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„Jurassic and Cretaceous diversity patterns of European dinosaurs“

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DANKSAGUNG

Die Fertigstellung dieser Arbeit dauerte länger als geplant und wurde durch viele private Krisen überschattet, umso erfreuter bin ich, diese nun vollendet zu haben. Dafür bedanke ich mich besonders bei meinem Betreuer Jürgen Kriwet welcher mich zu keinem Zeitpunkt unter zusätzlichen Druck setzte und geduldig an mir und meinem Thema festhielt und mir die besondere Chance gab, an meiner Leidenschaft für Archosaurier festzuhalten und diese vertiefen zu können. Ein weiterer wichtiger Faktor waren meine Studienkollegen, welche mich immer wieder motivierten, wenn es mal nicht so gut lief und mir mit Hilfe zur Seite standen. Außerdem bedanke ich mich bei meiner Familie und meinen Freunden, die mich auf diesem Weg begleiteten und immer bedingungslos unterstützten. Mein großer Dank gilt der Republik Österreich, welche mir in Form der Studienbeihilfenbehörde Wien, die finanziellen Möglichkeiten für dieses Studium gewährte.

In Gedenken an Jonathan Peter Tennant (06.05.1988 – 09.04.2020) der viel zu früh auf tragische Art verstarb und sich als einer der Ersten, speziell mit den Themen beschäftigte, die auch diese Arbeit beeinflussten.

ABSTRACT

English

Though diversity studies of the deep time are among the most discussed topics in palaeobiology, they are also confronted with major challenges. Although the beginnings of this field of research, as well as the first valid description of a dinosaur, are in Europe, the history of this group, on the continent has been little extensively studied. In particular, the Jurassic-Cretaceous transition is one of the least understood events in vertebrate palaeontology. Based on a comprehensive species database, palaeoenvironmental data, and specially adapted statistical methods, this work aims to contribute further insights into important developmental tendencies. Using recent studies and calculation analyses, the existing fossil record of the continent was compared with data on a global scale aiming at better understanding of faunal shifts and evaluating Cretaceous evolutionary patterns. In this thesis, for the first time, the course of European dinosaurs from the Tithonian to Berriasian across the Jurassic-Cretaceous boundary was studied in detail, which revealed a sharp decline in nearly all clades within a short period of time. Faunal analyses reveal major changes in palaeocommunity composition and indicate climatically induced adaptive trends. While the results of this work do not show a general long-term decrease in the diversity of European dinosaurs prior to the asteroid impact, they do suggest a state of structural instability that favoured vulnerability to extinction in the Maastrichtian.

Deutsch

Diversitätsstudien der Vergangenheit gehören zu den zentralsten Themen aber auch größten Herausforderungen in der Paläobiologie. Obwohl die Anfänge des Forschungszweiges, als auch die erste gültige Beschreibung eines Dinosauriers in Europa liegen, wurde die Entwicklung dieser Gruppe, auf dem Kontinent bisher wenig umfassend untersucht. Besonders der Jura-Kreidezeit Übergang ist eines der am wenigsten verstandenen Ereignisse in der Wirbeltierpaläontologie. Basierend auf einer umfassenden Artendatenbank, Paläoumweltdaten und speziell angepassten statistischen Methoden, soll diese Arbeit weitere Erkenntnisse zu wichtigen evolutionären Tendenzen beitragen. Mittels aktueller Studien und Kalkulationsanalysen wurde der vorhandene Fossilbericht des Kontinents mit Daten auf globaler Ebene verglichen, um Faunenumschwünge sichtbarer zu machen und die Entwicklungsmuster der Kreidezeit bewerten zu können. Zum ersten Mal wurde der Verlauf europäischer Dinosaurier am Übergang vom Tithonium zum Berriasium eingehend untersucht und zeigte einen starken Rückgang bei fast allen Kladen innerhalb kurzer Zeit. Faunenanalysen zeigen große Veränderungen in der Zusammensetzung der Paläogemeinschaften und weißen auf klimatisch induzierte Anpassungstrends hin. Die Ergebnisse dieser Arbeit zeigen zwar keinen allgemeinen Langzeit Rückgang der Diversität europäischer Dinosaurier vor dem Asteroideneinschlag aber lassen einen Zustand der strukturellen Instabilität erkennen, welcher die Anfälligkeit zum Aussterben im Maastrichtium begünstigte.

CONTENTS

INTRODUCTION

Research questions

The extinction event at the end of the Cretaceous is one of the best researched, many diversity studies focus on the sudden global extinction of non-avian dinosaurs at the end of the Maastrichtian and continuously more are being added (Brusatte et al., 2012, Chiarenza et al., 2020). The fascination and knowledge of what caused such a successful terrestrial vertebrate group to suddenly disappear after more than 160 million years of dominance is an important component to understanding other mass extinctions and important features of resilience as well as its effect on ecosystems (Marsicano et al., 2016). However, the transition from the Jurassic to the Cretaceous is among the least understood faunal changes in this regard (Tennant et al., 2017). For instance, extinction events from this time period previously were documented in marine and other terrestrial vertebrates, but aside from a few publications, little attention has been given to dinosaurs during this time, even though important environmental changes occurred (Tennant et al., 2017). Building on my bachelor's thesis from 2020, which included an investigation of the diversity of Jurassic theropods, the aim of this study is to provide for the first time a detailed picture, of the Jurassic and Cretaceous period of the European continent and its dinosaur fauna. Special attention will be given to the J/K transition, the features before the Cretaceous extinction event and diverse faunal communities. Specifically, the following research questions should be answered:

- Did an extinction event occur in European dinosaurs at the transition from the Jurassic to the Cretaceous?

- What are the evolutionary patterns between the global and European dinosaur faunas of the Jurassic and Cretaceous?

- Was the diversity of European dinosaurs already in decline before the mass extinction at the end of the Cretaceous?

Phylogenetic overview

To visualize evolutionary trends, a clear structuring of the investigated palaeobiodiversity is indispensable. Phylogenetic trees and family divisions of taxa are usually subject to constant change, each new finding like a piece of a puzzle that sheds new light on the ancestral history of living organisms. The more deeply and in detail a view goes into the individual lineages, the more exact differential diagnostic characteristics are necessary, in order to classify species, which can lead again to an increase of possible errors. To minimize artificial man-made classification errors, in this study, subdivisions into deep internal systematics were avoided and emphasis was placed on more stable clades. Since no more basal mixed forms of dinosaurs, which could be assigned to none of the large groups clearly had been existed in the observed period of the Jurassic and Cretaceous of Europe, no reference to these were taken in the following family tree (Figure 1).

For simplification, split groups which, could not be assigned to any of the major groups, or which have primitive characteristics, were defined as basal representatives (Coelophysoidea, Heterodontosauroidea). Birds, or avian-dinosaurs, belong to the clade Coelurosauria and have been excluded from most analyses, since their numerous appearance from the Cretaceous onwards significantly influences the course of diversity and can distort the underlying evolution of the non-avian dinosaurs (Benson & Choiniere, 2013). The genera *Alcmonavis*, *Archaeopteryx*, *Ostromia*, and *Wellnhoferia* from the Jurassic, were placed among the non-avian dinosaurs (if not otherwise noted) because they still share many characteristics with them (Xu et al., 2011, Lee & Worthy, 2012). A more detailed explanation can be found in the material and methods section. Contrary to the current scientific trend, information from the paleobiology database (PBDB) was not used to create the dataset. This was done to avoid errors in taxa identifications, systematic assignments, and inaccurate geographic as well as temporal distributions (Prothero, 2015).

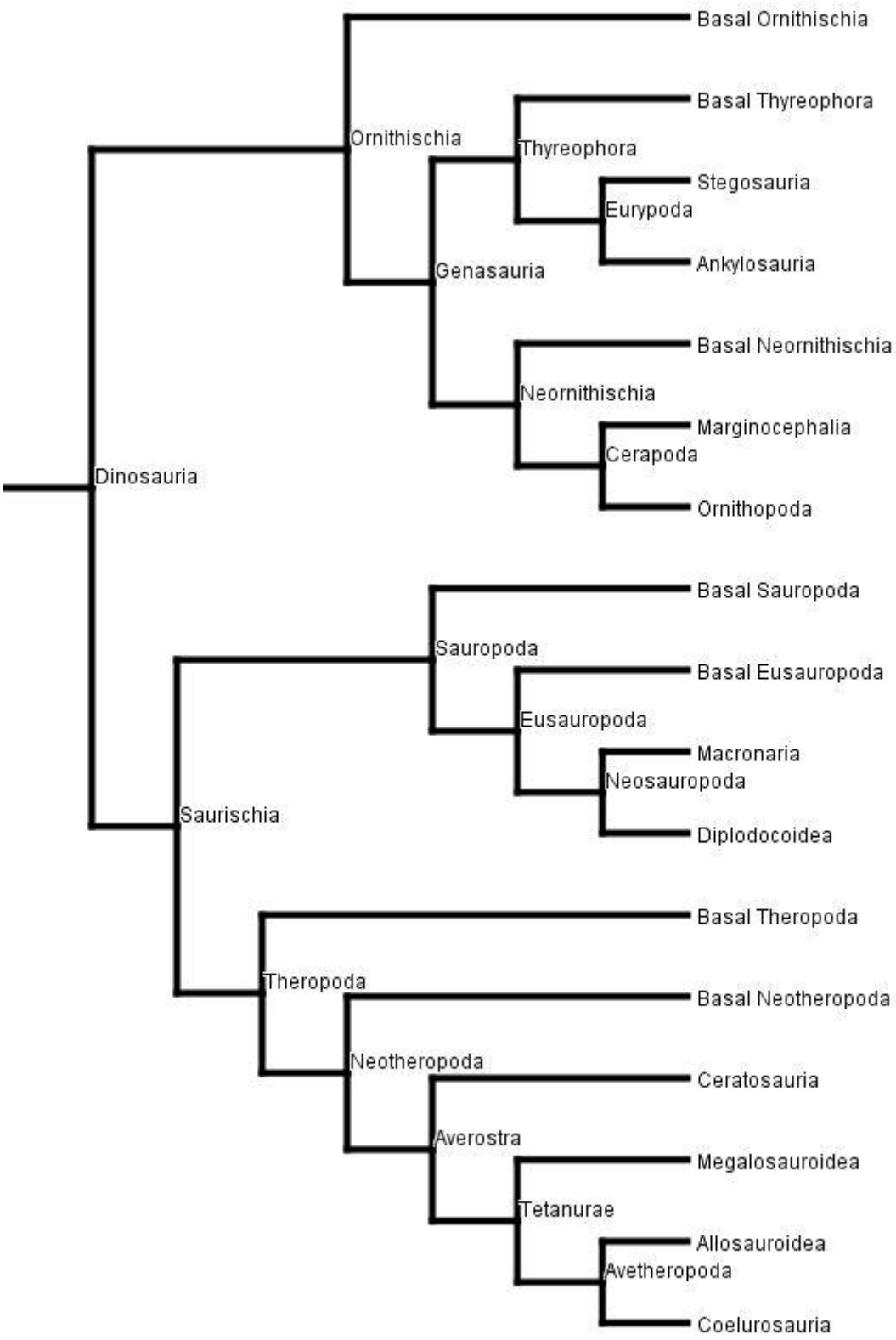

Figure 1: Highly simplified phylogenetic tree of the Jurassic and Cretaceous dinosaurs of Europe with all relevant clades discussed in this work (Modified after: Weishampel et al., 2004, Hendrickx et al., 2015, Madzia et al., 2021).

Jurassic World

The world of the Mesozoic was characterized by great changes in palaeogeography which had enormous effects on the palaeoclimate and are hard to imagine today (Holz, 2015). From greenhouse conditions to hothouse conditions and temperatures which are on average 6-9°C higher than the current ones. The sea level worldwide was much higher, the oxygen content in the atmosphere varied between 15-25% and the CO_2 concentration reached values that exceed those of nowadays up to 16 times (Holz, 2015). These different (often fast changing) environmental conditions required a high adaptability from organisms during past geological eras. These adaptations were evident in some theropods as well as ornithischians in the expression of feathering in various forms ranging from monofilaments to true feathers, which may have been genetically predisposed in all archosaurs and originally served as thermal insulation (Benton et al., 2019). Godefroit et al. (2020) discovered that feather-like structures occurred not only in ornithischians of the Late Jurassic and Early Cretaceous of China, but also in the Middle Jurassic *Kulindadromeus zabaikalicus*, a basal neornithischian from Siberia, which had scales as well as different filamentous structures distributed over its body. Giant animals such as the sauropods apparently developed physiological mechanisms that cooled their body temperature despite their excessive body mass (Eagle et al., 2011).

The Jurassic is defined as the middle period of the Mesozoic and lasts approximately from 201 to 145 Ma, and is already chronostratigraphically defined by GSSP's except for the Bathonian/Callovian/Oxfordian and Kimmeridgian/Tithonian transitions (ICS, 2022). The period was particularly characterized by a persistent rise (with large fluctuations) in sea level (Figure 2). In addition, the largest radiation of dinosaurs took place, including the origin of birds (Holz, 2015). Climate datasets are often based on isotopic measurements of marine shelled organism and therefore provide only limited information about terrestrial climates on a regional scale. By reconstructing the distribution of Jurassic fossil wood genera, direct terrestrial climate changes in Europe could possibly be determined. Accordingly, during the Early and Late Pliensbachian, Early Toarcian, and Early Middle Oxfordian, there may have been a strong cooling or strong increase in precipitation that favored a geographic expansion of northern genera (Philippe et al., 2017).

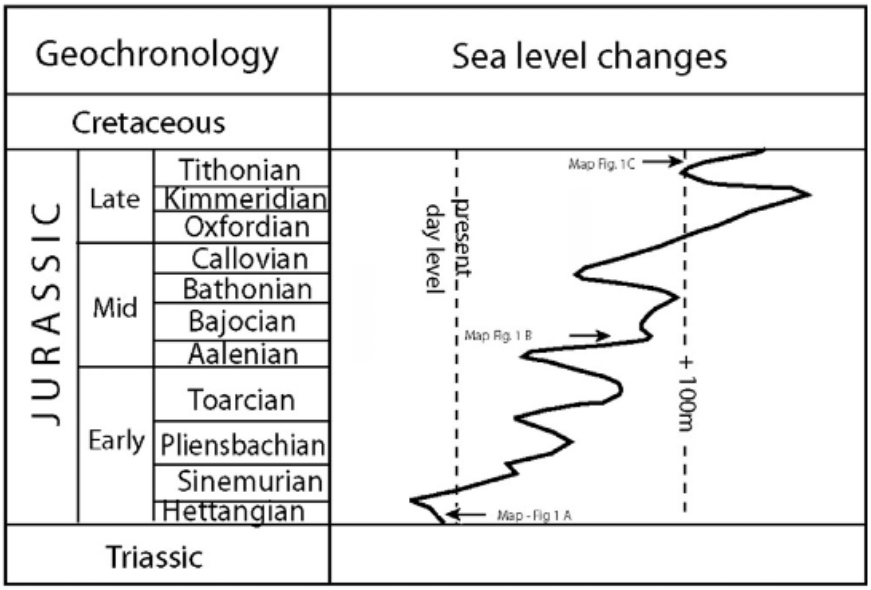

Figure 2: The rising trend of sea level peaked in the Late Jurassic but was characterized by strong fluctuations over the period (From: Holz, 2015).

These environmental factors had a direct impact on dinosaur evolution. Dunne et al. (2023) found that early sauropodamorphs lived geographically in cooler regions during the Late Triassic and Early Jurassic, but shifted to warmer locations during the Early Jurassic prior to sauropod evolution. Therefore, climatic changes favored the global distribution of sauropods, which preferred living conditions in geographically warmer areas. Rauhut et al. (2016) postulated that there was evidence of a faunal turnover in theropods from the Middle to Late Jurassic. Accordingly, the Middle Jurassic fauna dominated by Megalosauroidea was displaced by Coelurosauria among the smaller carnivores and by Allosauroidea among the large carnivores in the Late Jurassic (Figure 3). However, there appears to be an environmental preference of allosauroids for inland and megalosauroids for coastal environments. Within my bachelor thesis (2020), based on a recent dataset, I was able to partially verify the findings of Rauhut et al. (2016). The megalosauroids of the Middle Jurassic were strongly displaced by the coelurosaurs, among the large carnivores there was an approximate balance between the presence of megalosauroids and allosauroids (Figure 4).

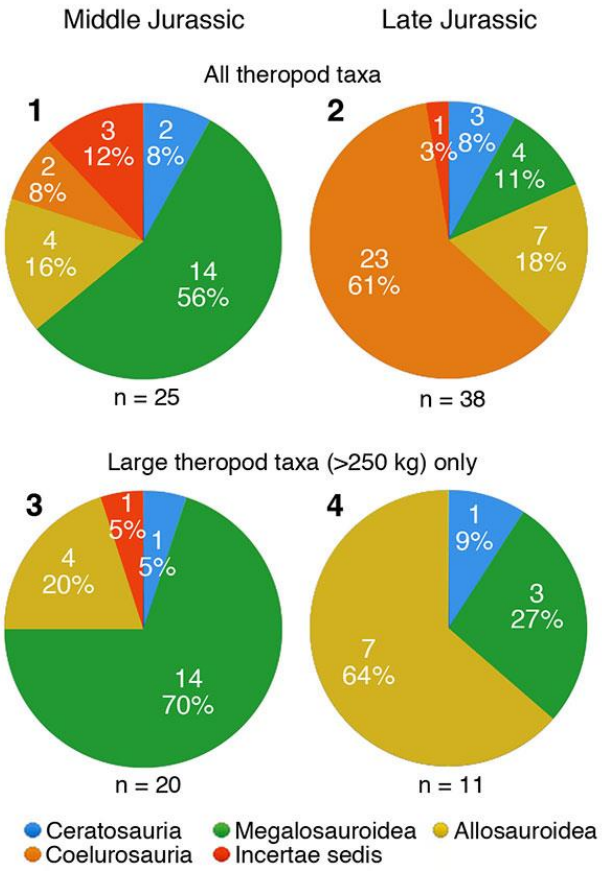

Figure 3: Changes in theropod clade composition from Middle to Late Jurassic (From: Rauhut et al., 2016).

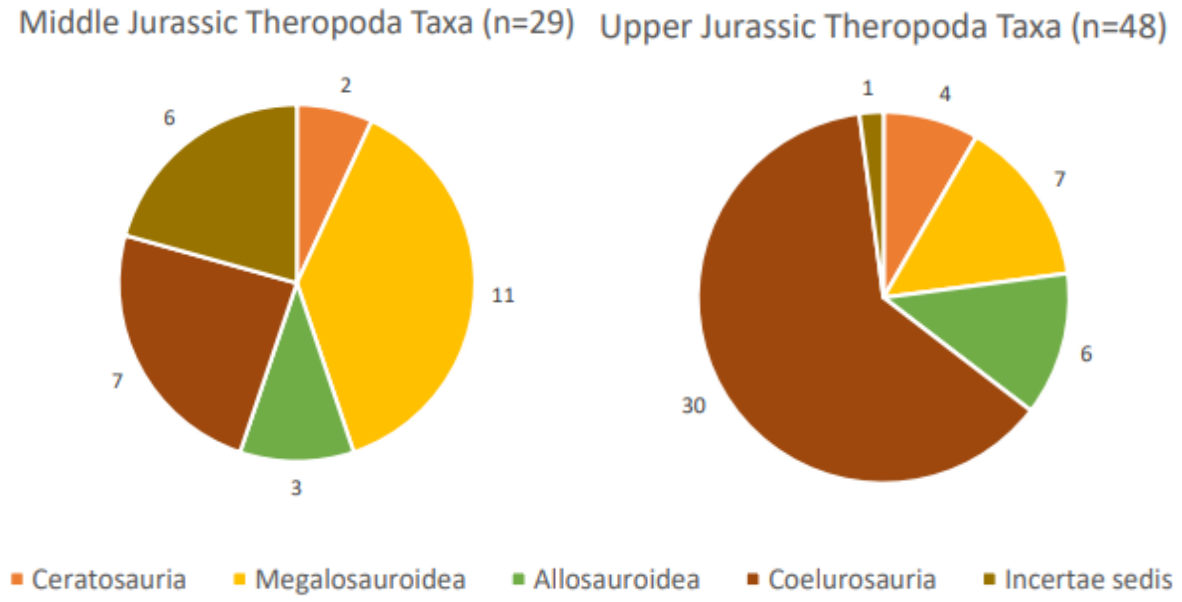

Figure 4: Changes in theropod clade composition from Middle to Upper Jurassic (From: Etzler, 2020).

Jurassic-Cretaceous transition

Although not a mass extinction by definition, the Jurassic-Cretaceous boundary appears to have been a major transformation for both terrestrial and marine ecosystems. Many groups disappeared at this time and new ones appeared, which are still represented today. The Late Jurassic and Early Cretaceous are characterized by enormous environmental disturbances (Tennant et al., 2016b). Probably affected by several asteroid impacts, large-scale tectonic processes, climate fluctuations from a greenhouse world that was interrupted by cold snaps and conditional dry periods. Eustatic sea level declined sharply, presumably leading to anoxic conditions and increased sulfur toxicity at the transition from the Tithonian to the Berriasian (Tennant et al., 2017). These environmental changes are evident in almost all tetrapod groups in form of taxonomic restructuring (Tennant et al., 2016b). Among the dinosaurs these are particularly visible, for example the diversity of sauropods decreased already before the J/K boundary, while the ornithischians were affected to an extent of about 33% and the theropods even by 75-80% only directly at the transition (Tennant et al., 2016b). Other groups, such as birds, lissamphibians, and also semiaquatic turtles, however, were able to diversify (Tennant et al., 2016b).

Furthermore, it was shown that especially due to strong sea level fluctuations, both marine and terrestrial crocodyliforms at the J/K boundary experienced a strong collapse in their palaeobiodiversity (especially in Europe) that can almost be described as a mass extinction (Tennant et al., 2016a). In contrast, the influence of palaeotemperature is unlikely to have been an influential factor (Tennant et al., 2016a).

At the transition from Tithonian to the Berriasian, there are signs of impact events, among them, a crater in Mjølnir, Norway, with a diameter of about 40 km, caused by an oblique impact (Dypvik et al., 2010). The Morokweng impact (South Africa), with a diameter of about 80 km, was geochronologically determined to be 146 million years old, predating the J/K boundary (Kenny et al., 2021). The definite chronostratigraphic boundary between the Jurassic and Cretaceous has not yet been defined by a GSSP (ICS, 2022).

Cretaceous World

The Cretaceous is the third and final period of the Mesozoic and lasted from about 145-66 Ma. The Early Cretaceous is not exactly defined yet, but the Late Cretaceous has GSSP's everywhere except for the Santonian/Campanian boundary (ICS, 2022). Also, during the Cretaceous, sea levels were much higher than today (Figure 5) and temperatures varied widely, especially toward the end (Holz, 2015). Most of Europe was in a warm-temperate climate zone during this period (Holz, 2015).

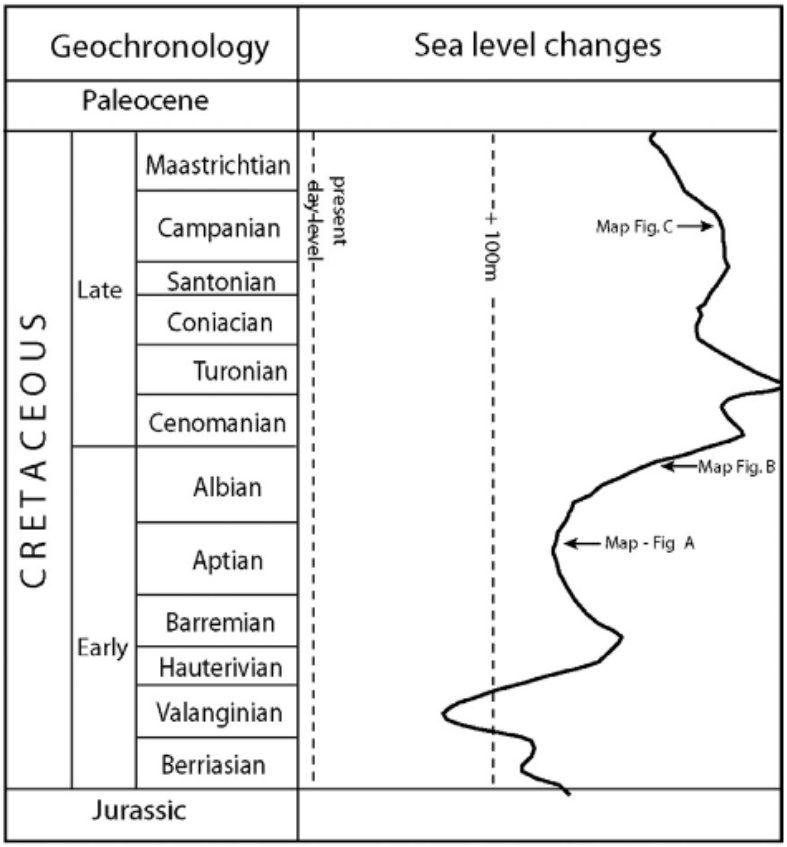

Figure 5: Sea level was rising for most of the Cretaceous period, reaching the highest peaks of the entire Mesozoic (From: Holz, 2015).

In Europe there were great changes in palaeogeography in the Late Cretaceous, which transformed the continent into an archipelago of islands through transgressions (Csiki-Sava et al., 2015). This makes of Europe a very special and difficult to understand continent during the Cretaceous, where there were many regional differences. But this special condition also led to an unique richness of different habitats, which indicate local endemism (Csiki-Sava et al., 2015). However, due to the particular palaeogeographic situation, there were repeated immigrants

from other continents, but these were not evenly distributed and resulted in a diverse mix of taxa, including relict species that survived longer in Europe than on other continents (Csiki-Sava et al., 2015).

This interplay of endemic partially isolated fauna and taxa, which were sometimes rare elsewhere in the world and clashed in Europe, also uniquely influenced the dinosaur evolution of the continent in the Late Cretaceous. Csiki-Sava et al. (2015) found no evidence of a gradual decline among European dinosaurs prior to the extinction at the end of the Cretaceous. However, it should be noted that the fossil record of Europe is characterized by inconsistent sampling and also by chronostratigraphic limitations.

From the Campanian to the Maastrichtian, a gradual change in the composition of the herbivorous dinosaur clades in southwestern Europe may have occurred due to sea level fluctuations, from a fauna dominated by sauropods, to one characterized by hadrosauroids (Fondevilla et al., 2019). Immigrant representatives of the Hadrosauroidea from North America, Eurasia, and Gondwana may have altered regional herbivore communities through a decline in sea level in a relatively short period of time and without major loss of biodiversity (Vila et al., 2016, Fondevilla et al., 2019). However, as early as the early Late Cretaceous, there is a so-called "sauropod hiatus" in North America and Europe, but this is likely due exclusively to sampling artifacts and is most likely due to a specific preference for inland habitats of titanosaurs for this time period (Mannion & Upchurch, 2011). The latitudinal biodiversity gradient (LBG) is unlikely to have played such a major role throughout the Mesozoic, as it does today (Mannion et al., 2012). There is no significant evidence that in the past the tropics served as a special place for dinosaur diversity and that this pattern was only consolidated on the mainland after the Eocene, conditioned by seasonality. Diversity was highest in the temperate palaeolatitudes and was particularly influenced by the distribution of land area in the Late Cretaceous (Mannion et al., 2012). The transition from the Cretaceous to the Paleogene marked the end of the long reign of dinosaurs, and birds, which are direct descendants of theropods, have been continued to populate the Earth until today. With about 9,700 species distributed on all continents, they are among the most successful vertebrates (Callaghan et al., 2021).

Extinction of non-avian dinosaurs

The impact of an asteroid in Chicxulub, can be counted today as the main cause of the sudden extinction of non-avian dinosaurs at the end of the Cretaceous. Although Deccan volcanism had already affected climate systems globally a few million years before the impact, a wide variety of modeling scenarios show no evidence that such negative results could have occurred (Chiarenza et al., 2020). Even for faunas in close proximity to the epicenter of the Deccan volcanism, there is no evidence of local mass extinctions (Chiarenza et al., 2020). In fact, it is likely that the Deccan volcanism softened the climatic and ecological consequences of the asteroid impact (Chiarenza et al., 2020). The importance of an objective look at palaeogeographical features shows the possible impact of the Deccan volcanism on southeast China, where a striking correlation was found between the amount of heavy metal anomalies and the decline of non-avian dinosaurs (Ma et al., 2022). Lerbekmo (2014) postulated that in addition to the known Chixculub impact with a crater diameter of about 180 km in Yucatan, Mexico, there was another impact in the southern Indian Ocean with a crater diameter of 450×600 km, called Shiva. This second impact occurred about 40,000 years later and indicates another catastrophe which occurred at the transition from the Cretaceous to the Paleogene.

Identifying the exact processes of extinctions is difficult, since only a few sites in the world provide accurate information about the last millions of years of the dinosaurs. Due to major fluctuations in sea level, temperature and increased volcanism, the Late Cretaceous period was characterized by changing environmental conditions (Wignall, 2001, Wilf et al., 2003, Miller et al., 2005). Despite these environmental changes, however, there is no global trend indicating a long-term decline of non-avian dinosaurs prior to the asteroid impact (Brusatte et al., 2015). The disappearance was abrupt by geological scales, and there is no evidence that long-term changes in sea level or temperature had a significant impact on the extinction (Brusatte et al., 2015).

Other approaches assume a gradual decline of dinosaurs in western Europe that started up to three million years before the great extinction and was carried out by magnetostratigraphic methods on egg shells preserved in situ (Galbrun, 1997). Sakamoto et al. (2016) also consider, based on statistical models, clear evidence of a decline in the rate of origin in all major groups of dinosaurs as early as about 10 Ma

before the mass extinction. As a result, they were no longer sufficiently resilient to crises. The only exception, according to the study, were specialized herbivores such as the Ceratopsidae and Hadrosauridae, whose new species emergence showed an increased origination rate throughout the Late Cretaceous. This could be due to global cooling of the climate during the Late Cretaceous, which resulted in extensive ecological changes and affected the diversity of herbivores (Condamine et al., 2021). The fact that this question is one of the most important and most discussed in palaeobiology and has not yet been clarified is shown, among others, by the work of Bonsor et al. (2020). According to this study, the phylogenetic methods currently used to capture the complexity of this question are not optimally suited as a test. Models that detect a negative trend in speciation rates of non-avian dinosaurs at the end of the Cretaceous, they argue, may have resulted from hierarchical sampling errors in the fossil record and the selection of inappropriate analytical methods. According to their results, diversity was not in a terminal stage and certainly still possessed the capacity for new taxa to evolve. Thus, the interpretation of these models, as well as the data set, are still highly controversial and continue to be the subject of research. Stanley (1979) described the theoretical macroevolution-derived accepted "Stanley Rule" that there is a positive correlation between rates of origin and extinction that applies to almost all taxa and geologic time periods. A rule, which could also have been valid for the dinosaurs.

Fossil record

In the end, the validity of such diversity analyses remains to be questioned, as they are almost always characterized by geological megabiases, especially in the terrestrial realm. Methods comparing estimated diversity from fossil-bearing strata with actual observable patterns showed that diversity curves of Theropoda as well as Ornithischia are sensitive to such geological factors (Barrett et al., 2009). Sauropodomorpha, on the other hand, appear to be more suitable as evidence for evolutionary patterns. These calculations also showed a decline in diversity millions of years before the mass extinction (Barrett et al., 2009). It is questionable how meaningful the popular example of North America as a model region actually is for answering this question. The commonly recognized diversity declines may not be a true biological signal, but may have been biased due to uneven geographic fossil

records. Areas in the Campanian, as an example, exhibit better taphonomic preservation than depositional environments in the Maastrichtian due to high sedimentation (Chiarenza et al., 2019).

Upchurch (2011) concluded that global environmental changes may have had some influence on the timing and magnitude of extinctions but that diversity on different continents still displays regional variations. Regional sampling at terrestrial scales is therefore not effective to reflect global signals. On the other hand, care must be taken with global datasets to ensure that there is no over-representation of diversity patterns from one specific region. The Mesozoic fossil record of Europe has poor quality outcrops, which are also unevenly distributed in time. The state of preservation of the fossils is often inferior and new potential sites are inaccessible due to built-up urban or agricultural areas. In addition, there are always large temporal and regional gaps (Csiki-Sava et al., 2015).

GEOGRAPHICAL SETTING

Since Europe, as a subcontinent, forms with Asia the continent of Eurasia, Europe is not clearly defined geographically and rather refers to a political-historical space (Figure 6). Therefore, Europe is considered the second smallest continent on Earth and covers an area of about 10 million km². One of the possible geographical boundaries is considered to be the Ural Mountains, which means that the western part of Russia can be considered European (Statista Research Department, 2022). Today's Ural Mountains exist in this form only since the Pliocene. As a cause for this plate tectonic events of the Eurasian southern margin are assumed, which could be related to the Alpidic mountain building (Ollier, 2006).

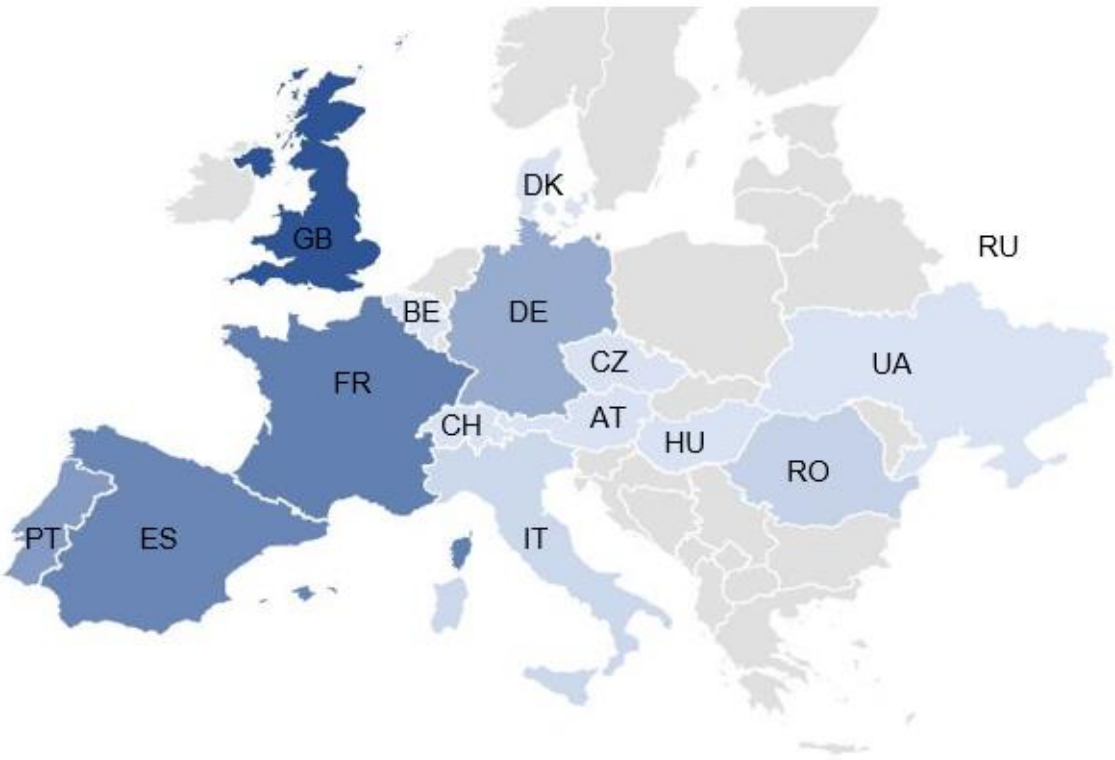

Figure 6: Graphical overview of Europe, colored (the darker, the more) are those countries with sites of Jurassic and Cretaceous dinosaur remains. Russia is not marked on the figure because of its largest area on the Asian continent, but it is still fossil-leading (Modified after: Microsoft PowerPoint).

