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The Current Status of *Globisporangium* Species in Iran: From *Pythium sensu lato* to Newly Described Species

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Abstract: The genus *Globisporangium* is a newly described taxon that has been recently separated from *Pythium sensu lato*. Although not many studies focused on isolating species assigned to this genus from Iran, some comprehensive studies showed that *Globisporangium* is an important genus with vast distribution in this part of the world. Even rare species assigned to *Globisporangium* have also been found in the country. Despite the importance of this genus, accurate identification and classification of *Globisporangium* is quite challenging worldwide. Morphological identification of *Globisporangium* is quite difficult due to the lack of identification keys, overlapping of some morphological features, the existence of species complexes, pleomorphism, and the absence of certain structures in some species. Furthermore, there is no universal DNA barcode for *Globisporangium* species yet, and most species cannot be delimitated using only one or two loci for the phylogenetic analyses. Besides, some studies in Iran do not include molecular investigations to support their morphological identification or make it possible to reidentify the reported species. Having no accurate checklist of the current species in the country also adds up to the problem. This review focuses on the current systematics of *Globisporangium* species in Iran, emphasizing the challenges in the morphological and molecular identification of the species in the country; it also proposes and discusses some solutions to resolve these problems.

Key words: Diversity, Ecology, *Oomycota*, Systematics, Plant Pathogens

INTRODUCTION

Oomycetes are fungus-like microorganisms related to diatoms. They occupy diverse ecological niches, including terrestrial, limnic, and marine environments. This group contains numerous genera which have diverse substrate preferences, such as plant pathogens (e.g., *Phytophthora* spp.), saprobes (e.g., most *Saprolegnia* spp.), human pathogens (e.g., *Pythium insidiosum* de Cock, Mend., Padhye, Ajello & Kaufman), animal pathogens (e.g., *Saprolegnia* spp., *Aphanomyces* spp.), and antagonists (e.g., *Pythium oligandrum* Dreschler, *Globisporangium nunn* [Lifsh., Stangh, & Baker] Uzhuhashi, Tojo & Kakish). Probably, the most well-known oomycete for the plant pathologists is *Phytophthora infestans* de Bary, the potato late blight pathogen, which has a historical role in the Irish famine and its sociological impacts. Apart from the genus *Phytophthora*, which largely encompasses plant pathogens, the genus *Pythium sensu lato* is also considered one of the most important oomycetes, causing mainly root and crown rot as well as pre- and post-emergence damping-off in seedlings. This genus causes substantial economic loss in the field crops as well as greenhouses. However, there are other species assigned to the genus *Pythium* that are considered antagonists (i.e., *P. oligandrum* and *P. acanthicum* Drechsler) or human pathogen (i.e., *P. insidiosum*). Iran is a vast and four-season country with a diverse oomycete biota. There are several reports of *Pythium sensu lato* species from the country on different hosts and substrates (Ershad 1977; Mostowfizadeh-Ghalamfarsa 2016; Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020).

The genus *Pythium sensu lato* is considered one of the most diverse groups, which was previously classified into 11 phylogenetic clades, i.e., A to K, based on its sporangial morphology as well as the sequences of ITS and LSU regions of rDNA (Lévesque & de Cock 2004). It soon was revealed that the genus *Pythium* is not a monophyletic one and was split into five genera (Uzuhashi *et al.* 2010). Except for the clades A, B, C, and D, other clades are now known by different names. In other words, only clades A, B, C, and D are now known as *Pythium sensu stricto* (Nguyen *et al.* 2022). *Pythium sensu stricto* produces filamentous to filamentous inflates sporangia with different types of oospores (Uzuhashi *et al.* 2010; de Cock *et al.* 2015; Uzuhashi *et al.* 2017; Nguyen *et al.* 2022). Clade K was later considered a separate genus called *Phytopythium*, with intermediate morphological

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features between *Phytophthora* and *Pythium*. *Phytopythium* produces ovoid to ellipsoid sporangia with external and internal proliferation similar to those of *Phytophthora* and has vesicles and zoospores differentiated in the vesicles like those of *Pythium* has (de Cock *et al.* 2015). Clade H is also known as *Elongisporangium* and is famous for producing clavate to elongated sporangia (Uzuhashi *et al.* 2010; Nguyen *et al.* 2022). A newly proposed genus, *Pilasporangium*, was also added to the popular clades of *Pythium sensu lato*. *Pilasporangium* is recognized for producing non-proliferated sporangia with complexed secondary hyphal branches (Uzuhashi *et al.* 2010; Nguyen *et al.* 2022). The genus *Pilasporangium* does not resemble any of the previous *Pythium sensu lato* clades and is considered a new genus (Uzuhashi *et al.* 2010). The remaining clades, i.e., E, F, G, and I, are now known as *Globisporangium* (Uzuhashi *et al.* 2010; Nguyen *et al.* 2022), which are thoroughly discussed below.

