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# DINOSTRAT: a global database of the stratigraphic and paleolatitudinal distribution of Mesozoic–Cenozoic organic-walled dinoflagellate cysts

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**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 evaluating underlying causes. For this reason, DINOSTRAT is here introduced – an open-source, iterative, community-fed database intended to house all regional chronostratigraphic calibrations of dinocyst events (https://github.com/bijlpeter83/DINOSTRAT.git, last access: 1 February 2022) (DOI – https://doi.org/10.5281/zenodo.5772616, Bijl, 2021). DINOSTRAT version 1.0 includes >8500 entries of the first and last occurrences (collectively called "events") of >1900 dinocyst taxa and their absolute ties to the chronostratigraphic timescale of Gradstein et al. (2012). Entries are derived from 199 publications and 188 sedimentary sections. DINOSTRAT interpolates paleolatitudes of regional dinocyst events, allowing evaluation of the paleolatitudinal variability in dinocyst event ages. DINOSTRAT allows for open accessibility and searchability, based 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, and (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, in fact many species have remarkable diachroneity. DINOSTRAT provides the data storage approach by which the community can now start to relate diachroneity to (1) inadequate ties 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 has 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 in restricted nearshore marine settings (e.g., Poulsen, 1994; Brinkhuis et al., 1998; Iakovleva et al., 2001; Śliwińska 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 the first and last stratigraphic occurrences (FOs and LOs, hereafter jointly referred to as "events") of easily recognized taxa. Through the past decades, 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, 1997a, b; Oosting et al., 2006; Awad and Oboh-Ikuenobe, 2019) and astrochronology (Versteegh, 1997). However, efforts to compile a global chronostratigraphic calibration of dinocyst events have 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 should the research field of dinocyst biostratigraphy progress?

Two questions arise from the notion of the 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 is, what is the impact of regional variability in the numerical ages of events on the regional consistency of the stratigraphic order of events?

- What are the underlying causes for the observed diachroneity? Broadly, three reasons could apply: (1) inaccurate or inadequate tie-in of dinocyst events to the chronostratigraphic timescale can lead to apparent (but perhaps false) diachroneity 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 of whether the last occurrence of a fossil dinocyst taxon reflects extinction of its producer, adjustment of cyst morphology by its producer (e.g., 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/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 (e.g., 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 that takes us towards answering these questions 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 the paleogeographic evolution of sites and the means of chronostratigraphic calibration. It further requires that such data compilations are constantly updated with new insights: updates to the geologic time scale and bio-magnetostratigraphic zonation schemes, altered taxonomic concepts, age models of sections, and stratigraphic sections. A complication on a logistical front is that dinocyst ranges are typically published in the closed-access peer-reviewed literature, which is not easily accessible to all, is inconsistent in its approach and is easily updated with new insights.

This paper introduces 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 1.0 currently contains over 8500 entries of the first and last occurrences of over 1900 dinocyst taxa tied to the international timescale. These entries originate from 199 peer-reviewed papers presenting data from 188 sites. Including as many reports/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/consistency in event ages and provides the basic information to evaluate the paleoceanographic signal that diachroneity may hold. Open accessibility of the basic dinocyst stratigraphic data will further allow a proper evaluation and update of evolutionary patterns in dinocyst families (MacRae et al., 1996) with full disclosure of the underlying data. The approach to the selection of appropriate data and entry and calculations of ages and paleolatitudes is explained in Sect. 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.

## 2 Approach

DINOSTRAT version 1.0 represents a compilation of dinocyst events from peer-reviewed literature, with a publication date predating 1 January 2021 (see Table 1). The taxonomic nomenclature, supra-generic classification and synonymy cited in Williams et al. (2022) are followed. One inherent assumption in the initial setup of 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. (2022). 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 (e.g., Hoyle et al., 2019), in part imposed by environmental conditions (e.g., Ellegaard, 2000). Some authors tend to lump species in complexes, while others split them 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 identifying them is considered a next step for when individual studies or sites are revisited.

For the subfamily Wetzelielloideae, DINOSTRAT deviates from the taxonomic index of Williams et al. (2022). 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., 2016). Therefore, for this subfamily, the calibration of dinocyst species is presented in the taxonomic classification of Wetzelielloideae prior to Williams et al. (2015).

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 the 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 2012 (GTS2012; Gradstein et al., 2012). 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 performed without the use of dinocyst biostratigraphy. Since magnetic reversals are globally synchronous, evaluating the synchroneity of dinocyst events with the 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 tools 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 geologic time scale (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.

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:

$$\begin{aligned}&[\mathrm{FO/LO}]\ \text{of}\ [\text{genus, species}] = [\#\#]\%\ \text{in}\\&\qquad([\text{stratigraphic tool}]\$[\text{zone}]),\end{aligned}\tag{1}$$

in which [##]% is linearly interpolated between the base (0 %) and top (100 %) of tie points; [stratigraphic tool]$[zone] is the name of the zone in the bio-magneto- or chronozonation in GTS2012 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:

$$\begin{aligned}&[\mathrm{FO/LO}]\ \text{of}\ [\text{genus, species}] = [\#\#]\%\ \text{between}\ [\#\#]\,\%\ \text{in}\\&\qquad[\text{stratigraphic tool}]\$[\text{zone}]\ \text{and}\ [\#\#]\%\ \text{in}\\&\qquad[\text{stratigraphic tool}]\$[\text{zone}].\end{aligned}\tag{2}$$

Outdated Jurassic and Cretaceous ammonite zonation schemes have been converted to those presented in GTS2012 (see Supplement File 1; following Ogg and Hinnov, 2012a, b, and citations therein). FOs in the bottom of sections and LOs at the top of sections are systematically omitted, unless they were specifically indicated to 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, and Mertens et al., 2014, for *Dapsilidinium pastielsii*) are entered with an LO of 0 Ma (modernst.csv in Bijl,

**Table 1.** Papers used in this review. Reference, geography, age base and age top (in Ma), tier (see Fig. 1), and means of calibration to the geologic time scale (GTS). The abbreviations of the microplankton zones indicated in the column "Calibrated to" (NJ, NC, NP, NN, CC, CP, CN, UC, N, P, E) are those commonly used in the literature and relate to the zones presented in the GTS2012 (Gradstein et al., 2012).

