Geoscience Frontiers 4 (2013) 87–93

Contents lists available at SciVerse ScienceDirect

China University of Geosciences (Beijing)

Geoscience Frontiers

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

Research paper

Were Late Cretaceous extinctions of gastropods selective by generic longevity?

Dmitry A. Ruban [a,b,*]

[a] P.O. Box 7333, Rostov-na-Donu, 344056, Russian Federation (for postal communication)
[b] Division of Mineralogy and Petrography, Geology and Geography Faculty, Southern Federal University, Zorge Street 40, Rostov-na-Donu, 344090, Russian Federation

ARTICLE INFO

Article history:
Received 11 February 2012
Received in revised form
11 April 2012
Accepted 17 April 2012
Available online 2 May 2012

Keywords:
Gastropods
Extinction
Longevity
Selectivity
Late Cretaceous

ABSTRACT

Many gastropod taxa went extinct during the Late Cretaceous. The stratigraphic ranges of 268 genera permit to establish the longevity of extinction victims for each stage of this epoch. “Young” taxa (originated within 3 epochs before the extinction) prevailed among victims of the extinctions in all stages. The proportion of “old” taxa (originated before the Cretaceous) that went extinct was the highest in the Cenomanian, and it was the lowest in the Coniacian and the Maastrichtian. It appears that the end-Cretaceous mass extinction affected chiefly “young” taxa. However, the comparison with the earlier time intervals suggests that this pattern of selectivity by generic longevity was not specific for the noted catastrophe, but, in contrast, it was typical for the entire Late Cretaceous. The latest Cenomanian environmental perturbation (OAE2) caused a stronger extinction of “old” taxa, and thus, this biotic crisis was less selective by generic longevity. This hypothesis, however, is not proven by the statistical test.

1. Introduction

Selectivity is a highly complex and yet to be fully understood phenomenon in the biotic evolution (Raup, 1994; McKinney, 1997; Smith and Jeffery, 1998; Jablonski, 2004; Peters, 2008; Clapham et al., 2009; Janevski and Baumiller, 2009; Bush and Bambach, 2011; Clapham and Payne, 2011; Payne et al., 2011). Generally, it means the ability of only certain fossil taxa to face extinctions or to escape them at critical boundaries in the geologic past. The other interesting phenomenon is the so-called longevity (=duration), which indicates the age of the fossil taxon from its origination to its extinction (Foote, 1988; Kammer et al., 1997, 1998; Miller and Foote, 2003; Escarguel and Bucher, 2004; Liow, 2006; Powell, 2007; Foote et al., 2008; Markov, 2009; Crampton et al., 2010; Heim and Peters, 2011; Ruban, 2012). It was previously hypothesized that some mass extinctions might have been selective by taxa longevity (Miller and Foote, 2003; Ruban, 2012). In other words, whether the taxa became victims or survivors of the environmental catastrophes depended on their age. However, it is not enough only to register such a selectivity of the mass extinction. More important is to understand whether this selectivity was a specific pattern of this biotic crisis or it was a characteristic feature of the long-term evolution of the studied fossil group.

Gastropods remained diverse fossils during the Late Cretaceous Epoch, and stratigraphic ranges of their taxa were long enough to be registered in the stage-resolution palaeontological record (Sepkoski, 2002). Extinction rate of this fossil group did not remain stable through the Late Cretaceous, and it peaked near the end of this epoch, when the end-Cretaceous (=Cretaceous/Paleogene, Cretaceous/Tertiary) mass extinction occurred (Fig. 1). The latter was among the most severe environmental catastrophes that took place in the Phanerozoic Era (Hallam and Wignall, 1997; Courtillot, 2007; Alvarez, 2008; Schulte et al., 2010; Alegret et al., in press). Thus, Late Cretaceous gastropods are very promising for a case test of the selectivity by generic longevity, which is an objective of the present study. Selectivity of extinctions that occurred in each stage of the Late Cretaceous is examined in order to understand whether the end-Cretaceous mass extinction was characterized by any peculiar selectivity.

2. Material and methods

This paper is based on gastropod stratigraphic ranges compiled in the most recent version of the palaeontological database by

* P.O. Box 7333, Rostov-na-Donu, 344056, Russian Federation (for postal communication).
E-mail addresses: ruban-d@mail.ru, ruban-d@rambler.ru.

