From bi-polar to regional distribution of modern dinoflagellate cysts, an overview of their biogeography

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**Abstract**

This paper examines the distribution of 91 modern dinoflagellate cyst taxa from 3636 locations across the world’s oceans. Patterns of distributions among the taxa included bi-polarity, cosmopolitan, northern versus southern hemispheres, and geographically restricted. Of the 91 taxa, three dominate these 3636 assemblages at the global scale, *Brigantedinium* species, *Operculodinium* *centrocarpum* sensu Wall and Dale 1966 and some species of *Spiniferites*. Whereas *Brigantedinium* is a true cosmopolitan taxon, with high abundances in each ocean, *Operculodinium centrocarpum* sensu Wall and Dale 1966 shows high abundances in polar to temperate regions in the Northern Hemisphere, and in tropical to sub-tropical waters in the Southern Hemisphere. *Spiniferites* species show highest occurrences in the Southern Hemisphere latitudes. This study also highlights three true bi-polar species, *Impagidinium pallidum*, *Islandinium minutum* and *Polarella glacialis*. Only a few taxa are strictly geographically restricted, either being relics of ancient seas such as the Paratethys (*Spiniferites cruciformis*) or linked to specific environmental conditions. However, recent studies have shown recent worldwide dispersal of these endemic species possibly due to human activities. Overall, this compilation has highlighted the progress made since early 1970s on our understanding of this important tracer of environmental conditions but also gaps in our knowledge of their distribution in pelagic regions on the Pacific and Indian Oceans as well as under Arctic sea ice.

Key-words: Dinoflagellate cyst; modern distribution; global; bi-polar; endemism

**1. Introduction**

The taxonomy and distribution of modern dinoflagellate cysts (= dinocysts) have been increasingly studied over the last few decades because they demonstrate significant potential as tracers of past marine environmental conditions, in particular where other microfossils are rare or negatively affected by preservation (e.g., Aksu and Mudie, 1984; de Vernal and Marret, 2007). The pioneering work of Williams (1971) describing the modern distribution of cysts in recent North Atlantic sediments first triggered a keen interest in this group of microfossils, and subsequent studies such as those from Davey and Rogers (1975), Wall et al. (1977), Williams and Bujak (1977), Harland (1983), Turon (1984), Edwards and Andrle (1992) and Rochon et al. (1999) have highlighted the relationship between dinocyst species assemblages and surface water masses of the ocean. Mudie and Harland (1996; text-fig.6) were the first to attempt a global-scale biogeographic synthesis for modern dinocyst-acritarch assemblages. Subsequently, a multitude of studies have helped to improve our knowledge on the biogeography of the dinocyst group from local (e.g., Radi et al., 2007; Limoges et al., 2010; Price et al. 2016) to global scale (Marret and Zonneveld, 2003; Zonneveld et al., 2013). The latest worldwide atlas published in 2013 illustrates the distribution of 71 taxa based on 2405 sites. Since 2013, additional studies (Table 1) investigating the modern distribution of dinoflagellate cysts regionally and worldwide have helped to refine ecological and biogeographical affinities of dinocyst taxa and confirmed biogeographical patterns, from endemism to bi-polarity. For example, a recent and regional atlas of the Black Sea corridor by Mudie et al. (2017) has filled some gaps in our knowledge of salinity tolerance for many modern taxa.

This paper provides a short overview of the global distribution of 91 modern dinoflagellate cyst taxa based on a literature review as well as an updated dinocyst database used for quantitative reconstructions, with a focus on bipolar and endemic species.

**2. Materials and Methods**

Global, regional and local cyst distributions were compiled mainly from the available literature (Table 1) reported since the publication of the worldwide Atlas of Zonneveld et al. (2013). These include dinocyst data from 21 Arctic Ocean sites not previously published in detail (Mudie, 1992), and now using up-to-date taxonomy. Where possible, cyst abundances and percentages were used except for some datasets reporting only the presence of taxa. All datasets were normalised (except for the ones with only presence available) and the relative abundance of each taxon was averaged within 2.5º band of latitude and longitude. The Tilia software of Grimm (1990) was used to create diagrams. Figure 1 was made using the software Ocean Data View (<https://odv.awi.de/>). Three diagrams were produced to illustrate the cyst taxa distribution against longitude, one with sites located north of 65ºN (780 sites), one with sites from the Pacific (857 sites), Atlantic (1048 sites) and Indians Oceans (540 sites) and excluding the Mediterranean, Marmara, Black, Caspian and Aral Seas, and finally, one illustrating only these five seas (411 sites).

[INSERT TABLE 1 HERE]

Taxonomical identification following Williams et al. (2017) was carefully checked for each dataset to ensure consistency. For the purpose of this compilation, we did not consider the type of sample preparation for palynological analysis as the focus of this paper is to depict distribution patterns. We also did not include species of *Alexandrium* as preservation issues and possible confusion with *Scrippsiella trifida* (Head et al. 2006) could introduce a bias in observation. A list of the taxa that were included in this compilation can be found in Table 2. We have also listed the cyst taxa found in recent sediments from studies published post 2013, but they were not included in the diagrams as they may have been previously ignored or grouped with other types such as round brown spiny cysts or peridinioids.

[INSERT TABLE 2 HERE]

**3. Biogeographical patterns**

A total of 3636 assemblages have been compiled for the global map (figure 1) that depicts the distribution of 91 dinocyst taxa. Figure 2 (a and b) presents the average relative abundance of each taxon according to a latitudinal gradient with a 2.5 degree resolution. Figures 3, 4 and 5 show these data against a longitudinal gradient for the Arctic Ocean, Pacific–Atlantic–Indian Oceans, and Mediterranean–Aral Seas, respectively.

The latitudinal and longitudinal distributions have highlighted specific patterns, from cosmopolitan to bimodal or endemic, all of which are discussed in the following sections.

[INSERT FIGURE 1 HERE]

The number of species per site, which we refer here to diversity, shows great variance across oceans and seas, with the highest being found in the Atlantic Ocean, around 50 to 30ºN (up to 70 taxa when binned into latitudinal bands, or up to 35 in individual assemblages), and the lowest in the Caspian/Aral seas (on average 6 taxa) and above 65ºN (on average 9 taxa). This pattern could be partly due to the number of sites studied in each ocean (1048 for the Atlantic, 857 for the Pacific and 540 for the Indian, and fewer in other regions) but also reflecting low temperature and short growing season in the semi-enclosed Arctic Ocean north of c. 80o N (>100 sites) and low salinity combined with extreme seasonal temperature change in the land-locked Caspian and Aral seas (49 sites). Most significantly, this compilation shows that three taxa globally dominate dinocyst assemblages, notably *Brigantedinium* spp. which include all identified species such as *Brigantedinium cariacoense* and *Brigantedinium simplex*, and similar cysts not identified at species level. Except for some studies, such as Mudie et al. (2017), it was not possible to map the distribution of species of *Brigantedinium* as they tend to be grouped together due to difficulty in the identification. The other two main taxa are *Operculodinium centrocarpum* sensu Wall and Dale 1966 and species of *Spiniferites* except for *Spiniferites elongatus/S. frigidus*, *Spiniferites* sp. granular type and *S. cruciformis* (note that *Spiniferites* spp. include all *Spiniferites* species that were only identified at genus level). Overall, the 91 dinocyst taxa can be assigned to five biogeographic groups: cosmopolitan, northern latitude, southern latitude, bipolar, and those of limited geographical range.

