

Universidade de Évora - Escola de Ciências e Tecnologia
Universidade Nova de Lisboa - Faculdade de Ciências e Tecnologias

Mestrado em Paleontologia

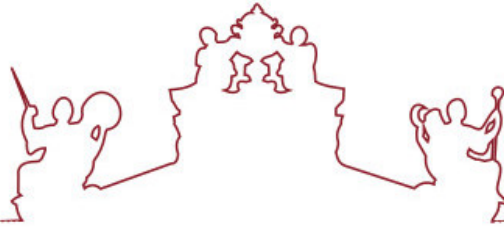
Dissertação

Contribuição da palinostratigrafia do Cretácico Superior da Nazaré (Portugal). Reconstituições peleambientais a biostratigráficas

André Filipe Martins Bonito

Orientador(es) | Lúgia Nunes de Sousa Pereira de Castro
Ausenda Cáceres Balbino
Pedro Miguel Callapez Tonicher

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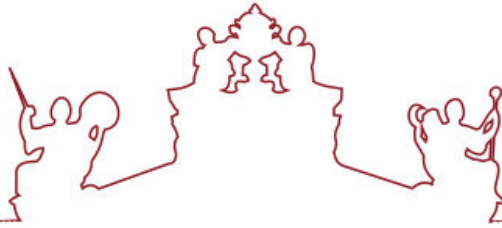
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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

Presidente | Carlos Alexandre Ribeiro (Universidade de Évora)

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Manuel Vieira (Shell U.K. Limited) (Arguente)

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RESUMO

É apresentada nesta dissertação uma análise estratigráfica e palinológica numa secção geológica do promontório da Nazaré, datada do Cretácico Superior, com incidência no estudo quantitativo dos palinomorfos, enfatizando os quistos de dinoflagelados de parede orgânica. Esta secção tem sido interpretada como ambiente marginal marinho restrito no Cenomaniano Médio. Foram recolhidas doze amostras em dez níveis margosos selecionados ao longo do perfil estratigráfico e preparadas através de técnicas palinológicas normalizadas, para observação ao microscópio. As amostras garantiam um conteúdo palinológico diversificado com quistos de dinoflagelados, esporos, grãos de pólenes, foraminíferos e acritarcas. As associações de dinoquistos apresentaram uma diversidade reduzida, sendo dominadas pelo peridinióide euralino *Subtilisphaera* sp. As inferências paleoambientais e paleoecológicas autorizadas pelos dinoquistos foram consistentes com reconstituições paleogeográficas de um ambiente lagunar propostas anteriormente para o Cenomaniano médio da região da Nazaré. As comparações com associações coevas de dinoquistos do Noroeste da Europa, do Cretáceo Superior da Plataforma Castelhana e das camadas inferiores da secção do mesmo promontório da Nazaré acentuaram, sobretudo, a especificidade paleoambiental marcada deste setor durante o Cenomaniano médio, com características de tipo lagunar.

Palavras-chave: Palinomorfos, Quistos de Dinoflagelados, Biostratigrafia, Paleoecologia, Cenomaniano Médio, Nazaré.

ABSTRACT

This dissertation presents a stratigraphic and palynological analysis in a geological section of the Nazaré promontory, dating from the Upper Cretaceous, focusing on the quantitative study of palynomorphs, emphasizing the organic-walled dinocysts. This section has been interpreted as a restricted marine marginal environment in the Middle Cenomanian. Twelve samples were collected at ten margin levels selected along the stratigraphic profile and prepared by standard palynological techniques for microscope observation. The samples provided diverse palynological content with dinoflagellate cysts, spores, pollen grains, foraminifera and acritarchs. The dinocysts assemblages presented a small diversity, being dominated by the eurialine peridinoid *Subtilisphaera* sp. Dinocysts-based paleoenvironmental and paleoecological inferences were consistent with paleogeographic reconstitutions of a lagoon environment previously proposed for the middle Cenomanian of the Nazaré region. Comparisons with coeval associations of Northwest European dinocysts, the Upper Cretaceous of the Castilian Platform and the lower layers of the section of the same Nazaré promontory emphasized the paleoenvironmental specificity of this sector during the Middle Cenomanian, with lagoon type characteristics.

Key-words: Palynomorphs, Dinoflagellate cysts, Biostratigraphy, Paleoecology, Middle Cenomanian, Nazaré.

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CHAPTER 1

INTRODUCTION

1.1 AIMS AND SCOPE OF THE RESEARCH

The Cretaceous Period is one of the major intervals of Earth's history best represented in the geological record of mainland Portugal, through a long and interesting historical of scientific researches and museological collections rich on type specimens. Together, all these accounts reveal the existence of a varied and rather complex stratigraphic setting with a highly abundant and diverse fossil record, yet partly studied until present day.

During my first months as student of the joined Master on Palaeontology of the universities of Évora and Nova de Lisboa, I had the opportunity to deep my knowledge on the Mesozoic Portuguese stratigraphy and its fossil assemblages, not just to complete my curricular year, but also as a prospect into a future specialization as a Palaeontologist. By that way, I became especially motivated for the study of Cretaceous Palynology, following the examples of other colleagues that essayed both fieldwork and the detailed laboratorial procedures that characterize this stimulating research area.

The theme here focused is thus the result of an interesting opportunity to pursuit the interdisciplinary study of a major and classic stratigraphic section of the Mesozoic Portuguese series, highly important for the characterization of the Cretaceous record in west central Portugal - the promontory of Nazaré. This coastal landscape area stands out in the northern range of a large rocky sector of Estremadura seashore, where nearly continuous exposures are available and allow exceptional conditions to observe Upper Jurassic and Cretaceous units of the continental margin of Iberia, studying aspects of their fossil content. In particular, the Cenomanian-Turonian carbonate platform beds of Nazaré have very interesting exposures with fine-grained organic rich facies where palynological investigations can be undertaken with good results. These favorable conditions and the relative lack of knowledge still

present regarding its dinocyst assemblages and their biostratigraphical and palaeoecological implications, are factors that also motivated me to pursue this research.

1.2 LOCATION OF STUDY AREA

The village and fishing harbor of Nazaré are situated on the Atlantic coast of West Central Portugal, about 100 km northward Lisbon (Fig. 1.1). Its landscape is dominated by a large promontory with a continuous exposure of sandstone and carbonate beds oriented as a monoclinical structure with a moderate dip angle oriented to NNW. The long southern side is vertical and plenty of blocks and cliffs on the base. The opposite side has steeped slopes from the hillcrests of Sítio and S. Miguel Arcanjo fortress to the northern beach, where the topmost Cretaceous succession is well exposed. The study area is located in a difficult access set of the southern side, where a small opened bay allow very complete observation and sampling of the mid Cenomanian beds.

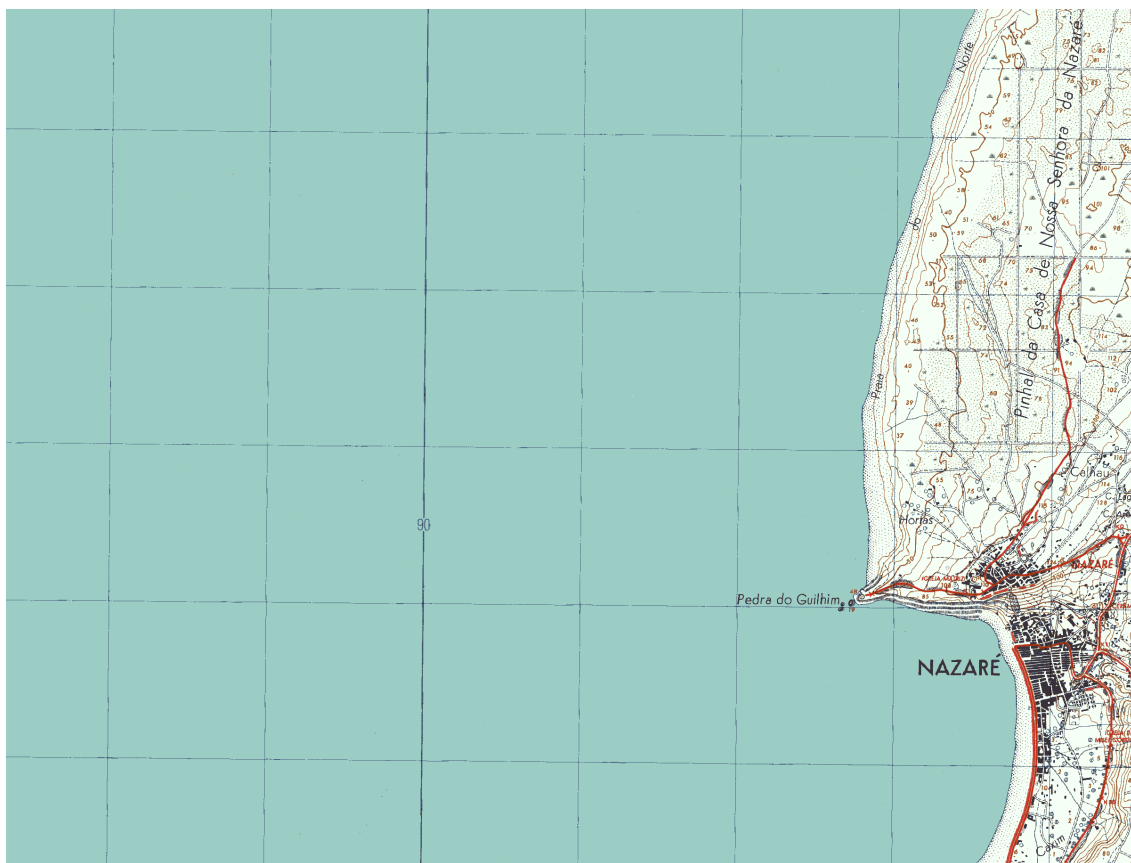


Fig. 1.1 - Location of Nazaré and the studied area in the 1/25,000 topographic map of the "Carta Militar de Portugal" of Serviços Cartográficos do Exército (1942).

1.3 OBJECTIVE OF THE STUDY

The objective of this study aims to integrate interdisciplinary aspects of general stratigraphy, taxonomy of dinocysts and paleocology relative to the same group of palynomorphs, and also to pollen and spores. The general purpose of this research is to contribute to the knowledge of the dinocysts of Portugal, with emphasis on those from middle Cenomanian of the Nazaré promontory, in the marl and limestone beds above those studied by our colleague Pedro Oliveira, in his Master thesis.

1.4. GEOLOGICAL SETTING

The break-up of Pangea developed a complex NNE-oriented system of graben structures in the western margin of Iberia, known as Lusitanian Basin (e.g. Dinis *et al.*, 2008). As several other Mesozoic peri-Tethyan basins, this narrow and North–South elongated basin located at the western border of the Iberian Massif between the Arrabida chain and the region of Aveiro, has its origin related to the opening of the North Atlantic Ocean. It is characterized by a thick sedimentary infill exclusively of Mesozoic age, which ranges from the Triassic to the Lower Cretaceous, and it contemporaneous of at least four major rifting phases. This diverse and complex succession deformed by several diapiric structures and reactivated Variscan structures is also covered by an Aptian-Albian and Late Cretaceous age, and overlain by Cenozoic deposits (Silva *et al.*, 2013). These post-rift sequences include several coarse-grained units related with regional uplift episodes, and a large carbonate platform of Albian-Turonian age related with the Cenomanian eustatic sea-level rises and highstands.

During the Cretaceous the palaeogeographic position of the Western Iberian Margin was around 30° N, with the palaeontological assemblages reflecting a dominant Tethyan influence. Nevertheless, the palaeontological record reveals increasing Boreal influence during the Late Cretaceous in response to the northward propagation of the Atlantic opening (Dinis *et al.*, 2008).

The Western Portuguese Carbonate Platform (WPCP) was one of the large rimmed shelves that bordered the European northern branch of the Tethys Realm, during the “Mid-Cretaceous” interval of accentuated sea-level rise and eustatic highstand (Fig. 1.2). This platform was gradually set up during the Albian and Cenomanian stages, and persisted until the end of lower Turonian, over large areas of the Western Iberian Margin. Presently, its carbonate facies are widely recorded on the onshore sectors of Portuguese Estremadura and Beira Litoral, between the parallels of Lisbon and Aveiro (Callapez, 2008).

The Late Cretaceous evolution of the West Iberian Continental Margin in the Estremadura and Beira Litoral Portuguese ranges and its correlation with contemporaneous Atlantic and Tethyan sedimentary basins of northwestern and southern Europe and northern Africa, including many

contexts of shallow carbonate platforms with highly diverse biotas, has long been a main subject for studies on Mesozoic stratigraphy and paleontology. Most researches have benefited from the existence of a diverse stratigraphic record with several highly fossiliferous units, ranging from the Cenomanian to the Maastrichtian and available in many onshore outcrops (Choffat 1885, 1900; Soares 1966, 1972, 1974, 1980; Berthou 1973, 1984a, b; Soares *et al.* 1982; Cunha 1992; Lauverjat 1992; Cunha and Reis 1995; Callapez 1998; Dinis 1999; Rey *et al.* 2006; Dinis *et al.* 2008; Callapez *et al.* 2010; Kullberg *et al.* 2013).

To the development of such ample and significant setting also has contributed the hinge location of the western border of the Iberian Plate in front of the expanding proto-Atlantic Ocean, in the first line of the climatic and biogeographic transitions between the northern branch of the Tethyan Realm and the European Temperate Domain, especially during the major Late Cretaceous transgressions and highstands. This context was a recurrent way for oceanic events and exchanging faunas, with repercussions on the stratigraphic record and its fossil assemblages (Callapez *et al.* 2019).

It is widely accepted that, in many aspects, the Cretaceous World was substantially different from our present day, full of geological and biotic events with remarkable developments. By this way, examples such as the paleogeographic scenery of a flooded Europe and North-Africa during the Late Cretaceous, with most of their emerged areas reduced to insular landscapes (Dercourt *et al.* 2000), are also interesting motivations for new researches, allowing the discovery of more aspects of the prevailing climates, lands and life. For the geological history of Iberia and its western border, the Late Cretaceous was also an important interval for the tectono-sedimentary evolution of the plate, when the Mesozoic successions of the Lusitanian Basin were overlain by a thick sedimentary succession that recorded the transition to a post-rift passive setting (Callapez *et al.* 2019).



Fig. 1.2 - Geographic framework of the succession outcroppings of the carbonate platform of the Cenomanian-Turonian, located in the Meso-Cenozoic Occidental Border of Iberia, north of the Lisbon parallel. Abbreviations and symbologies: NS - Sector North; SS - Southern Sector; Red line - boundary between both, expressed through the extension of reef and para-reef facies of said carbonated platform; Blue spot - place of study (adapted from Callapez & Soares, 2006).

Due to its location between North and Central Atlantic and North Africa, the WPCP has been the subject of recurrent interest concerning the biotic differentiation and mixing across the Tethyan and Temperate realms, particularly as regards the biogeographical distribution of rudist reefs and reef building corals, other benthic faunas and ammonites (Callapez, 2008).

The village and fisherman harbor of Nazaré are situated on the Atlantic coast of West Central Portugal, about 100 km northward Lisbon. From a geologic point of view, the landscapes and cliffs of Nazaré are plenty of interesting outcrops, cutting Jurassic and Cretaceous formations. This area also has

long been emphasized because of the close proximity to some regional structures that controlled the meso-cenozoic infill of the continental margin.

Among them are the diapiric and tectonic axis of Nazaré-Leiria-Pombal and Caldas da Rainha, which have acted as active borders between adjacent tectonic blocks of the Lusitanian Basin. The Upper Cretaceous stratigraphic succession of Nazaré is widely exposed on the slopes of a large promontory (Fig. 1.3), with slopes eroded from Cenomanian-Turonian platform carbonates and Campanian-Maastrichtian siliciclastics (Callapez, 2009). Besides the excellent conditions for detailed field observations, this continuous section occupies a strategic position, important to understand the regional palaeogeographic changes, and the tectono-sedimentary events that affected this sector of the Western Margin of Iberia, during Late Cretaceous times (Callapez, 2009).



Fig. 1.3 - General view of Nazaré promontory from the beach. Photograph taken by Luis Fernandes.

Until 2017, there was no Cenomanian dinocyst studies specifically performed on the Nazaré outcrop. Pedro Oliveira was the first to carry out a scientific project concerning the palynological investigation of dinocysts from the Upper Cretaceous of Portugal, particularly during the late early Cenomanian of the Nazaré promontory.

CHAPTER 2

STRATIGRAPHICAL FRAMEWORK

2.1 HISTORICAL OVERVIEW OF RESEARCH

Since the 1830s, the Portuguese Cenomanian carbonate units have been studied. Daniel Sharpe was the pioneer, followed by so many others, including Paul Choffat until the beginning of the 20th century. As a Swiss geologist based in Portugal, Choffat collaborated with the Geological Commission of the Kingdom for the detailed description of the stratigraphy, palaeontology and cartography of the Portuguese Mesozoic (Antunes, 1986), where the section of Nazaré was described in 1894. In the 1990s, the section was remade by Callapez (1998, 2001) and Callapez *et al.* (2014), which included the study of the vertebrates of Cenomanian lagoonal levels.

2.2 GENERAL STRATIGRAPHY OF THE CENOMANIAN

The Cenomanian carbonate succession of the Western Portuguese margin is part of a megasequence bounded by discontinuities, with a sedimentary record that ranges from the Upper Aptian to the Lower Campanian (Fig. 2.1) (Callapez, 1999). This megasequence is equivalent to the unconformity-bounded sequence *UBS4* defined by Cunha (1992). It is characterized by a succession of:

- (1) Alluvial coarse siliciclastic sediments and interbedded lutites drained westwards from the Hercynian Massif of Iberia;

- (2) Open and rimmed platform carbonates and mixed carbonate-siliciclastics;
- (3) Marine to alluvial micaceous sandstones (best represented in the northeast areas of the onshore);
- (4) Alluvial sandstones and conglomerates (Callapez, 2004).

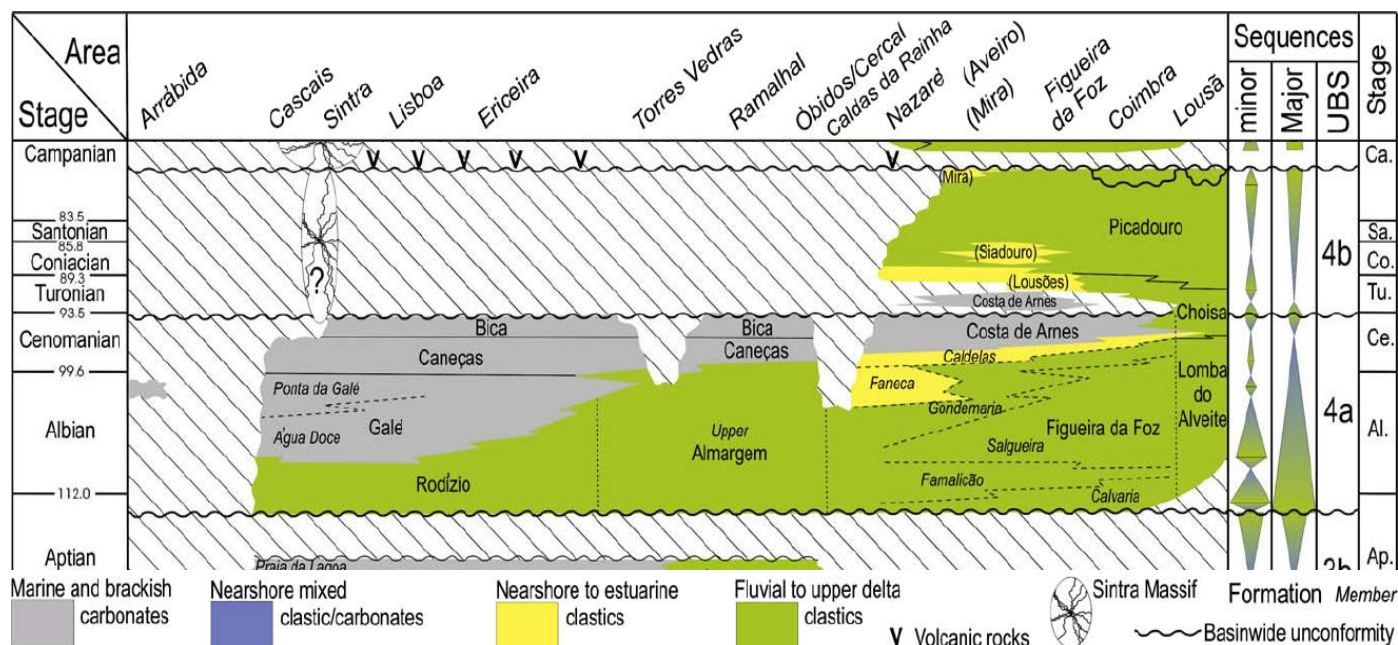


Fig. 2.1. Synthetic lithostratigraphic chart of the Cretaceous of the western Portuguese margin. Informal units within parenthesis. Triangles: blue - transgressive phase; green - regressive phase. UBS: unconformity bounded sequences after Cunha and Pena dos Reis (1995). Adapted from Dinis *et al.* (2008).

The Albian/Cenomanian transition corresponds to a discontinuity which is connected to a regressive episode within the carbonate platform. It can be related with increase in compression with Africa and transpression in the Pyrenees (Dinis *et al.* 2008). It was an ample and widespread sealevel drop recognized in the Boreal and the Tethyan main cycles, possibly eustatic considering its recognition in the cratonic Moscow depression.

The lithostratigraphy and the geological maps with Albian-middle Cenomanian deposits of the southern sector are based in a set of units defined by Choffat (1885, 1886, 1900): (1) the “*Knemiceras uhligi* level”,

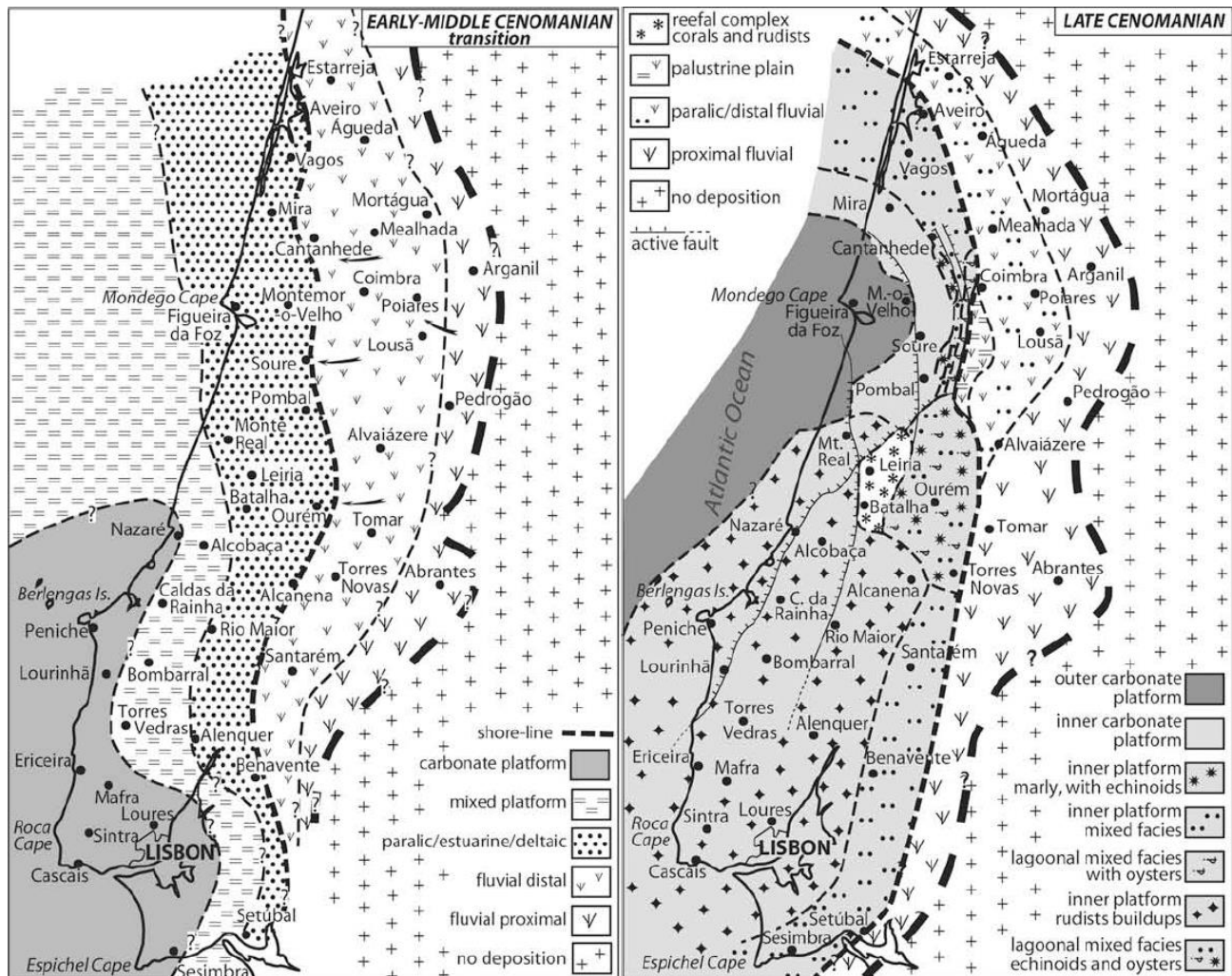


Fig. 2.2. Palaeogeographic maps of depositional environments for selected times of the late Early and Late Cenomanian (adapted from Dinis *et al.*, 2008).

(2) the “*Polyconites subverneuili* level”, (3) the “*Exogyra pseudafriicana* level” [*Ilymatogyra*], (4) the “*Pterocera incerta* level” [*Harpagodes*], (5) the “*Neolobites vibrayanus* beds” and (6) the “rudists limestone” (systematic update sensu Callapez, 2003). The four lower ones were grouped as “Bellasio” by Choffat (1886). Recently, the two lower levels define, respectively, the Água Doce and Ponta da Galé Members of the Galé Formation. The units (3) and (4) compose the Caneças Formation and the upper two levels correspond to the Bica Formation (Dinis *et al.*, 2008).

The Cenomanian T-R (transgressive-regressive) cycle: within the long-term eustatic rise (Fig. 2.2) the maximal Cretaceous transgression in the basin was during the initial upper Cenomanian (*Calycoceras guerangeri* Zone; Callapez, 2003). Afterward, individualization of open platform domains with ammonite facies took place in the northern sector (Baixo Mondego region; Choffat, 1900) (Fig. 2.2). Southwards, there was a rimmed platform with extensive calcarenitic shoals, a coral reef complex (Callapez, 2004) and

fringes of rudist buildups. Local uplift movements along the main diapiric axis also contributed to the diversification of the palaeogeography, particularly in the northern and central domains of the platform (Callapez, 2003). Marked by a hiatus and a karstified surface in the carbonate succession, the Cenomanian-Turonian transition exhibits an unconformity (Callapez, 2003) which is out of phase with the long-term eustatic trend, possibly due to increased compression in both, the Pyrenean and the Betic domains.

2.3 LOCAL STRATIGRAPHIC SETTING: THE “SÍTIO DA NAZARÉ FORMATION”

The Nazaré overall landscape is dominated by the Sítio, a large promontory with a hard ridge and tall cliffs of upper Cenomanian massive limestone beds, gently dipping towards the sea. This rocky area is bounded by several kilometers of sandy coast with dune fields, and by an alignment of *cuestas* with Upper Jurassic limestones (Fig. 2.3).

According to Callapez *et al.* (2014), the geology of the Nazaré region consists of a thick succession of Jurassic and Cretaceous shallow marine to continental units belonging to the onshore record of the West Iberian margin. This succession also records evidence of tectonic instability from the Late

Cretaceous onwards, due to the proximity of several diapiric structures adjacent to faulted blocks of the Mesozoic Lusitanic Basin (Dinis *et al.* 2008). The Cretaceous section of Nazaré is well-exposed in the steep slopes of the promontory, where a succession of Cenomanian–Turonian platform carbonates and “Garumnian” siliciclastic beds is available for detailed field-observations.

The sedimentary succession from the base of the promontory upwards displays the following main sequences (Fig. 2.4, 2.5), following Callapez *et al.*, 2014:

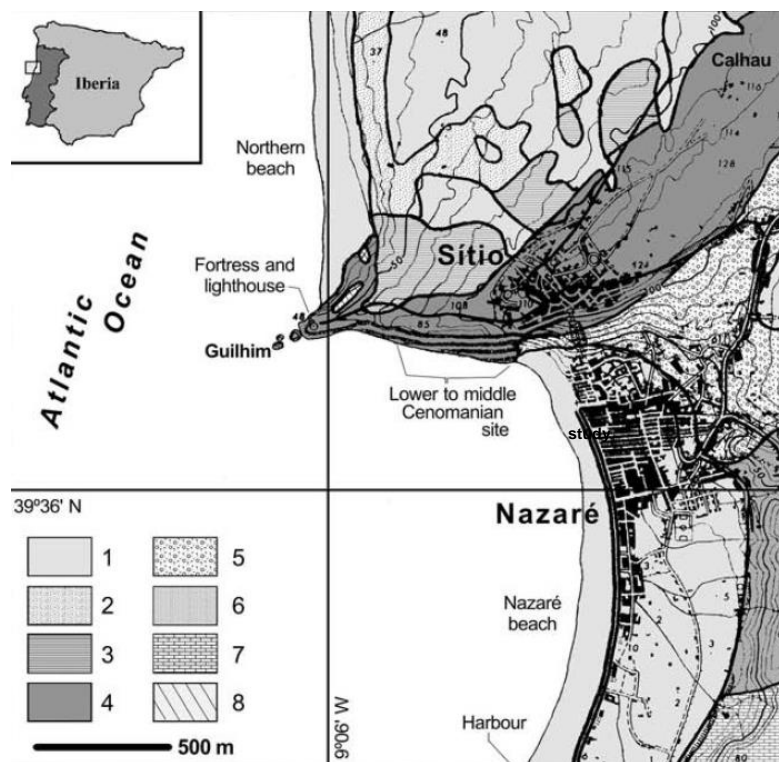


Fig. 2.3. General (Iberian Peninsula) and detailed maps of Nazaré. 1, beach sands; 2, dunes; 3, Campanian-Maastrichtian siliciclastics; 4, Cenomanian-Turonian platform carbonates; 5, Lower Cretaceous siliciclastics; 6, Upper Jurassic siliciclastics; 7, Upper Jurassic carbonates; 8, basaltic dykes (adapted from Callapez *et al.* 2014).

1) Albian to lower Cenomanian alluvial to marginal marine sandstones and lutites with plant remains (>30 m);

2) Upper lower Cenomanian littoral plain mixed facies with *Ilymatogyra* and *Ceratostreon biostromes*, changing laterally to inner shelf carbonates with abundant benthic invertebrates (“Unit with *Ilymatogyra pseudoafricana*”; 1-8 m);

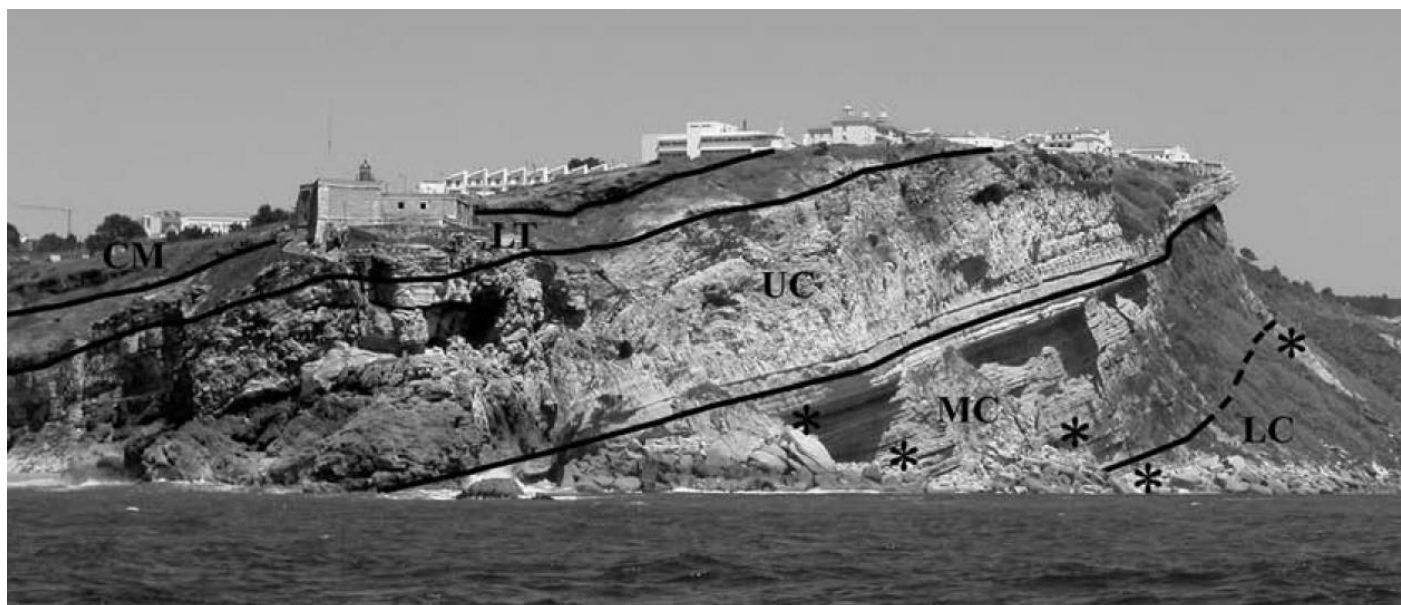


Fig. 2.4. Photographic view of Nazaré taken from west of the promontory: LC, upper lower Cenomanian; MC, middle Cenomanian; UC, upper Cenomanian; LT, lower Turonian; CM, Campanian-Maastrichtian; *, main beds with vertebrate samples (adapted from Callapez *et al.* 2014).

3) Middle Cenomanian lagoonal laminated marls and mudstones interbedded with oyster pavements and biostromes, and massive dolomitic beds with fish remains lying on the top (“Unit with *Gyrostrea ouremensis*”; 39 m);

4) Basal upper Cenomanian inner to middle shelf nodular limestones with *Neolobites* and a fully marine benthic palaeofauna (“Unit with *Neolobites vibrayanus*”; 11 m);

5) Upper Cenomanian outer reef and carbonated shoal biocalcarenic limestones with rudist debris (21 m);

6) Uppermost upper Cenomanian laminated limestones and bioturbated marls (9 m), correlative of the Bonarelli event and weathered by a local intra- Cretaceous endokarst system;

7) The topmost part of the section is exposed in the western slopes of the promontory. It starts with lower Turonian micaceous sandstones with *Radiolites* and *Actaeonella* shells (10.5 m) followed by Coniacian–Santonian alluvial sandstones (> 6 m), weathered basaltic dykes, and upper Campanian-Maastrichtian, alluvial-fan calciclastic conglomerates and red lutites with small terrestrial gastropods.

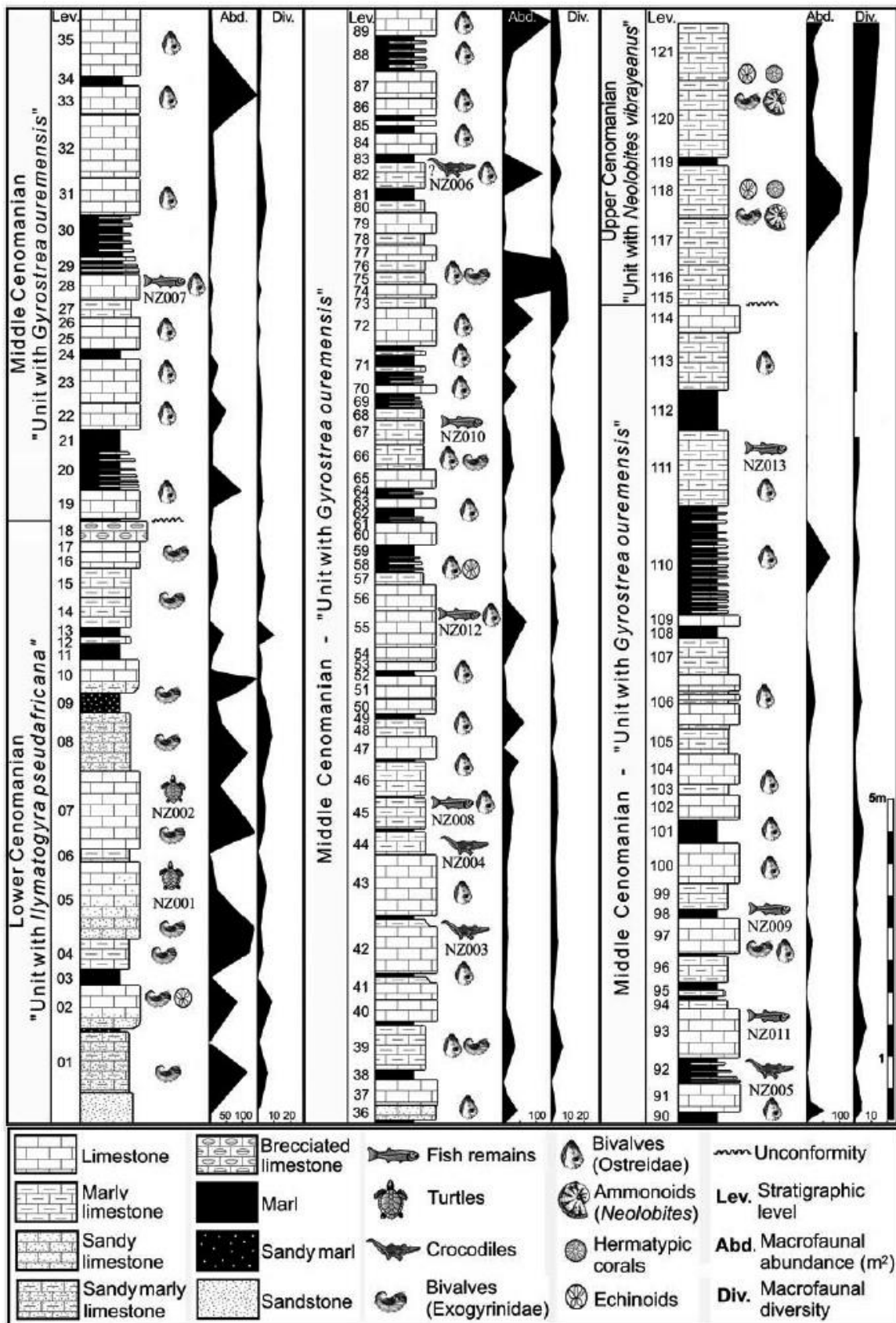


Fig. 2.5. Detailed biostratigraphic section of the Nazaré fossil site, with quantitative curves for the macrofaunal average density and taxonomic diversity, and the most relevant faunal elements. The average density values for each stratum are expressed as the minimal number of specimens per square meter of surface prospected. The most numerous valve was counted for each bivalve species, including fragments with hinge parts. Gastropods were counted as complete specimens and collumelar fragments (taken from Callapez *et al.*, 2014).

