RESEARCH PAPER

Upper Cenomanian and lower Turonian (Cretaceous) corals from the Tethyan West Portuguese Carbonate Platform

Hannes Löser[1] · Pedro M. Callapez[2]

Abstract

Scleractinian corals of late Cenomanian to early Turonian age from the western border of the Iberian Peninsula are described for the first time. They derive from middle to inner shelf limestones of the mid Albian-Turonian West Portuguese Carbonate Platform, near the localities of Figueira da Foz, Leiria, and Nazaré, where a succession of fossil-rich beds with cephalopods, rudists, and other invertebrates allows an accurate biostratigraphic control from the basal upper Cenomanian to the upper lower Turonian. During this interval, facies are deeper and carbonate-rich, that are more favourable to the occurrence of hermatypic corals and which are absent in previous sequences of the platform. The studied corals belong to the superfamilies Actinastreoidea, Cladocoroidea, Cyclolitoidea, Madreporoidea, Phyllosmilioidea, and Poritoidea. With a total of 11 species, the number of taxa is comparatively low when compared with other Late Cretaceous faunas. The corals show relationships to Albian coral faunas from the SE Iberian Platform and the Quillan Basin (SW France), both of which are located in the Tethyan Realm. The faunal turnover in scleractinian corals at the Cenomanian/Turonian (C/T) boundary is discussed. Scleractinian corals were rich in genera during the Cenomanian and reach about 110 co-existing genera at the base of the late Cenomanian. This number was reduced by 46 genera that became extinct at the Cenomanian/Turonian boundary, but were replaced rapidly after the boundary by 59 genera, of which six became extinct before the Coniacian. Sixty-six genera survived the C/T boundary, of which 11 became extinct before the middle Coniacian. This means that the Cenomanian richness in genera was almost restored in the Coniacian.

Keywords Scleractinia · Taxonomy · Palaeoecology · Early Late Cretaceous · Shelf carbonates · West Iberian Margin

Resumen

Se describen por primera vez los corales escleractinidos del periodo Cenomaniense superior - inicio del Turoniense del margen occidental de la península Ibérica. Los ejemplares fueron obtenidos en secciones de la plataforma carbonática media e interna de edad Albiense-Turoniense del oeste de Portugal, próximas a las localidades de Figueira da Foz, Leiria, y Nazaré. Este registro también contiene una sucesión de capas ricas en otros fósiles como cefalópodos, rudistas y otros invertebrados que permiten un control preciso sobre la bioestratigrafía desde el Cenomaniense superior hasta el Turoniense superior. Durante este intervalo de tiempo, las facies son más profundas y ricas en carbonatos, siendo más favorable a la aparición de corales hermatípicos que estaban ausentes en el registro anterior de la plataforma. Los corales estudiados pertenecen a las superfamilias Actinastreoidea, Cladocoroidea, Cyclolitoidea, Madreporoidea, Phyllosmilioidea y Poritoidea. Aunque muestran un total de 11 especies, la cantidad de taxones es comparablemente baja en comparación con otras faunas del Cretácico Superior. Los corales muestran relaciones con otros corales del Albiense del margen sureste de la plataforma

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Ibérica, y con la cuenca de Quillan (SO de Francia), ambas zonas localizadas en el mar de la Tethys. Se discute el cambio de las faunas de escleractinidos en el límite Cenomaniense/Turoniense (C/T). durante el Cenomaniense orden Scleractinia era rico en géneros en la zona estudiada, llegando a alcanzar aproximadamente 100 géneros en la base del Cenomaniense superior. Esta cantidad se reduce hasta 46 géneros en el límite Cenomaniense/Turoniense, pero se recuperó nuevamente después de dicho límite hasta alcanzar los 59 géneros, de los cuales 6 se extinguieron durante el Turoniense. Sesenta y seis géneros sobrevivieron el límite C/T, de cuales 11 géneros se extinguieron antes del Coniaciense medio. Eso indica que la riqueza de génerosque había en el Cenomaniense fue casi restaurada en el Coniaciense.

Palabras clave Scleractinidos · taxonomía · paleoecología · Comienzo del Cretácico Superior · Carbonatos de plataforma · Margen occidental de Iberia

1 Introduction

Scleractinian corals are a widespread invertebrate group in Mesozoic and Cenozoic shallow marine environments. Their skeletal remains are common on the margins and inner areas of rimmed carbonate platforms with reef or constratal structures, where an outstanding fossil record reveals the key importance of hermatypic corals as the frame builders, alongside sponges and microbialites (e.g., James, 1983; Tucker & Wright, 1992). When symbiotic with zooxanthellae, their modern representatives are stenotypic and live in fully marine warm environments with rather narrow ecological requirements. These biological constraints can be used to infer aspects that are related to the habitats and the way of life of Mesozoic fossil corals, using their occurrence for integrated palaeoecological studies and palaeoenvironmental characterisation of carbonate series.

The study of coral assemblages becomes even more interesting and well documented regarding the Cretaceous Period. During this long interval of Earth's history and until the late Maastrichtian major biotic changes occurred (Skelton, 2006). The same warm and shallow shelf environments of the Tethyan carbonate platforms where scleractinians had prospered, were extensively colonised by a large diversity of rudist bivalves, better adapted to a new range of ecological conditions that were allowed by high sealevel intervals, including reduced clastic input from the marginal marine areas of the continents, and changes in the Ca/Mg proportion (Gili & Götz, 2018). As a question of sub-environments, only rudists were major carbonate frame contributors, but they were not true reef builders. Coral richness at the genus level varied throughout the Cretaceous with peaks during the early Aptian and the Cenomanian, and considerable drops in the middle Albian and early to middle Turonian (Löser, 2016: 103). Generic richness varied not only through time but also from area to area such as, for example, in the Western Tethys where coral richness on the genus level was high from the Barremian to early Albian, and during the Cenomanian, Santonian and early Campanian, whereas in the Central Tethys it was high during the late Barremian and early Aptian, and during the early Cenomanian and Coniacian to Santonian. The Western Atlantic shows a completely different pattern where coral richness was high from the late Barremian into the early Albian and in the Maastrichtian (Löser, 2016: 125).

The present study focuses on the westernmost part of the Teythan platforms lying within the European branch of Tethys and its upper Cenomanian and lower Turonian coral assemblages, at present still poorly described regarding palaeontological aspects. The West Portuguese Carbonate Platform (WPCP) was set up at the palaeo-Atlantic margin of the Iberian microplate, acting as a post-rift shallow sea that was opened to repeated faunal changes between the Tethys Realm and the temperate Boreal domain. It was a wide shallow marine area colonised by scleractinian corals and rudists such as the Caprinulidae and Radiolitidae. Although these bivalves have long been studied, the Cenomanian–Turonian coral assemblages remained rather unknown concerning their taxonomy, age, palaeobiology and biogeographic range.

2 Location and stratigraphical setting

2.1 Geological setting

The studied area is located at the western border of the Iberian Peninsula, in the northern Estremadura and Beira Litoral ranges of west central Portugal, near the localities of Figueira da Foz, Leiria and Nazaré (Fig. 1). It is a low relief basin area with a geological setting of Mesozoic and Cenozoic sedimentary units from the Atlantic West Iberian Margin (WIM; Kullberg et al., 2013) bounded eastwards by a Variscan basement which acted as the main sediment source since the breakup of Pangaea (Soares et al., 2012).

The regional stratigraphy shows a thick succession of Mid Triassic to Upper Cretaceous siliciclastic, mixed and carbonate formations. They record the tectono-sedimentary evolution of the Lusitanian Basin, through four rifting phases of the proto-Atlantic opening and several intervals of thermal detumescense and accommodation of marine carbonates (Azerêdo et al., 2003; Wilson et al., 1989). The post-rift transition to a passive margin took place from the late Aptian

Fig. 1 Geographic location and geological context of the studied area. **A** Location on the western border of Iberia. **B** Detailed geographical and geological setting of the Beira Litoral and Estremadura ranges from the onshore region of the West Iberian Margin, with location of the sampled localities with upper Cenomanian and lower Turonian corals of the West Portuguese Carbonate Platform; **a** Caranguejeira, Leiria; **b** Nazaré; **c** Salmanha, Figueira da Foz. **1** Recent to Lower Cenozoic siliciclastics; **2** Turonian to Maastrichtian marginal marine and alluvial siliciclastics; **3** Middle Cenomanian to lower Turonian platform carbonates; **4** Aptian to middle Cenomanian alluvial siliciclastics; **5** Sinemurian to uppermost Jurassic syn-rift carbonates and Upper Jurassic interbedded sandstones of the Lusitanian Basin infill; **6** Triassic coarse siliciclastics and Hettangian evaporites; **7** Pre-Mesozoic Variscan basement
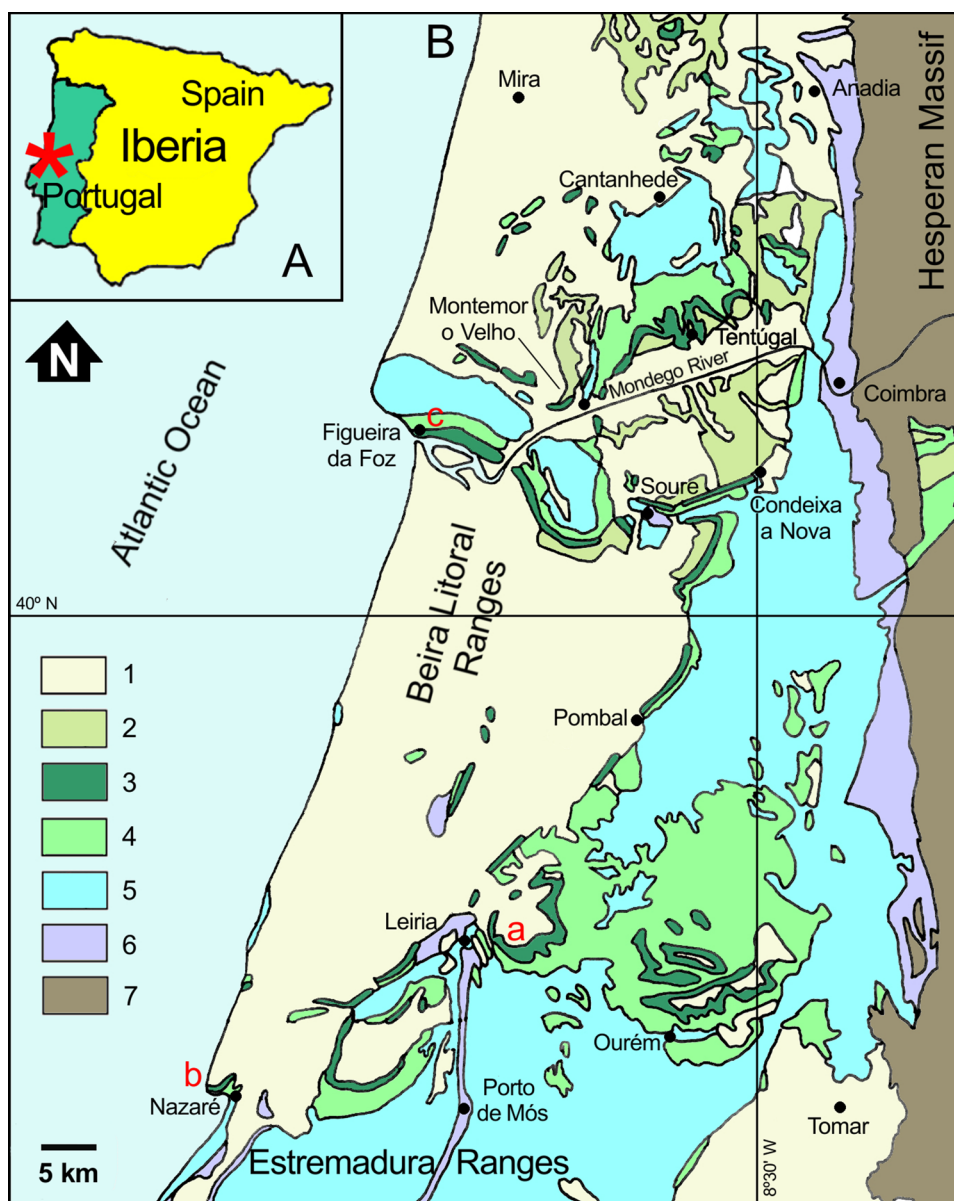
onwards, with the deposition of Albian to Maastrichtian siliciclastics and interbedded platform carbonates (Dinis et al., 2008; Segura et al., 2014).

