

EVOLUTIONARY HISTORY AND DIVERSITY OF WHITE BLISTER RUSTS (ALBUGINALES)*

MARCO THINES

Abstract. White blister rusts (Albuginales) are among the most common pathogen species on cultivated and wild angiosperms. Like the downy mildews, the second group of obligate plant parasitic oomycetes, they do not belong to the true fungi, the Mycota, but to the Straminipila, which also include seaweeds and diatoms. This review discusses recent findings on their diversity, evolution and systematics.

Key words: Albuginaceae, *Albugo*, biodiversity, oospore ornamentation, *Pustula*, taxonomy, *Wilsoniana*

Marco Thines, Johann Wolfgang Goethe University, Department of Biological Sciences, Siesmayerstr. 70, D-60323 Frankfurt (Main), Germany; Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, D-60325 Frankfurt, Germany; e-mail: marco.thines@senckenberg.de

HOST RANGES OF DOWNY MILDEWS AND WHITE BLISTER RUSTS

The white blister rusts (Albuginales) are ubiquitous pathogens which can be found on every continent except Antarctica. Like the second group of obligate biotrophic plant pathogens, the downy mildews, their sole hosts are flowering plants. Unlike downy mildews, however, white blister rust has also been reported from a member of the basal Angiosperm order, the Piperales, *Peperomia pelucida* (Patouillard & Langerheim 1892; Wilson 1907), and recently from Orchidaceae (Walker & Priest 2007). Although the main radiation of the Albuginales took place in the eurosids and euasterids *sensu* A.P.G. (2009), there are some species affecting Papaverales (for summary see Yu *et al.* 1998) and several parasitic to Caryophyllales. This is somewhat similar to downy mildews, which have also undergone significant radiation and diversification in eurosids, euasterids and Caryophyllales. In contrast to the situation in downy mildews, however, grasses (Poaceae) do not seem to be affected by white blister rusts. Interestingly, both downy mildews and white blister rusts show

a strong preference for weedy over woody hosts, and as yet no white blister rusts have been reported from any tree species.

TAXONOMIC HISTORY OF THE ALBUGINALES

In 1792 (Gmelin 1792) the first species of *Albugo* was described as *Aecidium candidum* (now *Albugo candida*) by Persoon, who later placed it in genus *Uredo*, subgenus *Albugo* (Persoon 1801). Based on differences in symptom development, Persoon (1801) described two different species of white blister rust, with *Uredo candida* subdivided into three varieties, parasitic to Brassicaceae and Asteraceae. A few years later, *Albugo* was established as an independent genus by de Roussel (1806), although erroneously Gray (1821) is often still given as the author for this genus. DeCandolle (for summary see Lamarck & DeCandolle 1806) added the species *Uredo portulacae* (now *Wilsoniana portulacae*) and *Uredo petroselini* (uncertain species), raised the variety *Uredo candida* beta *trogopogi* to species rank (*Uredo tragopogi*, now *Pustula tragopogonis*) and renamed *Uredo candida* as *Uredo cruciferarum*. In the remainder of

* This paper is dedicated to Professor Tomasz Majewski on the occasion of his 70th birthday.

the 19th century only a few additional species were described but a multitude of synonyms were introduced for the already established species, while it was generally perceived that the species had broad host ranges and were affecting whole host families. L veill  (1847) described the genus *Cystopus*, and later de Bary (1863) described the sexual state of *Albugo*, adopting the generic name *Cystopus*. Before Biga (1955) pointed out that names of sexual form have no precedence over anamorphs in oomycetes, many researchers considered white blister rusts to be members of the superfluous genus *Cystopus* (e.g., Wakefield 1927), while the older genus name, *Albugo*, also persisted.

In the early 20th century, several additional species of *Albugo* were described. Wilson (1907) recorded 13 species, and Biga (1955) accepted 30 species in this genus about 50 years later. Only a few new species were described thereafter; the key to the genus *Albugo* published forty years later (Choi & Priest 1995) recognized 10 species Biga had not included. Until molecular phylogenetic studies of the Albuginaceae became possible, *Albugo* was generally treated as a member of the Peronosporales (Dick 2001), in which it was placed along with the second group of obligate plant parasites, the downy mildews. This placement was challenged by molecular phylogenetic investigations, which revealed only a distant relationship between *Albugo* and the downy mildews (Riethm ller *et al.* 2002; Hudspeth *et al.* 2003). As a consequence, Thines and Spring (2005) described the order Albuginales to accommodate the white blister rusts. Based on molecular phylogeny and morphological investigations, two new genera were introduced. Of these, the genus *Wilsoniana* is parasitic on Caryophyllales, while *Pustula* affects Asterales and some affiliated orders. *Albugo* contains all the remaining species, but further phylogenetic and morphological investigations should be expected to lead to substantial revisions. The type species of the genus, *A. candida*, is usually affiliated with other Brassicales-infecting lineages, but so far it has not been established whether the host range of *Albugo s.str.* extends beyond Brassicales. The Convolvulaceae-affecting lineages of *Albugo* show high genetic distance from *Albugo*

on Brassicales and should thus probably be treated as an independent genus. The taxonomic changes throughout the past 100 years are illustrated in Figure 1.

