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Enhancing dinoflagellate cyst classification through combined LM and SEM analysis: A reassessment of *Spiniferites magnificus* and *Fibradinium annetorpense*

Manuel Vieira[a,b,*], David Jolley[c], Reinhard Zetter[d], Salih Mahdi[e], Friðgeir Grímsson[d,*]

[a] Aker BP ASA., Oksenøyveien 10, 1366 Lysaker, Oslo, Norway
[b] GEOBIOTEC, Department of Earth Sciences, NOVA School of Science and Technology, Campus de Caparica, P-2829 516 Caparica, Portugal
[c] Department of Geology & Geophysics, School of Geosciences, University of Aberdeen, King's College, Aberdeen AB24 3UE, UK
[d] University of Vienna, Department of Botany and Biodiversity Research, Rennweg 14, 1030 Vienna, Austria
[e] Petrostrat Ltd., Century House address to 6 Royal Mews, Gadbrook Park, Northwich CW9 7UD, UK

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ABSTRACT

Scanning Electron Microscopy (SEM) is underutilized in the taxonomic study of fossil dinoflagellate cysts, which are predominantly described through Light Microscopy (LM). However, SEM can complement LM by revealing detailed morphological features, such as ornamentation and perforations, that are often obscured under LM alone. This study applies the "single-grain method," combining LM and SEM, to refine the taxonomic descriptions of *Spiniferites magnificus* and *Fibradinium annetorpense*. SEM observations revealed previously undocumented features in *S. magnificus*, including variable intergonal processes, perforated sutural crests, and robust trifurcate gonal processes. These findings refine its taxonomy and suggest environmental influences, such as salinity variations, on its morphological variability. Similarly, SEM analyses of *F. annetorpense* allowed the determination of the cyst tabulation and clarified the previous described fibrous outer wall structure as the result of continuous ridges and indentations across the crests formed at the edge of each paraplate. This has also highlighted the presence of nano sized indentations forming rings around the paraplates.

Both species hold significant biostratigraphic value. *Spiniferites magnificus* serves as a key marker for the Late Danian in the North Sea Basin, with its extinction and inception coinciding with critical regional biozones. *Fibradinium annetorpense* has a wider stratigraphic range with reported occurrences from the Late Cretaceous to the Thanetian, but the specimens analyzed in this study are from upper Danian sediments collected in western Greenland.

1. Introduction

Scanning electron microscopy (SEM) is not routinely employed by palynologists in the taxonomic study of fossil dinoflagellate cysts. Most published species descriptions are based on morphological features observable through light microscopy (LM), often accompanied by photographic documentation of variable quality. This reliance on LM can lead to ambiguities concerning the identification of pertinent taxonomic characters. While SEM techniques do offer additional information, particularly regarding ornamentation and obscure features that may not be easily discernible with LM, they are not a direct substitute for LM observations. SEM can complement LM findings and provide a more comprehensive understanding of dinoflagellate cyst morphology allowing the description of species with a higher accuracy.

The "single-grain method," developed by Zetter, 1989, is a technique used to investigate the taxonomy of individual pollen grains by combining observations from both LM and SEM. This method, subsequently detailed by Halbritter et al., 2018, has been employed in numerous publications to provide a high level of detail in pollen grains that are often challenging to identify at the genus level using only LM. Examples of recent studies utilizing this method include those by Grímsson et al. (2011, 2015), Bouchal et al. (2016), Vieira and Zetter (2020), Vieira et al. (2022), Vieira et al. (2023a, 2023b), and Ulrich et al. (2024).

In this study, the single-grain method was utilized to examine the species *Spiniferites magnificus*, as formally described by Vieira et al.

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* Corresponding authors.
E-mail addresses: manuel.vieira@akerbp.com (M. Vieira), fridgeir.grimsson@univie.ac.at (F. Grímsson).

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(2018a), and *Fibradinium annetorpense*, as originally described by Morgenroth (1968). The aim was to identify additional morphological features that could enhance and refine their taxonomic descriptions.

2. Material and methods

2.1. Sample provenance

Specimens of *Spiniferites magnificus* were recovered from well 6305/8–2 drilled in the southern part of the Ormen Lange field. This well was drilled on the Norwegian Continental Shelf within the Møre Basin (Slørebotn Basin), approximately 100 km offshore north-west from Kristiansund. This well cored a section of Danian strata (see Vieira et al., 2018b), the specimens analyzed are from a sample at 2967.55 m.

The *Fibradinium* specimens were extracted from upper Danian (64 to 62 Ma) phosphoritic nodules present in the Agatdal Formation, Nuussuaq Group, Nuussuaq Peninsula, western Greenland (Grímsson et al., 2016, fig. 5). The phosphoritic nodules were collected from surface sedimentary rock layers at the Agatkløft and Turritellakløft outcrops in the Agatdalen valley (Grímsson et al., 2016, fig. 3).

2.2. Preparation of the samples

For the drill core samples, which yielded the *Spiniferites* specimens, standard laboratory processing for palynomorphs with HCl (55%) and HF (37%) for acid maceration was applied (see Vieira and Jolley, 2020). This was followed by 125 μm and 10 μm sieving to remove coarse and fine fractions, respectively. No oxidation of the kerogen was applied. The final residues were diluted in liquid glycerine and stored for further analysis. The phosphoritic nodules which yielded the *Fibradinium* specimens were processed following Grímsson et al. (2011) and Denk et al. (2012). Nodules were dissolved in HCl overnight, the residue was boiled for 10 min in HF and then for five minutes in HCl. The residue was washed, acetolized, washed again, and then mixed with glycerol and stored in small tubes for further investigation. In both preparation cases, small parts of the residue solution were mounted on LM slides without cover slips to allow selection and extraction of dinoflagellate cysts.

2.3. The single-grain method

The fossil dinoflagellate cysts were investigated both by LM and SEM using the single-grain method (Zetter, 1989; Vieira et al., 2009; Halbritter et al., 2018). The slides were scanned, and the specimens were extracted using a preparation needle with a single hair mounted on it. The cysts were placed into a small clean glycerol drop on a separate slide for study and photography with LM. The same cysts were then transferred onto SEM stubs with help of the preparation needle and washed with drops of ethanol to dissolve the remaining glycerol. The stubs with the palynomorphs were then sputter coated with gold and the objects studied and photographed with SEM.

The specimens of *Spiniferites magnificus* were observed with a Carl Zeiss Gemini SEM 300 Scanning Electronic Microscope, located in the University of Aberdeen (Scotland) – ACEMAC SEM facility. Specimens of *Fibradinium annetorpense* were studied at the University of Vienna, Austria, with a JEOL JSM-6400 Scanning Electron Microscope.

