Past, present, and future mass extinctions

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ABSTRACT

Enigmatic catastrophic events, involving mass extinction of life forms, have been recorded several times in the Earth history. In many cases, the causes and mechanisms of these major and minor mass extinctions can be traced via the fossil record. A synthesis of the available information is herein made on the major catastrophic events through Earth history to understand the processes in the past and present with speculation into the future. The selective nature of major mass extinctions from the fossil record indicates the vanishing of specific taxa and the survival of others. The sudden extinction of organisms is almost accompanied by a gradual disappearance of other forms, thus excluding any single cause for the killing mechanism. Consequently, the multiple causes' scenario is the plausible mechanism responsible for the vanishing of biota through the history of the fossil record. On the other hand, the recovery of biota after mass extinctions is also an intriguing phenomenon, in which some groups had rapid recovery whereas others took a long time for a revival. Based on multiple pieces of evidence from Africa, the end Permian extinction and the extinction of some Quaternary megafauna may be related to severe drought. In addition, the current mass extinction is progressively underway; arising from multiple causes and mainly related to anthropogenic activities, widespread diseases, as well as the possibility of extraterrestrial impacts. Reevaluation of the magnitude of the extinction event is urgently needed to judge if these extinctions represent natural episodic fluctuation of the biodiversity curve or unexpected catastrophe. Analyses of invertebrate occurrence data revealed that taxa originated during stressful crises intervals have a wider geographic range size and lower extinction rates. Moreover, species durations, geographic range, and diversity are influencing each other. In addition, the ecological traits of a species may control their extinction pattern and recovery speed-limit. Furthermore, the wide geographical distribution provides potentially to survive mass extinctions. Therefore, narrower geographic-range taxa are facing higher extinction risk.

1. Introduction

Mass extinctions are distinct phenomena as deduced from the fossil record that commonly indicates events excluded a large number of species in a short time span. The classic models such as that of Sepkoski (1982) suggested that mass extinctions take place when there is a sudden termination of numerous or the majority of species at a single horizon, or within a limited stratigraphic interval. However, Bambach et al. (2004) attributed two of the major mass extinctions (the late Frasnian and the end Triassic) to lowered rates of origination at the generic level rather than extinction. On the other hand, modern paleobiology places alert on sampling bias, where more samples mean finding more species (see Alroy et al., 2001; Peters, 2005; Alroy, 2008; Alroy, 2010). Holland and Patzkowsky (2015) demonstrated that taxon last appearance can be predicted at specific stratigraphic positions coincide. The difference in species duration among different taxonomic groups is determined by many biological and ecological factors

facilitating dispersion such as mode of life and mobility level (Abdelhady and Fürsich, 2015; Abdelhady et al., 2019a, b).

Although the Cretaceous-Paleogene (K-Pg) extinction is the most well-known event that excluded the dinosaur community, a series of other mass extinction events, include stronger events, were also recorded. The oldest known mass extinction, according to McMenamin (1992), occurred during the middle part of the Vendian, at about 650 Ma. Several authors attempted to formulate a common criterion to interpret the different mass extinctions. Thus, Twitchett (2006) concluded that understanding extinction and recovery processes in past events, especially those associated with climate disturbance (e.g. global warming) is essential to overcome current biodiversity threats. Models explain the recovery process after mass extinction has attributed the lag time between extinction and recovery phases to the increased biotic interactions during the recovery process (Solé et al., 2010). The body mass is the most important factor determining the upper limit of a taxon, where small taxa dying first. However, the trophic level is also
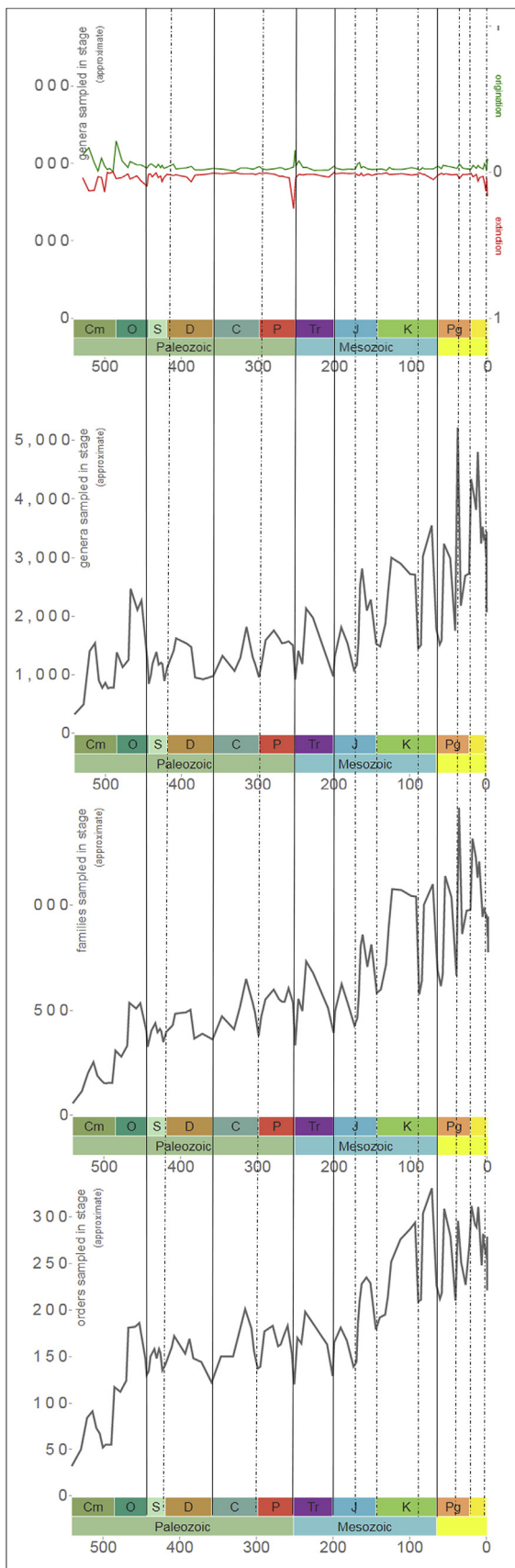
Fig. 1. Diversity, extinction, and origination curves of Phanerozoic taxa showing the five big mass extinctions. Curves were generated automatically in the User Interface of the Paleobiology Database in April 2019.

considered to exert significant control over the extinction. The survival/recovery processes during the recovery phase are responsible for the mass extinctions-induced evolutionary changes (Erwin, 1998). In recent work, Korn et al. (2013) proposed a method to quantify and classify the changes in morphospace across the extinction boundaries.

Despite the fact that there were repeated minor extinctions throughout the Earth's history, five well-known major mass extinction events have been identified from the fossil record (the big five; according to Raup and Sepkoski, 1982). However, other minor extinction events such as the Cambrian extinction and the Carboniferous events can also be added to the list. Thus, in this study, evaluation is not only focused on the well-established big five events, but also on the catastrophe to life during Precambrian (Ediacaran), Silurian, Carboniferous, Middle, Permian, Middle Triassic, Early Jurassic, Cretaceous, Paleogene, and Quaternary, as well as the current extinctions (see Fig. 1). These minor extinctions were investigated by many authors in the past decade (see Tennant et al., 2017; Wan et al., 2003; Abdelhady, 2008; Monnet, 2009; Caruthers et al., 2013). Raup and Sepkoski (1986) have introduced a list of ten severe biotic crises in earth history. Moreover, Sepkoski (1986) has highlighted twenty-nine potential mass extinction based on newly-compiled fossil marine genera. However, Twitchett (2006) indicated that a continuous magnitude of diversity loss between the smallest and biggest biotic crisis makes it hard to subdivide into two separate groups.

Mass extinctions of life in earth history involve complex catastrophic events, where the causes and mechanisms of which remained equivocal for a long time. Despite the existing debate between catastrophists, who believe in extraterrestrial impacts, and gradualists who rely on gradual kill mechanisms, the sudden disappearance of some organisms and the survival of others indicate a multiple causes' scenario. Moreover, our investigations indicate that the selective extinction is followed by a selective recovery of distinct taxa in most of the studied events (Table 2), reflecting an enigmatic strategy of some of the organisms to survive extinction. It appears that dwarfism (minimized body size) was one of the successful adaptive strategies to survive (see Elewa and Dakrory, 2008a). Small body size has two advantages over the big one; the ability to hide easily from predators, and the little need for nutrition. Other important surviving strategies include the body-chemical composition and the dormancy of a taxon (e.g. Robertson et al., 2013).

