



Variations in population structure of *Diplocraterion parallelum*: Hydrodynamic influence, food availability, or nursery settlement?

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ABSTRACT

In the Triassic of the Betic Cordillera, the U-shaped trace fossil *Diplocraterion parallelum* exhibits pronounced spatial variations in its abundance, size, and orientation. Higher density populations are found in small patches on bedding planes that were topographic lows on the palaeo-seafloor. These patches consist mainly of small specimens, separated into two size-groups: group A with larger specimens, and a similar preferred orientation, and group B of smaller individuals, densely distributed, and with a more variable orientation. Between the patches, isolated large individuals occur sparsely. Comparison with populations of crustaceans (which are among the potential trace makers of *Diplocraterion parallelum*) allows possible population dynamics of *D. parallelum* trace makers in this setting to be considered. Important factors determining changes in the abundance and distribution of crustacean populations are protection of small individuals against predators and/or comparatively high-energy conditions, nursery settlement, and/or temporal, typically seasonal, variations in environmental parameters. Depressions of the seafloor appear to have represented hospitable habitats in which juveniles of the producer of *D. parallelum* developed, reflecting either a deliberate reproductive strategy or the consequence of accumulation of eggs deposited elsewhere. In these depressions energy conditions may have been lower and food availability higher. During early ontogeny, defenseless young individuals used these areas as an ecological refuge against predators and high energy conditions. When the juveniles of the *D. parallelum* trace makers grew, they presumably spread from the nursery to settle in the surrounding area.

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1. Introduction

Ichnological analysis is important in a number of fields, including palaeobiology, palaeoecology, biostratigraphy, evolutionary biology, sedimentology, and sequence stratigraphy (e.g., Miller, 2003; McIlroy, 2004; Webby et al., 2004; Bromley et al., 2007; Miller, 2007; Seilacher, 2007; MacEachern et al., 2008; Buatois and Mángano, 2011). Ichnological and sedimentological data are often coupled in palaeoenvironmental and stratigraphic analyses (McIlroy, 2004). The spatial distribution of individual trace fossils and ichnocoenoses has been investigated in relation to lateral variation and spatial heterogeneity in both marine and terrestrial palaeoenvironments (e.g., McIlroy, 2004; Bromley et al., 2007; Miller, 2007). Ichnological analysis has been used much more rarely, however, to decipher the population dynamics of a single community. Distribution patterns within single populations of *Skolithos* and *Diplocraterion* have been related to potential trace makers, feeding strategy and to infer competition between individuals (Pemberton and Frey, 1984). Variations in the size and distribution pattern of associated examples of an ichnotaxon have high potential to

elucidate aspects of the structure of a palaeo-community, even this approach is scarcely applied. Analysis of size–frequency distribution from trace fossil assemblages reveals very useful for palaeoecological and palaeoenvironmental interpretations (Crimes, 1970; Marintsch and Finks, 1978; Kotake, 1994), including the reconstruction of the size-structure of fossil populations (Kowalewski and Demko, 1997). This study applies this approach to the trace fossil *Diplocraterion parallelum* from the Triassic of the Betic Cordillera, southern Spain, investigating the population dynamics of the trace maker, and considering the potential factors that controlled the variations observed.

2. Geological setting

The Triassic succession of the External Zone of the Betic Cordillera (southern Spain) is traditionally subdivided into the Buntsandstein, Muschelkalk, and Keuper facies. In the Huesa section (Fig. 1; RH-1, 3° 06' 30" W, 37° 45' 32" N, eastern sector of the Betic Cordillera, near the town of Huesa, Jaén Province; Rodríguez-Tovar et al., 2007; Rodríguez-Tovar and Pérez-Valera, 2008), the Muschelkalk sediments (Siles Formation, Middle Triassic; Pérez-Valera, 2005) consist of a 27-m-thick succession of dolomite, marlstone, and thin-bedded and fine-grained limestone, with bioclastic and nodular limestone intercalations. Seven facies (A to G), indicative of shallow carbonate

