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To cite this article: Kenneth Neil Mertens & Consuelo Carbonell-Moore (2018) Introduction to *Spiniferites* Mantell 1850 special issue, *Palynology*, 42:sup1, 1-9, DOI: 10.1080/01916122.2018.1465741

To link to this article: <https://doi.org/10.1080/01916122.2018.1465741>



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Published online: 14 Dec 2018.



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Introduction to *Spiniferites* Mantell 1850 special issue

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ABSTRACT

The first chapter of this special issue introduces the proceedings of two workshops concerning the cyst-based genus *Spiniferites* Mantell 1850. The historical background of the cyst-based genus *Spiniferites*, its closely related genera and the theca-based genus *Gonyaulax* Diesing 1866 is presented here.

KEYWORDS

Spiniferites; *Achomospaera*;
Nematosphaeropsis;
Gonyaulax

1. Introduction

This special issue presents the proceedings of two workshops concerning the dinoflagellate cyst-based genus *Spiniferites* Mantell 1850 and its closely related genera. During the first workshop problems surrounding species concepts in *Spiniferites* and related genera were highlighted and strategies to solve these issues were proposed; in the follow-up workshop results of new studies were presented. The first one was held at GEOTOP, Université du Québec à Montréal (UQAM), in Montréal (Canada) from 14 to 17 April 2014, and was hosted by Anne de Vernal, Audrey Limoges, Kenneth Neil Mertens and Nicolas Van Nieuwenhove. The follow-up workshop was held at Flanders Marine Institute (VLIZ), in Oostend, Belgium and Research Unit Palaeontology, from 6 to 9 July 2015 and was hosted by Kenneth Neil Mertens, Willemijn Quaijtaal, Thomas Steeman, Pieter Gurdebeke and Stephen Louwye.

The genus *Spiniferites* has representatives going back to the Cretaceous (Sarjeant 1970). Currently, it encompasses at least 100 species (Fensome et al. 2008), of which at least 13 species are extant [12 reported by Zonneveld et al. (2013) alongside the recently described *Spiniferites multisphaerus* Price and Pospelova 2014].

In contrast, there are currently 71 extant species that belong to the genus *Gonyaulax* Diesing (Gómez 2012), of which only 21 of these may be assigned to this genus using Dodge's 1989 *Gonyaulax* generic concept (17 species listed by Dodge, plus four new ones: *G. baltica* Ellegaard, Lewis and Harding 2002, *G. ellegaardiae* Mertens, Aydin, Takano, Yamaguchi and Matsuoka 2015, *G. membranacea* (Rossignol) Ellegaard et al. 2003, *G. elongata* (Reid) Ellegaard et al. 2003).

Only four of the 13 extant *Spiniferites* species (*S. elongatus* Reid 1974, *S. pachydermus* (Rossignol) Reid 1974, *S. membranaceus* (Rossignol) Sarjeant 1970, *S. ramosus* (Ehrenberg) Mantell) have been (albeit still disputable) related to four out of the 21 species of *Gonyaulax* (*G. elongata*, *G. ellegaardiae*, *G. membranacea*, *G. spinifera* Diesing), which reflects the large amount of

experimental and taxonomic work that still needs to be done. This work is urgently required since *Spiniferites* species are considered useful palaeoecological indicators (e.g. Zonneveld et al. 2013), valuable biogeographic indicators (Dale 1996), excellent biostratigraphic markers (e.g. Bujak and Matsuoka 1986), potentially toxic through yessotoxin production (e.g. Rhodes et al. 2006; Riccardi et al. 2009). In addition their long evolution and diversification since the Cretaceous is poorly understood and could shed a unique light on the evolution of unicellular life.

In this introduction we document the historical background of the cyst-based genus *Spiniferites* (1.1) and theca-based genus *Gonyaulax* (1.2) and how their biological affiliation was established (1.3).

1.1. History of the fossil-based genus *Spiniferites* and related genera

The history of the genus *Spiniferites* (along with other dinoflagellate cysts) was reviewed in great detail by Sarjeant (1964; 1970; 1974, p. 49–62) and Dale (1983). Sarjeant's reviews were obscurely presented, thus we feel the need to summarize and update them here. The first published observation of a *Spiniferites* was made by Christian Gottfried Ehrenberg from upper Cretaceous flint, although he attributed them to the genus *Xanthidium* because he thought these were siliceous zygospores of freshwater *Xanthidium*, a genus of desmidiacean fresh-water algae (Ehrenberg 1838). He erected two species, *Xanthidium furcatum* and *Xanthidium ramosum*. These and related taxa were called "xanthidia" for almost a century (e.g. White 1842). Mantell (1845) suggested they were of a flexible substance, probably organic, he suggested chitin or cutin, and in Mantell (1850, p. 191) proposed the name *Spiniferites* "in allusion to the numerous spines with which all the species are beset", but did not transfer any species to this new name. Mantell (1854) rectified this by attributing Ehrenberg's *Xanthidium ramosum*

to *Spiniferites ramosus* and White's *Xanthidium tubiferum* var. *palmatum* to *Spiniferites palmatus* and at the same time, he erected *Spiniferites reginaldi* (the last two species are problematic, see Sarjeant 1964, p. 66). Mantell did not designate a type species for *Spiniferites*, but this was not required before 1931 by the zoological code.

