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Characterization of marine environments from the aspiring Geopark Algarvensis Loulé-Silves-Albufeira

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Mestrado em Biologia Marinha

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Aleksandra Pierożyńska

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RESUMO

Os municípios de Loulé, Silves e Albufeira, em conjunto com a Universidade do Algarve, através do seu Centro de Investigação Marinha e Ambiental - CIMA, juntaram-se para trabalhar na candidatura do aspirante Geoparque Algarvensis Loulé-Silves-Albufeira a Geoparque Mundial da UNESCO. Este projeto intermunicipal do Sul de Portugal surgiu na sequência da descoberta paleontológica do *Metoposaurus algarvensis* - um anfíbio gigante extinto que viveu há 227 milhões de anos (Ma). O Geoparque encontra-se ainda na sua fase inicial de desenvolvimento, mas a importância desta candidatura para o futuro do território é significativa não só para a conservação do seu património geológico mas igualmente para o desenvolvimento local.

O aspirante Geoparque Algarvensis constitui um território com uma geodiversidade única, que permite revelar vários capítulos da história natural do planeta Terra, e da região do Algarve, que ficaram registados nas rochas das paisagens do Geoparque. O objetivo principal do presente trabalho consiste na caracterização dos paleoambientes marinhos das Eras Paleozóica e Mesozóica, que deram origem ao atual território do Geoparque Aspirante Algarvensis. Este projeto visa uma abordagem holística na educação, conservação, e desenvolvimento sustentável, através da valorização e promoção do património natural e cultural.

A base desta investigação paleoambiental e paleobiológica reside na pesquisa, organização e síntese de dados, principalmente bibliográficos, para desenvolver cenários relativos às alterações ambientais marinhas que ocorreram ao longo do tempo geológico e que deram origem às rochas do Geoparque Algarvensis. Esta abordagem científica sintetiza um vasto conjunto de dados da paleontologia, paleoecologia, (paleo)biologia marinha e geologia, a fim de reconstruir a natureza dos habitats e ambientes que existiram no passado, a partir de todas as evidências recolhidas. Estas evidências baseiam-se nas características ambientais dos sedimentos que originaram as rochas encontradas no tetrritório do Geoparque Algarvensis, mas principalmente no conteúdo fossilífero, e na sua paleobiologia, paleoecologia, ocorrência, e diversidade.

As rochas do Geoparque Algarvensis "contam" uma história notável, sobretudo marinha, que representa a evolução ambiental do sul de Portugal. A posição da charneira da região algarvia, e o seu património geológico das Eras Paleozóica e Mesozóica, permite vislumbrar mudanças paleoambientais importantes, que ocorreram nos últimos 360 Ma. A caracterização paleoambiental fornecida neste trabalho está dividida em três fases principais: Carbonífero Superior (Paleozóico – I.º Ciclo Wilson), representado pelo fecho do antigo Oceano Rheic e a formação do supercontinente Pangea); Triásico Superior e Jurássico (Mesozóico – II.° Ciclo Wilson), associado à fracturação do continente Pangea, que levou à abertura e evolução do Oceano Atlântico - uma parte notável das paisagens do território Algarvensis, o Barrocal. Todos estes paleoambientes contam uma história

única de organismos, ou grupo de organismos, e dos seus habitats, registados na geologia do território do aspirante Algarvensis.

O primeiro paleoambiente registado no território, e o único da Era Paleozóica (I.° Ciclo de Wilson), é representado pelo Grupo do Flysch do Baixo Alentejo (BAFG). Estas fácies resultantes de sedimentação em águas profundas incorporam diversos fósseis de goniatites. As espécies refereidas na bibliografia pertencem principalmente a oito famílias da ordem Goniatitida: Cravenoceratidae, Girtyoceratidae, Dimorphoceratidae, Homoceratidae, Reticuloceratidae, Gastroceratidae, Ramositidae, e Neoglyphioceratidae. Este associação fóssil de uma única ordem indica ambientes bastante peculiares, de águas profundas, nas quais as goniatites podiam habitar a diferentes profundidades na coluna de água. Os vários morfotipos das suas conchas indicam numerosos nichos ecológicos, tornando-os num dos grupos faunísticos marinhos mais bem sucedido do final do Período Carbonífero. Esta história baseia-se principalmente na síntese autoecológica, uma vez que não se encontrou outro conjunto fóssil nas fácies do BAFG, e como se trata de grupos extintos, seriam necessário estudos mais detalhados. Por ser o único hotspot de nautiloides no mundo, o Mar de Banda (Sul da Indonésia) pode ser considerado como um ambiente atual equivalente ao da "história do Paraíso das goniatites". Esta antiga história dos cefalópodes baseia-se sobretudo no conhecimento genérico dos taxa de amonóides planispirais, e não das goniatites em particular, devido ao número reduzido de publicações sobre a fauna amonóide do BAFG. Além disso, a maioria destas publicações são antigas e centram-se apenas na identificação, sistematização paleontológica, estratigrafia, e correlação, dentro da ordem Goniatitida. A futura investigação detalhada (principalmente sobre morfótipos de conchas) deste conjunto de fósseis, pode levar a uma melhor compreensão do paleoambiente paleozoico associado ao território do Algarvensis. No entanto, esta história não durou muito tempo. No final do Carbonífero Superior, as duas grandes massas terrestres colidiram, fechando assim o antigo Oceano Rheic, e criando um novo supercontinente – a Pangea. Esta fase tectónica representa o final do I.° Ciclo de Wilson, acabando com o "paraíso dos cefalópodes", e fechando assim o primeiro capítulo marinho da história geológica do aspirante Geoparque Algarvensis.

O segundo paleoambiente, e o primeiro dentro da Era Mesozóica (II.° Ciclo de Wilson), descrito no presente trabalho, está representado pela Formação do Grés de Silves do Triásico Superior. Esta formação inclui as camadas rochosas das recentes descobertas de várias jazidas fossilíferas com restos do anfíbio gigante - *Metoposaurus algarvensis*, que estão na origem do projeto do aspirante geoparque algarvensis Loulé-Silves- Albufeira. Além disso, foram também descobertos um crânio de fitossauro e pequenos ossos dérmicos de placodontes (que ainda estão por identificar), tornando a história geológica deste território ainda mais notável. Durante este período, também foi revelada uma história menos conhecida, a dos pequenos Conchostracea (*Euestheria minuta*, e

Pseudoasmussia destombesi). Todo este registo geológico e fossilífero apontam para uma deposição sedimentar numa bacia de rifte, de ambiente de transição de francamente continental para costeiro, caracterizado por condições áridas, que levaram à existência de lagoas temporárias. Por fim ocorreu a deposição de evaporitos, na recém-formada plataforma carbonatada marinha de pouca profundidade do período Jurássico. A região de Afar (África Oriental) é um exemplo atual deste tipo ambiente de transição. Tal como a atividade da Província Magmática do Atlântico Central (CAMP) do final do Triásico, e a consequente fracturação da Pangea, que levou à abertura de um novo mar tropical e estreito (a Bacia do Algarve), a elevada atividade vulcânica nesta região da África Oriental levou à abertura do Mar Vermelho, que à escala geológica é ainda bastante recente. Esta atividade tectónica relacionada com o rifte, abriu o segundo capítulo totalmente marinho da história geológica do aspirante Geoparque Algarvensis.

O terceiro paleoambiente (II.° Ciclo Wilson) do território geoparque algarvensis apresentado na presente dissertação, está associado ao desenvolvimento, durante o Jurássico, de uma plataforma carbonatada em águas pouco profundas da Bacia Algarvia, que evoluiu para um estreito mar tropical, com recifes altamente diversificados e abundantes, dominados por corais. Aqui, as bioconstruções complexas produziram um grande número de fósseis de invertebrados, de faunas marinhas semelhantes no atual (Cenozóico). Todos os grupos de invertebrados associados aos fósseis encontrados em fácies do Jurássico, ainda existem nos oceanos atuais. Estas diversas associações fossilíferas dos recifes do Jurássico, permitiram uma caracterização paleoambiental mais detalhada, das formações da Bacia do Algarve, permitindo a utilização da abordagem sinecológica. Em comparação com as fases geológicas anteriores, o período Jurássico conta uma história geológica singular baseada nas associações de fósseis e não num único grupo de fósseis. Estes antigos recifes dominados por corais já forneciam uma vasta gama de habitats marinhos para diversos grupos de invertebrados. Este cenário enquadra-se perfeitamente no equivalente atual da natureza do Mar Vermelho (também resultado de riftogénese), que suporta uma fauna abundante e diversificada de recife de corais tropicais. Finalmente, foi no Cretácico (o último período da Era Mesozóica) que se deu o fim da vasta história marinha dos paleoambientes registados na geodiversidade do aspirante Geoparque Algarvensis.

Palavras-chave: Geoparque Algarvensis, paleoambientes, goniatites, conchostráquios, *Metoposaurus*, paleo-recifes

ABSTRACT

The municipalities of Loulé, Silves and Albufeira, together with the University of Algarve, through its CIMA – Marine and Environmental Research Centre, are currently working on the application of the aspiring Geopark Algarvensis Loulé-Silves-Albufeira to become a UNESCO Global Geopark for which the present work aims to contribute. Accordingly, the main objective of the present study is the marine paleoenvironmental characterization of Paleozoic and Mesozoic Eras, recorded in the territory of the aspiring Algarvensis Geopark, in southern Portugal, through data synthesis (mainly bibliographic), and to present scenarios on the marine environmental changes that occurred along geologic times. This scientific approach synthesizes a wide range of datasets from paleontology, paleoecology, marine (paleo)biology and geology, in order to reconstruct the nature of ancient habitats and environments based on all the available evidences. These evidences consist in environmental characteristics from the sediment deposits that formed the rocks found in the Algarvensis Geopark territory, and mainly from their fossil content and their respective paleobiology, paleoecology, occurrence, and diversity.

The rocks of the Algarvensis Geopark territory "tell" remarkable stories, mostly marine, which are also representative of the environmental evolution of the south of Portugal. The hinge position of the Algarve region, and its geological heritage from Paleozoic and Mesozoic Eras, have given insights into the important paleoenvironmental changes that occurred within the last 360 Million years (Ma). The paleoenvironmental characterization provided in the present study is divided into three main phases: Late Carboniferous deep-sea of the Baixo Alentejo Flysch Group (Paleozoic – Ist Wilson's Cycle, represented by the closure of the ancient Rheic Ocean and formation of the super-continent Pangea); Late Triassic coastal (transitional) environment and Jurassic carbonate platform (Mesozoic – IInd Wilson's Cycle, associated with the Pangea break-up). All these paleoenvironments tell a unique story of the organisms or group of organisms, and their habitats, that are at the origin of the geodiversity recorded in the Algarvensis territory. Each of these three paleoenvironments is then related to a present-day equivalent environment for science communication purposes. This project aims for a holistic approach in education, conservation, and sustainable development, through the valorization and promotion of the natural and cultural heritage.

Key words: Algarvensis Geopark, paleoenvironments, goniatites, conchostracans, *Metoposaurus*, paleo-reefs

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LIST OF ACRONYMS AND ABBREVIATIONS

BAFG – Baixo Alentejo Flysch Group
CAMP – Central Atlantic Magmatic Province
CO_2 – carbon dioxide
dm - conch diameter
DO – Dissolved Oxygen
E – East
ECI - evaporites and carbonates intercalations
LPIA - Late Paleozoic Ice Age
Ma - Millions of years
ml/l – milliliter per liter
N – North
NE – Northeast
NW – Northwest
O_2 – Oxygen gas
OAE – Oceanic Anoxic Events
ºC – Degree Celsius
PSD – Portuguese Southwest Domain
S – South
SBM - São Bartolomeu de Messines
SE – Southeast
SPZ – South Portuguese Zone
SST – Sea Surface Temperature
SW – Southwest
swi – Surface-Water Interface
UNESCO – United Nations Educational, Scientific and Cultural Organization
uw - umbilical width
VS – Vulcano-sedimentary
W - West
ww - whorl width

CHAPTER 1. INTRODUCTION

The present master thesis contributes to characterize the (paleo) marine environments of the Aspiring Geopark Algarvensis Loulé-Silves-Albufeira from a marine biologist point of view.

1.1. Study justification

The municipalities of Loulé, Silves and Albufeira, together with the University of Algarve, through its CIMA – Marine and Environmental Research Centre, in southern Portugal, are currently working on the application of the aspiring Geopark Algarvensis Loulé-Silves-Albufeira to become a UNESCO World Geopark, containing geological sites (for instance Penina and Rocha da Pena) of recognized national and international importance for science, education and culture. Currently there are 169 UNESCO World Geoparks in 44 countries, among which 5 in Portugal (UNESCO, 2021). The importance of this application is significant due to the heritage of the Algarvensis Geopark and local development in the future. The aspiring Algarvensis Geopark covers part of the territory of Loulé-Silves-Albufeira. The area includes geological formations from the South Portuguese Zone (Paleozoic) and the Algarve Basin (Meso-Cenozoic). The geodiversity of this territory serves as the basis for telling the ancient history of the Algarve, which has potential for yielding insight into the dramatic (mostly marine) paleoenvironmental and faunal changes that occurred during Late Paleozoic and Mesozoic eras.

The discover of fossils of *Metoposaurus algarvensis,* an extinct amphibian resembling a giant salamander that lived 227 million years ago in Triassic (Brusatte *et al*., 2015), inspired the intermunicipal project that is still in its early phase of development. With a geological heritage of World reference and due to privileged location of the aspiring Algarvensis Geopark, it is a destination of high potential. It offers the visitors a wide range of options in terms of accommodation, gastronomy, uses and customs, traditions, heritage, and landscape, which allow an active participation and experiences in the local culture (Algarvensis Geoparque, 2021). However, for a better understanding of this territory's rich geological history, reconstructing past environments is important to evaluate the extent of natural environmental variability. Moreover, understanding past climatic changes and studying the response of organisms to those changes can represent a holistic approach that may engage the public with both, the geology and marine biology (Birks, 2008).

Paleontology is of fundamental importance to both geology and evolutionary biology. It is the biogeological memory of the Planet that should be valorised in the awareness of the future generations, and for the scientific, educational, and cultural benefit. Paleobiological heritage is recorded in fossils, thus conceptually the Paleontological Heritage, stretches far beyond the strict framework of geology, becoming also a part of the ancient story of life on Earth (Cachão *et al.*, 1999).

Therefore, the aspiring Algarvensis Geopark plays an important role in general attention to geoconservation and in promoting a greater awareness of Paleobiological importance in South Portugal. Although, dinosaur fossils have universal appeal, fossils of marine invertebrates seem to be less significant for the general public. Thus, in this dissertation, not only the case of famous amphibian is considered, but also the vaster marine story of the Algarve region. Moreover, this dissertation is an opportunity to contribute to the ambitious plan for the integrated development of the territory, which from the geological heritage point of view aims to give new life to this area, making the aspiring UNESCO Geopark a desirable destination for the future visitors. It aims to promote the knowledge about the territory, in its prehistorical and environmental aspects, using the natural heritage for the future generations, creating synergies related to scientific, educational, social and touristic activities (Algarvensis Geoparque, 2021).

1.2. Objectives of the dissertation

This dissertation aims to document and synthesize literature within a wide field of sciences in terms of its scopes and scales (as marine biology, paleontology, paleoecology, paleogeography, and geology), in order to explore (mostly marine) environmental and evolutionary changes that occurred in ancient times in the territory of the aspiring Algarvensis Geopark.

The main objective of the present study is thus a paleoenvironmental characterization of the past marine environments from Paleozoic and Mesozoic eras, recorded in the territory of the aspiring Algarvensis Geopark. Collecting and summarising existing data will allow to design an educational and scientific setting for future visitor's itinerary, with both educational and touristic purposes. The analysis of the study area (in the context of paleoenvironmental changes) is done by a broad literature synthesis. Therefore, the project aims to document and interpret in detail, most of the past marine environments and marine species found in the aspiring Geopark Algarvensis, as well as their evolution over space and time. These ancient stories and their main protagonists will give a new life of the landscapes of Algarve region in South of Portugal.

1.3. Methodology

The base of this paleoenvironmental and paleobiological research is the accumulation and ordering of data, mainly bibliographic, to develop the hypotheses about the marine environmental changes that occurred in the region of the Algarvensis Geopark. This approach synthesizes a wide range of data sets of paleontology, paleoecology, marine biology and geology, in order to reconstruct the nature of ancient habitats and environments from all the available evidence. These evidences are based on the environmental characteristics of the sediments found in the region of Algarvensis Geopark, but mainly on the fossil content, their biology, ecology, occurrence, and diversity. Moreover, it is significant to point, that this bibliographic evidence relies not only on the local data, but they are extended to a regional scale, and general knowledge of Earth sciences. It is applied, to allow the reader to understand the complex nature of the Algarvensis environmental evolution, and to show, that each paleoenvironment tells a different and very unique marine story, being continuously a part of global abiotic and biotic arrangements.

Characterization of the marine paleoenvironments is done on the basis of paleoecology, to investigate interactions between ancient environment and the organisms (fossils) as once living communities, bounded in space and time by limiting factors (Doyle and Lowry, 1996). Identification and interpretation of fossil assemblages, and determination of these factors, which controlled the diversity and abundance of each fossil group, allow for the environmental characterization and comparison with present-day equivalents on the principle of uniformitarianism (Doyle and Lowry, 1996).

Uniformitarianism is the theoretical basis for the interpretation of sedimentary facies and fossils. Comparison of the characteristics of ancient and modern sediments is therefore an important tool in paleoenvironmental characterization (*e.g.,* Doyle and Lowry, 1996). The uniformitarian is based on “the present is the key to the past” principle, and also refers to the paleoenvironmental research as “transferred ecology”, because it limits our ability to see how the ecology of the past was different from that of today (*e.g.,* Lyman, 2017). Thus, extinct species are assumed to have had ecological tolerances similar to those of their closest living relatives. This assumption is known as “taxonomic uniformitarianism” (*e.g.,* Reed *et al.,* 2013) or “taxonomic analogy” (*e.g.,* Bobe and Eck, 2001). Choosing its closest living relative as an appropriate ecological analogue for an extinct species assumes that the two species, because they are members of the same genus, family, or clade, not only share lots of genes but also have the same or similar ecological tolerances (*e.g.,* Lyman, 2017). The more distant the genetic relationship between the extinct and extant (modern analogue) taxon, the more tenuous the assumption becomes because as genetic relationship grows distant, the greater the chance that similarity in ecological tolerances decreases (*e.g.,* Jehl, 1966; Reed *et al.,* 2013).

Accordingly, this dissertation is organized in the following five chapters: Chapter 1 – presents the subject and the justification of the study, the outlined objectives and the methods used, to carry out this investigative and scientific work; Chapter 2 – briefly frames out the study area in the context of the Algarve region and its geological history, as well as, the main knowledge about the marine paleobiology and paleoecology of the Ancient Oceans; Chapter 3 and 4 – synthetize the fossil record of the study area, their biology and ecology, and propose interpretations of the paleoenvironments from the Late Paleozoic and the Mesozoic eras, and their present-day equivalents; Chapter 5 – takes stock of the work developed, summarizing and highlighting the main conclusions of the research, within the scientific dissemination, in the fields of Marine Biology, Paleoecology, Geosciences and Environmental Education, and the enhancement of paleontological heritage in the context of geoconservation.

CHAPTER 2. SCOPE OF THE STUDY

2.1. Study area and its natural heritage

The aspiring Algarvensis Geopark, covers part of the territories of Loulé, Silves and Albufeira (Figure 2.1). The geodiversity of this territory serves as the basis for telling the ancient history of Algarve – the region of recognized multidisciplinary interest due to its geological, geomorphological, biological, cultural and scientific importance (*e.g.*, Lopes, 2006).

Figure 2.1. Map of the aspiring Algarvensis Geopark in the southern Portugal (adapted from Algarvensis Geoparque, 2021).

2.1.1. Geomorphological setting

The Algarve is the southernmost province of mainland Portugal and is best known in Europe for its touristic coast of the Atlantic Ocean. The more inland part of the Algarve is called "Serra Algarvia", and it differs from the Algarve Basin in its geomorphological aspects (Figure 2.2). The Serra forms a mountainous barrier, marking the limit with the Lower Alentejo plains, to the north. This region comprises mostly Late Paleozoic sedimentary rocks that, in the western Algarve extend to the Littoral forming dramatic sea cliffs on the west coast, mostly in Alentejo region (Oliveira *et al.,* 2009)**.**

South of the Serra, there is the Meso-Cenozoic Algarve Basin that comprises carbonate rocks, and defines a region locally known as the "Barrocal" (Mesozoic Algarve Basin) and "Littoral" (Cenozoic sediments). In the western Algarve Basin, in Sagres area, the limestone lithologies form high cliff elevations with significant Jurassic outcrops, extending as a gentle elevations aligned in the east-west strike, from Cap Saint Vincent to the Guadiana River on the Portuguese-Spanish border (Oliveira *et al.*, 2009). Therefore, "Serra" and "Barrocal" constitute as two geomorphological components (landscapes) of the Algarvensis Geopark, which correspond to two ancient marine cycles in Earth history of Paleozoic and Mesozoic eras.

Figure 2.2. Regional map indicating the three geomorphological regions of Algarve, namely the Serra, Barrocal and Littoral (adapted from Oliveira et al., 2009).

2.1.2. Geological framework

Through the rocks of the aspiring Geopark Algarvensis territory we can read the history, beginning 360 million years ago, in the Late Paleozoic. At that time, South Portugal was at the bottom of a deep-sea – Rheic, between two supercontinents: Laurussia, to the north, and Gondwana, to the south. In this environment the sedimentary rocks are turbidites that became characteristic schists and greywackes of the Algarve mountain range. Millions of years later, the collision of these two supercontinents closed the sea between them, forming a new supercontinent: Pangea, and ending the I Wilson cycle. After that, the Algarve was located near the eastern bank of Pangea, and Geopark region was inhabited by amphibians and reptiles such as metoposaurus, phytosaurus and placodonts. In this environment the reddish rocks of Grés de Silves Group were formed, representing the beginning of a new Wilson cycle. With the continuous movement of the tectonic plates Pangea began to breakup, giving the origin of the Atlantic Ocean early in the Jurassic. These changes carved the complete story of southern Portugal (Algarvensis Geoparque, 2021).

Thus, the Algarvensis Geopark geology is divided in two major units – the Late Paleozoic Variscan basement of the South Portuguese Zone (SPZ), and the Meso-Cenozoic sedimentary rocks of the Algarve Basin (Figure 2.3). This geological partition is very well established and is affecting not only the shape of the natural landscapes but also some human aspects, as the use of soils for agriculture or the water resources, *etc.* (Oliveira *et al.*, 2009).

The southern end of the Iberian Massif (South Portuguese Zone) forms the basement of the Algarve Basin. The northern boundary of the SPZ with the Ossa-Morena Zone is defined by the Beja – Acebuches Ophiolite, whereas to the southern, by the angular unconformity with Mesozoic sedimentary rocks of the Algarve Basin (García-Navarro *et al.,* 2005). The Beja – Acebuches Ophiolite (390–350 Ma) is interpreted as a remnant of the Rheic Ocean, which separated the Euramerican SPZ from the Gondwanan Ossa– Morena Zone. The SPZ is divided into four domains (Figure 2.3), which are, from NE to SW, the Pulo do Lobo Suture Zone, the Pyrite Belt, the Baixo Alentejo Flysch Group (BAFG – the only one intercepted by the aspiring Algarvensis Geopark) and the Southwest Portuguese Domain (SPD). These domains trend NW–SE near the Atlantic coast to east–west inland and generally towards the SW (Rodrigues *et al.*, 2015).

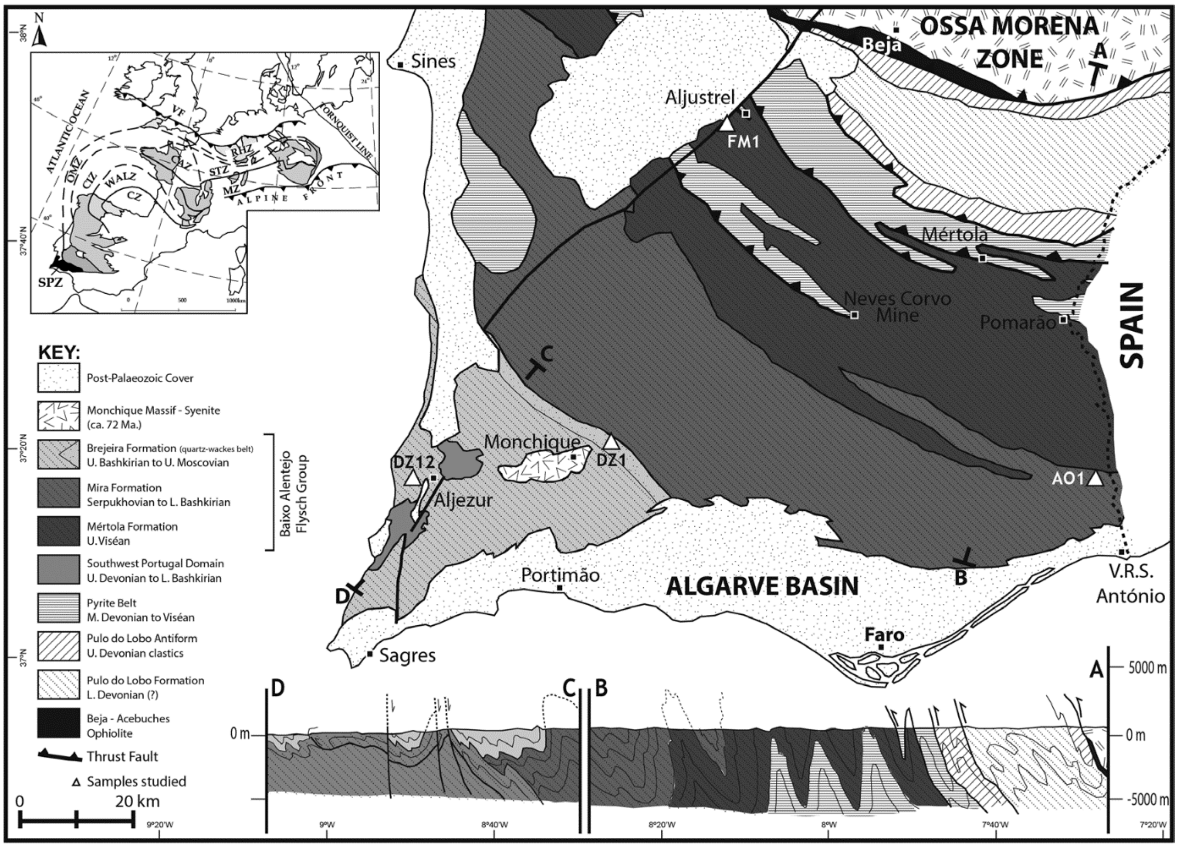


Figure 2.3. Simplified geological map of South Portugal illustrates the South Portuguese Zone (SPZ) and Ossa Morena Zone (adapted from Rodrigues et al., 2015).

Two significant evolutionary events of Algarve region can be defined in the Geopark terrane – the first between the Carboniferous and Middle Triassic (I Wilson Cycle – closure of the ancient Rheic ocean), represented by the Flysch Group of Baixo Alentejo (BAFG) of the SPZ, and the second (II Wilson Cycle – opening of the new Atlantic ocean), represented by to main groups of formations: the Grés of Silves Group, associated with Pangea breakup, and the transition from continental to coastal environment (from Middle Triassic to the earliest Jurassic); and the Algarve Basin (Meso-Cenozoic cover), which represent installation, evolution, and further "end" of carbonate platform in shallow tropical sea, which formed between Tethys and new Atlantic oceans (from Early Jurassic to earliest Cretaceous) (*e.g.*, Lopes, 2006).

The ages of the units, found in the aspiring Algarvensis Geopark outcrops, range from the topmost Lower Carboniferous to the Quaternary (however the Cenozoic is not included in the present work). As an example, the lithostratigraphic column from Rocha da Pena (Figure 2.4) can be introduced, to show general pattern of paleoenvironmental history of the Geopark: BAFG (the only one belonging to the I Wilson Cycle); Silves Sandstones; Pelites with evaporites and carbonate intercalations; Volcano-sedimentary Complex; and Algarve Basin (Lopes, 2006).

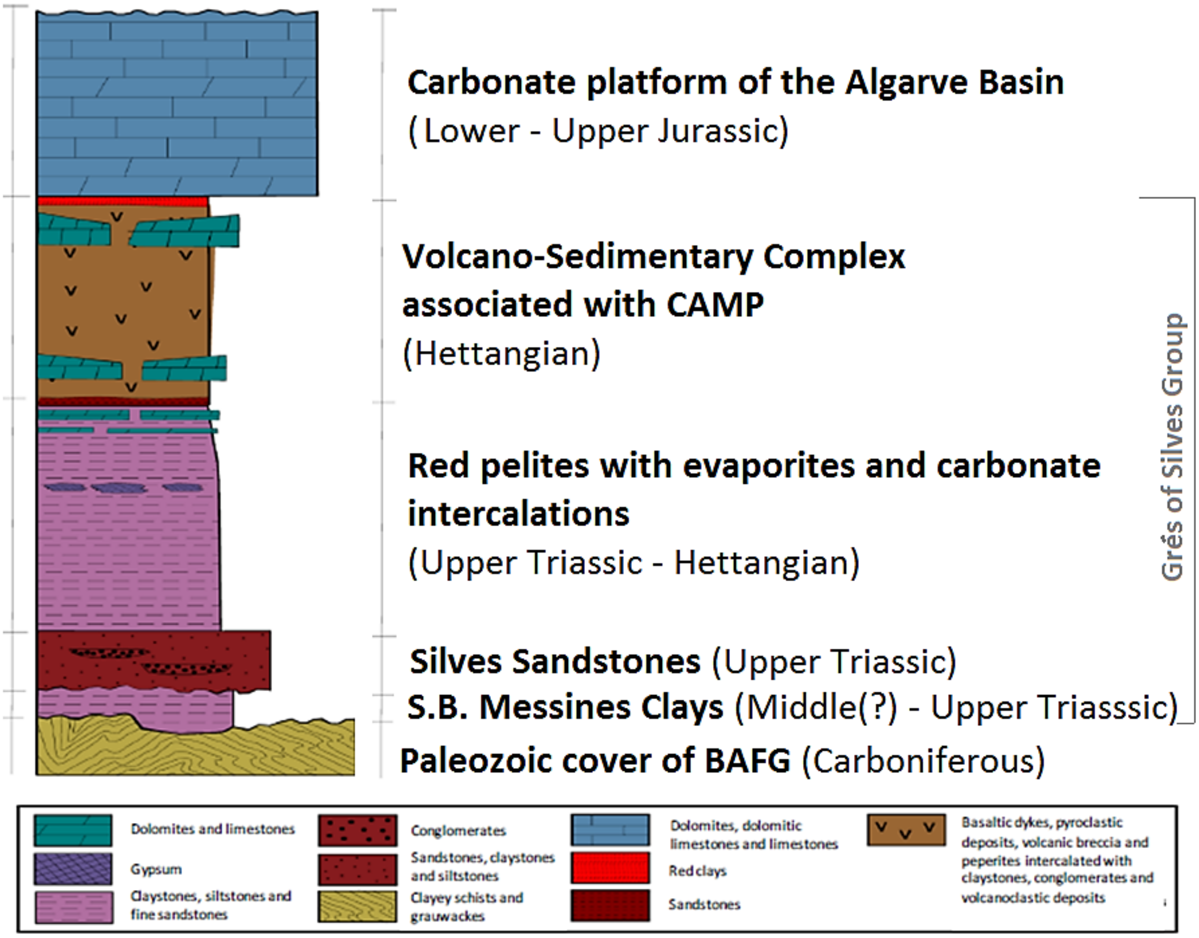


Figure 2.4. Lithostratigraphic Column of Rocha da Pena and Surrounding area. Each strata represents different marine/coastal paleoenvironment (adapted from Lopes, 2006).

Most of the strata found in the study area belong to marine sedimentary complexes. Although, some of the layers indicate fluvial or volcanic genesis, it is proven that there was a continuous, environmental input from surrounding marine areas (Lopes, 2006).

2.2. Fundamentals

Many of the key ecosystems and evolutionary processes are usually too slow to be studied on short periods of time. Sedimentary sequences show how environmental conditions have changed over time. Size, shape and arrangement of their particles, as well as geometry of the strata provide evidence about the environment in which sediment accumulated. Together with faunal succession, sedimentary rocks allow us to demonstrate the existence of ancient oceans, coasts, lagoons, lakes, etc. (*e.g.*, Murck and Skinner, 1999). Marine sediments can accumulate near the mouth of the streams, be moved along the coast by currents, accumulate on the continental shelves or at the foot of continental slopes. Most common marine sediments can be divided into seven categories: Estuarine and Deltaic sediments; Beach sediments, Offshore

Clastic sediments; Carbonate Shelves; Marine evaporite Basins; Turbidity Currents and Turbidites; and Deep-sea Oozes (Open University, 1978). Moreover, fossil contents enable us to find present-day equivalents. Using the climatic ranges of modern plants and animals as guides, we can conclude more detailed characteristics of the environment in which similar ancestral forms lived (*e.g.*, Murck and Skinner, 1999).

Paleoenvironmental reconstruction rely on fossils, which are an important component of sedimentary rocks, and, when they were living organisms, they were an integral part of their environment. Through the interpretation of their ancient ecologies, fossils act as a past climatic indicators; temperature, oxygen levels, salinity, and other environmental factors that can be determined due to the fossilized content. Moreover, the determination of ancient geographies and complex tectonic terranes are possible to be detected using the distribution patterns of fossil groups. Finally, they are highly important in stratigraphy as indicators of geological time periods (Figure 2.5) as they were restricted to particular environments (Doyle and Lowry, 1996).

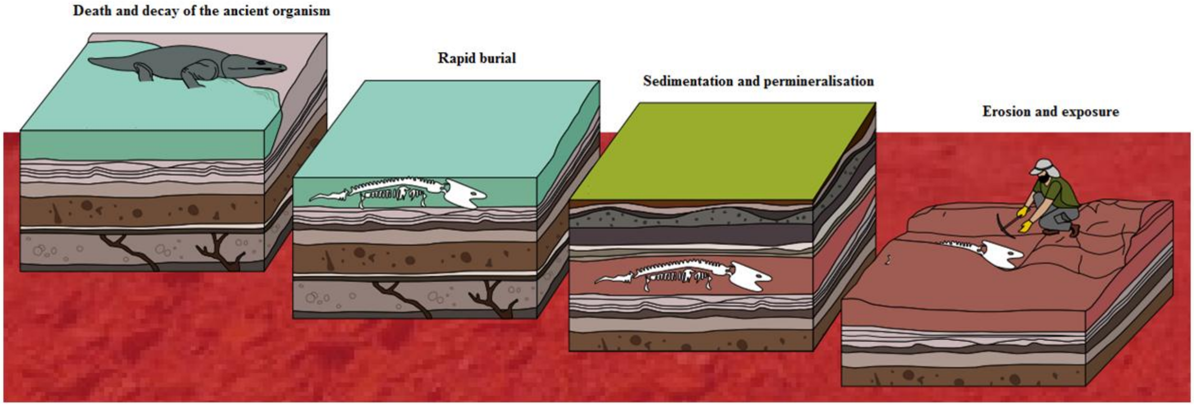


Figure 2.5. Fossilization process (Algarvensis Geoparque, 2021).

Lithology can give direct evidence of environment. For example, it is obvious that coral limestones are deposited in fully marine conditions, while red, oxidized sandstones form on land or in transitional environments (Open University, 1978). Equally, comparison of ancient and modern sedimentary structures serves information as paleowind or paleocurrent directions; while geometry determines spatial limits of the environment, like river channels or submarine fans (*e.g.*, Doyle and Lowry, 1996).

Paleoecology can be defined as the study of the interaction of ancient organisms with each other and with the environment in which they lived. Like in ecology, it is extremely important to determinate the nature of the biosphere and to record possibly all environmental changes (Doyle and Lowry, 1996). To make inferences about past conditions, paleoecology must rely on empirical data based on fossil assemblages and their enclosing sedimentary rocks. Experimental approaches and direct measurement of past environmental parameters as biotic, abiotic factors and species dispersal (which are critical components of modern ecology) are generally impossible in paleoecology (Brett, 2020; Lyman, 2017) . Furthermore, distortion and loss of information during fossilization processes indicates that fossil assemblages and their distributions are rarely coherent with living communities. Thus, the resolution of ancient ecosystems remains relatively imprecise. The lack of precision is compensated by the fact that paleoecology deals with processes occurring over vast intervals of time that are unavailable to modern ecology. Long-term evolutionary changes in communities may be related to patterns of environmental change. Therefore, the overall ecological changes in the global biosphere may be documented by evolutionary paleoecology which focuses on recognition and interpretation of long-term ecological trends that have been critical in shaping evolutionary patterns (Brett, 2020).

The origin and evolution of the higher taxonomic groups is consistent with macroevolution (*e.g.,* Hautmann, 2020; Hembry and Weber, 2020), and reflects the major cumulative changes in the fossil record through geological time (Annex – full Geological Time Scale). Paleontology has probably most to offer in the study of large-scale changes and broad patterns of evolution. Macroevolution (illustrated by the fossil record over a time) includes the appearance and disappearance of the higher taxonomic groups (*e.g.,* Grantham, 1995). It is also probable that macroevolutionary processes reflect large-scale environmental changes that result in processes like natural selection that lead to changes in a great number of taxonomic groups at the same time. Adaptive radiations and mass extinctions are two macroevolutionary processes that are of extreme importance in the development of the biosphere (Doyle and Lowry, 1996).

Among the major aspects of paleoecological application there is also taxonomic uniformitarianism (*e.g.,* Doyle and Lowry, 1996; Brett, 2020; Lyman, 2017). This concept relies on the investigation of modern organisms to specify limiting environmental factors, such as temperature preference, salinity tolerance, or depth ranges of their ancient relatives. Determination of similar environmental preferences of the closely related ancestors indicates that particular strata were deposited under a comparable range of environmental conditions. Such an approach is valid only for closely related organisms in relatively recent geologic time (Brett, 2020).

Species and even genera may have relatively uniform environmental ranges through time, however, the same cannot be said about higher taxa such as families. At the level of order or class, only the broadest uniformitarian generalizations apply. For instance, it is considered that fossils of nautiloids (*e.g.,* Westermann, 1996; Lukeneder, 2015) or echinoderms act as indicators of normal marine salinities, because all living representatives of these taxa have limited abilities for osmotic processes. Similarly, the restriction of photosynthetic organisms (such as algae) to the euphotic zone may be used in determining relative depth. However, the precision and reliability of taxonomic uniformitarianism principle breaks down in increasing age of ancient samples (Doyle and Lowry, 1996; Brett, 2020).

Moreover, some morphological features of fossils may be useful in interpretation of environmental inferences, avoiding reliance on evolutionary relationships. For example, delicately branched, inflexible colonies typify quiet areas and, commonly, areas of high turbidity where a branching skeleton may shed sediment more readily than a flat or globose form. Flexible or articulated skeletons or flat encrusting form in colonial marine animals are associated with highly turbulent shallow-water environments where streamlining becomes important; or growth forms of colonial organisms relate to environmental factors such as turbulence and sedimentation rates. Such ecologically related morphology may transcend taxonomic boundaries (Brett, 2020).

In the broad paleoenvironmental research two branches of paleoecology can be distinguished. The relationship of individual or small groups of organisms to their environment (paleoautecology) and the relationship of groups of organisms to each other and to their environment (paleosynecology). Moreover, trace fossils have a special role in paleoecology, as they directly represent the interaction between organisms and the substrate. Together the study of the ecological relationships among ancient organisms (recorded in the fossils assemblages, in their body fossils and trace fossils) are of paramount importance in paleoenvironmental analysis (Doyle and Lowry, 1996).

Through understanding the biology of the closest modern analogues, we can infer more about the extinct species by applying the concept of paleoautecology. If the species or close relatives are extant, then (with some confidence) its mode of life (physiology), and even behaviour can be inferred by taxonomic uniformitarianism, provided that the biology of living relatives is well understood. For instance, extant “fossil-like” Nautilus, and modern stalked crinoids provide valuable clues for interpreting the paleobiology of extinct organisms (Brett, 2020).

Paleoautecology investigates also the relationship of particular species or small groups of organisms to their environment, and their response to a series of external factors which limit their distribution and diversity. These limiting factors are important in the interpretation of the nature of ancient ecologies and in paleoenvironmental analysis (Doyle and Lowry, 1996).

Limiting factors directly influence the distribution and diversity of living organisms. Abiotic and biotic factors, the interaction between organisms (particularly in the competition for habitat space, and in the distribution of prey and predators), for example, may also limit organisms. However, their influence is often difficult to detect in the geological record. On a small scale, both sets of factors may affect individuals or communities, while on a much larger scale they have a direct influence on the distribution of plants and animals across the globe, the subject of biogeography and its geological counterpart, paleobiogeography (Doyle and Lowry, 1996).

Diversity is a valuable indicator of the nature and hostility of an environment, and, together with the density or abundance of individuals of a particular species, is an important paleoecological tool. Generally, environments of a relatively hostile nature, such as those with high or low salinities or low oxygen, are characterised by an assemblage which is low in diversity, often being monospecific (*e.g.,* Milsom and Rigby, 2009). Conversely, abundance of individuals may be high. In these stressed environments, most taxa are excluded, including most predators, so that the available resources are used by a limited number of successful species. This leads to the development of the low diversity but high density of the assemblage. Often, the colonisation of such habitats may be rapid, the species concerned being opportunists (Doyle and Lowry, 1996).

In less limited environments, such as normal marine salinities and fully oxygenated conditions, the biodiversity may be high, but the abundance of individuals may be correspondingly lower (*e.g.,* Oliveira *et al.*, 1985). This reflects the partitioning of the same resources available to the low-diversity assemblage between a greater number of species, with a corresponding increase in predators. In such environments, density is kept low through the competition for resources, and by the action of the predators. Species in these environments are known as equilibrium species, maintained in equilibrium by the quantity of the resource (Doyle and Lowry, 1996).

The study of relationships within groups of organisms (communities) that exist in the same time and space is known as synecology (Brett, 2020). In biology, this forms much of the detailed subject matter of ecology. A community is defined as a group of organisms from one or more species that occupy the same habitat in life. The identification of living communities is relatively straightforward, as it is possible to examine in detail a particular habitat (*e.g.*, freshwater lake, lagoon, and reef) and observe directly the interaction of its constituent organisms. In paleoecology, however, identification of communities is much more difficult. Relatively few fossils are found in their life position. Most have been transported, and some may be derived from a completely different habitat. It is preferable to use the term assemblage to describe a grouping of fossils preserved in each rock unit, as it may not necessarily reflect the nature of the original community. Recurring assemblages suggest a greater ecological significance, and these are referred to as associations (Doyle and Lowry, 1996).

Further, paleosynecology allows also to reconstruct trophic structure of ancient ecosystems, which are based on their comprehensive comparison with modern ecosystems, allowing the recognition of feeding strategies of individual organisms, and sequence of major trophic chains (Rozhnov, 2009). Most importantly, it must always be remembered that all fossil assemblages are extinct assemblages, as only in exceptional circumstances they come anywhere near the nature of the living community (Doyle and Lowry, 1996).

To sum up, among the goals of paleoecology are the reconstruction and characterization of ancient environments (primarily depositional environments), the inference of modes of life for ancient organisms from fossils, and the recognition of recurring groupings of ancient organisms that define relicts of communities (paleocommunities), thus the reconstruction of the interactions of these organisms with each other and with their environments. All these steps together document large-scale and long-term evolutionary patterns of changing ecosystems (Brett, 2020).

Chapters 3 and 4 combines mostly marine (with exception for the Triassic) fossil content found in the geological formations of the study area, and their biology, and ecology, as they were once living organisms, thriving in the ancient environments of the Algarvensis Geopark. Thus, it is a synthesis of general knowledge of paleobiology and paleoecology in order to understand the evolution pattern of faunas in the South of Portugal. This combined knowledge is crucial to characterize the dynamics of the ancient environments and the factors which controlled evolutionary paths of the Algarve region and its biota. Each subchapter is focusing on particular geological time of the Algarvensis Geopark, represented by different group of fossil organisms, in order to tell a story which is “one of its kind” for each period. Although, vertebrate fossils have universal appeal, fossils of marine invertebrates seem to be less significant for general public. Therefore, the following subchapters focus mainly to reveal a truly fascinate stories of the “less famous” invertebrates, which are essential part of all past and present marine, and aquatic ecosystems on Earth.

2.3. Review of knowledge on Marine Paleobiology

The major evolutionary trends unfolded in an interval of environmental instability, and in times of repeated global changes that punctuated longstanding periods of stability and termed ecological-evolutionary subunits. The bounding events (of greater or lesser intensity) kept creating restructuring in local to global ecosystems and are seen as major drivers of long-term patterns in species evolution (Becker *et al.*, 2016). The study of environmental changes, accompanied by global extinction events of the Phanerozoic, is fundamental for our understanding of the dynamics and stability of climate and marine ecosystems in Earth history, thus also in the study area (Kaiser *et al.*, 2015).