The following map (Figure 7) displays a temporal and geographical concentration of sites in certain individual regions (Portugal, Eastern Spain, Northern and Southern France, Southern England).

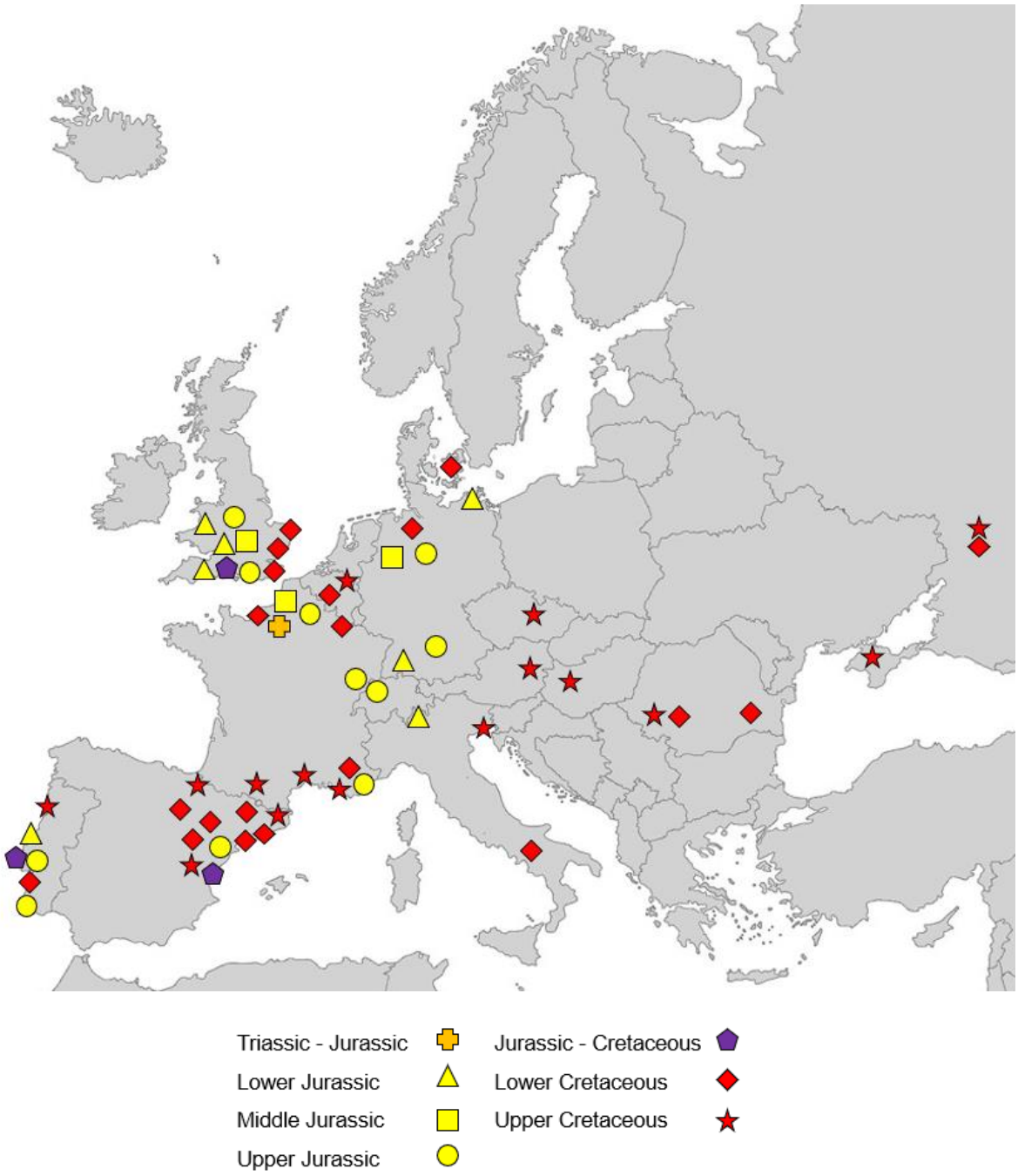

Figure 7: Localities of Jurassic and Cretaceous dinosaurs in Europe (including parts of Russia). The individual dots mark the respective series and may represent several sites due to the resolution (Modified after: europakarte.org).

Palaeogeographic maps (Figure 8a-e) show the approximate distribution of sites in past Europe. The individual time periods are marked with shapes and colors for the frequencies of localities (legend). Accordingly, most of the sites are located in coastal areas and from large parts of the presumed landmass there are (still) no finds at all. Reasons for some markers being located in the shelf area or even directly in the

ocean may be due to the strong fluctuations of the sea level, special taphonomic processes and or errors in the reconstruction of the exact geographic position. The largest aggregations are located between the palaeogeographical 30°-40° northern latitude.

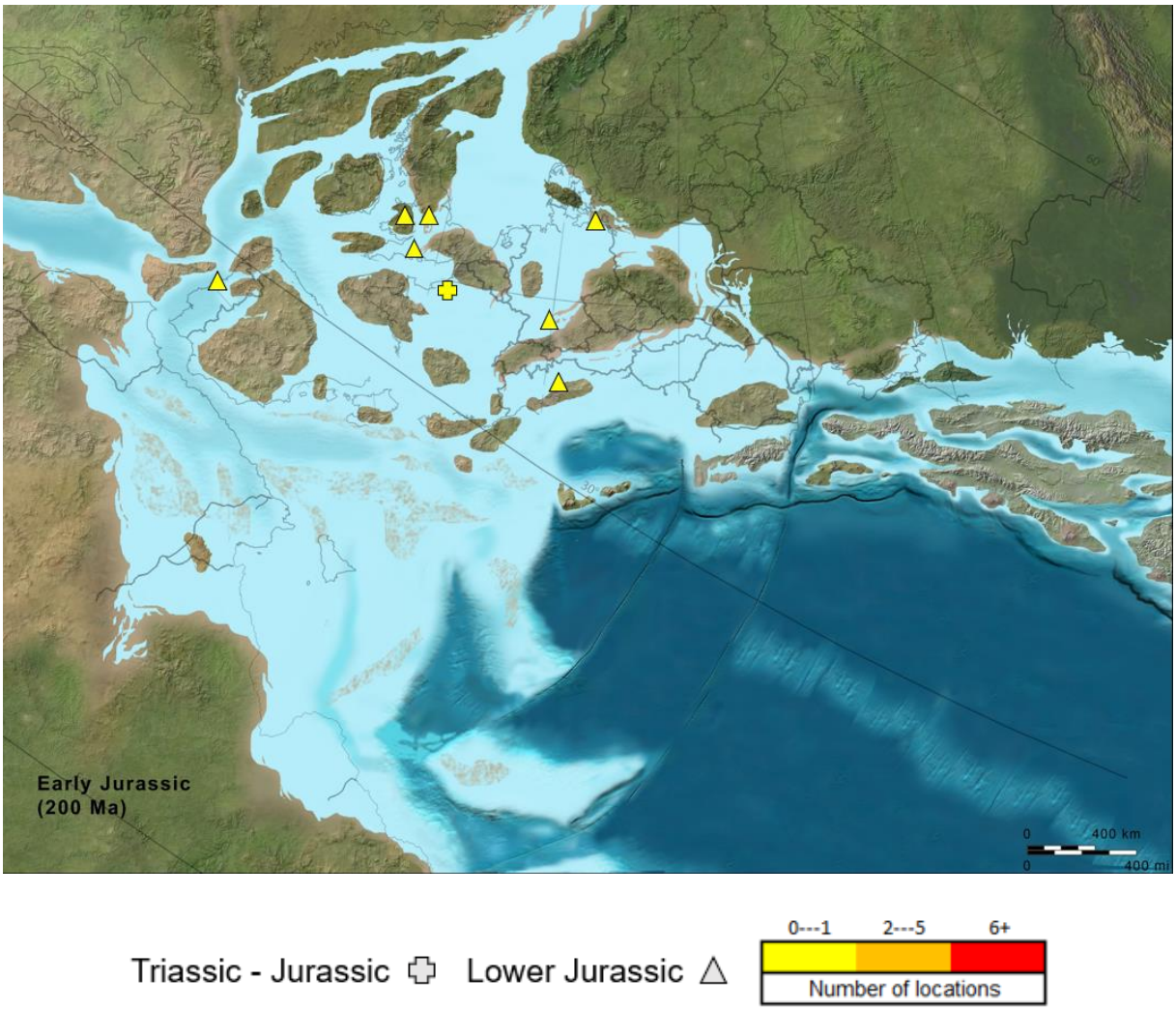

Figure 8a: Approximate palaeogeographic distribution of Lower Jurassic sites (Modified after: © Deep Time Maps™).

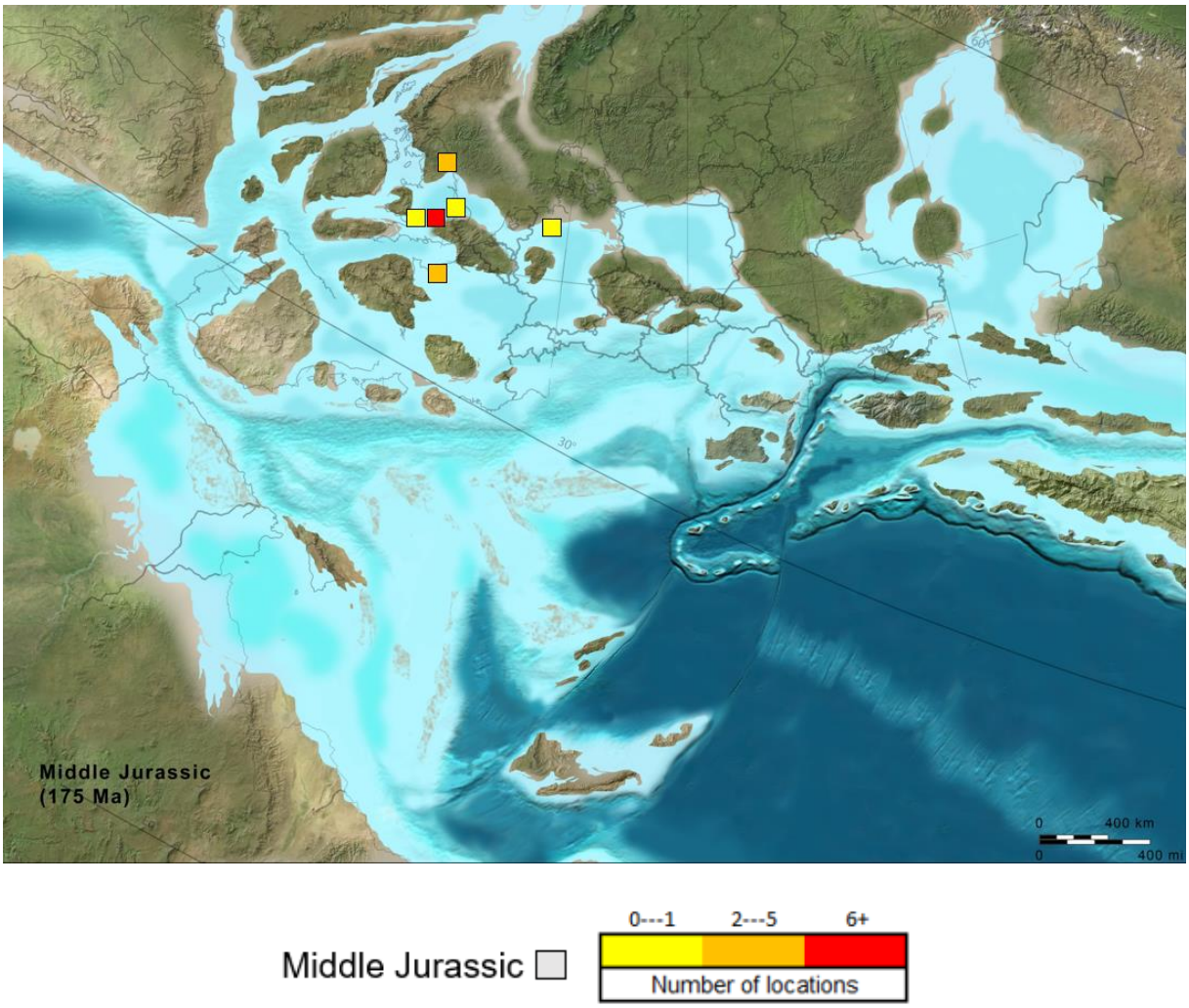

Figure 8b: Approximate paleogeographic distribution of sites in the Middle Jurassic (Modified after: © Deep Time Maps™).

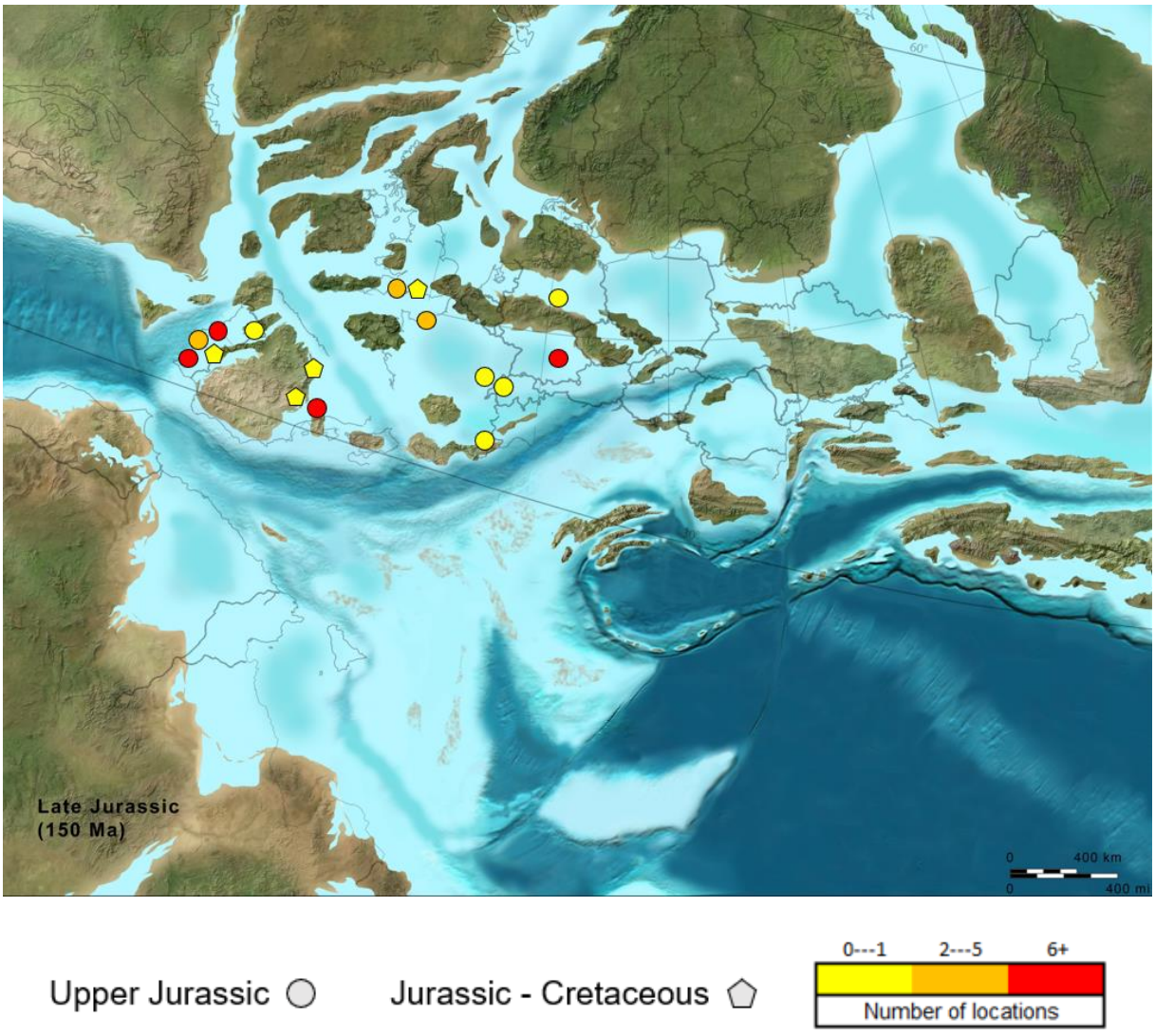

Figure 8c: Approximate palaeogeographic distribution of Upper Jurassic sites (Modified after: © Deep Time Maps™).

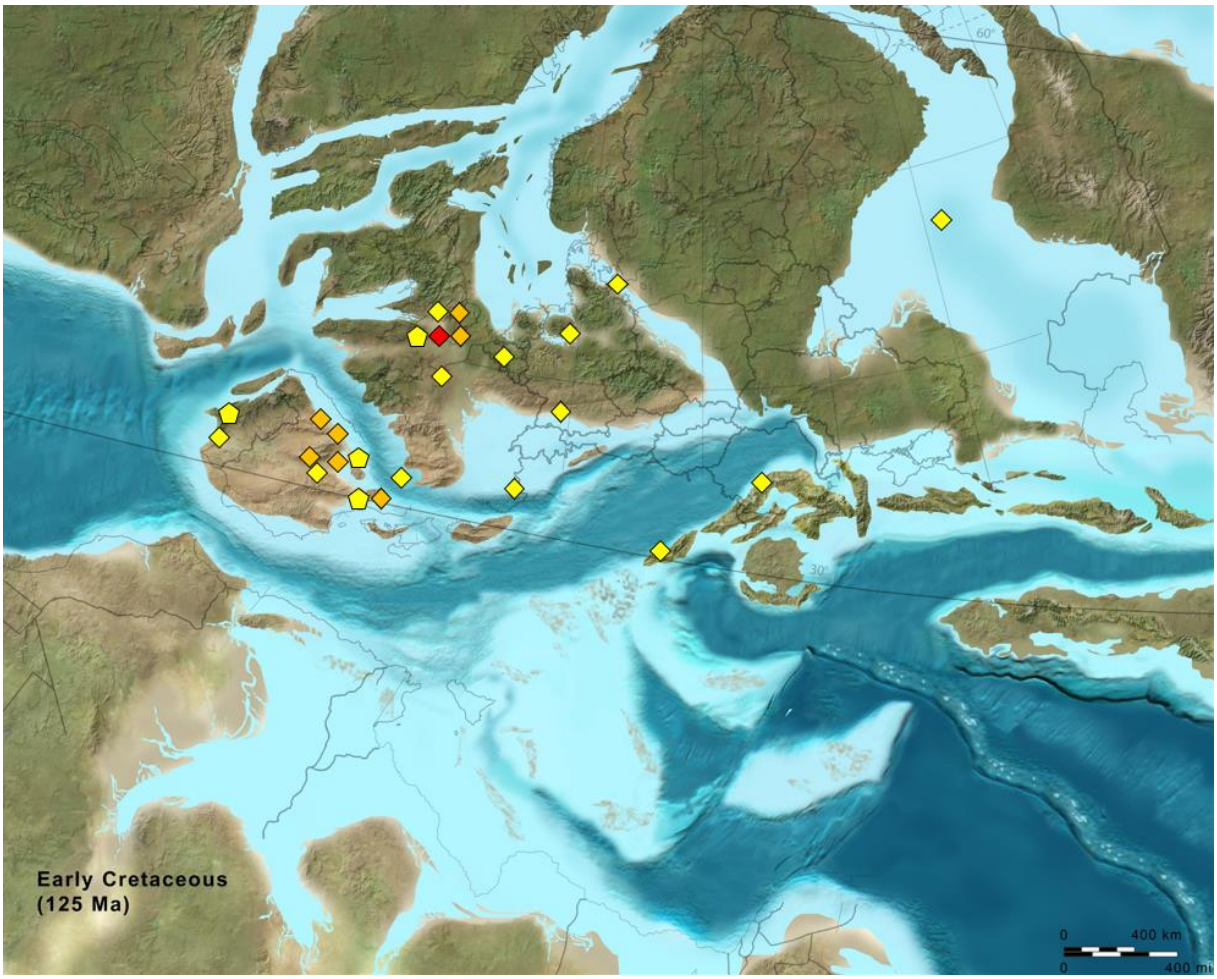

Figure 8d: Approximate palaeogeographic distribution of Lower Cretaceous sites (Modified after: © Deep Time Maps™).

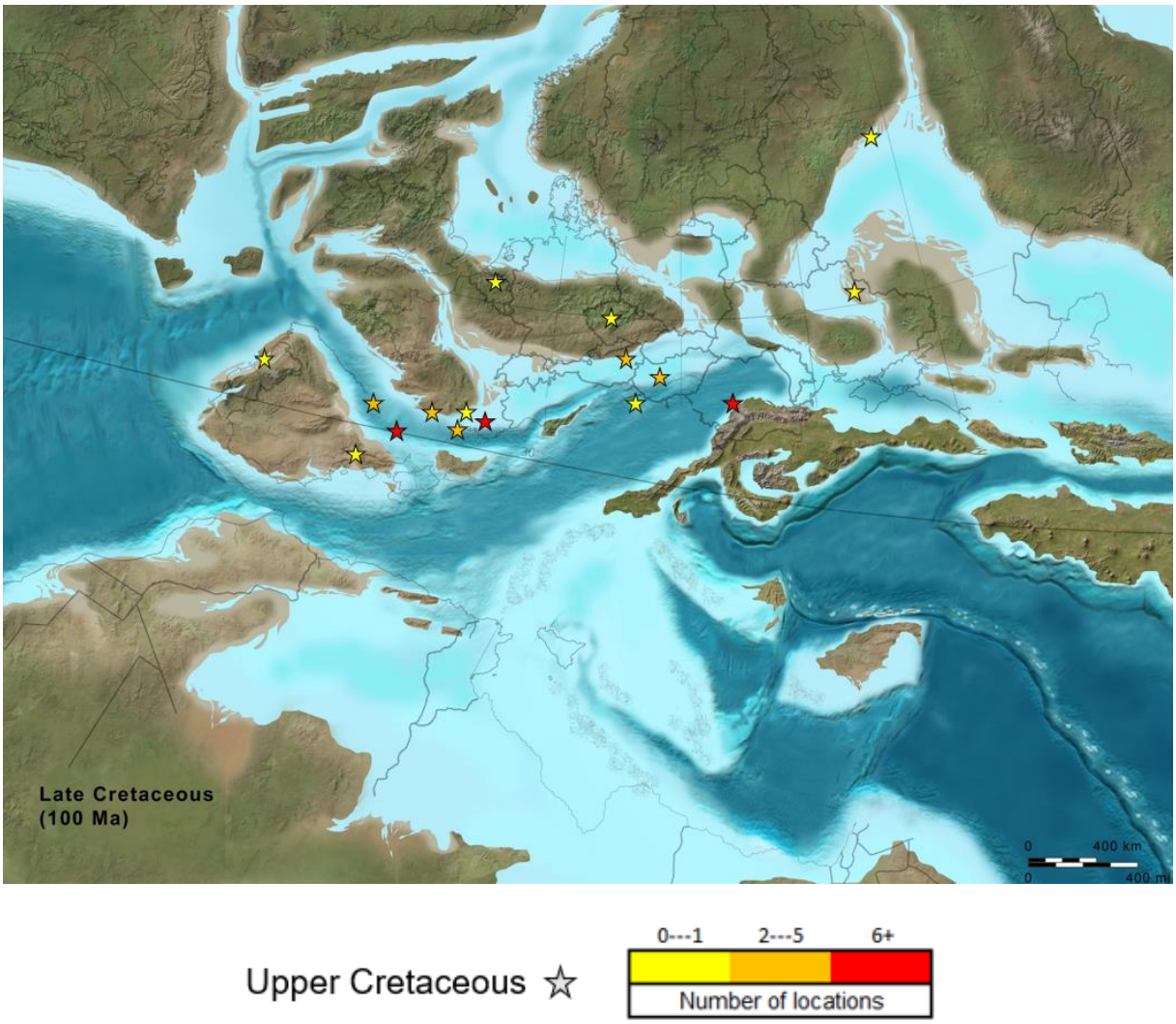

Figure 8e: Approximate palaeogeographic distribution of Upper Cretaceous sites (Modified after: © Deep Time Maps™).

MATERIAL AND METHODS

Data collection

Tables, charts, and graphs for data processing and visualization were created using Microsoft Office 365, statistical tests were conducted with the application RStudio PBC (now POSIT PBC) and iNEXT Online. The geographic overview map (Figure 6) was created using Microsoft PowerPoint (Version 2016). Deep Time Maps™ were used to represent the palaeogeographic sites (Figure 8a-e). The Mesquite program was used to generate the phylogram (Figure 1), which follows the systematic classification of Weishampel et al. (2004), Hendrickx et al. (2015) and Madzia et al. (2021). Numerical ages of stage and series boundaries were taken from the current

version of the International Chronostratigraphic Chart (IUGS) and used to classify the data. It should be noted that the methods used in this thesis may not be equally applicable to other studies at the global level without adapting them according to specific criteria.

A vast body of publications and standard reference works (as noted in the bibliography) were used to analyse the palaeobiodiversity of European dinosaurs over the Jurassic and Cretaceous period. In order to ensure the highest possible academic accuracy of the data in this study, sources in which contributions can be freely created and edited (Wikipedia & Paleobiology Database) were avoided. Nomina dubia and taxa of which only single fragments are available, which could not be classified more precisely were excluded. Possible synonyms of taxa were also avoided. A comprehensive overview of the data set can be found in the supplementary materials. The created dinosaur database is on the knowledge level of various publications until 15.03.2022.

Diversity estimation

The temporal and geographic occurrences of 156 (168, inclusive avian dinosaurs) valid European dinosaur species from 148 (160, inclusive avian dinosaurs) genera, ranging in age from the Hettangian (Lower Jurassic: 201.3 million years ago) to the end of the Maastrichtian (Upper Cretaceous: 66.0 million years ago), were extracted from recent publications and standard works. These time spans were used to generate estimates of taxic diversity by summing up the number of dinosaurs that occurred in each Jurassic and Cretaceous stage. Due to inaccuracies in the dating of geological formations with fossil material, the actual palaeobiodiversity may be biased. However, because of these occasionally large geological gaps, which only provide a sample-like picture of the past, the individual species and genera were also partly considered at the level of orders and clades in the diversity analyses. These divisions allow more consistent results, reduce the susceptibility to errors due to taxonomic mistakes, and provide a better overview.

Palaeodiversity classification and occurrence

The actual number of fossils found in a time period is the most basic indicator of the diversity of extinct organisms and gives a direct insight into past living worlds. Due to

various factors and influences in the fossilization and the discovery and identification of the same, there are large distortions of the actual palaeobiodiversity.

In order to guarantee a uniform structure in the diversity analysis, the species and genera were also considered at a higher taxonomic level. In the absence of a recognized common systematics, all dinosaurs of Europe were assigned to the following orders, clades, and superfamilies after selection of a suitable common association as shown in Figure 1 in a simplified way:

Superorder: **DINOSAURIA** Owen, 1842

Order: **SAURISCHIA** Seeley, 1888

Suborder: **THEROPODA** Marsh, 1881

"BASAL THEROPODA"

Clade: **NEOTHEROPODA** Bakker, 1986

"BASAL NEOTHEROPODA"

Clade: **AVEROSTRA** Paul, 2002

Clade: **CERATOSAURIA** Marsh, 1884

Clade: **TETANURAE** Gauthier, 1986

Superfamily: **MEGALOSAUROIDEA** Huxley, 1889

Clade: **AVETHEROPODA** Paul, 1988

Superfamily: **ALLOSAUROIDEA** Marsh, 1878

Clade: **COELUROSAURIA** von Huene, 1914

Clade: **AVIALAE** Gauthier, 1986

Clade: **SAUROPODA** Marsh, 1878

"BASAL SAUROPODA"

Clade: **EUSAUROPODA** Upchurch, 1995

Clade: "BASAL EUSAUROPODA"

Clade: **NEOSAUROPODA** Bonaparte, 1986

Clade: **MACRONARIA** Wilson & Sereno, 1998

Superfamily: **DIPLODOCOIDEA** Marsh, 1884

Order: **ORNITHISCHIA** Seeley, 1888

"BASAL ORNITHISCHIA"

Clade: **GENASAURIA** Sereno, 1986

Clade: **THYREOPHORA** Nopcsa, 1915

"BASAL THYREOPHORA"

Clade: **EURYPODA** Sereno, 1986

Suborder: **STEGOSAURIA** Marsh, 1877

Suborder: **ANKYLOSAURIA** Osborn, 1923

Clade: **NEORNITHISCHIA** Cooper, 1985

"BASAL NEORNITHISCHIA"

Clade: **CERAPODA** Sereno, 1986

Clade: **MARGINOCEPHALIA** Sereno, 1986

Clade: **ORNITHOPODA** Marsh, 1881

Under the term "basal" fall those representatives, which could not be clearly assigned taxonomically to any clade, or which stand between two larger clades and combine basal features from several taxa and their systematic position therefore could not be conclusively clarified (e.g. **COELOPHYSOIDEA** Nopcsa, 1928 or **HETERODONTOSAURIDAE** Romer, 1966 or Kuhn, 1966). In order to gain a more detailed insight into the course of palaeodiversity of European dinosaurs, avian dinosaurs were deliberately excluded from many analyses due to their abundant occurrence until today. Since a precise distinction in transitional forms from non-avian theropods to Mesozoic birds is controversial, only Cretaceous birds were actually counted as avian theropods unless otherwise noted in the results. A detailed list of all species and their classification can be found in the appendix.

Estimated mean standing diversity and origination/extinction rate

In order to compensate for inconsistencies in total diversity due to different (temporal) interval lengths and the number of origin and extinction events, the per taxon rate was used to calculate diversity according to the methods of Foote (2000). To avoid underestimation of taxonomic rates by excluding only singletons (taxa that are restricted to a single time interval), or overestimation of diversity by a high turnover rate, the estimated mean standing diversity was also included (Figure 9).

Diversity measures

Measure	Definition
Total diversity, N_{tot}	$N_{FL} + N_{bL} + N_{Ft} + N_{bt}$
Total diversity minus singletons	$N_{bL} + N_{Ft} + N_{bt}$
Bottom-boundary crossers, N_b	$N_{bL} + N_{bt}$
Top-boundary crossers, N_t	$N_{Ft} + N_{bt}$
Number of originations, N_o	$N_{FL} + N_{Ft}$
Number of extinctions, N_e	$N_{FL} + N_{bL}$
Estimated mean standing diversity	$(N_b + N_t) / 2$ $= (N_{bL} + N_{Ft} + 2N_{bt}) / 2$ $= (N_{tot} - N_o/2 - N_e/2)$

Rate measures

Measure	Definition
Per-taxon rate	Origination: $(N_{FL} + N_{Ft}) / (N_{tot}) / \Delta t$ Extinction: $(N_{FL} + N_{bL}) / (N_{tot}) / \Delta t$

Figure 9: Overview of the individual diversity calculation methods (From Foote, 2000).

Evaluation of locations

A total of 168 species from 104 sites in 16 different European countries were analyzed (Figure 6). In order to identify larger patterns of diversity across individual regions, the continent's finding countries, were divided into three geographic zones. These are not based on known political or historical definitions and have been self-established for use in annotated analyses that might reveal possible signals from a palaeogeographic point of view. For this purpose, all finding countries were assigned to the following broad geographic parts:

Western Europe: Belgium, England, France, Portugal, Spain, Wales

Central Europe: Austria, Czech Republic, Denmark, Germany, Hungary, Italy, Switzerland

Eastern Europe: Romania, Russia, Ukraine

Because of the palaeogeographical positions of the land masses there were sometimes considerable differences between the individual faunas. Therefore it is explicitly pointed out that the European continent of the Jurassic and Cretaceous was sometimes populated by other taxa, which did not (or no longer) occur on other continents.

Climate data calculations

To capture inferences about the impact of abiotic factors such as carbon dioxide levels or temperature on palaeodiversity, based on Supplementary Data 2 from Foster et al. (2017), global mean temperature and pCO2 probability maximum were reconstructed for the study period (201.5 million years - 66.0 million years).

At first, the radiative forcing had to be calculated by using the pCO2 values (From: Myhre et al., 1998, Foster et al., 2017):

$$\Delta F_{CO_2}(t) = 5.35 \cdot \ln\left(\frac{CO_2(t)}{280\ ppm}\right)$$

Equ. 1: *Equation for the radiative forcing, ΔF stands for the radiative forcing and increases logarithmically with relative change of CO2 concentration.*

By inserting the values of the radiative forcing, the global average temperature in 0.5 million year steps, could be determined by the following formula (From Foster et al., 2017):

$$T(t) = 14\,°C + 0.62\frac{K}{W/m^2} \cdot \Delta F_{CO_2}(t)$$

Equ. 2: *Equation for the effects of radiative forcing on the mean temperature T, ΔF stands for the radiative forcing.*

However, due to the many complex (feedback) processes that are not yet fully understood, this simple estimate can only serve as an approximate indication (Andrews & Forster, 2008).

Individual rarefaction method

The rarefaction method, by plotting a species accumulation curve diagram, allows a statistical estimate if a sample's material includes enough individuals to represent the species richness of a given sample area (Krebs, 2014). If the species accumulation curve reaches a plateau, it can be assumed that the sample is comprehensive, in which the entire species richness could be determined by extrapolating the rarefaction curve. If the sample does not represent comprehensive species richness, the curve will show an increase in the graph (Krebs, 2014).

