

New resinicolous *Chaenothecopsis* species from China

Hanna Tuovila¹

Department of Biosciences, P.O. Box 65, FIN-00014
University of Helsinki, Finland

Marie L. Davey

Arctic Biology Department, University Centre in
Svalbard, P.O. Box 156, N-9171 Longyearbyen,
Norway

Lihong Yan

Hunan Province Forest Botanical Garden, Botanical
Garden Road 111, Dongjingspu, Yuhua District,
Changsha, Hunan, P.R. China (P.C. 410116)

Seppo Huhtinen

Herbarium, University of Turku, FIN-20014 Turku,
Finland

Jouko Rikkinen

Department of Biosciences, P.O. Box 65, FIN-00014
University of Helsinki, Finland

Abstract: Four new resinicolous species of *Chaenothecopsis* are described from China: *Chaenothecopsis perforata* from exudate of *Rhus chinensis* (Anacardiaceae), *C. pallida* from exudate of *Ailanthus altissima* (Simaroubaceae), *C. resinophila* from exudate of *Kalopanax septemlobus* (Araliaceae) and *C. hunanensis* from resin of *Pinus massoniana* (Pinaceae). All the new species are compared with previously described resinicolous mycocalicioid taxa, and several new features in these species are presented. The newly described species cannot always be distinguished by any single character, but they all possess unique combinations of morphological, chemical and ecological features. Several aspects in the ecology and evolution of boreal and tropical resinicolous species are briefly discussed.

Key words: China, exudate, Mycocaliciales, resinicolous fungi, Sapindales

INTRODUCTION

Chaenothecopsis Vain. is a genus of small, pin-like ascomycetes in the order Mycocaliciales (Tibell and Wedin 2000). Molecular studies clearly suggest that the genus is polyphyletic (Tibell and Vinuesa 2005, Tuovila et al. 2013), but precise generic delimitations within the order remain unresolved. The substrate ecology of most mycocalicioid fungi has not been

studied in detail, but most species appear to be either saprotrophic on wood (lignicolous) or resin (resiniculous) or associate with atmophytic green algae (algalicolous) or the green algal symbionts of lichens (lichenicolous) (e.g. Tibell 1999).

The majority of previously known resinicolous mycocalicioid species live on the resin of conifers, especially on various species of *Abies* Mill, *Picea* A. Dietr. and *Tsuga* Carrière (Pinaceae) (Titov and Tibell 1993, Tibell and Titov 1995, Rikkinen 2003a, Tuovila et al. 2011b). These fungi have been found mainly from Eurasian and North American boreal and temperate forests. However, a few mycocalicioid species also have been described from angiosperm exudates (e.g. Funk and Kujt 1982, Samuels and Buchanan 1983, Tuovila et al. 2011a). Compared to conifers of the boreal and temperate zone, there are many more woody angiosperm species that produce resinous exudates, especially in the tropics and subtropics. This suggests that a plethora of mycocalicioid species might be found from such substrates in future studies.

Compared to the relatively uniform terpenoid resins of the Pinaceae, there is a wide diversity of different types of exudates in woody angiosperms. For example, tropical and subtropical trees of the orders Apiales and Sapindales and the families Dipterocarpaceae and Fabaceae, include many species that often produce substantial quantities of exudate. The chemical compositions of the exudates vary and are species specific and often even closely related plant species can produce distinctively different mixtures of phenolic and terpenoid products (Langenheim 2003a, Courtois et al. 2009). Here we describe four new resinicolous mycocalicioid fungi from the warm temperate forests of south central China, including three species from angiosperm exudates and one from conifer resin. Also a full description of *Chaenothecopsis khayensis* Rikkinen & Tuovila is provided in English in that this text was accidentally left out from the original species description (Tuovila et al. 2011a).

MATERIALS AND METHODS

Resiniculous fungi were collected from trunks and branches of *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), *Kalopanax septemlobus* (Thunb.) Koidz (Araliaceae), *Rhus chinensis* Mill. (Anacardiaceae) and *Pinus massoniana* Lamb. (Pinaceae) in warm temperate evergreen broadleaf forests in Hunan province in south central China. Specimens were obtained from Zhangjiajie National Forest Park in 1999,

TABLE I. NCBI GenBank accession numbers for the fungal ITS and LSU sequences used

Species	GenBank accession Nos. ITS/LSU	Reference ITS/LSU if not the same
<i>Pyrgillus javanicus</i> Nyl.	DQ826741/DQ823103	James et al. 2006
<i>Caliciopsis</i> sp.	GQ259981/GQ259980	Pratibha et al. 2011
<i>Chaenothecopsis</i> sp. 1	JX119110/JX119119	Tuovila et al. 2013
<i>Chaenothecopsis</i> sp. 2	KC590480/KC590485	This study
<i>Chaenothecopsis consociata</i> (Nádv.) A.F.W.Schmidt	AY795851/DQ008999	Tibell and Vinuesa 2005
<i>Chaenothecopsis debilis</i> (Sm.) Tibell	AY795852/AY795991	Tibell and Vinuesa 2005
<i>Chaenothecopsis diabolica</i> Rikkinen & Tuovila	JX119109/JX119114	Tuovila et al. 2013
<i>Chaenothecopsis dolichocephala</i> Titov	AY795854/AY795993	Tibell and Vinuesa 2005
<i>Chaenothecopsis epithallina</i> Tibell	AY795855/—	Tibell and Vinuesa 2005
<i>Chaenothecopsis fennica</i> (Laurila) Tibell	AY795857/AY795995	Tibell and Vinuesa 2005
<i>Chaenothecopsis golubkovae</i> Tibell & Titov	AY795859/AY795996	Tibell and Vinuesa 2005
<i>Chaenothecopsis khayensis</i> Rikkinen & Tuovila	JX122785/HQ172895	Tuovila et al. 2012/Tuovila et al. 2011a
<i>Chaenothecopsis montana</i> Rikkinen	JX119105/JX119114	Tuovila et al. 2013
<i>Chaenothecopsis nana</i> Tibell	AY795862/—	Tibell and Vinuesa 2005
<i>Chaenothecopsis nigripunctata</i> Rikkinen	JX119103/JX119112	Tuovila et al. 2013
<i>Chaenothecopsis pallida</i> Rikkinen & Tuovila	JX122779/JX122781	Tuovila et al. 2013
<i>Chaenothecopsis pusiola</i> (Ach.) Vain	JX119106/JX119115	Tuovila et al. 2013
<i>Chaenothecopsis quintralis</i>	—/ JQ267741	Messuti et al. 2012
Messuti, Amico, Lorenzo & Vidal-Russell		
<i>Chaenothecopsis resinicola</i> Tibell & Titov	AY795867/—	Tibell and Vinuesa 2005
<i>Chaenothecopsis resinophila</i> Rikkinen & Tuovila	JX122780/JX122782	Tuovila et al. 2013
<i>Chaenothecopsis sitchensis</i> Rikkinen	JX119102/JX119111	Tuovila et al. 2013
<i>Chaenothecopsis tsugae</i> Rikkinen	JX119104/JX119113	Tuovila et al. 2013
<i>Chaenothecopsis vainioana</i> (Nádv.) Tibell	JX119107/JX119116	Tuovila et al. 2013
<i>Mycocalicium</i> sp. 1	AF243133/—	Vinuesa et al. 2001
<i>Mycocalicium albonigrum</i> (Nyl.) Tibell	AF223966/AY796001	Vinuesa et al. 2001/Tibell and Vinuesa 2005
<i>Mycocalicium</i> sp. 2	KC590482/KC590487	This study
<i>Mycocalicium sequoiae</i> Bonar	—/AY796002	Tibell and Vinuesa 2005
<i>Mycocalicium subtile</i> (Pers) Szatala	AF225445/AY796003	Vinuesa et al. 2001/Tibell and Vinuesa 2005
<i>Phaeocalicium</i> sp.	KC590483/KC590484	This study
<i>Phaeocalicium interruptum</i> (Nyl.) Tibell	AY795873/—	Tibell and Vinuesa 2005
<i>Phaeocalicium polyporaenum</i> (Nyl.) Tibell ^a	AY789363/AY789362	Wang et al. 2005
<i>Phaeocalicium populneum</i>	AY795874/AY796009	Tibell and Vinuesa 2005
(Brond ex Duby) A.F.W. Schmidt		
<i>Phaeocalicium praecedens</i> (Nyl.) A.F.W. Schmidt	KC590481/KC590486	This study
<i>Sphinctrina leucopoda</i> Nyl.	AY795875/AY796006	Tibell and Vinuesa 2005
<i>Sphinctrina turbinata</i> (Pers. ex Fr.) de Not	AY795877/DQ009001	Tibell and Vinuesa 2005
<i>Stenocybe pullatula</i> (Ach.) Stein	AY795878/AY796008	Tibell and Vinuesa 2005

^aDeposited as *Mycocalicium* p.(Nyl.) Vain.

Badagongshan National Nature Reserve in 1999 and 2000, Yunshan National Forest Park in 2001 and Shunhuangshan National Forest Park in 2001. For information on the study area, see Koponen et al. (2000, 2004).

Morphological and chemical characters for the Chinese collections were determined with the methodology introduced in Tuovila et al. (2013). Additional material was obtained from the University of Helsinki Herbarium (H) and characterized both morphologically and chemically: *Chaenothecopsis asperopoda* Titov 3126 (isotype), *C. eugenia* Titov 6706 (paratype), *C. golubkovae* Titov 303 (isotype), *C.*

dolichocephala Titov 4458 (isotype; 4232, 4226 paratypes), *C. sitchensis* Rikkinen JR98446B, 98447, 98460A (paratypes), *C. khayensis* Rikkinen & Tuovila Rikkinen JR04G058 (holotype; Rikkinen JR04G001, JR04G051, JR04G057, JR04G60 isotypes).

Ascomata were imaged under a compound microscope with simultaneously incident and transmitted light. Images (FIGS. 2, 4, 6, 8) are digitally stacked photomicrograph composites obtained from several focal planes with the software package CombineZP for a better illustration of the three-dimensional objects.

