

RELATIONS BETWEEN WOOD-INHABITING INSECTS AND FUNGI

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INTRODUCTION

It is widely known that xylophagous insects do not usually attack healthy, resistant trees. In order to overcome these defenses, inner-bark feeding insects have developed symbiotic interrelationships with various organisms, fungi in particular. In this paper, using our own data together with that available in the literature, we analyze the forms of relationships between insects and fungi and the role of these interactions at various stages of wood decomposition. In doing so, we distinguish between the following fungal-insect relationships:

- 1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi
- 2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi (auxiliary ambrosia fungi according to Batra 1985)
- 3) xylophagous insects, symbiotically associated with fungi causing vascular mycoses
- 4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi.

The representatives of the first three groups develop in living wood or fresh timber. Representatives of the last group develop in dead wood, though in the earliest stages they can colonize living, but irreversibly weakened wood.

REVIEW

Ambrosia Mycetophagous Insects

This group includes insects which have necessary ectosymbiotic connections with a specific group of fungi imperfecti, the ambrosia fungi, and several characteristic features. The ambrosia fungi are highly sensitive to drought and develop only in moist wood. They are host specific, associated with certain species of insects, and are located only in colonized galleries or on the body of xylobionts. The fungi form the pellicle on the gallery walls--ambrosia--consisting of separate cells and fragments of filaments (Batra 1985 and others). Ambrosial cells can form vegetative mycelium under certain conditions.

Typical representatives of the ambrosia fungi are *Ascoidea*, *Ambrosiella*, *Raffaelea*, and *Phialophoropsis* (Batra 1967, 1985). The taxonomy of this group of fungi is poorly studied, representatives of other ecological groups, considered by us below, often being confused with them.

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Typical representatives of the ambrosia insects group are Platypodidae, Lymexylonidae, and some Scolytidae--*Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. (Francke-Grosmann 1967, Nakashima 1971, 1972, 1975, Mamaev 1977, Batra 1985, Nakashima et al. 1988). Some peculiar beetle representatives, Curculionidae and flies--Axymyiidae and Syrphidae--should also be classed among this group. The complex of ambrosia mycetophages is formed on both living wood and fresh timber. It has been said of the pin hole borer, *Austroplatypus incompertus* (Schedl.), that one and the same system of galleries can be used over 36 years (Harris et al. 1976). Ambrosia fungi have been obtained from the galleries of borers, pin hole borers, and bark beetles (Lymexylonidae, Platypodidae, Scolytidae) (Francke-Grosmann 1967, Baker and Norris 1968, and Nakashima 1971).

It has been ascertained that ambrosia fungi constitute the main food source for ambrosia insects (Kaneko and Takagi 1966, Norris and Baker 1967), and this determines insect behavior. The bark beetle *Xylosandrus compactus* Eichh. (Scolytidae) lays eggs only during the four to 14 days after colonization of the trunks of the coffee tree, i.e. after spreading of the ambrosia fungus mycelium throughout the surface of the gallery (Hara and Beardsley 1979). Successful larval development and imago reproduction are determined mainly by insect feeding on the ambrosia fungi (French and Roeper 1972, 1975, Barras 1973). Mamaev (1966) considered ambrosia insects xylomycetophagous. However, recent data show convincingly that they should be considered ambrosia mycetophages. This identification is indirectly confirmed by the peculiar intestinal structure of Axymyiidae larvae, without additional chambers or folds, which is pronounced in xylophages (Mamaev and Krivosheina 1966).

Apparently ambrosia insects are associated with fungi on a large number (up to 150 species) of host trees (Francke-Grosmann 1967). Colonization of new tree species occurs fairly quickly. For example, the ambrosia beetle, *Xylosandrus compactus* Eichh., was at first primarily on coffee trees on the Hawaiian Islands, but then spread throughout more than 100 tree species there (Hara and Beardsley 1979).

