but rather, patterns of correlations between character states can be used to predict how many combinations likely represent species. Thus, Messuti & Archer (2009) predicted 1,550 species of *Pertusaria* out of 4,660 possible character state combinations. Lücking (2012) used this approach to predict that in the large group of species centered around *Graphis scripta* (L.) Acharius (1809: 145) species richness might be about twice as high as the known number of species, based on 240 possible character state combinations and 90 combinations likely to exist in nature, 42 of them known in accepted species. This approach can be used for taxa in which the main characters are easily defined and determined and in which a certain level of combinations of presumably independent characters (such as ascospore type and secondary chemistry) is apparent, while it is impractical for groups that display complex morphologies or little overlap in character state combinations. It also depends on a certain level of knowledge already available, being more accurate for groups in which a larger number of species has already been described. Another study that in part used phenotype characters to predict species richness dealt with aquatic beetles (Nilsson-Örtman & Nilsson 2010).

In this paper, we used a parametric approach to predicting species richness based on a grid map and employing two measures: individual grid richness and average grid distribution per species. This novel approach was first applied by the first author and collaborators to another group of lichenized fungi in the Basidiomycota, the genera *Cora* and *Corella* (Lücking *et al.* 2014). The two measures are related to global diversity (over all grids) by a simple formula: global diversity is the sum of grid diversity divided by average grid distribution per species. Global diversity can thereby be interpreted as gamma diversity over all grids, while individual grid diversity corresponds to alpha diversity and grid distribution is a proxy for beta diversity or species turnover (Whittaker 1960). In the original formula (Whittaker 1960), gamma diversity is the product of average alpha diversity and average beta diversity, and it follows that in our formula, beta diversity corresponds to number of grids / average grid distribution. In other words, a higher number of grids combined with a lower average grid distribution results in higher beta diversity. Similar to Whittaker's (1960) formula, higher grid (alpha) diversity and lower grid distribution (higher beta diversity) will result in higher global (gamma) diversity. The challenge is to estimate individual grid diversity and average grid distribution. The first can be obtained through linear regression factoring in two independent parameters: habitat diversity and sampling effort per grid. The second can be estimated through interpolation of incomplete distribution ranges assumed to be caused by gaps in sampling effort. This approach corresponds to extrapolation from macroecological patterns, since we use biological traits of the taxa in question (correlation with habitat diversity) to predict individual grid richness. To compare this approach with other methods, we also employed two independent, non-parametric estimates: a species-area curve based on randomized subsampling of selected grids, and global species estimators based on frequencies of rare species.

Material and Methods

Since the current knowledge of diversity of Graphidaceae suggests that the majority of species in Graphidaceae are found in tropical areas, we focused in this study on (sub-)tropical regions. We assembled a grid map ranging from 30° northern to 30° southern latitude, with grids 15° wide and high, corresponding to approximately 1,600 km in each direction or approximately 2.5 million km² per grid, about 65% the extension of the United States (Fig. 1). This resulted in 46 grids covering land areas or archipelagos with known data on the three core subfamilies of Graphidaceae (Table 1). "Extratropical" areas (defined as outside the belt delimited by 30° northern to 30° southern latitude) and species exclusively occurring in these areas (Table 2) were excluded from the statistical prediction, since they contribute less than 5% to global species richness in the family and this proportion is within the error margin of the predictive model. However, since these areas do support substantial diversity in absolute numbers, we discuss species occurring exclusively in these areas separately.

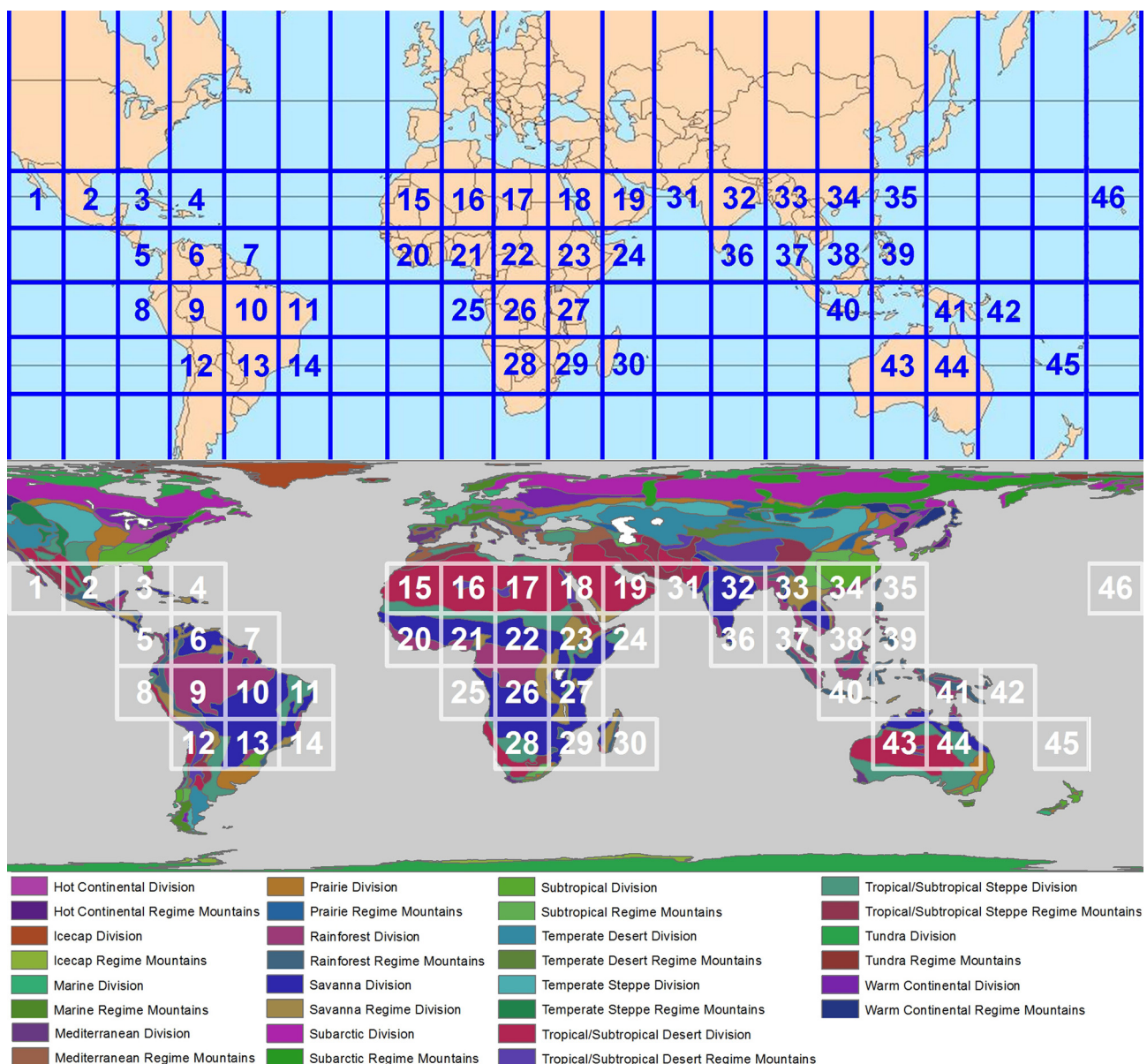


FIGURE 1. Global 15° x 15° gridmap used for the statistical approach to predict global species richness, including vegetation map from Bailey & Hogg (1986) and Bailey (1989) provided in ArcGIS.

TABLE 1. Global 15° x 15° grids, representative areas, and sampling score (from Table 3), GIS score, remote score, (Online Supplement T2) and total score (by multiplication of the three scores).

Grid	Region	Representative area	Sampling	GIS	Remote	Total
1	Neotropics	Sonoran Desert	5	83	1	414
2	Neotropics	Mexico	3	326	1	978
3	Neotropics	Florida, Cuba, Jamaica	8	297	1	2374
4	Neotropics	Hispaniola, Puerto Rico, Lesser Antilles	8	224	1	1792
5	Neotropics	Central America	10	326	1	3260
6	Neotropics	Colombia, Venezuela, Trinidad and Tobago	5	448	1	2238
7	Neotropics	Guayanas	3	288	1	864

.....continued on the next page

TABLE 1. (Continued)

Grid	Region	Representative area	Sampling	GIS	Remote	Total
8	Neotropics	Galapagos Islands, Ecuador, W and central Peru	2	316	1	632
9	Neotropics	W Amazon (Amazonas, Rondonia, Peru)	4	496	1	1984
10	Neotropics	E Amazonia (Pará)	1	363	1	363
11	Neotropics	northE Brasil	6	236	1	1417
12	Neotropics	Bolivia	0	245	1	0
13	Neotropics	central and S Brazil (Pantanal, Cerrado, Chaco)	2	391	1	782
14	Neotropics	SE Brazil (Minas Gerais, Rio de Janeiro)	5	299	1	1496
15	African Paleotropics	Morocco, W Algeria, Mauretania, W Mali	1	59	1	59
16	African Paleotropics	E Algeria and Mali, W Libya, N Nigeria	1	58	1	58
17	African Paleotropics	E Libya, W Egypt, N Chad, W Sudan	1	57	1	57
18	African Paleotropics	E Egypt, E Sudan, W Saudi-Arabia	1	113	1	113
19	African Paleotropics	E Saudi-Arabia, N Jemen, N Oman	1	100	1	100
20	African Paleotropics	Sierra Leone, Guinea, Ghana, Ivory Coast	2	317	1	634
21	African Paleotropics	S Nigeria, Cameroon, São Thomé and Príncipe	2	429	1	859
22	African Paleotropics	S Chad, southW Sudan, Central African Republic	0	419	1	0
23	African Paleotropics	E Sudan, Ethiopia, W Somalia	0	282	1	0
24	African Paleotropics	E Somalia, S Jemen, S Oman, Socotra	2	152	1	304
25	African Paleotropics	Equatorial Guinea, Gabun, Congo	0	252	1	0
26	African Paleotropics	Democratic Republic of Congo, Angola	0	436	1	0
27	African Paleotropics	Uganda, Kenya, Tanzania	3	317	1	950
28	African Paleotropics	Namibia, Botswana, N South Africa	4	173	1	693
29	African Paleotropics	Zimbabwe, Mozambique	3	217	1	652
30	African Paleotropics	Madagascar, Reunion, Mauritius	3	303	1	908
31	Eastern Paleotropics	Pakistan, northW India	0	120	1	0
32	Eastern Paleotropics	N and central India	5	418	1	2092
33	Eastern Paleotropics	Myanmar, N Thailand	3	475	1	1424
34	Eastern Paleotropics	S China, Hong Kong	4	335	1	1340
35	Eastern Paleotropics	Taiwan, Bonin Islands	2	208	1	417
36	Eastern Paleotropics	S India (Karnataka, Tamil Nadu, Kerala), Sri Lanka	10	278	1	2777
37	Eastern Paleotropics	Andaman Islands, S Thailand, Malaya, Singapore	8	354	1	2835
38	Eastern Paleotropics	Cambodia, Vietnam, Borneo, Labuan	2	347	1	693
39	Eastern Paleotropics	Philippines	8	259	1	2076
40	Eastern Paleotropics	Indonesia	2	337	1	673
41	Eastern Paleotropics	New Guinea	3	377	1	1131
42	Eastern Paleotropics	Solomon Islands	5	182	1	912
43	Eastern Paleotropics	NW Australia (Western Australia, Northern Territory)	3	126	1	378
44	Eastern Paleotropics	northE Australia (Queenslands, N New South Wales)	10	211	1	2108
45	Eastern Paleotropics	New Caledonia, Fiji Islands, Vanuatu, Tonga Islands	6	131	0.7	550
46	Eastern Paleotropics	Hawaii	9	129	0.7	813

TABLE 2. Species of Graphidaceae exclusively reported from regions outside the belt delimited by 30° northern and 30° southern latitude.

Species	Region
<i>Acanthothecis gyridia</i> (Stirt.) A.W. Archer	Australia
<i>Acanthothecis leucoxanthoides</i> Lendemer & R.C. Harris	North America
<i>Acanthothecis paucispora</i> Lendemer & R.C. Harris	North America
<i>Acanthothecis subaggregans</i> (Müll. Arg.) A.W. Archer	Australia
<i>Acanthothecis virguicola</i> Kantvilas	Australia
<i>Anomalographis madeirensis</i> (Tav.) Kalb	Europe
<i>Anomomorpha roseola</i> A. W. Archer & Elix	Australia
<i>Carbacanthographis iriomotensis</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Chapsa asteliae</i> (Kantvilas & Vězda) Mangold	Australia
<i>Chapsa lamellifera</i> (Kantvilas & Vězda) Mangold	Australia
<i>Chapsa lordhowensis</i> Mangold	Australia
<i>Chapsa minor</i> (Kantvilas & Vězda) Mangold & Lumbsch	Australia
<i>Clandestinotrema</i> aff. <i>antoninii</i>	Europe
<i>Crutarndina petractoides</i> (P. M. Jørg. & Brodo) Parnmen, Lücking & Lumbsch	Europe
<i>Fissurina alboscipita</i> (Coppins & P. James) Staiger	Europe
<i>Fissurina alligatorensis</i> Lendemer & R.C. Harris	North America
<i>Fissurina elixii</i> (A. W. Archer) A.W. Archer	Australia
<i>Fissurina flavicans</i> (Kashiw.) M. Nakan. & Kashiw.	Japan
<i>Fissurina fujisanensis</i> (Kashiw. & M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Fissurina howeana</i> (A. W. Archer) A.W. Archer	Australia
<i>Fissurina novae-zelandiae</i> C. Knight	New Zealand
<i>Fissurina psoromica</i> (A. W. Archer) A.W. Archer	Australia
<i>Fissurina subtropica</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Fissurina undulata</i> (Müll. Arg.) M. Nakan. & Kashiw.	Japan
<i>Graphis betulina</i> (Pers.) Ach.	Europe
<i>Graphis centrifuga</i> Räsänen	Australia
<i>Graphis flavopalmicola</i> Y. Joshi, Lücking & Hur	South Korea
<i>Graphis jejuensis</i> K. H. Moon, M. Nakan. & Kashiw.	South Korea
<i>Graphis koreana</i> S. Joshi & Hur	South Korea
<i>Graphis kousyuensis</i> (Horik. & M. Nakan.) Lücking	Japan
<i>Graphis macrocarpa</i> (Pers.) Röhl.	Europe
<i>Graphis parallela</i> Müll. Arg.	Japan
<i>Graphis pulverulenta</i> (Pers.) Ach.	Europe
<i>Graphis sophisticascens</i> Nyl.	North America
<i>Graphis sterlingiana</i> E.A. Tripp & Lendemer	North America
<i>Graphis uruguayensis</i> ined.	Uruguay
<i>Gymnographopsis chilena</i> C.W. Dodge	Chile
<i>Hemithecium argopholis</i> (C. Knight ex Müll. Arg.) A.W. Archer	Australia
<i>Hemithecium endofuscum</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Hemithecium polymorphum</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Leiorreuma yakushimensis</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Leucodecton desquamescens</i> (Vain.) Rivas Plata & Lücking	Japan

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TABLE 2. (Continued)

Species	Region
<i>Leucodecton isidioides</i> (Borrer) Lücking & Breuss	Europe
<i>Mangoldia atronitens</i> (A. W. Archer) Lücking, Parmen & Lumbsch	Australia
<i>Mangoldia australiana</i> Lücking, Parmen & Lumbsch	Australia
<i>Melanotopelia blepharostoma</i> Lumbsch & Divakar	South America
<i>Melanotopelia toensbergii</i> (Vězda & Kantvilas) Lumbsch & Mangold	North America
<i>Ocellularia pauciseptata</i> (Purvis & P. James) Aptroot	Europe
<i>Phaeographis oricola</i> Lendemer & R.C. Harris	North America
<i>Phaeographis patagonica</i> Zahlbr.	Chile
<i>Platygramme buxi</i> (Etayo) Etayo	Europe
<i>Platygramme pseudomontagnei</i> (M. Nakan.) M. Nakan. & Kashiw.	Japan
<i>Pseudoramonia richeae</i> Kantvilas & Vězda	Australia
<i>Pseudoramonia stipitata</i> (Vězda & Hertel) Kantvilas & Vězda	Tasmania
<i>Redonographa chilensis</i> (Zahlbr.) Lücking & Tehler	Chile
<i>Redonographa saxiseda</i> (Zahlbr.) Lücking & Tehler	Chile
<i>Schizotrema</i> aff. <i>schizoloma</i>	Australia
<i>Schizotrema subguadalupense</i> ined.	Australia
<i>Schizotrema subzebrinum</i> Mangold	Australia
<i>Thelotrema aemulans</i> Kremp.	New Zealand
<i>Thelotrema canescens</i> Tat. Matsumoto	Japan
<i>Thelotrema infundibularis</i> Tat. Matsumoto	Japan
<i>Thelotrema laurisilvae</i> Lücking & Breuss	Europe
<i>Thelotrema macrosporum</i> P.M. Jørg. & P. James	Europe
<i>Thelotrema nipponicum</i> Tat. Matsumoto	Japan
<i>Topeliopsis athallina</i> Lumbsch & Mangold	New Zealand
<i>Topeliopsis azorica</i> (P. James & Purvis) Coppins & Aptroot	Australia
<i>Topeliopsis</i> aff. <i>azorica</i> (P. James & Purvis) Coppins & Aptroot	Europe
<i>Topeliopsis decorticans</i> (Müll. Arg.) Frisch & Kalb	Australia
<i>Topeliopsis kantvilasii</i> Mangold & Lumbsch	Australia
<i>Topeliopsis lomatae</i> (Messuti, Lumbsch & Vězda) Messuti & Mangold	Argentina
<i>Topeliopsis macrocarpa</i> (C. W. Dodge) Mangold & Lumbsch	Subantarctic
<i>Topeliopsis patagonica</i> Mangold & Lumbsch	Chile
<i>Topeliopsis tasmanica</i> (Kantvilas & Vězda) Mangold	Australia

