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Fungal cortices in kauri resin from New Zealand as taphonomic and ecological analogues of Cretaceous amber cortices: an actualistic approach

Cortezas fúngicas en resina de pino kauri de Nueva Zelanda como análogos tafonómicos y ecológicos de cortezas en ámbar del Cretácico: una aproximación actualística

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Abstract: Several papers have been published in the last two decades about the peculiar cortices that commonly are present in Cretaceous amber pieces from diverse terrestrial western Tethyan localities. These cortices are constituted by networks of filamentous structures, and have been identified as mycelia composed of hyphae of resinicolous fungi according to a multidisciplinary research of Albian Spanish samples using diverse techniques. Main evidence indicating its fungal nature was the taphonomic scenario inferred and the detection of preserved chitin polysaccharides in the filamentous structures, using specific chitin markers visualized under confocal laser microscopy. Herein is present a similar fungal colonization pattern forming thin cortices observed in extant kauri pine resin (*Agathis australis*: Araucariaceae) from New Zealand. It has been compared with the typical pattern previously observed in the Spanish Cretaceous amber cortices. The similar fungal cortices in *Agathis* resins are considered as taphonomic and ecological analogues, but no phylogenetic relationship is suggested. The palaeoecological implications, with regard to Spanish Cretaceous forest environmental conditions that this extant correlate suggests, are discussed; also a new unusual growth of resinicolous fungus with the same microscopic hyphae features in Cretaceous amber are presented. Conclusions can be extended to Cretaceous amber cortices from other Laurasian localities.

Resumen: En las dos últimas décadas se han investigado unas cortezas peculiares que comúnmente están presentes en piezas de ámbar cretácico del margen occidental del Tetis. Están constituidas por estructuras filamentosas y han sido identificadas como micelios compuestos por hifas de un hongo resinícola, de acuerdo con una investigación multidisciplinar con el uso de técnicas diversas de muestras de ámbar español del Albiense. Su naturaleza fúngica se determinó principalmente por el escenario tafonómico inferido y la detección de polisacáridos de la quitina preservados en las estructuras filamentosas, utilizando marcadores específicos de quitina visualizados con microscopia láser confocal. Se presenta aquí un patrón similar de colonización fúngica, en forma de cortezas delgadas, en resina actual de pino kauri (*Agathis australis*: Araucariaceae) de Nueva Zelanda. Este patrón ha sido comparado con el observado en las cortezas del ámbar cretácico de España. En este estudio, las cortezas fúngicas similares en resinas de pino kauri son consideradas como análogos tafonómicos y ecológicos, pero no se sugiere una relación filogenética. Se discuten las implicaciones paleoecológicas que este correlato sugiere para las condiciones ambientales de los bosques cretácicos en Iberia; también se presenta aquí un crecimiento inusual de hongo resinícola en ámbar cretácico con idénticas características microscópicas de las hifas. Las conclusiones pueden extenderse a las cortezas en ámbar cretácico provenientes de otras localidades de Laurasia.

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INTRODUCTION

It is common the presence of light brown, opaque cortices in Cretaceous amber pieces from several western Tethyan localities, mainly from France (Breton, 2007; Girard *et al.*, 2009) and Spain (Peñalver & Delclòs, 2010; Speranza *et al.*, 2015; Lozano *et al.*, 2020), but absent in lower Albian Ariño amber in Spain (Álvarez-Parra *et al.*, 2021). They appear to be present in Cretaceous amber from Australia and absent in eastern Zealandian Cretaceous amber (Stilwell *et al.*, 2020). Despite the paucity of taphonomic studies on their macroscopic features, these cortices exhibit nearly identical characteristics at both the macroscopic and microscopic levels. The initial description of these cortices was provided by Casal (1762) in Latin, based

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on amber pieces discovered in the northern Spanish region of Asturias: "There are amber pieces below these laminae, whether of clay or shale, the size of which varies, with some like wallnuts and others like large apples or pears. These pieces do not appear cleanly; rather, their whole surface is covered by a crust very similar in appearance to Guayacan wood, so that, at first glance, it could be misinterpreted by the most expert botanists and specialists in these matters. Even though the substrate may be damp, these crusts are never soft but dry and hard, and when struck easily break into fragments, as indeed does the amber. It does not burn under a flame, but if thrown into the ambers of a fire it gives off a swampy, sulfurous smell." It was observed that, under both light microscopy (**LM**) and scanning electron microscopy (**SEM**), cortices are constituted by a profuse filamentous structure having each filament an empty core, as first observed by Waggoner (1994) in Cretaceous French amber. Because these cortices are typical in Cretaceous amber pieces from some Laurasian localities, and have not been found in Cenozoic ambers, at least with similar appearance, their presence in some incomplete amber pieces found into a middle Magdalenian cave in the North of Spain evidenced a local origin for the raw material, *i.e.*, Cretaceous amber collected in Spanish outcrops, instead of Cenozoic amber collected in other European areas (Corchón *et al.*, 2008).

The cortices constitute an important taphonomic factor, because they degraded the bioinclusions trapped in resin and later present in amber if they reached them. If not affected by these cortices, bioinclusions have an exceptional preservation that permits detailed taxonomical and palaeobiological studies. The empty core of the filamentous structure of the cortices enhances the amber degradation before and during exposition and erosion (weathering), and implies that the cortex is a more fragile part of the amber pieces (Speranza *et al.*, 2015), in line with the observations by Casal (1762) over two and half centuries ago.

The nature of these cortices has been treated in several papers (Breton, 2007; Girard *et al.*, 2009; Peñalver & Delclòs, 2010). However, notable confusion occurred due to partial studies based mainly on morphological features of the microscopic filamentous structure without the integration of important taphonomic evidence and the whole cortices' features. Now, there is consensus that the filamentous structure corresponded to a microorganism that grew inside the resin, forming the cortices, during the Cretaceous, not in Recent times (see Speranza *et al.*, 2015 and references therein). These authors also demonstrated that the microorganism involved in the origin of the cortices was a fungus and that the filamentous structure corresponds to a fossilized mycelium (but see Saint Martin & Saint Martin, 2018), in contrast to previous assignments to non-fungal microorganismal groups. A prime example of the misinterpretations in the literature, which has fueled differing interpretations, is the case of the filamentous structures observed under optical microscopy. These structures can be as transparent as the surrounding amber, making only the empty core visible (*e.g.*, Brasier *et al.*, 2010, fig. 3b). This has led to the mistaken identification of these fossil filaments as actinobacteria, as their true size and morphology are obscured by their transparent nature.

Here, an actualistic research analyzing several cortices from *Agathis australis* resin pieces from New Zealand is reported. It has been conducted for taphonomic comparison and its implications extend our knowledge of the Cretaceous resiniferous forests. A new Cretaceous amber piece containing an unusual growth, but with microscopic features typical of resinicolous fungi found in cortices, also sheds light on the nature and conditions of formation of the cortices.

