# Dimorphism of sporangia in Albuginaceae (Chromista, Peronosporomycetes)

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By using light- and scanning electron microscopy, the dimorphism of sporangia in Albuginaceae is demonstrated in 220 specimens of *Albugo*, *Pustula* and *Wilsoniana*, parasitic on plants belonging to 13 families. The presence of two kinds of sporangia is due to the sporangiogenesis and considered to be present in all representatives of the Albuginaceae. Primary and secondary sporangia are the term recommended to be used for these dissemination organs.

Key words: *Albugo*, morphology, sporangiogenesis, *Pustula*, *Wilsoniana*.

The Albuginaceae, a group of plant parasitic, fungus-like organisms traditionally restricted to the genus *Albugo* (Pers.) Roussel (*Cystopus* Lév.), but to which *Pustula* Thines and *Wilsoniana* Thines were recently added (Thines & Spring 2005), differs from other Peronosporomycetes mainly by the sub epidermal location of the unbranched sporangiophores, and basipetal sporangiogenesis resulting in chains of sporangia.

A feature only occasionally described is the presence of two kinds of sporangia. Tulasne (1854) was apparently the first to report this character in *Wilsoniana portulacae* (DC. ex Duby) Thines and, to a lesser extent, in *Albugo candida* (Pers.) Roussel. He also provided a detailed account of sporangiogenesis in *W. portulacae*. In the first taxonomic account of Peronosporales, de Bary (1863) mentioned the presence of one kind of sporangium in *A. candida* and closely related *A. capparidis* (de Bary) Ciferri, and two kinds in the remaining four species known at that time [*W. bliti* (Biv.) Thines, *W. portulacae*, *Pustula spinulosa* (de Bary) Thines, and *P. tragopogonis* (Pers.) Thines]. Zalewski (1883) commented upon the sporangiogenesis, particularly the blastic formation of sporangia. He described eight species, of which two were new, but omitted to specify any dimorphism. Berlese & De Toni (1888) and Berlese (1898, 1901) provided descriptions for 14 species. Of these, monomorphic

sporangia were mentioned in four species, dimorphic in five, and for another five species it is unclear whether they were considered mono- or dimorphic. Wilson (1907) provided a key for the identification of 13 species of which only eight were described in detail. He considered that sporangia are not dimorphic in *A. candida, A. ipomoeae-panduratae* (Schwein.) Swingle, and *A. occidentalis* G.W. Wilson, that the terminal (i.e. primary) sporangia only differ in size in *A. platensis* (Speg.) Swingle, *P. tragopogonis, W. bliti,* and *W. portulacae,* and that only in *A. lepigoni* they are truly dimorphic (dissimilar). Wilson (1908) also described larger (in *A. trianthemae* G.W. Wilson) or smaller (in *A. froelichiae* (G.W. Wilson) Sacc. & Trotter) terminal sporangia.

In describing the sporangiogenesis in *Albugo,* Gäumann (1928: 78) stated that the "first conidium in a chain" (i.e. primary sporangium) is larger and has uniformly thick wall. In the description of *Cystopus (Albugo) tilleae* Lagerh. (Patouillard & Lagerheim 1891) and *A. chardoni* G.W. Weston (Weston 1930) the dissimilarity of sporangia is clearly indicated in the descriptions. Jaczewski & Jaczewski (1931) treated eight species of which *A. candida* was described as having monomorphic sporangia, four dimorphic, and for three species only secondary sporangia were described. Of 12 species described and illustrated by Ito (1936) only three [*A. lepigoni* (de Bary) Kuntze, *A. molluginis* S. Ito, and *W. achyranthis* (Henn.) Thines] were considered as having dissimilar sporangia. Biga (1955) provided numerous measurements of sporangia size, in what was the most comprehensive compilation of the genus at the time, but did not indicate which type of sporangia have been measured. In publications where aspects other than the taxonomy were presented, but in which the sporangia were the main or at least one of the objects of study, the type of sporangia was not specified (Eberhardt 1904, Tsang 1929). More recent studies on Peronosporomycetes simply ignored this character (Waterhouse 1973, Shaw 1981, Saharan & Verma 1992, Dick 2001a, 2001b). The dimorphism was also ignored in monographs (Ananthanarayanan 1964, Jörstad 1964, Zhang & Wang 1998), in studies on germination (Melhus 1911, Bartaria & Verma 2001), cytology (Dangeard 1901, Stevens 1940, Safeeulla & Thirumalachar 1951, 1953, Berlin & Bowen 1964), and ultrastructure (Tewari *et al.* 1980), with the notable exception of Khan (1976).

