



# A re-evaluation of the Chaetothyriales using criteria of comparative biology

Yu Quan<sup>1,2,3</sup> · Lucia Muggia<sup>4</sup> · Leandro F. Moreno<sup>5</sup> · Meizhu Wang<sup>1,2</sup> · Abdullah M. S. Al-Hatmi<sup>1,6,7</sup> · Nickolas da Silva Menezes<sup>14</sup> · Dongmei Shi<sup>9</sup> · Shuwen Deng<sup>10</sup> · Sarah Ahmed<sup>1,6</sup> · Kevin D. Hyde<sup>11</sup> · Vania A. Vicente<sup>8,14</sup> · Yingqian Kang<sup>2,13</sup> · J. Benjamin Stielow<sup>1,12</sup> · Sybren de Hoog<sup>1,6,8,10</sup>

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## Abstract

Chaetothyriales is an ascomycetous order within Eurotiomycetes. The order is particularly known through the black yeasts and filamentous relatives that cause opportunistic infections in humans. All species in the order are consistently melanized. Ecology and habitats of species are highly diverse, and often rather extreme in terms of exposition and toxicity. Families are defined on the basis of evolutionary history, which is reconstructed by time of divergence and concepts of comparative biology using stochastic character mapping and a multi-rate Brownian motion model to reconstruct ecological ancestral character states. Ancestry is hypothesized to be with a rock-inhabiting life style. Ecological disparity increased significantly in late Jurassic, probably due to expansion of cytochromes followed by colonization of vacant ecospace. Dramatic diversification took place subsequently, but at a low level of innovation resulting in strong niche conservatism for extant taxa. Families are ecologically different in degrees of specialization. One of the clades has adapted ant domatia, which are rich in hydrocarbons. In derived families, similar processes have enabled survival in domesticated environments rich in creosote and toxic hydrocarbons, and this ability might also explain the pronounced infectious ability of vertebrate hosts observed in these families. Conventional systems of morphological classification poorly correspond with recent phylogenetic data. Species are hypothesized to have low competitive ability against neighboring microbes, which interferes with their laboratory isolation on routine media. The dataset is unbalanced in that a large part of the extant biodiversity has not been analyzed by molecular methods, novel taxonomic entities being introduced at a regular pace. Our study comprises all available species sequenced to date for LSU and ITS, and a nomenclatural overview is provided. A limited number of species could not be assigned to any extant family.

**Keywords** Black yeasts · Phylogeny · Ecology · Ancestral reconstruction · Evolution · Nomenclature

## Introduction

Chaetothyriales is an ascomycetous order within Eurotiomycetes of the subphylum Pezizomycotina (Gueidan et al. 2014; Wijayawardene et al. 2020). The order is renowned for containing so-called black yeasts and their filamentous relatives, among which are numerous opportunistic

agents of disease in humans and cold-blooded vertebrates. Well-known genera are *Cladophialophora*, *Exophiala*, *Fonsecaea* and *Phialophora* (Herpotrichiellaceae), but the order is much more diverse, in the literature of the last decades containing about 42 genera (with frequent additions) arranged in six families as summarized in the taxonomic browser of NCBI and 56 genera belonging to 11 families by Wijayawardene et al. (2020). A family that has been linked to Chaetothyriales, viz. Coccodiniaceae, contains four genera with few epilithic and epiphytic species having nondescript morphology and which are difficult to cultivate and sequence. Most researchers hypothesize an affinity to Capnodiales in Dothideomycetes (Hyde et al. 2013; Réblová et al. 2013; Kirk et al. 2001; Winka et al. 1998). Other families included in the order by Barr (1987a, b), i.e.

✉ Dongmei Shi  
shidongmei28@163.com

✉ Yingqian Kang  
kangyingqian@gmc.edu.cn

✉ Sybren de Hoog  
sybren.dehoog@radboudumc.nl

Extended author information available on the last page of the article

Metacapnodiaceae, Microtheliopsidaceae, Strigulaceae and Trichopeltidaceae, have also been suggested to belong to Dothideomycetes or are *incertae sedis* (Reynolds 1985). Pyrenotrichaceae (Herrera-Campos et al. 2005) has been suggested to belong to Chaetothyriales Wijayawardene et al. (2020) but no sequence data are available to support this. Also for family Lyrommataceae, containing the single genus *Lyromma* producing ascomata with antler-shaped appendages and pycnidia with filiform conidia (Flakus and Farkas 2013) no sequence data is available. Some other described families will be discussed below. The five remaining families that are currently accepted in the order are Chaetothyraceae, Cyphellophoraceae, Epibryaceae, Herpotrichiellaceae, and Trichomeriaceae (Réblová et al. 2013; Gueidan et al. 2014; Chomnunti et al. 2012a; Barr 1976; Barr and Makkai 1987).

A major problem in Chaetothyriales is that only a fraction of the extant species is likely to be known, as shown for other groups of fungi in Hyde et al. (2018). Members of Herpotrichiellaceae have limited morphological features and should be distinguished by molecular parameters observed on asexual states in culture. Conversely, species in the large family Chaetothyraceae have classically been distinguished by the morphology of their sexual state in nature, and for most no sequence data are available. Further, new monophyletic lineages of lichen-inhabiting fungi have been reported for fungi close to Chaetothyriales (Muggia et al. 2015, 2016, 2017, 2020), for which the exact taxonomic position still needs to be determined. Therefore, taxonomic boundaries at lower and higher levels are likely to appear unstable in the future when more extant biodiversity will be added and adequately described.

In summary, the taxonomy in Chaetothyriales is unsettled, for three reasons: (1) fragmentary representation of extant species, (2) limited availability of sequence data, and (3) conflicting concepts between traditional and modern taxonomic methods. As a consequence, the order is in need of detailed taxonomic revision. In view of taxonomic stability, the present paper aims to develop a polyphasic approach to classification, at least at the family level, since strict phylogenetic taxonomy may be subject to change as soon as new aspects of biodiversity of the order are revealed.

## Materials and methods

### Strains and sequences

Sequences of strains used in this study were retrieved from an in-house black yeast database maintained for research purposes at Westerdijk Fungal Biodiversity Institute, supplemented with data from GenBank (Table 1). In view of optimal resolution of phylogenetic relationships, all species sequenced to date were included with a single sequence per

species. Up to now (April 2020), GenBank records at NCBI list the order Chaetothyriales with 6 families, 42 genera and 273 species. Sequences in the present study comprise of 8 described families, 33 genera, 209 species, 45 undescribed species and two outgroup species. Species not included are either missing sequences for the LSU or ITS or both, or these sequences are obvious errors in NCBI. Undescribed species are mainly inhabitants of ant nests (carton-building ants or domatia) (Voglmayr et al. 2011; Nepel et al. 2014), or rock-inhabiting species of which a significant share belong to Chaetothyriales (Ruibal et al. 2018; Muggia et al. 2020); only a selection of these has been included.

### Phylogeny

To assess the phylogenetic position of Chaetothyriales, phylogenetic analyses of the ITS and LSU loci were performed for 254 sequences representing this order. Multiple sequence alignments were made by MAFFT v7 (<http://mafft.cbrc.jp/>) and optimized manually using MEGA v7.2 (Kumar et al. 2012) and BIOEDIT v7.2 (Hall 1999). Missing data for part of the sequences for some taxa were coded as ‘missing’, but still could be used in the final matrix (Wiens 2006, 2008).

Models of DNA sequence evolution for each locus partition were selected with jModelTest v.2.0 (Darriba et al. 2012), using the Akaike information criterion (AIC, Akaike 1974). To detect possible topological conflicts among loci, the CADM test (Campbell et al. 2011; Legendre and Lapointe 2004) was performed using the function ‘CADM.global’ implemented in the package ‘ape’ of R (Paradis et al. 2004). With congruence, three alignments, ITS, LSU and ITS combined with LSU were used to run the tree. Three algorithms, i.e. maximum likelihood (ML), Bayesian inference (BI) and Neighbor-Joining (NJ) were employed on phylogenetic analyses. *Capnodium coffeae*, CBS 147.52 and *Capnodium salicinum*, CBS 131.34 were taken as outgroups in most of the trees.

ML trees were obtained using RaxML-VI-HPC as implemented on the CIPRES portal web server (<http://www.phylo.org/>). Neighbor Joining (NJ) was performed by MEGA v6 (Tamura et al. 2013) with Kimura 2-parameter model and statistical bootstrapping procedure involving 1000 replicates. Bayesian command files were prepared using MESQUITE v2.75 (Maddison and Maddison 2007), and the analysis was done in MRBAYES v3.1.2 implemented in the CIPRES web server (<http://www.phylo.org/>). Two parallel runs with four Markov chain Monte Carlo (MCMC) simulations for each run were set for 10,000,000 generations and the result was checked using TRACER v1.5 (Rambaut and Drummond 2009) for effective sample size (ESS). The run was then extended for another 10,000,000 generations with a sample frequency of 1,000 per generation.

**Table 1** Strain GenBank data with proximate ecology per species

Clade	Species	Accession number	Ecology	ITS	LSU	References
Clade 1 Herpotrichiellaceae	<i>Exophiala spinifera</i>	D22I	Opportunistic	MH010942.1	MH012097.1	Nascimento et al. (2017)
	<i>Rhinocladiella similis</i>	PW3041	Opportunistic	LC158611.1	LC158635.1	de Hoog et al. (2003)
	<i>Exophiala exophialae</i>	CBS 668.76 (T)	Other	AY156973.1	NG059252.1	CBS
	<i>Exophiala nigra</i>	CBS 535.94 (T)	Other	KY115191.1	NG059253.1	Moussa et al. (2017a)
	<i>Exophiala oligosperma</i>	CBS 127587	Opportunistic	MH864631.1	MH876068.1	Zeng et al. (2007)
	<i>Exophiala polymorpha</i>	CBS 138920 (T)	Opportunistic	KP070763.1	NG059237.1	Yong et al. (2015)
	<i>Exophiala italica</i>	MFLUCC 16-0245	Epiphytic	KY496744.1	KY496723.1	Tibpromma et al. (2017)
	<i>Thysanorea aquatica</i>	MFLCC 15-0966	Other	MG922572.1	MG922576.1	Dong et al. (2018)
	<i>Thysanorea papuana</i>	CBS 212.96 (T)	Other	MH862572.1	MH874198.1	Pratibha and Prabhugaonkar (2015)
	<i>Capronia kleinmondensis</i>	CBS 122671 (T)	Other	MH863226.1	EU552107.1	Marincowitz et al. (2008)
	<i>Rhinocladiella atrovirens</i>	CBS 264.49 (T)	Epiphytic	MH856518.1	EU041869.1	de Hoog (1977)
	<i>Exophiala dermatitidis</i>	CBS 207.35 (T)	Opportunistic	MH855649.1	NG059225.1	Sudhadham et al. (2008)
	<i>Capronia mansonii</i>	CBS 101.67 (T)	Epiphytic	AF050247.1	AY004338.1	CBS
	<i>Capronia munkii</i>	CBS 615.96 (T)	Epiphytic	MH862601.1	EF413604.1	CBS
	<i>Exophiala hongkongensis</i>	HKU 32 (T)	Opportunistic	JN625231.2	NG059264.1	Woo et al. (2013)
	<i>Capronia dactylotricha</i>	CBS 604.96 (T)	Other	AF050243.1	KX712343.1	CBS
	<i>Capronia pilosella</i>	AFTOL-ID 657	Other	DQ826737.1	DQ823099.1	Müller et al. (1987)
	<i>Veronaea compacta</i>	CBS 268.75 (T)	Epiphytic	EU041819.1	NG057790.1	Papendorf (1976)
	<i>Exophiala brunnea</i>	CBS 587.66 (T)	Epiphytic	MH858890.1	KX712342.1	Papendorf (1969)
	<i>Exophiala jeanselmei</i>	CBS 507.90 (T)	Opportunistic	AY156963.1	KJ930161.1	Zeng et al. (2007)
	<i>Exophiala moniliae</i>	CBS 520.76 (T)	Epiphytic	KF881967.1	KJ930162.1	de Hoog (1977)
	<i>Exophiala bergeri</i>	CBS 353.52 (T)	Opportunistic	MH857080.1	NG059199.1	Zeng et al. (2007)
	<i>Exophiala sideris</i>	D88	Other	KC315801.1	HM627072.1	Seyedmousavi et al. (2011)
	<i>Exophiala capensis</i>	CBS 128771 (T)	Epiphytic	NR_121493.1	NG_059207.1	Crous and Groenewald (2011)
	<i>Capronia fungicola</i>	CBS 614.96 (T)	Other	KY484990.1	NG058761.1	Müller et al. (1987)
	<i>Capronia nigerrima</i>	CBS 513.69	Other	MH859363.1	AY605075.1	Barr (1991)
	<i>Phaeoannellomyces elegans</i>	CBS 101597	Opportunistic	NR_155687.1	KY115194.1	Moussa et al. (2017a, b)
	<i>Exophiala psychrophila</i>	CBS 191.87 (T)	Opportunistic	NR_145371.1	MH873750.1	de Hoog et al. (2011)
	<i>Exophiala lignicola</i>	CBS 144622 (T)	Epiphytic	NR_163358.1	NG_066324.1	Crous et al. (2019)
	<i>Exophiala nidicola</i>	FMR 3889 (T)	Other	NR_161045.1	MG701056.1	Crous et al. (2018)
	<i>Exophiala nishimurae</i>	CBS 101538 (T)	Epiphytic	NR_137092.1	KX712351.1	de Hoog et al. (2003)
	<i>Exophiala palmae</i>	UPCB 86822 (T)	Epiphytic	NR_158414.1	NG_064428.1	Nascimento et al. (2017)
	<i>Exophiala heteromorpha</i>	CBS 232.33 (T)	Epiphytic	NR_111184.1	NG_063975.1	de Hoog et al. (2003)
<i>Exophiala eucalypticola</i>	CBS 143412 (T)	Epiphytic	MH107891.1	NG_063955.1	Crous et al. (2018)	
<i>Exophiala eucalypti</i>	CPC 27630	Epiphytic	KY173411.1	KY173502.1	Crous et al. (2013)	

