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Putative Late Ordovician land plants

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The colonization of early terrestrial ecosystems by embryophytes (= land plants) irreversibly changed global biogeochemical cycles (Berner & Kothavala, 2001; Berner *et al.*, 2007; Song *et al.*, 2012). However, when and how the process of plant terrestrialization took place is still intensely debated (Kenrick & Crane, 1997; Kenrick *et al.*, 2012; Edwards *et al.*, 2014; Edwards & Kenrick, 2015). Current knowledge suggests that the earliest land plants evolved from charophycean green algae (Karol *et al.*, 2001) most probably during Early-Middle Ordovician times (Rubinstein *et al.*, 2010, and references therein). They were represented by small non-vascular bryophyte-like organisms (Edwards & Wellman, 2001; Wellman *et al.*, 2003; Kenrick *et al.*, 2012). The oldest fossil evidence from dispersed spores of presumable bryophytic nature is known from a Middle Ordovician locality (~ 470 Ma, Rubinstein *et al.*, 2010; Fig. 1) from Argentina (Gondwana palaeocontinent). The dispersed spore fossil record also suggests that the first radiation of vascular plants probably occurred during Late Ordovician times (~450 Ma, Steemans *et al.*, 2009). However, unequivocal macrofossils of vascular plants appear much later, during mid-Silurian (~430 Ma, Edwards *et al.*, 1992). This macrofossil evidence comes from the fossil-genus *Cooksonia*, an early polysporangiophyte (i.e., a plant with bifurcating axes and more than one sporangium), which is considered the earliest vascular land plant (Edwards *et al.*, 1992; Fig. 1). Further advances in knowledge about the origin and early dispersion of polysporangiophytes are needed for a better understanding of the initial plant diversification. Unfortunately, unravelling the initial steps of polysporangiophyte evolution is hindered by gaps in the fossil record of the earliest plants as well as by limitations of inference based on molecular clocks (Kenrick *et al.*, 2012; Edwards & Kenrick, 2015).

Assessing the affinities of fragmentary fossils is frequently only tentative. Most often, only partial evidence for land plant nature is visible on fossils of Silurian-Devonian age. Nevertheless, there are numerous examples in the deep-time fossil record of organisms that have been interpreted as early embryophytes even though unambiguous land plant characters were not demonstrated. For instance, Edwards and Feehan (1980) reported on some Silurian terminal sporangia and dichotomous axes interpreted as *Cooksonia*-type plants with no evidence for *in situ* spores nor for tracheids. Wellman *et al.* (2003) described the first plant

mesofossils with *in situ* spores from the Ordovician (Katian) fossil record, but the morphology of the parent plants remains unknown. More recently, Morris *et al.* (2011) reported on numerous fragments of Lower Devonian plants with terminal sporangia and dichotomous axes, again lacking preserved unambiguous land plant characters. Interestingly, some of the plants illustrated by Morris *et al.* (2011, pl. VI) appear closely similar to those reported in Fig. 2 (see below).

Here, we document an Ordovician (Hirnantian, ~445 Ma) putative plant macrofossil assemblage. The specimens come from an Upper Ordovician locality at Zbrza in the southern Holy Cross Mountains (HCM, central Poland, Laurussia palaeocontinent; Figs. S1-S2, see also Text S1). The fossils occur in mudstones of the uppermost Ordovician (Hirnantian) Zalesie Formation dated by trilobites, brachiopods and palynomorphs (Kielan, 1959; Temple, 1965; Masiak *et al.*, 2003; Trela *et al.*, 2009). The age of the plant-bearing sediments is confirmed by acritarchs and chitinozoans (Text S1). Reported evidence consists of dichotomously branched slender axes, some with terminal discoid or ovoid structures interpreted as sporangia, which could represent the earliest megafossil occurrence of polysporangiophytes (Fig. 1).