The mass extinction has been reviewed by several workers and specific events have also been evaluated in several recent studies such as Whiteside at al. (2010), Erwin et al. (2011), and Chen and Benton (2012). Elewa (2008, a, b, c, d, e, f, g, h) introduced summaries for the major mass extinctions in the fossil record and their causes. Herein, we reviewed published works dealing with different causes and the impact of major extinction events in the past and highlighting current/future extinction events. Although the literature on the subject is much diversified, we limited our review to and focused primarily on the causes and impact of these catastrophic events. Our review builds on a few previous works (e.g., Bambach et al., 2004; Harnik et al., 2012; Hull and Darroch, 2013).

2. Major mass extinctions

2.1. The end Ordovician

The end Ordovician (i.e. the Hirnantian) mass extinction is the oldest of the big five events and encompassing two separate phases. Both considered related in different ways to a strong but transitory glaciation at the South Pole (Hammarlund et al., 2012; Harper et al., 2014). Hammarlund et al. (2012) assigned the event to the anoxic water dominated the continental shelves, causing the extinction in shallower ecosystem biota, for the second pulse. According to Harper et al. (2014), it may be related to cooling and dominated ice and sea-level regression followed by global anoxia associated with highstand

sea level in the Late Hirnantian. Harper et al. (2014) noted, based on recent evidence, most of these factors were synchronous in the end Ordovician mass extinction.

According to Rasmussen and Harper (2011) temperature was not the only controlling factor for the end Ordovician mass extinction, and the mechanism that controlled the duration and magnitude of the sudden decrease in species diversity was the arrangement of the paleoplates. Based on data compiled from Laurentia and other continents, Adrain et al. (2000) noted that Silurian trilobite alpha diversities in all major environments are comparable to those of the Late Cambrian and Ordovician. These authors thus inferred a rapid recovery of trilobite alpha diversity following the end Ordovician extinction, whereas the global clade-level diversity remained depressed in the Silurian characterized by lower levels of provinciality. In spite of the apparent crisis that affected this extinction, the reasons have not been fully evaluated (Elewa, 2008c). Gong et al. (2017) suggested intense volcanism in South China during Late Ordovician based on high Hg values and Hg/TOC ratio.

2.2. The end Devonian

A series of extinction pulses within this period caused major destruction to life and McGhee (1996) estimated the losses to be 13%–38% at the family level, 55%–60% losses at the genus level, and 70%–82% at the species level. There is a general consensus among paleontologists concerning the enormity of the Late Devonian extinction, but the duration, number of events, and causes remain disputed. Algeo et al. (1995) suggested that the Late Devonian mass extinction occurred in the Frasnian before the appearance of first seed plants during a period characterized by the vegetation spread in swamps not. McGhee (1996) listed numerous major extinction events during the Devonian but considered the Kellwasser Event as the Late Devonian mass extinction.

Kaiho et al. (2013) believe that the Late Devonian event took place in a stepwise manner and reached a maximum near the Frasnian–Famennian (F–F) boundary. However, Streel et al. (2000) outlined two intervals of extended biodiversity fatalities, succeeded by two periodic extinction events of much shorter intervals. These are the Late Frasnian crisis pursued by the Kellwasser event, and the end Famennian crisis tracked by the Hangeberg event. Kaiser et al. (2016) found that the Devonian–Carboniferous boundary was marked by transgressive and hypoxic/anoxic phase, which has been associated with a global carbonate crisis and disturbance in the global carbon cycle. They indicated that the extinction patterns were similar in widely separate basins of the western and eastern Prototethys.

2.3. The end Permian

The end Permian mass extinction is ranked the biggest among the big five; it is considered as the largest biotic catastrophe in earth history and hence termed by different authors as "the Great Dying". Yet, the effect of this crisis on land varied widely from no effect on the terrestrial plants to complete destruction of the terrestrial ecosystems (see Hermann et al., 2011 for references therein). Erwin (2006) noted that about nine in ten marine animal species were lost at the Permian–-Triassic (P–T) boundary and terrestrial ecosystems were correspondingly destroyed. However, Nowak et al. (2019) and based on global data of macro- and micro plant fossils found that the fossil record is strongly biased and thus, there is no robust evidence for mass extinction.

Isozaki (2009) correlated the major catastrophe to the change in geomagnetism termed as the 'Illawarra Reversal', reflecting a significant change in the geodynamo in the outer core of the Earth. According to this author, the Illawarra reversal during the latest Guadalupian resulted in a series of events such as mass extinction, ocean redox change, C and Sr isotopic excursions, sea-level drop, and plume-

related volcanism. In recent work, Kaiho and Koga (2013) assigned the effect of the end Permian crisis on biota to the carbonate content. Thus, organisms with high carbonate content such as corals were particularly affected during the extinction, whereas organisms containing less carbonate in their skeletal structures were less affected. Villier and Korn (2004) suggested that the end Permian mass extinction was random with a non-selective strategy, which indicates a rapid catastrophic event. Although some life forms rapidly recovered, the delay of recovery in marine invertebrates after the end Permian mass extinction remains a mystery (Brayard et al., 2009; Stanley, 2009; Hautmann et al., 2011). For example, Brayard et al. (2009) showed that Triassic ammonoids began to diversify more than in the Permian only two million years after the Permian-Triassic boundary. The latter was not correlated to the slow recovery of other macroinvertebrates such as gastropods and bivalves. A similar situation has been recorded by Romano et al. (2013) on the Lower Triassic pectiniform conodont. The recovery after environmental perturbation in the fossil record such as intervals following mass extinctions has received more attention in recent studies (Dineen et al., 2014). Chen et al. (2014) indicated that the end Permian mass extinction event not only caused the biggest crises in global biodiversity but also influenced the successive biotic evolution. The end Permian mass extinction is receiving much attention in the light of rapid warming and potential ocean acidification caused by greenhouse gas emanation (Payne and Clapham, 2012) since it is analogous to the current environmental issues faced by our planet.

2.4. The end Triassic

The Triassic-Jurassic transition witnessed the initiation of dinosaurs (roughly 200 Ma). It seems that this mass extinction opened the door to the dinosaur world, where non-dinosaurian archosaurs and large amphibians became extinct leaving dinosaurs dominating the terrestrial life. Ward (2006) regarded the Triassic as important to terrestrial vertebrate life as the Cambrian was to modern life in general. On the other hand, Elewa (2008a, d) considered the end Triassic as the smallest among the big five events. McGhee et al. (2004) evaluated the marine Triassic-Jurassic extinction as category "IIa"; while Lucas and Tanner (2008) demoted it to category "IIb", indicating that the disturbance was of temporary nature. Zhang et al. (2018) reported, based on U-isotope data from the lattermost Permian to the earliest Middle Triassic in Iran, a global extent of redox conditions. They argued the late recovery of the biota to multiple oscillations in oceanic anoxia following the latest Permian mass extinction.

2.5. The end Cretaceous

The well-studied Cretaceous-Paleogene (K-Pg) is one of the five major mass extinction events of Earth's history (about 65 Ma ago). Ruban (2018) proposed a classification model for the events on the geologic records and concluded that the K-Pg represents the only anomalous event on the Phanerozoic biodiversity curve, where other minor mass extinctions may represent episodic events, where the marine biodiversity has naturally fluctuated. The demise of non-avian dinosaurs marked this terrible crisis leaving big questions on its mechanism and causes. The other organisms, which perished at the end of the Cretaceous, include ammonites, several flowering plants as well as pterosaurs. Cowen (2005) asserted that half of all living taxa became extinct due to the severe disturbance that occurred during this major event. Several common features, as well as differences between the K-Pg extinction and the end Permian extinction, were listed by Vajda and McLoughlin (2007), based on high-resolution palynofloral signatures. Lyson et al. (2011) suggested that the non-avian dinosaur fossils gap does not exist and thus no prior extinction has occurred. In general, there is no clear explanation until now of the rapid recovery of many animals and plants above the K-Pg boundary (Elewa and Joseph, 2009). Aberhan and Kiessling (2015) analyzed many ecological traits of the

mollusks such as life habits, level of mobility, feeding strategy, and position on the substrate. They found significant shifts in the ecospace utilization, where the predators and predator-resistant habits (e.g., infauna, mobile, and deposit-feeding mollusks) have dominated the post extinction assemblages.

3. Minor mass extinctions

3.1. The Precambrian (Ediacaran) extinction

The extinction of the Ediacaran biota was interpreted by Amthor et al. (2003) to be the result of environmental disturbance, which is comparable to Phanerozoic examples. Recently, Laflamme et al. (2013) tested three hypotheses to explain the vanishing of the Precambrian Ediacaran biota (mainly metazoans). These include mass extinction, biotic replacement, and as a result of changing preservation potential. These authors favored ecosystem engineering as the most likely cause although the other two possibilities were not fully excluded. On the other hand, Kataoka et al. (2014) assigned the mass extinctions of the Late Proterozoic and Cambrian to the encounters with nebulae termed as "Nebula Winter", where supernova remnants and dark clouds in the galaxy resulted in the depletion of oxygen and food scarcity as well as anoxia in the ocean. In another speculative proposal Joseph (2010), considered that the Earth was repeatedly assailed by gigantic rubble, and thus, rocks that are more than 4.2 Ga were destroyed, expunging any proof of primitive life on the surface.

