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ORIGINAL ARTICLE

The host range of *Albugo candida* extends from Brassicaceae through Cleomaceae to Capparaceae

Young-Joon Choi · Hyeon-Dong Shin · Marco Thines

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Abstract Capers (*Capparis spinosa*) are affected by white blister rust attributed to *Albugo capparidis* or, applying a broad species concept, to *Albugo candida*. Within the past 3 years, a great diversity within *Albugo* parasitic to the Brassicaceae has been observed. This has led to the description of two new specialized species within the parasites to Brassicaceae and the confirmation that *Albugo lepidii* is distinct from *Albugo candida*. In addition, it has been realized that *Albugo candida* has a broad host spectrum within the Brassicaceae, extending to the closely related Cleomaceae. Through molecular phylogenetic analysis of *cox2* sequences and morphological comparison, it is demonstrated that the host range of *A. candida* extends to the Capparaceae. These findings are both relevant for practical plant pathology and raise questions regarding the mechanisms involved in the exceptional broad host range of *Albugo candida*, compared to other *Albugo* species.

Keywords White blister rust · *Cleome* · *Capparis* · *cox2* mtDNA · Taxonomy

Y.-J. Choi · H.-D. Shin (✉)
Division of Environmental Science and Ecological Engineering, College of Life and Environmental Sciences, Korea University, Seoul 136-701, Korea
e-mail: hdshin@korea.ac.kr

Y.-J. Choi
e-mail: yjchoi@korea.ac.kr

M. Thines
Institute of Botany 210, University of Hohenheim, 70593 Stuttgart, Germany
e-mail: thines@uni-hohenheim.de

Introduction

Capers are widely grown in the Mediterranean and elsewhere for their edible flower buds. The caper bush (*Capparis spinosa* L.) is attacked by relatively few pathogens with one of the most prevalent being white blister rust caused by members of the Albuginaceae. This family of plant parasites is highly distinctive from the second obligate parasitic group of oomycetes, the Peronosporaceae (Riethmüller et al. 2002; Hudspeth et al. 2003; Thines and Spring 2005; Thines et al. 2008). The Albuginaceae contain four distinct lineages (*Albugo* s.str., parasitic to Brassicales; *Albugo* s.l., parasitic to Convolvulaceae; *Pustula*, parasitic to Asterales s.l.; and *Wilsoniana*, parasitic to Caryophyllales). Within the Albuginales, about 40 species responsible for white blister rust disease of economically important agricultural crops and common weeds have been described (Biga 1955; Choi and Priest 1995). The most widely recognized species, *Albugo candida* (Pers.) Roussel, had been thought to be the exclusive white rust pathogen of the Brassicaceae, infecting as many as 63 genera and 241 species (Mukerji 1975; Saharan and Verma 1992). Only recently was it realized that a high degree of genetic diversity is present within *Albugo* on Brassicaceae (Choi et al. 2006; Voglmayr and Riethmüller 2006) and that several of the observed lineages might constitute distinct species. Following the recent lectotypification of *A. candida*, the taxonomic status of which had previously been unclear (Choi et al. 2007), two specialized *Albugo* species parasitic to Brassicaceae have been described within *Albugo* (Choi et al. 2007, 2008). It was also demonstrated that *A. candida* s.str. has a broad host range extending over more than a dozen genera of the Brassicaceae and into the Cleomaceae, as the type of *A. chardonii* W. Weston (Chardón and Toro 1930; Vanev et al. 1993) was found to be nested within *A. candida* (Choi et al. 2007).

Albugo candida had also been reported from Capparaceae, (Choi and Priest 1995), but since no clear-cut morphological difference was given between *A. candida* and *A. capparidis* (de Bary) Kuntze, the second species of *Albugo* reported from Capparaceae, the identification of *A. candida* remained unsecured. Given that *Albugo* parasitic to Brassicales includes several distinct species (Choi et al. 2007, 2008) on the one hand, and the broad host spectrum for *A. candida* on the other, it was the aim of this study to clarify if the host spectrum of *A. candida* extends to Capparaceae, or if the lack of morphological characters for distinguishing *A. candida* from *A. capparidis* stated in prior studies (e.g., de Bary 1863; Berlese and DeToni 1888) are the reason for the reports of *A. candida* on Capparaceae.

Materials and methods

DNA was extracted for analysis of the *cox2* locus from two specimens of *A. chardonii*, (including the type; Plant Pathology Herbarium of Cornell University—CUP), and six specimens of *Albugo capparidis* (US National Fungus Collection—BPI; and the Jardin Botanique National de Belgique—BR).

