Mycorrhiza (1994) 5:71–88

ORIGINAL PAPER

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Arbuscular fungi and mycorrhizae (Glomales) of the Hel Peninsula, Poland

Abstract In the years 1985–1989, the occurrence of arbuscular fungi and mycorrhizae on the Hel Peninsula (Poland) was investigated with the help of 45 soil and root samples collected under 20 plant species of eight families. Except for *Zea mays*, the other plant species were from uncultivated sites. All soil samples contained spores of arbuscular fungi, of which about 45% were of the genus *Glomus*. *Acaulospora* spp. preferred members of the Cupressaceae. Spores of *Gigaspora* occurred rarely and only in two plant families. *Glomus* spp. were most frequently associated with plants of the Rosaceae, and species of *Scutellospora* were found at markedly higher frequencies among roots of plants of the Gramineae and Cupressaceae. A total of 29 spore-forming species and *Glomus tenue* (a fungus recognizable by its distinctive infections) were found. The most frequently recovered fungus, *Glomus tenue*, was present in roots of 56.8% of examined plants. Of the spore-forming fungi, the most frequently isolated spores were those of *Scutellospora dipurpurascens*, then *Glomus constrictum*, *Acaulospora* 61, and *Glomus microcarpum*. The overall spore density in examined samples averaged 99.8 in 100 g dry soil in the range 1 to 547, and was highest in a sample taken from around roots of *Festuca arundinacea*. The dominant fungi forming spores in sampled soils were *Glomus constrictum*, *Glomus microcarpum*, and *Scutellospora dipurpurascens*. The average species density was 3.9 in 100 g dry soil in the range 1 to 10, and was highest in *Corynephorus canescens*, *Rosa canina*, and *Thuja occidentalis*. Levels of colonization by arbuscular fungi ranged from 0.0 to94.0% (mean 23.3%) of the root length and were highest in *Festuca arundinaceae* and *Zea mays*.

Key words Glomales · Arbuscular fungi
Mycorrhizae · Occurrence

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Introduction

The Hel Peninsula (54°36′–54°47′N, 18°25′–18°48′E) is a narrow strip of land 200–3000 m wide, 34 km long and about 160 km^2 in area. It has been formed from sand brought by waves of the Baltic Sea. The mean annual precipitation and the mean precipitation in the vegetative period (May–July) are 528 mm and 156 mm, respectively. The hottest month is July, with a daily mean temperature ranging from 16.6 to 17.7° C. The mean number of frost days is 89.4 (Wojterski and Bednorz 1982).

The vegetation consists of 204 plant species in 155 genera and 50 families. The most numerously represented families are the Compositae (27 species in 22 genera), the Gramineae (19 species in 15 genera), the Rosaceae (13 species in 10 genera), and the Leguminosae (12 species in 10 genera) (Gerstmann et al. 1981).

In recent years, progressive erosion of the Hel Peninsula has been observed due to changes of the course of maritime streams generated by a pier in the fishing port at Władysławowo. At present, the losses are restored by mechanical transport of sand from the Puck Gulf. There are proposals for complex studies on the restoration and protection of the Hel Peninsula. A significant role in these enterprises will undoubtedly be played by arbuscular fungi.

Arbuscular fungi (Glomales) are probably amongst the most common soil fungi (Gerdemann 1968) and are associated with about 80% of the world's plants (Gianinazzi and Gianinazzi-Pearson 1986). Sand dune soils especially favour their development because of the low phosphorus content (Koske 1987). Numerous studies conducted in dune sites have shown them to be of frequent occurrence (Bergen and Koske 1984; Giovannetti and Nicolson 1983; Khan 1974; Koske 1975, 1987, 1988; Koske and Halvorson 1981, 1989; Koske and Tews 1987; Koske et al. 1975, 1990; Mohankumar et al. 1988; Nicolson and Johnson 1979; Puppi and Ries 1987; Sylvia 1986; Sylvia and Will 1988).

Arbuscular fungi significantly improve nutrition of plants, especially those growing in nutrient-poor sites (Harley and Smith 1983). Extramatrical hyphae of arbuscular mycorrhizae not only increase the absorptive area of a root (Bieleski 1973), but also stabilize sandy soils by binding sand grains into aggregates (Koske and Polson 1984; Sutton and Sheappard 1976). Reeves et al. (1979) suggested that mycorrhizal plants are more competitive than nonmycorrhizal plants. According to Hetrick et al. (1989) and Janos (1980), the presence of arbuscular fungi may affect both quantitatively and qualitatively the spectrum of plants in a community. Thus, the dispersion and occurrence of hosts within a site may be limited by the occurrence of fungal infection propagules (Miller 1987). However, the density of these propagules depends on the degree of fitness of a fungus-plant association (Dodd et al. 1990). In effective associations, a fungus significantly increases the rate of plant growth (Abbott and Robson 1981; Raju et al. 1990), and vigorously growing plants usually harbour both abundant mycorrhizal infections and numerous spore populations (Hetrick and Bloom 1986).

The sand being used in the recovery of the disturbed areas of the Hel Peninsula does not contain arbuscular fungi. Hence the stabilization of these areas may be hastened by introduction both of plants with high mycorrhizal dependency and fungi maintaining high effectiveness, i.e. the ability of a fungus to increase plant growth in a phosphate-deficient soil (Abbott and Robson 1981; Mosse 1972), and infectivity, i.e. the rate and extent of mycorrhizal infection formed by a fungus (Scheltema et al. 1987), in the Hel Peninsula soil conditions.

The aim of this present paper was to determine the occurrence of arbuscular fungi and mycorrhizae on the Hel Peninsula.

Materials and methods

Soil and root samples were collected from a depth of 5–30 cm using a small trowel. Samples of about 2 l were put into plastic bags and subsequently stored in a refrigerator at 4° C for 1–8 months. Because spore and species densities of arbuscular fungi are positively correlated with the degree of plant cover (Koske and Halvorson 1981), soils and roots were sampled under well-developed mature or maturing plants that grew in dense communities.

Spores of arbuscular fungi were recovered from soils by wet sieving and decanting (Gerdemann and Nicolson 1963). Both intact and crushed spores in polyvinyl alcohol/lactic acid/glycerol (PVLG) (Koske and Tessier 1983) and in Melzer's reagent were examined. Classitication, spore wall characteristics, and the spelling of scientific names are those suggested by Almeida (1989), Morton (1986), Morton and Benny (1990), and Walker (1983, 1986, 1991). Plant nomenclature follows that of Falkowski (1982) and Szafer et al. (1969). Spore colour was examined under a dissecting microscope on fresh specimens immersed in water. Colours were determined according to the *Methuen Handbook of Colour* (Kornerup and Wanscher 1983). Voucher specimens of recovered fungi have been deposited in the Department of Plant Pathology, Academy of Agriculture, Szczecin.

The mycorrhizal status of examined plant species was determined on roots washed away during wet sieving of soils. Mycorrhizal colonization of 50 stained (Phillips and Hayman 1970) root fragments with a length of about 1 cm was evaluated according to Giovannetti and Mosse (1980). The presence of *Glomus tenue* was determined in the same roots mounted on microscope slides.

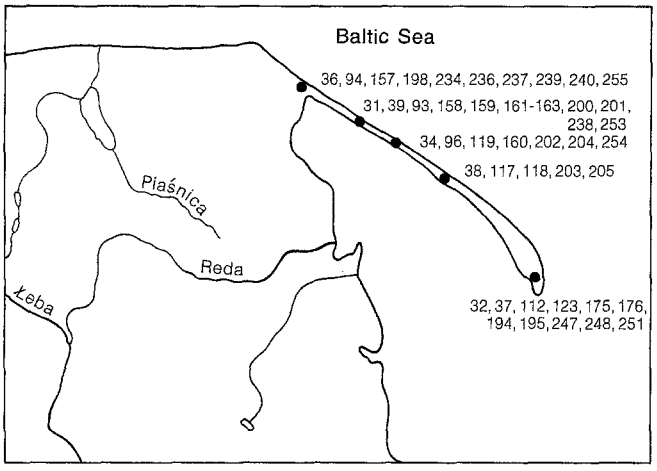


Fig. 1 Sites at which soil and root samples were collected

Differences in the structure of arbuscular fungal communities were investigated by determining the frequency of species and the spore and species densities, and by calculating dominance coefficients (Górny and Gruma 1981). The variability of spore and species densities was expressed by the coefficient of variability. The frequency of occurrence was calculated as the percentage of samples from which spores of a particular species was recovered. Spore and species density was defined by the number of spores and species occurring in 100 g dry soil. The dominance coefficient expresses the ratio of the number of spores of a particular species to the total number of spores of arbuscular fungi. The coefficient of variability is a quotient of a standard deviation and a mean expressed in percentages.

The localities and collection datas (see Fig. 1) were as follows: Chałupy: 31, 39, 23 August 1985; 93, 30 July 1986; 158, 159, 161, 162, 163, 4 June 1988; 200, 201, 28 September 1988; 238, 7 July 1989; 253, 26 August 1989; Hel: 32, 37, 21 August 1985; 112, 123, 20 August 1987; 175, 176, 194, 195, 28 September 1988; 247, 248, 251, 5 August 1989; Jastarnia: 38, 21 August 1985; 117, 118, 20 August 1987; 203, 205, 28 September 1988; Kuźnica: 34, 23 August 1985; 96, 22 July 1986; 119, 20 August 1987; 160, 4 July 1988; 202, 204, 28 September 1988; 254, 27 August 1989; Władysławowo: 36, 21 August 1985; 94, 29 July 1986; 157, 4 June 1988; 198, 28 September 1988; 234, 236, 237, 239, 240, 7 July 1989; 255, 27 August 1989.

Results and discussion

From 1985 to 1989, a total of 45 soil and root samples collected under 20 pland species of 8 plant families were examined (Fig. 1, Table 1). The chemical properties of 16 randomly chosen soil samples ranged as follows: pH (in 1 N KCl) 3.8–6.5; NO_3 12–240; P_2O_5 8–51; K_2O 5–138; Mg 6.4–362; Na 6–237; Cl 17–640 (mg/l); humus content 0.29–6.01 (%). Except for *Zea mays*, the other plant species grew in uncultivated sites. Most samples were taken from around roots of members of the Gramineae (23 samples, 11 plant species), followed by the Rosaceae (10 samples, 2 plant species) and the

Table 1 Plants examined and localities at which the occurrence of arbuscular fungi and mycorrhizae was investigated

Family and plant species	Locality (see Fig. 1)
Compositae	
Artemisia campestris L.	255
Cupressaceae	
Chamaecyparis lawsoniana (And.) Parl.	251
Thuja occidentalis L.	37, 112, 194, 195, 247, 248
Cyperaceae	
Bulboschoenus maritimus (L.) Palla	237
Ericaceae	
Calluna vulgaris (L.) Salisb.	198
Gramineae	
Ammophila arenaria (L.) Link	200, 202, 204, 205, 236
Corynephorus canescens (L.) P. B.	32, 160
Elymus arenarius L.	31
Festuca arundinaceae Schreb.	201
Festuca ovina L.	39, 157, 158
Festuca rubra spp. *fallax* (Thuill.) Hack.	36
Helictotrichon pubescens (Huds.) Pilg.	163
Holcus lanatus L.	*162*
Phragmites communis Trin.	161
Poa pratensis L.	159
Zea mays L.	38
Unknown grass	34, 94, 96, 176, 203
Juncaceae	
Juncus conglomeratus L.	237
Rosaceae	
Crataegus monogyna Jacq.	117, 254
Rosa canina L.	93, 118, 119, 123, 238, 239, 240, 253
Salicaceae	
Salix triandra L.	175

Cupressaceae (7 samples, 2 plant species). The other plant families were represented by both single soil samples and single plant species. The occurrence of arbuscular fungi was most frequently investigated in *Rosa canina* (8 samples), then in *Thuja occidentalis* (6 samples), *Ammophila arenaria* (5 samples), and *Festuca ovina* (3 samples). Mycorrhizal association in *Corynephorus canescens* and *Crataegus monogyna* were examined twice, and the other plant species were represented by single soil and root samples.