3. Systematic Paleontology

Division: Dinoflagellata (Bütschli, 1885) Fensome et al., 1993.
Subdivision: Dinokaryota Fensome et al., 1993.
Class: Dinophyceae Pascher, 1914.
Subclass: Peridiniphycidae Fensome et al., 1993.
Order: Gonyaulacales Taylor, 1980.
Family: Gonyaulacaceae Lindemann, 1928.
Genus: **Spiniferites** Mantell, 1850 emend. Sarjeant, 1970

This genus comprises fossil and extant proximochorate to chorate cysts of small to intermediate size exhibiting a central body of subspherical to subovoidal shape and a precingular archeopyle. Paratabulation in this genus is characterized by parasutural ridges or septa combined with processes, with a gonyaulacacean formula of 3–4′, 5–6″, 6c, 5–6″’, 1p, and 1’”“. However, parasutural boundaries may not consistently define paraplates such as 4’, 6”, 1″’ and sulcal paraplates. The archeopyle is precingular, Type P (3″ only), typically reduced, with a free operculum. A well-defined paracingulum is evident through the parasutural features, with ends that is often offset by more than one paracingulum width. The parasulcus is only partially delineated by parasutural features, with its constituent paraplates rarely distinguishable.

Spiniferites shows a considerable variation in surface ornament, size range (especially length) and the development of parasutural crests and membranes (raised ridges along the paraparaplate boundaries) between processes. Some of these crests can be raised close to the distal end of the processes forming flanges (eg. *Spiniferites mirabilis*) (see Limoges et al., 2018). The generally finely ornamented endophragm and periphragm are appressed except where the processes arise, although in some species a well-developed ventral pericoel can be observed.

All species belonging to this genus are known to always bear gonal processes (Williams et al., 1998). Nevertheless, some *Spiniferites* species can variably exhibit additional intergonal processes on sutures forming paraplate boundaries. Species with intergonal processes are recorded from Cretaceous to Quaternary deposits (Limoges et al., 2018).

Williams et al. (2017) identified approximately 150 accepted species of *Spiniferites*, highlighting its diversity. The genus *Hystrichosphaera* (Wetzel, 1933) was deemed a taxonomic junior synonym of *Spiniferites* by Sarjeant (1970). *Spiniferites ramosus* (Ehrenberg, 1837) was designated as the type species of *Spiniferites* by Loeblich Jr. and Loeblich III (1966). In the oil industry, “*Spiniferites ramosus* -group” is often used for specimens resembling the type species or non-distinctive forms.

Life-cycle studies of extant dinoflagellates indicate that *Spiniferites* represents cysts of certain *Gonyaulax* species (Diesing, 1866) and Fensome et al. (1993) consequently proposed that *Spiniferites* may be a taxonomic senior synonym of *Gonyaulax*. However, under current nomenclatural rules (Turland et al., 2018), *Gonyaulax* has priority as it is based on extant material. Despite this, most dinoflagellate cyst researchers prefer maintaining separate nomenclature for cysts and their extant counterparts (Head et al., 2016).

The taxonomic relationship between *Spiniferites* and other genera has been widely debated. Stover and Williams (1987) regarded *Hafniasphaera* (Hansen, 1977) as a junior synonym of *Spiniferites*, while Edwards (1996) retained it as a separate genus. Williams et al. (2017) noted that *Hafniasphaera* is characterized by vesiculate processes, often with a vesiculate central body, and is mainly restricted to the Late Cretaceous and Paleocene. Quattrocchio and Sarjeant (2003) proposed *Hafniasphaera* as a subgenus of *Spiniferites*, though this suggestion has not been widely adopted. Similarly, *Achomosphaera* (Evitt, 1963) was considered a junior synonym of *Spiniferites* by Duxbury (1983). However, Lentin and Williams (1989) and most researchers have treated *Achomosphaera* as a distinct genus due to its lack of sutures, although distinguishing it from *Spiniferites* often requires detailed examination. *Spiniferites* is also closely related to *Spiniferella* (Stover and Hardenbol, 1994), differing by having an L-type rather than an S-type ventral organization. *Hystrichostrogylon* (Agelopoulos, 1964) is cavate, with an extended pericoel typically in the ventral region, while *Rottnestia* (Cookson and Eisenack, 1961) is bicavate. Lastly, *Hystrichosphaeropsis* (Deflandre, 1935) can be distinguished by its sutural crests, which lack gonal and sutural processes.

Spiniferites magnificus Vieira et al., 2018a n. emend.
Figs. 1, 2 and 3.

Original description: Proximochorate dinoflagellate cyst with strong dorso-ventral compression. Cyst wall is relatively thin, smooth and hyaline. Processes are gonal and vary in width between 3.5 and 5 μm, and markedly expanded at the base. Processes are slightly membranous, distally bi- or trifurcated into foliate branches which can be, in turn, distally furcate. The processes are connected proximally with well-developed sutural crests. Septa are smooth with a regular distal margin. Paraplate boundaries indicated by sutural crests reflect the tabulation formula typical of the genus *Spiniferites*. Archeopyle is precingular, formed by loss of paraplate 3″ and the operculum is completely detached.

Emended description: The cysts are proximochorate and evidence dorsoventral compression. In LM, the cyst wall is relatively thin (Fig. 1), smooth and hyaline; in SEM the cyst main body have an ellipsoidal shape; endophragm and periphragm appressed between processes and sutural ridges. The wall is thin (<0,5 μm), smooth-scabrate and nannoperforate (Fig. 2E). The archeopyle is precingular, formed by loss of paraplate 3″ and the operculum is completely detached. Paraplate boundaries are indicated by well-developed sutural ridges/crests reflecting the typical paratabulation formula of the genus *Spiniferites*, although the paratabulation is often obscured by folding. Under SEM, the sutural crests evidence a variable width (between 2 and 4 μm) and continuous perforations also of variable size (up to 0.8 μm) forming a 'net' like structure (usually not easy to visualize in LM). The thickness of the sutural crests and development of these perforations shows some variation in the different specimens observed, from very well developed and perforated to thinner and with very few perforations. The observed specimens exhibit better developed perforations on the ventral side.

The processes are solid and originally described as gonal (common character among *Spiniferites*), although based on SEM investigations it is clear that the cysts have one or two intergonal processes. The presence and arrangement of these intergonal processes is variable between different individuals and they seem to be present more consistently on the ventral side. The gonal processes are formed at the intersection point of three paraparaplates (average process length of 12 μm); these are robust, markedly expanded at the base and vary in width between 4 and 6 μm. In most specimens they show the same perforations at the base as the sutural crest although others evidence a more robust and less perforate structure. The distal end of the gonal processes is usually trifurcated into foliate branches which can be, in turn, distally furcate (Fig. 1D; Fig. 2F, H). Some processes also evidence distal fenestrations which usually relate to better development of the sutural crest perforations (Fig. 2D).

