Phytotaxa 220 (3): 224–238
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.220.3.2

Unravelling the diversity behind the *Ophiocordyceps unilateralis* (Ophiocordycipitaceae) complex: Three new species of zombie-ant fungi from the Brazilian Amazon

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Abstract

In tropical forests, one of the most commonly encountered relationships between parasites and insects is that between the fungus *Ophiocordyceps* (Ophiocordycipitaceae, Hypocreales, Ascomycota) and ants, especially within the tribe Camponotini. Here, we describe three newly discovered host-specific species, *Ophiocordyceps camponoti-atricipis*, *O. camponoti-bispinosi* and *O. camponoti-indiani*, on *Camponotus* ants from the central Amazonian region of Brazil, which can readily be separated using morphological traits, in particular the shape and behavior of the ascospores. DNA sequence data support inclusion of these species within the *Ophiocordyceps unilateralis* complex.

Introduction

In tropical forests, social insects (ants, bees, termites and wasps) are the most abundant land-dwelling arthropods. Although they represent only 2% of the nearly 900,000 known insect species on Earth, they are estimated to compose more than half of the biomass (Fittkau & Klinge 1973; Höldobler & Wilson 2009). One of the better known members within this group are the ants, which form a single family (Formicidae), with close to 13,000 species described (Agosti & Johnson 2009). Ants occupy a wide range of habitats from high canopy to the leaf litter, forming huge colonies comprising tens to hundreds of thousands to millions of individuals.

Ants are associated with and susceptible to a variety of parasites. Amongst these, one group is particularly well adapted to live in tropical forests and to exploit this ant abundance, the entomopathogenic fungi of the genus *Ophiocordyceps* (Hypocreales; Ophiocordycipitaceae), currently comprising around 160 species (Robert *et al*. 2005; Sung *et al*. 2007). These parasites infect many different insects with a wide range of ecologies, from solitary wandering beetles to highly-organized ant societies. The orders infected include Blattaria, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mantodea, Odonata and Orthoptera (Araújo & Hughes bioRxiv). The functional morphology of *Ophiocordyceps* is equally diverse and has been linked to the host's ecology and biology (Evans *et al*. 2011).

Species of *Ophiocordyceps* were originally placed within *Cordyceps*, a genus established to accommodate fungal pathogens of arthropods bearing the sexual spore-producing structures (ascoma) on conspicuous stalks (stroma), arising from the host cadaver (Evans *et al*. 2011). However, due to the polyphyletic nature of *Cordyceps*—as evidenced by recent phylogenetic studies—species formerly assigned to the genus have now been reorganized into four genera (*Cordyceps*, *Elaphocordyceps* (currently *Tolypocladium,* see Quandt *et al*. 2014), *Metacordyceps* and *Ophiocordyceps*), within three families (*Cordycipitaceae*, *Clavicipitaceae* and *Ophiocordycipitaceae*) (Sung *et al*. 2007).

Within the Formicidae, *Ophiocordyceps* infections have been reported from the basal primitive groups (Ponerines) through to modern genera, such as *Camponotus* (Evans & Samson, 1982; Sanjuan *et al*. 2001; Evans *et al*. 2011), and often occur as epizootics, killing large number of ants in small patches of forest (Andersen *et al*. 2009; Pontoppidan *et al*. 2009). Such events are pan-tropical with records from Asia, Australasia, Africa and the Americas (Evans 1974;

 Accepted by Kevin Hyde: 6 May 2015; published: 24 Jul. 2015