Spores of arbuscular fungi were found in all examined soil samples. About 45% of isolated spores were of the genus *Glomus* (Table 2). The occurrence of members of the other genera in spore populations was similar and ranged from 14.7% (*Gigaspora*) to 20.7% (*Acaulospora*).

Koske (1975) found spores of arbuscular fungi in 21 of 23 examined soil samples from Australian sand dunes. Of 192 soil samples collected on the Tyrrhenian coast of central Italy, 167 ones contained arbuscular fungi (Puppi and Riess 1987). Mohankumar et al. (1988) recovered spores of these fungi from the root zone of all 53 investigated plant species of 30 families colonizing sandy beach soils of the Madras coast. Thus, the present author's results and those cited above support the suggestion of Gerdemann (1968) that arbuscular fungi are probably the most widely distributed soil fungi in the world. Their common occurrence suggests that they probably play an important role in the nutrition of plants (Harley and Smith 1983) and the stabilization of sands (Koske and Polson 1984; Sutton and Sheppard 1976) of the Hel Peninsula.

Species of *Glomus* also predominated in maritime sands of Madras (India) (Mohankumar et. al. 1988), Italy (Giovannetti and Nicolson 1983; Puppi and Ries 1987), Scotland (Nicolson and Johnson 1979), Florida (Sylvia 1986; Sylvia and Will 1988), Wisconsin (Koske and Tews 1987), Hawaii (Koske 1988), and San Miguel Island (California) (Koske and Halvorson 1989). In contrast, sand dunes in Australia (Koske 1975), Rhode Island (Koske and Halvorson 1981), Massachusetts (Bergen and Koske 1984; Gemma and Koske 1988; Gemma et al. 1989), and those extending from New Jersey to Virginia (Koske 1987) were dominated by species of the genera *Gigaspora* and *Scutellospora*.

There are at least three probable reasons for the strong predominance of fungi of the genus *Glomus* over those of *Gigaspora* and *Scutellospora* in soils of the Hel Peninsula. Firstly, *Gigaspora* species more frequently occur in soils with a large amount of sand (Day

Table 2 Frequency of occurrence of four genera of arbuscular fungi in seven plant families. The frequency was calculated from: (number of spores of a given genus/number of all spores in samples of a given plant family) × 100. Values in parentheses are coefficients of variation (%). *n*, Number of soil samples examined

Plant family	*n*	*Acaulospora*	*Gigaspora*	*Glomus*	*Scutellospora*
Compositae	1	—	—	48.0	52.0
Cupressaceae	7	35.5 (88.3)	—	24.1 (148.9)	26.1 (140.3)
Cyperaceae	1	—	—	100.0	—
Ericaceae	1	4.3	—	80.4	15.2
Gramineae	23	12.1 (137.1)	8.8 (406.1)	46.9 (190.9)	27.1 (230.1)
Juncaceae	1	—	100.0	—	—
Rosaceae	10	19.1 (210.0)	8.5 (599.9)	52.9 (118.2)	5.3 (109.2)
Salicaceae	1	90.7	—	4.1	5.2
Mean		20.2	14.7	44.6	16.4

Table 3 Frequency of occurrence of four genera of arbuscular fungi in 20 plant species. The calculation method and symbols are as in Table 2

Plant species	*n*	*Acaulospora*	*Gigaspora*	*Glomus*	*Scutellospora*
Ammophila arenaria	5	1.9 (193.9)	0.4 (200.0)	35.5 (133.4)	42.2 (96.2)
Artemisia campestris	1	—	—	48.0	52.0
Bulboshoenus maritimus	1	—	—	100.0	—
Calluna vulgaris	1	4.3	—	80.4	15.2
Chamaecyparis lawsoniana	1	—	—	90.0	10.0
Corynephorus canescens	2	24.7 (47.5)	—	46.3 (57.9)	29.1 (141.4)
Crataegus monogyna	2	15.4 (141.4)	28.9 (141.4)	5.6 (141.4)	50.2 (64.3)
Elymus arenarius	1	20.0	30.0	30.0	20.0
Festuca arundinaceae	1	7.9	—	91.0	1.1
Festuca ovina	3	39.1 (102.3)	—	21.6 (150.3)	39.3 (97.8)
Festuca rubra ssp. *fallax*	1	—	—	66.7	33.3
Helictotrichon pubescens	1	7.2	—	37.8	55.1
Holcus lanatus	1	14.3	—	71.4	14.3
Juncus conglomeratus	1	—	100.0	—	—
Phragmites communis	1	—	11.1	88.9	—
Poa pratensis	1	—	—	61.1	38.9
Rosa canina	8	23.9 (192.8)	3.4 (151.2)	66.1 (96.3)	6.6 (108.6)
Salix triandra	1	90.7	—	4.1	5.2
Thuja occidentalis	6	41.4 (71.7)	—	28.2 (171.1)	30.4 (141.5)
Zea mays	1	—	—	100.0	—

et al. 1987); the genus *Scutellospora* is an ancestral group of fungi (Morton 1990) and probably prefer similar sites. The soil samples from the Hel Peninsula were mainly collected under older vegetations where the amount of sand in soil is much lower than in the root zone of plants colonizing foredunes examined by most of the authors cited above. Secondly, species of *Glomus* seem to be more sensitive to drought than members of *Gigaspora* and *Scutellospora* (Daniels and Trappe 1980; Koske 1981), and this increases the competitive ability of the latter fungi, mainly in the foredunes. However, in the Hel Peninsula soils, the moisture is probably within the optimal range for *Glomus* spp. Thirdly, the soil temperature of the Hel Peninsula is more suitable for fungi of the genus *Glomus* than those of the genera *Gigaspora* and *Scutellospora*. Daniels and Trappe (1980) found that the optimal temperature for germination of spores of *Glomus* spp. was 14–22° C, whereas spores of *Gigaspora* and *Scutellospora* from two geographically and edaphically diverse sites germinated best at 25–35° C (Koske 1981; Schenck et al. 1975); this temperature rarely occurs in the region of the Hel Peninsula (Wojterski and Bednorz 1982).

With respect to families from which more than two species were examined, *Acaulospora* spp. were most frequently associated with members of the Cupressaceae (35.5%), and most rarely with plants of the Gramineae (12.1%) (Table 2). Spores of *Gigaspora* occurred at low frequency and only in two plant families. *Glomus* spp. were most frequently found among roots of plants of the Rosaceae (52.9%), followed by the Gramineae (46.9%) and then the Cupressaceae (21.4%). Spores of the genus *Scutellospora* occurred at markedly higher frequencies around roots of plants of the Gramineae (27.1%) and Cupressaceae (26.1%) than of the Rosaceae (5.3%).

The ocurrence of fungi of the genera *Acaulospora*, *Gigaspora*, *Glomus*, and *Scutellospora* in families with single plant species was in the range 0–90.7% (Compositae, Cupressaceae, Cyperaceae, Juncaceae versus Salicaceae), 0–100% (Compositae, Cupressaceae, Cyperaceae, Ericaceae, Salicaceae versus Juncaceae), 0–100% (Juncaceae versus Cyperaceae), and 0–52% (Cyperaceae, Juncaceae versus Compositae), respectively.

For the plant species examined more than twice, *Acaulospora* spp. occurred most frequently in the root zone of *Thuja occidentalis* (41.4%), then *Festuca ovina* (39.1%), *Corynephorus canescens* (24.7%), *Rosa canina* (23.9), and *Crataegus monogyna* (15.4%) (Table 3). Spores of *Gigaspora* were relatively frequently found in soils sampled under *Crataegus monogyna* (28.9%) but relatively rarely with roots of *Rosa canina* (3.4%) and *Ammophila arenaria* (0.4%). *Corynephorus canescens*, *Festuca ovina*, and *Thuja occidentalis* did not harbour fungi of this genus. Members of the genus *Glomus* predominated in the rhizosphere of *Rosa canina* (66.1%). In contrast, of the spore population associated with *Crataegus monogyna*, only 5.6% were of *Glomus*. *Glomus* spp. were also frequently present among roots of *Corynephorus canescens* (46.3%), *Ammophila arenaria* (35.5%), *Thuja occidentalis* (28.2%), and *Festuca ovina* (21.6%). Spores of *Scutellospora* were most frequently associated with *Ammophila arenaria* (42.2%) and most rarely with roots of *Rosa canina* (6.6%). A relatively high percentage of fungi of this genus was also found in rhizosphere soils of *Festus ovina* (39.3%), *Thuja occidentalis* (30.4%), and *Corynephorus canescens* (29.1%). The frequencies of occurrence of fungi of the genera *Acaulospora*, *Gigaspora*, *Glomus*, and *Scutellospora* in the root zone of plants represented by single species were in the ranges 0–90.7%, 0–100%, 0–100%, and 0–55.1%, respectively.

Arbuscular fungi are not specific to particular host plants and practically any fungal species can infect plants that usually form arbuscular mycorrhizae (Mosse 1975). Although there is evidence that some families and species of plants prefer particular genera or species of fungi (Abbott and Robson 1981; Ali 1969; Daft and Nicolson 1972; Dominik 1952; Graw et al. 1979; Koske and Halvorson 1981; Rabatin 1979; Schenck and Smith 1981), more recent results (Koomen et al. 1987; Koske 1987; McGonigle and Fitter 1990; Wilson 1984) suggest that both the quantitative and qualitative composition of spore populations of arbuscular fungi mainly results from complex fungus/plant/habitat interactions. In addition, fungal infectivity (Scheltema et al. 1987) and effectiveness (Abbott and Robson 1981; Mosse 1972), mycorrhizal dependency (Azcon and Ocampo 1981; Graham and Syversten 1985; Saif 1987), plant vigour (Daft and Nicolson 1972; Schenck and Schroeder 1974), and the strategies of fungi for minimizing simultaneous competition for host photosynthate or cortical cells (Gemma et al. 1989) may be important in this respect. The soil samples from the Hel Peninsula were mainly collected during the plant flowering period, and the preferences found by the author may only characterize the fungus/plant associations with respect to the time at which soils and roots were sampled. However, fungi dominant at the end of the plant growing cycle should play the most important role during plant colonization in the spring of the succeeding year and should determine both the species composition and the relative proportions of coexisting fungi throughout the vegetative period. According to Wilson (1984), prior colonization by one species may suppress the development of further fungi. Hence, seasonal sporulation of different species of arbuscular fungi is probably determined by periodic changes in the activity of the quantitatively dominant fungus in a particular fungus/plant combination which enable other arbuscular fungi to colonize and development. This needs to be tested using the technique of vital staining that Kough et al. (1987) applied to investigations of responses of arbuscular fungi to fungicides.

