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Fossil Chondrichthyes from the Neogene of Portugal: Diversity and Occurrence

Chondrichthyes Fósseis do Neogénico de Portugal: Diversidade e Ocorrência

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Abstract

Portugal has a rich fossil record both on the continent and in the Azores islands (Santa Maria). For decades, researchers have found thousands of fossils and identified hundreds of species from major taxonomic groups. The present work focuses on analyzing the scientific literature on fossils of Chondrichthyes collected in fossiliferous deposits of the Neogene. Fossils of sharks and rays, teeth, dermal denticles, and caudal spines were discovered in deposits from Aquitanian to Piacenzian (Neogene). About 105 deposits were identified and studied on the mainland and on the Island of Santa Maria, most of which have disappeared or are currently inaccessible. In total, 36 publications list 91 species of Chondrichthyes, 11 of which were described for the first time in Portugal, and 61 genera. Twelve orders are represented in the material published so far.

Keywords: Selachians; Literature; Paleodiversity

Resumo

Portugal possui um rico registo fóssil tanto no continente, como nas ilhas dos Açores (Santa Maria). Durante décadas, investigadores encontraram milhares de fósseis e identificaram centenas de espécies dos principais grupos taxonómicos. O presente trabalho foca-se na análise da literatura científica sobre fósseis de Chondrichthyes coletados em jazidas fossilíferas do Neogénico. Foram descobertos dentes, dentículos dérmicos e espinhos caudais em jazidas do Aquitaniano ao Piacenziano (Neogénico). Foram identificadas e estudadas cerca de 105 jazidas no continente e na Ilha de Santa Maria, a maioria das quais desapareceu ou encontra-se actualmente inacessível. No total, 36 publicações listam 91 espécies de tubarões e raias, 11 das quais descritas pela primeira vez em Portugal, e 61 géneros. Doze ordens estão representadas no material publicado até ao momento.

Palavras-chave: Seláceos; Literatura; Paleodiversidade

1 Introduction

Chondrichthyes are a numerous and diverse group, divided into two subclasses: Elasmobranchii (Selachii and Batoidea) and Holocephali (Amaral et al. 2018; Naylor et al. 2012). According to the "Shark References" database, in March 2021, there were 4.186 Chondrichthyes species known to science, 69.8% extinct, and 30.2% extant (Pollerspöck & Straube 2021). As presented in Figure 1, the majority of the forms of cartilaginous fishes are already extinct, with only 14 orders still represented in the recent biodiversity worldwide: Carcharhiniformes, Chimaeriformes, Echinorhiniformes, Hexanchiformes, Heterodontiformes, Lamniformes, Myliobatiformes, Orectolobiformes, Pristiophoriformes, Rajiformes, Rhinopristiformes, Squatiniformes, Squaliformes, Torpediniformes.

The first mentions of Chondrichthyes fossil forms in Portuguese sediments date back to 1885 with the work by Choffat (in Sauvage 1897-98), and with the reference of Portuguese fossil fishes in the British Museum collections by A. S. Woodward (1889). Only a few studies followed, but around 1940 the overall number of publications per decade steadily increased. New researchers further supported this research effort.

The works of Zbyszewski & Moitinho de Almeida (1950), Serralheiro (1954), and Jonet (1964) represent the starting point for broader studies. However, the former collections were made of fossils collected at the surface of outcrops. This practice distorted the collecting, with the lack of small specimens versus high amounts of indeed rarer but larger in size and more easily spotted fossils, such as the teeth of *Otodus (Megaselachus) megalodon*. M. T. Antunes introduced washing and sieving methods, which greatly improved the collecting of small fossils (Antunes & Jonet 1970), therefore contributing to a more complete understanding of the repartition of fossil Chondrichthyes in the Portuguese geological record. Other research projects were carried on afterwards by Antunes & Jonet (1970); Jonet (1964, 1966, 1968, 1976); Antunes & Balbino (2003, 2004, 2006, 2007); Antunes, Balbino & Cappetta (1999a, 1999b); Balbino & Cappetta (2000); Balbino & Antunes (2006); and more recently, Fialho, Balbino & Antunes (2019a), and Fialho et al. (2020).

One hundred and thirty-five years of Paleoichthyological research on Portuguese fossil material yielded a remarkable literature. However, the diversity found and published has not yet been analyzed as a whole. Future research would greatly benefit from information on the richest sites, the better-studied ages, and the diversity of fossil forms. The current work aims to further contribute to the subject by making available an exhaustive bibliographic analysis on the Chondrichthyes from the Neogene of Portugal.