[INSERT FIGURE 2A HERE]

[INSERT FIGURE 3A HERE]

*3.1 Cosmopolitan taxa*

Overall, *Brigantedinium* species are present in all oceans, with maximal occurrence south of 45ºS (Figure 2a) but they are not the dominant taxa in the Mediterranean-Black Sea corridor (Figure 5). Although the cysts are characterised as sensitive to degradation (e.g., Zonneveld et al., 2019), the heterotrophic *Brigantedinium* species appear to tolerate and thrive in a large range of environmental conditions, from brackish to high salinity conditions (e.g., Price et al., 2018), and from pack-ice margins where diatom food supplies are abundant in summer (e.g., Mudie and Harland, 1996; Harland and Pudsey, 1999) to tropical temperatures. The second most dominant species, found in both hemispheres is the autotrophic dinocyst *Operculodinium centrocarpum* sensu Wall and Dale 1966, although its relative abundance is higher in temperate to polar regions compared to subtropical and tropical areas. It also occurs in most oceans and seas except for the low salinity waters (*ca*. 5 to 17 psu) and the salinas of the inland Caspian and Aral seas, but has major occurrences in the Pacific and Atlantic Oceans. *Spiniferites* species, including all unidentified and recognised taxa, with *Spiniferites ramosus* being the most common and dominant, are also mostly present in all oceans and seas, although three of the species are geographically restricted to Arctic (*Spiniferites elongatus/Spiniferites frigidus*), in the Mediterranean and Okhotsk Seas (*Spiniferites* sp. granular type) or low salinity epicontinental seas (*Spiniferites* *cruciformis*) (see sections below). Furthermore, a recent overview of *Spiniferites* taxa distribution in the Northern Hemisphere has raised the issue of the existence of cryptic species, as illustrated by the cosmopolitan character and long biostratigraphic record of *Spiniferites ramosus* (de Vernal et al., 2018).

[INSERT FIGURE 3 HERE]

Several other less abundant species are also found almost everywhere, such as *Nematosphaeropsis labyrinthus*, with maximum occurrences in the South Pacific; however, this species is rare in the Black Sea and absent in the Caspian and Aral seas. The cyst of *Pentapharsodinium dalei* which has been found at all latitudes, is relatively common in the Pacific and Atlantic Oceans, and very occasional in the Indian Ocean. Its maximum occurrence is found north of 65ºN. It is worth noting that this taxon is also present in the low-salinity to brackish waters of the Black Sea-Caspian Sea corridor, which suggests also a large tolerance of environmental conditions. Within the less abundant species, *Impagidinium* taxa are also found almost everywhere seaward of estuarine environments, but again with two species (*Impagidinium caspienense* and *Impagidinium variaseptum*) geographically restricted (see sections below). Finally, although *Lingulodinium machaerophorum* has a quasi-cosmopolitan distribution, it is most abundant in the Mediterranean-Black Sea-Caspian Corridor and widespread in the Atlantic Ocean, but in the Pacific Ocean, it is sparse north of 40ºN in waters with sea surface temperature above 15ºC (e.g., Pospelova et al., 2008) and absent south of latitude 45ºS. This is quite surprising as relatively similar conditions in which this species thrives can be found in all oceans.

Overall, this compilation highlights that only few dinocyst taxa are found everywhere, which could imply their limited use as tracers of past global environmental conditions if used just individually. However, it is worth noting that their relative abundance is often related to specific oceanographic conditions as discussed in de Vernal et al. (2011), Zonneveld et al. (2013), Mudie et al. (2017) and de Vernal et al. (2018). The process morphology of *Operculodinium centrocarpum* sensu Wall and Dale 1966 and *Lingulodinium machaerophorum* is also very variable and correlates in some basins with temperature and/or salinity (e.g., Mertens et al., 2009, 2012b; Jansson et al.,2014; Gurdebeke et al., 2018). The case of the *Operculodinium centrocarpum* sensu Wall and Dale 1966 is very interesting as the relationship between process length and salinity shows strong positive correlation in the Baltic Sea and the opposite in the North Pacific (Mertens et al. 2009). This phenomenon can now be explained by cryptic speciation in *Protoceratium reticulatum* (a name of the motile stage for *Operculodinium centrocarpum* sensu Wall and Dale 1966) that was proposed by Mertens et al. (2012a) and supported by molecular evidence recently reported by Wang et al. (2019). Similarly, in low salinity seas, high variability of process development in *Spiniferites cruciformis* and the cyst of *Gonyaulax baltica* may be weakly correlated with surface salinity (Ellegaard et al. 2002; Mudie et al., 2002).

*3.2 Northern latitude taxa*

This compilation generally confirms previous studies on the distribution of taxa restricted to the Northern Hemisphere although it also has raised some questions with regards to the true occurrence of some species. Figure 2 shows that overall there is a greater diversity of dinocyst taxa in the Northern Hemisphere compared to the Southern Hemisphere, despite the relatively smaller area encompassed by the northern oceans. However, there is a greater number of samples in the Northern Hemisphere (3019) compared to the Southern Hemisphere (617). In both hemispheres, there is a strong decrease in dinocyst diversity poleward of about 50o latitude, this decline being steepest in the Southern Hemisphere where it corresponds to the outer margin of the drift ice zone (see Mudie, 1992; text-fig. 5).

Within these northern latitude taxa, only few species occur in relative high abundances north of 40ºN, such as *Echinidinium karaense*, cyst of *Polykrikos* sp. arctic morphology (previously assigned to *Polykrikos quadratus* and now excluded from the order Gymnodiniales (Potvin et al., 2018)), which are observed in most oceans. *Islandinium cezare*, *Echinidinium zonneveldiae*, *Trinovantedinium variabile*, S*piniferites elongatus*, *Achomosphaera andalousiense*, *Nematosphaeropsis rigida, Spiniferites* sp. granular type, Cyst type A (possibly cyst of *Protoperidinium fukuyoi* (Mertens et al., 2013)), and cyst of *Scrippsiella trifida* can also be characterised as strictly northern hemisphere taxa, with no occurrence south of 15ºN.

Other taxa apparently confined to the Northern Hemisphere may have been previously mis-identified as species with similar morphology or have recently been described and were possibly overlooked in earlier studies. One of such taxa is the cyst of *Protoperidinium nudum* which has only been identified in northern latitude assemblages. It is possible that the cyst of *P. nudum* occurs more widely but may have been mis-identified or grouped with *Selenopemphix quanta* as they share a very similar morphology. A similar situation may pertain for the cyst of *Polykrikos hartmannii*, which has morphology resembling *Echinidinium granulatum* (Zonneveld and Pospelova, 2015). Observations of the thecate stage of *P. hartmanii* have been reported for all oceans (e.g., Aktan and Keskin, 2017), notably along the eastern coast of the US and in the Gulf of Alaska. The only matching distribution between the thecate stage and its cyst can be found in the Black Sea. *Trinovantedinium pallidifulvum*, which has been recently described in Mertens et al. (2017a), has probably been identified as *Trinovantedinium applanatum* in previous studies. *Stelladinium bifidum* (see Head et al., this issue) and *Echinidinium bispiniformum* are also likely to have been mis-identified.

The cyst of *Biecheleria baltica* has been mapped in the Black Sea (Mudie et al., 2017) but also occurs in the Baltic Sea, possibly for at least the last 100 years (Kremp et al., 2018); it is therefore likely that these small transparent cysts have been ignored in previous studies. Alternatively, this species is a recent immigrant transported in ballast of ships that travel canals and rivers linking the low salinity waters from Baltic to Black seas. Other studies have also reported the presence of *Biecheleria* cysts, but due to their small size (<15 µm) some are likely to be lost during processing (e.g., Price and Pospelova, 2011) and therefore not included in total cyst counts (e.g., Bringué et al., 2013 Heikkilä et al., 2014; Price et al., 2017a; Gurdebeke et al., 2018). Finally, *Oblea acanthocysta*, revisited by Mertens et al. (2015), bears some resemblance with *Echinidinium* species and may have been included in this group in routine counts. However, it may also be geographically restricted off Japan, although it has recently been identified in the Izmir Bay (Aydin et al., 2011, 2015a,b) and British Columbian fjords (Gurdebeke et al., 2018).

