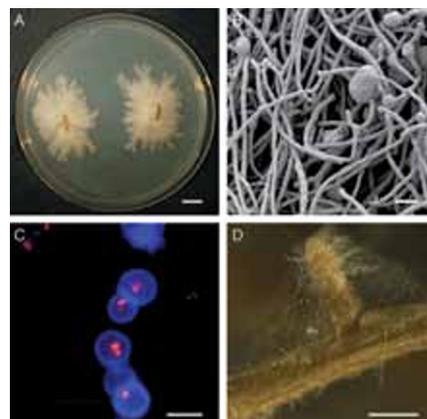


Archaeorhizomycetes: a new class for a major clade of soil fungi

The pioneering molecular study on Alaskan soils by Schadt *et al.* (2003) was a huge surprise to mycologists in claiming that there were even major fungal lineages in soils that did not correspond to known fungal groups. Subsequent work by many researchers has shown just how right their seemingly brash claims were. Two major clades of unnamed soil ascomycetes repeatedly emerge, that have come to be termed Soil Clone Groups 1 and 2. Group 1 is the most ubiquitous, especially in boreal and tundra soils, and data from 52 studies with 162 environmental sequences have been analyzed by Rosling *et al.* (2011). In addition, the authors obtained cultures of one species from soil in Sweden, and studied its behaviour on *Pinus* roots in the laboratory. It forms pale colonies and occurs

on root surfaces, often mixed with other fungi, but is not mycorrhizal. No sexual spores or undeniable conidia were found, but chlamyospore-like structures were noted. The fungus seems to have seasonal tendencies which the authors suggest may be indicative of a saprobic habit in which it depends on carbon compounds released by roots in the summer.

The new genus *Archaeorhizomyces* is introduced for *A. finlayi* and another unnamed species. The new class *Archaeorhizomycetes*, order *Archaeorhizomycetales*, and family *Archaeorhizomycetaeae* are introduced to accommodate these. The class is diagnosable by rRNA sequences, and is clearly extremely ancient as it belongs to the subphylum *Taphrinomycotina*, which includes *Neolecta*,



Archaeorhizomyces finlayi. Culture (A), SEM micrograph (B), chlamyospore-like structures (C), and growth on a *Pinus* root (D). Photos courtesy Anna Rosling.

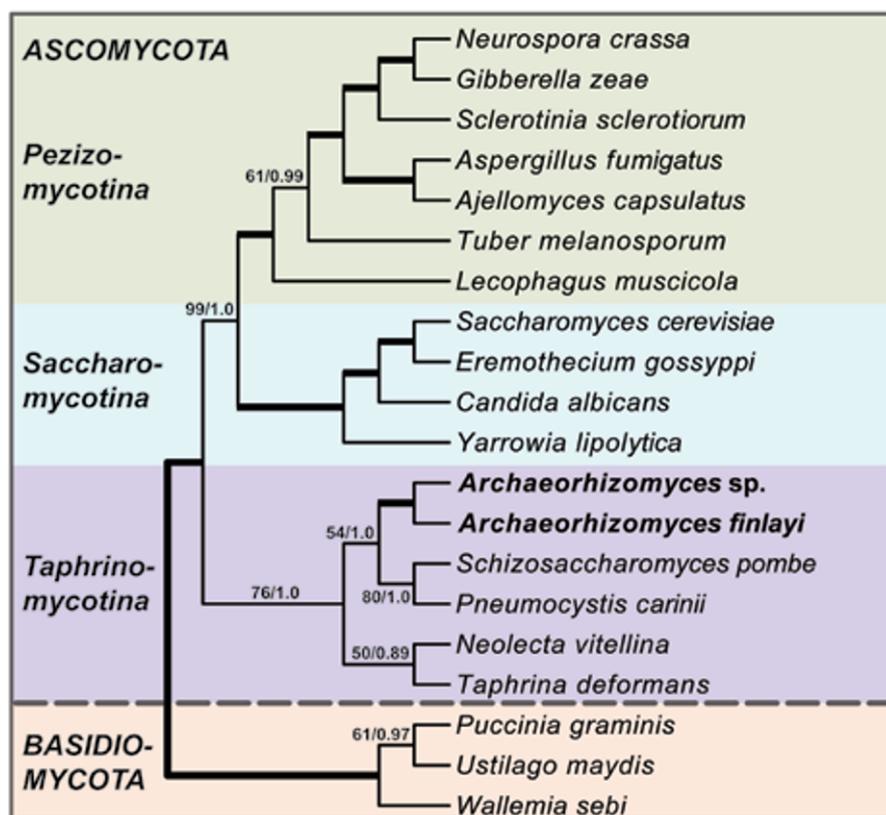
Pneumocystis and *Schizosaccharomyces*. It is notable that the new genus is filamentous as previously *Neolecta* seemed somewhat anomalous in the subphylum.

