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 evaluate underlying causes. For this reason, DINOSTRAT is here initiated – an open source, iterative, community-fed database intended to house all regional chronostratigraphic calibrations of dinocyst events (https://github.com/bijlpeter83/DINOSTRAT.git). DINOSTRAT version 1.0 includes >8500 entries of first and last occurrences (collectively called "events") of >1900 dinocyst taxa, and their absolute ties to the chronostratigraphic time scale 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 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 time scales; (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 et al., 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 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-Ikenobe, 2019), 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 diachroniety? Broadly, 3 reasons could apply: (1) inaccurate or inadequate tie-in of dinocyst events to the chronostratigraphic time scale, 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 (e.g., Rochon et a., 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 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 new insights: updated geologic time scales 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.

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 time scale and the (paleo-) geographic position of the site from which they were calibrated. DINOSTRAT version 1.0 currently contains over 8500 entries of first and last occurrences of over 1900 dinocyst taxa to the international time scale. 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 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 (MacRae 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.

2 Approach

DINOSTRAT version 1.0 represents a compilation of dinocyst events from peer-reviewed literature, with a publication date predating January 1st, 2021 (see Table 1). The taxonomic nomenclature, supra-generic classification and synonymy cited in Williams et al. (2017) is 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., 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 (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 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.

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., 2016). 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: 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	Geography (location)	Age base	Age top	Tier	Calibrated to
Açikalin 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 1)
Aubry et al., 2020	Labrador Sea, Greenland	3.2	2.25	1	Magnetostratigraphy on the same samples. Magnetic reversals were calibrated usingplanktonic foraminifera and nannofossils
Awad and Oboh-Ikenobe, 2016	Ivory Coast Margin	57	54	3	CP nannoplankton stratigraphy on the same section
Awad and Oboh-Ikenobe, 2019	Ivory Coast Margin	28	16	3	CP/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 controll shown (industry data)
Biffi and Manum, 1988	Central Italy	36	22	3	NP/NN nannoplankton and N/P planktonic foraminifer stratigraphies from the same sections

Bijl and Brinkhuis, 2015	East Antarctica	54	47	2	Magnetostratigraphy on the same section. Magnetochrons are 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 was calibrated to magnetostratigraphy, using dinocyst biostratigrapy
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/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	Tunesia, 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/NP nannoplankton stratigraphy on the same cores
Brown and Downie, 1985	Northern Bay of Biscay, France	60	10	3	NP/NN nannoplankton stratigraphy on the same cores
Bucefalo Palliani and Riding, 1997a	Italy	183	179	4	Tethyan ammonite stratigraphy, but no ammonite data was shown

Bucefalo Palliani and Riding, 1997b	France	199	170	4	Boreal ammonite stratigraphy, but no ammonite data was shown (see conversions in Supplement 1)
Bucefalo Palliani and Riding, 2000	United Kingdom	200	179	4	Tethyan ammonite stratigraphy, but no ammonite data was shown (see conversions in Supplement 1)
Bucefalo Palliani and Riding, 2003	Boreal/Tethys	191	180	4	Boreal ammonite stratigraphy, but no ammonite data was shown.
Bujak and Matsuoka, 1986	North Pacific, Japan	23	0	5	Independent age constraints from planktonic foraminifera, radiolaria, diatoms and nannoplankton are not shown in the paper.
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 are plotted but no ammonite data was presented. Campanian-Maastrichtian events were calibrated to stages (see conversions in Supplement 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; 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 was based on Ammonites, pelycepods and benthic foraminifera (see conversions in Supplement 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 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 1)
Duxbury, 2001	Scotland	139	100	4	Boreal ammonite zonation, not directly from the well cutting material (see conversions in Supplement 1)
Dybkjær and Piasecki, 2008, 2010	Denmark	23	0	3	NP/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 were 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 strat at the same site
Feist-Burkhardt and Monteil, 1997	France	171	167	3	Calibrated to Boreal ammonite stratigraphy (see conversions in Supplement 1)
Feist-Burkhardt, 1990	Southwest Germany	174	168	3	Boreal ammonite stratigraphy
Fensome et al., 2008	Scotian Margin, Eastern Canada	100	0	3	NN and NC nannoplankton stratigraphy, but because based on cuttings, only LOs are given
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 et al., 2009
Frieling et al., 2014	West Siberian Sea	60	45	2	Magnetostratigraphy and stable carbon isotope stratigraphy
Gradstein et al., 1992	North Sea, Netherlands	66	23	3	N/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 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	Magnetostrat 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 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 has 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 GPTS
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 1)
King et al., 2018	Crimea	59	48	3	NP nannofossil stratigraphy on the same samples
Kirsch, 1991	Bad Tolz, 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 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
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 1)
Leereveld, 1997a	Caravaca, Southern Spain	134	125	3	Tethyan ammonite stratigraphy on the same section (for conversions see Supplement 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	Ivory Coast Margin	140	112	3	CC nannofossil stratigraphy on the same section
Masure et al., 1998	Ivory Coast Margin	90	57	3	CP and CC nannoplaknton 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, 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 1)
Monteil, 1993	France	152	140	3	Some sections were calibrated to Tethyan ammonite stratigraphy, some only indicated stages (for conversions see Supplement 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-Shetland	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 1)
Nøhr-Hansen et al., 2002	West 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, then inferred for Site 263 (for conversions see Supplement 1)

Pearce, 2010	United Kingdom	95	70	4	UK ammonite zonations in nearby outcrops. Some intervals could not be correlated to the GTS2012
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 in 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	Barentz 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 1)
Riding and Thomas, 1988	United Kingdom	160	150	3	Boreal ammonite zonation on the same section (for conversions see Supplement 1)
Riding and Thomas in Powell, 1992	North Sea	202	145	4	Boreal ammonite zonations, but not directly shown in paper (for conversions see Supplement 1)
Riding and Thomas, 1997	North Scotland, Isle of Skye	166	155	3	Boreal ammonite stratigraphy on the same section (for conversions see Supplement 1)
Riding et al, 2010	Australia	237	145	4	Ammonites, conodonts, belemnite/bivalve, NJ nannoplankton stratigraphy and strontium isotopes, but these data are 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 1)
Skupien, 2004	Slovakia	123	99	3	Boreal ammonite stratigraphy (for conversions see Supplement 1)
Skupien and Vašíček, 2002	Czech Republic	131	113	3	Tethyan ammonite stratigraphy on the same section (for conversions see Supplement 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 1)
Smelror, 1988a	Greenland	167	160	3	Boreal ammonite stratigraphy on the same section (for conversions see Supplement 1)
Smelror, 1988b	Svalbard, Norway	168	160	3	NW European ammonite stratigraphy, herein calibrated to the Boreal zonation (for conversions see Supplement 1)
Smelror, 1994	Swabia	167	165	4	Ammonite and foraminifer stratigraphy, but herein calibrated against stages
Smelror and Dietl, 1994	South 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 1)
Soliman et al., 2012	Golf of Suez, Egypt	54	14	3	NP/NN nannoplankton stratigraphy on the same section
Steeman et al., 2020	Angola	60	35	3	P/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, South	110	95	3	Boreal ammonite stratigraphy on the same section (for conversions see Supplement 1)

	United Kingdom				
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 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
Versteegh, 1997	North Atlantic Ocean, Italy	3	2	1	Isotope stages, herein recalibrated to NN and CN nannoplankton zones
Versteegh and Zevenboom, 1995	South 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	Topical 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 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/NN nannoplankton stratigraphy on the same sections

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 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 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.

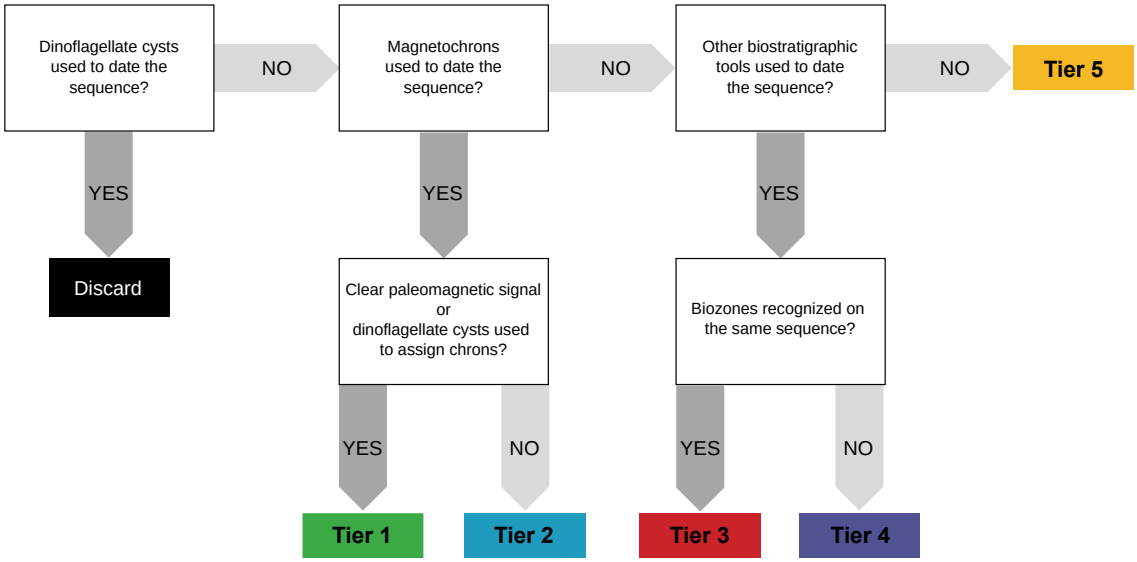

Figure 1: Decision tree for including studies in this review, and categorization criteria for the 5 tiers.

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:

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

in which [##]% is linearly interpolated between base (0%) and top (100%) of tie points, [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. 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 time scale, 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 to those presented in the GTS2012 (see Supplement 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, 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 Paleolatitude.org; 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.

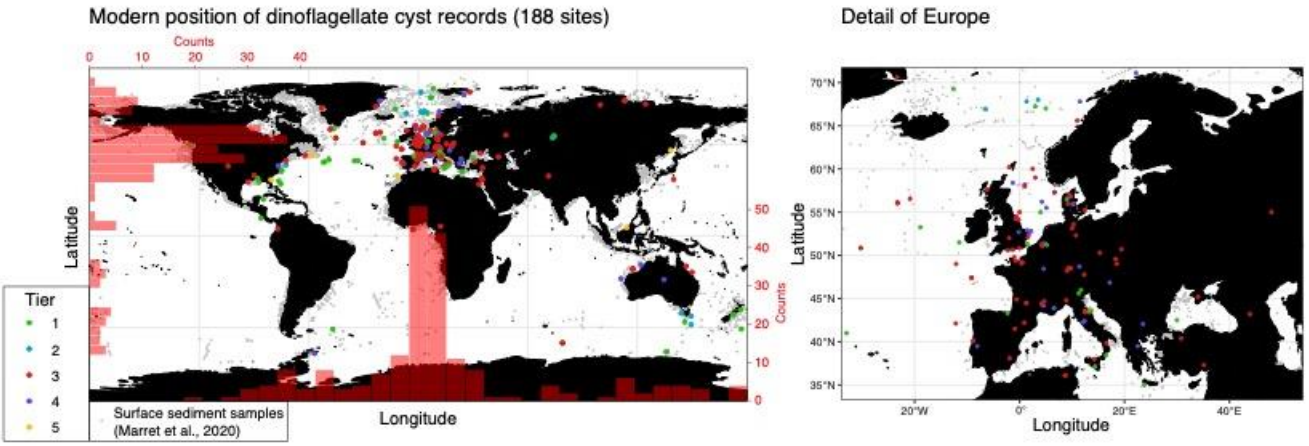

Figure 2: Present-day geographic distribution of sedimentary sequences used in DINOSTRAT (colors of the dots correspond to the to the tier status to which the site has been allocated), and surface sediment stations (in grey dots;

Marret et al., 2020 and Mertens et al., 2014). A. Global. Red scale bars on x/y axes represent number of sites per longitudinal/latitudinal bins, respectively B. Detailed map of sites in Europe.

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, 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.

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 (Tier 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 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 diachroniety 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 (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 families/subfamilies 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.

