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Taphonomy and morphology of the Ediacara form genus *Aspidella*

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ABSTRACT

Aspidella, the disk-like Ediacaran form genus, is a common and globally distributed member of the Ediacara Biota. In South Australia, it occurs prolifically ($n > 1000$) in locally dense assemblages on the bases of sandstone beds in the eponymous Ediacara Member of the Rawnsley Quartzite. Association with stalks, fronds and textured organic surfaces (TOS) has led to the interpretation of *Aspidella* as the holdfast of a frondose, *Charniodiscus*-like organism which lived with its holdfast secured within or under a sandy microbial mat and its stalk and frond protruding above the substrate and into the water column. As the dominant component of four fossiliferous beds and a minor component of most others, *Aspidella* exemplifies the bed-scale faunal heterogeneity characteristic of Ediacara fossil assemblages. *Aspidella* itself, moreover, is characterized by strong morphological variability, including variation in the presence or absence of particular distinct morphological features, variable preservation as internal and external molds, variable relief and a broad size range. However, the distribution of morphological characters is unrelated to either *Aspidella* specimen size or bed assemblage composition. Herein we demonstrate that this morphological diversity is an expression of neither ontogenetic nor species-level anatomical differences, but rather is the product of differential taphonomy related to variation in local substrate-related sedimentological and biogenic factors, particularly the presence or absence of TOS composed of the eukaryotic tubular organism *Funisia*.

1. Introduction

The appearance of the Ediacara Biota in the fossil record marks an unprecedented leap in morphological and ecological complexity (Clapham and Narbonne, 2002; Narbonne, 2005). Although the presence of trace fossils indicates a bilaterian animal presence in these ecosystems, the phylogenetic affinity and syn- and autecology of the majority of Ediacara organisms remain problematic, with interpretations ranging from crown-group or basal stem-group metazoans (e.g. Erwin et al., 2011; Gehling, 1991; Gehling et al., 2014; Glaessner, 1979, 1984; Sperling and Vinther, 2010) to protists (Zhuravlev, 1993), prokaryotic colonies (Grazhdankin and Gerdes, 2007; Steiner and Reitner, 2001), lichens (Retallack, 1994), fungal-grade organisms (Peterson et al., 2003), an extinct kingdom of life (Seilacher, 1992) or some combination thereof (Xiao and Laflamme, 2009).

In the Ediacaran deposits of South Australia, the majority of Ediacaran fossils, known as the Ediacara Biota, occur in the namesake Ediacara Member of the Rawnsley Quartzite. These diverse assemblages of morphologically enigmatic, predominantly soft-bodied forms are preserved in situ as casts and molds on the bases of medium- to coarse-grained sandstone beds (Droser et al., 2006). Nilpena Station, on the western margins of the Flinders Ranges, due to an exceptional combination of preservation and exposure, provides one of the few localities where Ediacara paleoecology can be explored both in great detail and on a very large areal and stratigraphic scale. Excavation and sequential reassembly of 26 fossiliferous beds (>300 m^2) at Nilpena reflects a growing realization of the need to move away from traditional individual-scale paleoecological methods and toward the more holistic approach of bed-scale community analysis (cf. Clapham et al., 2003; Darroch et al., 2013; Droser et al., 2006).

Traditionally, due to similarities in the diversity of fossil assemblages of the Ediacara Member and those of Russian Ediacaran deposits, the Ediacara Biota of South Australia has been assigned

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to the White Sea Assemblage (Waggoner, 2003). However, fossil assemblages at Nilpena also vary considerably, both between sedimentological facies and from bed to bed (Droser et al., 2006; Gehling and Droser, 2013). The nature and relative timing of this variability, especially the manner in which taphonomy may mediate ecological diversity, are questions of current interest (Droser et al., 2006; Gehling and Droser, 2013; Tarhan et al., 2010). In spite of the common tendency to liken Ediacara faunal assemblages to "census populations" (Clapham et al., 2003; Narbonne, 2005; Seilacher, 1992), i.e. pristine and complete equivalents of their living or recently deceased predecessors, even the most exceptionally preserved soft-bodied fossil assemblages must, as an inherent step in the process of fossilization, have undergone decay, deformation and alteration (Donoghue and Purnell, 2009). Fossil morphology is therefore not only a reflection of original anatomical characters, but also of the sedimentary, biostratinomic and diagenetic processes experienced by a fossil assemblage. Taphonomic variance, if confused with true anatomical diversity and organismal synapomorphies, may lead to false amplification of diversity. Morphologically disparate components of the Ediacara Biota have historically been assigned separate names and phylogenetic reconstructions (cf. Grazhdankin, 2000; Laflamme et al.,