Taxonomic status of the genus *Globisporangium*

The genus *Globisporangium* is recognized to produce globose to subglobose sporangia or hyphal swellings (Fig. 1). Most species do not produce any vesicle or zoospores as their asexual spores. Those species producing sporangia might sometimes have proliferated ones. Based on rDNA D1/D2 (18S) and *cox2* loci sequences, the genus *Pythium sensu lato* was split into five clades, 1 – 5 (Uzuhashi *et al.* 2010). The phylogenetic analyses results were in agreement with the sporangial morphology. Clade 4 was considered *Globisporangium*, which contained the previously described species within the clades E, F, G, and I of *Pythium sensu lato* (Lévesque & de Cock 2004). This genus is the largest group of the previously so-called *Pythium*, containing more than 80 species (Uzuhashi *et al.* 2010; Hyde *et al.* 2014; Nguyen *et al.* 2022). Even though the name *Globisporangium* was proposed by Uzuhashi and his colleagues in 2010 and it sounds morphologically, due to the lack of phylogenetic support, the researchers were reluctant to use this term, as well as other proposed genera names for the new classification. However, using the whole genome sequencing of 108 species assigned to the genus *Pythium sensu lato*, researchers confirmed that the names, *Elangisporangium*, *Globisporangium*, and *Pythium* are valid, and most be used from now on (Nguyen *et al.* 2022). *Globisporangium* has been reported several times worldwide. In Iran, there are also some reports of the genus available from different hosts and substrates (Table 1).

***Globisporangium* species as plant pathogens**

Most *Globisporangium* species are known to be plant pathogens worldwide. Some species are considered very aggressive plant pathogens with a wide host range. For instance, *G. ultimum* var. *ultimum* (Trow) Uzuhashi, Tojo & Kakish, and *G. ultimum* var. *sporangiiferum* (Drechsler) Uzuhashi, Tojo & Kakish all have wide host range causing root and crown rot on food crops (e.g., *Beta vulgaris* L.), ornamental crops (e.g., *Hydragena* sp.), and turf grasses and are responsible for significant economic loss in agriculture. These two varieties are members of *G. ultimum* (Trow) Uzuhashi, Tojo & Kakish species complex (see next sections) (Eggertson 2012). *Globisporangium ultimum* var. *ultimum*, and *G. ultimum* var. *sporangiiferum* are separated from each other based solely on their sporangial production and show no significant differences in other features, such as pathogenicity. While *G. ultimum* var. *sporangiferum* has only reported from *Actinia chinensis* Plunch. and turfgrass in Iran, it has wider host range worldwide (Ingram *et al.* 1990; Balk 2014). *Globisporangium ultimum* species complex has been reported several times in Iran on several plant species from various families (Table 1).

The second most important *Globisporangium* species is undeniably *G. irregulare* species complex causing root rot and seedling damping-off in a variety of plants worldwide and in Iran. The most important hosts of this species reported from Iran are *Aptenia cordifolia* Schwantes, *B. vulgaris*, *C. sativus*, *Salvia officinalis* L., and *Zinnia elegans* Jacq. Other species have rarely been reported from Iran and have a limited host range (Table 1).

***Globisporangium* species as antagonists**

Even though most *Globisporangium* species are categorized as plant pathogens, few and yet frequent reports of antagonistic species are available. With the first description of *G. nunn* (Lifsh., Stangh. & Baker) Uzuhashi, Tojo & Kakish 2010, it was revealed that this species has potential antagonistic activities against other plant pathogens (Paulitz & Baker 1987). *Globisporangium nunn* produces smooth oogonium with up to three antheridia per oogonium (Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017). Different reports of sporangial production of this species are available. The first reports revealed that this species produces two types of strains, i.e., the strains with sporangium and the strains lacking sporangium or hyphal swellings. In either case, none of the isolates could produce vesicles or zoospores (Kobayashi *et al.* 2010). In Iran, both cases have been observed in three different studies (Bolboli & Mostowfizadeh-Ghalamfarsa 2016; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019). Even though the rare distribution of *G. nunn* has been reported worldwide (Lévesque & de Cock 2004), recent studies showed that *G. nunn* is more abundant in Iran than expected. The antagonistic activity of *G. nunn* has been tested several times against *P. ultimum* var. *ultimum*, *Ph. cinnamomi* Rands, *Ph. citrophthora* Smith, *Ph. parasitica* Dastur, *Rhizoctonia solani* Kühn (Paulitz & Baker 1987; Fang & Tsao 1994; Kobayashi *et al.* 2010). *Globisporangium nunn* is the only antagonist among all *Globisporangium* species; however, it is considered one of the most important antagonists worldwide. This species is known to coil around the mycelium of the hosts, penetrate them, and lyse them by its lysing enzyme production (Paulitz & Baker 1987; Paulitz & Baker 1990). Nevertheless, it is not as

aggressive as *P. oligandrum* regarding its antagonistic activities (Kobayashi *et al.* 2010).