In a different proposal, Lindsay et al. (2005) considered that the abiotic organic output during Archean might be the prime cause of the extreme difficulty in recognizing the early biospheric record. Wacey et al. (2009) noted that improving our knowledge of the earliest fossil record enhances our understanding of the putative biological structures and signals which might be discovered in other planets. However, the question of whether Phanerozoic biota evolved from Ediacaran biota remains elusive. Many paleontologists believe in the relationships between Ediacaran biota and some of the present-day living organisms. Other workers, however, insist on differentiating between Ediacaran fossils and Phanerozoic biota. Brasier and Antcliffe (2004) tried to decode the Ediacaran mystery by studying the evolutionary development of the frondlike organism called Charnia. Investigations on the evolution and extinction of life also focus on the debate over the Neoproterozoic snowball versus slushball Earth hypothesis (see Micheels and Montenari, 2008). In an overview of the Snowball Earth events, Maruyama and Santosh (2008) summarized the major periods when the Earth is thought to have been frozen during the late Proterozoic. These include the Sturtian (715–680 Ma) and the Marinoan (680–635 Ma) global glaciations. They suggested that large multi-cellular animals of the Ediacaran fauna flourished immediately after the Marinoan event, as a prelude to the Phanerozoic world. Although several models have been proposed for the 'explosion' of life during Cambrian, and the appearance and extinction of the Ediacaran world (e.g., Santosh et al., 2014; Zhang et al., 2014 and references therein), the causes and mechanisms remain debated. Based on standardized quantitative data, Darroch et al. (2015) suggested that the latest Ediacaran was characterized by depauperate communities.

3.2. The Cambrian

The early Cambrian witnessed a distinct phase in evolution, when several groups of modern life forms, from worms to fishes, appeared (The Cambrian explosion). This radiation is shown by Shu (2008) to be a real biological event rather than an artifact of taphonomy or incomplete preservation of strata. Brasier (1990, 1992) referred to the Precambrian-Cambrian boundary as it is marked by the explosive evolution of invertebrate taxa. The biological modification of the Earth's atmosphere has taken four billion years to be consistent for generating and sustaining the evolution of complex life (Joseph, 2010).

The Cambrian explosion is considered by Brasier (1979) as superb adaptive radiation leading to the emergence of a new 'revealed life' (Phanerozoic eon) after an eon of 'hidden life' (Proterozoic eon). This explosion can be determined through exploring the original reason of genome evolution (Li and Zhang, 2010), keeping in mind the demonstrated link in the Neoproterozoic Earth history from the Galaxy to the genome level (Maruyama and Santosh, 2008). Meert and Lieberman (2008) regarded the biological changes as the main cause of the evolutionary events associated with the Cambrian radiation. Kirschvink and Raub (2003) proposed that a methane 'fuse' was the initiator of the Cambrian Evolutionary Explosion. Ginsburg and Jablonka (2010) provided a combined outline where both ecological and genomic issues are employed to interpret the enigma of the Cambrian explosion. In spite of the dispute concerning the causes of mass extinctions, Elewa and Joseph (2009) summarized four major extinctions during the Cambrian era (from 540 to 510 Ma), among which the fading of trilobites is the most important event. They cited multiple causes for these mass extinctions, including predation, as well as global cooling and reductions in sea level and oxygen leading to anoxia (according to Zhuravlev and Wood, 1996) and changes in ocean chemistry (as proposed by Saltzman et al., 1995).

3.3. The Silurian

In addition to the big five events, there were several minor mass extinctions which include the Silurian mass extinctions. Calner (2008) has evaluated three interesting events with a clear impact on marine environments include the Early Silurian Ireviken Event, the Middle Silurian Mulde Event, and the Late Silurian Lau Event. These three events were proposed to have caused significant catastrophe and ecosystem changes in both deep and shallow marine realms. Bowman et al. (2019) suggested a possible global expansion of anoxic and a paleoredox condition across portions of the late Silurian oceans.

3.4. The Carboniferous

One of the most important minor mass extinction events occurred during the Serpukhovian Stage in the Carboniferous, particularly during the late phase. Sepkoski (1996) regarded the Serpukhovian as the seventh most important mass extinction event of the fossil record whereas Stanley (2007) deemed it as the eighth, with a loss in biodiversity within the marine invertebrates of more than 26%. McGhee et al. (2012) considered the Serpukhovian as the fifth mass extinction, lesser than the Late Devonian mass extinction, but superior to that of the end Ordovician (see Fig. 1 for comparison).

3.5. The Guadalupian (middle Permian)

Applying the quantitative biostratigraphic constrained optimization method (CONOP) to the stratigraphic data of the tetrapod, a significant extinction event was recorded in the Karoo Basin, South Africa, where the generic richness in the mid-Permian (Guadalupian ~ 260 Ma) decreased by more than 75% (Day et al., 2015). Based on fossils and geochemical data on the Middle-Late Permian of Sverdrup Basin (Ellesmere Island, Arctic Canada), Bond et al. (2015) recorded a Capitanian brachiopods extinction in a chert/limestone redox interval documented by redox-sensitive trace metals and pyrite, which indicate a causal role for anoxia. They argue the latter to the smoking gun of volcanic eruptions based on mercury concentrations.

3.6. The ladinian (Middle Triassic)

Analyzing the Northwestern Caucasus macroinvertebrate revealed that Ladinian extinction was comparable in magnitude to other "minor" mass extinctions events such as Early Jurassic or end-Cenomanian (Ruban, 2017), where tetrapods, ammonoids, foraminifers, and

brachiopods genera were significantly dropped.

3.7. The early Jurassic

The Pliensbachian–Toarcian transition (Early Jurassic) is considered by Caruthers et al. (2013) as a global multi-phased event. They support the Volcanic Greenhouse Scenario as the most critical factor motivating the multi-phased extinction of the Pliensbachian–Toarcian. Raup and Sepkoski (1984) and Sepkoski (1996) reported that about 20% of the marine families and genera became extinct by this period. Brachiopods were strongly affected (Ruban, 2018).

3.8. The early Cretaceous

Extensive ammonite turnover took place by the end of the Hauterivian, which is well-documented in a corg-rich interval in the Mediterranean Tethys. This event coincides with a drastic sea-level fall, where large areas of the perimediterranean shelves have been exposed and eroded. In addition, there were a series of oceanic anoxic events during the Cretaceous (e.g. Early Aptian, Early Albian, Late Albian, Cenomanian-Turonian, and Coniacian-Santonian; see Schlanger and Jenkyns, 1976; Jenkyns, 1980, adding to OAE4 during the Late Campanian). The second event (OAE2) is the most important mid-Cretaceous OAE (Kaiho et al., 2014), where about eight percent of marine families, twenty-six genera, and 33–35% of species have been wiped out (Sepkoski, 1989, 1996). It is estimated by Raup and Sepkoski (1986) to represent one of the ten most severe biotic crises of Earth's history. However, MacLeod (2005) judged two extinction events to have occurred in the Cretaceous (an Aptian event and a Cenomanian event). He debated the importance and recognition of the Albian event in many paleontological datasets.

3.9. The Paleogene

Anoxia and Global warming at the Paleocene-Eocene Thermal Maximum (PETM) have left several extinctions and ecologic changes. Analyzing Molluscan assemblages, Ivany et al. (2018) find notable lasting impacts on diversity and functional ecology of some important clades, where Infauna and chemosymbiotic species increased, while body size and abundance have been dropped in one clade as result of hypoxic-driven selection. Similarly, Arcila and Tyler (2017) analyzed the Tetraodontiformes fishes and detected a major mass-extinction event during the PETM, followed by a marked increase in speciation rates.

3.10. The Quaternary

The late Quaternary extinctions (LQE) witnessed the death of hundreds of large-bodied taxa, which were mostly mammals, birds, and reptiles (Lima-Ribeiro et al., 2014). The extinction of many megafaunal taxa in the Late Pleistocene resulted in a diversity decrease and extinction across the entire globe Sandom et al. (2014). In addition, surviving taxa may have also experienced in terms of genetic diversity losses (Sandom et al., 2014; Hofreiter, 2007). This extinction was attributed by Johnson et al. (2016) to direct anthropogenic impact, while climate changes (e.g., glacial-interglacial climate) have played a minor role. Wang et al. (2019) suggested that megafauna was negatively affected by hunting and habitats destruction in Madagascar during the middle Holocene colonization and a significant increase in population, have caused the extinction by hunting and deforestation. Similarly, Faith (2014) suggested that the availability and productivity of the grassland habitats played a major role in the extinction of several large mammal species during the Quaternary of Africa.

