*Mycologist, Volume **17**, Part 1 February 2003. ©Cambridge University Press Printed in the United Kingdom.*
DOI: 10.1017/S0269915X03001150

Mushrooms and taphonomy: the fungi that mark woodland graves

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Two closely related chemoecological groups of fungi, the ammonia fungi and the postputrefaction fungi, have been associated with the decomposition by-products of cadavers. Sporocarps have been observed in disparate woodlands across the world and often mark sites of graves. These groups of fungi provide visible markers of the sites of cadaver decomposition and follow repeated patterns of successional change as apparent decomposition proceeds. We suggest these phenomena may become a useful tool for crime scene investigation, forensic archaeology and forensic taphonomy.

Keywords: forensic taphonomy, ammonia fungi, postputrefaction fungi, cadaver decomposition, postburial interval, grave markers

The burial of human cadavers in natural and semi-natural ecosystems occasionally takes place in an attempt to conceal evidence of crime. The ability to locate these clandestine graves can be an important part of the investigative process and allows closure for relatives of victims. There have been worldwide reports of sporocarp production in the proximity of decomposing cadavers and these have been termed the postputrefaction fungi (PPF) (Sagara, 1995). A closely related (sympatric) group of fungi have been found fruiting where a range of nitrogenous compounds has been introduced to the soil and these have been termed the ammonia fungi (AF) (Sagara, 1975). In this paper we review briefly the physiology and ecology of these fungal groups. We consider the possibility that sporophores may be used as a means of locating graves and that their fruiting sequence may enable estimations of time since burial.

Physiological ecology

Field experiments from geographically disparate regions have led to the recognition of ammonia fungi (Akira *et al.*, 1998; Bougher & Tommerup, 1999; Fukiharu & Hongo, 1995; Sagara, 1973; 1975; 1992; 1995). Fruiting has been induced on forest floors experimentally treated with urea, ammonia or other nitrogenous compounds that release ammonia upon decomposition (Sagara, 1975). Laboratory studies suggest that ammonia is a key substance required for the fruiting of these fungi (Morimoto *et al.*, 1981; 1982; Suzuki, 1978; Suzuki *et al.*, 1982). However, other forms of nitrogen, such as nitrate, amino acid and peptide, may also play a role in their fruiting. AF have only been reported in forest ecosystems and many are ectomycorrhizal. About 40 species have been recognised (Table 1).

When AF have become established in close proximity to decomposing or decomposed animal remains they may be termed postputrefaction fungi (Sagara, 1992; 1995). PPF have been reported in association with decomposed mammalian cadavers (Fukiharu *et al.*, 2000a; Hilton, 1978; Kuroyanagi et al., 1982; Miller & Hilton, 1986; Sagara, 1973; 1975; 1976; 1981; 1995; Takayama & Sagara, 1981), an avian cadaver (Fukiharu *et al.*, 2000b), mammalian excrement (Richardson & Watling, 1968; Sagara, 1973; 1975; 1978; 1980; 1989; Sagara *et al.*, 1981; 1993a; 1993b) and wasp nests (Sagara *et al.*, 1985). 25 species have been recognised (Table 1).

All PPF reported thus far have been found in woodlands. Sites of fruiting include Japan (Fukiharu *et al.*, 2000a; 2000b; Kuroyanagi *et al.*, 1982; Sagara, 1976; 1978; 1981; 1995; Sagara *et al.*, 1981; 1985; 1993a; 1993b), Australia (Hilton, 1978; Miller & Hilton, 1986), England (Sagara, 1989), Switzerland (Sagara *et al.*, 1988) and North America (Lincoff, 1981).

Table 1. Taxa described as either ammonia fungi (AF) or postputrefaction fungi (PPF).

