



# DINOSTRAT version 2.0-GTS2020

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**Abstract.** DINOSTRAT version 2.0-GTS2020 is now available (Bijl et al., 2023a; <http://dx.doi.org/10.5281/zenodo.7791273>). This version updates DINOSTRAT to the Geologic Time Scale 2020, and new publications are added into the database. The resulting database now contains over 9,450 entries from 209 sites. This update has not led to major and profound changes in the conclusions made previously. DINOSTRAT allows full presentation of first and last stratigraphic occurrences of dinocyst (sub-) families, as well as the evolutionary turnover throughout geologic history, as a reliable representation of dinoflagellate evolution. Although the picture of dinoflagellate evolution from DINOSTRAT is broadly consistent with that in previous publications, the underlying data is with DINOSTRAT openly available, reproducible, and up to date. This release of DINOSTRAT allows calibration of stratigraphic records to the Geologic Time Scale 2020 using dinoflagellate cysts as biostratigraphic tool.

## 15 1 Introduction

DINOSTRAT version 1.1 (Bijl, 2022) offers a comprehensive open access database of organic-walled dinoflagellate cyst first and last occurrences (dinocyst events). The dinocyst events in DINOSTRAT were calibrated to the Geologic Time Scale (GTS) 2012 (Gradstein et al., 2012). In 2020, a new geologic time scale was published (Gradstein et al., 2020). I here release DINOSTRAT version 2.0, in which stratigraphic ranges of dinocysts are calibrated to the GTS2020 of (Gradstein et al., 2020).

## 20 2 Methods

In the release of version 2.0 of DINOSTRAT, stratigraphic calibrations of dinoflagellate cyst first and last occurrences were updated to the GTS2020 (Gradstein et al., 2020). New papers that meet the criteria as laid out in DINOSTRAT version 1.1 (see Bijl, 2022 for more information about the approach) were added (see Table 1 for the new additions). The approach of data entry was not changed in this new release. Still published dinocyst ranges were included when they could be calibrated to a chrono-, bio-, or magnetostratigraphic zonation, whereby 5 reliability tiers were distinguished: 1) dinocyst events were calibrated against reliable magnetostratigraphy, 2) against compromised magnetostratigraphy, 3) against biostratigraphic zonations (nannofossils, foraminifer zones, ammonites), 4) indirectly against biostratigraphic zones (whereby the origin of those zones is not exactly clear, or these zones were not derived from the same material), and 5) from unclear



30 chronostratigraphic constraints. For more information see Bijl, 2022. The plotting tools were updated with extra features: the stages from the GTS2020 (Gradstein et al., 2020) are added to visually aid the interpretation of the plots.

### 3 Results: DINOSTRAT version 2.0-GTS2020

The database is released as Version 2.0-GTS2020 on Github and Zenodo (Bijl, 2023a); <http://dx.doi.org/10.5281/zenodo.7791273>), on which the new datasets and plotting tools can be found. The supplements (Bijl, 2023b) contain all the new figures for families, genera, species and sites in DINOSTRAT. The calibration of some entries in  
35 DINOSTRAT version 1.1 had to be adjusted for DINOSTRAT version 2.0-GTS2020, because of a revision of the Cretaceous ammonite zonations in GTS2020 (see Gradstein et al., 2020; Chapter Cretaceous). An overview of the changes induced by this can be found on Github (Bijl, 2023a). This update has not led to any major changes in the database. For most events, this update caused only minor adjustments in the calculated absolute age. The adjusted ammonite zonation scheme in the Cretaceous that GTS2020 proposed did lead to a lot of recalibrations of dinocyst events, but their absolute age should in  
40 principle not have changed much, since the ammonite zonation adjustment was mostly about redefining the index species and zone boundaries. With this update of DINOSTRAT, dinocyst events can now be used as chronostratigraphic indicator on the GTS2020 time scale.

