Chaetothiersia vernalis, a new genus and species of *Pyronemataceae* (*Ascomycota*, *Pezizales*) from California

Perry, B.A.[1*] and Pfister, D.H.[1]

Department of Organismic and Evolutionary Biology, Harvard University, 22 Divinity Ave., Cambridge, MA 02138, USA

Perry, B.A. and Pfister, D.H. (2008). *Chaetothiersia vernalis*, a new genus and species of *Pyronemataceae* (*Ascomycota*, *Pezizales*) from California. Fungal Diversity 28: 65-72.

Chaetothiersia vernalis, collected from the northern High Sierra Nevada of California, is described as a new genus and species. This fungus is characterized by stiff, superficial, brown excipular hairs, smooth, eguttulate ascospores, and a thin ectal excipulum composed of globose to angular-globose cells. Phylogenetic analyses of nLSU rDNA sequence data support the recognition of *Chaetothiersia* as a distinct genus, and suggest a close relationship to the genus *Paratrichophaea*.

Keywords: discomycetes, molecular phylogenetics, nLSU rDNA, Sierra Nevada fungi, snow bank fungi, systematics

Article Information
Received 31 January 2007
Accepted 19 December 2007
Published online 31 January 2008
*Corresponding author: B.A. Perry; e-mail: brian_perry@post.harvard.edu

Introduction

During the course of our recent investigation of the phylogenetic relationships of *Pyronemataceae* (Perry *et al*., 2007), we encountered several collections of an apparently undescribed, operculate discomycete from the northern High Sierra Nevada of California. Macroscopically, the taxon represented by these collections might be referred to genera of the *Pyronemataceae* such as *Trichophaea* Boud., *Trichophaeopsis* Korf & Erb, *Humaria* Fuckel, *Geopora* Harkn., *Tricharina* Eckblad, or *Wilcoxina* Chin S. Yang & Korf. These genera are characterized by medium- to large-sized apothecia with often pale hymenia and erect, pigmented marginal and superficial excipular hairs. Traditionally, these genera have been distinguished based upon differences in ascospore ornamentation, guttulation and reaction to various stains and media, as well as differences in the size and nature of the apothecial hairs and composition of the excipular tissues. Micromorphological examination of our collections, however, indicates that this taxon does not fit well within the limits of any of the described genera currently recognized in the family (Eriksson, 2006), and requires the erection of a new genus. We herein propose the new genus and species, *Chaetothiersia vernalis*, to accommodate this taxon.

The results of our previous molecular phylogenetic analyses of the family (Perry *et al*., 2007) suggest that this new genus and species are closely related to *Paratrichophaea* Trigaux, but fail to resolve this relationship with significant bootstrap support. In that study, which encompassed a broad sampling of taxa across the order *Pezizales*, several regions of the dataset were deemed ambiguous and therefore excluded from the analyses. In an attempt to further elucidate the relationships of this new genus and species within the family, we have analyzed an nLSU rDNA dataset focusing on the clade in which this new genus was previously resolved, and including additional macromorphologically similar genera, from which no nucleotide regions have been excluded (Table 1).

Table 1. List of taxa included in this study. Numbers in parentheses indicate multiple collections of a single taxon.