The choice of class name is perhaps somewhat unfortunate, however, in view of the class name *Archiascomycetes* Nishida & Sugiyama 1994. Although that name was not validly published, it has also been used by other authors and is essentially a synonym of *Taphrinomycotina* in circumscription.

It is to be anticipated that the numerous other taxa that appear in the class will eventually be named as they are obtained in culture or when procedures for naming taxa only known environmental sequences have been agreed. And Soil Clone Group 2 yet has to receive formal recognition.

Rosling A, Cox F, Cruz-Martinez K, Ihrmark K, Grelet G-A, Lindahl BD, Menkis A, James TY (2011) *Archaeorhizomycetes*: unearthing an ancient class of ubiquitous soil fungi. *Science* 333: 876–879.

Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301: 1359–1361.



Consensus phylogeny showing the position of *Archaeorhizomyces* species in the phylum *Ascomycota*. Modified from Rosling *et al.* (2011).

Inter-specific sex in grass smuts

Mating is of key importance to grass smut fungi (*Ustilaginaceae*) as it initiates parasitism by switching from a yeast phase

to a filamentous one with hyphae able to invade the plant tissues. The sexual identity is due to particular genomic alleles that

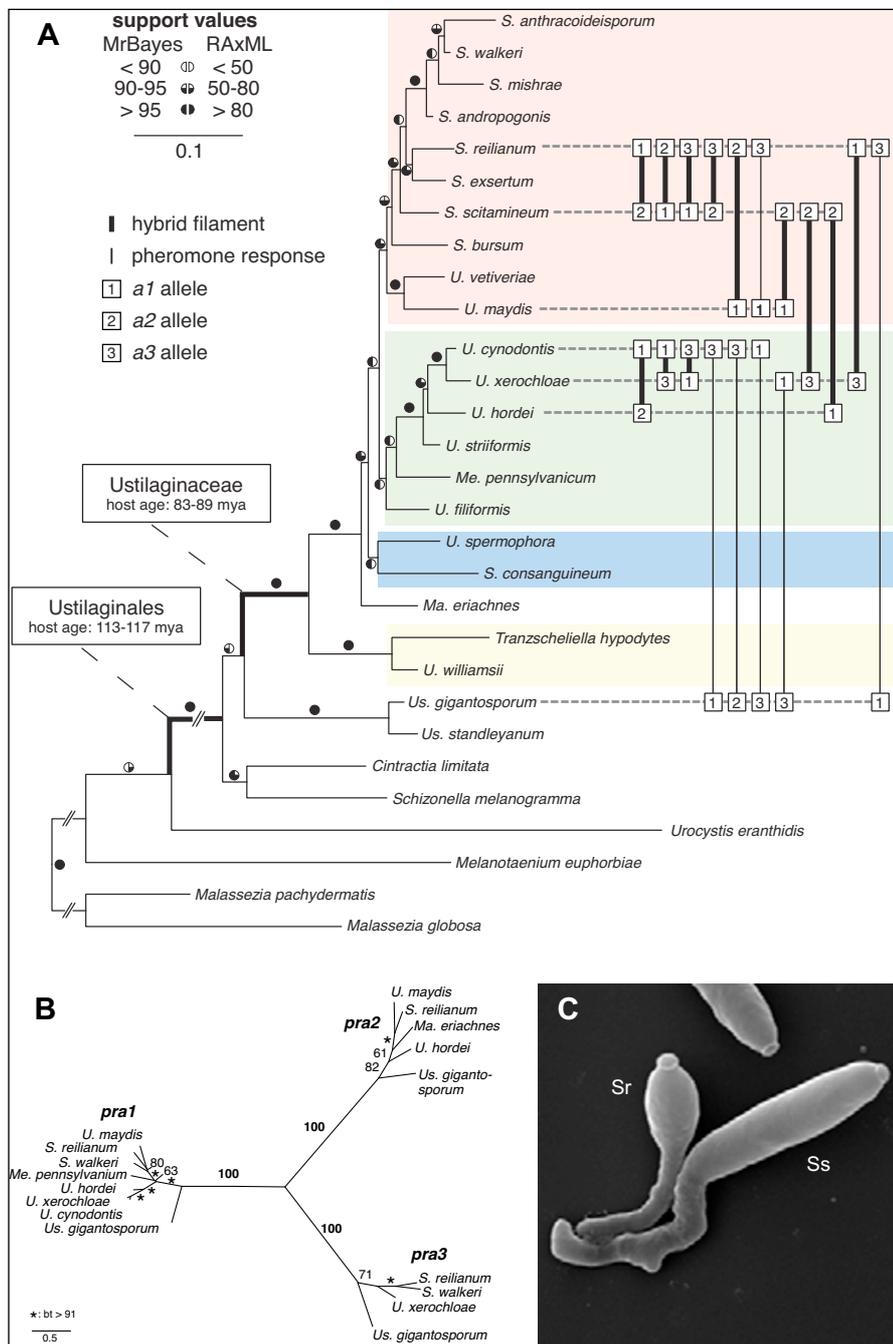
code for variants of a pheromone-receptor (PR) system and the transcription factors, operating in a bisphasic mating process;

this involves recognition, directed hyphal growth leading to conjugation, and then plasmogamy of compatible mating partners. In order to investigate this complex and fascinating system, last December Kellner *et*

al. (2011) reported on elegant investigations designed to illuminate our understanding of the evolution of the PR system. Ten species spanning 100 Myr of evolution of the system were selected for genomic and biological

