

Quantitative biostratigraphical ranges of some late Cenozoic species of the dinoflagellate genus *Spiniferites* and taxonomic considerations

Laurent Londeix

To cite this article: Laurent Londeix (2018) Quantitative biostratigraphical ranges of some late Cenozoic species of the dinoflagellate genus *Spiniferites* and taxonomic considerations, *Palynology*, 42:sup1, 203-220, DOI: [10.1080/01916122.2018.1465731](https://doi.org/10.1080/01916122.2018.1465731)

To link to this article: <https://doi.org/10.1080/01916122.2018.1465731>



© 2018 The Author(s). Published by AASP - The Palynological Society



Published online: 14 Dec 2018.



Submit your article to this journal [↗](#)



Article views: 668



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 2 View citing articles [↗](#)



Quantitative biostratigraphical ranges of some late Cenozoic species of the dinoflagellate genus *Spiniferites* and taxonomic considerations

Laurent Londeix

Université de Bordeaux/UMR 'EPOC' CNRS 5805 – allée Geoffroy St-Hilaire, Pessac cedex, France

ABSTRACT

A new quantitative biostratigraphical method, based on an 'index of stratigraphical abundance' (ISA), has been used to refine the stratigraphical range of 50 dinoflagellate cyst taxa. Most of these correspond to Quaternary representatives of *Achomosphaera* or *Spiniferites*. Some extinct taxa are also discussed when their morphology is close to that of recent species (e.g. *Spiniferites lenzii*, *S. twistringiensis* and *S. pseudofurcatus*), as well as some species possibly related to the motile *Gonyaulax spinifera* complex. The ISAs of *S. mirabilis* and *S. hyperacanthus* are similar, as well as for *S. elongatus* and *S. sphaericum*. Although initially presumed as indicating morphotypes of a same taxon, it seems rather that the ISAs similarities must be interpreted as an indication of close ecological preferences. The emergence of forms of *Spiniferites* with low to absent septa appears relatively late (compared to the range of the genus), but the first occurrence of intergonal processes is relatively early, indicating that it is probably a character deeply rooted into the generic genome. The previously calculated phylogeny of some *Gonyaulax* motile cells shows a different tree pattern than the stratigraphical first appearance succession of their presumed cyst equivalents.

KEYWORDS

Biostratigraphy; dinoflagellates; *Gonyaulax spinifera* complex; Neogene; Quaternary; *Spiniferites*

1. Introduction

Spiniferites Mantell 1850 is one of the most geographically widespread and stratigraphically long-ranging dinoflagellate cyst genus (Hultberg and Malmgren 1995). This finding holds true both in the ancient (post Jurassic) and recent (Pliocene-Quaternary) series as shown by the numerous records of this genus, especially for the type species, *Spiniferites ramosus* (Ehrenberg 1837) Mantell 1854. Indeed, this taxon presents an exceptional case of stratigraphic longevity, as it is reported in the fossil record from the Upper Jurassic to Present, with a thriving distribution. With a stratigraphical longevity exceeding 140 Ma, *Spiniferites ramosus* is probably one of the longest living among the Quaternary dinoflagellate species, and perhaps among all species in the living realm.

The genus *Spiniferites* encompasses more than 100 species (Fensome and Williams 2004) among which 20 have at least been recorded in Quaternary strata. In connection with the "Quaternary *Spiniferites* Workshops" held in Montreal (2014) and Ostend (2015) (see the general Introduction of this volume), we herein focus primarily on Quaternary and Neogene species. Stratigraphical range charts were published for some *Spiniferites* species (e.g. Harland 1978; Sarjeant 1979), and the one of 55 *Spiniferites* species by Hultberg and Malmgren (1995) remains a reference work, but over the last twenty years, new data were published and some new species have been erected. In addition, representations of species occurrences by a simple line between inception and extinction provide limited information.

To go beyond this method based on the only alternative presence/absence (i.e. occurrence), a new approach is here proposed based on an 'index of stratigraphical abundance' (ISA) calculated for various *Spiniferites* species. It is an occurrence probability of a taxon for each geological stage, which is the geochronological resolution selected here. On one hand, this allows to display the time interval in which a taxon is the most abundant relatively to other dinoflagellate cyst species, and secondly to compare the ISA's variations between different taxa.

The motile equivalent of *Spiniferites ramosus* is not clear and might be attributed to *Gonyaulax spinifera*-type (Claparède and Lachmann 1857) Diesing (1866) motile cells (e.g. Wall and Dale 1970; Lewis et al. 1999; Ellegaard et al. 2003; Rochon et al. 2009). Other types of cysts have been attributed to that motile complex, sometimes not belonging to the genus *Spiniferites* (e.g. *Bitectatodinium tepikiense*, *Nematosphaeropsis labyrinthus*, *Tectatodinium pellitum*; cf. 'Heterospor' in Head 1996; Lewis et al. 2001).

The present work is an opportunity to test whether dinoflagellate cyst taxa, which have been attributed to the motile *Gonyaulax spinifera* complex (Dodge 1989), present similarities in their 'index of stratigraphical abundance'. The study should also clarify the stratigraphical origin of the *Spiniferites* species still present in the modern seas.

2. Material and methods

2.1. The databases

In order to collect the occurrences of the selected taxa in the most exhaustive way possible, a very large number of records is needed. The PALYNODATA online database (Palynodata Inc. and White 2008) offers such an opportunity by providing a large number of species and references that list the geographical and stratigraphical local occurrences of each taxon. For the present work, a total of 2,279 publications from the organic-walled dinoflagellate cyst literature depicting 2,333 geological sequences (field sections or boreholes) was extracted from the PALYNODATA database. As the database has not been updated since 2006, it was completed with a personal database that contains data before and after 2006 for well-dated sequences, preferably with a dating not based on the dinoflagellate cysts themselves. It indexes occurrences of 1,585 organic-walled dinoflagellate cyst species from 214 additional publications (396 geological sequences) of global dinoflagellate cyst literature.

The merging of the two databases lead to 2,729 worldwide geological sequences from the Carnian (Upper Triassic) to today. Among them, 1,671 geological sequences provided species of *Spiniferites* or of the *Gonyaulax spinifera* complex. No stratigraphical synthesis (e.g. Sarjeant 1979; Powell 1992; Williams et al. 1993; Hultberg and Malmgren 1995) was integrated in the merged database, in order to not duplicate the data already included.

The final database therefore has two dimensions, with: the 46 geological stages, from the Carnian to the Holocene, in columns, and the taxa in rows. When a paper deals with several sites, each site was considered independently.

The occurrence of the taxon is 0 if it was not observed in the sequence and 1 if it has been recorded. The value of 0.5 is sometimes used when the dating is uncertain or imprecise (e.g. Senonian or Lower Miocene). The species referred as 'cf.' were not taken into account.

2.2. The index of stratigraphical abundance (ISA)

An 'index of stratigraphical abundance' (ISA) has been developed to get more information from the biostratigraphical records, allowing to go beyond the establishment of the stratigraphical range of a taxon by determining its oldest and youngest occurrences.

The ISA allows to not only to determine the stratigraphical range of a taxon as indicated by its earliest and latest occurrences but also to obtain a full occurrence probability distribution.

The ISA was calculated on the basis of the number of geological sequences in which a taxon was recorded during a time interval (= 'nOcc' for number of occurrences) versus the total number of sequences documented in the database (= 'nSeq' for total number of geological sequences) for the same time interval:

$$ISA = nOcc/nSeq$$

For each taxon, an ISA was calculated for each geological stage considering its worldwide occurrences. If necessary, the

geographical area of the record can be restricted to an oceanic basin, to a (paleo)hemisphere, etc. Overall, the ISA can be considered as an estimate for the occurrence probability of a taxon during each geological stage. For example, 157 sequences of the database span the Holocene. Among these sequences, 66 record *Spiniferites ramosus*. The ISA of *Spiniferites ramosus* for the Holocene is $66/157 = 0.42$. That means that in a global stratigraphical point of view, the probability to encounter a specimen of this species in a Holocene sequence is about 42%, implying that an ISA value cannot exceed 1. The database used here includes 2,729 different geological sequences and 1,585 organic-walled dinoflagellate cyst species. To calculate ISA, it is first needed to determine the number of sequences documented in the database for each geological stage (the time interval chosen here). Since the database from which it is calculated is substantial, featuring on average over a hundred publications for each geological stage (from 11 sequences for the Carnian to 308 for the Albian, cf. Table 1), the ISA constitutes a significant estimator.

3. Results

The stratigraphical occurrences of 50 taxa have been investigated. Most of them correspond to *Spiniferites* or *Achomosphaera* species recorded in Quaternary strata. Some extinct taxa are also depicted when their morphology is close to that of recent species (e.g. *Spiniferites lenzii*, *Spiniferites twistringiensis* and *Spiniferites pseudofurcatus*), as well as some species possibly related to the motile *Gonyaulax spinifera* complex.

3.1. *Spiniferites ramosus*, oldest occurrence of the genus?

Duxbury (1977), Davey (1979, 1982), Williams and Bujak (1985), Costa and Davey (1992), Stover et al. (1996) consider that, at least in NW Europe, the first appearance of *Spiniferites ramosus* marks the lowermost Valanginian. This is also what Hardenbol et al. (1998) followed by Ogg and Ogg (2008c) report for the Boreal/North Atlantic domain but, according to the lowermost Berriasian occurrences recorded by Monteil (1992, 1993), they consider an earlier occurrence in the Tethyan domain. That point of view is still confirmed by many experienced palynostratigraphers (James Riding, personal communication).

Such a statement deserves a closer scrutiny since several *Spiniferites ramosus* occurrences were recorded in Jurassic strata. Deflandre (1938) mentioned a single specimen attributed to *Hystrichosphaera furcata* (now *Spiniferites ramosus*) from the Lower Oxfordian cliffs of Villers-sur-Mer (France). The description given by the author was very succinct, with no mention of trifid processes. Due to its poor preservation, the specimen was not illustrated. Such a record seems not suitable for biostratigraphy. Sarjeant (1960) reported one specimen of *Hystrichosphaera furcata* that was illustrated (pl. 14, fig. 17) from the 'Upper Calcareous Grit' Formation from Yorkshire (England). The age of this formation is considered

as late Oxfordian (op. cit.). Still from Yorkshire in the 'Amphill Clay' Formation, Sarjeant (1962) reported two specimens (not depicted) of *Hystrichosphaera furcata* from an Oxfordian pit exposure. It is of note that the collective efforts of lots of reliable palynologists over many years have never replicated these occurrences in NW Europa. Gitmez and Ertug (1999) studied five Upper Jurassic sections from Turkey and mentioned few sparse specimens of *Spiniferites ramosus* in only one of them. The illustrated specimen (pl. 9, fig. 4-5) does not look like *Spiniferites ramosus* sensu holotype. In addition, this specimen appears very fresh and could be a contamination from the Neogene upper part of the outcrop. In their synthesis, Pestchevitskaya et al. (2011) recorded *Spiniferites ramosus* from a little below the Jurassic/Cretaceous (J/K) boundary (late Upper Volgian) in outcrops from Sub-Polar Ural, and from the J/K boundary near Laptev Sea. Unfortunately no specimen was depicted. Other specimens have been reported from Jurassic strata, but in boreholes for which the possibility of caving cannot be excluded (e.g. Brideaux 1977, Upper Jurassic of NW Canada; Chen 1978 early-middle Kimmeridgian and Portlandian from Madagascar; Thusu and Vigran 1985 unspecified Jurassic age from Libya, considered by the authors as caved; Guy-Ohlson 1986, Toarcien-Aalenian of Sweden). These borehole occurrences have not been considered in this work.

These records show that there are no unequivocal reports of *Spiniferites ramosus* from the Jurassic supported by photographic evidence. Cretaceous occurrences (particularly Neocomian one) are numerous enough to be considered as significant.

Berriasian (lowermost Cretaceous) records of *Spiniferites ramosus* show a scattered distribution since it was reported in various outcrops from Iran (Ashraf 1979), India (Kumar 1980), Gulf of Mexico (Riley and Fenton 1984), Libya (Thusu et al. 1989), SE France (Monteil 1992, 1993), NW Siberia (Lebedeva and Nikitenko 1999).

If we consider the bibliographical data as reliable, particularly those from outcrops, it appears that the geographical extension of *Spiniferites ramosus* appears restricted during the Berriasian, and almost worldwide during the Valangian.

Thus, we can consider that the first occurrence datum (FOD) of *Spiniferites ramosus* can be placed in the lowermost Berriasian and the Valangian worldwide extension could correspond to its first common occurrence (FCO). After that, the species presents consistent ISA values above ca 0.2 from the Valangian until present days (Figure 1). Two ISA optima are clearly distinct around Maastrichtian and Quaternary times with an interposed minimum centered on the Middle Miocene (Figure 1).

Davey (1979) defined *Spiniferites ramosus* as a biostratigraphical marker of the '*Spiniferites ramosus*' dinozone (Davey 1979) covering the mid-Early Valangian to the top Valangian in the Boreal realm. That marker could correspond to the FCO of the species.

Several other species of *Spiniferites* first appear during the Berriasian (e.g. *Spiniferites alatus* Duxbury 1977, *Spiniferites "multibrevis"* now *Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990) which makes uncertain whether

Spiniferites ramosus would be the oldest representative of the genus *Spiniferites*. *Achomosphaera* who is a genus morphologically very close to *Spiniferites* might have been the first of the two to appear since *Achomosphaera neptunii* (Eisenack 1958) Davey and Williams (1966) was recorded as early as the Tithonian (uppermost Jurassic; Harding et al. 2011).

3.2. Neogene and Quaternary *Spiniferites* plexus

The first and last occurrences of the selected species are presented in Table 2. Some species deserve further attention and are discussed below. The ISAs of the Quaternary and Pliocene species that first appear before the Cretaceous/Paleogene boundary are shown in Figure 1. Those which inception is post-Cretaceous are shown in Figure 2.

