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Geoglossomycetes cl. nov., *Geoglossales* ord. nov. and taxa above class rank in the *Ascomycota* Tree of Life

C.L. Schoch[1], Z. Wang[2], J.P. Townsend[2], J.W. Spatafora[3]

Key words

Bayesian inference
hybrid classification
maximum likelihood

Abstract Featuring a high level of taxon sampling across *Ascomycota*, we evaluate a multi-gene phylogeny and propose a novel order and class in *Ascomycota*. We describe two new taxa, *Geoglossomycetes* and *Geoglossales,* to host three earth tongue genera: *Geoglossum*, *Trichoglossum* and *Sarcoleotia* as a lineage of 'Leotiomyceta'. Correspondingly, we confirm that these genera are not closely related to the genera *Neolecta*, *Mitrula*, *Cudonia*, *Microglossum*, *Thuemenidum*, *Spathularia* and *Bryoglossum*, all of which have been previously placed within the *Geoglossaceae*. We also propose a non-hierarchical system for naming well-resolved nodes, such as 'Saccharomyceta', 'Dothideomyceta', and 'Sordariomyceta' for supraordinal nodes, within the current phylogeny, acting as rankless taxa. As part of this revision, the continued use of 'Leotiomyceta', now as a rankless taxon, is proposed.

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INTRODUCTION

The multi-gene sequence datasets generated by the research consortium 'Assembling the Fungal Tree of Life' (AFTOL) have resulted in several multi-gene phylogenies incorporating comprehensive taxon sampling across Fungi (Lutzoni et al. 2004, Blackwell et al. 2006, James et al. 2006). AFTOL generated a data matrix spanning all currently accepted classes in the *Ascomycota*, the largest fungal phylum. The phylogenies produced by AFTOL prompted the proposal of a phylogenetic classification from phylum to ordinal level in fungi (Hibbett et al. 2007). Although the Botanical Code does not require the principle of priority in ranks above family (McNeill et al. 2006), this principle was nevertheless followed for all taxa. The following ranked taxa were defined: subkingdom, phylum (suffix -mycota, except for Microsporidia), subphylum (-mycotina), class (-mycetes), subclass (-mycetidae) and order (-ales). As in Hibbett et al. (2007), several phylogenetically well-supported nodes above the rank of order could not be accommodated in the current hierarchical classification system based on the International Code of Botanical Nomenclature. To remedy this deficiency, rankless (or unranked) taxa for unambiguously resolved nodes with strong statistical support was proposed (Hibbett & Donoghue 1998). Hybrid classifications that include both rankless and Linnaean taxa have since been discussed elsewhere (Jørgensen 2002, Kuntner & Agnarsson 2006), and applied to diverse organisms from lichens (Stenroos et al. 2002) and plants (Sennblad & Bremer 2002, Pfeil & Crisp 2005) to spiders (Kuntner 2006). These studies all attempt to create a comprehensive code for phylogenetic nomenclature that retains the current Linnean hierarchical codes.

In keeping with the practice of previous hybrid classifications, we propose to use names corresponding to clades of higher taxa that were resolved in this phylogeny as well as preceding studies. The proposed informal, rankless names for well-supported clades above the class level in our phylogeny agrees with the principles of the Phylocode (http://www.ohio.edu/phylocode/). It is our hope that such names should function as rankless taxa, facilitating the naming of additional nodes/clades as they become resolved. Eventual codification will follow the example of Hibbett et al. (2007) by applying principles of type names and priority. A number of published manuscripts already provide background on other supraordinal relationships of Fungi; for more complete treatments of the various classes, see Blackwell et al. (2006).

During the AFTOL project a data matrix was generated spanning all currently accepted classes in the *Ascomycota*, the largest fungal phylum. A multi-gene phylogeny was recently inferred from these data, demonstrating relevant patterns in biological and morphological character development as well as establishing several distinct lineages in *Ascomycota* (Schoch et al. 2009). Here we test whether the relationships reported in Schoch et al. (2009) remain valid by applying both maximum likelihood (ML) and Bayesian analyses on a more restricted but denser set of taxa, including expanded sampling in the *Geoglossaceae*.

We will therefore address the taxonomic placement of a group of fungi with earth tongue morphologies that are shown to be unrelated to other known classes. This morphology is closely associated with the family *Geoglossaceae* (Corda 1838). With typical inoperculate asci and an exposed hymenium, *Geoglossaceae* has long been thought to be a member of *Leotiomycetes*, though the content of the family itself has experienced many changes (Nannfeldt 1942, Korf 1973, Spooner 1987, Platt 2000, Wang et al. 2006a, b). It is currently listed with 48 species and 6 genera in the Dictionary of the Fungi (Kirk et al. 2008). Several analyses using molecular data supported a clade including three earth tongue genera, *Geoglossum*, *Trichoglossum* and *Sarcoleotia* (Fig. 1), and cast doubt upon their positions in *Leotiomycetes* (Platt 2000, Gernandt et al. 2001, Lutzoni et al. 2004, Sandnes 2006, Spatafora et al. 2006, Wang et al. 2006b). Here we present a comprehensive phylum-wide phylogeny, including data from protein coding genes. We can confidently place the earth tongue family as separate from currently accepted classes in *Ascomycota*.

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[1] National Center for Biological Information (GenBank), National Library of Medicine, National Institute of Health, 45 Center Drive, MSC 6510, Bethesda, Maryland 20892-6510, USA;
corresponding author e-mail: schoch2@ncbi.nlm.nih.gov

[2] Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, CT 06520, USA.

[3] Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, USA.

