Earth-Science Reviews 140 (2015) 166–181

Contents lists available at ScienceDirect

Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev

Evidence and causes of the main extinction events in the Paleogene based on extinction and survival patterns of foraminifera

Eustoquio Molina *

Departamento de Ciencias de la Tierra and IUCA, Universidad de Zaragoza, Pedro Cerbuna, 12, E-50009 Zaragoza, Spain

ARTICLE INFO

Article history:
Received 17 July 2014
Accepted 14 November 2014
Available online 21 November 2014

Keywords:
Extinction
Survival strategy
Planktic foraminifera
Benthic foraminifera
Paleogene

ABSTRACT

We review the four main extinction events in the Paleogene, from the Cretaceous/Paleogene boundary to the Eocene/Oligocene boundary, integrating the results obtained from a study of foraminiferal assemblages with other paleontological and geological data. Different survival strategies followed by the species are described and the duration of the phases of extinction, survival, and recovery is estimated. The models and patterns of extinction of the foraminifera are highlighted. We present a range of evidence and paleo-environmental factors and analyze the possible causes of extinction. A new terminology for mass extinction events is proposed: sudden mass extinction would have happened virtually instantaneously and the process would have taken a few years or decades (Cretaceous/Paleogene boundary). Rapid mass extinction is defined as that which occurred in relatively short events, around 100 kyr (Paleocene/Eocene and Eocene/Oligocene boundaries). Slow mass extinctions are suggested to have lasted around 1 Myr (Bartonian/Priabonian transition) and may even have lasted for several million years.

Contents

1. Introduction

The first general insights into the extinction events of organisms were those of some naturalists in the 18th and early 19th centuries, such as Georges Louis Leclerc (Buffon) and Georges Cuvier, who drew attention to the extinction of species in the fossil record, which gave rise to the catastrophist paradigm (Rudwick, 2008). In the 19th century, the French naturalist Alcide d'Orbigny, founder of the field of Micropaleontology, proposed the existence of 27 total extinctions followed by as many successive periods of creation (Moreau and Dory, 2005). The catastrophist paradigm was soon replaced by the uniformitarian paradigm, which also accepted the concept of extinction. Darwin (1859) suggested the successive gradual extinction of species, one after another, and claimed that natural selection could adequately explain it. He attributed massive extinction events to imperfections in the fossil record. From the 19th century until relatively recently, there have been several authors who dealt with the subject such as the German Schindewolf (1963), but the question of extinction events had not aroused great interest until Alvarez et al. (1980) proposed the impact theory. This theory has revolutionized the field of Earth Sciences, contributing to the replacement of the gradual evolutionary paradigm by the neo-catastrophist evolutionary paradigm. In the past three decades, a large amount of data has been gathered on the various extinction events and theoretical concepts have been developed for

* Tel.: +34 976 761077; fax: +34 976 761106.
E-mail address: emolina@unizar.es.

http://dx.doi.org/10.1016/j.earscirev.2014.11.008

the phenomenon of extinction (Berggren and Van Couvering, 1984; Chaloner and Hallam, 1989; Donovan, 1989; Kauffman and Walliser, 1990; Raup, 1991; Glen, 1994; Molina, 1994; Hart, 1996; Hallam and Wignall, 1997; Palmer, 2003; Molina, 2004; Taylor, 2004; Twitchett, 2006, among others).

In addition to the background extinction process, which makes species disappear slowly and continually due mainly to biological causes (e.g. competition, endemism), there were periods of time in which the rate of extinction accelerated, giving rise to mass extinction events. There are basically two models: gradual mass extinction and catastrophic mass extinction, the latter of which should be more correctly termed 'sudden' as opposed to 'gradual' (Molina, 1995, 2006, 2007). Gradual mass extinctions can be subdivided according to their duration. Mass extinction events are mainly triggered by geological or extraterrestrial causes (Alvarez et al., 1980; Kaiho, 1994; Thomas, 2007; Schulte et al., 2010; McGowran, 2012, among others). Biological causes, such as the predominance of a single species, do not appear to have been the origin of mass extinctions, during the greater part of the Phanerozoic. However, recent data suggest that an event of this type is currently on-going: the most obvious cause of the mass extinction event is the extraordinary proliferation of the human species and its industrial activities (Leakey and Lewin, 1995).

Paleontologists have demonstrated that mass extinctions are selective and have affected some species more than others. During a mass extinction event, three phases or intervals can be identified: extinction, survival, and recovery (Kauffman and Erwin, 1995; Kauffman and Harries, 1996). In the course of these phases the different taxa react in a variety of ways, becoming extinct at the moment of the event (extinct taxa) or shortly thereafter (delayed extinction taxa), taking advantage opportunistically of the altered conditions (disaster taxa), fleeing from the altered conditions by migrating to refuges from which they return when conditions return to normal (Lazarus taxa), generating new more or less ephemeral forms that represent the beginning of new lineages (progenitor taxa), or resisting the altered environmental conditions (survivor taxa). Apart from the background extinctions, that result from normal competition and natural selection, it is generally accepted that throughout the Phanerozoic there have been five major mass extinction events, which occurred at the end of the Ordovician, the Frasnian (Late Devonian), the Permian, the Triassic, and the Cretaceous (Hallam and Wignall, 1997). Furthermore, there were many other significant mass extinction events, although of smaller amplitude than the five major extinctions, and several of them were in the Paleogene.