Simpson´s index

The Simpson's Index is a measure of the probability that two randomly selected individuals belong to the same species. The value D ranges from 0 to 1 and the higher the value, the higher the diversity (Krebs, 2014). As a deviation from the standard calculation, diversity was systematically analysed on a clade level across specific European zones.

$$1 - \hat{D} = 1 - \sum_{i=1}^{s}\left[\frac{n_i\left(n_i - 1\right)}{N\left(N - 1\right)}\right]$$

Equ. 3: *Equation of the Simpson´s Index, D stands for the index of species diversity, s for the number of species in the sample, n_i for the individuals of species in the sample and N for the total number of individuals in the sample.*

Shannon-Wiener index

The Shannon-Wiener Index is one of the most widely used diversity indices to estimate the species richness and abundance of a community (Omayio et al., 2019). There is no upper limit, the minimum value for the index is 0. The higher the value of H', the higher the diversity (Krebs, 2014). As a deviation from the standard calculation, diversity was systematically analysed on a clade level across specific European zones.

$$H' = -\sum_{i=1}^{s}(p_i)(\log_2 p_i)$$

Equ. 4: *Equation of the Shannon-Wiener Index, H' stands for the index of species diversity, pi describes the proportion of the respective individuals and s the number of species.*

Jaccard index

The Jaccard Index is one of the presence community coefficients and is used as a measure to evaluate the qualitative similarity of two habitats (Möseler et al., 2009). Within this work, deviations from the standard method were made at geographical and taxonomic levels.

$$\mathrm{JACC}[\%] = \frac{a}{a+b+c} \times 100$$

Equ. 5: *Equation of the Jaccard Index, JACC stands for the similarity measure, a for the number of common species, b for the number of species occurring only in habitat 1, c for the number of species occurring only in habitat 2.*

Biodiversity on spatial scales

Following the findings of Whittaker (1972), the diversity of European dinosaurs was analyzed over different geographical areas. Within this study, the classification of specific local areas and regions of Europe was examined at different geographic scales. The following definitions were distinguished (Krebs, 2014):

Alpha (α) Diversity: Describes the diversity in a given local area

Beta (β) Diversity: Describes the exchange of different individuals between two local areas

Gamma (γ) Diversity: Describes the overall diversity within a large region

Spearman´s correlation coefficient

Spearman's correlation coefficent was considered to be the most appropriate for the underlying data sample due to its properties as a non-parametric statistical test, which does not require assumptions about frequency distributions or a linear relationship between two variables (Xiao et al., 2016). A p-value lower than 0.05 is considered significant.

$$r_s = 1 - \frac{6\sum d_i^2}{N\left(N^2 - 1\right)},$$

Equ. 6: *Equation for the Spearman´s correlation coefficient, where r_s is the coefficient, N the total number of samples and d_i the difference between two ranks of the samples.*

Two different methods of statistical calculation were used, which underlie considerations by Alroy (2014) and the "Supplementary Data 2" by Foster et al. (2017). The first method was based on an average calculation of the global mean temperature, which are available in steps of 0.5 Ma, over a geological stage and compared the occurrence of dinosaurs per stage. Secondly, using a boundary crosser method, which only compares the (species/temperature) data directly at the transition of a stage (instead of within a stage), so that changes are measured directly and the different lengths of the individual geological stages have no influence. Nevertheless, the problem of a potential autocorrelation cannot be excluded even with two random and independent time series.

RESULTS

Standing diversity patterns of European non-avian dinosaurs

The following graphs (Figures 10 and 11) illustrate the raw standing diversity of non-avian dinosaurs throughout the Jurassic and Cretaceous of Europe. Due to gaps in the fossil record, there are no data from this continent for the Pliensbachian, Aalenian (both Early Jurassic), and for the Turonian, and Coniacian (both Late Cretaceous) geologic stages, which does not mean that there was an abstinence of dinosaurs.

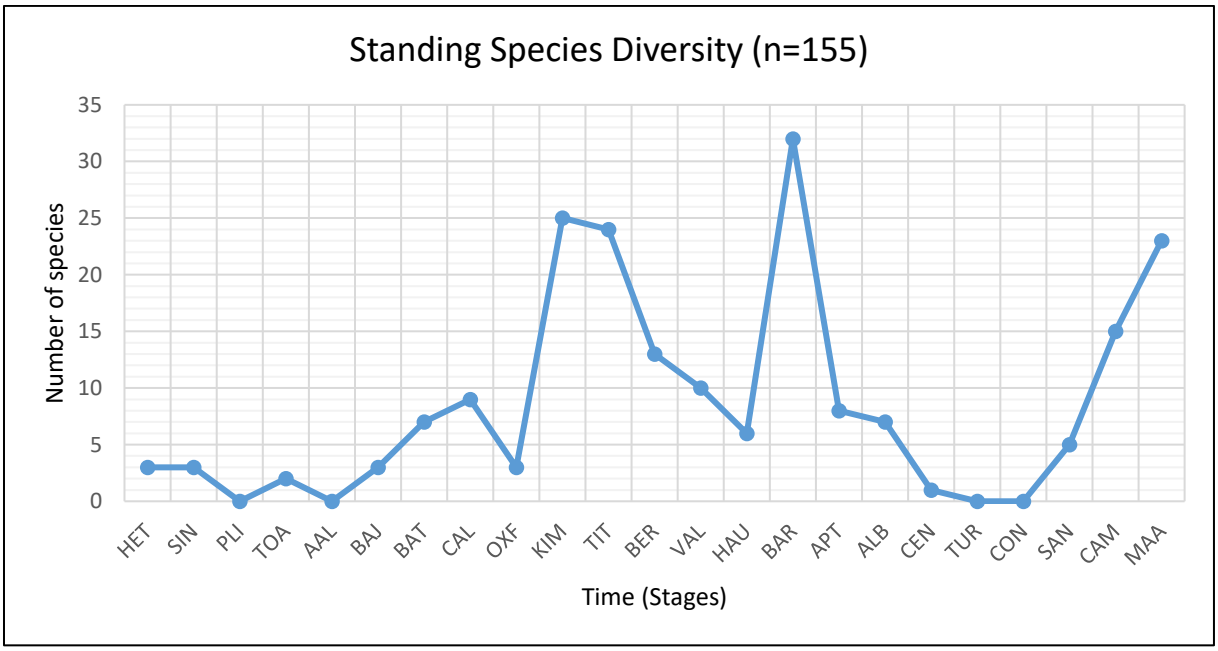

Figure 10: Standing species diversity of European Jurassic and Cretaceous non-avian dinosaurs.

The standing diversity (Figure 10) runs from the Hettangian to the Bathonian rather unremarkable on a low level, before a first increase appears in the Middle Jurassic. After a significant decline in the Oxfordian, the number of species in the Kimmeridgian and Tithonian increases enormously by 2.5 times the level that existed during the Callovian. At the transition from Jurassic to the Cretaceous, there is a sharp fluctuation in diversity, with a sudden decline of almost half of all species (-45.83%). This decline continues unabated until the Hauterivian. In the Barremian, a significant increase in species is recognizable, which even exceeds by far the diversity at the end of the Jurassic. This is followed by another strong decline in the Aptian, which continues into the Albian. From the Santonian on, which is on a relatively low diversity level, a last enormous increase of species occurrence sets in,

which reaches almost the height of the value from the Tithonian until the end of the Maastrichtian (Campanian/Maastrichtian +53.33%). To better understand evolutionary patterns, a subdivision of dinosaur diversity into their clades follows (Figure 11).

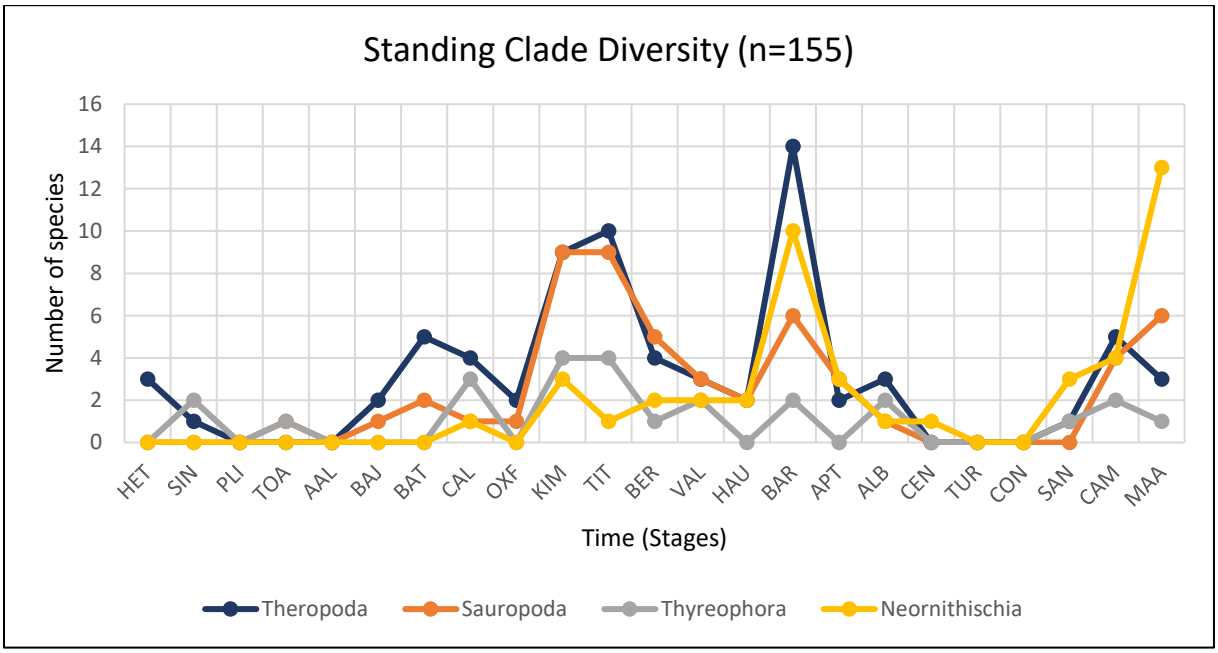

Figure 11: Standing diversity curve of European Jurassic and Cretaceous non-avian dinosaurs.

Theropoda

The number of species remains at a low level until the Bathonian and is completely interrupted in the Pliensbachian, Toarcian and Aalenian. From the Callovian to the Oxfordian, a decline before a significant peak occurs in the Kimmeridgian and Tithonian. At the transition to the Cretaceous in the Berriasian, a significant decline by about half of all species is identifiable. This decline continues until the Hauterivian with a further slight dip, before the sudden greatest diversity development occurs in the Barremian and even exceeds the peak from the Tithonian by far. In the Aptian, a drastic decline with a small increase in the Albian and complete absence of species through the Cenomanian, Turonian, Coniacian occurs. From the Santonian onwards, a renewed increase into the Campanian can be observed, which declines again in the Maastrichtian.

Sauropoda

Up to the Toarcian there is no evidence of sauropods, which from then on are at very low levels (absent in the Aalenian) until the Oxfordian. To the Kimmeridgian, a sudden significant increase occurs, which is maintained in the Tithonian and decreases by half to the Berriasian. In the Valanginian and Hauterivian, a slight decline in species number continues but increases again by more than double in the Barremian. In the Aptian and Albian, a collapse in diversity occurs. From the Cenomanian to the Santonian there is no record of sauropods. In the Campanian the diversity continues on a medium level and increases slightly in the Maastrichtian.

Thyreophora

The Thyreophora are present from the Sinemurian on with a low number of species and this rather low diversity continues until the Callovian. No records exist from the Pliensbachian, Aalenian, Bajocian, and Bathonian stages. In the Oxfordian they are also absent but reach again a stable diversity on a lower level in the Kimmeridgian and Tithonian. To the Berriasian a comparatively strong collapse of species numbers occurs, which continues from the Valanginian to the Maastrichtian on a similarly low level. In the meantime, there are no records from the Hauterivian, Aptian, Cenomanian, Turonian and Coniacian.

Neornithischia

The record of Neornithischia starts low in the Callovian, is absent in the Oxfordian, and increases slightly in the Kimmeridgian. A slight decline is recorded in the Tithonian. Towards the Berriasian there is a low level rise that continues until the Hauterivian. In the Barremian there is a strong increase in diversity with a first peak. A sudden sharp decline follows towards the Aptian, which persists with low diversity until the Santonian. In the Santonian and Campanian the diversity was stable with low diversities and increases enormously by more than three times in the Maastrichtian, forming the last but highest peak of the Neornitischia of Europe. Estimated mean standing diversity (Figure 12) shows genus richness from the Hettangian to the Maastrichtian without over- or underestimating the diversity.

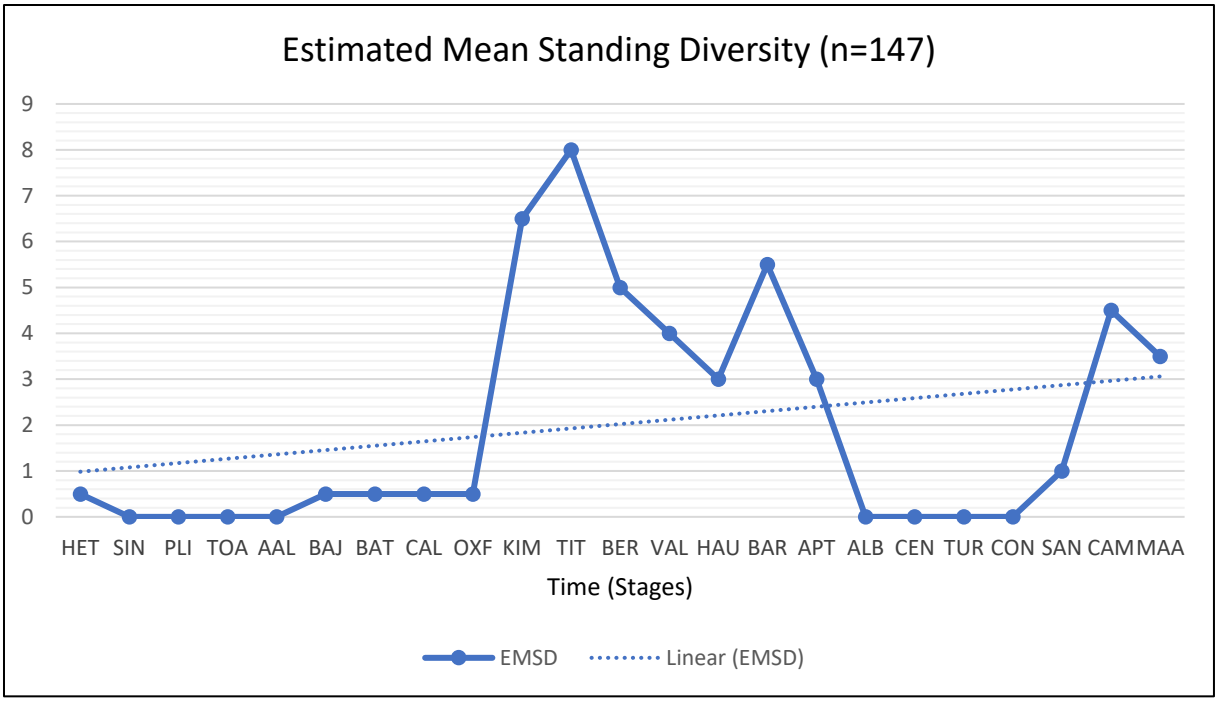

Figure 12: Estimated mean standing diversity (EMSD) of the genera of European Jurassic and Cretaceous non-avian dinosaurs.

From the Hettangian to the Oxfordian, a stable course on a low level is obvious. For the stages Sinemurian, Pliensbachian, Toarcian and Aalenian the value is zero due to the low occurrences. In the Kimmeridgian an enormous increase starts, which reaches its absolute peak in the Tithonian. In the Berriasian there is a decline (-37.5%), which gradually decreases until the Hauterivian. In the Barremian, a strong increase is recorded, which marks a high diversity. This subsequently decreases again in the Aptian and reaches zero again due to low occurrences in the Albian, Cenomanian, Turonian, Coniacian. In the Santonian an increase of the diversity starts, which reaches a last peak in the Campanian, before it comes to a small decrease (-22.22%) in the Maastrichtian. The tendency shows an increase from the beginning of the Jurassic to the end of the Cretaceous. In order to better understand the dynamics behind diversity, origination and extinction rates were calculated (Figure 13).

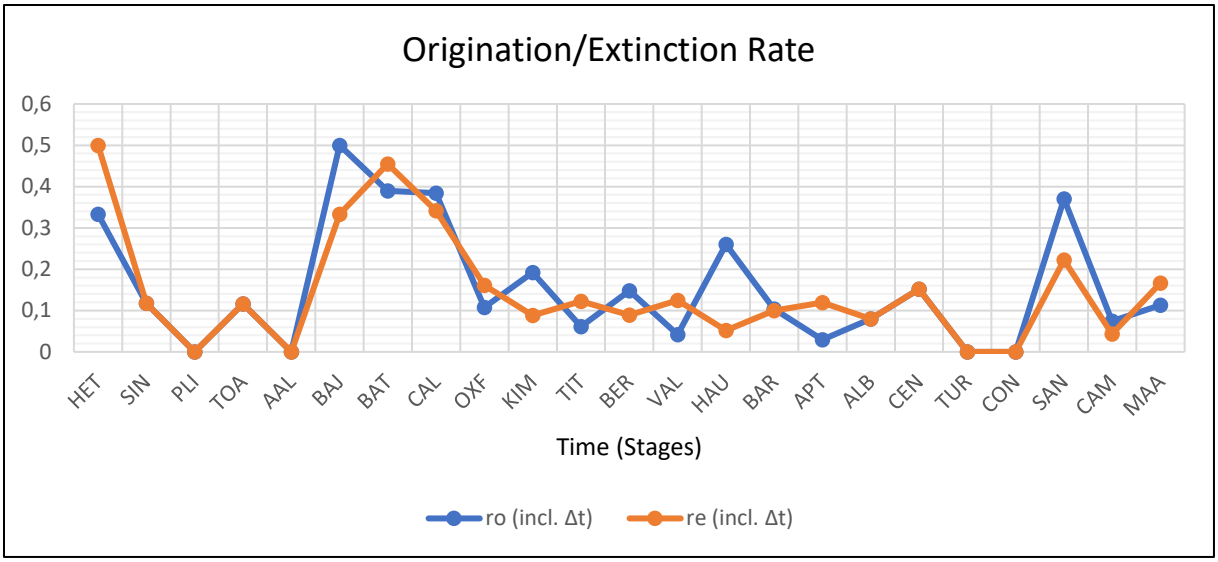

Figure 13: Calculated origination and extinction rate (per- taxon rate) of European non-avian dinosaurs by considering the duration of each stage.

The calculated per taxon rates shows that at the beginning of the Hettangian, the extinction rate is far above the origination rate. This levels off from the Sinemurian to the Aalenian on a congruent value. In the Bajocian, the origination rate increases significantly and is replaced by an increased extinction rate in the Bathonian. Both values converge from the Callovian to the Oxfordian. From the Kimmeridgian to the Valanginian, the rates of origination and extinction alternate in regular overlaps. In the Hauterivian the origination rate is in a large distance to the extinction rate, these coincide in the Barremian, before in the Aptian again the extinction rate predominates. There is a continuous overlap from the Albian to the Coniacian. In the Santonian, the origination rate is clearly higher than the extinction rate, as well as in the Campanian still with a small distance, before the extinction rate slightly predominates in the Maastrichtian.

Faunal composition of non-avian dinosaurs

As a supplement to the standing diversity, the following diagrams show the changes in faunal composition of the individual clades over time (Figures 14-19).

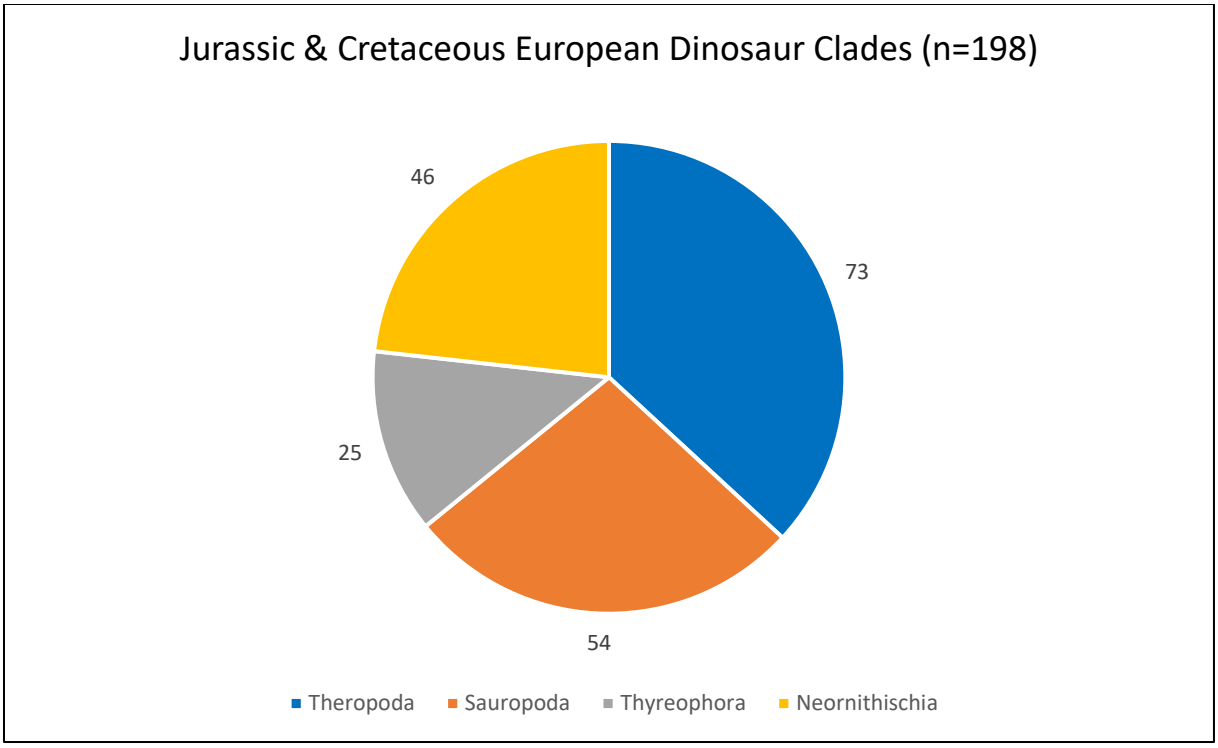

Figure 14: Total clade diversity of European Jurassic and Cretaceous non-avian dinosaurs.

Considering the entire investigation period (Figure 14), it shows that the largest percentage is represented by theropods (37%). Theropods are very diverse and common from the Jurassic to the end of the Cretaceous and still represented today by birds. Followed by the sauropods (27%), which also show a successful evolutionary history. Remarkable is the trend of the neornithischians (23%), which was a clade with rapid diversity increase in a short time on the European continent. The lowest proportion is provided by thyreophorans (13%).

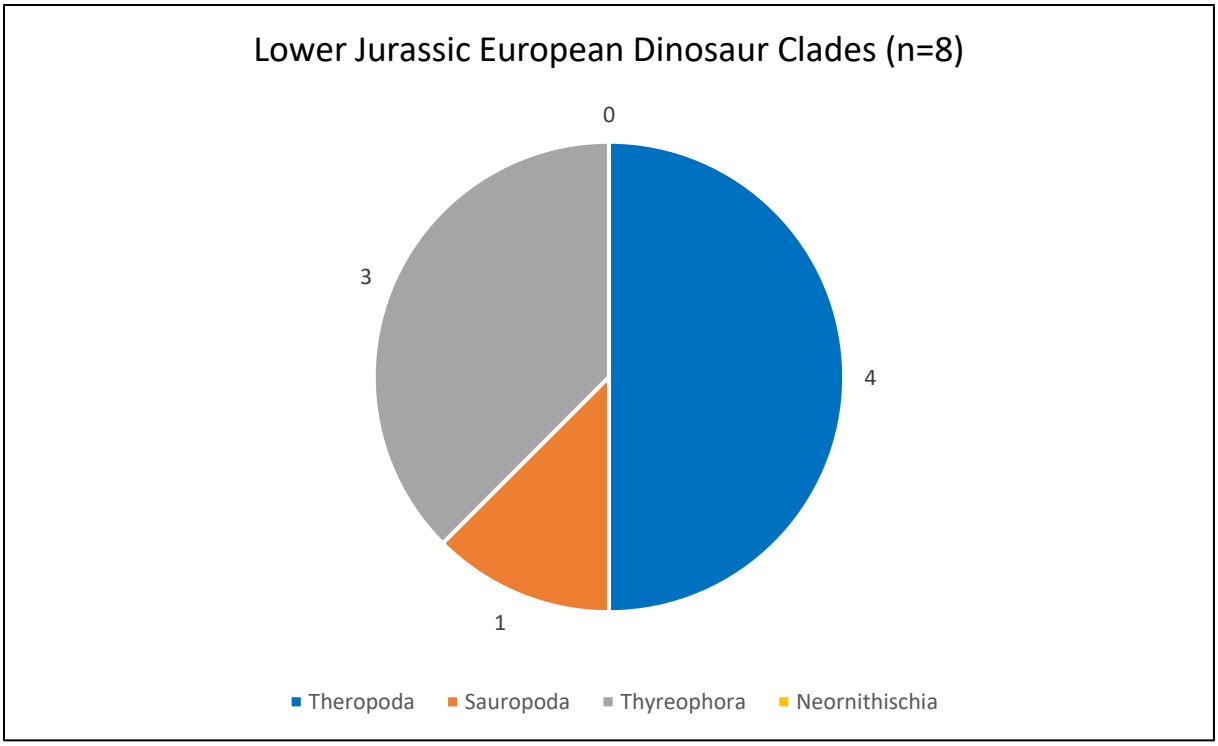

Figure 15: Diversity of Lower Jurassic European non-avian dinosaur clades.

Due to the low sample size in the Early Jurassic, the faunal composition results from this period are of little significance (Figure 15), but are included for a better understanding. It is obvious that half of the dinosaurs from this period belong to the theropods (50%). The thyreophorans (37.5%) also represent a significant proportion, compared to the rarer sauropods (12.5%). There are no findings of neornithischians from the Early Jurassic of Europe.

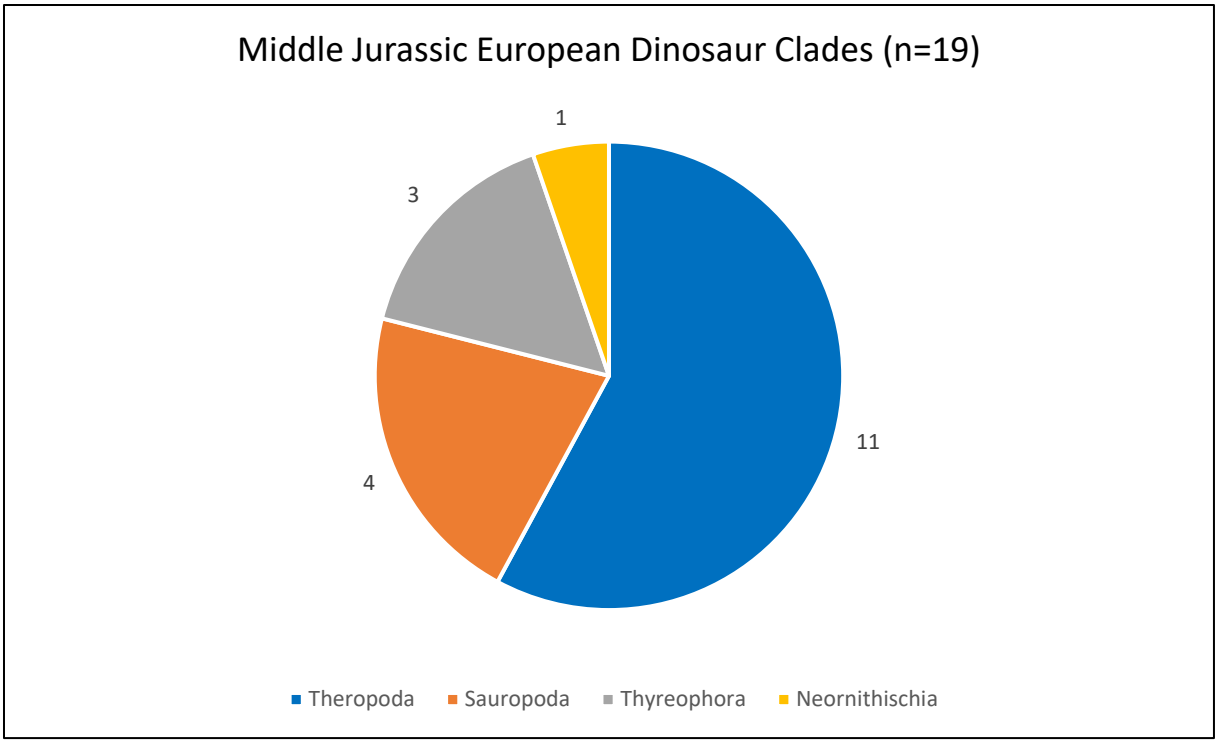

Figure 16: Diversity of Middle Jurassic European non-avian dinosaur clades.

Also in the Middle Jurassic, the largest proportion (Figure 16) is covered by theropods (58%). Among the herbivorous clades, the sauropods (21%), next to the thyreophorans (16%), are the most abundant representative. The neornithischians (5%) appear for the first time in the later Middle Jurassic.

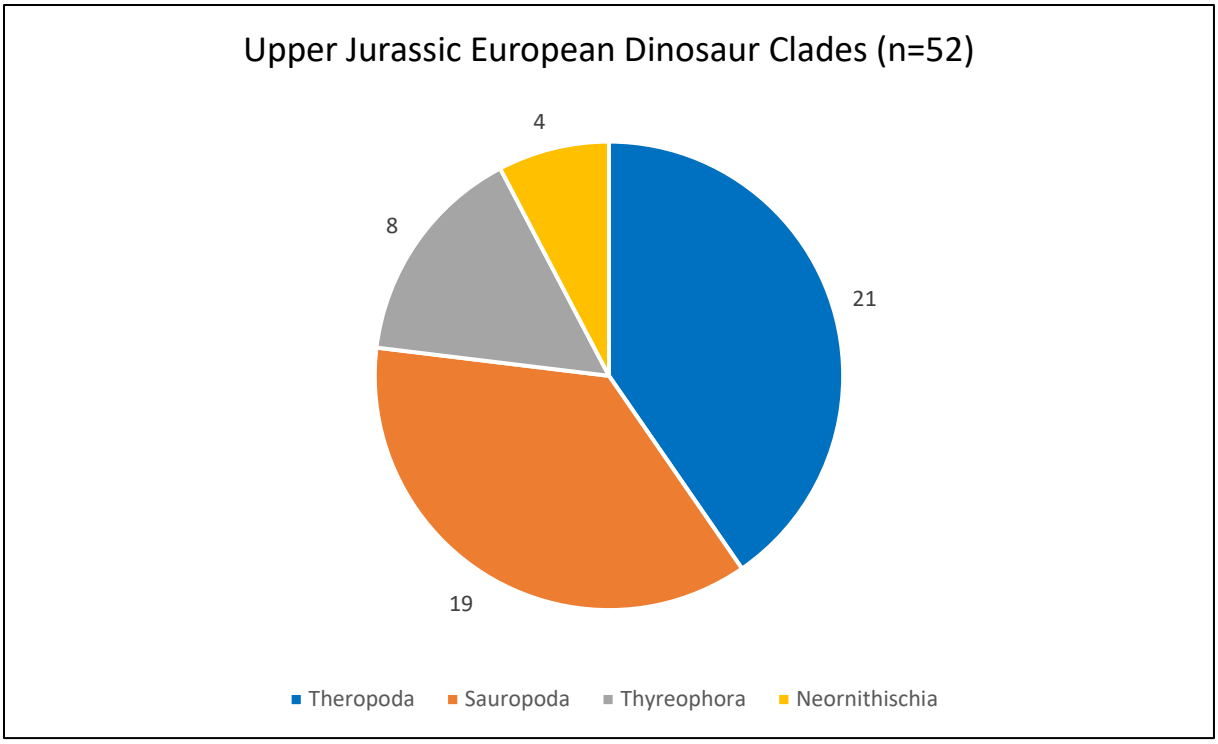

Figure 17: Diversity of Upper Jurassic European non-avian dinosaur clades.

Compared to the Middle Jurassic, the diversity in the Late Jurassic (Figure 17) has increased almostly three times. Theropods make up the largest proportion (40.5%), closely followed by sauropods (36.5%). The thyreophorans (15.5%) have remained stable in relation, and the number of neornithischians (7.5%) has increased slightly.

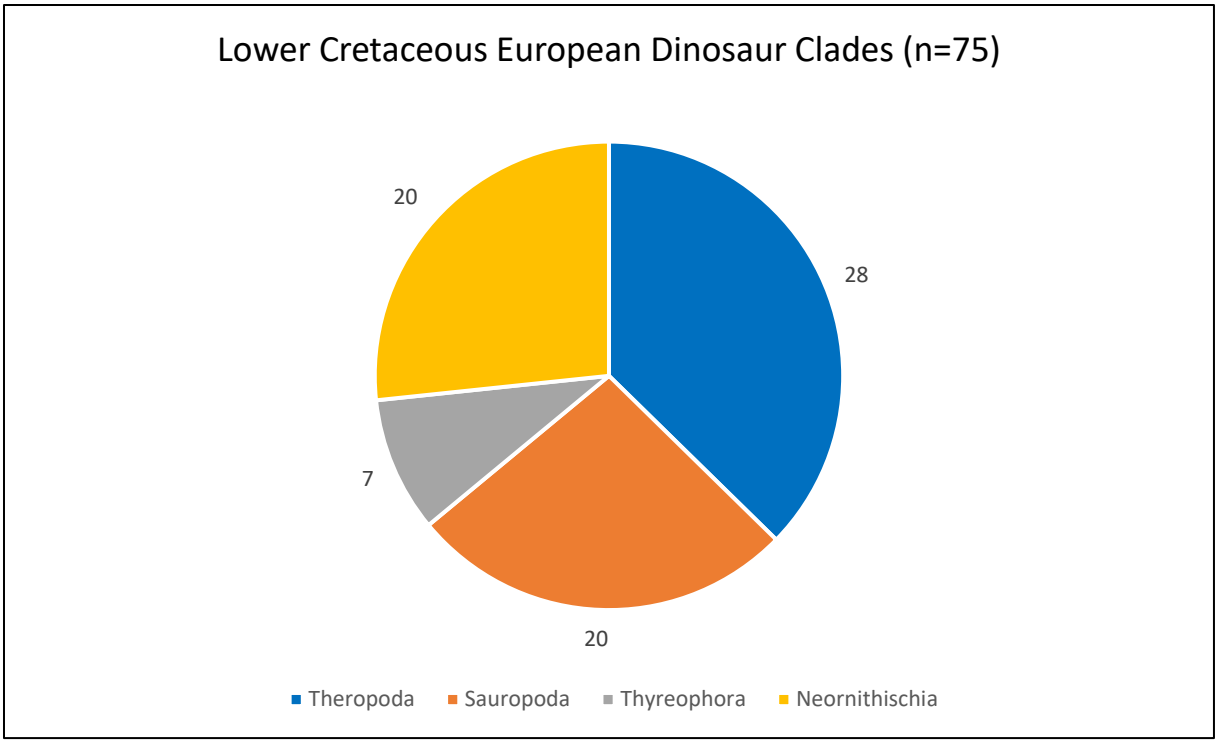

Figure 18: Diversity of Lower Cretaceous European non-avian dinosaur clades.

