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The unexpected ecological plasticity of *Phlegmacium herculeum* (Malençon) Bellanger & P.-A. Moreau, *comb. nov.*

EMANUELE CAMPO*, PIERRE-ARTHUR MOREAU**, DEMETRIS POLYCARPOU***
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Abstract

Due to conspicuous morphological features and a strict association with cedar trees, *Phlegmacium herculeum* has long thought to be one of the easiest *Cortinarius* to diagnose in the field. Recent collections with a deviant morphotype fruiting under *Pinus* trees, yet phylogenetically representing this species, are here introduced as *Phlegmacium herculeum* f. *pinophilum*. The combination *Phlegmacium herculeum* previously introduced was invalid and is validated here. Ecological interpretations of the discovery of a new host for *P. herculeum* are discussed.

Résumé

En raison de caractères morphologiques évidents et d'une association stricte avec les cèdres, *Phlegmacium herculeum* a longtemps été considéré comme l'un des cortinaires les plus faciles à identifier sur le terrain. Des récoltes récentes présentant un morphotype déviant et fructifiant sous des pins, bien que représentant phylogénétiquement cette espèce, sont présentées ici et formellement introduites comme *Phlegmacium herculeum* f. *pinophilum*. La combinaison *Phlegmacium herculeum* introduite précédemment n'était pas valide et est validée ici. L'interprétation écologique de la découverte d'un nouvel hôte pour *P. herculeum* est discutée.

Zusammenfassung

Aufgrund auffälliger morphologischer Merkmale und einer strikten Bindung an Zedern galt *Phlegmacium herculeum* lange Zeit als eine der am einfachsten im Feld zu diagnostizierenden *Cortinarius*-Arten. Neuere Aufsammlungen mit einem abweichenden Morphotyp, der unter *Pinus*-Bäumen wächst, aber phylogenetisch zu dieser Art gehört, werden hier als *Phlegmacium herculeum* f. *pinophilum* vorgestellt. Die zuvor eingeführte Kombination *Phlegmacium herculeum* war ungültig und wird hier validiert. Ökologische Interpretationen der Entdeckung eines neuen Wirts für *P. herculeum* werden diskutiert.

Riassunto

Per le caratteristiche morfologiche evidenti e la stretta associazione con gli alberi di cedro, *Phlegmacium herculeum* è stato a lungo considerato uno dei *Cortinarius* più facili da diagnosti-

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care sul campo. Recenti raccolte di un morfotipo fruttificante sotto alberi di *Pinus*, ma filogeneticamente rappresentative di questa specie, vengono qui descritte come *Phlegmacium herculeum* f. *pinophilum*. La combinazione *Phlegmacium herculeum* introdotta in precedenza non era valida e viene qui convalidata. Vengono discusse le interpretazioni ecologiche della scoperta di un nuovo ospite per *P. herculeum*.

Resumen

A causa de los evidentes caracteres morfológicos y la estricta asociación a los cedros, *Phlegmacium herculeum* ha pasado por ser durante muchos años uno de los *Cortinarius* más fáciles de diagnosticar en el campo. Recientes recolectas con un morfotipo diferente, fructificando bajo *Pinus*, aunque representa filogenéticamente esta especie, se presenta aquí como *Phlegmacium herculeum* f. *pinophilum*. La combinación *Phlegmacium herculeum*, previamente introducida, es inválida y se valida aquí. Se discute la interpretación ecológica de un nuevo huésped para el *P. Herculeum*.

Key words • Mots-clés • Schlüsselwörter • Parole chiave • Paraules clau: *Cortinarius*, *Cedrus*, *Phlegmacium herculeum* f. *pinophilum*, *Pinus*, phylogeny, taxonomy, host shift.

Introduction

Some taxa seem so well characterized that they evade taxonomic revisions with modern tools. This is the case for *Cortinarius herculeus* Malençon (1958), recently but invalidly (see below) recombined in genus *Phlegmacium* by Niskanen & Liimatainen (LIIMATAINEN et al., 2022), that is so far represented in public sequence databases by a single sequence each: KJ421098 in Genbank and UDB001104 in UNITE. These two sequences are however not identical and they were not generated from the type or authentic material (all preserved in G. Malençon's herbarium at MPU, in too poor condition to be suitable for sequencing), questioning their status of reference for the name. Despite this, no effort has been invested in past years to clarify the molecular signature of this species, in all likelihood because it is easily identified in the field by its stout habit, conspicuous smell of geosmin and its so far exclusive association with cedar trees.

