A taxonomic review of the Jurassic dinoflagellate cyst genus *Gonyaulacysta* Deflandre 1964 emend. nov.

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ABSTRACT

The Middle–Late Jurassic dinoflagellate cyst genus *Gonyaulacysta* is highly distinctive, being characterized by an epicyst which is substantially larger than the hypocyst. The sulcal region is typically longitudinal, but relatively rare specimens with sigmoidal venters have also been observed. The latter morphotypes may represent experimentation with a novel morphological trait. *Gonyaulacysta jurassica* is the nomenclatural type, and occurs in the Oxfordian–Kimmeridgian and the Bathonian–Kimmeridgian in the Northern and Southern Hemispheres respectively. A total of 151 species have been assigned to *Gonyaulacysta* although 126 of these have been transferred to other genera. Prior to this contribution, 15 species were accepted; this is herein reduced to eight. The species that are accepted are:

Gonyaulacysta adecta stat. nov., emend. nov.; *Gonyaulacysta australica* comb. nov., emend. nov.; *Gonyaulacysta ceratophora*; *Gonyaulacysta desmos* stat. nov., emend. nov.; *Gonyaulacysta dualis* emend. nov.; *Gonyaulacysta fenestrata* emend. nov.; *Gonyaulacysta jurassica* emend. nov.; and *Gonyaulacysta longicornis* stat. nov., emend. nov. These species form a closely related plexus with a unique morphology, and are distinguished on differences in cavation style, form of the sutural crests/ridges and size of the apical horn. All the species, except *Gonyaulacysta australica,* are reliable index taxa. Our main taxonomic proposals involve the elevation of all subspecies and varieties of species here retained in *Gonyaulacysta* to species status, or their synonymisation. This avoids use of cumbersome infraspecific names. At the species level, *Gonyaulacysta* exhibits substantial provincialism; for example *Gonyaulacysta dualis* is confined to the Oxfordian–Kimmeridgian of the Boreal Realm. *Gonyaulacysta adecta, Gonyaulacysta desmos* and *Gonyaulacysta longicornis* are present in the Bathonian–Oxfordian of Laurasia and surrounding areas. The species *Gonyaulacysta australica, Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* are restricted to the Oxfordian–Tithonian of Australasia. *Gonyaulacysta adecta* and the cosmopolitan *Gonyaulacysta jurassica* both exhibit overall size increases throughout the Bathonian–Kimmeridgian of Europe.

Keywords: biostratigraphy; dinoflagellate cysts; *Gonyaulacysta*; Middle–Late Jurassic; provincialism; taxonomy

1. Introduction

Georges Victor Deflandre (1897–1973) was a scientific polymath, and one of the pioneers of palynology (Sarjeant, 1973; Evitt, 1975; Noel, 1975; Riding and Lucas-Clark, 2016). He wrote the first major paper on Jurassic dinoflagellate cysts of the modern era (Deflandre, 1938). In this landmark publication, many important new taxa from the lowermost Oxfordian strata of northern France were established. The single sample studied was from the Marnes de Villers Formation (*Quenstedtoceras mariae* ammonite zone) and Georges Deflandre prepared the material by gently sieving with water (Riding and Schmitt, 2009; Riding, 2021).

One of the species described by Deflandre (1938) was the distinctive form that was named *Gonyaulax jurassica* (see Deflandre, 1938, p. 168–171, figs 1, 2; pl. 6, 2–6). He also described *Gonyaulax jurassica* var. *longicornis* (Deflandre, 1938, p. 171; pl. 6, 6), which is a variety with an elongate apical horn. *Gonyaulax* is a genus of living dinoflagellates, and *Gonyaulax jurassica* was therefore subsequently transferred to the fossil cyst-based genus *Gonyaulacysta* by Norris and Sarjeant (1965, p. 65) as the type. *Gonyaulacysta* has been emended by Sarjeant (1966, 1969, 1982), Stover and Evitt (1978) and Helenes and Lucas-Clark (1997). Major works on this important genus and similar forms include Stover and Evitt (1978), Sarjeant (1982), Helenes (1986), Jan du Chêne et al. (1986), Helenes and Lucas-Clark (1997), Riding and Helby (2001a) and Riding (2005a).

