A Phylogenetic Classification of the Inocybaceae

P. Brandon Matheny*

Abstract

Matheny *et al.* (2009) recently recognized seven major lineages composed of *Inocybe* and allies. Clade names were proposed for each lineage with a suggestion to recognize each informally at the generic rank within the family Inocybaceae. Here, additional taxonomic ramifications are discussed in contrast to other alternative classifications. Generic status for the seven major lineages of Inocybaceae is discussed, taking into consideration a global sample of taxa. A key to major clades and genera is provided.

Key Words: Agaricales, Crepidotaceae, homoplasy, monophyletic, nomenclature, phylogeny, polyphyletic

Introduction

Higher-level classification of fungi has undergone extensive revision recently, mainly in response to molecular phylogenetic research performed by the Assembling the Fungal Tree of Life (AFTOL) consortium (Hibbett *et al.* 2007). While this encompassing work presents a phylogenetic-based classification of fungal orders and above, including subclasses, classes, subphyla, phyla, and subkingdoms, no revisions were provided for families or lower-level taxa of fungi.

Many challenges exist to impart top-down comprehensive taxonomic revisions of fungal families, particularly of Agaricales, the largest order of mushroom-forming fungi. Some of these include rules of priority that govern names of families and lower-level taxa (tribes, genera, subgenera, sections, etc.) and lack of adequate taxon sampling in phylogenetic analyses, issues alluded to in Hibbett *et al.* (2007). An additional challenge is that investigators may elevate or create new taxonomic names without achieving some sort of consensus on the matter or may not rely upon explicit means of justifying their taxonomic decisions.

Unfortunately, not everyone operates under the principle that taxonomists need only recognize and name monophyletic groups or *clades*, taxa that include all the descendants of a common ancestor. Since 2001, when I first began publishing papers in systematics, I have operated under the principle

that only monophyletic groups should be named and recognized. I do this following rules outlined by the *International Code of Botanical Nomenclature* (ICBN), since my research primarily constitutes lower-level (family, genus, species) taxonomy. Rules for governing what groups to name following phylogenetic guidelines are fairly explicit (De Queiroz & Gauthier 1990, Hibbett & Donoghue 1998). While efforts against the principle of monophyly could be made, these arguments only hinder advancement of fungal systematics. Current tensions now exist whether to proceed with rank-free classifications (Cantino 2004, Jørgensen 2004), as implemented by the *PhyloCode*, or attempt to match phylogenies to limited Linnean hierarchical ranks.

The Inocybaceae is important because of its ectomycorrhizal ecology, toxicity, and large number of described species—500 per Kirk *et al.* (2008), 700 per Matheny *et al.* (2009). A significant number of *insufficiently* described species also exists in herbaria (as specimens) and on GenBank (as DNA sequences) (Horak 1979, Matheny & Bougher 2005, Ryberg *et al.* 2008, Ryberg *et al.* 2009, Singer 1986, Stuntz (n.d.), Stuntz 1965). In 2002 colleagues and I at the University of Washington (Matheny *et al.* 2002) presented the first molecular phylogeny of *Inocybe*. However, it was not until three years later with an increase in character and taxon sampling (Matheny 2005) that strong support developed in favor of a mildly surprising result: *Inocybe* was most closely related to the family Crepidotaceae and not to other ectomycorrhizal genera of Cortinariaceae, such as *Hebeloma* or *Cortinarius*, as predicted by Kühner (1980) and Singer (1986). This result

* Department of Ecology and Evolutionary Biology, Hesler 332, University of Tennessee, Knoxville, TN 37996 email: pmatheny@utk.edu

was reinforced by phylogenetic analysis of a dense DNA character supermatrix (six and three gene regions) for 274 and 175 species of Agaricales and outgroups (Matheny *et al.* 2006). An independent data matrix of two genes and analysis by Garnica and colleagues (Garnica *et al.* 2007) also suggests that *Inocybe* and the Crepidotaceae are each other's closest relatives, viz. sister groups.

