



A revised marine fossil record of the Mediterranean before and after the Messinian Salinity Crisis

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Abstract. The Messinian Salinity Crisis and its precursor events have been the greatest environmental perturbation of the
35 Mediterranean Sea to date, offering an opportunity to study the response of marine ecosystems to extreme hydrological
change and a large-scale biological invasion. The restriction of the marine connection between the Mediterranean and the
Atlantic Ocean already since the Tortonian–Messinian boundary resulted in stratification of the water column and increase
water temperature and salinity variations. Here, we present a unified and revised marine fossil record of the Mediterranean
that covers the Tortonian stage, the pre-evaporitic Messinian and the Zanclean stage and encompasses 22988 occurrences of



40 calcareous nannoplankton, dinoflagellates, foraminifera, corals, ostracods, bryozoans, echinoids, mollusks, fishes, and
marine mammals. This record adheres to the FAIR principles, it is updated in terms of taxonomy, and it follows the currently
accepted stratigraphic framework. Based on this record, knowledge gaps are identified, which are due to spatiotemporal
inconsistencies in sampling effort and the distribution of sedimentary facies, and the inherent differences in the preservation
potential between the groups. Additionally, sampling bias in old records may have distorted the record in favor of larger,
45 more impressive taxa within groups. This record is now ready to be used to answer both geological and biological questions,
and is amendable when new fossil data are brought to light.

1 Introduction

The Tortonian–Zanclean was a pivotal period in the evolution of the Mediterranean realm, predominantly due to the changes
in the marine gateway configurations that affected the hydrological budget and oceanographic conditions in the basin,
50 leading to the Messinian Salinity Crisis (MSC; Hsü et al., 1973). Even though the Neogene Mediterranean has been one of
the most intensely researched geoscience topics in the last 150 years, its fossil record is largely fragmented and outdated,
both in terms of taxonomy and stratigraphic assignment. Here, we provide a database of the revised marine fossil record of
the Mediterranean basin, before and after the MSC. The fossil record during the MSC has been addressed in previous works
(Carnevale et al., 2019; Carnevale and Schwarzahans, 2022) and is not included here. This open-access dataset meets FAIR
55 (findable, accessible, interoperable, and reusable) data standards. It can be enlarged and amended in the future, to enhance
our understanding of the response of marine ecosystems to large-scale connectivity changes. It includes marine species
occurrences in the Mediterranean Sea during the Tortonian age (13.8–7.25 Ma), the pre-MSC Messinian (7.25–5.97 Ma) and
the Zanclean age (5.33–3.6 Ma) for the following groups: calcareous nannoplankton, dinoflagellates, foraminifera, corals,
ostracods, bryozoans, echinoids, mollusks, fishes, and marine mammals.

60 2 Dataset structure

We collected the published fossil records of marine taxa in the Tortonian, the pre-evaporitic Messinian, and the Zanclean
(Agiadi et al., 2024). For each record, the database includes the name of the taxon as in the original publication, the higher
taxonomic group and the family it belongs to, the locality where it was found, the relative age of the sediments (separated
into the three above categories), the publication(s) providing evidence for the occurrence, and the initials of the experts who
65 collected and input the data (as given in the Authors Contribution statement).

An *Occurrence* was defined by the unique combination of three components: taxon, locality, age. To facilitate future
analyses at the genus and species levels, since we reported fossil occurrences at all taxonomic levels, we indicated the genus
and species identification status for each record. When the record was in open nomenclature, we indicated this as uncertain
(U) identification status of the species and/or the genus. However, when a species was described as a different morphotype,



70 but not named as a new species (e.g., sp. 1, sp. A etc.), we treated it as a separate species, if the corresponding expert(s) judged that the fossil material most probably belonged to a different, yet unnamed, species.

Locality was the distinct geographical site, where fossils were collected from. Often it was not possible to locate the origin of each record precisely, to the outcrop level, because several records were published many decades ago, and the outcrops had since then been destroyed and the authors are deceased. We therefore retained the most specific information we could find
75 based on the description of the locality in the publication. The coordinates of the localities were obtained either from the occurrence publication or by estimation based on the locality description. Each locality was assigned to one of three regions based on their paleogeographic placement in the Western Mediterranean (wMed), the Eastern Mediterranean (eMed), and the Po Plain–Northern Adriatic (PoA), following the currently accepted paleogeographic data (Amadori et al., 2018; Steininger and Rögl, 1984). The PoA region developed as a paleoceanographic sub-basin of the Mediterranean in the Tortonian–Early
80 Messinian, as evidenced by its distinct strontium isotopic signature (Cornacchia et al., 2021) and the absence of halite deposits. To facilitate comparisons, apart from the Messinian and Zanclean records, we placed also the Tortonian records from Piedmont and the Po Plain within the PoA region. Based on the Late Miocene paleogeographic evolution of Calabria and Sicily (Butler et al., 1995; Caracciolo et al., 2013; Henriquet et al., 2020), we included the records from these areas as part of the eMed, since the marine connection with the wMed was located near its present location, possibly along present
85 southern Sicily (Micallef et al., 2019) or at the Sicily Channel (Malta Plateau; Bache et al., 2012).