Table1. List of *Globisporangium* species reported from Iran

Species[1]	Matrix	Location[2]	Reference
G. attrantheridium (Allain-Boulé & Lévesque) Uzuhashi, Tojo & Kakish [*P. attrantheridium*, F]			
	Soil	Urmia	Badali *et al.* 2016
G. carolinianum (Mattews) Uzuhashi, Tojo & Kakish [*P. carolinianum*, E]			
	Beta vulgaris (rhizosphere)	West Azerbaijan (Khoy)	Badali *et al.* 2016
	Cupressus sempervirens (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Morus alba (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Prunus persica (rhizosphere)	Urmia	Badali *et al.* 2016
	Solanum lycopersicum (rhizosphere)	Urmia	Badali *et al.* 2016
	Zea mays (rhizosphere)	Fars (Mamasani)	Bolboli & Mostowfizadeh-Ghalamfarsa 2015
G. coniferarum Salmaninezhad & Mostowf. [G]			
	Cupressus arizonica (root tissue)	Fars (Shiraz)	Salmaninezhad *et al.* 2022
	Cupressus sempervirens (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2022
	Pinus elderica (crown tissue)	Fars (Shiraz)	Salmaninezhad *et al.* 2022
	Quercus sp. (crown tissue)	Fars (Shiraz)	Salmaninezhad *et al.* 2022
G. debaryanum species complex (Hesse) Uzuhashi, Tojo & Kakish [*P. debaryanum*, F]			
	Lens esculenta (rhizosphere)	Khuzestan (Dezful)	Ershad 1977
	Oryzae sativa (rhizosphere)	Fars (Kamfiruz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017
G. echinulatum (Mattews) Uzuhashi, Tojo & Kakish [*P. echinulatum*, E]			
	Citrus aurantium (roots)	Fars (Shiraz, Zarqan)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Cucumis sativus (rhizosphere)	Khorasan Razavi (Mashhad)	Askari Farsangi *et al.* 2011
	Soil	Khorasan Razavi (Mashhad)	Askari Farsangi *et al.* 2011
G. ershadii (Badali, Abrinbana, Abdollahz.) Nguyen *et al.* [*P. ershadii*, E]			
	Soil	East Azerbaijan	Abrinbana *et al.* 2017
G. glomeratum (Paul) Uzuhashi, Tojo & Kakish [*P. glomeratum*, I]			
	Prunus dulcis (rhizosphere)	West Azerbaijan (Eshnouye)	Badali *et al.* 2016
G. heterothallicum (Camp. & Hendrix) Uzuhashi, Tojo & Kakish [*P. heterothallicum*, I]			
	Triticum aestivum	Fars	Ravanlou & Banihashemi 2002
G. intermedium species complex (Mattews) Uzuhashi, Tojo & Kakish 2010 [*P. intermedium*, F]			
	Begonia seperflorens (rhizosphere)	Tehran	Ershad 1977
	Beta vulgaris	Khorasan	Afzali & Ershad 2006
	Prunus persica (rhizosphere)	Kermanshah	Azizi *et al.* 2012
G. iranense (Badali, Abrinbana & Abdollahz.) Nguyen *et al.* [*P. iranense*, J]			
	Soil	West Azerbaijan (Maku)	Badali *et al.* 2020
	Aptenia cordifolia	Fars (Shiraz)	Sabahi & Banihashemi 2013
	Beta vulgaris	Khorasan	Afzali & Ershad 2006
G. irregulare species complex (Buisman) Uzuhashi, Tojo & Kakish [*P. irregulare*, F]			
	Chamaecyparis lawsoniana (crown)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Cupressus sempervirens (root)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Phoenix canariensis (rhizosphere)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019

Table 1. Continued.

Species[1]	Matrix	Location[2]	Reference
G. irregulare species complex (Buisman) Uzuhashi, Tojo & Kakish [*P. irregulare,* F]			
	Pyrancantha coccinea (root)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Salvia officinalis	Hamadan	Abad *et al.* 2013
G. kandovanense (Chenari Bouket, Arzanlou, Tojo, Babai-Ahari) Nguyen & Spies [*P. kandovanense,* E]			
	Lolium perenne	East Azerbaijan	Chenari-Bouket *et al.* 2015
G. macrosporum (Vaartaja & Plaäts-Nit.) Uzuhashi, Tojo & Kakish [*P. macrosporum,* F]			
	Rosa hybrida	Hamadan	Abad *et al.* 2013
G. monoclinum (Abrinbana, Abdollahz. & Badali) Nguyen & Spies [*P. monoclinum,* Unknown]			
	Soil	East Azerbaijan	Badali *et al.* 2020
G. marsipium (Dreschler) Uzuhashi, Tojo & Kakish [*P. marsipium,* E]			
	Oryzae sativa (nursery soil)	Fars (Arsenjan, Kamfiruz)	Bolboli & Mostowfizadeh-Ghalamfarsa 2016
G. proliferatum (Cornu) Kirk [*P. middletonii,* E]			
	Beta vulgaris	West Azerbaijan (Khoy)	Badali *et al.* 2016
	Cucumis sativus	Kerman (Jiroft)	Hatami *et al.* 2010
	Cupressus sempervirens (rhizosphere, root)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
G. minor (Ali-Shtayeh) Uzuhashi, Toja & Kakish [*P. minor,* E]			
	Capsicum annuum (rhizosphere)	West Azerbaijan	Badali *et al.* 2016
G. nodosum (Paul, Galland, Bhatn. & Dulieu) Uzuhashi, Tojo & Kakish [*P. nodosum,* J]			
	Cuppressus sempervirens (roots)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Prunus armeniaca (rhizosphere)	West Azerbaijan (Maku)	Badali *et al.* 2016
G. nunn (Lifsh., Stangh. & Baker) Uzuhashi, Tojo & Kakish [*P. nunn,* J]			
	Acer pseudoplatanus (rhizosphere)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Beta vulgaris (rhizosphere)	West Azerbaijan (Khoy, Naqadeh)	Badali *et al.* 2016
G. nunn (Lifsh., Stangh. & Baker) Uzuhashi, Tojo & Kakish [*P. nunn,* J]			
	Cupressus arizonica (rhizosphere)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Helianthus annuus (rhizosphere)	West Azerbaijan (Khoy)	Badali *et al.* 2016
	Oryzae sativa (root)	Fars (Kamfiruz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017
	Prunus persica (rhizosphere)	Urmia	Badali *et al.* 2016
	Solanum lycopersicum (rhizosphere)	West Azerbaijan (Khoy)	Badali *et al.* 2016
	Zea mays (field soil)	Fars (Sormaq)	Bolboli & Mostowfizadeh-Ghalamfarsa 2016
	Vitis vinifera (rhizosphere)	West Azerbaijan (Sardasht)	Badali *et al.* 2016
G. okanoganense (Lipps) Uzuhashi, Tojo & Kakish [*P. okanoganense,* G]			
	Beta vulgaris	Tehran	Khodashenas Roudsari *et al.* 2010
	Pinus elderica	Fars (Shiraz, Zarqan)	Hamzeh Zarqani *et al.* 2010
	Soil	Khuzestan	Zamani Noor *et al.* 2004