45 **Table 1. New papers added to DINOSTRAT version 2.0-GTS2020. Reference, Geography, Age base and Age top (in Ma), Tier (see DINOSTRAT version 1) and means of calibration to the Geologic Time Scale. For the meaning of the acronyms of the microplankton zones indicated in the column “Calibrated to” the reader is referred to the GTS2020 (Gradstein et al., 2020).**

Reference	Geography	Age base	Age top	Tier	Calibrated to:
(Bujak et al., 2022)	Arctic	205	140	3	Calibrated to boreal ammonite stratigraphy
(Crouch et al., 2022)	Zealandia	63	56	3	Calibrated to NP nannoplankton stratigraphy
(González Estebenet et al., 2021)	Austral Basin	70	54	3	Calibrated to NP nannoplankton stratigraphy
(Guerrero-Murcia and Helenes, 2022)	Venezuela	100	65	5	Calibrated to stages
(Jarvis et al., 2021)	Germany	90	88	3	Calibrated to boreal ammonite stratigraphy



(Pearce et al., 2020)	UK	100	90	3	Calibrated to boreal ammonite stratigraphy
(Pearce et al., 2022)	France	86	70	3	Calibrated to UC nannofossil stratigraphy
(Thöle et al., 2022)	Antarctica	0	0	-	surface sediments
(Torricelli et al., 2022)	Angola	34	13	3	Calibrated to CP nannofossil stratigraphy
(Vasilyeva and Musatov, 2022)	Crimea	45	37	3	Calibrated to CNE nannofossil stratigraphy
(Vieira et al., 2020)	North Sea	66	56	3	Calibrated to stages with information from nannofossils
(Vieira and Mahdi, 2022)	Norway	85	62	3	Calibrated to stages with information from nannofossils

#### 4 Discussion

50 All the conclusions and interpretations made in the release paper of DINOSTRAT still stand with the addition of additional data and recalibration to the GTS2020. The North Atlantic Ocean is still strongly overrepresented in DINOSTRAT, and the Pacific Ocean underrepresented in the geographical distribution of sites used to calibrate dinocyst assemblages (Fig. 1), and equatorial regions and Southern Hemisphere remains underexplored, in spite of large ocean regions (Fig. 2). (Bujak et al., 2022) added crucial calibrated dinocyst events from the Jurassic Arctic Basin. The addition of the new Antarctic-proximal surface sediment data of (Thöle et al., 2022) adds geographic distribution information for modern dinocysts on the Southern Hemisphere, but still for a large number of modern species, their stratigraphic first occurrence remains largely unknown (see Supplements).

Further exploration of DINOSTRAT version 2.0-GTS2020 has allowed the presentation of the stratigraphic ranges of dinoflagellate cyst (sub-)families (Fig. 3). As in Fig. 2b, Fig. 3 presents counts of oldest first occurrences and youngest last occurrences of dinoflagellate cyst genera and species, but per (sub)family, which yields the calibrated age of origination and final extinction of dinoflagellate cyst (sub)families. This is a robust indication of the minimal stratigraphic range of these dincyst subfamilies.

Peridiniphyceidae have their first occurrence in the Ladinian (Middle Triassic), followed by Shublikodiniaceae, Suessiaceae and several miscellaneous Dinophyceae in the Carnian (Upper Triassic). The Heterocapsaceae, as first representatives of modern Peridiniales, the Mancodiniaceae as first representatives of the modern (but now non-cyst-forming) Cladopyxiineae, Nannoceratopsiaceae and Comparodiniaceae first occur in the Sinemurian (Lower Jurassic). Scrinocassiaceae and



Cladopyxiaceae (both part of the suborder of Cladopyxiineae) first occur in the Pliensbachian, and sees the last occurrence of the Shublikodiniaceae, the first of the cyst-forming dinocyst families to go extinct. The Toarcian sees the last occurrence of the Suessiales, as well as the first occurrence of the Pareodiniaceae, Areoligeraceae and Leptodinioideae of the family  
70 Gonyaulacaceae, with many modern representatives. The Aalenian (Middle Jurassic) sees the first occurrence of the Cribroperidinioideae. The Gonyaulacoideae first occur in the Bajocian, during which also many other Gonyaulacaceae taxa have first occurrences. The Scrinioicassiceae have their last occurrence in this stage. The Stephanelytraceae first occur in the Bathonian, while the Mancodiniaceae have their last occurrence. The Peridiniaceae first occur in the Callovian. The Deflandreoideae first occur in the Oxfordian (Upper Jurassic). The Nannoceratopsiaceae have their last occurrence and the  
75 Ceratiaceae their first occurrence in the Kimmeridgian. The Goniodomaceae have their first occurrence in the Tithonian. Palaeoperidinioideae first occur and Dollidiniaceae and Comparodiniaceae have their last occurrence in the Valanginian (Lower Cretaceous). Stephanelytraceae have their last occurrence in the Aptian. Heterocapsaceae last occur in the Albian, however motile cells still live in the modern ocean (Fensome et al., 1993). In the Cenomanian (Upper Cretaceous) Dinogymnioideae first occur, and Pareodiniaceae have their last occurrence. The Santonian sees the first occurrence of the  
80 Protoperidinioideae. The Ceratiaceae have their last occurrence at the end of the Maastrichtian. In the Danian (Paleocene), Wetzelielloideae have their first occurrence, the youngest subfamily to appear in the cyst record. Dinogymnioideae have their last occurrence in the Selandian, however motile cells of this subfamily still swim around in the modern ocean (Fensome et al., 1993). The Palaeoperidinioideae, Cladoxyxiaceae and Wetzelielloideae have their last occurrence in the Chattian (Oligocene). The Areoligeraceae have their last occurrence in the Burdigalian (Miocene). The Tortonian sees the last  
85 occurrence of the Leptodinioideae, and the Messinian the last occurrence of the Deflandreoideae.

