

Species of the Genus *Glomites* As Plant Mycobionts in Early Devonian Ecosystems

I. V. Karatygin, N. S. Snigirevskaya, and K. N. Demchenko

Komarov Botanical Institute, Russian Academy of Sciences, ul. Professora Popova 2, St. Petersburg, 197376 Russia
e-mail: ikar34@yandex.ru, natsnig@mail.ru, sardonio@yandex.ru

Received December 10, 2004

Abstract—Members of the genus *Glomites* played a prominent role as plant mycobionts in the Early Devonian paleoecosystems. Remains of fossil fungi are studied from silicified tissues of the axial organs of several specimens of the Early Devonian *Rhynia gwynne-vaughanii* Kidston et Lang and *Aglaophyton major* (Kidston et Lang) Edwards. Among them a symbiont of vesicular-arbuscular endomycorrhiza, the fungus *Glomites*, is studied. The morphology of its mycelium, vesicles, glomoid spores, and sporocarps is described in detail. The information obtained allows the description of a new species, *Glomites sporocarpoides* Karatygin, Snigirevskaya, K. Demchenko et Zdebska. This is the third species of this genus and the first species with sporocarps from Devonian deposits. Fungal sporocarps have been found in both dying plant tissues and in dispersed plant remains. Developmental stages of glomoid spores are revealed. *G. sporocarpoides* is characterized by the presence of both symbiotic and distinct pathogenic features. Similarities and dissimilarities in the formation of ancient and modern endomycorrhizae are discussed.

DOI: 10.1134/S0031030106050121

Key words: mycorrhiza, Early Devonian, Rhyniophyta.

INTRODUCTION

Endomycorrhizal fungi are currently known in more than 240 000 plant species, that is about 80% of the total number of all vascular plants. Members of the genus *Glomus* are the most common: this genus includes approximately 50 species growing on all continents and in virtually all ecosystems. This phenomenon repeatedly led to the hypothesis that endomycorrhiza is a very ancient type of symbiotic relationship, and that its significance for the colonization of the Devonian land might have been very high (Pirozynski and Malloch, 1975; Pirozynski and Dalpé, 1989; Karatygin, 1993, 2005; Remy et al., 1994; Taylor, 1990; Karatygin and Snigirevskaya, 2004; etc.).

The expansion and functioning of endomycorrhizae during the Early Devonian is crucial for understanding biotic relations between different elements of paleoecosystems, in particular, between plants and fungi. The study of associations between the first endophytic fungi and extinct plants clarifies one of the important characteristics of the most ancient terrestrial ecosystems, since it is known that the highly branching net of mycorrhiza facilitates the exchange of oxygen and phosphorus between symbionts. In addition, it was supposed that the transition from simple dichotomizing plants to sinuous recumbent forms was facilitated by the accelerated evolution of biosynthetic paths, which in early terrestrial plants included the transformation of primary metabolites into cellulose and lignin (Niklas, 1976). Such biosynthetic changes, which were obviously initiated by parasites or symbionts, were ar-

chemosis for vascular plants. The idea that lignification of Devonian plant cells originated as a protective reaction against parasitic and saprophytic fungi was first expressed as early as 1947 (Tauson, 1947).

Many questions concerning the biotic relationships between autotrophs and heterotrophs in ancient ecosystems can only be addressed by a comparative analysis of related living organisms and their ancestors. Thus, there is some evidence that signal molecules (e.g., flavonoids, cytokinins, phytohormones, and phenols) that are produced in cells of modern plants stimulated by fungal hyphae were present in paleoecosystems as early as the Devonian (Harrison, 1997).

In their classical study of the matrix of the Rhynie Chert Bed, Kidston and Lang (1921) described in the tissues of protostelic subterranean organs (rhizomoids) of the most ancient terrestrial plants (*Rhynia*, *Asteroxylon*, and *Horneophyton*) approximately 15 fungal forms, which were originally included in the heterogeneous genus *Palaeomyces*. Kidston and Lang were the first to pay attention to the similarity between certain structures of these fungi (cenocytic hyphae, terminal and intercalary vesicles, and spores) and endomycorrhizal fungi that grow, for example, on modern members of *Psilotum* and *Tmesipteris*, which among all modern plants show the maximal similarity to Rhyniophyta. In the same matrices, in subterranean organs of *Rhynia gwynne-vaughanii*, various spores of endophytic fungi were revealed as well as their clusters or, often, sporocarps (cluster enclosed in a joint coat; Boullard and Lemoigne, 1971; Sharma et al., 1993;

Lemoigne and Zdebska, 1980). These structures are also typical of modern mycobionts of endomycorrhiza. Later, the similarity of spores found in tissues of Devonian plants to modern analogues of spores of endomycorrhizal fungi of the genera *Glomus* and *Sclerocystis* was underlined (Pirozynski and Dalpé, 1989; Taylor and White, 1989).

