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# Silurian calcispheres (Calcitarcha) of Gotland (Sweden): Comparisons with calcareous dinoflagellates

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## Abstract

Scanning electron microscope examinations of polished and etched surfaces of sediments from the Silurian carbonate platform of Gotland, Sweden, revealed the presence of numerous, morphologically diverse “calcispheres” (Calcitarcha). Some of these spherical calcareous microfossils display wall structures that are surprisingly similar to those of calcareous dinoflagellate cysts. In analogy to the interpretation of the biological affinities of Palaeozoic acritarchs as cysts of organisms that might have been the ancestors of organic-walled dinoflagellates, the Calcitarcha from Gotland can be compared and may possibly be related to organisms that may have been the ancestors of calcareous cyst-producing dinoflagellates that so far have not been observed before the Late Jurassic. **To cite this article:** T. Servais et al., C. R. Palevol 8 (2009).

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## Résumé

**Calcisphères (Calcitarcha) du Silurien de Gotland (Suède) : comparaison avec les dinoflagellés calcaires.** L'examen au microscope électronique à balayage de surfaces polies et attaquées à l'acide d'échantillons de sédiments de la plate-forme carbonatée de Gotland, Suède, a révélé la présence de nombreux « calcisphères » (Calcitarcha) qui sont morphologiquement bien diversifiés. Certains de ces microfossiles calcaires sphériques montrent des structures de parois qui sont étonnamment similaires aux parois des kystes de dinoflagellés calcaires. En analogie avec l'interprétation des affinités biologiques des acritarches du Paléozoïque comme kystes provenant d'organismes qui auraient pu être les ancêtres des dinoflagellés à paroi organique, les Calcitarcha de Gotland peuvent être comparées et pourraient éventuellement être reliées à des organismes qui pourraient avoir été les ancêtres des dinoflagellés produisant des kystes calcaires qui jusqu'à maintenant ne sont connus qu'à partir du Jurassique terminal. **Pour citer cet article :** T. Servais et al., C. R. Palevol 8 (2009).

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## 1. Introduction

Dinoflagellates are mostly single-celled protists (apicomplexan alveolates) at or near the base of the

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food chain. They are found in most modern aqueous environments and constitute a major component of the marine microplankton biomass and biodiversity. They form a major part of primary producers in modern oceans. Some dinoflagellates produce resting cysts that may become fossilised. Most of these cysts are organic-walled, but fossil and living calcareous and siliceous cysts also occur.

Although comparative ultrastructural, molecular and biogeochemical studies indicate a Precambrian origin for the lineage [31,40], the first organic-walled microfossils considered to represent dinoflagellate cysts, only appeared in the Middle Triassic (~240 Ma) [10] before a major radiation in the Jurassic. Molecular clock calibrations often rely on this palaeontological evidence and thus place the derivation of the dinoflagellate lineage after the Permian–Triassic boundary [2]. However, there have been an increasing number of publications mentioning the presence of organic-walled dinoflagellates since the Early Palaeozoic, if not the Late Precambrian [28]. Known calcareous dinoflagellate cysts (calcareous dinocysts) date from the Late Jurassic (~180 Ma) [41] and thus played no role so far in the discussion on the possible pre-Mesozoic origin of the dinoflagellate lineage.

Here, we examine well-preserved carbonate sediments from the Silurian (~430–410 Ma) of Gotland, Sweden, a sequence that can be considered as a *Konservat-Lagerstätte* for calcareous micro- and nanofossils [36–39]. Among the numerous forms of spherical calcareous microfossils found in the studied sequence of Gotland, some morphotypes are possibly planktic, though the presence of planktic calcareous microorganisms in the Palaeozoic is still debated [37]. Some of the calcareous microorganisms of the Silurian of Gotland are very similar to calcareous cysts of dinoflagellates based on comparisons of their ultrastructure with that of modern and fossil taxa. However, other morphological characters of the modern dinoflagellate structure, such as serial tabulation, thecal plates, cingulum and sulcus, have not been observed. The objective of this article is to illustrate and describe the morphotypes from Gotland and to discuss their presence in the Silurian in the context of early dinoflagellate evolution.

## 2. The dilemma of the geological record of dinoflagellate cysts

Dinoflagellate life cycles commonly include resting cysts that represent a dormant stage [3]. Estimates indicate that about 13 to 16% of living dinoflagellates produce resting cysts that may be preserved in the fossil

record [15]. Most cyst-producing dinoflagellate species, both marine and freshwater, produce organic-walled cysts. However, some marine dinoflagellates produce calcified, partially calcified [51,52,54] or siliceous cysts [14].

