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RESEARCH/REVIEW ARTICLE

First records of aphid-pathogenic Entomophthorales in the sub-Antarctic archipelagos of Crozet and Kerguelen

Bernard Papierok,¹ Charles-Antoine Dedryver² & Maurice Hullé²¹ Pasteur Institute, 25 et 28, rue du Docteur Roux, FR-75015 Paris, France² Institute for Genetics, Environment and Plant Protection, French National Institute for Agricultural Research, Domaine de la Motte, FR-35653 Le Rheu, France**Keywords**

Natural enemies; introduced species; biological invasion; colonization; Zygomycetes; parasitism.

Correspondence

Maurice Hullé, Institute for Genetics, Environment and Plant Protection, French National Institute for Agricultural Research, Domaine de la Motte, FR-35653 Le Rheu, France. E-mail: maurice.hulle@rennes.inra.fr

Abstract

Since the 20th century, the sub-Antarctic islands have suffered an increasing number of biological invasions. Despite the large number of publications on this topic, there is a lack of knowledge on parasitism rates of invasive species and on the role of parasites and pathogens to regulate their populations. Six aphid species have been introduced in the archipelagos of Crozet (Île de la Possession, 46° 25' S–51° 51' E) and Kerguelen (49° 21' S–70° 13' E). Five of these species were found infected by entomopathogenic fungi of the order Entomophthorales. All these fungal species are cosmopolitan. *Conidiobolus obscurus* and *Entomophthora planchoniana* were the most frequently observed on Île de la Possession and in Archipel des Kerguelen, respectively. This is the first report of pathogenic fungi of aphids on the sub-Antarctic islands. We discuss these results in the light of our current knowledge of these insect pathogens. Their introduction by aphids surviving on plants during transportation is the most likely hypothesis to explain their presence on these remote islands.

As insular ecosystems in isolated and severe climatic environments, the sub-Antarctic archipelagos of Crozet and Kerguelen provide a unique field to address questions regarding invasive species in relation to increasing human impact and climate change (Gaston et al. 2002; Chown et al. 2005; Frenot et al. 2005; Chown et al. 2008). These remote islands have a cold oceanic climate and a depauperate native fauna and flora. Whalers and sealers were the main visitors during the 19th century and may be responsible for the first biological introductions. Kerguelen was increasingly visited from the beginning of the 20th century, whereas for Île de la Possession, in the Archipel Crozet, the increase in visits began in the mid-20th century (Frenot et al. 2001; Lebouvier & Frenot 2007). As sub-Antarctic islands, their food webs are poorly developed, with a high number of decomposers and very few herbivores, predators and parasites (Crafford et al. 1986; Chown et al. 1998; Vernon et al. 1998; Convey 2001). The success of invasive species in their new habitats can be explained at least in part by reduced control by natural enemies such as predators, pathogens and parasites—the enemy release hypothesis (Colautti et al.

2004; Liu & Stiling 2006)—but also by their own biological traits, such as dispersal, fitness and so on (Hayes & Barry 2008). However, there is a lack of knowledge about parasitism rates of invasive species and the role of parasites and pathogens in regulating their populations (Torchin et al. 2003; Prenter et al. 2004; Dunn et al. 2012).

Six species of aphids (Hemiptera, Aphididae) are known to occur on Île de la Possession and in Archipel des Kerguelen (Remaudière & Etienne 1988; Hullé, Pannetier, Maurice et al. 2003): *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), *Myzus ascalonicus* Doncaster, *Myzus ornatus* Laing, *Myzus persicae* (Sulzer) and *Rhopalosiphum padi* (L.). These species are cosmopolitan and are understood to have been introduced within the last 80 years (Hullé, Pannetier, Simon et al. 2003). *Myzus ascalonicus* is the most invasive (Hullé, Pannetier, Simon et al. 2003; Hullé 2012). This generalist feeder has colonized both introduced and native plants belonging to 14 families, and has spread widely, preferentially along the littoral zone and below 100 m above sea level (Hullé, Pannetier, Simon et al. 2003). To understand major biological traits that influence colonization success by

these cosmopolitan and polyphagous aphids in such sub-Antarctic environments, studies were carried out starting from the end of the 1990s. Host plant range, spatial and altitudinal distribution of aphids, their genetic variability, their role in the transmission of plant viruses and the vulnerability of native communities were especially investigated (Delmotte et al. 2001; Delmotte et al. 2003; Hullé, Pannetier, Maurice et al. 2003; Hullé, Pannetier, Simon et al. 2003; Lebouvier et al. 2011; Hullé 2012; Svanella-Dumas et al. 2013). Aphids killed by fungi of the order Entomophthorales (Zygomycetes) sensu Keller (2007) were first observed (by MH) in 2001 on Île de la Possession and in Archipel des Kerguelen, although the presence of natural enemies was not mentioned in the literature.

