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# New species of Ophiocordyceps unilateralis, an ubiquitous pathogen of ants from Thailand



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#### ABSTRACT

Ophiocordyceps unilateralis is an ubiquitous pathogen of ants with hidden phylogenetic diversity associated with host specificity. In this study, we describe two new species to this species complex: Ophiocordyceps septa and Ophiocordyceps rami. Both were found on unidentified ants of the genus Camponotus (C. sp.1 and C. sp2 respectively). Ophiocordyceps septa is very similar to Ophiocordyceps polyrhachis-furcata, Ophiocordyceps camponoti-leonardi, and Ophiocordyceps camponoti-saundersi (found respectively on the ants Polyrhachis furcata, Camponotus leonardi, and Camponotus saundersi) but differs in the size, the shape and the septation of the ascospores, while O. rami is clearly identifiable with macro-morphological features including multiple stromata similar to Ophiocordyceps halabalaensis on Camponotus gigas. A thorough morphological examination was also provided for O. polyrhachis-furcata, O. camponoti-leonardi, and O. camponoti saundersi, showing that the first was apparently distinguishable from the others by the absence of septation of the ascospores. A combined molecular phylogeny also supports O. septa and O. rami as distinct new species.

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## Introduction

Fungal ant pathogens were believed to be rare, and records of them were scarce (Allen & Buren 1974; Schmid-Hempel 1998). However, efforts have been made continuously to investigate their diversity and contribute to a better comprehension of their habitats (Evans & Samson 1982; Evans & Samson 1984, Evans et al. 2010, Evans et al. 2011). The most ubiquitous fungal pathogen of ants is the fungus Ophiocordyceps unilateralis (Tul.) Pech. Much attention has been given to this species because of

its outstanding way of life: infecting and modifying the ants' behaviour in order to favour its own transmission (Andersen et al. 2009, Pontoppidan et al. 2009; Hughes et al. 2011). The ants, infected by O. unilateralis, have been reported to die with their jaws clamped on elevated vegetal substrates, hanging themselves upside down.

This species was first described by Tulasne & Tulasne (1865) under the name Torrubia unilateralis. Successive collections of this species complex from around the world have demonstrated that it only attacks ants from the tribe

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Camponotini (subfamily Formicinae) (Evans & Samson 1984; Evans et al. 2011). This tribe is also attacked by Ophiocordyceps myrmecophila (Luangsa-ard et al. 2007), Ophiocordyceps irangiensis (Hywel-Jones 1996; Luangsa-ard et al. 2010), Ophiocordyceps lloydii (Evans & Samson 1984) and Ophiocordyceps pulvinata (Kepler et al. 2010). The taxonomy of O. unilateralis is problematic because its first description by Tulasne & Tulasne (1865) did not provide any description of sexual structures including ascomata, asci, and ascospores. Therefore, this species was characterised only by a lateral ascomatal cushion that developed on the stroma growing from the back of the ants' heads. Any specimen approximating this description is likely to be identified as O. unilateralis, thus the term "sensu lato" is frequently used in some literature (Evans et al. 2011; Kobmoo et al. 2012). The morphology of O. unilateralis s.l. is variable which was considered to represent intraspecific phenotypic variation and not a basis for the existence of co-occurring species (Evans & Samson 1984). However, recent studies have called for the delineation of distinct host-specific species and for a status change to a species complex rather than phenotypic plasticity (Evans et al. 2011; Kobmoo et al. 2012). Evans et al. (2011) described four new species of O. unilateralis s.l. found on four different ant species in Brazil: Ophiocordyceps camponoti-rufipedis on Camponotus rufipes, Ophiocordyceps camponoti-balzani on Camponotus balzani, Ophiocordyceps camponoti-melanotici on Camponotus melanoticus, and Ophiocordyceps camponoti-novogranadensis on Camponotus novogranadensis. Despite the lack of molecular data, sufficient micro-scale morphological characteristics were evident to indicate the differences between these host-specific taxa. These micromorphological differences were based on shape, size, and septation of ascospores; and also the types of phialides and

