

Arbuscular mycorrhizal fungi (*Glomeromycota*) of the Vistula Bar

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Błaszowski J., Adamska I., Czerniawska B.: *Arbuscular mycorrhizal fungi (Glomeromycota) of the Vistula Bar*. Acta Mycol. 37 (1/2): 39–62, 2002.

The occurrence of arbuscular mycorrhizal fungi (AMF) of the, phylum *Glomeromycota* associated with plants of maritime sand dunes of the Vistula Bar located in north-eastern Poland was investigated. The presence of AMF was revealed based on spores isolated from field-collected root-rhizosphere soil mixtures and two-cycle pot trap cultures established with parts of these mixtures. The mixtures came from under five species in four plant families. Spores of AMF occurred in 54.8% of the field samples and belonged to eight species. Additionally, culturing of root-soil mixtures in trap cultures revealed nine species and three undescribed morphotypes earlier not found in the field samples. Considering the number of records of species and morphotypes in the field samples and trap cultures, the fungal species most frequently occurring in dunes of the Vistula Bar is *Scutellospora dipurpurens*, followed by *Archaeospora trappei*, *Glomus laccatum*, and *Scu. armeniacae*. The overall average spore abundance in the field samples is low (4.48, range 0–31 in 100 g dry soil). The overall average species richness determined based on spores from both the field and trap cultures was 2.1 and ranged from 0 to 7 in 100 g dry soil. The plant harbouring the highest number of species of AMF was *Festuca rubra*. Of the maritime dune sites of Poland examined to date, the species composition of AMF of the Vistula Bar is most similar to that of the Słowiński National Park. When the comparisons included 15 maritime dune areas located outside Poland, the highest similarity occurred in the Vistula Bar/Canada comparison.

Key words: arbuscular mycorrhizal fungi, maritime dunes, occurrence, Vistula Bar

INTRODUCTION

Continuing investigations of the occurrence of arbuscular mycorrhizal fungi (AMF) in sand dune soils of Poland (Błaszowski 1993, 1994; Błaszowski, Tadych and Madej 2002; Tadych and Błaszowski 2000), the next area considered was the Vistula Bar.

The Vistula Bar is a narrow, sandy peninsula of a total length of ca. 90 km and a width of 1 to 2 km (Kondracki 1998). About 55 km and 193 km² of its length and area, respectively, belong to Poland, and the other part to the Kaliningrad district of

Russia. The Vistula Bar was created due to the influence of waves and the drift of sands coming from the abrasion of the shores of the Sambii Peninsula, Russia. These sands formed dunes of a height of extending 30 m. The northern border of the Vistula Bar is the shore of the Gdańsk Bay, and the southern one that of the Vistula Bay.

One of the most widely distributed fungal groups are arbuscular mycorrhizal fungi (AMF) of the order Glomerales, phylum Glomeromycota (Schüßler, Schwarzot and Walker 2001). These fungi are obligate symbionts co-occurring with most vascular plants (Smith and Read 1997).

The sites especially favouring the occurrence of abundant and diverse communities of AMF are sand dunes (e.g., Błaszczowski 1993; Dalpé 1989; Giovannetti and Nicolson 1983; Koske 1987; Mohankumar et al. 1988; Nicolson and Johnston 1979; Stürmer and Bellei 1994; Tadych and Błaszczowski 2000; Błaszczowski et al. 2002), mainly because of the exceptionally low content of soil phosphorous (Koske 1988; Nicolson and Johnston 1979).

AMF comprehensively influence plant and environment. For example, they increase the root absorptive area and, thereby, the plant nutrition (Bielecki 1973), influence the succession and composition of plant communities (Janos 1980; Tadych and Błaszczowski 2000), their competitiveness (Allen and Allen 1984) and phenology (Allen and Allen 1986), equalize the level of nutrition of co-existing plants by formation of hyphal bridges transferring nutrients between them (Newman 1988), and improve soil structure through binding sand grains into aggregates by extramatrical hyphae (Koske, Sutton and Sheppard 1975). Additionally, AMF alleviate the influence of high concentrations of, e. g., NaCl (Hildebrandt et al. 2001), increase the resistance of plants to water shortage (Augé 2001), pathogenic fungi and nematodes (Schönbeck 1978), as well as significantly modify the numerical and qualitative composition of rhizosphere microorganisms (Marschner, Crowley and Lieberl 2001).

The soils contain more abundant and diverse communities of AMF, the their plant associations have more persistent obligate mycorrhizal plant species (Miller 1979; Reeves et al. 1979).

Few investigations aimed at the utilization of AMF in stabilization and restoration of dune areas showed that inoculation resulted in more rapid establishment of transplants, stimulating the formation of AM hyphal networks and consequently accelerated the succession and stabilization of dunes (Gemma and Koske 1997; Tadych and Błaszczowski 2000). However, the influence of AMF on plants varied depending on both the fungal species used and the plant species compared (Tadych and Błaszczowski 1999; Sylvia and Burks 1988). Generally, the AMF most effectively assisting plants were local ecotypes (Saif 1986).

However, the numerical and qualitative composition of AMF of different dune areas of the world highly differed (Błaszczowski 1993; Koske and Tews 1987). Additionally, recent investigations using the technique of trap cultures showed that many species of AMF associated with roots of dune plants do not sporulate in the field (Stutz and Morton 1996; Błaszczowski et al. 2002). Therefore, the aim of the investigations presented here was to determine the occurrence of AMF associated with dune plants of the Vistula Bar based on spores isolated from field-collected

root-soil samples and pot trap cultures. The disclosure of the dominating species will enable to utilize them in protection or restoration of endangered areas of the Bar.

MATERIALS AND METHODS

Study site. The study was conducted on maritime dunes of the Polish part of the Vistula Bar located in north-eastern Poland (54°24'N, 19°30'E; Fig. 1). The dunes considered were those adjacent to the Gdańsk Bay.

Climate. The Vistula Bar is located within the central and eastern part of the climatic region of the shore of the Gdańsk Bay (Herbich and Markowski 1998). The mean annual sum of rainfalls is 550 mm, and the average annual air temperature ranges from 7.1 to 7.5°C.

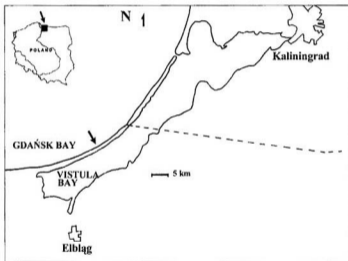


Fig. 1. Vistula Bar (arrow), from which root-rhizosphere soil samples were collected

Vegetation. Three plant associations consisting of ca. 370 taxa of vascular plants mainly represent the vegetation of the Vistula Bar (Piotrowska 1976; Piotrowska and Stasiak 1982). The wind-blow sand of white dunes is colonized by the *Elymo-Ammophiletum* Br.-Bl. et De Leeuw 1936 plant association. Apart from *Ammophila arenaria* Link and *Elymus arenarius* L., the plant species present in this association also are *Lathyrus japonicus* Willd. subsp. *maritimus* (L.) P. W. Ball, *Petasites spurius* (Retz.) Rechb., *Linaria odora* (M. Bieb.) Fisch., and *Festuca rubra* L. s. s.

The subsidiaries of the white dunes harbour the *Helichryso-Jasionetum litoralis* Libb. plant association with, e.g., *Artemisia campestris* var. *sericea* (Fr.) Lemke et Rothm., *Viola tricolor* L. s. s., and *Eryngium maritimum* L.

Carrying away from the shore of the Gdańsk Bay, the *Helichryso-jasionetum* plant association gradually transforms into *Empetro nigri-Pinetum* (Libb. et Siss. 1939 n.n.) Wojt. 1964 plant association.

Although the total number of plant species of the Vistula Bar is exceptionally high compared with that of other maritime dune areas, 84% of taxa are sporadic species, growing singly or in very sparse populations (Piotrowska and Stasiak 1984).