MATERIAL AND METHODS

Some aerial resin pieces obtained from the litter around a large *Agathis australis* (D. Don) Lindl. tree in the Waipoua Forest area in North Island, New Zealand (Steward & Beveridge, 2010) (Fig. 1), were examined in order to determine whether they showed similar resin cortices (Fig. 2A–2D) to those of Cretaceous ambers. The kauri pine tree is located on a slope (345 m above sea level) at the side of a road. Aerial resin samples were collected during two fieldwork campaigns for a taphonomic research carried out in 2008 and 2011. Two fallen kauri pine trees located close a river, with their root systems exposed, were also examined in order to obtain resin bodies originated from the roots in the soil (root resin bodies), but that survey was unsuccessful. Taphonomic observations of in situ copal pieces associated with Pleistocene kauri pine root systems, and collection of some of these pieces for comparison, were conducted by E. P. and X. D. with permission at a private propriety in Waipapakauri (35º00'32.83''S / 173º12'01.45'' E; 32 m above sea level), close to State Highway 1, North Island, New Zealand, during the 2011 campaign (Fig. 1).

Spanish Cretaceous amber cortices studied for comparison are the same as those studied in Speranza *et al.* (2015): from amber localities of Peñacerrada and Salinillas de Buradón (Basque-Cantabrian Basin), El Caleyu (Central Asturian Depression) and San Just (Maestrazgo Basin), all upper Albian in age (Lower Cretaceous). See Speranza *et al.* (2015) for the repositories. An additional Spanish upper Albian amber piece of the root amber type (SJ 2010-102) from the richest level of the San Just locality is studied and figured (housed at the *Fundación Conjunto Paleontológico de Teruel-Dinópolis*, Teruel Province, Spain). In addition, a new Spanish middle Albian amber piece of the stalactitic/aerial amber type from El Soplao locality (Cantabria) has been studied and figured in this work (CES-1202; it is housed at the Institutional Collection from El Soplao Cave, Government of Cantabria, Celis, Cantabria, Northern Spain). All these pieces were

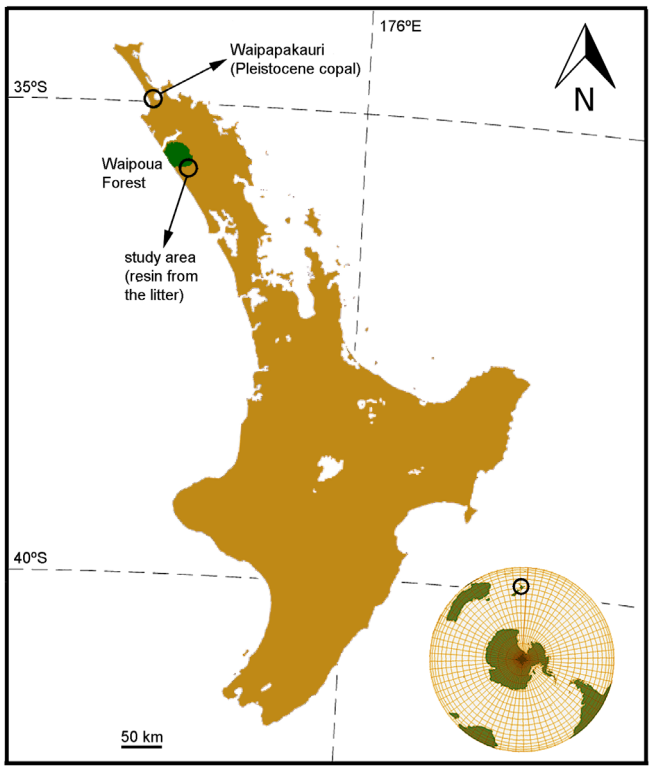

Figure 1. Geographical location of the studied *Agathis australis* resin samples and Pleistocene deposits at northern region of North Island, New Zealand.

obtained during palaeontological excavations with permits of the Spanish Autonomous Governments.

Resin slides and non-prepared samples of resin bodies with cortices, as well as some of the most scientifically interesting copal pieces, are in a comparison collection at the Geominer Museum of the Spanish Geological Survey (**IGME**, **CSIC**), in Madrid, and at the palaeontological collection of the Faculty of Earth Sciences of the University of Barcelona, both in Spain. For LM observations, two Olympus microscopes, BX51 and BX53 models, were used at the IGME (CSIC) facilities. During observation, incident and transmitted light were used simultaneously to resolve some structures. The SEM analyses were carried out using a HITACHI model S-4100 at the *Servei Central de Suport a la Investigació Experimental* (**SCSIE**) of the University of Valencia, Spain. For SEM examination, the resin samples were fractured in order to expose a clean, fresh surface, and then coated with gold. The SEM photomicrographs of a small sample of amber cortex obtained from one of the abundant amber pieces from El Caleyu outcrop, are included in this study only to illustrate the typical features of the Cretaceous filamentous structure; the original amber piece lacks an acronym.

Copal pieces from Waipapakauri, used for comparison, have an age of 39670 +/- 980 BP (and conventional radiocarbon age was 39640 +/- 970 BP (13C/12C ratio was -26.4 o/oo)), which is the measured radiocarbon age for Waipapakauri locality (in respect to 2 sigma calibration the result was outside of the calibration range). This age of Waipapakauri locality, where also taphonomic observations were done, was obtained by radiocarbon dating accomplished by Beta Analytic Inc. laboratory, in Miami in 2011. The analyzed sample was wood from a trunk. Alkali and acid washes were applied to remove humic acid and carbonate contamination.

RESULTS

Agathis australis resin from New Zealand

Cortices were observed in some samples of the collection of resin bodies obtained from the litter of a kauri pine (*Agathis australis*) (Fig. 2A, 2C, 2D). Cortices are present in the entire periphery of the resin bodies (Fig. 2C) and are thin, measuring 0.5–2 mm in depth (Fig. 2B, 2D). Hyphae inside the resin bodies are *ca*. 4.2 µm in width, having thick walls *ca*. 1.5 µm in width (Fig. 3B–3E). On the external surfaces have been observed assemblages of sclerotia (Fig. 2D), melanized hyphae (Fig. 2D) and hyphae with different characteristics, for example encrusted hyphae (hyphal width 2.5 µm; wall width *ca*. 0.7 µm) were observed together with hyphae presenting smooth surfaces (hyphal width 2 µm; wall width *ca*. 0.9 µm) (Fig. 3A, 3B). To note that the hyphae outside the resin bodies are thinner. Sections of the resin bodies under SEM revealed that cortices are constituted by extensive mycelia composed of hyphae growing toward the interior (Fig. 3). Hyphae are denser at the external zone (close the external surface of the resin bodies) of the cortices, and became sparse toward the amber core. They are strongly oriented to the interior of the resin bodies as is patent in these sections and all are homogeneous in their features, suggesting that only one of the morphotypes (one taxon) present on the external surface invaded the resin bodies. Under SEM, thick hyphal walls are constituted by an intact, homogenous material and are closely linked to the surrounding polymerized resin (see dotted arrows in Fig. 3E); in other words, the contact between the wall and the resin matrix is an inconspicuous limit, without holes and porous appearance. Under LM, these thick hyphae also show empty lumina and unaltered, homogeneous walls. In the interior of the resin bodies, free spores and structures that could definitely be interpreted as reproductive structures of fungal origin were not observed.