Peer-review under responsibility of China University of Geosciences (Beijing)

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http://dx.doi.org/10.1016/j.gsf.2012.04.002

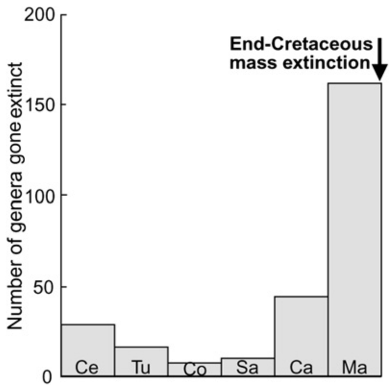

Figure 1. Changes in the number of gastropod genera gone extinct during the Late Cretaceous (on the basis of data by Sepkoski (2002) extracted for the purposes of this study; see Materials and methods). Stage abbreviations: Ce – Cenomanian, Tu – Turonian, Co – Coniacian, Sa – Santonian, Ca – Campanian, Ma – Maastrichtian.

Sepkoski (2002; see on-line: http://strata.geology.wisc.edu/jack/start.php). This appears to be comprehensive information on the global distribution of gastropod genera per stages. A total of 268 genera that went extinct in the Late Cretaceous, are considered for the purposes of the present study (Appendix). Some taxa are excluded from the analysis. These include genera with uncertain stratigraphic ranges (Sepkoski (2002) attributed their ranges to epochs only). The quantity of these taxa is just ∼7% of all genera gone extinct in the Late Cretaceous, and, thus, possible errors linked to the excluded taxa should be minimal.

The generic longevity is determined by the time interval between its origination and extinction. If so, one can consider the entity of genera gone extinct in the particular stage and then can measure the number of their originations in the precedent stages of the geologic history. The resulting graph will show the quantity of taxa with longer and shorter longevity. If genera with relatively longer longevity prevail among those gone extinct in the particular stage, this means that extinctions of this stage stressed "old" taxa. If, vice versa, genera with relatively shorter longevity prevailed among those gone extinct in the particular stage, this means that extinctions of this stage were aimed at "young" taxa. In the both cases, some kind of extinction selectivity will be outlined. But it is possible a situation when the both "old" and "young" taxa were stressed equally. In such a case, an absence of any selectivity can be postulated. For more evident conclusions, it is possible to measure the proportion of "young" and "old" genera for each stage. In the present analysis, the proportions of four kinds of gastropod genera are employed provisionally. These are genera that (1) originated in the same stage when they went extinct, (2) originated within 3 stages before extinction ("young" taxa), (3) originated in the Cretaceous and remained alive 3 stages before the extinction ("middle-age" taxa), and (4) originated before the Cretaceous ("old" taxa). Additionally, some descriptive statistical tools are used. The calculation of the median and mean longevity of gastropod genera that went extinct in each stage of the Late Cretaceous indicates whether there were changes in the relative age of taxa that went extinct in the particular time interval.

The present analysis of gastropods aims at the generic longevity of gastropods that went extinct in each of the Late Cretaceous stages, namely the Cenomanian, the Turonian, the Coniacian, the Santonian, the Campanian, and the Maastrichtian. Of course, these extinctions did not necessarily occur simultaneously at only particular critical boundaries. Therefore, selectivity of the so-called background extinction (Raup and Sepkoski, 1982; Wang, 2003; Taylor, 2004; Boucot, 2006; Lieberman and Kaesler, 2010) is evaluated. Indeed, the patterns of this selectivity might have changed through the geologic time. But tracing the selectivity of the background extinction is important for judgements about the selectivity of the end-Cretaceous mass extinction. If this biotic catastrophe demonstrated the same selectivity as was typical for the previous time intervals, when gastropods evolved "normally", it is impossible to say that this catastrophe was characterized by any specific selectivity by taxa longevity.

This study is based on the modern chronostratigraphic scale of the Late Cretaceous (Ogg et al., 2008), which should not appear significantly different from that time scale employed by Sepkoski (2002) for his palaeontological database. At least, the volume of the Late Cretaceous stages did not change fundamentally during two past decades (Rawson et al., 1996; Ogg et al., 2008). Refinement of results from the present study along the numerical time scale is avoided because of two main reasons. Firstly, the original data presented by Sepkoski (2002) were essentially attached to stages, not absolute time units. Secondly, a significant part these data indicate the time of originations and extinctions of taxa with a resolution limited to only stages. If one considers any stage with a long duration (like the Campanian), it will be impossible to say whether the particular taxa appeared near the beginning or the end of this stage, and thus, to link it to any absolute time point. Moreover, consideration of such time intervals as stages may help with the problem of the background extinction, which sometimes is treated as a sampling artefact (Boucot, 2006). It is evident that a moderate lowering of the time resolution increases an accuracy of the analysis linked to the distribution of taxa in the geologic time (cf. Ruban and van Loon, 2008).