A close relationship between *Inocybe* and Crepidotaceae was somewhat surprising because *Inocybe* is ectomycorrhizal, whereas the Crepidotaceae, recently itself revised by molecular phylogenetic analysis (Aime *et al.* 2005), is saprotrophic. Many species of Inocybaceae are also pharmacologically important because of their high concentration of muscarine (Brown *et al.* 1962, Stijve 1982, Malone & Brady 1987); species of Crepidotaceae do not contain the toxin (Benjamin 1995). The remainder of this paper will address decisions to promote *Inocybe* at a family rank and examine several alternative and recently proposed classifications.

Overview of Inocybe Classification

The genus *Inocybe* was originally conceived by Fries in 1821 as a "tribe" in the broad encompassing mushroom genus *Agaricus*. Today Fries's wide concept of *Agaricus* contains numerous families or clades, *i.e.*, monophyletic groups, of Agaricales (Moncalvo *et al.* 2000, 2002, Matheny *et al.* 2007a). In 1863 Fries elevated *Inocybe* to generic rank. This was done in response to observations by others that the basidiospores of some common species of *Inocybe* were unique by virtue of their nodulose, angular, or spinose state (Singer 1986), hereafter simply referred to as nodulose.

Later, Schroeter (1889) and Fayod (1889) simultaneously segregated nodulose-spored *Inocybe* from smooth-spored species and treated the former in the genus *Astrosporina* J. Schroet. or *Clypeus* (Britz.) Fayod, respectively. Because *Astrosporina* was published just before publication of *Clypeus* at the generic rank, the name *Clypeus* is superfluous as a genus name and is treated as a synonym of *Astrosporina* according to rules of the ICBN. In contrast to Schroeter and Fayod, most subsequent taxonomic agaricologists followed Fries and treated *Inocybe* as a single genus encompassing both smooth- and nodulose-spored taxa. There were at least two exceptions to this, however: (i) Earle (1909), who recognized four genera of *Ino-*

cybe (*Agmocybe*, *Astrosporina*, *Inocybe*, and *Inocibium*; and (ii) Horak (1967, 1979, 1980, 1981, 1987), who followed Schroeter (and essentially Fayod) in maintaining *Astrosporina* as a genus distinct from smooth-spored species of *Inocybe*.

Kühner (1980) argued against recognition of *Astrosporina* concluding that a subgeneric arrangement in *Inocybe* was best maintained if one stressed qualitative or discrete characters (e.g., the presence or absence of pleurocystidia) rather than quantitative or continuous characters (degree of uneven basidiospore wall topology). Kühner's argument was insightful from a biological point of view because intermediates between smooth- and nodulose-spored species could be found, e.g., *I. curvipes* and *I. lacera*, that questioned the hiatus between smooth- and nodulose-spored taxa. Thus, Kühner proposed subgenus *Inosperma* to encompass species of *Inocybe* lacking pleurocystidia (and having smooth spores) and circumscribed subgenus *Inocybe* to accommodate species with pleurocystidia (and having smooth or nodulose spores). No higher-level taxa were recognized that separated smooth- from nodulose-spored taxa. In effect, Kühner hypothesized that presence of pleurocystidia was a shared derived trait for species of subgenus *Inocybe*, a unique character state acquisition depicted in Figure 1A. In contrast, translation of Horak's classification of *Inocybe* into a phylogenetic hypothesis suggests that possession of nodulose spores is a diagnostic trait for *Astrosporina* (Fig. 1B). In a cladistic framework, shared derived traits, or *synapomorphies*, are evidence of monophyly. However, absence of a particular trait may be problematic, if its absence is considered the ancestral state (*symplesiomorphic*). Symplesiomorphic traits suggest paraphyletic groups: those that include descendants originally excluded from the group under question. Fish is a great example of a paraphyletic group because tetrapods are derived within the fish clade. Dicots and dinosaurs are two additional examples of paraphyletic groups because monocots are nested in dicots, and birds are derived from dinosaurs. Non-monophyletic groups, unfortunately, produce nomenclatural quandaries.