In general, there are two paradigms concerning the causes of these extinctions where some scientists believe in environmental change as principal (i.e. Graham and Lundelius, 1984; Guthrie, 1984; Graham and

Mead, 1987; Grayson and Meltzer, 2003; Nogués-Bravo et al., 2010), and some others blame human activities (i.e. Martin, 1973, 1984; Wesler, 1981; Miller et al., 1999; Holdaway and Jacomb, 2000; Alroy, 2001; Roberts et al., 2001; Fiedel and Haynes, 2004; Lyons et al., 2004; Martin, 2005; Surovell et al., 2005; Haynes, 2007, 2009; Gillespie, 2008; Surovell and Waguespack, 2008). A third opinion proposes disease as a cause of this event (Edwards, 1967; MacPhee and Marx, 1997); although the various models are debated (Barnosky et al., 2004; Koch and Barnosky, 2006; Owen-Smith, 1987). Extraterrestrial impact at 12,900 BP has also been speculated as to the major cause (Firestone et al., 2007).

4. Mass extinction evidences in Africa

The biogeographical imprint of mass extinctions may be uneven among geographic regions (Kiessling and Aberhan, 2007; Vilhena et al., 2013; Kocsis et al., 2018). Although sampling efforts are much lower in the south comparatively to Europe and North America (Abdelhady and Abdalla, 2018), many pieces of extinction events were recorded from the African continent. Three main mechanisms for the mass extinctions were reported in Africa; 1) Evidence for a plume event associated with volcanic activity of the Karoo igneous province were recorded in northeast and Western Africa during the Valanginian–Hauterivian (Segev, 2002; Maluski et al., 1995; Vaughan and Pankhurst, 2008), 2) Smithand Botha-Brink (2014) have introduced a drought-induced die-offs as a cause for the Permian-Triassic mass extinctions based on sedimentological and taphonomic pieces of evidence in the main Karoo Basin in South Africa, 3) The large (70–80 km diameter) Morokweng crater (Kalahari Desert, South Africa) about 145 Ma (i.e. J/K boundary 1; McDonald et al., 2006) provide an excellent evidence for an asteroid impact.

Kocsis et al. (2018) indicated that end Permian mass extinction show a dramatic loss of provinciality. In contrast, the end-Cretaceous mass extinction showed great geographical variability, where it has clear evidence in American marine bioregions and less-characterized effect on other Atlantic areas.

Two global anoxic events (the main Hangenberg Event and the lower/middle Tournaisian) associated with mass extinctions were recorded in the eastern Anti-Atlas successions (SE Morocco; Kaiser et al., 2011), where faunal and Sea-level changes and coincided with a glaciation phase. The Cenomanian-Turonian strata in Egypt are well exposed and contain diverse fauna. The stratigraphic data of the macro-invertebrates at this interval showed an obvious pattern of selectivity of the extinction, where the nektic organisms, which inhabited the upper water column (e.g. ammonites) and the epifaunal bivalves (e.g. Neithea, Plicatula, Inoceramus) were immune to extinction events (Abdelhady, 2008). According to Nagm (2015), less than ten percent of the late Cenomanian taxa were recorded in the lower Turonian strata. Elewa (2018) argued the migration and/or local turnover of the ostracod assemblages in North Africa and the Middle East in the Aptian-Turonian to cyclic environmental changes associated with the breakup of Gondwanaland and correlated to the orbital changes (for more details on migration of ostracods as a response to environmental changes see Elewa, 2002; Elewa, 2005c; Elewa and Mohamed, 2014, for examples on migration of organisms as a way of survival).

El-Sabbagh et al. (2004) indicated that the extinction patterns and turnover during the K/Pg boundary was preceded by another minor extinction interval at the Campanian-Maastrichtian in Western Sinai. In the Tarfaya Basin of Morocco, Planktic foraminifera turnover was accompanied by δ13C shift and accumulation of black shales (Keller et al., 2008). The Upper Cretaceous strata in Morocco documenting a major mass extinction of the pterosaurs at the K-Pg boundary, where a diverse assemblage was lived until late Maastrichtian (3 families and 7 species). Keller et al. (1996) have examined the most complete record of the K/Pg boundary at the stratotype section at El Kef, Tunisia found that planktic foraminifera and calcareous nannofossils are the most affected

Table 1
Possible causes of the important extinction events of the fossil record. XXX donates > 10 references; XX donates > 5, X donates < 5; and – donates 0 references.

Causes Event	Asteroid impact	Volcanism	Anoxia/euxinia	Sea level change	Glaciation/Global cooling	Supernova/Orbital change	Plate tectonic	Disease	Human	drought
Precambrian	-	X	X	-	X	X	-	-	-	-
Cambrian	-	-	X	X	XX	-	-	-	-	-
End Ordovician	-	X	XX	-	XXX	X	X	-	-	-
Late Devonian	X	X	XX	X	XX	-	-	-	-	-
End Permian	-	XXX	X	XX	X	X	XX	-	-	X
End Triassic	X	X	-	X	X	-	X	-	-	-
Cretaceous	-	-	X	-	-	X	-	-	-	-
K-Pg	XXX	X	-	-	-	X	-	X	-	-
Quaternary	X	X	-	-	X	-	-	X	XX	X
Current	X	-	-	-	-	-	-	X	XXX	X

groups among other invertebrates major changes across. They suggested that the event was gradual and selective. In contrast, Arenillas et al. (2000) indicated that the extinction at the Aïn Settara section took place over a short time period reflecting catastrophic large asteroid event. While the minor gradual decrease of some taxa can be related to other environmental changes.

The Lower Eocene Global Stratotype Section and Point (GSSP) has been defined by a distinct black anoxic clay bed in the Dababiya Quarry section in southern Egypt, where a sudden shift from light gray marls to black clay at the base of the Eocene and abrupt iridium increase (200 ppt) associated with a decrease in foraminiferal assemblages and δ13C occur (Schmitz et al., 2004; Alegret et al., 2005). Also, the stratigraphic data of the tetrapod in the Karoo Basin (South Africa) document the best well-known diversity loss in the mid-Permian (Guadalupian ~ 260 Ma). These strata documenting also global climate perturbations during the Permo-Triassic mass extinctions event Reyet al. (2016). Neritic sections in the southern shallow Tethys in Egypt have shown long-term changes in bottom-water chemistry and benthic foraminiferal extinction, where the benthic extinction event took place Schmitz et al. (1996).

Elewa and Morsi (2004) concluded that the turnover of the Paleocene-Early Eocene ostracods of east-central Sinai has resulted from migration rather than origination or extinction. One of the worthy examples of adaptation towards changes in the paleoenvironmental conditions (in this case water depth and salinity) is the morphological variability and adaptability of the Egyptian Eocene ostracod species Paracosta mokattamensis (Bassiouni). This ostracod species exemplifies adaptability as a parallel way to migration for organisms to survive by producing morphs capable of living in different water levels and conditions (for more details and examples, see Elewa, 2005a, b). On the other hand, the Cretaceous-Paleogene ostracods of West Africa, North Africa, and the Middle East showed a tendency towards endemism in the deep oceans caused by seafloor spreading as a result of the divergence of the continental plates (Elewa, 2017).

Although the Holocene was characterized by rapid climatic changes with strong droughts intervals, Wang et al. (2019) suggested that these changes were not the killer of the megafauna in Madagascar. They added that occurring of extinctions within stable climate intervals suggests that human colonization and a significant increase in population have caused the extinction by hunting and deforestation. Terrestrial records in Africa suggested that availability and productivity of the grassland habitats played a major role in the extinction of several large mammal species during the quaternary, where grazers and grasslands taxa are the most affected species (Faith, 2014). He added that grassland specialists were replaced by more ecologically flexible mammal communities. Thackeray et al. (2019) reported evidence supporting asteroid impact for the late Pleistocene extinctions during the Younger Dryas episode.

5. Causes of mass extinctions reconsidered

As many extinction events were associated with volcanogenic warming, anoxia, and acidification, Bond and Grasby (2017) suggested that the temporal association of igneous provinces and extinctions implies causality. They highlighted the atmospheric killers, which include toxic metal poisoning, acid rain, O3 damage, and UV-B radiation. The long-established classical models on the causes of mass extinctions do not take genetic or cellular mechanisms into account (Elewa and Joseph, 2009). Moreover, few scientists take into consideration the extinction of the microbial life when studying the major mass extinctions of the fossil record (e.g. Hoffman et al., 1998; Nagy et al., 2009). Therefore, Elewa and Joseph (2009) stated that the extinction of the Paleoproterozoic should be listed with the major extinction events.