Gonyaulacysta jurassica has a characteristic and unique morphology, which was first recognized and described in detail by Stover and Evitt (1978, p. 275–278). The two most distinctive and highly unusual characteristics of this species and the other species in *Gonyaulacysta* are the large epicyst, which is typically more than twice the length of the hypocyst, and an opisthopyle, which penetrates the ps plate (Fig. 1; Riding and Helby, 2001a, p. 151; Riding, 2005a, p. 14). Due to its distinctive morphology, abundance and wide geographical distribution, *Gonyaulacysta jurassica* is perhaps the quintessential Jurassic dinoflagellate cyst (Jan du Chêne et al., 1986; Riding, 2007). Seven other species share the distinctive cyst organisation, morphology and tabulation pattern of *Gonyaulacysta jurassica* (Fig. 2; Table 1). Three of these were previously subspecies or varieties.

The concept of *Gonyaulacysta jurassica* has embraced substantial intraspecific variability, prompting several taxonomic studies and resulting in three accepted subspecies and six accepted varieties (Fensome et al., 2019, p. 368–369). These nine infraspecific taxa were largely defined on differences in the cavation style and the size of the apical horn. This complex taxonomy of *Gonyaulacysta jurassica* makes the application of these taxa confusing and cumbersome. For example, *Gonyaulacysta jurassica* subsp. *adecta* var. *longicornis*, which is elevated to species status herein, is a highly distinctive large, late Callovian to middle Oxfordian form (e.g. Riding and Thomas, 1997, figs 5d, h). This contribution aims to simplify the taxonomy of *Gonyaulacysta* by emphasising the characteristic morphology of the genus and discontinuing the use of taxa below species level. This approach was presaged by Riding and Helby (2001a, p. 151), who stated that 'We consider *G. jurassica* has far too many subspecific and varietal subdivisions and the most important stratigraphical morphotypes should be elevated to specific status'.

Gonyaulacysta and its eight accepted species are treated systematically herein. The species retained in *Gonyaulacysta* are easy to recognize, and most of them are reliable biostratigraphical markers. They form a cosmopolitan and closely related plexus which is confined to the Middle and Late Jurassic (Bathonian–Tithonian; Fig. 3). Riding (2005a, p. 13) referred to this group as the '*Gonyaulacysta dualis/fenestrata/jurassica* complex'. Furthermore, two previous transfers of species into *Gonyaulacysta* are rejected and nine species previously attributed to this genus are transferred to more appropriate genera. The detailed morphology of the ventral area of *Gonyaulacysta* is documented and re-interpreted, and the spatial and temporal distributions of all the retained species are outlined. Finally the palaeobiology of this important genus is discussed.

(Figs 1, 2 and 3, and Table 1 near here)

2. The systematic palaeontology of *Gonyaulacysta*

In this section, the genus *Gonyaulacysta* and its eight accepted species are treated systematically. Original diagnoses and descriptions of the genus and the species are provided in Appendix 1 of the Supplementary material. A comprehensive inventory of the specimens figured herein comprising all relevant details such as the sample localities and coordinates, sample positions, biostratigraphy, lithostratigraphy, specimen dimensions, sample/slide numbers, England Finder references, and museum curation numbers are given in Table 2 and Appendix 2 of the Supplementary material. Where dimensions are given, the three measurements quoted in micrometres (μm) are minimum, (mean) and maximum respectively. Supplementary material Appendix 3 comprises nine data tables on five species of *Gonyaulacysta* which underpin the summary data herein. The material illustrated in this paper is housed in the collections of the British Geological Survey, Nottingham, UK, Geoscience Australia, Canberra, Australia and Museum Victoria, Melbourne, Australia (Table 2).

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

Suborder GONYAULACINEAE (autonym)

Family GONYAULACACEAE Lindemann, 1928

Subfamily GONYAULACOIDEAE (autonym)

Genus ***Gonyaulacysta*** Deflandre, 1964 emend. nov.

Selected synonymy list:

1964 *Gonyaulacysta* Deflandre: p. 5030.

1966 *Gonyaulacysta* Deflandre; Sarjeant: p. 111 (emendation).

1969 *Gonyaulacysta* Deflandre; Sarjeant: p. 7–8 (emendation).

1978 *Gonyaulacysta* Deflandre; Stover and Evitt: p. 157–158 (emendation).

1982 *Gonyaulacysta* Deflandre; Sarjeant: p. 27–28 (emendation).

1997 *Gonyaulacysta* Deflandre; Helenes and Lucas-Clark: p. 175–176 (emendation).