Cladistic analyses using morphological data (Kuyper 1986) provided important evidence that corroborates Kühner's hypothesis to some extent. Subgenus *Inocybe* was found to be monophyletic based on two shared derived features (Fig. 1C),

and taxa with nodulose spores were found to have evolved independently on multiple occasions, predictions implicitly made by Kühner. Kuyper's results also confirmed that subgenus *Inosperma*, as originally conceived by Kühner, is paraphyletic. Kuyper, however, found evidence for the monophyly of a group of species surrounding *I. terrigena*, which he named subgenus *Mallocybe*. This group was distinguished from others due to presence of two synapomorphies—necropigmented basidia and unique origin of cheilocystidia. Necrobasidia are easy to observe under the microscope as these collapse and be-
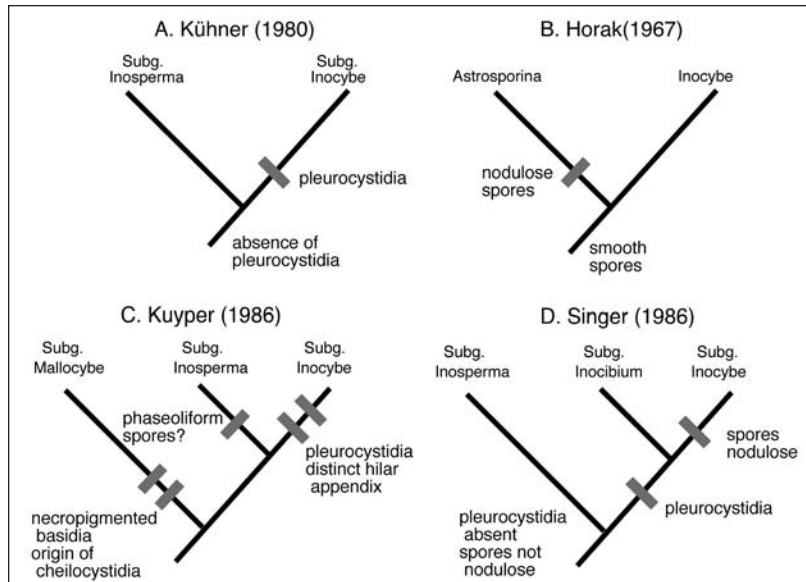

Fig. 1. A–D. Cladistic summaries of different family or genus level classifications of *Inocybe* and allies. Shared derived traits are indicated by thick gray bars. Share ancestral traits are included without gray bars. Bon's classification (1997) is the same as Singer's (1D) except for nomenclatural differences due to a disagreement over the generic type.

come ochraceous after spore release. Thus, Kühner's problem of a paraphyletic subgenus *Inosperma* was solved with removal and naming of the lineage containing *I. terrigena* and allies. Kuyper's analysis also suggested that subgenus *Inosperma s. str.* could be monophyletic or paraphyletic and that phaseoliform spores might be a shared derived state or shared ancestral state for the group, depending on the group's relationship to elliptic-spored species surrounding the *I. rimosa* complex.

Singer's classification (Singer 1986) is essentially a blend of Kühner's and Horak's classifications except nodulose-spored species are classified at a subgeneric rank (subg. *Inocybe*) rather than genus rank. Singer's nomenclatural decision (not taxonomic) was based on observations by Moser (1978) that the type of *Inocybe*, *I. relicina*, has nodulose spores in contrast to Heim's interpretation of this species in 1931. Horak (1967) had considered *I. geophylla* (smooth spores) as type of *Inocybe*. However, since Moser's publication there has been no debate about what constitutes the type of *Inocybe* with the exception of Bon (1997). Note that subgenus *Inocibium* (Fig. 1D) is recognized as a unique taxon in Singer's system, but no characters are pro-

vided that diagnose the group exclusively. Hence, one might predict that sugb. *Inocibium* (similar to Kühner's conception of subgenus *Inosperma*) is not monophyletic. Also note that Singer (1986) classified *Inocybe*, a single genus, as its own tribe, the Inocybeae, one of three tribes in his Cortinariaceae.

