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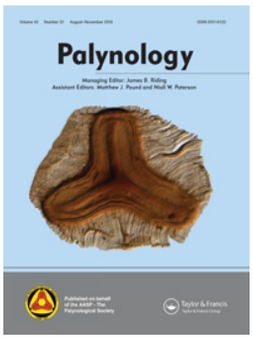

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Distribution and (palaeo)ecological affinities of the main *Spiniferites* taxa in the mid-high latitudes of the Northern Hemisphere

Anne de Vernal[a], Frédérique Eynaud[b], Maryse Henry[a], Audrey Limoges[c]*, Laurent Londeix[b], Jens Matthiessen[d], Fabienne Marret[e], Vera Pospelova[f], Taoufik Radi[a], André Rochon[g], Nicolas Van Nieuwenhove[c,h]* and Sébastien Zaragosi[b]

[a]Geotop Université du Québec à Montréal, Montréal, Canada; [b]Université de Bordeaux, UMR 5805 EPOC, Pessac cedex, France; [c]Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark; [d]Alfred Wegener Institute, Bremerhaven, Germany; [e]School of Environmental Sciences, University of Liverpool, Liverpool, UK; [f]School of Earth and Ocean Sciences, University of Victoria, Victoria, Canada; [g]Institut des sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski, Rimouski, Canada; [h]Department of Geoscience, Aarhus University, Aarhus, Denmark

ABSTRACT

In marine sediments of late Cenozoic age, *Spiniferites* is a very common genus of dinoflagellate cysts (dinocysts). Despite some taxonomical ambiguities due to large range of morphological variations within given species and convergent morphologies between different species, the establishment of an operational taxonomy permitted to develop a standardized modern database of dinocysts for the mid-high latitudes of the Northern Hemisphere. In the database that includes 1490 surface sediment samples, *Spiniferites mirabilis-hyperacanthus, Spiniferites ramosus* and *Spiniferites elongatus* were counted in addition to *Spiniferites belerius*, *Spiniferites bentorii*, *Spiniferites bulloideus*, *Spiniferites delicatus*, *Spiniferites lazus* and *Spiniferites membranaceus*. Among these taxa, *Spiniferites mirabilis-hyperacanthus*, *Spiniferites ramosus*, and *Spiniferites elongatus* are easy to identify and are particularly common. *Spiniferites bentorii* and *Spiniferites delicatus* also are morphologically distinct and occur in relatively high percentages in many samples. *Spiniferites lazus* and *Spiniferites membranaceus* also bear distinctive features, but occur only in a few samples. The identification of other taxa (*Spiniferites belerius*, *Spiniferites bulloideus,* notably) may be equivocal and their reported distribution has to be used with caution. The spatial distribution of *Spiniferites* species, with emphasis on the five most common taxa, is documented here with reference to hydrography (salinity and temperature in winter and summer, sea ice cover), primary productivity and geographical setting (bathymetry, distance to the coastline). The results demonstrate distinct ecological affinities for *Spiniferites elongatus,* which has an Arctic-subarctic distribution and appears abundant in low productivity environments characterized by winter sea ice and large temperature contrast between winter and summer. *Spiniferites mirabilis-hyperacanthus*, which occurs in warm temperate water sites, is more abundant in high salinity environments. It shares its environmental domain with *Spiniferites bentorii*, which appears to have a narrower distribution towards the warm and high salinity end of the *Spiniferites mirabilis-hyperacanthus* distribution. In contrast, *Spiniferites delicatus*, which occurs in warm-temperate to tropical environments, shows preference for relatively low salinity and low seasonal contrasts of temperature. *Spiniferites ramosus* exhibits a particularly wide distribution that overlaps both cold and warm *Spiniferites* taxa. Its cosmopolitan occurrence and its long-ranging biostratigraphical distribution suggest a high plasticity of the species and/or co-occurrence of several cryptic species. Hence, whereas *Spiniferites elongatus* and *Spiniferites mirabilis-hyperacanthus* are useful palaeoecological indicators despite their large morphological variability, *Spiniferites ramosus* is a taxon with an unconstrained ecological significance.

KEYWORDS
Dinocysts; Quaternary; palaeoceanography; temperature; salinity; sea-ice; productivity

1. Introduction

Spiniferites Mantell 1850 is a very common dinoflagellate cyst (dinocyst) genus in Mesozoic and Cenozoic sediments of the world oceans. More than one hundred species have been formally described and more than twenty of them were reported from Quaternary deposits (Williams et al. 2017; Londeix et al. 2018; Mertens et al. 2018). However, whereas *Spiniferites* is one of the most common genera of recent and past dinocyst populations, its use in palaeoecology and palaeoclimatology is not straightforward due to difficulties encountered for identification to species level. These difficulties arise from large morphological variations that characterize many species and/or morphological convergence between different species. Hence, the assignment of *Spiniferites* taxa to a given species from routine observation in optical microscopy is sometimes subjective and many

CONTACT Anne de Vernal devernal.anne@uqam.ca
*Present address: Department of Earth Sciences, University of New Brunswick, 2 Bailey Drive, Fredericton, NB E3B 5A3, Canada.

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Table 1. List of *Spiniferites* taxa in the reference modern database of the Northern Hemisphere (n = 1490) that are used here for statistical purpose, with summary information about their occurrence.

Name	Number of sites (nb)	Maximum %	nb > 0.5%	nb > 1%	nb > 10%
Spiniferites belerius	91	4.9	62	46	0
Spiniferites bentorii	89	10.8	71	58	2
Spiniferites bulloideus	108	6.3	56	40	0
Spiniferites delicatus	157	57.8	104	76	14
Spiniferites elongatus	1038	48.0	907	746	60
Spiniferites lazus	52	2.2	22	8	0
Spiniferites membranaceus	73	23.4	42	24	5
Spiniferites mirabilis-hyperacanthus	396	77.0	289	208	87
spiniferites pachydermus	1	0.3	0	0	0
Spiniferites ramosus	938	40.4	808	635	66
Spiniferites spp.	912	23.9	698	483	35
Spiniferites spp. granular	55	5.7	42	32	0

Table 2. Morphological features used to distinguish the main *Spiniferites* taxa in the reference database.

Central body		Processes		Sutural crests	Species
Proximo-chorate cysts with sutural processes	Pear-shaped with apical boss	Occasionnal intergonal		Low	*S. bentorii*
	Sphaerical to Subsphaerical or Ovoidal	Abundant intergonal		Low, but broad antapical flange with intergonal processes	*S. mirabilis*
				Low	*S. hyperacanthus*
		Occasionnal intergonal		Moderate, and well developed between gonal antapical processes	*S. membranaceus*
		Rare intergonal	Irregular processes	Septa developed mostly on the hypocyst	*S. belerius*
		Gonal only	Processes membranous with petaloid tips	High sutural crests	*S. delicatus*
			Process base large and fenestrate	Moderate sutural crests	*S. lazus*
			Processes short to long well defined terminal furcations	Moderate sutural crests	*S. bulloideus* *S. ramosus*
	Elongate	Gonal only	Processes shorter in cingular area	Sutural septa well developed at the apex and antapex	*S. elongatus*

researchers present their results after grouping specimens of *Spiniferites* at genus level. In order to deal with this issue, we developed an "operational taxonomy" with the aim to establishing standardized databases. The operational taxonomy is based on the definition of visually explicit taxa categories used for identification during routine observation and counting of dinocysts in optical microscopy under transmitted light at magnification of 400X to 1000X (Rochon et al. 1999; de Vernal et al. 1997, 2001, 2005, 2013; Bonnet et al. 2012). It thus requires morphological features clearly recognisable under optical microscope. In many cases, it results in the grouping of taxa that visually constitute a morphological continuum. The use of an operational taxonomy is a compromise. However, it is useful for systematic counts undertaken with the aim of statistical population analyses and quantitative palaeoecological studies, including the application of transfer functions or modern analogue techniques (Guiot & de Vernal 2007).

Here, we examine the distribution of the main *Spiniferites* taxa occurring in surface sediments of the Northern Hemisphere as reported in the most recent standardized dinocyst database (de Vernal et al. 2013). We first provide an overview of the operational taxonomy used to develop the database including the *Spiniferites* taxa and we report on the spatial distribution of the taxa and their relationships with sea-surface temperature and salinity, in both winter and summer, sea ice cover, primary productivity, bathymetry and distance to the coast. The objective of this work is to assess the ecological significance and usefulness of the main taxa in spite of taxonomical uncertainties and, therefore, to provide clues for a sound use of *Spiniferites* in qualitative and/or quantitative palaeoecological, palaeoceanographical and palaeoclimatic investigations.

2. Material and methods

2.1. The dinocyst data and the taxonomical status of spiniferites *taxa*

The standardized dinocyst database of the Northern Hemisphere was first developed in the 1990s with the aim to make transfer functions and/or to apply modern analogue techniques for quantitative palaeoceanographical reconstructions. The earliest works using the proto-database, which included mainly samples from the northwest North Atlantic and adjacent seas, were published in de Vernal et al. (1992a, 1993). Following this pioneering work, the enlargement of the database with samples from the Norwegian Sea was undertaken by adopting a systematic approach with regard to standardized palynological preparation techniques, implying treatments with warm hydrofluoric and hydrochloric acids but no oxidation, and sieving at 10 μm. The database

was developed using an operational taxonomy established after several workshops and reported in Rochon et al. (1999). Updates of the database using the same taxonomy were published using the studies by Radi & de Vernal (2004, 2008), Radi et al. (2007), Pospelova et al. (2008), Vasquez-Bedoya et al. (2008), Limoges et al. (2010) and Bonnet et al. (2012). Despite enlargement of the geographic coverage and taxonomic refinements, the list of *Spiniferites* taxa has remained the same since the initial versions of the reference database. In the last published update of the database, a total of 66 dinocyst taxa were reported including 12 *Spiniferites* taxa after grouping (de Vernal et al. 2013). The same database was used here with the exception of two sites and the grouping was not exactly the same. Hence, the data set reported in this manuscript comprises 1490 sites with counts for 67 taxa, including 12 *Spiniferites* categories. (Table 1) The entire data set is available online on the Geotop website (www.geotop.ca).

The general identification criteria for *Spiniferites* cysts distinguish light transparent specimens with a rounded to elongate body, where a Gonyaulacoid tabulation is distinct due to developed sutural ridges and numerous surrounding multifurcate processes in gonal and sometimes in intergonal position. Among these taxa, some have a morphology that permits unquestionable identification whereas others have more subtle characteristics making unequivocal assignment more uncertain, as briefly exposed below in alphabetical order of the species names (see also Table 2; Plates 1−3). More details about the taxonomical affinities of *Spiniferites* taxa and their morphological characteristics can be found in the reports published in this volume by Limoges et al., Londeix et al., Mertens et al. and Van Nieuwenhove et al.

Spiniferites belerius Reid 1974 (Plate 3) is a small cyst with an ovoidal central body and smooth surface, gonal and occasionally intergonal processes of irregular shape, and low sutural crests. *Spiniferites belerius* can bear processes of variable shapes and membranous septa between processes may develop, notably at the antapex (cf. Harland 1977; Rochon et al. 1999). The development of an antapical septum is also characteristic of *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 (see below and Plate 3). *Spiniferites belerius* and *Spiniferites membranaceus* were grouped together in an earlier version of the database (Rochon et al. 1999), but not here. Although *Spiniferites belerius* was counted as a distinct species, its morphological characteristics are a matter of discussion (Mertens et al. 2018). We cannot exclude the possibility that specimens of *Spiniferites belerius* were included in the *Spiniferites* spp. during routine counts. Therefore, caution is required when using the proportion of this taxon for quantitative purpose.

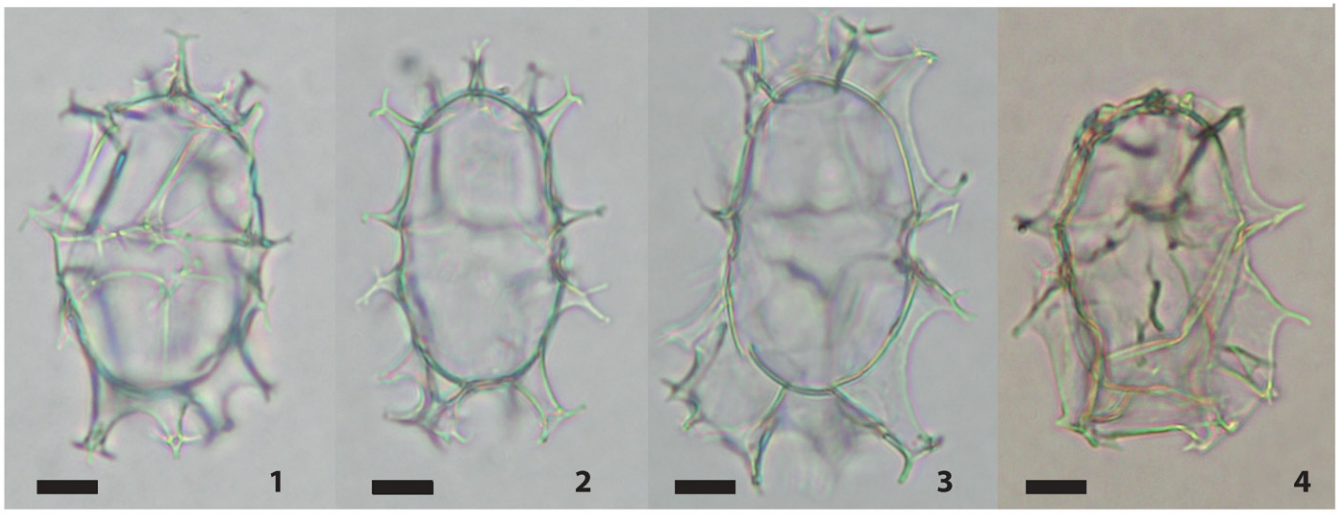
Spiniferites bentorii (Rossignol 1964) Wall & Dale 1970 (Plate 2) is easily distinguishable from other species based on its large pear-shaped central body, microgranular surface, relatively thick wall, and a pronounced apical boss (e.g. Rochon et al. 1999). Beyond these general characteristics, specimens assigned to *Spiniferites bentorii* may show morphological variations with regard to the length of processes, which are usually short, and with the shape of the processes, from conical to tapering and erect to curved (cf. Harland 1977). Moreover, intergonal processes can occur occasionally, as reported by Limoges et al. (2018).

