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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  $\mu\text{m}$  long by 21  $\mu\text{m}$  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 (Steemans *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.

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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.

## References

- Berner RA, Kothavala ZA. 2001.** Geocarb III. A Revised Model of Atmospheric CO<sub>2</sub> over Phanerozoic Time. *American Journal of Botany* **301**: 182–204.
- Berner RA, VandenBrooks JM, Ward PD. 2007.** Oxygen and evolution. *Science* **316**: 557–558.
- Bodzioch A, Kozłowski W, Popławska A. 2003.** *Cooksonia*-type flora from the Upper Silurian of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* **48**: 653–656.
- Cairns S, Den Hartog C, Arneson C. 1986.** Class Anthozoa (Corals, anemones). In: Sterrer W, Schoepfer-Sterrer C eds. *Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms*. Wiley, New York, 159–194.
- Clarke JT, Warnock R, Donoghue PC. 2011.** Establishing a time-scale for plant evolution. *New Phytologist* **192**: 266–301.
- Edwards D, Rogerson ECW. 1979.** New records of fertile Rhyniophytina from the late Silurian of Wales. *Geological Magazine* **116**: 93–98.
- Edwards D, Feehan J. 1980.** Records of *Cooksonia*-type sporangia from late Wenlock strata in Ireland. *Nature* **287**: 41–42.
- Edwards D, Wellman CH. 2001.** Embryophytes on land: The Ordovician to Lochkovian (Lower Devonian) record. In: Gensel P, Edwards D eds. *Plants Invade The Land: Evolutionary And Environmental Perspectives*. New York, USA: Columbia University Press, 3–28.

- Edwards D, Richardson JB. 2004.** Silurian and Lower Devonian plant assemblages from the Anglo-Welsh basin: A palaeobotanical and palynological synthesis. *Geological Journal* **39**: 375–402.
- Edwards D, Kenrick P. 2015.** The early evolution of land plants, from fossils to genomics: a commentary on Lang (1937) 'On the plant-remains from the Downtonian of England and Wales'. *Philosophical Transactions of the Royal Society B* **370**: 20140343.
- Edwards D, Fanning U, Richardson JB. 1986.** Stomata and sterome in early land plants. *Nature* **323**: 438–440.
- Edwards D, Davies KL, Axe LM. 1992.** A vascular conducting strand in the early land plant *Cooksonia*. *Nature* **357**: 683–685.
- Edwards D, Kerp H, Hass H. 1998.** Stomata in early land plants: An anatomical and ecophysiological approach. *Journal of Experimental Botany* **49**: 255–278.
- Edwards D, Morris JL, Richardson JB, Kenrick P. 2014.** Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytologist* **202**: 50–78.
- Fanning U, Richardson JB, Edwards D. 1988.** Cryptic evolution in an early land plant. *Evolutionary Trends in Plants* **2**: 13–24.
- Gerrienne P, Servais T, Vecoli M. 2016.** Plant evolution and terrestrialization during Palaeozoic times—The phylogenetic context. *Review of Palaeobotany and Palynology* **227**: 4–18.
- Gonez P, Gerrienne P. 2010a.** A new definition and a lectotypification of the genus *Cooksonia* Lang 1937. *International Journal of Plant Sciences* **171**: 199–215.
- Gonez P, Gerrienne P. 2010b.** *Aberlemnia caledonica* gen. et comb. nov., a new name for *Cooksonia caledonica* Edwards 1970. *Review of Palaeobotany and Palynology* **163**: 64–72.
- Gray J. 1985.** The microfossil record of early land plants: Advances in understanding of early terrestrialization, 1970–1984. *Philosophical Transactions of the Royal Society of London B* **309**: 167–195.
- Hemsley AR. 1989.** The ultrastructure of the spore wall of the Triassic bryophyte *Naiadita lanceolata*. *Review of Palaeobotany and Palynology* **61**: 89–99.
- Karol KG, McCourt RM, Cimino MT, Delwiche CF. 2001.** The Closest Living Relatives of Land Plants. *Science* **294**: 2351–2353.

