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A new species of *Albugo* parasitic to *Arabidopsis thaliana* reveals new evolutionary patterns in white blister rusts (*Albuginaceae*)

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Key words

Albuginales
effector gene
oospore morphology
phylogeny
plant pathogen
speciation

Abstract The obligate biotrophic lineages of the white blister rusts (*Albuginales*, *Oomycota*) are of ancient origin compared to the rather recently evolved downy mildews, and sophisticated mechanisms of biotrophy and a high degree of adaptation diversity are to be expected in these organisms. Speciation in the biotrophic *Oomycetes* is usually thought to be the consequence of host adaptation or geographic isolation. Here we report the presence of two distinct species of *Albugo* on the model plant *Arabidopsis thaliana*, *Albugo candida* and *Albugo laibachii*, the latter being formally described in this manuscript. Both species may occupy the same host within the same environment, but are nevertheless phylogenetically distinct, as inferred from analyses of both mitochondrial and nuclear DNA sequences. Different ways of adapting to their host physiology might constitute an important factor of their different niches. Evidence for this can be gained from the completely different host range of the two pathogens. While *Albugo candida* is a generalist species, consisting of several physiological varieties, which is able to parasitize a great variety of *Brassicaceae*, *Albugo laibachii* has not been found on any host other than *Arabidopsis thaliana*. Therefore, *Albugo laibachii* belongs to a group of highly specialised species, like the other known specialist species in *Albugo* s.s., *Albugo koreana*, *Albugo lepidii* and *Albugo voglmayrii*. The comparative investigation of the effector genes and host targets in the generalist and the specialist species may constitute a model system for elucidating the fundamental processes involved in plant pathogen co-adaptation and speciation.

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INTRODUCTION

The brassicaceous plant *Arabidopsis thaliana*, which has been the model system to study plant genetics and physiology since Laibach (1943) proposed it as a suitable candidate, has been the motor for fundamental discoveries in plant biology. During the past years, it has also become the focus of studies in plant pathogen interactions, especially in obligate pathogens, like downy mildews and powdery mildews (Holub 2007, 2008). Investigation of these obligate pathogens has provided many important insights into plant susceptibility and immunity (Austin et al. 2002, Muskett et al. 2002, Birch et al. 2006), but many aspects still remain enigmatic. With the discovery of a plethora of fast evolving effector genes involved in the pathogenesis of oomycetes (Morgan & Kamoun 2007), new approaches emerge for understanding the evolution of pathogenicity. The reference genome of the downy mildew of *Arabidopsis thaliana*, *Hyaloperonospora arabidopsidis,* for example, contains more than 100 effector-like genes (Win et al. 2007). The function of most of these is currently unknown, but they are expected to somehow be involved in manipulating their hosts to attenuate defence or to re-direct host metabolism and favour the parasite development. It can be expected that obligate biotrophic pathogens manipulate their hosts by highly evolved mechanisms to attenuate defence, and they are thus of particular interest for investigating host-pathogen interactions. For plant pathology, systems with different pathogens parasitic to the same host may constitute a promising approach to study plant defence mechanisms and the effectors involved in successful pathogen establishment. Recent reports demonstrate that white rust in *Arabidopsis thaliana* is also an important model pathosystem for molecular genetic investigation of broad spectrum induced susceptibility, and race-specific and non-host disease resistance (Holub et al. 1995, Parker et al. 1996, Borhan et al. 2004, 2008, Cooper et al. 2008).

The two highly distinct lineages of *Oomycota* (*Albuginaceae* and *Peronosporaceae*) that are obligate parasites of *Arabidopsis thaliana* (Gäumann 1918, Biga 1955) have until recently (Dick 2001) been thought to be closely related members of the order *Peronosporales*, and very distinct from the order *Pythiales*, which included the hemibiotrophic genera *Phytophthora* and *Pythium*. However, it became evident from the first comprehensive phylogenies of these organisms (Riethmüller et al. 2002, Hudspeth et al. 2003) that the downy mildews and white blister rusts are only distantly related. Along with morphological and cytological evidence, the order *Albuginales* was therefore introduced (Thines & Spring 2005), along with two new genera in the white blister rusts, *Pustula* (white blister rusts of *Asteridae*) and *Wilsoniana* (white blister rusts of *Caryophyllidae*). In the first phylogenetic reconstructions including *Albugo* s.s. (Rehmany et al. 2000, Choi et al. 2006, Voglmayr & Riethmüller 2006), it was observed that *Albugo* on *Brassicaceae* did not form a homogenous clade, but was separated into one clade comprising the majority of isolates and several additional distinct lineages. More detailed phylogenetic and morphological investigations revealed that in *Capsella bursa-pastoris* and in the genus *Draba*, two different specialist species are present (Choi et al. 2007, 2008). However, these new species were