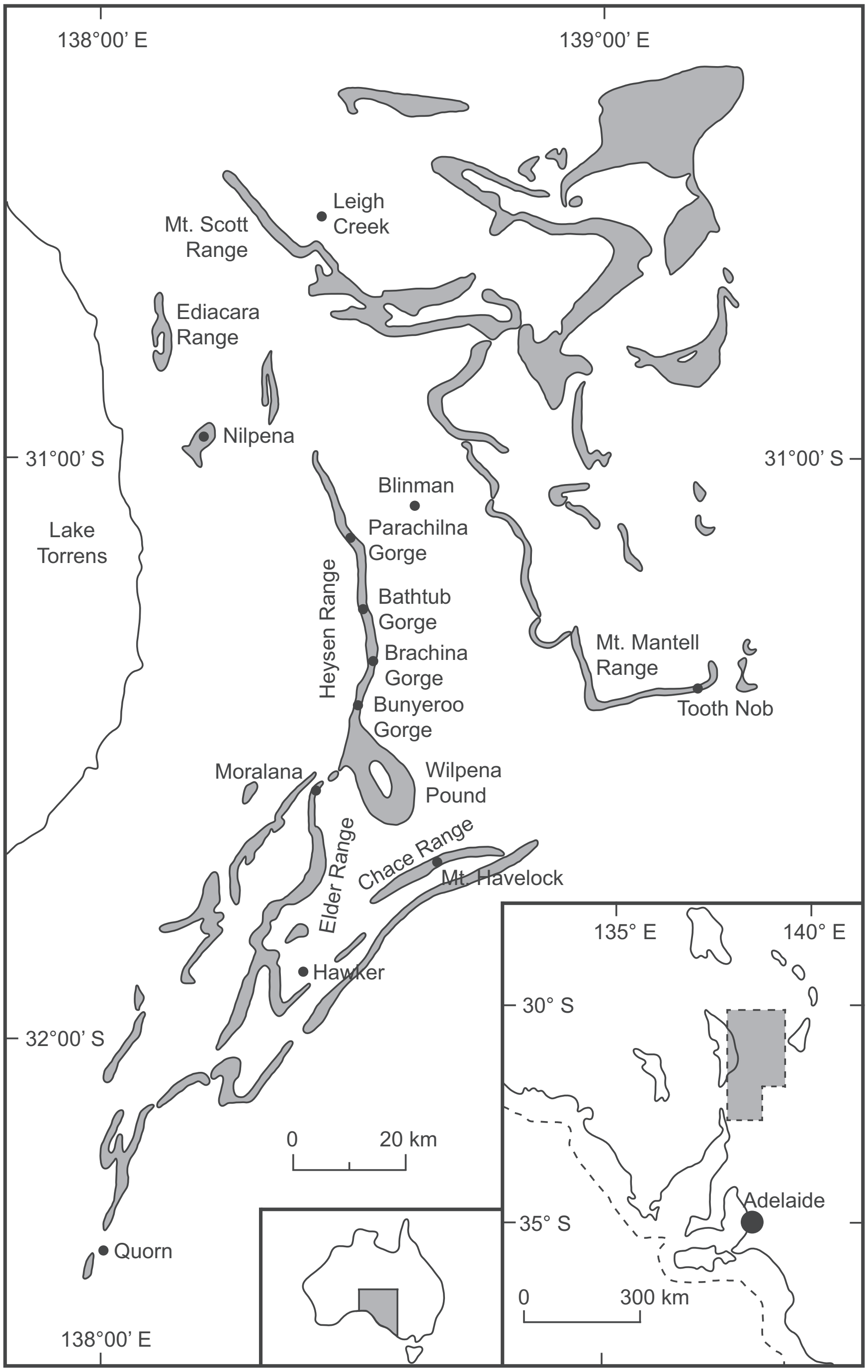

Fig. 1. Geographic context of Ediacara fossil deposits of the Flinders Ranges of South Australia. Modified from Droser et al. (2014). Gray denotes exposure of the Pound Subgroup.