Wetzel (1933) considered the *Xanthidia* were in an unknown systematic position (*incertae sedis*), and erected the genus *Hystrichosphaera*, placing the *Xanthidia* in a new family: the *Hystrichosphaeridae* (the ending shows Wetzel treated them under the zoological code). *H. ramosa* and *H. furcata* were designated as joint types. This was not permitted at that time under the zoological code, invalidating Wetzel's designation. *Hystrichosphaera* was emended by Deflandre (1937), to only include species with polygonal fields and an equatorial girdle (all other species lacking these features were placed in *Hystrichosphaeridium* Deflandre). Deflandre corrected Wetzel's mistake by designating *H. furcata* as type species, which was unfortunate, because the holotype is now lost (Sarjeant 1974, p. 54–55). From then on these type of organisms became popularly known as “hystrichospheres” or “hystrichosphaerids”, leading to a wide use of the name *Hystrichosphaera*. This and the lack of a type species of *Spiniferites* (*nomen nudum*), led Sarjeant (1964) to propose to the International Bureau of Plant Taxonomy (I.A.P.T.) to conserve *Hystrichosphaera* and reject *Spiniferites*. However, during the lengthy interim that the proposal awaited consideration, several other studies appeared. Davey and Williams (1966) further emended *Hystrichosphaera*, by describing its plate formula, cingular displacement, archeopyle and other details. Furthermore, based on a review of past studies, they proposed to treat *Hystrichosphaera furcata* as a synonym of *Hystrichosphaera ramosa*. In the same year, Loeblich and Loeblich (1966) validated *Spiniferites* by selecting *Spiniferites ramosus* as the type species. Loeblich and Tappan (1967) advocated the retention of the name *Spiniferites*. As a consequence of these events, the proposal was rejected by the Committee on Fossil Plants of the I.A.P.T. and the name *Spiniferites* was retained (Mamay 1969). Sarjeant (1970) accepted this conclusion and emended *Spiniferites* in accordance with the emendation of Davey and Williams (1966), and transferred all the *Hystrichosphaera* species into *Spiniferites*.

Several other fossil-based genera have been erected that are considered morphologically close to *Spiniferites*, through possession of a reflection of the same paratabulation. The most similar genera are *Achomosphaera* Evitt 1963 and *Hafniasphaera* Hansen 1977. *Achomosphaera* is differentiated from *Spiniferites* only by the lack of “sutural ridges or septa connecting their bases” (Evitt 1963, p. 163). *Hystrichosphaeridium ramuliferum*, a species described by Deflandre (1937) from the late Cretaceous, was transferred to *Achomosphaera ramulifera* and chosen as type species. *Hafniasphaera* differs from *Spiniferites* in containing “numerous evenly distributed vesicles (vacuoles)” inside the cyst wall (Hansen 1977, p. 13). Stover and Williams (1987) considered this a junior synonym of *Spiniferites*.

The genera *Rottnestia*, *Triblastula*, *Hystrichostrogylon*, *Hystrichosphaeropsis*, *Psaligonyaulax*, and *Tubotuberella* are only

differentiated from *Spiniferites* by having extensive pericoels. *Rottnestia* was erected by Cookson and Eisenack (1961), who transferred *Hystrichosphaera borussica* to *Rottnestia borussica* and designated it as the type species for the genus and it is characterized by the development of pericoel on the polar sides. *Triblastula* was erected by Wetzel (1933) and differs from *Rottnestia* “in that it lacks furcate processes of the *Spiniferites* type, and its periphragm is constricted near the apical and antapical ends of the endocyst” (Stover and Evitt 1978). *Hystrichostrogylon* was erected by Agelopoulos (1964) with *Hystrichostrogylon membraniphorum* as type species. The genus description was later emended by Stover and Evitt (1978) and is characterized by the development of a pericoel mainly on the dorsal side. *Hystrichosphaeropsis* was erected by Deflandre (1935) with *Hystrichosphaeropsis ovum* as type species. Species belonging to *Hystrichosphaeropsis* are bicavate, have smooth ridges and lack gonal processes. *Psaligonyaulax* was erected by Sarjeant (1966) with *Psaligonyaulax deflandrei* as type species. The cysts are bicavate, have denticulate ridges and lack gonal processes. *Tubotuberella* was erected by Vozzhennikova (1967) and differs from *Psaligonyaulax* in “having a more narrow, elongate hypoperiphragm which has a conspicuous antapical hole in the dorsal part of paraplate 1” (Stover and Evitt 1978).