3. Results

A total of 29 gastropod genera went extinct in the Cenomanian Stage (Appendix). Many of them were "young" taxa that appeared in the same Cenomanian or the late Early Cretaceous; however, victims also included some "old" genera, which originated in the Middle Triassic and the Jurassic (Fig. 2A). Especially, the Bathonian Stage was important in the appearance of taxa that did not cross the Cenomanian/Turonian boundary. A lesser number of gastropod genera (16 in total) went extinct in the Turonian Stage (Appendix). Many of them originated in the Turonian or the Cenomanian, i.e., they were "young" taxa, but some "old" taxa, which originated in the Ladinian and the Bathonian, also disappeared (Fig. 2A). Only 7 genera faced extinctions in the Coniacian Stage (Appendix). All of them were "young" taxa, which originated in the mid-Late Cretaceous (Fig. 2B). The number of gastropods gone extinct in the Santonian was also minimal (Appendix). These genera included chiefly "young" and "middle-age" taxa (Fig. 2B). However, one genus appeared in the pre-Cretaceous times.

The extinction rate accelerated in the Campanian Stage (Fig. 1), when 44 gastropod genera went extinct (Appendix). The majority of these genera were "young", and they appeared in the same Campanian (Fig. 2C). However, the number of late Early Cretaceous–early Late Cretaceous taxa ("middle-age" taxa) was also high. Moreover, some "old" genera that appeared in the Early and Middle Jurassic became victims of the Campanian extinctions (Fig. 2C). The most severe were extinctions of the Maastrichtian Stage (Fig. 1). A total of 162 gastropod genera disappeared in this time unit (Appendix). Many of these taxa were "young", but the number of Campanian genera was higher than that of Maastrichtian genera (Fig. 2D). Many Early and Late Cretaceous gastropods also went extinct in the Maastrichtian as well as some Triassic and Jurassic taxa; it should be noted that the relatively high number of pre-Cretaceous taxa that did not cross the Cretaceous/Paleogene boundary appeared in the Bathonian Stage (Fig. 2D). And one genus

