



Organic-walled dinoflagellate cysts in biostratigraphy: state of the art and perspectives for future research

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With 9 figures

Dedication: This contribution is dedicated to the memory of our dear friend and co-author Martin A. Pearce who sadly passed during the reviewing process of this contribution.

Abstract. Over the past 70 years, the potential of organic-walled dinoflagellate cysts (or dinocysts) for the dating and correlation of marine deposits from the Upper Triassic onwards has been increasingly realized, and dinocyst biostratigraphy has developed into a valuable stratigraphic method both in academic and industrial applications. Its utility is traditionally considered to be greatest in shelfal settings, but dinocyst biostratigraphy has also been successfully applied to deep-ocean sedimentary successions. As such, dinocyst-derived age information is complementary to that of other microfossil groups with typically more offshore distribution centers such as planktonic foraminifera, calcareous nannofossils, diatoms, and radiolaria. Due to the limited preservation potential of calcareous and siliceous microfossils in high-latitude settings, dinocysts are particularly important for age determinations in polar to sub-polar regions. The versatility of dinocyst signals is further enhanced in microscope slide preparations containing these microfossils because they typi-

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cally also include terrestrial palynomorphs such as pollen and spores, yielding direct land–sea correlations. Regardless of its impressive potential, dinocyst biostratigraphy comes with specific challenges. The present article aims to provide a critical and comprehensive review of dinocyst biostratigraphy. It first discusses the principles of dinocyst morphology and taxonomy, as well as current concepts in dinoflagellate (cyst) paleoecology, because accurate identification and an understanding of environmental tolerances are indispensable for successful dinocyst-based biostratigraphic analysis. It then considers the suitability of dinocysts as biostratigraphic markers in terms of morphological distinctiveness and abundances, taxonomic diversity, stratigraphic ranges, and (paleo-) geographic distributions. Finally, it identifies perspectives and potential for future work.

Keywords. dinoflagellate cyst; biostratigraphy; Mesozoic; Paleogene; Neogene; Quaternary

1. Introduction

Despite the recent advances in chemo- and cyclostratigraphy, microfossil biostratigraphy has remained a prominent and indispensable stratigraphic tool in both academic research and industry applications (e.g., [Gradstein et al. 2020](#), [Georgescu 2021](#)). Microfossils are particularly well suited for providing relative age control for drilling operations. Their commonly high abundance in sedimentary rocks allows the use of very small samples, and due to their small size, microfossils are easily recovered from subsurface drill cuttings without being destroyed by the mechanical action of the drill bit. Moreover, the rapid evolutionary rates in many microfossil groups yield age constraints at high temporal resolution (in the order of 100 kyrs or less). Accordingly, interest in microfossil biostratigraphy has long been driven by the exploration for hydrocarbons. The rapid expansion of hydrocarbon exploration, especially in northwestern Europe in the 1970s to 1990s, resulted in a boom in biostratigraphic research and funding. Factors such as the subsequent maturing of hydrocarbon provinces across northwestern Europe and beyond, instability in oil prices combined with a widespread recognition of accelerating global climate change, and the implementation of a moratorium at some universities on new funding from the hydrocarbon industry have led to a significant decline in industry-driven biostratigraphic research in recent decades.

From the late 1960s onwards, scientific drilling initiatives such as the Deep Sea Drilling Project (DSDP), Ocean Drilling Program (ODP), and Integrated/International Ocean Drilling/Discovery Program (IODP), as well as recognizing the acceleration of global change, promoted the interest in ocean drilling for paleoclimate research and consequently the use of microfossils as paleoenvironmental proxies. The increasing focus on paleoclimatic, paleoceanographic and paleoenvironmental change has resulted in classi-

cal biostratigraphy being undervalued and underfunded in many countries. However, biostratigraphy requiring high taxonomic precision remains an essential chronological foundation for many facets of process-oriented geoscientific research.

Within this context, organic-walled dinoflagellate cysts (hereafter dinocysts) have become increasingly relevant in biostratigraphy, and dinocyst biostratigraphy has evolved into a valuable tool for the dating and correlation of marine strata from the Upper Triassic onwards. The biostratigraphic value of dinocysts is enhanced by their co-occurrence with palynomorphs from terrestrial and freshwater settings, the groups commonly occurring in the same sample; this mixing has the potential to provide a direct land–sea correlation of environmental change. Dinocyst biostratigraphy is traditionally applied to marginal marine and epicontinental settings, mainly due to the limited water depths in which most cyst-forming dinoflagellates can complete their life cycle, and because other microfossil groups are often absent or have reduced diversities in such settings. Hence, dinocyst-based age information is complementary to that from other microfossil groups with distributions typically extending more distally, such as planktonic foraminifera, calcareous nannofossils, radiolaria, and diatoms. Because dissolution often affects calcareous and siliceous microfossils in polar to sub-polar environments, and fewer species of calcareous microfossils may be present in these environments, dinocyst biostratigraphy is particularly useful in high-latitude settings. As a result, dinocyst biostratigraphy has yielded a higher temporal resolution than that based on calcareous nannofossils in many high-latitude regions (e.g., Circum-Arctic: [Eldrett et al. 2004, 2019](#); [Nøhr-Hansen 2025](#); [Sluijs & Brinkhuis 2024](#); Circum-Antarctic: [Bijl et al. 2013, 2018a](#); [Bowman et al. 2016](#); [Clowes et al. 2016](#)).

Following a surge of regional dinocyst zonations published during the 1980s and 1990s (e.g., [Woollam & Riding 1983](#); [Heilmann-Clausen 1985, 1987](#); [Helby](#)

et al. 1987; Wilson 1988; Powell 1992; Bujak & Mudge 1994; Williams et al. 1993; Riding et al. 1999), Stover et al. (1996) and Williams et al. (2004) compiled these efforts into comprehensive, larger-scale schemes, partly in the multidisciplinary context of the ODP and IODP; in particular, Williams et al. (2004) differentiated the stratigraphic ranges of individual species for the low, mid- and high latitudes in the Northern and Southern Hemispheres. Two decades after the milestone compilation of Williams et al. (2004), dinocyst biostratigraphy has remained in high demand, but also faces new challenges. For instance, important progress has been made in directly tying dinocyst biohorizons to the international geological time scale (GTS; Gradstein et al. 2020), and substantial new biostratigraphic information from dinocysts has become available notably for the high latitudes. In light of these developments, we here aim to provide a critical and comprehensive review of dinocyst biostratigraphy. Emphasizing that accurate identification and an understanding of environmental tolerances are essential for successful biostratigraphic analysis, we first provide an overview of dinocyst morphology and taxonomy, and current concepts in dinoflagellate (cyst) paleoecology. Finally, we discuss potential future directions in dinocyst biostratigraphy.

2. Dinoflagellate nomenclature, morphology, and taxonomy

Dinoflagellates exhibit both plant-like and animal-like traits. Consequently, they have been classified both as protozoans, which are treated under the International Code of Zoological Nomenclature, and as algae, which are subject to the International Code of Nomenclature for algae, fungi and plants (ICN, until 2012 known as the International Code of Botanical Nomenclature). Today extant dinoflagellates are exclusively treated under the ICN, and indeed fossil dinocysts have generally been treated under this code (Head et al. 2024a). Biologically, dinoflagellates are nowadays treated as protists rather than protozoa or algae.

A particular challenge in studying dinoflagellates, especially in integrating the nomenclature of fossil and non-fossil taxa, is that biologists have traditionally used the morphology of the motile stage in classifying and typifying (and hence naming) taxa, whereas paleontologists studying the fossilized remains have based their classification by necessity on the morphology of the cyst, with rare exceptions the only part of the life

cycle that fossilizes. However, incubation experiments and other observations beginning in the 1960s (e.g., Wall & Dale 1966, 1968) revealed that cyst morphotypes already known by fossil-typified names could now be assigned to biologically-defined (non-fossil) species which carried different names. Thus, a dual nomenclature has developed where two names can be applied to the same specimen, one based on the fossil and the other based on its equivalent non-fossil (usually the motile stage). Dual nomenclature is explicitly allowed under the current ICN (Head et al. 2025). It means, for instance, that the names *Spiniferites* and *Impagidinium*, which represent large and geologically long-ranging fossil-genera, can be used independently of *Gonyaulax*, a large non-fossil genus, without concerns for priority of publication even when incubation studies show them to be related or “equivalent” (Head et al. 2024a, b). Dual nomenclature largely exists because fossil and non-fossil taxonomies cannot realistically be integrated at the generic level, but this is not the case at the supra-generic level where these taxonomies are linked by commonalities in tabulation (Fensome et al. 1993, Head et al. 2024a), as described below.

Dinoflagellates generally have complex life cycles of several stages. A biflagellate motile stage is known from nearly all extant dinoflagellates, and many taxa undergo cyst stages of one kind or another, including vegetative cysts, short-term temporary cysts, and long-term resting cysts (Fig. 1). The motile cells and the vegetative and temporary cysts of dinoflagellates are rarely preserved in the fossil record, a possible exception being *Dinogymnium* and related genera, which seem to represent fossilized ecdysal pellicles (May 1976). Hence, aside from the biogeochemical record of dinosterols and their diagenetic transformation products (e.g., Mouradian et al. 2007), dinoflagellate DNA in sediments (e.g., Armbrecht et al. 2024), and rare motile-stage fossils such as *Dinogymnium*, the fossil dinoflagellate record consists overwhelmingly of organic-walled, calcareous and (rarely) siliceous dinocysts that represent one life-cycle stage. The resting cysts in some taxa consist of highly resistant, eminently fossilizable biopolymers traditionally termed “dinosporin” or “bioplastic”, but having complex species-specific compositions (e.g., Versteegh et al. 2007; Gurdebeke et al. 2018). These organic-walled resting cysts are commonly preserved as microfossils and provide the basis for organic-walled dinocyst biostratigraphy.

As the fossil dinoflagellate record is based on only a part of the dinoflagellate life cycle, it is by nature

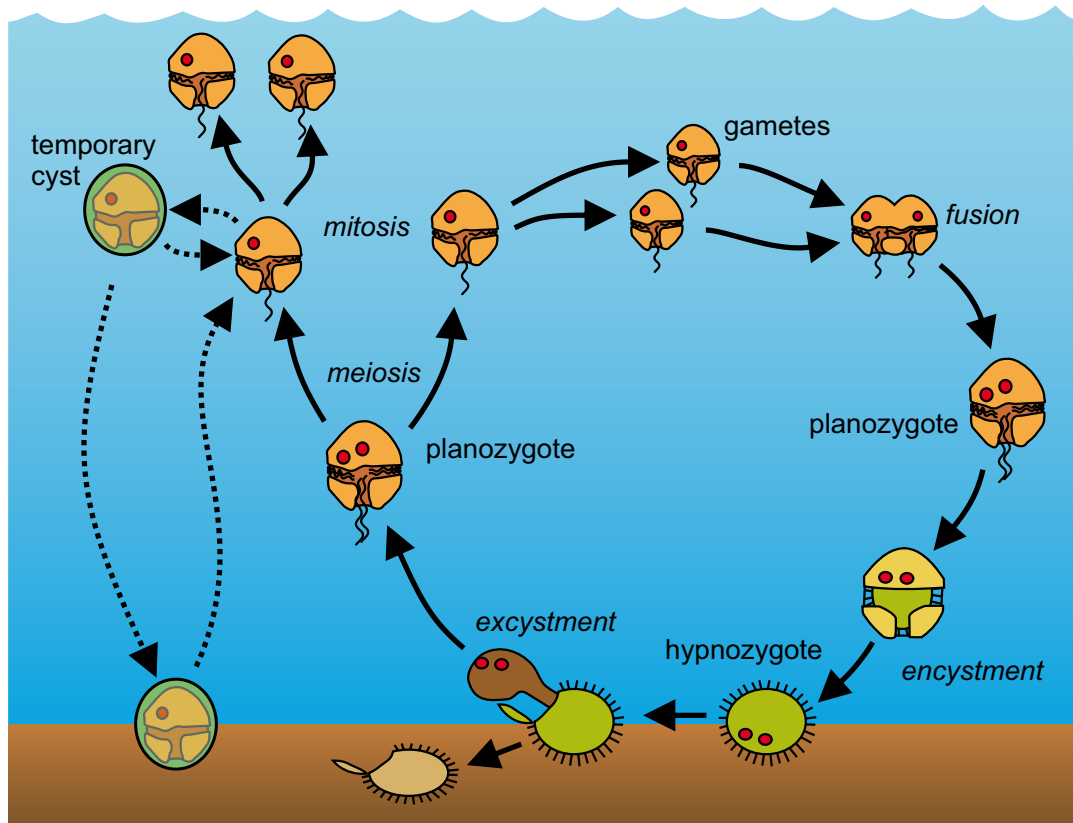


Fig. 1. Schematic illustration of the typical life cycle of cyst-forming dinoflagellates, including a motile stage with vegetative and sexual reproduction and a non-motile resting-cyst stage. Temporary cysts are generally not preserved in the fossil record. Modified from [Nehring \(1994\)](#).

incomplete and selective ([Evitt 1985](#)). In addition, only 13–16% of all extant dinoflagellate species produce fossilizable organic-walled resting cysts ([Head 1996](#)); this means that fossil dinocyst assemblages do not represent the full suite of dinoflagellate taxa that thrived in past oceans. However, while the selective nature of the dinoflagellate fossil record is undoubtedly a negative aspect, it compares favourably to the absent or minimal fossil records of many other protist groups.