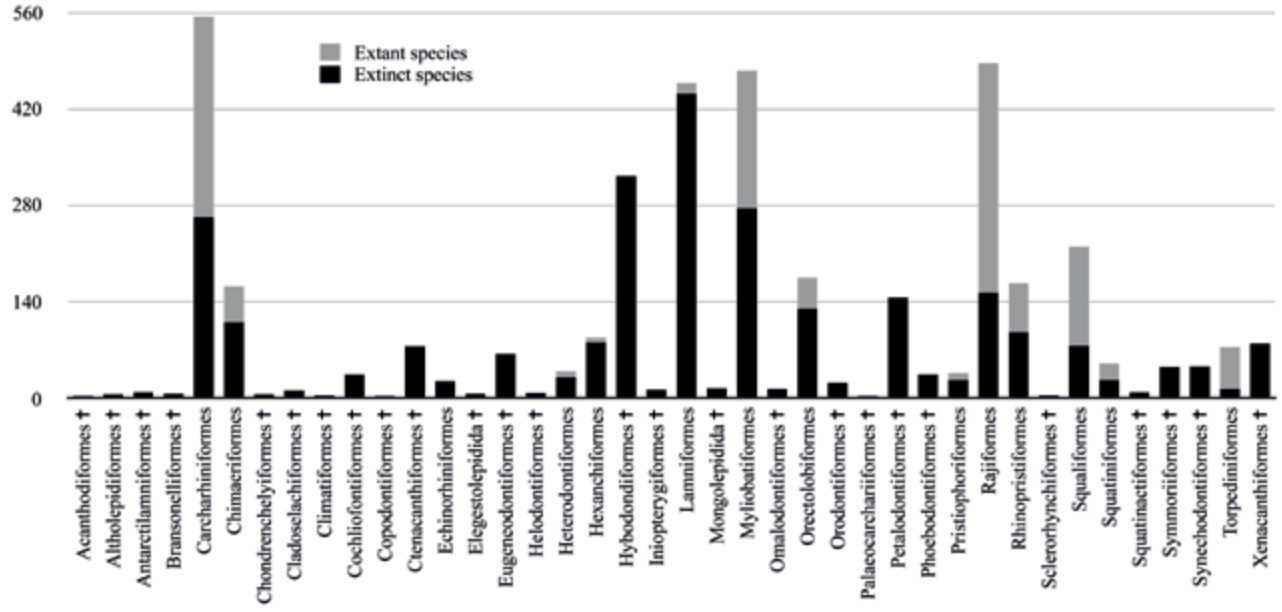

Figure 1 Number of extinct and extant species per Chondrichthyes's order, according to the shark-references database (Pollerspöck & Straube 2021). The cross symbol represents extinct orders.

2 Methodology and Data

Most of the paleoichthyological research done in Portugal was published in English, French, Spanish, and Portuguese. Therefore, this bibliographic search included the following keywords and respective translations: Chondrichthyes; Portugal; fossil; selachian; sharks; batoids; Neogene. The search was executed on the web search engine Google Scholar, the repository of the academic social network ResearchGate, and in the Portugal Open Access Scientific Repositories (RCAAP). In each study, the respective references' list was screened for older publications on the subject, which usually do not appear in the online databases and search engines. When necessary, paper versions were consulted at the University of Évora or acquired through the respective publisher.

The criteria for inclusion or exclusion of the publications screened were as follows:

- Type of publication: include if it is a peer-reviewed journal publication; exclude if it is not (e.g., congress abstract, master or doctoral dissertation).
- Type of data: include if it has reliable information on occurrences and if the fossils were attributed to a *taxon*; exclude if it only mentions selachians or preliminary data.
- Type of access: include if the publication was accessible; exclude if not.

From the 51 publications screened, only the following 36 met the conditions of the inclusion/exclusion criteria: Woodward (1889); Bonança (1891); Cotter (1888-1892) in Zbyszewski & Moitinho de Almeida (1950); Dollfus, Cotter & Gomes (1903-04); Zbyszewski (1947a, 1949, 1967); Zbyszewski (1947b, 1947c) in Zbyszewski & Moitinho de Almeida (1950); Zbyszewski & Moitinho de Almeida (1950); Serralheiro (1954); Cotter (1956); Zbyszewski & Ferreira (1962); Jonet (1964, 1965-66, 1968, 1976, 1978); Antunes (1967, 1970); Antunes & Jonet (1970); Jonet, Kotchetoff & Kotchetoff (1975); Antunes, Jonet & Nascimento (1981); Antunes, Balbino & Cappetta (1999a, 1999b); Antunes *et al.* (1999); Balbino & Cappetta (2000); Antunes & Balbino (2003, 2004, 2006, 2007, 2010a); Balbino & Antunes (2006); Ávila, Ramalho & Vullo (2012); Fialho, Balbino & Antunes (2019a); Fialho et al. (2020).