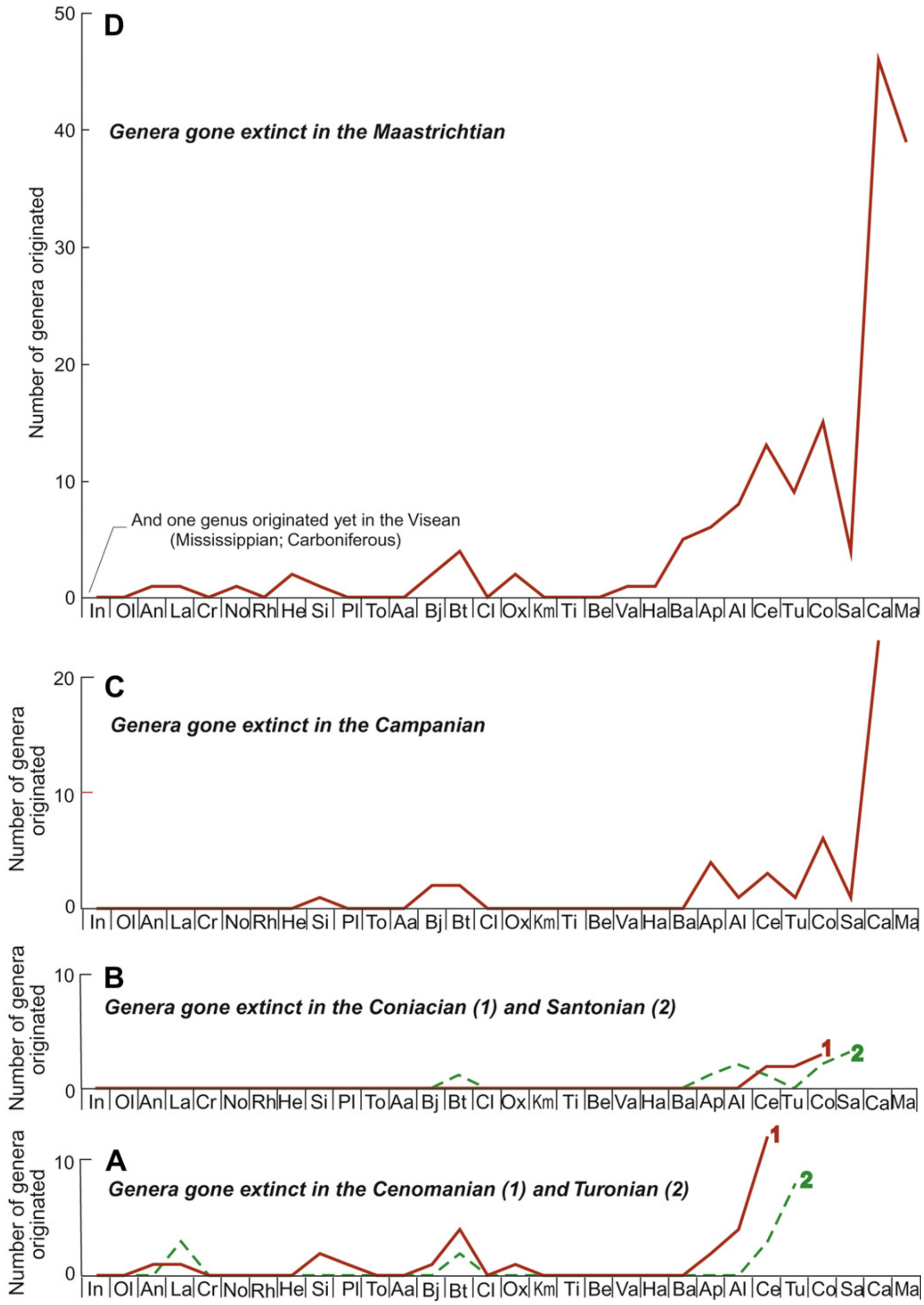

Figure 2. Changes in the number of gastropod genera gone extinct during the Late Cretaceous depending on the time of their origination. Stage abbreviations: In – Induan, Ol – Olenekian, An – Anisian, La – Ladinian, Cr – Carnian, No – Norian, Rh – Rhaetinan (Triassic stages), He – Hettangian, Si – Sinemurian, Pl – Pliensbachian, To – Toarcian, Aa – Aalenian, Bj – Bajocian, Bt – Bathonian, Cl – Callovian, Ox – Oxfordian, Km – Kimmeridgian, Ti – Tithonian (Jurassic stages), Be – Berriasian, Va – Valanginian, Ha – Hauterivian, Ba – Barremian, Ap – Aptian, Al – Albian, Ce – Cenomanian, Tu – Turonian, Co – Coniacian, Sa – Santonian, Ca – Campanian, Ma – Maastrichtian (Cretaceous stages).

that did not cross the Cretaceous/Paleogene boundary appeared yet in the Carboniferous.

The results presented above suggest that victims of the Late Cretaceous extinctions were chiefly "young" gastropod genera, i.e., those with a short longevity (Fig. 2). This reveals a long-term pattern of the selectivity. The latter is also indicated by the analysis of changes in the proportions of genera depending on their age (Fig. 3). For all Late Cretaceous stages, the number of genera originated in the same stages when they went extinct or within three stages before their extinction was significantly higher than the number of pre-Cretaceous genera. However, the above-mentioned proportions fluctuated significantly. E.g., victims of the Coniacian extinctions were dominated by "young" taxa, whereas victims of the Cenomanian extinctions included a lot of "old" taxa (Fig. 3). Moreover, the "middle-age" genera constituted a significant part of victims of the Santonian, Campanian, and Maastrichtian