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Capronia camelliae-yunnanensis</i>	CGMCC 3.19061 (T)	Epiphytic	NR_164589.1	NG_066425.1	Phookamsak et al. (2019)
	<i>Capronia leucadendri</i>	CBS 122672 (T)	Epiphytic	NR_156212.1	MH874754.1	Marincowitz et al. (2008)
	<i>Capronia parasitica</i>	CBS 123.88	Epiphytic	AF050252.1	FJ358225.1	Gueidan et al. (2008)
	<i>Rhinocladiella quercus</i>	CPC 26621 (T)	Epilithic/lichenicolous	KX306769.1	NG059698.1	Hernández-Restrepo et al. (2016)
	<i>Exophiala attenuata</i>	F10685 123.33	Opportunistic	KT013095.1	KT013094.1	Overy et al. (2015)
	<i>Exophiala lecanii-comi</i>	CBS 123.33 (T)	Opportunistic	MH855383.1	NG059200.1	Zeng et al. (2007)
	<i>Exophiala castellanii</i>	CBS 158.58 (T)	Opportunistic	MH857734.1	KF928522.1	CBS
	<i>Exophiala mesophila</i>	CBS 402.95	Other	MH862536.1	KX712349.1	Zeng et al. (2007)
	<i>Chaetothyriales sp.</i>	T210	Carton	KF614880	KF614880	Nepel et al. (2014)
	<i>Rhinocladiella phaeophora</i>	CBS 496.78 (T)	Other	EU041811.1	NG057785.1	Veerkamp et al. (1983)
	<i>Rhinocladiella aquaspersa</i>	CBS 122635	Opportunistic	GU017732.1	KX822357.1	Badali et al. (2010)
	<i>Rhinocladiella tropicalis</i>	RA776	Opportunistic	KU854928.1	KX356663.1	Gomes et al. (2016)
	<i>Rhinocladiella fasciculata</i>	CBS 132.86 (T)	Epiphytic	NR_145356.1	NG_057784.1	Arzanlou et al. (2007)
	<i>Rhinocladiella basitona</i>	CBS 101460 (T)	Opportunistic	AY163561.1	NG057783.1	de Hoog et al. (2019)
	<i>Exophiala salmonis</i>	CBS 157.67 (T)	Opportunistic	JF747137.1	AY213702.1	de Hoog et al. (2011)
	<i>Exophiala radialis</i>	P2854 (T)	Epiphytic	KT099204.1	KT723448.1	Madrid et al. (2016)
	<i>Exophiala equina</i>	CBS 116009 (T)	Opportunistic	KF928433.1	KF928497.1	de Hoog et al. (2011)
	<i>Exophiala pisciphila</i>	CBS 537.73 (T)	Opportunistic	DQ826739.1	NR121269	de Hoog et al. (2011)
	<i>Exophiala bonariae</i>	CCFEE 5792 (T)	Epilithic/lichenicolous	JX681046.1	KR781083.1	Isola et al. (2016)
	<i>Exophiala opportunistica</i>	CBS 122268	Opportunistic	KF928436.1	KF928500.1	de Hoog et al. (2011)
	<i>Exophiala cancerae</i>	CBS 115142	Opportunistic	MH862980.1	MH874540.1	de Hoog et al. (2011)
	<i>Exophiala abietophila</i>	CBS 145038 (T)	Epiphytic	NR_163357.1	NG_066323.1	Crous and Groenewald (2011)
	<i>Veronea constricta</i>	CBS 572.90	Other	MH862237.1	MH873920.1	Moustafa and Abdul-Wahid (1990)
	<i>Veronea japonica</i>	CBS 776.83 (T)	Epiphytic	MH861692.1	NG057789.1	Arzanlou et al. (2007)
	<i>Veronea botryosa</i>	CBS 254.57 (T)	Opportunistic	MH857711.1	MH869255.1	de Hoog et al. (2019)
	<i>Chaetothyriales sp.</i>	CBS 128956	Carton	KX822529	KX822529	Voglmayr et al. (2011)
	<i>Exophiala crusticola</i>	CBS 119970 (T)	Other	MH863070.1	NG059220.1	Dögen et al. (2013)
	<i>Minimelanolocus obscurus</i>	MFLUCC 15-0416	Other	KR215606.1	KR215611.1	Liu et al. (2015)
	<i>Minimelanolocus melanicus</i>	MFLUCC 15-0415 (T)	Other	KR215608.1	KR215613.1	Liu et al. (2015)
	<i>Minimelanolocus asiaticus</i>	MFLUCC 15-0237 (T)	Other	NR_154179.1	KR215610.1	Liu et al. (2015)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Minimelanolocus curvatus</i>	MFLUCC 15-0259 (T)	Other	KR215605.1	KR215609.1	Liu et al. (2015)
	<i>Minimelanolocus aquaticus</i>	MFLUCC 15-0414 (T)	Other	KR215607.1	KR215612.1	Liu et al. (2015)
	<i>Capronia acutisetata</i>	CBS 618.96 (T)	Epiphytic	NR_154744.1	NG058859.1	Müller et al. (1987)
	<i>Chaetothyriales sp.</i>	CBS 129051	Carton	KX822540	KX822540	Nepel et al. (2014)
	<i>Rhinocladiella anceps</i>	AFTOL ID 659	Other	DQ826740.1	DQ823102.1	CBS
	<i>Melanoctona tectonae</i>	MFLUCC 12-0389 (T)	Epiphytic	KX258778.1	KX258779.1	Tian et al. (2016)
	<i>Chaetothyriales sp.</i>	CBS 129050	Carton	KX822532.1	KX822532	Nepel et al. (2014)
	<i>Capronia coronata</i>	ATCC 56201 (T)	Other	NR_154745.1	AF050242.1	Müller et al. (1987)
	<i>Exophiala angulospora</i>	CBS 482.92 (T)	Opportunistic	MH862370.1	KF155190.1	Gjessing et al. (2011)
	<i>Rhinocladiella mackenziei</i>	CBS 368.92	Opportunistic	MH862361.1	EU041866.1	Moreno et al. (2018)
	<i>Rhinocladiella coryli</i>	CPC 26654 (T)	Epiphytic	KX306768.1	KX306793.1	Hernández-Restrepo et al. (2016)
	<i>Chaetothyriales sp.</i>	T171	Carton	KF614875	KF614875	Nepel et al. (2014)
	<i>Chaetothyriales sp.</i>	T22	Carton	KF614881	KF614881	Nepel et al. (2014)
	<i>Exophiala alcalophila</i>	CBS 520.82 (T)	Other	MH861524.1	NG059189.1	CBS
	<i>Fonsecaea minima</i>	CBS 125757 (T)	Epiphytic	MH863743.1	KF928520.1	Vicente et al. (2014)
	<i>Fonsecaea pugnacius</i>	CBS 139214 (T)	Opportunistic	NR_155089.1	NG058177.1	de Azevedo et al. (2015)
	<i>Fonsecaea pedrosoi</i>	CBS 271.37 (T)	Opportunistic	AB114127.1	KJ930166.1	Sutton et al. (2009)
	<i>Fonsecaea erecta</i>	CBS 125763	Epiphytic	KC886414.1	KF155186.1	Vicente et al. (2014)
	<i>Fonsecaea brasiliensis</i>	BMU 07620	Opportunistic	KJ701015.1	KJ930163.1	Vicente et al. (2012)
	<i>Cladophialophora devriesii</i>	CBS 147.84 (T)	Opportunistic	EU103985.1	KC809989.1	Badali et al. (2008)
	<i>Cladophialophora immunda</i>	CBS 834.96 (T)	Opportunistic	MH862619.1	KC809990.1	Badali et al. (2008)
	<i>Chaetothyriales sp.</i>	T367	Carton	KF614894	KF614894	Nepel et al. (2014)
	<i>Cladophialophora arxii</i>	CBS 306.94 (T)	Opportunistic	EU103986.1	NG058959.1	Badali et al. (2008)
	<i>Cladophialophora minourae</i>	CBS 556.83 (T)	Epiphytic	AY251087.1	NG058763.1	Badali et al. (2008)
	<i>Cladophialophora psammophila</i>	CBS 110553 (T)	Other	AY857517.1	NG058955.1	Badali et al. (2008)
	<i>Cladophialophora potulentorum</i>	CBS 114772	Other	EU035410.1	EU035410.1	Crous et al. (2007)
	<i>Cladophialophora australiensis</i>	CBS 112793	Other	EU137331.1	EU035402.1	Crous et al. (2007)
	<i>Cladophialophora matsushimae</i>	MFC1-P384 (T)	Epiphytic	FN549916.1	FN400758.1	Koukol (2010)
	<i>Cladophialophora lanosa</i>	KNU 16032 (T)	Other	LC387460.1	LC387461.1	Das et al. (2019)
	<i>Cladophialophora emmonsii</i>	CBS 640.96	Opportunistic	EU103995.1	KC809995.1	van den Ende and De Hoog (1999)
	<i>Chaetothyriales sp.</i>	CBS 128948	Carton	KX822492	KX822492	Voglmayr et al. (2011)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Chaetothyriales</i> sp.	CBS 128935	Carton	KX822479	KX822479	Voglmayr et al. (2011)
	<i>Chaetothyriales</i> sp.	CBS 128945	Carton	KX822487	KX822487	Voglmayr et al. (2011)
	<i>Cladophialophora mycetomatis</i>	CBS 122637 (T)	Opportunistic	FJ385276.1	NG058960.1	Badali et al. (2008)
	<i>Cladophialophora tumulicola</i>	JCM 28768	Epilithic/lichenicolous	LC192127.1	LC192092.1	Kiyuna et al. (2018)
	<i>Cladophialophora parmeliae</i>	CBS 129337	Other	JQ342180.2	JQ342182.1	Diederich et al. (2013)
	<i>Chaetothyriales</i> sp.	CBS 129044	Carton	KX822488	KX822488	Voglmayr et al. (2011)
	<i>Cladophialophora chaetospira</i>	CBS 114747	Epiphytic	EU035403.1	KF928514.1	Koukol (2010)
	<i>Cladophialophora boppii</i>	CBS 126.86 (T)	Opportunistic	MH861932.1	NG058762.1	de Hoog et al. (2019)
	<i>Cladophialophora yegresii</i>	CBS 114405 (T)	Epiphytic	EU137322.1	NG058855.1	de Hoog et al. (2007)
	<i>Cladophialophora subtilis</i>	CBS 122642 (T)	Opportunistic	FJ385273.1	NG058961.1	Badali et al. (2008)
	<i>Cladophialophora abundans</i>	CBS 126736	Epiphytic	KC776592.1	KC812100.1	Feng et al. (2014)
	<i>Cladophialophora samoensis</i>	CBS 259.83 (T)	Opportunistic	MH861581.1	NG058854.1	Badali et al. (2008)
	<i>Phialophora americana</i>	CBS 400.67	Opportunistic	MH859007.1	MH859007.1	Untereiner et al. (1999)
	<i>Phialophora verrucosa</i>	CBS 286.47	Opportunistic	KF928455.1	KF928519.1	Li et al. (2017)
	<i>Fonsecaea multimorphosa</i>	CBS 98096 (T)	Opportunistic	NR_111612.1	NG057983.1	CBS
	<i>Exophiala lacus</i>	FMR 3995	Other	KU705830.1	KU705847.1	de Hoog et al. (2011)
	<i>Cladophialophora tumbae</i>	JCM 28746 (T)	Epilithic/lichenicolous	LC192125.1	LC192090.1	Kiyuna et al. (2018)
	<i>Minimelanolocus thailandensis</i>	MFLUCC 15-0971	Other	MG922573.1	MG922577.1	Dong et al. (2018)
	<i>Minimelanolocus rous-selianus</i>	CBS 126086	Epiphytic	MH863784.1	MH875246.1	Ruiz et al. (2001)
	<i>Atrokyliandriopsis setulosa</i>	HMAS245592	Epiphytic	KP337330.1	KP337329.1	Ying-Rui Ma et al. (2015)
	<i>Uncispora</i> sp.	YMF 1.04133	Epiphytic	KU173860.1	KX131164.1	Yang et al. (2011)
	<i>Marinophialophora garethjonesii</i>	MFLUCC 16-1449(T)	Epiphytic	NR_164246.1	KY305176.1	Li et al. (2018)
	<i>Aculeata aquatica</i>	MFLUCC 11-0529	Epiphytic	MG922571.1	MG922575.1	Dong et al. (2018)
Clade 2 Cyphellophoraceae	<i>Cyphellophora euca-lypti</i>	CBS 124764 (T)	Epiphytic	KC455238.1	GQ303305.1	Cheewangkoon et al. (2009)
	<i>Cyphellophora guyanensis</i>	CBS 129342 (T)	Epiphytic	MH865228.1	MH876666.1	Decock et al. (2003)
	<i>Cyphellophora artocarp</i>	CHCJHBJBLM (T)	Epiphytic	KP010367.1	KP122930.1	Gao et al. (2015)
	<i>Cyphellophora musae</i>	GLZJSJ41 (T)	Epiphytic	KP010370.1	KP122932.1	Gao et al. (2015)
	<i>Cyphellophora olivacea</i>	CBS 122.74 (T)	Other	KC455247.1	KC455260.1	Réblová et al. (2013)
	<i>Cyphellophora phyllostachydis</i>	HLHNZWYZZ08 (T)	Epiphytic	KP010371.1	KP122933.1	Gao et al. (2015)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Cyphellophora gamsii</i>	CPC 25867 (T)	Epiphytic	KX228255.1	KX228307.1	Crous et al. (2016)
	<i>Cyphellophora oxyspora</i>	CBS 698.73 (T)	Other	MH860790.1	KC455262.1	CBS
	<i>Cyphellophora jindongensis</i>	IFRDCC 2659	Epiphytic	MF285234.1	MF285236.1	Yang et al. (2018)
	<i>Cyphellophora livistonae</i>	CPC 19433 (T)	Epiphytic	KC005774.1	NG042752.1	Madrid et al. (2016)
	<i>Phialophora intermedia</i>	CBS 235.93	Opportunistic	JQ766431.1	JQ766480.1	Iwatsu et al. (1988)
	<i>Cyphellophora pluriseptata</i>	CBS 286.85 (T)	Opportunistic	MH861881.1	KC455255.1	Feng et al. (2014)
	<i>Cyphellophora laciniata</i>	CBS 190.61 (T)	Opportunistic	EU035416.1	KF928547.1	Feng et al. (2014)
	<i>Cyphellophora suttonii</i>	CBS 449.91 (T)	Opportunistic	KC455243.1	KC455256.1	Feng et al. (2014)
	<i>Cyphellophora fusarioides</i>	CBS 130291 (T)	Opportunistic	MH865596.1	JQ766486.1	Feng et al. (2014)
	<i>Cyphellophora pauciseptata</i>	CBS 284.85 (T)	Opportunistic	JQ766438.1	JQ766519.1	Feng et al. (2014)
	<i>Cyphellophora sessilis</i>	CBS 243.85 (T)	Epiphytic	AY857542.1	EU514700.1	CBS
	<i>Cyphellophora europaea</i>	CBS 101466 (T)	Opportunistic	KF928473.1	KC455259.1	Lian and De Hoog (2010)
	<i>Cyphellophora vermisporea</i>	CBS 228.86 (T)	Other	MH861947.1	KC455257.1	Feng et al. (2014)
	<i>Cyphellophora reptans</i>	CBS 113.85 (T)	Other	EU514699.1	EU514699.1	Gao et al. (2015)
	<i>Chaetothyriales sp.</i>	CBS 128959	Carton	KX822542	KX822542	Voglmayr et al. (2011)
	<i>Phialophora capiguarae</i>	CBS 131954	Carton	KF928465.1	KF928529.1	Attili-Angelis et al. (2014)
	<i>Cyphellophora clematidis</i>	CBS 144983	Epiphytic	MK442577.1	MK442519.1	Crous et al. (2019)
	<i>Cyphellophora filicis</i>	DP002B	Epiphytic	MK404057.1	MK404053.1	Phookamsak et al. (2019)
	<i>Phialophora attae</i>	CBS 132767	Carton	KF928464.1	KF928528.1	Attili-Angelis et al. (2014)
	<i>Anthopsis deltoidea</i>	CBS 263.77(T)	Other	NR_153555.1	NG_057113.1	Moussa et al. (2017a, b)
Clade 3 Phaeosaccardinulaceae	<i>Paracladophialophora carceris</i>	CPC 27596 (T)	Epiphytic	NR_154360.1	KY173395.1	Crous et al. (2018)
	<i>P. cyperacearum</i>	CPC 33046 (T)	Epiphytic	NR_160625.1	MH327844.1	Crous et al. (2018)
Clade 4 Domatia	<i>Chaetothyriales sp.</i>	MACrb1	Domatium	HQ634654.1	HQ634654.1	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 135085	Domatium	KX822349	KX822349	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 132039	Domatium	KX822342	KX822342	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 129057	Domatium	KX822346	KX822346	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 132003	Domatium	KX822477	KX822477	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CR13Ceci2	Domatium	KX120978.1	KX120978.1	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	Cecr4	Domatium	KX822476	KX822476	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 135086	Domatium	KX822336	KX822336	Wang et al. (unpublished)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Chaetothyriales sp.</i>	Trii4	Domatium	KX822551	KX822551	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 134920	Domatium	KX822324	KX822324	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 134916	Domatium	KX822344	KX822344	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 128963	Domatium	KX822328	KX822328	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 128966	Domatium	KX822331	KX822331	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 128973	Domatium	KX822354	KX822354	Wang et al. (unpublished)
	<i>Chaetothyriales sp.</i>	CBS 134923	Domatium	KX822319	KX822319	Wang et al. (unpublished)
Clade 5 Melanina	<i>Chaetothyriales sp.</i>	A581	Epilithic/lichenicolous	MT193582	KT263163.1	Muggia et al (2020)
	<i>Chaetothyriales sp.</i>	A933	Epilithic/lichenicolous	MT193581	KT270641	Muggia et al (2020)
	<i>Chaetothyriales sp.</i>	A872	Epilithic/lichenicolous	MT193584	KT270601	Muggia et al (2020)
	<i>Chaetothyriales sp.</i>	A957	Epilithic/lichenicolous	MT193583	KT270659	Muggia et al (2020)
Clade 6 Trichomeriaceae	<i>Anthracoenomyces petraeus</i>	CGMCC 3.17315	Epilithic/lichenicolous	KP174843.1	KP174924.1	Su (2015)
	<i>Anthracoenomyces ramosus</i>	CGMCC 3.16367	Epilithic/lichenicolous	KP174846.1	KP174922.1	Su (2015)
	<i>Knufia perforans</i>	CBS 885.95 (T)	Epilithic/lichenicolous	MH862564.1	NG042586.1	Tsuneda et al. (2011)
	<i>Knufia petricola</i>	CBS 726.95 (T)	Epilithic/lichenicolous	MH862556.1	NG042775.1	Nai et al. (2013)
	<i>Knufia vaticanii</i>	CCFEE 5939 (T)	Epilithic/lichenicolous	KP791780.1	KR781068.1	Isola et al. (2016)
	<i>Knufia marmoricola</i>	CCFEE 6201	Epilithic/lichenicolous	KP791790.1	KR781077.1	Isola et al. (2016)
	<i>Knufia karalitana</i>	CCFEE 5921	Epilithic/lichenicolous	KP791784.1	KR781072.1	Isola et al. (2016)
	<i>Knufia epidermidis</i>	CBS 120353 (T)	Epilithic/lichenicolous	NR_111330.1	NG042475.1	Tsuneda et al. (2011)
	<i>Knufia cryptophialidica</i>	DAOM 216555 (T)	Epiphytic	JN040501.1	JN040500.1	Tsuneda et al. (2011)
	<i>Knufia mediterranea</i>	CBS 139721 (T)	Epilithic/lichenicolous	KP791794.1	KR781081.1	Isola et al. (2016)
	<i>Chaetothyriales sp.</i>	T261	Carton	KF614886.1	KF614886	Nepel et al. (2014)
	<i>Arthrocladium tropicale</i>	CBS 134926 (T)	Domatium	KX822543.1	NG057119.1	Nascimento et al. (2016)
	<i>Arthrocladium tardum</i>	CBS 127021 (T)	Epiphytic	KT337440.1	NG057089.1	Nascimento et al. (2016)
	<i>Arthrocladium caudatum</i>	CBS 457.67 (T)	Epiphytic	MH859032.1	NG_057084	Nascimento et al. (2016)
	<i>Arthrocladium fulminans</i>	CBS 136243 (T)	Opportunistic	KT337439.1	NG057088.1	Nascimento et al. (2016)
	<i>Chaetothyriales sp.</i>	CBS 128958	Carton	KX822541	KX822541	Voglmayr et al. (2011)
	<i>Chaetothyriales sp.</i>	CBS 129049	Carton	KX822531	KX822531	Voglmayr et al. (2011)



**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Chaetothyriales sp.</i>	CBS 129047	Carton	KX822533.1	KX822533	Voglmayr et al. (2011)
	<i>Exophiala placitae</i>	CBS 121716 (T)	Epiphytic	MH863143.1	MH874694.1	Crous et al. (2007)
	<i>Chaetothyriales sp.</i>	T179	Carton	KF614876.1	KF614876.1	Nepel et al. (2014)
	<i>Cladophialophora eucalypti</i>	CBS 145551 (T)	Epiphytic	MK876380.1	MK876419.1	Crous et al. (2019)
	<i>Cladophialophora pucciniophila</i>	KUS F23645	Other	JF263533.1	JF263534.1	Park and Shin (2011)
	<i>Cladophialophora proteae</i>	CBS 111667 (T)	Opportunistic	EU035411.1	EU035411.1	Crous et al. (2007)
	<i>Strelitziana albiziae</i>	CBS 126497 (T)	Epiphytic	MH864122.1	HQ599585.1	Crous et al. (2010)
	<i>Strelitziana eucalypti</i>	CBS 128214	Epiphytic	HQ599596.1	HQ599597.1	Crous et al. (2010)
	<i>Strelitziana australiensis</i>	CBS 124778 (T)	Epiphytic	GQ303295.1	GQ303326.2	Cheewangkoon et al. (2009)
	<i>Strelitziana cliviae</i>	CPC 19822 (T)	Epiphytic	KC005772.1	NG042750.1	Crous et al. (2012)
	<i>Bradymyces alpinus</i>	CCFEE 5493 (T)	Epilithic/lichenicolous	HG793052.1	GU250396.1	Hubka et al. (2014)
	<i>Bradymyces graniticola</i>	F6A	Epilithic/lichenicolous	KX179910.1	KX179912.1	Réblová et al. (2016)
	<i>Bradymyces oncorhynchi</i>	CCF 4369 (T)	Opportunistic	NR_132843.1	NG058643.1	Hubka et al. (2014)
	<i>Chaetothyriales sp.</i>	T333	Carton	KF614873.1	KF614873.1	Nepel et al. (2014)
	<i>Trichomerium foliicola</i>	MFLUCC 10-0078 (T)	Epiphytic	JX313655.1	JX313661.1	Chomnunti et al. (2011)
	<i>Trichomerium gloeosporum</i>	MFLUCC 10-0087 (T)	Epiphytic	JX313656.1	JX313662.1	Hongsanan et al. (2016a)
	<i>Trichomerium dioscoreae</i>	CBS 138870 (T)	Epiphytic	NR_137946.1	NG058126.1	Crous et al. (2014)
	<i>Trichomerium deniquelatatum</i>	MFLUCC 10-0884 (T)	Epiphytic	JX313654.1	JX313660.1	Chomnunti et al. (2012c)
	<i>Trichomerium eucalypti</i>	CBS 143443 (T)	Epiphytic	NR_156672.1	NG058525.1	Crous et al. (2017)
	<i>Chaetothyriales sp.</i>	T13	Carton	KF614778	KF614778	Nepel et al. (2014)
	<i>Chaetothyriales sp.</i>	T9	Carton	KF614780.1	KF614780.1	Nepel et al. (2014)
	<i>Chaetothyriales sp.</i>	CBS 128943	Carton	KX822485.1	KX822485	Voglmayr et al. (2011)
	<i>Chaetothyriales sp.</i>	CBS 129046	Carton	KX822526.1	KX822526	Voglmayr et al. (2011)
	<i>Knufia peltigerae</i>	CGMCC 3.17283	Epilithic/lichenicolous	KP174864.1	KP174935.1	Réblová et al. (2013)
	<i>Knufia tsunedae</i>	FMR 10621 (T)	Other	NR_132842.1	HG003672.1	Crous et al. (2013)
	<i>Metulocladosporiella musicola</i>	CBS 110960 (T)	Epiphytic	MH862870.1	DQ008153.1	Crous et al. (2006)
	<i>Brycekendrickomyces acaciae</i>	CBS 124104 (T)	Epiphytic	NR_132828.1	NG_058633.1	Crous et al. (2009)
	<i>Exophiala encephalarti</i>	CBS 128210	Epiphytic	HQ599588.1	HQ599589.1	Crous et al. (2010)
	<i>Ceramothyrium melastoma</i>	CPC 19837 (T)	Epiphytic	NR_111822.1	NG_042749.1	Crous et al. (2012)
	<i>Neostrelitziana acaciigena</i>	CBS 139903(T)	Epiphytic	NR_137987.1	NG_058165.1	Crous et al. (2015)
	<i>Strelitziana africana</i>	CBS 120037	Epiphytic	DQ885895.1	DQ885895.1	Arzanlou and Crous (2006)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
Clade 7 Chaetothyalceae	<i>Arthrophiale arthrospora</i>	COAD 658	Epiphytic	KY173473.1	KX447143.1	Crous et al. (2016)
	<i>Lithohypha aloicola</i>	CPC 35996(T)	Epiphytic	NR_166313.1	MN567611.1	Crous et al. (2019)
	<i>Ceramothyrium exiguum</i>	VTCCF-1209 (T)	Other	LC360297.1	LC360295.1	Tsurumi et al. (2018)
	<i>Nullicamycetes eucalypti</i>	CPC 32942 (T)	Epiphytic	MH327807.1	NG064546.1	Crous et al. (2018)
	<i>Ceramothyrium aquaticum</i>	VTCCF-1210 (T)	Other	LC360299.1	LC360296.1	Tsurumi et al. (2018)
	<i>Ceramothyrium phuquocense</i>	VTCCF-1206 (T)	Epiphytic	LC360298.1	LC360294.1	Tsurumi et al. (2018)
	<i>Camptophora schimae</i>	IFRDCC 2664	Epiphytic	MF285231.1	MF285233.1	Yang et al. (2018)
	<i>Camptophora hylomeconis</i>	CBS 113311 (T)	Epiphytic	EU035415.1	EU035415.1	Yang et al. (2018)
	<i>Aphanophora eugeniae</i>	CBS 124105 (T)	Epiphytic	FJ839617.1	NG056965.1	Réblová et al. (2013)
	<i>Phaeosaccardinula dendrocalami</i>	IFRDCC 2649 (T)	Epiphytic	NR_137820.1	NG060116.1	Yang et al. (2014)
	<i>Phaeosaccardinula multiseptata</i>	IFRDCC 2639 (T)	Epiphytic	NR_132894.1	KF667244.1	Yang et al. (2014)
	<i>Phaeosaccardinula ficus</i>	MFLUCC 10-0009 (T)	Epiphytic	HQ895840.1	NG059455.1	Chomnunti et al. (2014)
	<i>Ceramothyrium menglunense</i>	MFLUCC 16-1874 (T)	Epiphytic	KX524148.1	KX524146.1	Hyde et al. (2016)
	<i>Chaetothyrium brischoficola</i>	MFLUCC 10-0083 (T)	Epiphytic	HQ895839.1	HQ895836.1	Chomnunti et al. (2012c)
	<i>Vonarxia vagans</i>	CBS 123533 (T)	Epiphytic	FJ839636.1	NG057821.1	Réblová et al. (2013)
	<i>Chaetothyrium agathis</i>	MFLUCC 12-0113 (T)	Epiphytic	KP744437.1	KP744480.1	Liu et al. (2015)
	<i>Ceramothyrium podocarpus</i>	CPC 19826 (T)	Epiphytic	KC005773.1	NG042751.1	Crous et al. (2012)
	<i>Fumagopsis stellae</i>	CBS 145078 (T)	Epiphytic	NR_161138.1	NG_066293.1	Crous et al. (2018)
	<i>Exophiala eucalyptorum</i>	CBS 121638 (T)	Epiphytic	MH863133.1	NG_060793.1	Crous et al. (2007)
	<i>Ceramothyrium carnioolicum</i>	CBS 175.95	Epiphytic	KC978733.1	KC455251.1	CBS
<i>Ceramothyrium thailandicum</i>	MFLUCC 10-0008 (T)	Epiphytic	HQ895838.1	NG058817.1	Zeng et al. (2016)	
<i>Ceramothyrium ficus</i>	MFLUCC 15-0228 (T)	Epiphytic	KT588601.1	NG058927.1	Hongsanan et al. (2015a, b)	
<i>C. longivolcaniforme</i>	MFLUCC 16-1306 (T)	Epiphytic	KP324929.1	NG058904.1	Zeng et al. (2016)	
Clade 8 Epibryaceae	<i>Cladophialophora humicola</i>	CBS 117536 (T)	Epiphytic	EU035408.1	NG058850.1	Crous et al. (2007)
	<i>Cladophialophora minutissima</i>	CBS 121758 (T)	Bryophytic	MH863155.1	NG058851.1	Davey and Currah (2007)
	<i>Cladophialophora sylvestris</i>	CBS 350.83 (T)	Epiphytic	EU035413.1	EU035413.1	Crous et al. (2007)
	<i>Epibryon bryophilum</i>	CBS 126278	Bryophytic	MH863955.1	MH875414.1	Dobbeler (1978)
	<i>Epibryon interlamellare</i>	CBS 126286	Bryophytic	MH863958.1	MH875417.1	Dobbeler et al. (1979)
<i>Epibryon turfosorum</i>	CBS 126587	Bryophytic	MH864165.1	MH875627.1	Dobbeler (1978)	
Clade 9	<i>Chaetothyriales sp.</i>	L1992	Epilithic/lichenicolous	KT263083.1	KT263083.1	Muggia et al. (2015)