Information on the fossil record of dinoflagellates is based on palaeontological, molecular clock and biogeochemical evidence.

Palaeontologists record microfossils that can be related to fossilisable cysts of dinoflagellates (displaying the characteristic morphological criteria of modern dinoflagellate cysts, such as a serial tabulation, a cingulum and a sulcus) only since the Triassic. The dilemma of the discussion of when the first dinoflagellates appear in Earth's history is mostly a problem of the definition of the dinoflagellate cysts. Some authors consider that in order to be attributed to a dinoflagellate cyst, a microfossil must present the morphological criteria of modern dinoflagellates. Following this consideration, dinoflagellate cysts *sensu stricto* only appear at the base of the Mesozoic [10]. If one considers, however, that many living dinoflagellate species do not produce cysts and that several produce cysts that do not display these features, the first occurrence of dinoflagellates in the fossil record might be much older.

Besides the morphological criteria used by palaeontologists, ultrastructural [48] and molecular phylogenetic [11] data strengthen the suggestion that, together with the other groups of the alveolate lineage, such as the ciliates and apicomplexans, the dinoflagellates diverged possibly as early as the Precambrian (~1100–1000 Ma) [27].

In addition, the analyses of changes of the abundance of triaromatic dinosteroids through time have provided chemostratigraphic evidence of dinoflagellates (or other organisms with similar chemosynthetic capabilities) in rocks of Precambrian to Devonian age, which suggests that at least some acritarchs either were part of or close to the dinoflagellate lineage [32]. Subsequent biomarker investigations yielded dinoflagellate-related molecules that were extracted from Early Cambrian (~520 Ma) acritarchs [33] and the Mesoproterozoic (~1300 Ma) [31]. A marked increase of dinosteroids is observed in sediments since the Middle to Upper Triassic [32], which corresponds to the period of a major evolutionary radiation of the dinoflagellates in the Early Mesozoic [10].

There is now also additional palaeontological evidence to indicate that the dinoflagellate group may have been present much earlier. Butterfield and Rainbird [5] reported acritarchs from the Neoproterozoic of Arctic Canada (~900–800 Ma) with features they considered characteristic of dinoflagellate cysts. Leppig and Mon-

tenari [28] described possible dinoflagellates from the Permian (~300–280 Ma) of Mexico, while Servais et al. [45] interpreted the Late Cambrian–Early Ordovician (~500–480 Ma) galeate acritarchs as probably being resting cysts of a microorganism similar to modern dinoflagellates. The galeate acritarchs all display a large “polar” opening similar to a dinoflagellate archeopyle and some of them have a paratabulation, similar to many dinoflagellates [45,47].

The results from different disciplines therefore support the interpretation based on morphological criteria that some Palaeozoic acritarchs are possibly the ancestors of the dinoflagellates [7,30,43,44,45], although most of the morphological criteria of modern dinoflagellates (tabulation, cingulum, sulcus) usually are absent.

Although it is clear that microfossils with the distinctive morphological criteria of modern dinoflagellate cysts only appear during the Triassic, dinoflagellate related organisms that might have produced cysts without these criteria probably appeared much earlier, as molecular clock data and biogeochemical analyses, but also palaeontological data, now suggest.

### 3. Calcareous dinoflagellates

Deflandre [8] was the first to recognise some calcispheres as being of dinoflagellate origin. Wall and Dale [52] subsequently showed through culturing experiments that some modern dinoflagellate species produce calcareous cysts. Today, calcareous dinocysts form one of the three major components of modern carbonate rocks of biogenic origin, with a mean ratio of coccoliths:foraminifera:calcareous dinocysts of about 70:20:5; these groups forming 95% of the biogenic components of pelagic carbonates [1].

Calcareous dinocysts are formed during the life cycle of several species belonging to the Thoracospheraceae, a monophyletic family of the dinoflagellate order Peridiniales [9]. Although most calcareous dinocysts do not show signs of paratabulation, some calcareous cysts do reflect the peridinioid plate pattern of the corresponding motile dinoflagellate very clearly. The presence of a peridinioid paratabulation on the inside of the organic lining of *Pithonella patriciagreeleya* Bolli 1974 [4] (now attributed to the genus *Pirumella*) and on the surface of some otherwise non-tabulated species proved that many Mesozoic Thoracospheraceae are calcareous dinoflagellate cysts [20].