Both *Achomosphaera andalousiensis* Jan du Chêne (1977) and *Spiniferites septentrionalis* Harland (1977) possess processes with fenestrate/trabeculate distal tips and the distinction is not always easy (see Londeix et al. 2018). Some authors consider these species as synonym, and it is difficult, in the absence of clear illustrations, to know which of these two species has been recorded. It is probable that the compiled record of each of these species does not refer to a unique taxon. Nevertheless, the FAD of *Achomosphaera andalousiensis* seems to be upper Langhian (Powell 1986b; McCarthy and Mudie 1996, see also Dybkjær and Piasecki 2010) while the first appearance of *Spiniferites septentrionalis* is upper Tortonian-Messinian (Harland 1979). Spiniferate cysts with trabeculate/fenestrate distal tips are still present today. However, it is difficult to assign them to one or the other of these taxa since they present intermediate features (e.g. Morzadec-Kerfourn 1979; Mangin 2002). Nevertheless, *Spiniferites septentrionalis* is present in Upper Quaternary (Harland 1977) sediments and typical *Achomosphaera andalousiensis* have been recorded and illustrated by Head (1997) from Piacenzian strata. *Achomosphaera andalousiensis* gave its name to a dinozone established by Piasecki (1980) that covers almost the entire upper Miocene (e.g. Piasecki 1980; Manum et al. 1989; McCarthy et al. 2013).

Remarks: When Harland (1977) erected *Spiniferites septentrionalis*, he mentioned Philip C. Reid according who (personal communication) the new species was synonymous with *Spiniferites ramuliferus* as recorded by Reid (1974). In that work Reid considered the specimen figured by Downie and Singh (1970) as *Hystrichosphaera ramosa* (Figure 3) as synonymous of *Spiniferites ramuliferus*. Neither Reid nor Downie and Singh evoked the presence of perforated or trabeculate process terminations. Synonymy of *Spiniferites septentrionalis* with *Spiniferites ramuliferus* sensu Reid (1974) (non Deflandre) is not followed here, however *Spiniferites ramuliferus* sensu Reid (1974) and *Hystrichosphaera ramosa* sensu Downie and Singh (1970) (non Ehrenberg) seem to correspond to the same taxon.

The first formal occurrence of *Achomosphaera callosa* Matsuoka (1983) is Londeix and Lopes (2014) from Aquitanian stratotype, but it is likely that this species appeared earlier in the Chattian (Powell 1986b) as

Table 2. Taxonomical references of the taxa studied with the age of their first and last appearances. FAD: First appearance datum; LAD: Last appearance datum; FCO: First common occurrence; LCO: Last common occurrence. The arrow indicates the species is still living. See section 'References' for the full references of the citations.

Taxa	FAD	References	FCO	LCO	LAD	References
<i>Achomospaera andalousiensis</i> Jan du Chêne 1977	upper Langhian	Powell 1986c	Serravallian	Piacenzian/ ?lower Pleist.	—>	Morzadec-Kerfourn 1979
<i>Achomospaera andalousiensis</i> subsp. <i>suttonensis</i> Head 1997	Middle/Late Miocene	Kuhlmann 2004	lower Zanclean	—	Piacenzian	Louwyte et al. 2004
<i>Achomospaera callosa</i> Matsuoka 1983	Rupelian	Londeix, unpub. data	lower Aquitanian	Gelasian	Holocene	Zhu 2000
<i>Achomospaera granulata</i> Mao 1989	Late Pleistocene	Mao 1989	—	—	Late Pleistocene	Mao 1989
<i>Achomospaera ramosasimilis</i> (Yun 1981) Londeix et al. 1999	upper Valanginian	Londeix 1990	—	—	lower Zanclean	de Vernal and Mudie 1989
<i>Ataxiodinium choane</i> Reid 1974	Late Miocene	Warny 1999	—	—	—>	see Zonneveld et al. 2013
<i>Bitectatodinium tepikiense</i> Wilson 1973	upper Aquitanian	Powell 1988	Tortonian	—	—>	see Zonneveld et al. 2013
Cyst of <i>Gonyaulax baltica</i> Ellegaard, Lewis and Harding 2002	Recent	Ellegard et al. 2002	—	—	—>	Ellegard et al. 2002
<i>Impagidinium aculeatum</i> (Wall 1967) Lentin and Williams 1981	Middle/Late Eocene	Firth 1996, Gedl and Leszczynski 2005	Priabonian	—	—>	see Zonneveld et al. 2013
<i>Impagidinium patulum</i> (Wall 1967) Stover and Evitt 1978	Danian?	Moshkovitz and Habib 1993	Early Miocene	—	—>	see Zonneveld et al. 2013
<i>Impagidinium sphaericum</i> (Wall 1967) Lentin and Williams 1981	lower Chattian	Powell 1986c	lower Chattian	—	—>	see Zonneveld et al. 2013
<i>Nematosphaeropsis labyrinthus</i> (Ostenfeld 1903) Reid 1974	upper Ypresian	Köthe 1990	Lutetian	—	—>	see Zonneveld et al. 2013
<i>Rottnestia amphicavata</i> Dobell and Norris in Harland et al. 1980	Holocene	Harland et al. 1980	—	—	Holocene	Harland et al. 1980
<i>Spiniferites alaskensis</i> Marret et al. 2001	Middle Pleistocene	Marret et al. 2001	—	—	Middle Pleistocene	Marret et al. 2001
<i>Spiniferites asperulus</i> Matsuoka 1983	Late Miocene	Matsuoka 1983	—	—	Late Pleistocene	Bujak and Matsuoka 1986
<i>Spiniferites belerius</i> Reid 1974	Aquitani	Londeix and Lopes 2014	Pleistocene	—	—>	see Zonneveld et al. 2013
<i>Spiniferites bentorii</i> (Rossignol 1964) Wall and Dale 1970	Aquitani	Edwards 1986	Langhian	—	—>	see Zonneveld et al. 2013
<i>Spiniferites bentorii</i> subsp. <i>truncata</i> (Rossignol 1964) Wall and Dale 1970	Pleistocene	Rossignol 1964	—	—	—>	Liu et al. 2012
<i>Spiniferites bulloideus</i> Deflandre and Cookson 1955	Ypresian	Auffret and Gruas-Cavagnetto 1975	Aquitani	—	—>	see Zonneveld et al. 2013
<i>Spiniferites cruciformis</i> Wall and Dale in Wall et al. 1973	upper Middle Pleistocene	Koreneva and Kartashova 1978	Late Pleistocene	—	—>	see Zonneveld et al. 2013
<i>Spiniferites delicatus</i> Reid 1974	lower Rupelian	De Coninck 2001	Aquitani	—	—>	see Zonneveld et al. 2013
<i>Spiniferites ellipsoideus</i> Matsuoka 1983	lower Langhian	Matsuoka et al. 1987	—	—	upper Zanclean	Matsuoka et al. 1987
<i>Spiniferites elongatus</i> Reid 1974	lower Tortonian	Matsuoka 1983	—	—	—>	see Zonneveld et al. 2013
<i>Spiniferites falcipedi</i> Warny and Wrenn, 1997	upper Aquitanian	Londeix and Lopes 2014	Zanclean	Piacenzian	Piacenzian	De Schepper et al. 2009
<i>Spiniferites firmus</i> Matsuoka 1983	upper Burdigalian	Bujak and Matsuoka 1986	—	—	Early Pleistocene	Matsuoka 1983
<i>Spiniferites frigidus</i> Harland and Reid in Harland et al. 1980	Late Miocene	Matsuoka and Bujak 1988	Pleistocene	—	—>	Radi and de Vernal 2004
<i>Spiniferites hainanensis</i> Sun and Song 1992	Quaternary	Sun and Song 1992	—	—	—>	Limoges et al. 2018
<i>Spiniferites hyperacanthus</i> (Deflandre and Cookson 1955) Cookson and Eisenack 1974	upper Hauterivian	Kirsch and Below 1995	—	—	—>	see Zonneveld et al. 2013
<i>Spiniferites lazus</i> Reid 1974	Chattian	Strauss 1993	—	—	—>	see Zonneveld et al. 2013

(continued)

Table 2. Continued.

Taxa	FAD	References	FCO	LCO	LAD	References
<i>Spiniferites lenzii</i> Below, 1982c,	upper Valanginian	Londeix 1990	Hauterivian	—	lower Maastrichtian	Ashraf and Erben 1986
<i>Spiniferites ludhamensis</i> Head 1996	upper Gelasian (Antian),	Head 1996	—	—	upper Gelasian (Antian),	Head 1996
<i>Spiniferites membranaceus</i> (Rossignol 1964) Sarjeant 1970	lower Albian	Foucher 1975	upper Albian	—	—>	see Zonneveld et al. 2013
<i>Spiniferites mirabilis</i> (Rossignol 1964) Sarjeant 1970	Danian	Eshet et al. 1992	Rupelian	—	—>	see Zonneveld et al. 2013
<i>Spiniferites multisphaerus</i> Price and Pospelova 2014	Late Pleistocene	Price and Pospelova 2014	—	—	—>	Price and Pospelova 2014
<i>Spiniferites ovatus</i> Matsuoka 1983	lower Chattian	Powell 1986b,c	—	Zanclean	Holocene	Yun et al. 2000
<i>Spiniferites pachydermus</i> (Rossignol 1964) Reid 1974	Serravallian	Matsuoka 1983	Zanclean	—	—>	see Zonneveld et al. 2013
<i>Spiniferites pacificus</i> Zhao and Morzadec-Kerfourn 1994	Early Pleistocene	Zhao and Morzadec 1994	—	—	Late Pleistocene	Zhao and Morzadec 1994
<i>Spiniferites pseudofurcatus</i> (Klumpp 1953) Sarjeant 1970	upper Turonian	Foucher 1974	—	upper Messinian	Gelasian/Late Pleist.	Wrenn and Kokinos 1986
<i>Spiniferites pseudofurcatus</i> subsp. <i>obliquus</i> (Wall 1967) Lentin and Williams 1973	Late Pleistocene	Wall 1967	—	—	Holocene	Wall 1967
<i>Spiniferites ramosus</i> (Ehrenberg 1837) Mantell 1854 emend. Davey and Williams 1966	lower Berriasian	Monteil 1992	Valanginian	—	—>	see Zonneveld et al. 2013
<i>Spiniferites ramosus</i> subsp. <i>multiplicatus</i> (Rossignol 1964) Lentin and Williams 1973	Rupelian	Londeix, unpub. data	Berriasian	—	Zanclean	Londeix et al. 1999
<i>Spiniferites rhizophorus</i> Head in Head and Westphal 1999	upper Zanclean	Head and Westphal 1999	—	—	lower Gelasian	Head and Westphal 1999
<i>Spiniferites ristingensis</i> Head 2007	Late Pleist. (Eemian)	Head 2007	—	—	Late Pleist. (Eemian)	Head 2007
<i>Spiniferites rubinus</i> (Rossignol 1962) Sarjeant 1970	upper Burdigalian	McCarthy and Mudie 1996	Langhian	—	—>	see Zonneveld et al. 2013
<i>Spiniferites scabratus</i> (Wall 1967) Sarjeant 1970	middle Burdigalian	Londeix and Jan du Chêne 1998	Early Pleistocene	—	—>	see Zonneveld et al. 2013
<i>Spiniferites septentrionalis</i> Harland 1977	Late Miocene	Harland 1979	—	—	Late Pleistocene	Harland 1977
<i>Spiniferites serratus</i> Matsuoka 1983	Zanclean	Matsuoka 1983	—	—	Late Pleistocene	Matsuoka 1983
<i>Spiniferites splendidus</i> Harland 1979	Chattian	Zevenboom 1996	—	—	Late Pleistocene	McCarthy and Mudie 1996
<i>Spiniferites strictus</i> Matsuoka 1983	Serravallian	Matsuoka 1983	—	—	Gelasian	Matsuoka 1983
<i>Spiniferites twistringensis</i> (Maier 1959) Fensome et al. 1990	Berriasian	Ashraf 1979	—	Serravallian	Holocene	Grill and Quattrocchio 1996
<i>Tectatodinium pellitum</i> Wall 1967	lower Danian	Hansen 1977	lower Danian	—	—>	see Zonneveld et al. 2013
<i>Tuberculodinium vancampoeae</i> (Rossignol) Wall 1967	lower Ypresian	Fechner and Mohr 1988	Priabonian	—	—>	see Zonneveld et al. 2013

Achomosphaera cf. *crassipellis*) or in the upper Rupelian (Stampian, Londeix, unpub. data).

Achomosphaera ramosasimilis (Yun 1981) Londeix et al. 1999 was firstly recorded in the Santonian from Germany but the synonymy provided by the original author ranges from the Neocomian (as *Hystriospheraidium ramuliferum*, Gocht 1959) to the Upper Oligocene (as *Achomosphaera ramulifera*, Cookson and Eisenack 1974). Londeix (1990) recorded this species in the Upper Valanginian from SE France and it was also recorded in the Gelasian from Sicily

(Londeix et al. 1999). The youngest occurrence might be in Lower Pleistocene from Labrador Sea as *Achomosphaera ramulifera* (de Vernal and Mudie 1989).

Remarks: In the note accompanying the original description of *Achomosphaera ramosasimilis* Yun (1981) states that the shape and arrangement of the processes and the structure of the central body are equivalent to *Spiniferites ramosus ramosus*. This taxon is here considered as a concept that corresponds to *Spiniferites ramosus* without septa between the processes.

