VARIABILITY IN BIOLOGICAL DIVERSITY OF DINOSAURS AND DISTRIBUTION OF SPECIES BY FOOD TYPES

P I Egorov[1], E M Nesterov[1], S V Dubrova[1], K I Shmoylov[1] and M A Markova[1]

[1]Herzen State Pedagogical University of Russia

Abstract. Biodiversity analysis underlies macroevolutionary studies and allows to identify mass extinctions. Numerous studies of mass extinctions show that geological factors play a central role in determining the diversity dynamics. The late Cretaceous extinction is of interest to science as the closest to us extinction of the five mass extinctions that occurred in the Phanerozoic. There is currently no scientific consensus on the scenario in which the extinction occurred on land. In order to assess the features of superorder *Dinosauria* development during the Cretaceous-Paleogene, the authors have analysed the diversity of terrestrial taxa of Mesozoic dinosaurs. Based on data from the paleobiodb paleontological database using the Python programming language and its libraries, the features of the species diversity of *Dinosauria* have been studied. An attempt was made to quantify the species diversity of this group based on the ratio of predators to herbivores using data on dinosaur food types. The simulated diversity data were compared with observed patterns and existing estimates. It is likely that less than one-third of the dinosaurs that existed are currently known, as indicated by the geography of the fossils, and the proportions of dinosaurs by type of food.

Key words: biodiversity, mass extinctions, catastrophes, Mesozoic era, biotic crisis.

Introduction

The main purpose of paleoecology remains to establish the trajectory of biodiversity through time (Rosenzweig, 1995). Knowledge of biota development patterns at different taxonomic levels helps to identify important macroevolutionary signals, such as mass extinctions or species substitutions, and to reveal the rate and nature of adaptations (Stanley, 2007). To date, most of the Cretaceous-Paleogene research has centered on the study of marine sediments, whereas trends in terrestrial biodiversity over time have received less attention (Benton, 2008). The nature of the processes that took place in marine ecosystems is relatively well studied and there is a scientific consensus about it, consisting in the idea of reduction of the biological productivity of planktonic communities, which entailed a chain reaction of disruption of trophic chains of water bodies and extinction of individual groups of organisms, while there is no clear understanding about the course of the crisis on land.

According to Yeskov, the superorder *Dinosauria* with its companion pterosaurs is the only large group of organisms that became extinct on land at the end of the Cretaceous (Yeskov, 2020). That is why the *Dinosauria* superorder, which was the predominant terrestrial group for about 150 million years but had become completely extinct by the Danish Age, is central to the question of the nature of terrestrial extinction.

Diversity curves of Mesozoic dinosaurs have been proposed by several authors, the material for which were genera counts (Upchurch P. et al., 2005). However, most studies have concerned individual dinosaur clades rather than the diversity of dinosaurs in general. Fastovsky et al. (Fastovsky D. E. et al, 2004) and Wang and Dodson (2006) used more sophisticated statistical approaches, including population-based coverage estimates to estimate overall dinosaur diversity, but provided only a general temporal sample, which may have obscured or confounded important curve features. Lloyd et al. (Lloyd G. T. et al, 2008) provided the most comprehensive report of dinosaur diversity to date , using various indicators and attempting to correct for possible sampling errors in their diversity estimates.

Studies of marine invertebrate paleobiodiversity show that the quality and quantity of rock available to paleontologists to search for fossils (e.g., the area of outcrop of rocks containing fossils per unit time) have a major impact on the interpretation of diversity patterns. Diversity curves can result from changes in global sea level, tectonics, and other geologic processes affecting fossil conservation (McGowan, Smith, 2008). Thus, Wang and Dodson (2006) concluded that the availability of rocks had a strong influence on the observed pattern of dinosaur diversity in North America. Note that it is the United States that leads in the number of dinosaurs findings (Dodson, 1990).

The superorder *Dinosauria* is quite numerous and as of the current moment counts 1245 species. Some of them do not have genus affiliation yet and may belong to one of the duplication types.

Dinosaur diversity is constantly revised at different taxonomic levels. In 2008, Benton refuted the view that this superorder had 1,401 species (as of 2008), showing that 230 species were either synonymous, had insufficient basis for separation, or did not belong to dinosaurs (Benton, 2008). At the same time, we note that a large number of findings have already been made in the 21st century, which significantly complement the paleontological record.

