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 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, 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, 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of the most intensely researched geoscience topics in the last 150 years, its fossil record is largely fragmented and outdated, both in terms of taxonomy and stratigraphic assignment.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 Schwarzhans, 2022) and is not included here. This open-access dataset meets FAIR (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.

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 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,
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 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 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 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 synonyms 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 (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 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.

<table>
<thead>
<tr>
<th>Taxonomic group(s)</th>
<th># of Occurrences</th>
<th># of Localities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>all</td>
<td>eMed</td>
</tr>
<tr>
<td>Marine mammals</td>
<td>164</td>
<td>65</td>
</tr>
<tr>
<td>Sharks</td>
<td>216</td>
<td>55</td>
</tr>
<tr>
<td>Bony fishes</td>
<td>1601</td>
<td>365</td>
</tr>
<tr>
<td>Gastropods</td>
<td>5912</td>
<td>1113</td>
</tr>
<tr>
<td>Bivalves</td>
<td>3668</td>
<td>701</td>
</tr>
<tr>
<td>Bryozoans</td>
<td>833</td>
<td>319</td>
</tr>
<tr>
<td>Echinoids</td>
<td>217</td>
<td>27</td>
</tr>
<tr>
<td>Corals</td>
<td>902</td>
<td>235</td>
</tr>
<tr>
<td>Ostracods</td>
<td>4500</td>
<td>2215</td>
</tr>
<tr>
<td>Other molluscs</td>
<td>191</td>
<td>26</td>
</tr>
<tr>
<td>Benthic foraminifera</td>
<td>560</td>
<td>202</td>
</tr>
<tr>
<td>Planktic foraminifera</td>
<td>1306</td>
<td>651</td>
</tr>
<tr>
<td>Dinoflagellate cysts</td>
<td>1016</td>
<td>599</td>
</tr>
<tr>
<td>Calcareous nannoplankton</td>
<td>1902</td>
<td>922</td>
</tr>
<tr>
<td>Total</td>
<td>22988</td>
<td>7495</td>
</tr>
</tbody>
</table>
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 (Mascle and Mascle, 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.
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 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 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

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 Thivaiou: Data curation, Investigation (data collection: bivalves, gastropods), Writing – review & editing. Francesca Bosellini: Investigation (data collection: corals), Writing – review & editing. Marco Taviani: Investigation (data collection: corals), Writing – review & editing. Francesca Bulian: Investigation (data collection: marine mammals), Writing – review & editing. Alberto Collareta: Investigation (data collection: sharks), Writing – review & editing. Laurent Londeix: Investigation (data collection: dinoflagellates), Writing – review & editing. Costanza Faranda: Investigation (data collection: ostracods), Writing – review & editing. Francesca Lozar: Investigation (data collection: calcareous nannoplankton), Writing – review & editing. Alan Maria Mancini: Investigation (data collection: calcareous nannoplankton), Writing – review & editing. Stefano Dominici: Investigation (data collection: bivalves, gastropods), Writing – review & editing.

Competing interests

The authors declare that they have no conflict of interest.

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References


Muizon, C. de: Premier signalement de Monachinae (Phocidae: Mammalia) dans le Sahelien (Miocene superieur) d’Oran (Algerie), Palaeovertebrata, 11, 181–196, 1981.


WoRMS Editorial Board: World Register of Marine Species, 2024.