A total of 29 spore-forming species of arbuscular fungi were found, among which were seven *Acaulospora* spp., one *Gigaspora* sp., 16 *Glomus* spp., and five *Scutellospora* spp. (Table 4). Three species, *Acaulospora* 61, *Glomus* 93, and *Scutellospora* 72 probably are undescribed fungi. Other members of the genera *Acaulospora*, *Gigaspora*, *Glomus*, and *Scutellospora* also occurred in the spore populations, as well as spores of an unrecognized generic affiliation (without a subtending hypha or a sporiferous saccule). However, they were found rarely and in low amounts, and hence assignation of morphological features, especially spore wall structure, was impossible. In addition, 25 root samples were colonized by *Glomus tenue* (Greenall) Hall, a species rarely forming spores and recognizable by delicate hyphae less than 3.0 μm in diameter and staining darker than other arbuscular fungi (Hall 1977).

Table 4 Arbuscular fungi isolated from soils of the Hel Peninsula

Fungal species	Frequency of occurrence (%)	Dominance (%)
Acaulospora capsicula	10.9	1.66
Acaulospora cavernata	10.9	7.01
Acaulospora gedanskensis	8.7	1.53
Acaulospora lacunosa	17.4	3.34
Acaulospora paulinae	15.2	2.66
Acaulospora polonica	6.5	2.05
Acaulospora 61	28.3	2.82
Unknown *Acaulospora*	4.3	0.46
Gigaspora gigantea	19.6	1.55
Unknown *Gigaspora*	4.3	0.04
Glomus aggregatum	17.4	3.47
Glomus caledonium	10.9	3.40
Glomus constrictum	32.6	10.02
Glomus deserticola	13.0	2.86
Glomus dominikii	2.2	0.07
Glomus etunicatum	2.2	0.22
Glomus fasciculatum	23.9	8.05
Glomus geosporum	6.5	0.15
Glomus heterosporum	8.7	5.61
Glomus laccatum	2.2	0.39
Glomus macrocarpum	17.4	3.80
Glomus microcarpum	26.1	16.76
Glomus mosseae	15.2	1.00
Glomus occultum	4.3	0.22
Glomus pansihalos	2.2	0.07
Glomus 93	2.2	3.78
Unknown *Glomus*	13.0	1.53
Scutellospora calospora	17.4	1.31
Scutellospora dipurpurascens	50.0	11.09
Scutellospora nodosa	2.2	0.15
Scutellospora pellucida	4.3	0.33
Scutellospora 72	6.5	0.50
Unknown *Scutellospora*	13.0	2.25
Unrecognized spores	6.5	1.22

Frequency of occurrence

Glomus tenue was associated with roots of 56.8% of the examined plants and ranked first in frequency of occurrence of arbuscular fungi on the Hel Peninsula (Table 4). The most frequently recovered species forming spores was *Scutellospora dipurpurascens*, which occurred in 50% of the soil samples examined. Other frequently found spore-forming fungi were *Glomus constrictum* (32.6%), *Acaulospora* 61 (28.3%), and *Glomus microcarpum* (26.1%). Eight species had frequencies in the range 14.1–25%, of which *Glomus fasciculatum* ranked highest (23.9%). The frequency of occurrence of seven species was in the range 5.1–15%, with *Glomus deserticola* (13%) and *Glomus caledonium* (10.9%) having the highest frequencies. Eight species occurred in less than 5% of soil samples, including *Glomus occultum* (4.3%) and *Scutellospora pellucida* (4.3%).

Table 5 Mean spore and species density in 100 g dry soil of arbuscular fungi among roots of seven plant families. Symbols as in Table 2

Plant family	*n*	Spore density	Species density
Compositae	1	50.0	5.0
Cupressaceae	7	106.1 (76.5)	4.4 (65.4)
Cyperaceae	1	59.0	1.0
Ericaceae	1	46.0	3.0
Gramineae	23	105.4 (138.1)	4.0 (58.8)
Juncaceae	1	1.0	1.0
Rosaceae	10	99.1 (98.0)	4.4 (75.9)
Salicaceae	1	269.0	5.0

Table 6 Mean spore and species density in 100 g dry soil of arbuscular fungi among roots of 20 plant species. Symbols as in Table 2

Plant species	*n*	Spore density	Species density
Ammophila arenaria	5	60.8 (121.2)	3.2 (77.8)
Artemisia campestris	1	50.0	5.0
Bulboshoenus maritimus	1	59.0	1.0
Calluna vulgaris	1	46.0	3.0
Chamaecyparis lawsoniana	1	80.0	2.0
Corynephorus canescens	2	39.0 (58.0)	5.0 (28.2)
Crataegus monogyna	2	17.5 (68.7)	3.0 (0.0)
Elymus arenarius	1	10.0	4.0
Festuca arundinaceae	1	547.0	5.0
Festuca ovina	3	65.0 (102.4)	3.0 (33.3)
Festuca rubra ssp. *fallax*	1	6.0	1.0
Helictotrichon pubencens	1	445.0	10.0
Holcus lanatus	1	7.0	4.0
Juncus conglomeratus	1	1.0	1.0
Phragmites communis	1	9.0	1.0
Poa pratensis	1	54.0	3.0
Rosa canina	8	119.15 (82.5)	4.8 (77.0)
Salix triandra	1	269.0	5.0
Thuja occidentalis	6	84.3 (105.5)	4.8 (61.0)
Zea mays	1	230.0	5.0

Spore density

The overall spore density of arbuscular fungi for the 45 100-g soil samples examined was on average 99.8 and in the range 1–547. Spore density did not correlate with any soil chemical property determined, but correlated significantly with mycorrhizal colonization ($r=0.61$; $P=0.05$). The spore density was highest in samples from the Salicaceae (269) (Table 5). However, this family was represented only by one species and one soil sample. Relatively high and similar spore densities were found in the root zones of the Cupressaceae (106.1), Gramineae (105.4) and Rosaceae (99.1). The other plant families harboured arbuscular fungi in densities from 1.0 (Juncaceae) to 59 (Cyperaceae) spores in 100 g dry soil.

The average spore density of arbuscular fungi in soils of the Hel Peninsula is similar to densities found in sand dunes of Lake Huron (Canada) (0–632 spores in 100 g dry soil) (Koske et al. 1975) and in Florida foredunes (0–577) (Sylvia 1986). Lower spore densities were found in a coastal dune in Pakistan (1–29) (Khan 1974), a sand dune system on the Tyrrhenian coast of central Italy (0–250) (Puppi and Riess 1987), a barrier sand dune on the south coast of Rhode Island (101–336) (Koske and Halvorson 1981), sand dunes of Cape Cod in Massachusetts (0.2–16.2) (Bergen and Koske 1984), and a beach replenishment site in Florida (102–355) (Sylvia and Will 1988). More abundant spore populations have been found only in Australian sand dunes (0–1100) (Koske 1975).

The differences between the spore densities in the Hel Peninsula soils and other dune sites may result from: (1) differences in climatic conditions (Anderson et al. 1984; Koske 1987), (2) different species composition and different degree of plant cover of the compared areas (Anderson et al. 1984; Benjamin et al. 1989), (3) differences in microbiological, physical, and chemical soil properties (Anderson et al. 1984; Koske 1987, 1988), (4) seasonal fluctuations in spore abundance (Gemma et al. 1989), (5) presence of nonsporulating or infrequently sporulating arbuscular fungi (Koske 1988), and/or (6) decreased activity of arbuscular fungi due to parasitism by other arbuscular fungi (Koske 1984) or other soil microorganisms (Ross and Ruttencutter 1977).

The average densities of spores associated with roots of particular plant species were highest in *Festuca arundinaceae* (547), then in *Helictotrichon pubescens* (445), *Salix triandra* (269), and *Zea mays* (230) (Table 6). However, all these plant species were represented by single soil samples. Relatively dense spore populations also occurred around the roots of *Rosa canina* (119.5). Seven plant species harboured arbuscular fungi in densities of 50–100 spores, of which *Thuja occidentalis* (84.3) and *Chamaecyparis lawsoniana* (80) ranked highest. Less than 50 spores in 100 g dry soil were found in eight plant species, with *Calluna vulgaris* (46) and *Corynephorus canescens* (39) having the highest and *Juncus conglomeratus* the lowest average spore densities.

Dominance

Glomus microcarpum (16.76%), *Scutellospora dipurpurascens* (11.09%) and *Glomus constrictum* (10.02%) were the eudominants [dominance coefficient D at and above 10.0% (Górny and Gruma 1981)] among recovered species (Table 4). The dominants (D = 5.1–10.0%) were *Glomus fasciculatum* (8.05%), *Acaulospora cavernata* (7.01%), and *Glomus heterosporum* (5.61%). The subdominants (D = 2.5–5.0%) were *Glomus macrocarpum* (3.80%), *Glomus* 93 (3.78%), *Glomus aggregatum* (3.47%), *Glomus caledonium* (3.40%), *Acaulospora lacunosa* (3.34%), *Glomus deserticola* (2.86%), *Acaulospora* 61 (2.82%), and *Acaulospora paulinae* (2.66%). The coefficients of dominance of the other species ranged from 0.07% (*Glomus dominikii*) to 2.05% (*Acaulospora polonica*).

Dunes in New South Wales (Australia) were reported to be dominated by red-brown laminate spores and *Acaulospora scrobiculata* Trappe (Koske 1975). In Italian sand dunes, the predominant fungi were *Glomus mosseae*, *Scutellospora calospora* (Giovanetti and Nicolson 1983), *Glomus macrocarpum*, and *Glomus microcarpum* (Puppi and Riess 1987). *Glomus fasciculatum* was the only species found in maritime sand dunes in Scotland (Nicolson and Johnson 1979). According to Koske et al. (1975), the most abundant arbuscular fungi in dunes of the eastern shores of Lake Huron were *Glomus caledonium* and a species forming golden-brown spores. The dominant species of a barrier dune on the south coast of Rhode Island were *Acaulospora scrobiculata*, *Gigaspora gigantea*, and *Glomus aggregatum* (Koske and Halvorson 1981). *Gigaspora gigantea* was also the most frequently recovered species in the Cape Cod dunes of Massachusetts (Bergen and Koske 1984) and in dunes extending from New Jersey to Virginia (Koske 1987). The most abundantly occurring fungus in Wisconsin sand dunes was *Glomus etunicatum* (Koske and Tews 1987). Florida dunes were dominated by *Glomus deserticola* (Sylvia 1986; Sylvia and Will 1988). *Glomus microaggregatum*, an undescribed *Glomus* sp., *Sclerocystis sinuosa* Gerd. & Bakshi, and *Scutellospora* 816 were the most frequently recovered species from around roots of Hawaiian dune plants (Koske 1988).

Species density

The species density in soil samples from the Hel Peninsula averaged 3.9 and ranged from 1 to 10. The overall species density and soil chemical properties were not significantly correlated. The species density did not correlate with the spore density. Members of the Compositae and Salicaceae harboured most species in 100 g dry soil (each five species) (Table 5), but both plant families were represented only once. High average species densities were also recorded in soils sampled under the Cupressaceae (4.4), Rosaceae (4.4), and Gramineae (4). Rhizosphere soils of the other plant families contained from 1 species (Cyperaceae, Juncaceae) to 3 species (Ericaceae) in 100 g dry soil.