Intensive research on the calcareous cyst-wall ultrastructure since the 1980s induced considerable taxonomic revisions. The wall crystal orientation became the main diagnostic feature for the classification of calcareous

dinocysts. Based on the different wall types, Keupp [22] and Kohring [24] established four subfamilies of calcareous dinoflagellate cysts: Orthopithonelloideae (radial wall type with c-axes of the calcite crystals perpendicular to cyst surface), Obliquipithonelloideae (irregular oblique wall type), Pithonelloideae (uniquely declined c-axes), and Fuettererelloideae (radial wall type with c-axes to cyst surface). More calcareous dinocysts were reclassified giving archeopyle configuration priority over wall structure [23,46]. Recent molecular phylogenetic studies support this new interpretation [13].

Current knowledge of the stratigraphical range of the calcareous dinocysts indicates that they first appeared in the Late Jurassic [4,41] and they, therefore, played no role in the discussion of the origin of the dinoflagellate lineage so far. However, in the fossil record of the Mesozoic, but also the Palaeozoic, many spherical calcareous microfossils have been commonly described simply as “calcispheres”; generally, without a further taxonomical attribution and without interpretations of their biological affinity. Some of these “calcispheres” may possibly be related to ancestors of the calcareous dinoflagellates, but evidence is missing so far. The exact first appearance of calcareous dinoflagellates has thus not clearly been established to date.

### 4. Geological setting and sample preparation

The island of Gotland, Sweden, is formed from 450 m thick almost horizontal carbonate sediments. This geological sequence is considered as one of the best-preserved and most fossiliferous carbonate platform complexes of the Palaeozoic. It was deposited in a tropical, epicontinental sea near the Silurian palaeoequator. Although ~400 Ma old, the sediments are exceptionally well preserved because they have not experienced deep burial and strong tectonic stress due to their position on the stable Baltic Shield [35]. They contain numerous microfossil groups in an exceptional state of preservation, including acritarchs, chitinozoans and prasinophytes, but also calcareous microfossils, preserved in three dimensions [36,53].

With the aim of understanding the origin of the limestone–marl alternations from the Silurian of Gotland, Sweden, several hundred polished, slightly etched rock samples, were investigated with the scanning electron microscope (SEM) [34]. The material has allowed observations of the ultrastructure of numerous fossil groups, including brachiopods, ostracods and trilobites, bryozoans and corals [34]. Furthermore, several morphotypes of enigmatic, previously unknown calcareous micro- and nanofossils, have been recorded [38,39].