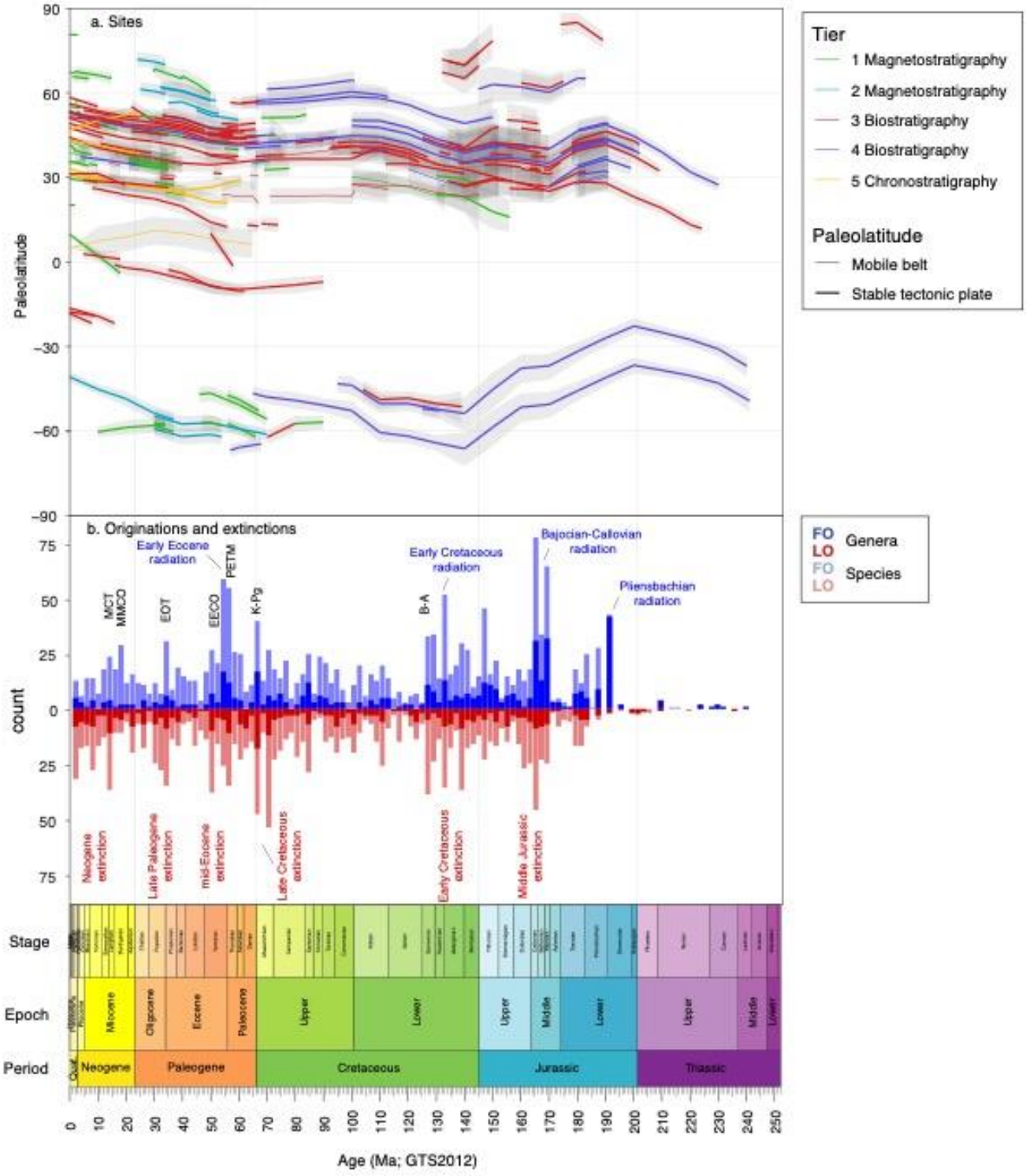
a. Sites
Paleolatitude
90
60
30
0
−30
−60
−90
Tier
1 Magnetostratigraphy
2 Magnetostratigraphy
3 Biostratigraphy
4 Biostratigraphy
5 Chronostratigraphy
Paleolatitude
Mobile belt
Stable tectonic plate
b. Originations and extinctions
count
75
50
25
0
25
50
75
MCT
MMCO
EOT
Early Eocene radiation
EECO
PETM
K-Pg
B-A
Early Cretaceous radiation
Bajocian-Callovian radiation
Pliensbachian radiation
Neogene extinction
Late Paleogene extinction
mid-Eocene extinction
Late Cretaceous extinction
Early Cretaceous extinction
Middle Jurassic extinction
FO Genera
LO Genera
FO Species
LO Species
Stage
Epoch
Period
Miocene
Oligocene
Eocene
Paleocene
Upper
Lower
Upper
Middle
Lower
Upper
Middle
Lower
Neogene
Paleogene
Cretaceous
Jurassic
Triassic
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
Age (Ma; GTS2012)

Figure 3: Data in DINOSTRAT. 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 (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), Miocene climatic transition (MCT). Extinction and radiation phases in dinocysts are highlighted in red and blue text, respectively.

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 modern latitudinal spread of these species to that of the past, and their age and latitude of oldest first occurrence (Supplement 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*, *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., *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).

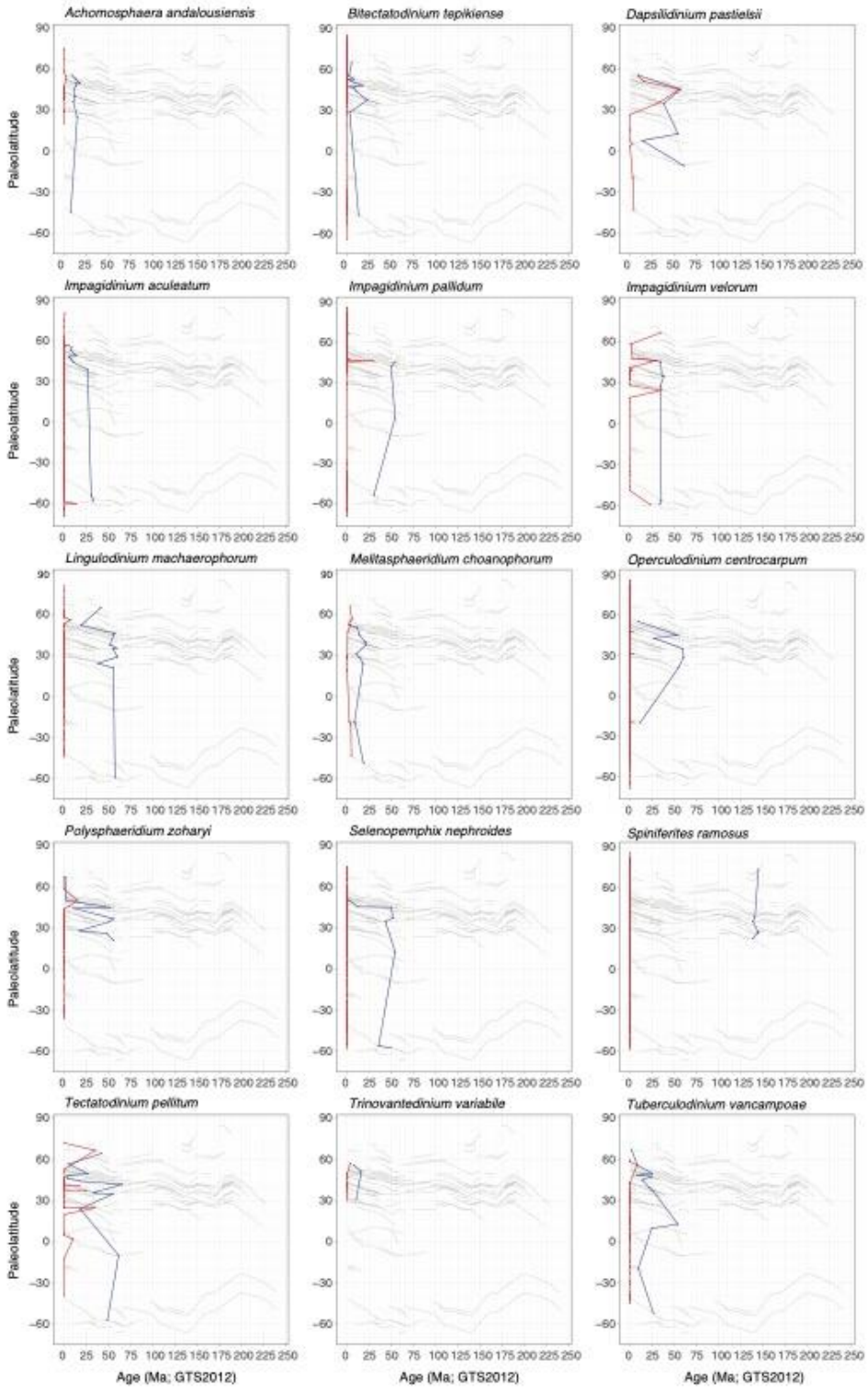
Achomosphaera andalousiensis
Bitectatodinium tepikiense
Dapsilidinium pastielsii
Impagidinium aculeatum
Impagidinium pallidum
Impagidinium velorum
Lingulodinium machaerophorum
Melitasphaeridium choanophorum
Operculodinium centrocarpum
Polysphaeridium zoharyi
Selenopemphix nephroides
Spiniferites ramosus
Tectatodinium pellitum
Trinovantedinium variabile
Tuberculodinium vancampoae
Paleolatitude
90
60
30
0
-30
-60
0 25 50 75 100 125 150 175 200 225 250
Age (Ma; GTS2012)

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.

3.2.2 Dinocyst (sub-) families

Range charts of the sites in DINOSTRAT are provided in the supplements (see "Sites" folder in Supplement 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 2). Users can produce/adapt these plots themselves with 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 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 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 (e.g., MacRae 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: 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 longer in Northern Hemisphere (NH) mid-latitudes (FO ~169 Ma; LO ~18 Ma) than in the rest of the world (FO ~145 Ma; LO ~36Ma), 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: 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.

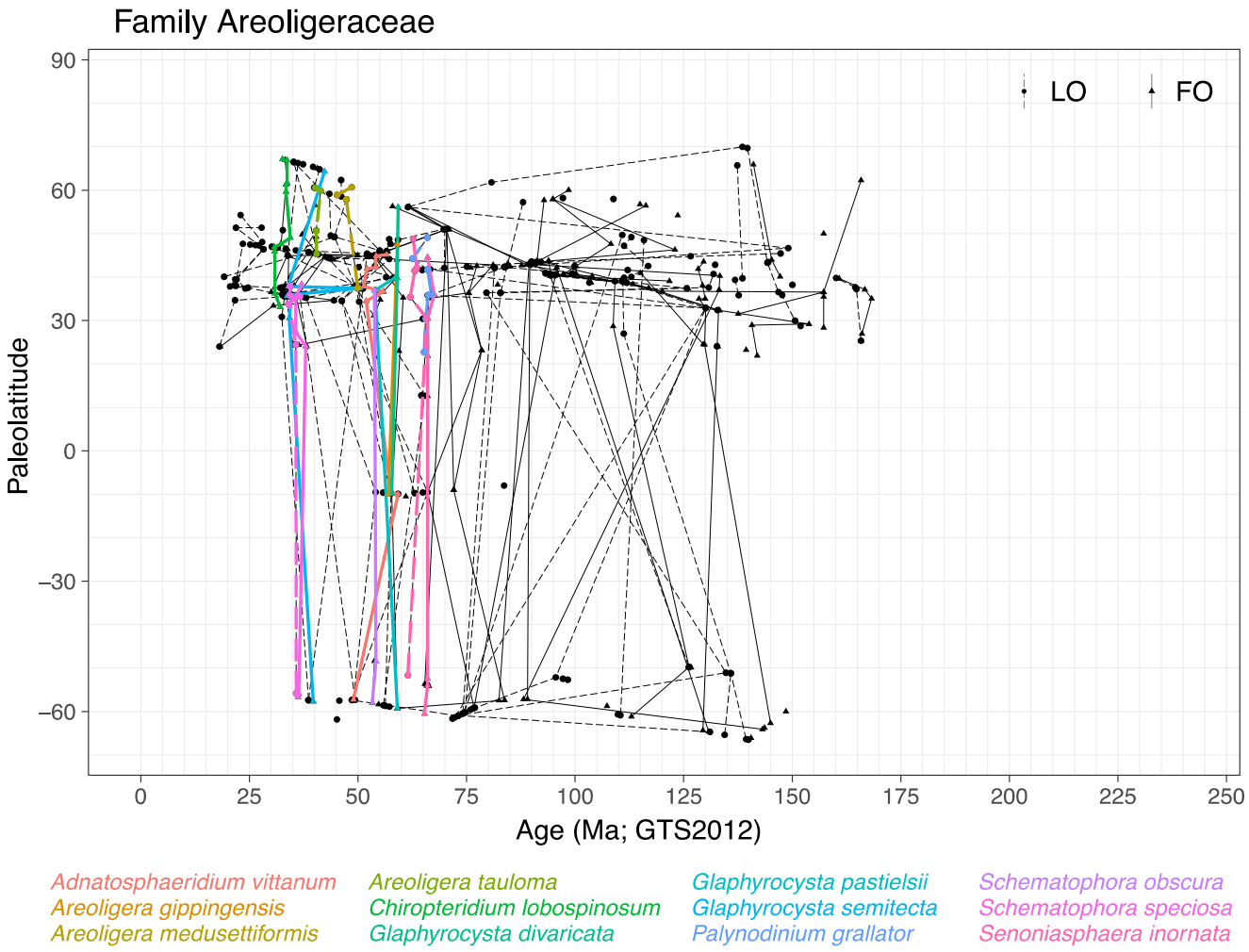

Figure 5: Ages and paleolatitudes of first (solid line and triangles) and last (dashed line and circles) occurrences of dinocyst species of the Family Areoligeraceae. Solid and dashed lines connect first and last occurrences, respectively, for each species, between sites. Colored lines represent quasi-synchronous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

Family Ceratiaceae (Fig. 6)

Range: The Ceratiaceae first appear in the Tithonian (~152Ma, 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: LO *Odontochitina costata*, LO *Phoberocysta neocomica*, range of *Pseudoceratium pelliferum* (Fig. 6).