*3.3 Southern latitude taxa*

Compared with the Northern Hemisphere there are very few dinocysts which have ranges that are restricted to the Southern Hemisphere. On average, diversity is also lower. Only two species are restricted south of 35ºS, *Selenopemphix antarctica* and *Cryodinium meridianum*.One other species, *Impagidinium variaseptum*,has an extended distribution just slightly above the equator. *Dalella chathamense* was initially described in the Southern Ocean (McMinn and Sun, 1994) but has now been found in low occurrences up to 42ºN (Pospelova et al., 2008; Bonnet et al., 2012), mostly in the Pacific Ocean.

It is also worth noting that among cosmopolitan taxa, some species seem to have their highest abundance in the South Pacific Ocean, such as *N. labyrinthus* and *Impagidinium aculeatum*. *Spiniferites ramosus* shows highest occurrences in the eastern region of the Indian Ocean.

*3.4 Bipolar taxa*

Of the 91 taxa compiled here, only two, *Impagidinium pallidum* and *Islandinium minutum*, are present in polar-subpolar regions of both poles. *Islandinium minutum* does not occur south of 15ºN and north of 40ºS and *I. pallidum* does not occur south of 25ºN and north of 30ºS. However, it is worth noting that *Polarella glacialis* is another true bipolar species, as it has been first described in Antarctica (Montresor et al., 1999) but was previously identified in Arctic sediments (Mudie et al., 1992). Subsequently, a phylogenetic study has confirmed that this species does occur in both polar regions (Montresor et al., 2003). In the Arctic Ocean, *Polarella glacialis* is mostly found north of 80o N and is apparently associated with multiyear sea ice duration over the Nansen Basin, but does not occur under permanent pack ice on the Canadian Polar Margin. It has also been observed in the subarctic waters of Hudson Bay (Heikkilä et al., 2014) as well as in plankton net samples from the Labrador Sea (July 2018), Baffin Bay in 2008 and 2014 (Rochon, unpublished data), and in faecal pellets from a sediment trap in the North Water polynya, southern Nares Strait (reported in Hargrave et al., 2002). *Polarella glacialis*, which produce small and fragile cysts, might have been missed due to sieving mesh and/or preservation issue (see Heikkilä et al., 2014; Limoges et al., 2018; de Vernal et al., this issue). It has, indeed, rarely been found in palaeosequences, although it has been detected in late Holocene Antarctic sediments through genomic studies (Boere et al., 2009) as well as in a very high sedimentation context where organic matter was very well preserved (Hartman et al., 2018).

***Impagidinium pallidum*:** There is one reported occurrence of this species in the Mediterranean Sea, south of Sicily (Zonneveld et al., 2013), but it is not present in the Marmara or Black Sea. Maximum occurrence of *Impagidinium pallidum* is found in the Northern Hemisphere, in particular in the Greenland Sea, with other large occurrences in the Norwegian and Barents Seas. In the Southern Hemisphere, it occurs in both coastal and oceanic locations. In the fossil record, it has been described in assemblages from the Mid Eocene in the Labrador Sea (Head et al., 1989), the Late Eocene from the Northern Pacific (Bujak, 1984) and the Pliocene of Alpha Ridge, central Arctic Ocean (Aksu and Mudie, 1984). In the Southern Hemisphere, *I. pallidum* is recorded for the Early Oligocene offshore Wilkes Land, Antarctica (Bijl et al., 2018). De Schepper et al. (2011) discuss the possibility that this species could have crossed the equator during periods of severe global cooling but it has not been recorded from equatorial Cenozoic sediments. The morphology of the dinocyst is the same in both hemispheres but the cyst-thecate relationship has yet to be described, although its phylogeny shows some closeness to *Impagidinium caspienense/Gonyaulax baltica* and *Spiniferites belerius* (Mertens et al., 2017b).

***Islandinium minutum***: Its distribution in modern sediments is mainly located in the Northern Hemisphere with only a couple of occurrences in the Southern Hemisphere. These are the north-west Weddell Sea (Pieńkowski et al., 2013) where it is found in relatively high abundances (~90% of some assemblages), and east of New Zealand but in very low relative abundances (<5%). Aksu and Mudie (1984) reported it (as *Multispinula minuta*) in Pleistocene sediments of the Arctic Ocean Alpha Ridge and Bijl et al. (2018) mention *Islandinium* sp. in early Miocene sediments from Wilkes Land, Antarctica. Williams et al. (2017) incorrectlygave an Holocene age for *Islandinium minutum*.

The existence of bipolar species, either in the dinoflagellates or other phytoplanktonic groups such as Radiolarians (e.g., Boltovskoy and Correa, 2016) is rather challenging to explain. An early study by Mudie et al. (1990) used records from ocean drilling cores to trace the migration of *I. pallidum* from the Pacific to Atlantic Oceans via the Panama gateway before c. 5 Ma and during successive opening of Arctic gateways. However, a mechanism of transport from the sub-Arctic to Antarctic regions between the Eocene and Oligocene remains enigmatic.

*3.5 Dinocysts with limited and small geographical ranges*

There are very few endemic dinocyst taxa, defined as those belonging to only one geographic region. *Stelladinium robustum* is currently limited to the Indian Ocean. *Peridinium ponticum* was thought to be restricted to the Black Sea until a recent study has observed this species on the Iberian margin (García-Moreiras et al., 2018). Two other species that are strongly associated with the Black Sea region are *Spiniferites cruciformis* and *Pyxidinopsis psilata*. In surface sediments, *S. cruciformis* is occasionally present in many areas of the Ponto-Caspian region but also rarely occurs off southern Italy in the Mediterranean Sea. It also has been reported, apparently with living cytoplasm, in modern freshwater lakes near the Marmara Sea (e.g., Leroy and Albay, 2010). This species is abundant in the lacustrine phases of the Pleistocene-early Holocene interval of the Black Sea and was a member of the Late Miocene Paratethyan basins in Europe, implying that the Mediterranean populations are relict. *P. psilata* was previously thought to be endemic to the Black Sea where it is common and widespread. However, it has been reported in southern Florida and in the east-coast of South America (Zonneveld et al., 2013; unconfirmed identification) and at one site on the west coast of Northern America (Zonneveld et al., 2013). There are no fossil records for occurrences of *P. psilata* outside of the Black Sea Corridor and it is likely that the trans-Atlantic and Pacific populations are recently introduced, transported from the Marmara-Black Sea region by ships (see Mudie et al., 2017). Two other species were found in the Caspian Sea (Marret et al., 2004), *Impagidinium caspienense* and *Caspidinium rugosum*, and were also thought to be endemic to this sea. However, a recent phylogenetic study by Mertens et al. (2017b) has related *I. caspienense* to *Gonyaulax baltica*, a species currently occurring in the Baltic Sea. A possible Arctic origin of *I. caspienense* at the end of the Pliocene has been recently discussed in Richards et al. (2018). *Caspidinium rugosum* is also thought to be a Paratethys relic, occurring in the European Pannonian Basin during the late Miocene. It is worth noting that the cyst of *Oblea acanthocysta* was initially observed solely off Japan (Omura Bay, Kawami et al., 2006) but has recently been identified in estuarine waters of British Columbia (Canada) (Gurdebeke et al. 2018) and the Izmir Bay (Turkey) (Aydin et al. 2011, 2015a,b). This example raises the question of the occurrence of this species in the eastern Mediterranean Sea, which could be the consequence of long-distance transport due to human activities or the result of being overlooked or lumped as a spiny brown cyst in other palynological studies.

Finally, observation of previously thought extinct taxa suggests that these taxa are probably extant in modern time as endemic species. This is notably the case of *Melitasphaeridium choanophorum* which occurs in recent sediments of the Gulf of Mexico (Limoges et al. 2013; Price et al., 2017b) and the South China Sea (Li et al., 2017 ), as well as *Dapsilidinium* *pastielsii* found in surface sediments from the Indo-Pacific warm pool region (Mertens et al., 2014).