The average species density of arbuscular fungi associated with plants examined at least twice was highest around roots of *Corynephorus canescens* (5), *Rosa canina* (4.8), and *Thuja occidentalis* (4.8) (Table 6). Relatively high densities also occurred under *Ammophila arenaria* (3.2), *Crataegus monogyna* (3), and *Festuca ovina* (3). Plants examined once harboured from 1 to 10 fungal species, of which *Helictotrichon pubescens* ranked highest.

The average species density of arbuscular fungi in soils of the Hel Peninsula was generally higher than densities found in dunes by Bergen and Koske (1984) on Cape Cod in Massachusetts (1.7), by Koske (1975) in Australia (1.5–2.4), by Koske (1988) on Hawaii (2.4), and by Koske and Halvorson (1981) on Rhode Island (3.1). Only plants colonizing dunes extending from New Jersey to Virginia harboured a higher average species density (4.9, in the range 4.2–6.3) (Koske 1987).

The generally higher average species density found in sites of the Hel Peninsula than at the sites mentioned above may be associated with the presence of more numerous populations of arbuscular fungi on this area (see above), because spore and species density are usually positively correlated (Anderson et al. 1984; Koske and Halvorson 1981). Sporulation of arbuscular fungi is seasonal (Gemma et al. 1989; Sylvia 1986). Thus, the sampling period may have coincided with the period of intensive sporulation of most species occurring on the Hel Peninsula. Most of the investigations in the literature were conducted at sites colonized by a few plant species, whereas the vegetation of the Hel Peninsula consists of a large number of herbaceous plants, shrubs, heaths, and trees (Gerstman et al. 1981). It has been shown that fungal and plant species diversity is positively correlated both in respect to arbuscular fungi (Anderson et al. 1984) and to other soil fungi (Christensen 1989). Another factor that could account for the higher species density is the higher soil heterogeneity of the Hel Peninsula than that of dune sites examined by other authors; higher environmental heterogeneity promotes niche differentiation (Christensen 1989).

Mycorrhizal colonization

The average mycorrhizal colonization of all examined plant species was 23.3% and was markedly lower than that of roots investigated by Giovannetti and Nicolson (1983), Koske (1988), Koske and Halvorson (1981, 1989), Koske et al. (1975), Nicolson (1960), Peterson et al. (1985), Puppi and Riess (1987), Sylvia (1986), and Sylvia and Will (1988). Only three of the 45 root samples tested contained no arbuscular fungi (numbers 118, 234, 248).

Highest mycorrhizal infections were found in *Festuca arundinaceae* (94.0%) and *Zea mays* (61.0%) (Table 7); however, these plants were examined only once. Other highly infected plant species were *Helictotrichon pubescens* (48.1%), *Rosa canina* (34.6%), *Ammophila arenaria* (30.3%), *Salix triandra* (28.1%), and *Bulboschoenus maritimus* (25.0%). The average percentage root length with mycorrhizal infections in the other plants ranged from 0 (*Juncus conglomeratus*) to 18.1 (*Chamaecyparis lawsoniana*).

Of the examined plant species, only the mycorrhizal status of *Bulboschoenus maritimus* is unknown in the literature. This species was reported to harbour relatively abundant mycorrhizal infections of *Glomus aggregatum* (Błaszkowski 1991c), despite the fact that members of the Cyperaceae are rarely associated with arbuscular fungi (Harley and Harley 1987) and that the habitat of this plant was regularly submerged by waves

Table 7 Mycorrhizal colonization of 20 plant species (%). *n*, Number of root samples examined

Plant species	*n*	Mean	Range
Ammophila arenaria	5	30.3	1.0–61.1
Artemisia campestris	1	13.2	—
Bulboshoenus maritimus	1	25.0	—
Calluna vulgaris	1	3.1	—
Chamaecyparis lawsoniana	1	18.1	—
Corynephorus canescens	2	11.6	11.1–12.1
Crataegus monogyna	2	11.1	6.1–16.1
Elymus aranarius	1	1.1	—
Festuca arundinaceae	1	94.0	—
Festuca ovina	3	12.4	0.1–26.1
Festuca rubra spp. *fallax*	1	11.1	—
Helictotrichon pubescens	1	48.1	—
Holcus lanatus	1	0.2	—
Juncus conglomeratus	1	0.0	—
Phragmites communis	1	0.1	—
Poa pratensis	1	4.1	—
Rosa canina	8	34.6	0.0–64.0
Salix triandra	1	28.1	—
Thuja occidentalis	6	15.7	0.0–51.0
Zea mays	1	61.0	—

of the Puck Gulf. Mycorrhizae seldom occur in wet soils (Anderson et al. 1984, 1986; Lodge 1989).

Ammophila arenaria, *Corynephorus canescens*, *Elymus arenarius*, *Festuca ovina*, *Holcus lanatus*, *Phragmites communis*, and *Poa pratensis* were consistently mycorrhizal in soils of the Hel Peninsula, although in other sites (Boullard 1963; Dominik 1952; Dominik and Pachlewski 1955; Dominik and Wojciechowska 1963; Harley and Harley 1987, 1990) they have been reported as mycorrhizal or nonmycorrhizal. According to Dominik (1952), *Ammophila arenaria* colonizing foredunes of the Słowinski National Park was autotrophic, whereas plants of this species in older dunes existed in association with arbuscular fungi.

Harley and Harley (1987) reported that *Rosa canina* and *Thuja occidentalis* were always associated with arbuscular fungi, whereas the present study revealed the presence of roots of these species both with and without mycorrhizal infections.

The distribution of mycorrhizae in roots is uneven and depends on the spatial distribution of infection propagules in the soil (Koide and Mooney 1987; Warner and Mosse 1983). In addition, spores of these fungi usually occur in aggregates (Sylvia 1986; Walker et al. 1982). Therefore, lack of mycorrhizae in roots may reflect either the complete absence of spores or their high dispersion, but only in the zone of sampled root fragments. This may partly explain the contradictions between the present results and those obtained by the authors cited above.

According to Harley and Harley (1987), *Crataegus monogyna*, *Festuca rubra*, and *Salix triandra* may be infected by both arbuscular and ectomycorrhizal fungi. All three plant species examined by the present author had only arbuscular infections.

Plants of the order Ericales routinely form ericoid mycorrhizae with fungi of Ascomycotina and Basidiomycotina (Harley and Smith 1983). Nevertheless, arbuscular fungi have been recorded in roots of this group of plants (see Koske et al. 1990); Koske et al. (1990) first illustrated the presence of these fungi in three species of the genus *Vaccinium* (Ericaceae) and in one species of the *Styphelia* (Epacridaceae). Thus, the observation of vesicles (no arbuscules were found) in roots of *Calluna vulgaris* growing on the Hel Peninsula extends the range of host plants of arbuscular fungi. *Calluna vulgaris*, which had arbuscular fungi in the roots, was growing alongside dense communities of grasses harbouring abundant spore populations of these fungi. This suggests that roots of *Calluna vulgaris*, usually available only to fungi forming ericoid mycorrhizae, may also be infected by arbuscular fungi when their spore concentration is high.

The distribution of arbuscular fungi on the Hel Peninsula and notes on their general occurrence

The number of soil samples in which a particular fungal species was found is given by *n*; the numbers following are those of the sites given in Table 1 and Fig. 1, and mentioned also in the list of localities and collection date.

Acaulospora capsicula Błaszk.
n = 5: 112, 175, 194, 195, 247

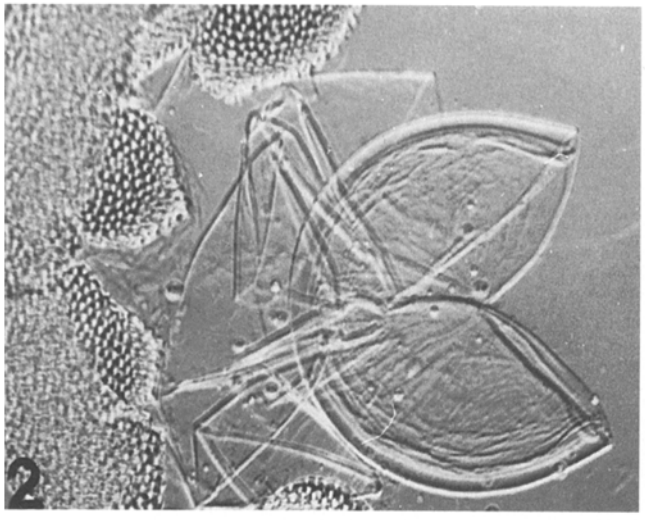
This species occurred only in the root zone of *Thuja occidentalis* and *Salix triandra* growing in a private garden at Hel. This site is about 200 m from the Baltic Sea (Błaszkowski 1990b). There is no other report of the occurrence of this species anywhere in the world.

Acaulospora cavernata Błaszk. (Figs. 2–6)
n = 5: 112, 175, 194, 195, 247

This fungus was associated only with roots of *Salix triandra* and *Thuja occidentalis*. Both plants grew in a private garden at Hel situated about 200 m from the Baltic Sea (Błaszkowski 1989).

Figs. 2–6 *Acaulospora cavernata*. Numbers indicate spore wall arrangement. **Fig. 2** Spore wall structure of crushed spore, differential interference contrast (DIC). ×282. **Fig. 3** Five inner walls (*arrows*); knobby surface of wall 6 is seen (DIC). ×457. **Fig. 4** Destroyed wall 6 of spore crushed slightly in Melzer's reagent (DIC). ×457. **Fig. 5** Inner walls with slightly disrupted wall 6 of spore vigorously crushed in polyvinyl alcohol/lactic acid/glycerol (DIC). ×353. **Fig. 6** Vigorously crushed spore in Melzer's reagent; wall 6 was torn and pushed beyond the spore (DIC). ×457