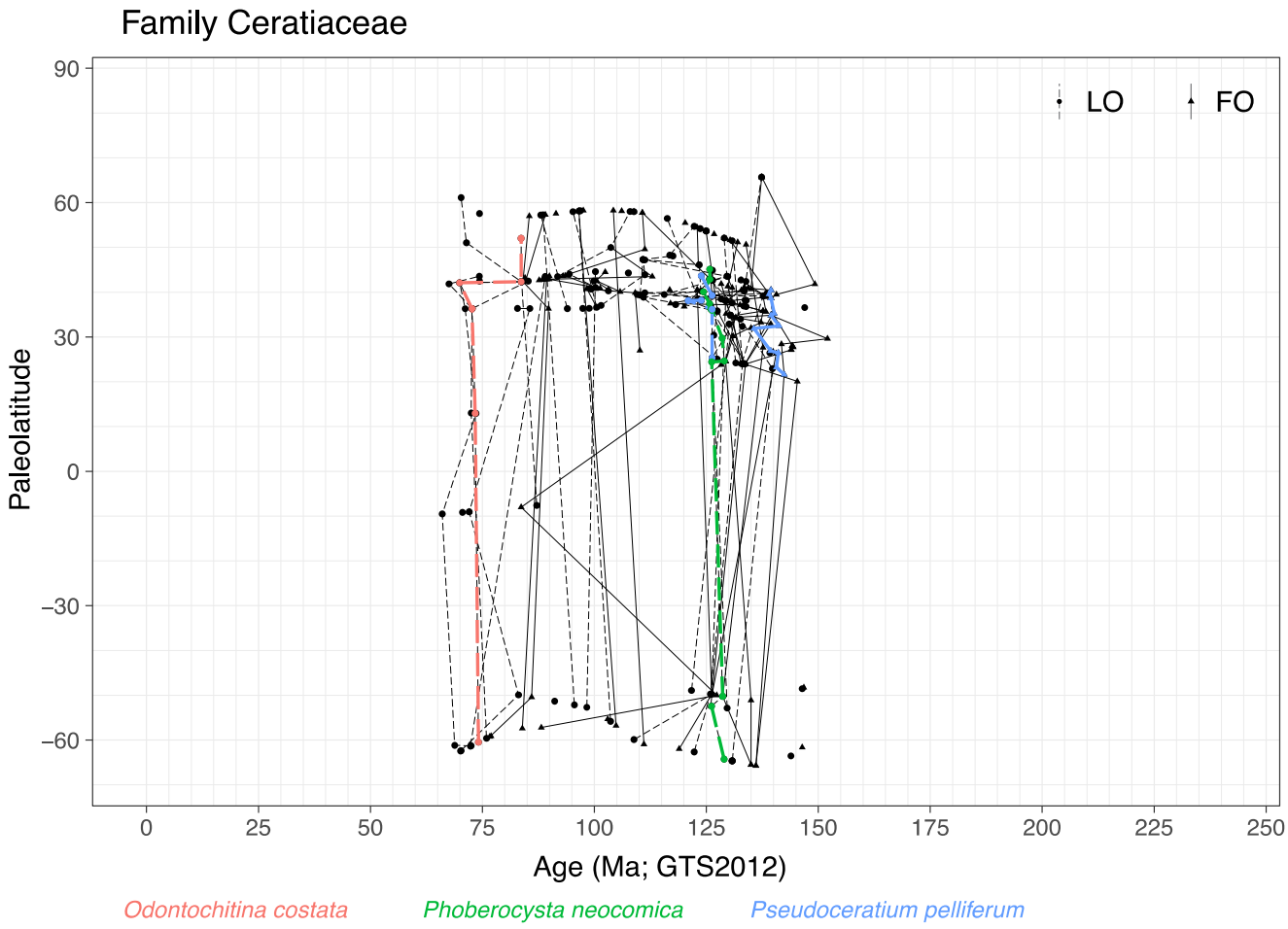

Figure 6: As Figure 5, but for the Family Ceratiaceae.

Family Cladopyxiaceae (Fig. 7)

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

Quasi-synchronous events: Several species of *Enneadocysta*. 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.

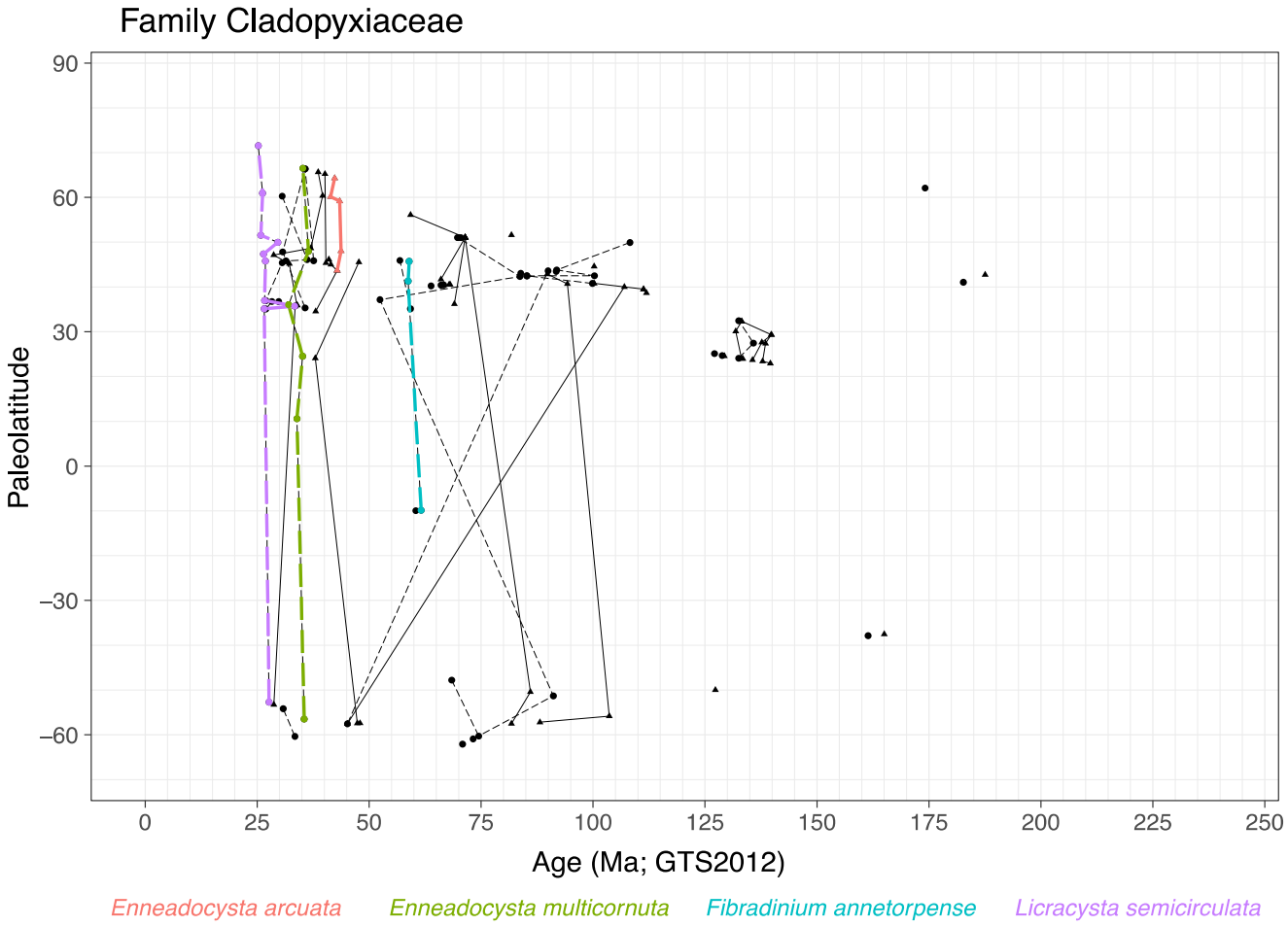

Figure 7: As Figure 5, but for the Family Cladopyxiaceae.

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 modern species *Polysphaeridium zoharyi* and *Tuberculodinium vancampoae*.

Quasi-synchronous events: species of *Alisocysta*, *Eisenackia*, *Heteraulacacysta* and *Homotryblium*. 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 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 into the geologic past species of this family exhibited much wider latitudinal ranges (65°S – 70°N).

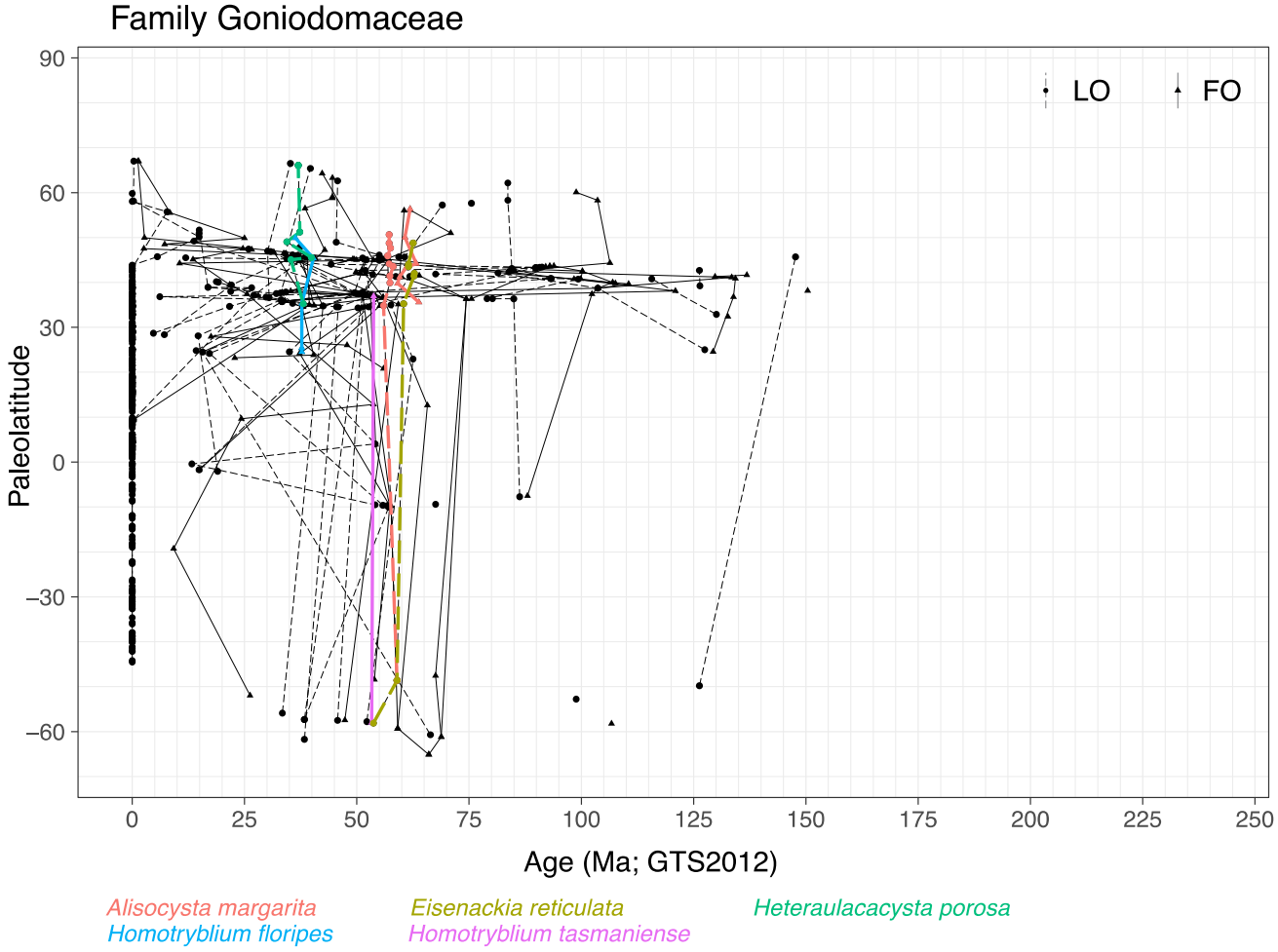

Figure 8: As Figure 5, but for the Family Goniodomaceae.

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 (~172 Ma) with *Kallosphaeridium* spp. and in the Bajocian (~169Ma) 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*. The subfamily has many entries in the Paleogene, but many of these events are not synchronous latitudinally.

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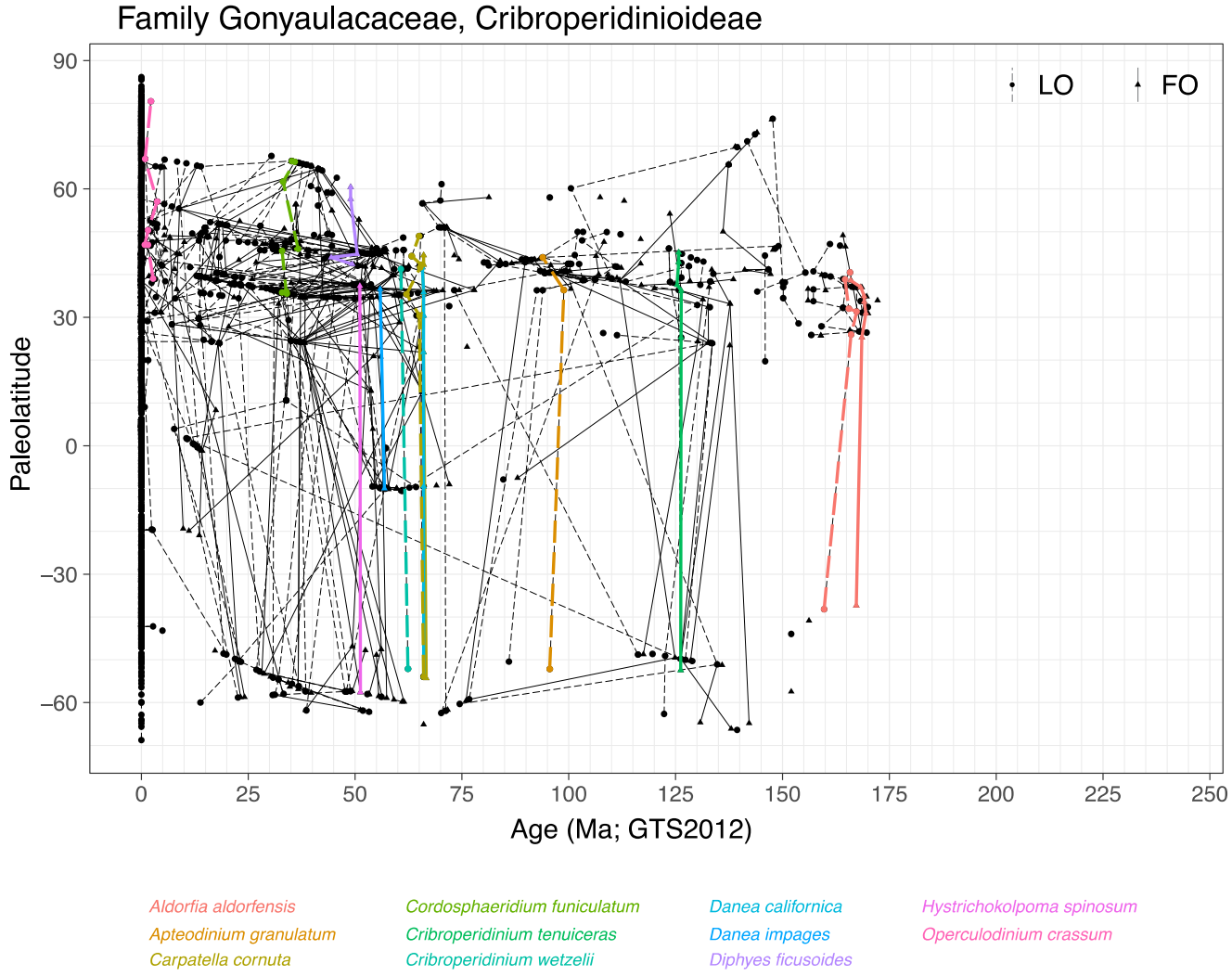


Figure 9: As Figure 5, but for the Family Gonyaulacoideae, subfamily Cribroperidinioideae.