Species	Collection	Geographic Origin	Collector	GenBank Access. no.
Chaetothiersia vernalis B.A. Perry & Pfister	BAP 492 (HOLOTYPE, FH)	USA, California	J. Laws	DQ220403
Chaetothiersia vernalis	HDT 53173 (SFSU)	USA, California	H.D. Thiers	DQ220400
Chaetothiersia vernalis	DHP & HDT 5.18.86 (FH)	USA, California	H.D. Thiers, D.H. Pfister	DQ220401
Genea arenaria Harkn.	Trappe 17288 (FH, dupl. OSC)	USA, California	J. Graham	DQ220332
Genea harknessii Gilkey	Trappe 13313 (FH, dupl. OSC)	USA, Washington	A. & D. Claridge	DQ220334
Geopora arenicola (Lév.) Kers	KS-94-173 (C)	Denmark	K. Hansen, S.K. Sandal	DQ220336
Geopora cooperi Harkn.	HDT 52489 (SFSU)	USA, Wyoming	J. Ammarati	DQ220341
Humaria hemisphaerica (F.H. Wigg.) Fuckel	BAP 320 (FH)	China, Tibet	B.A. Perry	DQ220352
Humaria velenovskyi (Vacek ex Svrček) Korf & Sagara	HK 24-IX-1975 (C)	Denmark	H. Knudsen	DQ220354
Lasiobolidium spirale Malloch & Cain	CBS 782.70	USA, Wyoming	R. F. Cain	DQ220363
Melastiza contorta (Massee & Crossl.) Spooner & Y.J. Yao	KH.01.06 (C)	Sweden	B.T. Olsen	AY500539
Parascutellinia carneosanguinea (Fuckel) T. Schumach.	KH.03.34 (FH)	Norway	K. Hansen, C. Lange	DQ220388
Paratrichophaea boudieri (Grélet) Bronkers	BAP 481 (FH)	USA, California	B.A. Perry	DQ220402
Pseudaleuria quinaultiana Lusk	NSW 7107	USA, Oregon	N. S. Weber	DQ220389
Pyronema omphalodes (Bull.) Fuckel	TL-11685 (QCNE, C)	Ecuador, Carchi	K. Hansen *et al*.	DQ220397
Spooneromyces laeticolor (P. Karst.) T. Schumach. & J. Moravec	C F-48310/HFG 88.013 (C)	Denmark	H.F. Gøtzsche	DQ220434
Tricharina gilva (Boud. ex Cooke) Eckblad	BAP 431 (FH)	USA, California	B.A. Perry	DQ220444
Tricharina ochroleuca (Bres.) Eckblad	C F-53062/HD Gr83.107 (C)	Greenland	H. Dissing	DQ220445
Trichophaea abundans (P. Karst.) Boud.	CBS 348.76	Finland	V. Hintikka	DQ220448
Trichophaea hemisphaerioides (Mouton) Graddon	KH.97.31 (FH)	USA, California	K. Hansen	DQ220457
Trichophaea hybrida (Sowerby) T. Schumach. (1)	DHP 30.VIII.2000 (FH)	USA, Vermont	D.H. Pfister	DQ220453
Trichophaea hybrida (2)	AMNH-49682/F-17491 (AMNH)	Iceland	G. G. Eyjólfsdóltir	DQ220455
Trichophaea woolhopeia (Cooke & W. Phillips) Arnould	BAP 453 (FH)	Norway	D.H. Pfister, B.A. Perry	DQ220459
Trichophaeopsis bicuspis (Boud.) Korf & Erb	NSW 8316 (OCS)	USA, Oregon	N. S. Weber	DQ220461
Trichophaeopsis tetraspora Dissing & M.D. Paulsen	C F-47525 (C)	Denmark	H. Dissing	DQ220463
Wilcoxina mikolae (Chin S. Yang & H.E. Wilcox) Chin S. Yang & Korf	WS 36 (SFSU)	USA, Wyoming	W. Stoll	DQ220468
Wilcoxina sp.	ITS RFLP RPC-10	USA, California	—	AF156926

Materials and Methods

Morphological observations

Macroscopic descriptions were compiled from field notes taken on the characters of fresh material for collections DHP & HDT May 1986 (FH) and BAP 492 (FH). Color terms and notations refer to those of Kornerup and Wanscher (1981). For micromorphological investigation, small pieces of dried apothecia were excised with a double-edged razor blade and allowed to rehydate in distilled H_2O for approximately 12 hours. Once fully rehydrated, excised portions were sectioned on a freezing microtome at a thickness of 20-35 µm, or used to prepare squash mounts. Sections were subsequently mounted in H_2O, congo red or cotton blue in lactic acid and viewed on a compound microscope utilizing both bright field and diffusion interference contrast (DIC) optics. All measurements were made from sections and squash mounts in H_2O. To adequately sample the range of ascospore dimensions, mature ascospores from each collection were measured at 1000X and the values pooled to determine an overall mean ascospore size. Photomicrographs were taken with a 35 mm camera body attached to an Olympus BX 60 microscope.

