DINOSTRAT version 2.0-GTS2020

Peter K. Bijl

Department of Earth Sciences, Utrecht University, 3584 CB, Utrecht, the Netherlands

Correspondence to: Peter K. Bijl (p.k.bijl@uu.nl)

Abstract. Mesozoic–Cenozoic organic-walled dinoflagellate cyst (dinocyst) biostratigraphy is a crucial tool for relative and numerical age control in complex ancient sedimentary systems. However, stratigraphic ranges of dinocysts are found to be strongly diachronous geographically. A global compilation of state-of-the-art calibrated regional stratigraphic ranges could assist in quantifying regional differences and evaluate underlying causes. DINOSTRAT (Bijl, 2023a; Bijl, 2023b) is an open source, iterative, community-fed database intended to house all regional chronostratigraphic calibrations of dinocyst events. DINOSTRAT version 2.0 includes >9,450 entries of first and last occurrences (collectively called "events") of >2,040 dinocyst taxa, and their absolute ties are now updated to the chronostratigraphic timescale of Gradstein et al., 2020. Entries are derived from 211 publications and 209 sedimentary sections. DINOSTRAT interpolates paleolatitudes of regional dinocyst events, allowing evaluation of the paleolatitudinal variability of dinocyst event ages. DINOSTRAT allows for open accessibility and searchability, on region, age, and taxon. This paper presents a selection of the data in DINOSTRAT: (1) the (paleo)latitudinal spread and evolutionary history of modern dinocyst species; (2) the evolutionary patterns and paleolatitudinal spread of dinocyst (sub)families; (3) a selection of key dinocyst events which are particularly synchronous. Although several dinocysts show – at the resolution of their calibration – quasi-synchronous event ages, indeed many species have remarkable diachroneity. DINOSTRAT provides the data storage approach by which the community can now start to relate diachroneity to (1) inadequate tie to chronostratigraphic timescales; (2) complications in taxonomic concepts and (3) ocean connectivity and/or the affinities of taxa to environmental conditions.

1 Introduction

Over 50 years of research efforts have established a framework to use organic-walled dinoflagellate cysts (dinocysts) as biostratigraphic and chronostratigraphic tools. Dinocyst biostratigraphy is particularly applied to sediments which are difficult to date otherwise, such as restricted, nearshore marine settings (e.g., Poulsen, 1994; Iakovleva et al., 2001; Sliwinska et al., 2012; Clyde et al., 2014), and polar regions (e.g., Sluijs et al., 2006; Bijl et al., 2013a; Houben et al., 2013; Radmacher et al., 2015; Śliwińska et al., 2020; Nøhr-Hansen et al., 2020). As with all biostratigraphy, the reliability of dinocyst biostratigraphy heavily depends on the accuracy, precision, and regional consistency of the numerical ages of first and last stratigraphic occurrences (FOs and LOs, hereafter jointly referred to as "events") of easily recognized taxa. Through the past decades,

Formatted: Dutch

Deleted: DINOSTRAT: A global database of the stratigraphic and paleolatitudinal distribution of Mesozoic-Cenozoic organic-walled dinoflagellate cysts

Deleted: Utrecht,

Deleted: For this reason,

Deleted: here initiated –

Deleted: (https://github.com/bijlpeter83/DINOSTRAT.git)

Deleted: 1.0

Deleted: 8500

Deleted: 1900

Deleted: time scale

Deleted: 2012

Deleted: 199

Deleted: 188

Deleted: time scale

Deleted: /

Deleted: (e.g.,

Deleted: Poulsen et al., 1994; Brinkhuis et al., 1998; Iakovleva et al., 2001; Śliwińska et al., 2012; Clyde et al., 2014)

Deleted: (e.g.,

Formatted: English (US)

Field Code Changed

Deleted: Sluijs et al., 2006; Bijl et al., 2013a; Houben et al., 2013; Radmacher et al., 2015; Śliwińska et al., 2020; Nøhr-Hansen et al., 2020) numerical ages of dinocyst events have become increasingly better chronostratigraphically constrained, using independent age control from magnetostratigraphy (e.g., Brinkhuis et al., 1992; Powell et al., 1996), other biostratigraphic tools (e.g., Davey, 1979; Leereveld, 1997b, a; Oosting et al., 2006; Awad and Oboh-Ikuenobe, 2016), and astrochronology (Versteegh, 1997). However, efforts to compile a global chronostratigraphic calibration of dinocyst events revealed strong diachroneity for many species between broad latitudinal bands, and endemism of many species within latitudinal bands (e.g., Williams et al., 2004). Because this impacts the development of quasi-global dinocyst zonation schemes, as have been proposed for other microfossil groups (e.g., Martini, 1971; Gradstein et al., 2020), the question is how the research field of dinocyst biostratigraphy should progress.

Two questions arise from the notion of geographic diachroneity of dinocyst events:

- What kind of error or uncertainty should be applied to the numerical ages of events? Now that diachroneity has been demonstrated, the next step is to quantify the uncertainty in numerical ages of dinocyst events for each species, and to assess regional consistency. This is particularly important when calibrated species ranges are geographically extrapolated over large distances. And a related question: What is the impact of regional variability in numerical ages of events on the regional consistency of the stratigraphic order of events?
- What are the underlying causes for the observed diachroneity? Broadly, 3 reasons could apply: (1) inaccurate or inadequate tie-in of dinocyst events to the chronostratigraphic timescale, which leads to apparent (but perhaps false) diachroniety of species events between sites; (2) complexities in taxonomic concepts could obscure comparison of species ranges between sites. This aspect relates to the ease by which subtle morphological differences between species can be recognized (e.g., Hoyle et al., 2019). It also relates to the question whether the last occurrence of a fossil dinocyst taxon reflects extinction of its producer, adjustment of cyst morphology by its producer (Rochon et al., 2009), or a change in its life cycle strategy (e.g., towards less-preservable pellicle cysts; Bravo and Figueroa, 2014); (3) finally, paleoenvironmental and paleoceanographic conditions can impact species occurrence: ocean connectivity (Van Simaeys et al., 2005; Bijl et al., 2013b; Van Helmond et al., 2016), leads and lags in the biotic response to climate change (Sluijs et al., 2007) or the temperature affinity of dinocyst taxa (Van Simaeys et al., 2005; Van Helmond et al., 2016). For instance, in geologic time intervals of global climate cooling, warm-loving plankton species have diachronous last occurrences which are progressively later at lower latitudes. A good example is the modern occurrence in the western Pacific warm pool of *Dapsilidinium pastielsii*, a species that was long thought to be extinct in the Pliocene (Head et al., 1989). This example serves as an indicator that asynchronous biostratigraphic events could actually be the result of paleoceanographic or paleoecologic influences, rather than just biostratigraphic error.

A process towards answering these, and improving the accuracy of dinocyst biostratigraphy, requires a data compilation approach that incorporates data from as many sites as possible, with detailed metadata on paleogeographic evolution of sites, and the means of chronostratigraphic calibration. It further requires that such data compilations are constantly updated with

Formatted: Dutch

Deleted: (e.g.,

Deleted: Brinkhuis et al., 1992; Powell et al., 1996)

Deleted: (e.g., Davey, 1979; Leereveld, 1997a,b; Oosting et al., 2006; Awad and Oboh-Ikenobe, 2019)

Deleted: (Versteegh, 1997)

Deleted: (e.g., Williams et al., 2004)

Deleted: (e.g.,

Deleted: Martini, 1971; Gradstein et al., 2020)

Deleted: time scale

Deleted: (e.g., Hoyle et al., 2019)

Deleted:

Deleted: (e.g., Rochon et a., 2009)

Deleted:

Deleted: (e.g., towards less-preservable pellicle cysts; Bravo and Figueroa, 2014)

Deleted: /

Deleted: (Van Simaeys et al., 2005; Bijl et al., 2013b; Van Helmond et al., 2016)

Deleted:

Deleted: (Van Simaeys et al., 2005; Van Helmond et al., 2016)

Deleted:

Deleted: (Head et al., 1989)

Formatted: Dutch

new insights: updated geologic timescales and bio- magnetostratigraphic zonation schemes, altered taxonomic concepts, age models of sections, stratigraphic sections. A complication on a logistical front, is that dinocyst ranges are typically published in the closed-access peer-review literature, which are not easily accessible to all, are inconsistent in their approach, and not easily updated with new insights.

Deleted: time scale

This paper initiates DINOSTRAT, an open-source, online platform intended to house, disseminate, and iteratively update all published chronostratigraphic calibrations of dinocyst ranges: the way in which they are tied to the chronostratigraphic timescale and the (paleo-) geographic position of the site from which they were calibrated. DINOSTRAT version 2.0-GTS2020 (Bijl, 2023a) currently contains over 9,450 entries of first and last occurrences of over 2,043 dinocyst taxa to the international timescale. These entries originate from 211 peer-reviewed papers presenting data from 209 sites. Including as many reports or sites as possible, with verifiable independent age control, and their latitudinal evolution through time, allows for proper evaluation of error and uncertainty. DINOSTRAT will allow assessment and quantification of regional variability and/or consistency in event ages and provides the basic information to evaluate the paleoceanographic signal that diachroniety may hold. Open accessibility of the basic dinocyst stratigraphic data will further allow a proper evaluation and update of evolutionary patterns in dinocyst families (Fensome et al., 1996) with full disclosure of the underlying data. The approach to the selection of appropriate data, entry and calculations of ages and paleolatitudes is explained in Section 2. Section 3 presents examples of calibrated dinocyst events: the stratigraphic and paleolatitudinal distribution of selected modern dinocysts, and that of extant and extinct dinocyst families, with selected taxa highlighted. Section 4 discusses the implications of the DINOSTRAT approach and future directions. This paper represents the start of a community-fed data assembly approach to iteratively improve regional constraints on dinocyst biostratigraphy.

Deleted: time scale

Deleted: 1.0

Deleted: 8500

Deleted: 1900

Deleted: time scale

Deleted: 199

Deleted: 188

Deleted: /

Deleted: /

Deleted: (MacRae et al., 1996)

2 Approach

DINOSTRAT version 2.0-GTS represents an updated compilation of dinocyst events from peer-reviewed literature, with a publication date predating 1 March 2023 (Table 1 provides a list of papers added to the previously published DINOSTRAT version 1.0 (Bijl, 2022)). The taxonomic nomenclature, supra-generic classification and synonymy cited in Williams et al., (2017) is followed. One inherent assumption in DINOSTRAT is that the authors of the reviewed literature have applied a consistent taxonomic framework. DINOSTRAT reports events of dinocyst species as they were presented in the papers, but applying the synonymy index of Williams et al. (2017). Most dinocyst species are easily recognized, have a stable morphology (both regionally and through time) and clearly defined species concepts. However, some species (and subspecies) diagnoses are more subtle or represent endmembers in a continuum (Hoyle et al., 2019), in part imposed by environmental conditions (Ellegaard, 2000). Some authors tend to lump species in complexes, while others split into subspecies. The international recognition of these lumps and splits may have evolved through time, and may have restricted, regional significance only. Therefore, subtle differences in species concept interpretation may exist between authors and regions, which the current approach was unable to account for, and is considered a next step, when individual studies or sites are revisited.

Deleted: 1

Deleted: January

Deleted: 1st,

Deleted: 1

Deleted: see

Deleted: the initial setup of

Deleted:

Deleted: (e.g., Hoyle et al., 2019)

Deleted:

Deleted: (e.g., Ellegaard, 2000)

For the subfamily Wetzelielloideae, DINOSTRAT deviates from the taxonomic index of Williams et al. (2017). The fundamental redefinition of species concepts in the taxonomic revisions for the Wetzelielloideae (Williams et al., 2015) eliminates many stratigraphically useful Eocene dinocyst taxa (Bijl et al., 2017). Therefore, for this subfamily, the calibration of dinocyst species is presented in the taxonomic classification of Wetzelielloideae prior to Williams et al. (2015).

Table 1. New papers added to DINOSTRAT version 2.0-GTS2020. Reference, Geography, Age base and Age top (in Ma), Tier (see DINOSTRAT version 1.0; Bijl, 2022) 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

Formatted: Dutch

Deleted:

Deleted: Williams et al. (2017)

Deleted:

Deleted: (Bijl et al., 2016)

(Vieira and Mahdi, 2022)	Norway	85	62	3	Calibrated to stages with information from nannofossils

A decision tree has been used to determine which papers to include in DINOSTRAT (Fig. 1). This tree first discards studies in which dinocysts were the only stratigraphic tool to date the sequence. Although these papers do provide valuable information on stratigraphic order of events, discarding them from this review eliminates the risk of circular reasoning and inherited chronostratigraphic ties. Only those dinocyst events are included that could be calibrated against a stratigraphic tool that can be traced back to the bio-, magneto- or chronozones in the Geologic Time Scale 2020 (GTS2020; Gradstein et al., 2020). This decision tree can be used to define five tiers of reliability in these papers (Fig. 1):

- Tier 1 studies present dinocyst events along with magnetostratigraphic constraints obtained from the same sedimentary section. The interpretation of magnetochrons from the paleomagnetic signal was done without the use of dinocyst biostratigraphy. Since magnetic reversals are globally synchronous, evaluating the synchroneity of dinocyst events with use of paleomagnetostratigraphy is most robust.
- Tier 2 studies present dinocyst events calibrated along with compromised or problematic magnetostratigraphic constraints on the same sedimentary section, for instance when the inclination signal suffers from a strong overprint, or when the magnetochron assignment is not clear. Studies in which dinocyst events served as biostratigraphic tool for magnetochron assignment are included in this tier as well.
- Tier 3 studies report dinocyst events together with biostratigraphic zones (from nannoplankton, foraminifer or ammonite zones), identified in the same sequence. These studies provide clear reports on the identification of these zones in the sequence.
- Tier 4 studies report dinocyst events with biostratigraphy, of which either the derivation is unclear, or the tie to the GTS (e.g., for outdated ammonite zonations), or biostratigraphic data does not come from the same sequence, but, for example, has been interpreted from nearby outcrops.
- Tier 5 studies report dinocyst events with independent chronostratigraphy, of which the derivation is unverifiable, or represents a regional synthesis.