The relationship between fossilizable resting cysts and the motile stage of dinoflagellate taxa is further complicated by the fact that the organic resting cysts of some extant dinoflagellate species show strong morphological variation in response to the physico-chemical characteristics of the surrounding waters (e.g., [Head 1996](#); [Mertens et al. 2009, 2011](#); [Rochon et al. 2009](#)); this highlights the exceptional sensitivity of dinoflagellates and their organic cysts to changes in water-mass characteristics, and thus their value as (paleo)environmental proxies (see Section 3). Despite

these complications, the fossil dinocyst record has proven extremely useful for providing age control as well as paleoenvironmental information in Upper Triassic to Quaternary strata.

The motile dinoflagellate cells have an outer layer of “amphiesmal” vesicles around the cell. In “thecate” (or armored) dinoflagellates, these vesicles contain cellulosic plates the number and arrangement of which constitute a tabulation or tabulation pattern. In athecate (or “naked”) dinoflagellates, amphiesmal vesicles lack cellulosic plates, although the vesicles often still occur in a pattern that can be referred to as tabulation. Tabulation is an important basis in the generic and suprageneric classification of the group ([Fensome et al. 1993](#)). Naked dinoflagellates include the symbionts of many corals and planktonic foraminifer species.

In contrast to most naked dinoflagellates, the thecate forms have a rich fossil record. Therefore, an understanding of tabulation is essential for the taxonomy of dinoflagellates, living and fossil. Thecal plates and

thus tabulation are primarily a functional feature of living motile dinoflagellates. Tabulation may be replicated, or “reflected”, in the morphologies of resting cysts, i.e., dinocysts (Gocht 1983; Evitt 1985). This “reflection” reveals equivalencies between extant motile cells and dinocysts, and thus facilitates taxonomic classifications. The thecate features reflected in cysts do not function as on the theca. Accordingly, the reflected features in cysts are often denoted by the prefix “para” (Evitt et al. 1977). However, “para-” terminology can be cumbersome, especially when applying to all features of the cyst, and the context usually makes it unnecessary. Accordingly, many authors use the standard thecal terminology for equivalent features on cysts, especially when dealing exclusively with cysts. We therefore do not use “para-” terminology in the present article. Detailed compilations on the morphologies realized during the different stages of the dinoflagellate life cycle, as well as the taxonomy of fossil

dinocysts have been provided previously by several authors (e.g., Evitt 1985; Fensome et al. 1993, 1996a). Aiming at a broad, biostratigraphically oriented audience, we provide only an overview of the key morphological features of dinocysts where they are directly relevant for biostratigraphic purposes.

The most basic features of motile cells that usually also occur on their cysts are two grooves, each hosting a flagellum, and to varying degrees the plate tabulation. In motile cells, the two grooves are related to the positions of the transverse and longitudinal flagella. The cingulum is a transverse groove that almost encircles the cyst, usually in an approximately equatorial position. Its two ends converge, but do not meet on what by definition is the ventral surface; the two ends of the cingulum are commonly offset relative to one another (Fig. 2). The side opposite to the ventral surface is hence the dorsal surface, and left and right are defined accordingly as in vertebrates. On the cyst, the

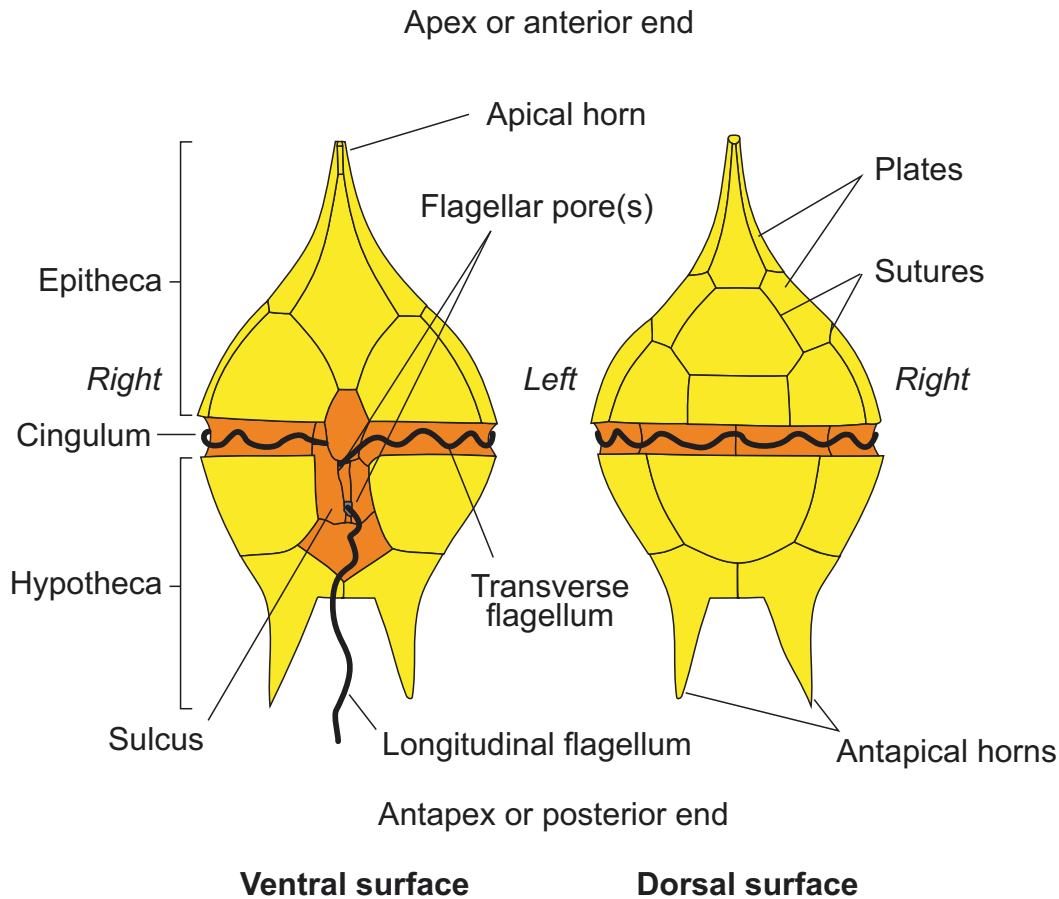


Fig. 2. Schematic illustration of the principal morphological features in a peridinialean dinoflagellate theca. With the exception of the flagella, features in the morphologies of hypnozygotic resting cysts often reflect features on the thecae of the dinoflagellates that they are derived from. Modified from Evitt (1985).

cingulum also divides the anterior epicyst (epithea on motile cells) from the posterior hypocyst (hypotheca on motile cells), the frame of reference being the direction of movement in the motile cell. The anterior and posterior ends are termed apex and antapex, respectively. The longitudinal groove on the ventral surface, which hosts the longitudinal flagellum on the motile cell, is termed the sulcus.

Many dinocysts have surface features that fully or more often partially reflect the tabulation on the motile theca through ridges, crests, or other linear arrangement of “ornament”. An important feature, sometimes the only evidence of tabulation on a cyst, is the archeopyle, an opening in the cyst wall through which excystment, or hatching, of the motile form occurs. Archeopyles almost invariably occur on the epicyst and mostly result from the loss of dorsal or apical plates. If these plates are removed as one piece, they are referred to as an operculum; if removed as several pieces, they constitute opercular pieces. The tabulation pattern is of prime importance in dinoflagellate classification, including dinocysts. Several systems have been developed to describe the tabulation patterns, which vary between taxa. The most widely used system is based on that developed by [Kofoid \(1907, 1909\)](#). Dinocyst tabulations can be grouped into six types; among fossil dinocysts, the gonyaulacoid and the peridinioid tabulations are the most widespread of these types, with well over 600 genera being included in the orders Gonyaulacales and Peridinales (Fig. 3; for details see reviews by [Evitt 1985](#); [Fensome et al. 1993, 1996a](#); [Fensome & Munsterman 2020](#)). It is important to note that tabulation patterns are commonly not obvious from individual fossils. Therefore, it is necessary to study multiple specimens and understand the broad affinities of particular morphological features. Nonetheless, the translucent nature of the dinocyst wall allows tabulation of both upper and lower surfaces of a single specimen to be examined under the light microscope.

The wall of fossil dinocysts as resolved under a light microscope is organized into one or more layers. If more than one layer is present, major cavities can occur between the different layers, thereby strongly influencing the cyst outline. Whereas the surface of some dinocysts is smooth, others exhibit surfaces that are covered with ornament of low relief such as granules or exhibit major elements such as septa or processes, the latter having different arrangements, shapes and terminations. The central body of a cyst in its simplest form is spheroidal, but may be dorsoventrally or

apically–antapically compressed, and its outline in dorsoventral view may extend to form apical, lateral and antapical horns.

To warrant maximum practical applicability of fossil dinocysts in biostratigraphy, their taxonomy must rely on distinguishable morphological features that allow straightforward identification of taxa under the light microscope (e.g., [Bijl et al. 2017](#)). These features comprise tabulation characteristics (including archeopyle type and shape, and distribution of ornament), cyst outline and size, number of wall layers and cavation, plate and suture ornamentation, and process location and morphology. In some cases, however, it is also necessary to consider the fine structure of the cyst wall (e.g., [Head 1994](#)).

3. Paleocology and paleogeography

Over the past decades, the paleoecological affinities of fossil dinocysts, and by extension their paleoenvironmental, paleoclimatic and paleoceanographic significance, have been the subject of a multitude of studies. Consequently, dinocyst-based paleoenvironmental reconstructions have become increasingly sophisticated. Generally, the most detailed information on dinocyst (paleo)ecology is available for the Quaternary due to the large number of extant dinocyst taxa in the respective assemblages that can be analyzed following an actuopaleontological approach (e.g., [de Vernal & Marret 2007](#) and references therein). A significant advance in this regard was the recording of cyst assemblages from modern oceanic sediments across large parts of the Northern Hemisphere and, later, globally. Such studies allowed the distributions of individual species to be mapped and quantitatively linked to a range of corresponding sea-surface parameters including temperature, salinity, macronutrients, and sea-ice cover, for each season of the year ([Rochon et al. 1999](#); [de Vernal et al. 2001, 2020](#); Fig. 4). Using this information, which was assembled using standardized protocols, statistical analyses including transfer functions and related approaches can generate numerical paleoenvironmental reconstructions from fossil assemblages throughout the Quaternary (e.g., [de Vernal et al. 2001](#); [Datema et al. 2019](#)). This information can be augmented with proxy datasets from the fossil record, such as planktonic foraminiferal geochemistry (Mg/Ca, $\delta^{18}\text{O}$) as an indicator of sea-surface temperature, to provide quantitative autecological information

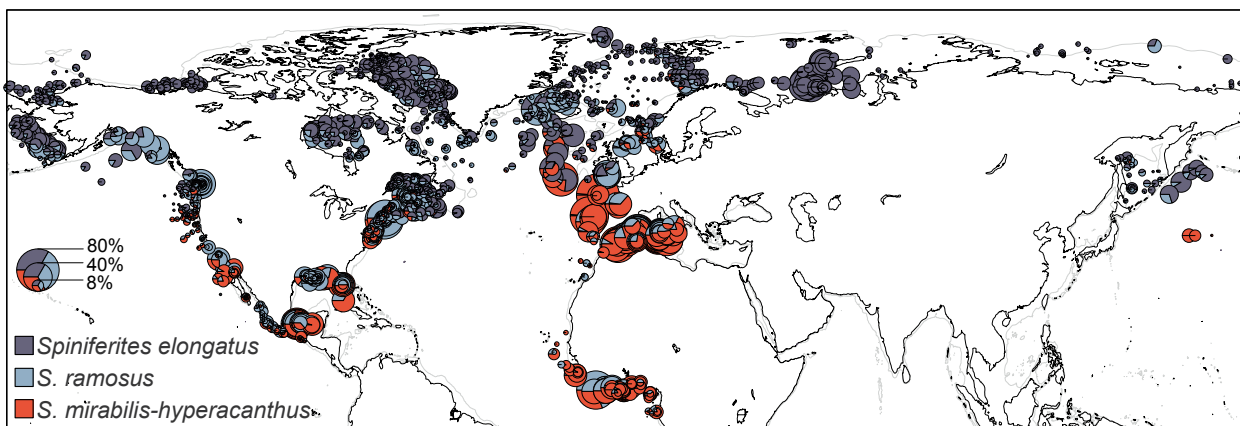


Fig. 4. Northern Hemisphere dataset of common modern dinocyst taxa based on surface sediments of the ocean floor. Sample processing and taxonomy follow standardized protocols. Because each modern dinocyst assemblage is linked to corresponding environmental parameters at the sea surface, the dataset is suitable for calibrating transfer functions that are used to reconstruct these environmental parameters from fossil assemblages. The figure shows the distributions of three common species of *Spiniferites* contained in the dataset (modified from de Vernal et al. 2020).

for extinct species (e.g., De Schepper et al. 2011, Hennissen et al. 2017).