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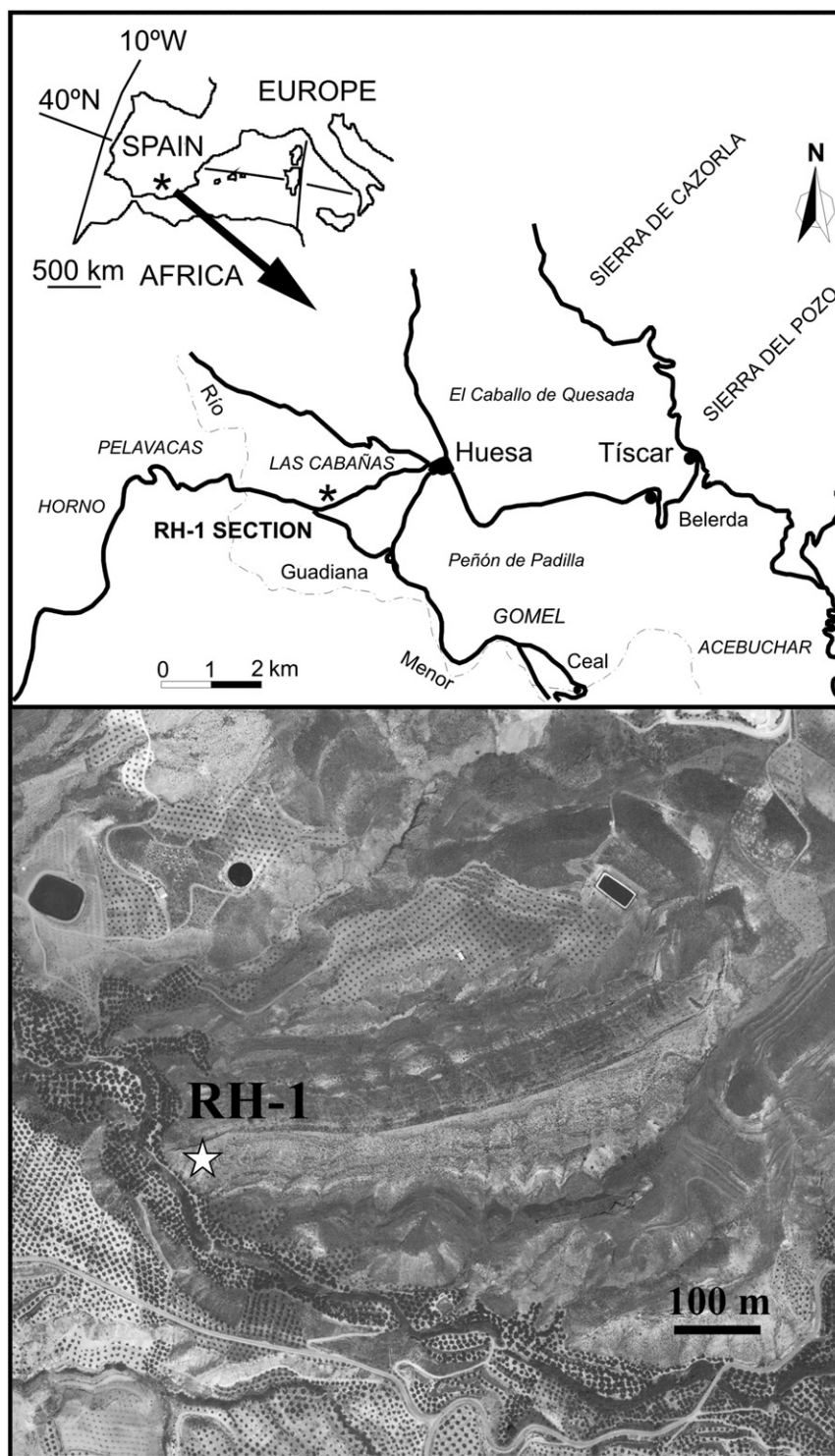


Fig. 1. Location of the Huesa section (HS-1, Betic Cordillera, southern Spain), indicated by a star.

environments, have been identified (Rodríguez-Tovar et al., 2007; Rodríguez-Tovar and Pérez-Valera, 2008). Facies E is a 3-m-thick package of alternating gray micritic limestone, marly limestone, and white marls. The marly limestones are mainly thin-bedded, with numerous gutter casts and frequent bioclastic shelly beds, and contain an abundant trace-fossil assemblage, mainly composed of *Rhizocorallium* and *Diplocraterion* (Fig. 2; Rodríguez-Tovar et al., 2007; Rodríguez-Tovar and Pérez-Valera, 2008). These sediments accumulated in an inner carbonate ramp influenced by storm currents (Pérez-Valera, 2005), above storm wave-base. Carbonate content varies widely within the facies, as

well as the frequency, size and shape of gutter casts. During deposition of facies E, the seafloor was characterized by planar to gently undulating surfaces reflecting minor changes in topographic relief, and creating small depressions.

3. *Diplocraterion parallelum* analysis

The burrows *Diplocraterion parallelum* are well-preserved. They do not exhibit cross-cutting, and there is no evidence for erosional surfaces that might indicate that the specimens were emplaced downwards

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