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Towards a new classification of the Arthoniales (Ascomycota) based on a three-gene phylogeny focussing on the genus *Opegrapha*

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ABSTRACT

A multi-locus phylogenetic study of the order Arthoniales is presented here using the nuclear ribosomal large subunit (nuLSU), the second largest subunit of RNA polymerase II (RPB2) and the mitochondrial ribosomal small subunit (mtSSU). These genes were sequenced from 43 specimens or culture isolates representing 33 species from this order, 16 of which were from the second largest genus, *Opegrapha*. With the inclusion of sequences from GenBank, ten genera and 35 species are included in this study, representing about 18 % of the genera and ca 3 % of the species of this order. Our study revealed the homoplastic nature of morphological characters traditionally used to circumscribe genera within the Arthoniales, such as exciple carbonization and ascomatal structure. The genus *Opegrapha* appears polyphyletic, species of that genus being nested in all the major clades identified within Arthoniales. The transfer of *O. atra* and *O. calcarea* to the genus *Arthonia* will allow this genus and family Arthoniaceae to be recognized as monophyletic. The genus *Enterographa* was also found to be polyphyletic. Therefore, the following new combinations are needed: *Arthonia calcarea* (basionym: *O. calcarea*), and *O. anguinella* (basionym: *Stigmatidium anguinellum*); and the use of the names *A. atra* and *Enterographa zonata* are proposed here. The simultaneous use of a mitochondrial gene and two nuclear genes led to the detection of what seems to be a case of introgression of a mitochondrion from one species to another (mitochondrion capture; cytoplasmic gene flow) resulting from hybridization.

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Introduction

The Arthoniales are one of the main lichenized groups of the Pezi-zomycotina and are currently classified in the Arthoniomycetes

(Hibbett *et al.* 2007; Spatafora *et al.* 2006). Their ascomata are usually apothecial in contrast to their closest relatives, the Dothideomycetes (Spatafora *et al.* 2006). Most species form lichen symbioses with trentepohlioid algae. The order currently

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includes three families (*Arthoniaceae*, *Chrysothricaceae*, and *Roccellaceae*), ca 55 genera and ca 1200 species. More than half of the species are included in the genera *Arthonia* and *Opegrapha* with ca 400 and 300 species, respectively (Kirk et al. 2001). The order is a major component of the lichen flora of many forest types, especially in the tropics where many corticolous and foliicolous species occur. It is also well represented in saxicolous habitats, especially in subtropical coastal habitats with a Mediterranean or desert type climate (Mediterranean area, Socotra island, southern California, the central Chilean coast and southern Africa) (Follmann & Werner 2003; Tehler 1983, 1990). Over 100 species belonging to the *Arthoniaceae* and *Roccellaceae* are known to grow as lichenicolous fungi on diverse hosts. Most of them are highly host-specific and commensalic (Lawrey & Diederich 2003).

The family concept within the *Arthoniales* has changed considerably during the past decades. Luttrell (1973) classified the *Arthoniaceae*, *Opegraphaceae* (including the *Roccellaceae*) and *Lecanactidaceae* in the order *Hysteriales* on the basis of their ascomata being somewhat similar to those of the *Hysteriaceae*, with boat-shaped to linear carbonaceous pseudothecia opening by a longitudinal slit. He suggested that the *Arthoniaceae* could be related to the *Myriangiales* owing to the structure of the ascomata being a tangled mass of hyphae in which the globoid asci are embedded. Henssen & Jahns (1974) distinguished the families *Arthoniaceae*, *Opegraphaceae*, *Lecanactidaceae*, and *Roccellaceae* in the *Arthoniales* assuming that the latter three families are more closely related than all to the *Arthoniaceae*. Earlier, Poelt (1973) suggested that the *Lecanactidaceae* should not be segregated from the *Opegraphaceae*. Arx & Müller (1975) placed the *Arthoniaceae* in the order *Dothideales*, omitting *Lecanactidaceae*, *Opegraphaceae*, and *Roccellaceae* from their classification. Barr (1979) placed the *Opegraphaceae* and *Roccellaceae* in the *Hysteriales*, and the *Arthoniaceae* in the *Myriangiales*. The *Arthoniales* (*Arthoniaceae*, *Chrysothricaceae*, and tentatively the *Seuratiaceae*) and *Opegraphales* (*Opegraphaceae* and *Roccellaceae*) were accepted as separate orders by Hawksworth & Eriksson (1986) who published both names validly. Within the *Opegraphales*, the species with a crustose, ecorticate thallus and lecideine ascomata were included in the *Opegraphaceae*, whilst the *Roccellaceae* (sensu Tehler 1990, 1993) included species with a crustose or fruticose, usually corticate thallus and ascomata with a well-developed thalline margin. Hafellner (1988) suggested a close relationship between the *Opegraphales* and *Arthoniales*, which were later merged in the class *Arthoniomycetes* (Eriksson & Winka 1997).