**4. Discussion**

The new biogeographic data we have presented, using 3636 assemblages in modern sediments of the global oceans and major inland seas, represent the enormous progress made since the first efforts of Williams in 1971 (with 44 taxa at 35 North Atlantic-Equatorial sites) and of Mudie and Harland in 1996 (65 taxa, 215 sites world-wide).These earlier studies also noted the very widespread distributions of most dinocyst species. However, Williams (1971) singled out four primary palaeoceanographic marker species: *Operculodinium centrocarpum* sensuWall and dale 1966 (forcoastal North America and northern Atlantic)*, Impagidinium aculeatum* (NW Africa), *Spiniferites mirabilis* (coastal eastern North Atlantic)and *Nematosphaeropsis* cf. *N. labyrinthus* (N. Atlantic Drift). Williams and Bujak (1977) then used data from 25 North Atlantic well sites and two deep-sea drilling cores to select *O. centrocarpum*, *L. machaerophorum, Polysphaeridium zoharyi* and *Homotryblium floripes* as important biogeographical and palaeoenvironmental indicators for North Atlantic water masses. These studies and the work of Wall et al. (1977) have subsequently strongly influenced the palaeoenvironmental interpretations assigned to pre-Quaternary dinocyst assemblages. Our new data show that caution is required in assigning palaeoenvironmental characteristics to assemblages based on single indicator taxa, such as *Polysphaeridium zoharyi* or *Tuberculodinium vancampoae*. The same caution now applies to the use of the ecofacies and biogeographical provinces delimited by Williams (1971) and Mudie (1992) using multivariate factor analysis to link assemblages with sea-surface temperature and salinity, and to relate geographic provinces with ocean circulation and sea-ice margins (Mudie and Harland, 1996) because the analytical methods tend to heavily weight the ecological characteristics of a dominant species.

Our new biogeographic data once again raise the question of whether cyst-producing dinoflagellate species live in/under sea ice within the Arctic Ocean (i.e., the ocean area north of Europe, Russia, Alaska and Canada), although that is not the case for the Antarctic sea ice region (see Zheng et al., 1992; Stoecker al., 1998). This question was first asked in 1980, at which time only *Protoperidinium* species were reported for plankton records from Canadian or West Greenland waters at 80ºN (the highest latitude with plankton records at that time; Mudie, 1992). Subsequently Okolodkov (1999) extended this database to 82ºN in the eastern Arctic Ocean and showed the absence of *Protoceratium reticulatum* north of ca. 70ºN, and only *Protoperidinium* spp. further north. Our new data show that within the Arctic region (figure 3), there is a notable decrease in dinocyst species diversity eastwards of 0 to 25ºE and westwards of 325ºE. This pattern appears to reflect the influence of relatively warm inflowing surface Atlantic water mass through the Fram Strait in the east, and warm Pacific water (Alaskan Coastal Current) through the Bering Strait in the west. The cyst diversity distribution pattern is also consistent with earlier biogeographical studies of theca-stage dinoflagellates (Okolodkov and Dodge, 1996; Okolodkov, 1999). These surveys correlated maximum species diversity with the Dunbar Line that encloses the Northern Hemisphere region with surface water of mixed Arctic and sub-Arctic or Boreal origin. Dinoflagellate studies from Antarctic sea ice clearly demonstrate the capacity of blooming population of *P. glacialis* (Zheng et al., 1992; Stoecker et al., 1998), which suggests that sea ice is not a limiting factor for some species.

The question of possible long-distance dinocyst transport to sediments beneath the pack-ice further north requires further research and is of particular importance because the inflow of warm, saline water of Atlantic origin increases with climate warming (Polyakov et al., 2012). However, the presence of *P. reticulatum* and *Gonyaulax* cf. *spinifera* as well as numerous cysts of *O. centrocarpum* and *S. ramosus* with cell content in plankton net samples in a polynya around 76ºN-73ºW suggests in-situ populations in waters south of the Arctic Ocean and therefore questions this long distance transport for these species (Rochon, unpublished data). It is possible that recent ice-thinning and/or increased shipping traffic within the Arctic Ocean will see the northern expansion of dinocyst diversity. There is a need for more data from moored, year-round Arctic sediment traps to avoid loss of small cysts in plankton nets and to cover seasons other than the summer ice-minimum interval when ships have access. A sediment trap sampling bi-monthly intervals that was moored under permanent pack-ice on the Canadian Polar margin in the Arctic Ocean north of Axel Heiberg in 1989-90 failed to capture any cysts (Hargrave et al., 1994), although a through-ice vertical plankton sample in August 1986 recovered *Peridiniella catenata, Protoperidinium depressum*, *P. pallidum* and *P. ovata.* Cysts of *P. catenata* were not recovered in the Polar Margin shelf sediments although they are common in deeper water sediments of the sub-arctic Baltic Sea (Spilling et al., 2006). Two subarctic sediment traps moored in eastern and western Hudson’s Bay (Canada) (Heikkilä et al., 2016) documented cyst assemblages at bi-weekly to bi-monthly interval from October 2005 to September 2006. These subarctic sites experience 5-7 months of consolidated sea ice. Over 20 cyst taxa were recorded in the traps, including *P. glacialis*, *E. karaense*, and *I. minutum*. Cyst production was negligible under ice during the Arctic winter, but ranged from 2700 to 394,800 cysts m-2 day-1 during spring and summer.

Despite a plethora of phytoplankton studies in the Antarctic region, very few focus only on dinoflagellates and even fewer on dinoflagellate cysts. The first studies at the beginning of the 20th century were focused on phytoplankton in general (Karsten, 1905; Magnin, 1915), with only few dinoflagellate species being described. It is with the work of Enrique Balech in 1974 that the richness in dinoflagellate species was discovered, with many new species being later described (e.g., Balech, 1975). In 1995, McMinn commented on the absence of dinoflagellate cysts in recent sediments around Antarctica but later on, several new and endemic species were discovered, such as S*elenopemphix antarctica* (Marret and de Vernal, 1997) and *Cryodinium meridianum* (Esper and Zonneveld, 2002). A recent study on dinoflagellate cysts near the Antarctic continent (Hartman et al., 2019) formally describes a new dinoflagellate cyst genus and species, *Nucicla umbiliphora*. It is therefore likely that there are still potentially new discoveries to be made in the southern polar regions.

**5. Conclusions**

This paper gives a brief overview of an updated worldwide distribution of 91 taxa of dinoflagellate cysts, highlighting the following observations:

* Of the 91 taxa that were studied here, their global distribution shows that only three modern taxa (*Brigantedinium* species, *Operculodinium centrocarpum* sensu Wall and Dale 1966 and some species of *Spiniferites*) dominate cyst assemblages worldwide. We therefore would cautiously recommend to not consider them as key-indicator taxa as previously done, and to interpret their occurrence in fossil sediments in combination with the full assemblage
* Only a few species are truly restricted geographically, such as *Stelladinium robustum* in the Indian Ocean and *Peridinium ponticum* in the Black Sea-Caspian Sea corridor (other taxa from this region are relicts of the former pan-Eurasian Paratethyan Sea, e.g., *Impagidinium caspienense, Spiniferites cruciformis*), although recent studies have highlighted recent dispersal possibly linked to human activities.
* Only three true bipolar species were identified — *Islandinium minutum*, *Impagidinium pallidum* and cyst of *Polarella glacialis* — but recent studies raise questions about cryptic species and morphological identification issues. Although there is no ambiguity with regards to the identification of *I. pallidum*, the recent finding of new *Islandinium* and morphologically similar speciessuggests higher diversity in this group, which would urge us to proceed with further culture experiments and phylogeny especially for Antarctic specimens, for which we have little information.
* The global distribution confirms the relatively rich diversity in environments where other palaeoceanographic tracers are rare or monospecific, in particular in polar environments or enclosed seas.
* This global overview highlights the need for more information from oceanic sites, in particular pelagic regions of the Pacific and Indian Oceans.
* Further information on cyst production beneath Arctic sea ice, seasonal and perennial would help to better understand life history of these important primary producers.