Fungal species	AF	PPF	Reference
ZYGOMYCETES			
Rhopalomyces strangulatus	-	+	Sagara (1973, 1975, 1995)
DEUTEROMYCETES			
Amblyosporium botrytis	+	+	Sagara (1973, 1975, 1992, 1995)
Cladorrhinum foecundissimum	+	+	Sagara (1973, 1975, 1992)
Doratomyces purpureofuscus	+	+	Sagara (1975)
Doratomyces putredinis	+	+	Sagara (1975)
Penicillium lividum	+	-	Sagara (1973, 1975)
ASCOMYCETES			
Ascobolus denudatus	+	+	Sagara (1973, 1975, 1992, 1995)
A. hansenii	+	+	Sagara (1973, 1975, 1992, 1995)
Byssonectria aggregata	+	-	Sagara (1973, 1975, 1995)
Humaria velenovskyi	+	+	Sagara (1973, 1975, 1992, 1995)
Iodophanus carneus	+	-	Sagara (1975)
Peziza (?) sp.[1]	+	+	Sagara (1973, 1975, 1992, 1995)
P. morovecii[2]	+	+	Sagara (1973, 1975, 1992, 1995)
Pseudombrophila deerata[3]	+	-	Sagara (1973, 1975, 1992)
Scutellinia scutellate	+	-	Sagara (1975)
BASIDIOMYCETES			
Coprinus echinosporus[4]	+	-	Sagara (1973, 1975, 1992)
C. neolagopus	+	+	Sagara (1973, 1975, 1992, 1995)
C. phlyctidosporus	+	+	Sagara (1973, 1975, 1992, 1995)
Hebeloma aminophilum	+	+	Hilton (1978); Miller & Hilton (1986)
H. luchuense	+	-	Fukiharu & Hongo (1995)
H. radicosoides[5]	+	+	Kuroyamagi *et al.* (1982); Sagara (1973, 1975,1989, 1992, 1995, 1993b); Sagara & Takayama (1982); Sagara *et al.* (1985, 2000)
H. radicosum	-	+	Sagara (1992, 1995)
H. spoliatum	+	+	Fukiharu *et al.* (2000a); Sagara (1973, 1975,1992, 1995); Sagara *et al.* (1985)
H. vinosophyllum	+	+	Fukiharu *et al.* (2000a); Sagara (1973, 1975, 1992, 1995); Takayama a& Sagara (1981)
Laccaria bicolor[6]	+	+	Sagara (1973, 1975, 1981, 1992, 1995)
L. amethystina	+	+	Sagara (1995)
Laccaria sp.	+	+	Sagara (1995)
Lactarius chrysorrheus	+	+	Sagara (1973, 1975, 1992, 1995)
Lepista nuda	+	+	Sagara (1995)
Panaeolina sagarae	+	-	Sagara (1973, 1975, 1992, 1995)
Rhizopogon succosus[7]	+	-	Sagara (1973, 1975, 1992)
Suillus luteus	+	+	Sagara (1995)
S. bovinus	+	+	Sagara (1995)
Tephrocybe ambusta[8]	+	-	Sagara (1973, 1975, 1992)
T. tesquorum[9]	+	+	Sagara (1973, 1975, 1992, 1995)

[1] *Gelatinodiscus* sp. in Sagara (1973)
[2] *Peziza* sp. no. 1 in Sagara (1973, 1975)
[3] *Fimaria* sp. in Sagara (1973, 1975)
[4] *Coprinus insignis* in Sagara (1973)
[5] *Hebeloma radicosum* in Kuroyamagi *et al.* (1982); Sagara (1973, 1975, 1989); Sagara & Takayama (1982); Sagara *et al.* (1985).
[6] *Laccaria proxima* in Sagara (1973, 1975, 1981)
[7] *Rhizopogon rubescens* in Sagara (1973, 1975)
[8] *Lyophyllum gibberosum* in Sagara (1973, 1975)
[9] *Lyophyllum tylicolor* in Sagara (1973, 1995)

Fruiting succession

Fruiting of different AF taxa has been divided into early and late stages based on time after chemical treatment of the forest floor (fertilisation) with nitrogenous compounds (Sagara, 1975). Early stage fungi comprise deuteromycetes, ascomycetes and saprotrophic basidiomycetes (Table 2). These have been observed to fruit from one to ten months after fertilisation (Fukiharu & Hongo, 1995; Sagara, 1992). Late stage

Table 2. Fruiting stage, trigger material, habitat and location of recorded postputrefaction fungi.