Genomic DNA was extracted and the ITS and LSU regions of rDNA were amplified and sequenced as described in Tuovila et al. (2013). Phylogenetic analysis of a concatenated dataset of ITS and LSU sequences was conducted as described in Tuovila et al. (2013), except MrBayes 3.2.1 (Ronquist et al. 2012) was used in the phylogenetic analyses. The models of evolution selected by jModelTest 2.0 (Darriba et al. 2012) for ITS1, 5.8SR, ITS2, and partial LSU respectively were: TPM2uf + G, TPM2 + I, TPM2uf + G, TrNef + I + G. GenBank accession numbers of sequences are provided (TABLE I). *Pyrgillus javanicus* Nyl. and *Caliciopsis* sp. were used as outgroups based on results of Schoch et al. 2009) (TABLE I).

RESULTS

Phylogenetic analyses.—We obtained ITS and partial LSU sequences for three of the four species described herein (*C. hunanensis*, *C. resinophila*, *C. pallida*). Despite repeated attempts we were not able to sequence *C. perforata*. *C. hunanensis* was excluded from the final analysis for reasons discussed in Tuovila et al. 2013. The concatenated matrix consisted of 35 species of Mycocaliciales and included 967 nucleotides. The resulting alignment was uploaded to TreeBASE, accession number TB2:S13910. The results of Bayesian and maximum likelihood phylogenetic analyses are illustrated on a maximum likelihood tree (FIG. 1). The overall tree topology is consistent with that found by Tuovila et al. (2013). The deeper nodes of the tree are unresolved or with low support. All crown clades are moderately or well supported. The monophyletic clades obtained in the analysis do not correspond to the generic delimitation of the classification in current use (e.g. Tibell 1999). However, the resinicolous species in each supported clade share some morphological and ecological characters. Clade A includes species with aseptate ascospores from angiosperm exudate; Clade B includes species with aseptate spores from conifer resins; Clade C includes resinicolous species from conifer resins that share some peculiar features in ascocarp morphology (see Tuovila et al. 2011b); and Clade D includes only species with septate, cylindrical ascospores from conifer resin.

TAXONOMY

Chaenothecopsis resinophila Rikkinen & Tuovila, sp. nov. FIGS. 2–3
Mycobank MB804598

Typus: Rikkinen 000424 (holotype, H). Etymology: refers to the ecology on resinous exudate.

Apothecia on exudate or exudate impregnated wood of *Kalopanax septemlobus* (Thunb.) Koidz., usually numerous, 800–1300 μm high. Stipe shining

black, straight, sometimes flexuous, occasionally branched once or more, 50–120 μm wide. Capitulum black, in young apothecia usually obovoid to ovoid, even obconical, later subspheric to hemispheric, 200–350 μm wide. Asci cylindrical, (28–) 32–45 \times (3–) 3.5–4 μm ($n = 30$), apex variously thickened, often penetrated by a short canal, mature asci usually without a thickening; formed without croziers, but croziers were observed occasionally in ascogenous hyphae. Ascospores uniseriate, sometimes partly biserially arranged, usually obliquely, rarely periclinally oriented or even disorganized in asci, aseptate, yellowish brown, ellipsoid to cylindrical, smooth, but each ascocarp with some free spores with minute, finely punctate ornamentation, visible under light microscopy at high magnification (1000 \times), (4–)4.8–6.3(–6.6) \times (2–)2.5–3.4(–3.8) μm ($n = 74$, from eight ascocarps, three populations), mean $5.4 \times 3 \mu\text{m}$, $Q = (1.5\text{--})1.6\text{--}2.2$ (–2.5), mean $Q = 1.8$. Paraphyses hyaline, filiform, 30–50 \times 1.5–2 μm ($n = 10$), occasionally with a simple branch in the upper part; septate, septal intervals 7–10 μm , paraphysis apices encrusted with strongly congophilous crystals. Stipe hyphae yellowish brown to dark brown, 3 μm wide, walls 1–1.5 μm , hyphae periclinally arranged (textura prismatica, slightly intertwined), basal cells large, irregular, walls 1.5–2 μm , stipe surface usually covered with a fragmenting pigment layer, thick-walled cells at the base of the stipe turn violet red in 1% IKI, reaction sometimes difficult to detect due to the pigmented cell walls; hyphae swell in KOH and brown pigment leaks into the medium; hyphae in inner part of stipe hyaline to light yellowish green, more or less periclinally arranged, thin-walled. Excipulum hyphae yellowish brown to greenish brown, 3 μm wide, wall 1–1.5 μm , periclinally arranged (textura prismatica, slightly intertwined); hyphae swell in KOH, some brown pigment leaks into the medium. Excipulum and upper part of stipe covered with sparse net of 2–3 μm wide, arching hyphae. Epithecium yellowish green, formed as a poorly developed, sparse net of moderately thick-walled, pigmented hyphae extending from the outer layer of the excipulum, hyphae 1.5–2 μm wide, hyphae swell in KOH, some brown pigment leaks into the medium. Hypothecium hyphae hyaline to light green, thin-walled, hyphae swell in KOH. All parts of the apothecium N– (or yellow on the ascoma slightly disappearing, green enhancing), all parts MLZ–.

Specimens examined: CHINA. Sangzhi County. Badagongshan National Nature Reserve (Badagongshan – Tianpingshan). Nan Mu Ping. Agricultural land with shade trees on mesic slope near forest edge, 29°45'N, 110°03'E, ca. 500 m. In trunk crevices of *Kalopanax septemlobus*, 23 Sep 2000, Rikkinen 000424 (holotype, H), 00398, 000425 (paratypes SKLM, H).

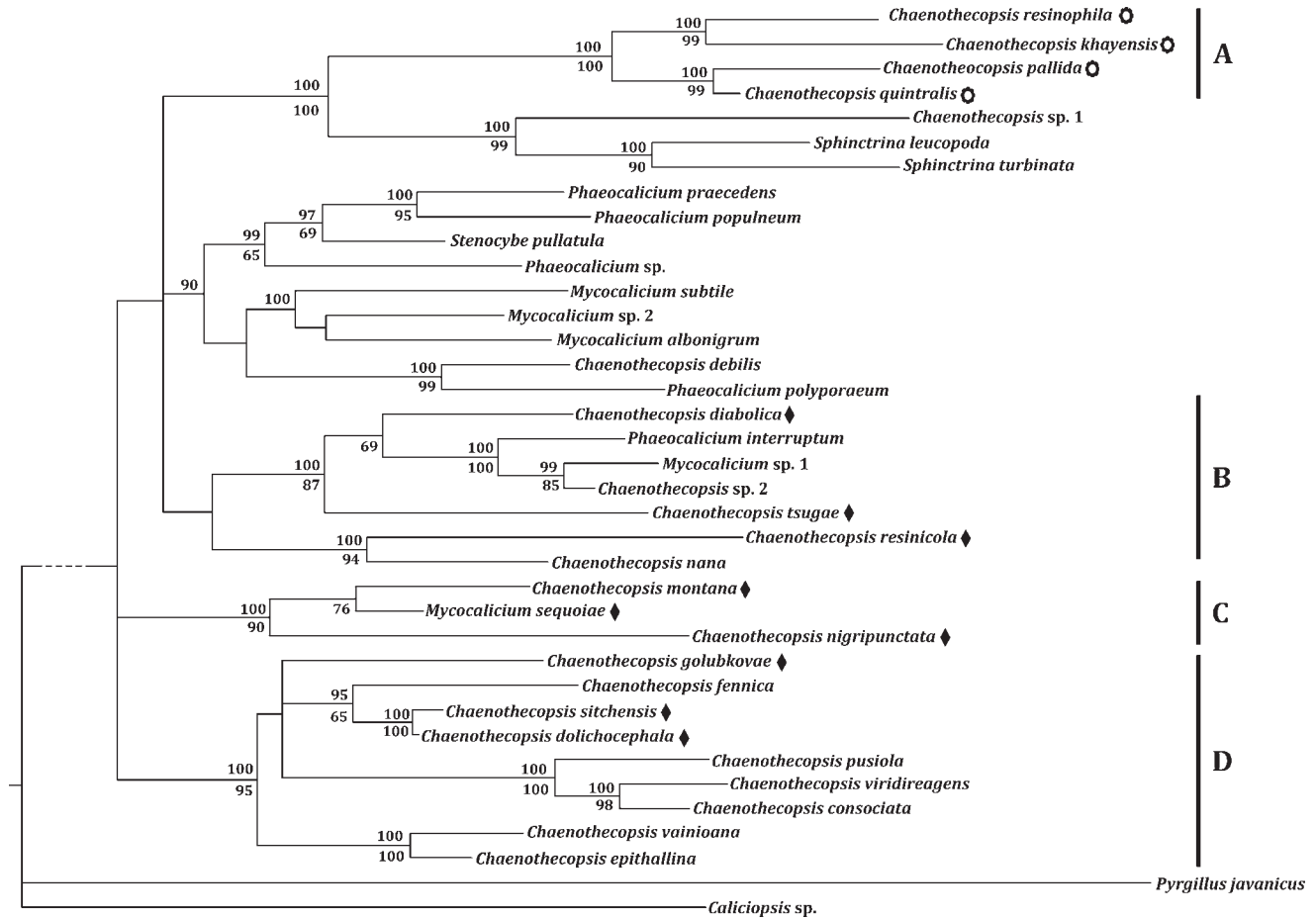


FIG. 1. Phylogenetic relationship of resinicolous mycocalicioids. Bayesian tree inferred from ITS1, 5.8S, ITS2 and 28S (partial) sequences (142, 154, 143 and 525 nucleotides respectively). Posterior probabilities $\geq 90\%$ for Bayesian inference (above node) and bootstrap values $> 60\%$ for maximum likelihood (below node) are given for supported nodes. Species from conifer resin indicated with a diamond and species from angiosperm resin indicated with flower.