We assembled a global working checklist of species in Graphidaceae (Online Supplement T1; http://www.fieldmuseum.org/sites/default/files/online_supplement_T1.txt), focusing on the three core subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae, from published literature and unpublished data (Wirth & Hale 1963, 1978; Hale 1973, 1974a, b, 1975, 1978, 1980, 1981; Lumbsch 1989, 1993; Harris 1989, 1990, 1995; Nagarkar & Hale 1989; Mies & Lumbsch 1990; Mies 1994a, b; Lumbsch & Aptroot 1993; Guderley & Lumbsch 1996; Marciano *et al.* 1996; Aptroot *et al.* 1997, 2007; Boonpragob *et al.* 1998; Staiger & Kalb 1999; Komposch & Hafellner 1999, 2000, 2003; Kalb & Staiger 2000; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Sipman 2001; Nakanishi *et al.* 2001, 2003, 2010; Staiger 2002; Wolseley *et al.* 2002; Nash *et al.* 2002, 2004, 2007; López de Silanes & Alvarez 2003; Messuti *et al.* 2003; Archer 2004, 2006, 2007, 2009; Kalb 2004, 2008, 2009; Adawadkar & Makhija 2004, 2005, 2006, 2007; Kalb *et al.* 2004, 2009a, b; Nayaka *et al.* 2004; Makhija & Adwadkar 2005a, b; Makhija *et al.* 2005, 2006, 2009; Frisch 2006; Frisch & Kalb 2006a, b; Frisch *et al.* 2006a, b; Cáceres 2007;

Galloway 2007; Aptroot & Sipman 2007; Jia & Wei 2007, 2008, 2009a, b; Lumbsch & Mangold 2007; Lücking 2007, 2008; Breuss & Neuwirth 2007; Tewari & Upreti 2007a, b; Jagadeesh Ram *et al.* 2007; Miao *et al.* 2007; Lücking *et al.* 2007, 2008, 2009a, b, 2010, 2011a, b, 2012a, b, c, 2013; van den Boom *et al.* 2007, 2013; Moon *et al.* 2008, 2011, 2012; Dal-Forno 2009; Archer & Elix 2009, 2013; Neuwirth & Lücking 2009; Sharma & Makhija 2009a, b; Chitale *et al.* 2009, 2011; Joshi *et al.* 2009, 2010a, b, 2012a, b, c, 2013a, b, c; Papong *et al.* 2009, 2010; Sérusiaux *et al.* 2009; Tripp *et al.* 2009; Lendemer 2010; Dal-Forno & Eliasaro 2010; Singh & Sinha 2010; Dubey *et al.* 2010; Kocourková *et al.* 2010; Nelsen *et al.* 2010, 2012; Rivas Plata *et al.* 2010a, b, 2012a, 2012b; Lumbsch *et al.* 2010, 2011a, b; Sharma *et al.* 2010a, b, 2012; Jia 2011; Mercado-Díaz 2009; Rincón-Espitia & Lücking 2011; Seavey & Seavey 2011; Sharma & Khadilkar 2011, 2012; Mongkolsuk *et al.* 2011; Rincón *et al.* 2011; Upreti *et al.* 2011; Lücking & Breuss 2012; Lücking & McCune 2012; Schumm & Aptroot 2012a, b; Cáceres *et al.* 2012a, b, 2013; Jia *et al.* 2012; Perlmutter *et al.* 2012; Rosabal *et al.* 2012; Sipman *et al.* 2012; Soto Medina *et al.* 2012; Weerakoon *et al.* 2012a, b; Wijeyaratne *et al.* 2012; Parnmen *et al.* 2012a, b, 2013; Jia & Kalb 2013; Rivas Plata & Lücking 2013; Bárcenas-Peña *et al.* 2014; Lendemer *et al.* 2013). For unpublished data, we included revision of herbarium material housed in the following herbaria: ABL, B, BM, F, FH, H, M, MSC, PC, S, TUR, US, W, hb. Henssen, hb. Kalb. All reported names were updated where possible using current genus and species concepts (Staiger 2002; Frisch *et al.* 2006a; Lücking *et al.* 2009a; Rivas Plata *et al.* 2010a). Subfamily Gomphilloideae, comprising an additional 400 known species, was excluded from the predictive model, as we currently do not have an extensive set of molecular data for this lineage to assess species concepts. We used a combination of morphological and molecular data (Parnmen *et al.* 2012a; Rivas Plata *et al.* 2012a, b, 2013), including revision of type material, to verify the status of each species included in the list. Molecular data are currently available for nearly 500 species within the core Graphidaceae (Staiger 2002; Frisch *et al.* 2006a; Staiger *et al.* 2006; Tehler *et al.* 2009; Lücking *et al.* 2013; Rivas Plata *et al.* 2013; Kraichak *et al.* 2014a; Lumbsch *et al.* 2014), allowing to evaluate the usefulness of phenotype characters for species delimitation in taxa where no molecular data are yet available (Berger *et al.* 2011; Parnmen *et al.* 2012a; Rivas Plata *et al.* 2012b). For example, since molecular data suggest that hymenium inspersion and secondary chemistry are uniform within a phylogenetically defined species in the family (Rivas Plata *et al.* 2012b, 2013), we generally separated species based on these characters. We then used the same source references to assess occurrences of each species within each grid. Specifically, where possible we critically revised data and material on taxa reportedly pantropical, and those kept in the dataset as pantropical or widely distributed were either supported by molecular data or else have a high likeliness of being correct, based on indirect evidence.

We employed detrended correspondence analysis (DCA) ordination to visualize the arrangement of grids in species space and patterns apparent from observed species distributions. DCA was performed by down-weighting rare species and rescaling the axes into 25 segments. In addition, we performed indicator species analysis using the three main tropical regions (Neotropics: grids 1–14; African Paleotropics: grids 15–30; Eastern Paleotropics: grids 31–46) as grouping variable. This approach uses Monte-Carlo randomization to shuffle the original data and tests species distributions among regions comparing them to a random distribution. Both approaches were done in PC-ORD 5.0 (McCune & Mefford 1999; McCune *et al.* 2002).

For each grid, we established three sets of scores: (1) scores representing the sampling effort per grid in graphidoid and thelotremoid Graphidaceae, ranging from 0 to 5 for each group (combined 0 to 10); (2) scores representing the presence of global vegetation types in each grid; and (3) scores indicating small, remote oceanic islands (more than 1,000 km from the next continent or large island). For the latter, we scored each grid as 1 except grids 45 and 46 (New Caledonia, Hawaii), which were scored as 0.7 (Table 1). Sampling scores were derived from data obtained from published literature and unpublished revisions of herbarium collections and recent field work (Table 3). We employed separate sampling scores for graphidoid and thelotremoid taxa since until recently, these were treated as separate families and hence available literature often results in a bias towards one or the other group in a given region. Three grids were defined as well-sampled, receiving the maximum score of 10: grids 5, 36, and 44. Although these grids have not been completely sampled, we applied the maximum score as conservative calibration for the model.

TABLE 3. Scoring system for the parameter sampling effort per grid.

Sampling score	
Score 0	Less than 10 species reported per group for grids with predominantly humid vegetation or less than five species for grids with semi-arid vegetation
Score 1	Less than 50 species reported per group for grids with predominantly humid vegetation or less than 10 species for grids with semi-arid vegetation
Score 2	Limited treatments available for one to several localities across grid, with 50 or more species reported per group for grids with predominantly humid vegetation or 10 or more species reported for grids with semi-arid vegetation
Score 3	Modern taxonomic treatments available for one locality within grid or limited treatments available for additional localities across grid
Score 4	Modern taxonomic treatments available for a one to three locality within grid and limited treatments available for additional localities across grid
Score 5	Modern taxonomic treatments available for more than three localities across grid

Vegetation types were defined the global vegetation map provided by Bailey & Hogg (1986), and Bailey (1989), using their intermediate division classification level (Online Supplement T2; http://www.fieldmuseum.org/sites/default/files/online_supplement_T2.txt). The land area of each division was calculated for each 15° latitude by 15° longitude grid cells (Fig. 1) using the "tabulate area" tool in ArcGIS version ArcGIS 10.1 with the Spatial Analyst extension. We used a cylindrical equal area projection for area calculations, which equally spaces longitudinal lines to form similarly sized rectangular grids (sub-tropical cells were 7% smaller than tropical cells). When comparing the land area of divisions, we used the relative area within grid cells rather than the absolute area between grid cells. We also accounted for ocean surface present within grid cells (Online Supplement T2). Since species richness is logarithmically correlated with area size, we transformed all area values using the exponent 0.25 (Online Supplement T2). This exponent was derived as best fitting model ($R_{\text{Pearson}} = 0.99$) from the following average species richness values of Graphidaceae observed in areas of a given size: ≈ 100 species (1 ha or 0.01 km²; Florida, Venezuela, Peru, Philippines: Lücking *et al.* 2011a, 2012c; Parnmen *et al.* 2012b; Rivas Plata & Lücking 2013); ≈ 300 species (50,000 km²; Costa Rica: Lücking *et al.* 2008; Sipman *et al.* 2012); ≈ 500 species (700,000 km²; Central America: combined from Wirth & Hale 1963, 1978; Hale 1978; Sipman 2001; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Breuss & Neuwirth 2007; van den Boom *et al.* 2007, 2013; Lücking *et al.* 2008; Sipman *et al.* 2012); ≈ 1000 species (1.8 million km²; Neotropics). The exponent depends only on relative species richness increasing with scale, independent of absolute species richness, and hence is not sensitive to sampling bias as long as reasonably similar sampling effort is assumed for each scale. We assigned each vegetation type (Bailey division) a score corresponding to the diversity of Graphidaceae expected within that vegetation type (Table 4), using data from quantitative studies to rank vegetation types according to expected diversity (Lücking 2003; Cáceres *et al.* 2008; Rivas Plata *et al.* 2008). These data also suggest that the vegetation types that contribute uniquely and substantially to overall species richness are the rainforest and rainforest mountains divisions, whereas the savanna and savanna mountains divisions mostly harbor species also found in the rainforest canopy. Therefore, to avoid overestimation of species richness when computing a cumulative score for grids in which both rainforest and savanna divisions were present, the diversity score for the savanna divisions was scaled back as follows: if the rainforest division area was larger than the savanna division area, it was set to 0 (then assuming that the savanna division would not contribute unique species); if the savanna division was larger but less than twice as large, it was set to 1; if the savanna division was between two and ten times as large, it was set to 2; and if the savanna division was more than ten times as large, it was set to the full score of 3 (Online Supplement T2). Sampling and vegetation scores were combined into a total prediction score for each grid by multiplication (Table 1). Since the Bailey vegetation map does not contain data for small islands, we assembled the data for grids 45 and 46 (New Caledonia, Hawaii) manually using the above criteria; also, the data for grid 4 (Hispaniola, Puerto Rico, Lesser Antilles) were manually corrected since they suggested absence of rainforest areas.

TABLE 4. Scoring system for the parameter Graphidaceae diversity versus vegetation type (Bailey divisions).

Sampling score	
Score 1	Prairie division
	Subtropical division
	Subtropical Mountains division
	Tropical/Subtropical Desert division
	Tropical/Subtropical Steppe division
	Tropical/Subtropical Desert Mountains division
	Tropical/Subtropical Steppe Mountains division
Score 3	Savanna division
	Savanna Mountains division
Score 5	Rainforest Mountains division
Score 10	Rainforest division

We compared the variation of observed species richness per grid with the variation in total prediction scores and established a linear regression as best fit for the correlation between the two variables, using the distribution fitting module in STATISTICA 6.0 and observed correlation coefficient *R* as evaluation parameter. We then computed predicted species richness per grid based on the linear model by using the maximum sampling score for each grid (10). From the predicted grid data, predicted global species richness was calculated by dividing the sum total of individual grid species richness by the average grid distribution per species, i.e. the average number of grids in which a species is present. Since the observed grid distribution is underestimated by biased sampling effort, we applied interpolation to estimate expected grid distribution per species, by assuming presence of each species in grids that connect grids with observed occurrences and share the same vegetation types in which the species occur. We thereby used a conservative approach, assuming no dispersal limitations for except between continental areas and hence occurrences of species in grids in which such occurrences cannot necessarily be expected for geographic reasons. For example, if a species was found in tropical rainforest in Mexico, Colombia, and southeastern Brazil, we assumed occurrence in all neotropical grids, including the Caribbean, whereas the species might actually be absent from that region due to dispersal limitations. This approach results in a higher estimate for average grid distribution and hence in a lower estimate for global species richness, thus balancing possible errors made in assuming that species do not occur outside the area determined by the grids in which a species was observed. The predicted global species richness was then calculated by dividing the sum total of predicted grid species richness by the interpolated average for species grid distributions.

To compare this approach with other methods, we also employed two separate, non-parametric extrapolation techniques. First, we computed a species-area curve based on eight well-sampled grids (3, 4, 5, 9, 36, 37, 39, 44), with sampling scores between 8 and 10, for an average of 8.9 (SD = 0.99). The species-area curve was computed using a randomized subsampling approach in PC-ORD 5.0 with 500 repetitions and the Sørensen distance measure (McCune & Mefford 1999; McCune *et al.* 2002). Since we included grids with incomplete sampling scores, for an average of 8.9 out of 10, this approach underestimates global diversity, as ideally each grid would have a maximum sampling score of 10 if completely sampled. Hence, we corrected each cumulative grid estimate resulting from the subsampling approach with the factor 1.12 (= 10 / 8.9). The corrected cumulative grid values were used to establish a non-linear model of species richness versus grid number via non-linear estimation in STATISTICA 6.0, employing the best-fitting formula $y = a + b \times \log_2(x)^c$, under least squares regression with a Levenberg-Marquart estimation, a maximum of 50 iterations, and 0.000001 as convergence criterion. The obtained model was used to predict global species richness by extrapolating from eight grids to the total of 46. Since this method is based on well-sampled grids only, it is biased towards sampling effort in ecogeographical terms, since no well-sampled grid represented tropical Africa and also no well-sampled grid represented one of the grids dominated by (semi-)desert vegetation. However, these two shortcomings have opposing effects on the extrapolated value and hence partially balance each other. Since the method assumes a continuous area rather than geographically separate regions, it will underestimate global species richness since it does not take into account that absences of species in particular grids are real, rather than sampling artifact; hence, the estimated species-area curve will appear flatter than it should be. On the other hand, since about 15% of the grids represent areas dominated by (semi-)desert vegetation, with low species richness to be expected, whereas the grids sampled for the species-area curve do not include such grids, the extrapolated model will overestimate global species richness. A way to correct for this uncertainty would be to

compute the model separately for each of the three major tropical regions and include low-diversity (semi-)desert dominated grids; however, the data did not allow this since too few grids had sufficiently high sampling scores.

In addition, we used the *specpool* function as part of the VEGAN package in R (Oksanen *et al.* 2013) to estimate global species richness based on rare species occurrences (singletons and doubletons) within all grids (Palmer 1990; Colwell & Coddington 1994). The method computes four different estimators for global species richness, plus their standard errors: Chao 2, first and second order Jackknife, and Bootstrap, with Chao 2 being the most progressive (likely overestimating) and Bootstrap the most conservative (likely underestimating) measure. We also employed the *betadiver* function in VEGAN to compute patterns of beta diversity between grids.

Results

We assembled a list of 2,079 taxa of Graphidaceae in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae (Online Supplement T1). Among these are 1,766 previously accepted species, plus 175 new species described in this issue, plus an additional at least 138 taxa that still await formal description. Among the 175 newly described species in this issue (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Kraichak *et al.* 2014a; Lumbsch *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Papong *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014), there are four novel generic lineages. By far most of the new species are in the genus *Ocellularia* (46 species), followed by *Fissurina* Fée (1825: xxxv; 24 species), *Graphis* (15), *Diorygma* Eschweiler (1824: 13, 25; 12 species), *Rhabdodiscus* Vainio (1921: 84; 10 species), and *Thelotrema* (nine species). Among the larger genera now containing 50 or more species, the genera with the highest proportion of newly described species are *Diorygma*, with 16.9%, *Ocellularia*, with 16.3%, and *Fissurina*, with 15.3% (Table 5). The highest proportion of new species was found in two small genera: *Myriochapsa* M. Cáceres, Lücking & Lumbsch in Parnmen *et al.* (2013: 128), with 66.7%, and *Compositrema* Rivas Plata, Lücking & Lumbsch (2012b: 1172), with 50%.

TABLE 5. Species per genus recognized in the core Graphidaceae and number and proportion of new species described in contributions in this volume.