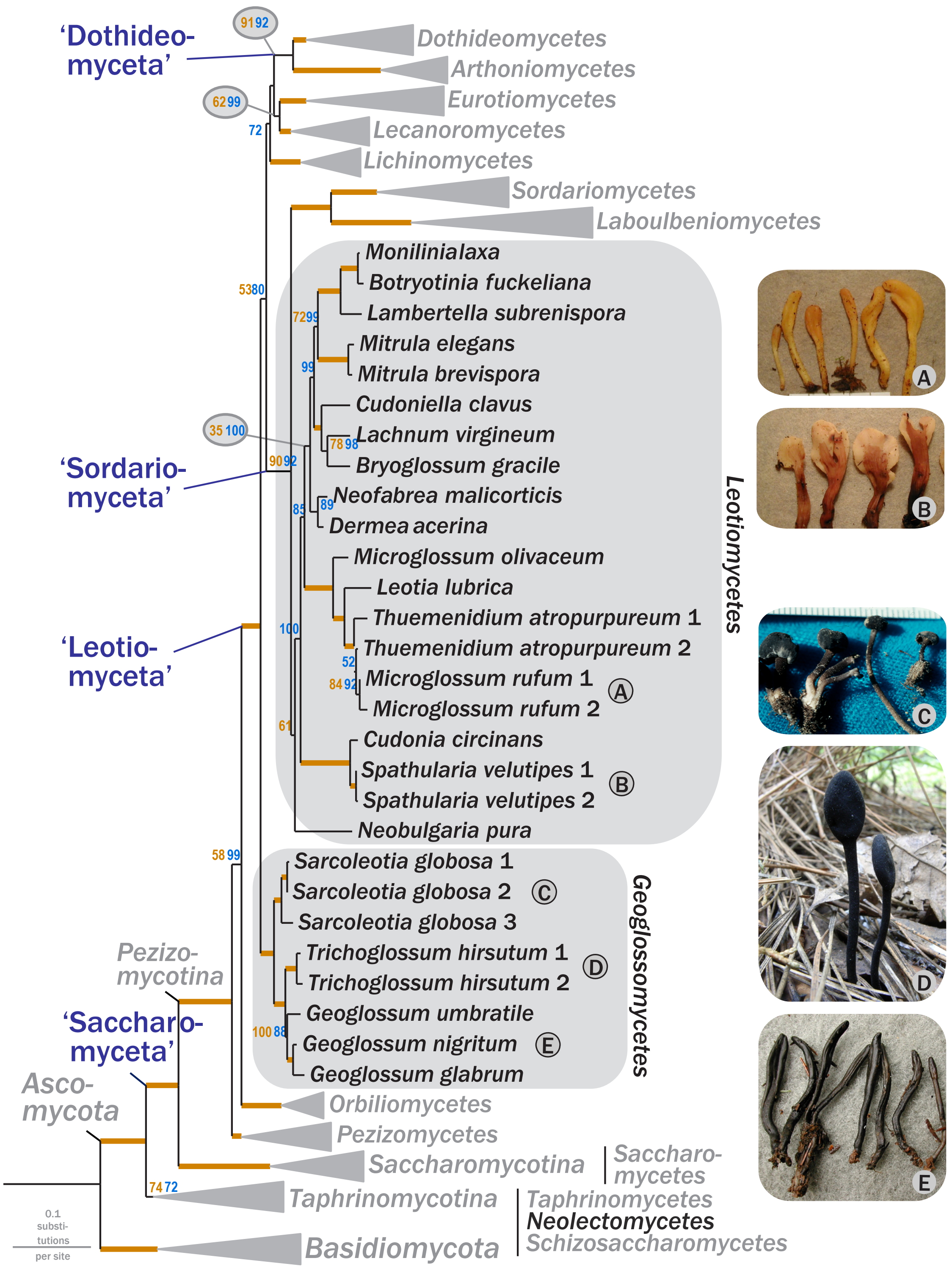

Fig. 1 A most likely tree obtained by RAxML for *Ascomycota*. Subphyla, class and rankless taxa are indicated. Classes containing fungi designated as earth tongues are indicated in black. The tree was rooted with outgroup *Rhizopus oryzae* (not shown). Bootstrap values are shown in orange and Bayesian posterior probabilities in blue. Orange, bold branches are supported by more than 80 % bootstrap and 95 % posterior probability, respectively. The full phylogeny, without collapsed clades, are shown in Fig. 2. The inset figures illustrate morphological ascomal diversity in the earth tongues. The species are as follows: A. *Trichoglossum hirsutum*; B. *Geoglossum nigritum*; C. *Microglossum rufum*; D. *Spathularia velutipes*; E. *Geoglossum nigritum.* Photo credits: A: Zhuliang Yang; B, D, E: Kentaro Hosaka; C: Dan Luoma.

MATERIALS AND METHODS

Data were extracted from the complete data matrix obtained from the WASABI database (www.aftol.org), incorporating representatives for all currently accepted classes, and maximizing the number of orders and available data. Following the approach of James et al. (2006) we performed a combined analysis, with both DNA and amino acid data, while allowing for missing data. This data was supplemented with additional ribosomal sequences from earth tongue genera obtained and deposited in GenBank from two previous studies (Wang et al. 2006a, b). To further minimise poorly aligned areas, 219 additional columns, which proved variable when viewed in BioEdit with a 40 % shade threshold, were excluded from the original AFTOL inclusion set. The refined dataset consisted of 161 taxa (including outgroups) and 4 429 characters for six different loci: the nuclear small and large ribosomal subunits (nSSU, nLSU), the mitochondrial small ribosomal subunit (mSSU) and fragments from three proteins: transcription elongation factor 1 alpha (*TEF1*) and the largest and second largest subunits of

RNA polymerase II (*RPB1*, *RPB2*). A complete table with the published GenBank numbers is listed in Table 1.

The phylogenetic analysis was run in RAxML v7.0.0 (Stamatakis 2006), partitioning by gene (six partitions) and estimating unique model parameters for each gene, as in Schoch et al. (2009). Models of evolution were evaluated as in Schoch et al. (2009) with the same models selected. For DNA sequences, this resulted in a general time reversible model (GTR) with a discrete gamma distribution composed of four rate classes plus an estimation of the proportion of invariable sites. The amino acid sequences were analysed with a RTREV model with similar accommodation of rate heterogeneity across sites and proportions of invariant sites. In addition, protein models for *TEF1* and *RPB2* incorporated a parameter to estimate amino acid frequencies. The tree shown in Fig. 1 was obtained by using an option in RAxML running a rapid bootstrap analysis and search for the best-scoring ML tree in one single run. This meant the GTRCAT model approximation was used, which does not produce likelihood values comparable to other programs. The full tree is shown here as Fig. 2 and was deposited in TreeBASE (www.treebase.org). We also ran 100 repetitions of RAxML under a gamma rate distribution option. The best scoring tree was included in TreeBASE.

A second analysis was run using Bayesian inference of maximum likelihood in MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, Altekar et al. 2004) using models and parameters that were comparable to the maximum likelihood run. Data were similarly partitioned and amino acids were analysed, so that a mixture of models with fixed rate matrices for amino acid sequences could be evaluated. In all cases rate heterogeneity parameters were used by a discrete gamma distribution plus an estimation of the proportion of invariable sites. A metropolis coupled Markov Chain Monte Carlo analysis was run for 9 million generations sampling every 200th cycle, starting from a random tree and using 4 chains (three heated and one cold) under default settings. Two separate runs were confirmed to converge using Tracer v1.4.1 (http://tree.bio.ed.ac.uk/software/tracer/). The first 10 000 sampled trees (2 million generations) were removed as burn in each run. A 50 % majority rule consensus tree of 70 000 Bayesian likelihood trees from the two combined runs was subsequently constructed, and average branch lengths and posterior probabilities determined. The numbers of nodes shared with the most likely tree in Fig. 1 was determined and plotted on the branches. This tree was deposited in TreeBASE, along with the inclusive character set.

RESULTS

The phylogeny presented in Fig. 1 supports 15 classes (11 in *Pezizomycotina*, 1 in *Saccharomycotina*, 3 in *Taphrinomycotina*) with good statistical support (both ML bootstrap and Bayesian posterior probability) for 14. Phylogenies with all lineages in the analysed data matrix are included in Fig. 2. A run with 100 repetitions of RAxML under a gamma rate distribution option resulted in a best scoring tree with a log likelihood of -111983. This tree shared the same supported nodes with the one presented in Fig. 1 but had changes in poorly supported nodes regarding placement of the *Eurotiomycetes* and *Dothideomycetes*. The two Bayesian runs produced trees with harmonic means of likelihood values of -112094 and -112076, respectively, with similar topological differences in poorly supported nodes.

As can be seen in Fig. 1, we continue to find low bootstrap and posterior probability support for *Leotiomycetes* as a monophyletic clade using a combined analysis of protein and nucleic acids. In our analysis, this includes *Neobulgaria pura* as the earliest diverging lineage. The node internal from this lineage is found in all ML bootstrap trees, suggesting that this taxon is unstable in our analyses. No conflicts were detected in *Neobulgaria* genes under a previous study and missing data did not affect important nodes (Schoch et al. 2009). A repeat run under maximum likelihood was done with *Neobulgaria pura* removed under the same settings but with only 100 bootstrap repetitions. This trimmed dataset yielded a congruent phylogeny with increased bootstrap for *Leotiomycetes* (78 %; data not shown). The instability of the placement of *Neobulgaria pura* does not compromise any of the conclusions we present here and may be due to various reasons. Improved taxon sampling will likely help to resolve its placement in future analyses.

We find support for numerous backbone nodes in *Ascomycota*, as did Schoch et al. (2009). Our phylum-wide sampling of *Ascomycota* classes in this study, combined with the results of a previous study (Schoch et al. 2009), facilitated addressing the placement of the previously problematic and unsampled lineages such as the *Geoglossaceae* in relation to all currently accepted *Ascomycota* classes.

Taxonomy

Given their unique ascomatal development, ultrastructure of ascus apical apparatus, mossy habitat, and our multilocus gene phylogeny, *Geoglossomycetes* cl. & ord. nov. is justified here as incertae sedis in *Pezizomycotina* and 'Leotiomyceta'.