Quantitative interpretations from older strata are more challenging, but semi-quantitative and qualitative analyses remain highly useful. Based on empirical information as well as the application of increasingly advanced statistical approaches, the understanding of dinoflagellate (cyst) paleoecology has made substantial progress for such deep-time assemblages. Accordingly, numerous studies have yielded information on the paleoecological significance of dinocyst assemblages of the Neogene (e.g., Versteegh 1994, Head 1998, Louwye et al. 2004, De Schepper et al. 2009, Boyd et al. 2018), Paleogene (e.g., Brinkhuis 1994, Pross & Schmiedl 2002, Rasmussen et al. 2003, van Simaëys et al. 2005a, Woods et al. 2014, Frieling & Sluijs 2018, Śliwińska 2019, Fig. 5), and, to a somewhat lesser degree, the Cretaceous (e.g., Pearce et al. 2003, 2009; Thorn et al. 2009; Bowman et al. 2013; Nøhr-Hansen et al. 2016; Eldrett et al. 2017), Jurassic (e.g., Riding et al. 1985, 2013; Bucefalo Palliani & Riding 1999; Correia et al. 2017), and Upper Triassic (Courtinat & Piriou 2002, Mantle et al. 2020). Integrating the findings of these studies, several reviews have appeared on the state of the art of Mesozoic and Cenozoic dinocyst paleoecology since the early 2000s (e.g., Matthiessen et al. 2005, Pross & Brinkhuis 2005, Sluijs et al. 2005, Frieling & Sluijs 2018). In the following paragraphs, we present a brief synopsis of dinoflagellate (cyst) paleoecology, focusing on aspects

that are particularly relevant from a biostratigraphic perspective.

Most dinoflagellates that form organic-walled resting cysts have neritic distribution centers across the continental shelves. This bathymetric preference is closely connected to the nature of the life cycle of most cyst-forming dinoflagellates. During their motile stage, dinoflagellates thrive in the (uppermost) photic zone of the water column. However, upon encystment they undergo a period of mandatory, endogenously controlled dormancy lasting weeks to months (Pfiester & Anderson 1987). During that time, they lose their mobility and typically sink through the water column, either ultimately reaching the sea floor or resting on a pycnocline that acts as an effective hydrodynamic barrier. After excystment, the new motile cells return to the photic zone. In fossil dinocysts, the hatching of the cyst is documented by opened archeopyles. Intact, non-excysted cysts are encountered only infrequently, which might suggest that excystment took place in the large majority of cysts. A notable exception are cysts that had settled in low-oxygen or even anoxic environments; evidence from modern (Anderson et al. 1987) and fossil (Pross 2001a) assemblages indicates that anaerobic conditions inhibit excystment. However, experiments have identified dinocysts from sediment with a remarkable viability of up to nearly 100 years (Ribeiro et al. 2011).

The paradigm has long been that the characteristics of this life cycle limit the maximum water depth of

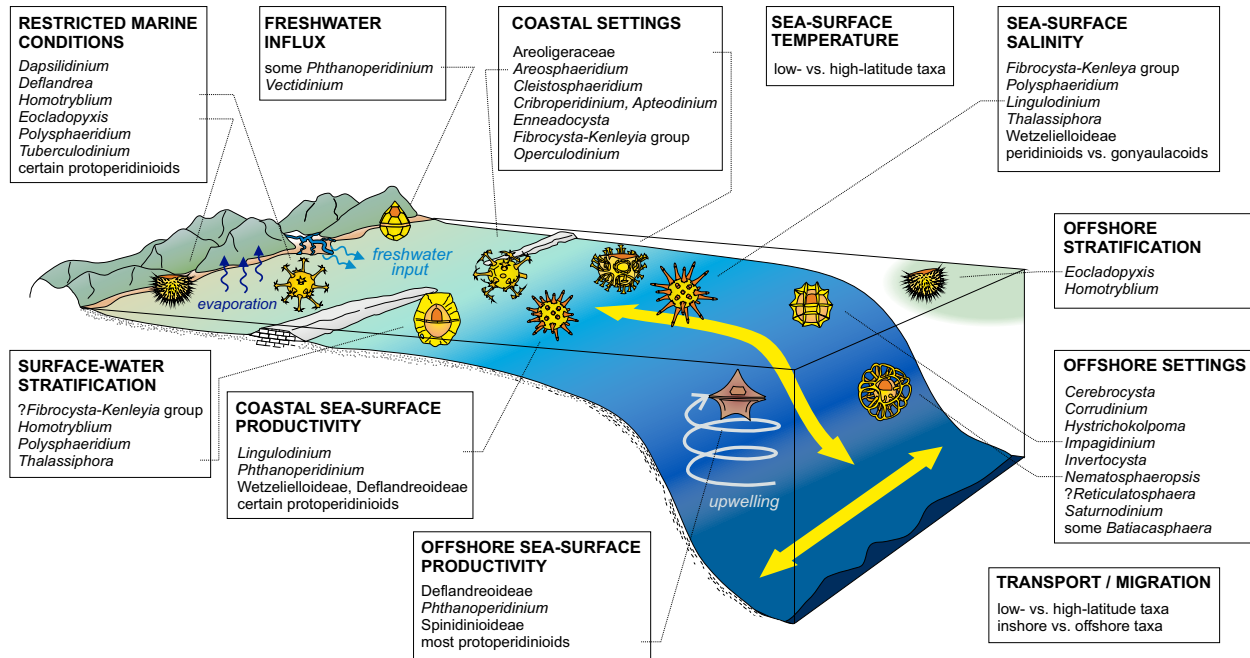


Fig. 5. Schematic representation of ‘deep-time’ (here: Paleogene) dinocysts indicative of specific paleoenvironmental conditions. See text for discussion. Modified from Pross & Brinkhuis (2005) and Frieling & Sluijs (2018).

their habitat, inhibiting the occurrence of cyst-forming taxa in oceanic settings unless these taxa have developed strategies that allow them not to sink to abyssal depths (see below). The paleoecological signal of dinocysts thriving in neritic settings may therefore bear both a surface-water and a bottom-water component, which has earned them at first glance, the apparently conflicting designation as “benthic plankton” (Dale 1983). However, recent work at open-ocean locations has questioned this paradigm. Notably, analyses of Paleocene through Pliocene dinocyst assemblages at open-ocean ODP Site 959 in the eastern equatorial Atlantic Ocean has revealed much higher dinocyst diversities than expected at open-ocean sites, with little sedimentological, lithological or provenance evidence for downslope transport (e.g., Frieling et al. 2018a, van der Weijst et al. 2022). It may suggest much higher flexibility in the geographic dispersal of dinoflagellates than previously thought, when any dinocyst that was not considered an open-ocean specialist was considered to reflect transport if found in deep-ocean sediments (e.g., Dale 1996). Still, because of the high abundances of dinocysts in shelfal sediments, the paleoenvironmental, paleoclimatic and paleoceanographic information gleaned from their assemblages, as well as their biostratigraphic potential, is comple-

mentary to that obtained from other, more pelagic plankton groups such as coccolithophores, planktonic foraminifera, and radiolaria.

An important feature that sets dinoflagellates apart from other fossilizable plankton is the variability of their trophic strategy. While many cyst-producing dinoflagellates are phototrophic, i.e., they respond primarily to factors connected to the availability of light, others are heterotrophic, i.e., are more dependent on the availability of suitable prey. Many otherwise phototrophic dinoflagellates have been shown to be mixotrophic, meaning that they can also utilize heterotrophic feeding strategies (e.g., Stoecker 1999). Cysts produced by dinoflagellates of all trophic modes are highly sensitive indicators of such oceanographic parameters as sea-surface temperature, salinity, productivity, and sea-ice cover (de Vernal et al. 2020, Thöle et al. 2023), surface-water stratification and upwelling (e.g., Reichart et al. 2004, Frieling & Sluijs 2018), and bottom-water oxygenation (e.g., Pross 2001a, Zonneveld et al. 2007). The fact that some dinocyst taxa occur predominantly in nearshore settings, whereas others are constrained to outer neritic or even oceanic environments, yields a strong proximal-distal signal in many assemblages both in the modern (e.g., Wall et al. 1977, Prebble et al. 2013) and deep-time domains (e.g., Brinkhuis

1994, Pross & Schmiedl 2002). Thus, dinocysts are invaluable in sea-level reconstructions and sequence stratigraphy (e.g., Habib et al. 1992). The long-distance transport of dinocysts provides information on potential downslope transport via mass-wasting events or for the reconstruction of paleo-currents (e.g., Huber et al. 2004, Pross et al. 2010, Bijl et al. 2018b). As already mentioned above, this sensitivity to environmental conditions makes dinocysts important proxies in paleoenvironmental, paleoclimatic and paleoceanographic research (see reviews by Dale 1996, Matthiesen et al. 2005, Pross & Brinkhuis 2005, Sluijs et al. 2005, de Vernal et al. 2020). By influencing the distribution of cyst-forming dinoflagellates in the world's oceans, it provides insight into paleoenvironmental signals that affect biostratigraphic datasets and introduce uncertainty in correlations. Neritic dinocyst taxa, with their more restricted distributions, may offer greater potential for high-resolution biostratigraphy than more cosmopolitan taxa.

Attempts have been made to utilize dinocysts as water-depth indicators, essentially attributing water depths to the response of dinocyst assemblages along proximal-distal gradients and associated generalized environmental conditions. Such efforts, which assume a relationship between surface-water conditions and water depth, should be treated with caution. They are strongly compromised by the ramifications of marine basin geometries (such as the steepness of the continental shelf; e.g., Somme et al. 2009), (paleo)oceanographic complexities, and the (paleo)ecological requirements of cyst-forming dinoflagellates. There is an extreme variability in the world's present and past oceans in relations between water depth and shoreline distance, and a similar, possibly even larger scatter exists for the correlation between water depth and surface-water conditions. Also, in their motile stage, cyst-forming dinoflagellates depend on surface-water conditions, which largely determine the proximal-distal signal in dinocyst assemblages (e.g., Dale 1996, de Vernal & Marret 2007). Water depth affects the signal from cyst-forming dinoflagellates primarily in the context that the protoplasts must be able to return to the photic zone after excystment. Numerous studies (e.g., Dale 1992, Bringué et al. 2019) suggest that dinocysts sink through the water column in aggregates, which reduces their buoyancy and greatly accelerates their descent. As a result, most cyst-forming dinoflagellates can thrive only in relatively shallow, shelfal settings. Cyst-forming dinoflagellates with oceanic habitats must have developed alternative strategies to

avoid the sinking of their cysts into depths from which they would be unable to return to the photic zone. These include enhancing the buoyancy of the cyst such that it remains in the upper water column, or accelerating completion of the cystal stage such that excystment occurs before the cysts sink too far towards the sea floor to re-establish the planktonic stage (Dale 1986, Dale & Dale 1992). Alternatively, cysts may rest on a strong and relatively shallow pycnocline that acts as a virtual sea floor, enabling cyst-forming dinoflagellates to complete their life cycle prior to sinking to deep water (e.g., Reichart et al. 2004). As such, oceanic cyst-forming dinoflagellates cannot yield information on water depth beyond that they indicate meso- to abyssopelagic settings. In light of the above, assigning depths to proximal-distal signals in neritic dinocyst assemblages would require the exclusion of the extreme scatter in the correlation between water depth and surface-water conditions on the shelf. As this appears impossible, exploiting the proximal-distal signals from neritic dinocyst assemblages in relation to water depth, or even providing absolute depth indications other than that the assemblages are from a shelfal setting, must be considered unrealistic.

A novel line of (paleo)ecological research based on dinocysts explores the carbon-isotopic composition of their walls (Sluijs et al. 2018). Moreover, this work, combining culturing work and analyses on cysts from core-top sediments also explores the ^{13}C fractionation in dinocysts as a potential proxy for seawater CO_2 concentrations (e.g., Frieling et al. 2023).