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Açıkalın et al. (2015) | Northwestern Turkey | 67 | 65 | 3 | Planktonic foraminifera stratigraphy on the same section |
| Århus et al. (1989) | Norway | 166 | 155 | 3 | Russian Platform zones, converted to Boreal ammonite zones (see Supplement File 1) |
| Aubry et al. (2020) | Labrador Sea, Greenland | 3.2 | 2.25 | 1 | Magnetostratigraphy on the same samples, magnetic reversals calibrated using planktonic foraminifera and nannofossils |
| Awad and Oboh-Ikuenobe (2016) | Côte D'Ivoire margin | 57 | 54 | 3 | CP nannoplankton stratigraphy on the same section |
| Awad and Oboh-Ikuenobe (2019) | Côte D'Ivoire margin | 28 | 16 | 3 | CP and CN nannofossil stratigraphy on the same samples |
| Bailey et al. (1997) | United Kingdom | 157 | 152 | 3 | Boreal ammonite stratigraphy from the same core samples. |
| Baruffini et al. (2002) | Southern Italy | 35 | 32 | 3 | CP nannoplankton stratigraphy from the same study |
| Besems (1993) | Borneo | 65 | 0 | 5 | Chronostratigraphy, no independent age control shown (industry data) |
| Biffi and Manum (1988) | Central Italy | 36 | 22 | 3 | NP and NN nannoplankton and N and P planktonic foraminifer stratigraphies from the same sections |
| Bijl and Brinkhuis (2015) | East Antarctica | 54 | 47 | 2 | Magnetostratigraphy on the same section, magnetochrons dated using dinocyst biostratigraphy |
| Bijl et al. (2013a, 2014) | Southwest Pacific | 57 | 35 | 2 | Complicated paleomagnetic signal – see Dallanave et al. (2016) and isotope stratigraphic constraints at Site 1171 and 1172 – U1356 calibrated to magnetostratigraphy, using dinocyst biostratigraphy |
| Bijl et al. (2018) | East Antarctica | 34 | 10 | 1 | Magnetostratigraphy with nannoplankton stratigraphy |
| Bowman et al. (2012) | Seymour Island, Antarctica | 68 | 65 | 4 | Inferred position of the K–Pg boundary |
| Bowman et al. (2016) | Seymour Island, Antarctica | 66 | 57 | 4 | Inferred position of the K–Pg boundary |
| Brinkhuis (1994) | Italy | 35 | 33 | 1 | Magnetostratigraphy with NP and CP nannoplankton and foraminifer stratigraphy in the same sections |
| Brinkhuis and Biffi (1993) | Central Italy | 37 | 32 | 1 | Magnetostratigraphy, based on nannoplankton stratigraphy and foraminifer stratigraphy |
| Brinkhuis et al. (1992) | Northwest Italy | 26 | 22 | 1 | Magnetostratigraphy, interpreted based on nannoplankton stratigraphy and foraminifer stratigraphy |
| Brinkhuis et al. (1998) | Tunisia, Denmark | 67 | 65 | 3 | Planktonic foraminifer stratigraphy at the same sections |
| Brinkhuis et al. (2003a) | Western Tasmania | 36 | 1 | 2 | Magnetostratigraphy with sparse nannoplankton in the Eocene, Oligocene and Neogene calibrated to nannoplankton, foraminifer and magnetostratigraphy |
| Brinkhuis et al. (2003b) | Eastern Tasmania | 70 | 30 | 2 | A complicated paleomagnetic signal with isotope stratigraphic constraints (see Dallanave et al., 2016) |
| Brown and Downie (1984) | Rockall Plateau, Ireland | 58 | 33 | 3 | CN and NP nannoplankton stratigraphy on the same cores |
| Brown and Downie (1985) | Northern Bay of Biscay, France | 60 | 10 | 3 | NP and NN nannoplankton stratigraphy on the same cores |
| Bucefalo Palliani and Riding (1997a) | Italy | 183 | 179 | 4 | Tethyan ammonite stratigraphy but no ammonite data shown |
| Bucefalo Palliani and Riding (1997b) | France | 199 | 170 | 4 | Boreal ammonite stratigraphy but no ammonite data shown (see conversions in Supplement File 1) |
| Bucefalo Palliani and Riding (2000) | United Kingdom | 200 | 179 | 4 | Tethyan ammonite stratigraphy but no ammonite data shown (see conversions in Supplement File 1) |
| Bucefalo Palliani and Riding (2003) | Boreal–Tethys | 191 | 180 | 4 | Boreal ammonite stratigraphy but no ammonite data shown. |
| Bujak and Matsuoka (1986) | North Pacific, Japan | 23 | 0 | 5 | Independent age constraints from planktonic foraminifera, radiolaria, diatoms and nannoplankton not shown in the paper. |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Bujak and Mudge (1994) | North Sea, United Kingdom | 57 | 53 | 4 | Synthesis, plots dinocyst events against NP nannoplankton and P planktonic foraminifer stratigraphy, not presenting independent stratigraphic data |
| Correia et al. (2019) | Portugal | 183 | 168 | 3 | Tethyan ammonite stratigraphy on the same sections. |
| Costa and Davey (1992) | North Sea, United Kingdom | 145 | 66 | 4 | Ammonite zones plotted but no ammonite data presented, Campanian–Maastrichtian events calibrated to stages (see conversions in Supplement File 1) |
| Costa and Downie (1979) | North Atlantic | 58 | 5 | 3 | Nannoplankton stratigraphy on the same section |
| Crouch et al. (2014) | New Zealand | 66 | 54 | 1 | Magnetostratigraphy and NP nannoplankton stratigraphy on the same samples |
| Dallanave et al. (2016);<br>Crouch et al. (2020) | New Zealand | 54 | 46 | 1 | Magnetostratigraphy and NP nannoplankton zones on the same section |
| Davey (1979) | North Atlantic | 124 | 100 | 3 | Nannoplankton stratigraphy on the same section |
| Davey (1982) | Denmark | 152 | 125 | 3 | Original stratigraphic account based on ammonites, pelecypods and benthic foraminifera (see conversions in Supplement File 1) |
| Davey (2001) | United Kingdom | 134 | 131 | 3 | Boreal ammonite stratigraphy on the section |
| Davey and Verdier (1971) | France | 113 | 103 | 4 | Boreal ammonite stratigraphy, not shown (see conversions in Supplement File 1) |
| De Lira Mota et al. (2020) | Gulf Coast, USA | 37 | 32 | 3 | NP nannofossil stratigraphy on the same samples |
| De Schepper and Head (2008, 2009) | North Atlantic | 6 | 0 | 1 | Magnetostratigraphy, NN nannofossil stratigraphy and N planktonic foraminifer stratigraphy |
| De Schepper et al. (2017) | North Atlantic | 7 | 1 | 1 | Magnetostratigraphy on the same section |
| De Vernal and Mudie (1989) | Labrador Sea, Greenland | 5.5 | 0 | 3 | Shipboard NN nannofossil stratigraphy |
| De Vernal et al. (1992) | North Atlantic | 1.5 | 0 | 1 | Magnetostratigraphy and NN nannofossil stratigraphy |
| De Verteuil and Norris (1996) | Chesapeake Bay, USA | 25 | 4 | 4 | Synthesized stratigraphic data, no independent age control presented |
| Dimter and Smelror (1990) | Southwest Germany | 166 | 163 | 3 | Boreal ammonite zonation on the same material |
| Dodsworth (2000) | USA and United Kingdom | 96 | 93 | 3 | Planktonic foraminifer and ammonite stratigraphy on the same section |
| Duffield and Stein (1986) | Gulf Coast, USA | 35 | 5 | 3 | N Planktonic foraminiferal zonation |
| Duque-Herrera et al. (2018) | Colombia | 18 | 5 | 3 | NN nannofossil events in the same core |
| Duxbury (1983) | North Sea | 126 | 110 | 3 | Boreal ammonite zonation (see conversions in Supplement File 1) |
| Duxbury (2001) | Scotland | 139 | 100 | 4 | Boreal ammonite zonation, not directly from the well cutting material (see conversions in Supplement File 1) |
| Dybkjær and Piasecki (2008, 2010) | Denmark | 23 | 0 | 3 | NP and NN nannoplankton stratigraphy |
| Egger et al. (2016) | Newfoundland, USA | 35 | 21 | 1 | Magnetostratigraphy with NN nannoplankton stratigraphy |
| Eldrett and Harding (2009) | Vøring Plateau, Norwegian Sea | 52 | 33 | 2 | Magnetostratigraphy on the same section – see Eldrett et al. (2004) |
| Eldrett et al. (2004) | Norwegian Sea | 50 | 30 | 2 | Magnetostratigraphy but chrons not independently interpreted |
| Eldrett et al. (2019) | North Atlantic | 34 | 24 | 2 | Magnetostratigraphy on the same section – see Eldrett et al. (2004) |
| Eshet et al. (1992) | Israel | 67 | 65 | 3 | NP nannoplankton stratigraphy at the same site |
| Feist-Burkhardt and Monteil (1997) | France | 171 | 167 | 3 | Calibrated to Boreal ammonite stratigraphy (see conversions in Supplement File 1) |
| Feist-Burkhardt (1990) | Southwest Germany | 174 | 168 | 3 | Boreal ammonite stratigraphy |
| Fensome et al. (2008) | Scotian margin,<br>eastern Canada | 100 | 0 | 3 | NN and NC nannoplankton stratigraphy but because based on cuttings, only LOs given |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Firth et al. (2013) | North Atlantic | 51 | 32 | 1 | Magnetostratigraphy with independent age control from nannoplankton and planktonic foraminifer stratigraphy |
| Firth (1996) | North Atlantic | 45 | 30 | 1 | Calibrated using magnetostratigraphy from Eldrett and Harding (2009) |
| Frieling et al. (2014) | West Siberian Sea | 60 | 45 | 2 | Magnetostratigraphy and stable carbon isotope stratigraphy |
| Gradstein et al. (1992) | North Sea, the Netherlands | 66 | 23 | 3 | N and P foraminifer stratigraphy but entered against NP nannoplankton stratigraphy |
| Grothe et al. (2017) | Black Sea | 6 | 5.5 | 1 | Magnetostratigraphy on the same section |
| Guasti et al. (2005) | Tunisia | 66 | 57 | 3 | NP nannoplankton and P foraminifer stratigraphy on the same section |
| Habib and Drugg (1983) | East Coast, USA | 157 | 138 | 1 | Magnetostratigraphy on the same section |
| Habib and Drugg (1987) | East Coast, USA | 145 | 66 | 2 | Magnetostratigraphy on the same section |
| Harding et al. (2011) | Southern Russia | 152 | 134 | 3 | Russian ammonite zonation on the same sections, correlated to Boreal ammonite zones (see conversions in Supplement File 1) |
| Harland (1979) | North Atlantic | 12 | 0 | 3 | Nannoplankton stratigraphy on the same section |
| Harland (1992) | North Sea | 23 | 0 | 4 | NN nannoplankton and N planktonic foraminifer stratigraphy but independent age constraints not explicitly shown |
| Head (1998) | North Sea | 4 | 1.6 | 4 | Stages, using known ages of sampled formations |
| Head and Norris (1989) | Western North Atlantic | 57 | 23 | 3 | NN nannoplankton stratigraphy |
| Head and Norris (2003) | North Atlantic | 7 | 1 | 1 | Magnetostratigraphy and NC nannoplankton stratigraphy from the same section |
| Head et al. (1989) | Labrador Sea | 9 | 5 | 3 | NN and CN nannoplankton stratigraphy at the same site |
| Heilmann-Clausen (1985) | North Sea | 62 | 54 | 3 | NP nannofossil zones on the same section |
| Heilmann-Clausen (1987) | Danish Basin | 152 | 100 | 4 | Synthesis of records from the North Sea area, correlation to Boreal ammonite zones (see conversions in Supplement File 1) |
| Heilmann-Clausen and Van Simaeys (2005) | Danish North Sea | 48 | 30 | 3 | NP nannofossil zonation |
| Helby and McMinn (1992) | Northwest Australia | 139 | 104 | 3 | CC nannofossil zonation on the same section |
| Helby et al. (1987) | Australia | 241 | 66 | 4 | Synthesis, calibrated to stages using industry information, Albian–Danian with independent age control from foraminiferal and nannoplankton zones |
| Hoek et al. (1996) | Israel | 73 | 69 | 3 | CC and UC nannofossil events |
| Hollis et al. (2009) | New Zealand | 51 | 46 | 3 | NP nannofossil stratigraphy on the same section |
| Houben et al. (2011) | Falkland Islands, South Atlantic | 35 | 32 | 1 | Oi-1 isotope event, the age of which is then transferred to the Geomagnetic Polarity Time Scale |
| Houben et al. (2019) | Alabama, USA | 37 | 30 | 1 | Magnetostratigraphy and NP nannoplankton stratigraphy on the same section |
| Iakovleva and Heilmann-Clausen (2010) | Siberia | 52 | 35 | 2 | Magnetostratigraphy on the same section |
| Ioannides et al. (1988) | France | 157 | 152 | 3 | Boreal ammonite stratigraphy (see conversions in Supplement File 1) |
| King et al. (2018) | Crimea | 59 | 48 | 3 | NP nannofossil stratigraphy on the same samples |
| Kirsch (1991) | Bad Tölz, southern Germany | 94 | 66 | 3 | Planktonic foraminifer stratigraphy, data not shown |
| Köthe (2012) | Northwest Germany | 65 | 0 | 3 | NP nannoplankton stratigraphy in the same sections (for conversions see Supplement File 1) |
| Köthe et al. (1988) | Pakistan | 58 | 50 | 3 | Nannoplankton stratigraphy on the same sections |
| Krijgsman et al. (1995) | Mediterranean (Gibliscemi) | 10 | 7 | 1 | Magnetostratigraphy with planktonic foraminifer stratigraphy on the same section |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Kuhlman et al. (2006) | Central North Sea | 4 | 0 | 1 | Magnetostratigraphy with foraminifer stratigraphy on the same section |
| Lebedeva et al. (2013) | Omsk, southwest Siberia | 83 | 68 | 1 | Magnetostratigraphy and CC nannoplankton stratigraphy on the same section |
| Leereveld (1995) | Caravaca, southern Spain | 145 | 105 | 3 | Tethyan ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Leereveld (1997a) | Caravaca, southern Spain | 134 | 125 | 3 | Tethyan ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Leereveld (1997b) | Caravaca, southern Spain | 146 | 134 | 3 | Tethyan ammonite stratigraphy on the same section |
| Londeix and Jan Du Chene (1998) | Bordeaux, France | 21 | 16 | 3 | NN nannoplankton stratigraphy |
| Louwye et al. (2004) | Belgium | 6 | 0 | 3 | NN nannoplankton stratigraphy on the same section |
| Louwye et al. (2008) | Porcupine Basin, Ireland | 17 | 11 | 1 | Magnetostratigraphy on the same section |
| Mao and Mohr (1992) | Kerguelen Plateau, Antarctica | 75 | 70 | 3 | CC nannofossil stratigraphy on the same section |
| Marret et al. (2020) | Global | 0 | 0 | – | Surface sediment data |
| Masure (1988) | Côte D'Ivoire margin | 140 | 112 | 3 | CC nannofossil stratigraphy on the same section |
| Masure et al. (1998) | Côte D'Ivoire margin | 90 | 57 | 3 | CP and CC nannoplankton stratigraphy on the same section |
| Matsuoka et al. (1987) | Japan | 20 | 0 | 3 | N foraminifer events on the same section |
| Matthiessen and Brenner (1996) | Spitsbergen | 3 | 0 | 1 | Magnetostratigraphy on the same section |
| McLachlan et al. (2018) | Western Canada | 77 | 71 | 1 | Magnetostratigraphy on the same site |
| McMinn (1992) | Northwest Australia | 16 | 3 | 3 | CP nannofossil stratigraphy and N planktonic foraminifer stratigraphy |
| McMinn (1993) | Northwest Australia | 9 | 0 | 3 | CN nannoplankton stratigraphy on the same section |
| Mohr and Mao (1997) | Kerguelen Plateau, Maud Rise, Antarctica | 73 | 70 | 1 | Magnetostratigraphy, CC nannoplankton stratigraphy |
| Montanari et al. (1997) | Contessa, Gubbio, Italy | 26 | 16 | 1 | Magnetostratigraphy, foraminifer and nannoplankton stratigraphy |
| Monteil (1992) | France | 152 | 134 | 3 | Tethyan ammonite stratigraphy, partly overwritten by Monteil (1993) (for conversions see Supplement File 1) |
| Monteil (1993) | France | 152 | 140 | 3 | Some sections calibrated to Tethyan ammonite stratigraphy, some only indicated stages (for conversions see Supplement File 1) |
| Mudge and Bujak (1996) | North Sea | 66 | 33 | 3 | Synthesis, using P planktonic foraminifer and NP nannoplankton events in the same section but no data shown |
| Mudge and Bujak (2001) | Faroe Islands–Shetland Islands | 66 | 54 | 3 | NP nannoplankton zones and P planktonic foraminifer zones in the same sections but no data shown |
| Mudie (1987) | North Atlantic | 8 | 0 | 1 | Magnetostratigraphy, N foraminifer stratigraphy and NN nannoplankton stratigraphy |
| Nikitenko et al. (2008) | Siberia | 150 | 134 | 3 | Siberian ammonite stratigraphy, in the paper correlated to Tethyan ammonite zones (for conversions see Supplement File 1) |
| Nøhr-Hansen et al. (2002) | Western Greenland | 66 | 62 | 3 | NP nannofossil stratigraphy on the same section |
| Nøhr-Hansen et al. (2020) | Northeast Greenland | 150 | 66 | 4 | Ammonite zonation on the same sections but ammonite data shown separately, calibrated to stages herein |
| Olde et al. (2015) | North Sea | 94 | 88 | 3 | Boreal ammonite stratigraphy on the same section |
| Oosting et al. (2006) | Australia | 131 | 120 | 4 | Tethyan ammonite stratigraphy on Angles, France, then inferred for Site 263 (for conversions see Supplement File 1) |
| Pearce (2010) | United Kingdom | 95 | 70 | 4 | UK ammonite zonations in nearby outcrops, not able to correlate some intervals to GTS2012 |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Piasecki et al. (1992) | Greenland | 65 | 57 | 3 | NP nannofossil stratigraphy on the same section |
| Poulsen and Riding (2003) | North Sea, United Kingdom | 210 | 137 | 4 | Synthesis of Danish and British dinocyst events, calibrated to Boreal ammonite stratigraphy but presented and herein plotted against stages |
| Poulsen (1992) | Denmark | 163 | 145 | 4 | Boreal ammonite stratigraphy, synthesis |
| Poulsen (1998) | Poland | 169 | 164 | 3 | Boreal and Tethyan ammonite zones |
| Powell et al. (1996) | North Sea, United Kingdom | 59 | 55 | 1 | Magnetostratigraphy on the same sections |
| Powell (1986) | Northwest Italy | 25 | 21 | 3 | NP nannofossil stratigraphy on the same section |
| Powell (1988) | Central North Sea | 63 | 54 | 3 | NP nannofossil stratigraphy on the same sediments, no nannoplankton data directly shown |
| Powell (1992) | North Sea, United Kingdom | 66 | 23 | 4 | P planktonic foraminifer and NP nannofossil stratigraphy, no direct calibration data shown |
| Prince et al. (2008) | United Kingdom | 89 | 83 | 3 | UK ammonite stratigraphy on the same sections, herein correlated to GTS2012 |
| Pross et al. (2010) | Italy | 35 | 22 | 1 | Magnetostratigraphy and independent age control from NP nannoplankton stratigraphy |
| Quaijtaal and Brinkhuis (2012) | Alabama, USA | 37 | 30 | 1 | Magnetostratigraphy from the same section, independently established using nannoplankton and foraminifer stratigraphy |
| Quaijtaal et al. (2014) | Porcupine Basin, Ireland | 17 | 11 | 1 | Magnetostratigraphy from the same section, independently established using nannoplankton stratigraphy |
| Radmacher et al. (2014a) | Barents Sea | 101 | 71 | 4 | Ages of the lithostratigraphic framework |
| Radmacher et al. (2014b) | Zumaia, Spain | 74 | 70 | 1 | Magnetostratigraphy and UC nannoplankton stratigraphy on the same section |
| Radmacher et al. (2015) | Norwegian Sea | 113 | 66 | 4 | Regional lithostratigraphy dated using foraminifers and nannoplankton but no direct independent age constraints shown |
| Riding and Helby (2001a–g) | Northwest Australia | 182 | 100 | 4 | Nannofossil and ammonite stratigraphy but with some correlation to European and Tethyan sections (for conversions see Supplement File 1) |
| Riding and Thomas (1988) | United Kingdom | 160 | 150 | 3 | Boreal ammonite zonation on the same section (for conversions see Supplement File 1) |
| Riding and Thomas (1992) | North Sea | 202 | 145 | 4 | Boreal ammonite zonations but not directly shown in paper (for conversions see Supplement File 1) |
| Riding and Thomas (1997) | North Scotland, Isle of Skye | 166 | 155 | 3 | Boreal ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Riding et al. (2010) | Australia | 237 | 145 | 4 | Ammonites, conodonts, belemnites, bivalves, NJ nannoplankton stratigraphy and strontium isotopes but these data not shown in the paper |
| Riley and Fenton (1982) | United Kingdom, France | 166 | 160 | 3 | Boreal ammonite stratigraphy on the same sections |
| Schiøler (1993) | Denmark | 72 | 66 | 4 | Stages, independent age constraints come from nannoplankton, not shown |
| Schreck and Matthiessen (2014) | Northern Iceland | 14 | 5 | 1 | Magnetostratigraphy with NN nannoplankton and diatom stratigraphy |
| Schreck et al. (2012) | Northern Iceland | 15 | 2 | 1 | Magnetostratigraphy with NN nannoplankton and diatom stratigraphy |
| Schreck et al. (2013) | Northern Iceland | 15 | 2 | 1 | Magnetostratigraphy with NN nannoplankton and diatom stratigraphy |
| Schreck et al. (2017) | Northern Iceland | 15 | 2 | 1 | Magnetostratigraphy with NN nannoplankton and diatom stratigraphy |
| Shulgina et al. (1994) | Siberia | 145 | 132 | 3 | Boreal ammonite stratigraphy on the same sections (for conversions see Supplement File 1) |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Skupien (2004) | Slovakia | 123 | 99 | 3 | Boreal ammonite stratigraphy (for conversions see Supplement File 1) |
| Skupien and Vasícek (2002) | Czech Republic | 131 | 113 | 3 | Tethyan ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Slimani and Louwye (2011) | Belgium | 75 | 62 | 4 | Regional lithostratigraphy calibrated to belemnite stratigraphy, tied to type Maastrichtian |
| Śliwińska et al. (2012) | Danish North Sea | 34 | 25 | 1 | Magnetostratigraphy and NP nannoplankton on the same section |
| Sluijs et al. (2003) | Tasmania | 37 | 30 | 2 | Magnetostratigraphy on the same section but no independent chron assignment |
| Smelror et al. (1991) | Spain | 168 | 158 | 3 | Tethyan ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Smelror (1988a) | Greenland | 167 | 160 | 3 | Boreal ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Smelror (1988b) | Svalbard, Norway | 168 | 160 | 3 | NW European ammonite stratigraphy, herein calibrated to the Boreal zonation (for conversions see Supplement File 1) |
| Smelror (1994) | Swabia | 167 | 165 | 4 | Ammonite and foraminifer stratigraphy but herein calibrated against stages |
| Smelror and Dietl (1994) | Southern Germany | 167 | 165 | 3 | Boreal ammonite stratigraphy on the same section |
| Smelror and Lominadze (1989) | Caucasus | 166 | 163 | 3 | Boreal ammonite stratigraphy from the same section (for conversions see Supplement File 1) |
| Soliman et al. (2012) | Gulf of Suez, Egypt | 54 | 14 | 3 | NP and NN nannoplankton stratigraphy on the same section |
| Steeman et al. (2020) | Angola | 60 | 35 | 3 | P and E foraminifer stratigraphy on the same section |
| Stover and Hardenbol (1994) | Belgium | 34 | 28 | 3 | NP nannoplankton stratigraphy on the same sections |
| Strauss and Lund (1992) | Germany | 18 | 6 | 3 | Nannoplankton stratigraphy on the same sections |
| Thorn et al. (2009) | Seymour Island, Antarctica | 68 | 65 | 4 | The position of the K–Pg boundary |
| Tocher (1987) | New Jersey Shelf, USA | 73 | 66 | 3 | Planktonic foraminifer stratigraphy on the same samples |
| Tocher and Jarvis (1994) | Fumichon, France | 100 | 95 | 3 | Boreal ammonite stratigraphy on the same section |
| Tocher and Jarvis (1995) | Northwest France | 101 | 92 | 3 | Boreal ammonite stratigraphy on the same section |
| Tocher and Jarvis (1996) | Northwest France, southern United Kingdom | 110 | 95 | 3 | Boreal ammonite stratigraphy on the same section (for conversions see Supplement File 1) |
| Torricelli (2000) | Southern Italy | 131 | 100 | 1 | Integrated bio-magneto-cyclostratigraphic framework but only stages shown in the paper |
| Torricelli (2006) | Piobbico, Italy | 113 | 100 | 3 | NC nannoplankton stratigraphy on the same section |
| Torricelli and Rosa Amore (2003) | Southern Italy | 101 | 72 | 3 | CC nannoplankton stratigraphy on the same section |
| Torricelli et al. (2006) | Tremp Basin, northern Spain | 53 | 51 | 3 | P planktonic foraminifer and NP nannoplankton stratigraphy on the same section |
| Türkecan et al. (2018) | Turkey | 18 | 14 | 3 | NN nannofossil and M foraminifer stratigraphy from the same section |
| Van de Schootbrugge et al. (2019a) | United Kingdom, Arctic | 189 | 174 | 3 | Boreal ammonite stratigraphy on the same section |
| Van de Schootbrugge et al. (2019b) | Northern Germany | 202 | 178 | 3 | Boreal ammonite stratigraphy |
| Van Mourik and Brinkhuis (2005) | Italy | 37 | 33 | 1 | Magnetostratigraphy on the same section |
| Van Mourik et al. (2001) | Offshore Florida | 39 | 35 | 1 | Magnetostratigraphy and CP nannoplankton stratigraphy on the same section |
| Van Simaeys et al. (2004) | Belgium | 33 | 22 | 3 | NP nannoplankton stratigraphy on the same sections |
| Van Simaeys et al. (2005) | Rhine Graben | 33 | 22 | 1 | Magnetostratigraphy on the same section |
| Vellekoop et al. (2015) | Tunisia | 67 | 65 | 3 | P foraminiferal zones on the same section |