2.4 SURVEYED STRATIGRAPHIC PROFILE

The succession considered for study in this work can be seen in Fig. 2.6. It extends upwards for 15 meters, covering an exposure of inner shelf and lagoonal marls and limestones of middle Cenomanian age, with a view to examining its fossil content in dinocysts and other palynomorphs.

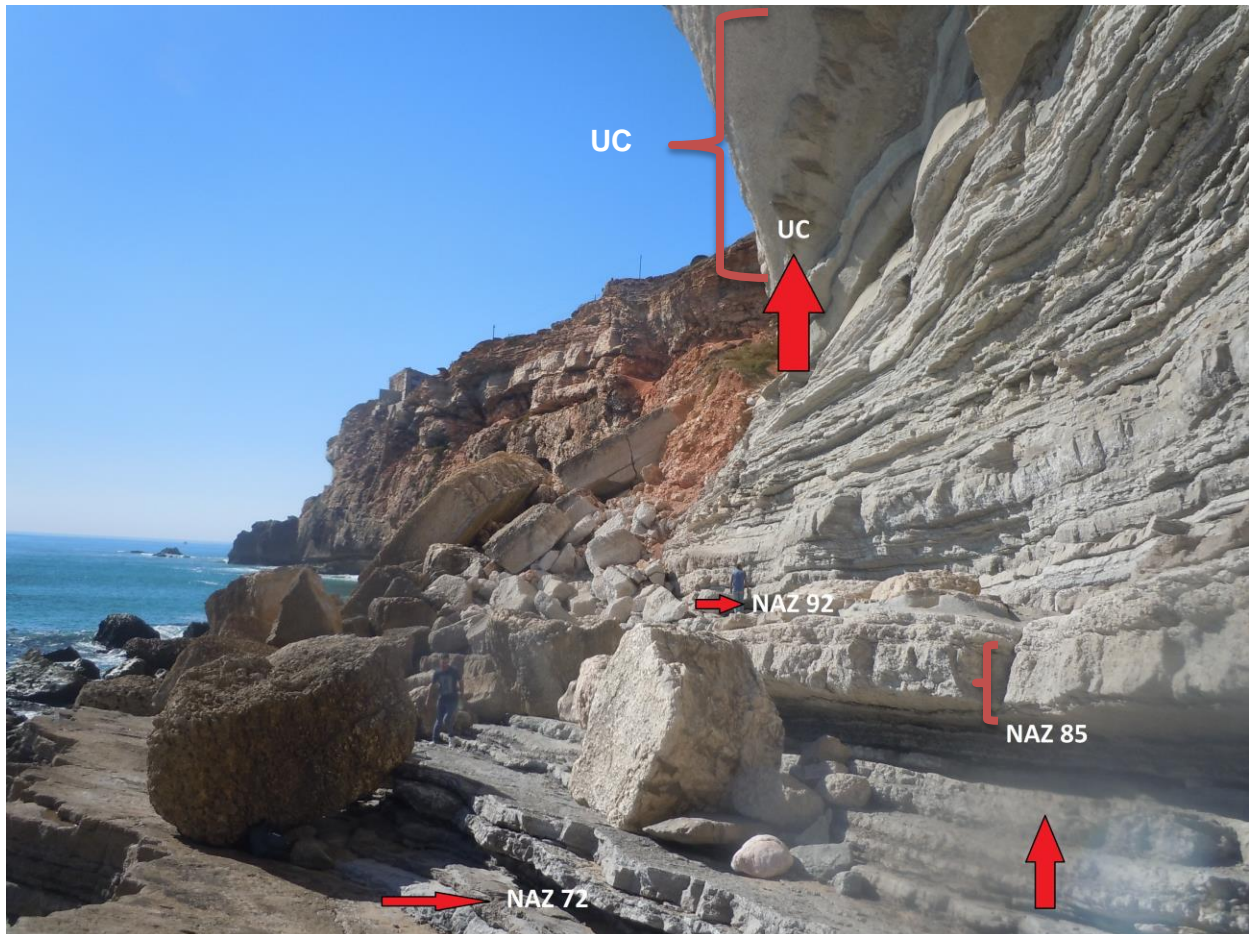


Fig. 2.6 - Photograph showing the sampling region, starting at NAZ 72 (Nazare level 72), in the middle Cenomanian. UC = upper Cenomanian.

The selected stratigraphic section is presented in Fig. 2.7 - distinguishing 27 levels. It contains a well-exposed succession of 27 levels, with interbedded limestones and marls finely laminated with oyster, biostromes and smaller concentrations of bivalves, gastropods and echinoids, centered on the lower layers. Between layers 76 and 79 some low scale slumping structures are visible. Layer 75 has a dolomitic level with thin sections, which may be an indication of regression. Layer 84 is a brecciated marly limestone rich on limestone intraclasts, suggesting a sequential rupture at this point. Just above, layer 85, a small turtle specimen was found, as well as fish teeth and traces of charcoal. Upwards in the series the content in ichnofossils markedly decreases.

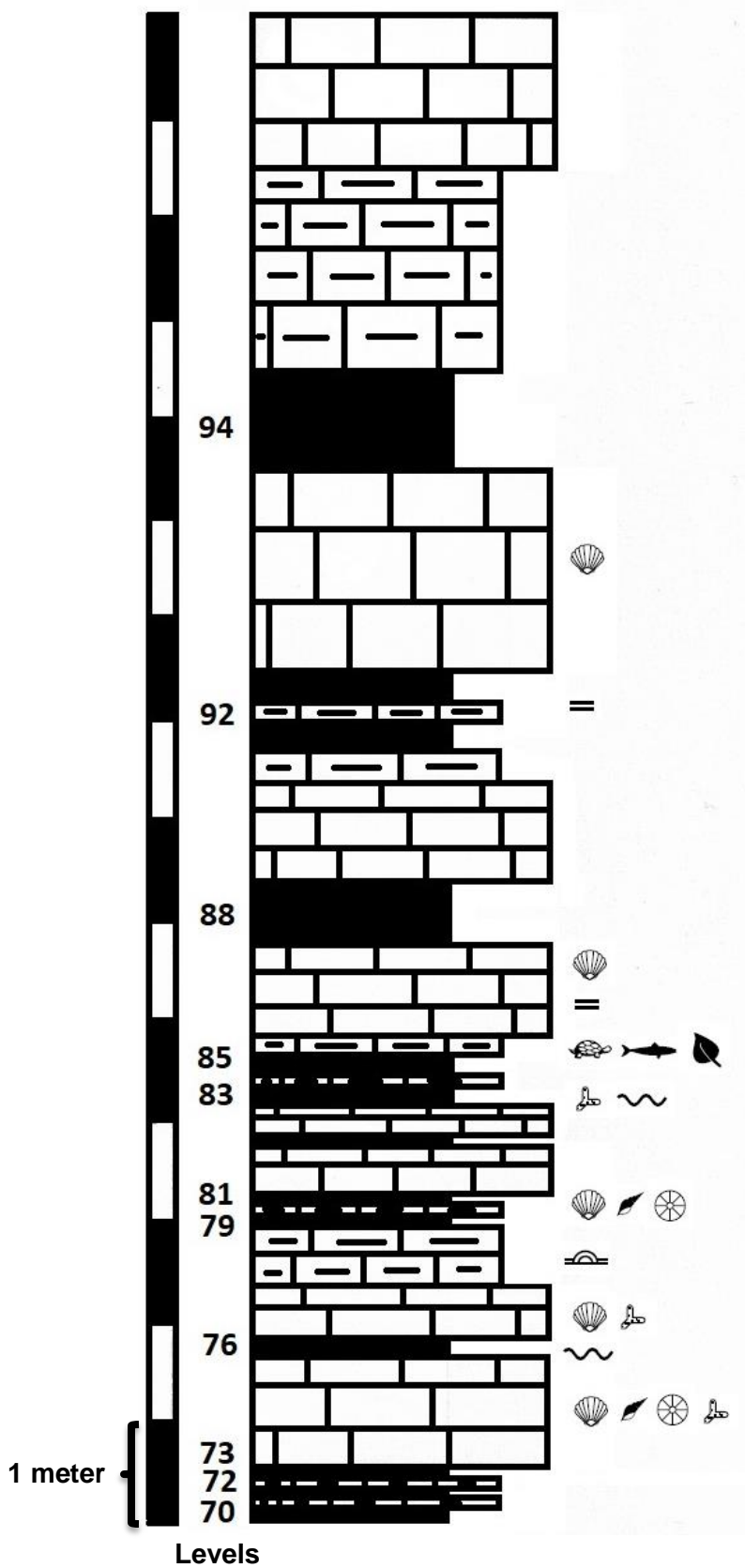


Fig. 2.7 – Stratigraphic profile of the studied succession.

CHAPTER 3

PALYNOLOGY AND PALYNOMORPHS

3.1 IMPORTANCE AND HISTORICAL PERSPECTIVE

Palynology is still a young science (Jansonius & McGregor, 1996). In the last four decades the number of palynologists increased rapidly as more and more applications were explored and developed. Spores and pollen are marvelous objects for study. Their morphology is infinitely varied, in a package so small that the wonder of their beauty never ceases to fascinate. This enchantment started as soon as the human eye was fortified by the magnifying property of the convex lens; without microscopes, there would be no palynology.

Several authors played a fundamental role in the development of the discipline of palynology, as listed below:

- The Englishman N. Green (1640) was the first to observe pollen grains under a microscope, according to Bradbury. The 70s was very remarkable for palynology as a scientific discipline, embracing more palynomorph groups as well as the importance of being linked to other areas;
- Kidston reviewed the then current state of affairs, starting with the first observation of spores in thin sections of Lancaster coal in 1833 by H. Witham who tentatively had interpreted them, however, as vessels of monocotyledonous plants;
- Reinsh (1881) discovered, in Carboniferous, Permian and Triassic coals, organically preserved plants remains that were comparable to modern equivalents. He first studied them in 1200 thin sections prepared by a few techniques;
- Sarjeant (1982, 1991, 1992) summarized research by Ehrenberg (1838), Mantell (1845) and White (1862), describing, illustrating and naming organically preserved dinoflagellate cysts so well that his names are still used;

The word palynology was first mentioned by Hyde & Williams (1944). It derives from the Greek *palunein* which means to pulverize, being also related to the latin word *pollen*, fine powder. The term palinomorph was created by Scott and introduced by Tschudy in 1961. It comprises microorganisms or organic wall structures of approximately 5 to 500 μm . palynomorphs are the pollen, spores, planktonic and bentic microorganisms with non-mineralized cell lining and the fungi (Castro, 2006).

Palynology is descriptive; identifications are the basic building blocks to construct and improve our knowledge. Descriptions must be precise, meticulous and perceptive: we must be aware of which criteria are important and which are of little consequence. Of course, our judgement is biased by our collective understanding and experience. We cannot interpret the past history of organic life without developing an affinity for, and knowledge of, recent organisms.

3.2 ACRITARCHS

Acritarchs are fossilized, organic-walled cysts of unicellular protists that cannot be assigned to known groups of organisms. Most acritarchs are probably the resting cysts of marine phytoplankton. Acritarchs can be found throughout the geological column, but are most common in the Lower Paleozoic.

Most individuals consist of a single, hollow vesicle (or theca) that may be ornamented with processes (most often spines) and surficial sculpturing elements (Castro, 2006). Vesicle symmetry varies from spherical or radial to bipolar to irregular. Many show simple excystment structures, which strengthens the suggestion that they are algal cysts (Fig. 3.1).

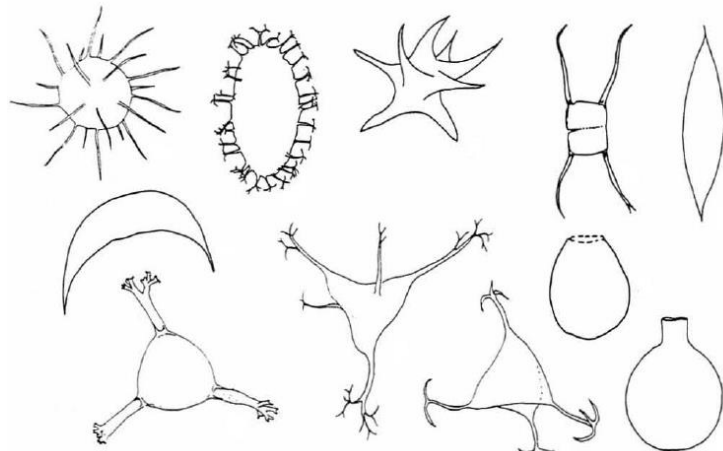


Fig. 3.1 – Basic acritarch shapes (adapted from Jansonius & McGregor, 1996).

Acritarchs are an important source of paleobiological information. The sheer numbers of acritarchs preserved in the rock record make them attractive for quantitative biostratigraphic and paleobiological studies. They represent the fossil record of the base of the global food chain during the Proterozoic and Paleozoic. Together with the cyanobacteria, they record the history of oxygen-producing autotrophes, organisms which have had a profound effect upon the composition of the atmosphere and the subsequent evolution of life on Earth.

3.3 DINOFLAGELLATES

Dinoflagellates are primarily single-celled organisms that occur typically as motile cells with two flagella (Fig. 3.2). The transverse flagellum is ribbon-like, encircles the cell, is usually within a transverse furrow known as the cingulum or girdle, and is thrown into many waves. The longitudinal flagellum is whip-like, trails posteriorly, is thrown only into a few waves and, proximally, is usually within a longitudinal furrow known as the sulcus (Castro, 2006). The flagella, together with the unique forward rotating motion which they impart, inspired Bütschli (1885) to propose the name “Dinoflagellata”, from the Greek *dinos*, “whirling rotation”, and the Latin *flagellum*, “small whip”. Hence, loosely translated, dinoflagellates are whirling, whip-bearing organisms. They have also been informally termed “the grass of the sea” (Bujak & Williams 1980) because of their importance as primary producers in the oceans, and “the dancing dust of the sea” (Harland 1985) in reference to their size and motility. Most dinoflagellates are distinguished by a dinokaryon, a special eukaryotic nucleus involving, among other distinctive features, fibrillary chromosomes that remain condensed during the mitotic cycle (Castro, 2006). Dinoflagellates have left a rich, if taxonomically selective, fossil record of organic-walled, calcareous and rare siliceous forms, almost exclusively cysts, in Mesozoic and Cenozoic rocks.

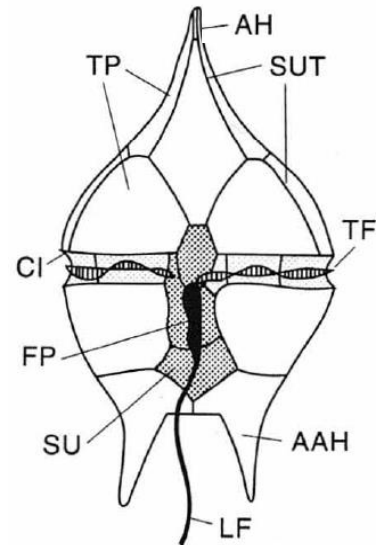


Fig. 3.2 - Basic morphology of a thecate motile cell. AAH = antapical horn, AH = apical horn, CI = cingulum, FP = flagellar pore, LF = longitudinal flagellum, SU = sulcus, SUT = suture, TF = transverse flagellum, TP = thecal plate (adapted from Jansonius & McGregor, 1996).

3.3.1 EXTANT CYSTS

A cyst is any nonmotile cell possessing a cell wall. Some cysts have walls composed of cellulose and are not preservable as fossils; others are fossilizable, having walls composed of a complex organic polymer similar to sporopollenin, termed dinosporin. Cysts can be categorized in terms of their function. Among living dinoflagellates, three functional types of cyst are prominent:

- 1) Resting cysts. Resting cysts represent a dormant stage in which normal life processes are greatly reduced. Dinoflagellate resting cysts have, so far, been found to result from sexual fusion; they are thus zygotic resting cysts, termed hypnozygotes. Walls of resting cysts are commonly strengthened by a sporopollenin-like material (dinosporin) and may comprise several layers. Most fossil dinoflagellates are probably hypnozygotes, although this is not directly demonstrable for extinct species.

- 2) Temporary cysts. A motile dinoflagellate cell with a well developed pellicle may, under adverse conditions, shed its flagella and outer wall (including plates, where present) and form a temporary cyst surrounded by the pellicle.
- 3) Vegetative cysts. Vegetative cysts are nonmotile cells surrounded by a continuous wall, probably the pellicle. These cells are metabolically and/or reproductively active, in contrast to resting and temporary cysts.

3.3.2 TABULATION

Conventionally, the term tabulation has been used to refer to the arrangement of thecal plates. However, as thecal plates occur within amphiesmal vesicles, and since there is a morphological continuum between taxa that have thecal plates and those that do not, tabulation can also be conceived of as the arrangement of amphiesmal vesicles, with or without thecal plates (Castro, 2006). It is generally assumed that thecal plates are composed of cellulose. Most plates are penetrated by trichocyst pores which may lie in pits (areolae). Cell growth, and hence increasing surface area, is accommodated by secondary growth of the plates at one or more of the plate margins. The growth bands thus produced are usually striated at right angles to the adjacent suture and have been termed “intercalary bands”. The six dinoflagellate tabulations are shown in figure 3.3.

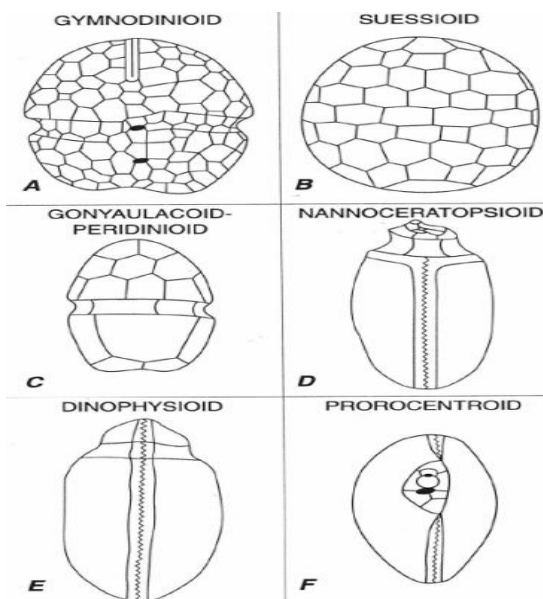


Fig. 3.3 - Tabulation types. A is in ventral view, B-E are in dorsal view, F is oblique apical view. (adapted from Jansonius & McGregor, 1996).

3.3.3 FOSSIL DINOFLAGELLATES

According to Jansonius & McGregor (1996), fossil dinoflagellates occur primarily in strata of Late Triassic to Recent age. They are mostly of marine origin, but some fresh water fossils are known. A cyst becomes fossilizable if one or more wall layers are impregnated with a resistant organic or inorganic substance. Most fossil dinoflagellate cysts have organic walls comprising dinosporin. Calcareous and siliceous cysts may have a fossilizable organic component in their wall, and some “organic-walled” fossil cysts in palynological preparations may represent the organic linings of calcareous cysts. Such fossils are thus somewhat analogous to the organic linings of foraminifera. Cysts are normally produced inside the

dinoflagellate theca. Cyst shape may approximate that of the motile cell, involving no long protrusions unrelated to thecal shape; such cysts are termed proximate (Fig. 3.4). Alternatively, the cyst may comprise a more or less spherical central body with processes or crests; such cysts are termed chorate or proximochorate, depending upon the height of the extensions relative to the central body (Castro, 2006). Although there is a morphological gradation between proximate, proximochorate and chorate cysts, these terms are useful in descriptions.

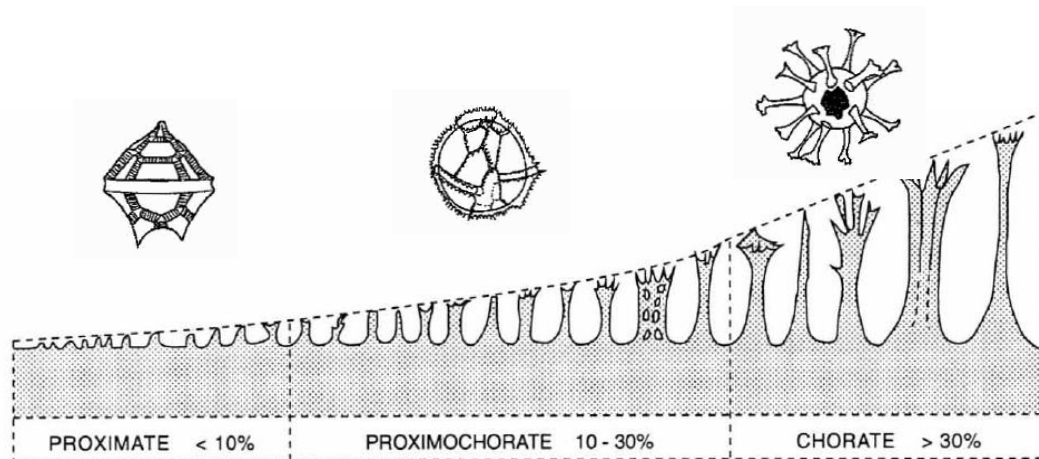


Fig. 3.4 - Use of the descriptive terms proximate, proximochorate and chorate based on process length as a percentage of the shortest diameter of the central body (adapted from Jansonius & McGregor, 1996; Sousa, Rivas-Carballo & Pais, 1999).

3.3.4 WALL LAYERS AND INTERVENING CAVITIES

The cyst wall may be one-, two- or three-layered. Four-layered walls have been reported, but are exceedingly rare; most cysts have one- or two-layered walls. Cysts with two or more wall layers and with cavities between these layers are termed cavate. Cysts with a single wall layer are termed acavate. Cavate cysts are usually proximate, but may be proximochorate or chorate.

3.3.5 SURFACE FEATURES

Certain thecal features can be reflected to varying degrees on the cyst. Following Evitt *et al.* (1977), many of these features are designated by the name of the corresponding thecal feature preceded by the prefix “para”. Thus, a paracingulum is that feature on the cyst which represents, or reflects, the cingulum on the theca. Parasulcus, paraplates, parasutures and paratabulation designate the features on the cyst which reflect, respectively, the sulcus, plates, sutures and tabulation of the theca. Paraterminology has not been accepted by all authors. It can be cumbersome and, once it is understood that “para” features are reflections of thecal features, the prefix can be omitted at an author’s discretion with, for example, the term “plate” substituting for “paraplate”.

3.3.6 EXCYSTMENT

To be viable, all cysts require a means of excystment. In dinoflagellates, excystment usually results from a suturing of the cyst wall. This suturing usually occurs along or parallel to a predetermined and intraspecifically consistent set of parasutures (Fig. 15). It may result in a slit-like aperture, but more commonly results in a flap-like opening or in the removal of a complete section of the cyst wall, the operculum corresponding to one or more paraplates (Castro, 2006). All of these types of openings have come to be referred to as archeopyles, although the term archeopyle was originally defined only for those apertures involving release of an operculum:

- An operculum involving a single paraplate is monoplacoid (Fig. 3.5E, F);
- One involving several plates is polyplacoid (Fig. 3.5A-C);
- An operculum comprising a single piece is said to be simple (Fig. 3.5B);
- An operculum involving several pieces is compound (Fig. 3.5D);
- An operculum or opercular pieces that are completely removed in the process of archeopyle formation are free (Fig. 3.5B, E, F);
- Those that remain attached are adnate (Fig. 3.5A, C).

An archeopyle may involve one or more paraplates from a single series:

- May constitute an apical archeopyle (Fig. 3.5B, C);
- An intercalary archeopyle (Fig. 3.5F);
- A precingular archeopyle (Fig. 3.5E);
- Or it may involve paraplates from two or more series (Fig. 3.5A, D).

Almost all known archeopyles occur on, or involve, the epitract and are especially common on the dorsal epitract. This is probably related to the fact that the episomal keystone plate is located dorsally, but why most cysts excyst on the epitract rather than on the hypotract is not known.

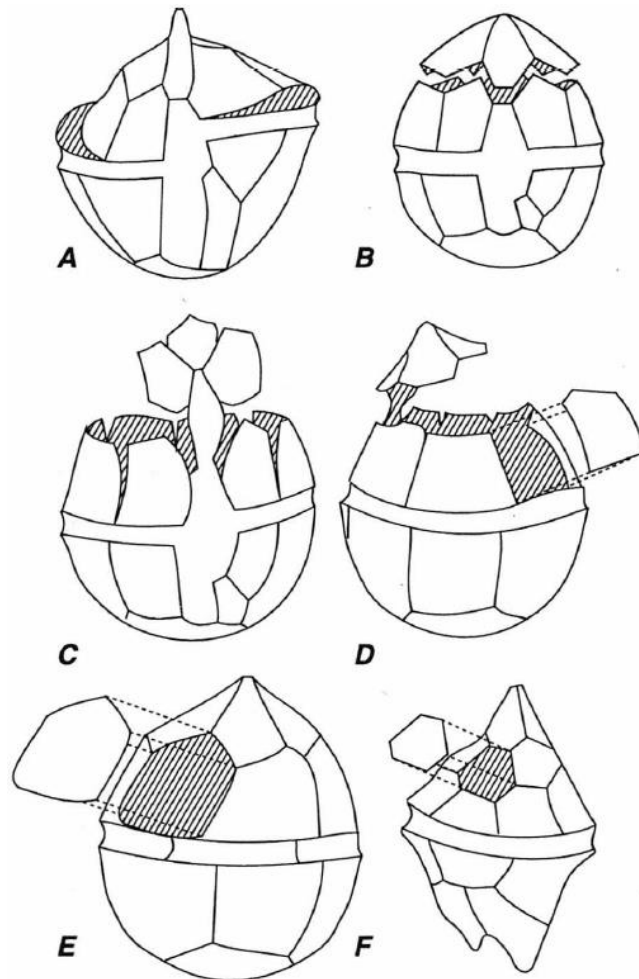


Fig. 3.5 - Types of excystment apertures. A. Epittractal archeopyle with operculum adnate ventrally. B. Apical archeopyle, involving complete removal of all four apical paraplates. C. An archeopyle involving four apical paraplates, adnate to each other and ventrally; accessory archeopyle sutures occur between precingular paraplates. D. An archeopyle similar to that shown in C but with, in addition, removal of a single precingular paraplate (combination archeopyle). E. A simple precingular archeopyle. F. A simple intercalary archeopyle (taken from Jansonius & McGregor, 1996).

3.3.7 PRACTICAL STUDY OF FOSSIL DINOFLAGELLATES

Paratabulation is the key to interpreting dinoflagellate taxonomy and phylogeny and these, in turn, are fundamental to meaningful biostratigraphic and ecological studies. The importance of tabulation thus acknowledged, it is also admittedly true that individual fossil specimens rarely show a complete paratabulation. In routine microscope studies, it is usually necessary to identify species, initially at least, on the basis of features such as cyst shape, process type and distribution, surface ornamentation or archeopyle type, rather than paratabulation. Dinoflagellate affinity of a specimen can be recognized by the presence of any characters reasonably relating to paratabulation: these include parasutural features, however incomplete; intratabular features; archeopyle outline; and the presence of a paracingulum. Even lacking any of these features, general shape (e.g. presence of a single apical horn and two antapical horns giving a peridinioid outline) may be considered convincing evidence. Once a specimen is confirmed as a dinoflagellate cyst, recognition of key morphological features is necessary to enable orientation. Paratabulation patterns, if present, will help, as will the following aids: archeopyles are virtually always on the epitract; single horns are almost invariably apical and pairs of horns antapical; the paracingulum is always interrupted ventrally by the parasulcus; an archeopyle involving one to a few (precingular or intercalary) paraplates is usually on the dorsal epitract; an apical archeopyle usually has a deep notch, the sulcal notch, on the ventral surface. Moreover, dinoflagellate cysts are commonly dorsoventrally flattened, presenting a dorsal or ventral view to the observer. When viewing in transmitted light, therefore, it is important to establish which surface, ventral or dorsal, is uppermost and which is lowermost.

3.4 SPORES

Spores, in the broadest sense, are produced in the life cycles of the so-called "lower plants" or cryptogams, comprising algae, fungi, bacteria, and the extensive array of seedless metaphytes. It is with the latter category that we are here concerned; thus, the term spore is used in the sense of a durable reproductive cell of bryophytes and of free-sporing pteridophytic vascular plants. In this context, spores of primarily land-based vegetation constitute an increasingly important and diverse element of the paleobotanical record from the middle Paleozoic onwards. Their wide dissemination in nonmarine and nearshore marine strata effectively transgresses the traditional ecological barrier between terrestrial and marine realms. While botanical information from them may be limited, fossil spores have proven exceptionally useful as biostratigraphic indices.

3.4.1 PRESERVATION

When initially deposited, spores are spheroidal or ellipsoidal, hollow bodies (normally disjunct, infrequently in tetrads) that become progressively flattened as the host stratum becomes compressed through sedimentary overburden or other post-depositional factors. The preservability of spore walls depends to a considerable extent on the chemical composition of the wall layers and on the chemical and physical characteristics of the depositional environment. Acidic environments are more favorable than alkaline, reducing than oxidizing, and low-energy than high-energy. Anaerobism is particularly important. Thus, spores are normally found, in conjunction with other, finely comminuted organic matter, in pale to dark grey-black argillaceous to fine-arenaceous rocks (claystones, siltstones, shales, fine-grained sandstones), and of course in coals, lignites, and peats.

3.4.2 HAPTOTYPIC FEATURES

In spores from tetrahedral tetrads, the haptotypic characters consist of three, more or less clearly defined contact areas that are in part delineated by a three-rayed structure centered at the proximal pole (Fig. 3.6). The three rays, commonly at about 120° to each other, constitute the so-called “Y-mark” or triradiate tetrad mark, and extend to, or some distance towards, the equator (the boundary between the proximal and distal hemispheres). This type of spore is the most common and easiest to identify because of the “Y-mark”.

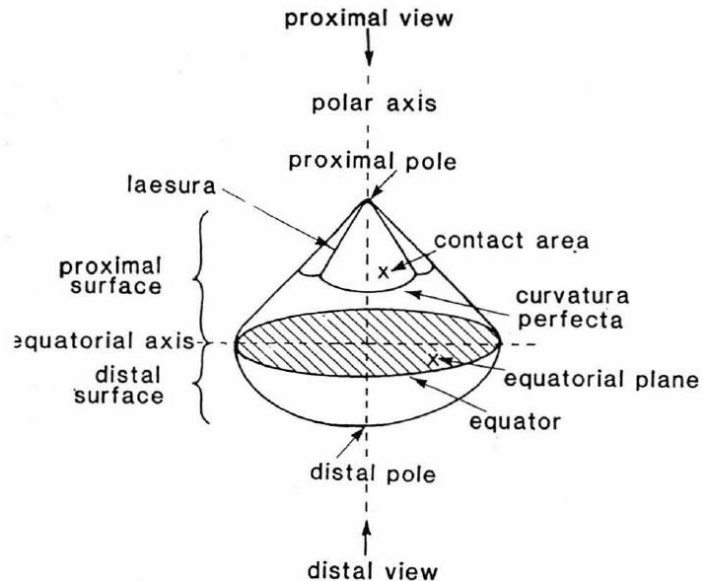


Fig. 3.6 - Equatorial view of trilete spore (adapted from Jansonius & McGregor, 1996).

3.4.3 WALL STRATIFICATION

Appropriate terms for spores are endospore (the inner cellulosic layer which rarely survives fossilization or laboratory-extractive procedures), exospore (the single-to multi-layered wall impregnated

with sporopollenin), and perispore (external to the exospore, and composed of sporopolleninous materials that are more electron dense and chemically less stable than the exospore).

3.4.4 APPLICATIONS OF FOSSIL SPORES

Spores have been important in the resolution of a host of geological and biological problems: in coal seam correlation, biostratigraphy, and age determination; in source rock, provenance, paleoenvironmental, paleoecological, paleogeographic, and phytogeographic studies; and in plant taxonomy, phylogeny, and evolution. Inherent in these applications is an interdisciplinary approach in elucidating relationships between biological, geological, and chemical processes. Dispersed organic matter (kerogen), including spore walls, coalifies at a rate similar to coal macerals when subjected to increasing temperature. The change in color of unoxidized exinite from pale yellow through orange, brown, and black, is a useful measure of carbonization which may be correlated with coal reflectance values and, in a generalized way, with progression through the oil and gas windows.

3.5 POLLEN

Palynological assemblages from Mesozoic and younger nonmarine deposits are mostly dominated by pollen of seed plants, both angiosperms and gymnosperms. To establish correlations between geographically separated regions, the paleopalynologist analyses the diversity of pollen, which provides information that can be used for paleoenvironmental reconstruction and to determine biostratigraphic sequences.

3.5.1 POLLEN TRANSPORT AND SEDIMENTATION

Anemophilous pollen grains are small, very abundant and present characteristics that facilitate pollination by the wind, travelling different distances varying greatly on the parent plant's species, depending also on the wind currents, the plant and its habitat's morphology. Some studies point out pollen distribution displays a bimodal pattern where the pollen is found close by and far from the parent plant. In order that some pollen will successfully land on receptive female organs of the same species, many wind-pollinated plants only release during favourable conditions (low humidity windy days) introducing enormous amounts of pollen in the atmosphere. Long-distance transport of pollen consists of a factor in large scale, regional correlations and age determinations using fossil pollen, although possibly the exception rather than the rule. Pollen reaching water and falling within it as an increased chance of

further transport, eventually being incorporated in sediment layers and becoming fossilized. Plants growing near ponds or small lakes may directly incorporate their pollen into the water body's sediments and therefore, in detailed analysis, reflect the type of plants growing with the pond/lake's surrounding area. The pollen grains preservability depends mainly on the amount of sporopollenin composing the exine, creating a thicker exine the higher sporopollenin value within its constitution.

3.5.2 APPLICATIONS

The application of fossil pollen of gymnosperms and angiosperms in palynological studies are similar in concept from the applications of other plant microfossils groups. Biostratigraphy, paleoclimatology and paleoenvironmental analysis are the center of stratigraphic applications, whilst botanical applications pertain to taxonomy and evolution. For example in applied palynological studies of terrestrial (nonmarine) rocks, pollen, along with spores, help to represent the land flora within the area of its formation also providing means for paleoenvironmental analyses of these rocks. Pollen and spore contained within the nonmarine strata may be the only fossils available to provide age data, consisting of a valuable terrestrial palynomorph asset to geology. Even open marine environment rocks may lack in fossil quantity, but still contain pollen residue. This also assists in the correlating marine rocks of strongly different facies, carrying specialized marine fossils. Pollen and other palynomorphs of terrestrial origin may also effect correlation of terrestrial with marine successions, which in turn, with the co-occurring with marine microfossils or invertebrate fossils such as ammonites, will help with the calibration afforded. In nonmarine rocks, pollen links mostly with palynostratigraphy and vertebrate biostratigraphy, an application sure to enhance both fields and with the utmost development necessity.

CHAPTER 4

TAXONOMY, STRATIGRAPHICAL DISTRIBUTION AND PALAEOECOLOGY

4.1 NOMENCLATURE AND TAXONOMY: SYSTEMATICS

Linnaeus, in the eighteenth century, made a great contribution to science by separating classification and nomenclature. Up to that time, scientific names of plants were (increasingly) long descriptive phrases. Linnaeus supplemented these phrases with binary names that eventually replaced the phrases—just two words, a generic name and a specific epithet as modifier. The binomial combination was unique to a particular species: no homonyms or synonyms allowed. Following Linnaeus, in the 19th century, the principles he had established began to be gathered into lists of rules to be followed. Homonyms (identical name for two different things) cannot be allowed in a rational nomenclature: scientific names need to be unique. Synonyms (different names for the same thing) are potentially also confusing. Synonyms in some instances were proposed independently by different persons for the same entity. In this case, if both names are legitimate in other respects, priority of publication determines which one is the “senior synonym” and hence the correct name. In other cases, different names were proposed for slightly variant entities which later were considered to be identical. The oldest name again survives, as it is the senior synonym. Unique identifiers are needed for items we want to refer to; yet the names selected should not be used themselves as classifiers. Nomenclature and classification in this respect need to be recognized as separate endeavors. Indeed, groups of fossils, including palynomorphs, can be separated and assigned different names on the basis of morphological features that depend on non-biologic matters such as the state of preservation.

4.1.1 CLASSIFICATION

Fensome *et al.* (1993) integrated the classification of fossil and living dinoflagellates by emphasizing wall structure, notably tabulation (and paratabulation); previously, living and fossil dinoflagellates had been largely classified separately. The overall classification of dinoflagellates is summarized on tables 1 and 2. All the information from tables was reproduced referring to DINOFLAJ3.

Table 1 - Classification of dinoflagellates within the Kingdom Protist down to the family rank (adapted from DINOFLAJ3).

Kingdom	Division	Subdivision	Class	Subclass	Order	Family	
Protist	Dinoflagellata	Dinokaryota	Dinophyceae	Gymnodiniphycidae	Gymnodinales	Gymnodiniaceae	
			Dinophyceae	Gymnodiniphycidae	Gymnodinales	Polykriaceae	
						Warnowiaceae	
						Actiniscaceae	
						Dicroerismaceae	
					Ptychodiscales	Brachydiniaceae	
						Amphitholaceae	
						Ptychodiscaceae	
					Suessiales	Symbiodiniaceae	
					Suessiaceae		
					Peridiniphycidae	See Table 2	
					Dinophysiphycidae	Nannoceratopsiales	Nannoceratopsiaceae
						Dinophysiales	Oxyphysiaceae
			Dinophysiaceae				
			Amphisoleniaceae				
			Prorocentrophycidae	Prorocentrales	Prorocentraceae		
			Uncertain	Desmocapsales	Desmocapsaceae		
				Phytodinales	Phytodiniaceae		
					Dinocloniaceae		
		Thoracosphaerales		Thoracosphaeraceae			
		Uncertain	Uncertain				
		Blastodiniiphyceae	Blastodinales	Blastodiniaceae			
				Protoodiniaceae			
Cachonellaceae							
Oodiniaceae							
Haplozoaceae							
Apodiniaceae							
Uncertain							
Noctiluiphyceae	Noctilucales	Noctilucaceae					
		Kofoidiaceae					
		Leptodiscaceae					
Uncertain	Uncertain	Uncertain					
Syndinea	Syndiniophyceae	Syndiniales	Duboscquellaceae				
			Syndiniaceae				
			Amoebophryaceae				
			Sphaeriparaceae				
			Uncertain				
Uncertain	Uncertain	Arpyloraaceae					

Table 2 - Subdivision of the subclass Peridiniphycidae (adapted from DINOFLAJ3).

