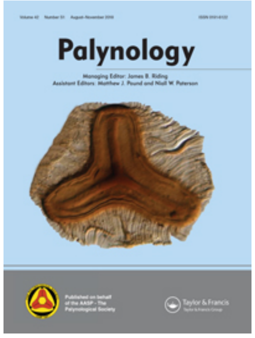

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ABSTRACT
The use of dinoflagellate cyst assemblages as a tool for palaeo-environmental reconstructions strongly relies on the robustness of cyst identification and existing information on the distribution of the different species. To this purpose, we propose a functional key for the identification of Pliocene and Quaternary *Spiniferites* bearing intergonal processes and depict the range of morphological variation of the different species on the basis of new observations from estuarine and coastal regions. Accordingly, the description of *Spiniferites mirabilis* is emended to include the new subspecies *Spiniferites mirabilis* subsp. *serratus*. We also report the occasional presence of intergonal processes in *Spiniferites bentorii* and *Spiniferites belerius*. This key aims to facilitate identification of this group of *Spiniferites* bearing intergonal processes and standardize cyst identification among researchers.

KEYWORDS
Dinoflagellate cyst; taxonomy; description; morphological variability; emendations

1. Introduction

All species belonging to the genus *Spiniferites* are known to always bear processes that are gonal, meaning located at the point of intersection (or triple junction) of three plates (e.g. Williams et al. 1978). However, some *Spiniferites* species can (consistently or occasionally) bear additional processes that are intergonal, meaning located between these intersections (or triple junctions) (e.g. Evitt 1985, p. 71) on so-called sutures that form the boundaries between plates (Evitt 1985, p. 69). Another important morphological feature for such species is the presence of crests or septa, which are raised ridges along the plate boundaries. Some of these crests can be raised close to the distal end of the processes (often located on the antapical side), and in such cases, are called flanges or wings.

Spiniferites species with intergonal processes are important components of the assemblages from Cretaceous to Quaternary deposits (Figure 1). Their distribution extends from estuarine to open ocean environments, in equatorial to subpolar regions (Zonneveld et al. 2013). In modern sediments, *Spiniferites mirabilis* (Rossignol 1964) Sarjeant 1970 and *Spiniferites hyperacanthus* (Deflandre and Cookson 1955) Cookson and Eisenack 1974 are the most often recognized species bearing intergonal processes and their cumulative abundances can reach more than 50% of the total dinoflagellate cyst (dinocyst) assemblage in the North Atlantic and adjacent seas (based on the Northern Hemisphere database of modern dinocysts compiled at Geotop (cf. de Vernal et al. 2013; see Figure 2; de Vernal et al. 2018)). These are accompanied by *Spiniferites bentorii* (Rossignol 1964) Wall and Dale 1970 and a few other species that will be discussed below.

During routine palynological counts, the assignment of *Spiniferites* specimens to previously described species is sometimes challenged by 1) the emergence of atypical features that are not listed in the original descriptions, such as an apical protuberance, sutural septa, wall surface ornamentation and 2) the presence of intergrading morphological features between distinct taxonomic identities. Deciphering whether a specimen found in sediment is a new form or within a range of acceptable morphological variation can thus be difficult. The decision is generally at the discretion of the analyst and may vary from one person to another. The final diagnostic can further depend upon the study area. As such, "uncommon" features are more common in estuarine environments than in open-ocean regions and palynologists working in estuarine environments might be

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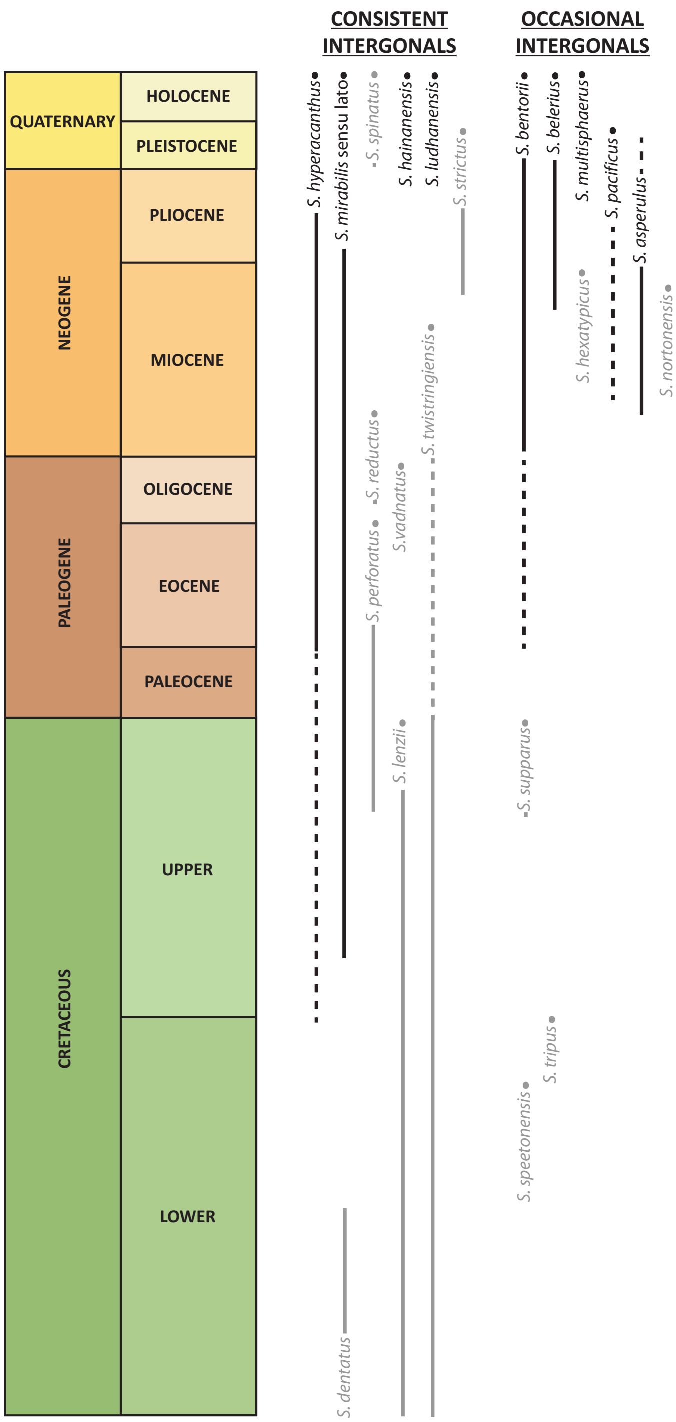


Figure 1. Known biostratigraphical ranges of *Spiniferites* species bearing intergonal processes. Taxa bearing intergonal processes on all the sutures (consistent intergonals) are distinguished from those occasionally bearing intergonal processes and rarely on all the sutures (occasional intergonals). Species names written in black are discussed in this contribution, whereas those in grey are not discussed.

tempted to refer to an operational species concept rather than to its strict formal description.

The use of a standardized taxonomy through an identification key with clear criteria is of paramount importance when trying to infer palaeoecological and palaeoceanographic information from the dinocyst assemblages. In order to facilitate cyst identification during routine counts, we present an overview of the Pliocene and Quaternary *Spiniferites* species described as having intergonal processes and we discuss their range of morphological variation.

2. Methodology

We present new observations of several *Spiniferites* species bearing intergonal processes extracted from sediment from various estuarine and coastal environments including Alvarado Lagoon (Southwestern Gulf of Mexico), West Lake (Florida, U.S.A.), northeast Pacific Ocean (Gulf of California), Isla San Jose Lagoon (southwest Gulf of California), Gulf of San Jorge (Argentina), Aegean Sea, Marmara Sea, and Mediterranean Sea (Figure 3). The large morphological variability depicted from these regions helps to highlight some parts of the original species descriptions that require further clarification. To ensure a good identification of the morphological features, some terms used in the species descriptions are reviewed in Table 1.

We also provide the current inventory of all *Spiniferites* species documented from Pliocene and Quaternary sediments that were formally described as consistently or occasionally bearing intergonal processes. Their original descriptions are reproduced, in addition to supplementary information based on available literature and our new observations. These descriptions are complemented with schematic illustrations and micrograph plates.

2.1. Sample preparations

Microscopy observations were performed on residues extracted from sediments processed using marine palynological analyses following standard laboratory procedures. Samples from the Gulf of Mexico, Gulf of San Jorge and Isla San Jose Lagoon were sieved between 106 and 10 μm and digested with warm hydrochloric acid (HCl 10%) and hydrofluoric acid (HF 40%) at Geotop, UQAM and UQAR (see de Vernal et al. 1999). Samples from the northeast Pacific Ocean (Gulf of California) and Aegean Sea were sieved between 120 and 15 μm and digested with room-temperature HCl (10%) and HF (40%) in the Paleoenvironmental and Marine Palynology Laboratory at the University of Victoria (cf. Pospelova et al. 2010). The organic residue was mounted onto microscope slides in glycerine gelatin. Light microscope observations were conducted by AL and TC at UQAM (Montréal, Canada), by AR at UQAR (Rimouski, Canada), KNM at Ghent University (Belgium), by LL at University of Bordeaux (France) and by VP at University of Victoria (Canada). For scanning electron micrographs, individual cysts were isolated from sediment samples using a micropipette onto a glass slide, subsequently air-dried and observed by KM using a Hitachi S-3400N (UQAM) and AR using a JEOL JSM-6460LV (UQAR).