Fungal species	Trigger Material	Dominant Vegetation	Location	Reference
		Early Fruiting Stage		
Rhopalomyces strangulatus	cadaver	not stated	not stated	Sagara (1975, 1995)
Amblyosporium botrytis	midden	not stated	not stated	Sagara (1995)
Ascobolus denudatus	cadaver, urine, faeces	*Pinus densiflora*	Kyoto, Japan	Sagara (1975, 1995)
Ascobolus hansenii	cadaver, faeces	*Pinus-Chamaecyparis*	Kyoto, Japan	Sagara (1995)
Tephrocybe tesquorum	cadaver, urine, faeces	*Pinus densiflora*	Kyoto, Japan	Sagara (1995)
Peziza (?) sp.	cadaver, urine, faeces	*Pinus-Chamaecyparis*	Kyoto, Japan	Sagara (1975, 1995)
Peziza morovecii	cadaver, urine, faeces	not stated	not stated	Sagara (1975, 1995)
Coprinus neolagopus	cadaver	not stated	not stated	Sagara (1995)
Coprinus phlyctidosporus	cadaver	not stated	not stated	Sagara (1995)
Coprinus stercorarius	faeces	*Pinus-Quercus*	Kyoto, Japan	Sagara (1995)
Crucispora rhombisperma	excrement	not stated	not stated	Sagara (1995)
Humaria velenovskyi	excrement	*Pinus-Chamaecyparis*	Kyoto, Japan	Sagara (1975)
		Late Fruiting Stage		
Hebeloma vinosophyllum	cadaver	*Castanopsis cuspidata*	Kyoto, Japan	Sagara (1976)
	cadaver	*Pinus densiflora*	Kyoto, Japan	Sagara (1976)
	cadaver	*Quercus serrata*	Saitama, Japan	Fukiharu *et al.* (2000b)
	avian cadaver	*Quercus serrata*	Tokyo, Japan	Fukiharu *et al.* (2000a)
Hebeloma aminophilum	cadaver	*Eucalyptus* spp.	Western Australia	Hilton (1978); Miller & Hilton (1986)
Hebeloma spoliatum	mammalian cadaver	*Pinus densiflora*	Kyoto, Japan	Sagara (1995)
	wasp nest	*Castanopsis cuspidata*	Kyoto, Japan	Sagara *et al.* (1985)
	mole midden	*Quercus serrata*	Kyoto, Japan	Sagara (1978, 1980)
	mole midden	*Pinus densiflora-Quercus serrata*	Aichi, Japan	Sagara (1981)
	mammalian cadaver	*Quercus serrata*	Tokyo, Japan	Fukiharu *et al.* (2000a)
Hebeloma radicosoides	wasp nest	*Castanopsis cuspidata*	Kyoto, Japan	Sagara *et al.* (1985)
	mole midden	*Quercus serrata*	Kyoto, Japan	Sagara (1978, 1980)
	mole midden	*Pinus-Quercus*	Aichi, Japan	Sagara (1981)
	mole midden	*Pinus densiflora*	New Forest, England	Sagara *et al.* (1989)
	mouse midden	N/A	Switzerland	Sagara *et al.* (1988)
	mammalian cadaver	*Pinus densiflora*	Aichi, Japan	Kuroyanagi *et al.* (1982)
Hebeloma radicosum	mole midden	*Fagus* sp.-*Quercus* sp.	Kyoto, Japan	Sagara *et al.* (1993b)
	mole midden	*Quercus* sp.-*Carpinus* sp.	Kyoto, Japan	Sagara *et al.* (1993b)
Hebeloma syrjense	cadaver	N/A	North America	Lincoff (1981)
Lactarius chrysorrheus	mammalian cadaver	*Pinus densiflora*	Kyoto, Japan	Sagara (1995)
	urine, faeces, midden	not stated	not stated	Sagara (1995)
Laccaria bicolor	mammalian cadaver	*Pinus densiflora*	Kyoto, Japan	Sagara (1981)
	excrement, midden	not stated	not stated	Sagara (1995)
Laccaria amethystina	cadaver	not stated	not stated	Sagara (1995)
Laccaria spp.	cadaver, midden	not stated	not stated	Sagara (1995)
Lepista nuda	excrement	not stated	not stated	Sagara (1995)
Suillus luteus	raccoon midden	not stated	not stated	Sagara (1995)
Suillus bovinus	raccoon midden	not stated	not stated	Sagara (1995)
Mitrula sp.	faeces, cadaver	not stated	not stated	Sagara (1995)