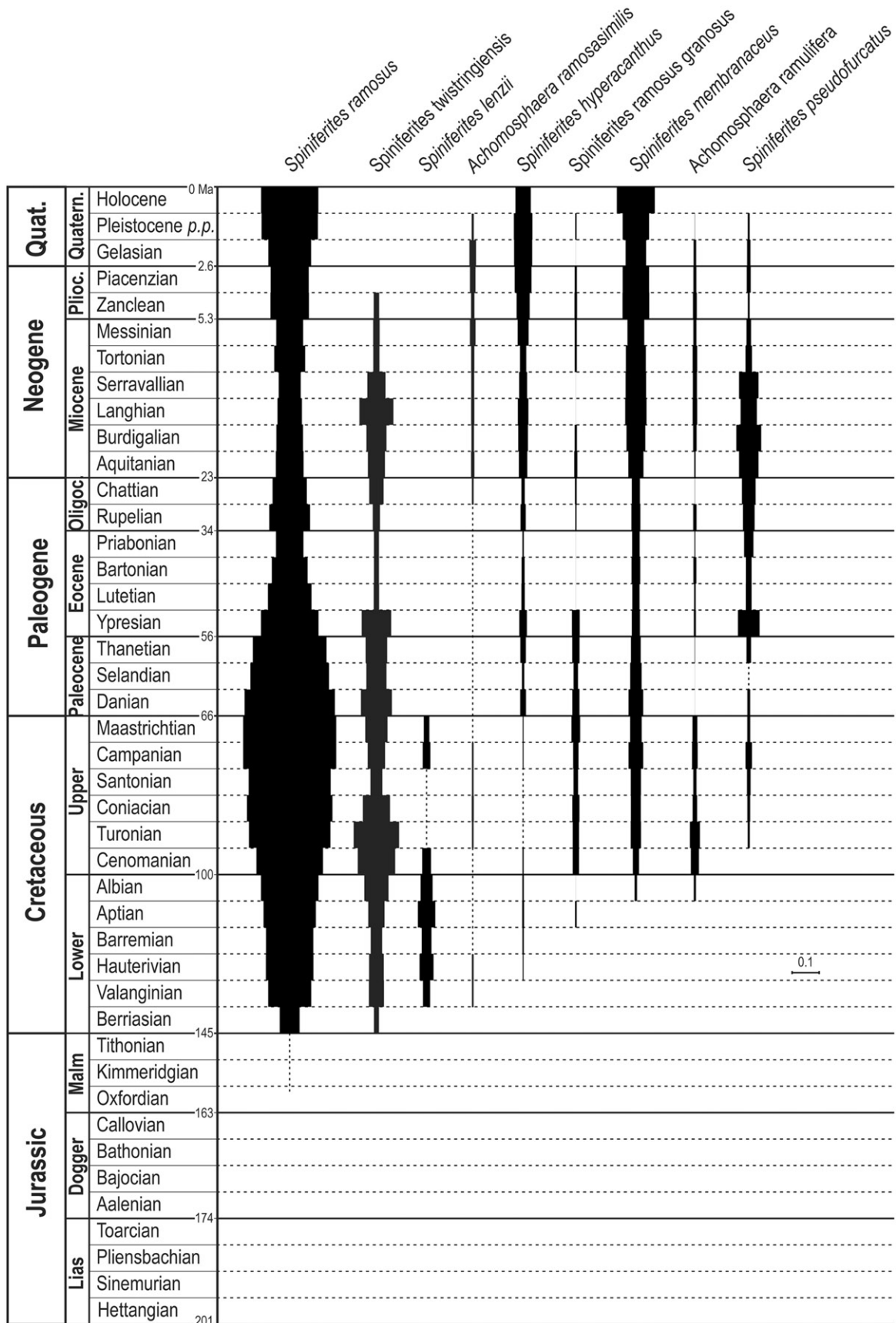


Figure 1. 'Index of stratigraphical abundance' (ISA) of some stratigraphically long ranging *Spiniferites* and *Achomosphaera* species. The chronostratigraphical framework (left column) is from ICS (2016). Species are presented in order of appearance. The scale bar corresponds to ISA = 0.1.

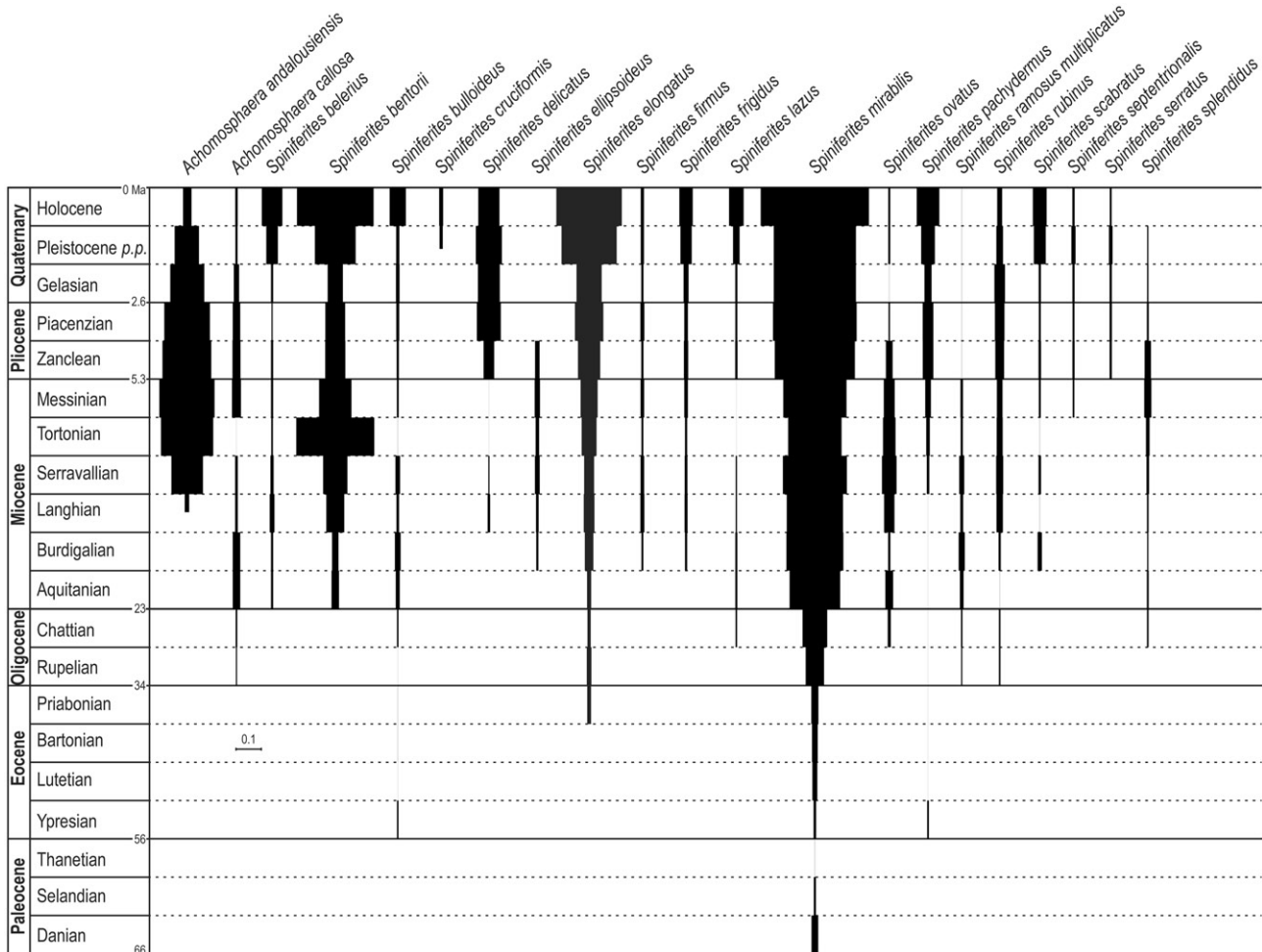


Figure 2. 'Index of stratigraphical abundance' (ISA) of some stratigraphically short ranging *Spiniferites* and *Achomospaera* species. The chronostratigraphical framework (left column) is from ICS (2016). Species are presented in alphabetical order. The scale bar corresponds to ISA = 0.1.

The earliest suitable records of *Spiniferites bentorii* (Rossignol 1964) Wall and Dale (1970) seem to be from Aquitanian by Edwards (1986) and Powell (1986b) respectively from South Carolina and NW Italy. The Paleogene records of *Spiniferites bentorii* (e.g. Frederiksen 1969; Bujak 1973; Islam 1984; Powell et al. 1996; Gedl 2005) are herein considered as not suitable since sparse, not illustrated, or with questionable identification.

The early record of *Spiniferites bentorii* subsp. *truncata* (Rossignol 1964) Wall and Dale (1970) in the Upper Cretaceous from Western Xinjiang (China) by Yu and Zhang (1980) appears very isolated compared to the other records for this taxon. This record is not taken into account here and the stratigraphical range of *Spiniferites bentorii truncata* is considered to be limited to its restricted and rare occurrences in the Quaternary.

The lowest occurrence of *Spiniferites bulloideus* Deflandre and Cookson 1955 might be Ypresian (Auffret and Graus-Cavagnetto 1975) but this record appears discrepant since the other oldest occurrences are significantly younger: Chattian (Londeix, unpub. data) and Aquitanian (Londeix and Lopes 2014).

Spiniferites cruciformis Wall and Dale in Wall et al. 1973 is endemic to the Black Sea, Marmara Sea, Caspian Sea, Aral Sea, and eastern Mediterranean (Zonneveld et al. 2013) and

occurs mainly in brackish environments. Applying biostratigraphy in a such context is generally not easy, and in the present case the oldest occurrences of this species are poorly dated: hypothetically within the range of Pliocene to Pleistocene (Eaton 1996) or Middle Pleistocene (Koreneva and Kartashova 1978). The undisputed oldest occurrences were recorded in the upper Pleistocene (Wall et al. 1973; Mudie et al. 2002, 2007; Londeix et al. 2009). Williams et al. (1998) consider the stratigraphical range of *Spiniferites cruciformis* from 0.17 to 0.01 Ma. The species might be not extinct since it is present in some surface sediments of the 'paratethysian' area (Zonneveld et al. 2013).

The earliest clear occurrence of *Spiniferites elongatus* Reid 1974 seems to be from Tortonian from Northern Japan (Matsuoka 1983; Matsuoka et al. 1987). Closely related morphologies to *Spiniferites elongatus* were sporadically found in Rupelian strata in a section from Belgium (De Coninck 2001) and from a borehole from the Norwegian-Greenland Sea (Poulsen et al. 1996). All these records are earlier than the Pleistocene FAD stated by Williams et al. (1998) and Ogg and Ogg (2008a) and are in agreement with the Late Miocene occurrence stated by Bujak and Matsuoka 1986 and Stover et al. (1996).

The stratigraphy of *Spiniferites hyperacanthus* (Deflandre and Cookson 1955) Cookson and Eisenack 1974 started in

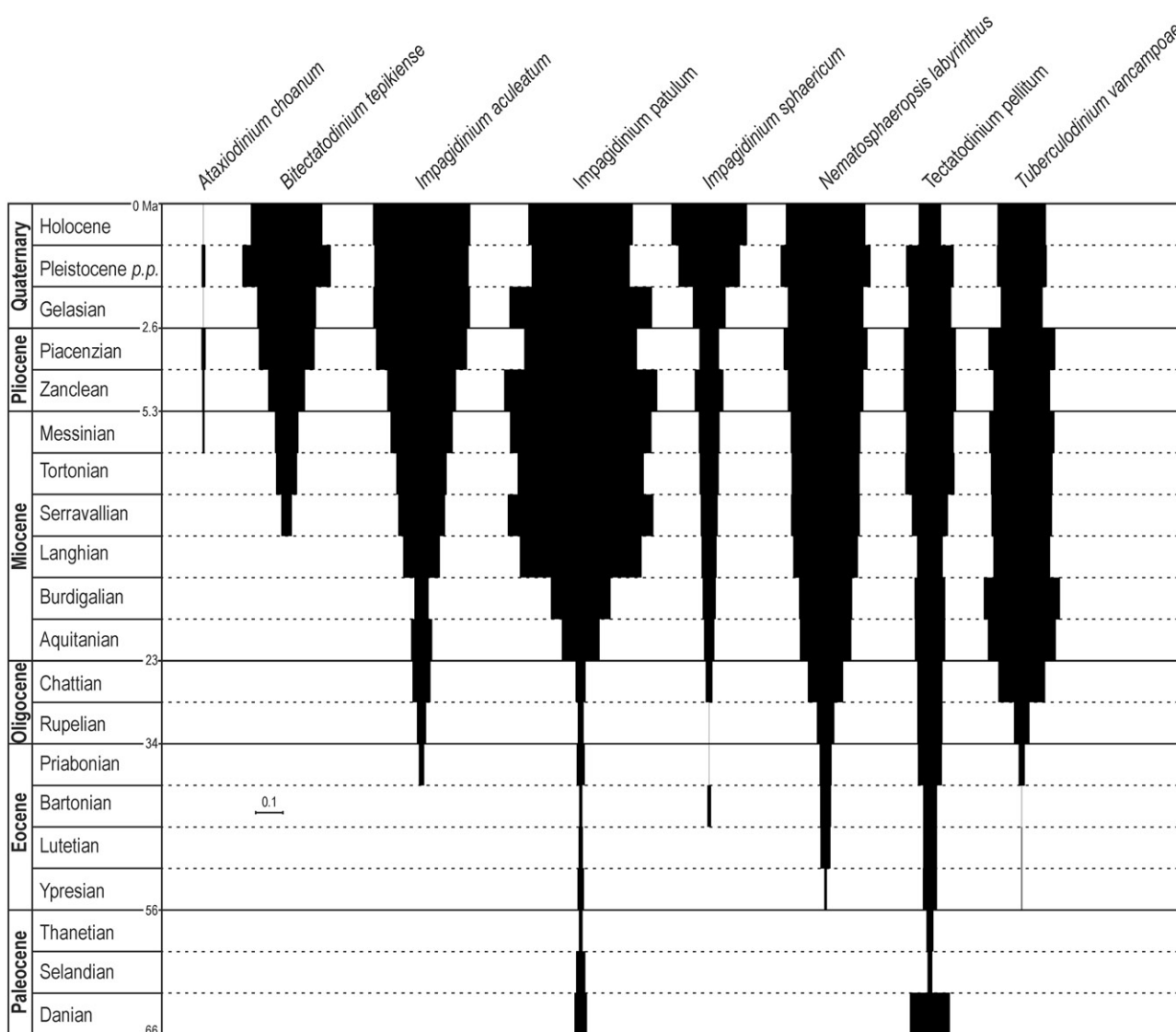


Figure 3. 'Index of stratigraphical abundance' (ISA) of some cyst species possibly related to the motile *Gonyaulax spinifera* complex. The chronostratigraphical framework on left column is from ICS (2016). Species are presented in alphabetical order. The scale bar corresponds to ISA = 0.1.

the Lower Cretaceous (Figure 1). Its lowest occurrence lies in the Hauterivian from Germany (Kirsch and Below 1995). Otherwise, the Cretaceous species *Spiniferites lenzii* Below 1982c (see Figure 1) is a morphologically very similar species since, although slightly smaller, it also bears numerous intergonal processes. This morphological similarity casts doubt on the identification of the Cretaceous cysts as *Spiniferites hyperacanthus*, and the absence of illustration for these records does not eliminate the doubt (e.g. Masure 1988; Below and Kirsch 1994; Fiet and Masure 2001). In the same way, the record of *Spiniferites lenzii* in Cenozoic strata (Matsuoka 1983) is remote from the latest (Maastrichtian) continuous occurrence. It might be the result of a reworking, and it is not considered here. All of these occurrences are discussed in Section 4 (see below).