Collection of samples. Mixtures of roots and rhizosphere soils of randomly selected plants were collected on 19 July 1997. The mixtures were excavated from a depth of 5–30 cm using a small trowel. A 0.5–1.0-L mixture represented each plant. The mixtures were placed in plastic bags and then stored at 4°C for 2–6 months until processed.

Isolation, trap culture establishment, and identification of AMF. In the laboratory, 100 g of each of the root-soil mixture collected was used to determine the abundance of spores and the richness of species produced in the field. The other part was mixed with an autoclaved coarse-grained sand (1:1 v/v). The mixtures were placed in 0.5-L plastic pots and seeded with *Plantago lanceolata* L. Hence, each plant growing in the field was represented by one root-soil sample collected from the field and one trap culture.

The cultures were grown in a greenhouse for four months with supplemental 16-h lighting provided by sodic lamps placed 1 m above pots. Plants were watered 2–3 times a week. No fertilization was applied. At harvest, watering was terminated and the cultures were allowed to dry *in situ* for 2 weeks. Plant tops were cut and a 100-g root-soil mixture was taken from each pot. The pots with their contents were subsequently stored at 4°C for 2 months. After that time, ca. 100 g of an autoclaved dune sand was added to each pot to complete the growing medium. The medium was seeded with the same plant host and the cultures were grown in conditions similar to those described above for next 4 months. The second-cycle trap cultures were dried *in situ* and stored at 4°C for 2 months. Another 100-g root-soil mixture was taken from each pot.

Spores of AMF were isolated from the root-soil mixtures by wet sieving and decanting (Gerdemann and Nicolson 1963). Both intact and spores crushed in polyvinyl/alcohol/glycerin (PVLG) and a mixture of PVLG and Melzer's reagent were investigated.

The fungi were identified according to their original descriptions (Schenck and Pérez 1990), revisions (Morton 1995; Franke and Morton 1994; Stürmer and Morton 1997), information and specimens obtained from Prof. R. E. Koske (Rhode Island University, U.S.A.), Prof. J. M. Morton (West Virginia University, U.S.A.), Prof. J. M. Trappe (Oregon State University, U.S.A.), and Dr. C. Walker (U.K.). Vouchers of all the fungal species recovered are preserved in the authors' collections. Nomenclature of the fungi mentioned in this paper follows Walker and Trappe (1993). The classification is that of Schüßler et al. (2001). Colour names are from Kornerup and Wanscher (1983).

Statistical analysis. Differences in the structure of arbuscular fungal communities were investigated by determining the frequency of occurrence of species, spore abundance and species richness, and by calculating dominance coefficients (Górny and Gruma 1981) and total spore volumes. Spore abundance, coeffi-

clients of dominance, and the total volume of spores of each species recovered were determined based on spores isolated only from field-collected samples. Frequency of occurrence and species richness were calculated based on spores isolated from both field-collected samples and trap cultures. The accepted values were the highest ones of those regarding the occurrence of a given species in the field samples, as well as in the first- and second-cycle trap cultures. Frequency of occurrence was calculated by determining the percentage of field-collected samples and trap cultures from which spores of a particular species were recovered. Spore abundance and species richness were defined by determining the number of spores and species, respectively, occurring in 100 g dry soil. Dominance coefficient expresses the proportion of the number of spores of a particular species in all spores of AMF recovered. The total spore volume was calculated by multiplying the total number of spores of a given species by the average volume of individual spores. The average volume of spores was calculated from their average diameter and equation of a sphere.

RESULTS AND DISCUSSION

General data. The occurrence of AMF associated with plants of maritime dunes of the Vistula Bar was determined based on 31 rhizosphere soil and root mixtures collected in 1997. The mixtures represented five species in four plant families (Table 1). The plant family most frequently examined was the *Poaceae*. The plant species most frequently sampled was *Am. arenaria*, followed by *F. rubra* and *R. rugosa*.

Table 1

Plants examined and soil samples in which the occurrence of arbuscular mycorrhizal fungi was investigated

Plant species	Number of soil sample
<i>Arrhenathera arenaria</i>	1147, 1155, 1159, 1160-1163, 1166, 1167, 1169, 1173-1176
<i>Festuca rubra</i>	1146, 1148, 1153, 1156-1158, 1164
<i>Artemisia campestris</i>	1149
<i>Lathyrus japonicus</i> subsp. <i>maritimus</i>	1150
<i>Rosa rugosa</i>	1151, 1152, 1154, 1170-1172

Spores of AMF occurred in 17 field-collected soil-root samples, i. e., 54.8% of all the samples investigated. They represented three of the eight existing genera of the phylum *Glomeromycota* (Schübler et al. 2001; Table 2). The spore populations isolated comprised eight species. Most taxa came from the genus *Glomus*.

Additionally, culturing of the soil-root mixtures in two cycles of trap cultures revealed nine species (1 *Archaeospora* and 8 *Glomus* spp.) and three undescribed morphotypes of the genus *Glomus* earlier not found in the field samples (Table 2). Of the species of AMF found to occur in the field, only four sporulated in trap cultures.

The relatively low percent of the field-collected root-soil mixtures with the exceptionally not numerous spores of AMF, the disclosure in trap cultures of seven species and four undescribed morphotypes not sporulating in the field, and the frequent occurrence of spores of species found in this study in the field of other dune sites of Poland and the world indicate that the dunes of the Vistula Bar do not favour AMF

and inhibit the development of arbuscular mycorrhizae. Sporulation of AMF is highly associated with the level of mycorrhizal colonization of their plant hosts (Gazey, Abbott and Robson 1992).

Table 2
Arbuscular mycorrhizal fungi isolated from field-collected root-soil mixtures and 1st and 2nd cycle trap cultures

Fungal species	Frequency of occurrence in			Dominance	Total spore volume $\mu\text{m}^3 \times 10^6$
	field-collected root-soil mixture	trap culture			
		1 st cycle	2 nd cycle		
		%			
<i>Acaulospora elegans</i>	3.2	-	-	0.7	1.8
<i>Archaeospora trappei</i>	-	25.8	25.8	-	-
<i>Glomus aggregatum</i>	3.2	-	3.2	8.8	3.2
<i>Glomus arenarium</i>	-	3.2	-	-	-
<i>Glomus clarum</i>	-	3.2	3.2	-	-
<i>Glomus claroidesum</i>	-	-	3.2	-	-
<i>Glomus constrictum</i>	3.2	-	-	0.7	0.03
<i>Glomus corymbiforme</i>	3.2	-	-	1.5	3.5
<i>Glomus fasciculatum</i>	9.7	-	6.5	25.7	9.4
<i>Glomus laccatum</i>	-	3.2	12.9	-	-
<i>Glomus lamellosum</i>	-	-	6.5	-	-
<i>Glomus microcarpum</i>	-	3.2	3.2	-	-
<i>Glomus minutum</i>	-	3.2	3.2	-	-
<i>Glomus verruculosum</i>	-	3.2	-	-	-
<i>Glomus 122</i>	-	-	6.5	-	-
<i>Glomus 123</i>	-	3.2	3.2	-	-
<i>Glomus 129</i>	-	3.2	-	-	-
<i>Scutellospora armeniaca</i>	12.9	9.7	-	19.9	113.0
<i>Scutellospora dipurpurescens</i>	35.5	38.7	35.5	43.4	285.9
<i>Scutellospora pellucida</i>	6.5	-	-	1.5	8.4

The high predominance of members of the genus *Glomus* in the communities of AMF of the Vistula Bar agrees with the species composition of these fungi recovered from dunes of the Baltic Sea (Błazkowski 1993), the Hel Peninsula (Błazkowski 1994), Italy (Giovannetti and Nicolson 1983; Puppi and Riess 1987), Scotland (Nicolson and Johnston 1979), Madras, India (Mohankumar et al. 1988), Canada (Dalpé 1989), Florida (Sylvia 1986; Sylvia and Will 1988), Wisconsin (Koske and Tews 1987), San Miguel, California (Koske and Halvorson 1989b; Koske, pers. comm.), and Hawaii (Koske 1988; Koske and Gemma 1996). In contrast, maritime dunes of Massachusetts (Bergen and Koske 1984; Gemma and Koske 1988; Gemma, Koske and Carreiro 1989), Rhode Island (Fries and Koske 1991; Koske and Halvorson 1981), the Atlantic coast from New Jersey to Virginia (Koske 1987), northern California (Rose 1988), and New South Wales, Australia (Koske 1975) were dominated by *Gigaspora* and *Scutellospora* spores.