Genus	Total	New	Percentage	Genus	Total	New	Percentage
<i>Graphis</i>	441	15	3.4%	<i>Halegrapha</i>	7	1	14.2%
<i>Ocellularia</i>	282	46	16.3%	<i>Wirthiotrema</i>	7	0	0.0%
<i>Fissurina</i>	157	24	15.3%	<i>Gyrotrema</i>	6	1	16.7%
<i>Phaeographis</i>	156	7	4.5%	<i>Acanthotrema</i>	5	1	20.0%
<i>Thelotrema</i>	106	9	8.5%	<i>Asteristion</i>	5	0	0.0%
<i>Diorygma</i>	71	12	16.9%	<i>Cruentotrema</i>	5	1	20.0%
<i>Myriotrema</i>	66	5	7.6%	<i>Glaucotrema</i>	5	1	20.0%
<i>Chapsa</i>	61	4	6.6%	<i>Kalbographa</i>	5	0	0.0%
<i>Acanthothecis</i>	56	5	8.9%	<i>Nitidochapsa</i>	5	1	20.0%
<i>Hemithecium</i>	51	0	0.0%	<i>Redonographa</i>	5	0	0.0%
<i>Rhabdodiscus</i>	42	10	23.8%	<i>Compositrema</i>	4	2	50.0%
<i>Sarcographa</i>	37	0	0.0%	<i>Dyplolabia</i>	4	0	0.0%
<i>Diploschistes</i>	31	0	0.0%	<i>Melanotopelia</i>	4	0	0.0%
<i>Platygramme</i>	30	3	10.0%	<i>Pseudotopeliopsis</i>	4	1	25.0%
<i>Astrochapsa</i>	28	4	14.2%	<i>Thecaria</i>	4	0	0.0%
<i>Carbacanthographis</i>	28	0	0.0%	<i>Leptotrema</i>	3	0	0.0%
<i>Leucodecton</i>	28	5	17.9%	<i>Myriochapsa</i>	3	2	66.7%

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TABLE 5. (Continued)

Genus	Total	New	Percentage	Genus	Total	New	Percentage
<i>Platythecium</i>	26	2	7.7%	<i>Phaeographopsis</i>	3	0	0.0%
<i>Topeliopsis</i>	20	0	0.0%	<i>Pseudoramonia</i>	3	1	33.3%
<i>Thalloloma</i>	19	2	10.5%	<i>Schistophoron</i>	3	0	0.0%
<i>Ampliotrema</i>	18	0	0.0%	<i>Thecographa</i>	3	0	0.0%
<i>Melanotrema</i>	18	1	5.6%	<i>Anomalographis</i>	2	0	0.0%
<i>Clandestinotrema</i>	17	1	5.9%	<i>Diaphorographis</i>	2	0	0.0%
<i>Pseudochapsa</i>	17	1	5.9%	<i>Gymnographopsis</i>	2	0	0.0%
<i>Fibrillithecis</i>	16	0	0.0%	<i>Heiomasia</i>	2	0	0.0%
<i>Leiorreuma</i>	15	1	6.7%	<i>Mangoldia</i>	2	0	0.0%
<i>Stegobolus</i>	15	1	6.7%	<i>Nadvornikia</i>	2	0	0.0%
<i>Chroodiscus</i>	14	0	0.0%	<i>Reimnitzia</i>	2	0	0.0%
<i>Schizotrema</i>	13	0	0.0%	<i>Sarcographina</i>	2	0	0.0%
<i>Pallidogramme</i>	12	0	0.0%	<i>Crutarndina</i>	1	0	0.0%
<i>Redingeria</i>	12	1	8.3%	<i>Enigmotrema</i>	1	0	0.0%
<i>Glyphis</i>	10	0	0.0%	<i>Malmographina</i>	1	0	0.0%
<i>Anomomorpha</i>	8	0	0.0%	<i>Phlegographa</i>	1	0	0.0%
				<i>Pycnotrema</i>	1	0	0.0%

Seventy-four taxa (3.5% of the total) are known exclusively from "extratropical" regions in the Northern and Southern Hemisphere north and south of 30° northern and southern latitude. These are mostly from North America, Europe, and eastern Asia (South Korea, Japan). Since the tropics are usually defined as the zone between 23° northern and southern latitude, we labeled these species "extratropical"; however, most of these are actually subtropical in nature, considering that the subtropics are defined as the zone between 23° and 35° northern and southern latitude. These were not included in the predictive computations but are listed separately (Table 2), leaving 2,005 (sub-)tropical or widely distributed species occurring within the grid area, with a total of 5,571 occurrences. "Subtropical" species included within the grid area are mostly those occurring in subtropical, (semi-)arid zones, such as in the genus *Diploschistes*.

Observed species richness per grid ranged from zero to 499 species (Table 6). The highest numbers were observed in grid 36 (southern India, Sri Lanka), with 499 species, grid 5 (Central America: Guatemala through Panama), with 443 species, grid 6 (Colombia, Venezuela, Trinidad), with 334 species, grid 37 (Andaman Islands, southern Thailand, Singapore, peninsular Malaysia), with 332 species, and grid 44 (Australia: Queensland and northern New South Wales), with 317 species. Other grids with high observed diversity were grid 3 (Louisiana, Florida, Cuba, Jamaica), grid 4 (Hispaniola, Puerto Rico, Lesser Antilles), grid 9 (western Amazon in Brazil and Peru), grid 32 (northern and central India), and grid 39 (Philippines). Comparatively low values were observed for all grids in tropical Africa and several grids in tropical Asia, as well as grids 10 and 12 (western Amazon, Bolivia) in tropical America.

Using DCA ordination, the grids separated well into four main groups (Fig. 2). On the vertical axis, grids were grouped into those dominated by subtropical, (semi-)arid desert areas and those with a substantial portion of tropical rainforest. Notably, the (semi-)arid grids are dominated by species of *Diploschistes* Norman (1852: 232) growing on inorganic substrata (soil, rock), whereas the tropical rainforest grids are dominated by all other genera (with mostly epiphytic species). On the horizontal axis, the grids separated well into neotropical, African paleotropical, and eastern paleotropical regions. Indicator species analysis showed that a large number of species (183) was significantly indicative for one of the three regions at $p < 0.05$ (Table 7), and another 107 marginally significant at $p < 0.1$. Considering that only species with presence in a certain number of grids will result in significant values and only 313 out of 2,005 species were found in five or more grids, this implies that almost all species have a biogeographical distribution bias with regard to one or two of the three main tropical regions and only very few species are truly pantropical. Indeed, only 155 species had occurrence data in two or more of the three main tropical regions; notably, one third of these were species of *Graphis*, and other well-represented genera included *Diploschistes*, *Dyplolabia* Massalongo (1854: 6), *Glyphis* Acharius (1814: 106), *Thecaria* Fée (1825: xlii,97), and *Thelotrema* (Online Supplement T1).

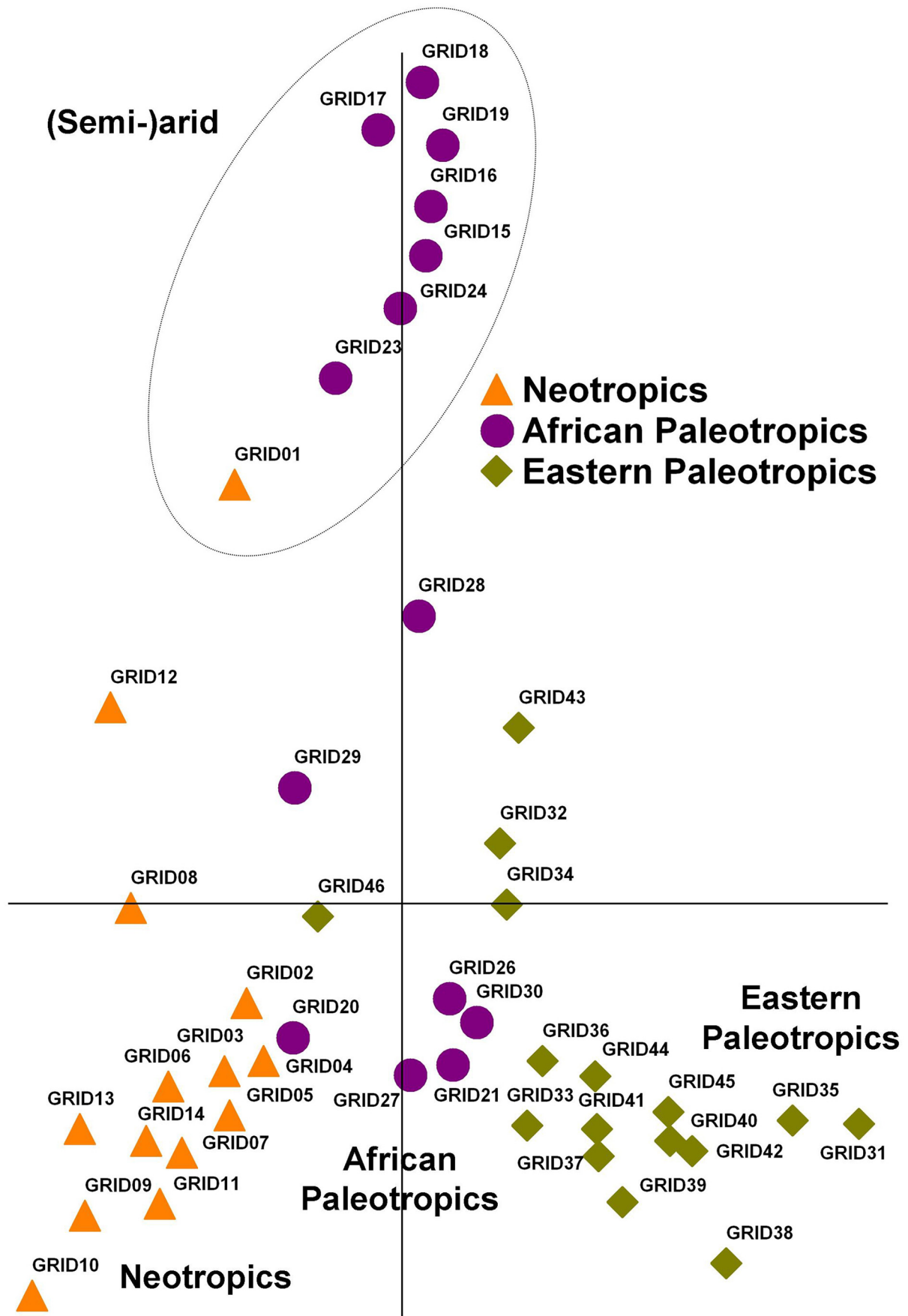


FIGURE 2. DCA ordination of the 46 grids based on observed species composition..

TABLE 6. Observed and predicted species richness per grid, difference, and indication of grids as "discovery hotspots" of undiscovered species based on difference between predicted and observed species richness; (+) difference 150–250 species, (++) difference 250–400 species, (+++) difference more than 400 species.

Grid	Region	Representative area	Observed	Predicted	Difference	Hotspot
1	Neotropics	Sonoran Desert	24	109	85	
2	Neotropics	Mexico	112	429	317	++
3	Neotropics	Florida, Cuba, Jamaica	282	391	109	
4	Neotropics	Hispaniola, Puerto Rico, Lesser Antilles	260	295	35	
5	Neotropics	Central America, Chocó	443	430	[–13]	
6	Neotropics	Colombia, Venezuela, Trinidad and Tobago	334	590	256	++
7	Neotropics	Guayanas	136	379	243	+
8	Neotropics	Galapagos Islands, Ecuador, W and central Peru	62	416	354	++
9	Neotropics	W Amazon (Amazonas, Rondonia, Peru)	260	653	393	++
10	Neotropics	E Amazonia (Pará)	24	478	454	+++
11	Neotropics	NE Brasil	134	311	177	+
12	Neotropics	Bolivia	14	322	308	++
13	Neotropics	Central and S Brazil (Pantanal, Cerrado, Chaco)	105	515	410	+++
14	Neotropics	SE Brazil (Minas Gerais, Rio de Janeiro)	162	394	232	+
15	African Paleotropics	Morocco, W Algeria, Mauretania, W Mali	8	77	69	
16	African Paleotropics	E Algeria and Mali, W Libya, N Nigeria	8	76	68	
17	African Paleotropics	E Libya, W Egypt, N Chad, W Sudan	4	75	71	
18	African Paleotropics	E Egypt, E Sudan, W Saudi-Arabia	4	148	144	
19	African Paleotropics	E Saudi-Arabia, N Jemen, N Oman	6	132	126	
20	African Paleotropics	Sierra Leone, Guinea, Ghana, Ivory Coast	49	418	369	++
21	African Paleotropics	S Nigeria, Cameroon	87	566	479	+++
22	African Paleotropics	S Chad, southW Sudan, Central African Republic	0	552	552	+++
23	African Paleotropics	E Sudan, Ethiopia, W Somalia	3	371	368	++
24	African Paleotropics	E Somalia, S Jemen, S Oman, Socotra	11	200	189	+
25	African Paleotropics	São Thomé and Príncipe, Equ. Guinea, Gabun, Congo	0	332	332	++
26	African Paleotropics	Democratic Republic of Congo, Angola	14	575	561	+++
27	African Paleotropics	Uganda, Kenya, Tanzania	79	417	338	++
28	African Paleotropics	Namibia, Botswana, N South Africa	61	228	167	+
29	African Paleotropics	Zimbabwe, Mozambique	55	286	231	+
30	African Paleotropics	Madagascar, Reunion, Mauritius	109	399	290	++
31	Eastern Paleotropics	Pakistan, northW India	1	158	157	+
32	Eastern Paleotropics	N and central India	248	551	303	+
33	Eastern Paleotropics	Myanmar, N Thailand	159	625	466	+++
34	Eastern Paleotropics	S China, Hong Kong	160	441	281	++
35	Eastern Paleotropics	Taiwan, Bonin Islands	24	275	251	++
36	Eastern Paleotropics	S India (Karnataka, Tamil Nadu, Kerala), Sri Lanka	499	366	[–133]	
37	Eastern Paleotropics	Andaman Islands, S Thailand, Malaya, Singapore	332	467	135	
38	Eastern Paleotropics	Cambodia, Vietnam, Borneo, Labuan	96	457	361	++
39	Eastern Paleotropics	Philippines	277	342	65	
40	Eastern Paleotropics	Indonesia	82	444	362	++
41	Eastern Paleotropics	New Guinea	129	497	368	++
42	Eastern Paleotropics	Solomon Islands	109	240	131	

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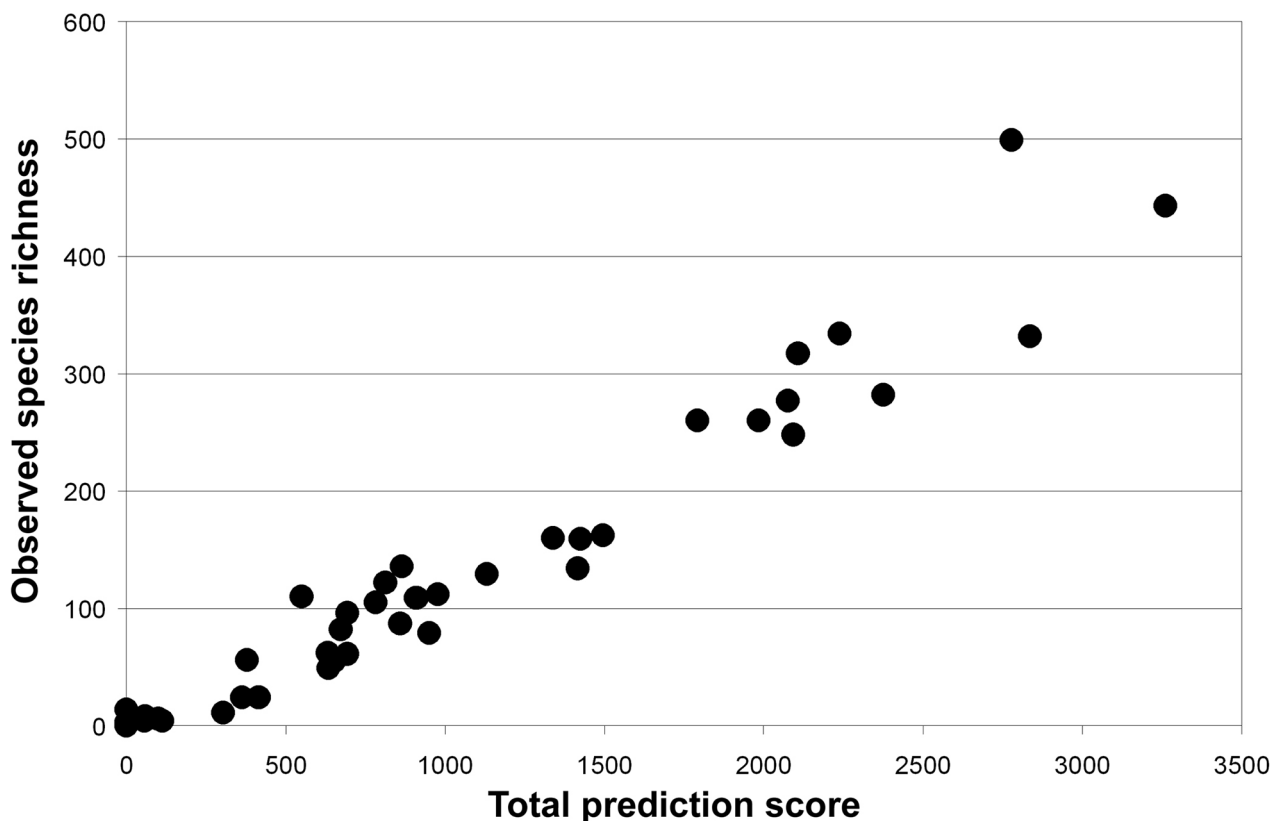
TABLE 6. (Continued)

Grid	Region	Representative area	Observed	Predicted	Difference	Hotspot
43	Eastern Paleotropics	NW Australia (Western Australia, Northern Territory)	56	166	110	
44	Eastern Paleotropics	northE Australia (Queenslands, N New South Wales)	317	278	[-39]	
45	Eastern Paleotropics	New Caledonia, Fiji Islands, Vanuatu, Tonga Islands	110	173	63	
46	Eastern Paleotropics	Hawaii	122	170	48	

TABLE 7. Results of indicator species test comparing observed species distribution with main tropical regions.