**Acknowledgements**

We are very grateful for the constructive comments from two anonymous reviewers, and warmly thank the Editor-in-Chief for his support and the Guest Editors of the Special Issue for inviting this paper.

**Funding**

This work was supported in part by the Zuckerman STEM Leadership Program through a postdoctoral scholarship to Andrea Price. So-Young Kim acknowledges support from the project titled 'Korea-Arctic Ocean Observing System (20160245)', funded by the MOF.

**References**

Aksu, A., Mudie, P., 1984. Palaeoclimate of Baffin Bay from 300,000-year record of foraminifera, dinoflagellates and pollen. Nature 312, 630-634.

Aktan, Y., Keskin, Ç., 2017. Second habitat record of *Polykrikos hartmannii* W. Zimm. (dinophyceae) in the south Aegean sea, Eastern Mediterranean. Turkish Journal of Fisheries and Aquatic Sciences 17, 1079-1083.

Aydin, H., Matsuoka, K., Minareci, E., 2011. Distribution of dinoflagellate cysts in recent sediments from Izmir Bay (Aegean Sea, Eastern Mediterranean). Marine Micropaleontology 80, 44-52.

Aydın, H., Yürür, E.E., Uzar, S., Küçüksezgin, F., 2015a. Modern dinoflagellate cyst assemblages of Aliağa and Nemrut bay: Influence of industrial pollution. Turkish Journal of Fisheries and Aquatic Sciences 15, 543-554.

Aydin, H., Yürür, E.E., Uzar, S., Küçüksezgin, F., 2015b. Impact of industrial pollution on recent dinoflagellate cysts in Izmir Bay (Eastern Aegean). Marine Pollution Bulletin 94, 144-152.

Balech, E., 1975. Clave illustrada de Dinoflagellados Antarcticos. Institut Antarctico Argentino, 99 p.

Balkis, N., Balci, M., Giannakourou, A., Venetsanopoulou, A., Mudie, P., 2016. Dinoflagellate resting cysts in recent marine sediments from the Gulf of Gemlik (Marmara Sea, Turkey) and seasonal harmful algal blooms. Phycologia 55, 187-209.

Bijl, P.K., Houben, A.J.P., Bruls, A., Pross, J., Sangiorgi, F., 2018. Stratigraphic calibration of Oligocene–Miocene organic-walled dinoflagellate cysts from offshore Wilkes Land, East Antarctica, and a zonation proposal. J. Micropalaeontol. 37, 105-138.

Boere, A. C., Abbas, B., Rijpstra, W. I. C., Versteegh, G. J. M., Volkman, J. K., Sinninghe Damsté, J. S., and Coolen, M. J. L., 2009. Late-Holocene succession of dinoflagellates in an Antarctic fjord using a multi-proxy approach: Paleoenvironmental genomics, lipid biomarkers and palynomorphs, Geobiology, 7, 265–281

Bonnet, S., de Vernal, A., Gersonde, R., Lembke-Jene, L., 2012. Modern distribution of dinocysts from the North Pacific Ocean (37-64 degrees N, 144 degrees E-148 degrees W) in relation to hydrographic conditions, sea-ice and productivity. Marine Micropaleontology 84-85, 87-113.

Boltovskoy, D., Correa, N., 2016. Biogeography of Radiolaria Polycystina (Protista) in the World Ocean. Progress in Oceanography 149, 82-105.

Bringué, M., Pospelova, V., Pak, D., 2013, Seasonal production of organic-walled dinoflagellate cysts in an upwelling system: A sediment trap study from the Santa Barbara Basin, California. Marine Micropaleontology 100, 34-51.

Bujak, J.P., 1984. Cenozoic dinoflagellate cysts and acritarchs from the Bering Sea and northern North Pacific, DSDP Leg 19. Micropaleontology 30, 180-212.

Candel, M.S., Radi, T., de Vernal, A., Bujalesky, G., 2012. Distribution of dinoflagellate cysts and other aquatic palynomorphs in surface sediments from the Beagle Channel, Southern Argentina. Marine Micropaleontology 96-97, 1-12.

Candel, M.S., Borromei, A.M., Martínez, M.A., Bujalesky, G., 2013. Palynofacies analysis of surface sediments from the Beagle Channel and its application as modern analogues for Holocene records of Tierra del Fuego, Argentina. Palynology 37, 62-76.

Crouch, E.M., Mildenhall, D.C., Neil, H.L., 2010. Distribution of organic-walled marine and terrestrial palynomorphs in surface sediments, offshore eastern New Zealand. Marine Geology 270, 235-256.

D'Silva, M.S., Anil, A.C., D'Costa, P.M., 2011. An overview of dinoflagellate cysts in recent sediments along the west coast of India. Indian Journal of Marine Sciences 40, 697-709.

D'Silva, M.S., Anil, A.C., Sawant, S.S., 2013. Dinoflagellate cyst assemblages in recent sediments of Visakhapatnam harbour, east coast of India: Influence of environmental characteristics. Marine Pollution Bulletin 66, 59-72.

Davey, R.J., Rogers, J., 1975. Palynomorph distribution in Recent offshore sediments along two traverses off South West Africa. Marine Geology 18, 213-225.

De Schepper, S., Fischer, E.I., Groeneveld, J., Head, M.J., Matthiessen, J., 2011. Deciphering the palaeoecology of Late Pliocene and Early Pleistocene dinoflagellate cysts. Palaeogeography Palaeoclimatology Palaeoecology 309, 17-32.

de Vernal, A., Marret, F., 2007. Organic-walled dinoflagellate cysts: tracers of sea-surface conditions., in: Hillaire-Marcel, C., De Vernal, A. (Eds.), Proxies in Late Cenozoic paleoceanography. Elsevier, Utrecht, pp. 371-408.

de Vernal, A., Rochon, A., 2011. Dinocysts as tracers of sea-surface conditions and sea-ice cover in polar and subpolar environments. IOP Conf. Series: Earth and Environmental Science 14: 012007.

de Vernal, A., Eynaud, F., Henry, M., Limoges, A., Londeix, L., Matthiessen, J., Marret, F., Pospelova, V., Radi, T., Rochon, A., Van Nieuwenhove, N., Zaragosi, S., 2018. Distribution and (palaeo)ecological affinities of the main *Spiniferites* taxa in the mid-high latitudes of the Northern Hemisphere. Palynology 42, 182-202.

Edwards, L.E., Andrle, V.A.S., 1992. Distribution of selected dinoflagellate cysts in modern marine sediments, in: Head, M.J., Wrenn, J.H. (Eds.), Neogene and Quaternary Dinoflagellate Cysts and Acritarchs. American Association of Stratigraphic Palynologists Foundation, pp. 259-288.

Ellegaard. M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects of temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp. nov. (Dinophyceae) from the Baltic Sea area. Journal of Phycology 38, 755-789.

Elshanawany, R., Zonneveld, K.A.F., 2016. Dinoflagellate cyst distribution in the oligotrophic environments of the Gulf of Aqaba and northern Red Sea. Marine Micropaleontology 124, 29-44.

Esper, O., Zonneveld, K.A.F., 2002. Distribution of organic-walled dinoflagellate cysts in surface sediments of the Southern Ocean (eastern Atlantic sector) between the Subtropical Front and the Weddell Gyre. Marine Micropaleontology 46, 177-208.

Gao, Y., Dong, Y., Li, H., Zhan, A., 2018. Influence of environmental factors on spatial–temporal distribution patterns of dinoflagellate cyst communities in the South China Sea. Marine Biodiversity, 1-13.

García-Moreiras, I., Pospelova, V., García-Gil, S., Muñoz Sobrino, C. 2018. Climatic and anthropogenic impacts on the Ría de Vigo (NW Iberia) over the last two centuries: a high-resolution dinoflagellate cyst sedimentary record. Palaeogeography, Palaeoclimatology, Palaeoecology, 504:201-218.