The present contribution compiles observations of aphid-pathogenic fungi in Archipel des Kerguelen and on Île de la Possession and discusses these data in the framework of our current knowledge on these insect pathogens and invasion biology.

Material and methods

Archipel des Kerguelen (49° 21' S–70° 13' E, 7200 km²) and Île de La Possession (46° 25' S–51° 51' E, 150 km²) in the Archipel Crozet are both in the sub-Antarctic area of the Southern Indian Ocean. Their mean annual temperatures are 4.85°C (Météo-France, 1951–2014 records) and 5.52°C (Météo-France, 1970–2014 records), respectively; little seasonal variation is recorded. The major climatic difference between these two archipels is rainfall: the total annual rainfall is 2400 mm on Île de la

Possession and varies from more than 3200 mm in the western part of Archipel des Kerguelen to less than 800 mm in the eastern part.

Entomophthorales-killed aphids were searched for during the austral growing seasons (December–May) in 2001/02 (Île de La Possession only) and 2011/12 and 2012/13 (Île de La Possession and Archipel des Kerguelen) at locations routinely used for botanical and entomological studies: Base Alfred Faure, Baie Américaine, Crique du Sphinx, Crique de Noël and Baie du La Pérouse on Île de la Possession (Fig. 1); and Base de Port-aux-Français, Île Haute, Île Mayes, Île aux Cochons and Île Verte in Archipel des Kerguelen (Fig. 2). Such aphids can be recognized by their peculiar brownish colour and, sometimes, their fixation on the substrate through fungal structures called rhizoïds or a layer of sporulating structures covering the body. When cadavers were found in aphid colonies, they were processed as follows to confirm the fungal nature of the infection and to identify the etiological agent. Leaves bearing colonies were cut out and placed in containers not completely closed, to prevent the atmosphere from becoming saturated. Back at the laboratory, leaves were observed with a binocular microscope. Aphids killed by Entomophthorales were gently removed from the leaf using forceps, and placed on a moistened piece of filter paper. That moistened piece was then attached to the inside of a Petri dish and the lid was inverted on slides to collect conidia forcibly discharged from cadavers. Following collection of conidia, slides were kept in dry conditions and corresponding cadavers stored in ethanol 70%. For observation of conidia, the slides were mounted in cotton blue in

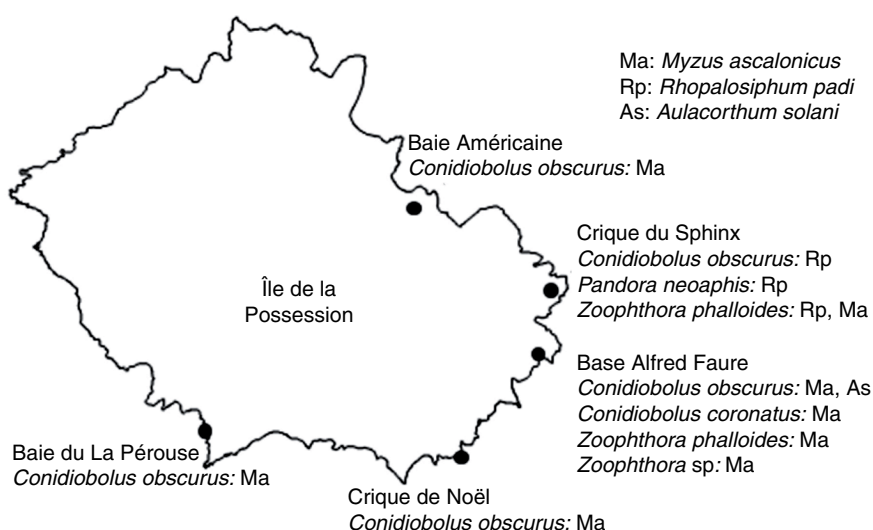


Fig. 1 Distribution of Entomophthorales on Île de la Possession (Archipel Crozet).