Formatted: Dutch

Formatted

Deleted: **Table 1: Papers used in this review. Reference, Geography, Age base and Age top (in Ma), Tier (see Figure 1) and means of calibration to the Geologic Time Scale (GTS). For the meaning of the acronyms of the microplankton zones indicated in the column "Calibrated to" the reader is referred to the GTS2012 (Gradstein et al., 2012.¶**
Reference ... [1]

Deleted: 2012

Deleted: (GTS2012

Deleted: ;

Deleted: Gradstein et al., 2012)

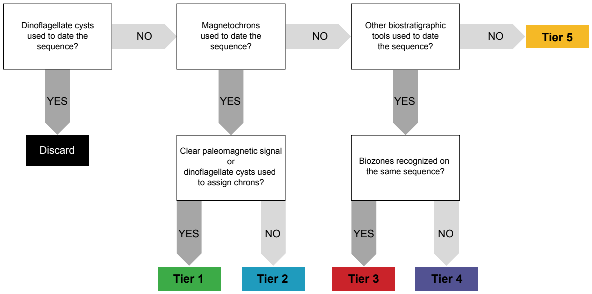

Figure 1: Decision tree for including studies in this review, and categorization criteria for the 5 tiers.

The numerical age of each dinocyst event is not explicitly entered into DINOSTRAT. Rather, its position within the zone it was calibrated to is entered. Ages are subsequently calculated via linear interpolation between these tie points, as follows:

[FO/LO] of [Genus, Species] = [##]% in ([stratigraphic tool]$[zone]) (1)

in which [##]% is linearly interpolated between base (0%) and top (100%) of tie points, and [stratigraphic tool]$[zone] is the name of the zone in the bio-magneto- or chronozonation in GTS2020 in which the dinocyst event falls. The rationale behind this approach instead of simple entry of the age is that while the numerical ages of dinocyst events are dependent on the evolving knowledge of the chronostratigraphic timescale, the stratigraphic position of the event relative to the tie points in the record is fixed. This approach makes it easier to update the ages of the dinocyst events when the ages of the chrono-, magneto- and biozones are updated in the future. If dinocyst events fall between two different stratigraphic ties, the event is noted as follows:

[FO/LO] of [Genus, Species] = [##]% between [##]% in [stratigraphic tool]$[zone] and [##]% in [stratigraphic tool]$[zone] (2)

Outdated Jurassic and Cretaceous ammonite zonation schemes have been converted first to those presented in the GTS2012 (see Bijl, 2022). The GTS2020 adjusted ammonite zonations further (Gale et al., 2020), which resulted in additional adjustments of calibrations of dinocyst events, notably in the Cretaceous (see Bijl, 2023a for specific adjustments made) FOs in the bottom of sections, and LOs at the top of sections are systematically omitted, unless they were specifically indicated to

Formatted: Dutch

Deleted: [stratigraphic tool] is the bio, magneto or chronozonation in the GTS2012, and [zone] is the name of the zone, chron or stage in which the dinocyst event falls.

Deleted: time scale

Deleted: GTS2012

Deleted:

Deleted: Supplement 1; following

Deleted: Ogg and Hinnov, 2012a, b and citations therein

Formatted: Dutch

represent an FO or LO. More recent publications presenting calibrations of dinocyst species from the same section overwrite older publications. Extant dinocyst species and their latitudes (from Marret et al., 2020; Mertens et al., 2014; Thöle et al., 2022) are entered with an LO of 0 Ma ("modernst.csv" in Bijl, 2023b for surface sediment station locations, "modernsp.csv" in Bijl, 2023b for dinocyst species at those stations).

Deleted: (from

Deleted: Marret et al., 2020, and Mertens et al., 2014 for *Dapsilidinium pastielsii*)

Each event entry in DINOSTRAT ("Dinoevents_FEB_23.csv" in Bijl, 2023b) includes the (paleo-) latitude of that event. This is interpolated using the age of the event and its location, which has a paleolatitude evolution through time ("Paleolatitude.csv" in Bijl, 2023b; with use of Paleolatitude.org, last access 10 May 2023; Van Hinsbergen et al., 2015). Paleolatitudes of sites in mobile orogenic belts are interpolated using regional tectonic reconstructions, and as such are prone to additional latitudinal uncertainty.

Deleted: Jan2021

Deleted:

Deleted: Bijl, 2021

Deleted:

Deleted: Bijl, 2021

Deleted:

Deleted: Van Hinsbergen et al., 2015

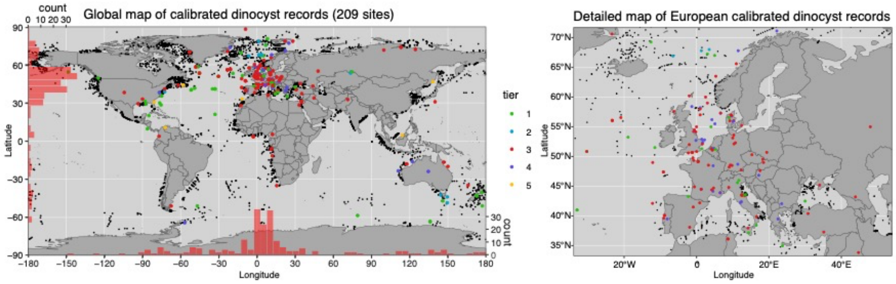

Figure 2: Present-day geographic distribution of sedimentary sequences used in DINOSTRAT (colors of the dots correspond to the to the tier status to which the site has been allocated), and surface sediment stations (in black dots; Marret et al., 2020; Mertens et al., 2014; Thöle et al., 2022). A. Global. Red scale bars on x and y axes represent number of sites in longitudinal and latitudinal bins, respectively B. Detailed map of sites in Europe.

Deleted: (in grey dots;

Deleted: Marret et al., 2020 and Mertens et al., 2014)

Deleted: /

Deleted: per

Deleted: /

3 The database

3.1 Sites

DINOSTRAT version 2.0-GTS2020 contains dinocyst events from 211 publications and 209 sites. The wider North Atlantic and European area is strongly overrepresented (Fig. 2). Few sites are from the Pacific, South Atlantic and Indian Ocean, and the equatorial region. This probably reflects a genuine bias in the available information, because of focus of the community

Deleted: currently

Deleted: 199

Deleted: 188

Deleted: /

Deleted: Ocean

Deleted: s

Deleted: ern

towards economically interesting regions (e.g., for hydrocarbon industry). It may also in part reflect a bias towards research from developed nations, and poor accessibility of publications from non-western societies.

The paleolatitudinal position of the sites through time confirms the strong over-representation of Northern Hemisphere mid-latitude sections (Fig. 3), and underrepresentation of the tropical regions, Pacific Ocean and southern mid-latitudes. The Paleogene has the largest latitudinal spread of records. The Mesozoic in particular has few entries from the Southern Hemisphere or equatorial regions. The Mesozoic records are predominantly calibrated to ammonite stratigraphy (tiers 3 and 4), and in some occasions to magnetostratigraphy (tiers 1 and 2; Fig. 3). Ammonite zones presented in the papers often had to be converted to those in the GTS2020, which is not always straightforward, as the zone definitions have changed through time (Hesselbo et al., 2020; Gale et al., 2020). The ammonite zonations are prone to strong endemism and regional diachroniety which was demonstrated particularly for the late Jurassic (Hesselbo et al., 2020). This may create a level of circular reasoning when dinocyst events are calibrated against these zones, because diachronous dinocyst events in DINOSTRAT may be the result of diachronous ammonite zones rather than actually being diachronous dinocyst events.

3.2 Calibrated dinocyst events

DINOSTRAT version 2.0 includes over 9,450 entries of calibrated dinocyst events (excluding the modern dinocyst database). On a species level, originations in DINOSTRAT peak in the middle Jurassic (Bajocian–Callovian) the Early Cretaceous (late Valanginian–Barremian) and the Eocene (Ypresian; Fig. 3b). Extinctions peak in the Early Cretaceous (Berriasian–Barremian), Late Cretaceous (Maastrichtian), Oligocene (Rupelian) and Miocene (Serravalian; Fig. 3b). This pattern is generally followed on a generic level, which likely has a stronger relation to the biologic diversity than dinocyst species diversity (Fensome et al., 1993).

The interpolated paleolatitudes for dinocyst events in DINOSTRAT allows detailed evaluation of the latitudinal synchroneity of dinocyst events. This paper presents a selection of the data in DINOSTRAT, focusing on the stratigraphic and geographic range of modern dinocyst species, of dinocyst (sub)families and of a selection of quasi-synchronous dinocyst events. Users can filter DINOSTRAT per locality (to present the stratigraphic order of events per site) and/or per taxon (to see the geographic variability of the range of any taxon), to serve their purposes.

Formatted: Dutch

Deleted: T

Deleted: GTS2012

Deleted: (

Deleted: Ogg and Hinnov, 2012a, b)

Deleted: (Ogg and Hinnov, 2012

Deleted: b)

Formatted: Not Highlight

Deleted: 1

Deleted: 8500

Deleted: upper

Deleted:

Deleted: (Fensome et al., 1993)

Deleted: /subfamilies

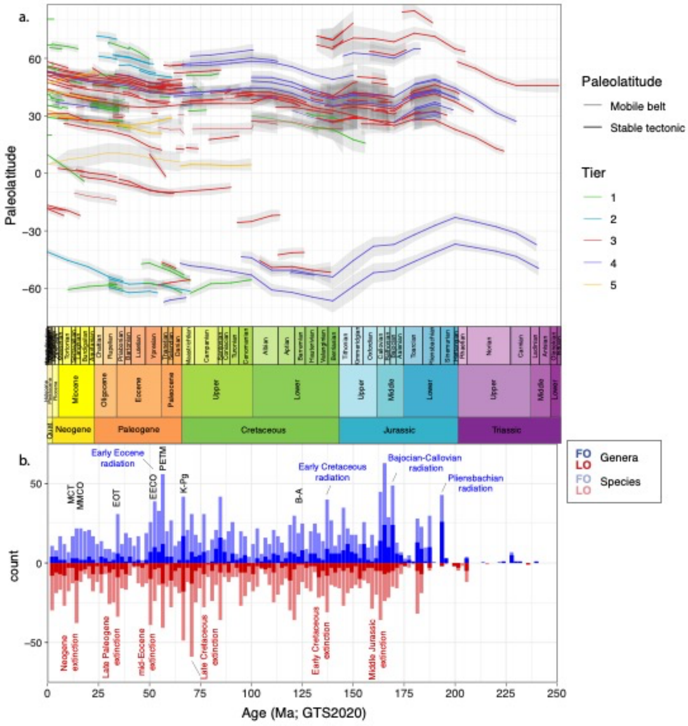

Figure 3: Data in DINOSTRAT version 2.0-GTS2020. a. Paleolatitude and age span of sites used in DINOSTRAT. Colors corresponds to tier, line thickness separates sites on stable oceanic or continental plates from those in mobile orogenic belts. Grey envelopes represent the error of the paleolatitude reconstruction inherited from the paleomagnetic reference frame (Van Hinsbergen et al., 2015). b. Dinocyst events in DINOSTRAT, filtered for oldest FOs (blue) and youngest LOs (red) of dinocyst species (lighter shade) and genera (darker shade), in 2 Myr bins. Several phases of climatic-environmental change are highlighted in black: Barremian-Aptian boundary (B-A), Cretaceous-Paleogene boundary (K-Pg), Paleocene-Eocene Boundary (PETM), Early Eocene Climatic Optimum (EECO), Eocene-Oligocene transition (EOT), mid-Miocene Climatic Optimum (MMCO), Miocene climatic transition (MCT). Extinction and radiation phases in dinocysts are highlighted in red and blue text, respectively.

Formatted: Dutch

Formatted: Normal, Line spacing: single

Formatted: Font: Bold

Deleted: (see Van Hinsbergen et al., 2015

Deleted:)

3.2.1 The stratigraphic range of modern dinocyst species

Modern dinocysts from surface sediment samples ((Marret et al., 2020), n=3600 and (Mertens et al., 2014), n=5, (Thöle et al., 2022), n=66) have a species-specific latitudinal spread. Sea surface temperature and nutrient conditions are the main controlling factors on modern assemblage compositions (Zonneveld et al., 2013). The database presented here allows comparison of modern latitudinal spread of these species to that of the past, and their age and latitude of oldest first occurrence (Supplement, and a selection in Fig. 4). Most modern species that have entries in DINOSTRAT have originations in the mid-Cenozoic: *Impagidinium* species, *Operculodinium centrocarpum*, *Tectatodinium pellitum*, *Tuberculodinium vancampoae* (Fig. 4). *Lingulodinium machaerophorum* has a first occurrence around 60 Ma. The exception is *Spiniferites ramosus*, a generalist species with a robust morphology through time, that has a remarkably consistent FO in the Berriasian (~145 Ma; Fig. 4). The dinocyst species that have geographic distributions restricted to one hemisphere today were also latitudinally restricted in the geologic past (e.g., *Spiniferites elongatus*, *Trinovantedinium variabile*; Fig. 4). *Achomosphaera andalousiensis, Dapsilidinium pastielsii, Impagidinium velorum, Melitasphaeridium choanophorum, Tectatodinium pellitum, Tuberculodinium vancampoae* had wider latitudinal distributions until the recent past, across both hemispheres. *Melitasphaeridium choanophorum* had progressively older LOs north and south of its restricted modern latitudinal distribution in northern mid-latitudes. *Lingulodinium machaerophorum* and *Polysphaeridium zoharyi* had a higher paleolatitudinal occurrence on only one hemisphere. Several modern taxa (e.g., *Bitectatodinium spongium*, *Polykrikos* spp., *Echinidinium* spp., most *Islandinium*

Formatted: Dutch

Deleted: Marret et al., 2020

Deleted:

Deleted: (Zonneveld et al., 2013)

Deleted: 2

Deleted: , *Protoperidinium* spp.

Formatted: Dutch

species, most *Stelladinium* species, *Polarella glacialis*) have no entry yet in DINOSTRAT. This could be because some species concepts are relatively novel or have poor preservation potential in the fossil record (Zonneveld et al., 2010).

Deleted: (e.g., because of selective degradation;

Deleted: Zonneveld et al., 2010)

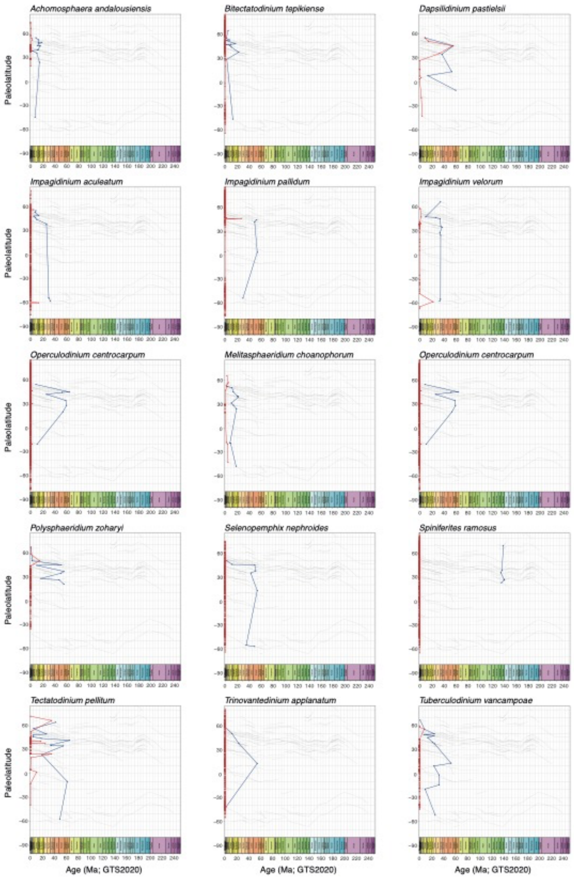

Figure 4: Age and paleolatitude of first (in blue) and last (in red) occurrences of selected modern dinocyst species. Last occurrences come from both the surface sediment database (Marret et al., 2020; Mertens et al., 2014; Thöle et al., 2022) and entries in DINOSTRAT.