Although the following publications did not met the criteria, and their data was not included, we consider important to mention them: Antunes (1972); Jonet (1981); Balbino (1995, 1996); Cardoso & Antunes (1995); Antunes & Balbino (2010b); Esteves & da Silva (2014); Antunes, Legoinha & Balbino (2015); Fialho (2015); Fialho, Balbino & Antunes (2016, 2017, 2018a, 2018b, 2019b); Azevedo (2017).

Three types of data were gathered in table format sets: (A) species occurrences and material; (B) stratigraphical occurrences (chronostratigraphic range); (C) geographical occurrences (geographic provenance). To organize the data sets were taken into account the synonymies of each taxon, the nomenclature qualifiers used, and that some of these authors consulted now outdated chronostratigraphic charts.

The following software was applied within the scope of this study: Numbers (version 10.1) for the statistical analysis and data visualization; Adobe Illustrator 2021 (25.2.1) for the creation of the dristibution map and the geochronological tables.

3 Results

By analyzing the available data, it was possible to register 1.156 individual occurrences of fossil Chondrichthyes taxa from geological sites throughout the territory.

3.1 Species Occurrences and Material

Some of the identified occurrences are attributed to *taxa* with a designation that was not listed on the shark-references database (Pollerspöck & Straube 2021). Such is the case of the material attributed to the taxon Catuloidei. According to Soares & de Carvalho (2013), this was a taxonomic group that included the families: Orectolobidae, Catulidae (Scyliorhinidae), and Pseudotriakidae. The genus was used with the open nomenclature qualifier sp. to include the corresponding data whenever possible.

In total, it was possible to list the occurrence of 16.106 fossils, 91 species, 61 genera, and 31 families from 11 selachian orders (Figure 2).

The major taxonomic group Selachii (Carcharhiniformes, Lamniformes, Squaliformes, Hexanchiformes, Hybodontiformes, Pristiophoriformes, Orectolobiformes, Squatiniformes) is the most diverse in Portugal's Neogene, with 58 species recorded (Figure 2A). The most abundant is the Batoidea (Myliobatiformes, Rhinopristiformes, Rajiformes, Torpediniformes), with 51,26% of the listed material (Figure 2B).

The most frequently found fossil selachian species were: *Carcharias taurus* Rafinesque, 1810, *Isurus oxyrinchus* Rafinesque, 1810, and *Otodus (Megaselachus) megalodon* (Agassiz, 1835). And the most abundant in the geological sites were *Myliobatis aquila* (Linnaeus, 1758), *Carcharias taurus*, and *Carcharhinus priscus* (Agassiz, 1843).

Some authors have also contributed to the global knowledge of fossil Chondrichthyes with the discovery of new species. From the 19 species originally presented, only the following 11 are currently listed on the shark-references database: *Pristis atlanticus* Zbyszewski (1947); *Paragaleus pulchellus* (Jonet, 1966); *Raja olisiponensis* (Jonet, 1968); *Pristis lanceolatus* Jonet (1968); *Rhinobatos antunesi* (Jonet, 1968); *Megascyliorhinus miocaenicus* (Antunes & Jonet, 1970); *Squalus almeidae* Antunes & Jonet (1970); *Mobula cappettae* Jonet (1976); *Galeorhinus goncalvesi* Antunes, Balbino & Cappetta (1999); *Paragaleus antunesi* Balbino & Cappetta (2000); *Aetobatus cappettai* (Antunes & Balbino, 2006). Some of these have so far only been found in Portugal.

3.2 Stratigraphical Occurrences

The study of Chondrichthyes' fossil diversity in Portugal has been mainly focused on the Miocene of the Lower Tagus and Alvalade Basins. It is associated with the lithostratigraphic units proposed by Cotter (1956), which remain valid and in general use (Pais et al. 2012). However, the correspondent chronostratigraphic designations have changed since. It was necessary to update these according to the calibrated general stratigraphic framework presented by Pais et al. (2012, Fig. 11) and the International Chronostratigraphic Chart by Cohen et al. (2013, version 2020/01).