Symbiotic connections with fungi lead to the formation in ambrosia insects of various structures for the transfer of fungi. These structures are known as mycangia or mycetangia and are situated on the body and in the internal organs. The organs have been studied well enough in bark beetle pinhole borers and have also been found in the attelabid beetles (Schneider 1976, Nakashima 1975, Sawada and Morimoto 1986). The synchronization of insect and fungi development is also of interest. It was discovered in *Corthylus punctatissimus* Zimm. (Scolytidae) that ambrosia fungus, *Amabrosiella xylebori*, reproduces intensively by gemmation in mycangia only prior to wood colonization by beetles (Roeper 1988).

In the European part of the U.S.S.R., the complex of ambrosia insects is represented by the borers *Elateroideus dermestoides* L. on deciduous trees and *E. flabellicornis* Sch. (Lymexylonidae) on conifers. Usually they are accompanied by the larvae of *Libnotes* Westw. (Limoniidae). The bark beetles *Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. are often found together with the borers (Mamaev 1974b, 1977). *Platypus cylindriciformis* Rtt., which is close to the more widely distributed *P. cylindrus* Hbst. (Platypodidae), develops in oak stumps in the Transcaucasus region. The ambrosia insect complex in the forests of the Far East (U.S.S.R.) is the most diverse, however. The most common ambrosia insects are *Platypus severini* Bl. (Platypodidae) and *Sipalinus gigas* Fabr. (Curculionidae), which occupy various tree species: cedar, fir, elm, and lime (Mamaev 1974a).

The ambrosia dipterans complex forms in moist dying or dead wood. It is represented by species of Axymyiidae, Syrphidae (*Temnostoma* St. Farg et Serv.) (Fig. 1a), Stratiomyidae (*Xylopachygaster* Kriv.), and Limoniidae (*Libnotes* Westw.).

Axymyiidae larvae colonize newly felled trunks, where they may exist for several years in the moist conditions. The larvae construct galleries, constantly removing boring dust and fungi. Both larvae and pupae are mobile, the latter having a sclerotized flat cover on the head for clearing galleries (Fig. 1).

A similar life pattern is typical to the species of the genus *Temnostoma* St. Farg. et Serv. (Syrphidae), which occupy the fresh wood of fallen trees. The peculiar keg-like shape of their larvae's bodies helps them to clear galleries (Fig. 1c).

Unfortunately, the composition of the fungi communities in the galleries of *Ambrosia dipterans* and the mechanism of their transfer have not yet been studied. It is very likely that, in addition to ambrosia fungi, yeast is of great importance there. The species of the genera *Libnotes* Westw. (Limoniidae) and *Xylopachygaster* Kriv. (Stratiomyidae) associate only with ambrosia insects and do not take part in fungi transport.

Ambrosia Xylomycetophagous (Phloeomycetophagous) Insects

The ambrosia xylomycetophagous insects are consistently associated with the cup and imperfecti fungi (micromycetes). The latter consume chiefly the contents of the cells and do not destroy cellular walls, though these traits do not strictly define them (Gorshin and Krapivina 1969).

Unlike the ambrosia fungi, the wood-coloring fungi are not closely associated with insects, appearing in the galleries after completion of insect development. Easily cultivated, they can be mistaken for ambrosia fungi because they are often associated with them.

The most typical representatives of this group are the *Ceratocystis*, causing the blue-stain disease of the wood. The spores of the blue-stain fungi are spread by the air flow and by xylobiont insects, particularly when insects transfer sticky secondary spores of the cup fungi (Beliakova 1954, Batra 1985). Wood-coloring fungi infest weakened, drying, and newly felled trees, which are characterized by the high humidity of wood and large amounts of easily assimilated substances.

Close connections between wood-coloring fungi and bark beetles of the genera *Dendroctonus* Er, *Ips* Deg., *Pityogenes* Bed., *Hylastes* Er., and *Hylurgops* Lec. have been established (Mathre 1964, Francke-Grosmann 1967, Barras and Perry 1971, Raffa and Smalley 1988, Furniss et al. 1988, and Bennet and Tattar 1988).