Spiniferites bulloideus (Deflandre & Cookson 1955) Sarjeant 1970 (Plate 3) is a small sub-spherical cyst with smooth wall surface, no apical boss, low sutural crests and bearing exclusively gonal processes. *Spiniferites bulloideus* is very similar to *Spiniferites ramosus* (Ehrenberg 1837b) Mantell 1854 (see also Mertens et al. 2018 and Londeix et al. 2018). *Spiniferites bulloideus* was considered to be a junior synonym of *Spiniferites ramosus* by Harland (1977). In the reference database, *Spiniferites bulloideus* was counted independently. However, many researchers agree on the difficulty to distinguish *Spiniferites bulloideus* in routine counts and tend to group them with *Spiniferites ramosus* or *Spiniferites* spp.

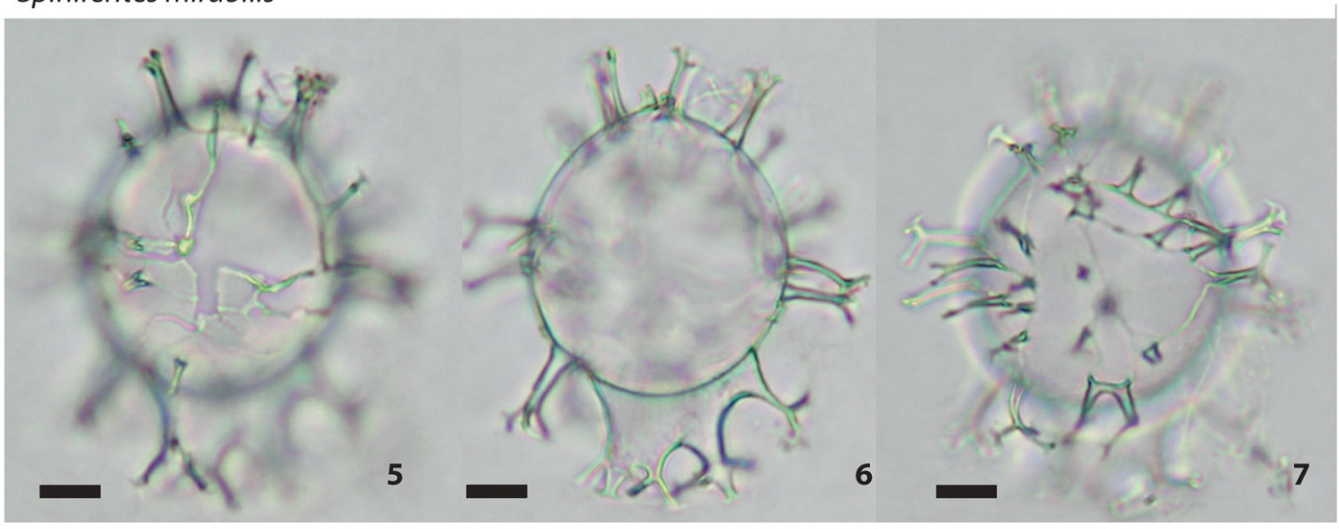
Spiniferites delicatus Reid 1974 (Plate 2) is characterized by membranous sutural crests and gonal processes with petaloid process tips. Its ovoidal central body sometimes bears a low apical boss. There are microgranulations on the outer wall layer, on the processes and sutural crests. *Spiniferites delicatus* is easy to distinguish from other *Spiniferites* taxa in the database. However, it might include *Spiniferites ristingensis* Head 2007, which is very similar (Mertens et al. 2018) and was described by Head (2007) from Eemian sediments of the Baltic Sea. *Spiniferites delicatus* was a minor component of assemblages in the early versions of the database, which included mostly cool temperate to polar North Atlantic sites (de Vernal et al. 1997; Rochon et al. 1999). In the most recent versions of the database that include samples from low latitudes (Vasquez-Bedoya et al. 2008; Limoges et al. 2010) it became an important taxon.

Spiniferites elongatus Reid 1974 (Plate 1) comprises all *Spiniferites* cysts having a conspicuously elongate cyst body and variably developed septa in the apical and antapical zones. *Spiniferites elongatus* as described by Reid (1974) has a smooth to finely microgranulate surface, exclusively gonal processes, and membranous hollow sutural septa varying in height, from low around the cingulum to high at the apex and antapex. Later observations showed that the height of sutural septa and their degree of development in these elongate *Spiniferites* cysts is very variable. At the end member, specimens with particularly extensive development of the membranous sutural septa and less prominent processes were assigned to *Spiniferites frigidus* described by Harland and Reid and/or *Rottnestia amphicavata* described by Dobell and Norris, both from recent Beaufort Sea sediments, in Harland et al. (1980). Synonymy between *Spiniferites frigidus* and *Rottnestia amphicavata* was proposed by Bujak (1984). However, in the systematic section of Rochon et al. (1999), Head recommended to maintain the species status of *Rottnestia amphicavata* arguing that it represents a distinct end member, notably because of the discrete structure of processes usually recognized only by presence of their distal furcations surmounting sutural septa in gonal position. More recently, it was suggested that both *Spiniferites frigidus* and *Rottnestia amphicavata* are junior synonyms of *Spiniferites elongatus* (Van Nieuwenhove et al. 2018). The main arguments in favor of synonymy are the

Spiniferites elongatus



Spiniferites mirabilis



Spiniferites ramosus

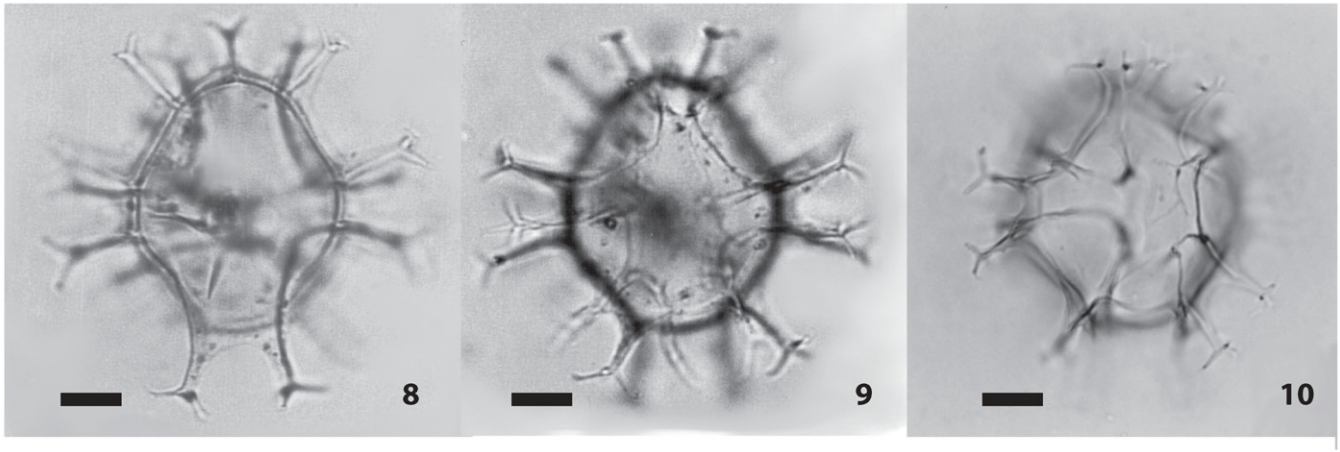


Plate 1. 1–4. Different specimens of *Spiniferites elongatus* (photos from AR, Gulf of St. Lawrence): continuum from *Spiniferites elongatus* (1) to morphotypes formerly assigned to *Spiniferites frigidus/Rottnestia amphicavata* (now *Spiniferites elongatus* – Beaufort morphotype) (4), central body length from 40 to 50 μm; 5–7. *Spiniferites mirabilis* (photos from AR, Gulf of St. Lawrence) in dorsal (5) and ventral (7) views and optical section (6), central body diameter 60 μm. 8–9. *Spiniferites ramosus* (figured in de Vernal & Mudie 1989; Labrador Sea) in dorsal (8) and ventral (9) views, central body length 40 μm. 10. *Spiniferites ramosus* (figured in Rochon et al. 1999; western North Atlantic) in ventral view, central body length 40 μm. All scale bars = 10 μm.

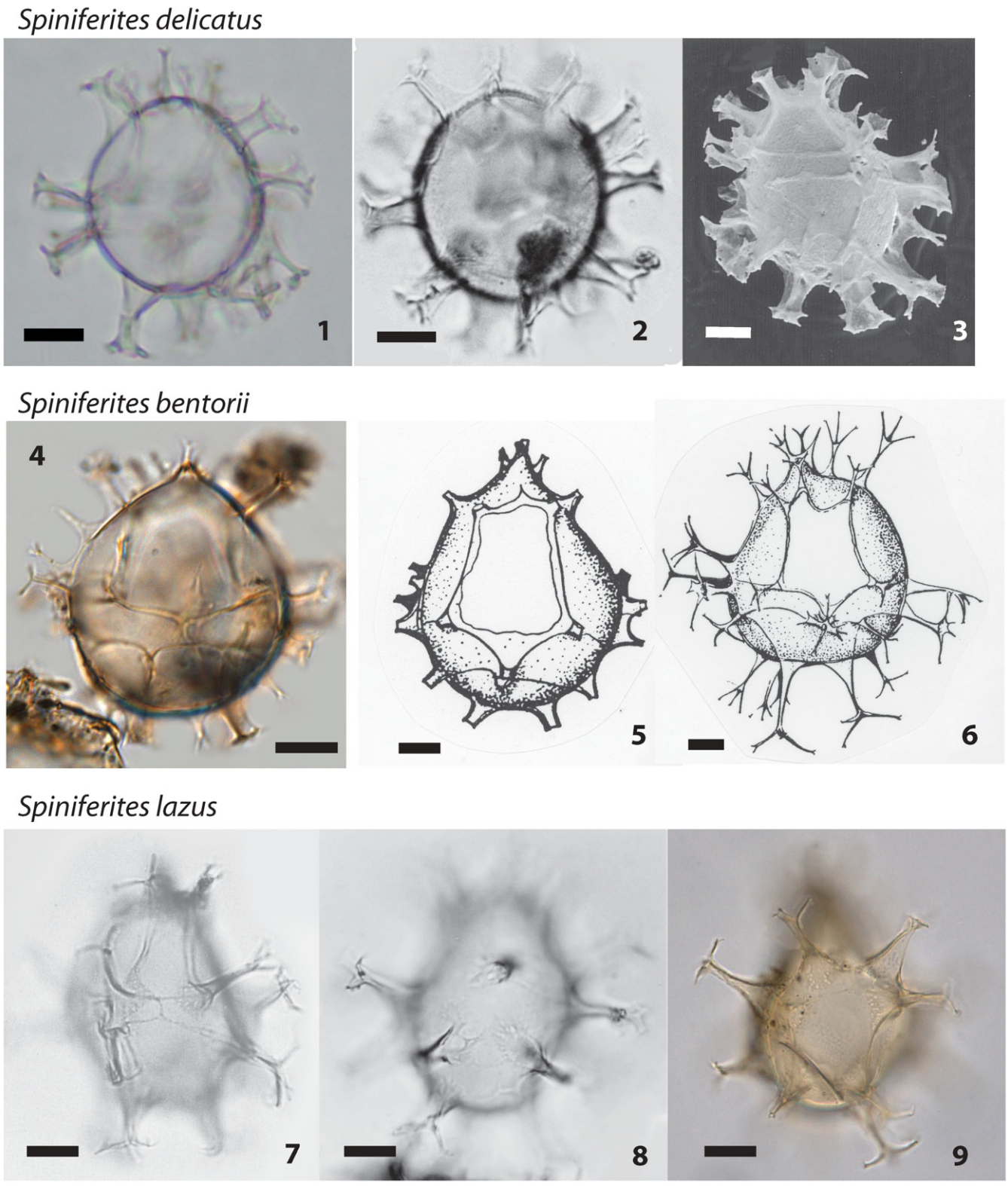


Plate 2. 1−3. Different specimens of *Spiniferites delicatus* in optical microscopy (1 Photo from AR; Gulf of St. Lawrence. 2 figured in Rochon et al. 1999; Western Mediterranean Sea) and scanning electron microscopy (3 figured in Turon & Londeix 1988; Western Mediterranean Sea), central body length 38–40 μm. 4−6. *Spiniferites bentorii* in optical microscopy (4 figured in Limoges et al. 2013; Gulf of Mexico) and original drawings (4–5) of the type species by Rossignol (1964) from the Mediterranean Sea, central body length 45 μm (4) and 60 μm (5–6). 7–9. Different specimens of *Spiniferites lazus* (7–8 figured in Rochon et al. 1999; North Sea; 9 photo from NVN, Iceland Plateau, North Atlantic Ocean), central body length 45 μm. All scale bars = 10 μm.

fact that there is a continuum between *Spiniferites elongatus* and that the morphological end-members were originally defined as *Spiniferites frigidus/Rottnestia amphicavata* without clear criteria to separate the entities for routine population counts (cf. Rochon et al. 1999; Heikkilä et al. 2014; Van Nieuwenhove et al. 2018). However, the latter