Fig. 7 *Acaulospora gedanskensis*. Intact spore with sporiferous saccule (DIC). ×245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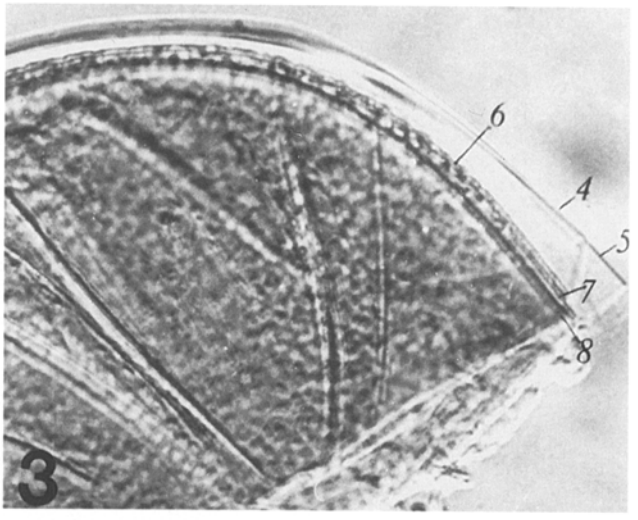
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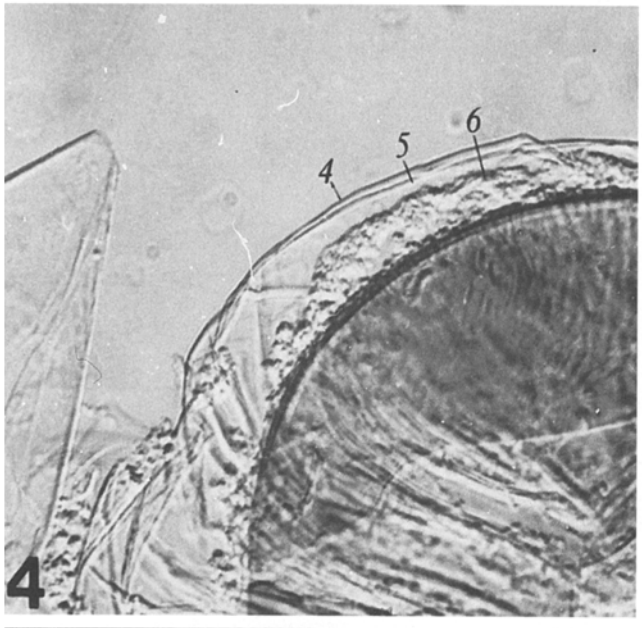
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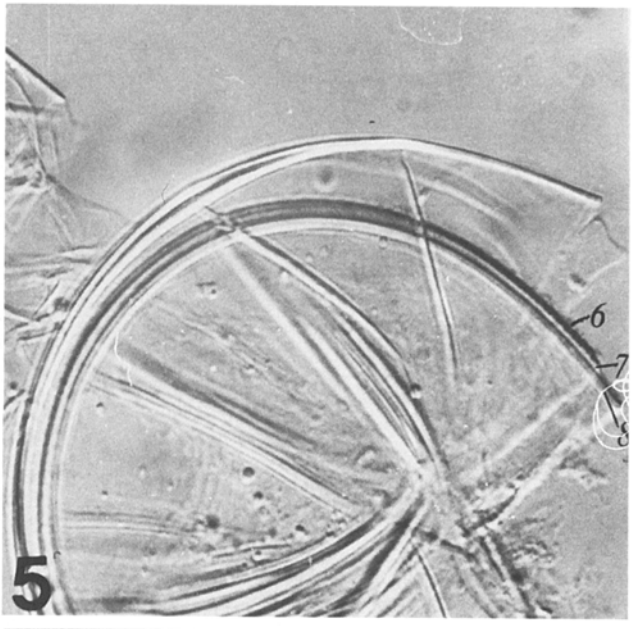
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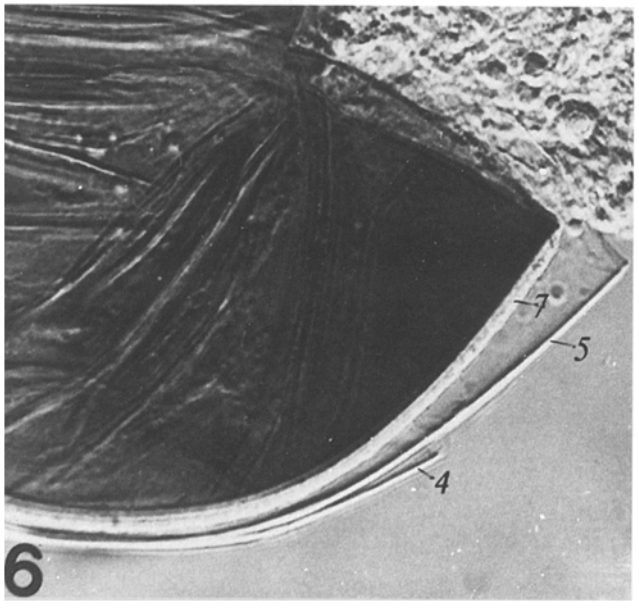
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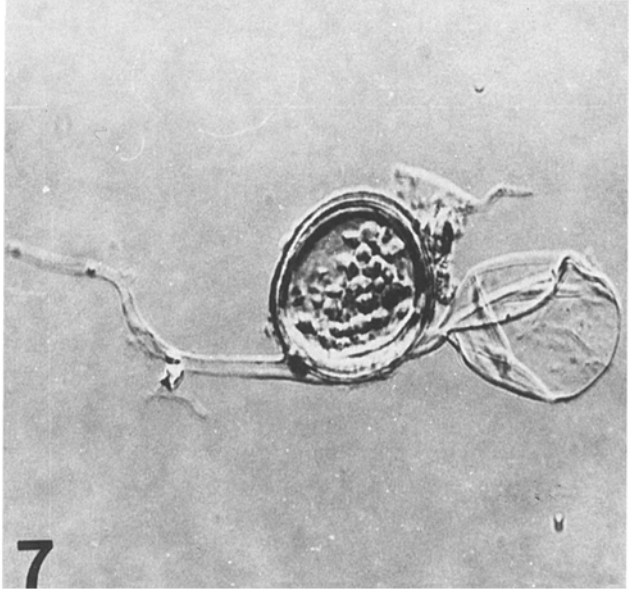
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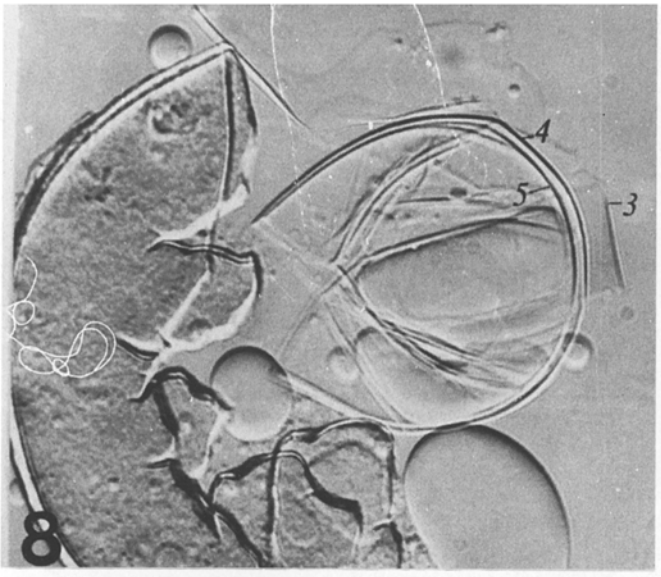
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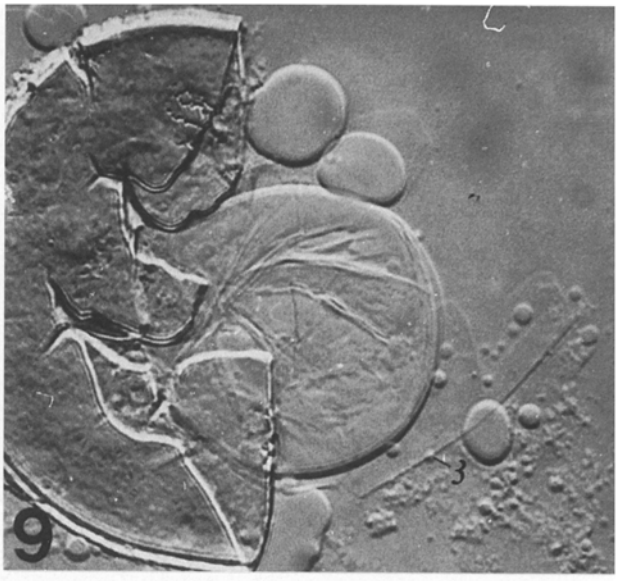
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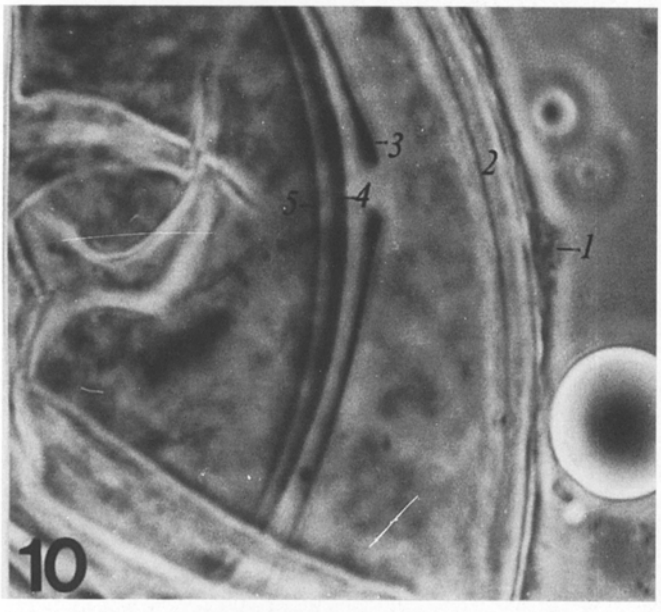
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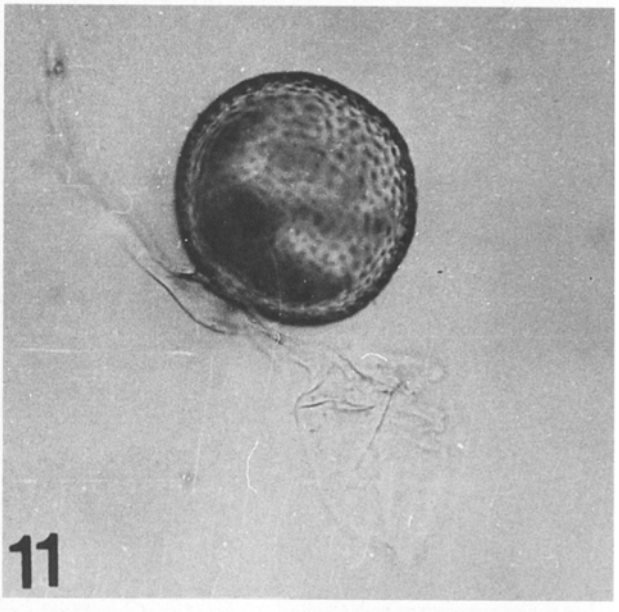
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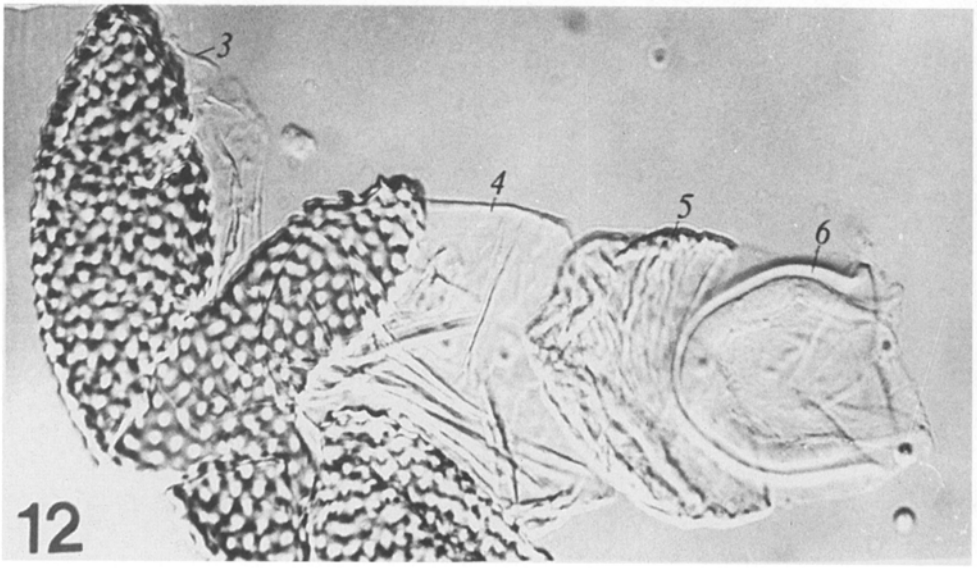
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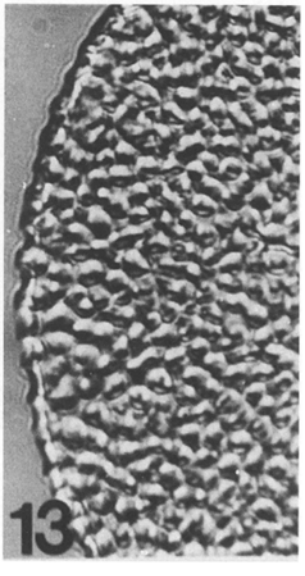
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The most distinctive feature of *A. cavernata* is the spore wall structure of eight walls (1–8) in three groups (A, B, C). Wall 1 is evanescent, hyaline, 0.8–1.5 μm thick, usually absent in field-collected spores. Wall 2 is laminated, yolk yellow (4B8) to light brown (6D8), (5.1–)5–(6.6) μm thick, evenly pitted with round, 2.0–5.0 μm, rarely ovate, 2.0–2.9 × 4.2–5.0 μm and 1.7–2.5 μm deep depressions. Wall 3 is unit, hyaline, (1.2–)2.0(–3.4) μm thick. Walls 4 and 5 are tightly adherent semi-rigid unit walls, hyaline, each 0.5–0.8 μm thick. Wall 6 is membranous, hyaline, up to 0.5 μm thick, evenly ornamented with small knobs; it usually completely tears and disappears in vigorously crushed spores. Wall 7 is coriaceous, hyaline, (1.5–)1.7(–2.9) μm thick. Wall 8 is amorphous, hyaline, 3.1–8.0 μm thick in PVLG. Only wall 8 stains beetroot purple (13D8) in Melzer's reagent. The muronym of *A. cavernata* spores is A(ELoU) B(*UU*) C(Mo*CA*).