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collected in isolated geographic regions in Korea or east Asia, and have so far not been reported from other parts of the world, suggesting that geographic isolation might have enabled independent adaptation to the same host. Closer inspection of the phylogeny presented by Voglmayr & Riethmüller (2006), in comparison with the one shown in Choi et al. (2007), reveals that in *Cardaminopsis halleri* (now *Arabidopsis halleri*), *Albugo candida* was observed in a specimen from Romania, while in a specimen of *Arabidopsis thaliana* from Austria a genetically distinct *Albugo* was found. If two related – yet distinct – species were parasitic to *Arabidopsis* in the same geographic region, this would suggest that sympatric speciation based on unknown niche adaptation mechanisms is possible in *Albugo*. This would create a promising model system for investigating plant defence and plant-pathogen interaction. In addition, it would raise fundamental questions regarding niche recognition, evolution and ecology in obligate, biotrophic plant pathogens. Therefore, it was the aim of this study to clarify whether two different species of *Albugo* might be present in the same geographic region and on a single host species – the model plant *Arabidopsis thaliana*.

MATERIALS AND METHODS

Specimens and morphological investigation

The details for the specimens examined and GenBank accession numbers are given in Table 1. Morphological investigation was done as described previously (Choi et al. 2008).

DNA extraction, PCR and sequencing

DNA extraction and *cox*2 amplification was performed as reported earlier (Hudspeth et al. 2000, McKinney et al. 1995, Thines et al. 2008). ITS regions were amplified from the specimens as described previously (Thines 2007), with elongation time set to 1 min. In addition to the primers reported in Thines (2007), the oomycete specific forward primer DC6 (Cooke et al. 2000) was employed. Sequencing was carried out by the commercial sequencing company GATC (Konstanz, Germany), SolGent (Daejeon, Korea) and the John Innes Genome Laboratory, (Norwich, UK), using the primers applied for PCR.

Alignment and phylogenetic reconstruction

Alignments for *cox*2 and ITS regions were produced using MUSCLE (Edgar 2004), v3.6, with the default settings. No manual 'improvements' were done. Alignments have been deposited in TreeBASE under the accession number S2375. Molecular phylogenetic reconstructions were done on concatenated *cox*2 and ITS alignments using MEGA v4.0 (Tamura et al. 2007) for Minimum Evolution (using Tajima-Nei distances) and Maximum Parsimony analyses, and RAxML v7.0 (Stamatakis 2006) for Maximum Likelihood analysis. In both cases, all parameters were set to default values. For Maximum Likelihood analysis, the GTRMIX variant was chosen. For all analyses, 1 000 bootstrap replicates (Felsenstein 1985) were performed.

Table 1 *Albuginaceae* specimens investigated in this study.