3. Observations from estuarine and coastal regions

Coastal and estuarine areas are characterized by stronger and more frequent fluctuations in environmental parameters

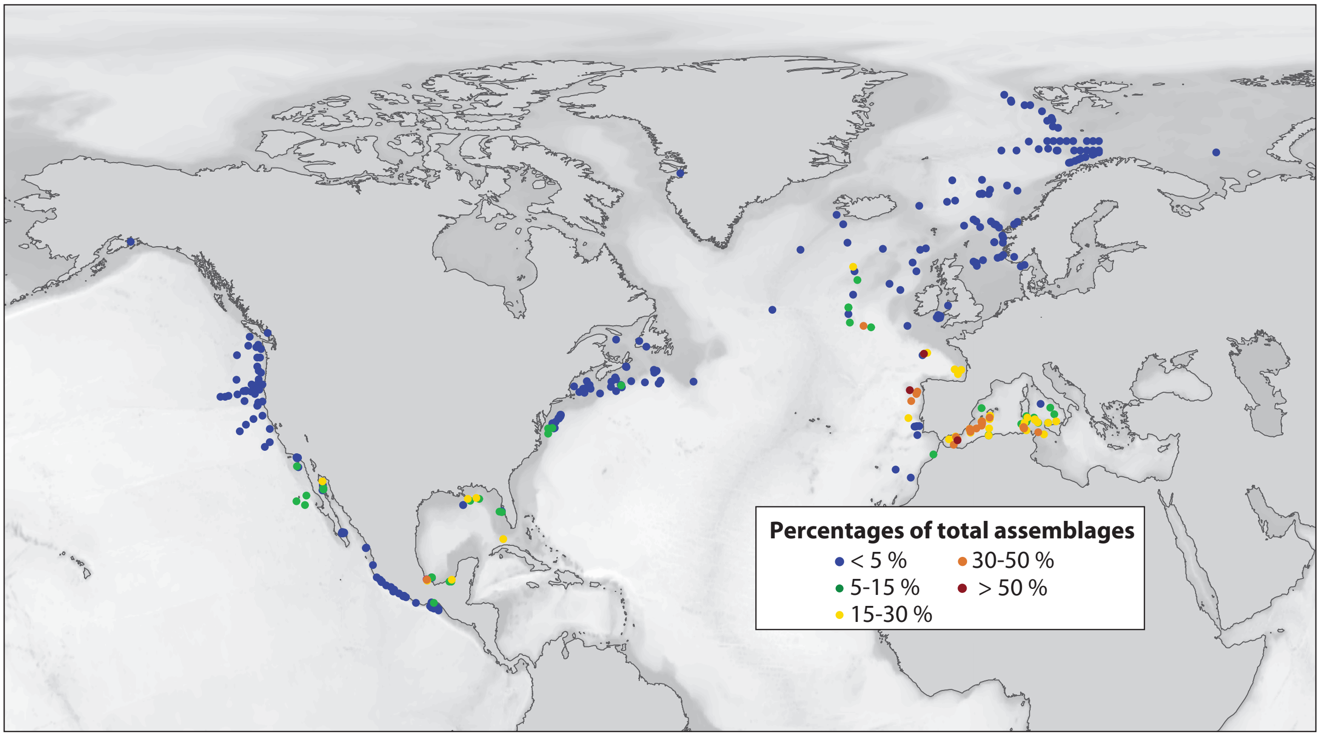


Figure 2. Modern distribution of *Spiniferites mirabilis* sensu lato together with *Spiniferites hyperacanthus* based on the Northern Hemisphere database of modern dinocyst compiled at Geotop ($n = 1492$; cf. de Vernal et al. 2013).

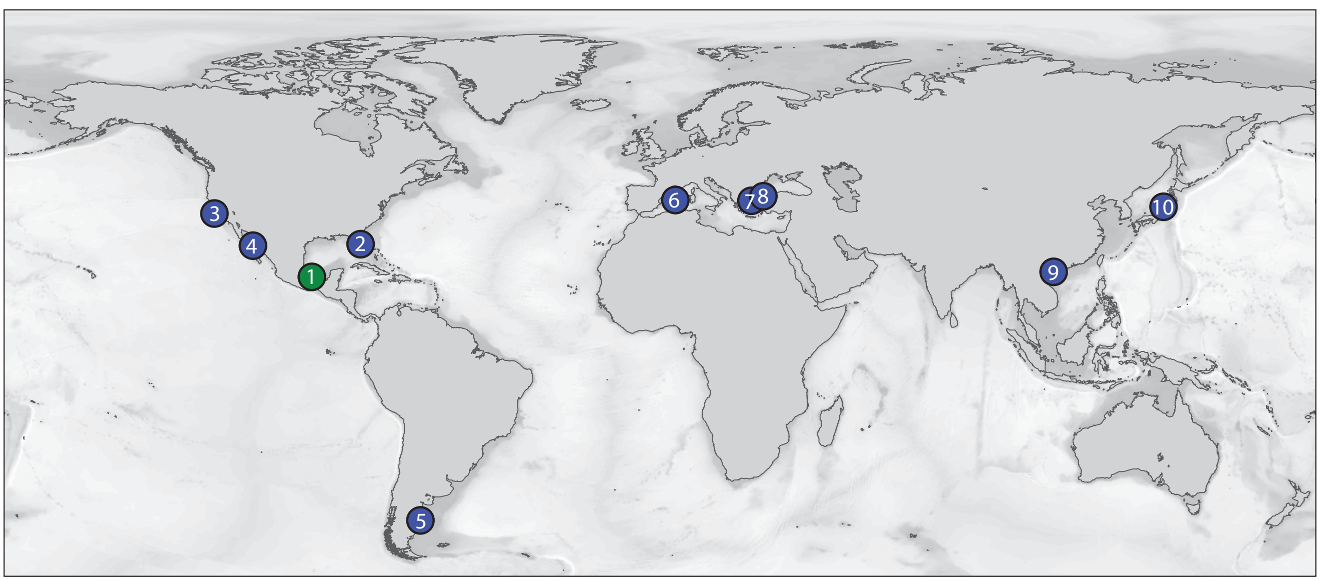
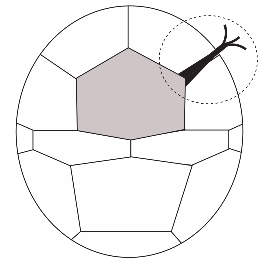
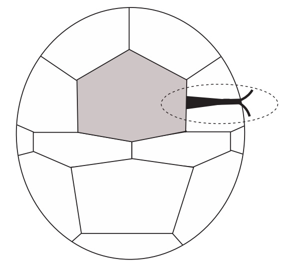


Figure 3. Map showing the locations of the various sites from which specimens are illustrated in plates 1–5: **1.** Alvarado Lagoon (Plates 1–2), **2.** West Lake (Florida; Plate 4), **3.** Northeastern Pacific Ocean (Gulf of California) (Plates 3–4), **4.** Isla San Jose Lagoon (Southwest Gulf of California) (Plates 4–5), **5.** San Jorge Gulf (Plate 3), **6.** Mediterranean Sea (Plate 3), **7.** Aegean Sea (Plate 3), **8.** Marmara Sea (Plates 3–4), **9.** Hainan Island (Plate 4), and **10.** Japan (Plate 4).

compared to the open ocean. As a consequence, cysts recovered from such marginal settings are more likely to display a wider range of morphological variability, as a response to fluctuating conditions (cf. Lewis et al. 1999; Ellegaard 2000, 2002; Kouli et al. 2001; Mudie et al. 2001; Pospelova et al. 2004; Mertens et al. 2009, 2012). In the shallow (~2 m depth) Alvarado Lagoon (Figure 3), *Spiniferites* species with intergonal processes are dominant and represent up to 48% of the dinocyst assemblages (see Limoges et al. 2015). However, many of the specimens identified did not match the original descriptions for Pliocene to Quaternary *Spiniferites* species with intergonal processes. They show a large range of variations with regards to the number, length and morphology of their processes, as well as the development of septa and the presence or absence of an apical protuberance (see Plates 1–2). Their identification is further complicated by ambiguities in the original descriptions or overlap between the descriptions. As a consequence, certain specimens could be attributed to either none or more than one of the formally established species. In spite of the individual features of the

Table 1. Definitions and illustrations of the morphological terms and concepts used to describe *Spiniferites* taxa with intergonal processes.

Morphological terminology	Definition	Illustrations
Gonal processes	Processes located at the intersection between three paraplates.	
Intergonal processes	Processes located on the parasutural boundary between two paraplates.	
Morphological concepts	**Signification**	
Species with occasional intergonal processes	Species that can carry one intergonal process (or two, but no more) along some sutures.	
Species with consistent intergonal processes	Species on which at least one intergonal process is present along each major suture.	

specimens, the apparently continuous range of morphologies would suggest that it seems rather unlikely that they belong to (a lot of) different species. It points to the need to define unambiguous diagnostic features that a specimen should display for assignation to a given palaeontological species, as well as the importance of including a potential range of morphological variations to the descriptions.

Comparison of *Spiniferites* morphologies from Alvarado Lagoon with those of other estuarine and coastal regions across different latitudes shows that the occurrence of morphotypes is not restricted to this specific subtropical site. For instance, the flange, an important characteristic of *Spiniferites mirabilis*, frequently displays important variations with respect to its height and number of processes included (Plate 3, Figures 1–20). The wall ornamentation of *Spiniferites mirabilis* is variable, ranging from smooth to microgranular (Plate 3, Figures 10–20). The number of intergonal processes in *Spiniferites hyperacanthus* and *Spiniferites mirabilis* varies (Plate 3). Many specimens of *Spiniferites mirabilis* show a well-developed apical protuberance. Furthermore, *Spiniferites* specimens from various estuarine regions exhibit fairly high sutural crests (Plate 1, Figures 13–15, Plate 2, Figures 13–14, Plate 3, Figure 6).

As such, on the basis of our new observations, a number of points could be made regarding the morphological characteristics of the taxa:

- *Spiniferites hyperacanthus* and *Spiniferites mirabilis* exhibit variations with regards to the number of intergonal processes, but always bear at least one intergonal process between gonal processes.
- In coastal and estuarine settings, *Spiniferites hyperacanthus* sometimes displays reduced processes (<3 µm).
- The development of an apical boss seems to be an occasional feature of *Spiniferites mirabilis* (Plate 2, Figures 4–6 and 9).
- Three to ten processes can be embedded in the flange of *Spiniferites mirabilis* (Plates 2–3).
- Specimens bearing intergonal processes and high sutural crests are relatively common in estuarine environments.

