Assoc. Prof. Wiesław Trela (PhD, DSc) works at the Polish Geological Institute – National Research Institute. For over 20 years he has been conducting sedimentological and stratigraphic research on the Paleozoic of Poland's Holy Cross Mountains. His research activity concentrates on studies of depositional environments and paleoecological conditions in the Ordovician period.

wieslaw.trela@pgi.gov.pl

Dr. Zbigniew Szczepanik (PhD) works at the Holy Cross Mountains Branch of the Polish Geological Institute – National Research Institute. He studies the stratigraphic, environmental and palaeogeographic aspects of acritrach microflora, as well as the thermal maturity of the organic matter of Lower Paleozoic palynomorphs.

zbigniew.szczepanik@pgi.gov.pl

The Conquest of Land in the Ordovician

Plant fossils discovered in Poland's Holy Cross Mountains are estimated to be 445 million years old, which changes our view of plant evolution, and above all proves that they appeared on land much earlier than we thought.

Wiesław Trela
Zbigniew Szczepanik

Polish Geological Institute – National Research Institute in Warsaw

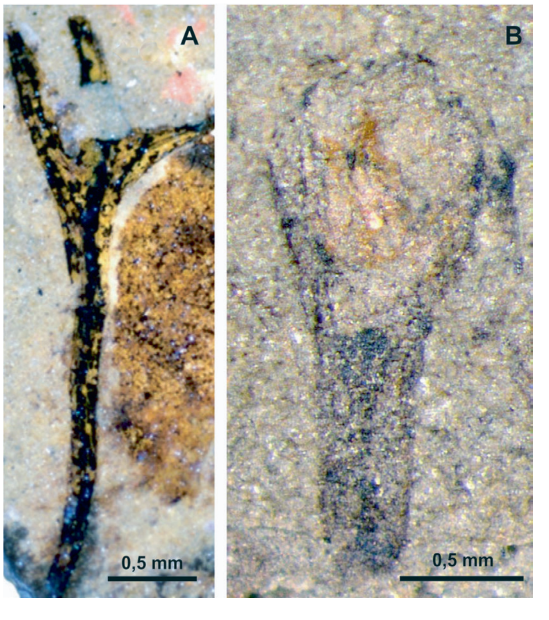
Paweł Filipiak, Mariusz Salamon

Faculty of Natural Sciences, Institute of Earth Sciences, University of Silesia in Katowice

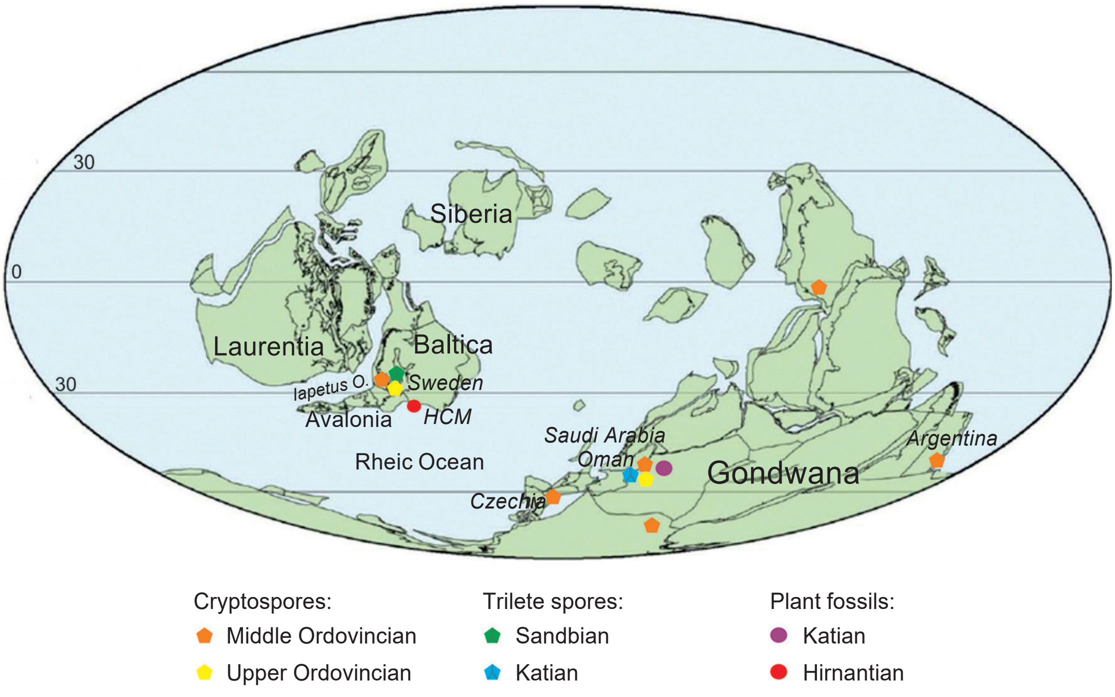
Przemysław Gorzelak

Institute of Paleobiology of the Polish Academy of Sciences in Warsaw

One of the most important issues in the evolution of life on Earth is how terrestrial habitats were colonized by plants. Molecular studies, as well as morphological, cytological and biochemical features show a great similarity between plants and certain green algae (Chara), indicating that they share a close relationship and common ancestor. According to paleontological data, plants first began to colonize land in the Ordovician period, between 475 and 450 million years ago. The terrestrialization of plants had a fundamental impact on changing the global biogeochemical cycle, weathering processes, soil structure, and, consequently, the state of the Earth's climate. With the appearance of terrestrial plants, carbon binding began, both in the gradually growing plant cover and the organic matter accumulated in the soil. The colonization of land by plants is