Type. *Gonyaulacysta jurassica* Deflandre, 1938, pl. 6, 2–3, figs 1–2.

Original description (in part). 'I place in the genus *Gonyaulacysta* nov. gen. (Genotype: *Gonyaulax jurassica* Defl. 1938), all species of *Gonyaulax* tabulate fossils represented by the more-or-less ornamented, projecting crests (pectinate, spiny, denticulate, etc.) with archeopyle (3rd pre-equatorial plate)...'. Deflandre (1964, p. 5030), translated by the present authors. See Appendix 1 of the Supplementary material for a complete translation.

Emended diagnosis. Cavate, elongate, tabulate gonyaulacacean dinoflagellate cysts with an apical horn. The cingulum is offset posteriorly so that the epicyst is markedly larger than the hypocyst. The sulcus is normally, but not always, L-type. Archaeopyle single-plate precingular, type $P_{3''}$. The operculum is free and formed from the endophragm only, as the periphragm representing the 3'' plate is entirely absent. An opisthopyle penetrates the ps plate.

Emended description. Elongate, usually dorsoventrally compressed dinoflagellate cysts with an ovoidal to subpolygonal (typically subpentagonal) pericyst, a prominent, truncate apical horn and a straight antapical margin. The endocyst is ovoidal, with or without a rounded apical protuberance. The epicyst is significantly larger than the hypocyst. Wall epicavate or bicavate but may occasionally be cornucavate or delphicavate respectively; locally suturocavate. Tabulation is indicated by sutural ridges or crests which may be discontinuous. Sutural features may be distally smooth, perforate or surmounted by denticles or small spines which, when developed, are distally pointed or bifurcate. The crests or ridges are typically markedly lower in height in the mid-ventral region. In the apical region the denticulation on the sutures, where developed, is reduced. The endophragm is moderately thick, with a smooth surface. The periphragm is markedly thinner than the endophragm and is normally smooth, but may bear isolated and scattered (nontabular) elements of low-relief such as granules and scabrae. Tabulation gonyaulacacean, formula 2pr, 4’, 1–2a, 6’’, 6c, 6’’’, 1p, 1’’’’, 5s; it differs from the standard gonyaulacalean pattern in the possession of one or two small anterior intercalary plates on the dorsal surface (Fensome et al., 1993; Fensome et al., 1996a, fig. 45). It exhibits neutral torsion and a porichnion at the 2pr/1’/4’ triple junction on the ventral side of the apical region. Archaeopyle precingular, type $P_{3''}$. The endoperculum may fall back into the empty endocyst; a perioperculum (the opercular piece in the periphragm) was never developed. Cingulum prominent and is located significantly closer to the antapex than to the apex; it is subdivided into six cingular plates and is laevorotatory, the displacement being typically equivalent to one cingulum width. The sulcus is mid-ventral, normally longitudinal (occasionally sigmoidal), delimited by low, sutural ridges; individual sulcal plates are not normally discernible. A circular to ellipsoid opisthopyle is developed in the periphragm which represents the ps plate. Size: intermediate to large.

Comments. The genus *Gonyaulacysta* was established by Deflandre (1964, p. 5030) and emendations were proposed by Sarjeant (1966, p. 111; 1969, p. 7–8; 1982, p. 27–28), Stover and Evitt (1978, p. 157–158) and Helenes and Lucas-Clark (1997, p. 175–176) (Appendix 1 of the Supplementary material). These emendations successively provided more morphological detail than was given in the original description.

Sarjeant (1966, p. 140) incorrectly considered that *Rhynchodiniopsis* "... was, at the time of its publication, effectively a junior homonym of *Gonyaulax*, none of the characters cited warranting the creation of a new name" (perhaps Sarjeant meant junior synonym). He proposed "that the name *Rhynchodiniopsis* be abandoned and the single species, *R. aptiana* ... be transferred to *Gonyaulacysta*." However, as Stover and Evitt (1978, p. 275) pointed out, such a transfer would have been been illegitimate as *Rhynchodiniopsis aptiana* is the type of *Rhynchodiniopis*, and that genus has priority over *Gonyaulacysta*; thus Stover and Evitt (1978, fig. 2) maintained the separation of *Gonyaulacysta jurassica* and *Rhynchodiniopsis aptiana.* We fully agree that *Rhynchodiniopsis* and *Gonyaulacysta* should be retained separately. *Rhynchodiniopsis* is an acavate to slightly cornucavate gonyaulacacean genus with an equatorial cingulum (e.g. Helenes, 1986, pl. 1, 1–6) and *Gonyaulacysta* is clearly not synonymous with it.