The ornamented membranous wall 7 in spores of *A. cavernata* is not homologous with a beaded membranous wall present in most members of *Acaulospora* because of differences in the position and nature of these walls. In *A. cavernata*, the knobby wall is the sixth wall in the eight-walled structure of spores, whereas a beaded membranous wall always adheres to an innermost wall. In contrast to the relatively loosely associated granular material of a beaded membranous wall, the knobs of the membranous wall of *A. cavernata* are its integral part.

Acaulospora gedanskensis Błaszk. (Figs. 7–10)
$n = 4$: 39, 198, 202, 239

This fungus probably occurs along the whole of the Hel Peninsula, but irregularly. It was present among roots of *Calluna vulgaris*, although the compatibility of these two organisms was not proved in pot cultures. The literature does not contain any information on the occurrence of this fungus in other regions of the world.

This fungus is recognizable by its small spores (55–88 μm diameter) and the distinctive spore wall structure consisting of an evanescent outermost wall (wall 1) adherent to a laminated wall (wall 2) in wall group A, of a single, very thin (0.3–0.5 μm thick) and rigid unit wall (wall 3) in wall group B, and of two smooth adherent membranous walls (walls 4, 5) in wall group C. None of the walls react in Melzer's reagent.

◀ **Figs. 8–10** *Acaulospora gedanskensis*. Numbers indicate spore wall arrangement. Outer and inner walls in PVLG. The spores in **Figs. 8, 9** were observed with DIC (×353) and those in **Fig. 10** with phase contrast (×490)

Figs. 11–13 *Acaulospora paulinae*. Numbers indicate spore wall arrangement. **Fig. 11** Intact spore with sporiferous saccule, bright-field microscopy. ×270. **Fig. 12** Outer and inner walls of spore crushed in PVLG (DIC). ×353. **Fig. 13** Pitted spore surface (DIC). ×457

Acaulospora lacunosa Morton
$n = 8$: 93, 94, 96, 119, 157, 160, 162, 204

This is a frequently occurring and abundantly sporulating fungus on the Hel Peninsula. This fungus was previously known only from West Virginia (Morton 1986) and has not been found at any maritime site.

Acaulospora paulinae Błaszk. (Figs. 11–16)
$n = 7$: 93, 119, 157, 163, 195, 200, 201

This species is a common inhabitant of the Hel Peninsula and of maritime dunes of the Słowinski National Park (Błaszkowski 1994). Only Koske (1988) found similar spores in the root zone of an unidentified grass growing in a marshy site behind a mine dune at Punaluu, Hawaii. However, these spores were of an undescribed species of the genus *Entrophosphora*, *Entrophospora* 838.

The distinctive features of this fungus are its small (60–95 μm diameter) and pitted spores, and the structure of the spore wall, which consists of an evanescent, hyaline outermost wall (wall 1) and a laminated, pitted, hyaline to yellowish-white (3A2) inner wall (wall 2) in wall group A, of two semi-rigid, hyaline walls (walls 3, 4) in wall group B, and of a beaded membranous, hyaline wall (wall 5) adherent to an amorphous, hyaline innermost wall (wall 6) [staining beetroot purple (13D8) in Melzer's reagent] in wall group C.

Acaulospora polonica Błaszk. (Figs. 17–19)
$n = 3$: 37, 112, 195

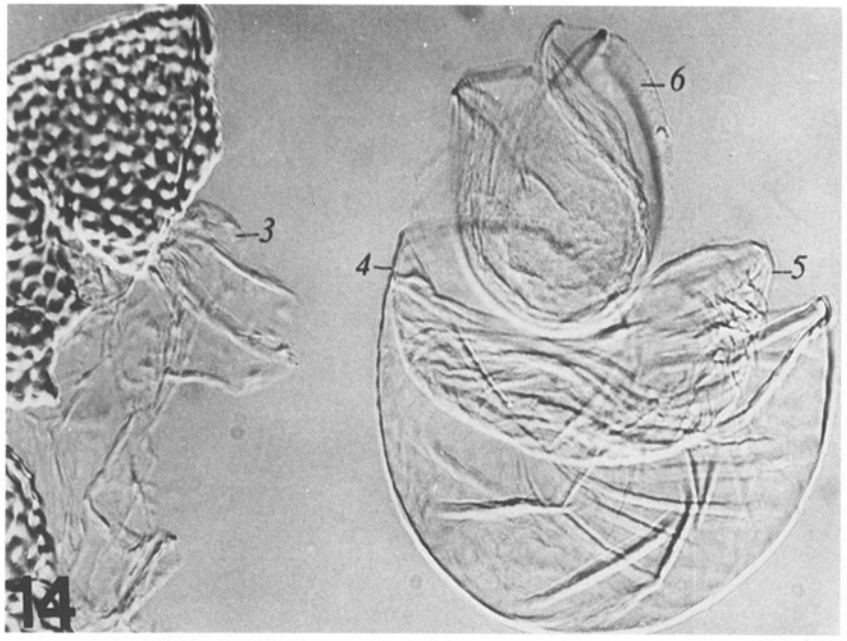
Spores of this species occur rarely and in low numbers. *A. polonica* is so far known only from the Hel Peninsula (Błaszkowski 1988).

It is distinguished by its small (70–120 μm diameter) and hyaline spores with the following muronym of the spore wall structure: A(EL) B(M) C(*M?M*). Under a light microscope, in slightly crushed spores, the innermost wall group seems to consist of only one wall, but vigorous crushing sometimes leads to separation of this group into two walls. This needs to be confirmed in studies using an electron microscope. None of the walls react with Melzer's reagent.

Acaulospora 61
$n = 13$: 31, 32, 34, 93, 119, 158, 163, 200, 201, 202, 240, 253, 254

This fungus is commonly associated with roots of various plants of the Hel Peninsula.