Glomites Taylor, Remy, Hass et Kerp was described from subterranean Early Devonian axes from the Rhynie Chert Bed (Taylor et al., 1995). The diagnosis of the genus is mostly based on the morphology of interstitial mycelium and arbuscles. To date, two species of *Glomites* have been known. The type species, *G. rhyniensis* Taylor, Remy, Hass et Kerp, grows on the axes of *Aglaophyton major* (Kidston et Lang) D. Edwards. From the Middle Triassic of Antarctica, Phipps and Taylor (1996) described *G. cycestris* Phipps et Taylor growing on roots of *Antarcticycas*. Later, the morphology of arbuscles and interstitial mycelium was used for the differentiation between *Glomites* and *Gigasporites*, another Triassic endomycorrhizal fungus (Phipps and Taylor, 1996). Recent evidence have revealed that supposed mycobionts of endomycorrhiza (or their ancestors) occur in even older deposits. In particular, the fungus *Palaeoglomus grayi* Redecker, Kodner et Graham was described from Ordovician dolomites (455–460 Ma, Wisconsin, United States). It is characterized by hyphae 3–5 µm in diameter and spores of 40–95 µm that are arranged in loose aggregates (Redecker et al., 2000a, 2002).

The present paper describes well-preserved remains of *Rhynia gwynne-vaughanii* Kidston et Lang and *Aglaophyton major* (Kidston et Lang) D. Edwards; a fossil fungus represented by a mycelium, vesicles, and sporocarps with glomoid spores is identified and described. Many morphological and functional characters of this fungus resemble symbionts of endomycorrhizae of modern plants, members of the genus *Glomus*, in particular, the thoroughly studied species *G. intraradicis* Schenck et Smith, which forms endomycorrhiza with *Lotus* and *Medicago* (Demchenko et al., 2004).

MATERIALS AND METHODS

Samples of flinty slates (= cherts) with embedded silicified remains of plants (collections of A.L. Takhtajan, St. Petersburg, and I.D. Zdebska, Kraków) were studied. The samples (collections nos. 1166 and 887) are housed in the Komarov Botanical Institute of the Russian Academy of Sciences (BIN). Transparent sections were made, 40–100 µm thick. Slides nos. 1166/1/3, 1166/1/8, 1166/1/2-2, 887/4/1, 887/2/1, and 1166/1/3-1, in which fungal remains are most distinctly seen, are studied in detail.

The Rhynie Chert Bed is situated in the Lower Old Red Sandstones and considered within the Pragian (Siegenian) Stage (Richardson, 1967; Trewin and Rice, 1992; Trewin, 1996; Trewin et al., 2003). Recent studies have shown that *Aglaophyton*, *Rhynia*, *Asteroxylon*,

and other plants of the Early Devonian flora of Rhynie grew on dry land rather than in swamps (Trewin, 1994; Anderson and Trewin, 2003). The silicified tissues of the axes of several Early Devonian plants that inhabited these ecosystems contain numerous fungal remains. Even in small samples of Rhynie chert, successive burials are distinct in the vertical section on the sites where *Rhynia* and accompanying plants *Aglaophyton*, *Asteroxylon*, and *Winfrenatia* (the most ancient lichen) grew. The particular value of the material under study is the prevalence of pure stands of plants, with small amounts of debris, and the high quality of preservation. Fungal remains at various ontogenetic stages are also perfectly preserved in the plant tissues. As a rule, these remains are distinguishable even through a stereoscope in reflected light with the aid of low magnification; therefore, some of the sections were purposefully made after preliminary screening of the surface of the samples. Photomicrographs were made using an Olympus BX51 microscope, a Zeiss camera, and KodakGold-100 film.

RESULTS

The most numerous fungal remains were found in axes of *Aglaophyton* and *Rhynia*. Both stomata and rhizoids were observed in the transverse section of a rhizomoid *Rhynia gwynne-vaughanii* (Pl. 18, fig. 1; rhizoids are not shown). This rhizomoid is most likely to be trailing and semisubterranean rather than subterranean. We identified the transverse section of an axis with numerous chlamyospores and vesicles as cf. *Aglaophyton major*.

The plant tissues contain two types of mycelium: vegetative and sporogenous. The former is formed by aseptate thin-walled hyphae that abundantly branch in the hypodermis. The diameter of the hypha of the vegetative mycelium is (2.5) 3.5–5.4 (11) µm. Usually hyphae vary in diameter and are irregularly thickened along their length. The hyphae develop both between (more often) and within cells (Pl. 18, figs. 2, 3). At early stages, rapid growth of hyphae in the cortex can apparently proceed without visible damage of cortical cells. The sporogenous mycelium forms terminal glomoid spores. In intercellular spaces, it forms glomoid spores, either solitary, or in groups of two or three spores, or in balls. Sporogenous mycelium may initiate the formation of sporocarps in intercellular spaces (Pl. 18, fig. 7). The hyphae of sporogenous mycelium located in the initial areas of their accumulation twist and intertwine to form numerous contacts between cellular walls (Pl. 18, figs. 2, 3, 7). Slimy and swollen cellular walls form gel-like hydrophilic matrix, in which spore differentiation takes place.

Most modern species of the Glomeraceae are known to form interstitial vesicles. The rate and modes of their development in the roots vary depending on the species of the host plant and changing ecological conditions (Tommerup, 1984; Morton, 1988). In our material, vesicles frequently occur both between and within cells (Pl. 18, figs. 4, 5). The size of the vesicles varies signif-

icantly. In some of them hyphal appendages or stalks 3–4 μm in diameter are distinguishable (Pl. 18, fig. 4). Some *Glomus* species have vesicles that can transform into thick-walled spores 160–320 μm in diameter that may be considered as true chlamydospores, or dormant spores. The transformation of vesicles into thick-walled rounded chlamydospores is often visible in slides (Pl. 18, figs. 8, 9). Very often, chlamydospores collapse and compress their content (Pl. 18, fig. 9).

