Crystallicutis gen. nov. (Irpicaceae, Basidiomycota), including C. damiettensis sp. nov., found on Phoenix dactylifera (date palm) trunks in the Nile Delta of Egypt

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**Crystallicutis** gen. nov. (Irpicaceae, Basidiomycota), including *C. damiettensis* sp. nov., found on *Phoenix dactylifera* (date palm) trunks in the Nile Delta of Egypt

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**Abstract**

The taxonomy of Polyporales is complicated by the variability in key morphological characters across families and genera, now being gradually resolved through molecular phylogenetic analyses. Here a new resupinate species, *Crystallicutis damiettensis* sp. nov. found on the decayed trunks of date palm (*Phoenix dactylifera*) trees in the fruit orchards of the Nile Delta region of Egypt is reported. Multigene
phylogenetic analyses based on ITS, LSU, EF1α, RPB1 and RPB2 loci place this species in Irpicaceae, and forming a distinct clade with Ceraceomyces serpens and several other hitherto unnamed taxa, which we also incorporate into a new genus Crystallicutis. We name two of these species, C. huangshanensis sp. nov. and C. rajchenbergii sp. nov. The distinctive feature of Crystallicutis gen. nov. is the presence of crystal-encrusted hyphae in the hymenium and subiculum. Basidiomes are usually honey-yellow with white margins but there is variability in the presence of clamp connections and cystidia, as noted for other genera within Irpicaceae. C. damiettensis is hitherto consistently associated with date palms killed by the red palm weevil Rhynchophorus ferrugineus, a highly damaging and invasive pest, recently spread to the Mediterranean region. C. damiettensis causes rapid wood decay by a potentially unusual white-rot mechanism and may play a role in the damage caused by R. ferrugineus.

**Keywords**: Brown rot; white-rot; insect vector; corticioid fungi; Agaricomycetes; phylogeny; PolyPEET
Introduction

Resupinate or corticioid fungi can be difficult to classify even to family level based on morphological characteristics (Larsson, 2007; Larsson et al., 2004). The deployment of molecular phylogenetics has led to substantial revision of the placement of many taxa within Polyporales, coordinated through focused initiatives such as the PolyPEET project (https://wordpress.clarku.edu/polypeet/) (Binder et al., 2013; Floudas and Hibbett, 2015; Justo et al., 2017). However, multigene phylogenies now provide a robust backbone at family level but there is an urgent need to reclassify many taxa which have been attributed to incorrect genera based on morphological data.

This problem is well-illustrated by the family Irpiceae Spirin & Zmitr. 2003 (Spirin, 2003), a well-supported clade which currently comprises 12 genera (Byssomerulius, Ceriporia, Cytidiella, Efibula, Emmia, Flavodon, Gloeoporus, Hydnopolyopus, Irpex, Leptoporus, Meruliopsis and Trametopsis) (Justo et al., 2017). Within multigene phylogenies of Irpiceae, it is also apparent that several clearly delineated clades within this family remain to be named (Justo et al., 2017).

The family Irpiceae also illustrates the fundamental problems associated with the classification of Polyporales based on morphological traits. In terms of macromorphology, three forms of basidiomes (pileate [Trametopsis], resupinate [Gloeoporus] and stipitate [Hydnopolyopus fimbriatus]) and four states for hymenophore configuration (poroid, daedaleoid/lamellate, smooth, hydnoid) are found (Justo et al., 2017; Sjökvist et al., 2012). A similar variation is evident in the diversity of hyphal systems (mostly monomitic but some dimitic [Flavodon/Irpex/Trametopsis]), which affects the consistency and longevity of fruiting bodies. Decay mode in
Polyporales is one of the most stable characters that has been used as the basis for segregating genera (Gilbertson and Ryvarden, 1986; Ryvarden, 1991) but within Irpicaceae, whilst most are white-rotting, a single genus \textit{Leptoporus} exhibits brown rot decay (Justo et al., 2017). With regard to other microscopic traits, most members of the family are rather nondescript, with consistently smooth hyaline spores but variation both within and between genera with regard to the presence of cystidia and clamped septa (e.g. cystidia in \textit{Irpex}, \textit{Emmia} and others; clamp-connections in \textit{Gloeoporus} and others).

These various morphological transitions have occurred repeatedly within this lineage (Floudas and Hibbett, 2015; Miettinen et al., 2016), making the construction of any dichotomous key based on morphological characteristics very unwieldy. Recognizing smaller, well-supported clades as independent families would not result in a more straightforward morphological grouping of these taxa.

In this study we describe a new resupinate fungus found on decaying trunks of \textit{Phoenix dactylifera} trees killed by red palm weevil (\textit{Rhynchophorus ferrugineus}). Based on the genetic and morphological similarities of this new species to \textit{Ceraceomyces serpens} and several other ‘orphan’ resupinate species, we include all four taxa in a new genus which we name \textit{Crystallicutis} gen. nov.

**Methods**

1. **Sampling and Morphological studies**

Basidiome samples were collected during a survey for wood-inhabiting fungi across orchards, and gardens of the North Nile Delta region of Egypt (2013-2020). Isolation
was conducted from basidiome tissues (Stalpers, 1978) at the Microbiological laboratory of Faculty of Science, Damietta University. Pure cultures were obtained on Potato dextrose agar (PDA) and 3% Malt extract agar (MEA), routinely incubated at 28°C. Cultures were stored at 4°C, on agar slopes and frozen at -80°C in 10% glycerol. Radial growth rate was quantified on MEA in 90 mm petri dishes, with mycelial plugs of actively growing cultures placed at the edge of the dish, according to the method of (Adaskaveg and Gilbertson, 1986). Optimal growth temperature was investigated across a range of temperatures (20-41°C). Culture compatibility tests were carried out for different isolates on MEA at 30°C for 3 weeks (Worrall, 1997). Vouchers from the samples were deposited at Aberystwyth University Herbarium (ABS). Herbarium acronyms follow Index Herbariorum (http://sweetgum.nybg.org/science/ih/).

The basidiome surface was observed with a dissecting microscope (Prior model 29362) at 50x. Basidiome sections were investigated by light microscopy (Olympus BX51M) mounted in 5% KOH, cotton blue or Melzer’s reagent at 1000x magnification. Photomicrographs were recorded with a Nikon Coolpix 995 digital camera. Measurements were taken using an objective micrometer or calibrated ocular.

Colony characters as colour, shape and size of hyphae and type of septa were checked after 1,2,4 weeks of incubation on MEA plates at 28°C (Stalpers, 1978). Hyphae were mixed with 20 µl of Calcofluor solution (200 µg/ml [w/v] in distilled water to stain the chitin cell walls), then visualized by epifluorescence microscopy (Olympus BX51). The spore shape index (Q; length/diameter) was calculated for 10 spores (Wu, 1990).
Scanning electron microscopy was performed at IBERS, Aberystwyth University.

Sections of air-dried samples were mounted directly on the surface of carbon stubs and coated with platinum and palladium (Pt/Pd; 4 nm thick layer) mixture using a High-Resolution Sputter Coater (Agar Scientific Ltd, UK) at 20 mA under vacuum, and the thickness was monitored with a quartz crystal micro-balance thickness controller. SEM was undertaken with a Hitachi S-4700 field emission scanning electron microscope (Hitachi, Tokyo, Japan) with the following emission settings: 10 µA/1500V and using Mixed (M) or upper (U) detectors.

2. DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from pure cultures using a CTAB-based method (Griffith and Shaw, 1998). PCR amplifications of several parts of DNA were carried out using different primer pairs. PCR reactions were performed in a volume of 25 µl (13 µl of Dream Taq [Green PCR Master mix] and 2 µl (ca. 1-10 ng) genomic DNA) using a thermal cycler (PTC-100 Techne, UK). PCR cycling conditions were as follows: one cycle of initial denaturation stage at 96°C for 5 min, 35 amplification cycles [Denaturation at 95°C for 30 sec, annealing at 48°-58°C (see below) for 30 sec, extension at 72°C for 45 sec], then final extension at 72°C for 5 min. The following primer pairs were used for different loci: ITS1, 5.8S, ITS2 (55°C anneal) (ITS1F [CTT GGT CAT TTA GAG GAA GTA A] and ITS4 [TTC TTC GCT TAT TGA TAT GC]) (Schoch et al., 2012); ITS2 and LSU (D1/D2 region) (53°C anneal)(ITS3 [GCA TCG ATG AAG AAC GCA] / HyglonR1 [TAA AGC CAT TAT GCC AGC ATC]) (Detheridge et al., 2016; El-Gharabawy et al., 2016); LSU (55°C anneal) (LR0R [ACCGCTGAACCTTAAGC] / LR5 [TCCTGAGGGAAAATTCG]); RPB1 (58°C touchdown anneal, with 1°C drop in annealing temperature per cycle to 48°C, then 30
cycles at 48°C for both amplicons) (rpb1:aA [GAG TGT CCG GGG CAT TTY GG] / rpb1:i2.2f [CGT TTT CGR TCG CTT GAT] and rpb1:aCr [ARA ART CBA CHC GYT TBC CCA T] / rpb1:940R [CTT CGT CYT TCG AAC GYT TRT A]) (Binder et al., 2010);

EF1α (58°C anneal) (EF1-1018F [GCY CCY GGH CAY CGT GAY TTY AT] / EF1-1620R [ACH GTR CCR ATA CCA CCR ATC TT]) (Rehner and Buckley, 2005).

PCR-DNA products were purified using spin column PCR purification kit (NBS Biologicals Ltd., Huntingdon, UK) and visualized on 1.5% agarose gel by gel electrophoresis system. The samples were then sent for Sanger sequencing at the IBERS Translational Genomics Facility (Aberystwyth University).

DNA sequences and chromatograms were curated and assembled using Geneious R10 (Kearse et al., 2012). The sequences generated in this study have been submitted to GenBank (Table 1).

In addition to sequences submitted to GenBank from previous phylogenetic studies of Irpicaceae (Table 1), sequences from Cytidiella melzeri (FP 102339) and Hydnopolyporus fimbritatus (CBS 384.51) were extracted from next-generation sequencing data deposited on NCBI database (SRX3006953- SRX3006967 and SRX2124808-SRX2124809, respectively) using an in-house developed pipeline.
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</tbody>
</table>

* Type species

*** sequences extracted from genome sequencing
3. Phylogenetic analyses

A dataset containing 169 sequences from 54 samples, including members of
Irpicaceae and three Phanerochaetaceae as outgroup, was created including ITS (54
sequences), LSU (54 sequences), EF1α (6 sequences), RPB1 (35 sequences), and
RPB2 (20 sequences). GenBank accession numbers and voucher details for the
sequences used in these analyses are provided in Table 1.

For all the following analyses the ITS region was divided into three subsets ITS1, 5.8S
and ITS2. Only the CDS from the protein-coding genes were used except for the third
intron from RPB1 that was included in a separate subset. Thus, eight subsets were
created: ITS1, 5.8S, ITS2, LSU, EF1α, RPB1, RPB2 and RPB1_I3. Each subset was
aligned separately with MAFFT v7.311 (Katoh and Standley, 2013) using the E-INS-i
algorithm for ITS1, ITS2 and RPB1_I3, and L-INS-i for the remaining subsets. The
alignments were curated manually with AliView v1.5 (Larsson, 2014) and trimmed to
remove uneven ends. With ITS1, ITS2 and RPB1_I3 alignments, morphological
matrices were constructed coding the indels as morphological characters using the
simple indel coding (Simmons and Ochoterena, 2000) implemented in SeqState
(Müller, 2005) and the nucleotide alignments were then trimmed with trimAl v1.4.rev22
(Capella-Gutiérrez et al., 2009) with the option -gappyout to remove unalignable
regions. Moreover, the protein-coding sequences were analysed in three partitions
accounting for each codon position. Therefore, 17 partitions were used for the
phylogenetic estimations: five nucleotide partitions (5.8S, LSU, ITS1, ITS2, RPB1_I3),
three morphological (ITS1_indel, ITS2_indel, RPB1_I3_indel) and nine accounting for
each codon position (EF1α_1, RPB1_1, RPB2_1, EF1α_2, RPB1_2, RPB2_2,
EF1α_3, RPB1_3, RPB2_3).
The separately aligned markers were combined into a single data matrix prior to phylogenetic reconstruction. Maximum-likelihood tree reconstruction was performed with IQ-TREE v2 (Minh et al., 2020). The best-fit evolutionary models and partitioning scheme for this analysis were estimated by the built-in ModelFinder (option -m MF+MERGE) allowing the partitions to share the same set of branch lengths but with their own evolution rate (−p option) (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017). Branch supports were assessed with ultrafast bootstrap (UFBoot; 1000 replicates) (Hoang et al., 2018), allowing resampling partitions and then sites within these partitions to reduce the likelihood of false positives on branch support (option --sampling GENESITE) (Gadagkar et al., 2005). Additionally, ultrafast jackknife (1000), SH-aLRT test (1000) (Guindon et al., 2010) and non-parametric bootstrap (100) were performed.

Bayesian Inference (BI) was conducted with MRBAYES v3.2 (Ronquist et al., 2012) with two independent Markov Chain Monte Carlo (MCMC) runs, each one with four chains and starting from random trees. The best-fit evolutionary models and partitioning scheme for these analyses were estimated as for the ML analysis but restricting the search to models implemented on MRBAYES (options -m TESTMERGEONLY -mset mrbayes). Chains were run for 10 million generations with tree sampling every 1000 generations. The burn-in was set to 25% and the remaining trees were used to calculate a 50% majority consensus tree and Bayesian Posterior Probability (BPP). The convergence of the runs was assessed on TRACER v1.7 (Rambaut et al., 2018) to ensure the potential scale reduction factors (PSRF) neared 1.0 and the effective sample size values (ESS) were sufficiently large (> 200).
Nodes with BPP ≥0.95 and/or UFBoot ≥95 were considered strongly supported.

Alignment and phylogenetic trees are available in Figshare (DOI: 10.6084/m9.figshare.13574255).

Results

1. Field investigation and sample collection

A resupinate fungus with honey-yellow basidiomes and white margins was initially collected as a single infection on the dead stump of a date palm tree (Phoenix dactylifera) in February, 2014 in a fruit farm at Baltim city, Kafr El-Sheikh (31.5764°N, 31.0796°E; a governorate of Nile Delta of Egypt). In more detailed surveys, basidiomes were found to be more widespread and present on dead date palm stumps and logs in several adjacent orchards (2017; five infected stumps in area of 200-250 m²). In 2018-2020, basidiomes were also found in orchards 60 km to the east in El-Sinaniah, Damietta (31.4429°N, 31.7798°E), always on dead date palm stumps or fallen trunks (10 different trees across an area of about ca. 400 m²). In all cases, the date palm stumps were in dense orchard with dense cover of planted trees (mainly mango, lemon, and date palm). Basidiomes were present throughout the year (Winter temp 10-20°C [RH 60-80%], Summer temp 25-35°C [RH 40-45%]).

Some of the basidiomes were formed on the bark (Fig. 1A/D) and others on decorticated areas of exposed wood (Fig. 1C/E/F) and the basidiomes were associated with advanced white-rot decay. The cause of death of the host trees was Rhynchophorus ferrugineus (red palm weevil), whose boreholes were readily visible in some stumps (Fig. 1B/C; arrowed).
**Fig. 1.** *Crystallicutis damiettensis* infecting date palm trunks. Honey-yellow basidiomes with white margins are visible emerging from the bark (A), often associated with bore holes of red weevil (B, arrowed) and batches of white-rot decay (C). Basidiome sometimes formed in long decay columns (D), also at trunk ends (E) and inside hollowed dead stumps (F).