The oldest record of *Spiniferites mirabilis* (Rossignol 1964) Sarjeant 1970 is from the lowermost Danian of Israel (Eshet et al. 1992), and is confirmed by the record of a *Spiniferites* sp. cf. *S. mirabilis* in Danian from Senegal (de Klasz et al. 1987; Jan du Chêne 1988).

The Dinoflagellate cyst Zone V of Costa and Downie (1979) covers the Upper Eocene and its lower boundary is marked by the first occurrence of *Spiniferites mirabilis*. It is now clear that the FAD of that species is older (Figure 2, Table 2).

The lowest occurrence of *Spiniferites pachydermus* (Rossignol 1964) Reid 1974 seems to be located in the Serravallian (Matsuoka 1983) or the Upper Miocene (Mudie 1989; McMinn 1993; Suc et al. 1995) but in all the cases older than the Gelasian age stated by Ogg and Ogg (2008a).

Spiniferites pseudofurcatus subsp. *obliquus* (Wall 1967) Lentin and Williams 1973 has almost exclusively been recorded by Wall in Quaternary sediments from the Caribbean Sea. The sole other record is by Wrenn and Kokinos (1986) from an Upper Pleistocene section in Gulf of Mexico in which reworking is frequent. The stratigraphical range of *Spiniferites pseudofurcatus* (Klump 1953) Sarjeant, 1970 appears to end before the onset of the Quaternary (Figure 1, Table 2), so the specific allocation of the *obliquus* subspecies is questioned.

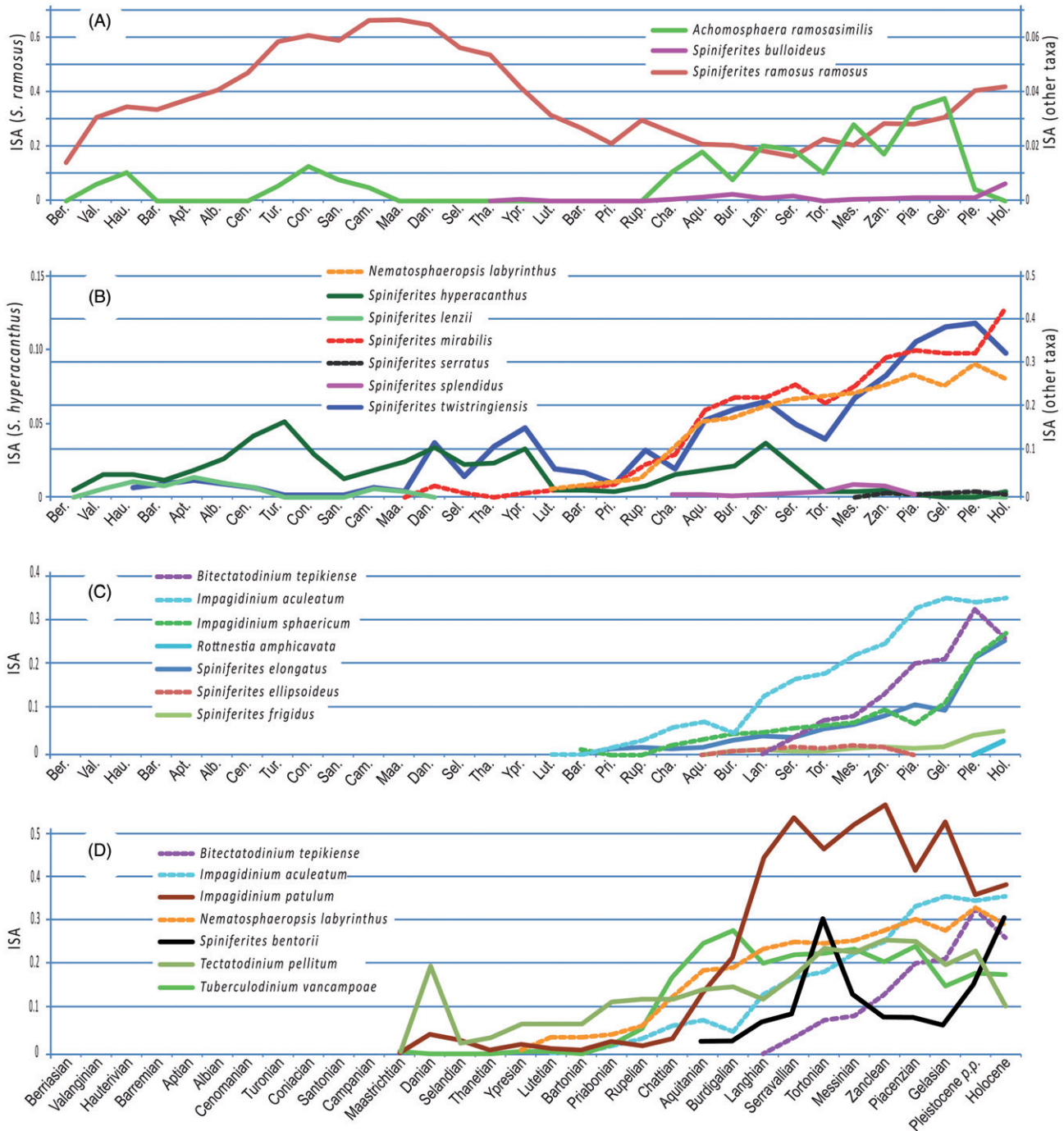


Figure 4. ISA comparison of some species. Abscissa: geological stages from the Berriasian (lowermost Cretaceous) to the Holocene.

Foucher (1974) recorded in the upper Turonian from France the oldest occurrence of *Spiniferites pseudofurcatus* (Klumpp 1953) Sarjeant, 1970. The highest ISA values of that species spans from the Ypresian to the Serravallian (Figure 3). Some specimens have been recorded in Plio-Quaternary strata, but they occur rarely except in Mediterranean area where reworking is frequent (Versteegh and Zonneveld 1994; Corradini in Guerrero et al. 1985; Londeix et al. 1999).

The FAD of *Spiniferites rubinus* (Rossignol 1962 ex Rossignol 1964) Sarjeant 1970 appears to lie in the upper Burdigalian (offshore Portugal, McCarthy and Mudie 1996). The morphology of the specimen illustrated by El Beialy

(1990, pl.4, fig.1) from the Middle/Late Oligocene from Egypt appears too different from Rossignol's species to be taken into account.

The lowest occurrence of *Spiniferites splendidus* Harland 1979 seems to be Chattian (Zevenboom 1996), even if there are few records of this taxon. Williams et al. (1998) and Ogg and Ogg (2008a) consider the last occurrence of *Spiniferites splendidus* as an index species for the mid/upper Zanclean boundary (synchronous with the top of Martini's (1971) NN13 calcareous nannofossils Zone). This datum should be considered obsolete since Mudie (1986) and Stoker et al. (1994) recorded *Spiniferites splendidus* in Gelasian strata.

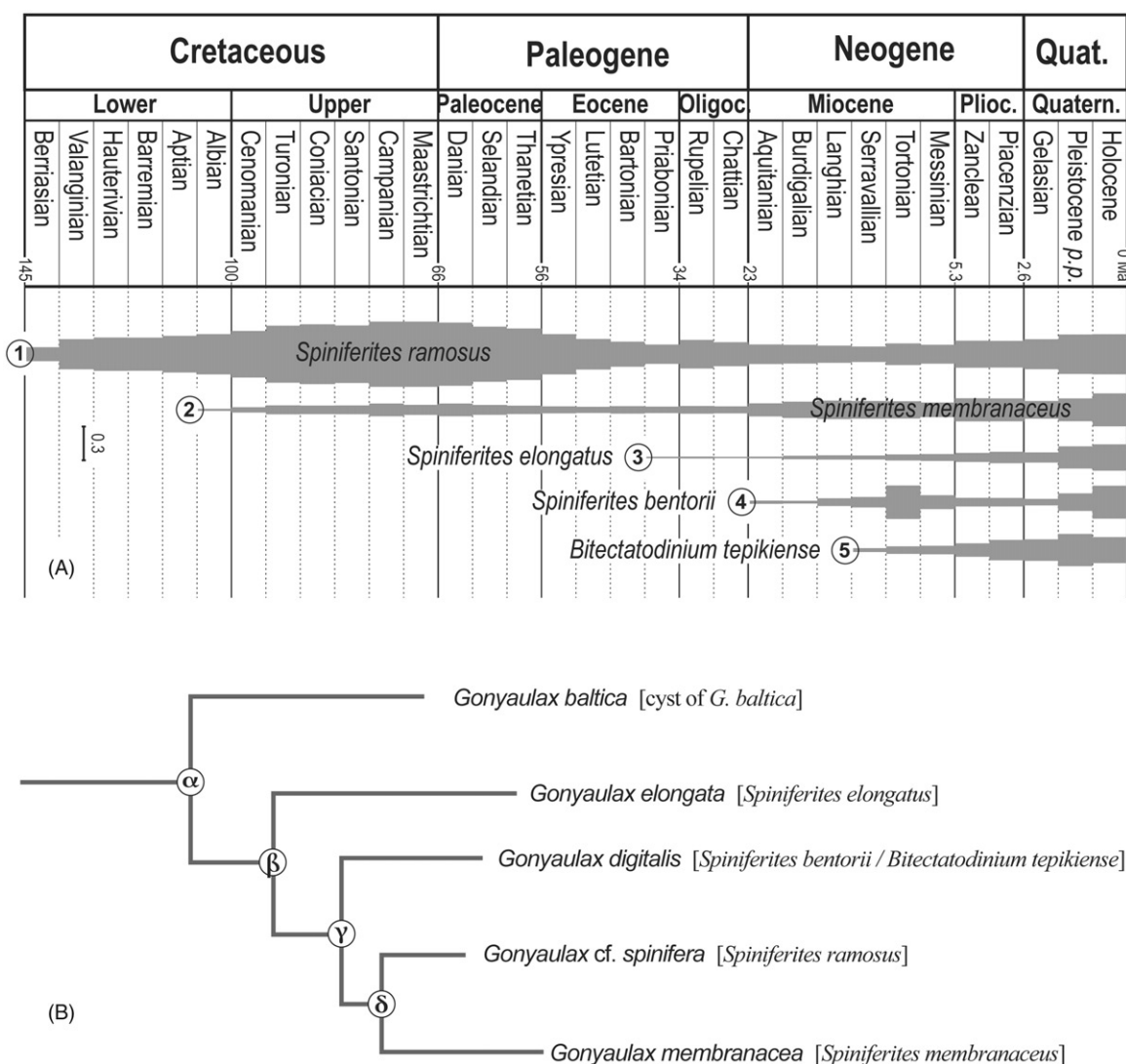


Figure 5. (A) Appearance chronology of five dinoflagellate cyst species according to their geological records as depicted by their 'index of stratigraphical abundance' (ISA). (B) Phylogeny of some living *Gonyaulax* species, inferred from partial LSU rDNA sequence data (redrawn after Ellegaard et al. 2003). The name of the cysts corresponding to their motile stage is enclosed in square brackets.

Furthermore, Mertens et al. (this volume) propose a synonymy with *Spiniferites mirabilis*.

The original description of *Spiniferites multibrevis* indicates the presence of intergonal processes, sometime up to three (Davey and Williams 1966). That feature being shared with *Spiniferites hyperacanthus*, the stratigraphy of this taxon is studied here. As *Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990 is considered to be a senior synonym of *Spiniferites multibrevis* (Davey and Williams 1966) Below 1982c (see Sarjeant 1983; Fensome and Williams 2004) the stratigraphical ranges of both species have been merged (Figure 1, Table 2). The overall range of *Spiniferites twistringiensis* appears to be Berriasian (as *Spiniferites multibrevis*: Ashraf 1979; Heilmann-Clausen 1987) to Serravallian (Figure 1) but it might be still present at Holocene (Grill and Quattrocchio 1996).

3.3. Cyst species possibly related to the motile *Gonyaulax spinifera* complex

The FAD of *Bitectatodinium tepikiense* Wilson 1973 appears to be Lower Miocene within the planktonic foraminiferal

Biozones N5 to N7, i.e. Burdigalian or may be upper Aquitanian (Powell 1988b, 1992; Stover et al. 1996) (Figure 3).