The drivers of extinction events may be identified from the selectivity patterns (Finnegan et al., 2015). In a recent study, Hull et al. (2015) introduced new insights related to the dynamics of mass extinction through mass rarity to provide the most robust measure of our current biodiversity crisis relative to the past. In general, there are repeated causes that have played important roles in the species extinction events (Table 1). According to Elewa and Joseph (2009), these include global warming (McAnena et al., 2013), major glaciation (Sheehan, 2001; Bornemann et al., 2008; Matthew, 2009), fluctuations in sea level, global anoxia (Abbas et al., 2000; Shen, 2008; Castle and Rodgers, 2009), volcanic eruptions (Courtillot, 1999; MacLeod, 2000, 2001), asteroid, comet, and meteor impacts (Alvarez et al., 1980; Firestone, 2009), plate tectonics (MacLeod, 2000, 2001), gamma rays (Melott and Thomas, 2009), and disease (Poinar and Poinar, 2008). Another example that may lead to the extinction of a definite group is predation (Reyment, and Elewa, 2002b; Elewa, 2007a, b, c, d). Adding to the preceding causes, Herbert (1992) and Mitchell et al. (2008) attributed the extinctions to the variations of the Earth's orbit, which cause cooling phases within warm conditions. Other hypotheses proposed include oceanic overturn (Wilde and Berry, 1984), tectonic factors leading to volcanism and sea-level fall (MacLeod, 2000, 2001), clathrate gun (Hecht, 2002), severe drought (Smith and Botha-Brink, 2014), hydrogen sulfide emissions from the seas (Kump et al., 2005), as well as a nearby nova, supernova or gamma-ray burst (Melott and Thomas, 2009).

Wei et al. (2014) attempted to evaluate the relationship between geomagnetic reversals and mass extinction. Their model is based on the proposal that accumulated oxygen will escape during an interval of increased reversal rate, leading to the dysoxia, which cause the mass extinction. Thereafter, Long et al. (2016) reported that Se depletion in the past oceans correlates with three major mass extinction events (e.g., the end Ordovician, end Devonian and end Triassic).

Hallam and Wignall (1999) elaborated Newell (1967) opinion and suggested that the majority of marine mass extinctions coincide with large eustatic inflections. Nonetheless, the work of Alvarez et al. (1980) on the K-Pg boundary highlighted the bolide impact hypothesis. Wignall (2001) countered the suggestion of Courtillot (1999) on the

Table 2
A matrix representing the important mass extinctions of the fossil record in relation to their causes.

Extinction event (older to younger)	% Extinction/ Origination	Loss % (Benton, 2003)	Cause(s)	Mechanism(s)	Extinction selectivity	Recovery selectivity	Distinct extinct organisms
Precambrian		-	3, 5, 6	Debatable	?	?	**Microbes**
Cambrian		-	3, 4, 5	Debatable	Selective	Selective	**-**
***End Ordovician**	81	27% F; 57% G	2, 3, 4, 5, 6, 8	Debatable	Selective	Selective	**Nautiloids**
***Late Devonian**	61	19% F; 50% G	1, 2, 3, 4, 5	Debatable	Selective	Selective	**Armoured fish**
***End Permian**	91	57% F; 83% G	2, 3, 4, 5, 7, 8	Debatable	Selective/ nonselective	Selective	**Trilobites and insects**
***End Triassic**	77	23% F; 48% G	1, 2, 4, 5, 8	Debatable	Selective	Selective	**Large amphibians**
Cretaceous	74	-	3, 7	Debatable	?	?	**-**
***K-Pg**		17% F; 50% G	1, 2, 6, 7, 9	Debatable	Selective	Selective	**Dinosaurs and ammonites**
Quaternary		-	1, 5, 9, 10	Debatable	Selective	Selective	**Mammoths**
Current		-	1, 9, 10	Debatable	Selective	-	**Human?**

* = The big five mass extinctions. 1 = Asteroid impact; 2 = Volcanism; 3 = Anoxia/euxinia; 4 = Sea level change; 5 = Glaciation/global cooling; 6 = Supernova/ Gamma rays; 7 = Orbital change; 8 = Plate tectonic; 9 = Disease; 10 = Human. F = Families; G = Genera.

perfect correlation between the age of flood basalt provinces and mass extinction. He believes the correlation exists but is imperfect, where only six of the major extinctions of the Phanerozoic coincide with major episodes of volcanicity. Seemingly, the multiple causes' scenario is the most convincing and acceptable hypothesis of mass extinctions to several scientists (see Molina et al., 1996; Twitchett, 2006; Elewa, 2008e; Elewa and Dakrory, 2008a, b; Elewa, 2014).

Darroch et al. (2015) argued the Ediacaran extinction, which is the first mass extinction of complex life, to innovative ecosystem changes and biological interactions. Laflamme et al. (2013) proposed that multiple causes including behavioral innovations together with the beginning of predation and ecosystem-wide changes, and the substitution of rigid, microbially-bound substrates by ventilated mixed grounds, led to the first large-scale extinction of macroscopic life. Kataoka et al. (2014) speculated that the late Neoproterozoic snowball Earth and the Cambrian explosion were possibly driven by a starburst, which took place around 600 Ma in the Milky Way Galaxy. Kirschvink (1992) argued the event to the raising planetary albedo. Extreme glaciation eventually affected the Neoproterozoic (e.g. Hambrey and Harland, 1985; Young and Gostin, 1989; Hoffman et al., 1998; Evans, 2000; Pazos et al., 2008). However, Micheels and Montenari (2008) suggested a moderate scenario of a slushball Earth instead of an extreme snowball hypothesis.

Among big five from oldest to youngest, the latest Ordovician mass extinction is well known to coincide with oxygenation episode in the Hirnantian Stage. Twitchett (2006) argued the first phase of the extinction event in the Late Ordovician to rapid global cooling. According to him, all major extinctions have resulted from climate changes associated with volcanism, while he minimizes the possible effect of an extraterrestrial cause.

The Late Devonian marine mass extinction, which is considered as one of the major crises of the fossil record, is linked to two Kellwasser simultaneous anoxic events, which have in turn been linked to changes in continental weathering, volcanic/hydrothermal fluxes, sea level and climate change (John et al., 2010). A link between marine anoxia associated with transgression and mass extinction in the Devonian was earlier suggested (see Johnson et al., 1985) the Late Devonian. Moreover, a global glaciation might be generated by a bolide impact (see Prothero, 1998; Joachimski and Buggisch, 2000, 2002). Kaiho et al. (2013) presumed a link between forest fire and soil erosion and the Late Devonian mass extinction. Marynowski and Racki (2014) argued against the proposal of Kaiho et al. (2013).

In their comparison of the causes of the end Permian mass extinction and those of the Cretaceous-Paleogene mass extinction, Vajda and McLoughlin (2007) noticed that the extended extinction-recovery succession at the Permian–Triassic boundary does not fit with an instant

causal mechanism such as an extraterrestrial body impact, but is well-matched with hypotheses related to extended environmental perturbations through flood-basalt volcanism and release of methane from continental shelf sediments. Meyer et al. (2011) supported the idea of euxinia as an explanation of the delayed biotic recovery during Early Triassic time. Winguth and Winguth (2012) attributed the end Permian extinction event to periodic anoxia evidenced by the orbital variability in the sedimentary record. Song et al. (2012) recorded the phenomenon of intense ocean anoxia, which is coincident with the end Permian mass extinction, through examining material of conodont albid crown apatite.

Hermann et al. (2011) assumed that recurrent patterns observed at the Permian-Triassic boundary suggest a common cause such as massive ejections of volcanic gases. Brand et al. (2012) concluded that Permian-Triassic mass extinction was the result of higher volcanic CO_2 and CH_4. Cui and Kump (2014) accepted global warming as a cause of the end Permian extinction event. The formation of Pangaea is another possible cause of this major event. Schobben et al. (2014) attributed the end Permian mass extinction event to multiple causes include global warming, intensified hydrological cycle, water column stagnation, eutrophication, and anoxia). Retallack et al. (2011) mentioned that the end Permian mass extinction was followed by unusually prolonged recovery.

Garbelli et al. (2015) indicated that global warming was an important factor in the biotic crisis for terrestrial and marine taxa of the late Paleozoic world through. Isozaki (2009) stated that the secular change in cosmic radiation can explain the global climatic changes that led to the end-Guadalupian extinction and the long-term global warming/cooling trend. Acidification has played an important role, as well, in the Permian-Triassic mass extinction (Clarkson et al., 2005). Liu et al. (2017), related the end-Permian extinction to massive volcanic eruptions based on direct geochemical evidence (e.g., Zinc isotope), which is an important micronutrient of marine phytoplankton.