Number in Fig. 1	Species	Host	Origin	Year	Herbarium code / strain identification	GenBank accession no. ITS	GenBank accession no. *cox*2
1	*Albugo candida*	*Arabidopsis arenosa*	Romania, Maramure_	1974	BP 54980	–	FJ468359
2		*Heliophila meyerii*	RSA, Vanrhynsdorp	1896	BPI 184888	DQ418493	DQ418515
3		*Arabidopsis thaliana*	UK, Norwich	2007	SL 11BB8	FJ468360	FJ468361
4		*Arabidopsis thaliana*	UK, Norwich	2007	SL 12T6	FJ468362	FJ468363
5		*Iberis amara*	USA, California	1938	BPI 184897	DQ418499	DQ418522
6		*Berteroa incana*	Austria, Krems	1987	BPI 184200	DQ418495	DQ418508
7		*Brassica juncea*	Korea, Namyangju	1998	KUS-F 15570	AY929826	AY927046
8		*Biscutella laevigata*	Switzerland, Valais	1903	BPI 184686	DQ418494	DQ418506
9		*Thlaspi arvense*	USA, New York	2002	CUP 065777	AY929847	AY913809
10		*Arabidopsis hallerii*	Romania, Suceava	1980	BPI 199991	DQ418502	DQ418513
11		*Arabis turrita*	Bulgaria	1955	SOMF 00337	AY929825	AY913803
12		*Erysimum cuspidatum*	Romania, Mehedinti	1979	BPI 199988	DQ418498	DQ418519
13		*Arabidopsis thaliana*	UK, Norwich	2007	SL 20DD5	FJ468364	FJ468365
14		*Aubrieta deltoidea*	Germany, Hessen	1953	BPI 184659	DQ418500	DQ418511
15		*Capsella bursa-pastoris*	Netherlands, Zuid-Holland		BPI 184451	DQ643916	DQ643944
16		*Arabidopsis thaliana*	UK, Norwich	2007	SL 30LL2	FJ468366	FJ468367
17		*Lunaria* sp.	USA, Oregon	2000	CUP 065639	AY929840	AY913797
18		*Capsella bursa-pastoris*	UK, 'East Malling'	2007	UW Acem2	–	FJ468368
19		*Arabidopsis thaliana*	Romania, Ilfov	1977	BP 75214	–	FJ468369
20		*Diplotaxis erucoides*	Palestine, Kiriat-Anabim	1935	BPI 184862	DQ418496	DQ418517
21		*Raphanus sativus*	Korea, Seoul	1990	KUS-F 10614	AY929841	AY927059
22		*Sisymbrium luteum*	Korea, Pyongchang	2002	KUS-F 19086	AY929844	AY913808
23		*Eruca sativa*	Pakistan, Daudkhel	1968	BPI 184870	DQ418503	DQ418514
24	*Albugo lepidii*	*Lepidium apetalum*	Korea, Seoul	1997	KUS-F 13747	AY929835	AY927054
25		*Lepidium virginicum*	Korea, Seoul	2000	KUS-F 17251	AY929838	AY927057
26		*Lepidium* sp.	Romania, Suceav	1980	BP 74488	–	FJ468370
27	*Albugo voglmayrii*	*Draba nemorosa*	Korea, Gapyong	1999	KUS-F 15732	AY929834	AY927053
28	*Albugo* sp.	*Descuraina sophia*	Russia	1977	SOMF 19655	AY929832	AY927051
29	*Albugo* sp.	*Diptychocarpus strictus*	Russia	1978	SOMF 19659	AY929833	AY927052
30	*Albugo laibachii* sp. nov.	*Arabidopsis thaliana*	Australia, Tasmania	1980	DAR 73071*	–	FJ468371
31		*Arabidopsis thaliana*	UK, 'East Malling'	2007	UW Acem1	–	FJ468372
32		*Arabidopsis thaliana*	UK, Norwich	2007	SL Nc14	FJ468373	FJ468374
33	*Albugo koreana*	*Capsella bursa-pastoris*	Korea, Namyangju	1997	KUS-F 13752	AY929829	AY927048
34		*Capsella bursa-pastoris*	Korea, Yongin	2000	KUS-F 17254	AY929831	AY927050
35		*Capsella bursa-pastoris*	Korea, Seoul	1999	KUS-F 15670	AY929830	AY927049
36	*Albugo ipomoeae-panduratae*	*Ipomoea hederacea*	Korea, Yangpyong	2003	KUS-F 19628	DQ643920	AY913804
37	*Wilsoniana amaranthi*	*Amaranthus spinosus*	Korea, Chunchon	2003	KUS-F 19835	AY929824	AY913805

BP = Herbarium of the Natural History Museum Budapest, BPI = Herbarium of the USDA Maryland, DAR = Herbarium of the Orange Agricultural Institute, KUS-F = Mycological Herbarium of the Korea University, SL = Sainsbury Laboratory (laboratory strains), SOMF = Bulgarian Academy of Sciences Mycological Collection, UW = University of Warwick. * type specimen. Numbers in **bold**face indicate specimens sequenced and investigated in light microscopy in this study.

