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How to explain a decapod crustacean diversity hotspot in a mid-Cretaceous coral reef

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ABSTRACT

The mid-Cretaceous (late Albian) decapod crustacean fauna from the Koskobilo quarry in Spain is the most diverse decapod fauna known thus far from the Cretaceous. This may be related to the coral reef environment in which these decapods were found within the Aldoirar patch reef. This diversity hotspot was further investigated by a detailed paleoecological study focusing on variation in lithology throughout the quarry using carbonate rock hand samples, thin sections, and acetate peels; and by studying decapod-rich sites within the quarry. The northern and stratigraphically oldest part of the Koskobilo quarry contained mostly wackestones and biomicrites, the middle to southern part contained floatstones and biosparites or biomicrites with many sponge remains, whereas the southernmost and stratigraphically youngest part consisted of coral-rich boundstones and biolithites. Fossils were more abundant and generally larger in the southern part of the quarry. Decapod-rich sites were restricted to the southern part of the quarry, possibly in part because of an increased possibility for shelter and food in a coral-rich area in the southernmost part of the quarry. Water depth was estimated to be between 20 and 80 m for at least the southern part, with energy levels apparently increasing from the northern to the southern part of the quarry. Systematic collecting was performed at four decapod-rich sites in the quarry to investigate differences in decapod diversity, composition, and size (width). The decapod fauna from the site within the coral-rich boundstones and biolithites appears to be the most diverse based on several diversity measures, has a statistically different faunal composition, contains species that were not found in other parts of the quarry, and consists of smaller decapods compared to other sites. More specimens of species with a smaller maximum width were found here as well as fewer specimens with a large maximum width. Smaller, presumed juvenile specimens of the crab *Goniodromites laevis* were also excavated here. This shows that decapod size can vary within a reef. Paguroids (hermit crabs) were mostly restricted to this coral-rich site. Some of the many decapods at this site may have been obligatory associates with the mostly branching corals. One site within the floatstone and biosparite zone contained hardly any decapods, which may be related to the abundance of hard-to-eat corallinacean red algae. A site in the Olazagutía quarry in the same patch reef consisting of massive colonial corals did not yield any decapods, presumably because of the inaccessible nature of the coral framestone leaving few places as shelter for decapods. The results suggest that different decapod sub- and microenvironments existed within this patch reef, thereby explaining at least in part the high diversity of decapods known from the Koskobilo quarry. This is one of the first times that a detailed paleoecological study has been performed for decapods in a fossilized coral reef. These results concur with modern reefs in that decapod communities also differ among subenvironments. The methodologies introduced herein for studying fossil decapods in reef environments can be used as well to study the paleoecology of decapods as well as other invertebrates from other periods in Earth's history.

1. Introduction

Both extant and fossil decapods have exhibited a preference for reef habitats, showing them to be important coral-reef inhabitants. Examples of decapod-rich faunas associated with corals from the fossil record are known from the Miocene of Malta (Gatt and De Angeli, 2010), the Eocene of Hungary (Müller and Collins, 1991), the Paleocene (Danian) of Denmark (Jakobsen and Collins, 1997), the Late Cretaceous (Maastrichtian) of the Netherlands (Collins et al., 1995; Leloux, 1999), and the Late Jurassic (Tithonian) of the Czech Republic and Austria (e.g., Robins, 2008; Schweitzer and Feldmann, 2008, 2009a,b; Robins et al., 2013). Diverse decapod faunas are also known from the Late Jurassic (Oxfordian) sponge-microbial reefs of Poland (Collins and Wierzbowski, 1985; Müller et al., 2000; Krobicki and Zatoń, 2008) and the Late Jurassic of Germany (Wehner, 1988; Müller et al., 2000), although the number of species is lower compared to faunas found in coral reefs. This link between a high number of decapod taxa and reefs is further supported by Fraaije (2003a) and Müller (2004), who qualitatively suggested that reef-associated fossil decapods show a