Table 1. Continued.

Species[1]	Matrix	Location[2]	Reference
G. okanoganense (Lipps) Uzuhashi, Tojo & Kakish [*P. okanoganense*, G]			
	Turfgrass	Tehran	Khodashenas Roudsari *et al.* 2010
G. orthogonon (Ahrens) Uzuhashi, Tojo & Kakish [*P. orthogonon*, J]			
	Triticum aestivum (field soil)	Fars	Mostowfizadeh-Ghalamfarsa & Banihashemi 2005
G. paroecandrum (Dreschler) Uzuhashi, Tojo & Kakish [*P. paroecandrum*, F]			
	Beta vulagris (rhizosphere)	West Azerbaijan	Babai-Ahari *et al.* 2004
	Cupressus sempervirens	Fars (Zarqan)	Zakeri *et al.* 1995
G. paroecandrum (Dreschler) Uzuhashi, Tojo & Kakish [*P. paroecandrum*, F]			
	Papaver somniferum	Fars, Tehran	Z. Banihashemi, Personal Communication, Ershad 1977
	Solanum lycopersicum (soil)	West Azerbaijan	Badali *et al.* 2014
	Soil	Razavi Khorasan	Askari Farsangi *et al.* 2011
G. perplexum (Kouyeas & Theoh.) Uzuhashi, Tojo & Kakish [*P. perplexum*, J]			
	Petunia sp.	Hamadan	Abad *et al.* 2013
	Rosa hybrida	Hamadan	Abad *et al.* 2013
G. pyrioosporum (Abdollahz., Badali & Abrinbana) Nguyen [*P. pyrioosporum*, E]			
	Soil	West Azerbaijan	Abarinbana *et al.* 2017
G. rostratum species complex (Butler) Uzuhashi, Tojo & Kakish [*P. rostratum*, E]			
	Pelargonium zonale	Fars (Shiraz)	Sabahi & Banihashemi 2013
	Soil	Fars (Bajgah)	Mostowfizadeh-Ghalamfarsa & Banihashemi 2005
G. salinum (Höhnk) Uzuhashi, Tojo & Kakish [*P. salinum*, Unknown]			
	Atropa belladonna	Hamadan	Abad *et al.* 2013
	Beta vulgaris	Khuzestan	Zamani Noor *et al.* 2004
G. ultimum species complex (Trow) Uzuhashi, Tojo & Kakish [*P. ultimum*, I]			
	Begonia semperflorens	Tehran	Ershad 1977
	Beta vulgaris	Alborz (Karaj)	Arzanlou *et al.* 2000
	Beta vulgaris	Kermanshah, West Azerbaijan	Younesi & Ravanlou 2004
	Beta vulgaris	Razavi Khorasan	Azimian *et al.* 2011
	Brassica napulus	Isfahan (Kashan)	Afshari-Azad *et al.* 2008
	Carthamus tinctorius	Tehran	Ershad 1977
	Carthamus tinctorius	West Azerbaijan	Afshari-Azad *et al.* 2008
	Cicer arietinum	Khuzestan (Dezful)	Vaziri 1973
	Cicer arietinum	Kurdistan	Amini 2006
	Cucumis sativus	Kerman (Jiroft)	Hatami *et al.* 2010
	Cucumis sativus	Tehran	Ershad 1977
	Cucumis sativus	Razavi Khorasan	Azimi *et al.* 2011
	Cupressus arizonica	Fars (Zarqan)	Zakeri *et al.* 1995
	Euphorbia pulcherrima	Mazandaran (Kelarabad)	Ershad 1977
	Fragaria ananassa	Kurdistan	Amini 2008
	Gossypium herbaseum	Isfahan (Isfahan)	Ershad 1977
	Hibiscus esculentus	Tehran	Ershad 1977
	Lens esculenta	Tehran	Kaiser *et al.* 1968
	Lycopersicum esculentum	East Azerbaijan (Marand)	Pouzeshi Miab *et al.* 2012
	Lycopersicum esculentum	North Khorasan (Garmkhan)	Azimian *et al.* 2011
	Lycopersicum esculentum	Semnan (Bastam, Damghan)	Ommati & Ershad 2004
	Orchidaceae	Tehran (Tehran)	Ershad 1977
	Phaseolus aureus.	Khuzestan (Dezful)	Vaziri 1973
G. spinosum species complex (Sawada) Uzuhashi, Tojo & Kakish [*P. spinosum*, F]			
	Cynodon dactylon (rhizosphere)	East Azerbaijan (Hashtroud)	Bouket *et al.* 2016
G. splendens (Hans Braun) Uzuhashi, Tojo & Kakish [*P. splendens*, I]			
	Papaver somniferum	Fars	Z. Banihashemi, Personal Communication

Table1. Continued.