Lastly, we must consider that Jülich (1982) elevated tribe Inocybeae to the family rank, Inocybaceae. In it Jülich simply applied Horak's classification (Fig. 1B) that circumscribed two genera, *Astrosporina* and *Inocybe*. *Astrosporina* was distinguished by spore walls with an "exosporial ornamentation."

Molecular Phylogenetic Analyses of Inocybe

This brings us back to the beginning of our story. Molecular data support recognition of a clade, *Inocybe sensu lato*, which is sister to the Crepidotaceae *sensu stricto*. Other analyses (Moncalvo *et al.* 2000, 2002, Matheny *et al.* 2006, Garnica *et al.* 2007) indicate the *polyphyly*, or independent origin of multiple groups that do not share a most recent common ancestor, of the family Cortinariaceae, the family in which *Inocybe* was traditionally classified. Thus,

I suggested re-recognition of *Inocybe* at the family level (Matheny 2005), as was formally validated by Jülich (1982). This results in a sister group arrangement of equal ranks (the Inocybaceae and Crepidotaceae) and contributes to the dismemberment of the highly polyphyletic Cortinariaceae. Incidentally, the name Inocybaceae is a valid family name as long as *Inocybe* is withdrawn from the Cortinariaceae, against which the Cortinariaceae is conserved (Pouzar 1985).

A close relationship between the Crepidotaceae *sensu stricto* and Inocybaceae presents a novel sister group relationship in the Agaricales, an arrangement first suggested by Moncalvo *et al.* (2002) but without strong statistical support. The two families differ substantially in their mode of nutrition but also differ in mode of development, spore karyology, and pharmacology (Table 1). However, both families do bear several similarities: spore deposit colors (dull brown), challenges in cultivation, and general absence of asexual reproductive propagules (but see Clemençon 2000). Members of *Crepidotus* and *Simocybe* require a period of basidiospore dormancy before germination (Senn-Irlet 1994, Aime 1999, Aime & Miller 2002), but spores of Inocybaceae are notoriously difficult to germinate (Fries 1982). Species of *Simocybe* and some *Crepidotus* share spore shapes (phaseoliform) similar to species of non-pleurocystidiate clades of Inocybaceae. This could suggest that phaseoliform spores might be a shared ancestral state in the Inocybaceae and Crepidotaceae clade, a topic that has not been explored. Additional similarities in cheilocystidia morphology occur between *Simocybe* and *Auritella* (Matheny & Bougher 2006). Other characters for this inclusive group, whether anatomical, physiological, or biochemical, require exploration using molecular phylogenetic hypotheses.

So, based on present evidence, *Inocybe* and allies are not closely related to *Cortinarius* or *Hebeloma*, genera that share some fruit body anatomical similarities with the Inocybaceae (filamentous pileipellis, presence of clamps, pigmented spores). Kühner (1984) pointed to a similar biology (ectomycorrhizal status) between *Cortinarius*, *Hebeloma*, and *Inocybe* as evidence for shared ancestry. Kühner also suggested a close relationship between *Cortinarius* and *Inocybe* justified by presence of similar violet cytoplasmic pigmentation and an ochraceous spore wall. These superficial similarities, however, are called *homoplasies* (or homoplasy in the singular), characters that are in conflict with the inferred phylogeny.

Should Inocybe Be Divided into Multiple Genera?

Matheny *et al.* (2009) recently produced a multi-gene phylogenetic analysis that unveiled seven major clades in the family, a summary of which is shown as a chronogram in Figure 2. It is ultimately an arbitrary choice whether the seven clades of the Inocybaceae are recognized at an infrageneric or sectional level, which would be consistent with some systematic treatments of *Inocybe* (Heim 1931, Kühner & Romagnesi 1953, Kühner 1980, Kuyper 1986, Singer 1986), or at the generic level, which would be consistent with others (Fayod 1889, Karsten 1889, Schroeter 1889, Earle 1909, Horak 1967, Jülich 1982, Matheny 2005, Matheny *et al.* 2009). The major groups recognized are monophyletic, a principle by which taxa are named and recognized (Kuyper 1994, Vilgalys *et al.* 1994, Singer 1994, Hibbett & Donoghue 1998). Other authors, such as Watling (2001), suggested that subgenus *Mallocybe* might warrant a unique generic disposition based only on morphological data. Thus, recognition of different groups of *Inocybe* at generic ranks is hardly novel.