The high predominance and diversity of members of the genus *Glomus* in dunes of the Vistula Bar supports earlier reports of a good adaptation of these fungi to a wide range of physical and chemical soil conditions (Anderson, Liberta and Dickman 1984; Grey 1991; Haas and Menge 1990; Porter, Robson and Abbott 1987). Daniels and Trappe (1980) found that the optimal temperature for germination of spores of *Glomus* spp. was 14–22°C, i. e., a temperature range of a vegetative period of the Vistula Bar (Herbich and Markowski 1998). In contrast, species of *Gigaspora* and *Scutellospora* prefer warmer soils (Koske 1981; Schenck, Graham and Green 1975). Koske (1987) proved statistically that temperature was the main abiotic factor determining the structure of AMF community in dunes extending from New Jersey to Virginia. *Acaulospora* and *Archaeospora* spp. rarely dominate in AMF communities (Błaszczowski 1991a, 1993a, 1994c; Gerdemann and Trappe 1974).

The main reasons of the lack of sporulation in both cycles of trap cultures of four of the eight species revealed in the field-collected samples and of the disappearance of spore production of four species in the second cycle of trapping probably were (1) expulsion or suppression of these fungi by species more competitive or faster adjusting to the conditions of the trap cultures and (2) incompatibility of the above- and underground conditions and the plant host of these cultures with the ecological requirements of these fungal species.

Frequency of occurrence. In the field, the fungi most frequently found were *Scu. dipurpureus* and *Scu. armeniaca* (Table 2). Other frequently encountered species were *Gl. fasciculatum* and *Scu. pellucida*.

In the first-cycle trap cultures, spores of *Scu. dipurpureus*, *Arch. trappei* and *Scu. armeniaca* were most frequently found (Table 2). Apart from *Arch. trappei*, these cultures also yielded spores of seven species and two morphotypes not revealed in the field-collected samples.

The fungal species most frequently encountered in the second-cycle trap cultures were *Scu. dipurpureus*, *Arch. trappei*, and *Gl. laccatum* (Table 2). Of the fungi found to sporulate in these cultures, only *Gl. aggregatum*, *Gl. fasciculatum* and *Scu. dipurpureus* produced spores in the field. The second cycle of trapping revealed two next species (*Gl. claroideum*, *Gl. lamellosum*) and an undescribed *Glomus* 122 that were not observed either in the field or in the first cycle-trap cultures. Compared with the first cycle, no sporulation of *Scu. armeniaca*, *Gl. arenarium*, *Gl. verruculosum*, and *Glomus* 129 was found.

Considering the number of records of species and morphotypes in the field samples and the two cycles of trap cultures (Table 2), the AMF most frequently occurring in dunes of the Vistula Bar were *Scu. dipurpureus* (35.5% of records), followed by *Arch. trappei* (25.8%), *Gl. laccatum* (12.9%), and *Scu. armeniaca* (12.9%).

Dominance. The eudominants (coefficient of dominance $D > 10.0\%$) of the Vistula Bar dunes were *Scu. dipurpureus*, *Gl. fasciculatum*, and *Scu. armeniaca* (Table 2). The dominant ($D = 5.1\text{--}10.0\%$) was only *Gl. aggregatum*. No species attained the level of subdominants ($D = 2.1\text{--}5.0\%$).

Scutellospora dipurpureus also dominated in dunes of the Słowiński National Park (SNP; Błaszczowski 1993; Tadych and Błaszczowski 2000). In contrast, the dunes of the Szczecin coast were dominated by *G. corymbiforme*, *G. pustulatum*

and *S. dipurpurescens*, and those of the Gdańsk coast by *G. constrictum* and *G. ?heterosporum* Smith et Schenck (Blaszkowski 1993). *Glomus microcarpum*, *S. dipurpurescens* and *G. constrictum* predominated in the Hel Peninsula dunes (Blaszkowski 1994). The dominant AMF of Italian dunes were *G. mosseae* (Nicol. et Gerd.) Gerd. et Trappe, *S. calospora* (Nicol. et Gerd.) Walker et Sanders, *G. macrocarpum*, and *G. microcarpum* (Giovannetti and Nicolson 1983; Puppi and Riess 1987). The maritime sand dunes of Scotland harboured only *G. aggregatum* (Nicolson and Johnston 1979; Koske pers. comm.). *Glomus aggregatum* also dominated in maritime sand dunes and shores of Quebec, New Brunswick and Nova Scotia, Canada (Dalpé 1989). In the Lake Huron dunes, Canada, the dominating AMF were *G. caledonium* (Nicol. et Gerd.) Trappe et Gerd. and a species forming yellow brown spores (Koske et al. 1975). The populations of AMF of dunes of the eastern coast of the U.S.A. were dominated by *A. scrobiculata* Trappe, *G. gigantea*, *G. deserticola*, *G. fasciculatum*, and *Scutellospora weresubiae* Koske et Walker (Bergen and Koske 1984; Koske 1987; Koske and Halvorson 1981; Sylvia 1986; Sylvia and Will 1988). The most abundantly sporulating fungus in the Wisconsin Great Lake dunes was *G. etunicatum* (Koske and Tews 1987). *Scutellospora coralloidea* (Trappe, Gerd. et Ho) Walker et Sanders, *S. heterogama* (Nicol. et Gerd.) Walker et Sanders, and *S. calospora* (Nicol. et Gerd.) Walker et Sanders predominated in the Lanphere-Christensen sand dunes of the Pacific Coastline (Rose 1988). *Scutellospora hawaiiensis* Koske et Gemma, *G. microaggregatum* Koske, Gemma et Olexia, *G. sinuosum* (Gerd. et Bashi) Almeida et Schenck, *Glomus* 807, *G. intraradices*, and *G. spurcum* Pfeiffer, Walker et Bloss belonged to the most abundant species in the root zone of plants of Hawaiian dunes (Koske 1988; Koske and Gemma 1996). In dunes of San Miguel Island, the species most frequently occurring were *Gl. etunicatum*, *Gl. pansihalos*, and *Gl. trimurales* (Koske, pers. comm.). Most spores isolated from sand dunes of Santa Catarina, Brazil, belonged to *A. scrobiculata* (Stürmer and Bellei 1994). The dune plants of the west coast of India most frequently hosted *Gl. albidum*, *Gl. clarum*, and *Gl. fasciculatum* (Kulkarni, Rawiraja and Sridhar 1997). The coastal sand dunes of New South Wales were predominated by *A. scrobiculata* and a red-brown-spored species (Koske 1975).

Table 3

Spore abundance* and species richness* of arbuscular mycorrhizal fungi among roots of four plant families of the Vistula Bar \pm S.D.

Family	n	Spore abundance	Species richness
Asteraceae	1	-	-
Leguminosae	1	4	2
Poaceae	23	4.5 \pm 7.6	2.1 \pm 2.1
Rosaceae	6	5.5 \pm 7.9	2.0 \pm 1.3

Explanation: *in 100 g dry soil

Spore abundance. The overall average (\pm S.D.) spore abundance of AMF in the field-collected soil-root mixtures was 4.5 ± 7.4 and ranged from 0 to 31 spores in 100 g dry soil. Most spores came from plants of the family Rosaceae (av. 5.5 ± 7.9) and Poaceae (av. 4.5 ± 7.6 ; Table 3). The plant species harbouring the most abundant spo-

re populations were *R. rugosa* (av. 5.5 ± 7.9) and *Am. arenaria* (av. 5.4 ± 9.2 ; Table 4), which also hosted numerous and diverse communities of AMF in other dunes of Poland (Błaszczkowski 1993, 1994; Tadych and Błaszczkowski 2000). No spores were found in the root zone of *Ar. campestris*, despite this plant has earlier been found to favor the sporulation of AMF (Błaszczkowski 1993). However, this plant was sampled only once.