No well-developed intercellular arbuscles comparable to those described in the other two *Glomites* species (Taylor et al., 1995) have been found. However, a concentrically situated zone of one layer of parenchymal cells is distinct in the second and third outer layers of the cortex in transverse sections of subterranean axes of *Rhynia* and *Aglaophyton* (Pl. 18, fig. 1). Most of these cells are filled with granular material apparently resulting from the collapse of arbuscles. Structurally, these cells do not differ from normal cells, either in size or in well-developed intercellular spaces. Among the normal cells, some cells show evidence of severe damage. In some cells it is possible to distinguish three-dimensional branching mycelial structures, which may be realistically considered as arbuscles during lysis (Pl. 18, fig. 6).

In some modern mycobionts, arbuscles are ephemeral and only exist for a short time, being totally destroyed in four to six days and leaving an amorphous mucous mass of fungal origin (Gorbunova, 1956). It is quite possible that we have not so far found more definite arbuscles because of their short life span. Destruction of arbuscles is usually considered as a result of the defense reaction of plant cells.

The formation in plant tissues of irregularly spherical sporocarps (250–350 μm in diameter) is a characteristic feature of *Glomites sporocarpoides* sp. nov. The number of glomoid spores in the sporocarps varies from two or three to a few tens (Pl. 19, figs. 1–4). The spores are spherical or ellipsoidal, 50–60 μm in diameter. The sporocarps are enveloped with a peridium, which is thin and one-layered at first stages of differentiation and multilayered in mature sporocarps. The peridium saves moisture in the developing sporocarp, forms stable microecological conditions, and protects spores from biotic and abiotic environmental factors.

The formation of sporocarps usually starts in intercellular spaces in clusters of sporogenous mycelium

(Pl. 19, fig. 7). As spores differentiate and their sizes increase, the total fungal mass in the sporocarps increases, causing the expansion of intercellular spaces and the constriction of cellular walls of the plant (Pl. 19, fig. 1). The cells of the cortex of the plant surrounding the sporocarps shrink and collapse. Spores within the sporocarp mature asynchronously. In the fully developed sporocarp there are many deformed and damaged spores and remains of their exosporia. The formation of sporocarps is most frequently completed in a tissue that has died completely.

In the tissues of *Rhynia gwynne-vaughanii* loose sporocarps or balls consisting of glomoid spores without peridium often occur (Pl. 19, figs. 5, 6). Such clusters of spores are most often situated in the outer cortex. The number of spores there varies from 3–5 to 30–40. Spores in the aggregates are spherical or elliptical, thin-walled, 18–24 μm in diameter, with a smooth coat 1.2–2.2 μm thick. The characteristic feature of the Glomeraceae and *Glomus* is the apical formation of glomoid spores on sporogenous mycelium. The formation of glomoid spores is most distinct in spore aggregates, where glomoid spores are formed by fusion of the apical regions of the hyphae (Pl. 19, fig. 6). The thickness of these hyphae is 6–9 μm on average. It gradually increases with the formation of spores, reaching 9–11 μm at the base of the spore and, occasionally, transforming into a cone-shaped stalk up to 30 μm long (Pl. 19, fig. 6). Rarely, sporogenous hyphae show evidence of branching. In this case, two or three spores are formed on one sporogenous hypha.

SYSTEMATIC PALEONTOLOGY
DIVISION GLOMEROMYCOTA
CLASS GLOMEROMYCETES

Order Glomerales

Family Glomeraceae C. Walker et Schussler, 2001

Genus *Glomites* Taylor, Remy, Hass et Kerp, 1995

Glomites sporocarpoides Karatygin, Snigirevskaya,
K. Demchenko et Zdebska, sp. nov.

Plate 18, figs. 1–9 and Plate 19, figs. 1–6

E t y m o l o g y. From the formation of glomoid spores in sporocarps.

H o l o t y p e. BIN, no. 887/4/1; Scotland, Aberdeenshire, vicinity of the village of Rhynie; Pragian