Field observations in New Zealand

During the two fieldwork campaigns carried out in North Island, New Zealand, was observed that *A. australis* roots can produce large amounts of resin. One individual, growing on the bank of a river with the roots exposed, had abundant resin of the aerial type from the roots due to the lack of confined conditions (Fig. 4).

In Pleistocene trees of *Agathis australis* exhumed for timber at Waipapakauri (Fig. 5), *ca*. 39,000 years old, root systems were observed with their original soil still attached and abundant large, kidney-shaped pieces of copal. Additionally, abundant aerial, stalactite-shaped copal pieces were recovered from the attached soil.

Spanish San Just amber

The studied upper Albian San Just amber piece (SJ 2010-102) is of the root amber type (Fig. 2E). It is nearly cuboidal and measures 3.5 × 2.5 × 1.5 cm. It has an opaque cortex and has been partially polished on each side to reveal the interior, showing an irregular cortex, thickness of 0.5 to 1 mm in deep in some parts (Fig. 2E).

Spanish El Soplao amber

The studied middle Albian El Soplao amber piece (CES-1202) is a fragment of stalactitic (aerial) amber which shows at least three flows, each partially wrapping the precedent (Fig. 6). On the cross-section surface, the sequence of flows can be observed and also the two dark surfaces of desiccation that separated them (resulting from external conditions and the time elapsed between resin flows). At level of the cross-section, the last flow (3rd) is completely invaded by the typical fungal mycelium that forms cortices (Fig. 6D). The 2nd flow is virtually uninvaded. Only in a small area the mycelium crossed the surface of desiccation and show a small growth in the 2nd flow (Fig. 6A, 6B).

DISCUSSION

Hyphal morphotypes observed in *Agathis australis* resin

Taking into account that the resin bodies were in contact with the litter/soil, where a high fungal diversity is present, the presence of diverse hyphal morphotypes on each resin external surface most likely indicates that more than one taxon of fungus are present externally. However, because one species of fungus can show hyphae with diverse ornamentation, it is not clear if the Figure 3B illustrates more than one fungal taxon. In any case, the dense and homogeneous mycelia present inside the resin bodies were formed probably by only one taxon that penetrated them; that homogeneity can be easily distinguished under stereomicroscope and LM (see Fig. 2B and white arrow in Fig. 2D) as a continuous whitish-yellow band. Beimforde and Schmidt (2011) observed external surfaces covered by associations of bacteria, fungal mycelia and algae in New Caledonian resin samples of *Agathis lanceolata* and *Agathis ovata* that hardened at the forest floor or close to it at the tree trunk, but apparently only one morphotype of resinicolous fungus penetrated these resin bodies.

Agathis australis resin as a suitable extant analogue

The study of extant analogues could be critical for the correct interpretation of fossils of simple morphologies such as the filamentous structures (hyphae) described herein. In this respect, Schmidt and Schäfer (2005) and Beimforde and Schmidt (2011) carried out actuotaphonomic experiments in order to determine various aspects of the growth and subsequent preservation of sheathed bacteria, cyanobacteria and fungi in newly exuded, non-hardened gymnospermous resins.

Based on diverse data, including the analysis of biomarkers of fossil plant cuticles and amber pieces, two plant groups have been proposed as the Spanish Cretaceous amber source: the family Cheirolepidiaceae, genus *Frenelopsis* (Menor-Salván *et al.*, 2009a, 2009b, 2010; Najarro *et al.*, 2010), and the family Araucariaceae, a taxon close to *Agathis* (Chaler & Grimalt, 2005). Both groups have also been indicated as producers of the Cretaceous resin that originated the French amber (Nohra *et al.*, 2015). The relationships of Cheirolepidiaceae to other conifers remain uncertain, but it is nested within the extant conifers in the phylogenetic analysis performed by Hilton and Bateman (2006). Some researchers have proposed a close relationship with Araucariaceae and Podocarpaceae, noting similarities in their reproductive structures (Jin *et al.*, 2023). However, other studies suggest that Cheirolepidiaceae may lie outside the crown group of modern conifers, aligning instead with the Voltziales (Andruchow-Colombo *et al.*, 2023). Other Cretaceous ambers have also been considered to be of *Agathis*-like origin (Langenheim, 2003), but see Grimaldi (2009) for a discussion on the difficulties to determine the plant origin of the ambers. Based on its close relationship, *Agathis australis* (Coniferales: Araucariaceae) or kauri pine could be considered a suitable analogue for comparison.

The resin from *Agathis australis* is also a suitable extant analogue for comparison due to the copious resin production of this species under natural forest conditions and its chemical composition, which implicates rapid polymerization and hardening (Langenheim, 1995), preventing rapid decomposition. Such production led to the formation of large copal deposits during the Quaternary, and also some Cretaceous and Paleogene–Neogene amber deposits (Ecroyd, 1982; Langenheim, 2003; Knapp *et al.*, 2007; Biffin *et al.*, 2010; Schmidt *et al.*, 2018). The environmental conditions in modern *A. australis* forests in New Zealand are generally consistent with those inferred for the resiniferous Cretaceous forests in Spain based on palaeobotanical and geological data, including the presence of forested areas near seacoasts under a subtropical climate.

Agathis produces an abundant resin that mainly contains diterpenoids with labdane structures, which is resistant to biodegradation (Langenheim, 2003). The