Geoglossomycetes, Geoglossales Zheng Wang, C.L. Schoch & Spatafora, *cl. & ord. nov.* — MycoBank MB513351, MB513352

Ascomata solitaria vel gregaria, capitata, stipitata; stipe cylindricus, atrum, glabrum vel furfuraceus. Regio hymeniali capitata, clavata vel pileata, indistinctum ex stipite; hymenium atrum, continuatcum stipite ad praematuro incrementi grado. Asci clavati, inoperculati, octospori, poro parvo in iodo caerulescentes. Ascosporae elongatae, fuscae, pullae vel hyalinae, multiseptatae. Paraphyses filiformes, pullae vel hyalinae. Distributio generalis, terrestris, habitaile locus fere uliginoso et muscoso.

Type genus. *Geoglossum* Pers., Neues Mag. Bot. 1: 116. 1794; *Geoglossaceae.*

Ascomata scattered to gregarious, capitate, stipitate; *stipe* cylindrical, black, smooth to furfuraceous. Ascigerous portion capitate, club-shaped to pileate, indistinguishable from stipe. *Hymenium* surface black, continues with stipe at early development stage. *Asci* clavate, inoperculate, thin-walled, J+, usually 8-spored. *Ascospores* elongate, dark-brown, blackish to hyaline, septate when mature. *Paraphyses* filiform, blackish to hyaline. Global distribution, terrestrial, habitat usually boggy and mossy.

DISCUSSION

In keeping with the phylogeny presented in Fig. 1, we endorse use of the -myceta suffix in order to circumscribe well-supported clades above class. The numbers of these clades are limited, and the use of such taxa will continue to become more practical as our biological knowledge base broadens. Use of this suffix will also allow for the continued use of *Leotiomyceta*, a taxon that has already been defined with a Latin diagnosis provided as a ranked superclass (Eriksson & Winka 1997) and remains in use (Lumbsch et al. 2005, Wang et al. 2006a). We propose its continued use, but as a rankless taxon together with the newly proposed rankless taxa, 'Saccharomyceta', 'Dothideomyceta' and 'Sordariomyceta'. Since these taxa are not currently accepted under the Code (McNeill et al. 2006), we will refrain from formal designations. The relevant clades are discussed below with the informal designations indicated in single quotations.

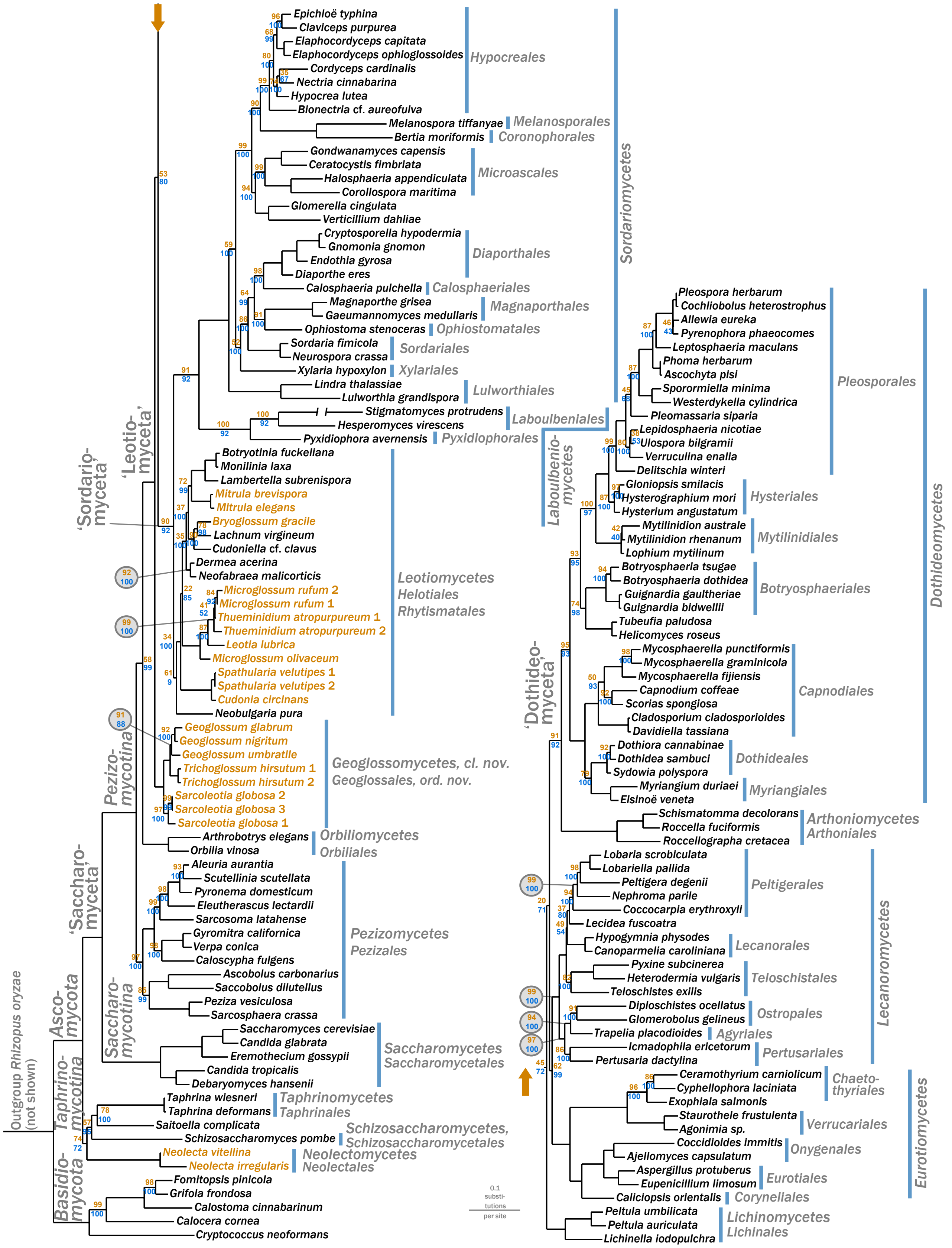

Fig. 2 A most likely tree obtained by RAxML for *Ascomycota* (as in Fig. 1). Phyla, subphyla, class, order and rankless taxa are indicated. Taxa designated as earth tongues are indicated in orange. The tree is displayed as two subtrees – orange arrows indicate where the subtrees were joined. The tree was rooted with outgroup *Rhizopus oryzae* (not shown). Bootstrap values are shown in orange above nodes and Bayesian posterior probabilities in blue below. Numbers were removed for nodes with 100 % bootstrap and 100 % posterior probability.

Subphylum Taphrinomycotina

As in recent studies using large multi-gene datasets (Spatafora et al. 2006, Sugiyama et al. 2006, Liu et al. 2009, Schoch et al. 2009), we find ML bootstrap support here for the monophyly of the *Taphrinomycotina*. The addition of sequences from protein coding genes has been vital to the establishment of statistical support for this grouping. Recent work has shown that the short generation times characteristic of species in this group make phylogenetic analyses particularly susceptible to long branch attraction artefacts (Liu et al. 2009). The placement of *Neolecta* in this subclade is also confirmed here. The club-shaped apothecia of the members of *Neolecta* share superficial similarity with those of the *Geoglossaceae*. *Neolecta* was long thought to be included in the *Geoglossaceae* until molecular work proved otherwise (Landvik 1996). In support of its placement in this early diverging group, *Neolecta* has several presumably ancestral features, such as simplified non-poricidal asci without croziers and the absence of paraphyses (Redhead 1979, Landvik et al. 2003). With additional sampling of both taxa and genes we find here moderate support for the monophyly of *Taphrinomycotina*, and thus demonstrate that the earliest diverging clade of the *Ascomycota* was dimorphic, with both filamentous and yeast growth forms. Nevertheless, it remains apparent that this part of the *Ascomycota* tree remains under sampled. This lack of adequate sampling is supported by the recent description of a clade labelled ‘Soil Clone Group I’ (SCGI). SCGI is ubiquitous in soil and is only known from environmental sequence data (Porter et al. 2008). It appears possible that they form a novel early diverging lineage outside of *Taphrinomycotina*. Very little remains known about their ecology, morphology and general biology.