In the past few years, we came across three puzzling *Phlegmacia* collections akin to *P. herculeum*, all from pure or mixed *Pinus* stands in Cyprus, Italy and southern France. Although they bore the typical odour of *P. herculeum*, none of these collections was identified as Malençon's taxon, mostly because of a different gross morphology and absence of cedars in the vicinity. Sequencing these collections revealed that they indeed represent *P. herculeum*, indicating that this species may sometimes be challenging to diagnose after all, especially when not fruiting under its assumed exclusive tree host. Here, we provide an unambiguous DNA barcode for this iconic taxon from multiple collections across the Mediterranean, and introduce a new form, *P. herculeum* f. *pinophilum*, for the atypical, pine-associated phenotype of this species.

Materials and methods

Morphological analyses

The collections were photographed in the field and detailed descriptions were made using fresh material. Microscopic structures were examined in fresh and dried material with light microscope Zeiss Primostar using plan-apochromatic objectives $\times 40$, $\times 60$ and $\times 100$ at oil immersion. The mounting media used were water, KOH 5%, anionic Congo red and anionic Melzer's reagent; dried material were previously rehydrated in ammonia solution 3%. Spores measurements were made by capturing images of spores taken from spore print, using GT CAM12 with camera control unit. Twenty spores were measured on three specimens of the holotype and ten spores from each

of the French and Cyprian collections; the minimum and maximum values detected are placed in brackets. Ten measurements were carried out for each other structure. All the material is deposited in the public herbarium AMB and in the private herbaria of EC and of the CEFÉ laboratory.

Molecular analyses

Five collections of *P. herculeum* were sequenced at the ITS locus, following methods described in LIIMATAINEN et al. (2017). Newly generated sequences were then compared with sequences published in Genbank and UNITE, through BLAST searches. Based on the results, an ITS dataset of 23 sequences spanning *Phlegmacium* sect. *Arguti*, was assembled, complemented by three other *Phlegmacia* sequences chosen as outgroup. Phylogenetic analyses of this dataset were conducted online at www.phylogeny.fr (DEREEPER et al., 2008). Multiple sequence alignment was performed with MUSCLE v. 3.7 (EDGAR, 2004). Maximum likelihood and Bayesian inference analyses were conducted, respectively, with PhyML v. 3.0 (GUINDON et al., 2010), using the GTR model of evolution (automatically selected), and MrBayes v. 3.1.2 (RONQUIST & HUELSENBECK, 2003), after 1 000 000 generations, tree and parameter sampling every 1 000 generations and an initial burn-in of 25 % (250 trees). Branch support was assessed, respectively, by the Shimodaira Hasegawa version of the approximate likelihood-ratio test (SH-aLRT), considered significant when ≥ 0.82 (ANISIMOVA et al., 2011; BELLANGER et al., 2015), and Bayesian posterior probabilities (BPP), considered significant when $\geq 95\%$ (RONQUIST & HUELSENBECK, 2003). Trees were built using TreeDyn 198.3 (CHEVENET et al., 2006) and edited with Inkscape 0.91 (<https://inkscape.org/fr>).

Results

The phylogenetic analysis of our ITS sequence dataset indicates that the two published sequences of *P. herculeum* KJ421098 and UDB001104, belong to the same clade, within sect. *Arguti* (Fig. 1). The UNITE sequence differs from KJ421098 and from all newly generated sequences mostly at the beginning of the ITS2 domain, by a few unique polymorphisms and deletions in the vicinity of a stretch of ambiguity letters. Together with a polyN stretch of undefined nucleotides at the beginning of the ITS1 domain, these features are hallmarks of poor quality sequences. In the same clade nest the sequences of two typical *P. herculeum* collections made by us under *Cedrus* in southern France (Fig. 2, 3). Interestingly, one of this collection (JMB2011112715, Fig. 2) fruited in a forest only 40 km south and with the same management history than that planted on slopes of the Mt Ventoux, where Moser collected the material represented by UDB001104. This finding further supports that the latter sequence does represent *P. herculeum* and that its long branch in Fig. 1 is artefactual. Taken together, our results confirm the phylogenetic identity of *P. herculeum* and establish e.g. KJ421098 as a proper barcode for this name, which can be safely assigned to the UNITE Species Hypothesis SH1942516.10FU.