Subclass	Order	Suborder	Family
Peridiniphycidae	Gonyaulales	Rhaetogonyaulacineae	Rhaetogonyaulacaceae
		Cladopyxiineae	Mancodiniaceae
			Cladopyxiaceae
			Scrinocassiaceae
			Lotharingiaceae
			Pareodiniaceae
			Uncertain
		Goniodomineae	Goniodomaceae
			Pyrocystaceae
		Gonyaulacineae	Gonyaulacaceae
			Areoligeraceae
			Ceratocoryaceae
		Ceratiineae	Ceratiaceae
		Uncertain	Heterodiniaceae
			Crypthecodiniaceae
			Uncertain
		Peridinales	Heterocapsineae
	Peridiniineae		Peridiniaceae
			Protoperidiniaceae
			Podolampaceae
			Uncertain
	Glenodiniineae		Glenodiniaceae
	Uncertain	Uncertain	
	Uncertain	Comparodiniaceae	
		Oxytoxaceae	
		Stephanelytraceae	
		Dollidiniaceae	
Uncertain			

4.1.2 THE MAJOR UNITS OF DINOFLAGELLATA

The dinoflagellates are encompassed within the division Dinoflagellata. Members of this division are distinguished by having, at some stage in their life cycle, a motile stage with two dissimilar flagella. The division Dinoflagellata includes subdivisions Syndinea and Dinokaryota. The former comprises a small group of parasites that have the basic dinoflagellate form but lack the typical dinoflagellate-style nucleus (i.e. a dinokaryon). Members of the Dinokaryota possess a dinokaryon during at least part of their life cycle.

Within the subdivision Dinokaryota, the classes Blastodiniophyceae and Noctiluophyceae have a dinokaryon during part of the life cycle only (i.e. a temporary dinokaryon) and have no known fossil representatives; the class Dinophyceae encompasses taxa with a permanent dinokaryon and contains all known fossils (Jansonius & McGregor, 1996). Within the class Dinophyceae, members of the subclass Gymnodiniophycidae have a gymnodinioid or suessoid tabulation type, members of the Peridiniphycidae have a gonyaulacoid-peridinioid tabulation type and members of the Dinophysiphycidae have a nannoceratopsioid tabulation type (Fig. 3.3).

4.2 EVOLUTIONARY PATTERNS

Evitt (1981) cautioned against a literal interpretation of the dinoflagellate fossil record on the basis that few living dinoflagellates have only a limited relevance in elucidating the pattern of dinoflagellate phylogeny. However, if there were no dinoflagellate fossils, we would be unaware of the Nannoceratopsiales – the “missing link” between the Peridiniphycidae and Dinophysiphycidae; we would not know that peridinialean and gonyaulacalean tabulations have been separate since Jurassic times; we would know nothing of the early Mesozoic Rhaetogonyaulacineae – a precursor of later gonyaulacaleans and possibly also of the Perdiniales (Jansonius & McGregor, 1996).

The dinoflagellate record has a distinctive distribution. Fossil dinoflagellates are rare, absent or unrecognized in pre-Mesozoic strata but, starting in the Triassic, increase steadily in species diversity until the late Cretaceous and early Cenozoic, then decline towards the present day (Fensome *et al.*, 1999).

Regardless of the constraints of the record, fossil dinoflagellates are a rich source of material for cladistics analyses. One of the principles of cladistics is that taxa are compared and arranged into *cladograms* such that the most efficient or parsimonious set of relationships is identified. Such cladistics analyses seek to analyze relationships through morphology and do not involve a historical perspective. The fossil record of dinoflagellates appears to show evolutionary patterns similar to those of other groups, such as a major adaptive radiation, which occurred in dinoflagellates in the Late Triassic and Early Jurassic (Fig. 4.1).

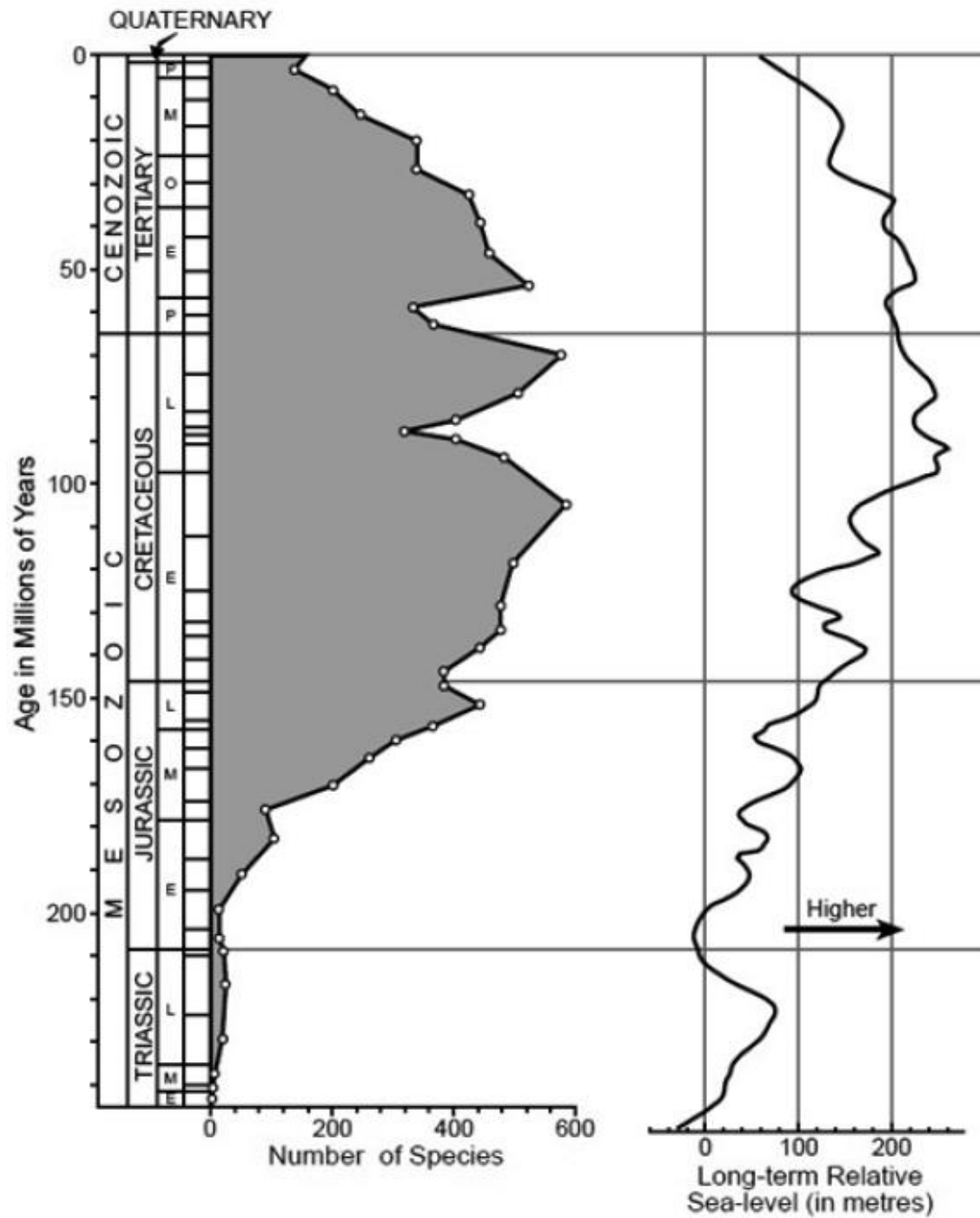


Fig. 4.1 - Fossil dinoflagellate diversity (number of species) during the Mesozoic and the Cenozoic (until the Quaternary) and its overall correlation with in long-term sea level (after McCrae *et al.*, 1996).

Fig. 4.2 relates the classification of dinoflagellates to geochronologic units (Mesozoic stages and epochs) by plotting the time of appearance of different taxonomic subclasses and orders and the number of species per family obtained in the fossil record. The red line corresponds to the Cenomanian Stage, which is the stratigraphic interval focused in the present work.

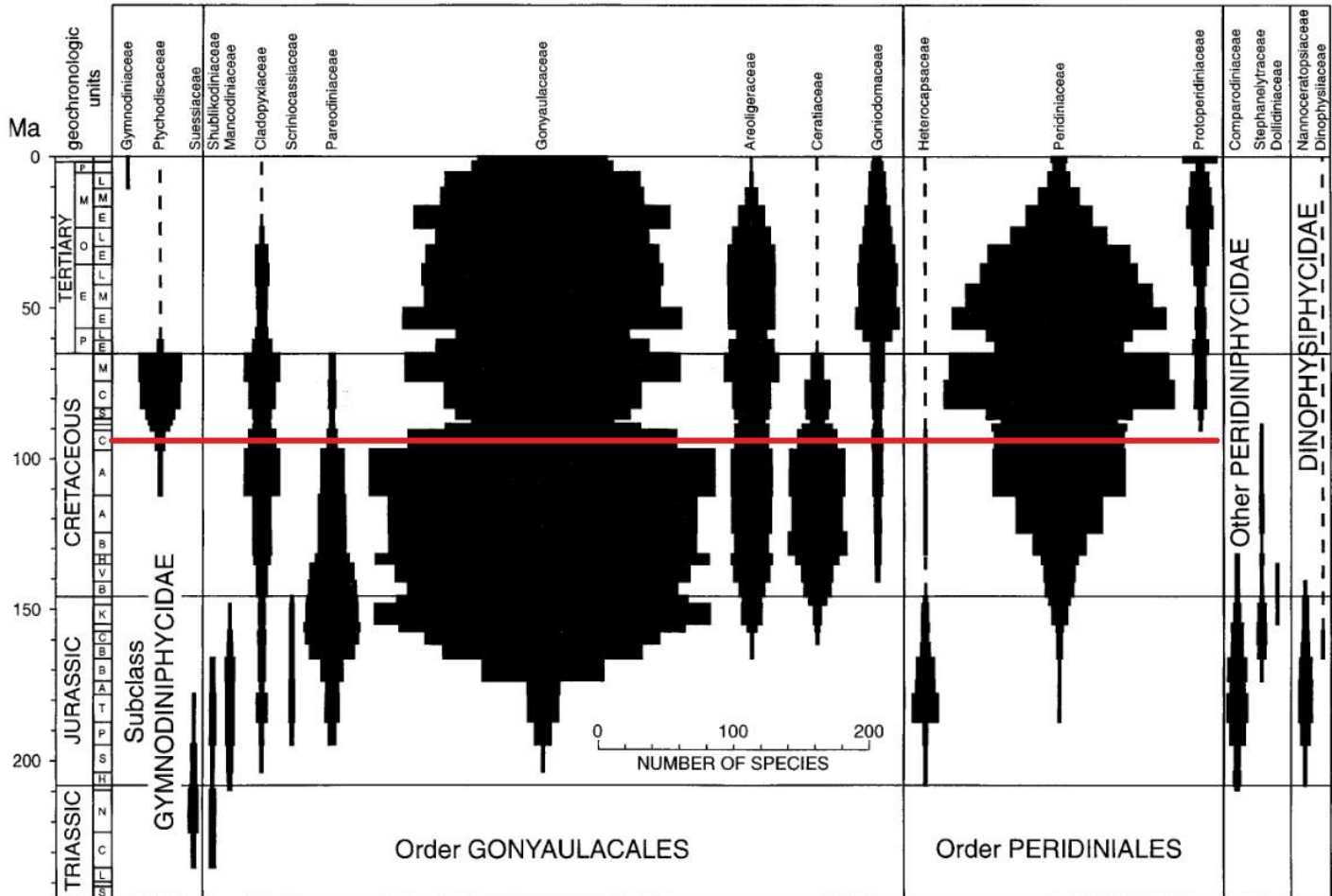


Fig. 4.2 - Number of known dinoflagellate fossil species per family and per time interval (Mezosoic stages and epochs) represented as spindle plots. The red line corresponds to the Middle Cenomanian time interval (adapted from Fensome *et al.*, 1999).

According to Fensome *et al.*, (1999) after dinoflagellates first appear in the Mesozoic record, there was a proliferation of morphological types as represented by individual families. By the mid Jurassic, practically all major variations within the gonyaulacoid-peridinioids were already present. Indeed, of the important groups that appeared after the mid Jurassic, relatively minor morphological changes are involved: ceratiaceans are essentially gonyaulacaceans with horns and minor changes in episomal tabulation; peridinia- ceans differ from the early heterocapsaceans in dropping a single apical plate boundary; and protoperidiniaceans derived from the peridiniaceans by the reduction in number of circular plates.

4.2.1 THE PHYLOGENY OF DINOFLAGELLATES

From cytological and biochemical evidence, dinoflagellates appear to be an ancient group of protists, most authorities now believing them to have originated in the Late Precambrian. These earliest dinoflagellates either produced no preservable cysts or generated cysts (acritarchs) whose morphology does not demonstrate their affinity. A study of openings and process distribution in Early Paleozoic acritarchs led Lister (1970) to conclude that some way be the cysts of thecate dinoflagellates. However, the tabulations produced by Lister were speculative, and not convincingly similar to any Mesozoic-Cenozoic or modern tabulations.

4.3 ECOLOGY AND PALAEOECOLOGY

Since the early work of Wall *et al.* (1977), many studies have documented the geographical distribution of modern dinocysts on the sea floor (Fig. 4.3). There are now regional data sets for the North Atlantic and the Arctic Oceans, the circum-Antarctic Ocean, the low latitudes of the Atlantic Ocean, the eastern and western Pacific Ocean margins. These data sets were used to define relationships between

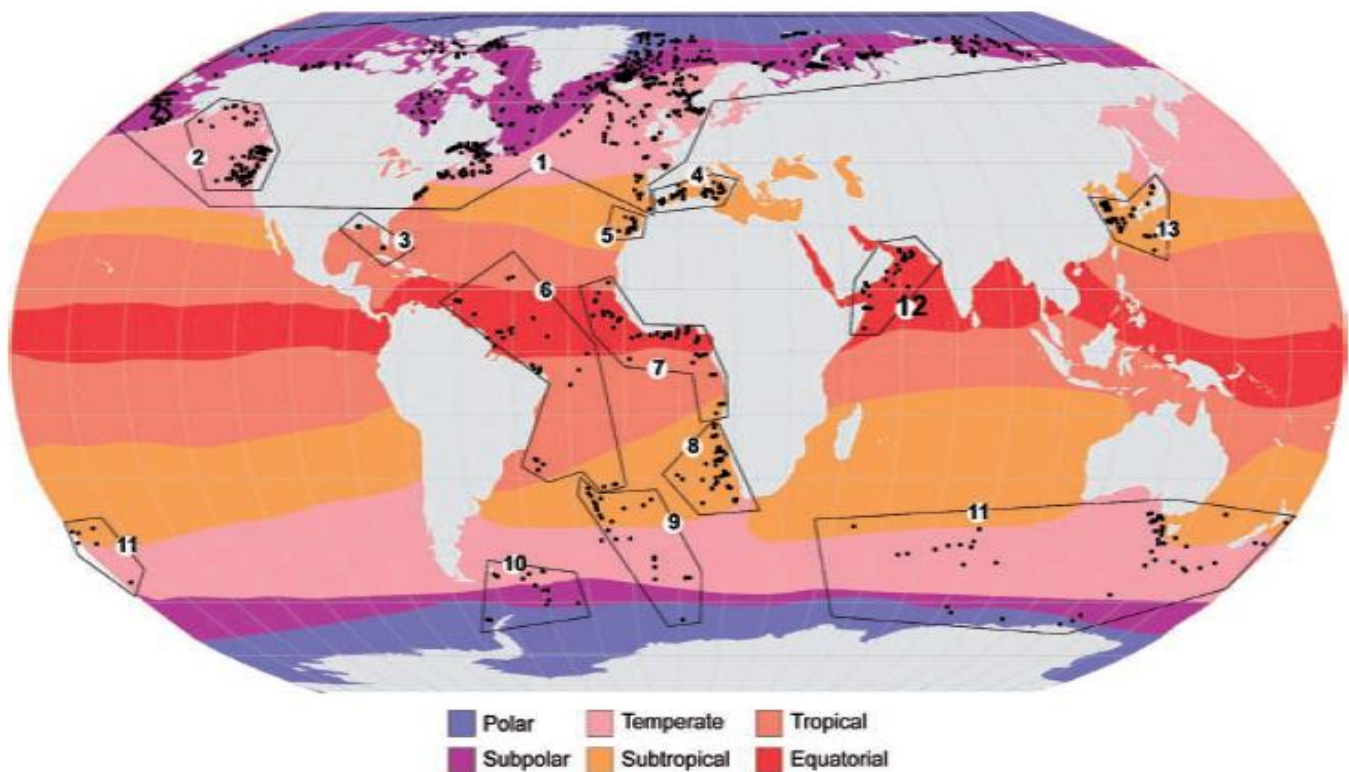


Fig. 4.3 - Map of the World Ocean showing the areas where the distributions of organic-walled dinoflagellate cysts in sediment have been documented from the study of assemblages in surface sediments. Climatic provinces after Gross and Gross (1994). Numbers from 1 to 13 indicate regional data sets. Taken from de Vernal & Marret, 2007.

the distribution of dinocyst assemblages and hydrographic parameters, notably the temperature, salinity, sea-ice cover and productivity or eutrophication. In parallel to studies dealing with modern distribution of assemblages, the number of paleoceanographical studies using dinocysts has increased significantly during the last two decades. Many of these studies present empirical interpretations of the assemblages in terms of productivity, salinity or temperature changes (de Vernal & Marret, 2007).

Following de Vernal & Marret (2007), dinocysts are found in marine sediment from polar to tropical environments. In general, the diversity of species decreases from the tropics to the poles, although the dinocyst concentration can be very high in Arctic seas and subpolar seas. More than 60 *taxa* have been recorded in the Northern Hemisphere, but only 10 to 12 *taxa* are common in the Arctic seas. In the southern hemisphere also, there is a gradient of decreasing diversity toward the pole. From high to low latitudes, the increase in the number of species is related to increased temperature (Figure 4.4). The relative abundance of many *taxa* also varies in relation with sea-surface temperatures (SST), either annually or seasonally. Multivariate analyses further support the determining influence of SST in *taxa* and assemblage distribution, both at regional or hemispheric scales. The existence of a relationship between SST and dinocyst assemblages is unquestionable. However, this relationship is most probably season-dependent. In high latitudes, the bloom of dinoflagellates, which is often followed by encystment, most frequently occurs during summer after the diatom bloom. Therefore, it can be assumed that dinocyst assemblages are mainly related to summer SSTs. However, dinoflagellates and their cyst population also appear dependent upon the temperature changes over the annual cycle. The overall life cycle of dinoflagellates and cyst production can take place over a few weeks to over a few months, depending upon the *taxon*. In polar seas where the ice-free season is very short, only the species having the ability to form cysts in a short time can develop. The seasonal constraint is low in intertropical environments, but possibly plays an important role on determining the abundance of *taxa* in temperate regions. Actually, the distribution of dinocyst assemblages in the North Atlantic and adjacent subpolar and polar seas suggests a relationship between dinocyst assemblages and the seasonality, as expressed by the difference between the coldest and warmest months.

Salinity tolerance

Thermic domain

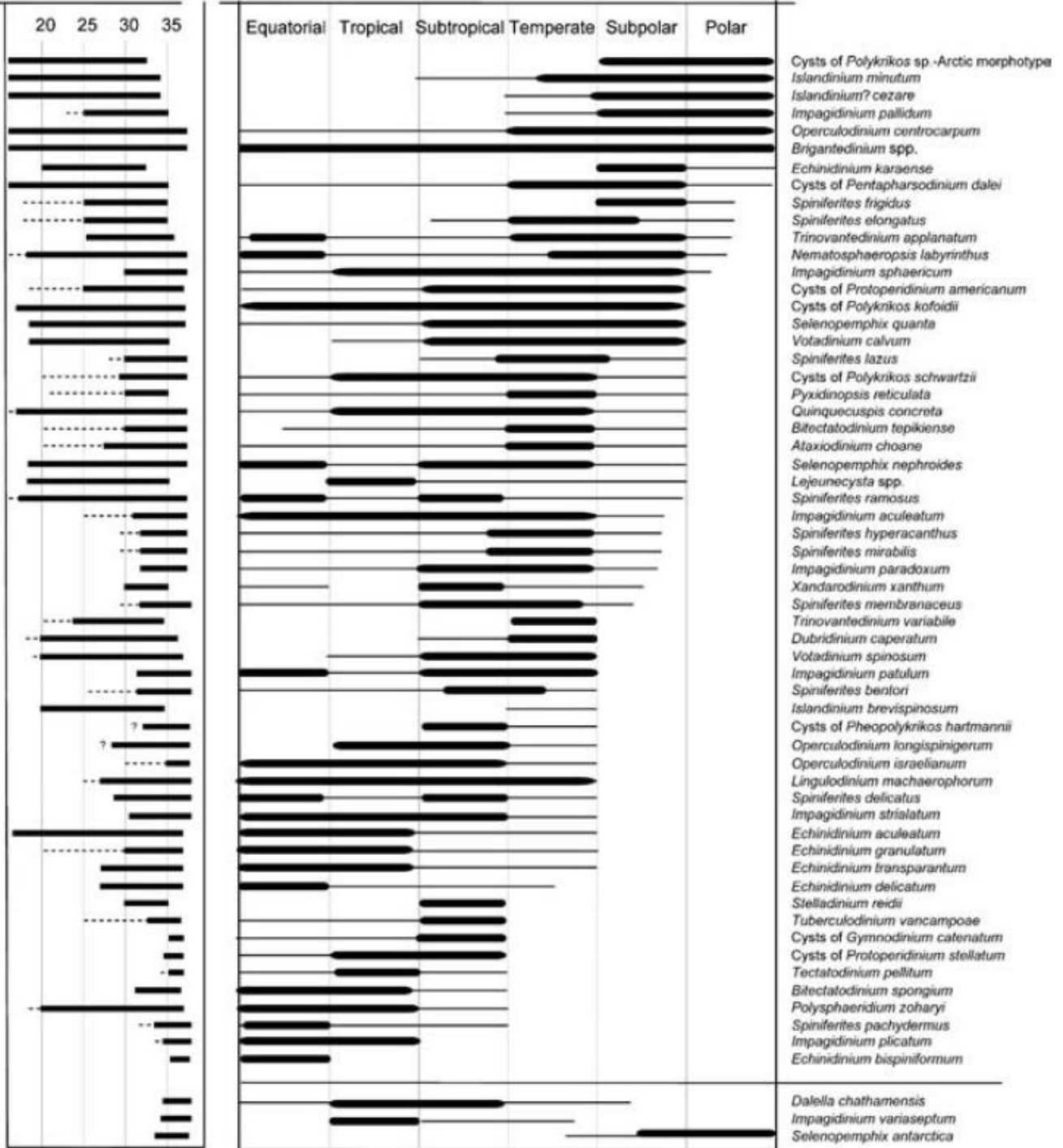


Fig. 4.4 - Diagram showing the known distribution of the main dinocyst taxa in surface sediments according to bioclimatic domains and their salinity tolerance (taken from de Vernal & Marret, 2007).

4.4 SPORES: NOMENCLATURE AND TAXONOMY

When naming dispersed fossil spores, paleopalynologists should adhere to the provisions of the International Code of Botanical Nomenclature (ICBN). The ICBN takes cognizance of the fragmental complexities of the paleobotanical record by formally recognizing, in addition to normal whole-plant *taxa* (modern “eutaxa”), form-genera and form-species (“parataxa”) that are applicable to the whole range of disjunct fossil-plants entities (i.e. dispersed spores and pollen grains, together with dissociated leaves, roots, fructifications, etc.). The essential raw materials of spore-paleopalynology are disjunct microfossils of diverse ages and diverse morphology. Morphology obviously provides the principal – and only really objective – basis for taxonomic discrimination; consequently, form-genera and –species are indeed aptly termed.

4.4.1 CHARACTERISTICS OF BRYOPHYTIC AND PTERIDOPHYTIC SPORES

Although much effort has been directed towards identification of pollen morphological characters that define angiospermy, little attention has been focused on ascertaining spore morphological features that discriminate between bryophyte and pteridophyte spores (Jansonius & McGregor, 1996). Apertural, sculptural, and architectural characters are reiterated throughout the Bryophyta and the various divisions of free-sporing pteridophytic plants; no single character or set of characters is unique to any division or class. Nonetheless, distinct trends are discernible with respect to the type and position of the aperture and to wall stratification and

ultrastructure (Table 3). For instance, spores with hilate apertures are restricted to hepatics (liverworts), hornworts, and mosses. The apertures of ferns and fern allies are consistently proximal, whereas they may be distal or proximal in the hepatics, hornworts, and mosses (Table 3). Although knowledge of spore-wall ultrastructures is far from complete for either living or fossil bryophytes and pteridophytes, preliminary results indicate lamellate stratal units in spores of bryophytes, fern allies, and the lower ferns, whereas in the higher ferns the exospore is generally homogeneous.

Table 3 - Distribution of selected characters among spores of bryophytes and pteridophytes (taken from Jansonius & McGregor, 1996).

Character	Hepatics/ Hornworts	Mosses	Fern Allies	Ferns
Aperture type:				
hilate	+	+		
trilete	+	+	+	+
monolete		+	+	+
Aperture position:				
proximal	+	+	+	+
distal	+	+		
Sporoderm components:				
mainly exospore	+	+	+	+
mainly perispore				+
Exospore ultrastructure:				
lamellate strata				
present	+	+	+	+
absent		?	?	+

4.4.2 EVOLUTION

Sporae dispersae – by far the most abundant and ubiquitous of plant organs in the fossil record – are preserved as tough, chemically resistant envelopes that contained protoplasmic units. The array of spore morphological features present in the fossil record and in living plants has been evaluated in both evolutionary and adaptive contexts (Jansonius & McGregor, 1996).

The progression of homospority to heterospority is reflected in the *sporae dispersae* record (Fig. 4.5). Earliest occurring spores are small, but larger spores appeared in the Late Silurian. In the Devonian, spores progressively assumed distinct size-differentiation, the largest spores representing megaspores of heterosporous plants. Heterospority is considered a derived character that arose independently in several divisions of the pteridophytes. Plots of apertural configuration against the time scale reveal the following oldest-to-youngest sequential introductions: alete, proximally hilate, trilete, monolete, and distally hilate (Fig. 4.5). Notwithstanding the controversy surrounding alliance of the earliest alete spores, their occurrence in tetrads suggests that the trilete condition is derived from alete. However, the possibility that the hilate condition was an independent innovation and not derived from alete should not be discounted.

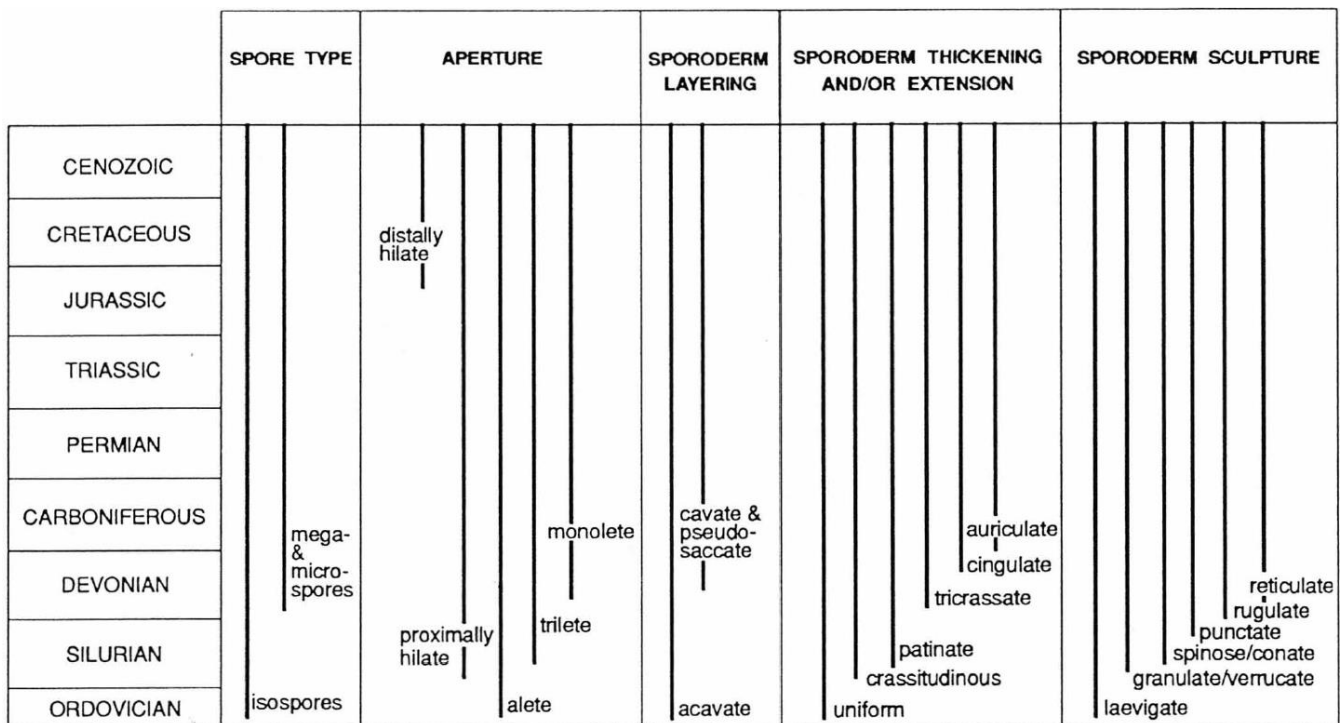


Fig. 4.5 - Chronological record of spore characters (taken from Jansonius & McGregor, 1996).

4.5 POLLEN EVOLUTION: ORGAN OR ORGANISM?

Traditionally, botanists consider the evolution of plants with reference to the sporophyte generation only. Paleopalynologists, however, focus on the evolution of pollen. The traditional caveat for anyone considering the “evolution of pollen” is that pollen does not evolve; only the plants that produce it evolve. At least in the conventional view, pollen is a plant part, or organ, not an organism. Although this view may be essentially correct, it is well to keep in mind that pollen grains are actually the free-living gametophyte generation of seed plants. They even have a genome that differs from that of the parent plant, at least in having only half the number of chromosomes of the parent, but conceivably in other small ways as well. Pollen grains clearly are not organs such as leaves, which truly are only parts of a whole plant.

4.5.1 OVERVIEW OF PHYLOGENETIC

Phyletic relationships among species may be suspected if it is difficult to differentiate species or to assign specimens to one species. Possible relationships among species can be elucidated only by careful taxonomic study. Probable ancestor-descendant relationships are indicated by the relative stratigraphic positions of fossils. The significance of phylogenetic studies of pollen is twofold: they suggest something of phyletic origins, which may aid in understanding past and living floras, and they provide a basis for age determination and zonation of stratigraphic successions. The use of palynological lineages in biostratigraphy appears to have much potential, yet it has been neglected in favor of interval zones based on individual species (Jansonius & McGregor, 1996).

4.5.2 EVOLUTION

The existence of two palynologically distinct major groups of flowering plants was first proposed by the Swedish palynologist Gunnar Erdtman (1960): those with a single (polar) pollen aperture (monosulcates) and those with three (equatorial) pollen apertures (tricolpates). Species with tricolpate pollen apertures (or aperture patterns derived from this) form a single major clade, now more commonly known as the eudicots, whereas species with monosulcate or monosulcate-derived apertures represent a series of basal angiosperm lineages, including Piperales and monocots (Fig. 4.6). A single polar aperture (sulcus) is found in many basal angiosperms and also in all the closest angiosperm relatives, such as conifers and Gnetales. Thus, optimization of this character on recent angiosperm phylogenies indicates an evolutionary transition at the base of the eudicot clade from one aperture to three (Furness & Rudall, 2004).

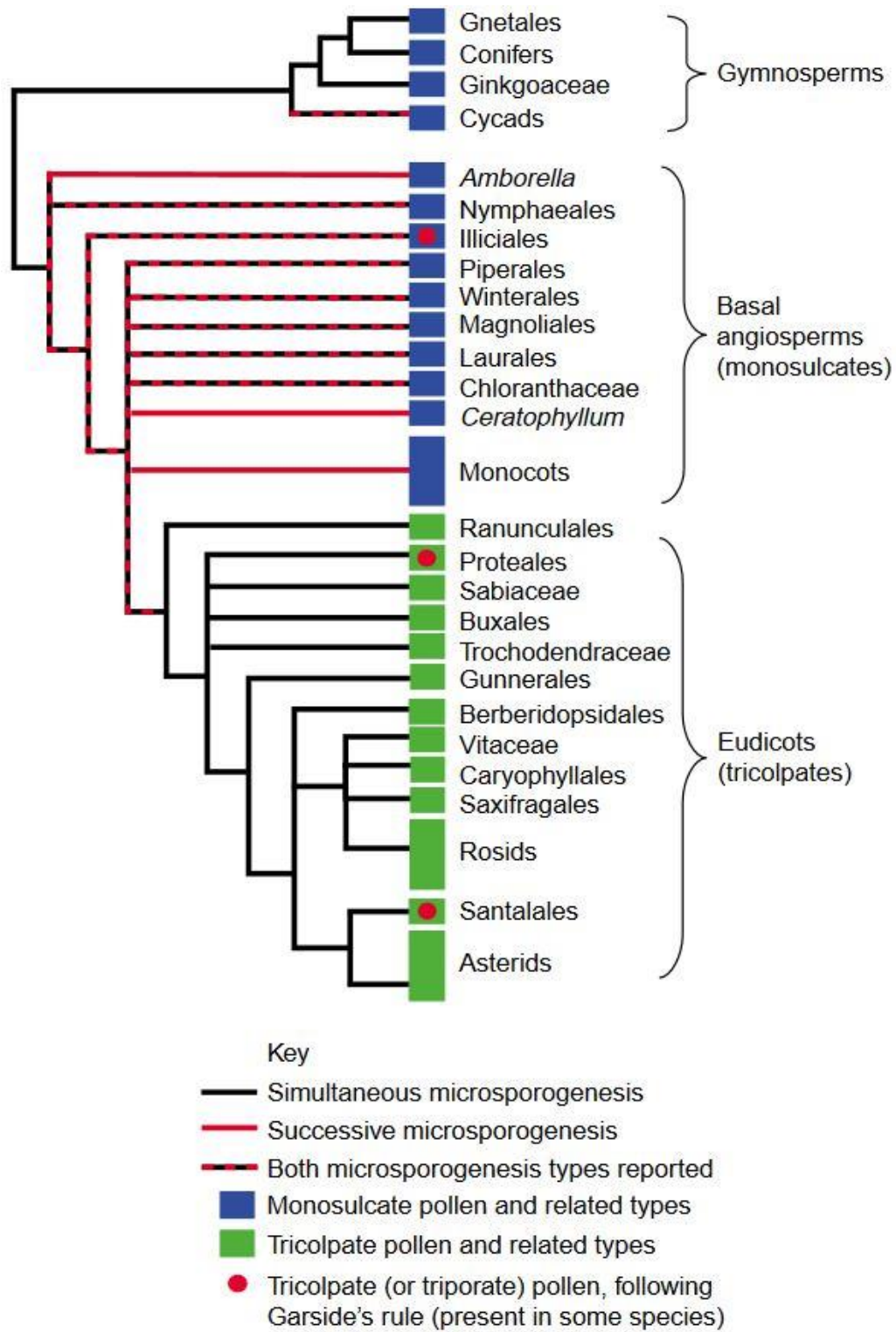


Fig. 4.6 - Diagram of phylogenetic relationships of major angiosperm clades, showing taxonomic position of families and orders in which simultaneous and successive microsporogenesis (lines) and tricolpate and monosulcate pollen (boxes) have been reported (Furness & Rudall, 2004).

Possession of three or more pollen apertures might offer a selective advantage because of the increased fertilization rate, perhaps contributing to the subsequent rapid radiation and success of eudicots. When coupled with a particular developmental pathway, this feature offers a phenotypic acquisition that could be seen as a key innovation crucial to eudicot success, particularly in the context of concomitant diversification of potential pollinators. In the same way, key innovations, including a faster reproductive cycle, specialized biotic pollination and double fertilization, have led to the success of the angiosperms relative to other seed plants (Furness & Rudall, 2004).

CHAPTER 5

MATERIAL AND METHODS

5.1 SAMPLING

The location of Nazaré and the proximity of its promontory facilitated the sample collection procedure. By this way, it was possible to draw the route taken through Google Earth (Fig. 5.1).



Fig. 5.1 - Sample collection location, shown on google earth with path taken from the center of Nazaré. (GPS coordinates: N:39.60435; W:009.08191)

Until the collection point, the path was made by foot from the city center. The base of the promontory required passage through rocks, some of them loose, so caution was needed (Fig. 5.2.).



Fig. 5.2 - Photograph of the path taken to the collection site. Professor Lígia Castro is in the photograph. Taken by Luís Fernandes.

Arriving at the desired location, a stratigraphic profile was elaborated, including a section with an altitude of 15 meters and 27 strata, alternating between layers of marl and limestone (Fig. 5.4). The criteria used to determine which layers offered the best lithology for sampling were essentially the type of particle size (thin) and the color of the sediment (as dark as possible as it indicates a higher amount of organic matter). Therefore, 12 samples of marl layers, about 200 grams each, were extracted from the geological profile (Fig. 5.3). The collection strata were: NAZ 72, NAZ 73 NAZ 76, NAZ 79, NAZ 81, NAZ 83, NAZ 85, NAZ 88, NAZ 92 and NAZ 94. Note that strata 85 and 92 were divided into Base (B) and Top (T), whereby 2 distinct samples were collected from these strata. Additional care was taken in keeping the sampling restricted to the inner sediments in each layer, avoiding the top sediments, typically more exposed and vulnerable to contamination. The collected sediments were placed in appropriate plastic bags which were properly identified and taken to the laboratory for analysis.



Fig. 5.3 - Collection of samples. Photographs taken by Luís Fernandes.