Molecular methods and analyses

DNA extraction, PCR and cycle sequencing protocols followed those outlined in Perry *et al*. (2007). The nLSU rDNA was symmetrically amplified using primers LROR and LR5 or LR7 (Moncalvo *et al*., 2000). In addition to these, internal primers LR3 and LR3R (Moncalvo *et al*., 2000) were also used for sequencing. Cleaned sequencing reactions were visualized on an ABI 3100 or 3730 Genetic Analyzer capillary sequencer (Applied Biosystems). Sequences were edited and assembled using the software package Sequencher 3.0 or 4.0 (Gene Codes Corp, Ann Arbor, MI). Sequences were aligned manually using MacClade 4 (Maddison and Maddison, 2000), Se-Al v.2.0 (Rambaut, 1996), and the editor window of PAUP* 4.0b4a (Swofford, 2003). Edited sequences have been deposited in GenBank (Table 1; http://www.ncbi.nlm.nih.gov/), and the aligned dataset is available via TreeBASE (http://www.treebase.org; S1764, M3216).

Parsimony analyses were conducted using PAUP* 4.0 (Swofford, 2003). Searches used a branch-and-bound algorithm with furthest sequence addition, MulTrees on, collapse of zero length branches and equal weighting of all characters. Nodal support of individual clades was assessed by bootstrap analyses (Felsenstein, 1985), using 1000 heuristic replicates, each consisting of 10 random addition sequences, with stepwise addition and tree bisection reconnection (TBR) branch swapping. Maximum likelihood (ML) searches were also conducted using PAUP*, under a GTR + I + G model of sequence evolution determined with the Akaike Information Criterion as calculated in the program Modeltest v.3.7 (Posada & Crandall, 1998). Parameter values were estimated from an initial tree generated using a simple Jukes-Cantor model. The resulting parameters were then fixed, and a search consisting of 500 heuristic replicates (random sequence addition, TBR branch swapping, collapse of zero length branches) was performed under the more complex model of sequence evolution as determined above. Clade support was assessed by nonparametric ML bootstrap analyses as implemented in the program PhyML (Guindon and Gascuel, 2003), and consisted of 1000 replicates using the same model of sequence evolution as the ML searches with all parameters estimated by the program. Bayesian analyses were performed using Metropolis-coupled Markov chain Monte Carlo (MCMCMC) methods as implemented in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) using the same model as the ML analyses. Bayesian analyses consisted of two parallel searches, run for 5 million generations and initiated with random starting trees. Chains were sampled every 500 generations for a total of 10,000 trees each, sampled from the posterior distribution. Those trees sampled prior to the runs reaching a split deviation frequency of 0.01 were discarded from the sample as the "burn-in," while the remaining trees were used to calculate the posterior probabilities of the