The face of Planet Earth has altered in many ways through prehistoric time. Active, till today, dynamic processes, such as plate tectonics and climate change, are differing the Earth’s surface and continue to impact biodiversity patterns. On the other hand, living organisms have their special role in shaping the surrounding environments. They have capacity to influence Earth’s hydrological and geochemical cycles, as well as its atmosphere, climate, sediments, and even the rocks in the geological substrate. Abiotic– biotic interactions characterize natural history and are the main trigger of evolutionary innovations, changes and biodiversity turnovers (Becker *et al.*, 2016).

The ocean may seem like a vast and unchanging environment, but the reality is way more complex down there – beneath the water surface. The life has continuously evolved over time and much of its history has taken place in the ancient seas. The first ocean lifeforms were so small that the naked eye would not see them. Later, “bizarre, and alien-like” creatures appeared, changing the water column into a “science fiction-like” movie (Hall, 2019). Even more familiar creatures, like fish, sharks, octopuses, etc., have a longer and more tangled past than we think, with ancestors very different from the modern organisms we know. Some species slowly adapted to changing seas, while others could not overcome surrounding changes, existing just for a “moment” in terms of geological time. Therefore, changing Earth resulted in constant reorganization of marine life. However, history shows that every “end” has a new beginning, creating new niches for those species, which are meant to survive (Hall, 2019).

The three "great" evolutionary faunas of the Phanerozoic oceans are sets of organisms (taxa) that have similar (not identical) histories of diversification and decline over geological time scale. Each marine evolutionary fauna appears to have its own level of diversity (increasing in stepwise succession), and characteristic rates of origination and extinction (Figure 2.6). Moreover they present different ecological styles: The Cambrian Fauna with generalized detritus- and suspension-feeders and low levels of faunal diversity; the Paleozoic Fauna with complexly tiered epifaunal suspension-feeders and intermediate alpha and beta diversities; and the Modern (Mesozoic-Cenozoic) Fauna with abundant shell-crushing predators, infaunal suspension and deposit-feeders, and highest diversities (Jablonski and Sepkoski, 1996).

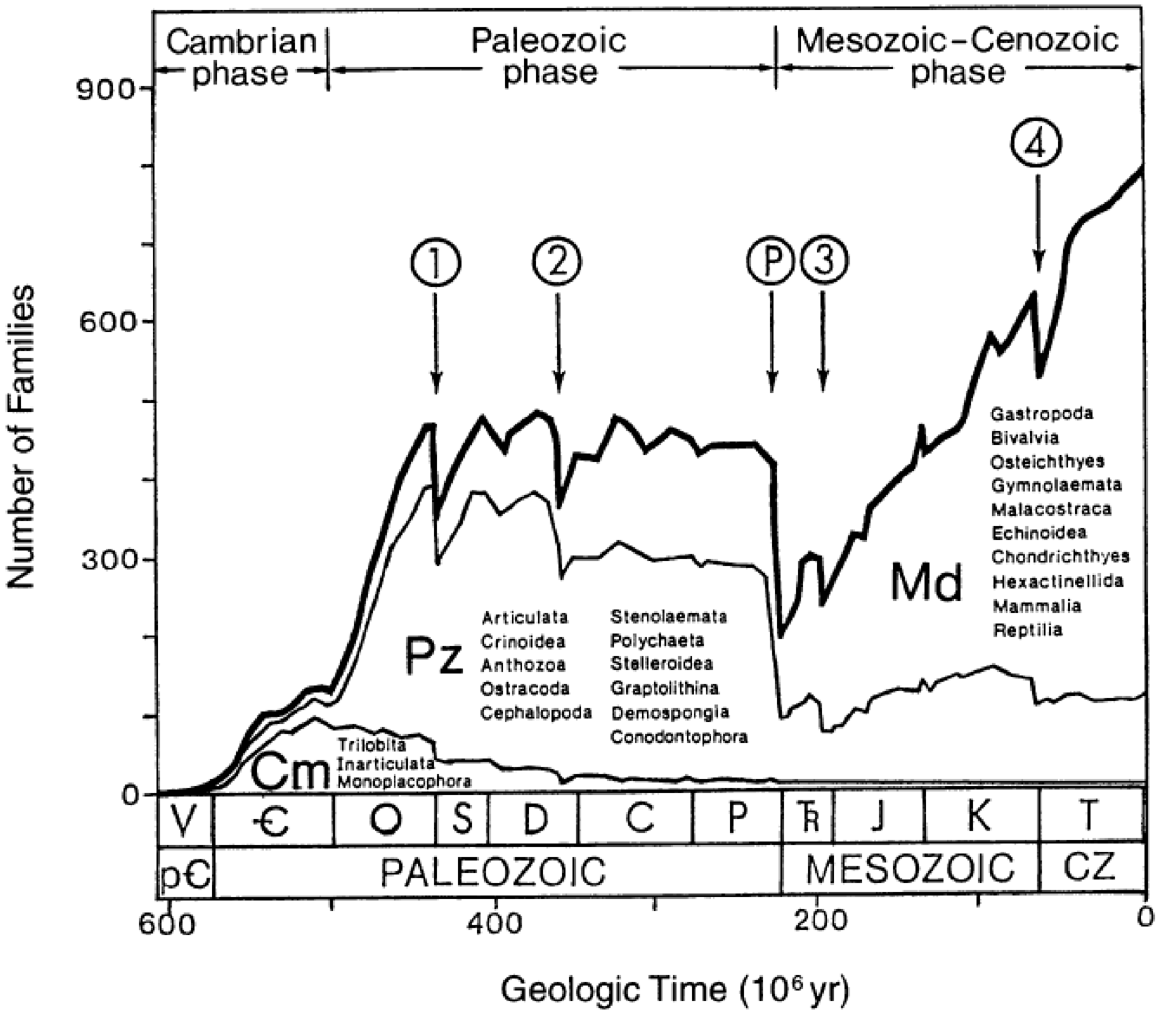


Figure 2.6. Diversity of marine animal families through the Phanerozoic, and the three Evolutionary Faunas. Arrows above the curve identify the five major mass extinctions of the Phanerozoic: P = end-Permian; 1 = end-Ordovician; 2 = late Devonian (Frasnian); 3 = end-Triassic; 4 = end-Cretaceous. Fields below the heavy curve delimit diversity histories of the three Faunas: Cm = Cambrian fauna; Pz = Paleozoic fauna; Md = Modern fauna (adapted from Jablonski and Sepkoski, 1996).

Figure 2.7 represents space above and below the sediment-water interface (swi), increasing through the Paleozoic, with stalked echinoderms, corals, bryozoans, and other groups extending above the sediment, and molluscs and arthropods burrowing below the the sediment-water interface. The Mesozoic was a time of maximum tiering breadth, followed by a drop of epifaunal forms in the Cenozoic (Jablonski and Sepkoski, 1996). At the community level, the evolutionary faunas dominate different marine habitats as they succeed one another through time. Members of the Cambrian fauna appeared across the shelf and became progressively more abundant on the outer shelf and basinal habitats during the Ordovician. Additionally, during the Ordovician, the early ancestors of the Modern fauna rose and started to dominate in shallow seas, then progressively expanded into the shelf zone and deeper habitats by the mid-Paleozoic. The great end-Permian mass extinction strongly reduced Paleozoic faunal communities, and the Mesozoic-Cenozoic fossil record occurred with mollusc-dominated taxa with preferences to shelf habitats. However, even if Upper Cretaceous outer-shelf habitats maintained diverse epifaunal communities, they certainly differed in the ecological modes of Paleozoic marine life (Jablonski and Sepkoski, 1996).

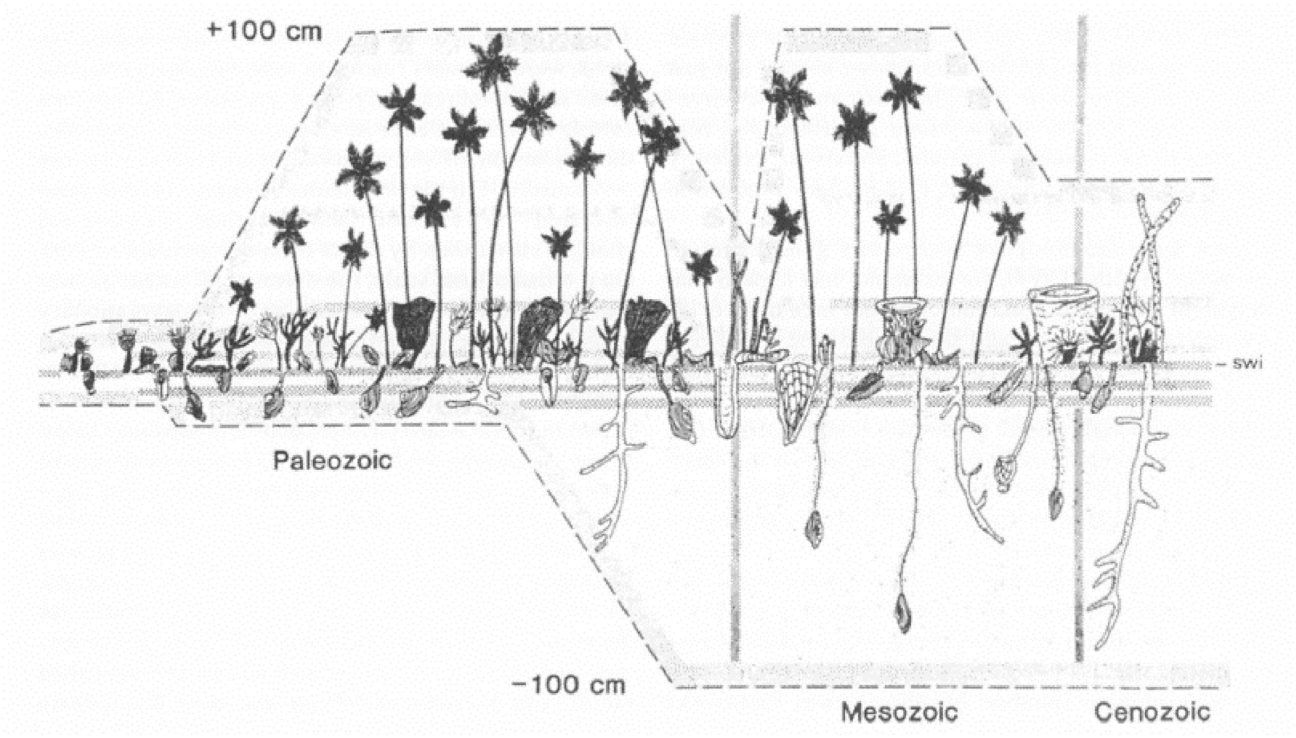


Figure 2.7. History of the tiering, or vertical ecological structure, of shallow-water benthic marine communities. Early Paleozoic communities dominated by the Cambrian Fauna showed little depth or complexity in tiering patterns. Dashed lines represent estimated maximum burrowing and elevation depths through time; vertical lines are boundaries between geologic eras; swi - the sediment-water interface (adapted from Jablonski and Sepkoski, 1996).

2.3.1. Paleozoic

Paleozoic Era literally translates as the "time of ancient life" and spans the time period between 544 and 245 million years ago. Paleozoic is the first of three eras within the Phanerozoic eon (the time of visible life). While life originated during the Archean and increased in complexity during the earlier Proterozoic, the Paleozoic era is marked by the spread of animals with hard parts such as shells and exoskeletons (Robison and Crick, 2021).

The story of life on Earth starts in the seas. The Cambrian explosion was a sudden increase in the rate of evolution. Intense diversification resulted in more than 35 new animal phyla; however, more recent discoveries show that the origin of "explosion" started around 575 million years ago (almost the end of the Proterozoic Eon) with the Ediacara fauna which was found as mostly soft-bodies animals (Robison and Crick, 2021). Moreover, non-stromatolitic algae of Early Paleozoic appeared within stromatolites and stromatolitic reefs (Levin, 2013). Representatives of almost all the major animal phyla evolved at the very beginning of the Paleozoic, during the Cambrian. The biota rapidly diversified throughout the Cambrian and Ordovician periods evolving in adaptation to almost all marine environments (Robison and Crick, 2021).

The Great Ordovician Biodiversification Event occurred only 40 million years after the Cambrian explosion. Tripling of global biodiversity in only 25 million years was accompanied by fragmentation of continents and proliferation of shallow, warm water habitats. In the middle of Ordovician new groups of marine fauna appeared: coralline animals, brachiopods, bivalves, and one of the most successful marine invertebrates – cephalopods (Levin, 2013).

Cephalopods are the most morphologically and behaviourally complex organisms in phylum Mollusca, which possess features such as a well-developed nervous system and brain, and a highly mobile, carnivorous lifestyle. The historical development of higher taxa, their diversity, and biostratigraphic significance have been fully studied over time. Research about ontogeny of Paleozoic ammonoids allowed to recognize the major evolutionary patterns, which became important in many fields of biology. All these numerous studies indicate that the Paleozoic cephalopods were one of the major elements of the ecological structure in marine ecosystems (Barskov *et al.*, 2008)**.**

The class Cephalopoda includes six subclasses (Figure 2.8), from which three share remarkable evolutionary history and are commonly fossilized around the World: the class Nautiloidea, Ammonoidea and Coleoidea (Sreepat, 2017). It is widely accepted that ammonoids are more closely related to extant coleoids than to Nautiloids. However, coleoids have internalized, and largely reduced shells, leaving *Nautilus* being the only living analogue to constrain the accretionary growth and function of the ammonoid shell (Ritterbush *et al.*, 2014).

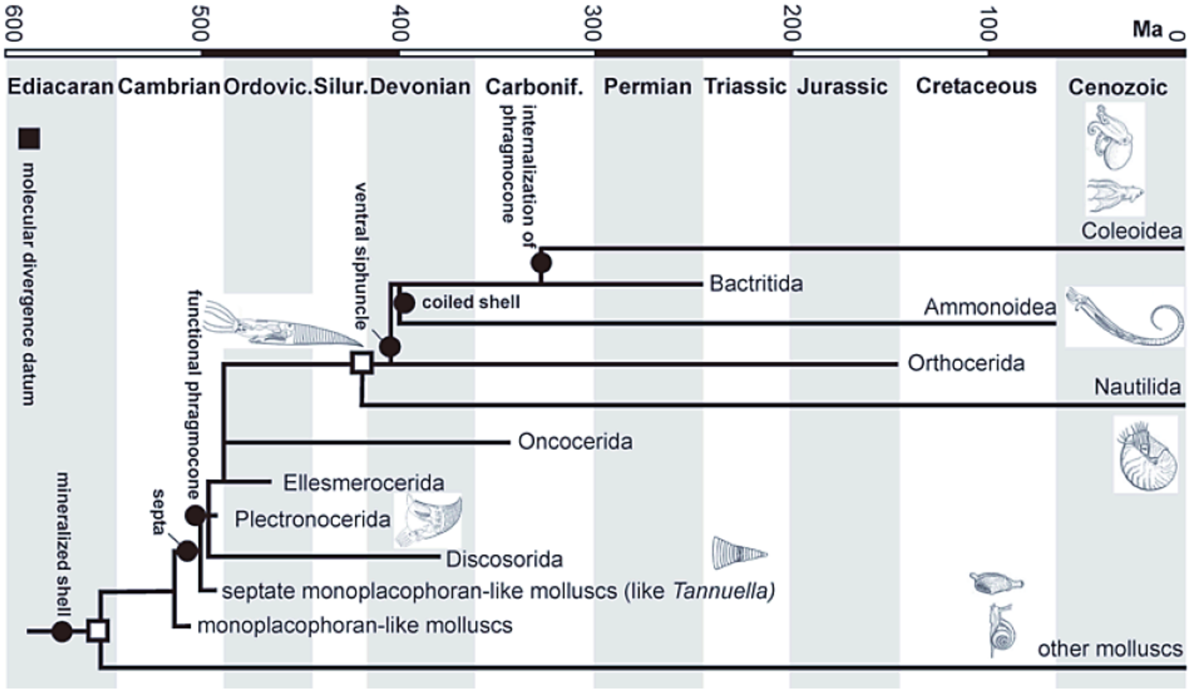


Figure 2.8. Cephalopod phylogeny (adapted from Klug et al., 2015).

The nautiloids dominated the Ordovician and Silurian seas, but by late Devonian, give way to the increasing presence of large predatory fish. About this time the ammonoids began to take over from the nautiloids, although still rare in the early Devonian, but they proliferated in the Carboniferous. The Coleoidea made their first appearance in the late Mississippian (Middle Carboniferous) but remained rare. Meanwhile, the sharp increase of ammonoids diversity occurred, and only two nautiloid orders persisted (Lacchia, 2012).

Ammonoids are the most diverse of all ectocochleate (externally shelled) cephalopods. These molluscs have developed a coiled phragmocone (the chambered portion of the shell). The coils (whorls) of the phragmocone may overlap the preceding ones almost completely (involute) or not at all, resembling a shape of a coiled snake (evolute). This is determined by the umbilicus-diameter of the early whorls left after overlap (Doyle and Lowry, 1996). A variety of shapes and sizes, with many ornament types, characterize the fossils of ammonoid shells, with a great range of variation even within a single species (different morphotypes). A great variety of terms have been involved to describe the shape of the ammonoid conch. It is assumed that these different shapes may reflect high adaptation to many modes of life using different swimming speeds and styles (Doyle and Lowry, 1996).

Line patterns on these shells are called sutures (pointing towards the aperture-saddles, pointing away from the aperture-lobes), and are known to have evolved in complexity through time.

Affiliation to specific order can be demonstrated in these zigzags: simple in most early ammonoids (goniatitic sutures), lobes modified with some frills in the ceratites (ceratitic suture) and completely frilled lobes and saddles in the ammonites themselves (ammonitic suture) (Figure 2.9). This contrasts with the nautiloid suture, which has only simple deflections and no pronounced lobes or saddles (Doyle and Lowry, 1996). Thus, the Carboniferous ammonoids are characterised as "goniatites", rather than "ammonites", which thrived in the later Mesozoic era.

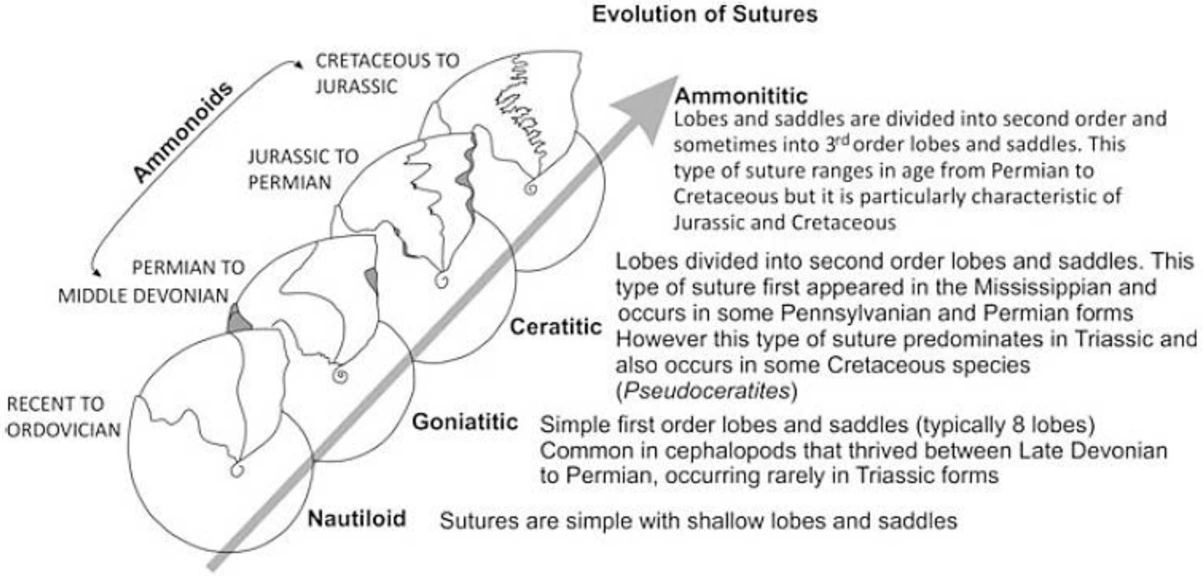


Figure 2.9. Schematic evolution of suture types, and their major characteristics through time. Overall an increase in sutural complexity is noted: from simple sutures with shallow lobes and saddles (goniatites) to those where lobes and saddles are divided into second order and sometimes into third-order lobes and saddles (adapted from Sreepat, 2017).

Ammonoids in general are common model organisms for the study of diversity, macroevolution, biostratigraphy, due to their high evolutionary rates, high diversity, and their geographical distribution. Although the fossils of ammonoid shells are very common, the preservation of soft-parts are very rare (hardly any) and based on assumptions. Thus, reconstructions of their appearance are often conjectural, and their ecology has been based primarily on the morphology, and facies distribution, of their fossilized shells (Korn and Klug, 2012). Thus, their internal anatomy is poorly known, mostly limited to muscle remains, traces of the digestive tract, and rarely, also their gills (*e.g.*, Lehmann, 1981). The morphology of the soft parts is completely unknown, so only inferences can be made. The great number of scientific reconstructions have been made on their appearance, by applying the phylogenetic bracket on the number of arms of recent embryonic nautiloids and belemnites. Some coleoids (including belemnites) are consider to have ten arms (based on the fossil record); nautiloid embryos five pairs of arm-buds, each with a pair of arms at an age of three months; thus, ten arms seem reasonable. Another unresolved problem is the hood. In nautiloid embryology, the hood develops from a clearly discernible bud; a non-mineralized hood may have formed similarly in ammonoids (Korn and Klug, 2012).

Finally, Paleozoic era is marked by an unprecedented boom of marine invertebrates, fish and a subsequent spread of higher plants, amphibians, and earliest reptiles (Table 2.1). Also, whole aquatic ecosystems developed in complexity, and further new land habitats were colonized. At the dawn of the Paleozoic, complex communities of multicellular organisms lived exclusively on the bottoms of shallow seas, while other environments were characterized by only very simple ecosystems or contained practically no life at all. By the end of the Paleozoic, shallow seas as well as ocean waters, seafloor sediments, lakes, rivers, and dry land were densely inhabited (Mikuláš and Chlupáč, 2009). Moreover, newly diverse life strategies were developed in marine environments: epifaunal and infaunal, filter and sediment feeding, herbivores, carnivores, and scavengers (Levin, 2013).

On land, a trend towards aridity and an increase in terrestrial habitat led to the increasing importance of the amniotic egg for reproduction. First primitive reptiles and mammal-like reptiles fully developed to the terrestrial life and started to spread in the Late Paleozoic. Anthracosaurs-basal tetrapods and amniotes appeared during the Carboniferous and were quickly followed by diapsids: (1) the marine reptiles, lizards, and snakes, and (2) the archosaurs-crocodiles, dinosaurs, and birds (Waggoner, 2011).

The Paleozoic history, thus does not only correspond to the emergence of life forms evolution, but also the gradual establishment of natural habitats and large ecosystems. Plants gave other organisms the opportunity to occupy new environments and thus, to alter their evolutionary paths. Without terrestrial plants, the bloom of insects, amphibians, reptiles and mammals would not have been possible (Mikuláš and Chlupáč, 2009).

Table 2.1. Summary of major Paleozoic marine groups and mass extinction (based on Levin, 2013; see also Figure 2.6 and text for more information).

Invertebrate Groups
– Plankton: not mineralized (cyanobacteria, green algae, architarchs); mineralized (foraminifera – calcareous microfossils and radiolarians – siliceous microfossils), – Colonial cup animals: sponges (Porifera), stromatoporoids, rugose and tabulate corals and other cnidarians, – Bryozoans, – Brachiopods,

- Mollusks: bivalves, gastropods, cephalopods,
- Arthropods: trilobites, ostracods,
- Echinoderms: Asteroidea (starfish); Ophiuroidea (brittle stars); Echinoidea (sea urchins); Crinoidea (crinoids),
- Graptolites: primitive chordates called pterobranchs.

Vertebrates Groups

- Agnathids (jawless fish): ostracoderms,
- Acanthodians and Placoderms (archaic jawed fish): placoderms,
- Chondrichthyans (cartilaginous fish),
- Osteichthyans (bony fish): ray-fined fish and lobe-finned fish,
- Conodonts: small parts of primitive jawless vertebrate with many teeth: range from Late Paleozoic to Triassic,
- Crossopterygians: transitional animals between fish and amphibians: Tiktaalik, Ichtyostega.

Main extinctions events with different impact on the biodiversity

- Late Ordovician: (1) First phase victims: planktonic and nektonic organisms; (2) Second phase victims: benthic organisms (great reduction in numbers of corals, conodonts, bryozoans, trilobites and brachiopods),
- Late Devonian: Decimated Devonian reef communities including tabulate corals and stromatoporoids; Severely reduced: rugose corals, brachiopods, goniatites, trilobites, conodonts, and placoderms; Marine invertebrates in general: loss of 70% of families,
- Late Permian (“Mother of All Mass Extinctions”).

2.3.2. Mesozoic

The fauna and flora of the Mesozoic were distinctly different from those of the Paleozoic. At the start of the Mesozoic, the remaining biota began to recover in diversity and total population numbers after the Permian Mass Extinction. Moreover, ecosystems began to resemble those of modern days. Vertebrates diversified throughout the Triassic. At the end of that period, terrestrial environments were dominated by the therapsids (mammal-like reptiles) and the thecodonts (ancestors of dinosaurs and crocodiles). The first true mammals, shrew-like omnivores, also appeared, as did the lizards, turtles, and flying pterosaurs. In the oceans, mollusks (ammonites, bivalves, and gastropods) became a dominant group. In addition, sharks and other fish, and marine reptiles (such as plesiosaurs, nothosaurs, and ichthyosaurs) started to refill new ecological niches, being at the top of the trophic web in marine environments (*e.g.*, Tang, 2021).

The Mesozoic era is known as the “Age of Dinosaurs”, but these famed organisms only diverge in the Middle Triassic. The proposed global zonations for tetrapod stratigraphy for Pangea is strongly based on widespread occurrences of semi-aquatic tetrapods (both reptiles and amphibians) whose well adapted thick skulls, body armours, and other resistant body parts are commonly preserved in the sediments. Moreover, in Triassic, Conchostracans (Figure 2.10) flourished in lacustrine environments. These small invertebrates, brought a great capacity in global biostratigraphy understanding, often appearing with tetrapod association (Ogg, 2012).

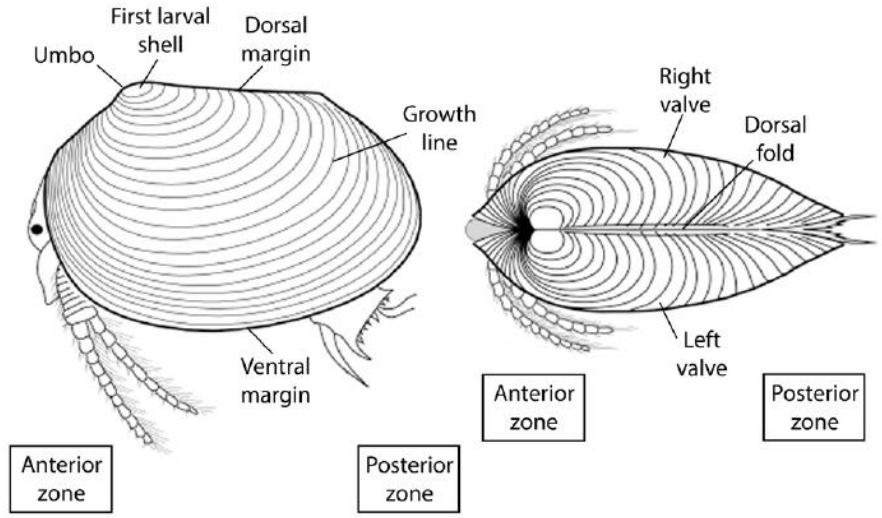


Figure 2.10. External morphology of the Conchostracans (adapted from Jessie and Gallego, 2015).

Among formerly named Conchostracans, order Diplostraca, is recognized worldwide. These small branchiopod-phyllopod crustaceans, also called “clam shrimp”, originated in Devonian and are present till now. Clam shrimps have a symmetrical, bivalved, chitinous carapace, which is the only part preserved in fossil record. They differ from the ostracods, which have a calcitic shell without preserved growth lines. Their size varies from 1 millimetre to a few centimetres (Jessie and Gallego, 2015). Their tiny drought-resistant eggs were easily dispersed by wind and water, and rapidly hatched upon exposure to suitable environments (Ogg, 2012). Limnic environments, for instance, the ephemeral water bodies, lakes, and riverbanks of dense subaqueous vegetation capable of providing protection against predators, are the niches where conchostracans thrive (Jenisch *et al.*, 2017**.** These characteristics and their brief life cycle (one to three weeks) enabled conchostracans to become widespread in lakes and temporary pools throughout super continent Pangea. Their distinctive carapaces were preserved in lacustrine, salt flat and floodplain deposits (Ogg, 2012). The geographical distribution of extant Diplostraca is worldwide. This very broad distribution can be explained, due to their time- and drought-resistant eggs, and possible, subsequent transportation by birds and winds. These latter characters made diplostracans useful for paleogeographical reconstructions (Jessie and Gallego, 2015).

These small aquatic invertebrates are filter or suspension feeders, being capable of swimming and burrowing into the sedimentary substrate. The development of clam shrimp carapaces is characterized by growth lines on both valves, acquired during ontogenesis (Figure 2.10). The spacing between them are called bands, which can be variable depending on local environmental conditions (Webb, 1979). Single body of water is usually occupied by one population of conchostracans, without any coexistence of other species of the same genus (Jenisch *et al.*, 2017).

In the Triassic oceans, the coccolithophores and pelagic algae made their first appearance. Marine green algae and cyanobacteria were abundant, whereas dinoflagellates rapidly diversified during the Late Triassic and Early Jurassic (*e.g.*, Tang, 2021). Moreover, the first of the scleractinian corals appeared in the Triassic and remained the most important skeletal coral group until today (Figure 2.11), replacing the rugose and tabulate corals.

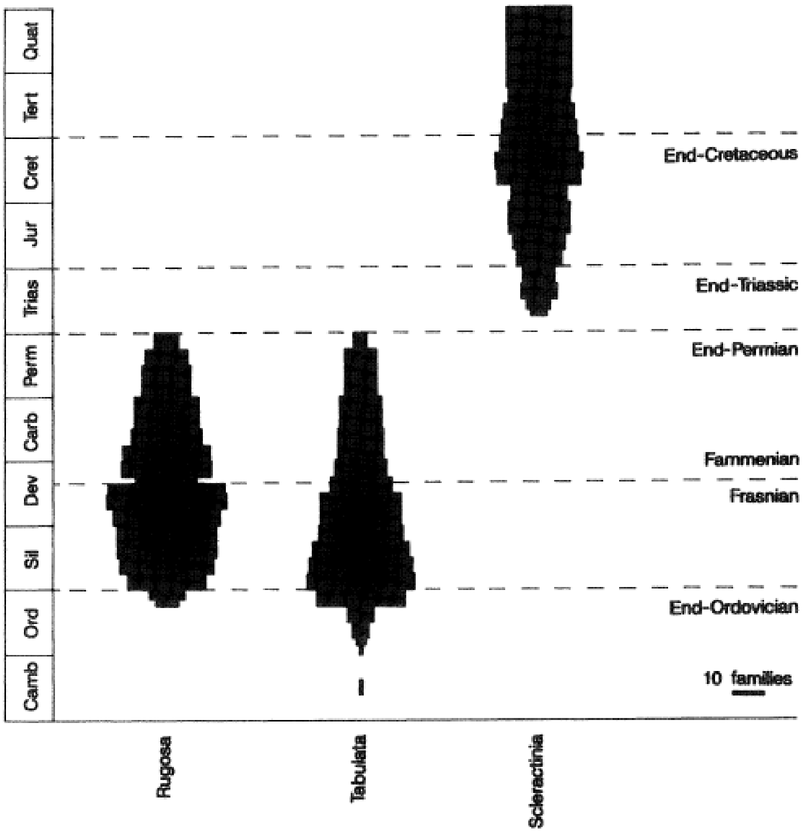


Figure 2.11. The diversity of coral families through geological time. The main extinction events are indicated (adapted from Doyle and Lowry, 1996).

The scleractinians developed along two lines, the reef-building hermatypic corals living in symbiosis with algae, the zooxanthellae; and the deeper water ahermatypic corals, without zooxanthellae. The hermatypic corals flourished in the later part of the Cenozoic, producing a great phase of reef development which has continued, with some interruption, to the present day (Doyle and Lowry, 1996). However, the origin of scleractinian corals is still debated, and involves two possible routes. The first involves direct derivation from the rugose corals. However, yet there is no evidence of an intermediate between the two groups, and there is a considerable time gap from the last appearance of the rugosa in the late Permian to the first appearance of the scleractinians in the Middle Triassic. The second possibility is that the scleractinians were derived from a soft-bodied anthozoan ancestor, such as a sea anemone, via a route involving the creation of a mineralised skeleton. Little evidence exists to be able to substantiate either hypothesis (Doyle and Lowry, 1996).

At the end of the Triassic and into the earliest Jurassic (Hettangian) flood basalts erupted across a large portion of North America, South America, Africa, and southern Europe (Scotese *et al*., 2021). The major cause of this event is thought to be the Central Atlantic Magmatic Province (CAMP), which led to Pangea fragmentation, and creation of sea ways and of new ocean basins. The general record from these rifting basins shows an evolution from continental to marginal marine sediments, interbedded with basalts, which indicate an extensive volcanic activity connected with Atlantic Ocean opening (*e.g.*, Kasprak *et al.*, 2010).

During this “brief episode” (of about 600,000 years), the CAMP released approximately 80,000 gigatons of CO2 into the atmosphere (Scotese *et al*., 2021). This exhalation of greenhouse gases led to a global warming, and following cascade of catastrophic environmental changes including increased terrestrial weathering and erosion, changes in ocean chemistry (oceanic acidification), photic zone euxinia (anoxic and sulfidic water conditions), falling marine productivity, and possible deep ocean anoxia (Scotese *et al*., 2021). As a result, the end of the Triassic was marked by another Mass Extinction Event, which is ranked as a third in terms of taxonomic severity. It is estimated that ca. 73% of marine genera, and a great number of non-marine clades of vertebrates went extinct, although some of the faunal groups like marine reptiles and fish flourished (Scotese *et al*., 2021). In the oceans, severe crisis was experienced by scleractinian corals, which had a catastrophic effect for the reef communities. Also the ammonoids became almost completely extinct at the end of the period, and only the phylloceratid ammonoids were able to survive, and gave rise to the explosive radiation of cephalopods later in the Jurassic (*e.g.,* Scotese *et al*., 2021; Tang, 2021).

Later, in the Early Jurassic epoch, biota rapidly started to refill the ecological niches. That was the perfect moment for dinosaurs to take over terrestrial and aerial habitats. However, some of the major developments took place under water. The ecology of the seas was changed by the diversification of marine fauna and consequently by the adaptations of these new organisms at the beginning of the Jurassic period (*e.g.,* Tang, 2021). With the evolution and radiation of the predators (crabs, gastropods, echinoderms, and marine vertebrates), predation pressures began to rise significantly. Therefore, the Jurassic marks the "Mesozoic Marine Revolution" – a survival race between predators and prey. For instance, increased level of depth of burrowing is found in sediments (Figure 2.7). These revolutions changed the nature of the seafloor, by modernizing marine (mostly benthic) habitats (*e.g.,* Tang, 2021).

By the Middle Jurassic, not only the seafloor was thriving, but also a turnover of the biotic composition of ancient reefs took place (Figure 2.12), changing the coral/calcisponge's reefs of the Late Triassic and Early Jurassic, to demosponge/coral-dominated reefs. Moreover, 'sponge/algal reefs' are unique in reef history because of their importance of microbial contribution and the siliceous sponge-dominated structures. Another turnover, this time to coral-dominated reefs, took place during the Late Jurassic, continuing in the Early Cretaceous (Flügel and Flügel-Kahler, 1992; Leinfelder *et al.*, 1996).

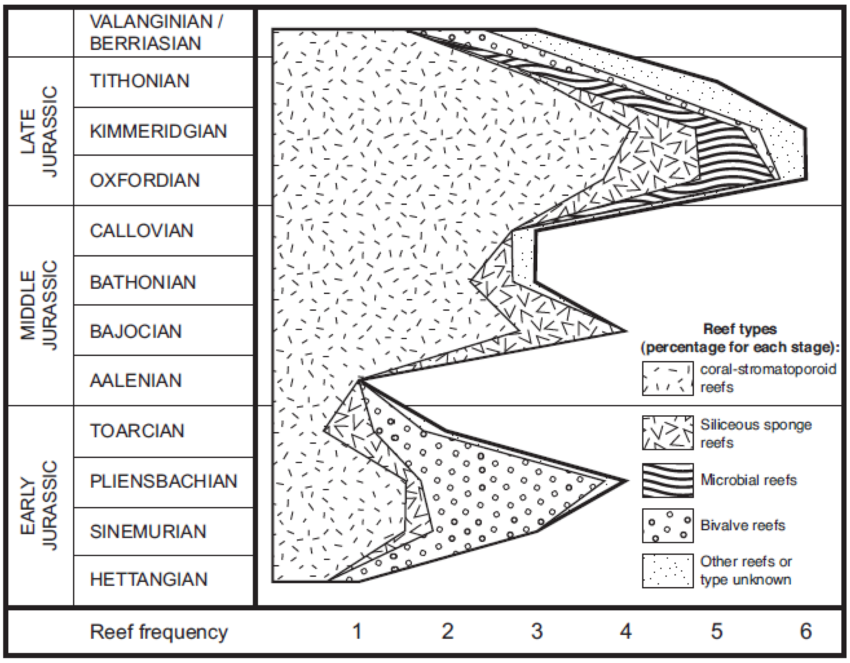


Figure 2.12. Fluctuations in the abundance of Jurassic reef types through time. Frequency of reefs and intensity of reef growth are classified into six categories considering the number of records and the geographical distribution: 1, Extremely rare (very few records, regionally very restricted); 2, very rare (few records, regionally restricted); 3, rare (some records but occurring in different regions); 4, common (common records, regionally ex-

panded); 5, abundant (many records, regionally widely expanded); 6, very abundant (abundant records, regionally widely expanded). Reef types are also indicated in five categories, each stage representing 100 percent (adapted from Leinfelder and Schmid, 2002).

In general reefs were more widespread and abundant in the Late Jurassic than earlier in the period. This significant phase of reef development is coeval with major tectonic plate reorganizations, marked by the breakup of Pangea, which started in the Late Triassic and led to the opening of the Central Atlantic and Alpine Tethys, followed by the North and South Atlantic, Indian Ocean and the Bay of Biscay (Nembrini *et al.*, 2021)**.** Rather than by an evolutionary radiation of reef biota, the difference in reef distribution and abundance (between the Middle and Late Jurassic) is more likely explained by a greater availability of suitable habitats, provided by the global sea level rise (sea level was about 100 to 150 m higher than today), and the opening of the new sea ways especially in the equatorial belt of Tethyan shelfs and marginal basins of the young Atlantic Ocean (Leinfelder *et al.*, 1994; Leinfelder, 2001; Leinfelder, 1993a). Jurassic reefs of different faunal compositions seem to have been mostly concentrated near 30N, especially in Europe (Figure 2.13) (Flügel and Flügel-Kahler, 1992). Moreover, during Upper Jurassic, the low latitude reef belt was probably wider than today. This indicates a more equilibrated greenhouse-type climate. In contrast to modern corals, Upper Jurassic scleractinians frequently occur in siliciclastic environments, due to the highly morphovariable taxa, which was able to cope with elevated sedimentation rates (Leinfelder *et al.*, 1996)**.**

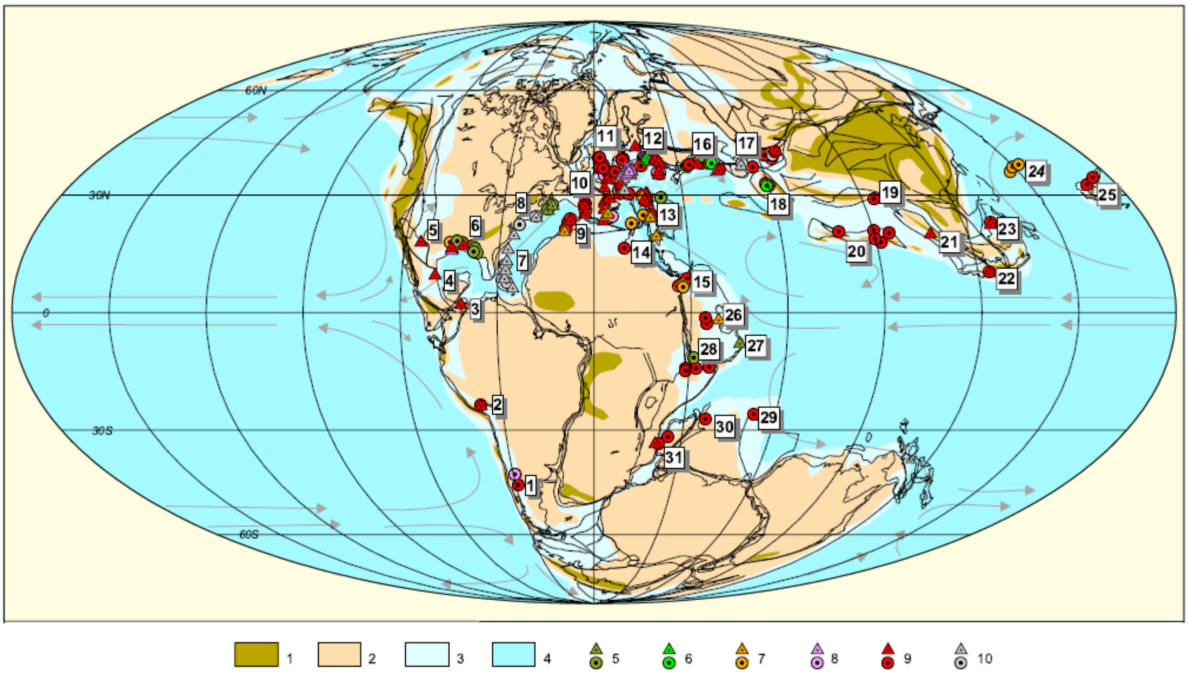


Figure 2.13. Global distribution of Callovian to lower Tithonian reefs, indicating probable current systems and dominant reef biota. Legend below the figure: 1, mountains; 2, land; 3, shelf; 4, deep water; dominant biota: 5, microbes; 6, algae; 7, coralline sponges; 8, siliceous sponges; 9, corals; 10 others/unknown; circles: Callovian–

Oxfordian reefs, Triangles: Kimmeridgian–early Tithonian reefs; reef sites (numbers in rectangles): 1, Neuquén Basin, Argentina; 2, Peru; 3, northern Colombia; 4, eastern Mexico; 5, Chihuahua, Mexico; 6, northeastern Florida to southern Texas; 7, Atlantic margin of eastern U.S.A.; 8, off Nova Scotia, Atlantic; 9, Morocco; 10, Portugal and Spain; 11, England; 12, Central Europe to Black Sea; 13, southern Europe; 14, Tunisia; 15, Egypt, Israel, and Lebanon; 16, Crimea, Ukraine to Caucasus, Russia; 17, Turkmenia, Uzbekistan, Tadzhikistan; 18, Iran; 19, Denchin, Tibet; 20, southern Tibet; 21, Klo Tho, Thailand; 22, Sumatra, Indonesia 23, Sarawak, Borneo, Malaysia; 24, Japan (yellow circle indicates the uncertain paleoposition); 25, Sakhalin, Russia (paleoposition hypothetical); 26, Saudi Arabia; 27, Oman; 28, Somalia, Ethiopia, and Yemen; 29, Karakorum; 30, Kachchh, India; 31, southern Tanzania and southwestern Madagascar (adapted from Leinfelder and Schmid, 2002).

Reef-building blocks, together with the ecological demands and capabilities of reef organisms, determine the actual character and the ecological position of the reefs. All potential reef environments of all reef types, in a given time slice, can be described and illustrated by one or more “reef windows”, i.e., the environmental conditions in which organisms are capable of forming reefs (Leinfelder and Schmid, 2002)**.**

Finally, marine Mesozoic is marked by steep increase of the diversification, and consequent adaptations of marine fauna (Table 2.2). The “Mesozoic Marine Revolution” changed the nature of the seafloor, which consequently led to include marine Mesozoic faunas in “Modern Fauna”, represented also by Cenozoic era (Figure 2.6) (*e.g.,* Tang, 2021).

Table 2.2. Summary of major Mesozoic marine groups and mass extinction (see Figure 2.6 and text for more information) (based on Levin, 2013).

Invertebrates Groups (Middle Triassic resurgence)

- Plankton: coccolithophorids, dinoflagellates, silicoflagellates, diatoms, foraminifera and radiolarians,
- Pelecypod bivalves (mainly oysters),
- Colonial cup animals: scleractinian corals (proliferated in equatorial Tethys), sponges, stromatoporoids and other cnidarians,
- Echinoderms: starfish, sea urchins, crinoids, ophiuroids,
- Mollusks: Gastropods, Cephalopods: Ammonoids (widespread, abundant index and guide fossils); Belemnites (highly successful in Jurassic – Cretaceous, related to squid and octopus),
- Crustaceans: barnacles, crayfish, lobsters, crabs, shrimp, ostracods (abundant during Jurassic – Cretaceous).