**Table 1** (continued)

Clade	Species	Accession number	Ecology	ITS	LSU	References
	<i>Chaetothyriales sp.</i>	L1993	Epilithic/lichenicolous	KT263084.1	KT263084.1	Muggia et al. (2015)
	<i>Chaetothyriales sp.</i>	L1994	Epilithic/lichenicolous	KT263085.1	KT263085.1	Muggia et al. (2015)
	<i>Lichenodiplis lecanorae</i>	L	Epilithic/lichenicolous	–	KT285909.1	Muggia et al. (2015)
Incertae sedis	<i>Cladophialophora modesta</i>	CBS 985.96	Opportunistic	KF928421.1	KF928485.1	Stielow and de Hoog (2014)
	<i>Cladophialophora scillae</i>	CBS 116461	Epiphytic	EU035412.1	EU035412.1	Crous et al. (2007)
	<i>Bacillicladium clematidis</i>	CBS 145035(T)	Epiphytic	NR_163355.1	NG_066322.1	Crous et al. (2019)
	<i>Cladophialophora hostae</i>	CBS 121637	Epiphytic	KX822478.1	KX822478.1	Crous et al. (2007)
	<i>Coccodinium bartschii</i>	CPC 13861	Epiphytic	EU019265.1	EU019265.1	Crous et al. (2007)
	<i>Capronia villosa</i>	ATCC 56206	Epiphytic	AF050261	AF050261	Untereiner et al. (1999)
	<i>Epibryon hepaticola</i>	M10 (T)	Bryophytic	EU725690.1	EU940091.1	Stenroos et al. (2010a, b)
Outgroup	<i>Capnodium coffeae</i>	CBS 147.52	Epiphytic	MH856967.1	MH868489.1	Hongsanan (2015a, b)
	<i>Capnodium salicinum</i>	CBS 131.34	Epiphytic	MH855469.1	MH866941.1	Mont (1849)

Of the 209 described species, four species were not recorded in the NCBI Taxonomy browser, but were described as *incertae sedis* by Wijayawardene et al. (2020), who listed ten genera as *incertae sedis*. We tested these as possible out- or in-groups by comparing the resulting bootstrap values. Similarly, species with long branches were re-analyzed as outgroup in ML trees that were run accordingly. All branches with bootstrap values  $\geq 70\%$  were collapsed, starting with the first group containing  $>1$  members. The absolute and relative numbers of collapsed clades were taken as a parameter of confidence, the ratios (supported/unsupported clades) were calculated (Table 2), criteria of quality of trees being a low number of unsupported trees, as well as a low number of collapsed trees indicating high support of branches of the backbone. Phylogenetic trees were edited using TREEVIEW v1.6.6 and completed with Adobe ILLUSTRATOR CS v5. The alignment was deposited in TREEBASE under accession number 26209.

### Divergence time and evolutionary rate estimation

Fossil-calibrated phylogeny was calculated by the BEAST2 tutorial (<https://beast2-dev.github.io>). The concatenated data set was used as a primary input to BEAST2 analyze and the choice of the GTR substitution model was based on pre-analysis using jModelTest v2.0 (Darriba et al. 2012) and the substitution rate was estimated. The divergence time

estimation was executed with a strict clock and birth-death models. Fossil data of the taxonomic group closest to Eurotiomycetes, i.e. the class Sordariomycetes studied e.g. by Pérez-Ortega et al. (2016), Liu et al. (2017) and Samarakoon et al. (2019) was used as calibration point (mean: 136 Mya; sigma: 0.5; credibility interval: 95 %). Tree sequences from Sordariomycetes were included: *Meliola centellae*, *Cordyceps agriota*, and *Colletotrichum agaves caricis* forcing the monophyletic mode. Similarly, a calibration point of 100 Mya to the order Capnodiales was included. Default MCMC options were used. The results were analyzed using TRACER v1.7.1 and to generate a maximum confidence of clades in the tree, TREEANNOTATOR v2.6.0 (burn-in option of 10%) and BEASTv.2.6.1. The tree was visualized by FIGTREE v1.4.4 and the geological axis was added using the GEOSCALEPHYLO function from the STRAP R package (<https://cran.r-project.org/web/packages/strap>) (Fig. 1).

### Ecology

We investigated broad ecological trends of 254 species by consulting original literature, NCBI database, Westerdijk database, MycoBank ([www.Mycobank.org](http://www.Mycobank.org)), and Index Fungorum ([www.indexfungorum.org](http://www.indexfungorum.org)); additional information to extend hypothesized ecological trends per species was abstracted from specific literature where available. Average ecologies were summarized as a single symbol per species,

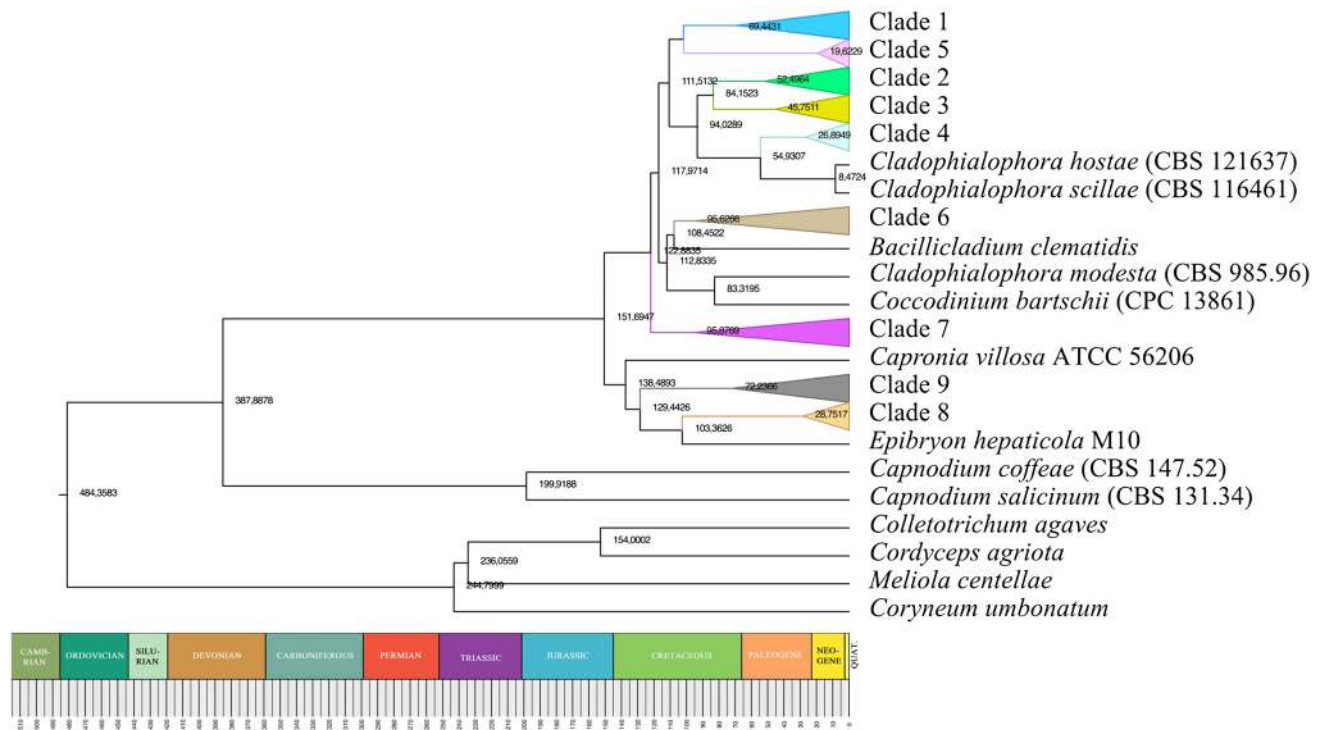
**Table 2** Outgroup test for long branches base on ML tree

Outgroups	Bootstrap										Supported/unsup-ported clades	Ratio
	Clade 1	cLade 2	Clade 3	Clade 4	Clade 5	Clade 6	Clade 7	Clade 8	Clade 9			
<i>Epibryon hepaticola</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Capronia villosa</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Cladophialophora modesta</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Cladophialophora hostae</i> , <i>C.scille</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Paracladophialophora</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Coccodinium bartschii</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Bacillicladium dematidis</i>	94	100	100	95	100	100	70	100	97	14/8	1.75	
<i>Capronia nigerrima</i>	-	100	100	95	100	100	70	100	97	23/32	0.72	
<i>Rhinocladiella mackenziei</i>	-	100	100	95	100	100	70	100	97	23/32	0.72	
<i>Arthrospiala arthrospora</i>	94	100	100	95	100	-	70	100	100	27/26	1.04	
<i>Strelitziana</i>	94	100	100	95	100	-	70	100	100	27/26	1.04	
Capnodium without incertae sedis	-	99	100	100	93	98	99	100	100	21/33	0.63	
Capnodium with incertae sedis	70	100	96	100	98	99	71	100	99	13/10	1.30	

and quantified relative to the number of species recognized per families (Table 1; Fig. 2). This aimed to extract broad evolutionary trends per family, which was used to strengthen or to falsify clades generated by ribosomal data.

### Ancestral character state reconstruction

Trends in evolutionary ancestry and its impact on lineage and species diversification was analyzed in the following steps: (i) simulation of quantitative traits among the phylogenetic tree, (ii) stochastic character mapping and inference of a multi-rate Brownian motion model fitting and its visualization, (iii) calculation of phylogenetic signals, and (iv) ecological disparity, and comparison to (v) lineage diversification over time. Discretely valued ecological character traits are listed in Table 1. Discrete characters were converted into continuous states to estimate their evolution along the previously inferred phylogeny based on ITS and LSU gene sequences (Fig. 3). Stochastic character mapping onto the phylogeny was done according to Hulslenbeck et al. (2003) with subsequent fitting of a multi rate Brownian motion model (Likelihood test for rate variation in a continuous trait) to estimate evolutionary rates (= Sigma parameter) for each character and to infer the ancestral state at the root node (O'Meara et al. 2006). Quantitative traits (= ecologies) were simulated among the phylogeny and were plotted as phenogram to visualize trait dynamics. To assess the phylogenetic signal of our data we computed the K statistic (Blomberg et al. 2003) and  $\lambda$  (Pagel 1999) to assess resolution quality of our dataset. Disparity relative to lineage diversification was calculated to assess success of species cladogenesis according to Pybus & Harvey (2000). Analyses were done with R statistical software (<https://www.r-project.org/>), employing mainly the packages APE (Paradis and Schliep 2019), PEGAS (Paradis 2010), GEIGER (Pennell et al. 2014), MAPS (<https://cran.r-project.org/web/packages/maps/index.html>), TAXONOMIZR (<https://cran.r-project.org/web/packages/taxonomizr/index.html>), PHYTOOLS (Revel 2011), and all their reverse dependencies. We used the functions 'MAKE.SIMMAP' for stochastically map characters (i), 'BROWNIE.LITE' to model in the Brownian motion process (ii), and to reconstruct the ancestral character state. Quantitative trait simulation (iii), was conducted via the 'TRAIGRAM' and 'PHENOGRAM' functions as well to plot the Brownian motion process of character evolution and to visualize the phenotype to the phylogeny (iv). Phylogenetic signal for K and  $\lambda$  were computed via the function 'PHYLOSIG' (vi). To assess lineage diversification rates we plotted a 'lineage through time' (LTT) via the function 'LTT' plot to define the relative time ratio required for the Chaetothyriales to give rise to its present lineages. Subsequently, to assess



**Fig. 1** Divergence time of the order Chaetothyriales based on ITS and LSU sequences. The bottom scale presents the main geological and periods and eras

morphological disparity we calculated and plotted a disparity through time (DTT) distribution via the function ‘DTT’ (vii). Details of the analysis and compiled scripts are available upon request.

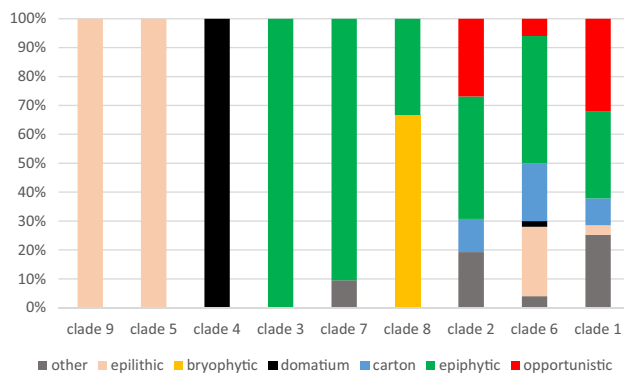
## Results

### Phylogeny

The single gene ITS and partial LSU, and combined sequences of ITS with partial LSU of 254 strains of black fungi were applied to determine phylogenetic trees of the entire order Chaetothyriales, using *Capnodium salicinum* and *Capnodium coffeae* as outgroups taxa. The alignment contained 522 characters for ITS, 497 for LSU, 1019 for combined sequences. The alignment of combined sequences had the following base frequencies:  $f(A) = 0.243$ ,  $f(T) = 0.247$ ,  $f(C) = 0.234$ ,  $f(G) = 0.275$ , among which 642 were variable and 548 parsimony-informative sites. When separate trees of LSU and ITS were compared with the tree based on the concatenated alignment, bootstrap values in the combined tree on average were higher than those found in single-gene trees. Some families did not form supported clades in single gene trees, but obtained higher

bootstrap support in combined trees. The non-collapsed NJ tree showed that this algorithm is not suitable for analysis of Chaetothyriales at ordinal level, judging from the low number of supported branches. With Bayesian analysis (BA) (Fig. 3) the combined tree contained a total of 153 supported clades (posterior probabilities  $PP \geq 95\%$ ), and with maximum likelihood (ML) 123 supported clades (bootstrap support  $BS \geq 70\%$ ). A total of 120 clades were recognized consistent in the two algorithms; in Fig. 3 both types of support are indicated by thickness of the branches.

For the reconstruction of the possible evolution of the order Chaetothyriales, the order of appearance of recognized groups is significant. In most literature on Chaetothyriales, topologies of phylogenetic inferences suggest the existence of six families (Réblová et al. 2013; Gueidan et al. 2014; Teixeira et al. 2017). The family Phaeosaccardinulaceae was introduced by Batista and Ciferri (1962) and is represented by three species (Wijayawardene et al. 2020). The recently described families Strelitzianaceae and Paracladophialophoraceae have four and two species in the tree, respectively. Three more groups were added in recent studies exploring novel habitats (Muggia et al. 2020; Wang unpublished data). These groups were mostly recognized as separate clades supported with high bootstrap in the bi-locus tree with all algorithms applied.