**Table 1.** Continued.

| Reference | Geography (location) | Age base | Age top | Tier | Calibrated to |
|---|---|---|---|---|---|
| Versteegh (1997) | North Atlantic Ocean, Italy | 3 | 2 | 1 | Isotope stages, herein recalibrated to NN and CN nannoplankton zones |
| Versteegh and Zevenboom (1995) | Southern Italy | 28 | 0 | 1 | Magnetostratigraphy on the same section |
| Vieira et al. (2020) | North Sea | 59 | 56 | 3 | NP nannofossil and P foraminifer stratigraphy |
| Williams and Bujak (1977) | Tropical and North Atlantic Ocean | 25 | 0 | 5 | Stages, no independent age control given |
| Williams et al. (1993) | Northern Hemisphere | 210 | 0 | 5 | Stages, no independent age control given |
| Willumsen (2012) | New Zealand | 70 | 64 | 3 | P foraminifer stratigraphy |
| Wilpshaar et al. (1996) | Central Italy | 35 | 22 | 3 | CP an NP nannoplankton and N planktonic foraminifer stratigraphy |
| Woollam and Riding (1983) | United Kingdom | 209 | 140 | 3 | Boreal ammonite stratigraphy (for conversions see Supplement File 1) |
| Wrenn and Kokinos (1986) | Gulf Coast | 10 | 0 | 1 | Magnetostratigraphy on the same section |
| Zegarra and Helenes (2011) | Equatorial eastern Pacific | 18 | 0 | 1 | Independent age model from magnetostratigraphy, nannoplankton and foraminifer stratigraphy |
| Zevenboom (1995) | Italy | 26 | 16 | 3 | NP and NN nannoplankton stratigraphy on the same sections |

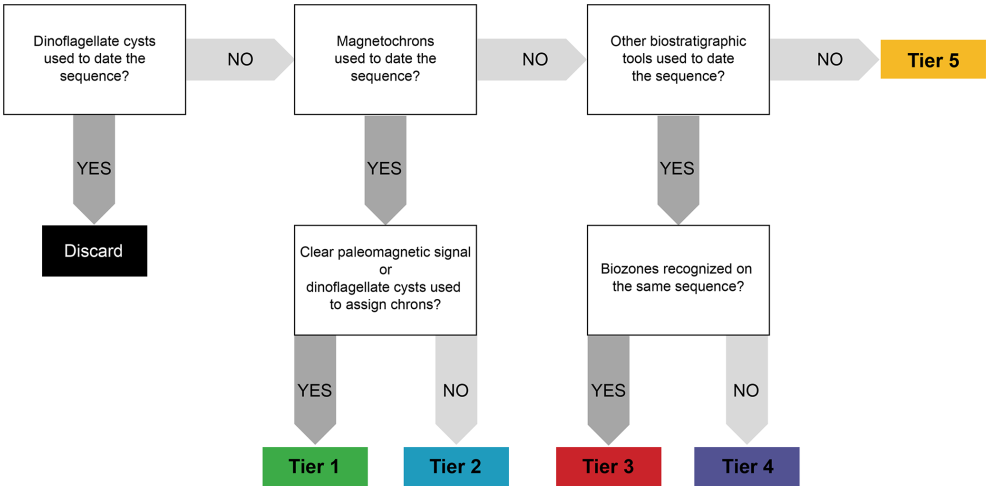

**Figure 1.** Decision tree for including studies in this review and categorization criteria for the five tiers.

2021, for surface sediment station locations, modernsp.csv in Bijl, 2021, for dinocyst species at those stations).

Each event entry in DINOSTRAT (Dinoevents_Jan2021.csv in Bijl, 2021) 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, 2021; with use of http://paleolatitude.org, last access: 1 February 2022 ; 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.

## 3 The database

### 3.1 Sites

DINOSTRAT currently contains dinocyst events from 199 publications and 188 sites. The wider North Atlantic–European area is strongly overrepresented (Fig. 2). Few sites are from the Pacific Ocean, the southern Atlantic and Indian Ocean, and the equatorial region. This probably reflects a genuine bias in the available information because of focus of the community 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.

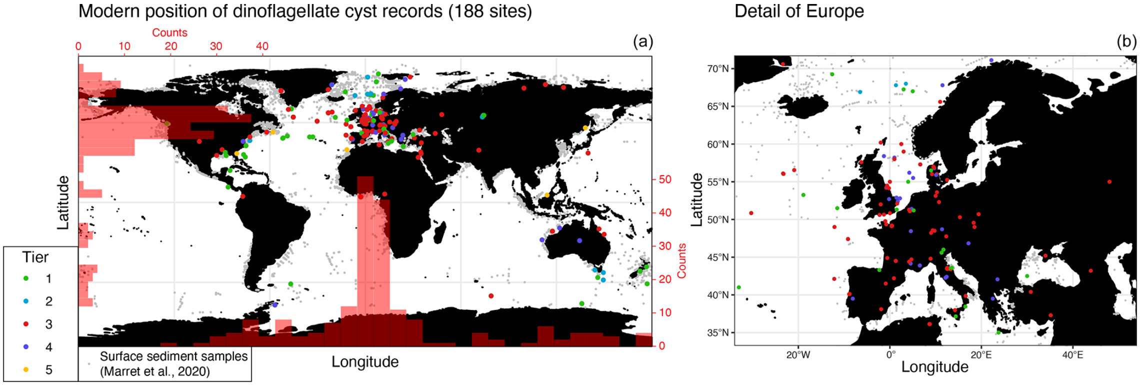

**Figure 2.** Present-day geographic distribution of sedimentary sequences used in DINOSTRAT (colors of the dots correspond to the to the tier status to which the site has been allocated) and surface sediment stations (in grey dots; Marret et al., 2020; Mertens et al., 2014). **(a)** Global. Red scale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

The paleolatitudinal position of the sites through time confirms the strong overrepresentation 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 on some occasions to magnetostratigraphy (tiers 1 and 2; Fig. 3). Ammonite zones presented in the papers often had to be converted to those in GTS2012, which is not always straightforward, as the zone definitions have changed through time (Ogg and Hinnov, 2012a, b). The ammonite zonations are prone to regional diachroneity, which was demonstrated particularly for the Late Jurassic (Ogg and Hinnov, 2012b). 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 1.0 includes over 8500 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), Upper Cretaceous (Maastrichtian), Oligocene (Rupelian) and Miocene (Serravallian; 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 allow 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 families/subfamilies and of a selection of quasi-synchronous dinocyst events. Users can filter DINOSTRAT by locality (to present the stratigraphic order of events per site) and/or by taxon (to see the geographic variability in the range of any taxon), to serve their purposes.