Vertebrates Groups

- Fishes (great diversification in body structures): cartilaginous fish like sharks and rays, bony fish (teleosts).

<u>New reptile groups</u>

- Archosaurs: crocodiles, flying reptiles, thecodonts, dinosaurs,
- Phytosaurs (crocodile-like forms),
- Turtles (toothed turtles).

<u>Marine Reptiles (return to sea)</u>

- Nothosaurs (paddle-shaped limbs): appearance during Triassic, ancestors of plesiosaurs,
- Placodonts: mollusc-eating reptiles, paddle-shaped flippers, pavement-type teeth in jaws and palate (shell crushing function),
- Plesiosaurs: long-neck and short-neck forms, first appearance during Jurassic,
- Ichthyosaurs: body-shape precoursors of modern toothed cetaceans; they were also giving birth to their young,
- Mosasaurs: giant sea-going lizards,
- Sea turtles: example Archelon, a 4m big turtle from Cretaceous.

Main extinction events with different impact on the biodiversity

- End Triassic; possibly related with the rift-related magmatism and fragmentation of the Pangea supercontinent,
- Cretaceous Life Crisis: Vertebrates groups completely lost were non-avian dinosaurs, ichthyosaurs, plesiosaurs, mosasaurs; Invertebrate groups completely lost: ammonoid cephalopods, belemnites, rudist bivalves; Loss of many invertebrate's families: echinoids, bryozoans, planktonic foraminifers, calcareous phytoplankton.

CHAPTER 3. LATE PALEOZOIC – I WILSON CYCLE

In the late Devonian, the evolution of land forests, and the increase in burial of their organic matter, had two first-order impacts on the composition of the atmosphere: a rise in O_2 and a drop in CO_2 (Figure 3.1a). The O_2 altered the track of evolution patterns, increasing the size of growth of animals on land (*e.g.*, giant insects). The general trend in lowering of CO_2 was a crucial driver for the Late Paleozoic glaciation, with the coldest peak in Serpukhovian (second occurred in Permian) (Royer, 2014).

Change in the oxygen content in the atmosphere had numerous biologically significant effects. Increase of O_2 in the air brought an increase in the concentration of dissolved oxygen in oceans (Figure 3.1b), seas, lakes, and rivers, as well as in benthic substrates. At present, many bodies of water serve as sinks for CO_2, acting as natural buffers and moderating the outward diffusion of metabolically produced gas (Cole *et al.*, 1994). Therefore, these changes in the partial pressure of oxygen and carbon dioxide in atmosphere, and further in the marine waters, would possibly open new opportunities for animals to invade previously anoxic waters (Gans *et al.*, 1999)**.** Sea surface temperatures (SST) estimated through Phanerozoic (Figure 3.1b) exhibit variations characterized by warm climate in the Early Paleozoic – Devonian and cool climate in the Late Paleozoic (Carboniferous – Permian). The average SST in the late Devonian were maintained at a high level around 30°C, followed by cool interval of Carboniferous, with SST fluctuations from 17°C to 12°C later in the period. This sea water temperature was having a positive relationship with salinity and atmospheric CO_2, and a negative with dissolved oxygen (DO) and atmospheric O_2 (Song *et al.*, 2019).

Dissolved oxygen in ocean is influenced by great number of factors, such as atmospheric oxygen level, temperature, ocean currents and organic productivity (Sarmiento *et al.*, 1988). However, for the surface seawater, it mainly depends on the first two since seawater oxygen dominantly comes from atmosphere by air-sea exchanging process. Marine primary producers, through process of photosynthesis, generate and release a major amount of oxygen to the photic zone (Song *et al.*, 2019). However, the Upper Carboniferous is known as a period of low diversity among the phytoplankton and reduced primary production (Riegel, 2008; Seuss *et al.*, 2020).

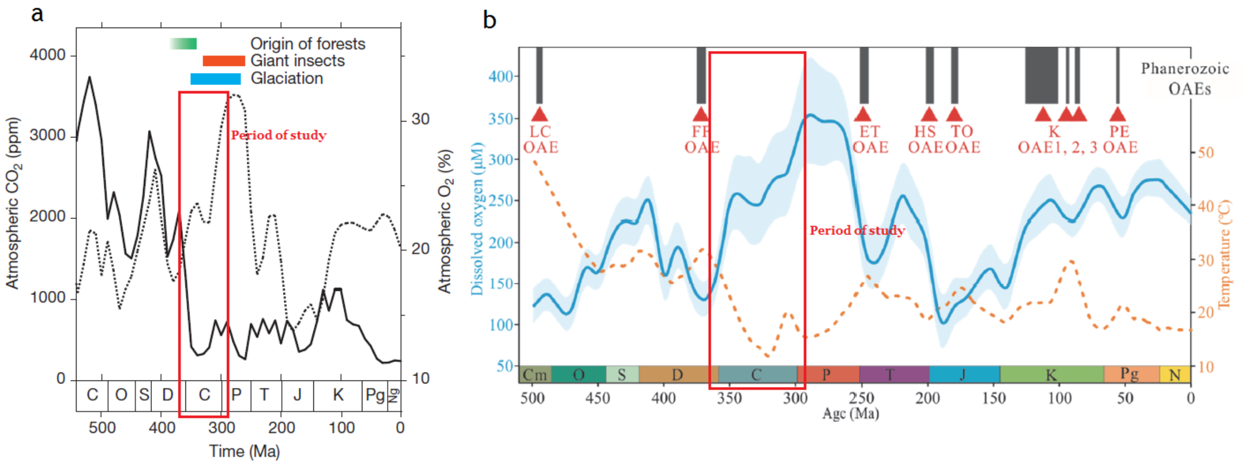


Figure 3.1. Climate (a) Phanerozoic history of atmospheric CO2 and O2 and key evolutionary and climatic events during the Paleozoic (adapted from Royer, 2014); and (b) Dissolved oxygen, sea surface temperature and oceanic anoxic events for the past 500 million years. The shade shows 90% confidence interval. Oceanic anoxic events (OAEs) of (LC) late Cambrian, (FF) Frasnian–Famennian, (ET) Lower Triassic, (HS) Hettangian–Sinemurian, (TO) Toarcian, (K) Cretaceous, (PE) Paleocene–Eocene; Blue peak represents Serpukhovian glaciation (adapted from Song et al., 2019).

In the Carboniferous, the Late Paleozoic Glaciation (approx. 372 – 254 Ma; Figure 3.1a, blue marker) occurred – the most intense and "long-lived" glaciation during the Phanerozoic, with the outstanding phase when the Earth underwent remarkable changes. At the beginning of the Late Paleozoic Ice Age (LPIA), one supercontinent Pangaea formed, with mountain chain extended almost from pole to pole, creating steep latitudinal temperature gradients with pronounced seasonality. Induced by these changes in the configuration of landmasses and landscape, together with the lowest atmospheric CO_2 and highest O_2 levels in the entire Phanerozoic, the Earth began to cool drastically (*e.g.,* Gans *et al.*, 1999; Royer, 2014; Song *et al.*, 2019; Seuss *et al.*, 2020).

Temperature fluctuations during the Late Paleozoic had a direct impact on the fauna and flora itself. In the Carboniferous, frequent sea level fluctuations often converged with episodic biotic turnover, as deepening and shallowing of ocean basins influenced the distribution of marine settings and their structural characteristics; such oscillations directly impact the benthos, plankton, and nekton and eventually led to biotic turnovers. Thus, the onset of the LPIA changed not only the landscape and sea level, but also the conditions in the marine environmental realms (Seuss *et al.*, 2020)**.**

More specifically, the biotic response of the Serpukhovian glaciation (Figure 3.1a, blue marker) was similar to the biotic response to last global Ice Age of the Pleistocene epoch (Cenozoic). The biogeographic differentiation, also called provinciality, of marine invertebrates raised dramatically in the early Pennsylvanian (Ziegler *et al.*, 1981). This increase reflected the biotic response to the establishment of a steep pole-to-equator temperature gradient because of glaciation. Crame and Rosen (2002) noted a similar biogeographic response to late glaciation of the Pleistocene (Raymond and Scotese, 2009).

Thus during time the Earth was cooling down, the global fauna was forced to react and adapt to the environmental changes by exploring new niches, migrating, or becoming more generalistic (*e.g.,* Carboniferous goniatites). In general, it is assumed that taxa living during the LPIA have been long-ranging and geographically widespread, resulting in a decreasing effect on evolutionary rates. Moreover, Alroy *et al.* (2008) found an overall drop in the global genus-level diversity throughout the late Carboniferous. The loss of specialized taxa and the dominance of generalists (also goniatites found in the study area) can be a possible reason for this phenomenon (Seuss *et al.*, 2020).

Based on the more detailed paleoenvironmental research from Carboniferous Maritimes Basin in Nova Scotia, which belonged to Avalonian-Meguma terrane (Calder, 1998), we can conclude more about the paleoclimate pattern of South Portugal, as both regions were getting closer, and were distributed in the same latitudinal position. Thus, in Carboniferous, the Algarvensis region was located within 0 – 30°S belt, and showed the tectonic trend towards the equatorial regions, with the general paleoclimate pattern of arid-humid-arid cycle. From the earliest to middle Namurian, the subtropical belt was changing from arid into semiarid, and to subhumid later in the stage. The maximum humidity occurred during the Westphalian, and further was followed by a sharp decline in the Stephanian (latest Carboniferous) (Calder, 1998; Raymond and Scotese, 2009).

The Devonian–Carboniferous boundary crisis represents a mass extinction that is of the same scale as the so-called “Big Five“ first-order Phanerozoic events (Figure 2.6). It brought an end to the extensive reefs; many nektonic organisms (like large bony fish); and phytoplankton richness (Riegel, 2008). Nevertheless, it is certain that the combination of multiple oceanographic factors was involved. However, sudden climate change appears to have been the major common trigger, possibly linked with episodes of significant drawdown of atmospheric CO_2. It played an important role in the evolution of many faunal groups and contributed to the decline, and further rise of entire ecosystems (Becker *et al.*, 2016).

One of the main Late Paleozoic rearrangement was very likely connected with the plate tectonic movement and the closure of the Rheic Ocean, which began in the late Silurian – early Devonian and continued until the Carboniferous (Fig 3.2). As a result, the Variscan mountain belt raised from the collision of Gondwanan terranes and Laurussia microplates (Baltica + Avalonia + Laurentia), which caused the closure of several oceans, among which the Rheic Ocean has been considered the most important (Königshof *et al.,* 2016)**.**

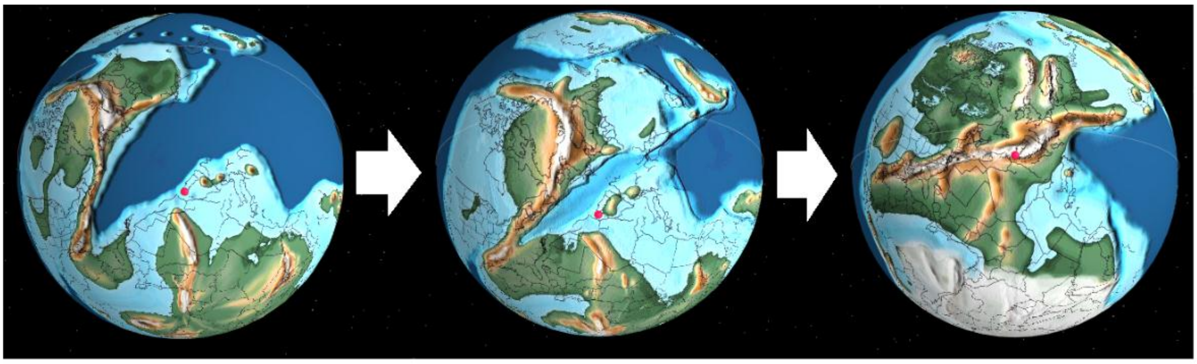


Figure 3.2. Late Paleozoic. Schematic plate tectonics movement, of the I Wilson Cycle (from the Ocean to the mountains). Algarve region is represented by the red dot (adapted from Scotese, 2021).

The Rheic ocean saw the evolution of bony and cartilaginous, endo-skeletal fish, coral reef and molluscs diversity spread. In the late Paleozoic more gastropod and cephalopod goniatite taxa appeared. On land, vascular plants and primitive trees had evolved, ready to develop into the rich flora of the upper Carboniferous swamp-forests preceding closure of the Rheic ocean. Meanwhile, the first amphibians crawled onto land which development quickly led to the reptile’s evolution early in Mesozoic (Königshof *et al.*, 2016)**.**

3.1. Carboniferous

Carboniferous depositional environments are recorded in the Algarve region in the formations the South Portuguese Zone (SPZ), which is one of the main units of the Variscan Iberian Massif. The Baixo Alentejo Flysch Group (BAFG) is a major component of SPZ, and it represents a development of the foreland basin that formed as a result of two approaching continents, and further collision of the Avalonian plate (containing SPZ) with the Gondwana (containing Ossa–Morena Zone) in the early Visean. The BAFG comprises three formations (from oldest to youngest) the Mértola, Mira and Brejeira (Rodrigues *et al.*, 2015).

3.1.1. Fossil content of the Baixo Alentejo Flysch Group

The rocks of BAFG found in the region of the Algarvensis Geopark belong to the Mira and Brejeira formations (Mértola does not belong to the study area) and are mainly composed of sandy turbidites (greywackes interbedded with black shales) of Visean to Moscovian age (Rodrigues *et al.*, 2015). In the South of Portugal, latest Devonian, Lower Carboniferous and early Upper Carboniferous sedimentary rocks contain ammonoid assemblages which are related to faunal associations known from central and western Europe, and British Islets (Korn, 1997). Despite some small differences during the Carboniferous ammonoid assemblages agree quite well with the ages of the strata, clearly indicating that the formations of Mira and Brejeira were in geographic continuity and were incorporated in the same paleogeographic realm (Oliveira *et al.,* 1979). Figure 3.3 depicts the ages of all formations of the Baixo Alentejo Flysch Group (BAFG), moreover, this data is combined with additional region of Southwest Portuguese Domain (SPD), due to its environmental importance.

The fossil content of the Baixo Alentejo Flysch Group is rather poor in faunal diversity (mainly Mira and Brejeira), however very rich in monospecific (at the order level) assemblage, consisting of great number of ammonoid species. Their distribution collected from Carboniferous formations of South Portugal uncovered the fact that the Flysch is stratigraphically oldest in the north and becomes gradually younger towards the southwest (Korn, 1997). All three units belong to the Carboniferous and are dated as Visean (345 – 326 Ma), Serpukhovian to early Bashkirian (Namurian: 326 – 315 Ma), and late Bashkirian to late Moscovian (Westphalian: 315 – 307 Ma) for the Mértola, Mira and Brejeira respectively (Rodrigues *et al.*, 2015).

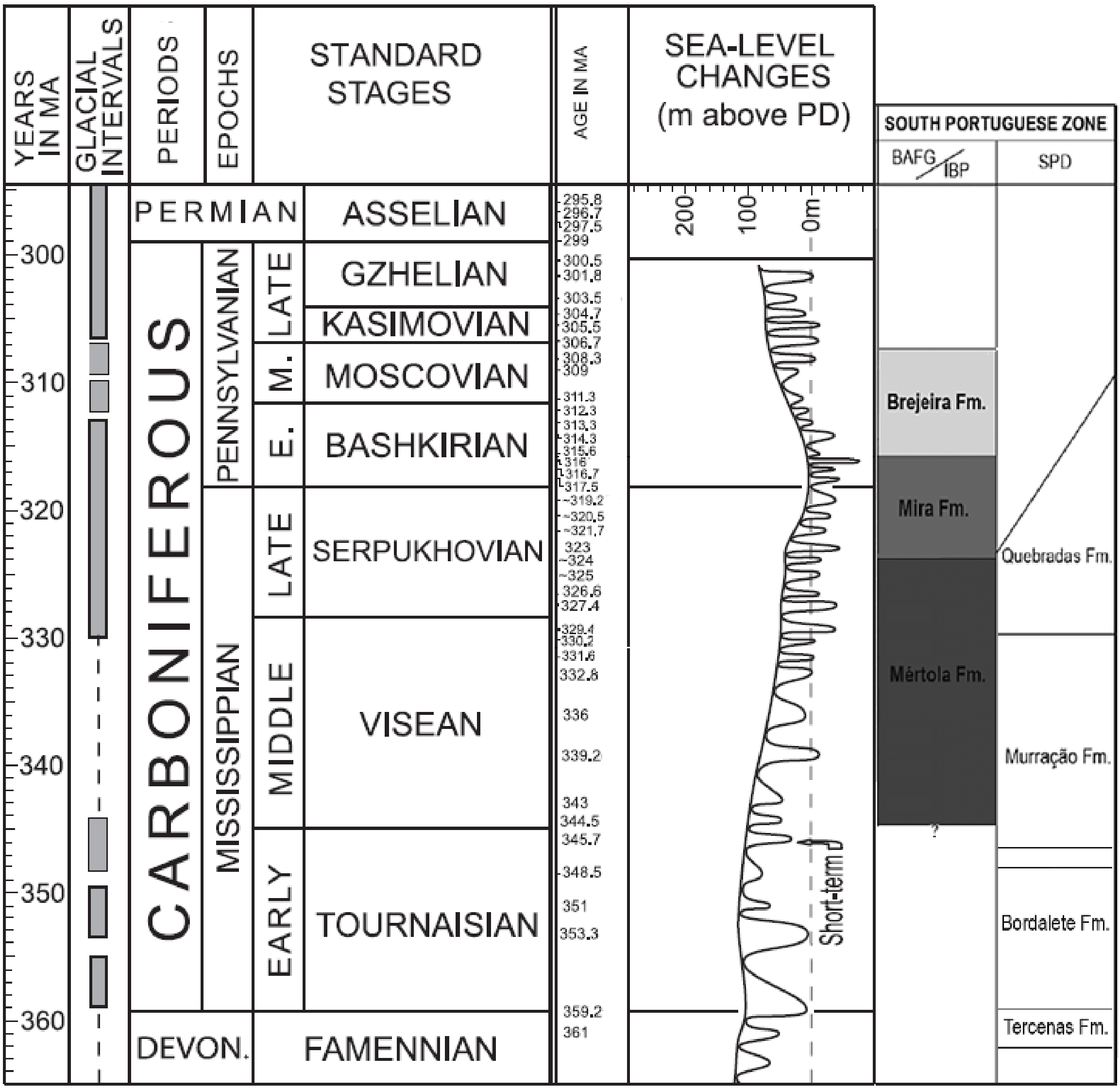


Figure 3.3. Considering geological time scale of Carboniferous formations found in study area, with additional group of Portuguese Southwest Domain (PSD) (adapted from Haq and Schutter, 2008; Rodrigues et al., 2015).

The Paleozoic fossil evidence has not yet been documented in the Algarvensis Geopark, however, in better exposed sites in the Algarve region, the geological formations of Mira and Brejeira reveal rich fossil assemblages of the ancient cephalopods. Thus, it is assumed, that those fossils, cannot be excluded in the characterization of the geopark paleoenvironments, as they are present in the facies also found in the aspiring Algarvensis Geopark, where no other fossil evidence was found so far. In addition, it needs to be also remembered, that majority of the fossil records are found in particular localities, where the erosive processes are more intense, therefore exposure is more likely (*e.g.*, walls of the hills along the roads, coast and sea cliffs, *etc.*), durinf the field work.

Table 3.1 represents species of ammonoids fossils found in the Carboniferous formations (but not in the study area, so far), which constitute the Paleozoic basement of the Algarvensis Geopark. The species belong mainly to eight families of order Goniatitida: Cravenoceratidae, Girtyoceratidae, Dimorphoceratidae, Homoceratidae, Reticuloceratidae, Gastroceratidae, Ramositidae, and Neoglyphioceratidae. The rest of families were excluded from this study due to the uncertainty of the taxonomy, or too small number of individuals in one genus. On the contrary, some species of Mértola are included to show the evolutionary continuity, as well as some of Quebradas (Southwest Domain, Carrapateira Group), due to environmental importance of this formation. In general, all the studies on marine Carboniferous fossils (of South Portugal) were made before 21st century, and are only concerned with biostratigraphy, biogeography, and basic shell morphology of goniatites. Table 3.1 contains species mainly from the surveys of Oliveira *et al.* (1979; 1983a; 1983b), however corrections were made based on the most recent listing (of all the genera found in South Portugal) made by Korn (1997). Taxonomy and distribution of the species was aligned with *GONIAT.org* database. Shell morphology (Figure 3.4), and their organism's modes of life (morphotypes), were based on bivariate plots from Korn (2010) illustrating the conch width index (ww/dm) and umbilical width index (uw/dm) (Barskov *et al.*, 2008; Korn, 2010; Klug *et al.*, 2015; Westermann, 1996).

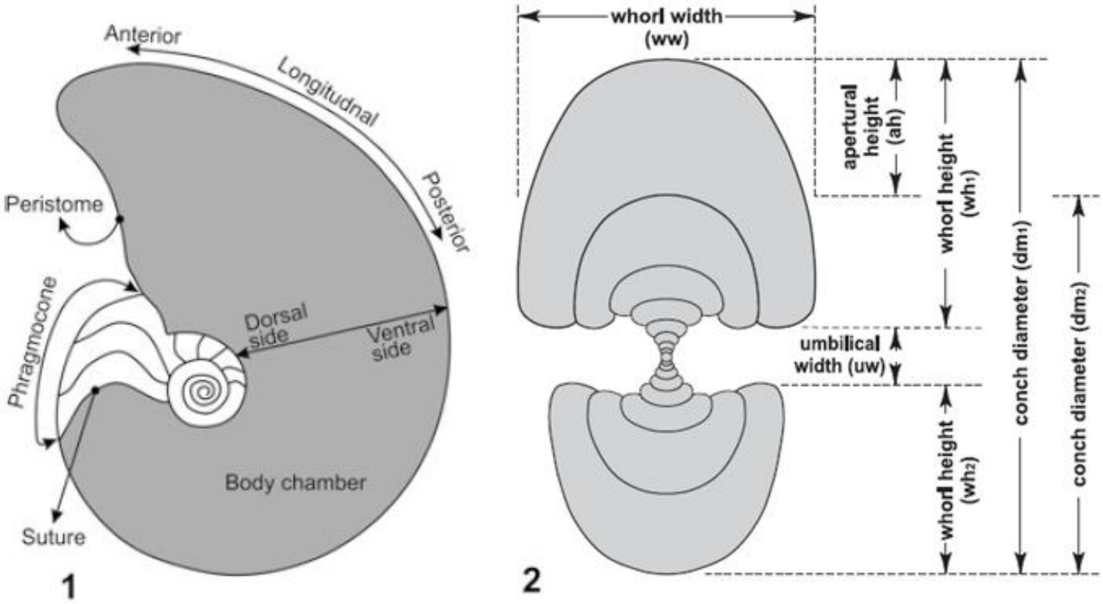
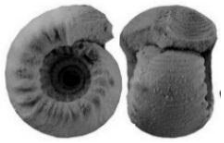
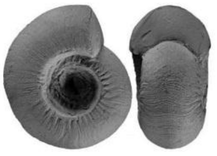
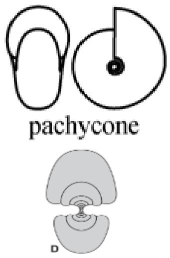
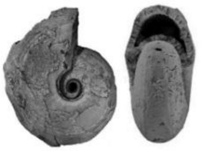
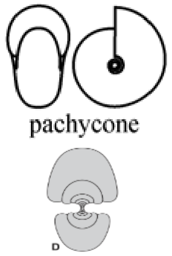
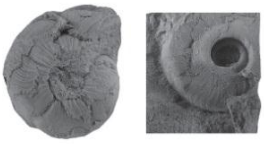
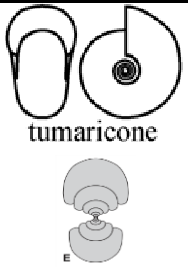
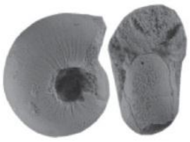
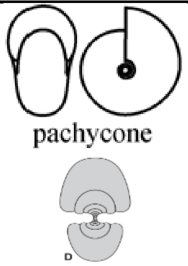
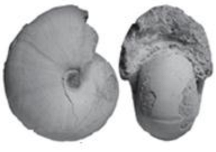
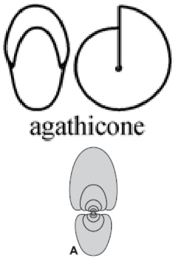
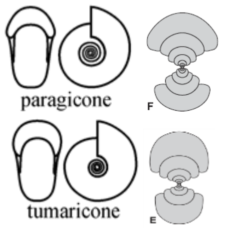
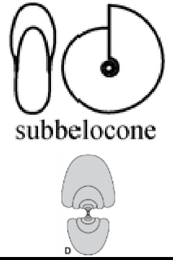
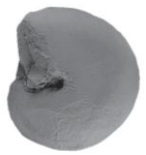


Figure 3.4. Schematic ammonoid shell morphology: 1: Common terminology (adapted from Sreepat, 2017); 2; Descriptive conch parameters of the cross-section used in analytical methods (adapted from Klug et al., 2015).

Table 3.1. Biostratigraphy of goniatites species found in formation of South Portugal, and their main characteristics. Late Visean goniatites, and few specimens of Namurian are lacking detail information, however, they remain in the table because of their evolutionary and biogeographical importance (besed on Oliveira et al., 1979; 1983a; Oliveira and Wagner-Genthis, 1983b; Korn, 1997; Barskov et al., 2008; Korn, 2010; Klug et al., 2015; Westermann, 1996; and GONIAT.org database).

`Age	**Biozone**	**Order Goniatitida,** Superfamily, Family, Genus	**Goniatites**	Mértola	**Mira**	**Brejeira**	Quebradas	**Shell morphology of the individuals found in the study area**	**Shell shape**	**Global distribution**
Lower Westphalian	Upper *Cancelloceras* zone, G2	Gastrioceratoidea, Gastrioceratidae, *Gastrioceras*	*Gastrioceras listeri*			●	●	 Size: 2 – 75mm diameter. Thickly pachyconic conch between 15 and 60mm diameter (at 15mm dm: ww/dm = 0.80, at 30 dm: ww/dm = 0.70, at 45mm dm: ww/dm = 0.60), umbilicus wide (uw/dm = 0.45) throughout these stages. *Gastrioceras listeri* has the widest conch of the European species of the genus.		Base of the G2 goniatite Zone of Great Britain, the Netherlands, Belgium, Germany (Rhenish Massif), Poland (Upper Silesia, Lublin Coal Basin), and possibly Ukraine.
Namurian	Lower *Cancelloceras* zone, G1	Neodimorphoceratoidea. Ramositidae, *Ramosites*	*Homoceratoides divaricatus* = *Ramosites sousai*			●	●	 Size: 13 – 34mm. Thickly discoidal conch (ww/dm about 0.45) and very narrow umbilicus (uw/dm = 0.1 in earlier stages and 0.05 in later stages).		Latest Namurian G1 Zone of South Portugal, and Great Britain.
		Gastrioceratoidea, Gastrioceratidae, *Cancelloceras*	*Gastrioceras crenulatum* = *Cancelloceras crencellatum*			●	●	 Size: 18 – 52mm. Pachyconic conch (ww/dm = 0.60 to 0.65), and moderately wide umbilicus (uw/dm = 0.35 to 0.40 at 20m dm and 0.40 to 0.45 at 40mm dm).		G1 Zone of Great Britain, Germany (Rhenish Massif), and South Portugal.
		Gastrioceratoidea, Gastrioceratidae, *Cancelloceras*	*Gastrioceras weristerense* = *Cancelloceras branneroides??*			●		 Size: 8 – 55mm diameter.	The conch form is not documented because of deformation of all the specimens.	G1 Zone of Great Britain (North Wales), and Southwest Portugal.
		Gastrioceratoidea, Gastrioceratidae, *Cancelloceras*	*Gastrioceras cancellatum* = *Cancelloceras cancellatum*			●	●	 Size: 2 – 70mm. Pachyconic conch at 15mm diameter (ww/dm = 0.65), with moderately wide umbilicus (uw/dm = 0.45). Conch thickly discoidal at 30mm diameter (ww/dm = 0.50), umbilicus moderately wide (uw/dm = 0.30 to 0.40).		G1 Zone of Great Britain (Yorkshire, Pembrokeshire), Belgium, the Netherlands, Germany (Rhenish Massif), and South Portugal
	Upper *Reticuloceras* zone, R2	Gastrioceratoidea, Reticuloceratidae, *Bilinguites*	*Reticuloceras superbilingue* = *Bilinguites superbilingue*		●	●	●	 Size: 4 – 15mm. Thickly discoidal conch at 12mm diameter (ww/dm = 0.55) and narrow umbilicus (uw/dm = 0.22); and thickly discoidal conch at 25mm dm (ww/dm = 0.50), and narrow umbilicus (uw/dm = 0.16).		R2 zone of Great Britain, Belgium, Germany (Rhenish Massif), Poland (Lublin Coal Basin), Ukraine, Russia (South Urals), Uzbekistan, China, and South Portugal.

	Gastrioceratoidea, Reticuloceratidae, *Bilinguites*	*Reticuloceras todmordenense* = *Bilinguites metabilinguis*				●	 Size: 3 – 31mm. Thickly discoidal conch at 12mm diameter (ww/dm = 0.60) and narrow umbilicus (uw/ dm = 0.22); thickly discoidal conch at 25mm dm (ww/dm = 0.50), and narrow umbilicus (uw/dm = 0.16).		R2 Zone of Great Britain, Belgium, Germany (Rhenish Massif), Russia South Urals, Uzbekistan, China, and South Portugal.
Lower *Reticuloceras* zone, R1	Gastrioceratoidea, Reticuloceratidae, *Phillipsoceras*	*Reticuloceras circumplicatile* = *Phillipsoceras circumplicatile*			●	●?	 Size: 5 – 16mm diameter. On the umbilical margin, they are a little strengthened, developing from ribs which can be seen in the inner whorls. The conch of the specimen is pachyconic with a moderately wide umbilicus.		R1 Zone of Great Britain, Ireland, Belgium, Germany (Rhenish Massif), France, Spain (West Pyrenees), and in South Portugal
	Gastrioceratoidea, Reticuloceratidae, *Bilinguites*	*Reticuloceras reticulatum*		●	●	●	 Size: 6 – 45mm. Thickly discoidal conch between 12 and 28mm diameter (ww/dm = 0.52 to 0.60), and narrow umbilicus (uw/dm = 0.22 - 0.30).		R1 Zone of Great Britain, Ireland, Belgium, the Netherlands, Germany (Rhenish Massif), Ukraine, and South Portugal.
	Neodimorphoceratoidea, Ramositidae, *Homoceratoides*	*Homoceratoides varicatus* = *Homoceratoides svetlanae*		●	●		 Size: 4.5 – 18mm. Pachyconic conch between 5 and 12mm diameter (ww/dm = 0.60 to 0.65), and thickly discoidal conch over 15mm diameter (ww/dm = 0.55 to 0.60); umbilicus moderately wide (uw/dm = 0.30 to 0.40) throughout these stages.		R1 of South Portugal, where the species accompanies *Vallites kullmanni*
	Gastrioceratoidea, Homoceratidae, *Vallites*	*Homoceras henkei* = *Vallites kullmanni*		●	●	●	 Size: 7 – 22mm. Pachyconic conch at 12mm diameter (ww/dm = 0.70), and thickly discoidal conch (ww/dm about 0.60) at 25mm diameter. Umbilicus narrow (uw/dm = 0.15).		R1 zone of Germany and South Portugal. In company with *Homoceratoides svetlanae* sp. nov.
Homoceras, H	Gastrioceratoidea, Homoceratidae, *Homoceras*	*Homoceras beyrichianum*		●	●	●	No data		H zone of Belgium, Germany, Great Britain, Ireland, Poland and Morocco
	Gastrioceratoidea, Homoceratidae, *Isohomoceras*	*Homoceras subglobosum* = *Isohomoceras subglobosum*			●		 Size: 10.5 – 27.8mm. Pachyconic conch (ww/dm = 0.60–0.85), with moderately depressed whorls, small umbilicus (uw/dm less than 0.30).		H zone of Great Britain, Belgium, Germany, South Portugal and questionably from northern Algeria

	Eumorphoceras zone, E	Dimorphoceratoidea, Dimorphoceratidae, *Dimomorphoceras*	*Metadimorphoceras sp.*		●		●	No data (no species classification)		
		Neoglyphioceratoidea Cravenoceratidae, *Cravenoceras*	*Cravenoceras sp*		●	●	●	No data (no species classification)		
		Neoglyphioceratoidea, Cravenoceratidae, *Cravenoceratoides*	*Cravenaceratoides sp.*		●			No data (no species classification)		
		Dimorphoceratoidea, Girtyoceratidae, *Eumorphoceras*	*Eumorphoceras sp.*		●		●	No data (no species classification)		
		Dimorphoceratoidea, Girtyoceratidae, *Girtyoceras*	*Girtyoceras modestum finale* = *Girtyoceras tomasi*		●	●	●	 Size: 8 – 16mm. Pachyconic conch at 8mm dm (ww/dm about 0.66), and moderately wide umbilicus (uw/dm = 0.38); conch thickly discoidal at 16mm dm (ww/dm = 0.55), umbilicus narrow (uw/dm = 0.20).		E zone of South Urals, and South Portugal (possibly of even late Visean age)
Late Visean	*Goniatites* zone, Go	Neoglyphioceratoidea Neoglyphioceratidae, *Lusitanites*	*Lusitanites subcircuralis* = *Lusitanites clitheroensis*		●		●	Size: 18 – 23mm. Discoidal conch at 20mm dm (ww/dm = 0.40). Umbilicus very narrow (uw/dm = 0.15), umbilical margin rounded.		Great Britain, South Portugal, France, Algieria, South Urals, Russia, Tajikistan, Uzbekistan, USA
		Goniatitoidea, Agathiceratidae, *Dombarites*	*Dombarites parafalcatoides*	●	●			No data		South Portugal, China, South Urals, Uzbekistan
		Neoglyphioceratoidea Cravenoceratidae, *Lyrogoniatites*	*Lyrogoniatites liethenis*	●	●			No data		South Portugal, Germany, Czech Republic
		Neoglyphioceratoidea Neoglyphioceratidae, *Neoglyphioceras*	*Neoglyphioceras spirale*	●				No data		Great Britain, Ireland Germany, South Portugal, Morocco, Czech Republic
		Goniatitoidea Goniatitidae, *Goniatites*	*Lusitanoceras algarviensis*	●				No data		South Portugal
		Goniatitoidea Goniatitidae, *Goniatites*	*Goniatites crenistria*	●					No data	Great Britain, Belgium, Germany, Poland, Czech Republic, and South Portugal, Morocco

Shell morphology analysis is limited just to a few species from the BAFG and made by Korn in 1997. The morphospace of the specimens from Table 3.1 was described using a schematic chart, therefore the life-modes are highly approximate. However, all these taxa belong to a single order, Goniatitida, which is the most numerous and morphologically diverse of all Paleozoic cephalopods, thus, general conclusions can be made regarding evolution and ecology of the four superfamilies: Dimorphoceratocea, Neoglyphioceratidae, Neodimorphoceratacea, Gastrioceratacea, found in the Mira and Brejeira formations. Most paleoecological studies focus on ammonoids as a whole, rather than on goniatites in particular. Therefore, any discussion (including the present one) assumes, that all results are valid for all ammonoid taxa, including goniatites (Lacchia, 2012).

Goniatites are extinct, and their distribution in space and time is much better known than their biology, thus interpretation of their mode of life can be made just by inference. Nevertheless, various approaches can be used, from the autecological studies, which focus on the morphology of the individual shell, to obtain physical constraints on the living organism, and from their synecology, which analyses associations and occurrences of ammonoids in the field (Lacchia, 2012). Intraspecific morphological variations have been studied intensively but remain still incomplete (in ecological context). Ammonoid synecology was significantly advanced at the end of th 20th century by the renewed interest in Paleozoic and Mesozoic dysoxic black shale facies (Westermann, 1996).

It is assumed, that after a drop in number of taxa at the end of the Devonian, the Carboniferous experienced the proliferation and diversification of ammonoids until the middle Moscovian (late Westphalian), when another crisis took place. Notwithstanding, these crises allowed the Carboniferous goniatites to refill environmental niches, and to evolve rapidly, becoming the richest and most diverse of all Paleozoic faunas (Lacchia, 2012).

In the early and middle Visean, diversity increased almost continuously toward the earliest Bashkirian. It is the most diverse interval within the history of Paleozoic ammonoids (possibly caused by increasing provincialism connected with the Variscan Orogeny), with a high number of species (Korn *et al.*, 2015). The ancestral stock of most Paleozoic Goniatitida was derived from the Prionoceratidae at the beginning of the Tournaisian age. Three superfamilies descended from the Goniatitina group: Dimorphocerataceae, Nomismocerataceae, and Goniatitaceae (Figure 3.5).

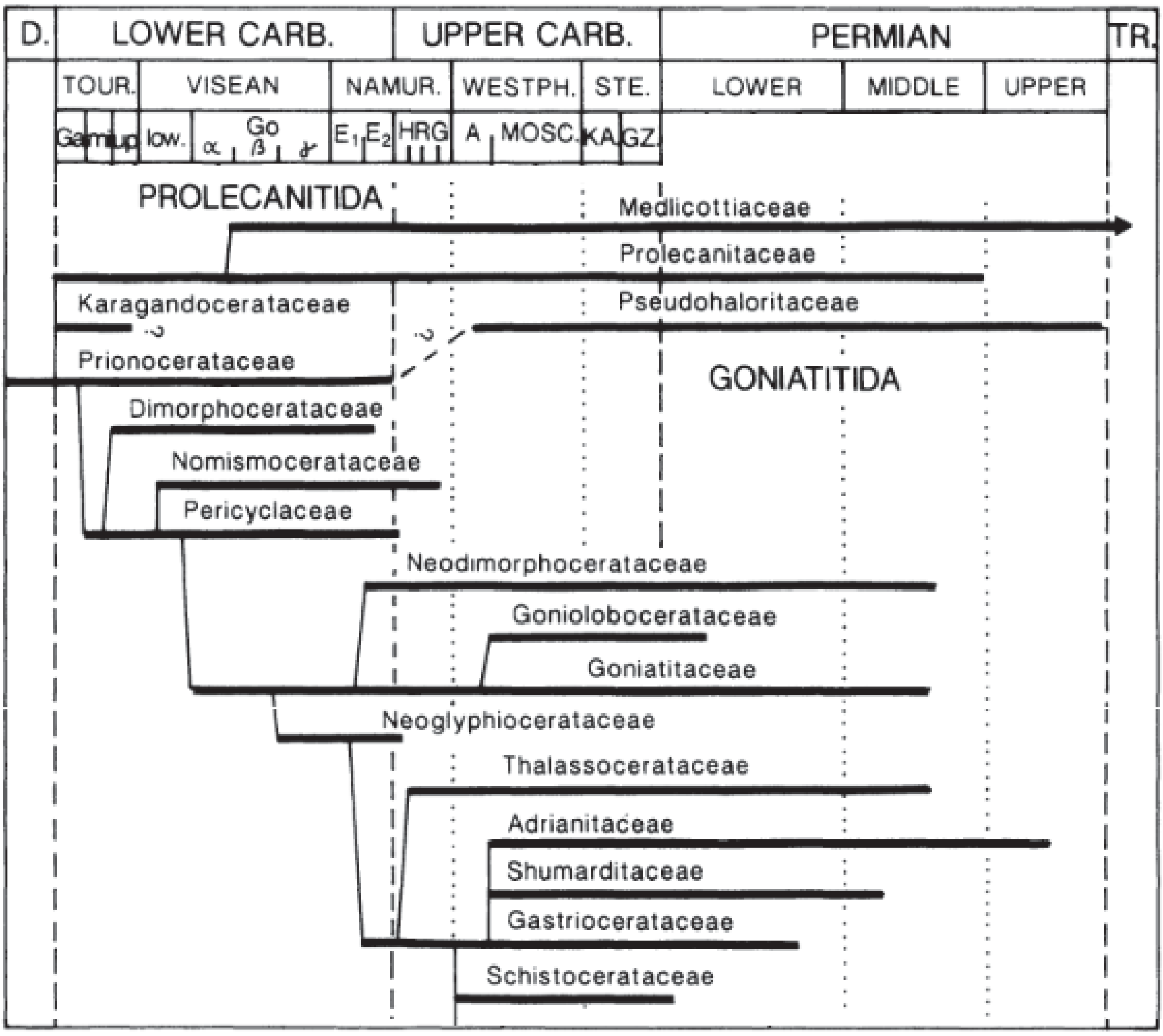


Figure 3.5. Chart showing the phylogeny and range of Carboniferous and Permian superfamilies. Abbreviations: Tour., Tournaisian; mi, middle Tournaisian; up, upper Tournaisian; Namur., Namurian; Westph., Westphalian; A, Westphalian A; Ste., Stephanian; Ga, Gattendorfia Biozone; Go, Goniatites Biozone; E, Eumorphoceras Biozone; H. Homoceras Biozone; R. Reticuloceras Biozone; G, Gastrioceras Biozone; Mosc., Moscovian; KA., Kasimovian; GZ, Gzhelian; AS (adapted from Becker and Kullmann, 1996).

The Dimorphocerataceae comprises genera with relatively wide ventral lobes. Among the families, the Girtyoceratidae exhibit well-rounded lateral saddles, and the Dimorphoceratidae show rather secondarily subdivided ventral or lateral lobes (Becker and Kullmann, 1996). The Goniatitaceae started to rule at the beginning of the late Visean. The conch formed discoidal to globular and involute shapes; many species are established as major global index fossils. At the end of the Visean, i) the Neoglyphiocerataceae arose from the Goniatitaceae, flourishing during the late epoch and early Namurian, with several index species belonging to the Neoglyphioceratidae and Cravenoceratidae families. The configuration of the suture is specific, rather narrow ventral lobe with low median saddle, and the broadly rounded first lateral saddle. Further, early in the Namurian, Neodimorphoceratacea superfamily descended from the

Goniatitaceae (*e.g., Ramositidae*), giving rise to the Gastriocerataceae with Homoceratidae, Reticuloceratidae, and Gastroceratidae families. The evolution of the suture lines, through the Upper Carboniferous, is shown in the Figure 3.6, with the evolutionary events represented by the different genre (Becker and Kullmann, 1996).

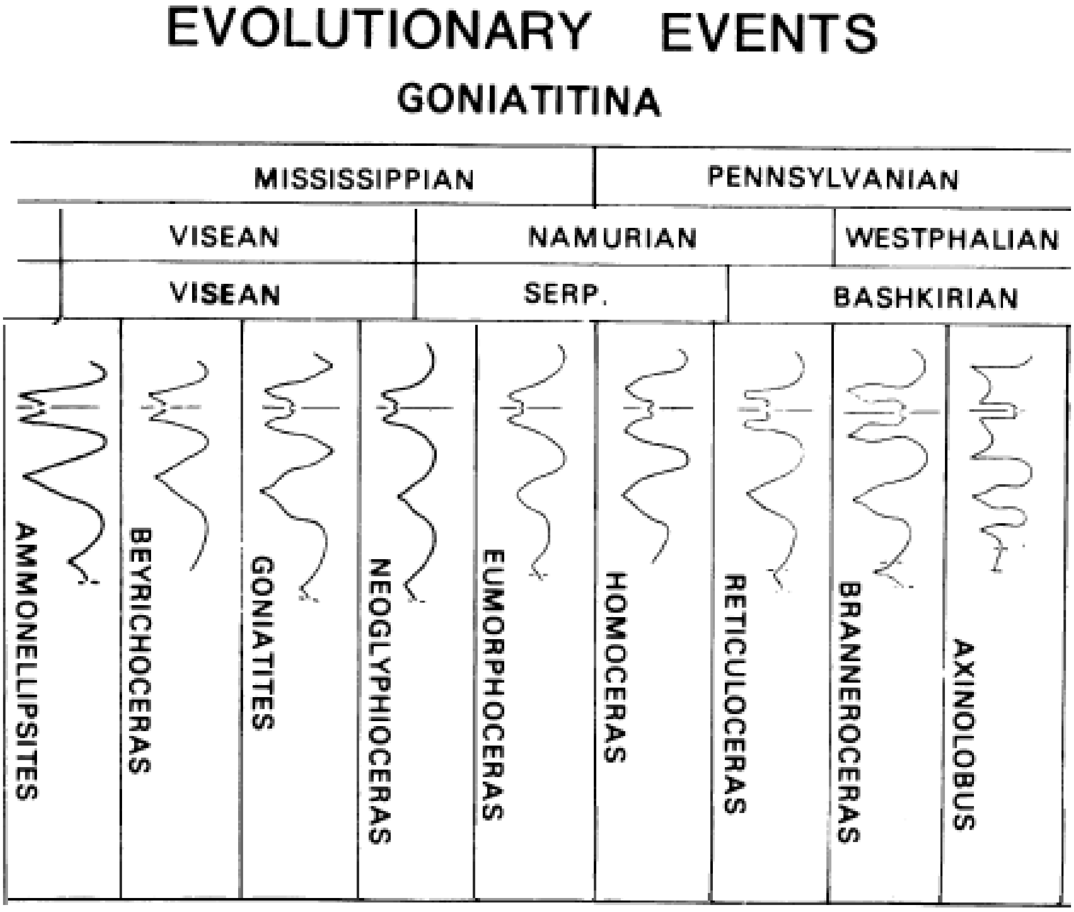


Figure 3.6. Evolutionary events of the order Goniatitida, represented in the suture lines of some of the major genre (adapted from Ramsbottom and Saunders, 1985).