Moshkovitz and Habib 1993 report *Impagidinium aculeatum* (Wall 1967) Lentini and Williams 1981 from Danian sediments. Although the material comes from outcrops, precluding caving, that record is far older from other ones that are Middle (Firth 1996, as *Impagidinium* sp. cf. *I. aculeatum*) to Upper Eocene (Brinkhuis 1992; Brinkhuis and Biffi 1993, as *Impagidinium* sp. cf. *I. aculeatum*; Gedl and Leszczynski 2005, as *Impagidinium aculeatum*).

It is recognized that *Impagidinium patulum* (Wall 1967) Stover and Evitt 1978 FCO is recorded since Lower Miocene (e.g. Powell 1986a, 1992; Brinkhuis et al. 2003; Dybkjaer 2004). Its first appearance is difficult to pinpoint since many occurrences were recorded from Danian strata (Moshkovitz and Habib 1993) to Upper Oligocene (e.g. Strauss 1993; Eidvin et al. 1998; Dybkjaer 2004), sometimes considered as caving (e.g. Eidvin et al. 1998) or with morphologies distant to the type material. Since illustration is not always provided, it is difficult to state.

Head and Nøhr-Hansen (1999) consider *Xenicodinium* (as *Tectatodinium*) *rugulatum* to be a taxonomic junior synonym

of *Tectatodinium pellitum*, therefore, the records taken into account herein are those of both names. The base of the dinoflagellate cyst 'X. *rugulatum* Zonule' proposed by Hansen (1977) and located at the base of the Danian marks the FAD of *Tectatodinium pellitum* which is just below the base of the calcareous nannofossil Zone NP2 (Stover et al. 1996; Ogg and Ogg, 2008b), and approximately corresponds to the base of the foraminiferal Zone Plb, according to Berggren et al. (1995). The older records of that taxon are thought doubtful (because questioned identification or not illustrated) by Head and Nøhr-Hansen (1999).

The FCO of *Tuberculodinium vancampoe* (Rossignol 1962) Wall (1967) is probably Priabonian as recorded by several authors (e.g. Costa et al. 1988; El-Bassiouni et al. 1988; Brinkhuis 1992; De Coninck 1999). The records by Fechner and Mohr (1988) and Kar (1985) respectively from Ypresian field section and Lutetian might indicate an earlier stratigraphical position for the appearance of this taxon. The record by Tea-yassia et al. (1999) from lower Maastrichtian is probably due to caving and is not considered here.

4. Discussion

4.1. About *Spiniferites ramosus* and some others

On the whole, the stratigraphical range of a species is only meaningful when we deal with the same taxon. Since the objective of this study is to depict the stratigraphical continuity of *Spiniferites* species recorded in Quaternary sediments, the reference morphologies are those of Quaternary species as described in Quaternary literature (e.g. Harland 1983; Powell 1992; Rochon et al. 1999). Many morphological, environmental and sometimes genetic data are available for Quaternary species. The genetic stability over time of the dinoflagellate species is impossible to establish, however, it has been agreed that *Spiniferites* species have sufficient taxonomical/morphological stability to follow them through geological times.

This is particularly the case for *Spiniferites ramosus* with a stratigraphical range of nearly 145 Ma, which seems (an oddity in the biosphere evolution) a very peculiar (even strange) case in the biosphere story. Without genetic fingerprinting, the concept of the morphological species is the lone guiding thread we can follow along such time intervals. In the case of *Spiniferites ramosus*, it corresponds to an ovoid central body with a smooth to shagreenate surface, with gonial processes only and distal trifid, then sometimes bifid, terminations (see Mertens et al. and Londeix et al. 2018). The length of the process is variable and intergonal process may occasionally be present (maximum one per suture). This morphological concept corresponds to the Cretaceous type of the species, illustrated by Davey in Davey and Williams (1966, fig.8) and is consistent with the Quaternary specimens (e.g. Rochon et al. 1999, pl.9, fig.4-6). Although stratigraphically distant, these two specimens illustrate the morphological standard of the species. The stratigraphical range depicted here concerns *Spiniferites ramosus ramosus* and excluded the many subspecies (> 32, Fensome and Williams 2004) assigned to *Spiniferites ramosus*.

If we accept that a species is ubiquitous because it is able to adapt to many environmental conditions, it is logical that its stratigraphical perenity is important. This is indeed what is observed for *Spiniferites ramosus* which proves to be a common species in modern sediments and whose current geographical distribution is very important, especially in environments with high seasonality (e.g. Zonneveld et al. 2013). Thus the long stratigraphical range of *Spiniferites ramosus* might be regarded as a taxonomical stability, at least in a paleontological point of view. The 'index of stratigraphical abundance' for *Spiniferites ramosus* shows two main optima: one during the Late Cretaceous and the second one during the Quaternary (Figure 1). In addition, *Spiniferites ramosus* ISA variations show that its FCO is in the base of Valanginian while its FOD is in the lowermost Berriasian.

The main features of *Spiniferites hyperacanthus* are the regular presence of several intergonal processes and low (or absent) septa. However, some modern specimens of this species show an unexpected morphological plasticity with the presence of well expressed septa (see Limoges et al. 2018). Such morphology is very close to that of *Spiniferites lenzii* and *Spiniferites twistringiensis* leading to wonder how to distinguish these taxa and whether they represent various morphotypes of the same species. The taxonomical identity of these taxa is not questioned here, but the discontinuous ISAs of *Spiniferites hyperacanthus* and *Spiniferites lenzii* are puzzling (Figure 1). Nevertheless, the presence of low to absent septa (i.e. *Spiniferites hyperacanthus*) appears to be a feature more frequent during Neogene and Quaternary times than in previous periods. This is also observed with *Spiniferites mirabilis* ISA (Figure 2), a species morphologically close to *Spiniferites hyperacanthus*. *Spiniferites* cf. *Spiniferites lenzii* illustrated by Oboh-lkuenobe et al. (1998, pl.9, figs. 2-3) from the upper Maastrichtian offshore Ivory closely resembles *Spiniferites hyperacanthus*. Caving is unlikely since many specimens were encountered (op. cit.). On the opposite, specimen illustrated by Lister and Batten (1988, pl.11, fig.6) as *Spiniferites hyperacanthus* appear very close to *Spiniferites lenzii*. Since it is difficult to evaluate the records of non-illustrated Cretaceous specimens, no occurrence of this period has been ruled out here. On the other hand, the Plio-Pleistocene record of *Spiniferites lenzii* from Japan (Matsuoka 1983) is not taken into account.

The emergence of *Spiniferites* morphologies with intergonal processes appears relatively early (Berriasian-Valanginian), showing that it is probably a character deeply rooted into the genus genome.

4.2. ISA comparison for some possibly related taxa

During the Montréal and Ostend round tables dealing with *Spiniferites* and *Achomosphaera* (see Mertens et al. this volume) the synonymization of some species was discussed. The ISAs of some of them are here discussed.

Spiniferites ramosus, *Achomosphaera ramosasimilis* and *Spiniferites bulloideus* are morphologically close species. The first appearance of *Spiniferites ramosus* and *Spiniferites bulloideus* appear far apart, respectively Berriasian and no older

than Ypresian (Figures 1 and 2). The time lapse between the first appearance of *Spiniferites ramosus* and *Achomosphaera ramosasimilis* appears closer, since the latter appears in the Valanginian. In addition, no similarity is observed between *Spiniferites ramosus* and *Spiniferites bulloideus* ISAs (Figure 4A) but variations of *Achomosphaera ramosasimilis* ISA are very similar to those of *Spiniferites ramosus* during the Neogene and the Pliocene, leading to consider a possible taxonomical relationship between these two taxa.

With the same approach, *Spiniferites mirabilis* and *Spiniferites hyperacanthus* ISAs appear to be correlated from the Rupelian to the Pleistocene (Figure 4B). The similarity of their ISAs reinforces the assumption they could be two morphotypes of a same taxon. The records of *Spiniferites serratus* and *Spiniferites splendidus* are too few to make significant the comparison of their ISA to that of *Spiniferites mirabilis*.

It is of note that the ISA of *Nematosphaeropsis labyrinthus* is very close to that of *Spiniferites mirabilis* (Figure 4B) This may suggest a possible link between the two taxa although the two morphologies are very different (intergonal processes and antapical veil in *Spiniferites mirabilis*, presence of trabeculae in *Nematosphaeropsis labyrinthus*).

Several types of cysts are possibly produced by *Gonyaulax spinifera*-type motile cells: e.g. *Spiniferites elongatus*, *Spiniferites membranaceus*, *Spiniferites ramosus*, *Spiniferites bulloideus*, *Spiniferites mirabilis*, *Nematosphaeropsis labyrinthus*, *Bitectatodinium tepikiense*, *Tectatodinium pellitum*, *Ataxiodinium choane* etc. (Rochon et al. 2009).

The ISAs variations through geological time of *Spiniferites elongatus* and *Impagidinium sphaericum* show an impressive covariance (Figure 4C). It gives substance to similar ecological affinities between the two species that are generally associated with sediments in polar to sub-tropical waters (Zonneveld et al. 2013; de Vernal et al. 2018). It also questions whether a biological affinity might exist between the two taxa. As respectively depicted by Helenes (1986) and Ellegaard et al. (2003) the paratabulations of *Impagidinium sphaericum* and *Spiniferites elongatus* show differences in the apical and precingular 6'' paraplates, indicating their ISA covariance is rather due to ecological similarities instead of taxonomical ones. According to Harland (1983), the motile cell of *Impagidinium sphaericum* would be a *Gonyaulax* sp. indet. That of *Spiniferites elongatus* is considered to be *Gonyaulax spinifera* or *Gonyaulax elongata* (Head 1996; Ellegaard et al. 2003). It is noteworthy that Helenes (1986) already indicated paratabulation similarities between what he called *Sphaericum* pattern (represented by *Impagidinium sphaericum*) and the *Spinifera* pattern related to *Gonyaulax spinifera*.

To a lesser extent, the ISA variations of *Spiniferites elongatus* and *Bitectatodinium tepikiense* also show a fair similarity (Figure 4C), which probably has to be interpreted as ecological similarities. The records of *Spiniferites ellipsoideus*, *Spiniferites frigidus* and *R. amphicavata* are too few to make the comparison of their ISAs significant to that of *Spiniferites elongatus*.

Cysts of the motile species *Gonyaulax digitalis* (Pouchet 1883) Kofoid 1911 are thought to be referable to *Spiniferites*

bentorii (cf. Head 1996) or to *Bitectatodinium tepikiense* (Ellegaard et al. 2003). The comparison of ISA of *Spiniferites bentorii* and *Bitectatodinium tepikiense* does not show any relationship between these two taxa (Figure 4D).

No other covariance has been detected between taxa related to *Gonyaulax spinifera*-type motile cells.

As inferred from partial LSU rDNA sequence data, Ellegaard et al. (2003, fig.46) propose a phylogeny of some *Gonyaulax* motile species. According to this method, *Gonyaulax baltica* would have appeared first and *Gonyaulax membranacea* would have appeared last (Figure 5A). In this tree, *Gonyaulax elongata*, *Gonyaulax digitalis* (= *Spiniferites bentorii* or *Bitectatodinium tepikiense*, Head 1996; Ellegaard et al. 2003) and *Gonyaulax* cf. *spinifera* (= *Spiniferites ramosus*, Ellegaard et al. 2003) appear successively between the two former species. That topology differs from the appearance chronology of the cyst equivalent of these species since *Spiniferites ramosus* first occurs at ca. 145 Ma (lowermost Berriasian) and the cyst of *Gonyaulax baltica* only in the Holocene (less than 11 ka). In addition, the order of appearance of *Bitectatodinium tepikiense*, *Spiniferites bentorii*, *Spiniferites elongatus*, *Spiniferites membranaceus* is respectively around 13 Ma (Serravallian), 23 Ma or maybe 58 Ma (Aquitanian or Thanetian), 37 Ma (Priabonian) and 112 Ma (Albian) (Figure 5A, Table 2). The stratigraphical appearances seem therefore to show a different pattern from that obtained by genetic analysis of motile cells, but this difference can simply mean that the stratigraphical range takes into account type morphologies, and not biological species.

5. Conclusion

The 'index of stratigraphical abundance' of the Quaternary *Spiniferites* species show only few similarities between them. Some couples of taxa show ISAs' similarities, such as *Spiniferites mirabilis* and *Spiniferites hyperacanthus*, and to a lesser degree, *Spiniferites ramosus* and *Achomosphaera ramosasimilis*. ISAs' comparisons with species outside of the *Spiniferites* genus sometimes show striking similarities such as for *Spiniferites mirabilis* and *Nematosphaeropsis labyrinthus*, and for *Spiniferites elongatus* and *Impagidinium sphaericum*. In a first approach, the similarities of ISA between two taxa could have been interpreted as indicative of cyst morphotypes belonging to the same species. The example of *Spiniferites elongatus* and *Impagidinium sphaericum* refutes this hypothesis since these two cysts do not have the same tabulation, which excludes the possibility that they could belong to the same species. This leads to dismiss the idea to use ISAs as a tool for taxonomical discrimination. However, it could be a suitable way to discern taxa having similar ecological preferences.

The fact remains that the ISAs allow a better visualization of abundance variations of a taxon, or a morphology, over time than the classic linear stratigraphical range. The ISA proves to be a valuable tool for locating in time the FCO and the LCO.

Moreover, it would be interesting to test the ISAs of some species (of *Spiniferites* and others) on a regional scale and

not on a global scale, as was carried out in this paper, to refine the stratigraphical interest of taxa.

Acknowledgements

I wish to express my gratitude to James Riding (British Geological Survey) for his review enriched by his subsequent advice and constructive exchanges. Stephen Louwey (Ghent University) is thanked for his helpful and constructive reviews of the manuscript and for his patience to improve the text, as well as Tristan Cantat-Gaudin (University of Padova) and Fabienne Marret (University of Liverpool).