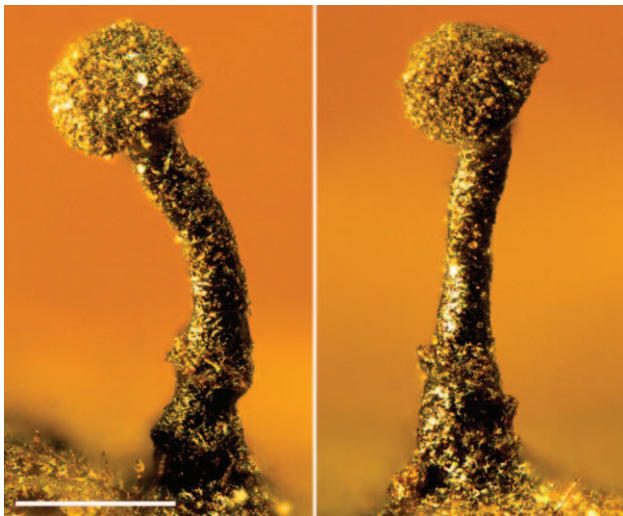


FIG. 2. *Chaenothecopsis resinophila* (holotype). Bar = 200 μm .

***Chaenothecopsis perforata* Rikkinen & Tuovila, sp. nov.**

FIGS. 4–5

Mycobank MB804599

Typus: Rikkinen 010540 (holotype, H).

Etymology: refers to the tight, perforated epithecium.

Apothecia on exudate or exudate impregnated bark and leaf scars of *Rhus chinensis* Mill., 800–1400 μm high. Stipe very dark brown, shiny when young, later black and matte, relatively short, straight, rarely flexuous, usually unbranched, 70–100 μm wide. Capitulum initially black, almost shiny, spherical, later brownish from released ascospores accumulating on top of epithecium, obovoid to hemispheric, 300–600 μm wide. Asci cylindrical, (26–)30–42 \times 3–4 μm ($n = 20$), apex variously thickened, often penetrated by a short canal, mature asci usually without a thickening; formed with croziers. Ascospores uniseriate, sometimes partly biseriately arranged, usually periclinally, rarely obliquely to almost vertically arranged in asci, aseptate, pale grayish to yellowish

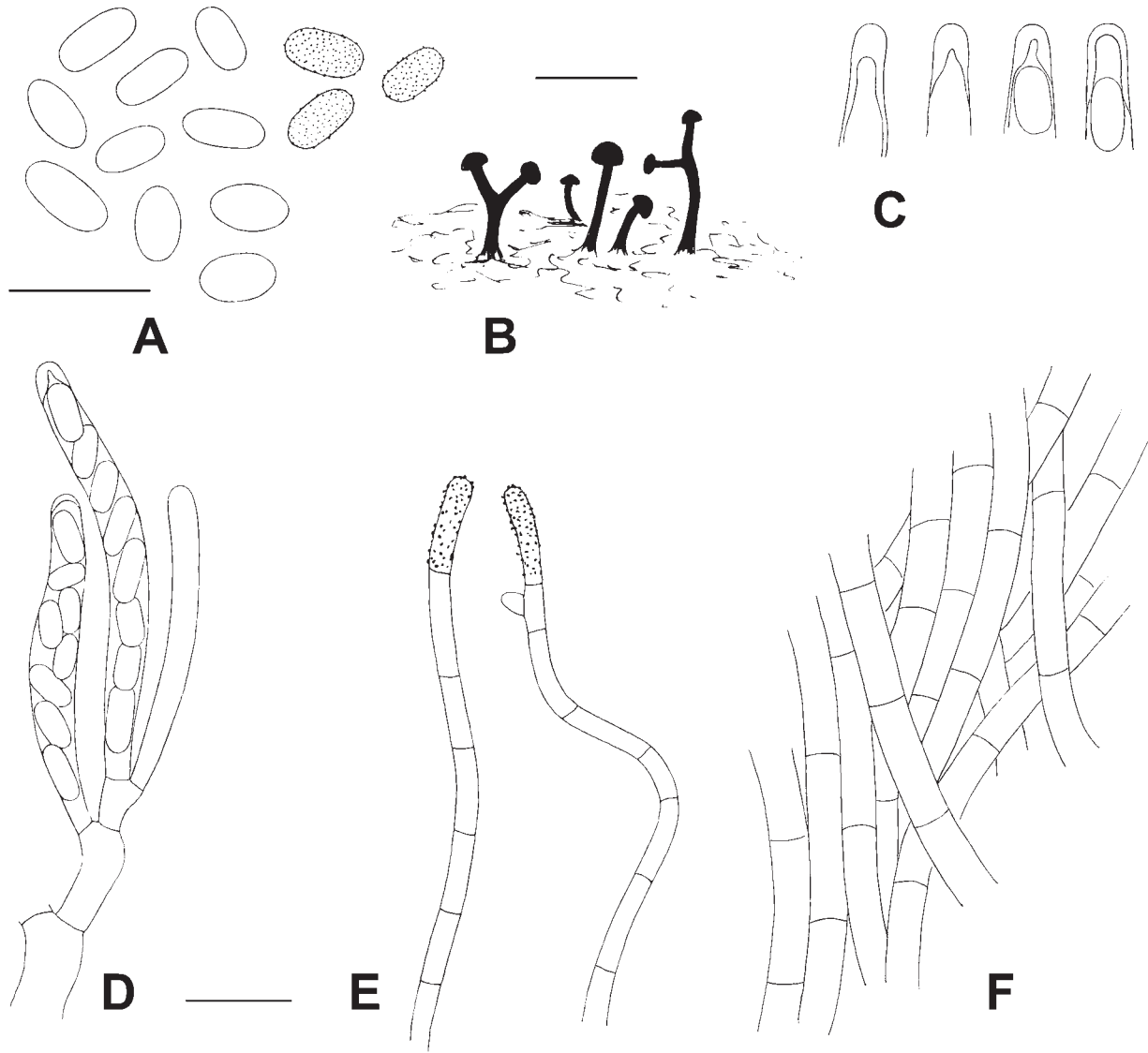


FIG. 3. *Chaenothecopsis resinophila* (A, C–F Rikkinen 000424, holotype; E, Rikkinen 00042, paratype). A. Mature ascospores. B. Ascocarps on resin. C. Ascus tip variation. D. Ascus formation (from left to right: mature, semimature, young) and ascospore orientation. E. Paraphyses. F. Textura type, excipulum. Bars: A, C, F = 10 μ m; D–E = 10 μ m; B = 1000 μ m. Drawings HT.

brown, ellipsoid to widely cylindrical, smooth, (4.2–) 4.8–6.1(–6.9) \times (2–)2.3–3.2(–3.5) μ m, mean 5.4 \times 2.8 μ m (n = 100, from nine ascocarps, four populations); Q = (1.4–)1.6–2.3(–2.5), mean Q = 1.9. Paraphyses hyaline, filiform, 30–40 μ m \times 1–2 μ m, rarely branched, septate, septal intervals 7–15 μ m. Stipe hyphae light grayish brown, almost hyaline, 3–4 μ m wide, walls 1–1.5 μ m, more or less periclinally arranged, partly intertwining (textura prismatica-intricata), hyphae strongly violet red in 1% IKI, moderately swelling in KOH; hyphae in inner part of stipe hyaline, slightly interwoven. Excipulum hyphae pale grayish brown, 2–3 μ m, walls 0.5–1 μ m, more or less periclinally arranged, less thick-walled near the margin, lower part strongly violet red in 1%

IKI, hyphae moderately swelling in KOH. Excipulum and upper part of stipe covered with sparse net of 2–3 μ m wide arching hyphae, walls 0.5 μ m. Epithecium grayish brown, formed as a continuum of excipulum, appearing as a uniform, pitted layer without obvious hyphal shapes, moderately swelling in KOH. Hypothecium hyphae hyaline, thin-walled, intertwined, moderately swelling in KOH. All parts of apothecium N– and MLZ–. A hyaline anamorphic fungus often was found covering the capitula of old ascocarps which gave capitula a white, hairy look.

Specimens examined: CHINA. Hunan Province. Xinning County. Shunhuangshan National Forest Park. Zheng Jiang Valley. Heavily grazed plantation forest with young *Cunninghamia lanceolata* and *Trachycarpus fortunei* mixed with

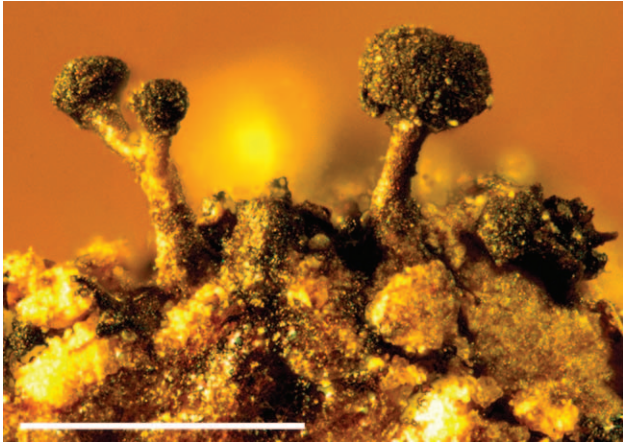


FIG. 4. *Chaenothecopsis perforata* (holotype). Bar = 500 μ m.

naturally regenerated evergreen trees, 26°24'35"N, 110°59'20"E, ca. 950 m. On branches of *Rhus chinensis*, 24 Sep 2001, *Rikkinen* 010540 (holotype H), 010538 (paratype UPS). Wugang County. Yunshan National Forest Park. Along road between Yunfeng Ge and Luhousi. Young plantation forests and secondary thickets along roadside, 26°35'55"N, 110°37'13"E, ca. 1250 m. On branches of *Rhus chinensis*, 19 Sep 2001, *Rikkinen* 010174, 010182, 010185, *Yan* 004889 (paratypes SKLM, H). Sangzhi County. Badagongshan National Nature Reserve (Badagongshan – Tianpingshan). Tuanping. Forest clearing with secondary thickets on steep ridge, 26°N, 110°E, ca. 1400 m. On branches of *Rhus chinensis*, 29 Sep 1999, *Rikkinen* 991084A, 991085B (paratypes H). Between Yuang Yang Ya and Yang Yang Ping. Low secondary evergreen forest, along roadside, 29°47'N, 110°05'E, ca. 1400 m. On branches of *Rhus chinensis*, 20 Sept 2000, *Rikkinen* 000120 (paratype H). Nan Mu Ping. Agricultural land with shade trees on mesic slope near forest edge, 29°45'N, 110°03'E, ca. 500 m. On branches of *Rhus chinensis*, 23 Sep 2000, *Rikkinen* 000398 (paratype H).