Species[1]	Matrix	Location[2]	Reference
G. ultimum species complex (Trow) Uzuhashi, Tojo & Kakish [*P. ultimum*, I]			
	Phaseolus vulgaris	Chahar Mahaal & Bakhtiari	Heidarian & Ershad 2002
	Solanum tuberosum	Semnan	Zaker 2008
	Triticum aestivum	Ilam, Lorestan, Markazi, Zanjan	Mansoori *et al.* 2002
	Triticum aestivum	Tehran	Amini *et al.* 1998
	Triticum aestivum	West Azerbaijan	Ravanlou 2000
G. ultimum* var. *sporangiiferum (Drechsler) Uzuhashi, Tojo & Kakish [*P. ultimum* var. *sporangiiferum*, I]			
	Actinidia chinesis	Fars (Shiraz)	Barzegar Marvasti & Banihashemi 2011
	Actinidia chinesis	Gilan, Mazandaran	Taheri *et al.* 2008
	Medicago sativa (rhizosphere)	Sardasht	Badali *et al.* 2016
	Solanum lycopersicum (rhizosphere)	West Azerbaijan (Khoy)	Badali *et al.* 2016
	Turfgrass	Fars (Shiraz)	Barzegar Marvdasti & Banihashemi 2011
G. ultimum* var. *ultimum (Trow) Uzuhahsi, Tojo & Kakish [*P. ultimum* var. *ultimum*, I]			
	Atropa belladonna	Hamadan	Abad *et al.* 2010
	Beta vulgaris	Ardabil (Ardabil), West Azerbaijan (West Azerbaijan (Khoy), Miandoab)	Babai-Ahari 2004
	Beta vulgaris	Hamadan	Kashi *et al.* 2000
	Beta vulgaris	Khorasan	Afzali & Ershad 2006
	Citrullus lanatus	Razavi Khorasan (Sarakhs, Torbat-e-Heydarieh, Torbat-e-Jam)	Askari Farsangi *et al.* 2011
	Caspicum annuum (rhizosphere)	West Azerbaijan (West Azerbaijan (Khoy))	Badali *et al.* 2016
	Crocus sativus	Razavi Khorasan	Afzali 2004
	Cucumis melo	Razavi Khorasan	Askari Farsangi *et al.* 2011
	Cucumis sativus	Hamadan	Abad *et al.* 2013
	Cucumis sativus	Razavi Khorasan	Askari Farsangi *et al.* 2011
	Cucurbita pepo	Razavi Khorasan (Mashhad, Quchan, Sarakhs)	Askari Farsangi *et al.* 2011
	Juglans regia	Hamadan	Abad *et al.* 2013
	Lycopersicum esculatum	Hamadan	Abad *et al.* 2013
	Lycopersicum esculatum	Razavi Khorasan	Askari Farsangi *et al.* 2011
	Malus domestica	Hamadan	Abad *et al.* 2013
	Nicotiana tabacum	Golestan	Sajjadi & Assemi 2012
	Phaseolus vulagris	Hamadan	Abad *et al.* 2013
	Solanum melongena	Razavi Khorasan (Chenaran, Fariman, Kashmar, Mashhad, Quchan, Sabzevar)	Abad *et al.* 2013
	Solanum lycopersicum (rhizosphere)	Urmia	Badali *et al.* 2016
G. stipitatum (Karaka & Paul) Nguyen & Spies [*P. stipitatum*, E]			
	Solanum lycopersicum (rhizosphere)	West Azerbaijan (Khoy)	Badali *et al.* 2016
G. sylvaticum species complex (W.A. Campb. & F.F. Hendrix) Uzuhashi, Tojo & Kakish [*P. sylvaticum*, F]			
	Pinus mugo	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019

Table 1. Continued.

Species[1]	Matrix	Location[2]	Reference
G. ultimum* var. *ultimum (Trow) Uzuhahsi, Tojo & Kakish [*P. ultimum* var. *ultimum*, I]			
	Soil	Razavi Khorasan (Chenaran, Fariman, Mashhad, Sabzevar, Sarakhs, Torbat-e-Heydarieh, Torbat-e-Jam)	Askari Farsangi *et al.* 2011
	Soil	West Azerbaijan	Badali & Abrinbana 2013
	Solanum tuberosum	Hamadan	Abad *et al.* 2013
	Triticum aestivum	Fars	Ravanlou & Banihashemi 2002
G. urmianum (Abrinbana, Badali & Abdollahz.) Nguyen *et al.* [*P. urmianum*, E]			
	Soil	West Azerbaijan	Abrinbana *et al.* 2017
	Cuppressus sempervirens (rhizosphere)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
	Pinus elderica (root)	Fars (Shiraz)	Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019
G. viniferarum (Paul) Nguyen & Spies [*P. viniferarum*, F]			
	Capsicum annuum (rhizosphere)	Urmia	Badali *et al.* 2016
G. yorkense (Blair, Nguyen, Spies) Nguyen *et al.* [*P. yorkense*, J]			
	Cupressus sempervirens (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Eucalyptus oliqua (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Melaleosa citrina (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Morus alba (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Phoenix canariensis (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Pinus elderica (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021
	Salix sp. (rhizosphere)	Fars (Shiraz)	Salmaninezhad *et al.* 2021