4. Taphonomy

Once the resting cyst has hatched by way of the archeopyle, the cyst wall may decay or become preserved in the sediment. The size of most dinocysts is between 30 and 100 μm , which suggests that their sedimentation regime is similar to that of silt; however, their hydrodynamic characteristics are further influenced by their relatively low density and cyst shape, including the potential presence of horns, processes and membranes that may affect buoyancy. Sediment-trap studies (Pospelova et al. 2018, Bringué et al. 2019) and modeling data for present-day oceans (Nooteboom et al. 2019) suggest consistently that the descent of dinoflagellates in the water column from the moment they lose mobility in their cyst-forming phase until they reach the sea floor occurs predominantly via small fecal pellets and aggregates. The significance of particle aggregation as a vehicle to bring

dinocysts to the sea floor may differ depending on the oceanographic setting and season. However, without this process, the bioprovinciality of dinocysts would be much less pronounced than is observed in modern ocean sediments (e.g., [Marret et al. 2020](#)).

The preservation of dinocysts in surface sediments and strata depends on several factors. A key impediment to preservation is the prolonged exposure to free oxygen dissolved in the water column and/or in pore water, which ultimately causes the destruction of all organic-walled dinocysts through oxidation. Oxygen exposure can occur during cyst transport prior to deposition in the sediment and/or after deposition, with oxygen supplied through extensive burrowing having the potential for further deleterious effects. Hence, preservation is strongly determined by the time the cysts remain suspended in the water column, seafloor oxygenation, burial rate, and biological activity on the sea floor.

There are strong indications that the differences in resistivity to oxidation are due to different molecular structures of the cysts ([Zonneveld et al. 2008](#), [Bogus et al. 2014](#)). Based on the susceptibility notably of protoperidiniacean cysts in the Quaternary, it is generally considered that protoperidinioid cysts may be generally less resistant to oxidation than gonyaulacoid cysts, although not all species within these groups were found to behave similarly ([Zonneveld et al. 2019](#) and references therein). Hence, the challenges connected to selective preservation are most relevant for dinocyst assemblages with high percentages of protoperidinioid cysts (e.g., [Zonneveld et al. 2008](#)), especially in sediments where bottom-water oxygen concentrations have strongly fluctuated (such as during and after the formation of sapropels; e.g., [Sangiorgi et al. 2006](#)). However, analyses have also shown that the down-core variations in *Protoperidinium* cyst concentrations still primarily reflect the productivity signal as evidenced in other proxies, even in relatively oxic settings (e.g., [Reichart & Brinkhuis 2003](#), [Bijl et al. 2018b](#), [Wubben et al. 2024](#)). Likewise, numerous multi-proxy studies involving early Paleogene dinocysts have yielded signals that are consistent with those from other, non-organic proxies (e.g., [Frieling et al. 2018a](#), [Crouch et al. 2020](#)). This suggests that the issue of selective preservation may be less consequential for dinocyst-based paleoenvironmental reconstructions and dinocyst biostratigraphy than earlier thought. In line with the above, laboratory experiments have also shown that notably heterotrophic (dominantly protoperidiniacean) taxa are particularly

sensitive to harsh chemical treatments during sample preparation (e.g., alkalis, oxidants, hot dilute HCl), which may result in a bias in the assemblages studied under the microscope relative to those originally preserved in the sediment (e.g., [Dale 1976](#), [Marret 1993](#)). Again, the challenges related to the sensitivity to such treatments appear to be most relevant for Quaternary assemblages with their often-high percentages of protoperidinioids. Nevertheless, there are instances where either depositional oxidation or post-depositional oxidation at outcrops has influenced the preservation of organic matter and associated dinocyst assemblages (e.g., [Radmacher et al. 2021](#)). Regardless, to minimize any processing-induced bias it is advisable to use gentle chemical treatment.

Another factor that may impose a preservation bias on dinocyst assemblages is post-depositional burial and thermal maturation. Under high burial temperatures and/or pressures the more labile organic matter content of the sediments, including dinocysts, can be converted and transformed into hydrocarbons through catagenesis. Thermal alteration of dinocysts can make identification challenging, and in extreme cases it can result in highly impoverished or barren intervals dominated by inertinite (e.g., [Vieira et al. 2021](#)). The chemical changes brought about by thermal maturation can, however, increase the resistance of protoperidinioid cysts to harsh chemical treatment during laboratory processing (M.J.H., pers. obs.).

Reworked specimens from older strata occur across all microfossil groups, but can be especially common in dinocyst assemblages owing to the often-complex depositional environments in nearshore settings. The preservation of reworked dinocysts may be as good or even better than the in-situ material. A spectacular example of extensive reworking occurs in the Oligocene of Antarctica: The rapid glaciation of the Antarctic continent at the Eocene–Oligocene transition removed sediments from the continent on a vast scale, and crustal reorganization connected to the emplacement of the ice sheet led to substantial submarine reworking of Eocene shelf sediments (including large numbers of Eocene dinocysts) into Oligocene deposits (e.g., [Houben et al. 2013](#), [Stocchi et al. 2013](#), [Bijl et al. 2018a](#)).

The differentiation between reworked and in-situ specimens is a crucial prerequisite for the biostratigraphic evaluation of dinocyst assemblages. As a first principle, reworking manifests itself by the presence of taxa that are stratigraphically discordant with the in-situ taxa. However, for long-ranging taxa it may be difficult to determine whether specimens are in situ or

reworked. To better identify reworking, a number of approaches have been developed. They either rely on statistical analyses (such as the covariance of taxa; [Bijl et al. 2018a](#)) or on differences between reworked and in-situ cysts as they result from different burial histories. Such differences may be reflected in color ([Bowman et al. 2016](#), [Riding et al. 2022](#)), fluorescence ([Strother et al. 2017](#)), susceptibility to biological staining ([Stanley 1965](#)), greater physical compression, and/or general physical degradation. The recognition of reworking also has a probability component. Species that occur abundantly within their natural stratigraphic ranges are more likely to be found as isolated reworked specimens above it in wells or core holes. For this reason, [De Schepper & Head \(2008\)](#) distinguished between a highest occurrence (HO), highest common occurrence (HCO) and highest persistent occurrence (HPO). Sporadic rare occurrences above a HPO might represent reworking. For species that are dominant or co-dominant, a HCO might represent the highest in-situ occurrence of the species in question, with specimens above this level being reworked. This approach obviously requires the counting of specimens, not merely the registering of presence or absence. Finally, ecological discordance may be considered, such as a warm-water species occurring in a glacial interval, although as many criteria should be applied as possible before a final decision is made.

While reworking is mostly seen as inconvenient, it can also yield valuable information. Once identified as reworked, such dinocysts can provide important insight into the nature and timing of base-level changes in their sedimentary source region and help unravel the origin of the sediments in which they occur. For example, [Lee et al. \(2002\)](#) used allochthonous palynomorphs including dinocysts extracted from glacial sediments to determine ice-flow paths during the Quaternary. In some cases, they can even serve as regional biostratigraphic markers. Hence, reworked cysts should be considered potentially useful elements of dinocyst assemblages.

5. Dinocyst biostratigraphy

5.1. Suitability of dinocysts as biostratigraphic markers

The earliest fossils that can be confidently identified as dinocysts have been described from the uppermost Middle Triassic (Ladinian, c. 239 Ma) of Australia, although this dating is based on indirect evidence only

([Stover & Helby 1987](#), [Riding et al. 2010](#)). Claims of pre-Mesozoic fossil dinoflagellates were countered by [Fensome et al. \(2000\)](#). Recently, [Dale \(2023\)](#) made comparisons between the morphologies of known dinocysts and Paleozoic acritarchs, for example the horn-bearing Early Cretaceous genus *Nyktericysta* with an unnamed horn-bearing Ordovician acritarch. Such morphological similarities are patently due to convergent evolution: there is a compelling understanding of the Mesozoic and Cenozoic patterns of dinoflagellate evolution supported by the fossil record and molecular phylogenetics ([Janouškovec et al. 2016](#)) that, for example, indicate an origin of the family Ceratiaceae (to which *Nyktericysta* belongs) in the Jurassic. Dinoflagellates must have had Paleozoic and earlier precursors, but the identity of these has so far not been convincingly demonstrated among body fossils. However, biogeochemical evidence offers tantalizing glimpses ([Moldowan et al. 1996](#)), as does ongoing work on the chemistry of palynomorph walls, including those of Paleozoic acritarchs (P. Meyvisch, pers. comm. 2024).

From the late Carnian onwards, dinocysts occur consistently, and they have been used for the dating and correlation of marine strata throughout the post-Carnian Mesozoic and Cenozoic ([Mangerud et al. 2019](#), [Gradstein et al. 2020](#), [Mantle et al. 2020](#)). For Paleozoic and pre-Carnian Mesozoic strata, acritarchs are similarly valuable index fossils as dinocysts for the Mesozoic and Cenozoic ([Molyneux et al. 1996](#)). For the Mesozoic and Cenozoic, however, the biostratigraphic potential of acritarchs has been overshadowed by dinocysts, although they are useful in the Cenozoic especially at higher latitudes ([De Schepper & Head 2014](#)). The biostratigraphic application of acritarchs is, however, beyond the focus of this paper.

Fossil dinocysts share many of the traits that make numerous microfossil groups excellently suited for age control. These include morphological distinctiveness in combination with high abundances, high diversity, short stratigraphic ranges, good preservation potential, and wide (paleo)geographic occurrences. In the following sections, we evaluate the critical traits of fossil dinocysts as stratigraphic markers.

5.1.1. Morphological distinctiveness and abundances

A crucial aspect of biostratigraphy is that age markers should be morphologically distinctive and easy to recognize. Although species occasionally exhibit morphological continua between end-members, this prerequi-

site is met by the vast majority of dinocyst taxa with regard to tabulation, archeopyle style, ornamentation, process numbers and shapes, outlines, and wall texture and fine structure (see Section 2 for details). In general, age-diagnostic taxa can be readily identified via transmitted light microscopy, although this process requires considerable human resources as well as expert knowledge. Over the past few years, substantial progress has been made in the digitalization of palynological slides. Given that fossil cysts are often crumpled owing to their flexible organic wall, it will be intriguing to see when and to what degree digital assistance and machine learning/artificial intelligence will be able to assist biostratigraphers in automatic species identification from scanned slides (see [Orenstein et al. 2022](#)).

A similarly important factor is that dinocysts occur in suitable concentrations across a broad range of sediment types. Maximum dinocyst abundances typically occur in silts and clays where tens of thousands of dinocysts may be present within one gram of dry sediment (e.g., [Eldrett & Harding 2009](#), [Faye et al. 2018](#)). Up to 256,000 dinocysts per gram of dry sediment have been reported from particularly favorable depositional settings ([Marret et al. 2004](#)). Much lower abundances are commonly found in sands, limestones and chalks; in such lithologies typical values are on the order of several hundred to a few thousand dinocysts per gram of dry sediment (e.g., [Westphal et al. 2004](#), [Dodsworth & Eldrett 2019](#), [Pearce et al. 2020](#)).

5.1.2. Taxonomic diversity

Relatively high taxonomic diversity is an important characteristic of the fossil dinocyst record. At suprageneric rank, dinocysts are classified largely through tabulation, and the pattern of evolution of family groupings provides a fairly coherent scheme that is reasonably explained in phylogenetic terms and consistent in a temporal sense. For example, the family Gonyaulacaceae, recognized through a common general tabulation in both fossils and extant taxa, appears to have originated in the Middle Jurassic. The family Ceratiaceae, fossil and extant forms of which exhibit a gonyaulacacean tabulation, but a distinctive compressed and horn-bearing shape, appears to have split from the Gonyaulacaceae in the Late Jurassic. Such distinctive groupings and their relationships are supported by molecular phylogenetics (e.g., [Janouškovec et al. 2016](#), [Gottschling et al. 2024](#)). Thus, the classification of fossil dinocysts, commonly misrepresented as arbitrarily based on morphology, can be demon-

strated to be coherent with the phylogeny of the group. Moreover, based on evidence from reflected tabulation, many, if not most dinocyst genera can be assigned to families and subfamilies that have a reasonable phylogenetic basis. Below family rank, the classification of genera and species becomes more randomly based on morphological features. There is generally a semi-consistent hierarchy of morphological features, with tabulation details and archeopyle as generally higher-ranking features than for example cyst outline and – lower still – wall ornamentation. Genera are commonly defined by tabulation and archeopyle type, but the development of horns and wall structure is used in cases such as the Ceratiaceae and Areoligeraceae in which the tabulation and archeopyle are remarkably stable over a long time. Species are commonly based on wall ornamentation or process morphology, and their separation can thus seem fairly random, with definitions less sharp than at higher ranks.

How fossil-species that are older than the Paleogene relate to extant (non-fossil) species is probably impossible to resolve. Through the Cenozoic and especially from the Miocene onwards an increasing number of fossil-species can be equated with non-fossil species, although occasionally two or more non-fossil species may produce a cyst morphotype assignable to a single fossil-species. Obviously, because fossil-species are invariably known only from the cyst, there will be uncertainty in comparing with non-fossil species where all stages of the life cycle are known. At the generic level, the classifications of fossil- and non-fossil dinoflagellates normally cannot be integrated ([Head et al. 2024a](#)).