Ultimately, I favor generic recognition of the seven inocyboid clades identified in this study and in Matheny *et al.* (2009) for reasons enumerated below, but pause to make these changes until data from undescribed and poorly known species come to light:

(1) The Inocybaceae is an ancient lineage that diversified between 99 and 191 million years ago (Fig. 2; Matheny *et al.* 2009). Initial diversification of the family pre-dated the K-Pg (Cretaceous-Paleogene) boundary but a star-burst radiation probably occurred during the Paleogene. The Inocybaceae is likely older than other ectomycorrhizal genera of Agaricales such as *Hebeloma* and *Alnicola*, and is just as old, if not probably older, than other ectomycorrhizal families of Boletales, such as the Pinaceae-specific Suillaceae.

(2) Discrete morphological traits can be used to distinguish *Inocybe sensu stricto* from non-pleurocystidiate clades similar to arrangements of sister genera *Pleurotus* and *Hohenbuehelia* (Thorn *et al.* 2000), now the Pleurotaceae, and many polyporoid

Table 1. Ecological and morphological comparison between Crepidotaceae and Inocybaceae

Characters	Crepidotaceae	Inocybaceae
Nutritional mode	Saprotrophic	Ectomycorrhizal
Development	Gymnocarpic or veil scarcely developed	Variable, mostly mono-velangiocarpus and pileo-stipitocarpus, also stipitocarpous or bivelangiocarpus
Clamp connections	Present or absent	Present
Spore deposit	Pale yellow to brown	Brown (rarely white)
Pileipellis	Filamentous, at times gelatinous, or with distinct pileocystidia	Filamentous, few species with pseudoparenchymatous subpellis, usually without distinct pileo-cystidia
Cheilocystidia	Always present, uniform	Heteromorphic in most species—paracystidia mixed with thick-walled cystidia
Pleurocystidia	Mostly absent but rarely thick-walled or originating from lamellar trama	Present in most species, (sub)hymenial origin, probably modified basidia
Germ pore	Absent	Absent (rarely present)
Spore topology	Smooth or ornamented, never angular or reticulate	Smooth or angular, wall protruding to form nodules or spines, never ornamented
Spore karyology	Uni- or binucleate	Binucleate
Anamorphic states	Infrequent	None observed
Spore germination	Dormancy required	Fail to germinate on standard agar plates
Pharmacology	No major toxins identified	Muscarine, psilocybin, aeruginascen, unclarified alkaloids, or none

and resupinate genera (Jülich & Stalpers 1980, Gilbertson & Ryvarden 1986).

(3) Communication about fungal diversity would be facilitated and improved by reference to genera or major clades instead of infrageneric ranks that have been variously interpreted by many authors (Heim 1931, Kühner 1980, Kuyper 1986, Singer 1986, Bon 1997, Kobayashi 2002). Recognition of the seven major lineages as genera or clades would no longer be encumbered by multiple interpretations of infrageneric names.

(4) Few new combinations at the specific level are necessary if *Inocybe* were split into multiple genera because *Inocybe sensu stricto* contains the bulk (about 85%) of *Inocybe* species, as extrapolated from a reasonable well-sampled German mycoflora (Stangl 1989). Thus, the nomenclature for the overwhelming majority of species would not change, which would counter arguments in favor of nomenclatural stability.

(5) Though taxon sampling of *Inocybe* species has not been exhaustive, the system proposed here

contains the highest predictive value to date for the evolution of inocyboid taxa. Additional taxon sampling might uncover additional clades or help resolve and support their inter-relationships, but the names of the major clades will not change.