From the mid Albian to the Cenomanian and early Turonian, during a long-term interval of eustatic rise and highstand with widespread marine sedimentation over many worldwide continental margins (Haq, 2014; Hardenbol et al., 1998), the Estremadura and Beira Litoral ranges of the WIM gradually become filled by inner shelf sediments of the West Portuguese Carbonate Platform (WPCP; Berthou, 1984; Soares, 1980; here Fig. 2). The first carbonated sequences were transgressive over post-rift coarse alluvial siliciclastics and confined to the region of Lisbon in south Estremadura (Rey, 2006). During the middle Cenomanian the platform carbonates gradually extended to the remaining onshore

sectors of the continental margin. This part of the succession is dominated by oyster-rich inner-shelf facies with a rather high siliciclastic input, more related to a mixed carbonate platform environment less favourable for the occurrence of scleractinian corals.

The basal upper Cenomanian is marked by widespread transgressive nodular limestone sequences (Callapez, 2008). They yield a typical Tethyan assemblage with the ammonite *Neolobites vibrayeanus* and a rich and diverse fauna of benthic invertebrates, including many molluscs and echinoids (Costa d'Arnes Formation; unit "C"; Berthou, 1984; Callapez, 2004; here Fig. 3A). These open shelf facies are overlain by a thick bed of coarse-grained bioclastic limestone with coral debris, nerineacean gastropods, and epibenthic
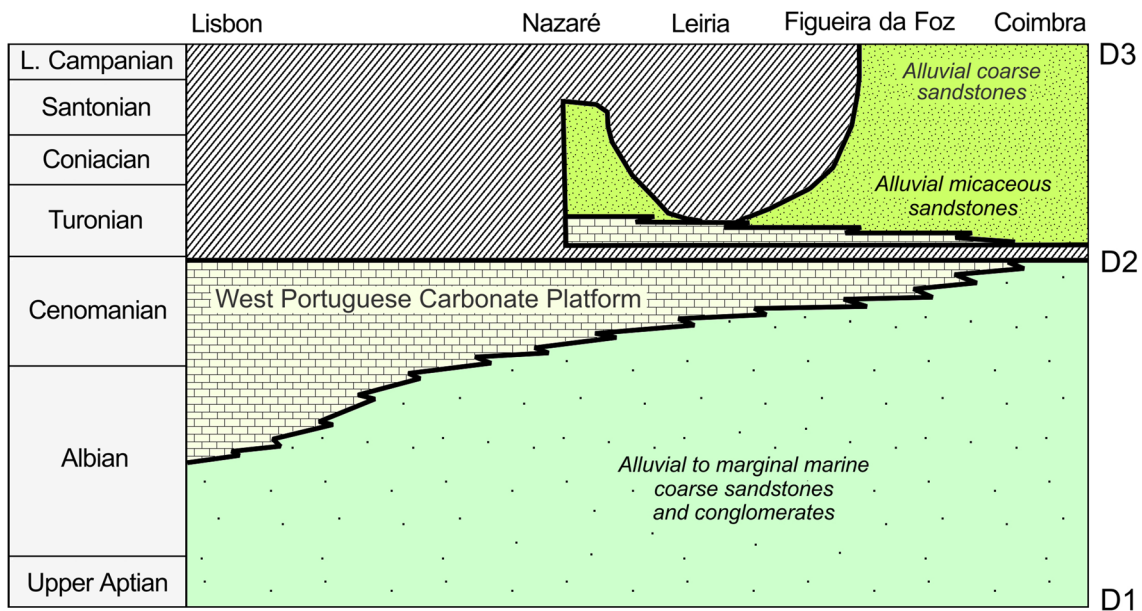
Fig. 2 Schematic diagram of the upper Aptian to lower Campanian post-rift series of the Atlantic West Iberian Margin with emphasis on the West Portuguese Carbonate Platform (WPCP) record of the Estremadura and Beira Littoral ranges of west central mainland Portugal. **D1** Main intra-Aptian unconformity related to tectonic

uplift and beginning of widespread coarse siliciclastic drainage; **D2** Cenomanian–Turonian unconformity related to uplift and subaerial exposure, and karst development on the WPCP; **D3** Main intra-Campanian unconformity followed by deep facies changes to alluvial reddish lutites ("Garum" series)
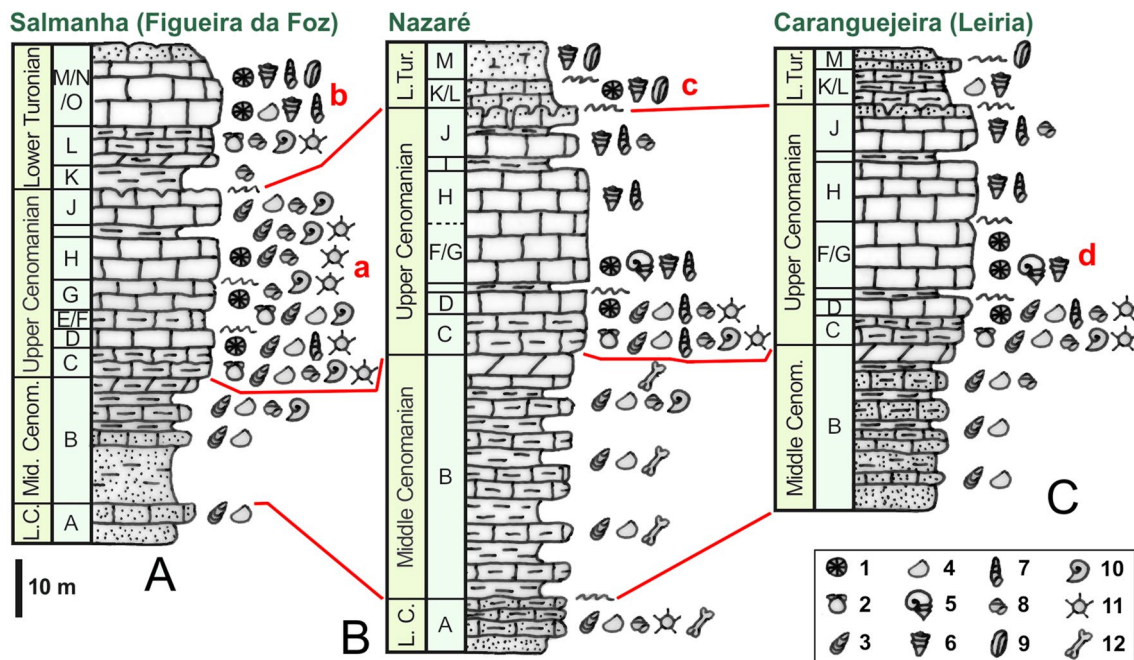

Fig. 3 Stratigraphic setting of the sampled localities with Cenomanian and lower Turonian corals of the West Portuguese Carbonate Platform: Salmanha (Figueira da Foz), Nazaré and Caranguejeira (Leiria). **A–C** Sections and local stratigraphic units; **a–d** Location of the collected samples; **a** Middle upper Cenomanian outer shelf limestones of Salmanha, **b** Middle lower Turonian coarse bioclastic limestones of Salmanha, **c** Middle lower Turonian coarse bioclastic micaceous limestones of Nazaré (northern beach), **d** Middle upper

Cenomanian rimmed shelf limestones of Caranguejeira. **1–12** Main fossil occurrences; **1** Scleractinian corals, **2** Pteriomorphia bivalves (except Ostreina), **3** Oysters and related bivalves, **4** Heterodonta bivalves (except rudists), **5** Caprinulid rudists, **6** Radiolitid rudists, **7** Nerineacean gastropods; **8** Tylostomid and other mesogastropods; **9** Acteonellid gastropods; **10** Cephalopods, **11** Echinoids, **12** Vertebrate remains

bivalves (unit"D"), showing a significant lateral persistence throughout the studied area.

The next upper Cenomanian succession shows a noteworthy lateral diversification of facies over the WPCP. In the northern areas between Figueira da Foz and Coimbra (Baixo Mondego region), they consist of open shelf limestones and marly limestones with *Vascoceras* ammonites, *Hemiaster* echinoids and *Tylostoma* gastropods, among others, and more locally they consist of small branched corals (units "E" to "J" Berthou, 1984; Callapez, 2008). To the south, the correlative sequences of Leiria contain thick limestone beds of a rimmed carbonate platform with platy corals present in slope areas (unit "G") and *Caprinula*, *Durania* and *Radiolites* buildups (unit "F" to "J"; here Fig. 3B). These rudist facies are also widespread across central and south Estremadura, from Nazaré towards the regions of Sintra and Lisbon (Berthou, 1984).

The uppermost Cenomanian record of the WPCP is limited by a large unconformity with subaerial exposure and palaeokarst development of the carbonate beds, which can be related to an uplift episode occurred at the Cenomanian–Turonian transition (Callapez, 2008). The overlying sequences are mid-early Turonian in age, showing a geographical range restricted to a few areas of Beira Litoral, Nazaré and Leiria. Near Figueira da Foz, they begin with massive micritic limestones (unit "K") followed by beds of coarse-laminated marly limestone with a rich assemblage of ammonites with North-African affinities (unit "L"; Barroso-Barcenilla et al., 2011). These sequences are correlative to a narrow fringe of *Radiolites* biostromes that lies around Leiria, and to several layers of micaceous, bioclastic limestone in the Nazaré area (Callapez, 2008). The upper part of the lower Turonian WPCP succession is markedly regressive, including carbonate sandstones with small massive corals, rudists and *Actaeonella* gastropods in the Nazaré exposure (Callapez, 2004; Fig. 3C). Near Figueira da Foz, a correlative succession of cross-bedded calcarenite shoals extensively outcrops with remains of scleractinian corals, *Radiolites* rudists and nerineacean (*Plesioptygmatis*) gastropods (units "M", "N", and "O"). The occurrence of *Actaeonella caucasica* also suggests a late early Turonian age. These sequences interfinger with a progradational body of littoral plain micaceous sandstones that marks the final retreat of the WPCP to offshore domains.