Region	Significant ($p < 0.05$)	Marginally significant ($p < 0.10$)	Total
Neotropics	94	63	157
African Paleotropics	3	3	6
Eastern Paleotropics	86	41	127
Total	183	107	290

Correlation between observed species richness per grid and total prediction score per grid resulted in a linear model, $y = 0.13 \times$ (Fig. 3), with a strong and highly significant correlation $R = 0.97$ and $p < 0.001$ and R^2 (variance explained) = 94%. Using the model by assuming a maximum sampling score (10) per grid, we predicted the highest species richness values for grid 9 (653 species) and grid 6 (590 species) in the Neotropics, grid 26 (575 species) and grid 21 (566 species) in tropical east Africa, and grid 33 (625 species) and grid 32 (551 species) in tropical Asia and Australia, respectively (Table 6). The predicted grid sum total was 16,217. Note that the prediction for three grids (5, 36, 44), including the two grids with the highest observed richness, was lower than the observed value in both cases, owing to the smoothing function of the linear model but also indicating that the model is conservative.

**FIGURE 3.** Observed species richness per grid plotted against total prediction score derived from sampling, vegetation diversity and landmass, and remote scores.

Observed grid distribution per species was $5,571 / 2,005 = 2.78$ grids, corresponding to 7 million km² on average per species. More than half of the species (1,110) were observed in a single grid only and another 313 species in two grids, together accounting for 70% of all (sub-)tropical species. The highest number of grids in which a species was observed was 28 (*Dyplolabia afzelii*), followed by 27 (*Glyphis cicatricosa*), 25 (*Glyphis scyphulifera*), 24 (*Graphis glaucescens*), and 22 (*Graphis tenella*). Notably, of the 25 species with the highest grid distribution, 20 represented graphidoid taxa formerly placed in Graphidaceae, and only five thelotremoid taxa of the former family Thelotremataceae. The low average grid distribution resulted in comparatively high measures of beta diversity between grids, ranging mostly between 0.8 and 1.0 and with an average of 0.91 (Fig. 4). After interpolating species distributions, the estimated grid distribution per species was 4.63 grids, or approximately 11.5 million km², which is about three times the size of the United States. Beta diversity then decreased to an average of 0.79 (Fig. 4). Using this value, global predicted species richness for (sub-)tropical core Graphidaceae was $16,217 / 4.63 = 3,503$ species. This corresponds to a 74% increase compared to the observed number of 2,005 species, or nearly 1,500 additional species.

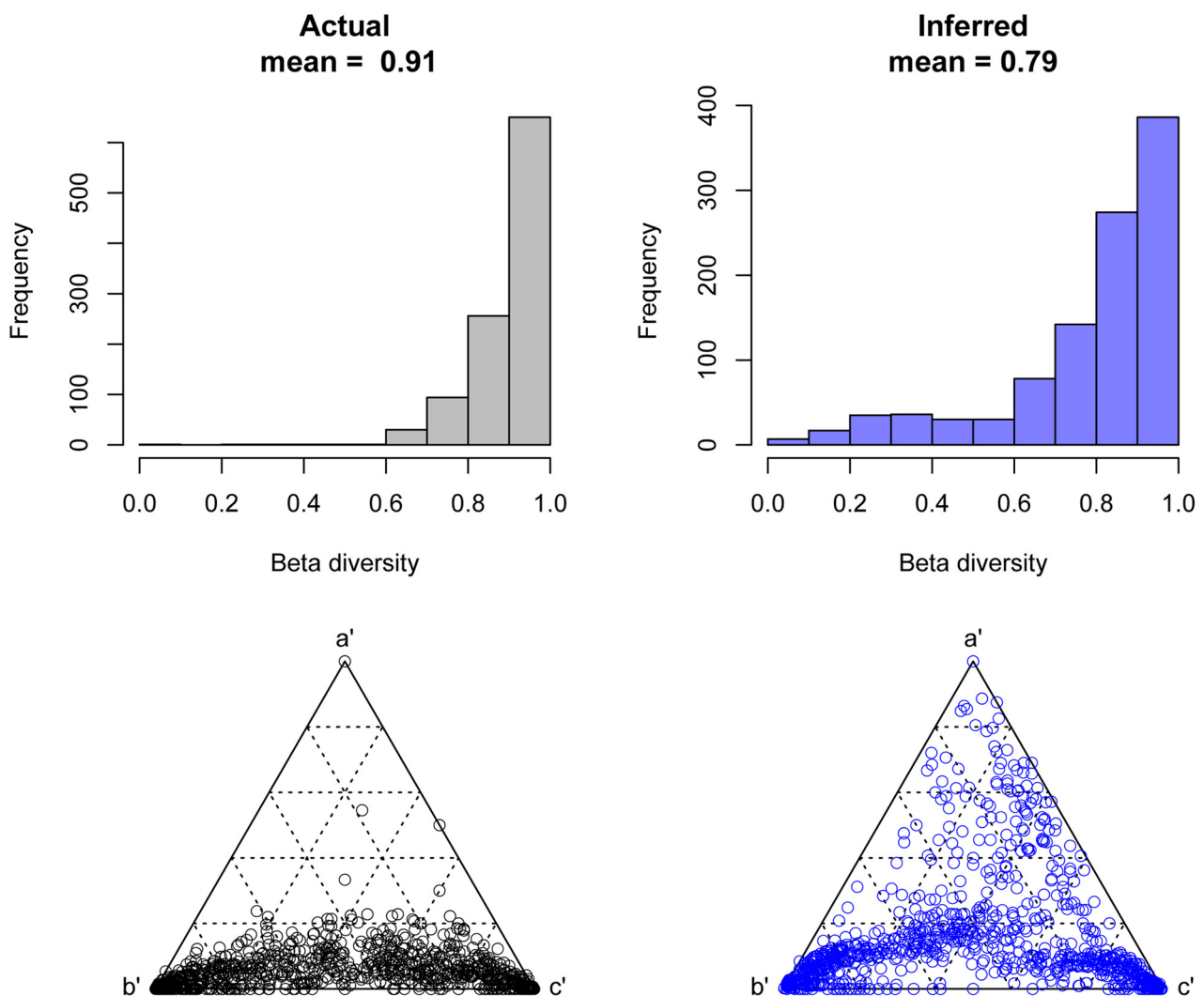


FIGURE 4. Beta diversity based on observed and interpolated grid occurrences.

The species-area curve reconstructed from eight well-sampled grids via subsampling showed absence of a plateau (Fig. 5). Based on this curve and corrected for sampling effort, the non-linear model was estimated as $y = 362 + 222 \times \log_2(x)^{1.50}$, with $R = 0.9996$, $p < 0.001$, explaining 99.9% of the variance in the data. Using this model, the global predicted species richness of (sub-)tropical core Graphidaceae projected to 46 grids was 3,244 species (Fig. 6). The *specpool* approach as part of the VEGAN package yielded the following estimates: Chao 2 = $3,962 \pm$

168 species; first order Jackknife = $3,084 \pm 253$; second order Jackknife = 3,850; Bootstrap = $2,454 \pm 139$. The average and the median over all predictors are 3,350 and 3,374 species, respectively; excluding the Bootstrap, which is generally considered a poor estimator (Chazdon *et al.* 1998), the average and median amount to 3,529 and 3,503 species, respectively. Thus, among all measures, the grid method provided the estimate closest to the central tendency of all estimators, rounding to approximately 3,500 species (Fig. 7).

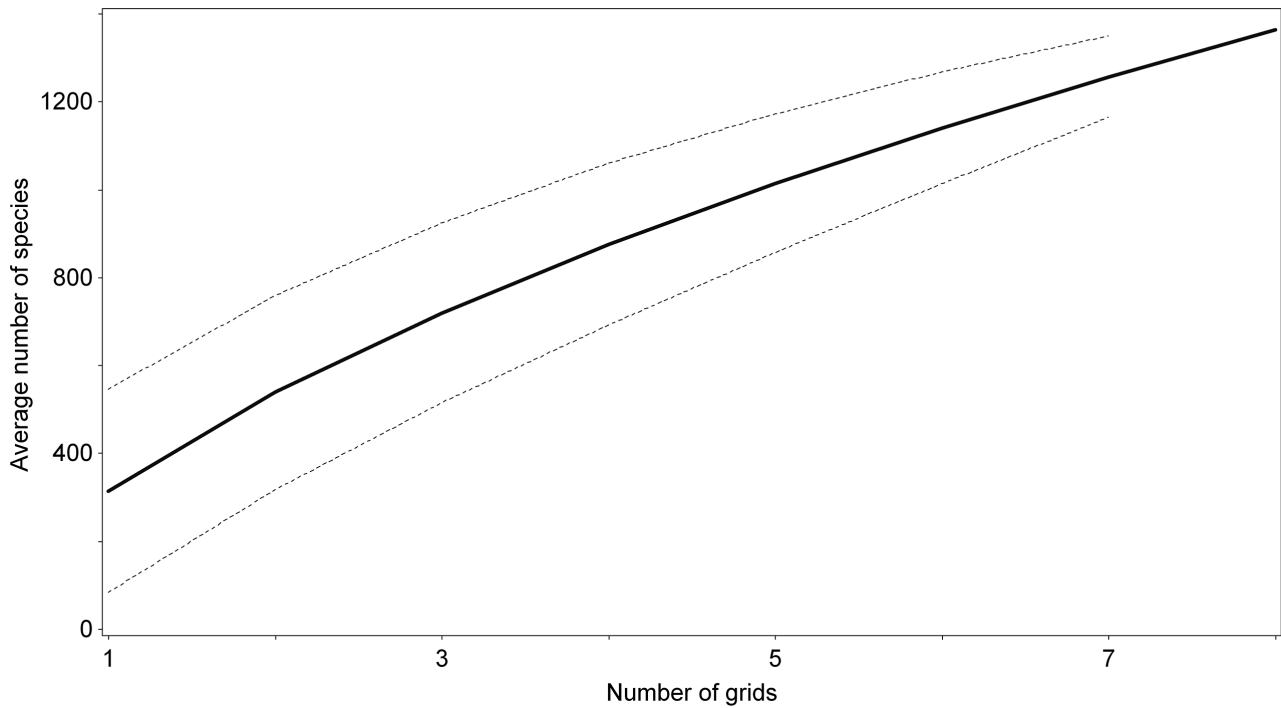


FIGURE 5. Species-area curve derived through randomized subsampling of eight selected grids with high sampling scores.

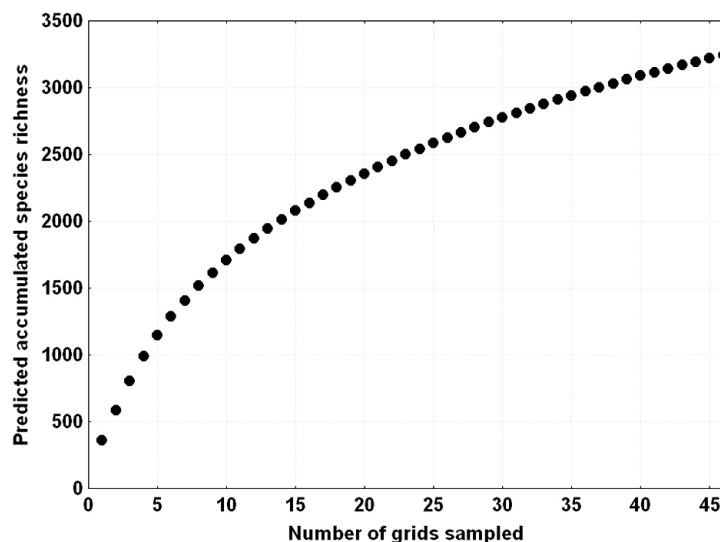


FIGURE 6. Non-linear estimation of global species richness derived from species-area curve and extrapolated to 46 grids.

Assuming the same proportional increase as found in species found within the grid area, the total species richness in extratropical regions could be estimated at $1.74 \times 74 \approx 130$ species. Likewise, global species richness in

subfamily Gomphilloideae, with currently 400 accepted species, could be estimated at $1.74 \times 400 \approx 700$ species. This is likely an underestimation, since many species in this subfamily are currently assumed to be pantropical, and no molecular data are available to test this assumption; in the core Graphidaceae, many supposedly subtropical species turned out to represent more than one species, usually with restricted distribution. This would result in a total of approximately $3,500 + 130 + 700 = 4,330$ species predicted for the entire family. Considering that approximately 2,326 have been formally described and accepted at this point (including subfamily Gomphilloideae), with further 140 awaiting description, an additional approximately 1,850 are awaiting discovery (Table 8), nearly 1,500 of which are (sub-)tropical taxa in the core Graphidaceae (subfamilies Fissurinoideae and Graphidoideae).

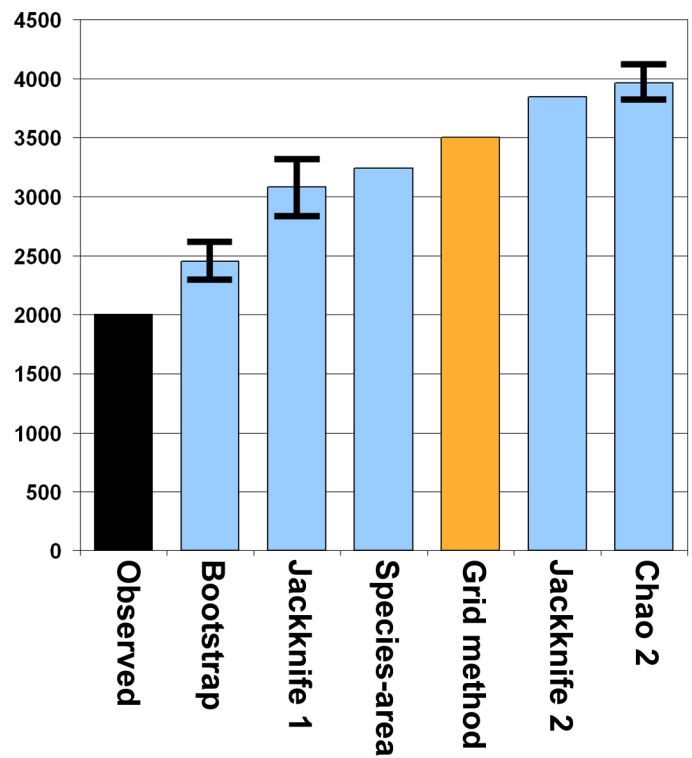


FIGURE 7. Comparison of prediction of global species richness of (sub-)tropical core Graphidaceae using different approaches.

TABLE 8. Observed (known) and predicted global species richness for Graphidaceae.

Group	Observed	Predicted	To be discovered
(Sub-)tropical core Graphidaceae (subfamilies Fissurinoideae, Graphidoideae, Redonographoideae)	2,005	≈ 3,500	≈ 1,500
Extratropical core Graphidaceae	74	≈ 130	≈ 55
Subfamily Gomphilloideae	400	≈ 700	≈ 300
Total	2,479	≈ 4,330	≈ 1,850

Our method allowed us to identify regions in which this predicted diversity is likely to be discovered, so-called "discovery hotspots" (Table 6, Fig. 8). These are in particular grid 2 (Mexico), grid 6 (Colombia, Venezuela), grid 8 (continental Ecuador, western and central Peru), grid 10 (eastern Amazon), grid 12 (Bolivia), grids 20–22 and 26 (tropical West Africa), grid 27 (tropical East Africa), grid 30 (Madagascar, Reunion, Mauritius), grid 33 (Myanmar, northern Thailand), grid 34 (China), grids 40 and 41 (Indonesia, Papua New Guinea), and grid 43 (Australia: Northern Territory).