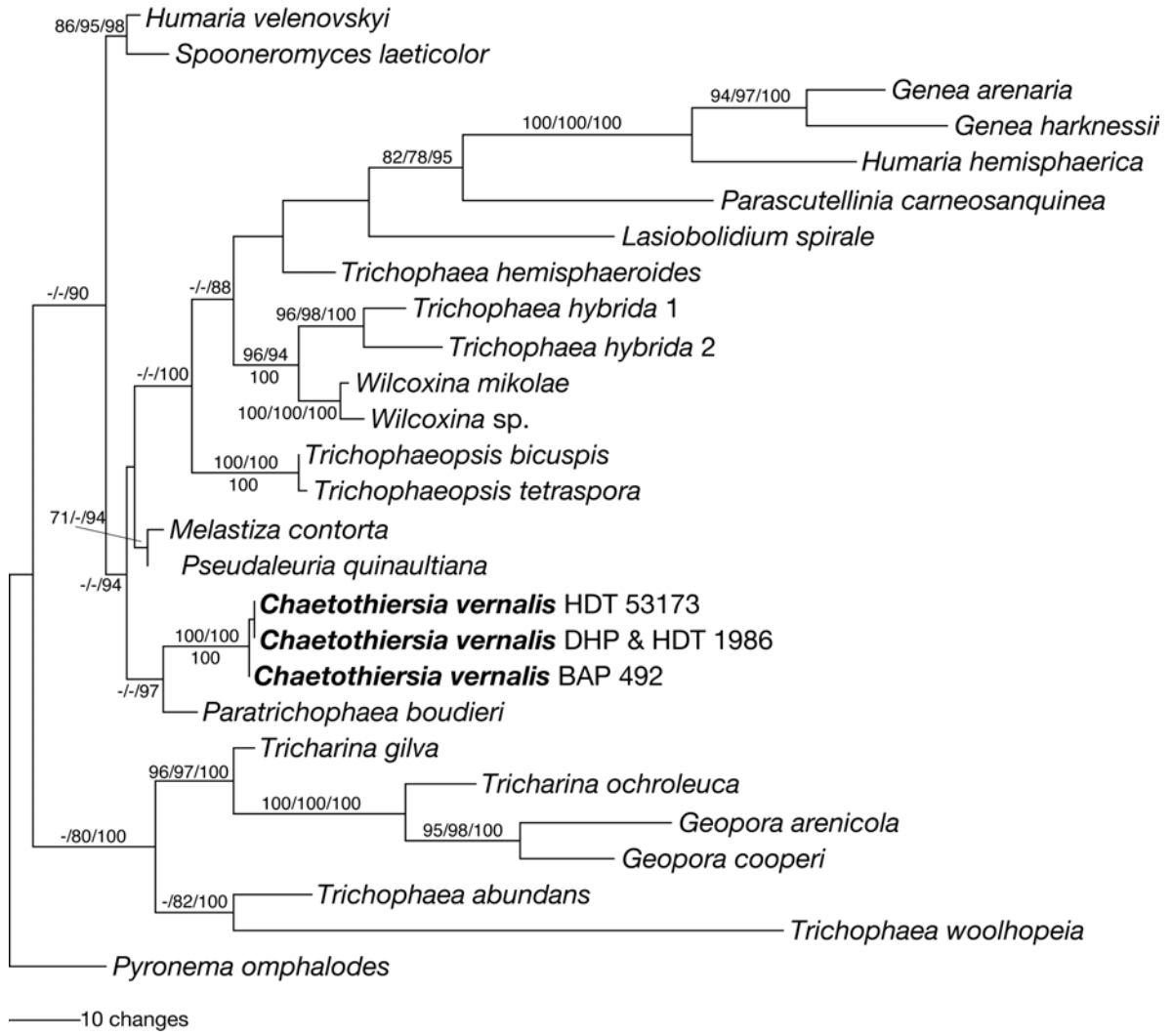


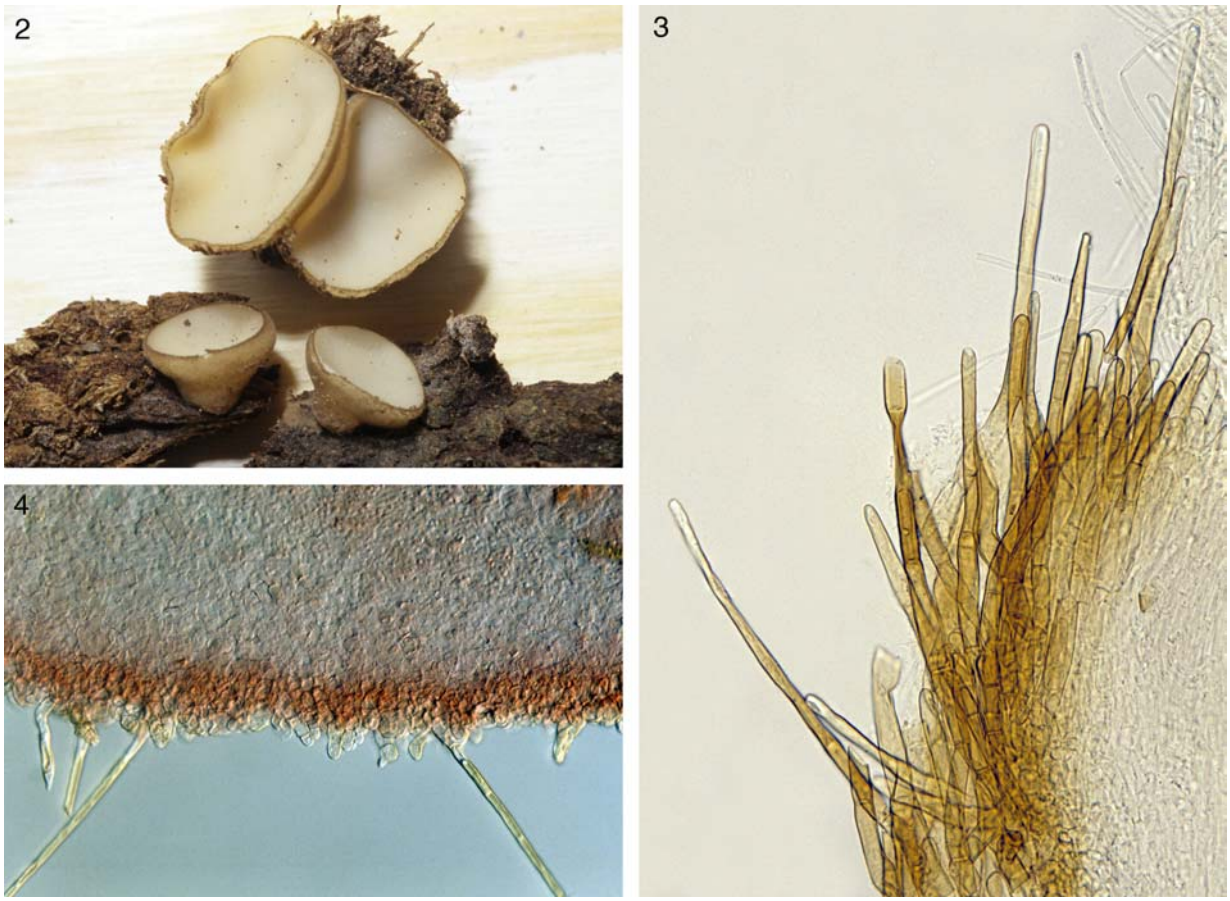
Fig. 1. Single parsimony tree of *Chaetothiersia* and other genera of *Pyronemataceae* inferred from nLSU sequence data (568 steps, CI = 0.609, RI = 0.666). Numbers separated by / represent parsimony bootstrap proportions, ML non-parametric bootstrap proportions, and Bayesian posterior probabilities greater than 70%, respectively (- designates a value below 70%). Numbers isolated below branches refer to Bayesian posterior probabilities, with associated bootstrap values located above the branch.

individual clades. The default settings were used in MrBayes to set the incremental heating scheme (i.e., 3 heated chains to one cold chain), unconstrained branch lengths [unconstrained: exponential (10.0)] and uninformative topology (uniform) priors.

Results

Phylogenetic analyses

The nLSU dataset consists of 834 aligned positions for 26 ingroup taxa, and contains 155 parsimony-informative positions. The parsimony analysis recovered a single tree of 568 steps (Fig. 1) similar to the tree produced by the ML analysis (-ln*L* = 3884.24117, not shown), differing only in the placement of *Lasiobolidium* and *Trichophaea hemisphaerioides* within the larger clade. Bayesian analyses reached an average standard deviation of split frequencies below 0.01 after approximately 250,000 generations, and the first 500 trees were excluded as the "burn-in." The three collections of *Chaetothiersia vernalis* are highly supported as a monophyletic group, but weakly supported by bootstrap analyses as the sister group to *Paratrichophaea boudieri*. These taxa are part of a large, weakly