Specimens examined: *Albugo chardonii*: Colombia, Dept. Cundinamarca, wet meadow above Salto de Tequendama, on *Cleome anomala* H.B. & K., 6 July 1929, Carlos Eugenio Chardón (CUP-CO-000668, Typus); USA, NY, Ontario Co., Geneva, on *Cleome hassleriana* Chodat cv. 'Rose Queen', 28 May 2002, Karen Snover (CUP-065770). *Albugo capparidis*: Ethiopia, Agaro, Kaffa Province, 15 km N. W. of Jimma, edge of woodland along low road to, alt. 1780 m. 7°43′N 36° 46′E, on *Capparis* sp., 5 January 1962, F.G. Meyer (BPI 185279); Italy, Rome, on living leaves of *Capparis* sp., May 1904 (BPI 184346; other herbaria: D. Saccardo Mycotheca Italica 1461); Italy, Environs de Roma, Mont Palatino, on *Capparis rupestris* Sibth. & Sm. (now, a synonym of *C. spinosa*), September 1887, E. Bommer and M. Rousseau (BR 075128-50); Italy, Bovezzano, on *Capparis rupestris* (now, a synonym of *C. spinosa*), Sept 1887, E. Bommer and M. Rousseau (BR 075128-51); Italy, Verona, on leaves of *Capparis spinosa*, Sept 1878, E. Bommer and M. Rousseau (BR 075128-52); USA, Hawaii, Kaalualu and Waiohinu, halfway between, on living leaves and stems of *Capparis* sp., 7 September 1929, Otto Degener (BPI 184347; other herbaria: Plants of Hawaii Herbarium Otto Degener 3761).

Morphological studies

Herbarium specimens were first moistened with 70% alcohol, and then the white blister rust organs were transferred with glass needles to a droplet of 60% lactic acid pipetted onto a microscope slide. These preparations were slowly warmed up, covered with coverslips and examined in brightfield- and DIC-light microscopy, using an Olympus BX51 microscope (Olympus, Tokyo, Japan) for measurements, and a Zeiss AX10 microscope (Carl Zeiss, Göttingen, Germany) mainly for photographs.

DNA extraction, amplification and sequencing

DNA was extracted from sporangiophores and sporangia formed on the lower surface of the infected leaves. DNA extraction was performed according to the methodology described in Lee and Taylor (1990). For *cox2* amplification, the primers designed by Hudspeth et al. (2000) were employed. The PCR products were purified using a QIAquick gel extraction kit (Qiagen, Hilden, Germany) and sequenced on an automatic sequencer (ABI Prism TM 377 DNA Sequencer), using the BigDye™ (Applied Biosystems, Foster City, CA, USA) cycle sequencing kit, version 3.1.

Phylogenetic analysis

Thirty-four sequences of partial *cox2* mtDNA, including *A. capparidis, A. chardonii*, and *A. candida*, were analyzed in this study. Information for the sequences is shown in Table 1. Herbaria abbreviations follow Holmgren and Holmgren (1998). The newly obtained *cox2* sequences were edited using the DNASTAR computer package (Lasergene, Madison, WI), version 5.05. Alignment of the sequences was performed using CLUSTAL X (Thompson et al. 1997), which is possible without ambiguity because of the presence of only few indels that are restricted to the outgroup. Phylogenetic trees were obtained from the data using maximum likelihood (ML) and maximum parsimony (MP) methods. For ML inference, RAxML (Stamatakis 2006) version 7.0.3 was used with all parameters set to default values, using the GTRMIX variant. A MP heuristic search was performed with 1,000 random sequence additions and branch swapping by tree bisection-reconnection (TBR), using PAUP* version 4b10 (Swofford 2002). For both analyses, the relative robustness of the individual branches was estimated by bootstrapping (BS) using 1,000 replicates. Bootstrapping was conducted based on heuristic searches by 100 rounds of random sequence addition and subsequent TBR branch swapping. The alignments and tree obtained were deposited in Treebase (accession number S2358).