Stover and Evitt (1978, p. 275–278) also undertook a comprehensive and incisive investigation of the type material of *Gonyaulacysta jurassica* and *Gonyaulacysta longicornis,* but did not formally emend these species (nor did they explicitly emend the genus, as was cited by Fensome et al., 2019, p. 357). William R. Evitt had visited Georges Deflandre in November 1959, and must have examined this material during his stay in Paris (Riding and Lucas-Clark, 2016, p. 37–39). The morphological analysis by Stover and Evitt (1978) was given as seven bullet points. Firstly, they described the bicavate and suturocavate cyst organisation and the shape of the endocyst. They noted that the midventral tabulation around the sulcus is consistently reduced, even partly suppressed. This phenomenon has also been observed in the closely related genus *Tubotuberella* (see Riding, 2012; Riding and Michoux, 2013). Stover and Evitt (1978) noted the presence of one or two small anterior intercalary plates on the dorsal side of the epicyst. The narrowness of plate 4' and the adjacent 6'' was also mentioned. A prominent circular–ellipsoid opisthopyle is consistently present in the periphragm of the ps plate, and hence penetrates the antapical pericoel. This feature occupies most of the ps plate in both epicavate and bicavate cysts, but is only clearly visible in forms which are bicavate. Stover and Evitt (1978) commented that the detailed tabulation on the slender apical horn is difficult to precisely resolve. These authors also stated that the endoarchaeopyle is smaller than the periarchaeopyle. However, Eaton (1984, figs 2–5) convincingly demonstrated that there is no perioperculum, and that the 3'' plate is represented by a primary opening on the pericyst.

Helenes (1986) outlined 12 tabulation styles in gonyaulacacean dinoflagellates. One of these is the *Jurassica* pattern, which was named after *Gonyaulacysta jurassica* (Helenes, 1986, fig. 15). This pattern is based on characteristic plate configurations in the apical (pr/2'), ventral (1'/6'') and antapical (symmetrical 1'''') regions (Helenes, 1986, fig. 15, table 1). This author merged his *Brixii, Ghermanii, Jurassica* and *Polyedra* patterns into the *Polyedra-Jurassica* complex (Helenes, 1986, table 2).

The most recent and comprehensive emendation of *Gonyaulacysta* was by Helenes and Lucas-Clark (1997, p. 175–176). These authors gave a synopsis and an emended description in six sections (i.e. shape, size, wall structure, archaeopyle, external features and tabulation), with most emphasis on the tabulation pattern. *Gonyaulacysta* has a distinctive tabulation with an L-type sulcus (of Evitt, 1985), contact between the 4' and 6'' plates, and the 1' and 6'' plates, a straight 1''' plate which lies within the sulcus and up to two anterior intercalary plates and a rectangular, symmetrical 1'''' plate (Helenes and Lucas-Clark, 1997, figs 1–3; table 1). This is however not consistent with Fensome et al. (1993, p. 92), who stated that *Gonyaulacysta* is in the subfamily Gonyaulacoideae which has S-type ventral organisation (of Evitt, 1985). *Gonyaulacysta* is distinguished from *Stanfordella* and *Wrevittia* by details of cavation style, equatorial cross section, the shape of the sulcus and other key plate configurations (Helenes and Lucas-Clark, 1997, table 1). The two ventral plate configurations proposed by Evitt (1985) are discussed in section 4 below.

In our view, the most characteristic feature of *Gonyaulacysta* is the large epicyst and the small hypocyst. The overwhelming majority of gonyaulacacean and peridiniacean fossil dinoflagellates have subequal epicysts and hypocysts, or the epicyst is smaller than the hypocyst (e.g. Lentin and Williams, 1976; Bujak and Davies, 1983; Jan du Chêne et al., 1986). In *Gonyaulacysta*, the epicyst approaches twice the length of the hypocyst (Figs 1, 2). This highly unusual phenomenon has previously been mentioned by Riding and Helby (2001a, p. 151), Riding (2005a, p. 14) and Riding and Lucas-Clark (2016, p. 79). In terms of tabulation, the apical region exhibits two preapical plates, two anterior intercalary plates and a porichnion (Fig. 1; Stover and Evitt, 1978, fig. 2; Evitt, 1985, figs 5.16D, 10.9B; Helenes, 1986, fig. 15; Fensome et al., 1993, figs 84B, 94; Helenes and Lucas-Clark, 1997, fig. 3). All these small areas are frequently difficult to observe in many specimens using transmitted light microscopy. Specifically, the porichnion at the 2pr/1'/4' triple junction on the ventral side of the apical region is normally only visible in well-preserved material using a scanning electron microscope (Helenes, 1986, pl. 4, 2). This small pore is a reflection of the adelopore of motile dinoflagellates and was first described by Evitt (1985, p. 74).