Due to the subdivision of the Cretaceous into only two geological series (Jurassic three series) and the different time spans, the data have to be considered more coarse (Figure 18). Still the theropods (37%) represent by far the largest percentage of taxa. Followed by the sauropods (26.5%) and the neornithischians (26.5%) which increased their diversity by five times compared to the Late Jurassic and together accounted for a considerable proportion. The diversity of thyreophorans (9%) decreased and forms a rather rare faunal element of this time.

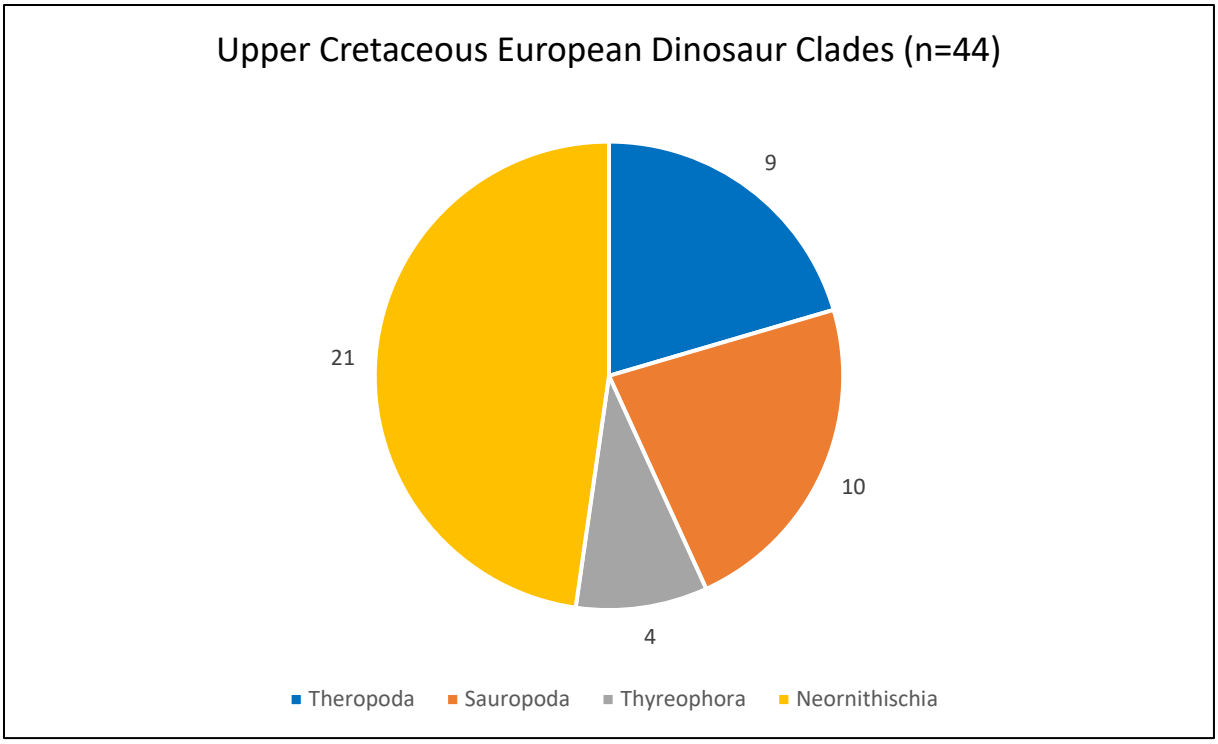

Figure 19: Diversity of Upper Cretaceous European non-avian dinosaur clades.

The diversity in the Late Cretaceous (Figure 19) is below to that of the Early Cretaceous. The proportion of neornithischians (48%) has again increased rapidly. They were by far the most abundant faunal element in this period and clearly dominated among the herbivorous representatives. The amount of sauropods (22.5%) has decreased in relation, but they still have a important share of diversity. Theropods (20.5%) appear more moderate in comparison with past ages, however, it is to be noted that the diversity of birds does not flow in here, whereby these, as is shown later, became more and more successful. The rarest clade continues to be that of thyreophorans (9%), their ratio to the other herbivorous dinosaurs has tended to remain at a stable but low level over the study period.

Theropod diversity patterns

Among the theropods, birds are the only representatives of the dinosaurs still living today and therefore are one of the most important and successful evolutionary adaptions within the clade. Their occurrence thus enormously influences the study of patterns of non-avian dinosaurs, which is why the following graphs show the impact on the palaeodiversity of theropods in Europe (Figure 20-23). Due to the small sample size, the analysis of the faunal composition starts with the Middle Jurassic (Figure 20).

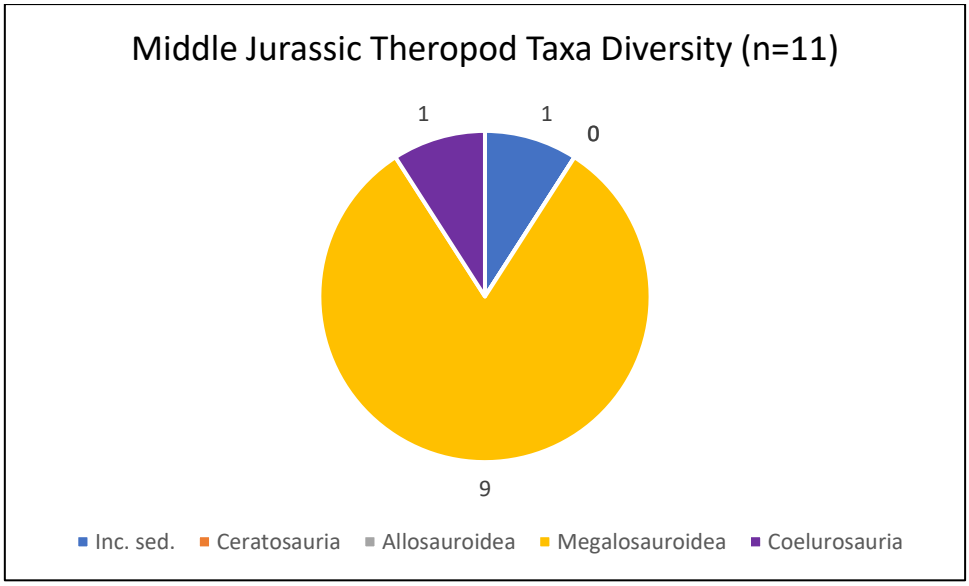

Figure 20: Diversity of Middle Jurassic European theropod clades.

Almost all of the Middle Jurassic theropods comprise representatives of the Megalosauroidea (82%), followed by Coelurosauria (9%) and species of taxa, incertae sedis (9%), which cannot be clearly assigned.

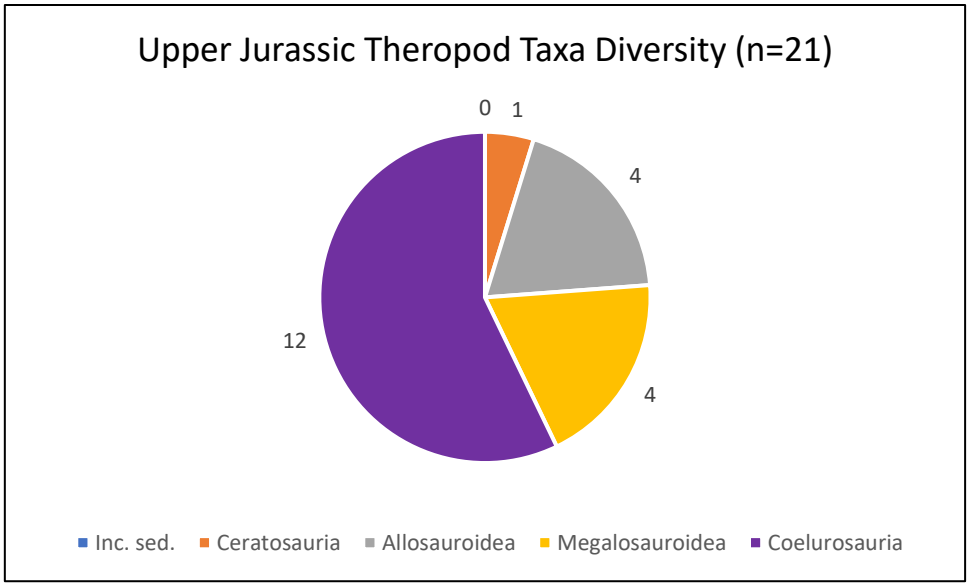

Figure 21: Diversity of Upper Jurassic European theropod clades.

The number of theropods compared to the Middle Jurassic has almost doubled to the Late Jurassic (Figure 21). The largest part of them is represented by Coelurosauria (57%), half of them could have already consisted of transitional forms to the avian dinosaurs, depending on the definition. The Megalosauroidea (19%) had to share their supremacy among the apex predators with the suddenly appearing Allosauroidea (19%). Ceratosauria (5%) belong to the rarer faunal elements.

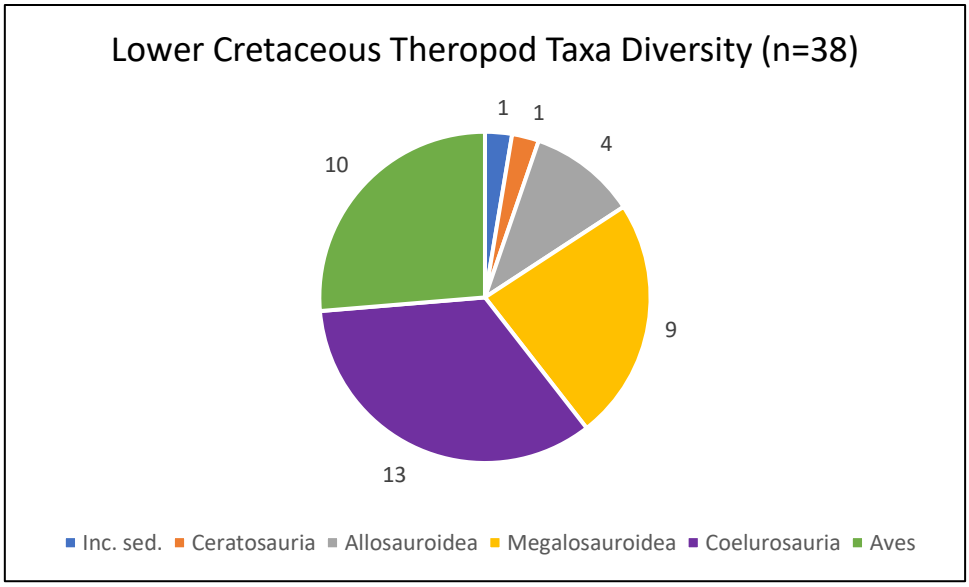

Figure 22: Diversity of Lower Cretaceous European theropod clades.

Due to the number of geological series in the Cretaceous and the different time spans, the results are to be considered more coarse in contrast to the Jurassic. The predominant part in the Early Cretaceous (Figure 22) is still dominated by Coelurosauria (34%), whereas the Mesozoic birds (26.5%), which are derived from them and can be assigned without doubt, already underlines the success of this group. The Megalosauroidea (24%) were able to increase their presence compared to the Allosauroidea (10.5%) again. Ceratosauria (2.5%) as well as not assignable representatives, incertae sedis (2.5%) were far rarer faunal elements.

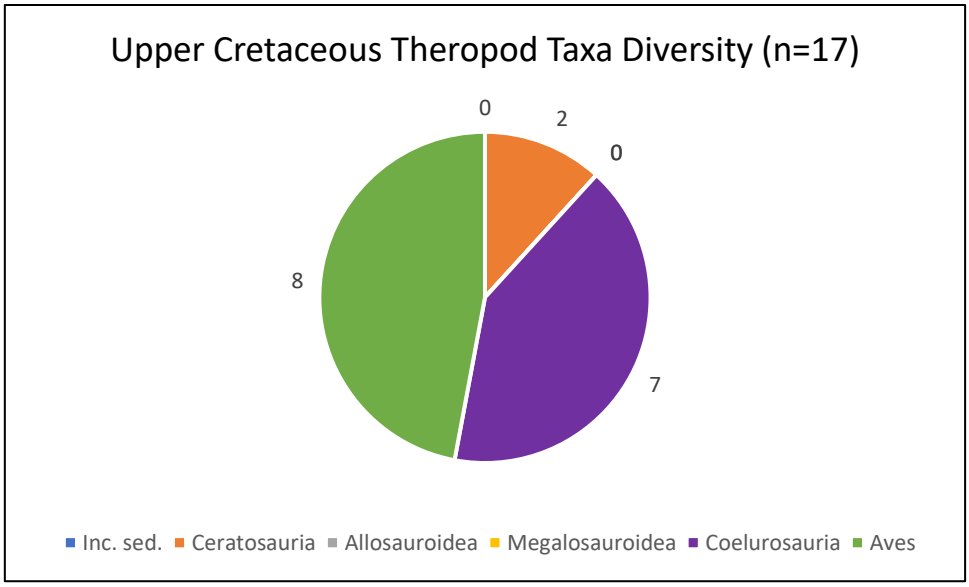

Figure 23: Diversity of Upper Cretaceous European theropod clades.

The number of representatives in the Late Cretaceous (Figure 23) is lower than in the Early Cretaceous. The dominance of avian dinosaurs (47%) has continued and for the first time is higher than that of Coelurosauria (41%). Ceratosauria (12%) continue to remain in the background, members of the Megalosauroidea and Allosauroidea suddenly do not appear in the fossil record of the Late Cretaceous of Europe. Figure 24 shows a comparison of the standing diversity between avian and non-avian theropods.

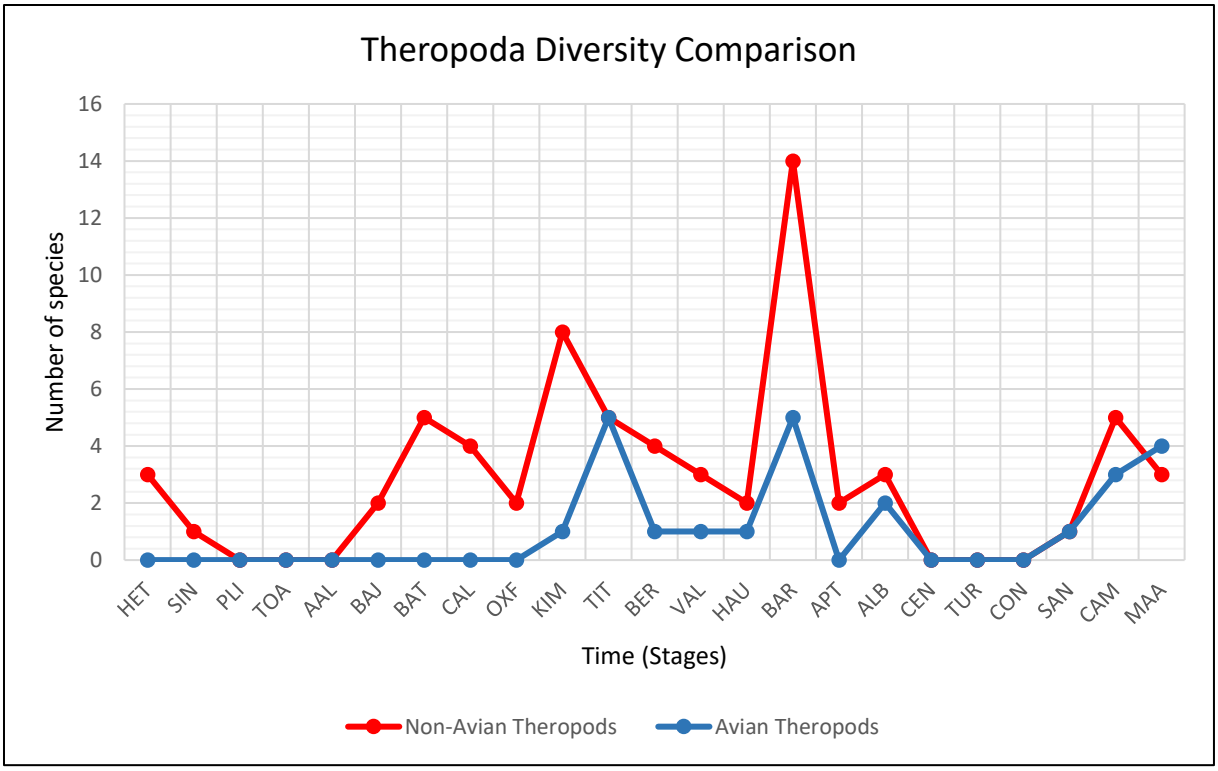

Figure 24: Comparison of the standing clade diversity of European Jurassic and Cretaceous theropods, including Jurassic birds as avian theropods.

The number of non-avian theropods remains at a low level until the Bathonian and is completely interrupted in the Pliensbachian, Toarcian, Aalenian. From the Callovian to the Oxfordian a decline is seen before a significant peak in the Kimmeridgian, which suffers a sharp decline in the Tithonian. At the transition to the Cretaceous, in the Berriasian, this gradual decline continues until the Hauterivian. In the Barremian the suddenly largest diversity increase occurs, which even exceeds the peak from the Kimmeridgian. In the Aptian, there is a drastic decline with little increase in the Albian and complete absence of species during the Cenomanian, Turonian, Coniacian. From the Santonian onwards, a renewed increase into the Campanian can be observed at a medium level, which declines again in the Maastrichtian. The occurrence of avian theropods in Europe starts inconspicuously in the Kimmeridgian, but reaches a significant peak already in the Tithonian. By the Berriasian, this high species occurrence has greatly reduced and continues into the Hauterivian at a very low level. In the Barremian, again a significant peak occurs, which is accompanied in the Aptian by a complete failure in the fossil record. In the Albian, is a small increase, which is again interrupted by a gap until the Coniacian. Diversity starts to increase gradually in the Santonian and reaches its final peak in the Maastrichtian. Figure 25

shows a comparison of the standing diversity between avian and non-avian theropods, with birds being counted only from the Cretaceous onward.

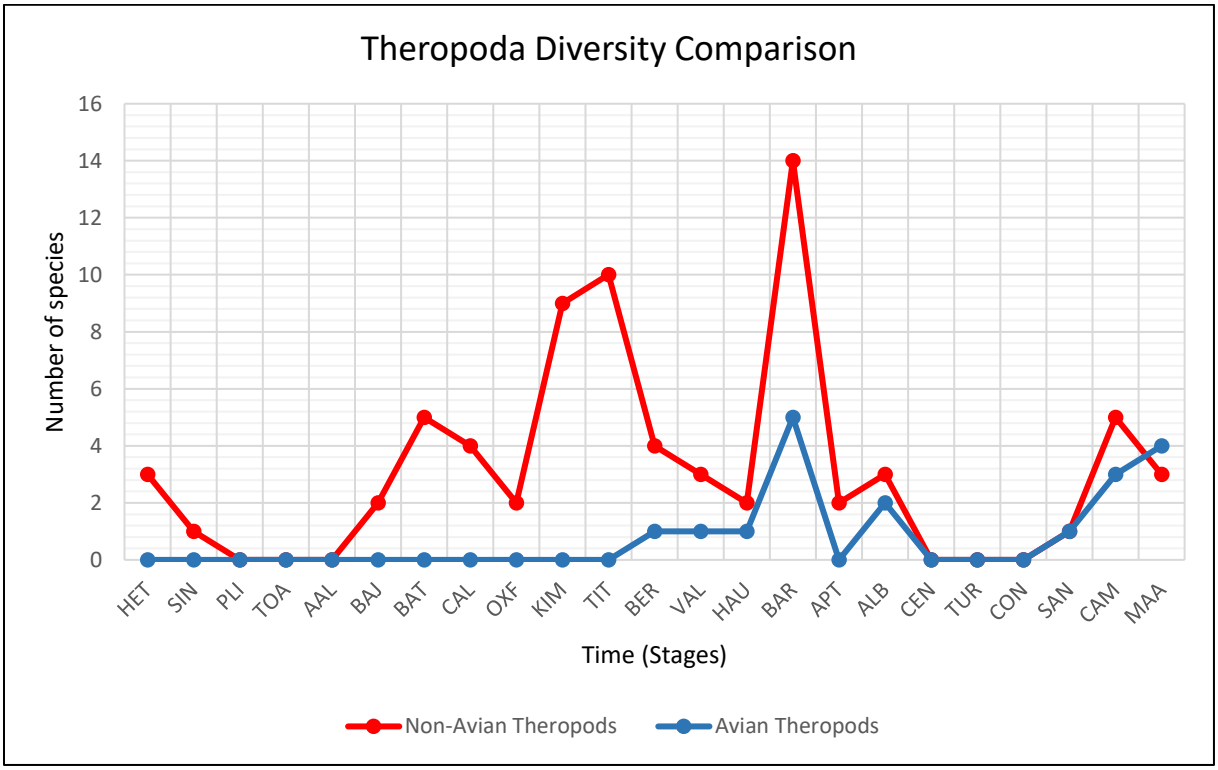

Figure 25: Comparison of the standing clade diversity of European Jurassic and Cretaceous theropods, excluding Jurassic birds as avian theropods.

The occurrence of avian theropods in Europe begins inconspicuously in the Berriasian and continues at a low level until the Hauterivian, before a significant peak occurs in the Barremian. Interrupted by a hiatus in the Aptian and a significantly lower number of species in the Albian. This is followed by a complete break in occurrence from the Cenomanian to the Coniacian. From the Santonian a strong gradual increase begins, which ended in the Maastrichtian with a renewed peak.

The data clearly show that the Aves had a strong influence on theropod diversity, especially in the Barremian and from the Santonian to the Maastrichtian, and therefore, taken as a whole, it would have significantly increased rather than decreased once again at the end of the Cretaceous. Figure 26 shows the total standing species diversity of European Jurassic and Cretaceous dinosaurs.

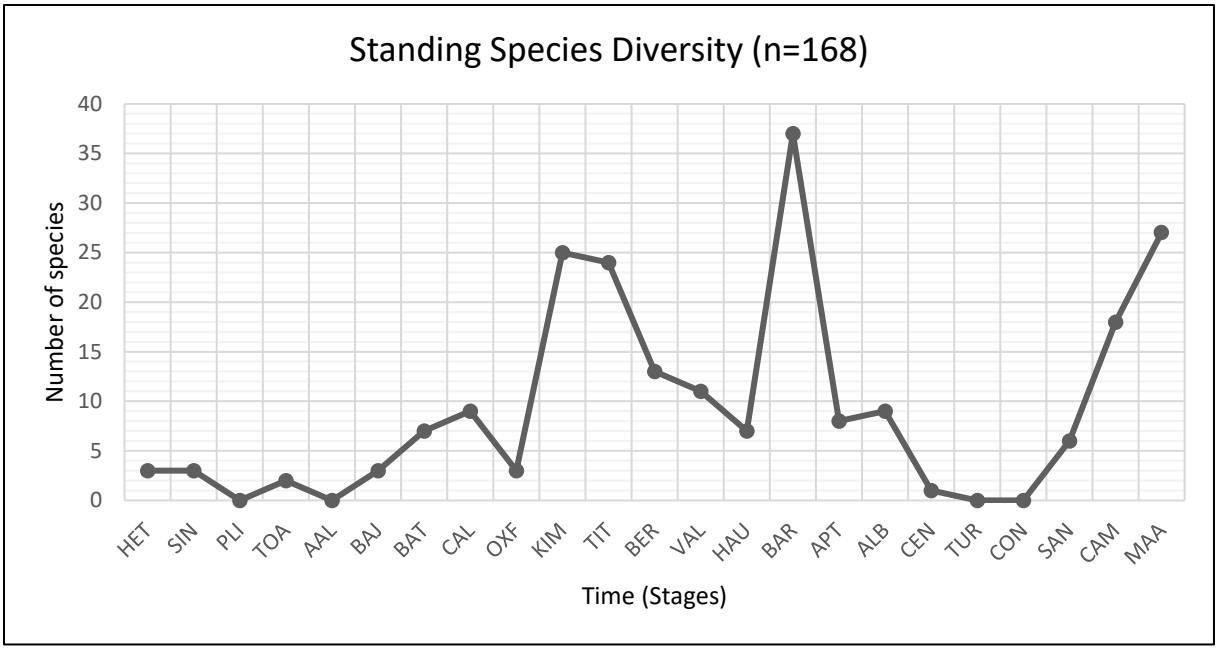

Figure 26: Standing species diversity of all European Jurassic and Cretaceous dinosaurs (incl. birds).

Compared to Figure 10, it can be seen that avian dinosaurs enhanced the peaks, but do not appear to have any effect on the diversity trend of the dinosaurs as a whole.

European fossil record

One of the most important direct influences on palaeodiversity is the actual number and distribution of sites, which can give an insight into the past. In the following graphs (Figure 27-29) the frequency and distribution of the individual fossiliferous regions were analysed, providing information about the fossil record of Jurassic and Cretaceous European dinosaurs.

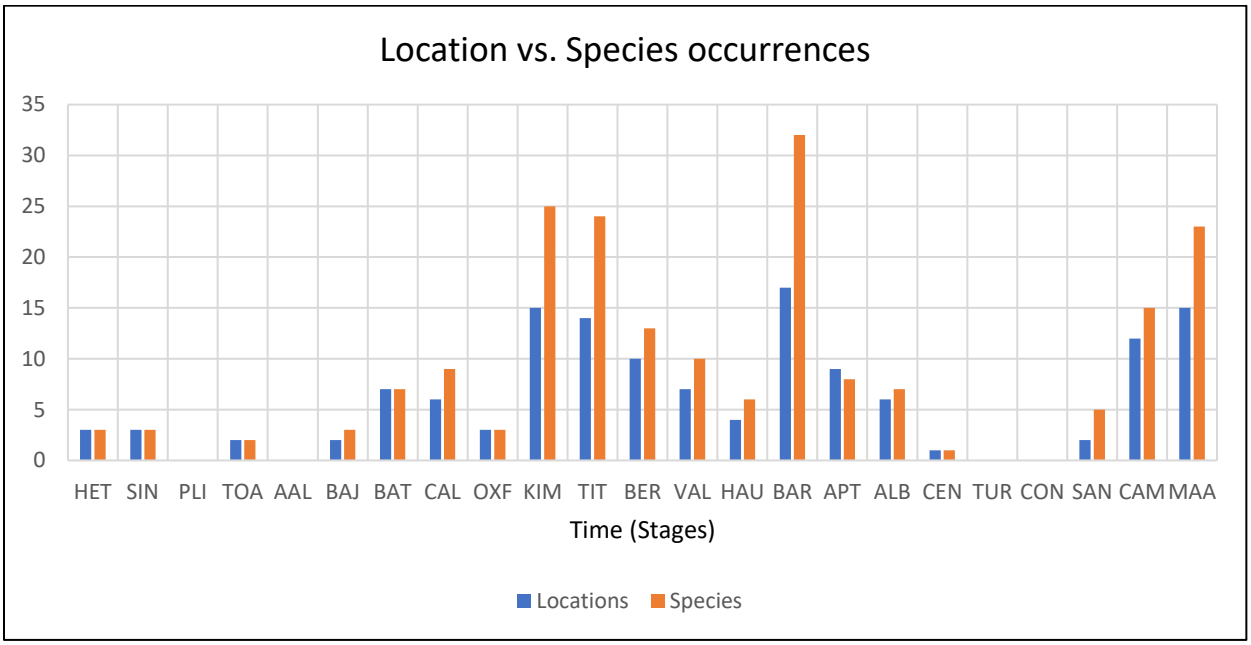

Figure 27: Species diversity against the number of fossil localities of European Jurassic and Cretaceous non-avian dinosaurs.

The number of non-avian dinosaurs detected is in most cases, as expected, equal to or higher than the number of sites (Figure 27). In the Kimmeridgian, Tithonian, Barremian, and Maastrichtian, the number of discovered species is even significantly higher than the number of available localities. In the Aptian and Albian, however, the number of sites outweighs the number of different species actually found, this is possible, for example, when a species occurs at several sites. From the Pliensbachian, Aalenian, Turonian and Coniacian unfortunately no fossils are available, which correlates with a lack of suitable deposits.

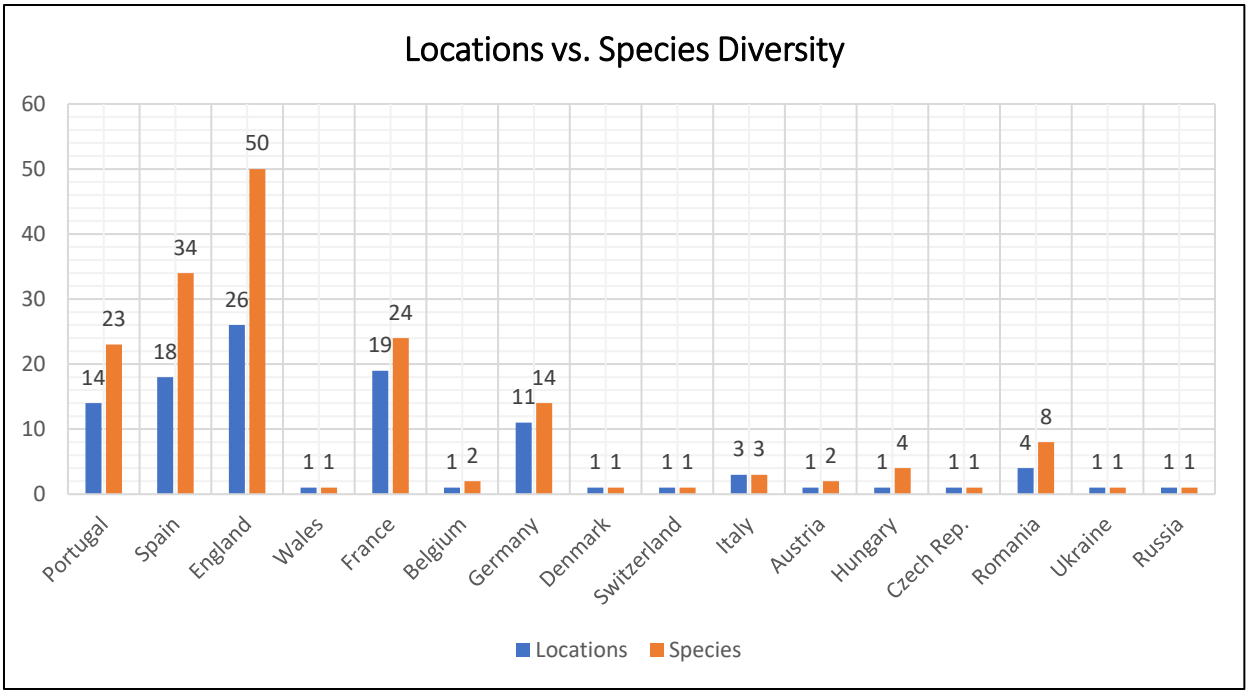

Figure 28: Number of sites and species diversity of European Jurassic and Cretaceous non-avian dinosaurs per country.

Figure 28 shows that the number of species detected is equal to or higher than the number of sites found. A clearly exceeding ratio is evident in England, Spain and Portugal (probably also Hungary and Romania). France and Germany may also be counted among the countries with the highest number of species. The remaining European countries conversely, show low occurrences.

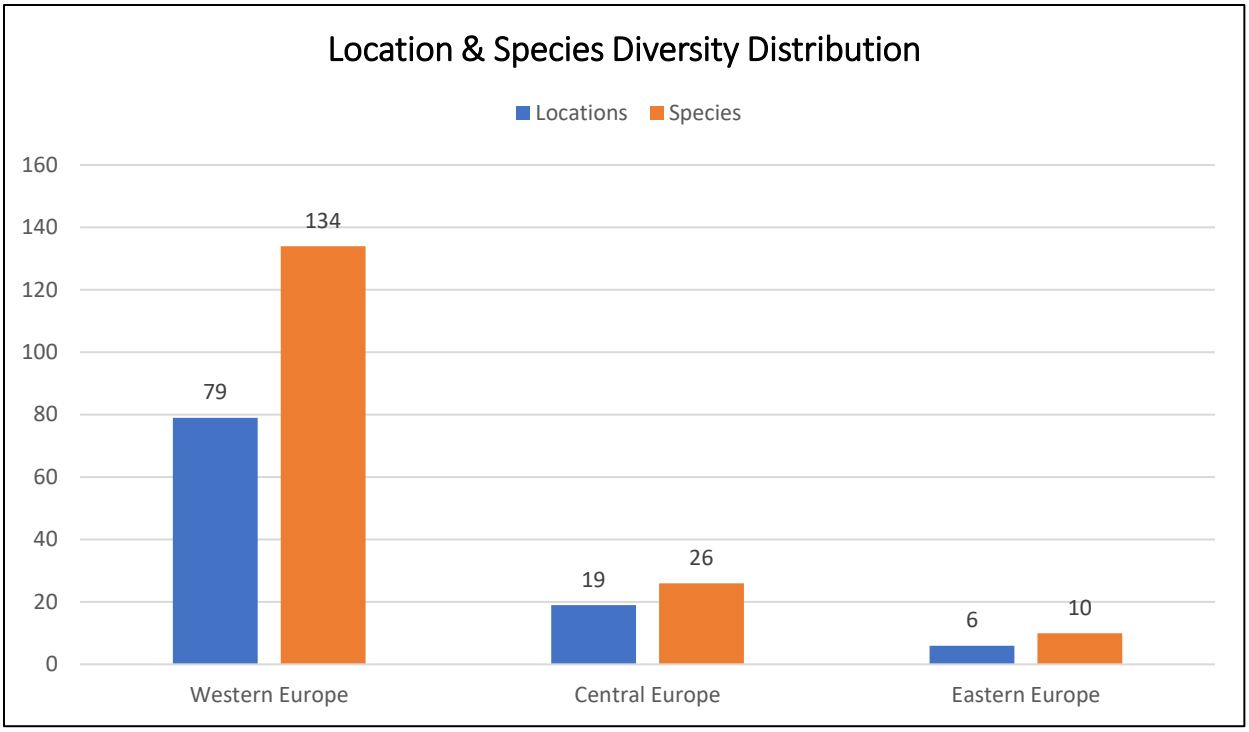

Figure 29: Distribution of the number of Jurassic and Cretaceous locations and species, by geographical regions.