The transition from the Triassic to Jurassic period (TJP; approximately 200 Ma) is called "the age of the dinosaurs". This period is known to encompass the end Triassic mass extinction. The causes of this major event, according to Deenen et al. (2010), are volcanism and associated greenhouse gases that paved the way for the dinosaurs to become the dominant species on Earth. Although McGhee et al. (2004) evaluated, as mentioned in a previous section, the marine Triassic-Jurassic extinction as category "IIa", Lucas and Tanner (2008) downgraded the TJB marine extinction to category IIb in their classification. They mentioned different causes of this event including physical processes, significant excursion in the carbon isotope composition of organic matter, the initiation of the Central Atlantic Magmatic Province (CAMP) eruptions, fluorine and chlorine volatile emissions during the

CAMP eruptions, and the effects of dramatic temperature fluctuations. Alternatively, the asteroid impacts which may have contributed to the breaking up of the Pangaea supercontinent is a possible cause of the end Triassic mass extinction (Joseph, 2000). Another assumption is the depletion of oxygen levels and increased anoxia (Ward et al., 2004) and dinosaurs survived this mass extinction because they developed respiratory systems far more proficient than other terrestrial species (Ward, 2006).

Raup (1992) noted that up to 85% of all species were nearly destroyed through the Cretaceous-Paleogene mass extinction. Since Alvarez et al. (1980) introduced the assumption of asteroid impact as a cause for the K-Pg extinction, several scientists tried to prove this theory through diversified studies (Thierstein, 1982; Smith et al., 1992; Molina et al., 1998). In an explanation of what was probably happened during the deposition of the K-Pg boundary layer, Goldin (2008, 2012) presented a new evaluation of the hypotheses for global wildfires and thermal destruction of the terrestrial biosphere following Chicxulub. Her results lie in two points; the first indicates that the deposition of Chicxulub ejecta spherules which formed the global K-Pg boundary layer did not occur as drops falling separately at their terminal velocities, but fell jointly as straight down concentrated currents under gravity; and the second demonstrates the limited pulse of thermal radiation reaching the surface of the atmosphere in both magnitude and duration as a result of absorption by spherules settling lower in the atmosphere. Keller et al. (2018) indicated that rapid warming and ocean acidification are directly linked to Deccan volcanism and the end Cretaceous mass extinction. They added that Anthropocene's dioxide input and environmental changes are faster than that of the end Cretaceous (12–16%).

On the other hand, some others excluded the asteroid impact as a single cause and relied on volcanic eruptions (see Li and Keller, 1998a, b, c). A third team preferred multiple causes' scenario (extraterrestrial bolide impact, volcanic eruptions, and climatic and environmental changes; see Elewa and Dakrory, 2008b; Arens and West, 2008). Poinar and Poinar (2008) proposed disease as a direct cause for the vanishing of dinosaurs. Punekar et al. (2016) suggested that Gigatons of carbon and silicon oxides have been introduced into the atmosphere, which was responsible for the carbonate crisis in the oceans and has resulted in several stressors in the marine realm causing the end Cretaceous mass extinction.

6. Selective vs. nonselective hypotheses

The heterogeneous of the biota (i.e. bioecological traits such as life-habit, feeding mode, mobility, etc.) may hide some extinction events. Testing the association between extinction threat and ecological traits using a database of 2497 marine vertebrate and molluscan genera, Payne et al. (2016) found a difference between modern and past extinction events, where modern extinction threatening large body size, while past extinction events were either nonselective or preferentially excluded smaller-bodied taxa. They added that pelagic animals were suffered more than benthic ones during previous mass extinctions but are not preferentially threatened in the modern ocean (for examples see Reyment, and Elewa, 2002a; Elewa, 2004; to see examples on the ability of benthic ostracods to adapt with the change in the environmental conditions through producing polymorphs).

Many scientists confirm the survival of eukaryotes after the snowball events. Accordingly, Hoffman and Schrag (2002) mentioned that refugia would have existed and their relative isolation and selective stresses could have contributed to their evolutionary diversification. Therefore, they considered the snowball events as an environmental filter on the evolution of life, and a biogeochemical pump that permanently changed the environment itself. On the other hand, selectivity might have occurred in the extinction and recovery phases during the end Ordovician events (Harper and Rong, 2008; Harper et al., 2014). Hammarlund et al. (2012) regarded the two discrete pulses of the end

Ordovician extinction as the first selectively affected nektonic and planktonic species, whereas the second was less selective. Korn et al. (2013) concluded that ammonoids demonstrate the similarity of the Devonian events (selective extinctions) but show a striking difference from the end Permian event (nonselective extinction). Kaiho et al. (2013) linked forest fire and soil erosion to the Late Devonian mass extinction with the highly selective decimation of shallow-water sedentary organisms. Lerosey-Aubril and Feist (2003) recorded implications for the selectivity of survivorship of trilobites during the Late Devonian crisis.

Selective nature of the end Permian mass extinction has been addressed by different authors (e.g. Bambach et al., 2002; Knoll et al., 2007; Dineen et al., 2014; Schobben et al., 2014). Song et al. (2011) assumed selective extinction of larger foraminifers at the end Permian mass extinction and consider them as the greatest victims of the event among the Permian foraminifer assemblages. A selective extinction of heavily calcified marine organisms has been reported for the end Permian event (Clapham and Payne, 2011 in Cui et al., 2013). Villier and Korn (2004) accounted for a high level of selective extinction of ammonoids at the end of the Capitanian and a nonselective extinction at the end of the Permian. Ruta et al. (2011) noticed particular selective survival of therapsids and diapsids of parareptiles after the end Permian mass extinction. Shen et al. (2010) presumed selective diversification of some surviving fossil groups after the end Permian mass extinction.

Brayard et al. (2009) detailed the extinction selectivity and patterns of recovery of the Triassic ammonoids. As to the K-Pg extinction event, a clear separation (selectivity) in the extinction rate is noticed by Schulte et al. (2010) between phytoplankton groups with calcareous shells and organic/siliceous shells. Feduccia (2014) deduced probable selective extinctions of the biota that suffered the K-Pg extinction event. Extinction selectivity was addressed by Wilson (2013) in the body size of mammals across the K-Pg boundary of northeastern Montana, USA. In general, less attention has been paid to the post-K-Pg biotic recovery as compared to the extinction event itself (Erwin, 1998). Robertson et al. (2013) recorded the role of dormancy in marine taxa as a selective recovery factor after the K-Pg extinction crisis. Lima-Ribeiro et al. (2014) noted selective extinction of large-bodied mammals of the late Quaternary.

A similar conclusion has been previously presented by Lyons et al. (2004), Brook and Bowman (2005), and Braje and Erlandson (2013). Wroe et al. (2004) proposed selective extinctions of large animals by human hunting and predation in the late Quaternary. Barnosky et al. (2011) emphasized the need to explore the relationship between extinction selectivity and extinction intensity. In conclusion, the common recorded selective extinctions exclude the hypotheses relying on the possibility of extraterrestrial bolide impacts to be a single cause of mass extinctions of the fossil record, although this could have served as one of the effective factors that led to these events. Alternatively, the recorded nonselective extinctions indicate that abrupt global destructions might have occurred.