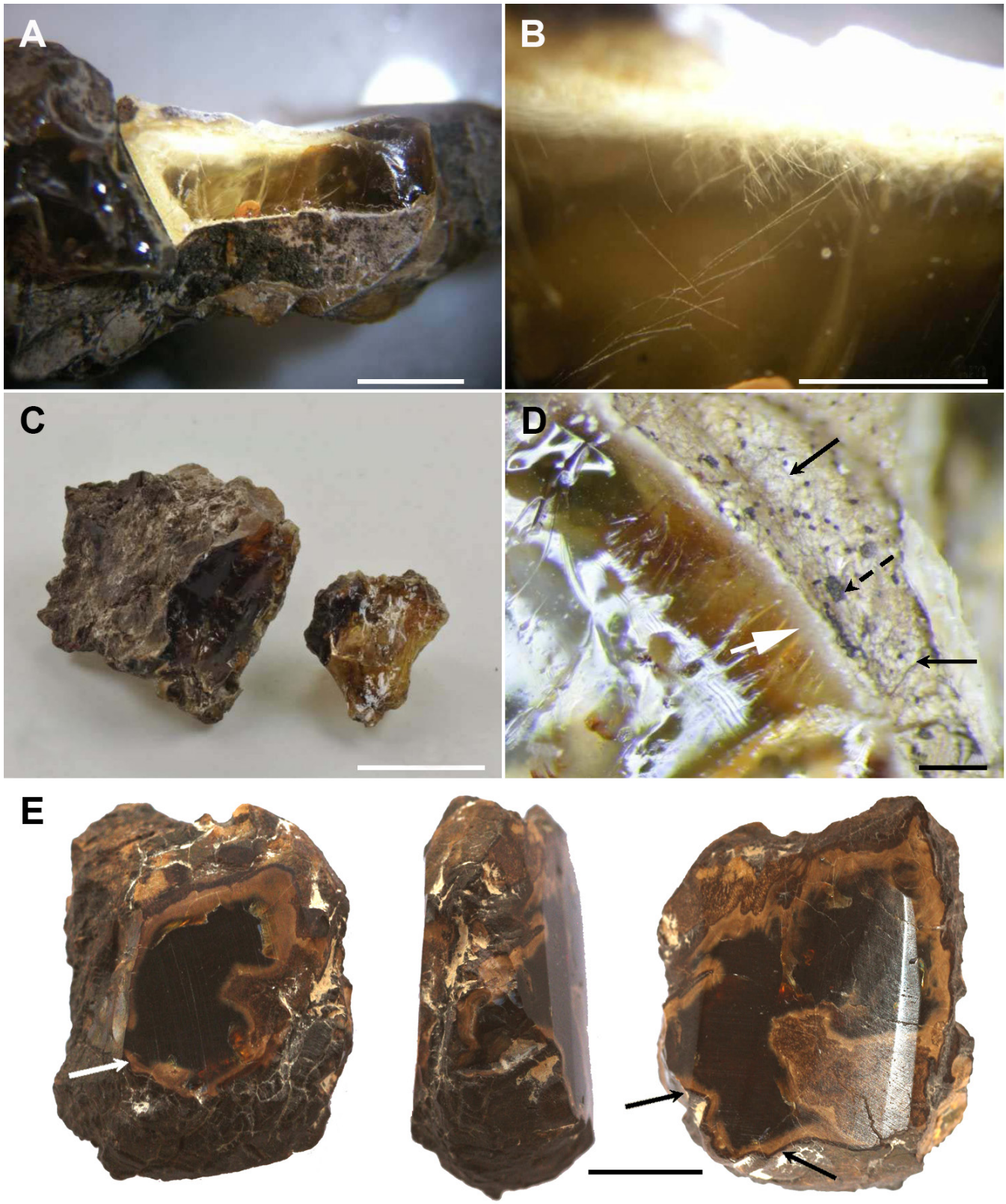

Figure 2. Cortices from semi-buried resin of kauri pine (*Agathis australis*) from New Zealand and Cretaceous amber from Spain. **A** and **C,** semi-buried resin aspect; **B** and **D,** fungal colonization showing a profuse fungal mycelium growing toward the interior of the resin body in the form of a thin cortex (white arrow in **D** indicates the homogeneous whitish-yellow band that constitutes the cortex as observed in a fresh section of the resin body), and melanized hyphae (black arrows) and sclerotia (dotted arrow) localized on the external surface of the *A. australis* resin bodies; **E,** root amber piece (SJ 2010-102) from San Just outcrop (Teruel Province), partially polished (two windows, one in each side) showing an irregular cortex (arrows indicate parts where the cortex is thinner); scale bars = 2 cm (C); 1 cm (E); 5 mm (A); 2 mm (B); 0.5 mm (D).