Figure 29 shows that the ratio of found species to sites is clearly more differentiated only in Western Europe. In terms of the number of sites, Western Europe (76%) represents the vast majority compared to Central Europe (18%) and Eastern Europe (6%). Also, the species richness reaches the absolute maximum in Western Europe (79%) clearly ahead of Central Europe (15%) and Eastern Europe (6%).

Individual rarefaction

In order to evaluate the significance of the diversity trends more precisely, the underlying collection success of the sites and species abundances per stage were examined by means of an individual rarefaction analysis. Due to a lack of data, the analyses excluded the Hettangian, Sinemurian, Pliensbachian, Toarcian and Aalenian.

The sample size for the Middle Jurassic is not complete enough after subjected rarefaction analysis for the stages Bajocian, Bathonian and Callovian (Figure 30). Only in the Bathonian an early plateau of species diversity could have been reached (Figure 31).

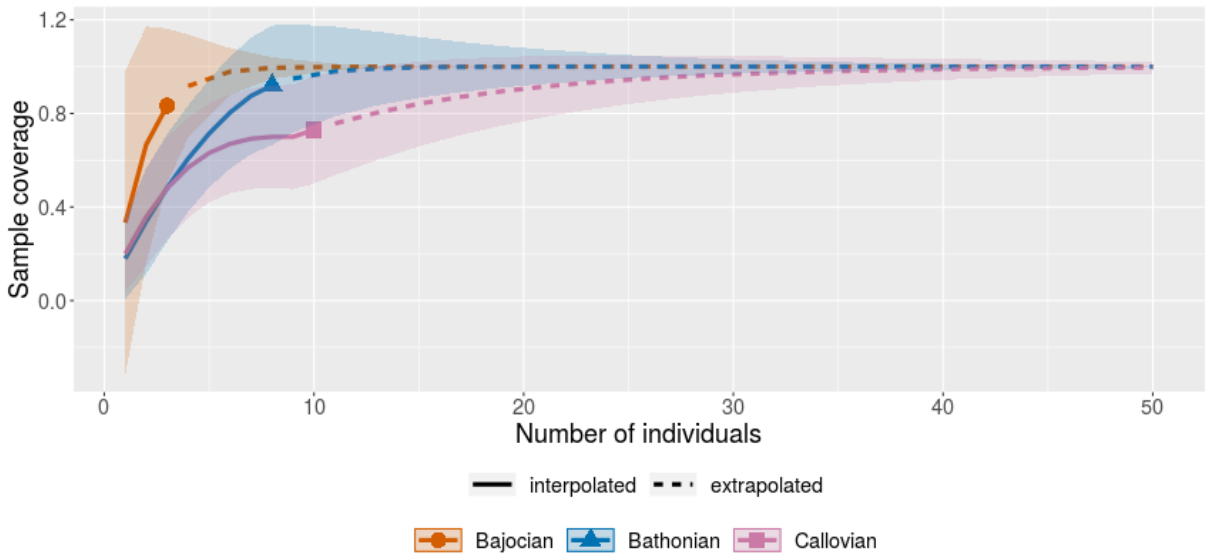

Figure 30: Performed rarefaction curves of the sample coverage for the Bajocian, Bathonian and Callovian are shown.

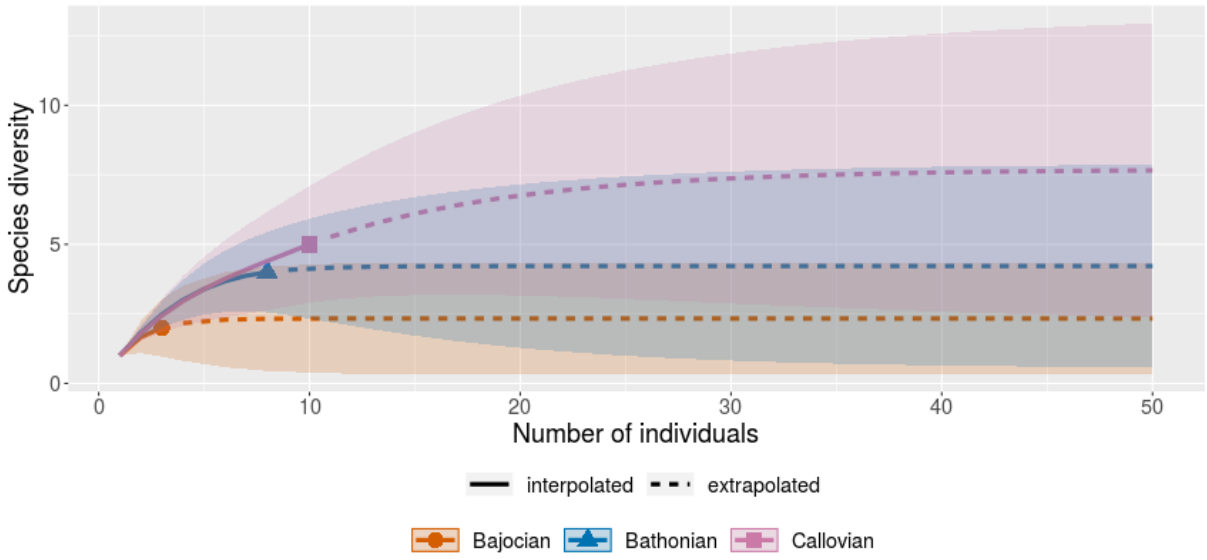

Figure 31: Performed rarefaction curves of species diversity for the Bajocian, Bathonian and Callovian.

For the Late Jurassic, acceptable sample coverage can be assumed for both the Kimmeridgian and Tithonian, whereas an incomplete quantity is present for the Oxfordian (Figure 32). The species diversity reached a decent value in the Kimmeridgian, whereas a somewhat higher value can be assumed in the Tithonian, too few data are available for the Oxfordian (Figure 33).

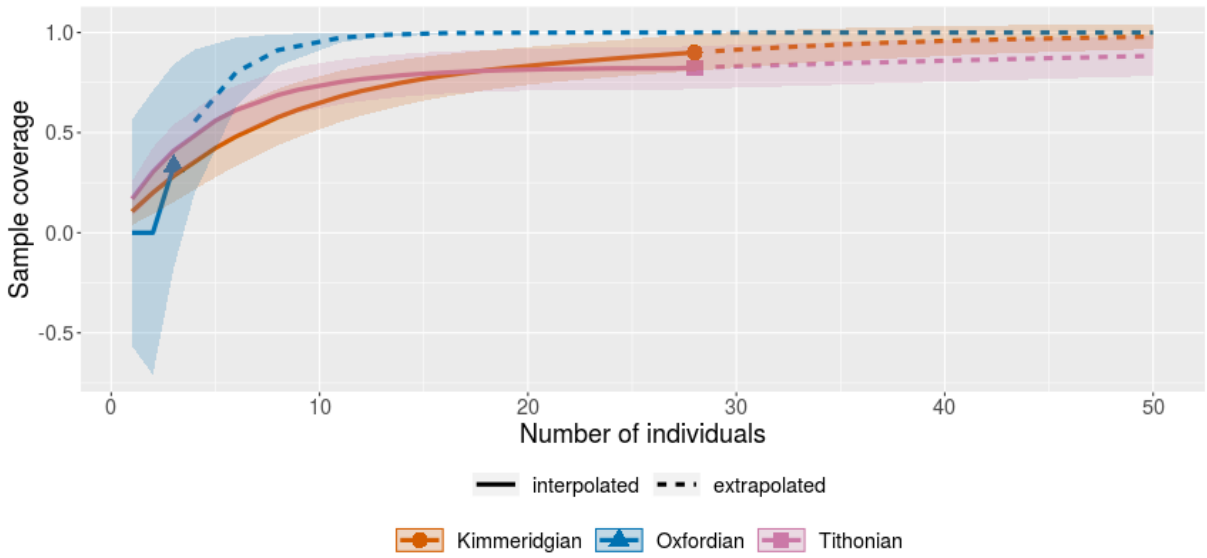

Figure 32: Performed rarefaction curves of the sample coverage for the Oxfordian, Kimmeridgian, and Tithonian.

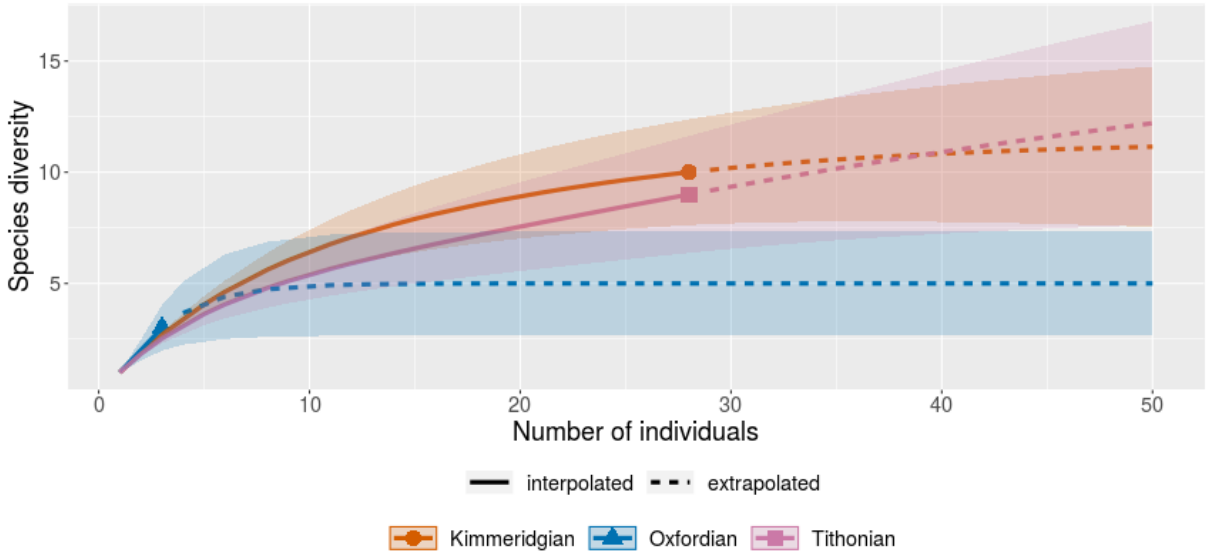

Figure 33: Performed rarefaction curves of species diversity for the Oxfordian, Kimmeridgian, and Tithonian.

Sample coverage for the Berriasian has reached a plateau, while calculations for the Valanginian and Hauterivian are higher but the number of individuals is low (Figure 34). The analysis of the species diversity shows a still slightly increasing curve in the Berriasian. In the Hauterivian no secure plateau was reached due to the low number of individuals. The deviations in the Valanginian are too large (Figure 35).

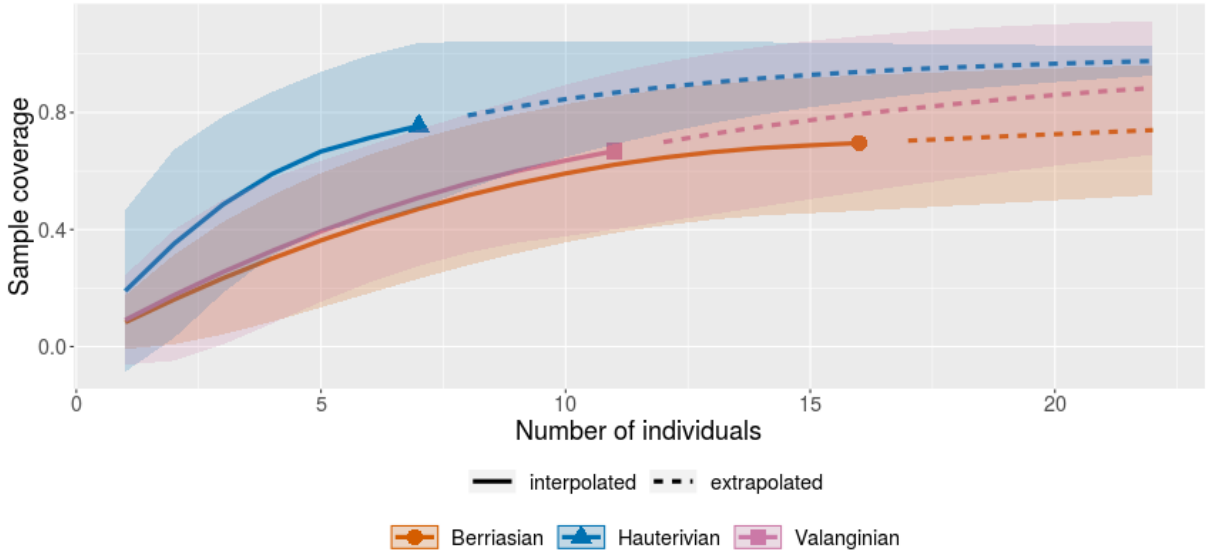

Figure 34: Performed rarefaction curves of the sample coverage for the Berriasian, Valanginian and Hauterivian.

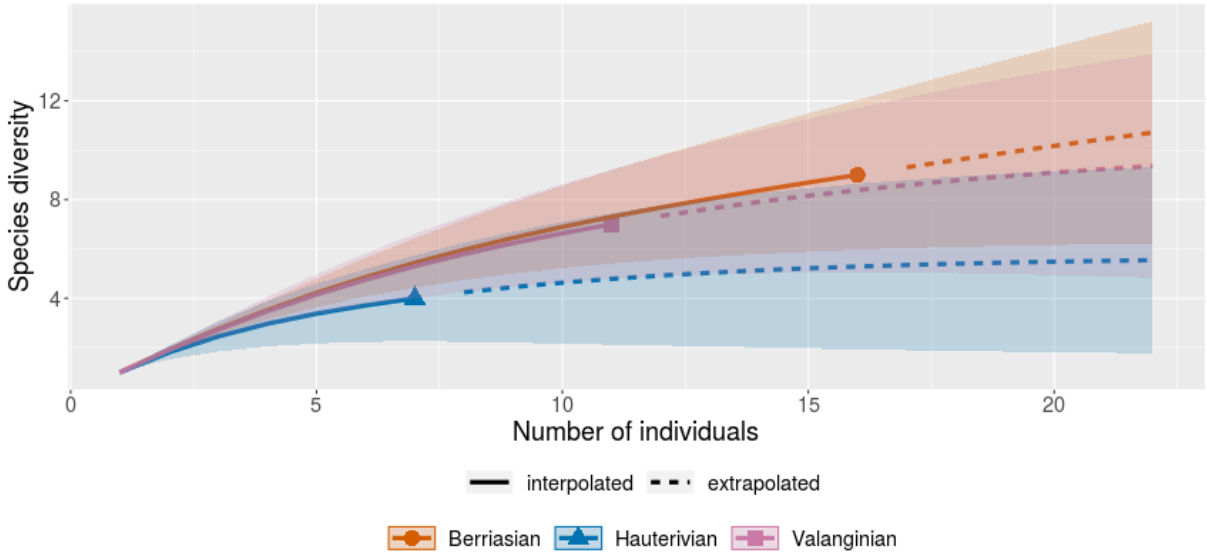

Figure 35: Performed rarefaction curves of species diversity for the Berriasian, Valanginian and Hauterivian.

Both the sample coverage and species diversity curves for the Barremian assume an acceptable sample size. The species diversity in the Aptian shows an approximately stable course, whereas the sample coverage is still increasing. In the Albian, both curves do not show an applicable trend (Figure 36 and 37).

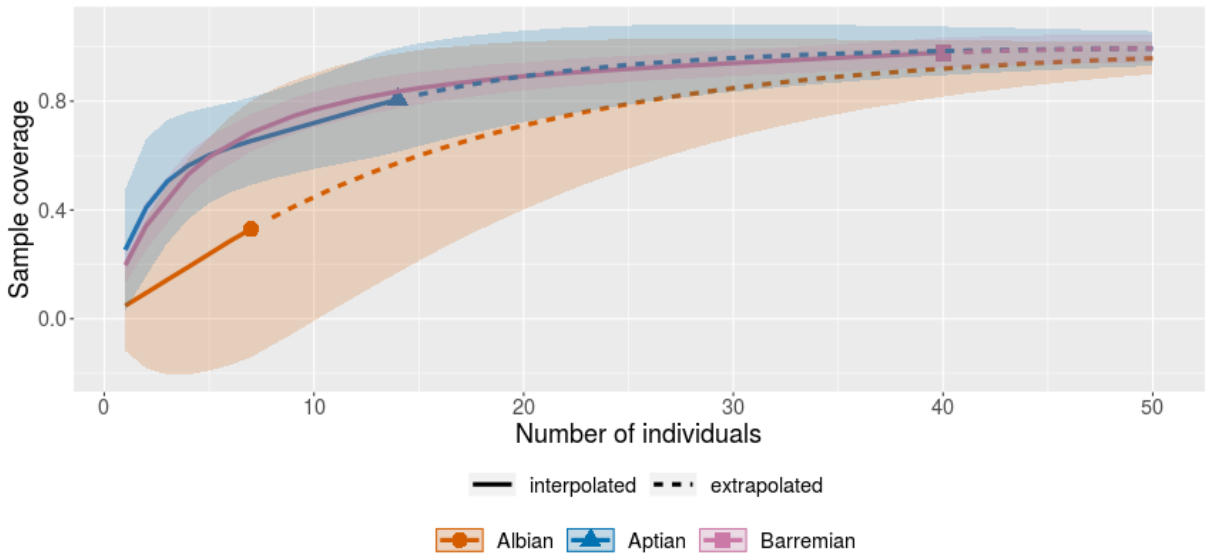

Figure 36: Performed rarefaction curves of the sample coverage for the Barremian, Aptian and Albian.

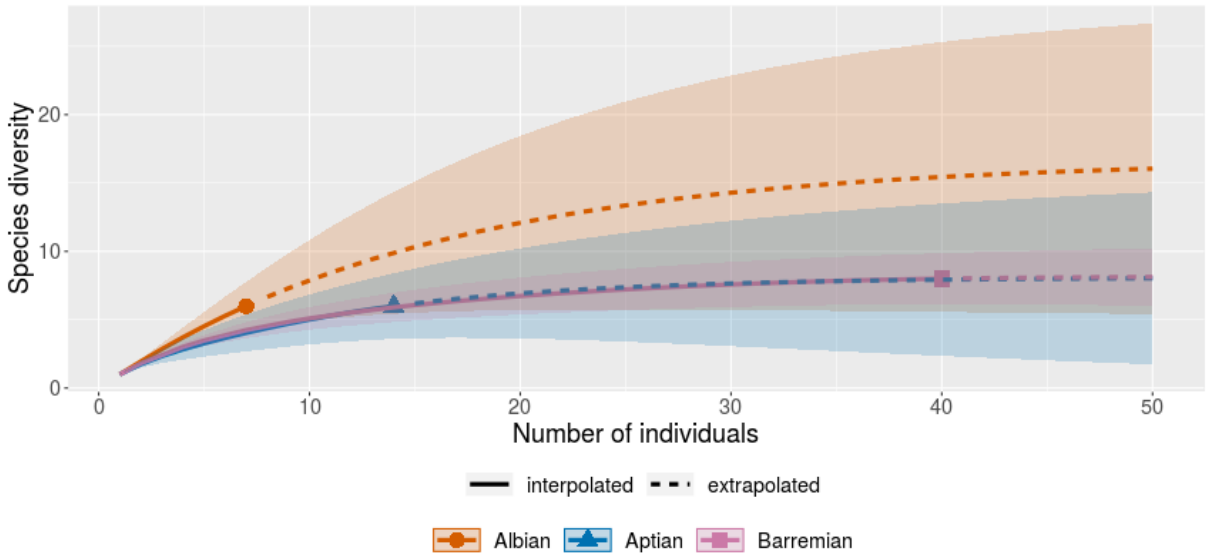

Figure 37: Performed rarefaction curves of species diversity for the Barremian, Aptian and Albian.

For the Cenomanian, Turonian and Coniacian of the Late Cretaceous, too few data for a rarefaction analysis are available. Both the sample coverage and species diversity curves assume, however, an acceptable amount of data for the Campanian and Maastrichtian, with too few finds for the Santonian (Figure 38 and 39).

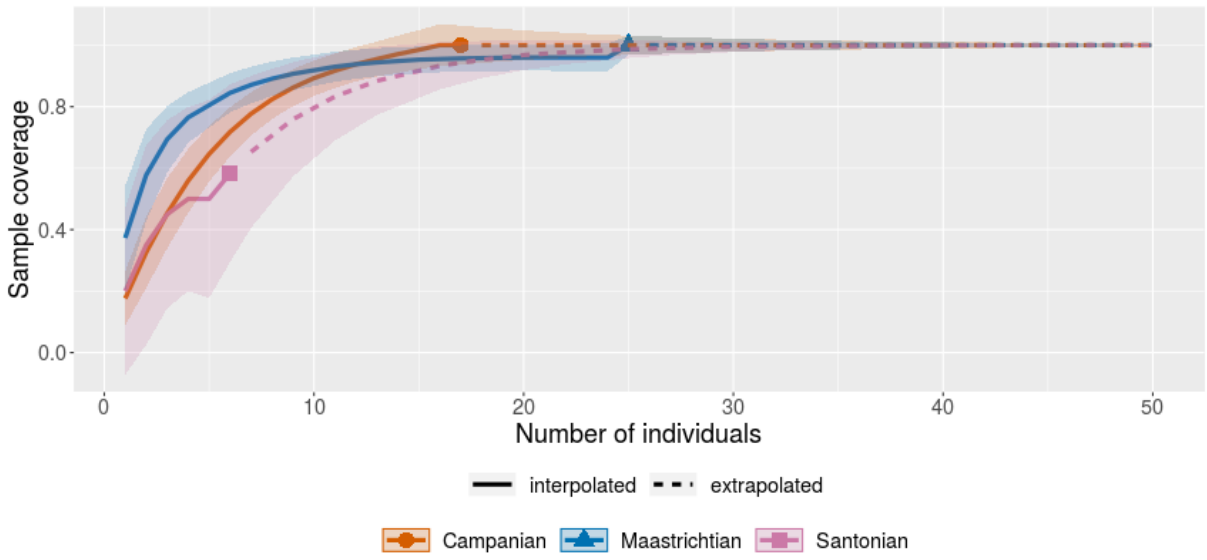

Figure 38: Performed rarefaction curves of the sample coverage for the Santonian, Campanian and Maastrichtian.

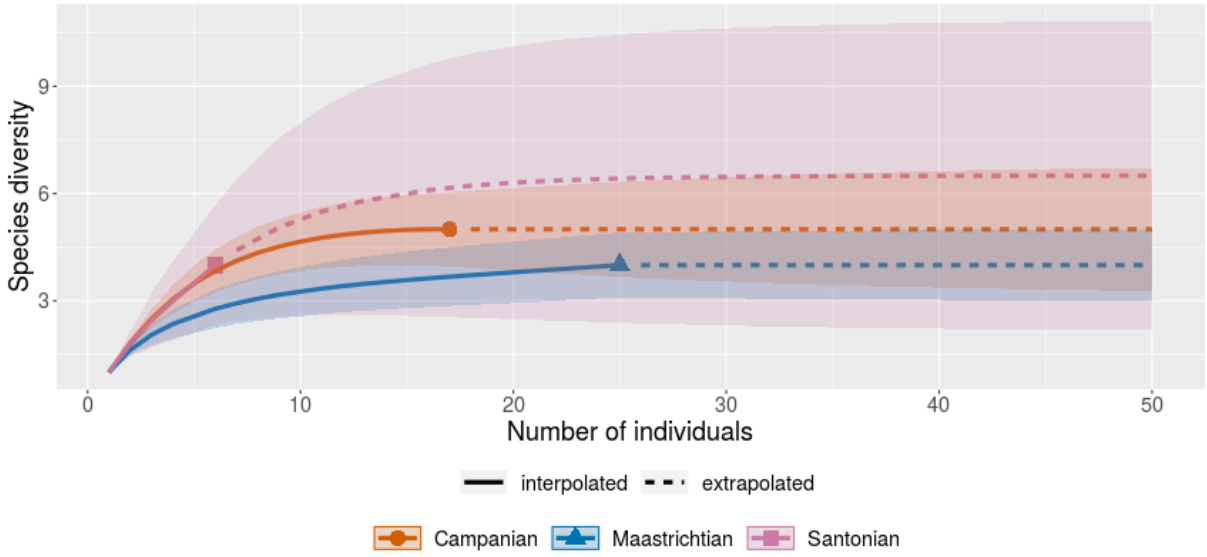

Figure 39: Performed rarefaction curves of species diversity for the Santonian, Campanian and Maastrichtian.

Simpson´s diversity index

The European non-avian dinosaurs were determined by applying the Simpsons Diversity Index (SD) for selected regions and geological periods (Table 1-3). A detailed breakdown of the calculations is shown in the appendix.

Table 1: Calculated SD value of European non-avian dinosaur clades of the Jurassic and Cretaceous.

Simpson´s Diversity Index (SD) - Total													
PT & ES		GB		BE & FR		DK & DE		IT & CH		AU & HU & CZ		RO & RU & UA	
D	0.85	**D**	0.9	**D**	0.83	**D**	0.65	**D**	0.9	**D**	0.8	**D**	0.6

The regions Great Britain (0.90) and Italy & Switzerland (0.90) achieve the highest diversity values (D), although the sample size of Italy & Switzerland with N=5 has little significance, followed by the regions Portugal & Spain (0.85) and Belgium & France (0.83). As a result of the significant West-East gradient, Western Europe was examined in more detail in the next tables.

Table 2: Calculated SD value of European non-avian dinosaur clades of the Jurassic.

Simpson´s Diversity Index (SD) - Jurassic					
Portugal & Spain		Great Britain		Belgium & France	
D	0.87	**D**	0.9	**D**	0.75

The highest SD value in the Jurassic is evident for Great Britain (0.90), closely followed by Portugal & Spain (0.87), with a distance to Belgium & France (0.75).

Table 3: Calculated SD value of European non-avian dinosaur clades of the Cretaceous.

Simpson´s Diversity Index (SD) - Cretaceous					
Portugal & Spain		Great Britain		Belgium & France	
D	0.79	**D**	0.87	**D**	0.73

Overall, the SD value in the Cretaceous is lower compared to the Jurassic of Western Europe. The highest value is achieved in Great Britain (0.87), followed by Portugal & Spain (0.79) and Belgium & France (0.73).

Shannon´s diversity index

The clades of European non-avian dinosaurs were determined by applying Shannon's Diversity Index (SH) for selected regions and geological periods (Table 4-6). A detailed breakdown of the calculations is shown in the appendix.

Table 4: Calculated SH value of European non-avian dinosaur clades of the Jurassic and Cretaceous.

Shannon´s Diversity Index (SH) - Total												
PT & ES		GB		BE & FR		DK & DE		IT & CH		AU & HU & CZ		RO & RU & UA	
H	2.12	**H**	2.3	**H**	1.79	**H**	1.31	**H**	1.33	**H**	1.27	**H**	1.03

Great Britain (2.30) and Portugal & Spain (2.12) display by far the highest diversity values (H), followed by Belgium & France (1.79). Due to the striking West-East discrepancy, Western Europe was examined again more closely with the results shown in the following tables.

Table 5: Calculated SH value of European non-avian dinosaur clades of the Jurassic.

Shannon´s Diversity Index (SH) - Jurassic					
Portugal & Spain		Great Britain		Belgium & France	
H	2.15	**H**	2.05	**H**	1.35

Portugal & Spain (2.15) display the highest SH score, just ahead of Great Britain (2.05), with a large gap to the region of Belgium & France (1.35).

Table 6: Calculated SH value of European non-avian dinosaur clades of the Cretaceous.

Shannon´s Diversity Index (SH) - Cretaceous					
Portugal & Spain		Great Britain		Belgium & France	
H	1.79	**H**	2.09	**H**	1.32

Overall, the SH value in the Cretaceous is lower compared to the Jurassic of Western Europe. The highest value is evident again, for Great Britain (2.09), with clear differences ahead of Portugal & Spain (1.79) and Belgium & France (1.32).

Jaccard index

To further investigate the interactions of clades of European non-avian dinosaurs within the continent, as well as the regions of Iberia (Portugal & Spain), Great Britain (England & Wales), and Belgium & France, through time, the similarity of faunas was calculated using the Jaccard Index (Table 7-9). A detailed breakdown of the calculation method is shown in the appendix.

Table 7: Calculated Jaccard Index value of European non-avian dinosaur clades of the Jurassic and Cretaceous showing the similarities between each region.

Jurassic	
Region	Jaccard Index [%]
Western - Central EU	42.86
Cretaceous	
Region	Jaccard Index [%]
Western - Central EU	23.08
Western - Eastern EU	33.33
Central - Eastern EU	60.00

During the Jurassic, the Jaccard Index indicates a weak similarity of dinosaur clades of 42.86% between Western and Central Europe. In the Cretaceous, the highest agreement is between Central and Eastern Europe with 60%, although the rather small sample size of both regions must be taken into account in the interpretation and increases the error rate.

Table 8: Calculated Jaccard Index value of European non-avian dinosaur clades of the Jurassic showing the similarities between each region.

Jurassic	
Region	Jaccard Index [%]
Iberia - Belgium & France	30.77
Iberia - Great Britain	61.54
Great Britain - Belgium & France	40.00

The Jurassic of Western Europe shows an above-average similarity between the region of Iberia and Great Britain, with 61.54%.

Table 9: Calculated Jaccard Index value of European non-avian dinosaur clades of the Cretaceous showing the similarities between each region.

Cretaceous	
Region	Jaccard Index [%]
Iberia - Belgium & France	45.45
Iberia - Great Britain	81.82
Great Britain - Belgium & France	45.45

The Cretaceous of Western Europe has a strong correspondence of clade presence between Iberia and Great Britain at 81.82%, with weak signals between the other regions as well.

Climate data analyses

Based on a global pCO2 dataset from Foster et al. (2017), radiative forcing (RF) and global mean temperature (GMT) values were calculated for the study period and plotted in five million year steps (Figures 40-42).

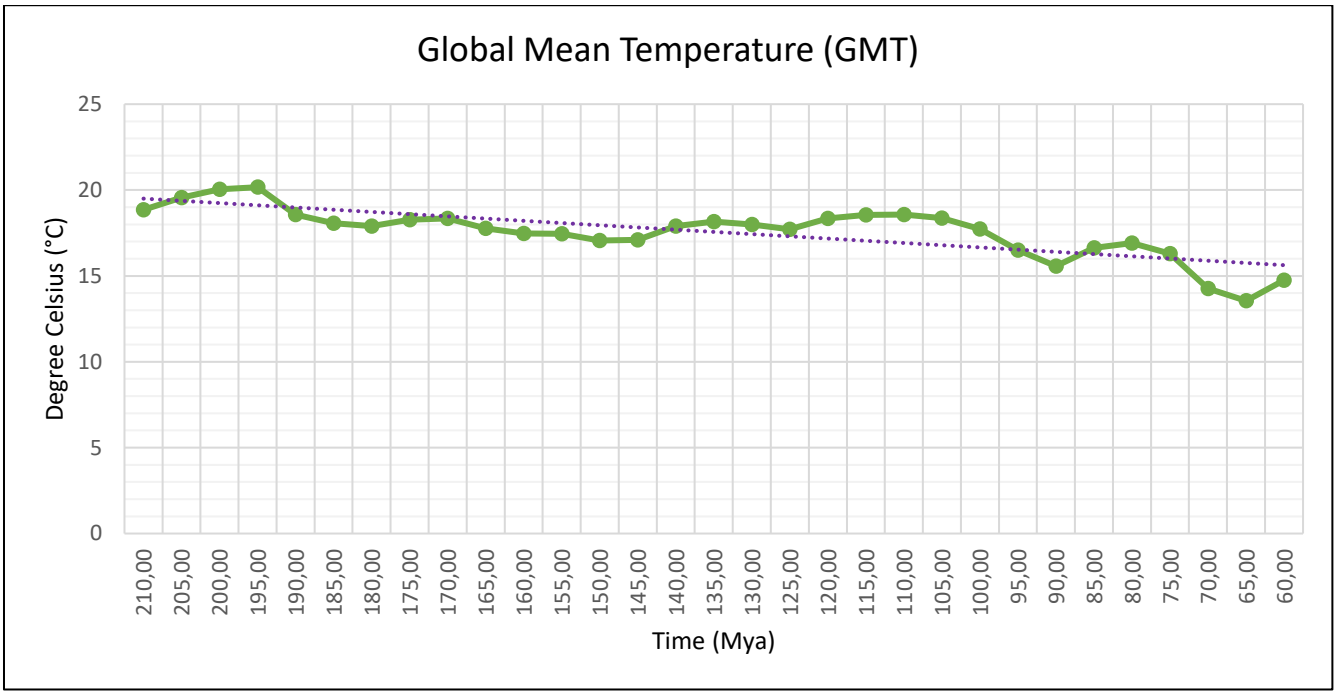

Figure 40: Progression of the global mean temperature (GMT) in degrees Celsius from the Norian (Triassic) to the Seladian (Paleogene) in time bins of 5 million years.

The calculated GMT (Figure 40) started at a rather high level in the Hettangian and continued to the middle Sinemurian at about 20°C before gradually decreasing to 17.8°C by the Toarcian boundary. From the Toarcian to the Late Bajocian, the temperature rises and holds around 18.2-18.4°C until the Early Bathonian. Thereafter, a slight cooling to 17.8°C occurred until the Oxfordian boundary. GMT only ranged between 17.8-17.0°C from the Early Oxfordian to the Late Tithonian, with intermittent peak variations of 0.6°C within 500,000 years. At the Jurassic-Cretaceous transition, the temperature dropped from about 17.2 to 16.8°C within a million years. From the early Berriasian, GMT steadily increased from 16.8 to 18.3°C into the Middle Valanginian. Over the next 36 million years, the temperature fluctuated only by about 1.2°C between 17.6-18.8°C with no noticeable abrupt collapses. A gradual cooling from about 17.8 to 15.5°C occurred along the Cenomanian to the Coniacian boundary, followed by another slow rise, up to 17.1°C

in the Middle Campanian. From the Middle Campanian onward, a significant cooling phase set in, changing the GMT from about 17.0 to 13.4°C by the Late Maastrichtian, well below the previous trend line. Overall, the global mean temperature was relatively stable over a period of nearly 100 million years, within a range of 2°C, experiencing slightly warmer and cooler episodes. Starting in the Cenomanian, the climate began to change significantly and was characterized by a strong cooling trend, with unique lows in the Maastrichtian that had not previously occurred over the entire study period.