**Fig. 2** Approximate types of ecology distributed over different families of Chaetothyriales, normalized to 100%. Pink represents ‘epilithic/lichenolytic’, orange ‘bryophytic’, black ‘ant domatium-associated’, blue ‘ant-made carton-associated’, green ‘epiphytic’, red ‘opportunistic’; brown unites ‘other’, remaining categories, mainly soil, water and fungus

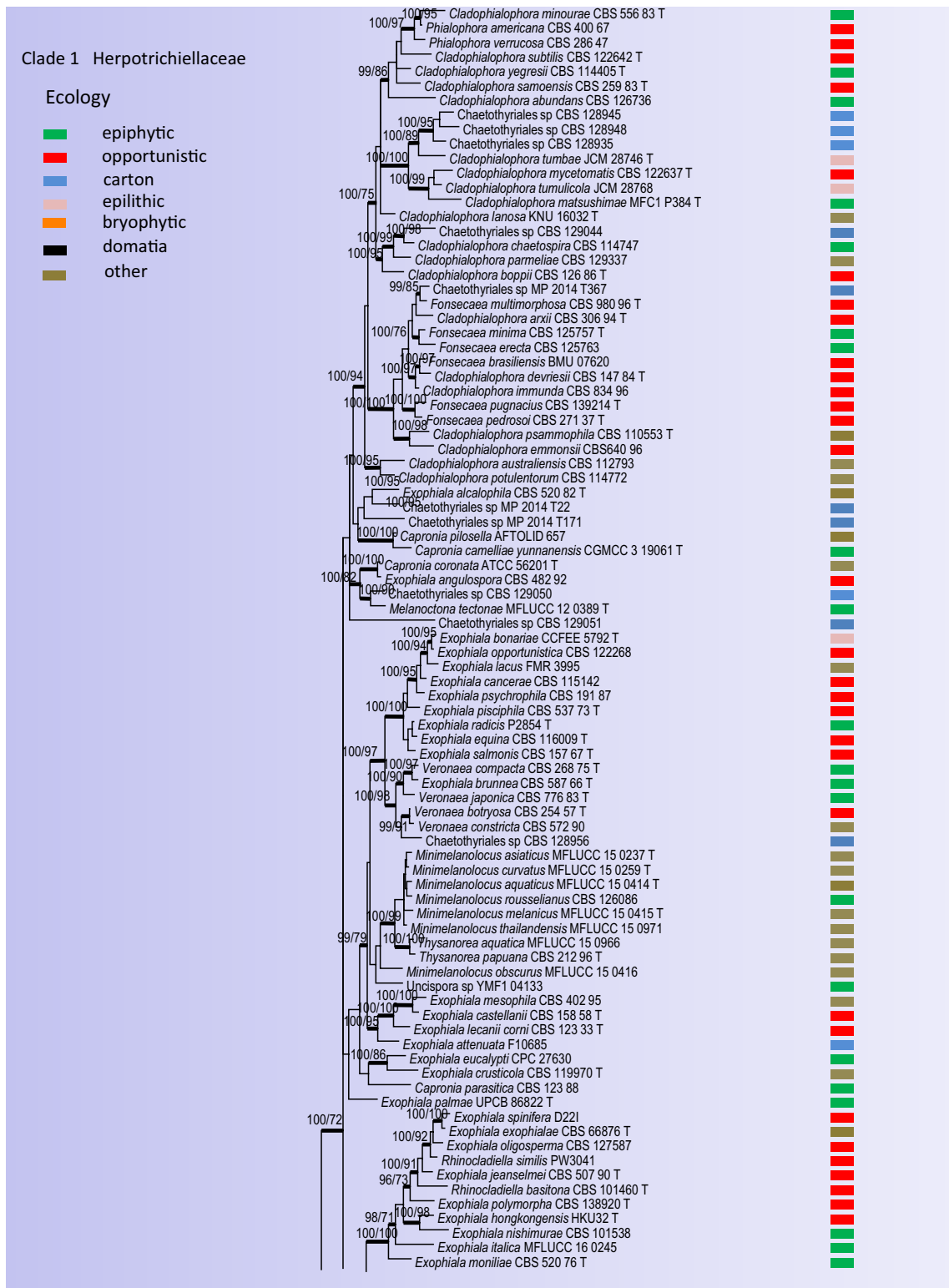
Six species, *Atrokyndriopsis* (Ma et al. 2015), *Lichenodiplis* (Hawksworth and Dyko 1979), *Melnikomyces* (Crous et al. 2014), *Bacillicladium* (Réblová et al. 2016), *Muellerella* (Muggia et al. 2020) and *Uncispora* (Sinclair 1979), mentioned as having an uncertain phylogenetic position by Wijayawardene et al. (2020), were included in the ML analysis. *Atrokyndriopsis setulosa* and *Uncispora* in Clade 1 had bootstrap support of 72 %. When *Neostrelitziana acaciigena* was added to the tree, it clustered in Clade 6, almost all species of this clade were described as Trichomeriaceae, with bootstrap support remaining at 100%. *Paracladophialophora* formed a sister clade to a cluster of undescribed ant-domatia associated fungi. *Lichenodiplis*, for which only an LSU sequence was available, formed a sister clade to a group of endolichenic fungi (Muggia et al. 2020). *Bacillicladium* was monophyletic next to Trichomeriaceae with low bootstrap support. The tree including the genera above is shown in Fig. 3. The genera *Melnikomyces* and *Muellerella* seemed remote from Chaetothyriales and were excluded from further analysis.

In the literature, the following fungi are treated as members of Chaetothyriales, at least by some authors, but were found at relatively long branches in the ML tree: *Epibryon hepaticola*, *Capronia villosa*, *Cladophialophora modesta*, *Cladophialophora hostae*, *Cladophialophora scillae*, *Paracladophialophora* spp., *Coccodinium bartschii*, *Arthrophia arthrospora*, *Capronia nigerrima*, *Bacillicladium dematidis*, *Rhinochlaediella mackenziei*, and *Strelitziana* spp., of which *Coccodinium* has been surmised to be dothideaceous (Hyde et al. 2013). Species were individually rearranged as outgroups and the effect on statistical support of resulting ML trees was compared with the supposition as to whether these are members or non-members, the bootstrap values should change significantly. Supported and unsupported clades were calculated; trees with highest ratios supported

vs. unsupported clades at a low number of supported clades in the backbone were considered to be optimal. The ratio of the combined ML tree including all *incertae sedis* above is 1.30 (Table 2). The highest ratios (1.75) were obtained when *Epibryon hepaticola*, *Capronia villosa*, *Cladophialophora modesta*, *Cladophialophora hostae* and *Cladophialophora scillae*, *Paracladophialophora* spp., *Bacillicladium dematidis*, or *Coccodinium bartschii* were used as outgroup, the ratios increased slightly compared to the reference tree (1.30, with *Capnodium* as outgroup); these species were consequently regarded as *incertae sedis*. Four of the items tested as outgroups, i.e. *Capronia nigerrima* (0.72), *Rhinochlaediella mackenziei* (0.72), *Arthrophia arthrospora* (1.04), and *Strelitziana* spp. (1.04) had a negative impact on the tree and taken as belonging in Chaetothyriales. *Bacillicladium dematidis*, *Cladophialophora modesta*, and *Capronia villosa*, similar to dothidealean *Coccodinium bartschii*, appeared as single-species branches in the tree, could not be affiliated to any of the known families and are therefore regarded as *incertae sedis*. Whether or not these species are members of Chaetothyriales could not be established. The complete tree including these species was compared to the same tree without these species, which led to drop of the ratio to 0.63. The complete tree with *Paracladophialophora* as outgroup remained the optimal tree, with a high ratio (1.75) of supported/unsupported branches and with a relatively low number of clades. This suggest that the group (Clade 3) represents a separate family, as proposed by Crous et al. (2016).

The best-fit models of evolution obtained for the different datasets were ITS = TVM+I+G, LSU = GTR+I+G, combined sequences = TIM2+I+G. No topological conflicts between the datasets were detected. The ML tree was constructed with GTRGAMMA + I in the CIPRES webserver. Robustness of trees was tested by comparing different algorithms on the individual datasets of LSU and ITS, and the combined dataset, placing accent on the backbone by collapsing all supported clades. The best tree is judged to be the one with the most resolved backbone, i.e. an optimal ratio of supported/unsupported branches, combined with high support values for all clades, starting at the outermost position (lowest value) which was variably taken by *Capronia villosa* or *Cladophialophora modesta* (Fig. 4; Table 3). With these criteria, the Bayesian tree of the combined dataset appeared to be optimal. Nine well-supported clades were recognized, which represent five existing families and several uncharacterized groups.

Clade 7 (**Chaetothyriaceae**) was relatively heterogeneous with low support, most likely caused by undersampling of sequence data as compared to the large diversity described on the natural substrate. One of the two *Chaetothyrium* species defining family and order, *C. brischoficola*, was found in this clade in several datasets (Fig. 3). The families



**Fig. 3** Phylogenetic tree of Chaetothyriales based on ITS and LSU sequences, obtained by Bayesian analysis and maximum likelihood (values of  $\geq 95\%$  for Bayesian probability and  $\geq 70\%$  for maximum

likelihood shown in bold branches). *Capnodium coffeae* and *Capnodium salicinum* were used as outgroup

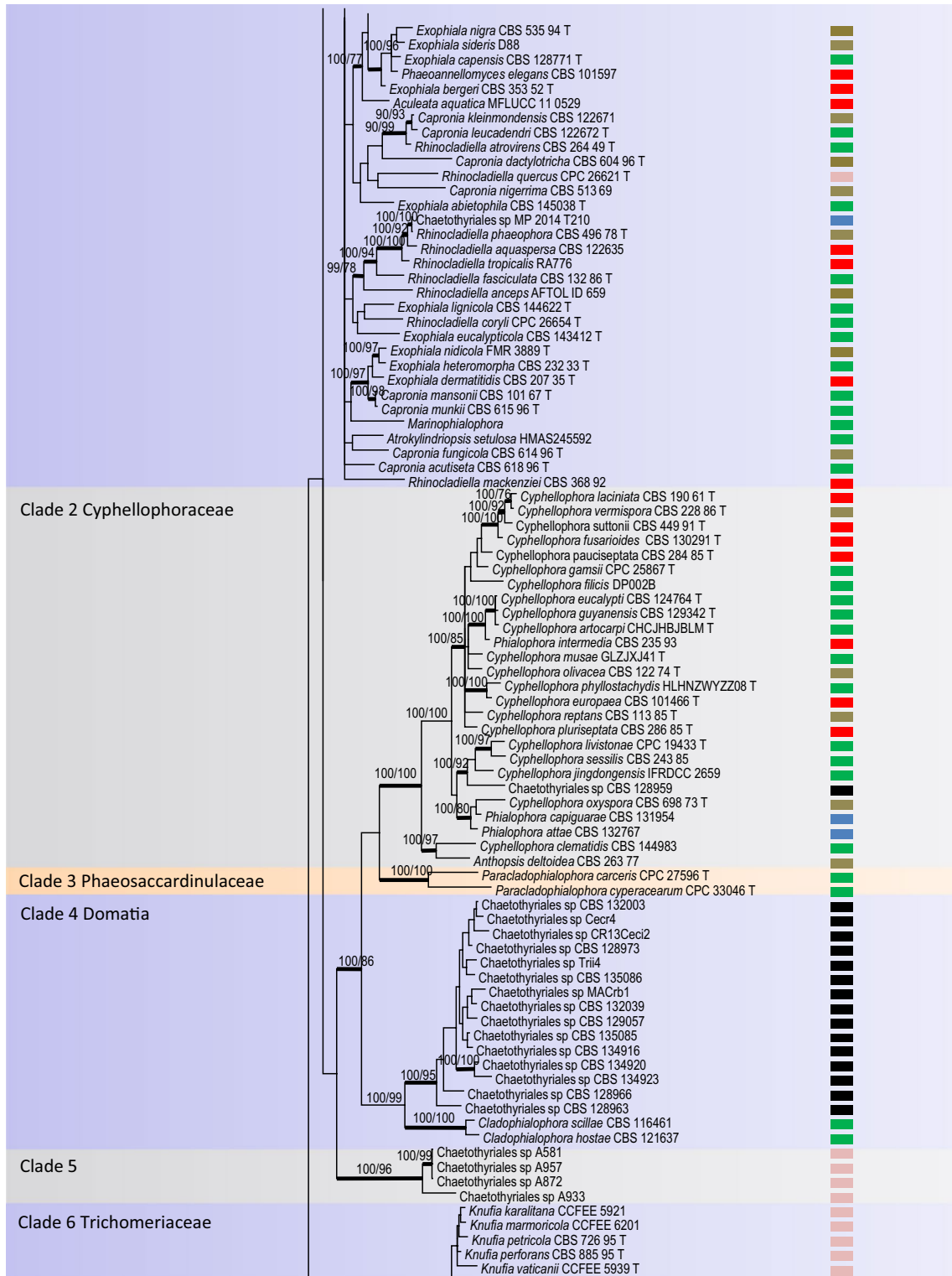


Fig. 3 (continued)



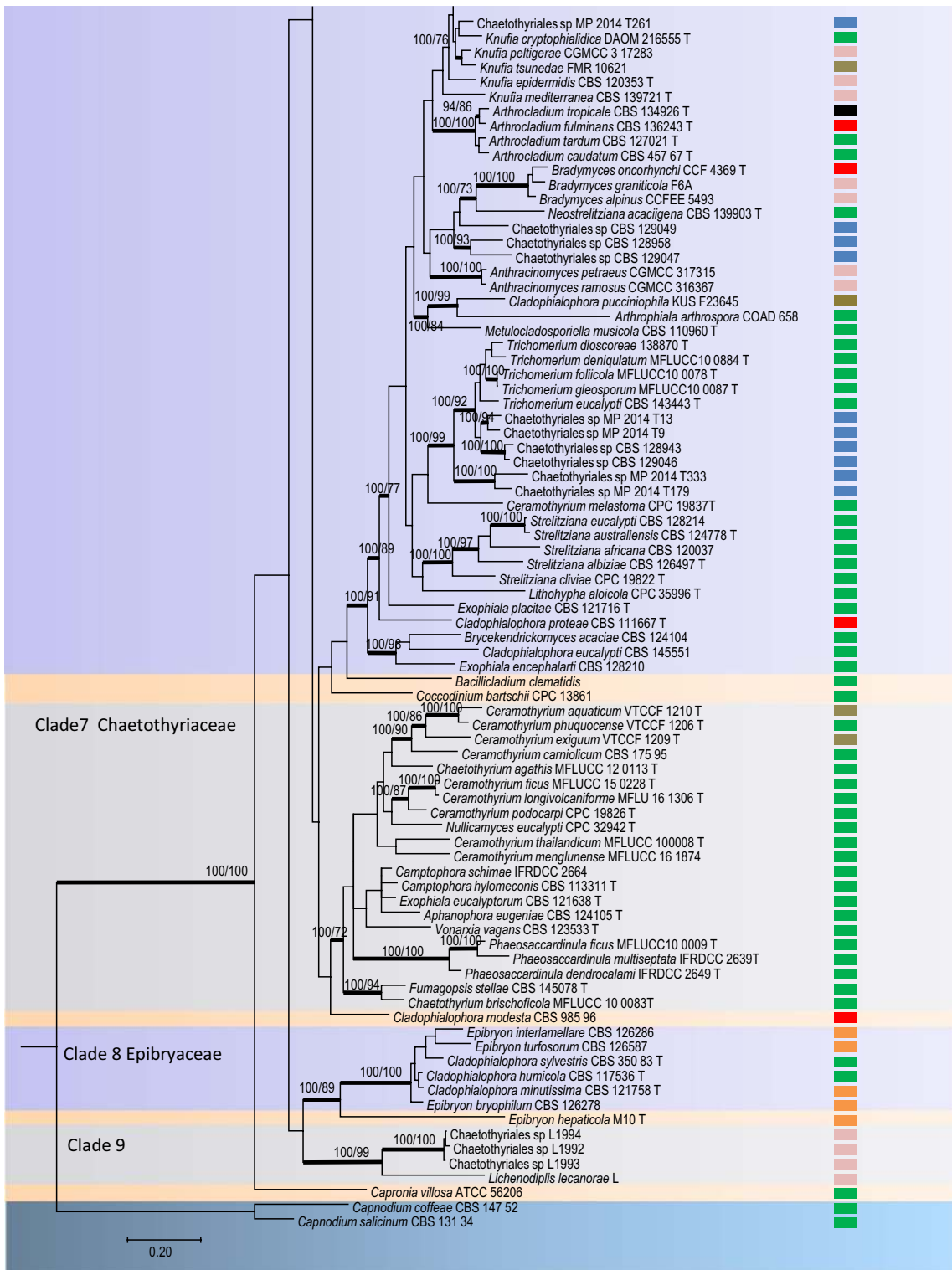
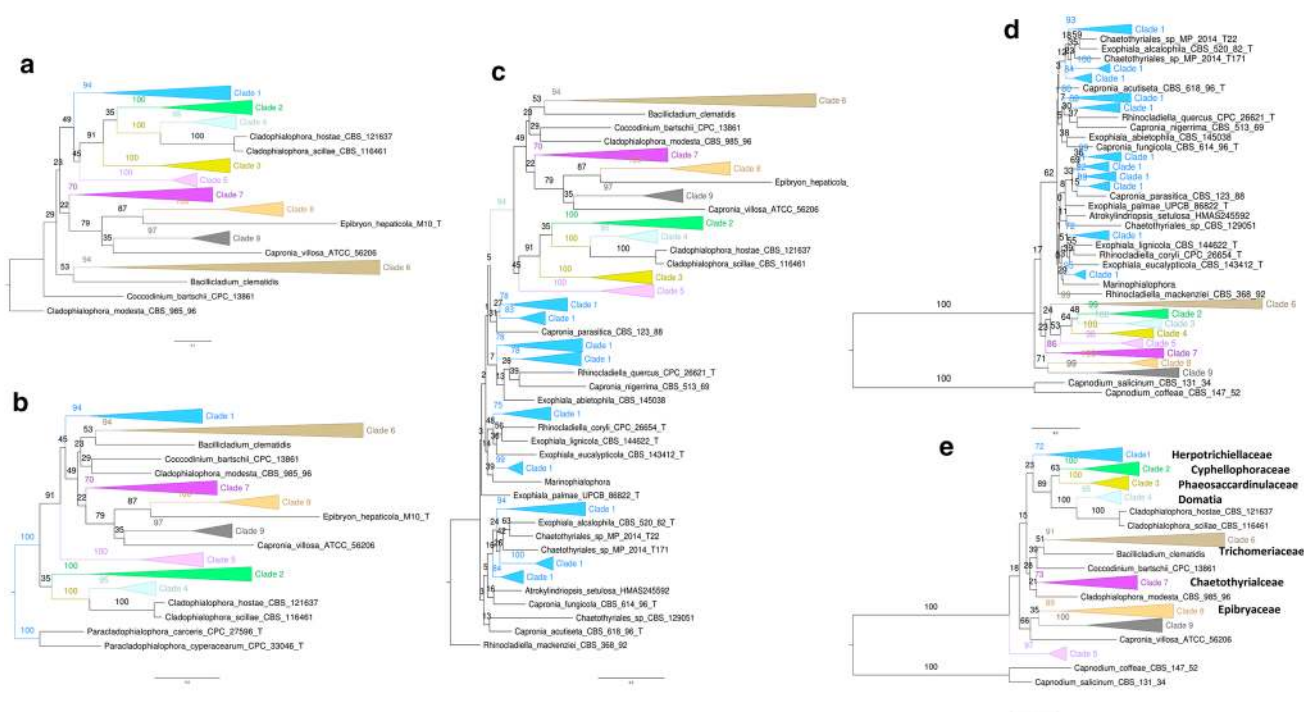


Fig. 3 (continued)



**Fig. 4** Outgroup test for long branches base on ML tree. **a** *Cladophialophora modesta* as outgroup; **b** *Paracladophialophora* sp. as outgroup; **c** *Rhinocladia mackenziei* as outgroup; **d** all species without *incertae sedis*; **e** all species including *incertae sedis*

Phaeosaccardinulaceae and Strelitzianaceae were found as part of the Chaetothyriaceae cluster; their family status is doubtful. Clade 1 (Herpotrichiellaceae) were also found to be diverse and resolved into two groups in some of the trees. The remaining families Cyphellophoraceae (Clad 2), Epibryaceae (Clade 8), and Trichomeriaceae (Clade 6) had consistent support. Three further clades had consistently high support values, i.e. a group of ant-domatia associated species (Clade 4) and two clusters of endolichenic species (Clade 5 and Clade 9).

Family **Trichomeriaceae** (Clade 6) comprised 50 strains, ten of which represented as yet undescribed species from an ant carton. Two species, *Metulocladosporiella musicola* and *M. musae*, were originally thought to belong to Herpotrichiellaceae (Crous et al. 2006), but in our tree clustered in Trichomeriaceae. The type strains of three species, *Cladophialophora pucciniophila*, *Cladophialophora proteae* and *Cladophialophora eucalypti* also clustered in this clade, although the type species of *Cladophialophora*, *C. ajelloi* (= *C. carrionii*) is a member of Herpotrichiellaceae. *Exophiala placitae* and *Exophiala encephalarti* should morphologically belong to Herpotrichiellaceae, but cluster in Trichomeriaceae.

Clade 4 comprised a total of 15 strains originating from **ant domatia** inside plant stems, known as domatia. Species typically produce sympodial conidia with flat conidial scars, and sometimes have additional catenate conidial states

(Wang unpublished data). The clade has sufficient support and ecological homogeneity to be recognized as a separate family. Two species, reported as causing leaf spots on different plant hosts (Crous et al. 2007), described after their plant hosts as *Cladophialophora scillae* and *C. hostae*, had exclusively catenate micromorphology. They cluster in one clade with a long branch, and upon taking them as outgroups, the general support values of tree improved (ratio rise from 1.30 to 1.75); consequently, *Cladophialophora scillae* and *C. hostae* are listed here as *incertae sedis*.