Despite this rather diverse set of stratigraphic units, the coral record of the WPCP is comparatively scarce in the number of localities where representatives of this group are present as a major part of the invertebrate assemblages. For this study, the sampling of coral remains was centred on upper Cenomanian and lower Turonian carbonate beds of three main sections of the northern and central ranges of the carbonate platform (Figs. 1B and 3) where these

invertebrates occur in significant numbers: Salmanha (Figueira da Foz), Souto de Cima and Carrasqueira (Caranguejeira, Leiria) and the Northern beach of Nazaré.

2.2 Localities

The samples of Salmanha, in the northern range of the WPCP, were collected from two distinct parts of the local composite section (Fig. 3A, sampling points "a" and "b"), all of them with accurate biostratigraphical data provided by ammonites, inoceramids and foraminifera (Barroso-Barcenilla et al., 2011; Berthou, 1984; Callapez, 1998, 2004, 2008; Segura et al., 2014). They include the Casal dos Touros quarry where the mid upper Cenomanian unit "H" is well exposed, always with a facies of whitish massive limestone (Fig. 4A, B) rich in *Pycnodonte vesiculare*, *Tylostoma ovatum* and *Hemiaster scutiger*, besides many coral representatives. Additional material was collected near the top of the WPCP succession, where the upper lower Turonian unit "M" extensively outcrops in slopes of the highway and a nearby supermarket storage area (Fig. 4C). Here, the local facies appears as a whitish limestone with low-angle planar cross-bedded structure and calcarenitic to calciruditic texture, sometimes with rather large concentrations of bioclasts, including many coral fragments. The geographical coordinates of both these sampling points are, respectively: 40° 9′ 4.75″ N; 8° 49′ 28.46″ W and 40° 8′ 54.86″ N; 8° 49′ 53.64″ W. To the South, in the central range of the WPCP, corals were sampled in the localities of Nazaré, and Souto and Carrasqueira, near Caranguejeira (Leiria), where an extensive area of mid upper Cenomanian rudist rich bioclastic limestones occurs. The first of these localities has an impressive exposure of the Cenomanian and Turonian WPCP units, with a continuous section (Fig. 3C, sampling point "c"). The topmost layers of the succession are accessible through the Northern beach way, where a coral-rich bed of whitish-pink micaceous limestone outcrops (Fig. 4D), which is overlain by yellowish cross-bedded coarse sandstones with abraded debris of *Radiolites* and *Actaeonella*. This sampled coral bed is correlative to the upper lower Turonian unit "M" of Figueira da Foz in the above, with geographical coordinates of 39° 36′ 23.59″ N; 9° 5′ 2.30″ W. Located about 30 km Northeast of Nazaré, the sampling area of Souto de Cima and Carrasqueira near Caranguejeira (Leiria) is known by its accessible large exposures of calcarenite limestone with rudist buildups and coral-rich levels in slopes of the roads to Caranguejeira and Padrão (Fig. 4E). Two sampling points where chosen: near Souto de Cima, from a thick whitish limestone with planar cross-bedded structure, and *Caprinula* and *Radiolites* massive debris, and along the Carrasqueira karstic valley where a set of platy coral-rich beds outcrop near the main road (Fig. 3C, sampling points "d" and "e"). These parts of the local WPCP
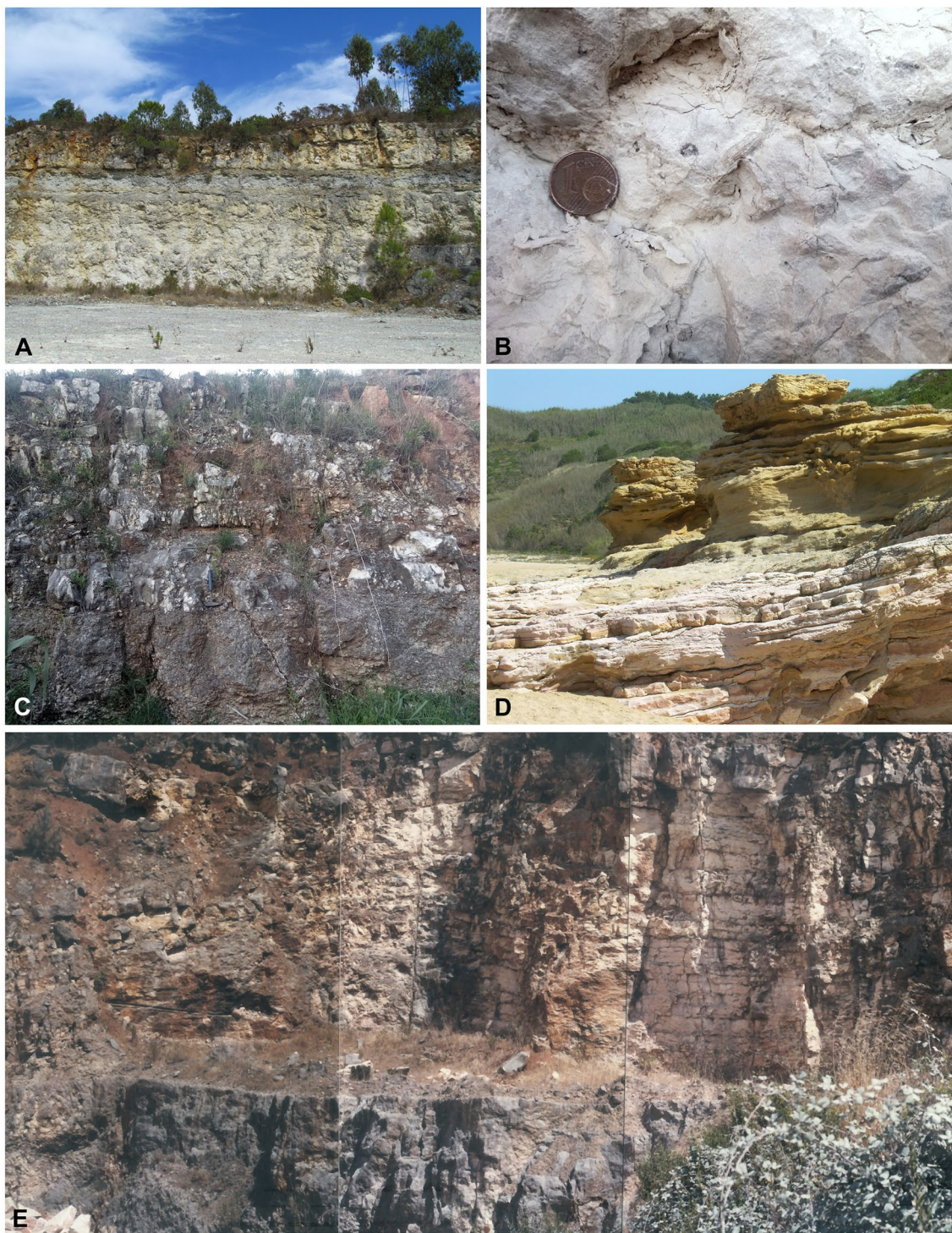
Fig. 4 Photographic views of the sampled sections from the Cenomanian–Turonian carbonate platform succession of West Central Portugal. **A** Salmanha (Figueira da Foz); aspect of the upper Cenomanian local units"H","I" and"J". Unit"H" is a massive whitish limestone with fragments of branched corals, infralittoral bivalves (*Pycnodonte*), gastropods (*Haustator*, *Tylostoma*), Vascoceratid ammonoids and infaunal echinoids (*Mecaster*); **B** Salmanha (Figueira da Foz); Detail of the sampled middle upper Cenomanian massive limestone with fragments of branched corals (Unit"H"; coin diameter = 1.6 cm); **C** Fontela (Figueira da Foz); aspect of the middle lower Turonian coarse limestone beds of unit"M" with scattered concentrations of corals and debris of rudist bivalves (*Radiolites*); **D** Nazaré (Northern beach of the Sítio); view of the local lower Turonian succession (units"L" and"M") with pink micaceous limestones with corals, rudist bivalves (*Radiolites*) and gastropods (*Actaeonella*) followed by strongly regressive, alluvial coarse limestones with abraided debris of the same fossil-association; **E** Padrão (Leiria); panoramic view of upper Cenomanian massive and laminated limestone beds (unit"G") with autochthonous concentrations of platy corals

succession are both mid-late Cenomanian in age and are the first correlative of unit "H" of Figueira da Foz and the Carrasqueira unit which is laterally equivalent to unit "G". Their geographical coordinates are: 39° 44′ 17.13″ N; 8° 43′ 15.44″ W, and 39° 45′ 28.06″ N; 8° 43′ 36.53″ W, respectively.

3 Materials and methods

Specimens were sampled during fieldwork research of the Cenomanian and lower Turonian carbonate successions of Figueira da Foz, Leiria and Nazaré. All samples were collected from stratigraphic sections with a detailed biostratigraphical setting based on ammonites and foraminifera (Barroso-Barcenilla et al., 2011; Berthou, 1984; Callapez, 1998, 2004, 2008; Segura et al., 2014), and they had been previously studied for invertebrate palaeoecology purposes (Callapez, 1998, 2008).

The selection of levels to sample was chosen based on specific criteria, namely the carbonate facies, abundance and diversity of coral specimens, preservation, accessibility of beds, and degree of biostratigraphical control. The coral specimens were collected from the local units "F", "G", "H" and "M" of the WPCP in the outcrops of Salmanha (Figueira da Foz), Carrasqueira (Leiria) and northern beach of Nazaré. The studied collection consists of around 50 samples that were collected and processed, twenty-four of which were included in the taxonomic study.

Coral specimens were cut and polished from samples with a rather embedded carbonate matrix. Thin sections in both transversal and longitudinal orientation were prepared where possible. Thin sections were scanned by passing light through them using a flatbed scanner with an optical resolution of 6400 dpi. Scanned images were then transferred to greyscale bitmaps. Their quality was amended by histogram contrast manipulation (contrast stretching) where possible. Corallite dimensions were systematically measured. Values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (https://www.paleotax.de/measure). The procedure and statistical background are described in Löser (2012). For each type of measurement (corallite diameter and distance) in one thin section the following values were obtained and/or calculated: n, number of measurements; min–max, lowest and highest measured value; μ, arithmetic mean (average); s, standard deviation; cv, coefficient of variation; μ ± s, first interval. The obtained morphometric values of the fossils were compared against those on specimens in worldwide fossil coral collections using a PaleoTax database (Löser, 2004) on post-Paleozoic corals and associated image database which has 27,600 specimens, around 15,800 of which are illustrated, that are located in the Noroeste Regional Station (ERNO) in Sonora,

Mexico which is a site of the National Autonomous University of Mexico (UNAM). The studied specimens and thin sections are housed in the Earth Sciences Department of the University of Coimbra (DCTUC) in Portugal under the numbers DCT/UC/CRET/2500, 2504, 2507, 2524, 5001–5019.