study. In addition to detailed comparative information on the alleles, they performed interspecific sex tests which revealed a high potential for hybridization between species linked to pheromone signalling. While the system is optimized for within-species sex, it reveals that there are possibilities for hybrid generation which could lead to smuts with new host specificities. This possibility was confirmed by the demonstration of actual fusions between not only species of the same genus, but ones in different genera, as illustrated in the accompanying figure. The authors comment that the system now revealed may serve as a valuable model for the study of the hybrid-based genesis of novel genotypes.

Kellner R, Vollmeister E, Feldbrügge M, Begerow D (2011) Interspecific sex in grass smuts and the genetic diversity of their pheromone-receptor system. *PLoS Genetics* 7: e1002436.



Interspecific sex in grass smuts (modified from Kellner *et al.* 2011). A, Multi-gene phylogeny and interspecific sexual compatibility of *Ustilaginales*. Concatenated Maximum Likelihood (ML) analysis of 2571 bp of *ssu*, *ITS*, *ITS* rDNA, *ef1-a* and *rpb1*. Circles next to branches indicate bootstrap support values and *a posteriori* probabilities of Bayesian and ML analyses, respectively. Branch lengths correspond to substitutions per site and abbreviated branches indicate longer branches. Connected squares illustrate hybrid filament formation (bold lines) or pheromone response (thin lines). Numbers in squares represent respective a mating types. Coloured boxes depict different phylogenetic clades (see text). Host ages refer to Prasad *et al.* (*Science* 310:1177–1180, 2005). B, Phylogeny of mating type-specific pheromone receptors. Maximum Likelihood analysis of complete pheromone receptor-coding sequences. Numbers and asterisks next to branches indicate bootstrap (bt) support values and branch lengths correspond to substitutions per site. C, Interspecific mating of haploid sporidia of *Sporisorium reilianum* (Sr) and *S. scitamineum* (Ss); SEM micrograph.