Clade 2 with 100% (ML/BI) bootstrap support contains 25 species belonging to family **Cyphellophoraceae**. Twenty strains described *Cyphellophora* species are clustered in this clade together with four *Phialophora* species (*P. livistona*, *P. attae*, *P. capiguarae*, and *P. intermedia*), together with a strain from the ant-made carton strain (CBS 128959). *Cyphellophora* and *Phialophora* traditionally differ by conidial shape, either lunate and septate, or subspherical, respectively, but the type species of *Phialophora*, *P. verrucosa*, is a member of the ‘carrionii-clade’ in Herpotrichiellaceae (de Hoog et al. 2011).

Clade 7 contains 21 species belonging to **Chaetothyriaceae**. The clade is well-supported in ML and BI trees (73/100). Inter-specific distances are relatively large due to incomplete taxon sampling. Members of this family have been reported since the 19th century after their ascomata on the natural substrate; culture and sequence data are available

**Table 3** Overview of genera described in Chaetothyriales, with number of species in brackets

Family	Genus	Type species	Type material	Suggested identity	
<b>Chaetothyriaceae</b> Hansf. ex M.E. Barr 1979 (T)	<i>Chaetothyrium</i> Speg. 1888 (T) (67)	<i>Chaetothyrium guaraniticum</i> Speg. 1888, NT <i>C. agathis</i>	IF550893	<i>Chaetothyrium</i>	
	<i>Actinocymbe</i> v. Hoehn. 1911 (3)	<i>Actiniopsis separato-setosa</i> Henn. 1908	Type unknown	Doubtful	
	<i>Ainsworthia</i> Bat. & Cif. 1962 (1)	<i>Ainsworthia zanthoxyli</i> Bat. & Costa 1962	Illeg., non <i>Ainsworthia</i> 1844	Invalid	
	<i>Aithaloderma</i> Syd. & P. Syd. 1913 (12)	<i>Aithaloderma clavatisporum</i> Syd. & P. Syd.	Syd. Fung. Exot No. 174	<i>Chaetothyrium</i>	
	<i>Almeidaea</i> Cif. & Bat. 1962 (1)	<i>Chaetothyrium vermisorum</i> Hansf. 1946	Illeg., non <i>Almeidaea</i> 1903	Invalid	
	<i>Aphanophora</i> Réblová & Unter. 2013 (1)	<i>Cyphellophora eugeniae</i> Crous & Alfenas 2009	CBS 124105	<i>Aphanophora</i>	
	<i>Arthrophia</i> Lisboa et al. 2016 (1)	<i>Arthrophia arthrospora</i> Lisboa et al. 2016	VIC 30505	<i>Arthrophia</i>	
	<i>Batistaella</i> Ciferri 1962 (2)	<i>Phaeosaccardinula coumae</i> Bat. & Vital 1955	Type lost	Doubtful	
	<i>Camptophora</i> Réblová & Unter. 2013 (2)	<i>Cyphellophora hylomeconis</i> Crous et al. 2007	CBS 113311	<i>Camptophora</i>	
	<i>Capnobatista</i> Cif. & Leal 1962 (1)	<i>Capnobatista serrulata</i> Cif. & Leal 1962	Reynolds 1982	<i>Trichomerium</i>	
	<i>Ceramothyrium</i> Bat. & Maia 1956 (39)	<i>Ceramothyrium paiveae</i> Bat. & Maia 1956, <b>REF</b> <i>C. thailandicum</i>	Type lost	<i>Ceramothyrium</i>	
	<i>Ceratocarpia</i> Rolland 1896 (3)	<i>Ceratocarpia cactorum</i> Rolland 1896	Type lost	Doubtful	
	<i>Chaetasterina</i> Bubak 1909 (1)	<i>Asterina anomala</i> Cooke & Harkness 1881	<i>Limacinula</i> (Coccodiniaceae)	Excluded	
	<i>Chaetopotius</i> Bat. 1951 (2)	<i>Chaetopotius commistum</i> Bat. 1951	Reynolds 1982	<i>Trichomerium</i>	
	<i>Chaetothyriomyces</i> Pereira-Carv. et al.	<i>Chaetothyriomyces brasiliensis</i> Pereira-Carv. et al.	UB12116	No sequence data	
	<i>Cyphellophoriella</i> Crous & A.J. Smith	<i>Cyphellophoriella pruni</i> Crous & A.J. Smith	CBS 140001	<i>Cyphellophoriella</i>	
	Euceramiaceae Bat. & Cif. 1962	<i>Eucерamia</i> Bat. & Cif. 1962 (1)	<i>Eucерamia palmicola</i> Bat. & Cif. 1962	Invalid	Invalid
		<i>Fumagopsis</i> Speg. 1910 (3)	<i>Fumagopsis triglifoides</i> Speg. 1911	LPS	<i>Fumagopsis</i>
		<i>Gilmania</i> Bat. & Cif. 1962	<i>Setella buchenaviae</i> Bat. & Lima 1955	Incertae sedis	Excluded
		<i>Kazulia</i> Nag Raj 1977 (2)	<i>Ypsilonia vagans</i> Speg. 1908	LPS	<i>Vonarxia</i>
<i>Microcallis</i> Syd. 1926 (9)		<i>Microcallis phoebes</i> Syd. 1926	Syd. Fung. Exot No. 161, 170h	Excluded	
<i>Neostrelitziana</i> Crous & Wingf. 2015		<i>Neostrelitziana acaciigena</i> Crous & Wingf. 2015	CBS 139903	<i>Neostrelitziana</i>	
<i>Nullicamyces</i> Crous 2018 (1)		<i>Nullicamyces eucalypti</i> Crous 2018	CBS 144426	<i>Ceramothyrium</i>	
<i>Phaeopeltis</i> Clem. 1909 (2)		<i>Phaeosaccardinula diospyricola</i> Henn. 1905	Name change	Superfluous	
Phaeosaccardinulaceae Bat. & Cif. 1962		<i>Phaeosaccardinula</i> Henn. 1905 (41)	<i>Phaeosaccardinula diospyricola</i> Henn. 1905, <b>REF</b> <i>P. ficus</i>	IFRD 9041	<i>Phaeosaccardinula</i>
	<i>Sphaerochaetia</i> Bat. & Cif. 1962 (1)	<i>Meliola loganiensis</i> Sacc. & Berl. 1885	Nom. inval., Art. 41.1	Doubtful	

**Table 3** (continued)

Family	Genus	Type species	Type material	Suggested identity
	<i>Stanhughesia</i> Constant. (4)	<i>Halbaniella linnaeae</i> Dearn. 1929	Anamorph	<i>Ceramothyrium</i>
Strelitzianaceae Crous & Wingf. 2015	<i>Strelitziana</i> Arzanlou & Crous 2006 (8)	<i>Strelitziana africana</i> Arzanlou & Crous 2006	CBS 120037	<i>Strelitziana</i>
	<i>Treubiomyces</i> v. Hoehn. 1909 (7)	<i>Treubiomyces pulcherrimus</i> v. Hoehn. 1907	Type lost	Doubtful
	<i>Trotterula</i> Speg. 1921 (1)	<i>Trotterula chilensis</i> Speg. 1921	Speg. 1918 Fig.	<i>Chaetothyrium</i>
	<i>Uloseia</i> Bat. 1963 (1)	<i>Halbaniella linnaeae</i> Dearn. 1929	Dearness	Superfluous
	<i>Vonarxia</i> Bat. 1960 (2)	<i>Vonarxia anacardii</i> Bat. & Bezerra 1960	ET CBS 123533	<i>Vonarxia</i>
	<i>Wiltshirea</i> Bat. & Peres 1962 (1)	<i>Wiltshirea quercifolia</i> Bat. et al. 1962	PH205	<i>Phaeosaccardinula</i>
	<i>Yatesula</i> Syd. <i>Zukalia</i> Sacc. 1891 (33)	<i>Yatesula calami</i> Syd. <i>Meliola loganiensis</i> Sacc. & Berl. 1885	PNH 25031 Type lost	Doubtful Doubtful
<b>Cyphellophoraceae</b> Reblova & Unter. 2013	<i>Cyphellophora</i> de Vries 1962 (25)	<i>Cyphellophora laciniata</i> de Vries 1962	CBS 190.61	<i>Cyphellophora</i>
	<i>Anthopsis</i> Fil. March. et al. 1977 (3)	<i>Anthopsis deltoidea</i> Fil. March et al. 1977	CBS 263.77	<i>Anthopsis</i>
	<i>Kumbhamaya</i> M. Jacob & Bhat 2000 (1)	<i>Kumbhamaya indica</i> Jacob & Bhat 2000	Jacob GUFCC-02 (PC)	<i>Cyphellophora</i>
<b>Paracladophialophoraceae</b> Crous 2018	<i>Paracladophialophora</i> Crous & Roets 2016 (2)	<i>Paracladophialophora carceris</i> Crous & Roets 2016	CBS 142068	<i>Paracladophialophora</i>
<b>Epibryaceae</b> Stenroos & Guiedan 2014	<i>Epibryon</i> Döbbeler 1978 (T) (47)	<i>Coleroa casaresii</i> var. <i>plagi-ochilae</i> Fragoso 1919	Type unclear	<i>Epibryon</i>
<b>Herpotrichiellaceae</b> Munk 1953	<i>Herpotrichiella</i> Petr. 1914 (T)	<i>Herpotrichiella moravica</i> Petr. 1914	Type lost	<i>Capronia</i>
	<i>Aculeata</i> Dong et al. 2018	<i>Aculeata aquatica</i> Dong et al. 2018	MFLU 11-1094	<i>Aculeata</i>
	<i>Ardhachandra</i> Subram. & Sudha (5)	<i>Pseudobeltrania selenoides</i> de Hoog 1977	IMI 107006-Ile	No sequence data
	<i>Atrokyndriopsis</i> Ma & Zhang 2015	<i>Atrokyndriopsis setulosa</i> Ma & Zhang 2015	HSAUP H4560	<i>Atrokyndriopsis</i>
	<i>Berlesiella</i> Sacc. 1888 (11)	<i>Sphaeria nigerrima</i> Bloxam 1859	CBS 513.69	<i>Capronia</i>
	<i>Botrytoides</i> Moore & Almeida (1)	<i>Botrytoides monopora</i> Moore & Almeida 1937	CBS 269.37	<i>Phialophora</i>
	<i>Capronia</i> Sacc. 1883 (81)	<i>Sphaeria sexdecimspora</i> Cooke 1871, <b>REF</b> <i>Capronia pilosella</i>	AFTOL 657	<i>Capronia</i>
	<i>Caproniella</i> Berl. 1896 (1)	<i>Melanomma pleisporum</i> Mouton 1886	Nomen confusum	Doubtful
	<i>Caproniella</i> Berl. 1899 (1)	<i>Sphaeria sexdecimspora</i> Cooke 1871	Illeg., non <i>Caproniella</i> Berl. 1896	Invalid
	<i>Carrionia</i> Bric.-Irag. 1939	<i>Hormodendrum pedrosoi</i> Brumpt 1922	Name change	Superfluous
	<i>Cladophialophora</i> Borelli 1980 (41)	<i>Cladophialophora ajelloi</i> Borelli 1980	CBS 160.54	<i>Cladophialophora</i>
	<i>Dictyotrichiella</i> Munk (6)	<i>Dictyotrichiella pulcherrima</i> Munk 1953	CBS 609.96	<i>Capronia</i>
	<i>Didymotrichiella</i> Munk (1)	<i>Didymotrichiella inconspicua</i> Munk 1953	Unknown	<i>Capronia</i>

**Table 3** (continued)

Family	Genus	Type species	Type material	Suggested identity
	<i>Exophiala</i> Carmichael 1967 (59)	<i>Exophiala salmonis</i> Carmichael 1967	CBS 157.67	<i>Exophiala</i>
	<i>Fonsecaea</i> Negroni 1936 (16)	<i>Hormodendrum pedrosoi</i> Brumpt 1922	CBS 271.37	<i>Fonsecaea</i>
	<i>Foxia</i> Castell. 1908 (1)	<i>Microsporum mansonii</i> Castell. 1905	Nomen nudum	Doubtful
	<i>Hormodendroides</i> Moore & Almeida (1)	<i>Hormodendrum pedrosoi</i> Brumpt 1922	CBS 271.37	<i>Phialophora</i>
	<i>Marinophialophora</i> Li et al. 2018 (1)	<i>Marinophialophora gareth-jonesii</i> Li et al. 2018	MFLUCC 16-1449	<i>Marinophialophora</i>
	<i>Melanchlenus</i> Calandron 1953 (2)	<i>Melanchlenum eumetabolus</i> Calandron 1953	CBS 264.49	<i>Rhinocladiella</i>
	<i>Melanostigma</i> Kirschst. 1939 (1)	<i>Sphaeria porothenia</i> Berk. & Curtis 1876	Type lost	Doubtful
	<i>Melanoctona</i> Tian 2016 (1)	<i>Melanoctona tectonae</i> Tian	MFLUCC 12-0389	<i>Melanoctona</i>
	<i>Metulocladosporiella</i> Crous et al. 2006 (6)	<i>Cladosporium musae</i> Mason 1945	CBS 161.74	<i>Metulocladosporiella</i>
	<i>Minimelanolocus</i> Castañeda & Heredia 2001 (34)	<i>Pseudospiropes navicularis</i> Castañeda 1987	Unknown	<i>Minimelanolocus</i>
	<i>Nadsoniella</i> Issatch. 1914 (4)	<i>Nadsoniella nigra</i> Issatch. 1914	CBS 535.94	<i>Exophiala</i>
	<i>Phaeoannellomyces</i> McGinnis & Schell 1985 (1)	<i>Phaeoannellomyces elegans</i> McGinnis & Schell 1985	CBS 122.95	<i>Exophiala</i>
	<i>Phialoconidiophora</i> Moore & Almeida 1937	<i>Phialoconidiophora guggenheimia</i> Moore & Almeida 1937	CBS 272.37	<i>Fonsecaea</i>
	<i>Phialophora</i> Medlar 1915 (63)	<i>Phialophora verrucosa</i> Medlar 1915	NT CBS 140325	<i>Phialophora</i>
	<i>Pleomelogramma</i> Speg. (1909)	<i>Pleomelogramma argentinensis</i> Speg. 1909	Type lost	Doubtful
	<i>Polytrichiella</i> Barr (3)	<i>Herpotrichiella polyspora</i> Barr 1959	Type lost	<i>Capronia</i>
	<i>Rhinocladiella</i> Nannf. 1934 (21)	<i>Rhinocladiella atrovirens</i> Nannf. 1934	CBS 264.49	<i>Rhinocladiella</i>
	<i>Sympodina</i> Subram. & Lodha 1964 (1)	<i>Sympodina coprophila</i> Subram. & Lodha 1964	CBS 350.65	<i>Veronaea</i>
	<i>Thysanorea</i> Arzanlou et al. 2007 (14)	<i>Periconiella papuana</i> Aptroot	CBS 212.96	<i>Thysanorea</i>
	<i>Veronaea</i> Cif. & Mont. 1957 (1)	<i>Veronaea botryosa</i> Cif. & Mont. 1957	CBS 254.57	<i>Veronaea</i>
	<i>Wangiella</i> McGinnis 1977 (3)	<i>Wangiella dermatitidis</i> McGinnis 1977	CBS 207.35	<i>Exophiala</i>
<b>Trichomeriaceae</b> Chomnunti et al. 2012	<i>Trichomerium</i> Speg. 1918 (36)	<i>Limacinia coffeicola</i> Puttemans 1904, NT <i>T. foliicola</i>	MFLUCC10-00780	<i>Trichomerium</i>
	<i>Arthrocladium</i> Papendorf 1969 (4)	<i>Arthrocladium caudatum</i> Papendorf 1969	CBS 457.67	<i>Arthrocladium</i>
	<i>Bacillicladium</i> Hubka et al. 2016 (2)	<i>Bacillicladium lobatum</i> Hubka et al. 2016	CBS 141.179	<i>Bacillicladium</i>
	<i>Bradomyces</i> Hubka et al. 2014 (3)	<i>Bradomyces oncorhynchi</i> Hubka et al. 2014	CBS 133066	<i>Bradomyces</i>
	<i>Brycekendrickomyces</i> Crous & Wingf. 2009 (1)	<i>Brycekendrickomyces aca-ciae</i> Crous & Wingf.	CBS 124104	<i>Brycekendrickomyces</i>
	<i>Brycekendrickomyces</i> Crous & Wingf. 2009 (1)	<i>Brycekendrickomyces aca-ciae</i> Crous & Wingf.	CBS 124104	<i>Brycekendrickomyces</i>

**Table 3** (continued)

Family	Genus	Type species	Type material	Suggested identity
	<i>Knufia</i> Hutchinson & Unter. 1996 (14)	<i>Knufia cryptophialidica</i> Hutchinson & Unter. 1996	DAOM 216555	<i>Knufia</i>
	<i>Lithohypha</i> Selbmann & Isola 2017 (1)	<i>Lithohypha guttulata</i> Selbmann & Isola 2015	CCFEE 5907	<i>Lithohypha</i>
	<i>Lithophila</i> Selbmann & Isola 2015 (1)	<i>Lithophila guttulata</i> Selbmann & Isola 2015	Illeg., non <i>Lithophila</i> 1788	<i>Lithohypha</i>
	<i>Neophaeococcomyces</i> Crous & Wingf. 2015 (2)	<i>Phaeococcomyces aloes</i> Crous & Wingf. 2013	CBS 136431	<i>Neophaeococcomyces</i>

Accepted families in bold

REF proposed reference, T type, ET epitype, NT neotype

of only a fraction of these. Appropriate description of the family Chaetothyriaceae is therefore as yet impossible.

Clade 8 contains members of **Epibryaceae**, with 100% ML and 100% BI bootstrap support. The phylogeny of this family also suffers from a severe taxon sampling effect, as of the 47 species listed in Index Fungorum, only seven are available in GenBank. Of these, *Epibryon hepaticola* clusters at some distance from remaining taxa, but given the poor representation of extant biodiversity this is probably insignificant. When *E. hepaticola* was treated as outgroup, the ratio rose from 1.30 to 1.75; consequently, the species is listed as *incertae sedis*. This clade also contained three species belonging to *Cladophialophora*, classified as such on the basis of catenate conidia. The original strain of *Cladophialophora minutissima* was isolated from bryophytes, while other *Epibryon* species had been described on the basis of their ascospores produced inside moss thalli; obviously this *Cladophialophora* is a cultural state of an *Epibryon* species. *Cladophialophora humicola* and *C. sylvestris* were derived from soil and decaying pine needles, respectively. The cladophialophora-type of conidiation is common throughout the entire order Chaetothyriales.

**Herpotrichiellaceae** (Clade 1) is best represented by sequence data, because a large part of the known species was described from isolates in culture, thus only representing the asexual state. Traditionally, species were described after their ascospores on the natural substrate, classified in the genus *Capronia*. Index Fungorum lists 89 described species, of which 85 belong to Herpotrichiellaceae and one to Trichomeriaceae. For a total of 119 strains in Herpotrichiellaceae, sequence data were available, including 11 carton fungi. It is unknown whether these are asexual isolates of known sexual species; the connection between sexual and asexual morphs has been made only occasionally (Müller et al. 1987; Untereiner 1997). The core structure of Herpotrichiellaceae was poorly resolved. The group fell apart into several, poorly supported subclusters. On the basis of LSU-data, de Hoog et al. (2011) distinguished a number of approximate clades within the family, of which the

‘bantiana-clade’ and the ‘carrionii-clade’ could be recognized. In a third, large remainder of species, numerous novel taxa had been added since 2011; no clades or clusters could be distinguished.

## Nomenclature

The order Chaetothyriales was validated by Barr (1987a, b) for epiphytic sooty molds mostly producing setose, clypeolate ascospores containing dark, multi-celled ascospores, with Chaetothyriaceae (Barr 1979) as type family. The invalidly described families Phaeosaccardinulaceae and Euceramiceae (Batista and Ciferri 1962) were regarded as synonyms (Barr 1987a, b).