Acaulospora 61 forms pale yellow (3A3) to orange (5B8) spores, 98–140 μm in diameter. Their wall structure consists of seven walls (1–7) in three groups (A, B, C). Group A consists of an evanescent, hyaline, outer-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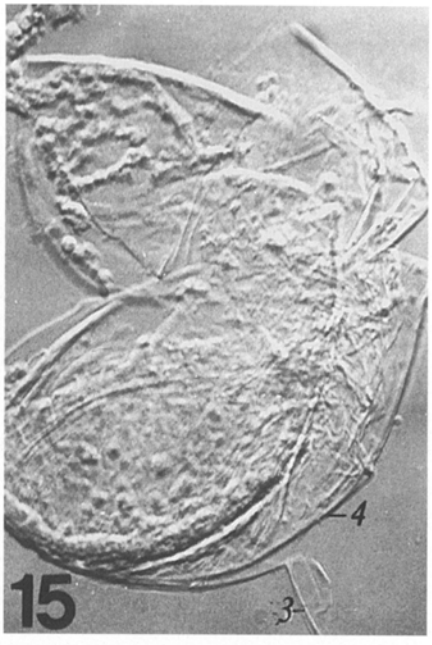
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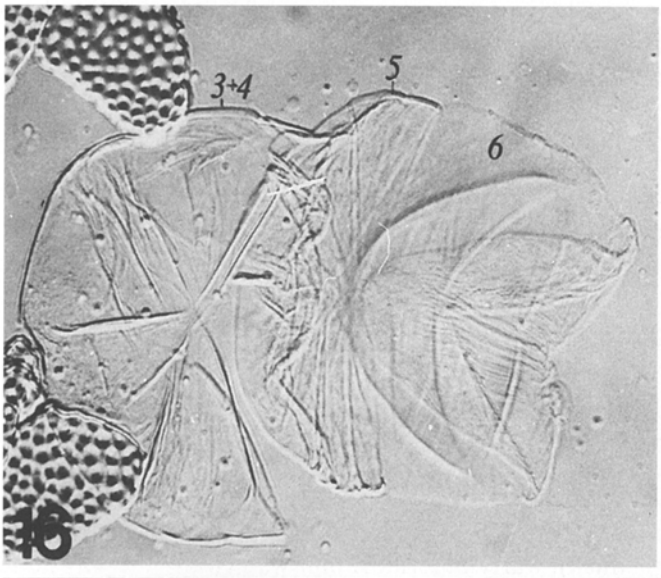
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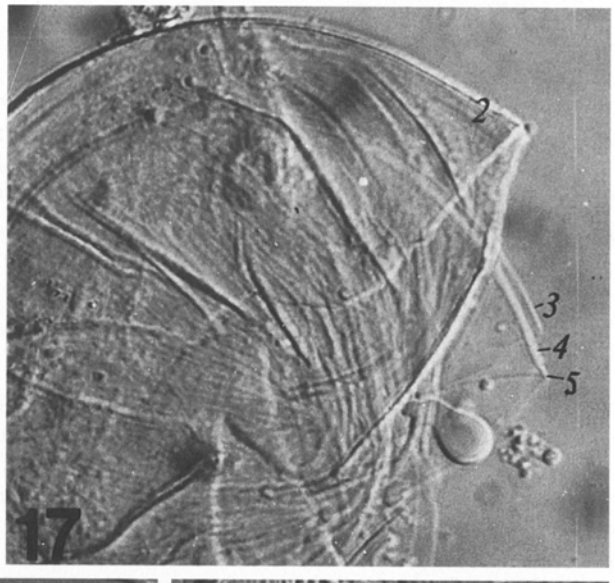
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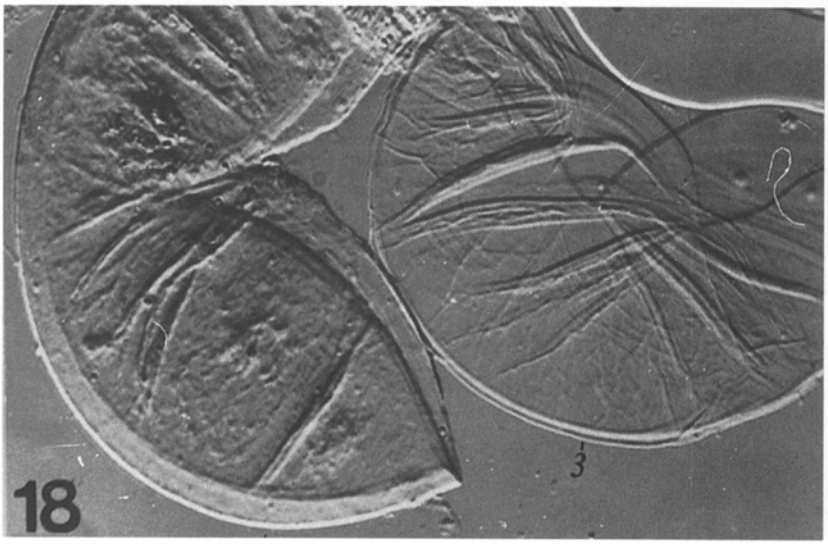
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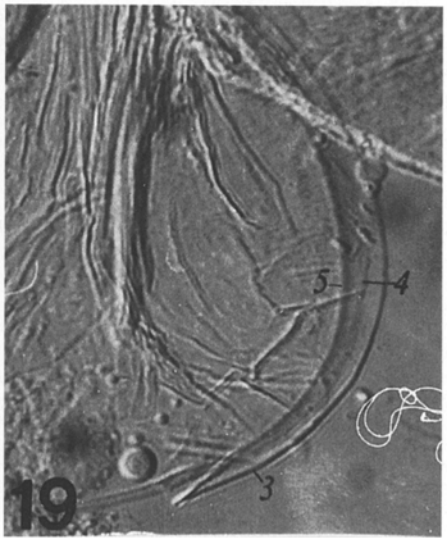
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most wall, 0.8–1.3 μm thick (wall 1), of a laminated, pale yellow (3A3) to orange (5B8) wall, 2.2–3.9 μm thick (wall 2), and of a unit, hyaline, separable wall, 0.5–0.8 μm thick (wall 3). Two tightly adherent hyaline, unit walls, 0.4–0.6 μm thick (walls 4, 5) form wall group B. Wall group C consists of a beaded membranous, hyaline wall, 0.5–1.0 μm thick (wall 6) and an amorphous, hyaline wall (wall 7) of variable thickness in PVLG, 0.8–1.2 μm thick and staining beetroot purple (13D8) in Melzer's reagent.

Gigaspora gigantea (Nicol. & Gerd.) Gerd. & Trappe
$n=9$: 31, 34, 96, 118, 119, 123, 161, 234, 254

G. gigantea is common and more often than not dominant in spore populations recovered from the root zones of dune plants of the USA (Bergen and Koske 1984; Gemma et al. 1989; Koske 1987; Koske and Halvorson 1981; Koske and Tews 1987; Sylvia and Will 1988). This species also occurs in Australia (Koske 1975).

Glomus aggregatum Schenck & Smith emend. Koske
$n=8$: 37, 38, 93, 123, 162, 163, 237, 255

G. aggregatum has been reported to be common inhabitant of sand dunes of the eastern coast of the USA and of the Great Lakes (Koske 1985, 1987; Koske and Halvorson 1981). It was present at Wisconsin dune sites (Koske and Tews 1987), among Hawaiian dune plants (Koske 1988), in sandy soils on San Miguel Island (Koske and Halvorson 1989), and in Florida dunes (Sylvia 1986; Sylvia and Will 1988).

The fungus probably plays an important role in the stabilization of dunes through its frequent occurrence in association with dune plants and because of the formation of extensive extramatrical hyphae binding sand grains into aggregates (Błaszkowski 1991b; Koske 1985).

G. aggregatum is easily recognizable by its occurrence in aggregates containing one-, two- or three-walled spores, frequently with inner proliferations (Błaszkowski 1991b; Koske 1985; Schenck and Smith 1982).

Glomus caledonium (Nicol. & Gerd.) Trappe & Gerd.
$n=5$: 38, 123, 159, 160, 238

Spores of this species have been reported in sand dunes on the eastern shores of Lake Huron (Koske et al. 1975) and in dunes from northern New Jersey to Virginia (Koske 1987).

Glomus constrictum Trappe
$n=15$: 112, 118, 119, 123, 158, 159, 160, 163, 175, 176, 194, 195, 200, 238, 251

G. constrictum has been reported to be of minor importance in the barrier sand dunes extending from northern New Jersey to Virginia (Koske 1987) and to be a rare arbuscular fungus of Hawaiian dune plants (Koske 1988).

This fungus is distinguished by its dark spores and constricted spore base. Difficulties may be encountered in the identification of the spores of this fungus because of the frequent lack of the outermost evanescent wall that adheres to a laminated wall in fully developed specimens (Błaszkowski 1990a).

Glomus deserticola Trappe et al.
$n=6$: 32, 37, 93, 160, 176, 195

G. deserticola has been reported to occur regularly as the most abundantly sporulating arbuscular fungus in Florida dunes (Sylvia 1986; Sylvia and Will 1988); other dune sites in the world did not contain this fungus.

Glomus dominikii Błaszk. (Figs. 20–23)
$n=1$: 93

This species has not been found at any other sites with maritime vegetation.

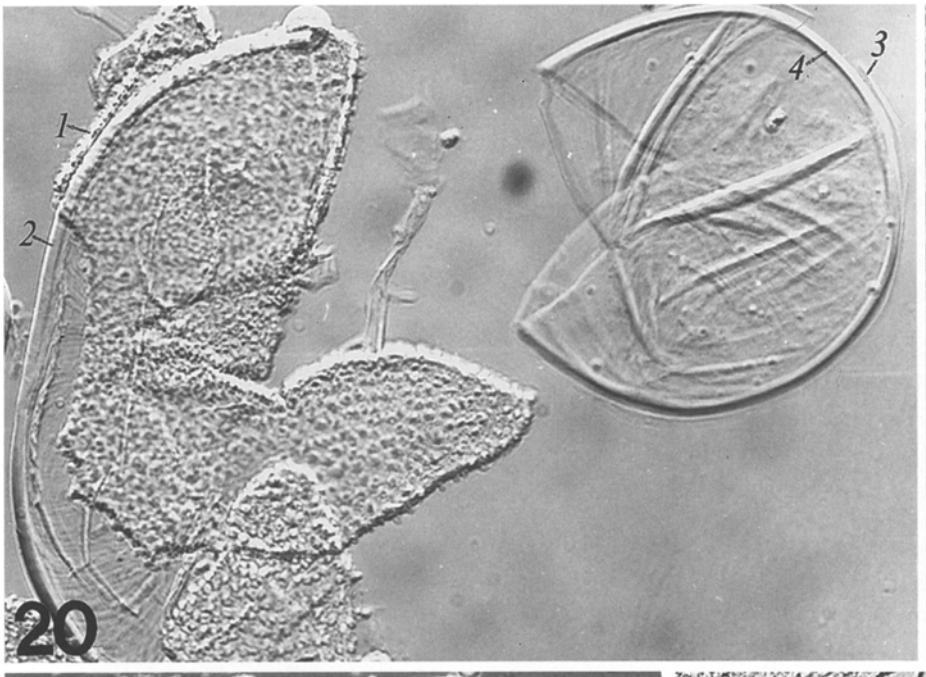
The distinctive features of this fungus are the white to orange-white (6A2) spores with a characteristic wall structure. Wall group A consists of a thin (0.7–1.5 μm thick), warty outermost unit wall (wall 1) tightly adherent to an inner laminated wall (wall 2), 2.0–3.5 μm thick. A hyaline, thin (0.5–0.8 μm thick) membranous wall (wall 3) and a relatively thick (1.5–2.8 μm thick) but flexible coriaceous wall (wall 4) forms wall group B. Wall 4 stains ruby red (12D8) in Melzer's reagent. The subtending hypha is straight, cylindric, often slightly broadening distally, occluded by a hyphal plug.

Glomus etunicatum Beck. & Gerd.
$n=1$: 255

G. etunicatum was regularly present in dunes of Rhode Island (Koske and Halvorson 1981), was the most frequently isolated arbuscular fungus from Wisconsin sand dunes (Koske and Tews 1987), and occurred in sandy soils on San Miguel Island (Koske and Halvorson 1989).

◀ **Figs. 14–16** *Acaulospora paulinae*. Numbers indicate spore wall arrangement. Outer and inner walls of spores crushed in PVLG (DIC). Magnification ×353 in **Figs. 14** and **15**, ×457 in **Fig. 15**