Figs 2-4. *Chaetothiersia vernalis* (BAP 492, **Holotype**, FH). **2.** Apothecia on bark of *Abies magnifica*, × 1.1. **3.** Light microscopic slide of superficial hairs arising from ectal excipulum of the apothecial margin, × 400. **4.** Light microscopic slide of ectal excipulum demonstrating the globose to angular-globose cells, formation of pustules, and the bases of two excipular hairs arising from this tissue layer, × 200. Photographs: B. A. Perry.

supported clade containing species of genera macromorphologically similar to *Chaetothiersia*, including *Genea*, *Trichophaea*, *Humaria*, *Trichophaeopsis* and *Wilcoxina*. The two species of *Genea* sampled form a well supported monophyletic group, as do both *Trichophaeopsis* and *Wilcoxina*. *Humaria* is non-monophyletic, with *H. hemisphaerica* forming the sister group to *Genea*, and *H. velenovskyi* grouping with *Spooneromyces laeticolor*. Taxa from *Tricharina* and *Geopora*, also morphologically similar to *Chaetothiersia*, form a separate, moderately supported clade with *Trichophaea abundans* and *T. woolhopeia*, rendering the later genus non-monophyletic. The two species of *Geopora* sampled, *G. arenicola* and *G. cooperi*, form a well supported monophyletic group, but *Tricharina* does not.