The most comprehensive overview of dinocyst-based species diversity through time yet compiled was presented by [MacRae et al. \(1996; Fig. 6\)](#), and [Fensome et al. \(1996b\)](#) explained the initial diversification in terms of an early Mesozoic radiation of the group. While [Stover et al. \(1996\)](#) suggested caution not to over-interpret the diversity trends of cyst “species” due to limitations of the input data and the biased nature of the cyst record, the general, overall trends in diversity are unequivocally robust (see discussion in [Bijl 2024](#)). It is evident that the Triassic and Early Jurassic were characterized by relatively low dinocyst diversity, with only a small number of families and few genera in these families (Fig. 7).

The inception of cyst-forming dinoflagellates as reflected in the fossil record is close to the Middle–Late Triassic transition, and diversity attained around 30 species during the Norian and Rhaetian in the Arc-

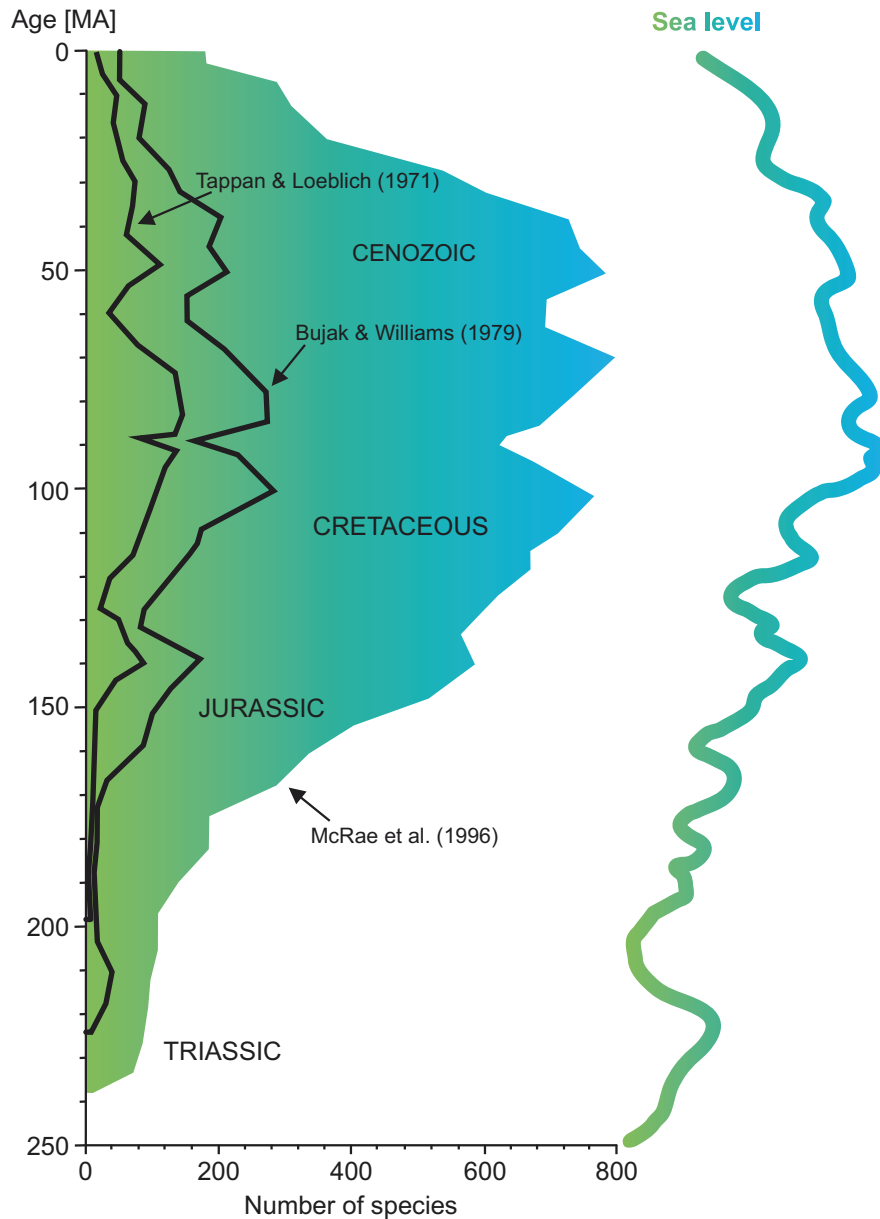


Fig. 6. Dinocyst diversity throughout the Mesozoic and Cenozoic as reconstructed by various authors in relation to the global sea-level curve of [Haq et al. \(1988\)](#). The observed correlation with the sea-level curve has been interpreted to reflect a positive relationship between sea level and the degree of ecological variance in shelf environments. Alternatively, this pattern may also reflect a research bias, as intervals of high sea level have a primary focus of hydrocarbon exploration, leading to more intensive studies of microfossils compared to intervals with lower sea levels. Modified from [MacRae et al. \(1996\)](#).

tic and east Gondwana. However, most of these taxa disappeared by the end-Triassic extinction. Diversity in the Early Jurassic was relatively low until minor radiations in the late Pliensbachian and Toarcian. In the Early Jurassic, several unusual cyst types (such as those assigned to the Nannoceratopsiaceae) appeared that did not continue into the Cretaceous. The Early

Jurassic also saw the inception of the Heterocapsaceae, a potential predecessor of the Peridiniaceae. By the Middle Jurassic most major groups of modern dinoflagellates had been established, most notably the families Gonyaulacaceae and Peridiniaceae. A substantial evolutionary radiation of the Gonyaulacaceae occurred in the Bajocian and Bathonian of the Middle

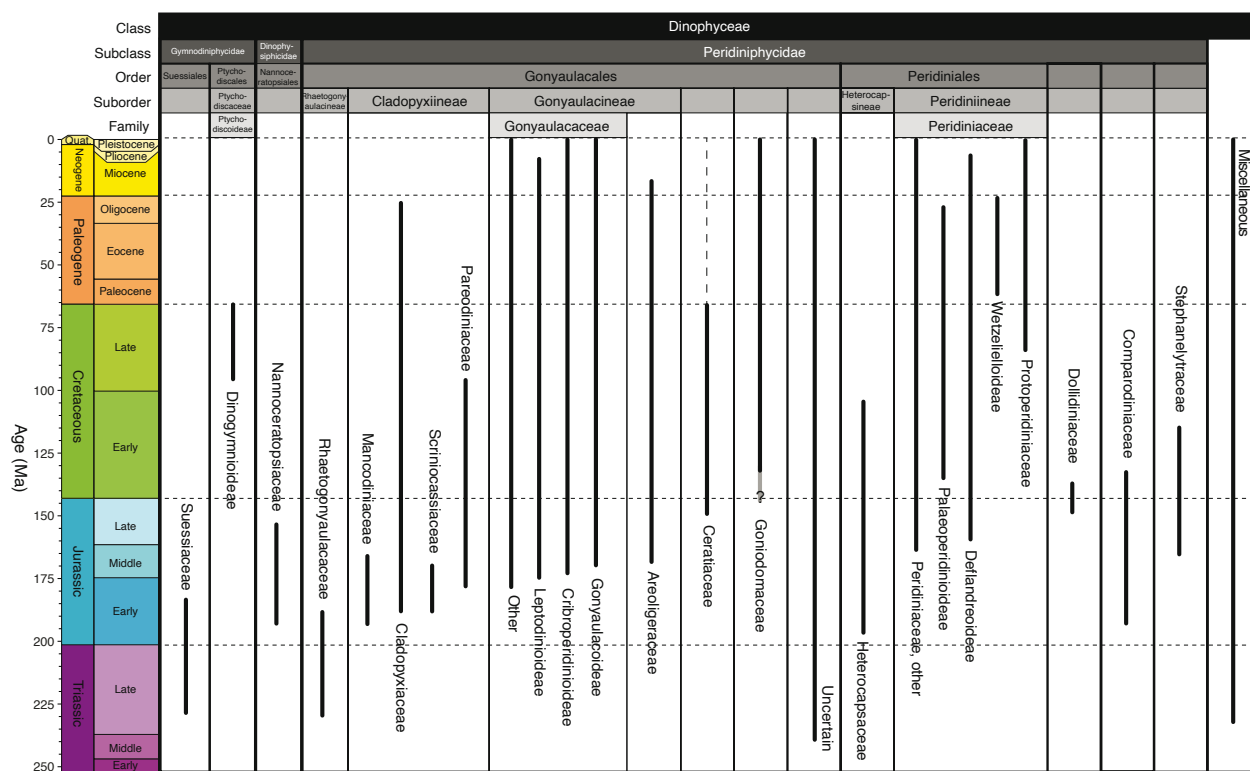


Fig. 7. Stratigraphic ranges of dinocyst (sub-)families. Black bars connect the oldest first occurrence and youngest last occurrence of (sub)families in DINOSTRAT version 2.1. Taxonomy follows Fensome et al. (1993); modified from Bijl (2024). The first appearance of the Goniodomaceae in the Late Jurassic is based on *Hystrichosphaeridium petilum* and *H. pattei*. However, these are apparently not quinqueform and should therefore not be included in the Goniodomaceae. Clearly quinqueform species of *Hystrichosphaeridium* first occur in the Early Cretaceous (Valanginian).

Jurassic. In the Late Jurassic, taxonomic expansion was mostly within the Gonyaulacaceae, but this epoch also included the first appearance of such families as the Areoligeraceae and Ceratiaceae.

The Cretaceous is characterized by high diversities in the Gonyaulacaceae and Peridiniaceae at both genus and species levels, which in part may reflect interest from oil and gas exploration. The high diversity in the Jurassic, Cretaceous, and the ensuing Paleogene results in the existence of many morphologically distinctive species with biostratigraphic significance. Following another peak during the Early Eocene, cyst diversity gradually declined during the Oligocene, with a loss of many long-ranging subfamilies and genera around the Oligocene–Miocene boundary.

Finally, the Neogene and Quaternary exhibit a further prominent diversity decline at family, genus and species levels, ultimately resulting in the lowest dinocyst diversity since the Jurassic in the Quaternary. This diversity decline is also reflected in databases focusing

on ‘modern’ dinocysts; they document a clear latitudinal gradient in diversity, with minimum diversity in the high and maximum diversity in the low latitudes (e.g., de Vernal et al. 2020). However, despite the reduced diversity during the Neogene, detailed dinocyst biostratigraphies have been developed, especially for the Miocene and Pliocene (e.g., de Verteuil & Norris 1996, Dybkjær & Piasecki 2010, De Schepper & Head 2009), even at high northern latitudes (e.g., Schreck et al. 2012). For the Quaternary, which has seen little evolutionary turnover, but is characterized by a strongly oscillating climate on Milankovitch time scales, ecostratigraphic schemes have been developed in place of classical biostratigraphic schemes to meet the high stratigraphic precision needed. Such schemes are not reliant upon high species diversity (see Section 7).

The evolutionary story of dinoflagellates has been punctuated by periods of apparent experimentation in different groups followed by a degree of stability. Examples are tabulation among thecate dinoflagellates as

a whole (as reflected in cysts) during the Triassic and Early Jurassic, and archeopyles among the Gonyaulacaceae during the Middle Jurassic and the Peridiniaceae during the mid-Cretaceous. In contrast, the stability in tabulations, aside from relatively minor adjustments, in the Gonyaulacaceae and Peridiniaceae has been remarkable. Fensome et al. (1993) provided a detailed phylogenetically based suprageneric classification of living and fossil dinoflagellates conventionally based on morphology. They clarified the definitions, content and relationships of many higher-level taxonomic dinoflagellate groups. During the past few decades, extant dinoflagellates have undergone molecular phylogenetic analyses (e.g., Saldarriaga et al. 2004, Gottschling et al. 2024). These analyses have supported many of the groupings recognized by Fensome et al. (1993), and a combination of evidence from fossils, extant taxa, and molecular sequencing is providing compelling advances in our understanding of dinoflagellate evolution.

5.1.3. Stratigraphic ranges

Dinocyst biostratigraphy is greatly facilitated by the very short evolutionary lifespans of many cyst taxa, which translates into relatively short-lived stratigraphic ranges and accordingly into a high temporal resolution of zonations. The relatively rapid evolution seen in the dinocyst record prompts considerations concerning the relationship between cyst-species turnover and phylogenetic turnover in the cyst-producing taxa. The biological relationships between fossilizable cysts and the non-fossilizable motile stage are not as straightforward as in other microfossil groups (compare Section 2). For instance, the motile-typified *Gonyaulax spinifera* species complex and its allies may produce as many as six fossil-genera (Head 1996, Head et al. 2024a), of which one, represented by the extant *Spiniferites ramosus*, was recorded close to the Jurassic–Cretaceous boundary (Monteil 1993). However, this complexity is of limited relevance for biostratigraphic purposes because the rapid turnover of dinocyst taxa and their sensitivity to ecological change can be used as a biostratigraphic signal irrespective of the genetic diversity of the cyst-forming dinoflagellates.

