EVIDENCE THAT DURING THE PALEOCENE-EOCENE THERMAL MAXIMUM PLESIADAPIFORM PRIMATES DID NOT FOLLOW THE LATITUDINAL DIVERSITY GRADIENT

Isabel-Yelena Andreev

ABSTRACT: A warming event occurred fifty-six million years ago, in the Paleogene, on the border of the Paleocene and Eocene, known as the Paleocene-Eocene Thermal Maximum. Many animals such as fish and insects suffered mass extinction, but primates increased in abundance and diversity. This study looks at whether there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene. A χ2 test was performed, with the latitudinal climate zone as the independent variable and the number of species of primates as the dependent variable. The results of this research are that the number of species of Plesiadapiform primates at higher latitudinal zones is significantly greater in the Eocene than in the Paleocene. The latitudinal diversity gradient (LDG) was lacking during the PETM, which allowed primates to migrate to higher latitudes because Earth's polar caps completely melted, and the tropical climate expanded far beyond the equatorial zone, meaning primates were able to migrate to higher latitudes through routes that would have previously been inaccessible because they were frozen and too cold.

Keywords: Plesiadapiform Primates, Paleocene-Eocene Thermal Maximum, Latitudinal Diversity Gradient (LDG), Diversity, Higher Latitudes, Global Warming.

Introduction

The climate on Earth has and is always changing. The planet becomes warmer or colder, the ocean levels change, the amount of precipitation in different regions around the world change, and the temperature of the water in the oceans also change. Scientists are aware of many large global warming and cooling events that have affected the entire planet. One of these sharp warming events occurred fifty-six million years ago, in the Paleogene, on the border of the Paleocene and Eocene. The average surface temperature of the Earth increased by five to eight degrees Celsius over several tens of thousands of years. This event is known as the Paleocene-Eocene Thermal Maximum (PETM) (McInerney, 2011). This climatic catastrophe led to the mass extinction of many classes of animals, such as fish (Zachos, 2005) and insects (Azevedo et al., 2019).

Earth's polar caps completely melted, and the tropics expanded far beyond the equatorial zones; therefore new species of primates spread to Asia, Europe, and North America all within a few thousand years (Bowen et al., 2002). Instead of following the latitudinal diversity gradient, primates migrated to higher latitudes through routes that would have previously been inaccessible because they were frozen over and too cold. As primates spread across the planet, they encountered less predators, more habitats to explore, and abundant food supplies, which led to the formation of tribes, groups, and then communities within species (Sluijs et al., 2007). These factors encouraged primates to socialize with each other, which ultimately led to new species of primates appearing all over the planet.

Primates, however, instead of becoming extinct, went through evolutionary and geographic changes, and adapted to the rapid increase of Earth's surface temperature by moving towards the poles, opening up new opportunities for primates to diversify.

This research paper specifically focuses on a subgroup of primates, called Plesiadapiform; these animals are precursors to other primates and mammals that originated and evolved during the Paleocene-Eocene Thermal Maximum. They adapted to being terrestrial herbivores. Even though their fossil record is limited, they are the first subgroup of primates whose geographical occurrence is unusual because their fossils have been found at higher latitudes, such as in Europe and North America (Bloch, et al., 2007).

In this paper, the hypothesis tested was whether there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene. I predicted that there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene because the latitudinal diversity gradient was lacking during the Paleocene-Eocene Thermal Maximum, so Plesiadapiform primates were able to migrate to higher latitudinal zones.

Materials and Methods

Data on the number of species of primates alive in the Paleocene and Eocene were downloaded from the Paleobiology Database on October 15, 2021 (https://paleobiodb.org) and exported as a Microsoft Excel file. The data was restricted to the Paleocene and Eocene period, restricted to the order of primates and further restricted to the family of Plesiadapiform and its genera. The geographic information included the minimum and maximum latitude at which the fossils of the genera were found. The data was reorganized, and a pivot table was created to display the genera name, minimum paleolatitude, maximum paleolatitude, and the climate zone. Furthermore, the minimum and maximum latitudes were categorized into six climate zones: tropical, temperate, polar, temperate, and polar, tropical, and temperate, and lastly, all three. The tropical zone had a latitudinal range of -23° S to 23° N. The temperate zone had a latitudinal range of -23° S to -60° S and 23° N to 60° N. The polar zone had a latitudinal range of -61° S to -90° S and 61° N to 90° N. The 'tropical and temperate' and 'all three' categories were omitted from statistical analysis and the graph because there were no species of primates' fossils found in those zones.