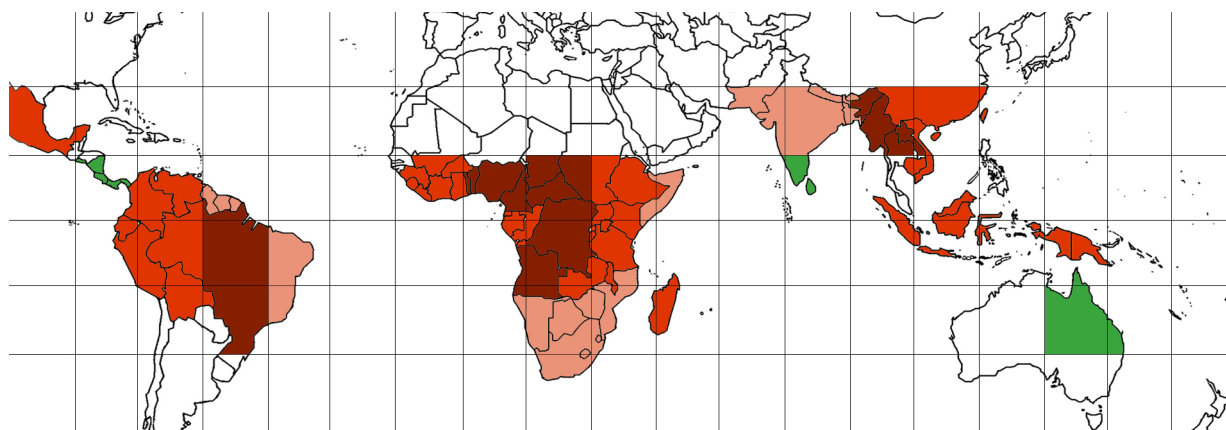


FIGURE 8. Predicted hotspots of undiscovered species richness in Graphidaceae (see Table 5; dark red +++, red ++, light red +) and areas of high observed species richness used to calibrate the predictive model (see Table 5; green; colors online only; the green regions are southern Central America, southern India, Sri Lanka and northwest Australia).

Discussion

Our statistical approach predicted approximately 1,850 species awaiting discovery in the lichen family Graphidaceae, most of them (about 1,500) representing (sub-)tropical taxa in subfamilies Fissurinoideae, Graphidoideae, and Redonographoideae. The approach we used is rather robust, since it relies on two simple measures: sum total of predicted grid richness, and average grid distribution. The predictive model assumes a simplified linear relationship between grid species richness and a score derived from sampling effort and vegetation diversity, as well as landmass. This model shows a high correlation, explaining nearly 95% of the variance in the data, but is not necessarily accurate for individual grid predictions. There are other parameters explaining grid species richness, such as evolutionary history of the area in question and dispersal limitations of individual species, often correlated with their ecological preferences. Not including these parameters in the model might lead to over- or underestimation of species richness in particular grids. However, since only the sum total of predicted grid richness is required for the prediction of global species richness, the global prediction is not especially sensitive against inaccurate individual grid predictions, since overestimates for certain grids are balanced by underestimates in other grids. For example, we observed the highest grid species richness in grid 36 (southern India, Sri Lanka), with 499 species, but the simplified model predicts only 366 species for this grid, which is a substantial underestimation. In this case, the particular evolutionary history of the Indian subcontinent as 'biotic ferry' between Gondwana and Laurasia (McKenna 1973; Scotese 2001; Conti *et al.* 2002; Hedges 2003) might have generated a unique lichen biota later mixed with southeast Asian elements, leading to an unusual high species richness that cannot be explained by vegetation diversity alone. Our predictive model takes a conservative approach in this respect by downweighting this unusual high grid species richness when used for calibration. Thus, our prediction might still be an underestimation of the real global species richness.

The highest values predicted for individual grids, ranging between 625 and 653 species, are not far off from the highest observed numbers found in grids 5 (Central America) and 36 (southern India, Sri Lanka), with 443 and 499 species, respectively. Partially ongoing surveys including or focusing on Graphidaceae in these two grids (Wirth & Hale 1963, 1978; Hale 1978; Breuss 2000, 2001, 2002, 2004, 2008, 2011; Adawadkar & Makhija 2004, 2005, 2006, 2007; Makhija & Adawadkar 2005a, b, 2007; Makhija *et al.* 2005, 2006, 2009; Breuss & Neuwirth 2007; van den Boom *et al.* 2007, 2013; Chitale *et al.* 2009, 2011; Lücking *et al.* 2008; Sharma & Makhija 2009a, b; Sharma *et al.* 2010a, b, 2012; Sharma & Khadilkar 2011, 2012; Sipman *et al.* 2012; Weerakoon *et al.* 2012a, b; Wijeyaratne *et al.* 2012; Bárcenas-Peña *et al.* 2013) have been rather thorough but are by no means complete, so that it is a rather safe to predict that individual grids may harbour more than 600 species.

Our results are further supported by the results from two separate, non-parametric methods. The approach of assembling a non-linear model based on a species-area curve derived from eight well-sampled grids yielded a very

similar prediction for global species richness of (sub-tropical) core Graphidaceae (3,244 versus 3,503 species). The species estimators yielded variable results, between 2,454 (Bootstrap) and 3,962 (Chao 2). The bootstrap estimator provided much lower estimates than the other estimators, only slightly higher than the observed number of species in the dataset. This estimator is generally considered a poor measure (Chazdon *et al.* 1998). The second order Jackknife is considered one of the best estimators for extrapolated species richness, supposed to be least susceptible to sampling bias (Chazdon *et al.* 1998; Hortal *et al.* 2006). The estimate of 3,850 species was about 10% above the estimate from the grid method and slightly lower than the Chao 2 estimate. Both Chao 2 and first order Jackknife are considered the most effective estimators if the number of samples is small relative to the sampling universe (Colwell & Coddington 1994; Brose *et al.* 2003; Walther & Moore 2005). Notably, many studies suggest that even progressive estimators such as Chao 2 and first order Jackknife underestimate true species richness. However, richness estimators are optimized to extrapolate from a small number of samples representing a fraction of the sampling universe and hence might not work effectively on grid data which cover the maximum number of samples but vary greatly in sampling effort. Hence, we consider the estimate from the grid method, which is close to the central tendency of all methods compared, as most realistic, also because it uses a broad set of underlying data, rather than focusing on the frequency of rare species.

An uncertainty level has to be attached to the interpolated estimation of grid distribution per species, since it can be assumed that increasing sampling will increase known species distributions not only by adding grids between disjunctions, but also by adding grids beyond the known range of a species. Interpolation techniques only consider the former, in our case increasing estimated average grid distribution from 2.78 to 4.63 grids, which corresponds to an area of approximately 11.5 million km² or almost three times the size of the United States. While this is a large area, lichen species are known to occupy much larger areas and pantropical or even cosmopolitan taxa have been confirmed through molecular data in Graphidaceae, such as *Dyplolabia afzelii* and *Thelotrema lepadinum* (Rivas Plata *et al.* 2013). On the other hand, molecular studies also suggest that the bulk of species in lichenized fungi have a much more restricted distribution than previously assumed, corresponding to areas smaller than the average estimated here and often to areas smaller than a single grid (Lücking *et al.* 2013; Moncada *et al.* 2013a, b; Rivas Plata *et al.* 2013). Notably, the confirmed widespread species are mostly graphidoid taxa found in more exposed microsites and often in disturbed habitats, which appears to facilitate dispersal even under changing climatic conditions through time. Thus far, none of the species that are more characteristic of tropical rainforest understories, such as in the genera *Fissurina*, *Ocellularia*, *Rhabdodiscus*, and *Stegobolus*, has been confirmed as being pantropical by means of molecular data (Rivas Plata *et al.* 2013). Using grid ordination and randomization of grid occurrences by means of an indicator species test, we could show that indeed most species in the family are confined to one of the three large tropical regions, and many are known from a single grid only. Hence, we can assume that the interpolated average calculated here is a rather realistic value. This is also supported when looking at the observed maximum grid distributions per species and the maximum expected values these can obtain. The maximum value of 28 grids in *Dyplolabia afzelii* corresponds to 61% of all grids, meaning that a proportional increase of grid distribution per species assuming the possible maximum of 46 for the species with the widest range would yield an increase in average grid distribution by the factor $46 / 28 = 1.64$. If we multiply the observed average grid distribution of 2.78 by 1.64, we obtain a predicted value of 4.56, very similar to the value of 4.63 obtained through interpolation of grid distribution ranges.

The predicted number of 1,850 undiscovered species, including 1,500 species in the core Graphidaceae, amounts to more than 75% of the currently known species. This proportion is rather close to the prediction made by Lücking *et al.* (2009b) for all lichenized species globally, with 28,000 predicted species compared to 17,500 currently known (Feurerer & Hawksworth 2007), or a 63% increase. Not all lichen groups have a similar proportion of unknown species; hence, with over 75% of the currently known species, the estimate for Graphidaceae, one of the larger and less well-studied families, seems in line with the global prediction for all lichenized species. Yes, 1,850 species is a huge number, which raises two important questions: (1) Where are these species to be found taxonomically and geographically and (2) how fast can they be discovered and described and what effort is necessary for this? In terms of taxonomic affinities, our data suggest that the bulk of undiscovered species richness is to be found in genera that already have a larger number of species and which are not well-studied, either because of lack of proper identification tools or because they largely occur in hard-to-reach virgin rain forest areas. Among the new species introduced in this issue, genera with a high number of new species (*Ocellularia*, *Fissurina*) combine the following attributes: (1) already containing a large number of species; (2) largely confined to well-

conserved tropical rain forest; (3) not well-studied but with increasing amount of molecular data becoming available; and (4) global identification tools becoming available, such as the interactive key to thelotremoid taxa including tribe Ocellularieae assembled by Gaswick & Lücking (2012) and a global key for species in the genus *Fissurina* (Lücking, in prep.). This contrasts with the comparatively low proportion of new species in the large genera *Graphis*, *Phaeographis*, and *Thelotrema*. Both *Graphis* and *Thelotrema* are mostly found in (semi-)exposed situations in montane regions, and for both genera, global identification tools have been available for a few years already. This could suggest that the rate of species discoveries in these genera is decreasing and the bulk of new species have been discovered in the past few years. The low number of new species in *Phaeographis*, on the other hand, is apparently due to the lack of reliable nomenclatural and taxonomic resources in this group, which makes formal new species descriptions difficult. We therefore predict that the majority of undiscovered species belong to the genera *Fissurina*, *Ocellularia*, and *Phaeographis* and their relatives, in particular *Myriotrema*, *Rhabdodiscus*, *Sacrographa*, and *Stegobolus*. Some of these species might not be genuinely new but correspond to names in historical publications that had been subsumed into synonymy or never revised after their original descriptions.

Geographically, our findings suggests that most of this unknown diversity is to be discovered in Mexico, the Andean countries from Venezuela down to Bolivia, the eastern Amazon, most of tropical West Africa, parts of continental southeast Asia (in particular China and adjacent areas to the southwest, such as Myanmar), and Indonesia and Papua New Guinea. Considering that substantial efforts in the past decade to catalogue the diversity of Graphidaceae have concentrated on a few regions only (southeastern North America, Costa Rica, the western Amazon, small parts of tropical Africa, India, Sri Lanka, Thailand, Australia, New Caledonia), and these efforts have unearthed over 600 new species, finding an additional 1,850 new species in the vast area covered by the aforementioned "discovery hotspot" regions seems not out of the ordinary. If we assume a similar-sized global task force and a continued collaborative effort as currently available, 600 species described in ten years translates to about 30 years required to describe an additional 1,850 species. However, this is only possible if there is continued substantial support for fieldwork, taxonomic work, and molecular work at a global scale, which will require increased efforts of taxonomists to explain the importance of this fundamental research for our understanding of the diversity of the globe to the public and funding agencies.

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Biodiversity of lichenized fungi tribe Ocellularieae, subfamily Graphidoideae in Thailand

ความหลากหลายทางชีวภาพของไลเคนไนซ์ฟังไจในเผ่า Ocellularieae



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INTRODUCTION

Graphidaceae contains four subfamilies, Fissurinoideae, Gomphilloideae, Graphidoideae, and Redonographoideae (Lumbsch *et al.*, 2014) (Fig. 1), among which Graphidoideae contains probably more than 75% of the species. Subfamily Graphidoideae is divided into three tribes: Graphideae (corresponding to the bulk of the former Graphidaceae), Thelotremateae (corresponding largely to the genus *Thelotrema* sensu Hale 1980), and *Ocellularieae* (corresponding largely to the genera *Myriotrema* and *Ocellularia* sensu Hale 1980). Lichenized fungi of tribe Ocellularieae belonging to subfamily Graphidoideae, currently number over 25,000 species worldwide, while the tribe Ocellularieae has been reported to have 11 genera; *Ampliotrema* Kalb ex Kalb, *Compositrema* Rivas Plata, *Fibrillithecis* Frisch, *Glaucotrema* Rivas Plata & Lumbsch, *Leptotrema* Mont. & v. d. Bosch, *Melanotrema* Frisch, *Myriotrema* Fée, *Ocellularia* G. Mey., *Redingeria* Frisch, *Rhabdodiscus* Vainio, *Stegobolus* Montagne (Kraichak *et al.*, 2014) (Fig. 2).

MATERIAL AND METHOD

All samples for this study were collected from different natural forests all over Thailand; tropical rainforest, lower montane rainforest, dry evergreen, dry dipterocarp, mangrove and beach forests. The reference collection was deposited at MSUT (Natural Medicinal Mushroom Museum) and F (The Field Museum). Sections of thalli and apothecia were cut using a razor blade and examined in water, a solution of KOH, and Lugol's solutions using a ZEISS Axioscope 2 plus compound microscope. Chemistry test by Thin Layer Chromatography technique using Horizontal Developing Chamber for TLC/HPTLC 10x10 cm plate with HPTLC Silica gel 60 F₂₅₄ with standard method on solvent C (Arup *et al.* 1993; Culberson 1972).

FIG. 1. Best-scoring maximum-likelihood tree based on a three-gene skeleton dataset of the core Graphidaceae. Thick branches indicate bootstrap support 70% or higher and/or posterior probabilities 95% or higher. Major lineages are highlighted. Novel genus lineages are marked with an asterisk. (Lumbsch *et al.*, 2014)