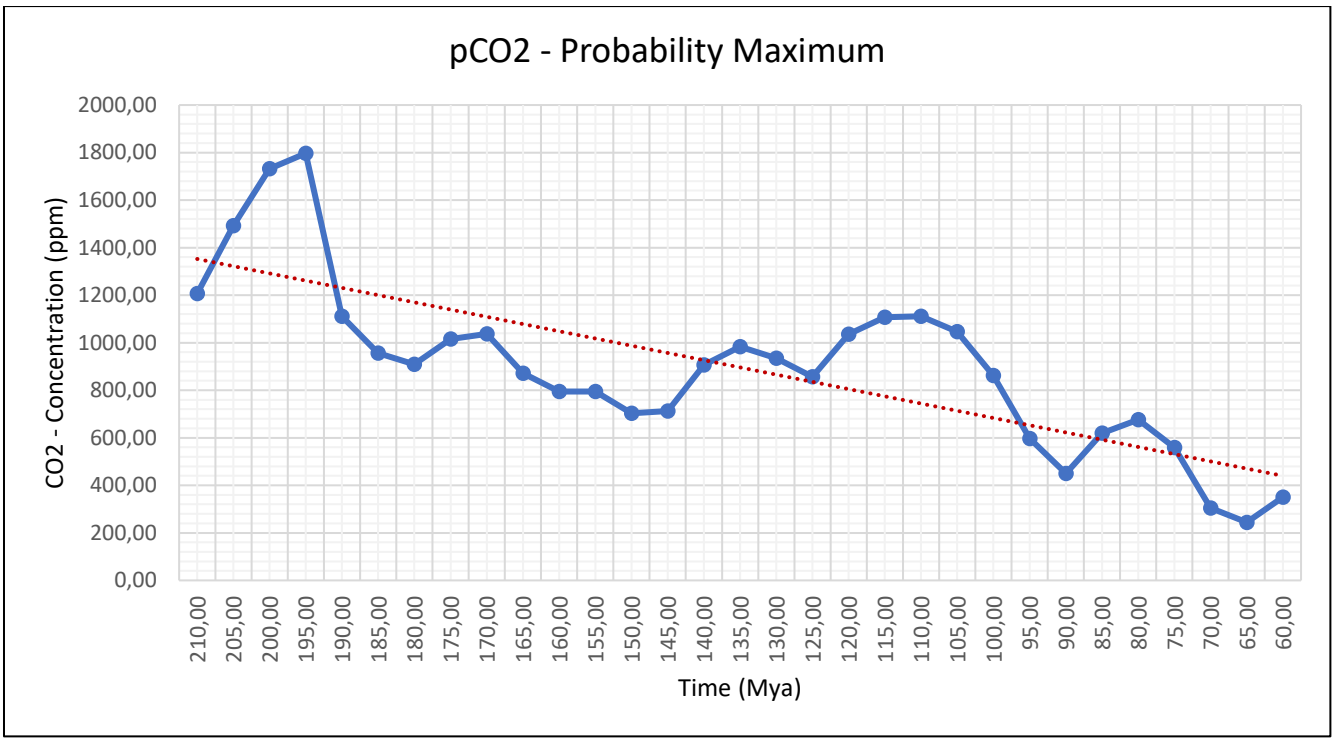

Figure 41: Progression of CO2 probability maximum in parts per million from the Norian (Triassic) to the Seladian (Paleogene) in bins of 5 million years. The graph shown is based on the data set of Foster et al. (2017).

At the beginning of the Jurassic the value was about 1732 ppm in the Hettangian and still increased to about 1800 ppm in the Sinemurian to the highest determined CO2 value. Up to the Toarcian boundary, the concentration decreased to 895 ppm, with a sharp drop from 300 ppm around 194 million years ago. From the Early Toarcian to the Late Bathonian, the pCO2 value fluctuated between 900-1070 ppm. Between the Callovian to the late Tithonian a decreasing trend in concentration occurred with fluctuations between 700-880 ppm, with a peak drop 150 million years ago (120 ppm). At the Jurassic-Cretaceous transition, the pCO2 value dropped by 62 ppm,

followed by a sharp increase (650-910 ppm) in concentration over the Berriasian. The period from the Valanginian to the Early Aptian was relatively stable with ranges between 825-1025 ppm, followed by a further increase with peaks up to 1200 ppm. Until the Late Albian, the value fluctuated between 1000-1200 ppm, before a downward tendency started at the transition to the Cenomanian. From the Cenomanian to the Coniacian boundary, the pCO2 level gradually dropped by nearly half, from 860 to 450 ppm. The concentration slowly increased again to 710 ppm by the Middle Campanian, before another significant reduction in the pCO2 value to only 230 ppm by the Late Maastrichtian. Despite large fluctuations (Figure 41), the transitions are, with a few exceptions, gradual with changes of at most 50 ppm within 500,000 years. The studied period showed a clear tendency for a decrease of the pCO2 level along the time, with changes starting in the Cenomanian which had a remarkable strong effect at the latest in the Campanian.

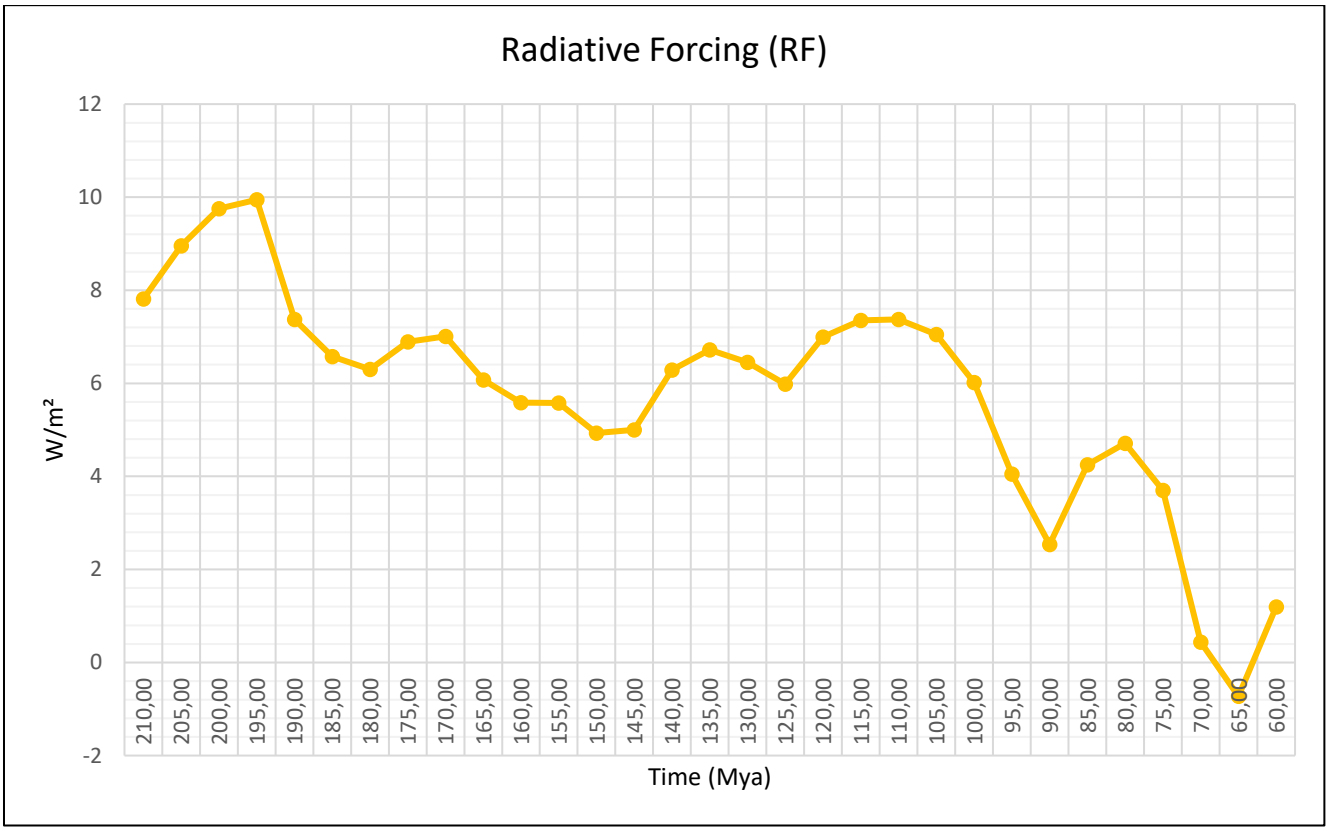

Figure 42: Course of radiative forcing with respect to solar radiation in W/m² from the Norian (Triassic) to the Seladian (Paleogene) in bins of 5 million years.

The plot of changes in radiative forcing (Figure 42) demonstrate agreement with the existing pCO2 data (Figure 41). Likewise, the effects of the factors on the calculated

global mean temperature (Figure 40) of the Jurassic and Cretaceous are shown, although at first sight in small magnitude.

Spearman's rank correlation test

The number of species of European non-avian dinosaurs (Figure 10) from the beginning of the Hettangian (201.3 Ma) to the end of the Maastrichtian (66.0 Ma) were tested for a possible correlation to global mean temperatures depicted in Figure 40 by using Spearman's rank correlation test.

The standard average calculation for the relationship between species abundance and global mean temperature (GMT) shows a very weak association with a p-value of 0.4633 (Figure 43).

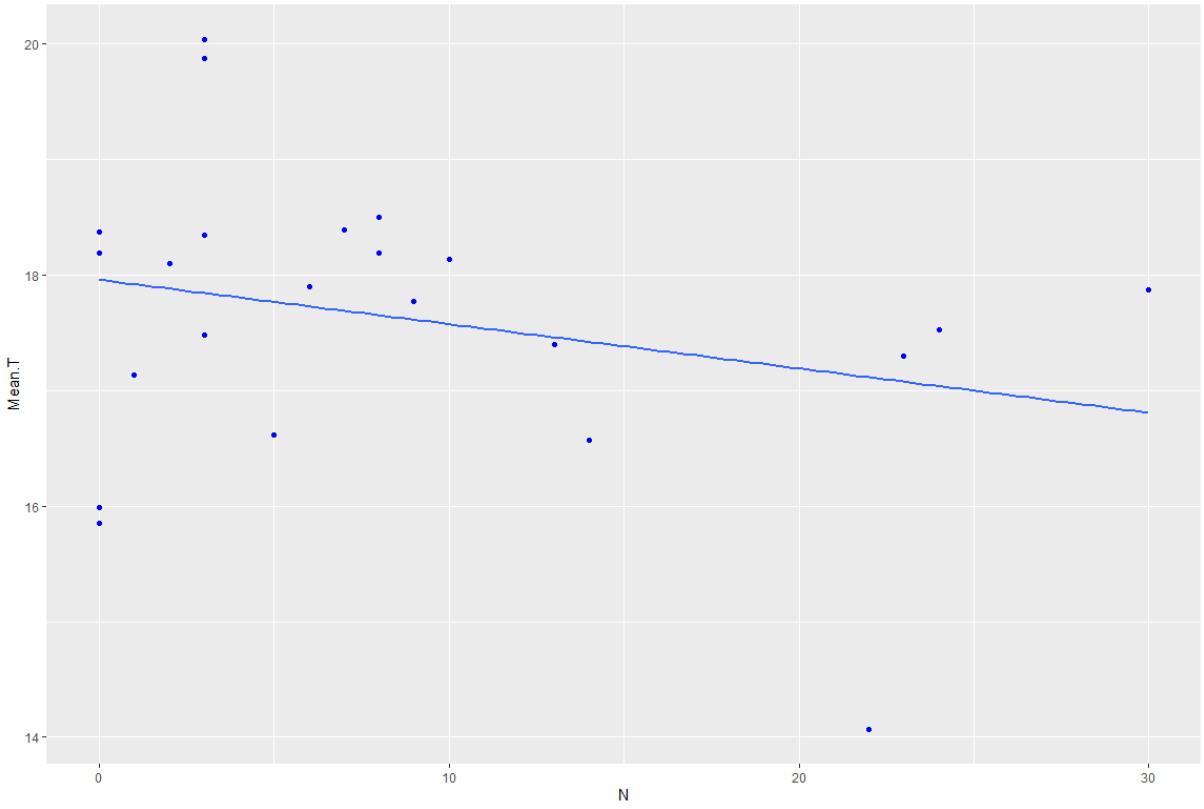

Figure 43: Spearman's rank correlation plot, shows the correlation of standard averages values between species abundance of European non-avian dinosaurs and the GMT of the Jurassic and Cretaceous.

The boundary crosser method for the relationship between species abundance and global mean temperature (GMT) shows a very weak association with a p-value of 0.5352 (Figure 44).

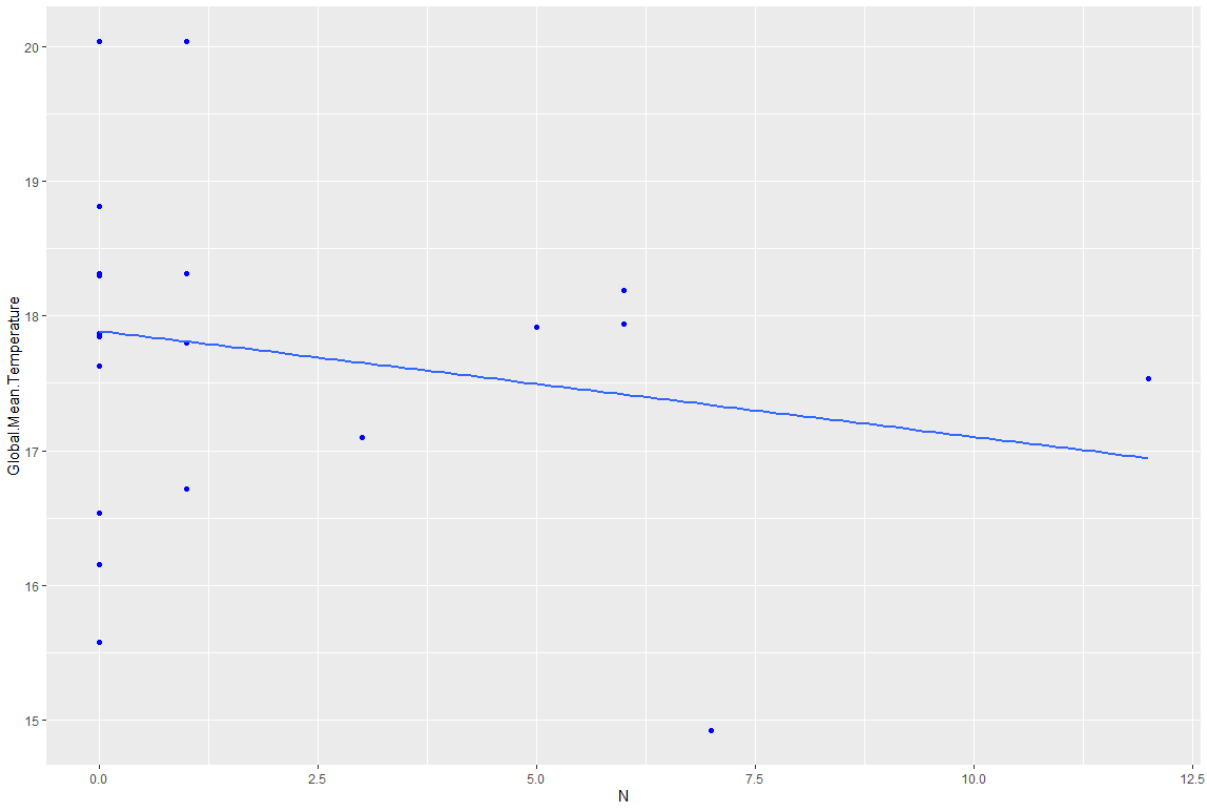

Figure 44: Spearman's rank correlation plot, shows the correlation of the boundary crosser method between the species abundance of European non-avian dinosaurs and the GMT of the Jurassic and Cretaceous.

No correlation between the number of species of European non-avian dinosaurs and the global average temperature over the Jurassic and Cretaceous could be found by using Spearman's rank correlation test.

DISCUSSION

Despite a long history of palaeontological research, many finds from different stages and the high public interest in the topic, the palaeobiodiversity of dinosaurs of Europe still is poorly known and understood. Numerous diversity analyses already dealt with the topic on a global scale or for North America and Asia. In the following, the relationships between abiotic factors and fossil availability are contrasted with the diversity on the European continent.

Availability and distribution of sites

It turned out that the fossil record from Europe during the Jurassic and Cretaceous is characterized by large irregularities. This refers to the geographic distribution of the

localities as well as to the temporal availability (Figure 6 and 7). The lack of finds from the Pliensbachian, Aalenian, Turonian and Coniacian means that there are time periods in the history of these animals, which still cannot be determined more precisely (Figure 27). The relationship between the number of sites and the number of remains recovered also varies enormously. For example, in the Barremian the number of species is much higher than the number of sites, indicating a high diversity density, whereas in the Bathonian both values are similar and thus indicate a lower abundance. In addition, there is a clear difference in the distribution of the sites among the countries (Figure 28), with England sporting the most fossil sites, followed by Spain and France. The West of Europe is much richer in sites and fossils than the middle or the east of the continent as defined here (Figure 29). This could be due to urban development, the associated lack of accessible layers or land ownership reasons (Csiki-Sava et al., 2015). However, geological conditions such as sedimentation rate, as well as palaeogeographic distribution of land mass are also of great importance to the taphonomic preservability of a cadaver and do not provide the same depositional environment in every area (Figure 8a-e). According to the findings of Chiarenza et al. (2019), the Campanian, for example, is more suitable for preservation than the Maastrichtian in many places. This does not seem to be the case in Europe, because the number of localities and the richness of species in the Maastrichtian far exceeds that of the Campanian (Figure 27). Furthermore, the exact chronostratigraphic units for the transitions of the Bathonian/Callovian/Oxfordian, Kimmeridgian/Tithonian/Berriasian/Valanginian, Hauterivian/Barremian/Aptian and Santonian/Campanian stages are still unclear (ICS, 2022). With these striking geologic impairments, it was essential to statistically test the significance of actual species abundance.

The individual rarefaction method showed that only the Kimmeridgian and Tithonian stages (Figures 32 and 33) in the Jurassic, and the Berriasian (Figures 34 and 35), Barremian (Figures 36 and 37), Campanian, and Maastrichtian (Figures 38 and 39) in the Cretaceous have an adequate collection success. This reduces the relevance and quality of many analyses to a few specific time periods.

Environmental conditions and feedback mechanisms

In addition to geological influences on the actual availability of fossils, environmental conditions have an impact on diversity itself. Based on the pCO2 dataset of Foster et al. (2017), global mean temperature was calculated for the study period. Due to the large time lag, the accuracy in reconstructing palaeoclimate and sea levels is insufficient. Since there can be large differences on a regional scale and most environmental data were obtained from marine organisms, there are uncertainties on the validity for terrestrial life. Figure 41 shows that globally there were huge variations in CO2 probability maximum during the Jurassic and Cretaceous. Dinosaurs were exposed to both highs of 1800 ppm in the Sinemurian and lows of 230 ppm just before the Masstrichtian asteroid impact. Among them, concentration fluctuated up to 300 ppm within 500 000 years (Sinemurian). The pCO2 level shows a strongly decreasing trend during the Jurassic and Cretaceous. Especially in the Upper Cretaceous the system became more and more unstable and shows considerable swings. Figure 42 shows that the radiative forcing was stable for most of the time, but fundamental changes occurred around the Cenomanian. In the Maastrichtian and Danian even a negative radiative forcing was reached, which means that the Earth lost more energy to space than it received. The Jurassic started very warm, reaching about 20°C on average in the Hettangian and Sinemurian. Despite the long period, the climate was characterized by great stability. For about 100 million years, the global mean temperature varied by only 2°C. From the Cenomanian on, the temperature started to decrease and reached only about 13.5°C in the late Maastrichtian (Figure 40).

A more detailed picture of past climate relationships, however, was obtained by comparing the pCO2 concentration (Figure 41) with sea levels (Figure 2 and 5), based on the work of Holz (2015). Due to the higher resolution, changes in CO2 concentration can be seen more clearly than in the global mean temperature, which does not provide relevant information on peak values. There is evidence for the presumed existence of two different feedback mechanisms during the Jurassic and Cretaceous. Since this focus was not the aim of the discussed study, only hypothetical indications can be explained. The beginning of the Jurassic, in the Hettangian and early Pliensbachian were characterized by particularly high

temperatures and CO2 concentrations. Simultaneously the sea level dropped to a minimum, which was even lower than today. From then on, the temperature and the CO2 value began to decrease strongly until the early Toarcian and the sea level was rising just as much, except for a short anomaly. Subsequently, during the Aalenian, a renewed rise in temperature with associated sharp decline in sea level occurred. At the transition to the Bajocian temperature dropped again and the sea level rose until the late Bathonian. From there, possibly at the beginning of the Callovian, a trend reversal began, with decreasing temperatures and CO2 concentrations, the sea level also decreased. During the Kimmeridgian, both temperature and sea level climbed and fell together again at the transition to the Tithonian. After another joint rise in levels toward the end, renewed changes occurred. Especially visible in the Valanginian, where the sea level decreased strongly but the temperature increased. This interplay continued according to the fluctuations until the Turonian, where the highest known sea level was accompanied by a low pCO2 or temperature value, which was also not usual until then. From the Santonian to the end of the Cretaceous, a rise in temperature again corresponded to a sea level rise related to it, and conversely, the increasingly falling temperature towards the end of the period led to a lower sea level, although this signal in the Maastrichtian did not respond as sensitively as it did in other periods. In summary, it can therefore be concluded that there may have had been two different climatic feedbacks during the Jurassic and Cretaceous. First, a parallel antagonistic mechanism, which lead to lower sea levels at high temperatures or pCO2 concentrations and vice versa. Secondly, a synchronic mechanism which leads at high temperature or pCO2 concentration to an increased sea level and reversed. The synchronic feedback effect is known to us from the present time and is based on the fact that a permanent ice sheet on a continent in pole position (Antarctica) exists. This suggests that there could have been extensive ice caps in the past during the Late Jurassic and Late Cretaceous. Such an event may also have occurred briefly in the Toarcian. Unfortunately, the phenomenon of antagonistic mechanism is difficult to explain. Nevertheless, the observed warm and cold periods are also consistent with the palaeobotanical findings of Philippe et al. (2017). They recognized, based on the increased dispersal of northern plant genera, that strong cooling or precipitation must have occurred during individual sections of

the Pliensbachian, Toarcian, and Oxfordian in Europe. European terrestrial findings, which are also reflected in the global data set used here.

Dinosaur diversity on the European continent

Statistically, no direct significant relationship between global mean temperatures and species richness could be determined. But the climate had far-reaching effects on eustatic sea level and thus on the availability of land masses. As a result, dinosaurs were at least indirectly affected in their dispersal or by habitat preferences and food accessibility. The course of the standing species diversity of non-avian dinosaurs in Europe (Figure 10) follows the expected development, despite the poor stratigraphic availability, especially, for the Lower Jurassic and the early Middle Jurassic, which largely matches the data on a global scale. In the Early Jurassic, a stable, but in comparison to later following periods, rather low occurrence can be assumed. Towards the end of the Middle Jurassic, a first rise should have set in, since the prime of the dinosaurs also in Europe was within the Late Jurassic. An even higher peak in species richness is evident during the Barremian and also the number of taxa in the Late Jurassic (n=52) is clearly lower than in the Early Cretaceous (n=75), but in this case the geological time lengths have to be considered. Figure 12 shows a more realistic course using the calculated estimated mean standing diversity (EMSD). Since singletons are excluded in this calculation, which are relatively high (especially for dinosaurs), interpretations have to be contrasted with the raw diversity. Unfortunately, there is, during the early Late Cretaceous a long period, in which no or very limited information about the diversity can be provided.

The overall distribution of clades from non-avian dinosaurs during the Jurassic and Cretaceous, shows a good mixture (Figure 14). Despite the supposedly better preservation of sauropod fossils, theropods are very strongly represented and also neornithischians are common. It should not be forgotten that there is a clear difference between the regions of the continent in the analyses. Both the Simpson and Shannon indices (Table 1 and 4) show that the highest diversity occurs in the West. This could be due to geological collection biases because of longer research history as mentioned at the beginning. In Western Europe, it can be concluded that most dinosaur taxa found particularly good conditions in Iberia and Great Britain throughout time (Table 2, 3, 5 and 6). The Jaccard Index (Table 7) indicates that the

faunas of western and central Europe were even closer in the Jurassic (42.86%) than in the Cretaceous (23.08%). While a higher agreement is found between Central and Eastern Europe (60%) in the Cretaceous, although this could also be biased by the low sample size and different durations of research history. It also is obvious, however, that there could have formed several parts more or less isolated from each other. Especially Western Europe shows low faunal similarities to the rest of the continent, but this could also be due to collecting bias. Within this region, in turn, a large faunal exchange seems to have taken place between Iberia and Britain (Tables 8 and 9) in both the Jurassic (61.54%) and Cretaceous (81.82%). The central and eastern parts of Europe remain poorly understood but is likely to have evolved independently in isolation due to palaeogeographical conditions, this also seems logical due to the postulated island association (Csiki-Sava, 2015).

Figure 11 shows the standing diversity of the individual clades and indicates that the Neornithischia first appeared in Europe during the Callovian. The dispersal probably was facilitated by sinking sea levels of that time (Figure 2). During the Middle Jurassic, their diversity was probably still very low and increased for the first time in the Kimmeridgian (Figure 16 and 17). However, their abundance remained low in the Late Jurassic and even declined again in the Tithonian. They were the only clade whose diversity increased toward the Berriasian and underwent radiation in the Early Cretaceous, particularly in the Barremian (Figure 11). Within this time there must have been major changes in food plants, a niche that the Neornitischia were apparently able to exploit. Their faunal share increased from 7.5% in the Late Jurassic to 26.5% in the Early Cretaceous (Figure 17 and 18). They surpassed the Thyreophora in this period and were equal to the Sauropoda in number of herbivorous clades. After this first radiation, diversity declined sharply from the Aptian onward and remained at an intermediate level until the Santonian. From then on, an increase started again and during the Maastrichtian the Neornithischia reached a second radiation phase (Figure 11). In the Late Cretaceous, they formed the most successful clade with a faunal proportion of 48% and definitively displaced the Sauropoda (22.5%) among the dominant herbivores (Figure 19). This faunal shift demonstrates success due to particular adaptations for ecological niches during the Campanian and Maastrichtian (Vila et al., 2016, Fondevilla et al., 2019). Surprisingly,

the clade was composed of 86.5% Ornithopoda, 8.1% basal forms, and only 5.4% Marginocephalia.

During the Early Jurassic the large Sauropoda were still very rare faunal elements of the palaeocommunities and were found in Europe only from the Toarcian on. In the Middle Jurassic they already had a faunal share of 21% (Figure 16) and experienced a radiation in the Late Jurassic. Their diversity jumped to very high values in the Kimmeridgian and Tithonian and with 36.5% (Figure 17) they were the most successful herbivores of that time. In the Early Cretaceous, they were still among the most abundant clades with a faunal percentage of 26.5% (Figure 18). During the Aptian and Albian, the diversity decreased again. For almost 17 million years (Cenomanian-Santonian), no significant records occur. Mannion & Upchurch (2011) also recognized this "sauropod hiatus", which is probably only caused by the known poor finding situation. In the Campanian, Sauropoda are back again and their diversity even increased strongly again in the Maastrichtian. With 22.5% (Figure 19) they did not represent the enormous faunal proportion they occupied in the Late Jurassic, but their diversity was still high. No indications for a special heat preference of sauropods in Europe could be found (Dunne et al., 2023).

The Thyreophora are known in Europe since the Sinemurian, but are rare representatives throughout the Early and Middle Jurassic. In the meantime, no remains were reported from the Pliensbachian, Aalenian, Bajocian and Bathonian. However, in the Middle Jurassic they make up the majority of the small to medium sized herbivores with 16% (Figure 16). After further lacking evidence in the Oxfordian, they reached their highest diversity in the Kimmeridgian and Tithonian (Figure 11). With a faunal share of 15.5% (Figure 17), they defended their place in the Late Jurassic ahead of Neornithischia. Throughout the Early and Late Cretaceous, they kept their diversity at stable but very low levels and could at no time keep up with the abundance of other herbivores (Figure 18 and 19). Thyreophora experienced their prime when the largest and probably most dangerous theropods appeared in Europe, due to their defensive weapons they were apparently able to resist the density of carnivores.

Due to their high abundance and temporal as well as geographic good distribution, theropods are one of the most interesting dinosaur clades. With 37% faunal

contribution over the entire Jurassic and Cretaceous, the non-avian theropods are the most dominant group among European dinosaurs (Figure 14). During the Jurassic, they are disproportionately represented even for carnivorous animals compared to herbivores (Figure 15-17). With early forms such as *Dracoraptor hanigani* to apex predators like *Allosaurus europeus* and *Asteriornis maastrichtensis,* a close relative of today's chickens and geese, there was a wide morphological variation in species that could occupy diverse ecological niches.

Theropods are already detectable at low levels in Europe at the beginning of the Jurassic and probably remained at this level until the Bajocian. From the Pliensbachian to the Aalenian no remains have been found. In the Middle Jurassic a first radiation apparently starts in the Bathonian. After a decline in species richness in the Oxfordian, another major radiation sets in, from which the ancestors of birds also evolved. In the Middle Jurassic, the non-avian theropods accounted 58% of the total fauna, in the Late Jurassic still 40.5% (Figure 16 and 17).

A closer look into the composition of the clades reveals exciting changes during this time. In the Middle Jurassic, Megalosauroidea (82%) was by far the most dominant group among theropods. This changed when a radiation among the Coelurosauria (57%) occurred in the Late Jurassic, but these were mainly small carnivores (Figures 20 and 21). Among the medium to large carnivores, the Megalosauroidea (19%) received strong competition from the Allosauroidea (19%). An observation already noted by Rauhut et al. (2016), who found a faunal turnover on global scale from a Megalosauroidea dominated fauna in the Middle Jurassic to a Coelurosauria dominated fauna in the Late Jurassic, and a displacement by Allosauroidea among the large theropod taxa (Figure 3).

Another analysis on global level with a broader data set confirms this faunal change, however, did not detect a change in favor of the Allosauroidea among the large representatives of the Late Jurassic (Figure 4), but rather a balance (Etzler, 2020).

On the European level, the faunal turnover by Coelurosauria could be confirmed here as well, but also on this continent the Megalosauroidea share the niche of the larger carnivores with the Allosauroidea during the Late Jurassic (Figure 21). It is also questionable how many of the coelurosaurians of the Late Jurassic already represent true birds. Figure 24 shows the diversity patterns of the non-avian theropods in the

Late Jurassic, which (if we consider the intermediate forms of the Jurassic already as birds) would have already declined strongly in the Tithonian. Figure 25, in which only Cretaceous birds were identified as such, shows, in my opinion, a more realistic gradual progression of the avian theropod diversity, which is why this direction will be pursued further on.

At the beginning of the Early Cretaceous, the diversity of non-avian theropods falls sharply, while that of avian theropods remains stable at a low level until the Hauterivian (Figure 25). For both groups, a further possible radiation occurs in the Barremian, which ends abruptly in the Aptian and recovers only slightly in the Albian. From the Cenomanian to the Coniacian, a large gap in the records is recognizable. Again, from the Santonian onwards, the occurrence increases for the last time towards the Late Cretaceous, with avian theropods ending with an increasing trend and the non-avian theropods with a slight decline in the Maastrichtian.

The impact of the bird emergence can be seen more detailed in a breakdown of the theropod community. Even in the Early Cretaceous the non-avian theropods are the most common clade among the European dinosaurs (37%, Figure 18). Within theropods, however, major compositional changes occur again. Coelurosauria (34%) are no longer the most common faunal element, birds (26.5%), which are closely related, represent a high proportion. Among the large carnivores, it is evident that the Megalosauroidea (24%) were able to displace the Allosauroidea (10.5%) again or occupied different ecological niches (Figure 22). Due to the high sea level and the spreading of coastal landscapes, spinosaurid representatives like *Baryonyx walkeri* or *Iberospinus natarioi*, which were particularly adapted to a shore life, were able to establish themselves and appeared more frequently at this time.

A completely different picture can be seen in the Late Cretaceous, where the non-avian theropods make up only 20.5% of the total fauna (Figure 19). Figure 23 depicts important changes within the clade. After the gap in the fossil record during the early Late Cretaceous, no representatives of the previously diverse megalosauroids and also the allosauroids are found anymore. Instead, avian theropods (47%) already represent the majority of the group followed by coelurosaurians (41%). The era of giant carnivores in Europe was obviously over, only ceratosaurians (12%), which existed in small abundances during the whole study period, still provided

representatives, but even these were only of medium size and are no longer detectable in the Maastrichtian. In the meantime the majority consisted of the smaller and agile dromaeosaurids belonging to the Coelurosauria. Avian theropods became a very successful clade shortly after their first appearance and are still present today. However, despite their abundant occurrences they have not fundamentally changed the course of the total diversity. Figure 26 shows that only the diversity peaks have been amplified and their evolutionary pattern is predominantly similar to that of the non-avian theropods.

On the basis of Figure 24 also another hypothesis can be proposed. Assigning the Jurassic avian-like forms to birds and supporting the assumption that there were indeed large polar ice caps during the Late Jurassic and Late Cretaceous, the climate may have had a decisive influence on the diversity evolution of theropods in particular, but also on dinosaurs as a whole. It would show that the mainly feathered, presumably warm-blooded and thus better insulated coelurosaurs, had evolutionary advantages over other dinosaurs in the corresponding much cooler high latitude habitats (Benton et al., 2019). As mentioned before, the diversity of non-avian theropods would have decreased already in the Tithonian and only the diversity of avian theropods would have increased in the Maastrichtian. More and more, Ornithischia are also reconstructed as partially feathered and Neornitischia show a slight increase as one of the few clades at the transition to the Berriasian (Benton et al., 2019, Godefroit et al., 2020). Especially in the Maastrichtian, during an unprecedented cooling, there was a radiation in Neornithischia and also among Theropoda, the feather-bearing Maniraptora were the ones that prevailed (Figure 11 and 23). The surprising diversity in the Barremian, in which all dinosaur clades showed an increase in species diversity, would therefore be due to the warm climate, in which also unfeathered theropods (Megalosauroidea and Allosauroidea) flourished again, which also shows the sudden increase of spinosauroids. Sauropods presumably were subject to different physiological conditions due to their sheer size and could regulate their body temperature differently as a result (Eagle et al., 2011). A more accurate assessment of this thesis would require a detailed look at global diversity trends, palaeogeography, palaeoclimatology, but also morphology, in which anatomical components such as metabolism must also be incorporated. This would imply that the dinosaurs were undergoing major phylogenetic restructuring due to

Late Cretaceous climate changes and were particularly vulnerable to catastrophes during this phase.