RESULTS

Molecular phylogenetic reconstruction

The phylogenetic reconstruction based on concatenated *cox*2 and ITS regions revealed a high degree of uniformity of *Albugo candida* isolates from 16 different host genera (Fig. 1). The genus *Arabidopsis* was among these genera, with five isolates from *Arabidopsis thaliana* and one isolate respectively from *Arabidopsis halleri* and *Arabidopsis arenosa*. This group, representing *A. candida,* was highly distinct from the other lineages, with maximum support in Minimum Evolution (ME) and Maximum Likelihood (ML) analyses and a bootstrap value of 99 in Maximum Parsimony (MP) analysis. Apart from *A. candida*, several other distinct lineages were observed, which correspond to the three additional species parasitic to *Brassicaceae*, *A. lepidii*, *A. koreana*, and *A. voglmayrii*. The specimens of *A. lepidii* and *A. koreana* each grouped together with maximum statistical support in ME and ML analysis, and a bootstrap value of 99 in MP analysis. The isolates from *Descuraina sophia* and *Diptychocarpus strictus* also clustered distinct from *A. candida,* and the other species so far described as parasites of the *Brassicaceae*. Notably, three isolates from *Arabidopsis thaliana* were also highly distinct from *A. candida,* and grouped together with maximum support in ME and ML analyses and a bootstrap value of 99 in MP analysis. Sequence similarity of these isolates in comparison to *A. candida* in ITS was only 86 %. This is a much lower degree of similarity than in closely related *Phytophthora* or downy mildew species, where ITS sequences were found to have 99 % similarity or more (Table 2). Relationships of the species of *Albugo* s.s. to each other could mostly not be resolved. However, some bootstrap support could be obtained for a clade consisting of all white blister pathogen lineages except for *A. candida* and *A. koreana* and for a clade containing the *Albugo* isolates from *Descuraina sophia*, *Diptychocarpus strictus* and *Arabidopsis thaliana*. All white blister pathogens on *Brassicaceae* formed a moderately (ML: bootstrap value 73) to highly (ME, MP: bootstrap value 99) supported clade.