### 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, $n=5$) 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 the modern latitudinal spread of these species to that of the past and of their age and the latitude of their oldest first occurrence (Supplement File 2 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* and *Tuberculodinium vancampoae* (Fig. 4). *Lingulodinium machaerophorum* has a first occurrence at 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* and *Tuberculodinium vancampoae* had

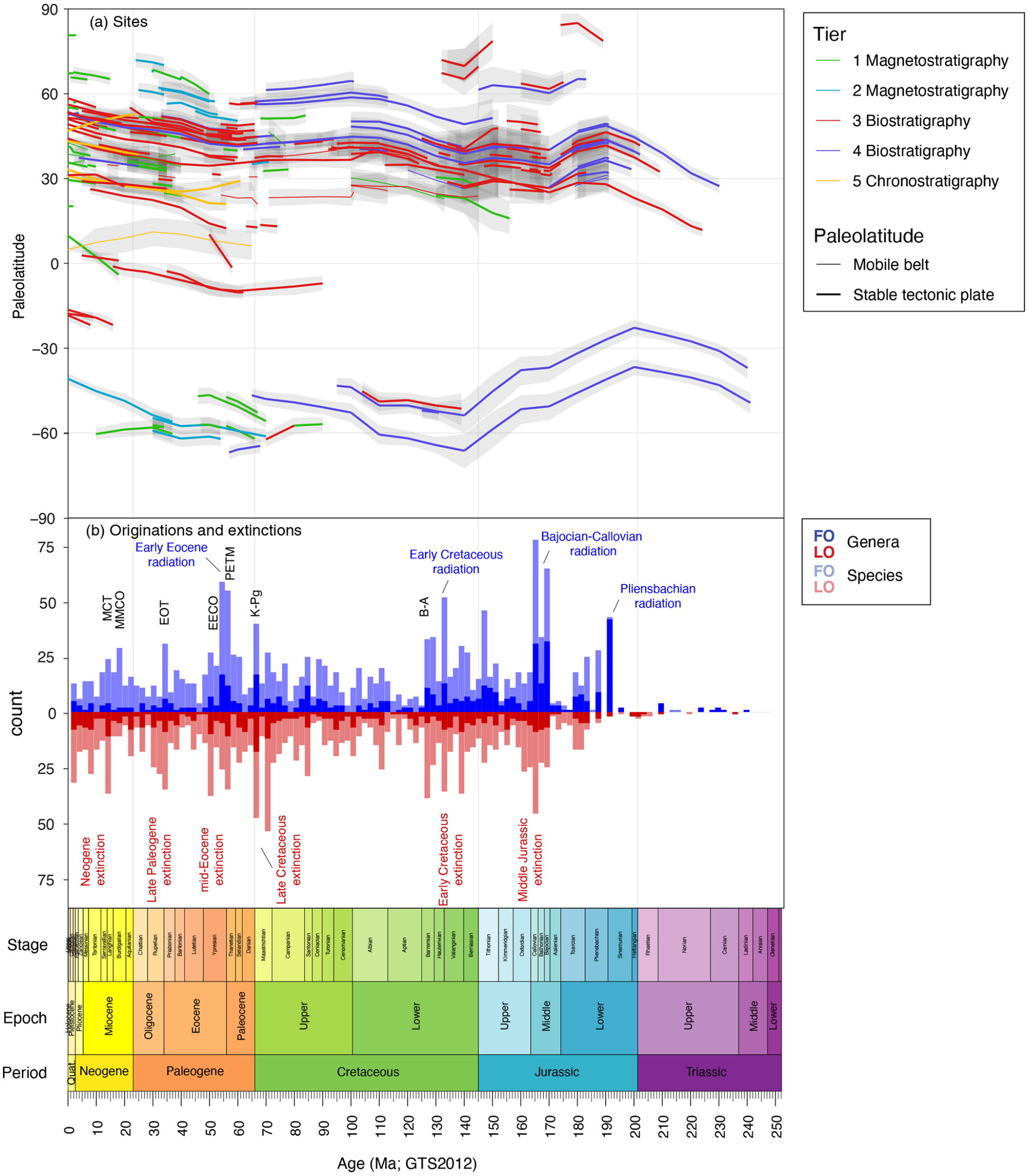

**Figure 3.** Data in DINOSTRAT. **(a)** Paleolatitude and age span of sites used in DINOSTRAT. Colors correspond to tier; line thickness separates sites on stable oceanic or continental plates from those in mobile orogenic belts. Grey envelopes represent the error of the paleolatitude reconstruction inherited from the paleomagnetic reference frame (see 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) and Miocene climatic transition (MCT). Extinction and radiation phases in dinocysts are highlighted in red and blue text, respectively.

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 in only one hemisphere. Several modern taxa (e.g., *Bitectatodinium spongium*, *Polykrikos* spp., *Protoperidinium* spp., *Echinidinium* spp., most *Islandinium* 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 (e.g., because of selective degradation; Zonneveld et al., 2010).

### 3.2.2 Dinocyst (sub)families

Range charts of the sites in DINOSTRAT are provided in the Supplement (see "Sites" folder in Supplement File 2). The age-over-paleolatitude entry in DINOSTRAT allows evaluation of the latitudinal difference in event ages for each individual species in DINOSTRAT ($n = 1914$), as well as for groupings per genus ($n = 460$) and family ($n = 28$) (Supplement File 2). Users can produce/adapt these plots themselves with the help of the R markdown script "plot creator.Rmd" in Bijl (2021). 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 of Supplement File 2). 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 of when and where phases of strong diversification and extinction occurred in that (sub)family. Second, as with the plots of modern species, they show not only 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 (e.g., MacRae et al., 1996), DINOSTRAT presents the fundamental spatio-temporal observations that underpin these compilations. Thirdly, the plots allow the presentation of the database in such 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.* The Areoligeraceae range from the Bathonian (∼ 168 Ma, FOs of *Adnatosphaeridium* spp. and *Senoniasphaera* spp.) to the mid-Miocene (∼ 18 Ma, LO of *Chiropteridium galea*). Areoligeraceae seem to range for longer in Northern Hemisphere (NH) mid-latitudes (FO ∼ 169 Ma, LO ∼ 18 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.* There are quasi-synchronous events of species of *Areoligera*, *Chiropteridium*, *Glaphyrocysta*, *Palynodinium*, *Schematophora* and *Senoniasphaera*,, particularly in the Late Cretaceous and Paleogene (Fig. 5). Many taxa in this subfamily however show strongly diachronous events between hemispheres.

Family Ceratiaceae (Fig. 6)

*Range.* The Ceratiaceae first appear in the Tithonian (∼ 152 Ma, FO of *Muderongia simplex*) in NH mid-latitudes, represent a diverse group in the Early Cretaceous and have an LO in the latest Cretaceous (∼ 66 Ma, LO of *Odontochitina operculata*).

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

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*).

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

Family Goniodomaceae (Fig. 8)

*Range.* Goniodomaceae first appear in the mid-Tithonian (∼ 150 Ma, FO of *Hystrichosphaeridium petilum*) in the NH mid-latitudes; most entries are from the Paleogene and continue with the modern species *Polysphaeridium zoharyi* and *Tuberculodinium vancampoae*.

*Quasi-synchronous events.* Species of *Alisocysta*, *Eisenackia*, *Heteraulacacysta* and *Homotryblium* have quasi-synchronous ranges. Many species ranges in this family are notably diachronous. Although some species do seem to show similar event ages between Southern Hemisphere (SH) high latitudes and NH mid-latitudes (Fig. 8), those with multiple entries in the northern 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 ago in the geologic past, species of this family exhibited much wider latitudinal ranges (65° S–70° N).

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 (∼ 172 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).

*Quasi-synchronous events.* Several species of *Cordosphaeridium* and *Danea* and species of *Aldorfia*, *Apteodinium*, *Carpatella*, *Cooksonidinium*, *Diphyes*, *Hystrichokolpoma* and *Operculodinium* have quasi-synchronous

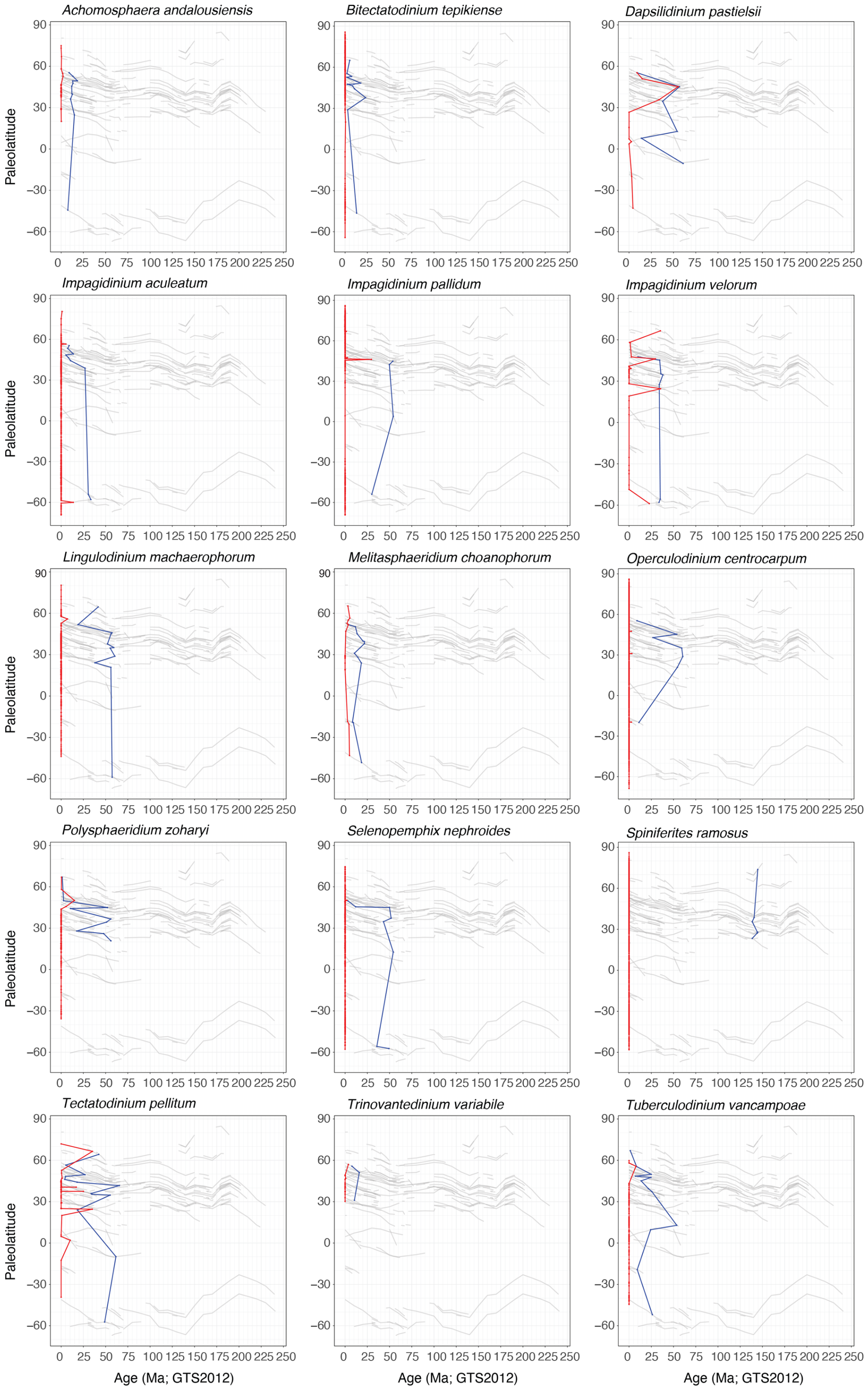

**Figure 4.** Age and paleolatitude of first (in blue) and last (in red) occurrences of selected modern dinocyst species. Last occurrences come from both the surface sediment database (Marret et al., 2020, with Mertens et al., 2014) and entries in DINOSTRAT.