Prions and phenotypic inheritance in wild yeasts

It has previously been recognized that self-perpetuating changes in protein structure can be heritable elements in yeasts separate from and preceding genetic change (True & Lindquist 2000); such self-perpetuating epigenetic structures are termed prions. Halfmann *et al.* (2012) investigated the yeast translation-termination factor prion

Sup35 that is not essential to the function of the protein and can adopt an amyloid configuration which self-perpetuates and leads to increased stops in codon read-through; that leads to a variety of new traits. The prions had been considered an artefact of strains kept in culture, but these authors examined occurrences and screened for new

prions in around 700 wild *Saccharomyces* strains. Prions proved to occur in about one third of the wild strains examined. Modifications of the Sip35 prion were demonstrated to confer characters likely to be beneficial to the yeasts under selective pressures, that is to develop beneficial phenotypes. Indeed, 40 % of the prions in

the wild yeasts were beneficial to growth under 12 sets of conditions tested. In yeasts, it has consequently now been established that prions are a naturally present supplementary source of inheritable material of adaptive value. The extent of prions in filamentous fungi as a whole has yet to be assessed, but they clearly have the potential to contribute to adaptability and fitness.

Halfmann R, Jarosz DF, Jones SK, Change A, Lancaster AK, Lindquist S (2012) Prions are a common mechanisms for phenotypic inheritance in wild yeasts. *Nature* 282: 363–368.

True HL, Lindquist SL (2000) A yeast prion provides a mechanism for genetic variation and phenotypic diversity. *Nature* 407: 477–478.

Yeast colonies, light and transmission electron micrograph photos of *Saccharomyces cerevisiae*.



Different fungal and algal genotypes demonstrated within one lichen specimen

Observations on the development of lichens in the field reveal that multiple propagules of a species developing on a surface often

coalesce to form a single structure. This is frequently observed where the propagules are asexual soredia or isidia, which may

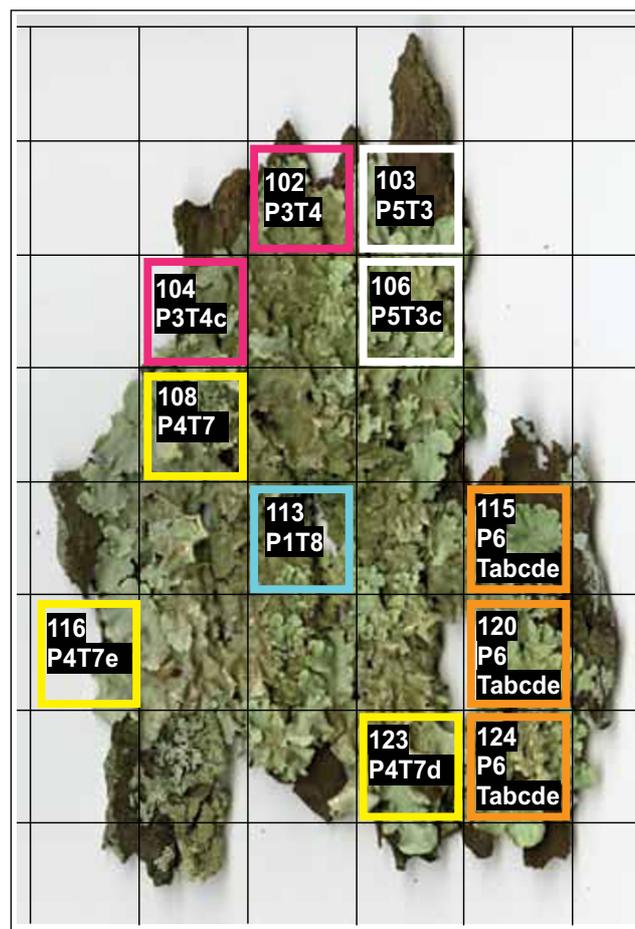
or may not have come from the same parent, and is well-documented. However, whether all had to be of a single genotype for this to occur was uncertain. The first study to suggest that a single lichen specimen might not just have a single fungal partner experimentally was the study of Larson & Carey (1986) who found that single specimens of two *Umbilicaria* species showed variations in physiological parameters and isoenzyme profiles. With the advent of DNA PCR technology, and especially the use of microsatellite (SSR) markers, it has become possible to explore the issue of the degree of individuality of single lichen specimens with respect to both the fungal and the algal populations that comprise them.