More surprising is the position within the same clade of three additional sequences of ours, generated from collections from southern France, Italy and Cyprus, none of them initially identified as *P. herculeum* based on their morphological and ecological characteristics (see Taxonomy below). The French and Italian collections were fruiting in forests dominated by *Pinus nigra* subsp. *salzmannii* and *P. pinea*, respectively, with no trace of living or dead cedar trees around. The Cyprian collection was found in a mixed *P. brutia* forest that also included *Quercus*, *Platanus* and other Mediterranean vegetation, but again devoid of cedars. Therefore, in contrast to its original and current concept, *P. herculeum* is not strictly associated with *Cedrus* as previously thought, but can also fruit under *Pinus*.

At first sight, these three harvests display similar morphological features that make them more reminiscent of *P. fraudulosum* or even of a mature and discoloured *P. caligatum* rather than *P. herculeum* (Fig. 4–11). Phylogenetically, the French and Italian collections display a unique C/T

polymorphism at the beginning of the ITS1. However, because the Cyprian material does not, no phylogenetic support for this deviant morphotype can be identified, therefore not supporting the introduction of a new species. For this reason, and to accommodate an appropriate rank for this morphotype also taking into account its apparent association with *Pinus* trees, we here describe it at an infraspecific rank, *Phlegmacium herculeum* f. *pinophilum*.

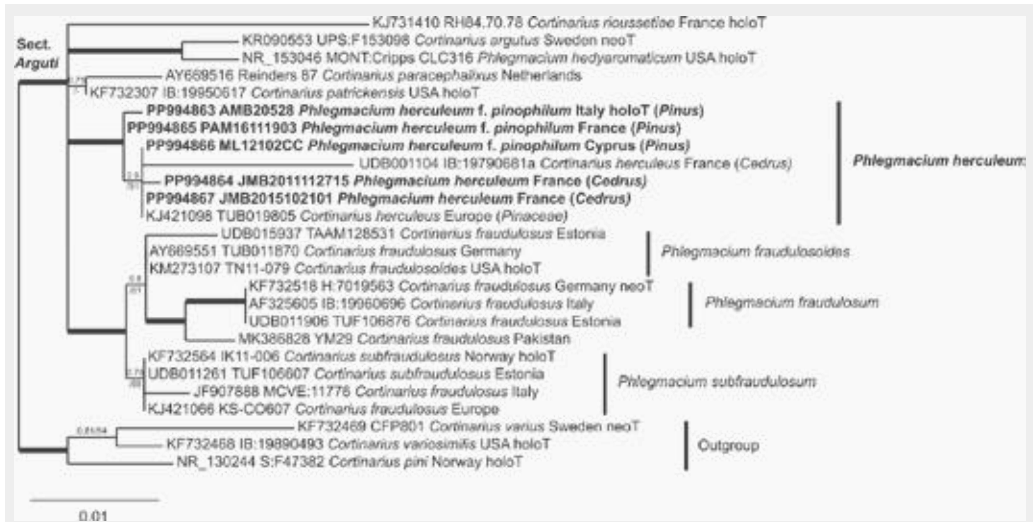


Figure 1 — ITS DNA phylogeny of *Phlegmacium* sect. *Arguti*

Phylogram resulting from the Bayesian Inference analysis of all available sequences of *P. herculeum*, as well as sequences representing sect. *Arguti*. Maximum likelihood (SH-aLRT) and Bayesian inference (BPP) branch support values are indicated by branches. Significantly supported branches (SH-aLRT 0.82 and BPP 95 %) are thickened. Sequences generated for the present work are highlighted in Bold.

Taxonomy

Phlegmacium herculeum (Malençon) Bellanger & P.-A. Moreau, *comb. nov.* **Fig. 2, 3**
Mycobank MB854728.

Basionym: *Cortinarius herculeus* Malençon in G. Malençon & R. Bertault, *Travaux de l'Institut Scientifique Chérifien, Série Botanique et Biologie Végétale* 33: 503 (1970). Mycobank MB854739.

Protonym: *Cortinarius herculeus* Malençon, *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* 7, p. 159 (1958), invalid (TURLAND et al., 2018, art. 40.1: type not indicated). Mycobank MB295872.

