Evolutionary Theory for
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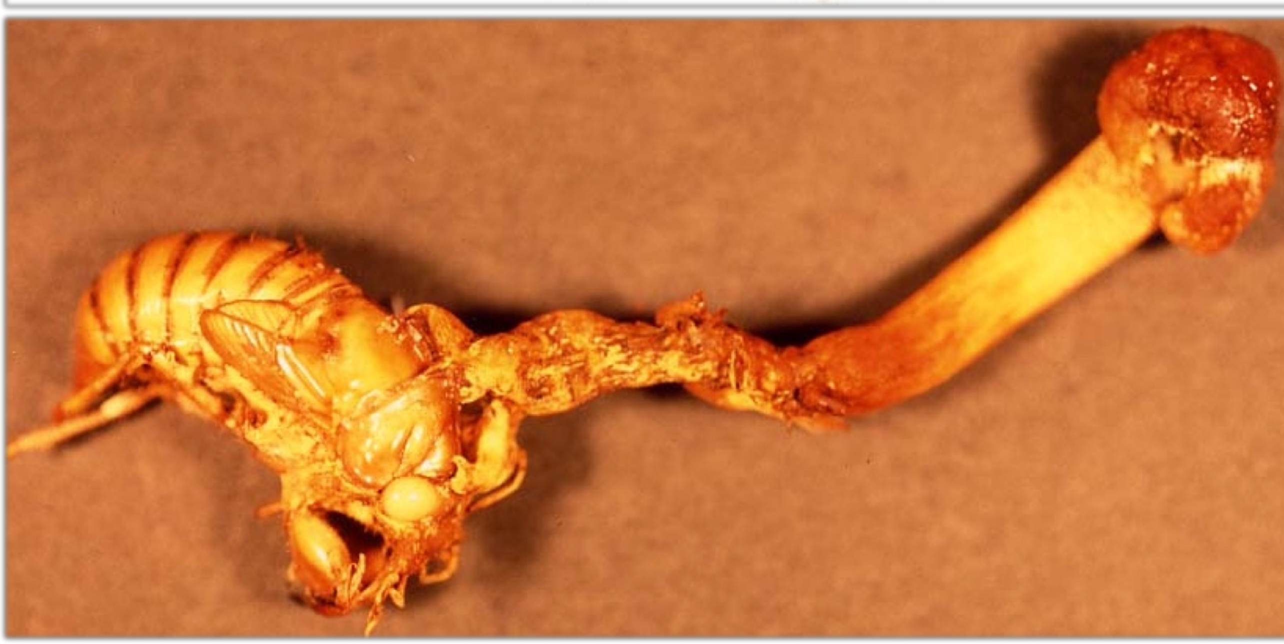

Recurrent symbiont recruitment from fungal parasites in cicadas

Cover image:
The large brown cicada *Graptopsaltria nigrofuscata* and the cicada-parasitic fungus *Ophiocordyceps heteropoda*
(Takema Fukatsu, AIST)

Recurrent symbiont recruitment from fungal parasites in cicadas

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Diverse insects are associated with ancient bacterial symbionts, whose genomes have often suffered drastic reduction and degeneration. In extreme cases, such symbiont genomes seem almost unable to sustain the basic cellular functioning, which comprises an open question in the evolution of symbiosis. Here, we report an insect group wherein an ancient symbiont lineage suffering massive genome erosion has experienced recurrent extinction and replacement by host-associated pathogenic microbes. Cicadas are associated with the ancient bacterial co-obligate symbionts *Sulcia* and *Hodgkinia*, whose streamlined genomes are specialized for synthesizing essential amino acids, thereby enabling the host to live on plant sap. However, our inspection of 24 Japanese cicada species revealed that while all species possessed *Sulcia*, only nine species retained *Hodgkinia*, and their genomes exhibited substantial structural instability. The remaining 15 species lacked *Hodgkinia* and instead harbored yeast-like fungal symbionts. Detailed phylogenetic analyses uncovered repeated *Hodgkinia*-fungus and fungus-fungus replacements in cicadas. The fungal symbionts were phylogenetically intermingled with cicada-parasitizing *Ophiocordyceps* fungi, identifying entomopathogenic origins of the fungal symbionts. Most fungal symbionts of cicadas were uncultivable, but the fungal symbiont of *Meimuna opalifera* was cultivable, possibly because it is at an early stage of fungal symbiont replacement. Genome sequencing of the fungal symbiont revealed its metabolic versatility, presumably capable of synthesizing almost all amino acids, vitamins, and other metabolites, which is more than sufficient to compensate for the *Hodgkinia* loss. These findings highlight a straightforward ecological and evolutionary connection between parasitism and symbiosis, which may provide an evolutionary trajectory to renovate deteriorated ancient symbiosis via pathogen domestication.

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