Chaetothiersia vernalis B.A. Perry & Pfister, **gen. et spec. nov**. (Figs 2-4) MycoBank: 510434.

Etymology: *Chaeto* (Latin) indicating the long hairs of the excipulum, and *thiersia* in reference to and in honor of Dr. Harry D. Thiers (1919-2000), professor of Biology and curator of mycological collections at San Francisco State University (H.D. Thiers Herbarium), and one of the first to collect specimens of this new genus and species; *vernalis* (Latin) pertaining to Spring; in reference to the fruiting of this species during the Spring months in the High Sierra Nevada.

Apothecia cupulatum vel disciforme, pallide canum ad cretaceum, margo distinctus; externus pilosus, pilus superficialis, rigidus ad curvus, hyalinus vel plus saepe fuscus, obtusus. *Excipulum* medullare crassum, densum, texturae intricatae; excipulum ectale tenue, perexiguum, cellulae globosae vel angulara-globosae. *Asci* octosporae, non-amyloideus, operculate. *Ascosporae* leaves, ellipsoidia, eguttulatae, hyalinae. *Paraphyses* simplices, angustae, rectae, septatae. *Gregarium*, lignatile.

***Holotypus*:** BAP 492 (FH), Sierra Co., California, USA.

Apothecia 5-30 mm diam, deep cupulate with a narrowed base at first, expanding to discoid and tending to become ±convoluted, larger forms often appressed to the substrate. *Hymenium* pale gray (2-3A3) to nearly white, smooth; margin distinct, covered with erect, dark brown hairs that are often borne in fascicles. *Receptacle* ± concolorous with hymenium, densely to sparsely covered with dark to pale brown, ± appressed and occasionally projecting hairs. *Ectal excipulum* only a few cells thick, up to 40 µm, extending beyond hymenium to form distinct margin, composed of angular-globose to broadly clavate cells 4.8-16 µm diam, tending to form small irregular pustules. *Medullary excipulum* thicker, up to 840 µm in sections 1-2 mm inwards from margin, composed of densely compacted *textura intricata*, cells 1.6-6.4 µm diam. *Excipular hairs* 60-720 × 4-14.4 µm, brown to nearly hyaline, multiseptate, thick-walled (up to 2.4 µm), apically rounded, arising from angular-globose cells of the ectal excipulum, those near the margin typically straight and projecting, those of the receptacle often flexous and quite narrowed apically (~2 µm), interspersed with shorter, broader forms. *Hymenium* 300-400 µm thick. *Asci* 8-spored, 304-380 × 8-16 µm, operculate, cylindrical, J–, arising from a pleurorhynchous base. *Ascospores* 16.8-18.4(-19.2) × 10-11.2 (-12) µm ($\bar{x}$ = 17.8 × 10.6 µm, n = 60 spores), ellipsoid, smooth, eguttulate, hyaline, not refractive in media containing lactic acid, with granular cytoplasmic contents, often collapsing in media other than H_2O. *Paraphyses* narrow, 1.6-2.4 µm diam, equal to barely expanding apically, straight, multiseptate, unbranched, hyaline, exceeding asci by up to 10.4 µm.

Habit and habitat: Gregarious to caespitose on decaying wood and bark of conifers (*Abies magnifica* A. Murray), and on woody debris in soil.

Known distribution: Northern High Sierra Nevada mountains, California, U.S.A., April to June.