Deleted: ¶

Formatted: Font: Bold

Deleted: (Marret et al., 2020, with Mertens et al., 2014)

3.2.2 Dinocyst (sub)families

Range charts of the sites in DINOSTRAT are provided in the supplements (see “Sites” folder in (Bijl, 2023b)). The age over paleolatitude entry in DINOSTRAT allows evaluation of the latitudinal difference in event ages for each individual species in DINOSTRAT (n=2043), as well as for groupings per genus (n=470) and family (n=28; see Supplement). Users can produce and adapt these plots themselves with help of the R markdown script “stratigraphy plots.R” in Bijl, 2023b). The most robust dinocyst events will have synchronous ages of FOs and LOs per paleolatitude (i.e., vertical blue and red lines in the plots in the Supplement (Bijl, 2023b)). The FOs and LOs connected per species and grouped in (sub)families are plotted and described below, with particularly synchronous taxa highlighted. The purpose of these plots is threefold: first, they show the total stratigraphic range and latitudinal spread of these dinoflagellate (sub)families, and time intervals when and where phases of strong diversification and extinction occurred in that (sub)family. Second, as with the plots of modern species, they show in which paleolatitudes these supra-generic groups first appear, but also where they last became extinct. Although earlier compilations of the evolution of dinocyst families do exist (Fensome et al., 1996), DINOSTRAT presents the fundamental spatio-temporal observations that underpin these compilations. Thirdly, the plots allow presentation of the database in a way that the validity of extrapolating dinocyst events on a supra-regional scale can be critically evaluated in the discussion.

Order Gonyaulacales

Family Areoligeraceae (Fig. 5)

Range. Areoligeraceae range from the Bathonian (~168 Ma, FOs of *Adnatosphaeridium* spp. and *Senoniasphaera* spp.) to the Burdigalian (~16 Ma, LO of *Glaphyrocysta reticulosa*). Areoligeraceae seem to range longer in Northern Hemisphere (NH) mid-latitudes (FO ~168 Ma; LO ~16 Ma) than in the rest of the world (FO ~145 Ma; LO ~36 Ma), although this can be in part related to a sampling bias. The oldest FOs in NH mid-latitudes are species with a stratigraphic occurrence restricted to that area.

Quasi-synchronous events. The events of species of *Areoligera, Chiropteridium, Glaphyrocysta, Palynodinium, Schematophora* and *Senoniasphaera* are quasi-synchronous, particularly in the late Cretaceous and Paleogene (Fig. 5). Many taxa in this subfamily however show strongly diachronous events between hemispheres.

Formatted: Dutch
Deleted: **(sub-) f**
Deleted: Supplement
Deleted: 2
Deleted: 1914
Deleted: 460
Deleted:) (
Deleted: 2
Deleted: /
Deleted: plot creator.Rmd
Deleted:
Deleted: Bijl, 2021
Deleted: of
Deleted: 2
Deleted:
Deleted: (e.g., MacRae et al., 1996)
Deleted: *e*
Deleted: the
Deleted: mid-Miocene
Deleted: 8
Deleted: *Chiropteridium galea*
Deleted: 169
Deleted: 8
Deleted: :
Formatted: Font: Not Italic
Formatted: Font: Not Italic

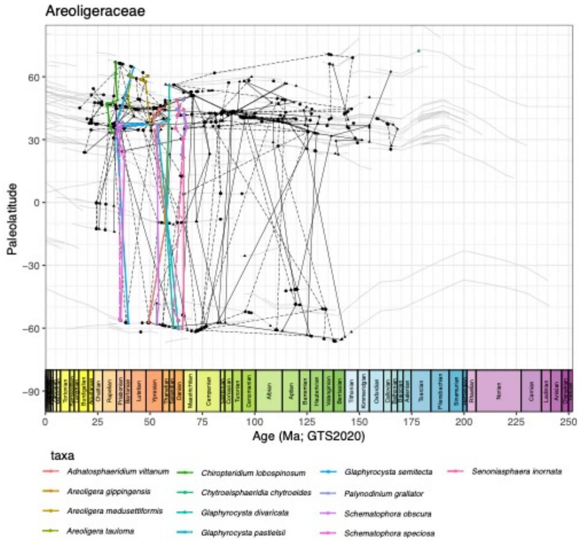

Figure 5: Ages and paleolatitudes of first (solid line and triangles) and last (dashed line and circles) occurrences of dinocyst species of the Family Areoligeraceae. Solid and dashed lines connect first and last occurrences, respectively, for each species, between sites. Colored lines represent quasi-synchronous species events.

Family Ceratiaceae (Fig. 6)

Range The Ceratiaceae first appear in the Tithonian (~149 Ma, FO of *Muderongia simplex*) in NH mid-latitudes, represents a diverse group in the Early Cretaceous and has an LO in the latest Cretaceous (~66 Ma, LO of *Odontochitina operculata*).

Quasi-synchronous events The LO of *Odontochitina costata,* LO of *Phoberocysta neocomica,* the range of *Pseudoceratium pelliferum* are quasi-synchronous (Fig. 6).

Formatted: Dutch

Deleted: :

Deleted: 152Ma

Deleted: :

Formatted: Font: Not Italic

Formatted: Dutch

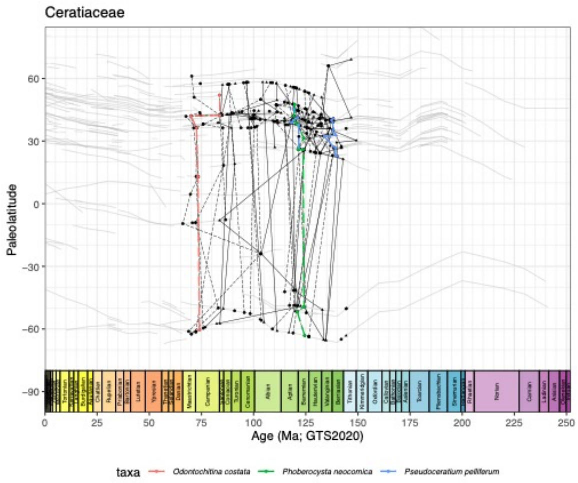

Figure 6: As Figure 5, but for the Family Ceratiaceae.

Family Cladopyxiaceae (Fig. 7)

Range. This family first appears in the Pliensbachian (~188 Ma, FO of *Freboldinium* spp.), and ranges until the late Oligocene (~25 Ma; *Licracysta semicirculata*).

Deleted: :

Quasi-synchronous events. Several species of *Enneadocysta*. LO of *Fibradinium annetorpense* around 60 Ma and the LO of *Licracysta semicirculata* around 26 Ma are quasi-synchronous. Most entries in the Late Cretaceous and Paleogene are highly diachronous.

Deleted: :

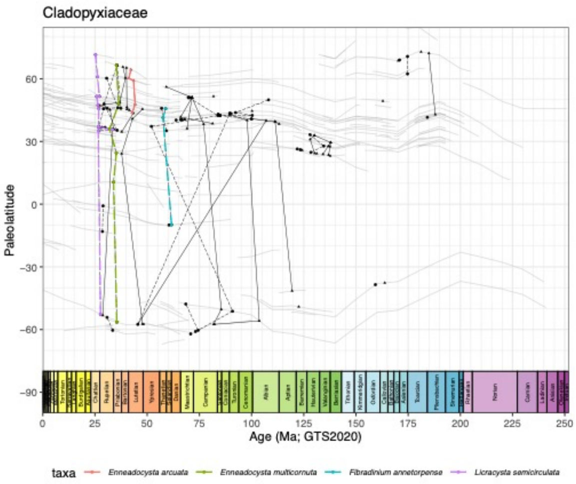

Figure 7: As Figure 5, but for the Family Cladopyxiaceae.

Family Goniodomaceae (Fig. 8)

Range. Goniodomaceae first appear in the mid-Tithonian (~147 Ma, FO of *Hystrichosphaeridium petilum*) in the NH mid-latitudes, most entries are from the Paleogene, and continue with modern species *Polysphaeridium zoharyi* and *Tuberculodinium vancampoae*.

Quasi-synchronous events. Species of *Alisocysta, Eisenackia, Heteraulacacysta* and *Homotryblium* are quasi-synchronous. Many species ranges in this family are notably diachronous. Although some species do seem to show similar event ages between southern hemisphere (SH) high and NH mid-latitudes (Fig. 8), those with multiple entries in the NH mid-latitudes, where site density is highest, show strong diachroneity over short latitudinal distances. Modern species have a restricted latitudinal spread to subtropical and tropical regions, but not too long into the geologic past species of this family exhibited much wider latitudinal ranges (65°S – 70°N).

Formatted: Dutch

Deleted: *Range:*

Deleted: 150

Deleted: *Quasi-synchronous events:*

Deleted: s

Deleted: northern

Formatted: Dutch

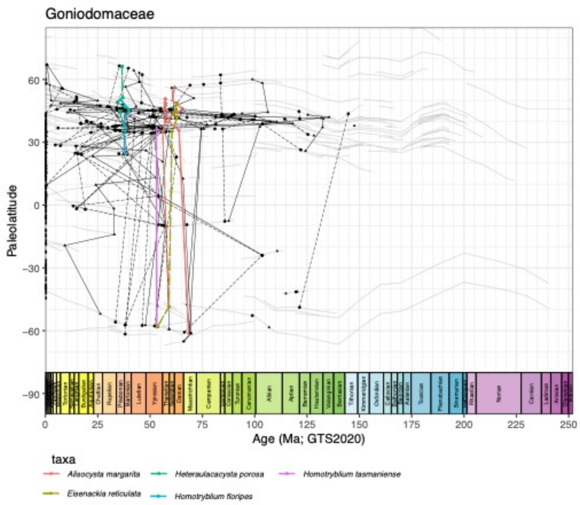

Figure 8: As Figure 5, but for the Family Goniodomaceae.

Family Gonyaulacaceae

Subfamily Cribroperidinioideae (Fig. 9)

Range. This subfamily includes the extant species *Operculodinium centrocarpum* and *Lingulodinium machaerophorum*. The subfamily first appears in NH mid-latitudes in the Aalenian (~173 Ma) with *Kallosphaeridium* spp. and in the Bajocian (~169 Ma) with *Cribroperidinium* spp., and shortly thereafter *Aldorfia* and *Korystocysta*. *Cribroperidinium* is a long-ranging genus. Many entries are from the early Cretaceous (~125 Ma) and early Paleogene (66–34 Ma).

Deleted: *Range:*

Deleted: t

Deleted: 2

Quasi-synchronous events. Several species of *Cordosphaeridium* and *Danea*, and species of *Aldorfia*, *Apteodinium, Carpatella, Cooksonidinium, Diphyes, Hystrichokolpoma* and *Operculodinium* are quasi-synchronous. The subfamily has many entries in the Paleogene, but many of these events are not synchronous latitudinally.

Deleted: *Quasi-synchronous events:*

Deleted: s

Deleted: .

Formatted: Dutch

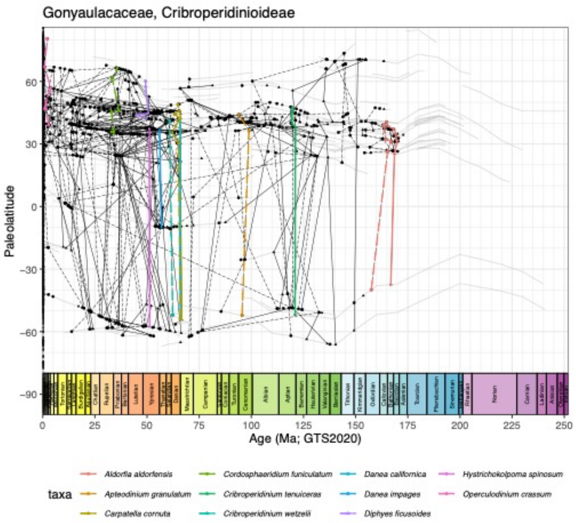

Figure 9: As Figure 5, but for the Family Gonyaulacaceae, subfamily Cribroperidinioideae.

Deleted: **Gonyaulacoideae**

Subfamily Gonyaulacoideae (Fig. 10)

Range. the subfamily of Gonyaulacoideae includes common modern cyst genera such as *Spiniferites* spp., *Achomosphaera* spp., *Impagidinium* spp., *Nematosphaeropsis* spp. and *Tectatodinium* spp. The subfamily first occurs in the Bajocian (~170 Ma), with the FO of *Gonyaulacysta* spp. and *Tubotuberella* spp.

Deleted: *Range:*

Quasi-synchronous events. Species of *Achomosphaera, Ataxiodinium, Callaiosphaeridium, Corrudinium, Ectosphaeropsis Hystrichodinium, Impagidinium, Spiniferites* and *Unipontidinium* seem quasi-synchronous (Fig. 10). Events of species of *Escharisphaeridia* spp., *Gonyaulacysta* spp., and *Tubotuberella* spp., range slightly longer in NH high latitudes than in mid-latitudes. Many species in this subfamily are strongly diachronous.

Deleted: *Quasi-synchronous events:*

Deleted: s

Deleted: Northern Hemisphere

Formatted: Dutch

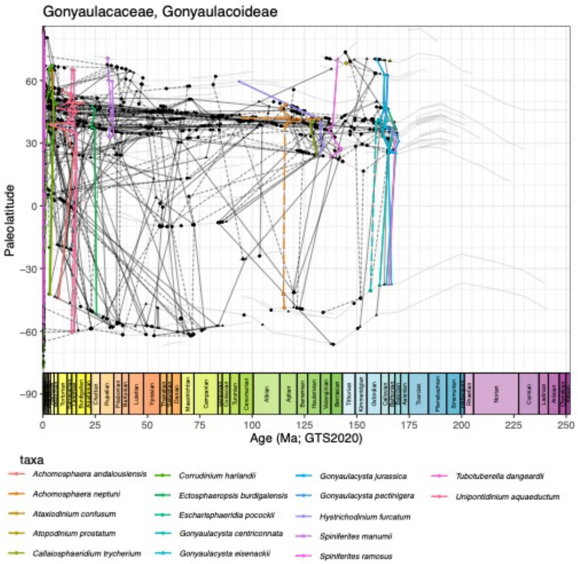

Figure 10: As Figure 5, but for the Family Gonyaulacaceae, subfamily Gonyaulacoideae.