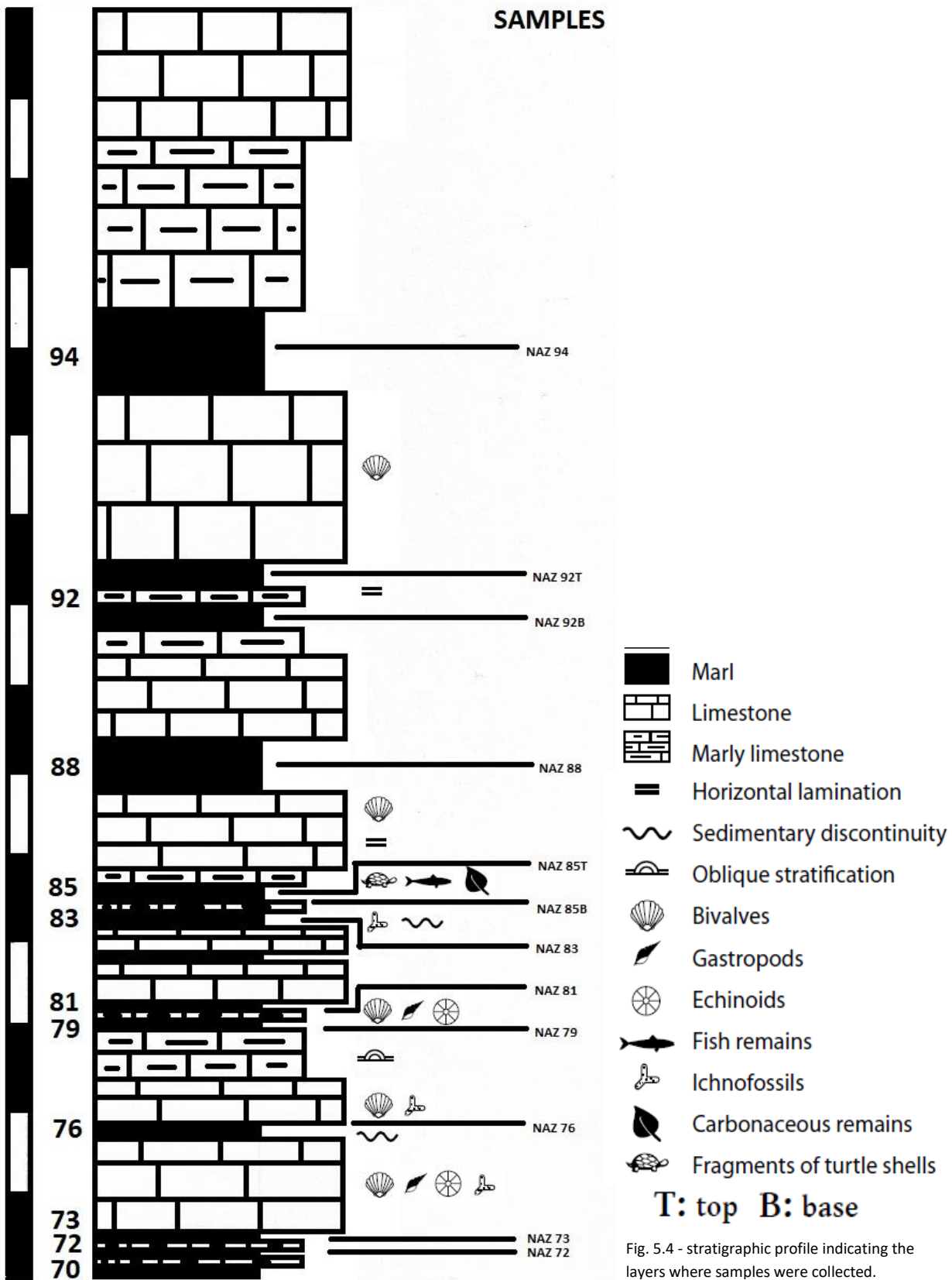


Fig. 5.4 - stratigraphic profile indicating the layers where samples were collected.

5.2 PALYNOLOGICAL TECHNIQUES

According to Jansonius & McGregor (1996), the foundation of any palynological research is technique. Accurate taxonomic, biostratigraphic, paleoecological and quantitative inferences depend on proper procedure. Effective comparisons between and within specific studies require a certain standardization of methods, with accommodation for innovation. Indifferent execution of maceration and extraction techniques will adversely impact all subsequent analyses. Figure 5.5 illustrates the basic steps for paleopalynological processing as outlined by these authors.

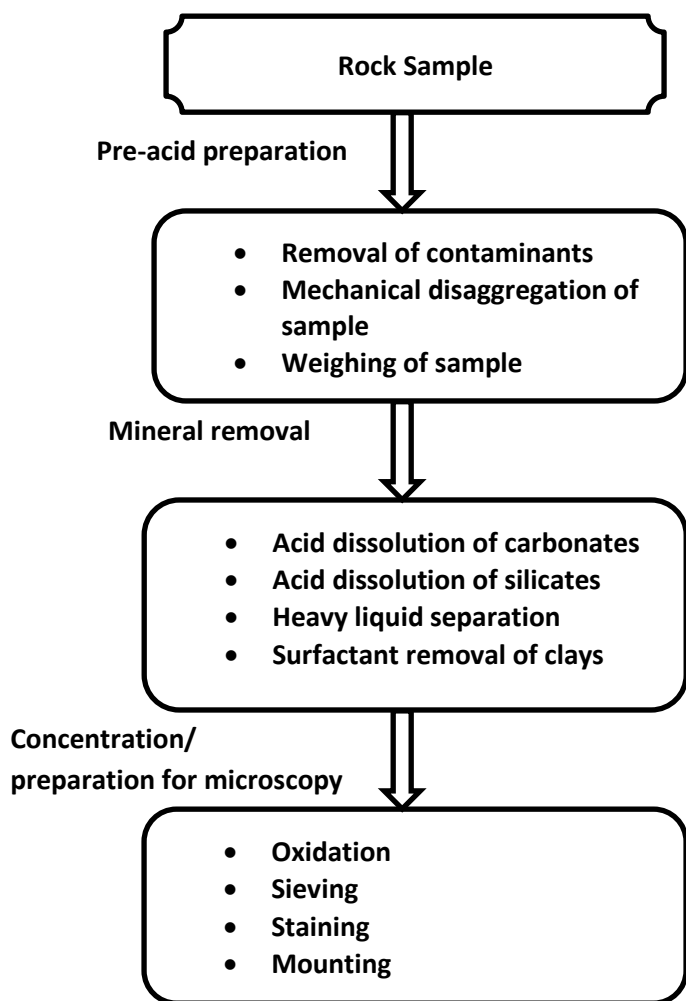


Fig. 5.5 - Standart paleopalynological processing procedures

Discussions with palynologists and/or palynological processors made it clear that each laboratory has developed its own unique processing methods. Techniques are often hybrids, and the available labware may reflect local circumstances.

5.3 LABORATORY SAFETY STANDARDS

Jansonius & McGregor (1996) noted that efficient laboratory equipment arrangement, knowledge of safety features and procedures, and understanding of chemical reagents and the by-products of processing are imperative for all personnel. There should be clear pathways between work stations and safety equipment such as shower, eye wash and fire extinguisher. This is particularly important in event of exposure to toxic fumes or irritants that may impair or temporarily disorient an individual. Fume hoods should have sufficient power to exhaust all toxic vapors. Bulk acid should be housed in properly ventilated storage bunkers. Chemical containers and processing utensils should be washed and neutralized before being properly discarded. Used reagents must be decanted into neutralizing bunkers. These bunkers must be serviced regularly by a responsible toxic/hazardous waste company.

Five general rules apply when working with chemicals: 1, never work alone; 2, always work with acids in a well ventilated fume hood; 3, add acids to water, never vice versa; 4, use specified and appropriate emergency and first aid procedures; and, 5, always consult a physician after exposure to caustic chemicals. All reagents used in palynological processing are potentially harmful. Initial treatments for neutralizing commonly used acids and reagents are listed below:

- Ethyl alcohol (C_2H_5OH). Inhalation of undiluted vapor may cause nausea, vomiting and irritation of mucus membranes. Contact of 100% ethanol with eyes or skin will cause irritation. Readily absorbed through skin. Flush affected areas with water. If swallowed, drink water and call a physician. This reagent, in pure form, is flammable, and may burn with a nearly invisible flame.
- Hydrochloric acid (HCl). Both aqueous and vapor states can disfigure or destroy tissue. Inhalation of fumes will irritate or damage mucous membranes. Serious burns are susceptible to infection. Flush affected area with copious amounts of water. If ingested, drink several glasses of water and seek medical attention.
- Hydrofluoric acid (HF). Both liquid and gaseous states are extremely dangerous. This acid is severely corrosive to the skin even in low concentration. If concentration is 20% or less, burns may not be felt until several hours after contact. Concentrations of 21% to 60% are usually detected earlier, but 61% to 100% are felt instantly. The acid is readily absorbed and often affects tissues below the skin. The reaction between hydrofluoric acid and silicate rock is exothermic, so great caution must be exercised. Never add hydrofluoric acid and stir at the same time because the explosive response may be delayed. Violent reactions in beakers may be slowed by applying ethanol or methanol from spray bottles.

5.4 MATERIAL

For a laboratory procedure, it is important to have a good understanding and perception of all materials to be used for the process to be successful. Below is a list of all materials used during laboratory preparation (Figure.5.6).

- ✓ Laboratory equipment coat and gloves);
- ✓ Toilet paper;
- ✓ Hydrochloric acid 37% (HCl);
- ✓ Hydrofluoric acid 48% (HF);
- ✓ Ultrasonic cleaner;
- ✓ 125 μm sieves;
- ✓ 15 μm sieves;
- ✓ Heating plate;
- ✓ Straws;
- ✓ Electric kettle;
- ✓ 12 Samples;
- ✓ White paper sheets;
- ✓ Precision scale;
- ✓ Electrothermal magnetic stirrer;
- ✓ Reusable Plastic Measuring Cups (100 ml);
- ✓ Vials;
- ✓ Plastic pipettes;
- ✓ Electrothermal plate;
- ✓ Goblet;
- ✓ Soft toothbrush;
- ✓ Fume Hoods;
- ✓ Teflon cups;
- ✓ Hammer;
- ✓ Distilled water;
- ✓ Distiller water machine;
- ✓ Calgon® or Sodium hexametaphosphate;
- ✓ Labels;
- ✓ Alcohol (90%);
- ✓ Glycerin;
- ✓ Microscopic slides and lamellae;
- ✓ Varnish.



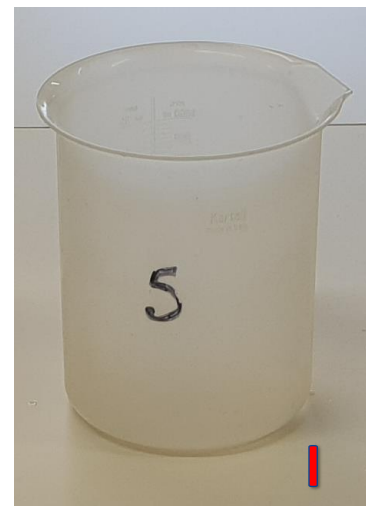
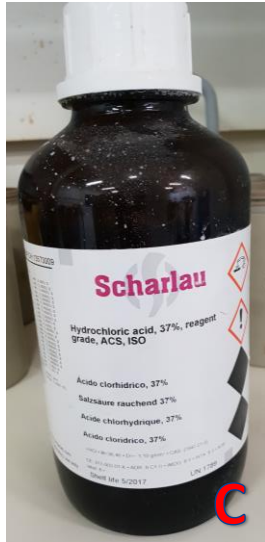


Fig. 5.6 - Various materials used in the laboratory. The images are not to scale. A – Shaker; B – Ultrasound cleaner; C – Brand of Acids used in demineralization; D – Calgon and sieve; E – Lamellae, glycerin, straws, micro slides and toothbrush; F – Overview of lab set; G – Teflon cup; H – Vial; I – 1-liter cup.

5.5 LABORATORY PREPARATION

Castro (2006) noted that good palynological procedure is an individualistic art requiring astute skill, knowledge and hands-on involvement, and depends on the “know-how” of each researcher and technique, along with some personal involvement. It is essential to have access to adequate lab equipment. Below, the steps related to the entire laboratory procedure, performed at Departamento de Ciências da Terra (DCT) at Faculdade de Ciências e Tecnologias (FCT) from Universidade NOVA de Lisboa, are described:

1. Clearly identified teflon cups and their lids were cleaned with alcohol, in order to avoid contamination;
2. The samples were smashed into thinner particles, which potentiates the action of the acids, with a suitable hammer;
3. A sheet of white paper was placed on top of a precision scale. The tare was removed and about 30 grams were weighed for each sample;



Fig. 5.7 - Sample weighing

4. The fragments were placed in the cups, which allow treatment with hydrochloric and hydrofluoric acids;
5. The sediment underwent several attacks with acids with different concentrations, in order for the mineral fraction to be progressively removed. This was performed in a laboratory hood that limited exposure to toxic fumes and facilitated the handling of the chemical products;

6. The first acid applied was hydrochloric acid 37% (for the elimination of carbonates). Some



samples had more carbonates, so it was necessary to add a little alcohol to slow down the reaction. Every 15 minutes the cups were shaken to try to dissolve the contents retained on the walls;

7. After 1 hour, distilled water was added to the cups, without filling completely and attempting to clean the walls;
8. After 4 hours, the water was removed, being careful not to lose sediment, and distilled water was added again for more 4 hours;



9. The water was removed, always being careful not to lose sediment, and hydrofluoric acid 48% (for the elimination of silicates) was added. This process can be quite dangerous, so the user should always use mask and laboratory gloves. The cups were closed with the lids and placed on a electrothermal magnetic stirrer, where they remained at least 4 hours;

10. The electrothermal magnetic stirrer was turned off and the samples rested for 1 hour. As in some cups reaction still occurred, more HF was placed in all the cups and allowed to stir until

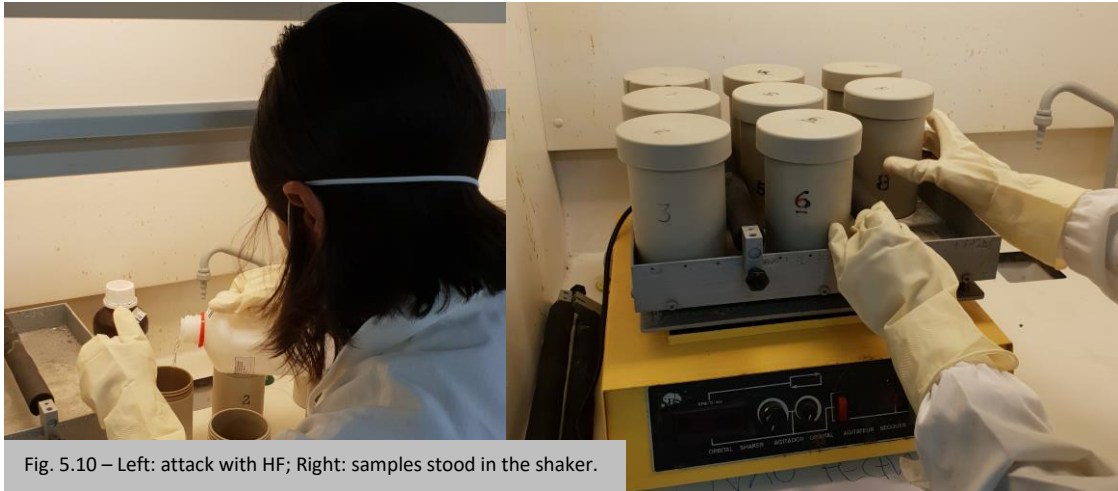


Fig. 5.10 – Left: attack with HF; Right: samples stood in the shaker.

- the next day;
11. The electrothermal magnetic stirrer was turned off and the samples stood for 4 hours;
12. The cups were opened (be careful when removing the lids because drops may fall) and hydrochloric acid 37% (for the elimination of fluorides and sulfides) was added;
13. The cups were filled with distilled water and waited 4 hours;
14. The water was removed, without losing sediment, and the cups were stored in the laboratory hood with more distilled water overnight;
15. An ultrasonic cleaner was disinfected and distilled water was added in. 1-liter laboratory sample cups were cleaned with alcohol. 125 μm sieve were used to filter samples of teflon cups into the 1-liter cups. With a squirt of distilled water, the maximum amount of sample possible for filtration, which may contain palynomorphic material, was cleaned. Everything that went through the 125 μm sieve was the intended content. The sieves were washed with running tap water by the hand, so the net did not burst. The sieves were immersed in the ultrasonic cleaner for 10 minutes;



Fig. 5.11 - Filtration with 125 μm sieves

16. The water was removed from the cups and a half *calgon* lid diluted in a jug of warm distilled water (for the elimination of mudstone) was added;
17. After 4 hours, the water was again removed and distilled hot water was added with an electric kettle. The samples rested during the weekend;



Fig. 5.12 - Attack with Calgon

18. The water was removed and distilled water was added again;
19. Sieves of 15 μm were used to filter samples from the 1-liter laboratory cups. Everything that remained inside the sieve was the intended content. The sieves were gently rotated to



Fig. 5.13 - Filtration with 15 μm sieves

- facilitate filtering, which proved to be more difficult and time consuming. Vials were labeled for each sample. The contents of the sieves were drained into the respective vial. The samples rested for 4 hours. The sieves were placed in the ultrasonic cleaner;
20. With a plastic pipette for each sample, water was withdrawn from the vials to remove unwanted contents in suspension. One drop of HCl was added in each vial so that the fungi did not proliferate;
 21. A sheet of paper was placed on top of a heating plate at less than 50°C. A small goblet with melted suppository glycerin (because it is cheap, transparent, serves as a glue and a good

anti fungus) was placed on top of the plate. The slides were placed on the sheet of paper, previously cleaned with alcohol;

22. Two slides were labeled for each sample. Straws were used to place a small amount of sample from the vials in the slides, to favor the dispersal of the palynomorphs (1 straw for each sample). These were left to dry;

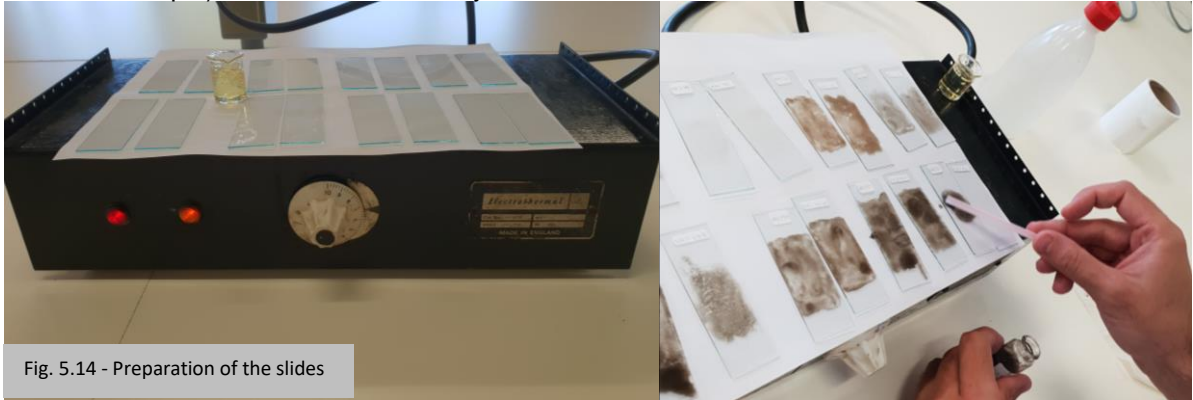


Fig. 5.14 - Preparation of the slides

23. After drying, 3 drops of glycerin were placed in each slide. The lamellae were placed on top and, with a straw, were straightened, trying to keep the same thickness across, removing air bubbles. With a soft toothbrush, the excess of glycerin was removed, holding the slides through the lamellae. Varnish was placed on the ends of the lamellae to glue to the slides and were left to dry once again;

24. The next day, the microscopic slides were ready to be observed.



Fig. 5.15 - Fixation of the slides and observation

5.6 CHALLENGES

During the laboratory work, some processes were challenging and had to adapt the conditions of the laboratory, the availability of materials and the logistics of the workers. It should also be noted that the samples reacted differently to the different acids, so repeats were necessary for the palynomorphs to be visible under the microscope afterwards.

The differences between samples are indicated when reacting to the various attackers within 3 months (Table 4). Several factors determined the differences between samples such as: nature of the sample composition, abundance of organic matter and poor preparation and / or fixation of the slides and / or lamellae.

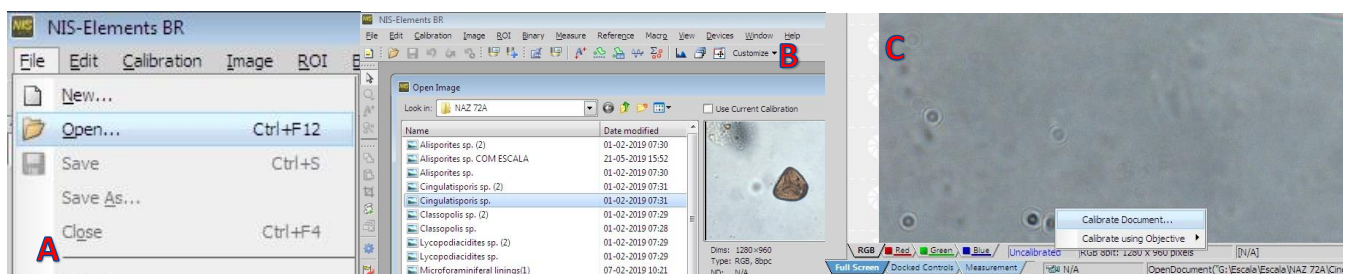
Table 4 - Number of times the demineralization and filtration processes were used for each sample throughout the laboratory procedure.

SCHEDULE PROCEDURE (October 16 – January 16)					
Sample	Demineralization			Filtration	
	HCl	HF	Calgon	125 µm sieve	15 µm sieve
NAZ72	10x	2x	16x	1x	9x
NAZ73	7x	2x	9x	1x	5x
NAZ76	7x	2x	9x	1x	5x
NAZ79	9x	2x	15x	1x	9x
NAZ81	7x	2x	9x	1x	5x
NAZ83	3x	1x	7x	1x	5x
NAZ85B	2x	1x	3x	1x	2x
NAZ85T	3x	1x	12x	1x	9x
NAZ88	3x	1x	12x	1x	9x
NAZ92B	3x	1x	12x	1x	9x
NAZ92T	3x	1x	7x	1x	5x
NAZ94	2x	1x	3x	1x	2x

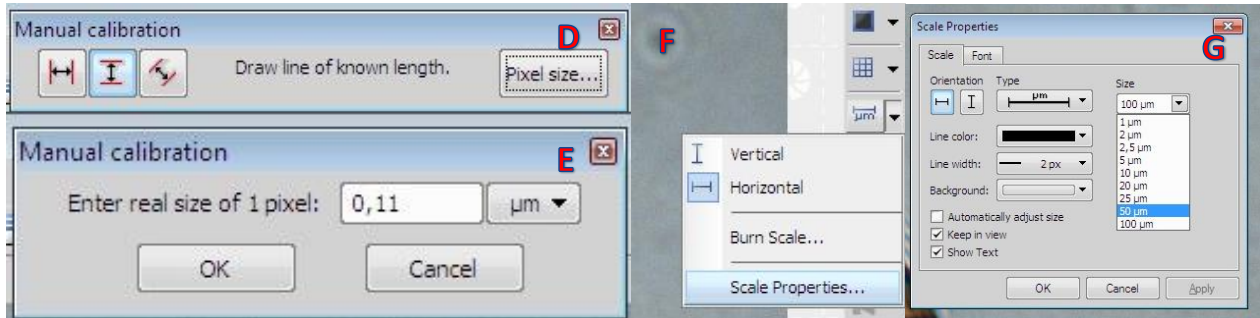
5.7 PHOTOGRAPHY AND IMAGE EDITING

After observation under the microscope, the next step was to obtain photographs of the studied palynomorphs and to edit them. For this, a photographic camera was used together with a small monitor attached to the microscope. In addition, NIS - Elements BR 4.00.00® computer software was also required. Below are the steps that were performed in the software for photo editing (Fig. 5.16A-J):

1. Open software;
2. File – Open – Select image;
3. Right-click on “Uncalibrated” (lower left corner) and left-click on “Calibrate Document”;



4. Left-click on pixel size;
5. Enter the value for 1 pixel (x60 = 0,11 μm ; x40 = 0,19 μm) and select "OK";
6. Left-click on "Show Scale" on right menu. Click on the right arrow and then "Scale Properties" to edit the scale;
7. Change size to 50 μm and select "OK";



8. Click again on the right arrow "Show Scale" and select "Burn Scale". Press "OK";
9. Click on "File", select "Save As" to save the image with scale.



All edited images of the studied palynomorphs are available in the Appendix.

CHAPTER 6

DISCUSSION OF RESULTS

6.1 ANALYSIS OF THE PALYNOLOGICAL CONTENT

Analysis of the palynological content of the samples disclosed the occurrence of distinct groups of palynomorphs, including 15 dinocysts *taxa*, 21 sporomorph *taxa* (of which 12 pollen types, and 9 spores), common to abundant microforaminiferal linings and 1 acritarch specimen. The identified *taxa* of dinocysts, spores and pollen are alphabetically listed in Tables 5 and 6, along with their suprageneric affiliations and an associated code referring to their microphotographic illustration in the plates provided in Annex 1. The relative abundances of the palynological groups are shown in table 7 and the respective graphical representations in figures 6.1 and 6.2.

Table 5 – *Taxa* of found dinocysts. Suprageneric affiliations are given in the middle column. The rightmost column identifies the corresponding photomicrograph illustrations (“PI”. stands for “plate”; the number before the colon identifies the plate; number(s) after the colon specify an image or a set of images in the plate). Table reproduced following Fossilworks.org.

Dinoflagellate cysts Taxa	Botanical affinity	Figure
<i>Bourkidinium sp.</i>	Gonyaulacales	Pl.1:1
<i>Canningia sp.</i>	Areoligeraceae	Pl.2:1-5

<i>Cribooperidinium sp.</i>	Gonyaulacales	Pl.3:1-2
<i>Cyclonephelium sp.</i>	Areoligeraceae	Pl.4:1-4
<i>Dingodinium sp.</i>	Gonyaulacales	Pl.3:3
<i>Florentinia sp.</i>	Cribooperidinioideae	Pl.5:1-6
<i>Heterosphaeridium sp.</i>	Gonyaulacales	Pl.6:1-3
<i>Impletosphaeridium sp.</i>	Gonyaulacales	Pl.7:1-3
<i>Kiokansium sp.</i>	Gonyaulacales	Pl.8:1-3
<i>Odontochitina sp.</i>	Ceratiaceae	Pl.9:1-2
<i>Palaeohystrichophora sp.</i>	Palaeoperidinioideae	Pl.10:1-4
<i>Spiniferites sp.</i>	Gonyaulacoideae	Pl.11:1-3
<i>Subtilisphaera sp.</i>	Palaeoperidinioideae	Pl.12:1-5
<i>Xenascus sp.</i>	Ceratiaceae	Pl.13:1-2
<i>Xiphophoridium sp.</i>	Gonyaulacales	Pl.14:1-4

Table 6 – *Taxa* of found spores and pollen grains. Suprageneric affiliations are given in the middle column. The rightmost column identifies the corresponding photomicrograph illustrations. Table reproduced following Fossilworks.org.

Spores Taxa	Botanical affinity	Figure
<i>Cicatricosisporites sp.</i>	Schizaeaceae	Pl.24:1-6; Pl.25:1-4
<i>Cingulatisporis sp.</i>	Uncertain	Pl.26:1-6
<i>Contignisporites sp.</i>	Pteridaceae	Pl.27:1
<i>Densoisporites sp.</i>	Selaginellaceae	Pl.27:2
<i>Kraeuselisporites sp.</i>	Lycopsida	Pl.27:3-4
<i>Leptolepidites sp.</i>	Lycopsida	Pl.27:5
<i>Patellasporites sp.</i>	Pteridophyta	Pl.28:1-6

<i>Triorites</i> sp.	Magnoliopsida	Pl.29:1
<i>Triplanosporites</i> sp.	Pteridophyta	Pl.29:2-4

Pollen Taxa	Botanical affinity	Figure
<i>Alisporites</i> sp.	Pinaceae	Pl.15:1-6
<i>Basopollis</i> sp.	Magnoliopsida	Pl.17:1-4
<i>Classopolis</i> sp.	Cheirolepidiaceae	Pl.18:1-6
<i>Concavisporites</i> sp.	Pteridophyta	Pl.19:1-3
<i>Cyathidites</i> sp.	Pteridopsida	Pl.20:1-5
<i>Echitriporites</i> sp.	Proteaceae	Pl.21:1-3
<i>Podocarpidites</i> sp.	Podocarpaceae	Pl.16:1-3
<i>Proteacidites</i> sp.	Proteales	Pl.22:1-6
<i>Steevesipollenites</i> sp.	Gnetales	Pl.23:1
<i>Syncolporites</i> sp.	Loranthaceae	Pl.23:2
<i>Taxodiaceapollenites</i> sp.	Uncertain	Pl.23:3
<i>Tricolpites</i> sp.	Magnoliopsida	Pl.23:4

Table 7 – Relative abundances of the palynological groups of the samples from the geological cut of the Cenomanian middle of the promontory of Nazaré.

Stage	Samples	Dinocysts (%)	Pollen (%)	Spores (%)	Acritarchs (%)	Microforaminiferal linings (%)	Total (n°)
Middle Cenomanian	NAZ 72	7	53	12	0	28	293
	NAZ 73	57	14	4	1	24	324
	NAZ 76	64	6	8	0	22	469
	NAZ 79	43	7	2	0	48	403
	NAZ 81	24	26	2	0	48	398
	NAZ 83	7	35	1	0	57	496
	NAZ 85B	2	93	5	0	0	952
	NAZ 85T	16	42	16	0	26	749
	NAZ 88	5	63	6	0	26	258
	NAZ 92B	8	82	3	0	7	555
	NAZ 92T	3	80	2	0	15	589
	NAZ 94	36	50	13	0	1	317
	Total		20	51	6	0	23

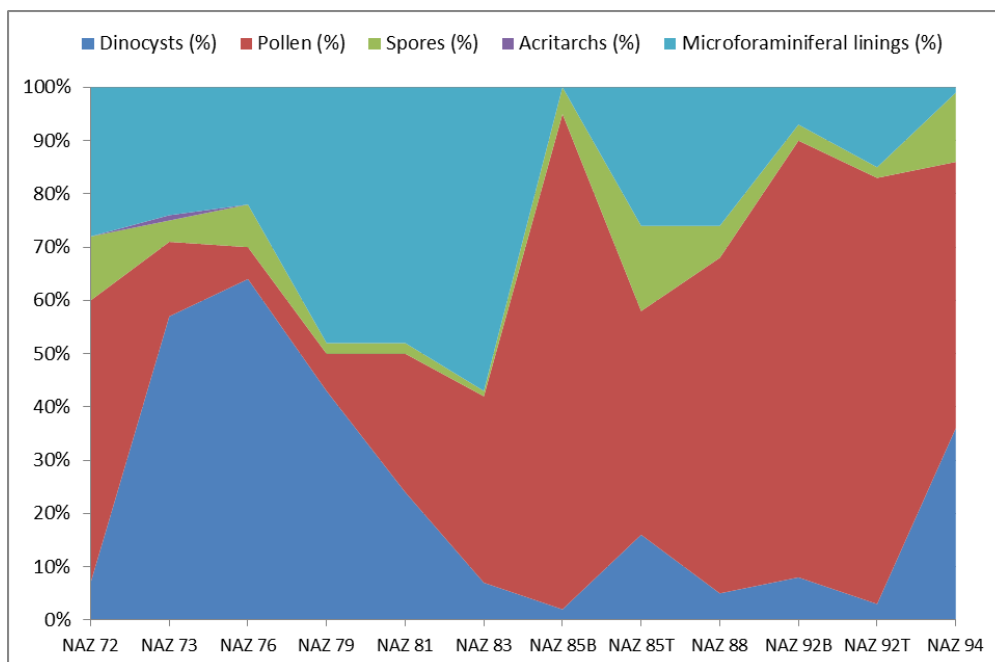


Fig. 6.1 – Graphical representation in area of the information contained in table 7.

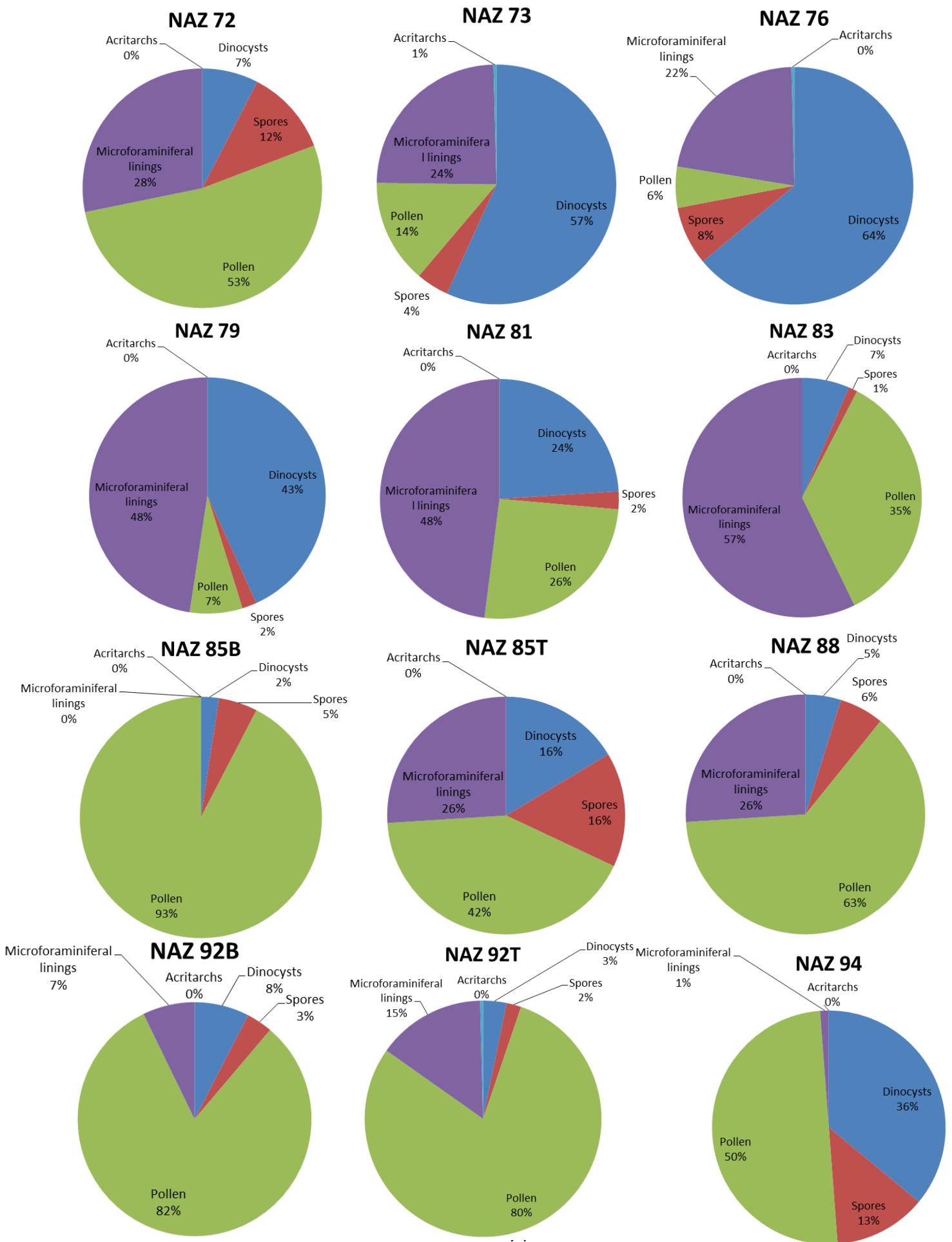


Fig. 6.2 - Pie charts showing the relative percentages of different categories of palynomorphs in each productive sample. These same data are resumed in aggregate form (100% stacked area chart, matched to the samples in the stratigraphic sequence).

In Fig. 6.2 is graphically represented the relative abundance of the distinct groups of palynomorphs in each of the 12 samples. These percentages were based on a counting of 250 palynomorphs/sample. Samples are vertically arranged so as to reflect, from bottom to top, the location of the sampled layers in the stratigraphic column (number 72 corresponds to the layer more towards the base of the profile and number 94 to the layer more towards to the top). On layers 85 and 92 samples are also arranged in a bottom-up order, with B standing for the base and T for the top of the corresponding layer. The predominance of pollen over all other palynomorphs is clear in all samples which constitute 51% of the palynomorphs (table 7), with a largest value of 93% in sample NAZ 85 (base layer) and a lowest value of 7% in sample NAZ 79. The second and third dominant groups are the microforaminiferal linings and dinocysts, constituting 23% and 20% of the identified palynological groups, respectively. For those two groups, the values show a large discrepancy along the layers. The largest value for dinocysts is 64% in sample 76 and the lowest is 2% in sample 85 (base layer). For microforaminiferal linings, the values are between 57% and 0%. The spores are less abundant, constituting only 6% of palynomorphs ranging from 16% to 1%.

A joint comparative appreciation of how these percentages vary across samples can be obtained from the stacked area chart of Fig. 6.3. The largest reductions in dinocysts relative abundance (to 2%) occur at NAZ 85B followed by NAZ 92T (3%) and 88 (5%). These reductions are related to somewhat distinct patterns of increase of other groups of palynomorphs: in NAZ 85B it is the huge increase of pollen grains (i.e., the terrestrial component) that associates with the reduction in the percentage of dinocysts; in NAZ 92T, an increase of the relative abundance of microforaminiferal linings (included in the aquatic-marine component) contributes as well to that reduction; and in NAZ 88, in addition to important relative increases of pollen and spores, increased relative abundance of microforaminiferal (aquatic component) is also associated with the diminished percentage of dinocysts.

The largest increases in dinocysts percentages occur in turn at NAZ 76 (to 64%) and NAZ 73 (to 57%): in NAZ 76 it associates primarily with a strong reduction of the pollen content, accompanied by an also significant reduction of spores (i.e., it is chiefly correlative of a reduction of the terrestrial component); in NAZ 73 this is correlative of a decrease of all other groups.