Parmotrema tinctorum is a rather common tropical lichen that reproduces mainly by asexual isidia. Mansournia *et al.* (2012) studied populations growing on *Pinus thunbergii* in Japan, and used microsatellite markers to characterize the partners at different levels: within single specimens, on single trees, and within 10 x 10 cm quadrats. Of particular interest were the results from single specimens in which they studied numerous small pieces of tissue. They found that a single specimen could be formed from a single fungal partner with or without changes in the algal partner, or fusion of several independent partners. In total 12 fungal genotypes and 37 algal genotypes were recognized. An example in which there were five fungal genotypes and a single algal genotype is illustrated here. Further, specimens from individual trees or which were close together tended to have similar genotypes, suggesting limited dispersal in the site.

This study provides evidence to support what has long been suspected, that one cannot presume that what looks like a single individual lichen specimen represents a single fungal genotype.

Larson DW, Carey CK (1986) Phenotypic variation within “individual” lichen thalli. *American Journal of Botany* 73: 214–223.

Mansournia MR, Wu B, Matsushita N, Hogetsu T (2012) Genotypic analysis of the foliose lichen *Parmotrema tinctorum* using microsatellite markers: association of mycobiont and photobiont, and their reproductive modes. *Lichenologist* 44: 419–440.



A single specimen of *Parmotrema tinctorum* showing the different fungal and algal genotypes determined with PCR of SSR markers. Codes prefixed by P are of the fungal partner, and those by T are of the algal partner; five fungal genotypes and one algal genotype were detected within this particular specimen. Adapted from Mansournia *et al.* (2012).