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higher diversity than those living in other habitats. Coral reefs also provide preferred habitats for many extant decapods. Abele (1974, 1976) found that decapods were especially diverse in a subtidal *Pocillopora* coral community and in a rocky intertidal habitat in Panama, part of which consisted of *Porites* corals. In addition, he noted that the number of decapod species increased with increasing complexity of the habitat; that is, with more substrates in a certain habitat (Abele, 1974). Abele (1979) also suggested that 80–96% of all macrofaunal specimens and 76–89% of all species associated with live *Pocillopora* coral heads off the Pacific coast of Panama were decapods. Austin et al. (1980) found similar results for coral heads of *Pocillopora damicornis* in the Great Barrier Reef as Crustacea, predominantly Decapoda, comprised 72% of the species and 86% of the individuals on the coral heads.

Studies on extant decapods have provided a variety of ecological knowledge concerning decapods in coral reef habitats. Decapods use reefs for numerous purposes including as a place of shelter, as a feeding site, and as a source of nutrition (Abele, 1974). A coral reef contains different sub- and microenvironments, such as in between coral branches, on the corals, distal to the corals themselves in unprotected parts of the reef, etc. Grajal and Laughlin (1984) noted that shelters may not only be used as resting places, but the commensal brachyuran *Domecia acanthophora* Desbonne and Schramm, 1867 also uses them for reproduction and brood care. Many of the decapod species associated with the Great Barrier Reef in Australia appear to be obligatory associates with the branching coral *Acropora* by virtue of the fact that they live on the coral (Patton, 1994), whereas facultative associates (ones that can live in other habitats as well) were usually absent from the coral heads. The same author also noted that the spaces between the branches contained decapods.

Decapod communities are known to differ within extant reef environments (e.g., Thomassin, 1974; Martínez Iglesias and García Raso, 1999). Different subenvironments may favor slightly different decapod communities within the reefs, thereby in part explaining the high decapod biodiversity of reefs in general. For example, Martínez Iglesias and García Raso (1999) found that decapod species richness was higher in the lagoon and on the slope than on the reef flat based on three Cuban reefs. This low diversity on the reef flat was explained by higher hydrodynamics and a lower diversity of substrates related to fewer coral species. The decapod communities in these subenvironments consisted of a combination of exclusive species and shared species but differing in abundance per subenvironment. Interestingly, Edwards and Emberton (1980) found that the number of decapod specimens and species on the coral *Stylophora pistillata* was greater in reef flats than in the smaller, deeper water colonies, which was, in part, attributed to the higher openness of the coral branches in deeper waters in the Red Sea. Here, they argued, fishes would be better able to enter the coral complex and prey upon the decapods. These observations are consistent with the ecological "species-sorting hypothesis", which postulates that diversity is related to environmental gradients and thus the density of niches within a given region (e.g., Whittaker, 1962, 1972; Leibold et al., 2004). Similar results have been found for arthropods in tropical rainforest environments relative to adjacent non-rainforest sites (Basset et al., 2012), the only other type of environment known to rival the diversity found in reef environments.

The goal of this paper is to investigate the high decapod crustacean diversity found in the mid-Cretaceous (upper Albian) strata exposed in the Koskobilo quarry (N 42.8823°, W 2.1990°) near Alsasua in northern Spain. The number of decapod species found in the Koskobilo quarry is currently unsurpassed for a single locality in the Cretaceous with 36 species (Klompmaker, 2013). This paper will test the hypothesis that this high diversity in the Koskobilo quarry can at least in part be explained by the presence of multiple sub- and microenvironments that favored different decapod faunas. The systematics and taxonomy of the decapods from this quarry have been investigated in detail recently (Fraaije et al., 2009, 2012a; Klompmaker et al., 2011a,b,c, 2012a,b; Artal et al., 2012; Klompmaker, 2013) and provide the basis for this study.