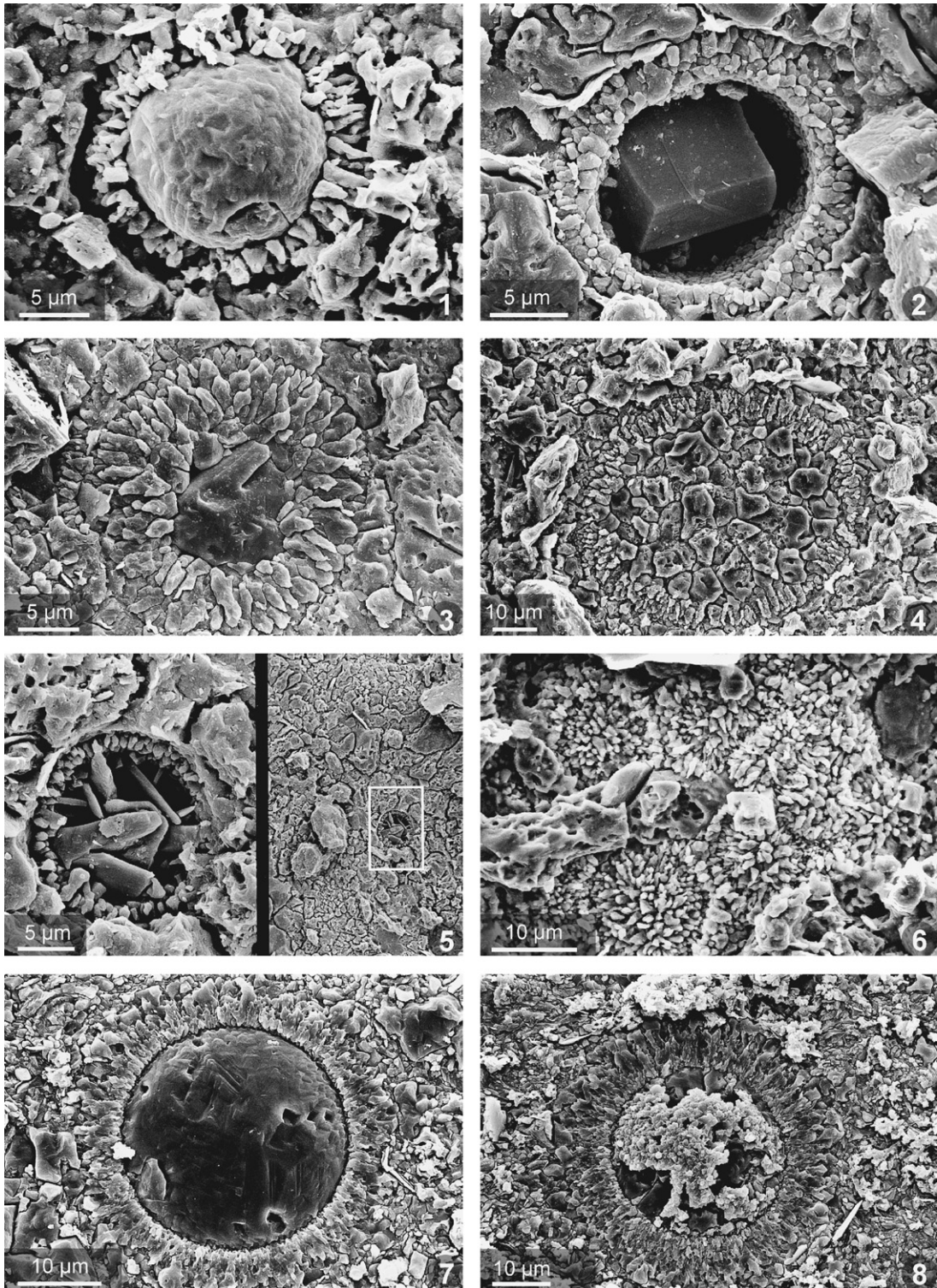


Fig. 1. Calcitarcha from the Silurian of Gotland (1–6) and the Cretaceous of New Zealand (7–8). **1.** and **2.** Högklint Formation (Lower Sheinwoodian, locality Häftingsklint 3 [26]). **3.** Slite Group (Middle Sheinwoodian, locality Stora Mafriids 4 [42]). **4.** Lower Visby Fm. (2.6 m below *Phaulactis* layer, ?Lowermost Sheinwoodian, locality Buske 1 [26]). **5.** Lower Visby Fm. (4.0 m below *Phaulactis* layer, ?Uppermost Telychian, locality Rönnlint 1 [17]). **6.** Högklint Fm. (Lower Sheinwoodian, locality Ireviken 3 [26]). **7.** and **8.** Upper Cretaceous (New Zealand [6]).

Indeed, the carbonate platform of Gotland can be considered a *Konservat-Lagerstätte* for Palaeozoic carbonate microorganisms [38].

The calcareous microorganisms from Gotland still retain the original wall ultrastructure, because the tiny calcite crystals that constitute the wall have not been destroyed by a late diagenesis [34]. The calcispheres investigated and partly illustrated herein come from samples collected by Munnecke [34]. The methodology used is that of SEM of polished, slightly etched rock surfaces. The samples are cut perpendicular to the bedding, polished with corundum powder (granulation=2000) and etched in 0.1 M hydrochloric acid for 20 sec. Subsequently, they are coated with gold/palladium for the examination with SEM.

For comparison, many samples have also been examined from other well-preserved limestones from various geological periods, including the Devonian, Carboniferous, Permian, Triassic, Jurassic and Cretaceous. Calcispheres with possible dinoflagellate affinities are present in all these periods. In the present paper, two calcispheres from the Cretaceous of New Zealand [6] are illustrated for comparison with the Silurian specimens from Gotland.

Although it is difficult to extract individual microfossils from the matrix of the micritic limestone, observation of polished, etched surfaces gives an insight into the morphology and ultrastructure of the calcispheres, allowing comparison with the ultrastructure of modern and fossil calcareous microorganisms and calcareous dinocysts.