References

- Ashraf AR, Erben HK. 1986. Palynologische Untersuchungen an der Kreide/Tertiär-Grenze west-mediterraner Regionen. *Paläontographica Abteilung B*. 200(1):111–163.
- Ashraf AR. 1979. Die rätio-jurassischen floren des Iran und Afghanistans. 6; Jurassische und unterkretazische dinoflagellaten und acritarchen aus Nordafghanistan. *Paläontographica Abteilung B*. 169(4–6):122–158.
- Auffret JP, Graus-Cavagnetto C. 1975. Les formations Paléogènes sous-marines de la Manche Orientale. Données palynologiques. *Bull Soc Géol France Ser 7*. 17(5):641–655.
- Below R, Kirsch K-H. 1994. Die verteilung des palynophytoplanktons einer Dunkel/Hell/Dunkel sequenz des Hochsten Apt (Jacobi-Zone) von Vohrum (Niedersachsen/Deutschland) – neue methodische Ansätze bei der quantitativen Analyse Mariner Floren. *Paläontographica Abt B*. 232(1):59–102.
- Berggren WA, Kent DV, Swisher CC III, Aubry M-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren WA, Hardenbol J, editors. *Geochronology, time scales and global stratigraphic correlation*. Vol. 54. Tulsa: SEPM Special Publication; p. 130–212.
- Brideaux WW. 1977. Taxonomy of upper jurassic – lower cretaceous microplankton from the Richardson Mountains, District of MacKenzie, Canada. *Geological Survey of Canada Bulletin* 281, 89 p.
- Brinkhuis H, Biffi U. 1993. Dinoflagellate cyst stratigraphy of the Eocene/Oligocene transition in Central Italy. *Mar Micropaleontol*. 22(1):131–183.
- Brinkhuis H, Munsterman DK, Sengers S, Sluijs A, Warnaar J, Williams GL. 2003. Late Eocene – Quaternary dinoflagellate cysts from ODP Site 1168, off Western Tasmania. *Proc Ocean Drill Prog Sci Results*. 189:1–36.
- Brinkhuis H. 1992. Late Eocene to early Oligocene Dinoflagellate cysts from central and northeast Italy. PhD Rijksuniversiteit, Utrecht, 169 p.
- Bujak JP. 1973. Microplankton from the Barton Beds of the Hampshire Basin, England [Unpublished Ph.D. Thesis]. Sheffield: University of Sheffield, 455 p.
- Bujak N, Matsuoka K. 1986. Late Cenozoic dinoflagellate cyst zonation in the western and northern Pacific. *Am Assoc Stratigraphic Palynologists*. 17:7–25.
- Chen YY. 1978. Jurassic and Cretaceous palynostratigraphy of a Madagascar well [Unpublished PhD Thesis]. Arizona: Department of Geosciences, University of Arizona; 264 p.
- Claparède E, Lachmann J. 1857. Etudes sur les infusoires et les Rhizopodes. *Mémoires de l'Institut Générois*. 6:392–412.
- Cookson IC, Eisenack A. 1974. Mikroplankton aus Australischen Mesozoischen und Tertiären Sedimenten. *Paläontographica Abt B*. 148(1):44–93.
- Costa LI, Davey RJ. 1992. Dinoflagellate cysts of the Cretaceous System. In: Powell AJ, editor. *A stratigraphic index of dinoflagellate cysts*. London: Chapman and Hall; p. 99–153. (British Micropaleontological Society Publication Series).
- Costa LI, Downie C. 1979. Dinoflagellates. In: Montadert L. et al., editors. Sites 405 and 406. Deep Sea Drilling Project, Initial Reports 48: Washington: U.S. Government Printing Office; p. 228–232.
- Costa LI, Manum SB, Meyer KJ. 1988. Great Britain/Norway;The Viking Graben. In: R. Vinken, compiler. *The Northwest European tertiary basin*. Vol. 100. Hannover: Geologisches Jahrbuch Reihe A; p. 330–332.
- Davey RJ, Williams GL. 1966. The genera *Hystrichosphaera* and *Achomosphaera*. In: Davey RJ, Downie C, Sarjeant WAS, Williams GL, editors. *Studies on Mesozoic and Cainozoic Dinoflagellate Cysts*. British Museum (Natural History) Geology, Bulletin, Supplement 3: London; p. 28–52.
- Davey RJ. 1979. The stratigraphic distribution of dinocysts in the Portlandian (latest Jurassic) to Barremian (Early Cretaceous) of north-west Europe. *Am Assoc Stratigraphic Palynol Contrib Ser*. 5B:49–81.
- Davey RJ. 1982. Dinocyst stratigraphy of the latest Jurassic to Early Cretaceous of the Haldager No. 1 borehole, Denmark. *Geological Survey of Denmark, Series B, No. 6*, 57 p.
- De Coninck J. 1999. Organic-walled phytoplankton biostratigraphy of the Eocene – Oligocene transition in the Kallø Borehole and the Rupelian stratotype area (northwestern Belgium). *Bull Soc Belge Géol Paléontol d'Hydro*. 105(4):171–209.
- De Coninck J. 2001. Organic-walled microfossils in the Oligocene Grimmeringen and Neerreppe Sand Members from the Grimmeringen Type Locality. *Geological Survey of Belgium, Mineralogical Paper* 2001/2, 294:58 p.
- de Klasz I, de Klasz S, Colin J-P, Jan du Chêne R, Ausseil-Badie J, Bellion Y, Peypouquet J-P. 1987. Apport de la micropaléontologie (foraminifères, ostracodes, dinoflagellés) à la connaissance stratigraphique et paléogéographique de la Formation des Madeleines (Danien du Sénégal). *Cahiers de Micropaléontologie, special issue*. 2(3–4):5–27.
- De Schepper S, Head MJ, Louwey S. 2009. Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geol Mag*. 146 (1):92–112.
- de Vernal A, Eynaud F, Henry M, Limoges A, Londeix L, Matthiessen J, Marret F, Pospelova V, Rochon A, Van Nieuwenhove N. 2018. Distribution and (paleo)ecological affinities of the main Spiniferites taxa in the Northern Hemisphere. *Palynology*. 42 Suppl:1.
- de Vernal A, Mudie P.J. 1989. Pliocene and Pleistocene palynostratigraphy at ODP Sites 646 and 647, eastern and southern Labrador Sea. *Proc Ocean Drilling Prog Sci Results*. 105:401–422.
- Deflandre G. 1938. Sur le microplancton des mers Jurassiques, conservé à l'état de matière organique dans les Marnes de Villers-Sur-Mer. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*. 206:687–689.
- Diesing KM. 1866. Revision der Prothelminthen. Abtheilung: Mastigophoren. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. Abteilung 1, Mineralogie, Botanik, Zoologie, Anatomie, Geologie und Paläontologie*. 52:287–401.
- Dodge JD. 1989. Some revisions of the Family Gonyaulacaceae (Dinophyceae) based on a scanning electron microscope study. *Bot Mar*. 32:275–298.
- Downie C, Singh G. 1970. Dinoflagellate cysts from estuarine and raised beach deposits at Woodgrange, Co. Down, N. Ireland. *Grana Palynol*. 9:124–132.
- Duxbury S. 1977. A palynostratigraphy of the Berriasian to Barremian of the Speeton Clay of Speeton, England. *Paläontographica Abt B*. 160(1–3):17–67.
- Dybkaer K. 2004. Dinocyst stratigraphy and palynofacies studies used for refining a sequence stratigraphic model—uppermost Oligocene to lower Miocene, Jylland, Denmark. *Rev Palaeobot Palynol*. 131:201–249.
- Dybkaer K, Piasecki S. 2010. Neogene dinocyst zonation for the eastern North Sea Basin, Denmark. *Review of Palaeobotany and Palynology*. 161:1–29.
- Eaton GL. 1996. *Serilodinium*, a new Late Cenozoic dinoflagellate from the Black Sea. *Rev Palaeobot Palynol*. 91:151–169.
- Edwards LE. 1986. Late Cenozoic dinoflagellate cysts from South Carolina, U.S.A. In: Wrenn JH, Duffield SL, Stein JA, editors. *Papers from the First Symposium on Neogene Dinoflagellate cyst biostratigraphy*. College Station (TX): American Association of Stratigraphic Palynologists, Contribution Series 17: p. 47–58.

- Ehrenberg CG. 1837. Über das Massenverhältniss der jetzt lebenden Kiesel-Infusorien und über ein neues Infusorien-Conglomerat als Polierschiefer von Jastraba in Ungarn. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, aus dem Jahre 1836, Physikalische Klasse. 1:109–135.
- Eidvin T, Goll RM, Grogan P, Smelror M, Ulleberg K. 1998. The Pleistocene to Middle Eocene stratigraphy and geological evolution of the Western Barents Sea Continental Margin at Well Site 7316/5-1 (Bjornoya West area). *Norsk Geologisk Tidsskrift*. 78(1):99–123.
- Eisenack A. 1958. Mikroplankton aus dem norddeutschen Apt, nebst einigen Bemerkungen über fossile Dinoflagellaten. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*. 106:383–422.
- El-Bassiouni AE, Ayyad SN, El-Beialy SY. 1988. On the Eocene-Oligocene boundary in Alam El-Bueib. IX:Western Desert, Egypt. *Rev Esp Micropaleontología*. 20(1):59–70.
- El-Beialy SY. 1990. Palynology, palaeoecology, and dinocyst stratigraphy of the Oligocene through Pliocene succession in the Quantara-1 Well, Eastern Nile Delta, Egypt. *J Afr Earth Sci*. 11(3):291–307.
- Ellegaard M, Daugbjerg N, Rochon A, Lewis J, Harding IC. 2003. Morphologic and genetic (LSU rDNA) variation within *Spiniferites/Gonyaulax* (Dinophyceae), including the cyst-theca relationship of *Spiniferites elongatus* and phylogenetic analysis of the position of *Spiniferites* and *Bitectatodinium* within the Gonyaulacales. *Phycologia*. 42:151–164.
- Ellegaard M, Lewis J, Harding IC. 2002. Cyst-theca relationship, life cycle, and effects of temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp. nov. (Dinophyceae) from the Baltica Sea area. *J Phycol*. 58:775–789.
- Eshet Y, Moshkovitz S, Habib D, Benjamini C, Magaritz M. 1992. Calcareous nannofossil and dinoflagellate stratigraphy across the Cretaceous/Tertiary boundary at Hor Hahar, Israel. *Mar Micropaleontol*. 18(3):199–228.
- Fechner GG, Mohr B. 1988. Early Eocene spores, pollen and microplankton assemblages from Fehmarn Island, North Germany. *Tertiary Res*. 9(1):147–168.
- Fensome RA, Williams GL. 2004. The Lentin and Williams Index of fossil dinoflagellates 2004 Edition. *Am Assoc Stratigr Palynol Contrib Ser*. 42:909 p.
- Fensome RA, Williams GL, Barss MS, Freeman JM, Hill JM. 1990. Acritarchs and fossil prasinophytes: an index to genera, species and infraspecific taxa. *Am Assoc Stratigr Palynol Contrib Ser* 25:771 p.
- Fiet N, Masure E. 2001. Les dinoflagellés albiens du bassin de Marches-Ombrie (Italie): proposition d'une biozotation pour le domaine thétyisien. *Cretaceous Res*. 22(1):63–77.
- Firth JV. 1996. Upper Middle Eocene to Oligocene dinoflagellate biostratigraphy and assemblage variations in Hole 913B, Greenland Sea. *Proc ODP Sci Res*. 151:203–242.
- Foucher J-C. 1974. Microfossiles des silex du Turonien suprieur de Ruyaulcourt (Pas-de-Calais). *Ann Paléontol Invert*. 60:113–164.
- Foucher J-C. 1975. Dinoflagellés et acritarches des silex créacés du Bassin de Paris: une synthèse stratigraphique. *Ann Sci Univ Reims Assoc Rég pour l'étude Recherche Sci*. 13(1):8–10.
- Frederiksen NO. 1969. Stratigraphy and palynology of the Jackson Stage (Upper Eocene), and adjacent strata of Mississippi and Western Alabama [Unpublished Ph.D. Thesis]. University of Wisconsin; 355 p.
- Gedl P. 2005. Late Eocene – early Oligocene organic-walled dinoflagellate cysts from Folsz, Magura Nappe, Polish Carpathians. *Acta Palaeobot*. 45(1):27–83.
- Gedl P, Leszczynski S. 2005. Palynology of the Eocene-Oligocene Transition in the Marginal Zone of the Magura Nappe at Folsz (Western Carpathians, Poland). *Geol Carpathica (Geologicky Zbornik)* 56(2):155–167.
- Gitmez GU, Ertug K. 1999. Dinoflagellate cysts and acritarchs from the Jurassic-Cretaceous boundary, Northwest Anatolia, Turkey. *Micropaleontology*. 45(1):69–98.
- Gocht H. 1959. Mikroplankton aus dem nordwestdeutschen Neokom (Teil II). *Paläontologische Zeitschrift*. 33(1):50–89.
- Grill SC, Quattrocchio ME. 1996. Fluctuaciones eustaticas durante el Holoceno a partir del regis de paleomicroplancton; Arroyo Napostá Grande, sur de la Provincia de Buenos Aires. *Ameghiniana*. 33(4):435–442.
- Guerrera F, Coccloni R, Corradini D, Bertoldi R. 1985. Caratteristiche lito-sedimentologiche e micropaleontologiche (foraminiferi, dinoflagellati, pollini e spore) di successioni tripolacee plioceniche del bacino di Caltanissetta. *Boll della Soc Geol Ital*. 103:629–660.
- Guy-Ohlson D. 1986. Jurassic palynology of the Vilhelmsfält bore no.1, Scania, Sweden: Toarcian-Aalenian. Stockholm: Swedish Museum of Natural History, Section of Palaeobotany, 127 p.
- Hansen JM. 1977. Dinoflagellate stratigraphy and echinoid Dinoflagellate biostratigraphy and depositional environment distribution in Upper Maastrichtian and Danian deposits ment of the type Maastrichtian (Late Cretaceous, ENCI from Denmark. *Bulletin of the Geological Society of Den- Quarry, The Netherlands*). *Mar Micropaleontology*. 31(26):1–26.
- Hardenbol J, Thierry J, Farley MB, Jacquin T, De Graciansky P-C, Vail PR. 1998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. In De Graciansky P-C, Hardenbol J, Jacquin T, Vail PR, editors. *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins*. Vol. 60. Tulsa: SEPM Special Publication, Chart 5.
- Harding IC, Smith GA, Riding JB, Wimbledon WAP. 2011. Inter-regional correlation of Jurassic/Cretaceous boundary strata based on the Tithonian-Valanginian dinoflagellate cyst biostratigraphy of the Volga Basin, western Russia. *Rev Palaeobot Palynol*. 167:82–116.
- Harland R, Reid PC, Dobell P, Norris G. 1980. Recent and sub-recent dinoflagellate cysts from the Beaufort Sea, Canadian Arctic. *Grana*. 19(3):211–225.
- Harland R. 1977. Dinoflagellate cysts from the Bearpaw formation (upper campanian to Maastrichtian) of Montana. *Palaeontology*. 20(1):179–193.
- Harland R. 1978. Quaternary and Neogene dinoflagellate cysts. In: Thusu B, editor. *Distribution of biostratigraphically diagnostic dinoflagellate cysts and miospores from the Northwest European continental shelf and adjacent areas*. Vol. 100. College Station (TX): Continental Shelf Institute; p. 7–17.
- Harland R. 1979. Dinoflagellate biostratigraphy of Neogene and Quaternary sediments at holes 400/400A in the Bay of Biscay (Deep Sea Drilling Project Leg 48). In: Montadert L, Roberts DG, editors. *Initial Reports of the DSDP 48*: p. 531–545.
- Harland R. 1983. Distribution maps of recent dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Palaeontology*. 26(2):321–387.
- Head MJ, Nøhr-Hansen H. 1999. The extant thermophilic *Tectatodinium pellitum* (al. *Tectatodinium rugulatum*) from the Danian of Denmark. *J Paleontol*. 73(4):577–579.
- Head MJ, Westphal H. 1999. Palynology and Paleoenvironments of a Pliocene Carbonate Platform: The Clino Core, Bahamas. *J Paleontol*. 73(1):1–25.
- Head MJ. 1996. Chapter 30. Modern dinoflagellate cysts and their biological affinities. In: Jansonius J, McGregor DC, editors. *Palynology: principles and applications*. Dallas: American Association of Stratigraphic Palynologists Foundation; 3: p. 1197–1248.
- Head MJ. 1997. Thermophilic dinoflagellate assemblages from the Mid-Pliocene of eastern England. *J Paleontol*. 71(2):165–193.
- Head MJ. 2007. Last Interglacial (Eemian) hydrographic conditions in the southwestern Baltic Sea based on dinoflagellate cysts from Ristinge Klint, Denmark. *Geol Mag*. 144(6):987–1013.
- Heilmann-Clausen C. 1987. Lower Cretaceous dinoflagellate biostratigraphy in the Danish Central Trough. *Danmarks Geologiske Undersøgelse*. 17:1–89.
- Helenes J. 1986. Some variations in the paratabulation of gonyaulacoid dinoflagellates. *Palynology*. 10(1):73–110.
- Hultberg SU, Malmgren BA. 1995. Evolutionary patterns in the dinoflagellate cyst genus *Spiniferites* (Cretaceous through Quaternary): relationships to sea-level changes. *Hist Biol*. 10:341–357.
- ICS. 2016. International Chronostratigraphic Chart, v2016/04. International Commission on Stratigraphy. <http://www.stratigraphy.org/ICSchart/ChronostratChart2016-04.jpg>.