Explanation of Plate 18

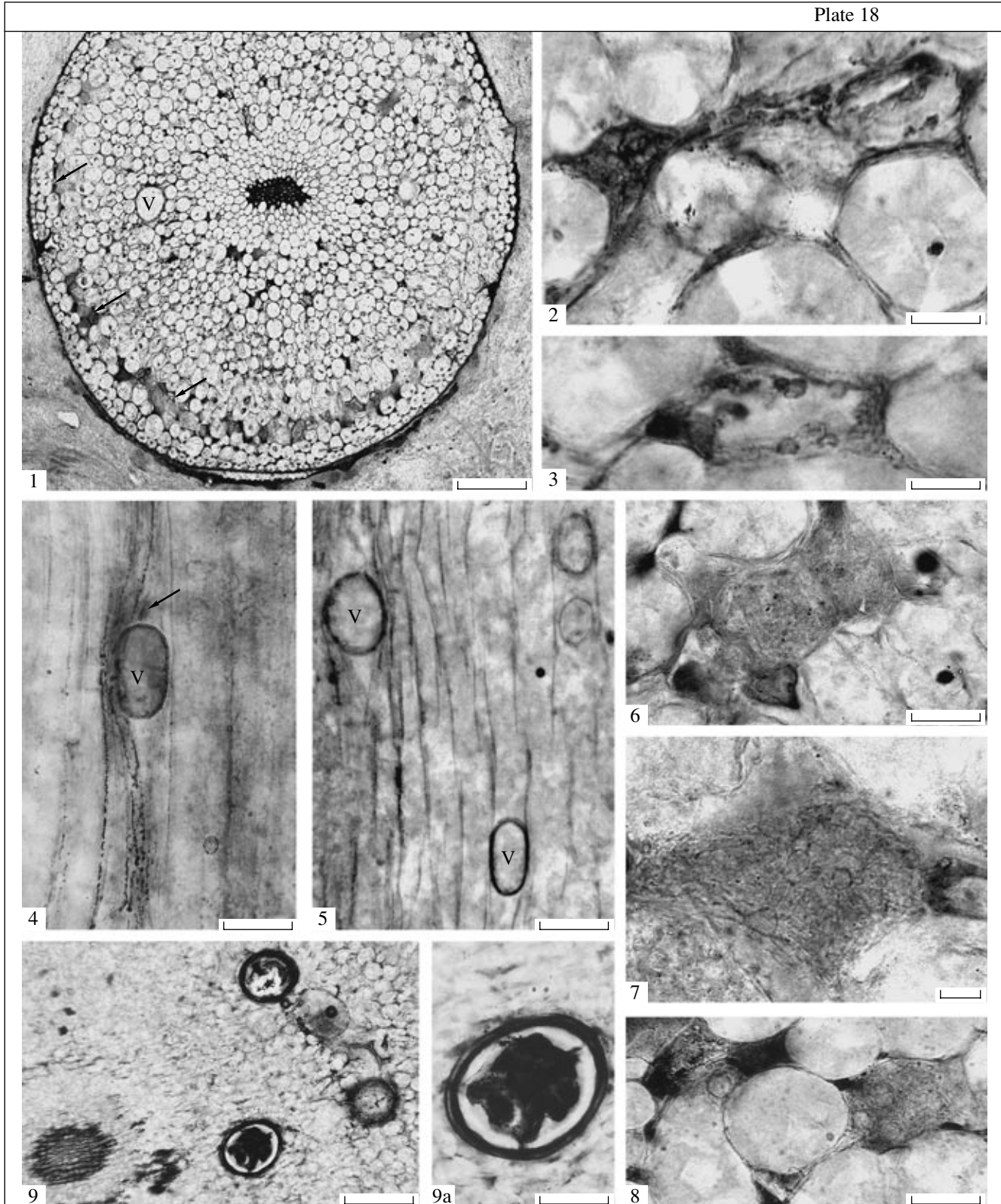
Figs. 1–9. Endophytic mycobiont *Glomites sporocarpoides* in silicified tissues of higher plants: (1) BIN, no. 1166/1/3, zone of the maximal occurrence of the mycobiont in the outer parenchyma cortex of rhizomoid of *Rhynia gwynne-vaughanii* (arrows) and a thin-walled vesicles (V) in the inner cortex; (2, 3) BIN, no. 1166/1/3, hyphae in oblique and transverse sections in intercellular spaces of inner cortex parenchyma; (4, 5) BIN, no. 1166/1/8, intercellular and intracellular fungal vesicles in the conductive tissue of an axis of cf. *Aglaophyton major*, (4) intercellular vesicle with an adjacent hypha (arrow); (5) to the left, cellular walls of the cortex are widened because of hypha intrusion into intercellular space; to the right, vesicles are visible within cells of the cortex; (6) BIN, no. 1166/1/3, arbuscle at a late stage of “digestion”; (7) BIN, no. 1166/1/2-2, hyphae of sporogenous mycelium within cells and in intercellular space, initial stage of the sporocarp formation; (8, 9, 9a) BIN, no. 887/2/1, chlamydospores of various maturity in the middle and inner cortex of *Aglaophyton major*, (8) vesicles transforming into chlamydospores; (9, 9a) solitary thick-walled chlamydospore. Scale bar (1, 8) 300 μm ; (2, 3) 25 μm ; (4, 5) 50 μm ; (6) 40 μm ; (7) 100 μm ; (9) 160 μm ; (9a) 420 μm .