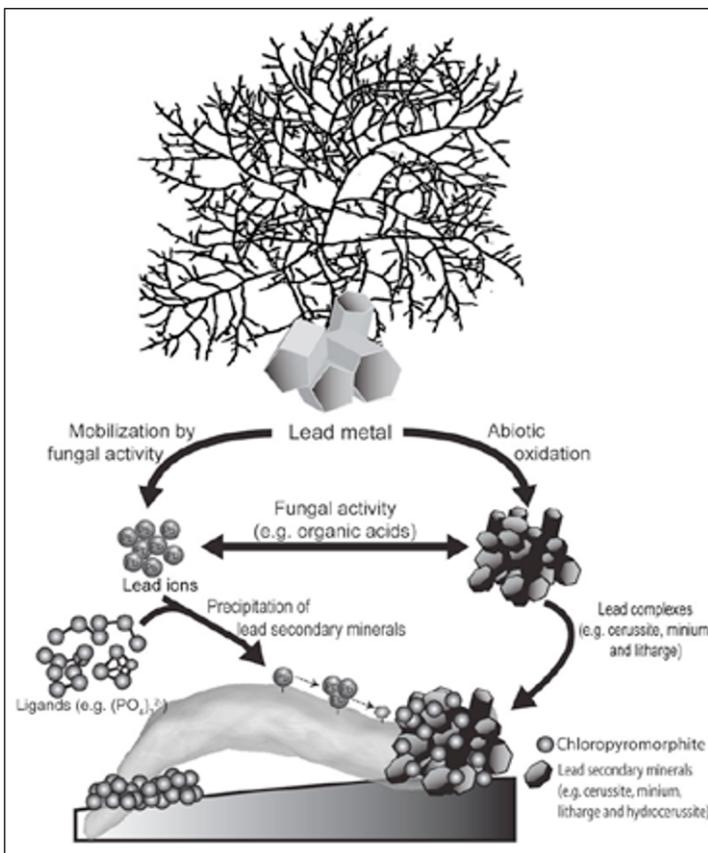
Fungi that can transform lead

Soil and rock-inhabiting fungi, especially lichen-forming fungi, are well known to be able to convert different minerals to oxalates through the extracellular secretion of oxalic acid. Now, Rhee *et al.* (2012) have found that two fungi, *Metarhizium anisopliae* and *Paecilomyces javanicus*, are able to act directly on lead metal to form chloropyromorphite, the most stable lead mineral known. The strains were isolated from a former lead-

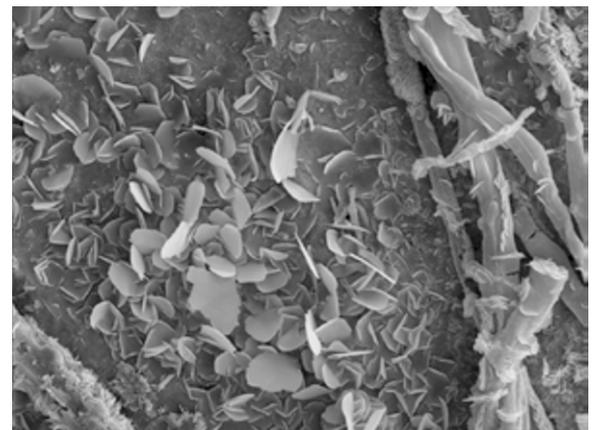
mining area in Scotland, and their activity was demonstrated using incubated lead shot, and examination by two methods of X-ray analysis; it should be noted that in controls without the fungi, different compounds were formed. The lead shot was visibly corroded after one month, and minor amounts of some other lead compounds were also noted. The paper includes superb environmental scanning electron (ESEM)

micrographs, and amazingly shows that the pyromorphite develops as minute spherules even inside the fungal hyphae. This finding is not only of interest in demonstrating a previously unknown biogenic step in the corrosion of lead metal and as a contribution to lead biogeochemistry, but could have applications. Soils can become lead-contaminated through, for example, the deposition of industrial wastes, battery casings, pipes, paints, inks, and shot, and lead has dangerous toxic effects on humans. The potential of using the tested strains, and other isolates of those and additional species of fungi, in the bioremediation of actual lead-contaminated soils clearly merits further exploration and assessment.

Rhee YJ, Hillier S, Gadd GM (2012) Lead transformation to pyromorphite by fungi. *Current Biology* 22: 1–5.



Schematic representation of the processes involved in lead transformation by fungi. Courtesy Geoffrey M. Gadd.



Secondary mineral formation on the surface of metallic lead resulting from the activities of *Metarhizium anisopliae*. Photo courtesy Geoffrey M. Gadd.

Nutritional value of fungi in animal diets

Humans along with many other animals, including a wide range of terrestrial mammals, eat fungi as components of their diets to various degrees. The actual nutritional value of fungi has, however, been unclear and much-debated. This is as while chemical analyses can give very positive indications, the extent to which they are digestible is unclear. In order to ascertain the extent of digestibility, Wallis *et al.* (2012) analyzed the fibre, amino acid composition, and both total and available nitrogen in a about 60 samples of sporocarps of diverse

epigeous and hypogeous macrofungi from Australia and the USA; they then examined the digestibility *in vitro*. Amongst the genera of fungi studied, were species of *Agaricus*, *Boletus*, *Cantharellus*, *Gauteria*, *Hysterangium*, *Morchella*, *Rhizopogon*, and *Tricholoma*. The results showed that while in general the mushrooms and truffles tested