Grimm, E.C., 1990. Tilia 2.0 Program. State Museum, Research and Collections Center, Springfield, Illinois, USA.

Gurdebeke, P.R., Pospelova, V., Mertens, K.N., Dallimore, A., Chana, J., Louwye, S., 2018. Diversity and distribution of dinoflagellate cysts in surface sediments from fjords of western Vancouver Island (British Columbia, Canada). Marine Micropaleontology 143, 12-29.

Hardy, W., Marret, F., Penaud, A., Le Mezo, P., Droz, L., Marsset, T., Kageyama, M., 2018. Quantification of last glacial-Holocene net primary productivity and upwelling activity in the equatorial eastern Atlantic with a revised modern dinocyst database. Palaeogeography Palaeoclimatology Palaeoecology 505, 410-427.

Hargrave, B.T., Vonbodungen, B., Stoffynegli, P., Mudie, P.J., 1994. Seasonal variability in particle sedimentation under permanent ice cover in the Arctic-Ocean. Continental Shelf Research 14, 279-293.

Hargrave, B.T., Walsh, I.D., Murray, D.W., 2002. Seasonal and spatial patterns in mass and organic matter sedimentation in the North Water Polynya. Deep-Sea Research II 49 (22-230, 5227.

Harland, R., 1983. Distribution maps of recent dinoflagellate cysts in bottom sediments from the North-Atlantic Ocean and adjacent seas. Palaeontology 26, 321-387.

Harland, R., Pudsey, C.J., 1999. Dinoflagellate cysts from sediment traps deployed in the Bellingshausen, Weddell and Scotia seas, Antarctica. Marine Micropaleontology 37, 77-99.

Hartman, J.D., Bijl, P.K., Sangiorgi, F., 2018. A review of the ecological affinities of marine organic microfossils from a Holocene record offshore of Adélie Land (East Antarctica). Journal of Micropalaeontology, 37 (2), pp. 445-497

Hartman, J.D., Sangiorgi, F., Bijl, P.K., Versteegh, G.J.M., 2019. *Nucicla umbiliphora* gen. et sp. nov.: a Quaternary peridinioid dinoflagellate cyst from the Antarctic margin. Palynology 43(1), 94-103

Head, M.J., Norris, D.R., Mudie, P.J., 1989. 26. New species of dinocysts and a new species of acritarch from the upper Miocene and lowermost Pliocene, ODP Leg 105, site 646, Labrador Sea in: Srivastava, S.P. et al. (Eds.), Ocean Drilling Program, Proceedings, Scientific Results Leg 105, p.453-466, pl.1-5; College Station, Texas.

Head, M.J., Lewis, J., De Vernal, A., 2006. The cyst of the calcareous dinoflagellate *Scrippsiella trifida*: Resolving the fossil record of its organic wall with that of *Alexandrium* *tamarense*. Journal of Paleontology 80, 1-18.

Heikkilä, M., Pospelova, V., Hochheim, K.P., Kuzyk, Z.Z.A., Stern, G.A., Barber, D.G., Macdonald, R.W., 2014. Surface sediment dinoflagellate cysts from the Hudson Bay system and their relation to freshwater and nutrient cycling. Marine Micropaleontology 106, 79-109.

Heikkilä, M., Pospelova, V., Forest, A., Stern, G.A., Fortier, L., Macdonald, R.W., 2016. Dinoflagellate cyst production over an annual cycle in seasonally ice-covered Hudson Bay. Marine Micropaleontology 125, 1-24.

Hessler, I., Young, M., Holzwarth, U., Mohtadi, M., Lückge, A., Behling, H., 2013. Imprint of eastern Indian Ocean surface oceanography on modern organic-walled dinoflagellate cyst assemblages. Marine Micropaleontology 101, 89-105.

Jansson, I.M., Mertens, K.N., Head, M.J., de Vernal, A., Londeix, L., Marret, F., Matthiessen, J., Sangiorgi, F., 2014. Statistically assessing the correlation between salinity and morphology in cysts produced by the dinoflagellate *Protoceratium reticulatum* from surface sediments of the North Atlantic Ocean, Mediterranean-Marmara-Black Sea region, and Baltic-Kattegat-Skagerrak estuarine system. Palaeogeography Palaeoclimatology Palaeoecology 399, 202-213.

Karsten, G., 1905. Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898–1899. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer “Valdivi 2, 1-136.

Kawami, H., Iwataki, M., Matsuoka, K., 2006. A new diplopsalid species *Oblea acanthocysta* sp. nov. (Peridiniales, Dinophyceae). Plankton and Benthos Research 1, 183-190.

Kremp, A., Hinners, J., Klais, R., Leppänen, A.-P., Kallio, A., 2018. Patterns of vertical cyst distribution and survival in 100-year-old sediment archives of three spring dinoflagellate species from the Northern Baltic Sea. European Journal of Phycology 53, 135-145.

Leroy, S.A.G., Albay, M., 2010. Palynomorphs of brackish and marine species in cores from the freshwater Lake Sapanca, NW Turkey. Review of Palaeobotany and Palynology 160, 181-188.

Li., Z., Pospelova, V., Liu, L., Zhou, R., Song. B., 2017. High-resolution palynological record of Holocene climatic and oceanographic changes in the northern South China Sea. Palaeogeography, Palaeoclimatology, Palaeoecology, 483, p. 94-124.

Limoges, A., Kielt, J.-F., Radi, T., Ruíz-Fernandez, A.C., de Vernal, A., 2010. Dinoflagellate cyst distribution in surface sediments along the south-western Mexican coast (14.76° N to 24.75°N). Marine Micropaleontology 76, 104-123.

Limoges, A, Londeix L, de Vernal A. 2013. Organic-walled dinoflagellate cyst distribution in the Gulf of Mexico. Marine Micropaleontology 102:51-68

Limoges, A., Ribeiro, S., Weckstrom, K., Heikkila, M., Zamelczyk, K., Andersen, T.J., Tallberg, P., Masse, G., Rysgaard, S., Norgaard-Pedersen, N., Seidenkrantz, M.S., 2018. Linking the modern distribution of biogenic proxies in high Arctic Greenland shelf sediments to sea ice, primary production, and Arctic-Atlantic pnflow. J Geophys Res-Biogeo 123, 760-786.

Liu, D., Shi, Y., Di, B., Sun, Q., Wang, Y., Dong, Z., Shao, H., 2012. The impact of different pollution sources on modern dinoflagellate cysts in Sishili Bay, Yellow Sea, China. Marine Micropaleontology 84-85, 1-13.

Magnin, L., 1915. Phytoplancton de l′Antarctique. Deux Expéditions Antarctique Francaises 1908-1910, 1-96.

Marret, F., de Vernal, A., 1997. Dinoflagellate cyst distribution in surface sediments of the southern Indian Ocean. Marine Micropaleontology 29, 367-392.

Marret, F., De Vernal, A., Benderra, F., Harland, R., 2001. Late Quaternary sea-surface conditions at DSDP Hole 594 in the southwest Pacific Ocean based on dinoflagellate cyst assemblages. Journal of Quaternary Sciences 16, 739-751.

Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. Review of Palaeobotany and Palynology 125, 1-200.

Marret, F., Leroy, S., Chalie, F., Gasse, F., 2004. New organic-walled dinoflagellate cysts from recent sediments of Central Asian seas. Review of Palaeobotany and Palynology 129, 1-20.

Marret, F., Scourse, J., Kennedy, H., Ufkes, E., Jansen, J.H.F., 2008. Marine production in the Congo-influenced SE Atlantic over the past 30,000 years: a novel dinoflagellate-cyst based transfer function approach. Marine Micropaleontology 68, 198-222.

McMinn, A., Sun, X., 1994. Recent dinoflagellate cysts from the Chatham Rise, Southern Ocean, east of New Zealand. Palynology 18, 41-53.

McMinn, A., 1995. Why are there no post-Paleogene dinoflagellate cysts in the Southern Ocean? Micropaleontology 41, 383-386.