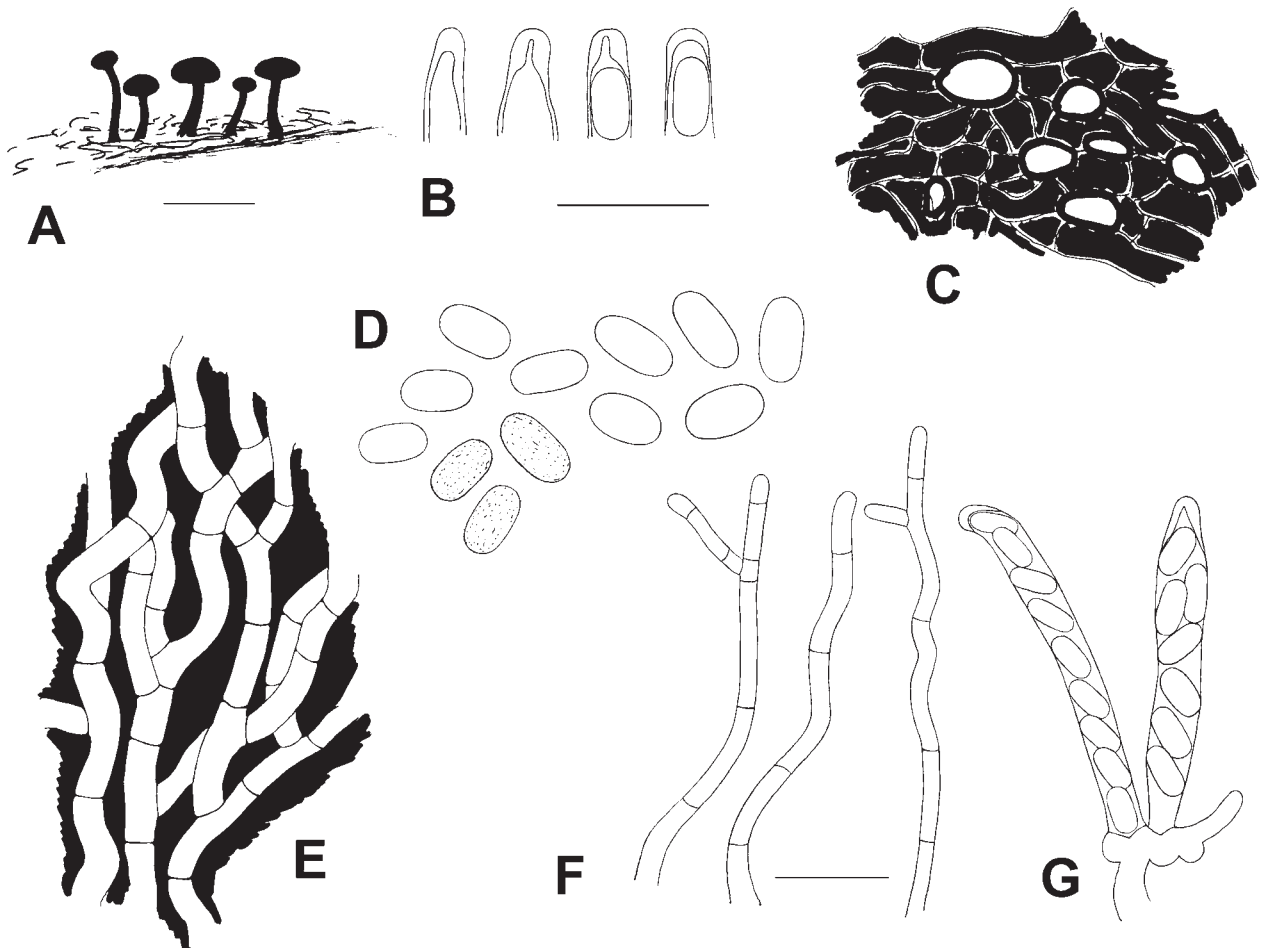


FIG. 5. *Chaenothecopsis perforata* (A–D, F–G *Rikkinen* 010540, holotype; B *Rikkinen* 010538, paratype). A. Ascocarps on resin. B. Ascus tip variation. C. Epithecium, surface view. D. Mature ascospores. E. Textura type, stipe. F. Paraphyses. G. Ascus formation (from left to right: mature, semimature, emerging) and ascospore orientation. Bars: A = 1000 μ m, B–E = 10 μ m, F–G = 10 μ m. Drawings HT.

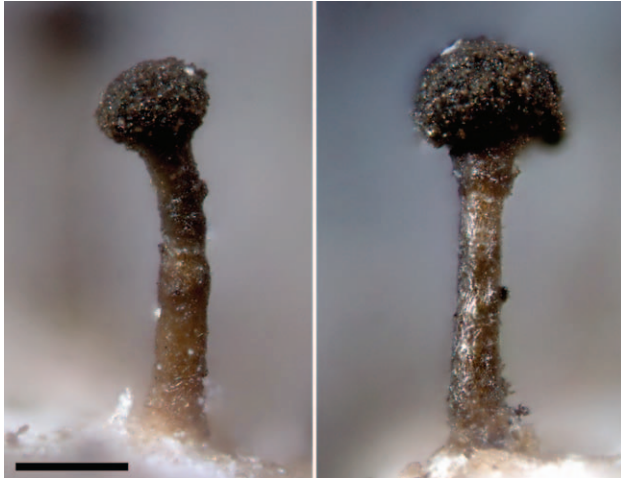


FIG. 6. *Chaenothecopsis pallida* (holotype). Bars = 100 μ m.

Chaenothecopsis pallida Rikkinen & Tuovila, sp. nov.

FIGS. 6–7

Mycobank MB804600

Typus: Rikkinen 010652 (holotype, H).

Etymology: refers to the pale stipe.

Apothecia on exudate or exudate impregnated wood of *Ailanthus altissima* (Mill.) Swingle, 750–1100 μ m high. Stipe brown, shiny when young, matte when older, straight, sometimes slightly flexuous, occasionally branched, 60–120 μ m wide. Capitulum initially black, lentil-shaped or obovoid, later subspherical to hemispheric, later dark brown from released ascospores accumulating on top of the epithecium, 200–320 μ m wide. Asci cylindrical, (33–)36–50 \times 3–4 μ m ($n = 50$), apex variously thickened, often penetrated by a short canal, mature asci usually without a thickening; formed without croziers. Ascospores uniseriate, obliquely or periclinally arranged in asci, aseptate, yellowish brown, cylindrical, smooth, (4.8–)5.0–6.6(–6.9) \times (2.1–)2.3–3.8(–4) μ m, mean 5.8 \times 3 μ m ($n = 70$, from seven ascocarps, three populations); $Q = (1.5–)1.7–2.4(–2.7)$, mean $Q = 1.9$. Paraphyses hyaline, filiform, 27–45 \times 1–1.5 μ m ($n = 10$), often branching in upper part, septate, septal intervals 4–10 μ m. Stipe hyphae light brown to almost hyaline, 5 μ m wide, periclinally arranged, agglutinated walls (textura oblita) between two lumina 3–5 μ m, hyphae strongly violet red in 1% IKI, strongly swelling in KOH; hyphae in inner part of the stipe more loosely arranged, hyaline, slightly intertwined, thin-walled. Excipulum hyphae yellowish brown, of similar structure than in stipe, in lower part of excipulum strongly violet red in 1% IKI. Epithecium yellowish brown, formed as a continuum of excipulum, of strongly pigmented, thin-walled hyphae, 3 μ m wide. Hypothecium hyaline, hyphae thin-walled. All parts of apothecium N– and MLZ–.

Specimens examined: CHINA. Hunan Province. Xinning County. Shunhuangshan National Forest Park. Li Zhu Jiang Valley. Mature riparian secondary evergreen broadleaf forest in narrow valley, 26°24'N, 110°59', 980 m. On exudate in basal crevice of large *Ailanthus altissima*, 25 Sep 2001, Rikkinen 010652 (holotype H), 010638, 010639 (paratypes SKLM, H).

Chaenothecopsis hunanensis Rikkinen & Tuovila, sp. nov.

FIGS. 8–9

Mycobank MB804601

Typus: Rikkinen 990059 (holotype, H).

Etymology: refers to Hunan province, China, where the species first was discovered.