4. Original descriptions of Pliocene and Quaternary *Spiniferites* species with intergonal processes, comments about occurrence and discussion

We present an overview of Pliocene and Quaternary *Spiniferites* species described as having intergonal processes. These are reported in alphabetical order. We provide the original descriptions of the cysts together with translations, and a discussion. Note that in the section below, *Spiniferites nanus* Matsuoka 1976 has not been included because it is not possible to unambiguously distinguish its morphology from already described species. We recommend restricting its identification to the holotype. Furthermore, although *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970, *Spiniferites lazus* Reid 1974 and *Rottnestia amphicavata* Dobell and Norris in Harland et al. 1980 (now considered a junior synonym of *Spiniferites elongatus* Reid 1974; see Van Nieuwenhove et al. 2018) have previously been reported to occasionally exhibit intergonal processes (Rochon et al. 1999), new observations could not confirm this to be part of their intraspecific morphological variability. These species are therefore not included here, but are respectively discussed in Gurdebeke et al. (2018) and Van Nieuwenhove et al. (2018).

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993, emend. Adl et al. 2005

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

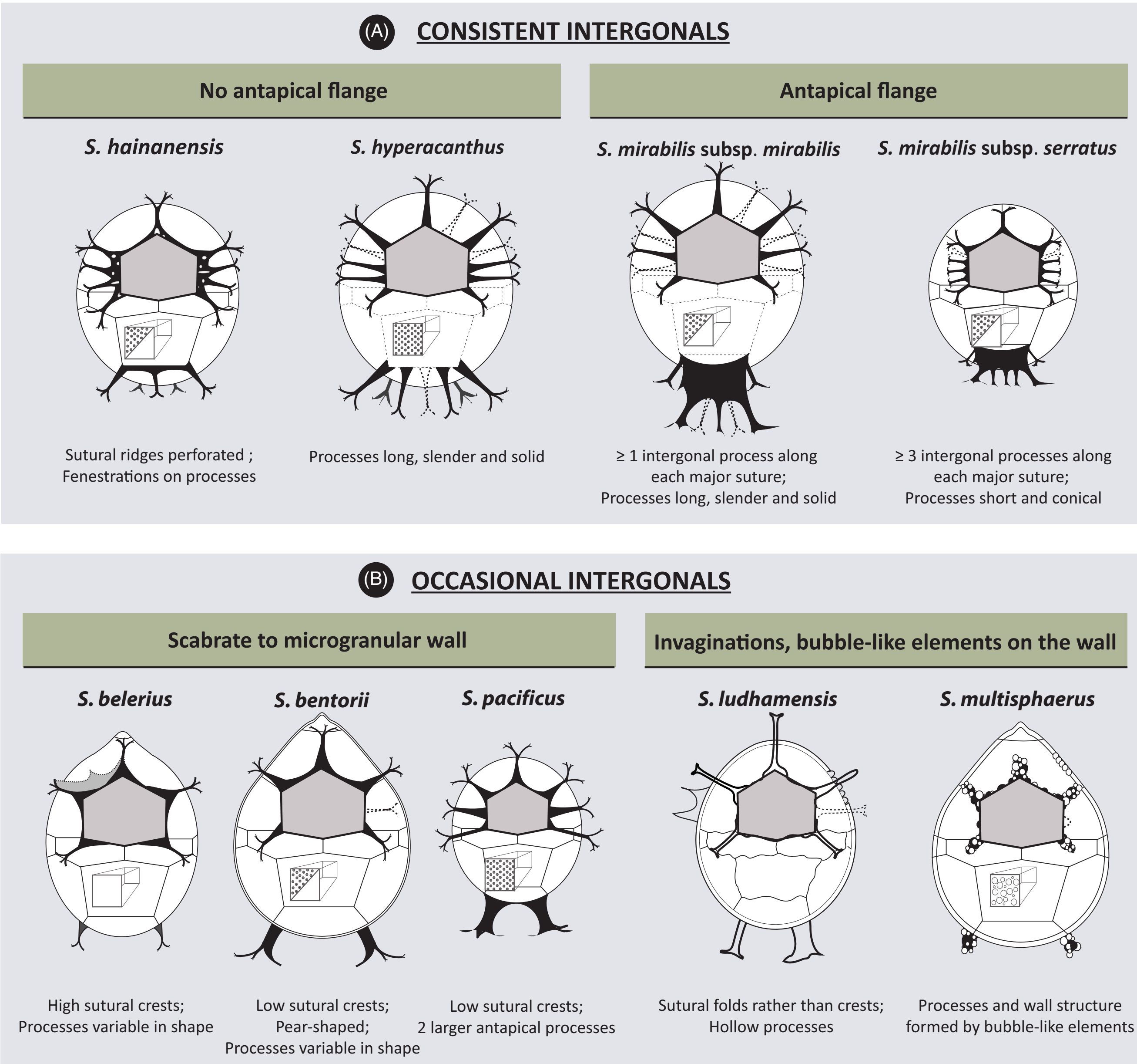


Figure 4. Schematic representations of the Pliocene and Quaternary *Spiniferites* species with intergonal processes, divided in two groups of taxa (see also Table 2): A) those with consistent intergonals, which include species characterized by intergonal processes on all sutures: *Spiniferites hainanensis*, *Spiniferites hyperacanthus*, *Spiniferites mirabilis* subsp. *mirabilis* and *Spiniferites mirabilis* subsp. *serratus*, and B) those with occasional intergonals, which correspond to the species on which intergonal processes are sometimes present, but rarely on all sutures. This group includes *Spiniferites belerius*, *Spiniferites bentorii, Spiniferites pacificus, Spiniferites ludhamensis* and *Spiniferites multisphaerus*.

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order GONYAULACALES Taylor 1980

Suborder GONYAULACINEAE (Autonym)

Family GONYAULACACEAE Lindemann 1928

Subfamily GONYAULACOIDEAE (Autonym)

Genus *SPINIFERITES* Mantell 1850 emend. Sarjeant 1970

- ***Spiniferites asperulus*** Matsuoka 1983, p. 131–132, Plate 12, Figures 2, 3a–b, 4

Original description (from Matsuoka 1983). The intermediate proximochorate cyst is subspherical to ovoidal in shape, and consists of two layers, periphragm and endophragm. The endophragm is relatively thick and smooth. The periphragm is thin and granular. The gonal processes are conical, and distal ends of secondary furcate branches are bifid. At the proximal base of these processes, parasutural septa become membraneous. Their surface has small grana. This ornamentation is especially well developed in both apical and antapical areas. The parasutural septa are weak but almost complete. The archeopyle is a simple and reduced precingular type made up of loss of the 3′′ paraplate. The paratabulation basically coincides with the gonyaulacacean type.

Dimensions. Central body: 48–69 µm in length and 45–64 µm in width. Process length: up to 16 µm (Matsuoka 1983).

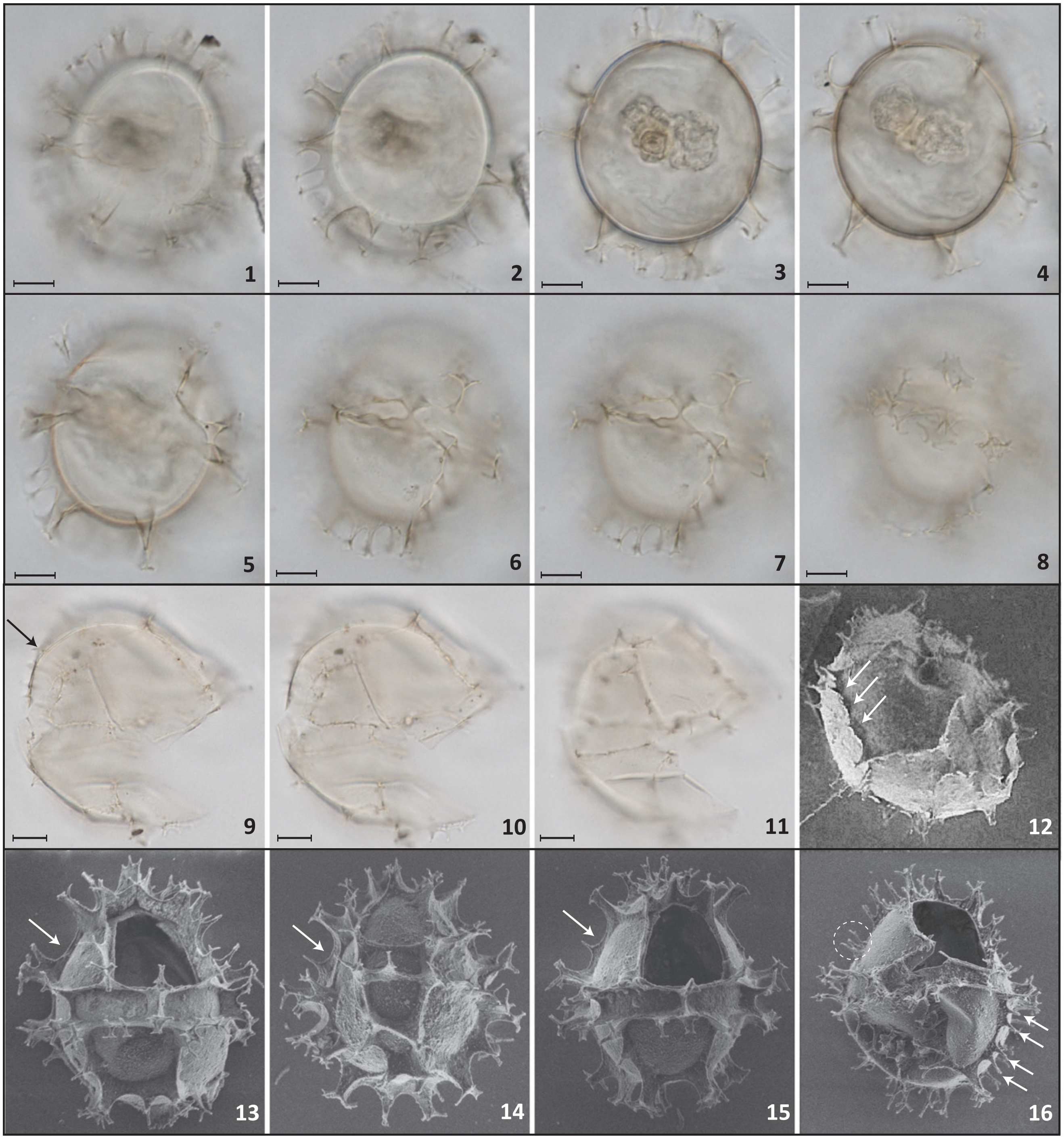


Plate 1. Figures 1–16. Bright field light and SEM micrographs of cysts of *Spiniferites* with intergonal processes that do not show an antapical flange. All specimens were observed in recent sediment from Alvarado Lagoon. **1–8.** *Spiniferites hyperacanthus*. Low to high focal planes of a specimen with up to three intergonal processes. **9–11.** *Spiniferites hyperacanthus* – short-processed morphotype. Low to high focal views of the same specimen. Note the presence of several short intergonal processes and low sutural crests. **12.** *Spiniferites hyperacanthus* – short-processed morphotype, **13–15.** Atypical specimens of *Spiniferites hyperacanthus* showing high sutural crests. **16.** Specimen of *Spiniferites hyperacanthus* – multi-intergonal morphotype. Specimen displaying fusion between processes and up to four intergonal processes. Scale bars = 10 μm.