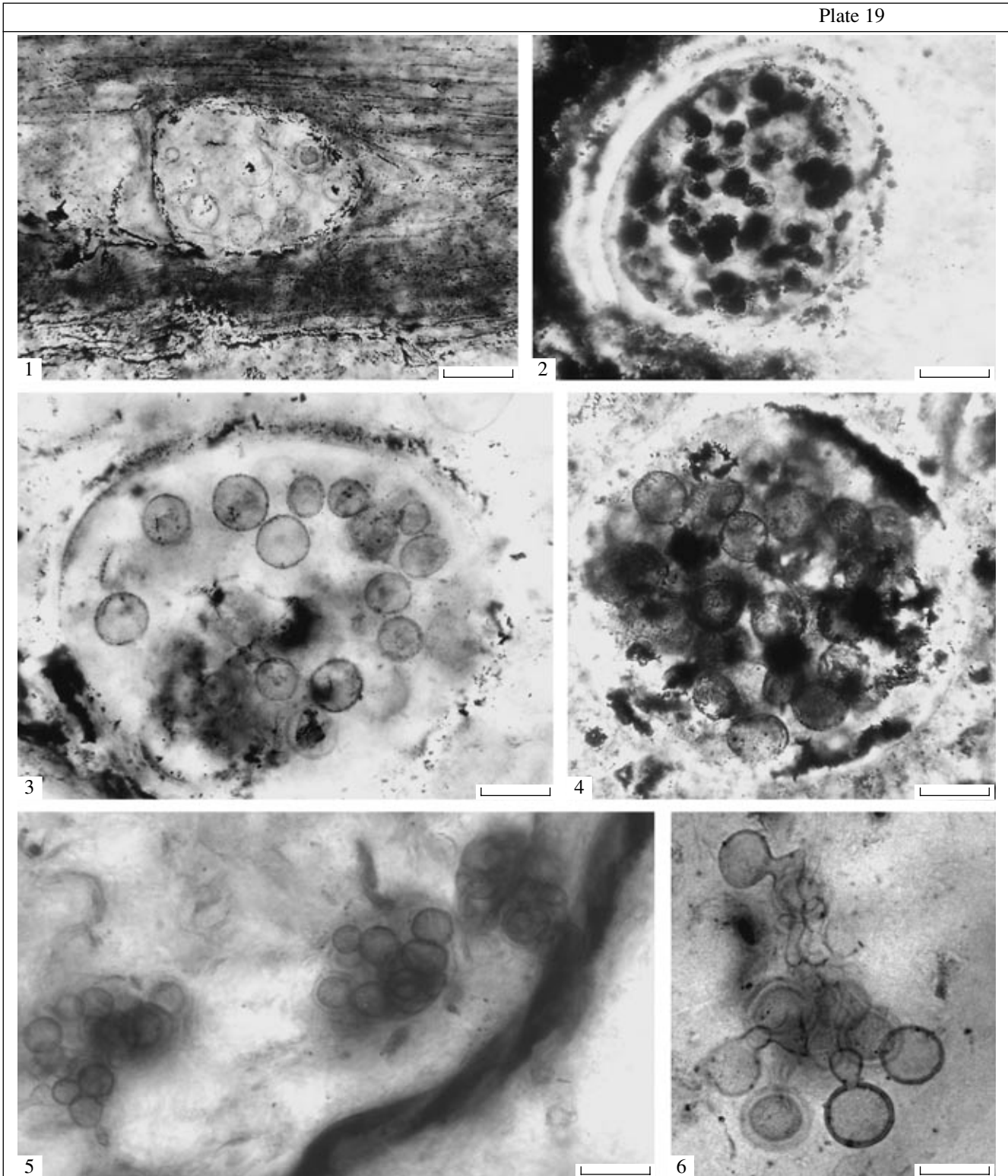
(= Siegenian), Lower Old Red Sandstone; Early Devonian (Pl. 19, fig. 4).

Diagnosis. Glomoid spore in sporocarps or in loose aggregates (spore balls) in axes and debris of

Aglaophyton major and *Rhynia qwynne-vaughanii*. Intraradical hyphae of two types: one consisting of aseptate hyphae 8–15 μm in diameter, other sporogenous hyphal branches 10–18 μm giving rise to solitary

Plate 18





Explanation of Plate 19

Figs. 1–6. Sporocarps and glomoid spores of *Glomites sporocarpoides* in the axes of *Aglaophyton major*: (1) BIN, no. 887/4/1, (2–4) BIN, no. 887/4/1, mature sporocarps in degrading tissue of the cortex; (5, 6) BIN, no. 1166/1/3-1, agglomerates and glomoid spores at different developmental stages on sporogenous mycelium in the inner cortex of the axis; (1–3) syntypes; (4) holotype. Scale bar (1) 80 μm ; (2) 60 μm ; (3, 4) 70 μm ; (5) 50 μm ; (6) 20 μm .

or multiple terminal globose–elongate glomoid spores. Sporocarps 250–350 μm in diameter, irregularly globose; peridium of sporocarps 8–13 μm in diameter; 30–80 glomoid spores in each sporocarp. In sporocarps, glomoid spores ranging 50–60 μm in diameter, globose to subglobose; in loose aggregates glomoid spores ranging (18) 20–24 (25) μm in diameter.

Description. Glomoid spores arranged in sporocarps or loose aggregates were found in axes of *Aglaophyton major* and *Rhynia gwynne-vaughani* and in plant remains near the subterranean axes of these plants. There are two types of interstitial mycelium: one type consists of cenocytic hyphae 8–15 μm in diameter, the other is formed by sporogenous hyphae 10–18 μm in diameter that produce glomoid spores, either solitary or in groups of a few spores. The sporocarps are 280–430 μm in diameter, irregularly spherical; the peridium of sporocarps is 8–13 μm in diameter; each sporocarp yields about 30–80 glomoid spores. In sporocarps, glomoid spores are spherical, 50–60 μm in diameter; in aggregates, their diameter is (18) 20–24 (25) μm .