**Chaetothyriaceae** had provisionally been introduced by Hansford (1946) with *Chaetothyrium*, based on *C. guaraniticum* Speg., as the type species. The original dried material of the type species, described in 1888, insufficiently allows interpretation. The Index Fungorum lists 76 published names in *Chaetothyrium*, of which 67 are accepted as members of Chaetothyriaceae. However, GenBank contains only two sequenced species, viz. *Chaetothyrium agathis* (Liu et al. 2015) and *C. bischoficola* (Chomnunti et al. 2012b), both isolated on a single occasion from leaves of tropical plants. It remains uncertain whether this is in accordance with the intention of Spegazzini (1888), but numerous authors maintained the ecological concept of ‘sooty moulds’, i.e. epiphytic colonizers of living plants: at least 64 of the 67 species mentioned above were described from plant leaves, generally without symptoms. In order to stabilize the nomenclatural reference of Chaetothyriales, we herewith propose *Chaetothyrium agathis* Hongsanan & K.D. Hyde (Liu et al. 2015) as a **neotype** of *Chaetothyrium*. *Chaetothyrium agathis* takes a central position in the clade of Chaetothyriaceae (Fig. 3) and is the reference point of the order Chaetothyriales. Wijayawardene et al. (2020) listed the genus *Aithaloderma* in the Chaetothyriaceae. Hansford (1946) reexamined the type of *A. clavatisporum* which

displayed a *Triposporium* asexual state, and reclassified it in *Chaetothyrium*.

Chaetothyriaceae further comprises the genus *Ceramothyrium*. This genus is listed with 41 names in Index Fungorum, of which 39 are surmised to belong to Chaetothyriaceae. The type species is *Ceramothyrium paivieae* (Batista 1956), originally reported from leaves of *Paivea langsdortii* (= *Copaifera langsdorfii*; Leguminosae) in Brazil. No molecular data are available for this species. Judging from older literature, this genus is also reserved for species colonizing plant leaves, with 37 of 39 species demonstrating this ecology, including the nine species of which LSU sequences are available in GenBank. Of these, *Ceramothyrium thailandicum* colonizes living leaves of *Lagerstroemia* (Lythraceae) in Thailand. Awaiting selection of neotype material which is closer to the original type location of Batista (Batista 1956), we regard *Ceramothyrium thailandicum* as the reference species for *Ceramothyrium* in the present paper.

*Phaeosaccardinula*, introduced by Hennings (1905) with type species *P. diospyricola* on leaves of *Diospyros* (Ebenaceae) in Amazonian Brazil, contains 47 species in Index Fungorum, of which 41 were regarded as members of Chaetothyriaceae. The genus currently has six synonymous generic names (Table 3), all containing a very small number of species that were mostly discarded for nomenclatural reasons. In accordance with the type species *P. diospyricola*, nearly all authors in older literature classified plant-colonizing species in the genus. Of three species, LSU sequences are available in GenBank, i.e. *P. dendrocalami* and *P. multiseptata* (Yang et al. 2014), and *P. ficus* (Chomnunti et al. 2012b), all from living plant leaves, in (sub)tropical China and Thailand, respectively. In absence of sequence data of the remaining 39 species of *Phaeosaccardinula*, we regard these species as representative for the genus, with *P. ficus* as **reference**.

Two species are known in *Vonarxia* of which *V. anacardii* is the type species (Batista 1960). The species is in poor condition (van der Aa and von Arx 1986) and is currently judged to be of uncertain affinity (Index Fungorum), while *V. vagans* has been sequenced and described by several authors (Réblová et al. 2013; Crous et al. 2009). That taxon, based on *Ypsilonia vagans* Speg. on leaves of *Spiraea cantonensis* (Rosaceae) in Brazil, has setose sporodochia with splayed stauroconidia. Crous et al. (2009) epitypified the species with CBS 123533 as the type culture. Given the unclear status of the type species *V. anacardii*, we might regard *V. vagans* as a reference species for the genus *Vonarxia*, but it should be noted that it is also the type species of *Kazulia* (Raj 1977). The morphologically similar genus *Fumagopsis* was described by Spegazzini (1910) with *F. triglifoides*, on living leaves of *Lucuma neriifolia* (Sapotaceae) in Argentina, as the type species. Using the dried herbarium specimen of the holotype, van der Aa and van

Oorschot (1985) redescribed this specimen. It is characterized by setose sporodochia bearing stauroconidia, similar to those of *Vonarxia vagans* but differing by the conidia being pronouncedly multicellular. *Fumagopsis triglifoides* has as yet not been sequenced. Three species records of *Fumagopsis* are listed in Index Fungorum, but only one, *F. stellae*, CBS 145078 from leaves of *Eucalyptus* (Myrtaceae) in Australia, has been deposited in NCBI. This species had similar morphology, with setose sporodochia and multicellular stauroconidia on the natural substrate, and sequences placed it in Chaetothyriales (Crous et al. 2018). Numerous other sporodochial, morphologically reminiscent genera have been described, such as *Zelopelta* (Sutton and Gaur 1984), *Phalangispora* (Nawawi and Webster 1982), which are in need of modern sequence data.

Four small genera were recently described for which sequence data are available, i.e. *Aphanophora*, *Arthrophia*, and *Camptophora*. All type species of these genera (Table 3) cluster in the supported clade of Chaetothyriaceae (Fig. 3), all at relatively long branches, underlining their position as separate genera. *Nullicamyces* clusters amidst species of *Ceramothyrium* in a cluster that is however not supported (Fig. 3). *Stanhughesia* was described as *Ceramothyrium* asexual states (Constantinescu et al. 1989). Species of *Microcallis* have been reclassified in *Chaetothyria* which is a genus of Micropeltidaceae.

**Cyphellophoraceae** was introduced by Réblová and Untereiner (Réblová et al. 2013) with *Cyphellophora* (de Vries 1962) as the type genus and *C. laciniata* as the type species. CBS 190.61 is available as the type strain, and the taxon has several genes in GenBank. Currently, 28 species have been described in the genus, two of which were transferred as independent genera of Chaetothyriaceae (*C. eugeniae* as type of *Anaphora*, and *C. hymeloconis* as type of *Camptophora*) and one, *C. suttonii*, has been excluded. Another genus of this family is *Anthopsis*, based on *A. deltoidea* as type species with CBS 263.77 as type strain (Moussa et al. 2017a, b).

**Trichomeriaceae** was introduced by Chomnunti et al. (2012b) with *Trichomerium* as type genus. This genus is based on the sooty mold *Limacinia coffeicola* Puttemans [non *Phaeosaccardinula coffeicola* (Maharachchikumbura et al. 2018)] as the type species (Puttemans 1904). Reynolds (1983) judged this species as being close to or identical to *T. grandisporum*, which he considered as the only recognized species in *Trichomerium* with a large number of synonymous names. No living ex-type material was available to recent authors (Chomnunti et al. 2012a), who consequently took *T. foliicola*, with sequence data, as reference for genus and family. From their extensive illustrations of the sexual state of this fungus, it appears that the ascigerous fruit bodies of *Trichomerium* are morphologically very similar to those of *Capronia*, the rather monomorphic sexual state observed

in numerous species of Herpotrichiellaceae. Conidia were not observed, but several members of Trichomeriaceae [e.g. *Trichomerium gloeosporum* (Hongsanan et al. 2016a) and *T. changmaiensis* (Maharachchikumbura et al. 2018)] produce elaborate stauroconidia.

The family **Epibryaceae** was introduced by (Gueidan et al. (2014) with *Epibryon* (Döbbeler 1978, 1980) as type genus which has *Epibryon plagiochilae* as the type species. This species was described with molecular data by Stenroos et al. (2010a, b) in a detailed overview of the genus, and is accepted here as reference for this group of phylogenetically consistent moss endophytes.

The best-known family in the order Chaetothyriales is **Herpotrichiellaceae**, introduced by Munk (1953) with *Herpotrichiella* (Petraik 1914) as the type genus. *Herpotrichiella moravica* was selected as the type species, which is considered to be a synonym of *Capronia pilosella* (Untereiner 1997). Consequently, the currently accepted name for *Herpotrichiella* is that of its older synonym *Capronia*, introduced by Saccardo (1883) with *Capronia sexdecimspora* (Cooke) Sacc. as type species, characterized by setosa ascumata with asci containing 16 hyaline, 3–4-septate ascospores. As no interpretable type material of this species is available, the identity of this species remains uncertain. As yet, none of the species with 16-spored asci has been sequenced, and thus replacement of *C. sexdecimspora* by an extant neotype is difficult and the exact position of the reference for *Capronia* in the Herpotrichiellaceae remains uncertain. We propose to stabilize the nomenclature of Herpotrichiellaceae by selecting *Capronia pilosella* AFTOL 657 as **reference** for the family.

A large number of *Capronia* species has been subsequently described (e.g. Barr 1987a, b; Friebe 2012), of which Index Fungorum considers 81 to be of chaetothyrialean affinity. The family Herpotrichiellaceae comprises 30 generic names (Table 3), which are principally available for a future taxonomic rearrangement with phylogenetic affinity as leading principle and which therefore are in need of redefinition with reference material. The oldest name of these is *Berlesiella*, based on *Sphaeria nigerrima* Bloxam 1859, which in spite of absence of usable type material is now considered to be *Capronia nigerrima* (Barr 1991). Sequenced material of this species is available from Untereiner and Naveau (1999) who used strain CBS 513.69 described by Müller et al. (1987). *Caproniella* was introduced (Berlese 1896) with *Melanomma pleiosporum* as a single species, now known as *Capronia pleiosporum* (MycoBank), but no recent material is known to be available. Berlese (1899) used *Caproniella* with *Sphaeria sexdecimspora* as the type. This generic name is superfluous as *S. sexdecimspora* was the type of *Capronia*, and *Caproniella* Berlese 1899 is a later homonym of *Caproniella* Berlese 1896. For these reasons we consider *Caproniella* as a *nomen confusum*. Moussa et al.

(2017a, b) noted that *Foxia* and *Melanchlenus* were invalid due to absence of descriptions in the protologues. Most of the remaining genera are represented by extant type strains with molecular data (Table 3).

## Ecology and evolution

Members of Chaetothyriales have a rich ecological diversity, with a general tendency to extremotolerance (Gostincar et al. 2019) and toxin management (Teixeira et al. 2017). The difficulty to isolate the fungi from the environment (Sudhaham et al. 2008, Vicente et al. 2008) interferes with understanding of the preferred ecological niche. Available data may provide distorted information since unspecific habitats may have been sampled thus far. For example, *Cyphellophora europaea* is commonly encountered colonizing human nails. It has been found in bathrooms where this fungus is likely to have been acquired by the patients. A natural habitat has not been found, but colonization of moist surfaces suggests oligotrophy. For only a small number of species of Cyphellophoraceae, environmental data are available. Numerous species have been described from a single strain on a single host plant, without indication of a specific plant-pathogenic lifestyle. We have assumed oligotrophy for these species as well, listing them as colonizers of the phyllosphere with an epiphytic lifestyle.

Ecologies of 254 strains and their relatives in Chaetothyriales were investigated (Table 1). Many species of Chaetothyriales have been described from single collections and hence epidemiological investigations are problematic. Habitat data were abstracted from the sampling sites of strains described in the original publications, supplemented with a summary of ecological trends per species abstracted from the literature. Seven categories were summarized as follows, ‘epilithic/lichenolytic’ (on bare or parasitizing on lichens), ‘epiphytic’ (colonizing plant leaves without symptoms), ‘opportunistic’ (deep, single- or multi-organ infection in humans, also infection in cold-blooded vertebrates), ‘carton’ (carton of chewed wood in ant nests), ‘domatium’ (ant nest inside living plant stem), ‘bryophytic’ (endophytic in mosses), and ‘other’ (aquatic, fungicolous, in soil). Members of the family Herpotrichiellaceae showed highly diverse ecological sources. In a total of 119 strains, five ecologies were distinguished. In the main categories, 38 strains derived from opportunistic infections, 30 from other, 36 were epiphytic, 4 were epilithic/lichenolytic, while 11 as yet undescribed strains had been isolated from carton material in ant nests.

Available information on members of Cyphellophoraceae was scant, not allowing definitive conclusions. Several species were isolated from living plants, but it remained unclear whether this was an infectious process, or epiphytic growth without notable invasion. Data are abstracted from a



summary given by Feng et al. (2014). *Cyphellophora europaea* is the only common species of the family. It is a commensal or mild infectious agent on human skin and nails, and was repeatedly isolated in bathrooms where the fungus was suggested to be picked up (Lian and de Hoog 2010); for this reason, we prefer ‘opportunistic’ as its ecology. In total, four ecology types are observed in this family. Given the frequent plant origin without clear description of disease, we listed the main ecology as ‘epiphytic’ (44%).

Members of Trichomeriaceae are surface colonizers: 42 % of the species were isolated from rock. *Knufia epidermidis* was originally described as repeatedly being involved in mild nail infections (Li et al. 2008), but Zakharova et al. (2013) found the same fungus occurring as a rock colonizer with an ecology similar to remaining *Knufia* species. 38 % of members of Trichomeriaceae reportedly were derived as ‘sooty molds’ from plants which often had somewhat leathery leaves. Since these were single sampling events and no reports about plant disease have been published, we listed all species as being epiphytic. The species of *Bradomyces* had single isolation events (rock and fish) for which no common denominator could be found.

Members of Chaetothyriaceae have nearly always been reported from living plants. Detection was generally by ascospores on the natural substrate, which eventually were immersed on a stroma fixed to the undamaged host tissue. We listed those members as ‘epiphytic’; only 10% of the species were described from other habitats.

Clade 4 contains a major subclade of 15 strains that were derived exclusively from domatia of tropical ants. The second subclade contained two species with cladophialophora-like morphology which caused leaf spots on their host plants; they are known from single sampling events. Two more undescribed clades (Clades 5 and 9) were noted which all were derived from rock environments (Muggia et al. 2020).

*Epibryon* species are fungi forming small ascospores inside moss tissue. Index Fungorum lists 48 species, most of which have been described after material on the host and could not be included in this study for lack of sequence information. Three cladophialophora-like species clustered in the Epibryaceae, of which *C. minutissima* was derived from mosses without observation of the ascigerous state. The ecologies of the five cultured *Epibryon* species are consistently bryophilous.

Of the distinguished ecological categories, epilithic and epiphytic are commonly encountered in several families (Herpotrichiellaceae, Trichomeriaceae, Cyphellophoraceae, Chaetothyriaceae, and Clades 5 and 9). Also carton-material of ant nests and tunnels is widely distributed (Herpotrichiellaceae, Trichomeriaceae and Cyphellophoraceae). Human infection is nearly exclusively found in Herpotrichiellaceae, occasionally in Trichomeriaceae, and restricted to mild,

superficial infections in Cyphellophoraceae. Infections in cold-blooded vertebrates are restricted to Herpotrichiellaceae. Dominant ecology in Clades 9 and 5 is ‘epilithic’; in Epibryaceae this is ‘bryophytic’, in Clade 4 ‘ant-domatium associated’, in Chaetothyriaceae ‘epiphytic’, and in Trichomeriaceae it is ‘epiphytic’. The overview contains 39 ant-associated strains, isolated either from carton material of nests and tunnels, or from domatia inside living plants. The latter type (15 entries) is restricted to Clade 4, while carton-associated species (24 entries) have a wide distribution in Herpotrichiellaceae, Trichomeriaceae and Cyphellophoraceae and are not found in Clade 4, confirming data of Voglmayr et al. (2011) and Nepel et al. (2014).

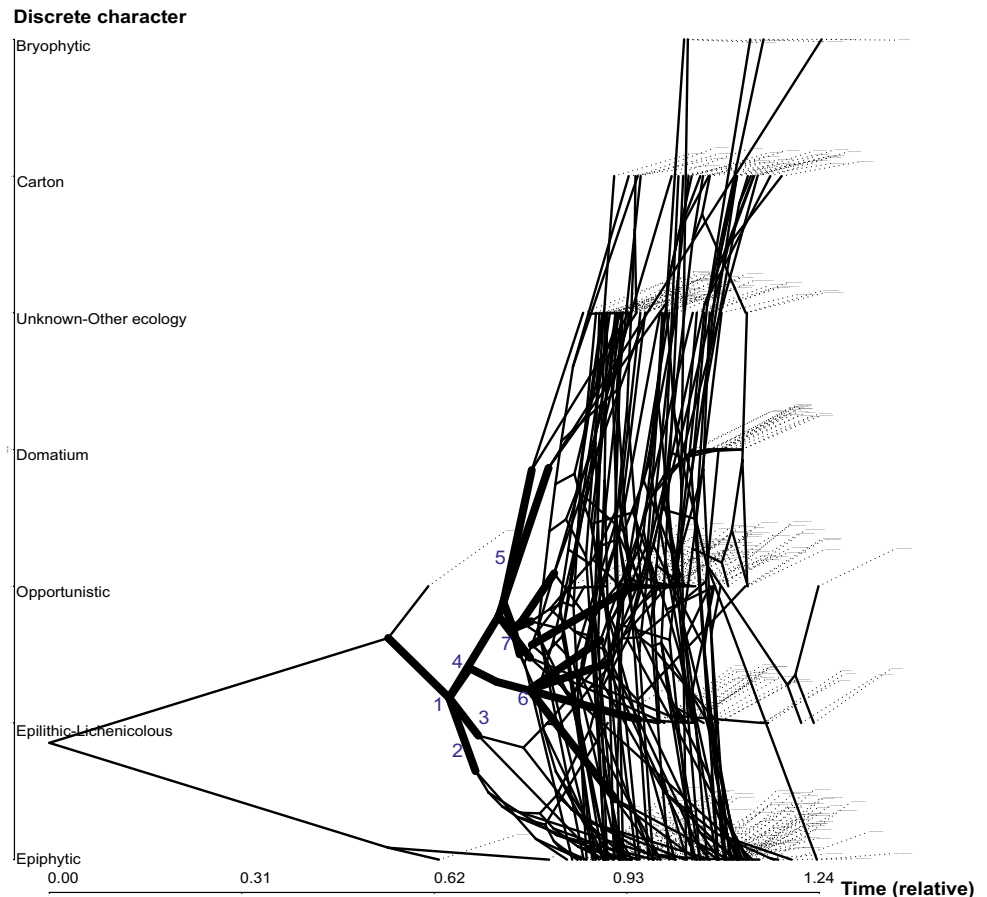
The evolutionary time estimation (Fig. 1) reveals that the Chaetothyriales crown order emerged in the late Devonian Period. Between the end of the Cretaceous, i.e. 151.69 Mya, the family was split, separating Clade 8, *Epibryon hepaticola* M10, Clade 9 and *Capronia villosa* from the remaining species. Fundamental speciation events occurred through the Cretaceous and Paleocene periods. The formation of the family Chaetothyriaceae (Clade 7) appears ancestral, starting about 122 Mya. The diversification of the family Herpotrichiellaceae was later, around 111 Mya (Fig. 1).

### Ancestral character state reconstruction

In a first step, ecological traits were plotted model-free onto the phylogeny via the function ‘phenogram’ over time, in order to determine approximate number of ancestral trait changes (Fig. 5). Seven major directions of trait evolution are obvious (1–7 in Fig. 5). Although the phenogram does not indicate the exact ancestral state to the Chaetothyriales, particularly the traits ‘epiphytic’ and ‘epilithic-lichenicolous’ (branching point 1) suggests ancestry as a ‘epilithic-lichenicolous-epiphytic’ type. This assumption is strongly supported by absence of early overlapping trait changes. Branching point 1 gave rise to at least 3 major traits (branching points 2–4), which subsequently led to a strong lineage diversification and occupation of vacant ecological space leading to extant traits. During this process, most traits underwent multiple trait shifts visualized by overlapping branches, which is apparent for the epiphytic (branching points 2, 3 and 6) and the opportunistic characters (branching points 6, 7). Particularly the opportunistic trait appears to have sourced its extant trait from a strong random walk of ancestral intermediate traits (strong branch/line overlap). Traits ‘carton’, ‘domatia’ and ‘bryophytic’ have a non-random distribution. ‘Carton’ has diversified from early ancestral branching point (5), with almost no overlap to other traits.