- Islam MA. 1984. A study of early Eocene palaeoenvironments in the Isle of Sheppey as determined from microplankton assemblage composition. *Tertiary Res.* 6:11–21.
- Jan du Chêne RE. 1988. Étude systématique des kystes de dinoflagellés de la Formation des Madeleines (Danien du Sénégal). *Cahiers de micropaléontologie*, Nouvelle série. 2:147–174.
- Kar RK. 1985. The fossil floras of Kachchh. IV– tertiary palynostratigraphy. *Palaeobotanist.* 34:1–280.
- Kirsch KH, Below R. 1995. Quantitative Untersuchung der Dinoflagellatenverteilung in den hell/dunkel-Rhythmiten des Hauterive-Barrême-Grenzbereichs im Niedersächsischen Becken (Norddeutschland) am Beispiel des Profils der Tongrube Otto Gott bei Sarstedt. *Paläontographica Ab B.* 236(4):105–146.
- Klump B. 1953. Beitrag zur Kenntnis der Mikrofossilien des mittleren und oberen Eozän. *Palaeontographica. Abteilung A.* 103:377–406.
- Kofoid CA. 1911. Dinoflagellata of the San Diego region, IV. The genus *Gonyaulax*, with notes on its skeletal morphology and a discussion of its generic and specific characters. University of California Publications in Zoology. 8:187–286.
- Koreneva EV, Kartashova GG. 1978. Palynological study of samples from holes 379A, 380A, Leg 42B. Initial Rep DSDP. 42(2):951–992.
- Köthe A. 1990. Paleogene dinoflagellates from Northwest Germany; biostratigraphy and paleoenvironment. *Geol Jahrbuch Reihe A.* 118:3–111.
- Kuhlmann G. 2004. Hoge resolutie stratigrafie en paleo-milieu veranderingen in de zuidelijke Noordzee tijdens het Neogeen Een geïntegreerde studie van Laat Cenozoïsche marine afzettingen in het noordelijke gedeelte van het Nederlandse offshore gebied (met een samenvatting in het Nederlands). *Geologica Ultraiectina, Mededelingen van de Faculteit Geowetenschappen Universiteit Utrecht.* 245:1–205.
- Kumar A. 1980. Early Cretaceous dinocysts and acritarchs from the Krishna-Godavari Basin, Andhra Pradesh, India. *International Palynological Conference, 5th, Abstracts*, 210. Cambridge.
- Lebedeva NK, Nikitenko BL. 1999. Dinoflagellate cysts and microforaminifera of the Lower Cretaceous Yatria River section, Subarctic Ural, northwest Siberia (Russia). *Biostratigraphy, palaeoenvironmental and palaeogeographic discussion.* *Grana.* 38(2–3):134–143.
- Lentin JK, Williams GL. 1973. Fossil dinoflagellates: index to genera and species. Geological Survey of Canada. Paper 73–42; p. 176.
- Lewis J, Rochon A, Ellegaard M, Mudie P, Harding I. 2001. The cyst–theca relationship of *Bitectatodinium tepikiense* (Dinophyceae). *Eur J Phycol.* 36(2):137–146.
- Lewis J, Rochon A, Harding IC. 1999. Preliminary observations of cyst–theca relationships in *Spiniferites ramosus* and *Spiniferites membranaceus* (Dinophyceae). *Grana.* 38:113–124.
- Limoges A, Londeix L, Mertens KN, Rochon A, Pospelova V, de Vernal A, del Carmen Cuéllar T. 2018. Towards an identification key for Pliocene and Quaternary *Spiniferites* taxa bearing intergonal processes based on observations from estuarine and coastal environments. *Palynology.* 42 Suppl:1 (this volume).
- Lister JK, Batten DJ. 1988. Stratigraphic and palaeoenvironment distribution of Early Cretaceous dinoflagellate cysts in the Hurlands Farm Borehole, West Sussex, England. *Paläontographica Abt B.* 210(1):9–89.
- 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. *Mar Micropaleontology.* 84–85:1–13.
- Londeix L, Benzakour M, de Vernal A, Turon J-L, Suc J-P. 1999. Late Neogene dinoflagellate cyst assemblages from the Strait of Sicily, Central Mediterranean Sea: paleoecological and biostratigraphical implications. In: Wrenn JH, Suc J-P Suc, Leroy SAG, editors. *The Pliocene: time of change.* Dallas: American Association of Stratigraphic Palynologists Foundation; p. 65–91.
- Londeix L, Herreyre Y, Turon J-L, Fletcher W. 2009. Last glacial to holocene hydrology of the Marmara Sea as inferred by the dinoflagellate cysts record. *Rev Palaeobot Palynol.* 158:52–71.
- Londeix L, Jan du Chêne R. 1998. Stratigraphie des kystes de dinoflagellés du Burdigalien stratotypique bordelais (France). *Geobios.* 30(3):283–294.
- Londeix L, Lopes S. 2014. Les dinokystes de l'Aquitainien stratotypique: biostratigraphie et quantification de paramètres environnementaux. In: Londeix L (coord.), editor. *Stratotype aquitainien.* Paris: Muséum national d'Histoire naturelle, Biotope; 416 p. (Patrimoine géologique, 5).
- Londeix L, Zonneveld K, Masure E. 2018. Operational taxonomy of Quaternary *Spiniferites* sensu lato and identification. *Palynology.* 42 Suppl:1 (this volume).
- Londeix L. 1990. La distribution des kystes de dinoflagellés dans les sédiments hémipélagiques, (Ardèche), et pélagiques, (Arc de Castellane, S.E. de la France), en Domaine Vocontien, du Valanginien terminal au Barrémien inférieur. *Biostratigraphie et relations avec la stratigraphie séquentielle.* Bordeaux 1 University [PhD thesis] 478; 606 p.
- Louwey S, Head MJ, De Schepper S. 2004. Dinoflagellate cyst stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea Basin. *Geol Mag.* 141(3):353–378.
- Maier D. 1959. Planktonuntersuchungen in tertiären und quartären marinen Sedimenten. Ein Beitrag zur Systematik, Stratigraphie und Ökologie der Coccolithophoridae, Dinoflagellaten und Hystrichosphaerideen vom Oligozän bis zum Pleistozän. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen.* 107:278–340.
- Mangin S. 2002. Distribution actuelle des kystes de dinoflagellés en Méditerranée occidentale et application aux fonctions de transfert. *Diplôme d'Etudes Approfondies dissertation.* Bordeaux: Bordeaux 1 University; 34 p.
- Manum SB, Boulter MC, Gunnarsdottir H, Rangnes K, Scholze A. 1989. Eocene to Miocene palynology of the Norwegian Sea (ODP Leg 104). In: Eldholm O, et al. editors. *Proceedings Ocean Drilling Program, College Station (TX): Scientific Results 104.* p. 611–639.
- Mao S. 1989. V. Dinoflagellata. In: Hao Y, Mao S, Ruan P, Su X, Sun S, Wang Z, Yin J, Zheng H, editors. *Quaternary microbiotas and their geological significance from northern Xisha Trench of South China Sea.* Wuhan, China: China University of Geosciences Press; p. 132–147.
- Marret F, de Vernal A, Pedersen TF, McDonald D. 2001. Middle Pleistocene to Holocene palynostratigraphy of Ocean Drilling Program Site 887 in the Gulf of Alaska, northeastern North Pacific. *Can J Earth Sci.* 38(3):373–386.
- Martini E. 1971. Standard tertiary and quaternary calcareous nannoplankton zonation. In: Farinacci A, editor. *Proceeding 2nd international conference on Planktonic Microfossils;* Roma, 2:p. 739–785.
- Masure E. 1988. Le genre *Maghrebinia* Below, 1981, nouvelle interprétation et amendement. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine.* 12(1):361–381.
- Matsuoka K. 1983. Late Cenozoic dinoflagellates and acritarchs in the Niigata district, Central Japan. *Palaeontographica Abt B.* 187(1–3):89–154.
- Matsuoka K, Bujak JP, Shimazaki T. 1987. Late Cenozoic dinoflagellate cyst biostratigraphy from the west coast of northern Japan. *Micropaleontology.* 33:214–229.
- McCarthy FMG, Katz ME, Kotthoff U, Browning JV, Miller KG, Zanatta R, Williams RH, Drljepan M, Hesselbo SP, Bjerrum CJ, et al. 2013. Sea-level control of New Jersey margin architecture: palynological evidence from Integrated Ocean Drilling Program Expedition 313. *Geosphere.* 9(6):1457–1487.
- McCarthy FMG, Mudie PJ. 1996. Palynology and dinocyst biostratigraphy of Upper Cenozoic sediments from ODP Leg 149 Sites 898 and 901, Iberian Abyssal Plain. *Proc ODP Sci Res.* 149:241–265.
- McMinn A. 1993. Neogene dinoflagellate cyst biostratigraphy from Sites 815 and 823, Leg 133, Northeastern Australian Margin. *Proc ODP Sci Res.* 133:97–105.
- Mertens KN, Van Nieuwenhove N, Gurdebeke PR, Aydin H, Bogus K, Bringué M, Dale B, De Schepper S, de Vernal A, Ellegaard M, et al. 2018. Summary of round table discussions about *Spiniferites* and *Achomospaera* occurring in Pliocene to modern sediments. *Palynology.* 42 Suppl:1.
- Monteil E. 1992. Kystes de dinoflagellés index (Tithonique-Valanginien) du sud-est de la France. Proposition d'une nouvelle zonation palynologique. *Revue de Paléobiologie.* 11(1):299–306.