Within the last 80 years, independent zonations have been developed for several of the regions with a succession of ammonoid faunas. These zonations are often based on species with a limited geographical distribution and hence a correlation between the regions is often difficult (Korn and Klug, 2015). The subdivision of the Carboniferous by means of ammonoid genera leads to several genus zones, which at least in part can be correlated with the chronostratigraphic stages. However, a global zonation based on species is not applicable because of the limited geographical distribution of many of the species (Korn and Klug, 2015).

3.1.1.1. Latest Visean, *Goniatites* biozone (*Go)*

A remarkable change came in the late Visean. The appearance of *Girtyoceras* and the radiation of *Goniatites* mark the beginning of a series of goniatite biozones of rather short duration (Kullmann *et al.*, 1990). Most goniatitid genera were cosmopolitan (*e.g., Goniatites).* At the end of the latest Visean, a world-wide increase in ammonoid diversity took place, which is especially notable in Europe, Asia, and North America. The maximum of the faunal changeover in Europe was reached in the latest Visean, with goniatites with triangular inner whorls *(e.g., Dombarites, Platygoniatites)*. Neoglyphioceratids with their distinct ornamentation are also useful as index fossils. Distinctive cravenoceratids marked the Visean-Namurian boundary, followed by the appearance of the sculptured genus *Eumorphoceras* (Becker and Kullmann, 1996).

During the middle late Visean, the biogeographic relationships between ammonoid faunas changed drastically. Only a few genera appear to be globally distributed, *e.g*., *Lusitanoceras, Neoglyphioceras,* and *Lusitanites* (Table 3.1). Late Visean ammonoids are nearly globally distributed in the tropical and subtropical realms and their rapid evolution makes them excellent stratigraphical index fossils. Interestingly, most assemblages of the early late Visean are dominated by the cosmopolitan genus *Goniatites*, such as those in South Portugal (Korn, 1997), the Cantabrian Mountains of Spain (Kullmann, 1961), the British Isles (Bisat 1934; Korn and Tilsley 2006), Central and Eastern Europe (Nicolaus 1963; Korn 1988), the Moroccan Maseta (Korn and Ebbighausen 2008), the Anti-Atlas of Morocco (Klug *et al.* 2006; Korn *et al.* 2007). Many of these regions, however, possess their own endemic species of *Goniatites* (Korn and Klug, 2015).

Increasing provincialism, later in the late Visean, makes a global correlation of ammonoid successions even more difficult. Three major paleogeographical realms with characteristic sets of genera (Figure 3.7, presented in the different shades of dots) can be separated, each of which possesses an independent ammonoid biostratigraphy. The North Variscan realm (Figure 3.7, white dots) is dominated by the genera *Arnsbergites*, *Hibernicoceras, Paraglyphioceras, Neoglyphioceras* and *Lusitanoceras* (only the two last ones found in the study area), which occur in South Portugal (Korn, 1997), Ireland (Moore and Hodson 1958; Hodson and Moore 1959), northern England (Bisat 1924; Moore 1936), Germany (Korn 1988; 1996) and the Moroccan Maseta (Korn and Ebbighausen 2008; Korn and Klug, 2015).

Figure 3.7. Paleogeographic map for the ancient Rheic Ocean region for the latest Visean and early Serpukhovian. (After Scotese, 1997 and Korn et al., 2012 [NV Nevada; UT Utah; TX Texas; OK Oklahoma; AR Arkansas; KY Kentucky; MM Moroccan Maseta; SP South Portugal (in the red zone); IR Ireland; BE Belgium; RM Rhenish Mountains; GB England; MS Moravia and Silesia; SU South Urals; NU North Urals; CM Cantabrian Mountains; AA Anti-Atlas; SV Saoura Valley; JB Jadar *Block of Serbia] (adapted from Korn and Klug, 2015).*

3.1.1.2. Early Namurian (Serpukhovian), *Eumorphoceras* zone *(E)* and Middle Namurian (early Bashkirian), *Homoceras* zone (*H*)

In the early Namurian, close to the end of the Early Carboniferous, the Gastrioceratacea originated**.** A change in morphological characteristics, especially in the configuration of the suture, appeared in the middle Namurian (end of Serpukhovian, *Eumorphoceras* zone, E biozone; Table 3.1). Goniatitina with a subdivided lateral, agathiceratids with subdivided ventral and lateral lobes *(e.g., Agathiceras),* as well as the conservative Gastrioceratidae *(e.g., Gastrioceras, Cancelloceras*) are characteristic of the Upper Carboniferous and Lower Permian strata (Becker and Kullmann, 1996).

At the end of the Early Carboniferous, a severe crisis in ammonoid evolution occurred in which the number of genera and species dropped considerably. The first recognizable interval of the Upper Carboniferous is rather short *Homoceras* biozone, which is not well documented because of the incompleteness of most sections around the beginning of Upper Carboniferous boundary in many parts of the world. The duration of the entire subperiod, which is roughly equivalent to the Pennsylvanian, comprised approximately 25 million years (Becker and Kullmann, 1996).

In the late Serpukhovian, the paleobiogeographic separation of the various regions was completed. The North Variscan realm (occurrences on the British Isles and Central Europe) became isolated becoming mainly characterized by the absence of taxa typical for the other realm. Assemblages in the North Variscan realm are characterized by the genera *Anthracoceras*, *Cravenoceras*, *Cravenoceratoides*, and *Eumorphoceras* (Korn and Klug, 2015).

The paleogeographical separation of shelf areas in the Visean was maintained during the Serpukhovian, thus stratigraphical schemes had to be proposed for the various regions (Korn and De Baets, 2015). The principal subdivision was developed by British researchers and, later on, adapted by workers on correlative successions in other parts of Europe such as Ireland (Hodson, 1957; Yates, 1962), South Portugal (Korn, 1997), the Netherlands (Dorsman, 1945), Belgium (Dorlodot and Delépine, 1930; Demanet, 1938; 1941; 1943), northern France (Chalard, 1960), the Rhenish Mountains (Schmidt, 1934; Patteisky, 1959; Horn, 1960; Korn and Horn, 1997), North Moravia (Patteisky, 1936), the Lublin Coal Basin of Poland (Bojkowski, 1979), the Moroccan Maseta (Delépine, 1941) and the Donetz Basin (Popov, 1979). The stratigraphical subdivision of the sediments in these regions is mainly based on girtyoceratid, homoceratid, reticuloceratid and gastrioceratid ammonoids (Korn and Klug, 2015).

The base of the Upper Carboniferous subsystem, namely Middle Namurian (lower Bashkirian, *Homoceras* zone, *H*) is defined by the Homoceratidae appearance. The morphology of the new forms belonging to the Homoceratidae was very conservative; conch form, sculpture, and suture line remained almost unchanged. But as in the early Tournaisian prionoceratids and earliest Namurian cravenoceratids, there was a tendency to develop widely umbilicate shells, predominantly starting in the early whorls. In general, the ammonoid faunas were impoverished (Becker and Kullmann, 1996).

3.1.1.3. Upper Namurian (*R1, R2, G1*) to Westphalian (Bashkirian to Moscovian, *G2*)

After the drastic decline at the beginning of the upper Carboniferous, the middle and late Namurian ammonoids proliferated intensively. Most species of the *Homoceras* Biozone continued into the *Reticuloceras* Biozone (R) and gave rise to a great variety of sculptured forms of worldwide distribution (Table 3.1). The general morphological aspect, however, did not change much. The number of species increased to more than 200, belonging to 45 goniatitid genera (Becker and Kullmann, 1996).

The time interval under consideration comprises three well-documented goniatite biozones, with a high number of short-ranging taxa that provide detailed biostratigraphic resolution: the lower *Reticuloceras* Biozone (R1), the upper *Reticuloceras* Biozone (R2), and the *Cancelloceras* Biozone (G1). Ammonoids from this time interval are recorded from 400 localities, mainly in Ukraine, Russia, Kazakhstan (southern Urals), South China, Europe, and North Africa but also from North America (Becker and Kullmann, 1996).

During this rather long period of about 10 to 11 million years, more than 160 species belonging to 60 goniatitid genera were present. Some groups exhibited a slight increase of sutural elements leading to more complex sutures. Sculptures were very diverse and common in goniatites from the upper *Cancelloceras* Biozone (G2) of Westphalian age (approximately 400 localities are known) (Becker and Kullmann, 1996). However, later in the epoch (beginning of the late Pennsylvanian), the Rheic Ocean vanished, together with its marine habitats and algarvian goniatites. Closure of the Rheic Ocean was accompanied by collision between Gondwana and Laurussia forming the Variscan Orogen of western Europe (Henderson *et al.*, 2016)**.**

3.1.2. Story of the Goniatite’s Paradise

It has been common to assume that the great majority of ammonoids lived close to the epicontinental (epeiric) sea floor, where they obtained their prey and that they were either "nektobenthic" or "benthopelagic" (= demersal) (*e.g.*, Westermann, 1990). This has been a consequence of the belief that all ammonoids were poor swimmers and thus, unable to catch the prey in midwater. However, more recent studies, about numerous well "streamlined" morphotypes, assumed that they were also active swimmers, able to chase their prey in the water column. In fact, in the Carboniferous the majority of ammonoids seem to have been pelagic (Westermann, 1996). Epipelagic-mesopelagic boundary for ammonoids (Figure 3.8) is considered to have been at 240 m depth. This is because of the physiology of phragmocone-bearing cephalopod shell; 240 m is the lower limit of effective liquid removal from the chambers by osmosis, at a 2% salinity differential across the siphuncular membrane (Ward and Westermann, 1985). Therefore, it is assumed that mesopelagic ammonoids had to rise regularly to epipelagic depths to compensate for flooding (Westermann, 1996).

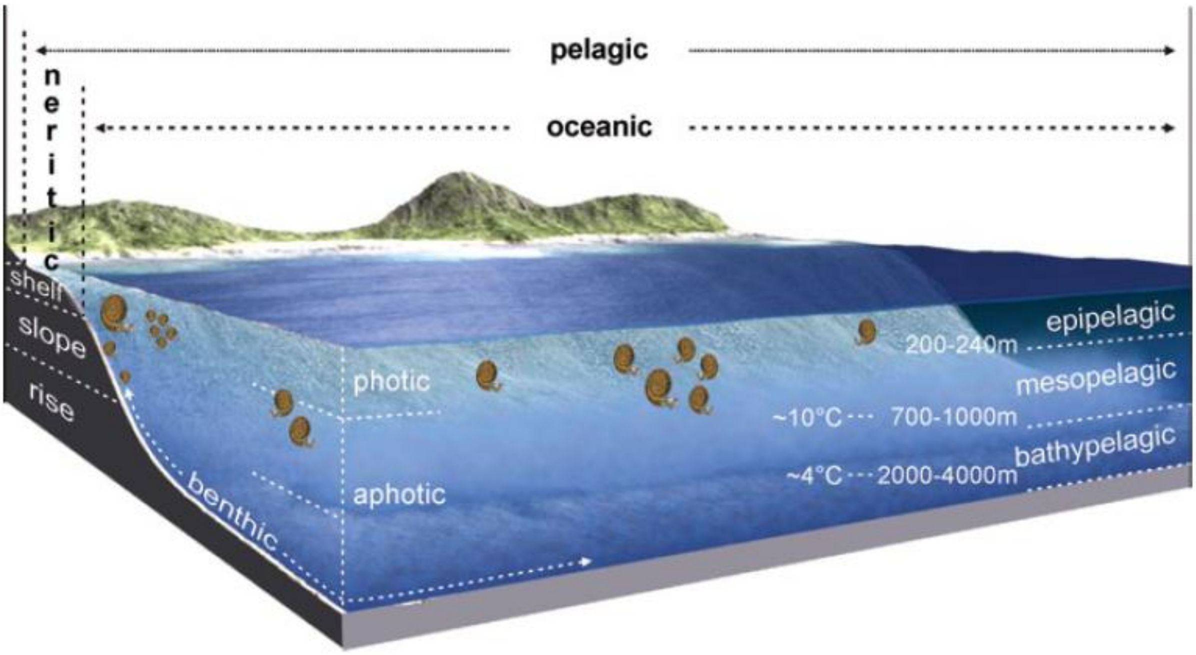


Figure 3.8. Schematic diagram showing the pelagic zone and its horizontal layers, marine environments inhabited by ammonoids. For details and explanations see the text. Ammonoid size and paleogeographic distances not to scale (adapted from Lukeneder, 2015).

Furthermore, water paleotemperatures have been estimated based on isotopic proxies. Indeed, oxygen and carbon isotopic signatures are a proxy for water temperature in aragonitic and calcitic shells such as those of extant *Nautilus*, *Spirula* and *Sepia* (Lukeneder, 2015). Isotopic records of modern and fossil cephalopod shells from embryo, juvenile, mid-age and adult stages allows interpretation of transitions in habitat temperature and indirectly water depth (Lukeneder *et al*., 2010). Various strategies are documented in t stable isotope records of ammonoids' shells (mostly for the Mesozoic ammonites), which (in some degree of confidence) can be compared with modern cephalopods. For instance, isotopic records of extant *Nautilus* and the cuttlefish *Sepia* suggest that those species are planktonic migrants travelling from warm shallow to cool deep waters, then returning to the shallows to spawn. In contrast, deep-sea squid *Spirula*, rises from cold, deep habitats to warmer, shallower habitats in adulthood. Habitat temperature of extinct ammonoids in estimated to change from 6 to 10°C, which would imply a depth range from 50–700 m today (Lukeneder *et al*., 2010). Nevertheless, these values may be overestimates because the chambers of ammonoid shells have been considered to only resist hydrostatic pressure of depths up to 400– 500 m in most of the species (Hewitt, 1996). Alternatively, changes in temperature might also be related to horizontal migrations through water column or seasonal changes in water temperatures (Lécuyer and Bucher, 2006; Ritterbush *et al*., 2014).

Therefore, it seems reasonable to assume that ammonoids initiated migrations due to their ontogeny (Figure 3.9), changes in diet or later in the mating/spawning phase, as in modern cephalopods (Ritterbush *et al.*, 2014)**.** In this case interesting might be also the discovery of sexual dimorphism in ammonoids (Figure 3.10) (Klug *et al.*, 2015)**.** Detailed examination of early ontogenetic stages of the Jurassic ammonites showed, that in many cases, larger (macroconch) and smaller (microconch) ammonoid specimens were just morphological types belonging to one species, and the differences in size were established as the sexual dimorphism (Doyle and Lowry, 1996). This assumption was based on the discovery of juvenile macroconchs with adult microconchs in dysoxic basin facies, and adult macroconchs concentrations in carbonate platform facies. That might lead to the conclusion, that the adult females left the hypoxic, cold basins to spawn (and possibly die) in the warmer and oxygenated waters of the adjoining shallower platforms (Westermann, 1996).

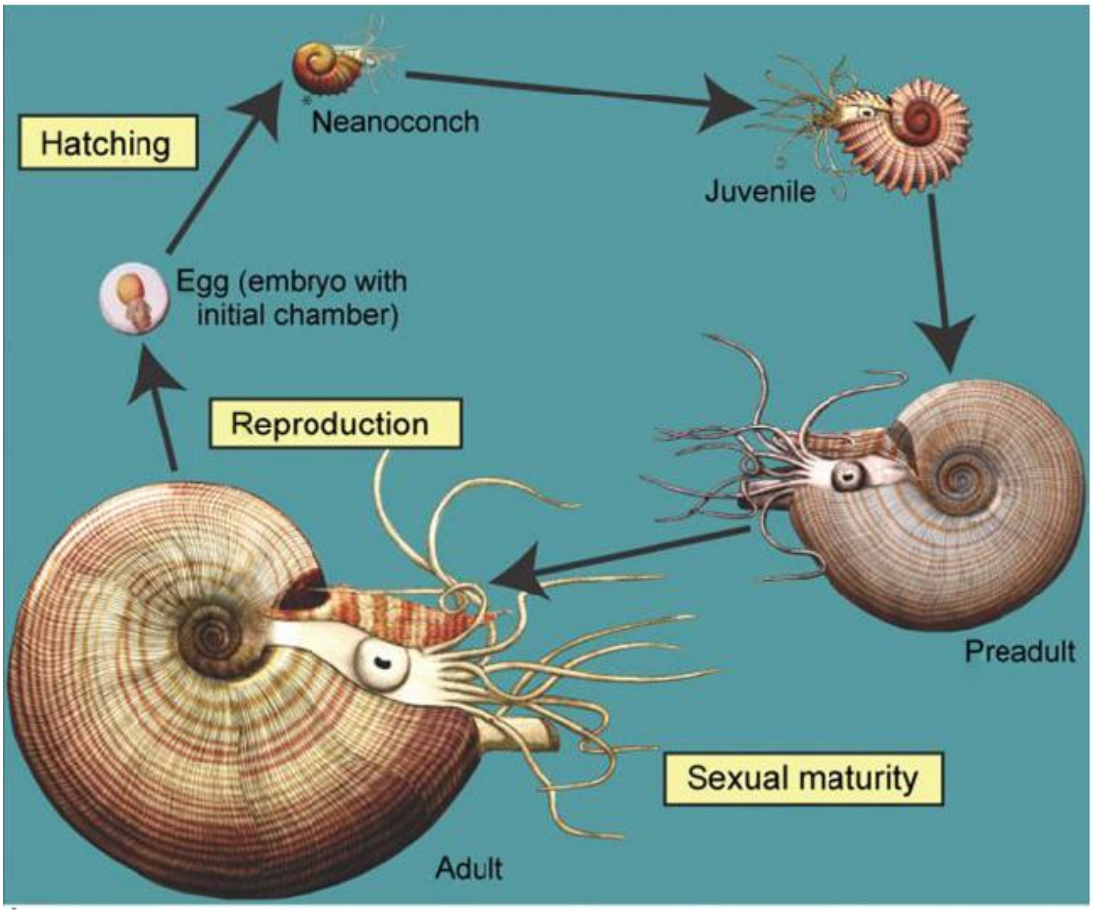


Figure 3.9. General ontogeny of ammonoids (adapted from Ritterbush et al., 2014)

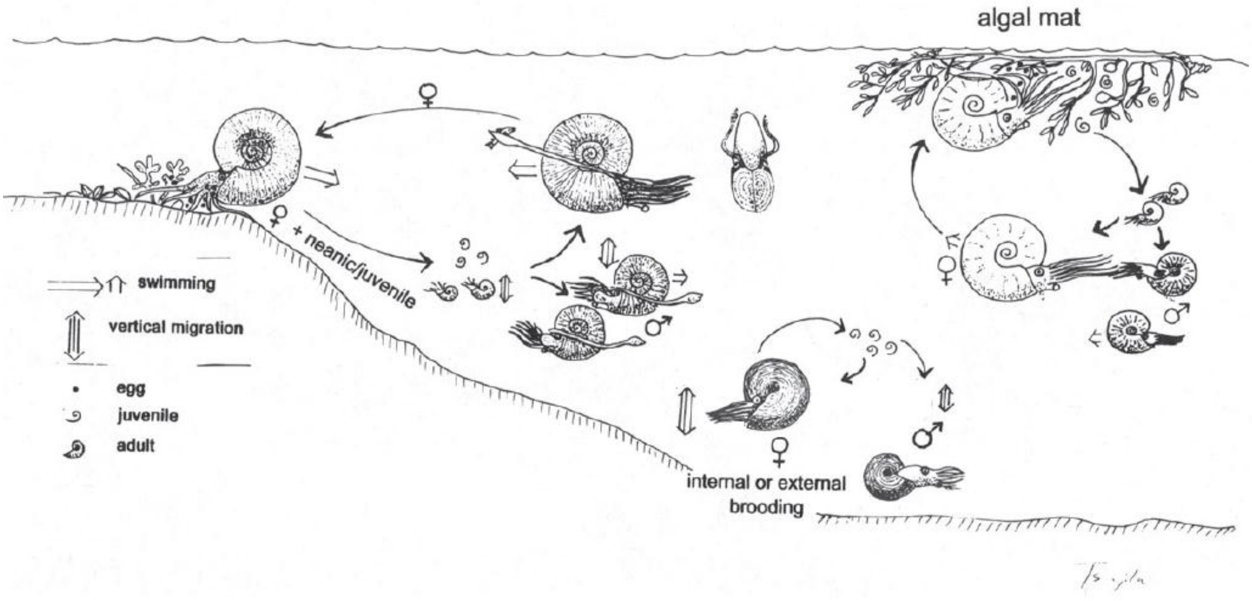


Figure 3.10. Three life-cycle scenarios of dimorphic ammonoids (from left to right): nektic with benthic eggs, planktic with planktic eggs, and planktic with pseudoplanktic eggs laid in floating algal mats (adapted from Westermann, 1996).

However, detail isotopic measurements of the ammonoids for estimating habitat depth is possible only when the aragonite composition of the external shells and septa is pristine. This case is very rare for such old fossils like Paleozoic goniatites shells, because aragonite (the chief mineral that makes up the ammonoid shell) transforms into calcite, during taphonomy, as a function of time, pressure, and temperature (Dullo and Bandel, 1988). Thus, it is also highly difficult to obtain specimens, which are preserved well enough to observe fine details of their microstructure (Kulicki *et al.*, 2015). Therefore, majority of the studies drew attention to the relation between the ecology of individual ammonoid taxa and morphological shell parameters (shown in Figure 3.4), such as conch whorl index (ww/dm) and umbilical width index (uw/dm) based on conch diameter (dm), whorl width (ww), umbilical width (uw) (*e.g.*, Westermann, 1996; Korn and Klug, 2001, 2012; Barskov *et al.*, 2008; Lukeneder, 2015).

Numerous authors (*e.g.*, Batt 1989; 1991; 1993; Westermann, 1996; Ritterbush and Bottjer, 2012) argued that each shell morphogroup had its own special habitats and motility (e.g., passive drifting, vertical migration, or swimming), making shell architecture directly dependent on habitat. Furthermore, environment and water depth were assumed, regarding the lithology, geochemistry, and fossil assemblages. However, detailed knowledge on the habitat is still speculative and based on spatial distribution (Lukeneder, 2015). Westermann (1996) identified two major shell types in ammonoids, the homomorphs and the heteromorphs (varying in coiling-axis). The major seven morphogroups of planispiral shape, and their special habitats, include spherocone (planktic), discocone (planktic-nektic), cadicone (planktic), oxycone (nektic), platycone (demersal), planorbicone (planktic-demersal), serpenticone (planktic) (Figure 3.11) (Westermann, 1996; Lukeneder, 2015).

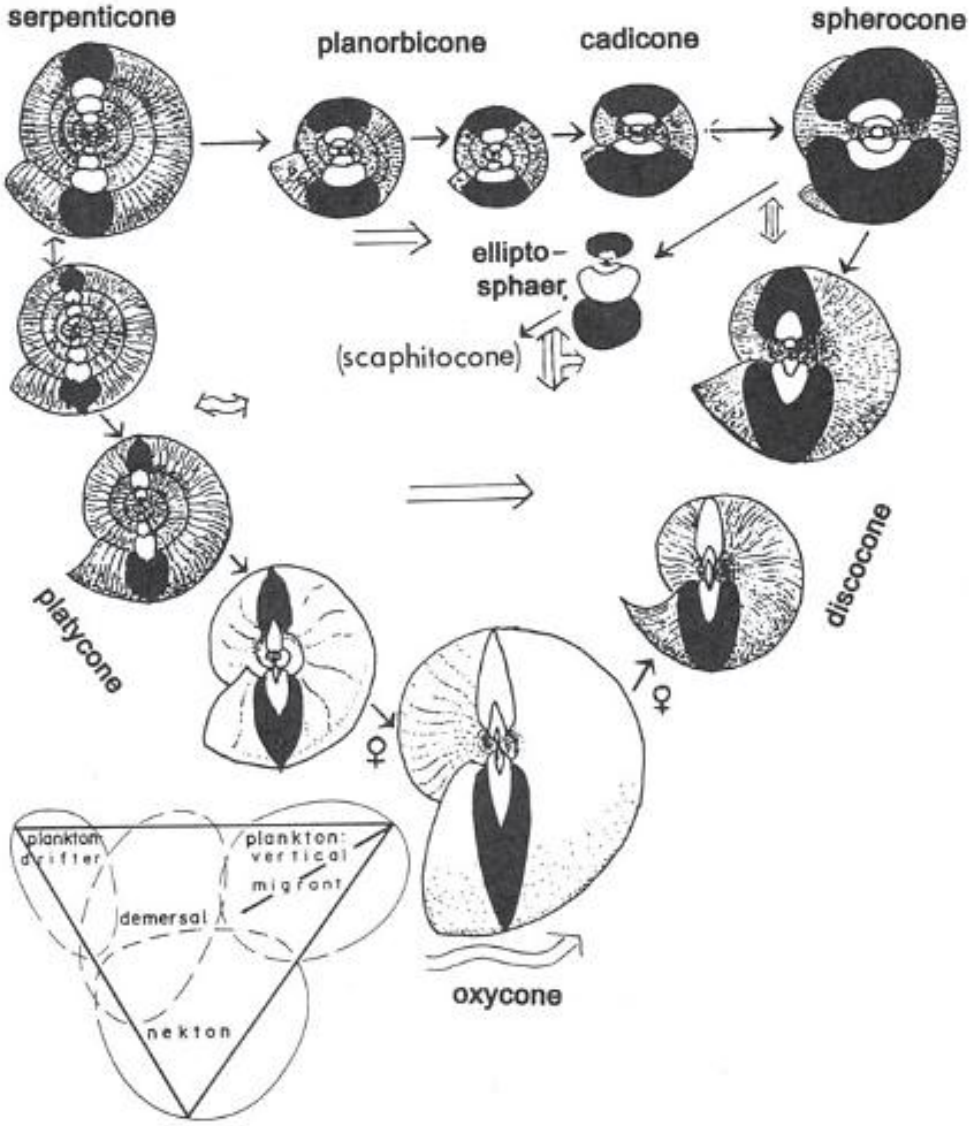


Figure 3.11. The basic planispiral shell shapes, their most common ontogeny (simple arrows), and their principal modes of life (small diagram) (adapted from Westermann, 1996).

However, swimming ability remains still controversial in all ammonoids. On the other hand, the worldwide distribution of goniatites indicates the ability to invade various types of habitat. The most frequent was a nekton-pelagic habit, while neanic and mostly small juveniles were quasiplanktic, which became more mobile at maturity. In general, lenticular shells with bilateral symmetry are associated with locomotion, while prominent ornamentation is associated with reduced mobility. In goniatites, the growth lines are generally not very prominent, which is consistent with a nektonic habit. However, the globose shape of most goniatites suggests they might be more associated with vertical migration than with high swimming skills (Lacchia, 2012).

In conclusion, the three major life modes were established (concerning shell morphology and present-day analogues) as following: active swimmers, drifters (planktic), and vertical migrants, in the epeiric basins, shelf seas and deep oceans (Westermann, 1996). However, more detailed characterisation was previously made by Nesis (1976), who distinguished five, general life-habits of extant cephalopods, also used by paleobiologists in detail analysis:

- Benthic life-form: bottom-dwelling, mainly crawling, rarely using their hyponome. Size from small to large. Solitary scavengers. Produced eggs are large, with direct development, without pelagic stages. This group mostly comprises octopuses.
- Benthopelagic life-form: bottom-dwelling, do not crawl on the bottom, but slowly move above the bottom using their hyponome in a very short distance. Possibly good at manoeuvring. Scavengers and stealth predators. Development is direct, without a pelagic stage. Deep-water octopuses. The only extant representative with an outer shell is *Nautilus*.
- Nektobenthic life-form, represented by two types:
  - sepia type – intermediate forms between benthic and pelagic, closely connected with the sea floor where they spend nights, ambush, and lay large size eggs. Small and medium-sized. Feed on moving prey and capable of darting forward. Ambush predators, often live in groups,
  - neritic squid type – forms close to nektonic cephalopods. Live on the shelf, connected with the bottom only to lay small size eggs. Fast, active predators, hunting in groups. The development has a pelagic stage.
- Nektonic life-form: permanently in the pelagic zone, not connected with the sea bottom. Active group predators, Swimming quickly using the hyponome. Eggs are small, in large numbers and the development includes a pelagic “larval” stage, which differs in appearance from the adult. This group is represented by modern oceanic squids.
- Planktonic life-form: strictly pelagic, small to medium size (sometimes also large). Feed on plankton and sometimes live in groups. Incapable of moving for long time using the hyponome. Eggs are usually pelagic, and the development is very long-standing. Larvae are often completely different from the adults, *e.g*, larval stage of small octopuses.

It is thus clear that the ecological structure of ammonoids communities underwent a great alternation through Paleozoic era. Biotic changes in trophic conditions (predator-prey relationships), food supply (diet differs in different water layers), and natural enemies (other cephalopods, fishes) triggered changes in populations and morphotypes (Lukeneder, 2015).

In the Devonian (when ammonoids appeared), community structure started to become more dominated by pelagic forms. The number of benthic and benthopelagic forms halved and the number of planktonic and nektonic forms increased (while the number of higher taxa decreased). From the Carboniferous onward, no benthic forms appeared in the cephalopod community (Barskov *et al.*, 2008). This restructuring (the largest in the Paleozoic history of cephalopods), was more likely caused not by change of the proportions of life-forms in the community, but rather related to the global events from the end of Devonian through Carboniferous. The drop in the number of benthic forms was possibly a result of the sea floor reduction, sea level fluctuations, and the distribution of anoxic conditions, which led to the degradation of bottom habitats. Thus, ecological structure of the community resulted more from the changes in the environment – by inhabiting mostly the water column from off-shore, they were successfully avoiding a loss of benthic habitats caused by the sea floor reduction (due to the closure of the Rheic Ocean) and continuous sea level changes shown in the Figure 3.3 (Barskov *et al.*, 2008)**.**

Detail conclusion on the life-modes of the goniatites, found in the Carboniferous formations of the Algarve region, is impossible at this stage. Life-forms from the Table 3.1 (shell shape) are highly approximate, and might contain significant errors, due to the lack of statistical analysis of the conch parameters, poor preservation, and low number of specimens collected from the studied formations. Moreover, in many cases, the systematic identification brings uncertainty even at the genus level. This might be due to the fact that, the Upper Carboniferous ammonites from the BAFG were poorly studied over time (limited to the one source made by Korn (1997), in comparison to the ones from the Southwest Domain (Carrapateira Group). To conclude more about biology and ecology of the species found in the BAFG, more specimens should be collected, and statistical analysis of the conch parameters should be applied.

Nevertheless, different morphotypes (shell shapes) shown in the Table 3.1 indicate that numerous ecological niches were present among algarvensis goniatites. Thus, at this stage, general assumptions can be made based on the global data collection for the order Goniatitida. As it is noted by Barskov *et al.* (2008), from the general ecological point of view, order

Goniatitida (with planispiral shells), contains nektobenthos (~ 37%), plankton (~ 35%), and benthopelagic forms (~28%) (Figure 3.12a). From the time of their appearance in the Middle Tournaisian and during the entire Carboniferous goniatitids played a dominant role in the cephalopod communities, determining their morphological and ecological structure. The main feature of the ecological structure of the order is high taxonomic diversity of benthopelagic forms. The structure of the order changed significantly in the course of its evolution (Figure 3.12b). The main trend was towards a gradual decrease in the diversity of nektobenthic genera (~45% in the Lower Carboniferous,~25% at the end of the Permian) due to the increase in the proportions of planktonic and benthopelagic forms (Barskov *et al.*, 2008).

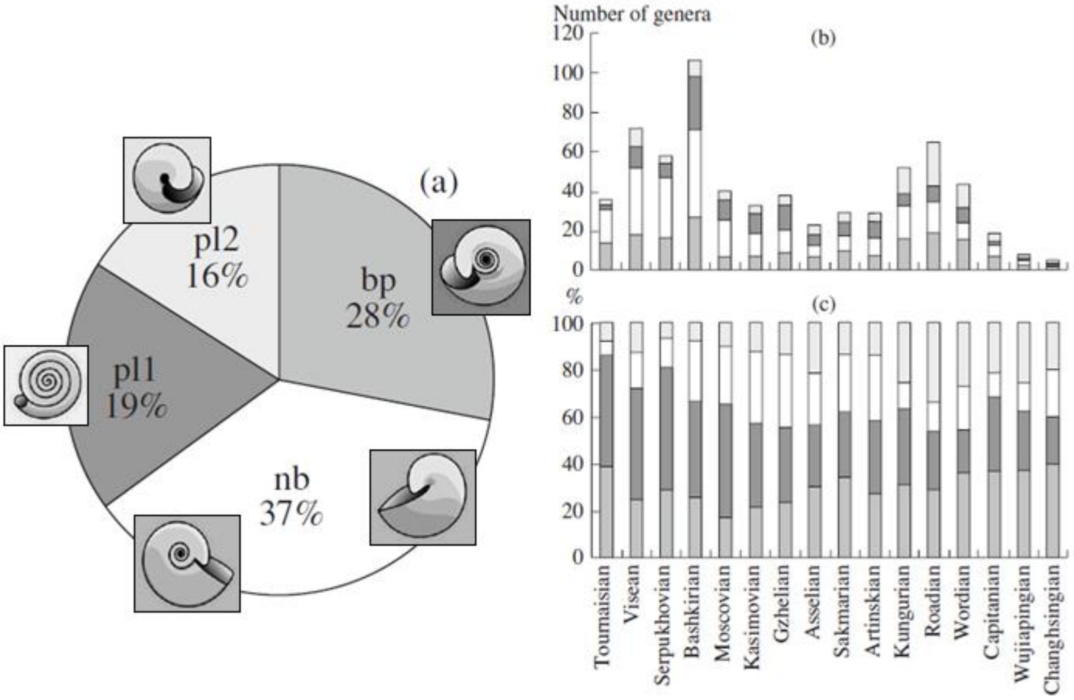


Figure 3.12. Order Goniatitida, (a) Ecological structure: pl, evolute planktonic forms; pl2, involute planktonic forms; nb, nektobenthic forms; bp, benthopelagic forms; (b and c) changes in the ecological structure during their existence: b, absolute values; c, percentage (adapted from Barskov et al., 2008).

The proportion of goniatites life-forms through time are highly generalized, simply because of their ontogenetic disparity during their growth stages, thus, also because of the changes in the life-mode. Earliest evolution of ammonoid reproductive strategies in Devonian shows decreasing trend in egg size and increase in fecundity. Thus, further shift to *r*-strategy in late Devonian through Carboniferous was done (Landman *et al.*, 1996). Eventually egg dimensions of ammonoids became closely resembling those of modern epi-mesopelagic coleoids, more specific, some of the squid families (*e.g.*, Brachioteuthidae, Heteroteuthinae, Pyroteuthidae) and octopods (*e.g.,* Argonautoidea), which hatchlings are epipelagic (Sweeney *et al*., 1992). Other extant cephalopods that live either at the bottom or in the meso-bathypelagic layers produce larger eggs (with some exceptions). Generally, adult ammonoids might spawn anywhere, even in deep ocean, whereas their hatchlings might quickly rise to surface waters to forage, as happens in the modern abundant squid families like Onychoteuthidae Gonatidae, Cranchiidae and some others (Laptikhovsky *et al.*, 2013)**.** Throughout evolutionary history, nautiloids always produced much larger eggs than ammonoids, being more *K*-selected, with a life-span longer than 20 years, and with an iteroparous reproductive strategy – the females spawn once a year, survive, feed, grow and regenerate their gonads for a further reproductive event the following year (Rocha *et al.*, 2001)**.**

On the other hand, the trophic status of ammonoids exhibit a wide range of feeding strategies through time, from planktotrophic to active carnivorous. They were prayed by vertebrates like fishes, sharks (however, no evidence was found in the study area), and invertebrates (*e.g.,* other cephalopods, crustaceans). Ammonoids ate possibly everything they were able to catch and hold, leading to the interpretation that their strategies varied from demersal herbivores, scavengers via microphagous carnivorous to active, nektonic predators (Kennedy and Cobban, 1976; Lukeneder, 2015).

As noted by Westermann (1996) and further Lukeneder (2015), numerous feeding strategies can be assumed, especially for neanic and juvenile ammonoids. It is envisioned, that they fed on a mobile prey, on essentially planktic organisms (ammonoid hatchlings, pseudo planktic and planktic microorganisms such as ostracods or microgastropods), using their ejectile tentacles, and those with non-ejectile tentacles or velar webs, on tactile or chemosensory feeding by "pseudoscavenging" of organic particles floating and sinking at all depths (Reyment, 1988; Westermann, 1996). The preying behaviour is crucial for understanding the ammonoid habitat and ecology, because ammonoids might have actively followed prey. This can cause ontogenetic or diurnal migrations, preying on different resources during their lifespan, or preying at night when some other predators sleep, like recent *Nautilus* (Reyment 1988; Lukeneder, 2015).

Data on prey and buccal organs is extremely scarce, especially for Paleozoic ammonoids, however the results of autecology and synecology, from last decades, might help to conclude some highly possible trophic scenario. Following Westermann (1996), Carboniferous goniatites from the Algarvensis Geopark might belong to the pelagic food chain, possibly at multiple number of trophic levels. Smallest taxa together with neanic stages and juveniles of larger species, fed directly on the microplankton, perhaps nocturnally with modest vertical migration or at the lower limit of the photic zone. They were eaten by mid-sized ammonoids which, in turn, fell prey to the larger, relatively good swimmers among the ammonoids. Some of them were vertical migrants in deep water, including the oceans, where some fed on mesopelagic organisms including sluggish juvenile ammonites, and others zooplankton (Westermann, 1996). During the nektoplanktic juvenile phase and subsequent stages, they fed on various nutrients and nano- and microplankton members as trophic resources. Taxonomic groups can therefore appear or vanish due to changes in trophic levels (Lukeneder, 2015).

This scenario presents mostly monospecific trophic relations (also due to the lack of other evidence), possibly limited to several families of order Goniatitida. In the Carboniferous, diverse marine life was mainly distributed to the shallow seas, leaving epi and mesopelagic zones (including more distance offshore waters), into cephalopod communities. In the Carboniferous, the morphological restructuring of goniatite shells (the largest in the Paleozoic history of cephalopods), gave them an opportunity to occupy all the marine environmental niches, and to create a “cephalopod paradise” in the closing ancient Rheic Ocean.

3.1.3. The Rheic Ocean Basin

As mentioned before, formations of Mira and Brejeira filled ancient foreland basin from the Rheic Ocean (Figure 3.13). This system is made of elongated regions of potential sediment deposition that form on continental crust between orogenic belts with associated subduction, and cratons. Numerous studies of foredeep zones (*e.g.,* Covey, 1986; Sinclair and Allen, 1992) have documented a transition from early deep marine sedimentation (flysch) to later shallow marine or even nonmarine sedimentation. This transition most likely reflects the fact that foreland basin systems originated in oceanic trenches and later become shallow marine or nonmarine. Modern submarine foredeeps on continental crust are characterized by shallow shelf deposits that are accumulating in depths lower than 200 m deep (DeCelles and Giles, 1996). In Carboniferous, similar situation is established for SW Britain (Oliveira and Quesada, 1998), SW Poland (Górecka-Nowak, 2008), and the Rhenish Massif (Korn and Horn, 1997; Königshof, Becker and Hartenfels, 2016), which indicate clear progradation towards the foreland. However, in South Portugal, lithostratigraphic sequence ends in Brejeira formation, due to the subsequent erosion, which create a hiatus, and no shallow shelf is recorder for this region.

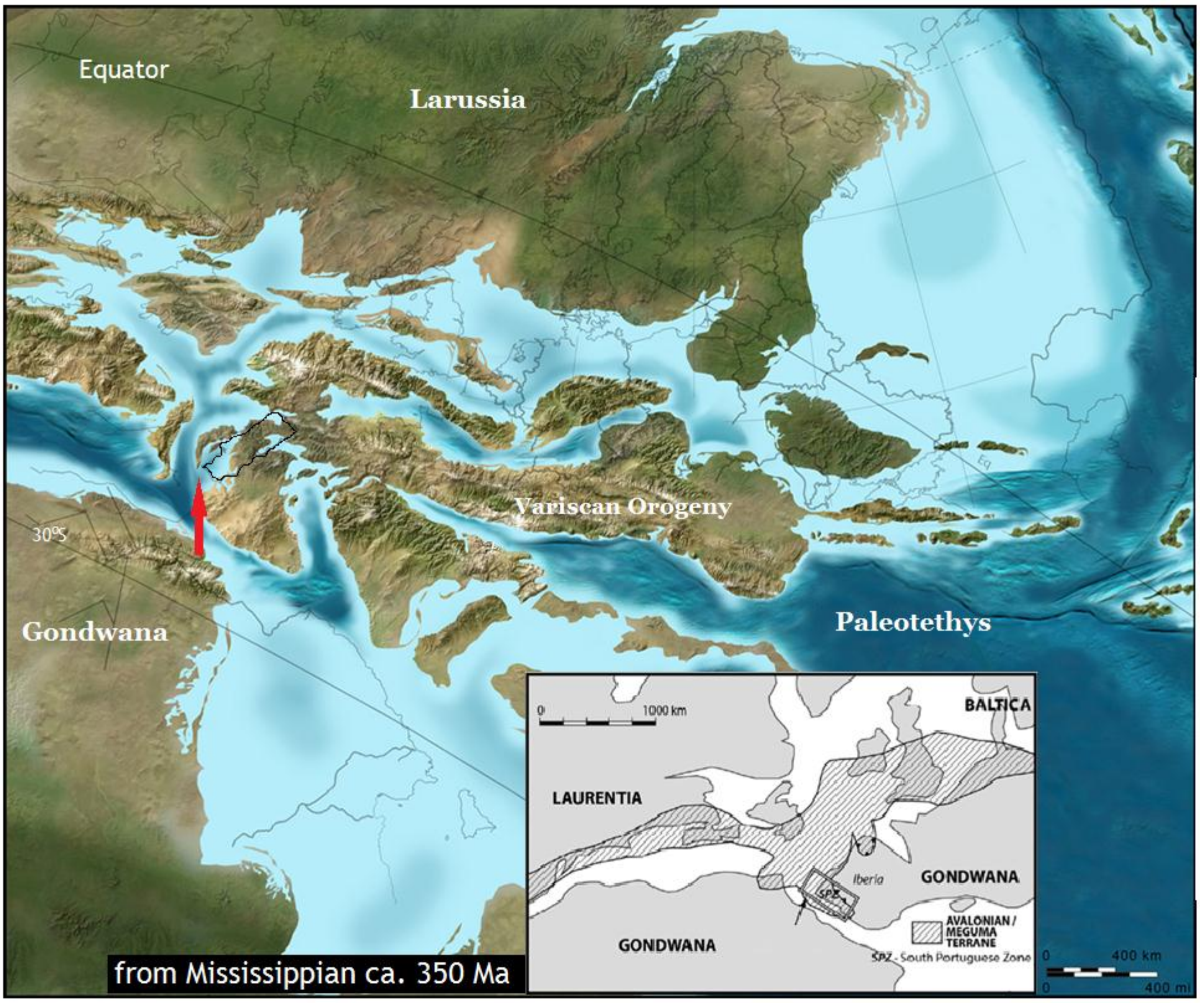


Figure 3.13. Carboniferous paleomap of Europe, with the South Portugal indicated by the red arrow (adapted from Deep Time Maps, 2021 and Rodrigues et al., 2015).

The Mira and Brejeira formations, are in stratigraphic continuity, but they show different provenances through time. Basal part of the Mira formation indicates a deep ocean sedimentation from two different sources: extrabasinal deposits (related to fully turbulent flows having possibly long-lived river discharge) from Ossa–Morena Zone; and intrabasinal (unsteady flows that initiate from a cohesive debris flow that accelerates along the slope) from Avalonian South Portuguese Zone (Figure 3.14a) (Rodrigues *et al.*, 2015; Zavala and Arcuri, 2016). The second provenance scenario for the BAFG units (Figure 3.14b) is attributed to the presence of a physical barrier (forebulge) that formed during the high tectonism and development of the foreland basin. This barrier was active from middle Visean times and separated the subbasins of upper Mira and Brejeira. In the late Bashkirian (middle Westphalian) Mira became a part of the Variscan mountain chain, and only Brejeira remained, leaving the last legacy of the Rheic Ocean. It exhibits flow directions mainly to the SE and E with some paleocurrent measurements indicating flow towards the SW and north (Rodrigues *et al.*, 2015), probably because the turbidite flows had to fill up the submarine topography build on the carbonate platform represented by the Carrapateira Group (the Southwest Domain). During Moscovian, the colliding margins of the SPZ and the outer margin of Gondwana, became a part of the Variscan orogeny (Pereira *et al.*, 2007; Pereira *et al.*, 2008).