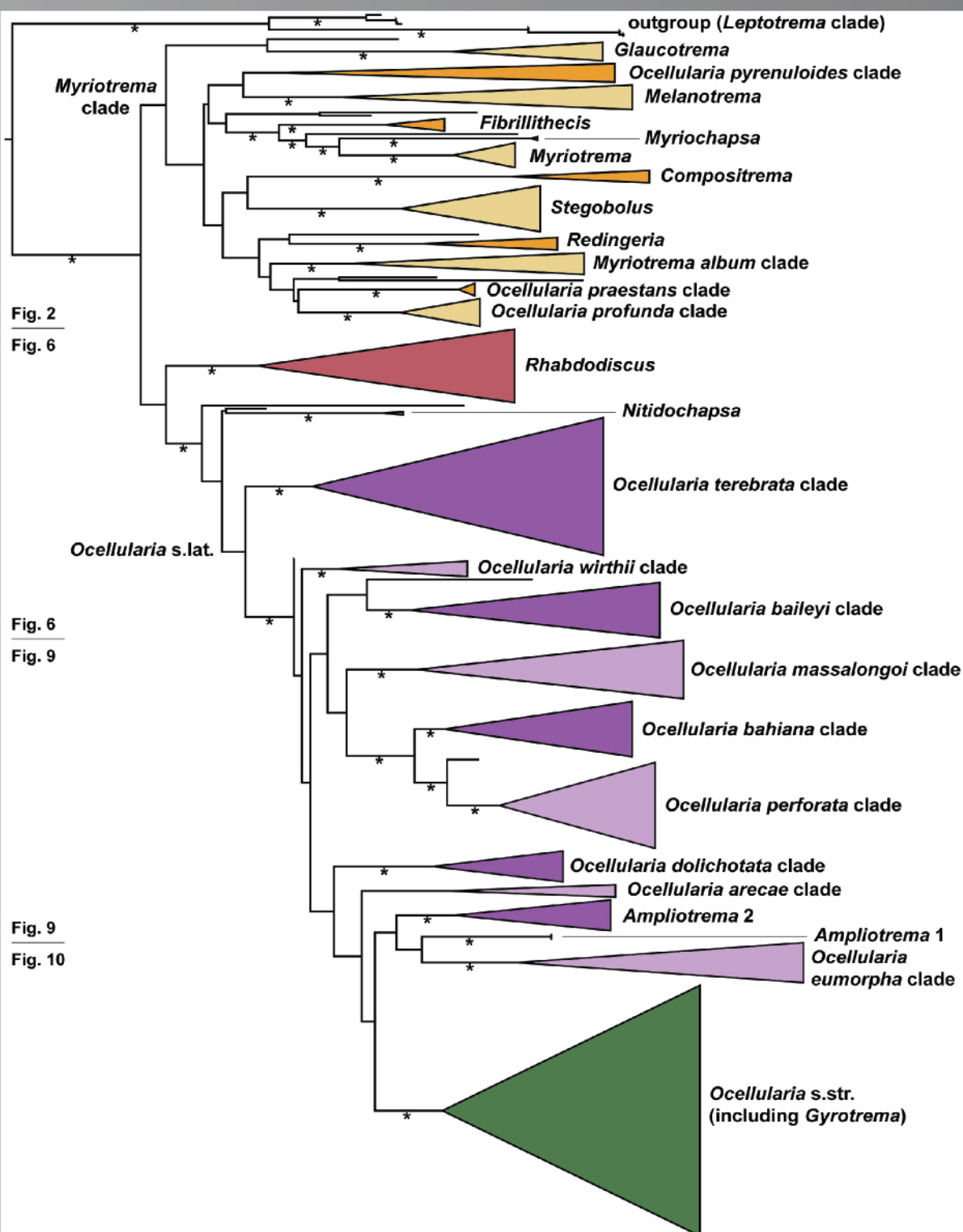
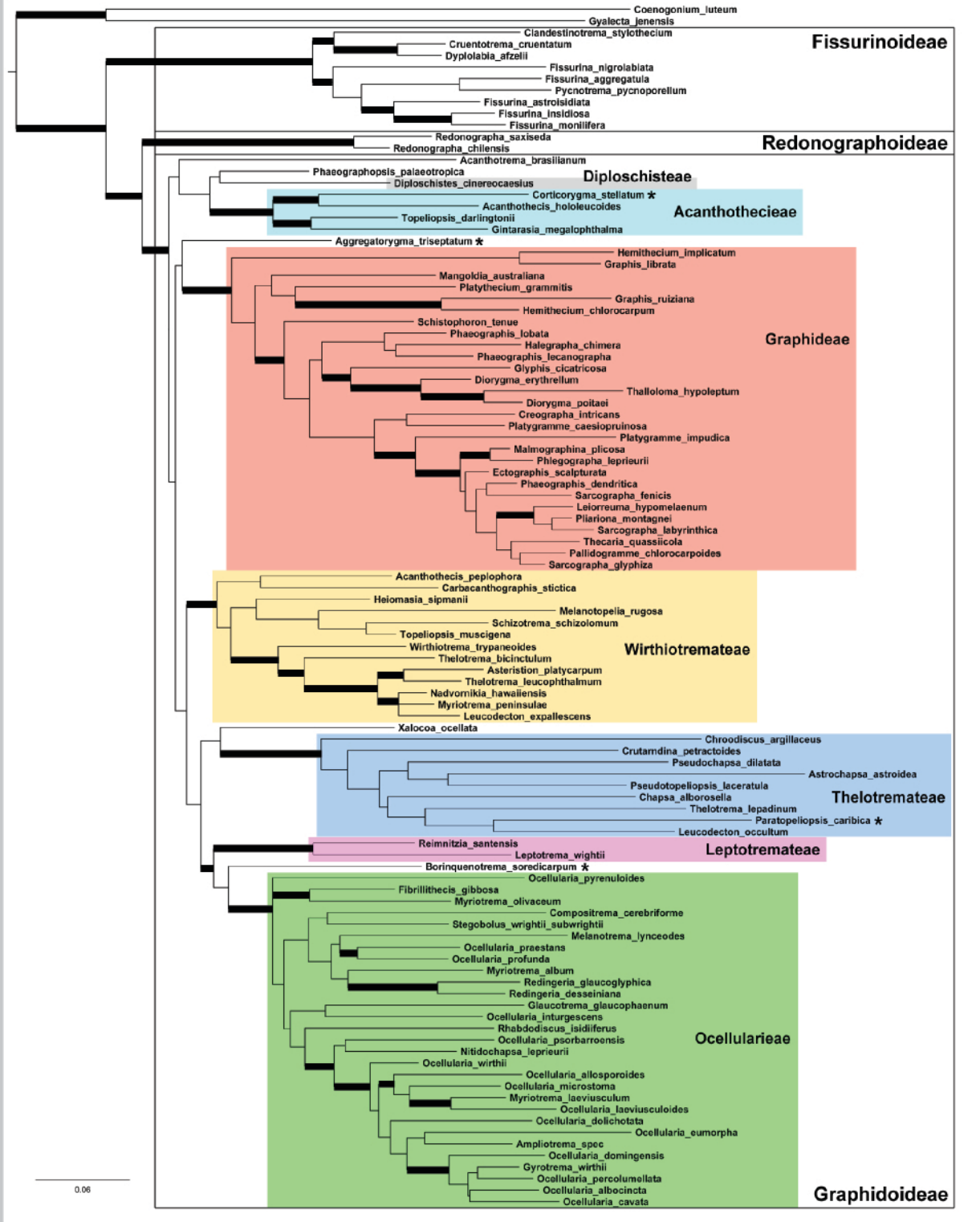
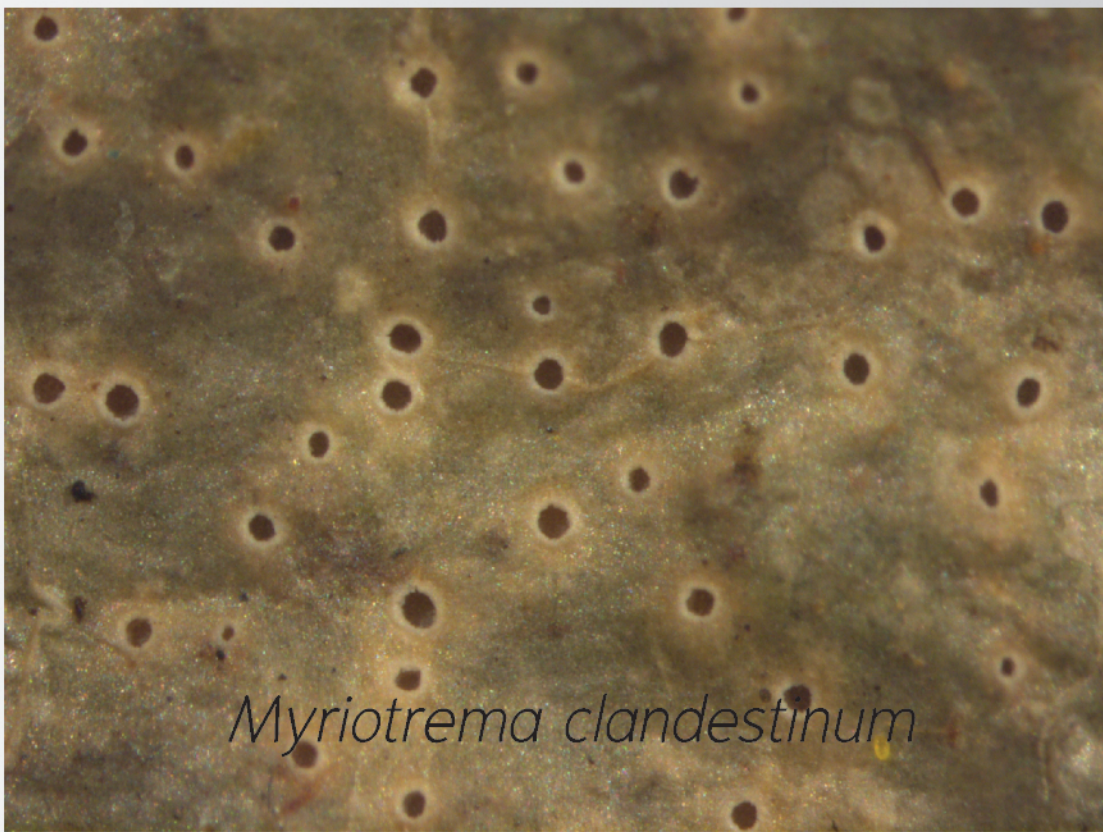
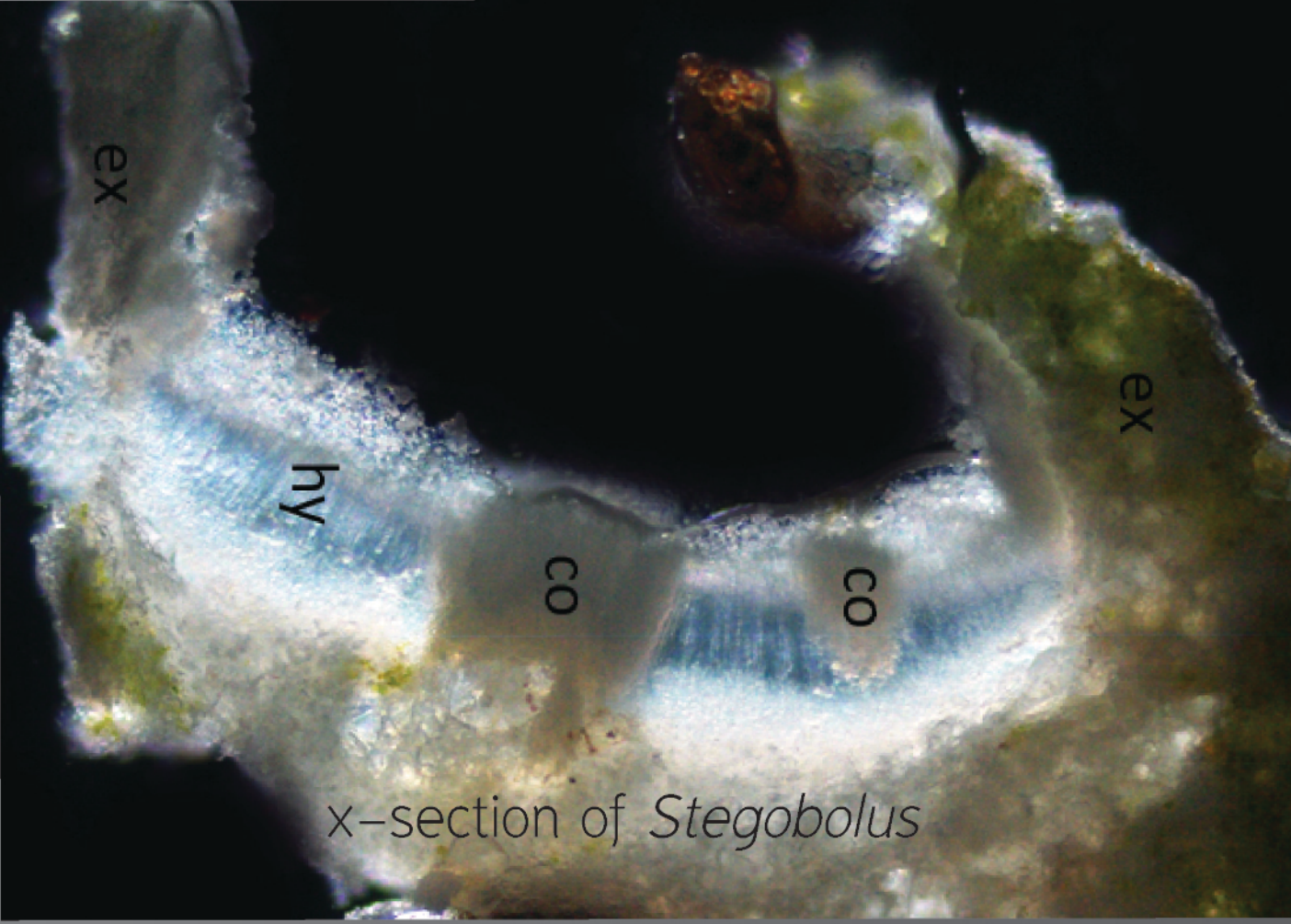
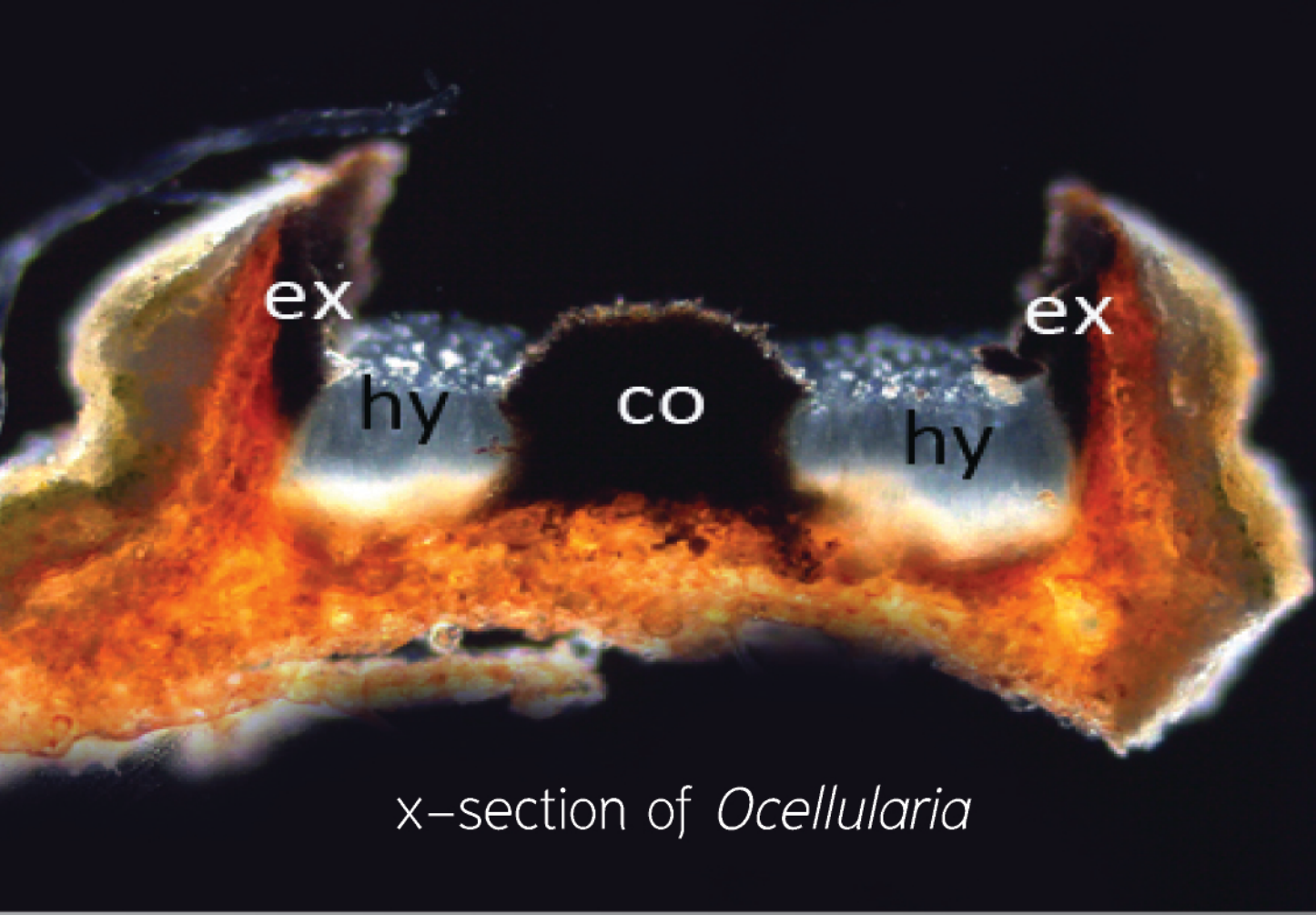


FIG. 2. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing major clades. Supported clades are marked with an asterisk. Detailed phylogenies for each portion of the tree, as well as numeric support values. (Kraichak *et al.*, 2014)



RESULTS AND DISCUSSION

The results found 8 genera and 55 taxa such as *Compositrema thailandicum*, *Fibrillithecis thailandica*, *Leptotrema phaeosporum* var. *vainiona*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. aff. myriotremoides*, *My. olivaceum*, *Ocellularia albocincta*, *O. allosporoides*, *O. aff. allosporoides*, *O. ascidioidea*, *O. aff. ascidioidea*, *O. cavata*, *O. cerebriiformis*, *O. croceoisidiata*, *O. cruentata*, *O. dolichotata*, *O. fumosa*, *O. aff. fumosa*, *O. granulifera*, *O. guianensis*, *O. interponenda*, *O. interposita*, *O. aff. interposita*, *O. isidiophora*, *O. khunantensis*, *O. kohphangangensis*, *O. laeviusculoides*, *O. aff. laeviusculoides*, *O. massalongoi*, *O. nitida*, *O. papillata*, *O. percolumnellata*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. rimosa*, *O. salazinica*, *O. subcalvescens*, *O. subdolichotata*, *O. subleucina*, *O. subgranulosa*, *O. thelotremoides*, *O. terebrata*, *O. violacea*, *O. viridipallens*, *O. wolseleyana*, *O. xanthostromiza*, *O. aff. zamboangensis*, *O. exigua*, *Rhabdodiscus crassus*, *Rh. marivelensis*, *Rh. subcavatus*, *Rh. subemersus* and *Stegobolus berkeleyanus*. High species diversity was found in tropical rainforest, lower montane rainforest and dry evergreen forest respectively. No lichens of tribe Ocellularieae were collected from dry dipterocarp, mangrove or beach forests.

CONCLUSIONS

Most of species in tribe Ocellularieae were found genus *Ocellularia* 74% (37 species), *Rhabdodiscus* 8% (4 species), *Myriothema* 6% (3 species), *Melanotrema* 4% (2 species) respectively. Genera *Compositrema*, *Fibrillithecis* and *Leptotrema* were found only one species. Kraichak *et al.* (2014) also reported phylogenetic analysis of tribe Ocellularieae show member presented in *Ocellularia* clade than other. The collection specimen is unidentified was found in Thailand need to be study by meolecular work in the future. Lichenized fungi of tribe Ocelluarieae in Thailand also reported the new species and new records in Papong *et al.* (2014).