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

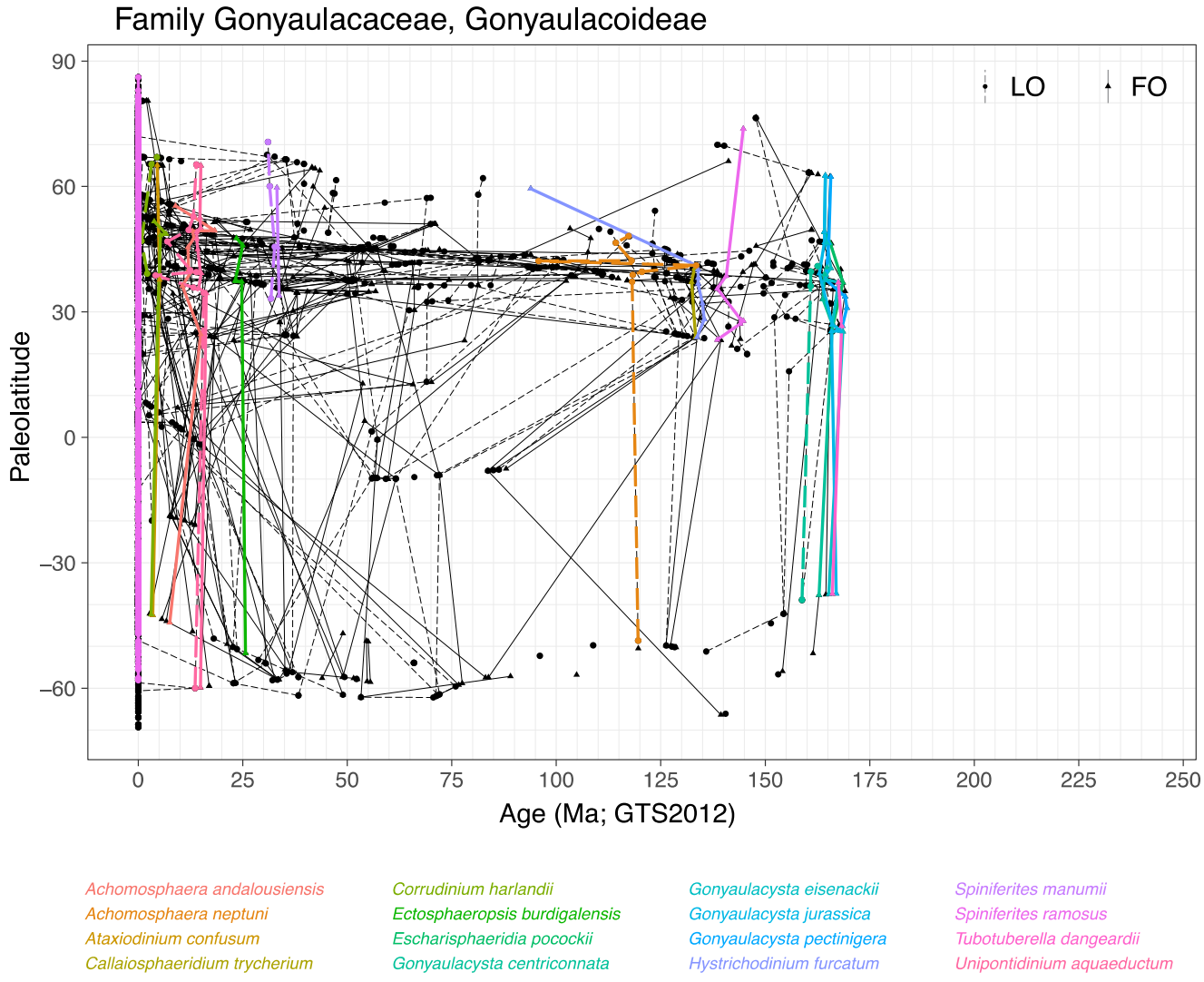


Figure 10: As Figure 5, but for the Family Gonyaulacaceae, subfamily Gonyaulacoideae.

Subfamily Leptodinioideae (Fig. 11)

Range: Leptodinioideae first appear in the Aalenian (~172 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*).

325 *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.*

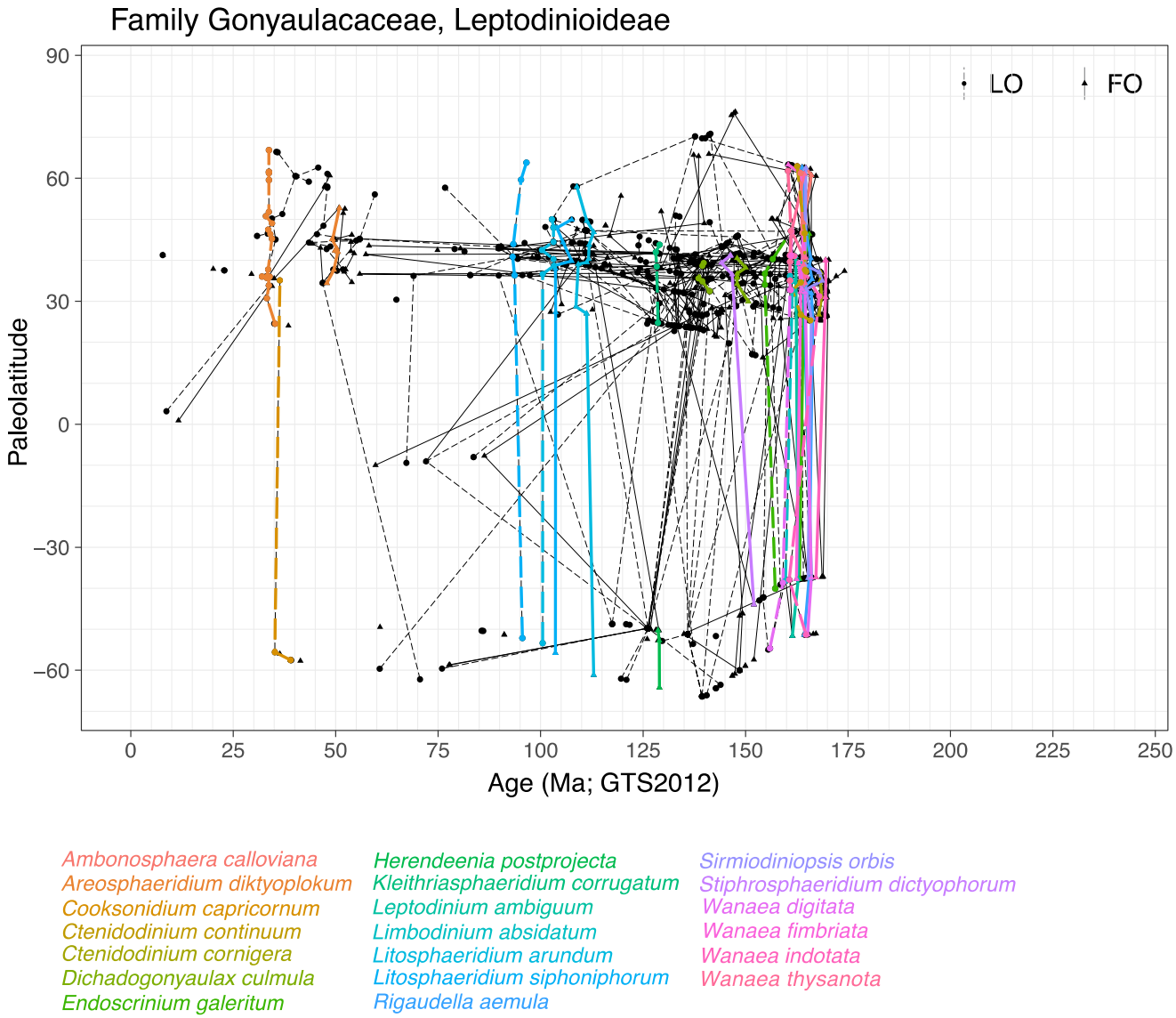


Figure 11: As Figure 5, but for the Family Gonyaulacoideae, subfamily Leptodinioideae.

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.

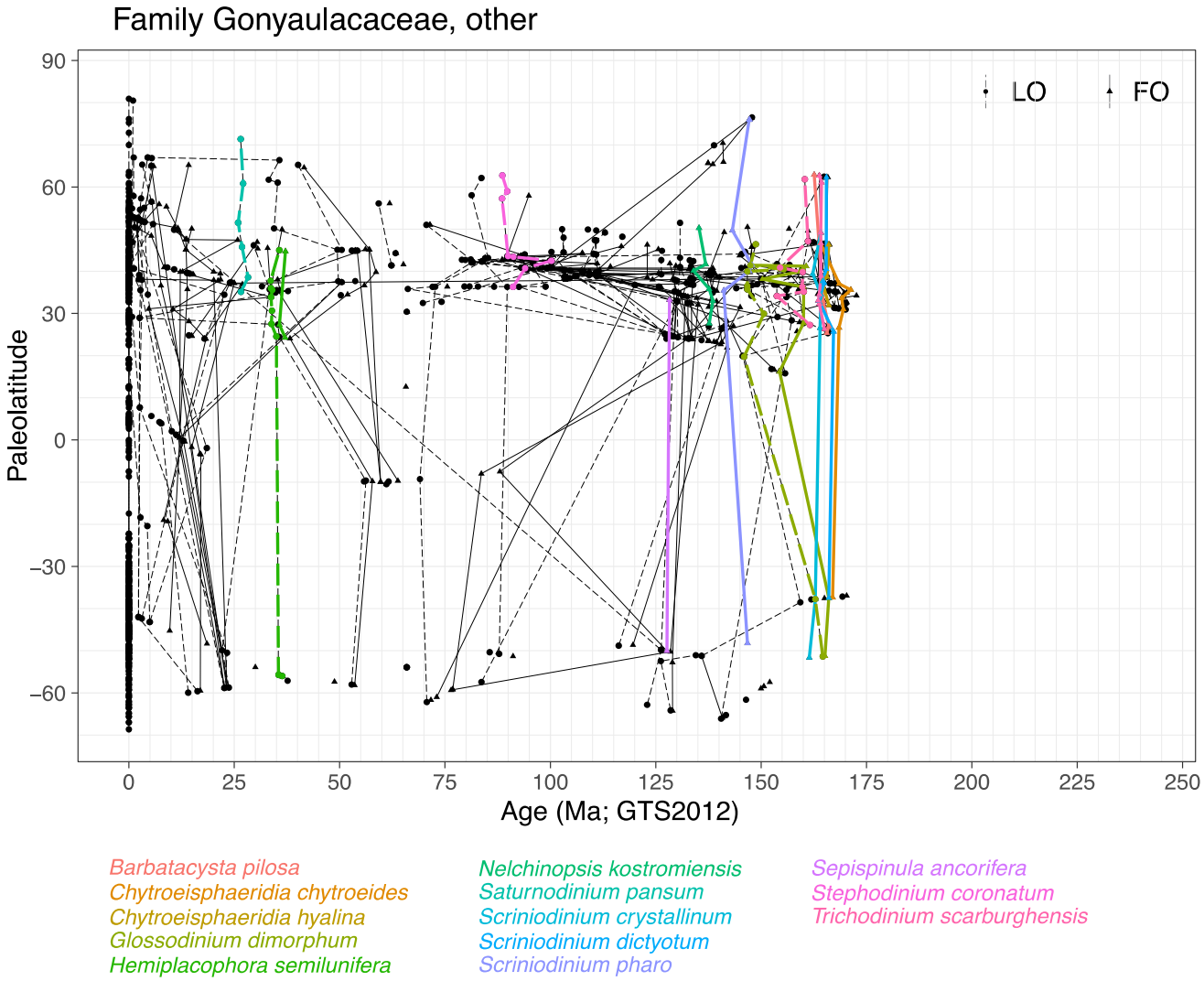


Figure 12: As Figure 5, but for other genera in the Family Gonyaulacoideae.

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.

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

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 quasi-synchronous.