- Kenrick P, Crane PR. 1997.** The origin and early evolution of plants on land. *Nature* **389**: 33–39.
- Kenrick P, Kvaček Z, Bengtson S. 1998.** Semblant land plants from the Middle Ordovician of the Prague Basin reinterpreted as animals. *Palaeontology* **42**: 91–102.
- Kenrick P, Wellman CH, Schneider H, Edgecombe D. 2012.** A timeline for terrestrialization: Consequence for the carbon cycle in the Palaeozoic. *Philosophical Transactions of the Royal Society of London B* **367**: 519–536.
- Kielan Z. 1959.** Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. *Palaeontologia Polonica* **11**: 1–198.
- Kotyk M, Basinger JF, Gensel PG, de Freitas TA. 2002.** Morphologically complex plant macrofossils from the Late Silurian of Arctic Canada. *American Journal of Botany* **89**: 1004–1013.
- Lang WH. 1937.** On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London B* **227**: 245–291.
- Masiak M, Podhalańska T, Stempień-Sałek M. 2003.** Ordovician-Silurian boundary in the Bardo Syncline (Holy Cross Mountains)—New data on fossil assemblages and sedimentary succession. *Geological Quarterly* **47**: 311–329.
- Morris JL, Richardson JB, Edwards D. 2011.** Lower Devonian plant and spore assemblages from Lower Old Red Sandstone strata of Tredomen quarry, South Wales. *Review of Palaeobotany and Palynology* **165**: 183–208.
- Nøhr-Hansen H, Koppelhus EB. 1988.** Ordovician spores with trilete rays from Washington Land, North Greenland. *Review of Palaeobotany and Palynology* **56**: 305–311.
- Raymond A, Gensel P, Stein WE. 2006.** Phytogeography of late Silurian macrofloras. *Review of Palaeobotany and Palynology* **142**: 165–192.
- Rayner RJ. 1986.** *Promissum pulchrum*: The unfulfilled promise? *South African Journal of Science* **82**: 106–107.
- Rubinstein CV, Gerrienne P, de la Puente GS, Astini RA, Steemans P. 2010.** Early Middle Ordovician evidence for land plants in Argentina (Eastern Gondwana). *New Phytologist* **188**: 365–369.

- Snigirevskaya IS, Popov LE, Zdeska D. 1992.** New discovery of the oldest higher plant remains in the Middle Ordovician of Kazakhstan (Novie nakhodni ostatkov dreveishchikh veschikh rastenii I srednem ordovike juusnogo kazakhstana). *Botanicheskii Zhurnal* 77: 1–10.
- Song Z, Wang H, Strong PJ, Li Z, Jiang P. 2012.** Plant impact on the coupled terrestrial biogeochemical cycles of silicon and carbon: Implications for biogeochemical carbon sequestration. *Earth-Science Reviews* 115: 319–331.
- Stemans P. 1999.** Paléodiversification des spores et des cryptospores de l'Ordovician au Dévonien inférieur. *Geobios* 32: 341–352.
- Stemans P, Le Hérisse A, Bozdogan N. 1996.** Ordovician and Silurian cryptospores and miospores from southeastern Turkey. *Review of Palaeobotany and Palynology* 93: 25–76.
- Stemans P, Le Hérisse A, Melvin J, Miller MA, Paris F, Verniers J, Wellman CH. 2009.** Origin and radiation of the earliest vascular land plants. *Science* 324: 353.
- Strother P, Al-Hajri S, Traverse A. 1996.** New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. *Geology* 24: 55–58.
- Temple JL. 1965.** Upper Ordovician brachiopods from Poland and Britain. *Acta Paleontologica Polonica* 10: 379–450.
- Theron JN, Rickards RB, Aldridge RJ. 1990.** Bedding plane assemblages of *Promissum pulchrum*, a new giant Ashgill conodont from the Table Mountain Group, South Africa. *Palaeontology* 33: 577–594.
- Trela W, Szczepanik Z. 2009.** Lithology and acritarch assemblage of the Zalesie Formation in the Holy Cross Mountains on the background of the Late Ordovician paleogeography and sea-level changes. *Przegląd Geologiczny* 57: 147–157.
- Wellman CH, Osterloff PL, Mohiuddin U. 2003.** Fragments of the earliest land plants. *Nature* 425: 282–285.
- Wellman CH, Stemans P, Vecoli M 2013.** Palaeophytogeography of Ordovician-Silurian land plants. In: D. A. T. Harper, T. Servais eds. *Early Palaeozoic Biogeography and Palaeogeography*. London: Geological Society, 461–476.

**Zhong B, Fong R, Collins LJ, McLenachan PA, Penny D. 2014.** Two new fern chloroplasts and decelerated evolution linked to the long generation time in tree ferns. *Genome Biology and Evolution* **6**: 1166–1173.