Results

Morphological analysis

Eight specimens of *Albugo chardonii* on *Cleome anomala* (1) and *C. hasslerana* (1) and white blister rusts labelled as *A. capparidis* on *Capparis spinosa* (3) and *C.* sp. (3) were

Table 1 Summary of information about the sequences used for phylogenetic analysis

Species	Host	Herbarium number	GenBank Acc. No.
Albugo candida s.str.	*Arabidopsis halleri*	BPI 199991	DQ418513
	Arabis turrita	SOMF 00337	AY913803
	Aubrieta deltoidea	BPI 184659	DQ418511
	Berteroa incana	BPI 184200	DQ418508
	Biscutella laevigata	BPI 184686	DQ418506
	Brassica juncea	KUS F 15570	AY927046
	Capsella bursa-pastoris	BPI 184451	DQ643944
	Diplotaxis erucoides	BPI 184862	DQ418517
	Eruca sativa	BPI 184870	DQ418514
	Erysimum cuspidatum	BPI 199988	DQ418519
	Heliophila meyeri	BPI 184888	DQ418515
	Iberis amara	BPI 184897	DQ418522
	Lepidium campestre	KUS F 13747	AY927054
	Lunaria sp.	CUP 065639	AY913797
	Raphanus sativus	KUS F 10614	AY927059
	Sisymbrium luteum	KUS F 19086	AY913808
	Thlaspi arvense	CUP 065777	AY913809
A. candida s.l.	*Descurainia sophia*	SOMF 19655	AY927051
A. candida s.l.	*Diptychocarpus strictus*	SOMF 19659	AY927052
A. capparidis	*Capparis spinosa*	BR 75128-50	FJ390871[a]
	Capparis spinosa	BR 75128-51	EF655654[a]
	Capparis sp.	BPI 184346	FJ390872[a]
	Capparis sp.	BPI 184347	FJ390873[a]
A. chardonii	*Cleome anomala* (Typus)	CUP CO-000668	AY913799[a]
	Cleome hassleriana	CUP 065770	EU877955[a]
A. ipomoeae-panduratae	*Ipomoea hederacea*	KUS F 19628	AY913804
A. koreana	*Capsella bursa-pastoris*	BPI 871286	AY927049
A. occidentalis	*Spinacia oleracea*	-	AY286220
A. voglmayrii	*Draba nemorosa*	BPI 87775	EU240590
Pustula tragopogonis	*Helianthus annuus*	-	AY286221
Wilsoniana achyranthis	*Achyranthes japonica*	KUS F 19955	AY913807
W. bliti	*Amaranthus spinosus*	KUS F 19835	AY913805
W. portulacae	*Portulaca oleracea*	KUS F 18991	AY913806

[a] Sequences obtained during this study

morphologically compared with *A. candida* from various brassicaceous hosts. In *Cleome anomala* infected by *A. chardonii*, the leaf surface had sparse yellow to straw-colored lesions, with sori mostly on the lower surface, but occasionally on the upper surface. The sori were formed subepidermal, color primarily white, but occasionally light-yellow, shape elongated and irregular, often confluent, covering mostly large areas of the lower and rarely upper side of the leaf (Fig. 1a). The grouped sporangiophores were hyaline, cylindrical or clavate, 25–43 μm long, 10–15 μm wide (n=131), thick-walled, especially towards the base (up to 5.5 μm; Fig. 1b, c). The sporangia were arranged in basipetal chains, hyaline, globose to subglobose, (13.8–)15.5–20.9(−23.5) μm diam. (n=108), the primary sporangia were similar to the secondary sporangia, although the former exhibit a slightly thicker wall (1.2–2 μm) than the latter (0.5–0.8 μm) (Fig. 1d, e, respectively). Resting organs were not seen. Similar symptoms were observed on *Capparis* materials. The sori were formed on both upper and lower surface of infected leaves, and were subepidermal, colour white to yellowish, shape elongated and irregular, often confluent (up to 10 mm) and sometimes rounded, with irregularly torn epidermis. The morphological characteristics of sporangiophores and sporangia are indeed identical to those of *A. chardonii*, excluding minor difference in sporangial size; (13.3–)14.5–18.4(–22.5) μm diam. (n=115) in the primary sporangia, which were similar to the secondary sporangia, although the former exhibit a slightly thicker wall (1.2–1.8 μm) than the latter (0.5–1.0 μm). Resting organs were