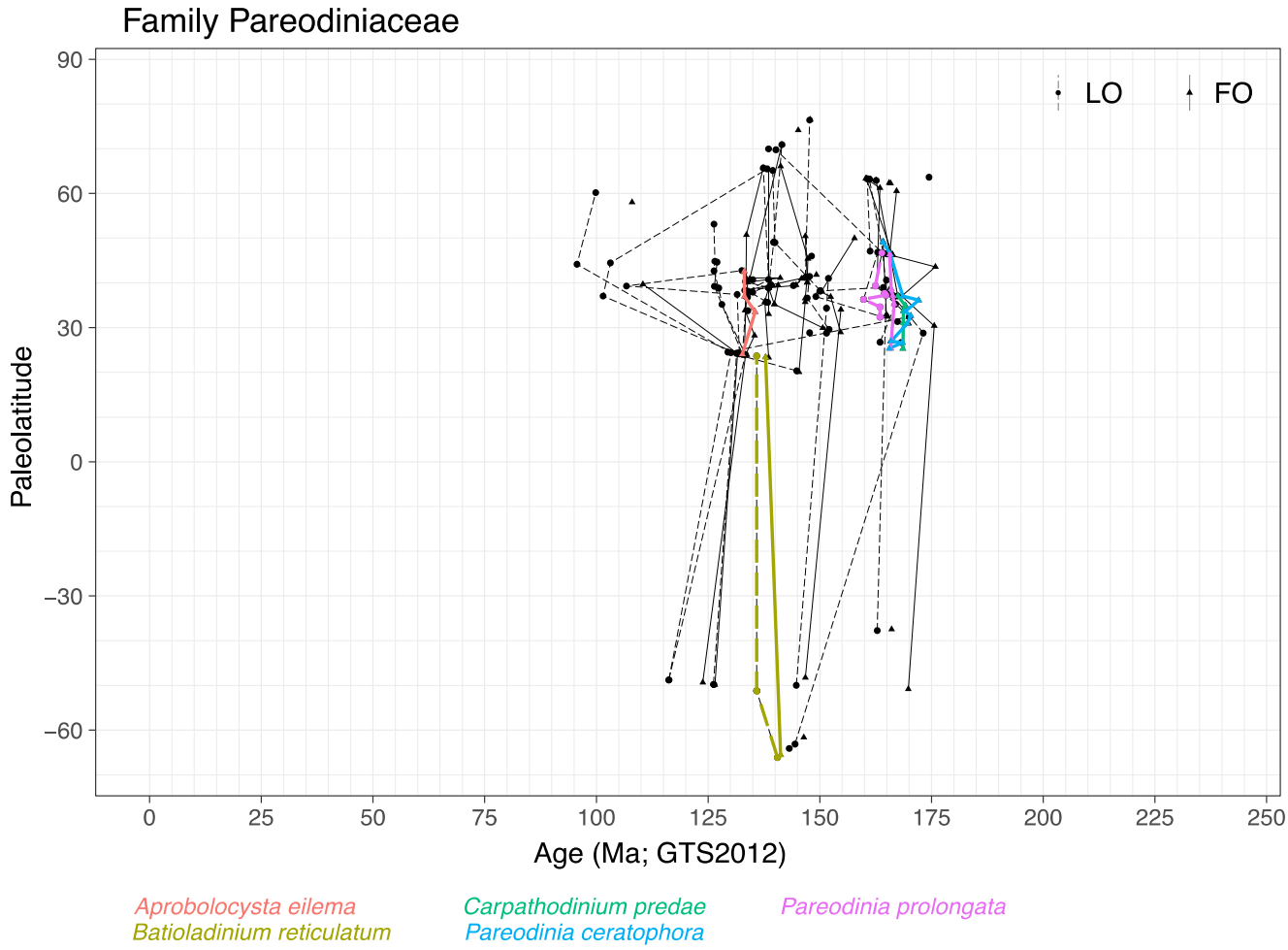


Figure 14: As Figure 5, but for the Family Pareodiniaceae.

355 Family Scriniocassiaceae (Fig. 15)

Range: Scriniocassiaceae range from the Pliensbachian (~187 Ma, FO of *Scriniocassis weberi*) to the Bajocian (~169Ma, LO of *Scriniocassis weberi*) and comprise of only 3 species. Events from this family are only reported from the 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, ~230 Ma) to early Jurassic (LOs of *Dapcodinium sacculus* and *Dapcodinium ovale* in the mid-Pliensbachian, 187 Ma).

Quasi-synchronous events: LO of *Rhaetogonyaulax rhaetica* close to the Triassic-Jurassic boundary, LO of *Dapcodinium priscum*.

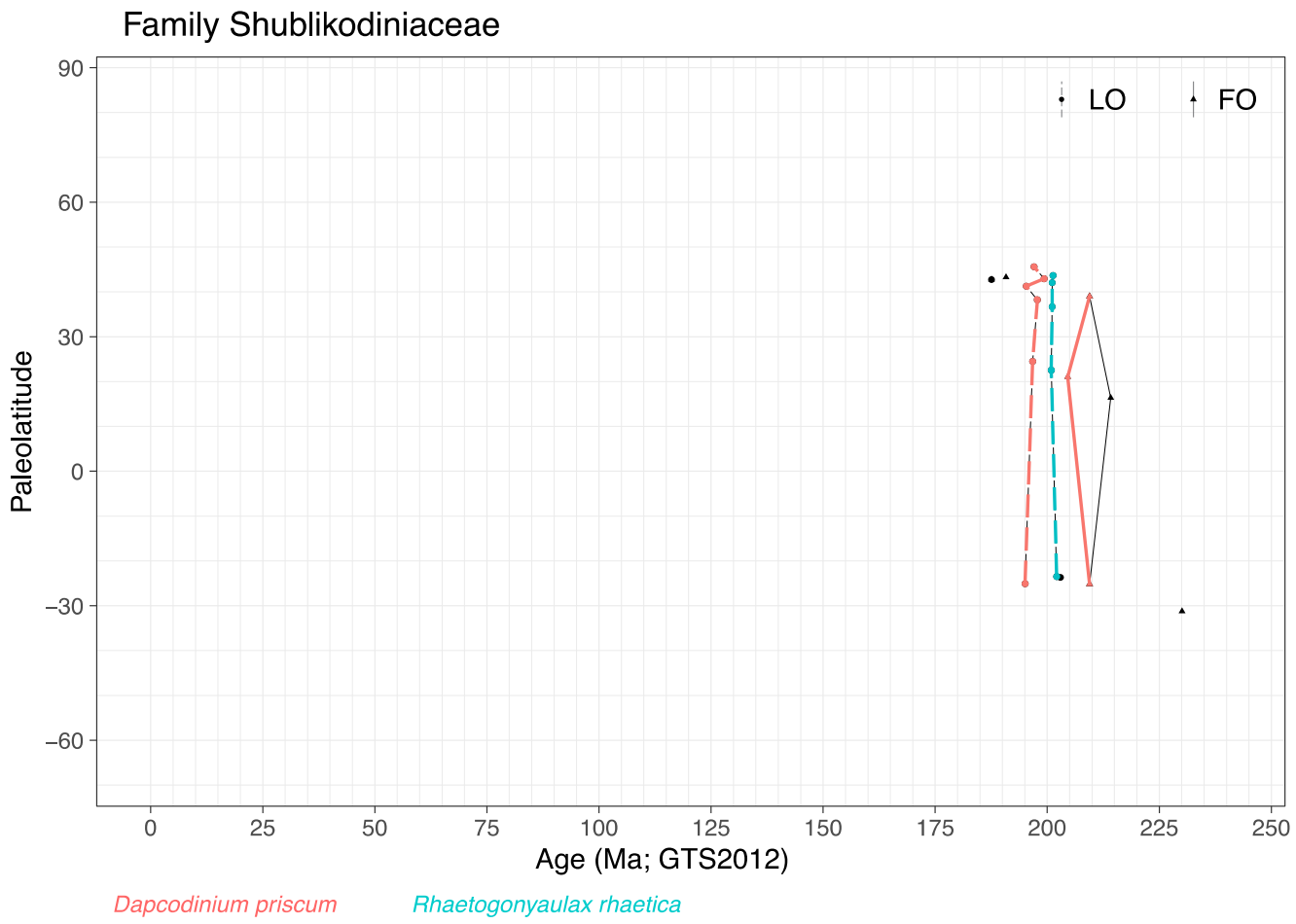


Figure 16: As Figure 5, but for the Family Shublikodiniaceae.

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 *Amiculosphaeridia*, *Atopodinium*, *Batiacasphaera*, *Cleistosphaeridium*, *Dingodinium*, *Distatodinium*, *Heslertonia*, *Labyrinthodinium*, *Membranilarnacia*, *Mendicodinium*, *Oligokolpoma* and *Valensiella* are quasi-synchronous.

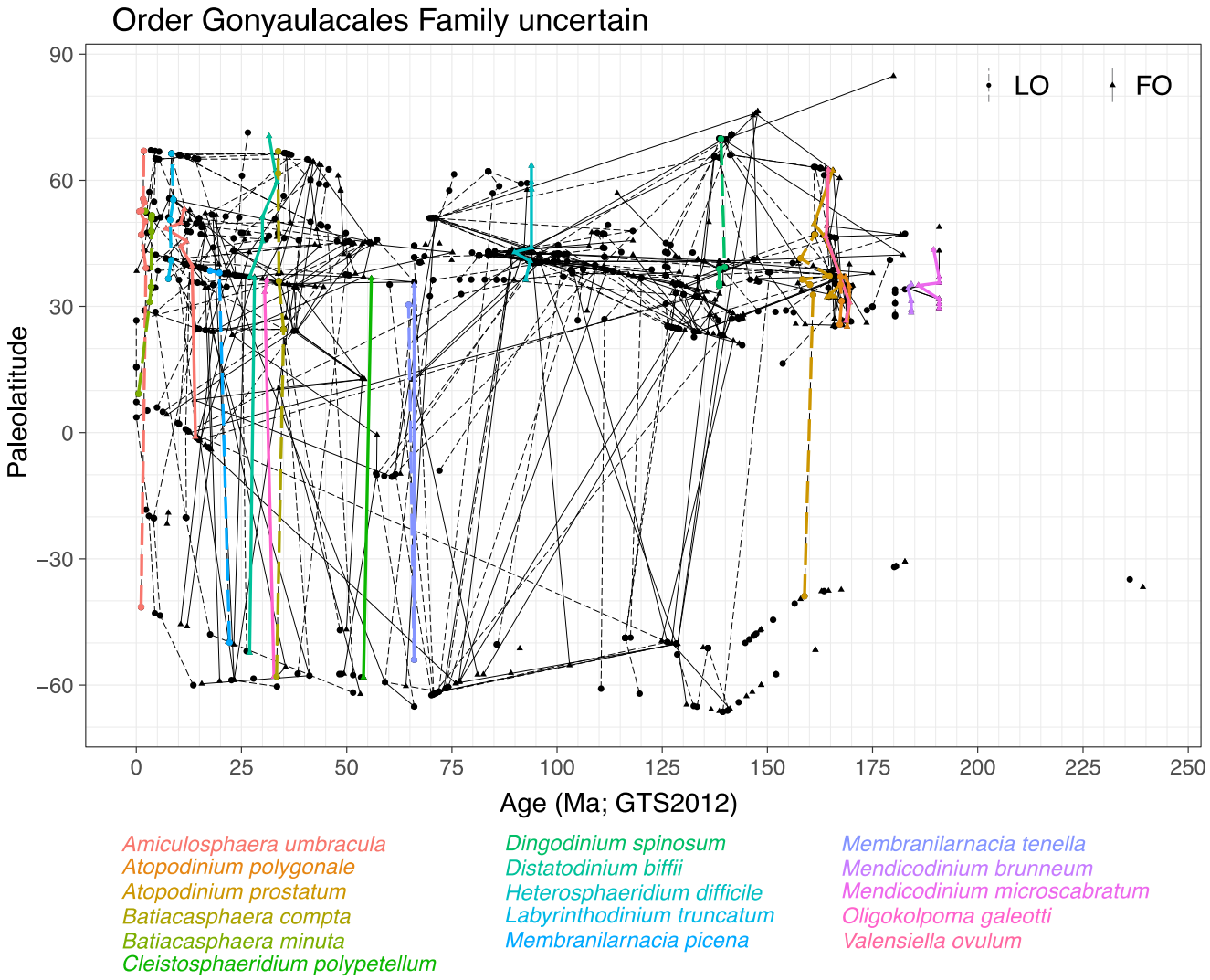


Figure 17: As Figure 5, but for the Order Gonyaulacales, Family uncertain.

Order uncertain

Family Comparodiniaceae (Fig. 18)

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

Quasi-synchronous events: Range of *Biorbifera johnwingii*, FO of *Valvaeodinium spinosum*, LO of *Valvaeodinium koessenium*.