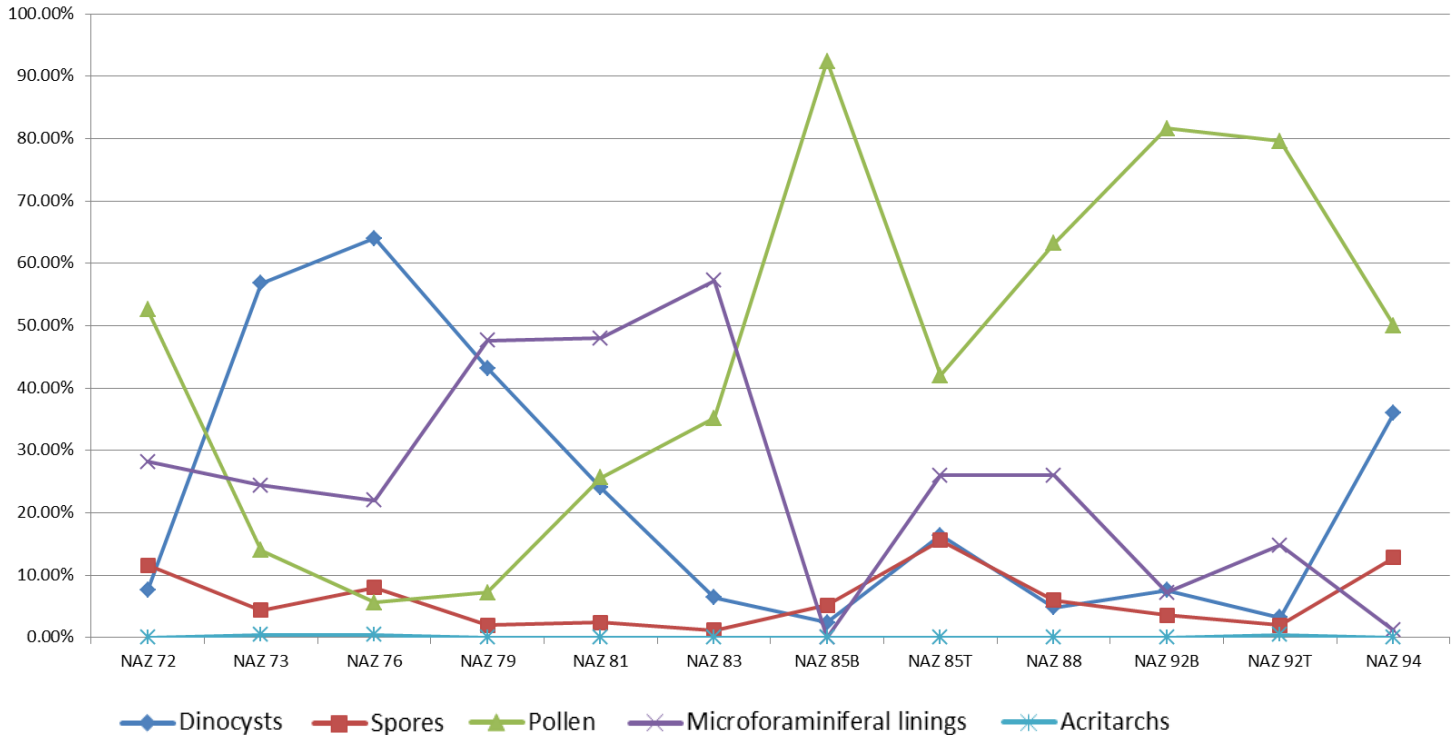


Fig. 6.3 - Graphic showing the relationship between the percentages of the different palynomorph groups

6.2 PALYNOLOGICAL RATIOS

Several quantitative indexes of palaeoenvironmental and palaeoecological features have been proposed based on ratios between different types of palynomorphs. Among them, one of the most common is the terrigenous versus marine ratio, computed as the sum of pollen grains and spores (representing the terrestrial influx) divided by the number of dinocysts (representing the marine influx). Although complicated by a possible differential impact of oxidation conditions on the preservation of dinocysts and sporomorphs or by the importance of long-distance transport mechanisms, higher values of this ratio can be taken to signal greater proximity to the shoreline.

Graph in Fig. 6.4 plots this ratio (on the ordinate) as a function of the productive samples (on the abscissa, ordered from the bottom to the top of the stratigraphic column). Values are in most cases greater than 1, reflecting the predominance of terrestrial influx. With the exception of samples NAZ 73, NAZ 76 and NAZ 79, where the ratio is below 1, showing a presence of marine component. The red line helps to highlight the tendency for higher values of this ratio for samples located towards the top of the stratigraphic succession.

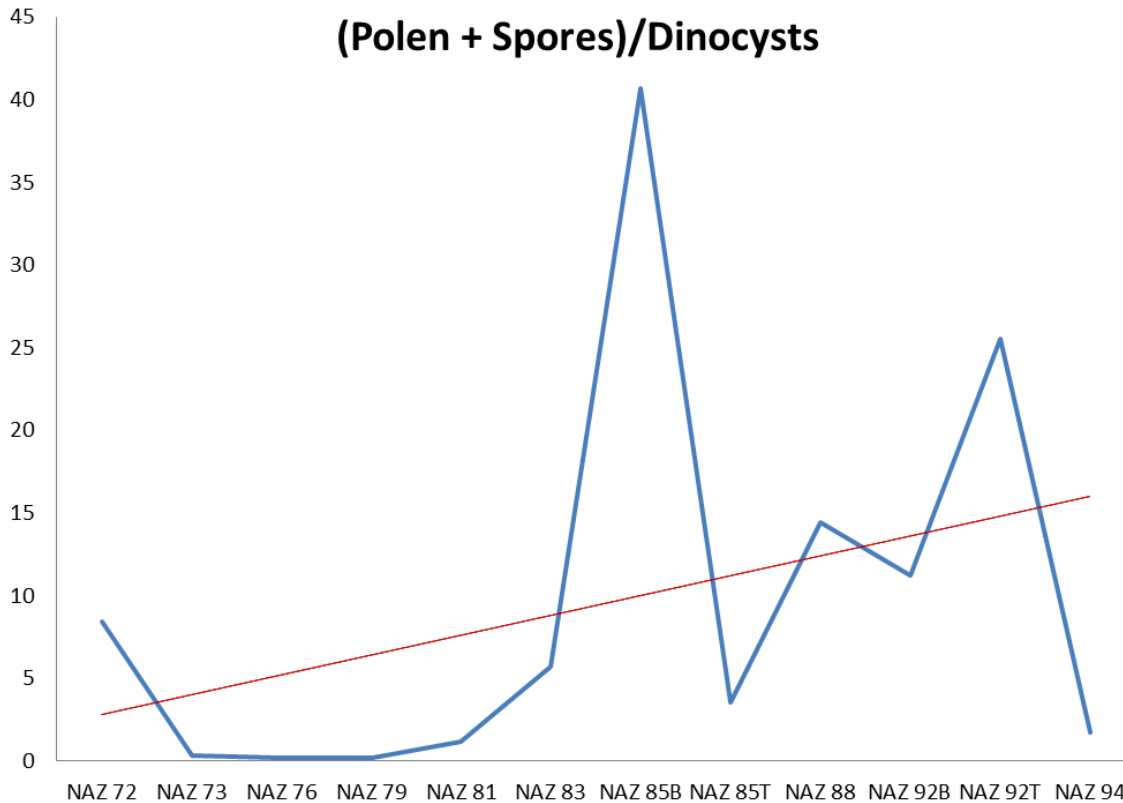


Fig. 6.4 – Changes of the pollen to dinocysts ratio [(pollen + spores)/dinocysts] across samples (on the abscissa, moving upward in the stratigraphic sequence).

Another proposed palynological ratio for evaluating increases/decreases in distance from seashore is the bisaccate pollen versus other pollen ratio (B:O). Due to their sac-like appendices, which make them more aero- and hydrodynamically efficient for long distance transport, bisaccate conifer pollen tends to increase their relative proportion as overall pollen concentration decreases with distance from the coastline. As any other single palynological ratio, this one may alternatively reflect factors other than an onshore-offshore gradient, such as changes in the plant communities at the source of the terrestrial influx.

Graph in Fig. 6.5 plots the B:O ratio as a function of the productive samples, ordered according to their location (from bottom to top) in the stratigraphic profile. Bisaccate pollen, represented in the examined samples by *Alisporites* sp. and *Podocarpidites* sp., correspond in every sample to a small proportion of the pollen grains, which is reflected in the consistently low values of this ratio. A small trend for an decrease of the B:O ratio in samples located more towards the top of the profile can also be noticed, but still associated with rather low ratio values.

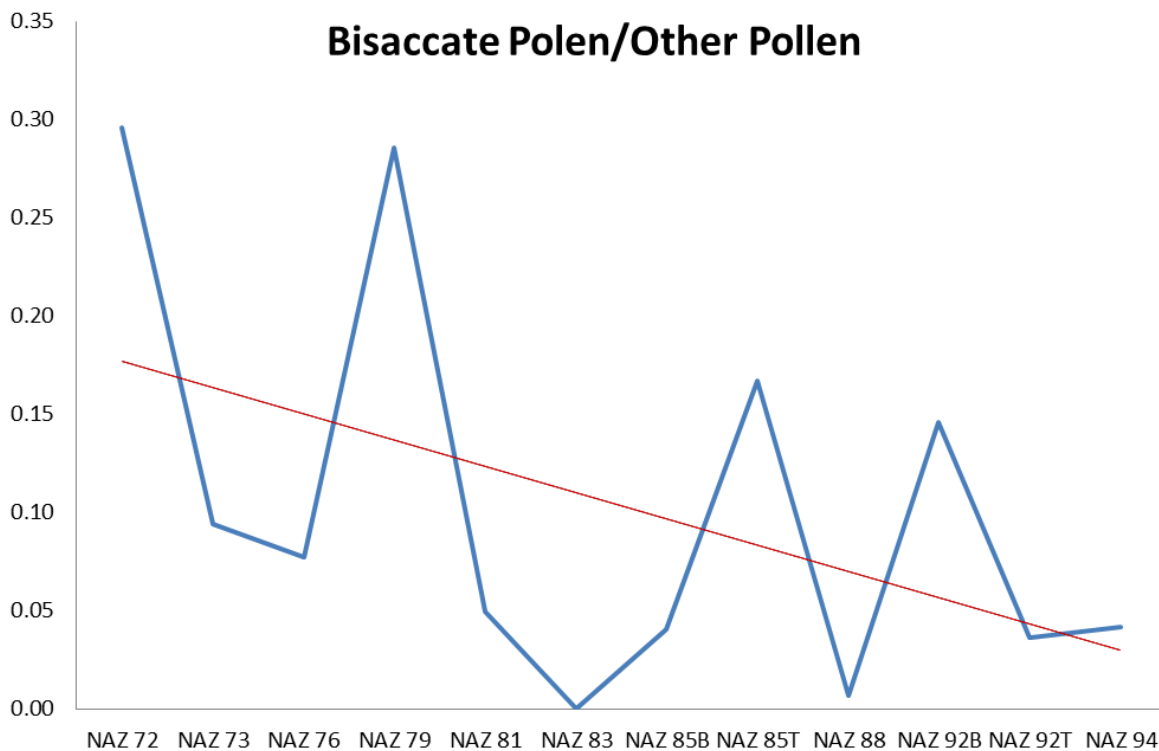


Fig. 6.5 – Ratio of bisaccate pollen to other pollen across the samples.

The ratio of pollen grains versus spores (P:S) has also been used as a proxy for distance to the shoreline, given the greater ease with which pollen can be wind or water-transported away from their origin, but mostly as a proxy for palynomorph oxidation. Since spores resist better to oxidation, the ratio P:S tends to be higher in environments of rapid sediment accumulation and burial.

The Graph in Fig. 6.6 expresses this ratio (on the ordinate) as a function of the bottom-up succession of productive samples, on the abscissa. Except for sample NAZ 76, pollen predominate over spores in all samples, resulting in ratio values above 1. The red line helps detecting a trend for higher values in samples more towards the top of the profile, suggestive of higher rates of sediment accumulation than those associated with layers lower down in the succession.

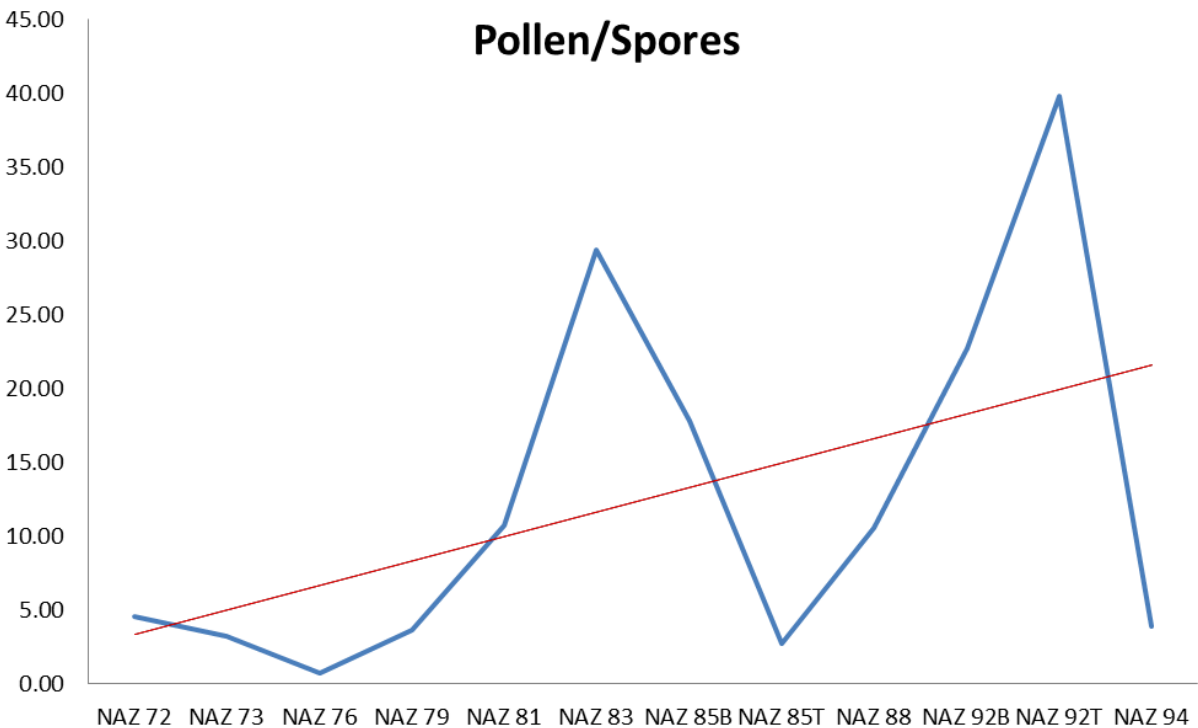


Fig. 6.6 – Ratio of pollen to spores across the samples.

The dinocyst-based identification of productivity variations strongly relies on changes in the ratio of peridinioid (P) versus gonyaulacoid (G) cysts of dinocyst assemblages. This approach, which has its basis in observations of Quaternary dinocyst assemblages, is founded on the different life styles and feeding strategies in dinoflagellates forming peridinioid (P) and gonyaulacoid (G) cysts. In analogy to modern *Protoperidinium*, P-cysts are considered to predominantly represent heterotrophic dinoflagellates thriving on, whereas G-cysts mainly represent autotrophic dinoflagellates (Pross & Brinkhuis, 2005). Nevertheless, several externally calibrated studies (e.g., using satellite data on primary productivity as a criterion) supported the potential usefulness of this ratio for productivity reconstruction.

Peridinioids comparative increase in nearshore conditions characterized by strong fluctuations in salinity and/or nutrient levels has also been signalled (Peyrot *et al.*, 2012). Also, certain palynomorphs have different tolerances to chemical oxidation. For example, Quaternary heterotrophic protoperidiniacean dinoflagellate cysts are much more susceptible than autotrophic gonyaulacacean genera (Hopkins & McCarthy, 2002). A decrease in the P:G ratio may thus reflect oxidation related processes such as rate of sedimentation, which differentially affect these two groups of cysts. Both the link of this ratio to primary productivity and to the rate of sedimentation open up the possibility of cautiously using it to estimate a nearshore-offshore gradient, with lower values of the ratio indicating more distal environments (de Vernal & Marret, 2007).

Graph in Fig. 6.7 plots a simple ratio of number of Peridinioids/(number of Periodinioids + Gonyaulacoids) expressed as a relative percentage (0 to 100 %) as a function of the bottom-up succession of productive samples. The presence of both dinocyst groups is quite balanced, i.e. there is no clear predominance of one group over the other, which does not guarantee relevant information about the paleoenvironment and paleecology by itself.

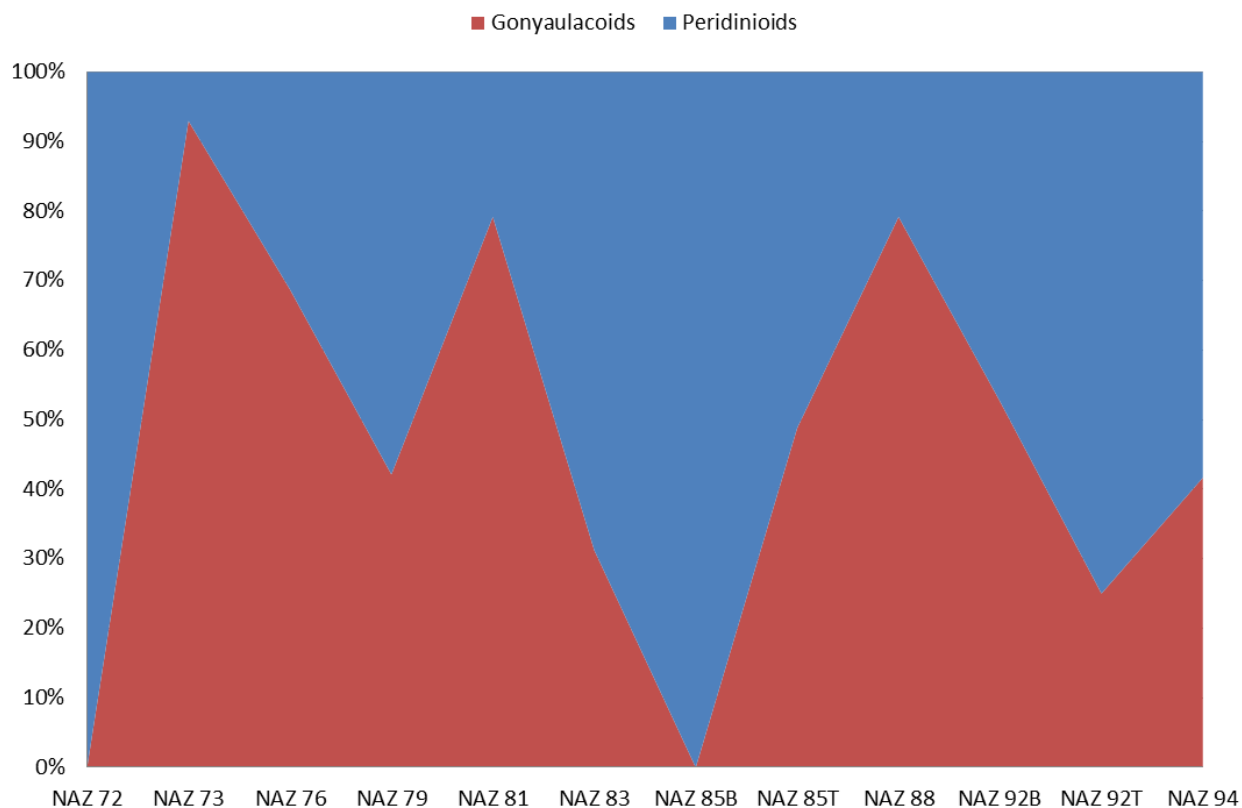


Fig. 6.7 - 100% stacked area chart presenting the percentage of peridinioid and gonyaulacoid dinocysts across samples (on the abscissa, moving upward in the stratigraphic sequence).

However, a relevant feature is the total absence of gonyaulacoids in samples NAZ 72 and NAZ 85B. That would point to closer proximity to marine environment at these layers, in agreement with the suggestions of bissacate/other pollen ratio (Fig. 6.5); considered from the standpoint of oxidation processes, to an increased rate of sedimentation/burial on the same layers – in agreement with the suggestion of the Pollen/Spores ratio (Fig. 6.6). In this context, the increase of the terrestrial component in those samples suggested by the (pollen + spore)/dinocyst ratio (Fig. 6.4) appears as either discrepant with the remaining indicators or as requiring explanation by factors other than higher proximity to marine environments.

Other palynological-based signals have been proposed, namely regarding the inshore-offshore gradient, which are not based on quotients and can be used for cross-checking the indications arising from palynological ratios. According to Wall *et al.* (1977), dinocysts diversity has come to be recognized in itself as a relevant palaeoenvironmental indicator, overall dependent on the stress in ecosystems, which is often related to shoreline proximity. Changes in assemblage composition and diversity may be used to determine transgressive-regressive phases and can be related to changes in relative sea level. This has led to the successful application of dinocyst studies in sequence stratigraphy (Pross & Brinkhuis, 2005).

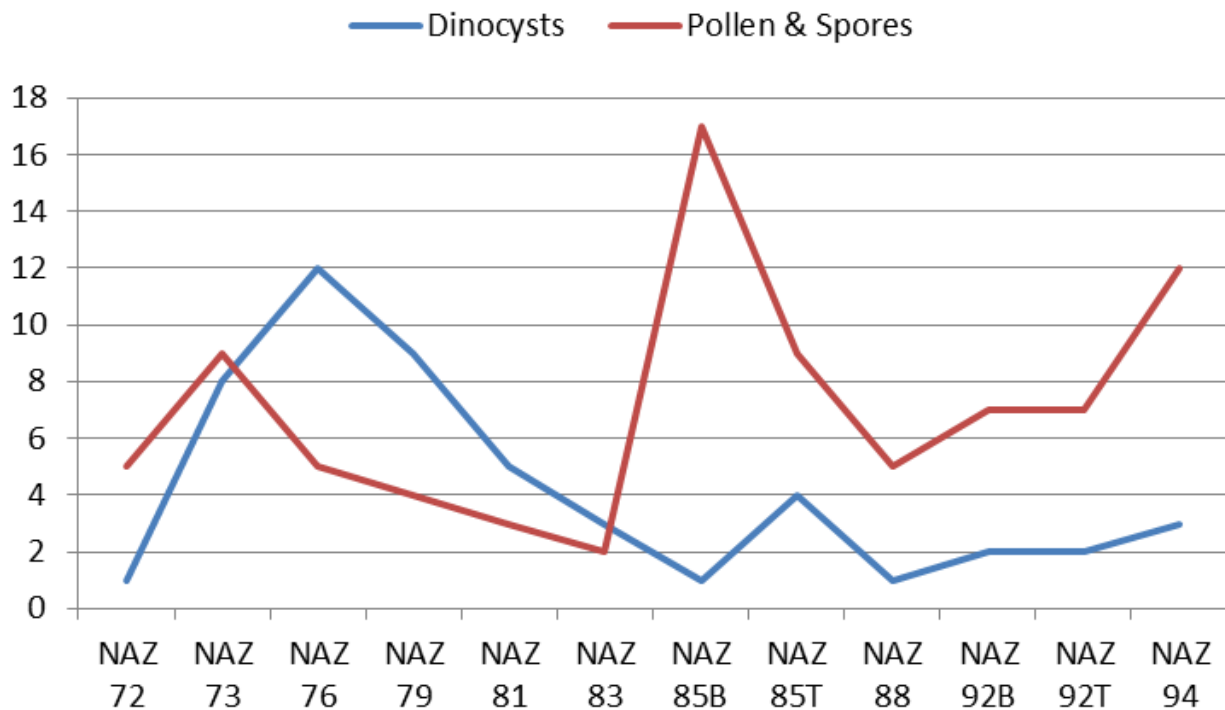


Fig. 6.8 -Dinocysts (blue line) and pollen and spores (red line) genera richness across samples: richness was indexed simply by the number of genera identified in a sample.

Graph in Fig. 6.8 plots a straightforward measure of dinocysts diversity (the number of recorded distinct *taxa*, or genera richness) as a function of the productive samples ordered from the bottom towards the top of the profile. An equivalent measure of diversity was also taken for the terrestrial component represented by spores and pollen grains and is additionally plotted for comparison. The number of distinct dinocyst *taxa* in each sample is overall rather low (its maximum being 12) and thus suggestive of a near shore, proximal setting, rather than open marine. A similar pattern is apparent for the pollen + spore diversity, with the exception of a somewhat noticeable rise in NAZ 83 (extending, to a bigger degree, to NAZ 85B). Pollen + spore richness was for the most part greater than dinocysts richness.

6.3 CHARACTERIZATION OF DINOCYST ASSEMBLAGES

Subtilisphaera sp. was the dominant *taxon* in most samples, accounting for around 7,3 % of the total of recorded dinocysts. Its representation across samples varied from a minimum of 1 % (sample NAZ 88) to a maximum of 21 % (sample NAZ 94). The second most abundant *taxa*, at a close distance from the third one, was *Impletosphaeridium* sp., accounting for 2,6% of the total number of dinocysts, and with percentages across samples varying in between 0 % (samples NAZ 72, NAZ 81, NAZ 85B, NAZ 88, NAZ 92B and NAZ 92T) and 12 % (sample NAZ 73). *Florentinia* sp. was the third most common *taxa*, with an overall representation of 2,5%, varying from 0% (in NAZ 72, NAZ 79, NAZ 83, NAZ 85B, NAZ 85T, NAZ 88, NAZ 92B, NAZ 92T and NAZ 94) to 25% (NAZ 73) across samples.

Goodman (1979) noted that low dominance-high diversity assemblages reflect more offshore conditions and high dominance-low diversity assemblages more inshore conditions. The dominance found in all samples thus converges with the low number of dinocysts *taxa* recorded (low diversity) in signaling an innershore marine setting. Also, assemblages including only a few dinocyst species and overwhelmingly dominated by one single *taxon* have been particularly associated with ecologically restricted nearshore and estuarine (brackish) environments (Li & Habib, 1996), with relatively low energy and little water movement, what seems to happen in this study.

Relatively small fluctuations of the percentage representation of each *taxon* across samples are apparent in Fig. 6.9. A comparatively higher peak of *Florentinia* sp. can be seen at NAZ 73, of *Impletosphaeridium* sp. at NAZ 94, of *Palaeohystrichophora* sp. at NAZ 79, or of *Xiphophoridium* sp. at NAZ 81 samples. These fluctuations are associated with some degree of change in the genera composition across samples and may involve either inverse or direct relations between the percentage representations of different genera.

Another look at the distribution of dinocysts across samples is provided in Table 8, which classifies each *taxon* in terms of abundance (percentage of the total count of palynomorphs in each sample). Three classification categories were used, following the terminology and percentage criteria offered in Balme (1970): rare, for percentages $\leq 1\%$; common, for percentages from 1.1 to 9.9%; abundant, for percentages $\geq 10\%$.

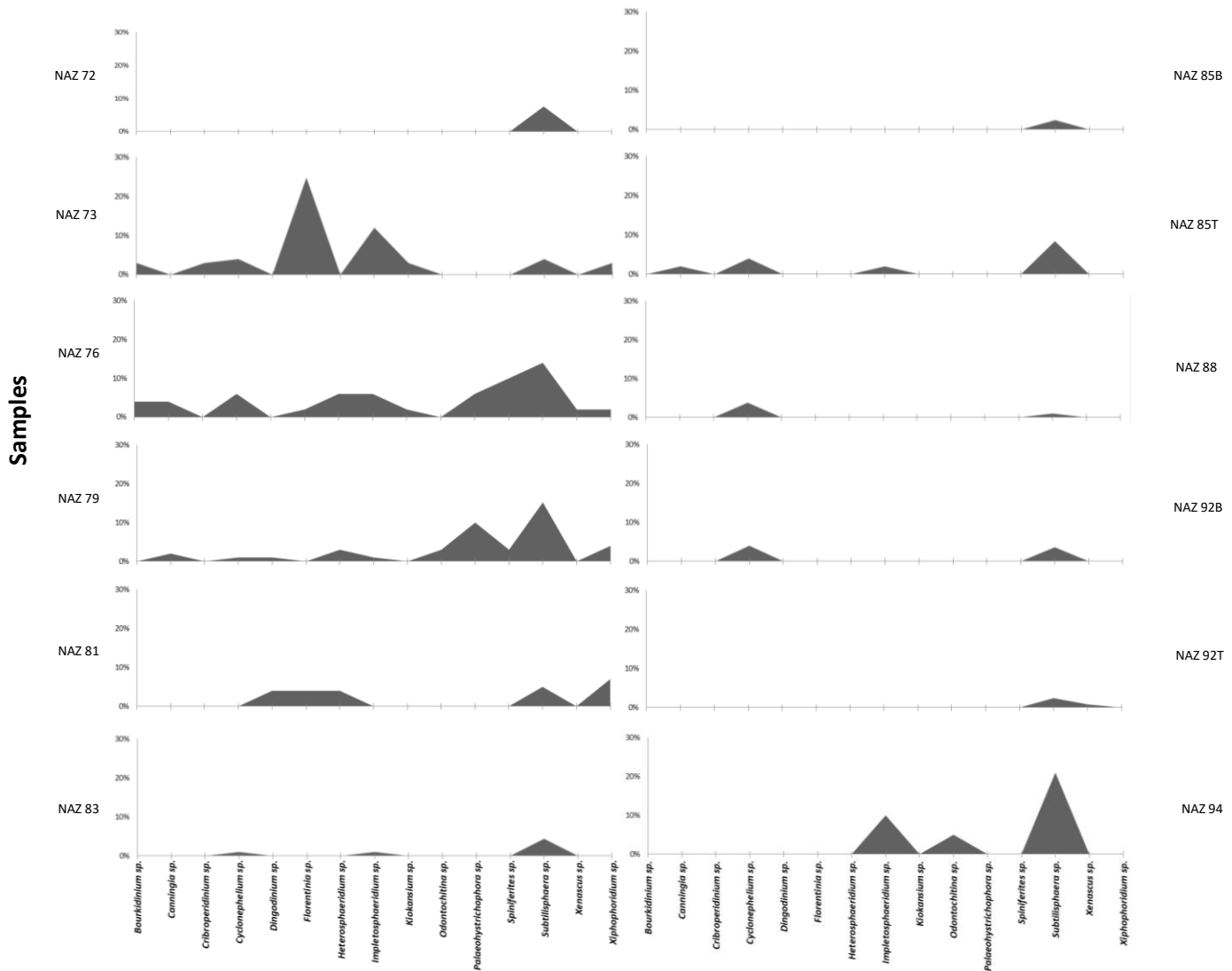


Fig. 6.9 –Dinocyst percentage diagrams for the set of productive samples (ordered vertically as in the lithostratigraphic column).

Considering the abundant (A) and common (C) categories to characterize the prevalent genera association, *Subtilisphaera* sp. (abundant in 3 samples and common in almost every other), *Impletosphaeridium* sp. (abundant in 2 samples and common in also 2 samples), *Florentinia* sp. (abundant in 1 sample and common in 2 samples) and *Palaeohystrichophora* sp. and *Spiniferites* sp. (both abundant in 1 sample and common in 1 another), appear as the most widely shared taxa across samples. Commonly represented in five out of seven samples, *Cyclonephelium* sp. is also fairly transversal across assemblages.

Table 8 – Stratigraphic distribution of dinocysts. Occurrences in each sample are classified as R-Rare ($\leq 1\%$), C-Common (1.1 – 9.9 %) and A-Abundant ($\geq 10\%$) (Balme, 1970).

Dinocysts															
Samples	<i>Bourkidinium</i> sp.	<i>Canningia</i> sp.	<i>Cribroperidinium</i> sp.	<i>Cyclonephelium</i> sp.	<i>Dingodinium</i> sp.	<i>Florentinia</i> sp.	<i>Heterosphaeridium</i> sp.	<i>Impletosphaeridium</i> sp.	<i>Kiokansium</i> sp.	<i>Odontochitina</i> sp.	<i>Palaeohystrichophora</i> sp.	<i>Spiniferites</i> sp.	<i>Subtilisphaera</i> sp.	<i>Xenascus</i> sp.	<i>Xiphophoridium</i> sp.
NAZ 72													C		
NAZ 73	C		C	C		A		A	C				C		C
NAZ 76	C	C		C		C	C	C	C		C	A	A	C	C
NAZ 79		C		R	R		C	R		C	A	C	A		C
NAZ 81					C	C	C						C		C
NAZ 83				R				R					C		
NAZ 85B													C		
NAZ 85T		C		C				C					C		
NAZ 88				C									R		
NAZ 92B				C									C		
NAZ 92T													C	R	
NAZ 94								A		C			A		

The environmental preferences of dinocysts taxa have been recognized as important palaeoenvironmental and palaeoecological indicators. Even though many of the recorded species in this study are cosmopolitan and may be qualified as opportunistic, as is typical of most dinocysts assemblages (Wall *et al.*, 1977), remaining differences in the degree of tolerance to variations in trophic, salinity or water depth conditions may still afford a basis for palaeoenvironmental inferences.

Cyclonephelium sp. is an important uppermost Cenomanian and Turonian dinocyst marker in NW Europe (Lignum, 2009). *Heterosphaeridium* sp. and *Florentinia* sp. are biostratigraphic marker genera that have Lower Turonian bases in NW Europe as well. In the high northern latitudes, *Heterosphaeridium* sp. has been recorded in the Cenomanian suggesting that it is a cold water tolerant genus that migrated southward with the predominant Late Cretaceous cooling (Lignum, 2009). *Subtilisphaera* sp. has been considered as a littoral type genus (Skupien & Vacísek, 2002). These authors also noted that the increased number of peridinioid cysts, present most frequent in the environment of the higher supply of nutrients, indicates a possibility of a high drift from the continent (which is shown by the considerably high content of sporomorphs as well) and also the reduction of salinity of the sea surface. Fresh water and

nutrient influx implies increased runoff, possibly as a result of increased precipitation. High productivity and limited water circulation at the bottom cause anoxic conditions of sedimentation. *Xenascus* sp., *Odontochitina* sp., *Palaeohystrichophora* sp. and *Spiniferites* sp. indicate a shallow marine environment with high terrestrial influx (Skupien & Mohammed, 2008). *Kiokansium* sp., *Canningia* sp. and *Cribroperidinium* sp. are associated as euryhaline genera (tolerate or perhaps prefer lowered salinities (Skupien, 2007) and have been related to lagoonal and restricted marine. Harris & Tocher (2003) also noted that many of the dinocyst genus *Xiphophoridium* sp. showed no environmental preference. About the palaeoecological preferences of *Impletosphaeridium* sp., its occurrence has been recorded at a brackish, marginal or restricted marine environment (Skupien, 2007). Finally, data about environmental preference of *Bourkidinium* sp. and *Dingodinium* sp. is very poor.

Taken altogether, the overall composition of the assemblages is thus suggestive of a low salinity, possibly brackish setting, and involving restricted shallow conditions consistent with lagoonal and/or tidal flat environments. Several taxa exhibit preferences for warm water such as *Spiniferites* sp. (Prauss, 2002) and *Palaeohystrichophora* sp. (Uwins & Batten, 1988). *Impletosphaeridium* sp. and *Heterosphaeridium* sp. appear in turn to prefer cooler water temperatures (Arai, 2007; Warny *et. al*, 2007). The decreased representation of *Spiniferites* sp. and *Palaeohystrichophora* sp., two taxa with a specific affinity for well oxygenated waters (Courtinat & Shaaf, 1990), at samples higher up in the succession, might signal upward decreasing oxygenation in the associated palaeoenvironmental. This is supported with the presence of *Cyclonephelium* sp. in the upper layers, a *taxa* with affinity for low oxygenated waters.

In the end, nutrient availability under a restricted shallow water environment with reduced (and eventually varying) salinity seems to be the most important palaeoenvironmental controls for the genera composition of the assemblages.

6.4 CHARACTERIZATION OF OTHER PALYNOMORPHS ASSEMBLAGES

Tables 9 and 10 provide a classification of sporomorphs, microforaminiferal linings and acritarchs in terms of abundance (percentage of the total count of palynomorphs in the sample), based on the same criteria used above for dinocysts: R-Rare ($\leq 1\%$), C-Common (1.1 – 9.9 %) and Abundant-A ($\geq 10\%$).

Table 9 – Stratigraphic distribution of pollen. R-Rare ($\leq 1\%$), C-Common (1.1 – 9.9 %) and Abundant-A ($\geq 10\%$).

Samples	Pollen											
	<i>Alisporites</i> sp.	<i>Basopollis</i> sp.	<i>Classopollis</i> sp.	<i>Concavisporites</i> sp.	<i>Cyathidites</i> sp.	<i>Echitriporites</i> sp.	<i>Podocarpidites</i> sp.	<i>Proteacidites</i> sp.	<i>Steevesipollenites</i> sp.	<i>Syncolporites</i> sp.	<i>Taxodiaceapollenites</i> sp.	<i>Tricolpites</i> sp.
NAZ 72	A		A									
NAZ 73	R		A	R			R					
NAZ 76	R		C									
NAZ 79	C		C									
NAZ 81	R		A									
NAZ 83			A									
NAZ 85B	C	C	A		R	R	C	R		C		C
NAZ 85T			A	R	R	R						
NAZ 88		R	A					R				
NAZ 92B	C		A		R			C	R			
NAZ 92T	C		A	R			R	R				
NAZ 94	C	R	A		R			R			R	

Gymnosperm pollen grains, particularly of the conyphera type, predominate, with *Classopollis* sp. as the most ubiquitous and abundant. *Alisporites* sp. and *Podocarpidites* sp. are the only two bisaccate pollen, much less represented than other pollen types, suggesting a low influence of transportation and a deposition close to the production site of the pollen grains. Classopolis-dominated assemblages have been interpreted as corresponding to coastal vegetation (Peyrot *et al.*, 2011). A similar association of conifer pollen, predominantly *Classopollis*, with spores of pteridophytes, chiefly *Pattelasporites*, has been reported for the Lower Cretaceous of the Lusitanian Basin (Mendes *et al.*, 2014), and interpreted to indicate a warm, seasonally dry climate.

Table 10 – Stratigraphic distribution of spores, foraminifera and acritarchs. R-Rare ($\leq 1\%$), C-Common (1.1 – 9.9 %) and Abundant-A ($\geq 10\%$).

Samples	Spores										For.	Acr.
	<i>Cicatricosisporites</i> sp.	<i>Cingulatisporis</i> sp.	<i>Contignisporites</i> sp.	<i>Densoisporites</i> sp.	<i>Kraeuselisporites</i> sp.	<i>Leptolepidites</i> sp.	<i>Patellasporites</i> sp.	<i>Triorites</i> sp.	<i>Triplanosporites</i> sp.	Microforaminiferal linings		
NAZ 72		R					C				A	
NAZ 73	R			R			C		R		A	R
NAZ 76	R		R				C				A	R
NAZ 79		R					R				A	
NAZ 81											A	
NAZ 83		R									A	
NAZ 85B	R	C		R		R	R	R	R			
NAZ 85T	C	C					R		R		A	
NAZ 88		R				R					A	
NAZ 92B	R	R			R						C	
NAZ 92T	R				R						A	R
NAZ 94	R		R				R	R	R		R	

The pteridophyte spores *Pattelasporites* sp., *Cicatricosisporites* sp. and *Cingulatisporis* sp. were the three most abundant taxa whose can be found in many diverse environments, from marine to lagoonal and terrestrial (see: Fossilworks). Combined with the much larger representation of pollen grains versus spores (see Fig. 6.6), the strong predominance of spores of pteridophytes, and the absence of bryophytes spores (more dependent on water for their reproduction) may signal a moderately humid palaeoclimate (Villanueva-Amadoz *et al.*, 2011).