Lowest stratigraphic occurrence. Early Miocene (Yun 1994)

Comment on occurrence. This species was identified only by a few authors in sediment from the Pacific Ocean (Matsuoka 1983; Kurita and Obuse 2003).

Discussion. The most distinctive features for this species are the gonal processes with granular and membraneous stalks, and the long secondary branches of the processes. While the diagnosis of this species mentions the presence of occasional intergonal processes, no intergonal process is visible on the holotype of *Spiniferites asperulus*. This species is therefore not included in our identification key.

- ***Spiniferites belerius*** Reid 1974, p. 596–598, Plate 2, Figures 12–13

Plate 4, Figure 16

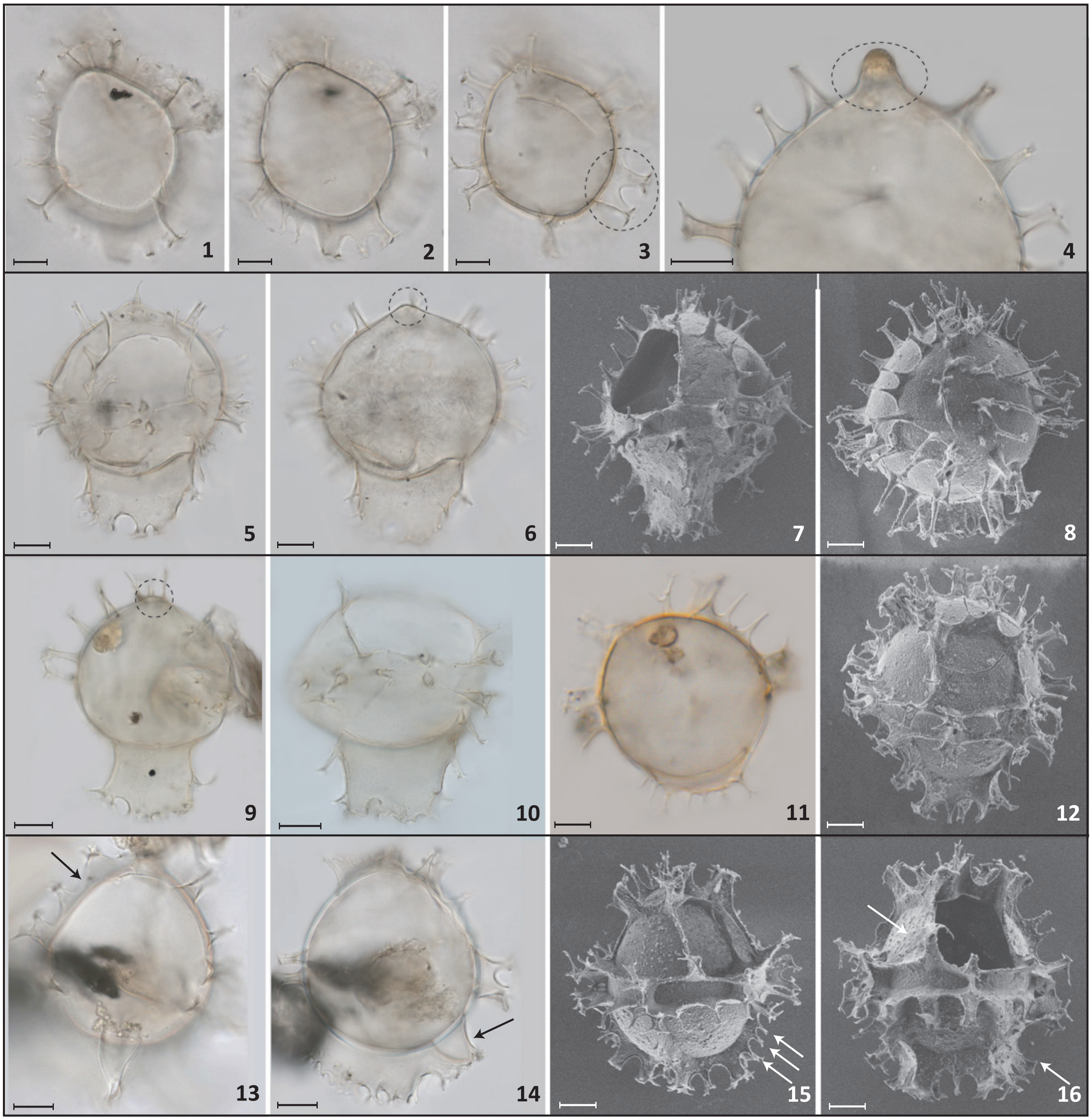


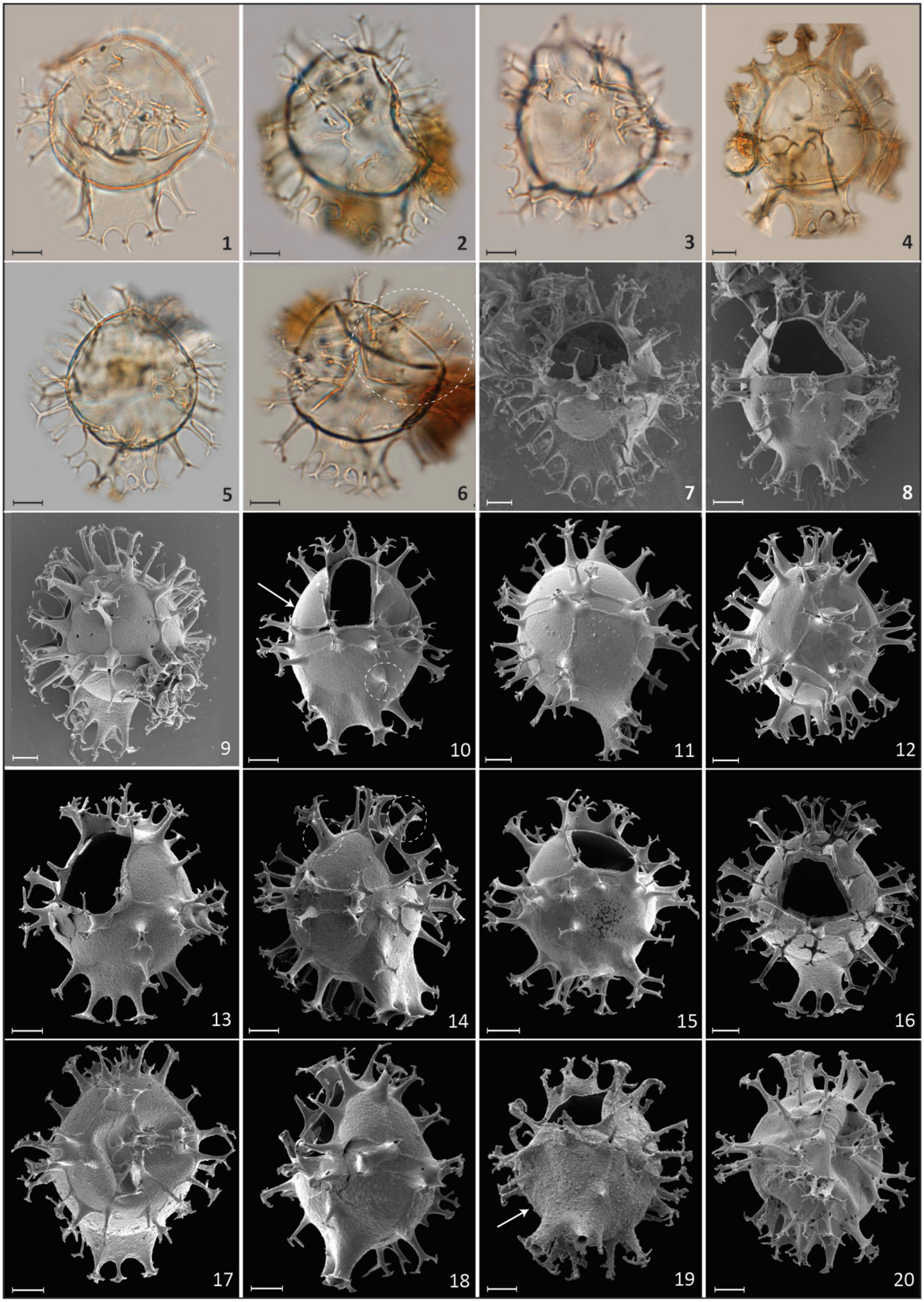
Plate 2. Figures 1–16. Bright field light and SEM micrographs of cysts of *Spiniferites* with intergonal processes and characterized by a flange or the development of a relatively high crests on the antapical region. All specimens were observed in recent sediment from Alvarado Lagoon. **1–3**. *Spiniferites mirabilis*. Note the ovoidal shape of the central body and the development of a membrane between some processes, **4**. *Spiniferites mirabilis* with very well developed apical protuberance, **5–11**. Different specimens of *Spiniferites mirabilis* showing well developed flanges. Note that the processes are solid and slender and the sutural crests are very low or absent. **12–16**. Specimens showing high sutural crests and the development of a moderately high membrane at the antapical region. Scale bars = 10 µm.