Moreover, in studies dedicated to the genus *Albugo* (Săvulescu 1946) or to *A. candida* (Togashi *et al.* 1930, Togashi & Shibasaki 1934, Mäkinen & Hietajärvi 1965, Lakra & Saharan 1989), in which extensive measurements of sporangia were performed, the authors failed to specify which type of sporangia were measured.

Although Tulasne (1854) mentioned the dimorphism of sporangia in *A. candida,* albeit to a lesser degree compared to

*W. portulacae*, subsequent authors either did not specify this character (Mukerji 1975a), or claimed that no dimorphism is present in the former species (Bary 1863, Berlese & De Toni 1888, Fischer 1892, Berlese 1898, 1901, Jaczewski 1901, Wilson 1907, Wakefield 1927, Jaczewski & Jaczewski 1931, Ito 1936, Săvulescu 1946, Baker 1955).

During studies on various members of Peronosporomycetes, we remarked that the morphology of sporangia in Albuginaceae, as revealed in LM and SEM, is more complex than previously thought. The aim of this study is to clarify some details of the sporangial morphology, the extent of sporangial dimorphism distribution within Albuginaceae, to explain the cause of this phenomenon, and why this feature was sometimes overlooked or misunderstood.

## Materials and Methods

### Specimens

Some 220 specimens of Albuginaceae parasitic on plants belonging to 13 families were examined (complete list at UPS) but only those that were used for illustration in this study are included in Table 1.

### Light microscopy and SEM

For LM examination, pustules, particularly young ones, were moistened with 70 % alcohol under a dissecting microscope. Using a scalpel, the top portion of the pustule was cut parallel to the leaf surface, turned upside down and placed in a drop of 60 % lactic acid in distilled water. The slide was warmed up on a smoothing iron, and covered with a cover slip. The examination of slides was performed with either a Diaplan or Laborlux K (Leitz, Wetzlar, Germany) microscope, and pictures were taken with a Nikon Coolpix 4500 digital camera attached to the first microscope. Line drawings were made with the aid of a Leitz drawing tube, attached on the above mentioned microscopes, using a 100 × oil immersion objective, at a final 2000 × enlargement.

### Scanning electron microscopy

For SEM, small pustules or fractions of a pustule were cut from the herbarium specimens and glued on aluminium object holders, the pustule oriented face down. Afterwards, the leaf tissue was broken away using a needle to open the pustule. The object holder was then

held close to vertical and hit against a hard surface to liberate the secondary sporangia. Subsequently, the samples were desiccated for two days, sputtered and examined as described previously (Thines & Spring 2005).