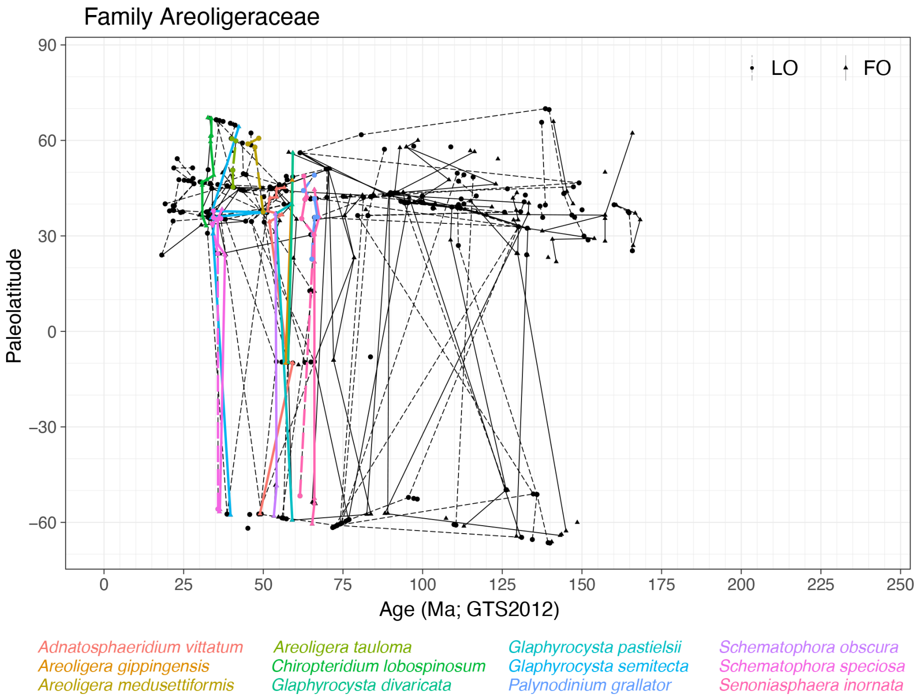

**Figure 5.** Ages and paleolatitudes of first (solid line and triangles) and last (dashed line and circles) occurrences of dinocyst species of the family Areoligeraceae. Solid and dashed lines connect first and last occurrences, respectively, for each species, between sites. Colored lines represent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

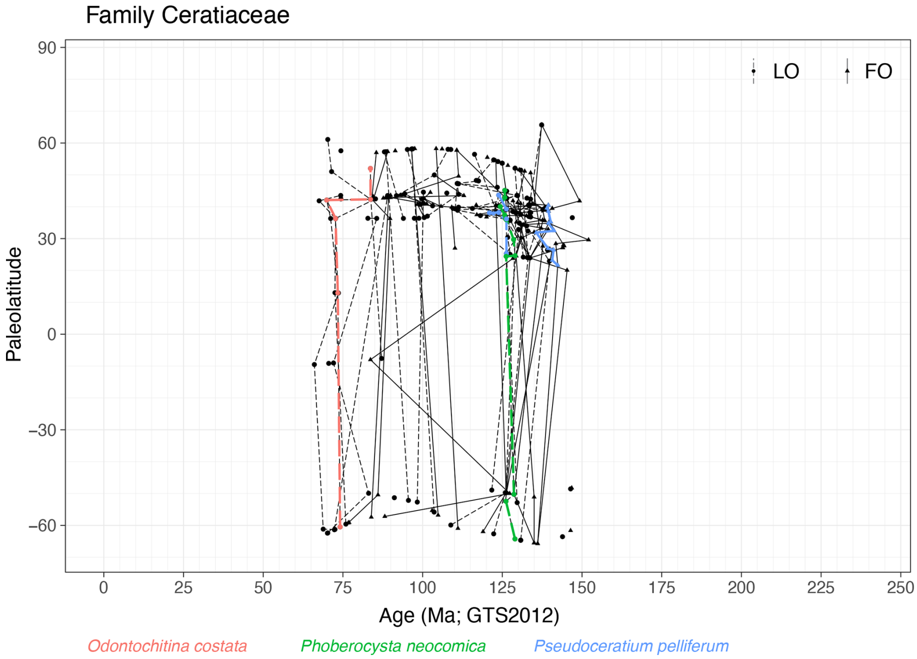

**Figure 6.** Same as Fig. 5 but for the family Ceratiaceae.

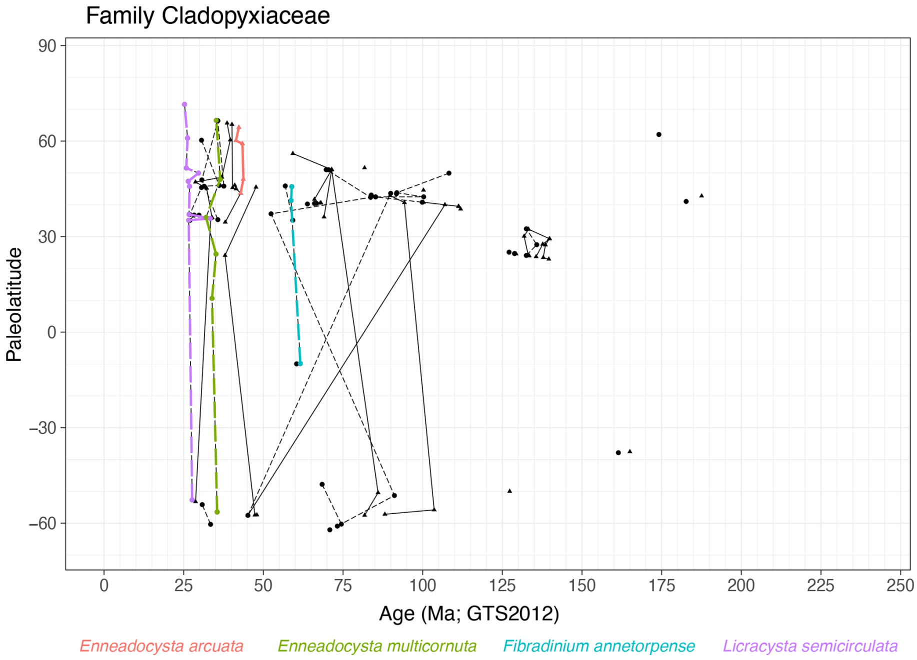

**Figure 7.** Same as Fig. 5 but for the family Cladopyxiaceae.

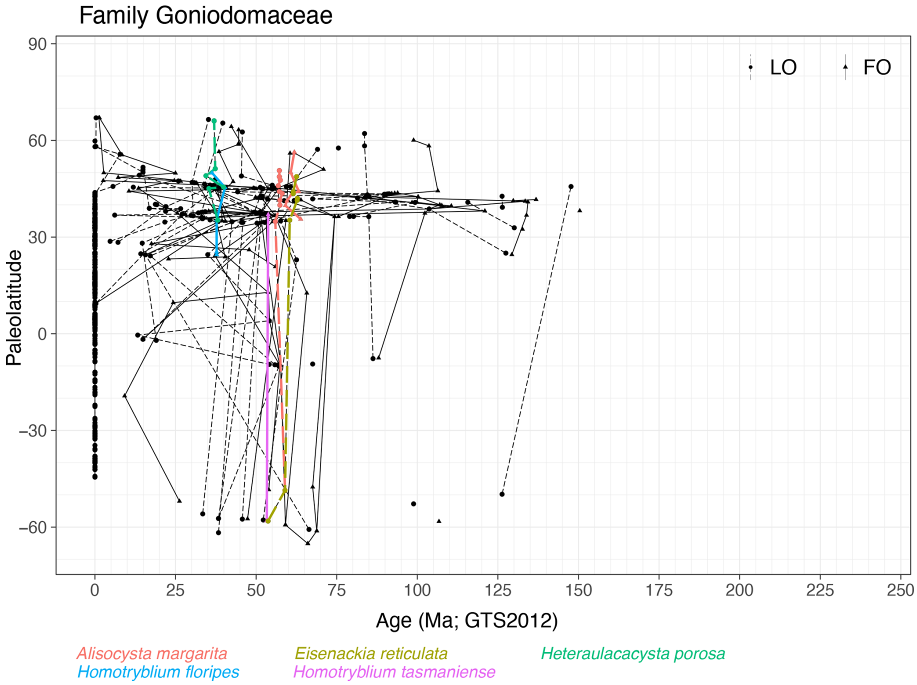

**Figure 8.** Same as Fig. 5 but for the family Goniodomaceae.

ranges. The subfamily has many entries in the Paleogene, but many of these events are not synchronous latitudinally.

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.

*Quasi-synchronous events.* Species of *Achomosphaera*, *Ataxiodinium*, *Callaiosphaeridium*, *Corrudinium*, *Ec-*

*tosphaeropsis Hystrichodinium*, *Impagidinium*, *Spiniferites* and *Unipontidinium* have quasi-synchronous events (Fig. 10). Events of species of *Escharisphaeridia* spp., *Gonyaulacysta* spp. and *Tubotuberella* spp. range for slightly longer in Northern Hemisphere high latitudes than in mid-latitudes. Many species in this subfamily are strongly diachronous.

### Subfamily Leptodinioideae (Fig. 11)

*Range.* Leptodinioideae first appear in the Aalenian (∼ 172 Ma, FO of *Meiourogonyaulax valensii*) and include 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*).

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

### 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* and *Trichodinium* spp. have remarkably consistent events.

### Family Mancodiniaceae (Fig. 13)

*Range.* Species of Mancodiniaceae occur in sediments from the late Sinemurian (∼ 190 Ma) to the mid-Bathonian (∼ 167 Ma) and seem quasi-synchronous latitudinally.

### Family Pareodiniaceae (Fig. 14)

*Range.* Pareodiniaceae first appear in the late Toarcian (∼ 176 Ma, FO of *Pareodinia halosa*) and range in NH mid-latitudes into the Cenomanian (∼ 95 Ma, LO of *Batioladinium jaegeri*). Events of species in *Carpathodinium*, *Pareodinia* (both NH only), *Aprobolocysta* and *Batioladinium* appear to be quasi-synchronous.

### Family Scriniocassiaceae (Fig. 15)

*Range.* Scriniocassiaceae range from the Pliensbachian (∼ 187 Ma, FO of *Scriniocassis weberi*) to the Bajocian (∼ 169 Ma, LO of *Scriniocassis weberi*) and comprise only three species. Events from this family are only reported from the Northern Hemisphere.

### Family Shublikodiniaceae (Fig. 16)

*Range.* Cysts from the family Shublikodiniaceae occur in the Late Triassic (FO of *Rhaetogonyaulax wigginsii* in the Carnian, ∼ 230 Ma) to Early Jurassic (LOs of *Dapcodinium sacculus* and *Dapcodinium ovale* in the mid-Pliensbachian, 187 Ma).

*Quasi-synchronous events.* The LO of *Rhaetogonyaulax rhaetica* close to the Triassic–Jurassic boundary and LO of *Dapcodinium priscum* are quasi-synchronous.

### Family uncertain (Fig. 17)

*Remarks.* This group of which the family is uncertain contains 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.

### Order uncertain

### Family Comparodiniaceae (Fig. 18)

*Range.* Cysts from this family range from the late Sinemurian (191 Ma, FO of *Valvaeodinium* spp.) to the mid-Valanginian (134 Ma, LO of *Biorbifera johnwingii*). All species except *Valvaeodinium spinosum* and *Biorbifera ferox* have ranges restricted to the Northern Hemisphere.

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

### Family Stephanelytraceae (Fig. 19)

*Range.* Stephanelytraceae cysts comprise one genus, which ranges from the Callovian (∼ 166 Ma) to the late Aptian (∼ 117 Ma) and seems quasi-synchronous.

### Order Peridiniales

### Family Heterocapsaceae (Fig. 20)

*Range.* Heterocapsaceae range from the mid-Sinemurian (195 Ma, FO of *Liasidium variabile*) to the mid-Albian (105 Ma, LO of *Angustidinium acribes*).

*Quasi-synchronous events.* Range of *Liasidium variabile* and *Parvocysta bullula*, restricted to NH mid-latitudes.

### Family Peridiniaceae

### Subfamily Deflandroideae (Fig. 21)

*Range.* Deflandroideae first occur in the Southern Hemisphere in the Oxfordian (∼ 161 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