Mertens, K.N., Ribeiro, S., Bouimetarhan, I., Caner, H., Combourieu Nebout, N., Dale, B., De Vernal, A., Ellegaard, M., Filipova, M., Godhe, A., Goubert, E., Grøsfjeld, K., Holzwarth, U., Kotthoff, U., Leroy, S.A.G., Londeix, L., Marret, F., Matsuoka, K., Mudie, P.J., Naudts, L., Peña-Manjarrez, J.L., Persson, A., Popescu, S.-M., Pospelova, V., Sangiorgi, F., van der Meer, M.T.J., Vink, A., Zonneveld, K.A.F., Vercauteren, D., Vlassenbroeck, J., Louwye, S., 2009. Process length variation in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: Investigating its potential as salinity proxy. Marine Micropaleontology 70, 54-69.

Mertens, K.N., Bringue, M., Van Nieuwenhove, N., Takano, Y., Pospelova, V., Rochon, A., de Vernal, A., Radi, T., Dale, B., Patterson, R.T., Weckstrom, K., Andren, E., Louwye, S., Matsuoka, K., 2012a. Process length variation of the cyst of the dinoflagellate *Protoceratium reticulatum* in the North Pacific and Baltic-Skagerrak region: calibration as an annual density proxy and first evidence of pseudo-cryptic speciation. J. Quat. Sci. 27 (7), 734–744.

Mertens, K.N., Bradley, L.R., Takano, Y., Mudie, P.J., Marret, F., Aksu, A.E., Hiscott, R.N., Verleye, T.J., Mousing, E.A., Smyrnova, L.L., Bagheri, S., Mansor, M., Pospelova, V., Matsuoka, K., 2012b. Quantitative estimation of Holocene surface salinity variation in the Black Sea using dinoflagellate cyst process length. Quaternary Science Reviews 39, 45-59.

Mertens, K.N., Yamaguchi, A., Takano, Y., Pospelova, V., Head, M.J., Radi, T., Pienkowski, A.J., de Vernal, A., Kawami, H., Matsuoka, K. 2013. A new heterotrophic dinoflagellate from the North Pacific, *Protoperidinium fukuyoi*: cyst–theca relationship, phylogeny, distribution and ecology. Journal of Eukaryotic Microbiology, 60(6):545–563.

Mertens, K.N., Takano, Y., Head, M.J., Matsuoka, K., 2014. Living fossils in the Indo-Pacific warm pool: a refuge for thermophilic dinoflagellates during glaciations. Geology 42, 531-534.

Mertens, K.N., Takano, Y., Gu, H.F., Yamaguchi, A., Pospelova, V., Ellegaard, M., Matsuoka, K., 2015. Cyst-theca relationship of a new dinoflagellate with a spiny round brown cyst, *Protoperidinium lewisiae* sp. nov., and its comparison to the cyst of *Oblea acanthocysta*. Phycological Research 63, 110-124.

Mertens, K.N., Gu, H.F., Takano, Y., Price, A.M., Pospelova, V., Bogus, K., Versteegh, G.J.M., Marret, F., Turner, R.E., Rabalais, N.N., Matsuoka, K., 2017a. The cyst-theca relationship of the dinoflagellate cyst *Trinovantedinium* *pallidifulvum*, with erection of *Protoperidinium* *lousianensis* sp nov and their phylogenetic position within the Conica group. Palynology 41, 183-202.

Mertens, K.N., Takano, Y., Gu, H., Bagheri, S., Pospelova, V., Pieńkowski, A.J., Leroy, S., Matsuoka, K., 2017b. Cyst-theca relationship and phylogenetic position of *Impagidinium caspienense* incubated from Caspian Sea surface sediments: relation to *Gonyaulax baltica* and evidence for heterospory within gonyaulacoid dinoflagellates. Journal of Eukaryotic Microbiology 64(6): 829-841.

Montresor, M., Procaccini, G., Stoecker, D.K., 1999. *Polarella glacialis*, gen. nov., sp. nov. (Dinophyceae): Suessiaceae are still alive! Journal of Phycology 35, 186-197.

Montresor, M., Lovejoy, C., Orsini, L., Procaccini, G., Roy, S., 2003. Bipolar distribution of the cyst-forming dinoflagellate *Polarella glacialis*. Polar Bio. 26, 186-194.

Mudie, P.J., 1992. Circum-arctic Quaternary and Neogene marine palynofloras: paleoecology and statistical analysis, in: Head, M.J., Wrenn, J.H. (Eds.), Neogene and Quaternary Dinoflagellate Cysts and Acritarchs. American Association of Stratigraphic Palynologists Foundation, Dallas, pp. 347-390.

Mudie, P.J., de Vernal, A., Head, M.J., 1990. Neogene to recent Palynostratigraphy of circum-Arctic basins: results of ODP leg 104, Norwegian Seam, leg 105, Baffin Bay, and DSDP site 611, Irminger Sea, in: Bleil, U., Thiede, J. (Ed.), Geological history of the Polar Oceans: Arctic versus Antarctic. Kluwer Academic Publishers, pp. 609-646.

Mudie, P.J., Harland, R., 1996. Aquatic Quaternary, in: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologist Foundation, Salt Lake City, pp. 843-878.

Mudie, P.J., Rochon, A., Aksu, A.E., Gillespie, H., 2002. Dinoflagellate cysts, freshwater algae and fungal spores as salinity indicators in Late Quaternary cores from Marmara and Black seas. Marine Geology 190, 203-231.

Mudie, P.J., Marret, F., Mertens, K.N., Shumilovskikh, L., Leroy, S.A.G., 2017. Atlas of modern dinoflagellate cyst distributions in the Black Sea Corridor: from Aegean to Aral Seas, including Marmara, Black, Azov and Caspian Seas. Marine Microplaeontology 134, 1-152.

Okolodkov, Y.B., Dodge, J.D, 1996. Biodiversity and biogeography of planktonic dinoflagellates in the Arctic Ocean. Journal of Experimental Marine Biology and Ecology 202,19-27.

Okolodkov, Y.B., 1999. Species range types of recent marine dinoflagellates recorded from the Arctic. Grana 38, 162-169.

Orlova, T.Y., Morozova, T.V., 2013. Dinoflagellate cysts in recent marine sediments of the western coast of the Bering Sea. Russian Journal of Marine Biology 39, 15-29.

Pieńkowski, A.J., Marret, F., Scourse, J.D., Thomas, D.N., 2013. Organic-walled microfossils from the north-west Weddell Sea, Antarctica: records from surface sediments after the collapse of the Larsen-A and Prince Gustav Channel ice shelves. Antarctic Science 25, 565-574.

Polyakov, I.V., Pnyushkov, A.V., Timokhov, L.A., 2012. Warming of the Intermediate Atlantic Water of the Arctic Ocean in the 2000s. Journal of Climate 25, 8362-8370.

Pospelova, V., de Vernal, A., Pedersen, T.F., 2008. Distribution of dinoflagellate cysts in surface sediments from the northeastern Pacific Ocean (43-25°N) in relation to sea-surface temperature, salinity, productivity and coastal upwelling. Marine Micropaleontology 68, 21-48.

Pospelova, V., Kim, S.J., 2010. Dinoflagellate cysts in recent estuarine sediments from aquaculture sites of southern South Korea. Marine Micropaleontology 76, 37-51.

Potvin, E., Kim, S.Y., Yang, E.J., Head, M.J., Kim, H.C., Nam, S.I., Yim, J.H., Kang, S.H., 2018. Islandinium minutum subsp barbatum subsp nov (Dinoflagellata), a New Organic-Walled Dinoflagellate Cyst from the Western Arctic: Morphology, Phylogenetic Position Based on SSU rDNA and LSU rDNA, and Distribution. J Eukaryot Microbiol 65, 750-772.Prebble, J.G., Crouch, E.M., Carter, L., Cortese, G., Bostock, H., Neil, H., 2013. An expanded modern dinoflagellate cyst dataset for the Southwest Pacific and Southern Hemisphere with environmental associations. Marine Micropaleontology 101, 33-48.