4 Description of the material

The determination of the taxonomic position (superfamilies and families) of the corals is principally based on the micromorphological characteristics of the septal blades. The genus assignment follows the organisational form of the coral and the species morphometric data. In its outline, the classification follows the traditional scheme that was introduced by Alloiteau (1952) and later improved by Löser (2016). The descriptions for superfamilies, families, and genera are principally based on the characteristics of the type material of the respective type species that were studied by the first author between 1990 and 2015 (and that resulted in the systematic revision published in Löser, 2016). All below given descriptions are not based on the literature because it often neither shows nor mentions important microstructural features. This is mainly because most literature published before 1960 and also many current publications do not show thin sections and do not allow to recognize important microstructural characteristics.

As for instance, the superfamily Actinastreoidea is based on the genus *Actinastrea*. To understand the characteristics of the superfamily the type material of *Actinastrea goldfussi* Orbigny, 1850, and additional topotypical material from the type locality was studied (the latter using thin sections). When several families are collected in one superfamily, the classification into families follows the name giving genera of the families. As for instance the family Agatheliidae is based on the genus *Agathelia* with the type species *Agathelia asperella*. In order to understand the constitution of the family, the type material of *Agathelia asperella* and topotypical material from the type area was studied (the latter by thin sections).

The following abbreviations are used in describing the dimensions of the corals: ccd, distance between corallite centres; cdw, distance between corallite centres within corallite series; clmax, large lumen; clmin, small lumen; cmax, larger outer corallite diameter; cmin, smaller outer corallite diameter; crd, distance of corallite series; septa, number of septa in the adult corallite.

Order Scleractinia Bourne, 1900.

Remarks A general classification system that covers all Scleractinian corals (Triassic-today) and is valid for Mesozoic, Cenozoic, as well as extant coral is not available. For Mesozoic and Cenozoic/extant corals, different classification

systems are still applied. The classification system of the order Scleractinia since Vaughan and Wells (1943) and Alloiteau (1952) is the application of suborders and families. The use of suborders is not practical for various reasons. Firstly, not all suborders are well-defined and/or limited to a relatively small group of genera. Secondly, when suborders are applied strictly, many families would remain without a suborder. These families would require the creation of new suborders. The creation of new taxa of higher levels always increases noise and may cause confusion. To avoid this scenario, a preliminary classification system was introduced by Löser (2016), which does not apply suborders, but rather superfamilies that group families together. Practically, suborders are for the moment replaced by superfamilies. Superfamilies have the advantage that they are covered by the rules of nomenclature, hence a superfamily has always a reference to a genus. This is not the case in suborders. A comparison of the former classification system using suborders and the new system is published in Löser (2016) and Löser et al. (2018). The concept of superfamilies was followed by Garberoglio et al., (2020, 2021) and Kolodziej (2020). Baron-Szabo (2021) only applies families but does not apply suborders. The relationship between former suborders and superfamilies is shown in Löser (2016) and Löser et al. (2018).

Ranges of genera, families, and superfamilies (as given in Löser, 2016) are principally based on material that was personally exa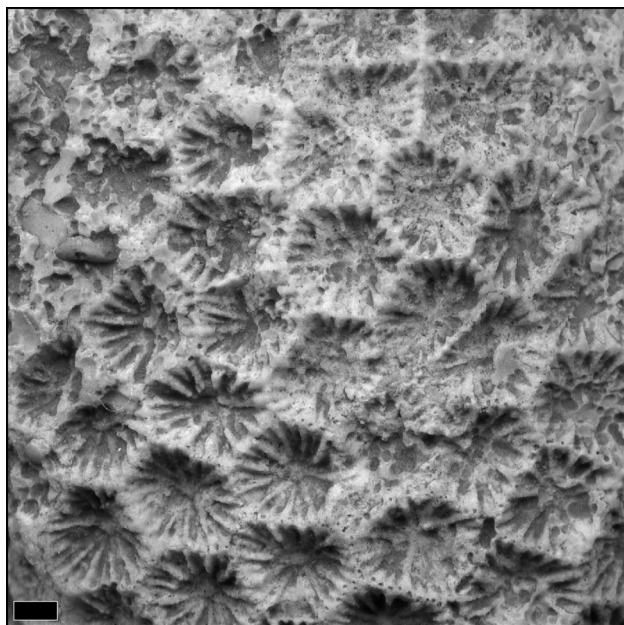mined and that come from properly dated strata. Material without an exact stratigraphic control was not included. Of course, these ranges may change when new material is observed. Mesozoic corals have a low biostratigraphic value because the ranges of most species and genera are long. But at least they allow to apply probabilistic estimations based on associations (Löser, 2002, 2021).

Superfamily Actinastreoidea Alloiteau, 1952

Description Cerioid, phaceloid or plocoid colonies. Septa compact, mostly in a regular radial symmetry. Septa often connected to each other. Lateral faces with thorns, upper margin granulated. Microstructure of septa of medium-sized trabeculae. Lonsdaleoid septa present in one genus, main septa absent. Synapticulae absent. Pali in some genera present, columella in most genera. Endotheca varies, generally made of thin tabulae. Wall compact or subcompact, mainly septothecal. Marginarium in one genus. Coenosteum generally present, consists of isolated trabeculae or costae. Budding extracalicinal and intracalicinal.

Family Actinastreidae Alloiteau, 1952

Remarks The family was formerly assigned to the suborder Archeocaeniina Alloiteau, 1952. The suborder has no reference to any family or genus, and should encompass corals with septa made of a few 'simple' trabeculae without a divergence system. The suborder cannot be identical with the suborder Astrocoeniina Vaughan & Wells, 1943 that is based on the Eocene genus *Astrocoenia*, which for a long period of time was poorly known. The material of *Astrocoenia* that is illustrated by Vaughan and Wells (plates 5 and 14) belongs to *Actinastrea* or *Stelidioseris* and corresponds to the definition of the suborder. The name-giving genus *Astrocoenia* has, in contrast, very small trabeculae (Löser, 2016: 186, fig. A55). The suborder Astrocoeniina is still applied to Cenozoic corals, but in a questionable sense.

Stelidioseris Tomes, 1893

Type species—*Stelidioseris gibbosa* Tomes, 1893.

Description Plocoid colony with a very narrow coenosteum that is made up of confluent costae. Corallites circular or polygonal. Septa in a regular radial symmetry. Septa of the first and second generation can be connected to the columella, younger septa can be connected to the older septa. Septa of the second generation may be centrally swollen. Columella styliform and large. No pali.

Stelidioseris retifera (Stoliczka, 1873).

Figure 5

Fig. 5 *Stelidioseris retifera* (Stoliczka, 1873), DCTUC CRET 5003, coral surface, scale bar 1 mm

Material DCTUC CRET 5003.

Dimensions

(CRET 5003)

	n	min–max	μ	s	cv	μ ± s
clmin	25	1.64–2.36	1.97	0.19	10.0	1.77–2.17
clmax	25	2.04–3.01	2.45	0.20	8.2	2.25–2.66
ccd	27	1.79–2.61	2.21	0.19	8.7	2.02–2.41
septa	24					

Remarks The species has a worldwide distribution between the Barremian and Coniacian.

Occurrence Upper lower Turonian (Nodosoides zone) of Portugal (Coimbra) Figueira da Foz, Casal dos Touros, Salmanha/M.

Superfamily Cladocoroidea Orbigny, 1851

Description Solitary and colonial (cerioid, phaceloid, plocoid) corals. Septa compact. Septal in regular thickness. Septal symmetry radial, regular or sub-regular. Septa often connected to each other. Septal lateral faces with thorns and/or granulae, septal upper margin with fine granulations. Lonsdaleoid septa and main septum absent. Microstructure of medium-sized trabeculae. Synapticulae absent. Pali present in some genera. Columella present in most genera, styliform, lamellar, parietal or by septal fusion. Endotheca generally present. Marginarium absent. Wall present, septothecal or parathecal. Coenosteum present in plocoid genera. Budding extracalicinal (cerioid, plocoid) or intracalicinal (phaceloid).

Family Cladocoridae Orbigny, 1851

Description Phaceloid colonies. Septal symmetry sub-regular radial. Pali present in some genera. Columella styliform, lamellar, or parietal.

Remarks Most genera of the family are poorly documented due to the small size of the type specimens or the lack of thin sections. The family was formerly assigned to the suborder Faviina. As shown in Garberoglio et al. (2021), the septal microstructure of the name giving genus *Favia* differs from the Cretaceous families assigned to the suborder Faviina.

Procladocora Alloiteau, 1952

Type species—*Calamophyllia gracilis* Orbigny, 1850.

Description Phaceloid colony. Corallites with a small diameter (< 6 mm). Septa in a irregular radial symmetry; systems can be recognised. The number of septa increases with the corallite diameter. The septa of the first two cycles have pali. The columella is lamellar.

Procladocora arnaudi (Alloiteau, 1957).

Figure 6a, b

Material DCTUC CRET 5000; 2 thin sections.

Dimensions

(CRET 5000)

	n	min–max	μ	s	cv	μ ± s
cmin	7	3.59–6.20	4.79	0.78	16.4	4.00–5.58
cmax	6	3.89–8.32	5.80	1.44	24.8	4.36–7.24
clmin	7	2.46–4.79	3.86	0.74	19.2	3.12–4.61
clmax	6	2.67–7.11	4.81	1.41	29.4	3.40–6.23
septa	4	24–34	26.50	5.0	18.8	22–32

Remarks P. *arnaudi* to date is only known from the Maastrichtian of France.

Occurrence Upper Cenomanian (Juddii zone) of Portugal (Coimbra) Figueira da Foz, Casal dos Touros, Salmanha/H1.

Superfamily Cyclolitoidea Milne Edwards & Haime, 1849

Description Solitary and colonial corals. Septa with regular perforations, with perforations only in certain parts of the septa, or almost compact. Septa generally thick, without notable symmetry (except Negoporitidae). Septa often connected to each other. Septal lateral faces with pennulae and thorns. Septal distal margin with large granulae. Lonsdaleoid septa and main septum absent. Microstructure of large trabeculae. Synapticulae present. Pali in some genera probably present but difficult to distinguish from the perforated inner margins of the septa. Columella poorly defined. Endotheca present or absent. When present, mostly thin tabulae. Marginarium absent. Wall poorly defined. Coenosteum varies depending on the organisation type. Budding varies.