The counts of oldest first occurrences and youngest last occurrences through time (Fig. 3) provide a rough indication of the amount of turnover within that (sub)family, although for here caution must be taking not to overinterpret the data. Unlike previous overviews of dinoflagellate cyst evolution the overview presented here is strictly *not* intended to represent dinoflagellate diversity through time. This has several reasons. First of all, dinocyst diversity does not necessarily reflect  
90 biological diversity of dinoflagellates, as only 10% of modern dinoflagellates include a cyst-phase in their life cycle (Bravo and Figueroa, 2014). It is impossible to assess whether this fraction of cyst-producing dinoflagellates has changed through time. Yet, the representation of many dinoflagellate families in the fossil record of dinocysts (Fig. 3) does suggest that a cyst-phase was ubiquitous among a wider scope of dinoflagellate taxa in the past. Second, and on top of the above, many entries in DINOSTRAT have only a first occurrence or last occurrence logged, not both (because of their long range or because of  
95 calibration limitations), which prevents assessing the full stratigraphic range of many species, and therefore, prevents the assessment of total diversity through time. Incorporating more publications, e.g., those with perhaps poorer independent age control, could in the future result in a more complete database of full ranges of cyst taxa but would compromise the reliability of entries. Thirdly, interpreting what dinoflagellate cyst turnover would mean for the paleobiology of dinoflagellates remains complex due to the apparent ability for dinocyst (sub)families to switch cyst formation on and off: the Cladopyxiaceae,  
100 Nannoceratopsiae and Dinogymniae are known as modern motile cells (Fensome et al., 1993) yet their stratigraphic occurrence



as cysts in the fossil record ended long before modern times (Fig. 3). Finally, and most importantly, dinoflagellate cyst taxonomy is not a biological but a morphological taxonomy, whereby it remains a question to what extent morphological species of cysts are produced by genetically distinctly different dinoflagellate species. On genus level, defining morphological differences comprise more fundamental characteristics related to plate tabulation (Fensome et al., 1993), and that gives more confidence that it reflects biological diversity. What the overview presented here does reflect at minimum is how important certain dinoflagellate cyst subfamilies are for chronostratigraphy in any particular time interval.

The stratigraphic ranges of dinocyst (sub)families (Fig. 3) from DINOSTRAT match closely the dinocyst diversity plot of (Fensome et al., 1996). This was expected, as both syntheses probably use overlapping literature resources as basis for the inferred dinoflagellate evolution. DINOSTRAT delivers a verifiable, reproducible database, that underpins dinoflagellate evolution, and that is updated to the most recent Geologic Time Scale. It provides a platform that allows iterative improvement of the communities' collective knowledge of dinoflagellate cyst biostratigraphy. The similarity to other overviews of evolution (Fensome et al., 1996) demonstrates the completeness of the DINOSTRAT database.

## 5 Data and code availability

DINOSTRAT version 2.0-GTS2020, including R-code to make the figures, is available on Github and Zenodo (Bijl, 2023a);  
http://dx.doi.org/10.5281/zenodo.7791273.

## 6 Supplements

Supplementary figures are available in (Bijl, 2023b) for those not familiar with R programming:

- Paleolatitude distributions of dinocyst (sub-)families (2034 plots)
- Paleolatitude distributions, stratigraphic ranges and distribution maps of dinocyst genera (470 plots)
- Paleolatitude distributions, stratigraphic ranges and distribution maps of dinocyst species (28 plots)
- Paleolatitude distributions of modern dinocyst species (95 plots)
- Stratigraphic ranges of dinocysts per site (211 plots)