Disturbances at the Jurassic-Cretaceous boundary

The transition from the Jurassic to the Cretaceous and its impact on dinosaurs has been poorly studied up to now. Tennant et al. (2017) mentioned the major environmental changes during this time in form of asteroid impacts, increased tectonic processes, a strong decrease of the eustatic sea level, as well as climate fluctuations which led to cold and dry periods. Furthermore, sauropod diversity is thought to have declined prior to the J/K boundary, while ornithischians (-33%) and theropods (up to -80%) started to decline just at the transition (Tennant et al., 2016b). This master's thesis is the first concrete study of the diversity patterns of non-avian dinosaurs at the Tithonian-Berriasian transition on the European continent. A noticeable decline of European dinosaurs at the J/K boundary was also found in this work. The total number of the standing species diversity of non-avian dinosaurs has dropped considerably from the Tithonian to the Berriasian by -45.83% (Figure 10). An analysis of the data (Figure 11) shows that theropods (-60%) and sauropods (-44.44%) were most affected. The thyreophorans showed mathematically (-75%) the strongest decrease but also the smallest sample size, whereas the neornithischians doubled their species richness. The EMSD indicates a decline of 37.5% of genus diversity (Figure 12). The extinction rate of 0.12 was also clearly higher than the origination rate of 0.06 (Figure 13).

Although the number of localities from the Tithonian to the Berriasian shows a decrease of 28.57%, the site/fossil ratio should also be considered here (Figure 27). In the Tithonian there is a difference of 71.43% between the number of localities and the number of species found, but in the Berriasian it accounts for only 30%, which could be interpreted as an indicator for a decreasing palaeobiodiversity density. The individual rarefaction analysis indicates an adequate collection success at the J/K boundary (32 and 34) supporting these interpretations.

Figures 2 and 5 show that the sea level receded within a short time at the transition (Holz, 2015). Across the J/K boundary, the pCO2 concentration decreased by 62 ppm and the GMT by 0.4°C (Figure 40 and 41). Since there had been major changes in these factors during other geologic time periods that did not result in such an

incision, there are no valid arguments for considering palaeoclimate or fluctuating sea level as the main driver (Tennant et al., 2016a). It was demonstrated that during the transition from the Tithonian to the Berriasian, a highly increased extinction rate among the major European dinosaur clades occurred, but not a mass extinction by definition. The reason why theropods and sauropods were particularly affected is difficult to explain. Neither climatic conditions, sea level changes, or faunal shifts could be identified as the primary cause. Not to be underestimated are short-term effects of the asteroid impact in Norway, which could have had devastating due to the palaeogeographical setting in Europe (Dypvik et al., 2010). However, a collecting bias as a cause cannot be ruled out.

Evolutionary patterns during the Late Cretaceous

During the Maastrichtian, the dinosaur world began to change dramatically. The pCO2 value gradually decreased throughout the Maastrichtian from 369 ppm 72 million years ago to 228 ppm 66 million years ago, and the GMT decreased from 14.9°C to 13.3°C. The Maastrichtian therefore marked an exceptionally cool period, unprecedented in the entire history of non-avian dinosaurs (Figures 40 and 41). Sea level decreased gradually compared to the Campanian (Figure 5) but was still above average. The number of sites in Europe increased directly from the Campanian to the Maastrichtian, and also the site/fossil ratio shows an increasing trend, which can be considered as a positive development (Figure 27). The individual rarefaction analyses also confirms a good sampling success for the Campanian and Maastrichtian (Figure 38 and 39).

The evolution of non-avian dinosaurs at the end of the Cretaceous is still much debated. Whether they already suffered a loss of global diversity before the asteroid impact or their diversification rate remained constant over time (Brusatte et al., 2015) should be considered in relation on regional scale (Upchurch, 2011). The standing species diversity (Figure 10) indicates an increase from the Campanian to the Maastrichtian of 53.33% in the non-avian dinosaurs of Europe, even when birds are included there was an increase of 50% (Figure 26). However, not all clades were equally successful (Figure 11). The diversity of Neornithischia (+225%), after a first peak in the Barremian, actually developed towards the Maastrichtian. Also the Sauropoda (+50%) increased again, while the values of Thyreophora (-50%) again

fluctuated extremely due to the low sample size. The non-avian Theropoda (-40%) diversity obviously decreased strongly during the Late Cretaceous. This is also shown by changes in the faunal composition (Figure 22 and 23). In contrast, the birds (33.33%) originating from Coelurosauria gained again towards the end of the Cretaceous.

The EMSD shows a genus loss of 22.22% (Figure 12) in non-avian dinosaurs from the Campanian to the Maastrichtian and also the origination rate, which was still solidly positive in the Campanian, was overlapped by the extinction rate in the Maastrichtian (Figure 13). However, the significance of the EMSD must be considered in the appropriate context due to the singletons problem with dinosaur fossils. A clear trend change of palaeodiversity in the Maastrichtian of Europe can be seen, but a general decline prior to the mass extinction cannot be assumed (Galbrun, 1997). Some clades, such as the Neornitischia were very successful until the end (Sakamoto et al., 2016), the diversity of Sauropoda was stable, whereas Theropoda seems to have been in a phase of restructuring and change. An inconspicuous but stable existence was led by the Thyreophora, which probably occupied very specific ecological niches or geographic regions (Schade et al., 2022). There is no significant evidence that environmental impacts had a direct effect on species richness, but possibly they required morphological adaptations from the dinosaurs. Although the diversity of European dinosaurs at the end of the Cretaceous could not match those of the Late Jurassic or the curious high in the Barremian, it remains questionable whether they were actually already in decline or adapted to the unique conditions of that time. Observing the "Stanley Rule," which is particularly evident in Neornithischia, a high diversity rate also leads to an increased extinction rate (Stanley, 1979).

CONCLUSION

The objective of the present master thesis is to provide an overview of the diversity patterns of European Jurassic and Cretaceous dinosaurs. For this purpose, a dataset of 168 species belonging to 160 genera from 104 sites in 16 European countries was created and analyzed by using a multi-method approach of global environmental data and various statistical calculations. Consideration was given to both the frequency of the species and the connections between the individual clades at a higher taxonomic

level, in order to provide a comprehensive but still detailed picture of the faunal developments of the past. The focus of this study is to gain knowledge on the course of palaeobiodiversity at the Tithonian/Berriasian transition and before the Maastrichtian mass extinction, as well as on faunal dynamics of major clades in general.

Based on the assumptions of other papers about a global hidden mass extinction of tetrapods at the Jurassic/Cretaceous boundary, the diversity of European dinosaurs at this transition was investigated in more detail here for the first time. Indeed, a significant decline of -45% in standing species diversity occurred and the estimated mean standing diversity shows a loss of -37% in genera. Especially affected were theropods (-60%), sauropods (-44%) as well as thyreophorans. Neornithischians were the only clade that showed an increase. The reasons for this could not be determined, although there was a sea level decline at this transition and climate data also showed a slight change, but nothing that did not exist before and led to a similar situation. A possible trigger could have been an impact in Norway. Despite the observed decline in diversity of European dinosaurs, it cannot be considered a mass extinction by definition.

No evidence of a general long-term decline in palaeobiodiversity among European dinosaurs at the end of the Cretaceous was found. It was shown that there was a high diversification ability especially among the neornitischians and avian theropods. The progress of sauropods was stable, whereas the non-avian theropods and the thyreophorans experienced a strong loss in diversity. The data indicate that the asteroid impact occurred at an unstable moment in time, when great faunal shifts and morphological adaptations to changing environmental conditions were taking place.

No statistical correlation between the global mean temperature and species abundance was found in the performed analyses. Enormous fluctuations in sea level, pCO2 (230-1800 ppm) and global average temperature (13.5-20 °C) during the study period show the special ability of dinosaurs to constantly adapt to their environment. The course of sea level could apparently have had a major influence on the exchange of faunas among the individual regions. For some families of the Neornithischia in particular, the possibilities for migration may have offered opportunities to spread out in Europe as well, which is shown by their remarkably

successful development. Among the individual clades, the Neornithischia may have possessed a decisive advantage over other herbivores due to special physiological adaptations. The sauropods have established themselves as a successful model of evolution and were able to maintain a stable high level even after their peak in the Late Jurassic. Due to the small sample size, not much is known about the diversity of Thyreophora. Their species richness was low throughout the Jurassic and Cretaceous. After their maximum in the Middle or Late Jurassic, they possibly occupied increasingly specialised niches and were able to maintain themselves at a stable low level.

The largest percentage of clade composition over the entire study period was accounted for by non-avian theropods (37%), which seems unusually high for carnivorous representatives. An incipient change from a Megalosauroidea dominated fauna in the Middle Jurassic to one by Coelurosauria in the Late Jurassic, could also be shown in this work. Coelurosauria, from which the ancestors of today's birds developed at least in the Early Cretaceous, were the most successful group among the theropods, despite predominantly small representatives. Among the medium to large predators, Europe was particularly dominated by Megalosauroidea, which after an increase of Allosauroidea in the Late Jurassic, in the Early Cretaceous could again represent the clear majority among the carnivores. Within it, especially a peak of diversity in all European dinosaur clades can be observed, which took place during a warm phase in the Barremian. Remarkable is the large amount of spinosauroids which might have found ideal coastal conditions. After a period of gaps in the Upper Cretaceous fossil record, the group of Allosauroidea and Megalosauroidea suddenly disappeared. The theropod fauna in the Late Cretaceous of Europe is almost exclusively composed of feathered Coelurosauria from the group of Maniraptora and birds. Also, the Ceratosauria which were on a very low level over the whole period, appear the last time in the Campanian.

Furthermore, a hypothesis for a system of two different feedback mechanisms between global sea level changes and pCO2 levels was presented, suggesting polar ice caps in the Late Jurassic and Late Cretaceous. This could have had a far-reaching impact on high-latitude faunas, driving the development of feathers as insulation and providing an important evolutionary advantage for some members of the Coelurosauria and possibly Neornithischia. However, this assumption could

neither be statistically tested nor explained by physical models within this work and would have to be compared with diversity data on a global scale.

Despite large gaps in the fossil record, which make it impossible to draw more precise conclusions about large parts of the study period, the Kimmeridgian/Tithonian/Berriasian/Barremian/Campanian and Maastrichtian stages were satisfactorily collected. The data show a strong west-east divide, which means that most of the data provide solid information on Western Europe, but Eastern Europe is underrepresented. Even with the palaeogeographical proximity to France, there seems to have been an increased faunal exchange between Iberia and Britain, especially during the Cretaceous.

Basically, the aims of this work could be fulfilled and fundamental features about the diversity patterns from European dinosaurs of the Jurassic and Cretaceous could be recognized. The lack of geographically and temporally well distributed sites, as well as the small sample size of the continent, leave large parts of the past still in the dark. Despite the long history of palaeontological research, many fossil remains and geological formations are deficiently described or of poor preservation. Compared to China or North and South America, some of the existing literature on dinosaur research in Europe is outdated or limited to specific regions. Especially Middle and East Europe are under-researched. The availability of (regional) Mesozoic environmental data which can provide information about terrestrial systems is equally low. A large gap that could possibly be filled by palaeobotany. New discoveries in Northern, Central and Eastern Europe, as well as more accurate palaeoclimatological reference indicators, would improve future palaeobiodiversity studies. Also of great importance are studies which additionally deal with other vertebrates but also plants, in order to work out a comprehensive ecological picture. Due to the complexity of the topic, it was unfortunately not possible to go into more detail about the morphological development of the individual clades over time.

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SUPPLEMENTARY MATERIALS

European Dinosaur Taxa

Clade	Genus	Species	From	To	Country
Macronaria	Abditosaurus	kuehnei	Maastrichtian	Maastrichtian	ES
Ornithopoda	Adynomosaurus	arcanus	Maastrichtian	Maastrichtian	ES
Marginocephalia	Ajkaceratops	kozmai	Santonian	Santonian	HU
Coelurosauria	Alcmonavis	poeschli	Tithonian	Tithonian	DE
Allosauroidea	Allosaurus	europeus	Kimmeridgian	Tithonian	PT
Megalosauroidea	Altispinax	dunkeri	Berriasian	Valanginian	GB
Eusauropoda	Amanzia	greppini	Kimmeridgian	Kimmeridgian	CH
Macronaria	Ampelosaurus	atacis	Maastrichtian	Maastrichtian	FR
Ankylosauria	Anoplosaurus	curtonotus	Albian	Albian	GB
Macronaria	Aragosaurus	ischiaticus	Tithonian	Berriasian	ES
Coelurosauria	Archaeopteryx	lithographica	Kimmeridgian	Tithonian	DE
Coelurosauria	Archaeopteryx	albersdoerferi	Tithonian	Tithonian	DE
Ceratosauria	Arcovenator	escotae	Campanian	Campanian	FR
Ornithopoda	Arenysaurus	ardevoli	Maastrichtian	Maastrichtian	ES
Coelurosauria	Aristosuchus	pusillus	Barremian	Barremian	GB
Avialae	Asteriornis	maastrichtensis	Maastrichtian	Maastrichtian	BE
Macronaria	Atsinganosaurus	velauciensis	Campanian	Campanian	FR
Coelurosauria	Aviatyrannis	jurassica	Kimmeridgian	Kimmeridgian	PT
Avialae	Balaur	bondoc	Maastrichtian	Maastrichtian	RO
Megalosauroidea	Baryonyx	walkeri	Barremian	Aptian	GB
Avialae	Bauxitornis	mindszentyae	Santonian	Santonian	HU
Ornithopoda	Blasisaurus	canudoi	Maastrichtian	Maastrichtian	ES
Ornithopoda	Brighstoneus	simmondsi	Barremian	Barremian	GB

Ornithopoda	Burianosaurus	augustai	Cenomanian	Cenomanian	CZ
Ornithopoda	Callovosaurus	leedsi	Callovian	Callovian	GB
Megalosauroidea	Camarillasaurus	cirugedae	Barremian	Barremian	ES
Ornithopoda	Canardia	garonnensis	Maastrichtian	Maastrichtian	FR
Eusauropoda	Cardiodon	rugulosos	Bathonian	Bathonian	GB
Ceratosauria	Ceratosaurus	dentisulcatus	Kimmeridgian	Kimmeridgian	PT
Megalosauroidea	Ceratosuchops	inferodios	Barremian	Barremian	GB
Eusauropoda	Cetiosauriscus	stewarti	Callovian	Callovian	GB
Eusauropoda	Cetiosaurus	oxoniensis	Bajocian	Bathonian	GB
Coelurosauria	Compsognathus	longipes	Tithonian	Tithonian	DE/FR
Allosauroidea	Concavenator	corcovatus	Barremian	Barremian	ES
Avialae	Concornis	lacustris	Barremian	Barremian	ES
Tetanurae	Cruxicheiros	newmanorum	Bathonian	Bathonian	GB
Ornithopoda	Cumnoria	prestwichii	Kimmeridgian	Kimmeridgian	GB
Stegosauria	Dacenturus	armatus	Kimmeridgian	Berriasian	ES/GB/PT
Stegosauria	Dacenturus	lennieri	Kimmeridgian	Kimmeridgian	FR
Diplodocoidea	Demandasaurus	darwini	Barremian	Aptian	ES
Diplodocoidea	Dinheirosaurus	lourinhanensis	Kimmeridgian	Tithonian	PT
Ornithopoda	Draconyx	loureiroi	Tithonian	Tithonian	PT
Ankylosauria	Dracopelta	zbyszewskii	Tithonian	Tithonian	PT
Basal Neotheropoda	Dracoraptor	hanigani	Hettangian	Hettangian	GB-WLS
Coelurosauria	Dromaeosauroides	bornholmensis	Berriasian	Valanginian	DK
Megalosauroidea	Dubreuillosaurus	valesdunensi	Bathonian	Bathonian	FR
Macronaria	Duriatitan	humerocristatus	Kimmeridgian	Tithonian	PT
Megalosauroidea	Duriavenator	hesperis	Bajocian	Bajocian	GB
Basal Ornithischia	Echinodon	becklesii	Berriasian	Berriasian	GB
Basal Ankylosauria	Emausaurus	ernsti	Toarcian	Toarcian	DE
Avialae	Enaliornis	barretti	Albian	Albian	GB
Avialae	Enaliornis	sedgwicki	Albian	Albian	GB

Avialae	Eoalulavis	hoyasi	Barremian	Barremian	ES
Coelurosauria	Eotyrannus	lengi	Barremian	Barremian	GB
Ornithopoda	Eousdryosaurus	nanohallucis	Kimmeridgian	Kimmeridgian	PT
Allosauroidea	Erectopus	superbus	Albian	Albian	FR
Macronaria	Eucamerotus	foxi	Barremian	Barremian	GB
Coelurosauria	Euronychodon	portucalensis	Campanian	Maastrichtian	PT
Macronaria	Europasaurus	holgeri	Kimmeridgian	Kimmeridgian	DE
Macronaria	Europatitan	eastwoodi	Barremian	Aptian	ES
Ankylosauria	Europelta	carbonensis	Albian	Albian	ES
Megalosauroidea	Eustreptospondylus	oxoniensis	Callovian	Callovian	GB
Ornithopoda	Fylax	thyrakolasus	Maastrichtian	Maastrichtian	ES
Macronaria	Galvesaurus	herreroi	Kimmeridgian	Tithonian	ES
Avialae	Gargantuavis	philoinos	Campanian	Maastrichtian	ES/FR
Macronaria	Garrigatitan	meridionalis	Campanian	Campanian	FR
Ceratosauria	Genusaurus	sisteronis	Albian	Albian	FR
Ornithopoda	Gideonmantellia	amosanjuanae	Barremian	Barremian	ES
Macronaria	Haestasaurus	becklesii	Berriasian	Valanginian	GB
Avialae	Hesperornis	rossicus	Campanian	Campanian	RU
Ankylosauria	Hungarosaurus	tormai	Santonian	Santonian	HU
Ankylosauria	Hylaeosaurus	armatus	Valanginian	Valanginian	GB
Ornithopoda	Hypselospinus	fittoni	Valanginian	Valanginian	GB
Basal Neornithischia	Hypsilophodon	foxii	Barremian	Aptian	ES/GB
Avialae	Iberomesornis	romerali	Barremian	Barremian	ES
Megalosauroidea	Iberospinus	natarioi	Barremian	Barremian	PT
Ornithopoda	Iguanodon	bernissartensis	Barremian	Aptian	BE/DE/ES/FR/GB
Ornithopoda	Iguanodon	galvensis	Barremian	Barremian	ES
Coelurosauria	Juratyrant	langhami	Tithonian	Tithonian	GB
Coelurosauria	Juravenator	starki	Kimmeridgian	Kimmeridgian	DE
Stegosauria	Lexovisaurus	durobrivensis	Callovian	Callovian	FR/GB

Macronaria	Lirainosaurus	astibiae	Campanian	Maastrichtian	ES
Macronaria	Lohuecotitan	pandafilandi	Campanian	Maastrichtian	ES
Basal Neotheropoda	Lophostropheus	airelensis	Rhaetian	Hettangian	FR
Stegosauria	Loricatosaurus	priscus	Callovian	Callovian	GB
Eusauropoda	Losillasaurus	giganteus	Kimmeridgian	Tithonian	ES/PT
Coelurosauria	Lourinhanosaurus	antunesi	Kimmeridgian	Tithonian	PT
Macronaria	Lourinhasaurus	alenquerensis	Kimmeridgian	Tithonian	PT
Basal Thyreophora	Lusitanosaurus	liasicus	Sinemurian	Sinemurian	PT
Macronaria	Lusotitan	atalaiensis	Tithonian	Tithonian	PT
Allosauroidea	Lusovenator	santosi	Kimmeridgian	Kimmeridgian	PT
Ornithopoda	Machlodon	suessi	Campanian	Campanian	AT
Ornithopoda	Machlodon	vorosi	Santonian	Santonian	HU
Macronaria	Madeupposeidon	ruffordi	Berriasian	Valanginian	GB
Ornithopoda	Magnamanus	soriaensis	Hauterivian	Barremian	ES
Megalosauroidea	Magnosaurus	nethercombensis	Bajocian	Bajocian	GB
Macronaria	Magyarosaurus	dacus	Maastrichtian	Maastrichtian	RO
Ornithopoda	Mantellisaurus	atherfieldensis	Barremian	Aptian	BE/GB
Avialae	Martinavis	cruzyensis	Campanian	Maastrichtian	FR
Ornithopoda	Matheronodon	provincialis	Campanian	Campanian	FR
Megalosauroidea	Megalosaurus	bucklandii	Bathonian	Bathonian	GB
Allosauroidea	Metriacanthosaurus	parkeri	Oxfordian	Oxfordian	GB
Stegosauria	Miragaia	longicollum	Kimmeridgian	Tithonian	PT
Ornithopoda	Morelladon	beltrani	Barremian	Barremian	ES
Allosauroidea	Neovenator	salerii	Hauterivian	Barremian	GB
Avialae	Noguerornis	gonzalezi	Berriasian	Barremian	ES
Macronaria	Normanniasaurus	genceyi	Albian	Albian	FR
Coelurosauria	Nuthetes	destructor	Berriasian	Berriasian	GB
Macronaria	Oceanotitan	dantasi	Kimmeridgian	Tithonian	PT
Basal Sauropoda	Ohmdenosaurus	liasicus	Toarcian	Toarcian	DE

Macronaria	Oplosaurus	armatus	Barremian	Barremian	GB
Coelurosauria	Ornithodesmus	cluniculus	Barremian	Barremian	GB/RO
Macronaria	Ornithopsis	hulkei	Barremian	Barremian	GB
Coelurosauria	Ostromia	crassipes	Tithonian	Tithonian	DE
Macronaria	Paludititan	nalatzensis	Maastrichtian	Maastrichtian	RO
Ornithopoda	Pararhabdodon	isonensis	Maastrichtian	Maastrichtian	ES
Ornithopoda	Pareisactus	evrostos	Maastrichtian	Maastrichtian	ES
Coelurosauria	Pelecanimimus	polyodon	Hauterivian	Barremian	ES
Basal Neornithischia	Phyllodon	henkeli	Kimmeridgian	Kimmeridgian	PT
Megalosauroidea	Piveteausaurus	divesensis	Callovian	Callovian	FR
Coelurosauria	Pneumatoraptor	fodori	Santonian	Santonian	HU
Megalosauroidea	Poekilopleuron	bucklandii	Bathonian	Bathonian	FR
Ankylosauria	Polacanthus	rudgwickensis	Barremian	Barremian	GB
Ankylosauria	Polacanthus	foxii	Barremian	Barremian	GB
Ornithopoda	Portellsaurus	sosbaynati	Barremian	Barremian	ES
Ornithopoda	Proa	valdearinnoensis	Albian	Albian	ES
Coelurosauria	Proceratosaurus	bradleyi	Bathonian	Bathonian	GB
Coelurosauria	Pyroraptor	olympius	Campanian	Maastrichtian	ES/FR
Stegosauria	Regnosaurus	northamptoni	Valanginian	Valanginian	GB
Ornithopoda	Rhabdodon	priscus	Santonian	Maastrichtian	ES/FR
Ornithopoda	Riabininohadros	weberae	Maastrichtian	Maastrichtian	UA
Megalosauroidea	Riparovenator	milnerae	Barremian	Barremian	GB
Ceratosauria	Saltriovenator	zanellai	Sinemurian	Sinemurian	IT
Ankylosauria	Sarcolestes	leedsi	Callovian	Callovian	GB
Basal Neotheropoda	Sarcosaurus	andrewsi	Hettangian	Hettangian	GB
Basal Thyreophora	Scelidosaurus	harrisonii	Sinemurian	Sinemurian	GB
Coelurosauria	Scipionyx	samniticus	Albian	Albian	IT
Megalosauroidea	Sciurumimus	albersdoerferi	Kimmeridgian	Kimmeridgian	DE
Macronaria	Soriatitan	golmayensis	Hauterivian	Barremian	ES

Stegosauria	Stegosaurus	ungulatus	Kimmeridgian	Tithonian	PT
Marginocephalia	Stenopelix	valdensis	Berriasian	Berriasian	DE
Megalosauroidea	Streptospondylus	altdorfensis	Callovian	Oxfordian	FR
Ankylosauria	Struthiosaurus	austriacus	Campanian	Campanian	AT
Ankylosauria	Struthiosaurus	languedocensis	Campanian	Campanian	FR
Ankylosauria	Struthiosaurus	transylvanicus	Maastrichtian	Maastrichtian	RO
Coelurosauria	Tamarro	insperatus	Maastrichtian	Maastrichtian	ES
Ceratosauria	Tarascosaurus	salluvicus	Campanian	Campanian	FR
Macronaria	Tastavinsaurus	sanzi	Aptian	Aptian	ES
Ornithopoda	Telmatosaurus	transsylvanicus	Maastrichtian	Maastrichtian	RO
Ornithopoda	Tethyshadros	insularis	Campanian	Maastrichtian	IT
Megalosauroidea	Torvosaurus	gurneyi	Kimmeridgian	Tithonian	PT
Eusauropoda	Turiasaurus	riodevensis	Tithonian	Berriasian	ES
Coelurosauria	Valdoraptor	oweni	Berriasian	Valanginian	GB
Ornithopoda	Valdosaurus	canaliculatus	Berriasian	Barremian	GB/RO
Megalosauroidea	Vallibonavenatrix	cani	Barremian	Barremian	ES
Coelurosauria	Variraptor	mechinorum	Campanian	Campanian	FR
Tetanurae	Vectaerovenator	inopinatus	Aptian	Aptian	GB
Coelurosauria	Vectiraptor	greeni	Barremian	Barremian	GB
Macronaria	Volgatitan	simbirskiensis	Hauterivian	Hauterivian	RU
Macronaria	Vouivria	damparisensis	Oxfordian	Oxfordian	FR
Coelurosauria	Wellnhoferia	grandis	Tithonian	Tithonian	DE
Megalosauroidea	Wiehenvenator	albati	Callovian	Callovian	DE
Avialae	Wyleyia	valdensis	Barremian	Barremian	GB
Diplodocoidea	Xenoposeidon	proneneukos	Berriasian	Valanginian	GB
Coelurosauria	Yaverlandia	bitholus	Barremian	Barremian	GB
Ornithopoda	Zalmoxes	robustus	Maastrichtian	Maastrichtian	RO
Ornithopoda	Zalmoxes	shqiperorum	Maastrichtian	Maastrichtian	RO
Eusauropoda	Zby	atlanticus	Kimmeridgian	Kimmeridgian	PT

Diversity Rate Calculations

	t	Δt	N_{FL}	N_{bL}	N_{Ft}	N_{bt}	N_b	N_t	N_{tot}	$N_{TOT\ (ex.\ sgt)}$	EMSD	N_o	N_e	$r_{o\ (incl.\ \Delta t)}$	$r_{e\ (incl.\ \Delta t)}$
HET	201,3	2	2	1	0	0	1	0	3	1	0,5	2	3	**0,33333333**	**0,5**
SIN	199,3	8,5	3	0	0	0	0	0	3	0	0	3	3	**0,11764706**	**0,11764706**
PLI	190,8	8,1	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
TOA	182,7	8,6	2	0	0	0	0	0	2	0	0	2	2	**0,11627907**	**0,11627907**
AAL	174,1	3,8	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
BAJ	170,3	2	2	0	1	0	0	1	3	1	0,5	3	2	**0,5**	**0,33333333**
BAT	168,3	2,2	6	1	0	0	1	0	7	1	0,5	6	7	**0,38961039**	**0,45454545**
CAL	166,1	2,6	8	0	1	0	0	1	9	1	0,5	9	8	**0,38461538**	**0,34188034**
OXF	163,5	6,2	2	1	0	0	1	0	3	1	0,5	2	3	**0,10752688**	**0,16129032**
KIM	157,3	5,2	11	0	13	0	0	13	24	13	6,5	24	11	**0,19230769**	**0,08814103**
TIT	152,1	7,1	8	12	2	1	13	3	23	15	8	10	20	**0,06123699**	**0,12247397**
BER	145	5,2	3	3	7	0	3	7	13	10	5	10	6	**0,14792899**	**0,0887574**
VAL	139,8	7,2	3	6	0	1	7	1	10	7	4	3	9	**0,04166667**	**0,125**
HAU	132,6	3,2	1	0	4	1	1	5	6	5	3	5	1	**0,26041667**	**0,05208333**
BAR	129,4	8	19	5	6	0	5	6	30	11	5,5	25	24	**0,10416667**	**0,1**
APT	121,4	8,4	2	6	0	0	6	0	8	6	3	2	8	**0,0297619**	**0,11904762**
ALB	113	12,5	7	0	0	0	0	0	7	0	0	7	7	**0,08**	**0,08**
CEN	100,5	6,6	1	0	0	0	0	0	1	0	0	1	1	**0,15151515**	**0,15151515**
TUR	93,9	4,1	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
CON	89,8	3,5	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
SAN	86,3	2,7	3	0	2	0	0	2	5	2	1	5	3	**0,37037037**	**0,22222222**
CAM	83,6	11,5	6	1	6	1	2	7	14	8	4,5	12	7	**0,07453416**	**0,04347826**
MAA	72,1	6,01	15	7	0	0	7	0	22	7	3,5	15	22	**0,11344728**	**0,16638935**

Simpson's Diversity Index Calculations

SD Index Total Calculation

Subfamily	Portugal & Spain			Great Britain			Belgium & France		
	n	n-1	n(n-1)	n	n-1	n(n-1)	n	n-1	n(n-1)
Allosauroidea	4	3	12	3	2	6	1	0	0
Ceratosauria	1	0	0	0	-1	0	3	2	6
Coelurosauria	10	9	90	10	9	90	4	3	12
Megalosauroidea	5	4	20	10	9	90	5	4	20
Theropoda inc. sed.	0	-1	0	4	3	12	1	0	0
Diplodocoidea	4	3	12	2	1	2	0	-1	0
Eusauropoda	7	6	42	4	3	12	0	-1	0
Macronaria	21	20	420	7	6	42	5	4	20
Sauropoda inc. sed.	0	-1	0	0	-1	0	0	-1	0
Marginocephalia	0	-1	0	0	-1	0	0	-1	0
Ornithopoda	20	19	380	12	11	132	11	10	110
Neornithischia inc. sed.	3	2	6	3	2	6	0	-1	0
Ankylosauria	2	1	2	5	4	20	1	0	0
Stegosauria	10	9	90	6	5	30	2	1	2
Thyreophora inc. sed.	1	0	0	1	0	0	0	-1	0
N	88			67			33		
		∑	1074		∑	442		∑	170

D	0,85971787
PT & ES	

D	0,90004523
GB	

D	0,83901515
BE & FR	

Subfamily	Denmark & Germany			Italy & Switzerland			Austria & Hungary & Czech Rep.			Romania & Russia & Ukraine		
	n	n-1	n(n-1)	n	n-1	n(n-1)	n	n-1	n(n-1)	n	n-1	n(n-1)
Allosauroidea	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Ceratosauria	0	-1	0	1	0	0	0	-1	0	0	-1	0
Coelurosauria	10	9	90	1	0	0	1	0	0	1	0	0
Megalosauroidea	2	1	2	0	-1	0	0	-1	0	0	-1	0
Theropoda inc. sed.	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Diplodocoidea	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Eusauropoda	0	-1	0	1	0	0	0	-1	0	0	-1	0
Macronaria	1	0	0	0	-1	0	0	-1	0	3	2	6
Sauropoda inc. sed.	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Marginocephalia	1	0	0	0	-1	0	1	0	0	0	-1	0
Ornithopoda	2	1	2	2	1	2	3	2	6	8	7	56
Neornithischia inc. sed.	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Ankylosauria	0	-1	0	0	-1	0	2	1	2	1	0	0
Stegosauria	0	-1	0	0	-1	0	0	-1	0	0	-1	0
Thyreophora inc. sed.	1	0	0	0	-1	0	0	-1	0	0	-1	0
N	17			5			7			13		
		∑	94		∑	2		∑	8		∑	62

	D	0,65441176		D	0,9		D	0,8095238		D	0,602564103	
	DK & DE			IT & CH			AU & HU & CZ			RO & RU & UA		

SD Index Calculation Jurassic Western Europe

Simpson´s Diversity Index - Jurassic									
Subfamily	Portugal & Spain			Great Britain			Belgium & France		
	n	n-1	n(n-1)	n	n-1	n(n-1)	n	n-1	n(n-1)
Allosauroidea	3	2	6	1	0	0	0	-1	0
Ceratosauria	1	0	0	0	-1	0	0	-1	0
Coelurosauria	3	2	6	2	1	2	1	0	0
Megalosauroidea	2	1	2	4	3	12	5	4	20
Theropoda inc. sed.	0	-1	0	3	2	6	1	0	0
Diplodocoidea	2	1	2	0	-1	0	0	-1	0
Eusauropoda	6	5	30	4	3	12	0	-1	0
Macronaria	10	9	90	0	-1	0	1	0	0
Sauropoda inc. sed.	0	-1	0	0	-1	0	0	-1	0
Marginocephalia	0	-1	0	0	-1	0	0	-1	0
Ornithopoda	2	1	2	2	1	2	0	-1	0
Neornithischia inc. sed.	1	0	0	0	-1	0	0	-1	0
Ankylosauria	1	0	0	1	0	0	0	-1	0
Stegosauria	8	7	56	4	3	12	2	1	2
Thyreophora inc. sed.	1	0	0	1	0	0	0	-1	0
N	40			22			10		
		∑	194		∑	46		∑	22

D	0,87564103
PT & ES	

D	0,9004329
GB	

D	0,75555556
BE & FR	

SD Index Calculation Cretaceous Western Europe

Simpson´s Diversity Index - Cretaceous									
Subfamily	Portugal & Spain			Great Britain			Belgium & France		
	n	n-1	n(n-1)	n	n-1	n(n-1)	n	n-1	n(n-1)
Allosauroidea	1	0	0	2	1	2	1	0	0
Ceratosauria	0	-1	0	0	-1	0	3	2	6
Coelurosauria	7	6	42	8	7	56	3	2	6
Megalosauroidea	3	2	6	6	5	30	0	-1	0
Theropoda inc. sed.	0	-1	0	1	0	0	0	-1	0
Diplodocoidea	2	1	2	2	1	2	0	-1	0
Eusauropoda	1	0	0	0	-1	0	0	-1	0
Macronaria	11	10	110	7	6	42	4	3	12
Sauropoda inc. sed.	0	-1	0	0	-1	0	0	-1	0
Marginocephalia	0	-1	0	0	-1	0	0	-1	0
Ornithopoda	18	17	306	10	9	90	11	10	110
Neornithischia inc. sed.	2	1	2	3	2	6	0	-1	0
Ankylosauria	1	0	0	4	3	12	1	0	0
Stegosauria	2	1	2	2	1	2	0	-1	0
Thyreophora inc. sed.	0	-1	0	0	-1	0	0	-1	0
N	48			45			23		
		∑	470		∑	242		∑	134