Several studies have shown an increase in microforaminiferal linings in shallower waters (Melia, 1984; Powell *et al.*, 1990), allowing to interpret the common to abundant occurrence of microforaminifera across samples (with the single exception of 85B, where no microforaminifera linings were recorded) as an indication of an overall shallow water palaeoenvironment. No particular shallowing trend upwards in the succession is suggested.

Taken overall, the study of the assemblages of palynomorphs other than dinocysts concurs with the same general indications of a shallow water nearshore palaeoenvironment with reduced salinity, possibly of a lagoonal/brackish type and allowing for some contribution of river freshwater input.

6.5 DINOCYSTS-BASED BIOSTRATIGRAPHY

The usefulness of dinocysts as biostratigraphic markers is highly dependent on the occurrence of biostratigraphically relevant species/genera, that is, *taxa* with a narrow chronostratigraphical range in between their first occurrence (FO) and their last occurrence (LO), allowing thereby for low resolution correlation. This was not the case of the studied assemblages, which individually do not add diagnostic value as regards the proposed age of the succession of middle Cenomanian on the basis of foraminifera, benthic faunas of invertebrates, and even ammonoid and vertebrate assemblages (e. g. Berthou, 1973, 1984; Berthou *et al.*, 1979; Lauerjat, 1982; Callapez, 1998, 2008; Callapez *et al.*, 2014).

Fig. 6.10 illustrates the range of the recorded dinocysts *taxa* across samples with reference to the geological time scale (Gradstein *et al.*, 2018). The correspondence between the stratigraphic column and the geological time information was obtained through the alignment of the LEP/B discontinuity with the proposed onset of middle Cenomanian in Williams *et al.* (2004).

The genera *Bourkidinium* sp. and *Kiokansium* sp. appear at the exact same time in the studied cut (FO in NAZ 73 and LO in NAZ 76), an indicator that both *taxa* were part of the same ecosystem. The same is true for the genera *Palaeohystrichophora* sp. and *Spiniferites* sp. (FO in NAZ 76 and LO in NAZ 79) and also *Florentinia* sp. and *Xiphophoridium* sp. (FO in NAZ 73 and LO in NAZ 81). *Dingodinium* sp. has a very short occurrence range (FO in NAZ 79 and LO in NAZ 81). The *taxon* with the highest occurrence period is *Subtilisphaera* sp. (FO in NAZ 72 and LO in NAZ 94). *Criproperidium* sp. presents a unique and distinct case in which its first and last occurrence was verified in the same layer (NAZ 73).

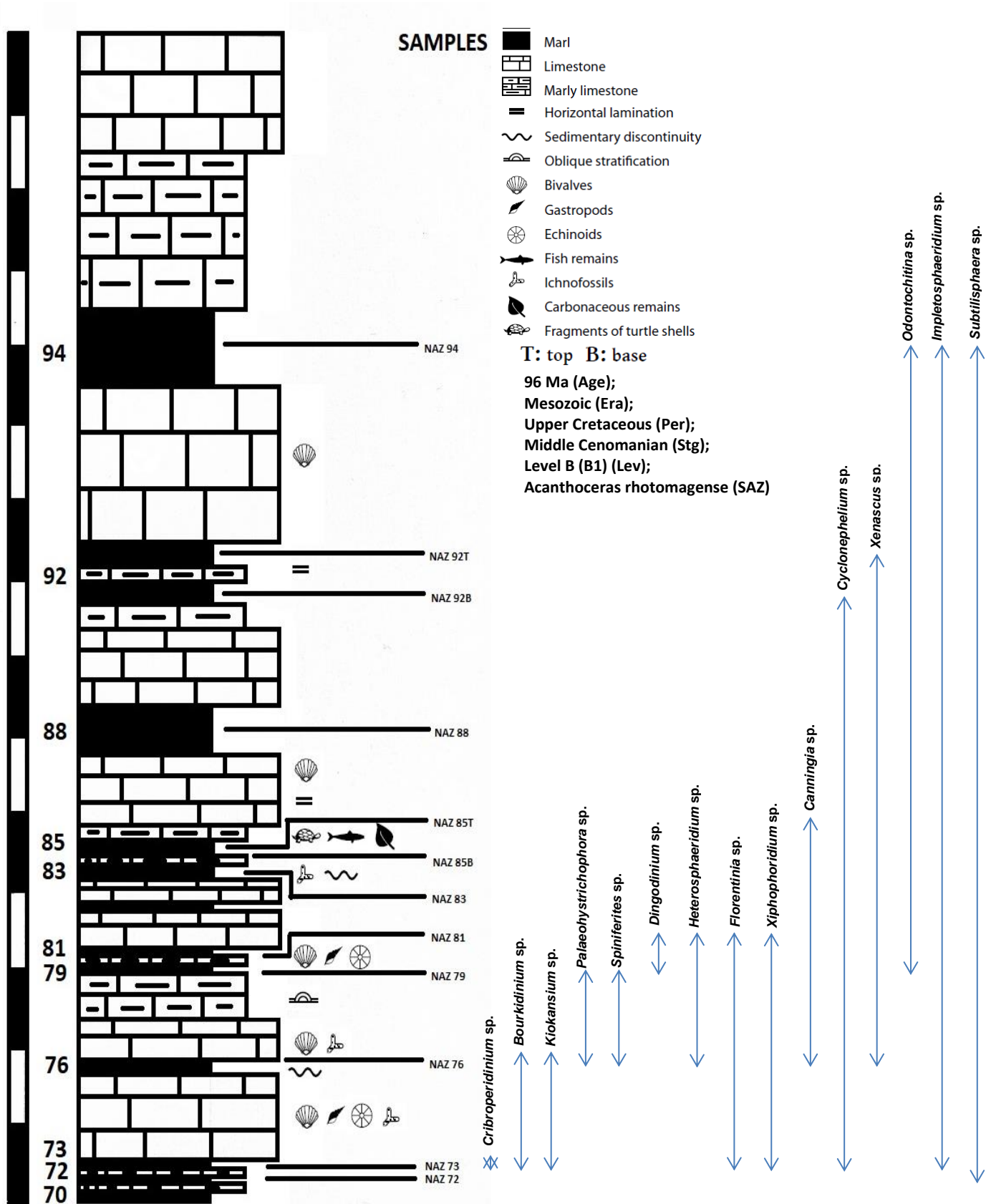


Fig. 6.10 – Stratigraphic ranges of dinocysts taxa identified in the sampled section. Age (Ma) refers to Gradstein et al.’s (2012) timescale for the Mesozoic. Per = Period, Stg = Stage, Lev = Level, SAZ = Standard Ammonite Zonation.

6.6 COMPARISON WITH OTHER CRETACEOUS DINOCYSTS ASSEMBLAGES

The majority of the studies of Upper Cretaceous dinocysts focus the Cenomanian-Turonian boundary, given its association with the major biotic event known as OAE 2 or Bonarelli Event (Barroso-Barcenilla *et al.*, 2011). Two earlier studies conducted in Portugal which allow a comparison with the present one are those of Berthou *et al.* (1980) and Berthou & Hasenboehler (1982). They both investigate the Albian and Cenomanian dinocysts associations in the region of Lisbon (south of Nazaré) and distinguish furthermore between the early, middle and late Cenomanian stage. Berthou *et al.* (1980) report that dinocysts occurrences were rare in the middle Cenomanian, with *Trichodinium castaneum* as the single identified species. These findings are not in accordance from those in the present study, where diverse and relatively well represented dinocyst *taxa* were found, though not the very single *taxa* identified by Berthou *et al.* (1980) for this time interval (*Trichodinium castaneum*). This discrepancy might signal coeval diverging local sedimentological and palaeoenvironmental conditions at the Lisbon and Nazaré sectors.

The study of Berthou & Hasenboehler (1982) has provided a much larger diversity of *taxa* occurring during the early and middle Cenomanian. A comparative summary of Berthou & Hasenboehler's (1982) reported *taxa* is given in Table 11. All *taxa* shared with the present study are represented in bold (as long it includes the same genera): dominant *taxa* in a given Cenomanian substage and do not occurring in any other substages are additionally reported and signaled with one asterisk (*), and *taxa* within brackets ([]) are not of interest for the current comparison. Six of the 15 dinocysts *taxa* (as genera) identified in the present study (i.e., 40%) were also reported in Berthou & Hasenboehler (1982). However, rather than being specific to one stage, they largely spread across the three Cenomanian substages. While all occurred at the middle Cenomanian, four were also reported in the early Cenomanian and three in the late Cenomanian. With the exception of *Palaeohystrichophora infusorioides* identified only in the Cenomanian (across all substages), all other *taxa* also range across several Albian substages. Berthou & Hasenboehler's (1982) in their study, noted that as far as the lower, middle and upper Cenomanian are concerned, dinocyst-based studies do not seem to add significantly to the biostratigraphic precisions in the studied regions. However, they can still be useful for integrated biostratigraphic purposes with other taxonomic groups. Another relevant indication supported by the fact that 60 % of the *taxa* in the current study, among which the dominant (*Subtilisphaera* sp.) and the second most abundant genera (*Impletosphaeridium* sp.), were absent from Berthou & Hasenboehler's (1982) samples, which could mean, again, that palaeoenvironmental conditions in the regions of Lisbon and Nazaré were very likely divergent. This suggests that, dinocyst-based studies may be important sources in assessing palaeoenvironmental conditions and palaeoecological communities, and differences among distinct palaeogeographical regions.

		Pevrot (2011) Pevrot <i>et al.</i> (2011) Pevrot <i>et al.</i> (2012)	Berthou & Hasenboehler (1982)	Oliveira (2017)	Fernandes (2019)	Present Study
Stratigraphic sections		Tamaion, Condemios, Fuentetoba, Puentedeved	Casal da Cova e Fontanelas	Nazaré	Nazaré	Nazaré
Turonian	Lower	<i>P. infusorioides</i> <i>Spiniferites ramosus</i> <i>Canningia reticulata</i> [<i>E. phragmites</i>] [<i>T. castanea</i>] <i>Xenascus ceratioides</i>				
Cenomanian	Upper	<i>Trithyrodinium suspectum</i> <i>Florentinia mantellii</i> <i>Florentinia</i> sp. <i>Soiniferites</i> sp.	<i>P. Infusorioids</i> <i>X. ceratioides</i> <i>X. alatum</i> [<i>T. castanea</i>]			
	Middle		<i>P. infusorioides</i> <i>S. ramosus</i> <i>X. ceratioides</i> <i>X. alatum</i> <i>Florentinia</i> sp. <i>Canningia</i> spp. <i>Epelidosphaeridia spinosa</i> <i>Oligosphaeridium</i> sp. <i>O. pulcherrimum</i> <i>Protoellips. corollum</i> *	<i>Subtilisphaera</i> sp. <i>Spinidium</i> sp.** <i>Spiniferites ramosus</i> <i>Canningia</i> sp. <i>Florentinia</i> sp. <i>Xiphophoridium alatum</i> <i>Impletosphaeridium</i> sp. <i>Epelidosphaeridia spinosa</i> <i>Spiniferites</i> sp. <i>Trithyrodinium suspectum</i> <i>Xenascus ceratioides</i> <i>Palaeohystric. infusorioides</i> <i>Xenascus</i> sp. <i>Trithyrodinium</i> sp. <i>Florentinia mantellii</i> <i>Heterosphaeridium</i> sp. <i>Canningia reticulata</i> <i>Oligosphaeridium</i> sp. <i>O. pulcherrimum</i> <i>Palaeohystrichophora</i> sp.	<i>Laciniadinium</i> sp. <i>Soinidium</i> sp. <i>Palaeohystrichophora infusorioides</i> <i>Canningia</i> sp. <i>Canningia reticulata</i> <i>Circulodinium</i> sp. <i>Coronifera oceanica</i> <i>Downiesphaeridium</i> sp. <i>Exochosphaeridium</i> sp. <i>Florentinia</i> sp. <i>Florentinia aff. Cooksoniae</i> <i>Florentinia cf. deanei</i> <i>Florentinia mantellii</i> <i>Impletosphaeridium</i> spp. <i>Oligosphaeridium</i> sp. <i>Oberculodinium</i> sp. <i>Rhaetogonyaulax</i> sp. <i>Sentusidinium</i> spp. <i>Spiniferites</i> sp. <i>Spiniferites ramosus</i> <i>Xenascus</i> sp. <i>Xenascus ceratioides</i> <i>Xiphophoridium alatum</i>	<i>Bourkidinium</i> sp. <i>Canningia</i> sp. <i>Criboeridinium</i> sp. <i>Cyclonephelium</i> sp.* <i>Dingodinium</i> sp. <i>Florentinia</i> sp. <i>Heterosphaeridium</i> sp. <i>Impletosphaeridium</i> sp. <i>Kiokansium</i> sp. <i>Odontochitina</i> sp. <i>Palaeohystrichophora</i> sp. <i>Soiniferites</i> sp. <i>Subtilisphaera</i> sp. <i>Xenascus</i> sp. <i>Xiphophoridium</i> sp.
	Lower		<i>P. infusorioides</i> <i>X. alatum</i> <i>Canningia</i> sp. <i>Oligosphaeridium</i> sp. <i>O. pulcherrimum</i> <i>Florentinia</i> sp. <i>Epelidosphaeridia spinosa</i> <i>Protoellips. corollum</i> * <i>Spinid. vestitum</i> <i>Exochosph. truncatum</i>			

Table 11 – Shared taxa (bold type) between the dinocysts assemblages of the present study and those from the same section of Nazaré, but in the lower layers and also those from Cenomanian-Turonian sections of the Castilian Platform (Spain) and from Albian-Cenomanian sections of the Western Portuguese Basin (Lisbon region). All observed taxa at Nazaré are listed (both from present study as from Oliveira, 2017). As for the other sections, only taxa shared with the Nazaré section are reported, exception made to dominant or especially abundant taxa. * Dominant taxon not represented in any stage of another section; ** Dominant taxon represented in Oliveira, 2017 section but not in present study; [] Taxa among the most abundant in Peyrot *et al.*, 2011. (Adapted from Oliveira, 2017).

In the left column of Table 11, a summary comparison with the findings of three dinocysts studies conducted at different sites of the Castilian Platform, Northern- Central Spain, (Peyrot, 2011; Peyrot *et al.*, 2011, and Peyrot *et al.*, 2012) concerned with late Cenomanian-early Turonian stratigraphic intervals, is

presented. The three Spanish studies involve distinct outcrop sections corresponding to an outer shelf to coastal and terrestrial transect (Peyrot *et al.*, 2011), opening a possibility to compare assemblages in different paleoenvironment environments. Despite differences in assemblage's diversities and composition, a transversal predominance of *Palaeohystrichophora infusorioides* and *Spiniferites ramosus* was found in all Spanish studies (Peyrot, 2011; Peyrot *et al.*, 2011; Peyrot *et al.*, 2012). This concurs with a common dominance of *Palaeohystrichophora infusorioides* during the middle and late Cenomanian in most NW areas (Lignum, 2009), very often associated with *Spiniferites ramosus*, leading to the recognition of an Upper Cretaceous "Spiniferites-Palaeohystrichophora (S-P) Assemblage" (Prince *et al.*, 1999), expressing eutrophic conditions of the middle shelf. As shown in Table 11 (left column), five of the 15 genera recorded in the present study (i.e., 33%) are represented in the late Cenomanian-early Turonian assemblages of the Castilian Platform. Conversely, 67% of the *taxa* in the present study are absent in the Castilian Platform assemblages, among which the dominant *Subtilisphaera* sp. and the second most abundant *taxon* *Impletosphaeridium* sp., expressing a rather different species composition (and namely, an important divergence as regards the P-S assemblage, which seems to provide the basic association in the Spanish samples). Given the interpretation of the P-S assemblage as a marker of eutrophic middle-shelf environments, the contrasting dominance of *Subtilisphaera* sp. in the present study, with reported affinities to restricted marginal low salinity environments, should be taken as a clear signal of a local palaeoenvironmental divergence.

Another study of Cenomanian dinocyst assemblages used for comparison was provided in Oliveira (2017). This study concerned the interval section from late early to middle Cenomanian from Nazaré in the lower layers than those of the present study. Despite some differences found in the diversity of genera, *Subtilisphaera* sp. predominance was verified in both studies. As shown in Table 11, nine of the 15 genera recorded in the present study (60%) are represented in the layers studied by Oliveira, 2017, and thus 40% are not. This includes the abundant genus *Cyclonephelium* sp. which is not represented in any of the studies mentioned above. Also, the dominant *taxon* *Spinidinium* sp., which is signaled with two asterisks (**) is absent in the present study, comparing with the results obtained by Oliveira, 2017. Again, this contributes to a different *taxon* composition, even if both sections are part of the same platform, and could possibly mean that, transversely, new genera appear while others disappear.

Finally, the last study was done by Fernandes (2019). Presenting exactly the same age, this comparison of studies is the most interesting from the biostratigraphic point of view. Fernandes, 2019, provided data starting at layer NAZ 43 up to the layer NAZ 70. Even so, several differences in the diversity of genera were presented in both studies. Following Table 11, eight of the 15 genera recorded in the present study (53%) are represented in the layers from NAZ 43 to NAZ 70. Again, *Subtilisphaera* sp. was the most dominant *taxon* verified in both studies. Considering all the *taxa* only found at the layers studied by Fernandes, 2019 as well those only found at the present study, this supports the idea that the *taxon* composition can vary widely in the environment, even in sections so close to each other.

These results support and generalize the indications of the present study that studies based on Cenomanian dinocysts offer a valid tool for paleoenvironmental and paleoecological reconstructions, but not much for additional biostratigraphic calibrations.

CHAPTER 7

CONCLUSION

7.1 PALAEOENVIRONMENTAL AND PALAEOECOLOGICAL IMPLICATIONS

Recognizing the potential of dinoflagellates cysts, fossil spores and fossil pollen grains as palaeoenvironmental markers, one of the study's purported goals was to contribute to a palaeogeographic reconstruction of the Nazaré sector during the middle Cenomanian. This particular section has been previously interpreted, based on the sedimentary facies and an extensive analysis of (mostly) macro invertebrate and vertebrate faunas, as reflecting to a restricted lagoonal environment yielding benthic palaeocommunities dominated by the oyster *Gyrostrea ouremensis* (Callapez *et al.*, 2014). An interesting perspective in this context is to evaluate the convergence of microbial data caused by the study of palynomorph assemblages with the proposed regional paleogeographic scheme (Callapez *et al.*, 2014), and whether other constraints on paleoenvironmental interpretations can be obtained in this way.

Three structural features of the recorded palynomorphs assemblages were: (1) predominance of pollen grains non-bisacatte, (2) dinocysts high dominance-low genera diversity, and (3) no clear predominance of peridinioids dinocysts over gonyaulacoids. *Classopolis*-dominated assemblages of pollen grains is taken as an indicator of coastal vegetation (Peyrot *et al.*, 2011), along with the scarce representation of bisacatte pollen, suggest a nearshore deposition, close to the production source. As previously signaled, dinocysts high dominance-low diversity assemblages are a common indicator of proximal innershore conditions (Goodman, 1979), with strong domination by one single taxon, as is the case here, often related to restricted nearshore and estuarine (brackish) low energy environments (Li & Habib, 1996). Despite the non-predominance of peridinioids over gonyaulacoids, there is a complete absence of gonyaulacoides in two layers of the section which can be an accepted proxy for reduced/variable salinity under nearshore conditions (Harker *et al.*, 1990) and/or abundant nutrient supply

associated with upwelling zones or with enriched terrestrial input (Peyrot *et al.*, 2012). All mentioned structural features thus converge in pointing towards a markedly nearshore, rather restricted, variable to low-saline, possibly brackish, environment with a rich nutrient supply, plausibly of terrestrial origin.

The environmental preferences of the genera identified in the assemblages supported these indications and added further details. Diverging from the *Spiniferites-Palaeohystrichophora* (S-P) Assemblage (Prince *et al.*, 1999), predominant during middle-late Cenomanian times in Northwest Europe and reflecting middle to outer shelf eutrophic conditions, the dominant cyst was the strongly euryhaline *Subtilisphaera* sp., with reported affinities to restricted marine environments, including salt marshy, intertidal, deltaic, estuarine and lagoonal habitats (Skupien & Vacísek, 2002). Among the remaining *taxa*, several display a similar propensity towards restricted environments of low to varying salinities, along with documented occurrences in diverse marginal marine and lagoonal habitats: *Xenascus* sp., *Odontochitina* sp., *Kiokansium* sp., *Impletosphaeridium* sp., *Canningia* sp. and *Cribroperidinium* sp. (Skupien & Mohammed, 2008; Skupien, 2007). This agrees with several studies where various environmental and ecological factors influence a greater distribution of dinocysts in this type of environment (see Fig. 7.1).

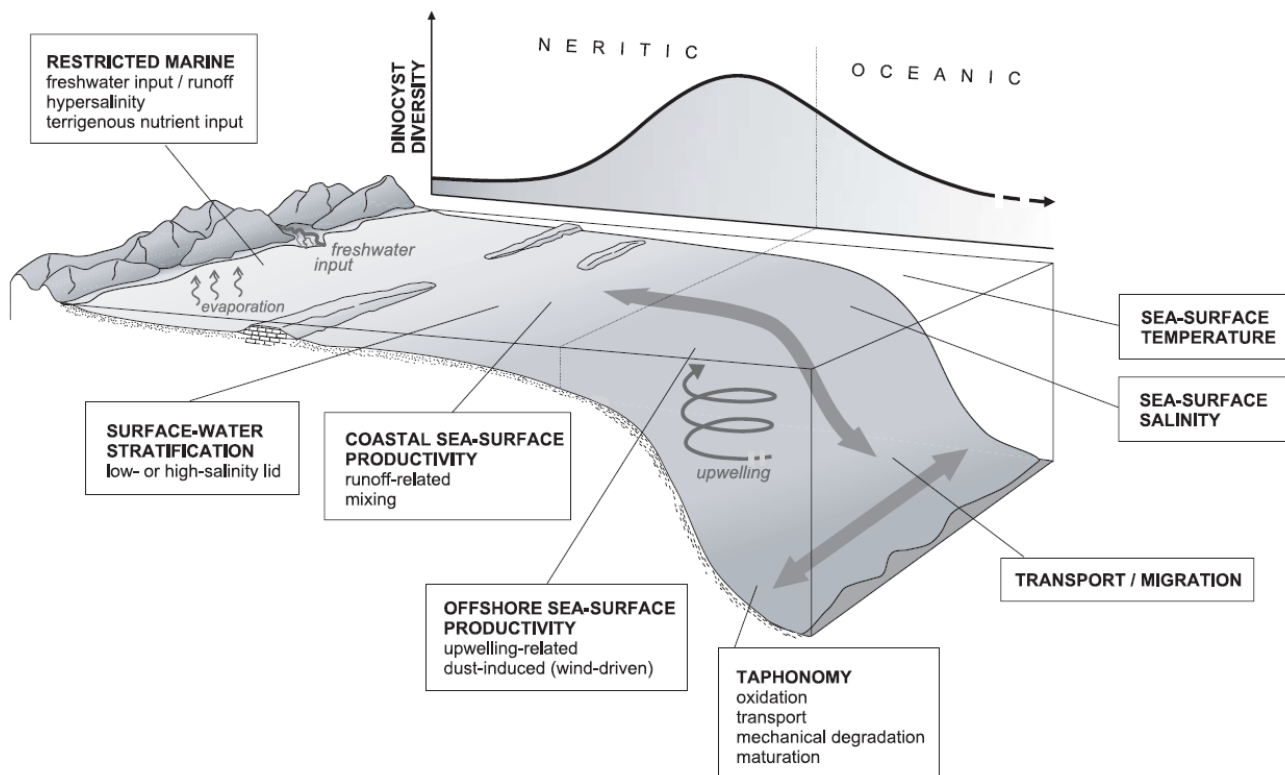


Fig. 7.1. Schematic illustration of main factors influencing the distribution of dinoflagellates and their organic-walled cysts (taken from Pross & Brinkhuis, 2005).

Also, the occurrence of common to abundant microforamineferal linings is taken as an indication of shallow waters (Powell et al., 1990). All taken together, the overall picture provided by the palynomorphs-based analysis fits well the palaeoenvironmental interpretation of the middle Cenomanian of Nazaré based on the sedimentary and macro-faunal (invertebrate and vertebrate) evidence, namely the schematic reconstruction proposed by Callapez et al. (2014), articulating an idealized tidal flat model and a marginal marine lagoon partially separated from an open shelf environment by barrier shoals (see Fig. 7.2).

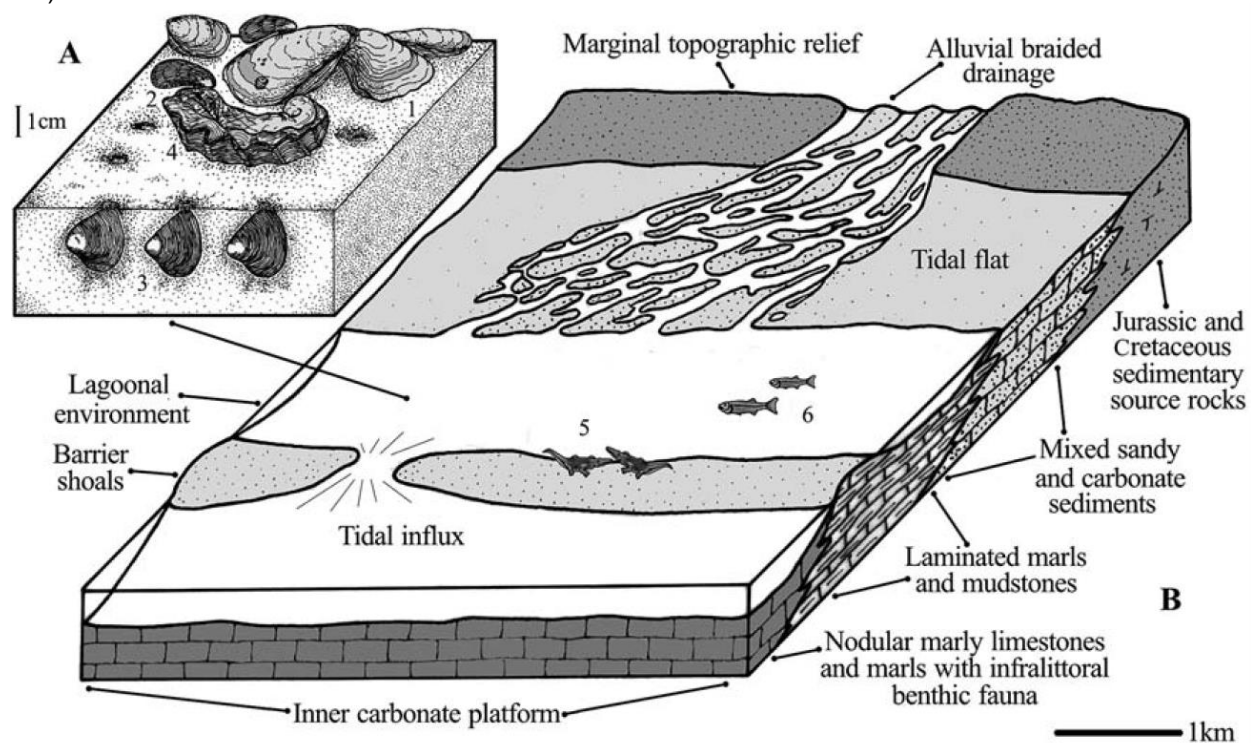


Fig. 7.2 - B. Schematic palaeoenvironmental reconstruction for the Nazaré sector during the Middle Cenomanian and a vertebrate fauna including fishes, turtles and crocodyliforms. The lagoonal environment is represented by oyster communities with *Gyrostroma ouremensis*, illustrated in A. (taken from Callapez et al., 2014).

7.2 COMPARATIVE VIEWS WITH OTHER CRETACEOUS DINOCYSTS ASSEMBLAGES

Comparing dinocysts assemblages at stratigraphically equivalent regions is crucial for an exploratory view of the similarities and differences between them. Segura et al., 2014 noted that, during the Late Cretaceous, the Iberian Peninsula was a relatively independent tectonic block. Its privileged palaeogeographical location favoured the arrival of boreal faunas from the Protoatlantic and temperate-warm faunas from the Tethys to its epicontinental flooded regions. The assemblages found at the Nazaré sector reflect a predominance of taxa with a recognized/probable Tethyan affinity, such as *Subtilishphaera* sp., *Florentinia* sp., *Spiniferites* sp. and *Xenascus* sp. (Arai et al., 2000; Skupien & Vasicek, 2002), and environmental preferences for warm water, such as *Spiniferites* sp. and

Palaeohystrichophora sp. (Prauss, 2002; Uwins & Batten, 1988), while also including species sometimes taken to reflect more northern, Protoatlantic influences, such as *Impletosphaeridium* sp. and *Heterosphaeridium* sp. (Arai, 2007; Warny *et al.*, 2007).

Unlike assemblages of the Castilian Platform (Northern-Central Spain), where characteristic high latitude species such as *Isabelidium acuminatum* were recorded, no taxa with a recognized specific Temperate-Boreal affinity were found at the Nazaré site. Both the Cenomanian-Turonian Spanish assemblages (Peyrot, 2011; Peyrot *et al.*, 2011; Peyrot *et al.*, 2012) and those from the different parts of Northwest Europe (Lignum, 2009) exhibited a predominance of *Palaeohystrichophora infusorioides* and *Spiniferites ramosus*, which could mean that the genera identified in the present study belong to these same species. This also suggests a rather specific local palaeoenvironment of the Nazaré sector during the middle Cenomanian, departing from the widespread open shelf marine environments reflected in the studies used for comparison.

The earlier studies of Albian-Cenomanian dinocysts in the region of Lisbon (Berthou *et al.*, 1980; Berthou & Hasenboehler, 1982) supported this palaeocological specificity of Nazaré and harmonizes well with the suggested role of local tectonics structures close by diapiric structures of Caldas da Rainha and São Pedro de Moel acting as barriers) in sustaining the development of a marginal-marine lagoonal system in early-middle Cenomanian time (Callapez *et al.*, 2014).

However, the paleoecological specificity of Nazaré appear to be quite varied along the platform itself, taking into account the results obtained in the lower-middle Cenomanian layers from Oliveira, 2017. This is supported by the abundant presence of *Spinidium* sp. in the lower layers, but in total absence in the present study. The opposite occurs with *Cyclonephelium* sp., which suggests a change in dinoflagellate communities sometime during the Middle Cenomanian.

Adding the results obtained by Fernandes, 2019, these inferences are even clearer. Both studies present genera of dinocysts that did not occur in the other. This is the case with the presence of *Spinidium* sp., *Circulodinium* sp. and *Oligosphaeridium* sp. only in the lower layers and *Cyclonephelium* sp., *Kiokansium* sp. and *Odontochitina* sp. only in the present study, even in sections with a relatively low distance range. Plus, the determination of the species *Palaeohystrichophora infusorioides*, *Canningia reticulata*, *Florentinia mantelli*, *Spiniferites ramosus*, *Xenascus ceratioides* and *Xiphophoridium alatum* by Fernandes, 2019, could mean that the genera identified in the present study belong to these same species.

The new palynological data allowed to identify new *taxa*, mainly of dinocysts, and to refute the palaeoenvironmental, paleoecological and paleogeographic conditions proposed in previous studies. However, it would be important for future work to also include observation under the scanning electron microscope, in order to recognize even more shapes, namely details that could lead to the species, thus increasing the taxonomical listing and, consequently, recognizing palaeoenvironments and biostratigraphy of these organisms. It would be equally important to continue the studies in these units to confirm possible phenomena of provincialism in the middle Cenomanian of Nazaré.

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APPENDIXES

PLATES 1 TO 31

(The scale in all photographs is set to 50µm)

Plate 1

1. *Bourkidinium* sp., Sample 73 Slide 73 A; x: 37,9; y: 115,1.

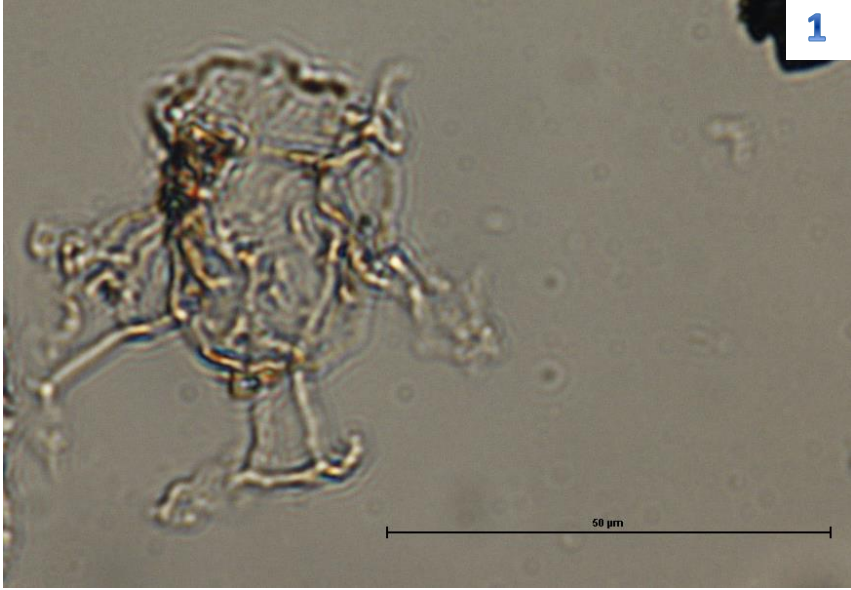


Plate 2

1. *Canningia sp.*, Sample 76 Slide 76 B; x: 25,7; y: 92,3.
2. *Canningia sp.*, Sample 76 Slide 76 B; x: 29,4; y: 92,4.
3. *Canningia sp.*, Sample 79 Slide 79 A; x: 25,5; y: 90,2.
4. *Canningia sp.*, Sample 79 Slide 79 A; x: 54,0; y: 102,9.
5. *Canningia sp.*, Sample 85T Slide 85T A; x: 52,3; y: 102,5.

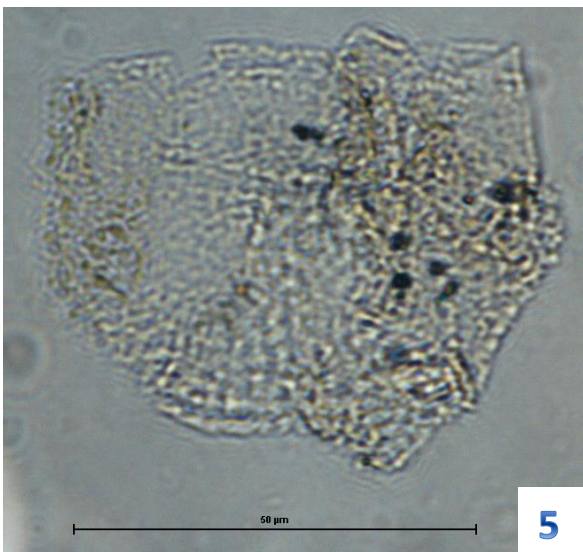
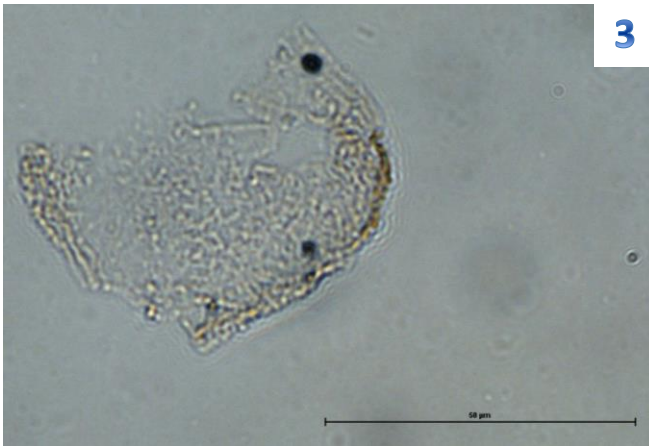
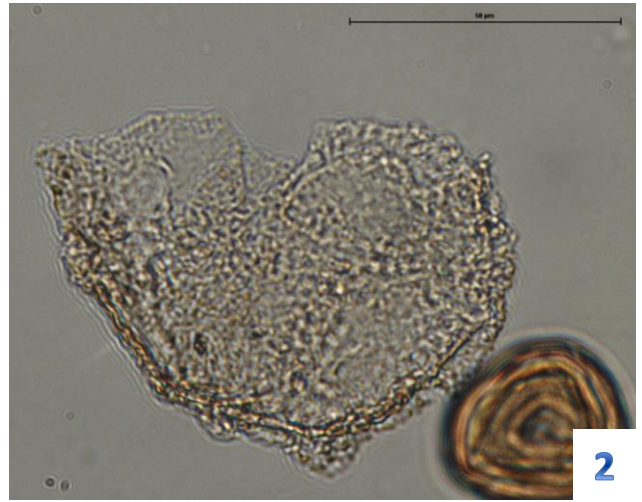
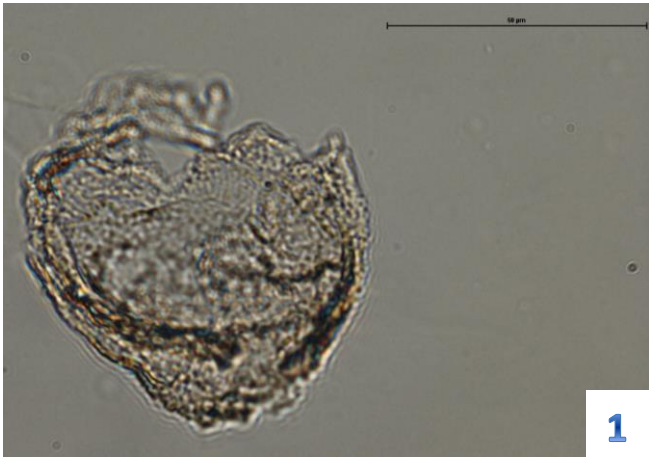


Plate 3

1. *Cribroperidinium sp.*, Sample 73 Slide 73 A; x: 50,4; y: 114,7.
2. *Cribroperidinium sp.*, Sample 85T Slide 85T A; x: 21,8; y: 115,6.
3. *Dingodinium sp.*, Sample 79 Slide 79 A; x: 24,0; y: 108,0.