ALBUGINALES ARE AN ANCIENT BIOTROPHIC GROUP

Unexpectedly, the Albuginales were revealed to be a group only distantly related to the downy mildews (Riethm ller *et al.* 2002; Hudspeth *et al.* 2003; Thines *et al.* 2008), and it is worth noting that obligate dependence on living angiosperm cells has evolved independently at least twice in the oomycetes. Obligate biotrophy in the downy mildews arose in evolutionarily recent times, with some basal downy mildews still exhibiting several characteristics commonly attributed to the hemibiotrophic genus *Phytophthora* (Thines 2009); the Albuginales are a highly divergent lineage and are not closely related to any culturable species. Considering the deep branching of the Albuginales within the peronosporalean lineage, obligate biotrophy can be assumed to be a more ancient phenomenon in the Albuginales. Thus it is not surprising that the Albuginales share several derived character states unique to oomycetes. For example, white blister rust species do not depend on moist conditions for asexual sporulation. Spore production takes place below the epidermal layer of the host plants, and seems to be a highly regulated process in which lytic enzymes play a key role (Heller & Thines 2009), and not force as was generally thought previously (Webster & Weber 2007).

A unique feature of the Albuginales is the production of small, stalked haustoria, which ensure optimal exposure of the interacting surface of the pathogen inside the host cell. Baka (2008) showed that tubular structures extend from the haustorial membrane inside the host cell, probably owing to defense mechanisms or to recruitment of the host secretion and uptake machinery by the pathogen. The high degree of reduction and shape conservation of the haustoria in white blister rust can be seen as another characteristic derived from their longstanding relationship with angiosperm hosts.

Historic classification

Current phylogenetic classification

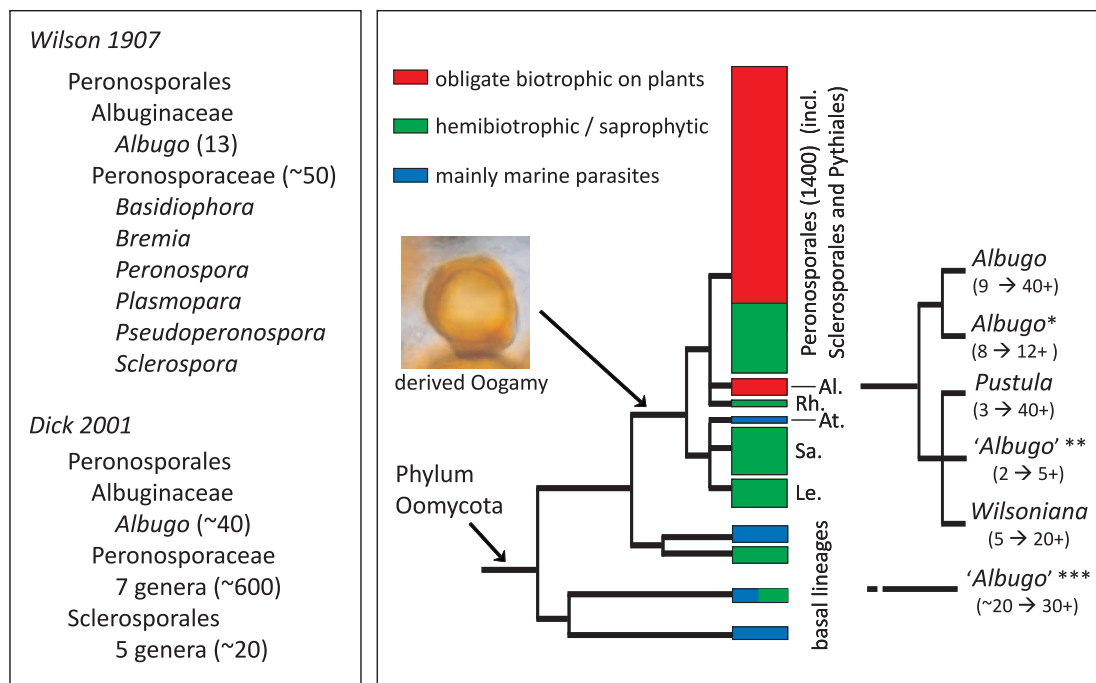


Fig. 1. Historical and current taxonomy of white blister rusts. Species numbers at left are published species numbers, followed by conservative species estimates of the actual diversity. * – *Albugo s.l.* on Convolvulaceae, ** – *Albugo s.l.* on some Caryophyllales, *** – unsequenced species of *Albugo* with uncertain phylogenetic affinity. Rh. – Rhipidiales, At. – Atkinsiellales (informal designation), Sa. – Saprolegniales, Le. – Leptomitales.