Apothecia on resin or resin impregnated wood and bark of *Pinus massoniana* Lamb., 700–1200 μ m high. Stipe slender, shining black, 30–50 μ m wide. Capitulum matte black, later dark brownish, obconical to conical or obovoid to hemispheric, 150–300 μ m wide; also often irregularly shaped and/or strongly flattened, agglomerated, almost heart-shaped or stretched and then as narrow as stipe. New apothecia can proliferate from old capitula, even repetitiously. Asci cylindrical, 55–74(–85) μ m \times (3–)3.5–4(–4.5) μ m ($n = 20$), apex variously thickened, often penetrated by a short canal, mature asci usually without a thickening; formed with distinct croziers. Ascospores uniseriate, usually periclinally, sometimes obliquely arranged in asci, green to yellowish green-brown, septate, septa thinner (and less visible) than spore wall, slightly thickened at the septal junction, cylindrical, smooth to finely pointed, (7–)7.3–10.3(–11.1) \times (2–)2.5–3.8(–4) μ m, mean 8.7 \times 3.2 μ m ($n = 110$, from 14 ascocarps, six populations); $Q = (1.9–)2.1–3.6(–4.5)$, mean $Q = 2.8$. Paraphyses filiform, unbranched proportion of paraphyses 50–75 μ m \times 1–1.5 μ m, septate, septal intervals 11–13 μ m, shorter or as long as asci, occasionally branching once or twice, or longer than asci, and then branching at ascus apex or above, intertwining to form a loose net above the asci, covered with small colorless, strongly congophilous crystals. Stipe hyphae dark green to brownish, 4–5 μ m wide, walls 1.5 μ m, strongly pigmented, the green pigment often unevenly agglomerated on walls as small lumps or plates, periclinally arranged (textura prismatica); hyphae in inner part of the stipe hyaline or light green, more thin-walled, intertwined. Excipulum hyphae light yellowish green, textura prismatica, pigmented as in the stipe. Epithecium light green, formed as a loose net of the excipular hyphae, partly of branching and intertwining paraphyses, hyaline to light green, congophilous pigment covers cells in epithecium. Hypothecium hyaline to light green. Hymenium and hypothecium IKI– or often with fast and faint blue

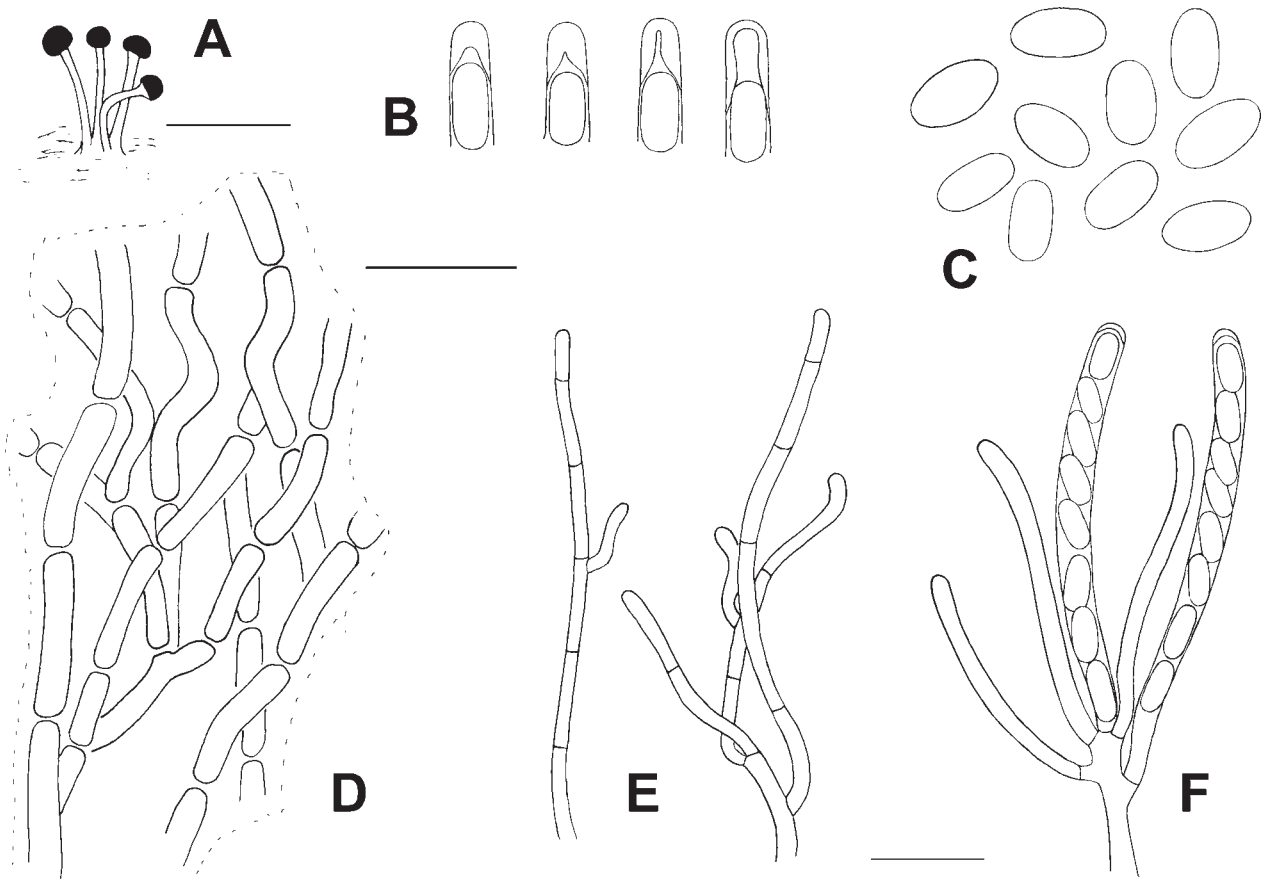


FIG. 7. *Chaenothecopsis pallida* (A–B, E Rikkinen 010652, holotype; D Rikkinen 010390 paratype; C, F Rikkinen 010638 paratype). A. Ascocarps on resin. B. Ascus tip variation. C. Mature ascospores. D. Textura type, stipe. E. Paraphyses. F. Ascus formation (mature with spores and very young without spores) and ascospore orientation. Bars: A = 1000 μm , B–F = 10 μm . Drawings HT.

reaction (see Tuovila et al. 2013). All green or greenish parts of apothecium turn brown in KOH, brown leaks into the medium, sometimes faint reddish reaction in excipulum. All parts N–, MLZ–. A brown hyphomycetous fungus was often found growing among the ascocarps, and rarely on top of the old ascocarps.

Specimens examined: China. Hunan province. Dayong County. Zhangjiajie National Forest Park. Fuqiyuan, along trail to view point above Zhangjiajie Hotel. Young *Cunninghamia*-angiosperm forest with large remnant pines, 29°19'N, 110°25'E, 650 m. In basal crevice of large *Pinus massoniana*, 15 Sep 1999. Rikkinen 990059 (holotype H), 990055 (paratype UPS), 990058 (paratype SKLM). Matianya, young plantation forest with *Cunninghamia lanceolata*, *Pinus massoniana* mixed with naturally regenerated broad-leaf trees and bamboo stands, 29°19.05'N, 110°27.47'E, ca. 900 m. Resiniculous on basal trunks of mature *Pinus massoniana*, 16 Sep 1999, Rikkinen 990139, 990164–990167 (paratypes H). Xiejiayu. Naturally regenerated evergreen forest with grassy openings on steep slope of narrow stream valley. 29°18'N, 110°25'E, ca. 750 m. Resiniculous on basal

trunk of large *Pinus massoniana*, 19 Sep 1999, Rikkinen 990413 (paratype H).

Chaenothecopsis khayensis Rikkinen & Tuovila
Tuovila H., Cobbinah J.R., Rikkinen J. (2011).

Chaenothecopsis khayensis, a new resinicolous calicioid fungus on African mahogany. *Mycologia* 103:610–615.

Apothecia on exudate of *Khaya* spp. (Meliaceae), 400–650 μm high. Stipe straight, sometimes flexuous, occasionally branched once or more, shiny, almost black with olive-green tinge, 50–100 μm wide. Capitulum obovoid to ovoid, even obconical, later subspherical to hemispherical, black; 100–260 μm wide. Asci cylindrical, (46–)49–66(–70) \times (3–)3.5–5.5 μm ($n = 25$), apex variously thickened, often penetrated by a short canal, mature asci usually without a thickening; formed without croziers. Ascospores uniseriate, usually periclinal, rarely obliquely oriented in asci, aseptate, grayish olive green, ellipsoidal to cylindrical, with minute ornamentation of low ridges consisting of

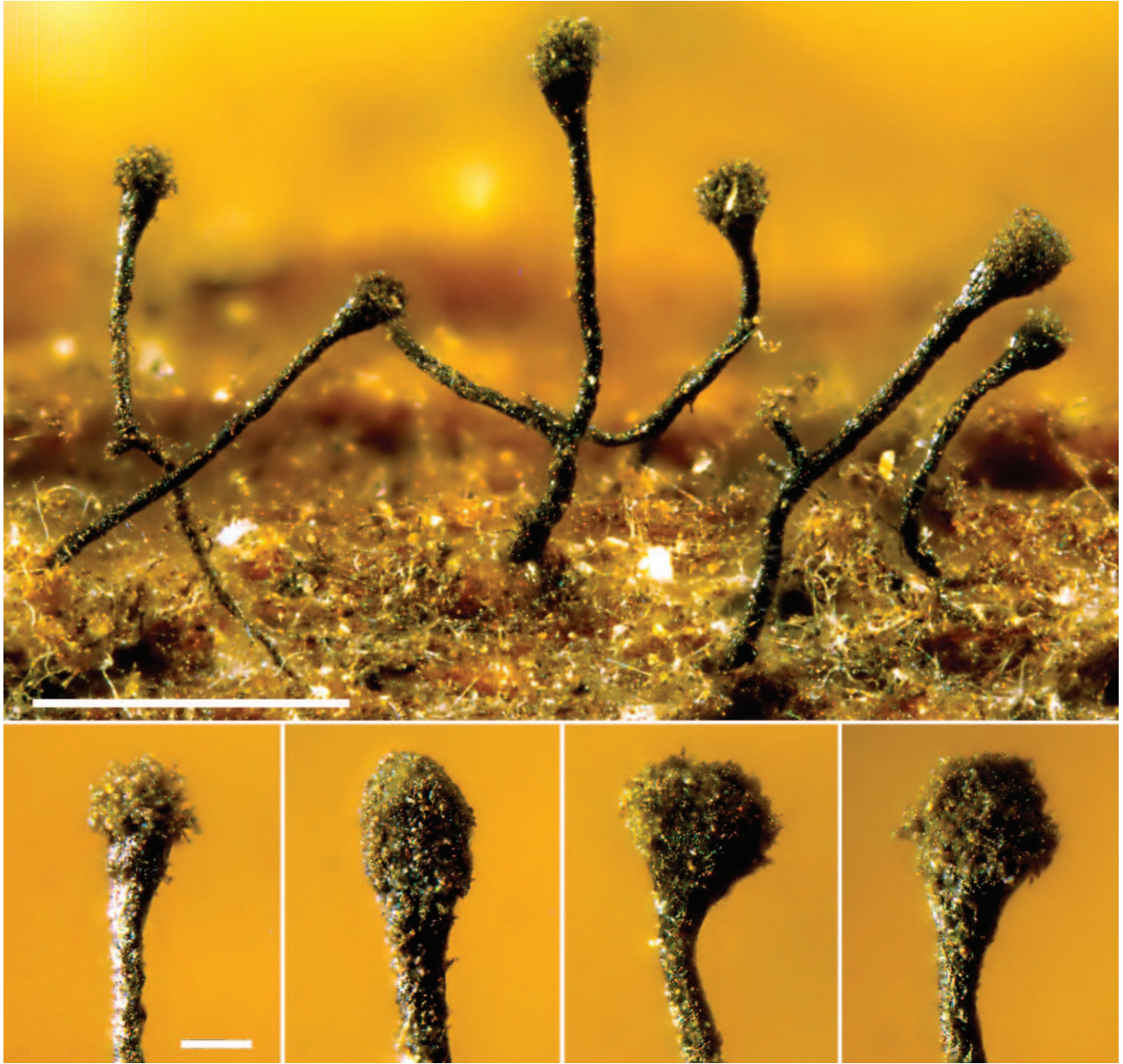


FIG. 8. *Chaenothecopsis hunanensis* (holotype). Bars: upper image = 500 μm , lower images = 50 μm .