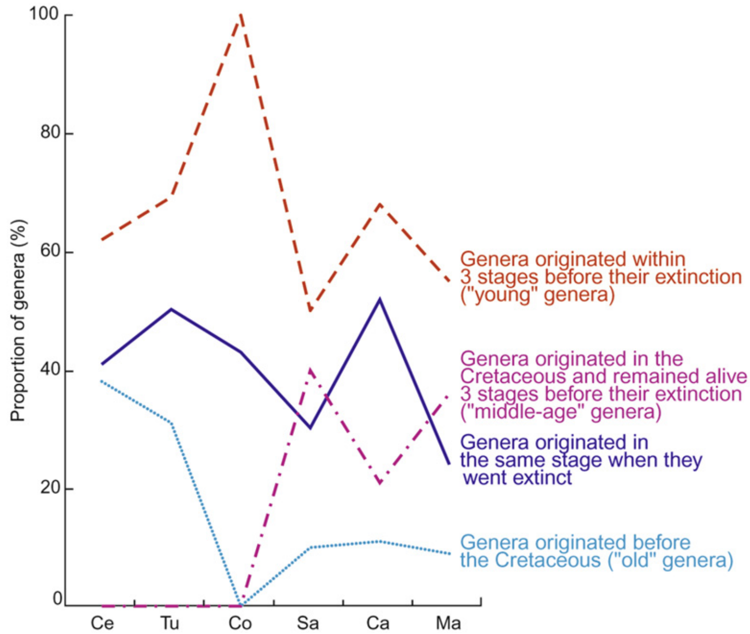

Figure 3. Changes in the proportion of gastropod genera gone extinct during the Late Cretaceous depending on the time of their origination. See Fig. 1 for stage abbreviations.

extinctions. Results of the statistical analysis imply significant variations in the both median and mean longevity (Fig. 4), i.e., the dynamics of the registered selectivity by taxa longevity. However, it is evident that younger taxa prevailed among victims of extinctions in all stages, because the median value in none case is larger than 3.

4. Discussion

High extinction rate of gastropods in the Maastrichtian Stage can be linked to the influence of the end-Cretaceous mass extinction (Fig. 1). As shown above, "young" and "middle-age" genera prevailed among victims of Maastrichtian extinctions. Indeed, this is a kind of selectivity. But is it different from the selectivity of background extinction observed at the precedent intervals? Most probably, the answer should be negative because (1) the proportions between "young" and "old" gastropod genera that gone extinct in the Maastrichtian were comparable to those observed for some other Late Cretaceous stages (Fig. 3), and (2) the median and

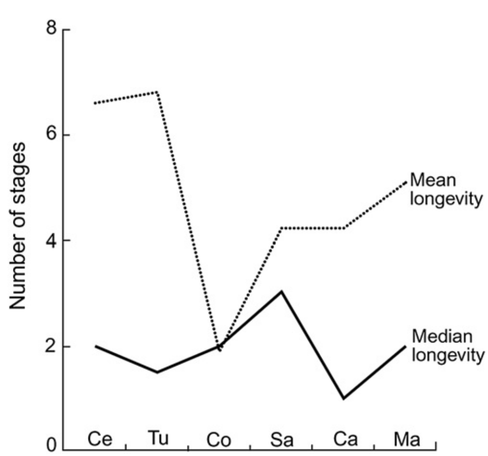

Figure 4. Changes in the median and mean longevity of gastropod genera gone extinct during the Late Cretaceous.

mean longevity of victims of the Maastrichtian extinctions do not differ significantly from values calculated for victims of the earlier extinctions (Fig. 4). One may propose two alternative hypotheses about possible influences of the end-Cretaceous mass extinction on marine fossils, including gastropods. Firstly, the mass extinction might have been focused on either very "old" or very "new" taxa. The formers seem to be potential victims, because they might have lost their evolutionary potential, whereas the latters might have been vulnerable to environmental perturbations because of their young age and "underdeveloped" abilities for adaptation and resistance to unfavourable environments. Secondly, the mass extinction might have affected fossils in a haphazardous way and, thus, caused extinctions of both many "old" and "young" taxa. The both hypotheses should be rejected with regard to our results. Moreover, as shown above, the selectivity end-Cretaceous mass extinction was not a specific pattern in comparison to the selectivity established for the other stages of the Late Cretaceous.