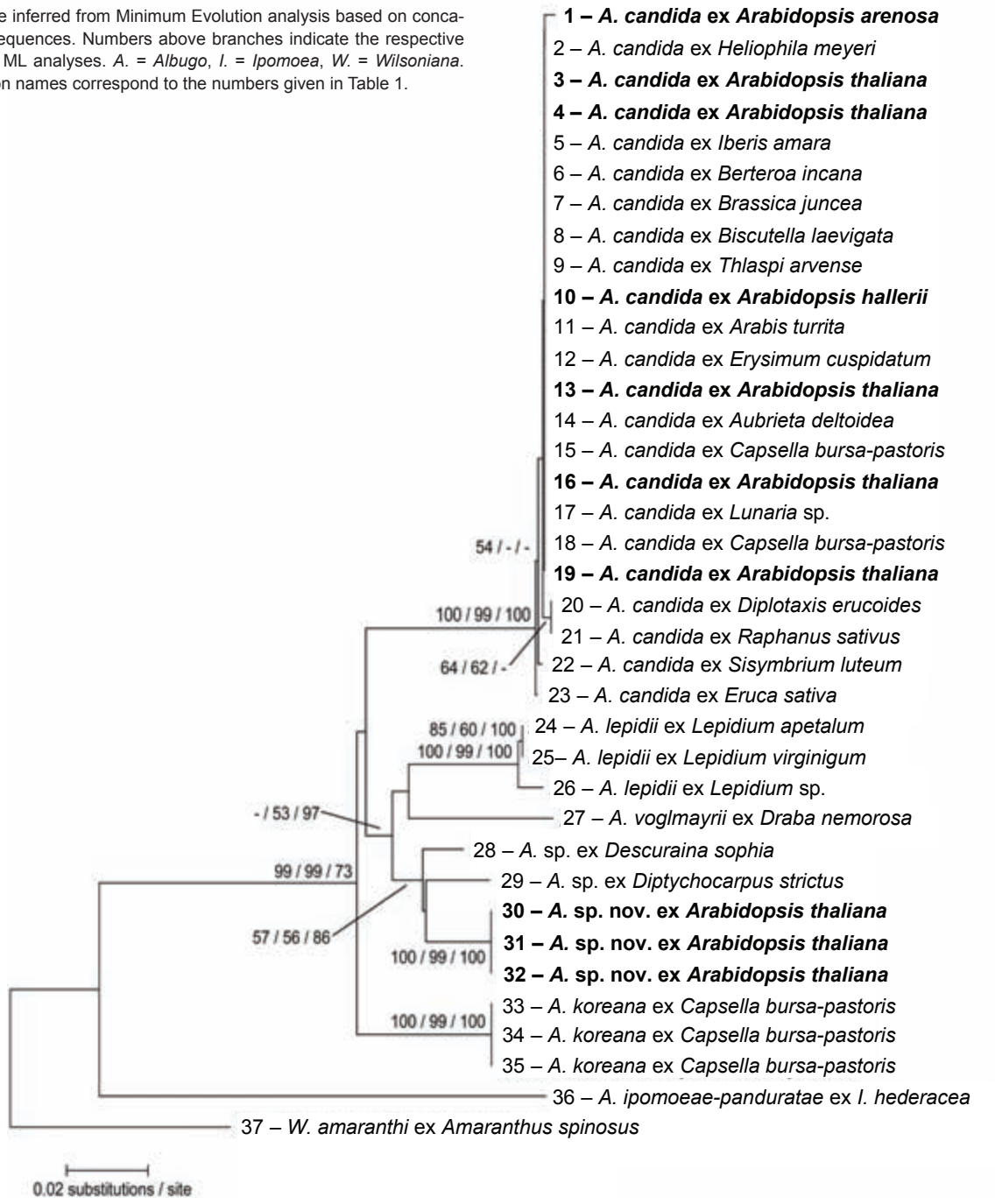

Fig. 1 Phylogenetic tree inferred from Minimum Evolution analysis based on concatenated ITS and *cox*2 sequences. Numbers above branches indicate the respective support in ME, MP and ML analyses. *A.* = *Albugo*, *I.* = *Ipomoea*, *W.* = *Wilsoniana*. Numbers preceding taxon names correspond to the numbers given in Table 1.

Table 2 Comparison of the ITS similarity of various oomycete species.

GenBank No.	GenBank No.	Maximum identity in blastn*
Albugo laibachii FJ468373	*Albugo candida* AF271231	86 %
Albugo koreana AY929830	*Albugo candida* AF271231	85 %
Peronospora tabacina AY198289	*Peronospora rumicis* DQ643903	92 %
Peronospora effusa DQ643901	*Peronospora rumicis* DQ643903	99 %
Hyaloperonospora arabidopsidis AY531434	*Hyaloperonospora parasitica* AY210987	88 %
Hyaloperonospora hesperidis AY531455	*Hyaloperonospora parasitica* AY210987	90 %
Phytophthora capsici AB367371	*Phytophthora infestans* EU200321	90 %
Phytophthora nicotinae FN263242	*Phytophthora infestans* EU200321	91 %
Phytophthora phasaeoli DQ821179	*Phytophthora infestans* EU200321	99 %
Phytophthora mirabilis AF266777	*Phytophthora infestans* EU200321	99 %

* Searches were performed at NCBI (http://blast.ncbi.nlm.nih.gov/Blast.cgi), with all parameters set to default values.