Table 4

Spore abundance* and species richness* of arbuscular mycorrhizal fungi among roots of five plant species \pm S.D.

Plant species	n	Spore abundance	Species richness
<i>Ammophila arenaria</i>	14	5.4 ± 9.2	1.9 ± 1.8
<i>Artemisia campestris</i>	1	0	0
<i>Festuca rubra</i>	9	3.0 ± 4.4	2.4 ± 2.5
<i>Lathyrus japonicus</i> subsp. <i>maritimus</i>	1	3.0	1.0
<i>Rosa rugosa</i>	6	5.5 ± 7.9	2.0 ± 1.3

Explanation: *in 100 g dry soil

Such a low spore abundance of AMF has been recorded only in dunes of Cape Cod, Massachusetts (0.2-16.2 spores in 100 g dry soil; Bergen and Koske 1984), Santa Catarina, Brasil (0-69; Stürmer and Bellei 1994), and Pakistan (1-29; Khan 1974). In Poland, the average abundances of spores in 100 g dry soil of the Baltic Sea coastal dunes located in the former Gdańsk and Szczecin voivodeships were 96.7 and 72.0, respectively (Błaszczkowski 1993), the Hel Peninsula - 99.8 (Błaszczkowski 1994), and SNP 75.9 (Tadych and Błaszczkowski 2000).

Species richness. Taking into account the spores isolated from both the field-collected samples and trap cultures, the overall average (\pm S.D.) species richness of AMF in dunes of the Vistula Bar was 2.1 ± 1.9 and ranged from 0 to 7 in 100 g dry soil. The plant families harbouring most species were the Poaceae (av. 2.1 ± 2.1) and the Rosaceae (av. 2.0 ± 1.3 ; Table 4). On an average, most species were associated with *F. rubra* (av. 2.4 ± 2.5) and *R. rugosa* (2.0 ± 1.3 ; Table 4). *Ammophila arenaria* hosted on an average of 1.9 ± 1.8 species in 100 g dry soil.

Total spore volume. The species of AMF of the Vistula Bar forming spores of the greatest total spore volume were *Scu. dipurpureus* and *Scu. armeniaca* (Table 2). Great spore volumes also came from *Scu. pellucida* and *Gl. fasciculatum*.

Plant-AM fungal species associations. Considering the spores revealed in both the field-collected soil-root samples and the two cycle-trap cultures (Table 2), the plant species associated with the highest number of species of AMF was *Am. arenaria* (10 species and 2 undescribed morphotypes), followed by *F. rubra* (8 species) and *R. rugosa* (6 species and 1 undescribed morphotype).

Ammophila arenaria harboured most species of AMF in SNP, when sampled 69 times in 1993-1996 (Tadych and Błaszczkowski 2000). Its close American relative, *Am. breviligulata* also hosted diverse populations of these fungi (Koske 1987; Koske, pers. comm.).

Fungal community similarity. The occurrence of AMF in maritime dunes of Poland and the world has so far been determined based on spores isolated only

from field-collected samples. Therefore, in the comparisons presented below, species of the fungi isolated only from the field of the Vistula Bar were first considered. Subsequent comparisons included species also revealed in trap cultures.

The species composition of AMF of the field soils of the Vistula Bar most resembled that revealed in dunes of the New South Wales, Australia ($C=0.77$; Koske 1975), followed by Szczecin ($C=0.37$; Błaszczkowski 1993), and SNP ($C=0.37$; Tadych and Błaszczkowski 2000).

When the comparisons considered species also revealed in trap cultures, the species composition of AMF of the Vistula Bar was most similar to that of SNP ($C=0.41$; Tadych and Błaszczkowski 2000), followed by Szczecin ($C=0.37$), and Gdańsk ($C=0.34$; Błaszczkowski 1993).

Taking into account all the AMF recognized in the Vistula Bar and those revealed in 15 maritime dune sites located outside Poland (Bergen and Koske 1984; Dalpé 1989; Giovannetti and Nicolson 1983; Koske 1975, 1987; Koske and Gemma 1996, 1997; Koske and Halvorson 1981, 1989; Koske and Tews 1987; Mohankumar et al. 1988; Kulkarni et al. 1997; Stürmer and Bellei 1994; Sylvia 1986), the highest similarity occurred in the Vistula Bar/Canada comparison ($C=0.33$).

The unexpected high similarity of the Vistula Bar/New South Wales comparison probably mainly resulted from the poor recognition of species diversity of AMF at the time when the Australian investigations were conducted; of the five morphotypes revealed, only two received species names (Koske 1975).

The high similarity of the communities of AMF of dunes of the Vistula Bar, the former Gdańsk and Szczecin voivodeships, and Canada supports earlier suggestions that the main factor influencing the distribution of AMF is climate (Anderson et al. 1984; Błaszczkowski 1993; Koske 1987).

The occurrence of arbuscular mycorrhizal fungi in dunes of the Vistula Bar and notes on their general distribution

Comments on the reports of the species from other localities refer only to collections made in sand dunes.

Abbreviations: n – the number of field-collected samples with spores of a given fungus; \underline{n} – the number of first cycle-trap cultures with spores of a given fungus; $\underline{\underline{n}}$ – the number of second-cycle trap cultures with spores of a given fungus. The numbers following are those of soil-root samples listed in Table 1.

Acaulospora elegans Trappe et Gerd.

$n=1$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1150.

Only one spore of this fungus in one field sample collected from under *L. japonicus* subsp. *maritimus* was found in the study discussed here. *Acaulospora elegans* did not sporulate in trap cultures.

This species has been reported from sand dunes in Washington, Oregon, and northern California (Gerdemann and Trappe 1974; Rose 1988) and Brazil (Trufem 1995).

Archaeospora trappei (Ames et Linderman) Morton et Redecker

n=0, \bar{n} =8, \underline{n} =8: 1146, 1147, 1149, 1152, 1154, 1159, 1160, 1174, 1146, 1147, 1149, 1152, 1154, 1159, 1160, 1174.

Spores of *Arch. trappei* were only revealed in trap cultures of the first and second cycles. Of the plants sampled, only *L. japonicus* subsp. *maritimus* did not host this fungus.

The lack of finding of *Arch. trappei* in the field may have resulted from either the omission of its spores or their absence at the time of collection of the soil-root samples because of decomposition or seasonality of sporulation. *Archaeospora trappei* produces small, colourless spores with one wall consisting of thin and delicate layers. Seasonal sporulation has been revealed in many species of AMF (e.g., Gemma et al. 1989).

This paper is the third report of the occurrence of *Arch. trappei* in maritime dunes. In Poland, this fungus has earlier been found in maritime dunes of SNP (Tadych and Błaszowski 2000) and inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

The only other report of the occurrence of *Arch. trappei* in dunes is the original description of this fungus made from spores recovered from under *Lilium longiflorum* Thunb. colonizing southern Oregon and northern California coastal areas (Ames and Linderman 1976).

Glomus aggregatum Schenck et Smith emend. Koske

n=1, \bar{n} =0, \underline{n} =1: 1154, 1163.

At the Vistula Bar, *Gl. aggregatum* was associated with roots of *Am. arenaria* and *R. rugosa*.

In Poland, *Gl. aggregatum* has earlier been found in many coastal dunes of the Baltic Sea (Błaszowski 1991), the Hel Peninsula (Błaszowski 1994), and SNP (Tadych and Błaszowski 2000). This fungus has also been encountered in sands of the bank of the Odra river (Błaszowski 1991) and inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

Additionally, *Gl. aggregatum* is known from dunes of the eastern coast of North America (Dalpé 1989; Friese and Koske 1991; Gemma and Koske 1989; Koske 1987; Sylvia 1986; Sylvia and Will 1988), Wisconsin (Koske and Tews 1987), Florida (Sylvia 1986; Sylvia and Will 1988), San Miguel Island (Halvorson and Koske 1987; Koske and Halvorson 1989b), Hawaii (Koske 1988), Brazil (Trufem et al. 1994), Italy (Giovannetti 1985), and Japan (Abe and Katsuya 1995).