After the mass extinction at the Cretaceous/Paleogene boundary, organisms started new evolutionary trends as a greenhouse world evolved into an icehouse world, including rapid global warming and cooling events during the Paleogene. Foraminiferal extinctions are mainly related to meteorite impacts, hyperthermal events, glaciation events and other geologic phenomena. The chronology of the Paleogene Period has recently been updated (Wade et al., 2011; Vandenberghe et al., 2012), allowing a more accurate evaluation of the patterns and duration of the Paleogene extinction events. The aim of this review paper is to analyze the extinction events of the Cretaceous/Paleogene, Paleocene/Eocene, Middle–Late Eocene and Eocene/Oligocene, evaluating the magnitude of each event, its causes, extinction patterns, and survival strategies of planktic and smaller benthic foraminifera. In addition, we propose a new terminology for mass extinction events and we estimate the duration of the principal extinction events of the Paleogene.

2. Materials and methods

Not all groups of fossilized organisms allow us to ascertain with the same degree of precision their extinction patterns and survival strategies, since they require highly detailed biostratigraphic studies which for many groups are just not possible. A good number of groups were highly restricted to particular environments or were very rarely fossilized, making it difficult to establish their models and causes of extinction. The best example of this is the dinosaur fossil record, which is often so patchy that it will probably take a long time to determine definitively whether they became extinct in a gradual or sudden manner, as their study is strongly influenced by what is known as the "Signor–Lipps effect" (Signor and Lipps, 1982). The foraminifera, on the other hand, due to their small sizes, wide distribution and abundance in ocean environments, are enormously useful and allow us to study their ecological patterns and strategies in detail, based on which we can then deduce the causes of extinction, especially in the Paleogene (Molina, 1995, 2006). In order to facilitate comparison among different sections and make world-wide correlations, foraminiferal taxonomy has been revised and updated according to Olsson et al. (1999) and Pearson et al. (2006). Furthermore, standard chrono-biostratigraphy has been updated (Fig. 1) and range charts (Figs. 2 to 6) have been simplified to better show the patterns of extinction.

The outcrop sections and boreholes (DSDP and ODP sites) studied, on which this paper is based, cover a wide range of locations around the world, mainly in intermediate and low latitudes. In Spain, they include the Betics (Agost, Alamedilla, Aspe, Caravaca, El Navazuelo, Fuente Caldera, Molino de Cobo, and Torre Cardela) and the Pyrenees (Arguis, Artieda, Campo, Osinaga, and Zumaya). In Italy: Gubbio, Massignano and Possagno. In France: Bidart and the Bay of Loye. In Tunisia: El Kef, Aïn Settara and Elles. In Egypt: Dababiya. In Mexico: Coxquihui, El Mimbral, La Lajilla, and La Ceiba. In Cuba: Loma Capiro, Peñalver and Santa Isabel. In the Atlantic Ocean: DSDP sites 94, 116, 363, 366, 401, 402, and 612. In the Indian Ocean: DSDP sites 214, 216, 219, 223, 242, and 253. In the Pacific Ocean: DSDP sites 277, 292, and 462 (see Molina et al., 1993, 1998, 2009).

Detailed samplings were conducted on a metric scale, but where extinction or meteorite impact events were located, sampling density was from 2 to 20 cm. At the levels closest to the event, continuous samples were taken with a resolution of 2 cm. The samples were disaggregated with water and washed, and the fractions greater than 150 μm, 100 μm or 63 μm were studied according to the size of the foraminifera in each section and event. In many sections, quantitative studies were conducted, separating a representative fraction of more than 300 specimens in each sample, using an Otto microsplitter and also checking the rest of the sample for less frequent species.

3. The Cretaceous/Paleogene boundary event

The Cretaceous/Paleogene boundary event (K/Pg) is one of the most widely studied as it is the most recent of the 5 major mass extinctions, it has been dated to 66.04 Ma (Vandenberghe et al., 2012). The stratotype for the K/Pg boundary was defined at the base of the clay that contains the iridium anomaly in the El Kef section in Tunisia (Molina et al., 2006a, 2009). This event, which constitutes one of the most significant biological crises in geological history, is used to define the boundary between the Mesozoic and Cenozoic Eras.

Alvarez et al. (1980) proposed that the collision of a large meteorite measuring some 10 km in diameter may have produced a level abnormally rich in iridium that coincided with the sudden catastrophic mass extinction. This evidence was recorded in a thin clay interval at the K/Pg boundary in Gubbio (Italy), Stevns Klint (Denmark) and Woodside Creek (New Zealand), as well as in Caravaca (Spain) (Smit and Hertogen, 1980). In addition, other evidence at the K/Pg boundary has been found, such as microtektites, Ni-rich spinels, shocked quartz, which, combined with the discovery of a large impact crater structure in the Yucatan peninsula, the sedimentological evidence of tsunamis and gigantic gravitational flows as well as the dating by $^{40}Ar/^{39}Ar$ of the impact silica glass have enabled to confirm the validity of the impact theory (Schulte et al., 2010).

However, since the classic sections of Gubbio and Caravaca are composed of rocks that were formed in deep ocean settings, they do not