Of course, not all extinctions of gastropods that occurred in the Maastrichtian were linked to the end-Cretaceous mass extinction. Some of them took place a bit earlier. From 162 genera that went extinction in the last stage of the Late Cretaceous Epoch, Sepkoski (2002) indicated 30 taxa disappeared in the Early Maastrichtian and 34 taxa disappeared in the Late Maastrichtian. For other 98 genera, he did not specify the stratigraphic range at the level of substages. Despite the evident data incompleteness, it is intriguing to pay some attention to victims of the only Late Maastrichtian extinctions (Appendix). The most of them were "young" and "middle-age" taxa, whereas the numbers of "old" genera and those originated in the Maastrichtian were little (Fig. 5). This reveals selectivity, which is a bit different from that established for the entire Maastrichtian. However, one should note that (1) many "old" and Maastrichtian taxa do not bear precise stratigraphic ranges in the original database by Sepkoski (2002), and (2) many Maastrichtian genera went extinct already in the Early Maastrichtian. If so, the available evidence does not allow to question the lack of any specific pattern in the selectivity by generic longevity linked to the end-Cretaceous mass extinction.

The Late Cretaceous was not a "calm" epoch in the biotic evolution. At least, two environmental perturbations stressed

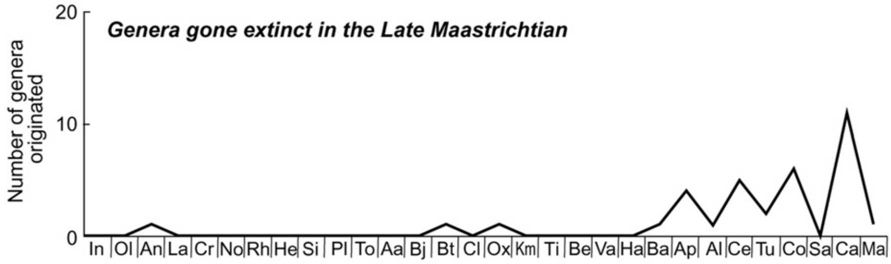

Figure 5. Changes in the number of gastropod genera gone extinct during the Late Maastrichtian depending on the time of their origination [measured on the basis of incomplete data extracted from Sepkoski (2002)]. See Fig. 2 for stage abbreviations.

marine invertebrates. These were the Oceanic Anoxic Event 2 in the latest Cenomanian (Jenkyns, 1980, 2010; Hallam and Wignall, 1997; Harries and Little, 1999; Takashima et al., 2006; Keller et al., 2008) and the Oceanic Anoxic Event 3 in the Santonian (although this dating is a subject of debates) (Jenkyns, 1980; Toshimitsu and Hirano, 2000; Rey et al., 2004; Takashima et al., 2006; Jones et al., 2007). From some regional records, it is known that these events might have affected gastropods (e.g., Ruban et al., 2011). The present results suggest that many genera gone extinct in the Cenomanian were either "young" or "old" (Fig. 2A) and the proportion of "old" taxa among extinction victims was the highest for the Late Cretaceous (Fig. 3). This differs from the selectivity established for the Maastrichtian. One may hypothesize that the relatively little proportion of "old" taxa among victims of the Maastrichtian extinctions was the result of massive disappearance of these taxa within the earlier stages and subsequent impoverishment of the Maastrichtian assemblage in taxa with longer longevity. This permits to assume that the Maastrichtian extinctions were, in fact, severe for the "old" taxa similarly to the Cenomanian extinctions. Let's imagine that none "old" taxon went extinct from the Cenomanian and until the Maastrichtian to disappear in the latter stage. This would increase the proportion of "old" taxa among victims of the Maastrichtian extinctions up to 20%. But this is anyway lower than the relative quantity of genera gone extinct in the Cenomanian and the Turonian. Thus, the tested hypothesis and the above-mentioned assumption should be rejected. Anyway, it appears that the Cenomanian was characterized by the least selectivity by generic longevity of gastropods from all Late Cretaceous stages. Was this a haphazardous effect of the latest Cenomanian event? Answering this intriguing question requires additional studies, which are beyond the scope of the present paper. However, the median longevity of gastropod genera gone extinct in the Cenomanian does not differ significantly from that of genera gone extinct in the other stages (Fig. 4). This permits to doubt in the specificity of the selectivity of the Cenomanian extinctions. As for the Santonian, it did not provoke multiple extinctions of "old taxa" (Fig. 2B), and the low number of gastropod extinctions in this stage (Fig. 1) does not permit to consider the latter as a critical interval in the evolution of Cretaceous gastropods. However, the statistical analysis shows that the median longevity was maximal in the Santonian (Fig. 4).