The genera *Nematosphaeropsis*, *Trabeculidium*, *Cannosphaeropsis*, *Unipontidium*, *Dalella* and *Evittosphaerula* are differentiated from *Spiniferites* by the presence of trabeculae connecting the distal ends of the processes. *Nematosphaeropsis* and *Trabeculidium* are characterized by having pairs of trabeculae, whilst *Unipontidium*, *Dalella*, *Evittosphaerula* and *Cannosphaeropsis* have single trabeculae. *Nematosphaeropsis* was first proposed by Deflandre and Cookson (1954), but the name was invalid because the authors did not provide a description. In 1955 the same authors corrected this by providing a description, recognizing the strong morphological similarity to *Spiniferites* (then still called *Hystrichosphaera*) though stressing the difference of the distal ends of the processes as they are “joined to one another by trabeculae or filaments”. *Nematosphaeropsis balcombiana* was chosen as type species. Wrenn (1988) further emended *Nematosphaeropsis*, and emphasized the importance of pairs of trabeculae connecting the distal ends. *Trabeculidium* was erected by Duxbury (1980) to encompass trabeculate species with pairs of trabeculae connecting the distal ends, possessing both gonal and intergonal processes, but lacking sutural septa. Wrenn (1988) chose to ignore the genus *Trabeculidium*, and placed these species under *Nematosphaeropsis*. *Cannosphaeropsis* was first erected by Wetzel (1933) with *Cannosphaeropsis utinensis* as type species, and is characterized by the presence of single trabeculae connecting the distal ends of the processes. Williams and Downie (1966) emended the description of the genus, and restricted the genus to species lacking sutural septa connecting their bases and possessing exclusively gonal processes and a precingular archeopyle. Wrenn (1988) erected the genus *Unipontidium* to encompass species that have single trabeculae, can bear sutural septa and have “parasutural trabeculae joining processes at their distal