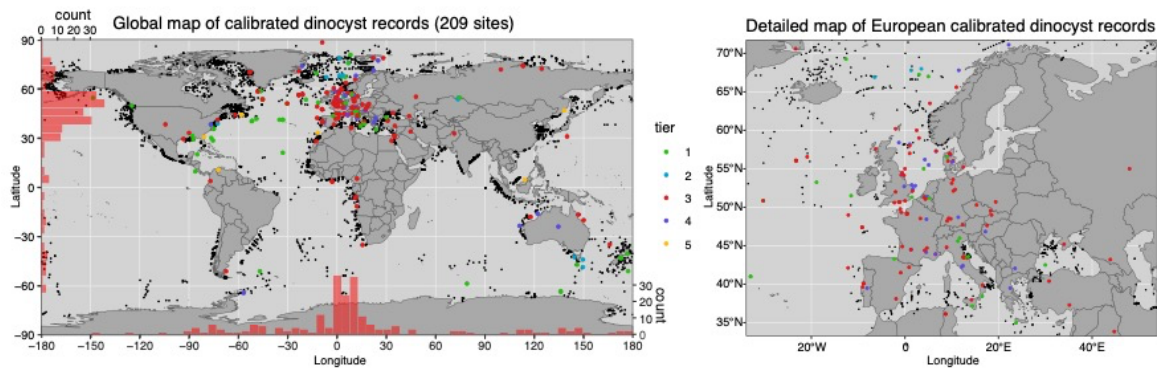
## 7 Competing interests

Author declares no conflict of interest



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130 **Figure 1:** Map of sites included in DINOSTRAT version 2.0-GTS2020. Maps produced using ggplot in R (Wickham, 2016).