Glomus arenarium Błasz., Tadych et Madej

n=0, \bar{n} =1, \underline{n} =0: 1167.

Only one trap culture of the first cycle indicated the existence of the *Am. arenaria*-*Gl. arenarium* association.

Other sites found to harbour *Gl. arenarium* were only maritime dunes adjacent to Świnoujście (Błaszowski, Tadych and Madej 2001) and inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

Glomus claroideum Schenck et Smith

$n=0$, $\underline{n}=0$, $\underline{\underline{n}}=1$: 1163.

Only one trap culture of the second cycle showed *Gl. claroideum* associated with roots of *Am. arenaria* of the Vistula Bar.

This fungus has earlier infrequently been recorded in dune areas. Błaszowski et al. (2002) recovered its spores from inland dunes of the Błędowska Desert, Poland, and Mohankumar et al. (1988) recognized *Gl. claroideum* in sandy beach soils of the Madras coast.

Glomus clarum Nicol. et Schenck

$n=0$, $\underline{n}=1$, $\underline{\underline{n}}=1$: 1165, 1165.

Although not found in the field samples, the first and second cycles of trapping of AMF revealed *Gl. clarum* associated with roots of *F. rubra* growing in dunes of the Vistula Bar.

In Poland, this is the first record of this fungal species in maritime dunes, although *Gl. clarum* occurred in inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

Glomus clarum has been found in dunes of the province Lands Area of Cape Cod National Seashore, Massachusetts (Koske and Gemma 1997), Someshawa, Mangalore Coast of Karnataka, India (Kulkarni et al. 1997), and Quebec, New Brunswick and New Scotia, Canada (Dalpé 1989).

Glomus constrictum Trappe

$n=1$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1151.

As indicated one trap culture of the second cycle, *Gl. constrictum* was hosted by *R. rugosa* growing at the Vistula Bar.

In Poland, this fungal species has earlier many times been revealed in dunes adjacent to the Baltic Sea (Błaszowski 1993, 1994; Tadych and Błaszowski 2000) and in inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

Glomus constrictum has also been recovered from dunes of Quebec, New Brunswick and New Scotia, Canada (Dalpé 1989), New Jersey to Virginia (Koske 1987), and those of Santa Catarina, Brazil (Stürmer and Bellei 1994).

Glomus corymbiforme Błasz.

$n=1$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1176.

This fungus was found only in one field-collected sample representing *Am. arenaria*.

In Poland, *Gl. corymbiforme* occurred in maritime dunes of Świnoujście (Błaszowski 1995), SNP (Tadych and Błaszowski 2000), and inland dunes of the Błędowska Desert (Błaszowski et al. 2002).

Recently, this fungus was revealed in dunes of the Mediterranean Sea adjacent to Karabucak-Tuzla, Turkey, and Tel Aviv, Israel (Błaszowski, pers. observ.).

Glomus fasciculatum (Thaxter) Gerd. et Trappe emend. Walker et Koske

$n=3$, $\underline{n}=0$, $\underline{\underline{n}}=2$: 1150, 11152, 1176, 1162, 1163.

Glomus fasciculatum was encountered in three field-collected root-rhizosphere soil mixtures and two pots of the second-cycle trap cultures. The plants harbouring this fungus in the field were *Am. arenaria*, *L. japonicus* subsp. *maritimus*, and *R. rugosa*.

In Poland, *Gl. fasciculatum* has been isolated from dunes of the Baltic Sea coast and the Hel Peninsula (Błaszczkowski 1993, 1994), SNP (Tadych and Błaszczkowski 2000), as well as from inland dunes of the Błędowska Desert (Błaszczkowski et al. 2002).

Other reports of the presence of *Gl. fasciculatum* in dunes are those from the eastern and western shores of North America (Dalpé 1989; Bergen and Koske 1984; Gemma and Koske 1989; Koske and Halvorson 1981; Rose 1988).

Glomus laccatum Błaszcz.

n=0, \bar{n} =1, \bar{n} =4: 1165, 1162, 1163, 1164, 1165.

No spores of *Gl. laccatum* were found in the field soils of the Vistula Bar. However, this fungus sporulated in first- and second-cycle trap cultures representing *Am. arenaria* and *F. rubra*.

Other Polish dune areas earlier found to be inhabited by *Gl. laccatum* were those of the Gdańsk coast and SNP (Błaszczkowski 1993). There is no record of this fungal species in other regions of the world.

However, examination of many trap cultures with soils of different cultivated and non-dune uncultivated areas of Poland indicated that *Gl. laccatum* rather is a frequently occurring AMF. It forms small and colourless spores with a delicate wall. Hence, the infrequent finding of this fungus in field-collected root-soil samples probably results from the same reasons that make difficult the disclosure of, e.g., *Arch. trappei* (see above).

Glomus lamellosum Dalpé, Koske et Tews

n=0, \bar{n} =0, \bar{n} =2: 1164, 1167.

Two trap cultures of the second cycle revealed *Gl. lamellosum* to co-occur with *Am. arenaria* and *F. rubra* colonizing dunes of the Vistula Bar.

In Poland, *Gl. lamellosum* also occurred in maritime dunes of the Western Pomerania and Pomerania voivodeships, as well as in inland dunes of the Błędowska Desert (Błaszczkowski et al. 2002).

Dalpé, Koske and Tews (1992) isolated *Gl. lamellosum* from under *Am. breviligulata* Fern colonizing the sandy shore of Nottawasaga Bay in Georgian Bay, Ontario, Canada and sand dunes of Baile's harbor, Wisconsin, U.S.A.

Glomus microcarpum Tul. et Tul.

n=0, \bar{n} =1, \bar{n} =1: 1164, 1164.

Glomus microcarpum was present only in the first and second cycle trap cultures representing *F. rubra* growing in the field.

This fungus is known from dunes of the Baltic Sea coast (Błaszczkowski 1993a, b, 1994a), SNP (Tadych and Błaszczkowski 2000), Poland, Madras, India (Mohan Kumar et al. 1988), and Italy (Puppi and Riess 1987).

Glomus minutum Błaszcz., Tadych et Madej

n=0, \bar{n} =1, \bar{n} =1: 1146, 1167.

Only the first- and second-cycle trap cultures revealed *Gl. minutum* associated with *Am. arenaria* and *F. rubra* growing in the Vistula Bar dunes.

Glomus minutum has originally been described based on spores produced in trap cultures with dune soils adjacent to Świnoujście in north-western Poland (Błaszkowski, Tadych and Madej 2000). No other literature report exists of this fungus.

The spores of *Gl. minutum* are one of the smallest among those produced by all the species of AMF recognized to date. Additionally, they are colourless and have a very thin wall. Thus, the reasons of the lack of records of this fungus in the field soils probably are as those regarding, e. g., *Arch. trappei* and *Gl. laccatum* (see above).

Glomus verruculosum Błaszk.

n=0, \bar{n} =1, \bar{n} =0: 1172.

At the Vistula Bar, *Gl. verruculosum* was found to be hosted only by *R. rugosa*. This is the first record of this fungus in dune sites of Poland and the world.

Glomus verruculosum was discovered among roots of *Glyceria aquatica* (L.) Wahlb. growing at the sandy bank of the river Odra (Błaszkowski and Tadych 1997).

Glomus 122. Figs 2-6

n=0, \bar{n} =0, \bar{n} =2: 1163, 1165.

Two trap cultures of the second cycle revealed *Glomus* 122 to be present in the Vistula Bar dunes.