Remarks The superfamily is a very important element in all Cretaceous faunas. The families are numerous in genera and some of their genera are very common. The superfamily continues at least into the Eocene.
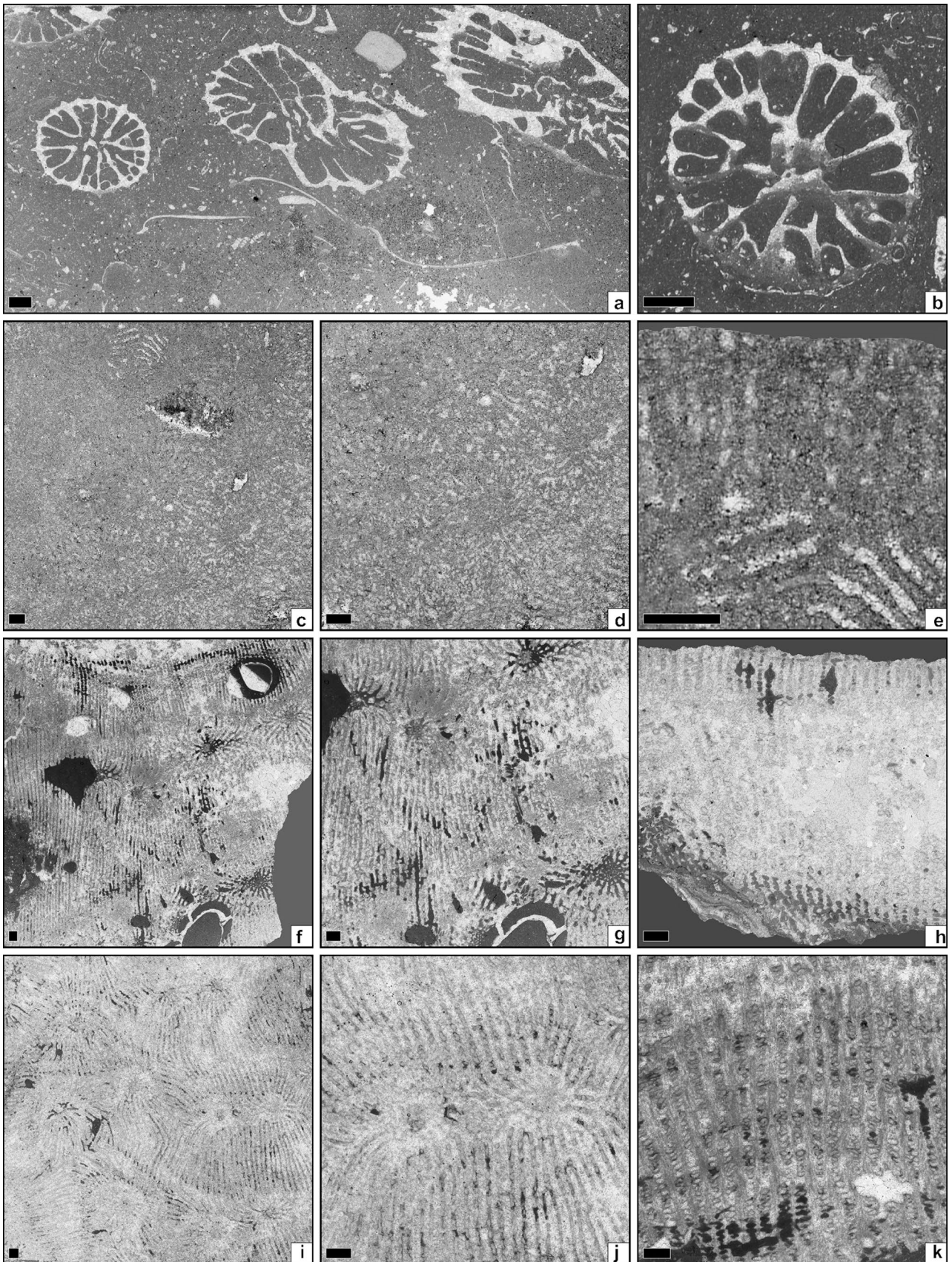
◄Fig. 6 **a**, **b** *Procladocora arnaudi* (Alloiteau, 1957), DCTUC CRET 5000, **a** transversal thin section, **b** transversal thin section, detail, scale bar 1 mm. **c–e** *Astraeofungia cenomana* (Orbigny, 1850), DCTUC CRET 5018, **a** transversal thin section, **d** transversal thin section, detail, **e** longitudinal thin section, scale bar 1 mm. **f–h** *Dimorphastrea* cf. *duparci* (Koby, 1898), DCTUC CRET 5005, **f** transversal thin section, **g** transversal thin section, detail, **h** longitudinal thin section, scale bar 1 mm. **i–k** *Dimorphastrea fallax* Becker, 1875, DCTUC CRET 5007, **k** transversal thin section, **j** transversal thin section, detail, **k** longitudinal thin section, scale bar 1 mm

Family Latomeandridae Fromentel, 1861

Description The family encompasses numerous solitary and colonial coral genera that show septa with perforations that are concentrated in the inner margin of the septa. The septa are thinner than in the Synastraeidae and less perforated than the Microsolenidae. The thickness of septa and the space between them is equilibrated.

Remarks For this group of genera, formerly the family name Leptophylliidae was applied (e.g., Löser, 2016). Since *Leptophyllia* was found to belong to the Synastraeidae (see for instance Löser et al., 2019), the family name can no longer be applied. For the moment, we decided to reinstall the Latomeandridae. The family is not well defined since the type material of the type species of *Latomeandra* is silicified. The family was formerly assigned to the suborder Microsolenina Morycowa and Roniewicz, 1995. The suborder encompasses families that were originally assigned to the Fungiina suborder. The main characteristic is the presense of pennulae, balkon-like formations related to a rhythmical growth that are visible on the septal lateral faces. The genus *Microsolena* itself is poorly defined; the type material of the type species is not available. The genus, family, and suborder are conceptual.

Astraeofungia Alloiteau, 1952

Type species—*Astrea decipiens* Michelin, 1841.

Description Thamnasterioid colony, with mostly only at the inner margin perforated septa, that distinguish hardly in length and thickness. The corallites are regularly distributed, and generally not in rows as in *Dimorphastrea*. Costae run between all corallites.

Astraeofungia cenomana (Orbigny, 1850).

Figure 6c–e

Material DCTUC CRET 5018; 2 thin sections.

Dimensions

(CRET 5018)

	n	min–max	μ	s	cv	μ ± s
ccd	7	3.76–4.94	4.23	0.45	10.8	3.77–4.69
septa	4	25–28	26.50	1.73	6.5	25–28

Remarks A. cenomana is a very common species. It has a worldwide distribution between the Aptian and Cenomanian.

Occurrence Early Turonian (Nodosoides zone) of Portugal (Coimbra) Nazaré, beach section/2.

Dimorphastrea Orbigny, 1850

Type species—*Dimorphastrea grandiflora* Orbigny, 1850.

Description Thamnasterioid colony with corallites arranged in concentric rows. The colony surface is plane, the corallite centres may be slightly depressed. Septa connect more between corallites of neighboured rows than with corallites of the same row. *Dimorphastrea* is similar to *Astraeofungia* and juvenile colonies of *Astraeofungia* and *Dimorphastrea* are difficult to distinguish.

Dimorphastrea cf. *duparci* (Koby, 1898).

Figure 6f–h

Material DCTUC CRET 5005; 2 thin sections.

Dimensions

(CRET 5005)

	n	min–max	μ	s	cv	μ ± s
crd	3	14.2–17.6	15.5	1.80	11.6	13.7–17.3
cdw	4	4.54–11.5	8.42	2.88	34.2	5.53–11.3
septa	5	33–48	41.4	5.89	14.2	36–47

Remarks The present material differs from *D. duparci* by slightly larger distances between the corallite rows and higher septal counts. The species is known from the Kimmeridgian to Cenomanian of the Tethys.

Occurrence Upper Cenomanian (Geslinianum zone) of Portugal (Coimbra) Leiria, Carrasqueira/F.
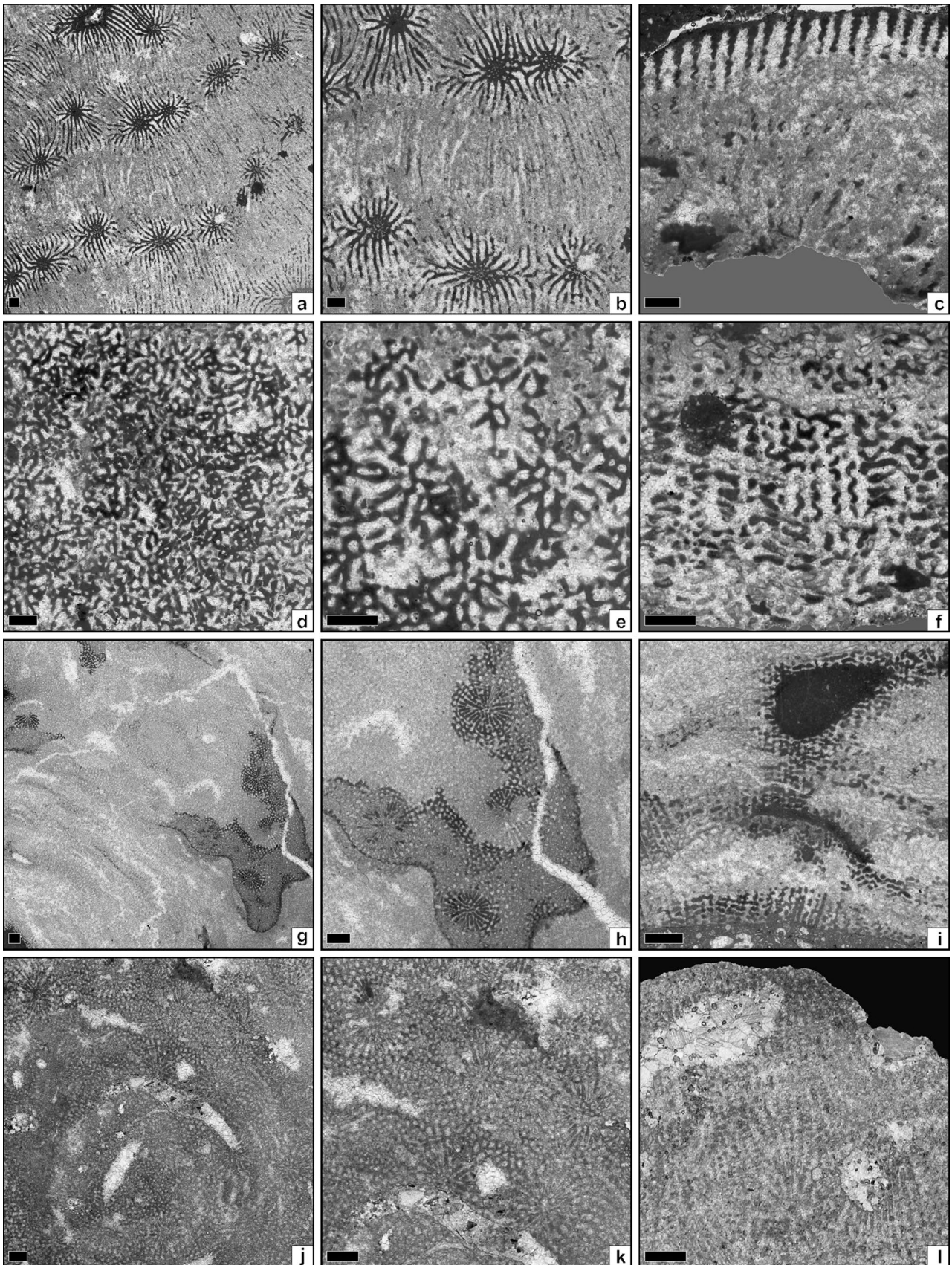
Fig. 7 a–c *Dimorphastrea* cf. *lorioli* Koby, 1898, DCTUC 2500, **a** transversal thin section, **b** transversal thin section, detail, **c** longitudinal thin section, scale bar 1 mm. **d–f** *Eocomoseris* sp., DCTUC CRET 5006, **d** transversal thin section, **e** transversal thin section, detail, **f** longitudinal thin section, scale bar 1 mm. **g–i** *Negoporites quartus* Eliášová, 1995, DCTUC CRET 5008, **g** transversal section, **h** transversal thin section, detail, **i** longitudinal thin section, scale bar 1 mm. **j–l** *Actinacis* ? *remesi* Felix, 1903a, DCTUC CRET 5016, **j** transversal thin section, **k** transversal thin section, detail, **l** longitudinal thin section, scale bar 1 mm

Dimorphastrea fallax Becker, 1875

Figure 6i–k

Material DCTUC 2517, CRET 5004, CRET 5007; 6 thin sections.