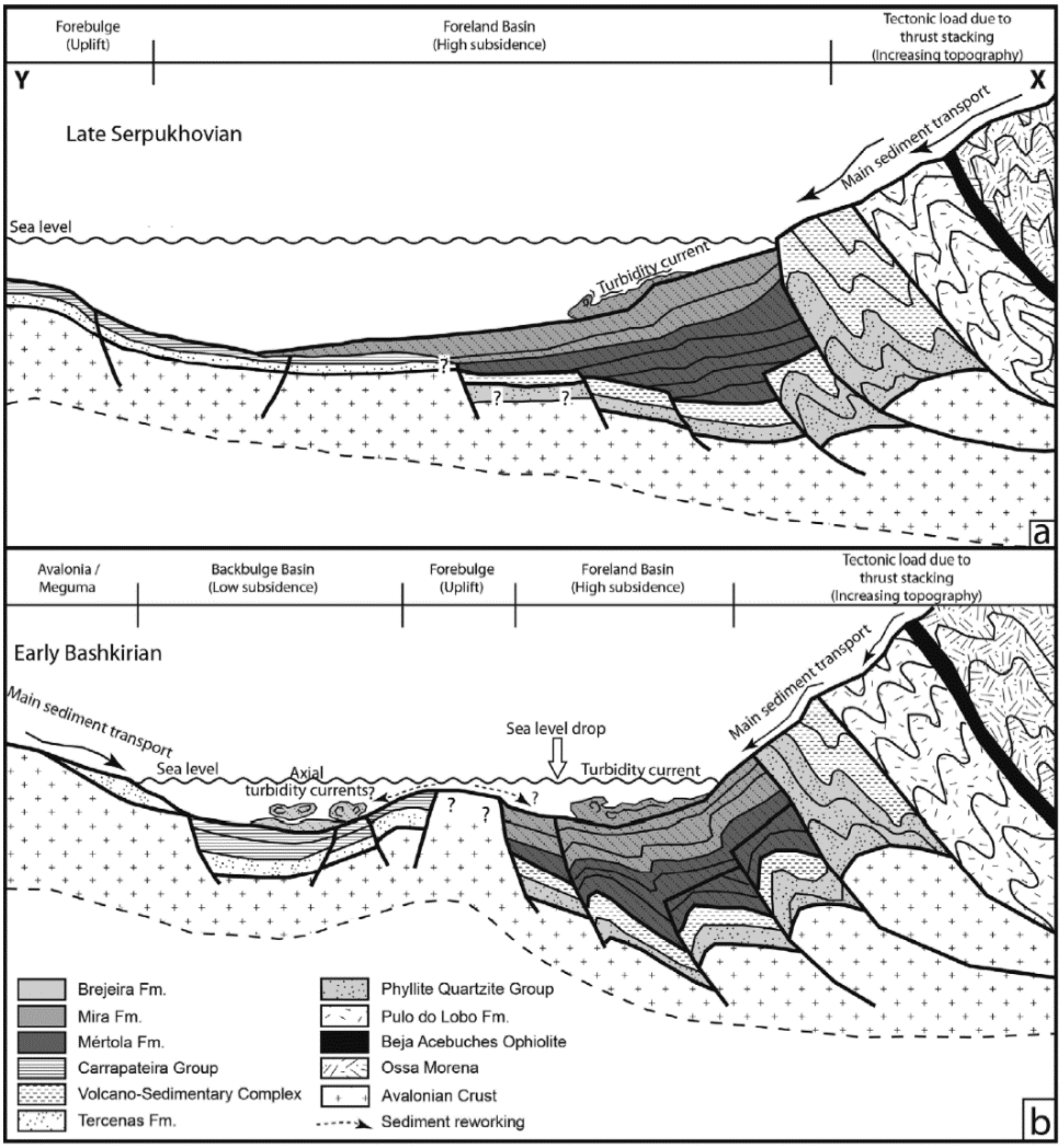


Figure 3.14. Schematic cross-section illustrating the tectonic and basin fill evolution of the Baixo Alentejo Flysch Group. (a) Late Serpukhovian. Prograding flysch sedimentation (Mértola and Mira formations) (b) Early Bashkirian. There is continuous uplift of the forebulge owing to the increase in the tectonic load in the foreland basin and the formation of a physical barrier. The Brejeira Formation is deposited in the backbulge basin, onto the platform-facies of the SW Portugal Domain. Figure is not to scale (adapted from Rodrigues et al., 2015).

The Algarvensis territory was thus a part of the narrowing Rheic Ocean, surrounded by the warm and shallow tropical seas, from late Visean to Moscovian age. This ancient basin was filled by the flysch type sediments of the Baixo Alentejo Flysch Group, deposited by gravity flow of turbidity currents (density currents resulting from an increase in sediment concentration), at the bottom of the deep-sea. Marine turbidite facies are known to have accumulated in moderate to deep (up to 2000 m) waters, in tectonically active regions (Geology Science, 2021). Accordingly, Mira and Brejeira are composed of mainly greywackes (sandy turbidites) interbedded with thin layers of black shales (Rodrigues *et al.*, 2015).

Greywackes are thought to be formed from muds and sands, that have been eroded and then transported by rivers and glaciers down to coastal waters. Further, the sediment continues to flow from the shelf, where it is transported down the continental slope, as turbidity currents, onto deep ocean floor, where they accumulate over a long period of time. These sediments become deeply buried and undergo change by being compressed and cemented together, due to the highly active tectonism. A deep grey colour indicates environment with low oxygen concentration. The thin black shale beds formed between turbidites, indicate events with greater concentration of organic matter, which slowly settled on the sea floor, and may represent thousands of years (Stow and Smillie, 2020; Geology Science, 2021). “Black shales” are dark, because of being especially rich in unoxidized carbon. They were deposited in anoxic, reducing environments, such as in stagnant water columns or very high sediment accumulation. Therefore, in environments such as deep water slope, or ocean floor, where the oxygen concentration is relatively low, periodic black shale events are highly suspected. They are the results of external factors, like climate change, greater productivity or sediment input, tripping the balance in favour of anoxia and organic matter preservation (Tourtelot, 1979; Stow *et al.*, 2001).

Throughout the Phanerozoic, hypoxic (O_2 = 0.3–1.0 ml/l) sea water conditions were important for pelagic organisms such as ammonoids (Westermann, 1996). The geochemical and biotic conditions are important in seawater, at the seawater–sediment interface, and in sediment itself (Lukeneder, 2015). Ammonoids, as indicators for environmental conditions, reacted to changes in water geochemistry. Anoxic (O_2 < 0.3 ml/l) black shales were mostly (not always) characterized by the absence of fossils of ammonoids, as in general anaerobic conditions tends to eliminate metazoans taxa. The high metabolism of larger taxa excluded most of them from dysoxic–anoxic conditions. However, some smaller forms might tolerate such conditions, but only for short period of time, for preying or during migration phases. Such species, in the adult stage, lived in the water column and were perhaps able to survive briefly in dysoxic waters as reported for the recent *Nautilus,* which inhabits aerobic waters but is able dive shortly into dysoxic zones (Wells *et al*., 1992; Mapes and Nützel, 2009**;** Lukeneder, 2015).

In hypoxic basins, some of the Carboniferous goniatites might be perhaps euryoxic or even adapted to slight dysoxia (Westermann, 1996). Based on Wells *et al.* (1992) aquarium experiments with *Nautilus,* suggest that at mid water depth in hypoxic basin, pelagic ammonoids: (1) were just below the photic zone where they had better chances to escape predators; (2) they were below the base storm waves, which would have influenced buoyancy even of the relatively good swimmers; and (3) they could escape periodic anoxic waters (Westermann, 1996).

Well-oxygenated waters probably contained great food supply and enhanced the growth of eggs. Accordingly, aerobic waters of the primary habitats are required for early ontogenetic development (Westermann, 1996; Laptikhovsky *et al.*, 2013), therefore adult females of goniatites are thought to have spawned in well-oxygenated habitats (Lukeneder, 2015). Therefore, here the question arises – how they got to the deep ocean of BAFG? Goniatites belonged mostly to the pelagic environments. They occupied continental slopes and open distal waters, possibly, till depths of 500 m, or possibly even deeper, taking in consideration the fact, that living *Nautilus pompilius* can reach depths of 700 m (Dunstan *et al.*, 2011). Thus, the fossils found in the BAFG were very likely transported and deposited on the bottom of the deep-sea through the gravity of the water column or transported by the turbidity currents from the continental slope.

However, it is worth to pointed out, that nearby the deep environment of the BAFG, the Southwest Portugal Domain (still part of the siliciclastic sea during the late Devonian) evolved to a Carboniferous carbonate/shale platform (Carrapateira Group) in the Carboniferous, as an Avalonian epicontinental sea (Oliveira et al., 2019)**.** During Pennsylvanian, when deposition of the Mira started, just the Quebradas formation remained, as a part of elevated shallow platform. This unit is composed of mainly black shales with interbedded carbonates (limestones), which increase in frequency towards the top of the formation, with numerous horizons of phosphatic nodules (Korn, 1997). It means, that deposition occurred in a restricted marine environment of quiet waters, with bottom anoxic conditions, and the interbedded phosphatic nodules may represent upwelling near its external border (Oliveira *et al.*, 2009). This unit is rich in ammonoids of Serpukhovian and Bashkirian age (R1 to G2 biozone). The goniatites are represented by characteristic species, including *Vallites kullmanni, Reticuloceras reticulatum Bilinguites metabilinguis, Cancelloceras* cf. *crencellatum,* and *Gastrioceras listeri* (Pereira *et al.*, 2007) , also found in the formations from the Algarve region.

The Quebradas shales are characteristically black coloured, organic-rich (kerogen), finely laminated, with disseminated pyrite, and often weathered into "paper shales" with a strictly pelagic and pseudoplanktic fauna, as in the classical *Posidonia* Shales of northwest Europe (found in Murração formation of Lower Carboniferous) (Oliveira *et al.*, 1985; Pereira *et al.*, 2007). These paleoenvironments are characterised by high nutrient input from the surrounding highland causing plankton blooms and is typically associated with early transgressive phases (Westermann, 1996). Besides the rich goniatitic assemblage, similar to the one from BAFG, these shallow tropical waters were inhabited also by other benthopelagic forms as conodonts, and benthic invertebrates, such as brachiopods, and scattered planktonic radiolarians (Oliveira *et al.*, 1985). In the upper part, laminated shales with few thin limestone beds occurs. This means, that the transition to the Brejeira Formation was slow, and marked by distal turbidites (Korn, 1997).

Close association of the carbonate platform is highly important in fact, due to the diverse life modes of the goniatites, also found in the Carboniferous formations of the Algarvensis Geopark. Even though, the highest percentage of the species belong to pelagic, nektobenthic lifestyle, on some point in their life span, they depended on the shallower waters, to feed, spawn, or to migrate, depending on the growth stage. The Namurian scenario of goniatites diverse life-modes is represented in Figure 3.15. It shows a close association of pelagic forms with the deeps water and carbonate platform.

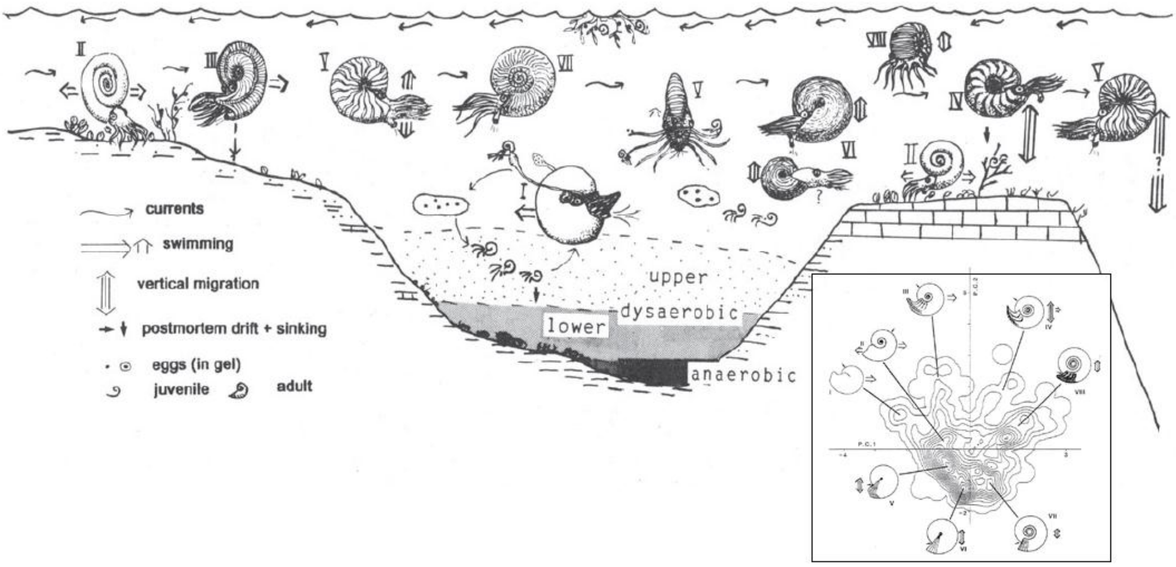


Figure 3.15. Carboniferous (Namurian) scenario of basin and platform environments with the major ammonoid morphotypes I – VIII defined by the graph in the right bottom corner (adapted from Westermann, 1996).

The deep-sea paleoenvironments of Mira and Brejeira formations contain monospecific fossil assemblage (at the order level) of numerous species of order Goniatitida. Generally, in the Paleozoic, more stressed environments (*e.g.*, with high or low salinities; low oxygen; greater depth), are characterised by an assemblage which is low in faunal diversity, but abundant in individuals of a particular species. In these environments, most taxa are excluded, including some other predators, so that the available resources are used by a limited number of successful species. Often, the colonisation of such habitats may be rapid, and the species concerned being opportunists (Doyle and Lowry, 1996). Regarding the Carboniferous goniatites, a high morphological diversity of the structure of their shells, already determine a wide range of habitat adaptations. Goniatitids occupied many ecological niches in the Late Paleozoic seas and, unlike other orders cephalopods (dominated just by few families), their representation in various life forms was reasonably uniform. Through their evolutionary history, goniatitids inhabited the entire water column including sea bottom, and surface water. Morphometrically, they never overlapped the morphospace of other orders (Barskov *et al.*, 2008)**.**

Even though, Paleozoic goniatites were thriving until the end of Carboniferous, the two approaching continents of Lauretania and Gondwana brought the end of the Rheic Ocean, thus the end of the Goniatites paradise in Algarve. This tectonic event closes the first “Chapter” of the ancient marine story of the Algarvensis Geopark (Rodrigues *et al.*, 2015).

3.1.4. Present-day equivalent – Banda Sea (Southern Indonesia)

Finding a present-day equivalent, which would perfectly illustrate the deep-sea environment of the Algarvensis Geopark is difficult from the biological point of view, due to the significant differences between Paleozoic and modern faunas. However, the approximate analogue can be assumed from the geological point of view. We know that at the time of the Carboniferous, the ancient Rheic Ocean was closing, due to the collision of two continents, with the tropical marine waters of the South Portuguese zone between them. Thus, the first clue should be connected with the latitudinal position of the present-day equivalent and the existence of the ophiolite sequence, also associated with the South Portuguese Zone (Beja – Acebuches Ophiolite).

Following definition made by Haldar (2020) ophiolite is “a thrust sheets of ancient oceanic crust and upper part of mantle rocks that have been uplifted and exposed above sea level and often emplaced on top of the continental lithosphere. It occurs close to the oceanic ridges, orogenic belt, documenting the existence of former ocean basins that have now been absorbed by thrusts, subduction zone, and plate tectonics”. Thus, investigating the modern system is fundamental because it provides a key to understanding the ancient deposits (Pirouz *et al.*, 2011)**.**

The geological record of the evolution of ocean basins from the rift-drift and seafloor spreading stages to the initiation of subduction and final closure (the Wilson cycle) is well preserved in most orogenic belts (Dilek and Furnes, 2011). Nevertheless, the algarvian Carboniferous environment could be assimilated to the one found in the Indonesian and New Guinea regions, mainly because of its latitudinal position, and the existence of ophiolite.

The Indonesian and New Guinea region is an active collisional fusion of the complex Asian and Australian continental margins with of the western Pacific. The continent-continent collision has progressed to the stage where the Sunda Shelf of Asia and the Sahul Shelf of Australia are now partially connected by a collage of island arcs and continental fragments separated by trapped and partially obducted ocean basin lithosphere (Harris, 2003). Taking into consideration the cross section showed in the Figure 3.16, we can conclude that Banda Sea acts like a present-day equivalent for the deep basin of the BAFG, together with Timor Sea which corresponds to the shallower cratonic sea of Avalonia (represented by the Quebradas formation). However, a foreland basin has not yet developed in the Banda Orogen (Harris, 2011).

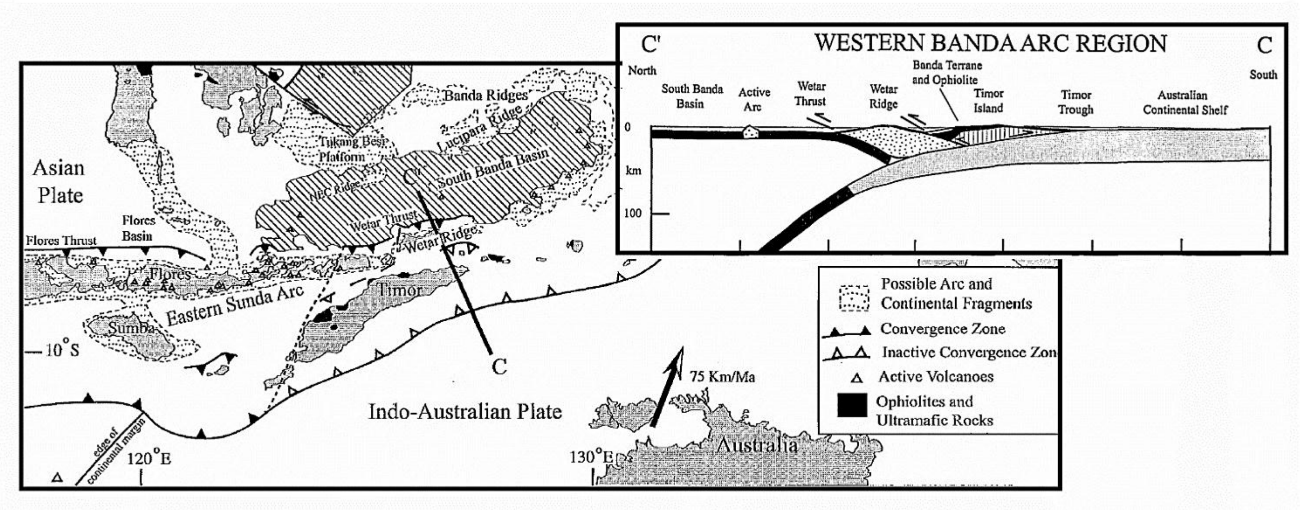


Figure 3.16. Map of the Indo-Australian junction, and the cross section of the Western Banda Arc region (adapted from Harris, 2003).

The Banda Sea is one of several seas located in the Indonesian archipelago between Australia and mainland of Asia. All seas together create the route for the Indonesian “Throughflow” (a crucial gateway for ocean circulation and regulation of global climate) between the Indian and Pacific oceans. The formation of this narrow seaways, and the juxtaposition of different flora and fauna, are the result of the collision of Australia and Southeast Asia, thus the closure of the Tethys Ocean that once separated them (Figure 3.17). It is this place, where an elevated continental plateau lies together with a complex array of oceanic basins, continental fragments, volcanic arcs, and carbonate platforms (Pownall *et al.*, 2018).

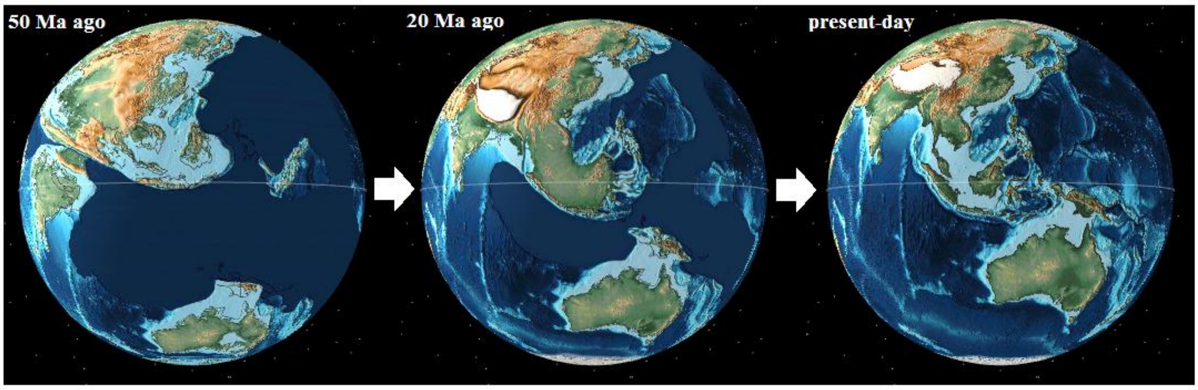


Figure 3.17. Australia–Asia collision, and Tethys Ocean closure (adapted from Scotese, 2021).

Accordingly, the Banda Sea seems to fit quite well as a present-day equivalent to the ancient depths of the Algarvensis Geopark. However, there is here a question remaining – what happened to the island arc of the ancient Rheic Ocean? No magmatic arcs of Middle to Upper Devonian age have been discovered in the paleogeographically adjacent continental crust of Laurussia or Gondwana. However, Korn (1997) found out that, in some parts of Quebradas, tuffitic layers deserves a special interest. This component was interpreted as deriving from an eroded volcanic complex. Pereira *et al.* (2012) suggest that an oceanic arc, which developed in response to intra-oceanic subduction of the Rheic Ocean, was eroded immediately following ocean closure. The Middle and Upper Devonian detrital zircons (minerals, derived from the erosion of pre-existing rocks) of South Portuguese Zone are attributable to a magmatic event, as a consequent subduction of the oceanic crust. It is inferred that the source terrane, with an intra-oceanic magmatic arc, was subsequently eroded, yielding the clastic detritus that was deposited in the Upper Devonian – Upper Carboniferous basins (Oliveira *et al.*, 2019; Pereira *et al.*, 2012).

Moreover, Indo – Pacific is the only hotspot of the living nautiloids. They inhabit the deep slopes and fore-reef habitat within 30° N to 30° S belt, and are also found in Banda Sea (Ambon), were species *Nautilus pompilius* was registered (Saunders *et al.*, 2017). However, the deepest occurrence of *Nautilus pompilius* is assigned for Queensland region (Australia), where they were found at the depth of 703 m, during feeding behaviour in the daytime (Figure 3.18) (Dunstan *et al.*, 2011).

Figure 3.18. Deepest record of Nautilus– 703 meters. Nautilus pompilius recorded feeding during daytime at 703 m on the sea floor (adapted from Dunstan et al., 2011).

These data support the hypothesis that, in contrast to previously observed diurnal migrations, more complex vertical movement patterns may exist in *Nautilus pompilius,* and perhaps in all other *Nautilus* populations (Dunstan *et al.,* 2011). These patterns are very likely dictated by optimal feeding substrate, avoidance of daytime visual predators, requirements for resting periods at 200 m to regain neutral buoyancy, upper temperature limits of around 25 °C and implosion depths at 800 m. The slope, terrain and biological community of the various geographically separated *Nautilus* populations may provide different permutations and combinations of the above factors, resulting in preferred vertical movement strategies most suited for each population (Dunstan *et al.*, 2011).

3.2. Permian – Lower Triassic

At the final stages of a I Wilson cycle, the two continents – Lauretania and Gondwana collided, closing the ancient Ocean and forming one single supercontinent – Pangea, which continued until the Upper Triassic. In that period of compressive tectonics (from the end of the Upper Carboniferous to the Upper Triassic), Variscan mountains were formed, however, continuous elevation of the mountain chain, and the consequent erosion and elimination of the geological record (mostly during Permian period), resulted in a stratigraphic gap in Algarve (Figure 3.19). During this erosive period, of at least 110 Ma (in emerged region of Algarve), no sedimentary and fossil record was found (Lopes, 2006; Weil *et al.*, 2019).

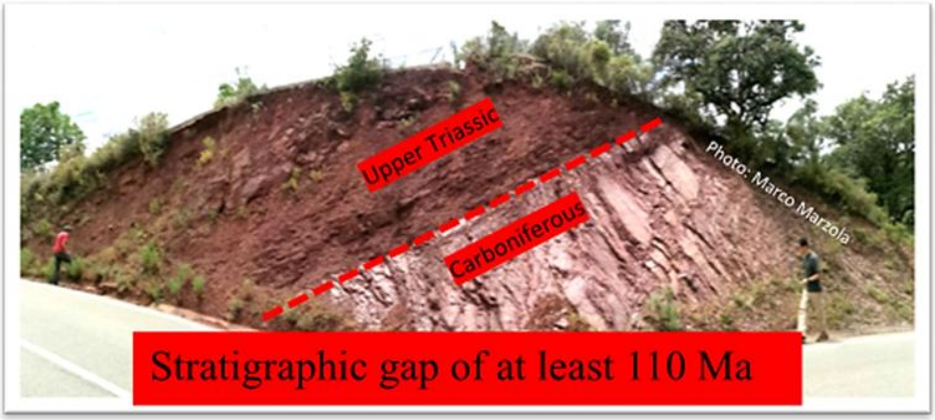


Figure 3.19. Stratigraphic gap between Upper Carboniferous and Upper Triassic formations, as can be observed at Pirineu geosite of the algarvensis geopark.

In parallel, shortly after the closure of the Rheic Ocean, and the assemblage of Pangea supercontinent, at the end of Permian, the "Mother of Extinctions" occurred, devastating most of the life in the oceans, seas and on land. This global life devastation was a series of extinction pulses that contributed to the greatest mass extinction in Earth's history, until today. The Permian-Triassic extinction was characterized by the elimination of over 95 percent of marine and 70 percent of terrestrial species. Over half of all taxonomic families disappeared. This event is the greatest of the five major mass extinctions that span the history of our planet (Ross and Ross, 2021).

Shallow-water marine invertebrates including the trilobites, rugose, and tabulate corals, and two large groups of echinoderms (blastoids and crinoids), suffered the most. A great number of invertebrate families, which were highly successful prior to these extinctions, were affected (Ross and Ross, 2021). Several groups of aquatic vertebrates, such as the earliest jawed and heavy armour fish were eliminated. In addition, sharks, bony fishes, brachiopods, bryozoans, ammonoids, therapsids, reptiles, and amphibians experienced significant decrease by the end of the Permian Period (Ross and Ross, 2021).

The cause of the Permian extinction was probably connected with the Siberian Traps (massive lava flow in eastern Asia). Ages of the lava flows suggest that the traps formed over a one-million-year interval, with the original volume estimated to be between 1 million and 4 million cubic km of lava expelled (Farabee, 2021). This Permian event triggered drastic climate changes followed by extreme global warming, greenhouse gas effects; carbon-dioxide poisoning; ozone layer damage or loss; and complete devastation of the worldwide ecosystems (Levin, 2013).

CHAPTER 4. MESOZOIC – II WILSON CYCLE

The Mesozoic era began with the a "formative" phase in the Earth history. During the Triassic, the Algarve was once again (after Late Paleozoic) in the centre of drastic changes that were finalised late in the Triassic. Further, the Jurassic was a time of the stabilization and rapid faunal evolution. The story of the beginning of the II Wilson Cycle (from the land to the ocean; Figure 4.1) is well represented in the sediments of the Algarve region. The Mesozoic paleoenvironments of the Algarvensis Geopark constitute as the complete sequences of this world reorganization, which continues till today.

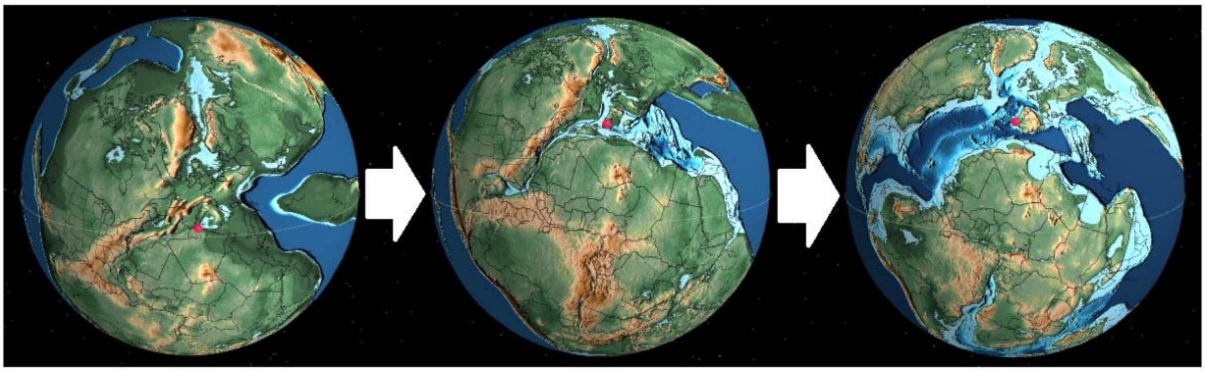


Figure 4.1. Mesozoic (from Triassic until Cretaceous). Schematic plate tectonics movement, of the II Wilson Cycle (from the Land to the Ocean). Algarve region is represented by the red dot (adapted from Scotese, 2021).

4.1. Late Triassic – Hettangian (Jurassic)

The Algarve Basin is a sedimentary basin, oriented in the E-W direction, which in the submerged part is approximately 150 km long and up to 25 km wide. This basin is formed by more than 4000 m thick of Meso-Cenozoic sediments (Terrinha *et al*., 2013). The Triassic and the lowermost Jurassic sediments, of the Algarvensis Geopark (Figure 4.2), are represented by the Grès de Silves Formation (corresponding to the II Wilson Cycle – opening of the new ocean), and is composed of the following units (from the base to the top): Clays of São Bartolomeu de Messines (SBM Clays, "AA unit", ca. Middle – Upper Triassic age); Silves Sandstones (S Sandstones, "AB1 unit" of Carnian age, Upper Triassic); Pelites with evaporites and carbonates intercalations (ECI Pelites, "AB2 unit" of latest Triassic (Norian) and earliest Jurassic (Hettangian)); Vulcano – Sedimentary Complex (VS Complex, "AB3 unit", Hettangian) (after Palain, 1976; 1979; Terrinha *et al.*, 2013; Lopes, 2014; Pereira *et al.*, 2016). For Palain (1976; 1979) the stratigraphic succession is changing from a continental alluvial environment to a marginal coastal environment in a warm climate and with periods of severe drought (Lopes, 2014).

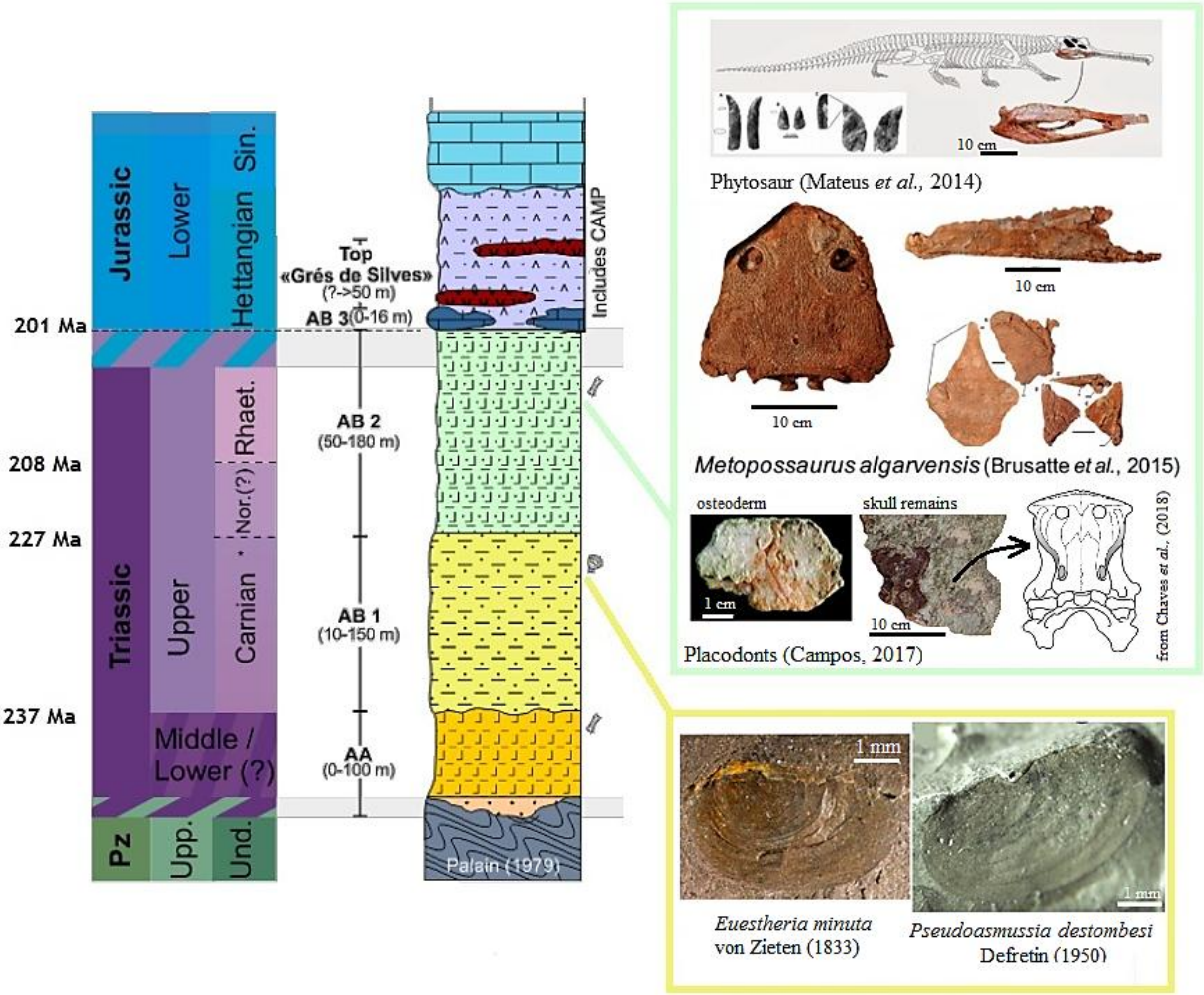


Figure 4.2. Schematic lithostratigraphic column with the Triassic to Lowest Jurassic units found in the Algarvensis Geopark (Algarve Basin) (modified after Palain, 1976 and Lopes, 2014), and their fossil content (see also references in the respective panels).

The SBM Clays (AA) are essentially a red pelite layer with intercalated beds of fine sandstone. The top strata show bioturbation and fragments of bones belonging to the Stegocephalia clade (four-limbed stem-tetrapods, and their amphibian-grade descendants) (Palain, 1976; 1979; Russell and Russell, 1977). However, no detail systematic was applied for this specimen. According to Antunes (2010), this assemblage allows to attribute this unit to the Middle Triassic (Lopes, 2014).

Silves Sandstones (AB1) are mainly red sandstones, interbedded with clay-silty layers. Near the top of the strata bioturbation (ichnofossils) and specimens of the order Diplostraca – *Euestheria minuta* (von Zieten, 1833) and *Pseudoasmussia destombesi* (Defretin, 1950) have been found, which made it possible to date the unit of Carnian, Upper Triassic age (Figure 4.2) (Palain, 1976; 1979). The facies appear to be essentially continental in nature, but slowly tending towards a marginal coastal domain (Palain, 1976; 1979; Lopes, 2014).

The EIC Pelites (AB2) correspond to a unit formed by rhythmic sequences of fine sandstones, siltites, clays, sometimes including evaporites (Palain, 1976; 1979). The top of this sequence is marked by dolomitic levels, the uppermost part of which is already Lower Jurassic in age (Figure 4.2). The unit is interpreted by Palain (1976; 1979) as a set of deposits formed at the edge of a basin subject to variations in column height and water salinity and with continental contributions (water and sediments) (Lopes, 2014). In these sediments, the remains of an unique species have been found, that gives name to the Geopark – *Metoposaurus algarvensis* (Brusatte *et al.*, 2015), which is about 227 million years old, and has only been described so far in this region of the world. In these formations, some unidentified bivalves and ganoid fish scales were also found (Mateus and Campos, 2017), and other fossils of animals from the Triassic period, such as a skull of phytosaurs and remains of placodontes – osteoderms (Brusatte *et al.*, 2015; Campos *et al.*, 2017).

The VS Complex (AB3) is composed mostly of extrusive sequences interspersed with contemporary sediments and with discontinuous levels of dolomites (from the term AB3) (Figure 4.2) (Terrinha *et al.*, 2013). This magmatism probably occurred during the Hettangian - Sinemurian (Verati *et al.*, 2007). The Volcano-sedimentary Complex caused by Central Atlantic Magmatism Province (CAMP), associated with the disruption of Pangea and the opening of the Atlantic Ocean (Font *et al.*, 2015)**.**

4.1.1. Fossil content of the Grés of Silves Group

Table 4.1 depicts systematics paleontology of the species found in the Triassic formations of the Algarvensis Geopark (unidentified faunal assemblage from below a “family” level was not included in the analysis). The geological age of Grés de Silves has been discussed mainly in context of vertebrate’s fossil assemblage, which is perhaps, the most accurate indicator of geological age. The genus *Metoposaurus* is restricted to Carnian and Norian (237 to 208 Ma), with the transition from Carnian and Norian at 227 Ma. Another useful dating occurrence is the reptile Cyamodontoid placodont of genus *Henodus*, which has a chronological distribution restricted to the lower Carnian, 235 to 228.4 Ma. *Henodus* fossils occur in most of Grés de Silves, indicating that most of the deposition of this formation is relatively restricted in time, possibly to Carnian (Mateus and Campos, 2017).

Table 4.1. *Systematic paleontology of the fossil species found in the AB1 unit (Silves Sandstones) and AB2 unit (ECI Pelites) units of the Grés of Silves Group.*

SYSTEMATICS	AB1		AB2		
PHYLUM	ARTHROPODA		CHORDATA		
SUBPHYLUM	CRUSTACEA		VERTEBRATA		
CLASS	BRANCHIOPODA		AMPHIBIA	REPTILIA	
SUPERORDER/ ORDER/ CLADE	DIPLOSTRACA		TEMNOSPONDYLI	DIAPSIDA	PLACODONTIA
SUBORDER/ CLADE	SPINICAUDATA		STEREOSPONDYLI	ARCHOSAURIFORMES	SAUROPTERYGIA
FAMILY	EUESTHERIIDAE		METOPOSAURIDAE	PHYTOSAURIDAE	HENODONTIDAE
GENUS	*Euestheria*	*?Pseudoasmussia*	*Metoposaurus*	*unidentified*	*?Henodus*
SPECIES	*Euestheria minuta*	*Pseudoasmussia (=”Estheria”) destombesi*	*Metoposaurus algarvensis*		unidentified

Due to the fact, that *Metoposaurus* and the *Phytosaurus* fossil from the Grés of Silves Group belong to the terrestrial realm, and are well studied in the recent decade, this subchapter provides only synthetized and basic information on their ecology and distribution. The fossil assemblage of Placodonts give affinities to the fully aquatic lifestyle, but these fossils are still under the study. In addition, unit AB1 reveals less famous story of the small invertebrate, which actually brought a great capacity in global biostratigraphy understanding. Palain (1976; 1979) was the first one to mention euestheriids in the Algarve region, however, no photo-documentation of the fossil assemblage was found. Therefore, the pictures of the conchostracans fossils (Figure 4.2) are adapted from Morton *et al.*, (2017) for *E. minuta*, and from Gallego *et al.*, (2020) for *P. destombesi*. Even though, no detail description of the algarvian specimens was published, this discovery made it possible to assign this unit to the lowermost Upper Triassic age – Carnian (Gallego *et al.*, 2020).

4.1.2. Story of the less famous Conchostracans

Regarding fossil record, conchostracans are present in pre-Permian through modern sediments. However, their potential for biostratigraphy and inter-regional correlation has only been fully developed in Triassic strata (Kozur and Weems, 2010; Ogg, 2012). They have the greatest biostratigraphic resolution power of all Triassic continental aquatic and even terrestrial fossils, and in some intervals this resolution is as high as the one of ammonoids in marine sediments. With the widest distribution of identical species in both low and high latitudes, they pose the lowest level of endemism, and the lowest provincialism to paleolatitudes, of all investigated Triassic continental fossils (Kozur and Weems, 2010). Approximately 30 conchostracans zones and regional variants have been defined for the Triassic (Jenisch *et al.*, 2017). Additionally, their potential for correlation with marine facies is high because they are not only common in fresh water deposits, but they also can be found in brackish deposits or in the deltaic marginal marine beds of very shallow marine deposits (Kozur and Weems, 2010)**.**

The present-day systematics of Diplostraca is based on the anatomy of the soft parts of the animal, not on the carapace, therefore, there are no cross checks between living and fossil organisms. Furthermore, several species were based on only one fossil specimen, although recent studies suggest the comparison between fossil and extant taxa (Martin and Davis, 2001; Astrop and Hegna, 2015). Morphological studies have shown that uniform characteristics used to describe the Diplostraca fossils are (after Jessie and Gallego, 2015): 1) the angle between dorsal and posterior margin; 2) the shape of the shell; 3) the presence or absence and the number of growth lines on the carapace; 4) the position of the umbo, which is placed between the median point and the anterior end of the dorsal margin; 5) the presence of different structures such as spines, nodes and ribs in the umbonal region, the type of structure in the interspaces of growth lines; and 6) the presence or absence and number of radial ornaments (*e.g.,* Raymond, 1946; Tasch, 1969; Chen and Shen, 1985; Jessie and Gallego, 2015). These characteristics are based on the shell parameters (measurements) used in the statistical analysis by paleobiologists (Figure 4.3).

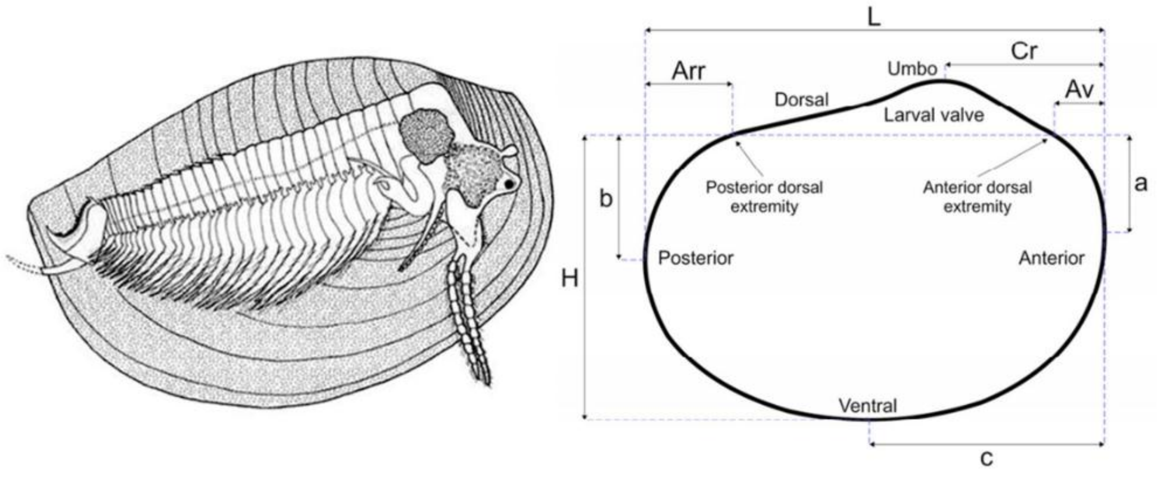


Figure 4.3. From the left: schematic anatomy of the living clam shrimp; and the carapace characteristics used by paleontologists. 'L' is the total length of the specimen; 'H' is height; 'Arr' is the distance between the posterior dorsal extremity and the vertical. 'Av' is the distance between the anterior dorsal extremity and the vertical extension of the anterior-most point of the carapace; 'Cr' is the distance between the highest point of the umbo and the vertical extension of the anterior-most point of the carapace; 'a' is the distance between the anterior-most point of the carapace and the horizontal extension of the anterior dorsal extremity. 'b' is the distance between the posterior-most point of the carapace and the horizontal extension of the posterior dorsal extremity. 'c' is the distance between the lowest point on the ventral margin and the vertical extension of the anterior-most point on the carapace (adapted from Jessie and Gallego, 2015; Morton et al., 2017).

The Diplostraca order contains the Spinicaudata suborder (Figure 4.4), to which all Triassic conchostracans belong. Their shells have spines, which may be present along the dorsal and posterodorsal margins, while the spaces between the growth lines are smooth (Kozur and Weems, 2010; Cáceres and Rogers, 2015). However, spinicaudatans fossils are difficult to classify, and the establishment of their hierarchical diagnostic characters bring doubts in diagnosis, due to the morphological similarities of their carapaces (Olempska, 2004). Furthermore, generic assignment of many of the specimens is not yet clear. Among all described fossil species, many are synonyms, established as new, while being already described by different authors, from other regions. In addition to these considerable issues, many of them were established on poorly preserved material that was neither well described nor well documented and needs to be revised by resampling from the same localities (Kozur and Weems, 2010).