[1.] *Globisporangium* species [*Pythium sensu lato* name, Clade *sensu* Lévesque & de Cock 2004]
[2.] Province (place)

Challenges in morphological identification of *Globisporangium* species

Accurate identification of isolates is an essential step for understanding the precise biology of *Globisporangium* species and characterizing the evolutionary relationships among them. Although molecular tools have facilitated the identification process, using morphological features in identification is inevitable. Morphological identification of a particular species has always been problematic for researchers, and *Globisporangium* species are no exception. Classification of this genus has always been challenging due to difficulties in isolation of certain species, the lack of identification data for species, and the identification of morphological features of different species. Hence, Hence, it is quite challenging to identify *Globisporangium* species based solely on their morphological characteristics. This difficulty would enhance due to the low number of typical isolates, non-homothallic species, sexually sterile isolates, similar morphological features among different species groups, and considerable fluctuations in sexual and asexual structures' size and shapes within species (Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020). Moreover, while the morphological classification of the genus *Globisporangium* has been used as a traditional tool to the plant pathologists, it has been confirmed that several morphological species are polyphyletic assemblages (Villa *et al.* 2006).

One of the major concerns of the taxonomists is the recovering of both pathogenic and saprophyte *Globisporangium* species. Because most plant pathologists prefer to obtain information about the plant pathologists, or in rare cases, antagonists, little information would be acquired about saprobic or marine species (Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020). Hence, the current reported number of oomycetes, and in particular, *Globisporangium* species, does not reflect the true number of species. Furthermore, most species could not be easily isolate from soil or plant material, and if they do, they might not produce the required structures for the morphological identification (Kageyama 2014; Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020).

Globisporangium species can show different growth patterns on different media. In other words, the growth pattern is considered an important factor in morphological identification. Nevertheless, even

multiple strains of a single species show variations in their growth habit. Consequently, specific identification of a particular *Globisporangium* species should not rely merely on its growth rate and pattern (Zitnick-Anderson 2013; Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020).

Morphological identification and classification of *Globisporangium* species could be quite challenging due to several reasons. Lacking certain structures is one of the most important obstacles in recognizing *Globisporangium* species. Most *Globisporangium* species do not produce any zoospores (Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019) or in rare cases, such as *G. nunn*, any sporangia (Uzuhashi *et al.* 2010; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017). This could cause serious problems with species that do not produce any sexual structures readily, such as *G. heterothallicum* (Campb. & Hendrix) Uzuhashi, Tojo & Kakish, which makes it quite difficult to identify based on morphological features (Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020). Moreover, species such as *G. heterothallicum* is morphologically very similar to its closely related species, *G. glomeratum* (Paul) Uzuhashi, Tojo & Kakish. These two species cannot be morphologically delimitated (Paul 2003).

Having multiple variations of a specific morphological feature is called pleomorphism which has been reported several times from *Pythium sensu lato* species and specifically *Globisporangium* spp. Pleomorphism is considered one of the significant obstacles to the morphological characterization of a particular species. Take *G. multisporum* (Poitras) Uzuhashi, Tojo & Kakish as an example. This species produces different types of sporangia, i.e., subglobose, globose, oblong, and limoniform, as well as both monoclinous and diclinous antheridia (Van der Plaäts-Niterink 1981). In Iran, *G. irregulare* (Buisman) Uzuhashi, Tojo & Kakish producing both smooth and ornamented oospores is an excellent example of pleomorphism and the challenges posed through the morphological identification of a certain *Globisporangium* species (Badali *et al.* 2016).

Species complex is another major problem in the morphological identification of a *Globisporangium* species. The term "species complex" is usually used in taxonomy regarding three main situations: I. It is believed that a group of organisms may represent more than one species; II. No species boundaries could be discerned with certainty, *e.g.*, because of morphological similarity or insufficient data; and III. It is hypothesized that these species are related in some way. *Globisporangium debaryanum* (Hesse) Uzuhashi, Tojo & Kakish, *G. intermedium* (de Bary) Uzuhashi, Tojo & Kakish, *G. irregulare*, *G. rostratum* (Hendrix & Papa) Uzuhashi, Tojo & Kakish, *G. spinosum* (Sawada) Uzuhashi, Tojo & Kakish, and *G. sylvaticum* (Campbel & Hendrix) Uzuhashi, Tojo & Kakish and *G. ultimum* are species complexes reported from Iran (Babai-Ahary *et al.* 2004; Bouket *et al.* 2016; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019; Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020, Salmaninezhad *et al.* 2021). Some of the *Globisporangium* species complex problems have been resolved in recent years. For instance, using a multiple gene genealogy approach, researchers could successfully resolve the problem of *G. ultimum* complex, which is now known as *G. ultimum* var. *ultimum* and *G. ultimum* var. *sporangiiferum* (Eggertson 2012). Even though attempts addressed the problem of *G. intermedium* and *G. irregulare* complexes, some skepticism remained. For instance, using a multiple gene genealogy approach, *G. intermedium* has been divided into three main groups, including *G. intermedium*, *G. attrantheridium* (Allain-Boulé & Lévesque) Uzuhashi, Tojo & Kakish, and another yet unresolved group (Li *et al.* 2021). The problem remains for *G. irregulare*, which has been split into three main groups, i.e., *G. irregulare sensu stricto*, *G. cryptoirregulare* (Garzón, Yánez & G.W. Moorman) Uzuhashi, Tojo & Kakish, and *G. irregulare sensu lato.* The status of *G. irregulare sensu lato* is still a challenge for the taxonomists because it contains *G. regulare* (Paul) Uzuhashi, Tojo & Kakish, and *G. cylindrosporum* (Paul) Uzuhashi, Tojo & Kakish (Spies *et al.* 2011).