Sporocarps unknown. Spores borne singly in the soil, in aggregates (Fig. 2) or inside roots; produced from straight or dichotomously branched sporophores. *Aggregates* usually oblong, 60–130 x 80–240 μm , with 2 to 4 spores. *Sporophore* consisting of single or dichotomously branched, coenocytic to sparsely septate; hyaline; (5.6-) 6.2 (-7.1) μm wide hyphae with a wall (0.5-) 0.6 (-0.7) μm thick; either continuous with extramatrical mycorrhizal hyphae or developed from the outermost spore wall layer 1, mostly at the opposite of the subtending hypha (Fig. 3), sometimes from other places of a spore; bearing spores blastically at hyphal tips. *Spores* yellowish white (3A2) to pale yellow (3A3); mostly ovoid to oblong or irregular; 60–130 x 80–240 μm , very rarely globose to subglobose (Fig. 2); (70-) 83 (-100) μm diam; with a highly plicate or indented margin (Fig. 3); indentations 7.5–25.0 μm deep; with a single subtending hypha. *Subcellular structure of spores* composed of one wall (Figs. 4-6) with three layers (layers 1-3). Outermost layer 1 sloughing, smooth, hyaline, (0.5-) 0.8 (-1.0) μm thick before disintegration, frequently forming a branch, 10–75 μm long and 5–12.5 μm wide, to form a sporophore bearing a new spore (Fig. 3). Layer 2 sloughing, smooth, hyaline, (0.5-) 0.7 (-1.0) μm thick before disintegration. Layers 1 and 2 usually closely adherent to each other but separable from layer 3 and present in most mature spores. Layer 3 laminate, smooth, yellowish white (3A2) to pale yellow (3A3), (0.7-) 0.9 (-1.5) μm thick, staining pale orange (6A3) to reddish orange (7A6) in Melzer's reagent. *Subtending hypha* yellowish white (3A2) to pale yellow (3A3); straight or recurvate, mostly funnel-shaped, rarely cylindrical or constricted; (2.5-) 6.8 (-10.0) μm wide at the spore base. *Wall of subtending hypha* yellowish white (3A2) to pale yellow (3A3); (0.5-) 1.1 (-2.5) μm thick at the spore base; continuous with spore wall layers 1-3 in both young and most mature spores. *Pore* open in most mature spores or occlu-

ded by a septum, (3.9-) 5.9 (-8.6) μm wide, continuous with the innermost lamina of spore wall layer 3.

The unique properties of *Glomus* 122 are (1) the formation of irregular spores with deep indentations, (2) the production of spores most frequently clustered in aggregates originating from either a branched sporophore continuous with an extramatrical mycorrhizal hypha or a new sporophore developing from the outermost spore wall layer 1, and (3) the reactivity of the laminate innermost spore wall layer in Melzer's reagent.

The only two species of arbuscular fungi of the genus *Glomus* superficially resembling *Glomus* 122 are *G. aggregatum* Schenck et Smith emend. Koske and *G. intraradices* Schenck et Smith. They produce spores both singly in the soil and in aggregates present in the soil or inside roots (Błaszowski 1991; Błaszowski, pers. observ.; Koske 1985; Schenck and Smith 1982). Their spores also are similar in size, somewhat in shape, and in having a 3-layered wall structure with two sloughing, hyaline, outer layers and a laminate, innermost layer.

Although *G. aggregatum* frequently forms irregular spores, they have no deep indentations (Fig. 3) distinguishing spores of *Glomus* 122. Spores of *Glomus* 122 with indentations also occur inside roots, suggesting the indentations to be a genetically conserved property of this fungus rather than that caused by the occurrence of particular conditions during development of spores, e.g., the lack of sufficient place for originating, neighbouring spores.

In contrast to *Glomus* 122, *G. aggregatum* may also produce inside spores by internal proliferation (Błaszowski 1991; Koske 1985). Additionally, the thickness of the laminate spore wall of *G. aggregatum* usually is greater than the total thickness of their two outer layers and much greater than the thickness of the laminate spore wall layer of *Glomus* 122 (1.5 μm thick in *G. aggregatum* vs. 0.7-1.5 μm thick in *Glomus* 122). Hence, spores of the former new fungus usually are lighter coloured than those of the latter species.

The main properties distinguishing *Glomus* 122 from *G. intraradices* are the number and compactness of the sublayers of the laminate spore wall layer (Schenck and Smith 1982; Stürmer and Morton 1997). This layer of *Glomus* 122 spores usually consists of two, inseparable laminae, whereas the laminate layer of *G. intraradices* spores is composed of many, easily separating sublayers.

Additionally, *Glomus* 122 differs from both *G. aggregatum* and *G. intraradices* in properties of the outermost spore wall layer and the reactivity in Melzer's reagent (Błaszowski 1991; Błaszowski, pers. observ.; Koske 1985; Schenck and Smith 1982; Stürmer and Morton 1997). Although the outermost layer of *Glomus* 122 deteriorates with age, it is much more compact and, thereby, much more permanent than the short-lived, mucilaginous layer of both *G. aggregatum* and *G. intraradices* spores. Finally, the staining spore wall layer of *Glomus* 122 in Melzer's reagent is only the innermost, laminate layer (Figs 4-6), whereas the reactive wall layer of spores of *G. aggregatum* and *G. intraradices* is the mucilaginous outermost layer. The laminate spore wall layer of none of the known species of arbuscular fungi of the genus *Glomus* stains in Melzer's reagent.

Glomus 123. Figs 7-9

n=0, n=1, n=1: 1159, 1159.

The first and second cycles of trapping revealed *Glomus* 123 to be associated with roots of *Am. arenaria* growing in dunes of the Vistula Bar.

Sporocarps unknown. Spores borne singly in the soil; produced from straight sporophores. *Sporophore* coenocytic to sparsely septate; hyaline; (3.5-) 4.4 (-5.3) μm wide; with a wall (0.3-) 0.5 (-0.7) μm thick; bearing spores by swelling at hyphal tips. *Spores* hyaline; globose to subglobose; (35-) 55 (-75) μm diam; sometimes ovoid; 50-70 x 45-90 μm ; with a single subtending hypha (Figs 7, 8). Subcellular structure of spores consisting of one wall (Figs 7, 8) with two layers (layers 1-2). Outermost layer 1 evanescent, smooth, hyaline, (0.3-) 0.6 (-0.7) μm thick before disintegration, closely adherent to layer 2, rarely present in mature spores (Figs 8, 9). Layer 2 hyaline, smooth, (1.0-) 2.7 (-5.1) μm thick. Spore wall layers 1-2 not reacting in Melzer's reagent. *Subtending hypha* hyaline; straight or recurvate; cylindrical or funnel-shaped (Fig. 9); (1.2-) 3.3 (-4.9) μm wide at the spore base. *Wall of subtending hypha* hyaline; (0.5-) 0.7 (-1.0) μm thick at the spore base; continuous with spore wall layers 1-2 (Fig. 8) in young spores, then consisting of a single layer continuous with spore wall layer 2 (Fig. 9). *Pore* occluded by a septum, 0.3-0.6 μm wide, continuous with the innermost lamina of spore wall layer 2.

Discussion. *Glomus* 123 is characterized by its small, hyaline spores having a simple wall structure and a strikingly narrow subtending hypha.

When viewed through a dissecting microscope, *Glomus* 123 may be indistinguishable from *G. diaphanum* Morton et Walker, *G. laccatum* Blaszk., and *Paraglomus occultum* (Walker) Morton et Redecker (Blaszkowski 1988; Morton and Walker 1984; Morton 2000; Morton and Redecker 2001). All the three fungal species produce ectocarpic and hyaline spores of similar size and shape.

At this level of observations and from the same reasons, *Glomus* 123 spores may also be easily confused with spores of *G. pallidum* Hall and *G. viscosum* T. H. Nicolson occurring singly in the soil. However, compared with *Glomus* 123 always producing single spores in the soil, those of the latter two fungi may additionally occur in compact sporocarps (*G. pallidum*; Hall 1977) or loose aggregates (*G. pallidum*, *G. viscosum*; Hall 1977; Walker et al. 1995).