**2. Basidiome morphology of voucher UN63A**

The basidiomes are annual, effuse-resupinate, comprising a thin layer of patchy of tissue tightly attached to the host. When young and fresh, basidiomes are lemon to olive/honey-yellow coloured with a crenulate/papillate/tuberculate hymenium surface, up to 20 x 45 cm in extent, up to 0.3 mm thick (Fig. 2). Sometimes, basidiomes appear as a thicker velvety mat, deep yellow-coloured, warty (bullate or phlebioid) irregularly crenulated surface with waxy (ceraceous) appearance. Basidiomes have white, thin, loose cobweb-like fibrous margins. With age, the flesh of the basidiome becomes thinner and more compressed, with a pinky-buff or ochraceous to pale brown or olive brown colour, smoother surface, and dull (not waxy) appearance. The flesh is yellowish white, soft, loose when fresh, more fragile with small cracks when dry, assuming a dark or brownish colour with addition of KOH solution. No pores were observed on the hymenium. Fresh basidiomes have a strong but pleasant mushroom-like odour. No mycelial cords or rhizomorphs were observed (Fig. 2).

**Fig. 2.** Detailed view of resupinate basidiomes of *Crystallicutis damiettensis* in the field. The resupinate basidiomes are honey yellow coloured with a granulated (papillate) surface and white thin fibrous margin when young (A). Thicker velvety mats with a warty (bullate) surface, irregularly crenulated and a waxy appearance are also found (B). Older basidiomes are buff to pale brown with white margins and cracked (C), with the surface becoming smoother with a dull (not waxy) appearance, concolorous flesh and soft dense texture (D). Scale bar indicates 1cm.

**3. Cultural characteristics**
Cultures were obtained from eight basidiomes collected from Damietta and Kafr El-Sheikh. In axenic culture (MEA), the mycelium is yellowish or creamy white to pale buff coloured, sparse adpressed mycelium, with slow radial growth rate (1.6-2.2 mm/day) (Fig. 3A). On PDA growth is more cottony/downy, with occasionally denser growth on the inoculum plug. Maximal growth rate was obtained at 30°C and no growth was observed above 35°C.

**Fig. 3.** *Crystallicutis damiettensis* in pure culture on PDA. Floccose appearance of young colonies of isolate UN63A (2 weeks old), with slight yellow colouration (A). Colonies incubated in the light exhibited pigmentation similar to that seen in basidiomes (B). Assessment of somatic incompatibility between isolates from Kafr El-Sheikh (UN63A, UN63B, UN63C). Yellow pigmentation after incubation in the light for 4 weeks is visible on the upper surface (C), with zone lines between genetically different cultures (B vs A/C), more clearly visible from beneath (D).

In older cultures (>4 weeks), following growth at ambient light levels, yellowish brown pigmentation developed as a waxy-leathery thin layer at the edges of colonies (Fig. 3B). Thus, there was some differentiation of hymenial structures but basidia and basidiospores were not observed. The pigmentation and differentiation did not occur when cultures were incubated in the dark.

Hyphae from pure cultures are hyaline, thin-walled (3-4 µm diameter; Fig 4A/B/C), with large clamps abundant. Chlamydospores, both intercalary and terminal (Fig. 4B/C), were present in older cultures (after 3-4 weeks of growth); these, are numerous, globose or fusiform (7.5-9.5 µm diam) with encrustation by small irregularly shaped crystals visible on some hyphae (Fig. 4D, inset). Amorphous areas of brown resinous material were also visible in some areas but it was not clear whether these were associated with the crystals (Fig. 4D).
Fig. 4. Micromorphology of *Crystallicutis damiettensis*. In pure culture, abundant clamp connections are visible in brightfield (A) and under epifluorescence microscopy with Calcofluor B staining (B,C; arrowed). Spherical-ellipsoid chlamydospores, both intercalary and terminal, are abundant (B-D), alongside brown resinous agglomerations (D) and encrustation by small crystals of individual hyphae (D, inset). In basidiomes examined by scanning electron microscopy, large crystals are visible, embedded in the matrix of the hymenium surface (E; arrowed) and smaller crystals encrusting the surface of hyphae in the subhymenium and subiculum (F). Scale bar indicates 10 µm.

Pairings of isolates obtained from different trees at Kafr El-Sheikh revealed the formation of zone lines due to somatic compatibility (Fig. 3. C,D). This result is suggestive of an outcrossing breeding strategy (Griffith and Hedger, 1994).

4. Basidiome micromorphology of voucher UN63A

Basidia, rarely observed, are clavate (6.0-7.5 x 12.0-15.0 µm), smooth, thin-walled, 4-spored (Fig. 5A; SuppFigS1G). Basidioles are similar in shape but smaller (4-5 µm diameter) (Fig. 5A; SuppFigS1G). Basidiospores are short, ovoid to ellipsoid, tear-shaped, smooth, sometimes thick-walled, 3.0-3.5 x 4.0-5.0 µm in size (Q =1.42-1.66), colourless, non-cyanophilous (not staining with Cotton Blue), with no colour change associated with KOH or Melzer’s reagent (i.e. non-amyloid and non-dextrinoid) (Fig. 5A; SuppFig1H). Cystidia are abundant, long, smooth (not encrusted), hyaline, thin-walled, septate (2-celled), spear-shaped or with a sharply pointed apex (4.0-5.0 x 22-25 µm) (Fig. 5B; SuppFigS1J/K). Cystidioles are fusiform, 3.0-4.0 x 18-22 µm (Fig. 5C; SuppFigS1L).

Fig. 5. Diagram of microscopic structures of *Crystallicutis damiettensis* basidiome. Hymenium layer with clavate 4-spored basidia, thick-walled basidiospores, smaller basidioles and basal clamps (A). Cystidia are spear-shaped (B) or fusiform (C), with cystidioles also present (D). Large and small hyaline crystals (E) and other encrustation on hyphae were observed (F). Generative hyphae with abundant clamps (G) and pseudo-skeletoid subicular hyphae (H) are present. Scale bar indicates 10 µm.
The subhymenial layer is composed of tightly packed hypha (SuppFigS1E/F), with clamps present on all primary septa, (subicular, subhymenial and sub-basidial). The hyphal system is monomitic; generative hyphae bear abundant clamps (Fig. 5F; SuppFigS1F) and frequent stumpy branches (hyaline and thin-walled, 3.0-4.5 µm diam) (Fig. 5A/B/C). Some generative hyphae are thick-walled to nearly solid (pseudo-skeletoid, sparsely branched, fewer clamps, 6.5-8.0 µm diam) (Fig. 5G).

Large irregularly-shaped hyaline crystals (10-30 x 20-50 µm) are visible on the hymenium surface (Fig. 4E) and also in the subhymenium and subiculum (SuppFigS1C/D/E). More widespread, in the hymenium, subhymenium and subiculum were smaller (1-4 µm) rhomboid-shaped hyaline crystals (Fig. 4F; SuppFigS1F), found mainly forming encrustations of hyphae. The latter were similar to those observed on hyphae in pure cultures. The larger crystals and also the smaller crystals when not forming hyphal encrustations were soluble in KOH but the hyphal encrustations of smaller crystals remained intact in KOH. Brown, resinous agglomerations, similar to those observed in pure cultures, were also visible (SuppFigS1A) but it was not clear how these were associated with the crystalline deposits. No chlamydospores were seen within basidiome tissues.

**SuppFigS1.** Microscopic features of *Crystallicutis damiettensis* basidiome. A smooth/non-perforated, honey-yellow hymenium encrusted with brown clumps/resinous granules (A: 50x light magnification), which were visible under SEM (B); also clusters of large, amorphous, hyaline crystals observed under SEM (C) and LM (D). In transverse section; the basidiome is composed of a compact mat of mycelia (E) with a monomitic hyphal system consists of three types of generative hyphae, as arrowed (normal generative hyphae with clamps, crystal-encrusted basal hyphae and pseudo-skeletoid hyphae) (F). Clavate 4-spored basidia (arrowed), smaller basidioles (G) are visible on the hymenium, as are sometimes thick-walled ovoid basidiospores (H), showing no reaction with Melzer’s reagent (H; right). Generative hyphae with basal clamps (I; Cotton Blue stain) are visible, as are spear-shaped (2-celled) cystidia (J, K) and fusiform cystidioles (L). Scale bar indicates 10 µm (except A = 400 µm).
5. Phylogenetic reconstruction

The final alignment consisted of 54 sequences with 4291 characters and 2133 parsimony-informative sites. The BI analysis converged in both runs as indicated by the effective sample sizes (ESS) of all parameters above 4500 and the potential scale reduction factors (PSRF) equal 1.000 for all the parameters according to the 95% highest posterior density interval. Details about evolutionary models and partitioning schemes used and all trees generated in the analyses can be found in SuppData1.