Nevertheless, according to estimates (Gradstein et al. 2008; Fassett, 2005), about 30 new species of *Dinosauria* superorder are discovered every year (see Fig. 1), while for the 20th century this indicator was only 3–4 species per year. Specialists estimate the possible biodiversity of this order with a rather large range. Thus, Wand and Dodson in 2006 estimated the biodiversity of dinosaurs at the genus level at 1850 genera (Wang, Dodson, 2006), a decade earlier Russell gave an estimate of 3400 genera (Russell, 1995). These values are 3.5 or more times exceeding the proven representations for 2006: 556 genera (Wang and Dodson, 2006), and are much more relevant than 1090 genera obtained by the authors from the open base (Nesterov et al., 2020). At the same time, it should be noted that the allocation of dinosaur genera at the current time remains a controversial part of their systematics.

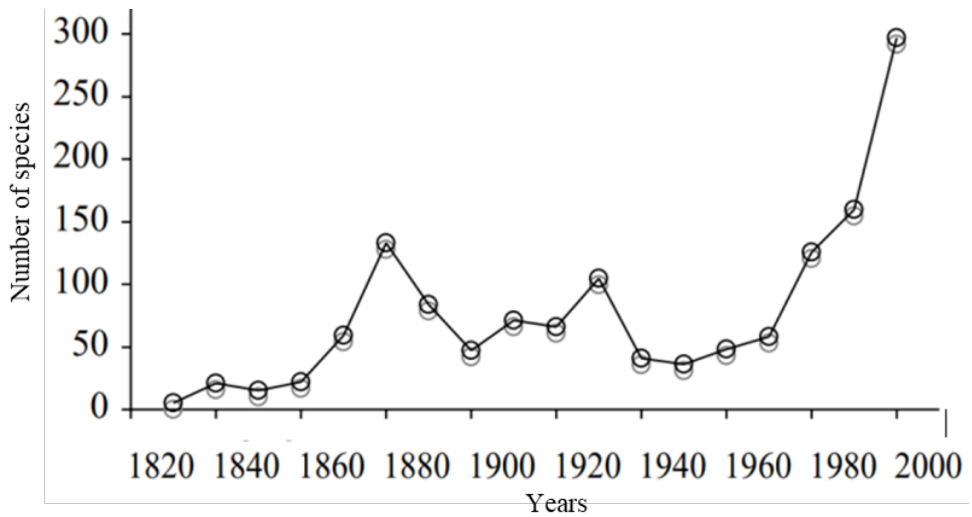

Fig. 1. Number of discovered species of the superorder *Dinosauria* by decades (based on M. Benton)

The purpose of the present study is to relate the dynamics of dinosaur diversity at the level of families, genera, and species in the Mesozoic Era as well as to propose the ratio of dinosaur diet type as an alternative way of specifying the possible number of species.

Methods

To perform the work, the authors analysed data on all representatives of the superorder *Dinosauria* listed in the database (The Dinosaur Genera List, 2022) as of 01/11/2022.

The paleobiodb paleontological database, which operates according to the Application Programming Interface principle, was used as a source of biodiversity data. The database (PBDB; https://paleobiodb.org) consists of taxonomically identified fossil occurrence data with geographic and temporal references. The taxonomy used by PBDB is not static, but is dynamically generated using an algorithm applied to separately managed verified taxonomic data. PBDB owes its existence to researchers who have entered more than 1.25 million fossil findings over the course of their work (Peters et al, 2016).

Raw data on paleontological findings were collected by the author into a .csv file, which was processed using the Python programming language (ver. 3.21) and the numpy, pandas, and matplotlib data visualization libraries.

The cleaned data included, in addition to taxonomic, geographical, and chronological references, also information about the type of dinosaur's diet divided into three categories "herbivore", "carnivore", and "omnivore". The information on the ratio of dinosaurs with different types of feeding was used by us as an alternative way of calculation of a potential quantity of dinosaurs about which we do not know due to the incompleteness of the paleontological record.