The plant fossils described herein are scattered among various fragments of coalified material. Two branching axes broken at both ends (3 mm long by 0.1 mm wide and 2 mm long by 0.3 mm wide, respectively; Fig. 2a,b) are attributable to the fossil-genus *Hostinella* that includes vegetative isotomously branched axes. Another specimen shows a trichotomous axis division (3.2 mm long by 0.3 mm wide; Fig. 2c), a feature known to occur in some late Silurian/Early Devonian plants (Gonez & Gerrienne, 2010a,b). The studied samples also yielded several probably fertile axes. A small, dichotomously branched, slender and leafless stem (1.5 mm long by 0.2 mm wide; Fig. 2d) bears terminal structures interpreted as sporangia (0.4 mm long by 0.3 mm wide; Fig. 2d). The two other fertile specimens are not branched. They consist of a short axis (1.1 mm long by 0.3 mm wide; Fig. 2e) ending either in a horizontally stretched, presumably cup-shaped, structure interpreted as a sporangium (0.8 mm long by 1.1 mm wide; Fig. 2e) or in an ovoid/hemispherical sporangium-like body (1.3 mm long by 1 mm wide; Fig. 2f). Their form, size and structure seem to be close to the observed from *Cooksonia pertoni* (Fig. 2e; Lang, 1937; Edwards & Feehan, 1980) and *C. hemisphaerica* (Fig. 2f; Edwards & Rogerson, 1979; Edwards & Feehan, 1980), respectively.

Moreover, the specimen illustrated at Fig. 2d looks quite similar to the bifurcating axis showing the basal part of a sporangium described by Edwards *et al.* (2014, fig. 3f). Furthermore, within a macerated residue, we found rare trilete spores resembling the *Ambitisporites avitus-dilutus* (Stemans *et al.*, 1996; Fig. 2g,h), a morphon interpreted as indicative of vascular plants (Fanning *et al.*, 1988; Stemans *et al.*, 2009); however the trilete marks of our specimens are not regularly formed, which casts doubts on their trilete spore nature. Interestingly, there are a variety of Ordovician spores with irregular trilete-like folds, such as *Besselia nunaatica* (Nøhr-Hansen & Koppelhus, 1988) that are well known from mosses and hornworts. The last important feature shown by our specimens has been found on an indeterminate dispersed axis. It is a small structure that we interpret as a stoma (Fig. 3a). This probable stomatal complex (29 μm long by 21 μm wide; Fig. 3b) fits with the structure and morphology of those described from Silurian-Early Devonian plant fossils by Edwards *et al.* (1986, fig. 3b; 1998, figs. 2b-c, 3e-h, 10b; 2014, fig. 3b), which again suggests a land plant status for our specimens.

On the other hand, the sporangia figured remind those of the sphaerocarpalean liverwort *Naiadita lanceolata*, as described in Hemsley (1989). Although *Naiadita* is Triassic in age, it is generally considered that liverworts were abundant in the Ordovician as inferred from the presence of their dispersed spores (i.e., cryptospores; Gray, 1985; Wellman *et al.*, 2003). We also note that the illustrated stomatal apparatus (Fig. 3) is similar to that of *Akdalophyton caradocki* from the Sandbian (Late Ordovician) of Kazakhstan (Snigirevskaya *et al.*, 1992, pl. II.4). *Akdalophyton* has no tracheids, but does have what appear to be hydroids, and has been interpreted as a moss, with helically arranged leaves, distinct but reminiscent of the axis shown here in Fig. 2b. This evidence suggests that the macrofossil remains presented herein, like the Late Ordovician *Akdalophyton*, are indeed land plants, but probably non-vascular specimens, which is consistent with their occurrence in the early Eoembryophytic phase of plant evolution (Gerrienne *et al.*, 2016, fig. 3).

Distinguishing the earliest land plants, which are characterized by a very simple morphology, from other phyla occasionally showing superficial resemblances, is challenging. This is because (1) several types of organism (e.g. some invertebrates and hemicordates) produce axial fragments resembling land plant axes (see Kenrick *et al.*, 1998, for further discussion), and (2) the characters that confirm the land plant status (e.g. sporangia

and/or stomata) are usually missing, difficult to discern or ambiguous. Importantly, our specimens neither show appendage-bearing ("spiny") axes nor laminated collagenous substance, which may be indicative of graptolite or octocoral affinities (Cairns *et al.*, 1986; Kenrick *et al.*, 1998), respectively. Instead, they are smooth and heavily coalified (which excludes conodont affinity; Rayner, 1986; Theron *et al.*, 1990), and one of them possesses a possible stoma, which is an unambiguous character of land plants.

The three fertile specimens illustrated at Figs. 2d-f show three different sporangial morphologies. This lack of morphological consistency may seem odd because assemblages of the earliest land plants have long been considered to show rather uniform fertile morphologies, with only cryptic variations (see e.g. Fanning *et al.*, 1988). This morphological uniformity is however only apparent: in recent years, a great variety of sporangial shapes, sizes and organizations has been reported (among others: Edwards & Wellman, 2001; Edwards & Richardson, 2004; Edwards *et al.*, 2014). Additionally, it should be noted that Ordovician-Silurian cryptospores, which are considered the earliest evidence of land plants, are reported from throughout the globe and display already a wide range of morphologies (Steemans, 1999; Wellman *et al.*, 2003, 2013). This is further consistent with the variety of cryptospore producers documented to date (see Edwards *et al.*, 2014, and references therein). In this context, the disparity on the reproductive structures illustrated here appears less surprising.