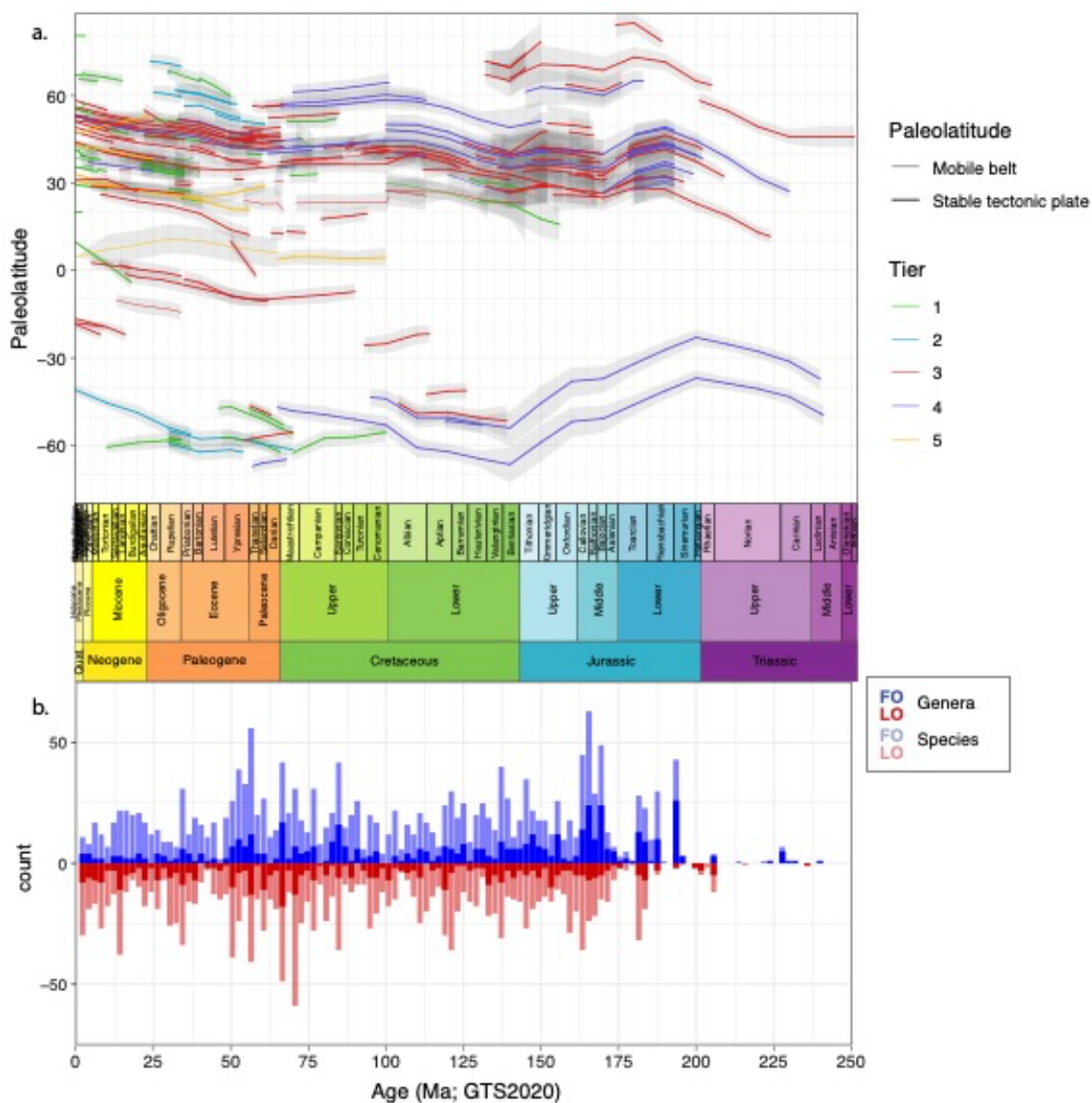
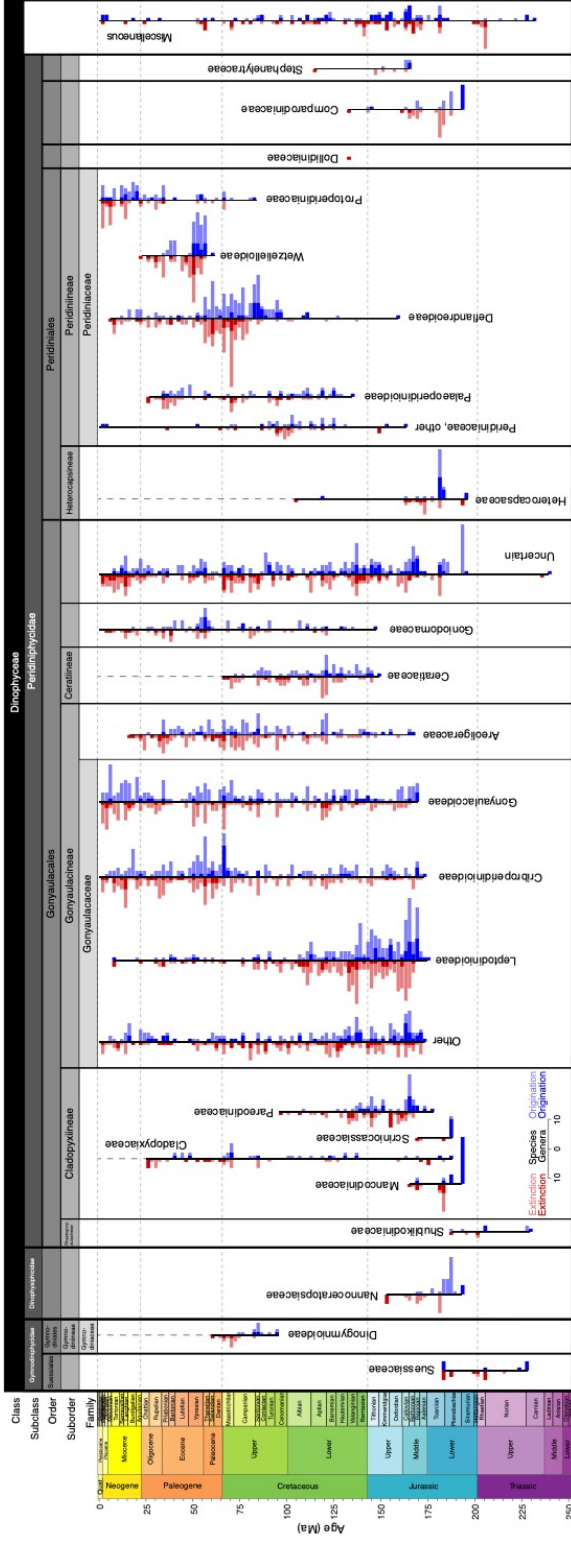


Figure 2: a Paleolatitude through time of sites used in DINOSTRAT version 2.0-GTS2020. b. The number of oldest first occurrences and youngest last occurrences of dinocyst species, plotted in 2Myr bins. Plot produced using ggplot in R (Wickham, 2016).



DINOSTRAT: Dinoflagellate cyst biostratigraphy and evolution







← **Figure 3: Number of dinoflagellate cyst species and genera oldest first occurrence and youngest last occurrence, plotted per dinoflagellate cyst (sub)family, in 2 Myr bins.**

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