Nomenclatural note: When combining most *Cortinarius* species names into their ten newly defined genera, LIIMATAINEN et al. (2022) designated as basionym for *Phlegmacium herculeum* (Malençon) Niskanen & Liimat., *Cortinarius herculeus* Malençon, «*C.R. Soc. Sci. nat. Maroc*: 159 (1958)», following the data provided at this date by the online databases Mycobank and Index Fungorum. After carefully checking the whole publication by Malençon (1958), we concluded that the latter name was introduced invalidly, because no holotype was designated, despite this becoming mandatory by Jan 1st, 1958 (art. 40.1 of the International Code of Nomenclature, TURLAND et al., 2018). Malençon was probably aware of this omission and added the citation of the holotype when reproducing the diagnosis of his species in Malençon & Bertault (1970: 503), thus validating the name. As a result, the combination based on an invalid basionym proposed by the Finnish authors is invalid (art. 41.2, see also 41.8). We here fix this issue by repeating their nomenclatorial move, but

citing as basionym the earliest valid publication of *Cortinarius herculeus* by Malençon, dating back to 1970, in the first part of the French author's monograph.

Holotype: MOROCCO. Azrou, in cedar forest, 13 Nov 1937, G. Malençon, n°769/MPUC00484.

Original diagnosis: *Pileo magno*, 10–15(–20) cm lato, plerumque 12–15 cm, hemisphaerico, deinde e convexo plano, margine inflexa, aetate paulum medio depresso; firmo, crasso, gravi, primum ex ochraceo stramineo, deinde sordide alutaceo, postremo fulvido, cortina ex argentea candida, flavescente, disco excepto, velato, quae 1–2 cm super marginem lineam orbicularem submembranaceam, ex albam sulfurinam, relinquit; medio punctato, alibi tenuissimus fibrillis radialibus virgato, udo viscidulo, siccum paulum lustrato; margine inflexa-involuta, paulum excedente, atque cortinae vestigiis appendiculata. Stipite pleno, robusto, 10–15 cm x 20–32 mm (in parte media), elato, interdum erecto, saepius ad basim arcuato, quae in clavam dilatata est et in parvum mucronem subradicatum designit, imposito, striolato, primum albedo, deinde coloribus ex luteolis sordide argillaceis e basi ad apice tincto, levi et sursum paulum fibrilloso, ubi cortina annuliformis plus minusve, manifesta videtur, inferius squamulis vel furfuribus sulfurinis vel ex argillaceis sulfurinis in annulos superpositos et plus minusve integros dispositis, variato.

Lamellis latis (8–13 mm), parum stipatis, inaequalibus, adnatis-sinuatis vel subliberis, pallidis, e roseis pallide avellaneis, deinde argillaceis, acie concolore, integra, deinde inaequaliter denticulata.

Carne albida vel flavescente in pileo, sordide argillacea, in imo stipite paulum luteis, firma, odore terrae vel mucoris, gravissimo, sapore dulci, terram revocante. Sporis e ferrugineis cinnamomeis vel brunneis (fulvis, castaneo addito, secundum Chromotaxia Sacc., vel Séguy 131), amygdaliformibus, sub lente fulvis, maxime punctatis, praesertim in apice, area hilari reducta, sublaevi vel rugulosa, magnis, 11–13 x 6.5–7.25 µm. Hab. - Ad terram in cedretis, singularibus vel in circulas vigenis, automno. Moyen Atlas et Rif (Maroc).

Studied material: FRANCE. Gard, Montdardier, under *Cedrus atlantica* in the mixed forest of the pic d'Anjeau, calcareous soil, elev. ca 700 m, 21 Oct 2015, J.-M. Bellanger, JMB2015102101, Genbank ITS PP994867; Vaucluse, Bonnieux, under *Cedrus atlantica*, calcareous soil, elev. ca 720 m, 27 Nov 2015, J.-M. Bellanger, JMB2011112715, Genbank ITS PP994864. ITALY. Sardinia, Villagrande Strisaili (NU), Luas, Bosco di Santa Barbara, under *Cedrus atlantica*, 9 Nov 2017, E. Campo & M.C. Magnozzi, AMB17723 (CAMPO 2018, not sequenced).