The validity of each record was then assessed by the corresponding expert(s), considering changes in the stratigraphic placement of the sedimentary formation from which it derived, new taxon synonymies or reassignment since the publication of the record, and previous misidentifications, leading to a revised name for that record, if necessary. Taxonomy followed the World Register of Marine Species (WoRMS Editorial Board, 2024) and the systematic schemes of: Kroh and Smith
90 (2010) for echinoids; Nelson et al. (Nelson et al., 2016) for fishes; Marx et al. (2016) for cetaceans; and Berta et al. (2018) for pinnipeds. The state of knowledge was accordingly noted in each case, as: E. if the identification was confirmed by the expert based on own sample examination, C. if the identification was confirmed by the expert based on photographs of the material that are available in the literature, R. if the identification was revised by the expert in the present study, and L. if the identification was not confirmed due to lack of access to the fossil material and absence of photographs in the literature, and
95 the record relied only on the literature reference.



3 Fossil record overview

The assembled dataset comprised 22988 occurrences including 4959 species, 1764 genera and 642 families (Table 1; Fig. 1).

Table 1. Overview of the collected fossil dataset in the three regions: Eastern Mediterranean (eMed), Western Mediterranean (wMed), Po Plain-Northern Adriatic (PoA). The group ‘other molluscs’ includes scaphopods, chitons and cephalopods.

Taxonomic group(s)	# of Occurrences				Species	Genera	Families	# of Localities			
	all	eMed	wMed	PoA				all	eMed	wMed	PoA
Marine mammals	164	65	60	39	26	24	20	114	42	47	25
Sharks	216	55	110	51	85	56	26	37	7	23	7
Bony fishes	1601	365	695	541	426	265	127	70	22	32	16
Gastropods	5912	1113	2056	2743	1760	535	150	129	50	36	43
Bivalves	3668	701	2173	794	479	233	70	161	42	101	18
Bryozoans	833	319	514	0	265	170	83	6	3	3	0
Echinoids	217	27	173	17	109	38	22	42	12	22	8
Corals	902	235	514	153	133	57	23	242	73	149	20
Ostracods	4500	2215	938	1347	1086	168	29	124	59	37	29
Other molluscs	191	26	53	112	77	30	16	23	10	2	11
Benthic foraminifera	560	202	233	125	117	62	42	20	6	10	4
Planktic foraminifera	1306	651	468	187	97	17	3	79	37	29	13
Dinoflagellate cysts	1016	599	300	117	174	70	13	38	20	17	2
Calcareous nannoplankton	1902	922	707	273	125	40	18	56	26	20	10
Total	22988	7495	8994	6499	4959	1765	642	836	279	424	135