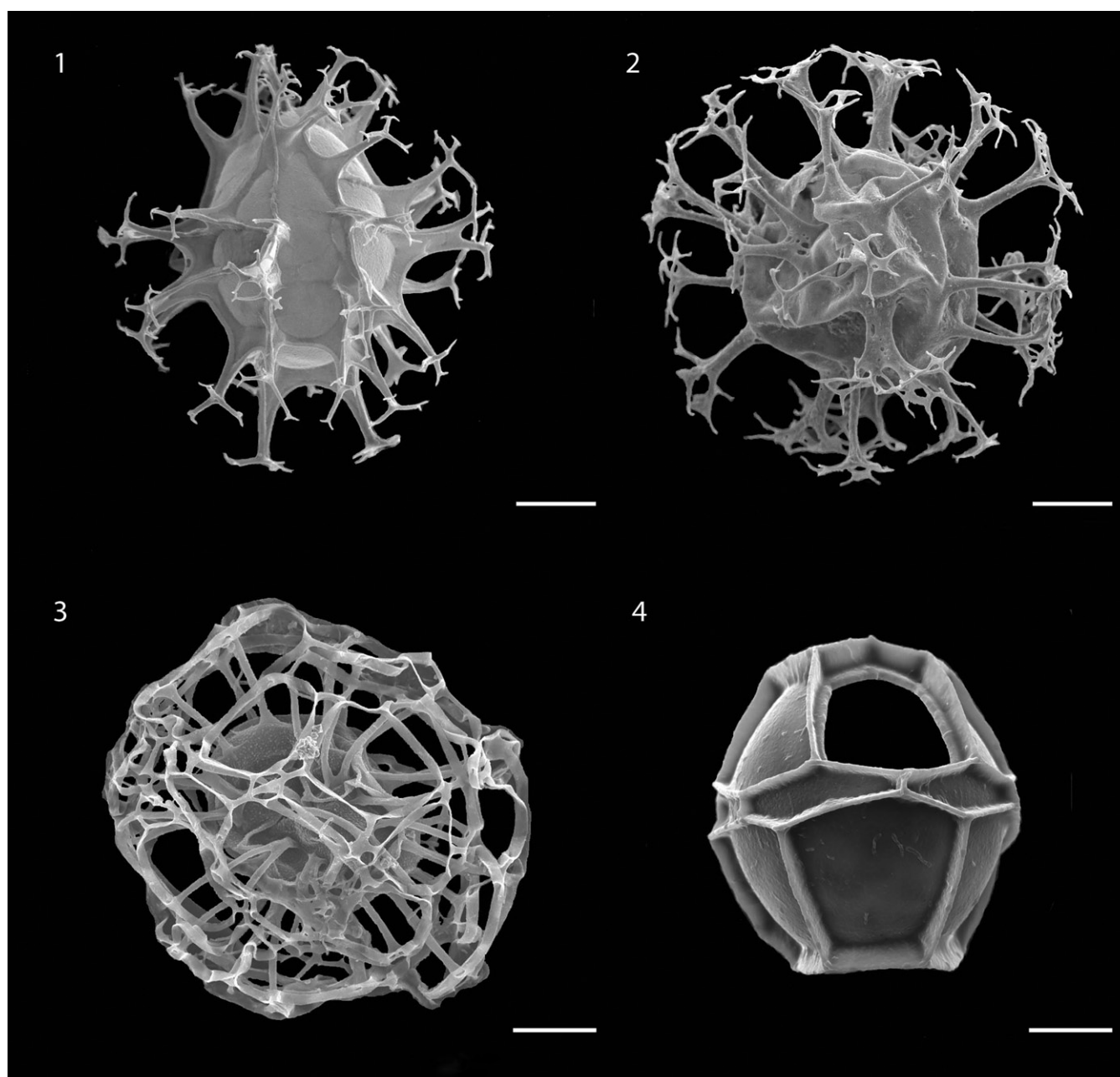


Plate 1. Scanning electron micrographs of the four modern cyst-based genera mentioned in the text: *Spiniferites* (1), *Achomosphaera* (2), *Nemosphaeropsis* (3) and *Impagidinium* (4). 1. *Spiniferites ramosus* from modern surface sediment in Baie de Vilaine (Bretagne, France). 2. *Achomosphaera andalusiense* from Pleistocene sediments of the Israelian coastal plain (Reading Borehole, 167–168 m depth). 3. *Nemosphaeropsis labyrinthus* from the lower Pleistocene of the North Atlantic (U1308A-19-4, 14–16 cm, 174.74 mbsf). 4. *Impagidinium patulum* from the Holocene of the Gulf of Cadiz. All scale bars = 10 μ m.

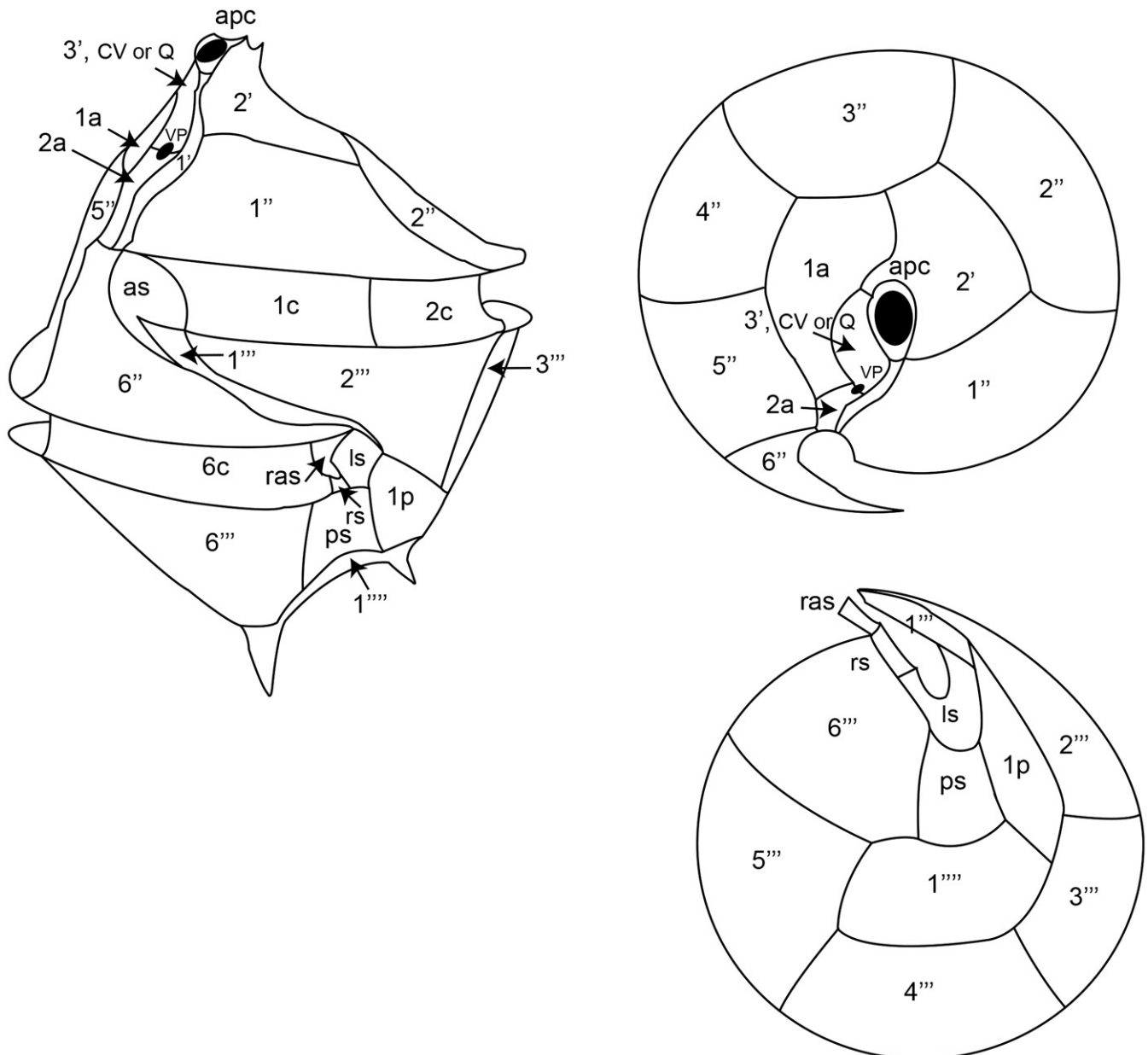
terminations, rather than along the process shafts, proximal of their distal terminations" (Wrenn 1988, p. 148). *Dalella*, described by McMinn and Sun (1994), differs from other trabeculate genera in having the trabeculum joined only to the central body at the archeopyle margin, parasulcus and apex. At the extreme end of this morphology is the peculiar genus *Evittosphaerula*, erected by Manum (1979), with *Evittosphaerula paratabulata* as type species. It was described as showing dinosporin threads tracing out a gonyaulacoidean tabulation; a central body is missing.