Variable reasons may be influencing the species duration (i.e. longevity). Understanding these reasons is essential for conservation biology. Based on occurrence data in the Paleobiology Database, longevity, geographic range size, and diversity show a cyclic complex pattern, in which there is no compelling evidence that one variable determines the others more or less than do any variable (see Abdelhady et al., 2019b, Fig. 2). The linear regression model indicates a circular dependency among genus duration (longevity), geographic distribution (range size), and diversity (expressed by genus richness). Fig. 2 shows a positive correlation between every two pairs of the three measures. Generally, the correlation remains highly significant (high values of Pearson's correlation, r between 0.62 and 0.67). These results are in accordance with the previously documented correlation between range and duration in many groups that have been studied. Although Kreft and Jetz (2010) found that range size or geographic distribution has no effect on the species richness and only minority of the wide-range taxa
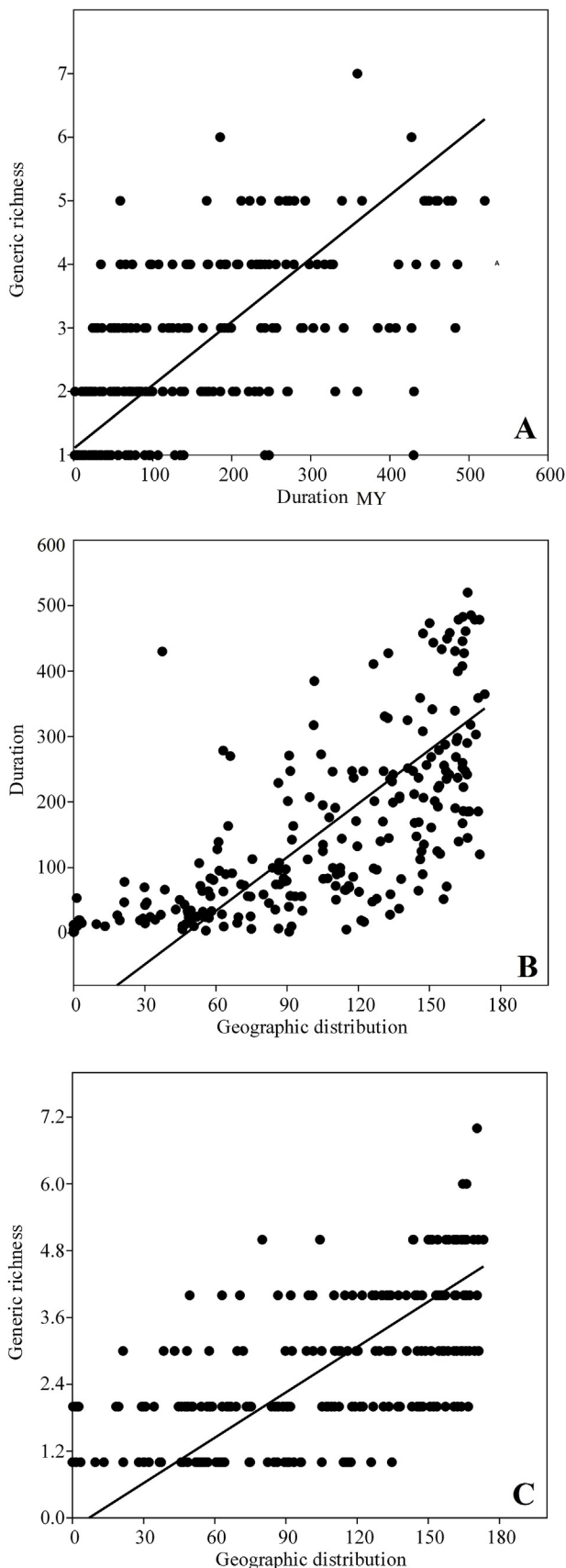
dominated a diverse community (only 20%), which in turn limiting the role of distribution on the total diversity pattern, a strong positive correlation between range size and diversity for the Phanerozoic was indicated (see Fig. 2).

Theoretically, genera with long duration have higher potential to be collected, than those of short duration; however, Ruban (2012) found that older brachiopod superfamilies had more chances to be extinct during four of the five major mass extinction, which may tolerate the sampling potentiality. Consequently, both longevity and range size may be derived by other factors rather than diversity. Based on standardized data sets of more than fifty-thousand taxonomic occurrences from the Paleobiology Database, Nürnberg and Aberhan (2013) found that mean values of extinction and speciation rates are significantly lower for broadly adapted genera than narrowly doing adapted ones.

Miller and Foote (2003) analyzed the longevities of marine taxa originated throughout the Phanerozoic and found that marine taxa originated during recoveries from mass extinctions have a wider geographic range than those originating at stable times. In addition, they recognized a correlation between the geographic range-sizes and species duration of marine taxa. Simpson and Harnik (2009) indicated an important role for the abundance in the extinction pattern of the marine bivalves in the Mesozoic and Cenozoic. It is also possible that living in a diverse community may facilitate the development of adaptation to overcome extinction.

Krug and Jablonski (2012) suggested that origination during major extinction events provide longer stratigraphic durations relatively to genera originated at normal stable intervals. In addition, taxa originated under stress such as global crises event have longer geographic ranges (Miller and Foote, 2003; Ros et al., 2011; Abdelhady and Abdalla, 2018). To test these hypotheses, the range of the bivalve taxa at the five major earth crises, namely the end Ordovician, end Devonian, end Permian and the end-Cretaceous were analyzed. Spatial and temporal ranges of the taxa (which represent the geographic distribution and Longevity of the taxa) originated at the crises interval are much wider than those originated whenever (i.e. normal or stable conditions; Table 3). During and soon after environmental crises new taxa originate and start gradually to fill out the spaces of the extinct ones. Origination under an unstable environment may govern the ecological characteristics of the newly evolved taxa. According to community succession models, the first taxa occupied niche tends to be 'opportunistic'. These opportunistic taxa make the environmental suitability for the coming animals, which are mainly 'equilibrium' taxa and thus may be more eurytopic (see also Levinton, 1970; Abdelhady and Fürsich, 2014).

Table 3
Comparing average and maximum duration and range size of the bivalve originated at environmental crises (5-Major mass extinction events) to those originated during normal conditions. Genera originated at crises interval have wider range size and longer durations. The occurrence and range data of the major invertebrates including bivalves, cephalopods, gastropods, and brachiopods were downloaded in December 2016 from Paleobiology Database (http://paleobiodb.org/#/).

Stage	Crisis event	Stage top (MY)	Average duration (longevity) (MY)	Maximum duration (longevity) (MY)	Maximum range size (lat. degree)
Maastrichtian	**Cretaceous**	**66**	**8.69**	**63.41**	**144.89**
Danian		61.6	1.78	5.60	106.79
Rhaetian	**Triassic**	**201.3**	**24.38**	**135.30**	**145.01**
Toarcian		174.1	7.43	29.10	139.89
Changhsingian	**Permian**	**252.17**	**12.77**	**50.87**	**147.86**
Olenekian		247.2	6.65	12.20	131.55
Famennian	**Devonian**	**358.9**	**55.85**	**157.60**	**74.94**
Tournaisian		346.7	15.80	15.80	1.00
Hirnantian	**Ordovician**	**443.4**	**12.14**	**24.20**	**89.27**
Telychian		433.4	8.57	14.20	122.43

Fig. 2. Linear regression model and relationship between (A) Longevity and genus richness, r = 0.63. (B) Longevity and geographic range size, r = 0 0.67. (C) Diversity and range size, r = 0.62.
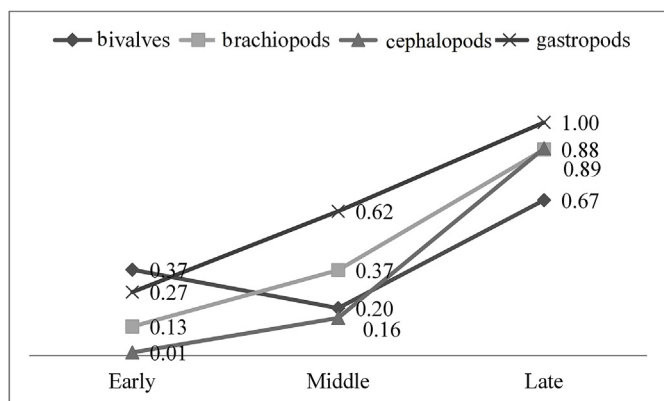
Fig. 3. Extinction rates (boundary crosser method; Foote, 2000) of the Triassic macroinvertebrate during the Early, Middle, and Late Triassic.

Table 4
Important ecological traits of the bivalves survived the end Permian and end Cretaceous mass extinction events.

Autecology		End Permian	End Cretaceous
Shell composition%	Aragonite	55	70
	Calcite	45	**30**
Life habit%	Epifauna	52	51
	Infauna	48	49
Feeding mode (Diet) %	Deposit-feeders	**15**	**10**
	Suspension-feeders	85	90
Mobility %	Mobile	49	51
	Stationary	51	49

Examining the Triassic macroinvertebrates revealed that extinction rates of the Early Triassic were very low and rates increase with increasing environmental stability at the Middle and Late Triassic (Fig. 3). Thus, taxa originated at crises intervals have a wider range size (Table 3) and lower extinction rates (Fig. 3). Hence, geographic range size, the result of ecophysiology, plays a major role in determining extinction risk.

Roopnarine and Angielczyk (2015) examined the Permian-Triassic communities in South Africa and found that functional diversity regardless of species richness is an important stability factor. The diversity-stability relationship has been indicated previously (i.e., 'more complex ecological systems are more stable'; for details see Abdelhady and Fürsich, 2014; Abdelhady and Mohamed, 2017). Based on evidence from multiple ecosystems at a variety of temporal and spatial scales, Tilman et al. (2006) suggested that biological diversity acts to stabilize ecosystem functioning in the face of environmental fluctuation.

7. Recovery from mass extinction

As the world faces an ongoing extinction crisis, which includes but not limited to climate change, habitat destruction, biodiversity loss. Past recovery from mass extinctions provides a basic idea for modern ongoing extinction (Clarkson et al., 2016; Zhang et al., 2017). Mass extinctions in the fossil record are followed by prolonged intervals of ecological instability due to the destruction of the biosphere –geosphere interactions (Hull, 2015). According to Erwin (2001), the ecospace collapse during mass extinctions needs to be rebuilt during the recovery phase. However, if the extinction catastrophe is rapid, recovery will begin faster, while continued deteriorations will give the chance for some groups to radiate and diversify while others may still be suffering extinctions (Budd and Johnson, 1999).