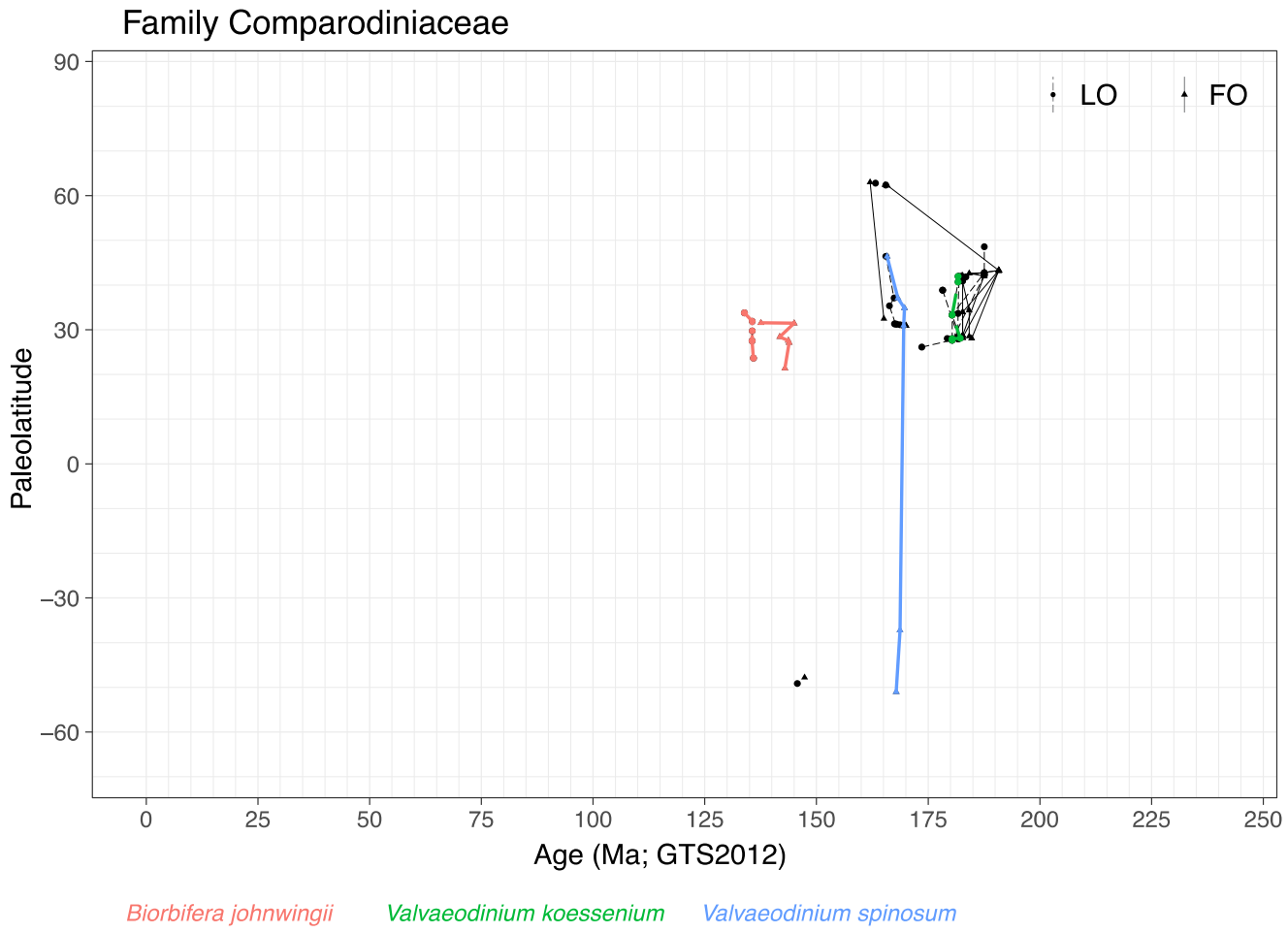


Figure 18: As Figure 5, but for the Family Comparodiniaceae.

390

Family Stephanelytraceae (Fig. 19)

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

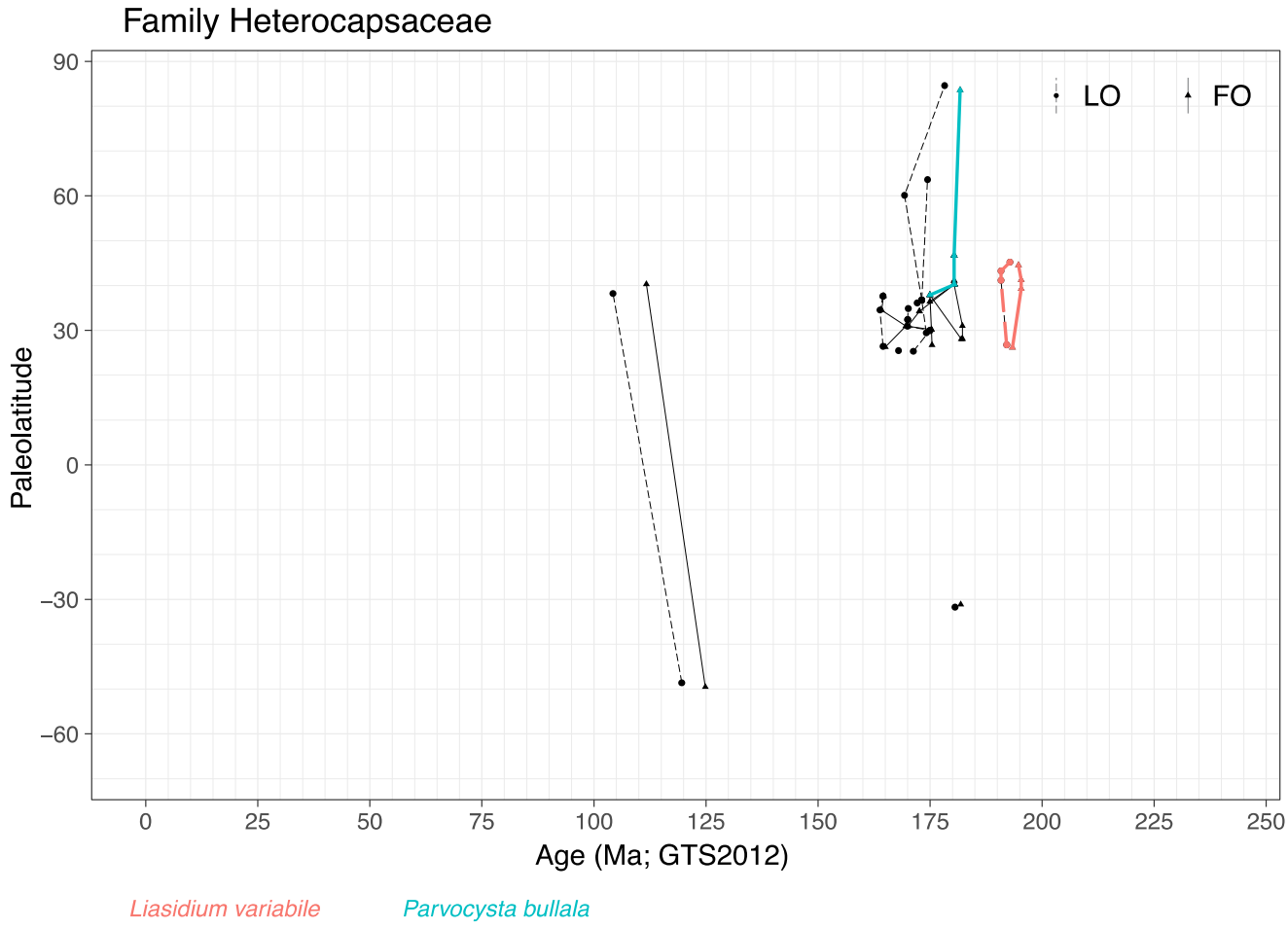
Figure 19: As Figure 5, but for the Family Stephanelytraceae.

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 bullala*, restricted to NH mid-latitudes.



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

Family Peridiniaceae

Subfamily Deflandreoideae (Fig. 21)

Range: Deflandroideae first occur on the Southern Hemisphere in the Oxfordian (~ 161 Ma) with *Pyxidiella* spp. *Isabelidinium* 410 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 5 Ma and appears to range longest in low and mid-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 415 events in the Maastrichtian-Paleocene (70–60 Ma).

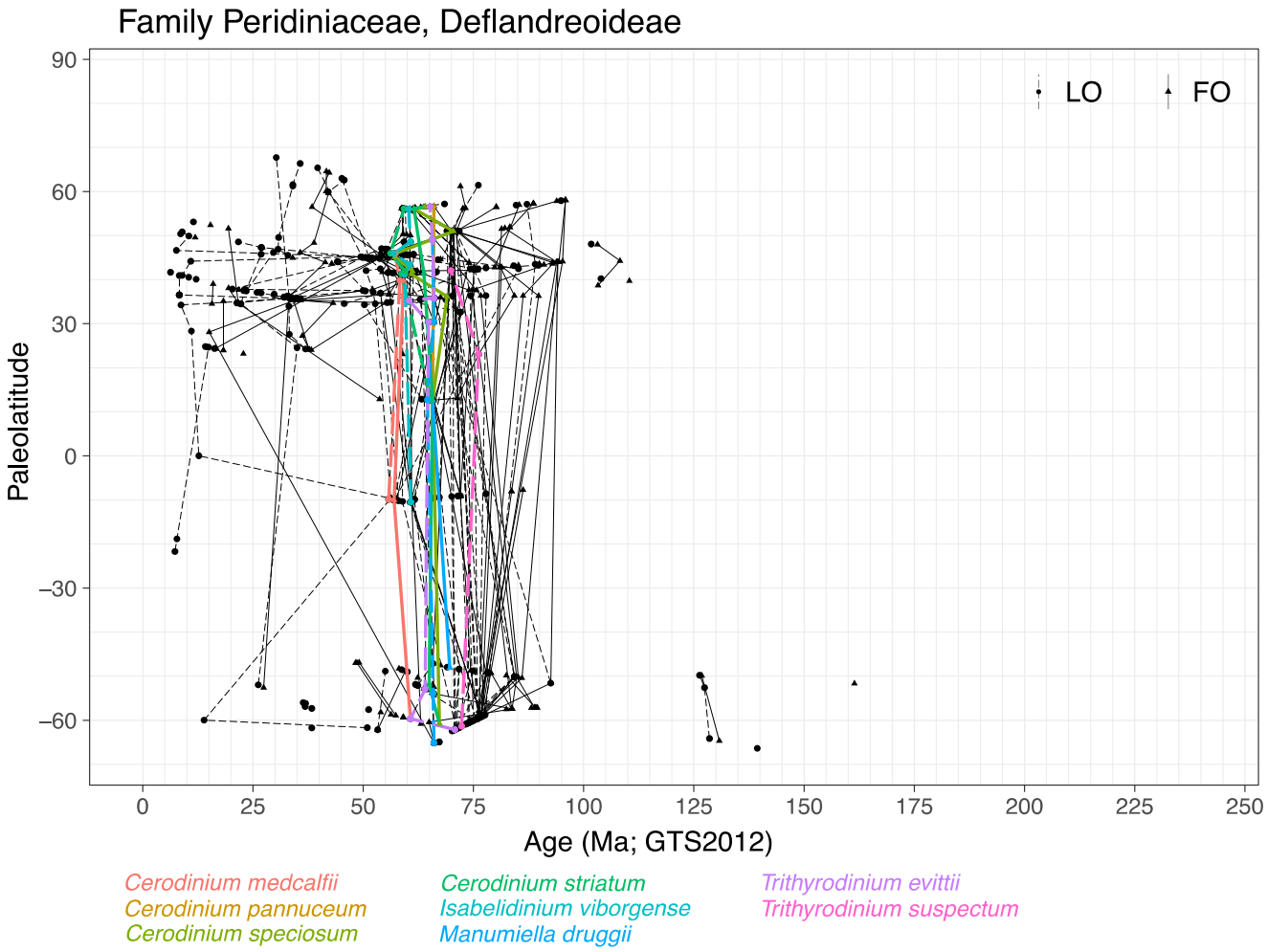


Figure 21: As Figure 5, but for the Family Peridiniaceae, subfamily Deflandreoideae.

Subfamily Palaeoperidinioideae (Fig. 22)

Range: the Palaeoperidinioideae range from the mid-Valanginian (~135 Ma, FO of *Subtilisphaera perlucida*) to the late Oligocene (~26 Ma, LO of *Phthanoperidinium comatum*).

Quasi-synchronous events: range of *Palaeoperidinium pyrophorum* and the LO of *Phthanoperidinium comatum*.