As shown in Figure 3, batoid fossil material has been associated with sediments of all Miocene stages. However, only *Raja olisiponensis* and *Rhynchobatus pristinus* seem to maintain their presence from the Aquitanian to the Messinian (Figure 3).

In Figure 4, we observe that the fossil shark species are present throughout all the Neogene, with several species occurring in all stages.

3.3 Geographical Occurrences

Through the current work, it was possible to approximately identify the geographic location of 105 geological sites with fossil selachian material in the continent and Santa Maria's Island (Azores). Unfortunately, most of these deposits have already been lost. The expansion of residential areas, Lisbon's Airport, roadways, and even the construction of Expo'98, are some of the reasons that led to the disappearance of these outcrops currently referred to only in the bibliography.

In Figure 5, it is possible to observe the geographic distribution of the referred Neogene outcrops in a 10x10km2 grid. The diversity of fossil selachian species, including the location of the new species described, and the abundance of material collected are highlighted. Due to the in-depth studies focused on the marine Miocene of Lisbon and Setubal's Peninsula, and in the Alvalade Basin, these were the regions with the most identified sites (Figure 5).

Despite the disappearance of the majority of these Neogene deposits, it is still possible to revisit some through the researchers own photographic records. Such is the case for the following geological sites: Quinta dos Durões (Figure

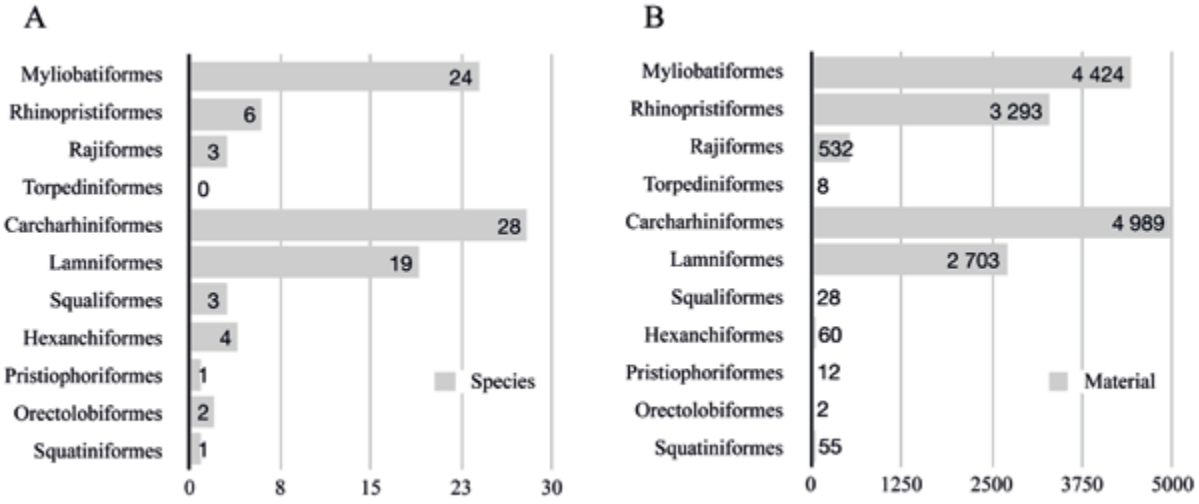

Figure 2 Graphic representation of (A) the number of species identified per order (species left in open nomenclature sp. were not accounted for); (B) amount of material identified per order (all fossils were accounted for).