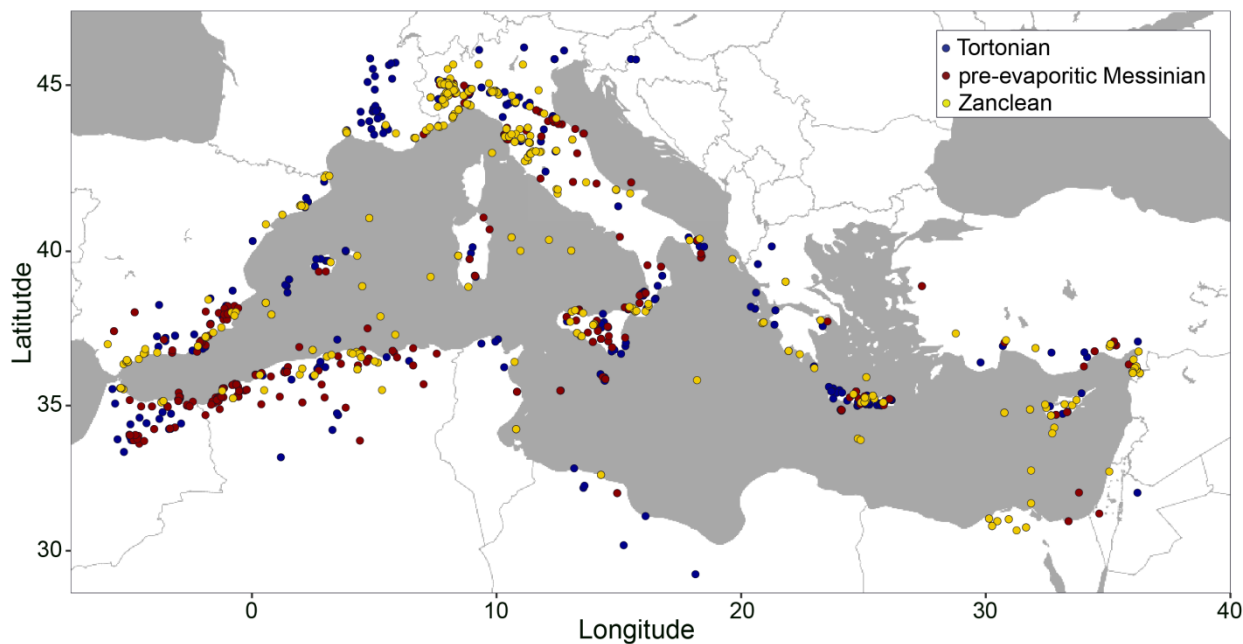


Figure 1. Mediterranean map with the localities included in this record. The coordinates of the localities were obtained from the original publications, whenever possible. When the exact coordinates for a locality had not been published or when the locality was too vague (e.g. Libya), we included approximate coordinates based on the description of the locality in the original publication.

110 The map was produced using ggmap (Kahle and Wickham, 2013).

4 Record gaps

Some gaps are detected in the fossil record. Spatiotemporal gaps are attributed to: a) the spatial distribution of outcrops of Late Miocene–Early Pliocene deposits (Masclé and Masclé, 2012); and b) socioeconomic and political conditions favoring research in the northwestern Mediterranean countries (Cappelletto and et al., 2021). The spatial distribution of the localities within the Mediterranean is strongly skewed toward the West and the North (Fig. 1; e.g., for molluscs Monegatti and Raffi, 2010). However, there are notable exceptions. For example, most Tortonian data on gastropods derive from the eastern Mediterranean, whereas almost all Messinian and Zanclean localities are in the western sub-basin or the Po Plain-Northern Adriatic region. On the other hand, rarity is inherent in the fossil record of large animals. Only a single diverse shark tooth assemblage is currently known from the pre-evaporitic Messinian of the Mediterranean Basin, from the vicinities of Oran (Algeria; Arambourg, 1927). Similarly, the fossil record of pinnipeds from the Late Miocene–Early Pliocene of the Mediterranean Basin only consists of two Monachinae (Phocidae) species: *Messiphoca mauritanica* from the Messinian (during the MSC) of Algeria (Muizon, 1981) and fragmentary remains referred of *Pliophoca cf. etrusca* from southern France, Italy and Spain (Berta et al., 2015).



Moreover, large species, especially those with more robust remains, have generally been favored in the fossil record of some groups, such as molluscs, as they were generally easier to sample (Dominici et al., 2020). This was in spite of the fact that a large proportion of the species in modern biodiversity hotspots are smaller than 4 mm (Bouchet et al., 2002). Particularly for the case of molluscs, bivalves, contrary to gastropods, include calcitic forms that have a higher preservation potential than aragonitic forms. In contrast to gastropods, there are many more pre-evaporitic Messinian localities with rich bivalve faunas than either Tortonian and Zanclean localities. This is largely due to a few large expeditions in North Africa (Cornée et al., 2014; el Kadiri et al., 2010; Merzeraud et al., 2019), which yielded however only faunal lists of large-sized, mostly calcitic forms extracted from calcarenites, a lithology underrepresented in Zanclean collections (Dominici and Forli, 2021; Dominici et al., 2019).

Important gaps in the Late Miocene–Early Pliocene marine fossil record of the Mediterranean derive from the uneven distribution of the different facies. This affects especially the records of benthic organisms, whose distribution depends on the type of substratum. In the case of molluscs, knowledge of the onshore-offshore facies gradient is fragmentary (Dominici and Forli, 2021; Dominici et al., 2019). As a result, for gastropods, Tortonian and Zanclean data represent a wider facies range, from onshore to offshore siliciclastic, whereas the pre-evaporitic Messinian data are mainly confined to open shelf mudstones, so that littoral and bathyal taxa of the pre-evaporitic Messinian may be underrepresented in the database. Moreover, the Messinian mollusc data include records from hybrid carbonates (e.g., Dominici et al., 2019), which are lacking in the Zanclean (Dominici and Forli, 2021). Such gaps do not appear consistently across groups, however: for ostracods, both shallow and deeper siliciclastic facies are represented from the three geographic areas and the three stratigraphic intervals, rendering the dataset rather more complete.