### 5. Calcispheres, Calcitarcha and calcareous dinoflagellate cysts

The term “calcisphere” is informal and refers generally to spherical, calcareous microfossils. The term calcispheres lacks an official diagnosis and, until recently, remained informal, although many authors use the term in various ways. In order to resolve this issue, Versteegh et al. [50] proposed, in analogy with the erection of the Acritarcha for organic microfossils of unknown origin, the new group called Calcitarcha, that includes all calcareous microfossils with a central cavity for which the biological affinities are unknown.

Flügel [12] noted that “calcisphere” is a term referring to spherical microfossils regarded for a long time as “microproblematica”, but today considered by most authors as algal cysts, some perhaps as planktic algae. According to Flügel [12], most Palaeozoic calcispheres occur in shallow-marine platform and ramp carbonates, while most of the Jurassic and Cretaceous calcispheres occurring in pelagic limestones represent calcareous dinoflagellate cysts.

Devonian and Carboniferous Calcitarcha have been taxonomically differentiated according to wall structure, ornamentation and differences in size [12]; some represent dasycladacean algae, for example, *Acetabularia* [29], others are regarded as planktic green algae [19], or possible foraminifera [49]. For Flügel [12], “some fossils formerly considered to be microproblematica are no longer problematic with regard to their position” because most Mesozoic and Cenozoic “calcispheres” are now considered to be “calciodinoflagellate” cysts; that is, calcareous dinoflagellate cysts, following the detailed investigations of Keupp [21].

Although many of the Mesozoic calcareous spherical microfossils can now be attributed to the calcareous dinoflagellates, not all Mesozoic and Cenozoic forms should be assigned to this group. Other biological affinities for some of them have been proposed, including a freshwater chlorophyte affinity for the recent species *Phacotus lenticularis* for example [18,25].

The Calcitarcha should thus be considered a polyphyletic group, with most of the Mesozoic microfossils being probably calcareous cysts of dinoflagellate species.

For Palaeozoic Calcitarcha, the biological affinities are especially difficult to establish, as many Palaeozoic carbonate rocks are poorly preserved and diagenetically altered, so many Palaeozoic “taxa” only represent diagenetic forms. In a similar way as some Palaeozoic acritarchs now are interpreted as the cysts of a possible ancestor of organic-walled dinoflagellates [7,30,43–45], some Palaeozoic Calcitarcha could be interpreted as the calcareous cysts of organisms that may have been the ancestors of calcareous dinoflagellates, although it must be emphasised that many other Calcitarcha should most probably be attributed to other biological phyla, such as other algal groups, foraminifera or radiolaria.

Fig. 1. Calcitarcha du Silurien de Gotland (1–6) et du Crétacé de Nouvelle-Zélande (7–8). 1. et 2. Formation Högklint (Sheinwoodien inférieur, localité Häftingsklint 3 [26]). 3. Groupe Slite (Sheinwoodien moyen, localité Stora Mafrids 4 [42]). 4. Formation Visby inférieur (2,6 m en dessous du niveau à *Phaulactis*, ? Sheinwoodien le plus inférieur, localité Buske 1 [26]). 5. Formation Visby inférieur (4,0 m en dessous du niveau à *Phaulactis*, ? Telychien le plus supérieur, localité Rönnlint 1 [17]). 6. Formation Högklint (Sheinwoodien inférieur, localité Ireviken 3 [26]). 7. et 8. Crétacé supérieur (Nouvelle-Zélande [6]).

## 6. Calcitarcha from the Silurian of Gotland

Besides many other calcareous microorganisms [34,38,39], the Silurian sequence of Gotland includes numerous Calcitarcha that display a wide morphological variety of very well preserved ultrastructures. In a preliminary report, Munnecke et al. [38] illustrated several calcareous microfossils from Gotland that were tentatively attributed to blue green algae, brown algae, parathuramminid foraminifera and sponge spicules, as well as few spherical calcareous microfossils, named “calcispheres” and “nanospheres”, with varied wall structures; among these was a specimen with an originally aragonitic wall that had been replaced by calcite. The biological affinity of these “calcispheres” and “nanospheres” is as yet unknown [50].