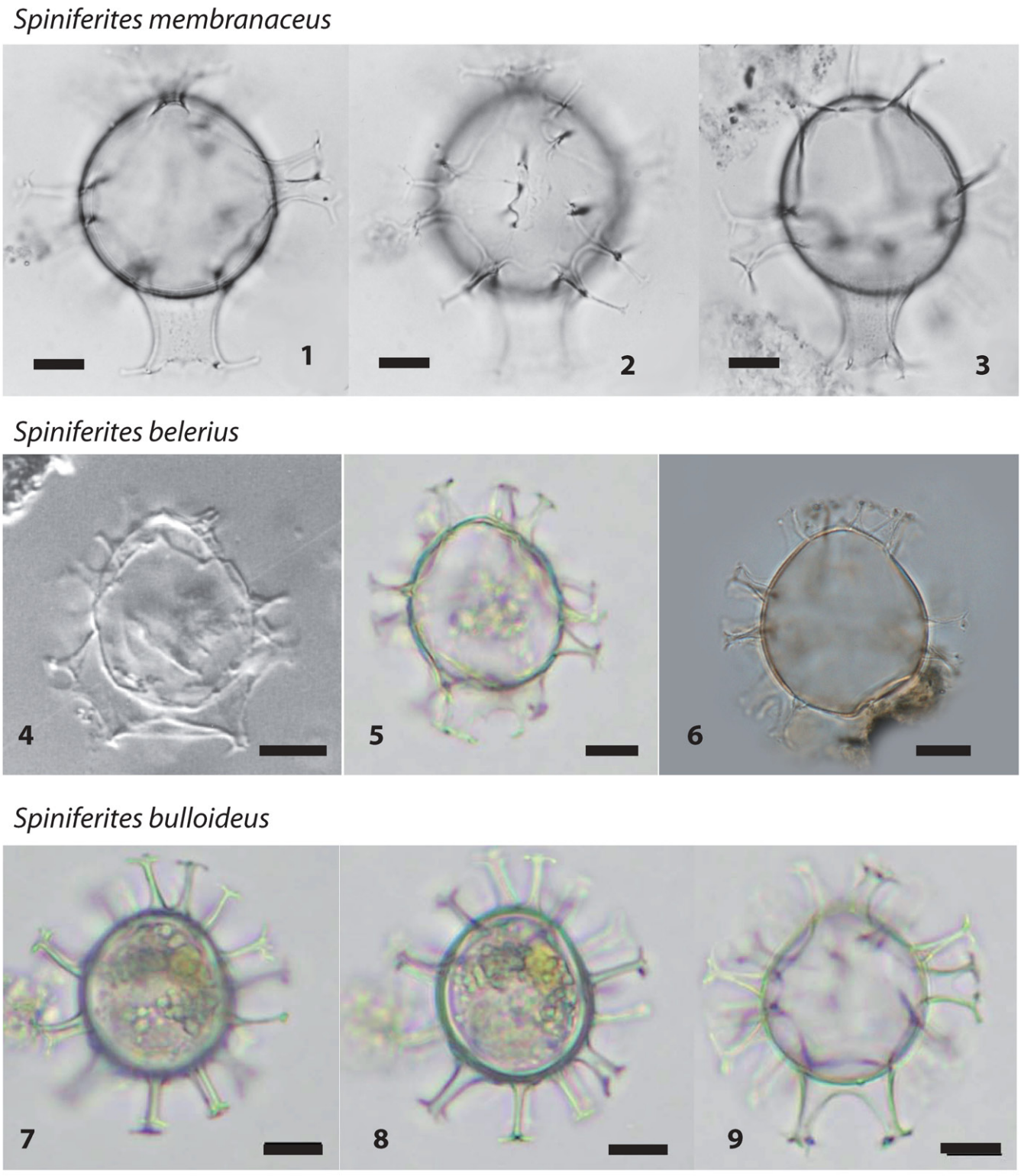
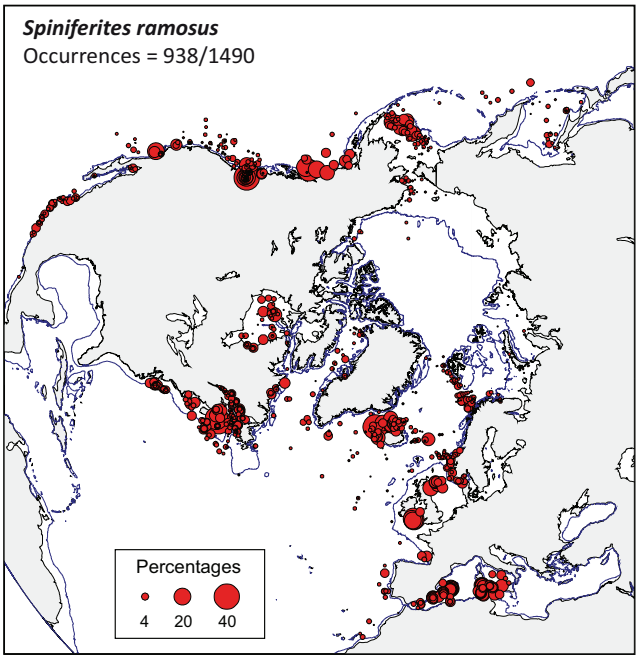


Plate 3. 1–3. *Spiniferites membranaceus* (figured in Rochon et al. 1999; North Sea), central body length 46 µm. 4–6. Different specimens of *Spiniferites belerius* in optical microscopy (4 figured in de Vernal et al. 1992b; Western Mediterranean Sea; 5 Photo from AR; Gulf of St. Lawrence; 6 Photo from VP; East China Sea). 7–9. *Spiniferites bulloideus* in optical microscopy (photos from AR; Gulf of St. Lawrence). All scale bars =10 µm.

authors introduced an informal type, *Spiniferites elongatus* – Beaufort morphotype, to refer to specimens with the extreme morphology formerly attributed to *Spiniferites frigidus* or *Rottnestia amphicavata*. Hence, all these morphologies are herein simply referred to as *Spiniferites elongatus*, corresponding to the grouping under *Spiniferites elongatus* sensu lato that has been used in most publications dealing with the Quaternary palaeoceanography of cool temperate to subarctic seas.

Spiniferites lazus Reid 1974 (Plate 2) has an ovoidal central body with microgranular to microreticulate surface, and very often a small apical boss. The processes are exclusively gonal



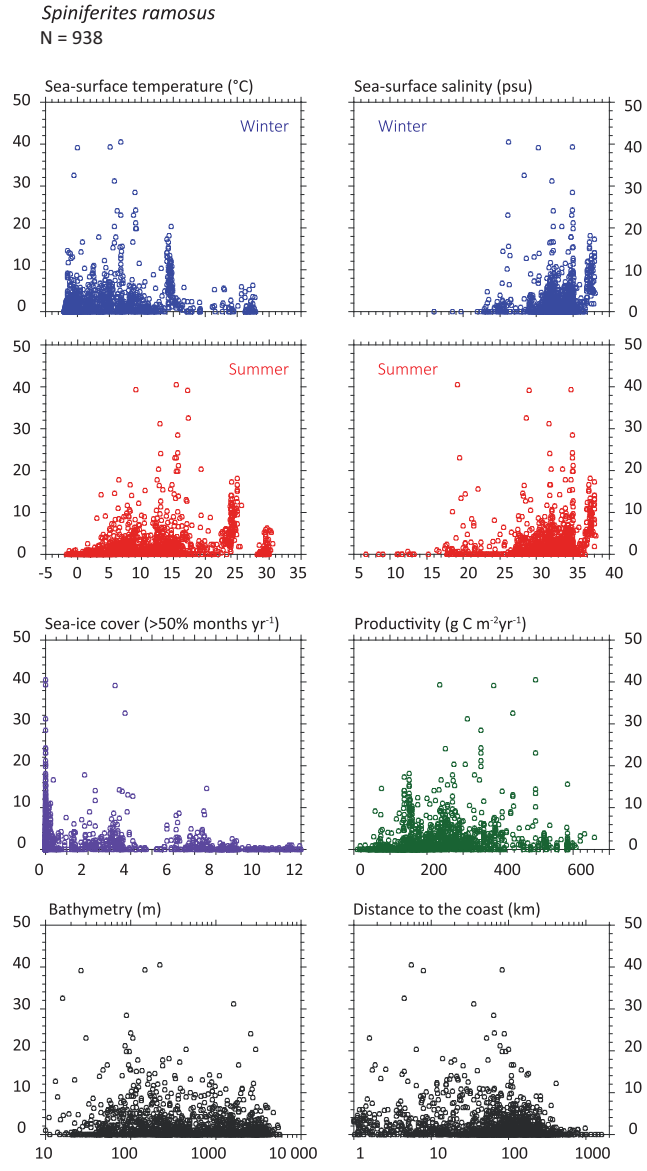


Figure 1. Distribution of *Spiniferites ramosus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

and are distally furcate with recurved bifurcate tips and the sutural crests are low. The distinctive feature of *Spiniferites lazus* is the fenestration on the expanded process bases (cf. Rochon et al. 1999). *Spiniferites lazus* is easy to distinguish, but is rarely abundant in the modern database.

Spiniferites membranaceus (Rossignol 1964) Sarjeant 1970 (Plate 3) has an ovoidal central body without apical boss. The processes are exclusively gonal and are distally furcate with recurved bifurcate tips. Sutural crests are low, except on the dorsal side of the antapex, where they form a conspicuous membrane. The well-developed antapical septa are a feature that permits distinction from *Spiniferites ramosus*.

Spiniferites mirabilis (Rossignol 1964) Sarjeant 1970 (Plate 1) is a taxon recording large morphological variations. It is typically characterized by a large spheroidal to sub-spheroidal central body, low to absent sutural crests, the presence of gonal and intergonal processes and a conspicuous flange linking gonal and intergonal processes at the antapex. Beyond this general description, *Spiniferites mirabilis* may display important variations in the ornamentation of the outer wall from smooth to densely microgranular, the development of sutural crests, the number and height of intergonal processes, including those making up the antapical flange, and the presence/absence of an antapical boss (cf. Limoges et al. 2018). With the exception of the antapical flange, the same characteristics and ranges of variations apply to *Spiniferites hyperacanthus* (Deflandre & Cookson 1955) Cookson & Eisenack 1974. Because the orientation of the cysts or folding may prevent observation of the antapical zone to see the flange, *Spiniferites mirabilis* and *Spiniferites hyperacanthus* are grouped together as *Spiniferites mirabilis-hyperacanthus*. The morphology and taxonomic affinities of *Spiniferites hyperacanthus,* which was described from Miocene deposits, are discussed with more details by Londeix et al. (2018).

Spiniferites ramosus (Ehrenberg 1837b) Mantell 1854 (Plate 1) is one of the most commonly recorded *Spiniferites* species. Under this name, there are very variable morphologies, which led to the description of many subspecies (n = 32; Williams et al. 2017). The main characteristic of the ovoid cyst is to exclusively bear gonal processes, have a smooth wall surface and no apical boss. Sutural crests are low but more developed towards the processes (cf. Rochon et al. 1999). Normally, the processes are long, often hollow at their base with distal trifurcations having bifurcate tips. However, the length of the processes is highly variable and the morphology of their distal ends is not always well expressed (e.g. Lewis et al. 1999). Moreover, there is occasional development of narrow trabeculae between adjacent process tips. In some (perhaps teratologic) cases, the trabeculae are well developed and form a network (e.g. Rochon et al. 2009), which may lead to confusion with *Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid 1974 or *Nematosphaeropsis rigida*

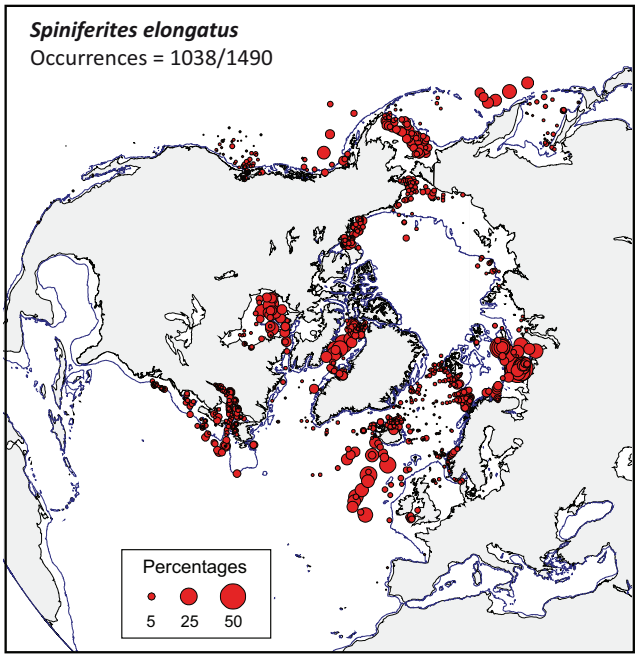


Figure 2. Distribution of *Spiniferites elongatus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

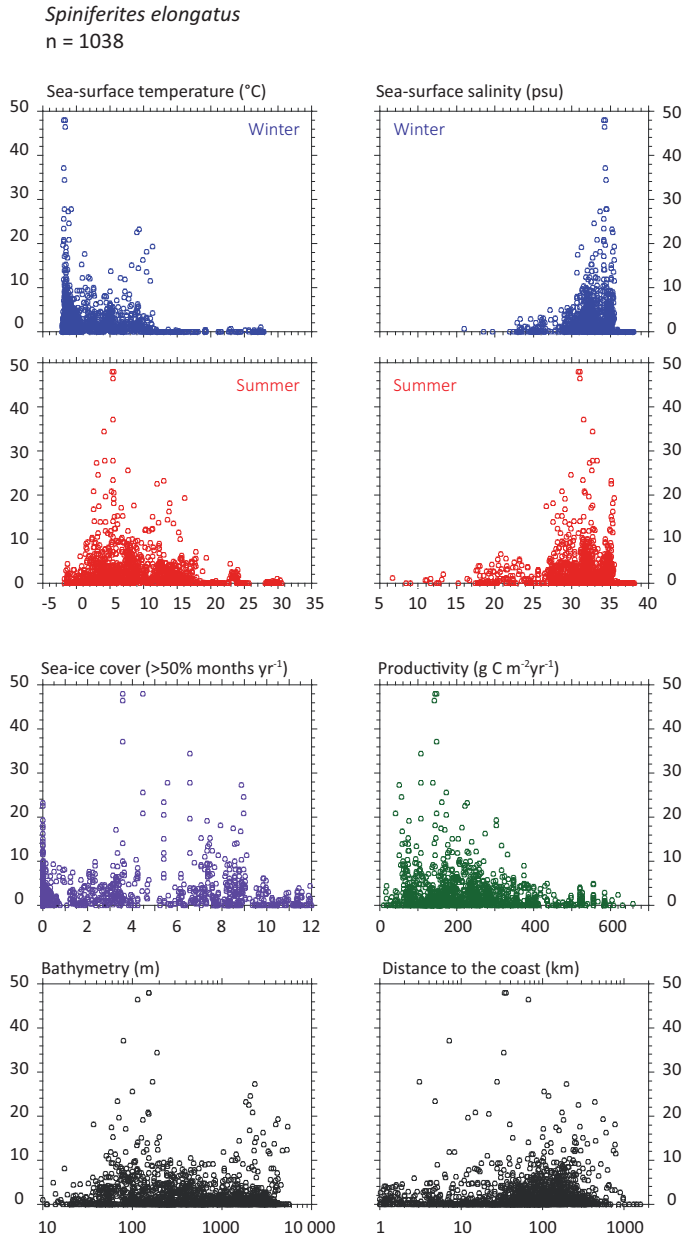


Figure 2. Continued.