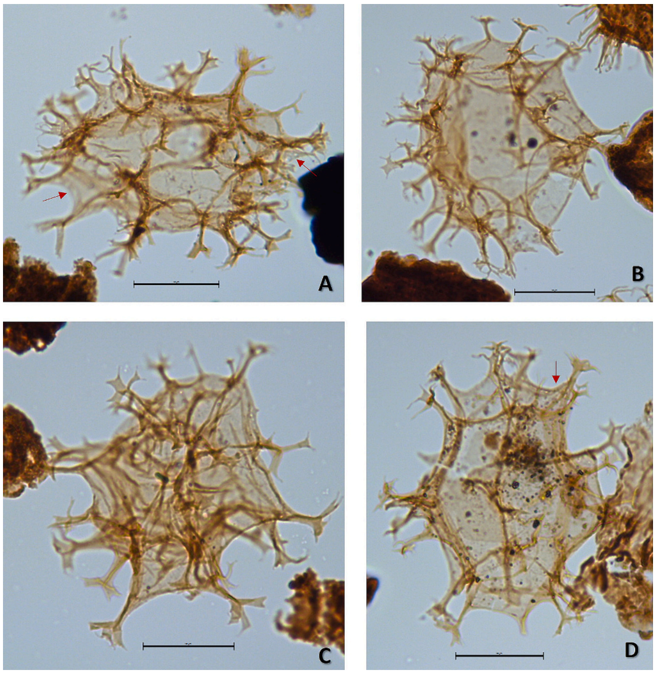

Fig. 1. The scale bar represents 20 μm for all specimens. A–D. Light microscope photographs of *Spiniferites magnificus*. Red arrows evidence the perforations across the sutural crests, which are usually not easy to visualize in LM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The intergonal processes are less robust than the gonal processes; are proximally connected with the sutural crests, and distally terminate in variable shapes, from a simple termination to bi- or trifurcate ends which can furcate again at the end. The length is also generally shorter than the gonal processes (between 6 and 9 μm) (Fig. 1H; Fig. 2B).

Dimensions: Diameter of cyst body varies between 50 and 62 μm, cyst with processes varies between 60 and 82 μm, length of gonal processes between 9 and 13 μm, length of the intergonal processes between 6 and 9 μm. Number of specimens measured under SEM = 7.

Remarks: Comparable perforations in the sutural crests have been recently reported in the extant species *Spiniferites hainanensis* (see Limoges et al., 2018, plate 4–2,6), although these perforations exhibit a larger size but a smaller number. Process tips in *Spiniferites hainanensis* are described as trifurcate (gonal) or bifurcate (intergonal), although in *Spiniferites magnificus* the intergonal processes are more variable, they can be simple, bifurcate or trifurcate.

According to Limoges et al. (2018), in *Spiniferites hainanensis* the number of intergonal processes differs from one specimen to another and even from one suture to another on the same specimen. Similar observation can be made with *S. magnificus*. Vieira and Mahdi (2019) highlighted the morphological similarities between *Spiniferites magnificus* and *Spiniferites rhomboideus*. However, the latter exhibits several (usually 3–4) intergonal (sutural) processes with similar dimensions to the gonal processes. These are smaller and less robust then observed in *S. magnificus*. Some perforations along the distal ends of the sutural crests, resembling the ones observed in *S. magnificus*, have also been observed in *Spiniferites rhomboideus* specimens (Vieira and Mahdi, 2019, pls. 1, 3). More detailed research should be done across these species to better understand the degrees of variations.

Family: CLADOPYXIACEAE von Stein, 1883

The family Cladopyxiaceae von Stein, 1883 comprises numerous types of small, subspherical and tabulate gonyaulacacean cysts which are commonly found in Cretaceous and Paleogene sediments. According to published data, this group appears in the fossil record from the Toarcian (Early Jurassic) and extends until the?Miocene (Goodman, 2017). The representatives of this family exhibit common morphological characteristics such as small size (maximum dimension 40 μm), ellipsoidal to subspherical shape, and the lack of prominent projections. The cyst wall is composed of either an autophragm exclusively or both an autophragm and an ectophragm. The tabulation is expressed by sutural features and the composition of the apical paraplates varies within this family. Goodman (2017) did a comprehensive review of this family, although did not discuss *Fibradinium* due to being a less understood form.

Genus: **Fibradinium** Morgenroth, 1968 n. emend.

Type-species: *Fibradinium annetorpense*

Original description: Morgenroth (1968) named the genus *Fibradinium* from the latin word "fibratus" (fibrous). The original description comprises subspherical to ellipsoidal cysts with a theca composed of two layers. The inner layer is a smooth membrane while the outer layer presents a fibrous (spaghetti type) structure. Paraplate organization:?7′, 6″, 6c, 6″', 1p, 1″". Cingulum is equatorial and the sulcus is undifferentiated. The archeopyle is apical.

Remarks: Morgenroth (1968) segregated this genus from other dinoflagellate cysts with 6 pre and 6 post equatorial paraplates, like *Eisenackia*, *Microdinium*, and *Gonyaulax* due to the double wall layer and the fibrous structure of the theca. The division of the apex into 7 apical paraplates was not differentiated in the original description.

Taxonomic senior synonym: *Phanerodinium* (Deflandre, 1937a) Slimani (1994), according to Below (1987, p.36), although Lentin and