5.1.4. (Paleo-)geographic distribution

Organic-cyst-forming dinoflagellates occur across a wide range of ecological settings – from polar regions

to the equator and from open-ocean upwelling zones to estuaries and freshwater systems. By extension, their absence from the stratigraphic record may be due to taphonomic processes rather than original non-occurrence. Their appearance across a wide spectrum of ecosystems also means that dinocysts are often present in sediments where other microfossils are absent. As a result, dinocyst biostratigraphy is typically applied to sedimentary successions on the continental shelf, in restricted marine basins, and in polar oceans. At a basinal scale, the relatively narrow ecological niches of most cyst-forming dinoflagellates also assist in biostratigraphy, with blooms or “acmes” of taxa helping to identify lithostratigraphic units in event stratigraphy and yielding intricate basin-specific stratigraphies (e.g., Paleogene of the North Sea: Bujak & Mudge 1994, King 2016; Cretaceous of Greenland: Bjerager et al. 2020). However, such local- to regional-scale biostratigraphic markers are rarely applicable on wider geographic scales. The best-known exception to this rule is the worldwide proliferation of the dinocyst genus *Apectodinium* during the Paleocene–Eocene Thermal Maximum at the transition between the two epochs (e.g., Bujak & Brinkhuis 1998, Crouch et al. 2001), which was associated with several more poleward expansions of taxa (Frieling et al. 2018b). Other examples are migrations of characteristically Arctic species such as *Tubotuberella dentata* at the Middle–Late Jurassic transition (Riding 2012), the *Cyclonephelium compactum–membraniphorum* plexus during a Late Cretaceous cold spell (van Helmond et al. 2016 and references therein), and the genus *Svalbardella* during Oligocene glaciation events (van Simaeyns et al. 2005a, Śliwińska & Heilmann-Clausen 2011, Śliwińska 2019).

5.2. Challenges in dinocyst biostratigraphy and solutions

As noted previously, dinocyst biostratigraphy is predominantly applied to marginal marine settings where other commonly used microfossil groups such as calcareous nannoplankton and planktonic foraminifers may be poorly represented. This, together with the fact that neritic, siliciclastic settings often exhibit a complex sedimentation history with considerable variability in sediment-deposition rates and discontinuous sedimentation, complicates the calibration of dinocyst ranges to the GTS. The highest potential for integrated biostratigraphic schemes that allow chronostratigraphic assessment of dinocyst ranges comes from ex-

tended sedimentary successions on the outer shelves or slopes, or in drift deposits along the path of bottom currents, where various microfossil groups are preserved in thick sections with more continuous sedimentation. Importantly, the deposition of silt and clay from the nearby continental margins in these settings can preserve paleomagnetic signals enabling ties to magnetostratigraphy. Because magnetic reversals are globally synchronous and occur within a few thousand years, magnetostratigraphy is instrumental in time-scale development (Tauxe 2010). Increasingly, chemostratigraphy and orbital tuning are applied to sedimentary archives from more offshore settings, which may have resolution down to the Milankovitch frequencies (e.g., Sluijs & Brinkhuis 2024). Hence, a crucial step in correlating biostratigraphic signals to chronostratigraphy is when specific magnetochrons, carbon-isotope excursions, and/or orbital cycles are identified in a dinocyst-bearing sedimentary succession.

Dinocyst biostratigraphers have long recognized that many Mesozoic–Cenozoic dinocyst assemblages have distributions that are restricted in space as well as time (“bioprovinces” or “suites”). The primary factors influencing these bioprovinces were surface-water conditions, including sea-surface temperature, productivity, and salinity, together with circulation patterns and paleogeography. During the Jurassic, dinocyst bioprovinces comprised a Boreal and a Tethyan Province in the Northern Hemisphere, and an Austral Province in the Southern Hemisphere (e.g., Norris 1975, Helby et al. 1987, Smelror 1991; see Stover et al. 1996 for details). A classic example from the Cretaceous is the regional differentiation of Campanian peridinialean cyst assemblages into Boreal, Warm-temperate, and Tropical-subtropical suites (Lentin & Williams 1980). A notable case of dinocyst provincialism during the Cenozoic is the so-called “Transantarctic Flora”, an Eocene dinocyst association endemic to Antarctic-derived surface currents. This assemblage has been widely documented at paleolatitudes south of c. 60°S and is easily distinguishable from assemblages with more cosmopolitan or tropical affinities (e.g., Wrenn & Beckmann 1982; Bijl et al. 2011, 2013).

At the same time, the first and/or last appearances of various globally distributed cyst taxa may be diachronous across different, otherwise well-dated sections primarily due to gradients in surface-water conditions and/or paleogeographic barriers (e.g., Williams & Bujak 1977, Stover et al. 1996, Pross 2001b, Williams et al. 2004, Śliwińska et al. 2020). However,

ground-truthing this observation for the full spectrum suite of biostratigraphically important dinocyst taxa requires that information from the literature is internally consistent; only then will it be possible to fully compare and quantitatively assess potential regional differences in the stratigraphic ranges of taxa. For example, a species might be known by different names in different regions, masking the potential for interregional correlations. Also, different names have likely been applied in different parts of the geological column to what is probably the same species. These issues are uncommon and resolvable. Further challenges to be resolved in such efforts are that different geologic time scales have been used in the respective studies and that taxonomic concepts have evolved over time (Bijl 2022).

Acknowledging the inconsistencies in dinocyst biostratigraphic schemes worldwide, Bijl (2022) revisited all existing literature data where dinocyst ranges had been calibrated independently to various versions of the GTS. The rationale of this approach was to establish consistent regional stratigraphic information that could then be compared on a global scale, instead of averaging stratigraphic ranges into one biostratigraphic scheme that would supposedly be applicable worldwide. The results were fed into the database DINOSTRAT, which offers a free-to-use, public open-access platform where regional dinocyst stratigraphic information can be stored, compared and updated in response to any new developments of the GTS (Bijl 2022, 2024). Presenting existing publications in tiers based on the quality of the calibration (e.g., magnetostratigraphy or other biostratigraphic information from microfossils, planktonic foraminifers, and/or ammonites), DINOSTRAT yields a spatial pattern of stratigraphic ranges per species, genus, and family; for intervals where the tie to the GTS is not sufficiently well defined, geologic stages are given. The database further includes metadata of the sites studied such as paleolatitude, which allows us to assess the past latitudinal differences in the stratigraphic ranges of different taxa. Iterative, straightforward updates of the entire database are possible e.g., when a new version of the GTS is published or when the database is to be augmented with new publications. Currently, DINOSTRAT contains information from c. 200 publications and c. 210 sites.

The review of Bijl (2022) and the subsequent update to GTS 2020 (Gradstein et al. 2020) by Bijl (2024) indicate that the first and/or last appearances of many dinocyst taxa indeed show strong diachroneities. For

many taxa, these diachroneities are in the order of millions of years. In addition, the more information becomes available, the more and longer diachroneities are recognized. By extension, the current selection of available records appears to underestimate the diachroneity of ranges. The causes behind these diachroneities are many. For instance, restricted paleoceanographic connectivity can obstruct the biogeographic spread of taxa, thereby altering their stratigraphic ranges in one region compared to another. As discussed above, paleoclimatic gradients can also cause pronounced diachroneities in the stratigraphic occurrences of taxa, and unidentified reworking can obscure the true stratigraphic range of taxa. Besides these natural factors, there are also other, non-natural causes for diachroneities in dinocyst data. These include ambiguous taxonomic concepts (Section 2), sampling at low stratigraphic resolution, identification errors by the analyst, and – particularly in industrial wells – the effect of downhole caving of rock material and hosted microfossils that can extend the reported stratigraphic ranges downwards. In any case, the results imply that the development of a global dinocyst zonation scheme is unrealistic as it would not take into account the specific traits of dinoflagellates and their cysts. These comprise the relatively narrow ecological requirements of many cyst-forming dinoflagellates as well as their distribution center in neritic rather than in oceanic settings (Section 3), both of which work towards a marked paleo-provincialism or endemism in many dinoflagellate (cyst) assemblages. It is therefore recommended to compare the lowest and highest occurrences of dinocysts to regional calibrations, with the aim of developing regional biostratigraphic schemes. These measures can maximize the biostratigraphic utility of dinocysts, particularly for regions and settings that are difficult to date otherwise.

6. Biozonation schemes

As discussed above, the distribution of dinocysts is strongly influenced by paleoenvironmental forcing (through sea-surface temperature, salinity, productivity, and water-mass structure, but also through ocean currents). Most cyst-forming dinoflagellates have a marginal marine distribution center, but discussion has been reopened to what extent taxa considered to be shelf-constrained may produce cysts in more open-ocean settings. However, not only dinoflagellates, but all organisms exhibit to varying degrees a dependence on environmental factors, and environmental condi-

tions are obviously not uniform throughout their habitats. It can thus be argued that a biozonation scheme based on truly globally synchronous first and last appearance datums is unrealistic for any group of organisms. However, this complexity can be addressed through the development of regional biostratigraphic schemes that are independently calibrated to the GTS. The spatial extent that such schemes should be suitable for depends on the gradients in environmental conditions and paleogeography.

The dinocyst zonations that have been established comprise mainly formal or informal (concurrent) range, interval, assemblage, Oppel, and lineage zones (e.g., Brinkhuis & Biffi 1993, Bujak & Mudge 1994, Stover et al. 1996). However, besides being potentially affected by diachronous stratigraphic ranges of the marker taxa employed, these zones partially also rely on different concepts, which bears considerable potential for confusion particularly among non-experts. A classic example of this is the Early to Middle Jurassic *Nannoceratopsis gracilis* Zone, which – depending on the region proposed and its definition by different authors – starts as early as the late Pliensbachian to as late as the late Bajocian (Woollam & Riding 1983). Similarly ambiguous is its termination, which may be as early as the latest Toarcian or as late as the middle Bathonian (Stover et al. 1996 and references therein). This apparent paradox does not reflect an uncertainty as to the range of the species *Nannoceratopsis gracilis*. This distinctive and widespread species has a total reported range from the late Pliensbachian to Bathonian. However, it is consistently present between the early Toarcian and early Bajocian, and is sparse in the late Pliensbachian and the late Bajocian to Bathonian (Woollam & Riding 1983, Wiggan et al. 2017). Having the potential to avoid or at least reduce these complexities, the concept of dinocyst biohorizons has received considerable attention. A dinocyst biohorizon is commonly understood as “a surface where a biostratigraphical change takes place, or that has a distinctive biostratigraphical character”; examples are the lowest and highest occurrences of taxa in a given region (Norwegian Committee on Stratigraphy 1989, Stover et al. 1996).

Some authors have avoided the vagaries of zonation schemes by using biostratigraphic “events” because these, unlike biozones, can be used in isolation of other events. The events mainly used are the first and last appearances of species (FA and LA, respectively). These are geochronologic terms, and their equivalents in chronostratigraphy are lowest and high-

est occurrences (LO and HO), which refer to each of the two biohorizons representing the two events. For reasons given above, dinocyst events are not usually assumed to be isochronous, at least on a global scale, so the terms first and last appearance datum (FAD, LAD, and their chronostratigraphic equivalents LOD and HOD) are rarely used in dinocyst stratigraphy. The biostratigraphic event/horizon approach has been used, for example, for the Labrador–Baffin Seaway (Nøhr-Hansen et al. 2016) and the Arctic (Bujak et al. 2021, 2022). It may better facilitate integration of dinocyst stratigraphic data from other disciplines, especially in databases (Bringué et al. 2020). It might be mentioned that in industry, the terms first and last downhole occurrences (FDO and LDO) have been used respectively in place of highest and lowest occurrences: a more consistent terminology in this case would be highest and lowest downhole occurrences.

7. Correlation and integration

High-quality biostratigraphic information requires the calibration of biohorizons (such as the regional lowest and highest occurrences of stratigraphically useful dinocysts) to chronostratigraphic information from the same archives. Such chronostratigraphic data can come from paleomagnetic reversals, but can also be based on astrochronology, isotope stratigraphy, and/or radiometric ages. Importantly, the last three approaches provide chronostratigraphic information for intervals of the geological record with prolonged near-constant geomagnetic polarity such as the Cretaceous Normal Superchron (~ 121–84 Ma) or, on markedly shorter timescales, Chrons such as C33n (79.90–74.20 Ma), C26r (62.28–59.24 Ma), or C20r (46.24–43.46 Ma; Ogg 2020). The magnetostratigraphic and/or isotope stratigraphic data used must have been calibrated independently, such as by means of distinctive patterns of polarity reversal or biostratigraphies based on other fossil groups, to avoid potential circular reasoning.