The genus *Impagidinium* Stover and Evitt 1978 can be described as *Spiniferites* cysts consistently lacking furcated processes, with *Impagidinium dispersitum* as the type species.

The genera *Exiguosphaera* Duxbury 1979, *Gonyaulacysta* Deflandre 1964, *Pentadinium* Gerlach 1961, *Prionodinium* Leffingwell and Morgan 1977, *Pterodinium* Eisenack 1958 and *Leptodinium* Klement 1960 are similar to *Imagidinium* but differ in paratabulation and other details (e.g. Stover and Evitt 1978; Jan du Chêne et al. 1986).

The genera *Galeacysta* Corradini and Biffi 1988, *Seriliodinium* Eaton 1996 and *Pterocysta* Rochon et al. 2002 are closely related to the cruciform species *Spiniferites cruciformis* Wall and Dale in Wall et al. 1973 and form a peculiar group of morphologies. These are discussed in more detail by Mudie et al. (2018).

The four modern genera are illustrated in Plate 1.



Figures 1. Interpretation of the tabulation of *Gonyaulax spinifera* based on SEM observations; 1. Ventral view, 2. Apical view, 3. Antapical view. Kofoidian plate numbering is used.

1.2. History of the theca-based genus *Gonyaulax* and related genera

The taxonomic history of the genus *Gonyaulax* is complicated and was reviewed in detail by Lewis et al. (1999). Since the cyst-based genus *Spiniferites* has been related only to *G. spinifera* Diesing, *G. digitale* (Pouchet) Kofoid, *G. scrippsae* Kofoid (and the new species erected in the 21st century) through incubation experiments (see next section), we will only focus on these species. Its history starts with Claparède and Lachmann who in 1858 described a new species of dinoflagellate from the North Sea, close to Glesnæsholm (Norway), which they named *Peridinium spiniferum*. Its tabulation was not studied; it was 40 µm in length, and presented an overhanging cingulum with a large offset. The genus *Gonyaulax* was erected by Diesing (1866), to include

dinoflagellates such as *Peridinium spiniferum* Claparède and Lachmann, which became the type species *Gonyaulax spinifera* (Claparède and Lachmann) Diesing. The name *Gonyaulax* is derived from the Greek: *gonu*, knee (or *gonio*-, angular) and *aulax*, furrow (Kofoid 1911a; Sournia 1986). Pouchet (1883) described another species, *Protoperidinium digitale*, from waters close to Concarneau (France), a larger species with a less displaced cingulum. He used the epithet *digitale* because its form reminded him of a "dé à coudre" (thimble). Stein (1883) illustrated several dinoflagellates under the name of *Gonyaulax spinifera* (pl. 4, figs 10–14) (although Dodge [1989, p. 275] suggested that Stein's *G. spinifera* was *Gonyaulax verior*, however, only figs 10 and 11 might be this species). Stein also described other species of *Gonyaulax*, though no detailed tabulation was provided. Tabulation was