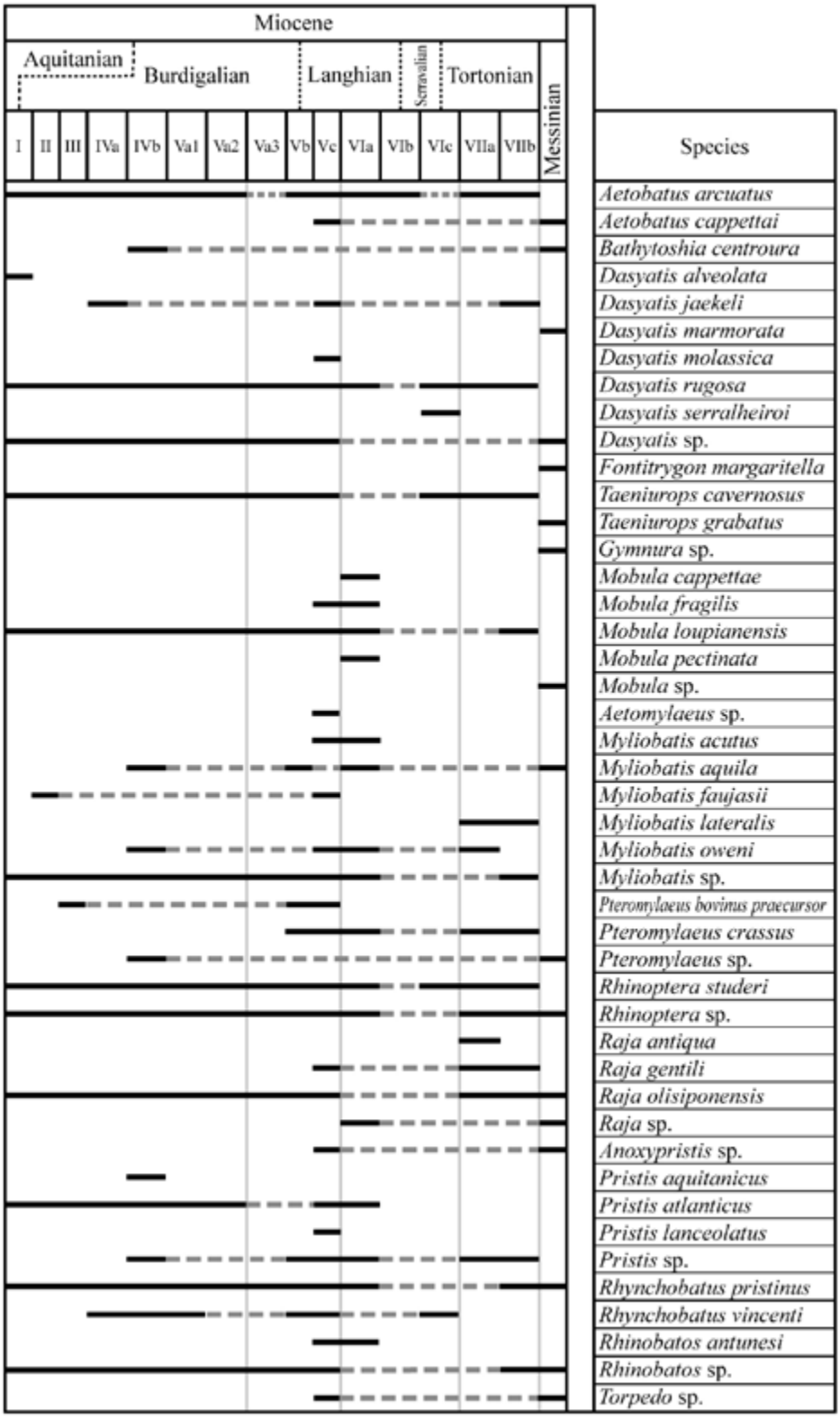

Figure 3 Chronostratigraphic ranges of the 45 batoid species identified in fossiliferous geological sites in Portugal. The continuous line corresponds to identified occurrences; the dashed line corresponds to expected occurrences.