A compilation of presently available chronostratigraphically calibrated dinocyst biostratigraphies indicates that such information is strongly skewed towards the Cenozoic (Fig. 8). While more than 50 studies are on intervals of the Paleogene, Neogene, and Quaternary, fewer than 20 studies cover parts of the Cretaceous, and only one study extends into the Upper Jurassic; no chronostratigraphically constrained dinocyst biohorizons are yet available for the Triassic (Fig. 8). Geographically, the coverage is best for the mid- to

higher latitudes of the Northern Hemisphere, whereas little information is available for the equatorial regions. Over the past two decades, an increasing number of magnetostratigraphically calibrated dinocyst bioevents has become available for the higher latitudes of the Southern Hemisphere (Fig. 8). This spatiotemporal distribution pattern can be ascribed to several factors. It may partly reflect the fact that older parts of the geological record have traditionally been worked on by fewer researchers and so they have remained understudied in comparison to younger intervals. However, it may also reflect the progress and integrating effects of scientific ocean drilling. The DSDP, ODP and IODP initiatives have yielded a wealth of high-quality sediment archives particularly for the Cenozoic and, to a lesser extent, the Cretaceous; pre-Cretaceous strata are rarely encountered in today's ocean basins due to destruction via subduction. Ocean drilling has also prompted stratigraphers from different disciplines to collaborate on the same material, thereby providing an important impetus for interdisciplinary collaborations.

Encompassing just 2.6 million years, the Quaternary dinocyst record has relatively few evolutionary and extinction events. Thus, the classical approach of using range tops and range bases for stratigraphic correlation cannot yield the orbital- to suborbital-scale resolution required to understand the high-frequency climate dynamics of the Quaternary. Fortunately, the dinocyst record is amenable to ecostratigraphy owing to the sensitivity of dinoflagellates to environmental change. Dinocyst ecostratigraphy is best achieved when integrated with an independent chronostratigraphical framework (e.g., marine isotope stratigraphy and/or magnetostratigraphic reversals).

Such a scheme exists at the Chiba composite section in Japan, its Global boundary Stratotype Section and Point (GSSP) defining the Chibanian Stage and Middle Pleistocene Subseries (Suganuma et al. 2021). The GSSP aligns closely with the Matuyama–Brunhes reversal, has an astronomical age of 774.1 ka, and falls within Marine Isotope Stage (MIS) 19. During MIS 19, full interglacial conditions developed within MIS 19c, followed by the inception of glaciation as marked by the bases of MIS 19b and stadial 1 (Fig. 9). The GSSP occurs just below the MIS 19c/b boundary. Of the many proxies used to recognize stadial 1 in the Chiba composite section, dinocysts are the most decisive. Between 772.9 and 770.4 ka, the dinocyst record at Chiba is dominated by *Protoceratium reticulatum* (also known as *Operculodinium centrocarpum sensu*

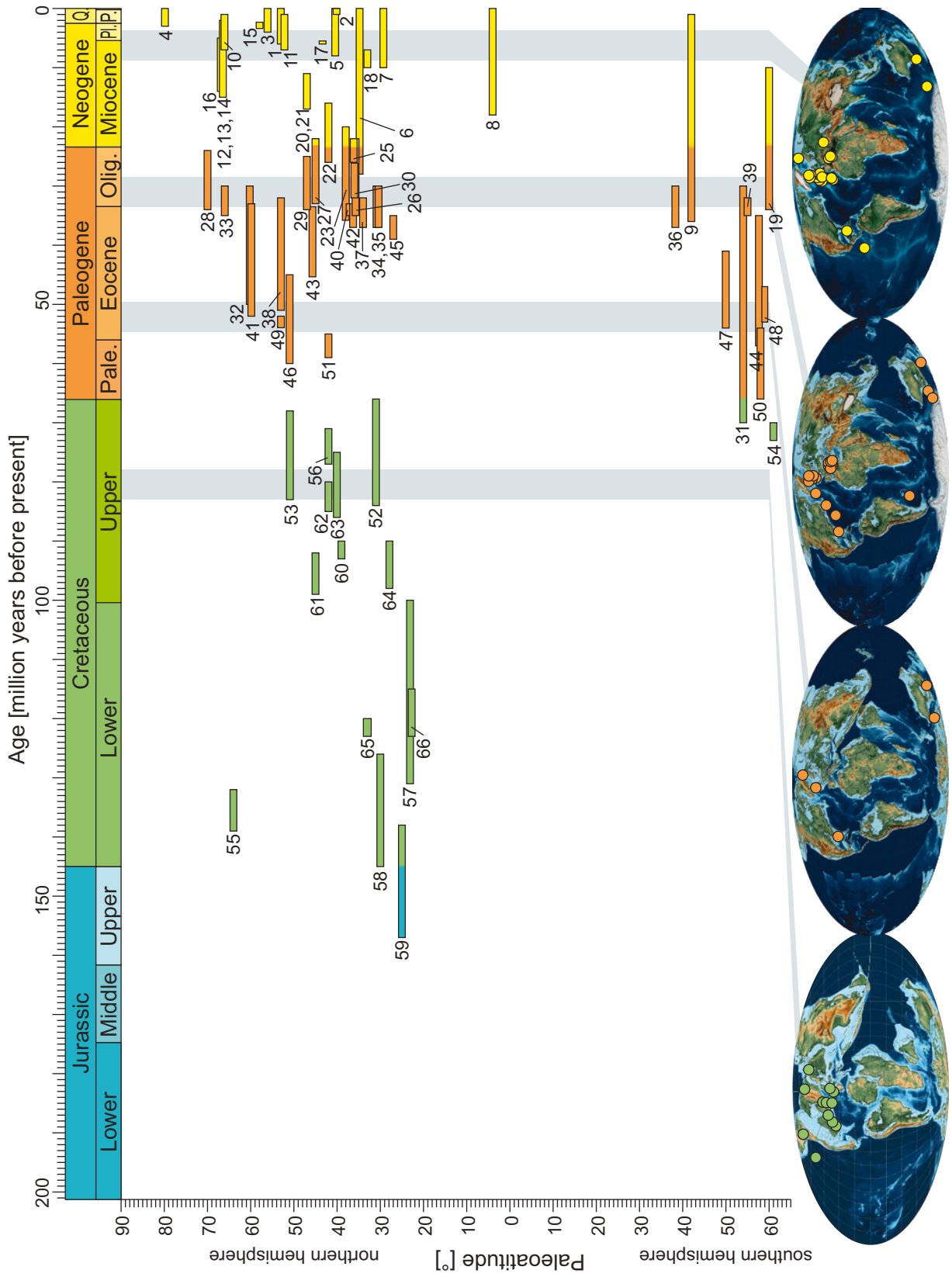


Fig. 8. Stratigraphic and paleolatitudinal distribution of yet available chronostratigraphically (i.e., via magnetostratigraphy, isotope stratigraphy, radiometric dating, and astrochronology) calibrated records of dinocyst bioevents. List of records has been taken from the DINOSTRAT database and augmented by own research. Bar lengths indicate lengths of individual records. Approximate positions of individual records are indicated on the paleogeographic maps. Paleolatitudes of study sites have been recalculated following van Hinsbergen et al. (2015), paleogeographic maps for the Late Miocene, Early Oligocene, Early Eocene, and middle Late Cretaceous (from right to left) are after Scotese (2014a, b; 2021), and ages are according to GTS 2020 (Gradstein et al. 2020). Numbering of records according to their age tops, from young to old. Colored dots on paleogeographic maps indicate approximate positions of records shown in the main panel. 1 – De Schepper & Head (2008, 2009), 2 – de Vernal et al. (1992), 3 – Kuhlmann et al. (2006), 4 – Matthiessen & Brenner (1996), 5 – Mudie (1987), 6 – Versteegh & Zevenboom (1995), 7 – Wrenn & Kokinos (1986), 8 – Zegarra & Helenes (2011), 9 – Brinkhuis et al. (2003a), 10 – De Schepper et al. (2017), 11 – Head & Norris (2003), 12 – Schreck et al. (2012), 13 – Schreck et al. (2013), 14 – Schreck et al. (2017), 15 – Aubry et al. (2020), 16 – Schreck & Matthiessen (2014), 17 – Grothe et al. (2017), 18 – Krijgsman et al. (1995), 19 – Bijl et al. (2018a), 20 – Louwey et al. (2008), 21 – Quaijtaal et al. (2014), 22 – Montanari et al. (1997), 23 – Wilpshaar et al. (1996), 24 – Egger et al. (2016), 25 – Brinkhuis et al. (1992), 26 – Pross et al. (2010), 27 – van Simaey et al. (2005b), 28 – Eldrett et al. (2019), 29 – Śliwińska et al. (2012), 30 – Coccioni et al. (2008), 31 – Brinkhuis et al. (2003b), 32 – Eldrett et al. (2004), 33 – Firth (1996), 34 – Houben et al. (2019), 35 – Quaijtaal & Brinkhuis (2012), 36 – Sluijs et al. (2003), 37 – Brinkhuis & Biffi (1993), 38 – Firth et al. (2013), 39 – Houben et al. (2011), 40 – Brinkhuis (1994), 41 – Eldrett & Harding (2009), 42 – Van Mourik & Brinkhuis (2005), 43 – Thomsen et al. (2012), 44 – Bijl et al. (2013, 2014), 45 – Van Mourik et al. (2001), 46 – Frieling et al. (2014), 47 – Dallanave et al. (2016) and Crouch et al. (2020), 48 – Bijl & Brinkhuis (2015), 49 – Iakovleva & Heilmann-Clausen (2010), 50 – Crouch et al. (2014), 51 – Powell et al. (1996), 52 – Habib & Drugg (1987), 53 – Lebedeva et al. (2013), 54 – Mohr & Mao (1997), 55 – Jelby et al. (2020), 56 – McLachlan et al. (2018), 57 – Torricelli (2000), 58 – Habib & Drugg (1987), 59 – Habib & Drugg (1983), 60 – Olde et al. (2015), 61 – Pearce et al. (2020), 62 – Jarvis et al. (2023), 63 – Pearce et al. (2022), 64 – Eldrett et al. (2015), 65 – Oosting et al. (2006), 66 – Unida & Patruno (2016).

Wall & Dale 1966), a cyst that today can be abundant at high-latitude sites and has an affinity for meso- to eutrophic and cold to temperate environments, especially where the upper water column is unstable (Balogh et al. 2021). The interval dominated by *P. reticulatum* is therefore interpreted to document a rapid change to cooler, mixed, nutrient-rich waters resulting from a southward shift of the Kuroshio Extension. This shift reflects a sharp global cooling event interpreted from multiple proxies to represent glacial inception at the onset of MIS 19b. The abrupt percentage increase of *Protoceratium reticulatum* at 772.9 ka can therefore serve as a local ecostratigraphic marker to identify glacial inception and hence approximate the Lower–Middle Pleistocene boundary, which it follows by just 1200 years. Worldwide similarities in the climatic structure of MIS 19 suggest that abrupt, near-synchronous changes in ocean currents at the onset of MIS 19b will be widely recognized in the dinocyst record. This example highlights the potential of dinocyst ecostratigraphy for intervals of the dinocyst record that exhibit few evolutionary and extinction events and/or are marked by particularly pronounced environmental variability.

