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Diversity and ecology of sponges in the Early Ordovician Fezouata Biota, Morocco

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ABSTRACT

Sponges form a significant component of the diversity of the Tremadocian (Early Ordovician) Fezouata Biota in the Anti-Atlas of Morocco, but are distributed intermittently and have so far received only limited attention. New material reveals a high diversity of undescribed taxa (a total of at least 27 species), including numerous representatives of protomonaxonid groups such as the Leptomitidae, Piraniidae and "Choiidae". Some of these taxa show unusually complex skeletal architecture, and represent derived variations of their lineages relative to those in the Cambrian Burgess Shale-type faunas, although most species are assignable to described families. Reticulosan sponges are rare in the Fezouata Biota, and usually fragmentary. The palaeoecology of the sponge fauna is unusual, with most species known only from single sites (frequently single bedding planes), but are often abundant where they occur. It is very rare for two species of sponge to be found on the same slab, or at precisely the same horizon. With some species of protomonaxonid, particular bedding planes are crowded with individuals of species that are rarely, if ever, found isolated. Only two species (*Pirania auraeum* Botting, 2007 and an undescribed hazeliid) are found at numerous levels, and these are not known from crowded assemblages; this may relate to differences in reproductive strategy. The dense, usually monospecific populations can best be explained through repeated colonisation events in a frequently hostile environment, rather than representing a range of different stable communities.

1. Introduction

Sponges (Porifera) are often (though not universally) the second-largest animal group in Cambrian Burgess Shale-type biotas, in terms of diversity and often also abundance (Caron and Jackson, 2006; Wu et al., 2014). In almost all such deposits that have been described in detail, only arthropods are more diverse, and in these deposits sponges are in some cases the dominant group by biomass (Conway Morris, 1986). A significant diversity of sponges is also seen in the early Cambrian, carbonate-hosted Sinsk Biota of Siberia (Ivantsov et al., 2005). In combination with the other Burgess Shale-type faunas, this shows that sponges were not limited to deeper-water environments, but were a constant presence among Cambrian marine communities in at least shelf-depth habitats.

Ordovician faunas are much more diverse ecologically than Cambrian communities (Harper, 2006; Servais et al., 2010), but there is no equivalent suite of soft-bodied biotas; those that are known are taphonomically and ecologically disparate, often with highly specialised or taxonomically limited communities (Balinski and Sun, 2015; Farrell et al., 2009; Gabbott et al., 2010; Liu et al., 2006; Young et al., 2007; Botting and Muir, 2012; Botting et al., 2011). The Fezouata Biota (Van Roy et al., 2010, 2015) strongly resembles some of the Cambrian Lagerstätten (especially the Chengjiang Biota; Gabbott et al., 2004; MacKenzie et al., 2015) in appearance and general preservation, and to some extent also in palaeoenvironment (Martin et al., in press); it therefore allows an assessment of ecological continuity from the middle Cambrian into the Early Ordovician, at least at high latitudes. The Fezouata Biota is believed to have been situated at around 75 to 80 degrees South (Torsvik and Cocks, 2011), within the Antarctic Circle, but this is mistakenly given as around 65 degrees South by Martin et al. (in press) and Van Roy et al. (2015). Sponges are moderately well known from Ordovician rocks worldwide, but their record is extremely patchy (Muir et al., 2013). Excluding the mainly carbonate platform-based lithistids, the best-known Ordovician sponge faunas are from siliciclastic sediments of Wales, where an ecological framework is now available for at least the Middle Ordovician (Muir and Botting, 2015). A good understanding of the Fezouata Biota sponge assemblage and its ecology is therefore important for establishing by how much sponge ecology changed from the middle Cambrian to the Early Ordovician, and potentially provides a way to assess the broader applicability of poriferan ecological patterns described from elsewhere.

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2. Materials and methods

This study is based on collections accumulated over many years, by many people. Peter Van Roy acquired and donated many of the new specimens, obtained primarily from the Moroccan commercial collector Mohammed Ben Moula, who ultimately sourced much of the known Fezouata Biota material. This material is housed in the National Museum Wales, under accession number NMW.2015.34G. Other material was collected during the French ANR project "RALI", and made available by Bertrand Lefebvre and Emmanuel Martin; this includes material housed in the museums of Marrakech, Marseille and Lyon universities. Additional specimens were provided by Lucy Muir, or collected in the field by JPB. All the material immediately available in Europe was examined; sponges were identified in stratigraphic collections of the Fezouata Biota, and some were also identified on slabs in collections compiled to represent other groups (notably echinoderms). The extensive Yale Peabody Museum collections have not been accessed for this project, although a preliminary list of sponge material has been studied, together with some photographs; some of this has helped to inform the distribution of particularly distinctive species (notably *Pirania auraeum* Botting, 2007).

Understanding the stratigraphic and distributional framework of the sponges in these collections has been made possible by the work of the RALI project, and the stratigraphic context is based on that provided by Martin et al. (in press). Locality numbers given are those used by this project, and stratigraphic positions are based on the logs of Martin et al. (in press); localities from earlier collections have been correlated into this new numbering scheme by Emmanuel Martin where possible.