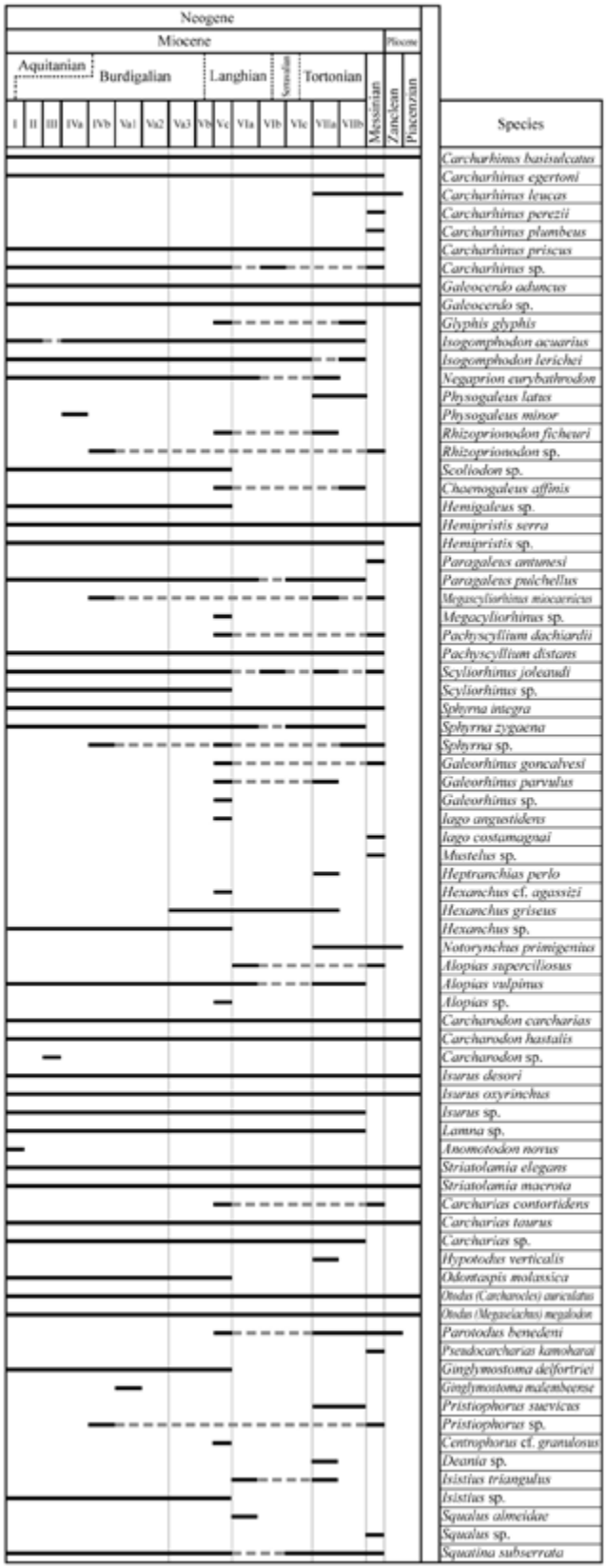

Figure 4 Chronostratigraphic ranges of the 77 shark species identified in fossiliferous geological sites in Portugal. The continuous line corresponds to identified occurrences; the dashed line corresponds to expected occurrences.

