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Cryptospores from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of Saudi Arabia: taxonomy and systematics

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ABSTRACT

Well preserved palynomorphs from the Hanadir Shale Member of the Qasim Formation (Darriwilian) from Saudi Arabia were recovered from wells KAHF-1 and TAYM-4, which include a variety of cryptospore tetrads, dyads and monads. An assemblage of these cryptospores is described systematically for the first time. Two new cryptospore genera, *Cryptotetras* and *Didymospora* are described; one new species of *Rimosotetras*, *R. subsphaerica*, is also erected to accommodate loosely arranged tetrads comprised of sub-spherical spore-members. The palynoflora appears to have more in common with younger assemblages of latest Ordovician and earliest Silurian age than it does with problematic spore-like microfossils from older strata, indicating that these cryptospores were produced by early embryophytes, true land plants. Given the somewhat advanced evolutionary spore character of the Hanadir assemblage, the gap between the megafossil record of plant axes and spores might indicate that the plants of the Ordovician were at a bryophyte grade of evolution. The possibility remains, however, that spore characters evolved in advance of other defining characters associated with the evolution of sporophytic plant phases on land.

1. Introduction

Neither the chlorophyte nor the charophyte algae produce resistant walled tetrahedral spore tetrads. This simple morphological fact allows us to track the presence of land plants in the stratigraphic record through their more widely distributed spore remains. Cryptospore dyads have also become accepted as proxies for embryophytes, in part because they occur in the sporangia of early land plants (Fanning et al., 1991; Wellman et al., 1998a,b, 2003; Edwards and Wellman, 2001). Occurrences of cryptospores from Ordovician rocks are somewhat rare and the description and systematic characterization of any assemblage of this age is apt to significantly affect our understanding of the origin of land plants. The cryptospores from the Hanadir Member of the Qasim Formation in Saudi Arabia (Figs. 1–2), are no exception in this regard: they are Darriwilian in age which places them at the base of the record of cryptospore dyad and tetrad populations that show unambiguous affinities with embryophytic spores. Given a paucity of Ordovician macroscopic plant remains, the diversity of cryptospore tetrad and dyad species is our only proxy of true plant diversity at this time. To the extent that cryptospore morphology and topology are a reflection of the evolution of meiosis in plants, they can inform us as well of fundamental biological processes that were actively evolving during the algal-plant transition (Taylor and Strother, 2009; Strother, 2010) or in the early establishment of bryophyte lineages (Brown and Lemmon, 2011).

The stratigraphic and systematic record of the cryptospores presents us with a range of evolutionary scenarios, and the primary goal of providing a proper systematic treatment of the cryptospores from the Hanadir is to get a sense of where they fit into these early models of plant evolution. Steemans noted, that in spite of its early age, the Hanadir assemblage already contains characteristic elements that range into the Llandovery (Steemans, 1999a). Wellman, in his study of cryptospores from the type Caradoc area, concluded that the later portion of the Ordovician Period represented a period of evolutionary stasis for the cryptospores (Wellman, 1996). This aspect of cryptospore evolution has been supported by subsequent reviews and systematic comparisons (Steemans, 1999b, 2000; Wellman and Gray, 2000; Kenrick et al., 2012). Wellman has argued that the early cryptospore assemblages are dominated by membrane-enclosed taxa (Wellman, 1996; Wellman and Gray, 2000) with a shift toward naked forms dominating post-Llandoverian assemblages. The systematics of the Hanadir cryptospores presents a mixed response to these ideas, although it is clear that this early assemblage does indeed include taxa which can be also be found in the Silurian, supporting the original observation of Steemans (1999a).

There is little doubt that the Hanadir assemblage contains elements that are related to subsequent plant evolution and the dispersed