During the study of predator-prey relationships, more than 10 models have been proposed which attempt to predict and explain the population dynamics of predator and prey. Among them there is one of the most famous but already outdated Lotka-Voltaire model (Trubetskov, 2011), as well as alternative models of Gause-Kolmogorov, Arditi-Hinzburg (Tyutyunov, Titova, 2018) and others. However, all of these models were created to describe population dynamics in real time and are not designed to reveal the relationship between predator and herbivore species of dinosaurs over millions of years. Therefore, the authors used the ideas of these models for a preliminary attempt to estimate species diversity.

Results

Numerical characteristics of species diversity are important for statistical processing of data on the development of the superorder *Dinosauria* and for understanding the features of extinction of this superorder.

Thirty-four dinosaur families, 165 genera, and 252 species of 782 species that existed during the Cretaceous period survived to the last century of the Cretaceous, including 104 species estimated (J. Le Loeuff, 2012) that disappeared at the Cretaceous-Paleogene boundary. Thus, for the Late Triassic extinction, data show 11 families and 18 genera, 54 species out of 133 species that inhabited the Triassic, for the Jurassic 23 families, 62 genera 131 species (Fig. 2, 3).

The species diversity of the Triassic was not so significant. From the appearance of the first dinosaurs to the Triassic extinction passed about 35–40 million years, according to studies (Brusatte, 2012) the exact moment of the separation of dinosaurs from dinosauromorphs is rather difficult to determine.

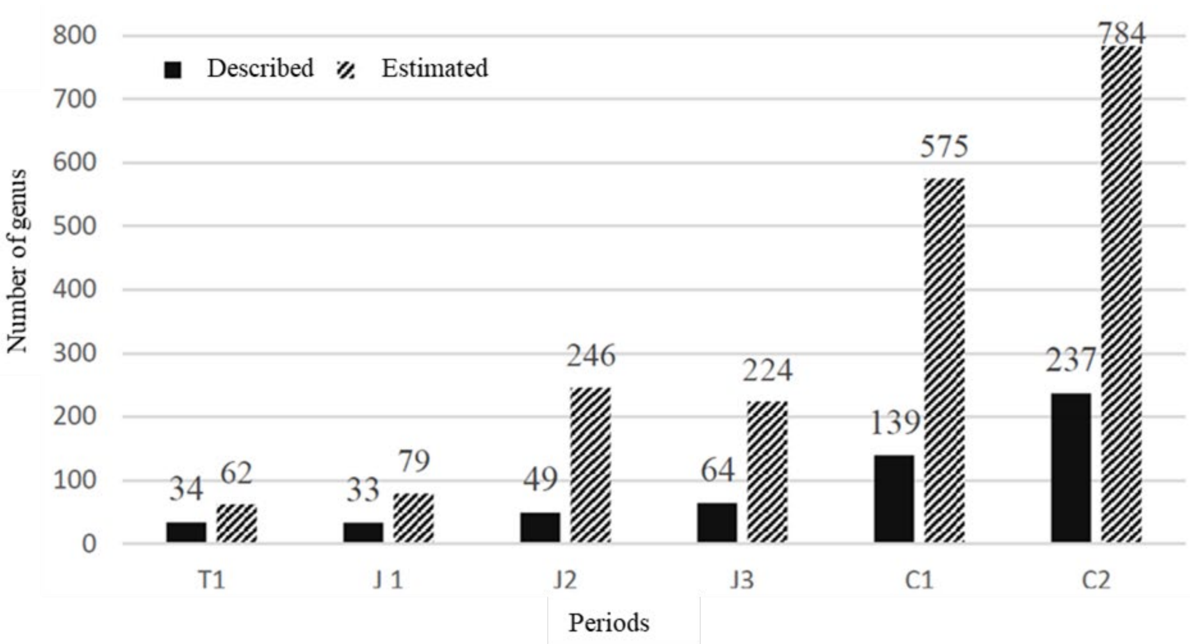

Fig. 2. Diversity at the level of genera during the Mesozoic Era

The Triassic-Jurassic biotic crisis provided an opportunity for dinosaurs to evolve, freeing up some ecological niches. From the Early Jurassic to the last centuries of the Late Cretaceous there was an increase of dinosaur biodiversity at all taxonomic levels.

Thus, dinosaurs reached their greatest flowering in terms of species diversity in the Late Cretaceous (Fig. 3). This thesis contradicts the opinion that by the end of the Cretaceous dinosaurs were in decline (Yeskov, 2020; Sarjeant and Currie, 2001) and an external impact (an asteroid according to Alvarez (Alvarez W. et al, 1982) or the outflow of Deccan traps (Keller et al, 2009) ended the ecosystem, already out of ecological balance.