Trichotomously branching plant axis (A) and oval sporangium (B) from the Upper Ordovician (Hirnantian) in the HCM



Occurrence of spores and plant fossils on the paleogeographic map of the Late Ordovician (445 million years ago); HCM – the Holy Cross Mountains

currently considered to be one of the most important factors (if not the key factor) responsible for the cooling of the Ordovician climate, through their effect on reducing CO_2 concentration and increasing O_2 in the atmosphere. This process ended about 445 million years ago, when the CO_2 concentration dropped to 8 times today's level (or less). This triggered the formation of the ice sheet in the southern part of the Gondwana continent, which lasted from 0.5 to 1 million years, which in turn resulted in a global sea level fall (the Hirnantian regression) and a biotic crisis, which finished the Great Ordovician Biodiversity. It should be noted, however, that other important factors contributing to the reduction of CO_2 in the atmosphere could also be responsible for the Ordovician climate cooling, such as: 1) declining volcanic activity associated with the super mantle plume, 2) mass blooming of phytoplankton (the Ordovician planktonic revolution) and the related increasing supply of organic carbon in bottom sediments, and 3) increased weathering of siliciclastic rocks.

First plants

According to some researchers, the presence of permanent tetrads and dyadas in Middle Cambrian sediments, or sporomorphs (forms morphologically resembling spores), permanently linked together into biologically undivided aggregates, point to the Cambrian colonization of land by pioneer plants representing the transition from algae. However, the oldest definite fossils of terrestrial plants are cryptospores found in the Ordovician period, which have many features in common with modern liverwort spores. Their presence has been documented in deposits of the Middle Ordovician period, in Argentina (470 million years ago) and Saudi Arabia (460 million years ago). In addition, in the Upper Ordovician (Katian stage), sedimentary records of Oman sporangium fragments were found together with cryptospores, which are similar to modern liverworts. This is why liverworts were considered to have been the first plants which colonized land. The Late Ordovician period was also time span when the first trilete spores appeared, which are regarded to be a spore morphology typical for vascular plants, although these type forms are also found among some bryophytes. However, unequivocal macrofossils of vascular plants are known from the Middle Silurian period (430 million years ago) and are represented by the fossil-genus *Cooksonia*, characterized by bifurcating axes and more than one sporangium. In the late Silurian, colonization of land by plants was so advanced that it left a signature of wildfires.

The oldest fossils

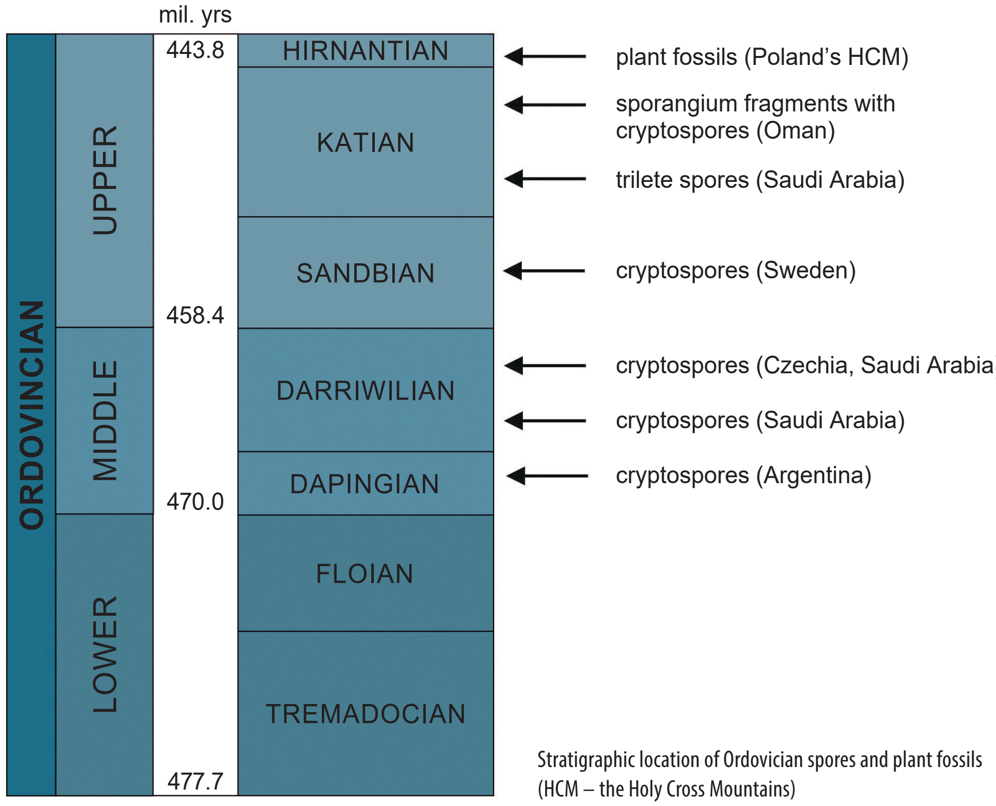
In 2018, an international team of researchers published the results of a study in the journal *New Phytologist* regarding the oldest macrofossils presumably of terrestrial plants from 445 million years ago found in Po-