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Biodiversity of lichenized fungi tribe Ocellularieae, subfamily Graphidoideae in Thailand

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Abstract

Lichenized fungi of tribe Ocellularieae belonging to subfamily Graphidoideae and family Graphidaceae, currently number over 25,000 species worldwide, while the tribe Ocellularieae has been reported to have 11 genera. All samples for this study were collected from different natural forests all over Thailand; tropical rainforest, lower montane rainforest, dry evergreen, dry dipterocarp, mangrove and beach forests. The reference collection was deposited at MSUT and The Field Museum. All samples were studied by taxonomy and chemistry test by Thin Layer Chromatography technique using Horizontal Developing Chamber for TLC/HPTLC 10x10 cm plate with HPTLC Silica gel 60 F₂₅₄ with standard method on solvent C. The results found 8 genera and 55 taxa such as *Compositrema thailandicum*, *Fibrillithecis thailandica*, *Leptotrema phaeosporum* var. *vainiona*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. aff.myriotremoides*, *My. olivaceum*, *Ocellularia albocincta*, *O. allosporoides*, *O. aff.allosporoides*, *O. ascidioidea*, *O. aff.ascidioidea*, *O. cavata*, *O. cerebriformis*, *O. croceosidiata*, *O. cruentata*, *O. dolichotata*, *O. fumosa*, *O. aff.fumosa*, *O. granulifera*, *O. guianensis*, *O. interponenda*, *O. interposita*, *O. aff.interposita*, *O. isidiophora*, *O. khunantensis*, *O. kohphangangensis*, *O. laeviusculoides*, *O. aff. laeviusculoides*, *O. massalongoi*, *O. nitida*, *O. papillata*, *O. percolumnellata*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. rimosa*, *O. salazinicola*, *O. subcalvescens*, *O. subdolichotata*, *O. subleucina*, *O. subgranulosa*, *O. thelotremoides*, *O. terebrata*, *O. violacea*, *O. viridipallens*, *O. wolseleyana*, *O. xanthostromiza*, *O. aff.zamboangensis*, *O. exigua*, *Rhabdodiscus crassus*, *Rh. marivelensis*, *Rh. subcavatus*, *Rh. Subemersus* and *Stegobolus berkeleyanus*. High species diversity was found in tropical rainforest, lower montane rainforest and dry evergreen forest respectively. No lichens of tribe Ocellularieae were collected from dry dipterocarp, mangrove or beach forests.

Keywords: Ascomycota: Ostropales/ phytotaxa/ Graphidaceae/ thin layer chromatography/ taxonomy



ความหลากหลายทางชีวภาพของไลเคนไชน์ฟงใจในเผ่า Ocellularieae วงศ์ย่อย Graphidoideae ในประเทศไทย

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บทคัดย่อ

ไลเคนไชน์ฟงใจหรือราที่ก่อให้เกิดไลเคนเผ่า Ocellularieae จัดอยู่วงศ์ย่อย Graphidoideae และอยู่ในวงศ์ Graphidaceae ปัจจุบันมีรายงานจำนวนสมาชิกในวงศ์นี้มากกว่า 25,000 ชนิด ส่วนไลเคนเผ่า Ocellularieae มีรายงานการค้นพบ 11 สกุล ตัวอย่างไลเคนจากการสำรวจและเก็บตัวอย่างจากป่าธรรมชาติในประเทศไทยในชนิดป่าที่แตกต่างกันได้แก่ป่าดิบชื้นป่าดิบเขา ป่าดิบแล้งป่าเต็งรังป่าชายหาดและป่าชายหาดตัวอย่างอ้างอิงเก็บรักษาไว้ที่ MSUT และ F โดยทำการศึกษาอนุกรมวิธานของไลเคนไชน์ฟงใจเผ่า Ocellularieae และศึกษาสารไลเคนด้วยวิธีรังเคลสผิวบางด้วยเครื่อง Horizontal Developing Chamber For TLC/HPTLC 10x10 cm plate โดยใช้แผ่น HPTLC Silica gel 60 F₂₅₄ ใช้ตัวทำละลายระบบ C และใช้วิธีมาตรฐานพบไลเคนทั้งหมด 8 สกุลและ 55 แทกซาได้แก่ *Compositrema thailandicum*, *Fibrillithecia thailandica*, *Leptotrema phaeosporum* var. *vainiona*, *Melanotrema melanophthalmum*, *M. platystomum*, *Myriotrema clandestinum*, *My. aff. myriotremoides*, *My. olivaceum*, *Ocellularia albocincta*, *O. allosporoides*, *O. aff. allosporoides*, *O. ascidioidea*, *O. aff. ascidioidea*, *O. cavata*, *O. cerebriformis*, *O. croceosidiata*, *O. cruentata*, *O. dolichotata*, *O. fumosa*, *O. aff. fumosa*, *O. granulifera*, *O. guianensis*, *O. interponenda*, *O. interposita*, *O. aff. interposita*, *O. isidiophora*, *O. khunantensis*, *O. kohphangangensis*, *O. laeviusculoides*, *O. aff. laeviusculoides*, *O. massalongoi*, *O. nitida*, *O. papillata*, *O. percolumnellata*, *O. pseudopapillata*, *O. rhicnoporoides*, *O. rimosa*, *O. salazinicola*, *O. subcalvescens*, *O. subdolichotata*, *O. subleucina*, *O. subgranulosa*, *O. thelotremoides*, *O. terebrata*, *O. violacea*, *O. viridipallens*, *O. wolseleyana*, *O. xanthostromiza*, *O. aff. zamboangensis*, *O. exigua*, *Rhabdodiscus crassus*, *Rh. marivelensis*, *Rh. subcavatus*, *Rh. Subemersus* และ *Stegobolus berkeleyanus* จำนวนชนิดของไลเคนเผ่า Ocellularieae พบมากที่สุดที่ป่าดิบชื้นป่าดิบเขาและป่าดิบแล้งตามลำดับ ส่วนป่าเต็งรังป่าชายหาดและป่าชายหาดไม่พบไลเคนในเผ่านี้

คำสำคัญ: ไลเคนไชน์ฟงใจ/ ไลเคนเผ่า Ocellularieae/ ความหลากหลายทางชีวภาพ

(Ostropales, Ascomycota)

Graphidaceae of THAILAND 1: The genus *Ocellularia*

1

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.
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1 *Ocellularia allosporoides*



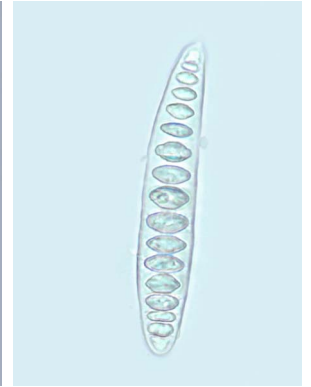
2 *Ocellularia allosporoides*



3 *Ocellularia allosporoides*
Asci with ascospores



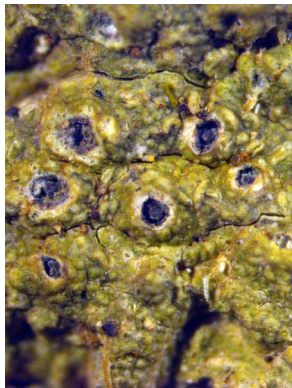
4 *Ocellularia allosporoides*
Transversely septate ascospore



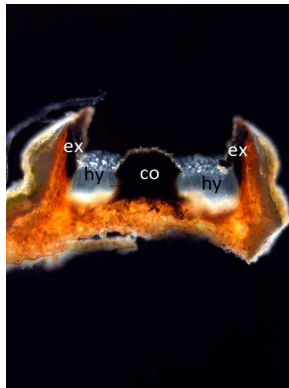
5 *Ocellularia allosporoides*
Transversely septate ascospore



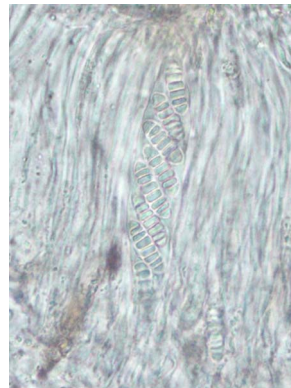
6 *Ocellularia ascidioidea*



7 *Ocellularia ascidioidea*



8 *Ocellularia ascidioidea*
Cross section through ascus



9 *Ocellularia ascidioidea*
Asci with ascospores



10 *Ocellularia ascidioidea*
Transversely septate ascospores



11 *Ocellularia cavata*



12 *Ocellularia cavata*



13 *Ocellularia cavata*



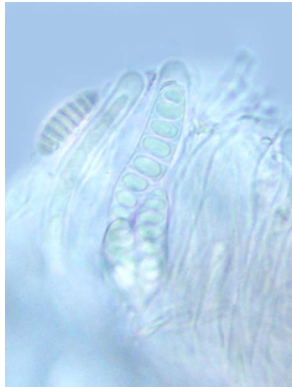
14 *Ocellularia cavata*
Yellow medulla



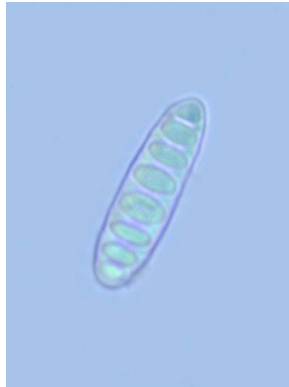
15 *Ocellularia cavata*



16 *Ocellularia cavata*



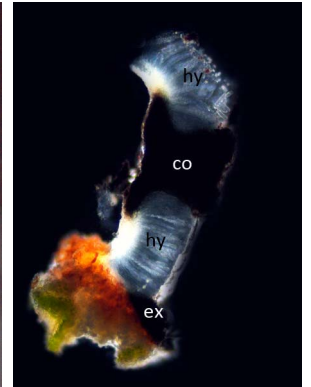
17 *Ocellularia cavata*
Asci with ascospores



18 *Ocellularia cavata*
Transversely septate ascospore



19 *Ocellularia cavata*
Transversely septate ascospores



20 *Ocellularia cavata*
Cross section through ascus

co = columella, ex = exciple, hy = hymenium

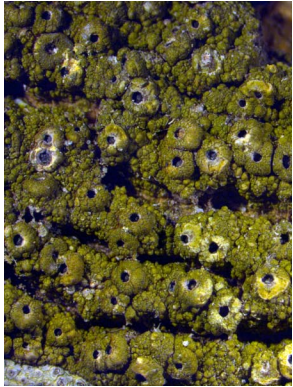
(Ostropales, Ascomycota)

Graphidaceae of THAILAND 1: The genus *Ocellularia*

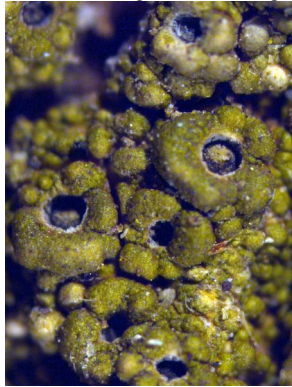
2

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

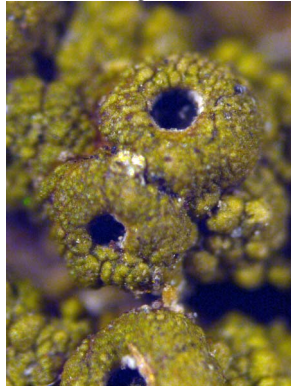
Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.
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21 *Ocellularia croceoisidiata*



22 *Ocellularia croceoisidiata*



23 *Ocellularia croceoisidiata*



24 *Ocellularia croceoisidiata*
Asci with ascospores



25 *Ocellularia croceoisidiata*
Transversely septate ascospore



26 *Ocellularia ascidioidea*



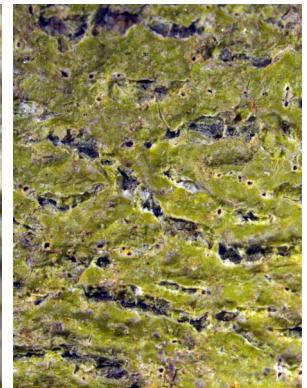
27 *Ocellularia ascidioidea*



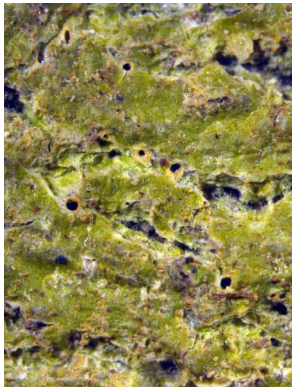
28 *Ocellularia fumosa*



29 *Ocellularia fumosa*



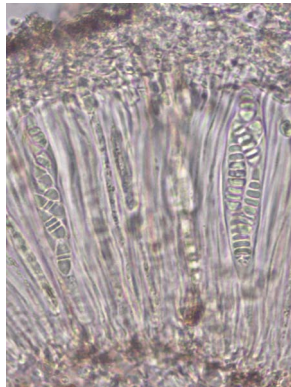
30 *Ocellularia interponenda*



31 *Ocellularia exigua*



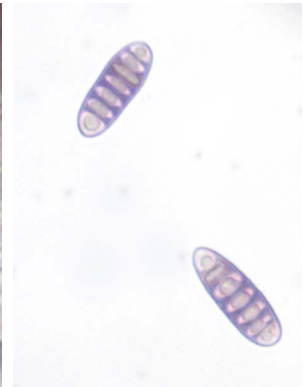
32 *Ocellularia exigua*



33 *Ocellularia exigua*
Asci with ascospores



34 *Ocellularia exigua*
Transversely septate ascospores



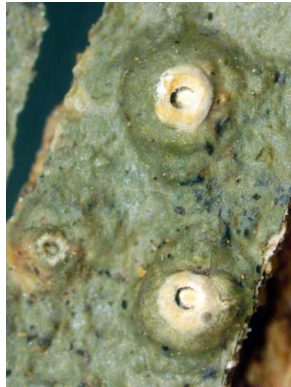
35 *Ocellularia exigua*
Transversely septate ascospores



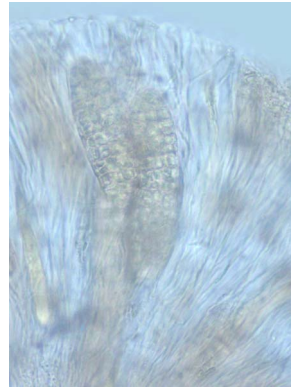
36 *Ocellularia interponenda*



37 *Ocellularia interponenda*



38 *Ocellularia interponenda*
Cross section through ascoma



39 *Ocellularia interponenda*
Asci with ascospores



40 *Ocellularia interponenda*
Muriform ascospore

co = columella, ex = exciple, hy = hymenium

(Ostropales, Ascomycota)

Graphidaceae of THAILAND 1: The genus *Ocellularia*

3

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

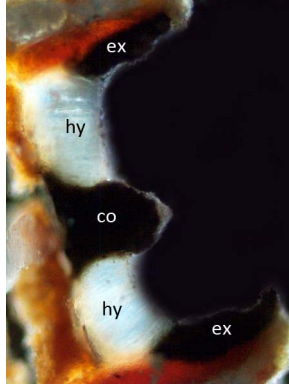
Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.
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41 *Ocellularia isidiophora*



42 *Ocellularia isidiophora*



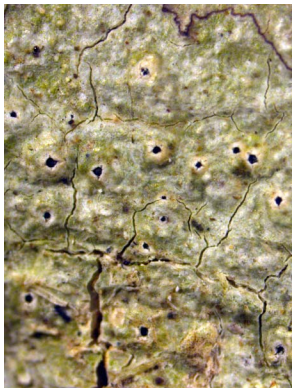
43 *Ocellularia isidiophora*
Cross section through ascoma



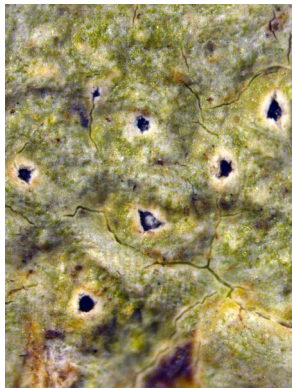
44 *Ocellularia isidiophora*
Asci with ascospores



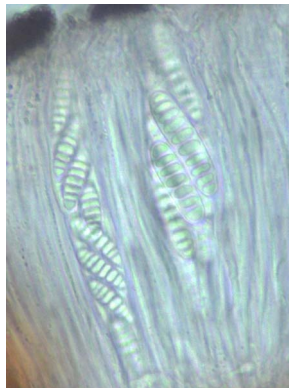
45 *Ocellularia isidiophora*
Transversely septate ascospores



46 *Ocellularia laeviusculoides*



47 *Ocellularia laeviusculoides*



48 *Ocellularia laeviusculoides*
Asci with ascospores



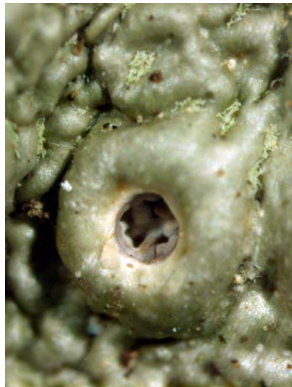
49 *Ocellularia laeviusculoides*



50 *Ocellularia laeviusculoides*
Muriform ascospore



51 *Ocellularia nitida*



52 *Ocellularia nitida*



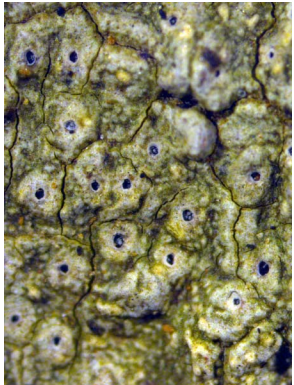
53 *Ocellularia nitida*



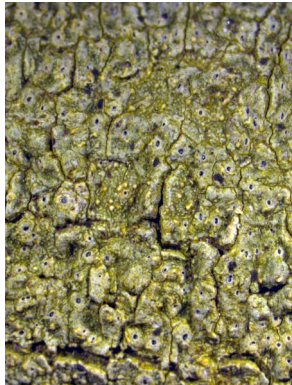
54 *Ocellularia nitida*
Submuriform ascospores



55 *Ocellularia nitida*
Submuriform ascospore



56 *Ocellularia papillata*



57 *Ocellularia papillata*



58 *Ocellularia papillata*
Cross section through ascoma



59 *Ocellularia papillata*
Transversely septate ascospores



60 *Ocellularia papillata*
Transversely septate ascospores

co = columella, ex = exciple, hy = hymenium

(Ostropales, Ascomycota)