**Tab. 1.** – List of specimens used to depict the primary and secondary sporangia in Albuginales

| Fungus | Host | Collection | Figure No |
|---|---|---|---|
| *Albugo candida* | *Capsella bursa-pastoris* | Germany, Stetten, Airfield, Jun 2002, M. Thines (HUH) | 15, 20 |
| *Albugo candida* | *C. bursa-pastoris* | Hungary, 1884 (Linhart – Fungi hung. 391a in UPS) | 1, 3 |
| *Albugo candida* | *C. bursa-pastoris* | Finland, Turku, Muhkuri, 20 Jun 1935, L. A. Kari (UPS) | 2 |
| *Albugo ipomoeae-aquaticae* | *Ipomoea aquatica* | China, Yunnan, S of Jinghong, 3 Sep 2004, M. Thines (HUH) | 14, 19 |
| *Albugo ipomoeae-panduratae* | *Ipomoea hederacea* | USA, KS, Belvue, 28 Sep 1906, E. Bartholomew (UPS) | 8 |
| *Albugo lepigoni* | *Spergularia marina* | Finland, Brännboda, Järnskär, 18 Jun 1968, H. Roivanen (UPS) | 7 |
| *Pustula spinulosa* | *Cirsium arvense* | Germany, Bayern, Bayreuth, A. Walther (UPS) | 2, 4 |
| *Pustula tragopogonis* | *Helianthus annuus* | Germany, Esslingen, Oberesslingen, 10 Oct 2004, M. Thines (HUH) | 11, 16 |
| *Pustula tragopogonis* | *Tragopogon porrifolius* | Sweden, Uppsala, Botanical Garden, 1 Sep 1933, J. Ax. Nannfeldt (UPS) | 9 |
| *Wilsoniana bliti* | *Amaranthus blitoides var. reverchonii* | Romania, Mamaia, 15 Aug 1991, G. Negrean & M. Costea (BUCM 121331) | 5 |
| *Wilsoniana bliti* | *Amaranthus blitum* | Italy, 1873 (Saccardo – Mycoth. veneta 66 in UPS) | 10 |
| *Wilsoniana bliti* | *Amaranthus cruentus* | Germany, Baden, Krotzingen, Jul 2002, M. Thines (HUH) | 13, 18 |
| *Wilsoniana portulacae* | *Portulaca oleracea* | China, Yunnan, S of Jinghong, 3 Sep 2004, M. Thines (HUH) | 12, 17 |

## Abbreviations and acronyms

Abbreviation and/or acronyms of herbaria are those from Holmgren & Holmgren (1998), most fungal names are from Choi & Priest (1995) and Thines & Spring (2005), and plant names from The International Plant Names Index (2004); published on the Internet http://www.ipni.org [accessed 2006]. The authorities of both

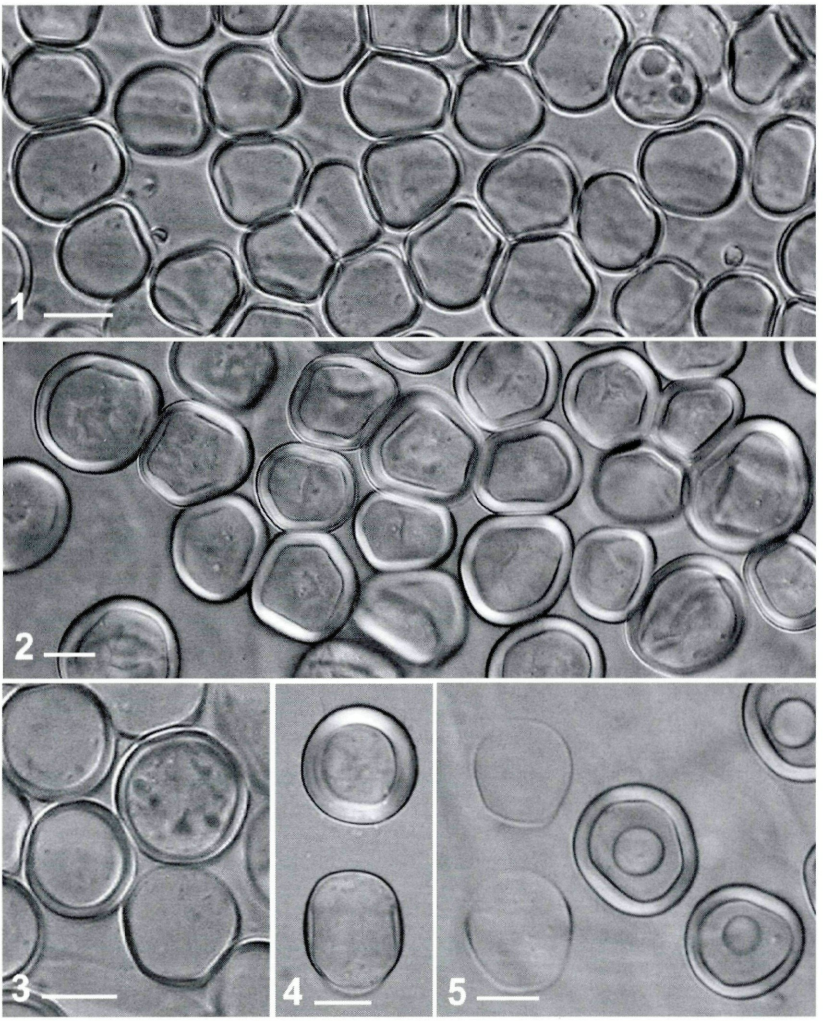
fungi and plants are available at the mentioned sites. The following acronyms of generic names and sporangia are used throughout the text: A. = *Albugo,* P. = *Pustula,* W. = *Wilsoniana,* Psp = primary sporangia, and Ssp = secondary sporangia.