To assess trait transitions, we calculated conditional likelihood for each character state at each node of the phylogenetic tree, including the root and simulated ancestral states at

**Fig. 5** Quantitative trait simulation among the phylogeny inferred via the R package ‘PHYTOOLS’. The plot depicts phenotypic distribution over the phylogeny and its associated changes over time. While it is similar the Brownian motion phenogram, the quantitative trait simulation does not depict the stochastically mapped character on to the phylogeny, and with that the phenotypic changes estimated for each branch, neither the relative evolutionary rate ratio ( $\sigma$  parameter) for each phenotype. Instead, it visualizes trait changes, uniformity and discreteness of such changes over time in a more comprehensive way. Branching points indicate approximated major directions of phenotypic changes at the root node to the entire order Chaetothoriales. X-axis depicts relative time for the phenotype (ecology) to evolve given the underlying phylogeny. Y-axis depicts relative phenotypic categories



**Table 4** Brownian rate parameters  $\sigma$  estimated via the Brownian model, including the approximated standard error for each phenotype (ecology)

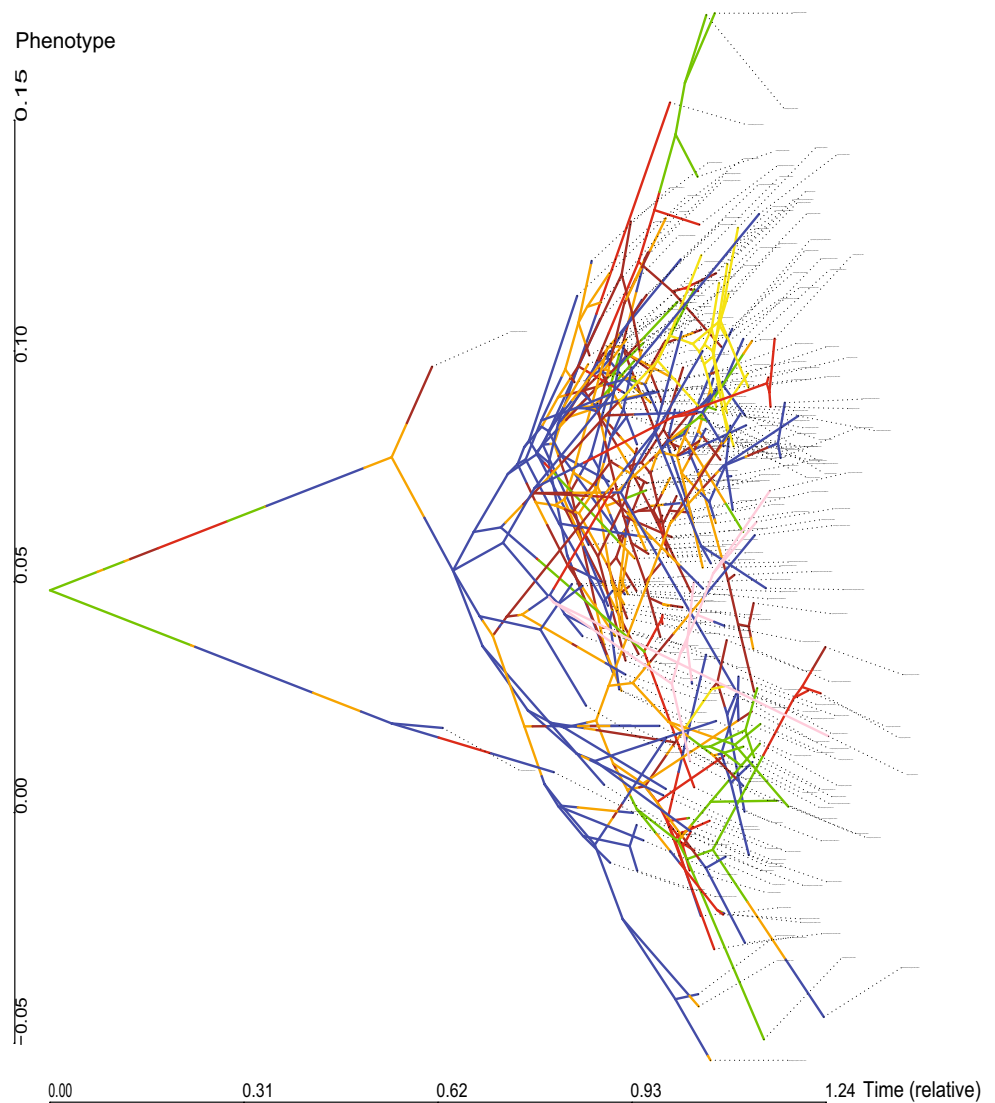
	Epiphytic	Epilithic	Opportunistic	Domatium	Other	Carton	Bryophytic
$\sigma^2$ (Brownian rate)	8.9783	0.0056	46.019	0.0056	227.9022	194.7455	518.9015
Standard error	2.5921	0	12.1818	0	40.3123	30.1685	262.1754

The higher the rate, the more likely a given phenotype is diversifying at present time. Lower rates indicate a slow down for ancestral, but an increase (with higher rates) for derived phenotypes

each internal node by sampling from the posterior distribution of states (stochastic character mapping). The waiting times between substitutions are drawn from an exponential distribution with the rate being the diagonal elements of the model’s instantaneous rate matrix ( $Q$ ), conditioned on the current state to infer a character transition matrix (Table 6). This matrix served as input for the Brownian motion model fitting to estimate evolutionary rate changes (Table 4), and are visualized by mapped character changes along each individual branch (Fig. 6). The plotted Brownian motion process (Fig. 6) indicated that three traits can be considered as ancestral: ‘epilithic’, ‘carton’, and, at a more derived position, ‘epiphytic’. Short sections of ‘opportunistic’ among initial branches indicate that these traits, although later subject of a

diversification burst, had precursor traits at a very early stage of evolution (as a result of the stochastically mapped characters). Conversely, the Brownian null model inferred the ancestral state as being quantitatively in between ‘epilithic’ and ‘epiphytic’, with tendency towards ‘epilithic’ (recoded discrete character ‘epiphytic’ = 1, ‘epilithic’ = 2, Brownian null model ancestral state = 1.71). The more ancestral characters ‘epilithic’ and ‘epiphytic’, as well the highly derived character ‘domatia’ have low evolutionary rates (Brownian rates  $\sigma^2$ ); remaining traits, which are randomly distributed over the taxa, experience a strong rate burst. Paucity of niche shifts on internal branches decreases covariances among tips relative to the neutral expectation and repress phylogenetic signals; conversely, an initially high rate of niche

**Fig. 6** Brownian motion phenogram inferred via the R package ‘PHYTOOLS’. Brownian rate parameter  $\sigma$  was set to 0.1 to simulate trait evolution under Brownian motion. X-axis depicts relative time for the phenotype (ecology) to evolve given the underlying phylogeny. Y-axis depicts relative phenotypic variation under the Brownian rate parameter. Color coding for the various ecologies derived from stochastic character mapping: epiphytic (blue), epilithic/lichenolytic (red), opportunistic (brown), domatium (yellow), other (orange), carton (green) and bryophytic (pink). If lines do not cross, vertically and/or horizontally the phenotype (= character = ecology) does not tend to be randomly distributed (the situation towards the base, ancestral state), while phenotypic changes towards the tips of the phenogram underlay in many cases (not all eg. ‘domatium’ or ‘bryophytic’) a strong random distribution. Topological distribution is equivalent to a late-burst model of phenotypic evolution



**Table 5** Statistical values obtained from calculations for the phylogenetic signal given the inferred phylogeny (Pagel’s  $\lambda$  and Blomberg’s K)

	Pagel’s $\lambda$	Blomberg’s K	Pybus’s $\gamma$
Stastical value	0.726	0.114	2.384
p-Value	NA	NA	0.017
LogLikelihood	– 499.2	NA	NA

Pybus’s  $\gamma$  statistic equates for speciation rates. The higher lambda and K the higher the phylogenetic signal. If gamma is negative, it equates for a slow down in speciation, if positive (in the case of our data) it equates for increased speciation

differentiation which decreases towards the present, tends to increase phylogenetic signal relative to the neutral expectation. Thus the most drastic niche shifts are concentrated near the root of the tree during early evolutionary history. The likelihood matrix for individual character transitions

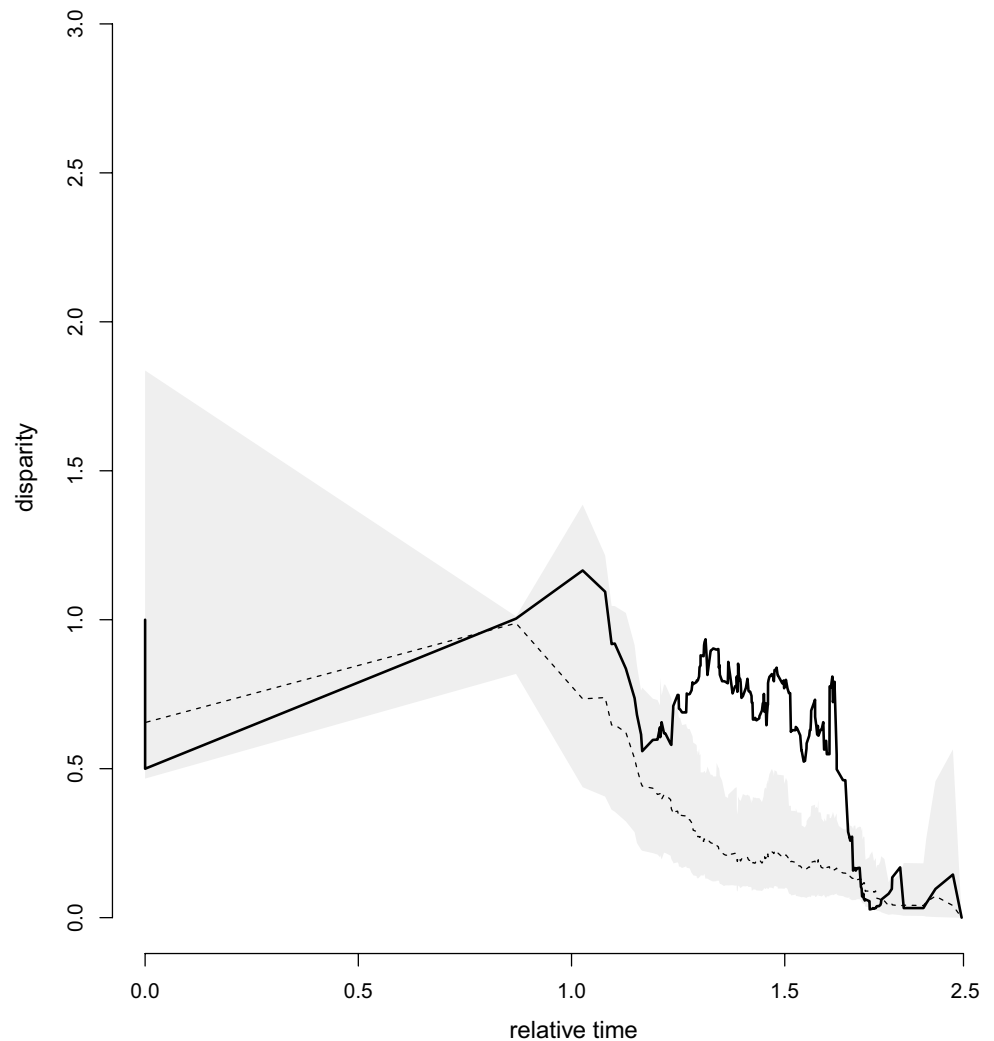
is given in Table 6, where higher values indicate a higher likelihood that the character was derived from another entity. The monophyletic character ‘domatia’ has a single character origin likelihood shared by ‘opportunistic’ (Table 6). The derived characters with high evolutionary rates (i.e. ‘domatia’ and ‘bryophytic’) expose a likelihood for a single character origin. Testing for the resolution of our dataset, assessment over the phylogenetic signal for the K and  $\lambda$  (lambda) statistic was performed. While the K statistic indicates a low phylogenetic signal for the global dataset, which is equivalent to a ‘tip-swap’ model, it is obvious from the Brownian motion process (Fig. 6), that character evolution towards the tips cannot be fully resolved given the current phylogeny comprising solely ribosomal gene data, which indicate (e.g. as for ‘opportunistic’ or ‘carton’) a strong random distribution (Brownian random walks) towards the tips. In contrast, Pagels’ lambda indicates a higher phylogenetic signal, which taken together as a result of the K statistic and the Brownian

**Table 6** Transition matrix; Character (trait=ecologies) transition matrix derived from stochastic character mapping

	Epiphytic	Epilithic	Opportunistic	Domatium	Other	Carton	Bryophytic
Epiphytic	− 8.4913879	0.6391623	1.5957816	0.0000000	13.235969	0.0000000	− 0.3100787
Epilithic	0.6391623	− 4.2168518	1.7859090	0.0000000	0.0000000	1.791780	0.0000000
Opportunistic	0.6391623	1.7859090	1.7859090	0.5035451	13.235969	0.0000000	0.0000000
Domatium	0.0000000	0.0000000	0.5035451	0.0000000	0.0000000	0.0000000	0.0000000
Other	5.9463653	0.0000000	13.2359694	0.0000000	− 23.377706	4.195371	0.0000000
Carton	0.0000000	1.7917805	0.0000000	0.0000000	4.195371	− 5.987151	0.0000000
Bryophytic	0.3100787	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	− 0.3100787

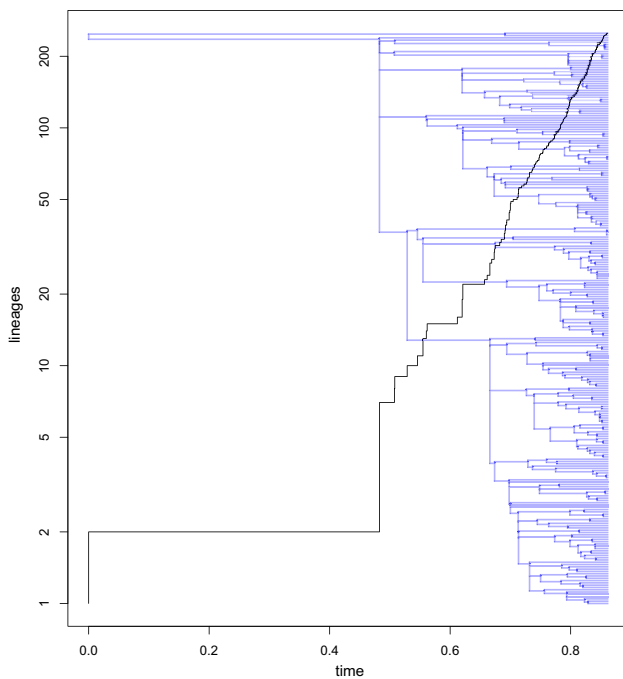
Higher values indicate higher likelihood that a character is derived from another entity (Read in rows to columns). For example, the character state ‘domatium’ has a single value indicating that a key transition to this constrained lifestyle with highly specialized ants, was derived from the ‘opportunistic’ character (and associated intermediate character changes of ‘opportunistic’)

**Fig. 7** Disparity through time (DTT) plot inferred via the R package ‘GEIGER’. The plot depicts morphological disparity between phenotypes over time. X-axis depicts relative time for the lineages to disparate given the underlying phylogeny and phenotypic data (ecologies). Y-axis depicts relative disparity between phenotypes (ecologies). Remarkably, and in concordance with the Brownian motion phenogram and the ‘LTT’ plot, morphological disparity peaked very early in Chaetothyrialian evolution prior to most lineages being born. This indicates that major phenotypic innovations occurred very early in Chaetothyrialian evolution, with a significant slow down in novelty and evolutionary rates (as of the Brownian model) to mostly the ancestral phenotypes and increase towards more derived phenotypes (e.g. ‘domatium’). Multiple small phenotypic disparate fluctuations (birth/extinctions) equates to the rise of the extant species



distribution, equates to a medium resolution quality of the dataset (phylogenetic signal, discrete character evolution), similar to Munkemüller et al. (2012) and Ackerly (2009), supporting validity over the assumptions on trait transitions above (Table 5).

Lineage diversification and disparity distribution over time was demonstrated with a lineage through time plot (LTT; Fig. 8). Given the late burst of lineage diversification in Chaetothyriales, major phenotypic innovations occurred very early in the evolution. Highest disparity coincides with



**Fig. 8** Lineage through time (LTT) plot inferred via the R package ‘PHYTOOLS’. The plot depicts lineage diversification (accumulation) over time. X-axis depicts relative time for the lineages to diversify given the underlying phylogeny. Y-axis depicts relative number of lineages identified from the phylogeny. In concordance with the Brownian motion phenogram, the ‘LTT’ plot equates for a late burst model of diversification since a step increase (accumulation) in lineages accelerates only late in time. While establishing niche conservatism and occupation of niches took almost as much time for the early Chaetothyalian taxa to evolve relative to the total number of lineages, lineage diversification and speciation events for all extant taxa in the present niches equates for less than one quarter of the total time. The underlying phylogeny, depicted as ultrametric tree where evolutionary rates are set equal is shown as background graph in blue

earliest diversification events, and with novelty for vacant niches (Fig. 7). After the late burst of diversification, beyond the greatest disparity peak, niche conservatism limits further character innovation; major trait innovation is subsequently declining. However, significantly positive Pybus’s  $\gamma$  statistics (+2.384) indicates that cladogenesis increases over time leading to pronounced and continuous species diversification in existing niches (Table 5).

## Discussion

### The study of biodiversity

The scientific history of the order Chaetothyaliales consists of two parts, i.e. a phenotypic era using the sexual state in its natural habitat, and a prevalently molecular phase mostly applying asexual states in culture. The order attained

recognition particularly through the contributions of M.E. Barr (1923–2008) on Loculoascomycetes. Studies in that time were performed by morphology of the sexual state on the natural substrate, such as lichenized rock or decorticated wood, of which dried voucher specimens were preserved in herbaria. Only very few species were studied in culture. Numerous older, previously described species became assigned to the order ([www.indexfungorum.org](http://www.indexfungorum.org)). Among these were members of the group that had already been recognized in the 19th century. As the early descriptions have nomenclatural priority, comparison of type material would be necessary to stabilize generic and specific names in the order. However, much of this material is now lost or is otherwise inaccessible, so that we are unsure about the identity of reference material defining families, genera and species. Even the identity of the species defining the order, *Chaetothrium guaraniticum* Spegazzini, described in 1888, is uncertain, and hence an epitype will be designated below.

A similar line of research, after studies of Barr and others, has been on so-called ‘sooty moulds’, i.e. black fungi colonizing plants, rock or other inert material without invasion, forming a moss-like black felt. Most of these studies (Reynolds 1982; Reynolds 1983; Reynolds 1985; Chomnunti et al. 2014) comprised members of Capnodiales as well as Chaetothyaliales. Only a fraction of these species, mainly belonging to Chaetothriaceae and Trichomeriaceae, have cultures.

In the second half of the 20th century, an independent line of research emerged that almost exclusively used living cultures. Schol-Schwarz (1968) systematically revised phialophora-like organisms, and after studies of de Hoog (1977) and Hermanides-Nijhof (1977) and the term ‘black yeasts’ became adopted in the literature. Reference material of these studies was deposited in culture collections, and today sequence data are commonly available for almost all species cultured after 1970. The great majority of novel taxa initially belonged to a single family, Herpotrichiellaceae. Later, diversity studies discovered a gamut of fungi that phylogenetically clustered in other families of the Chaetothyaliales. These studies take GenBank data as reference for novelty of their isolates, neglecting older, nomenclaturally valid but unsequenced taxa.

Müller et al. (1987) and Untereiner (1997) were the first to make systematic connections between sexual and asexual phases by either bringing ascospores to germinate, or by stimulating asexual strains to produce ascospores, respectively. Today, the connection between the ascigerous state in nature and the conidial state in culture can be verified by sequence data. Remarkably, Haase et al. (1999), as confirmed in subsequent studies, noted that only very few of the sexual strains brought into culture appeared to match with any of the numerous available names of asexual herpotrichiellaceous species. In our data, only possible

connections between *Capronia coronata/Exophiala angulospora* and *Capronia semiimmersa/Phialophora americana* have been confirmed by sequencing. This suggests a preponderance of clonal reproduction as a survival strategy in Herpotrichiellaceae.