It is possible to observe mutualistic interactions between wood-coloring fungi and bark beetles. The wood infested by blue-stain fungi is the most attractive and accessible to the bark beetles (Goheen et al. 1985). This can be explained by several facts. The fungi facilitate wood assimilation by the insects and promote xylophage aggressiveness, and fungi activity is known to increase the protein content of the wood (Hodges et al. 1968) and to decrease the water supply (Horntvedt et al. 1983). Together this results in the most favorable conditions for bark beetle development. On the other hand, mutualistic interactions promote special adaptations for fungi transmitting (Barras and Perry 1972, Furniss et al. 1988). The mechanism of fungi transfer is not simple. Secondary spores are fixed not only in mycangia, but directly on the body surface as well (Barras and Perry 1972, Livingston et al. 1983, Paine and Birch 1983).

Some data testify to the complex interactions between the ambrosia fungi and the ambrosia xylomycetophagous insects. The connection between tree colonization by bark beetles and intensive mycelium growth in mycangia was noted by Paine and Birch (1983). The bark beetles inoculate the wood with several *Ceratocystis* species. At the same time, however, the species preventing intensive blue-stain fungi development and favoring beetle breeding are also transferred in mycangia (Bridge and Perry 1985, Wood et al. 1988).

The interactions between bark beetles and wood-coloring fungi are considered by some authors to be facultative (Mamaev 1977, Batra et al. 1985). That supposition is partially confirmed by the peculiarities of the ecology of the fungi--they can develop without interactions with insects--and by

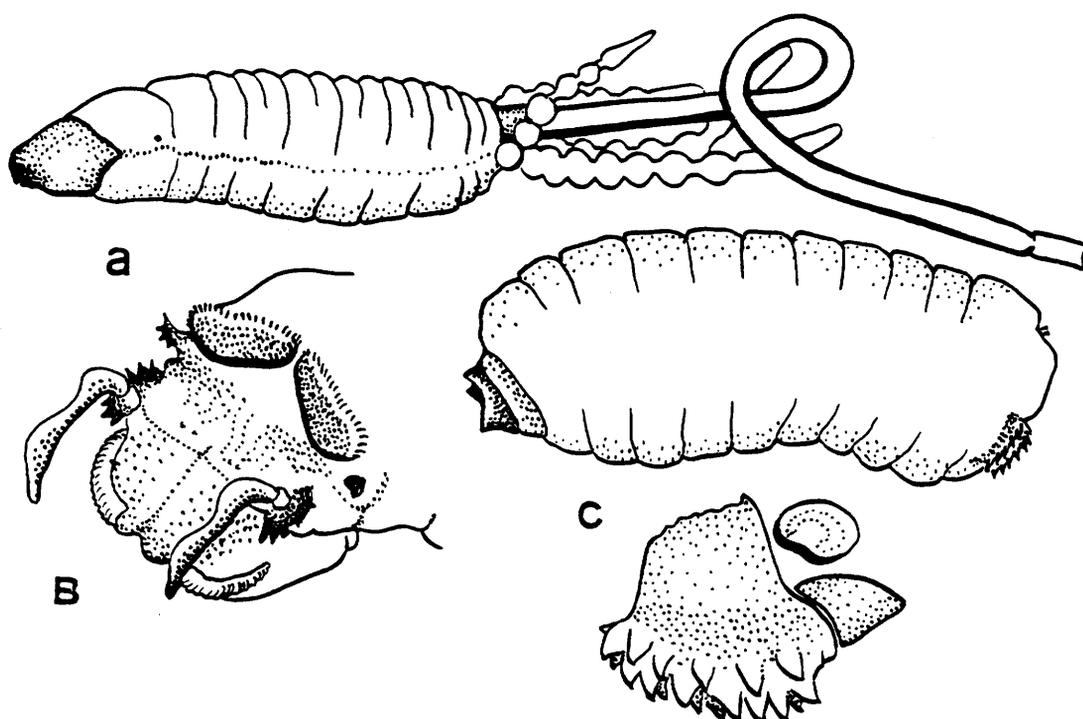


Figure 1. Preimaginal stages of xylobiont dipterans. A - the larvae of *Mesaxymyia kerteszi* Duda (Axymyiidae), B - the fore end of the head of pupa *Mesaxymyia kerteszi* Duda (Axymyiidae), and C - the larvae of *Temnostoma vespiforme* L. (Syrphidae).

features of the ecology of the insects--their capacity for development without symbiotic fungi has been documented (Grosmann 1931, Holst 1937). At the same time, more recent data do not resolve this question definitively. The bark beetles of this community feed on wood infested by fungi. We classify these beetles as xylo- or phloeomycetophages.