Regarding stratigraphic gaps, the main issue when assembling the dataset derived from the fact that in some cases the chronostratigraphic framework provided in the initial publication is considered questionable (e.g., Benson, 1976; Doruk, 1979; Sissingh, 1972). Additionally, several new species were established without either descriptions or illustrations (*nomina nuda*; Doruk, 1979). In the case of echinoids for example, many finding localities in the rich Italian Pliocene are generically reported in the geologic maps and publications as ‘Zanclean–Piacenzian’, thus preventing the precise temporal collocation of numerous citations from the Argille Azzurre Formation of the PoA region (e.g., Airaghi, 1901; Botto-Micca, 1896) and from Tuscany (e.g., Desor, 1858; Meneghini, 1862). There are two different problems here: old citations rarely indicated the precise stratigraphic position, whereas several precise layers yielding echinoids have not been studied (and dated) yet by modern methods. For the Pliocene, records were only included in the database if they could be securely placed in the Zanclean based on the current knowledge on the stratigraphic placement of the deposits they were recovered from. The result is a limited record for the Messinian and possibly the Zanclean, both potentially leading to an underestimation of echinoid diversity.



155 **Data availability**

The dataset described in the paper is openly accessible under a CC BY license at <https://doi.org/10.5281/zenodo.10782429> (Agiadi et al., 2024).

Code availability

No code was used for assembling the database. The code to generate Table 1 and Figure 1 is available at
160 <https://zenodo.org/doi/10.5281/zenodo.10782634>.

5 Conclusions and Outlook

This dataset includes a Tortonian–Zanclean marine fossil record of the Mediterranean before and after the Messinian Salinity Crisis. The Late Miocene–Early Pliocene Mediterranean fossil record is invaluable, not only for large-scale paleobiogeographic studies, but also for evaluating the indigenous/non-indigenous status of tropical marine species detected
165 today in the eastern Mediterranean, establishing resilience thresholds for marine organisms and their ecosystems, and investigating evolutionary dynamics, particularly of higher trophic-level groups. Nevertheless, we highlight the need for further targeted sampling expeditions and collaborative paleontological investigations facilitated by science diplomacy (Soler and Perez-Porro, 2021) to fill in these spatial gaps in the fossil record of the Mediterranean.

Author contribution

170 **Konstantina Agiadi**: Conceptualization, Data curation, Funding acquisition, Investigation (data collection: osteichthyes), Methodology, Project administration, Writing – original draft preparation. **Niklas Hohmann**: Data curation, Formal analysis, Methodology, Writing – review & editing. **Elsa Gliozzi**: Investigation (data collection: ostracods), Writing – review & editing. **Danae Thivaïou**: Data curation, Investigation (data collection: bivalves, gastropods), Writing – review & editing. **Francesca Bosellini**: Investigation (data collection: corals), Writing – review & editing. **Marco Taviani**:
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Pierre Moissette: Investigation (data collection: bryozoans), Writing – review & editing. **Ildefonso Bajo Campos**: Investigation (data collection: echinoids), Writing – review & editing. **Enrico Borghi**: Investigation (data collection: echinoids), Writing – review & editing. **George Iliopoulos**: Investigation (data collection: marine mammals), Writing – review & editing. **Assimina Antonarakou**: Investigation (data collection: planktic foraminifera), Writing – review & editing. **George Kontakiotis**: Investigation (data collection: planktic foraminifera), Writing – review & editing. **Evangelia Besiou**: Investigation (data collection: planktic foraminifera), Writing – review & editing. **Stergios D. Zarkogiannis**: Investigation (data collection: planktic foraminifera), Writing – review & editing. **Mathias Harzhauser**: Investigation (data collection: bivalves, gastropods), Writing – review & editing. **Francisco Javier Sierro Sánchez**: Investigation (data collection: benthic foraminifera), Writing – review & editing. **Angelo Camerlenghi**: Conceptualization, Funding acquisition, Writing – review & editing. **Daniel García-Castellanos**: Conceptualization, Funding acquisition, Writing – review & editing.

Competing interests

The authors declare that they have no conflict of interest.

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