ALBUGINALES ARE HIGHLY DIVERSE ON SEVERAL PLANT FAMILIES

Except in Convolvulaceae, Biga (1955) and Choi and Priest (1995) accepted only single or a few species per host family, and they considered them synonymous in many cases when more than one species had been described on a single host family. Thus it was assumed that the species were host-family-specific, and this stance led to mostly broad species concepts (Wilson 1907; Biga 1955; Kochman & Majewski, 1970; Vanev *et al.* 1993; Choi & Priest 1995). During the last decade, however, molecular phylogenetic studies have revealed some genetic diversity within *Albugo* on Brassicaceae (Rehmany *et al.* 2000; Choi *et al.* 2006; Voglmayr & Riethmüller 2006). Detailed molecular phylogenetic and morphological studies have confirmed the validity of *Albugo lepidii* (Choi *et al.* 2007b)

and turned up several previously overlooked species (Choi *et al.* 2007b, 2008; Thines *et al.* 2009a; Ploch *et al.* 2010). Using *Cardamine*, Ploch *et al.* (2010) recently demonstrated that even within a single host genus there may be multiple specialized species. In Caryophyllales as well, species diversity seems to be higher than previously thought: Voglmayr and Riethmüller (2006) demonstrated that *Wilsoniana amaranthi* and *W. bliti*, both parasitic on species of *Amaranthus*, are indeed independent species. However, We have only scratched the surface of the complex of *Albugo* from Caryophyllales, however; several species may await discovery. Oospore morphology and ornamentation, previously used mostly for species delimitation on distinct plant families only (with the notable exception of species in Convolvulaceae), have now been shown to be the most important characters for their delimitation (Voglmayr & Riethmüller 2006;

Choi *et al.* 2007b). Detailed investigations in the Convolvulaceae are lacking, but judging from the morphological diversity of the species described (for an overview see Choi and Priest 1995), most of these can be expected to prove phylogenetically distinct. For Asteraceae, which contain *ca* 300 reported host genera (Wilson 1907; Biga 1955; Whipps & Cooke 1978; Voglmayr & Riethmüller 2006), about four times the *ca* 70 host genera known for Brassicaceae (Wilson 1907; Biga 1955; Kochman & Majewski 1970), no detailed investigations using both molecular phylogenetic and morphological evidence have yet been published. However, Voglmayr and Riethmüller (2006) have already observed some genetic diversity in nrLSU in this group, its species diversity may be comparable to that of the Brassicaceae-infecting lineages. If species of Asteraceae are as host-specific as in Brassicaceae, dozens of new species await discovery.

SPECIALISM AND GENERALISM ARE KNOWN IN WHITE BLISTER RUSTS

Against what was previously thought, most white blister rust species are host-specific, apparently at least at the genus level (Choi *et al.* 2007b, 2008; Thines *et al.* 2009a) but sometimes even below that (Ploch *et al.* 2010). *Albugo candida* has an exceptionally broad host range, however, with hosts throughout various Brassicaceae tribes and extending to Cleomaceae and Capparaceae (Choi *et al.* 2009a). As genetic exchange throughout this vast host range is thus highly likely, it may be misleading to give race designations to strains collected from a specific host solely on the basis of the host species affected (Borhan *et al.* 2008). Interestingly, so far there are three cases known in which the same host genus can be affected by both the generalist species *A. candida* and a specialized species (Choi *et al.* 2007b, 2008; Thines *et al.* 2009a). The underlying mechanisms allowing *A. candida* to parasitize a broad range of Brassicales, while the specialized species seem to have restricted host ranges, remain obscure, but as Thines *et al.* (2009a) suggested, the reason for this difference be that *A. candida* employs effectors which target

basal defense pathways conserved throughout Brassicales. Another still unresolved question is the basis for the co-occurrence of specialist and generalist species, that is, the underlying niche partitioning for the species. So far no generalist species seem to have been observed in Asteraceae and Caryophyllales (Voglmayr & Riethmüller 2006), but only limited sampling has been done in these groups.

MANY SPECIES ARE TO BE DISCOVERED

The pace of species discovery in both downy mildews (Cunnington 2006; Voglmayr *et al.* 2006; Choi *et al.* 2007a, 2009b; Voglmayr & Constantinescu 2008; Thines *et al.* 2009b) and white blister rusts (Choi *et al.* 2007b, 2008; Thines *et al.* 2009a, Ploch *et al.* 2010) has dramatically increased in the last five years. Ongoing studies are turning up several undescribed species in Brassicaceae and Asteraceae, and in view of the narrow host specialization characteristic for most species of white blister rusts, new species are likely to be discovered in other host families. Figure 1 gives estimates of species diversity in each of the groups, based on distinct phylogenetic lineages recently found (both published and unpublished) and the number of known hosts.

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