Xylophagous Insects Associated with Vascular Mycoses

Vascular mycoses are common among elms (Ulmaceae) and beeches (Fagaceae) and are caused by *Ceratocystis* fungi. The most familiar is Dutch elm disease, caused by the fungus *C. ulmi*. Among its vectors are now considered all the species of *Scolytus* Geoffr., the species of *Pteleobius* Bed., *Hylurgopinus rufipes* Eichn., the weevil *Magdalis armigera* Geoffr. (Curculionidae), and the capricorn beetle *Saperda punctata* L. (Cerambycidae) (Pfeffer 1979, Bejer 1979, Covassi 1980, Sengonca and Leisse 1984). The insects infect living trees during their feeding in the crown. Dying of the branches and tree weakening create favorable conditions for occupation of the stems by the insects. A similar disease causing oak mortality is widely distributed throughout Europe and North America. The pathogen of oak mycosis in the U.S.A. is *Ceratocystis fagacearum* (Rexrode and Jones 1970, 1971); in Europe it is the species of *Ceratocystis*, *Diaporthe*, and *Fusarium* (Kriukova and Plotnikova 1979, Kuzmichev 1982). The bark beetles *Pseudopityophthorus minutissimus* Zimm., *P. pruinosus* Eichh., and *Scolytus intricatus* Ratz. are considered vectors. In recent years, the role of sap beetles (Nitidulidae) in fungi transmitting has been discussed (Appel et al. 1986). These diseases caused by insect vectors are

likely to be distributed widely. Accordingly, the role of *Platypus subgranosus* Schedl. as a *Chalara australis* vector causing the drying wilt of beech myrtle (Fagaceae) has recently been identified (Elliott et al. 1988). Similar interactions have been observed between the sawyer beetle, *Monochamus urussovi* Fisch., and the fungi, *Ceratocystis* spp. (Isaev et al. 1988). Isaev et al. (1988) attach no less importance to these fungi than to the well-known pathogen of Dutch elm disease.

Infection of the beetle by the secondary spores takes place in the pupal chamber, on the walls of which the perithecium develops. Coincidence of the development cycles of both fungus and insect points to the historical connections between these species. Thus Vasechko (1981) and Lindeman (1986) thought this fungi to be an adventive species, against which the trees have not yet developed a pronounced resistance. It is possible, however, that the cause of such wide disease distribution is sufficient pathogen variability; if anything, it is represented now by several strains (Bazzigher 1981).

There are essential differences in the interactions between the fungi and the ambrosia xylomycetophages communities associated with wood-coloring fungi and those of the xylophages associated with vascular mycosis pathogens. In the first case, the bark beetle galleries occur on the trunk sections infected by the blue-stain fungi or in the parts nearby. In the case of vascular mycosis, there is asynchrony of trunk colonization by fungus and insects. With respect to insects, the fungi are a factor of tree weakening. As a result, insect species of this community have neither trophic nor biotopic connections with fungi and are typical phloeoxylophages.

It is important to remember that two ecologically distinct groups of fungi, having qualitatively different connections with insects, exist within the genus *Ceratocystis*.

Destructive Xylomycetophages Occupying Mainly Dead Wood

Wood-destroying fungi affect cellulose and lignin--the main components of the cell walls--causing wood rotting. Various species of fungi are characterized by different selectivity, causing rots distinct in color and structure: corrosive or destructive, brown or light. In the final stages of a tree's decay, the xylophagous insects prefer destructive light and brown rots. The greatest numbers of wood-destroying fungi are among the basidium fungi, but trunk rot is caused by cup and imperfecti fungi as well.

Insects associated with wood-destroying fungi can be placed in three large groups: species-vectors of fungi, which are not trophically related to infected wood; species transferring the fungi spores and preparing the substrate for their brood; species trophically related to fungus infecting the wood, but lacking special structures for fungi transfer. Representatives of the first group, while promoting wood-destroying fungi development, weaken trees and create conditions favorable to xylophage breeding.