Comparison. *G. sporocarpoides* differs from the two earlier described species of *Glomites* (*G. cycetris* Phipps et Taylor and *G. rhyniensis* Taylor, Remy, Hass et Kerp) in having well-developed sporocarps that form in dying and decaying plant tissues.

Remarks. The new species most closely resembles the common modern species *Glomus microcarpus* Tul. et C. Tul., the type species of this genus, which has the smallest sporocarps (smaller than 5 mm) in comparison to the other members of the genus (Gerdemann and Trappe, 1974). In nature, in *G. microcarpus* both sporocarps and ectocarpous spores develop (Godfrey, 1957). Another recent species resembling *Glomites sporocarpoides* is *Glomus mosseae* (T. Nicolson et Gerd.) Gerd. et Trappe, which is characterized by sporocarps with a well-developed peridium. Most modern members of *Glomus* and *Sclerocystis* do not form glomoid spores in root tissues (Morton, 1988). Only a few of them (*G. aggregatum* Schenck et Smith and *G. intraradicis* Schenck et Smith) have spores that are morphologically similar to the spores of fossil fungi and are able to form spores within mycorrhizal roots.

Material. Holotype and several specimens from the same locality, BIN, nos. 1166/1/3, 1166/1/8, 1166/1/2-2, 1166/1/3-1, 887/4/1, and 887/2/1.

DISCUSSION

In the last few years, the taxonomy of endomycorrhizal fungi has undergone fundamental changes caused by application of molecular methods, with description of new high-level taxa (orders, families, and genera). In particular, a new phylum (division), Glomeromycota, was described to include an ecologically important group of endomycorrhizal fungi. Glomeromycota includes four orders: Glomerales, Archaeosporales, Paraglomerales, and Diversisporales with several

families (Schu bler et al., 2001). It is supposed that Glomeromycota diverged from the same common ancestor as Ascomycota and Basidiomycota. The rDNA sequencing of hyphae and spores of the Ordovician species *Palaeoglomus grayi* Redecker, Kodner et Graham (Redecker et al., 2002) revealed a high diversity of genotypes within Glomerales, thus indicating that the origin of this order is even older (up to 600 Ma ago) than was earlier believed (Berbee and Taylor, 2000; Redecker et al., 2000a, 2000b).

The concept of long-term symbiotic coevolution between plants and fungi has significant factual grounds. Among them is the presence of mycophytic associations of most ancient plants, which resemble modern endomycorrhiza. Paleomycological data show that higher plants have been mycotrophic since their origin and over the entire period of their existence. Mycobionts found in the lower parts of axes have been found in Devonian members of virtually all ancestral groups of main phylogenetic lineages. The division Rhyniophyta is known to be a primary phylogenetic node, where the initial links of the evolution of higher plants intervene. The occurrence of fungal endosymbionts in members of ancestral groups of different phylogenetic lineages of higher plants in the Devonian allows us to hypothesize that the original mycophytic association appeared much earlier. It is possible that rhyniophytes and lycopsids had a common stalk rooting in the earliest Silurian or, even, the Ordovician.

It should be particularly emphasized that endomycorrhiza as absorption organs were more important for early vascular plants than for modern plants because the former lacked a true root system. Subterranean organs of the first vascular plants were rhizomes with rhizomoids, the main function of which was attachment to the substrate. In this context, it would be more correct to refer to the symbiotic organs of Devonian plants under discussion as mycorrhizoids or mycorrhizomes, which are quite different from the endomycorrhiza of modern plants both functionally and structurally.

The endomycorrhizal fungi of the genus *Glomites* that are known from plants *Aglaophyton major* and *Rhynia gwynne-vaughanii* from the Rhynie Chert show (at all developmental stages) an obvious similarity to mycobionts of endomycorrhizae of modern plants. It is clear that *Glomites* species are ancestors of modern members of the Glomerales. The presence of arbuscles, vesicles, and sporocarps in all three *Glomites* species proves that endomycorrhiza were common and actively functional in the Early Devonian. These fungi already had signal mechanisms for long coexistence with photobionts. It is possible that cytogenetic mechanisms that determined the activity of endomycorrhizae in the Devonian are analogous or extremely similar to those of endomycorrhizae of modern plants (Taylor, 1990). Similarly, mechanisms of transfer of phosphates and carbon between the fungus and plant are also of very ancient origin. In many respects, this fact determined their further coevolution.

Kizil'shtein and Spitsgluz (1999, p. 33) correctly underlined that "cardinal rearrangement of organic matter in geological processes does not lead to transformation of initial biochemical compounds into homogeneous geological polymer; contrariwise, initial biopolymers transforming into so-called 'molecular fossils' pertain structural individuality, and it is not lost even at high metamorphic stages."