Fig. 1/1–6 illustrates a selection of morphotypes of spherical calcareous organisms. The specimens illustrated herein are from the Högklint and Lower Visby formations and from the Slite Group of Llandovery and Wenlock (Early Silurian) age. The nomenclature of the sample localities of Gotland, mentioned in Fig. 1, follows the stratigraphical scheme introduced by Laufeld [26]. Etched sections of a total of 132 samples from the Silurian of Gotland produced small Calcitarcha (usually 10 to 25  $\mu\text{m}$  in diameter) that were informally termed “nanospheres” by Munnecke and Samtleben [35]. These organisms are observed in all formations of the Silurian of Gotland, from the Latest Llandovery to the Late Ludlow. In addition, larger Calcitarcha, 60 to 100  $\mu\text{m}$  in diameter, have been observed in the Visby and Högklint formations (Fig. 1/4 [34,37]). However, as these larger Calcitarcha often show pores and a festoon-like inner surface, they probably are not related to dinoflagellates. In comparison to the Palaeozoic specimens, two morphotypes of Calcitarcha from the Cretaceous of New Zealand are illustrated in Fig. 1/7–8. These specimens are from sediments of probably Campanian–Maastrichtian age, from the North Island of New Zealand [6].

Several comparisons can be made between the Silurian small Calcitarcha and Mesozoic–Cenozoic calcareous dinoflagellate cysts.

Firstly, the spherical shapes of the non-compacted Calcitarcha from micritic limestones correspond to those of calcareous dinoflagellate cysts observed in etched surfaces of Mesozoic and Cenozoic sediments.

Secondly, the size-range (between 10 and 25  $\mu\text{m}$ , mostly around 20  $\mu\text{m}$ ) of the Silurian small Calcitarcha (nanospheres) is similar to Recent calcareous dinoflagellate cysts such as *Thoracaspheara heimii* and to many Mesozoic and Cenozoic Calcitarcha (Fig. 1/7–8).

Finally, the ultrastructure of the Silurian small Calcitarcha is very similar to that of fossil and Recent calcareous dinocysts, so similar in fact that it is virtually impossible to distinguish the two.

However, it is impossible to attribute the Silurian specimens to the dinoflagellates because they are not isolated, only etched sections of the Calcitarcha being available, making the comparison with calcareous dinoflagellates only possible through the observation of the ultrastructure. Mesozoic dinoflagellates can be isolated, for example, from comparatively soft chalk samples, while it is difficult to extract the Silurian Calcitarcha from the well-lithified micritic limestones, but also from the marls. It remains therefore impossible so far to observe a peridinialean paratabulation of the inside of the Calcitarcha, which would indicate a biological affinity without doubt, although not all Recent cysts show paratabulation. It has also been impossible so far to clearly distinguish an archaeopyle (polar opening) that is formed by removal of one or more paraplates in the dinoflagellates. However, such an archaeopyle opening is absent even in some recent calcareous dinoflagellates, for example in the case of the slit archaeopyle of *Scrippsiella trifida* [16], although this feature is not known for the Mesozoic taxa which are characterised by a circular opening considered to be formed by the removal of the 2nd intercalary paraplate.

## 7. Conclusions

Observations from thin sections and slightly etched polished surfaces of many Palaeozoic micritic limestones show spherical calcareous microfossils that can be attributed to the Calcitarcha previously usually termed “calcispheres”. The biological affinities of these microfossils are complex and the informal category of the Calcitarcha is most probably polyphyletic.

Some of the wall ultrastructures of the Calcitarcha from the Silurian of Gotland seem indistinguishable from those of Mesozoic or Cenozoic calcareous dinoflagellate cysts. However, as it is difficult to extract these microfossils from the micritic limestones and marls, the diagnostic elements of dinoflagellate cysts, such as a paratabulation or an archaeopyle are not observed. It is thus not possible to unequivocally attribute these Calcitarcha to the calcareous dinoflagellates.

A same dilemma exists for the organic-walled equivalents of the organic-walled microphytoplankton in the Palaeozoic. Although of similar size range and morphology and comparable palaeoecological and palaeogeographical distribution, most Palaeozoic

acritarchs cannot be attributed to the dinoflagellates because some of the diagnostic elements that are characteristic for dinoflagellates, such as a paratabulation and an archaeopyle are missing within the acritarchs, although, as mentioned above, some living dinoflagellate species produce cysts that do also not display these characteristic morphological features.

Today, most Palaeozoic acritarchs are considered to be organic-walled cysts of organisms that were possibly the ancestors of the dinoflagellates. In a similar way, some Palaeozoic Calcitarcha could be interpreted as the calcareous cysts of organisms that might have been the ancestors of dinoflagellates. These results suggest that among the Palaeozoic Calcitarcha some might have been ancestors of the calcareous dinoflagellates, which so far are recognised in the fossil record only since the Late Jurassic (~180 Ma ago).

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