8. Conclusions and potential for future work

Dinocyst biostratigraphy has come far since its early pre-World War II foundations and its acceleration in the 1950s and 1960s that was driven by hydrocarbon exploration. Over the decades, the biostratigraphic information from these microfossils has become increasingly refined both in terms of temporal resolution and regional coverage; these observations have also provided critical insights into dinoflagellate evolution that are now being integrated with molecular phylogenetic studies. This development is reflected in an increasing number of papers proposing formal dinocyst zonation from the 1960s onwards. Important advances were the calibration of dinocyst data with ammonite zonation for the Jurassic and Cretaceous (e.g., Woollam & Riding 1983), and with calcareous nannoplankton and planktonic foraminifer zonation for the Cretaceous and Cenozoic (e.g., Stover et al. 1996). Owing to the neritic distribution center of cyst-forming dinoflagellates and the more offshore habitats of calcareous microplankton (notably planktonic foraminifera and calcareous nannofossils), the latter step

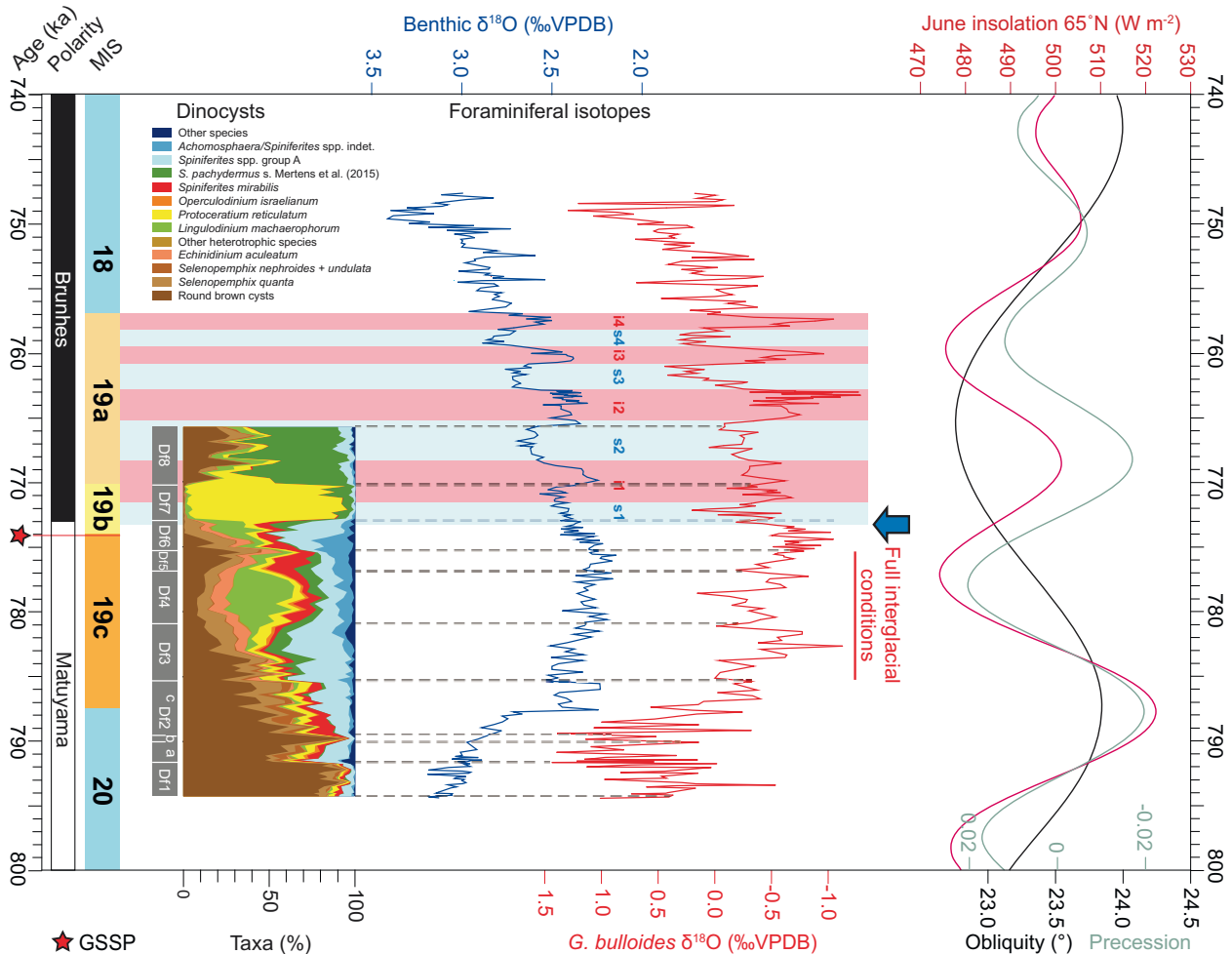


Fig. 9. An example of dinocyst ecostratigraphy from the Chiba section (Japan), global stratotype for the Lower–Middle Pleistocene boundary. Also shown are magnetostratigraphic polarity, foraminiferal isotope stratigraphy, and orbital parameters. The eight dinocyst-defined local assemblage biozones are effectively ecozones reflecting oceanographic conditions across the boundary. The sharp rise in percentages of *Protoceratium reticulatum* cysts just above the GSSP marks an abrupt shift to cooler conditions that persisted throughout the first stadial of MIS 19. It represents the inception of glaciation in MIS 19 and is a world-wide, near-synchronous event. Modified from Balota et al. (2021).

allowed the biostratigraphic correlation of shelfal and oceanic settings.

A further major advance has been the calibration of dinocyst biohorizons to the GTS via chronostratigraphic information derived primarily from magnetostratigraphy, chemostratigraphy, and orbital stratigraphy. As outlined above, such studies must utilize age information independently, such as from microfossil groups other than dinocysts (e.g., calcareous nannoplankton and/or planktonic foraminifers) or radiometric dates (such as from volcanic ash layers) from the same archive to avoid circular logic. These efforts started in the 1980s and are still expanding. However,

substantial further work is required to obtain a spatiotemporally highly resolved, comprehensive record of chronostratigraphically calibrated dinocyst biohorizons. As already emphasized in the milestone review of dinocyst biostratigraphy by Stover et al. (1996) and illustrated in Fig. 8 herein, more data from the low latitudes are particularly needed to fully understand the diachroneities in the first and/or last appearances of globally distributed cyst taxa. Regarding the stratigraphic record of dinocysts, the largest knowledge gaps in the open literature are for the Mesozoic, and particularly the Upper Triassic, Lower Jurassic, and Upper Cretaceous.

Integrations of dinocyst biostratigraphic and magnetostratigraphic information from the same sedimentary archive have presently been carried out mainly for Cenozoic records, and only few studies have yet exploited it for the Cretaceous (with the exception of the Cretaceous Normal Superchron, ~ 121–84 Ma) and the Jurassic. In fact, many Mesozoic dinocyst biostratigraphies have been developed from sections that lack magnetostratigraphic age control. Perplexingly, there are even sections for which magnetostratigraphies as well as microfossil (including dinocyst) biostratigraphies have been published, but these stratigraphies have not been converted into calibrated biostratigraphies. In such cases, there appears a shortage of coordination efforts between the involved disciplines, and/or a lack of (interested) dinocyst biostratigraphers and the necessary funding. Overcoming this gap between disciplines – as has been impressively done through, for example, the DSDP, ODP, and IODP initiatives – will be instrumental in establishing more magnetostratigraphically calibrated dinocyst biohorizons.

Further possibilities for directly tying dinocyst biohorizons to chronostratigraphy come from astrochronology, carbon-isotope stratigraphy, and radiometric dating. In particular the astronomical calibration of sedimentary cycles can yield a considerably higher temporal resolution and accuracy than timescales based on linear interpolation between magnetostratigraphic reversals. Hence, besides yielding direct connection to the absolute time scale in their own right, they are ideally suited to complement efforts of integrating dinocyst biohorizons with magnetostratigraphic data for intervals with polarity quiescence such as the Cretaceous Normal Superchron. Whereas there is abundant information available on astronomically dated nannoplankton and planktonic foraminifer biohorizons of the Paleogene, Neogene, and Quaternary (e.g., Raffi et al. 2006, Wade et al. 2011), the enormous potential of this approach has yet remained underexplored for dinocyst biostratigraphy.

Progress in directly tying dinocyst biohorizons to the GTS may provide new momentum for an old question – why should dinocyst biostratigraphy use zones when events/horizons such as lowest and highest occurrences of selected taxa (Stover et al. 1996) could be used more conveniently? The answer is not straightforward. Assemblage zones are used commonly in Quaternary studies where they serve effectively as ecostratigraphic biozones. These zones can be precise to within a hundred years or less (e.g., Balota et al. 2021; Fig. 9). They are also used in industry where

high stratigraphic precision is needed, such as in well biosteering. However, they are not applicable over wide geographic areas. Other kinds of zones, such as interval zones based on the successive lowest occurrences of designated species (or highest occurrences in some Quaternary and most industry applications) are conceptually based on the event/horizon approach. Therefore, it may be simpler to reference the events/horizons directly. This approach was followed by the Circum-Arctic Palynological Event Stratigraphy project (CAPE), which documented selected palynological events (such as taxon appearances and disappearances) across the present-day Arctic region from the Silurian to the Cenozoic (Bujak et al. 2021). The advantage of such an approach is that any one event can be recognized in isolation of the others, and in extreme environments this may be useful or even obligatory. It also more readily facilitates the inclusion of data from different subdisciplines in integrated schemes (e.g., Fensome et al. 2008). In other cases, such as the mid-latitude Miocene biozonation of de Verteuil & Norris (1996), successive events are indeed usually recognizable, and the biozones they define may contain characteristic features within them. These units then have descriptive value in the same way that lithostratigraphic units are useful. Whether to use a biozone or event approach accordingly depends on the circumstances, but in correlating the biostratigraphic record of dinocysts to the GTS, the event approach seems the more practical.

Palynological processing has traditionally involved the use of hydrochloric (HCl) and hydrofluoric (HF) acids. The toxicity and corrosive nature of these acids necessitate extensive precautions and safety measures that can be a major obstacle to the application of dinocyst biostratigraphy. Moreover, their use becomes increasingly part of a discussion regarding science's transition to a more sustainable future. The consequences of accidental spillages notably of HF are particularly serious in mobile laboratory facilities such as on offshore drilling rigs. In response to these chemical hazards, alternative non-acid methods have been developed, although no widely practiced “standard” processing method is yet in use (Riding 2021 and references therein). The further establishment of such techniques will be instrumental in making palynological processing safer, more environmentally friendly, quicker, and cheaper, thereby increasing the practicality of dinocyst biostratigraphy.

The identification of biostratigraphic index taxa necessitates considerable expert knowledge. Over the

past decades, international, non-profit short courses in dinocyst analysis have proven to be a highly efficient and effective means of sharing such knowledge within the dinocyst research community. Organized under the motto “by and for the people,” these courses began in the early 1970s in North America and have been held at irregular intervals across Europe from 1994 onward. In addition to providing direct access to the latest advancements in dinocyst morphology, stratigraphy, and paleoecology, these courses have significantly fostered collaboration and knowledge exchange among researchers, playing a pivotal role in shaping the field of dinocyst research. Such community-driven international short courses should be continued on a regular basis to sustain and further advance the discipline. A similarly important forum are the international conferences on modern and fossil dinoflagellates. Established in 1978, these conferences have been a cornerstone of the dinoflagellate research community, convening every three to five years at different locations worldwide. They bring together palynologists based in earth sciences with researchers studying dinoflagellates in other disciplines such as phycology, genetics, ecology, and public health. Sustaining and extending these conferences in the future will be essential for promoting interdisciplinary exchange and advancing innovative ideas and concepts.

The community of dinocyst researchers has also greatly benefited from the extensive taxonomic knowledge base provided by the series of publications known as “The Lentin and Williams Index”. Listing all fossil dinoflagellate taxa at and below generic rank known to the authors and providing information on synonymies, nomenclature, history, and broad geologic age of the type, this index has proven to be an invaluable resource for the field. The index is published at irregular intervals, with the most recent, digital version released in 2019 (Fensome et al. 2019). It is the basis of the DINOFLAJ database, an easily accessible online resource that also incorporates information on suprageneric classification (Williams et al. 2017). Both resources provide indispensable support to the community of dinocyst researchers, and it is essential to ensure their ongoing maintenance and frequent updates to sustain their value.

With the rapid evolution of digital science and machine learning/artificial intelligence, the possibility of automating some of the particularly time-consuming aspects of dinocyst biostratigraphy – notably the logging of microscope slides – appears to be just around the corner. However, certain characteristics of organic-

walled dinocysts pose specific challenges for automatic recognition: Their flexible walls make them susceptible to folding and compression, although their typical translucency enables a near-complete elucidation of their morphologies. Given the rapid advancements in cognitive computing the prospect exists that the time-consuming task of logging microscope slides will be alleviated in the future. This is an opportunity rather than a threat for dinocyst biostratigraphy. Instead of making dinocyst biostratigraphers redundant, the successful application of cognitive computing will require substantial expert human analysis: a key to its success will be the integration of in-depth knowledge of dinocyst morphology, taxonomy, and biostratigraphy with expertise in statistics and coding.

The effective application of machine learning and artificial intelligence in dinocyst biostratigraphy also requires that the training material – such as reference collections and taxonomic descriptions – be of high quality and clarity. However, many of the currently available taxonomic definitions of dinocyst taxa fall short of this standard. With the prospect of making dinocyst biostratigraphy more cost-effective and potentially faster, the application of machine learning/artificial intelligence for taxonomic identification may also drive a surge in demand for fundamental dinocyst taxonomy and biostratigraphy. Additional benefits of automated recognition and identification in dinocyst biostratigraphy include the potential for remote work and the assurance that results will be fully traceable and reproducible, which could help reduce interpretation bias and improve consistency.

A key limitation to the application and further development of dinocyst biostratigraphy has been the decline in funding. With regard to the hydrocarbon industry, this decline was driven to some extent by industry maturation and a shift toward funding research in energy-transition technologies. However, for many emerging energy solutions such as hydrothermal energy, natural hydrogen exploration, carbon capture and storage, and wind power, understanding the subsurface in terms of stratigraphy and correlation remains crucial. As a result, the transition to new energies may lead to a resurgence in funding and demand for dinocyst biostratigraphy. By embracing the challenges ahead – some of which we have outlined above – dinocyst biostratigraphy can maintain, and potentially expand, its role as a unique discipline in both academic research and industrial applications.

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