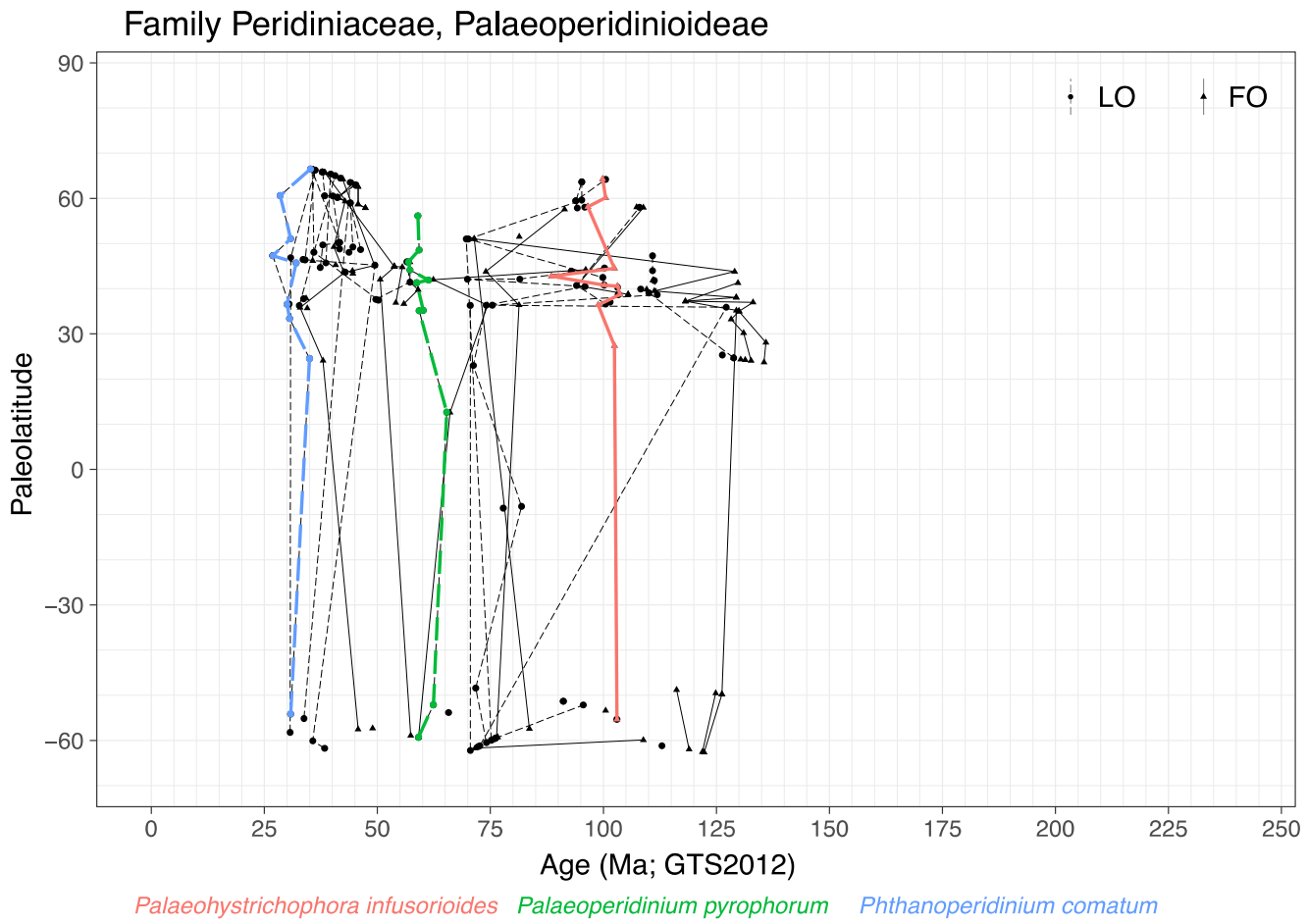
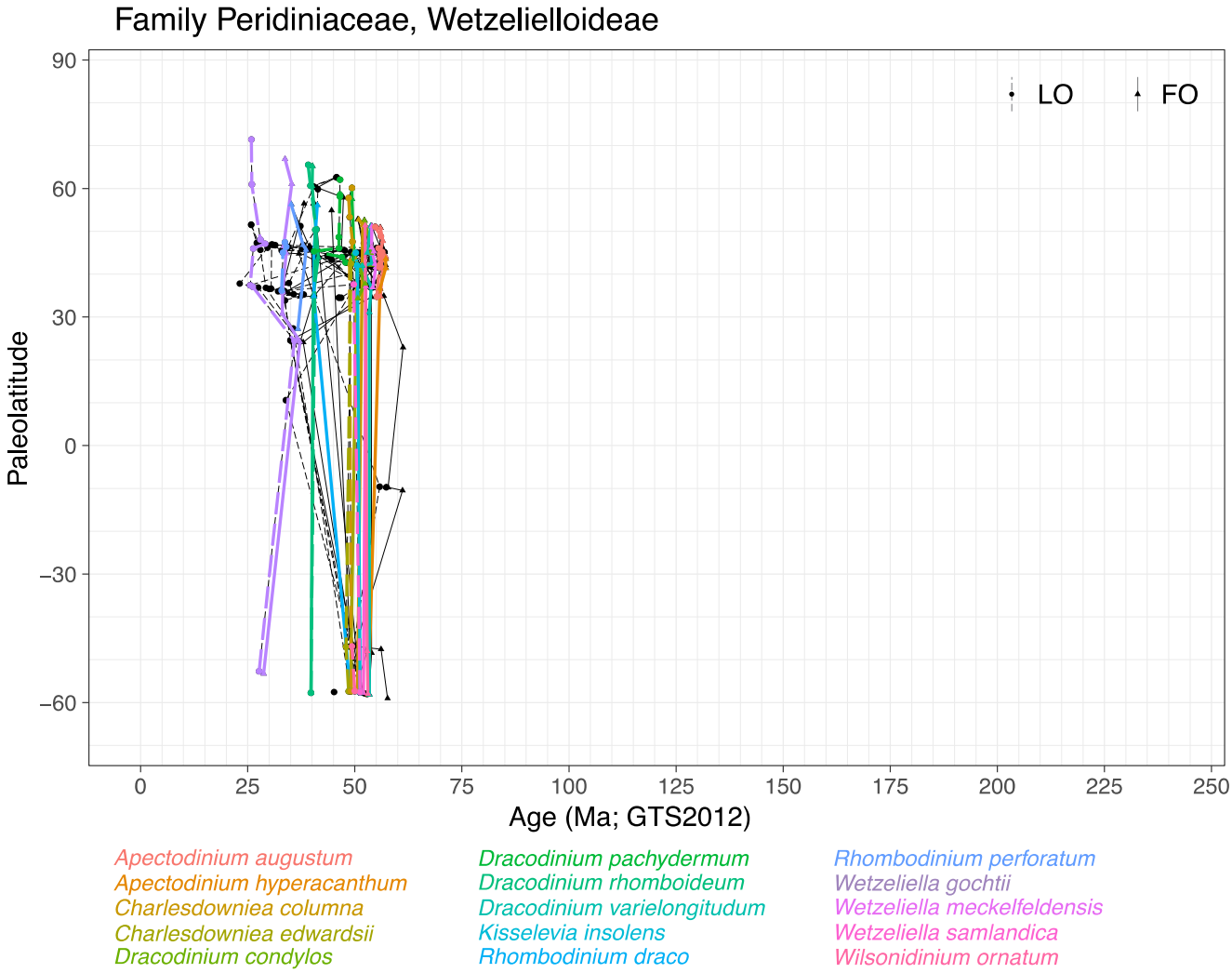


Figure 22: As Figure 5, but for the Family Peridiniaceae, subfamily Palaeoperidinioideae.

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



435 **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 129 Ma.

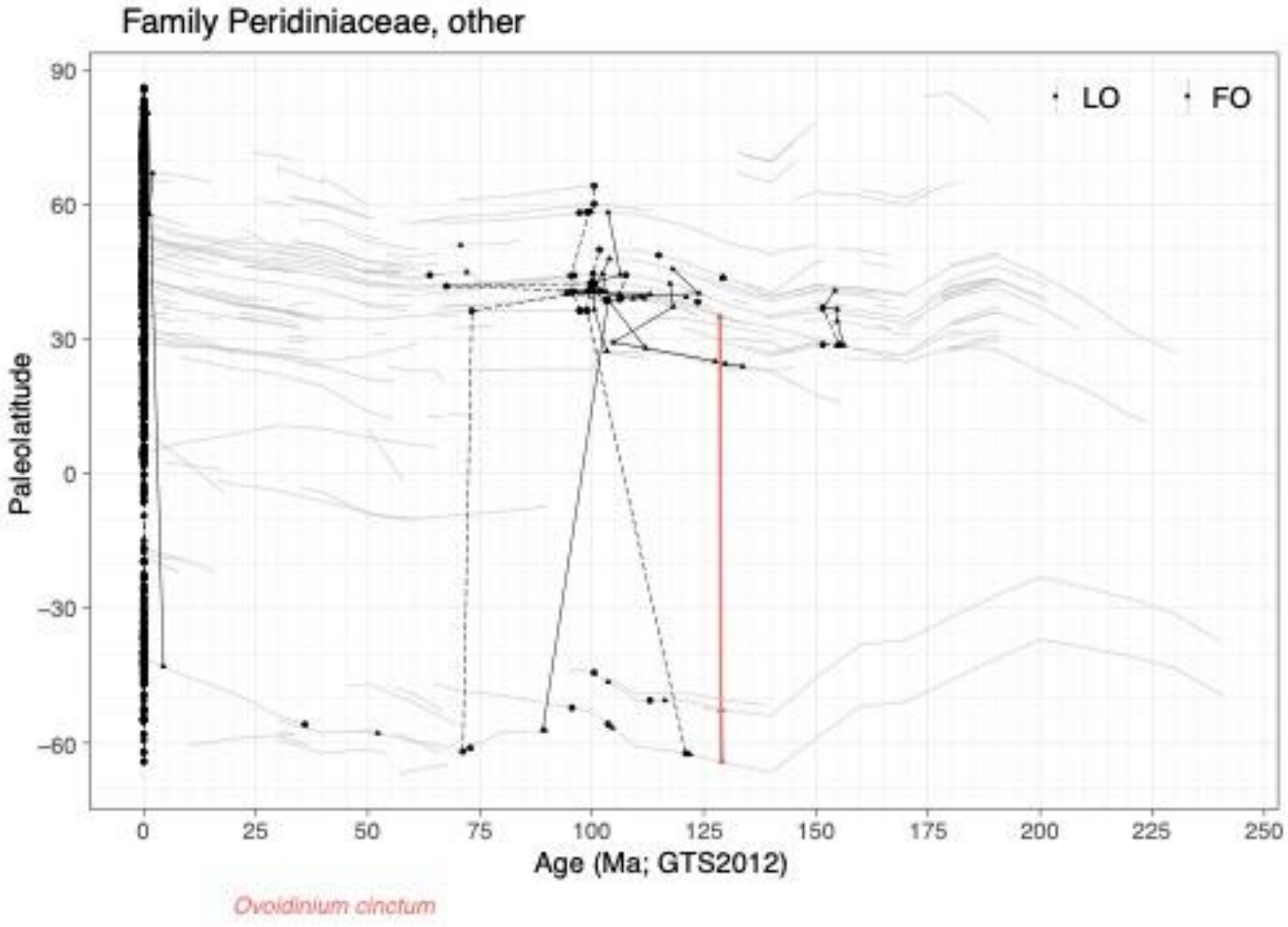


Figure 24: As Figure 5, but for other subfamilies in the Family Peridiniaceae.

Family Protoperidiniaceae (Fig. 25)

Range: Protoperidiniaceae first appear in the Santonian (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.

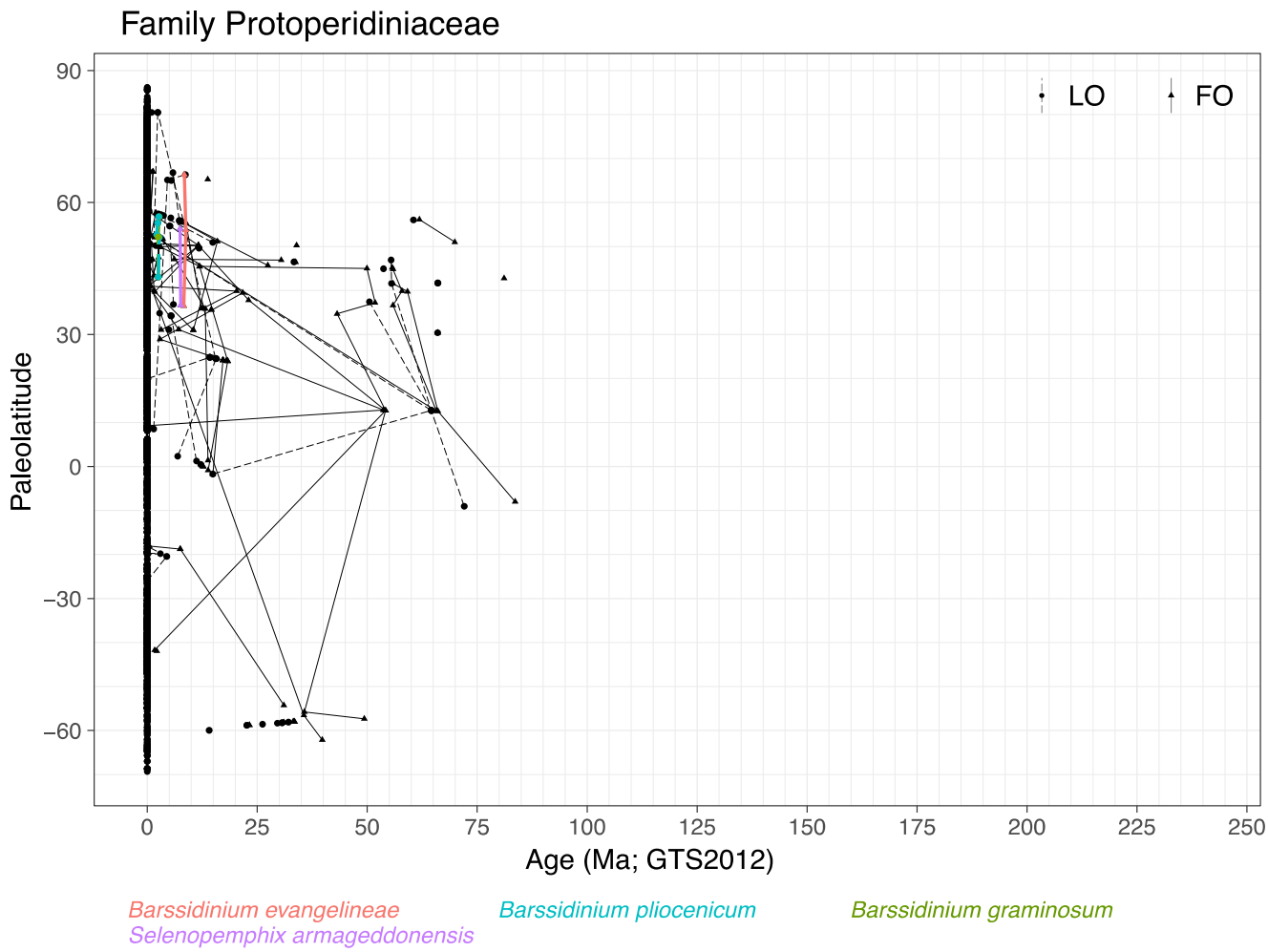


Figure 25: As Figure 5, but for the Family Protoperidiniaceae.