5. Conclusions

The analysis of the selectivity of Late Cretaceous gastropod extinctions by generic longevity permits three interesting conclusions:

(1) in each stage of the Late Cretaceous Epoch, "young" genera prevailed among all taxa gone extinct;
(2) the proportions of "young", "middle-age", and "old" genera among victims of extinctions changed significantly through the Late Cretaceous;
(3) the end-Cretaceous mass extinction affected chiefly "young" gastropod genera, but this was not a specific pattern of this biotic catastrophe.

Generally, this study demonstrates that the selectivity of mass extinctions cannot be considered without a close attention to the fossil evolution before these events and that the registered selectivity of mass extinctions can be an only expression of the long-term evolutionary pattern. Further studies of the extinction selectivity by generic longevity of gastropods (and other organisms) should extend the scope of the present analysis and consider, for instance, short-term and along-term survivors as well as other mass extinction events.

Acknowledgements

The author gratefully thanks the journal editor Prof. M. Santosh (Japan) and the anonymous reviewer for their constructive suggestions, Dr. I.Yu. Safonova (Russia) for her invitation to "GSF" and preliminary check of the paper, and also Dr. W. Riegraf (Germany), Prof. A.J. van Loon (Netherlands), and some other colleagues for their help with literature.

Appendix

Taxonomic lists of gastropod genera that went extinct in the Late Cretaceous stages. Extracted from Sepkoski (2002; see on-line: http://strata.geology.wisc.edu/jack/start.php). For more explanations see the text (Materials and methods).

Genera gone extinct in the Cenomanian Stage:

Aplocus, *Bicarinella*, *Blackdownia*, *Buckmanina*, *Ceritella*, *Chilocyclus*, *Cirsocerithium*, *Coronatica*, *Craginia*, *Diarthema*, *Eotrochactaeon*, *Fictoacteon*, *Harpagodes*, *Helicocryptus*, *Horizostoma*, *Jaccardiella*, *Liocium*, *Mrhilaia*, *Naricopsina*, *Oligoptyxis*, *Palaeotrochactaeon*, *Paraturbo*, *Phyllocheilus*, *Pirsila*, *Pseudomelania*, *Pterodonticeras*, *Pyrgotrochus*, *Stelzneria*, and *Turboidea*.

Genera gone extinct in the Turonian Stage:

Aphanoptyxis, *Blancia*, *Eustoma*, *Gargania*, *Gonzagia*, *Hamlinia*, *Italoptygmatis*, *Laevinerinea*, *Mesotrochactaeon*, *Microschiza*, *Myagrostoma*, *Oncochilus*, *Pholidotoma*, *Ptychoris*, *Purpuroidea*, and *Tanaliopsis*.

Genera gone extinct in the Coniacian Stage:

Armenostoma, *Cerithina*, *Cerithiomorpha*, *Eovolutilithes*, *Haploptyxis*, *Plectocion*, and *Sevanella*.

Genera gone extinct in the Santonian Stage:

Banis, *Coninoda*, *Cuphosolenus*, *Hacobjania*, *Hexaglauconia*, *Parapuractaeon*, *Pchelincevella*, *Pseudogaleodea*, *Pseudomesalia*, and *Struthiolariopsis*.

Genera gone extinct in the Campanian Stage:

Actaeonella, *Afrocypraea*, *Araratella*, *Astandes*, *Ataphrus*, *Beisselia*, *Cassiope*, *Caucasella*, *Christitys*, *Closteriscus*, *Coelobolma*, *Crossotrema*, *Dicroloma*, *Discotectus*, *Eccliseogyra*, *Echinobathra*, *Eosolarium*, *Eripachya*, *Ficulomorpha*, *Fusimilis*, *Gigantocapulus*, *Glauconiella*, *Globiconcha*, *Glosia*, *Gymnentome*, *Haydenia*, *Holzapfelia*, *Lissapiopsis*, *Margaritella*, *Mexicotrochaetaeon*, *Neotrochaetaeon*, *Parvivoluta*, *Proconulus*, *Protopirula*, *Pseudorapa*, *Pterodonta*, *Seminola*, *Sogdianella*, *Spiractaeon*, *Sycodes*, *Tetraplica*, *Tibiaporrhais*, *Troostella*, and *Tundora*.