It is common knowledge that most modern species of *Glomus* and *Sclerocystis* do not form spores within roots, and the formation of spores usually takes place in soil in the close vicinity of roots of photobionts (Morton, 1988; Morton and Benny, 1990). Among modern members of *Glomus*, only a few species have distinct sporocarps, which develop in soil near mycorrhizal roots. The presence of these structures is considered as an advanced character (Walker, 1987; Redecker et al., 2000b). Only in some of them (*G. aggregatum* Schenck et Smith and *G. intraradicis* Schenck et Smith) glomoid spores develop in the tissues of mycorrhizal roots. Morphologically, they greatly resemble spores of the fossil fungus *Glomites*.

The discovery of well-developed sporocarps in *Glomites sporocarpoides* in living and dying tissues of Devonian rhyniophytes leads to the conclusion that these are ancient and primitive structures. In the Early Devonian, the development of sporocarps in living and dying plant tissues may be explained by weak soil formation. Later, as the soils enriched with organic matter and coevolutionary relationships between endomycorrhizal fungi and plants improved, the formation of sporocarps in the majority of glomoid fungi shifted to the soil. Moreover, during coevolution with plants many *Glomus* species completely lost the ability to form sporocarps.

Distinct pathogenicity is a characteristic feature of *Glomites sporocarpoides*: the mycelium actively invades the plant axes, vast necrotic zones form in the plant tissues, and assimilative tissues of the plant are replaced by vesicles and forming sporocarps. The volume of the plant tissue that is replaced by developing fungal sporocarps may be very high, particularly at later developmental stages. We can conclude that at the early stages of the coevolution of mycobionts and photobionts an unstable equilibrium existed between mutualistic and antagonistic features. An evaluation of relationships between the fungus and plant in terms of *advantage* is debatable, whereas the ecological and evolutionary profits of symbiosis are obvious, taking into consideration processes at the levels of tissues and cells. In this case, the term *adaptation* seems to be much more suitable for mycorrhiza, since it is better suited to determination of evolutionary prospects and ecological flexibility of the partners. It is possible that in the course of further coevolution between *Glomus* species and plants the relationships between the symbionts became more and more mutualistic, and the pathogenic effect of the fungus on the plant reduced.

ACKNOWLEDGMENTS

We are grateful to the academician of the Russian Academy of Sciences A.L. Takhtajan (St. Petersburg) and to Prof. D. Zdebska (Kraków, Poland) for providing for this study chert samples of the Early Devonian of Scotland.

The study was supported by the Program of the Presidium of the Russian Academy of Sciences "Origin and Evolution of the Biosphere," grant of the President of the Russian Federation (MK-1824), and Foundation of Russian Science Promotion.

REFERENCES

1. L. I. Anderson and N. H. Trewin, "An Early Devonian Arthropod Fauna from the Windyfield Chert, Aberdeenshire, Scotland," *Palaeontology* **46**, 467–509 (2003).
2. M. L. Berbee and J. W. Taylor, "Fungal Molecular Evolution: Gene Trees and Geological Time," in *The Mycota, V, VII, Part B: Systematics and Evolution* (Springer-Verlag, Berlin, 2000), pp. 229–245.
3. B. Boullard and Y. Lemoigne, "Les champignons endophytes du *Rhynia gwynne-vaughanii*: étude morphologique et déductions sur leur biologie," *Le Botaniste* **54** (1–6), 49–89 (1971).
4. K. N. Demchenko, T. Winzer, J. Stougaard, et al., "Distinct Roles of *Lotus japonicus* SYMRK and SYM15 in Root Colonization and Arbuscule Formation," *New Phytol.* **163** (2), 381–392 (2004).
5. J. W. Gerdemann and J. M. Trappe, "The Endogonaceae of the Pacific Northwest," *Mycol. Mem.* **5**, 1–76 (1974).
6. R. M. Godfrey, "Studies of British Species of *Endogone*: II. Fungal Parasites," *Trans. Brit. Mycol. Soc.* **40**, 136–144 (1957).
7. N. P. Gorbunova, "On Interrelationships between a Fungus and a Higher Plant in a Mycorrhiza," *Usp. Sovrem. Biol.* **42** (2) (1956).
8. M. J. Harrison, "The Arbuscular Mycorrhizal Symbiosis: An Underground Association," *Trends in Plant Sci.* **2**, 54–60 (1997).
9. I. V. Karatygin, *Coevolution between Fungi and Plants* (Gidrometeoizdat, St. Petersburg, 1993) [in Russian].
10. I. V. Karatygin, "Fungi as Components of Ancient Ecosystems," *Bot. Zh.* **90** (9), 1297–1318 (2005).
11. I. V. Karatygin and N. S. Snigirevskaya, "Paleontological Evidence for the Origin of the Main Taxonomic Groups of Fungi," *Mikol. Fitopatol.* **38** (5), 15–31 (2004).
12. R. Kidston and W. H. Lang, "On Old Red Sandstone Plants Showing Structure from the Rhynie Chert Bed, Aberdeenshire: Part V. The Thallophyta Occurring in the Peat-Bed; the Succession of the Plants throughout a Vertical Section of the Bed, and the Conditions of Accumulation and Preservation of the Deposit," *Trans. R. Soc. Edinburgh* **52** (33), 855–902 (1921).
13. L. Ya. Kizil'shtein and A. L. Spitsgluz, *Atlas of Microscopic Components and Petrogenetic Types of Anthracites Anatomical Atlas of Paleozoic Coal-Forming Plants* (Sev.-Kavkazsk. Nauchn. Tsentr Vyssh. Shkoly, Rostov-on-Don, 1999) [in Russian].