## 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.

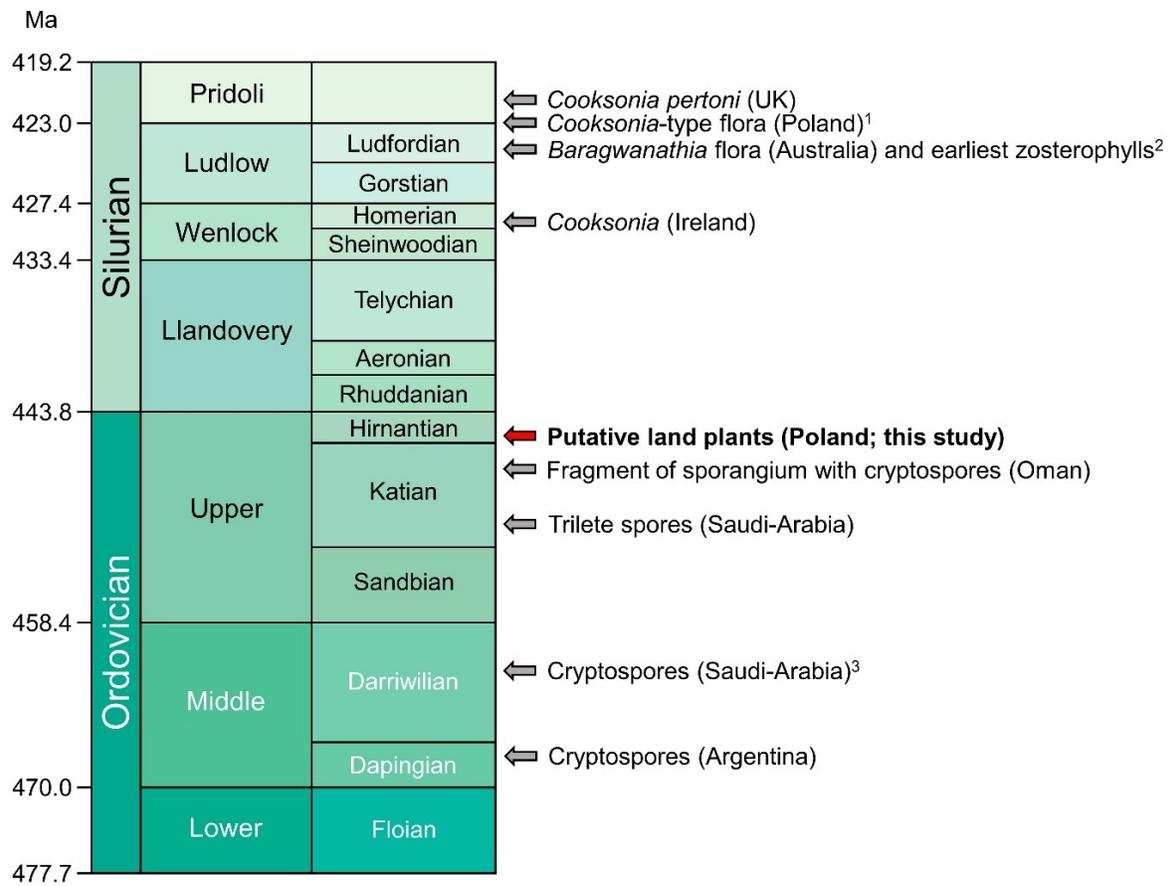
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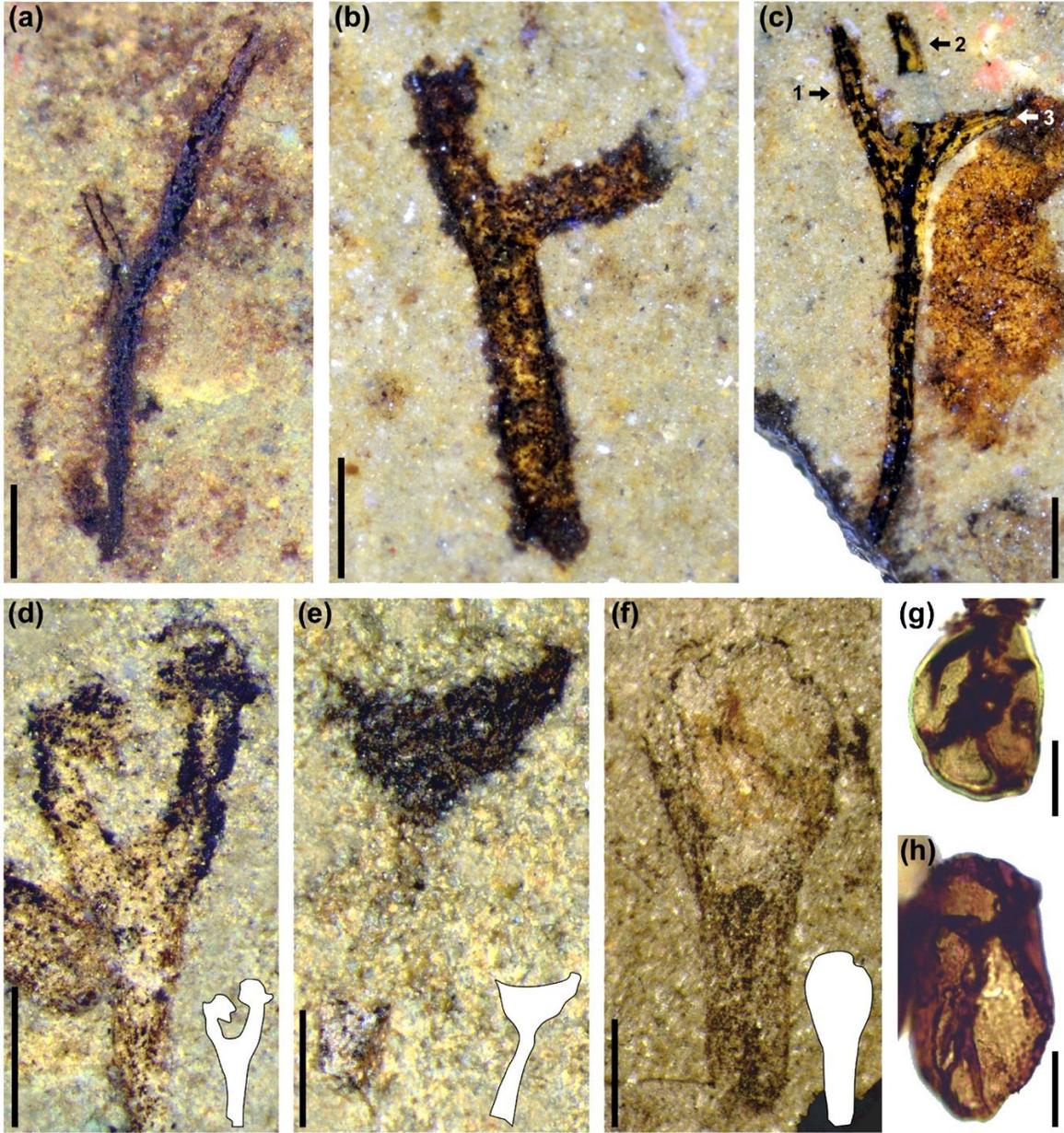
**Fig. 1.** Stratigraphic occurrences of the oldest fossils of land plants and spores. Bold text identifies the fossil assemblage described in this paper. Ages (Ma) from the *International Chronostratigraphic Chart of the International Commission on Stratigraphy* v2016/12. References: <sup>1</sup>Bodzioch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