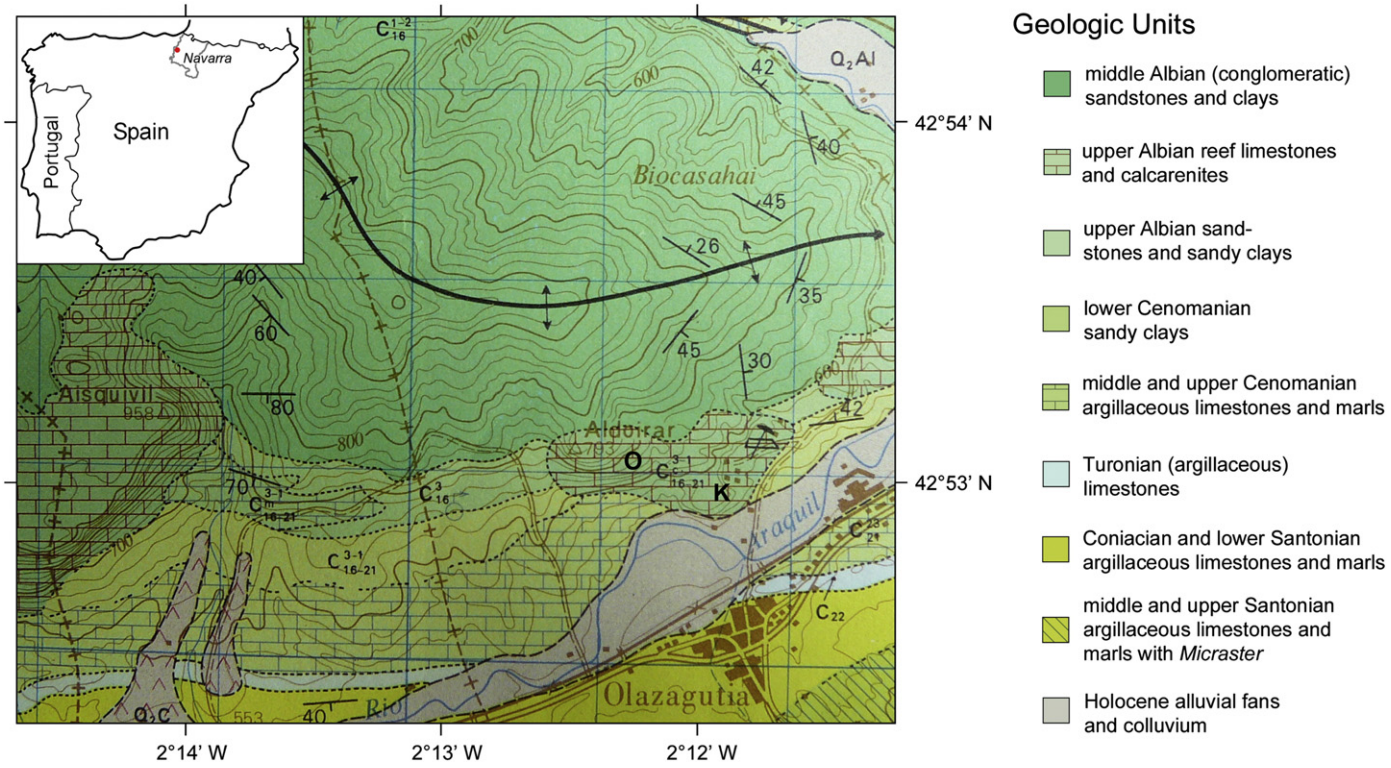

Fig. 1. A geological map of the area north of Olazagutía with an inset showing the location of the study area (red dot) in the Navarra region, northern Spain. The Aldoirar patch reef contains two quarries: the abandoned Koskobilo quarry (K = southern part of this quarry) and the active Olazagutía quarry (O). An anticlinal structure can be found north of the patch reef. The hammer symbol NE of the Koskobilo quarry is not part of this quarry. The distance between 53′ and 54′ is 1853 m.
From: Mapa Geologico de España, E. 1:50,000, Salvatierra, Segunda serie — Primera edición, 1978.