Comments: This species is remarkable due to the macroscopic stability of its concept, which has been abundantly documented in literature for over half a century. As defined by Malençon (1958), it represents a stout fungus, first compared to *C. cephalixus* sensu Konrad & Maublanc (now *Phlegmacium cliduchum* (Secr. ex Fr.) Ricken), earlier cited by Maire (1914) as *Cortinarius claricolor* (Fr.) Fr. or *Cortinarius turmalis* Fr., with a strong odour of earth or dust and strictly associated with *Cedrus* trees. All later authors endorsed this definition (e.g. MOSER, 1978; CETTO, 1983; HENRY, 1986; BIDAUD et al., 1999, CONSIGLIO, 2009) and only the extent of lilac hues on lamellae and veil prompted Robert Henry to introduce var. *ionophyllus* and later f. *violascens* (HENRY, 1986, 1989). It should be noted, however, that already in the original description, Malençon did mention the variability of these blue tinges in some basidiomata, which led him to informally introduce a «var. *lilaceus*» for one of his collection (n°1830, MALENÇON, 1958).

Regarding the ecology, the consensus is absolute as we could not find a single report (both in printed books and on the web) of *P. herculeum* mentioning a putative host tree other than cedar. In this respect, it is interesting to note that when describing the obscure but morphologically similar *Cortinarius herculoides* Bertault from a *Quercus suber* forest in north Morocco, BERTAULT (1983) wrote: «First of all, it should be noted that the cork oak forest habitat immediately eliminates the strictly cedar-associated *C. herculeus*» (*Remarquons d'abord que l'habitat en forêt de chêne-liège élimine d'emblée le C. herculeus strictement cédricole*). Although the author points to some additional distinguishing criteria, mostly the localization of the smell in the lamellae vs the context, the association with cedars was considered so strong, that it is clear for Malençon's

collaborator that any *P. herculeum* lookalike not collected under a cedar tree, belongs to a different species.

In contrast to the wide consensus over the macroscopic, organoleptic and ecological defining criteria of *P. herculeum*, spore size of this species seems to vary a bit among collections and among different descriptions. In the original diagnosis, Malençon reports large amygdaliform spores of $11\text{--}13 \times 6.5\text{--}7.25 \mu\text{m}$, but the revision of the holotype material (MPU) by the authors of the *Atlas des Cortinaires* (BIDAUD et al., 1999) and then by CONSIGLIO (2009), yielded slightly different values: «slightly smaller» and « $11.6\text{--}14.5 \times 6\text{--}8.2 \mu\text{m}$, most of the time $12\text{--}13 \times 6.8\text{--}7 \mu\text{m}$ (one collection $10\text{--}11 \times 6\text{--}7 \mu\text{m}$)», respectively. Our two sequenced collections from cedars somehow confirm this micro-anatomical plasticity, as JMB2015102101 and JMB2011112715 deliver spores of $12.5\text{--}14 \times 6\text{--}7 \mu\text{m}$ and $10.5\text{--}12.5 \times 6.5\text{--}7 \mu\text{m}$, respectively, while an unsequenced collection from cedars in Cyprus has spores measuring $10\text{--}14 \times 6.5\text{--}7.5 \mu\text{m}$ (data not shown). They are otherwise fully consistent with most published descriptions and illustrations of the species, in its slightly lilacinous form (Fig. 2).



Photo: J.- M. Bellanger

Fig. 2 — *Phlegmacium herculeum*, in situ basidiomata, coll. JMB2011112715, France



Photo: E. Campo

Fig. 3 — *Phlegmacium herculeum*, in situ basidiomata, coll. AMB17723, Italy

Phlegmacium herculeum* f. *pinophilum E. Campo, P.-A. Moreau, Polycarpou & Bellanger, *f. nov.* **Fig. 4-12**

Mycobank MB854729.

Etymology: refers to the apparent association of this form with *Pinus* spp.

Holotype: ITALY. Venezia, Oasi di Vallevicchia-Brussa, in coastal place under *Pinus pinea* on calcareous and sandy soil, elev. 0 m, 4 Dec 2023, E. Campo, Herbarium number AMB20528, Genbank ITS PP994863.

Isotype in private herbarium (E. Campo) EC23120428.

Diagnosis: differs from the type by a less robust habit, the lack of lilac hues in any part of basidiomata and by occurrence in pure or mixed pine forests, without the presence of cedar trees.