It is possible to use the average lifespan of dinosaur genera to establish their probable distribution at the time of the biotic crisis. The total duration of the Maastrichtian age is estimated at 5.1 Ma (70.6–65.5 Ma) according to (Gradstein et al, 2008) the late Maastrichtian starts with the planktonic foraminifer zone SR4 68.3 Ma (Li at el, 1999), thus the total duration of the late Maastrichtian age is about 2.8 Ma. The average life span of the dinosaur genus calculated by Dodson (Dodson, 1990) is 7.7 Ma. Thus, the given data testify that dinosaurs were capable to survive this frontier that does not agree with the universal extinction of all 104 species by the beginning of the Danish century (it is estimated that there could be 628–1078 species surviving till the Late Maastrichtian) (Le Loeuff, 2012). Thus, Late Maastrichtian dinosaurs were able to survive the Cretaceous-Paleogene boundary, provided the ecological trends of the Late Cretaceous persisted.

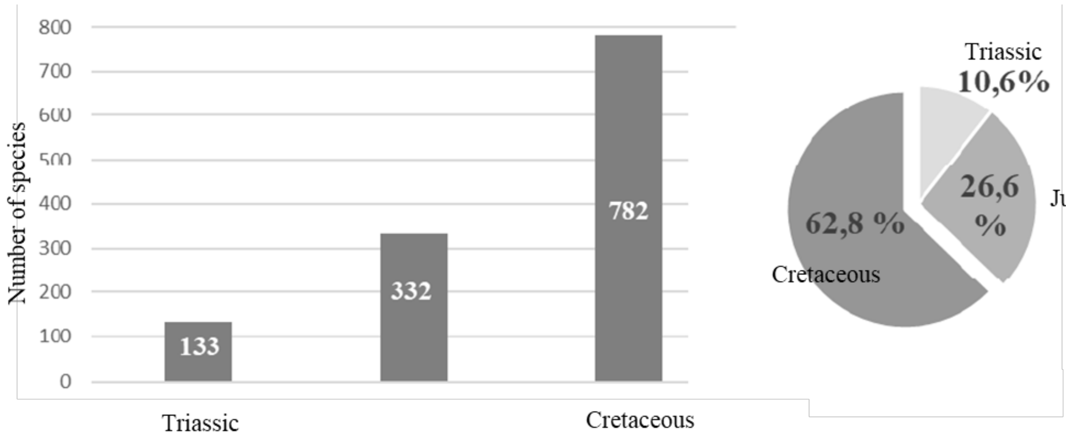

Fig. 3. Species diversity of dinosaurs and proportion of each period

To study the distribution of dinosaurs by type of feeding, a set of 1071 species for which the feeding pattern is known was used. The distribution of dinosaurs by the type of nutrition turns out to be the most contradictory and rather indicates the extreme incompleteness of the paleontological record (Fig.4).