## Results

In every examined specimen two types of sporangia were detected: primary, first formed (Psp) and secondary, subsequently formed (Ssp) sporangia. The Psp are smaller or larger than the Ssp, and their wall is 1 – 3 µm thick and occasionally yellowish (Figs. 1 – 20). The Psp are mostly apparent when attached to, and usually flattened against the lower side of the host's epidermis (Figs. 1, 2). In plan view they appear more or less circular (Figs. 3, 4, 6 –10, 12, 14) or, due to mutual pressure, polyangular (Figs. 1, 2, 11, 13). Their walls appear more or less uniformly thick. In lateral view, the walls are often of variable thickness, i.e. lesser thickening of a small or larger portion of the basal part (Figs. 7, 9, 10).

The structures in the centre of Psp, as seen in Figs. 10, 12, and 13, are part of the 'disjunctor' or 'suspensor' that connects the sporangia in chains. In some Psp the disjunctor continues to be attached to the lower wall after sporangial release and disintegration of the chains. This morphological structure was noticed already by Berkeley (1848), illustrated long ago by Tulasne (1854) and Mangin (1891), and recently in both LM and SEM by Mims & Richardson (2003).

In Ssp the shape, as well as the wall structure, shows more variation. These sporangia may be almost globose in *P. tragopogonis* (Fig. 9), oblong in *A. ipomoeae-panduratae* (Fig. 8), or obovoidal with only slightly *(A. eurotiae)* or distinctly truncate (*A. lepigoni, W. bliti* Figs. 7, 10) base. The wall may be uniformly, ca. 0.4 – 0.5 µm thin in *A. lepigoni* (Fig. 7) ca. 0.7 µm in *A. trianthemae,* or evenly ca 1.5 – 2 µm thick as in *A. ipomoeae-panduratae* (Fig. 8). In *A. candida* (Figs. 3, 6), *A. capparidis,* and to a lesser degree in *W. portulacae,* the basal and lateral portions of Ssp wall are more or less thicker than the apical part. In many species the wall of Ssp shows a thickening, mostly as an equatorial ring (Figs. 4, 5, 9, 10). In lateral view, the ring appears as a very slight thickening of the wall, which is characteristic for *Wilsoniana* (Figs. 5, 10) or lenticular, which is typical for *Pustula* (Fig. 9). It seems that the equatorial thickening of the wall confers more rigidity to the sporangium. In dehydrated, collapsed sporangia, both the apical and the basal part of the sporangial wall collapse, but the equatorial ring will stay rigid (Fig. 16).