14. Y. Lemoigne and D. Zdebska, "Structures problématiques observées dans des axes provenant du chert Dévonien de Rhynie," *Acta Palaeobot.* **21** (1), 3–8 (1980).
15. J. B. Morton, "Taxonomy of VA Mycorrhizal Fungi: Classification, Nomenclature, and Identification," *Mycotaxon* **32**, 267–324 (1988).
16. J. B. Morton and G. Benny, "Revised Classification of Arbuscular Mycorrhizal Fungi (Zygomycetes): A New Order Glomales, Two New Suborders, Glominae and Gigasporinae, and Two Families, Acaulosporaceae and Gigasporaceae, with an Emendation of Glomaceae," *Mycotaxon* **37**, 471–491 (1990).
17. K. J. Niklas, "The Role of Morphological Biochemical Reciprocity in Early Land Plant Evolution," *Ann. Bot.* **40** (170), 1239–1254 (1976).
18. C. J. Phipps and T. N. Taylor, "Mixed Arbuscular Mycorrhizae from the Triassic of Antarctica," *Mycologia* **88** (5), 707–714 (1996).
19. K. A. Pirozynski and Y. Dalpé, "Geological History of the Glomaceae with Particular Reference to Mycorrhizal Symbiosis," *Symbiosis* **7** (1), 1–35 (1989).
20. K. A. Pirozynski and D. W. Malloch, "The Origin of Land Plants: A Matter of Mycotrophism," *BioSystems* **6** (3), 153–164 (1975).
21. D. Redecker, R. Kodner, and E. Graham, "Glomalean Fungi from the Ordovician," *Science* **289** (5486), 1920–1921 (2000a).
22. D. Redecker, J. B. Morton, and T. D. Bruns, "Ancestral Lineages of Arbuscular Mycorrhizal Fungi," *Mol. Phylog. Evol.* **14**, 276–284 (2000b).
23. D. Redecker, R. Kodner, and E. Graham, "*Palaeoglomus grayi* from the Ordovician," *Mycotaxon* **84**, 33–37 (2002).
24. W. Remy, T. N. Taylor, H. Hass, and H. Kerp, "Four Hundred-Million-Year-Old Vesicular Arbuscular Mycorrhizae," *Proc. Natl. Acad. Sci. USA* **91** (25), 1841–1843 (1994).
25. J. B. Richardson, "Some British Lower Devonian Spore Assemblage and Their Stratigraphic Significance," *Rev. Palaeobot. Palynol.* **1**, 11–129 (1967).
26. A. Schußler, D. Schwarzott, and C. Walker, "A New Fungal Phylum, the Glomeromycota: Phylogeny and Evolution," *Mycol. Res.* **105** (12), 1413–1421 (2001).
27. B. D. Sharma, D. R. Bohra, and R. Harsh, "Vesicular Arbuscular Mycorrhizae Association in Lower Devonian Plants of the Rhynie Chert," *Phytomorphology* **43** (1–2), 105–110 (1993).
28. V. O. Tauson, *Inheritance of Microbes* (Akad. Nauk SSSR, Leningrad, Moscow, 1947) [in Russian].
29. T. N. Taylor, "Fungal Associations in the Terrestrial Paleoecosystems," *Tree* **5** (1), 21–25 (1990).
30. T. N. Taylor and J. F. White, "Fossil Fungi Endogonaceae from the Triassic of Antarctica," *Am. J. Bot.* **76** (3), 389–396 (1989).
31. T. N. Taylor, W. Remy, H. Hass, and H. Kerp, "Fossil Arbuscular Mycorrhizae from the Early Devonian," *Mycologia* **87** (4), 560–573 (1995).
32. I. C. Tommerup, "Development of Infection by a Vesicular-Arbuscular Mycorrhizal Fungus in *Brassica napus* and *Trifolium subterraneum* L.," *New Phytol.* **98**, 487–495 (1984).
33. N. H. Trewin, "Depositional Environment and Preservation of Biota in the Lower Devonian Hot-Springs of Rhynie, Aberdeenshire, Scotland," *Trans. R. Soc. Edinburgh, Earth Sci.* **84** (3), 433–442 (1994).
34. N. H. Trewin, "Preface," in R. Kidston and W. H. Lang "On Old Red Sandstone Plants Showing Structure from the Rhynie Chert Bed, Aberdeenshire," *Trans. R. Soc. Edinburgh, Earth Sci.* **87** (3), 423–425 (1996).
35. N. H. Trewin and C. M. Rice, "Stratigraphy and Sedimentology of the Devonian Rhynie Chert Locality," *Scottish J. Geol.* **28**, 37–47 (1992).
36. N. H. Trewin, S. R. Fayers, and R. Kelman, "Subaqueous Silicification of the Contents of Small Ponds in an Early Devonian Hot-Spring Complex, Rhynie, Scotland," *Can. J. Earth Sci.* **40** (11), 1697–1712 (2003).
37. C. Walker, "Systematics and Taxonomy of the Arbuscular Endomycorrhizal Fungi (Glomales)—a Possible Way Forward," *Agronomie* **12**, 887–897 (1992).