(6) A bias exists unnecessarily in favor of large agaric genera (Smith & Hesler 1968, Romagnesi 1977). One encompassing genus *Inocybe* undermines the phylogenetic diversity uncovered in the clade and its sister position to the Crepidotaceae. In short, a subgeneric classification would, in my opinion, fail to facilitate future studies that attempt to explore the evolution, biodiversity, ecology, and genomics of the group.

(7) *Inocybe s. lato* appears to be paraphyletic. However, the monophyly of *Inocybe* and a possible sister position to *Auritella* cannot be rejected using a statistical approach (Ryberg 2009).

Distinguishing Features of Each Major Clade of Inocybaceae

Auritella is distinguished by its geographic distribution (known only from the wet tropics of west Africa and temperate parts of Australia), typically tough fruit bodies, long cheilocystidia, necropigmented basidia, mostly elliptic, cylindrical, or globose smooth spores, lack of pleurocystidia, and non-rubescent context (Matheny & Bougher 2006). It is not known whether any of the known seven species contain muscarine. *Auritella* is a relict lineage that first split between African and Australian lineages about 70 million years ago. Plant associations for this genus probably include genera of Fabaceae and Myrtaceae.

The Mallocybella clade is known only by two species, one of which is undescribed and poorly characterized from Zambia (Villarreal *et al.* 1998, Matheny *et al.* 2009). This pair of species groups together on a consistent basis but is not significantly supported by statistical analyses. Nevertheless, its present geographic distribution includes the Mediterranean area of Europe (Spain and Corsica; see Moreau *et al.* 2007) and dry tropical Africa (Zambia). Salient features of the clade might include abundant caulocystidia and possibly small fruit body size. Both species associate with angiosperms—Cistaceae in the Mediterranean and Phyllanthaceae and/or Fabaceae in Africa. Both are characterized by necropigmented basidia and non-rubescent context.
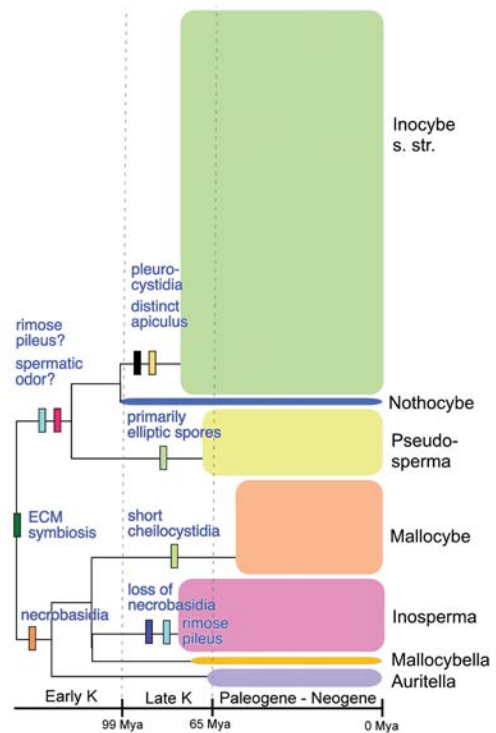

Fig. 2. Summary chronogram of the Inocybaceae. Seven major clades or lineages are designated. Topology and geological timeline are based on averaged branch lengths and dates produced by Matheny *et al.* (2009). Major character transitions (synapomorphies or symplesiomorphies) or potential diagnostic traits are suggested by bars. Clade size is roughly proportional to number of species estimated in a given clade. K = Cretaceous; Mya = millions of years ago.

