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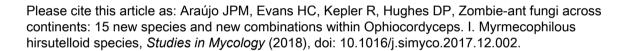
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Zombie-ant fungi across continents: 15 new species and new combinations within *Ophiocordyceps*. I. Myrmecophilous hirsutelloid species

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Abstract: Ophiocordyceps species infecting ants – the so-called zombie-ant fungi – comprise one of the most intriguing and fascinating relationships between microbes and animals. They are widespread within tropical forests worldwide, with relatively few reports from temperate ecosystems. These pathogens possess the ability to manipulate host behaviour in order to increase their own fitness. Depending on the fungal species involved the infected ants are manipulated either to leave the nest or ascend understorey shrubs, to die biting onto vegetation, or descend from the canopy to die at the base of trees. Experimental evidence has demonstrated that the behavioural change aids spore dispersal and thus increases the chances of infection, because of the existing behavioural immunity expressed inside ant colonies that limits fungal development and transmission. Despite their undoubted importance for ecosystem functioning, these fungal pathogens are still poorly documented, especially regarding their diversity, ecology and evolutionary relationships. Here, we describe 15 new species of Ophiocordyceps with hirsutella-like asexual morphs that exclusively infect ants. These, form a monophyletic group that we identified in this study as myrmecophilous hirsutelloid species. We also propose new combinations for species previously described as varieties and provide for the first time important morphological and ecological information. The species proposed herein were collected in Brazil, Colombia, USA, Australia and Japan. All species could readily be separated using classic taxonomic criteria, in particular ascospore and asexual morphology.

Key words: Behaviour manipulation, Camponotini, entomopathogenic fungi, entomopathogens, Formicidae, host association, *Hypocreales*, insect pathogen, multigene phylogeny, myrmecophyly, *Ophiocordyceps, Ophiocordyceps unilateralis*, *Ophiocordycipitaceae*, zombie-ant fungi.

Taxonomic novelties: New combinations: Ophiocordyceps dolichoderi (H.C. Evans & Samson) Araújo, H. C. Evans & D. P. Hughes.; Ophiocordyceps monacidis (H.C. Evans & Samson) Araújo, H. C. Evans & D.P. Hughes.; New species: Ophiocordyceps albacongiuae Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps blakebarnesii Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-chartificis Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-floridani Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-floridani Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-nidulantis Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-nidulantis Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps camponoti-sexguttati Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps daceti Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps kimflemingiae Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps naomipierceae Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps occophyllae Araújo, S. Abell, T. Marney, R. Shivas H.C. Evans & D.P. Hughes.; Ophiocordyceps octakii Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordyceps satoi Araújo, H. C. Evans & D.P. Hughes.; Ophiocordycep

INTRODUCTION

Fungi associated with insects are one of the most spectacular and diverse interactions found in nature. There is an enormous variety to consider: mutualistic symbionts (Suh *et al.* 2005); fungi serving as an obligate food source, such as those found in fungus-gardening ants (Currie *et al.* 2003); sexually- and behaviourally-transmitted parasites – e.g. Laboulbeniales (DeKesel 1996); and entomopathogenic fungi that are highly virulent and are considered to have pronounced effects on host populations (Evans 1974). Despite this increasing knowledge, fungal-insect associations still remain an understudied area of fungal biodiversity and likely harbour one of the largest reservoirs of undocumented species among Fungi.

Insects, with more than a million described species (Foottit & Adler 2009) are distributed among 29 orders (Misof *et al.* 2014). The fungal pathogens are able to colonize 19 of these orders, resulting in the evolution of a wide diversity of morphologies and strategies that enable infection and onward transmission using the insect body as the ecological niche (Araújo & Hughes 2016). Among these different strategies, one of the most impressive and sophisticated interactions between insects and entomopathogenic fungi is that involving ants and species of fungi in the genus *Ophiocordyceps* (Andersen *et al.* 2009). The genus is estimated to have arisen about 100 million years ago (Sung *et al.* 2008) and since then has colonized ten orders of insects (Sanjuan *et al.* 2015, Araújo & Hughes 2016), comprising about 200 species of entomopathogens (Crous *et al.* 2004). Although ants account for less than 2 % of insect species, they contribute as much as 50 % of animal biomass in tropical forests (Holldobler & Wilson 2009, Agosti & Johnson 2009). Ants occupy a wide range of habitats, from high canopy to the leaf litter, forming colonies comprising from a few dozen (Jahyny *et al.* 2002) to millions of individuals (Currie *et al.*, 2003), especially in tropical forests. As such dominant members of most terrestrial biomes, ants are the most commonly encountered hosts for species in the genus *Ophiocordyceps* in tropical forests worldwide.

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