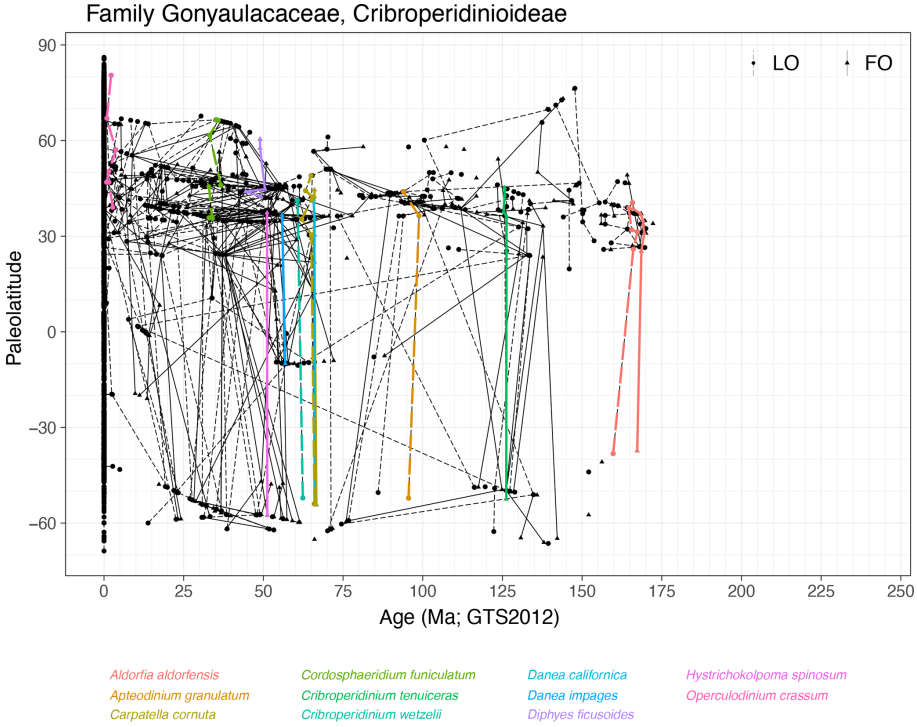

**Figure 9.** Same as Fig. 5 but for the family Gonyaulacaceae, subfamily Cribroperidinioideae.

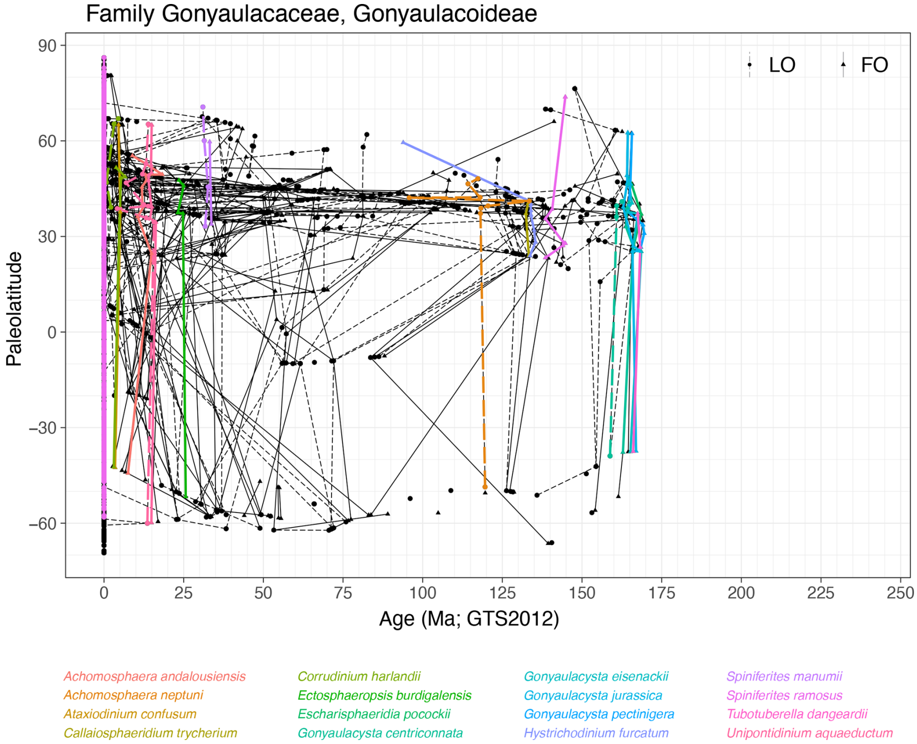

**Figure 10.** Same as Fig. 5 but for the family Gonyaulacaceae, subfamily Gonyaulacoideae.

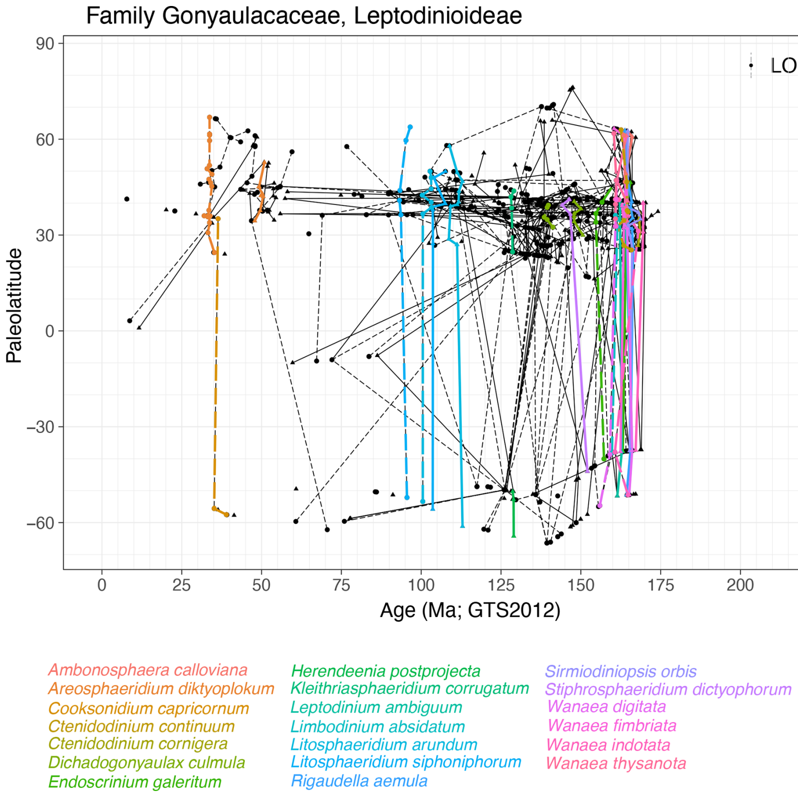

**Figure 11.** Same as Fig. 5 but for the family Gonyaulacaceae, subfamily Leptodinioideae.

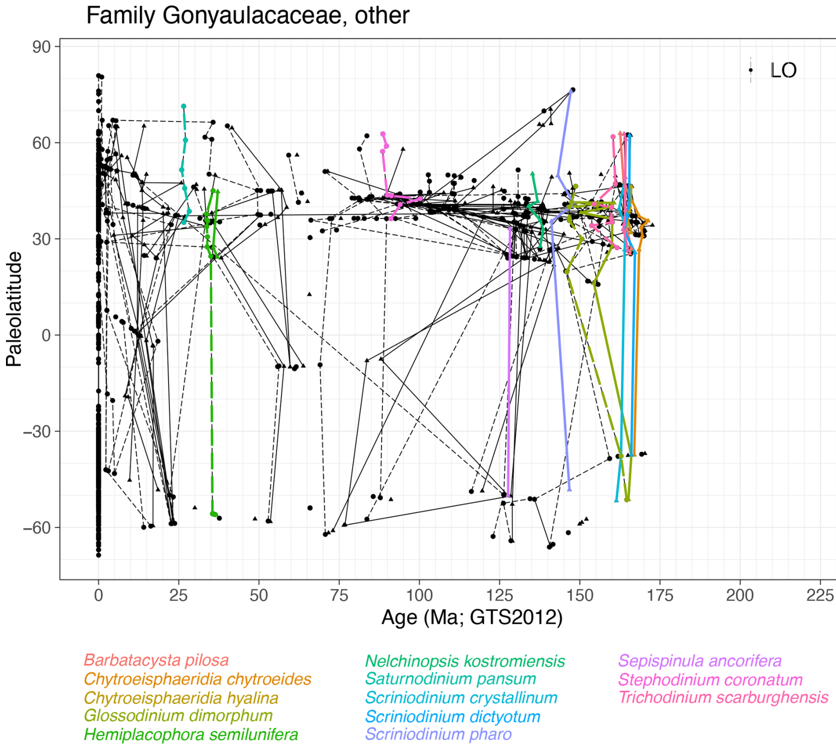

**Figure 12.** Same as Fig. 5 but for other genera in the family Gonyaulacaceae.

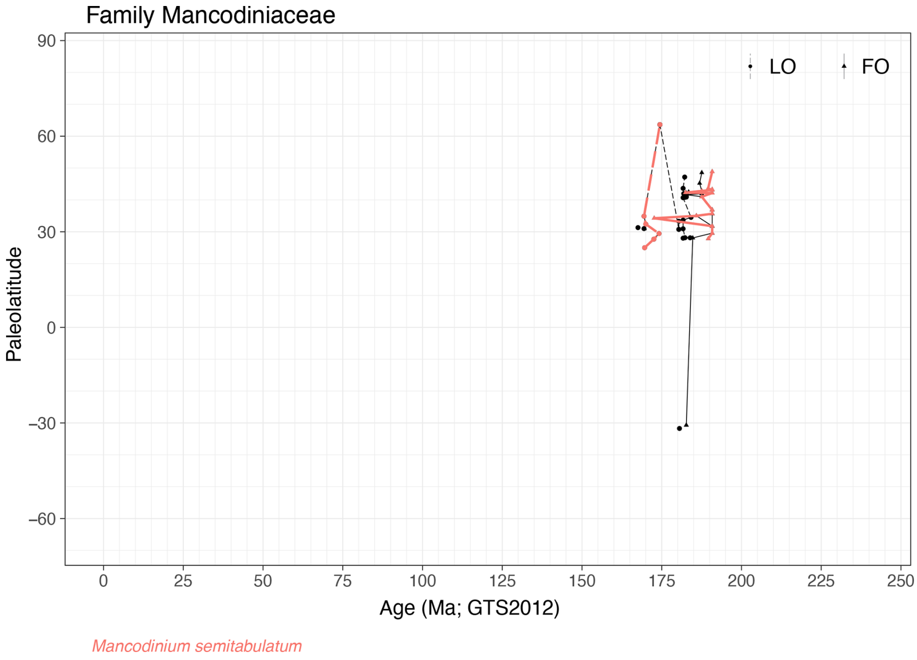

**Figure 13.** Same as Fig. 5 but for the family Mancodiniaceae.

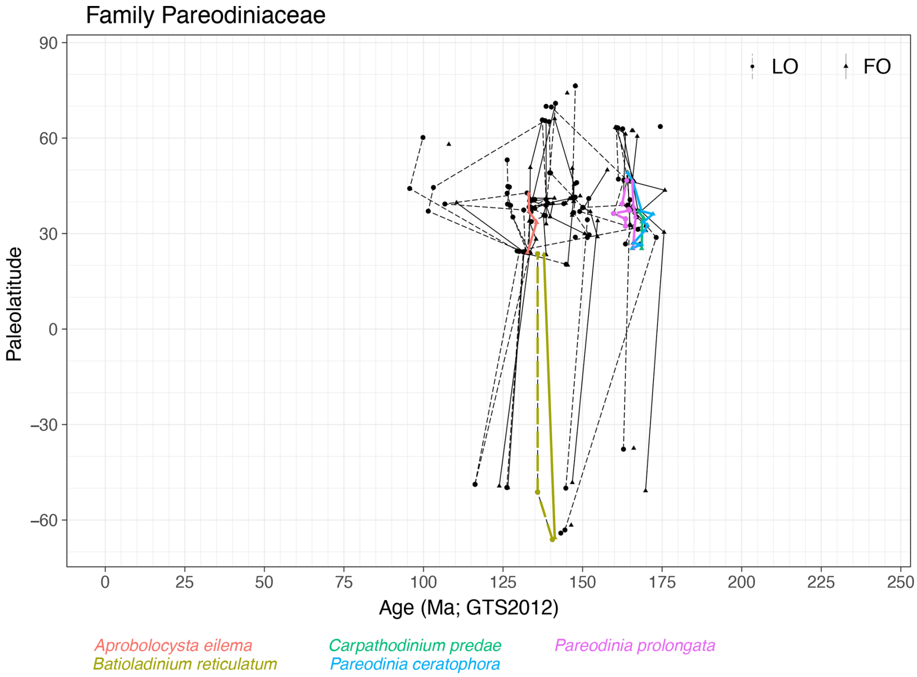

**Figure 14.** Same as Fig. 5 but for the family Pareodiniaceae.

LO of *Sumatradinium* spp. around 5 Ma and appears to range for the longest in low and middle latitudes. Deflandeoideae have many FO and LO entries in both hemispheres, particularly in the Late Cretaceous and early Paleogene.

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

Subfamily Palaeoperidinioideae (Fig. 22)

*Range.* The Palaeoperidinioideae range from the mid-Valanginian (∼ 135 Ma, FO of *Subtilisphaera perlucida*) to

**Figure 15.** Same as Fig. 5 but for the family Scriniocassiaceae.

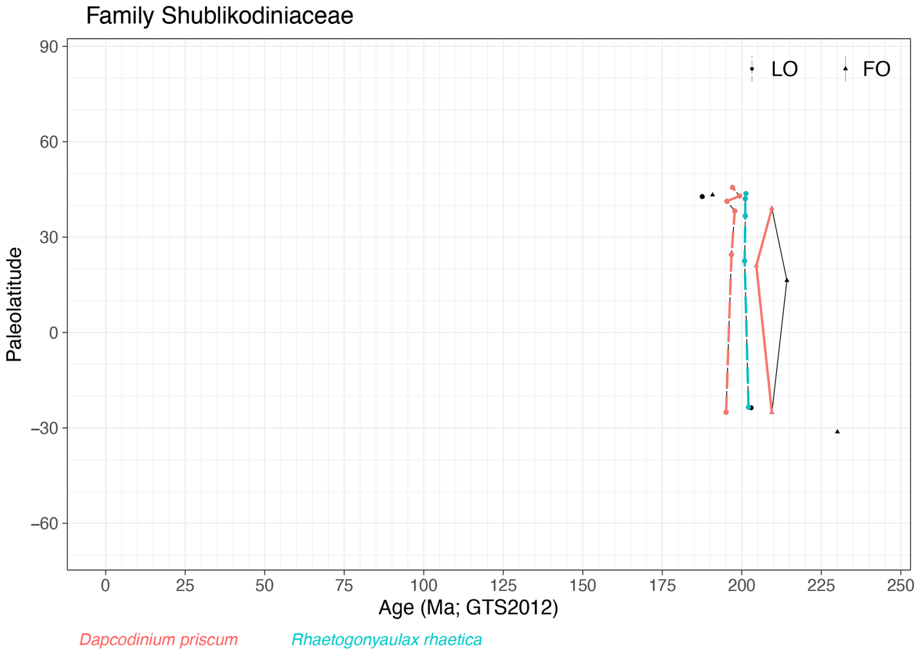

**Figure 16.** Same as Fig. 5 but for the family Shublikodiniaceae.

the late Oligocene (∼ 26 Ma, LO of *Phthanoperidinium comatum*).