Material examined: USA. California: El Dorado County, Crystal Basin Recreation Area, caespitose on woody debris in soil under conifers, 4 May 1974, *HDT 32218*, coll. by Harry D. Thiers (SFSU). El Dorado County, Silver Fork Road, near China Flat Campground, elev. ca. 1525 m, on woody debris in soil and rotting wood, 26 April 1986, *HS 3068*, coll. by Herb Saylor (SFSU). Sierra County, Highway 49, 3 miles east of Yuba Pass, solitary on woody debris in soil, 15 June 1983, *HDT 45925*, coll. by Harry D. Thiers (SFSU). Sierra County, Highway 49, "Steele Gulch," elev. ca. 1770 m, on conifer log, 18 May 1986, coll. by Donald H. Pfister & Harry D. Thiers (FH, paratype). Sierra County, Highway 49, Yuba Pass, elev. ca. 2400 m, on woody debris in soil under conifer bark, 6 June 1990, *HDT 53173*, coll. by Harry D. Thiers (SFSU, paratype). Sierra County, Highway 49, Yuba Pass, elev. ca. 2400 m, on backside of bark on decaying stump of *Abies magnifica*, 2 June 2003, *BAP 492*, coll. by Jack Laws (FH, holotype). Tuolumne County, Pinecrest Lake, on woody debris near dead logs, 1 April 1972, *HDT 28743*, coll. by Harry D. Thiers (SFSU). Tuolumne County, Pinecrest Lake, on woody debris near melting snow, 1 April 1972, *HDT 28744*, coll. by Harry D. Thiers (SFSU).

Discussion

Chaetothiersia vernalis is characterized by the following combination of features: smooth, eguttulate, ellipsoid ascospores, brown, non-rooting, stiff superficial excipular and marginal hairs with obtuse apices; a dense medullary excipulum composed of *textura intricata*; a very thin ectal excipulum of globose to angular-globose cells; medium to rather large apothecia (relative to other members of *Pyronemataceae*); and growth on wood and woody debris associated with moisture produced by the Spring snowmelt in the High Sierra Nevada. Our morphological observations, as well as the results of the phylogenetic analyses, indicate a close relationship between *Chaetothiersia* and *Paratrichophaea*. These genera are quite similar in the presence of smooth, ellipsoid ascospores and long, projecting excipular hairs. However, the hairs of *Paratrichophaea* are typically rooting, arising from the medullary excipulum, are apically acuminate, and often bifurcating basally. The hairs of *Chaetothiersia* are superficial in nature, arising from the cells of the thin ectal excipulum, obtuse apically, and have not been observed to branch basally. Additionally, the apothecia of the *Chaetothiersia* attain sizes quite a bit larger than those typically reported for *Paratrichophaea* (1-4 mm). *Paratrichophaea* appears to be a rather rare or easily overlooked genus, and we have sampled only a single species in our phylogenetic analyses. Aside from the original

description of the genus by Trigaux (1985), three species of *Paratrichophaea* have been treated from North America by Pfister (1988), and more recently Bronkers (2003) has treated two of the same species from Europe. An additional taxon, *Cheilymenia albescens* Dissing et Raitv., was transferred to *Paratrichophaea* by Schumacher (1988) due to the obvious affinities this species has with the other members of the genus.

Additional genera that may superficially resemble *Chaetothiersia* include *Trichophaea*, *Trichophaeopsis*, *Tricharina*, *Geopora*, *Humaria* and *Wilcoxina*. Of these genera, both *Humaria* and some *Trichophaea* species can be distinguished from *Chaetothiersia* by the presence of ornamented, guttulate spores. The smooth-spored species of *Trichophaea*, such as *T. woolhopeia* and *T. abundans*, are also characterized by guttulate spores. Similarly, *Geopora* is also characterized by ascospores containing 1-2 large guttules, and produces generally subhypogeous apothecia. *Wilcoxina* species have eguttulate spores, hair and excipular structure similar to *Chaetothiersia*, but can be distinguished by generally smaller ascospores (up to 9.5 × 16), which are yellow-refractive when mounted in media containing lactic acid. Additionally, the apothecia of *Wilcoxina* are often orange to ochraceous, and with the exception of *W. sequoia* (W. Phillips) T. Schumach., which is reported to grow on bark, foliage and decayed wood, the apothecia of most species occur on soil. The eguttulate ascospores of *Tricharina* are also often yellow-refractive in media containing lactic acid, and unlike *Chaetothiersia*, typically occupy more than half to nearly the entire length of the ascus. The excipular hairs of *Tricharina* are also generally restricted to the margin, and the apothecia are not known to occur on woody substrates. *Trichophaeopsis* species generally produce smaller apothecia (up to 4 mm diam.) than those of *Chaetothiersia*, and can be distinguished by the presence of ectal cells arranged in distinct vertical rows, and often forked excipular hairs which tend to have a long branch pointing upwards, relative to the orientation of the apothecium, and a shorter branch pointing down.