The combination of subcellular spore wall and subtending hypha properties readily separates *Glomus* 123 from the other species listed above. *Glomus* 123 and *G. laccatum* form two-layered spores with a sloughing outermost layer not reacting in Melzer's reagent (Blaszkowski 1988). However, the laminate layer of *Glomus* 123 consists of many, very thin, adherent, usually inseparable sublayers (Figs 7-9), whereas that of *G. laccatum* is composed of four to five easily separating laminae, each (0.5-) 1.2 (-2.2) μm thick.

Apart from two outer wall layers similar phenotypically to those of *Glomus* 123 spores, *G. diaphanum* has another flexible or semiflexible innermost layer (Morton 2000; Morton and Walker 1984), which never occurs in *Glomus* 123. Additionally, the sloughing layer of *G. diaphanum* spores can stain light pink in Melzer's reagent (vs. no reaction in *Glomus* 123 in this reagent).

The main properties distinguishing *Glomus* 123 from *P. occultum* are the number and characteristics of spore wall layers. While a sloughing layer and a laminate layer

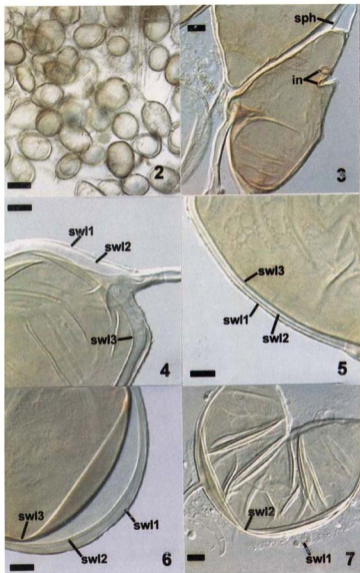
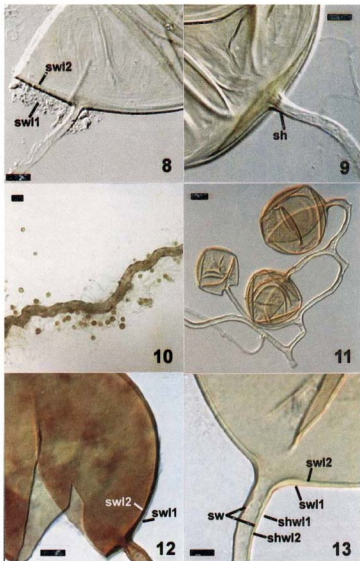


Fig. 2-6. *Glomus* 122. 2. Intact spores. 3. Spore with indentations (in) and terminal sporophore (sph) continuous with the outermost spore wall layer. 4-6. Three spore wall layers (swl 1-3) with the innermost laminate layer 3 stained in spores crushed in Melzer's reagent. Fig. 2, bright field microscopy; Figs 3-6, differential interference contrast. Scale bars: Fig. 2, - 100 μ m; Figs 3-6 - 10 μ m.
 Fig. 7. *Glomus* 123. Spore wall layers 1 (swl 1) and 2 (swl 2). Scale bar - 10 μ m.



Figs 8-9. *Glomus* 123.8. Highly deteriorated spore wall layer 1 (swl 1) adherent to spore wall layer 2 (swl 2). 9. Narrow subtending hypha (sh). All differential interference contrast, Scale bars - 10 μ m. Figs 10-13. *Glomus* 129. 10. Intact spores associated with roots, bright field microscopy. 11. Cluster of spores. 12. Stained spore wall layer 1 (swl 1) adherent to spore wall layer 2 (swl 2) of a spore crushed in Melzer's reagent. 13. Open funnel-shaped subtending hypha with wall layers 1 and 2 (shwl 1 and 2) continuous with spore wall layers 1 and 2 (swl 1, 2). Fig. 10, bright field microscopy; Figs 11-13, differential interference contrast. Scale bars: Fig. 10. - 200 μ m; Fig. 11 - 20 μ m; Figs 12-13 - 10 μ m.

are the component parts of the *Glomus* 123 spore wall, a sloughing layer and two permanent layers constitute the wall of *P. occultum* spores (Morton and Redecker 2001).

Despite single spores of *G. viscosum* also are reminiscent of *Glomus* 123 spores due to the possession of a two-layered wall structure with a laminate inner layer, their outer layer is permanent (a unit wall vs. an evanescent wall *sensu* Walker 1983 in *Glomus* 123) and exudes a mucigel-like substance absorbing soil particles with age (Walker et al. 1995), a phenomenon not found in the newly encountered arbuscular fungus.

Additionally, the subtending hypha of *Glomus* 123 spores is narrower than that of spores of the other fungi discussed here [(1.2-) 3.3 (-4.9) μm wide vs. 5.4–11.2 μm (*G. diaphanum*), 7.4–12.9 μm (*G. laccatum*), 3–10 μm (*P. occultum*), 5–20 μm (*G. pallidum*), 8–11 μm (*G. viscosum*); Błaszczowski 1988; Hall 1977; Morton and Walker 1984; Walker 1982; Walker et al. 1995].

Other arbuscular fungi with lightly coloured spores likely to be confused with those of *Glomus* 123 are *G. albidum* Walker et Rhodes, *G. gibbosum* Błaszcz., *G. lacteum* Rose et Trappe, *G. leptotichum* Schenck et Smith, and *G. spurcum* Pfeiffer, Walker et Bloss emend. Kennedy, Stutz et Morton. However, all these fungi form markedly larger spores of different quantitative and qualitative properties of a subcellular wall structure and have a wider subtending hypha (Błaszczowski 1997; Kennedy, Stutz and Morton 1999; Rose and Trappe 1980; Schenck and Smith 1982; Walker and Rhodes 1981). Additionally, in contrast to *Glomus* 123, both *G. albidum* and *G. leptotichum* stain in Melzer's reagent, and spores of *G. gibbosum* and *G. spurcum* may occur in aggregates or sporocarps (*G. gibbosum*) enclosed by a common hyphal mantle.

Glomus 129. Figs 10-13

n=0, n=1, n=0: 1151.

Glomus 129 occurred only among roots of *R. rugosa*, as one trap culture of the first cycle showed.

Sporocarps unknown. Most spores strongly associated with roots of the plant host (Fig. 10), more rarely occurring in loose aggregates (Fig. 11) or singly in the soil; produced from straight sporophores. *Sporophore* coenocytic to sparsely septate; hyaline to yellowish white (3A2); (4.9-) 6.0 (-7.8) μm wide; with a wall 0.5–0.8 μm thick; bearing spores by swelling at hyphal tips. *Spores* pale yellow (3A3) to light orange (6A6); globose to subglobose; (25-) 60 (-100) μm diam; sometimes ovoid; 40–70 x 50–120 μm ; with a single subtending hypha (Figs 10, 11). Subcellular structure of spores consists of one wall (Figs 12, 13) with two layers (layers 1-2). Outermost layer 1 mucilaginous, hyaline, (0.5-) 0.6 (-1.0) μm thick when not deteriorated, tightly adherent to layer 2, sloughing with age, staining reddish white (10A2) to bluish red (11B8) in Melzer's reagent. Layer 2 laminate, pale yellow (3A3) to light orange (6A6), (1.2-) 2.4 (-3.9) μm thick. *Subtending hypha* pale yellow (3A3) to light orange (6A6); straight or recurved; funnel-shaped or slightly flared (Figs 11-13), rarely constricted; (6.4-) 9.9 (-15.7) μm wide at the spore base. *Wall of subtending hypha* pale yellow (3A3) to light orange (6A6); (2.2-) 2.6 (-2.9) μm thick at the spore base; consisting of two layers continuous with spore wall layers 1 and 2 (Fig. 13). Pore (1.7-) 4.7 (-8.6)

μm wide, open or occluded by a curved septum continuous with the laminate spore wall layer 2.

When observed under a dissecting microscope, the species of the genus *Glomus* most resembling *Glomus* 129 are *G. aggregatum* Schenck et Smith emend. Koske, *G. fasciculatum* (Thaxter) Gerd. et Trappe emend. Walker et Koske, *G. intraradices* Schenck et Smith, and *G. hoi* Berch et Trappe (Berch and Trappe 1985; Koske 1985; Stürmer and Morton 1997; Walker and Koske 1987). Spores of all the fungi occur singly or in aggregates in the soil, are yellow-coloured, and have a similar shape and size range. *Glomus pustulatum* Koske et al. and *G. trimurales* Koske et Halvorson also produce spores similar in colour and size, but they are formed only singly in the soil (Koske et al. 1986; Koske and Halvorson 1989a).

