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The dawn of terrestrial ecosystems on Baltica: First report on land plant remains and arthropod coprolites from the Upper Silurian of Gotland, Sweden

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ABSTRACT

Sporangia, with their *in situ* cryptospores, spore masses, and a possible axis were identified in marginal marine Ludlovian deposits from Gotland, Sweden by means of light- and scanning electron microscopy.
The sporangia identified are elongate, with fragments of the sporangia covering preserved, and contain well-preserved *in situ* embryophyte cryptospores identified as *Laevolancis divellomedia* (monad) and *Dyadospora murusdensa* (dyad). A single detached axis was identified possessing superficial longitudinal striations resembling epidermal cell patterning. The axis ends in a cup-shaped structure that possibly represents the basal part of a sporangium. Masses of cryptospore monads shrouded in amorphous organic material, most probably representing coprolites of terrestrial arthropods, were found in the same beds. The spores in these masses are degraded in sharp contrast to the excellent preservation of the dispersed and sporangia-hosted spores. The monad, *L. divellomedia,* a common local constituent of the dispersed microflora, was identified in the coprolites. This is the first report of undisputed Silurian land plant remains in Baltica and the study reveals one of the earliest examples of arthropod–plant interactions.

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1. Introduction

Elucidating the evolution of the earliest terrestrial flora has been largely based on the records of dispersed spores, due to macro- and mesofossils seldom being found in Ordovician and early Silurian rocks. The enigmatic cryptospores, which to a large extent lack extant analogues (Shute et al., 1996), first appear in the fossil record in mid-Ordovician rocks (Rubinstein et al., 2010), generally occurring in the form of dyads (two spores fused) and tetrads (four spores fused). They differ from trilete spores in lacking haptotypic contact features and in some cases by bearing an envelope. The bonding of the units ranges from being permanent to facultative in character. The earliest cryptospores recorded are encountered in Argentinean lower Middle Ordovician (Dapingian, about c. 473–471 Ma; Rubinstein et al., 2010) rocks. Five genera of naked and enveloped monads (single spores) and tetrads have been identified in these Argentinean early cryptospore assemblages.

The first hilate cryptospore monads appeared by the Late Ordovician (Katian), all probably derived from dissociated dyads (Steemans et al., 2009). Through the course of the Silurian, cryptospores in dyad form became progressively less common, although they persisted into the Lochkovian (Wellman et al., 1998b; Gensel, 2008). The monads increased, however, in both diversity and abundance until the end of the Silurian or the beginning of the Devonian and then they decreased in the end of Lochkovian and finally disappeared in the Late Devonian (Wellman et al., 1998b).

In situ records of early spores are important since they combine information on the palaeogeographic radiation and evolution of dispersed spores with knowledge of the ecological and structural development of the plants that produced them. Morris et al. (2011a) describes several *in situ* spore-containing sporangia of Lockhovian age from the Welsh Borderline. They found two groups of sporangia, one containing monads of the cryptospores genus *Cymbohilates* and one containing trilete spores of the genera *Ambitisporites*, *Aneurospora* and *Streelispora*. They erected two new plant genera that produced these spores; *Lenticulatheca* (that produced the monads) and *Paracooksonia* (that produced the trilete spores). These two genera show a close relationship and they consider both genera to be rhyniophytoids (Morris et al., 2011a). Another study by Morris et al. (2011b) discusses plant and spore assemblages of Lower Devonian age from the Lower Old Red Sandstone in South Wales. Rhyniophytes and Rhyniophytoids of the genera *Cooksonia*, *Salopella* and *Tarrantia* were found together with a diverse group of minute axial plants and dispersed spores. The minute plants were found to have both tracheophytic and bryophytic characters and are considered to be stem-group embryophytes apart from rhyniophytes and rhyniophytoids (Morris et al., 2011b).

Pridolian–Lochkovian sporangia of various forms encompassing a wide range of cryptospore types have been described from localities in the Welsh Borderland in Britain, as summarized by Edwards and

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Richardson (2004). Thus far, however, only cryptospore-bearing sporangia with short axes preserved have been described, and these provide only limited information on the stature of the whole plants. Based on the morphology of various sporangia fragments Edwards (1996) and Wellman et al. (1998b), suggested that some of the mesofossils containing *in situ* hilate cryptospores were produced by rhyniophytoids, i.e. plants of rhyniophyte design but without proven tracheophyte affinity. TEM studies of the ultrastructure of the outer spore wall of cryptospores suggest a liverwort affinity for the earliest land plants producing these spores (Wellman et al., 2003).

The earliest trilete spores have been recognized in Ordovician (mid-Katian) rocks of Saudi Arabia and have been suggested to derive from the earliest vascular plants (Steemans et al., 2009).

Dispersed laevigate trilete spores resembling those of basal vascular plants became common during the early Silurian (Burgess and Richardson, 1991; Steemans, 2000; Wellman and Gray, 2000). Although mesofossils of land plants have been identified throughout the Silurian, they do not occur in substantial numbers until the late Silurian (Edwards, 1990; Steemans, 2000; Edwards and Wellman, 2001; Gensel, 2008).

The earliest plant fragments containing *in situ* spores were discovered in Oman and are of Late Ordovician (Caradoc) age (Wellman et al., 2003). Parts of what is presumed to be a sporangium cover were found on spore masses. The spore masses consist of cryptospores in the form of naked tetrads, envelope-enclosed tetrads and naked dyads and are suggested to be of liverwort affinity based on the spore wall ultrastructure (Wellman et al., 2003). More extensive evidence of early land plants has been found in Upper Silurian and in Lower Devonian sediments from Britain in the form of meso- and macrofossils (Edwards, 2000; Edwards and Wellman, 2001; Edwards and Richardson, 2004).