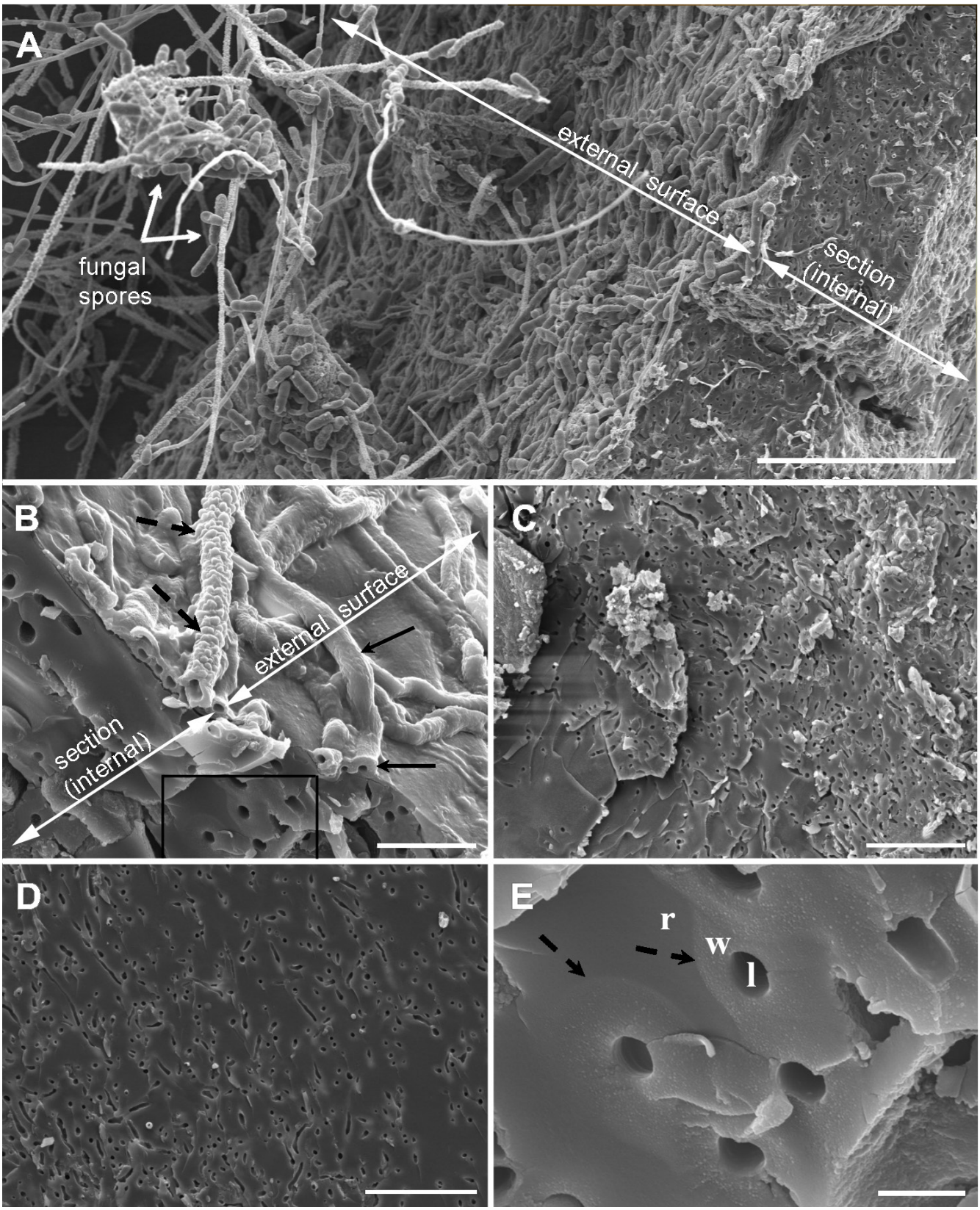

Figure 3. SEM photomicrographs of the mycelia that constitutes the cortices in kauri pine (*Agathis australis*) resin. **A,** Mycelium and abundant fungal spores on the external surface of the resin body and a section of the cortex sowing a mycelium into the resin; **B,** external mycelium consisting of individual strands of thick-walled hyphae (continuous black arrows) and encrusted hyphae (dotted black arrows), and internal fungal colonization; **C** and **D,** internal fungal colonization as seen on fracture surfaces; **E,** detail of some sectioned hyphae present into the resin body showing the cell walls with the appearance of a halo around the empty lumina (dotted black arrows indicate the limits of the walls); these are very similar to those from western Tethyan Cretaceous ambers in fracture surfaces (like in Fig. 6D and unlike in Fig. 7). Abbreviations: **l,** lumen, **r,** resin, **w,** hyphal wall; scale bars = 80 µm (A); 30 µm (C, D); 8 µm (B); 2 µm (E).

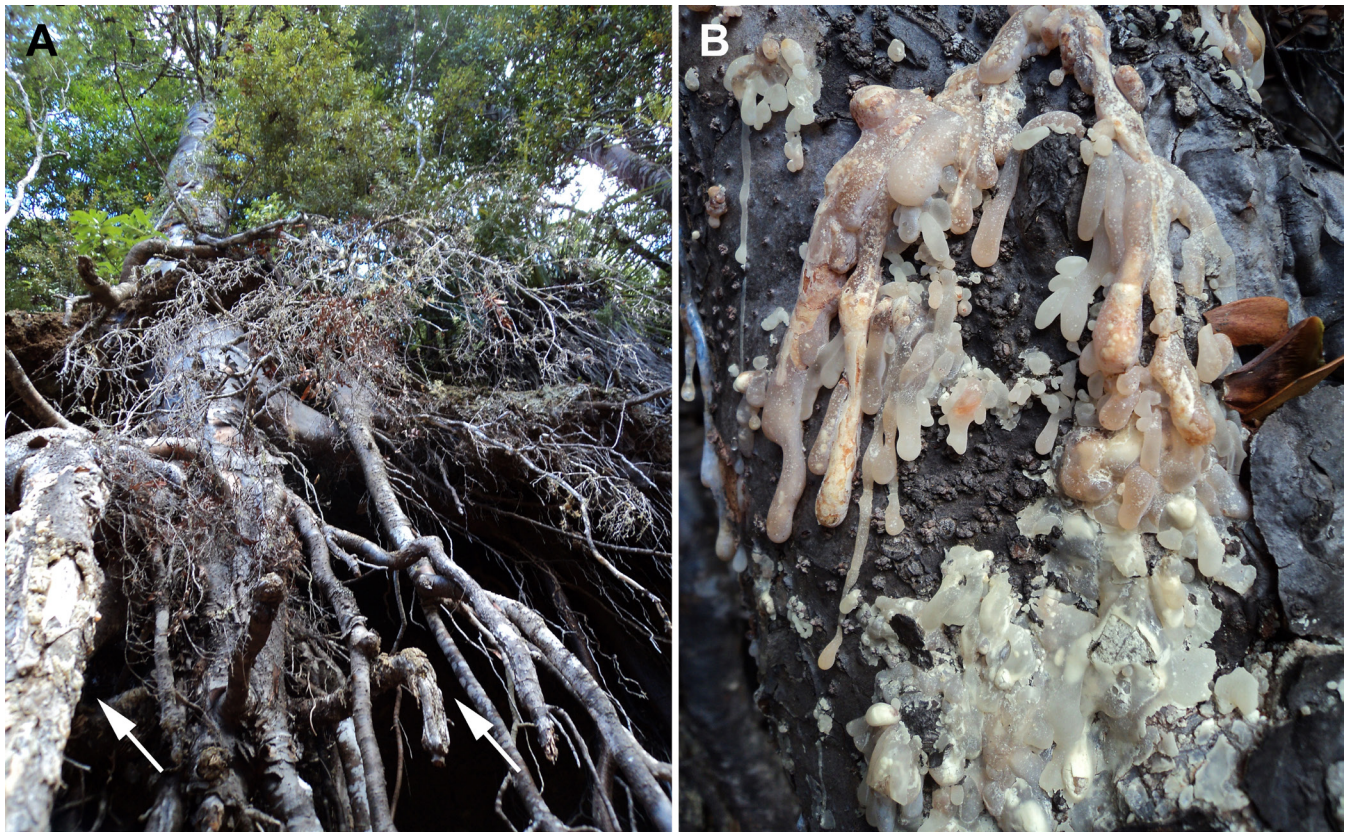

Figure 4. Aspect of stalactitic (aerial) resin exudations from exposed roots. **A,** Large resin exudations (arrows indicate two large sets of exudations) of *Agathis australis* tree at the bank of a river, photographed from below, with the roots exposed; **B,** detail of large resin exudations from a root (set of resin exudations is *ca.* 7 cm width). Photographs taken in March 2011 at the limits of the Waipoua Forest (North Island, New Zealand).

kauri resin constitutes chemical and/or mechanical barriers against invading organisms like insects and fungi (Langenheim, 2003). The chemical composition and stability of fresh kauri resins, along with their low oxygen concentration and low water availability, determine that only specialized fungi, mainly ascomycetes and basidiomycetes saprotrophic fungi, can colonize them (Hintikka, 1970; Blanchette & Biggs, 1992; Rikkinen & Poinar, 2000).

Literature on true fungi associated to *Agathis* kauri pine in New Zealand is scarce (*e.g.*, Ecroyd, 1982; McKenzie *et al.*, 2002; Hood, 2009; Padamsee *et al.*, 2016; Byers *et al.*, 2020). Most of the fungal records related to *A. australis* are saprobes found in dead and fallen wood and litter (Ecroyd, 1982; McKenzie *et al.*, 2002; Hood, 2009; Byers *et al.*, 2020). Only nineteen species have been cited (McKenzie *et al.*, 2002; Hood, 2009), including wood- and bark-inhabiting ascomycetes species, such as *Colpoma agathidis*, *Helotium allantosporum* and *Lophodermium agathidis*, and basidiomycetes decay fungi like *Heterobasidion araucariae* and *Coltricia schweinitzii*.