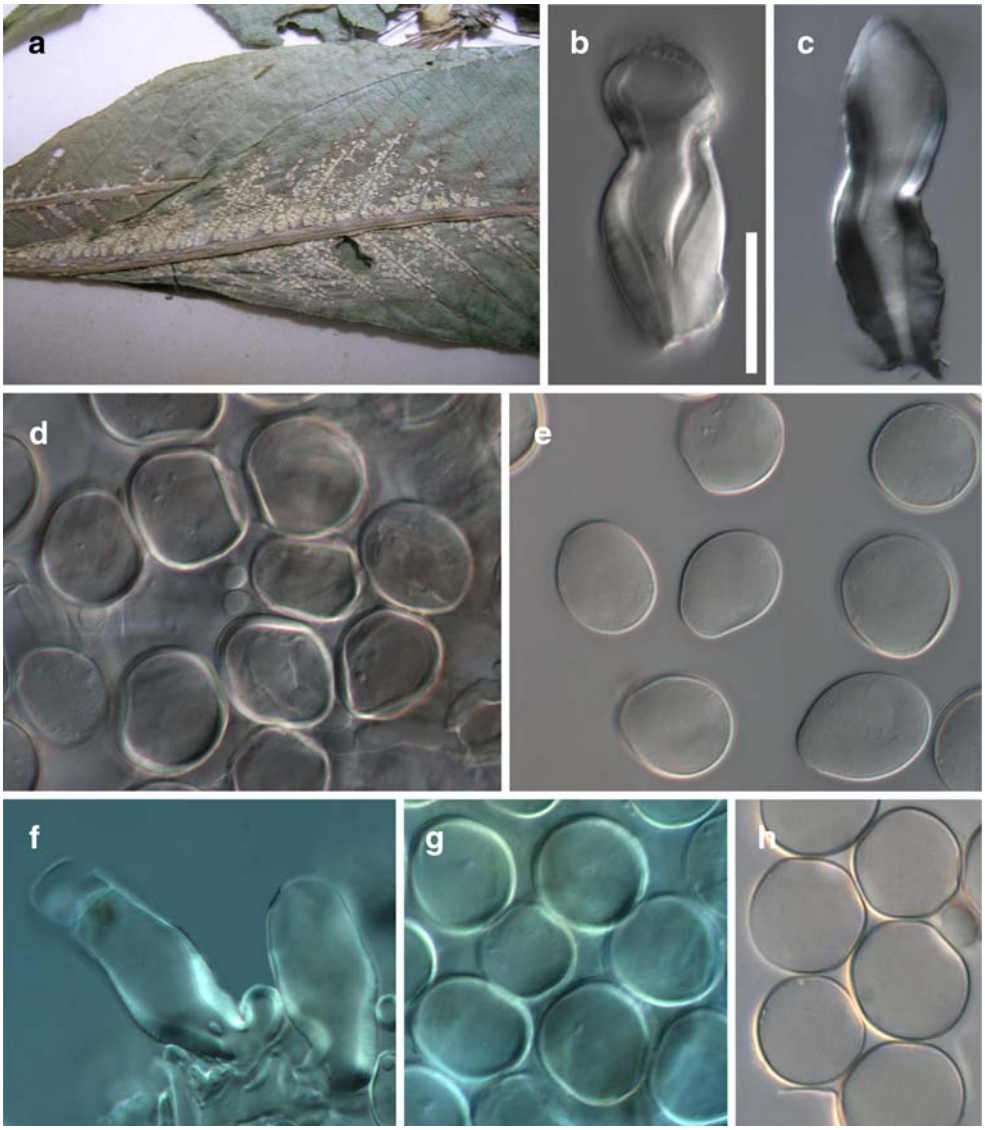

Fig. 1 *Albugo chardonii* (**a**–**e**) on *Cleome anomala* and *A. capparidis* (**f**–**h**) on *Capparis spinosa*. **a** Sori on infected leaves; **b**, **c**, **f** sporangiophore; **d**, **g** primary sporangia; **e, h** secondary sporangia. *Scale bars* 15 µm for **b**, **c**, **f**; 20 µm for **d**, **e**, **g**, **h**. Source: CUP CO-000668 (typus) for *A. chardonii*; BR 75128-50 for *A. capparidis*

not seen. The morphological characteristics of *A. chardonii* and the specimens labelled as *A. capparidis* are identical to those of *A. candida* s.str. from *Arabis*, *Brassica*, *Capsella*, *Lunaria*, *Raphanus*, *Sisymbrium*, and *Thlaspi*. Therefore, two species could not be differentiated from *A. candida* by their morphological comparison.