Genera gone extinct in the Maastrichtian Stage:

Actaeonina, *Aliofusus*, *Amplostoma*, *Amuletum*, *Anchura*, *Anisomyon*, *Anomalofusus*, *Anteglossia*, *Atira*, *Auriala*, *Avellana*, *Bajanerita*, *Bathrotomaria*, *Bellifusus*, *Belliscala*, *Beretra*, *Biplica*, *Boltenella*, *Buccinopsis*, *Bullopsis*, *Caveola*, *Cenomanella*, *Chilodonta*, *Cimolithium*, *Closteroides*, *Columbellaria*, *Cryptorhytis*, *Cylindrotruncatum*, *Damesia*, *Deussenia*, *Dircella*, *Discohelix*, *Drilluta*, *Echinimathilda*, *Eoacteon*, *Eoharpa*, *Exechocirsus*, *Ficulopsis*, *Forsia*, *Fulgerca*, *Garramites*, *Goniocylichna*, *Graciliala*, *Graphidula*, *Gymnarus*, *Gyrotropis*, *Haplovoluta*, *Helicaulax*, *Hercorhynchus*, *Hippocampoides*, *Hydrotribulus*, *Itieria*, *Itruvia*, *Kaunhowenia*, *Lacriforma*, *Latiala*, *Laxispira*, *Lemniscolittorina*, *Libycerithium*, *Liopeplum*, *Lispodesthes*, *Lomirosa*, *Longoconcha*, *Lowenstamia*, *Lupira*, *Lutema*, *Lutima*, *Lyosoma*, *Lysis*, *Mataxa*, *Medionapus*, *Metriomphalus*, *Michaletia*, *Millosevichia*, *Mitridomus*, *Monilriretusa*, *Morea*, *Murphitys*, *Myobarbum*, *Nairiella*, *Napulus*, *Neocylindrites*, *Nerinea*, *Nerinella*, *Nipponitys*, *Nummocalcar*, *Odontobasis*, *Odontofusus*, *Oligoptycha*, *Ooliticia*, *Ornopsis*, *Paladmete*, *Palaeopsephaea*, *Paleofusimitra*, *Parafusus*, *Paramorea*, *Parasimplotyxis*, *Parietiplicatum*, *Perustrombus*, *Piestochilus*, *Pleurotomaria*, *Pornosis*, *Procampanile*, *Procancellaria*, *Protodolium*, *Pseudobuccinum*, *Pseudocymia*, *Pseudohercynella*, *Pseudoliotina*, *Pseudoperissitys*, *Pterocerella*, *Ptychosyca*, *Ptygmatis*, *Pugnellus*, *Punctospira*, *Pyktes*, *Pyrazella*, *Pyrifusus*, *Quadrinervus*, *Rapopsis*, *Remera*, *Remnita*, *Rhombopsis*, *Ripleyella*, *Rostellana*, *Rostellinda*, *Sargana*, *Schizobasis*, *Scobinodola*, *Scorbinidola*, *Semisolarium*, *Serrifusus*, *Sohlella*, *Sohlitella*, *Spirgvaleia*, *Spironema*, *Stantonella*, *Striaticostatum*, *Tanimasanoria*, *Tectaplica*, *Teneposita*, *Tephlon*, *Tessarolax*, *Thylacus*, *Tintorium*, *Torgnellus*, *Torquesiella*, *Trajanella*, *Tridactylus*, *Trobus*, *Trochacanthus*, *Trochactaeon*, *Tryonella*, *Turbinopsis*, *Uchauxia*, *Urceolabrum*, *Velatella*, *Volutoderma*, *Volutomorpha*, *Weeksia*, *Woodsella*, and *Zikkuratia*.

Genera gone extinct in the Late Maastrichtian:

Anchura, *Anisomyon*, *Anomalofusus*, *Atira*, *Bellifusus*, *Buccinopsis*, *Caveola*, *Chilodonta*, *Eoacteon*, *Graphidula*, *Haplovoluta*, *Helicaulax*, *Hercorhynchus*, *Kaunhowenia*, *Latiala*, *Laxispira*, *Liopeplum*, *Longoconcha*, *Lowenstamia*, *Lupira*, *Napulus*, *Oligoptycha*, *Ornopsis*, *Paladmete*, *Palaeopsephaea*, *Piestochilus*, *Pleurotomaria*, *Pyktes*, *Quadrinervus*, *Rostellana*, *Sargana*, *Thylacus*, *Trochacanthus*, and *Weeksia*.

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