SuppData1. Additional details of the phylogenetic analyses, including various trees.

DNA sequence was obtained for the full ITS region of all seven isolates and all were identical (KX428470). Additionally, for isolate UN63A, the D1/D2 region of the large (28S) ribosomal subunit (GenBank MW508515), the EF1α gene (GenBank MW523002) and also the RPB1 gene (GenBank MW523003) were sequenced. In all cases, the sequences obtained were quite distinct from any other sequences present on GenBank but more detailed phylogenetic analysis placed the fungus at the base of the *Byssomerulius* clade, as defined by Floudas and Hibbett (2015) and intermediate between *Meruliopsis* sp. and *Ceriporia* spp. (Fig. 6).

Sequences were also extracted from two genome sequence projects (*Cytidiella melzeri* and *Hydnopolyporus fimbriatus*). Alignment and phylogenetic trees are are available in Figshare (DOI:10.6084/m9.figshare.13574255).

Fig. 6. Multigene maximum-likelihood tree of Irpicaceae. Support values are presented as numbers (UFBoot/BPP) on branches and shown only for UFBoot ≥ 70 and BPP ≥ 0.70. Type species for other genera within Irpicaceae are represented by a star. Outgroups are *Bjerkandera adusta* and *Terana caerulea* (Phanerochaetaceae). *Crystallicutis* gen. nov. is boxed in red. Asterisks (*) represent maximum UFBoot/BPP
values, dashes (−) represent values below the cut-off threshold (70%), and dots (.) represent ML clades that were not recovered in the BI tree. Scale bar indicates number of substitutions per site. More details on supporting values can be found in SuppData1.

The clades recovered here within Irpicaceae correspond well with those recovered by Justo et al. (2017) (Fig. 4). Clade /crystallicutis (BS=98; BPP=1) is strongly supported in our phylogeny and occupies a similar position in the phylogeny presented by Justo et al. (2017), basal to the subclade containing Trametopsis, Efibula, Byssomerulius and Irpex. Within clade /crystallicutis, UN63 occupies a basal position, with the other samples forming two distinct pairs. The first of these contains the well-established and widely distributed Ceraceomyces serpens (Bernicchia and Niemelä, 1998; Ginns, 1975) alongside Dai6090, a specimen collected from Huangshan Mountain, Anhui, China and which was named as Ceriporia sulphuricolor by Cui and Jia (2011).

The type specimen of Ceriporia sulphuricolor Bernicchia & Niemelä originates from Italy (Bernicchia and Niemelä, 1998; Ginns, 1975) but the type specimen (voucher 6591 [HUBO fungarium]) was recently moved to the University of Oslo, Natural History Museum Fungarium (O) following retirement of the HUBO curator Dr. Annarosa Bernicchia. Sequencing of the ITS spacer region and partial LSU of HUBO- 6591 (now named O-F-76351; GenBank: MW508516) revealed it to be identical to several specimens of Ceriporia alachuana, and therefore unrelated to Dai6090 and other members of /crystallicutis (SuppData2).

SuppData2. Phylogenetic analysis of the type specimen of Ceriporia sulphuricolor alongside Ceriporia alachuana.
Also falling within /crystallicutis are sequences derived from voucher MR-4310, labelled in GenBank as *Phlebia cf. griseoflavescens*. We obtained this voucher and microscopic examination revealed the presence of hyphae encrusted with small and large crystals, as detailed below (SuppFigS2).

**SuppFigS2A. Morphology of the basidiome of *Crystallicutis rajchenbergii*;**
resupinate honey-yellow basidiome on deciduous wood (A) smooth non-ceraceous surface with small cracks when old/dry, with brownish centre (B) whitish yellow fibrous margins (C) 0.1-0.3 mm thickness (black arrowed in D). Scale bar is 5mm for A-D. Under light microscope; thin-walled clamped generative hypha (2.5-3.0 μm diam, red arrow in E/H, stained with Congo Red), most hyphae heavily-encrusted (3-4 μm diam, black arrow in E/F), thinner (1.5-2 μm diam) densely branched hyphae in the subhymenium (G). Thick-walled pseudo-skeletoid hyphae with larger diameter (5-6 μm diam, white arrow in F). Ovoid to clavate, thick-walled 4-spored basidia and basidioles on the hymenium surface, 5-6 x 8-10 μm in size (black arrows in H). Subellipsoid, thick-walled basidiospores (3-6 x 10–15 μm) (I), cyanophilous (CB+ in J), non-amyloid/dextrinoid in Melzer’s reagent (K). Clusters of free large regular rhomboid crystals (on left; 25-37 μm across) and other irregular crystals (on right; 3 x 4μm to 30 x 35 μm) spread through the subhymenium and subiculum (L). Fusiform cystidioles (10 x 3 μm), thick-walled with a basal swelling (M), flame shaped cystidia (2-cells) with sharp apex (25-30 x 4-5 μm) (N with cotton blue), appear thick-walled and non-encrusted in Congo Red (O), while others were top encrusted (P). Scale bar indicates 10 μm for E-P.

**Taxonomy**

*Crystallicutis* El-Gharabawy, Leal-Dutra and G.W. Griff., gen. nov.

IndexFungorum. IF557789

**Type species.** *Crystallicutis damiettensis* El-Gharabawy, Leal-Dutra and G.W. Griff.

**Etymology.** Derived from the Latin words *crystallus* = crystal and *cutis* = rind/surface, due to the presence of crystals in the hymenium and subiculum of the basidiomes.
**Diagnosis.** Differs from other members of family Irpicaceae due to the presence of hyphae encrusted with crystals in the subiculum and usually yellow colour of the hymenial surface when fresh.

**Description.** Basidiomes resupinate with smooth, tuberculate, papillate, merulioid or sometimes poroid hymenophores, usually honey-yellow (not bright yellow) in colour (but occasionally rosy, reddish or greenish), waxy with white margin. Hyphae of subiculum and sometimes hymenium/subhymenium encrusted with crystals associated with darker (brown) resinous granules. Hyphal system is monomitic, usually with abundant clamp connections present. Basidia cylindric-clavate, basidiospores hyaline, smooth, ellipsoid, and non-amyloid and non-dextrinoid. Found forming white-rot on heavily decayed trunks of woody monocot and dicot angiosperms, as well as coniferous trees. Rhizomorphs and mycelial cords absent.


**Crystallicutis damiettensis** El-Gharabawy, Leal-Dutra and G.W. Griff., sp. nov.

IndexFungorum. IF557790

**Etymology.** The species epithet “*damiettensis*” refers to Damietta University (North Nile Delta, Egypt), close to the location where the fungus was first discovered.
**Diagnosis.** Basidiome resupinate, honey-yellow, tuberculate to papillate-warty, with waxy texture, white margin. Basidia clavate (6.0-7.5 x 12.0-15.0 µm), smooth, thin-walled, 4-spored. Basidioles similar in shape but smaller (4-5 µm diameter). Basidiospores short, ovoid to ellipsoid, tear-shaped, smooth, sometimes thick-walled (3.0-3.5 x 4.0-5.0 µm), non-amyloid and non-dextrinoid. Cystidia abundant, long, smooth, hyaline, thin-walled, septate (2-celled), spear-shaped (4.0-5.0 x 22-25 µm). Cystidioles are fusiform, 3.0-4.0 x 18-22 µm. Monomitic hyphal system, with generative hyphae bearing abundant clamps and frequent stumpy branches. Brown, resinous agglomerations and large irregularly-shaped hyaline crystals (10-30 x 20-50 µm) are present on the hymenium surface, subhymenium and subiculum. Smaller (1-4 µm) rhomboid-shaped hyaline crystals are present forming encrustations of hyphae. Differs from other members of this genus in having abundant cystidia and cystidioles.