small warts, visible under light microscope at high magnification (1000 \times), a small proportion of smooth spores seen in each ascocarp, (6.1–)6.8–9.1 $\mu\text{m} \times$ (2–)2.5–4(–4.2) μm ($n = 50$, from four populations), mean = 7.6 \times 3.2 μm , $Q = (1.6\text{--})1.8\text{--}3.2\text{(–}3.5)$, mean $Q = 2.4$. Paraphyses hyaline, filiform, 30–50 \times 2 μm ($n = 10$) occasionally branching at the lower part, septate, septal intervals 15–17 μm . Stipe hyphae grayish or brownish olive green, 5–7 μm wide, walls 1.5–2.5 μm , hyphae periclinally arranged (textura prismatica), thick-walled hyphae turn violet red in 1% IKI, hyphae in inner part of stipe hyaline to light green, more or

less periclinally arranged. Excipulum hyphae grayish to brownish olive green, 2–4 μm wide, walls 0.5–1.5 μm ; hyphae periclinally arranged (textura prismatica), excipulum and upper part of stipe covered with sparse to dense net of horizontally to vertically arranged, 2 μm wide arching hyphae, walls 0.5 μm wide. Epithecium olive green, formed as a continuum of the outer layer of excipulum, appearing as a sparse to dense net, hyphae 2 μm wide, walls 0.5 μm . Hypothecium hyphae hyaline to light green, thin-walled. All parts of apothecium swell and turn brown in KOH, all parts N– and MLZ–.

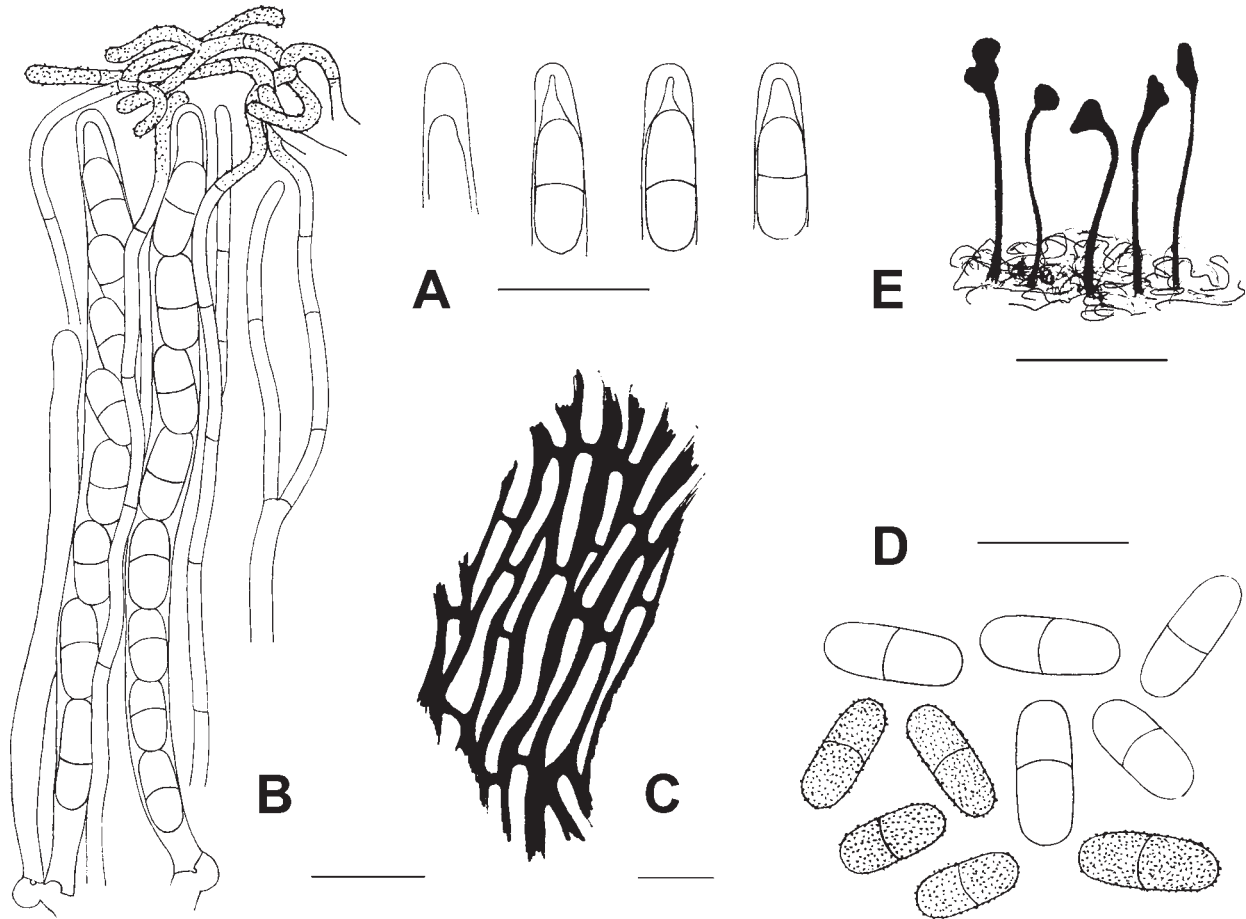


FIG. 9. *Chaenothecopsis hunanensis* (A, D–E Rikkinen 990059, holotype; A Rikkinen 990055, paratype; B–C Rikkinen 990167 paratype). A. Ascus tip variation. B. Paraphyses, ascus formation (mature with spores and very young without spores) and ascospore orientation. C. Textura type, stipe. D. Mature ascospores. E. Ascocarps on resin. Bars: A–D = 10 μ m, E + 1000 μ m. Drawings HT.

DISCUSSION

Taxonomy and systematics.—The overall topology recovered in the phylogenetic analysis is consistent with Tuovila et al. (2013). The same major clades, also supported by consistent morphology and ecology, are maintained. Our phylogeny demonstrates that the majority of genera in the Mycocaliciales (*Chaenothecopsis*, *Mycocalicium*, *Phaeocalicium*) are polyphyletic (see also Tibell and Vinuesa 2005). Unfortunately the lack of resolution in the deep nodes makes it impossible to delimit monophyletic genera at this point. Hopefully the generic boundaries and relationships can be resolved in studies using additional gene regions and a wider taxon sampling. However, some concluding remarks are possible, especially concerning the position of the genus *Sphinctrina* Fr. (Fries 1825) within Mycocaliciales. In some studies *Sphinctrina* has been found to be nested within Mycocaliciaceae (Gueidan et al. 2008, Prieto et al. 2013, Prieto and Wedin 2013), but

this position was dubious due to the relatively few representatives of species in the order included in the analyses. Although Tibell and Vinuesa (2005) analyzed the family with wider taxon sampling, the position of *Sphinctrina* was not well resolved. Our study (Tuovila et al. 2013) was the first to demonstrate strong support for the inclusion of *Sphinctrina* within Mycocaliciaceae, and our current results indicate that this relationship is robust. The additional taxon sampling in these studies has provided improved resolution of the position of Sphinctrinaceae and indicates the taxon is superfluous and should not be used.

While Tuovila (2013) suggests possible solutions to reassign generic names to certain clades in Mycocaliciales, she indicates that sample depth is low in most geographic areas (especially from the southern hemisphere) and more data is needed to elucidate the morphological and phylogenetic affiliations of mycocalicioid species. At this point we still lack sufficient knowledge to make appropriate taxonomi-

TABLE II. Distinguishing features of four *Chaenothecopsis* species from angiosperm exudates

	<i>Chaenothecopsis khayensis</i>		<i>Chaenothecopsis resinophila</i>		<i>Chaenothecopsis perforata</i>		<i>Chaenothecopsis pallida</i>	
Epitechium	Loose net		Loose net		Solid with small holes		Loose net	
Hypphae in stipe	Textura prismatica, olive green		Textura prismatica, yellowish to dark brown		Textura prismatica/intricata, light grayish brown		Textura oblita, light brown to hyaline	
Crystals on paraphyses	-		+		-		-	
Spores (μm) / average	(6.1–)6.8–9.1 \times (2.0–)2.5–4.0 / 7.6 \times 3.2		(4–)4.8–6.3 (–6.6) \times (2–)2.5–3.4 (–3.8) / 5.4 \times 3 (1.5–)1.6–2.2(–2.5) / 1.8		(4.2–)4.8–6.1(–6.9) \times (2–)2.3–3.2(–3.5) / 5.4 \times 2.8 (1.4–)1.6–2.3(–2.5) / 1.9		(4.8–)5–6.6(–6.5) \times (2.1–)2.3–3.8(–4) / 5.8 \times 3 (1.5–)1.7–2.4(–2.7) / 1.9	
Q value / average	(1.6–)1.8–3.2(–3.5) / 2.4		Yellowish brown, ornamented		Grayish to yellowish brown, some very finely ornamented		Yellowish brown, smooth	
Spore color and ornamentation	Olive green, ornamented							
IKI reaction	Strong red in stipe		Weak red in stipe		Strong red in stipe and lower part of excipulum		Strong red in stipe and lower part of excipulum, very fast and faint blue in hymenium	
Crozier	-		-		+		-	
Hypphae swell with KOH	+		+		++		+++	

cal changes, despite the well characterized incongruencies between the nomenclature and evolutionary relationships within the group.