Kobmoo et al. (2012) used a molecular phylogenetic approach to demonstrate host-specific divergence between O. unilateralis specimens found on Polyrhachis furcata, Camponotus leonardi, and Camponotus saundersi ants. Interestingly, macromorphological examinations did not reveal any significant differences, suggesting cryptic speciation within this species complex. The specimens found on these three ants were thus given new species names Ophiocordyceps polyrhachis-furcata, Ophiocordyceps camponoti-leonardi, and Ophiocordyceps camponoti-saundersi, respectively. In the same study, some molecular data were presented on specimens found on unidentified ants of the genera Camponotus and Polyrhachis but morphological examinations have yet to be performed on those specimens.

Luangsa-ard et al. (2011) described Ophiocordyceps halabalaensis found on C. gigas ants in the south of Thailand. This species fit the broad description of O. unilateralis s.l., having a stipitate stroma emerging between the head and the thorax of the ants. However, it also displayed two other stromata emerging from the top joints between the left and right forelegs and the thorax. These morphological differences justified the nomination of a new species, a decision that was supported by the molecular data showing it to be closely related to, but different from O. unilateralis on the ant C. leonardi. Finally, O. pulvinata was found on the ant Camponotus obscuripes in Japan. Based on its morphological characteristics, this species did not fit the broad description of O. unilateralis because it

lacked a stipitate stroma supporting an ascomatal cushion. However, it also shows an extended phenotype similar to *O. unilateralis*: the ant demonstrates a behaviour modification by biting a twig; and the molecular data showed its very close relationship to *O. unilateralis* (Kepler et al. 2010).

In the current study, we describe two new species of the O. unilateralis species complex which have been found in Thailand on ant species different from those reported previously. Their species status is supported by a molecular phylogeny, as is their close phylogenetic relationship to species of O. polyrhachis-furcata, O. camponoti-leonardi, O. camponoti-saundersi. The morphology of these three taxa was also re-examined in comparison to the two species described in this studies.

#### Material and methods

#### Collection and management of specimens

During ongoing biodiversity survey in Thailand, we discovered new specimens of Ophiocordyceps unilateralis on ant species different to those found in previous studies (Evans et al. 2011; Kobmoo et al. 2012). Two groups of specimens could be distinguished based on hosts, distinct unidentified Camponotus ants (C. sp.1 and C. sp.2) (Figs 1 and 2). Actually, O. unilateralis on C. sp.1 was already found in Kobmoo et al. (2012) but there were too few samples for complete morphological descriptions and were thus used for molecular work instead. In contrast, O. unilateralis on C. sp.2 is being reported here for the first time. Both types of specimens have morphological characteristics of O. unilateralis in a broad sense (sensu lato) in that they possess lateral ascomatal cushions on a stroma growing from the joint between the head and the thorax of the ants. However, those found on C. sp.2 also have another two stroma growing from the joints between the thorax and both forelegs of the ants (Fig 1). We were not able to isolate the specimens into pure culture. Therefore, some specimens were used for DNA extraction from fresh stroma. Others were subjected to morphological examination. After the extraction, the ants were dried in a food dehydrator for one day and deposited at BIOTEC Bangkok Herbarium (BBH).

New specimens of O. unilateralis on the ants Polyrhachis furcata, Camponotus leonardi, and Camponotus saundersi were also collected for thorough morphological examinations and additional molecular data (Table 1).

### Morphological examinations

The important component of the sexual state, i.e. perithecial plate, was prepared for microscopic observation by rehydration in sterile water until become soft. Free-hand longitudinal sections of tissues were mounted in cotton blue and lactophenol; perithecia, asci, and ascospores were measured using a light microscope. For asexual state, samples were examined by using Scanning Electron Microscopy. The type of Hirsutella phialides (A-type, B-type and C-type) were identified according to Evans & Samson (1982, 1984) and Evans et al. (2011).

We re-examined specimens of Ophiocordyceps polyrhachisfurcata, Ophiocordyceps camponoti-leonardi, and Ophiocordyceps camponoti-saundersi to compare with the two new species

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