From an evolutionary viewpoint, the early land plant flora reported herein suggests that polysporangiophytes had already evolved by Late Ordovician times (Fig. S2, Text S1). This pushes back the first occurrence of polysporangiophytes for about 15 million years (Fig. 1), which is consistent with the age of the clade recently estimated through molecular clock analysis (Clarke *et al.*, 2011; Zhong *et al.*, 2014). In addition, some of these Late Ordovician putative plants (Fig. 2e,f) are very closely comparable, in size and morphology, to the earliest macrofossil floras described elsewhere in the world from younger (mid-upper Silurian to lowermost Devonian) localities (Edwards & Richardson, 2004; Raymond *et al.*, 2006; Edwards *et al.*, 2014). This fact suggests a very low evolutionary rate for the earliest polysporangiophytes. Then again, the presence of early polysporangiophytes in worldwide-distributed Silurian-Devonian localities suggests a dispersal of the earliest Gondwanan floras quicker than expected.

Current available data show a rather conflicting and incomplete picture of early plant terrestrialization (Kenrick *et al.*, 2012), leaving many key questions unanswered. A major discrepancy in time of appearance of spores and plant macrofossils is particularly intriguing. Importantly, a major change in spore types in the Late Ordovician-early Silurian, leading to the decrease of cryptospores and increase in diversity of trilete spores, was attributed to the initial radiation of vascular or pre-vascular plants (Stemans *et al.*, 2009). It has however to be noted that, although the fossilization potential and the evolutionary value of palynomorphs are clearly assessed, their attribution to source plants is most often problematic. For instance, trilete spores, commonly interpreted as indicative of vascular plants, are also linked to some living bryophytes (see e.g., Kenrick *et al.*, 2012, and references therein). The plant remains presented herein most probably document the oldest macrofossils of polysporangiophytes in the Upper Ordovician sedimentary record. This new evidence strongly supports that the major floral turnover seen in the microfossil record might indeed also be interpreted in terms of the evolution of macrofossil floras.

Acknowledgments

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Author contributions

M.A.S, P.G. and T.B. discovered and collected plant specimens. P.G. conducted microstructural observations. Ph.G., Ph.S, B.C.M. provided intellectual contributions to interpretation and description of fossils. P.F., A.H. and F.P. performed palynological

investigations and verified the age of sediments. M.M., R.N. and W.T. made petrographic observations and/or provided geological information. M.A.S, P.G., P.F., Ph.G., Ph.S., B.C.M., R.N., A.H., F.P., R.N. and W.T. contributed to writing the manuscript and supplementary materials.

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Supporting Information

Fig. S1. Sampling site. (a) Map of Europe with Poland and Holy Cross Mountains (HCM) indicated. (b) Geological map of Holy Cross Mountains. Asterisk indicates the investigated locality. Slightly modified from Malec *et al.* (2010).

Fig. S2. Geological settings. (a) Section through Cambrian to Silurian sediments in the Zbrza Anticline (based on observations from core drills and field outcrops); location of fossil plants is marked with an asterisk. (b) Hirnantian mudstone with location of fossil plants marked with an arrow.

Text S1. Geological settings and stratigraphy, sample processing and palynological analysis.