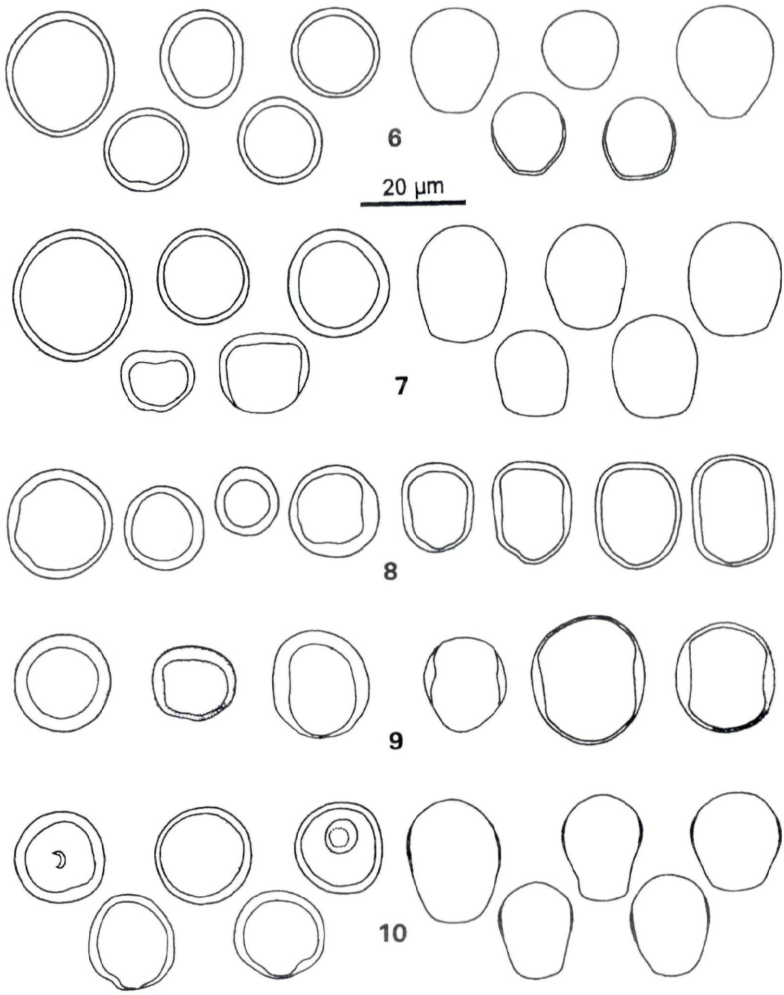



**Figs. 1 – 5.** Primary and secondary sporangia in various Albuginaceae. **1.** Primary sporangia agglomerated and partially deformed by mutual pressure, on the inner face of the epidermis in *Albugo candida*. **2.** Idem in *Pustula spinulosa*. **3 – 5.** Primary (thick wall) and secondary (thin wall) sporangia in *A. candida* **(3)**, *P. spinulosa* **(4)**, and *Wilsoniana bliti* **(5)**. Bars = 10 µm. Sources indicated in Table 1.