**Typification.** The holotype (Fig. 2, Fig. 5) was collected from: EGYPT. Kafr El-Sheikh, Baltim (31.5764°N, 31.0796°E; North Nile Delta), growing on fallen trunk of date palm (Phoenix dactylifera) killed by Rhynchophorus ferrugineus, 14 Feb 2014, coll. HM El-Gharabawy, Voucher UN63A is held at <ABS>(Aberystwyth University biorepository). The ex-type culture UN63A is held in the Aberystwyth University fungal culture collection and also at the Faculty of Science at Damietta University. GenBank: KX428470 (ITS1 spacer, 5.8S rRNA gene, ITS2 spacer, D1–D2 28S rRNA).

**Additional specimens examined.** Four additional basidiomes found on trunks and stumps of fallen date palms killed by Rhynchophorus ferrugineus in the same orchard at Baltim, Kafr El-Sheikh (31.5764°N, 31.0796°E), Aug-Dec 2017; vouchers UN63B, UN63C, UN63X, UN63Y; coll. HM El-Gharabawy, held at the Faculty of Science at
Damietta University. Ten basidiomes, on trunks and stumps of fallen date palms killed by *Rhynchophorus ferrugineus*, at El-Sinaniah, Damietta (31.4429°N, 31.7798°E), Jan 2018-Feb 2020; vouchers UN1-UN10; coll. HM El-Gharabawy, held at the Faculty of Science at Damietta University.

**Distribution.** Nile Delta region of Egypt. Hitherto only found on fallen and heavily-rotted trunks or stumps of *Phoenix dactylifera* (datepalm).

**Notes:** White-rot decay mechanism with secretion of Mn-dependent and Mn independent peroxidases, but only low and transient secretion of laccase (El-Gharabawy et al., 2016).

*Crystallicitis serpens* (Tode ex Ginns) El-Gharabawy, Leal-Dutra and G.W. Griff., comb. nov.

IndexFungorum: IF557791


**Synonyms.**

*Merulius ceracellus* Berk. & M.A. Curtis, Grevillea 1(no. 5): 69 (1872)


*Merulius porinoides subsp. serpens* (Tode) Bourdot & Galzin, Hyménomyc. de France (Sceaux): 348 (1928) [1927]

*Merulius stratosus* Pilát, Bull. trimest. Soc. mycol. Fr. 52(3): 322 (1937) [1936]

*Xylomyzon crustosum* Pers., Mycol. eur. (Erlanga) 2: 34 (1825)
**Description.** (Ginns, 1975): 147

**Notes.** A widespread and common species in Europe and North America. The species was placed in the genus *Ceraceomyces* by Ginns (1975). Ginns (1975) distinguished this white-rot forming species from its ‘relative’ *C. borealis* on the basis that the latter formed a brown rot. However, he noted that whilst *C. serpens* formed a white-rot of angiosperm hosts, on conifers this was less clear (“incipient brown rot”). The type species of *Ceraceomyces* is *C. tessulatus* (Amylocorticiales), only very distantly related to *C. serpens* which Ginns placed in *Meruliopsis*. Ginns (1975) also noted that the subhymenial area of basidiomes was “often heavily impregnated with fine granules or a resin-like substance”.

**Crystallicutis huangshanensis** El-Gharabawy, Leal-Dutra and G.W. Griff., sp. nov

IndexFungorum. IF557792

**Etymology.** The species epithet “huangshanensis” refers to Huangshan Mountain, Anhui Province China where the type specimen was found.

**Diagnosis.** (Cui and Jia, 2011): 534-535. Honey-yellow to olivaceous-buff pore surface, margin thin, cream. Subiculum cream, cottony, up to 0.5mm thick with tubes concolorous with pore surface, Hyphal system monimitic, generative **hyphae** with simple septa. Generative hyphae in subiculum hyaline, coarsely encrusted with small crystals (2-4 μm across).
**Typification.** The holotype (Fig. 3, Fig. 4 in (Cui and Jia, 2011)) was collected from Huangshan Mountain Anhui Province, China (30.139°N; 118.164°E) on rotten angiosperm wood, 12th December 2004 by Y.C. Dai (Dai 6090).

**Additional specimens examined.** None

**Notes.** Specimen Dai6090 was incorrectly named as *Ceriporia sulphuricolor* by Cui and Jia (2011) based on its morphological similarity to the description of *C. sulphuricolor* (HUBO6591 / O-F-76351), which was described from Italy (Bernicchia and Niemelä, 1998). Our genetic analysis reveals the two samples to be unrelated, with the type specimen of *C. sulphuricolor* being very similar to *Ceriporia alachuana* (Suppdata2). Jia et al. (2014) undertook DNA sequencing of the ITS/ and partial LSU region of Dai 6090, placing the specimen basal to the main *Ceriporia* clade, with Chen et al. (2020) later placing it close to *C. serpens* in their analyses.

The description of Dai 6090 by Cui and Jia (2011) differs from that of Bernicchia (Bernicchia and Niemelä, 1998) in that the basidiome is “honey-yellow to ochraceous buff” (Fig. 3 in (Cui and Jia, 2011)) rather than bright yellow (Fig. 3 in (Cui and Jia, 2011)). Unlike other members of genus *Crystallicutis*, pores are present on the hymenium. Unlike HUBO6591 / O-F-76351, Dai 6090 lacks hyphoid cystidia and the tramal hyphae are interwoven, not parallel. The hyphae of the subiculum are heavily encrusted, with small (2-4 µm diameter) hyaline crystals (Cui and Jia, 2011) but the larger free crystals seen in *C. damiettensis* and *C. serpens* are not reported. Cui et al. (2011) noted the similarity of voucher Dai 6090 to *Ceriporia subspissa*, collected in Guyana (Aime et al., 2007) but the latter species is reported to bear cystidia in the hymenium and have a deep reddish brown hymenium/subiculum.
Suppdata2. Phylogenetic analysis of the type specimen of Ceriporia sulphuricolor

**Crystallicutis rajchenbergii** El-Gharabawy, Leal-Dutra and G.W. Griff., sp. nov

IndexFungorum. IF556941

**Etymology.** The species epithet “rajchenbergii” in honour of the mycologist Mario Rajchenberg who collected this specimen.

**Diagnosis.** Fruitbody resupinate, adnate, effused-elongate, 0.1-0.3 mm thick, smooth continuous surface, non-ceraceous with small cracks when old/dry, honey-yellow coloured with tan to brownish compact centre, bright yellow to whitish fibrous thinner margins. Hyphal system monomitic hyphae, generative hypha thin-walled, 2.5-3.0 µm, thinner (1.5-2 µm) and more densely branched in subhymenial hyphae (SuppFigS2A,B). Some distinct thick-walled, smooth (pseudo-skeletoid) hyphae with larger diameter (5-6 µm) are visible. Hyphae (3-4 µm) in the hymenium and subiculum are heavily encrusted with small crystals (0.5-1 µm), Large regular rhomboid crystals (25-37 µm across) and some irregular-shaped crystals (3x4-30 x 35 µm) are present throughout the subhymenium and subiculum. Cystidia (4-5 x 25-30 µm) are frequent, two-celled and clavate with a sharp apex, mostly non-encrusted, thick walled. Cystidioles are fusiform (3 x 10 µm), thick-walled, with a basal swelling. Basidia/basidioles are 4-spored, ovoid to clavate (5-6 x 8-10 µm). Basidiospores subellipsoid with a small rounded apiculus (3-6 x 10–15 (occasionally 6 x 22µm), smooth, thick-walled, IKI-, non-amyloid / dextrinoid but cyanophilous (CB+). Habitat. On decayed, deciduous wood, USA: North Carolina.
**Typification.** The holotype (voucher MR-4310; SuppFigS2A,B) is kept at the Forest Disease Herbarium, USDA Northern Research Station. It was collected by Dr. Mario Rajchenberg (12<sup>th</sup> July 1988) from Rustic Falls Area (off horse Cove Road), south-east of Highlands, Macon County, North Carolina (35.039°N; -83.156°W) and originally named as *Phlebia cf. griseoflavescens*.