Original description (from Reid 1974). Test oval, always widest at the girdle; at times constricted towards the poles to give a rounded diamond shape with a clear apical node. The thin smooth surfaced wall is ornamented by gonal trifurcate processes formed from sutural septae [sic]. Septae [sic] form the high antapical "trumpet" shaped process, which characterises the species and may also form high membranous flanges. Process tips are trifurcate with recurved bifurcate tips. A relatively narrow 6–8 µm girdle is displaced by one to three times its own width.

Dimensions. Central body: 35–42 µm. Maximum process length 7–10 µm, with posterior process length between 10–15 µm (Reid 1974).

Lowest stratigraphic occurrence. late Miocene (Bertini et al. 1998).

Comment on occurrence. Since *Spiniferites belerius* is generally grouped with *Spiniferites membranaceus* in global databases (cf. de Vernal et al. 2013; Zonneveld et al. 2013), it is difficult to assess its individual distribution. However, the list of publications in which *Spiniferites belerius* is reported (see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PALYNODATA online database 2015) highlights a wide distribution ranging from tropical to subpolar environments, from coastal to open-ocean regions.

Discussion. Single specimens of *Spiniferites belerius* can bear variable process shapes. The wall is smooth and thin. Well-developed sutural membranes are often observed between processes, which are frequently truncated. Intergonal processes are occasionally observed one some sutures.

- ***Spiniferites bentorii*** (Rossignol 1964, p. 84–85, Plate 1, Figures 3, 3bis. 5–8, Plate 3, Figures 1–3) Wall and Dale 1970, p. 47–48

Plate 4, Figures 14–15

Original description (from Rossignol 1964). *Le test est formé de deux couches, d'épaisseur variable; l'interne participe à la protubérance apicale, et n'est interrompue que par l'archéopyle; l'externe donne naissance aux processus et aux très légères crêtes qui forment les « sutures » ou limites des plaques. L'archéopyle est préformé par une ligne de moindre résistance plus transparente à quelque distance du bord de la 3e plaque précingulaire. Les processus sont en général longs, fins, déliés, aux points de jonction de trois plaques. Parfois apparaissent des processus surnuméraires bifurqués au long des sutures méridiennes des grandes plaques pré et post-cingulaires. Certains processus sont particuliers: celui qui occupe le sommet de la protubérance apicale semble seulement bifurqué: en réalité la troisième branche est latérale et réduite; le processus situé à la suture de la première plaque apicale, la plaque ventrale et le sommet de la 6e précingulaire triangulaire résulte de la coalescence de trois processus, il est large et complexe; enfin, des six processus de la plaque antapicale, les deux dorsaux, à la base de la plaque 3''', sont toujours beaucoup plus développés, plus grands et plus larges que tous les autres; ces grands processus antapicaux sont d'ailleurs un caractère très constant du genre* Hystrichosphaera; *ils occupent la même situation que les deux protubérances antapicales de nombreux Dinoflagellés. Les quatre autres processus antapicaux, de taille normale, peuvent être réunis deux par deux du même côté par des voiles à leur base, et plus ou moins fusionnés.*

Translation (by AL). The cyst is formed by two layers, of variable thickness; the internal layer is part of the apical protuberance, and is only interrupted by the archeopyle; the external layer gives rise to the processes and very slight ridges that form the "sutures" or the plate boundaries. The archeopyle is pre-formed by a more transparent line near the edge of the third precingular plate boundary. The processes are generally long, fine and slender at the junction between three plates. Occasionally, surmounting bifurcate processes appear along the longitudinal sutures of the major pre- and postcingular plates. Some processes are very distinctive: the one located at the top of the apical protuberance appears only bifurcate: in fact, the third branch is lateral and reduced; the process located on the suture of the first apical plate, the ventral plate and on the top of the triangular sixth precingular plate results from the coalescence of three processes, it is large and complex; finally, of the six processes of the antapical plate, the two dorsal on the basis of plate 3''' are always much more developed, longer and larger than all others; these two large antapical processes represent in fact a very constant feature of *Hystrichosphaera*; they are located at the same position as the two antapical protuberances of several dinoflagellates. The other four antapical processes, of normal size, can be joined pairwise at the same side by low veils at their basis, and can be more or less fused together.

Dimensions. Central body length: 60–73 µm, width: 45–63 µm. Length of processes: 15–20 µm, 25 µm for the antapical processes (Rossignol 1964).

Lowest stratigraphic occurrence. Miocene (Mudie 1989; Manum et al. 1989).

Comment on occurrence. In modern sediment, *Spiniferites bentorii* has until now only been observed from equatorial to temperate regions, dominantly in coastal environments (Zonneveld et al. 2013).

Discussion. *Spiniferites bentorii* is recognized due to its distinctive pear-shaped central body and a pronounced apical boss. The processes are highly variable in shape and length with the two antapical processes being the longest. In rare cases, the bases of the processes can be fenestrate. The wall surface is smooth to microgranular. Intergonal processes are occasionally present on some sutures.

Comparison. *Spiniferites bentorii* differs from *Spiniferites hainanensis* Sun and Song 1992 by its typical pear-shaped central body and in only carrying occasional intergonal processes. On the contrary, *Spiniferites hainanensis* bears at least one intergonal process on all major sutures. In addition, *Spiniferites lazus* differs from *Spiniferites bentorii* by its ovoidal to elongate central body shape and by the occasional presence of intergonal processes on *Spiniferites bentorii*. *Spiniferites bentorii* differs from *Spiniferites multisphaerus* Price and Pospelova 2014 only by the absence of bubble-like elements on its wall structure.

- ***Spiniferites hainanensis*** Sun and Song 1992, p. 49, Plate 1, Figure 12, Plate 2, Figures 1–2

Plate 4, Figures 1–11

Original description (from Sun and Song 1992). Body ellipsoidal. Endophragm and periphragm appressed between processes and parasutural ridges. Surface smooth or finely granulated. Processes solid, bases connected by low parasutural ridges, which are uniformly perforated at the distal ends. Process tips trifurcate (gonal) or bifurcate (intergonal), primary furcations may be additionally bifurcate. One or two small holes are generally seen in the base or middle part of

◀

Plate 3. Figures 1–20. Bright field light and SEM micrographs of cysts of *Spiniferites mirabilis* from different estuarine and coastal regions. These pictures illustrate the range of variability regarding the number of processes included in the flange, the number of intergonal processes between two adjacent gonal processes, the development of relatively high sutural crests between processes on some individuals and the wall ornamentation varying from smooth to microgranular. Note that on all specimens, processes are solid and mostly slender. **1–3**. Specimens from the Gulf of California. **4**. Specimen from the Aegean Sea. **5–6**. Specimens from the Gulf of California. **7**. Specimen from the Mediterranean Sea. **8–9**. Specimens from the Marmara Sea. **10–20**. Specimens from the Gulf of San Jorge. Scale bars = 10 µm.

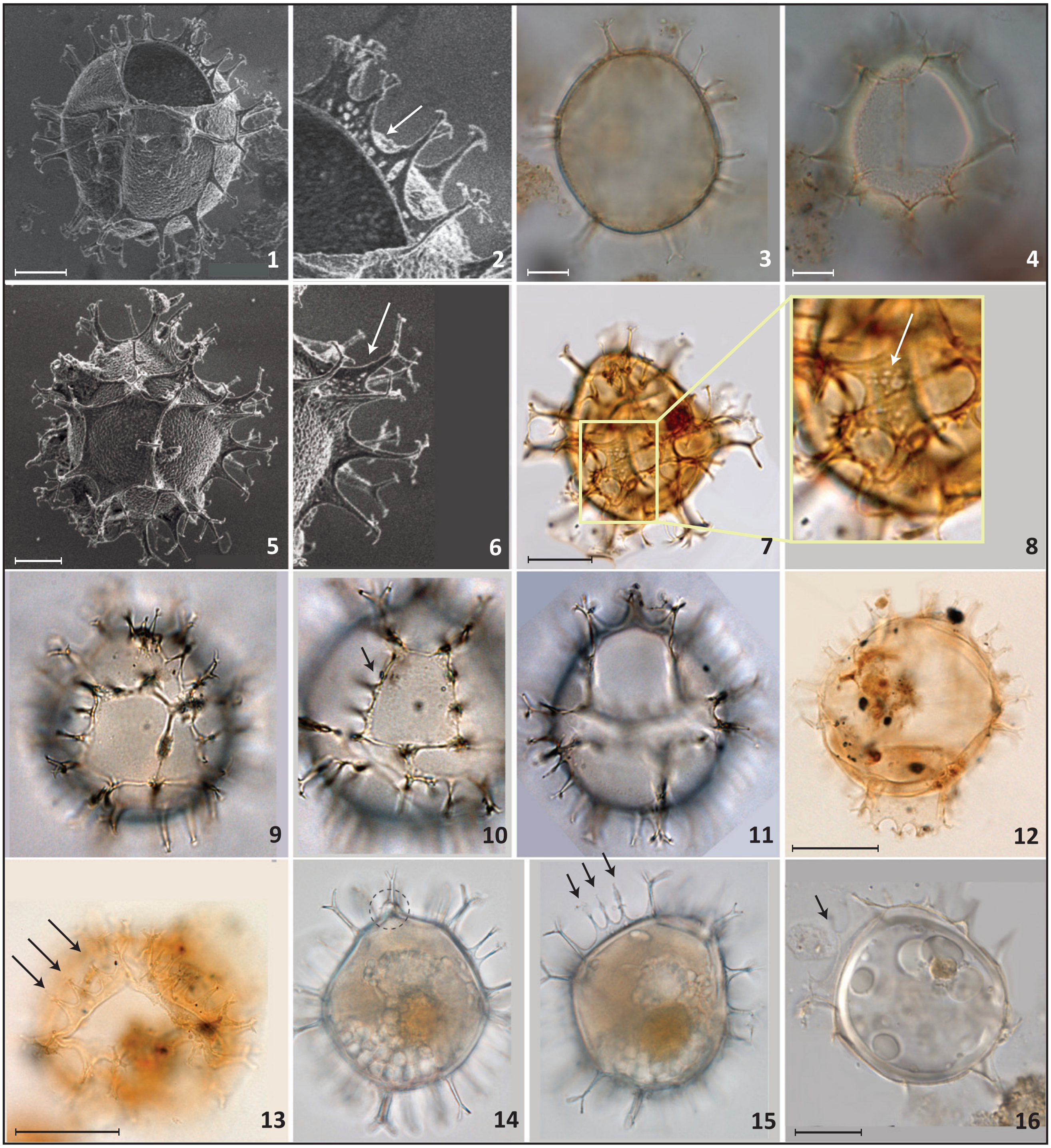

Plate 4. Figures 1–16. Bright field light and SEM micrographs of cysts of *Spiniferites* bearing intergonal processes. **1–6**. *Spiniferites hainanensis* from the Marmara Sea and Black Sea **7–8**. *Spiniferites hainanensis*, from Isla San Jose Lagoon. Note the fenestration on the crests connecting the processes. **9–11**. *Spiniferites hainanensis* from location S1, Fangchenggang, Guangxi province (very close to Hainan island). **12–13**. Holotype of *Spiniferites mirabilis* subsp. *serratus* from the Nishiyama formation, Japan. **14–15.** Different views of the same specimen of *Spiniferites bentorii* showing intergonal processes. Note the typical pear-shaped central body and the well-developed apical protuberance. **16.** *Spiniferites belerius* from Alvarado Lagoon. Scale bars = 10 μm.