The disruptive scientific history of Chaetothyriales provides an unbalanced view on the order, due to current accent on molecular data. As a result, most molecular studies focus on Herpotrichiellaceae at the expense of other families within the order. Generic circumscriptions before the year 2000 have been phenotypic, while simple forms of asexual sporulation such as catenate cladophialophora-like conidia are now known to occur widely throughout the order. For example, members of *Cladophialophora* (Feng et al. 2013) can be found scattered in four families, Herpotrichiellaceae, Trichomeriaceae, Epibryaceae and Clade 4. Many morphological genera thus are obviously polyphyletic. Novel species are introduced at a regular pace, phylogenetic trees suffering from a significant taxon sampling problem, and therefore redefinition of genera is recommended to be postponed until a more complete overview of extant and still-to-be-described species is obtained.

## Origin and evolution of Chaetothyriales

Judging from results of divergence time estimations (Fig. 1), the order Chaetothyriales emerged about 387 Mya, during the end of Devonian (416–359 Mya), but the speciation events occurred in the Jurassic (201–145 Mya), which was initiated by the major Triassic–Jurassic extinction event, possibly as a result of rapid climate change due to volcanism or methane production during the active split into continental plates of the ancient Pangea continent (Ivanov 2007). During the early period, animal and plant life on earth became very scarce. Our hypothesis is that for a long time, the ancestral Chaetothyriales colonized rock surfaces, and under these extreme and oligotrophic conditions grew slowly without much diversification.

A significant change in diversity in Chaetothyriales was observed around 151 Mya. One possible hypothesis is that the interaction of Chaetothyriales with toxin-containing lichens and Cyanophytes on rock became a driver towards toxin-management, which opened other windows of opportunity. As a result of the subsequent Cretaceous–Paleogene extinction event (66 Mya), global species diversity greatly declined again, resulting in many vacant ecological niches. It took a long time for the ecosystem to restore general diversity (MacLeod et al. 1997; Wilf and Johnson 2004), but the Chaetothyriales, which were not significantly impacted by the extinction event, began an explosion of diversification.

Ancestral groups of Chaetothyriales had an epilithic, lichen-associated strategy (Muggia et al. 2020). This is in line with earlier assumptions, where black lichenized fungi

of Verrucariales were listed in ancestral position to Chaetothyriales (Gueidan et al. 2008, 2011). Several clades with identical non-lichenized, endolichenic lifestyles (Clades 8, 5 and 9) emerged, including the basal clade, oldest clade (Clade 9). We speculate that the oldest Chaetothyriales co-evolved with lichens that live on the surface of rocks. Metabolic products are accumulated in the lichen thallus during the growth, known as lichenic acid or lichen substances (Barnes 2000). Usnic acid, a dibenzofuran derivative, is one of the most common and abundant lichen metabolites (Cochietto et al. 2002). The Cyanobacteria that occur in the lichens as photosynthetic accessory contain other toxins, such as microcystins (Oksanen et al. 2004) which are larger molecules containing benzene rings. Early fungi living under these conditions must have the ability to tolerate or to degrade these chemicals.

Cytochrome p450 genes (CYPs) play a fundamental role in primary, secondary, and xenobiotic metabolism (van den Brink et al. 1998). Some black yeasts are among the Ascomycota species with the highest number of CYPs (Teixeira et al. 2017). Also genes related to alcohol dehydrogenase (ADH), aldehyde dehydrogenase (ALDHs) and drug efflux pumps were copied in large quantity, which helps the black fungus adapt to the toxic environment better. The gene replications may have become the basis of metabolic versatility observed in modern black yeast. These genetic adaptations acquired in the common ancestor of the studied species are maintained throughout the evolution of Chaetothyriales. The apparent rapid explosion of diversification in the order, underlined by the low rate of extinction and giving rise to all within a very short time frame (Fig. 8) certainly has contributed to opening of numerous windows of opportunity for members of the order.

## Chaetothyrialean main families

**Herpotrichiellaceae** is the largest family within the order, containing 19 recognized genera and 179 species (as per 01-10-2019); 117 species were analyzed in this study. Excluded species were those without known ITS or LSU sequences, or with obviously incorrect sequences as concluded from large distances to any of the taxa in the chaetothyrialean tree. In all trees, species published as being members of the family Herpotrichiellaceae showed instability and low bootstrap values with different algorithms. In the single-gene LSU or ITS trees, the family was not supported but deteriorated into many subclades. With LSU + ITS, they clustered together but the bootstrap values remained relatively low.

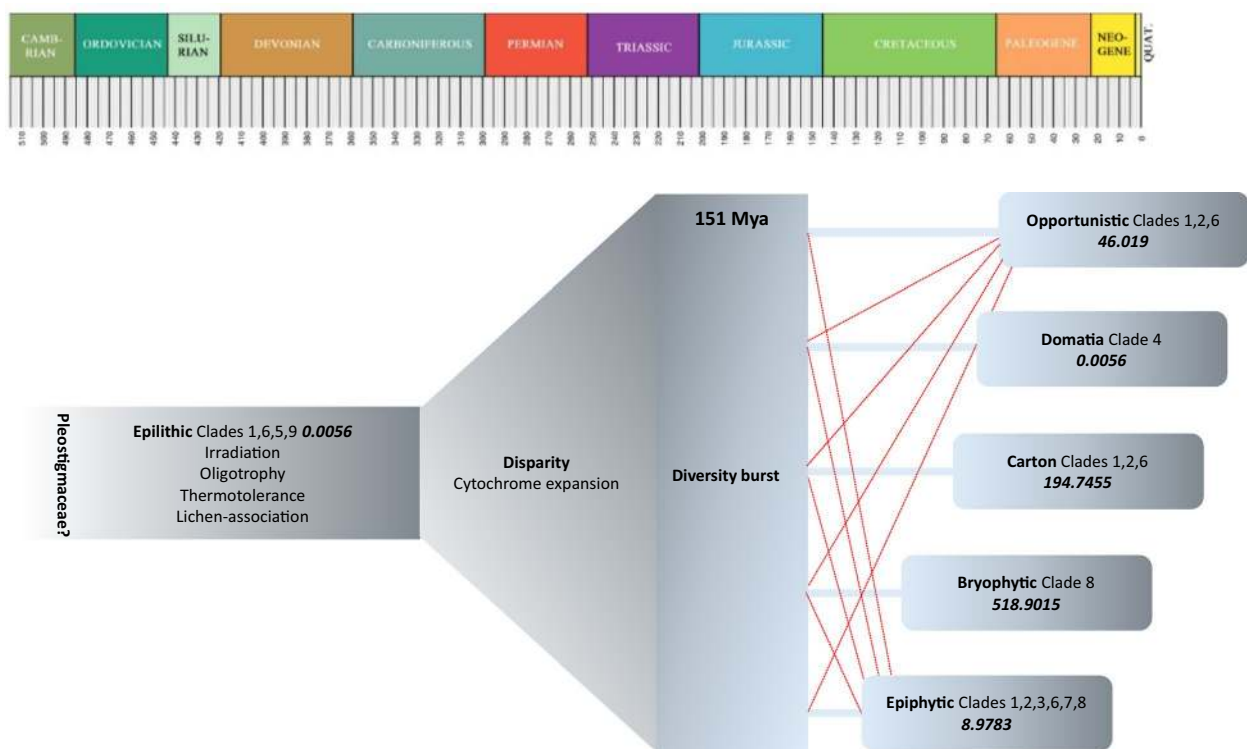
In search of common ecological features for Herpotrichiellaceae, Gostinčar et al. (2018) referred to these fungi as being polyextremotolerant, i.e. combining tolerance of e.g. temperature, dryness, toxin, and nutrient limitation.

Numerous, as yet undescribed members of the family are epilithic, colonizing hard, sun-exposed rock (Ruibal et al. 2008). The medical counterpart of the meristematic ecotype on exposed habitats is the muriform cell formed in tissue of patients with chromoblastomycosis, but members of the family are known from a plethora of opportunistic diseases (de Hoog et al. 2019). Species are notoriously difficult to isolate from natural environments (Sudhaham et al. 2008; Vicente et al. 2014), but are enriched in human-created habitats, such as oil-contaminated soil (Prenafeta-Boldú et al. 2001), creosoted railway sleepers (Gümral et al. 2014), gasoline (Isola et al. 2013), dishwashers (Raghupathi et al. 2018), bathing facilities (Matos et al. 2002), or household sinks (Nishimura et al. 1987). These environments suggest, in line with suggestions of Gostincar et al. (2018), oligotrophy in addition to extremotolerance and toxin management. Infective ability seems to be consistently present in the family, as waterborne species without thermotolerance infect numerous cold-blooded vertebrates instead of humans (de Hoog et al. 2011). Quan et al. (2019) developed an isolation method based on enrichment with hydrocarbons, underlining the significance of toxicity in the biology of these fungi, while earlier authors successfully implemented experimental inoculation of environmental samples into laboratory animals (Gezuele et al.

1972; Dixon et al. 1980), high incubation temperature and low pH (Sudhaham et al. 2008), extraction with mineral oil (Satow et al. 2008; Vicente et al. 2008), and cycloheximide as suppressor of contaminants (Wang et al. 2018). Generally, low competitive ability with co-occurring saprobes has been hypothesized, as a result of which they prevalently occupy (micro-)habitats that are hostile to microbial life and are inaccessible for their competitors (Gueidan et al. 2008).

The **Cyphellophoraceae** were previously known as the ‘europaea-clade’ within Herpotrichiellaceae (de Hoog et al. 2011) and were raised to family level by Réblová et al. (2013). As yet, insufficient data are available to recognize an unambiguous ecological trend in the family. Several species are known from individual reports from plants, but mostly without clear information on the type of growth, whether as an endophyte, a pathogen, or a colonizer. *Cyphellophora europaea* is a common species causing mild infections on human skin and nails (de Hoog et al. 2000). Lian and de Hoog (2010) hypothesized a life style as an oligotrophic colonizer of moist, warm environments, where it could accidentally be picked up by human hosts. This might also hold true for other clinical *Cyphellophora* species.

The clade representing **Trichomeriaceae** contained 48 strains, in addition to some undescribed species isolated



**Fig. 9** Diagrammatic representation of evolution of Chaetothyriales over geological times. Epilithic lifestyle is ancestral, possibly emerging from groups with uncertain phylogenetic position such as Pleistigmaceae. Ecological disparity increased at an early stage,

followed by diversification with several ecotypes shortly after each other and at low levels of innovation as expressed by Brownian rates (Table 4). The red lines indicate multiple origins

from ant nest carton and four species of the genus *Strelitziana* described from living plants. *Strelitziana australiensis*, *S. eucalypti*, *S. albiziae* and *S. cliviae* were all named after their host plants and have been classified in a separate family, Strelitzianaceae (Crous et al. 2015). In our study, these species cluster in the Trichomeriaceae clade albeit at rather long branches; this result is different from previous studies (Cheewangkoon et al. 2009; Crous et al. 2010) and is possibly explained by our larger dataset. Morphologically, the asexual states of the species resemble those of *Cyphellophora*, and their growth on decaying leaves are not suggestive for primary pathogenicity. Thus we have reason to believe that no separate family status is necessary and the genus *Strelitziana* might well be maintained in the family Trichomeriaceae. Members of this family are ‘sooty moulds’ colonizing inert substrates such as leathery plants (Chomnunti et al. 2014), while *Knufia* and relatives contains rock-colonizing species (Isola et al. 2016).

**Chaetothyriaceae** is the type family of the order Chaetothyriales. Although the family is monophyletic, bootstrap values were relatively low, and distances between taxa rather large. This clearly demonstrates a taxon sampling error, as explained above. The majority of species has been isolated from plants, with small populations as colonizers without significant invasion of living tissue. Their epiphytic life style is not associated with significant disease (Crous et al. 2006; Crous et al. 2007; Gueidan et al. 2014; Hongsanan et al. 2016b).

Clade 4 mainly consists of **ant-domatia colonizing species**. The pronounced ability to metabolize monoaromatic hydrocarbons explained the overabundance of members of Herpotrichiellaceae in human-dominated environments; in nature, this may be an association with ants (Voglmayr et al. 2011, Nepel et al. 2014), as these insects communicate with similar compounds. Their nest materials of cartons, tunnels or domatia are antimicrobial. Schlick-Steiner et al. (2008) was the first to find a relationship between ants and Chaetothyriales. Defosse et al. (2009) revealed a symbiotic tripartite of domatia-forming plant, ant and fungus. In our study, the domatia fungi all belong to a single, novel clade. Mayer and Voglmayr (2009), Voglmayr et al. (2011), Nepel et al. (2014) and Vasse et al. (2017) revealed a stunning biodiversity, of which the carton-associated species were divided over families Herpotrichiellaceae, Trichomeriaceae and Cyphellophoraceae. Attili-Angelis et al. (2014) described some species in Cyphellophoraceae from leaf-cutting ants in Brazil. Probably only a fraction of these fungi is known, because there are thousands of tropical ants which build specific tunnel structures which may carry ant-specific black yeasts.

## Ancestral character state reconstruction

Phenotypic plasticity (i.e. the sum of morphotypes and growth abilities) enables a fungus to respond differentially to novel environmental conditions. Most organisms are able to survive outside their original and preferred habitat. In the theory of ecological fitting (Janzen 1985), this operational environment is known as the ‘sloppy fitness space’ (Agosta and Klemens 2008). Under conditions of survival stress, adaptation of the organism is promoted, whereas in absence thereof, or with populations occupying different environments and connected by gene flow, and thus being subjected to heterogeneous pressure, more likely leads to evolutionary stasis.

Brownian motion is an effective model as the sum of a large number of very small, random forces relative to the given trait changes. The wide species richness, the diverse and fairly consistent ecotypes and the size of our dataset provides an opportunity for modelling evolutionary transitions in comparison with the evolutionary timing of Chaetothyriales since its origin (Fig. 1). To this aim, ecological traits are plotted along phenogram branches via stochastic character mapping, revealing which traits in a population follow a uniform pattern, and which may have evolved as products of other traits and or transitions. While ecological disparity peaked very early in Chaetothyriales evolutionary history, interestingly a general trend in biology (e.g. as for animals and plants; Harmon et al. 2012; Hughes et al. 2013), it logically leads to a strong decline in occupying new niches given the combinations of ancestral phenotypes and associated genetic abilities. While a Brownian process by means of evolutionary history is driven by two indicators of a clade’s success, i.e. diversity as measured by the number of species, and disparity which is an estimate of the lineage’s occupancy of a defined ecological space (Minelli 2016; Foote 1997; McGhee 1999; Wills 2001; Erwin 2007), these attributes are not mutually exclusive. Success in disparity does not necessarily go together with success in diversity.

Ancestral, epilithic Chaetothyriales, possibly preceded by rock-colonizing groups such as Pleostigmaceae (Muggia et al. 2020) colonized harsh and extreme environments, with low diversity, while significant disparity is observed with the abrupt evolution of e.g. ‘domatia’ and ‘bryophytic’ ecotypes in highly derived lineages. After these innovations, disparity decreased, but with explosive diversification in similar habitats. As a general rule many large organism genera show high diversity with low disparity, while others are highly diverse but also exhibit high disparity, the latter being an important attribute to the Chaetothyriales (= early high disparity burst lead to large diversity). The largest taxonomic genera are often characterized by key innovations that often, but not necessarily, coincide with their diagnostic



apomorphies. A key principle in the black fungi strongly supported by our data (=ecologies).

How is the evolution of fungal clades with high diversity and/or disparity be explained? It can be addressed from three main perspectives: (1) evolvability, in terms of release from previous constraints and of the presence of genetic or developmental conditions favoring multiple parallel occurrences of a given evolutionary transition and its reversal (clearly supported by the Brownian analysis); (2) phenotypic plasticity as a facilitator of speciation; and (3) modularity, heterochrony and a coupling between the complexity of the life cycle and the evolution of diversity and disparity in a clade. The possible role of saltational evolution in the origination of high diversity and/or disparity (eg. when considering our transition matrix results, indicating highly abrupt evolution of eg. ‘domatia’ or ‘bryophytic’ ecologies) in Chaetothyriales needs to be further explored. While under the simplest conditions (neutral genetic drift) there is no relationship between evolutionary rate and phylogenetic signal however, such a relationship can exist when evolution is not entirely neutral. For other circumstances, such as functional constraint, fluctuating selection, niche conservatism, and evolutionary heterogeneity, the relationship between process, rate, and phylogenetic signal is complex. While our data precisely reflects this complex case, it is due to its completeness an example for macroevolutionary modelling and stochastic effect discovery in kingdom fungi.

## Conclusions

Numerous fungi with rock-inhabiting life styles have been described, but the Chaetothyriales are special by representatives with intimate relationships with lichens, which led to expansion of cytochromes providing windows of opportunity for diversification. Colonization of toxic environments is an alternative way to escape microbial competition. Toxic hydrocarbons are found in nature e.g. in ant-dominated habitats. In human-made environments, toxic hydrocarbons are present as compounds of oil- and gasoline-pollution and industrial exhaust of xenobiotic volatiles. Members of Herpotrichiellaceae have been proposed as agents of bioremediation, for example in industrial biofilters, where they survive the conditions of acidification and dryness much better than the bacteria that are currently used in air clean-up (Cox et al. 1993; Groenestijn and Kraakman 2005). The vertebrate nervous system also contains aromatic hydrocarbon neurotransmitters, which might be used by black yeasts once they are introduced into the human body. This would explain opportunism of these fungi, in analogy of hypotheses put forward in *Cryptococcus* (Esher et al. 2018). A summarizing diagram of the possible lines of adaptation in Chaetothyriales leading to species-rich families is given in Fig. 9.

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## Affiliations

Yu Quan<sup>1,2,3</sup>  · Lucia Muggia<sup>4</sup> · Leandro F. Moreno<sup>5</sup> · Meizhu Wang<sup>1,2</sup> · Abdullah M. S. Al-Hatmi<sup>1,6,7</sup>  · Nickolas da Silva Menezes<sup>14</sup> · Dongmei Shi<sup>9</sup> · Shuwen Deng<sup>10</sup> · Sarah Ahmed<sup>1,6</sup> · Kevin D. Hyde<sup>11</sup> · Vania A. Vicente<sup>8,14</sup> · Yingqian Kang<sup>2,13</sup> · J. Benjamin Stielow<sup>1,12</sup> · Sybren de Hoog<sup>1,6,8,10</sup> 

<sup>1</sup> Centre of Expertise in Mycology of Radboud University Medical Centre/Canisius Wilhelmina Hospital, Nijmegen, The Netherlands

<sup>2</sup> Key Laboratory of Environmental Pollution Monitoring and Disease Control, Ministry of Education of Guizhou & Key Laboratory of Medical Microbiology and Parasitology,

School of Basic Medical Sciences, Guizhou Medical University, Guiyang, China

<sup>3</sup> College of Food and Pharmaceutical Engineering, Guizhou Institute of Technology, Guiyang, China

<sup>4</sup> Department of Life Sciences, University of Trieste, Trieste, Italy

- <sup>5</sup> Amsterdam Medical Center, Amsterdam, The Netherlands
- <sup>6</sup> Foundation Atlas of Clinical Fungi, Hilversum, The Netherlands
- <sup>7</sup> Ministry of Health, Directorate General of Health Services, Ibri, Oman
- <sup>8</sup> Postgraduate Program in Microbiology, Parasitology and Pathology, Biological Sciences, Department of Basic Pathology, Federal University of Parana, Curitiba, Brazil
- <sup>9</sup> Department of Dermatology & Laboratory of Medical Mycology, Jining No. 1 People's Hospital, Jining, Shandong, China
- <sup>10</sup> Department of Medical Microbiology, People's Hospital of Suzhou National New & Hi-Tech Industrial Development Zone, Suzhou, China
- <sup>11</sup> Center of Excellence in Fungal Diversity, Mae Fah Luang University, Chiang Rai, Thailand
- <sup>12</sup> Thermo Fisher Diagnostics, Specialty Diagnostics Group, Landsmeer, The Netherlands
- <sup>13</sup> Guizhou Academy of Tobacco Science, Guiyang, China
- <sup>14</sup> Engineering Bioprocess and Biotechnology Post-graduation Program, Department of Bioprocess Engineering and Biotechnology, Federal University of Parana, Curitiba, Brazil