The Mallocybe clade is presently composed of about 30 species, many undescribed from North America, southeast Asia, and tropical Africa. The group is similar to *Auritella* and the Mallocybella clade (necropigmented basidia, non-rubescent context), but differs in having short cheilocystidia (the only exception is *I. unicolor* Peck (=*I. caesariata sensu amer. auct.*), which possibly represents the earliest branch in the clade). Unlike *Auritella* and the Mallocybella clade, the Mallocybe clade has primarily radiated with conifers in the north temperate zone and has probably made recent switches to Salicaceae. The earliest diverging lineages associate with Myrtaceae in Australia and Fagales in eastern

North America. Kuyper (1986) suggests the chei-locystidia originate as terminal elements of the hyphae of hymenophoral trama, in contrast to aris-ing from modified basidia, as observed elsewhere in the family. This trait could represent a second synapomorphy for Mallocybe.

The Inosperma clade has been slowly reduced to a monophyletic group since first introduced by Kühner (1980). Kuyper (1986) first segregated taxa with necropigmented basidia (Mallocybe clade), but subg. *Inosperma* remained paraphyletic in some analyses. Molecular analyses confirm that most species in this clade bear phaseoliform spores for the most part and/or have rubescent context. Characters that identify the clade will not be entire-ly known until several dry tropical African species and wet tropical Asian species are studied in detail (see Matheny *et al.* 2009). A rimose pileus appears to be symplesiomorphic for the clade as species of section *Cervicolores*, which are derived within the group, bear a squamulose pileus. Section *Cervicolores* is also noteworthy for species that lack muscarine. Odors are often distinctive in the Inosperma clade and include notable smells described as truffle-like, aromatic, bruised *Geranium* leaves, fishy, moldy, or like honey. I anticipate at least 35 species will be assigned to this clade, many undescribed or poorly known from Papua New Guinea, southern India, Thailand, Malaysia, dry tropical Africa, and North America. Northern European species have been recently delimited by a combination of molecu-lar and morphological data (Larsson *et al.* 2009), results that will aid eventual clarification of taxa from North America and elsewhere.

The Nothocybe lineage is known from a single unclarified species possibly with affinities to *I. cutifracta* Petch (pers. com. Egon Horak) originally described from Sri Lanka (Petch 1917; see Pegler 1986 and Turnbull 1995 for their in-terpretations of *I. cutifracta*). The only collection sequenced originates from southern India and is a reported associate with *Casuarina*, which can form ectomycorrhizas (Wang & Qiu 2006). Some spores of the sequenced specimen actually exhibit a slight angular outline, a feature at odds with the protologue for *I. cutifracta*. According to Pegler (1986) the cheilocystidia are unique in being capi-tate (also mentioned in the protologue), similar to some species of *Auritella*. However, a type study by Horak (1980) depicts clavate shaped cheilocystidia.

Despite what appear to be different interpretations of *I. cutifracta*, the sequenced collection is ancient, long isolated, and a relict lineage known so far only from tropical India.

The Pseudosperma clade is diagnosed by spe-cies that have mostly elliptic or regular spores and typically a rimose pileus. ITS sequences of species sampled worldwide are extremely divergent and are challenging to tie to morphological descrip-tions (Matheny, unpublished). Many species are undescribed or poorly known from southeast Asia, the neotropics, Australia, and North America. At least 25 species occur in the Pseudosperma clade, but this will likely increase as more collections are sequenced, especially from under-explored geographic localities. Some species, e.g., *I. flavella* in Europe, are composed of multiple cryptic spe-cies (Ryberg *et al.* 2008). Spermatic odors may have first evolved in the common ancestor of the Pseu-dosperma, Nothocybe, and *Inocybe s. str.* clades, a potential name for which could be Inocybeae *s. str.* Larsson *et al.* (2009) prefer to label the Pseudo-sperma clade as section *Rimosae s. str.* in accordance with an infrageneric classification. This work will help to clarify species boundaries for taxa that oc-cur outside northern Europe.