Despite these challenges in the identification, there are some other taxonomic obstacles in identifying different *Globisporangium* species. Lack of valid morphological identification keys, lack of certain species morphological descriptions, illustrations, imageries, and morphometric data sets are some of the problems facing an oomycete taxonomist dealing with *Globisporangium* species identification especially those who work in Iran. In addition, most species have only been reported once or, in rare cases, twice in the country, for example, *G. urmianum*, *G. nunn*, and *G. carolinianum* (Bolboli & Mostowfizadeh-Ghalamfarsa 2016; Abrinbana *et al.* 2016; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017; Salmaninezhad *et al.* 2021). Furthermore, metadata recordings of the recovered *Globisporangium* species are unavailable for several isolates. Only in recent comprehensive studies, metadata recordings, such as matrices, host information, location coordinates, and date of isolation are mentioned (Abrinbana *et al.* 2016; Badali *et al.* 2016; Bolboli & Mostowfizadeh-Ghalamfarsa 2016; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019). Besides, host information is quite important in the recordings and generalization of the host names, such as turf grass, cucumber, etc., could be problematic in future studies. Moreover, most papers are still using the previous names of the species assigned to *Globisporangium* as *Pythium*, which is false. Recent studies strongly urged the authors to correctly use *Globisporangium* for the species previously known as *Pythium* clade E, F, G, and I (Uzuhashi *et al.* 2010; Nguyen *et al.* 2022).

Challenges in molecular barcodes for identification of *Globisporangium* species

The ITS region of the rDNA has been exclusively used for all oomycetes identification. Using this region for identification provides several advantages, such as the availability of many sequences in public databases, ease of the amplification, and interspecific variation level (Robideau *et al.* 2011; Mostowfizadeh-Ghalamfarsa & Salmaninezhad 2020). However, using the ITS region cannot solely differentiate *Globisporangium* species. Besides, in rare cases, the ITS region amplification and sequencing would be difficult. For instance, there are some records from Iran that some novel *Globisporangium* species do not show high-quality ITS sequences despite several attempts using different primers due to some unexpected indels in their spacer regions (Salmaninezhad *et al.* 2022). One could resolve this problem by cloning the PCR products of the ITS region. Apart from the ITS region, other genes, such as cytochrome oxidase c subunit I (*cox1*) can be used for species identification in *Globisporangium*. Nevertheless, no universal DNA barcode for *Globisporangium* species has been introduced. Most *Globisporangium* species cannot be identified even using ITS and *cox1* loci simultaneously. It seems that using multiple gene genealogies phylogenetic approach could be a time-consuming but accurate answer. Recently, several species assigned to *Globisporangium* have been reported from Iran, e.g., *G. debaryanum, G. irregulare, G. nodosum* (Paul) Uzuhashi, Tojo & Kakish, *G. yorkense* (Blair) Nguyen & Spies, *G. nunn*, *G. urmianum* (Abrinbana, Badali & Abdollahz.) Nguyen & Spies, and *G. carolinianum* (Matthews) Uzuhahsi, Tojo & Kakish (Badali *et al.* 2016; Bolboli & Mostowfizadeh-Ghalamfarsa 2016; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2017; Salmaninezhad & Mostowfizadeh-Ghalamfarsa 2019; Salmaninezhad *et al.* 2021). None of the mentioned species can be separated using both ITS and *cox1* loci. Hence, using other loci such as cytochrome oxidase c subunit II (*cox2*) and beta-tubulin (*Btub*) would also help resolve this problem (Salmaninezhad *et al.* 2021).