Rankless taxon ‘Saccharomyceta’

‘Saccharomyceta’ includes the two remaining subphyla of *Ascomycota*, *Saccharomycotina* and *Pezizomycotina*. *Saccharomycotina* comprises the ‘true yeasts’ (e.g., *Saccharomyces cerevisiae*), although hyphal growth has been documented in some taxa (e.g., *Eremothecium*). The *Pezizomycotina* consists of the majority of filamentous, ascoma producing species, but numerous species are additionally capable of yeast and yeast-like growth phases. Thousands of species are only known to reproduce asexually. These two subphyla form a well-supported, monophyletic group that has been recovered in a large number of studies across a diversity of character and taxon sets. The recognition of ‘Saccharomyceta’ highlights the shared common ancestry of these two taxa and the inaccurate characterisation of *Saccharomycotina* as a primitive or basal lineage of the *Ascomycota*. Rather, its small genome size (Dujon et al. 2004) and dominant yeast growth phase can be characterized as derived traits for this subphylum.

Rankless taxon ‘Leotiomyceta’

We apply ‘Leotiomyceta’ as a rankless taxon containing the majority of fungi with a diversity of inoperculate asci (e.g., fissitunicate, poricidal, deliquescent). ‘Leotiomyceta’ excludes the earliest diverging classes of *Pezizomycotina*, *Pezizomycetes* and *Orbiliomycetes*. It was first defined as a superclass (Eriksson & Winka 1997). This definition has remained in use (Lumbsch et al. 2005, Spatafora et al. 2006). Included in this clade are the informal, rankless taxa ‘Dothideomyceta’, ‘Sordariomyceta’, as well as the classes *Eurotiomycetes*, *Lecanoromycetes*, *Lichinomycetes*, and a newly proposed class, *Geoglossomycetes.*

The type genus of *Geoglossaceae*, *Geoglossum* was initially proposed by Persoon (1794). Persoon described it as club-shaped, with unitunicate, inoperculate asci, with the type species given as *Geoglossum glabrum* Pers. *Trichoglossum* have historically been classified in *Geoglossaceae*, and *Sarcoleotia* has historically been classified in the *Helotiaceae* (*Leotiomycetes*). These inoperculate *Discomycetes* produce terrestrial, stipitate, clavate ascomata, commonly referred to as earth tongues, which include *Leotia*, *Microglossum*, *Cudonia*, and *Spathularia*. In terms of ascomatal development, species of *Geoglossum*, *Trichoglossum*, and *Sarcoleotia* possess a hymenium that freely develops towards the base, while other earth tongue fungi feature a distinct ridge to their hymenium, implying a developmental stage during which the hymenium is enclosed (Schumacher & Sivertsen 1987, Spooner 1987, Wang et al. 2006b). An enclosed hymenium has been observed as well in several other lineages, such as *Cyttaria*, *Erysiphales* and *Rhytismatales* in the *Leotiomycetes* (Korf 1983, Gargas et al. 1995, Johnston 2001). Although the name earth tongue implies these fungi are terrestrial and have no direct association found with other organisms, *Trichoglossum*, *Geoglossum* and *Sarcoleotia globosa* have often been recorded in boggy habitats abundant with bryophytes (Seaver 1951, Dennis 1968, Schumacher & Sivertsen 1987, Spooner 1987, Jumpponen et al. 1997, Zhuang 1998). Ascus apical morphology is one of the major features in distinguishing higher ascomycetes, and operculate ascomycetes as members of *Pezizales* have an apical or subapical operculum which is thrown back at spore discharge while a definite plug is present in the thickened ‘inoperculate’ ascus apex as in species of the *Helotiales* (Korf 1973). Ultrastructure of the ascus apical apparatus suggested no close relationship between *Leotia lubrica* and species of *Geoglossum* and *Trichoglossum*. A structure known as a tractus connects the uppermost spore to the apical wall and the spores to each other in *Trichoglossum hirsutum*, but is never found in other species of the *Helotiales* and is possibly homologous to structures in *Sordariomycetes* and *Pezizomycetes* (Verkley 1994). Recent molecular phylogenetic analyses (Sandnes 2006, Wang et al. 2006a, b) confirmed that the earth tongue fungi are not monophyletic. At least two origins occurred in *Leotiomycetes*: in *Leotia* and allies in *Helotiales*, and in *Cudonia* and allies in *Rhytismatales*. *Geoglossum*, *Trichoglossum*. *Sarcoleotia* (*Geoglossomycetes* as we define it) represent a third, independent lineage of earth tongues, which we confirmed does not belong within the *Leotiomycetes*.

DNA-only and combined model analyses produced conflicting placements of *Geoglossaceae* within *Pezizomycotina*. Previous analyses applying nucleotide sequences only placed the order as a sister group to the *Lichinomycetes* (Lutzoni et al. 2004, Spatafora et al. 2006), which includes a small number of lichenised species mainly associated with cyanobacteria (Reeb et al. 2004). Our sampling of *Lichinomycetes* includes two genera, *Peltula* and *Lichinella* that encompass at least some of the ascal diversity, i.e., rostrate and deliquescent, present in the class. In contrast, our combined amino acid and nucleotide model analyses resolved *Geoglossaceae* as an isolated, unique lineage of ‘Leotiomyceta’ with no supported sister relationship, in agreement with Schoch et al. (2009). Different levels of missing data underlie these two conflicting topologies, and several phenomena can potentially explain this conflict, ranging from model misspecification to long-branch attraction. Regardless of these concerns, our conclusion that the *Geoglossaceae* is a monophyletic lineage, unallied with members of the *Leotiomycetes* and any of the other large fungal classes remains strongly supported.

Eurotiomycetes and *Lecanoromycetes* are the two remaining classes in ‘Leotiomyceta’. *Eurotiomycetes* is arguably the most ecologically diverse class within *Ascomycota* including lichenised species, saprobes and pathogens of animals and plants. As currently defined, this class incorporates several distinct orders and three subclasses spanning virtually all known fun-

Table 1 Taxa and sequences used in this study.