Asst. Prof. Paweł Filipiak (PhD, DSc)
works at the Faculty of Natural Sciences, Institute of Earth Sciences, University of Silesia. He studies the palynology of Devonian and Carboniferous deposits and macroflora. Member of the editorial board of the journal *Annales Societatis Geologorum Poloniae*.
pawel.filipiak@us.edu.pl

Assoc. Prof. Mariusz Salamon (PhD, DSc)
is a Professor at the Institute of Earth Sciences, Faculty of Natural Sciences, at the University if Silesia. His studies the taphonomy, paleoecology, systematics and evolution of fossil crinoids. Member of the editorial board of the journal *Annales Societatis Geologorum Poloniae*.
mariusz.salamon@us.edu.pl

Asst. Prof. Przemysław Gorzelak (PhD, DSc) works at the PAS Institute of Paleobiology in Warsaw. He studies the paleoecology, functional morphology, evolution and biomineralization of contemporary and fossil echinoderms. He has received scholarships from the Foundation for Polish Science and the Minister of Science and Higher Education.

pgorzelak@twarda.pan.pl



Stratigraphic location of Ordovician spores and plant fossils (HCM – the Holy Cross Mountains)

land's Holy Cross Mountains (HCM). They occurred in the latest Ordovician (the Hirnantian stage) mudstones, shales and marls with sandstone interbeds, which are a regional record of sea level fall, forced by glaciation in Gondwana. The stratigraphic position of these deposits was determined on the basis of trilobite fossils of *Mucronaspis* and brachiopods of the Hirnantia Fauna. In addition, these sediments yielded a typical Upper Ordovician microfossil assemblage, including chitinozoa and acritarchs. Particularly noteworthy is acritarch microflora consisting of Hirnantian forms, accompanied by Cambrian and Middle Ordovician redeposited taxa, such as the genus *Frankea*, typical for the Middle Ordovician in Gondwana.

The plant fragments found in the HCM have dichotomously branched axes. These specimens are small, only 2–3 mm long and about 3 mm wide. One specimen with a trichotomous axis division (3.2 mm long and 0.3 mm wide) was also documented, which is a feature noted in some late Silurian and Early Devonian plants (430–410 million years ago). The single not branched specimens end in cup-shaped and oval sporangia (about 0.4–0.8 mm long and 0.3–1.1 mm wide), which in form, size and morphology are similar to the Silurian genus *Cooksonia*, and resemble structures found in Triassic liverworts. In addition, sporomorphs morphologically similar to trilete spores were identified in samples from the HCM, and stomatal apparatus resembling that in *Akdalophyton caradocki*, a plant from the late Sandbian (453–455 million years ago). Thus the Hirnantian plant fossils from the HCM are the oldest macrofossils of polysporangiophytes in the sedimentary record.

In the late Ordovician the HCM were located close to the southwestern margin of the Baltica, between 30° and 40° southern latitude. The latest research on Hirnantian sediments on the Polish side of the Baltic Sea indicates that at that time icebergs from Gondwana were reaching its southwestern shelf, from which thicker terrigenous material, such as sand and fine gravel, was melted. It is likely that the Late Ordovician icebergs also influenced the HCM region. In this context, the presence of *Frankea* in the Hirnantian acritarch assemblage of the HCM may be interpreted in two ways, as a result of 1) redeposition from the collision zone of the Avalonia microcontinent with Baltica, or 2) transport by icebergs from the marginal zone of Gondwana. Therefore, it cannot be rule out that fossils of terrestrial plants found in the HCM may have been redeposited and in fact are older than the Hirnantian age.

A recently reported assemblage of sporomorphs from the Middle and Upper Ordovician in Sweden is noteworthy in that it consists of cryptospores and trilete spores. These data challenge the current opinion that the first plants originated in Gondwana. They also suggest that vascular plants may have appeared on Baltica as early as the Late Ordovician, although according to some researchers, trilete spores may also occur in some bryophytes.

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