Carnivorous Fungi from Cretaceous Amber

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arnivorous or predatory fungi have developed distinctive trapping devices such as adhesive hyphae, knobs, and networks or constricting and nonconstricting rings that enable them to exploit nematodes, other small animals, and protozoans as their main nutrition source (1-3).

Here, we report fossil evidence of carnivorous fungi that have hyphal rings as trapping devices preserved together with their prey, small nematodes, in circa (ca.)-100-millionyear-old amber. A later fossil carnivorous fungus is known from Oligocene-Miocene Mexican amber (4), but its trapping devices are not clearly identifiable.

Our fossil specimens originate from the highly fossiliferous amber deposit of Archingeay/Les-

> Nouillers in southwestern France, which is Late Albian in age (5, 6). The specimens are deposited in the Museum of Natural History in Paris (accession numbers MNHN AR-C115.5a, ARC115.13, ARC115.20, and ARC115.22a).

> The mycelium consists of irregularly septated branched hyphae, which are 1.5 to 2 μm in diameter. The rings originate from ca.-2-um-thick lateral branches of the hyphae, forming a loop. In contrast to modern trapping rings consisting of three cells, the rings, which are seen in three specimens of the fungus, are unicellular, forming just a single septum at the junction. Fully developed rings (inner diameter of 8 to 10 µm and outer diameter of 11 to 15 μm) probably detached easily from the supporting hypha and are found disassociated from the mycelium (Fig. 1, A, B, and E). Adhered particles (Fig. 1B and fig. S1A), which are numerous in some samples, indicate that the rings produced a sticky secretion, improving the efficiency of trapping, as known from modern carnivorous fungi trapping with adhesive networks or knobs. Once trapped, the nematodes were probably penetrated and digested by infestation

In addition to rings, the fossil fungus also developed blastospores. They are ellipsoid to oviform, are 2 to 4 μm by 1 to 3 μm in size, and bud laterally in whorled position at the hyphae (Fig. 1, C and E). Secondary spores are seen budding primarily apically from the blastospores and form nearly acropetal chains. These cells established yeast colonies (Fig. 1, D and E, and fig. S1B).

Several small nematodes of ca. 100 µm in length are located close to a trapping ring (fig. S1, C and D).

Because their maximum diameter falls within the width range of the rings, these animals can be identified as potential prey of the fungus. As a saprotrophic organism and consumer, the fossil fungus was a part of a highly diverse and complex soil biocenosis of an ancient coastal amber forest (6). Budding cells of yeast stages are ecologically important in liquid media and are reduced during the course of adaptation to terrestrial habitats. Aquatic representatives of modern carnivorous fungi are considered secondarily aquatic and belong to the same groups as terrestrial soil fungi (7). In contrast, the dimorphism exhibited by these fossils may represent an early transitional stage from wet to drier limnetic-terrestrial habitats.

These fossils show that by the Early Cretaceous soil fungi had already developed complex trapping devices to catch motile organisms. As in modern ecosystems, carnivorous fungi formed an ecological group of specialized consumers of small metazoans and protozoans. Today this ecological niche is occupied by more than 200 species of the Zygomycetes and imperfect stages of the Ascomycetes and the Basidiomycetes (3). On the basis of the mode of ring formation and the dimorphic mode of life, the fossils cannot be assigned to any recent carnivorous fungus, providing evidence that different groups occupied this ecological niche in the age of dinosaurs and that trapping devices were developed independently multiple times in the course of Earth history. The occurrence of carnivorous fungi in the Mesozoic is an example of complex interactions in early soil ecosystems and suggests that carnivory in fungi may be of ancient origin.