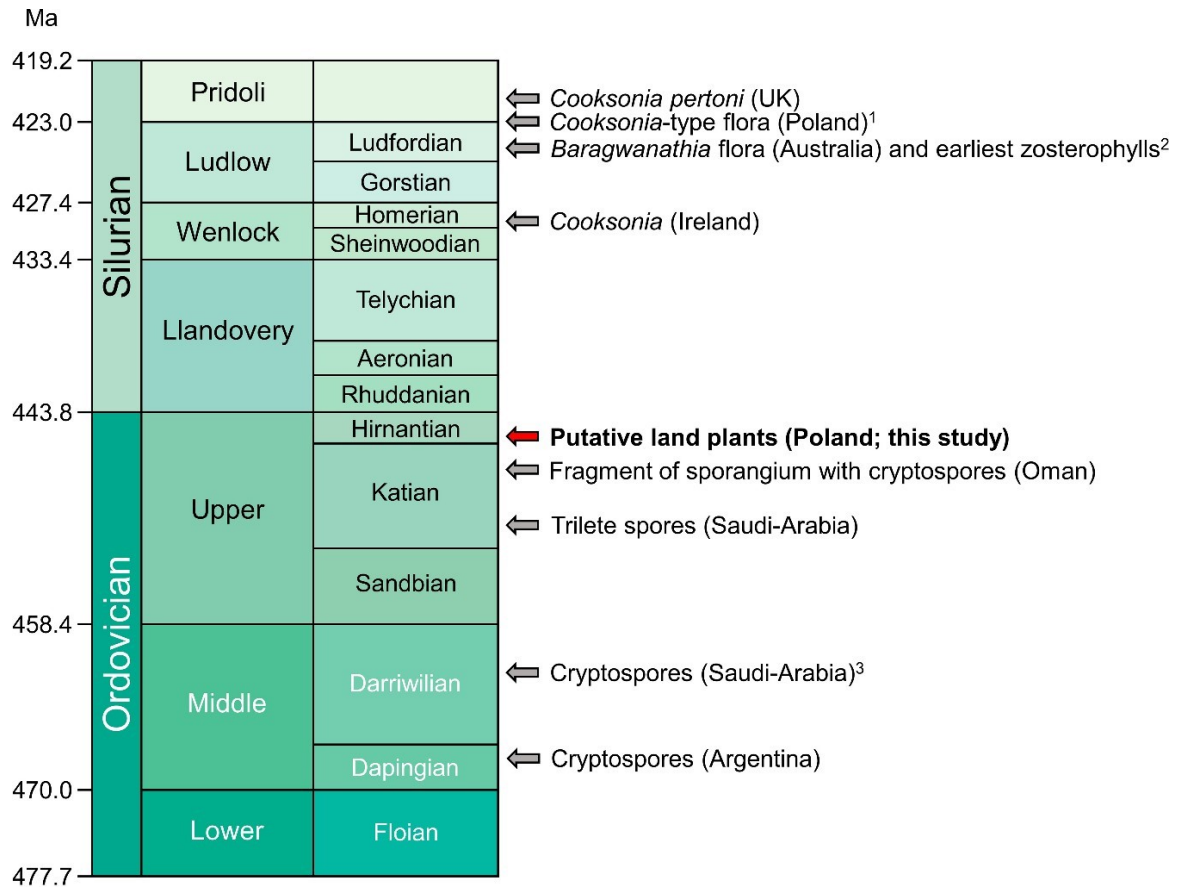
Figure legends

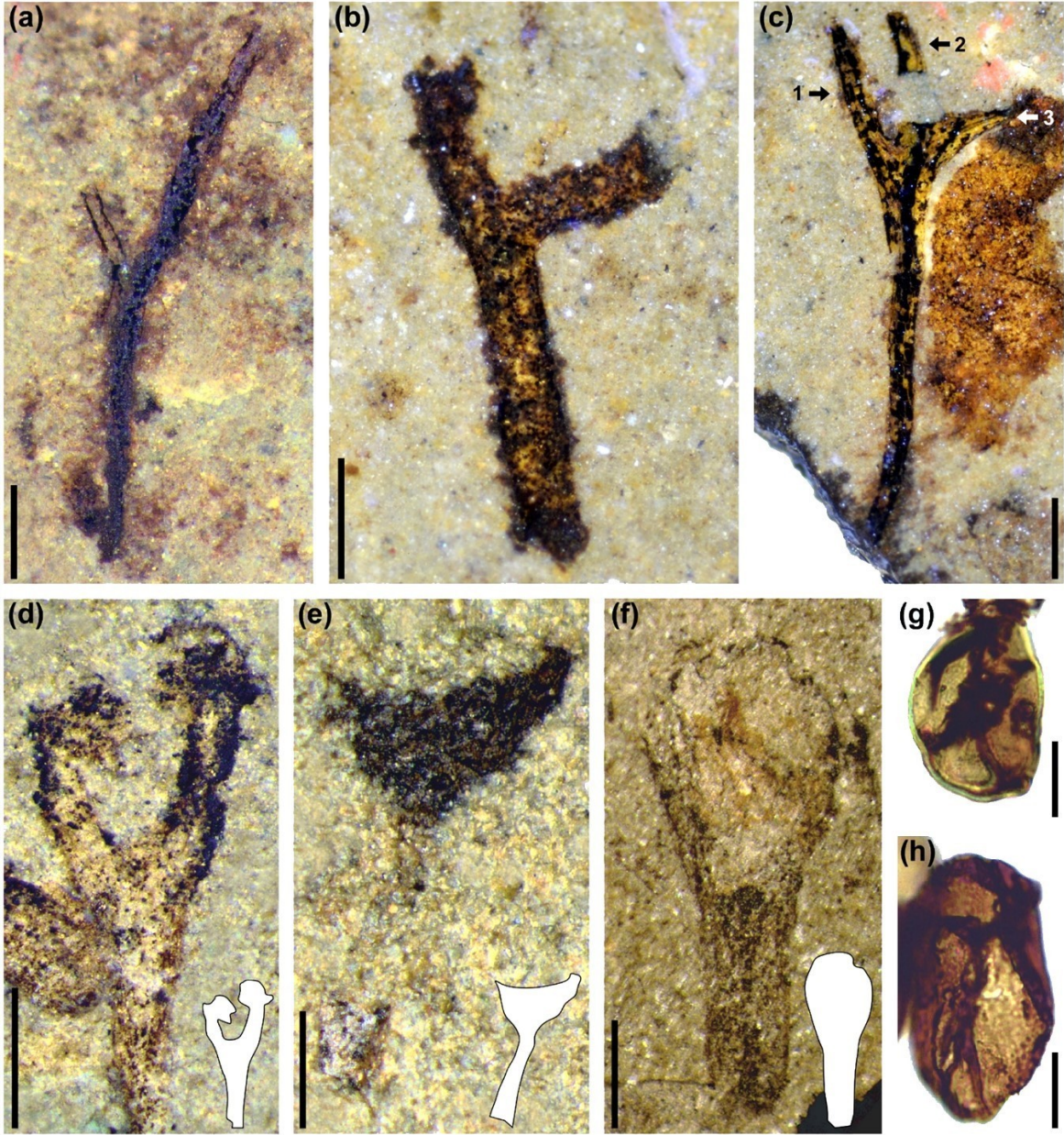
Fig. 1. Stratigraphic occurrences of the oldest fossils of land plants and spores. Bold text identifies the fossil assemblage described in this paper. Ages (Ma) from the *International Chronostratigraphic Chart of the International Commission on Stratigraphy* v2016/12. References: ¹Bodzioch *et al.* (2003), ²Kotyk *et al.* (2002), ³Strother *et al.* (1996). Modified from Edwards & Kenrick (2015, fig. 1).

Fig. 2. Plant remains and spores from Zbrza (Poland). (a, b) Dichotomously branched axes attributed to *Hostinella* sp. (c) Trichotomous axis. Daughter axes are indicated by an arrow and numbered 1-3. (d) Dichotomously branched, slender and leafless stem bearing terminal structures interpreted as sporangia. (e) Short axis