Analyzing range data from the fossil record and found that regardless of the magnitude of the extinction peak, there are 10 million years lag before the origination reaches the same peak, which is known as the speed limit (Clarkson et al., 2016). The latter may be related to environmental factors. Anoxic and related toxics are the main reasons for both extinction and prolonged recovery episodes (Clarkson et al., 2016). Thibodeau et al. (2016) found that significant biotic recovery started only after the eruption of the Central Atlantic Magmatic Province ceased.

Examining recovery from the end Permian mass extinction, Grasby et al. (2016) based on stable isotope data suggested a greenhouse world and reduced marine productivity during the Early Triassic have created an Early Triassic nutrient gap. These persistent environmental perturbations may be responsible for the delayed recovery (Foster et al., 2017). Similarly, Zhang et al. (2017) indicated that the intrusion of the sulfide-rich waters on the shallower marine ecosystem may be responsible for both mass extinction and delayed recovery. The latter may highlight the present-day challenges (i.e. global warming and eutrophication of modern continental shelves). Away from the marine realm, Donovan et al. (2016) and based on well-dated macrofossil spanning the Maastrichtian-Danian found that the total diversity of the insect damage decreased from the Cretaceous to the Paleocene, where the recovery to pre-extinction levels occurred within 4 Ma.

Schueth et al. (2015) suggested a large-scale geographic heterogeneity in both extinction and recovery of the end Cretaceous crises. Examining the (Griesbachian) microbialite unit on the Great Bank of Guizhou in South China, Foster et al. (2018) stated that the benthic community such as brachiopods, crinoids, echinoids, bivalves, gastropods, microconchids, and ostracods are more diverse relative to other coeval deposits, where there are no temporal trends in any diversity index or body size during the recovery phase. They added that the dominance of the small body-sizes and opportunistic taxa point to a high-stress environment (Abdelhady and Fürsich, 2014). Urbanek (1993) studied the Upper Silurian graptoloids and stated that post-
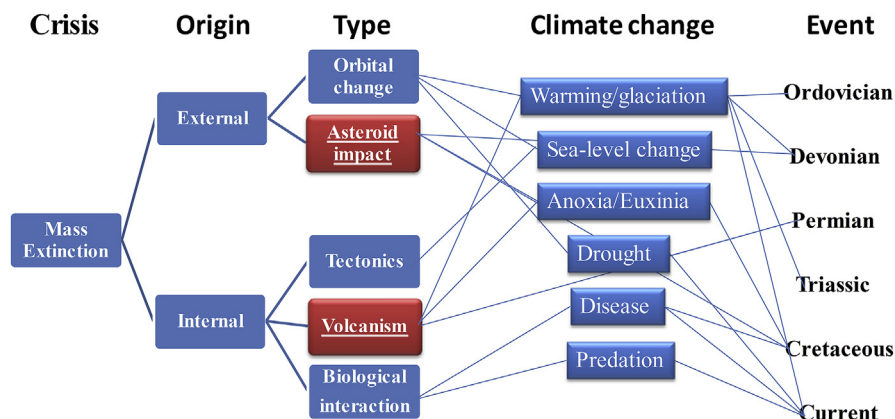

Fig. 4. Mechanisms of the major mass extinction events in earth history.

extinctions taxa are usually dwarfed (small-size) in comparison to pre-extinction ones (Lilliput Effect; see also Elewa, 2018). Elewa and Dakrory (2008a) noticed the Lilliputian planktonic foraminiferal assemblages of the K-Pg boundary of the North African Plate. The dominance of the small-body taxa was also highlighted again (see Sallan and Galimberti, 2015). Therefore, the latter authors based suggested a similar pattern for the current extinction (i.e. loss of large-bodied taxa). Although our expectations are the slower recovery rates near the crater, Lowery et al. (2018) found that proximity to the impact has no significant effect on the recovery. They found that in nearby areas many fauna has reappeared just years after the impact, where within 30 kyr, a high-productivity ecosystem has been established.

In addition to the environmental stress, Schueth et al. (2015) indicated that competition between newly-appeared and survivors taxa may be an important factor controlling the K/Pg recovery of nannoplankton. According to Krug and Jablonski (2012), both species richness and geographic range expand rapidly in the recovery stage than before extinction. They argued the higher origination rates of post-Paleozoic times to the past recovery from a mass extinction event. Based on stratigraphic range data of the marine bivalves, they added that origination rates are constant throughout the Phanerozoic and shifted only during the major biotic crises. Based on Erwin (2001) and Hofmann et al. (2013), three main phases following the extinction event can be distinguished. The first is a lag interval with no significant increase in alpha diversity, where the duration of this lag phase may be extended (e.g., end Permian; Erwin, 2001) or absent. The lag interval followed by a recovery interval, on which competition within habitats increases (i.e. alpha diversity). Finally, when alpha diversity reaches a critical threshold (habitat saturation of species), beta diversity (habitat heterogeneity) starts to increase.

Herein, testing if ecological traits such as life habit (i.e., infaunal vs. epifaunal), diet (suspension vs. deposit feeders), shell composition (aragonite vs. calcite), substrate type (clastics vs. carbonate), and locomotion (stationary vs. mobile) influencing the species duration in the Phanerozoic bivalves (Abdelhady and Abdalla, 2018; https://doi.org/10.1594/PANGAEA.854072), revealed some significant variation, occasionally between deposit and suspension feeders (Table 4). In addition, we have tested whether wide geographical distribution provides potentially to survive mass extinctions, and we found a significant variation among the average duration of narrow and wide range sizes (66 and 230 Ma).

7.1. Current mass extinction is underway

Many scientists believe that our planet is moving towards witnessing the sixth mass extinction (e.g. Wilcove et al., 1998; Crutzen and Stoermer, 2000; Steffen et al., 2007; Elewa, 2008b, e; Elewa and Joseph, 2009). Some scholars alerted that man is accelerating the current mass extinction (i.e. the sixth mass extinction) through various anthropogenic activities (Elewa, 2008e; Andryszewski, 2008; Elewa and Joseph, 2009; Braje and Erlandson, 2013; Elewa, 2014). Some workers speculate asteroid impact as one of the possible leading causes of the earliest phases of the expected sixth mass extinction (Chyba et al., 1993; Firestone et al., 2007). Braje and Erlandson (2013) argued that late Pleistocene and Holocene extinction can be seen as part of a single complex continuum progressively more motivated by anthropogenic factors that continue today. They view the current extinction event as having multiple causes, with humans playing an increasing role through time. It is one of the serious problems to underestimate the major events, as Barnosky et al. (2011) confirmed that the current extinction rate is higher than our expectations based on data from the fossil record, which required enhanced and intensive efforts for conserving current biota.

Stanley (2016) argued the species rarity (reduction in geographic ranges and/or population sizes) to humans through wholesale, through modification of terrestrial habitats, appropriation of primary

productivity for humanity, overexploitation, and pollution, among other factors. Ceballos et al. (2015) showed that the average rate of species loss of vertebrate animals in the last century is100 times higher than the background rate, which indicates that a sixth mass extinction is already underway. The latter is accompanied by a decrease in population size ($> 40\%$) and a range of many animals, occasionally mammals, (up to 80% shrinking geographic range; see Ceballos et al., 2017). The need to pay much attention to conservational biology and reconciliation ecology has been emphasized (Rosenzweig, 2005). However, the intrinsic risk may provide a baseline for highlighting potential threats to marine biodiversity (Finnegan et al., 2015). Anthropogenic-induced environment changes have threatened biodiversity and induced evolutionary changes (see Díaz et al., 2006; Mora and Sale, 2011; Abdelhady, 2016; Abdelhady et al., 2018, 2019a).

8. Conclusions

The current synthesis leads to the following salient conclusions.

- Mass extinctions of the fossil record have distinct origins, mechanisms, and causes.
- Minor mass extinctions should be reconsidered, in which some should be ranked as major events (e.g. the Ediacaran extinction).
- The 'multiple causes' scenario is the plausible mechanism for mass extinction events, where geomagnetic reversals, volcanic activity, and asteroid impact all will be followed by anoxic episodes (see also, Wei et al., 2014). Moreover, transgression will be accompanied by marine anoxia (Johnson et al., 1985). Furthermore, a global glaciation might be generated by bolide impact (see Prothero, 1998; Joachimski and Buggisch, 2000, 2002, Fig. 4)
- Taxa range, duration, and diversity can be correlated but there is no compelling evidence that one variable determines the others more or less than do any variable.
- Taxa originated at crises intervals have a wider range size and lower extinction rates.
- The ecological traits of a species may control their extinction pattern and recovery speed-limit.
- The wide geographical distribution provides potentially to survive mass extinctions.
- Current mass extinction is underway through anthropogenic activities, widespread diseases, and the possibility of extraterrestrial bolide impacts.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jafrearsci.2019.103678.

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