Wrenn 1988. *Spiniferites bulloideus* is morphologically very similar to *Spiniferites ramosus* but it is more spherical, smaller, and more delicate in structure than the typical *Spiniferites ramosus* (Harland 1977). Hence, *Spiniferites bulloideus* has been treated as a junior synonym of *Spiniferites ramosus* (Harland 1977) and is often grouped with *Spiniferites ramosus*. In recent sediments, *Spiniferites ramosus* is one of the most commonly reported taxa of the genus, but its taxonomical identification is very lax as large morphological variations are usually accepted. For typical specimens (i.e., Plate 1, figures 8-9), we may recommend to use the name *Spiniferites ramosus* subsp. *ramosus* and to use *Spiniferites ramosus* sensu lato for other morphologies of the species, including *Spiniferites bulloideus*.

Spiniferites pachydermus (Rossignol 1964) Reid 1974 is a large (>50 µm) spherical to subspherical cyst often with a low apical boss, low sutural crests and gonal trifurcate processes, which is distinguished by a very thick (~ 3 µm) microgranulate to fibrous wall (cf. Reid 1974; cf. also Londeix et al. 2018). The diagnostic criteria of *Spiniferites pachydermus* are discussed by Mertens et al. (2018). *Spiniferites pachydermus* was reported only once in the database.

Spiniferites spp. is a category often used to group specimens of *Spiniferites* that are not identified at species level because of unsuitable orientation, folding or poor preservation, or because ambiguous characteristics make its unequivocal assignment to species level difficult. This category also corresponds to specimens belonging to undescribed species or to species occurring rarely and not yet introduced in the standardized database. Hence, *Spiniferites* spp. is a wide category without precise significance. It should not be used for ecological purpose, except as being an indicator of taxonomic diversity.

Spiniferites spp. granular is an informal name for all *Spiniferites* specimens with gonal processes and a thick (~ 1 µm) and granular outer wall. The specimens assigned to *Spiniferites* spp. granular have variable sizes and morphologies, the only common feature being the relatively thick granular wall. The nomenclature of this informal taxonomic category is questionable as discussed by Londeix et al. (2018). *Spiniferites* spp. granular is mentioned here but not used for ecological inference.

2.2. The environmental data

The surface sediment samples used to develop the dinocyst database were collected in nearshore to offshore sites and are representative of estuarine, coastal, neritic and oceanic

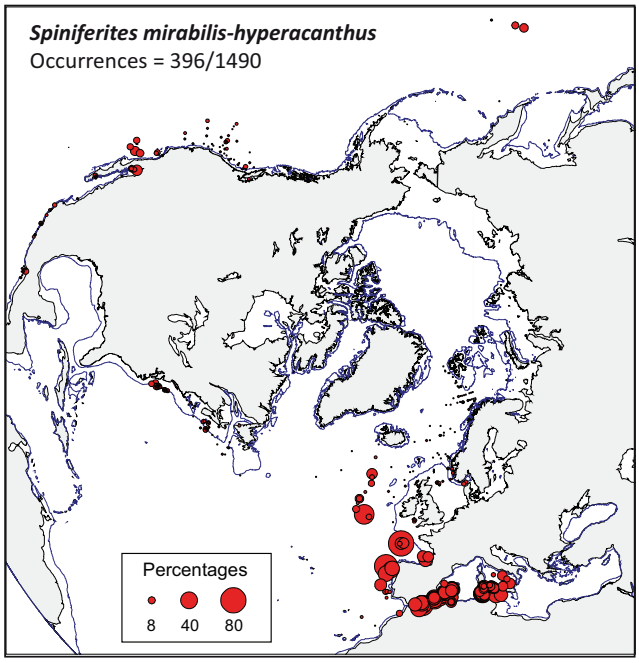
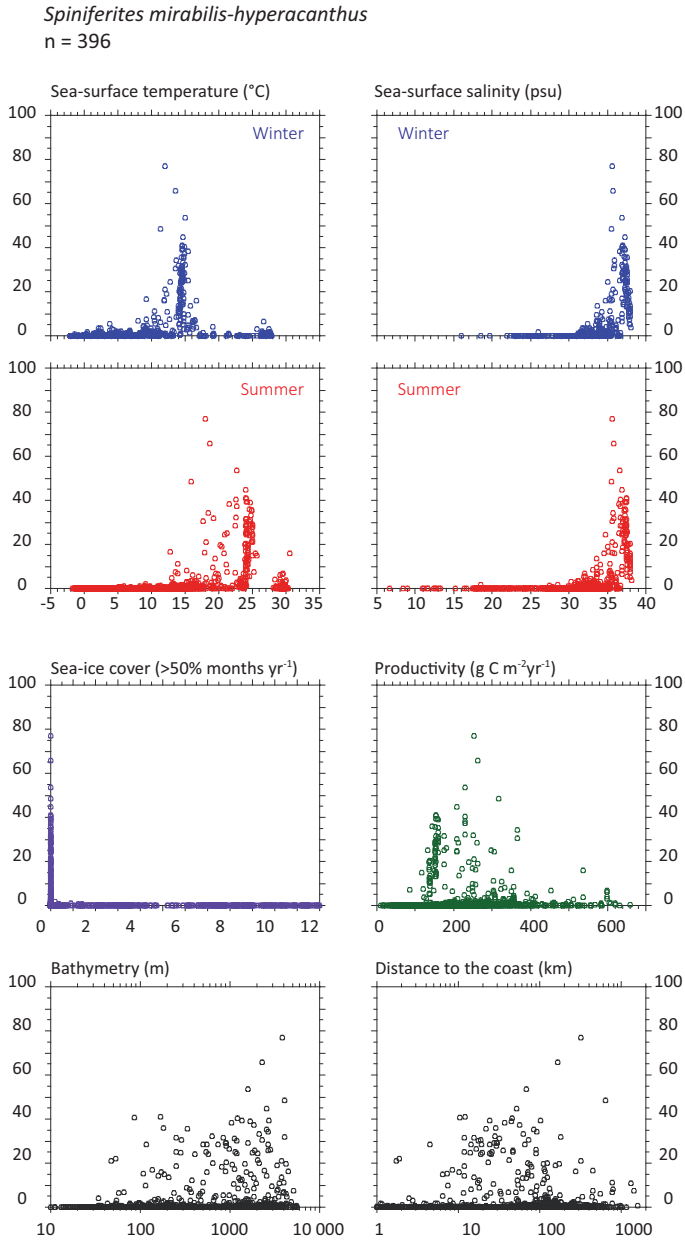


Figure 3. Distribution of *Spiniferites mirabilis-hyperacanthus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.



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conditions. The environmental data compiled here include sea-surface temperature (SST), salinity (SSS), sea ice cover and primary productivity in addition to the bathymetry and distance from the coast. Sea-surface temperature (SST) and salinity (SSS) were compiled from the 2001 version of the World Ocean Atlas (cf. Conkright et al. 2002). The mean February, August, winter (January-February-March) and summer (July−August−September) SSTs and SSSs were calculated from values collected within a radius of 30 nautical miles around each station. The sea-ice cover data were compiled on a 1x1 degree grid scale based on data spanning 1953−2003, which were provided by the National Snow and Ice Data Center (NSIDC) in Boulder. We express sea ice as the number of months per year of sea ice with concentration >50%, which correlates with the mean annual concentration (cf. de Vernal et al. 2013). The primary productivity data are from satellite observation of water properties of the oceans as calculated with the Vertical Generalized Production Model (VGPM) described by Behrenfeld & Falkowski (1997). The data used here have a spatial resolution of 4.63 km and were provided by the MODerate resolution Imaging Spectroradiometer (MODIS) program. MODIS was launched by the National Aeronautics and Space Administration (NASA) in 2000 (cf. Radi & de Vernal 2008). Primary productivity is referred as productivity for the remainder of this text. The bathymetry and the distance to the coastline were calculated mostly from the 2014 version of the General bathymetric map of the ocean (GEBCO) in addition to complementary information from the European Marine Observation and Data Network (EMODnet) and the International Bathymetric Chart of the Arctic Ocean (IBCAO) for the European margins and Arctic, respectively.

The sample sites cover a wide domain of SSTs, which range from freezing to 30.6 °C. They also cover a wide domain of SSSs, which range from 7 to 38 psu. SSS and SST of both winter and summer were considered in addition to SST and SSS of February and August, which are typically the coldest and warmest months of the year. The data set includes a large number of sites (n = 774) marked by the occurrence of sea ice for more than 0.1 monthy^{-1} and many sites are characterized by contrasted SSTs in summer and winter. The seasonal duration of sea ice, which is proportional to the mean annual concentration, is a very important parameter of the data set as it determines the life cycle of the biota (e.g., Vancoppenolle et al. 2013).

The parameters (n = 13) used for quantitative data treatments are listed in Table 3 and the corresponding values

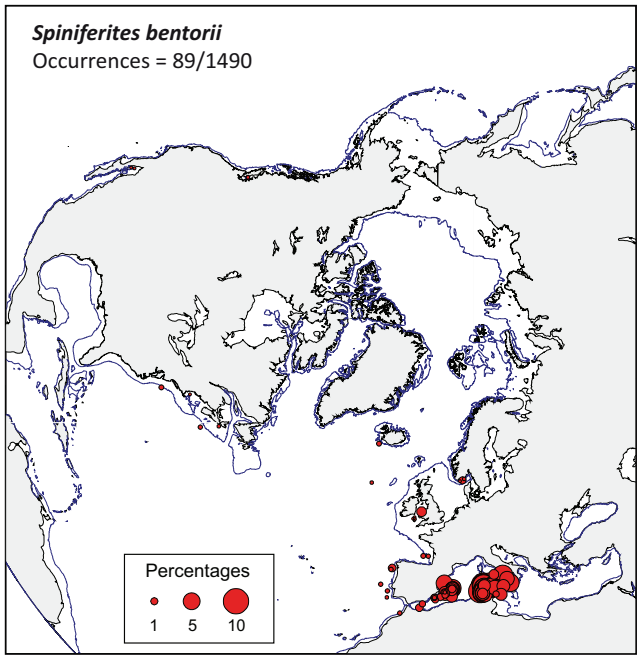

Figure 4. Distribution of *Spiniferites bentorii* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

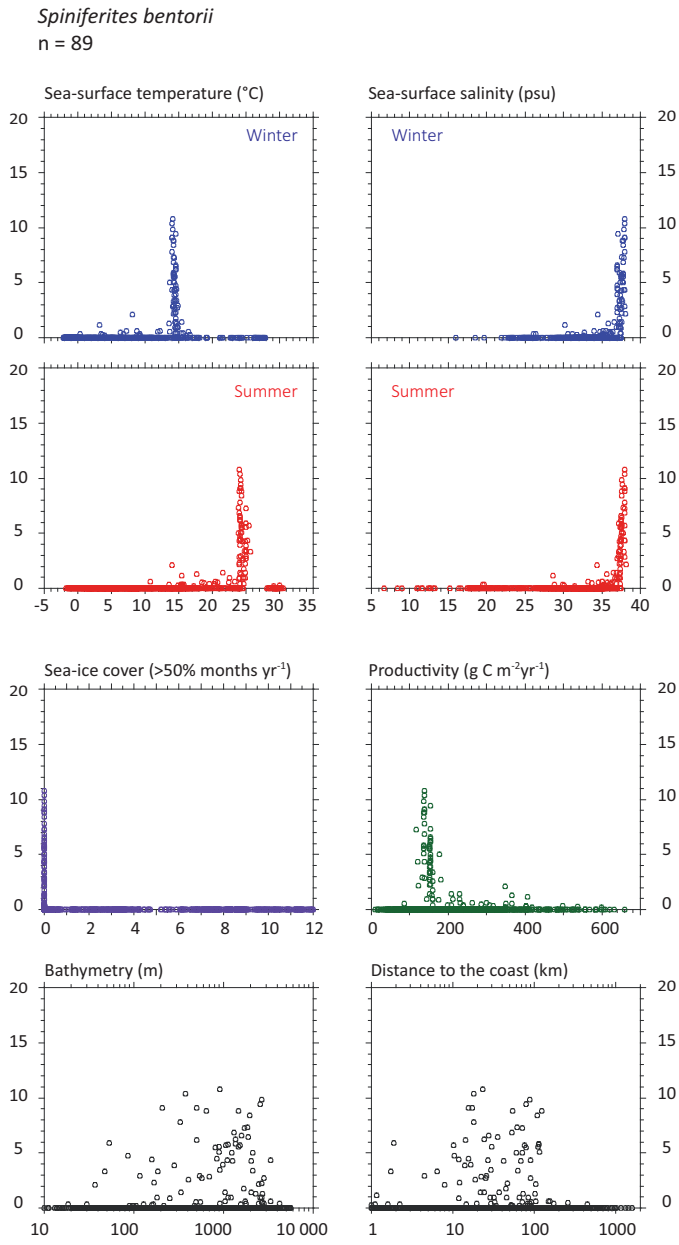

Figure 4. Continued.

at the 1490 sites can be found on the Geotop website. Among selected parameters, the hydrographic factors such as seasonal temperature and salinity in addition to sea ice cover are critical as they are used for applications in palaeoclimatology and palaeoceanography. Productivity, bathymetry and distance to the coast are important too, but more from an ecological or taphonomical point of view. There are other parameters likely playing a role on the distribution of dinoflagellates and their cysts, and they may include turbulence, water mass stratification, competition with primary producers, sedimentation rates and selective preservation of organic compounds, etc. In-between site comparison of seasonal, annual, and inter-annual *Spiniferites* cyst production in eight sediment traps from different geographic regions highlights that such parameters are not easily available or quantifiable although their importance increases in highly heterogeneous estuarine systems (Pospelova et al. 2018).