Description

Basidiomata large-sized, but less robust or more slender than the type, fruiting scattered to gregarious. Pileus 40–80 mm, hemispherical at first, then convex or widely campanulate with the margin remaining involuted for a long time, and often becoming sinuous at maturity. Cuticle smooth, shiny, dry to slightly viscid in moist weather, usually with some remnants of whitish veil at the margin, pale buff or ochraceous-buff when young, then turning more ochraceous, sometimes fibrillose on the margin in old specimens. **Lamellae** rather thick, emarginate, whitish to pale clay-coloured, then hazelnut brown, light rusty brown at the end; edges very thin, entire and concolorous. **Stipe** 40–120 mm long, 10–20 mm wide, flexuose, rooting, cylindrical or slightly attenuated at the base, rarely clubbed, whitish to light lemon-yellow and fibrillose in the upper part, covered by a white membranous veil that forms a well-defined ascending ring, veil breaking into bands of scales on the lower part that soon become salmon-orange to tawny-brownish. **Context** white, firm, slightly yellow on mature specimens and when exposed to the air, greenish grey by oxidation in stipe medulla, in parts greyish-green in exsiccata; with a mild taste and a strong and earthy odour. **Macrochemical reaction** to KOH negative or dull red-brown on the cuticle, yellowish or dull red-brown in the context of the pileus, weakly yellow-orange in that

of the stipe; guaiac, phenol and FeSO₄ all negative, slowly grey-greenish in the context with the latter chemical.

Basidiospores (10.5–)11.2–14(–14,5) × (5.5–)6–7(–7.5) μm, Q = 1.80–2.10, amygdaloid with medium and low warts; weakly dextrinoid. **Basidia** 35–45 × 9–10 μm, tetrasporic, clavate with sterigmata up to 6 μm long, clamped. **Marginal cells** scattered, 20–30 × 4–8 μm, cylindrical, clavate or subulate, clamped. **Lamellar trama** composed of parallel hyaline hyphae 4–12 μm wide, up to 15–30 μm wide in the middle layers, slightly constricted at the septa. **Pileipellis** an epicutis of loosely intertwined, 4–8 μm wide hyphae, slightly gelatinized with obtuse terminal articles, strongly incrustated in a yellow-ochre pigment, surrounding larger hyphae 10–18 μm wide with weak yellowish-brown parietal pigment. **Clamp** connections present everywhere.

Habitat & distribution: So far confirmed in pure or mixed *Pinus* forests of the Mediterranean area, in southern France, north-eastern Italy and Cyprus. Probably more widespread but misidentified in the absence of DNA sequencing.

Other studied material: CYPRUS. Lythrodontas, mixed forest with *Pinus brutia*, *Platanus orientalis* and other deciduous trees, 20 Jan 2021, D. Polycarpou, ML12102CC, Genbank ITS PP994866. FRANCE. Hérault, Pégairolles-de-Buèges, *Pinus nigra* subsp. *salzmanii* with a few *Quercus ilex* on calcareous soil, 19 Nov 2016, P.-A. Moreau & F. Richard, PAM16111903, Genbank ITS PP994865.

Comments: This form displays morphological and ecological features that make it quite distinct from the type and other previously published forms. Basidiomata are more slender and less robust than those of cedar-associated populations. According to our sampling, the pine-associated form is totally devoid of blue-lilac tinges in any part of basidiomata. Basidiospores are quite variable in size among our three collections, but values are in the same broad range as that reported for *C. herculeus*. Lastly, this form appears to exclusively occur in *Pinus*-dominated forests, without any trace of cedar trees around.



Photo: E. Campo

Fig. 4 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidiomata, coll. AMB20528 (holotype), Italy



Photo: E. Campo

Fig. 5 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidiomata, coll. AMB20528 (holotype), Italy



Photo: E. Campo

Fig. 6 — *Phlegmacium herculeum* f. *pinophilum*, exsiccata, coll. AMB20528 (holotype), Italy



Photo: P.-A. Moreau

Fig. 7 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidiomata, coll. PAM16111903, France



Photo: P.-A. Moreau

Fig. 8 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidiomata, coll. PAM16111903, France



Photo: D. Polycarpou

Fig. 9 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidioma, coll. ML12102CC, Cyprus



Photo: D. Polycarpou

Fig. 10 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidioma, coll. ML12102CC, Cyprus



Photo: D. Polycarpou

Fig. 11 — *Phlegmacium herculeum* f. *pinophilum*, in situ basidioma, coll. ML12102CC, Cyprus