**Additional specimens examined.** None but a BLAST search using the *C. rachjenbergii* ITS and LSU sequences revealed a strong match to an unidentified culture (isolate code 6/1-30) isolated from leaf litter in Sussex County, New Jersey (ITS: AF241321 [99.5%ID]; LSU: AF241355 [99.9%ID]) in a hitherto unpublished study (Polishook et al.).

**Notes.** This specimen was subject to DNA barcoding and phylogenetic analysis (KY948797 [ITS]; KY948888 [LSU]; KY948963 [RPB1]) by Justo et al. (2011), who place it in a well-supported clade alongside *Ceraceomyces serpens* and *Ceraceomyces* sp. Miettinen-16854.3. Our attempts to obtain voucher Miettinen-16854.3 from H have hitherto been unsuccessful. Mario Rajchenberg originally named as *Phlebia cf. griseoflavescens*. *Phlebia griseoflavescens* was recently renamed as *Antrodia griseoflavescens* (Runnel et al., 2019). Although known only from the single voucher MR-4310, we consider that the detailed phylogenetic analyses conducted by Justo et al. (2011) and ourselves (which show it to be distinct), combined with our microscopic analysis of the voucher merit is formal naming.

**SuppFigS1.** Microscopic features of *Crystallicutis damiettensis* basidiome. A smooth/non perforated, honey-yellow hymenium encrusted with brown clumps/resinous granules (A: 50x light magnification), which were visible under SEM (B); also clusters of large, amorphous, hyaline crystals observed under SEM (C) and
LM (D). In transverse section; the basidiome is composed of a compact mat of mycelia (E) with a monomitic hyphal system consists of three types of generative hyphae, as arrowed (normal generative hyphae with clamps, crystal-encrusted basal hyphae and pseudo-skeletoid hyphae) (F). Clavate 4-spored basidia (arrowed), smaller basidioles (G) are visible on the hymenium, as are sometimes thick-walled ovoid basidiospores (H), showing no reaction with Melzer’s reagent (H; right). Generative hyphae with basal clamps (I; Cotton Blue stain) are visible, as are spear-shaped (2-celled) cystidia (J, K) and fusiform cystidioles (L). Scale bar indicates 10 µm (except A = 400 µm).

**SuppFigS2B.** Diagram of the microscopic structures of the basidiome of *Crystallicutis rajchenbergii*: Hymenium layer with ovoid to clavate thick-walled basidia and basidioles (5-6 x 8-10 µm), thick-walled, subellipsoid basidiospores (3-6 x 10-15 µm) (A). Fusiform thick-walled cystidioles with a basal swelling (10 x 3 µm) (B). Flame-shaped cystidia (2-cells) with sharp apex, thick walled and non-encrusted (25-30 x 4-5 µm), some were top encrusted (C). Free large regular rhomboid crystals (25-37 µm across), other irregular crystals (3 x 4µm to 30 x 35 µm) (D). Thin-walled clamped generative hypha (2.5-3.0 µm diam) (E), heavily-encrusted hyphae (3-4 µm diam), getting thinner (1.5-2 µm diam) densely branched hyphae in the subhymenium (F). Thick-walled pseudo-skeletoid hyphae (5-6 µm diam) (G). Scale bar indicates 10 µm.

**Discussion**

Resupinate fungi are among the most important wood-decay fungi. Not only do they contribute to nutrient cycling by decomposing wood debris, but they are also a potentially valuable source of novel pharmacologically-active biomolecules (Stošić-Grujičić et al., 2011; Zapora et al., 2016). During a survey of basidiomycetes growing on North Nile Delta of Egypt, resupinate basidiomes with unusual morphology were found growing on fallen, dead trunks of *P. dactylifera* in a fruit farm.

Following initial DNA barcoding, generic placement of this taxon could not be determined readily from its morphological features because it possessed characters assignable to several genera. However, following more detailed phylogenetic analysis using RPB1 and EF1α locus, UN63A was placed close to *Ceraceomyces serpens* and voucher Dai6090 (labelled as *Ceriporia sulphuricolor*), with strong statistical support.

Previous phylogenetic reconstructions including these two species, also placed them
in the same clade (Chen et al., 2020; Justo et al., 2017), and it was already apparent that the generic names attributed to these species were incorrect, since the type species of *Ceraceomyces* is in Amylocorticiales, whilst *Ceriporia viridans* (type species for this genus, also in Irpicaceae) is placed close to *Meruliopsis*. Sequence data was obtained for the type specimen of *C. sulphuricolor* (Bernicchia 6591, from Italy; (Bernicchia and Niemelä, 1998)). Our phylogenetic analyses showed it to be unrelated to voucher Dai6090 from China (Cui and Jia, 2011; Chen et al., 2020) and to be identical to *Ceriporia alachuana* (SuppData2).

As has been found to be the case with other genera within Irpicaceae and other families within Polyporales (Floudas and Hibbett, 2015; Justo et al., 2017), morphological comparisons of the four species which we now place within *Crystallicutis*, revealed relatively few consistent features but all four form basidiomes with crystalline encrustations of the hymenium, subhymenium and subiculum. Basidiomes are usually yellow-coloured with a white margin, though *C. serpens* basidiomes are sometimes pinkish or greenish-coloured. Other features such as presence of cystidia and clamp connections, as well as the macromorphology of the hymenophore surface, are not conserved within the genus.

Ginns (1975)(p. 147) observed that *C. serpens* exhibited some unusual traits in wood decay, “with a white-rot of angiosperms and what, visually, appears to be an indistinctive white or incipient brown rot of conifers”. In pure culture, he observed it to oxidise gallic acid strongly but did not detect laccase activity using gum guaiac substrate. We have previously examined the ligninolytic capability of isolate UN63A using the model substrate ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic
acid)) (El-Gharabawy et al., 2016). It was found to secrete Mn-dependent and Mn-independent peroxidase, as well as laccase. Despite its slow growth rate and low enzymatic activity relative to the other Polyporales with which it was compared, it caused rapid loss of substrate dry weight in ash sawdust culture. In nature, *C. damiettensis* causes a white-rot on decaying datepalm trunks but enzymatic evidence suggests that it may have an unusual mechanism of wood decay. *C. huangshanensis* (Dai 6090) was reported to produce a white-rot (Cui and Jia, 2011) but to our knowledge, no pure cultures of this species exist. However, a culture derived from voucher MR-4310 (*C. rajchenbergii*) is available at CFRM. The presence of crystal-encrusted hyphae in several of the species in this clade may relate to the unusual mechanism of wood decay alluded to above.

There have been very few previous studies of macrofungi associated with datepalm logs. Of these, Rattan et al. (1980) was the most detailed with regard to resupinate fungi but none of the organisms they describe (from Iraq) matches the features of *Crystallicutis damiettensis*. Egypt is globally the largest grower of date palm and the arrival of red palm weevil in 1993 has caused a drop in production exceeding 30% (Al-Dosary et al., 2016). It is possible that this fungus has only recently arrived in the Mediterranean region, following the spread of the red palm weevil *Rhynchophorus ferrugineus* (since the 1980’s). This highly invasive pest attacks more than 40 palm species and has spread from Asia widely across the Mediterranean region in recent decades (Al-Ayedh, 2008; Al-Dosary et al., 2016).