2.3. The data treatments

In the database, the average sum of dinocysts counted is 356 (minimum 60 and maximum 4012) and the total number of taxa is 67, including 12 *Spiniferites* categories (see Table 1). The relative occurrences or percentages of *Spiniferites* taxa were calculated vs. the total dinocyst count (cf. Figures 1−8). Multivariate analyses were conducted from the percentages of *Spiniferites* taxa vs. the sum of total dinocysts (Figure 9) and also vs. the sum of *Spiniferites* cysts only in order to emphasize the significance of the taxa within the *Spiniferites* group (Figure 10).

The multivariate analyses were performed with the Canoco software version 4.5 (Ter Braak & Smilauer 2002) on the taxa distribution and sea-surface conditions in the n = 1490 database after logarithmic transformation of relative percentages of dinocyst taxa. The transformation aims at giving more weight to accompanying taxa, which can be more diagnostic of environmental conditions than the dominant taxa that are often cosmopolitan (cf. for ex. de Vernal et al. 2001).

Detrended correspondence analyses (DCA) were first performed to identify the type of function between assemblages and environmental variables (cf. Ter Braak & Smilauer 2002). When taking into account the 1490 sites, 66 taxa and 13 environmental parameters, the results show that the length of the first axis (2 standard deviations) is close to 4, which

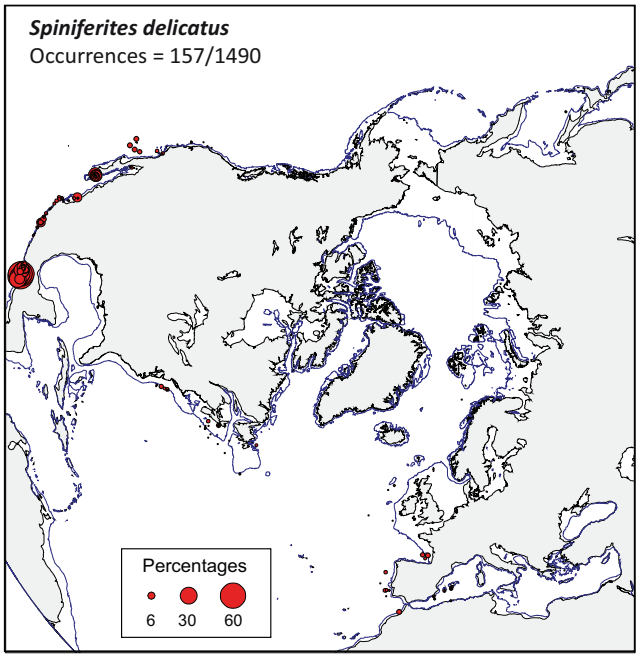

Figure 5. Distribution of *Spiniferites delicatus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

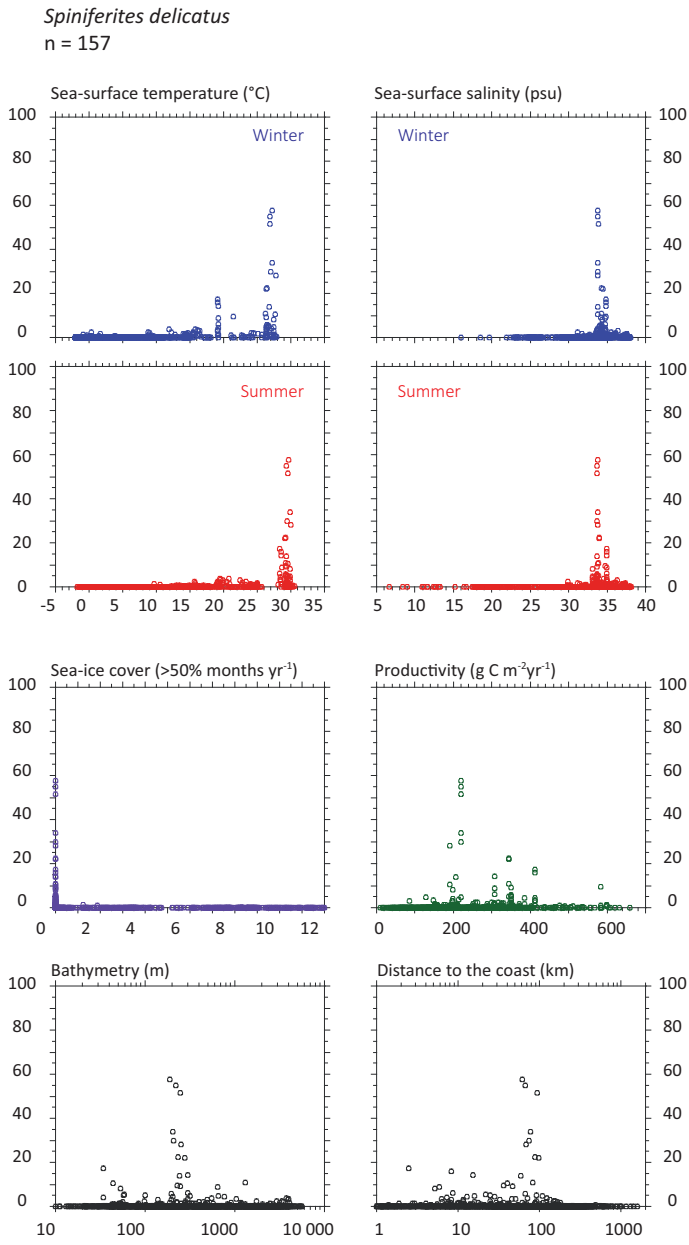

Figure 5. Continued.

suggests unimodal-type functions suitable for Canonical Correspondence Analysis (CCA) (e.g. Jongman et al. 1995). This is consistent with results obtained previously (cf. de Vernal et al. 2013).

The subset of data built from *Spiniferites*-only assemblages includes 697 sites. It corresponds to surface sediment samples in which the total share made up by *Spiniferites* species represents at least 5% of the entire dinocyst assemblages. This subset comprises the 12 *Spiniferites* taxa and 13 environmental parameters. In this case, DCA showed that the length of the first axis is lower than two, which rather corresponds to linear relationships and makes Redundancy Analysis (RDA) more appropriate (e.g. Jongman et al. 1995).

3. Results

3.1. The distribution of the main spiniferites taxa in the Northern hemisphere

The occurrence of the 12 *Spiniferites* taxa in the n = 1490 database is summarized in Table 1. Among these taxa, *Spiniferites ramosus*, *Spiniferites mirabilis-hyperacanthus* and *Spiniferites elongatus* are particularly common and *Spiniferites bentorii* and *Spiniferites delicatus* also record relatively high percentages at many sites. More importantly, these five taxa are morphologically distinct from each other, allowing routine counting with high confidence regarding their taxonomical assignment. Hence, we present herein some information on the distribution of the main modern *Spiniferites* species, with emphasis to the five taxa mentioned above, in addition to *Spiniferites membranaceus* and *Spiniferites lazus*, which are also morphologically distinct.

Spiniferites ramosus (Figure 1) - this taxon is particularly cosmopolitan and occurs in a wide range of environments with regard to SST, SSS, productivity, bathymetry and nearshore to offshore locations. However, it is rare in areas marked by very dense sea ice cover and low salinity (<20 psu).

Spiniferites elongatus (Figure 2) can occur in relatively high percentages, ranging 10−50% in subarctic seas. It is outer neritic to oceanic and tolerates extensive sea-ice cover. Its maximum occurrence is recorded where summer SST is close to 6 °C but SSS > 28 psu, and where productivity is lower than 300 gC $m^{-2}y^{-1}$. The modern distribution of *Spiniferites elongatus* as documented here from 1490 sites of the Northern Hemisphere including both Pacific and North Atlantic data does not show a bimodal pattern supporting the existence of two entities with distinct

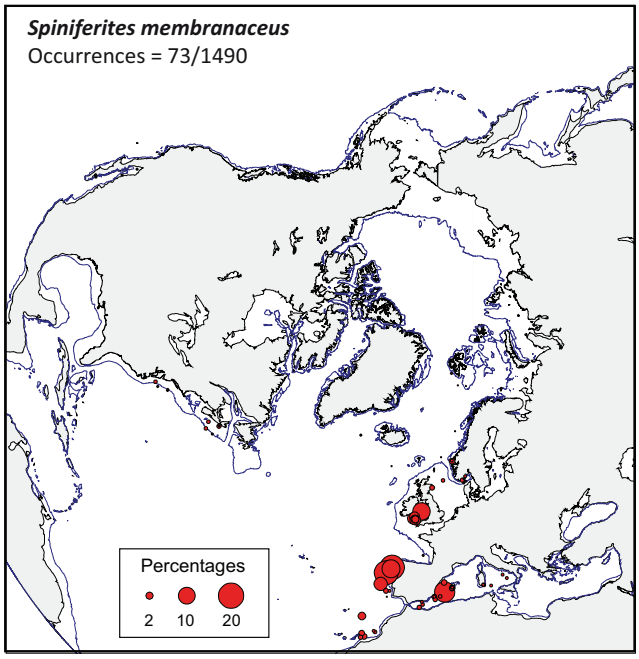

Figure 6. Distribution of *Spiniferites membranaceus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

ecological affinities, unlike what was suggested in Rochon et al. (1999).

Spiniferites mirabilis-hyperacanthus (Figure 3) occurs in low numbers in many samples but may reach very high percentages (>10% and up to 80%) in offshore areas where relatively high SSTs (10−15 °C in winter; >18 °C in summer) and SSSs (>35 psu) are recorded. It is abundant in the North Atlantic in the vicinity of the Gibraltar Strait and in the northeastern sector of the subtropical gyre.

Spiniferites bentorii (Figure 4) occurs in a small number of samples and with low percentages, rarely exceeding 10%. In the database, the maximum abundance of *Spiniferites bentorii* is recorded in the Algerian and Tyrrhenian basins of the western Mediterranean Sea where SSTs (13−15 °C in winter, 23−25 °C in summer) and SSSs (>36 psu) are high, but productivity is low (<150 gC $m^{-2}y^{-1}$).

Spiniferites delicatus (Figure 5) is a neritic taxon that gained importance in the Northern Hemisphere database with the addition of low-mid latitudes samples (e.g. Vasquez-Bedoya et al. 2008; Limoges et al. 2010). It occurs in relatively high percentages (>5%) in warm-temperate to tropical environments (SSTs ranging 25−30 °C) and shows preference for low seasonal contrasts of SST and SSS around 34 psu.

Spiniferites membranaceus (Figure 6) occurs mostly along the southwest European margins off the Eastern Atlantic coasts and western Mediterranean Sea. It is rarely abundant, with low number of sites recording >5%. At the few sites where is it relatively abundant, it shows affinities for saline (>34) environments with a wide SST range (from 6 °C in winter to 26 °C in summer), and productivity (up to 400 gC $m^{-2}y^{-1}$).

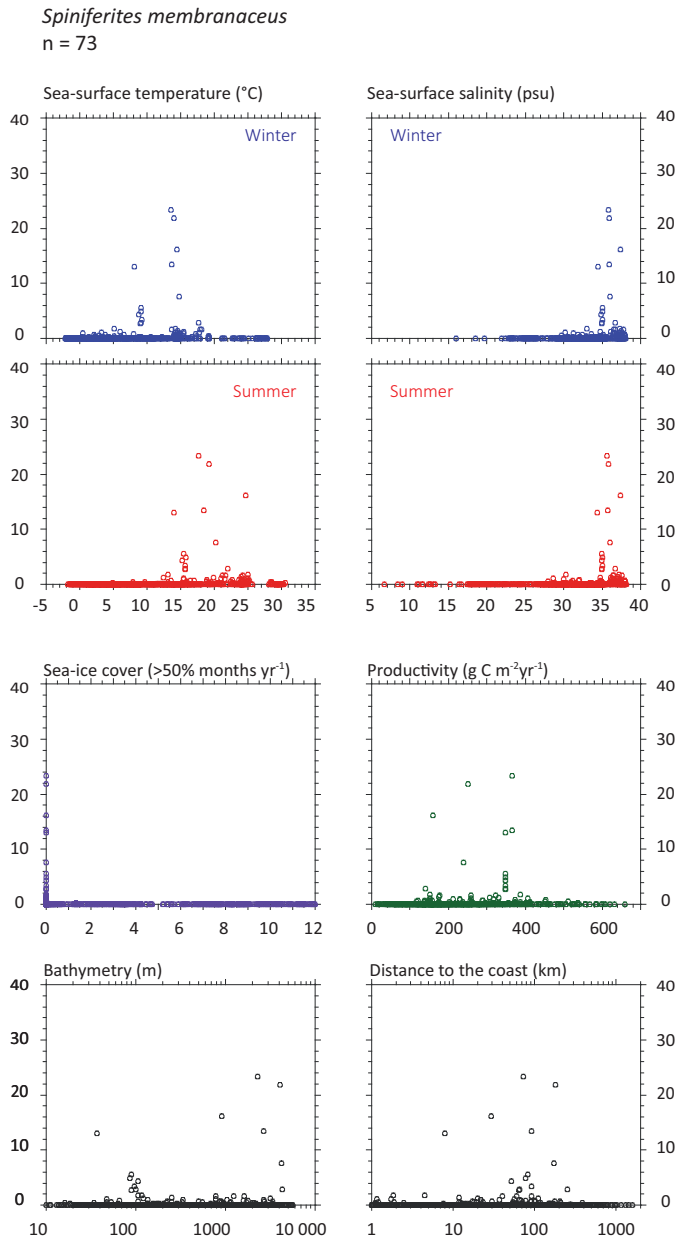

Figure 6. Continued.