Morphological investigation

Morphological comparison of *Albugo candida* from *Arabidopsis thaliana* and other hosts with the undescribed species of *Albugo* on *Arabidopsis thaliana* revealed marked differences in oospore size, which clearly separates *A. candida* from *Albugo* sp. on *Arabidopsis thaliana*. The oospores of *Albugo candida* were (42.5–)47.9–57.6(–62.5) (av. 51.8) µm diam in the type host *Capsella bursa-pastoris*, (37.5–)43.8–52.1(–57.5) (av. 48) µm diam in *Eruca* sp., (40–)43.1–49.4(–51.3) (av. 46.3) µm diam in *Heliophila* sp. and (42–)45.9–53.0(–55) (av. 49.5) µm diam in *Arabidopsis thaliana*. In the undescribed species on *Arabidopsis thaliana*, the oospores were significantly smaller with (36.8–)38.3–43.3(–47) (av. 40.8) µm diam. Oospore surface ornamentation was similar to *A. candida*, but markedly different from the other *Albuginaceae*. While branching lines on the oospore surface is a prominent character of oospores in *A. candida* (Fig. 2g, h), and also in the undescribed species (Fig. 2e, f), all other hitherto described species exhibit irregular, rounded protuberances on their oospore surface, which do not become confluent and branched. In addition, the lines formed on oospores of *Albugo* sp. (Fig. 2e) are mostly less regular in appearance than those in *A. candida* (Fig. 2g). Primary and secondary sporangia, as well as sporangiophores, were similar in shape and size in all specimens investigated and did not allow unambiguous species identification, which is in line with previous investigations.

Taxonomy

Due to its distinct phylogenetic placement and morphological characteristics differing from all other *Albuginaceae* hitherto known, a new species is introduced here to accommodate the undescribed species on *Arabidopsis thaliana*.

Albugo laibachii Thines & Y.J. Choi, *sp. nov*. — MycoBank MB509563; Fig. 2

Mycelia intercellularia, haustoria intracellularia, vesicularia. Sori hypophylli, distincti, rotundi vel irregulares, saepe confluentes, albi, 0.5–4(–11) mm diam. Sporangiophora hyalina, clavata vel cylindracea, (20–)23.3–33.9(–37.5) (av. 28.6) µm longa, (10.5–)11.5–13.8(–15) (av. 12.7) µm diam (n = 102). Sporangia hyalina, globosa vel subglobosa, sporangia primaria (11.8–)12.5–14.5(–15.3) (av. 13.5) µm diam (n = 94), sporangia secondaria (11.5–)14.3–17.1(–18.5) (av. 15.7) µm diam (n = 113), parietibus uniformibus. Oogonia in folia, globosa vel irregularia, flavida, (45–)47.4–54.3(–58) (av. 50.9) µm diam (n = 63). Oospora luteola vel brunnea, globosa, verruculosa vel tuberculata, (36.8–)38.3–43.3(–47) (av. 40.8) µm diam (n = 34).

Etymology. Dedicated to Friedrich Laibach, who first suggested *Arabidopsis thaliana* as a model plant for plant genetics.

Mycelium intercellular. *Haustoria* knob-like to globose, 3–5 µm diam, surrounded by thick sheath, with narrow and short stalk, 1–2 µm in length, one to several in each host cell. *Sori* hypophyllous, distinct, rounded or irregular, 0.5–4(–11) mm diam, often confluent, whitish, sometimes present in stems and inflorescences. *Sporangiophores* hyaline, clavate or cylindrical, straight to slightly curved, (20–)23.3–33.9(–37.5) (av. 28.6) µm long, (10.5–)11.5–13.8(–15) (av. 12.7) µm wide (n = 102), mostly grouped, thick-walled, especially towards the base up to 6 µm. *Sporangia* arranged in basipetal chains, hyaline, primary sporangia similar to the secondary sporangia, but the former exhibit a slightly thicker wall; primary sporangia globose or polyangular due to mutual pressure, (11.8–)12.5–14.5(–15.3) (av. 13.5) µm diam (n = 94), with wall uniformly 1.5(–2) µm thick; secondary sporangia globose to subglobose, (11.5–)14.3–17.1(–18.5) (av. 15.7) µm diam (n = 113), with uniformly thin wall, tip round, base mostly rounded, but rarely subtruncate, pedicel mostly absent. *Resting organs* rarely present as pale brown dots on both the upper and lower surface of the leaf spots. *Oogonia* broadly globose or irregular, yellowish, (45–)47.4–54.3(–58) (av. 50.9) µm diam (n = 63), wall smooth, 1–2 µm thick. *Oospores* plerotic, yellowish to pale brownish, globose, (36.8–)38.3–43.3(–47) (av. 40.8) µm diam including the height of tubercles (n = 34), wall 2–4 µm thick, irregularly tuberculate, with blunt ridges; tubercles mostly connected, but very rarely single, often branched, up to 4 µm long.