The attached Microsoft Excel spreadsheet shows the setup of the table used in statistical analysis. A $\chi 2$ test was performed in Microsoft Excel 2019 with a significance level of $\alpha = 0.05$ (since this test is not high-risk), using latitudinal climate zone as the independent variable and the number of species of primates as the dependent variable to determine whether there is a significant difference in the number of species of primates at higher latitudinal zones in the Eocene than in the Paleocene. I predicted a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene due to the lack of latitudinal diversity gradient during the Paleocene-Eocene Thermal Maximum, so Plesiadapiform primates were able to migrate to higher latitudinal zones. My null hypothesis was that there is no significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene.

Results

A $\chi 2$ test was performed to determine whether there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene. Findings show that there is a significant difference in the frequency of species of primates at higher latitudinal zones in the Eocene than in the Paleocene, which indicates that the *latitudinal diversity* gradient

was lacking during the Paleocene-Eocene Thermal Maximum (Figure 1). The probability of getting these results by random chance of the statistical null hypothesis - that there is no significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene - is only 2.62 x 10-32; therefore, I reject my null hypothesis and accept my alternative hypothesis; there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene. The distribution of species of Plesiadapiform primates is statistically different in the Eocene than in the Paleocene.

Discussion

Based on the results of the $\chi 2$ test, the research hypothesis is accepted; there is a significant difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene. Figure 1 and the p-value from the $\chi 2$ test illustrates that the number of species of Plesiadapiform primates in the tropical and temperate climate zones is significantly higher in the Eocene than in the Paleocene.

Absence of the Latitudinal Diversity Gradient (LDG) During the Paleocene-Eocene Thermal Maximum

During the Paleocene, there was only one species of Plesiadapiform primates in the tropical zone and thirty-three species of Plesiadapiform primates in the tropical zone during the Eocene. Similarly, during the Paleocene there were only twenty-three species of Plesiadapiform primates in the temperate zone and 117 species of Plesiadapiform primates in the temperate zone in the Eocene.