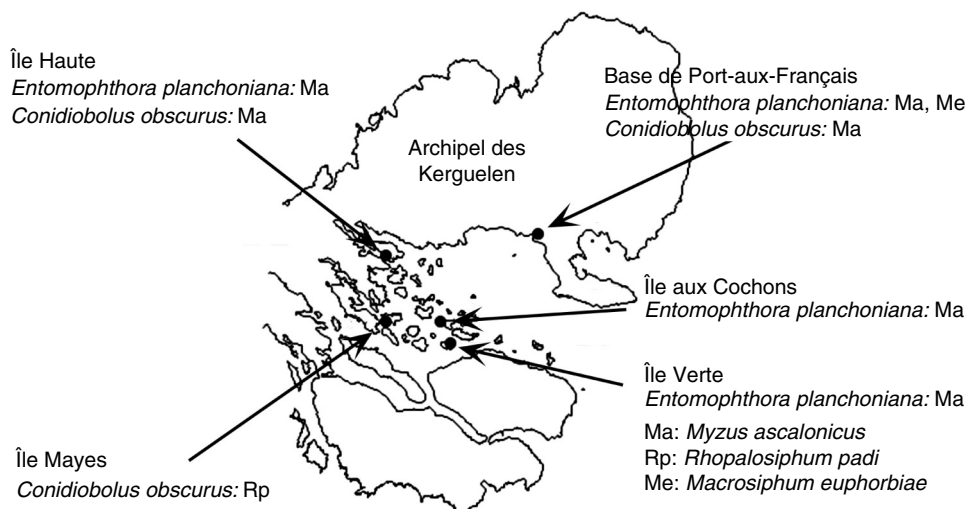


Fig. 2 Distribution of Entomophthorales in Archipel des Kerguelen (Golfe du Morbihan).

lactophenol. Shapes of spores were systematically noted, and the length and width of 10–50 spores per cadaver were measured, using a light microscope (200 ×). Cadavers kept in ethanol were also mounted in anilin blue or cotton blue in lactophenol after being teased apart using fine forceps or fine insect pins for observation and measurement of possible resting spores; detailed procedures are described by, for example, Papierok and Balazy (2007). The fungal species were identified on the basis of the combination of the following phenotypic characters: shape and size of primary and possibly secondary conidia, branched or unbranched conidiophores, shape and size of resting spores, and presence and type of rhizoids (Latgé & Papierok 1988; Keller 2006; Keller 2007).

Results

A total of 114 fungus-killed aphids were collected: 98 *Myzus ascalonicus*, seven *Rhopalosiphum padi*, seven *Aulacorthum solani* and two *Macrosiphum euphorbiae*. The distribution of entomophthoralean species and their aphid hosts are shown in Figs. 1, 2 and Table 1.

Six different Entomophthorales were distinguished from dead aphids collected on Île de La Possession, namely: *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller (in 2001–02 and 2011–13); *Entomophthora planchoniana* Cornu (in 2001–02); *Pandora neoaphidis* (Remaudière & Hennebert) Humber (in 2001–02); *Zoophthora phalloides* Batko (in 2001–02); *Zoophthora* sp. (in 2001–02); and *Conidiobolus coronatus* (Costantin) Batko (in 2011–13).

In Archipel des Kerguelen, only two species were observed (in 2011–13): *Entomophthora planchoniana* and *Conidiobolus obscurus*.

The principal morphological characteristics of these fungal species are given in Table 2, together with the sizes of the locally collected corresponding spores.

Conidiobolus obscurus was found on *Myzus ascalonicus*, *Aulacorthum solani* and *Rhopalosiphum padi*, but the situation differed between the two regions. On Île de la Possession, *C. obscurus* was observed on both periods of collection and was the main aphid pathogen at the five studied locations (57 out of 68 aphids), especially on *M. ascalonicus* (49 specimens out of a total of 55). In Archipel des Kerguelen, *C. obscurus* was found at three out of the

Table 1 The Entomophthorales and their aphid hosts. Numbers correspond to the number of collected aphids: in boldface 2001–02; in roman: 2011–13.