Spiniferites lazus (Figure 7) occurs only at a few sites of the modern database and it is rarely more abundant than 2%. The data show that *Spiniferites lazus* occurs in temperate areas (cool in winter and up to 25 °C in summer) where salinity is relatively high and productivity variable (up to 500 gC $m^{-2}y^{-1}$) is recorded.

3.2. Summary of spiniferites taxa distribution in the hydrographical space

Beyond the distribution of individual taxa (Figures 1 − 7), a summary figure of the distribution of key species was built from the mean summer SSS and SST corresponding to the occurrences from low (>0.5%) to relatively high relative occurrences (>5% or >10%; see Figure 8 and Table 3). Figure 8 shows that *Spiniferites ramosus* has a very wide

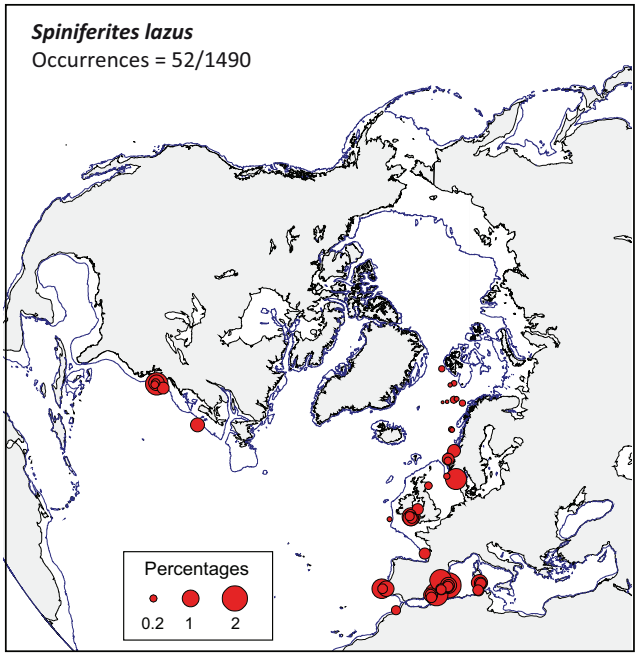

Figure 7. Distribution of *Spiniferites lazus* in the n = 1490 database: (a) Map of relative abundance in percentages relative to total dinocyst counts and (b) graphs of percentage vs. sea-surface temperature in winter and summer, sea-surface salinity in winter and summer, sea-ice cover, productivity, bathymetry and distance to the coast. In the map, the isobath corresponds to 200 meters of water depth. Source: figures drafted by the authors using MapInfo.

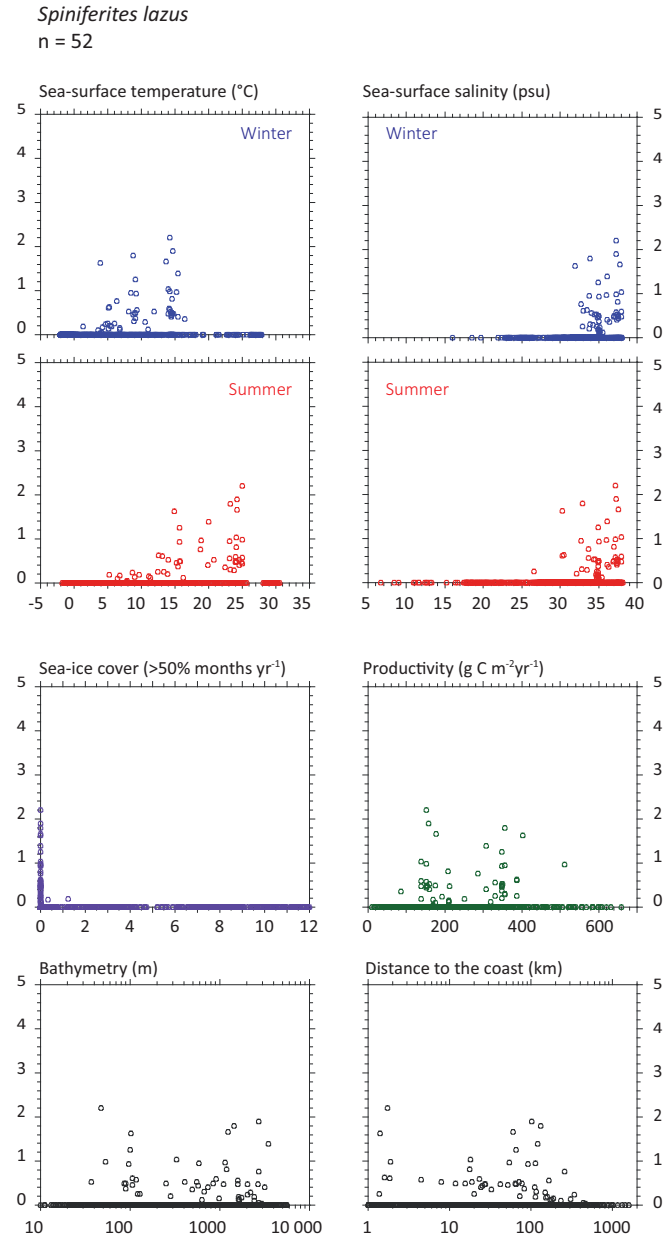

Figure 7. Continued.

distribution overlapping with that of the other taxa, but that *Spiniferites elongatus* has a distribution distinct from that of *Spiniferites mirabilis-hyperacanthus*, *Spiniferites bentorii* and *Spiniferites delicatus*. It also shows that, when considering relatively high percentages, *Spiniferites bentorii* and *Spiniferites mirabilis-hyperacanthus* share very similar hydrographic domains, but that *Spiniferites delicatus* stands out as a high temperature, relatively low salinity taxon. A marked temperature gradient separates this taxon from the low SST pole where *Spiniferites elongatus* largely dominates.

The distribution of *Spiniferites* taxa in the Northern Hemisphere can be further described from multivariate analyses. The results of the CCA on the occurrence of the 67 taxa in relation to 13 environmental parameters at the 1490 sites of the database (Figure 9; Table 4) clearly show that the dinocyst assemblages closely relate to hydrographical conditions. The first axis explains about 42% of the covariance of the species-environments relationship. It primarily correlates with temperature and sea-ice parameters. The second axis explains about 25.4% of the covariance and correlates best with salinity parameters. The third and fourth axes explain about 12.8% and 7.9% of the covariance and are mostly related to productivity and bathymetry and/or distance to the coast, respectively. All *Spiniferites* taxa have positive scores with regard to the first axis and correlate positively with temperature, except *Spiniferites elongatus* that stands out as a low temperature-seasonal sea ice taxon. Similarly, the scores of most *Spiniferites* taxa correlate with salinity, except for *Spiniferites delicatus*, which shows preference for relatively low salinity. Actually, CCA indicates three poles with *Spiniferites elongatus* at the low temperature-low salinity end, *Spiniferites delicatus* at the high temperature-low salinity end, and a cluster with *Spiniferites mirabilis-hyperacanthus*, *Spiniferites membranaceus*, *Spiniferites bulloideus, Spiniferites lazus* and *Spiniferites belerius* aligned towards the high temperature-high salinity end, and *Spiniferites bentorii* at the extremity of this cluster. By contrast, the central position of *Spiniferites ramosus* in the ordination diagram would indicate no clear affinity of the taxon with any of the selected environmental parameters.

The multivariate analyses performed with *Spiniferites* taxa only (Figure 10; Table 5) show similar results, although the relationship was established from redundancy analysis (RDA). The first axis explains about 32% of the species variance and 71.1% of the species-environment covariance. It primarily correlates with temperature and sea-ice parameters. The second axis explains about 12.8% of the covariance and correlates best with salinity parameters. The third axis, explaining about 10.5% of the covariance, mostly relates to

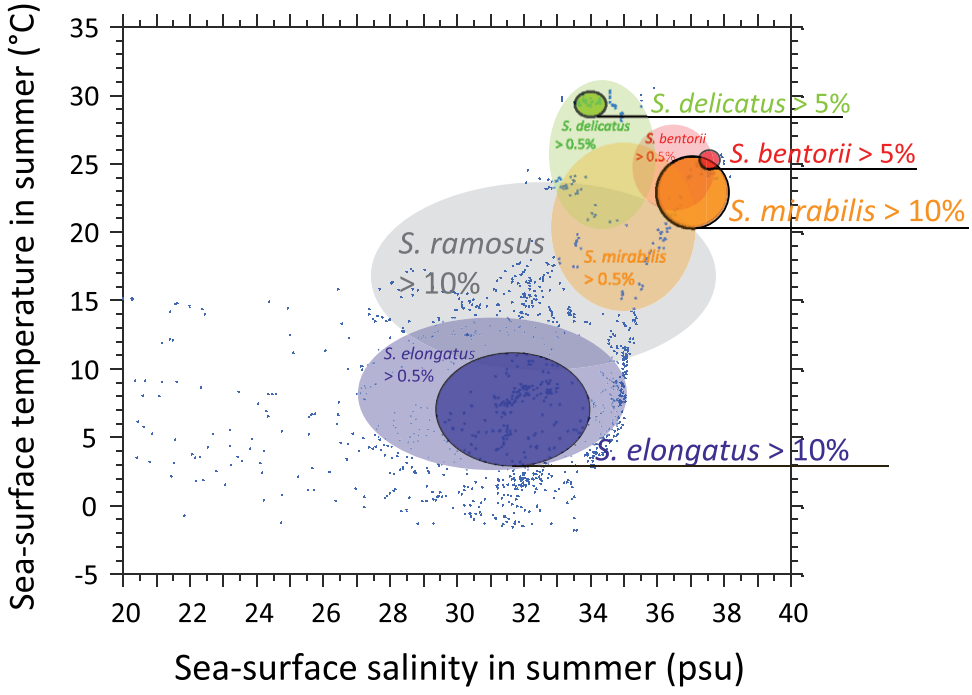

Figure 8. Schematic illustration of the hydrographical domain for the main *Spiniferites* taxa. The ellipses correspond to the average ± one standard deviation of the summer temperature and salinity at sites where *Spiniferites bentorii*, *Spiniferites delicatus*, *Spiniferites elongatus* and *Spiniferites mirabilis-hyperacanthus* occur (>0.5%) and are common-dominant (>10% for all, except *Spiniferites bentorii* >5%). The central transparent ellipse corresponds to the average ± one standard deviation of the summer temperature and salinity at sites where *Spiniferites ramosus* is common or dominant (>10%). Numerical results for averaged environmental parameters corresponding to occurrences of the *Spiniferites* taxa are presented in table 3.

productivity and bathymetry and/or distance to the coast. The ordination diagram also shows three extremes. One extreme is defined by *Spiniferites elongatus* in the low temperature/seasonal sea-ice domain. A second extreme is defined by *Spiniferites delicatus* in the low salinity-high temperature domain. The third extreme is defined by *Spiniferites mirabilis-hyperacanthus* and *Spiniferites bentorii* in the high temperature and high salinity domain. All other taxa have a relatively central position.

4. Discussion

4.1. The spiniferites taxa: their diversity and occurrences

Spiniferites is one of the most common genera of modern dinocyst assemblages, but it includes many species that are difficult to distinguish from each other in palynological slides. Nevertheless, there are taxa that cannot be misidentified based on the concepts used here. These taxa include *Spiniferites ramosus*, *Spiniferites elongatus*, *Spiniferites mirabilis-hyperacanthus, Spiniferites bentorii* and *Spiniferites delicatus*, which are distinct from each other in terms of the shape of their body and/or the distribution-shape of their processes and sutures (Table 2; Plates 1 – 3). They also include *Spiniferites lazus* (Plate 2), which is easy to identify when the base of the processes is clearly visible.

The identity of the other *Spiniferites* taxa in the Northern Hemisphere database (Rochon et al. 1999; de Vernal et al. 2013) is less straightforward. They are usually not very abundant (Table 1) and lack unequivocal criteria of identification: the close similarity of *Spiniferites bulloideus* to *Spiniferites ramosus* explains why both taxa are often grouped together; *Spiniferites belerius* with more or less expanded septa, mostly in the antapical area is not always easy to identify. In case of doubt in the identification to species level, specimens of *Spiniferites belerius* may have been counted as *Spiniferites* spp. or grouped with *Spiniferites membranaceus* during routine analyses. In addition, the informal taxon *Spiniferites* spp. granular, which was introduced to identify granulate thick-walled specimens (mostly) from the Mediterranean Sea (Mangin 2002) and the northwest North Pacific (Bonnet et al. 2012), may include several species and would require further observations for standardization of consensual operational taxonomy.