Subfamily Leptodinioideae (Fig. 11)

Range. Leptodinioideae first appear in the Aalenian (~175 Ma, FO of *Meiourogonyaulax valensii*), and includes many species events in the Bajocian and Bathonian. Although most entries are in the Jurassic and Early Cretaceous, the subfamily ranges into the late Miocene (~8 Ma, LO of *Acanthaulax miocenica*).

Deleted: *Range:*

Deleted: 2

Quasi-synchronous events. Events in species of *Ambonosphaera*, *Areosphaeridium* (NH), *Cooksonidium, Ctenidodinium, Dichadogonyaulax, Endoscrinium, Herendeenia, Kleithriasphaeridium, Leptodinium*, *Limbodinium, Litosphaeridium*, *Rigaudella aemula*, *Sirmiodiniopsis*, *Stiphrosphaeridium* and *Wanaea* seem quasi-synchronous.

Deleted: *Quasi-synchronous events:*

Deleted: events

Deleted: .

Formatted: Font: Not Italic

Formatted: Dutch

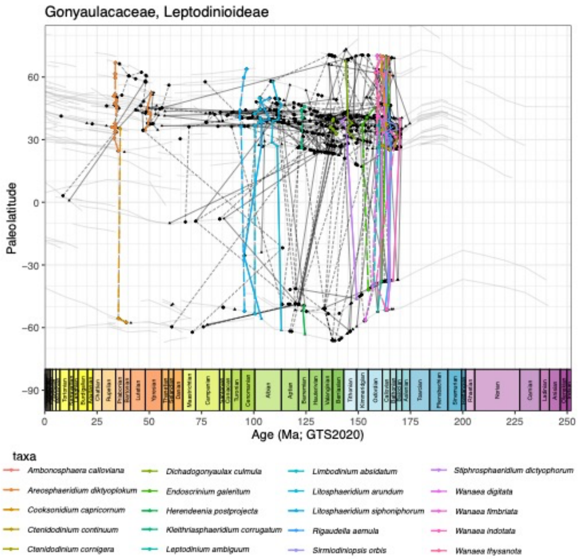

Figure 11: As Figure 5, but for the Family Gonyaulacaceae, subfamily Leptodinioideae.

Deleted: **Gonyaulacoideae**

Family Gonyaulacaceae, other (Fig. 12)

Remarks. Other species in the Family Gonyaulacaceae could not be assigned to a subfamily. Species of *Barbatacysta*, *Chytroeisphaeridia*, *Glossodinium*, *Hemiplacophora, Nelchinopsis, Saturnodinium, Scriniodinium*, *Sepispinula, Stephodinium, Trichodinium* spp. have remarkably consistent events.

Deleted: :

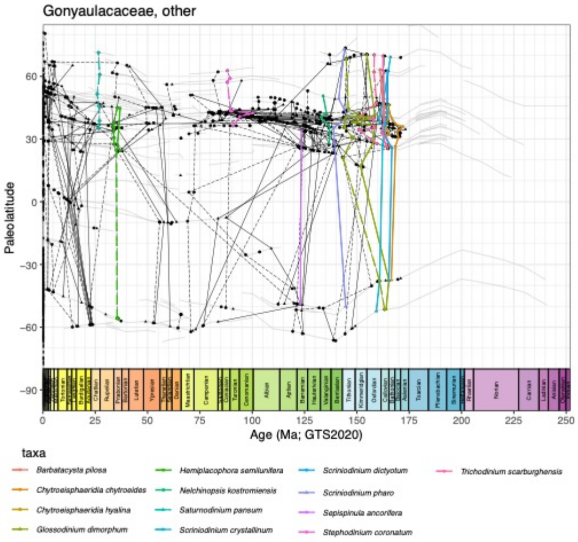

Figure 12: As Figure 5, but for other genera in the Family Gonyaulacaceae.

Family Mancodiniaceae (Fig. 13)

Range. species of Mancodiniaceae occur in sediments from the Pliensbachian (~193 Ma) to the mid-Bathonian (~166 Ma) and seem quasi-synchronous latitudinally.

Formatted: Dutch

Deleted: **Gonyaulacoideae**

Deleted: *Range:*

Deleted: late Sinemurian

Deleted: 0

Deleted: 7

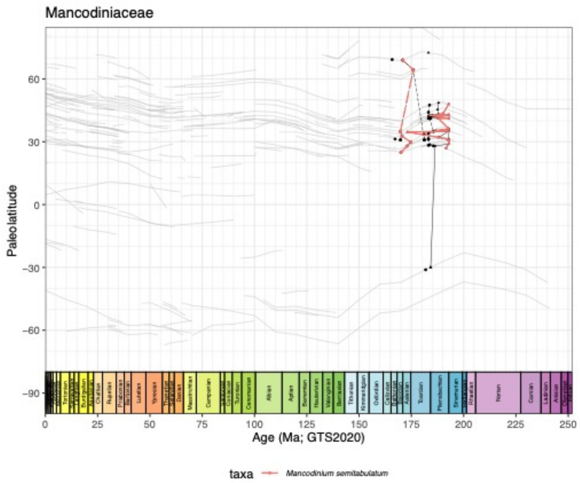

Figure 13: As Figure 5, but for the Family Mancodiniaceae.

Family Pareodiniaceae (Fig. 14)

Range. Pareodiniaceae first appear in the late Toarcian (~178 Ma, FO of *Pareodinia halosa*) and range in NH mid-latitudes into the Cenomanian (~96 Ma, LO of *Batioladinium jaegeri*). Events of species in *Carpathodinium, Pareodinia* (both NH only), *Aprobolocysta* and *Batioladinium* appear quasi-synchronous.

Formatted: Dutch

Deleted: *Range:*

Deleted: 6

Deleted: 5

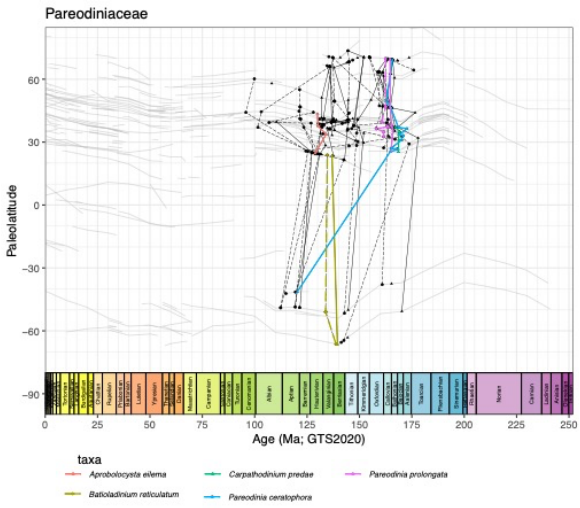

Figure 14: As Figure 5, but for the Family Pareodiniaceae.

Family Scriniocassiaceae (Fig. 15)

Range. Scriniocassiaceae range from the Pliensbachian (~188 Ma, FO of *Scriniocassis weberi*) to the Bajocian (~170 Ma, LO of *Scriniocassis weberi*) and comprise of only 3 species. Events from this family are only reported from the NH.

Formatted: Dutch

Deleted: *Range:*

Deleted: 7

Deleted: 69

Deleted: Northern Hemisphere

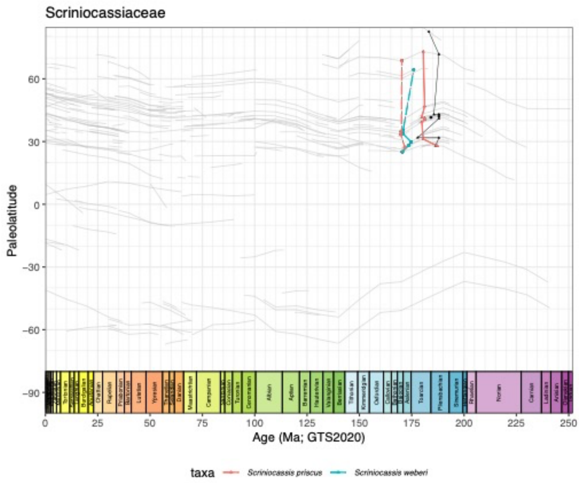

Figure 15: As Figure 5, but for the Family Scriniocassiaceae.

Family Shublikodiniaceae (Fig. 16)

Range. Cysts from the Family Shublikodiniaceae occur in the late Triassic (FO of *Rhaetogonyaulax wigginsii* in the Carnian, ~229 Ma) to early Jurassic (LOs of *Dapcodinium sacculus* and *Dapcodinium ovale* in the mid-Pliensbachian, 188 Ma). *Quasi-synchronous events.* The LO of *Rhaetogonyaulax rhaetica* close to the Triassic-Jurassic boundary, LO of *Dapcodinium priscum* are quasi-synchronous.

Formatted: Dutch

Deleted: *Range:*

Deleted: c

Deleted: 230

Deleted: 7

Deleted: *Quasi-synchronous events:*

Deleted: .

Formatted: Dutch

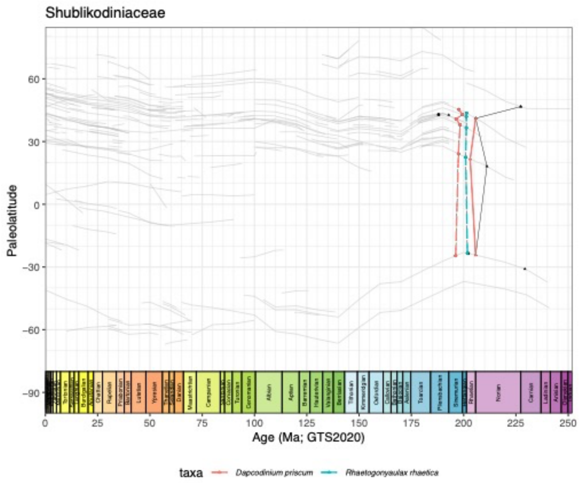

Figure 16: As Figure 5, but for the Family Shublikodiniaceae.

Family uncertain (Fig. 17)

Remarks: this group of which the family is uncertain does contain several stratigraphically synchronous species (Fig. 17). Ranges of species of *Amiculosphaera*, *Atopodinium, Batiacasphaera, Cleistosphaeridium, Dingodinium, Distatodinium, Heslertonia, Labyrinthodinium, Membranilarnacia, Mendicodinium, Oligokolpoma* and *Valensiella* are quasi-synchronous.

Deleted: *idi*

Formatted: Dutch

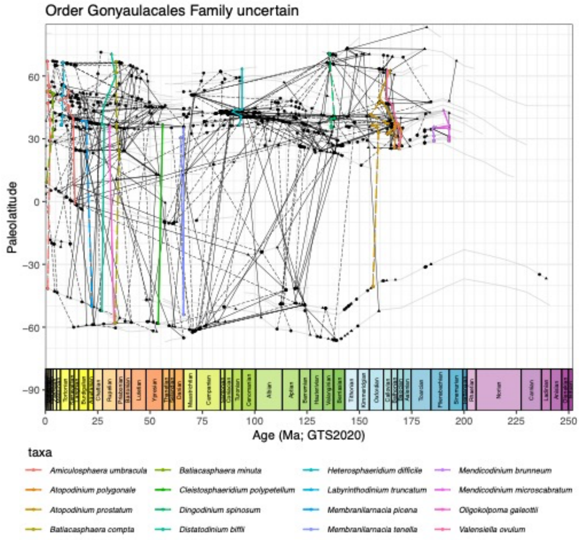

Figure 17: As Figure 5, but for the Order Gonyaulacales, Family uncertain.

Order uncertain

Family Comparodiniaceae (Fig. 18)

Range. cysts from this family range from the Pliensbachian (193 Ma, FO of *Valvaeodinium* spp.) to the mid-Valanginian (133 Ma, LO of *Biorbifera johnwingii*). All species except *Valvaeodinium spinosum* and *Biorbifera ferox* have ranges restricted to the NH.

Quasi-synchronous events. The range of *Biorbifera johnwingii*, FO of *Valvaeodinium spinosum*, LO of *Valvaeodinium koessenium* are quasi-synchronous.

Deleted: *Range:*

Deleted: late Sinemurian

Deleted: 1

Deleted: 134

Deleted: Northern Hemisphere

Deleted: *Quasi-synchronous events:*

Deleted: R

Deleted: .

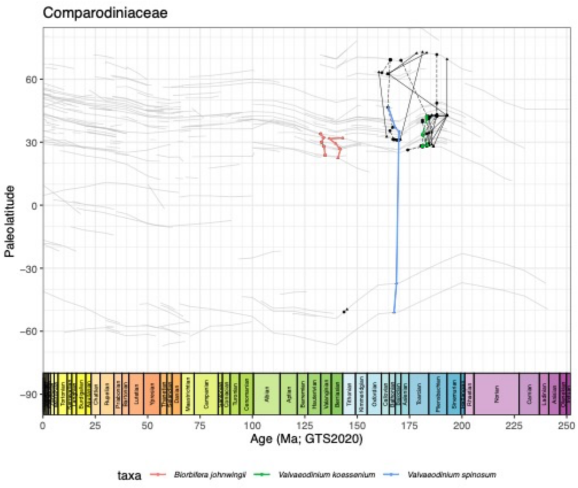

Figure 18: As Figure 5, but for the Family Comparodiniaceae.

Family Stephanelytraceae (Fig. 19)

Range. Stephanelytraceae cysts comprise of one genus, which ranges from the Callovian (~165 Ma) to the late Aptian (~115 Ma) and seems quasi-synchronous.