| Entomophthorales | Île de la Possession | | | Archipel des Kerguelen | | |
|-----------------------------------|--------------------------|---------------------------|---------------------------|--------------------------|-------------------------------|---------------------------|
| | <i>Myzus ascalonicus</i> | <i>Aulacorthum solani</i> | <i>Rhopalosiphum padi</i> | <i>Myzus ascalonicus</i> | <i>Macrosiphum euphorbiae</i> | <i>Rhopalosiphum padi</i> |
| <i>Conidiobolus coronatus</i> | 1 | | | | | |
| <i>Conidiobolus obscurus</i> | 27 +22 | 7 | 1 | 5 | | 1 |
| <i>Entomophthora planchoniana</i> | 3 | | | 38 | 2 | |
| <i>Pandora neoaphidis</i> | | | 2 | | | |
| <i>Zoophthora phalloides</i> | 1 | | 3 | | | |
| <i>Zoophthora</i> sp. | 1 | | | | | |
| Total | 55 | 7 | 6 | 43 | 2 | 1 |

Table 2 The six entomophthoralean species found on aphids in Crozet and Kerguelen archipelagos: main morphological characteristics and corresponding spore sizes of the local collected material.

| Entomophthoralean species | Main morphological characteristics | Primary conidia Extreme length × extreme width in μm | Secondary conidia Length × width in μm | Resting spores in μm |
|-----------------------------------|---|---|---|--|
| <i>Conidiobolus obscurus</i> | Unbranched conidiophores, absence of rhizoids, almost globose primary conidia, spherical resting spores | 32.7–45.7 × 32.3–40.7 mean: 40.1 × 34.5 | – | Diameter: 34.1–34.7 Wall thickness: 2.4–3.3 |
| <i>Entomophthora planchoniana</i> | Unbranched conidiophores, thick rhizoids, subspherical campanulate conidia, resting spores with dark, uneven episporium | 16.7–19.0 × 15.1–16.2 mean: 18.3 × 14.7 | – | No resting spores observed |
| <i>Pandora neoaphidis</i> | Branched conidiophores, thin rhizoids with discoid holdfast, primary conidia ovoid to elongate ovoid, absence of resting spores | 21.1–25.0 × 12.6–14.9 | – | – |
| <i>Zoophthora phalloides</i> | Branched conidiophores, thin rhizoids with specialized holdfast, long and slim primary conidia, with a papilla demarcated with a light bulge from the conidial body, capilliconidia | 33.4–35.1 × 8.7–8.9 | 31.9 × 8.7 | No resting spores observed |
| <i>Zoophthora</i> sp. | Id. but ellipsoid primary conidia | 22.8 × 10.8 | 23.1 × 7.5 | No resting spores observed |
| <i>Conidiobolus coronatus</i> | Unbranched conidiophores, absence of rhizoids, almost globose primary conidia, absence of resting spores, presence of villose conidia | 41.2 × 36.1 | – | – |

five studied locations, on *M. ascalonicus* and *R. padi* only, and there were fewer of them (six out of 46 aphids).

As for *C. obscurus*, the situation regarding *Entomophthora planchoniana* differed between the two regions. On Île de la Possession, the fungus was found at one location during one period of collection (2001–02) and on three specimens of *M. ascalonicus*. By contrast, in Archipel des Kerguelen, *E. planchoniana* was observed at four out of the five locations, and was the main aphid pathogen (40 specimens out of 46), mainly on *M. ascalonicus* (38 specimens), and twice on *M. euphorbiae* at one location.

Aphids parasitized by *C. obscurus* and *E. planchoniana* were found continuously between December and May, suggesting that the infection persisted over several aphid generations.

Pandora neoaphidis was collected only at Crique du Sphinx (Île de la Possession) in 2001–02 on two specimens of *R. padi*. *Zoophthora phalloides* was observed on Île de la Possession at two of the five studied locations, on four specimens only: three *R. padi* and one *M. ascalonicus*. From the single *M. ascalonicus* specimen found infected by *Z. phalloides*, another type of primary and secondary conidia typical from the genus *Zoophthora* was observed.

Unfortunately very few conidia were obtained. That material resembled *Zoophthora radicans* (Brefeld) Batko, but the poverty of our collection could not allow a proper identification. The fungus was therefore referred to as *Zoophthora* sp.

Conidiobolus coronatus was found on one occasion only on Île de la Possession, on *M. ascalonicus*.