Dimensions

(CRET 5007)

	n	min–max	μ	s	cv	μ ± s
crd	8	9.23–11.9	10.82	0.99	9.1	9.83–11.8
cdw	13	4.34–9.08	6.39	1.65	25.9	4.73–8.05
septa	10	32–53	41.40	7.10	17.1	34–49

Remarks The species occurs between the Kimmeridgian and Turonian of the Western and Central Tethys, in Boreal regions, and in the Western Atlantic.

Occurrence Upper Cenomanian (Geslinianum zone) of Portugal (Coimbra) Leiria, Carrasqueira/F.

Dimorphastrea cf. *lorioli* Koby, 1898

Figure 7a–c

Material DCTUC 2500, 2504, CRET 5009, CRET 5010; 8 thin sections.

Dimensions

(CRET 2500)

	n	min–max	μ	s	cv	μ ± s
crd	15	7.04–11.0	9.15	1.22	13.3	7.93–10.4
cdw	15	2.79–9.29	5.50	1.71	31.1	3.78–7.21
septa	15	26–40	31.40	4.48	14.2	27–36

Remarks The present material differs from *D. lorioli* by higher septal counts. The species is known from the Hauterivian and Cenomanian of France based on the study of unpublished material observed by the first author.

Occurrence Upper Cenomanian (Geslinianum zone) of Portugal (Coimbra) Leiria, Carrasqueira/F.

Family Microsolenidae Koby, 1889

Description Solitary and colonial (cerioid, hydnophoroid, meandroid, phaceloid, plocoid, thamnasterioid) colonies. Septa completely and regularly perforated. Interseptal space larger than or equal to septal thickness.

Remarks The family was formerly assigned to the suborder Microsolenina (see above).

Eocomoseris Melnikova et al., 1993

Type species—*Eocomoseris gurumdyensis* Roniewicz, 2011 nom. nov. pro *Eocomoseris ramosa* Melnikova et al., 1993 non *Heptastylopsis ramosus* Frech, 1890.

Description Astreoid colony with small corallites. Symmetry of septa irregular, but two size orders can be distinguished. Number of septa up to 30. Septa occasionally connected to each other. Costae sub-confluent to non-confluent. Synapticulae fairly common. Columella styliform. Endotheca and wall absent. Coenosteum narrow.

Eocomoseris sp.

Figure 7d–f

Material DCTUC CRET 5006, CRET 5011; 4 thin sections.

Dimensions

(CRET 5006)

	n	min–max	μ	s	cv	μ ± s
ccd	20	1.89–2.68	2.25	0.23	10.5	2.01–2.48
cmin	10	1.73–2.11	1.92	0.11	5.8	1.81–2.03
septa	12	17–23	19.16	1.89	9.9	17–21

Remarks The genus *Eocomoseris* was originally only described with one Cretaceous species. Later revisions of type material revealed that another two formerly described
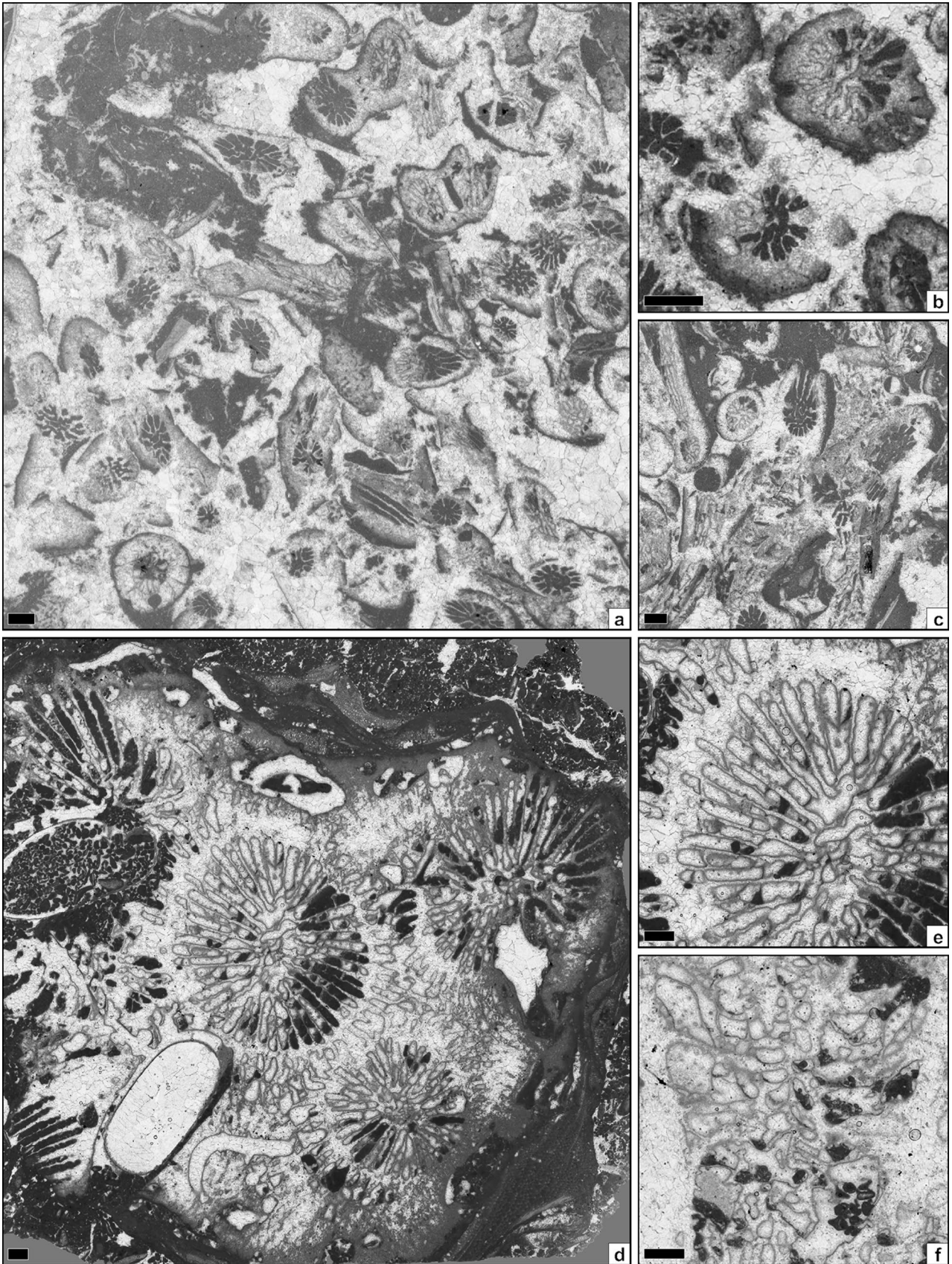
◀**Fig. 8** **a–c** *Palaeohelia* sp., DCTUC 2524, **a** transversal thin section, **b** transversal thin section, detail, **c** longitudinal thin section, scale bar 1 mm. **d–f** ?*Barysmilia* sp., DCTUC CRET 5002, **d** transversal thin section, **e** transversal thin section, detail, **f** longitudinal thin section, scale bar 1 mm

species are in existence. The distinction of species is difficult because the principal characteristic—the distance of the corallite centres—varies within one colony. In other genera of the family (*Microsolena*, *Dimorpharaea*) the distance of corallites presents a lower variability (see as for instance Pandey et al., 1999) and hence the corallite distance is more suitable for the distinction of species. The material presented here is not well enough preserved to establish a new taxon. Material that coincides in the corallite diameter and septal counts with the present specimens occurs worldwide from the Valanginian to Cenomanian.

Occurrence Upper Cenomanian (Geslinianum zone) of Portugal (Coimbra) Leiria, Carrasqueira/F.

Family Negoporitidae Eliášová, 1995

Description Colonial (plocoid) corals. Septa with perforations. Septal symmetry bilateral. Septa connected to each other. Pali and columella present. Endotheca with tabulae. Wall incomplete, synapticulothecate. Coenosteum extended, with isolated trabeculae. Budding extracalicinal.

Remarks The family was formerly assigned to the suborder Microsolenina (see above).

Negoporites Eliášová, 1989

Type species—*Porites michelini* Reuss, 1846.

Description Plocoid colony. Corallite outline circular, corallites small (generally below 3 mm in diameter). Septa irregularly perforated. Symmetry of septa bilateral. Septal cycles differ in length, but hardly at all in thickness. Septa of younger cycles often and regularly connected to the septa of preceding cycles. Not well-separated pali irregularly present. Costae non-confluent. Synapticulae fairly common, mainly in the wall. Columella small, substyliform. Endotheca consists of numerous thin tabulae. Wall subcompact, synapticulothecal. Coenosteum medium broad, consists of trabeculae and tabulae.

Negoporites quartus Eliášová, 1995

Figure 7g–i

Material DCTUC CRET 5008; 2 thin sections.

Dimensions

(CRET 5008)

	n	min–max	μ	s	cv	μ ± s
cmin	12	2.19–2.80	2.45	0.18	7.4	2.26–2.63
cmax	12	2.50–3.30	2.93	0.21	7.3	2.71–3.14
ccd	13	3.42–6.31	4.67	0.89	19.2	3.77–5.56
septa	10	28–36	32.90	2.51	7.6	30–35

Remarks The genus *Negoporites* is restricted to the Cenomanian. The species *N. quartus* to date is only known from the Cenomanian of the European Boreal.

Occurrence Upper Cenomanian (Geslinianum zone) of Portugal (Coimbra) Leiria, Carrasqueira/F.