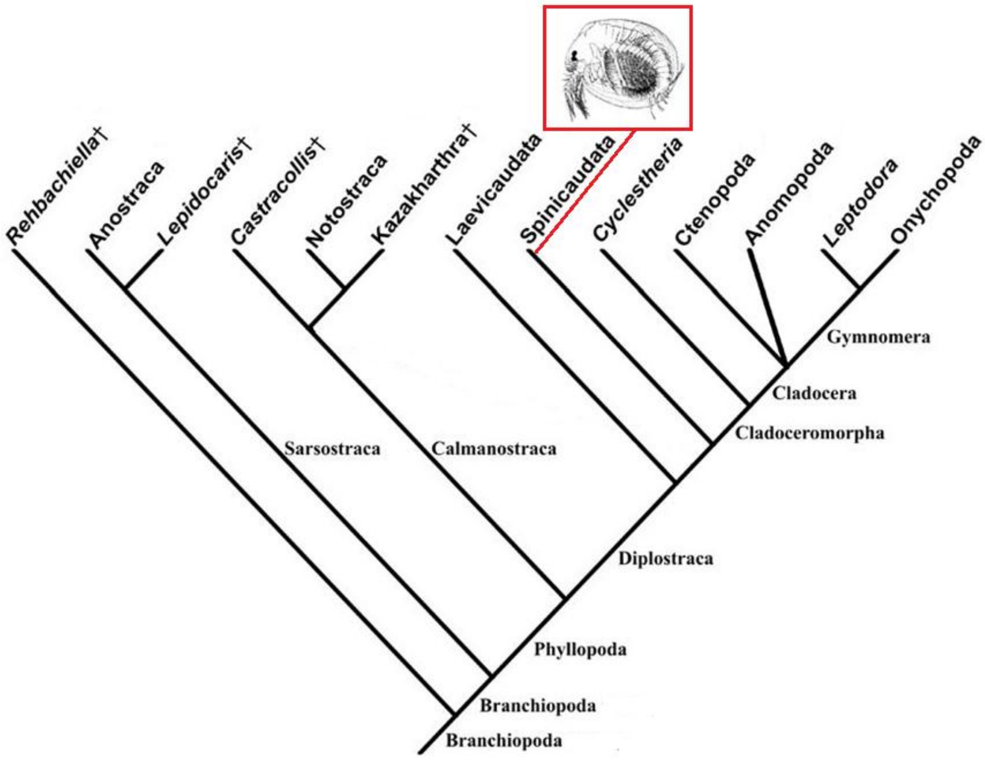


Figure 4.4. Phylogeny of Branchiopoda based on morphological information pointing out the position of Spinicaudata suborder (adapted from Olesen, 2007).

Euestheriidae is an extinct and extremely diverse family, containing the majority of taxa from the Eosetherioidea superfamily (Figure 4.5). The euestheriids are small in size (in comparison to other families), with the larval carapace positioned anteriorly, often rised above the dorsal margin (but is by no means a guaranteed feature). Larval carapaces are typically small, with regular, tightly spaced growth bands. A broad, telliniform carapace (Figure 4.5) is typical for this group never registered in living taxa. Division and the exact relationship between Euestheriidae taxon remains is still unclear, and more detail studies are in need (Astrop and Hegna, 2015)**.** This family contains two genera that are known from the Upper Triassic strata found in the Algarvensis Geopark: *Euestheria* and *Pseudoasmussia* as described by Palain (1976, 1979).

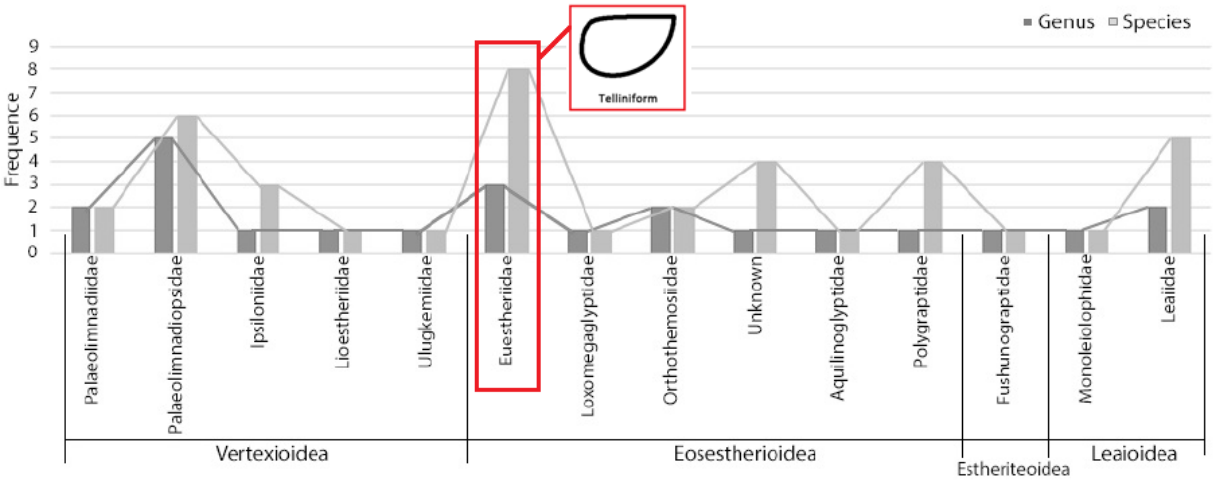


Figure 4.5. Histogram of Diplostraca genera and species corresponding to families housed in Lille University (adapted from Jessie and Gallego, 2015; Astrop and Hegna, 2015).

The original designation of the *Pseudoasmussia* “*Estheria*” *destombesi* was made by Defretin (1950) and further Cuvelier *et al.*, (2015) agreed with previous arguments implying an absence of any ornamentation, which consequently prevented the assignment to any other known genera. However, the name “*Estheria*” cannot be used as a genus of diplostracans because it is already preoccupied by the insect (parasite flies). *P. destombesi* was recorded in AB1 unit of the Grés of Silves (Algarve, Portugal), Argana-Bigoudine area (western High-Atlas, Morocco), Saint-Menge, Mine (Vosges, France) and in Borehole of Lacoste (Gard, France) (Cuvelier *et al.*, 2015; Gallego *et al.*, 2020)

Euestheria minuta was first described by von Zieten, (1833), who assigned specimen to a posidoniform bivalve species “*Posidonia minuta”,* due to its carapace similarities. In 1946, Raymond made a correction on the systematic by attaching specimens to Branchiopoda. *Euestheria minuta* displays large variations in morphology and outline, probably related to geographic and stratigraphic varieties. Due to its restricted stratigraphic distribution (Middle to Upper Triassic) and cosmopolitanism, this species is an interesting paleontological tool (Cuvelier *et al.*, 2015)**.** *Euestheria minuta* zone is the youngest Triassic conchostracan zone that occurs not only in the entire northern hemisphere, (Middle to Upper Triassic) from Europe (South Portugal, France, Germany), China, United States, Canada and Greenland, but also in the southern hemisphere of Gondwana (North and South Africa, Argentina Brazil and Australia) (Kozur and Weems, 2010; Jenisch *et al.*, 2017; Gallego *et al.*, 2020). Moreover, *Euestheria minuta* was documented in the same localities in France, and Northern Africa as *Pseudoasmussia* “*Estheria*” *destombesi.*

4.1.3. Story of the famous Triassic Tetrapods

In the Upper Triassic, among the most prominent groups of tetrapods, the Metoposauridae, a clade of temnospondyl amphibians, and the Phytosauridae, “crocodile-like” diapsids occurred, and were globally distributed in low paleolatitudes during the Upper Triassic, filling crocodile-like predatory niches in lacustrine and fluvial environments (Brusatte *et al.*, 2015). Moreover, numerous groups of reptiles invaded the fully aquatic realm, colonizing many marine environments. Like the Cenozoic marine mammals, they exemplify convergent evolution, gaining morphological, physiological and ecological characteristics adapted to fully aquatic life mode (Bardet *et al.*, 2014)**.** Soon after the end-Permian extinction, the Sauropterygia group developed from terrestrial ancestors, with their unique body structure, which enabled them to move their tail vertically like modern cetaceans (Sennikov, 2019). Among them, the sauropterygians (including the famous Plesiosauria and Nothosauria) appeared and more important – the Placodontia, which filled the shallow marine and brackish waters of the Tethys (Bardet *et al.*, 2014)**.**

4.1.3.1. THE PLACODONT

The placodontes are extinct aquatic reptiles, belonging to the Sauropterygia group, that lived during the Triassic. This short-necked animals with robust skulls generally bearing a characteristic low crushing dentition, traditionally regarded as durophagous bottom dwellers (Bardet *et al.*, 2014)**.** Placodontia is composed by two clades, corresponding to unarmored placodonts (Placodontoidea), and placodonts with carapace (Cyamodontoidea) (Chaves *et al.*, 2018a), which was made up of bone plates called osteoderms. This bony part gave them a similar appearance to turtles but with which they are not related, although it is a curious case of convergent evolution. Unlike turtles, the osteoderms of the placodontes are much more numerous, in the order of hundreds, small size, in multiple rows (only three in turtles), not being fused to the ribs (Mateus and Campos, 2017). Both placodontoids and cyamodontoids were well adapted to walk on the shallow seafloor thanks to their peculiar morphologies, coupled to a pachyostotic skeleton, which increased their body weight and procured them a thick skeleton used as ballast (Bardet *et al.*, 2014)**.**

The paleoecology of placodonts shows they were mainly linked to coastal environments of the Tethys Ocean margins (Bardet *et al.*, 2014). Most of the placodonts lived in the sea, in shallow-waters, feeding on molluscs that crushed with their large flat teeth (Mateus and Campos, 2017). The only (so far) described exception to this lifestyle is the small cyamodontoid *Henodus* (Huene, 1936) (Figure 4.6), which is recognized as a monospecific genus, found in deposits (Upper Triassic of Tethyan affinity) of Germany (Huene 1936), and Spain (Chaves *et al.*, 2018a; 2018b). Poorly preserved skull remains and many hexagonal, flat, elongated, and unadorned osteoderms (Figure 4.2), collected from the Algarvensis Geopark territory indicate affiliation to the cyamodontoid *Henodus*. This taxon, so far, is the only placodont which lived in brackish water, instead of living in the sea, and which fed by filtering (Mateus and Campos, 2017).

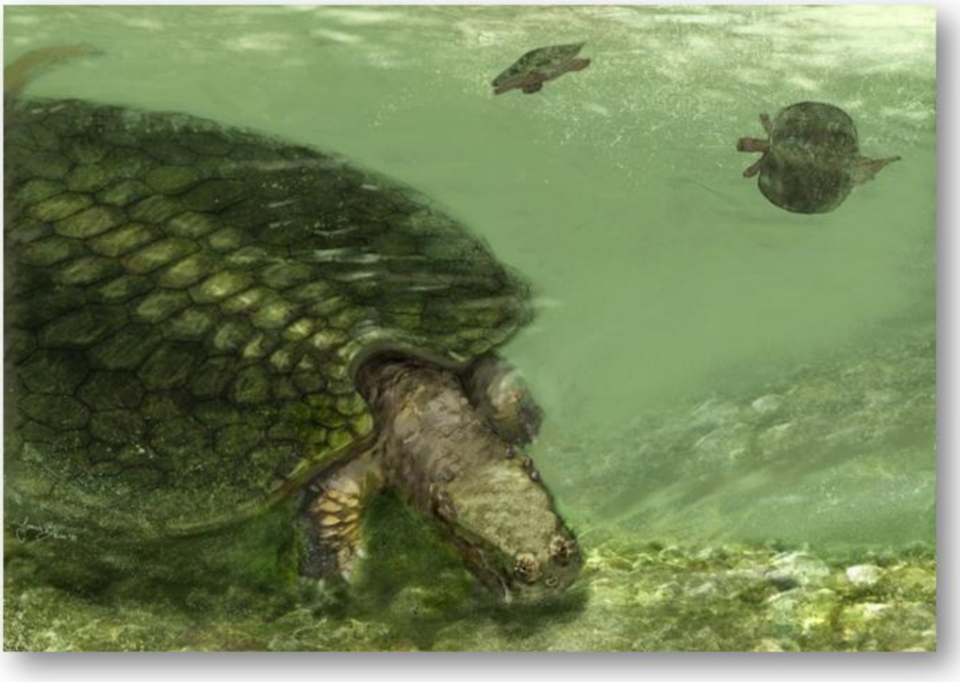


Figure 4.6. Reconstruction of the Henodus species found in the Algarvensis Geopark (adapted from Mateus and Campos, 2017).

This genus is represented by the species *Henodus chelyops* (Huene 1936), which is recognized as being highly autapomorphic. Some distinct characters of this taxon point different feeding adaptations from those of the other known placodontes. This genus is considered a brackish water and lagoon inhabitant, of herbivorous habits (Chaves *et al.*, 2018b)**.** These forms were possibly equipped with jaw adapted to feed on small organisms found in the water and muddy substrate, just like flamingos do today (Mateus and Campos, 2017). This interpretation is based on almost total absence of teeth in *H. chelyops***.** Thus, the feeding strategy of *H. chelyops* apparently diverged from those adopted by the exclusively durophagous placodonts, probably being one of the earliest herbivorous marine reptiles known so far (Li *et al.*, 2016; Chaves *et al.*, 2018a)**.**

Through all sauropterygians, the placodonts gained special attention among paleontologists, because they were typical inhabitants of coastal habitats of the Tethys Ocean, especially its western part where they mostly inhabited Europe, North Africa, and Middle East. It is common to assume that the combination of both biological characteristics (they were pachyostotic durophagous bottom-dwellers) and favourable paleoenvironmental conditions (warm and shallow marine regions) could explain why their geographical distribution was limited and remained restricted to the Tethys Ocean shores, from China to Europe (Bardet *et al.*, 2014)**.**

4.1.3.2. THE METOPOSAURUS ALGARVENSIS

Metoposaurids are some of the most common and characteristic vertebrates from the Triassic Pangea (Brusatte *et al.*, 2015). These amphibians of the stereospondyls group are extinct predators with an appearance similar to that of a salamander , but with lengths that could reach more than two meters. They had a similar lifestyle to crocodiles and were common in aquatic environments (Brusatte *et al.*, 2015; Mateus and Campos, 2017). Their occurrence is limited to the Upper Triassic and they are distributed worldwide. The morphological description of the fossil organisms and the link with the geological setting are the most common methods used in paleontology to gain information about their mode of life and living environment (Teschner and Konietzko-Meier, 2018). Their distinctly ornamented skulls, spool-shaped vertebrae, and atrophied limb elements are found at numerous sites in Africa, Europe, India, and North America (Brusatte *et al.*, 2015).

The fossils found in the Algarvensis territory are clearly of the genus *Metoposaurus* (Figure 4.7), but distinct from those known in Poland, Morocco, France and Germany, which enabled the establishment of the new species in 2015. It received the name *Metoposaurus algarvensis*, found only in the municipality of Loulé and named after the Algarve (Brusatte *et al.*, 2015; Mateus and Campos, 2017). This flat skull species lived in bodies of water like ponds and lakes, which were often severely affected by long periods of drought that gradually reduced them, confining the *Metoposaurus* that concentrated in last water bodies where they were dying in groups. This resulted in a large and exceptional concentration of bones, with more than ten individuals found in Penina. This Portuguese bonebed appears to be monodospecific at this time, but future investigation may reveal a more diverse assemblage (Brusatte *et al.*, 2015)**.**

Being amphibians, the *Metoposaurus* were highly dependent on aquatic environments and perhaps they would not have a musculature properly prepared to wander and look for survival alternatives during the drought seasons, which is the evidence that metoposaurids often congregated in groups in freshwater systems and regularly succumbed to mass death events. This apparently occurred across their entire geographic range, given the widespread distribution of bonebeds (Mateus *et al*., 2014; Mateus and Campos, 2017).

Figure 4.7. Reconstruction of the Metoposaurus algarvensis found in the Algarvensis Geopark (adapted from Mateus and Campos, 2017).

4.1.3.3. THE PHYTOSAUR

The phytosaurus are non-archosaur archosauriforms found in Middle – Upper Triassic rocks, that are part of the great post-Permian archosauromorph radiation (Mateus *et al*., 2014). These semi-aquatic reptiles were the largest predators of the Triassic, and possibly fed on animals such as *Metoposaurus algarvensis*. With long-snouted skulls, rostrums, and armoured body, the phytosaurs were physically very similar to crocodiles and would have similar lifestyles (Mateus and Campos, 2017). However, phytosaurus are not related to crocodiles These carnivorous reptiles show remarkable convergence with unrelated extant crocodilians. This convergence and the postcranial characteristics has been helpful in understanding their ecology and potential lifestyle; some species of phytosaurs may have had a semi-aquatic lifestyle, while others may have had a more terrestrial lifestyle (Grimes and McLain, 2019).

The taxonomy and phylogeny of non-archosaur archosauriform reptiles of phytosaurs affinities, found in Middle – Upper Triassic rocks, have proven to be contentious and confusing. All current phylogenies are based on cranial characters, thus, descriptions of phytosaur postcranial materials have become increasingly needed. In addition, describing the morphology of postcranial parts may also be useful in understanding the ecological roles of phytosaurs. As it was noted in the past, particular morphologies (such as a strongly curved femur) seem to be more accurate for an aquatic lifestyle, while others (a nearly straight shaft), would more likely fit to a terrestrial lifestyle (Grimes and McLain, 2019).

The phytosaurus (Figure 4.8) lived only during the Triassic, in several regions of the globe, but in the Iberian Peninsula the only known phytosaurus fossil is a jaw and a set of teeth found in the municipality of Loulé, that was discovered 2.7 m above and about 5 m lateral to the bonebed of the temnospondyl *Metoposaurus* in the same stratigraphic section as Central Atlantic Magmatic Province (CAMP) basalts of northern Pangean rift sequence (Mateus *et al.*, 2014). Nevertheless, due to the lack of the most useful element of the phytosaurus jaw, the detail identification on the species level is impossible, being however probably close to *Nicrosaurus* (Mateus and Campos, 2017).

Figure 4.8. Reconstruction of the Phytosaurus found in the Algarvensis Geopark (adapted from Mateus and Campos, 2017).

4.1.4. The Pangean riftogenesis

At the beginning of the Mesozoic era, most of the continents were concentrated in the C-shaped supercontinent known as Pangea (Figure 4.1). Climate was generally very dry across the continent with very hot summers and cold winters in the interior. A highly seasonal monsoon climate appeared nearer to the coastal regions. Although the climate was more moderate further from the equator, it was generally warmer than today with no polar ice caps. Late in the Triassic, seafloor spreading in the Tethys Sea led to the separation of the northern and southern parts of the supercontinent, with the beginning of the rifting phase of Pangea into Laurasia and Gondwana (Figure 4.1) (Bagley, 2014).

The Triassic was first defined based on the characteristic terrestrial deposits sequences that crop out across much of Europe, in which many of the first Triassic tetrapod vertebrates were discovered. These discoveries helped to paint a general picture of the Triassic as a formative phase, of the critical transitional interval in Earth's history during which life recovered and stabilized from a devastating end-Permian extinction (Mateus *et al*., 2014). Although faunas were clearly "modernizing", some archaic groups remained diverse and abundant, and some underwent their final bursts of evolutionary radiation before being ravaged by another mass extinction at the end of the Triassic**.** During much of the Triassic, the Pangea supercontinent fossil record was dominated by widespread tetrapod and conchostracans association, which brought significant contribution for the global stratigraphic correlation (Ogg, 2012).

The Algarve Basin was a deformed, extensional basin in the south of Portugal, at the edge of the triple junction, were three tectonic plates (Iberian, African and North American) started to drift from each other (Figure 4.9). This basin experienced significant paleoenvironmental, and faunal changes during the latest Triassic and earliest Jurassic (Hettangian). At this time the Earth started again changing its "face" by the initiation phase of the next Wilson Cycle, which last till today. The Upper Triassic / Lower Jurassic fossil record of stereospondyls in the territory of the Algarvensis Geopark may mark some of the latest surviving members of the tetrapod groups in Europe, represented primarily by fragmentary materials found in isolated locations. Even though, the geological and chronologic framework of the Algarve Basin is still not completely understood, its fossil assemblage corresponds as a critical record of this time, which yield beginning of another marine chapter of the Algarvensis Geopark (Kasprak *et al.*, 2010).

Occurrence of the *Metoposaurus* fossils in the Upper Triassic deposits of Portugal is an evidence that these large amphibians were widespread at low latitudes in the Late Triassic. All known *Metoposaurus* fossils have been discovered within a narrow belt between approximately 30° N and 30° S (modern tropical zone). This paleogeographic distributional pattern has long been recognized and continues to hold with the discovery of new metoposaurid specimens in Europe and elsewhere (Brusatte *et al.,* 2015)**.** The metoposaurid fossil localities in eastern North America, Morocco, the Iberian Peninsula, and Central Europe are positioned in or near rift basins that were precursors to the later break-up of Pangaea. Metoposaurids may have favoured interconnected stream or lake environments that were situated in the rift valleys, but their tolerance for marine conditions remains unclear (Witzmann and Gassner, 2008)**.** The distribution of metoposaurids is similar (not identical) to the distribution of phytosaurs during the Late Triassic (Figure 4.10) (Brusatte *et al.*, 2015)**.**

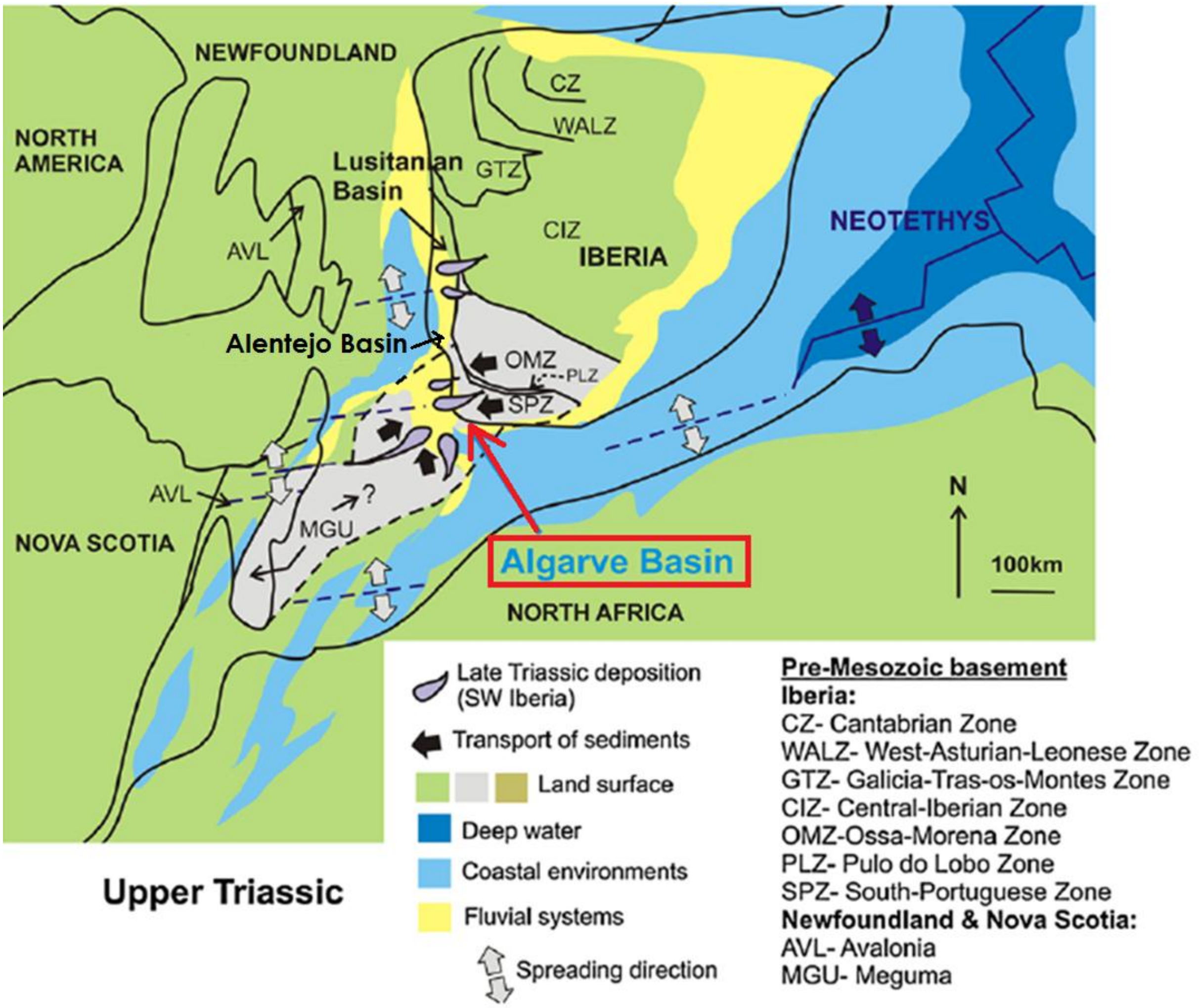


Figure 4.9. Paleogeographic reconstruction of the Upper Triassic continental rifting in southwest Iberia (adapted from Pereira et al., 2016).

Phytosaurs are also commonly found in the belt between 30° N and 30° S, and were once thought to be restricted to these zones, however, their fossil discoveries extend into latitudes as high as 45°–50° N. It is possible that also metoposaurids extended into these regions, but no fossil record has yet been discovered. The low latitudes are represented by the richly sampled Pangean rift sections in Africa, Europe, and North America (Mateus *et al*., 2014). Both phytosaurs and metoposaurids were notably rare in the southern hemisphere during the Triassic. Brusatte *et al.*, (2012) hypothesized, that the low number of occurrences in these regions may have been caused by local climatic conditions in southwestern Pangea, which is thought to have been more arid than the monsoonal environments in low-to-mid latitudes during the Late Triassic. If correct, this hypothesis may indicate that climate was a major driver of the paleoenvironmental distributions of many vertebrate groups during the Upper Triassic (Mateus *et al.*, 2014). The case of the placodonts fossils remains still open and a detail research is required to conclude on its paleontological systematics. However, if the specimens found in the Algarvensis Geopark are of *Henodontidae* family, we can assume that its occurrence is very likely connected with the Tethyan subsidence in the Algarve Basin.

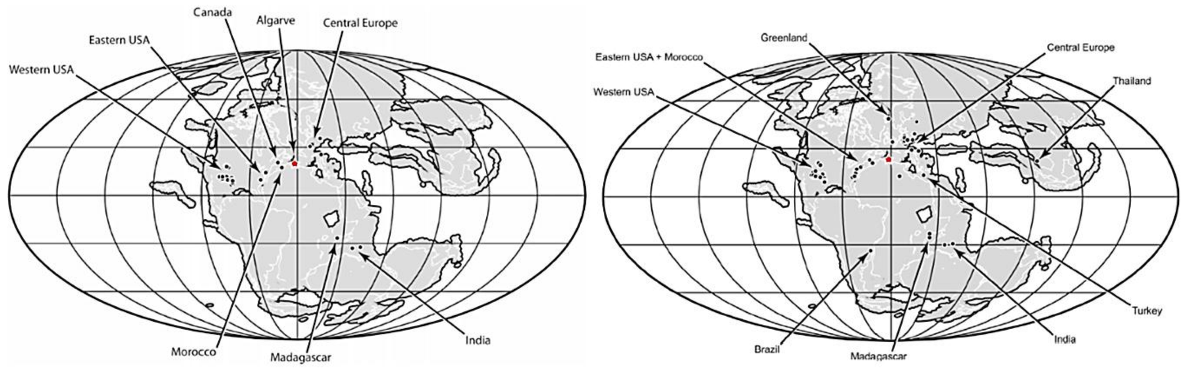


Figure 4.10: Global distribution of the Metoposaurus (left)and Phytosaurus (right) fossil localities. Algarve region marked by the red dot (adapted from Brusatte et al., 2012; 2015).

The Upper Triassic terrigenous sequence of the Grès of Silves Group was deposited in continental rift basins under semi-arid, equatorial climate. The environments were characterized by alluvial fans separated by alluvial plains with temporary ponds and meanderform rivers (Figure 4.11A), with evaporites near the coastal areas (Pereira *et al.*, 2016). The terrestrial successions of tetrapods (giant amphibians and reptiles), and lacustrine conchostracans, together with flora (spores/pollen, macroflora), are broadly inter-correlated in different regions of Pangea. The evolution of terrestrial ecosystems to marine-based Triassic stages and substages is fairly well established across the globe (Ogg, 2012). The sediments from the Upper Triassic of Algarve rift basin evolved, from continental, essentially fluvial, to shallow marine coastal lagoon environments in the earliest Hettangian (Figure 4.11B). These include evaporites mentioned before and the Volcano-sedimentary Complex of CAMP, whose temporal boundaries are difficult to date (Lopes, 2006; Pereira *et al.*, 2016).

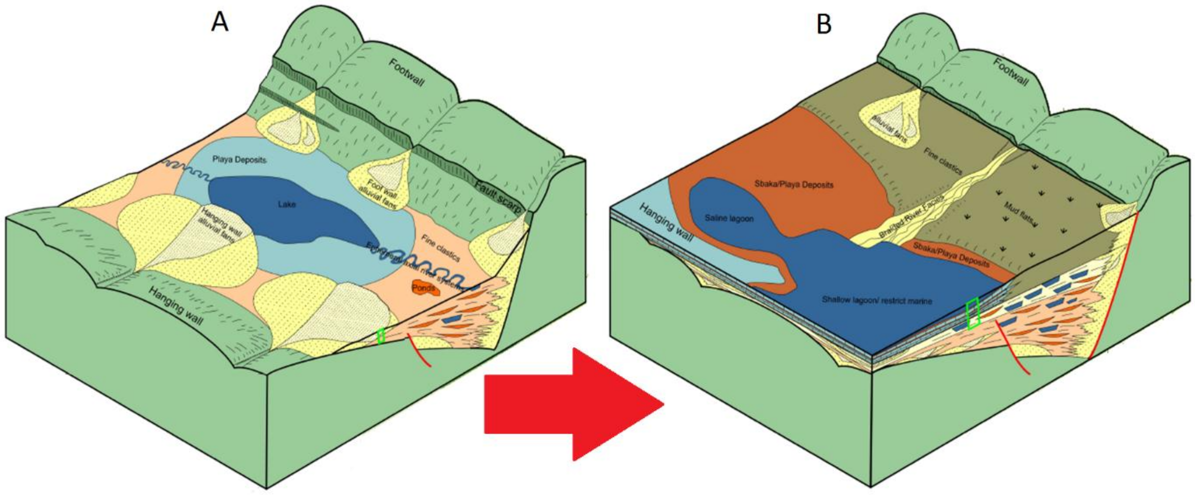


Figure 4.11. Transformation of the Algarve Basin. (A) alluvial fans separated by alluvial plains with temporary ponds and meander-form rivers of the Late Triassic; (B) shallow marine coastal lagoon of the Hettangian age (adapted from Barreto, 2018).

The Central Atlantic Magmatic Province (CAMP; Figure 4.12) is one of the Mesozoic continental Large Igneous Provinces associated with the disruption of Pangea and the opening of the Atlantic Ocean. The CAMP relates to one of the major mass extinctions of the Phanerozoic that occurred at around 200 Ma ago in the Triassic/Jurassic transition. The synchronism between this volcanism and the end-Triassic Extinction has been established indirectly, by comparing geological data from circum-Atlantic CAMP lavas flows, as well as from underlying Triassic red beds. Paleomagnetic data of the CAMP is well documented in North America, Morocco and South America but are still scarce in Iberia (Font *et al.*, 2015).

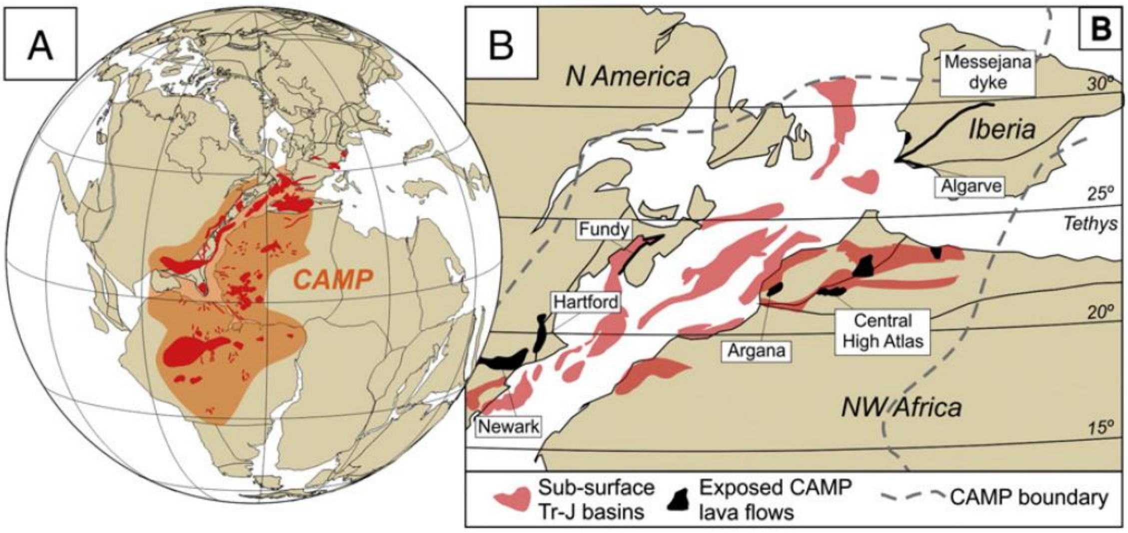


Figure 4.12. (A) Map of Pangea at Triassic showing the distribution of the Central Atlantic Magmatic Province. (B) Onset showing the distribution of sub-surface Triassic–Jurassic basin and exposed CAMP lavas in North America, Northwest Africa, and Iberia (adapted from Font et al., 2015).

The Volcano-sedimentary Complex corresponds to the first phase of riftogenesis in the Mesozoic, which led to the opening of the Atlantic Ocean. The rifting in Portugal was complex with the development of a broad rift zone including several subbasins within three main basins (Figure 4.9), with highly variable geometries and different environmental conditions. The materials that compose the Complex were originated in a continental magmatism along the system of faults developed as a result of this riftogenic process (Frizon De Lamotte *et al.*, 2015). However, the presence of intercalated clay beds suggests volcanic interruptions in the midst of aquatic environment. In addition, these volcanic materials are sometimes cemented with calcium carbonate. This presence could be associated with interruptions of volcanic activity under shallow marine waters (Lopes, 2006; Pereira *et al.,* 2016). From a stratigraphic point of view, this event is coeval with important paleoenvironmental changes in the Algarve Basin. It occurs always between the sabkha-like continental to peritidal deposits. Renewed subsidence followed the volcanism and carbonate platform conditions were established, which would last until the end of the Jurassic. This phase marked Algarve region as an ecotone type environment, which, according to Kark (2013), it is an area of a steep transition between ecological communities, and/or ecological regions along an environmental gradient. The end of the supercontinent, gave rise to the widespread shallow tropical seas within tropical regions across fragmentating Pangea, were the fully marine fauna, of Tethyan affinities, thrived from the Early Jurassic until the Early Cretaceous period. The first sediments to be deposited on this marine platform were the Sinemurian dolomites (Pena Dos Reis and Pimentel, 2014).

4.1.5. Present-day equivalent – the Afar Triangle (Eastern Africa)

The latest Triassic is another paleoenvironment with the present-day equivalent mainly based on the geology. In the northeastern part of Ethiopia, at the junction of the Red Sea and the Gulf of Aden, lies a region known as the Afar triangle (Figure 4.13). It is a wild and generally hostile region, featured by below sea level deserts, towering escarpments, active volcanoes and craters (Tazieff, 1970). In the Afar, the African, Arabian, and Indian plates are characterized as the triple junction (Figure 4.13), like the one existing in Algarve in the Late Triassic. The Red Sea itself has opened around 30 Ma years ago and is still widening (Figure 4.14). At first, the Arabian plate moves away from the African Plate. This divergent boundary continues east along the floor of the Gulf of Aden, and ultimately extends into the Carlsberg Ridge and the mid-Indian Ocean ridge. The African Plate is breaking apart along the well-known East African Rifts, separating the Somalian Plate from the main continental block (often known as the Nubian Plate in the north) (Migoń, 2010). The triangle seems to be a focal point for new oceans in the making. What is more, whereas elsewhere the process that is producing continental separation is hidden in the depths of the ocean, here we can see it taking place in direct view on dry land (Tazieff, 1970).

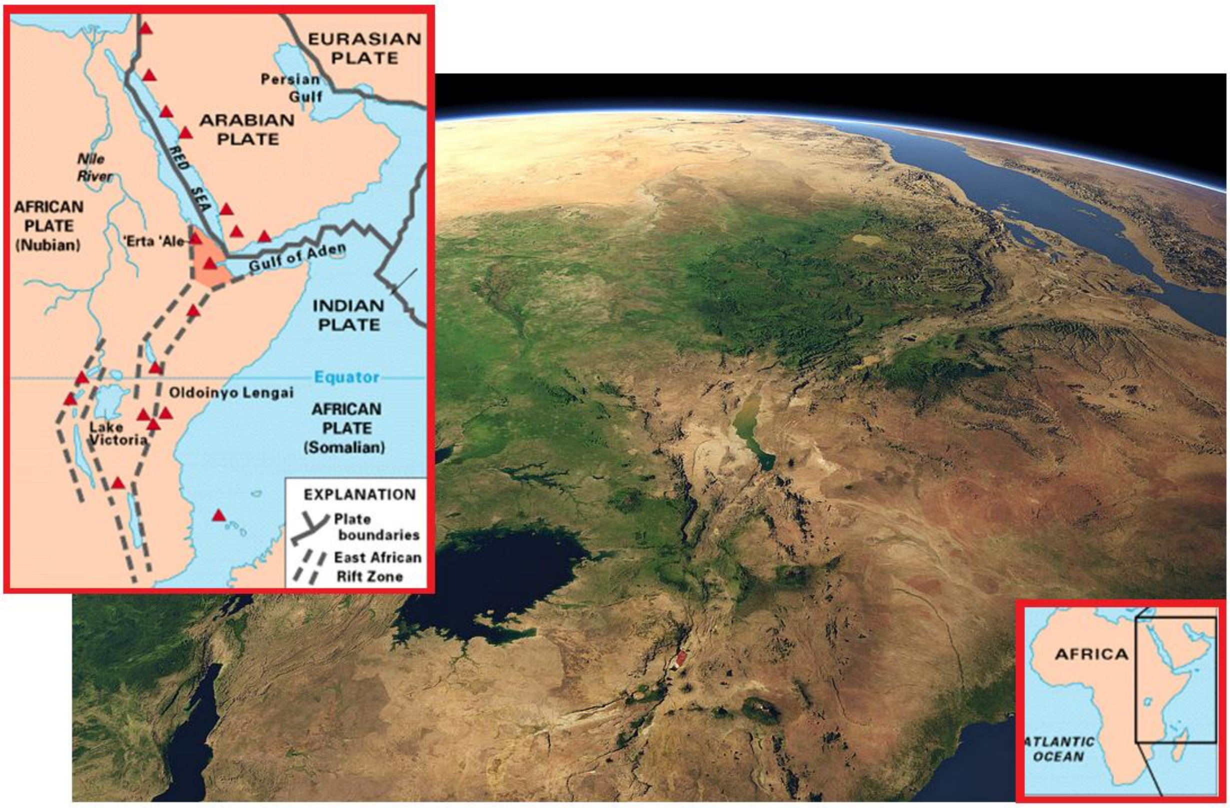


Figure 4.13. Map of East Africa showing the Afar Triangle (shaded, center), so-called triple junction, where three plates are pulling away from one another: the Arabian Plate, and the two parts of the African Plate (the Nubian and the Somalian) splitting along the East African Rift Zone. Some of the historically active volcanoes are presented in red triangles (adapted from USGS, 2021, and Migoń, 2010).

The Triangle is the one place where the coastlines and plateau margins cannot fit perfectly into their preexisting configuration because the major constructive process of basaltic flows have been a little excessive and has created a new lowland that is the Afar. The entire Assal-Ghoubbet rift is similar to the Algarve Rift Basin, covered mostly by lacustrine limestones being overload by recent-aged basalts which would correspond to the CAMP (Migoń, 2010; Iltireh *et al.*, 2018). There is a valid concept that the East African Rift marks the line of a super-plume rising within the mantle beneath the continental slab, and a hot-spot along this mega-feature has created the enhanced volcanic activity that built the Afar (Migoń, 2010).

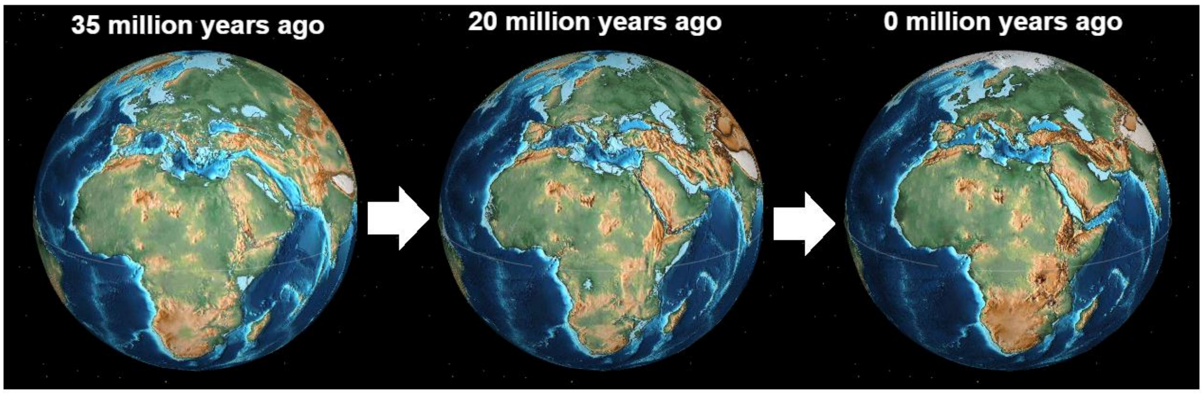


Figure 4.14. Riftogenesis of the African and Arabian plate, and the Red Sea opening (adapted from Scotese, 2021).

The most active area of the Triangle lay in Djibouti. This region has a hot desert climate with two main seasons: October to April is the cool season with high humidity and rainfall on the coast; May to September is the hot season with tropical rain inland. In May, June, September, and October the variable north-easterly winds blow, and in the summer, very violent, dry, hot and dusty winds will blow from the west. There is no permanent river in Djibouti, and surface flow is directly related to rainfall, which is extremely variable, and takes the form of floods lasting anywhere from several hours to two to three days (Ott *et al.*, 2008).

Deepest point in the whole Afar region contains Lake Assal and the marine bay of Ghoubbet (Djibouti). This massive, curved rift valley covering a surface area of 115 km^2, surrounded by mountains, with cliffs rising 600 m along its southern fault boundary. The lake is separated from the Gulf of Tadjourah by approximately 10 km of land and the semi-enclosed basin of Ghoubbet al Kharâb, on the south-eastern side of the lake (Ott *et al.,* 2008). Between Lake Assal and the bay of Ghoubbet Kharâb, the Assal-Ghoubbet Rift fault appears, which permits percolation of seawater into the lake. The sea in Ghoubbet is over 200 m deep, and the surface of Lake Assal fluctuates around 155 m below sea level. Lake Assal lies over sediments up to 200 m deep, has thick beds of upper Holocene gypsum exposed around its shores, and is depositing salt on its marginal flats, as its main recharge is by seawater infiltration through the porous basalts (Migoń, 2010; Waltham, 2009).

Lake Assal can be considered as reflecting the last phase of the terrestrial environment recorded in the uppermost Triassic sequences exposed in the territory of the Algarvensis geopark and reflecting the Iberian riftogenesis. Multiple bonebeds of *Metoposaurus algarvensis* correspond to the mass deaths of this tetrapods, which concentrated in the places where the last fresh water bodies in Algarvensis territory were found. This fresh water ponds, fully disappeared shortly after, together with the giant amphibians, reptiles and conchostracans. It is very likely that in the future Afar region will experience the marine water subsidence and spreading mid-ocean ridge will create a new ocean.

4.2. Jurassic – Berriasian (Cretaceous)

Jurassic climates can be reconstructed from the analyses of fossil and sediment distribution and from geochemical analyses. Fossil organisms of warm-adapted organisms are found up to 60° N and 60° S paleolatitude, suggesting an expanded tropical zone. The fossil record of higher paleolatitudes indicates that in this time slab there was a less abrupt temperature difference between the Equator and the poles than today. Despite this decreased temperature gradient, there was a marked difference in marine invertebrates from northern higher latitudes—the Boreal Realm—and the tropical Tethyan Realm (Tang, 2021).

"Tethyan" referred to the warm water/tropical biota of the Tethys Ocean that separated Eurasia from Gondwana. Recent research on biota and paleomagnetism has shown that the Tethyan subrealms differed not only in longitude, but also greatly in latitude (Westermann, 2000). The West Tethyan subrealm, was located in the Equatorial Belt. Studies on the Upper Jurassic ammonites has demonstrated that typically "West Tethyan" faunas ranged from the east-central Pacific (Panthalassa) along southern Laurasia and northern Africa all the way to Japan and East Russia. Similar affinities along southern Eurasia probably existed throughout the Mesozoic for marine bivalves (*e.g.*, Liu *et al.*, 1998). The West Tethyan (also called Mediterranean and Sub-Mediterranean) contains significant fossil record bearing witness to the ecotone (transitional boundary) for mainly ammonoids of the Boreal and Tethyan Realms (Westermann, 2000). It is assumed that, at every taxonomic level, the Tethyan faunas are more diverse than the Boreal, which is well documented, for example, among cosmopolitan Lower Jurassic ammonite genera. This difference in faunal diversity allows a distinction between the two realms throughout the entire Jurassic (Hallam, 1969).