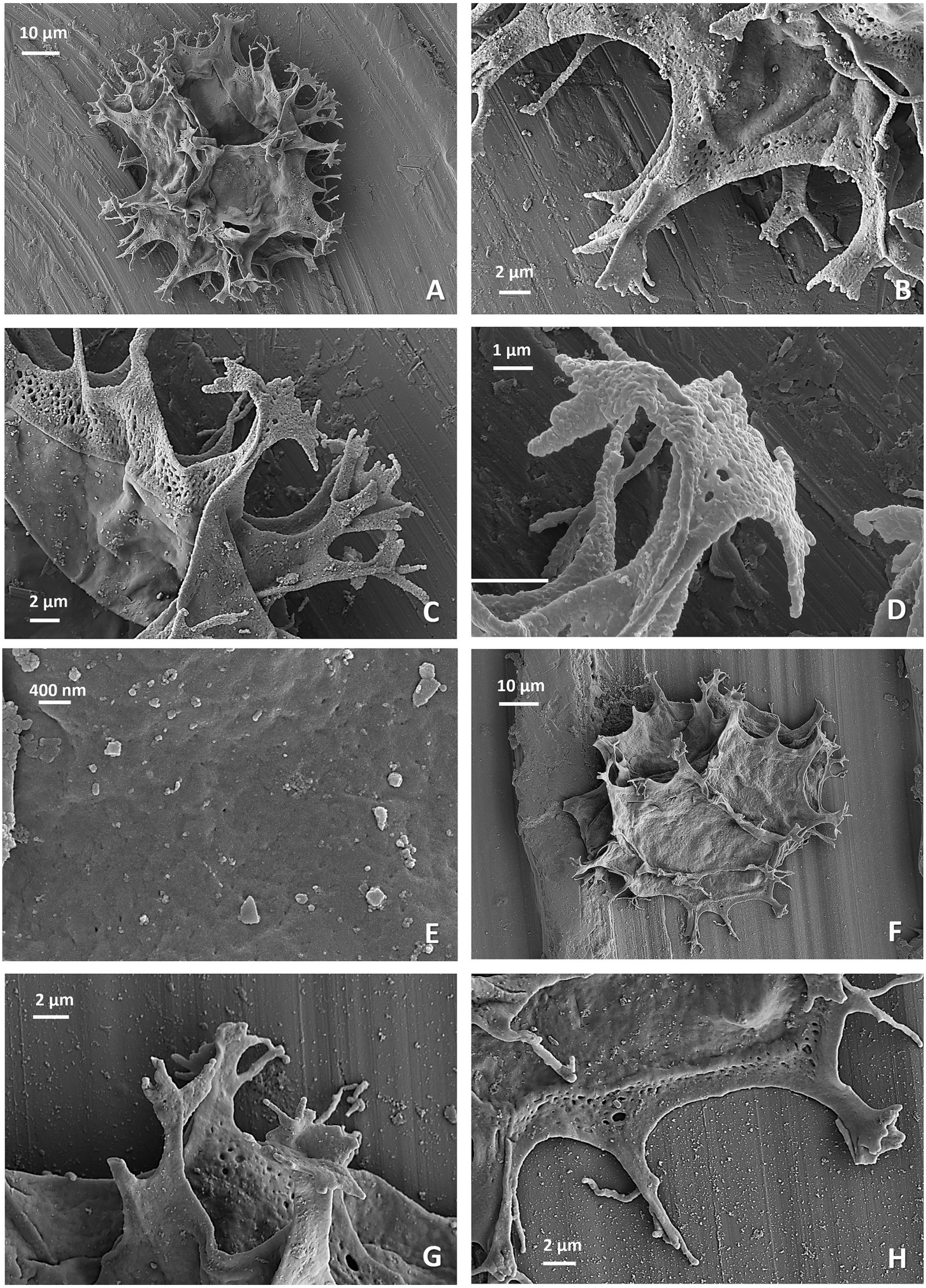

Fig. 2. A – SEM photos of *Spiniferites magnificus* specimen (ventral side) very well preserved. The archeopyle is clear. B and C – detail of the sutural crests evidencing well developed continuous perforations also of variable size. D – detail of a gonal processes formed at the intersection point of three paraplates. The distal end is trifurcated into foliate branches which distally furcate. E – Detail of the cyst wall evidencing a smooth surface with nano perforations. F – *Spiniferites magnificus* specimen (dorsal side). G and H – Details of the sutural crests and gonal and intergonal processes.

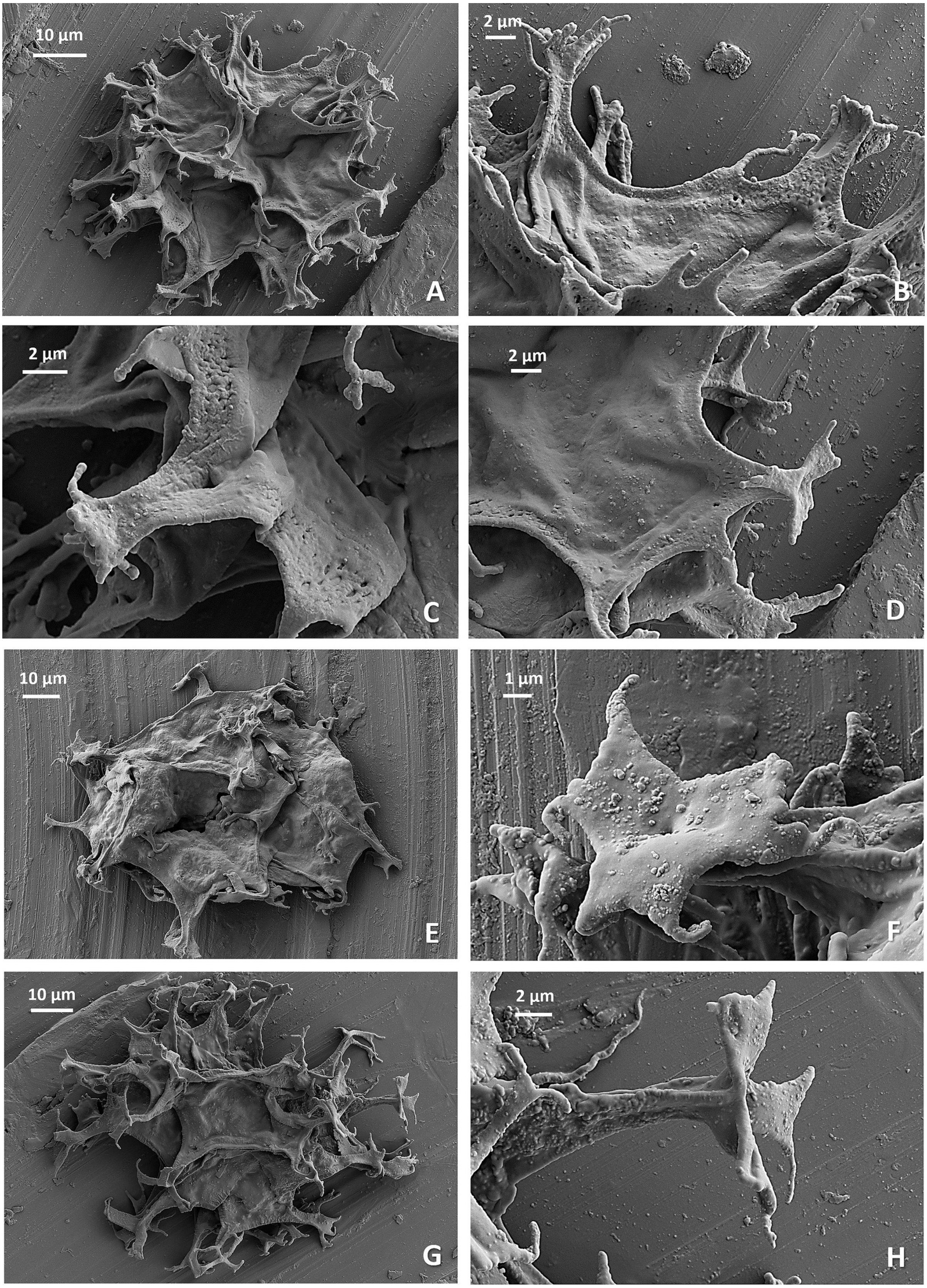

Fig. 3. A, E, G – SEM photos of *Spiniferites magnificus* full specimens. B, C, D – Details of the sutural crests and gonal and intergonal processes. F and H – details of gonal processes evidencing the trifurcated distal which distally furcate.

Table 1
List of published *Fibradinium* species.

Species	Author	Notes
Fibradinium annetorpense	Morgenroth, 1968	
Fibradinium densibaculatum	Below, 1987	Originally *Phanerodinium*, subsequently (and now) *Fibradinium*? Questionable assignment: Lentin and Williams (1989, p. 135)
Fibradinium diatretiforme		
Fibradinium follis		
Fibradinium lacertum		
Fibradinium squamosum		
Fibradinium variculum	Stover and Helby, 1987	

Williams (1993, p.221) retained the genus *Fibradinium*. To date, there are seven published species of *Fibradinium*, although five have a questionable assignment (Table 1).