Molecular analysis

The phylogenetic relationship among the *Albugo* species was inferred from the ML and MP analyses of the aligned sequences of the partial *cox2* mtDNA. A ML tree is presented in Fig. 2. Out of 572 total characters, 133 were parsimony-informative, and parsimony analysis resulted in 117 most parsimonious trees of 370 steps with a consistency index (Kluge and Farris 1969) of 0.6513 and a retention index (Farris 1989) of 0.8740. Since no statistically significant differences were found between the tree topologies of the ML and MP analyses, only the ML tree is shown in Fig. 2. The phylogenetic inferences revealed that the sequences from *Capparis spinosa*, *Capparis* sp., *Cleome anomala*, and *C. hasslerana* were embedded within *A. candida* materials from *Arabidopsis, Arabis*, *Aubrietia*, *Berteroa*, *Biscutella*, *Brassica*, *Capsella*, *Diplotaxis*, *Eruca*, *Erysimum*, *Heliophila*, *Iberis*, *Lunaria*, *Raphanus*, *Sisymbrium*, and *Thlaspi*, with maximum support in both analyses. The close relationship of *A. chardonii*, the specimens labeled as *A. capparidis* and *A. candida* was also supported by high sequence similarity of 99.8–100% (none or 1 out of 572 characters different). The level of sequence identity between these three species exceeds that found among *A. candida* materials from various brassicaceous hosts, indicating that they are indeed to be considered conspecific.

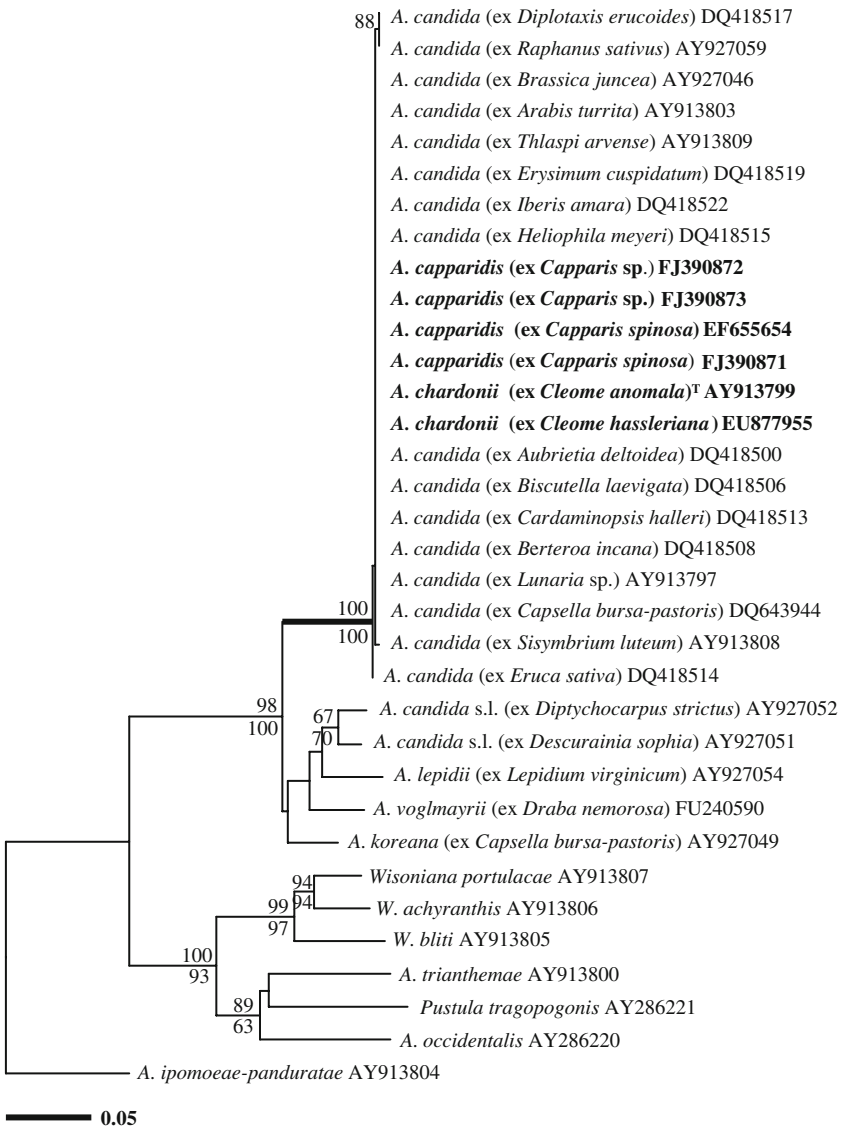

Fig. 2 Phylogenetic tree of Albuginaceae species inferred by ML analysis using the partial *cox2* mtDNA. ML and MP BS values above 50% are given *above/below* the branches, respectively. The number of nucleotide changes between taxa is represented by branch length and the *scale bar* equals the number of nucleotide substitutions per site. *Albugo* specimens from *Cleome and Capparis* are in *bold*