Superfamily Madreporoidea Dana, 1846

Description Colonial (phaceloid, plocoid) corals. Septa compact, very thin, in an irregular radial symmetry. Septa often connected to each other. Lateral faces with fine thorns, upper margin unknown. Lonsdaleoid and main septa absent. Microstructure of septa of small trabeculae. Synapticulae absent. Pali absent, columella present in most genera, lamellar or by septal fusion. Endotheca present. Marginarium absent. Wall thick, lamellar. Coenosteum made of lamellae. Budding extracalicinal and intracalicinal.

Family Madreporidae Dana, 1846

Palaeohelia Alloiteau, 1958

Type species—*Palaeohelia collignoni* Alloiteau, 1958.

Description Phaceloid colony with thin branches. Septa without symmetry. A weak columella is formed by the fusion of septa in the corallite centre.

Remarks The family was formerly assigned to the suborder Meandrinina Alloiteau, 1952. The definition of this suborder was rather conceptual when it was established. It should gather genera with compact septa and smooth lateral septal faces and smooth septal upper margins. No data were provided on the septal microstructure. Subsequently, a large amount of material with very small trabeculae was assigned to this suborder. Indeed, the name-giving genus *Meandrina* Lamarck, 1801 shows septal ornamentation as described

above, but it possesses rather large trabeculae (Löser, 2016: Fig. 3.3.1.3A). So, the family Madreporidae cannot remain here.

Palaeohelia sp.

Figure 8a–c

Material DCTUC 2524; 4 thin sections.

Dimensions

(CRET 2524)

	n	min–max	μ	s	cv	μ ± s
cmin	20	1.56–2.71	2.14	0.37	17.2	1.77–2.51
cmax	20	2.34–3.48	2.88	0.29	10.3	2.58–3.17
clmin	25	1.03–1.47	1.20	0.13	11.2	1.07–1.34
clmax	25	1.06–2.02	1.56	0.26	16.8	1.30–1.83
septa	24					

Remarks *Palaeohelia* received little attention since its creation. Four species are known: *P. albiensis* Beauvais, 1982, *P. collignoni* Alloiteau, 1958, *P. dartoni* (Wells, 1933), and *P. graeca* (Baron-Szabo & Steuber, 1996). There exists more undescribed material. The present specimen belongs with certainty to a new species, that is only known from the Cenomanian of Portugal. In its morphology it does not differ from other species of the genus, except for its corallite dimensions. These are very small compared to the other species. The material described by Löser et al. (2019) as *Palaeohelia* sp. from the Upper Cretaceous of Austria has even smaller dimensions.

Occurrence Upper Cenomanian (Juddii zone) of Portugal (Coimbra) Leiria, Souto de Cima/H.

Superfamily Phyllosmilioidea Felix, 1903b

Description Solitary and colonial (astreoid, flabelloid, meandroid, phaceloid, plocoid) corals. Septa compact. First septal generation thicker than all others. Symmetry irregular or subregular radial. Septa in some genera connected to each other. Septal distal margins smooth, lateral faces with fine thorns, inner margins often swollen or T-shaped. Lonsdaleoid septa very rare. Main septum absent. Microstructure of very small trabeculae, only marked by a dark line. The costae are made by medium-sized trabeculae that result in granulated costal surfaces. Synapticulae and pali absent.

Columella present or absent. Endotheca mostly present. Marginarium absent. Wall generally present, septothecal. Coenosteum present in some genera. Budding varies.

Family Phyllosmiliidae Felix, 1903b

Remarks The family was formerly assigned to the suborder Meandrinina Alloiteau, 1952 (see above for discussion).

Barysmilia Milne Edwards & Haime, 1848

Type species—*Dendrophyllia brevicaulis* Michelin, 1841.

Description Plocoid colony with elliptical corallites, often as very short corallite rows. The septal symmetry is irregularly radial. The coenosteum is present, often very narrow.

?*Barysmilia* sp.

Figure 8d–f

Material DCTUC CRET 5001, CRET 5002, CRET 5013, CRET 5015; 6 thin sections.

Dimensions

(CRET 5002)

clmin	7.4–9.5
clmax	8.3–11.2
septa	48

Description Plocoid colony. Corallite outline circular. Septa compact, in cross section tapering towards the centre. Septal maximum thickness 300 μm. Septal microstructure of small trabeculae. Symmetry of septa radial and irregularly hexameral with subregular cycles of septa. Septal cycles differ in length and thickness. First two septal cycles extend to the corallite centre, later cycles are shorter. Younger septa are regularly connected to older septa. Septa of the first two cycles irregularly connected in the corallite centre. Septal distal margin unknown, lateral face with few thorns, inner margin swollen in places. Costae very short, non-confluent or sub-confluent. Synapticulae absent. Columella probably lamellar but difficult to distinguish from the inner margins of the septa. Endotheca consists of numerous tabulae. Wall compact, parathecal. Coenosteum narrow. Budding extracalicinal.

Remarks This material very probably represents a new genus, but the material is too poorly preserved to be formally

established as a new taxon. It differs from *Barysmilia* by the formation of the wall (parathecal in place of septothecal), the columella (parietal in place of lamellar) and the formation of the first septal cycles (normal thickness in place of thickened). Even the position within the family Phyllosmiliidae is questionable. The material is also similar to members of the Placocoeniidae family but differs clearly in its septal microstructure.

Occurrence Upper lower Turonian (Nodosoides zone) of Portugal (Coimbra) Figueira da Foz, Casal dos Touros, Salmanha/M; Nazaré, beach section/1; Nazaré, beach section/2.

Superfamily Poritoidea Gray, 1842

Description Colonial (astreoid, plocoid) corals. Septa irregularly perforated. Symmetry of septa irregular radial or bilateral. Septa connected to each other. Septal distal margin coarsely dentated, lateral face with rare granulae, inner margin slightly swollen in places. Lonsdaleoid septa and main septum absent. Microstructure of medium-sized trabeculae. Synapticulae abundant. Pali present in some genera. Columella and endotheca present. Marginarium absent. Wall varies. Coenosteum generally present. Budding extracalicinal.

Family Actinacididae Vaughan & Wells, 1943

Description Astreoid colonies. Septa in a regular radial or bilateral septal symmetry.

Remarks The family was formerly assigned to the suborder Fungiina Verrill, 1870. The suborder was applied by Alloiteau (1952) and subsequent authors in a very broad sense for any coral with perforate septa and/or synapticulae (except the suborder Dendrophylliina). The suborder collects families that vary considerably in their septal microstructure and has a very informal character. Fungiina sensu stricto are corals with futurae (see Gill, 1981) (e.g., only the Fungiidae, and perhaps the Asteroseriidae families). All other families cannot remain in this suborder. Some families have already been separated into the suborder Microsolenina.

Actinacis Orbigny, 1849

Type species—*Actinacis martiniana* Orbigny, 1849.

Description Astreoid colony. The corallites are small, elliptical, well marked and with large distances to each other. Septal symmetry is between radial and bilateral. Septa often and regularly connected to each other. Pali present but because of the septal perforations not well visible.

Actinacis ? *remesi* Felix, 1903a

Figure 7j–l

Material DCTUC CRET 5012, CRET 5014, CRET 5016, CRET 5017; 7 thin sections.

Dimensions

(CRET 5016)

	n	min–max	μ	s	cv	μ ± s
clmin	15	1.62–2.26	1.90	0.19	10.1	1.71–2.09
clmax	15	2.07–2.83	2.38	0.26	11.2	2.11–2.65
ccd	20	2.50–4.24	3.17	0.49	15.5	2.67–3.66
septa	12	24–30	27.33	2.01	7.3	25–29

Remarks The material can clearly be assigned to the genus *Actinacis*, but could not be assigned to an existing species with certainty. Closely related is material labelled as *Actinacis vignyensis* Alloiteau, 1957 (MNHN; but never formally described) and material labelled as *Actinacis remesi* Felix, 1903a (NHMW, coll. Trauth; PU, coll. Zuffardi-Comerci) from the Eocene of Klokocov (Moravia, Czech Republic) but the type of *Actinacis remesi* itself is unknown. The unnamed species is distributed worldwide between the Upper Albian and Eocene.

Occurrence Upper lower Turonian (Nodosoides zone) of Portugal (Coimbra) Nazaré, beach section/1; Nazaré, beach section/2.

5 Discussion

The Cenomanian/Turonian (C/T) boundary was a prominent event in the Cretaceous Period. Oceanic Anoxic Event II and a global sea level highstand had an impact on coral diversity and evolution. At the Cenomanian/Turonian boundary, 46 coral genera disappeared (Fig. 9). This number is constituted by genera that occurred at least in the late Cenomanian but did not pass the C/T boundary. Genera that had their last occurrence during the early or middle Cenomanian are not counted. Sixty-six genera survived the C/T boundary, but 11 of them did not reach the middle Coniacian. Another 59 genera evolved after the C/T boundary, but six of them occurred only during the Turonian. At the base of the late Cenomanian 110 genera occurred. The richness of genera almost recovered in the Coniacian and reached 115 genera in the late Santonian.

Genera	U.A	Cen.	Tur.	Co.
Ambiguastraea				
Asteroseris				
Coelosmilia				
Microseris				
Ovalastrea				
Thalamocoenia				
Confusaforma				
Microphyllia				
Placophora				
Thalamocaeniopsis				
Preverastraea				
Sakalavastraea				
Canleria				
Actinoseris				
Aplopsammia				
Aspidiscus				
Cryptocoenia				
Cyclocyathus				
Diplocteniopsis				
Latohelia				
Paramontlivaltia				
Placoseris				
Polyphylloseris				
Sinaimeandra				
Stylocyathus				
Thamnasteria				
Eocomoseris				
Kobyphyllia				
Eocolumastrea				
Helladastraea				
Dactylosmilia				
Stelloria				
Negoporites				
Carcicocaenia				
Cyclastraea				
Diegosmilia				
Phyllotrochus				
Plesioparasmilia				
Colonicyathus				
Columellophora				
Elasmocoenia				
Leptophyllaraea				
Placohelia				
Valliseris				
Rhabdocora				
Stylocorella				
Astraeofungia				
Latiphyllia				
Silingastraea				
Pleurocoenia				
Actinaraea				
Comophyllastraea				
Complexastrea				
Dimorpharaea				
Dimorphocoenia				
Microsolena				
Protrochocyathus				

(groups labelled E, se)

Genera	U.A	Cen.	Tur.	Co.
Glenarea				
Actinacis				
Ahrdorffia				
Aulosmilia				
Brachycoenia				
Caryophyllia				
Columastrea				
Conicosmilotrochus				
Dimorphastrea				
Heliopora				
Heterocoenia				
Meandrastrea				
Meandraraea				
Pachygyra				
Pachyphyllia				
Palaeohelia				
Placocoenia				
Platycyathus				
Plesiosmilia				
Polyastropsis				
Pseudopolytremacis				
Siderastrea				
Stephanocoenia				
Synastrea				
Trochophyllia				
Vallimeandra				
Stelidioseris				
Heterocyathus				
Hydnophoropsis				
Stephanocyathus				
Eosiderastrea				
Montlivaltoides				
Palaeosiderofungia				
Geroastrea				
Actinastrea				
Glyphephyllia				
Hydnophoraraea				
Micrabacia				
Moltkia				
Nefophyllia				
Onchotrochus				
Parasmilia				
Phyllosmilia				
Placosmilia				
Procladocora				
Synhelia				
Elasmophyllia				
Paractinacis				
Pachyheterocoenia				
Felixaraea				
Leptophyllia				
Neocoenia				
Barysmilia				
Epiphaxum				
Loboseris				
Anisastraea				
Brachymeandra				