Inocybe s. str. represents a massive radiation of several hundred species that are distributed pri-marily in temperate areas. However, many species are undescribed or poorly known from the neo-tropics, southern South America, New Zealand, Africa, and Australia. Two traits appear unique to the group: a distinct apiculus on the spores and presence of pleurocystidia. Species with nodulose spores probably evolved independently on numer-ous occasions. Hence, taxa such as *Astrosporina*, *Clypeus*, and subg. *Inocybe sensu* Singer, introduced earlier in the text, are not monophyletic. Devel-opmental traits such as absence of a cortina, stipe with a marginate bulb, and entirely pruinose stipe, are also homoplasious (Matheny *et al.* 2002, Kropp *et al.* 2009, Ryberg 2009). This is undoubtedly the most evolutionary 'successful' group of Inocyba-ceae as approximately 85% of the species in the family occur in *Inocybe s. str.*

Table 2. Comparison of classifications for Inocybaceae since 2006

Kirk *et al*. 2008	Knudsen & Vesterholt 2008	Matheny *et al*. 2006	Cannon & Kirk 2007
Inocybaceae =Crepidotaceae	Crepidotaceae =Inocybaceae	Crepidotaceae	Crepidotaceae[c]
Auritella	*Crepidotus*	*Crepidotus*	*Crepidotus*
Chromocyphella?	*Episphaeria*	*Pleuroflammula*	*Simocybe*
Crepidotus	*Inocybe*	*Simocybe*	
Episphaeria?	*Mythicomyces*[b]		
Flammulaster[a]	*Pellidiscus*	Inocybaceae	Inocybaceae[c]
Inocybe	*Pleuroflammula*	*Auritella*	*Auritella*
Simocybe	*Simocybe*	*Inocybe* s. str.	*Inocybe*
Pellidiscus	*Stagnicola*[b]	Inosperma clade	
Phaeomarasmius[a]		Mallocybe clade	
Phaeomyces		Mallocybella clade	
Phaeosolenia?		Nothocybe clade	
Pleuroflammula		Pseudosperma clade	
Tubaria[a]			

a. Genera classified in the Tubarieae (now Tubariaceae, see Vizzini 2008) in Matheny *et al*. (2006)

b. Genera positioned as the sister group to Psathyrellaceae (Moncalvo *et al*. 2002) or in the Psathyrellaceae (Matheny *et al*. 2006).

c. Only significant genera are indicated.

Alternative Family-level Classifications, or Why Not Classify Inocybe in the Crepidotaceae?

Table 2 presents a synopsis of classifications of the Inocybaceae and Crepidotaceae since 2006. Four different classifications have been proposed, and remarkably all four differ substantially. In Kirk *et al*. (2008) the two families Inocybaceae and Crepidotaceae are lumped together, but the younger name of the two (Inocybaceae) is given nomenclatural priority. However, Pouzar (1985) suggests the name Crepidotaceae has been a legitimate family name since 1951, when it was raised to family rank by Singer, and the name Inocybaceae has only existed since 1982. Kirk *et al*. (2008) indicate 13 genera belong to this inclusive family. However, *Flammulaster* (doubtfully monophyletic), *Phaeomarasmius* (doubtfully monophyletic), and

Tubaria (monophyletic when *T. minima* is excluded) (see Matheny *et al*. 2007b) do not form a monophyletic group together with the Inocybaceae and Crepidotaceae in Matheny *et al*. (2006) but do so with significant statistical support in Garnica *et al*. (2007). The publication by Cannon & Kirk (2007) treats the Crepidotaceae and Inocybaceae as separate families.

The new Nordic flora edited by Knudsen & Vesterholt (2008), like Kirk *et al*. (2008) lumps together the families Crepidotaceae and Inocybaceae, with the name Crepidotaceae having nomenclatural priority. Two genera, *Mythicomyces* and *Stagnicola*, are also classified in their Crepidotaceae *s. lat.*, but this is inconsistent with previous phylogenetic studies by Moncalvo *et al*. (2002) and Matheny *et al*. (2006), both of which suggest the placement of either one or both of these genera sister to the Psathyrellace-

ae. Both of these genera should be excluded from their Crepidotaceae. Ultimately, I favor recognition of the Inocybaceae due to several traits that diagnose the group (mycorrhizal status, presence of muscarine, general antiquity) from its sister group the Crepidotaceae *s. str.* (Aime *et al.* 2005).

Acknowledgments

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