Formatted: Dutch

Deleted: *Range:*

Deleted: 6

Deleted: 7

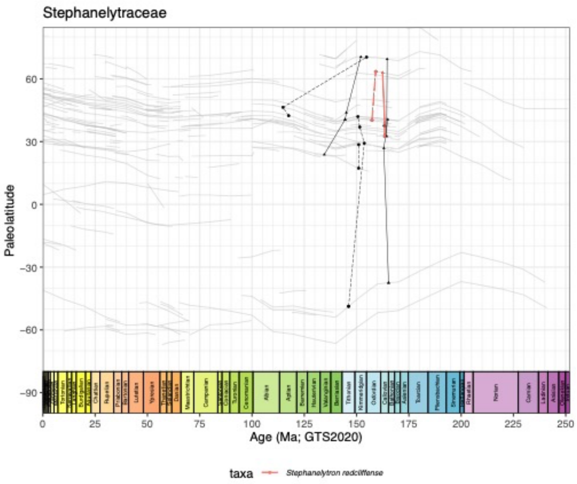

Figure 19: As Figure 5, but for the Family Stephanelytraceae.

Order Peridiniales

Family Heterocapsaceae (Fig. 20)

Range. Heterocapsaceae range from the mid-Sinemurian (196 Ma, FO of *Liasidium variabile*) to the mid-Albian (104 Ma, LO of *Angustidinium acribes*).

Quasi-synchronous events. The range of *Liasidium variabile* and *Parvocysta bullula*, restricted to NH mid-latitudes, are quasi-synchronous.

Formatted: Dutch

Deleted: *Range:*

Deleted: 5

Deleted: 5

Deleted: *Quasi-synchronous events:*

Deleted: *a*

Formatted: Dutch

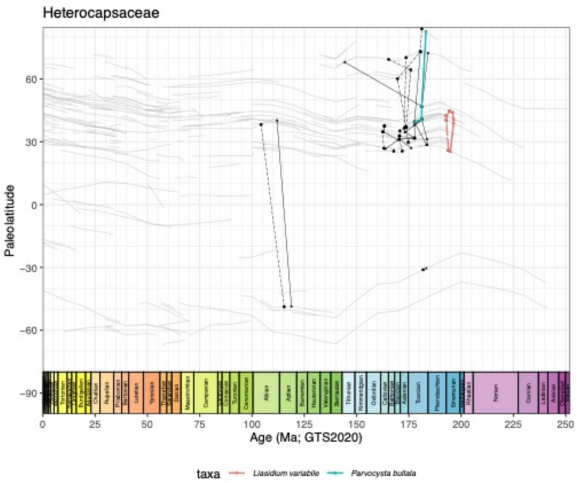

Figure 20: As Figure 5, but for the Family Heterocapsaceae.

Family Peridiniaceae

Subfamily Deflandreoideae (Fig. 21)

Deleted: e

Range. Deflandreoideae first occur on the Southern Hemisphere in the Oxfordian (~159 Ma) with *Pyxidiella* spp. *Isabelidinium* and *Eurydinium* first appear in the Albian (~109 Ma), and many species first appear in the Late Cretaceous (~95–66 Ma). The subfamily became extinct with the LO of *Sumatradinium* spp. around 6 Ma and appears to range longest in low and mid-latitudes. Deflandreoideae have many FO and LO entries in both hemispheres, particularly in the Late Cretaceous and early Paleogene.

Deleted: *Range:*

Deleted: 161

Deleted: 5

Deleted: e

Quasi-synchronous events. Several species of *Cerodinium*, *Manumiella, Trithyrodinium*, and *Isabelidinium* have quasi-synchronous events in the Maastrichtian-Paleocene (70–60 Ma).

Deleted: *Quasi-synchronous events:*

Deleted: s

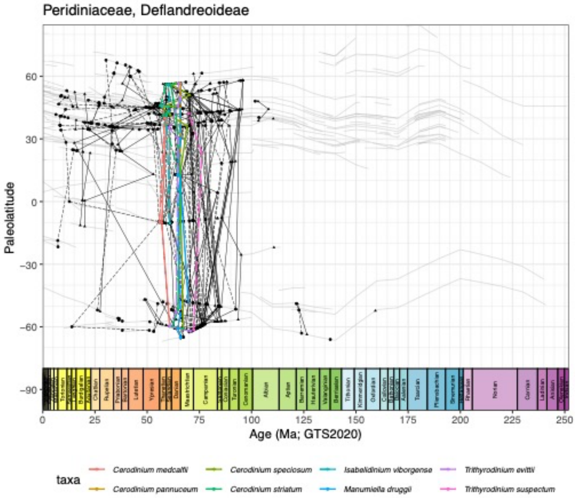

Figure 21: As Figure 5, but for the Family Peridiniaceae, subfamily Deflandreoideae.

Subfamily Palaeoperidinioideae (Fig. 22)

Range. The Palaeoperidinioideae range from the mid-Valanginian (~135 Ma, FO of *Subtilisphaera perlucida*) to the Chattian (~27 Ma, LO of *Phthanoperidinium comatum*).

Quasi-synchronous events. The range of *Palaeoperidinium pyrophorum* and the LO of *Phthanoperidinium comatum* are quasi-synchronous

Formatted: Dutch

Deleted: *Range:*

Deleted: t

Deleted: late Oligocene

Deleted: 6

Deleted: *Quasi-synchronous events:*

Deleted: .

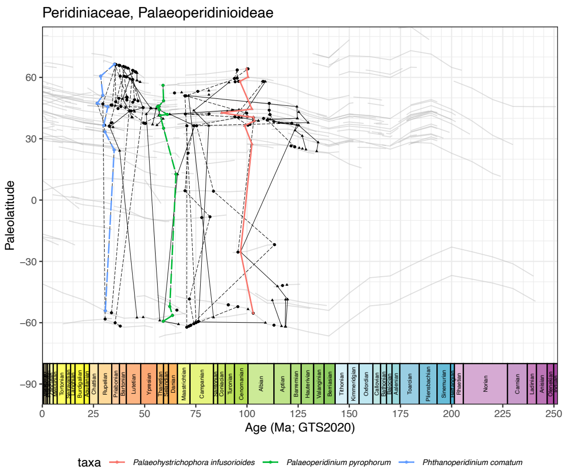

Figure 22: As Figure 5, but for the Family Peridiniaceae, subfamily Palaeoperidinioideae.

Subfamily Wetzelielloideae (Fig. 23)

Range. Wetzelielloideae range from the Selandian (~61 Ma, FO of *Apectodinium homomorphum*) to the Chattian (~23 Ma, LO of *Wetzeliella symmetrica*). Diversification particularly in the Ypresian leads to many species with short stratigraphic ranges, many of which are relatively synchronous latitudinally. Several species appear to range longer in the NH than on equal paleolatitudes on the SH. Many species lack chronostratigraphic ties in equatorial records.

Formatted: Dutch

Deleted: *Range:*

Deleted: mid-Paleocene

Deleted: 2

Deleted: late Oligocene

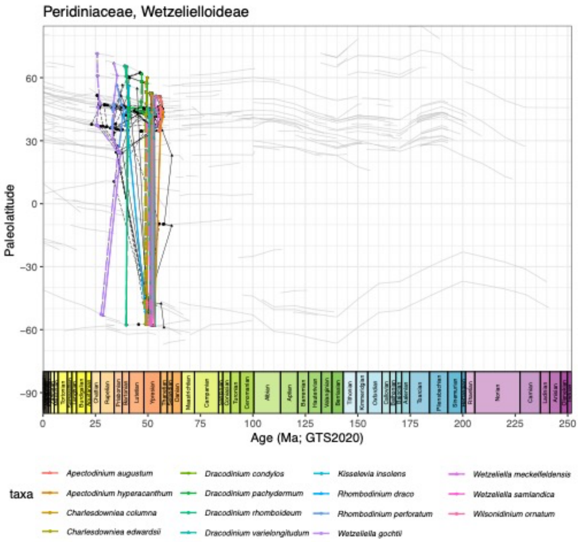

Figure 23. As Figure 5, but for the Family Peridiniaceae, subfamily Wetzelielloideae.

Family Peridiniaceae, other (Fig. 24)

Remarks. There is one quasi-synchronous event in this rest group: the FO of *Ovoidinium cinctum* around 124 Ma.

Formatted: Dutch

Deleted: :

Deleted: t

Deleted: 129

Formatted: Dutch

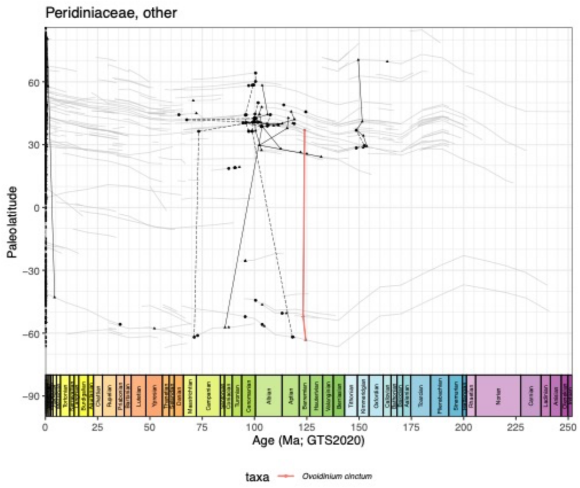

Figure 24: As Figure 5, but for other subfamilies in the Family Peridiniaceae.

Family Protoperidiniaceae (Fig. 25)

Range. Protoperidiniaceae first appear in the Santonian (~84 Ma; FO of *Phelodinium magnificum*) and range into the modern with 30 species in 13 genera, which is exceptionally diverse for modern cyst families. Species have oldest first occurrences in low latitudes than in high latitudes. Events are extremely diachronous.

Deleted: *Range:*

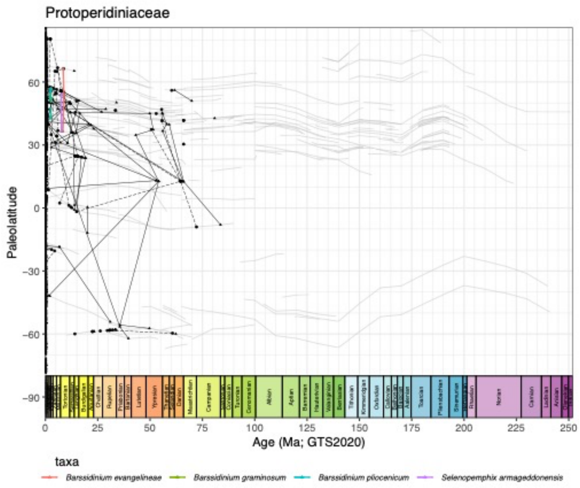

Figure 25: As Figure 5, but for the Family Protoperidiniaceae.

Order Nannoceratopsiales

Family Nannoceratopsiaceae (Fig. 26)

Range. Cysts from the Family Nannoceratopsiaceae occur from the Pliensbachian (193 Ma, FO of *Nannoceratopsis deflandrei* subsp. *senex*) to the mid-Kimmeridgian (~153 Ma, LO of *Nannoceratopsis pellucida*).

Formatted: Dutch

Deleted: *Range:*

Deleted: c

Deleted: late Sinemurian

Deleted: 1

Deleted: 5

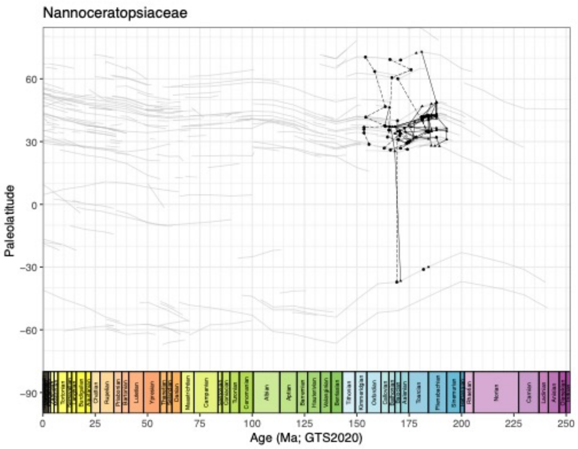

Figure 26: As Figure 5, but for the Family Nannoceratopsiaceae.

Order Ptychodiscales

Family Ptychodiscaceae (Fig. 27)

Range. This family only has entries in the Late Cretaceous (96–66 Ma), where species represent fairly synchronous stratigraphic markers. Although cysts are only found in a relatively short geologic time interval, motile cells of Ptychodiscaceae are known from modern plankton.

Formatted: Dutch

Deleted: *Range:*

Deleted: t

Deleted: 1

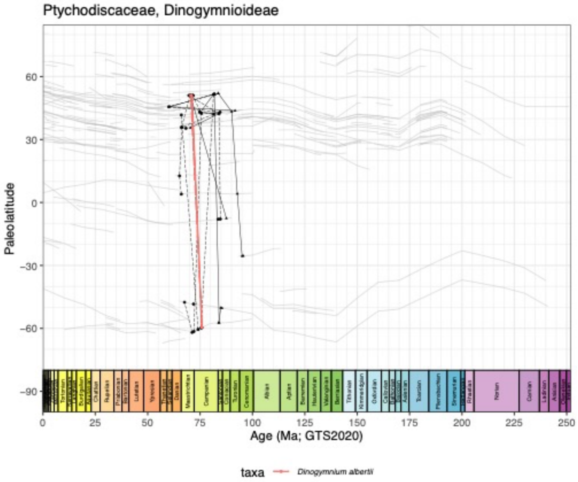

Figure 27: As Figure 5, but for the Family Ptychodiscaceae, subfamily Dinogymnioideae.

Order Suessiales

Family Suessiaceae (Fig. 28)

Range. Suessiaceae occur in the Carnian–Toarcian (228–183 Ma).

Quasi-synchronous events. The LO of *Suessia swabiana* is quasi-synchronous. Other events are highly diachronous.

Formatted: Dutch

Deleted: *Range:*

Deleted: Triassic

Deleted: Early Jurassic

Deleted: 9

Deleted: 2

Deleted: *Quasi-synchronous events:*

Formatted: Dutch

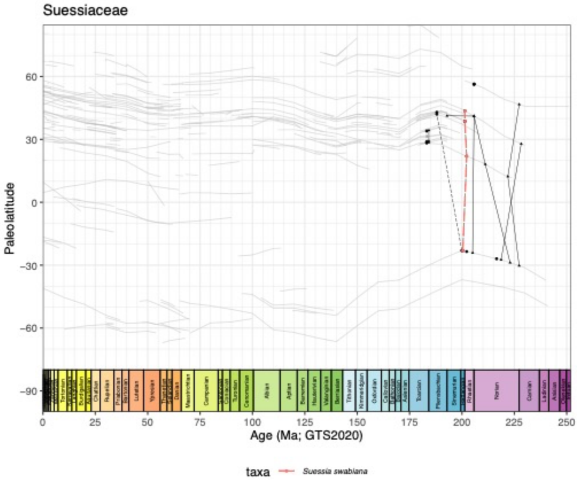

Figure 28: As Figure 5, but for the Family Suessiaceae.