also not provided by other authors such as Murray and Whitting (1899). This caused great confusion in the literature. Aware of these difficulties, Kofoid (1911a, p.189) decided to study in detail the genus utilizing mostly plankton samples offshore southern California. He transferred *Protoperidinium digitale* to *Gonyaulax digitale*, and provided more detailed descriptions of *G. spinifera* as well as other species. *Gonyaulax spinifera* and *G. digitale* are so closely related, that even Kofoid (1911a, p. 191) did not make the distinction of the two species during the progress of his study. Kofoid also described several new *Gonyaulax* species (*Gonyaulax alaskensis*, *Gonyaulax diegensis*, *Gonyaulax scrippsae*, *G. sphaeroidea*), and provided - albeit now considered incorrect - tabulation formulas (except for the sulcal plates). He had a relatively broad concept of the genus *Gonyaulax*. He divided the genus into four subgenera, the first one being the subgenus *Gonyaulax*. Kofoid once more divided the subgenus *Gonyaulax* into four groups, the second of which was the "spinifera group", which included *G. spinifera*, *G. digitale*, *G. diegensis* and *G. triacantha* (the latter had been transferred to *Amylax* by Meunier (1910)). In the same year, Kofoid and Michener (1911) described several *Gonyaulax* species, but unfortunately the illustrations were not published and are now lost. Many more species were later described and Kofoid's relatively broad genus concept of *Gonyaulax* was followed in subsequent publications (e.g. Schiller 1935). One of the factors that may contribute to the difficult taxonomy of the genus *Gonyaulax* is the large variability of the theca morphology depending of its growth stage; this was first shown by Taylor (1962) for *Gonyaulax polygramma* Stein who showed significant variation in size, shape and ornamentation.

The next major revision of the genus was done by Dodge (1989). Through scanning electron microscopy observations, Dodge (1989, p. 281) emended *Gonyaulax* to only include species with the tabulation Po, 3', 2a, 6'', 6c, 4-8s, 5''', 1p, 1'''. However, later studies by Lewis et al. (1999) and Ellegaard et al. (2002, 2003) found in principle the same tabulation, but have interpreted this tabulation differently, specifically for the *Gonyaulax* species that may be related to *Spiniferites* type cysts. Lewis et al. (1999) applying the Taylor-Evitt plate homology described in Fensome et al (1993) interpreted Dodge's 3' as a separate plate called the Cv plate and considered Dodge's 1a and 2a as the third (*3') and fourth (*4') apical plates homologues. They also observed a ventral pore between plate Cv and *4' and considered the small plate on the left side of the sulcus as the first postcingular plate (as Kofoid (1911a) did), so six postcingular plates would be found in the hypotheca. Ellegaard et al. (2002) presented a very similar plate formula with one exception: they located the ventral pore between plates 1' and *4'. Ellegaard et al. (2003) called the Cv plate "Q" (termed used by Helenes 1984 for the same plate) and located the ventral pore at the junction of plates 1', Cv (Q) and *4'. The tabulation formula using Kofoid (1909) and Balech (1980) nomenclature would be summarized as Po, Cp, 4', 6'', 6c, 4-6s, 6''', 1p, 1'''. The tabulation of *Gonyaulax spinifera* is illustrated in Figure 1.

The combination of molecular characterization of cyst and thecal morphology studies greatly contributed to the

clarification of the taxonomy of *Gonyaulax*, providing unequivocal characterization of some species (e.g. Ellegaard et al. 2003; see next section).

In accordance to Dodge (1989)'s revision, several species previously assigned to *Gonyaulax* have been transferred to other genera, primarily based upon their different tabulations. This transfer is also supported by their different cyst morphologies, which cannot be classified under the genus *Spiniferites*. A few examples are mentioned here. The toxigenic gonyaulacoid species *Gonyaulax tamarensis* -group was allocated in the genus *Alexandrium* Halim (Balech 1995). *Gonyaulax polyedra* Stein 1883 was transferred by Dodge (1989) to the cyst-based genus *Lingulodinium* Wall 1967. *Gonyaulax catenata* (Levander) Kofoid was transferred to the genus *Peridiniella* Kofoid and Michener 1911 by Balech (1977). *Protoceratium reticulatum* (Claparède and Lachmann) Bütschli has also been known as *Gonyaulax grindleyi* Reinecke (Stosch 1969) but Dodge (1989) considered that *Protoceratium reticulatum* was not a *Gonyaulax* according to his interpretation of the genus *Gonyaulax*. Murray and Whitting (1899) described *Gonyaulax jollifei*, for which Kofoid (1911b) created the new genus *Spiraulax* based upon the differences with *Gonyaulax* he observed in Murray & Whitting's organism. This was ratified by Carbonell-Moore (1996).