AFTOL no.	Class	Order	Voucher[1]	Taxon	nSSU	nLSU	mSSU	*RPB1*	*RPB2*	*TEF1*
1241	*Zygomycota* outgroup		GB	*Rhizopus oryzae*	AF113440	AY213626	AY863212	Genome	Genome	Genome
438	*Basidiomycota* outgroup		GEL 5359	*Calocera cornea*	AY771610	AY701526		AY857980	AY536286	AY881019
439	*Basidiomycota* outgroup		AW 136	*Calostoma cinnabarinum*	AY665773	AY645054		AY857979	AY780939	AY879117
1088	*Basidiomycota* outgroup		GB	*Cryptococcus neoformans*	Genome	Genome		XM_570943	XM_570204	Genome
770	*Basidiomycota* outgroup		MB 03-036	*Fomitopsis pinicola*	AY705967	AY684164	FJ436112	AY864874	AY786056	AY885152
701	*Basidiomycota* outgroup		DSH s.n.	*Grifola frondosa*	AY705960	AY629318		AY864876	AY786057	AY885153
126	*Arthoniomycetes*	*Arthoniales*	Diederich 15572	*Roccella fuciformis*	AY584678	AY584654	EU704082	DQ782825	DQ782866	
93	*Arthoniomycetes*	*Arthoniales*	BG Printzen1981	*Roccellographa cretacea*	DQ883705	DQ883696	FJ772240		DQ883713	DQ883733
307	*Arthoniomycetes*	*Arthoniales*	DUKE 0047570	*Schismatomma decolorans*	AY548809	AY548815	AY548816	DQ883718	DQ883715	DQ883725
946	*Dothideomycetes*	*Botryosphaeriales*	CBS 115476	*Botryosphaeria dothidea*	DQ677998	DQ678051	FJ190612	EU186063	DQ677944	DQ767637
1586	*Dothideomycetes*	*Botryosphaeriales*	CBS 418.64	*Botryosphaeria tsugae*	AF271127	DQ767655			DQ767644	DQ677914
1618	*Dothideomycetes*	*Botryosphaeriales*	CBS 237.48	*Guignardia bidwellii*	DQ678034	DQ678085			DQ677983	
1784	*Dothideomycetes*	*Botryosphaeriales*	CBS 447.70	*Guignardia gaultheriae*		DQ678089	FJ190646		DQ677987	
939	*Dothideomycetes*	*Capnodiales*	CBS 147.52	*Capnodium coffeae*	DQ247808	DQ247800	FJ190609	DQ471162	DQ247788	DQ471089
1289	*Dothideomycetes*	*Capnodiales*	CBS 170.54	*Cladosporium cladosporioides*	DQ678004	DQ678057	FJ190628	EU186064	DQ677952	DQ677898
1591	*Dothideomycetes*	*Capnodiales*	CBS 399.80	*Davidiella tassiana*	DQ678022	DQ678074			DQ677971	DQ677918
2021	*Dothideomycetes*	*Capnodiales*	OSC 100622	*Mycosphaerella fijiensis*	DQ767652	DQ678098	FJ190656		DQ677993	
1615	*Dothideomycetes*	*Capnodiales*	CBS 292.38	*Mycosphaerella graminicola*	DQ678033	DQ678084			DQ677982	
942	*Dothideomycetes*	*Capnodiales*	CBS 113265	*Mycosphaerella punctiformis*	DQ471017	DQ470968	FJ190611	DQ471165	DQ470920	DQ471092
1594	*Dothideomycetes*	*Capnodiales*	CBS 325.33	*Scorias spongiosa*	DQ678024	DQ678075	FJ190643		DQ677973	DQ677920
274	*Dothideomycetes*	*Dothideales*	DAOM 231303	*Dothidea sambuci*	AY544722	AY544681	AY544739		DQ522854	DQ497606
1359	*Dothideomycetes*	*Dothideales*	CBS 737.71	*Dothiora cannabinae*	DQ479933	DQ470984	FJ190636	DQ471182	DQ470936	DQ471107
1300	*Dothideomycetes*	*Dothideales*	CBS 116.29	*Sydowia polyspora*	DQ678005	DQ678058	FJ190631		DQ677953	DQ677899
	Dothideomycetes	*Hysteriales*	CBS 114601	*Gloniopsis smilacis*	FJ161135	FJ161174			FJ161114	FJ161091
	Dothideomycetes	*Hysteriales*	EB 0324	*Hysterium angustatum*	FJ161167	FJ161207			FJ161129	FJ161111
	Dothideomycetes	*Hysteriales*	EB 0249	*Hysterographium mori*	FJ161155	FJ161196				FJ161104
1613	*Dothideomycetes*	Incertae sedis	CBS 283.51	*Helicomyces roseus*	DQ678032	DQ678083			DQ677981	DQ677928
1580	*Dothideomycetes*	Incertae sedis	CBS 245.49	*Tubeufia paludosa*	DQ767649	DQ767654			DQ767643	DQ767638
1853	*Dothideomycetes*	*Myriangiales*	CBS 150.27	*Elsinoë veneta*	DQ767651	DQ767658	FJ190650			DQ767641
1304	*Dothideomycetes*	*Myriangiales*	CBS 260.36	*Myriangium duriaei*	AY016347	DQ678059	AY571389		DQ677954	DQ677900
	Dothideomycetes	*Mytilinidiales*	EB 0248	*Lophium mytilinum*	FJ161163	FJ161203			FJ161128	FJ161110
	Dothideomycetes	*Mytilinidiales*	CBS 301.34	*Mytilinidion australe*		FJ161183				
	Dothideomycetes	*Mytilinidiales*	CBS 135.34	*Mytilinidion rhenanum*	FJ161136	FJ161175			FJ161115	FJ161092
267	*Dothideomycetes*	*Pleosporales*	DAOM 195275	*Allewia eureka*	DQ677994	DQ678044			DQ677938	DQ677883
1583	*Dothideomycetes*	*Pleosporales*	CBS 126.54	*Ascochyta pisi* var. *pisi*	DQ678018	DQ678070			DQ677967	DQ677913
54	*Dothideomycetes*	*Pleosporales*	CBS 134.39	*Cochliobolus heterostrophus*	AY544727	AY544645	AY544737		DQ247790	DQ497603
1599	*Dothideomycetes*	*Pleosporales*	CBS 225.62	*Delitschia winteri*	DQ678026	DQ678077	FJ190644		DQ677975	DQ677922
1576	*Dothideomycetes*	*Pleosporales*	CBS 101341	*Lepidosphaeria nicotiae*		DQ678067			DQ677963	DQ677910
277	*Dothideomycetes*	*Pleosporales*	DAOM 229267	*Leptosphaeria maculans*	DQ470993	DQ470946		DQ471136	DQ470894	DQ471062
1575	*Dothideomycetes*	*Pleosporales*	CBS 276.37	*Phoma herbarum*	DQ678014	DQ678066	FJ190640		DQ677962	DQ677909
1600	*Dothideomycetes*	*Pleosporales*	CBS 279.74	*Pleomassaria siparia*	DQ678027	DQ678078			DQ677976	DQ677923
940	*Dothideomycetes*	*Pleosporales*	CBS 541.72	*Pleospora herbarum* var. *herbarum*	DQ247812	DQ247804	FJ190610	DQ471163	DQ247794	DQ471090
283	*Dothideomycetes*	*Pleosporales*	DAOM 222769	*Pyrenophora phaeocomes*	DQ499595	DQ499596	FJ190591		DQ497614	DQ497607
1256	*Dothideomycetes*	*Pleosporales*	CBS 524.50	*Sporormiella minima*	DQ678003	DQ678056	FJ190624		DQ677950	DQ677897
1598	*Dothideomycetes*	*Pleosporales*	CBS 110020	*Ulospora bilgramii*	DQ678025	DQ678076			DQ677974	DQ677921
1601	*Dothideomycetes*	Pleosporales	CBS 304.66	*Verruculina enalia*	DQ678028	DQ678079			DQ677977	DQ677924
1037	*Dothideomycetes*	Pleosporales	CBS 454.72	*Westerdykella cylindrica*	AY016355	AY004343	AF346430	DQ471168	DQ470925	DQ497610
1063	*Eurotiomycetes*	*Chaetothyriales*	CBS 175.95	*Ceramothyrium carniolicum*	EF413627	EF413628		EF413629	EF413630	
1033	*Eurotiomycetes*	*Chaetothyriales*	CBS190.61	*Cyphellophora laciniata*	EF413618	EF413619				
671	*Eurotiomycetes*	*Chaetothyriales*	CBS 157.67	*Exophiala salmonis*	EF413608	EF413609	FJ225745	EF413610	EF413611	EF413612
1911	*Eurotiomycetes*	*Coryneliales*	CBS 138.64	*Caliciopsis orientalis*	DQ471039	DQ470987	FJ190654	DQ471185	DQ470939	DQ471111
5007	*Eurotiomycetes*	*Eurotiales*	CBS 658.74	*Aspergillus protuberus*	FJ176842	FJ176897			FJ238379	
2014	*Eurotiomycetes*	*Eurotiales*	CBS 339.97	*Eupenicillium limosum*	EF411061	EF411064			EF411068	EF411070