fungi comprise ectomycorrhizal basidiomycetes that can fruit from one to four years after fertilisation (Table 2) (Fukiharu & Hongo, 1995; Sagara, 1992). Most early stage fungi fruit on soil containing high concentrations of ammonia and do not apparently utilise nitrate (Yamanaka, 1995a; 1995b). Late stage fungi fruit in response to organic nitrogen and high concentrations of ammonium and nitrate (Yamanaka, 1995a; 1995b). This suggests that nitrogen utilisation is related to the type of nitrogen, which may be useful as nitrogen form is related to the decomposition stage of nitrogenous substrates in soil. For example, protein nitrogen is broken down into amino nitrogen, which in turn will release ammonia that may then be nitrified into nitrate. The nitrate accumulation that might be expected at the end of these processes may favour some taxa (late stage fungi) while proteins and amino acids may favour the selection of other taxa (early stage fungi). Preferential utilisation of different nitrogen forms may, in part, explain the shift from early to late stage fruiting fungi. Thus, this sequence of fruiting may be similar to the succession of ectomycorrhizal fungi during forest development (e.g. Visser, 1995) and could possibly represent a metabiotic relationship ‘in which one organism must modify the environment before the second is able to live in it' (Waid, 1997).

Nutrient utilisation

Two species of PPF, *Rhopalomyces strangulatus* and *Hebeloma radicosum*, do not fruit following chemical fertilisation and hence are not recognised as AF (Sagara, 1995). From this we might hypothesise that these species are similar to 'protein fungi' (Abuzinadah and Read, 1986) in that they utilise nitrogen directly from proteins and/or amino acids (Abuzinadah & Read, 1988; Tibbett *et al*., 1998; Tibbett *et al*., 1999). *Rhopalomyces strangulatus* and *H. radicosum* may have an active role in the decomposition process as opposed to solely utilising decomposition by-products as sources of nitrogen.

Some ectomycorrhizal fungi (strains of *Hebeloma* spp.) display a clear preference for organic nitrogen (glutamic acid) over mineral nitrogen (ammonium) (Tibbett *et al*., 1998; 2000) and are capable of the decomposition and nutrient utilisation of seeds in axenic culture and in symbiosis (Tibbett *et al*., 1998; Tibbett & Sanders, 2002). Of the *Hebeloma* spp. tested, strains from colder regions showed a greater bias toward organic nitrogen than strains from more temperate climes. This may be of importance in colder regions where decomposition and mineralisation can be inhibited by temperature (Swift *et al*., 1979) and direct utilisation of organic nitrogen may be the preferred ecological strategy (Tibbett *et al*., 1998; 1999). This in turn may cause a shift in successional patterns among otherwise synonymous taxa.

To date, all cadavers associated with PPF comprise little more than bones and possibly hair (Fukiharu *et al*., 2000a; 2000b; Hilton, 1978; Kuroyanagi *et al*., 1982; Miller & Hilton, 1986; Sagara, 1976; 1981) although Sagara (1981) notes the presence of adipocere (hydrolysed fat) in association with PPF. Other than this, little is known about the temporal relationship between cadaver decomposition and fungal fruiting.

Potential applications in forensic science

Fungal species have been regarded by forensic science as an 'agent' of decomposition (Killam, 1990) possibly restricted to growth on the surface of a cadaver (Evans, 1963; Janaway, 1996). The work reviewed above suggests that PPF can be highly visible markers of soil disturbance and cadaver decomposition in wooded areas. The use of PPF for estimations of time since burial would be based upon early and late fruiting species. Current experimental evidence suggests that early and late stage AF can be generally viewed as occurring within the first year and two to four years after fertilisation, respectively (Fukiharu & Hongo, 1995; Sagara, 1992). However, how this relates to cadaver decomposition by PPF is unknown and may only be inferred by field observations and comparisons with AF fertilisation experiments. The stage of cadaver decomposition responsible for producing sufficient nutrients (simple organic nitrogen, ammonium, nitrate) for specific fungal fruiting stages needs to be determined if the full forensic potential of the PPF is to be exploited. Experimental conditions such as temperature must be taken into account as these can affect the rate of tissue decomposition (Carter and Tibbett, 2001) and nitrogen mineralisation (Swift *et al*., 1979) in soils. A greater understanding of grave soil characteristics may facilitate the use of PPF as a tool in forensic taphonomy for the location of graves and estimating the time since burial.

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