The double wall layer is not exclusive to *Fibradinium* and can be observed in other microdinioids (Slimani, 1994). Furthermore, the fibrous structure of the theca, which Morgenroth (1968) used to differentiate this genus, cannot be observed with scanning electron microscopy (SEM) for *Fibradinium annetorpense*. Therefore, we propose amending the genus to accommodate the new observations.

Emended diagnosis: Cysts subspherical; gonyaulacacean, paratabulation indicated by parasutural ridges, formula 5′, 5a, 7″, 6c, 7″’, 1p, 1″“.

Emended description: Cysts are small, subspherical, with a smaller epicyst than the hypocyst. The periphragm displays ridges and shallow penitabular indentations“. SEM analysis shows that the latter features form complete rings around some paraplates. The tabulation, determined through SEM, follows a pattern of 5’, 5a, 7”, 6c, 7″’, 1p, 1″“. The archeopyle is apical-intercalary (tAtI)a, with an operculum typically attached to the anterior sulcal paraplate.

Fibradinium annetorpense (Morgenroth, 1968) n. emend.
Figs. 5, 6

Original description: The species original description is similar to the genus, although a few extra notes have been added. The archeopyle is formed by the fall of the apical paraplate 6 resulting in a pentagonal opening. On the hypotheca there are 6 post equatorial paraplates, 1 intercalary paraplate and 1 antapical paraplate. The small longitudinal sulcus has a shape of a drop, with paraplate 1′ being the continuation towards the apex. Boundaries between paraplates are well defined with thicker fibrous outer layer (Morgenroth, 1968).

Emended description: Cysts are cavate, ovoidal to ellipsoidal where the epicyst is smaller than the hypocyst. The cyst wall is composed of endophragm and smooth periphragm. The cyst size has a width between 23 and 31 μm and a length of 28–36 μm. When observed with SEM, it becomes clear that the fibrous outer layer described by Morgenroth

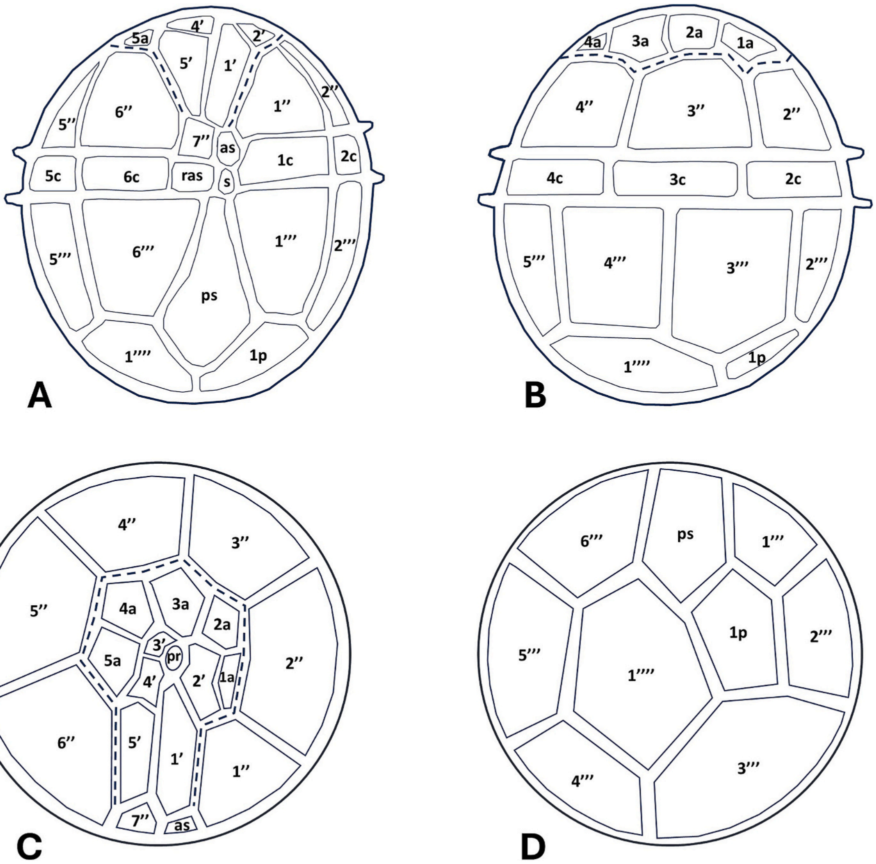

Fig. 4. Schematic tabulation for *Fibradinium annetorpense* n. emend. based on SEM observations. (A) Ventral, (B) dorsal, (C) apical, (D) antapical tabulation scheme.

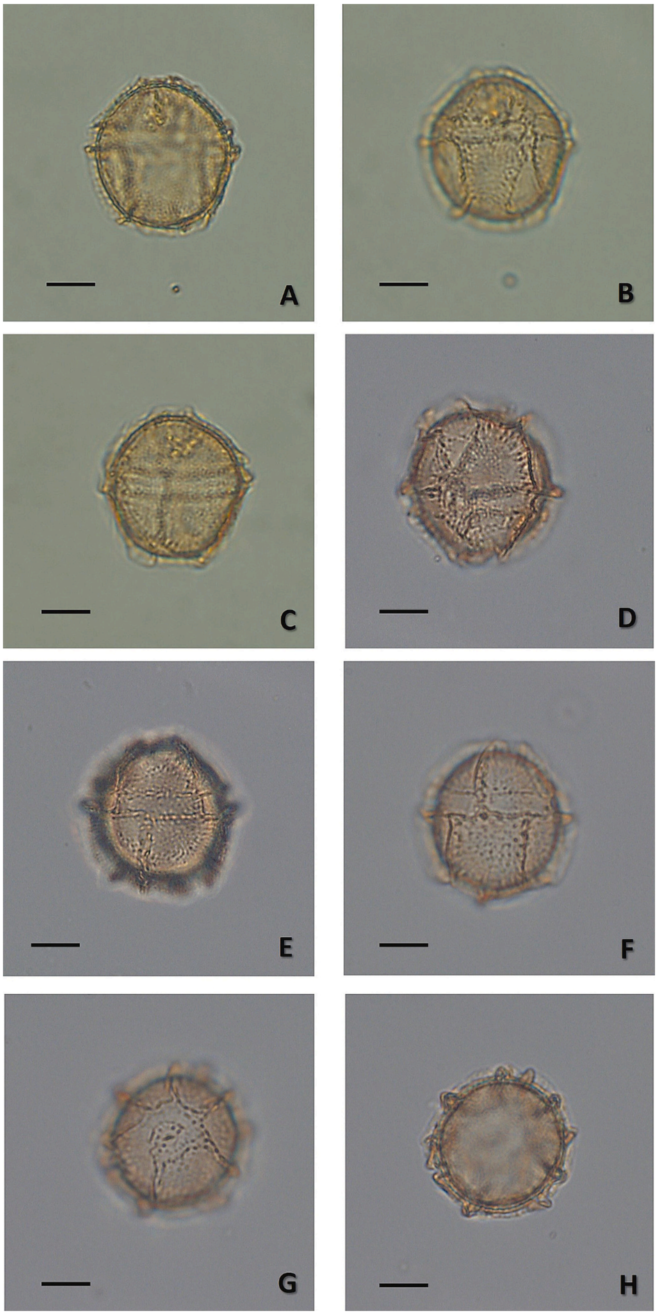

Fig. 5. Light microscope photographs of *Fibradinium annetorpense* n. emend. A–C – same cyst in equatorial view. A and B – ventral side photos with different focus. C – dorsal side of the cyst. D–H same cyst in different orientations. D – apical view. E–F – equatorial view dorsal side. G–H – antapical view with different focus. The scale bar represents 20 μm for all specimens.