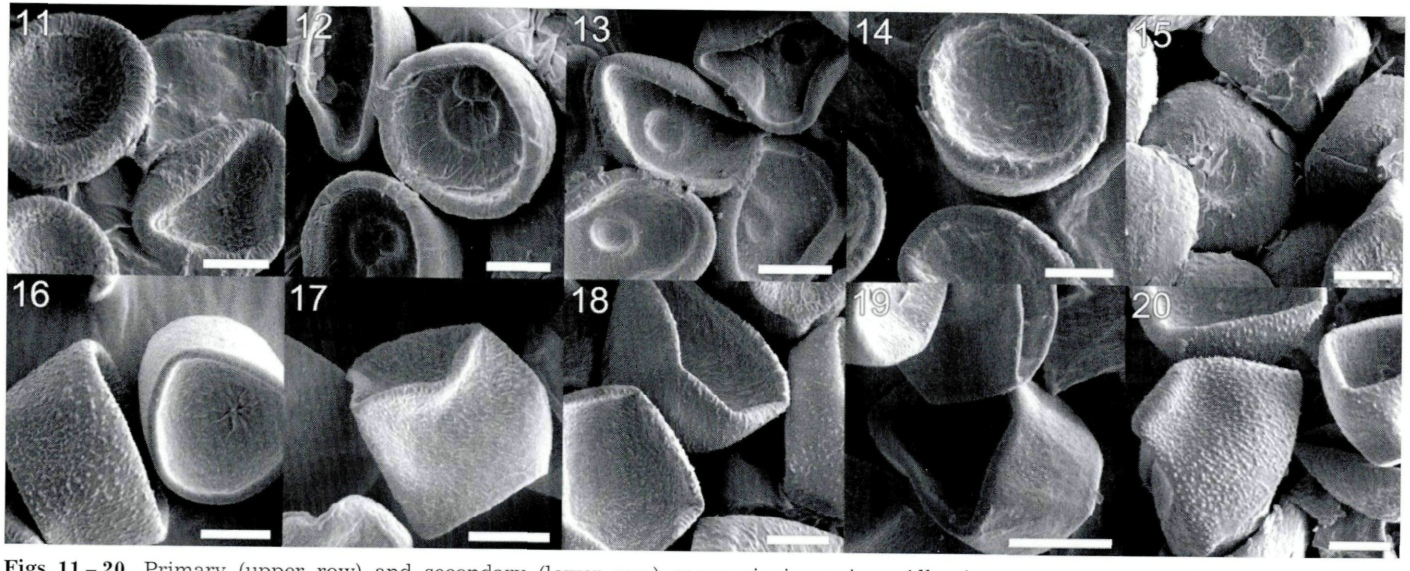
## Discussion

The mode of sporangiogenesis in Albuginaceae, i.e. basipetal succession from the top of the sporangiophore, was first described by Tulasne (1854). This process is similar to one type of blastic conidiogenesis known in some anamorphic fungi (Subramanian 1971, Cole & Samson 1979 and references herein). The first sporangium

(Psp) is formed holoblastically, the (thick) wall of the sporangiophore taking part in the formation of the sporangium wall. The subsequent sporangia (Ssp) are formed presumably enteroblastically, their (thin) wall being newly formed. As a result, the first formed sporangium has a thick wall, especially in the apical region, whereas the subsequent ones have a thin wall. Ultrastructural details of the sporangiogenesis in *A. candida* are presented by Soylu *et al.* (2003: Fig. 2, d) where not




**Figs. 6 – 10.** Primary (left) and secondary (right) sporangia in various Albuginaceae. **6.** *Albugo candida*. **7.** *A. lepigoni*. **8.** *A. ipomoeae-panduratae*. **9.** *Pustula tragopogonis*. **10.** *Wilsoniana bliti*. Secondary sporangia in **7, 9, 10** in plan view (round, symmetrical with uniform wall thickness) and side view (asymmetrical, with thinner wall at the base). Sources indicated in Table 1.




**Figs. 11 – 20.** Primary (upper row) and secondary (lower row) sporangia in various Albuginaceae as seen in SEM. **11, 16.** *Pustula tragopogonis*. **12, 17.** *Wilsoniana portulacae*. **13, 18.** *W. bliti*. **14, 19.** *Albugo ipomoeae-aquaticae*. **15, 20.** *A. candida*. Sources indicated in Tab. 1.

only two sporangiophores bearing thin-walled Ssp are seen, but also a thick-walled Psp detached from the chain. Although the blastic mode of sporangiogenesis in *Albugo* was not questioned, the percurrent character of this process, claimed by Hughes (1971) and Thakur (1977) was contested by Khan (1977). Irrespective whether or not the percurrent character of the process is accepted, the dimorphism of these sporangia is the result of the sporangiogenesis. This type of sporangiogenesis is common to all Albuginaceae. Consequently, all species possess two kinds of sporangia.