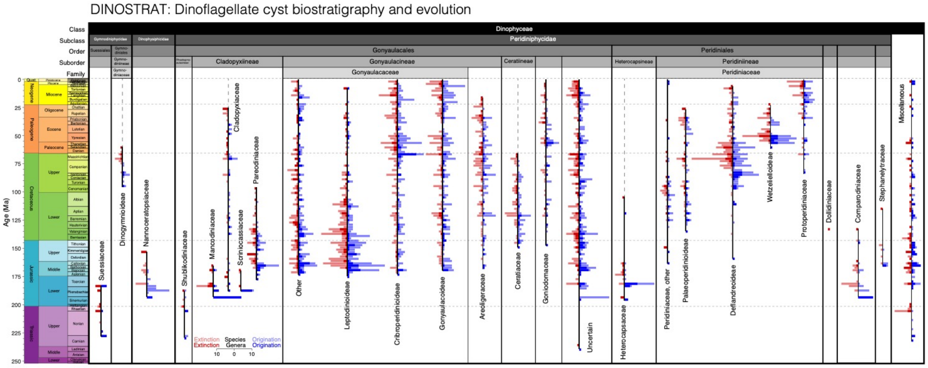

Figure 29: Overview of dinoflagellate evolution from the dinocyst record. Number of first and last occurrences of genera and species per dinocyst (sub)family through time.

Formatted: Dutch

4 Discussion

4.1 Geographic extrapolation of dinocyst events

A suite of dinocyst events throughout the entire stratigraphic record have quasi-synchronous ages across all latitudes (Fig. 5–28). Uneven geographic spread of data, with voids in the equatorial region and the Pacific Ocean, makes global synchroneity of these events highly uncertain. Still, the synchronous events confirm the potential and value of dinocyst biostratigraphy to date complex sedimentary systems. It also implies that ocean connectivity did allow dinocyst species to migrate globally, as far as their environmental tolerances permit.

Yet, the majority of dinocyst species have very diachronous ranges in DINOSTRAT, as well as latitudinally restricted geographic spreads, which confirms previous interpretations (Williams et al., 2004). By using DINOSTRAT the underlying causes of this diachroniety can now be further explored. The shortness of some of the records used in this review may lead to 'false' events, i.e., those that represent re-appearance or temporal disappearance rather than 'true' first or last occurrences (FO and LO, respectively). The obvious false FOs and LOs have been removed from DINOSTRAT by omitting events that occur at the base or the top of the sections. Particularly rare species, or those occurring at the end of their preferred environmental niche, come and go in stratigraphic sections, and these lead to 'false' events in DINOSTRAT. Although such 'false' FOs and LOs may obscure a uniform age of events over latitudes, they may still have important regional stratigraphic significance, which is why their entries are retained in DINOSTRAT. As a result, the age and region of the oldest FOs and youngest LOs have the most significance for reconstruction of evolutionary patterns. Although caving of material typically falsely increases the age of oldest FOs, this is unlikely a large influence on the entries in DINOSTRAT, as most studies come from core or outcrop material, and not from ditch cuttings, for which caving is much more likely. Reworking could falsely extend the age of youngest LOs of species. Although species that were reported as reworked in the papers have been omitted from DINOSTRAT, some reworked dinocysts could have been falsely identified as *in situ* in the original papers. It cannot be excluded that this causes some level of diachroniety in LOs, although this is unlikely a large factor.

Deleted:

Deleted: (Williams et al., 2004)

The complexity of taxonomic concepts in some dinocyst genera (species definitions, or morphological continua) hinders proper evaluation of latitudinal synchroneity of events. The reviewed literature covers 50 years, during which taxonomic concepts of dinocysts species have iteratively evolved. The extensive synonymy database of Williams et al. (Williams et al., 2017) does deliver crucial organization of the taxonomic framework. Still, some of the subtle morphological differences in species are limited to the expert eye of individual researchers, and these may not have been recognized by others (which occasionally led to the presentation of taxa on a generic level, instead of further specification to species level). Making the taxonomic framework consistent for all studies now included in DINOSTRAT would be a cardinal effort and will be part of the iterative setup of DINOSTRAT. For example, reviews of dinocyst taxonomic frameworks on a per-family basis, such as has been initiated for the *Spiniferites* complex (Mertens and Carbonell-Moore, 2018) could help adjusting inconsistencies in species concepts, and their stratigraphic occurrence. In any case, it must be stressed that the quality of any biostratigraphic marker is defined not

Deleted: (2017

Deleted:)

Deleted: (e.g., Mertens and Carbonell-Moore, 2018) only by the accuracy of the tie to the chronostratigraphic timescale, or global consistency of the age of FO or LOs, but also by their morphological distinctiveness.

Events may also appear diachronous in DINOSTRAT because of inadequate or inaccurate ties to the chronostratigraphic timescale. In such cases, minor diachroniety (~10^{4-5} years) may be related to the inherent assumption of linear sedimentation rates between age tie points. Larger diachroniety (~10^{5-6} years) may be because the zonation through which dinocyst events were calibrated to the chronostratigraphic timescale is diachronous. For calibrations against magnetostratigraphy (tiers 1 and 2) this is unlikely, and could occur only when magnetochrons were wrongly interpreted in the sites used. For events calibrated against Cenozoic nannoplankton and foraminifer zonations (in tiers 3 and 4) this is also unlikely, as these events are relatively robustly calibrated to chronostratigraphy (Watkins and Raffi, 2020). Less robust are the Mesozoic ammonite zonation schemes, which have shown to be quite latitudinally diachronous themselves (Hesselbo et al., 2020; Gale et al., 2020). The geographic variability in ages of zone boundaries, but also numerous adjustments of zone definitions throughout the past 50 years, further complicates accurate tie of dinocyst events with ammonite data to the GTS2020. So far, the majority of Mesozoic dinocyst events have been calibrated against these ammonite zonations, which makes their absolute tie to the chronostratigraphic timescale most uncertain. A major challenge for future versions of DINOSTRAT is to improve the independent age control of Mesozoic calibrated dinocyst events.

Also, ecological reasons could cause geographically diachronous events. When local environmental or depositional conditions change, assemblages adjust, which leads to local and temporal (dis)appearances of species that may be falsely interpreted as extinction or origination events. If so, dinocyst taxa associated to the most dynamic environmental niches on the continental shelf are expected to have the most diachronous events. Indeed, there are particularly diachronous events in Goniodomaceae and Protoperidinioideae – both families are associated with near-shore depositional settings (Zonneveld et al., 2013; Sluijs et al., 2005; Frieling and Sluijs, 2018), that are most environmentally dynamic. Settings in which these species occur offshore, such as upwelling regions (Sangiorgi et al., 2018), or hyperstratified waters (Reichart et al., 2004; Cramwinckel et al., 2019), are environmentally equally dynamic. In contrast, families typically associated with offshore conditions, such as the Wetzeliellioideae (Frieling and Sluijs, 2018) reveal much more synchronous events. For regional stratigraphy, the diachroniety is of less concern because these events can still be used for regional stratigraphic correlation (Vieira et al., 2020). It does mean that for such species, dinocyst biostratigraphy applies regionally, and caution should be taken to extrapolate event ages far outside of these regions. There are also species that clearly show regional inconsistency of origination or extinction ages because of climate change – e.g., *Melitasphaeridium choanophorum* had a much wider geographic distribution during warmer past climates and a progressively younger LO in lower latitudes as climate cooled (Fig. 4).

Diachroniety is usually larger between latitudinal bands than within latitudinal bands. The sparsity of records from the SH high latitudes complicates robust assessment of interhemispheric differences in dinocyst event ages. In the Mesozoic, the diachroneity is likely related to the inadequate calibration of events to the international timescale. DINOSTRAT is short of Mesozoic records that are tied to other stratigraphic tools than ammonites. For the Cenozoic, the diachroneity between hemispheres cannot be explained by inadequate calibration since many events are calibrated against magnetostratigraphy. For

Formatted: Dutch

Deleted: time scale

Deleted: time scale

Deleted: time scale

Deleted: (Watkins and Raffi, 2020; Petrizzo et al., 201

Deleted: 2)

Formatted: Not Highlight

Deleted: (e.g., Ogg and Hinnov, 2012a, b and references therein)

Deleted: GTS2012

Deleted: time scale

Deleted: (Zonneveld et al., 2013; Sluijs et al., 2005; Frieling and Sluijs, 2018)

Deleted: (Sangiorgi et al., 2018)

Deleted: (Reichart et al., 2004; Cramwinckel et al., 2019)

Deleted: (Frieling and Sluijs, 2018)

Deleted: time scale

those, environmental reasons must be at play. While in the early Paleogene many dinocyst events are quasi-synchronous (events within the Wetzeliellioideae, of *Cerodinium* and *Palaeoperidinium*), in the late Paleogene and Neogene diachroneity seems to become stronger. This may be in part because of stronger latitudinal temperature gradients as global average climate cools (Cramwinckel et al., 2018; Westerhold et al., 2020), which creates more diverse ecological niches and complicates latitudinal migration.

Many dinocyst species and higher generic ranks have their oldest first occurrence and youngest last occurrence in NH mid-latitudes (for example Areoligeraceae, Cladopyxiaceae, Comparodiniaceae, Goniodomaceae, Nannoceratopsiaceae, Palaeoperidinioideae, Wetzeliellioideae; Figs. 5, 7, 18, 8, 26, 22, 23). This may be because of a much higher density of records at those latitudes. However, the vast continental shelf area in Europe throughout the Mesozoic and much of the Cenozoic did likely serve as the perfect habitat for taxa to find a new niche and to linger on. A higher record density in SH and equatorial regions should shed light on this idea.

4.2 Evolutionary patterns in dinocyst (sub)families

DINOSTRAT refines with coherent, independent, open-access and up-to-date data, the evolutionary patterns presented previously (Fensome et al., 1996; Fensome et al., 1993), and adds their latitudinal distribution through time. Following up on 60 million years of experimentation in cyst-formation among a wide group of dinoflagellates (Fig. 29), gonyaulacoid dinocysts developed their most fundamental taxonomic features in a rapid diversity phase in the Bajocian (~169 Ma) likely on vast continental shelf areas on the European continent. The extremely high turnover in Gonyaulacoid dinocysts in the late Jurassic and Cretaceous is reflected in the density of the events in DINOSTRAT (Fig. 29). Peridinioid dinocyst taxa strongly proliferated in the Late Cretaceous and Paleogene (Fig. 29). The decline in dinocyst diversity in the Neogene is visible in the scarcity of FOs from 25 Myrs onwards (except in Protoperidinioideae). 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 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. 29) does suggest that a cyst-phase was ubiquitous among a wider scope of dinoflagellate taxa in the past. Second, many entries in DINOSTRAT have only a first occurrence or last occurrence logged, not both, which prevents assessing the full stratigraphic range of many species, and therefore, prevents the assessment of total diversity through time. Incorporating more publications 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 Cladopxiaceae, 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. 29). Finally, and most importantly, dinoflagellate cyst taxonomy is not a biological but a

Formatted: Dutch

Deleted: (Cramwinckel et al., 2018; Westerhold et al., 2020)

Deleted: (sub-) f

Deleted: presents for the first time a quantitative overview of stratigraphic and paleolatitudinal distribution of fossil and modern dinocyst taxa. Through that, it

Deleted:

Deleted: (e.g., Fensome et al., 1993; MacRae et al., 1996)

Deleted: (Figs. 13, 15, 16, 18–20, 26, 28)

Deleted: (Figs. 5, 9–12, 17)

Deleted: diversity

Deleted: g

Deleted: diversified

Deleted: (Figs. 21–25)

Deleted: DINOSTRAT allows to further explore spatial patterns in dinocyst evolution in the future.

Formatted: Dutch

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. 29) 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 demonstrates the completeness of the DINOSTRAT database.

4.3 Functionality of DINOSTRAT

Once downloaded, DINOSTRAT can be filtered by location, allowing users to compare newly generated dinocyst chronologies to nearby calibrated regional dinocyst events. DINOSTRAT can also be filtered by species, genus or higher taxonomic rank, for further evaluation of the latitudinal spread of any species of interest. The data in DINOSTRAT is readily visualized in the Supplement, and these plots can be adjusted and reproduced using the R markdown file "plot creator" in (Bijl, 2023a). The community is invited to contact the author either via email or through GitHub, with suggestions, error reports, and/or additional papers or data to be entered, so that the data content of DINOSTRAT is iteratively improved.

Deleted: 2

4.4 Future directions

DINOSTRAT will be regularly updated. Annual minor updates include addition of sites, adjustments in the current entries (e.g., through the feedback process), or minor revisions in taxonomy or stratigraphy. Major updates will occur in a 3-year cycle and will be the result of new geologic timescales, or profound revisions in dinocyst taxonomic concepts. Major updates will be accompanied by a short communication in this journal, minor updates will be communicated through the GitHub repository. Updates of the Geologic Time Scale (e.g., to GTS2020; Gradstein et al., 2020) will be implemented once the metadata of that Geologic Time scale have become available. All versions of DINOSTRAT will remain archived on GitHub.

Deleted: /

Deleted: G

Deleted: T

Deleted: S

Deleted: (e.g., to GTS2020; Gradstein et al., 2020

Deleted:)

5 Data availability

The DINOSTRAT database is available under a CC-BY 4.0 license on GitHub (Bijl, 2023a; https://github.com/bijlpeter83/DINOSTRAT.git, last access 10 May 2023; and zenodo https://doi.org/10.5281/zenodo.7791273; last access 10 May 2023). The database consists of 7 csv files: (1)

Deleted: ;

Deleted: DOI

Deleted: :

Deleted: 4471204

Deleted: 4

"Paleolatitude.csv"; paleolatitude and present-day position of sites in DINOSTRAT, (2) "modernst.csv"; the site locations of core top sediments, (3) "modernsp.csv"; a modified modern dinocyst dataset, and (4) "Dinoevents_FEB_23.csv"; the calibrated dinocyst events, (5) "stages.csv"; a csv with stage names, (6) "Changes GTS2012_2020.csv"; the calibration changes due to changes in ammonite zonations, (7) "CMGW_ICS_colour.csv", color codes for the stages. "stratigraphy plots.R" is an R script to reproduce the figures presented in this paper.

6 Conclusions

This paper presents the database DINOSTRAT version 2.0-GTS2020 (Bijl, 2023a) a database containing >9,450 entries of regional dinocyst first and last occurrences (events) from over 2,043 species, in 209 sites. Geographic distribution of sites used in DINOSTRAT is strongly concentrated in the northern hemisphere mid-latitude, notably in Europe and the North Atlantic, and few sites are in the Pacific or Southern Hemisphere. Ages of events were calibrated using their ties to the Geologic Time Scale. The paper presents the location and age of origin of modern dinocyst species, genera, subfamilies and families. it reviews the age range and geographic spread modern and extinct dinocyst taxa and highlights the most latitudinally synchronous dinocyst events.