Up until now, not enough attention has been paid to the role of insects in the transferring of wood-destroying fungi. The assumption has often been made that the role of the bark beetles is secondary, only associated with wood-destroying fungi (Beaver 1976). In fact, however, much data document bark beetles--*Dendroctonus* Er., *Hylurgops* Lec., *Ips* Deg., *Scolytus ratzeburgi* Jans.--occupying trees infected by tinder or gill fungi (Livingston et al. 1984). At the same time the role of *Dendroctonus* in transferring spores of *Fomitopsis pinicola* has been demonstrated by Harrington et al. (1981). The connection between the bark beetles *D. ponderosae* Hopk. and *Pityogenes fossifrons* Lec. and tree infection by the honey-fungus *Armellaria mellea* was discovered by Kulhavy et al. (1984). Bark beetles and weevils, particularly *Hylobius abietis* L., are thought to be vectors of the pine-fungus *Fomitopsis annosa* (Nuorteva and Laine 1968). The role of the representatives of the above mentioned group in the tree-fungus-insects system is not simple; they are likely to be both fungi associates and their vectors.

Typical representatives of the second species group, transmitting fungus infection and preparing the substrate for brood development, are the horntails. A connection has been found between horntails and the fungi *Polyporus*, *Daedalia*, *Daldinia*, and others (Stillwell 1960, 1964, Vaartaja and King 1964), the spores of which are transmitted by females during oviposition (Stillwell 1964). A dual effect of horntails on wood has been discovered. The horntails inoculate the tree with a special secretion which causes needle yellowing and weakening of tree resistance to fungi (Coutts 1969). Inoculation by the fungi causes changes in wood properties that facilitate tree occupation by horntails (Sinadsky 1967, Schimitschek 1974). On wood sections, the direct correlation between horntail attacks and fungus mycelium infections is vividly evident.

Strong preference for wood infected by basidium fungi was also found in some Peltidae and Buprestidae species. *Peltis grossum* L. (European-West Siberian species) and *P. giganteum* Rtt. (East Siberian species) are typically found with the brown rots of conifers and *Ostoma ferrugineum* L. with the brown birch rots caused by the fungus *Piptoporus betulinus*. The larvae develop only in the wood infected by mycelium. The possibility of spore transmission by species of Peltidae has not yet been studied.

Direct connections between damage to asian poplars *Populus pruinosa*, *P. ariana*, and other species by the popylore *Inonotus pseudohispidus* and the buprestid beetle *Eurythyrea oxiana* Sem. were recorded in the riparian forests of Middle Asia. Both the fungus and the beetle species are extremely common there. The fungus infects weakened, but visibly vigorous trees. The infected wood takes on a brownish or red color due to pigment accumulation (Sinadsky and Bondarceva 1956). The buprestid larvae occupy only those wood sections infected by the fungus. Conditions for spread of the fungus have not been studied. The spores are thought to penetrate to the wood at various injury sites (Sinadsky and Bondarceva 1956). At the same time, the close connections between the buprestid larvae and the fungus (common area, beetle habitation only in fungus-infected wood zones, initial occupation by both beetle and fungus of the trunk base) testify to the possibility of spore transmission by beetles. It is quite possible that the connections between this insect group and the fungi are not simple and belong to a different category of insect/fungal relationship. This supposition is confirmed by the example of the horntails, for many of which mutualistic, symbiotic relations are evident. Thus *Xeris spectrum* L. (Siricidae) with poorly developed mycetangia injure wood only during the year following occupation by another horntail species (Spradbery 1974), which infect it with fungi.

Species Trophically Associated with Fungus-Infected Wood and Lacking Special Structures for Fungal Transmission

This group includes the destructive xylophages breeding in light and brown wood rots. Wood occupation takes place quite long after fungi inoculation. The imago of this insect group tries to locate tree trunks suitable for colonization (Mamaev 1974c). By wood boring, xylophages promote various microorganisms and fungi activity (Callaham and Shifrine 1960, Mamaev 1960) and favor their penetration of the wood through galleries (Hesterberg et al. 1976).

