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Reinitialization of evolutionary clocks during sublethal environmental stress in some invertebrates

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Abstract

This paper describes the influence of high environmental stress on evolutionary trends in some selected Mesozoic ammonite lineages and some protists. During extinction periods, many ammonoids are affected by drastic simplifications of their shell geometry, ornamentation and suture line. We observe that relatively tightly coiled ammonites can give rise to highly evolute forms or uncoiled heteromorphs with simple ornamentation and almost ceratitic suture line—a phenomenon called “proteromorphosis”. Such simplifications often correspond to a reappearance of ancestral geometries (primitive ornamentation, evolute coiling or uncoiling) which suggest that the evolutionary clock of these organisms can be reinitialized by extreme, sublethal, environmental stress such as giant volcanism (including its consequences on diverse pollutions and on climatic changes) and major regressive events.

Keywords: evolution; proteromorphosis; atavisms; environmental stress; ammonoids; silicoflagellates; planktonic organisms

1. Introduction

An abundant literature based on compilations of published paleontological data deals with the variations of biodiversity through time and provides useful information about extinction and recovery periods. That kind of investigations started with the well-known works of Sepkoski [1] and Benton [2] and has been recently reviewed by Courtillot and Gaudemer [3].

The diverse possible origins of extinctions have also been investigated by plenty of authors and recent collections of papers review the classical causes like extraterrestrial impacts, marine regressions, climatic changes, anoxic events, etc. [4,5]. At the moment, it seems that Courtillot’s [6] theory involving giant volcanism has the most general explanatory power, with enormous potential consequences on the chemistry of sea waters and also on global climatic changes. Fig. 1 shows that there is an almost perfect correlation between the major extinctions and periods of volcanism [6].

On the other hand, there are very few papers which analyse the modes of evolution during major extinction events: What are the characteristics of the organisms surviving major crises: are they stable or modified? What kind of transformations have affected them? The goal of the present paper is to analyze in detail how some invertebrates react during major stress episodes. To do this, we will start our discussion with a description of the evolution of some ammonoids during major crisis periods. Fig. 2 illustrates a generalized

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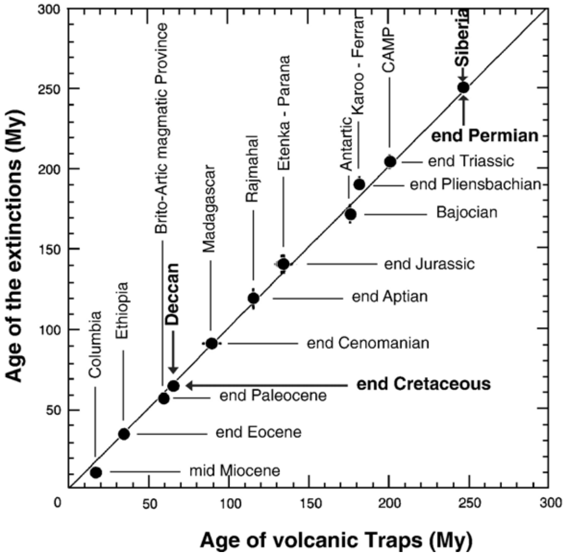

Fig. 1. Age of the major extinctions vs. age of volcanic traps (redrawn from [6]).

phylogenetic tree of this group, and shows the major extinction events which occurred during its history.

Generally speaking, the basic stratigraphic observations on which our interpretations of the "gradual" evolutionary lineages developing during environmentally stable periods are well established and widely accepted. Our main new contribution concerns the phylogenetic relationships between successive lineages during periods of severe ecological stress. These questions are poorly investigated in current literature because the fossil record, during such periods, is often weak. The main reasons for this are (1) the collapse of general productivity during these phases and (2) major crises are often associated with more or less pronounced marine regressions and stratigraphic gaps.

We will compare the theoretical and schematic evolutionary model which can be built for ammonites with the morphogenetical behaviour of some living micro-organisms when they are submitted to a variety of high environmental stresses.

2. Evolutionary trends

In itself, the morphology of an isolated organism tells us very little about the evolution of that organism. By contrast, the morphological variations occurring in a given phyletic lineage are of outstanding importance. Such variations have the potential to reveal evolutionary rules and, of course, can be observed only by paleontologists working on well-documented stratigraphic sequences. We generally use the term "evolutionary trend" to describe the oriented morphological transformations occurring in stratigraphic sequences of one particular species or in phyletic series of closely related species. When the paleontological data are accurate, the trends are obvious and can be considered as observed facts: they do not need to be demonstrated using methods like cladistics.

In some cases, trends seem to be more or less gradual and are used as a biochronological clock for stratigraphic correlations [7–9]. However, in most cases, they appear as discrete sequences of closely related species belonging to a single lineage showing an oriented morphological variation which includes all transitional forms.

The phyletic increase in body size is the most frequently quoted evolutionary trend. It is known as Cope's Rule, named after the American vertebrate paleontologist who first observed it in the 19th century [10,11]. The most famous case, illustrated in many paleontological textbooks, is the evolution of horses.

It should be noticed that size increase is by no mean a true evolutionary "rule" because many lineages do not increase in size during their evolution and numerous cases of size decrease, occurring during sporadic ecological perturbations, are well known in the fossil record. The case of the planktonic foraminifera size decrease during the few hundred thousand years preceding the KT boundary [12], generated by the Deccan volcanism and its catastrophic consequences, is particularly instructive. Generally speaking, such size fluctuations and trends reversals are mostly dependent on environmental variations and increasing size mainly affects the beginning of phyletic lineages [13]. A common belief is that most new lineages begin with forms which are smaller than their direct ancestor. The case of

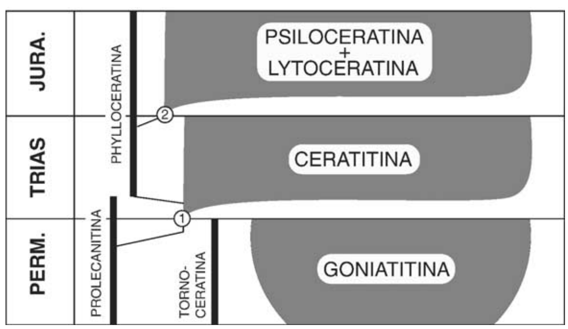

Fig. 2. Schematic phylogeny of ammonoids from the Permian to the Jurassic: (1) position of the genus *Ophiceras* at the origin of all *Certatitina* and (2) position of *Psiloceras* at the origin of all Jurassic ammonites (see Fig. 4 below).