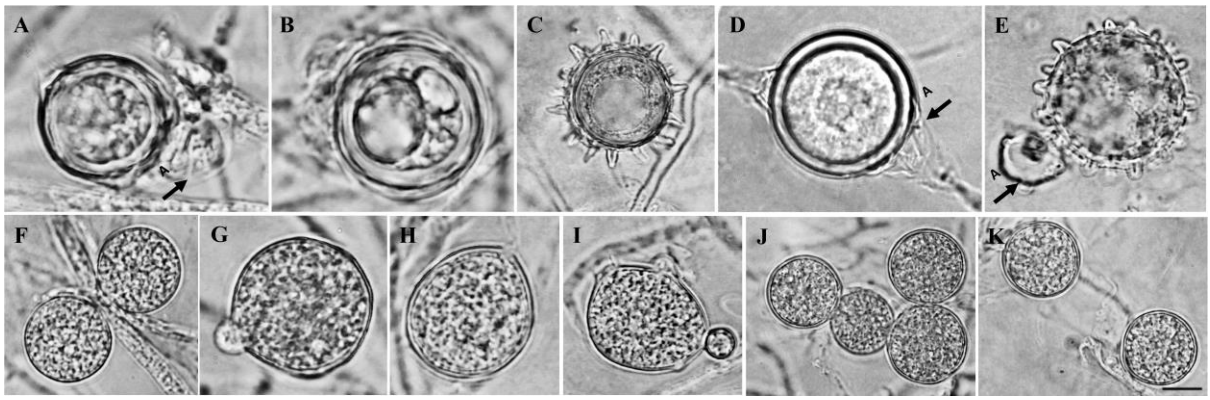

Fig 1. Morphological characteristics of *Globisporangium* species from Iran. A-E: Sexual structures (oospores). A: Mostly plerotic oospores with paragynous antheridium in *G. sylvaticum;* B: aplerotic oospore in *G. middletonii;* C: Ornamented oospore in *G. echinulatum;* D: hypogynous antheridium in *Globisporangium* sp.; E: Ornamented oospore with a paragynous antheridium in *G. echinulatum*; F-K: Asexual structures. F: Hyphal swellings in *Globisporangium* sp.; G-I: Various types of sporangia in *G. yorkense;* J: Terminal chlamydospores in *Globisporangium* sp.; K: intercalary chlamydospores in *Globisporangium* sp. Bar = 10 µm.

CONCLUSION

This study highlights the current taxonomic status of *Globisporangium* species in Iran and the challenges to its morphological and molecular identification. According to the recent studies, we conclude that, in general, Iran, as a four-season country, is an oomycete-rich area with a potential for the existence of new taxa. Among all the oomycetes, *Globisporangium* genus containing more than 80 described species could be of great significance. There are several reports of the isolation of *Globisporangium* species, regardless of their lifestyles, from Iran, which highlights the importance of this species in agricultural and forest studies. However, fast and accurate identification of these species is of great importance because researchers could address the problem in a proper time for disease management, especially in the case of *G. ultimum*, *G. ultimum* var. *sporangiiferum*, and *G. ultimum* var. *ultimum*, due their aggressive nature as plant pathogens with vast host range.

In general, only a few studies focused on the comprehensive species description of *Globisporangium* species from limited areas of Iran, so it is important to conduct more samplings from other parts of Iran, especially forests and ornamental trees. Ornamental trees have been shown to be a preferable host for *Globisporangium* species, especially new taxa. So, performing more samplings would result in the identification of new species assigned to *Globisporangium.* Due to the challenges in morphological and molecular identification of *Globisporangium* species,It is suggested that one should take extreme caution in using the correct name when describing new species. It is also essential that the researchers provide their morphological results together with the phylogenetic analyses to confirm their inferences. Moreover, it is important to have an updated morphological identification key with high-quality pictures and illustrations. Therefore, we call oomycete experts to design and objectively evaluate an interactive online key for identifying *Globisporangium* species. These electronic keys, especially when accompanied by geographical distribution maps, hosts metadata, and DNA barcode sequences, would take the identification process of the species to another level and resolve some of the challenges we are facing.

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وضعیت فعلی گونه‌های *Globisporangium* در ایران: از *Pythium sensu lato* تا گونه‌های توصیف شده‌ی اخیر

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چکیده: جنس *Globisporangium*، از آرایه‌های جدید توصیف شده، به تازگی از *Pythium sensu lato* تفکیک گردیده است. اگرچه مطالعات زیادی بر جداسازی گونه‌های این جنس از ایران تمرکز نداشته‌اند، تعدادی مطالعات جامع نشان داده‌اند که *Globisporangium* جنسی مهم با پراکنشی وسیع در این منطقه از جهان است. حتی گونه‌های نادری از *Globisporangium* در ایران یافت شده‌اند. علی‌رغم اهمیت این جنس، شناسایی دقیق و رده‌بندی *Globisporangium* در سراسر دنیا، چالش‌برانگیز است. شناسایی ریخت‌شناختی *Globisporangium* به دلیل فقدان کلیدهای تشخیصی، هم‌پوشانی برخی خصوصیات ریخت‌شناختی، وجود گونه‌های مرکب، چندشکلی ساختاری و نبود ساختارهای مشخص در برخی گونه‌ها، بسیار دشوار است. علاوه بر این، هنوز هیچ بارکد دی‌اِن‌ای عمومی برای گونه‌های *Globisporangium* وجود ندارد و اکثر گونه‌ها را نمی‌توان تنها با یک یا دو ژن‌گاه با واکاوی‌های فیلوژنتیکی تفکیک کرد. به علاوه، برخی مطالعات در ایران به منظور تأیید شناسایی ریخت‌شناختی یا شناسایی مجدد گونه‌های گزارش شده، هیچ‌گونه بررسی مولکولی انجام نداده‌اند. فقدان فهرست گونه‌های گزارش شده نیز به این مشکل افزوده است. تمرکز نقد حاضر روی سیستماتیک گونه‌های *Globisporangium* در ایران با تأکید بر چالش‌های شناسایی ریخت‌شناختی و مولکولی این گونه‌ها در کشور قرار دارد؛ همچنین راه‌کارهایی را برای حل این مشکلات، بحث و پیشنهاد کرده است.

کلمات کلیدی: اُمیکوتا، بوم‌شناسی، بیمارگرهای گیاهی، تنوع، سیستماتیک

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