The capacity of this group to feed on poorly assimilated, less nutritional wood pulp in the absence of ectosymbiotic associations with fungi can be explained by the presence of cellulases in the intestine. So, unlike bark and capricorn beetles feeding on bark and sap-wood and possessing hemicellulase, the capricorns as typical inhabitants of destructive rots have a set of cellulases, promoting cellulose utilization by the insect (Chararas 1983, Chararas and Chipoulet 1983, Kukor and Martin 1986). The high cellulases concentration in the intestine is thought to result from fungi reproducing in the folds of the intestine (Schlottke 1948, Mamaev 1960, 1974c). At the same time, capricorn beetles breeding in weakened trunks on the border of xylem and phloem were discovered to possess an extra set of enzymes and yeast, favoring assimilation of the carbohydrates (Chararas and Pignal 1981).

Brown rots most often form under the influence of the polypore *Fomitopsis pinicola* and are most common to conifers. The typical inhabitants of brown wood rots in the European part of the U.S.S.R. are *Toxotus cursor* L. (Cerambycidae), *Ceruchus chrysomelinus* Hochw., and *Aesalus scarabeoides* Pz. (Lucanidae). In the mountains of the Caucasus, the last of these species is replaced by *Aesallus ulanovskyii* Gglb. (Kosarjevskaya and Mamaev 1962, Mamaev 1977).

The typical destroyers of brown rot wood in the Far East are the cockroach, *Cryptocercus relictus* B. Bien., the beetles *Prostomis mordax* Rtt. (Cucujidae), *Istrisia rufobrunnea* Lew. (Salpingidae), *Nematoplus semenovi* Nik. (Nematoplidae), *Phellopsis amurensis* Heyd. (Zopheridae), and others (Mamaev 1973a, 1973b, 1974b). Among Diptera, the most common inhabitant of brown rots is *Hyperoscelis eximia* Bohem. (Canthyscelidae).

The light rots, usually developing under the influence of the tinder fungus *Fomes fomentarius*, are most typical to leaf-bearing trees. The light rot wood in the European part of the U.S.S.R. are usually destroyed by the larvae of common stag beetles, *Lucanus cervus* L., *Dorcus parallelipedus* L., and *Sinodendron cylindricum* L. (Lucanidae), and the larvae of dipterans, *Tanyptera atrata* L., *Dictenidia bimaculata* L. (Tipulidae), and *Epiphragma ocellaris* L. (Limoniidae). The main consumers of light rots in the Far East are the stag beetles, *Prismognathus subaeneus* Motsch. and *Eurytrachelus rubrofemoratus* Voll. (Lucanidae), the darkling beetles, *Misolampidius tentyrioides* Sols (Tenebrionidae), and the dipterans, *Phoroctenia vittata* Mg., *Tanyptera nigricornis* Mg. (Tipulidae), *Hesperinus rohdendorfi* Kriv. et Mam. (Hesperinidae), and *Pachyneura oculata* Kriv. et Mam. (Pachyneuridae). In this group one can also find the beetles *Melandrya mongolica* Motsch. (Melandryidae) and *Dentisca serridens* Ter.-Min. (Curculionidae).

Among the ecological groups considered, two groups of destroyers (bark and capricorn beetles) can be classified as xylophages, and the last horntails, peltids, and some buprestids as xylomycetophages, because of their feeding on wood infected by fungus mycelium.

CONCLUSIONS

Vigorous trees have diverse properties for facilitating their resistance against consumers. Moreover, wood is a substance resistant to degradation. Therefore, representatives of the "tree-fungus-insect" system have evolved allowing insects to exploit a vast resource.

My attempt to classify these relations is no doubt far from being complete, partly because the delicate mechanisms of insect-fungi interactions have as yet been insufficiently studied. Nevertheless, the examples presented permit us to conclude that complicated insect-fungi relationships exist at all successional stages of wood degradation (Lindemann 1986).

SUMMARY

Based on the forms of their interrelationships with fungi, we distinguished four groups of insects: 1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi; 2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi; 3) xylophagous insects, symbiotically associated with vascular mycosis fungi; and 4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi. Among the destructive xylo-, mycetophagous insects, three ecological subgroups were identified in terms of their trophic and symbiotic connections with fungi.

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