The consistent association of *C. damiettensis* with *R. ferrugineus* suggests that a mutualistic interaction between these organisms, as has been found in other wood-
and that the presence of *C. damiettensis* exacerbates the damaging effects of the weevil. For example, the white-rot fungus *Donkioportia expansa* (Polyporaceae) is found in consistent association with the deathwatch beetle (*Xestobium rufovillosum*) (Belmain et al., 2002; Campbell and Bryant, 1940). Similarly, *Flavodon ambrosius* (also Irpicaceae) is found as mycosymbiont of *Ambrosiodmus* ambrosia beetles (Li et al., 2015), being transported by their vector in specialised mycangia (Simmons et al., 2016) and suppressing the activity of other wood decay fungi (Skelton et al., 2019b). There is hitherto no direct evidence at present that *C. damiettensis* contributes to the tree damage caused by *R. ferrugineus* (subfamily Dryophthorinae). However, it lies within the same family (Curculionidae; order Coleoptera) as Ambrosia beetles (subfamilies Platypodinae and Scolytinae) and bark beetles (subfamily Scolytinae) so the coincidence in the distribution of *R. ferrugineus* and *C. damiettensis* raises the possibility that the former may be a targeted vector of the latter (Jacobsen et al., 2017).

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Declaration

Ethics approval and consent to participate
Not applicable

Adherence to national and international regulations
For samples obtained from fungarium collections, appropriate permissions were granted. Field sampling was undertaken with appropriate permissions from Egyptian authorities.

Consent for publication
All authors have approved the manuscript for submission

Availability of data and material
All the sequences generated in this study are deposited in GenBank (accession numbers can be found in Table 1). Alignments used to generate the phylogenies are available in Figshare (DOI:10.6084/m9.figshare.13574255). Samples are deposited in the biorepository <ABS>

Competing interests
The authors have declared that no competing interests exist.

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Author contributions

HME - undertook fieldwork and labwork; writing of the paper; CALD - Phylogenetic analyses; writing of the paper; GWG - conceived the paper; analysis of data; drafted the manuscript.
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Fig. 1. *Crystalllicutis damiettensis* infecting date palm trunks. Honey-yellow basidiomes with white margins are visible emerging from the bark (A), often associated with bore holes of red weevil (B, arrowed) and batches of white-rot decay (C). Basidiome sometimes formed in long decay columns (D), also at trunk ends (E) and inside hollowed dead stumps (F).
Fig. 2. Detailed view of resupinate basidiomes of *Crystallicutis damiettensis* in the field. The resupinate basidiomes are honey yellow coloured with a granulated (papillate) surface and white thin fibrous margin when young (A). Thicker velvety mats with a warty (bullate) surface, irregularly crenulated and a waxy appearance are also found (B). Older basidiomes are buff to pale brown with white margins and cracked (C), with the surface becoming smoother with a dull (not waxy) appearance, concolorous flesh and soft dense texture (D). Scale bar indicates 1cm.
**Fig. 3.** *Crystallicutis damettensis* in pure culture on PDA. Floccose appearance of young colonies of isolate UN63A (2 weeks old), with slight yellow coloration (A). Colonies incubated in the light exhibited pigmentation similar to that seen in basidiomes (B). Assessment of somatic incompatibility between isolates from Kafr El-Sheikh (UN63A, UN63B, UN63C). Yellow pigmentation after incubation in the light for 4 weeks is visible on the upper surface (C), with zone lines between genetically different cultures (B vs A/C), more clearly visible from beneath (D).
**Fig. 4.** Micromorphology of *Crystalllicutis damiettensis.* In pure culture, abundant clamp connections are visible in brightfield (A) and under epifluorescence microscopy with Calcofluor B staining (B,C; arrowed). Spherical-ellipsoid chlamydospores, both intercalary and terminal, are abundant (B-D), alongside brown resinous agglomerations (D) and encrustation by small crystals of individual hyphae (D, inset). In basidiomes examined by scanning electron microscopy, large crystals are visible, embedded in the matrix of the hymenium surface (E; arrowed) and smaller crystals encrusting the surface of hyphae in the subhymenium and subiculum (F). Scale bar indicates 10 µm.
Fig. 5. Diagram of the microscopic structures of the basidiome of *Crystallidicus damiettensis*. Hymenium layer with clavate 4-spored basidia, thick-walled basidiospores, smaller basidioles and basal clamps (A). Cystidia are spear-shaped (B) or fusiform (C), with cystidioles also present (D). Large and small hyaline crystals (E) and other encrustation on hyphae were observed (F). Generative hyphae with abundant clamps (G) and pseudo-skeletoid subicular hyphae (H) are present. Scale bar indicates 10 µm.
Fig. 6. Multigene maximum-likelihood tree of Irpicaceae. Support values are presented as numbers (UFBoot/BPP) on branches and shown only for UFBoot ≥ 70 and BPP ≥ 0.70. Type species for other genera within Irpicaceae are represented by a star. Outgroups are Bjerkandera adusta and Terana caerulea (Phanerochaetaceae). *Crystallicuts* gen. nov. is boxed in red. Asterisks (*) represent maximum UFBoot/BPP values, dashes (−) represent values below the cut-off threshold (70%), and dots (.) represent ML clades that were not recovered in the BI tree. Scale bar indicates number of substitutions per site. More details on supporting values can be found in SuppData1.
Supplementary data for:-

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Crystallicutis gen. nov. (Irpicaceae, Basidiomycota), including C. damiettensis sp. nov., found on Phoenix dactylifera (date palm) trunks in the Nile Delta of Egypt

https://doi.org/10.1016/j.funbio.2021.01.004
SuppFig1. Microscopic features of *Crystallicuts damiettensis* basidiome. A smooth/non perforated, honey-yellow hymenium encrusted with brown clumps/resinous granules (A: 50x light magnification), which were visible under SEM (B); also clusters of large, amorphous, hyaline crystals observed under SEM (C) and LM (D). In transverse section; the basidiome is composed of a compact mat of mycelia (E) with a monomitic hyphal system consists of three types of generative hyphae, as arrowed (normal generative hyphae with clamps, crystal-encrusted basal hyphae and pseudo-skeletoid hyphae) (F). Clavate 4-spored basidia (arrowed), smaller basidioles (G) are visible on the hymenium, as are sometimes thick-walled ovoid basidiospores (H), showing no reaction with Melzer’s reagent (H; right). Generative hyphae with basal clamps (I; Cotton Blue stain) are visible, as are spear-shaped (2-celled) cystidia (J, K) and fusiform cystidioles (L). Scale bar indicates 10 µm (except A = 400 µm).
SuppFigS2. Morphology of the basidiome of *Crystallicutis rajchenbergii*; resupinate honey-yellow basidiome on deciduous wood (A) smooth non-ceraceous surface with small cracks when old/dry, with brownish centre (B) whitish yellow fibrous margins (C) 0.1-0.3 mm thickness (black arrowed in D). Scale bar is 5mm for A-D. Under light microscope; thin-walled clamped generative hypha (2.5-3.0 µm diam, red arrow in E/H, stained with Congo Red), most hyphae heavily-encrusted (3-4 µm diam, black arrow in E/F), thinner (1.5-2 µm diam) densely branched hyphae in the subhymenium (G). Thick-walled pseudo-skeletoid hyphae with larger diameter (5-6 µm diam, white arrow in F). Ovoid to clavate, thick-walled 4-spored basidia and basidioles on the hymenium surface, 5-6 x 8-10 µm in size (black arrows in H). Subellipsoid, thick-walled basi­diospores (3-6 x 10-15 µm) (I), cyanophilous (CB+ in J), non-amyloid/dextrinoid in Melzer’s reagent (K). Clusters of free large regular rhomboid crystals (on left; 25-37 µm across) and other irregular crystals (on right; 3 x 4µm - 30 x 35 µm) spread through the subhymenium and subiculum (L). Fusiform cystidioles (10 x 3 µm), thick-walled with a basal swelling (M), flame shaped cystidia (2-cells) with sharp apex (25-30 x 4-5 µm) (N with cotton blue), appear thick walled and non-encrusted in Congo Red (O), while others were top encrusted (P). Scale bar indicates 10 µm for E-P.
SuppFig3. Diagram of the microscopic structures of the basidiome of Crystallicutis rajchenbergii: Hymenium layer with ovoid to clavate thick-walled basidia and basidioles (5-6 x 8-10 µm), thick-walled, subellipsoid basidiospores (3-6 x 10-15 µm) (A). Fusiform thick-walled cystidioles with a basal swelling (10 x 3 µm) (B). Flame-shaped cystidia (2-cells) with sharp apex, thick walled and non-encrusted (25-30 x 4-5 µm), some were top encrusted (C). Free large regular rhomboid crystals (25-37 µm across), other irregular crystals (3 x 4µm to 30 x 35 µm) (D). Thin-walled clamped generative hypha (2.5-3.0 µm diam) (E), heavily-encrusted hyphae (3-4 µm diam), getting thinner (1.5-2 µm diam) densely branched hyphae in the subhymenium (F). Thick-walled pseudo-skeletoid hyphae (5-6 µm diam) (G). Scale bar indicates 10 µm.
**SuppData1: Parameters for phylogenetic analyses**