(1968) is the result of continuous ridges and indentations across the crests formed at the edge of each paraplate. The cysts also evidence the presence of nanno “indentations” forming a ring around the precingular, cingular, postcingular, posterior, and posterior sulcal paraplates. The number can vary from paraplate to paraplate and be more or less clear depending on the stage of preservation. The apical and anterior intercalary paraplates exhibit at least 1 nanno “indentation” depending on the size of the paraplate.

It was possible to determine the tabulation using SEM as indicated by sutural features which are expressed by crests: 5′, 5a, 7″, 6c, 7″’, 1p, 1″“(see Figs. 4, 5, 6, Supplementary material).

The archeopyle is apical-intercalary of the type (tAtI)a with an adnate operculum ventrally usually attached to the anterior sulcal paraplate; the operculum is composed of eleven paraplates of which there are 1 preapical, 5 apicals, and 5 anterior intercalaries. The 1′ and 5′ paraplates are elongated and larger than the other apical paraplates. The epicist has 7 precingular paraplates, a typical microdinioid feature that contrasts with other gonyaulacaceans. In the ventral area the presence of 1 anterior right sulcal paraplate (ras) and 1 anterior sulcal paraplate (as), close to the sulcus. The posterior sulcal paraplate is large and omegaform as observed in other microdinioids. There are 6 postcingular paraplates and two relatively large plates (1p and 1″“) form the antapex. Paraplate 1″“is significantly larger than 1p (Fig. 6E).

Remarks: Slimani (1994) described *Fibradinium annetorpense*? as resembling Morgenroth’s original illustrations of *F. annetorpense* but differing in tabulation, with an archeopyle formed by the loss of nine apical and intercalary paraplates. Slimani (op. cit., p. 24) also revised the genus *Microdinium* (Cookson and Eisenak, 1960) to emphasize its apical-intercalary archeopyle (type tAtl)a, similarly composed of nine small paraplates. These differences in tabulation and archeopyle types distinguish *Fibradinium*, *Microdinium* (apical-intercalary), and *Phanerodinium* (precingular, no anterior intercalary paraplates), contradicting Below’s (1987) proposal to synonymize these genera.

However, Slimani (1994) questioned whether intraspecific variability in *F. annetorpense* might blur distinctions between *Fibradinium* and *Microdinium*, potentially supporting Below’s synonymization of the two under *Phanerodinium*. Slimani did not formalize this synonymization, and in 2011, Slimani and Louwye (2011) recognized *Microdinium* as distinct by referencing “*Microdinium* Cookson and Eisenack, 1960 emend. Slimani, 1994“and assigning two new *Druggidium* species to the “*Microdinium* Complex of Gp-cysts”. Duxbury (2019) also made a detailed discussion of these same remarks.

As mentioned above, there are currently seven published species of *Fibradinium*, although five of them have a questionable assignment (Table 1). Stover and Helby (1987) distinguished *F. variculum* from *F. annetorpense* by noting the absence of sutural features that outline paraplates. Based on Morgenroth’s (1968) findings, the size, shape, wall layering, position of the paracingulum, and archeopyle of both species appear to be identical. Duxbury (2019) raised questions about whether *F. variculum* should remain classified within this genus. Although it is a small species, exhibiting a fibrous-like structure like that *of F. annetorpense* observed under LM, it lacks clear tabulation beyond what is indicated by the cingulum and sulcus. Additionally, the archeopyle type for *F. variculum*, as described by Stover and Helby (1987), is apical (type [tA]), while Slimani (1994) noted the loss of apical and intercalary paraplates, totalling nine for this genus.

The type material for *F. variculum* dates from the Barremian to early Aptian age, and Duxbury (2019) recorded it from similar-aged material in the Heslerton No. 2 borehole in northern England. Duxbury (2024) also documented Valanginian/Berriasian and Hauterivian/Barremian GSSP sites at Vergol and La Charce, confirming the species’ wide geographic distribution and marking its oldest published record to date.

In the future, SEM analysis of *F. variculum* should be used to clarify if this species indeed possesses a true fibrous structure. Additionally, such analysis would assist in distinguishing its tabulation, which may influence the decision whether or not to retain the genus *Fibradinium*.