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

### Subfamily Wetzelielloideae (Fig. 23)

*Range*. Wetzelielloideae range from the mid-Paleocene (∼ 62 Ma, FO of *Apectodinium homomorphum*) to the late Oligocene (∼ 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

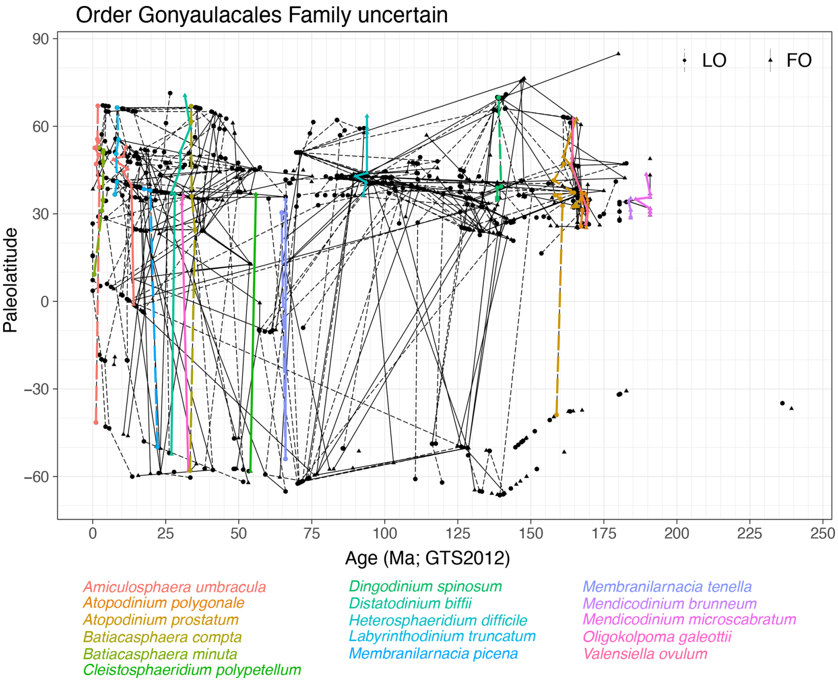

**Figure 17.** Same as Fig. 5 but for the order Gonyaulacales, family uncertain.

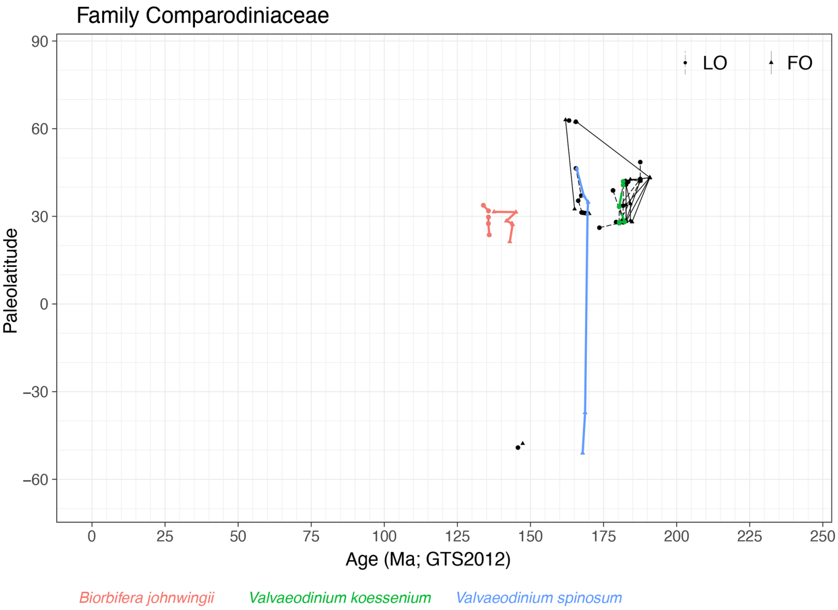

**Figure 18.** Same as Fig. 5 but for the family Comparodiniaceae.

for longer in the NH than on equal paleolatitudes in the SH. Many species lack chronostratigraphic ties in equatorial records.

### Family Peridiniaceae, other (Fig. 24)

*Remarks.* There is one quasi-synchronous event in this remaining group: the FO of *Ovoidinium cinctum* at around 129 Ma.

### Family Protoperidiniaceae (Fig. 25)

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

**Figure 19.** Same as Fig. 5 but for the family Stephanelytraceae.

**Figure 20.** Same as Fig. 5 but for the family Heterocapsaceae.

### Order Nannoceratopsiales

### Family Nannoceratopsiaceae (Fig. 26)

*Range.* Cysts from the family Nannoceratopsiaceae occur from the late Sinemurian (191 Ma, FO of *Nannoceratopsis deflandrei* subsp. *senex*) to the mid-Kimmeridgian (∼ 155 Ma, LO of *Nannoceratopsis pellucida*).

### Order Ptychodiscales

### Family Ptychodiscaceae (Fig. 27)

*Range.* This family only has entries in the Late Cretaceous (91–66 Ma), where species represent fairly synchronous stratigraphic markers. Although cysts are only

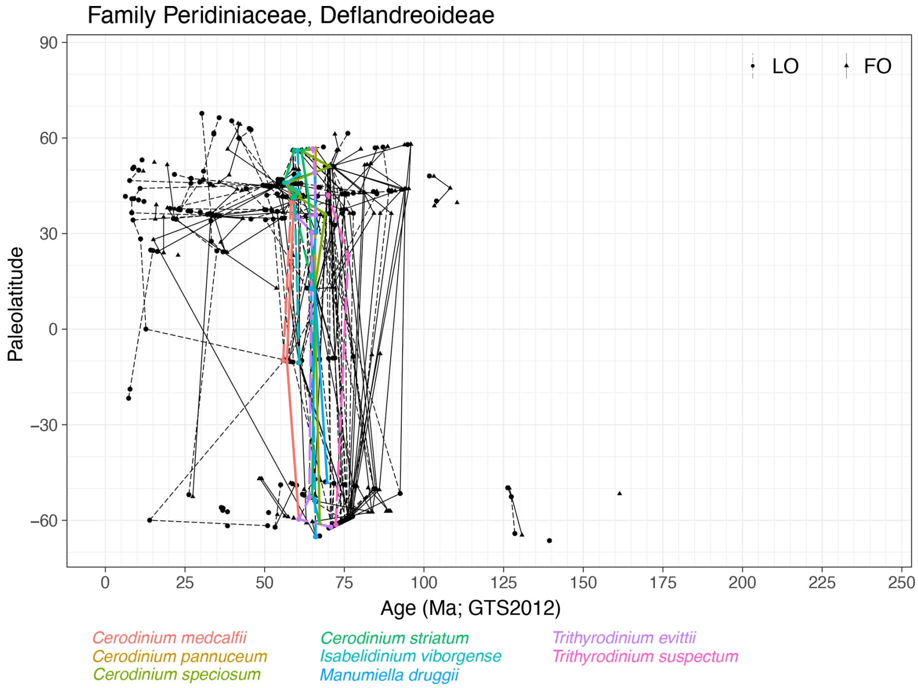

**Figure 21.** Same as Fig. 5 but for the family Peridiniaceae, subfamily Deflandreoideae.

found in a relatively short geologic time interval, motile cells of Ptychodiscaceae are known from modern plankton.

Order Suessiales

Family Suessiaceae (Fig. 28)

*Range.* Suessiaceae occur in the Triassic–Early Jurassic (229–182 Ma).

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

## 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 (Figs. 5–28). The 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. They also imply that ocean connectivity did allow dinocyst species to migrate globally, as far as their environmental tolerances permitted.

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 diachroneity 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 (FOs and LOs, respectively). The obviously 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 the reconstruction of evolutionary patterns. Although caving of material typically falsely increases the age of the oldest FOs, this is unlikely to have 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 the 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 diachroneity in LOs, although this is unlikely a large factor.