Plate 4

1. *Cyclonephelium sp.*, Sample 73 Slide 73 A; x: 40,7; y: 113,3.
2. *Cyclonephelium sp.*, Sample 73 Slide 73 A; x: 43,7; y: 115,7.
3. *Cyclonephelium sp.*, Sample 83 Slide 83 B; x: 55,7; y: 99,5.
4. *Cyclonephelium sp.*, Sample 85T Slide 85T A; x: 58,5; y: 112,9.

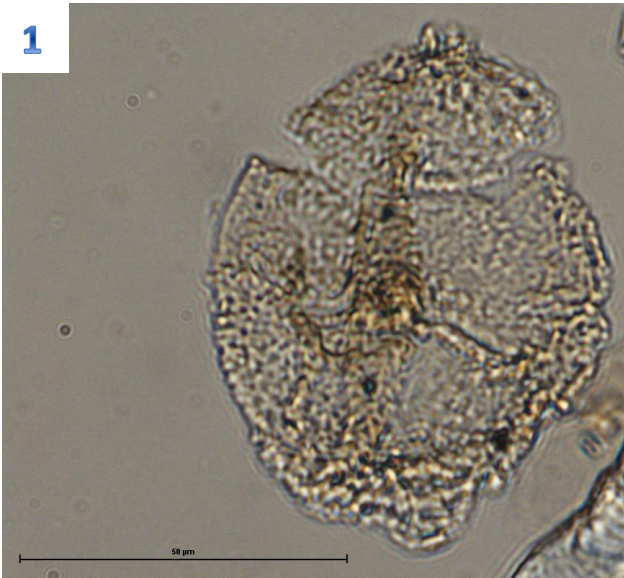


Plate 5

1. *Florentinia sp.*, Sample 73 Slide 73 A; x: 48,9; y: 113,9.
2. *Florentinia sp.*, Sample 73 Slide 73 A; x: 23,5; y: 114,6.
3. *Florentinia sp.*, Sample 73 Slide 73 A; x: 29,6; y: 112,5.
4. *Florentinia sp.*, Sample 73 Slide 73 A; x: 18,6; y: 109,3.
5. *Florentinia sp.*, Sample 81 Slide 81 A; x: 42,7; y: 98,7.
6. *Florentinia sp.*, Sample 76 Slide 76 B; x: 35,7; y: 91,7.

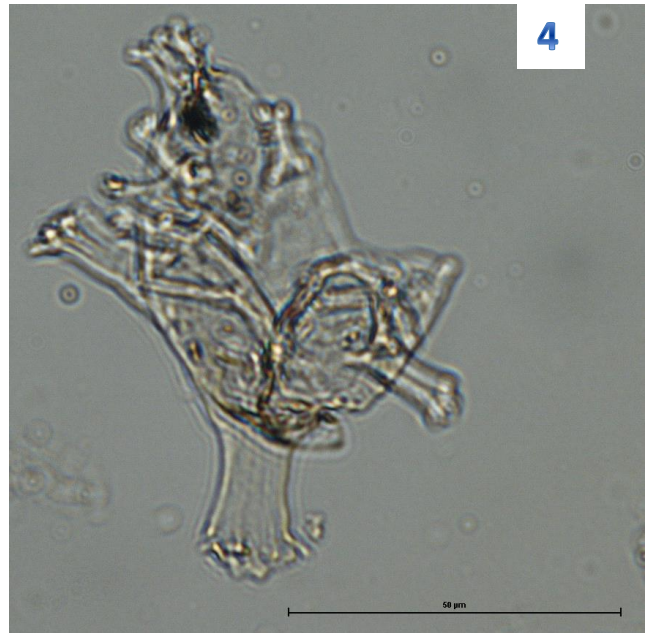
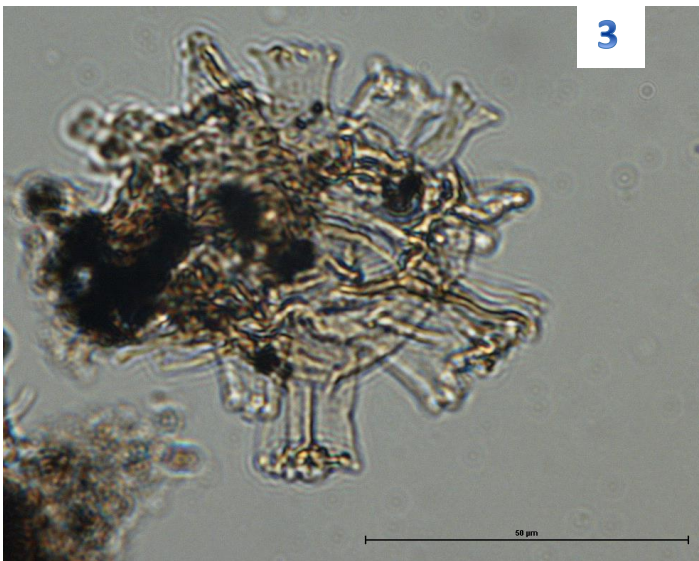
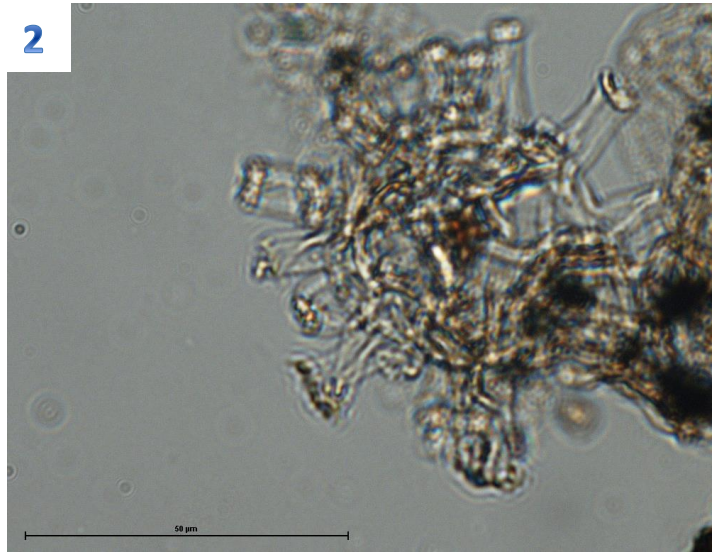
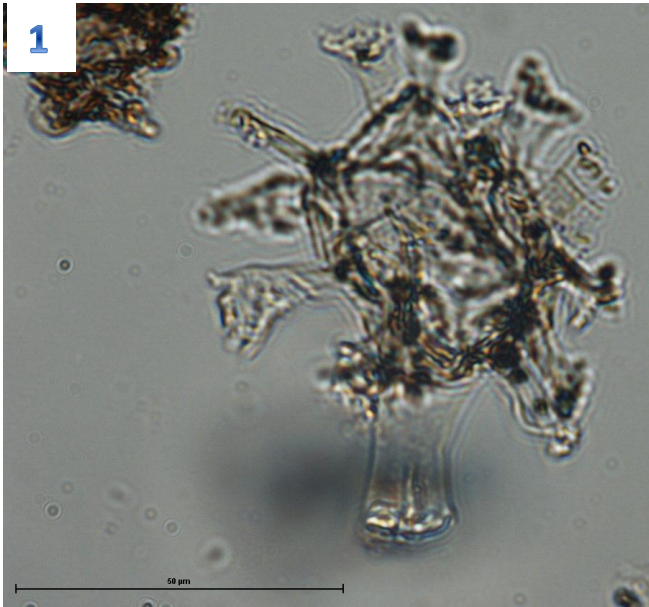


Plate 6

1. *Heterosphaeridium* sp., Sample 79 Slide 79 A; x: 25,6; y: 98,5
2. *Heterosphaeridium* sp., Sample 79 Slide 79 A; x: 35,6; y: 92,7.
3. *Heterosphaeridium* sp., Sample 81 Slide 81 A; x: 52,3; y: 97,1.



Plate 7

1. *Impletosphaeridium sp.*, Sample 73 Slide 73 A; x: 26,1; y: 114,2.
2. *Impletosphaeridium sp.*, Sample 73 Slide 73 A; x: 21,4; y: 109,0.
3. *Impletosphaeridium sp.*, Sample 83 Slide 83 B; x: 45,8; y: 106,3.

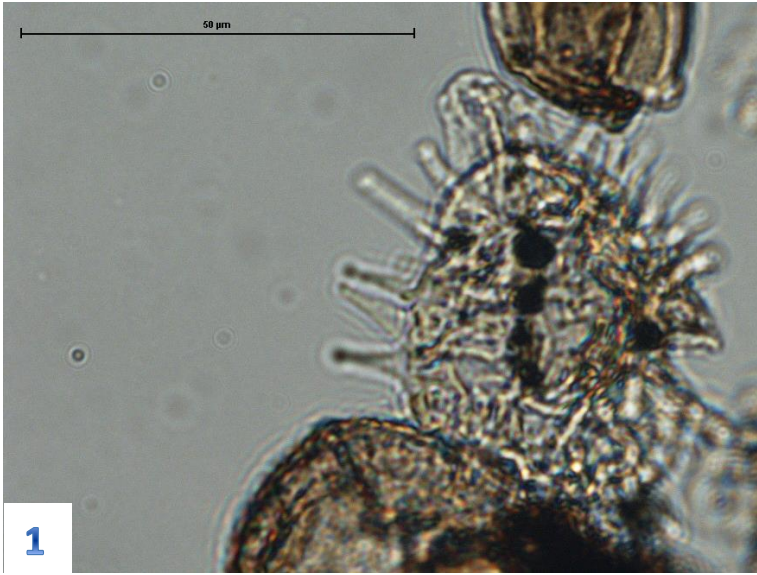


Plate 8

1. *Kiokansium sp.* Sample 76 Slide 76 B; x: 54,1; y: 99,4.
2. *Kiokansium sp.*, Sample 76 Slide 76 B; x: 46,9; y: 105,8.
3. *Kiokansium sp.*, Sample 76 Slide 76 B; x: 42,4; y: 101,0.

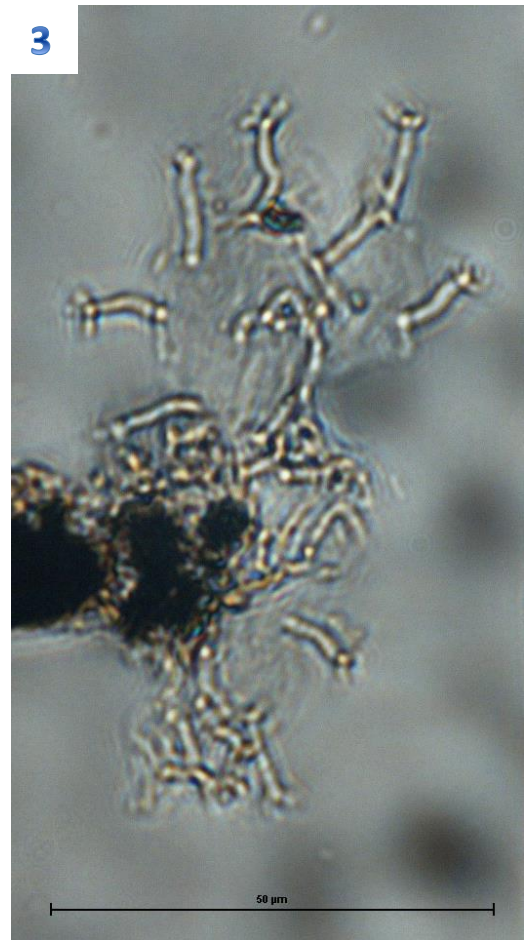
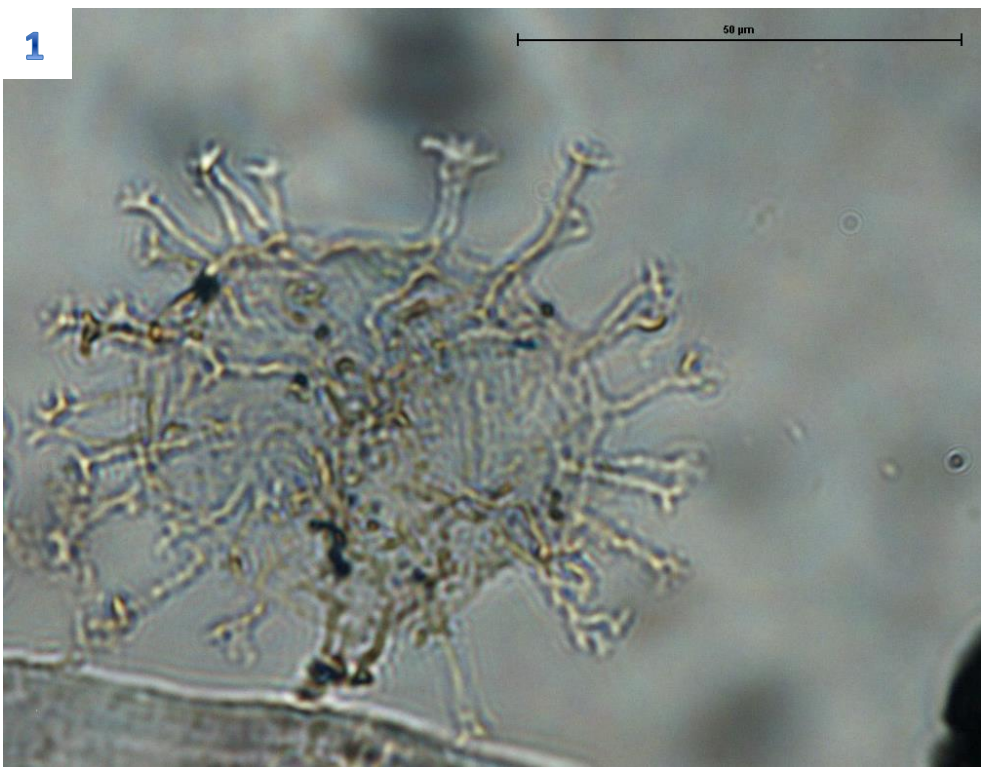


Plate 9

1. *Odontochitina* sp., Sample 79 Slide 79 A; x: 42,5; y: 94,4.
2. *Odontochitina* sp., Sample 79 Slide 79 A; x: 23,0; y: 98,6.



Plate 10

1. *Palaeohystrichopora* sp. Sample 76 Slide 76 B; x: 45,8; y: 91,9.
2. *Palaeohystrichopora* sp. Sample 76 Slide 76 B; x: 40,7; y: 94,4.
3. *Palaeohystrichopora* sp. Sample 79 Slide 79 A; x: 13,3; y: 93,8.
4. *Palaeohystrichopora* sp. Sample 79 Slide 79 A; x: 33,7; y: 95,5.

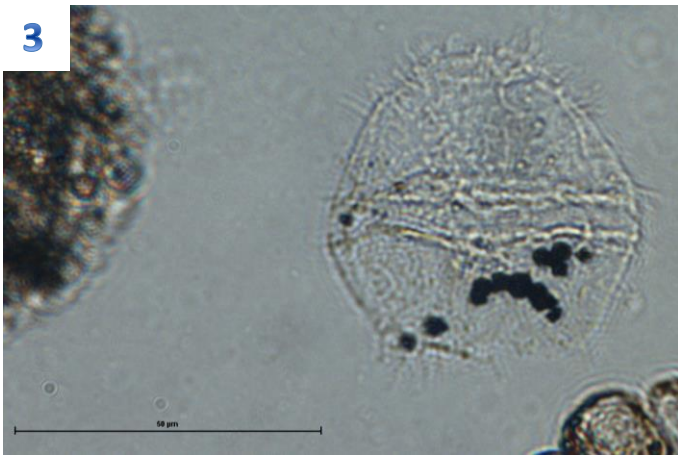
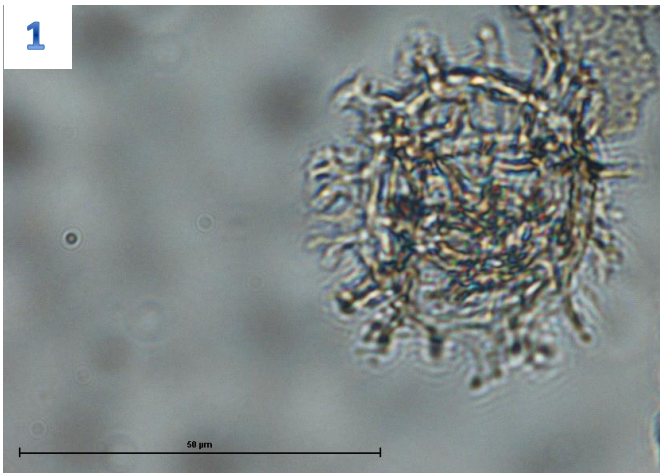


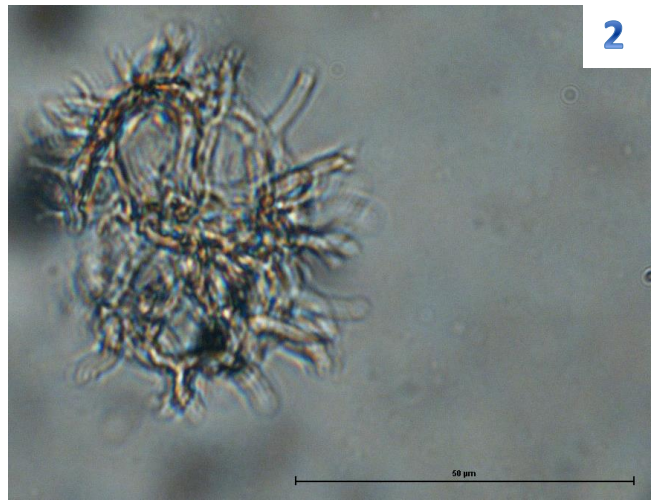
Plate 11

1. *Spiniferites sp.*, Sample 76 Slide 76 B; x: 38,4; y: 107,0.
2. *Spiniferites sp.*, Sample 76 Slide 76 B; x: 51,4; y: 101,7..
3. *Spiniferites sp.*, Sample 73 Slide 73 A; x: 26,7; y: 115,7.1

1



2



3

Plate 12

1. *Subtilisphaera sp.*, Sample 72 Slide 72 A; x: 43,5; y: 107,5.
2. *Subtilisphaera sp.*, Sample 73 Slide 73 A; x: 43,0; y: 103,6.
3. *Subtilisphaera sp.*, Sample 76 Slide 76 B; x: 46,7; y: 113,6.
4. *Subtilisphaera sp.*, Sample 83 Slide 83 B; x: 43,7; y: 101,2.
5. *Subtilisphaera sp.*, Sample 94 Slide 94 A; x: 31,9; y: 108,2.

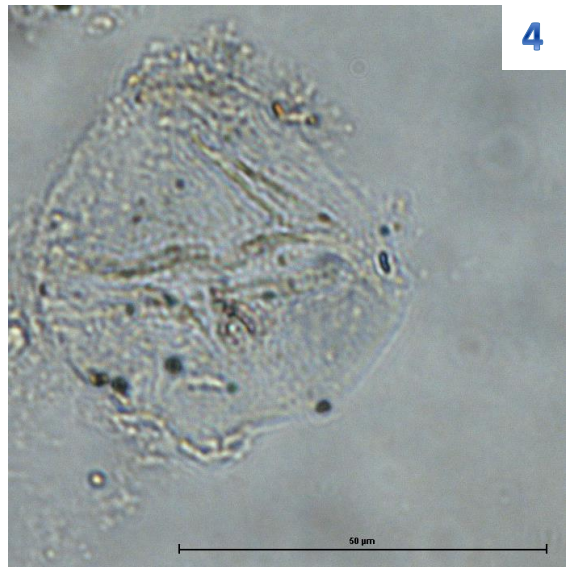
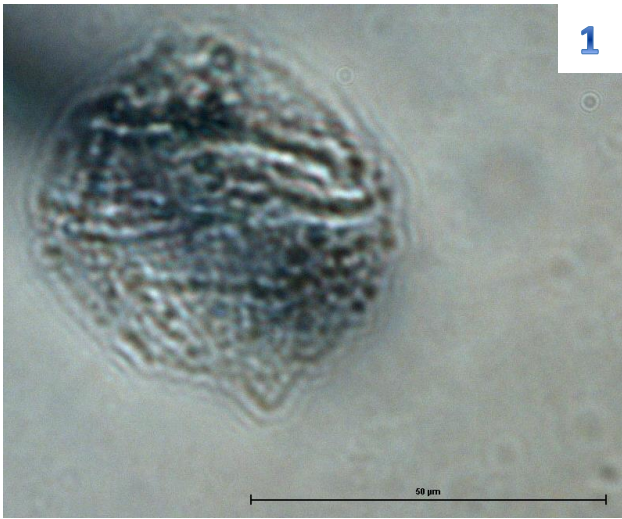


Plate 13

1. *Xenascus sp.*, Sample 76 Slide 76 B; x: 46,7; y: 93,5.

2. *Xenascus sp.*, Sample 92T Slide 92T A; x: 30,7; y: 98,4.

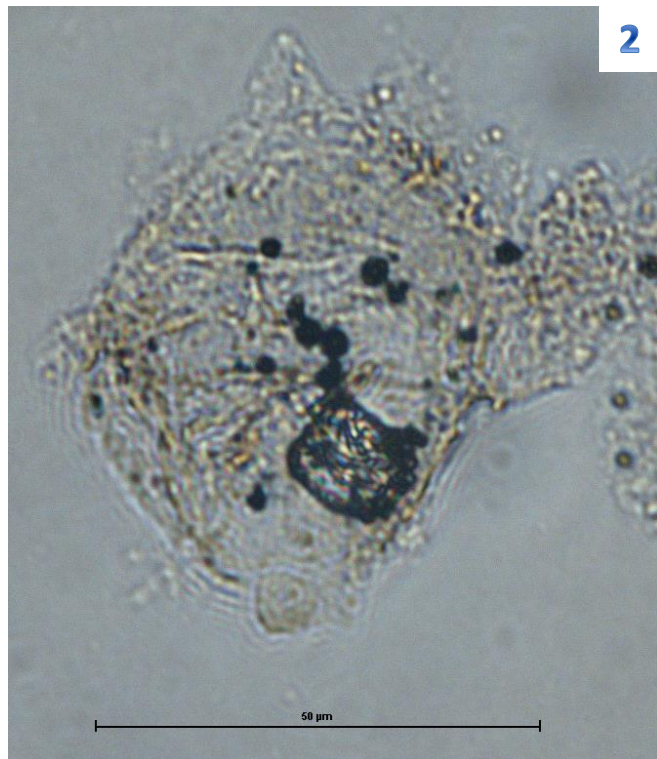
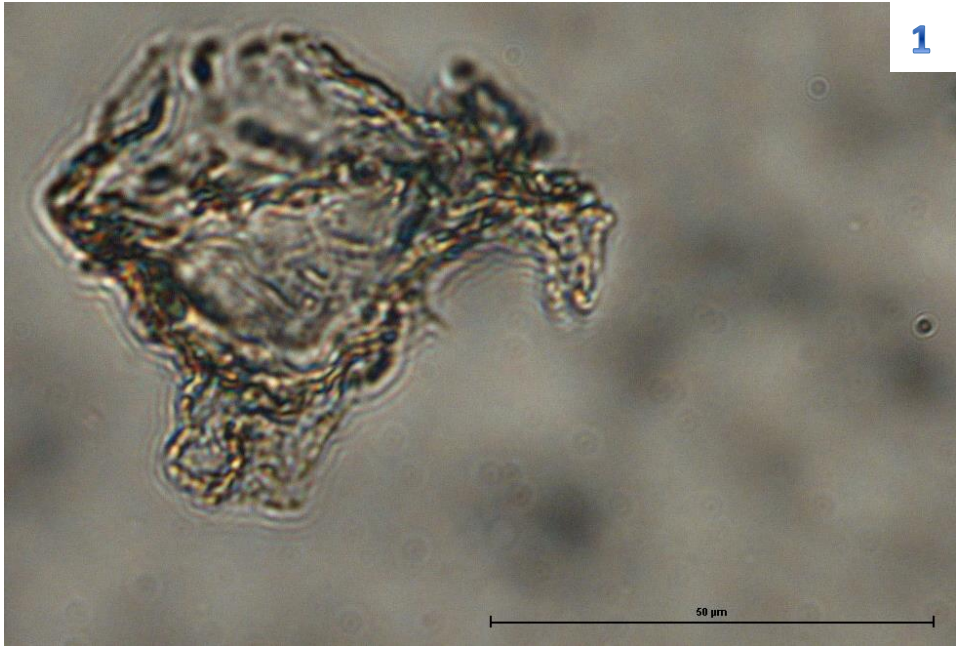


Plate 14

1. *Xiphophoridium sp.*, Sample 73 Slide 73 A; x: 26,7; y: 115,7.
2. *Xiphophoridium sp.*, Sample 76 Slide 76 B; x: 21,6; y: 105,5.
3. *Xiphophoridium sp.*, Sample 79 Slide 79 A; x: 23,6; y: 103,5.
4. *Xiphophoridium sp.*, Sample 81 Slide 81 A; x: 40,7; y: 98,3.

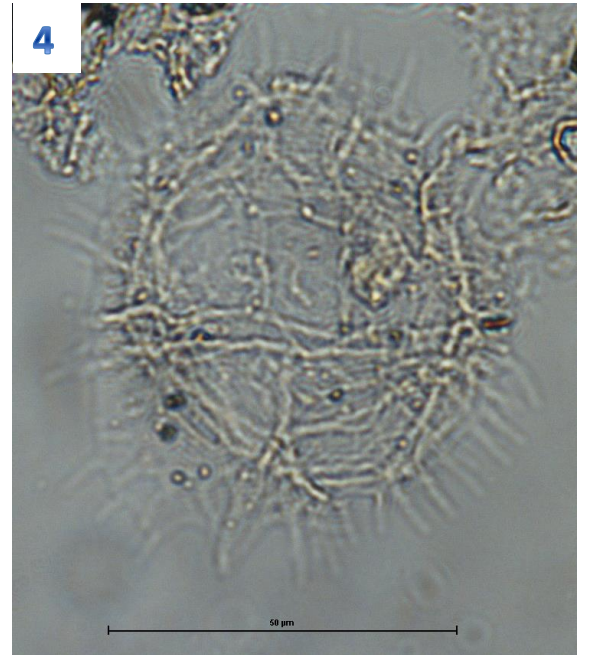
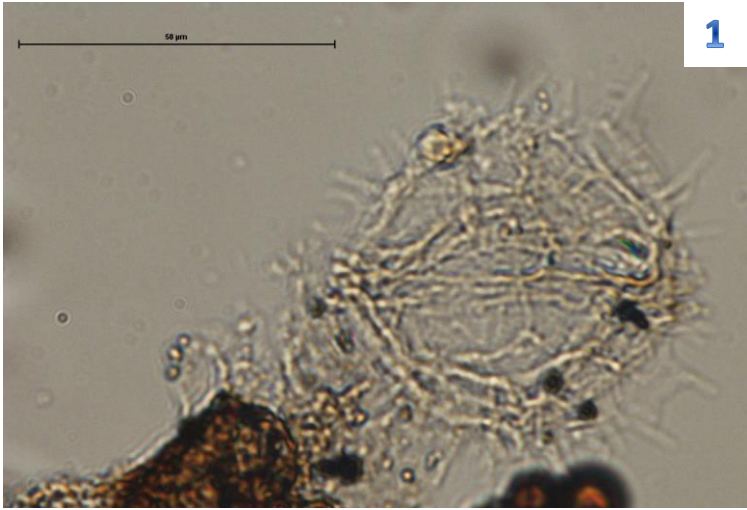


Plate 15

1. *Alisporites* sp., Sample 72 Slide 72 A; x: 49,6; y: 95,4.
2. *Alisporites* sp., Sample 73 Slide 73 A; x: 50,6; y: 114,6.
3. *Alisporites* sp., Sample 79 Slide 79 A; x: 27,7; y: 93,3.
4. *Alisporites* sp., Sample 85B Slide 85B A; x: 35,0; y: 92,0.
5. *Alisporites* sp., Sample 92T Slide 92T A; x: 49,0; y: 100,9.
6. *Alisporites* sp., Sample 94 A Slide 94 A; x: 94,3; y: 47,6.

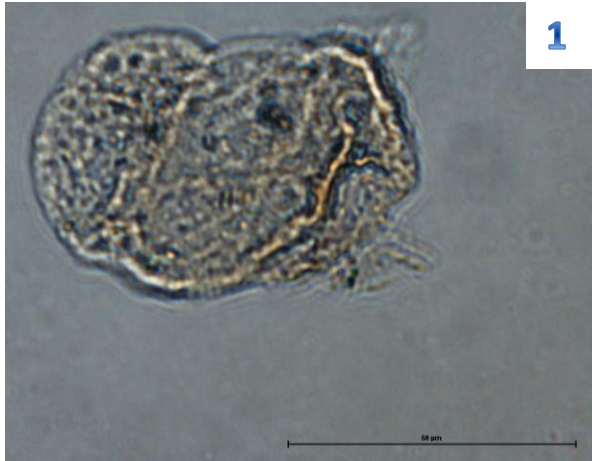


Plate 16

1. *Podocarpidites* sp., Sample 73 Slide 73 A; x: 50,6; y: 114,6.
2. *Podocarpidites* sp., Sample 85B Slide 85B A; x: 46,2; y: 94,5.
3. *Podocarpidites* sp., Sample 92T Slide 92T A; x: 52,2; y: 102,3.

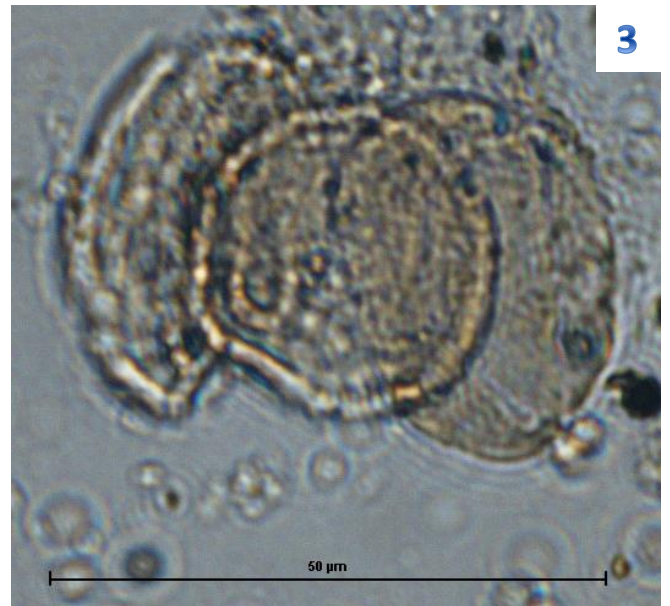


Plate 17

1. *Basopollis* sp., Sample 85B Slide 85B A; x:46,0; y: 92,3.

2. *Basopollis* sp., Sample 85B Slide 85B A; x: 9,0; y: 93,0.

3. *Basopollis* sp., Sample 88 Slide 88 A; x: 32,2; y: 105,5.

4. *Basopollis* sp., Sample 94 Slide 94 A; x: 23,6; y: 111,8.

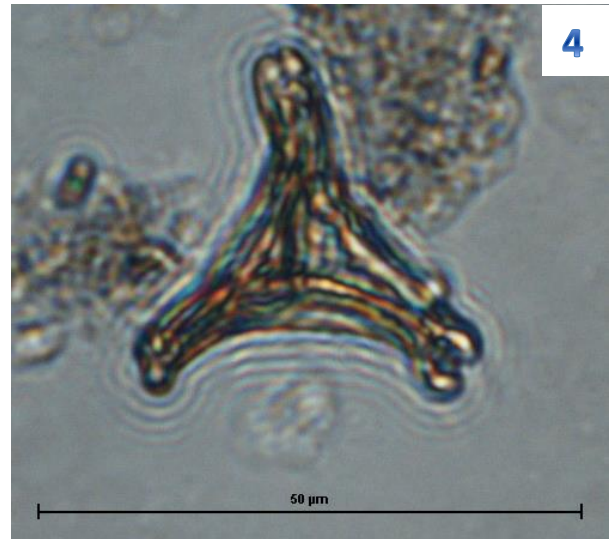
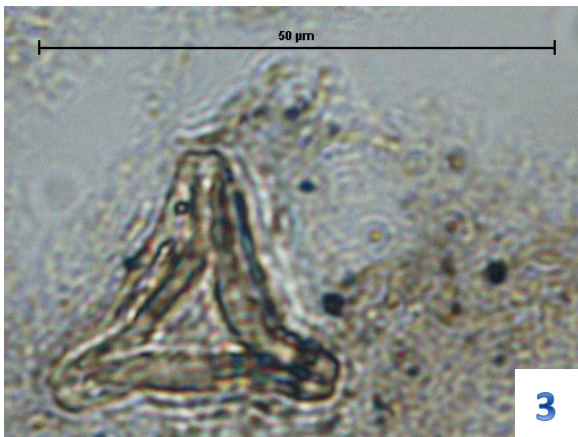
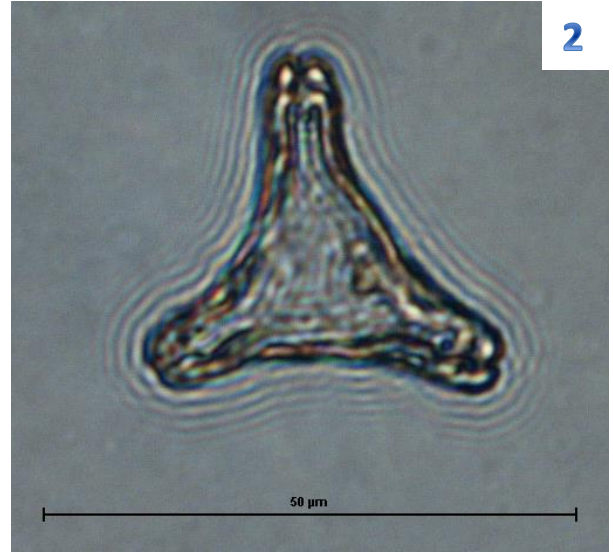
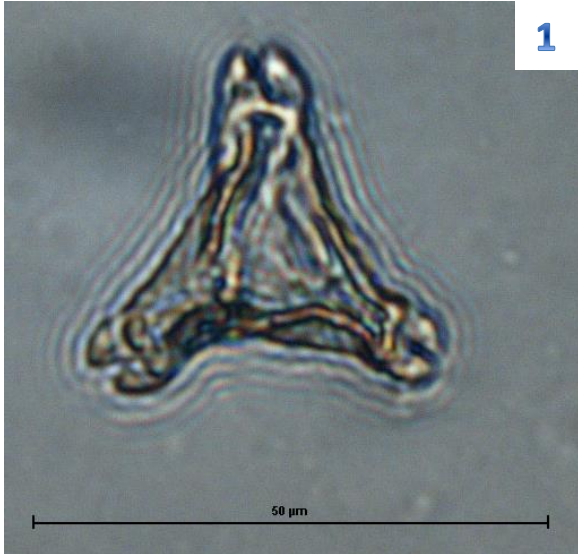


Plate 18

1. *Classopolis sp.*, Sample 72 Slide 72 A; x: 53,3; y: 111,4.
2. *Classopolis sp.*, Sample 73 Slide 73 A; x: 33,5; y: 115,0.
3. *Classopolis sp.*, Sample 73 Slide 73 A; x: 44,7; y: 113,4.
4. *Classopolis sp.*, Sample 73 Slide 73 A; x: 49,9; y: 104,3.
5. *Classopolis sp.*, Sample 76 Slide 76 B; x: 39,4; y: 114,9.
6. *Classopolis sp.*, Sample 81 Slide 81 A; x: 30,2; y: 99,6.

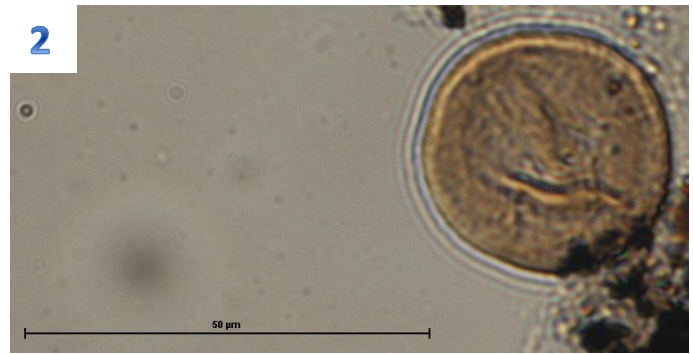


Plate 19

1. *Concavisporites* sp., Sample 73 Slide 73 A; x: 24,6; y: 114,3.
2. *Concavisporites* sp., Sample 85T Slide 85 A; x: 37,7; y: 112,3.
3. *Concavisporites* sp., Sample 92T Slide 92T A; x: 48,7; y: 110,3.