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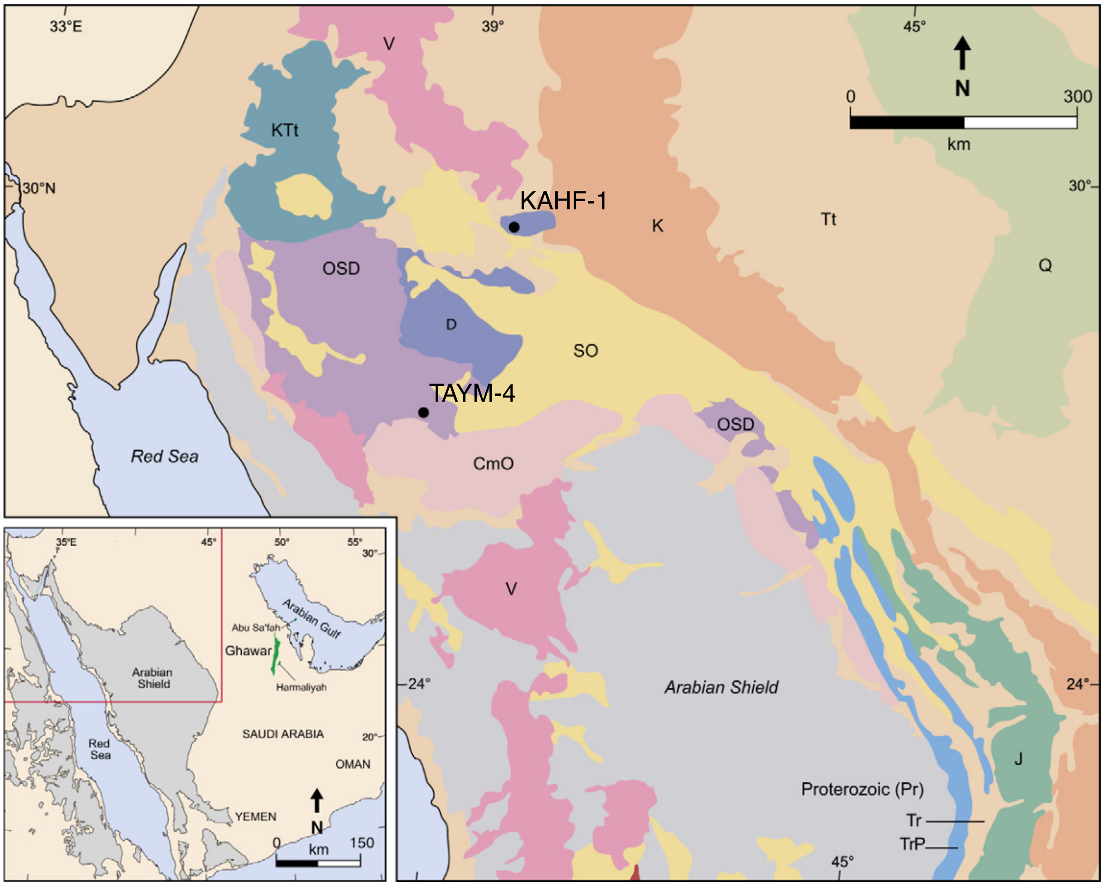

Fig. 1. Geological setting and location of study core holes KAHF-1 and TAYM-4. CmO, undifferentiated Cambrian-Ordovician; SO, undifferentiated Ordovician-Silurian; D, Devonian; OSD, undifferentiated Ordovician-Silurian-Devonian.

cryptospore and trilete spore record that followed throughout the remainder of the Ordovician and Silurian Periods. But there is a second question with respect to land plant evolution that should be addressed in the Hanadir assemblage and that is, to what extent are these microfossils tracking transitory phases during the evolution of plants from algae? Are there any aspects of the Hanadir assemblage that appear to be related to older fossils in the stratigraphic record? In order to examine this question, one needs to compare with what is known about earlier Ordovician and Cambrian occurrences of cryptospores (Taylor and Strother, 2009) and spore-like palynomorphs (Strother, 2000; Baldwin et al., 2004; Strother et al., 2004; Taylor and Strother, 2008; Taylor, 2009), in spite of the fact that such forms may or may not be considered relevant to land plant evolution (Wellman, 2003; Steemans and Wellman, 2004; Kenrick et al., 2012).

2. Geologic setting, material and methods

The present work expands on an initial report (Strother et al., 1996) which did not include systematic or taxonomic characterization of the Hanadir palynoflora. The original material was based on cuttings (well RA: see Strother et al., 1996) and from core (wells TAYM-4 and KAHF-1, Figs. 1–2). Rock samples were processed using conventional acid maceration (HF and HCl) treatment following Traverse (2008). The extracted organic residues were not oxidized. In this report, all described material comes from well TAYM-4, although some additional preparations from the cores were examined. The geological setting of the Hanadir palynoflora can be found in Strother et al. (1996; and references therein). Additional information about the regional and basinal setting of the Hanadir can be found in Al-Hajri and Owens (2000) and more specifically, in Le Hérissé et al. (2007) who illustrated several cryptospores recovered from the Hanadir Member at a different location in central Saudi Arabia.

The assemblage is well preserved, but it occurred in a mixed setting in which clearly marine elements, chitinozoa and acritarchs, dominate over cryptospores (Strother et al., 1996). The underlying Saq Formation, considered to represent fluvial to near-shore settings, appears to be conformable in places with the Hanadir Member (Le Hérissé et al., 2007), which clearly was deposited in marine conditions. In general, based on the palynomorph content alone, the Hanadir Member was deposited in a shallow marine setting which received some terrestrial input and was either rapidly buried or accumulated under low O_2 levels. This latter conclusion is based on the excellent organic preservation that is seen in the TAYM-4 specimens and the ubiquitous presence of pyrite, often embedded in the specimens themselves (Plate I, 1, 4 and throughout).

All images were photographed using a Fujifilm S5 Pro IS camera body attached to a Zeiss Axiomat compound microscope. A B+W 486 filter was used to block Infrared (IR) and ultraviolet (UV) ends of the spectrum, as the Fujifilm camera is both UV and IR sensitive. A 100 W halogen light source was set to a color temperature of 3200 °K, and the raw files were captured using "Tungsten" to set the white balance. Neutral density filters were used to control light level during exposure. Raw files were opened in Adobe Bridge using the Camera Raw interface to adjust exposure. Final color balance was achieved by setting the white point of the image background to 218 in the Levels menu in Adobe Photoshop.

Type specimens are housed in the Micropalaeontology Department at the Natural History Museum, Cromwell Road, London. Supporting