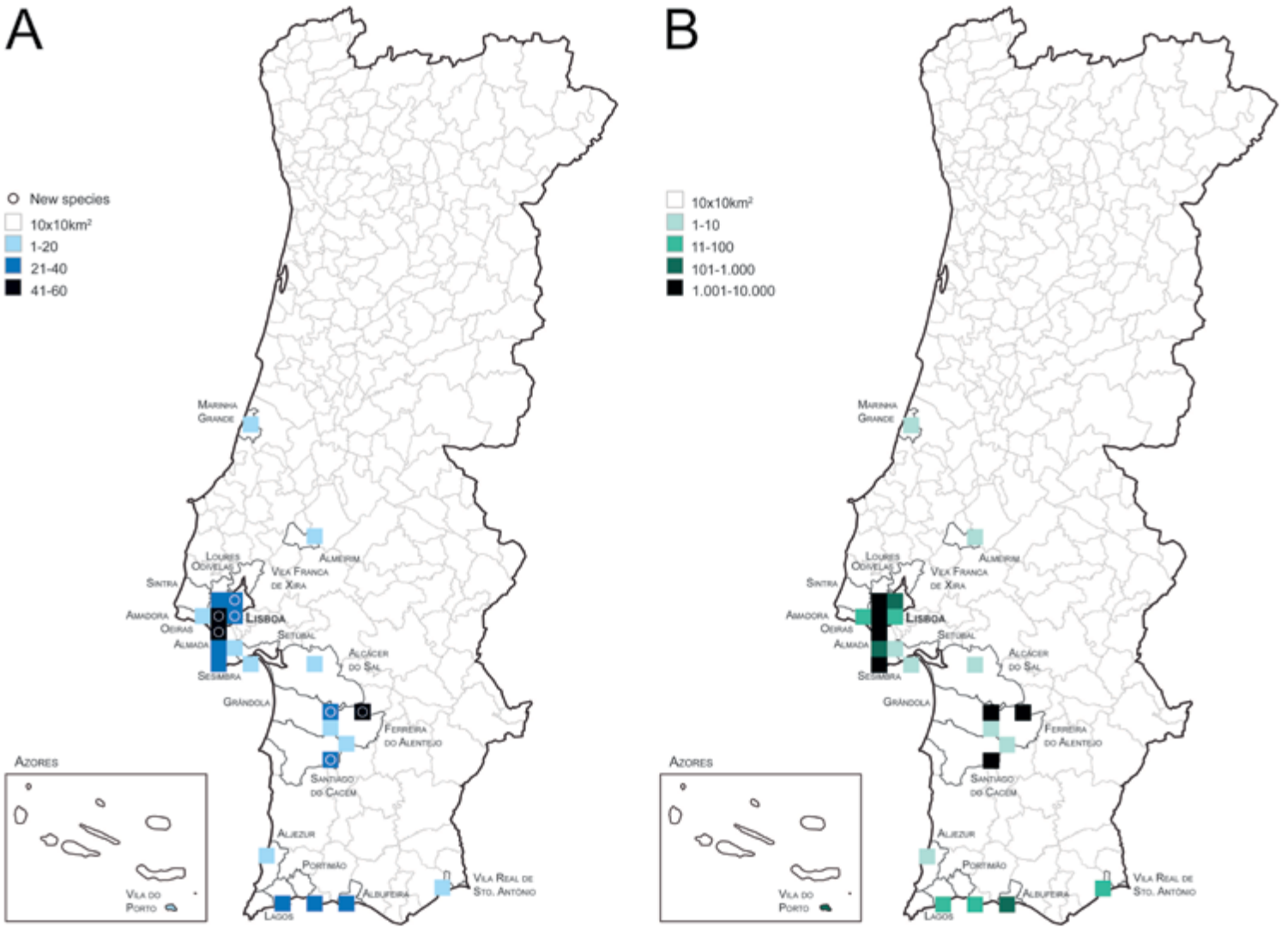

Figure 5 Geographic distribution of the occurrence of fossil selachians in Portugal's Neogene outcrops. The 10x10 km² UTM grids were adapted from Loureiro & Sillero (2008). The counties with occurrences of fossil Chondrichthyes were named. (A) depicts the number of species identified in each zone, highlighting the zones with new species. (B) represents the number of fossils found in each zone.

6A-B), Olival da Susana (Figure 6C-D), and Quinta do Narigão (Figure 6E). The photographs included in Figure 6, kindly provided by M. T. Antunes, portrait the conditions of these geological sites at the time of the sediments removal.

The site of Quinta dos Durões was studied by Antunes & Jonet (1970). In Figure 6A-B, it is possible to observe the *strata* corresponding to the Cotter geological units Vc (Langhian) and VIIa (Tortonian) (Cotter, 1956).

The upper *strata* of Areeiro do Olival da Susana and Quinta Grande are visible in Figure 6C. Cited in the works of Zbyszewski & Moitinho de Almeida (1950) and Serralheiro (1954), this site clearly presents (Figure 6D) a marine transgression depositional sequence. Coarse sands at the base, overlaid by beds of finer white sands from coastal cords with clayey dune intercalations, followed by clays with oysters (Vb), and limestones in the upper *strata* (Vc).