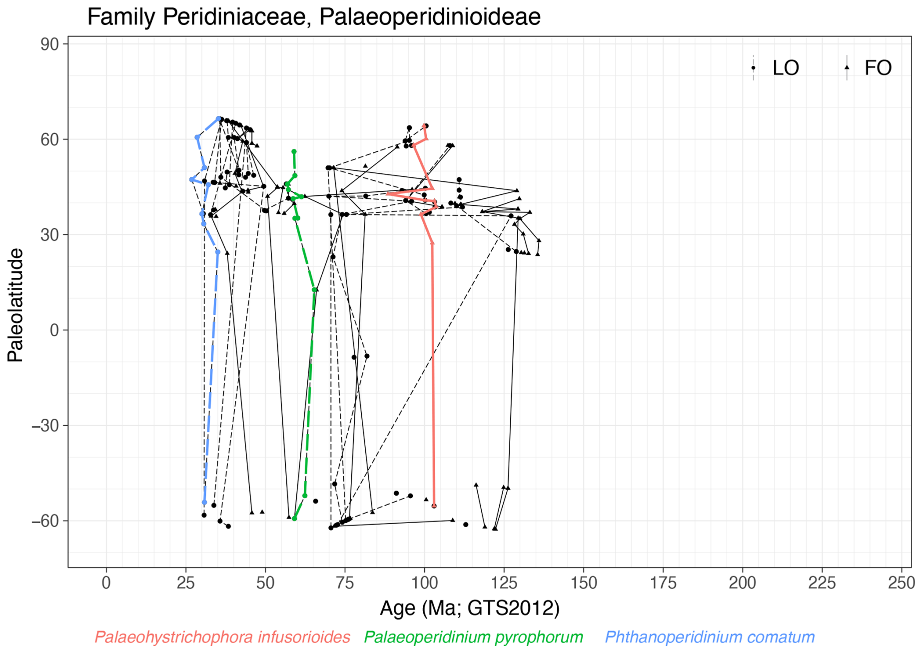

**Figure 22.** Same as Fig. 5 but for the family Peridiniaceae, subfamily Palaeoperidinioideae.

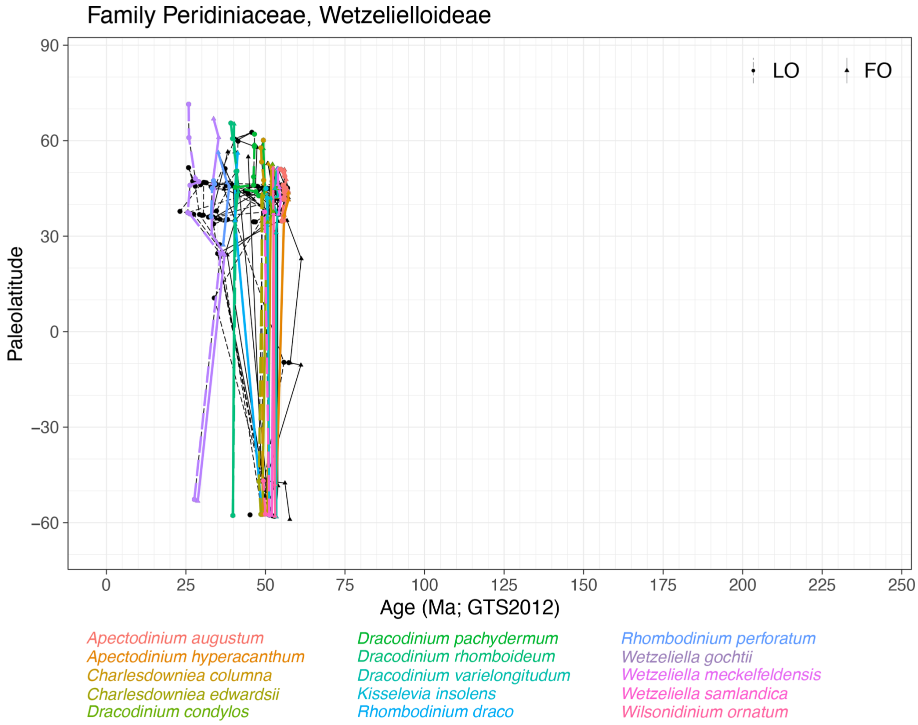

**Figure 23.** Same as Fig. 5 but for the family Peridiniaceae, subfamily Wetzelielloideae.

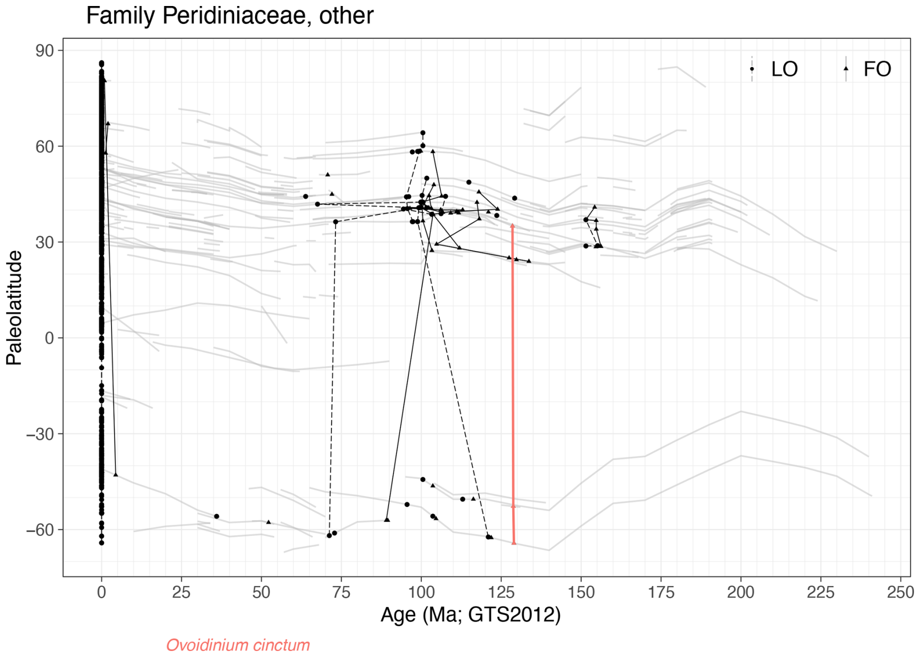

**Figure 24.** Same as Fig. 5 but for other subfamilies in the Family Peridiniaceae.

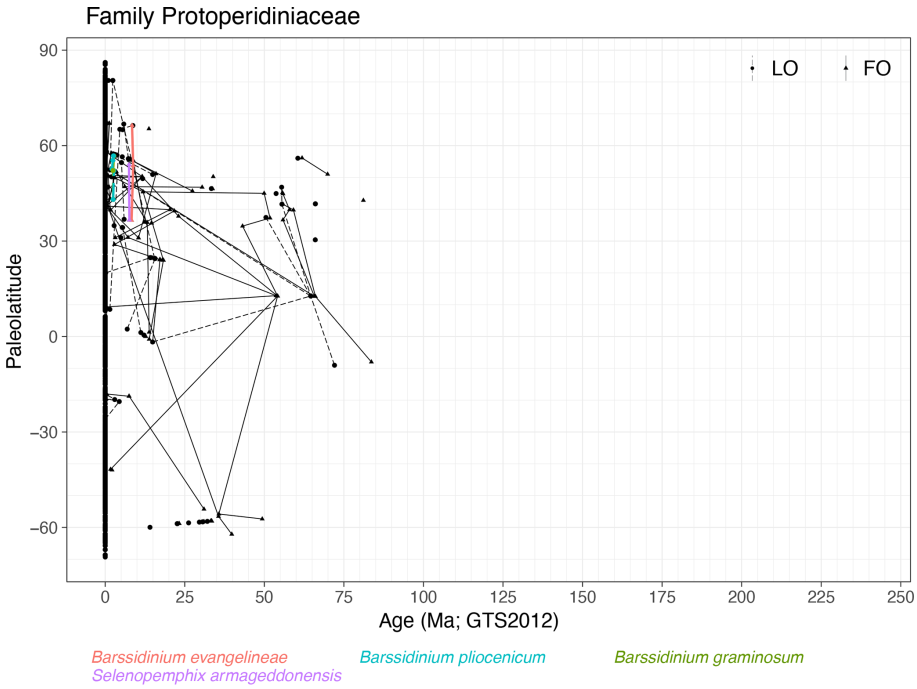

**Figure 25.** Same as Fig. 5 but for the family Protoperidiniaceae.

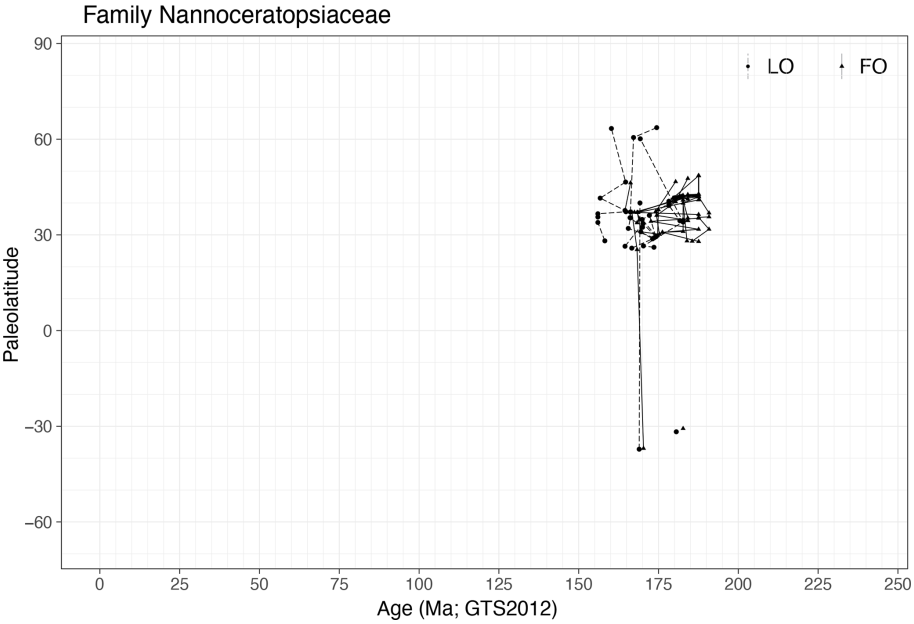

**Figure 26.** Same as Fig. 5 but for the family Nannoceratopsiaceae.

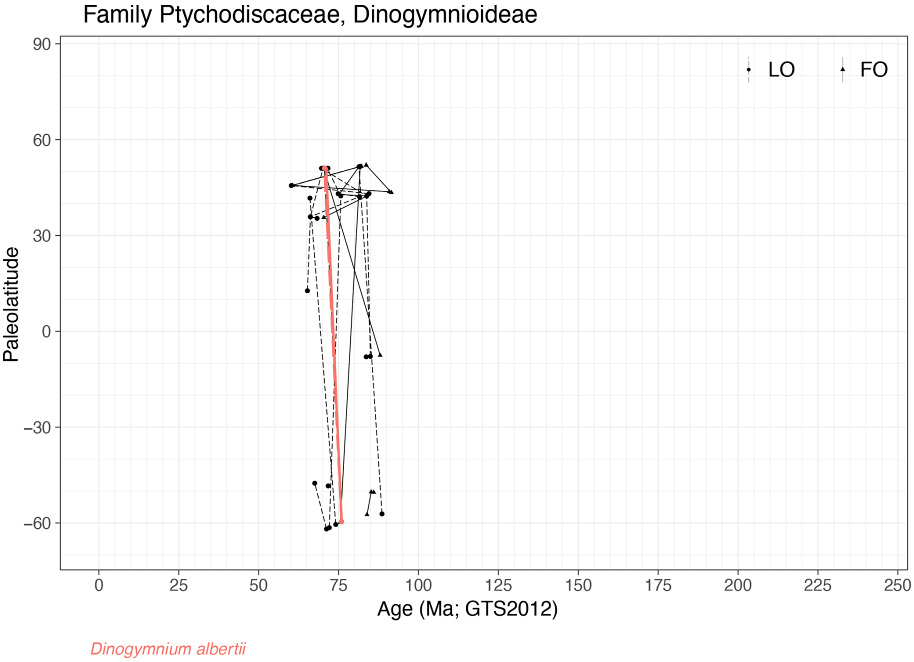

**Figure 27.** Same as Fig. 5 but for the family Ptychodiscaceae, subfamily Dinogymnioideae.

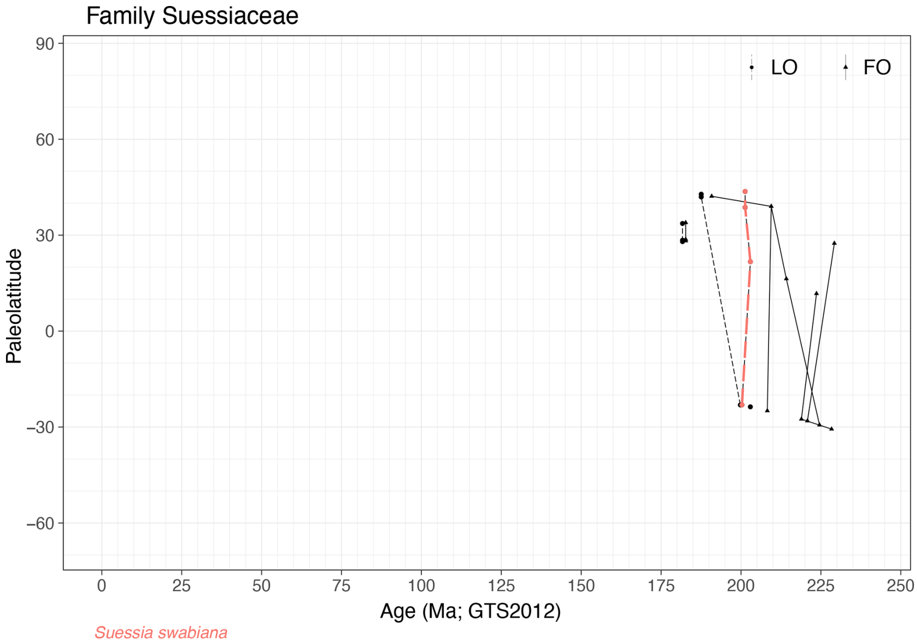

**Figure 28.** Same as Fig. 5 but for the family Suessiaceae.

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. (2022) 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 has 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 (e.g., Mertens and Carbonell-Moore, 2018), could help in 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 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 ($\sim 10^{4–5}$ years) may be related to the inherent assumption of linear sedimentation rates between age tie points. Larger diachroneity ($\sim 10^{5–6}$ 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; Petrizzo et al., 2012). Less robust are the Mesozoic ammonite zonation schemes, which have been shown to be quite latitudinally diachronous themselves (e.g., Ogg and Hinnov, 2012a, b, and references therein). The geographic variability in the ages of zone boundaries and also numerous adjustments of zone definitions throughout the past 50 years further complicate accurate tying of dinocyst events with ammonite data to GTS2012. 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 calibrated Mesozoic 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 with 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 nearshore depositional settings (Zonneveld et al., 2013; Sluijs et al., 2005; Frieling and Sluijs, 2018) that are the most environmentally dynamic. Settings in which these species occur offshore, such as in 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 diachroneity is of less concern because these events can still be used for regional stratigraphic correlation (e.g., as in Vieira and Jolley, 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 in 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).

Diachroneity 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 stratigraphic tools other than ammonites. For the Cenozoic, the diachroneity between hemispheres cannot be explained by inadequate calibration since many events are calibrated against magnetostratigraphy. For 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 the 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 presents for the first time a quantitative overview of the stratigraphic and paleolatitudinal distribution of fossil and modern dinocyst taxa. Through that, it refines with coherent, independent, open-access data the evolutionary patterns presented previously (e.g., Fensome et al., 1993; MacRae et al., 1996) and adds their latitudinal distribution through time. Following up on 60 million years of experimentation in cyst formation among a wide group of dinoflagellates (Figs. 13, 15, 16, 18–20, 26, 28), gonyaulacoid dinocysts developed their most fundamental taxonomic features in a rapid diversity phase in the Bajocian ($\sim 169$ Ma), likely on vast continental shelf areas on the European continent (Figs. 5, 9–12, 17). The extremely high diversity in gonyaulacoid dinocysts in the Late Jurassic and Cretaceous is reflected in the density of the events in DINOSTRAT. Peridinioid dinocyst taxa strongly diversified in the Late Cretaceous and Paleogene (Figs. 21–25). The decline in dinocyst diversity in the Neogene is visible in the scarcity of FOs from 25 Ma onwards (except in Protoperidinioideae). DINOSTRAT allows the further exploration of spatial patterns in dinocyst evolution in the future.

### 4.3 Functionality of DINOSTRAT

Once downloaded, DINOSTRAT can be filtered by location, allowing users to compare newly generated dinocyst chronologies to calibrated regional dinocyst events nearby. 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 are readily visualized in Supplement File 2, and these plots can be adjusted and reproduced using the R markdown file plot creator.Rmd in Bijl (2021). 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.

### 4.4 Future directions

DINOSTRAT will be regularly updated. Annual minor updates include the addition of sites, adjustments in the current entries (e.g., through the feedback process) or minor revisions in taxonomy/stratigraphy. Major updates will occur in a 3-year cycle and will be the result of updates to the geologic time scale 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.

## 5 Data availability

The database is available under a CC BY 4.0 license on GitHub (Bijl, 2021; https://github.com/bijlpeter83/DINOSTRAT.git, last access: 1 February 2022; DOI https://doi.org/10.5281/zenodo.5772616). The database consists of four .csv files: (1) 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_Jan2021.csv – the calibrated dinocyst events. plot creator.Rmd is an R markdown file to reproduce the figures presented in this paper.

## 6 Conclusions

This paper presents the database DINOSTRAT version 1.0 (Bijl, 2021), a database containing >8500 entries of regional dinocyst first and last occurrences (events) from over 1900 species, in 188 sites. The geographic distribution of sites used in DINOSTRAT is strongly concentrated in the Northern Hemisphere mid-latitudes, 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 the origin of modern dinocyst species, genera, subfamilies and families. It reviews the age range and geographic spread of 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 inadequate calibration to the chronostratigraphic timescale, false interpretations of true events, complicated species concepts or paleoceanographic reasons. In any case, this dictates caution when extrapolating ages of dinocyst events to far distances and demonstrates the need for regionally calibrated dinocyst zonations, which DINOSTRAT here provides. It further provides a solid foundation to review spatio-temporal patterns in dinocyst evolution, dispersal and extinction. DINOSTRAT is freely available under a CC BY 4.0 license. It allows the user to filter by region or by species, genus or higher taxonomic rank.

**Supplement.** Supplement File 1 is a table of conversions of published zones to those in GTS2012. Supplement File 2 is a zip file containing ages and latitudes of events in individual dinocyst species (1914 plots), grouped by genus (459 plots) and by family (27 plots), including modern cyst species (92 plots) and the range charts for all sites (188 plots). The supplement related to this article is available online at: https://doi.org/10.5194/essd-14-579-2022-supplement.

**Competing interests.** The contact author has declared that there are no competing interests.

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