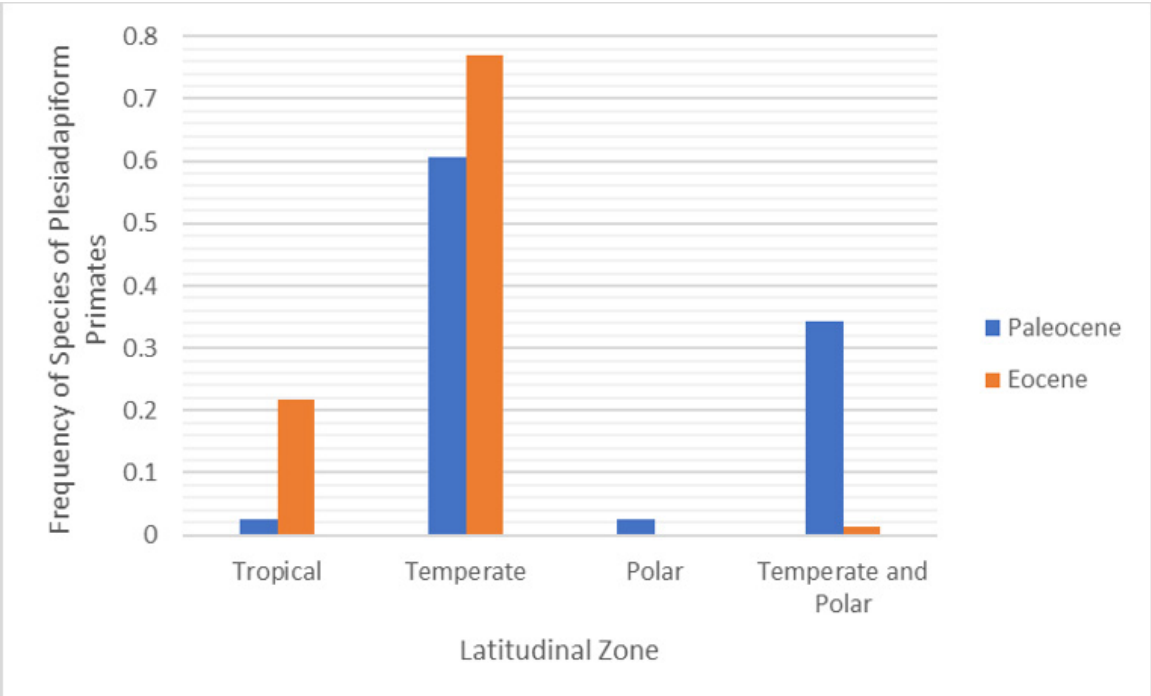

Figure 1:
The frequency of species of Plesiadapiform primates at higher latitudinal zones is significantly greater in the Eocene than in the Paleocene. After performing the $\chi 2$ test, the results indicate that the latitudinal diversity gradient (LDG) was lacking during the Paleocene-Eocene Thermal Maximum (as indicated by a p-value of 2.62 x 10-32 with a significance level of $\alpha = 0.05$).

Since these results indicate that there is a difference in the number of species of Plesiadapiform primates at higher latitudinal zones in the Eocene than in the Paleocene, it is presumed that the latitudinal diversity gradient (LDG) was lacking during the Paleocene-Eocene Thermal Maximum. This allowed Plesiadapiform primates to migrate to higher latitudes because Earth's polar caps completely melted, and the tropical climate expanded far beyond the equatorial zone. A more thorough analysis using the oxygen isotope composition of primate bones from the Paleocene and Eocene showed that the LDG was flat, indicating the LDG was shallow during the warming intervals on Earth (Rose et al., 2011). These results are consistent and in agreement with my results, indicating that Plesiadapiform primates migrated to higher latitudes through routes that would have previously been inaccessible because they were frozen and too cold.

Tropical & Temperate and Polar Latitudinal Zones

I would like to zoom in on a specific set of data points in the 'polar' and 'tropical and temperate' categories because the results were opposite of what I expected. During the Paleocene, there was only one species of Plesiadapiform primates in the polar zone and zero species of Plesiadapiform primates in the polar zone during the Eocene. Similarly, during the Paleocene there were thirteen species of Plesiadapiform primates in the temperate and polar zone and two species of Plesiadapiform primates in the temperate and polar zone in the Eocene. A possible explanation for these results is perhaps the geographic changes of Plesiadapiform primates were small and did not favor the migration of primates to higher latitudes during the Paleocene-Eocene Thermal Maximum, meaning primates simply went extinct because they were unable to adapt to the increase in Earth's temperature (Soligo, 2007).

Migration Patterns of Primates during the Paleocene-Eocene Thermal Maximum

However, I disagree with this explanation because instead of becoming extinct during the Paleocene-Eocene Thermal Maximum, primates (including Plesiadapiform primates) went through evolutionary and geographic changes and adapted to the rapid increase of Earth's surface temperature by moving towards the poles, opening up new opportunities for primates to diversify. Ancestors of new species of primates such as Hyaenodontids in Mongolia and Perissodactyl in Bayan Ulan (Bowen et al., 2002) originated in the tropics and the new species were found in Asia, Europe, and North America all within a few thousand years. It makes sense that primates from the Eocene were discovered in Asia, Europe, and North America due to the temperate zone having a latitudinal range of -23° S to -60° S and 23° N to 60° N and Asia, Europe, and North America are within that range. Primates (including Plesiadapiform primates) were able to move between continents on land bridges at high latitudes, which only became accessible during the Paleocene-Eocene Thermal Maximum (Sluijs et al). The rapid increase of Earth's surface temperature allowed primates to migrate to higher latitudes through routes that would have previously been inaccessible because they were frozen and too cold, thus indicating that the number of species of primates would be higher at higher latitudes. My results are consistent with the findings mentioned above: during the Paleocene there were only twenty-three species of Plesiadapiform primates in the temperate zone and 117 species of Plesiadapiform primates in the temperate zone during the Eocene.

Unusual Geographical Occurrence of the *Teilhardina*

As I was conducting my research on the Paleocene-Eocene Thermal Maximum and the latitudinal diversity gradient (LDG), I came across a general scientific problem that paleobiologists and other scientists have been

unable to agree upon. Paleobiologists and other scientists have been studying the *Teilhardina* genus, the first known primate, for an exceedingly long time, but they cannot come to an agreement on why species in the *Teilhardina* genus originated in and spread to various locations around the world during the Paleocene-Eocene Thermal Maximum. Currently, four hypotheses have been proposed to explain the distribution of the *Teilhardina* genus during the Paleocene-Eocene Thermal Maximum, which included continents such as Africa, Asia, Europe, and North America (Beard, 2008). By researching my research question, I potentially produced a different explanation on how the *Teilhardina* genus dispersed to higher latitudes, resulting in an increase in their abundance and diversity.