1.3. History of the affiliation of *Spiniferites* and related genera to the theca-based genus *Gonyaulax*

It took a long time before *Spiniferites* cysts were associated with cells of *Gonyaulax*. Reinsch (1905) was the first to suggest that Ehrenberg's "Xanthidia", were cysts of dinoflagellates, but this correct observation was largely ignored. The relation of some of Wetzel's "hystrichospheres" to the tabulation seen on dinoflagellates was first proposed by Deflandre (1935, 1936, 1937), but "since he considered that the position of the spines meant that the girdle could not have contained a flagellum, he did not believe they were dinoflagellates" (Sarjeant 2002, p. 283). Later, Deflandre (1947, p. 14-15) mentioned Reinsch's hypothesis but was skeptical because the only dinoflagellate cysts he had observed inside thecae had smooth walls and did not bear any processes. Later, several researchers started observing "hystrichospheres" in modern sediments. Erdtman (1950) noted having seen *Hystrichosphaera furcata* in marine sediments of the Gullmarn Fjord (Sweden), which he later described as *Hystrichosphaera* cf. *furcata* (Erdtman 1954). McKee et al. (1959) noted hystrichospheres in a Pacific atoll and Muller (1959) noted hystrichosphaerids on the Orinoco River delta and shelf. Around the same time, plankton ecologist Ramón Margalef depicted an organism, which he had observed in the plankton of Ría de Vigo (Spain), and which he called "cyst of *Gonyaulax spinifera*" (Margalef 1956, Fig. 6), unaware that this was actually a "hystrichosphere".

It was Evitt (1961) who convincingly suggested that some of the "hystrichospheres" were not motile forms but cysts of dinoflagellates. Later, Evitt and Davidson (1964) made the first link of the genus *Hystrichosphaera* to one of the *Gonyaulax* species: they observed a *Hystrichosphaera* type

cyst inside a theca of *Gonyaulax digitale*. The definite proof of a relation between *Hystrichosphaera* cysts and *Gonyaulax* thecate stages was accomplished by Wall (1965) through incubation experiments. He related *Hystrichosphaera bentorii*, now known as *Spiniferites bentorii* (Rossignol) Wall & Dale to *Gonyaulax digitale* (Pouchet) Kofoid. Wall's pioneering work was continued in collaboration with Barrie Dale. They related *Hystrichosphaera bentorii* and *H. nodosa* to *G. digitale*, *H. bulloidea* to *G. scrippsae*, *H. scabrata* to *Gonyaulax* sp. 2, *H. ramosus* and *H. mirabilis* to *G. spinifera* (Wall and Dale 1966, 1967, 1968, 1970; Wall et al. 1967). They also showed for the first time that other cyst-based genera, in casu *Nematosphaeropsis balcombiana* and *Tectatodinium pellitum*, could also be related to *Gonyaulax spinifera*. Wall and Dale (1968) suggested that these theca-based species (except for *G. scrippsae*) might belong to a complex called "spinifera complex" which corresponds to *G. spinifera*, *G. digitale* and *G. diegensis*, three species that are difficult to discriminate and which form part of the "spinifera group" of Kofoid (1911). *Gonyaulax triacantha* Jörgensen was also included in the same group by Kofoid (1911) but was later transferred to *Amylax* Meunier by Sournia (1984), though its cyst is not known. The fact that five cyst species could be related to two theca-based species suggested to them that part of the life cycle of this complex is at least to some extent "heterosporous", meaning that one thecate stage may produce two or more types of a cyst-based species. Later, Dale (1976) applied the informal term "*Gonyaulax spinifera* group" to those cysts that apparently correlate to either *G. spinifera*, *G. digitale* or *G. scrippsae*. Dale (1976) also related *Spiniferites elongatus*, *Spiniferites membranaceus*, *Ataxiodinium choanophorum* (known at that time as *Planinosphaeridium membranaceum*) and *Bitectatodinium tepikiense* to *Gonyaulax spinifera*. Unfortunately a detailed description of the motile stage was never published. Dale (1983) mentioned once again the possibility of "heterospory", but stressed that this could be due to the theca-based taxa being under classified or the cyst-based taxa being over classified.

Few cyst-theca experiments took place in the following decades and these incubation studies largely confirmed the relationships proposed by Wall and Dale. Dobell and Taylor (1981) related two *Spiniferites* type cysts with an operculum consisting of two precingular plates to two *Gonyaulax* species, which they considered close to *Gonyaulax alaskensis*. Taylor and Gaines (1989) studied cyst formation in *Gonyaulax spinifera* though not in detail. Sonneman and Hill (1997) incubated cysts from Australian sediments and related *S. mirabilis* to *G. spinifera*, while Persson et al. (2000) isolated cysts from the West coast of Sweden, and also largely confirmed earlier Wall and Dale results.

Several other authors have proposed empiric relationships based upon cyst morphological observations, which were thoroughly reviewed by Head (1996).

