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Evolution of complexity and natural selection: Suture complexity and its relation to taxonomic longevity in Cretaceous ammonoids

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ABSTRACT

A sample of 682 suture lines belonging to 204 Cretaceous planispiral ammonoid genera shows a positive, significant relationship between suture complexity (measured as fractal dimension [Df]) and generic longevity. However, during the Cretaceous there was no increase in the mean fractal dimension. This paradox is due to the evolutionary dynamic during this time span comprising mainly the appearance, disappearance (or anagenetic transformation) of those genera with simpler sutures and, consequently, the maximal values of fractal dimension were more stable in time. These results contrast with (i) the hypothesis that simple morphologies are linked to low ecological specialization and (ii) the idea that the role of natural selection can be unambiguously deduced from stratigraphic ranges.

1. Introduction

There is wide consensus about the general evolutionary trend towards an increase in morphological complexity (Bonner, 1988; McShea, 1996; Carroll, 2001). This becomes obvious by comparing, for example, the earliest Archaean microfossils with the current biota – a result of a myriad of evolutionary transitions.

From a neontological point of view, the number of genes related to the number of biochemical events, cell-type number, internal complexity (as the number of germ layers) or biological diversity are some of the potential ways of quantifying biological complexity (Carroll, 2001). However, the fossil record – the primary data source to illustrate the evolution of morphological complexity – does not provide many examples that allow detailed studies over long periods of time. Among the exceptions is the evolution of the septal complexity in ammonoids, manifested as suture complexity. The suture complexity has been quantified using different metrics, such as the ISC index (Ward, 1980), the SCI index (Saunders and Work, 1996, 1997; Saunders et al., 1999) or the fractal dimension (e.g., Boyajian and Lutz, 1992; Lutz and Boyajian, 1995; Pérez-Claros et al., 2002, 2007; Pérez-Claros, 2005, [Fig. 1]), which provide comparable results. The evolution of suture complexity has been analysed by Boyajian and Lutz (1992) during the long history of this group from the Early Devonian to the end of the Cretaceous. Their results illustrate adequately how many other morphological traits have evolved: the group starts from a single species of simple morphology, which becomes more complicate as the group diversifies and finally, the mean and the maximum degree of complexity level off. On the other hand, the behaviour of the minimum complexity is important in order to study the nature of this trend, as it stays close to the initial value in passive systems, whereas it increases over time in driven trends (McShea, 1994). In this case, the results are equivocal, as minimum complexity increased slightly until the end-Permian mass extinction but decreased somewhat until the extinction of the group at the end of the Cretaceous (McShea, 1994). There are additional tests to study the passive or driven nature of trends (i.e., resulting from diffusion in bounded spaces or consequence of pervasive biases in the direction of change) although each with its own caveats (McShea, 1994). The application of those tests to Palaeozoic ammonoids (Saunders et al., 1999) shows, in fact, a scenario compatible with a driven trend for this initial part of the evolutionary history of this group of cephalopods. The levelling off of complexity reached after the Permian/Triassic extinctions may suggest that optima were reached by the time of the final extinction of the ammonoids at the Cretaceous/Paleogene boundary (Saunders et al., 1999).

On the other hand, both driven and passive systems can result from external factors (selection processes) or internal factors (as developmental constraints) or both (McShea, 1994). Boyajian and

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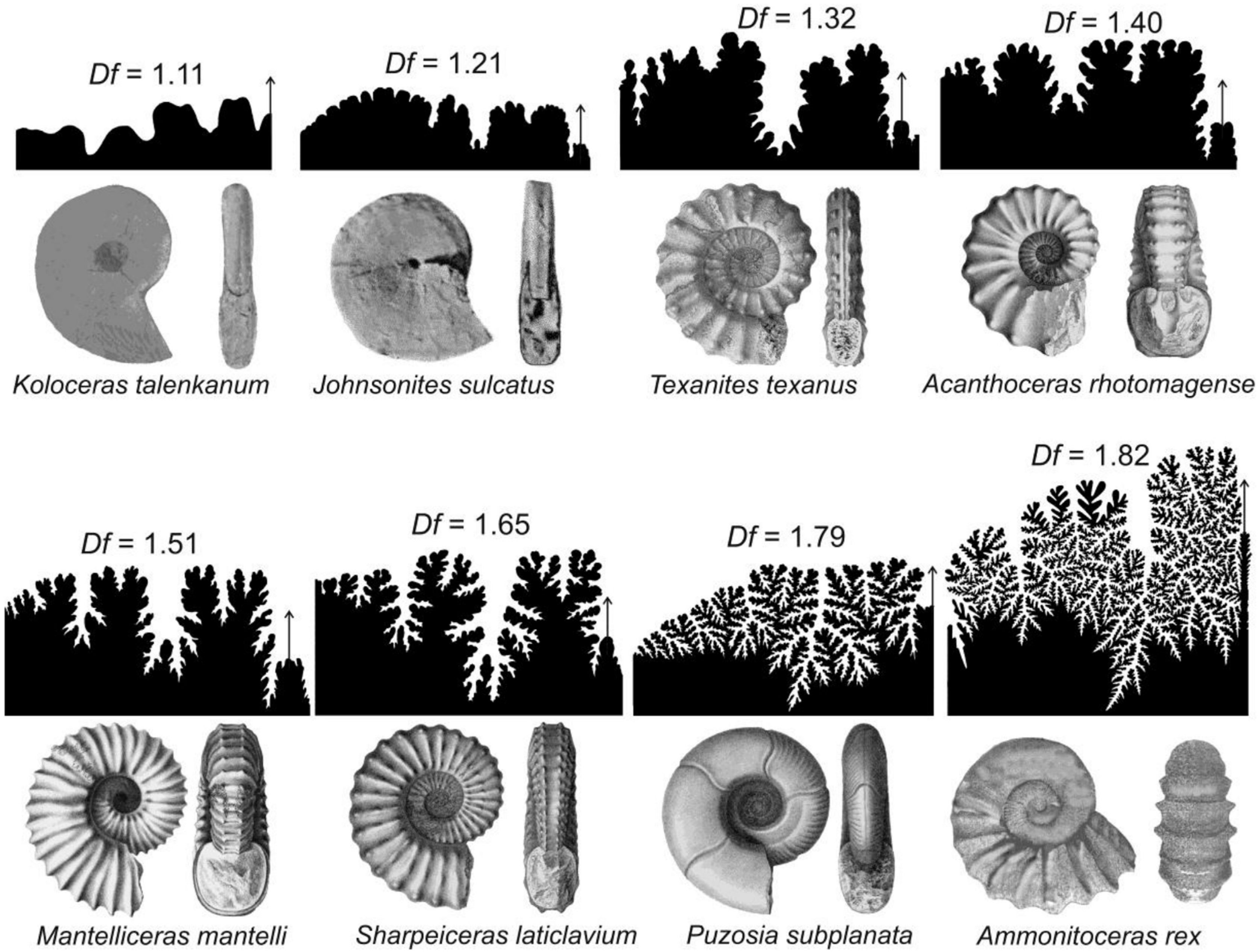

Fig. 1. Examples of Cretaceous ammonoid sutures showing increasing degree of complexity. Note that as fractal dimension of sutures approaches 2, septum peripheries begin to fill a volume.