1083	*Eurotiomycetes*	*Onygenales*	GB	*Ajellomyces capsulatum*	Genome	Genome		Genome	Genome	Genome
1084	*Eurotiomycetes*	*Onygenales*	TIGR	*Coccidioides immitis*	Genome	Genome		Genome	Genome	Genome
684	*Eurotiomycetes*	*Verrucariales*	NYBG 808041	*Agonimia* sp.	DQ782885	DQ782913		DQ782853	DQ782874	DQ782917
697	*Eurotiomycetes*	*Verrucariales*	DUKE 0047959	*Staurothele frustulenta*	DQ823105	DQ823098	FJ225702	DQ840553	DQ840560	
	Geoglossomycetes	*Geoglossales*	OSC 60610	*Geoglossum glabrum*	AY789316	AY789317				
56	*Geoglossomycetes*	*Geoglossales*	OSC 100009	*Geoglossum nigritum*	AY544694	AY544650	AY544740	DQ471115	DQ470879	DQ471044
	Geoglossomycetes	*Geoglossales*	Mycorec1840	*Geoglossum umbratile*	AY789302	AY789321				
	Geoglossomycetes	*Geoglossales*	HMAS 71956	*Sarcoleotia globosa 1*	AY789298	AY789299				
	Geoglossomycetes	*Geoglossales*	OSC 63633	*Sarcoleotia globosa 2*		AY789409				
	Geoglossomycetes	*Geoglossales*	MBH 52476	*Sarcoleotia globosa 3*		AY789428				
64	*Geoglossomycetes*	*Geoglossales*	OSC 100017	*Trichoglossum hirsutum 1*	AY544697	AY544653	AY544758	DQ471119	DQ470881	DQ471049
	Geoglossomycetes	*Geoglossales*	OSC 61726	*Trichoglossum hirsutum 2*	AY789312	AY789313				
229	Incertae sedis	Incertae sedis	IAM 12963	*Saitoella complicata*	AY548297	AY548296		DQ471133	AY548300	DQ471133
	Laboulbeniomycetes	*Laboulbeniales*	GB	*Hesperomyces virescens*	AF298233	AF298235				
	Laboulbeniomycetes	*Laboulbeniales*	GB	*Stigmatomyces protrudens*	AF298232	AF298234				
2197	*Laboulbeniomycetes*	*Pyxidiophorales*	CBS 657.82	*Pyxidiophora avernensis*	FJ176839	FJ176894			FJ238377	FJ238412
962	*Lecanoromycetes*	*Agyriales*	GB	*Trapelia placodioides*	AF119500	AF274103	AF431962	DQ366259	DQ366260	DQ366258
589	*Lecanoromycetes*	Incertae sedis	DUKE 0047522	*Lecidea fuscoatra*	DQ912310	DQ912332	DQ912275	DQ912355	DQ912381	
6	*Lecanoromycetes*	*Lecanorales*	DUKE 0047740	*Canoparmelia caroliniana*	AY584658	AY584634	AY584613	DQ782817	AY584683	DQ782889
195	*Lecanoromycetes*	*Lecanorales*	DUKE 0047550	*Hypogymnia physodes*	DQ973006	DQ973030	DQ972978		DQ973091	
958	*Lecanoromycetes*	*Ostropales* s.l.	Lumbsch 995	*Diploschistes ocellatus*	AF038877	AY605077		DQ366252	DQ366253	DQ366251
1349	*Lecanoromycetes*	*Ostropales* s.l.	JK 5548K	*Glomerobolus gelineus*	DQ247811	DQ247803	DQ247784		DQ247793	
128	*Lecanoromycetes*	*Peltigerales*	DUKE 0047503	*Lobaria scrobiculata*	AY584679	AY584655	AY584621	DQ883736	DQ883749	DQ883768
314	*Lecanoromycetes*	*Peltigerales*	DUKE 0047520	*Lobariella pallida*	DQ883788	DQ883797	DQ912297	DQ883740	DQ883753	DQ883772
131	*Lecanoromycetes*	*Peltigerales*	DUKE 0047548	*Nephroma parile*	46411421	46411445	46411390	DQ973061	DQ973075	FJ772246
134	*Lecanoromycetes*	*Peltigerales*	DUKE 0047504	*Peltigera degenii*	AY584681	AY584657	AY584628	DQ782826	AY584688	DQ782897
333	*Lecanoromycetes*	*Peltigerales*	DUKE 0047747	*Coccocarpia erythroxyli*	DQ883791	DQ883800	DQ912294	DQ883743	DQ883756	DQ883775
875	*Lecanoromycetes*	*Pertusariales*	DUKE 0047641	*Icmadophila ericetorum*	DQ883704	DQ883694	DQ986897	DQ883723	DQ883711	DQ883730
224	*Lecanoromycetes*	*Pertusariales*	DUKE 0047506	*Pertusaria dactylina*	DQ782880	DQ782907	DQ972973	DQ782828	DQ782868	DQ782899
320	*Lecanoromycetes*	*Teloschistales*	DUKE 0047507	*Heterodermia vulgaris*	DQ883789	DQ883798	DQ912288	DQ883741	DQ883754	DQ883773
686	*Lecanoromycetes*	*Teloschistales*	DUKE 0047544	*Pyxine subcinerea*	DQ883793	DQ883802	DQ912292	DQ883745	DQ883758	DQ883777
87	*Lecanoromycetes*	*Teloschistales*	DUKE 0047925	*Teloschistes exilis*	AY584671	AY584647	FJ772245	DQ883779	DQ883759	DQ883764
59	*Leotiomycetes*	*Helotiales*	OSC 100012	*Botryotinia fuckeliana*	AY544695	AY544651	AY544732	DQ471116	DQ247786	DQ471045
	Leotiomycetes	*Helotiales*	MBH 52481	*Bryoglossum gracile*	AY789419	AY789420				
166	*Leotiomycetes*	*Helotiales*	OSC 100054	*Cudoniella* cf. *clavus*	DQ470992	DQ470944	FJ713604	DQ471128	DQ470888	DQ471056
941	*Leotiomycetes*	*Helotiales*	CBS 161.38	*Dermea acerina*	DQ247809	DQ247801	DQ976373	DQ471164	DQ247791	DQ471091
49	*Leotiomycetes*	*Helotiales*	OSC 100002	*Lachnum virgineum*	AY544688	AY544646	AY544745	DQ842030	DQ470877	DQ497602
1262	*Leotiomycetes*	*Helotiales*	CBS 811.85	*Lambertella subrenispora*	DQ471030	DQ470978		DQ471176	DQ470930	DQ471101
1	*Leotiomycetes*	*Helotiales*	OSC 100001	*Leotia lubrica*	AY544687	AY544644	AY544746	DQ471113	DQ470876	DQ471041
	Leotiomycetes	*Helotiales*	FH-DSH -97103	*Microglossum olivaceum*	AY789396	AY789397				
	Leotiomycetes	*Helotiales*	Ingo-Clark-Geo163	*Microglossum rufum 1*	DQ257358	DQ257359				
1292	*Leotiomycetes*	*Helotiales*	OSC 100641	*Microglossum rufum 2*	DQ471033	DQ470981		DQ471179	DQ470933	DQ471104
	Leotiomycetes	*Helotiales*	ZW02-012	*Mitrula brevispora*	AY789292	AY789293				
	Leotiomycetes	*Helotiales*	WZ-Geo47-Clark	*Mitrula elegans*	AY789334	AY789335				
169	*Leotiomycetes*	*Helotiales*	OSC 100063	*Monilinia laxa*	AY544714	AY544670	AY544748	FJ238425	DQ470889	DQ471057
1259	*Leotiomycetes*	*Helotiales*	CBS 477.97	*Neobulgaria pura*		FJ176865		FJ238434	FJ238350	FJ238397
149	*Leotiomycetes*	*Helotiales*	OSC 100036	*Neofabraea malicorticis*	AY544706	AY544662	AY544751	DQ471124	DQ470885	DQ847414
	Leotiomycetes	*Helotiales*	1100803	*Thueminidium atropurpureum 1*		AY789307				
	Leotiomycetes	*Helotiales*	1136126	*Thueminidium atropurpureum 2*		AY789305				
353	*Leotiomycetes*	*Rhytismatales*	DUKE 0047585	*Cudonia circinans*	AF107343	AY533013	AY584700		AY641033	
	Leotiomycetes	*Rhytismatales*	OSC 100640	*Spathularia velutipes 1*	FJ997860	FJ997861			FJ997863	FJ997862
	Leotiomycetes	*Rhytismatales*	ZW Geo58	*Spathularia velutipes 2*	AY789356	AY789357				
896	*Lichinomycetes*	*Lichinales*	Schultz16319a	*Lichinella iodopulchra*				DQ782857	DQ832328	DQ832327
892	*Lichinomycetes*	*Lichinales*	DUKE 0047648	*Peltula auriculata*	DQ832332	DQ832330		DQ782856	DQ832331	
891	*Lichinomycetes*	*Lichinales*	DUKE 0047527	*Peltula umbilicata*	DQ782887	DQ832334	DQ922954	DQ782855	DQ832335	DQ782919
1363	*Neolectomycetes*	*Neolectales*	DAH-3	*Neolecta irregularis*	DQ842040	DQ470986				DQ471109
1362	*Neolectomycetes*	*Neolectales*	DAH-11	*Neolecta vitellina*	DQ471037	DQ470985			AAF19058	