each process. Paratabulation gonyaulacacean, indicated by processes and parasutural ridges. Archeopyle precingular, operculum free. Paracingulum indicated by parasutural features. Parasulcus not clear.

Dimensions. Central body length: 42.8–49.0 μm, width 35.0–42.0 μm. Length of processes: ~10.5 μm (Sun and Song 1992).

Lowest stratigraphic occurrence. Quaternary (Sun and Song 1992)

Comment on occurrence. This form has rarely been recognized from recent sediment and possibly has been grouped with *Spiniferites hyperacanthus* or within *Spiniferites* spp. We nonetheless currently consider that this morphology is not restricted to the region where this species was described

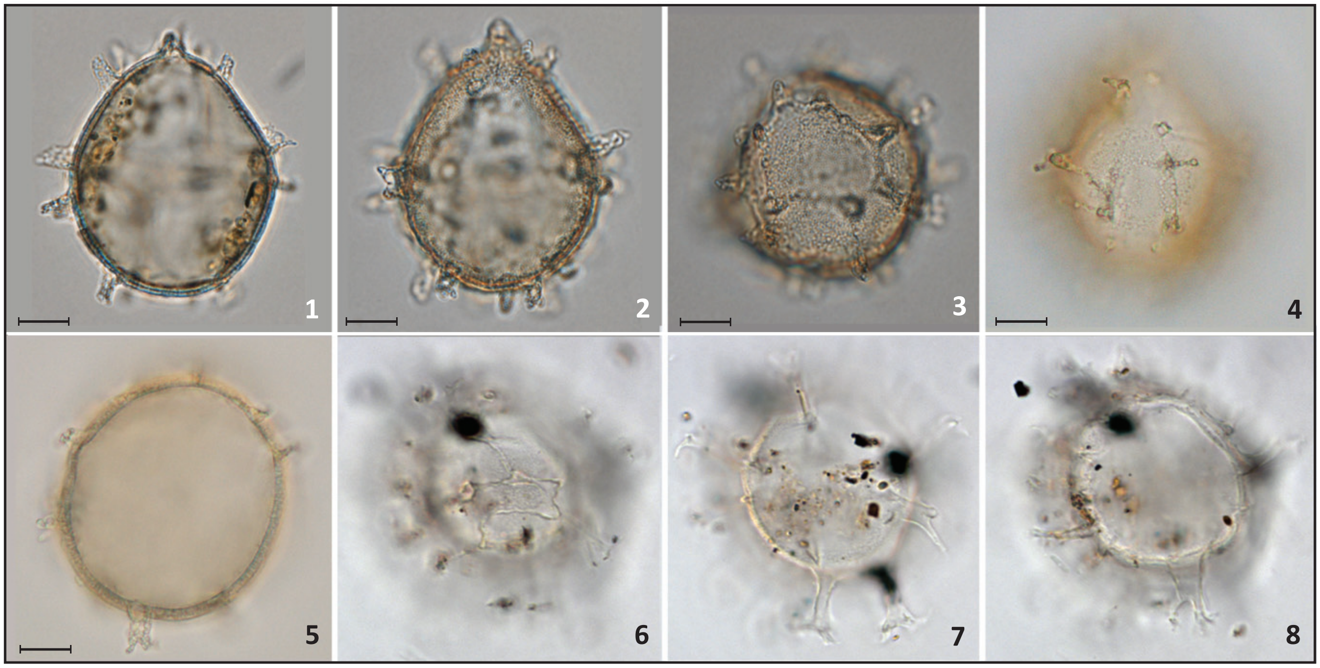

Plate 5. Figures 1–8. Bright field light micrographs of cysts of *Spiniferites* bearing intergonal processes. **1–-3.** *Spiniferites multisphaerus* (photos credit: Andrea Price). **4–6.** *Spiniferites multisphaerus.* **7–8.** Different views of the same specimen of *Spiniferites ludhamensis* from the Israelian coastal plain (Ashdod borehole Reading 167 cm). Scale bars = 10 µm.

(Hainan Island, China) and is, at least, present in other warm environments such as the Gulf of California and Marmara Sea.

Discussion. As observed in specimens from the Marmara Sea, Black Sea and Isla San Jose Lagoon (Southwest Gulf of California), the distinctive features of *Spiniferites hainanensis* are the fenestrate, moderately elevated crests between the bases of the processes (Plate 4, Figures 1–11). The number of intergonal processes differs from one specimen to another (from one to two between pairs of gonal processes) and even from one suture to another on the same specimen. Development of trabeculae between adjacent process tips also is occasionally observed (see Plate 4, Figure 7).

Comparison. *Spiniferites hainanensis* is distinguished from *Spiniferites hyperacanthus* by the presence of uniformly perforated parasutural ridges.

- ***Spiniferites hyperacanthus*** (Deflandre and Cookson 1955, p. 264–265, Plate 6, Figure 7) Cookson and Eisenack 1974, p. 59

Plate 1, Figures 1–16

Original description (from Deflandre and Cookson 1955). Shell globular, spherical or almost spherical; polygonal fields characteristic of the genus with fine, sometimes almost indistinguishable outlines, the equatorial series recognizable by the alignment of the processes. Stalks of processes long, stiff, often slender, dividing into 3 distinct branches with simple or bifurcate apices, inserted both at the angles of the fields and along their sides, the usual arrangement being 1 process to each angle of the field and 2 along each side.

Dimensions. Central body diameter: 54–59 µm. Length of processes: 13–20 µm (Deflandre and Cookson 1955).

Lowest stratigraphic occurrence. Cretaceous (Cookson and Eisenack 1974; Manum et al. 1989)

Comment on occurrence. *Spiniferites mirabilis* and *Spiniferites hyperacanthus* are commonly grouped in global datasets making the assessment of their individual distribution difficult. As a group, they are observed in sediment from tropical to subpolar environments. High occurrences are notably found around the Iberian Peninsula, in the Mediterranean Sea and in the Gulf of Mexico (see Figure 1).

Discussion. Although the morphology of *Spiniferites hyperacanthus* shows variations with regard to the length of the processes, these are systematically slender. Specimens usually exhibit two intergonal processes between the gonal processes, but this number can vary from one specimen to another: from one to several intergonal processes. Importantly, the sutural crests are low or absent and are inconspicuous at the antapex (i.e. not higher than anywhere else on the cyst). Morphotypes with short processes (<3 µm) were observed from different estuarine regions (Plate 1, Figures 9–12). It would be interesting to investigate if the process length variations are driven by environmental factors, as it is the case for some other dinocyst taxa (i.e. changes in salinity and temperature; Wall et al. 1973; Nehring 1994; Dale 1996; Lewis et al. 1999; Ellegaard 2000; Kouli et al. 2001; Mudie et al. 2001; Ellegaard et al. 2002; Mertens et al. 2009, 2012).

Recommendations. In order to keep potentially useful environmental information, we recommend the use of two informal types during routine counts: specimens with short processes (<3 µm) can be identified as *Spiniferites hyperacanthus* – short-process morphotype, and specimens with three or more intergonals between pairs of gonal processes as *Spiniferites hyperacanthus* – multi-intergonal morphotype.

- ***Spiniferites ludhamensis*** Head 1996, p. 557, Figure 12, nos. 3–14, Figure 13, Figure 14, nos. 1–3

Plate 5, Figures 6–8

Original description (from Head 1996). Spiniferate cyst with egg-shaped central body. Pedium thin (ca. 0.1 µm), appearing as black line in optical section. Luxuria consists of tegillum (< 0.3 µm thick) which, across intratabular areas, has funnel-shaped invaginations whose solid, rod-like bases connect with pedium. Bases generally less than 0.3 µm in diameter, mostly spaced about 1.0 µm or less apart, appearing as closely spaced dots in surface view. Invaginations absent from parasutural areas, and unsupported tegillum forms parasutural folds about 1–2 µm high delineating gonyaulacoid paratabulation. Gonal and intergonal processes arise from folds. Processes bifurcate or multifurcate, in some cases with second-order branching, and hollow along their entire length including distal terminal branches. Surface of processes finely and faintly granulate. A tapering, spine-like apical process with smaller side branches, also present. Archeopyle precingular, type P(3″). Operculum monoplacate, free.
Dimensions. Central body diameter: 38 (42.2) 49 µm. Length of processes: 10 (12.9) 15 µm (Head 1996).
Lowest stratigraphic occurrence. Quaternary (ca. 2.4–1.8 Ma) (Head 1996)
Comment on occurrence. Originally described from the Gelasian of the Royal Society borehole at Ludham, eastern England (Head 1996), this species was also recognized from upper Quaternary sediment of the Mediterranean Sea (see Mertens et al. 2018).
Discussion. The numerous invaginations that characterize the wall structure as well as the thin, hollow processes constitute the most important diagnostic features for this species. This species also exhibits parasutural folds rather than solid crests. The central body is ovoidal and to date, no specimen with an apical protuberance has been observed.