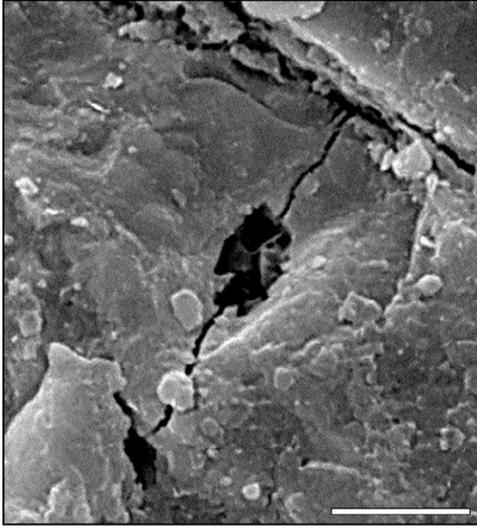
just below it. (g, h) Compressed spores of cf. *Ambitisporites avitus-dilutus* (slide code: ZbrzaA). Scale bars equal 0.5 mm (a-f) and 20  $\mu\text{m}$  (g,h). Light microscope photographs (a-f), interpretative line drawings (d-f). GIUS numbers 2-3675/1-8.

**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  $\mu\text{m}$ . GIUS number 2-3675/9.





(a)



(b)