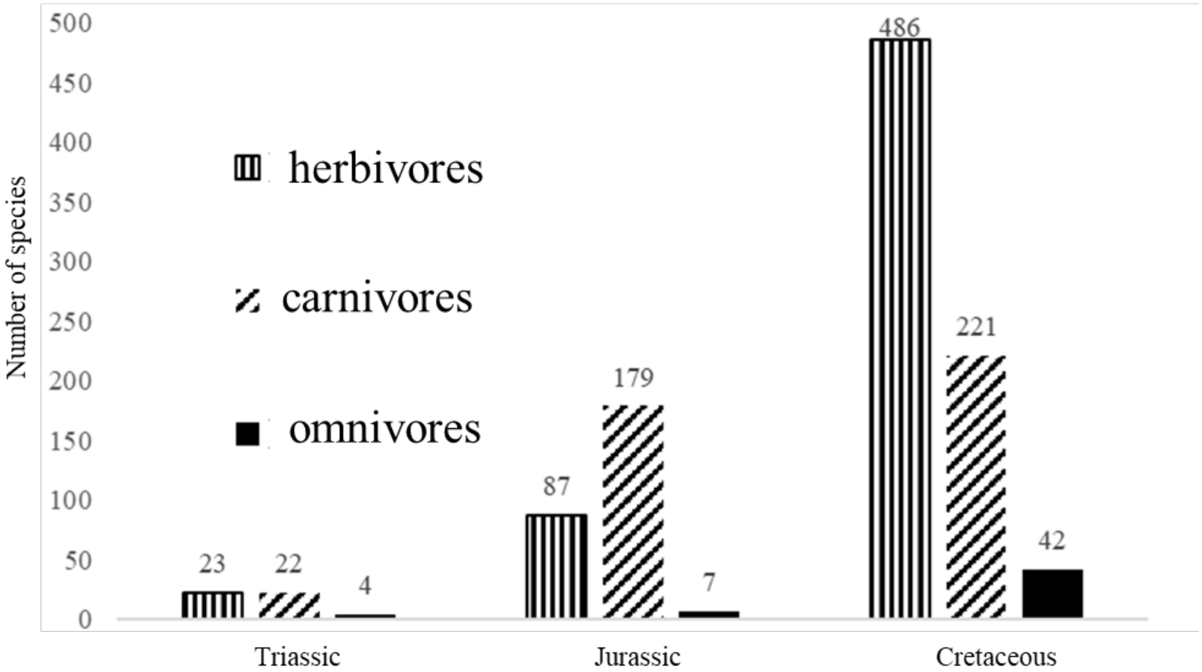

Fig 4. Species distribution of dinosaurs by type of feeding

Usually, when describing the ratio of biological mass of predators and herbivores, the rule of 10 % is resorted to, which says that no more than ten percent of the energy from the previous one is transferred to each successive trophic level. The remaining 90 % is spent on the vital processes of organisms and is dissipated in the form of thermal radiation. Predatory dinosaurs did not necessarily feed only on other dinosaurs. Their diet could include birds, mammals, and other reptiles. However, it is impossible to ignore the predominance of predatory dinosaurs over herbivores in the Jurassic period and the approximate equality between these categories in the Triassic. Even the predominance of herbivores over predators by more than a factor of two in the Cretaceous is insufficient in terms of the generally accepted ecological models. Such a relationship suggests that now we do not know more than one third of the dinosaur species, while their total number may exceed 3500 species.

Conclusions

At the present time, the hypothesis of sudden extinction of dinosaurs as a result of impact is widely accepted and this fact can be indirectly confirmed by the obtained data. Thus, we cannot speak about «casual» disappearance of some dinosaur species, as by the end of Cretaceous dinosaurs represented evolutionarily advanced and various group of organisms.

Obviously, the contemporary paleontological record is extremely incomplete. The ratio of herbivorous dinosaurs to all other dinosaurs has a clear shift towards predators, which is anomalous for the structure of modern ecosystems.

As a continuation of this work, it is necessary to further compare the rates of appearance of taxa and extinction of representatives of the superorder *Dinosauria* throughout all ages of the Mesozoic Era, as well as to construct a mathematical model of the distribution of dinosaurs on the surface of continents based on the density of their findings.

Acknowledgements

The publication is prepared for the project "Geochemical indication of paleoecological conditions of the Late Cretaceous biotic crisis based on the results of the study of Cretaceous-Paleogene geological sections", supported for the competition of implementation of promising fundamental research works by young scientists of the Herzen State Pedagogical University of Russia.

References

[1] Rosenzweig M. L. Species diversity in space and time. – Cambridge university press, 1995.

[2] Stanley S. M. Memoir 4: an analysis of the history of marine animal diversity //Paleobiology. – 2007. – V. 33. – No. S4. – P. 1-55. doi:10.1666/06020.1

[3] Benton, M. J. How to find a dinosaur, and the role of synonymy in biodiversity studies //Paleobiology. – 2008. – V. 34. – P. 516–533.

[4] Yeskov K. Y. The Great Extinction // Speech on the Postnauka Channel. URL: https://postnauka.ru/video/33782 (circulation date 15/11/2020).

[5] Upchurch P. et al. Phylogenetic and taxic perspectives on sauropod diversity. – 2005.