Many dinocyst taxa show quasi-synchronous events latitudinally, which can be widely used to stratigraphically date complex sedimentary sequences. Latitudinal diachroneity in events can be the result of either inadequate calibration to the chronostratigraphic timescale, false interpretations of 'true' events, complicated species concepts or paleoceanographic reasons. In any case, it dictates caution to extrapolate ages of dinocyst events to far distances, and demonstrates the need for regionally calibrated dinocyst zonations, which DINOSTRAT here provides. It further provides solid foundation to review spatio-temporal patterns in dinocyst evolution, dispersal, and extinction. DINOSTRAT is freely available under CC-BY 4.0 license. It allows the user to filter by region, or by species, genus, or higher taxonomic rank.

7 Supplements

Supplementary figures can be found in (Bijl, 2023b). Zip file containing plots showing the ages and latitudes of events in individual dinocyst species (2043 plots), grouped per genus (470 plots), per family (28 plots), of modern cyst species (95 plots), and the range charts for all Sites (211 plots).

8 Competing interests

Author declares no conflict of interests

Formatted: Dutch

Deleted: p

Deleted: Jan2021

Deleted: Plot creator

Deleted: .Rmd

Deleted: markdown file

Deleted: 1.0 (Bijl, 2021),

Deleted: 8500

Deleted: 1900

Deleted: 188

Deleted: time scale

Deleted: Supplement 1: Table of conversions of published zones to those in GTS2012

Formatted: Highlight

Formatted: No bullets or numbering

Deleted: **Supplement 2: Zip file containing ages and latitudes of events in individual dinocyst species (1914 plots), grouped per genus (459 plots), per family (27 plots), of modern cyst species (92 plots), and the range charts for all Sites (188 plots).**

9 Acknowledgements

I thank Henk Brinkhuis, Bas vd Schootbrugge, Francesca Sangiorgi and Appy Sluijs for useful discussions. The ‘Advanced course in organic-walled dinoflagellate cyst taxonomy, stratigraphy and paleoecology’ has been a great ‘playground’ to discuss progress in the field, and for that I have Martin Head, Martin Pearce, Jörg Pross, Jim Riding, and Poul Schiøler to thank. I acknowledge the then research assistants who helped building predecessors of DINOSTRAT: Tjerk Veenstra, Keechy Akkerman and Caroline van der Weijst. Thanks to Martin Schobben and Ilja Kocken for help with the data analysis and visualization in R, and Douwe van Hinsbergen for help reconstructing the paleolatitudes of the sites. James Ogg is thanked for providing the data from GTS2020. The constructive and detailed comments from Henrik Nøhr-Hansen and Ian Harding greatly improved the first version of the manuscript.

10 Financial support

The *LPP* Foundation has financially supported the development of DINOSTRAT.

Formatted: Dutch

Moved down [1]: The *LPP* Foundation has financially supported the development of DINOSTRAT.

Deleted: GTS2012

Deleted: the final manuscript

Moved (insertion) [1]

References

Awad, W. K. and Oboh-Ikuenobe, F. E.: Early Paleogene dinoflagellate cysts from ODP Hole 959D, Côte d'Ivoire-Ghana Transform Margin, West Africa: New species, biostratigraphy and paleoenvironmental implications, Journal of African Earth Sciences, 123, 123-144, 10.1016/j.jafrearsci.2016.07.014, 2016.

Bijl, P. K.: DINOSTRAT: A global database of the stratigraphic and paleolatitudinal distribution of Mesozoic-Cenozoic organic-walled dinoflagellate cysts, Earth System Science Data, 14, 579-617, 10.5194/essd-14-579-2022, 2022.

Bijl, P. K.: DINOSTRAT version 2.0-GTS2020, 10.5281/zenodo.7791273, 2023a.

Bijl, P. K.: DINOSTRAT version 2.0-GTS2020 Supplements, 10.5281/zenodo.7930060, 2023b.

Bijl, P. K., Sluijs, A., and Brinkhuis, H.: A magneto- and chemostratigraphically calibrated dinoflagellate cyst zonation of the early Palaeogene South Pacific Ocean, Earth-Science Reviews, 124, 1-31, 10.1016/j.earscirev.2013.04.010, 2013a.

Bijl, P. K., Brinkhuis, H., Egger, L. M., Eldrett, J. S., Frieling, J., Grothe, A., Houben, A. J. P., Pross, J., Sliwinska, K. K., and Sluijs, A.: Comment on 'Wetzeliella and its allies–the 'hole' story: a taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae' by Williams et al. (2015), Palynology, 41, 423-429, 10.1080/01916122.2016.1235056, 2017.

Bijl, P. K., Bendle, A. P. J., Bohaty, S. M., Pross, J., Schouten, S., Tauxe, L., Stickley, C. E., McKay, R. M., Roehl, U., Olney, M., Sluijs, A., Escutia, C., Brinkhuis, H., and Expedition, s.: Eocene cooling linked to early flow across the Tasmanian Gateway, Proceedings of the National Academy of Sciences of the United States of America, 110, 9645-9650, 10.1073/pnas.1220872110, 2013b.

Bravo, I. and Figueroa, R. I.: Towards an Ecological Understanding of Dinoflagellate Cyst Functions, Microorganisms, 2(1), 11–32, https://doi.org/10.3390/microorganisms2010011, 2014.

Brinkhuis, H., Powell, A. J., and Zevenboom, D.: High-resolution dinoflagellate cyst stratigraphy of the Oligocene / Miocene transition interval in northwest and central Italy, in: Neogene and Quaternary Dinoflagellate Cysts and Acritarchs, edited by: Head, M. J., and Wrenn, J. H., American Association of Stratigraphic Palynologists Foundation, Dallas, 219-258, 1992.

Bujak, J., Bringué, M., Goryacheva, A. A., Lebedeva, N. K., Pestchevitskaya, E. B., Riding, J. B., and Smelror, M.: Jurassic palynoevents in the circum-Arctic region, Atlantic Geoscience, 58, 055 - 098, 10.4138/atlgeo.2022.003, 2022.

Clyde, W. C., Wilf, P., Iglesias, A., Slingerland, R. L., Barnum, T., Bijl, P. K., Bralower, T. J., Brinkhuis, H., Comer, E. E., Huber, B. T., Ibañez-Mejia, M., Jicha, B. R., Krause, J. M., Schueth, J. D., Singer, B. S., Raigemborn, M. S., Schmitz, M. D., Sluijs, A., and Zamaloa, M. C.: New age constraints for the Salamanca Formation and lower Río Chico Group in the western San Jorge Basin, Patagonia, Argentina: Implications for cretaceous-paleogene extinction recovery and land mammal age correlations, Bulletin of the Geological Society of America, 126, 289-306, 10.1130/B30915.1, 2014.

Cramwinckel, M. J., van der Ploeg, R., Bijl, P. K., Peterse, F., Bohaty, S. M., Röhl, U., Schouten, S., Middelburg, J. J., and Sluijs, A.: Harmful algae and export production collapse in the equatorial Atlantic during the zenith of Middle Eocene Climatic Optimum warmth, Geology, 47, 247-250, 10.1130/G45614.1, 2019.

Cramwinckel, M. J., Huber, M., Kocken, I. J., Agnini, C., Bijl, P. K., Bohaty, S. M., Frieling, J., Goldner, A., Hilgen, F. J., Kip, E. L., Peterse, F., Van Der Ploeg, R., Röhl, U., Schouten, S., and Sluijs, A.: Synchronous tropical and polar temperature evolution in the Eocene letter, Nature, 559, 382-386, 10.1038/s41586-018-0272-2, 2018.

Crouch, E. M., Clowes, C. D., Raine, J. I., Alegret, L., Cramwinckel, M. J., and Sutherland, R.: Latest Cretaceous and Paleocene biostratigraphy and paleogeography of northern Zealandia, IODP Site U1509, New Caledonia Trough, southwest Pacific, New Zealand Journal of Geology and Geophysics, 10.1080/00288306.2022.2090386, 2022.

Davey, R. J.: The stratigraphic distribution of dinocysts in the Portlandian (latest Jurassic) to Barremian (Early Cretaceous) of northwest Europe, Am.Assoc.Stratigr.Palynol., Contrib.Ser., 5B, 48-81, 1979.

Ellegaard, M.: Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark, Review of Palaeobotany and Palynology, 109, 65–81, 2000.

Fensome, R. A., MacRae, R. A., Moldowan, J. M., Taylor, F. J. R., and Williams, G. L.: The Early Mesozoic Radiation of Dinoflagellates, Paleobiology, 22, 329-338, 1996.

Fensome, R. A., Taylor, F. J. R., Norris, G., Sarjeant, W. A. S., Wharton, D. I., and Williams, G. L.: A Classification of Modern and Fossil Dinoflagellates, Book, Whole, Micropalaeontology, Special Paper, Salem, 351 pp.1993.

Frieling, J. and Sluijs, A.: Towards quantitative environmental reconstructions from ancient non-analogue microfossil assemblages: Ecological preferences of Paleocene – Eocene dinoflagellates, Earth-Science Reviews, 185, 956-973, 10.1016/j.earscirev.2018.08.014, 2018.

Gale, A. S., Mutterlose, J., and Batenburg, S.: The Cretaceous Period, in: The Geologic Time Scale 2020, edited by: Gradstein, F. M., Ogg, J. G., Schmitz, B., and Ogg, G. M., Elsevier, Amsterdam, 1023–1087, 2020.

Formatted: Dutch

Deleted: References¶

Açıkalın, S., Vellekoop, J., Ocakoğlu, F., Yılmaz, İ. Ö., Smit, J., Altıner, S. Ö., Goderis, S., Vonhof, H., Speijer, R. P., Woelders, L., Fornaciari, E. and Brinkhuis, H.: Geochemical and palaeontological characterization of a new K-Pg Boundary locality from the Northern branch of the Neo-Tethys: Mudurnu – Göynük Basin, NW Turkey, Cretaceous Research, 52, 251–267, 2015.¶

Århus, N., Birkelund, T. and Smelror, M.: Biostratigraphy of some Callovian and Oxfordian cores off Vega, Helgeland, Norsk Geologisk Tidsskrift, 69, 39–56, 1989.¶

Aubry, A. M. R., De Schepper, S. and de Vernal, A.: Dinocyst and acritarch biostratigraphy of the Late Pliocene to Early Pleistocene at Integrated Ocean Drilling Program Site U1307 in the Labrador Sea, Journal of Micropaleontology, 39(1), 41–60, doi:10.5194/jm-39-41-2020, 2020.¶

Awad, W. K. and Oboh-Ikuenobe, F. E.: Early Paleogene dinoflagellate cysts from ODP Hole 959D, Côte d'Ivoire-Ghana Transform Margin, West Africa: New species, biostratigraphy and paleoenvironmental implications, Journal of African Earth Science, 123, 123–144, doi:10.1016/j.jafrearsci.2016.07.014, 2016.¶

Awad, W. K. and Oboh-Ikuenobe, F. E.: Paleogene-early Neogene paleoenvironmental reconstruction based on palynological analysis of ODP Hole 959A, West Africa, Marine Micropaleontology, 148, 29–45, 2019.¶

Bailey, D. A., Milner, P. and Varney, T.: Some dinoflagellate cysts from the Kimmeridge Clay Formation in North Yorkshire and Dorset, U.K., Proceedings of the Yorkshire Geological Society, 51, 235–243, 1997.¶

Baruffini, L., Lottaroli, F. and Torricelli, S.: Integrated high-resolution stratigraphy of the lower oligocene tusa tuffite formation in the Calabro-Lucano area and sicily (southern Italy), Rivista Italiana di Paleontologia e Stratigrafia, 108(3), 457–478, 2002.¶

Besems, R.: Dinoflagellate cyst biostratigraphy of Tertiary and Quaternary deposits of offshore NW Borneo, Geological Society of Malaysia, bulletin, 33, 65–93, 1993.¶

Biffi, U. and Manum, S. B.: Late Eocene-Early Miocene dinoflagellate cyst stratigraphy from the Marche region (Central Italy), Bulletino della Società Paleontologica Italiana, 27(2), 163, 1988.¶

Bijl, P.K.: DINOSTRAT V1.0, available at https://github.com/bijlpeter83/DINOSTRAT.git; DOI:10.5281/zenodo.4471204, 2021.¶

Bijl, P. K. and Brinkhuis, H.: A new genus and two new species of dinoflagellate cysts from lower Eocene marine sediments of the Wilkes Land Margin, Antarctica, Review of Palaeobotany and Palynology, 220, 88–97, doi:10.1016/j.revpalbo.2015.05.004, 2015.¶

Bijl, P. K., Sluijs, A. and Brinkhuis, H.: A magneto- chemo-stratigraphically calibrated dinoflagellate cyst zonation of the early Paleogene South Pacific Ocean, Earth-Science reviews, 124, 1–31, 2013a.¶

Bijl, P. K., Bendle, A. P. J., Bohaty, S. M., Pross, J., Schouten, S., Tauxe, L., Stickley, C. E., McKay, R. M., Roehl, U., Olney, M., Sluijs, A., Escutia, C., Brinkhuis, H. and scientists, E. 318: Eocene cooling linked to early flow across the Tasmanian Gateway , PNAS, 110(24), 9645–9650, doi:https://doi.org/10.1073/pnas.1220872110, 2013b.¶

Bijl, P. K., Sluijs, A. and Brinkhuis, H.: Erratum to "A magneto- and chemostratigraphically calibrated dinoflagellate cyst zonation of the early Paleogene South Pacific Ocean" [Earth Sci. Rev. 124 (20 ... [2]

Formatted: Dutch

González Estebenet, M. S., Guler, M. V., and Pérez Panera, J. P.: Late Maastrichtian to Danian organic-walled dinoflagellate cysts and calcareous nannofossils from eastern Austral Basin, Patagonia, Argentina, Review of Palaeobotany and Palynology, 285, 10.1016/j.revpalbo.2020.104342, 2021.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., and Ogg, G. M.: The Geologic Time Scale 2012, 2012.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., and Ogg, G. M.: Geologic Time Scale 2020, in, edited by: Gradstein, F. M., Ogg, J. G., Schmitz, M. D., and Ogg, G. M., Elsevier, https://doi.org/10.1016/B978-0-12-824360-2.00032-2, 2020.