Table 1 (cont.)

AFTOL no.	Class	Order	Voucher[1]	Taxon	nSSU	nLSU	mSSU	*RPB1*	*RPB2*	*TEF1*
1252	*Orbiliomycetes*	*Orbiliales*	CBS 397.93	*Arthrobotrys elegans*	FJ176810	FJ176864			FJ238349	FJ238395
905	*Orbiliomycetes*	*Orbiliales*	CBS 917.72	*Orbilia vinosa*	DQ471000	DQ470952		DQ471145		DQ471071
65	*Pezizomycetes*	*Pezizales*	OSC 100018	*Aleuria aurantia*	AY544698	AY544654		DQ471120	DQ247785	DQ466085
70	*Pezizomycetes*	*Pezizales*	KH-00-08	*Ascobolus carbonarius*	AY544720	AY544677		FJ238423		
152	*Pezizomycetes*	*Pezizales*	OSC 100062	*Caloscypha fulgens*	DQ247807	DQ247799		DQ471126	DQ247787	DQ471054
933	*Pezizomycetes*	*Pezizales*	CBS 626.71	*Eleutherascus lectardii*	DQ471014	DQ470966	FJ190606	DQ471160	DQ470918	DQ471088
176	*Pezizomycetes*	*Pezizales*	OSC 100068	*Gyromitra californica*	AY544717	AY544673	AY544741	DQ471130	DQ470891	DQ471059
507	*Pezizomycetes*	*Pezizales*	TL-6398	*Peziza vesiculosa*	DQ470995	DQ470948		DQ471140	DQ470898	DQ471066
949	*Pezizomycetes*	*Pezizales*	CBS 666.88	*Pyronema domesticum*	DQ247813	DQ247805	FJ190613	DQ471166	DQ247795	DQ471093
1299	*Pezizomycetes*	*Pezizales*	CBS 472.80	*Saccobolus dilutellus*	FJ176814	FJ176870		FJ238436	FJ238353	FJ238402
954	*Pezizomycetes*	*Pezizales*	CBS 733.68	*Sarcosoma latahense*	FJ176806	FJ176860		FJ238424		FJ238392
153	*Pezizomycetes*	*Pezizales*	OSC 100049	*Sarcosphaera crassa*	AY544712	AY544668		FJ238430		
62	*Pezizomycetes*	*Pezizales*	OSC 100015	*Scutellinia scutellata*	DQ247814	DQ247806	FJ190587	DQ479935	DQ247796	DQ471047
74	*Pezizomycetes*	*Pezizales*	NRRL 22338	*Verpa conica*	AY544710	AY544666	AY544761			FJ238389
1073	*Saccharomycetes*	*Saccharomycetales*	GB	*Candida glabrata*	AY198398	AY198398		XM_447415	XM_448959	Genome
1269	*Saccharomycetes*	*Saccharomycetales*	GB	*Candida tropicalis*	M55527	Genome		Genome	Genome	Genome
1077	*Saccharomycetes*	*Saccharomycetales*	GB	*Debaryomyces hansenii*	DHA508273	AF485980		XM_456921	CR382139	Genome
1072	*Saccharomycetes*	*Saccharomycetales*	GB	*Eremothecium gossypii*	AE016820	AE016820	AF442353	NM_209535	AE016819	Genome
1069	*Saccharomycetes*	*Saccharomycetales*	GB	*Saccharomyces cerevisiae*	SCYLR154C	SCYLR154C	AF442281	X96876	SCYOR151C	Genome
1199	*Schizosaccharomycetes*	*Schizosaccharomycetales*	GB	*Schizosaccharomyces pombe*	X54866	Z19136	X54421	X56564	D13337	Genome
5086	*Sordariomycetes*	*Calosphaeriales*	CBS 115999	*Calosphaeria pulchella*	AY761071	AY761075				FJ238421
	Sordariomycetes	*Coronophorales*	SMH4320	*Bertia moriformis*		AY695260			AY780151	
2124	*Sordariomycetes*	*Diaporthales*	CBS 171.69	*Cryptosporella hypodermia*	DQ862049	DQ862028			DQ862018	DQ862034
935	*Sordariomycetes*	*Diaporthales*	CBS 109767	*Diaporthe eres*	DQ471015	AF408350	FJ190607	DQ471161	DQ470919	DQ479931
1223	*Sordariomycetes*	*Diaporthales*	CBS 112915	*Endothia gyrosa*	DQ471023	DQ470972		DQ471169	DQ470926	DQ471096
952	*Sordariomycetes*	*Diaporthales*	CBS 199.53	*Gnomonia gnomon*	DQ471019	AF408361	FJ190615	DQ471167	DQ470922	DQ471094
187	*Sordariomycetes*	*Hypocreales*	GJS 71-328	*Bionectria* cf. *aureofulva*	DQ862044	DQ862027	FJ713625		DQ862013	DQ862029
189	*Sordariomycetes*	*Hypocreales*	GAM 12885	*Claviceps purpurea*	AF543765	AF543789		AY489648	DQ522417	AF543778
162	*Sordariomycetes*	*Hypocreales*	OSC 93609	*Cordyceps cardinalis*	AY184973	AY184962	EF469007	DQ522370	DQ522422	DQ522325
192	*Sordariomycetes*	*Hypocreales*	OSC 71233	*Elaphocordyceps capitata*	AY489689	AY489721	FJ713628	AY489649	DQ522421	AY489615
193	*Sordariomycetes*	*Hypocreales*	OSC 106405	*Elaphocordyceps ophioglossoides*	AY489691	AY489723	FJ713629	AY489652	DQ522429	AY489618
163	*Sordariomycetes*	*Hypocreales*	ATCC 56429	*Epichloë typhina*	U32405	U17396	FJ713624		DQ522440	AF543777
156	*Sordariomycetes*	*Hypocreales*	ATCC 208838	*Hypocrea lutea*	AF543768	AF543791	FJ713620	AY489662	DQ522446	AF543781
159	*Sordariomycetes*	*Hypocreales*	CBS 114055	*Nectria cinnabarina*	U32412	U00748	FJ713622	AY489666	DQ522456	AF543785
1265	*Sordariomycetes*	Incertae sedis	FAU 553	*Glomerella cingulata*	AF543762	AF543786	FJ190626	AY489659	DQ522441	AF543773
237	*Sordariomycetes*	Incertae sedis	ATCC 16535	*Verticillium dahliae*	AY489705	DQ470945	FJ713630	AY489673	DQ522468	AY489632
413	*Sordariomycetes*	*Lulworthiales*	JK 5090A	*Lindra thalassiae*	DQ470994	DQ470947	FJ190593	DQ471139	DQ470897	DQ471065
747	*Sordariomycetes*	*Lulworthiales*	JK 4686	*Lulworthia grandispora*	DQ522855	DQ522856	FJ190595		DQ518181	DQ497608
734	*Sordariomycetes*	*Magnaporthales*	JK 5528S	*Gaeumannomyces medullaris*	FJ176801	FJ176854				
1081	*Sordariomycetes*	*Magnaporthales*	Broad	*Magnaporthe grisea*	AB026819	AB026819		Genome	Genome	Genome
	Sordariomycetes	*Melanosporales*	ATCC 15515	*Melanospora tiffanyae*	AY015619	AY015630			AY015637	
1906	*Sordariomycetes*	*Microascales*	TCH C89	*Ceratocystis fimbriata*	U32418	U17401			FJ238372	
5011	*Sordariomycetes*	*Microascales*	728a	*Corollospora maritima*	FJ176846	FJ176901	FJ190660		FJ238381	FJ238415
1907	*Sordariomycetes*	*Microascales*	CBS 122611	*Gondwanamyces capensis*	FJ176834	FJ176888			FJ238373	
409	*Sordariomycetes*	*Microascales*	CBS 197.60	*Halosphaeria appendiculata*	U46872	U46885				FJ238390
1038	*Sordariomycetes*	*Ophiostomatales*	CBS 139.51	*Ophiostoma stenoceras*	DQ836897	DQ836904	FJ190618		DQ836891	DQ836912
1078	*Sordariomycetes*	*Sordariales*	Broad	*Neurospora crassa*	X04971	AF286411		XM_959004	XM_324476	Genome
216	*Sordariomycetes*	*Sordariales*	CBSC 15-5973	*Sordaria fimicola*	AY545728	AY545724				DQ518175
51	*Sordariomycetes*	*Xylariales*	OSC 100004	*Xylaria hypoxylon*	AY544692	AY544648	AY544760	DQ471114	DQ470878	DQ471042
1234	*Taphrinomycetes*	*Taphrinales*	CBS 356.35	*Taphrina deformans*	DQ471024	DQ470973	FJ713610	DQ471170	DQ470927	DQ471097
265	*Taphrinomycetes*	*Taphrinales*	IAM 14515	*Taphrina wiesneri*	AY548293	AY548292	AY548291	DQ471134	AY548298	DQ471134