The newly described *Chaenothecopsis* species from hardwood exudates differ from most previously known species in the genus in having relatively short, aseptate ascospores and in growing on the exudates of tropical or subtropical broadleaf trees. In both of these features they most closely resemble *Chaenothecopsis khayensis* and the recently described South American *Chaenothecopsis quintralis* Messuti, Amico, Lorenzo & Vidal-Russell (Messuti et al. 2012). Indeed, in our phylogenetic analyses two of the new species, *C. pallida* and *C. resinophila*, formed a strongly supported monophyletic clade with *C. khayensis* and *C. quintralis*, supporting a close evolutionary relationship between these hardwood exudate species.

The species described herein cannot always be distinguished from each other by any unique character but instead are separated by species-specific combinations of morphological and chemical characters (TABLE II). *Chaenothecopsis quintralis* is easily distinguished from *C. khayensis*, *C. resinophila* and *C. pallida* by the presence of croziers. It differs from *C. perforata*, another species with croziers, in the shape and size of spores (spore width 3.2–5 μm vs. 2.3–3.2 μm) and in the hyphal structure of the stipe. All four species presented herein are similar in several morphological attributes, which distinguish them from other species of resinicolous mycocalicioids. Most of the other species are confined on conifer resins and have longer, septate ascospores. Four of the seven previously known resinicolous mycocalicioid species that have aseptate spores can be conveniently distinguished from the present group on the basis of these characters: *C. diabolica* Rikkinen & Tuovila (Tuovila et al. 2011b) has distinctively ornamented, fusoid spores, *C. resinicola* Tibell & Titov (Tibell and Titov 1995) has a distinct pruina on the stipe and *C. tsugae* Rikkinen (Rikkinen 1999) is a robust species with large spores. *Chaenothecopsis oregana* Rikkinen (Rikkinen 2003a), *C. schefflerae*, and *Mycocalicium chaudhari* Tewari & Pant (Tewari and Pant 1966) are superficially more similar, but also they have for example the following distinguishing characters: *C. oregana* grows on conifer resin and its hyphae are wine red, *C. schefflerae* produces a pseudostroma and has almost round spores and *M. chaudhari* has ellipsoid, strongly ornamented spores. *Mycocalicium viscinicola* Funk & Kujt (Funk and Kujt 1982) has much larger spores than any other mycocalicioid species from hardwood exudates.

Chaenothecopsis humanensis differs clearly from the other species described here, both in morphology and in its association with conifer resin, but it closely

TABLE III. Distinguishing features of seven *Chaenothecopsis* species with septate spores from conifer resins

	<i>Chaenothecopsis humanensis</i>	<i>Chaenothecopsis dolicocephala</i>	<i>Chaenothecopsis golubkovae</i>	<i>Chaenothecopsis proliferatus</i>	<i>Chaenothecopsis sitchensis</i>	<i>Chaenothecopsis eugenia</i>	<i>Chaenothecopsis asperopoda</i>
Epithelium	Loose net of excipular hyphae and branching paraphyses	Branching paraphyses and amorphous pigment	Excipular hyphae in a very tight structure	Excipular hyphae and branching paraphyses in a very tight structure	Long, branching paraphyses and amorphous pigment	Loose net of excipular hyphae	Loose net of excipular hyphae and very long branching paraphyses
Stipe	Textura prismatica, partly intertwined, dark green	Textura prismatica, brownish green	Textura epidermoidea, yellowish brown	Textura prismatica, partly intertwined, dark green - dark brown	Textura prismatica, -intricata, light to dark green; covered with amorphous pigment	Textura prismatica, light green, almost colorless	Somewhat textura prismatica, difficult to observe, green - yellow green - brown green
Excipulum	Textura prismatica, light yellowish green	Textura prismatica, yellowish green	Textura epidermoidea, yellowish brown	Textura prismatica, dark green to dark brown	Textura prismatica, -intricata, light to dark green; covered with amorphous pigment	Textura prismatica	Somewhat textura prismatica, difficult to observe
Crystals	10-30 µm thick layer beneath the epithelium + on top of the paraphyses	Colorless crystals scattered in hymenium and hypotechium,	No crystals	5-20 µm thick layer beneath the epithelium + on top of the paraphyses,	Colorless crystals scattered in the whole ascoma; red pigments especially in older ascomas,	Colorless crystals scattered in the whole ascoma, orange crystals at the base of the stipe especially in older ascomas,	Colorless crystals in the whole ascoma, orange crystals at the base of the stipe especially in older ascomas, K+ red
Spores /average	K-, sometimes + faint reddish (7.0-)7.3-10.3 (-11.1) × (2.0-) 2.5-3.8 (-4.0)/ 8.7 × 3.2 µm	K+ red in fresh specimens (8.0-)8.1-10.5(-11.9) × (2.8-)3.0-4.3 / 9.3 × 3.8 µm	(7.2-)8.0-10.6 (-13.2) × (2.0-) 2.9-4.0(-4.1)/ 9.2 × 3.4 µm	(6.2-) 7.6-12.0 (-13.5) × (2.6-)2.9-4.2 (-4.8)/9.5 × 3.6 µm	K- (7.5-)7.6-10.1 (-10.5) × (3.0-) 3.1-4.1(-4.4)/8.7 × 3.6	K- 7.2-8.2 × 2.4-2.8 ^a (6.1-)6.3-7.9 (-8.2) × (2.0-) 2.1-2.8(-3.2) / 7.1 × 2.5	(5.5)6.0-7.0(7.0) × (3.0)2.0-2.5(2.5) ^b (6.1-)6.2-7.8 (-8.1) × (2.0-) 2.1-3.0(-3.2) / 6.9 × 2.5
Q value/average	(1.9-)2.1-3.6(-4.5)/ 2.8	(2.0-)2.1-3.7(-4.0)/ 2.6	(2.1-)2.2-3.5(-4.3)/ 2.8	(1.9-)2.1-3.6(-4.4)/2.7	2.0-2.9/2.4	(2.1-)2.5-3.5 (-3.6)/2.9	(2.2-)2.3-3.5 (-3.7)/2.8
Spore ornamentation and color	Ornamented, Yellowish, dark green to brown	Ornamented, yellowish brown	Smooth, yellowish brown	Smooth (only a fraction ornamented)	Ornamented, yellowish brown	Smooth, yellowish dark green	Smooth, yellowish green

TABLE III. Continued

	<i>Chaenothecopsis humanensis</i>	<i>Chaenothecopsis dolicocephala</i>	<i>Chaenothecopsis golubkova</i>	<i>Chaenothecopsis proliferatus</i>	<i>Chaenothecopsis sitchensis</i>	<i>Chaenothecopsis eugenia</i>	<i>Chaenothecopsis asperopoda</i>
Spore septa	Thinner than spore wall, slightly thickened at the septal junction	Thinner than spore wall, thickened at the septal junction	Thinner than spore wall, thickened at the septal junction	As thick as spore wall, thickened at the septal junction	As thick as spore wall, strongly thickened at the septal junction	Thinner than spore wall, slightly thickened at the septal junction	Thinner than spore wall, slightly thickened at the septal junction
IKI reaction	Blue faint and fast or nonexisting in hymenium, no red reaction	Blue faint or nonexisting, red only in stipe (and lower part of excipulum) or nonexisting	Fast blue in hymenium, persisting red in stipe, difficult to see	Fast blue in hymenium, persisting red in stipe, excipulum, and epitecium, difficult to see	Fast blue in hymenium, no red reaction	Fast blue in hymenium, persisting red in stipe and excipulum, easy to see	Fast blue in hymenium, persisting red in stipe and excipulum, easy to see

^aFrom original description (Titov 2001).

^bFrom original description (Titov and Tibell 1993).

resembles several previously known species with septate spores. It can be distinguished from these by a combination of spore, ascocarp and chemical characters. For example, *C. nigripunctata* Rikkinen, in addition to having a characteristic macroscopic appearance, has larger spores than *C. hunanensis* (Rikkinen 2003b). *Chaenothecopsis edbergii* Selva & Tibell, has a lime green pruina on its ascocarps (Selva and Tibell 1999) and a blue MLZ+ (euamyloid) reaction of the hymenium. All the other species on conifer resin with septate spores, including *C. sitchensis* Rikkinen (Rikkinen 1999), *C. proliferatus* Rikkinen, A.R. Schmidt & Tuovila (Tuovila et al. 2013), *C. dolichocephala* Titov (Tibell and Titov 1995), *C. golubkova* Tibell & Titov, *C. asperopoda* Titov (Titov and Tibell 1993) and *C. eugenia* Titov (Titov 2001) have similar characters but in different combinations. All these species are compared with *C. hunanensis* (TABLE III).

The identification of resinicolous mycocalicioid species is often complicated by the co-occurrence of several species in the same collection (Tuovila et al. 2011b). For example, the examination of type material of *C. asperopoda* and *C. dolichocephala* revealed the presence of two undescribed species. The isotype material of *C. asperopoda* kept in Helsinki has two distinct species, which may explain the odd variation in stipe color noted in the original species description by Titov (Titov and Tibell 1993). The differences between the two species will be addressed in a forthcoming paper, and the characters and spore size indicated herein are from the ascocarps corresponding best to the original description (light green stipe). In addition, the paratype material of *C. dolichocephala* kept in Helsinki contains two specimens collected from resin of *Pinus koraiensis* Siebold & Zucc. These specimens differ from the isotype material from resin of *Abies holophylla* Maxim. They are similar to *C. hunanensis* and actually might belong to the same species. The spores however are consistently wider than those of *C. hunanensis*. All the species with septate spores from conifer resin are obviously closely related, and it is quite likely that additional taxa will be found when additional conifer hosts from eastern Asia are examined in more detail.