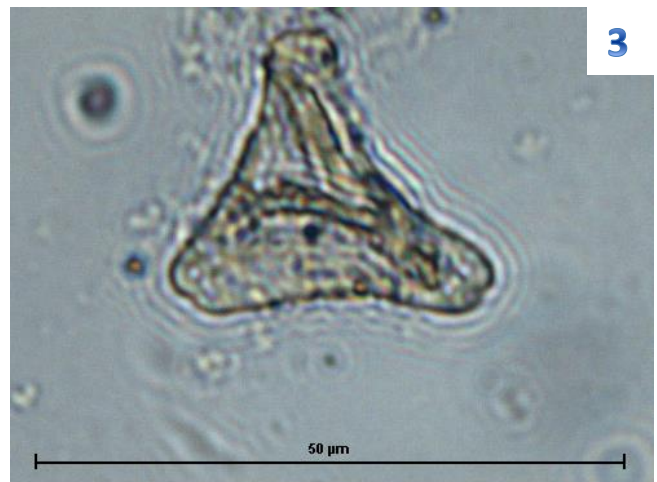
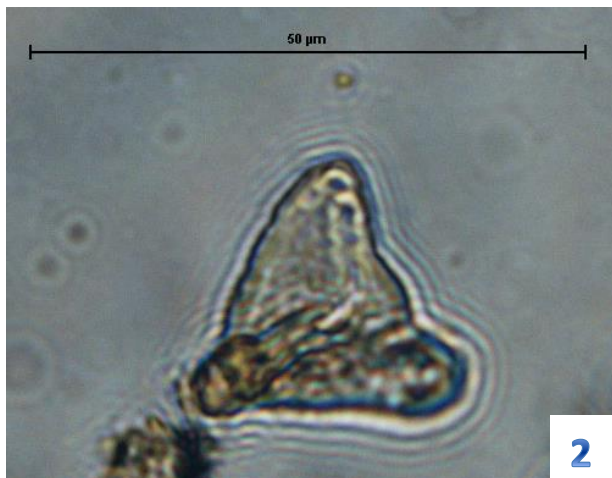
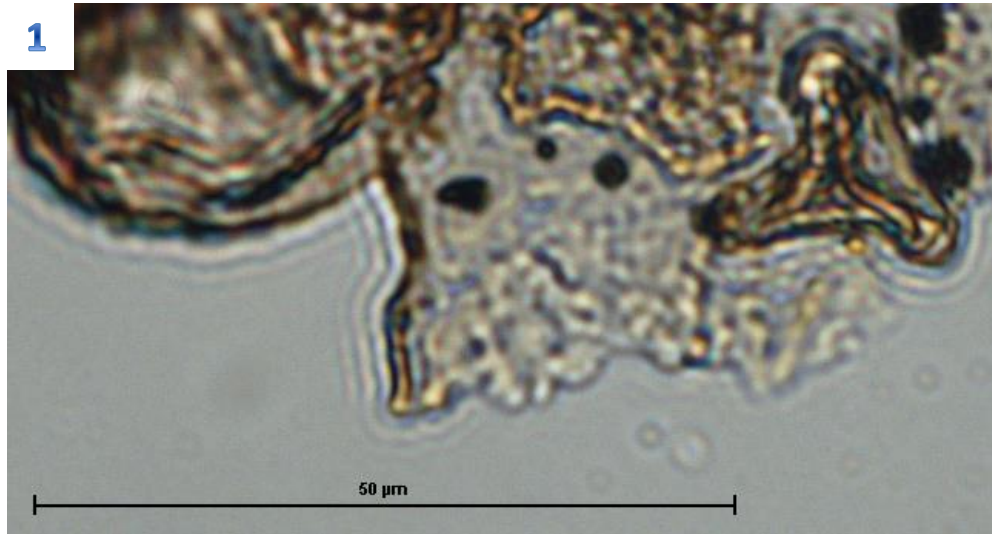


Plate 20

1. *Cyathidites sp.*, Sample 85B Slide 85 A; x: 23,0; y: 99,6.
2. *Cyathidites sp.*, Sample 85T Slide 85T A; x: 42,0; y: 114,5.
3. *Cyathidites sp.*, Sample 92B Slide 92B A; x: 18,7; y: 99,0.
4. *Cyathidites sp.*, Sample 94 Slide 94 A; x: 44,3; y: 98,7.
5. *Cyathidites sp.*, Sample 94 Slide 94 A; x: 42,1; y: 113,2.

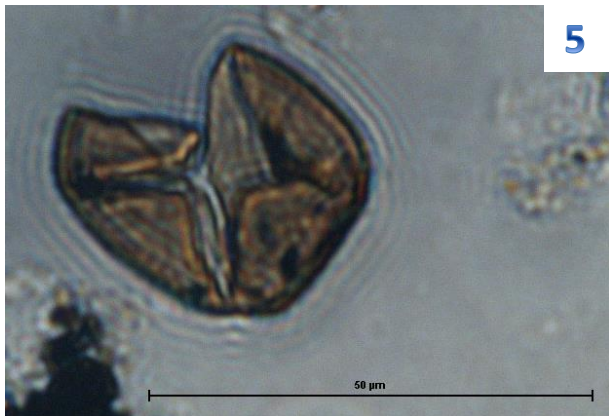
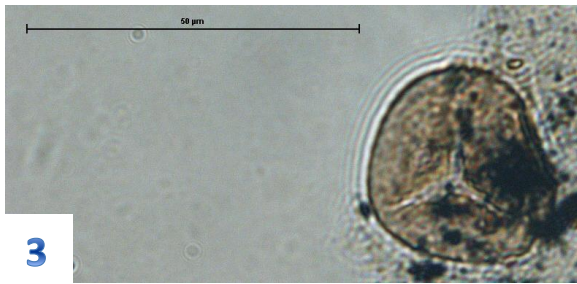
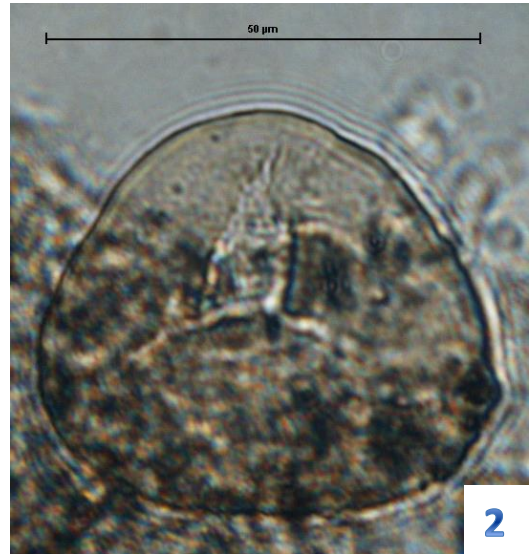
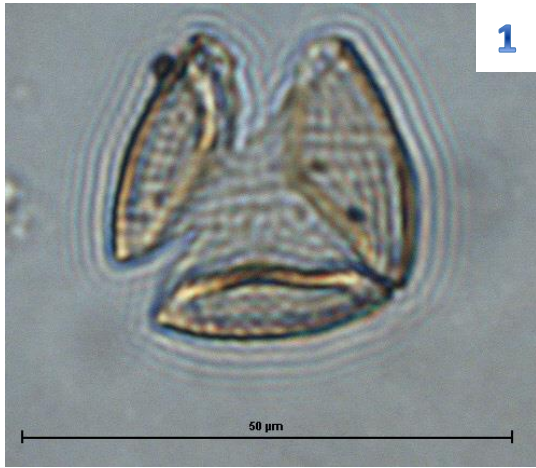


Plate 21

1. *Echitriporites* sp., Sample 85B Slide 85B A; x: 47,0; y: 91,6.
2. *Echitriporites* sp., Sample 85B Slide 85B A; x: 45,2; y: 91,5.
3. *Echitriporites* sp., Sample 85T Slide 85T A; x: 37,7; y: 112,3.

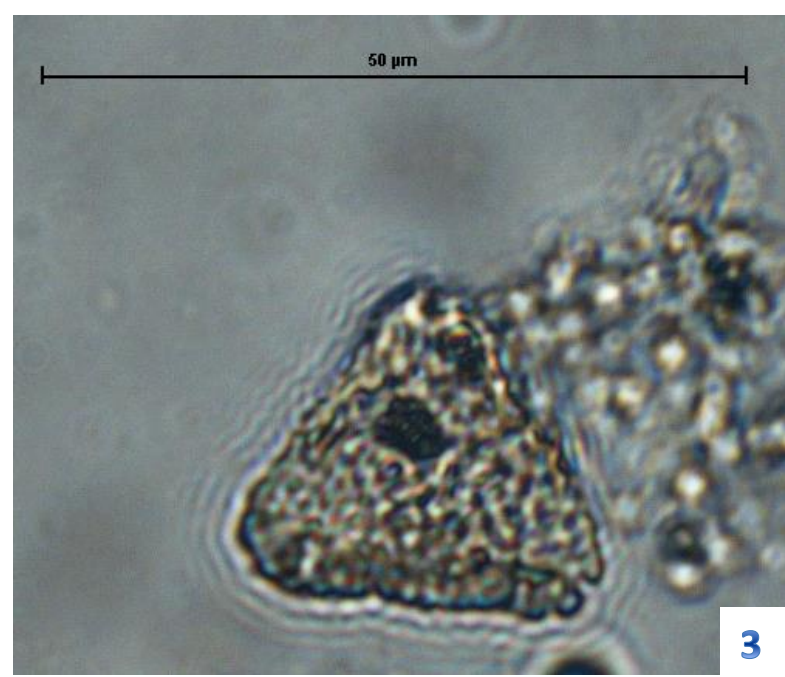
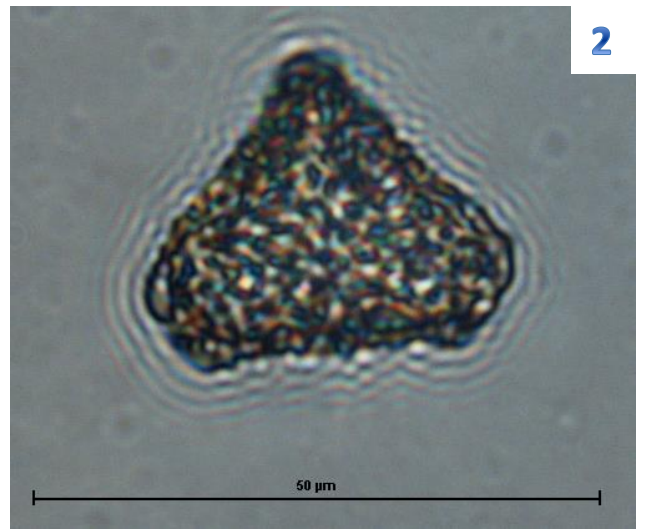
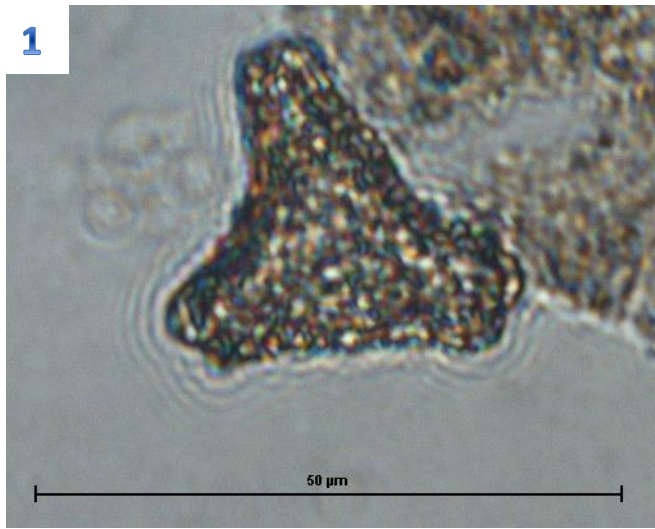


Plate 22

1. *Proteacidites sp.*, Sample 85B Slide 85B A; x: 11,7; y: 107,0.
2. *Proteacidites sp.*, Sample 88 Slide 88 A; x: 40,2; y: 96,7.
3. *Proteacidites sp.*, Sample 92B Slide 92B A; x: 43,7; y: 104,5.
4. *Proteacidites sp.*, Sample 92B Slide 92B A; x: 17,0; y: 110,0.
5. *Proteacidites sp.*, Sample 94 Slide 94 A; x: 41,2; y: 111,0.
6. *Proteacidites sp.*, Sample 92T Slide 92T A; x: 18,4; y: 110,8.

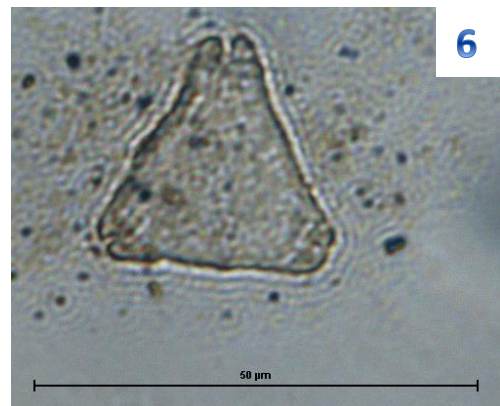
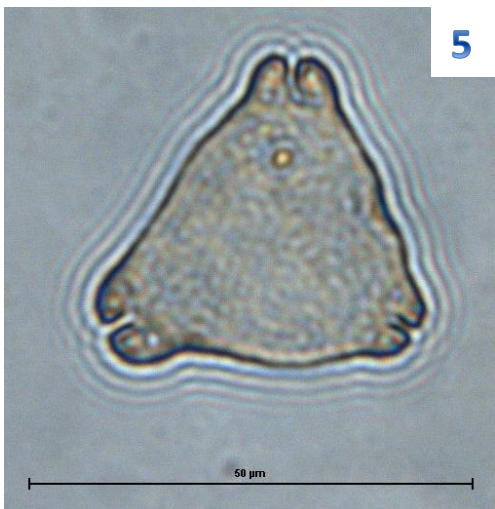
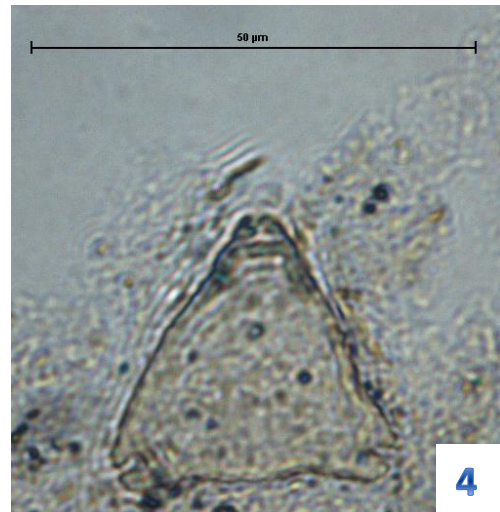
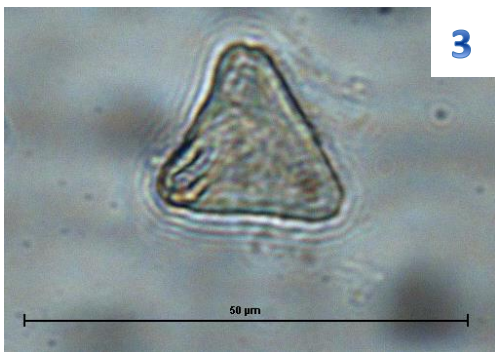
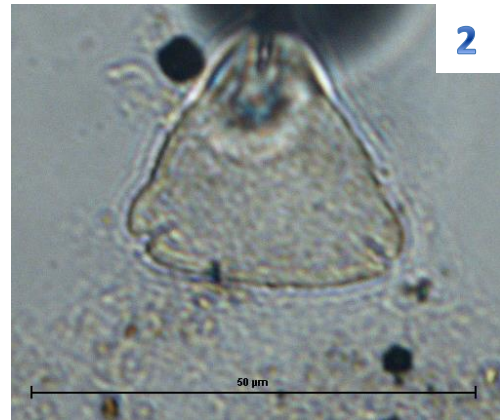
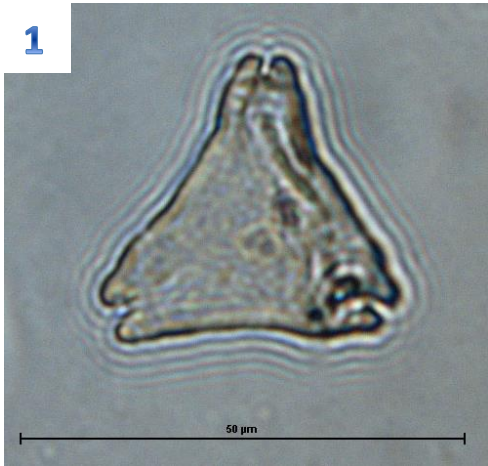


Plate 23

1. *Steevesipollenites sp.*, Sample 92B Slide 92B A; x: 20,0; y: 112,0.
2. *Syncolporites sp.*, Sample 85B Slide 85B A; x: 9,9; y: 93,3.
3. *Taxodiaceapollenites sp.*, Sample 94 Slide 94 A; x: 48,2; y: 94,2.
4. *Tricolpites sp.*, Sample 85B Slide 85B A; x: 19,5; y: 92,2.

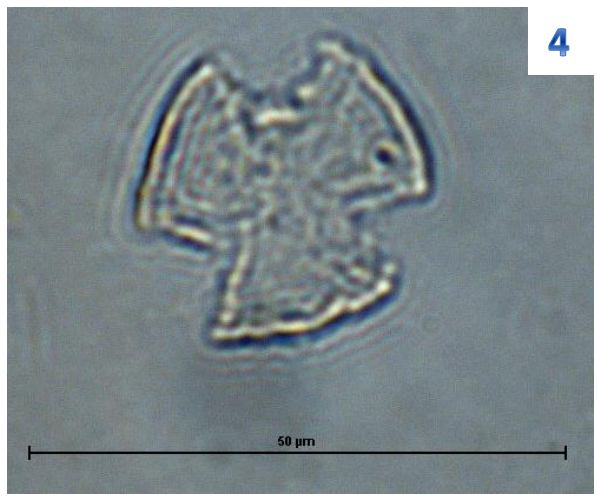
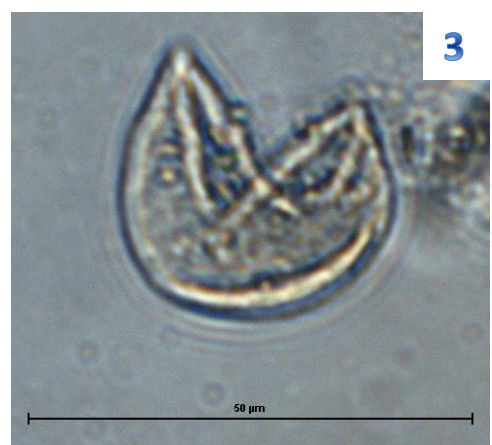
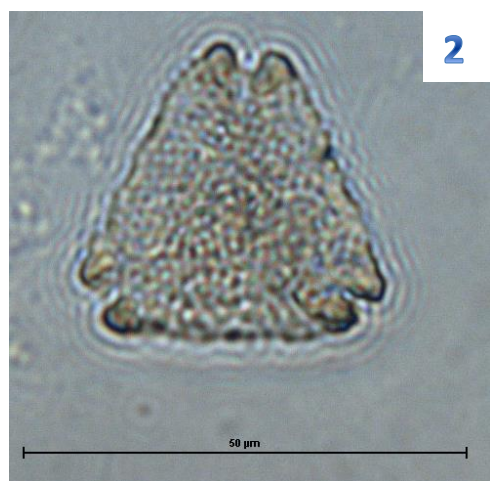


Plate 24

1. *Cicatricosisorites sp.*, Sample 73 Slide 73 A; x: 21,0; y: 107,0.
2. *Cicatricosisorites sp.*, Sample 73 Slide 73 A; x: 24,4; y: 108,4.
3. *Cicatricosisorites sp.*, Sample 76 Slide 76 B; x: 31,4; y: 111,4.
4. *Cicatricosisorites sp.*, Sample 85B Slide 85B A; x: 9,0; y: 111,0.
5. *Cicatricosisorites sp.*, Sample 85T Slide 85T A; x: 39,8; y: 109,0.
6. *Cicatricosisorites sp.*, Sample 94 Slide 94 A; x: 50,5; y: 96,4.

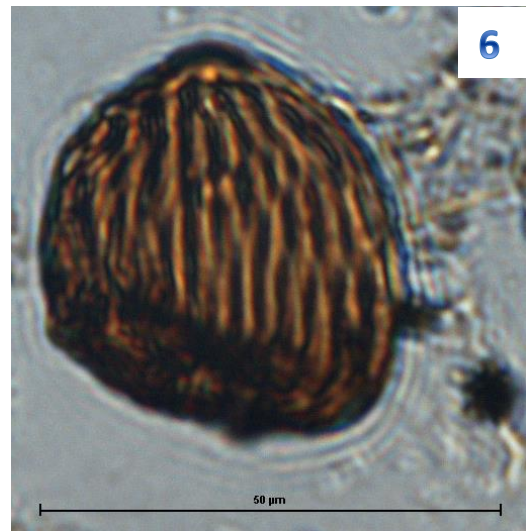
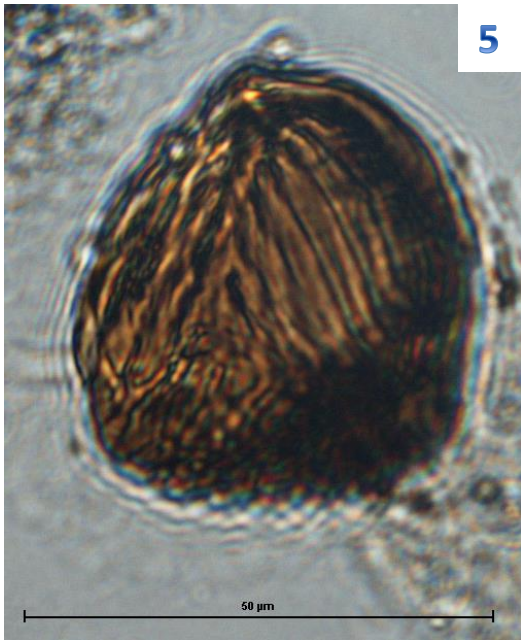
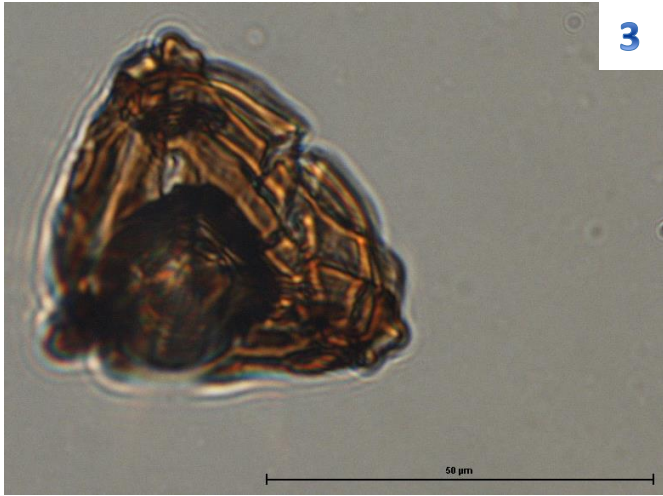
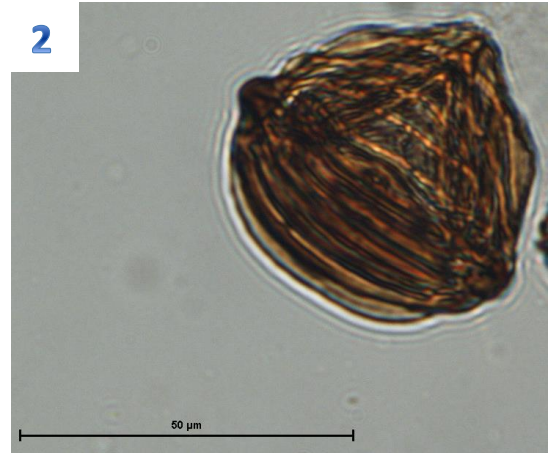
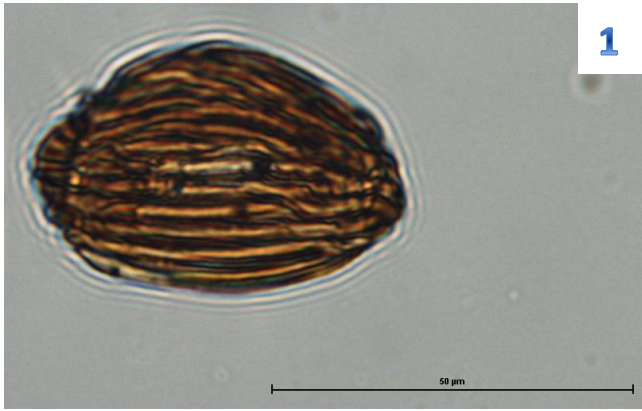


Plate 25

1. *Cicatricosisorits sp.*, Sample 85T Slide 85T A; x: 23,0; y: 112,8.
2. *Cicatricosisorits sp.*, Sample 85T Slide 85T A; x: 48,4; y: 101,5.
3. *Cicatricosisorits sp.*, Sample 85T Slide 85T A; x: 42,0; y: 97,0.
4. *Cicatricosisorits sp.*, Sample 94 Slide 94 A; x: 23,5; y: 109,0.

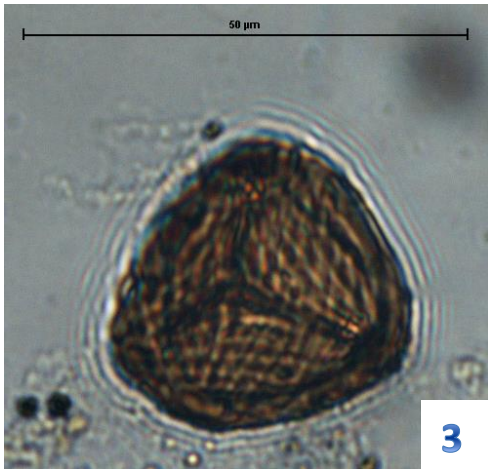
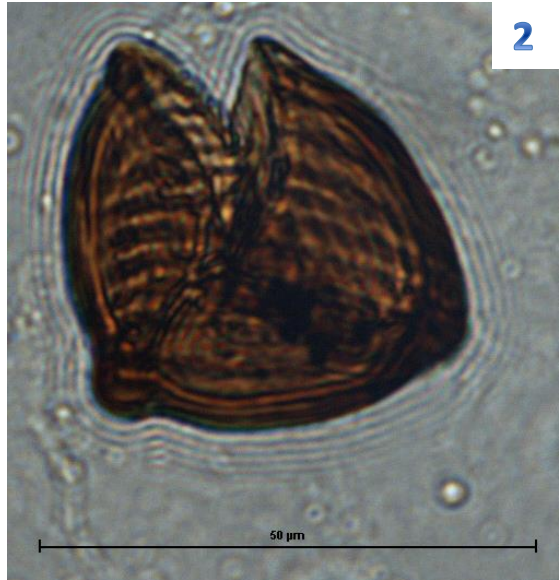
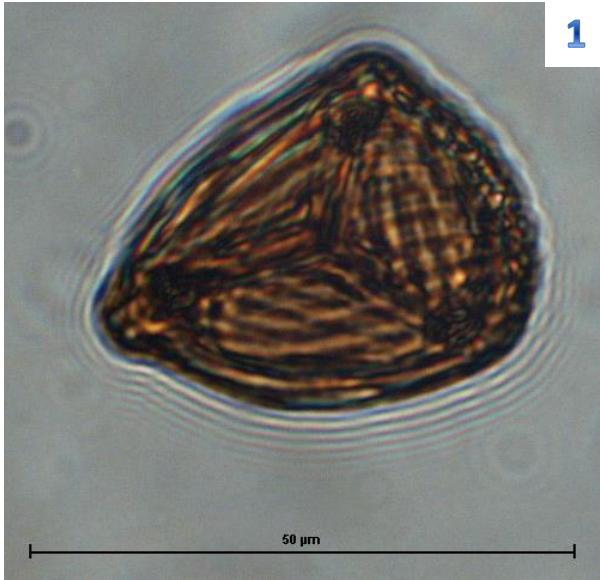


Plate 26

1. *Cingulatisporis sp.*, Sample 72 Slide 72 A; x: 38,5; y: 97,7.
2. *Cingulatisporis sp.*, Sample 79 Slide 79 A; x: 30,0; y: 93,0.
3. *Cingulatisporis sp.*, Sample 83 Slide 83 B; x: 58,9; y: 102,5.
4. *Cingulatisporis sp.*, Sample 85B Slide 85B A; x: 10,0; y: 95,7.
5. *Cingulatisporis sp.*, Sample 85T Slide 85T A; x: 48,4; y: 104,5.
6. *Cingulatisporis sp.*, Sample 88 Slide 88 A; x: 33,5; y: 111,5.

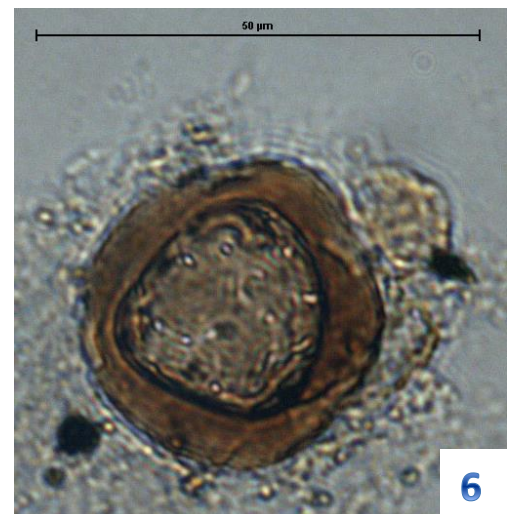
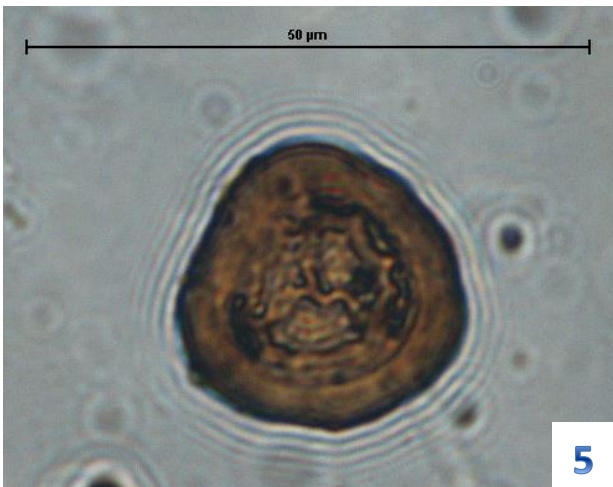
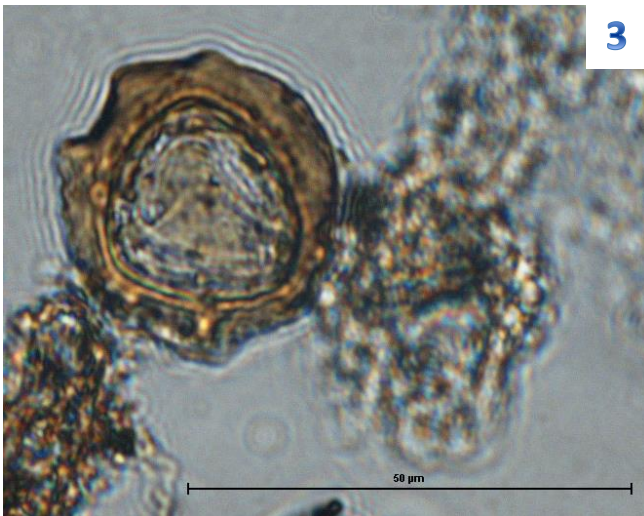


Plate 27

1. *Contignisporites sp.*, Sample 76 Slide 76 B; x: 42,9; y: 92,2.
2. *Densoisporites sp.*, Sample 73 Slide 73 A; x: 18,7; y: 114,7.
3. *Krauselisporites sp.*, Sample 92B Slide 92B A; x: 16,7; y: 106,3.
4. *Krauselisporites sp.*, Sample 92T Slide 92T A; x: 43,3; y: 95,4.
5. *Leptolepidites sp.*, Sample 88 Slide 88 A; x: 33,8; y: 105,5.

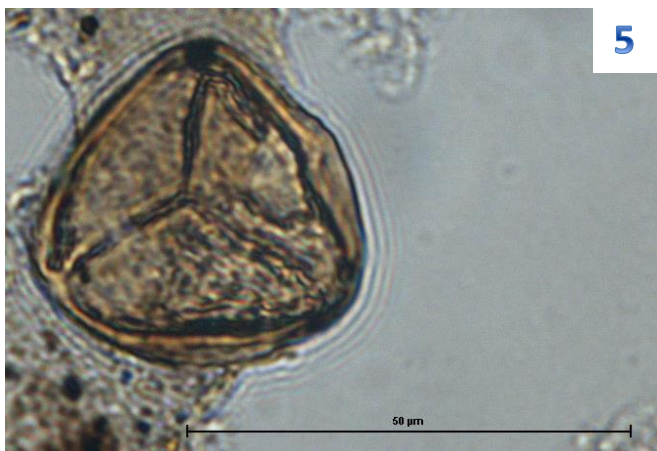
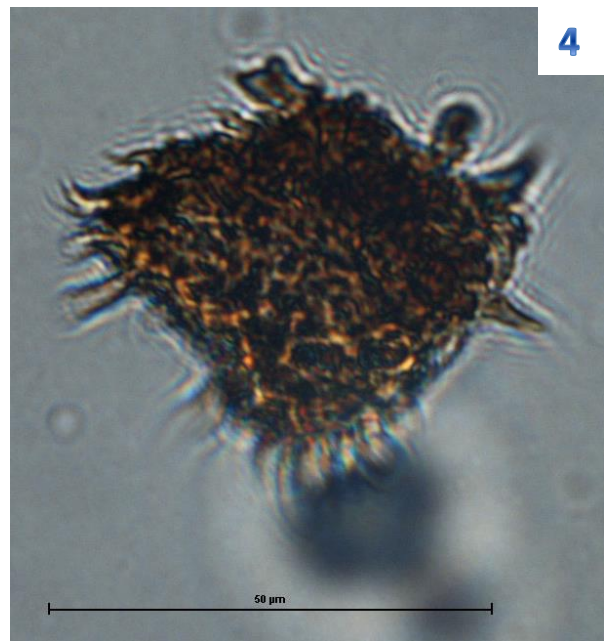
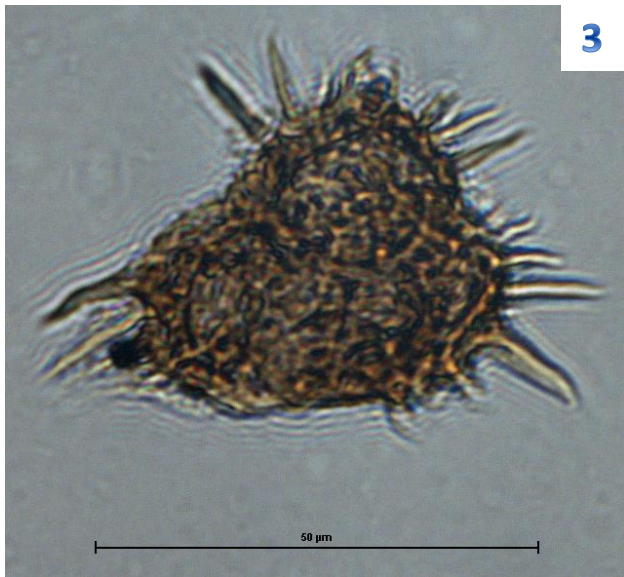


Plate 28

1. *Patellasporites sp.*, Sample 72 Slide 72 A; x: 50,7; y: 101,8.
2. *Patellasporites sp.*, Sample 73 Slide 73 A; x: 51,7; y: 113,7.
3. *Patellasporites sp.*, Sample 73 Slide 73 A; x: 18,4; y: 115,8.
4. *Patellasporites sp.*, Sample 76 Slide 76 B; x: 49,7; y: 93,5.
5. *Patellasporites sp.*, Sample 79 Slide 79 A; x: 30,0; y: 93,0.
6. *Patellasporites sp.*, Sample 94 Slide 94 A; x: 41,9; y: 95,4.

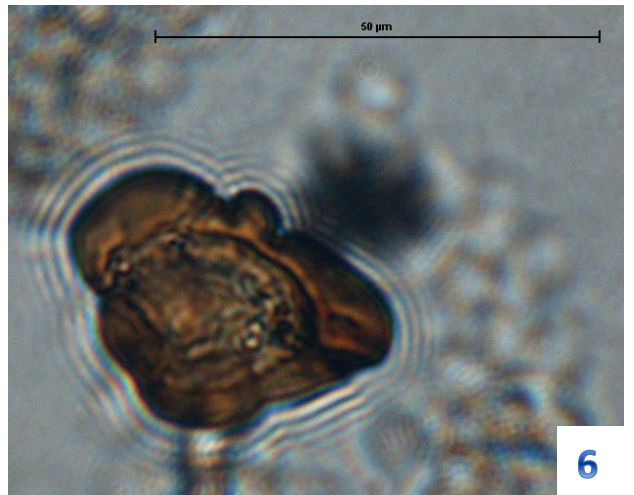
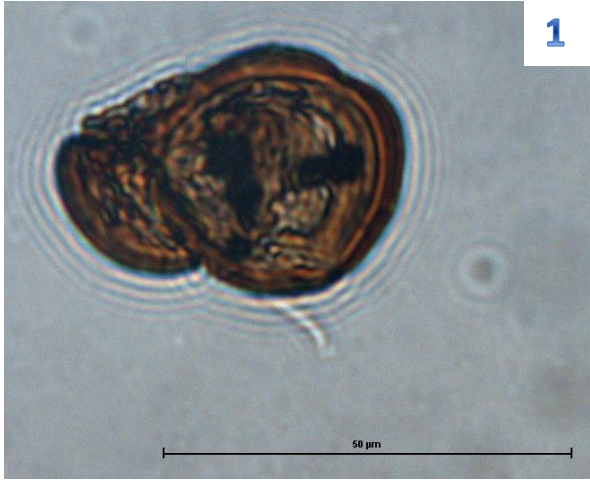


Plate 29

1. *Triorites sp.*, Sample 85B Slide 85B A; x: 45,6; y: 103,5.
2. *Triplanosporites sp.*, Sample 73 Slide 73 A; x: 23,1; y: 109,2.
3. *Triplanosporites sp.*, Sample 85T Slide 85T A; x: 31,3; y: 104,8.
4. *Triplanosporites sp.*, Sample 94 Slide 94 A; x: 48,2; y: 93,7.

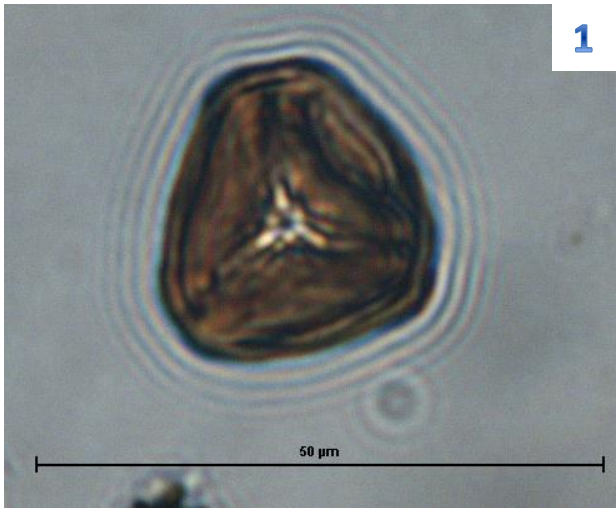


Plate 30

1. *Microforaminiferal linings*, Sample 72 Slide 72 A; x: 46,8; y: 92,4.
2. *Microforaminiferal linings*, Sample 72 Slide 72 A; x: 26,0; y: 95,6.
3. *Microforaminiferal linings*, Sample 76 Slide 76 B; x: 49,7; y: 102,0.
4. *Microforaminiferal linings*, Sample 76 Slide 76 B; x: 21,6; y: 111,4.



Plate 31

1. *Micrhystridium sp.*, Sample 76 Slide 76 B; x: 36,2; y: 107,3.

2. *Micrhystridium sp.*, Sample 92T Slide 92T A; x: 48,3; y: 105,8.