Graphidaceae of THAILAND 1: The genus *Ocellularia*

3

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

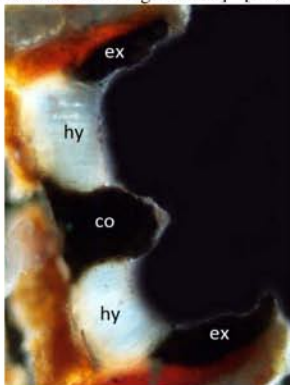
Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.
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41 *Ocellularia isidiophora*



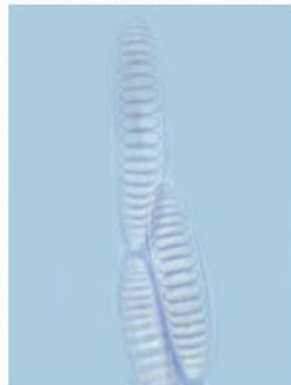
42 *Ocellularia isidiophora*



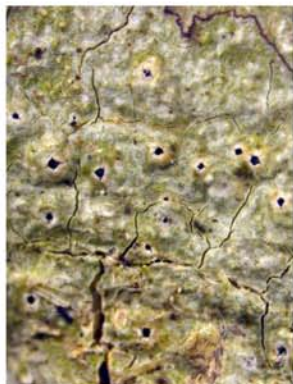
43 *Ocellularia isidiophora*
Cross section through ascus



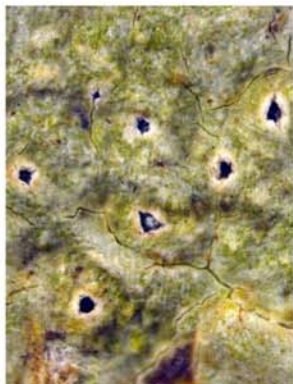
44 *Ocellularia isidiophora*
Asci with ascospores



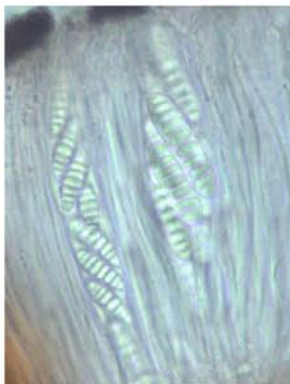
45 *Ocellularia isidiophora*
Transversely septate ascospores



46 *Ocellularia laeviusculoides*



47 *Ocellularia laeviusculoides*



48 *Ocellularia laeviusculoides*
Asci with ascospores



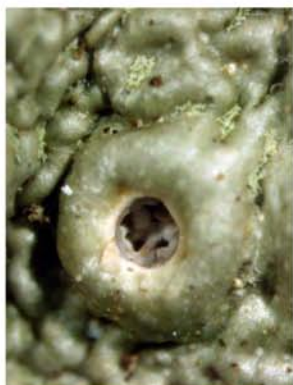
49 *Ocellularia massalongoi*



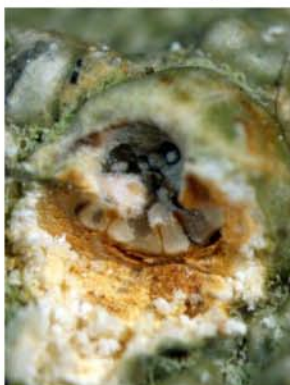
50 *Ocellularia massalongoi*
Muriform ascospore



51 *Ocellularia nitida*



52 *Ocellularia nitida*



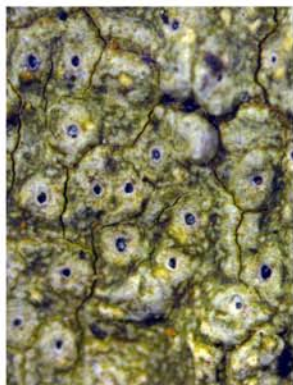
53 *Ocellularia nitida*



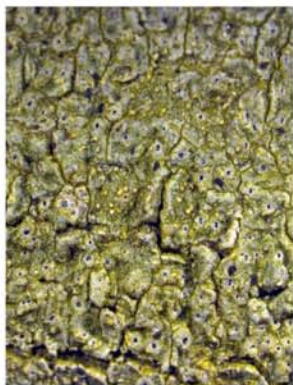
54 *Ocellularia nitida*
Submuriform ascospores



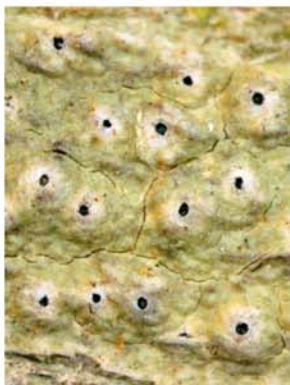
55 *Ocellularia nitida*
Submuriform ascospore



56 *Ocellularia papillata*



57 *Ocellularia papillata*



58 *Ocellularia papillata*
Cross section through ascus



59 *Ocellularia papillata*
Transversely septate ascospores



60 *Ocellularia papillata*
Transversely septate ascospores

co = columella, ex = exciple, hy = hymenium

(Ostropales, Ascomycota)
Graphidaceae of THAILAND 2:

1

The genera *Astrochapsa*, *Chapsa*, *Compositrema*, *Nitidochapsa*, *Pseudochapsa* & *Pseudotopeliopsis*

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

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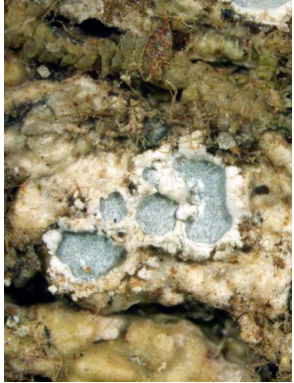
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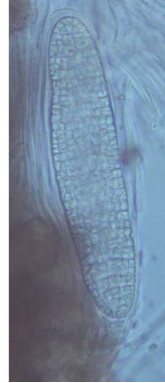
1 *Astrochapsa astroidea*



2 *Astrochapsa thailandica*



3 *Astrochapsa thailandica*



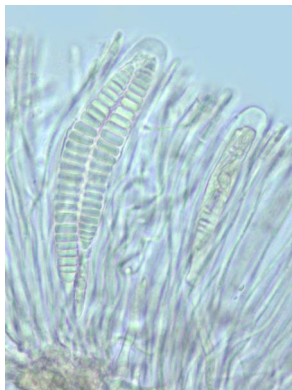
4 *Astrochapsa thailandica*
Ascus with ascospore



5 *Astrochapsa thailandica*
Muriform ascospore



6 *Chapsa indica*



7 *Chapsa indica*
Asci with ascospores



8 *Chapsa leprocarpoides*



9 *Chapsa patens*



10 *Chapsa patens*



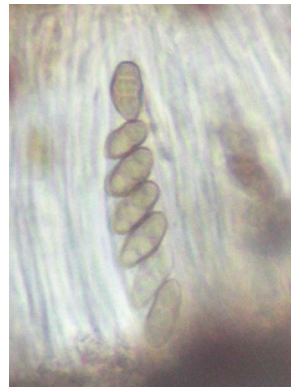
11 *Chapsa pulvereodiscus*



12 *Chapsa pulvereodiscus*



13 *Chapsa pulvereodiscus*



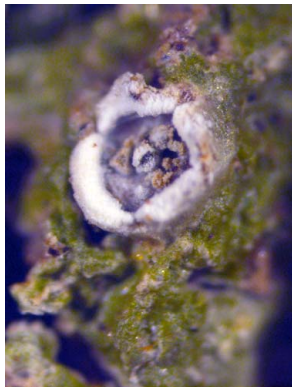
14 *Chapsa pulvereodiscus*
Asci with ascospores



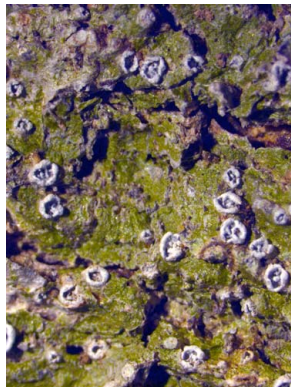
15 *Chapsa pulvereodiscus*
Submuriform ascospores



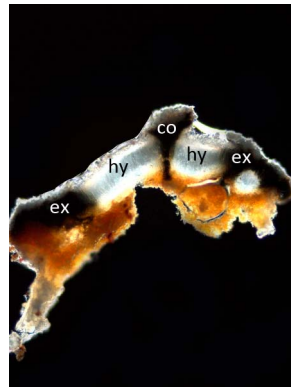
16 *Compositrema thailandicum*



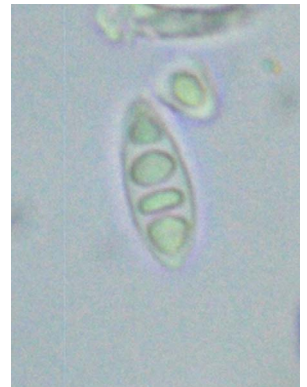
17 *Compositrema thailandicum*



18 *Compositrema thailandicum*



19 *Compositrema thailandicum*
Cross section through ascoma



20 *Compositrema thailandicum*
Transversely septate ascospore

co = columella, ex = exciple, hy = hymenium

The genera *Astrochapsa*, *Chapsa*, *Compositrema*, *Nitidochapsa*, *Pseudochapsa* & *Pseudotopeliopsis*

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

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21 *Nitidochapsa leprieurii*



22 *Nitidochapsa leprieurii*



23 *Nitidochapsa leprieurii*



24 *Nitidochapsa leprieurii*



25 *Pseudochapsa pseudophlyctis*



26 *Pseudochapsa pseudophlyctis*



27 *Pseudochapsa pseudophlyctis*



28 *Pseudochapsa pseudophlyctis*



29 *Pseudochapsa pseudophlyctis*



30 *Pseudochapsa pseudophlyctis*



31 *Pseudotopeliopsis aggregata*



32 *Pseudotopeliopsis aggregata*



33 *Pseudotopeliopsis aggregata*



34 *Pseudotopeliopsis aggregata*



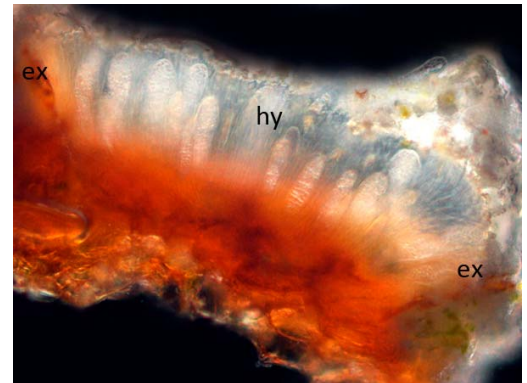
35 *Pseudotopeliopsis aggregata*



36 Tropical rainforest



37 Habitat for Graphidaceae lichens



38 *Pseudochapsa pseudophlyctis*
Cross section through ascoma

co = columella, ex = exciple, hy = hymenium

(Ostropales, Ascomycota)
Graphidaceae of THAILAND 3:

The genera *Glaucotrema*, *Leucodecton*, *Melanotrema*, *Myriotrema* & *Thelotrema*

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.

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1 *Glaucotrema glaucophaenum*



2 *Glaucotrema glaucophaenum*



3 *Leucodecton compunctum*



4 *Leucodecton compunctum*



5 *Leucodecton compunctum*
Muriform ascospore



6 *Melanotrema platystomum*



7 *Melanotrema platystomum*



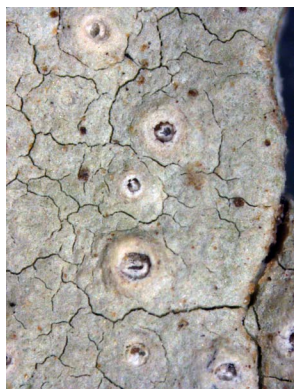
8 *Myriotrema clandestinum*



9 *Myriotrema clandestinum*



10 *Thelotrema butsatronii*



11 *Thelotrema butsatronii*



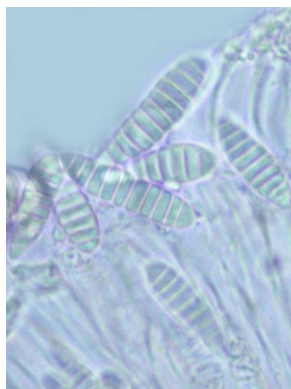
12 *Thelotrema butsatronii*
Muriform ascospore



13 *Thelotrema defossum*



14 *Thelotrema defossum*



15 *Thelotrema defossum*
Transversely septate ascospores



16 *Thelotrema porinoides*



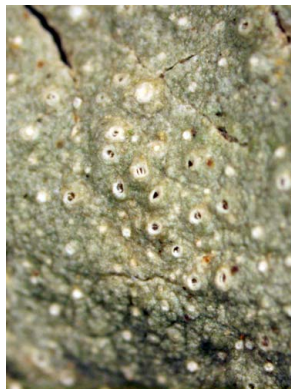
17 *Thelotrema porinoides*



18 *Thelotrema rugatulum*



19 *Thelotrema triseptatum*



20 *Thelotrema triseptatum*

(Ostropales, Ascomycota)

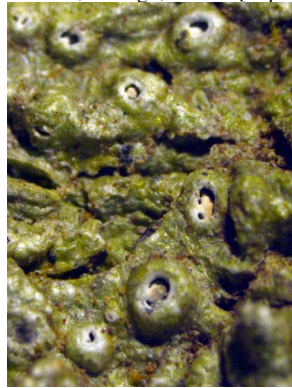
Graphidaceae of THAILAND 4: The genera *Rhabdodiscus* & *Stegobolus*

Khwanruan Butsatorn-Papong, H. Thorsten Lumbsch & Robert Lücking

Photos by K. Butsatorn-Papong. Produced by K. Butsatorn-Papong, H.T. Lumbsch, R. Lücking. Support from the Thailand Research Fund, C. Keller, A.Mellon Foundation.
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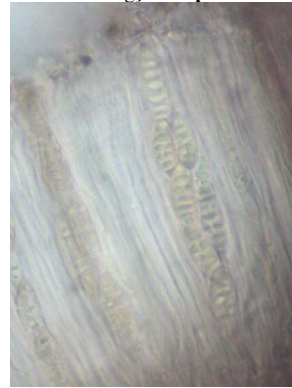
1 *Rhabdodiscus crassus*



2 *Rhabdodiscus crassus*



3 *Rhabdodiscus crassus*



4 *Rhabdodiscus crassus*
Asci with ascospores



5 *Rhabdodiscus crassus*
Submuriform ascospore



6 *Rhabdodiscus subcavatus*



7 *Rhabdodiscus subcavatus*



8 *Rhabdodiscus subcavatus*



9 *Rhabdodiscus subemersus*



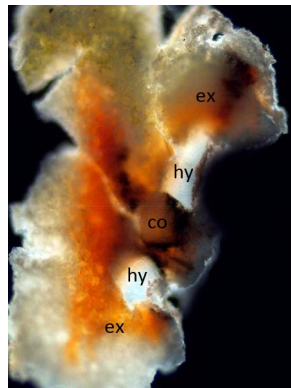
10 *Rhabdodiscus subemersus*



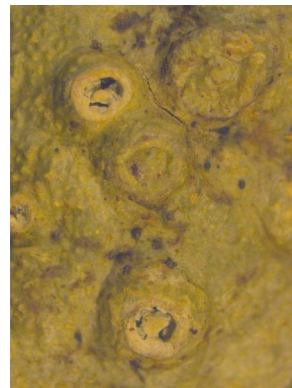
11 *Stegobolus berkeleyanus*



12 *Stegobolus berkeleyanus*



13 *Stegobolus berkeleyanus*
Cross section through ascoma



14 *Stegobolus kophangangensis*



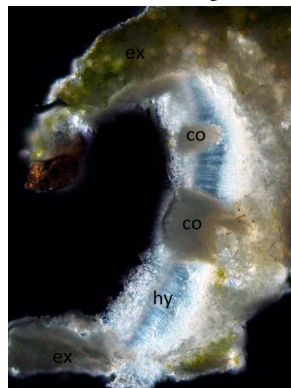
15 *Stegobolus kophangangensis*
Muriform ascospores



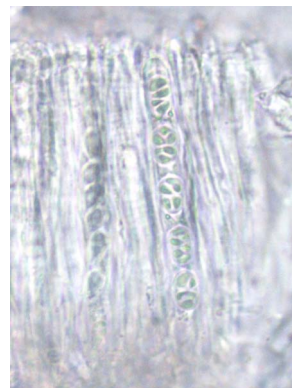
16 *Stegobolus neowrightii*



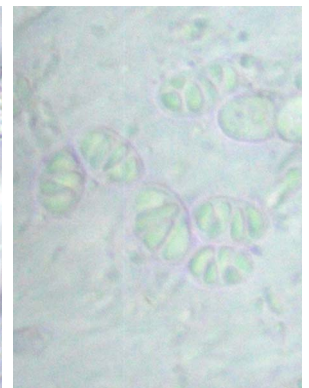
17 *Stegobolus neowrightii*



18 *Stegobolus neowrightii*
Cross section through ascoma



19 *Stegobolus neowrightii*
Asci with ascospores



20 *Stegobolus neowrightii*
Submuriform ascospores

co = columella, ex = exciple, hy = hymenium