- ***Spiniferites mirabilis*** (Rossignol 1964, p.86–87, Plate 2, Figures 1–3, Plate 3, Figures 4–5) Sarjeant 1970, p. 76 emend.

Plate 2, Figures 1–16; Plate 3, Figures 1–20

Synonymy. *Hystrichosphaera mirabilis* Rossignol 1964, p. 86–87, Plate 2, Figures 1–3, Plate 3, Figures 4–5 (the species was first invalidly published by Rossignol 1962, p. 132, because no image was provided); *Spiniferites mirabilis* (Rossignol) Sarjeant 1970, p. 76; *Spiniferites splendidus* Harland 1979, p. 537, Plate 3, Figures 1–2.
Original description (from Rossignol 1964). *La paroi est fine, à deux couches. Les «sutures» des plaques sont peu discernables à cause du grand nombre de processus qui s'y dressent. Au pôle antapical, là où chez* Hystrichosphaera furcata *s'élèvent les deux grands processus dorsaux, la série des 5 à 7 processus insérés sur la face dorsale et les faces latérales de la plaque antapicale est noyée dans un voile commun qui les empâte jusqu'à la fourche; il est constitué comme les processus eux-mêmes, par la couche externe du test, décollée de la couche interne; vus de face, ces processus forment une sorte d'éventail; vu de profil, leur base commune prend l'aspect de doigts de gant les uns derrière les autres; en vue antapicale, cet éventail forme un fer à cheval ouvert sur la face ventrale de l'hystrichosphère.*
Translation (by AL). The wall is thin and consists of two layers. The plate "sutures" are weakly discernible due to the presence of the large number of processes that they carry. At the antapical pole, where two large dorsal processes rise on *Hystrichosphaera furcata*, a series of five to seven processes located on the dorsal and lateral sides of the antapical plates are embedded in a shared veil, which rises to the distal end of the processes; just like the processes, the veil forms from the external layer of the cyst, detached from the internal layer; in frontal view, these processes appear like a hand fan; in lateral view, their joined basis looks like the fingers of a glove, one behind the other; in antapical view, this fan takes on the appearance of a horseshoe that opens to the ventral side of the hystrichosphere.
Emended diagnosis. Ovoidal to spheroidal cyst characterized by a noticeable flange between dorsal antapical processes. Processes are both gonal (trifurcate) and intergonal (bifurcate) with recurved bifurcate tips – at least one intergonal process is present on all sutures. The wall surface ornamentation ranges from smooth to granulate. Sutural crests are absent to moderately high. The archeopyle is precingular and formed by loss of plate 3″.
Emended description. Central body ovoidal to spheroidal. The wall is thin and consists of two layers. The wall surface ornamentation ranges from smooth to granulate. Sutural crests are generally low, and can be nearly absent. However, the emergence of moderately high sutural crests between processes can be observed on certain specimens (see Plate 3, Figure 6). Gonal processes are trifurcate with bifurcate tips. Intergonal processes are bifurcate with bifurcate tips. Although *Spiniferites mirabilis* exhibits significant variations with regards to the number of intergonal processes (from one to more than three) (Plates 2–3 and specimen illustrated in Rochon et al. 1999), at least one intergonal process is present on all sutures. A flange, composed of a variable number of processes, is present on the dorsal side of the antapical plate. The number and length of the processes included in the flange varies from one specimen to another and up to 10 processes were counted on specimens illustrated here (see Plates 2 and 3). The antapical flange can be asymmetric (e.g. Mao and Harland 1993, Plate 1, Figure 3; Morzadec-Kerfourn 2002, Plate 1, Figure 3; Limoges et al. 2013, Plate 2, Figure 17) and is located along the suture separating plates 4‴ and 1⁗. The paratabulation formula is 4′, 6″, 6c, xs, 6‴, 1p, 1⁗
Dimensions. Central body diameter: 40–84 µm in length, 35–76 µm in width. Length of processes: 7–44 µm.
Lowest stratigraphic occurrence. Late Cretaceous (Kedves 1999).
Discussion about subdivision of the species. The description of *Spiniferites mirabilis* is here emended to include its

range of morphological variability. There is no clear biological evidence to know whether the number of intergonal processes has any importance to differentiate species (interspecific variation), subspecies (intraspecific variation) or can vary within a single strain. This missing evidence results in inconsistency in the current descriptions of species. Some species have been differentiated based on their number of intergonal processes, notably to differentiate *Spiniferites serratus* Matsuoka 1983 from *Spiniferites mirabilis*, whilst other species such as *Spiniferites hyperacanthus* have been allowed variation of the number of intergonal processes. Given the missing biological evidence, in this paper we chose to try to retain as much as possible information. Hence, considering the large range of morphological variability associated to *Spiniferites mirabilis*, we here propose to retain two subspecies: *Spiniferites mirabilis* subsp. *serratus* new subspecies, and *Spiniferites mirabilis* subsp. *mirabilis* (autonym). This subdivision is based on the number of intergonal processes between pairs of gonal processes and on the general shape of the processes. *Spiniferites mirabilis* subsp. *mirabilis* exhibits at least one intergonal process between adjacent gonal processes, whereas *Spiniferites mirabilis* subsp. *serratus* exhibits at least three intergonal processes between gonal processes. The processes of *Spiniferites mirabilis* subsp. *serratus* are shorter and flatter than those of *Spiniferites mirabilis* subsp. *mirabilis*.

Note. The holotype could not be localized; it is therefore impossible at this moment to comment on it.

Comparison. The main feature to distinguish *Spiniferites mirabilis* from *Spiniferites hyperacanthus* is the presence of a well-developed flange along the suture between the antapical (1'''') and 3''' plates. This feature is absent on *Spiniferites hyperacanthus*.

- ***Spiniferites mirabilis* subsp. *mirabilis*** (autonym) (Rossignol 1964, p. 86–87, Plate 2, Figures 1–3, Plate 3, Figures 4–5) Sarjeant 1970, p. 76 emend.

Diagnosis. A subspecies of *Spiniferites mirabilis* on which one or two intergonal processes are present between two adjacent gonal processes. Processes are generally long and slender.

Dimensions. Central body diameter: 40–70 μm in length, 35–60 μm in width. Length of processes: 15–22 μm (Rossignol 1964).

Discussion. *Spiniferites mirabilis* subsp. *mirabilis* differs from *Spiniferites mirabilis* subsp. *serratus* in having less than three intergonal processes between pairs of gonal processes.

- ***Spiniferites mirabilis* subsp. *serratus*** (Matsuoka 1983) stat. nov. = *Spiniferites serratus* Matsuoka 1983, p. 135–136, Plate 14, Figures 1a–c, 2a–c, 3

Plate 4, Figures 12–13

Synonymy. *Spiniferites serratus* Matsuoka 1983, p. 135–136, Plate 14, Figures 1a–c, 2a–c, 3, Figure 20, A–B (proposed here).

Diagnosis. A subspecies of *Spiniferites mirabilis*, which exhibits three or more intergonal processes between two adjacent gonal processes, and relatively shorter and flatter processes than that of *Spiniferites mirabilis* subsp. *mirabilis*.

Description. Central body ovoidal to spheroidal. The wall is thin and consists of two layers. Sutural crests are generally low, except at the antapex, where they form a flange. Processes are conical to subconical. Three or more intergonal processes are present on all major sutures. The archeopyle is a reduced pentagonal and simple precingular type derived from loss of the 3'' paraplate.

Dimensions. Central body diameter: 45–54 μm in body length, 47–50 μm in body width. Length of processes: 7–9 μm (Matsuoka 1983).

Lowest stratigraphic occurrence. late Neogene (Matsuoka 1983; Bujak and Matsuoka 1986)

Comment on occurrence. A few authors have reported this form in samples from the Pacific Ocean (Yun et al. 1999, 2000; Kurita and Obuse 2003).

Discussion. Most of the morphologic features (archeopyle, flange, central body shape) of *Spiniferites serratus* conform to those of *Spiniferites mirabilis*. However, *Spiniferites serratus* was described by Matsuoka (1983) as a species distinct from *Spiniferites mirabilis* on the basis of its relatively smaller size and the presence of at least three intergonal processes between each gonal process. Here, we propose the following change in rank: *Spiniferites mirabilis* subsp. *serratus* (Matsuoka 1983) stat. nov. = *Spiniferites serratus* Matsuoka 1983, p. 135–136, Plate 14, Figures 1a–c, 2a–c, 3.

- ***Spiniferites multisphaerus*** Price and Pospelova 2014, p. 101–116, Plate 1–2, Plate 3, Figures 7–9, Plate 4, Figures 4–11, Plate 5, Figures 4–9

Plate 5, Figures 1–5

Original description (from Price and Pospelova 2014). Oval to pear-shaped, proximochorate cyst with a pronounced apical protuberance. Wall is relatively thick and is constructed of small bubble-like elements. Processes are stubby, furcate and contain hollow bubble-like elements. Tabulation is clearly expressed and is typical of the genus. Archeopyle precingular, formed by release of Plate 3''.

Dimensions. Range central body length (including apical protuberance): 42.6 (52.4) 66.5 μm. Mean length of processes: 1.5 (4.4) 8.0 μm (Price and Pospelova 2014).

Lowest stratigraphic occurrence. Late Pleistocene (Price and Pospelova 2014)

Comment on occurrence. To date, this species has only been documented from the central to northern Gulf of California, where it was described.

Discussion. This species differs from the others by the wall structure, sutural septa and processes that feature bubble-like elements (Plate 5, Figures 1–5). The wall surface is pitted or reticulate. We refer to the round table discussion (Mertens et al. 2018) for comparison with other *Spiniferites* species that have a bubble-like surface texture.