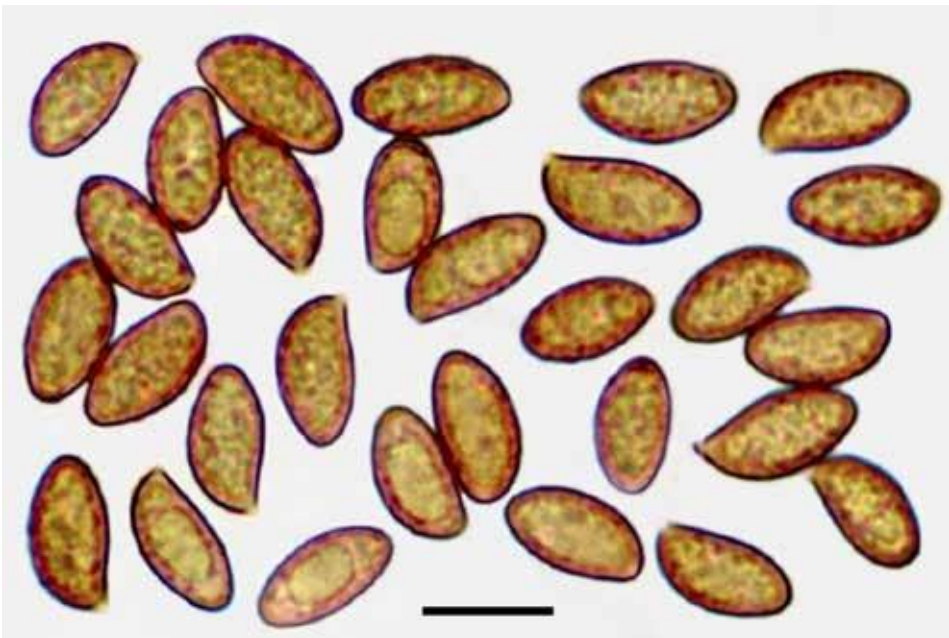


Photo: E. Campo

Fig. 12 — *Phlegmacium herculeum* f. *pinophilum*, spores, coll. AMB20528 (holotype), Italy.

Scale bar = 10 μ m

Discussion

Cedar forests are known to host a limited number of specific ectomycorrhizal (EcM) fungi, which usually dominate their communities, in association with opportunistic or rare species of *Inocybe* s.lat. and *Hebeloma* species (e.g. MAIRE, 1914; MALENÇON & BERTAULT, 1975). *Cedrus*-specific taxa are abundant and distinct enough to have been thoroughly documented, at least since their official descriptions; namely: *Geopora sumneriana* (Berk.) Torre as early fruiting Ascomycota, *Phlegmacium herculeum* and *Tricholoma cedretorum* Bon as fall-fruiting species, apparently exclusively associated with this host. Other species thought to be originally specific to cedars, such as *Cortinarius cedretorum* Maire or *Ramaria cedretorum* Maire, revealed to be at least as common in ecogeographically homologous pine forests and occasionally other host trees in continental Europe. Rarer species are less documented, but interestingly, some emblematic ones, such as *Gomphus crassipes* (Kuntze) Maire, *Paralepistopsis amoenolens* (Malençon) Vizzini or *Cantharocybe gruberi* var. *luteosaturata* (Malençon) Esteve-Rav. et al. (the last two probably saprobes), originally described from cedar forests from North African stands and also found in plantations in Europe, were also reported from natural pine forests in Southern Europe (PÉREZ DANIÉLS & PALAZÓN LOZANO, 2005; MOREAU et al., 2001; ESTEVE-RAVENTÓS et al., 2011).