Substratum — Living leaves of *Arabidopsis thaliana.*

Known distribution — Australia, England, France, Germany.

Specimens examined. Australia, Tasmania, Gretna, 29 Sept. 1980, *D. Morris,* DAR 73071, holotype. – Additional specimens examined are listed in Table 1.

DISCUSSION

Before the molecular phylogenetic studies of Choi et al. (2006) and Voglmayr & Riethmüller (2006), it was generally believed that only a single species of *Albugo* is parasitic to *Brassicaceae*, with a very broad host range, encompassing 63 genera and 241 species (Biga 1955, Saharan & Verma 1992). These include cultivated species of economic importance, in particular *Eutrema*, *Armoracia*, *Brassica* and *Raphanus* species. Only recently, it was found that a high genetic diversity exists within *Albugo* on *Brassicaceae* (Choi et al. 2006, 2007, 2008, Voglmayr & Riethmüller 2006). In addition, it was realised that oospore morphology and ornamentation provide characters of high phylogenetic significance (Voglmayr & Riethmüller 2006, Choi et al. 2007, 2008), which is contrasted by a low degree of variability of the dimorphic sporangia (Constantinescu & Thines 2006) as has been revealed in several studies (Biga 1955, Makinen & Hietajarvi 1965).

Mainly on the basis of oospore ornamentation two new species, *Albugo koreana*, parasitic to *Capsella bursa-pastoris* in Korea and *A. voglmayrii*, parasitic to *Draba nemorosa* in East Asia, were described. For the host genera of these species it has been known that *Albugo candida* may infect them in Europe. In case of *A. koreana*, even the same host species may be affected by either *A. koreana* or *A. candida*. But even with the rather broad sampling presented by Choi et al. 2007, no case of *A. koreana* from any other country than Korea could be confirmed.