- ***Spiniferites pacificus*** Zhao and Morzadec-Kerfourn 1994, p. 268–269, Plate 1, Figures 1 a–c, 2 a–b, 3, Plate 2, Figures 1–2–3 a–b

Original description (from Zhao and Morzadec-Kerfourn 1994). *Kyste proximochorate de forme sphérique à ovoïde dont la paroi est composée d'un endophragme et d'un périphragme à surface microgranuleuse. Présence de processus gonaux à extrémité trifurquée puis bifurquée, de processus intergonaux à extrémité bifurquée et de deux processus antapicaux, creux, plus développés que les autres, reliés par une membrane septale basse et ouverts à leur extrémité divisée en trois longues branches à terminaison bifurquée.*
Translation (by AL). Proximochorate cyst, subspherical to ovoidal in shape, having a wall that consists of an endrophragm and a periphragm with a microgranular surface. Presence of gonal processes with trifurcate terminations and birfurcate tips, intergonal processes with bifurcate terminations, and two hollow antapical processes, that are more developed than the others, linked together by a low septal membrane and open at their extremity, which is divided in three long branches with bifurcated terminations.
Dimensions. Central body diameter: 30–35 µm. Mean length of processes: 10 µm. Mean length of antapical processes: 13 µm (Zhao and Morzadec-Kerfourn 1994).
Lowest stratigraphic occurrence. Pleistocene (Zhao and Morzadec-Kerfourn 1994)
Comment on occurrence. This species was described from the northwest Pacific Ocean.
Discussion. In the original description, *Spiniferites pacificus* differs from the other *Spiniferites* species in having stout and distally open antapical processes. Processes are sometimes connected by low crests.

- ***Spiniferites spinatus*** (Song et al. 1985, p. 43, Plate 2, Figure 5) Lentin and Williams 1989

Translation (by Haifeng Gu, Third Institute of Oceanography, Xiamen – China, February 2017). Cyst ovoid to subspherical, epicyst and hypocyst equal in size separated by a wide and clear cingulum. The cyst wall probably consists of two relatively thin layers, whose surface is coarse to granular. The archeopyle is difficult to be identified. The cyst is a typical spiniferate, with large and marked plates of epicyst and hypocyst, and cingular plates extending in horizontal direction. The paraplates are demarcated by subtle ridges 2–3 µm high, like one layer of thin membrane surrounding the cyst body. There are short tubular processes at the junctions of ridges, which are narrow, hollow with trifurcate or bifurcate distal ends. There are ca. 2 spiny processes in the middle of the ridges whose bases are wide and taper abruptly with pointed distal end. The ridges are smooth. The diameter of the cyst body is 38 µm and the processes can be as high as 5 µm. The current specimen has a plate pattern identical to *Spiniferites cingulatus* Sarjeant 1970 (Eisenack, Katalog, Bd. II, pp. 537). *Spiniferites cingulatus* comprises several varieties based on the ornamentations of cyst body and overall cyst shape, which all possess high ridges and clear plate boundaries. The current variety has weak ridges and spiny processes in the ridges, which can be differentiated from previous varieties.
Dimensions. Central body: 47–60 x 35–56 µm. Length of processes: 5 µm (Song et al. 1985).
Lowest stratigraphic occurrence. Early Pleistocene (Lentin and Williams, 1989)
Comment on occurrence. To date, this taxon was observed exclusively in the type material of the Pacific Ocean, East China Sea.
Recommendation. We recommend restricting the identification of *Spiniferites spinatus* to the holotype. This species is therefore not included in the identification key.

- ***Spiniferites splendidus*** Harland 1979, p. 537, Plate 3, Figures 1–2. = *Spiniferites mirabilis* emend.

Original description (from Harland 1979). Some specimens of this species are broader than long and exhibit some separation of the wall layers beneath the processes giving rise to bulbous process bases. The cyst is characterized, however, by its large size and by the distinctive morphology of the processes. The membranous processes are particularly conspicuous especially those in the posterior intercalary position. The tabulation is outlined by low ridges or membranes, which are confluent with the process structure.
Dimensions. Central body: 62.0–84.0 µm in length, 52.0–76.0 µm in width. Length of processes: 22.0–44.0 µm (Harland 1979).
Lowest stratigraphic occurrence. Senonian, Cretaceous (Kedves 1999)
Comment on occurrence. *Spiniferites splendidus* has been mainly identified from Neogene sediment in the North Atlantic region (e.g. McCarthy and Mudie 1996).
Discussion. *Spiniferites splendidus* was described by Harland (1979) as a separate species from *Spiniferites mirabilis* on the basis of its larger size and the presence of numerous flamboyant membranous processes. After examination of new photographs of the holotype of *Spiniferites splendidus* and given the large intraspecific variability within *Spiniferites mirabilis*, *Spiniferites splendidus* is now considered to be a junior synonym of *Spiniferites mirabilis.*

- ***Spiniferites strictus*** Matsuoka 1983, p. 136–137, Plate 12, Figures 4a–b, 6

Original description (from Matsuoka 1983). The intermediate proximochorate cyst is subspherical to ovoidal in shape, and consists of two layers, moderately thick periphragm with a smooth to granular surface and endophragm, adpressed between processes. The processes comprise relatively short tapering gonal and intergonal types. They have bi- or trifurcate second branches with bifid tips. Small perforations are sometimes observed near the proximal base of the processes. The parasutural septa are distinctive and somewhat membraneous. Some specimens have a small apical boss, but not always. The archeopyle is a reduced pentagonal

Table 2. Identification key for Pliocene and Quaternary *Spiniferites* taxa bearing intergonal processes (see also Figure 4).

Consistent intergonals	One or more intergonal processes along each major[a] parasutural boundaries	No antapical flange	Sutural ridges uniformly perforated at the base of the processes	***Spiniferites hainanensis***
			Long processes (R*>0.20)	***Spiniferites hyperacanthus***
			Short processes (R*<0.06)	***Spiniferites hyperacanthus*** **– short-process morphotype**
		Antapical flange	At least 1 intergonal along each major boundary; Processes long, slender and solid	***Spiniferites mirabilis*** **subsp.** ***mirabilis***
			At least 3 intergonals along each major boundary; Short, conical processes	***Spiniferites mirabilis*** **subsp.** ***serratus***
Occasional intergonals	Occasional intergonal processes (not more than one or two) along some meridian parasutural boundaries	Wall bi-layered with scabrate to microgranular periphragm	High sutural crests; Processes variable in shape within a same specimen and frequently truncated	***Spiniferites belerius***
			Low sutural crests; Pear-shaped central body	***Spiniferites bentorii***
			Processes connected by low crests; Two larger and thicker processes near the antapex	***Spiniferites pacificus***
		Wall bi-layered with invaginations or buble-like elements	Sutural folds rather than solid crests; Processes are hollow along their entire length and arise from folds	***Spiniferites ludhamensis***
			Pitted surface to micro-vesicular periphragm; Processes and wall structure formed by multiple bubble-like elements	***Spiniferites multisphaerus***

[a]Meridian pre- and post-cingular plate boundaries.
*R = length of processes/diameter of the central body.

precingular type derived from release of the 3″ paraplate. The paratabulation is that of the genus.

Dimensions. Central body: 53–67 in length, 50–62 μm in width. Length of processes: 10–14 μm (Matsuoka 1983).

Lowest stratigraphic occurrence. Miocene (Suzuki and Kurita 1998)

Comment on occurrence. This species was rarely reported from the Pacific and Atlantic Oceans (Matsuoka 1983; Engel 1992; Yun et al. 2000).

Discussion. It is difficult to unambiguously differentiate this morphology from that of *Spiniferites bentorii*. We therefore suggest restricting the name to the holotype. This species is not included in the identification key.

6. Identification key for *Spiniferites* taxa with intergonal processes

On the basis of our observations and the available literature, we propose to separate the *Spiniferites* taxa with intergonal processes into two morphological groups (Table 2, Figure 4):

1. Those bearing consistent intergonal processes, which include species characterized by at least one intergonal process on all sutures. For Pliocene and Quaternary strata, this group includes *Spiniferites hainanensis*, *Spiniferites hyperacanthus*, *Spiniferites mirabilis* subsp. *mirabilis* and *Spiniferites mirabilis* subsp. *serratus* stat. nov.
2. Those bearing occasional intergonal processes, which correspond to the species on which such processes are sometimes present, but rarely on all sutures. This group includes *Spiniferites belerius*, *Spiniferites bentorii* as the most common species, in addition to *Spiniferites ludhamensis*, *Spiniferites multisphaerus* and *Spiniferites pacificus*.

Beyond the distribution of intergonal processes, consistent or occasional, a number of criteria have to be taken into account. The shape and number of intergonal processes, the height of the sutural crests and the presence or absence of a flange are the most important features for assigning a specimen to a given species. We do not consider the presence or absence of an apical boss to be a significant morphological trait to separate species or even subspecies. For instance, we demonstrated that such feature is recurrent for *Spiniferites mirabilis*. Indeed, cysts formed in batch cultures of single strains have also shown the presence and absence of an apical boss (e.g. Lewis et al. 2001).

7. Conclusion

The list of eight species of *Spiniferites* bearing intergonal processes observed from Pliocene and Quaternary sediments is provided. Although some morphological variations can be accepted and should not compromise routine cyst identification, especially when working in estuarine environments, we highly recommend illustrating forms that show atypical features to allow for site-to-site comparison of the different morphotypes. This might help to extract a potential environmental significance for the emergence of certain structures.

A few suggestions were made according to our observations:

- We recommend the originally defined *Spiniferites serratus* to be regarded as a morphological variability of *Spiniferites mirabilis*, i.e. *Spiniferites mirabilis* subsp. *serratus*.
- We propose *Spiniferites splendidus* to be regarded as a junior synonym of *Spiniferites mirabilis*.
- We suggest the occasional presence of intergonal processes to be part of the intraspecific variability of *Spiniferites bentorii* and *Spiniferites belerius*.
- We informally suggest identifying specimens of *Spiniferites hyperacanthus* with three or more intergonal processes between pairs of gonal processes as *Spiniferites hyperacanthus* – multi-intergonal morphotype. Similarly, we suggest identifying specimens of *Spiniferites hyperacanthus* with short processes (<3 μm) as *Spiniferites hyperacanthus* – short-process morphotype.

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