Resiniculous ecology.—A considerable proportion of all currently known mycocalicioid species are resinicolous with different species colonizing terpenoid resins of conifers and phenolic resins of angiosperms. The early evolution of this ecology remains unclear in that the exact relationships of the five well supported clades with resinicolous species could not be resolved. However, all clades with species on conifer resins are clearly distinct from the clade of species on angiosperms. This indicates that either the resinicolous ecology has evolved

independently in each group or that there have been multiple switches to lichenicolous and lignicolous ecologies in some lineages. The fossilized specimens preserved in Miocene and Eocene ambers demonstrate that the association between mycocalicalean fungi and conifer exudates is ancient (Rikkinen and Poinar 2000, Tuovila et al. 2013). Also the well defined group of species on angiosperm exudates may be quite old in that these species share several unique morphological and chemical traits but have highly disjunct ranges in Africa, Asia and South America.

Most resinicolous species of Mycocaliciales seem to be host specific, with individual plant species hosting different fungi. It is known that pathogenic organisms sometimes can accidentally infect foreign hosts and when doing so they can be subjected to strong selective pressures leading to highly directional evolutionary development (Giraud et al. 2006). Because the chemical compositions of angiosperm exudates vary more than those of conifer resins (Langenheim 2003a), the fungi on angiosperms could show higher substrate specificity. However, it must be noted that also the terpene composition of different conifers can be variable (Zamponi et al. 2007, Nikolić et al. 2011) and thus also the mycocalicioid species on conifer resin may be more host specific than originally thought.

Of the nine presently known mycocalicioid species from angiosperm exudates, five (including *C. perforata*, *C. pallida*, *C. khayensis*) colonize host plants in the Sapindales. This order includes numerous tropical hardwoods with moderate to copious exudate production (Langenheim 2003b). Given the apparent host specificity in this group of mycocalicioid fungi, and the great diversity of potential host plants, it seems likely that many more resinicolous will be found from the exudate flows of other sapindalean genera (e.g. *Boswellia* Roxb. ex Colebr., *Bursera* Jacq. ex L., *Commiphora* Jacq. and *Canarium* L.).

ACKNOWLEDGMENTS

The field work in Hunan province was conducted in cooperation with the Forestry Department of Hunan Province, its Forest Botanical Garden, the Department of Biosciences (formerly Department of Ecology and Systematics) and the Botanical Museum, University of Helsinki. We thank Timo Koponen whose Academy of Finland project (No. 44475) made the field work possible. Hanna Tuovila's research was supported by grants from the Jenny and Antti Wihuri Foundation, Ella and Georg Ehrnrooth Foundation and Oskar Öflund Foundation.

LITERATURE CITED

Courtois EA, Paine CET, Blandinieres P-A, Stien D, Bessiere J-M, Houel E, Baraloto C, et al. 2009. Diversity of the

- volatile organic compounds emitted by 55 species of tropical trees: a survey in French Guiana. *J Chem Ecol* 35:1349–1362, doi:10.1007/s10886-009-9718-1
- Darriba D, Taboada G, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat Methods* 9:772, doi:10.1038/nmeth.2109
- Fries E. 1825. *Systema orbis vegetabilis I. Plantae homonemae*. Lund: Typographia Acad. 367 p.
- Funk A, Kujt J. 1982. *Mycocalicium viscinicola* sp. nov. (Caliciales) on mistletoe viscin in South America. *Can J Bot* 60:191–193, doi:10.1139/b82-024
- Giraud T, Villaréal LMMA, Austerlitz F, le Gac M, Lavigne C. 2006. Importance of the life cycle in sympatric host race formation and speciation of pathogens. *Phytopathology* 96:280–307, doi:10.1094/PHYTO-96-0280
- Gueidan C, Villaseñor CR, de Hoog GS, Gorbushina AA, Untereiner WA, Lutzoni F. 2008. A rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. *Stud Mycol* 61:111–119, doi:10.3114/sim.2008.61.11
- Koponen T, Cao T, Huttunen S, Hyvönen J, Juslén A, Peng C, Piippo S, Rao PC, Vána J, Virtanen V. 2004. Bryophyte flora of Hunan province, China 3: Bryophytes from Taoyuandong and Yankou Nature Reserves and Badagongshan and Hupingshan National Nature Reserves, with additions to floras of Mangshan Nature Reserve and Wulingyuan Global Cultural Heritage Area. *Acta Bot Fenn* 177:1–47.
- , Enroth J, Fang YM, Huttunen S, Hyvönen J, Ignatov M, Juslén A, Lai MJ, Piippo S, Potemkin A, Rao PC. 2000. Bryophyte flora of Hunan province, China 1. Bryophytes from Mangshan Nature Reserve and Wulingyuan Global Cultural Heritage Area. *Ann Bot Fenn* 37:11–39.
- Langenheim JH. 2003a. What plant resins are and are not. *Plant resins*. Portland, Oregon: Timber Press. p 23–50.
- . 2003b. Resin-producing plants. *Plant resins*. Portland, Oregon: Timber Press. p 51–103.
- Messuti MI, Vidal-Russell R, Amico GC, Lorenzo LE. 2012. *Chaenothecopsis quintralis*, a new species of calicioid fungus. *Mycologia* 104:1222–1228, doi:10.3852/12-006
- Nikolić B, Ristić M, Tešević V, Marin PD, Bojović S. 2011. Terpene chemodiversity of relict conifers *Picea omorika*, *Pinus heldreichii* and *Pinus peuce* endemic to Balkan. *Chem Biodivers* 8:2247–2260, doi:10.1002/cbdv.201100018
- Prieto M, Baloch E, Tehler A, Wedin M. 2013. Mazaedium evolution in the Ascomycota (Fungi) and the classification of mazaediata groups of formerly unclear relationship. *Cladistics* 29:296–308, doi:10.1111/j.1096-0031.2012.00429.x
- , Wedin M. 2013. Dating the diversification of the major lineages of Ascomycota (Fungi). *PloS One* 8: e65576, doi:10.1371/journal.pone.0065576
- Rikkinen J. 1999. Two new species of resinicolous *Chaenothecopsis* (Mycocaliciaceae) from western North America. *Bryologist* 102:366–369, doi:10.2307/3244223
- . 2003a. Calicioid lichens and fungi in the forests and woodlands of western Oregon. *Acta Bot Fenn* 175:1–41.
- . 2003b. *Chaenothecopsis nigripunctata*, a remarkable new species of resinicolous Mycocaliciaceae from western North America. *Mycologia* 95:98–103, doi:10.2307/3761966

- , Poinar G. 2000. A new species of resinicolous *Chaenothecopsis* (Mycocaliciales, Ascomycota) from 20 million year old Bitterfeld amber, with remarks on the biology of resinicolous fungi. *Mycol Res* 104:7–15, doi:10.1017/S0953756299001884
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Large B, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61:539–542, doi:10.1093/sysbio/sys029
- Samuels GJ, Buchanan DE. 1983. Ascomycetes of New Zealand 5. *Mycocalicium schefflerae* sp. nov., its ascus ultrastructure and *Phialophora* anamorph. *NZ J Bot* 21: 163–170, doi:10.1080/0028825X.1983.10428540
- Schoch CL, Sung G-H, López-Giráldez F, Townsend JP, Miadlikowska J, Hofstetter V, Robbertse B, et al. 2009. The Ascomycota tree of life: a phylumwide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Syst Biol* 58:224–239, doi:10.1093/sysbio/syp020
- Selva SB, Tibell L. 1999. Lichenized and nonlichenized Calicioid fungi from North America. *Bryologist* 102: 377–397, doi:10.2307/3244225
- Tewari VP, Pant DC. 1966. Ascomycetes of India I. *Mycologia* 58:57–66, doi:10.2307/3756988
- Tibell L. 1999. Calicioid lichens and fungi. *Nordic Lichen Flora I*, 20–94.
- , Titov A. 1995. Species of *Chaenothecopsis* and *Mycocalicium* (Caliciales) on Exudate. *Bryologist* 98: 377–397, doi:10.2307/3243587
- , Vinuesa M. 2005. *Chaenothecopsis* in a molecular phylogeny based on nuclear rDNA ITS and LSU sequences. *Taxon* 54:427–442, doi:10.2307/25065370
- , Wedin M. 2000. Mycocaliciales, a new order for nonlichenized calicioid fungi. *Mycologia* 92:577–581, doi:10.2307/3761518
- Titov A, Tibell L. 1993. *Chaenothecopsis* in the Russian Far East. *Nord J Bot* 13:313–329, doi:10.1111/j.1756-1051.1993.tb00055.x
- Tuovila H. 2013. Sticky business—diversity and evolution of Mycocaliciales (Ascomycota) on plant exudates. *Publications in Botany from the University of Helsinki* 44. 142 pages. (<https://helda.helsinki.fi/handle/10138/39265>)
- , Cobbinah JR, Rikkinen J. 2011a. *Chaenothecopsis khayensis*, a new resinicolous calicioid fungus on African mahogany. *Mycologia* 103:610–615, doi:10.3852/10-194
- , Larsson P, Rikkinen J. 2011b. Three resinicolous North American species of Mycocaliciales in Europe with a re-evaluation of *Chaenothecopsis oregana* Rikkinen. *Karstenia* 51:37–49.
- , Schmidt AR, Beimforde C, Dörfelt H, Grabenhorst H, Rikkinen J. 2013. Stuck in time—a new *Chaenothecopsis* species with proliferating ascomata from *Cunninghamia* resin and its fossil ancestors in European amber. *Fungal Divers* 58:199–213, doi:10.1007/s13225-012-0210-9
- Zamponi L, Michelozzi M, Capretti P. 2007. Terpene response of *Picea abies* and *Abies alba* to infection with *Heterobasidion* s.l. *For Pathol* 37:243–250, doi:10.1111/j.1439-0329.2007.00493.x