Images of the Fezouata Biota do not translate well to greyscale, because the red fossils are a similar shade to the green sediment. Some images in the printed version of this paper have therefore been processed using the software The Gimp to adjust the brightness of specific hues, thus increasing contrast in desaturated images.

This study is not a systematic work, as it does not include material currently in the Yale Peabody Museum, and primary taxonomy is not the purpose of this volume. The aim of this paper is instead to summarise the known diversity, distribution, palaeoecology and wider significance of the fauna, both in terms of how it informs our understanding of the Fezouata Biota and for its implications for understanding Ordovician sponge evolution, at high latitudes or more generally. Generic assignments and species distinctions are therefore tentative at this stage.

3. Taphonomy

Like all elements of the Fezouata Biota, sponges are unevenly distributed through the lower and upper Fezouata formations (also known collectively as the Fezouata Shale, since there is little if any distinction between the two). With non-biomineralised taxa, this can partly be explained as a taphonomic constraint on their distribution; however, this is less obvious in the case of sponges, which in most cases have a siliceous (or calcareous or biminerallic; Botting et al., 2012) skeleton. Siliceous spicule skeletons can be preserved relatively easily in offshore environments, although silica dissolves readily in warm, shallow water (Land, 1976; Rützler and Macintyre, 1978). Rapid burial and protection from subsequent scavenging frequently resulted in preservation of intact sponge skeletons in early Palaeozoic rocks, even where little or no soft tissue preservation occurs (e.g. Botting, 2004; Mehl et al., 1993; Xiao et al., 2005). Such material forms the bulk of the early sponge fossil record.

Even without abrupt burial, sponges often leave a recognisable fossil record. If sponge skeletons become disarticulated before burial, then the dissociated spicules can be dissolved under hostile chemical conditions (Land, 1976), and are often lost from shallow-water siliciclastic sediments. In offshore argillaceous deposits, however, spicules are frequently preserved either as moulds or as pyritic replacements, with the largest spicules retaining some traces of silica (e.g. Botting et al., 2012). In offshore deposits that represent episodic abrupt burial of temporally continuous ecosystems rather than continuous sedimentation, a high proportion of sponges would have died and disarticulated on the sea floor between burial events, leading to a high ratio of spicules to articulated sponges. Episodic burial in turbid gravity flows is believed to be the primary depositional mode of the Fezouata Biota (Martin et al., in press) and unless dissociated spicules were systematically dissolved, spicule-rich sediments should substantially outnumber complete sponges. This is not the case.

In the available collections from the Fezouata Biota, there are few examples of disarticulated sponges known, and no known spiculite layers. There are also very few examples of articulated or near-articulated skeletons without any associated soft tissues, and the only ones seen during this study are reticulosan sponges from a small number of sites. In contrast, there are many horizons crowded with dense monospecific assemblages of protomonaxonid sponges (Fig. 2A) and, in one case, of the reticulosan *Valospongia* Rigby, 1983 (Fig. 2B and C) preserving complete sponges preserved mainly as soft tissues (Fig. 2C), with no sign of disarticulation. Except in very rare cases, neither these nor adjacent horizons preserve isolated spicules in association with the entire sponges, either on the same surface or within the beds in which the mass assemblages occur.

Sponges are always at least partly flattened, with spicules (where visible) three-dimensionally replaced by iron oxides, and almost invariably also a dense deposit of oxides filling the spaces between spicules, and providing a clear margin to the soft tissues of the body wall and osculum. This is typical of exceptionally-preserved pyritized sponge faunas preserved in mudstones elsewhere (e.g. Botting and Muir, 2013; Botting et al., 2015), and implies a two-stage process affecting the soft tissues and the spicules separately.

No sponges (either body fossils or spicules) have been recovered from many of the productive beds for the biota as a whole, despite the widespread presence of soft-tissue pyritization. The apparent absence of sponges from these locations, where pyritization of both biomineralized and non-biomineralized tissues is known, is unlikely to be a taphonomic artefact, and must be assumed to represent an ecological pattern.

4. Fauna

It has taken many years for the extent of the Fezouata Biota sponge fauna to be revealed, largely because of their unusual distribution patterns. Diversity at almost any site within the Fezouata Biota is very low, and most species are restricted to individual exposures. In practise, this means that species are in many cases known only from a single lensiform deposit or thin bed, and each species' discovery is therefore dependent on fortuitous excavation. This has the implication that many other sponges are likely to exist in the Fezouata formations, and many new taxa should be anticipated both in the present collections housed in the Yale Peabody Museum, and from further excavations in future. Although examination of the Peabody collections will presumably affect our understanding of the distribution patterns of the sponges, the collections on which this work is based are large enough to provide a robust outline.

A map of the well-located localities known to produce sponges is provided in Fig. 1, and localities are referred to in the text below; localities referred to as B2007 numbers are those referred to by Botting (2007) for the species described there. Where heights are provided for localities within the measured section, this refers to the stratigraphic framework of Martin et al. (in press); see also Section 5.1.1 for the stratigraphic distribution of the taxa recorded.

4.1. "Protomonaxonida"

The majority of species encountered in the Fezouata Biota, and the great majority of specimens, belong to the informal grouping known