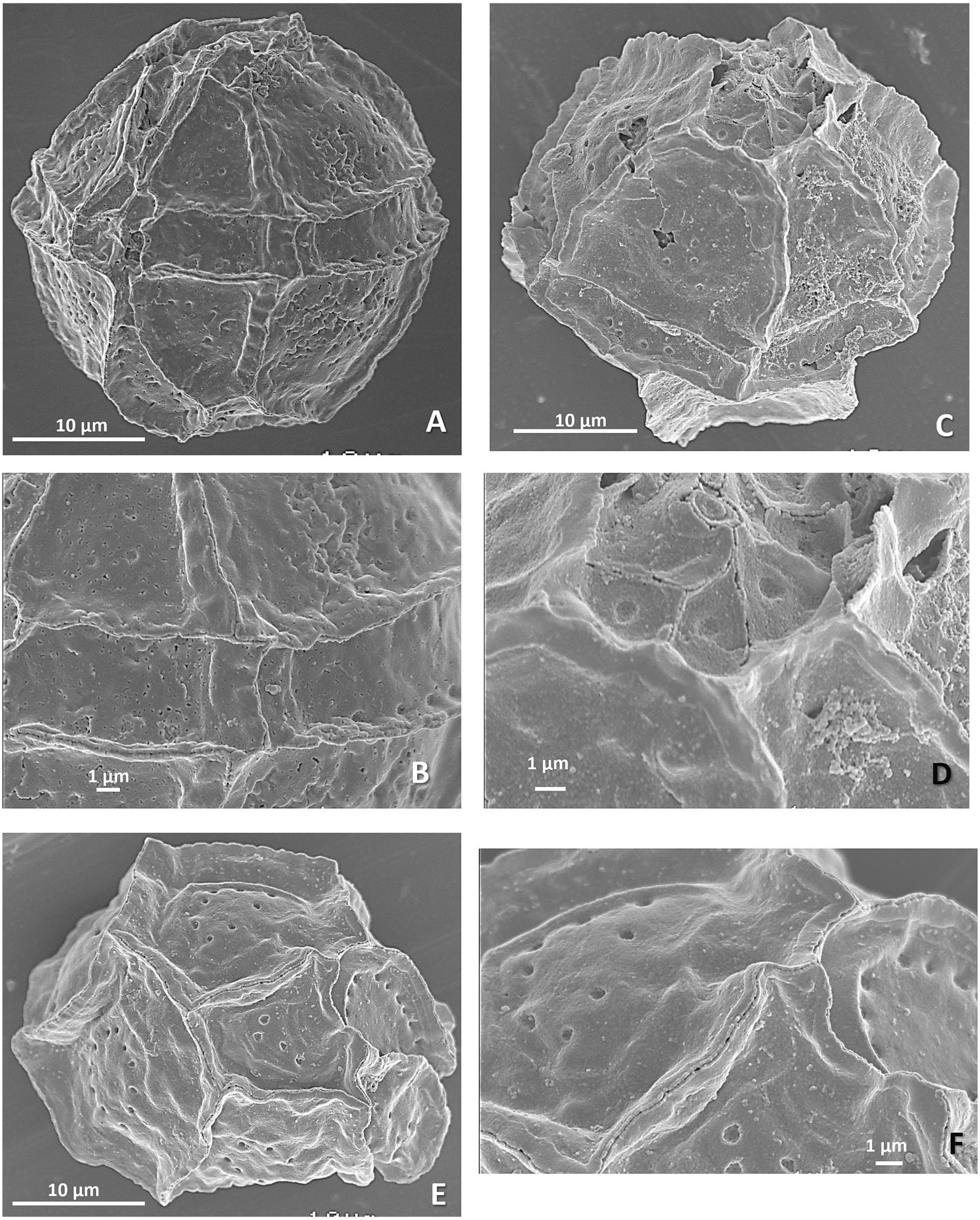

Fig. 6. SEM photos of *Fibradinium annetorpense* n. emend. (3 different specimens) A – ventral side evidencing the presence of 1 anterior right sulcal paraplate (ras) and 1 anterior sulcal paraplate (as), close to the sulcus and the large and omegaform posterior sulcal paraplate. B – detail of the cingular paraplates evidencing the continuous ridges and indentations across the crests formed at the edge of each paraplate. C – apical view of a specimen evidencing the archeopyle area. D – detail of the apical area (in appendix 2 the tabulation interpretation is drawn on top of the images). E – Antapical view of a very well-preserved specimen evidencing the postcingular paraplates and the two relatively large antapical (1p and 1’’“) paraplates. Is possible to see that paraplate 1’’“ is largen than 1p. F – detail of the paraplate junctions evidencing ridges and indentations. Also clear the presence of nanno “indentations” forming a ring around each paraplate.

4. Stratigraphic and paleoenvironmental relevance of these species

Spiniferites magnificus was formally described by Vieira et al. in 2018, although its initial identification dates back to 1983 by palynologists from Robertson (UK) Ltd. This species has become an important biostratigraphic marker for the late Danian in the greater North Sea Basin. Despite its frequent mention in various biostratigraphic publications, including works by Williams and Bujak (1985), Mudge and Bujak (1996), Stover et al. (1996), and Williams et al. (1998, 2004), it remained informal until Vieira et al. (2018b) provided a formal taxonomic designation. In the North Sea Basin, this species has its LO (Last Occurrence = extinction datum) at the boundary between the Danian and Selandian at the same stratigraphic level as *Operculodinium magnum* and the FO (First Occurrence) of *Thalassiphora lacunata*; and stratigraphically just above the LO of *Eisenackia reticulata*. This event was used to define the North Sea Dinocyst Biosubzone P2b of Mudge and Bujak (1996) and the Biozone P2: *Spiniferites magnificus* Zone (Bio subzone P2.3) of Vieira et al. (2020). In the same stratigraphic interval, the presence of additional microfossil markers, such as the LO of planktonic foraminifera like *Globanomalina* cf. *compressa*, *Eoglobigerina trivialis*, *E. spiralis*, and *Globorotalia inconstans* further supports the assignment of a Danian age (Vieira et al., 2020). The FO of *Spiniferites magnificus* is observed in the Biosubzone P1.3 as per Vieira et al. (2020), occurring before the LO of *Senoniasphaera inornata*. Due to its relatively short stratigraphic range, this taxon serves as an excellent regional stratigraphic marker across the greater North Sea Basin.

Mudge and Bujak (1996) initially observed that *Spiniferites magnificus* had only been documented within the North Sea region. However, in a subsequent publication by the same authors in 2001, they reported the presence of this species in wells from the Faroe-Shetland Basin at the same stratigraphic level. Furthermore, *S. magnificus* was utilized to define the top of the lower Paleocene in the Våle Formation of the Grane Field, as noted by Mangerud et al. (1999). Nøhr-Hansen (2012) also documented its occurrence in the uppermost Danian strata within the Kangerlussuaq Basin in southern East Greenland. Additionally, Vieira et al. (2018a) presented a species distribution map encompassing the North Sea, Faroe-Shetland, and Norwegian Sea basins, highlighting occurrences in Danian sediments in various wells within the Jeanne d'Arc Basin in Canada.

The presence of intergonal processes and high sutural crests in *Spiniferites magnificus* is noteworthy, as similar features are observed in extant *Spiniferites* species, which are relatively common in estuarine environments (Limoges et al., 2018). In that relation, it is relevant to note that *Spiniferites magnificus* from the Late Danian occurred in fully marine environments. There, *S. magnificus* was associated with diverse dinoflagellate cyst assemblages comprising taxa such as *Eisenackia reticulata*, *Spiniferites ramosus* 'group', *Glaphyrocysta expansa*, *Cerodinium diebelii*, *Palaeoperidinium pyrophorum*, *Palaeocystodinium bulliforme*, P. *golzowense*, P. *lidiae*, *Hystrichosphaeridium tubiferum*, *Desmocysta plekta*, *Cribroperdinium wetzelii*, *Areoligera constricta*, *Operculodinium magnum*, O. *centrocarpum*, *Spongodinium delitense*, and *Xenicodinium lubricum* (see Vieira et al., 2020). The presence of abundant planktic foraminifera species such as *Globanomalina* cf. *compressa*, *Eoglobigerina trivialis*, *E. spiralis, Globorotalia inconstans*, *Eoglobigerina edita*, and *Globorotalia planocompressa* in the same stratigraphic interval also indicates open marine conditions. We speculate that the variations in the development of sutural crests observed in different specimens of *Spiniferites magnificus* may indicate that they were transported from various regions of the shelf. This variation could potentially reflect differences in salinity conditions.

Currently, *Spiniferites hainanensis*, is present in warm environments such as around the Hainan Island (China), the Gulf of California (Mexico), and in the Marmara Sea (Turkey) (Limoges et al., 2018). *Spiniferites magnificus* also occurred across the greater North Sea area in relatively warm sea waters during the Late Danian (Vieira et al., 2020).