The wall of Psp is definitely thicker than in the Ssp. Nevertheless, it should be taken into account that, particularly when Psp are flattened against the host epidermis, what appears as a single wall is in fact the image of a folded wall. This might be less obvious in light microscopy (Figs. 1 – 5) but is clearly visible in SEM (Figs. 12, 14).

According to Tulasne (1854), a sporangiophore produces 6 – 8 sporangia. This results in a Psp/Ssp ratio of 1/5 to 1/7. This is one of the reasons why the Psp are more rarely seen and reported. In addition, because Psp often remain attached to the lower side of the epidermis, a feature again firstly reported by Tulasne (1854). As the slides are usually made from free sporangia after the epidermis is removed, the chance of finding Psp in a microscopic slide is rather low. Due to the predominance of Ssp, it is likely that most studies in which the type of sporangia was not specified were based on the observation of Ssp.

## Terminology

Several pairs of terms have been used to differentiate the first vs. subsequently formed sporangia (sometimes called conidia) in Albuginaceae: some/others (Tulasne 1854), terminal/others (Bary 1863, Wakefield 1927, Baker 1955), first/subsequent (Zalewski 1883), terminal/unnamed (or lower) (Wilson 1907), first (apical) or buffer cells/others (Gäumann & Dodge 1928, Gäumann 1949), terminal/later (Weston 1930), apical/basal (Biga 1955), terminal/lower (Mukerji 1975 b), terminal/subterminal (Waterhouse 1975), terminal/normal (Choi & Priest 1995), distal/proximal (maturing) (Khan 1976), etc. In most cases the terms used refer to the position of sporangium in a chain, i.e. terminal, apical, vs. basal, lower, and subterminal, etc. In fact, the arrangement of sporangia in chains is rarely maintained and observed when microscopic slides are made. Even more rarely the terminal/first formed sporangium continues to be attached to the chain. The position of a sporangium in the chain correlates with the time when it was produced. Therefore, we consider that primary vs. secondary sporangia are more appropriate terms for the two types of sporangia.

Function of the sporangia

Not only the morphological dimorphism but also a functional dissimilarity between the two kinds of sporangia was reported. Tulasne (1854) was apparently the first to claim that the germination by production of zoospores occurs only in Ssp. De Bary (1863) stated that at germination the Psp either produce a tube, or are sterile, whereas the Ssp produce zoospores. Palm (1932) showed that in *P. tragopogonis, W. bliti,* and *W. portulacae,* sporangia produce germ tubes inside the pustules. He concluded that this type of germination occurs more often than previously reported, but omitted to specify on which kind of sporangia his studies were based upon. Palm (1932) also reviewed the divergences on this matter as expressed in various plant pathology books. According to Edie & Ho (1970), in *A. ipomoeae-aquaticae* the type of germination is temperature-dependent. Jaczewski & Jaczewski (1931) described the Psp in *A. lepigoni, P. tragopogonis, W. bliti,* and *W. portulacae* as sterile. Gäumann & Dodge (1928: 78) and Gäumann (1949: 60) claimed that the Psp, called „buffer cells", are probably not germinating and serve only to lift the epidermis. Gäumann's findings were supported by Khan (1976) who observed some minor differences in the ultrastructure or cell organelles of Psp, compared to the Ssp., in *A. candida.* Interestingly, he did not comment upon the wall thickness difference.

Conclusions

Although the dimorphism of sporangia in Albuginaceae has been observed for about 150 years, uncertainty about its presence, morphological features, and ontogeny still exist. Contrary to previous knowledge, we demonstrate that dimorphism is present in all representatives of the Albuginaceae. We also show that the dimorphism is due to the sporangiogenesis. The recommended terms to be used are the ontogenetic ones, namely primary and secondary sporangia.

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