Figs. 17–19 *Acaulospora polonica*. Numbers indicate spore wall arrangement. Wall structure of crushed spores in PVLG (DIC). ×457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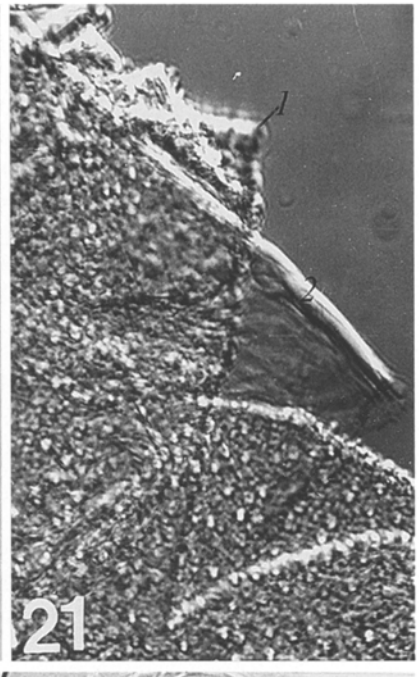
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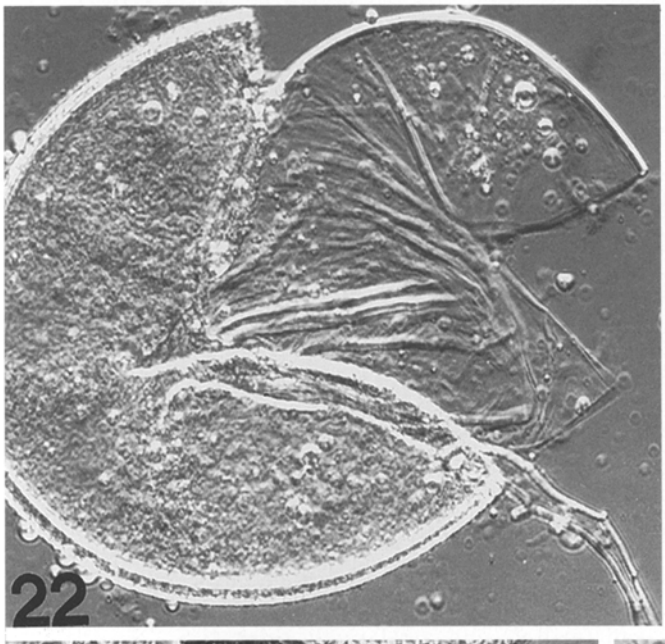
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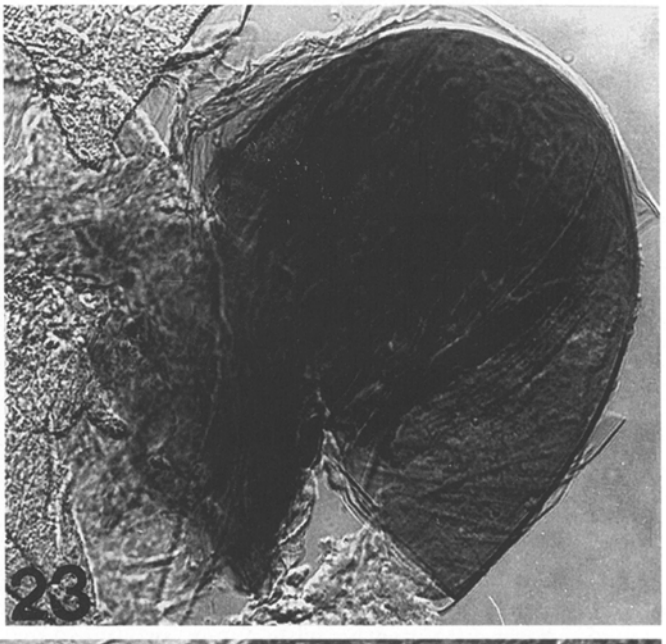
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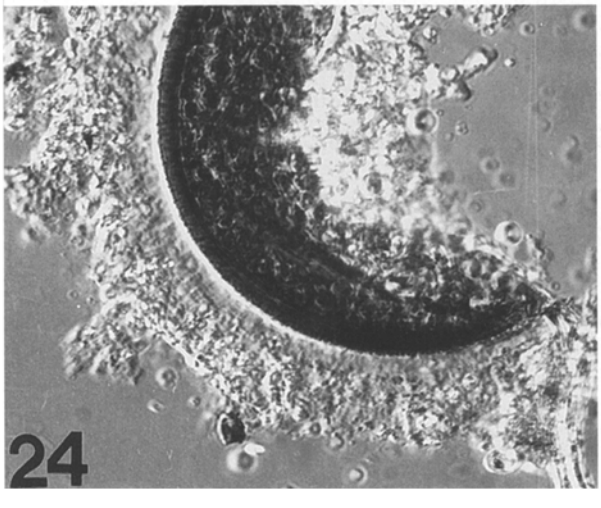
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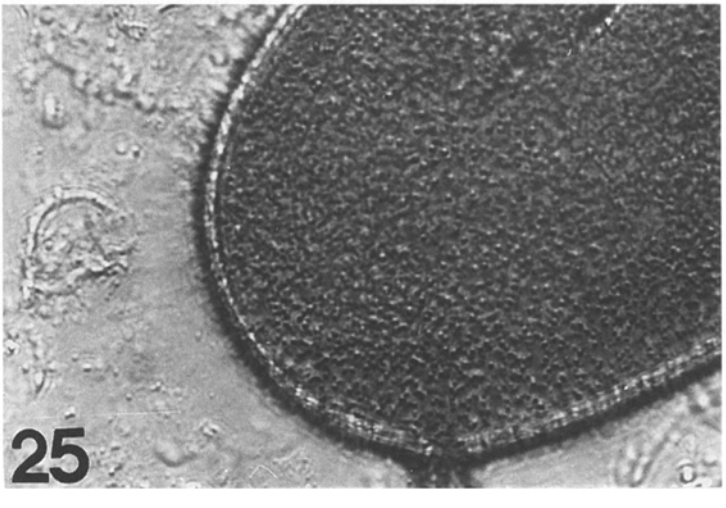
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Glomus fasciculatum (Thaxter) Gerd. & Trappe emend. Walker & Koske
$n=11$: 32, 33, 37, 38, 94, 96, 119, 123, 162, 200, 202

This species was found in Italian sand dunes (Giovannetti and Nicolson 1983; Puppi and Riess 1987), occurred in a maritime dune in the United Kingdom (Nicolson and Johnson 1979) and in dunes of Cape Cod, Massachusetts (Bergen and Koske 1984).

Glomus geosporum (Nicol. & Gerd.) Walker
$n=3$: 31, 32, 37

This species was present in a sand dune in Italy (Puppi and Riess 1987) and occurred commonly in Wisconsin dunes (Koske and Tews 1987).

Glomus heterosporum Smith & Schenck
$n=3$: 200, 202, 239

There is no report of the occurrence of this species at other dune sites.

Glomus laccatum Błaszk.
$n=1$: 163

This species was associated only with roots of *Helictotrichon pubescens*. The original site of this fungus (Błaszkowski 1988) is about 30 km from the Hel Peninsula, and it was here that *Glomus laccatum* was found for the second time in the world.

Glomus macrocarpum Tul & Tul.
$n=8$: 33, 36, 37, 39, 93, 96, 163, 201

G. macrocarpum has been recorded in dunes on the Tyrrhenian coast of central Italy (Puppi and Riess 1987) and commonly in Wisconsin dunes (Koske and Tews 1987).

Glomus microcarpum Tul. & Tul.
$n=12$: 34, 38, 39, 96, 119, 123, 163, 198, 200, 201, 202, 204

This species was present in a sand dune system on the Tyrrhenian coast of central Italy (Puppi and Ries 1987) and in beach soils of Madras (Mohankumar et al. 1988).

Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe
$n=7$: 31, 34, 37, 38, 93, 94, 161

G. mosseae was present in Italian sand dunes (Giovannetti and Nicolson 1983; Puppi and Ries 1987) and in sandy soil but not in dunes of Wisconsin (Koske and Tews 1987).

Glomus occultum Walker
$n=2$: 93, 117

This species was found at low densities in the barrier dunes from New Jersey to Virginia (Koske 1987). Mohankumar et al. (1988) recovered spores of *G. occultum* from sandy beach soils of the Madras coast.

Glomus pansihalos Berch & Koske (Figs. 24, 25)
$n=1$: 112

G. pansihalos was present in sand dune soils in California, New Jersey and Michigan (Berch and Koske 1986) and in dunes extending from New Jersey to Virginia (Koske 1987). Koske and Halvorson (1989) found spores of this fungus in sandy soils on San Miguel Island.

Glomus 93
$n=1$: 253

This species was associated with roots of *Rosa canina*. In pot cultures, it formed vesicular-arbuscular mycorrhizae with *Festuca rubra* L., *Sorghum sudanensis* (Piper) Stapf, and *Trifolium pratense* L.

This fungus forms hyaline to yellowish-white (3A2) spores, 80–140 μm in diameter. Spores have three walls (1–3) in one group (A). Wall 1 is evanescent, hyaline, 0.8–2.0 μm thick. Wall 2 is laminated, hyaline to yellowish-white (2A2), 1.0–7.5 μm thick. Wall 3 is membranous, hyaline, 0.3–0.6 μm thick, tightly adherent to wall 2. The subtending hypha is straight or recurvate, cylindric, 5.0–12.5 μm wide at the spore base, occluded by both the innermost membranous wall 3 and a septum in the subtending hypha.

Scutellospora calospora (Nicol. & Gerd.) Walker & Sanders
$n=8$: 32, 93, 94, 96, 117, 119, 123, 163

S. calospora has been recovered from dunes in Australia (Koske 1975), Italy (Bergen and Koske 1984; Gemma et al. 1989; Giovannetti and Nicolson 1983; Puppi

◀ **Figs. 20–23** *Glomus dominikii*. Numbers indicate spore wall arrangement. **Figs. 20–22** Wall structure of crushed spores in PVLG (DIC). ×353 (**Figs. 20, 22**); ×457 (**Fig. 21**). **Fig. 23** Wall 4 stained dark in a spore crushed in Melzer's reagent (DIC). ×353

Figs. 24, 25 *Glomus pansihalos*. **Fig. 24** Crushed spore with expanded outermost wall in PVLG (DIC). ×282. **Fig. 25** Warty ornamentation of wall 2 (DIC). ×353

and Ries 1987) and the USA (Koske 1987; Koske and Halvorson 1981; Koske and Tews 1987).

Scutellospora dipurpurascens Morton &. Koske
$n=23$: 34, 94, 96, 112, 117, 157, 159, 162, 163, 175, 195, 198, 200, 201, 204, 205, 236, 247, 248, 251, 253, 254, 255

This species also predominated in maritime dunes of the Słowinski National Park (Błaszkowski 1994) and is probably the most frequently occurring arbuscular fungus of the genus *Scutellospora* in other soils in Poland (Błaszkowski 1991c). There is no report of the presence of *S. dipurpurascens* at other dune sites of the world.

Scutellospora nodosa Błaszk.
$n=1$: 175

This species only occurred around the roots of *S. triandra* growing in a private garden at Hel (Błaszkowski 1991a). There is no report of the occurrence of this fungus in other regions of the world.

Scutellospora pellucida (Nicol. & Schenck) Walker
$n=2$: 123, 255

Spores of this fungus have been rarely found in sand dunes of Cape Cod, Massachusetts (Bergen and Koske 1984) and in the barrier dunes extending from northern New Jersey to Virginia (Koske 1987). This species was also present at maritime site in Dartmouth, Massachusetts (Gemma et al. 1989).

Scutellospora 72
$n=3$: 118, 119, 255

This species probably occurs along the whole of the Hel Peninsula, but irregularly and usually in low numbers.

The distinctive features of this fungus are the apricot yellow (5B8) to yellowish-brown (5E8), smooth or slightly roughened spores, 140–240 μm in diameter, with eight walls (1–8) in two groups (A, B). Group A consists of a unit, smooth or slightly roughened, greyish orange (5B5), outermost wall, 0.7–1.2 μm thick (wall 1) adherent to a laminated, apricot yellow (5B6) to yellowish-brown (5E8) wall, 5.4–13.0 μm thick (wall 2) and a membranous, hyaline wall, 0.4–0.7 μm thick (wall 3). Walls 4–8 form wall group B. Wall 4 is coriaceous, hyaline, 1.0–1.7 μm thick. Wall 5 is membranous, hyaline, 0.7–1.5 μm thick and usually adheres to wall 4. Wall 6 is coriaceous, hyaline, 2.2–4.4 μm thick. Wall 7 is membranous, 0.5–0.7 μm thick and tightly adheres to wall 6. Wall 8 is amorphous and hyaline. Walls 2, 7, and 8 stain in Melzer's reagent.

Acknowledgement This research was supported in part by The Committee of Scientific Researches, grant no. PB 5.0271.91.01.

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