Other *Spiniferites* species have been described from recent or modern sediments of the Northern Hemisphere. They notably include *Spiniferites cruciformis* Wall & Dale in Wall et al. 1973, reported to occur in the Caspian Sea, Black Sea and eastern Mediterranean Sea (cf. Zonneveld et al. 2013), but has also been assigned questionably to freshwater or brackish-water environments (Kouli et al. 2001). They also include *Spiniferites hainanensis* Sun & Song 1992 described from sediments along the Chinese coast and reported by Limoges et al. (2018) to occur in other warm environments such as the Marmara Sea and Gulf of California. The cyst of *Gonyaulax baltica* Ellegaard et al. 2002 reported from the Baltic Sea and showing similarities with *Spiniferites bulloideus* is possibly another distinct species (Ellegaard et al. 2002). A few species described from upper Quaternary sediments and possibly extending towards modern can also be mentioned. One of them is *Spiniferites alaskensis* Marret et al. 2001b ex Marret in Fensome & Williams 2004, described from last

interglacial sediments of the northeast Pacific Ocean (Marret et al. 2001b). The cysts referred to as *Achomosphaera andalousiensis* Jan du Chêne 1977, which are very recognizable by their fenestrate processes tips (Head 1993, 1997; Penaud et al. 2008), represent another one. *Achomosphaera andalousiensis* occurs occasionally in recent sediments of the western Mediterranean Sea but seems to be more important in the Miocene, Pliocene and Pleistocene (e.g. de Vernal et al. 1992b). The number of modern *Spiniferites* species might well be higher than what reported in the database. Because the species diversity is usually higher under warm climate (cf. de Vernal & Marret 2007), special care in the taxonomy of *Spiniferites* taxa will be critical when extending the reference database towards low latitudes (cf. for ex., Limoges et al. 2013). In this context, the newly described taxon *Spiniferites multisphaerus* Price & Pospelova 2014 reported from the Gulf of California (cf. Price & Pospelova 2014) has to be mentioned here. There are a few other *Spiniferites* species that were reported from Quaternary deposits (see Mertens et al. 2018), but there are not discussed here because of their very low occurrences.

4.2. The usefulness of *spiniferites* taxa in palaeoceanography

In its present state, the standardized database of the Northern Hemisphere (de Vernal et al. 2013) includes seven taxonomic entities of *Spiniferites* that are distinct from each other, some of them occurring in high number in many surface sediment samples: *Spiniferites bentorii*, *Spiniferites delicatus*, *Spiniferites elongatus*, *Spiniferites mirabilis-hyperacanthus, Spiniferites ramosus, Spiniferites lazus* and *Spiniferites membranaceus*. The question whether or not these taxa are useful for assessing hydrographical conditions is discussed below.

Spiniferites elongatus* vs. *Spiniferites mirabilis-hyperacanthus – The hydrographical conditions under which high numbers of *Spiniferites elongatus* (>10%) and *Spiniferites mirabilis-hyperacanthus* (>10%) occur in the n = 1490 database clearly illustrate their respective affinities for two distinct hydrographical domains. Maximum relative abundances of *Spiniferites elongatus* characterize relatively low saline (31.8 ± 2.4 psu) and cool (7.1 ± 3.8 °C) marine waters in summer and seasonal sea-ice cover (4.5 ± 3.4 months/y^{-1} >50%) in winter, whereas *Spiniferites mirabilis-hyperacanthus* is rather associated to mild-warm (14.2 ± 1.1 °C in winter and 23.2 ± 2.7 °C in summer) highly saline waters (37.0 ± 0.9 psu in both winter and summer). The distribution of these two taxa with occurrence greater than 0.5% does not show any overlap (Figure 8). Therefore, these taxa represent endmembers within a subpolar to warm temperate gradient, respectively. Such pattern is also obvious from Holocene and late Quaternary sedimentary records. *Spiniferites elongatus* is a typical component of Holocene assemblages in subarctic basins such as the Labrador Sea and Baffin Bay (e.g. Gibb et al. 2015), the Greenland Sea (e.g. Solignac et al. 2006; Van Nieuwenhove et al. 2016), the Barents Sea (Voronina et al. 2001), the Laptev Sea (Klyuvitkina & Bauch 2006), the

Table 3. Surface ocean parameters (mean and standard deviation) at sites where the *Spiniferites* taxa occur from occasionally (>0.5%) to significantly (>5% or >10%). SST and SSS are respectively sea-surface temperature and sea-surface salinity. The data are schematically illustrated in Figure 8.

	S. belerius	*S. bentorii*		*S. bulloideus*	*S. delicatus*		*S. elongatus*		*S. lazus*	*S. membranaceus*	*S. mirabilis-hyperacanthus*		*S. ramosus*		*S. spp. granular*
Occurrence	Present (>0.5%)	Present (>0.5%)	Common (>5%)	Present (>0.5%)	Present (>0.5%)	Common (>5%)	Present (>0.5%)	Common (>10%)	Present (>0.5%)	Present (>0.5%)	Present (>0.5%)	Common (>10%)	Present (>0.5%)	Common (>10%)	Present (>0.5%)
n	62	71	28	56	104	22	907	60	22	42	289	87	808	66	42
SST - summer (°C)*	22.9 ± 3.1	23.5 ± 2.6	24.3 ± 0.4	22.1 ± 4.2	25.3 ± 5.4	29.2 ± 0.5	8.9 ± 5.6	7.1 3.8	20.6 ± 4.4	19.9 ± 4.1	20.4 ± 5.8	23.2 ± 2.7	13.9 ± 7.1	17.2 ± 6.4	22.2 ± 4.9
SST - August (°C)	23.7 ± 3.3	24.4 ± 2.8	25.2 ± 0.4	23.0 ± 4.4	25.7 ± 5.1	29.5 ± 0.5	9.6 ± 5.8	7.7 ± 4.0	21.4 ± 4.6	20.6 ± 4.3	21.0 ± 5.8	24.1 ± 2.8	14.6 ± 7.1	18.0 ± 6.5	23.4 ± 4.7
SSS - summer (psu)*	36.7 ± 1.3	37.1 ± 1.4	37.7 ± 0.2	35.8 ± 3.1	34.3 ± 1.6	34.0 ± 0.6	31.1 ± 3.8	31.8 ± 2.4	35.1 ± 2.5	35.3 ± 2.6	34.6 ± 2.4	37.0 ± 0.9	32.0 ± 4.0	33.2 ± 5.2	36.6 ± 1.9
SSS - August (psu)	36.7 ± 1.4	37.0 ± 1.5	37.7 ± 0.2	23.0 ± 4.4	34.3 ± 1.6	34.0 ± 0.6	30.9 ± 4.0	31.4 ± 2.5	35.0 ± 2.5	35.3 ± 2.6	34.6 ± 2.4	37.0 ± 0.9	31.9 ± 4.0	33.2 ± 5.1	36.6 ± 1.9
SST - winter (°C)	13.7 ± 2.6	13.8 ± 2.1	14.3 ± 0.2	12.4 ± 4.5	18.6 ± 8.0	24.9 ± 3.4	1.9 ± 4.1	0.9 ± 4.3	11.1 ± 3.8	11.7 ± 4.8	12.2 ± 5.9	14.2 ± 1.1	5.9 ± 6.9	8.5 ± 5.5	12.2 ± 5.4
SST - February (°C)	13.5 ± 2.5	13.7 ± 2.0	14.1 ± 0.3	12.3 ± 4.4	18.4 ± 8.0	24.6 ± 3.5	1.9 ± 4.0	1.0 ± 4.2	10.9 ± 3.7	11.6 ± 4.7	12.1 ± 5.9	14.0 ± 1.1	5.8 ± 6.9	8.3 ± 5.5	12.0 ± 5.6
SSS - winter (psu)	36.8 ± 1.2	37.1 ± 1.4	37.7 ± 0.2	36.1 ± 2.4	34.6 ± 1.4	34.3 ± 0.4	32.6 ± 2.2	33.7 ± 1.3	35.5 ± 1.9	35.3 ± 2.6	35.0 ± 1.9	37.0 ± 0.9	33.1 ± 2.7	34.1 ± 3.6	36.7 ± 1.8
SSS - February (psu)	36.8 ± 1.2	37.1 ± 1.2	37.7 ± 0.2	36.2 ± 2.5	34.6 ± 1.4	34.2 ± 0.2	32.8 ± 2.3	33.7 ± 1.3	35.6 ± 1.9	35.7 ± 2.0	35.0 ± 1.9	37.0 ± 0.9	33.1 ± 2.8	34.2 ± 3.6	36.7 ± 1.8
Productivity (gC/m^{2}y)	199 ± 78	173 ± 65	144 ± 11	211 ± 97	298 ± 115	302 ± 97	227 ± 116	159 ± 75	279 ± 112	268 ± 96	272 ± 109	191 ± 70	277 ± 128	267 ± 121	169 ± 39
Sea-ice cover (months/y^{-1})	0	0	0	0.2 ± 1.2	0 ± 0.2	0	3.2 ± 3.6	4.5 ± 3.4	0	0	0 ± 0.1	0	1.3 ± 2.4	0.6 ± 1.4	0.3 ± 0.6
Sea-ice concentration (/10)	0	0	0	0.2 ± 1.0	0 ± 0.2	0	2.6 ± 2.9	3.6 ± 2.7	0	0	0 ± 0.1	0	1.1 ± 1.9	0.5 ± 1.2	0.2 ± 0.4
Bathymetry (m)	1299 ± 1133	1250 ± 914	1227 ± 680	1049 ± 1092	691 ± 1015	252 ± 270	817 ± 1017	1202 ± 1520	859 ± 1300	1077 ± 1285	1415 ± 1305	1468 ± 1177	819 ± 1041	530 ± 743	992 ± 802
Distance to the coast (km)	70 ± 117	53 ± 46	57 ± 39	63 ± 108	52 ± 67	50 ± 33	126 ± 128	193 ± 205	60 ± 67	66 ± 60	139 ± 202	93 ± 180	95 ± 108	50 ± 62	80 ± 205

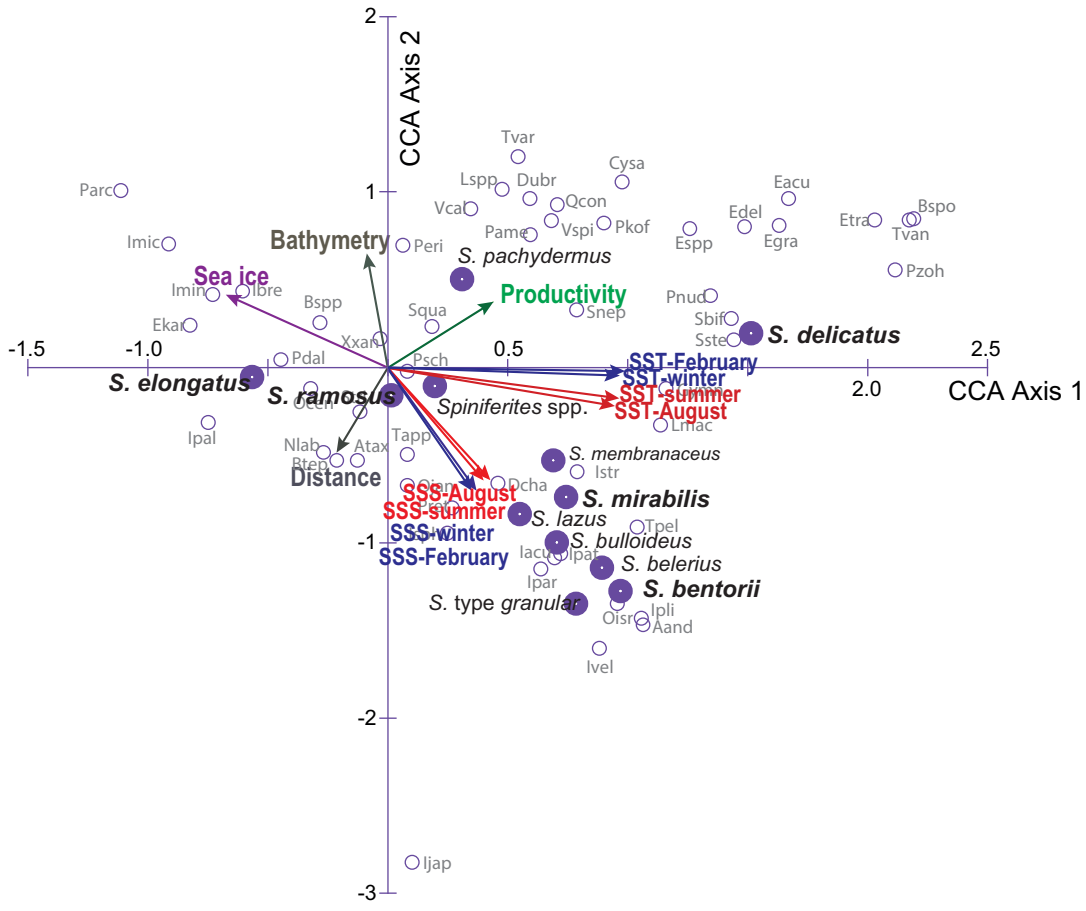

Figure 9. Ordination diagram of the results of canonical correspondence analyses (CCA) on the taxa distribution and sea-surface conditions in the database that includes 67 taxa and 13 environmental parameters at 1490 sites (cf. Table 4 for numerical results).