Lewis et al. (1999) showed that *Spiniferites ramosus* and *Spiniferites membranaceus* form two morphologically different motile stages of *Gonyaulax*, thus providing evidence for the under classification of the theca-based taxa. Lewis et al. (2001) convincingly showed through detailed culture

experiments that the cyst-based *Bitectatodinium tepikiense* should be related to *G. digitale*, not *G. spinifera* as formerly suggested by Wall and Dale. Ellegaard et al. (2002) described a new species of *Gonyaulax*, *Gonyaulax baltica* from the Baltic Sea area, a species that forms cysts similar to *Spiniferites bulloideus* sensu Wall and Dale (1968). Additionally, these authors found that the length of the processes of the cyst of *Gonyaulax baltica* diminishes with the increase of salinity.

A new era was heralded through careful study of batch grown cultures in combination with molecular data of cyst-based cultures. As touched upon in the section 1.2, Ellegaard et al. (2003) established cultures from cysts of *Spiniferites membranaceus* and *Spiniferites elongatus* and showed that, based on morphology and LSU rDNA sequences, both form two new, distinct theca-based species, which they respectively called *Gonyaulax membranacea* and *Gonyaulax elongata*. They also sequenced cultures of *Gonyaulax baltica*, *Gonyaulax digitale* and *Gonyaulax* cf. *spinifera*, and confirmed that these form distinct species in the phylogenetic tree. Mertens et al. (2015) described the cyst-theca relationship of *Spiniferites pachydermus* Reid, and described a new species of its motile stage called *Gonyaulax ellegaardiae*. The phylogenetic position of *Gonyaulax ellegaardiae* showed that it was close to strains from New Zealand and the Adriatic identified as *Gonyaulax spinifera* by Rhodes et al. (2006) and Riccardi et al. (2009) respectively, suggesting that these strains might have been misidentified.

As remarked by Head (1996), most cysts belonging to the genus *Spiniferites* are more distinctive in morphology, and hence more significant taxonomically, than the respective thecae belonging to the genus *Gonyaulax*. This suggests that the thecate-stage morphology has been more conservative evolutionarily than the cysts, which might explain the difficulty of biologists to differentiate the *Gonyaulax* species, in comparison to the relative ease of identification of the *Spiniferites* species by the palaeontologists.

The batch culture studies mentioned above have shown that some morphological characteristics are identical between the respective cyst and theca. Detailed comparison of cysts and theca of batch cultures show that the tabulation of the cysts and thecae corresponds to 2po, 4', 6'', 6c, 5-6s, 6''', 1p, 1''''', except for the sulcal plates which are not always reflected on the cyst (Lewis et al. 1999; Ellegaard et al. 2002, 2003; Mertens et al. 2015). On both there is a ventral S-type organization, i.e. where the first apical plate has no contact with the sixth precingular plate. However, several fossil cyst species have been described with aberrant tabulations (particularly three instead of four apical plates, e.g. *Spiniferites bentorii* (Rossignol) Wall & Dale and *Spiniferites multisphaerus* Price & Pospelova), but these are likely due to a weakly visible suture between plates 1' and 4'. In addition, an apical protrusion is, when present, almost always seen on both cyst and theca.

In contrast there are morphological characteristics that are not identical or not even shared. The Q plate (the homologue to Kofoid's 3', or Cv plate according to Taylor-Evitt's model) is only visible on the thecate stage. The overhang

and displacement of the cingulum is different on the cyst compared to the theca, with the overhang not visible on the cyst, and with less displacement. The archeopyle is only visible on the cyst; it corresponds to the third precingular plate, which is also the keystone plate on the thecate stage (the only plate in the epitheca that overlaps all the surrounding plates). An aberrant archeopyle type was reported by Dobell and Taylor (1981), corresponding to the third and fourth precingular plates. The processes are only visible on the cyst stage, and are of taxonomic importance. Some species have exclusively gonal processes (which are always trifurcate), whereas other have both gonal and intergonal processes (the latter are always bifurcate, as opposed to the former which are always trifurcate). For the cyst of *Gonyaulax baltica*, variations in size of body and processes have been related to variations in temperature and salinity, and are not related to phylogeny (Ellegaard et al. 2002).

For the other genera morphologically close to *Spiniferites*, the biological affiliation is largely unknown, and has only been inferred based on morphological comparison between cyst and theca, e.g. for *Achomosphaera ramulifera* to be *Gonyaulax spinifera* by Reid (1974). Rochon et al. (2009) suggested that the genus *Nematosphaeropsis* might also be related to *Gonyaulax spinifera*. They used batch cultures of *Gonyaulax spinifera* to show that this motile stage can produce both *Spiniferites ramosus* as well as *Nematosphaeropsis labyrinthus* type cysts. However, *Nematosphaeropsis labyrinthus* type cysts still need to be hatched and sequenced to confirm this suggestion.

Acknowledgements

We acknowledge Nicolas Chomérat and Elisabeth Nézan who helped us to understand the correct ending of *Gonyaulax digitale*. Two anonymous reviewers are acknowledged for constructive comments.

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