Phylogenetic analyses of the nLSU data support the recognition of *Chaetothiersia* as a distinct genus in the *Pyronemataceae*, and confirm, with weak bootstrap support, our morphological observations suggesting a sister relationship between this genus and *Paratrichophaea*. The relationships of *Chaetothiersia* to other morphologically similar genera of the family, however, are not resolved with high support. *Chaetothiersia* and *Paratrichophaea* are part of a clade containing several genera with morphologically similar features, but this clade is not well supported. With the exception of *Trichophaea*, *Humaria* and *Tricharina*, the other genera sampled by more than one taxon all form well supported monophyletic groups. In agreement with our previous investigation (Perry *et al*., 2007), the species of *Trichophaea* sampled are nested in two independent clades. *Trichophaea woolhopeia*, the type of the genus, and *T. abundans*, which are both smooth-spored species, are isolated from the rough-spored species *T. hybrida* and *T. hemisphaerioides*. *Humaria* displays a similar pattern, with the brightly pigmented *H. velenovskyi* forming the sister group to *Spooneromyces laeticolor*. These results suggest that the generic placement of both *H. velenovskyi* and the rough-spored species of *Trichophaea* are in need of reconsideration (Perry *et al*., 2007). Also in agreement with our previous analyses, the phylogenetic delimitation of *Tricharina* from *Geopora* remains unclear, indicating that the limits of these genera need to be re-examined.

Acknowledgements

We would like to thank Dennis E. Desjardin, curator of the herbarium at SFSU, for the loan of specimens HDT 28743, 28744, 32218, 45925, 53173, and HS 3068, used in this study. We would also like to thank Genevieve Lewis-Gentry for her invaluable assistance with the Latin diagnosis. This research was funded in part by NSF Grant DEB-0315940 to DHP and Karen Hansen, and a Harvard University research grant to BAP.

References

Bronkers, R.J.C. (2003). Een sleutel tot de Europese soorten van de genera *Trichophaea*, *Tricho-*

phaeopsis en *Paratrichophaea*. Sterbeeckia 23: 9-27.

Eriksson, O.E. (2006). Outline of Ascomycota. Myconet 12: 1-82.

Felsenstein, J. (1985). Confidence limits on phylogenies - an approach using the bootstrap. Evolution 39: 783-791.

Guindon, S. and Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52: 696-704.

Huelsenbeck, J.P. and Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754-755.

Kornerup, A. and Wanscher J.H. (1981). *Taschenlexikon der Farben*. 3rd edition. Muster-Scmidt, Zürich.

Maddison, D.R. and Maddison, W.P. (2000). *MacClade 4: Analyses of phylogeny and character evolution*. Version 4.0. Sinuaer Associates, U.S.A.

Moncalvo, J.M., Lutzoni, F.M., Rehner, S.A., Johnson, J. and Vilgalys R. (2000). Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Systematic Biology 49: 278-305.

Perry, B.A., Hansen, K. and Pfister, D.H. (2007). A phylogenetic overview of the family *Pyronemataceae* (*Ascomycota*, *Pezizales*). Mycological Research 111: 549-571.

Pfister, D.H. (1988). *Paratrichophaea* (*Pezizales*) in North America. Mycologia 80: 515-519.

Posada, D. and Crandall, K.A. (1998). Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817-818.

Rambaut, A. (1996). *Se-Al: Sequence Alignment Editor*. Available at http://evolve.zoo.ox.ac.uk/.

Ronquist, F. and Huelsenbeck, J.P. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572-1574.

Schumacher, T. (1988). The *Scutellinia* battle; the lost, missing and dead. Mycotaxon 33: 149-189.

Swofford, D.L. (2003). *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, U.S.A.

Triquax, G. (1985). *Paratrichophaea macrocystis* genre et espece nouveaux. Documents Mycologiques 16: 1-6.