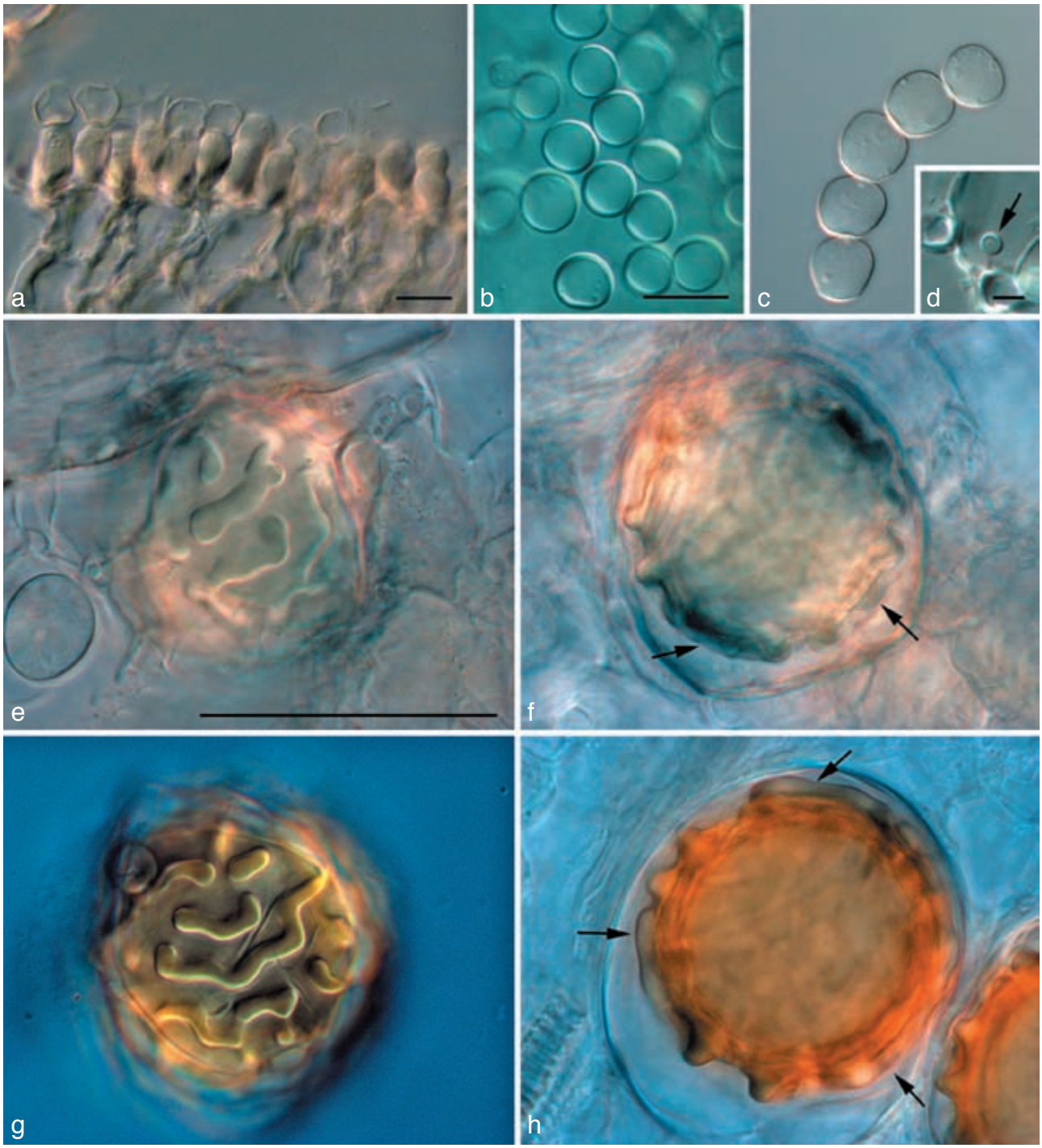

Fig. 2 Morphological characteristics of *Albugo* species on *Arabidopsis thaliana*. a–f. New species discovered on *Arabidopsis thaliana*; g, h. *Albugo candida* on *Arabidopsis thaliana*. — a. Sporogenous hyphae; b. primary sporangia; c. secondary sporangia; d. haustorium; e, g. surface ornamentation of oospores; f, h. protuberances (arrows) as seen in lateral view. — Scale bars: a–c = 20 µm, d = 10 µm, e–h = 50 µm. Sources: a–f (DAR 73071), g, h (BP 75214).

Therefore, it could be argued that *A. candida* and *A. koreana* are the result of an allopatric speciation event, i.e. speciation took place primarily due to geographic isolation.

However, this is in contrast to the situation observed in this study for northern Europe. Both *A. candida* and *A. laibachii* were found to co-occur in the same geographic region, and even in the same locality. Therefore, to explain the presence of two distinct species on the same host plant, either sympatric speciation (i.e. speciation within the same geographical region) or later migration has to be considered. In the former case the occupation of different ecological niches has to be postulated, which was also in line with the finding that the two species may coexist in the same region. As the host plant for both species is identical, these niches could be in different strategies for exploiting their host. Interestingly, the broad host spectrum of *A. candida* could be confirmed in general, with a host range covering a large array of the common tribes of the *Brassicaceae* (Choi et al. 2006, 2007, 2008, Voglmayr & Riethmüller 2006). Within the generalist species *A. candida*, several more restricted or specialised lineages seem to be present (Pound & Williams 1963, Petrie 1988). However, inoculation experiments with other isolates have shown, that some are able to parasitize largely unrelated plants, even from two distinct families, as recently Khunti et al. (2000) showed that an isolate from *Brassica juncea* could successfully infect *Cleome viscosa*. It is also possible that in some of the infection trials so far unrevealed specialised species have been used.

Apart from *A. candida*, which encompasses all isolates from *Brassica* sequenced so far, several highly distinct lineages exist, many of which have so far not been described as independent species (Choi et al. 2006, 2007, 2008, Voglmayr & Riethmüller 2006). The basis for these highly different strategies likely is a consequence of different sets of effector genes employed during compatible interaction. It will be the privilege of future studies, to investigate the molecular basis of the host specialisation in *A. laibachii* and the broad host spectrum of the species *A. candida*, from which in turn several isolates with a restricted host range have recently been found (for a discussion see Borhan et al. 2008). The two *Albugo* pathogens of *Arabidopsis thaliana* might therefore become an important model system for investigating the basic processes involved in plant defence and pathogen specialisation.

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