A northern flying squirrel (*Glaucomys sabrinus*) holding a truffle in its paws, evidently devouring the white flesh. Photo Jim Grace.



were a reasonable source of amino acids and digestible nitrogen, there were large differences between species, and the protein had a poor balance of digestible amino acids. The authors consider that this explains why mammals that are primarily mycophagous tend to eat a wide range of sporocarps, and in some cases have developed foregut-fermentation to maximise the available nutritional value. In addition, they note that many mycophagous mammals supplement their diets with insects which are a source

of high-quality protein. In Australia, the combination of mycophagy, foregut fermentation, and coevolution may explain the potorine marsupials which are obligate or preferential mycophagists. It is suggested that their use of hypogeous fungi enables them to survive the destructive effects of devastating fires as the hypogeous fungi tend to remain in the aftermath. The authors, perhaps tactfully, largely avoid the issue of the dietary value of fungal sporocarps in the human diet . . . A single experience can

hardly be taken as representative but, after repeatedly consuming meals with different mushrooms as the major component over several weeks about 15 years ago, I found I had shed quite a few pounds.

Wallis IR, Claridge AW, Trappe JM (2012)

Nitrogen content, amino acid composition and digestibility of fungi from a nutritional perspective in animal mycophagy. *Fungal Biology* 116: 590–602.

Archaeolichenology: a novel use of lichens

A novel application of lichens has just been developed by lichenologists at the Royal Botanic Garden Edinburgh. These are being used to reconstruct species' regional distributions, and so indicate habitat types, for the historic period prior to the industrial revolution that started in the mid-18th century. The rationale is that epiphytic lichens grow on the outer-bark surface of trees, and trees harvested and used as the frame for pre-industrial buildings were not likely to have been transported far from where they were used. Consequently, where bark occurs on the timber structures of pre-industrial buildings, it might be possible to find preserved lichens which may suggest something of both past distributions and local ecologies.

This proved to be the case, and Yahr *et al.* (2011) discovered 87 epiphytic lichen species in a survey of 78 buildings dating from the period 1300-1750 across southern England. The best-preserved material tended to be found in the roof-spaces of low-status homes with continuous occupancy, where conditions are not so dissimilar to those of many herbaria today. Many of the pre-industrial records are from outside the species' current range, and estimates

suggest an 80 % loss of epiphyte diversity from areas such as south-east England (Ellis *et al.* 2011). This study has demonstrated an intriguing new tool for environmental reconstruction, with the potential of re-evaluating environmental and conservation base-lines. This is of particular interest as current knowledge from the literature and preserved specimens is necessarily biased towards the mid-18th century onwards, a period where industrialization was already starting to become widespread in much of lowland Britain.

Information related to changes over time can be accrued, but to ensure accuracy, it was necessary to consider the accurate dating of the timbers (based on styles of carpentry), possible timber re-use within buildings, and the local transport networks. The group plans to focus on increasing the resolution of the data, using data available from wattles, and also dendrochronology. The work is being undertaken in collaboration with archaeologists at University College London.

Based on material kindly supplied by Christopher J. Ellis.

Ellis CJ, Yahr R, Coppins BJ (2011)

Archaeobotanical evidence for a massive loss of epiphyte species richness during industrialisation in southern England. *Proceedings of the Royal Society of London, Biological Science, B*, 278: 3482–3489.

Yahr R, Coppins BJ, Ellis CJ (2011) Preserved epiphytes as an archaeological resource in post-medieval vernacular buildings. *Journal of Archaeological Science* 38: 1191–1198.



A specimen of a *Physconia* species preserved on the bark of a 400 year-old timber. Photo courtesy Christopher J. Ellis.