The rock samples yielding the *Fibradinium annetorpense* n. emend. Specimens are of Late Danian age, between 64 Ma - 62 Ma, and corresponding to the calcareous nannoplankton biozones NP3-NP4 (Dam et al., 2009; Grímsson et al., 2016).

In the same sample other dinoflagellate cysts were identified such as *Achomosphaera ramulifera*, *Areoligera coronata*, *A. senonensis*, *Cerodinium speciosum*, *Cordosphaeridium inodes*, *Deflandrea variabilis*, *Operculodinium centrocarpum*, *Palaeocystodinium bulliforme*, *Palaeoperidinium pyrophorum*, *Senegalinium iterlaaense, Tanyosphaeridium xanthiopyxides,* and *Thalassiphora pelagica.* The occurrence of *Deflandrea variabilis* is stratigraphically relevant, this species was recently described from sediments in the Ormen Lange field (Norwegian Sea) associated with other Danian marker species such as *Alisocysta reticulata* and *Spiniferites magnificus* (Vieira et al., 2018b). The presence of *Senegalinium iterlaaense* has been previously documented in Greenland sediments, specifically within the upper NP3 to upper NP4 zones of Martini (1971), as reported by Nøhr-Hansen and Heilmann-Clausen (2001). It has also been recorded in Denmark below the top of the Danian limestone (Nøhr-Hansen and Heilmann-Clausen, 2001). Additionally, this taxon was identified in the

Fig. 7. Map of published occurrences of *Fibradinium annetorpense in sediments from the Santonian to Thanetian (see Appendix 1 for reference details).*

uppermost part of the Danian limestone at Limhamn Quarry in southern Sweden, where it was referred to as *Deflandrea* sp. A by De Coninck (1975), within the NP3 Zone of Martini (1971). Furthermore, *Senegalinium iterlaaense* has been consistently recorded in the Norwegian Sea, associated with other Danian markers (Vieira et al., 2018b).

The *Fibradinium annetorpense* n. emend. holotype was collected from Danian sediments at the Annetorp locality, from which the species name is derived (Morgenroth, 1968). The specimens analyzed in this study were extracted from phosphoritic nodules dated to the late Danian (64 to 62 Ma) on the Nuussuaq Peninsula, western Greenland. A review of published occurrences and the PALSYS database (Bijl, 2023) reveals that this taxon has a broader stratigraphic range than *S. magnificus*, spanning from the Santonian to the Thanetian. Fig. 7 illustrates these published occurrences, which are further detailed in Appendix 1. The majority of recorded occurrences are concentrated in Europe and along the eastern coast of North America, with additional scattered reports from northern and western Africa. To date, no occurrences have been documented in Australia, South America, or most parts of Asia. However, a Maastrichtian occurrence has been reported in southern Western Siberia (Lebedeva et al., 2013).

The earliest occurrence of *F. annetorpense* is Santonian, confirming a Late Cretaceous inception for this species. It subsequently experienced significant geographic expansion in the Paleocene. The Maastrichtian and Danian intervals exhibit the widest distribution, with occurrences in North America, Europe, and Africa. In contrast, the Selandian and Thanetian intervals show fewer records. Notably, the species reached its broadest geographic distribution during the Danian, as evidenced by its consistent presence across a wide range of locations.

5. Conclusion

This study highlights the value of integrating SEM observations into the taxonomic study of fossil dinoflagellate cysts, emphasizing the enhanced resolution and morphological detail achievable with the single-grain method. By applying this methodology, we refined the descriptions of *Spiniferites magnificus* and *Fibradinium annetorpense*, identifying key features that were previously obscured under LM, such as perforations in sutural crests, variable intergonal processes, and intricate wall ornamentation. These advancements provide a more nuanced understanding of these species, underscoring the significance of SEM in complementing LM for dinoflagellate cyst taxonomy.

Future work should focus on extending SEM-based analyses to other dinoflagellate cyst taxa, especially those with uncertain taxonomic assignments. By systematically documenting fine-scale morphological features, it may be possible to resolve long-standing taxonomic ambiguities and deepen our insights into the evolutionary and ecological dynamics of Paleocene dinoflagellates.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2025.105300.

Appendix B. Appendix

This appendix alphabetically lists all formally described taxa below the generic level which are mentioned in this contribution, with full author citations.

Dinoflagellate cysts:

Achomosphaera ramulifera (Deflandre, 1937b) Fensome et al., 1991
Areoligera constricta Vieira et al. (2018b)
Areoligera coronata (Wetzel, 1933) Lejeune-Carpentier (1938)
Areoligera senonensis (Lejeune-Carpentier, 1938) Lejeune-Carpentier and Sarjeant (1981)
*Cerodinium diebelii (*Alberti, 1959*)* Lentin and Williams (1987)
Cerodinium speciosum (Alberti, 1959) Lentin and Williams (1987)
Cordosphaeridium inodes (Klumpp, 1953) Eisenack (1963)
Cribroperidinium wetzelii (Lejeune-Carpentier, 1939) Helenes (1984)
Deflandrea variabilis Vieira et al. (2018b)
Desmocysta plekta Duxbury (1983)
Eisenackia reticulata (Damassa, 1979) Quattrocchio and Sarjeant (2003)
Glaphyrocysta expansa (Cyclonephylium expansum) (Corradini, 1973) Roncaglia and Corradini (1997)
Hystrichosphaeridium tubiferum (Ehrenberg, 1837) Davey and Williams (1966)
Operculodinium centrocarpum (Deflandre and Cookson, 1955) Wall (1967)
Operculodinium magnum Vieira et al. (2018a)
Palaeocystodinium bulliforme Ioannides (1986)
Palaeocystodinium golzowense Alberti (1961)
Palaeocystodinium lidiae (Górka, 1963) Davey (1969)
Palaeoperidinium pyrophorum (Ehrenberg, 1837) Sarjeant (1967)
Senegalinium iterlaaense Nøhr-Hansen and Heilmann-Clausen, 2001
Senoniasphaera inornata (Drugg, 1970) Stover and Evitt (1978)
Spiniferites hainanensis Xuekun and Zhichen, 1992)
Spiniferites mirabilis (Rossignol, 1964) Sarjeant, 1970
Spiniferites ramosus Ehrenberg, 1837
Spiniferites rhomboideus Vieira and Mahdi, 2019
Spongodinium delitiense (Ehrenberg, 1837) Lucas-Clark (1987)
Tanyosphaeridium xanthiopyxides (Wetzel, 1933) Sarjeant (1985)
Thalassiphora lacunata Vieira et al. (2018a)
Thalassiphora pelagica (Eisenack, 1954) Benedek and Gocht (1981)
Xenicodinium lubricum Morgenroth (1968)

Microfossils:

Eoglobigerina spiralis Bolli (1957)
Eoglobigerina trivialis Subbotina (1953)
Globanomalina compressa Plummer (1927)
Globorotalia inconstans Subbotina (1953)

Data availability

Data will be made available on request.

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