Partitions file with partition schemes and evolutionary models implemented in the Maximum likelihood analyses (IQTREE partitions file):

```nexus
begin sets;
  charset ITS1_ITS2_I3_RPB1 = Irpiceae_all.fas: 1-883;
  charset 58S_EF1a_2_RPB1_2_RPB2_2 = Irpiceae_all.fas: 884-1042 1044-3418\3;
  charset LSU = Irpiceae_all.fas: 3419-4291;
  charset EF1a_1_RPB1_1_RPB2_1 = Irpiceae_all.fas: 1043-3418\3;
  charset EF1a_3 = Irpiceae_all.fas: 1045-3418\3;
  charset RPB1_3_RPB2_3 = Irpiceae_all.fas: 1657-3418\3;
  charset I3_RPB1_indel = Irpiceae_all_indel.fas:MORPH, 1-98;
  charset ITS2_indelITS1_indel = Irpiceae_all_indel.fas:MORPH, 99-329;
charpartition mymodels =
  TPM2+F+I+G4: ITS1_ITS2_I3_RPB1,
  TPM3+F+I+G4: 58S_EF1a_2_RPB1_2_RPB2_2,
  GTR+F+I+G4: LSU,
  TIM+F+I+G4: EF1a_1_RPB1_1_RPB2_1,
  GTR+F+I+G4: EF1a_3,
  TPM2+F+G4: RPB1_3_RPB2_3,
  MK+FQ+ASC+G4: I3_RPB1_indel,
  MK+FQ+ASC+R2: ITS2_indelITS1_indel;
end;
```

Partitions file with partition schemes and evolutionary models implemented in the Bayesian Inference analysis:

```nexus
Models and partition schemes:
  GTR+F+I+G4: ITS1_ITS2_I3_RPB1,```
HKY+F+I+G4: 58S_EF1a_2_RPB1_2_RPB2_2,

GTR+F+I+G4: LSU,

GTR+F+I+G4: EF1a_1_RPB1_1_RPB2_1,

GTR+F+I+G4: EF1a_3,

GTR+F+G4: RPB1_3_RPB2_3;

MrBayes partitions file:

#nexus

begin mrbayes;

execute irpicaceae_mb.nex;

charset ITS1_ITS2_I3_RPB1 = 1101-1982;

charset 58S_EF1a_2_RPB1_2_RPB2_2 = 330-488 490-1100\3 2857-4619\3;

charset LSU = 1983-2855;

charset EF1a_1_RPB1_1_RPB2_1 = 489-1100\3 2856-4619\3;

charset EF1a_3 = 491-1100\3;

charset RPB1_3_RPB2_3 = 2858-4619\3;

charset INDEL = 1-329;

partition favored = 7: ITS1_ITS2_I3_RPB1, 58S_EF1a_2_RPB1_2_RPB2_2, LSU,

EF1a_1_RPB1_1_RPB2_1, EF1a_3, RPB1_3_RPB2_3, INDEL;

set partition = favored;

lset applyto=(1,3,4,5) nst=6 rates=invgamma ngammacat=4;

lset applyto=(6) nst=6 rates=gamma ngammacat=4;

lset applyto=(2) nst=2 rates=invgamma ngammacat=4;
lset applyto=(7) rates=gamma;

prset applyto=(1)

statefreqpr=fixed(0.210937,0.227899,0.237667,0.323497)
shapepr=fixed(0.873065)
pinvar=fixed(0.218331)
revmat=fixed(1.65262,5.79093,2.15199,0.799527,5.85249, 1);

prset applyto=(2)

statefreqpr=fixed(0.304123,0.220815,0.203096,0.271967)
shapepr=fixed(0.649635)
pinvar=fixed(0.709309)
revmat=fixed(1, 2.66487, 1, 1, 2.66487, 1);

prset applyto=(3)

statefreqpr=fixed(0.263434,0.194104,0.297374,0.245088)
shapepr=fixed(0.536896)
pinvar=fixed(0.556043)
revmat=fixed(1.49914,6.55845,2.31922,0.676263,14.4049, 1);

prset applyto=(4)

statefreqpr=fixed(0.261993,0.234213,0.352613,0.151181)
shapepr=fixed(0.797382)
pinvar=fixed(0.548203)
revmat=fixed(1.13561,1.77856,0.720257,0.482009,6.51285, 1);
prset applyto=(5)  
statefreqpr=fixed(0.124654,0.392391,0.247792,0.235163)  
shapepr=fixed(1.76944)  
pinvar=fixed(0.109357)  
revmat=fixed(2.75686,8.85939,0.0001,2.26517,21.744, 1);  

prset applyto=(6)  
statefreqpr=fixed(0.139993,0.3014,0.312622,0.245986)  
shapepr=fixed(1.40007)  
revmat=fixed(2.68707,18.3327,5.29837,1.80452,19.1293, 1);  

prset applyto=(7) ratepr=variable;  

end;
SuppData1; Tree 1. Bayesian Inference tree of Iplicaceae. Supporting values on branches are Bayesian Posterior Probability (in %). Red box shows the new genus and species clade. Scale bar: nucleotide substitutions per site.
SuppData1; Tree 2. Maximum likelihood tree of Iripaceae. Supporting values on branches are Non-parametric Bootstrap. Red box shows the new genus and species clade. Scale bar: nucleotide substitutions per site.
SuppData1; Tree 3. Maximum likelihood tree of Irpicaceae. Supporting values on branches are SH-rt / Ultrafast Jackknife. Red box shows the new genus and species clade. Scale bar: nucleotide substitutions per site.
SuppData1; Tree 4. Maximum-likelihood tree of Irpicaceae using the same genes and methods as main text Figure 6, with additional sequences of C. serpens supporting the position of this species within Cristallicutis.
**SuppData 2:** Sequence data were obtained from the type specimen (HUBO6591 / O-F-76351) of *Ceriporia sulphuricolor* for the ITS spacer region (GenBank: MW508516).

Phylogenetic reconstruction indicates that this sequence (arrowed) was identical to several sequences labelled as *Ceriporia alachuana* (red font), which are placed in Meruliaceae close to *Hydnophlebia*, as noted by Chen et al. (2020). The six sequences within this clade show broad geographical distribution (Italy, Iran, USA, China). A second group of unrelated sequences (green font), also labelled as *Ceriporia alachuana*. All originate from China or South Korea, and fall within Irpicaceae but closer to *Meruliopsis* than *Ceriporia* sensu stricto. The type specimen of *C. alachuana*, (from Florida, USA) has not been DNA barcoded, so it is at present unclear which of the two clades represent the true *C. alachuana*. Voucher L-11510-Sp from Florida (KP135340.1; bold font) represents a potential epitype being from a nearby location, if the type specimen is lost or degraded, as suggested by Chen et al. (2020). The type species of the genera *Ceriporia* and *Meruliopsis* are indicated by blue and green stars respectively. Salient bootstrap values (>70%) are indicated at nodes. Scale bar indicates number of substitutions per site.