Discussion

Entomophthorales are considered as the main fungal pathogens of aphids throughout the world (Latgé & Papierok 1988; Pell et al. 2001; Barta & Cagán 2006). The present work is the first report of any aphid-pathogen member of that fungal group on the sub-Antarctic islands. One species of the genus *Neozygites*, parasitizing mites, was recorded in the west coast of Antarctica (Bridge & Worland 2004). The situation appears similar in the Arctic, where these fungi have been very rarely observed: on aphids in Finland north of the Arctic Circle (Papierok 1989), on Muscoid flies in Greenland (Eilenberg et al. 2007) and in larval populations of a noctuid moth in west Greenland (Avery & Post 2013).

Except for *Zoophthora* sp., the main characteristics of the five other identified entomophthoralean species match overall the data from the literature. However, slight differences in the size of primary conidia (*Conidiobolus obscurus*) or length of capilliconidia (*Z. phalloides*) were observed compared to the literature (Remaudière et al. 1979; Bałazy 1993; Keller 2006), underlining the morphological variation within these species.

Conidiobolus obscurus and *Entomophthora planchoniana*, the two species most frequently found in the sub-Antarctic Archipel des Kerguelen and Île de la Possession,

are two of the three most frequent and numerous pathogens in aphid populations in temperate and continental climates (Thaxter 1888; Shands et al. 1963; Gustafsson 1965; Remaudière, Latgé et al. 1981; Pell et al. 2001). The third species, *P. neoaphidis*, was in contrast found on one aphid species at one location only (Île de la Possession) during our investigations. One could hypothesize that this fungus was a late introduction that has not yet established itself across the archipelagos. In any case, the presence of *C. obscurus* in both periods of study, that is, at an interval of 10 years, shows the ability of Entomophthorales to be established successfully in the sub-Antarctic.

Entomophthora planchoniana is the most abundant species in Archipel des Kerguelen and *C. obscurus* on Île de la Possession. This difference in distribution could be explained by differences in rainfall between both locations, with annual rainfall much higher in Crozet than in eastern Kerguelen. In Europe, *E. planchoniana* seems to be able to tolerate lower relative humidity than *C. obscurus* (Dedryver 1981; Remaudière, Keller et al. 1981).

A few hypotheses can be invoked to explain the presence of Entomophthorales infecting aphids on sub-Antarctic islands. First, all entomophthoralean species recorded could have been introduced, along with aphids, by people. *Zoophthora phalloides*, for instance, is found only on aphids of the sub-family of Aphidinae, to which belong *M. ascalonicus* and *R. padi* (Remaudière, Latgé et al. 1981), the most abundant aphid species introduced in Crozet and Kerguelen (Hullé, Pannetier, Simon et al. 2003). Introduction of fungi by aphids surviving on plant foods (e.g., onions for *M. ascalonicus* infected by *Z. phalloides*) transported by boat appears as the most likely scenario. Second, Entomophthorales could have been introduced without human intervention by transient airborne winged aphids. Transportation of Entomophthorales by winged aphids is common, but infected aphids cannot fly actively long distances (Feng et al. 2007) and must be transported passively by wind. Long-distance passive flights by aphids (about 1300 km) have been mentioned to explain the presence of the aphid *Cinara abieticola* Cholodkovsky in Svalbard (Heikinheimo 1968). However, the nearest possible sources of infected aphids to colonize Crozet and Kerguelen are more than 3000 km away, so this hypothesis seems to be less probable than the previous one to explain the presence of Entomophthorales (and of their hosts) in these archipelagos. Third, some fungal species could have been present before the arrival of aphids, on other insects or in the soil. All but one of the entomophthoralean species found in this study are aphid-specific and seem only to survive some months in soil without any aphid

host (Lateur 1977). Indeed, only *Conidiobolus coronatus* is known to cause mortalities in other insect species (Ben-Ze'ev & Kenneth 1980; Papierok & Coremans-Pelseneer 1980; Papierok 1985; Papierok et al. 1986; Keller 1987). *Conidiobolus coronatus* is mainly a saprophytic fungus that can be easily isolated from temperate and tropical soil samples. Although possible, this third hypothesis has not been yet supported by observations of infected insect species other than aphids or the detection of fungal material in the soil.

In conclusion, on the basis of the situation observed with the aphid–Entomophthorale model in the insular ecosystems of the sub-Antarctic archipelagos of Crozet and Kerguelen, the in-depth study of the introduction of these insects and their pathogens into such environments could contribute to a better understanding of the role of natural enemies in biological invasions (Dunn 2009).

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