Glomus 129 differs from the species listed above in number, as well as in phenotypical and staining properties of its spore wall layers. They are most evident when spores crushed in a mixture of PVLG and Melzer's reagent are examined under a compound microscope.

While the spore wall of *Glomus* 129 consists of two layers: a mucilaginous layer adherent to a laminate layer (Figs 12, 13), that of spores of *G. aggregatum*, *G. fasciculatum*, and *G. intraradices* comprises three layers. *Glomus* 129 lacks the flexible innermost layer of *G. fasciculatum* (Walker and Koske 1987) and *G. aggregatum* (Błaszowski 1991) and the semiflexible middle layer of *G. intraradices* (Stürmer and Morton 1997). Additionally, the outermost wall layer of *G. fasciculatum* spores is permanent and the innermost spore wall layer of *G. intraradices* consists of readily separating sublayers (laminae). In contrast, the outer layer of *Glomus* 129 spores sloughs with age, and their inner laminate layer consists of tightly adherent laminae (Figs 12, 13). Finally, only the outermost mucilaginous layer of spores of *Glomus* 129 and *G. intraradices* reacts in Melzer's reagent, whereas all three layers of *G. fasciculatum* spores stain in this reagent. No data of the reactivity of the spore wall components of *G. aggregatum* in Melzer's reagent exist. There is an urgent need to receive a living culture of this fungal species to examine its properties so far known only from field-collected spores. Spores of arbuscular mycorrhizal fungi isolated from the field are frequently completely devoid of their outer short-living spore wall components and the reactivity of spore wall layers in Melzer's reagent has been frequently unrecorded in early descriptions of arbuscular fungi (Morton 1995, 1996). Nevertheless, the unique property of *G. aggregatum* is the production of spores by internal proliferation (Koske 1985; Błaszowski 1991).

Although *G. hoi* produces two-layered spores as does *Glomus* 129, compared with their inner spore wall layer, the outer layer of the former fungus is thicker and coloured, and that of the latter species is thinner and colourless (Berch and Trappe 1985; Morton 2000).

The spores of *G. pustulatum* and *G. trimurales* have a wall composed of three permanent layers, of which none stains in Melzer's reagent (Błaszowski, pers. observ.; Koske and Halvorson 1989a; Koske et al. 1986; Morton 2000; vs. two layers with an outer layer staining reddish white to bluish red in this reagent in *Glomus* 129).

Scutellospora armeniaca Błaszk.

n=4, \bar{n} =3, \bar{n} =0: 1146, 1146, 1148, 1153, 1153, 1154, 1164.

At the Vistula Bar, *Scu. armeniaca* was associated only with *F. rubra* and *R. rugosa*, as showed its spores isolated from both the field and the first-cycle trap cultures. This fungus stopped to sporulate in cultures of the second cycle.

In Poland, *Scu. armeniaca* has earlier been found in maritime dunes of the Hel Peninsula (Błaszkowski 1994) and SNP (Błaszkowski and Tadych 2000), as well as in inland dunes of the Błędowska Desert (Błaszkowski et al. 2002).

No other report exists of *Scu. armeniaca* outside Poland.

Scutellospora dipurpurescens Morton et Koske

n=11, n=12, n=11: 1146, 1146, 1146, 1147, 1150, 1151, 1151, 1151, 1153, 1153, 1153, 1158, 1159, 1159, 1159, 1160, 1160, 1160, 1161, 1161, 1162, 1162, 1162, 1162, 1163, 1163, 1163, 1164, 1164, 1168, 1170, 1170, 1171, 1175, 1175.

At the Vistula Bar, *Scu. dipurpurescens* co-occurred with *Am. arenaria*, *F. rubra*, *L. japonicus* subsp. *maritimus*, and *R. rugosa*.

In maritime dunes of Poland, *Scu. dipurpurescens* dominated in soils of the Hel Peninsula (Błaszkowski 1994) and has been among the most frequently occurring AMF in SNP (Tadych and Błaszkowski 2000). Additionally, *Scu. dipurpurescens* has been a frequent inhabitant of inland dunes of the Błędowska Desert (Błaszkowski et al. 2002).

Scutellospora dipurpurescens probably has a worldwide distribution and has frequently been cited in the literature as *Scu. calospora* (Nicol. et Gerd.) Walker et Sanders, a species very closely related with and indistinguishable from *Scu. dipurpurescens* under a dissecting microscope (Dalpé 1989; Giovannetti and Nicolson 1983; Koske and Gemma 1997; Koske and Halvorson 1981, 1989).

Scutellospora pellucida (Nicol. et Schenck) Walker et Sanders

n=2, \bar{n} =0, \bar{n} =0: 1153, 1164.

At the Vistula Bar, spores of *Scu. pellucida* were found only in the field as associated with roots of *F. rubra*.

In other dune areas of Poland, this fungus has been encountered in soils of the Hel Peninsula, the Gdańsk and Szczecin coasts (Błaszkowski 1993), SNP (Tadych and Błaszkowski 2000), and the Błędowska Desert (Błaszkowski et al. 2002).

Other dune sites containing spores of *Scu. pellucida* have been those of the North American Atlantic coast (Bergen and Koske 1984; Dalpé 1989; Friese and Koske 1991; Gemma and Koske 1989; Gemma et al. 1989; Koske 1987; Koske and Gemma 1997; Koske and Walker 1986), California (Rose 1988), San Miguel Island (Koske, pers. comm.), Italy (Giovannetti 1985), as well as Israel and Turkey (Błaszkowski, pers. observ.).

Acknowledgment: This study was supported in part by the Committee for Scientific Research, project no. 6 P04G 100 19.

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Arbuskularne grzyby mikoryzowe (*Glomeromycota*)

Mierzei Wiślanej

Streszczenie

Zbadano występowanie arbuskularnych grzybów mikoryzowych (AGM) z rzędu *Glomerales*, gromady *Glomeromycota* związanych z roślinami nadmorskich wydm piaszczystych Mierzei Wiślanej. Obecność AGM ujawniono na postawie zarodników wyizolowanych z mieszaniny korzeni i gleby ryzosferowej zebranych z wydm i dwóch cykli wazonowych kultur pułapkowych utworzonych z części tych mieszanin. Mieszaniny te pochodziły spod pięciu gatunków z czterech rodzin roślin. Zarodniki AGM występowały w 54,8% prób polowych i należały do 8 gatunków. Ponadto uprawianie mieszanin korzeni i gleby w kulturach pułapkowych ujawniło 9 gatunków i 3 nieopisane morfotypy wcześniej nie znalezione w próbach polowych. Uwzględniając liczbę notowań gatunków i morfotypów w próbach polowych i dwóch cyklach kultur pułapkowych, grzybem najczęściej występującym w wydmach Mierzei Wiślanej była *Scutellospora dipurpureascens*, następnie *Archaeospora trappii*, *Glomus laccatum* i *Scu. armeniaca*. Ogólne średnie zagęszczenie zarodników w próbach polowych było niskie (4,48, zakres 0-31 w 100 g suchej gleby). Ogólne średnie zagęszczenie gatunków określone na podstawie zarodników wyodrębnionych z prób polowych i kultur pułapkowych wynosiło 2,06 i wahało się od 0 do 7 w 100 g suchej gleby. Rośliną utrzymującą

najwięcej zarodników była *Acanthophila arcuaria*. Spośród zbadanych stanowisk wydmyowych Polski, skład gatunkowy AGM Mierzei Wiślanej był najbardziej podobny do tego ze Słowińskiego Parku Narodowego. Gdy do porównań włączono 15 nadmorskich stanowisk wydmyowych położonych poza Polską, najwyższe podobieństwo wystąpiło w porównaniu Mierzeja Wiślana/Kanada.