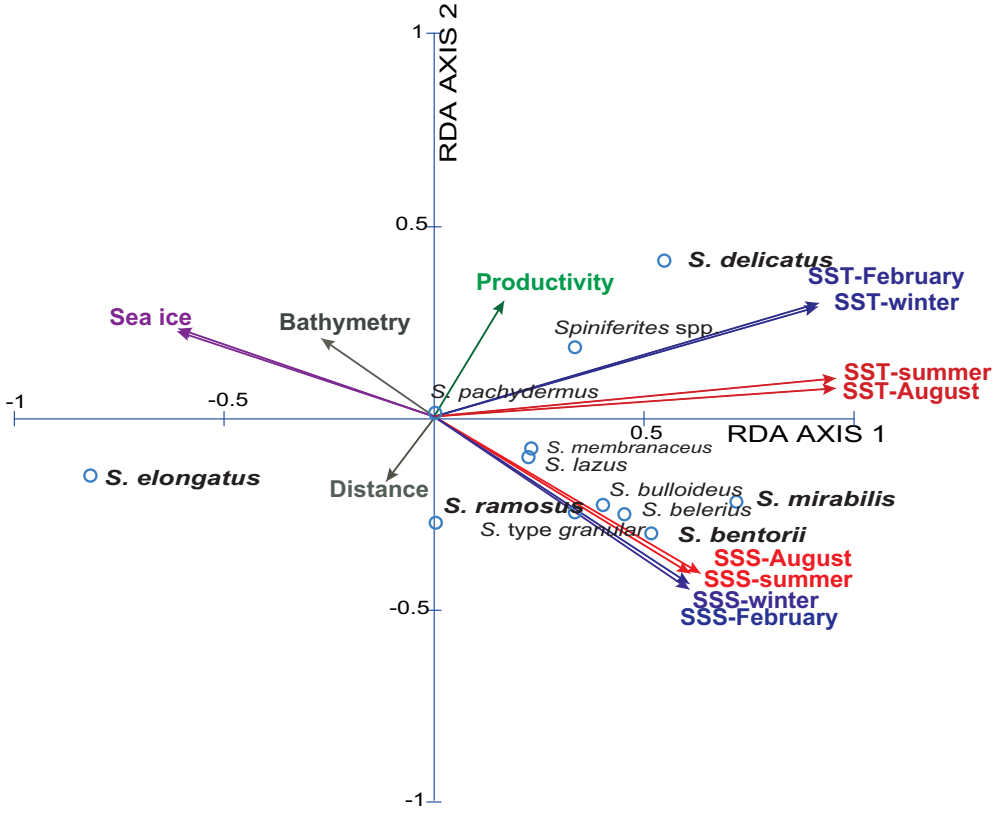

Figure 10. Ordination diagram of the results of redundancy analyses (RDA) on the taxa distribution and sea-surface conditions in the database that includes 12 *Spiniferites* taxa and 13 environmental parameters at 697 sites (cf. Table 5 for numerical results).

Table 4. Results of canonical correspondence analysis (CCA) on the taxa distribution and sea-surface conditions in the database that includes 67 taxa and 13 environmental parameters at 1490 sites (cf. Figure 9 for the ordination diagram). SST and SSS are respectively sea-surface temperature and sea-surface salinity.

Canonical Correspondence Analysis (CCA) - 1490 sites
67 taxa (log transformed)
13 environmental parameters

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	.4339	.2629	.1327	.0819
***Spiniferites* taxa scores**				
S. belerius	.8961	−1.1475	.5918	−.6370
S. bentorii	.9767	−1.2800	.7971	−.8380
S. bulloideus	.7076	−1.0036	.4151	−.5974
S. delicatus	1.5206	.1895	.4802	−.0509
S. elongatus s.l.	−.5614	−.0608	−.0077	−.0831
S. lazus	.6261	−.7548	.0709	−.6222
S. membranaceus	.6957	−.5362	−.0332	−.4142
S. mirabilis-hyperacanthus	.7488	−.7462	.1552	−.0976
S. ramosus	.0193	−.1640	−.1977	−.3374
S. pachydermus	.3160	.4973	−.8615	−.8468
Spiniferites spp.	.2007	−.1122	−.1234	−.1473
Spiniferites spp. granular	.7896	−1.3540	.7841	−.8788
Correlation of environmental variables with axes				
SST-February	.9454	−.0064	.0534	.0859
SSS-February	.3051	−.5248	.1701	−.0712
SST-winter	.9480	−.0077	.0468	.0852
SSS-winter	.3222	−.5280	.1576	−.0683
SST-August	.8833	−.1660	−.0147	−.1095
SSS-August	.3791	−.4774	.0453	−.0317
SST-summer	.8990	−.1419	−.0174	−.0951
SSS-summer	.3519	−.4812	.0828	−.0131
Sea-ice cover (months/y-1)	−.6133	.2865	.4994	.0601
Sea-ice concentration	−.6163	.2865	.5005	.0626
Productivity	.3902	.2662	−.5635	−.0560
Distance to the coast	−.1770	−.3655	−.0885	.5698
Bathymetry	−.0752	.4687	.0933	−.5378

Table 5. Results of redundancy analysis (RDA) on the taxa distribution and sea-surface conditions in the database that includes 12 *Spiniferites* taxa and 13 environmental parameters at 697 sites (cf. Figure 10 for the ordination diagram).

Redundancy Analysis (RDA) - 697 sites
12 taxa (log transformed)
13 environmental parameters

	Axis 1	Axis 2	Axis 3
Eigenvalues	.3230	.0584	.0484
***Spiniferites* taxa scores**			
S. belerius	.4564	−.2562	.1001
S. bentorii	.5195	−.3064	.0963
S. bulloideus	.4037	−.2327	.0461
S. delicatus	.5500	.4049	.0364
S. elongatus	−.8171	−.1563	.0361
S. lazus	.2268	−.1072	−.0195
S. membranaceus	.2338	−.0845	−.0176
S. mirabilis-hyperacanthus	.7231	−.2249	.1023
S. ramosus	.0054	−.2792	−.4406
S. pachydermus	.0043	.0081	−.0150
Spiniferites spp.	.3374	.1782	−.3555
Spiniferites spp. granular	.3382	−.2527	.0861
Correlation of environmental variables with axes			
SST-February	.8099	.1896	.0503
SSS-February	.5238	−.2789	.3143
SST-winter	.8123	.1912	.0473
SSS-winter	.5288	−.2851	.3273
SST-August	.8342	.0523	−.1229
SSS-August	.5463	−.2599	.2016
SST-summer	.8415	.0706	−.1128
SSS-summer	.5354	−.2612	.2362
Sea-ice cover (months/y^{-1})	−.5385	.1444	.2640
Sea-ice concentration	−.5408	.1409	.2657
Productivity	.1486	.1884	−.4079
Distance to the coast	−.1021	−.1023	.2883
Bathymetry	−.2387	.1300	−.1779

Chukchi Sea (de Vernal et al. 2005b; McKay et al. 2008), the Bering Sea (Radi et al. 2001) and the Gulf of Alaska (de Vernal & Pedersen 1997; Marret et al. 2001b). In contrast, *Spiniferites mirabilis-hyperacanthus*, which is absent from the above mentioned subarctic environment, is common in Holocene sediments of warm environments such as the Mediterranean Sea (e.g. Rouis-Zargouni et al. 2010), the Bay of Biscay (e.g. Zumaque et al. 2017), and the Gulf of Mexico (Limoges et al. 2014). Moreover, *Spiniferites mirabilis* recorded a maximum occurrence peak during the last interglacial or marine isotope stage (MIS) 5e (ca. 128–117 ka), both in the North Atlantic (Eynaud et al. 2004; Penaud et al. 2008; Van Nieuwenhove et al. 2011; Harland et al. 2016) and in the South Pacific (Marret et al. 2001a). The maximum occurrence peak of *Spiniferites mirabilis* during the last interglacial is compatible with the particularly warm conditions that characterized the last interglacial worldwide (e.g. PIGS 2016).

Spiniferites elongatus is a useful taxon despite variations in its morphology concerning the length vs. width ratio of the cyst body and the expansion of the apical and antapical septa. Specimens characterized by a particularly elongate shape and well developed apical-antapical septa, originally assigned to *Spiniferites frigidus,* were reported to be abundant in Baffin Bay, Barents Sea, Bering Sea and Beaufort Sea (e.g. Harland et al. 1980; Harland 1982; Mudie & Short 1985; Radi et al. 2001). Hence, it is tempting to associate the most elongated morphotypes to cold settings. However, systematic observations and measurements of the length and width of the cyst and septa have still not provided a statistically clear relationship between morphometry and environmental parameters (Van Nieuwenhove et al. 2018).

The case of *Spiniferites ramosus* – In contrary to *Spiniferites elongatus* and *Spiniferites mirabilis-hyperacanthus, Spiniferites ramosus* is not a taxon with distinctive and thus easy to identify ecological affinities as it can be found in a wide range of environmental settings. It occurs in high proportions (>10%) in cool to warm waters (8.5 ± 5.5 °C in winter and 17.2 ± 6.4 °C in summer) and at very variable salinity (33.2 ± 5.2 psu). It encompasses areas occupied by *Spiniferites elongatus* and *Spiniferites mirabilis-hyperacanthus* and often occurs as the most common *Spiniferites* taxon at mid latitudes (cf. this study) as well as low latitudes (e.g. Limoges et al. 2013; Hessler et al. 2013). As concluded by Marret & Zonneveld (2003) and Zonneveld et al. (2013) from global data compilations, *Spiniferites ramosus* seems to be very cosmopolitan. However, *Spiniferites ramosus* records a large morphological variability, possibly including more than one species or genotype. What is identified as *Spiniferites ramosus* can relate to co-existing cryptic species. The variable morphology could also reflect a true morphological plasticity of the species that might be a response to environmental stress. In any case, the cosmopolitan distribution of *Spiniferites ramosus* possibly results from the clustering of different species or subspecies that are difficult to distinguish on a routine basis. It is also of note that *Spiniferites ramosus* is a long ranging taxon (lowermost Cretaceous to modern) and that more than 30 infra-specific taxa of *Spiniferites ramosus* have been described (Williams et al. 2017). It can thus be concluded that the current morphological concept of *Spiniferites ramosus* constitutes an entity with poorly constrained taxonomy, ecological affinity and biostratigraphy.

***Spiniferites bentorii* and *Spiniferites delicatus* as thermophilic species** - In the warmer part of the database, the distribution of *Spiniferites bentorii* and *Spiniferites delicatus* shows distinct characteristics with regard to hydrographic conditions (Figure 8, Table 3). Moreover, both taxa seem to have a neritic distribution as their occurrence is exclusive to sites located relatively close to the coast (<120 km; see Figures 4b and 5b). Relatively high percentages of *Spiniferites delicatus* (>5%) characterize year-round warm environments (22.9 ± 0.5 °C in winter and 24.9 ± 3.4 °C in summer), rather low salinity around 34 ± 0.6 psu and high productivity (302 ± 97 gC $m^{-2}y^{-1}$). *Spiniferites delicatus*, however, is still represented by a limited number of data points in the Northern Hemisphere reference database (de Vernal al. 2013), but its known global distribution tends to support affinities for tropical waters (cf. Zonneveld et al. 2013). For example, the ecological affinities identified here from the mid latitudes of the Northern Hemisphere are consistent with the distribution pattern of *Spiniferites delicatus* in the Gulf of Guinea, equatorial Atlantic, where maximum occurrences (up to 80%) are also recorded under temperature and salinity ranging 23–29 °C and 34–35 psu (Marret 1994; Marret & Zonneveld 2003).

The environments with relatively high occurrence of *Spiniferites bentorii* (>5%) are different from those recording high percentages of *Spiniferites delicatus* (>5%). In the mid latitude of the Northern Hemisphere, *Spiniferites bentorii* seems to characterize areas with important contrast of seasonal temperature gradients (14.3 ± 0.2 °C in winter and 24.3 ± 0.4 °C in summer), high salinity (37.6 ± 0.3 psu) and lower productivity (144 ± 11 gC $m^{-2}y^{-1}$). However, *Spiniferites delicatus* is also present in the Black Sea (up to 10%), where salinity can be very low, thus suggesting tolerance for lower salinity (e.g. Mudie et al. 2007). The species has also been reported (up to 6%) from North American temperate, nutrient-rich estuarine systems with an average SSS of ~27 psu (Pospelova et al. 2002; Price & Pospelova 2011). From its worldwide distribution compiled by Zonneveld et al. (2013), *Spiniferites bentorii* tends to display affinities for warm conditions with large seasonal temperature contrasts, and with tolerance for wide salinity ranges.

Spiniferites membranaceus* and *Spiniferites lazus – *Spiniferites membranaceus* and *Spiniferites lazus* are distinct entities, but they are not often abundant. In the mid-high latitudes of the Northern Hemisphere, they share similar warm temperate domains. However, their preferred environments might be at lower latitudes and for warmer conditions (cf. Zonneveld et al. 2013). For example, *Spiniferites membranaceus* is common in intertropical areas of the Indian Ocean (e.g. Hessler et al. 2013) and the South China Sea (Kawamura 2004). The known distribution of *Spiniferites lazus* in time and space is limited, with documented occurrence mostly restricted to late Quaternary sediment of British Isles (Reid 1974; Marret & Scourse 2002) and Mediterranean Sea (Turon & Londeix 1988; Mangin 2002). *Spiniferites lazus*, however,

recorded peaks of abundance during cold episodes of the last glacial stage in the subtropics (Marret & Turon 1994; Penaud et al. 2010) and is quite abundant (more than 20%) in the sediments of the Holocene thermal optimum of the Celtic Sea (Marret et al. 2004).

5. Conclusions

Despite a wide range of morphological variations, taxonomic uncertainties and the possibility of cryptic species, some of the main species of *Spiniferites* routinely identified and counted for population analyses are very useful tracers of sea-surface conditions. These species principally include *Spiniferites elongatus*, *Spiniferites mirabilis-hyperacanthus*, *Spiniferites bentorii* and *Spiniferites delicatus*, which are diagnostic to identify subpolar, cool temperate, warm temperate and tropical conditions. In particular, the occurrence of *Spiniferites elongatus* and *Spiniferites mirabilis-hyperacanthus*, which are common in marine sediments, is very useful to distinguish subpolar from warm temperate environments. *Spiniferites bentorii* and *Spiniferites delicatus* are also diagnostic to document warm conditions although their occurrence is not as common. Other species might well be useful at mid-low latitudes but some effort to develop an operational taxonomy to ascertain consistent identification of taxa is needed.

One particularity of the dinocyst database as compared to other palaeoceanographical tracers such as planktic foraminifers or coccoliths is the possibility to include both nearshore and offshore, shallow and deep sites. This results in large ranges of SSSs and in various combinations of SST and SSS and winter vs. summer extremes. Shelf environments are indeed often prone to stratification of the upper water masses, which leads to low thermal inertia and therefore large temperature changes from winter to summer in high latitudes. Hence, among *Spiniferites* taxa, some show more affinities for nearshore environments characterized by low salinity. This seems to be the case for *Spiniferites delicatus*. The large morphological plasticity displayed by other taxa such as *Spiniferites ramosus*, might actually be an illustration of the adaptation to various and variable conditions. Attentive examination of their morphological ranges can be relevant as they might well reflect different environmental conditions.

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No potential conflict of interest was reported by the author.

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