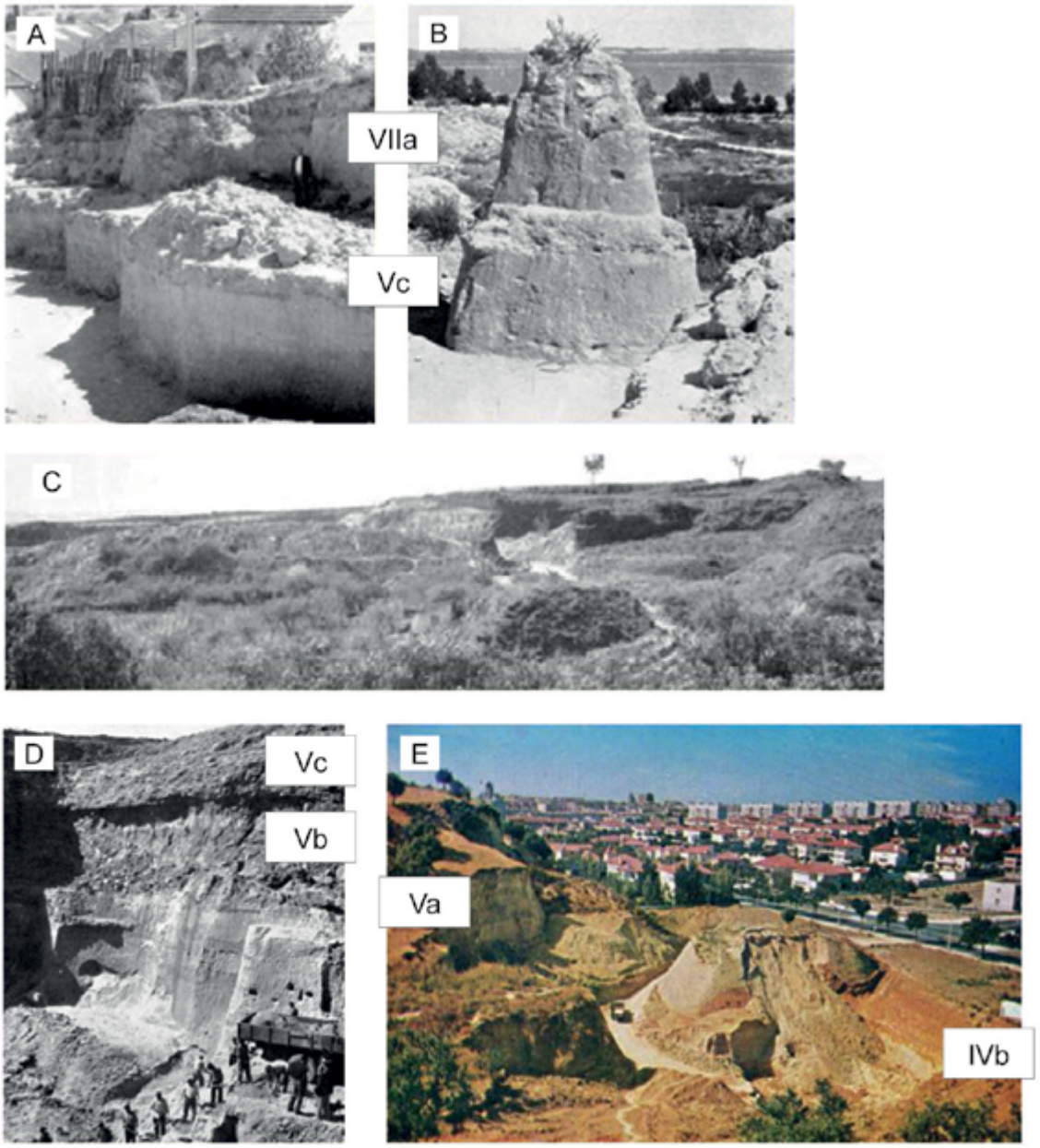

Figure 6 Photographic record of Portuguese geological sites located in sand extraction zones, with correspondent Cotter (1956) geological units indicated. All photos were taken by M. T. Antunes. A-B Quinta dos Durões, Mutela (Almada, 1957). C-D Areeiro do Olival da Susana and Quinta Grande, located in Charneca do Lumiar (Lisbon, 1959). E Quinta do Narigão to Avenida Gago Coutinho (Lisbon, 1960).

The Figure 6E shows the geological site Quinta do Narigão, with fluvial lower levels (IVb) followed at the top by the Cotter geological unit Va.

4 Conclusions

The extensive noncontinuous research of 135 years on the Portuguese fossil marine sediments presented in the current work supports the conception of high selachian diversity (extinct and extant) present in the geological record of the country. The Neogene period has been the main focus of study for researchers, especially the Miocene of Lisbon. Through the in-depth studies so far conducted, it was possible to detail the chronostratigraphic range of the identified species and the geographic distribution of the studied geological sites.

By considering the results of this literature analysis on the subject, it was possible to assess the Chondrichthyes' fossil diversity present in Portugal's Neogene. There have been at least 105 geological sites found, and 16.106 fossils studied. A total of 91 species were registered, 11 of which were first discovered in Portugal. 61 genera, and 31 families attributed to Hybodontiformes, Carcharhiniformes, Hexanchiformes, Lamniformes, Orectolobiformes, Squaliformes, Squatiniformes, Pristiophoriformes, Myliobatiformes, Rajiformes, Rhinopristiformes, Torpediniformes.

In light of the current knowledge, Selachii is the most diverse *taxon*, while Batoidea stands as the most abundant in the Portuguese geological record.

In conclusion, separately, each publication and their respective findings enrich the regional knowledge of the paleo selachian fauna diversity. However, by considering the total results of 36 studies, from 1885 to 2020, we can assess the total paleodiversity of selachians found in Portugal's Neogene record and highlight the diversity and abundance per order and the geographic distribution of the geological sites analyzed in these studies.

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