Resinicolous fungi, probably of the family Mycocaliciaceae, forming cortices have been reported in extant *Agathis* species from New Caledonia (Beimforde & Schmidt, 2011), but detailed descriptions of the mycelial growths inside the resin bodies and their hyphal features for comparison await publication. Seyfullah *et al.* (2018) observed that many resin bodies on the forest floor associated with *Agathis lanceolata* in New Caledonia showed traces of resinicolous fungal mycelia on their surfaces, with the holes formed by the fungal hyphae potentially leading to further resin degradation over time. Many resinicolous fungal species seem to be host and/or substrate specific, between them mycocalicioid species specialized to live in resin substrates (Tuovila *et al.*, 2013). However, the ability to grow in resin could not be exclusive of Mycocaliciaceae. Taking into account the high rate of resin accumulation during the Cretaceous (Delclòs *et al.*, 2023) and Eocene (Grimaldi, 1996), and the vast extant diversity of the fungal kingdom —estimated at 0.8 million to 5.1 million species, though only 100,000 have been described—, most likely more lignicolous fungi acquired the ability to degrade diterpenoids and to colonize kauri resin bodies (Blackwell, 2011).

A different resinicolous fungus, a mycocalicioid, which does not form cortices, has been reported in *Agathis* resin (Rikkinen *et al.*, 2014). In addition, resinicolous fungi have been observed in *Araucaria* resin (Beimforde *et al.*, 2016), unlike in *Wollemia* resin, the third araucarian genus.

Cortices formation conditions

The cortices observed in semi-buried kauri pine resin bodies are similar to those commonly found in Spanish Cretaceous ambers (Figs. 2, 3). As presented in Results section, the studied yellow-brown cortices in resin bodies are thin, measuring just a few millimeters. Only a few Spanish amber pieces show cortices of comparable thinness. Curing of the resin is mainly due to the loss of its volatile compounds (Martínez-Delclòs *et al.*, 2004; Seyfullah *et al.*, 2018), a process that varies depending on the type of resin and environmental conditions. More likely, the *A. australis* resin cortices are thin due to the

Figure 5. Pleistocene kauri pine root systems accumulated during removal of trees from the ground to market timber, at a private propriety in Waipapakauri, New Zealand, in 2011. **A,** Root system of an individual, or maybe of diverse individuals pilled together, exposed because lacks value as timber for arts and crafts; **B,** detail of the original Pleistocene soil retained by the roots containing abundant in situ copal in the form of balls and kidney-shaped pieces; **C,** detail of the large size of one of the pilled roots in the area.

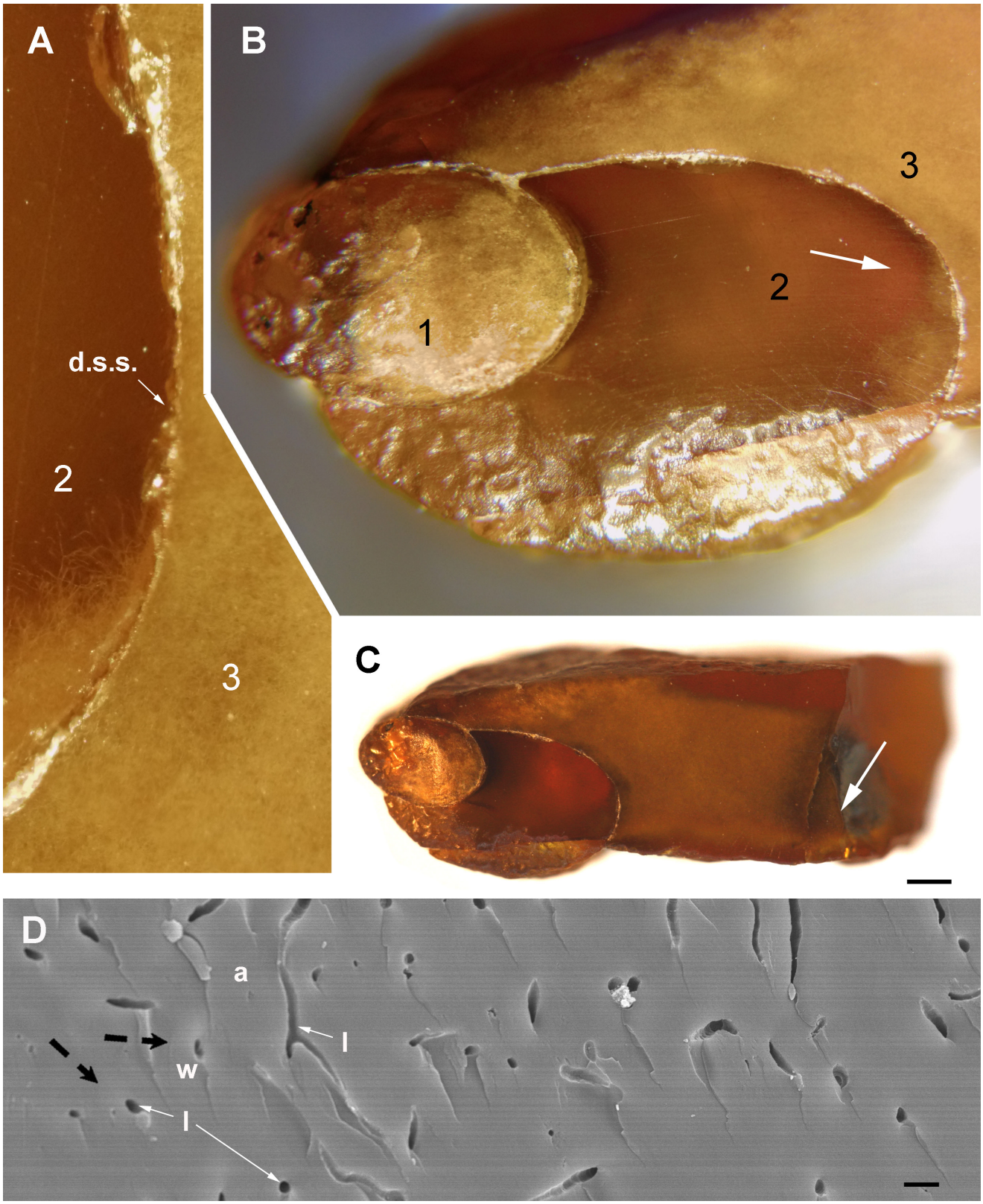

Figure 6. New resinicolous fungal growth in a stalactitic (aerial) amber piece (acronym CES-1202) from El Soplao locality and its identical preserved hyphae like the typical Cretaceous Spanish amber cortices and virtually identical to those in kauri pine resin cortices. **A**–**C,** Cross-section of the stalactitic (aerial) amber piece showing three consecutive flows (1 to 3) with the flow 3 entirely invaded by the mycelium in this section and how the desiccation surface was a barrier to invade the flow 2 from it, but incipiently invaded in a point (detail in **A**); the white arrow in **B** indicates the detail enlarged in **A**; **D,** SEM image of a sampled small flake (fracture surface) from piece in **C** (white arrow in **C**) showing the hyphal cell walls sectioned with the appearance of a halo around the empty lumina (dotted black arrows indicate the limits of the walls); it shows hyphae in the stage 1 of degradation (intact walls) according to the sequence of Speranza *et al.* (2015) (like in Fig. 3E and unlike in Fig. 7). Abbreviations: **a,** amber, **l,** lumen, **d.s.s.,** desiccation surface section, **w,** hyphal wall; scale bars = 1 mm (C); 2 µm (D).