Guerrero-Murcia, L. A. and Helenes, J.: Statistic biostratigraphy and paleoecology of tropical Upper Cretaceous dinoflagellate cysts, Journal of South American Earth Sciences, 115, 10.1016/j.jsames.2022.103730, 2022.

Head, M. J., Norris, G., and Mudie, P. J.: Palynology and dinocyst stratigraphy of the Upper Miocene and lowermost Pliocene, ODP Leg 105, Site 646, Labrador Sea, In: Srivastava, S.P.et al.Ocean Drilling Program, Proceedings , Scientific Results, Leg 105, College Station, Texas, 105, 423-451, 1989.

Hesselbo, S. P., Ogg, J. G., and Ruhl, M.: The Jurassic Period, in: The Geologic Time Scale 2020, edited by: Gradstein, F. M., Ogg, J. G., Smitz, M. D., and Ogg, G. M., Elsevier, Amsterdam, 955–1022, 2020.

Houben, A. J. P., Bijl, P. K., Pross, J., Bohaty, S. M., Passchier, S., Stickley, C. E., Röhl, U., Sugisaki, S., Tauxe, L., Van De Flierdt, T., Olney, M., Sangiorgi, F., Sluijs, A., Escutia, C., Brinkhuis, H., Brinkhuis, H., Dotti, C. E., Klaus, A., Fehr, A., Fehr, A., Williams, T., Bendle, J. A. P., Bohaty, S. M., Carr, S. A., Dunbar, R. B., Gonzalez, J. J., Hayden, T. G., Iwai, T. G., Jimenez-Espejo, F. J., Katsuki, K., Kong, G. S., McKay, R. M., Nakai, M., Olney, M. P., Passchier, M. P., Passchier, M. P., Pekar, S. F., Pross, J., Pross, J., Riesselman, C. R., Sakai, T., Shrivastava, P. K., Stickley, C. E., Sugisaki, S., Tauxe, L., Tuo, S., van de Flierdt, T., Welsh, K., and Yamane, M.: Reorganization of Southern ocean plankton ecosystem at the onset of antarctic glaciation, Science, 340, 341-344, 10.1126/science.1223646, 2013.

Hoyle, T. M., Sala-Pérez, M., and Sangiorgi, F.: Where should we draw the line between dinocyst "species"? Morphological continua in Black Sea dinocysts, Journal of Micropaleontology, 38, 55–65, 2019.

Iakovleva, A. I., Brinkhuis, H., and Cavagnetto, C.: Late Palaeocene-Early Eocene dinoflagellate cysts from the Turgay Strait, Kazakhstan; correlations across ancient seaways, Palaeogeogr.Palaeocl., 172, 243-268, 2001.

Jarvis, I., Pearce, M., Püttmann, T., Voigt, S., and Walaszczyk, I.: Palynology and calcareous nannofossil biostratigraphy of the Turonian – Coniacian boundary: The proposed boundary stratotype at Salzgitter-Salder, Germany and its correlation in NW Europe, Cretaceous Research, 123, 10.1016/j.cretres.2021.104782, 2021.

Leereveld, H.: Upper Tithonian-Valanginian (Upper Jurassic-Lower Cretaceous) dinoflagellate cyst stratigraphy of the western Mediterranean, Cretaceous Research, 18, 385-420, 1997a.

Leereveld, H.: Hauterivian-Barremian (Lower Cretaceous) dinoflagellate cyst stratigraphy of the western Mediterranean, Cretaceous Research, 18, 421-456, 1997b.

Marret, F., Bradley, L., de Vernal, A., Hardy, W., Kim, S.-Y., Mudie, P., Penaud, A., Pospelova, V., Price, A. M., Radi, T., and Rochon, A.: From bi-polar to regional distribution of modern dinoflagellate cysts, an overview of their biogeography, Marine Micropaleontology, 159, doi:10.1016/j.marmicro.2019.101753, 2020.

Martini, E.: Standard Tertiary and Quaternary calcareous nannoplankton zonation, in: Proceedings 2nd International Conference Planktonic Microfossils Roma, edited by: Farinacci, A., Tecnosci., Rome 739–785, 1971.

Mertens, K. N. and Carbonell-Moore, C.: Introduction to Spiniferites Mantell 1850 special issue, Palynology, 42, 1-9, 10.1080/01916122.2018.1465741, 2018.

Mertens, K. N., Takano, Y., Head, M. J., and Matsuoka, K.: Living fossils in the Indo-Pacifi c warm pool: A refuge for thermophilic dinofl agellates during glaciations, Geology, 42, 531-534, 10.1130/G35456.1, 2014.

Nøhr-Hansen, H., Piasecki, S., and Alsen, P.: A Cretaceous dinoflagellate cyst zonation for NE Greenland, Geological Magazine, 157, 1658–1692, 2020.

Oosting, A. M., Leereveld, H., Dickens, G. R., Henderson, R. A., and Brinkhuis, H.: Correlation of Barremian-Aptian (mid-Cretaceous) dinoflagellate cyst assemblages between the Tethyan and Austral realms, Cretaceous Research, 27, 792-813, 10.1016/j.cretres.2006.03.012, 2006.

Pearce, M. A., Jarvis, I., Ball, P. J., and Laurin, J.: Palynology of the Cenomanian to lowermost Campanian (Upper Cretaceous) Chalk of the Trunch Borehole (Norfolk, UK) and a new dinoflagellate cyst bioevent stratigraphy for NW Europe, Review of Palaeobotany and Palynology, 278, 10.1016/j.revpalbo.2020.104188, 2020.

Pearce, M. A., Jarvis, I., Monkenbusch, J., Thibault, N., Ullmann, C. V., and Martinez, M.: Coniacian-Campanian palynology, carbon isotopes and clay mineralogy of the Poigny borehole (Paris Basin) and its correlation in NW Europe, Comptes Rendus - Geoscience, 354, 10.5802/crgeos.118, 2022.

Poulsen, N. E.: Dinoflagellate cyst biostratigraphy of the Late Jurassic of Poland, GEOBIOS, 17, 401–407, 1994.

Powell, A. J., Brinkhuis, H., and Bujak, J. P.: Upper Paleocene-lower Eocene dinoflagellate cyst sequence biostratigraphy of southeast England, in: Correlation of the Early Paleogene in Northwest Europe, edited by: Knox, R. W. O. Ä., Corfield, R. M., and Dunay, R. E., Geol. Soc. Spec. Publ, 145-183, 1996.

Radmacher, W., Mangerud, G., and Tyszka, J.: Dinoflagellate cyst biostratigraphy of Upper Cretaceous strata from two wells in the Norwegian Sea, Review of Palaeobotany and Palynology, 216, 18–32, 2015.

Formatted: Dutch

Reichart, G. J., Brinkhuis, H., Huiskamp, F., and Zachariasse, W. J.: Hyperstratification following glacial overturning events in the northern Arabian Sea, Paleoceanography, 19, PA2013, doi:2010.1029/2003PA000900, 2004.

Rochon, A., Lewis, J., Ellegaard, M., and Harding, I. C.: The Gonyaulax spinifera (Dinophyceae) “complex”: Perpetuating the paradox?, Review of palaeobotany and palynology, 155, 52-60, https://doi.org/10.1016/j.revpalbo.2008.12.017, 2009.

Sangiorgi, F., Bijl, P. K., Passchier, S., Salzmann, U., Schouten, S., McKay, R., Cody, R. D., Pross, J., Van De Flierdt, T., Bohaty, S. M., Levy, R., Williams, T., Escutia, C., and Brinkhuis, H.: Southern Ocean warming and Wilkes Land ice sheet retreat during the mid-Miocene, Nature Communications, 9, 10.1038/s41467-017-02609-7, 2018.

Sliwinska, K. K., Abrahamsen, N., Beyer, C., Brünings-Hansen, T., Thomsen, E., Ulleberg, K., and Heilmann-Clausen, C.: Bio- and magnetostratigraphy of Rupelian-mid Chattian deposits from the Danish land area, Review of Palaeobotany and Palynology, 172, 48-69, 2012.

Śliwińska, K. K., Jelby, M. E., Grundvåg, S.-A., Nohr-Hansen, H., Alsen, P., and Olaussen, S.: Dinocyst stratigraphy of the Valanginian-Aptian Rurikfjellet and Helvetiafjellet formations on Spitsbergen, Arctic Norway, Geological Magazine, 157, 1693-1714, 2020.

Sluijs, A., Pross, J., and Brinkhuis, H.: From greenhouse to icehouse; organic walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene, Earth-Science Reviews, 68, 281-315, 10.1016/j.earscirev.2004.06.001, 2005.

Sluijs, A., Brinkhuis, H., Schouten, S., Bohaty, S., John, C. M., Zachos, J. C., Reichart, G. J., Sinninghe Damsté, J. S., Crouch, E. M., and Dickens, G. R.: Environmental precursors to rapid light carbon injection at the Palaeocene/Eocene boundary, Nature, 450, 1218-1221, 2007.

Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Sinninghe Damsté, J. S., Dickens, G. R., Huber, M., Reichart, G. J., Stein, R., Matthiessen, J., Lourens, L. J., Pedentchouk, N., Backman, J., Moran, K., and scientists, E.: Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum, Nature, 441, 610-613, 2006.

Thöle, L. M., Nooteboom, P. D., Hou, S., Wang, R., Nie, S., Michel, E., Sauermilch, I., Marret, F., Sangiorgi, F., and Bijl, P. K.: An expanded database of Southern Hemisphere surface sediment dinoflagellate cyst assemblages and their oceanographic affinities, Journal of Micropalaeontology, in review, 10.31223/X54948, 2022.

Torricelli, S., Menichetti, E., and Knezaurek, G.: Climate-driven dinoflagellate cyst stratigraphy of the Oligocene-lower Miocene turbidite succession of the Lower Congo Basin (offshore NW Angola), Journal of African Earth Sciences, 192, 10.1016/j.jafrearsci.2022.104536, 2022.

Van Helmond, N. A. G. M., Sluijs, A., Papadomanolaki, N. M., Plint, A. G., Gröcke, D. R., Pearce, M. A., Eldrett, J. S., Trabucho-Alexandre, J., Walaszczyk, I., Van De Schootbrugge, B., and Brinkhuis, H.: Equatorward phytoplankton migration during a cold spell within the Late Cretaceous super-greenhouse, Biogeosciences, 13, 2859–2872, doi:10.5194/bg-13-2859-2016, 2016.

Van Hinsbergen, D. J. J., De Groot, L. V., Van Schaik, S. J., Spakman, W., Bijl, P. K., Sluijs, A., Langereis, C. G., and Brinkhuis, H.: A paleolatitude calculator for paleoclimate studies, PLoS ONE, 10, 2015.

Van Simaeys, S., Munsterman, D., and Brinkhuis, H.: Oligocene dinoflagellate cyst biostratigraphy of the southern North Sea Basin, Review of Palaeobotany and Palynology, 134, 105-128, 10.1016/j.revpalbo.2004.12.003, 2005.

Vasilyeva, O. N. and Musatov, V. A.: Dinoflagellate cyst and nannoplankton assemblages from the Middle Eocene Kuma Formation of Crimean Peninsula — biostratigraphy and palynofacies, Palaeoworld, https://doi.org/10.1016/j.palwor.2022.11.006, 2022.

Versteegh, G. J. M.: The onset of major Northern Hemisphere glaciations and their impact on dinoflagellate cysts an acritarchs from the Singa section, Calabria (southern Italy) and DSDP Holes 607/607A (North Atlantic), Marine Micropaleontology, 30, 319-343, 1997.

Vieira, M. and Mahdi, S.: New Late Cretaceous to earliest Paleogene (Campanian–Danian) dinoflagellate cysts from the Møre Basin, offshore Norway, Palynology, 46, 1-19, 10.1080/01916122.2021.2006817, 2022.

Vieira, M., Mahdi, S., and Holmes, N.: High resolution biostratigraphic zonation for the UK central North Sea Paleocene, Marine and Petroleum Geology, 117, 104400, https://doi.org/10.1016/j.marpetgeo.2020.104400, 2020.

Watkins, D. and Raffi, I.: Calcareous Nannofossils, in: The Geologic Time Scale 2020, Elsevier, Amsterdam, 69–73, 2020.

Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretano, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A., and Zachos, J. C.: An astronomically dated record of Earth’s climate and its predictability over the last 66 million years, Science, 369, 1383-1387, 10.1126/science.aba6853, 2020.

Williams, G. L., Fensome, R. A., and MacRae, R. A.: DINOFLAJ3, American Association of Stratigraphic Palynologists, Data Series, 2, 2017.

Williams, G. L., Damassa, S. P., Fensome, R. A., and Guerstein, G. R.: Wetzeliella and its allies - The 'hole' story: A taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae, Palynology, 39, 289-344, 10.1080/01916122.2014.993888, 2015.

Williams, G. L., Brinkhuis, H., Pearce, M. A., Fensome, R. A., and Weegink, J. W.: Southern Ocean and global dinoflagellate cyst events compared: Index events for the late Cretaceous - Neogene, in: Proceedings of the Ocean Drilling Program, Scientific Results, volume 189, edited by: Exon, N. F., Kennett, J. P., and Malone, M. J., 1-98, 2004.

Zonneveld, K. A. F., Versteegh, G. J. M., Kasten, S., Eglinton, T. I., Emeis, K. C., Huguet, C., Koch, B. P., De Lange, G. J., De Leeuw, J. W., Middelburg, J. J., Mollenhauer, G., Prahl, F. G., Rethemeyer, J., and Wakeham, S. G.: Selective preservation of organic matter in marine environments; Processes and impact on the sedimentary record, Biogeosciences, 7, 483-511, 2010.

Zonneveld, K. A. F., Marret, F., Versteegh, G. J. M., Bogus, K., Bonnet, S., Bouimetarhan, I., Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K., Henry, M., Holzwarth, U., Kielt, J. F., Kim, S. Y., Ladouceur, S., Ledu, D., Chen, L., Limoges, A., Londeix, L., Lu, S. H., Mahmoud, M. S., Marino, G., Matsouka, K., Matthiessen, J., Mildenhal, D. C., Mudie, P., Neil, H. L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J. L., Verleye, T., Wang, Y., Wang, Z., and Young, M.: Atlas of modern dinoflagellate cyst distribution based on 2405 data points, Review of Palaeobotany and Palynology, 191, 1-197, 10.1016/j.revpalbo.2012.08.003, 2013.

Formatted: Dutch

Formatted: Level 1, Space Before: 24 pt, After: 12 pt, Keep with next

Page 5: [1] Deleted **Bijl, P.K. (Peter)** **07/05/2023 20:33:00**

Page 43: [2] Deleted **Bijl, P.K. (Peter)** **07/05/2023 20:34:00**