(group labelled S)

Genera	U.A	Cen.	Tur.	Co.
Delphinastraea				
Phyllocoeniopsis				
Pseudocycloseris				
Paramoltkia				
Astraraea				
Hemiporites				
Polyseris				
Astrogyra				
Brachyseris				
Columactinastraea				
Cyclolites				
Dasmiopsis				
Diploctenium				
Gyroseris				
Gosaviaraea				
Pseudofavia				
Mycetophylliopsis				
Strotogyra				
Valliculastraea				
Crinopora				
Litharaeopsis				
Micralcyonarites				
Somalites				
Astraraeatrochus				
Placogyropsis				
Agathelia				
Brachyphyllia				
Elephantaria				
Felixastraea				
Flabellosmilia				
Haimesiphyllia				
Hydnophorastraea				
Hydnoseris				
Koilomorpha				
Lasmogyra				
Maeandrella				
Nefocoenia				
Ogilviastraea				
Orbignygyra				
Leptophyllastraea				
Reussicoenia				
Siderocoenia				
Phragmosgyra				
Taxogyra				
Cycloria				
Proplesiastraea				
Lamnastrea				
Synhydnophora				
Pachyphylliopsis				
?Lasmogyra				
?Astraraea				
?Leptophyllastraea				
?Agathelia				
Paradimorphastraea				
Diblasus				
Thecoseriopsis				
Actinocoenia				

(group labelled T, U)

◄**Fig. 9** Coral genera with their stratigraphic range between the upper Albian to Coniacian. Genera that became extinct before the upper Cenomanian are not shown. Genera endemic in one faunule in red. E, genera that became extinct during the upper Cenomanian; se, genera that survived the CT boundary but hardly reached the Coniacian; S, genera that survived the C/T boundary; T, exclusive Turonian genera; U, newly evolved, post-Cenomanian genera. Range data from Löser (2016). Only genera for which a range could be obtained are included

The reduction of taxa at the C/T boundary is the same predicament that occurred at the Cretaceous/Paleogene boundary (Löser, 2016: 123). The loss of taxa during the Turonian is not only related to the sea level fall during the same period that reduced the available shallow marine area for colonisation; the low number of lower to middle Turonian coral localities to any extent (Löser, 2016: 119) is also caused by the regression during the Turonian that eroded the faunas deposited from the C/T boundary on. It is noteworthy that among all of these genera are numerous examples that are endemic, monospecific and/or poorly known.

5.1 Species richness

When outcrops with shallow marine corals are sampled thoroughly, they always yield large faunas. Particularly for Cenomanian faunas this has been shown in multiples occasions for Boreal (Bohemian Basis, Eliášová, 1997; Westphalian Basin, Löser, 1994; Saxonian Basin, Löser, 2014, 2015) and Tethyan faunas (Penninic Ocean, Löser et al., 2013; Quillan Basin, Löser & Bilotte, 2017; West Pelagonian zone, Löser et al., 2018). For each of the three Boreal faunas nearly sixty species were found, and for the three Tethyan faunas values between 16 and 40 species are reported.

The 11 coral species described here are distributed among six localities or levels. With the exception of the Carrasqueira locality with five species, the localities have between one and three species. Since the report is not based on collection material but rather on systematic field studies, complete sampling was achieved. Compared to other shallow marine coral faunas, the number of species is very low and conditions seemed to be unfavourable for corals. The level that was richest in species is the Carrasqueira locality (Leiria) with an association of platy corals that are exclusively made up by pennular corals thus supposing low-level light conditions. A comparable situation was described from the upper Cenomanian of southern France (Löser & Bilotte, 2017) with 16 coral species. The Carrasqueira locality is the only place to have yielded rich coral material per number of specimens; in all other outcrops, corals have been searched for.

The level H1 in the Salmanha section yielded only one species, at the same level as the Souto de Cima outcrop (Leiria). Both species are phaceloid, inferring low water

energy and probably also a slightly deeper environment. The lower Turonian localities at the Nazaré beach yielded a total of three species. The low number is due to the low concentration of corals and their very poor state of conservation. The lower Turonian level M in the Salmanha section yielded only two species. Compared to other coral localities of a comparable age, this number is very low.

5.2 Palaeoecology

The study of several Portuguese coral faunas has shown that even profound sampling cannot yield numerous species when the environment was not favourable for corals. Unfavourable conditions are mostly related to temperature or salinity. So low temperature has inhibited coral growth in the Western Pacific from the Albian on (Iba & Sano, 2007), and low salinity has inhibited coral growth in the Western Atlantic between the late Cenomanian and the Santonian because of the opening of the Western Interior Seaway (Hay, 2008; Löser, 2013a). Nevertheless, for the case of the Cenomanian–Turonian WPCT the surface water temperatures should have been sufficiently high to support benthic communities with corals, along with many examples of Tethyan invertebrates. Salinity variations and high turbidity related to the influx of fine-grained siliciclastics could have been much more effective in explaining the rather low diversity values, and coral growth inhibition. This can be partly explained by the palaeogeographic setting of the carbonate platform during the late Cenomanian and early Turonian, when its inner shelf ranges of Figueira da Foz, Leiria, and Nazaré were bordered by a depositional system of siliciclastic alluvial plains, which provided fine-grained micaceous sediments to the shallow platform. Besides progradation during regressive intervals, the fluvial drainage to the platform and significant volumes of sediment transported in suspension were certainly responsible for frequent episodes of salinity decrease and higher turbidity, which would have affected coral diversity and growth.

The presence of corals does not automatically imply the existence of reefs. Corals can construct reefs when the conditions are favourable. The Cretaceous was characterised by high temperatures, on the one hand (Forster et al., 2007), and a seawater chemistry that was unfavourable for the scleractinian corals which build their skeletons from aragonite, on the other hand (Stanley & Hardie, 1998). Throughout the Cretaceous, coral colonies remained small, rarely reaching dimensions beyond 20 cm. There are very few exceptions (Bover Arnal et al., 2012). Coral reefs—here understood as rigid biogenic constructions that are clearly elevated above the sea floor—are rarely reported from the Cretaceous (Bonilla González et al., 2018; Fernández Mendiola et al., 2015). Most of these rare reefs are built up by phaceloid corals of the genus *Actinastreopsis* (Löser, 2013a). Therefore,
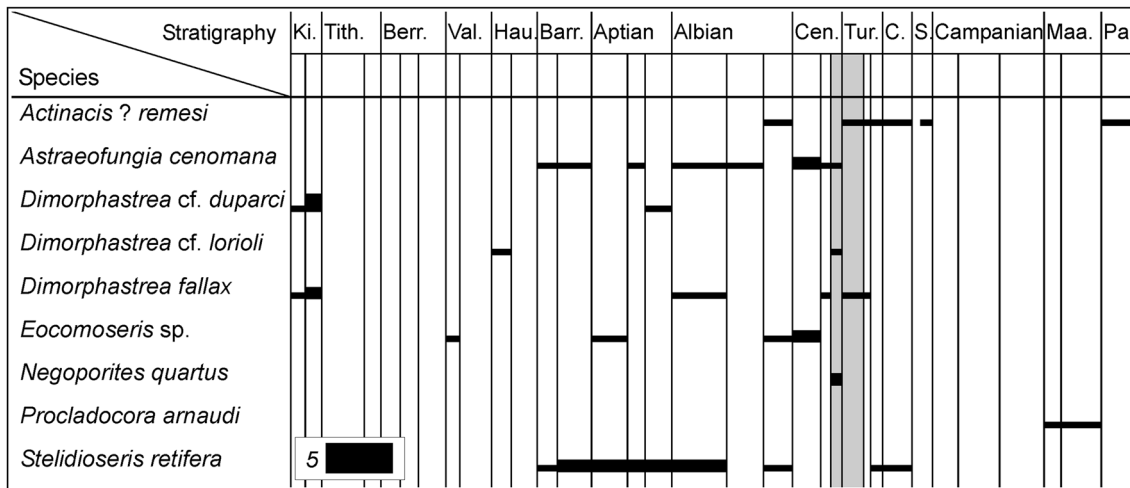
Species / Stratigraphy	Ki.	Tith.	Berr.	Val.	Hau.	Barr.	Aptian	Albian	Cen.	Tur.	C.	S.	Campanian	Maa.	Pa
Actinacis ? remesi															
Astraeofungia cenomana															
Dimorphastrea cf. *duparci*															
Dimorphastrea cf. *lorioli*															
Dimorphastrea fallax															
Eocomoseris sp.															
Negoporites quartus															
Procladocora arnaudi															
Stelidioseris retifera	5														

Fig. 10 Stratigraphic distribution of species found in the study area. The thickness of bars corresponds to the number of localities. The material of the present study is not shown but the age of the study area is marked in grey
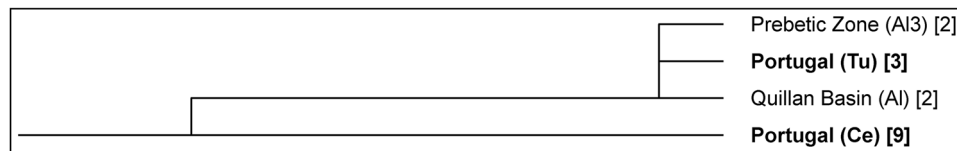
Fig. 11 Correlation of faunules with the studied faunas. Only the time period Albian to Coniacian was analysed, and only faunules with more than one species. The Correlation Ratio coefficient was applied. The Prebetic zone corresponds geographically to SE Spain, the Quillan Basin principally to SW France

we cannot discuss coral reef formations in the Cretaceous of Portugal.

5.3 Distribution

The low number of species makes a comparison to other localities very difficult. The species from the study area all have long ranges (Fig. 10) with slightly more occurrences in the Albian and Cenomanian, and less in the Turonian to Maastrichtian. The palaeobiogeographic comparison with other areas does not show many results because of the paucity of data (Fig. 11). Species of the study area were found in boreal regions, such as the Bohemian-Saxonian Basin (Eliášová, 1997; Löser, 2014), and in two other areas of the Iberian Peninsula and the Quillan Basin (Löser & Bilotte, 2017; Löser et al., 2013).

6 Conclusion

Shallow marine strata of the West Portuguese Carbonate Platform of the upper Cenomanian to lower Turonian have yielded coral associations from six sample points with a surprisingly low number of exclusively hermatypic corals. The number of species varies between one and five per sample point, even though profound searching was carried out. The rarity of corals in the strata and the resulting low number of species is explained by a certain variation in salinity and a high water turbidity. This situation compares well to the Western Interior Seaway where coral growth was inhibited by lower temperatures and a lower salinity. Its occurrence stopped during the middle Cenomanian and returned in the Campanian.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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