Order Nannoceratopsiales

Family Nannoceratopsiaceae (Fig. 26)

Range: cysts from the Family Nannoceratopsiaceae occur from late Sinemurian (191 Ma, FO of *Nannoceratopsis deflandrei senex*) to the mid-Kimmeridgian (~155 Ma, LO of *Nannoceratopsis pellucida*).

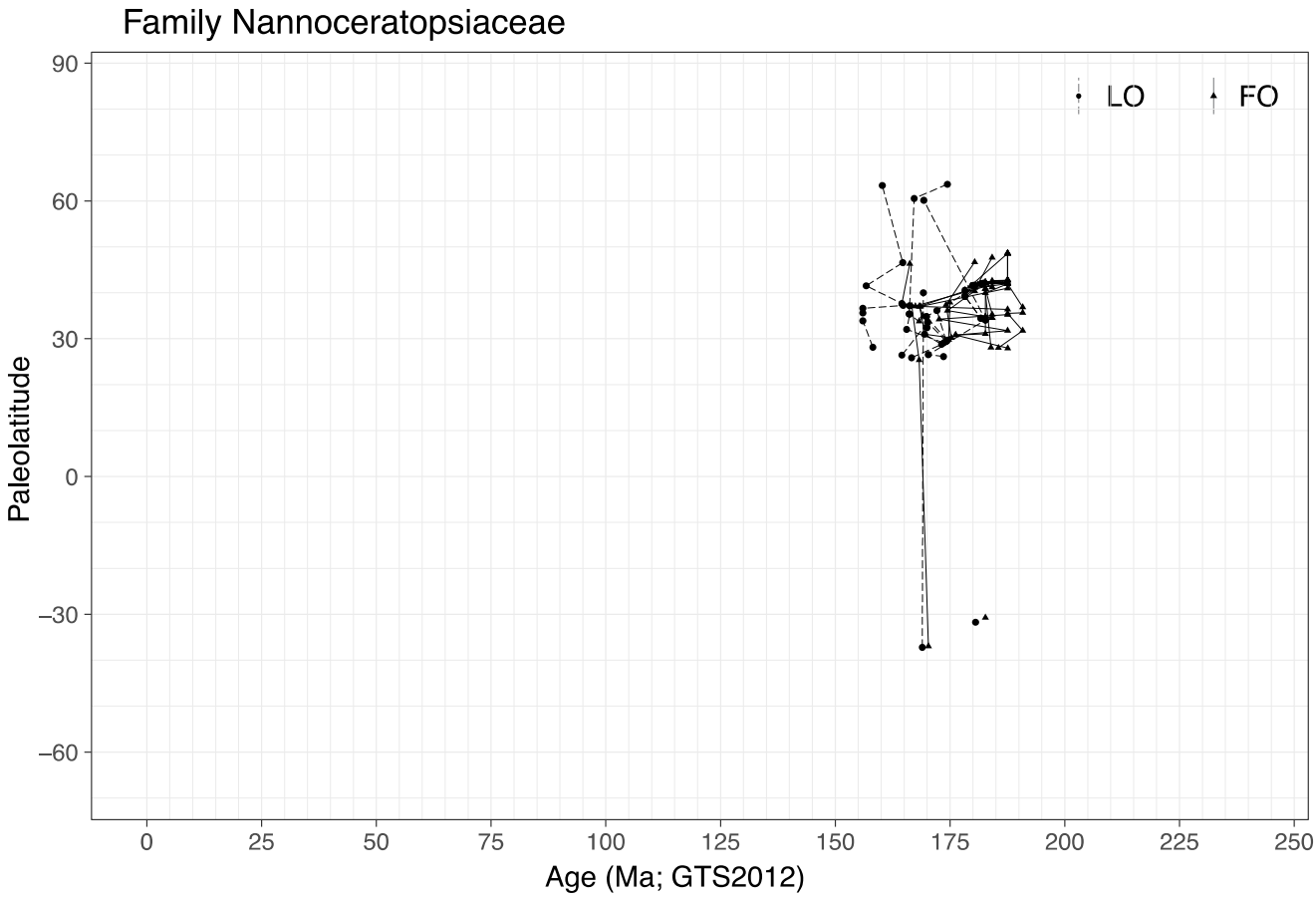


Figure 26: As Figure 5, but for the Family Nannoceratopsiaceae.

Order Ptychodiscales

Family Ptychodiscaceae (Fig. 27)

Range: this family only has entries in the Late Cretaceous (91–66 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.

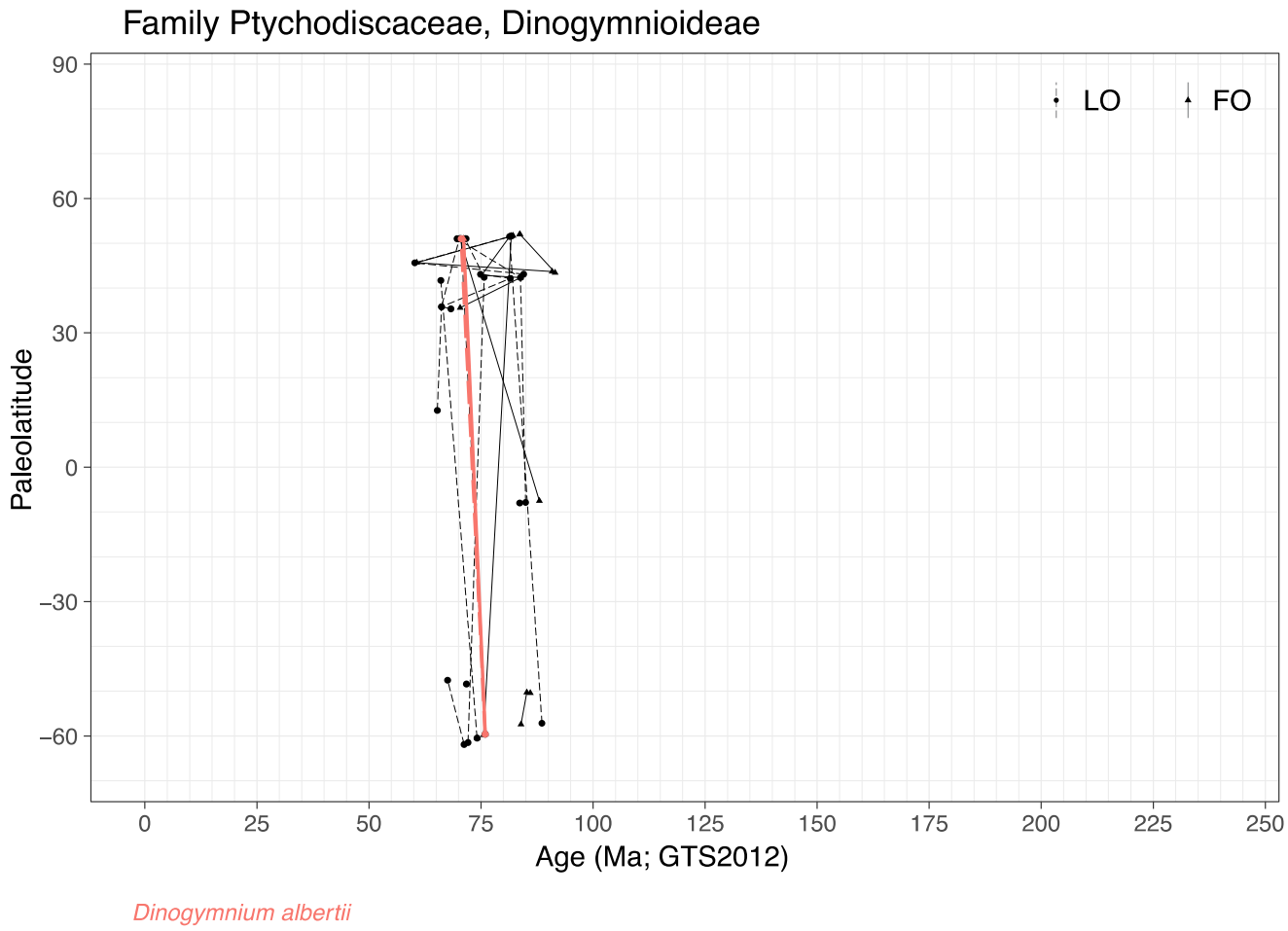


Figure 27: As Figure 5, but for the Family Ptychodiscaceae, subfamily Dinogymnioideae.

Order Suessiales

Family Suessiaceae (Fig. 28)

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

Quasi-synchronous events: LO of *Suessia swabiana*. Other events are highly diachronous.

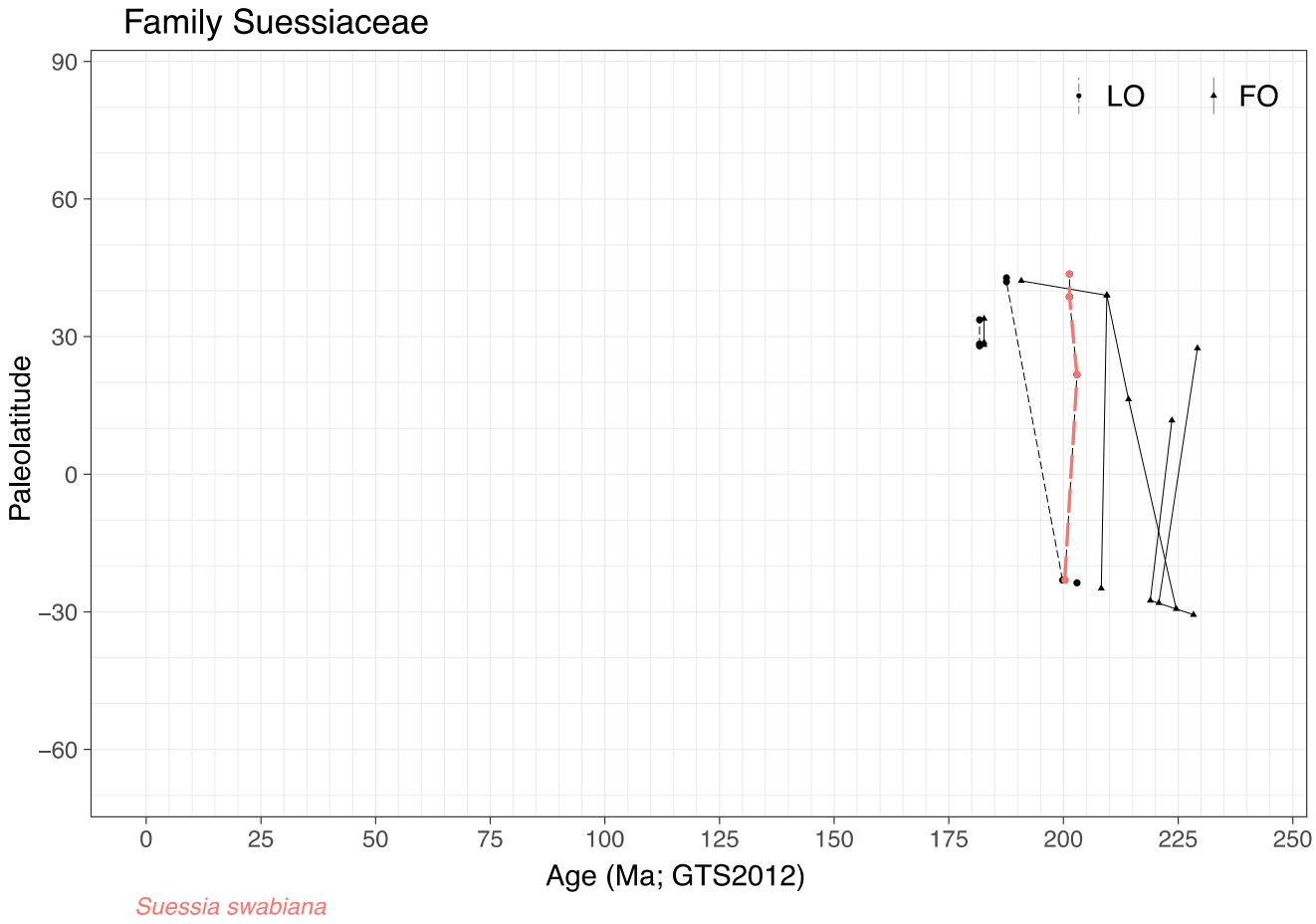


Figure 28: As Figure 5, but for the Family Suessiaceae.

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.

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. (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 (e.g., 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 only by the accuracy of the tie to the chronostratigraphic time scale, 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 time scale. In such cases, minor diachroniety (~10^{4-5} yr) may be related to the inherent assumption of linear sedimentation rates between age tie points. Larger diachroniety (~10^{5-6} yr) may be because the zonation through which dinocyst events were calibrated to the chronostratigraphic time scale 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 shown to be quite latitudinally diachronous themselves (e.g., Ogg and Hinnov, 2012a, b and references therein). 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 GTS2012. So far, the majority of Mesozoic dinocyst events have been calibrated against these ammonite zonations, which makes their absolute tie to the chronostratigraphic time scale 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 (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 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 time scale. 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 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 presents for the first time a quantitative overview of 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 (~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 Myrs onwards (except in Protoperidinioideae). DINOSTRAT allows to further explore 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 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 Supplement 2, and these plots can be adjusted and reproduced using the R markdown file "plot creator" 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 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 new Geologic Time Scales, 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; DOI:10.5281/zenodo.4471204). The database consists of 4 csv files: (1) "Paleolatitude.csv"; paleolatitude and present-day position of sites in DINOSTRAT, (2) "modernsp.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. 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 time scale, 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

- Supplement 1: Table of conversions of published zones to those in GTS2012
- 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).

8 Competing interests

Author declares no conflict of interests

9 Acknowledgements

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