Discussion

For the white blister rust parasitic on *Cleome anomala*, the epithet "*chardoni*" was first introduced as a dedication to Carlos Eugenio Chardón. This epithet is generally used in most taxonomy and plant pathology related works. However, ICBN Article 60.11 (McNeill et al. 2006) requires that when a male personal name ends with a consonant, the epithet should be formed by adding -ii- (stem augmentation plus the genitive inflection) in conformity with Recommendation 60C.1. If known not to be so, the termination is to be corrected orthographically. Therefore, the termination was corrected here as "*chardonii*" throughout.

Until now, *Albugo* strains infecting *Cleome* species were regarded as both *A. candida* and *A. chardonii,* because of unclear morphological difference. The only previously reported morphological difference between *A. chardonii* and *A. candida* is the thickness of the sporangial wall. *A. candida* has been reported to have a uniform wall thickness of the sporangia, while those of *A. chardonii* have wall thickening across the base and sides (Chardón and Toro 1930; Choi and Priest 1995). In the present observation, however, the wall thickness of the sporangia showed no obvious morphological difference of the two species. The wall thickness in the sporangia of *A. chardonii* was mostly uniform, while only a few sporangia, particularly secondary ones, had irregular thickened walls, the basal and lateral portions being slightly thicker than the apical part. In a previous study (Constantinescu and Thines 2006) and the present one, however, this morphological feature was also commonly observed in most materials of *A. candida*. Phylogenetic analyses (Choi et al. 2007; this study) have shown *A. chardonii* grouped together with *A. candida* s.str. from various plants of the Brassicaceae with a high level of

sequence homology. This hints at the possibility that the two species are indeed conspecific. Interestingly, the morphological and molecular identity among them is in agreement with previous inoculation experiments; Safeeulla (1952) and Jörstad (1964) reported that *A. candida* can attack plants in the Cleomaceae, and recently Khunti et al. (2000) showed that an isolate from *Brassica juncea* could successfully infect *Cleome viscosa*. Therefore, we conclude that *A. chardonii* is to be regarded a synonym of *A. candida*.

Similar to the situation in *Cleome*, *Albugo* from *Capparis* was also classified either as *A. capparidis* or as *A. candida*. *A. capparidis* was formally introduced by de Bary (1863), based on a variety of *A. candida* previously described by Rabenhorst (1844). But de Bary notes in his description that the species was "*in speciminibus C. Candida* [*A. candida*] *omnino similia*". Also Pirotta (1884, as cited in Fischer 1892) and Berlese and DeToni (1888) could not find differences between *Albugo* accessions from Brassicaceae and from Capparaceae. In the monographic work of Biga (1955), the species is recognised on the basis of host preference, but both sporangia and oospore features are identical to *A. candida* var. *macrospora*. The ornamentation of the oospore wall has proven to be possibly the most important character to distinguish between closely related species in the Albuginaceae (Voglmayr and Riethmüller 2006; Choi et al. 2007, 2008). Interestingly, Choi and Priest (1995), who unfortunately do not mention any specimens they might have scrutinized, cite Biga (1955) and Saccardo (1888) and state the oospore ornamentation was "tuberculate", a feature that could indicate that this species might be unrelated to *A. candida*, depending on the interpretation of the character state "tuberculate". As Voglmayr and Riethmüller (2006) have shown that a specimen from *Cleome* was placed distinct from *A. candida* among the specialized species, two lineages can obviously parasitize the genus *Cleome*, *A. candida* and an additional possibly undescribed species. Our findings presented here demonstrate that *A. candida* may also parasitize *Capparis spinosa* and its natural host range therefore extends to the family Capparaceae. Whether the situation in Capparaceae is similar to the situation found in Cleomaceae, where two distinct *Albugo* species may occur as parasites, has to be revealed by future studies. In addition, it will be necessary to determine and investigate the specimen on which Rabenhorst (1844) had based the variety later granted species rank by de Bary (1863), to clarify if *A. capparidis*, similar to *A. chardonii*, needs to be relegated into synonymy with *A. candida*.

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