It has been suggested that increased volcanic and seafloor-spreading activity during the Lower Jurassic released large amounts of carbon dioxide (a greenhouse gas) and led to higher global temperatures. Warm temperatures and decreased latitudinal gradients also may be related to the Tethys Sea, which distributed warm, tropical waters around the world. Ocean circulation was probably quite sluggish because of the warm temperatures, lack of ocean density gradients, and decreased winds. As stated in the previous subchapter, there is no evidence of glaciation or polar ice caps in the Jurassic. This may have been caused by the lack of a continental landmass in a polar position or by generally warm conditions; however, because of the complex relationships between temperature, geographic configurations, and glaciations, it is difficult to state a definite cause and effect (Tang, 2021).

The average temperature of the waters in the Tethys Sea is assumed to have been 5º higher than in the surrounding oceans and seas (MacSotay, 1981). It is now known that some groups of organisms appeared, developed, and disappeared with the Tethys Sea, without ever having left the tropical marine environments. The latitudinal boundary between the Boreal and Tethyan domains, during the Jurassic-Cretaceous, would have fluctuated between 20 and 40º N paleolatitude; there, the temperature gradient seems to have been low, the two domains being separated by temperature differences. The parameter that seems to control most of the horizontal distribution of organisms is undoubtedly the temperature of the waters (Terrinha *et al.*, 2013).

Iberia occupies a key position for the understanding of Mesozoic paleoenvironmental changes. Since the beginning of the II Wilson Cycle, it stands at a hinged position between the Western Tethys and the newly formed North Atlantic Ocean (Figure 4.15), and between two contrasting climatic belts reflected in floral provinces: a hot arid belt to the south, and a warm humid one to the north (Dinis *et al.*, 2020).

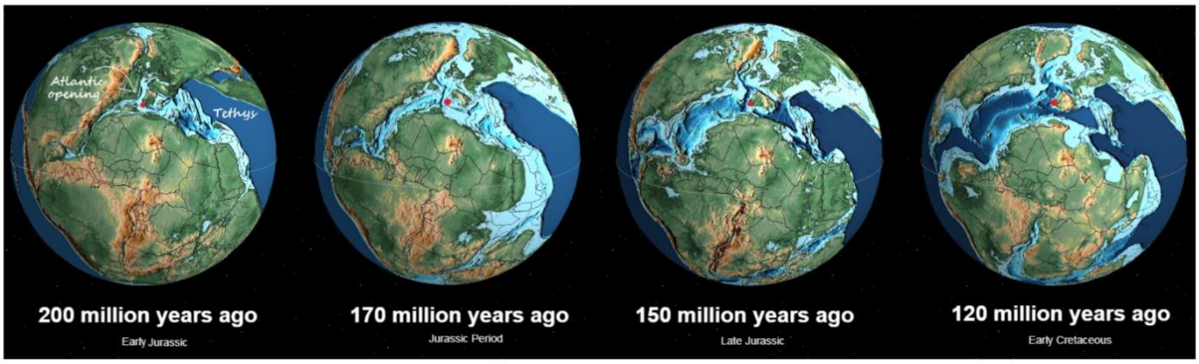


Figure 4.15. Plate tectonics movement and the Oceans distribution, from the early Jurassic till the early Cretaceous. Algarve region is marked by a red dot (adapted from Scotese, 2021).

4.2.1. The Algarve Basin and its fossil content

From the latest Triassic, the South of Portugal belonged to one of the numerous rifting basins of the Iberia-North America-North Africa junction margins. However, most of these basins, (including some of the Iberian basins), which formed early in the Mesozoic, lie offshore and generally there is not much known of their fossil contents, or at least their macrofossils. However, some of the significant Jurassic onshore outcrops are found in Portugal, in two main Mesozoic basins connected by the ancient seaway (faunal migration route) – the Lusitanian

Basin (western Iberian margin), and the Algarve Basin (south Iberian margin) (Figure 4.16) (Borges *et al.*, 2011; Dommergues *et al.*, 2011). The Algarve rift basin was located in the western part of the Tethys Sea, between 15N and 30N latitude, in a tectonic regime of lithospheric stretching and thinning, related to the generalized fracturing of Pangea, and creation of the new shallow carbonate platforms. It is along these seas, that Boreal and Tethyan faunas mixed, due to the hinge position between two margins – one associated to the future Atlantic Ocean and the other to the Neo-Tethys Ocean, thus resulting in the paleobiogeographic importance of the Portuguese basins, particularly during Jurassic times (Terrinha *et al.*, 2013).

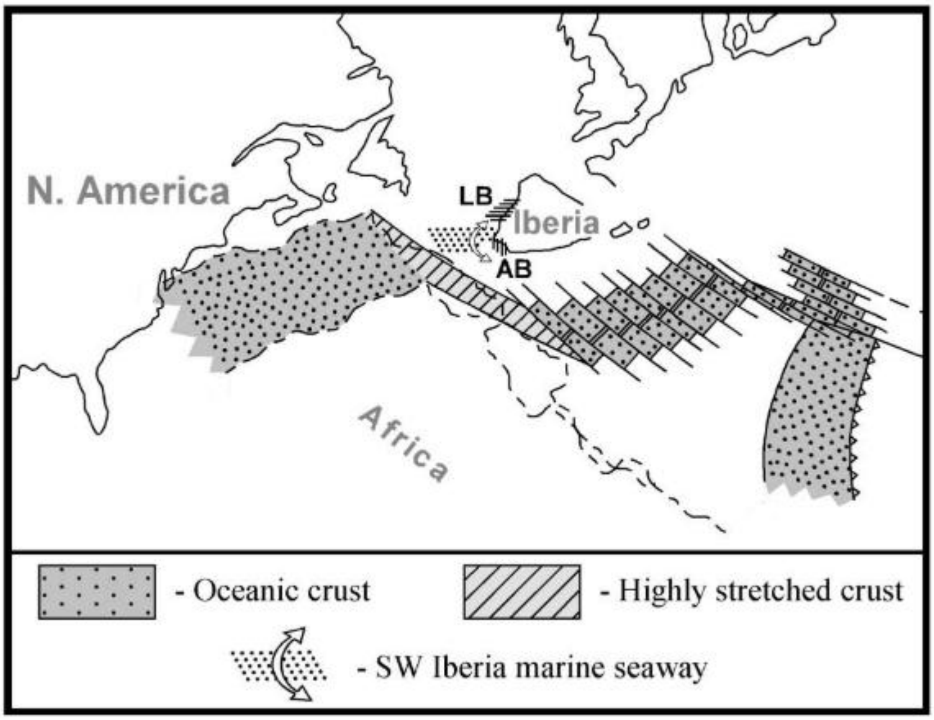


Figure 4.16. Tectonic setting of Iberia during Mesozoic times. Speculative highly stretched area separates the Neo-Tethys to the east from the Central Atlantic to the west. Also shown is the seaway around the SW corner of Iberia through which the ammonoids migrated between the Algarve (AB) and Lusitanian Basins (LB); when emerged, the white dotted area constituted a geographic barrier between the Tethyan and Boreal realms (adapted from Terrinha et al., 2002).

The sedimentary infill of the Algarve Basin comprises Upper Triassic continental deposits followed by mostly marine and marginal marine Jurassic to Lower Cretaceous units (Dinis *et al.*, 2020). The Jurassic marine carbonates are well-established across the Algarve basin. From the Sinemurian (second stage of the Lower Jurassic) to the Tithonian (last stage of the Upper Jurassic), three main sedimentary cycles of marine carbonates (separated by regional unconformities) are recognized. These cycles consist mainly in shallow-water limestones, sometimes with reef facies and alternations of marls with pelagic limestones, which are related to sea level variations or regional tectonic events, contributing to the formation of deep and shallow zones in the platform. The first cycle starts from the Sinemurian to early Toarcian (Lower Jurassic, known in Europe as Lias), the second from the Aalenian to Callovian (Middle Jurassic, Dogger) and the third from the middle Oxfordian to Tithonian (Upper Jurassic, Malm) (García-Navarro *et al.*, 2005; Borges *et al.*, 2011; Rodrigues *et al.*, 2012).

After a period of uniform sedimentation from the Hettangian to the Sinemurian, the Algarve Basin begins to split into two subbasins, separated by a structural high (Terrinha *et al.*, 2013). According to Manuppella *et al.*, (1987), since the beginning of the Middle Liasic (lower Pliensbachian), the following subbasin division appear (due to the Jurassic lithofacies variability): western subbasin (Algarve Occidental, mainly Sagres area); the structural high Budens-Lagoa-Algoz, characterised by confined sedimentation domain during the entire Jurassic; and the eastern subbasin (Algarve Oriental), between Lagoa and Vila Real de Santo Antonio, to which the region of the Algarvensis Geopark belongs (Figure 4.17) (Borges *et al.*, 2011; Rodrigues *et al.*, 2012; Terrinha *et al.*, 2013).

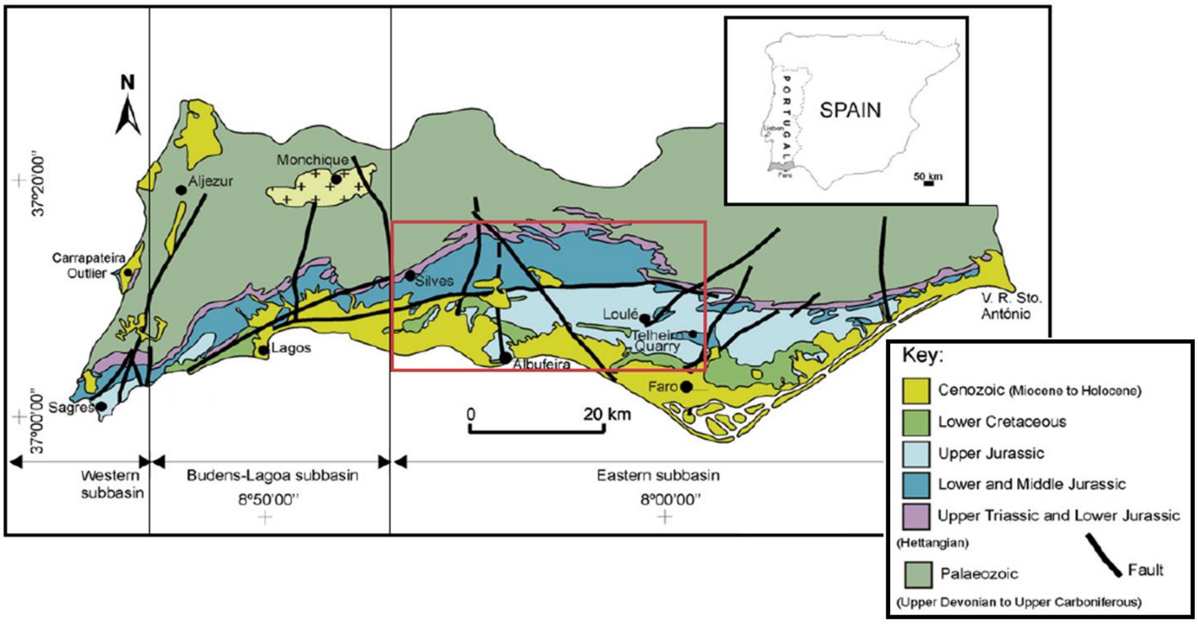


Figure 4.17. Simplified geological map of the Algarve Basin, with the division into subbasins. Red square represents the region of the Algarvensis Geopark (adapted from Lopes, 2006).

The story of the Jurassic of the Algarvensis Geopark is more complex than the previous chapters. The geology compromises a great number of the formations which yield different environmental settings, depending on the location and the exact age (Figure 4.18). Detailed description of all depositional environments and the paleontological systematics of the fossil assemblage would require too many pages, possibly leading to a development of a too heavy set of data, on the Master Thesis level. Therefore, the paleoenvironmental characterization of the Jurassic needs to be compressed and simplified.

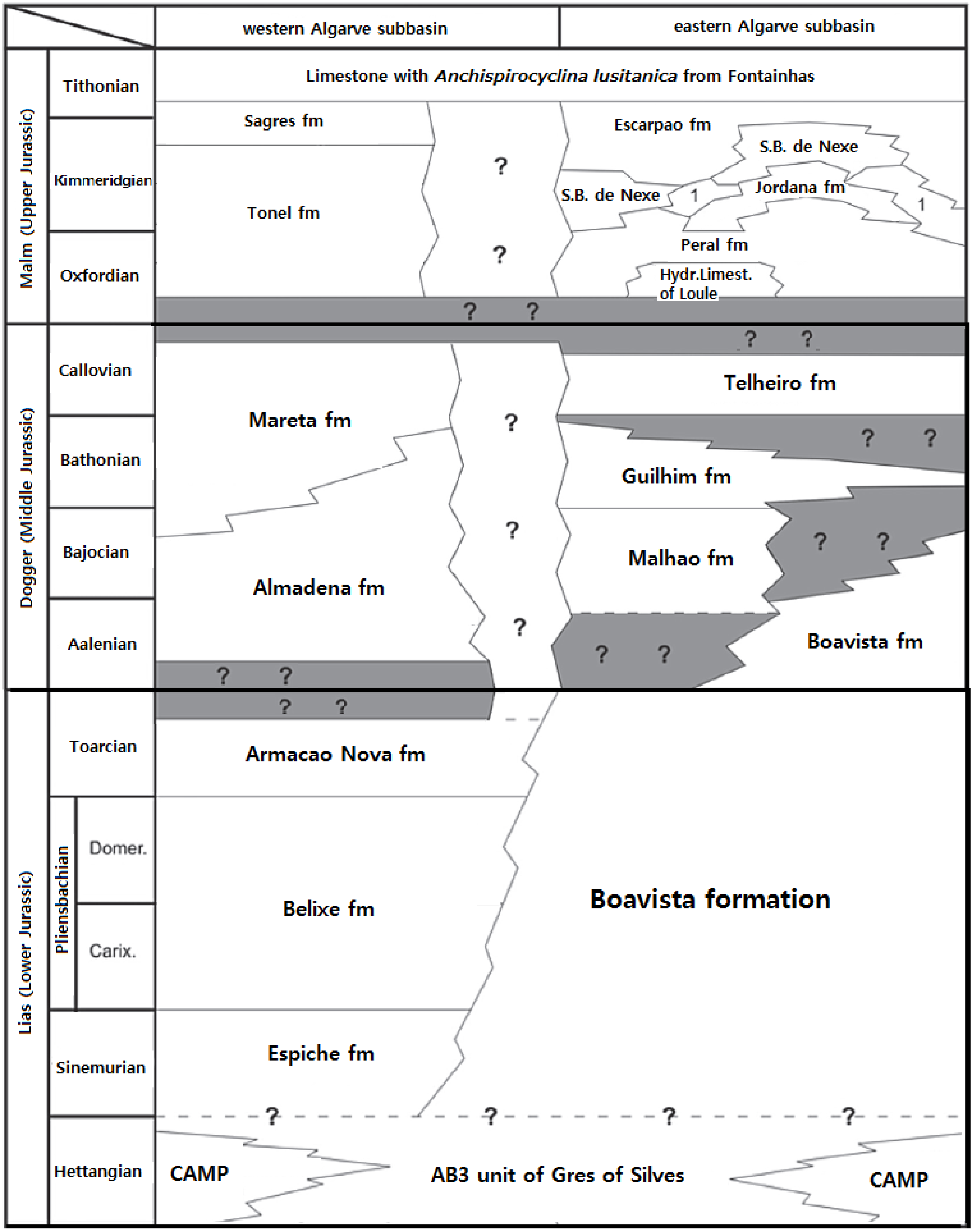


Figure 4.18. Correlations of the Jurassic lithostratigraphic units in the Algarve Basin (adapted from Terrinha et al., 2013).

In general, paleoenvironmental studies of the Jurassic are very well constrained for the Algarve region. However, until the end of the Middle Jurassic, the faunal biodiversity of the Algarvensis Geopark is mostly limited to stratigraphically significant microfossils and ammonites. The turnover is observed during the Upper Jurassic, when the highly diverse reef-building fauna appeared in the shallow tropical Algarvensis Basin. This scenario seems to be very predictable since the Triassic/Jurassic boundary was marked by mass extinction event assumed to be caused by the Pangea breakup and creation of the new seaways, also in western Iberian Peninsula. Therefore, the Upper Jurassic acts like a final stage of the marine evolutionary path, which needed several millions of years to recover and bloom later in the period.

The story of the Jurassic from the Algarvensis region corresponds to the eastern part of the Algarve Basin. This subbasin is divided into two main sedimentary cycles: first one from the Lower Lias till Dogger, and the second cycle during the Malm. This division is (also) greatly supported by the difference in number of formations (less in the first cycle than in the second) and in diversity of the faunal realm. While Upper Jurassic macroinvertebrates are highly diverse and abundant, Lower and Middle Jurassic fossils are mostly dominated by microorganisms, and ammonites (Borges *et al.*, 2011; Dommergues *et al.*, 2011). Earliest Cretaceous (Berriasian) represents the end of the second cycle, and the end of the fully marine Mesozoic deposition in the eastern Algarve; therefore, it is not included in the paleoenvironmental characterisation.

Due to the fact, that Jurassic contains many different faunal groups (mostly represented by “modern type” organisms), all fossil assemblages (with some examples of the species) is already incorporated in the paleoenvironmental characterization. Moreover, many groups are lacking paleontological systematics and photo-documentation, thus, both stories are focusing more directly on the environment’s evolution, instead of just one organism. However, a slightly different scenario, was obtained for the Upper Jurassic, where the faunal assemblage is dominated by the abundant reef-building organisms, especially corals. Table 4.2 presents all fossil groups mentioned in the literature, and all the main formations found in the eastern subbasin of Algarve, thus, in Algarvensis Geopark region.

Table 4.2. All the fossil groups found in the formations of the eastern Algarve subbasin. Thickness of the rows does not correspond to the age scale (based on Palain, 1976; Rocha 1976; Marques and Rocha, 1981; Mouterde et al., 1981; Rosendahl, 1985; Azerêdo et al., 2003; Borges et al., 2011; Dommergues et al., 2011; Terrinha et al., 2013; Rocha et al., 2014).

			Eastern Algarve Subbasin	
Period	Epoch	Stage (Age)	Fossil groups	Formations
JURASSIC	**Malm** (Upper)	Tithonian 152 Ma	Scleractinian corals (hermatypical and ahermatypical), Stromatoporoides (calcareous sponges), Chaetetids (hyper-calcified demosponges), other Sponges (siliceous, calcareous), Red algae, (Solenoporaceae and Corallinaceae), Green algae (Dasycladaceae and Characeae), Blue-green algae, Foraminifera, Ostracods, Serpulids, Bryozoans, Brachiopods, Bivalves (*e.g.*, oysters, pectinids), Gastropods (*e.g.*, Nerineae), Ammonites, Belemnites, Echinoderms (Echinoids, Crinoids)	Escarpão; Fontaínhas with *Anchispyrocyclina lusitanica*
		Kimmeridgian 157 Ma		Jordana (with Moinho do Cotovio, Nossa Senhora da Rocha, and Amendoeira sections); Cerro da Cabeça; Santa Bárbara de Nexe; Escarpão
		Oxfordian 163 Ma		"Hydraulic limestones" of Loulé; Peral
	Dogger (Middle)	Callovian 166 Ma	Foraminifera, Dinoflagellates, Ammonites, Belemnites, Brachiopods, Bivalves, Corals	Telheiro Quarry
		Bathonian 168 Ma		Guilhim
		Bajocian 170 Ma		Malhão
		Aalenian 174 Ma		
	Lias (Lower)	Toarcian 182 Ma	Foraminifera, Green algae (dasycladaceae), Porostromata (cyanobacteria), Rare reef intercalations (coral/sponge fragments), Ostracods, Serpulids (tube-worms), Brachiopods, Gastropods, Bivalves and Echinoids	Picavessa and Boavista (with Alte section)
		Pliensbachian 190 Ma		
		Sinemurian 199 Ma		
		Hettangian 201 Ma	Gastropods, Bivalves	AB3 unit of Grès of Silves Group

4.2.2. Story of the Shallow Tropical Sea (Lower – Middle Jurassic)

4.2.2.1. Lower Jurassic

In the earliest Jurassic, the Algarve Basin, thus Algarvensis area, was subjected to large continental influence from the nearby Iberian Massif. The upper part of the Grés of Silves Group (AB3 unit in Palain, 1976) correspondsis assigned to the first Jurassic stage (Hettangian), and is mainly composed of evaporites, marls, limestones, dolomites, and layers of volcanic rocks of CAMP. The sedimentation environment (equal for the western and eastern subbasin) indicates, coastal shallow marine domain, sheltered (more or less) from currents, and marked by periods of alternately agitated and calm deposition (Terrinha *et al.*, 2013). These conditions have only been favourable to the development of lamellibranches (bivalves) and gastropods, which are scarce in diversity (Mouterde *et al.*, 1981; Youbi *et al.*, 2003). Only a few forms were listed by Marques and Rocha (1981) and Rocha *et al.* (2014), and are considered as the most characteristic, and the most convenient forms for the correlation of the Hettangian stage. The two gastropod, and two bivalve species are shown in the Figure 4.19 and they belong to: A) gastropod *Neritopsis algarbiensis*, (Rocha *et al.*, 2014); B) gastropod *Promathildia turritella*, (Mouterde *et al.*, 1981); C) bivalve *Isocyprina* aff. *germari,* which is one of the most abundant fossils in the Hettangian of Portugal (Mouterde *et al.*, 1981); D) bivalve *Homomya (?)cuneata*, common form in the AB3 unit (Mouterde *et al.*, 1981).

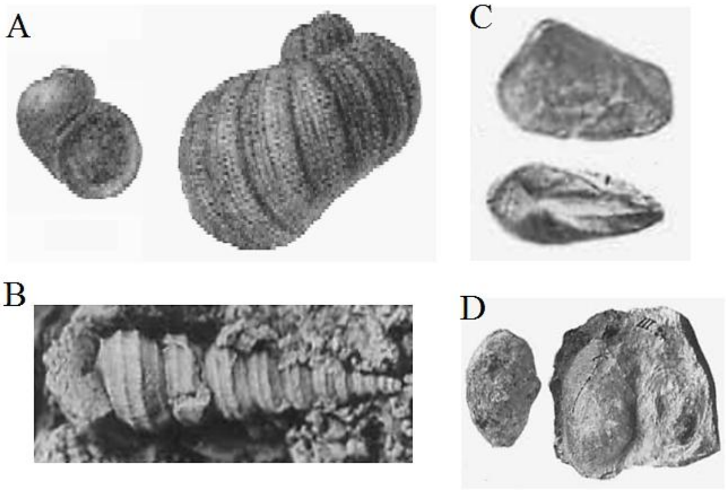


Figure 4.19. Hettangian fossils found in the AB3 unit of the Grés of Silves Group: A) gastropod Neritopsis algarbiensis, occurrence from Vila do Bispo to Castro Marim; B) gastropod Promathildia turritella, also known from the deposits of France, Germany, England, Luxembourg; C) bivalve Isocyprina aff. Germari, one of the most abundant fossils in the Hettangian of Portugal; D) bivalve Homomya (?)cuneata, common form in the AB3 unit (adapted from Mouterde et al., 1981 and Rocha et al., 2014).

Towards the end of the Hettangian and beginning of the Sinemurian, the carbonate dolomitic sedimentation was continuous throughout the entire basin. These facies suggest the existence of a vast platform, which was gradually opening to marine influences. The great extension of this carbonate platform allows to conclude that, during the Early Jurassic, a rather uniform paleoenvironment reigned in the Algarve Basin (Terrinha *et al.*, 2013). A similar evolution is postulated for the Lusitanian Basin. This suggests that epicontinental seas bordered the Iberian Peninsula at this time. However, paleontological data suggest that communication between the Algarve and Lusitanian Basins was not effective until the middle Pliensbachian, which implies that these basins were probably interior epicontinental seas (Terrinha, 1998).

The Sinemurian carbonates of the eastern Algarve Subbasin outcroping in the Algarvensis Geopark represented by the eastern Algarve subbasin, are composed by shallow-water dolomitic limestones and dolomites, which dominate until the late Liassic (Rocha, 1976; Manuppella, 1988). This thick unit corresponds to the Boavista formation (including the Alte section), also called (informally) Picavessa formation (from Serra da Picavessa). The age of the rocks is reaching the lower Toarcian, locally even Aalenian stage (near Tavira) (Azerêdo *et al.*, 2003; Terrinha *et al.*, 2013). The Sinemurian is marked by dolomitic, mostly unfossiliferous series (Dommergues *et al.*, 2011). However, locally, as at the Alte section, dolomites are intercalated with limestones rich in microfossil assemblages, and microbial fabrics (commonly encountered in carbonate rocks). This deposition might result from repeated wetting and drying of carbonate mud in supratidal setting, with cyanobacterial mat surfaces, and/or from degassing of decaying organic material (Azerêdo *et al.*, 2003). In these environments, bacteria can play an important role, especially in less agitated waters (*e.g.,* Lopes, 2006).

A carbonate succession recognized at Alte contains the first typical Tethyan fossil assemblage, particularly microfossils (Figure 4.20). It comprises calcareous green algae (dasyclads), porostromates (calcified cyanobacteria), calcispheres (undiagnosed spherical, calcareous microfossils), rare reef intercalations (coral/sponge fragments), ostracods, gastropods, bivalves, serpulids (tubeworms) and echinoids (Azerêdo *et al.*, 2003). In regard to the biostratigraphy, the most significant are the larger imperforate foraminifera (*e.g., Lituosepta recoarensis* and *Paleomayncina termieri*, among others). The presence of these species allowed to date the succession as the topmost Sinemurian. The dasyclads (*e.g., Palaeodasycladus mediterraneus*, *Thaumatoporella parvovesiculifira)* are the most important group of the typical Lower Jurassic (Liasic) microflora (Azerêdo *et al.*, 2003).

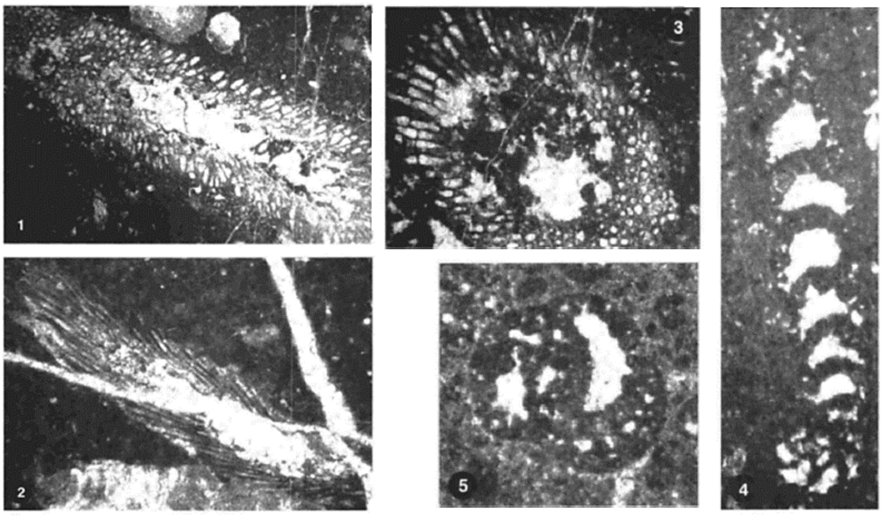


Figure 4.20. Some microfissils from the Alte section. 1,3) Palaeodasvcladus mediterrcmeus (longitudinal section and oblique section); 2) Palaeodasvcladus gracilis (longitudinal section); 4) Lituolid (axial section); Pseudocyclammina? sp. (oblique section) (adapted from Azerêdo et al., 2003).

The succession of Alte is mainly composed of intertidal – supratidal sediments, with subtidal sediments, suggesting very shallow, marginal-marine deposition, with a dominant low-energy, frequently subaerially exposed setting, as it is indicated by the fenestra micrite-rich textures, microbial-mats and bioherms (lens shaped organic reef) (Azerêdo *et al.,* 2003). Salinity probably ranged from normal-marine (dasyclads, relatively high paleobiodiversity at some levels, remains of open-marine fauna) to slightly lower (restricted-marine macrofauna with predominance of benthic foraminifera, and presence of microbial laminations). Occasionally, higher-energy events occurred, as reflected by the coarser grained limestones. Erosional contacts are present in some of the thin sections. Occurrence of microbial/algal micritic clasts, reworked algae, and foraminifera, beachrock clasts, and some features of open marine fauna clearly suggest that these are storm deposits (Azerêdo *et al.,* 2003).

Among all the basins of the Iberia-North America-North Africa junction margins, the Algarve and Lusitanian basins are the only ones with onshore fossiliferous Pliensbachian outcrops, and the only ones to yield Pliensbachian ammonites. However, this assemblage is in the West of the Algarve Basin (Sagres area), where the succession is composed of open-marine marls and limestones with ammonoid fossils, representing marine external platform (Rocha, 1976; Terrinha, 1998; Manuppella *et al.*, 1987; Dommergues *et al.*, 2011). That was the time when Algarve Basin started to differ between subbasins. Nevertheless, as a whole, South of Portugal occupied an interesting paleobiogeographic position in the westernmost Tethyan Realm (Dommergues *et al.*, 2011).

In the eastern Algarve Basin, the Pliensbachian and Toarcian age correspond to the upper part of Boavista (informal Picavessa) formation (Terrinha, 1998; Azerêdo *et al.*, 2003). This paleoenvironment is considered as correlative of the Espiche formation (western subbasin). The upper part of the Boavista dolomites does not seem to overpass the middle Pliensbachian. This unit is overlain by Boavista limestones (probably of middle Pliensbachian/Toarcian age) with rare reef intercalations and oolitic limestones in thick layers, rich in foraminifera and dasycladaceous algae (*Paleodasycladus* sp.). At the Serra da Picavessa, north of Loulé, a thick limestone sequence was dated as middle Pliensbachian based on the existence of *Paleodasycladus* sp.. This formation contains flint micro-nodules similar to the ones occurring in the Pliensbachian “calcários dolomiticos com nodulos de sílex” of Praia de Belixe (Sagres) (Terrinha, 1998; Terrinha *et al.*, 2013).

Speculations regarding the paleobiogeography of the Algarve region during the Pliensbachian to Toarcian time interval are mainly based on comparison of faunal affinities of the Tethyan and Boreal realms, from distinct geological provinces of Iberia. First occurrences of ammonite taxa in the Algarve Basin are recorded in the lower Pliensbachian of western subbasin (Rocha, 1976; Terrinha, 1998). Together with numerous fossils of benthic (bivalves, gastropods, brachiopods) and pelagic (belemnites) organisms, these ammonites were collected in dolomitic limestones from the Belixe formation (near Fortaleza do Belixe) and the Cabo de São Vicente (western subbasin). Even though, no ammonites of the earliest Pliensbachian were found in the eastern sector, the assemglage found in the western subbasin is common for all the Tethys Sea provinces (*e.g.,* Andalusia, Provence, southern French Alps, Middle French Alps, Middle Atlas), and not found in the Pliensbachian of Lusitanian Basin (Rocha, 1976; Terrinha, 1998; Dommergues *et al.*, 2011; Terrinha *et al.*, 2013).

Typical boreal ammonites migrated southwards into the Algarve Basin during the late Pliensbachian, however they never became dominant (Rocha, 1976). Nevertheless, this fact represents an evidence that, in the Algarve Basin, both Tethyan and Boreal paleogeographical realms overlapped, making it an extremely important region in terms of the Jurassic biogeography in Western Europe (Borges *et al.*, 2011). However, from the Toarcian stage, short term compressional phases, within the broad extensional framework occurred (Terrinha *et al*., 2002). These tectonic events may have, at least partially, isolated the basins, thus, preventing the mixing of Tethyan and Boreal faunas, especially during the Toarcian-Aalenian interval. Moreover, most of the Toarcian and Aalenian (possibly except for its uppermost part) have not been recognized in the eastern Algarve Basin, as the Lower-Middle Jurassic transition is marked by a basin wide hiatus (Azerêdo *et al.*, 2003).

4.2.2.2. Middle Jurassic

The transition from the Lower to Middle Jurassic is marked by a hiatus since no sediments of the middle Toarcian to middle Aalenian interval are known in the basin. In this time interval, only near Tavira, dolomitic limestones and dolomites of Boavista are recognized, dated as Sinemurian-Aalenian age (Manuppella, 1992; Terrinha *et al.*, 2013). In general, the Middle Jurassic of the eastern subbasin is extensively covered by Upper Jurassic, Cretaceous and Cenozoic sediments. The eastern sedimentation pattern is highly similar to the western sector, and it is presented in three Middle Jurassic formations (Terrinha *et al.*, 2013): Limestones of Malhão (Aalenian – Bajocian) with foraminifera (*e.g., Lucasella cayeuxi* and *Timidonella sarda),* and rare coral reef intercalations (example of unidentified species shown in Figure 4.21) (Terrinha *et al.*, 2013); Guilhim limestones and marls (lower to middle Bathonian) with foraminifera (*e.g., Protopeneroplis striata)*, ammonoids (*e.g., Ebrayiceras sp.*) (Terrinha *et al.*, 2013), and brachiopods (*e.g., "Terebratula " algarbiensis)*, from the upper Bajocian – Bathonian (Rocha *et al.*, 2014); Marlitic limestones and marls of Telheiro Quarry (Callovian) with rare ammonites (example of unidentified species shown in Figure 4.21) (Terrinha *et al.*, 2013), and abundant dinoflagellate cysts (Borges *et al.*, 2012).

Figure 4.21. Unidentified coral (Malhão Formation) and ammonite (Guilhim Formation) specimens, from the Middle Jurassic of the Algarvensis Geopark.

In the Algarve, the first formations of the Middle Jurassic present systematic thickness reduction and gaps (Terrinha *et al.*, 2013). After deposition of the pelagic lower Toarcian facies, the sedimentation was interrupted, and further replaced by shallow-water limestones in late Aalenian–Early Bajocian. Altogether, these features point toward a tectonic origin (*e.g.*, a basin uplift) for the paleogeographic modifications, that once more disconnected the Algarve and Lusitanian basins, and exposed the Algarve Basin to erosion during late Toarcian–Aalenian times (Terrinha *et al.*, 2002). It was the time, when a barrier reef existed in the Sagres area, separating the internal domain of the eastern subbasin, from the open marine platform with pelagic fauna to the west. This reef regime remained until the end of the Bajocian (Rocha, 1976; Terrinha *et al.*, 2013). From the late Bathonian–middle Callovian, the faunal associations are mostly Tethyan (with occasional ammonites of Boreal affinities, *e.g.*, *Ebrayceras* sp.), due to the confinement of the Algarve Basin, possibly associated with a sea level drop (Terrinha *et al.*, 2002). In the late Callovian migration of the Boreal *Kosmoceratidae* into the Algarve Basin coincided with the end of the confinement of the basin. The migration of the Tethyan *Phylloceratidae* into the Lusitanian Basin occurred immediately after the late Callovian–Early Oxfordian compressive/uplift event when subsidence and stretching resumed (Rocha, 1976; Terrinha *et al.*, 2002; Terrinha *et al.*, 2013).

The presence of an almost exclusively pyritic fossils (increased fragility of the fossil assemblage, caused by the pyrite oxidation), of the Callovian age, associated with the gypsum suggests, that these facies developed in a more or less closed basin, without bottom circulation, or in areas where upwelling currents originated with a great concentration of organic material. This must correspond to the infralittoral zone of the neritic domain (Borges *et al.*, 2012; Terrinha *et al.*, 2013). In this type of environment mostly macrofauna dominate, such as nektonic and planktonic ammonites and belemnites. While benthonic forms are very scarce or entirely absent, the dinoflagellates thrive, as they are diverse in shallow shelfal environments (especially in estuarine neritic settings), where many forms are adapted to unstable regimes. Despite this, it is assumed, that the relatively enclosed nature of this depocenter (during the Callovian) explains the low diversity of the dinoflagellate cyst associations. Typical Callovian species (which were not recorded in the formation) may have been especially sensitive to enclosed depositional settings, thus, just a few species adapted to the changing conditions (Borges *et al.*, 2012).

Late Callovian is marked by an extensive depositional hiatus along all Algarve Basin. No sediment record was found until the middle Oxfordian. This was possibly caused by basin uplift, and nondeposition, since the long-term eustatic curve shows a constant sea level rise during this time interval, and the short-term fluctuations of low amplitude. These episodes of sedimentary gaps of the Callovian-Oxfordian are common in all Iberian basins (Terrinha *et al.*, 2002).

4.2.3. Story of the Ancient Reefs (Oxfordian – Berriasian)

A new sedimentary cycle, that began in the middle Oxfordian, allowed the installation of a shallow gulf (from Albufeira to Tavira), centred in the Loulé region (to the west, sedimentation on a carbonate platform was maintained). This gulf reached its greatest extent in the upper Oxfordian, supporting diverse fauna, within abundant reef habitats. There are notable differences in the western and eastern facies, especially up to the base of the upper Kimmeridgian. The Upper Jurassic of the Algarvensis Geopark is composed of seven main formations, based on the eastern subbasin (after Terrinha *et al.*, 2013; and Rosendahl, 1985):

- "Hydraulic limestones" of Loulé attributed to the middle Oxfordian,
- Marly limestones and marls of Peral (middle Oxfordian – lower Kimmeridgian) with abundant ammonites, belemnites, sponges, corals, and frequent plant remains (leaves and stems). The upper part of the unit presents, in the Albufeira sector, important siliciclastic passages where, sometimes, more carbonate rich levels of corals are interspersed; on the

other hand, in the Rocha sector (Sao Brás de Alportel), a stromatolitic bioconstruction with siliceous sponges were noted,

- Limestones of Jordana (Kimmeridgian) with mostly fragmented and silicified sponges, corals, brachiopods, crinoids, belemnites and ammonoids. This formation is well exposed in Moinho do Cotovio, Nossa Senhora da Rocha, and Amendoeira sections,
- Bioconstructed limestones of Cerro da Cabeça (Kimmeridgian) with corals, rich in fragments of ahermatypic polychaetes, sponges, crinoid fragments, cidarid radials, gastropods, and bivalves. The base of this unit is a probable lateral equivalent of the Jordana Limestones with flint nodules,
- Dolomitic limestones of Santa Bárbara de Nexe (Kimmeridgian) corresponds to a secondary dolomitization of the previously described formations,
- Limestone of Escarpão (Kimmeridgian – Tithonian) with abundant microfauna and constituted by three members (from bottom to top): Limestones with *Alveosepta jaccardi* (foraminifera), with fossils of Nerineae and small primitive rudists; Limestones with *"Vaginella" striata* and *Clypeina jurassica* (algae); and transitional limestones,
- Limestones with *Anchispyrocyclina lusitanica* from Fontaínhas (Tithonian) with foraminifera, algae, bivalves and gastropods. In the top of the unit, an occurrence of calpionellids (extinct genus of single celled eukaryotes, *e.g.*, *Calpionella alpine* and *Crassicolaria parvula),* allowed to attribute it to the upper Tithonian.

In the Late Jurassic, the Algarve Basin of southern Portugal, still represented a part of the shelf of Tethyan epicontinental sea. Eastern subbasin successions exhibit a clear shallowing-upward trend, passing from an ammonite-rich, marl-dominated Oxfordian facies; through lower Kimmeridgian limestones overlain by coralliferous carbonate platform sediments of the middle to upper Kimmeridgian; to the Tithonian lagoonal and Purbeck-type sediments. In this period, a great number of corals, thrombolites, siliceous sponges, and mixed coral-siliceous sponge reefs occurred (Figure 4.22) with a wide variety of different coral associations (Leinfelder *et al.*, 1993).

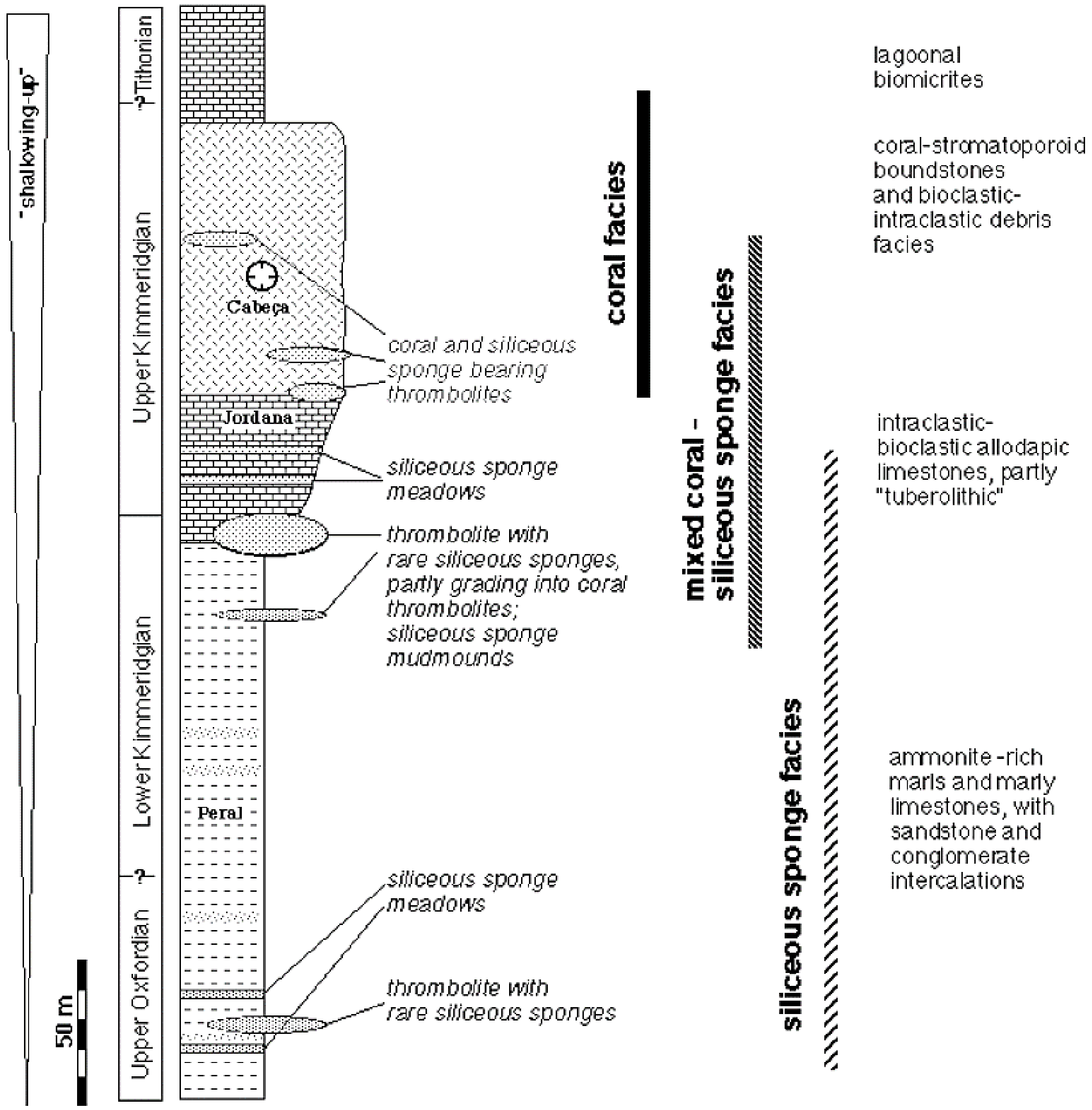


Figure 4.22. Generalized Upper Jurassic shallowing upward succession from the eastern Algarve Basin (Portugal). Siliceous sponge reef facies, mixed reef facies and coral reef facies are bathymetrically separated but show distributional overlaps. Thrombolites may occur throughout the succession (adapted from Leinfelder, 1993).

Scleractinians seems to be a dominant element. The reef-bearing facies of the eastern subbasin (listed before), as well as their coral associations and compositions, are presented in Figure 4.23. This reef-building faunal assemblage is an extremely important tool in paleoenvironmental reconstruction of the Upper Jurassic in Algarve. The scleractinian coral fauna, of the eastern Algarve Basin (together with São Bras de Alportel-Tavira section, which is not included in this study) consists of 131 species in total. Most of them belong to the hermatypical shallow-water taxa. Just two species – *Trochocyathus* cf. *laminus* and *Stylocyathus coarctatus* are ahermatypical. The scleractinians corals are distributed in the suborders Archaeocaeniina, Stylinina, Faviina, Amphiastreina, Fungiina, Rhipidogyrina and Caryophyllina (Rosendahl, 1985). Some unidentified fragments of scleractinian reefs, from Cerro de Cabeça (formation with the highest abundance and diversity of corals), are shown in the Figure 4.24.