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Supporting Online Material

www.sciencemag.org/cgi/content/full/318/5857/1743/DC1 Materials and Methods

References

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Scale bars represent 10 µm. (A) Trapping ring (MNHN ARC115.13). (B) Trapping ring with attached detritus. The arrowhead indicates the only septum (MNHN ARC115.22a). (C) Formation of blastospores at a hypha (MNHN ARC115.20). (D) Formation of yeast colonies at a hypha (MNHN ARC115.20). (E) Reconstructed life cycle with ring formation, fully developed ring at the supporting hypha, disassociated ring, trapped nematode,

formation of blastospores, and yeast colonies.

Fig. 1. Dimorphic carnivorous fungus from Cretaceous amber.

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Materials and Methods

Amber piece no. ARC 115 was found in the Archingeay/Les-Nouillers quarry in Charente-Maritime (southwestern France), which has already produced numerous fossils, mainly insects (S1, S2). The amber is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). In the regional stratigraphical section, this amber-bearing stratum corresponds to the subunit A1 (S3) and was dated as Late Albian (ca 100 million years old) by palynological studies (S4, S5). The reconstructed paleoenvironment corresponds to a coastal tropical forest and representatives of the Araucariaceae were probably the main resin-producing trees (S1, S6).

The carnivorous fungi were originally fossilized in a single piece of amber (ARC 115) alongside 79 arthropods and numerous microorganisms such as bacteria, algae and testate amoebae. Most arthropods are litter-living taxa. The find of a mole cricket, in particular, indicates that the resin solidified in a soil habitat, not at the tree bark (S7). The original 4 x 3 x 2 cm piece of amber was divided into 31 pieces in order to separate the inclusions for investigation. This preparation followed the method described by Perrichot (S1). The polished amber pieces were investigated using transmitted-light differential-interference-contrast microscopes.

The four fungi-containing amber fragments are deposited in the amber collection of the Department of Earth History in the National Museum of Natural History in Paris. MNHN ARC115.13 contains a fragment of decomposed wood with a mycelium and the trapping ring shown in Figs. 1A and S1D as well as dispersed yeast cells and several nematodes. MNHN ARC115.22a contains a mycelium with two trapping rings (Figs. 1B and S1A) and yeast cells. MNHN ARC115.20 yields mycelia as well as a loop representing an initial stage of ring formation. Attached to a piece of detritus, several hyphae forming blastospores and secondary spores are preserved (Fig. 1C). A plethora of yeast colonies is preserved, some of which are still connected to hyphae (Fig. 1D). MNHN ARC115.5a contains a mycelium and numerous small yeast colonies as well as several nematodes (Fig. S1, B and C).

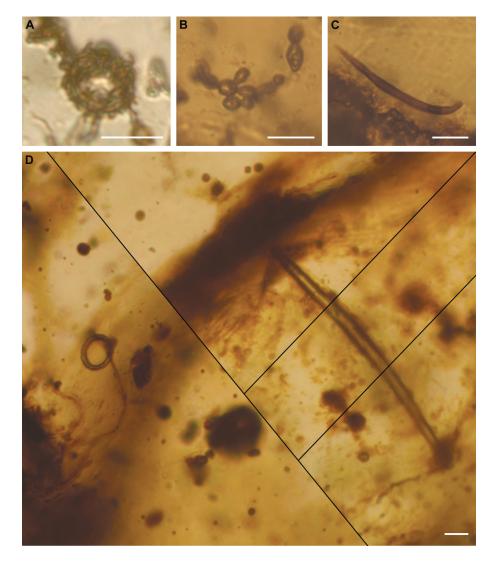


Fig. S1. Dimorphic carnivorous fungus from Cretaceous amber with its prey. (**A**) Trapping ring polluted by tiny detritus particles indicating that the rings were sticky (MNHN ARC115.22a). (**B**) Yeast colony disassociated from the hypha (MNHN ARC115.5a). (**C**) Syninclusion of a small nematode (MNHN ARC115.5a). (**D**) View of a trapping ring and a nematode close to it reconstructed from four optical sections (MNHN ARC115.13). Scale bars represent 10 μm.

Supplementary References

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