[1] voucher GB = obtained from GenBank, or genome databases without clear voucher numbers.

gal ecological niches (Geiser et al. 2006). *Lecanoromycetes* contain the majority of the lichenised fungi (Miadlikowska et al. 2006). Earlier large-scale phylogenies (e.g. Lutzoni et al. 2004) have suggested a sister relationship between these two classes, but we find that such a relationship remains without strong statistical support (Fig. 1). Despite this, internal nodes are well supported enough to provide good support for the hypothesis that lichenisation evolved multiple times in the *Ascomycota*, with losses being rare (Gueidan et al. 2008, Schoch et al. 2009).

The remaining classes are discussed in relation to their respective rankless taxa listed below.

Rankless taxon ‘Dothideomyceta’

This taxon is well supported, with ML bootstrap of 91 % and a moderate Bayesian posterior probability of 92 %. It includes two classes of fungi which produce fissitunicate asci, *Arthoniomycetes* and *Dothideomycetes*. *Arthoniomycetes* consists of ± 1 600 species of lichenised and lichenicolous fungi with fissitunicate asci and exposed hymenia (Grube 1998, Ertz et al. 2009). Unlike other species with fissitunicate asci, these taxa have ascohymenial development, prompting their placement in a transitory group, or ‘Zwischengruppe’ that is intermediate between ascohymenial and ascolocular development (Henssen & Jahns 1974). The class is resolved as sister to *Dothideomycetes*, consistent with recent studies (Lutzoni et al. 2004, Spatafora et al. 2006, Wang et al. 2006a). *Dothideomycetes* is a large class containing two subclasses, *Dothideomycetidae* and *Pleosporomycetidae* (Schoch et al. 2006). Our analysis contains members of all known orders in the class, including recent additions (Boehm et al. 2009). This broad representation yields increased resolution in the placement of an order previously labelled incertae sedis, *Botryosphaeriales* (Schoch et al. 2006). Placement of *Botryosphaeriales* within subclass *Pleosporomycetidae* is well supported, as is a close relationship with the unplaced family *Tubeufiaceae* (Fig. 2).

Rankless taxon ‘Sordariomyceta’

‘Sordariomyceta’ contains three classes, *Leotiomycetes*, *Laboulbeniomycetes* and *Sordariomycetes*. We find similar resolution for this clade as for the ‘Dothideomyceta’. These three classes are characterised by the production of unitunicate, poricidal asci, or derivatives of such asci (e.g., deliquescent asci). *Leotiomycetes* and *Sordariomycetes* include numerous fungi associated with plants as pathogens, endophytes and epiphytes. The sordariomycete phylogeny is comparatively well resolved with 15 orders and 3 subclasses named (Zhang et al. 2006, Kirk et al. 2008). In contrast, the leotiomycete classification still poorly matches its inferred phylogeny. A recent class-wide effort to assess morphological and ecological data in a phylogenetic context continued to find high levels of diversity unaccounted for in the current classification (Wang et al. 2009). In addition to the aforementioned two classes, Fig. 1 also supports the placement of the *Laboulbeniomycetes* reported in Schoch et al. (2009) as part of a monophyletic lineage. The relationship between the *Sordariomycetes* and *Laboulbeniomycetes* is also well supported but we will refrain from naming this node until sampling can be expanded for the *Laboulbeniomycetes*. The class *Laboulbeniomycetes* encompasses an enigmatic lineage of insect symbionts and mycoparasites that have long proved problematic with respect to placement in higher-level classification schemes. *Laboulbeniomycetes* comprises two orders, *Laboulbeniales* and *Pyxidiophorales*, that are united by an ascospore synapomorphy of a darkened holdfast region and by molecular data (Weir & Blackwell 2001, 2005). Members of *Pyxidiophorales* possess globose perithecia with a single layer of wall cells, and long perithecial necks that release their ascospores passively in droplets at the tips of their necks; this mechanism is repeatedly derived within *Ascomycota* for insect dispersal of ascospores (Blackwell 1994). For this reason, they have been likened to other insect-dispersed perithecial ascomycetes (e.g., *Ophiostomatales*) that now are strongly supported as members of *Sordariomycetes*. *Laboulbeniales* includes ectoparasites of insects and displays morphological traits not found elsewhere in the *Ascomycota*. They form apomorphic ascomata produced by the division and enlargement of ascospores that are difficult to characterize in existing ascomatal terms. *Laboulbeniales* feature an ostiole, however, which is consistent with perithecia produced by hyphal growth. Determinate growth of the ascospore with a series of predictable cell divisions produces a thallus of a finite number of cells that is characteristic at the genus and species level (Tavares 1979). The analyses presented here strongly support *Laboulbeniomycetes* as sister to *Sordariomycetes*. This placement corresponds with the terminology originally applied to this group (Thaxter 1896). It is interesting to note that while species of *Pyxidiophorales* are endowed with a diverse group of anamorphs, members of *Laboulbeniales* are mainly known to reproduce sexually.

Summary

In conclusion, we propose two monotypic formal taxa and describe continued support for four informal rankless taxa. Important improvements in the resolution of deep nodes within the *Ascomycota* may be attributed to multi-gene sequence data produced by AFTOL and other projects during the last 5 years. The accelerating accumulation of genome-scale sequence data will continue to challenge and improve existing phylogenetic hypotheses. However, in order to direct limited resources towards under-sampled areas in the fungal phylogeny, an accurate, up-to-date classification is required. By placing three earth tongue genera in a separate newly described class, we underscore and communicate the genetic diversity that is found in the fungi producing these very convergent morphologies.

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