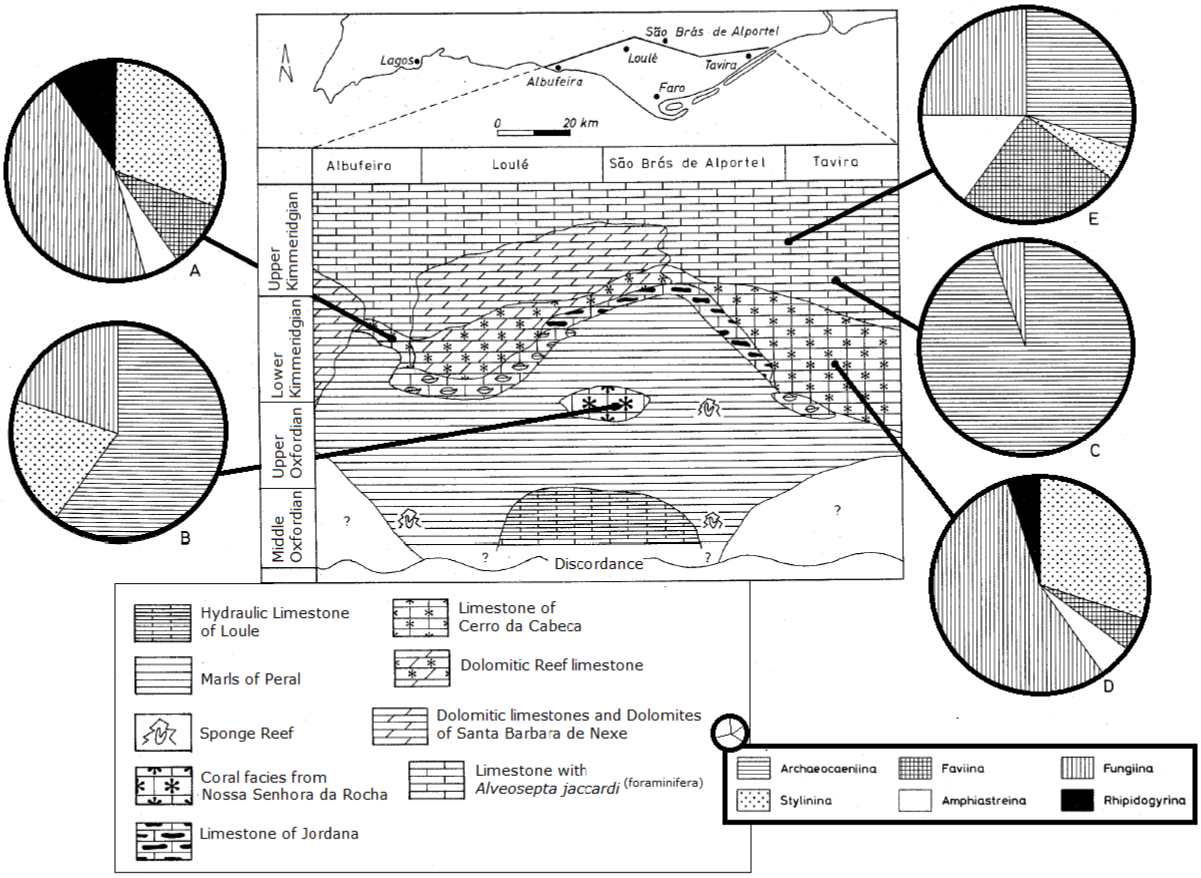


Figure 4.23. Different faunal spectra in the lithostratigraphic units of the slid Portuguese Upper Jurassic. Pie charts represent different coral association in the eastern Algarve Basin. A: Albufeira and Moinho do Cotovio; B: Amendoeira; C: Lagoa dos Cavalos; D: Sao Bras de Alportel, Peral, Cerro da Cabeca, Marco and Tavira; E: Varzeas (adapted from Rosendahl, 1985).

Figure 4.24. Unidentified fragments of scleractinian corals, from Cerro de Cabeça Formation.

The first Upper Jurassic fossiliferous formation is the marl limestone and marl layers of Peral, as well as "hydraulic limestone" of Loulé (very poor in fossil assemblage). This formation is dated from the middle Oxfordian to the lower Kimmeridgian, and represents the deposition on the flat, external platform of open sea (50 – 200m in depth), where quite strong currents prevailed. These conditions allowed the formation of sponge reefs facies (Figure 4.22) in the shallowest part of 30 – 40m depths, which might resulted from an increase of terrigenous input (Rosendahl, 1985; Leinfelder *et al.*, 1996; Terrinha *et al.*, 2013). These biostromes were dominated particularly by tube-shaped siliceous sponges (chaetetids). Tube shapes possibly evolved to elevate the animal rapidly above the sea floor which might still have been subject to oxygen depletion. The water depth (below the upper euphotic zone) and the nutrient concentration determine the composition of the sponge assemblage and other organisms (Leinfelder *et al.*, 1996).

Later, during the early Kimmeridgian, development of the Peral facies reached its peak in the area of Nossa Senhora da Rocha and NE of Loulé, where the reef formations can reach up to 80m and represent a large part of the layers of Peral. Corals, stromatopores, chaetetids, other sponges, bivalves (often with oysters), gastropods, bryozoans, and sea urchins occur mainly in this reef complex. The coral fauna is particularly rich and well preserved. Furthermore, sandstone bodies of Moinho do Cotovio may indicate proximity to land (Rosendahl, 1985; Terrinha *et al.*, 2013).

Branchy stromatopores (*Cladocoropsis mirabiIis*) occur in the Nossa Senhora da Rocha (Amendoeira site from Rosendahl, 1985). In general, Portuguese stromatoporoids in lagoonal facies, are dominated by branching forms. Stromatoporoids may be relatively frequent within certain horizons of a mixed salinity, mud-dominated carbonate succession. The occurrence of these calcified “sponges” in the basin suggest deposition of "back-reef" facies in shallow-water, low-energy environment (Leinfelder *et al.*, 2005). In addition, corals, algal crusts and dasycladacean algae are particularly common in subtidal flats of 3 – 5m depths. Generalizing, all these indicators suggest a sedimentary environment in a protected "back-reef" or lagoon area, no deeper than 10m (Rosendahl, 1985).

With the appearance of increasingly more coastal facies, the reduction of the gulf started, with a transitional mixed coral-siliceous sponge (chaetetids) facies of Jordana limestones (Figure 4.22), to Cerro da Cabeça coral-dominated limestone (Figure 4.22; 4.24, Upper Kimmeridgian) and partially dolomitized limestone of Santa Bárbara de Nexe (Rosendahl, 1985; Terrinha *et* *al.*, 2013). The coral-dominated, laterally persistent Cerro da Cabeça reef complex is of diachronic age, but it is mostly assigned to the upper Kimmeridgian (Figure 4.23). Acompanying fauna is partially silicified, and is based on sponges, stromatopores, chaetetids, echinoderms, molluscs and brachiopods. Most of these coral reef structures seem to have grown on a steepened ramp (Figure 4.25) of the shelf or platform, within a tectonic regime, which is interpreted to be a result of intense rifting, where the seaway widened considerably. This setting explains the rapid transitions from coral-dominated into thrombolitic microbial reefs and siliceous sponge reefs of greater depths (Leinfelder *et al.*, 1994; Leinfelder and Schmid, 2002).

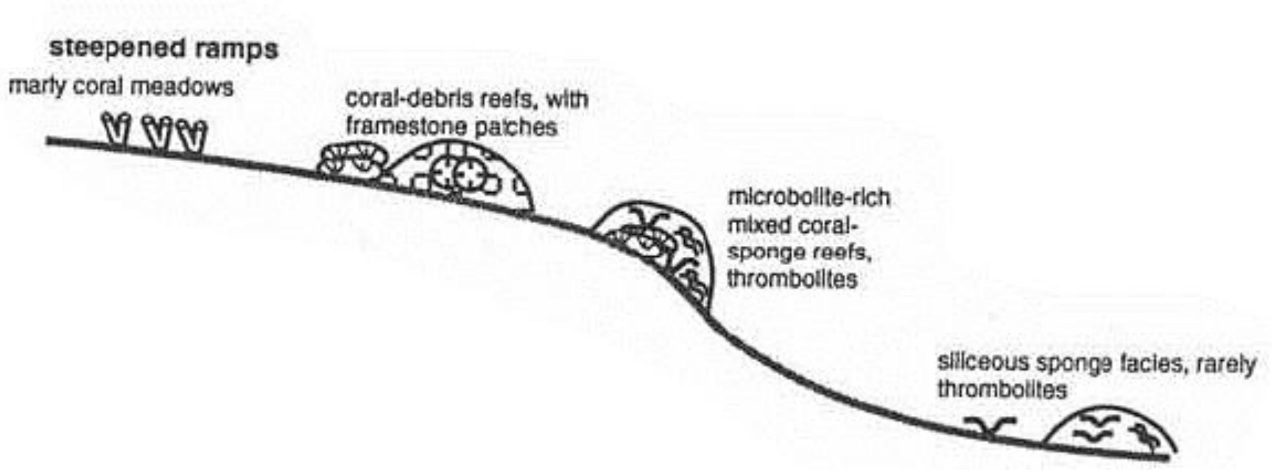


Figure 4.25. Schematic representation of the different reef settings on the steep ramp (adapted from Leinfelder et al., 1996).

During the Kimmeridgian, the reef facies of the eastern Algarve underwent a fundamental change from siliceous sponge facies to coral-dominated facies (always in association with stromatoporoids and chaetetids). Because of a steep ramp gradient, different types of coral-dominated structures occurred in the eastern Algarve Basin (Figure 4.25; 4.26). In the shallow inner ramp, highly diverse coral-stromatoporoids-chaetetids reefs are found, rich in debris (Leinfelder and Schmid, 2002). Medium to high diversity communities formed low relief biostromes, or elevated bioherms with cumulative thicknesses up to 150 m, mostly in moderate to high-energy shallow-water environments. Slopes were occupied by coral-microbolite reefs, and microbial mounds of pure thrombolites deeper setting (Leinfelder *et al.*, 1994; Leinfelder *et al.*, 1996). This special reef type grew in a deeper outer ramp setting. Coral-siliceous sponges with microbial crust were also present, but they were highly restricted to certain levels, whereas the pure thrombolites probably formed under dysoxic conditions (Leinfelder and Schmid, 2002).

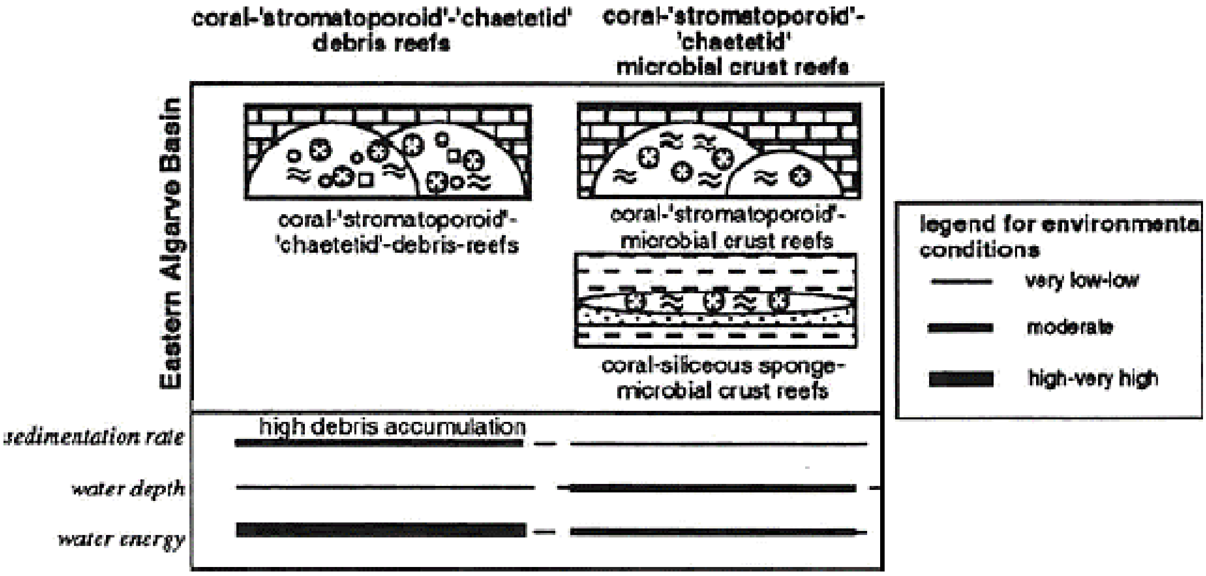


Figure 4.26. Coral-dominated reef types from the Upper Jurassic of the eastern Algarve subbasin (adapted from Leinfelder et al., 1994)

To summarize, the Jurassic reefs demonstrate that the “reef window” was relatively wide, especially in the Late Jurassic. It was the time of evolution in photic algal symbiosis in scleractinian corals, and the high adaptation to the mesotrophic and increasingly oligotrophic environments (Leinfelder and Schmid, 2002)**.** In the eastern South Portugal, almost all reef types, presented in the Upper Jurassic “reef window”, occurred (being less or more widespread). This means that the story of the ancient Algarvensis reefs fits well in the Late Jurassic “reef window” (Figure 4.27).

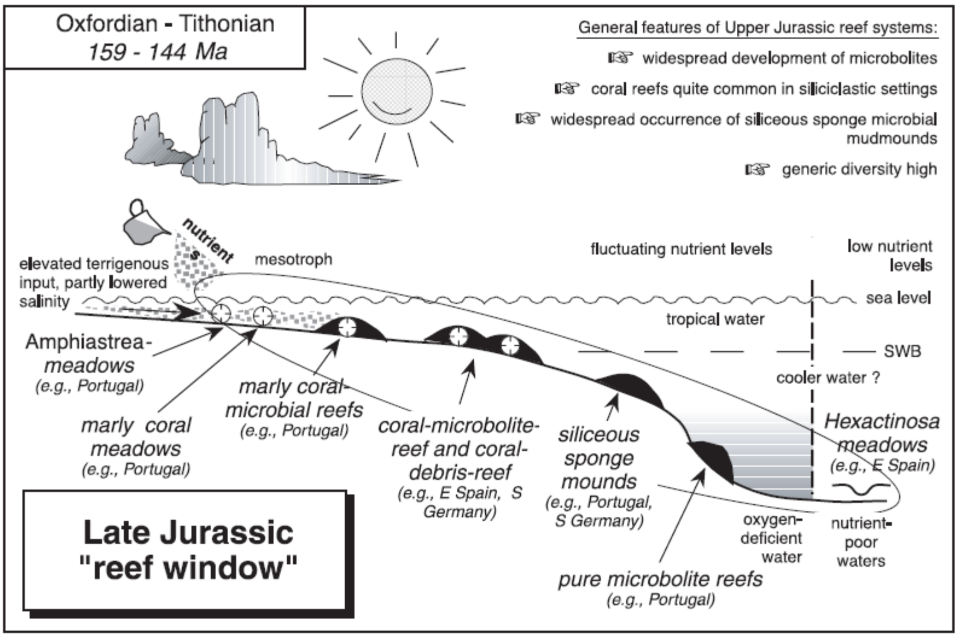


Figure 4.27. Late Jurassic “reef window” (adapted from Leinfelder and Schmid, 2002).

The uppermost Jurassic sediments of the Escarpão limestone (Kimmeridgian) and Fontainhas limestone with *Alveosepta jaccardi* (Kimmeridgian – Tithonian), were deposited in the very internal platform. In general, the Upper Jurassic sedimentation cycle is of transgressive nature from Oxfordian to Kimmeridgian, followed by a regressive period, that lasted until the end of the Berriasian. The shallowest water formations occurred with the Fontainhas formation, which made the regression tendency clear. Here, too, biostromes can occasionally occur with built up of corals, stromatopores and chaetetids. However, the continental influence grows stronger until the Purbeck facies from the Tithonian and brackish-limnic formations from the Berriasian age (Rosendahl, 1985; Terrinha, 1998)

The lack of ammonite assemlage in the lowest Cretaceous of the Algarve and lack of paleoecological data, based on other taxa, does not allow a of correlation between paleoecological modifications. This was associated with closure of seaway between the Algarve and Lusitanian Basins and the onset of compressive episodes that caused uplift and erosion of the formations of the Algarve Basin (Terrinha, 2002). Thus, the earliest Cretaceous ends the second, and the last sedimentary cycle of the fully marine Jurassic of the Algarvensis.

4.2.4. Present-day equivalent – the Red Sea (Northern Africa)

The present-day equivalent of the Jurassic palaeoenvironments recorded in the Algarvensis Geopark formations is based on the story of the Upper Jurassic reefs. This choice is based on the last evolutionary stage of the period, when faunal adaptation reaches its peak. In addition, it is a type of environment, which can be associated with its equivalent regarding plate tectonism and, what is more important, from the biological and ecological point of view. In the Late Jurassic mostly scleractinian coral-dominated reefs flourished, being the most abundant and diverse reef-building organisms, of shallow tropical Algarvensis Rift Basin.

In terms of its large size, and the previous present-day equivalent (Afar Triangle), the Red Sea is a unique analog for carbonate deposition in an ancient marine rift setting. The Red Sea covers a full 20° of latitude in Northern Europe, of clear tropical waters, which support vigorous coral reef growth associated with production of carbonate detritus (Purkis *et al.*, 2015). The environments from the Gulf of Suez–Red Sea–Gulf of Aden (Figure 4.28) provide probably the best examples of the diversity found within rift basin carbonate platforms (Bosence, 2012).

Figure 4.28. Red Sea and the Gulf of Suez represented by the red dot (adapted from Google Maps).

The Red Sea represents a young, already oceanic basin, which started to open in the late Oligocene (~30 Ma; Figure 4.29), when the Arabian plate started to pull apart from African plate. After advanced continental rifting, oceanic spreading began in the Pliocene (~5 Ma) and continues till today, as it is demonstrated by the intense volcanic and seismic activity in the area (Schettino *et al.*, 1970). Constant rifting is pulling apart two plates, which will result in the opening of the new seaway between the Red Sea and Mediterranean Sea, in the eastern region of Nile delta.

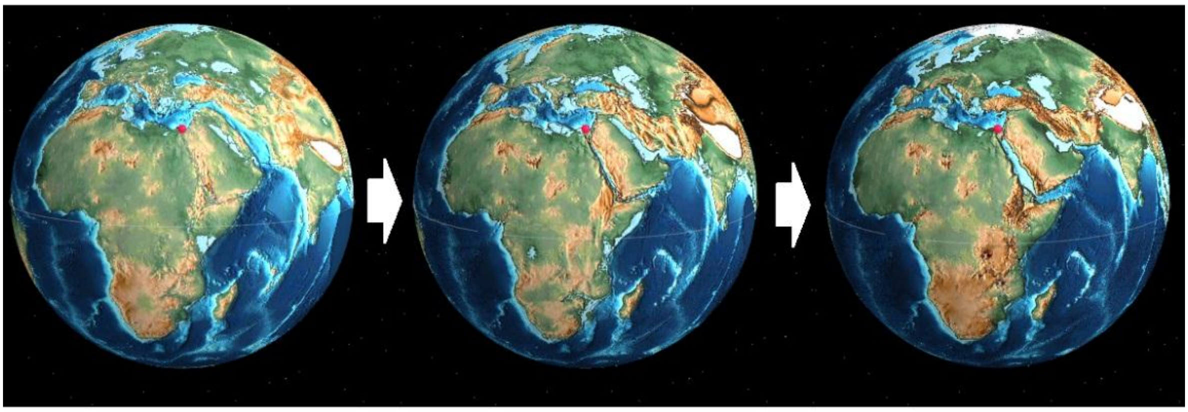


Figure 4.29. Riftogenesis of the African and Arabian plate, and the Red Sea opening (adapted from Scotese, 2021).

Modern reefs are well developed in the shallow, coastal settings of the Red Sea, especially along Egyptian coast, and in the Gulfs of Suez and Aqaba. However, the northern region fits particularly well as an analogue, regarding the position of the future seaway. In these regions, reef organisms are growing luxuriously in depths of 0.5 to 30m, along a generally steep to vertical reef-fronts. A great variety of corals was found , along with all the usual reef-associated fauna and flora (Tucker, 2003). In general, the coral reefs of the Red Sea provide a most valuable natural laboratory. They are highly diverse ecosystems, which have attracted reef researchers from many different countries. The Red Sea is characterised by changing environmental conditions which span the entire range, from those which can support vigorously growing corals to those where environmental stresses exceed the tolerances of coral or reef growth (Behairy *et al.,* 1992).

Jurassic coral reefs were nearly as complex as modern reefs (also due to the similarities in associated fauna), and they also seemed to provide a wide range of habitats, for highly diverse marine invertebrates. However, their relationship with the coralline red algae was poorly developed (Leinfelder and Nose, 1999; Leinfelder, 2001). These algae are essential binding and cementic organisms of many reefs today. During the Jurassic, stabilization in reefs was mostly provided by microbolite crusts. However, they were normally unable to develop in the very high-energy zones, giving Jurassic windward shallow-water reefs a distinct debris pile aspect. Calcareous red algae did exist in Jurassic reefs, but they did not play important roles in reef communities. Whereas, microbial calcification is also important in modern reefs, but it is mostly restricted to certain environments, probably due to the competition with coralline algae (Leinfelder, 2001). In addition, Jurassic corals grew more slowly than today. That was probably caused by the photosymbiotic relation, which was not yet as well developed. Many Jurassic photosymbiotic corals were apparently still more dependent on heterotrophic nutrition. Consequently, Jurassic coral reefs are more frequently found in terrigeneously influenced, mesotrophic settings than today (Leinfelder, 2001).

Both modern and Jurassic coral reefs are mainly composed of scleractinians, but their ecological and biological demands are not the same. All this differences indicate distinct environmental settings, which can be seen in the schematic “reefs windows” for both periods (Figure 4.30).

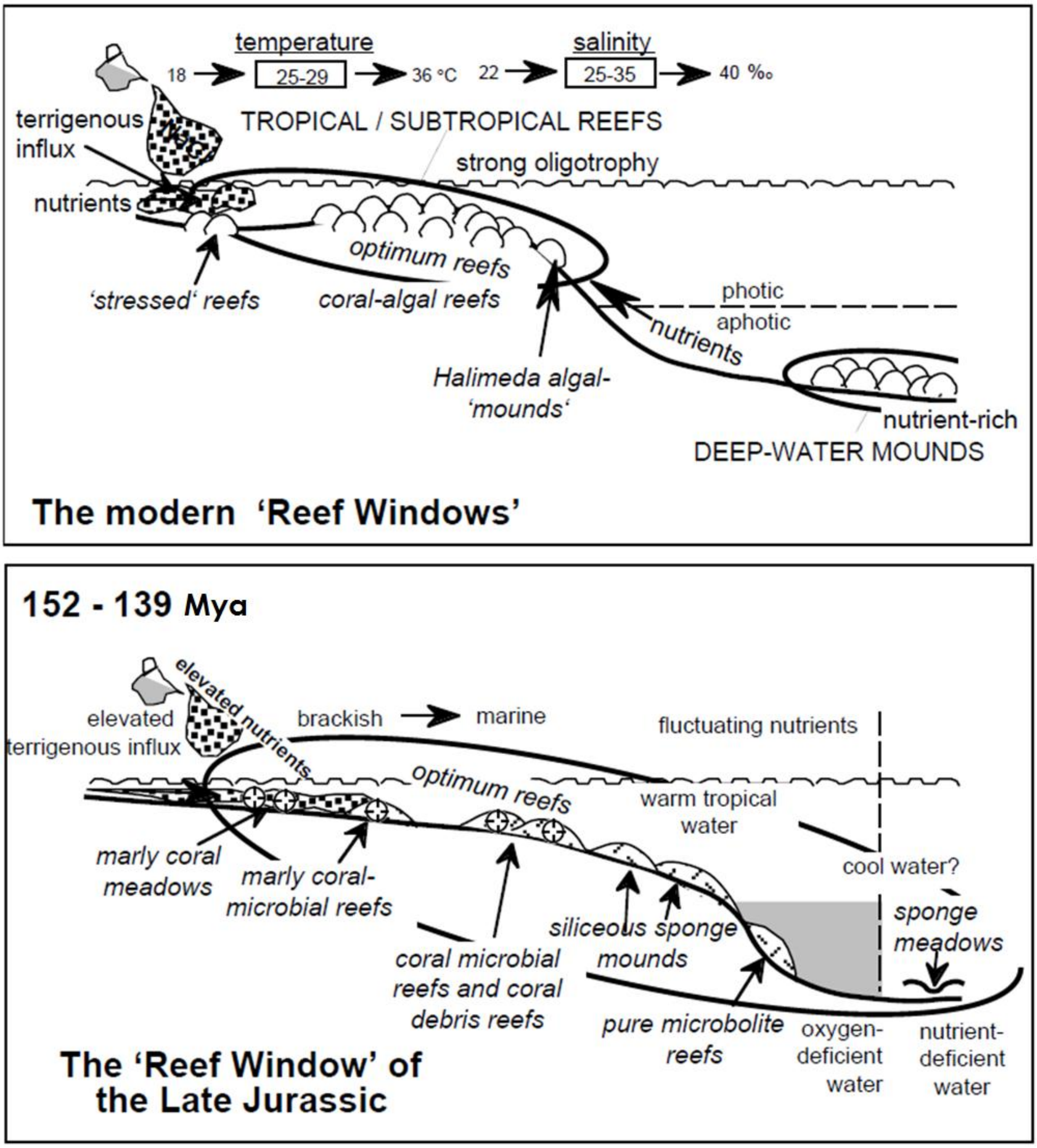


Figure 4.30. The Late Jurassic and the modern, "reef windows", showing generalized reef types and their environmental conditions. Note that the Late Jurassic reef window was much larger than the modern tropical/subtropical one, due to both better habitat availability (higher sea level) and lesser specialization or reefs. Deep-water coral mounds also are present in modern settings but occur in a distinct window separated from the tropical and subtropical reef window. The optimum for Late Jurassic coral reefs (as reflected by maximum diversities and pronounced reef growth) was slightly deeper and closer to coastlines than for modern coral reefs (adapted from Leinfelder, 2001).

CHAPTER 5. GENERAL CONCLUSION

The rocks of the Algarvensis Geopark “tell” remarkable, mostly marine story, which represents the environmental evolution of the south of Portugal. The hinge position of Algarve region, and its geological evolution of the Paleozoic and Mesozoic eras, has given insight into “dramatic” paleoenvironmental changes, which occurred within the last 360 Ma. These changes are divided by two main tectonic events: I Wilson Cycle, represented by the closure of the ancient Rheic Ocean and creation of the supercontinent Pangea; and II Wilson Cycle, connected with the Pangea brake-up, which led to the opening and evolution of the Atlantic Ocean – a remarkable part of the Algarvensis landscapes.

The paleoenvironmental characterisation provided in this study is divided into three main periods: Late Carboniferous (Paleozoic); Late Triassic (Mesozoic); and Jurassic (Mesozoic). This classification is based on the geology and the fossil assemblage found in the study area. All these paleoenvironments tell a particular and unique story of the aancient faunas, and their habitats located in the Algarvensis region.

The first paleoenvironment, and the only one of the Paleozoic era (I Wilson Cycle), is represented by the Baixo Alentejo Flysch Group. These deep-water facies yield diverse goniatite assemblages. The species belong mainly to eight families of order Goniatitida: Cravenoceratidae, Girtyoceratidae, Dimorphoceratidae, Homoceratidae, Reticuloceratidae, Gastroceratidae, Ramositidae, and Neoglyphioceratidae. This monospecific fossil assemblage indicates quite hostile, deep-ocean environments, where goniatites inhabited a wide range of water column. Their various shell morphotypes indicate numerous ecological niches, making them one of the most successful pelagic faunal group of the marine Late Carboniferous period. This story relies strongly on autecological synthesis, as there is no other fossil assemblage found in BAFG facies. In addition, as they are extinct organisms, they required a more detailed explanation. The “Story of the Goniatites Paradise” is well represented by a present-day equivalent of Banda Sea (Southern Indonesia), where the only hotspot (in the World) of nautiloids exists. The “ancient cephalopods story” of the Algarvensis Geopark is based on the general knowledge, attributed to planispiral ammonoids taxa, rather than on goniatites particularly. The main reason behind it, is a very low number of publications focusing on the ammonoids fauna from BAFG. Most of these publications are old and focus only on the paleontological systematics, stratigraphy, and correlation, within the Goniatitida order. Future detailed research (mostly on shell morphotypes) of this faunal assemblage, may lead to a better understanding of the Paleozoic Algarvensis paleoenvironment. However, this story did not last long. In the latest Late Carboniferous time, the two great landmasses collided, consequently closing the ancient Rheic Ocean, and creating one supercontinent – the Pangea. This final stage of the I Wilson Cycle, ended the cephalopod’s paradise, thus, closing the first marine chapter of the Algarvensis Geopark.

The second paleoenvironment, and the first within the Mesozoic era (II Wilson Cycle), consists of Upper Triassic Grés of Silves Group. Those are the rocks, that inspired the municipalities of Loulé-Silves-Albufeira to start this unique project, based on recent discoveries of multiple bonebeds of the giant amphibian – *Metoposaurus algarvensis*. Moreover, a skull of phytosaurus and new findings of Henodontidae remains (which are still under determination), made this “story” even more remarkable. Within this period, the “less famous” story of the small Conchostracans was also revealed. All these facies, together with their fossil assemblages, indicate a deposition in a rift basin, of transitional, continental to coastal environment, characterised by arid conditions, that led to the existence of temporary ponds, and ultimately the formation of evaporites, in the newly formed shallow marine carbonate platform of Jurassic period. The nature of this transitional environment is well known from the Afar region (Eastern Africa). Just as the Late Triassic CAMP activity, and consequent Pangea brake-up, led to the opening of a new narrow tropical sea (the Algarve Basin), the high volcanic activity in the eastern African region led to the opening of the Red Sea, which on a geological scale, is still quite young. This rift-related tectonism opened the second fully marine chapter of the Algarvensis Geopark.

The third paleoenvironment (II Wilson Cycle) is associated with the installation of the shallow-water carbonate platform in the Jurassic of Algarve Rift Basin, which further evolved into a narrow tropical sea, with highly diverse and abundant, coral-dominated reefs. Here, complex bioconstructions yield a great number of invertebrate fossils, which are of modern, Meso-Cenozoic Evolutionary Faunas. All these invertebrate groups, found in Jurassic facies, are found in the present-day oceans. This diverse associations, within Jurassic reefs, allowed for more detailed paleoenvironmental characterisation as the fossil communities, found in the formations of the Algarve Basin enable the use of the synecological approach. Therefore, due to the great number of species, within many faunal groups, systematic paleontology was less detailed. In comparison to previous subchapters, Jurassic period tells a unique “story” focused on a group of organisms, instead, on a particular one. These ancient coral-dominated reefs were (possibly) already providing a wide range of marine habitats for diverse invertebrate groups. This scenario fits perfectly in the nature of the Red Sea (also a result of rifto-genesis), which supports abundant and diverse fauna of tropical coral reefs. However, every beginning has an end, thus, the earliest Cretaceous (the last period of Mesozoic era) closed a vast marine story of the aspiring Algarvensis Geopark.

The Algarvensis Geopark of Loulé-Silves-Albufeira constitutes a territory with a unique geodiversity, that reveals several chapters of the natural history of planet Earth, and the Algarve region, which is written in the rocks of the Geopark landscapes (Figure 5.1). This project aims for a holistic approach in education, conservation, and sustainable development, through the valorisation and promotion of the natural and cultural heritage: The Aspiring Loulé-Silves-Albufeira Geopark (Veiga-Pires *et al.*, 2019).

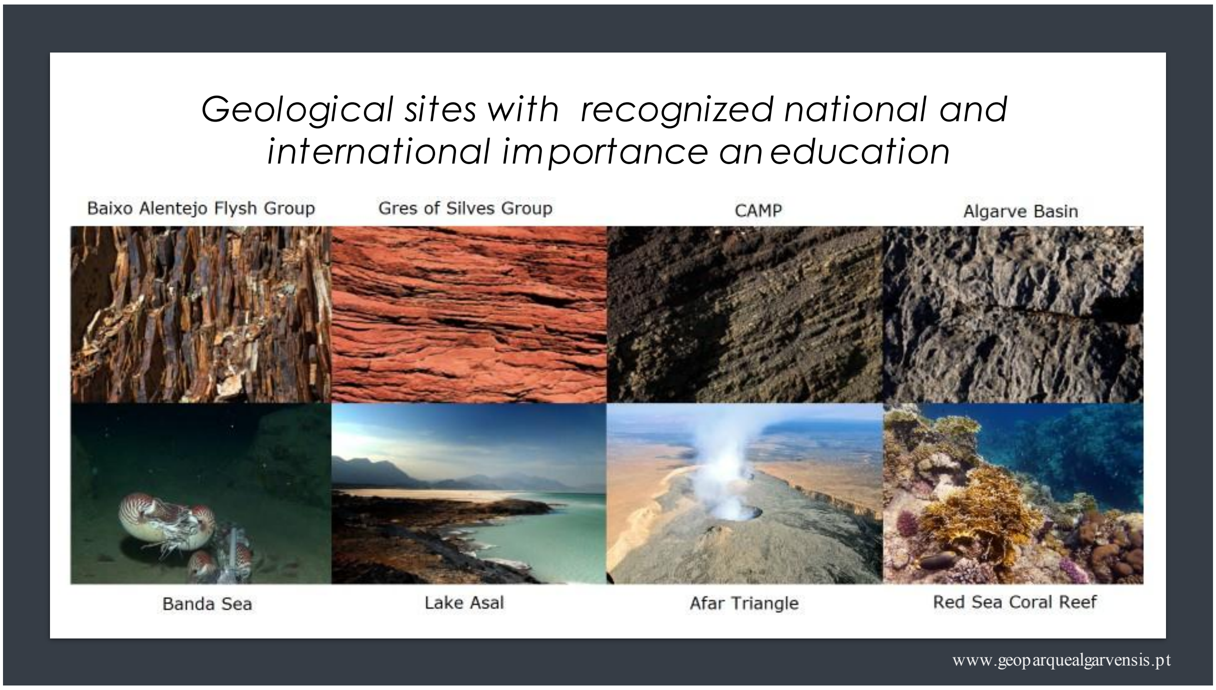


Figure 5.1. Rock formations and associated with them present-day equivalents from the Algarvensis Geopark. From the left to right: Mira formation of BAFG; Pelites from Grés of Silves Group; Vulcano-Sedimentary Complex of CAMP, and carbonates of the Algarve Basin.

The paleoenvironmental characterisation from the present work was made from the marine biologist point of view…

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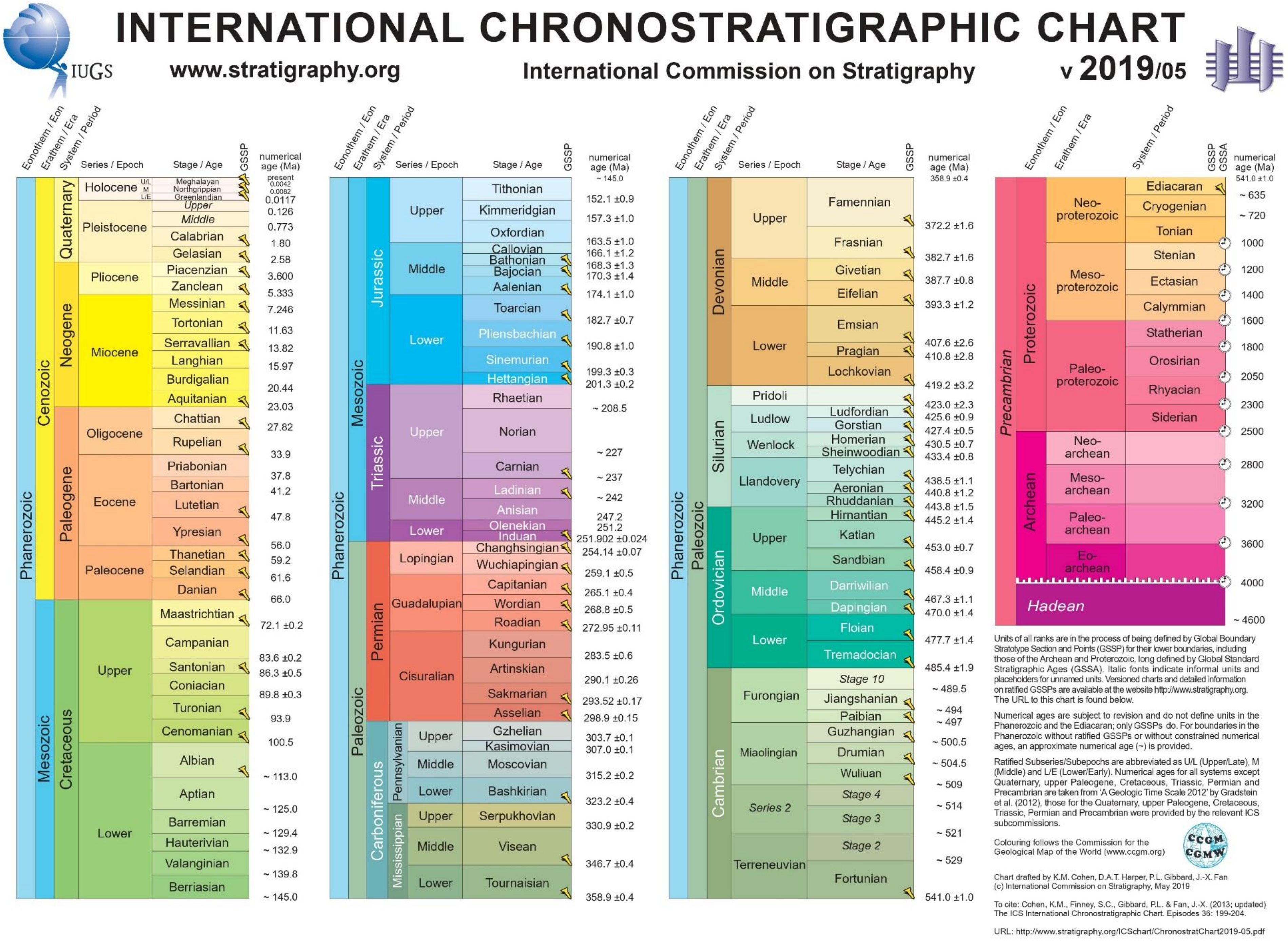
ANNEX



INTERNATIONAL CHRONOSTRATIGRAPHIC CHART

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v 2019/05

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch		Stage / Age	GSSP	numerical age (Ma)
							present
Phanerozoic	Cenozoic	Quaternary	Holocene	U/L	Meghalayan	✓	0.0042
				M	Northgrippian	✓	0.0082
				L/E	Greenlandian	✓	0.0117
			Pleistocene		*Upper*		0.126
					Middle		0.773
					Calabrian	✓	1.80
					Gelasian	✓	2.58
		Neogene	Pliocene		Piacenzian	✓	3.600
					Zanclean	✓	5.333
			Miocene		Messinian	✓	7.246
					Tortonian	✓	11.63
					Serravallian	✓	13.82
					Langhian		15.97
					Burdigalian		20.44
					Aquitanian	✓	23.03
		Paleogene	Oligocene		Chattian	✓	27.82
					Rupelian	✓	33.9
			Eocene		Priabonian		37.8
					Bartonian		41.2
					Lutetian	✓	47.8
					Ypresian	✓	56.0
			Paleocene		Thanetian	✓	59.2
					Selandian	✓	61.6
					Danian	✓	66.0
	Mesozoic	Cretaceous	Upper		Maastrichtian	✓	72.1 ±0.2
					Campanian		83.6 ±0.2
					Santonian	✓	86.3 ±0.5
					Coniacian		89.8 ±0.3
					Turonian	✓	93.9
					Cenomanian	✓	100.5
			Lower		Albian	✓	~ 113.0
					Aptian		~ 125.0
					Barremian		~ 129.4
					Hauterivian		~ 132.9
					Valanginian		~ 139.8
					Berriasian		~ 145.0

Eonothem / Eon	Erathem / Era	System / Period		Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
							~ 145.0
Phanerozoic	Mesozoic	Jurassic		Upper	Tithonian		152.1 ±0.9
					Kimmeridgian		157.3 ±1.0
					Oxfordian		163.5 ±1.0
				Middle	Callovian		166.1 ±1.2
					Bathonian	✓	168.3 ±1.3
					Bajocian	✓	170.3 ±1.4
					Aalenian	✓	174.1 ±1.0
				Lower	Toarcian	✓	182.7 ±0.7
					Pliensbachian	✓	190.8 ±1.0
					Sinemurian	✓	199.3 ±0.3
					Hettangian	✓	201.3 ±0.2
		Triassic		Upper	Rhaetian		~ 208.5
					Norian		~ 227
					Carnian	✓	~ 237
				Middle	Ladinian	✓	~ 242
					Anisian		247.2
				Lower	Olenekian		251.2
					Induan	✓	251.902 ±0.024
	Paleozoic	Permian		Lopingian	Changhsingian	✓	254.14 ±0.07
					Wuchiapingian	✓	259.1 ±0.5
				Guadalupian	Capitanian	✓	265.1 ±0.4
					Wordian	✓	268.8 ±0.5
					Roadian	✓	272.95 ±0.11
				Cisuralian	Kungurian		283.5 ±0.6
					Artinskian		290.1 ±0.26
					Sakmarian	✓	293.52 ±0.17
					Asselian	✓	298.9 ±0.15
		Carboniferous	Pennsylvanian	Upper	Gzhelian		303.7 ±0.1
					Kasimovian		307.0 ±0.1
				Middle	Moscovian		315.2 ±0.2
				Lower	Bashkirian	✓	323.2 ±0.4
			Mississippian	Upper	Serpukhovian		330.9 ±0.2
				Middle	Visean	✓	346.7 ±0.4
				Lower	Tournaisian	✓	358.9 ±0.4

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
						358.9 ±0.4
Phanerozoic	Paleozoic	Devonian	Upper	Famennian	✓	372.2 ±1.6
				Frasnian	✓	382.7 ±1.6
			Middle	Givetian	✓	387.7 ±0.8
				Eifelian	✓	393.3 ±1.2
			Lower	Emsian	✓	407.6 ±2.6
				Pragian	✓	410.8 ±2.8
				Lochkovian	✓	419.2 ±3.2
		Silurian	Pridoli		✓	423.0 ±2.3
			Ludlow	Ludfordian	✓	425.6 ±0.9
				Gorstian	✓	427.4 ±0.5
			Wenlock	Homerian	✓	430.5 ±0.7
				Sheinwoodian	✓	433.4 ±0.8
			Llandovery	Telychian	✓	438.5 ±1.1
				Aeronian	✓	440.8 ±1.2
				Rhuddanian	✓	443.8 ±1.5
		Ordovician	Upper	Hirnantian	✓	445.2 ±1.4
				Katian	✓	453.0 ±0.7
				Sandbian	✓	458.4 ±0.9
			Middle	Darriwilian	✓	467.3 ±1.1
				Dapingian	✓	470.0 ±1.4
			Lower	Floian	✓	477.7 ±1.4
				Tremadocian	✓	485.4 ±1.9
		Cambrian	Furongian	*Stage 10*		~ 489.5
				Jiangshanian	✓	~ 494
				Paibian	✓	~ 497
			Miaolingian	Guzhangian	✓	~ 500.5
				Drumian	✓	~ 504.5
				Wuliuan	✓	~ 509
			Series 2	*Stage 4*		~ 514
				Stage 3		~ 521
			Terreneuvian	*Stage 2*		~ 529
				Fortunian	✓	541.0 ±1.0

	Eonothem / Eon	Erathem / Era	System / Period	GSSP GSSA	numerical age (Ma)
					541.0 ±1.0
Precambrian	Proterozoic	Neo-proterozoic	Ediacaran	✓	~ 635
			Cryogenian		~ 720
			Tonian	◷	1000
		Meso-proterozoic	Stenian	◷	1200
			Ectasian	◷	1400
			Calymmian	◷	1600
		Paleo-proterozoic	Statherian	◷	1800
			Orosirian	◷	2050
			Rhyacian	◷	2300
			Siderian	◷	2500
	Archean	Neo-archean		◷	2800
		Meso-archean		◷	3200
		Paleo-archean		◷	3600
		Eo-archean		◷	4000
	Hadean				~ 4600

Units of all ranks are in the process of being defined by Global Boundary Stratotype Section and Points (GSSP) for their lower boundaries, including those of the Archean and Proterozoic, long defined by Global Standard Stratigraphic Ages (GSSA). Italic fonts indicate informal units and placeholders for unnamed units. Versioned charts and detailed information on ratified GSSPs are available at the website http://www.stratigraphy.org. The URL to this chart is found below.

Numerical ages are subject to revision and do not define units in the Phanerozoic and the Ediacaran; only GSSPs do. For boundaries in the Phanerozoic without ratified GSSPs or without constrained numerical ages, an approximate numerical age (~) is provided.

Ratified Subseries/Subepochs are abbreviated as U/L (Upper/Late), M (Middle) and L/E (Lower/Early). Numerical ages for all systems except Quaternary, upper Paleogene, Cretaceous, Triassic, Permian and Precambrian are taken from 'A Geologic Time Scale 2012' by Gradstein et al. (2012), those for the Quaternary, upper Paleogene, Cretaceous, Triassic, Permian and Precambrian were provided by the relevant ICS subcommissions.

Colouring follows the Commission for the Geological Map of the World (www.ccgm.org)

Chart drafted by K.M. Cohen, D.A.T. Harper, P.L. Gibbard, J.-X. Fan

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