During the Paleocene-Eocene Thermal Maximum, tons of carbon were released from locations around the world previously cold and frozen, which resulted in the surface temperature of the Earth to rapidly increase. This event led to a significant drop in sea levels around the world, thus creating accessible land bridges between continents that were previously inaccessible, since they were frozen over. Therefore, the *Teilhardina* genus could have originated in the tropics and then spread to Asia, Africa, Europe, and North America. However, carbon isotope composition analysis of teeth from the *Teilhardina* genus revealed that species in North America had fewer evolved features than those of species in Belgium (Marris, 2008). These findings indicate that North America was the last migration stop for species within the *Teilhardina* genus. These primates could have originated in the tropics and then dispersed to Africa, Asia, Europe, and finally to North America on high-latitude land bridges.

Limitations and Future Work

Bias may have occurred in this research when restricting the data to the order of primates, and further restricting to the subgroup Plesiadapiform and its genera because the dataset for all primates was too large and advanced for this research. The geographic information included the minimum and maximum latitude at which the fossils of the genera were found, but not anywhere between the minimum and maximum latitude. It could be possible that the Plesiadapiform primate fossils found at the minimum or maximum latitude were outliers, and the majority of fossils were saturated somewhere in-between. Future studies should take into account more than just latitude for considering the difference in the number of species of Plesiadapiform primates in the Paleocene and Eocene. Further, future studies should analyze the number of species of Plesiadapiform primates at different latitudes and their body size to see if there is any correlation between latitudinal location and body size.

Acknowledgments

I would like to thank my professor, Dr. Price, for helping and navigating me through the course of this research, from helping format the data needed to test my hypothesis to providing thoughtful feedback on all assignments leading up to this research paper. I would also like to thank my classmates for peer reviewing this paper and providing valuable feedback.

References

Azevedo Schmidt LE, Dunn RE, Mercer J, Dechesne M, Currano ED. 2019. Plant and insect herbivore community variation across the Paleocene-Eocene boundary in the Hanna Basin, southeastern Wyoming. PeerJ. 7(e7798): e7798. DOI:10.7717/peerj.7798

Beard KC. 2008. The oldest North American primate and mammalian biogeography during the Paleocene-Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences of the United States of America.* 105(10):3815–3818. DOI:10.1073/pnas.0710180105

Bloch JI, Silcox MT, Boyer DM, Sargis EJ. 2007. New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proceedings of the National Academy of Sciences of the United States of America*. 104(4):1159–1164. DOI: 10.1073/pnas.0610579104

Bowen GJ, Clyde WC, Koch PL, Ting S, Alroy J, Tsubamoto T, Wang Y, Wang Y. 2002. Mammalian dispersal at the Paleocene/Eocene boundary. *Science* (New York, N.Y.). 295(5562):2062–2065. DOI:10.1126/science.1068700

Marris E. 2008. How primates crossed continents. *Nature*. DOI:10.1038/news.2008.637

McInerney FA, Wing SL. 2011. The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual review of earth and planetary sciences*. 39(1):489–516 DOI: 10.1146/annurev-earth-040610-133431

Rose PJ, Fox DL, Marcot J, Badgley C. 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology*. 39(2):163–166. DOI:10.1130/g31099.1

Sluijs A, Bowen GJ, Brinkhuis H, Lourens LJ, Thomas E. 2018. The Palaeocene–Eocene Thermal Maximum super greenhouse: biotic and geochemical signatures, age models and mechanisms of global change. In: Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies. T*he Geological Society of London on behalf of The Micropalaeontological Society*. p. 323–349. DOI: 10.1144/tms002.15

Soligo C. 2007. Invading Europe: did climate or geography trigger early Eocene primate dispersals? Folia primatologica; *International Journal of Primatology*. 78(5–6):297–313. DOI: 10.1159/000105146

Zachos JC, Röhl U, Schellenberg SA, Sluijs A, Hodell DA, Kelly DC, Thomas E, Nicolo M, Raffi I, Lourens LJ, et al. 2005. Rapid acidification of the ocean during the Paleocene-Eocene thermal maximum. *Science* (New York, N.Y.).308(5728):1611–1615. DOI:10.1126/science.1109004