Price, A.M., and Pospelova, V. 2011. High-resolution sediment trap study of organic-walled dinoflagellate cyst production and biogenic silica flux in Saanich Inlet (BC, Canada). Marine Micropaleontology 80, 18-43.

Price, A.M., Pospelova, V., Coffin, M.R.S., Latimer, J.S., Chmura, G.L., 2016. Biogeography of dinoflagellate cysts in northwest Atlantic estuaries. Ecology and Evolution 6, 5648-5662.

Price, A.M., Coffin, M.R.S., Pospelova, V., Latimer, J.S., Chmura, G.L., 2017a. Effect of nutrient pollution on dinoflagellate cyst assemblages across estuaries of the NW Atlantic. Marine Pollution Bulletin 121, 339-351.

Price, A.M., Baustian, M.M., Turner, E., Rabalais N. , Chmura , G.L., 2017b. *Melitasphaeridium choanophorum* – a living fossil dinoflagellate cyst in the Gulf of Mexico, Palynology, 41:3, 351-358,

Price, A.M., Baustian, M.M., Turner, R.E., Rabalais, N.N., Chmura, G.L., 2018. Dinoflagellate cysts track eutrophication in the Northern Gulf of Mexico. Estuaries and Coasts 41, 1322-1336.

Radi, T., Pospelova, V., de Vernal, A., Barrie, J.V., 2007. Dinoflagellate cysts as indicators of water quality and productivity in British Columbia estuarine environments. Marine Micropaleontology 62, 269-297.

Richards, K., van Baak, C.G.C., Athersuch, J., Hoyle, T.M., Stoica, M., Austin, W.E.N., Cage, A.G., Wonders, A.A.H., Marret, F., Pinnington, C.A., 2018. Palynology and micropalaeontology of the Pliocene - Pleistocene transition in outcrop from the western Caspian Sea, Azerbaijan: Potential links with the Mediterranean, Black Sea and the Arctic Ocean? Palaeogeography Palaeoclimatology Palaeoecology 511, 119-143.

Rochon, A., de Vernal, A., Turon, J.-L., Matthiessen, J., Head, M.J., 1999. Distribution of dinoflagellate cyst assemblages in surface sediments from the North Atlantic Ocean and adjacent basins and quantitative reconstructions of sea-surface parameters. American Association of Stratigraphic Palynologists, Dallas.

Shin, H.H., Yoon, Y.H., Kim, Y.O., Matsuoka, K., 2011. Dinoflagellate Cysts in Surface Sediments from Southern Coast of Korea. Estuaries and Coasts 34, 712-725.

Shin, H.H., Lim, D., Park, S.Y., Heo, S., Kim, S.Y., 2013. Distribution of dinoflagellate cysts in Yellow Sea sediments. Acta Oceanologica Sinica 32, 91-98.

Spilling, K., Kremp, A., Tamelander, T., 2006. Vertical distribution and cyst production of *Peridiniella catenata* (Dinophyceae) during a spring bloom in the Baltic Sea. Journal of Plankton Research 28(7), 659–665.

Stoecker, D.K., Gustafson, D.E., Black, M.M.D., Baier, C.T., 1998. Population dynamics of microalgae in the upper land-fast sea ice at a snow-free location. J. Phycol. 34, 60-69.

Turon, J.L., 1984. Le palynoplancton dans l'environnement actuel de l'Atlantique Nord-Oriental. Evolution climatique et hydrologique depuis le dernier maxrimum glaciaire. Mémoires de l'Institut de Géologie du Bassin d'Aquitaine 17, 313 p.

Uddandam, P.R., Prasad, V., Rai, J., 2017. Dinoflagellate cyst distribution in sediments of western Bay of Bengal: Role of sea surface conditions. Palaeogeography, Palaeoclimatology, Palaeoecology 483, 31-48.

Verleye, T.J., Louwye, S., 2010. Recent geographical distribution of organic-walled dinoflagellate cysts in the southeast Pacific (25-53 degrees S) and their relation to the prevailing hydrographical conditions. Palaeogeography Palaeoclimatology Palaeoecology 298, 319-340.

Wall, D., Dale, B., Lohmann, G.P., Smith, W.K., 1977. The environmental and climatic distribution of dinoflagellate cysts in the North and South Atlantic Oceans and adjacent seas. Marine Micropaleontology 2, 121-200.

Wang., N., Mertens, K.N., Krock, B., Luo., Z., Derrien, A., Pospelova, V., Liang, Y., Bilien, G., Smith, K.F., De Schepper, S., Wietkamp, S., Tillmann, U., Gu, H., 2019. Cryptic speciation in *Protoceratium reticulatum* (Dinophyceae): evidence from morphological, molecular and ecophysiological data. Harmful Algae.

Williams, D.B., 1971. The occurence of dinoflagellates in marine sediments, In: The Micropalaeontology of Oceans: Proceedings of the Symposium Held in Cambridge from 10 to 17 September 1967 Under the Title 'Micropalaeontology of Marine Bottom Sediments'. Cambridge University Press, p.91-96.

Williams, D.B., Fensome, R.A., MacRae, R.A., 2017. The Lentin and Williams index of fossil dinoflagellates 2017 edition. AASP Contribution Series Nº48.

Williams, G.L., Bujak, J.P., 1977. Distribution patterns of some North-Atlantic Cenozoic dinoflagellate cysts. Marine Micropaleontology 2, 223-233.

Zheng, S.X., Wang, G.Z., Lin, S.J., 2012. Heat shock effects and population survival in the polar dinoflagellate *Polarella glacialis*. Journal of Experimental Marine Biology and Ecology 438, 100-108.

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

Zonneveld, K.A.F., Pospelova, V., 2015. A determination key for modern dinoflagellate cysts. Palynology 39, 387-409.

Zonneveld, K.A.F., Gray, D.D., Kuhn, G., Versteegh, G.J.M., 2019. Postdepositional aerobic and anaerobic particulate organic matter degradation succession reflected by dinoflagellate cysts: The Madeira Abyssal Plain revisited. Marine Geology 408, 87-109.

**Figure Captions**

Figure 1: Location of modern dinoflagellate cyst assemblages compiled from all available datasets.

Figure 2: Latitudinal variation in modern dinocyst relative abundance. 2a. Most abundant and common species. 2b. Uncommon species. Relative abundance for each species was averaged in a 2.5-degree latitudinal band. Number of taxa (diversity) is plotted against a 2.5 degree latitudinal band. Bipolar species are coloured in purple, Southern Ocean species, in light blue.

Figure 3: Longitudinal distribution of dinocyst taxa found above 65ºN. Relative abundance for each taxon was averaged in a 2.5-degree longitudinal band. Number of taxa (diversity) is plotted against a 2.5 degree longitudinal band.

Figure 4: Longitudinal distribution of dinocyst taxa found below 65ºN. Relative abundance for each taxon was averaged in a 2.5-degree longitudinal band. Number of taxa (diversity) is plotted against a 2.5 degree longitudinal band. Colour bands highlight the Pacific Ocean (blue), Atlantic Ocean (green) and Indian Ocean (orange).

Figure 5: Longitudinal distribution of dinocyst taxa found from the Marmara Sea to the Aral Sea. Relative abundance for each taxon was averaged in a 2.5-degree longitudinal band. Number of taxa (diversity) is plotted against a 2.5 degree longitudinal band. Colour band highlights the Caspian and Aral seas.

**Table caption**

Table 1: Location of datasets used for this compilation with type of data and references.

Table 2: List of dinoflagellate cyst species (with code name used for the metadata in supplementary material) with motile stage name included in this compilation and/or observed in surface sediments from studies listed in Table 1. T is for Trophic habit, with P including phototrophic and autotrophic species, H for heterotrophic species and M for mixotrophic. P+ includes species known to be phagotrophic.