rapid polymerization and hardening of this resin under aerial conditions as suggested by Langenheim (1995). Our own field observations in New Zealand during February 2008 also support rapid hardening (see also Peñalver *et al.*, 2008): fresh resin exudations lost their stickiness, at least superficially, after just three days without rain. Beimforde and Schmidt (2011) observed similar mycelia in *Agathis lanceolata* resin from New Caledonia, forming an opaque and fragile surface layer (or cortex), *ca*. 3 mm in deep, constituted by hyphae 1.5–3 µm in diameter.

As previously described, under SEM (Fig. 3B–3E), the fungal mycelium in *A. australis* resin presents hyphal walls embedded in the resin, namely, there is an inconspicuous limit between the hyphal walls and the surrounding resin (Fig. 3E). This is similar in fossil analogues and, in both cases, indicates that the hyphae invaded the resin bodies from the exterior and grew inward before complete hardening.

Speranza *et al.* (2015) proposed two main scenarios for the origin of cortices in Spanish Cretaceous amber. The fungal growth on aerial resin bodies, mainly on stalactite-shaped ones, was less frequent and generally produced thin cortices. This probably occurred on the bark of branches and trunks, mainly near the soil, where the low colonization intensity was related to the rapid hardening of the resin and/or lower fungal aerial inoculum. In contrast, fungal growth on resin bodies originated from roots within the soil and litter, mainly larger, kidney-shaped resin bodies, was more common and produced thicker cortices. This was related to an extensive tree root system that produced higher quantities of resin, potentially induced by pathogenic fungi under moist conditions in the soil and litter, with a higher fungal inoculum potential (Speranza *et al.*, 2015). The prolonged period required for resin polymerization and the fungal ability to use fresh resin as a carbon source supported this extensive fungal growth. At this regard, it was argued that some aerial resin bodies that had not fully hardened may have fallen into the litter, and be invaded from their entire external surface similarly to those originating from roots. This scenario is the most plausible explanation for the cortices on the aerial kauri pine resin bodies studied here.

The field observations in New Zealand, both abundant resin of the aerial type from exposed roots and abundant large kidney-shaped pieces of copal associated with root systems, align with the two main scenarios inferred by Speranza *et al.* (2015) regarding the origin of the cortices in Spanish Cretaceous amber pieces.

Hyphae's preservation

A sequence of hyphal degradation occurred during the fossil diagenesis of the Spanish Cretaceous amber pieces was described by Speranza *et al.* (2015), mainly based on LM and SEM observations (Figs. 6, 7). As expected, the kauri pine resin bodies show mycelia/hyphae in the stage 1 of degradation of Speranza *et al.* (2015) (Fig. 3), as they only remained in the litter for a short time. In contrast, the taphonomic history of Cretaceous amber involved subsequent transport, a second burial (following an initial presumed burial in the litter) in estuarine deposits, and a long fossil diagenesis. The observed preservation in kauri

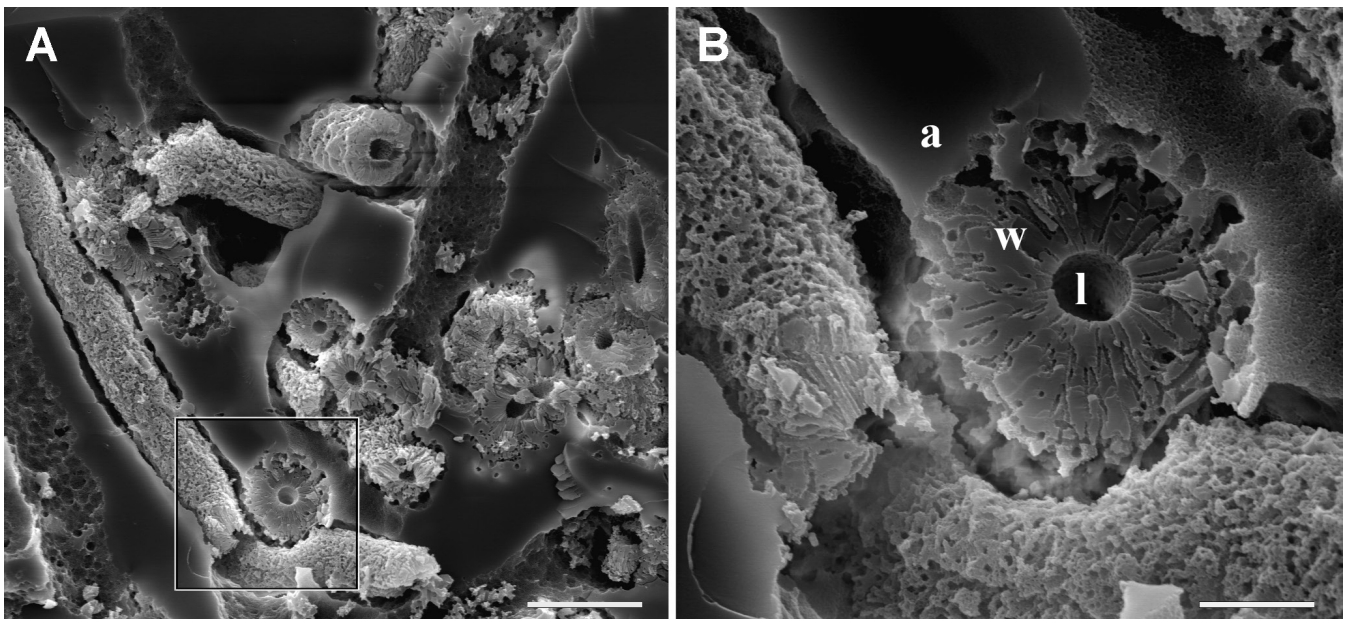

Figure 7. SEM photomicrographs of a cortex sample from El Caleyu amber (upper Albian), obtained by simple fracture of the amber piece. **A,** Hyphae partially degraded in longitudinal and transversal views. These hyphae are in degradation stage 3, *sensu* Speranza *et al.* (2015), evidenced by the irregularly eroded appearance of the wall, crossed by abundant empty radial fibrillary structures, and incipient isolation of the wall from the degraded amber (unlike the intact walls in Figs. 3E, 6D); **B,** detail from the inset of the left photomicrograph. Abbreviations: **a,** amber, **l,** lumen, **w,** hyphal wall; scale bars = 10 µm (A); 2.5 µm (B).

resin bodies is different in some aspects to that of the degraded hyphae in Cretaceous ambers due to taphonomic reasons (see Fig. 7 and Speranza *et al.* (2015) for details about the fossil hyphae preservation), but identical to hyphae in stage 1 of degradation in other amber pieces (Fig. 6D). Particular caution should be taken, because some putative features of the original hyphae could be artifacts of preservation.