ending in a horizontally stretched, presumably cup-shaped, sporangium. (f) Short axis ending in an ovoid/hemispherical sporangium. Sporangium is approximately as high as wide, and the subtending axis widens

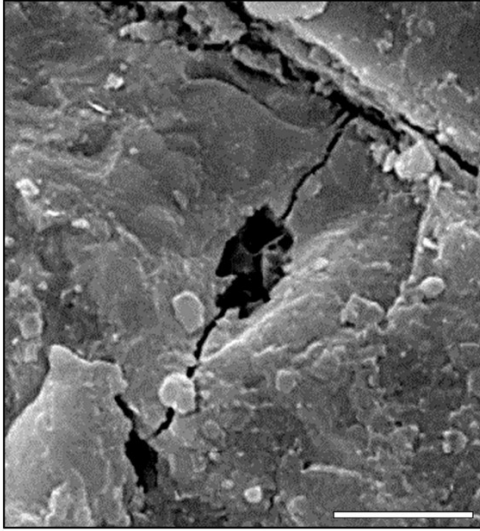
just below it. (g, h) Compressed spores of cf. *Ambitisporites avitus-dilutus* (slide code: ZbrzaA). Scale bars equal 0.5 mm (a-f) and 20 μm (g,h). Light microscope photographs (a-f), interpretative line drawings (d-f). GIUS numbers 2-3675/1-8.

Fig. 3. Probable stomatal complex from Zbrza (Poland). (a) SEM image of a stoma from an indeterminate axis, with elongated stomatal pore and traces of guard cells. (b) Line drawing showing the main structure (guard cells and stomatal pore) of stoma illustrated in (a). Scale bar equal 10 μm . GIUS number 2-3675/9.





(a)



(b)