Cedrus atlantica is endemic of the Atlas Mts (Algeria and Morocco, North Africa) and was only massively introduced in Western Europe (especially Southern France) in the late XIXth century (PONS, 1998). *Cedrus libani* has a broader natural area spanning the Eastern Mediterranean Basin and has been planted all over Europe as an ornamental tree since the XVIIth century. The endemic Cyprian species *Cedrus brevifolia* and the Himalayan species *Cedrus deodara* have been planted in Western Europe during the second half of the XXth century and remain ornamental (TOTH, 1980; BOU DAGHER-KHARRAT et al., 2007). The fungal communities in natural cedar stands are relatively well-documented for *C. atlantica* in North Africa (MALENÇON & BERTAULT, 1970, 1975) and to a lesser extent *C. brevifolia* (LOIZIDES et al., 2011; LOIZIDES, 2021), also documented by local surveys from Turkey concerning *C. libani*. All available data suggests that the profiles of ectomycorrhizal communities in mature stands are dominated by generalist species (*Hebeloma* spp., *Inocybe* spp., *Tricholoma* spp.), but include the same host-selective species *Geopora sumneriana*, *Phlegmacium herculeum* and *Tricholoma cedretorum*, found across the entire range of *Cedrus* spp. distribution. The recent discovery of two apparently *Cedrus*-specific species, *Cortinarius viridans* Bellanger & Loizides (in BIDAUD et al., 2021), so far only known from Cyprus, and *Tricholoma anatolicum* H. H. Doğan & Intini, apparently specific of *Cedrus libani* in Turkey and *C. atlantica* in North Africa (INTINI et al., 2003; BENAZZA, 2017), remain noticeable exceptions. Other taxa described from North African cedar forests, such as *Hygrophorus purpurascens* var. *cedretorum* Maire (MAIRE, 1914), *Inocybe dolichospora* Malençon (in MALENÇON & BERTAULT, 1970), *Tricholoma cedrorum* Maire (MAIRE, 1928; MALENÇON & BERTAULT, 1975), or *Cortinarius malenconii* Bidaud et al. (= *C. aurasiacus* ss. Malençon & Bertault, 1970; BIDAUD et al., 1993) could represent additional examples of endemic host-specific EcM fungi. However, since the latter four taxa are not documented outside their original localities, their apparent host specificity may just reflect a paleoendemism with very few relictual stations (or rarely fruiting), that makes unlikely a fortuit introduction in other continents with other host trees.

Regarding *Gomphus crassipes*, *Ramaria cedretorum* or *Cantharocybe gruberi* var. *luteosaturatus*, the hypothesis of a host extension of *Cedrus*-specific species to European coniferous trees is possible although rather unlikely, since the concerned European localities are not especially artificialized, nor close to *Cedrus*-planted areas. Thus, these taxa were more likely originally associated with mixed coniferous forests in Mediterranean mountains, either with loose EcM associations to their hosts, or having shifted from pines to cedars (or reverse) during the long palaeartic coexistence of cedars and pines, before the disparition of the first from Europe about 700 000 years ago (PONS & QUÉZEL, 1998). Consistently, species known to occur in both pine and cedar forests are mostly species with

no strict host specificity (such has *Hebeloma eburneum* Malençon or *H. subtortum* P. Karst., amongst the most commonly cited in literature; see BEKER et al., 2016). Some of them prefer *Pinaceae*, such as *Tricholoma terreum* (Schaeff.) P. Kumm., *Boletopsis mediterraneensis* G. Moreno et al. (CROUS et al., 2019), *Cortinarius dibaphus* Fr., and *Sarcosphaera coronaria* (Jacq.) J. Schröt. Finally, most species originally described from *Cedrus* forests and initially thought to be host-specific and characteristic of cedar stands such as the spring-fruited Ascomycota *Neourmula pouchetii* (Berthet & Rioussset) Paden and *Tarzetta insignis* (Berthet & Rioussset) Korf & J. K. Rogers (FOUCHIER & NEVILLE, 1998) were recently reported under pines or other conifers (PFISTER et al., 2008; VAN VOOREN et al., 2019).

In this context, *Phlegmacium herculeum* and *Tricholoma cedretorum* represent noticeable exceptions within a *Cedrus*-associated fungal community that is globally non-specific. The evidence that *P. herculeum* can also be found in natural pine stands without *Cedrus* trees in the vicinity suggests that the apparent specificity of EcM fungi to *Cedrus* may result from a relict, pre-glaciation period, when pines and cedars co-existed and might have shared part of their fungal communities. The subsequent geographical split of pine- and cedar-dominated forests during ice-ages and the isolation of *Cedrus* spp. in confined relictual areas during these times, may have selected a few, apparently hyper-specialized fungal species remaining with cedars, whilst pines maintained more diversified fungal communities across a much broader geographical range. As suggested by Pozzi et al. (2018) about *Alnus cordata*, EcM trees with a reduced area such as *Cedrus atlantica* tend to have either lost their specific fungal partners, or to have kept a few, hyper-competitive ones, simultaneously increasing their capacity of association with partners of surrounding trees. This hypothesis finally questions the strict specificity of *Tricholoma cedretorum*, which identification is usually strongly directed by the host-tree. This species would be easily confused with *T. pessundatum* (Fr.) Quél. or *T. stans* (Fr.) Sacc. if it also happened to occur in pine forests with a deviant morphology such as here observed with *P. herculeum*.

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