Comments on the unusual growth of resinicolous fungus

The cortices in Cretaceous amber sometimes have a non-homogeneous thickness around the amber pieces (Fig. 2E), which depends on the irregularities of the external surfaces of the original resin bodies. Other rare cases show growing spots isolated by parts of the external surface without fungal alteration. In middle Albian of El Soplao amber, it has been discovered that fungi grew preferentially along resin layers richest in phloem sap (pseudoinclusions) toward the interior (Lozano *et al.*, 2020, fig. 1d–1g). In this last case the phloem sap plus the resin medium constituted a more nutritious option for the fungi than the resin alone, as concluded by Lozano *et al.* (2020).

In a fragment of a middle Albian stalactitic (aerial) amber piece (CES-1202) from El Soplao, a hardened surface, or desiccation layer, prevented fungal growth from penetrating the resin body from the outer resin layers. In a small area of the desiccation surface separating the 2nd and 3rd flows, the fungus crossed it, most likely due to a lower desiccation/hardening at that point, and then continued a small growth in the 2nd flow up to a critical hardening of the resin (Fig. 6). As indicated by Speranza *et al.* (2015), the low intensity of colonization observed in a few stalactitic amber pieces is related to rapid hardening of the resin in aerial conditions and/or a lower aerial fungal inoculum. Because these fungal mycelia are not bioinclusions *s.s.* (they were not trapped and embedded by the original resin like, for example, a flying insect), they could be present in different resin flows, hence the concepts of syninclusion, eusyninclusion and parasyninclusion (see Solórzano-Kraemer *et al.*, 2023) cannot be applied.

Resin and amber compared: the fungal nature of the cortices

In summary, relevant macro- and micro-morphological similarities between New Zealand (extant) fungal mycelia (Fig. 3) and Spanish (Albian) (Figs. 6D, 7) fungal mycelia have been observed: 1) both produced cortices, 2) both had similar spatial patterns of fungal colonization of resin bodies, 3) both showed similar sizes of hyphae and cell walls, 4) no reproductive structures were present inside the resin/amber bodies, and 5) in both cases only one morphotype constituted the mycelia, thus lacking evidence of other microorganisms inside the resin/amber bodies. Obviously, these similarities do not indicate a phylogenetic relationship between the two mycelial assemblages, neither that the fungus growing today in *A. australis* resins is a relict from Cretaceous times. Several diagnostic data are lacking in these fossils because only mycelia are preserved, preventing a supported phylogenetic relationship. It is likely that different taxa are involved, considering the long time between the Cretaceous and Recent records. Hyphae on the external surface of the studied kauri resin bodies show varied characteristics, likely indicating the presence of more than one taxon (Fig. 3A, 3B); however, apparently only one invaded the resin bodies forming the thin cortices.

Saint Martin and Saint Martin (2018) criticized the research and results of Speranza *et al.* (2015) indicating putative erroneous methodological aspects of the analyses and putative misinterpretations. They advocated for a sheathed bacterial nature of these filamentous growths ("the bacterial hypothesis"), in line with the earlier conclusions of Schmidt and Schäfer (2005), instead of the fungal nature advocated by Speranza *et al.* (2015). They also published excellent images showing new and interesting features of the structure of the filaments present in some French Cretaceous amber samples, but unusual, which await taphonomic study and some of them most likely may be preservational artifacts. Saint Martin and Saint Martin (2018) largely misinterpreted the analyses done and the results obtained by Speranza *et al.* (2015), and underestimated the chemical evidence confirming that the widespread Cretaceous filamentous growths in Cretaceous ambers forming cortices are, in fact, fungal mycelia. Two important misinterpretations were that they underconsidered or did not note that Speranza *et al.* (2015) used specific chitin markers when detected chitin polysaccharides in the filamentous structure from Spanish Cretaceous amber and, at the same time, used a sophisticated method to discriminate the specific fluorescence, due to specific signal under confocal laser microscopy, from the natural fluorescence.

CONCLUSIONS

The extant *A. australis* resin cortices, present in aerial resin bodies, are herein interpreted as mainly originated in the litter, where fungi grew on the external surfaces of resin bodies, which had fallen from the branches or the trunk in an unhardened condition.

In general, under LM, the resin bodies showed a pattern of fungal colonization, hyphal distribution and hyphal morphology, forming mycelia very similar to those observed in Cretaceous amber cortices. Under SEM, the hyphal lumen, fungal cell wall, and extracellular material also resembled the microscopic appearance of the fossil hyphae, lacking sings of degradation.

It seems that the existence of resinicolous fungal taxa that form cortices, trophically related to coniferous resins, occurred over a long geological period from the Valanginian to the Recent. Although a phylogenetic

affinity cannot be established between the fungi present in Cretaceous amber and those in *Agathis australis* resin, the diverse taxa involved could at least be considered ecological analogues, and they clearly are taphonomic (biostratinomic) analogues. The study of this Recent analogue sheds light into the various conditions under which Cretaceous cortices formed, supporting some recently inferred conditions for both Cretaceous litter and forest soil. Similarly, observations on Pleistocene copal from New Zealand support the two main scenarios previously inferred for the origin of fungal cortices present in western Tethyan (Iberia Island) amber pieces.

The actualistic research carried out, along with the newly described and unusual growth pattern in Spanish Cretaceous amber, strongly reinforce the fungal nature of the Cretaceous cortices (mycelia), previously evidenced with the detection of preserved chitin polysaccharides in the filamentous bodies. In our view, the most important aspects in order to carried out suitable research on these cortices and their filamentous microscopic structures are: 1) to integrate actualistic observations, 2) to consider a solid taphonomic framework, 3) to study cortex samples obtained by the own researcher who will observe and interpret the microscopic structures and will consider the features of the cortex, 4) to combine LM and SEM observations in the description of the filaments of samples from the same cortex and same part of it, 5) to compare anatomical and taphonomic features observed in samples of the same cortex obtained from the more external, middle and more internal parts, and 6) to perform suitable and specific chemical detection.

Supplementary information. This article has no additional data.

Author contributions. EP conceived the study. EP and XD carried out fieldwork and collected the specimens and samples. EP prepared the figures. All the authors analyzed and discussed the data and wrote the manuscript.

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