This investigation aims to evaluate the regional terrestrial ecosystem of Baltica toward the end of the Silurian period by documenting the occurrence of cryptospore-producing plants and highlighting the fauna–flora interaction in this early ecosystem. Attention is also directed at taxonomic problems stemming from the occurrence of monads and dyads within the same sporangium. The Gotland material contributes to an emerging picture of diversity and ecological interactions in early terrestrial ecosystems.

2. Geological background

During the Ludlovian, palaeo-Gotland was situated in a shallow bay in the central part of the southern shore of the palaeocontinent of Baltica, which at the time was located close to the palaeoequator (Fig. 1); (Bassett et al., 1989; Scotese and McKerrow, 1990).

The bedrocks on Gotland consist of upper Llandoverian to upper Ludlovian marine sediments that mainly developed as a regressive sequence of marlstones and limestones, including reefs (Fig. 2). The clastic sedimentary components of this bedrock were probably transported to the area by rivers draining land to the northwest (Tullborg et al., 1995). For detailed stratigraphical and sedimentological information on Gotland, see Calner and Eriksson (2006) and Eriksson and Calner (2008) and the references cited therein.

Land-derived palynomorphs are only common in the partly argillaceous Ludfordian Burgsvik Beds exposed in southern Gotland (Fig. 2). The dispersed palynomorph assemblages there contain both the remains of marine organisms (acritarchs, prasinophycean algae, and scolecodonts) and terrestrial life (cryptospores, trilete spores, fungal spores, hyphae, tubular structures and cuticles) (Hagström, 1997).

The maximum thickness of the Burgsvik Beds is recorded in the Burgsvik core 1 at 47 m (Hede, 1919) (Fig. 2). That core served as a basis for Manten's (1971) subdivision of the Burgsvik Beds into three members. Biostratigraphical investigations based on conodont elements indicated the sequence to be of Ludfordian (Whitcliffian) age (Jeppson, 2005). Marine macrofossils in the Burgsvik Beds are rare, in contrast to the otherwise highly fossiliferous deposits found in other units on Gotland (Laufeld and Bassett, 1981). Sedimentary structures present in the arenitic portions of the Burgsviks Beds indicate deposition in shallow water, probably as offshore bars in a storm-influenced environment.

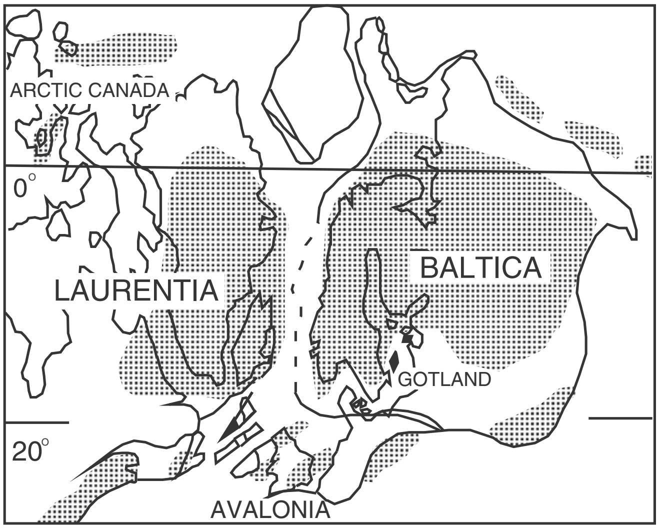

Fig. 1. A palaeogeographic reconstruction of Baltica during the Ludlovian. The positions indicated are from Scotese and McKerrow (1990). The shaded areas show schematic distribution of land (Bassett et al., 1989; Witzke, 1990).

No unequivocal plant macrofossils have previously been found on Gotland. Halle (1920) reported the presence of *Psilophyton*(?) *hedei* from the lower Ludlovian Hemse Beds represented by several branching spiny axes a few centimetres in length each. Re-examination of

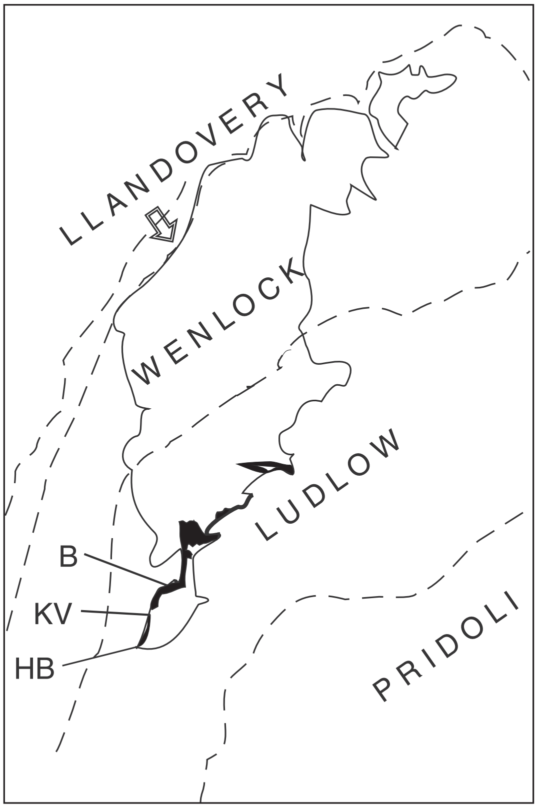

Fig. 2. Silurian series on Gotland and the location of the Burgsvik Beds (in black). Localities: B = Burgsviksborrningen 1 well, KV = Kättelvik 1 and 2 cores, HB = Hoburgen 1 outcrop.

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