Tehler's (1990) first phylogenic hypothesis of the *Arthoniales*, focusing mostly on the *Roccellaceae* and based on morphological, chemical, and anatomical data, confirmed *Arthoniales* and *Opegraphales* together as a monophyletic group. He suggested including the *Opegraphales* in the *Arthoniales*. Hawksworth et al. (1995) and Grube (1998) expanded the *Roccellaceae* to include the *Opegraphaceae* and other genera, such as *Chiodecton*, *Schismatomma*, and *Synoesia*, considered of uncertain family affiliation by Tehler (1993). Current generic concepts are mainly based on characters such as thallus structure, chemistry, and ascomatal anatomy, including the degree of ascomatal carbonization, internal ascomatal structure, ascus types, and ascospore septation.

So far, only few representatives of *Arthoniales* have been included in molecular phylogenetic studies, and almost no

molecular data have been published for the crustose taxa, including the important genera *Arthonia* and *Opegrapha*, and very few taxa had more than one locus in GenBank. Tehler (1995a,b), who published the first *Arthoniales* sequences (nuSSU), found incongruence between molecular and morphological datasets. In Tehler (1995a), *Lecanactis abietina* did not cluster with other members of the *Arthoniales* (*Arthonia radiata*, *Dendrographa leucophaea*, and *Schismatomma pericleum*), but strangely was found to be closely related with *Porpidia crustulata* (sub. *Lecidea crustulata*) of the *Lecanorales*. When the same sequences were included in a broader phylogenetic context, including representative species from the *Ascomycota* and *Basidiomycota*, the monophyly of the *Arthoniales* was found to be well-supported (Gargas et al. 1995). Based on multilocus phylogenetic analyses, the *Arthoniomycetes* have been reported to be sister to the *Dothidiomycetes* by Lutzoni et al. (2004) but with low support. Spatafora et al. (2006) confirmed this result using a more extensive taxon and locus sampling.

Myllys et al. (1998) used partial sequences from the nuSSU rDNA of 18 taxa to investigate the phylogenetic relationships in the order *Arthoniales* focusing on the family *Roccellaceae*. Because this locus was too conservative for solving phylogenetic relationships among closely related genera, ITS data were added to an extended dataset including 33 taxa to provide more resolution (Myllys et al. 1999). Significant incongruence between the molecular and morphological datasets were shown and assumed to be due to a high level of homoplasy in the morphological data (e.g. placement of *Schismatomma*, *Lecanactis*). Tehler & Irestedt (2007) investigated the phylogenetic relationships within the family *Roccellaceae* s. str. based on LSU and RPB2 sequences from 48 taxa including mainly members of the genera *Roccella* and *Roccellina*. The results of these phylogenetic analyses also suggest that the fruticose/crustose habits have evolved multiple times in the family *Roccellaceae* s. str. and that character states, such as fruticose and crustose, may have been overemphasized in morphologically based classifications.

The order *Arthoniales* was never subjected to a broad and exhaustive molecular phylogenetic study. The two main genera of this order, *Arthonia* and *Opegrapha*, are considered as heterogeneous assemblages (Grube et al. 1995; Matzer 1996; Pentecost & Coppins 1983) based on morphology. Some allied genera, including the recently monographed genus *Enterographa* (Sparrius 2004), can also be considered as heterogeneous. No sequences from these crustose genera have ever been included in analyses focusing on the *Arthoniales*. The aim of this paper is to confront the current morphology-anatomy-based classification with a multi-locus phylogeny of the *Arthoniales* and to discuss the taxonomic value of diagnostic characters used to define genera and families within this order.

Material and methods

Contaminations with co-occurring fungi are frequent when using standard DNA isolation protocols on lichen thalli (see Hofstetter et al. 2007). This is especially the case with taxa having inconspicuous thalli and collected in the tropics (see Arnold et al. in press), such as most *Opegrapha* species. DNA amplifications have been particularly difficult for

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