- Monteil E. 1993. Dinoflagellate cyst biozonation of the Tithonian and Berriasian of south-east France. Correlation with the sequence stratigraphy. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*. 17:249–273.
- Morzadec-Kerfourn MT. 1979. Etude des organismes les kystes de dinoflagelles. In: Burolet PF, Clairefond P, Winnock E, editors. *La mer Pelagienne. Géologie Méditerranéenne*. 6(1):221–248.
- Moshkovitz S, Habib D. 1993. Calcareous nannofossil and dinoflagellate stratigraphy of the Cretaceous-Tertiary boundary, Alabama and Georgia. *Micropaleontology*. 39(2):167–191.
- Mudie PJ, Rochon A, Aksu AE, Gillespie H. 2002. Dinoflagellate cysts, freshwater algae and fungal spores as salinity indicators in Late Quaternary cores from Marmara and Black Seas. *Mar Geol*. 190(1–2):203–231.
- Mudie PJ. 1986. Palynology and dinoflagellate biostratigraphy of Deep Sea Drilling Project Leg 94, Sites 607 and 611, North Atlantic Ocean. *Deep Sea Drilling Proj Initial Rep*. 94:785–812.
- Mudie PJ. 1989. Palynology and dinocyst biostratigraphy of the Late Miocene to Pleistocene, Norwegian Sea; ODP Leg 104, Sites 642 to 644. *Proc ODP Sci Res*. 104:587–610.
- Mudie PJ, Marret F, Aksu AE, Hiscott RN, Gillespie H. 2007. Palynological evidence for climatic change, anthropogenic activity and outflow of Black Sea Water during the Late Pleistocene and Holocene: centennial- to decadal-scale records from the Black and Marmara Seas. *Quaternary Int*. 167–168:73–90.
- Oboh-Ikuenobe FE, Yepes O, Greggs JM. 1998. Palynostratigraphy, palynofacies, and thermal maturation of Cretaceous-Paleocene sediments from the Côte d'Ivoire-Ghana Transform Margin. *Proc Ocean Drilling Prog Sci Res*. 159:277–318.
- Ogg JG, Ogg G. 2008a. Pliocene/Pleistocene. (0–6 Ma Time-Slice). Update to Geological Time Scale 2004 (Gradstein, F.M., Ogg, J.G., Smith, A.G., et al., Cambridge Univ. Press) and The Concise Geologic Time Scale (Ogg, J.G., Ogg, G., Gradstein, F.M., 2008). https://engineering.purdue.edu/Stratigraphy/charts/Timeslices/0_Plio_Pleist.pdf.
- Ogg JG, Ogg G. 2008b. Paleogene. (33–66 Ma time-slice). Update to Geological Time Scale 2004 (Gradstein, F.M., Ogg, J.G., Smith, A.G., et al., Cambridge Univ. Press) and The Concise Geologic Time Scale (Ogg, J.G., Ogg, G., Gradstein, F.M., 2008). https://engineering.purdue.edu/Stratigraphy/charts/Timeslices/2_Paleogene.pdf.
- Ogg JG, Ogg G. 2008c. Late Jurassic. (139–169 Ma time-slice). Update to Geological Time Scale 2004 (Gradstein, F.M., Ogg, J.G., Smith, A.G., et al., Cambridge Univ. Press) and The Concise Geologic Time Scale (Ogg, J.G., Ogg, G., Gradstein, F.M., 2008). https://engineering.purdue.edu/Stratigraphy/charts/Timeslices/5_JurCret.pdf.
- Palynodata Inc. & White JM. 2008. Palynodata Datafile: 2006 version, with Introduction by J.M. White. Geological Survey of Canada Open File 5793. <http://paleobotany.ru/index.php?id=25>.
- Pestchevitskaya E, Lebedova N, Ryabokon A. 2011. Uppermost Jurassic and lowermost Cretaceous dinocyst successions of Siberia, the Subarctic Urals and Russian Platform and their interregional correlation. *Geol Carpathica*. 62(3):189–202.
- Piasecki S. 1980. Dinoflagellate cyst stratigraphy of the Miocene Hodde and Gram Formations, Denmark. *Geol Soc Denmark Bull*. 29:53–76.
- Pouchet G. 1883. Contribution à l'étude des cilioflagellés. *Journal of Anatomy and Physiology*. 19:399–455.
- Poulsen NE, Manum SB, Williams GL, Ellegaards M. 1996. Tertiary dinoflagellate biostratigraphy of Sites 907, 908 and 909 in the Norwegian-Greenland Sea. In: Thiede J, Myhre AM, Firth JV, Johnson GL, Ruddiman WF, editors. *Proceedings of the Ocean Drilling Program*. Vol. 151. College Station (TX): Scientific Results; p. 255–287.
- Powell AJ. 1986a. A dinoflagellate cyst biozonation for the Late Oligocene to Middle Miocene succession of the Langhe Region, northwest Italy. *Am Assoc Stratigraphic Palynol Contrib Ser*. 17:105–127.
- Powell AJ. 1986b. The stratigraphic distribution of Late Miocene dinoflagellate cysts from the Castellian superstage stratotype, Northwest Italy. *Am Assoc Stratigraphic Palynol Contrib Ser*. 17:129–149.
- Powell AJ. 1988. A preliminary investigation into the Neogene dinoflagellate cyst biostratigraphy of the British southwestern approaches. *Bulletin des Centres de Recherche Exploration-Production Elf-Aquitaine*. 12(1):277–311.
- Powell AJ, editor. 1992. A stratigraphic index of dinoflagellate cysts. London: British Micropalaeontological Society Publications Series; 290 p.
- Powell AJ, Brinkhuis H, Bujak JP. 1996. Upper Paleocene-Lower Eocene dinoflagellate cyst sequence biostratigraphy of Southeast England. In: Knox RWO, et al. editors. *Correlation of the early Paleogene in Northwest Europe*. Vol. 101. London: Geological Society Special Publication; p. 145–183.
- Price AM, Pospelova V. 2014. *Spiniferites multisphaerus*, a new dinoflagellate cyst from the Late Quaternary of the Guaymas Basin, Gulf of California, Mexico. *Palynology*. 38:101–116.
- Radi T, de Vernal A. 2004. Dinocyst distribution in surface sediments from the northeastern Pacific margin (40–60°N) in relation to hydrographic conditions, productivity and upwelling. *Rev Palaeobot Palynol*. 128:169–193.
- Reid PC. 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia Beihefte*. 25:579–637.
- Riley LA, Fenton JPG. 1984. Palynostratigraphy of the Berriasian to Cenomanian sequence at Deep Sea Drilling Project Site 535, Leg 77, southeastern Gulf of Mexico. *Deep Sea Drilling Proj Initial Rep*. 77:675–690.
- Rochon A, de Vernal A, Turon J-L, Matthiessen J, Head MJ. 1999. Distribution of Recent dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent areas in relation to sea-surface parameters. *Am Assoc Stratigr Palynol Contrib Ser*. 35:146 p.
- Rochon A, Lewis J, Ellegaard M, Harding IC. 2009. The *Gonyaulax spinifera* (Dinophyceae) “complex”: Perpetuating the paradox? *Rev Palaeobot Palynol*. 155:52–60.
- Rosignol M. 1962. Analyse pollinique de sédiments marins quaternaires en Israël II. — Sédiments pleistocènes. *Pollen et Spores*. 4:121–148.
- Rosignol M. 1964. Hystrichosphères du Quaternaire en Méditerranée orientale, dans les sédiments pléistocènes et les boues marines actuelles. *Revue de Micropaléontologie*. 7(2):83–99.
- Sarjeant WAS. 1960. Microplankton from the Corallian rocks of Yorkshire. *Proc Yorkshire Geol Soc*. 32(4):389–408.
- Sarjeant WAS. 1962. Microplankton from the Amphill Clay of Melton, South Yorkshire. *Palaeontology*. 5(3):478–497.
- Sarjeant WAS. 1970. The genus *Spiniferites* Mantell, 1850 (Dinophyceae). *Grana*. 10:74–78.
- Sarjeant WAS. 1979. Middle and Upper Jurassic dinoflagellate cysts: the world excluding North America. *Am Assoc Stratigr Palynol Contrib Ser*. 5B:133–157.
- Sarjeant WAS. 1983. A restudy of some Dinoflagellate cyst holotypes in the University of Kiel Collections. IV. The Oligocene and Miocene holotypes of DOROTHEA MAIER (1959). *Meyniana*. 35:85–137.
- Stoker MS, Leslie AB, Scott WD, Briden JC, Hine NM, Harland R, Wilkinson IP, Evans D, Ardu DA. 1994. A record of Late Cenozoic stratigraphy, sedimentation and climate change from the Hebrides Slope, north-east Atlantic Ocean. *J Geol Soc Lond*. 151(2):235–249.
- Stover LE, Brinkhuis H, Damassa SP, De Verteuil L, Helby RJ, Monteil E, Partridge AD, Powell AJ, Riding JB, Smelror M, et al. 1996. Chapter 19. Mesozoic-Tertiary dinoflagellates, acritarchs and prasinophytes. In: Jansonius J, McGregor DC, editors. *Palynology: principles and applications*. Vol. 2. Dallas: American Association of Stratigraphic Palynologists Foundation; p. 641–750.
- Stover LE, Evitt WR. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. *Stanford University Publications, Geological Sciences*. 15:300 p.
- Strauss C. 1993. Taxonomie und biostratigraphie des marinen mikroplanktons mit organischer wandung im Oligo-Miozan Ostdeutschlands. *Dissertation Bergakademie Freiberg*, 110 p.
- Suc J-P, Violanti D, Londeix L, Poumot C, Robert C, Clauzon G, Gautier F, Turon J-L, Ferrier J, Chikhi H, et al. 1995. Evolution of the Messinian Mediterranean environments; the Tripoli Formation at Capodarso (Sicily, Italy). *Rev Palaeobot Palynol*. 87(1):51–79.
- Sun XK, Song ZC. 1992. Quaternary dinoflagellates from arenaceous dolomite in Hainan Island. (in Chinese with English summary). *Acta Micropalaeontologica Sinica*. 9(1):45–52.

- Tea-Yassia J, Digbehil ZB, Yaa KR, Glohia BV. 1999. Étude de quelques palynomorphes du crétacé supérieur du bassin offshore de Côte d'Ivoire: implications biostratigraphiques et paléoenvironnementales. *J Afr Earth Sci.* 29(4):783–798.
- Thusu B, van der Eem JGLA, El-Mehdawi A, Bu-Argoub F. 1989. Jurassic–Early Cretaceous palynostratigraphy in northeast Libya. In Arnauti E, et al., editors. *The subsurface palynostratigraphy of Northeast Libya*. Libya: Special Publication of the University of Garryounis; p. 171–213.
- Thusu O, Vigran JB. 1985. Middle – Late Jurassic (Late Bathonian – Tithonian) Palynomorphs. *J Micropalaeontol.* 4(1):113–130.
- Versteegh GJM, Zonneveld KAF. 1994. Determination of palaeoecological preferences of dinoflagellates by applying detrended and canonical correspondence analysis to Late Pliocene dinoflagellate cyst assemblages of the South Italian Singa section. *Rev Palaeobot Palynol.* 84(1):181–199.
- Wall D, Dale B, Harada K. 1973. Descriptions of new fossil dinoflagellates from the Late Quaternary of the Black Sea. *Micropaleontology.* 19:18–31.
- Wall D, Dale B. 1970. Living hystrichosphaerid dinoflagellate spores from Bermuda and Puerto Rico. *Micropaleontology.* 16:47–58.
- Wall D. 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology.* 10(1):95–123.
- Warny S. 1999. Mio-Pliocene palynology of the Gibraltar Arc: a new perspective on the Messinian Salinity Crisis [Unpublished Ph.D. dissertation]. Louvain (BE): Université Catholique de Louvain, Faculté des Sciences; 347 p.
- Williams GL, Brinkhuis H, Bujak J, Damassa S, Hochuli PA, De Verteuil L, Zevenboom D. 1998. Cenozoic Biochronostratigraphy – Dinoflagellate cysts. In: De Graciansky PC, Hardenbol J, Jacquín T, Vail PR, editors. *Mesozoic and Cenozoic Sequence Chronostratigraphic Framework of European Basins. Mesozoic and Cenozoic Sequence Stratigraphy of European Basins*. Vol. 60. Tulsa: SEPM Special Publication.
- Williams GL, Bujak JP. 1985. 18. Mesozoic and Cenozoic dinoflagellates. In: Bolli HM, Saunders JB, Perch-Nielsen K, editors. *Plankton stratigraphy*. Cambridge: Cambridge University Press; p. 847–964. (Cambridge Earth Science Series).
- Williams GL, Stover LE, Kidson EJ. 1993. Morphology and stratigraphic ranges of selected Mesozoic–Cenozoic dinoflagellate taxa in the northern hemisphere. Geological Survey of Canada paper 92–10, Ottawa (CA); 137 p.
- Wrenn JH, Kokinos JP. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico. College Station (TX): American Association of Stratigraphic Palynologists, Contributions Series 17:169–225.
- Yu J, Zhang W. 1980. Upper Cretaceous dinoflagellate cysts and acritarchs of Western Xinjiang. (Sinkiang Uighur). *Bull Chinese Acad Geol Sci.* 2(1):93–119. (in Chinese with English summary).
- Yun H. 1981. Dinoflagellaten aus der Oberkreide (Santon) von Westfalen. *Palaeontographica, Abteilung B.* 177:1–89.
- Yun H, Byun H, Park YA. 2000. Palaeoenvironments interpretation based on microfossil assemblages from intertidal sediments of the Haenam Bay. *J Paleontol Soc Korea.* 16(2):123–144.
- Zevenboom D. 1996. Late Oligocene – Early Miocene dinoflagellate cysts from the Lemm Carrosio Section, (northwest Italy): Biostratigraphy and palaeoenvironmental interpretation. *G Geol Ser 3A.* 58(1):81–93.
- Zhao YY, Morzadec-Kerfourn MT. 1994. Nouveaux kystes de dinoflagellés: *Spiniferites pacificus* nov. sp. et *Pentadinium netangei* nov. sp. du Pléistocène du nord-ouest Pacifique. *Geobios.* 27(3):261–269.
- Zhu H. 2000. On the dynamics of Permian phytoprovincial succession of the Tarim Plate. In: Song Z, editor. *Palynofloras and Palynomorphs of China*. Hefei: Press of University of Science and Technology of China; p. 28–40.
- Zonneveld KAF, Marret F, Versteegh GJM, Bonnet S, Bouimtarhan I, Crouch E, de Vernal A, Elshanawany R, Edwards L, Esper O, et al. 2013. Atlas of modern dinoflagellate cyst distribution based on 2405 datapoints. *Rev Palaeobot Palynol.* 191:1–197.