D	0,79166667
PT & ES	

D	0,87777778
GB	

D	0,73517787
BE & FR	

Shannon's Diversity Index Calculations

SH Index Total Calculation

Subfamily	Portugal & Spain				Great Britain				Belgium & France			
	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi
Allosauroidea	4	0,04545455	-3,09104245	-0,14050193	3	0,04477612	-3,10608033	-0,13907822	1	0,03030303	0	0
Ceratosauria	1	0,01136364	-4,47733681	-0,05087883	0	0	0	0	3	0,09090909	-2,39789527	-0,21799048
Coelurosauria	10	0,11363636	-2,17475172	-0,24713088	10	0,14925373	-1,90210753	-0,28389665	4	0,12121212	-2,1102132	-0,25578342
Megalosauroidea	5	0,05681818	-2,8678989	-0,1629488	10	0,14925373	-1,90210753	-0,28389665	5	0,15151515	-1,88706965	-0,28591964
Theropoda inc. sed.	0	0	0	0	4	0,05970149	-2,81839826	-0,16826258	1	0,03030303	-3,49650756	-0,10595477
Diplodocoidea	4	0,04545455	-3,09104245	-0,14050193	2	0,02985075	-3,51154544	-0,10482225	0	0	0	0
Eusauropoda	7	0,07954545	-2,53142667	-0,20136348	4	0,05970149	-2,81839826	-0,16826258	0	0	0	0
Macronaria	21	0,23863636	-1,43281438	-0,34192161	7	0,10447761	-2,25878247	-0,2359922	5	0,15151515	-1,88706965	-0,28591964
Sauropoda inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0
Marginocephalia	0	0	0	0	0	0	0	0	0	0	0	0
Ornithopoda	20	0,22727273	-1,48160454	-0,3367283	12	0,17910448	-1,71978597	-0,30802137	11	0,33333333	-1,09861229	-0,3662041
Neornithischia inc. sed.	3	0,03409091	-3,37872453	-0,11518379	3	0,04477612	-3,10608033	-0,13907822	0	0	0	0
Ankylosauria	2	0,02272727	-3,78418963	-0,08600431	5	0,07462687	-2,59525471	-0,19367572	1	0,03030303	-3,49650756	-0,10595477
Stegosauria	10	0,11363636	-2,17475172	-0,24713088	6	0,08955224	-2,41293315	-0,21608357	2	0,06060606	-2,80336038	-0,16990063
Thyreophora inc. sed.	1	0,01136364	-4,47733681	-0,05087883	1	0,01492537	-4,20469262	-0,06275661	0	0	0	0
∑	88	1		-2,12117357	67	1		-2,30382662	33	1		-1,79362746
			H	2,12117357			**H**	2,30382662			**H**	1,79362746

Subfamily	Denmark & Germany				Italy & Switzerland				Austria & Hungary & Czech Rep.				Romania & Russia & Ukraine			
	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratosauria	0	0	0	0	1	0,2	-1,60943791	-0,32188758	0	0	0	0	0	0	0	0
Coelurosauria	10	0,58823529	-0,53062825	-0,31213427	1	0,2	-1,60943791	-0,32188758	1	0,14285714	-1,94591015	-0,27798716	1	0,07692308	-2,56494936	-0,1973038
Megalosauroidea	2	0,11764706	-2,14006616	-0,25177249	0	0	0	0	0	0	0	0	0	0	0	0
Theropoda inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplodocoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusauropoda	0	0	0	0	1	0,2	-1,60943791	-0,32188758	0	0	0	0	0	0	0	0
Macronaria	1	0,05882353	-2,83321334	-0,16665961	0	0	0	0	0	0	0	0	3	0,23076923	-1,46633707	-0,33838548
Sauropoda inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marginocephalia	1	0,05882353	-2,83321334	-0,16665961	0	0	0	0	1	0,14285714	-1,94591015	-0,27798716	0	0	0	0
Ornithopoda	2	0,11764706	-2,14006616	-0,25177249	2	0,4	-0,91629073	-0,36651629	3	0,42857143	-0,84729786	-0,36312765	8	0,61538462	-0,48550782	-0,29877404
Neornithischia inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ankylosauria	0	0	0	0	0	0	0	0	2	0,28571429	-1,25276297	-0,35793228	1	0,07692308	-2,56494936	-0,1973038
Stegosauria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyreophora inc. sed.	1	0,05882353	-2,83321334	-0,16665961	0	0	0	0	0	0	0	0	0	0	0	0
∑	17	1		-1,31565807	5	1		-1,33217904	7	1		-1,27703426	13	1		-1,03176711
			H	1,31565807			H	1,33217904			H	1,27703426			H	1,03176711

SH Index Calculation Jurassic Western Europe

Shannon´s Diversity Index - Jurassic												
Subfamily	**Portugal & Spain**				**Great Britain**				**Belgium & France**			
	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi
Allosauroidea	3	0,075	-2,59026717	-0,19427004	1	0,04545455	-3,09104245	-0,14050193	0	0	0	0
Ceratosauria	1	0,025	-3,68887945	-0,09222199	0	0	0	0	0	0	0	0
Coelurosauria	3	0,075	-2,59026717	-0,19427004	2	0,09090909	-2,39789527	-0,21799048	1	0,1	-2,30258509	-0,23025851
Megalosauroidea	2	0,05	-2,99573227	-0,14978661	4	0,18181818	-1,70474809	-0,3099542	5	0,5	-0,69314718	-0,34657359
Theropoda inc. sed.	0	0	0	0	3	0,13636364	-1,99243016	-0,27169502	1	0,1	-2,30258509	-0,23025851
Diplodocoidea	2	0,05	-2,99573227	-0,14978661	0	0	0	0	0	0	0	0
Eusauropoda	6	0,15	-1,89711998	-0,284568	4	0,18181818	-1,70474809	-0,3099542	0	0	0	0
Macronaria	10	0,25	-1,38629436	-0,34657359	0	0	0	0	1	0,1	-2,30258509	-0,23025851
Sauropoda inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0
Marginocephalia	0	0	0	0	0	0	0	0	0	0	0	0
Ornithopoda	2	0,05	-2,99573227	-0,14978661	2	0,09090909	-2,39789527	-0,21799048	0	0	0	0
Neornithischia inc. sed.	1	0,025	-3,68887945	-0,09222199	0	0	0	0	0	0	0	0
Ankylosauria	1	0,025	-3,68887945	-0,09222199	1	0,04545455	-3,09104245	-0,14050193	0	0	0	0
Stegosauria	8	0,2	-1,60943791	-0,32188758	4	0,18181818	-1,70474809	-0,3099542	2	0,2	-1,60943791	-0,32188758
Thyreophora inc. sed.	1	0,025	-3,68887945	-0,09222199	1	0,04545455	-3,09104245	-0,14050193	0	0	0	0
∑	40	1		-2,15981703	22	1		-2,05904437	10	1		-1,3592367
			H	2,15981703			**H**	2,05904437			**H**	1,3592367

SH Index Calculation Cretaceous Western Europe

Shannon´s Diversity Index - Cretaceous												
Subfamily	Portugal & Spain				Great Britain				Belgium & France			
	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi	n	pi	ln pi	pi * ln pi
Allosauroidea	1	0,02083333	-3,87120101	-0,08065002	2	0,04444444	-3,11351531	-0,13837846	1	0,04347826	0	0
Ceratosauria	0	0	0	0	0	0	0	0	3	0,13043478	-2,03688193	-0,26568025
Coelurosauria	7	0,14583333	-1,92529086	-0,28077158	8	0,17777778	-1,72722095	-0,3070615	3	0,13043478	-2,03688193	-0,26568025
Megalosauroidea	3	0,0625	-2,77258872	-0,1732868	6	0,13333333	-2,01490302	-0,26865374	0	0	0	0
Theropoda inc. sed.	0	0	0	0	1	0,02222222	-3,80666249	-0,0845925	0	0	0	0
Diplodocoidea	2	0,04166667	-3,17805383	-0,13241891	2	0,04444444	-3,11351531	-0,13837846	0	0	0	0
Eusauropoda	1	0,02083333	-3,87120101	-0,08065002	0	0	0	0	0	0	0	0
Macronaria	11	0,22916667	-1,47330574	-0,33763256	7	0,15555556	-1,86075234	-0,28945036	4	0,17391304	-1,74919985	-0,30420867
Sauropoda inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0
Marginocephalia	0	0	0	0	0	0	0	0	0	0	0	0
Ornithopoda	18	0,375	-0,98082925	-0,36781097	10	0,22222222	-1,5040774	-0,33423942	11	0,47826087	-0,73759894	-0,35276471
Neornithischia inc. sed.	2	0,04166667	-3,17805383	-0,13241891	3	0,06666667	-2,7080502	-0,18053668	0	0	0	0
Ankylosauria	1	0,02083333	-3,87120101	-0,08065002	4	0,08888889	-2,42036813	-0,21514383	1	0,04347826	-3,13549422	-0,13632584
Stegosauria	2	0,04166667	-3,17805383	-0,13241891	2	0,04444444	-3,11351531	-0,13837846	0	0	0	0
Thyreophora inc. sed.	0	0	0	0	0	0	0	0	0	0	0	0
∑	48	1		-1,79870871	45	1		-2,09481341	23	1		-1,32465972
			H	1,79870871			H	2,09481341			H	1,32465972

Jaccard Index Calculations

	Jurassic				
	FA		Presence		
Clades	**Western-EU**	**Central-EU**	**a**	**b**	**c**
Allosauroidea	4	0	0	1	0
Ceratosauria	1	1	1	0	0
Coelurosauria	6	8	1	0	0
Megalosauroidea	11	2	1	0	0
Theropoda inc. sed.	4	0	0	1	0
Diplodocoidea	2	0	0	1	0
Eusauropoda	10	1	1	0	0
Macronaria	11	1	1	0	0
Sauropoda inc. sed.	0	1	0	0	1
Marginocephalia	0	0	0	0	0
Ornithopoda	4	0	0	1	0
Neornithischia inc. sed.	1	0	0	1	0
Ankylosauria	2	0	0	1	0
Stegosauria	14	0	0	1	0
Thyreophora inc. sed.	2	1	1	0	0
Total			6	7	1
Total a+b+c			14		
		Jaccard Index [%]	**42,86**		

	Cretaceous				
	FA		Presence		
Clades	**Western-EU**	**Central-EU**	**a**	**b**	**c**
Allosauroidea	4	0	0	1	0
Ceratosauria	4	0	0	1	0
Coelurosauria	18	4	1	0	0
Megalosauroidea	9	0	0	1	0
Theropoda inc. sed.	1	0	0	1	0
Diplodocoidea	4	0	0	1	0
Eusauropoda	1	0	0	1	0
Macronaria	22	0	0	1	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	2	0	0	1
Ornithopoda	39	7	1	0	0
Neornithischia inc. sed.	5	0	0	1	0
Ankylosauria	6	2	1	0	0
Stegosauria	4	0	0	1	0
Thyreophora inc. sed.	0	0	0	0	0
Total			3	9	1
Total a+b+c			13		
		Jaccard Index [%]	**23,08**		

	Cretaceous				
	FA		Presence		
Clades	**Western-EU**	**Eastern-EU**	**a**	**b**	**c**
Allosauroidea	4	0	0	1	0
Ceratosauria	4	0	0	1	0
Coelurosauria	18	1	1	0	0
Megalosauroidea	9	0	0	1	0
Theropoda inc. sed.	1	0	0	1	0
Diplodocoidea	4	0	0	1	0
Eusauropoda	1	0	0	1	0
Macronaria	22	3	1	0	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	39	8	1	0	0
Neornithischia inc. sed.	5	0	0	1	0
Ankylosauria	6	1	1	0	0
Stegosauria	4	0	0	1	0
Thyreophora inc. sed.	0	0	0	0	0
Total			4	8	0
Total a+b+c			12		
		Jaccard Index [%]	**33,33**		

	Cretaceous				
	FA		Presence		
Clades	**Central-EU**	**Eastern-EU**	**a**	**b**	**c**
Allosauroidea	0	0	0	0	0
Ceratosauria	0	0	0	0	0
Coelurosauria	4	1	1	0	0
Megalosauroidea	0	0	0	0	0
Theropoda inc. sed.	0	0	0	0	0
Diplodocoidea	0	0	0	0	0
Eusauropoda	0	0	0	0	0
Macronaria	0	3	0	0	1
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	2	0	0	1	0
Ornithopoda	7	8	1	0	0
Neornithischia inc. sed.	0	0	0	0	0
Ankylosauria	2	1	1	0	0
Stegosauria	0	0	0	0	0
Thyreophora inc. sed.	0	0	0	0	0
Total			3	1	1
Total a+b+c			5		
		Jaccard Index [%]	**60,00**		

	Jurassic				
	FA		Presence		
Clades	**Iberia**	**Belgium & France**	**a**	**b**	**c**
Allosauroidea	3	0	0	1	0
Ceratosauria	1	0	0	1	0
Coelurosauria	3	1	1	0	0
Megalosauroidea	2	5	1	0	0
Theropoda inc. sed.	0	1	0	0	1
Diplodocoidea	2	0	0	1	0
Eusauropoda	6	0	0	1	0
Macronaria	10	1	1	0	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	2	0	0	1	0
Neornithischia inc. sed.	1	0	0	1	0
Ankylosauria	1	0	0	1	0
Stegosauria	8	2	1	0	0
Thyreophora inc. sed.	1	0	0	1	0
Total			4	8	1
Total a+b+c			13		
		Jaccard Index [%]	**30,77**		

	Jurassic				
	FA		Presence		
Clades	**Iberia**	**Great Britain**	**a**	**b**	**c**
Allosauroidea	3	1	1	0	0
Ceratosauria	1	0	0	1	0
Coelurosauria	3	2	1	0	0
Megalosauroidea	2	4	1	0	0
Theropoda inc. sed.	0	3	0	0	1
Diplodocoidea	2	0	0	1	0
Eusauropoda	6	4	1	0	0
Macronaria	10	0	0	1	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	2	2	1	0	0
Neornithischia inc. sed.	1	0	0	1	0
Ankylosauria	1	1	1	0	0
Stegosauria	8	4	1	0	0
Thyreophora inc. sed.	1	1	1	0	0
Total			8	4	1
Total a+b+c			13		
		Jaccard Index [%]	**61,54**		

	Jurassic				
	FA		Presence		
Clades	**Great Britain**	**Belgium & France**	**a**	**b**	**c**
Allosauroidea	1	0	0	1	0
Ceratosauria	0	0	0	0	0
Coelurosauria	2	1	1	0	0
Megalosauroidea	4	5	1	0	0
Theropoda inc. sed.	3	1	1	0	0
Diplodocoidea	0	0	0	0	0
Eusauropoda	4	0	0	1	0
Macronaria	0	1	0	0	1
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	2	0	0	1	0
Neornithischia inc. sed.	0	0	0	0	0
Ankylosauria	1	0	0	1	0
Stegosauria	4	2	1	0	0
Thyreophora inc. sed.	1	0	0	1	0
Total			4	5	1
Total a+b+c			10		
		Jaccard Index [%]	**40,00**		

	Cretaceous				
	FA		Presence		
Clades	**Iberia**	**Belgium & France**	**a**	**b**	**c**
Allosauroidea	1	1	1	0	0
Ceratosauria	0	3	0	0	1
Coelurosauria	7	3	1	0	0
Megalosauroidea	3	0	0	1	0
Theropoda inc. sed.	0	0	0	0	0
Diplodocoidea	2	0	0	1	0
Eusauropoda	1	0	0	1	0
Macronaria	11	4	1	0	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	18	11	1	0	0
Neornithischia inc. sed.	2	0	0	1	0
Ankylosauria	1	1	1	0	0
Stegosauria	2	0	0	1	0
Thyreophora inc. sed.	0	0	0	0	0
Total			5	5	1
Total a+b+c			11		
		Jaccard Index [%]	**45,45**		

	Cretaceous				
	FA		Presence		
Clades	**Iberia**	**Great Britain**	**a**	**b**	**c**
Allosauroidea	1	2	1	0	0
Ceratosauria	0	0	0	0	0
Coelurosauria	7	8	1	0	0
Megalosauroidea	3	6	1	0	0
Theropoda inc. sed.	0	1	0	0	1
Diplodocoidea	2	2	1	0	0
Eusauropoda	1	0	0	1	0
Macronaria	11	7	1	0	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	18	10	1	0	0
Neornithischia inc. sed.	2	3	1	0	0
Ankylosauria	1	4	1	0	0
Stegosauria	2	2	1	0	0
Thyreophora inc. sed.	0	0	0	0	0
Total			9	1	1
Total a+b+c			11		
		Jaccard Index [%]	**81,82**		

	Cretaceous				
	FA		Presence		
Clades	**Great Britain**	**Belgium & France**	**a**	**b**	**c**
Allosauroidea	2	1	1	0	0
Ceratosauria	0	3	0	0	1
Coelurosauria	8	3	1	0	0
Megalosauroidea	6	0	0	1	0
Theropoda inc. sed.	1	0	0	1	0
Diplodocoidea	2	0	0	1	0
Eusauropoda	0	0	0	0	0
Macronaria	7	4	1	0	0
Sauropoda inc. sed.	0	0	0	0	0
Marginocephalia	0	0	0	0	0
Ornithopoda	10	11	1	0	0
Neornithischia inc. sed.	3	0	0	1	0
Ankylosauria	4	1	1	0	0
Stegosauria	2	0	0	1	0
Thyreophora inc. sed.	0	0	0	0	0
Total			5	5	1
Total a+b+c			11		
		Jaccard Index [%]	**45,45**		

Climate Dataset Calculations

Age (Ma)	pCO2 prob. max.	Radiative Forcing	Global Mean Temperature	Stages
60,00	350,14	1,195888537	14,74145089	
60,50	336,38	0,981423308	14,60848245	
61,00	328,65	0,85702364	14,53135466	
61,50	315,58	0,639896286	14,3967357	Selandian
62,00	309,78	0,540711953	14,33524141	
62,50	304,22	0,44392292	14,27523221	
63,00	288,17	0,153855874	14,09539064	
63,50	275,40	-0,088533842	13,94510902	
64,00	261,70	-0,361513723	13,77586149	
64,50	256,67	-0,465471356	13,71140776	
65,00	244,44	-0,726599916	13,54950805	
65,50	235,40	-0,928189548	13,42452248	
66,00	228,84	-1,079391178	13,33077747	Danian
66,50	238,80	-0,851452362	13,47209954	
67,00	247,76	-0,654441973	13,59424598	
67,50	245,15	-0,711044377	13,55915249	
68,00	244,28	-0,73018273	13,54728671	
68,50	247,71	-0,655493444	13,59359406	
69,00	261,65	-0,362632629	13,77516777	
69,50	278,05	-0,037366756	13,97683261	
70,00	304,07	0,441202837	14,27354576	
70,50	334,70	0,954751627	14,59194601	
71,00	345,49	1,124425206	14,69714363	
71,50	355,69	1,280068666	14,79364257	
72,00	369,23	1,480032693	14,91762027	Maastrichtian
72,50	397,26	1,871483506	15,16031977	
73,00	435,21	2,359616108	15,46296199	
73,50	454,20	2,588098483	15,60462106	
74,00	487,96	2,971598723	15,84239121	
74,50	515,38	3,26414998	16,02377299	
75,00	559,27	3,701398204	16,29486689	
75,50	584,05	3,933338734	16,43867001	
76,00	611,01	4,174764548	16,58835402	
76,50	624,52	4,291747649	16,66088354	
77,00	649,32	4,500099436	16,79006165	
77,50	680,95	4,754560307	16,94782739	
78,00	714,54	5,012111889	17,10750937	
78,50	696,89	4,878305386	17,02454934	
79,00	692,48	4,844351038	17,00349764	
79,50	685,23	4,788039452	16,96858446	
80,00	675,53	4,711792406	16,92131129	

80,50	677,98	4,731161079	16,93331987	
81,00	659,94	4,586863451	16,84385534	
81,50	668,49	4,655775122	16,88658058	
82,00	683,89	4,777559282	16,96208675	
82,50	699,49	4,898262935	17,03692302	
83,00	680,80	4,753326431	16,94706239	
83,50	634,30	4,374839554	16,71240052	Campanian
84,00	623,45	4,282577953	16,65519833	
84,50	614,81	4,207902651	16,60889964	
85,00	619,42	4,247909012	16,63370359	
85,50	629,72	4,336080564	16,68836995	
86,00	611,63	4,180153006	16,59169486	
86,50	601,04	4,086722488	16,53376794	Santonian
87,00	574,15	3,841807368	16,38192057	
87,50	574,37	3,843912418	16,3832257	
88,00	558,55	3,694477106	16,29057581	
88,50	498,70	3,088069108	15,91460285	
89,00	477,51	2,855782554	15,77058518	
89,50	455,56	2,604079843	15,6145295	
90,00	450,16	2,540301615	15,574987	Coniacian
90,50	473,13	2,806536117	15,74005239	
91,00	481,15	2,896415269	15,79577747	
91,50	479,48	2,87778701	15,78422795	
92,00	462,19	2,681290608	15,66240018	
92,50	467,86	2,746629575	15,70291034	
93,00	496,03	3,059328187	15,89678348	
93,50	522,13	3,333685442	16,06688497	
94,00	535,30	3,466989901	16,14953374	Turonian
94,50	568,52	3,789151029	16,34927364	
95,00	596,80	4,048818602	16,51026753	
95,50	609,86	4,164609981	16,58205819	
96,00	622,05	4,270522084	16,64772369	
96,50	650,13	4,50671798	16,79416515	
97,00	691,83	4,839340219	17,00039094	
97,50	730,74	5,132064521	17,18188	
98,00	777,35	5,462867013	17,38697755	
98,50	814,98	5,715774539	17,54378021	
99,00	805,80	5,655176309	17,50620931	
99,50	833,61	5,836729406	17,61877223	
100,00	862,05	6,016222008	17,73005765	
100,50	898,53	6,237922845	17,86751216	Cenomanian
101,00	945,01	6,507781267	18,03482439	
101,50	965,86	6,624511363	18,10719705	
102,00	986,66	6,738493483	18,17786596	

102,50	1006,27	6,843829678	18,2431744	
103,00	1013,91	6,8842464	18,26823277	
103,50	1012,72	6,877994682	18,2643567	
104,00	1027,05	6,953160734	18,31095965	
104,50	1040,37	7,022121964	18,35371562	
105,00	1046,47	7,053394332	18,37310449	
105,50	1019,65	6,914454463	18,28696177	
106,00	1037,44	7,006990909	18,34433436	
106,50	1033,25	6,98534007	18,33091084	
107,00	1028,16	6,958933294	18,31453864	
107,50	1039,07	7,015393204	18,34954379	
108,00	1040,79	7,0242499	18,35503494	
108,50	1055,28	7,098243529	18,40091099	
109,00	1058,74	7,115740103	18,41175886	
109,50	1069,77	7,171188645	18,44613696	
110,00	1110,78	7,372438383	18,5709118	
110,50	1112,36	7,380050543	18,57563134	
111,00	1148,07	7,549124403	18,68045713	
111,50	1171,66	7,657913474	18,74790635	
112,00	1084,42	7,243957302	18,49125353	
112,50	1095,61	7,29890437	18,52532071	
113,00	1194,91	7,76303978	18,81308466	Albian
113,50	1207,55	7,81932223	18,84797978	
114,00	1123,15	7,43169923	18,60765352	
114,50	1112,02	7,378442082	18,57463409	
115,00	1107,09	7,354631657	18,55987163	
115,50	1102,52	7,332541313	18,54617561	
116,00	1103,25	7,336067687	18,54836197	
116,50	1093,39	7,288031069	18,51857926	
117,00	1077,79	7,21113765	18,47090534	
117,50	1155,01	7,581333055	18,70042649	
118,00	1132,44	7,475767987	18,63497615	
118,50	1109,51	7,366343139	18,56713275	
119,00	1085,07	7,247151712	18,49323406	
119,50	1065,49	7,149731823	18,43283373	
120,00	1035,66	6,997840187	18,33866092	
120,50	1016,73	6,89911617	18,27745203	
121,00	1004,47	6,83421564	18,2372137	
121,50	990,70	6,760367531	18,19142787	Aptian
122,00	983,18	6,719632734	18,1661723	
122,50	968,78	6,640698621	18,11723315	
123,00	987,36	6,742306959	18,18023031	
123,50	931,03	6,428031774	17,9853797	
124,00	878,83	6,119349643	17,79399678	
124,50	861,74	6,014297614	17,72886452	

125,00	856,72	5,982990562	17,70945415	
125,50	867,26	6,048443139	17,75003475	
126,00	899,52	6,243816869	17,87116646	
126,50	935,43	6,453242825	18,00101055	
127,00	925,84	6,398124024	17,96683689	
127,50	856,06	5,978878594	17,70690473	
128,00	848,35	5,930496911	17,67690808	
128,50	836,78	5,857054443	17,63137375	
129,00	846,83	5,920910305	17,67096439	
129,50	913,11	6,324042688	17,92090647	Barremian
130,00	935,09	6,451309857	17,99981211	
130,50	950,58	6,53918544	18,05429497	
131,00	906,95	6,287829451	17,89845426	
131,50	879,94	6,126121589	17,79819539	
132,00	886,48	6,165686297	17,8227255	
132,50	892,13	6,199682428	17,84380311	Hauterivian
133,00	909,10	6,300537778	17,90633342	
133,50	925,75	6,397612791	17,96651993	
134,00	949,64	6,533909998	18,0510242	
134,50	972,22	6,659626388	18,12896836	
135,00	983,04	6,718853265	18,16568902	
135,50	993,36	6,774733557	18,20033481	
136,00	1003,59	6,829521899	18,23430358	
136,50	1024,47	6,939716297	18,3026241	
137,00	1011,73	6,872767491	18,26111584	
137,50	1014,20	6,885825299	18,26921169	
138,00	1007,19	6,848721275	18,24620719	
138,50	991,33	6,763762881	18,19353299	
139,00	947,70	6,522990349	18,04425402	
139,50	919,17	6,359442732	17,94285449	Valanginian
140,00	906,23	6,283593324	17,89582786	
140,50	890,40	6,189293922	17,83736223	
141,00	848,21	5,929614758	17,67636115	
141,50	841,34	5,886124376	17,64939711	
142,00	831,85	5,825423531	17,61176259	
142,50	831,68	5,82429435	17,6110625	
143,00	738,70	5,190055709	17,21783454	
143,50	725,03	5,090088517	17,15585488	
144,00	664,43	4,623141453	16,8663477	
144,50	651,10	4,514722291	16,79912782	
145,00	713,01	5,000699316	17,10043358	Berriasian
145,50	742,41	5,216854738	17,23444994	
146,00	766,99	5,391131238	17,34250137	
146,50	754,86	5,305805516	17,28959942	
147,00	746,00	5,242655852	17,25044663	

147,50	737,93	5,184457292	17,21436352	
148,00	725,33	5,092340096	17,15725086	
148,50	717,12	5,031447763	17,11949761	
149,00	738,03	5,18522364	17,21483866	
149,50	717,24	5,032327348	17,12004296	
150,00	703,38	4,927896915	17,05529609	
150,50	824,47	5,777720118	17,58218647	
151,00	834,46	5,842169411	17,62214503	
151,50	799,60	5,613854505	17,48058979	
152,00	812,24	5,697801342	17,53263683	Tithonian
152,50	809,92	5,682497622	17,52314853	
153,00	815,46	5,71892578	17,54573398	
153,50	827,93	5,800118903	17,59607372	
154,00	813,72	5,707513552	17,5386584	
154,50	807,17	5,66431421	17,51187481	
155,00	794,32	5,578456232	17,45864286	
155,50	756,06	5,314316428	17,29487619	
156,00	722,07	5,068203913	17,14228643	
156,50	897,28	6,230484343	17,86290029	
157,00	858,14	5,991852975	17,71494884	
157,50	835,77	5,850567511	17,62735186	Kimmeridgian
158,00	822,84	5,767160447	17,57563948	
158,50	814,67	5,713756284	17,5425289	
159,00	797,35	5,598786784	17,47124781	
159,50	796,50	5,593064355	17,4676999	
160,00	795,33	5,585232571	17,46284419	
160,50	782,89	5,500897851	17,41055667	
161,00	785,35	5,517651572	17,42094397	
161,50	793,06	5,569949336	17,45336859	
162,00	775,16	5,447804626	17,37763887	
162,50	785,09	5,51590638	17,41986196	
163,00	771,41	5,421827934	17,36153332	
163,50	881,36	6,134742459	17,80354032	Oxfordian
164,00	855,45	5,975057989	17,70453595	
164,50	861,99	6,015802082	17,72979729	
165,00	871,25	6,073012198	17,76526756	
165,50	877,20	6,109430385	17,78784684	
166,00	895,90	6,222247031	17,85779316	Callovian
166,50	929,99	6,422027215	17,98165687	
167,00	974,75	6,673542765	18,13759651	
167,50	1004,32	6,833425963	18,2367241	
168,00	1011,74	6,872828619	18,26115374	
168,50	1029,62	6,966537626	18,31925333	Bathonian
169,00	1045,27	7,047262452	18,36930272	

169,50	1041,41	7,027467961	18,35703014	
170,00	1037,52	7,007408901	18,34459352	
170,50	1029,03	6,963449074	18,31733843	Bajocian
171,00	1071,40	7,17934594	18,45119448	
171,50	1064,67	7,145604448	18,43027476	
172,00	1048,07	7,061541011	18,37815543	
172,50	1043,98	7,040623365	18,36518649	
173,00	1040,97	7,025203285	18,35562604	
173,50	1027,70	6,956526127	18,3130462	
174,00	1022,63	6,930085388	18,29665294	Aalenian
174,50	1018,11	6,906406374	18,28197195	
175,00	1015,82	6,894316505	18,27447623	
175,50	1012,49	6,876767664	18,26359595	
176,00	1020,94	6,921241383	18,29116966	
176,50	1015,73	6,893846284	18,2741847	
177,00	1008,42	6,855203569	18,25022621	
177,50	999,39	6,807107357	18,22040656	
178,00	998,07	6,80001574	18,21600976	
178,50	983,26	6,72005149	18,16643192	
179,00	971,06	6,653272584	18,125029	
179,50	941,81	6,489647421	18,0235814	
180,00	909,50	6,302839752	17,90776065	
180,50	908,94	6,299582935	17,90574142	
181,00	912,62	6,321199714	17,91914382	
181,50	926,38	6,40122914	17,96876207	
182,00	920,92	6,369646919	17,94918109	
182,50	921,06	6,370418186	17,94965928	
183,00	895,84	6,22191776	17,85758901	Toarcian
183,50	896,31	6,224707157	17,85931844	
184,00	923,15	6,382543317	17,95717686	
184,50	859,47	6,000139897	17,72008674	
185,00	956,90	6,574677739	18,0763002	
185,50	965,18	6,620781239	18,10488437	
186,00	945,03	6,507904494	18,03490079	
186,50	950,25	6,537360877	18,05316374	
187,00	947,85	6,523802984	18,04475785	
187,50	952,48	6,549920059	18,06095044	
188,00	972,15	6,659239173	18,12872829	
188,50	985,24	6,730817509	18,17310686	
189,00	1005,13	6,837756221	18,23940886	
189,50	1074,93	7,196916982	18,46208853	
190,00	1111,68	7,376791624	18,57361081	
190,50	1156,62	7,588790416	18,70505006	
191,00	1196,72	7,77115268	18,81811466	Pliensbachian
191,50	1246,89	7,990839444	18,95432046	

192,00	1345,54	8,398234618	19,20690546	
192,50	1436,28	8,747375124	19,42337258	
193,00	1466,45	8,858588971	19,49232516	
193,50	1449,82	8,797566631	19,45449131	
194,00	1740,76	9,77598539	20,06111094	
194,50	1769,77	9,864416656	20,11593833	
195,00	1796,57	9,94481357	20,16578441	
195,50	1800,11	9,955349235	20,17231653	
196,00	1783,74	9,906483136	20,14201954	
196,50	1772,47	9,87256431	20,12098987	
197,00	1768,36	9,860161684	20,11330024	
197,50	1770,42	9,866366831	20,11714744	
198,00	1767,68	9,858076345	20,11200733	
198,50	1768,01	9,859102454	20,11264352	
199,00	1725,17	9,727872325	20,03128084	
199,50	1731,48	9,747394792	20,04338477	Sinemurian
200,00	1732,56	9,750725561	20,04544985	
200,50	1730,60	9,744682705	20,04170328	
201,00	1723,92	9,723989889	20,02887373	
201,50	1732,22	9,749688422	20,04480682	Hettangian
202,00	1689,51	9,616121294	19,9619952	
202,50	1550,94	9,158274995	19,6781305	
203,00	1521,18	9,054627733	19,61386919	
203,50	1602,61	9,333604391	19,78683472	
204,00	1583,01	9,267758403	19,74601021	
204,50	1545,19	9,138416151	19,66581801	
205,00	1492,68	8,953421721	19,55112147	
205,50	1461,27	8,839661106	19,48058989	
206,00	1543,67	9,133120189	19,66253452	
206,50	1540,96	9,123729387	19,65671222	
207,00	1505,03	8,997514558	19,57845903	
207,50	1437,95	8,753574799	19,42721638	
208,00	1368,30	8,487945038	19,26252592	
208,50	1348,82	8,411247539	19,21497347	Rhaetian
209,00	1277,87	8,12215225	19,0357344	
209,50	1240,43	7,96306529	18,93710048	
210,00	1206,60	7,815131449	18,8453815	Norian

Addendum

During the review of this thesis, a new representative of spinosaurids was described from the Arcillas de Morella Formation (Spain). *Protathlitis cinctorrensis* from the Barremian, assigned to the Baryonychinae, indicates a high diversity of spinosaurids in the region of that time (Santos-Cubedo et al., 2023). Apart from this new discovery, *Baryonyx walkeri*, *Ceratosuchops inferodios*, *Riparovenator milnerae* from England, as well as *Iberospinus natarioi*, *Camarillasaurus cirugedae* and *Vallibonavenatrix cani* already were known from Spain. The finding of *Protathlitis* could not be included in the database and calculations for this study. Since the genus can be included into the clade Megalosauroidea, this highlights the faunal similarity between the regions of Iberia and Britain, despite their palaeogeographic position during the Cretaceous. The occurrence during a time of increased coastal area discussed in this work, reinforces the impression of a climatically driven diversity push of the Megalosauroidea in the Barremian and underlines the suggestion that the origin of spinosaurids was in Europe before they spread further across Africa.

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