[6] Fastovsky D. E. et al. Shape of Mesozoic dinosaur richness //Geology. – 2004. – V. 32. – No. 10. – P. 877-880. doi:10.1130/0091-7613(2005)31<e75:R>2.0.CO;2

[7] Wang S. C., Dodson P. Estimating the diversity of dinosaurs //Proceedings of the National Academy of Sciences. – 2006. – V. 103. – No. 37. – P. 13601-13605. doi:10.1073/pnas.0606028103

[8] Lloyd G. T. et al. Dinosaurs and the Cretaceous terrestrial revolution //Proceedings of the Royal Society B: Biological Sciences. – 2008. – V. 275. – No. 1650. – P. 2483-2490.

[9] McGowan A. J., Smith A. B. Are global Phanerozoic marine diversity curves truly global? A study of the relationship between regional rock records and global Phanerozoic marine diversity //Paleobiology. – 2008. – V. 34. – No. 1. – P. 80-103.

[10] Dodson P. Counting dinosaurs: how many kinds were there? //Proceedings of the National Academy of Sciences. – 1990. – V. 87. – No. 19. – P. 7608-7612.

[11] Gradstein F. M., Ogg J. G., Van Kranendonk M. On the geologic time scale 2008 //News-letters on stratigraphy. – 2008. – V. 43. – No. 1. – P. 5-13.

[12] Fassett J. E., Heaman L. M., Simonetti A. Direct U-Pb dating of Cretaceous and Paleocene dinosaur bones, San Juan Basin, New Mexico //Geology. – 2011. – V. 39. – No. 2. – P. 159-162.

[13] Russell D. A. China and the lost worlds of the dinosaurian era //Historical Biology. – 1995. – V. 10. – No. 1. – P. 3-12.

[14] Dynamics of Dinosauria superorder biodiversity on different taxonomic levels / E. M. Nesterov, P. I. Egorov, A. E. Miroshkina, S. M. Zagashev // Geology, geoecology, evolutionary geography: a collective monograph / Ministry of Education of the Russian Federation, Russian State Pedagogical University named after A. I. Herzen. A. I. Herzen. Volume XIX. - Saint-Petersburg : Herzen State Pedagogical University of Russia., 2020. - P. 51-56. - EDN FTQAYV.

[15] The Dinosaur Genera List. URL: https://www.polychora.com/dinolist.html (circulation date 01.11.2022).

[16] Peters S. E., McClennen M. The Paleobiology Database application programming interface //Paleobiology. – 2016. – V. 42. – No. 1. – P. 1-7.

[17] Trubetskov D. I. The phenomenon of the mathematical model of Lotka-Volterra and similar models // Izvestiya vysokikh obrazovaniye. Applied Nonlinear Dynamics. – 2011. – V. 19. – No. 2. – P. 69-88.

[18] V. Tyutyunov, Yu. V. From Lotka-Volterra to Arditi Ginzburg: 90 years of evolution of trophic functions / Yu.V. Tyutyunov, L.I. Titova // Journal of General Biology. – 2018. – V. 79. – No. 6. – P. 428-448. – DOI 10.1134/S004445961806009X. – EDN VMAANI.

[19] Le Loeuff J. Paleobiogeography and biodiversity of Late Maastrichtian dinosaurs: how many dinosaur species went extinct at the Cretaceous-Tertiary boundary? //Bulletin de la So-ciéte Géologique de France. – 2012. – V. 183. – No. 6. – P. 547-559

[20] Brusatte S. L. Dinosaur paleobiology. – John Wiley & Sons, 2012.

[21] Sarjeant W. A. S., Currie P. J. The «Great Extinction» that never happened: the demise of the dinosaurs considered //Canadian Journal of Earth Sciences. – 2001. – V. 38. – No. 2. – P. 239-247.

[22] Alvarez W. et al. Iridium anomaly approximately synchronous with terminal Eocene extinctions //Science. – 1982. – V. 216. – No. 4548. – P. 886-888.

[23] Keller G., Sahni A., Bajpai S. Deccan volcanism, the KT mass extinction and dinosaurs //Journal of biosciences. – 2009. – V. 34. – No. 5. – P. 709-728.

[24] Li L., Keller G., Stinnesbeck W. The Late Campanian and Maastrichtian in northwestern Tunisia: palaeoenvironmental inferences from lithology, macrofauna and benthic foraminifera //Cretaceous Research. – 1999. – V. 20. – No. 2. – P. 231-252.