The original, and all the five emended diagnoses and descriptions of *Gonyaulacysta*, are given in full in Appendix 1 of the the Supplementary material. We deem it necessary to emend *Gonyaulacysta* herein in order to stress the variety of cavation, the very large epicyst in comparison to the hypocyst, the lack of a periarchaeopyle and the opisthopyle in the ps plate. The genus *Gonyaulacysta* is cosmopolitan, and has a highly characteristic morphology; the eight species outlined herein form a tightly defined genus which is confined to the Middle and Late Jurassic. The oldest species, *Gonyaulacysta adecta*, is largely of Middle Jurassic age, but the other species are confined to the Late Jurassic. The genus is most abundant in the Oxfordian (Fig. 3). The species are principally differentiated on the morphology of the sutural ridges/crests and the cavation style. Due to the very specific morphology and tabulation of *Gonyaulacysta* recognized herein, the transfer nine species out of *Gonyaulacysta* into more suitable genera is considered to be neccessary. Additionally, two previous transfers of species into *Gonyaulacysta* are not supported herein.

Comparison. *Gonyaulacysta* is easily distinguished from acavate gonyaulacaean genera with single-plate precingular archaeopyles, such as *Acanthaulax*, *Apteodinium*, *Leptodinium*, *Rhynchodiniopsis* and *Trichodinium*, by exhibiting clear separation of the endophragm and periphragm.

However, *Gonyaulacysta* shares some features with other cavate gonyaulacacean genera. For example, *Psaligonyaulax* and *Tubotuberella* are also prominently bicavate and often exhibit sutural crests and ridges. However, like most other dinoflagellate genera, the cingulums of *Psaligonyaulax* and *Tubotuberella* are positioned equatorially, such that the epicyst and hypocyst are of more or less equal length. *Psaligonyaulax* lacks an opisthopyle. Furthermore, the hypocystal opening in the periphragm of *Tubotuberella* is in the 1'''' plate (Jan du Chene et al., 1986, pl. 123). *Stanfordella* and *Wrevittia* are also superficially similar to *Gonyaulacysta*, but have circular cross sections, equatorial cingulums and consistently an S-type ventral configuration. They also differ in having a cornucavate epicyst and a suturocavate hypocyst. Moreover, they typically lack any anterior intercalary plates and differ in several key plate contacts (Helenes and Lucas-Clark, 1997, figs 1, 2; table 1). Duxbury (1977, p. 37) deemed the monotypic genus *Nelchinopsis* to be a taxonomic junior synonym of *Gonyaulacysta*. *Nelchinopsis*, which was retained as a separate genus by Stover and Williams (1987, p. 11), is holocavate and its archaeopyle type is not known with certainty (Harding, 1996, p. 353). *Triblastula* displays a small, subspherical endocyst, is strongly bicavate with extensive pericoels and has prominent processes surrounding the cingulum. *Hystrichosphaeropsis* is strongly bicavate and can be circumcavate with extremely large pericoels; it also has a subspherical endocyst, lacks sutural ornamentation, and has typically weakly expressed tabulation.

Gonyaulacysta jurassica (Deflandre, 1938) Norris and Sarjeant, 1965 emend. nov.

Fig. 2A; Plate I, 1–9; Plate II, 1–9

Selected synonymy list:

1938 *Gonyaulax jurassica* Deflandre: p. 168–170, pl. 6, 2–5, figs 1, 2.

1965 *Gonyaulacysta jurassica* (Deflandre) Norris and Sarjeant: p. 65.

1982 *Gonyaulacysta jurassica* (Deflandre); Sarjeant: p. 30 (emendation).

1986 *Gonyaulacysta jurassica* (Deflandre); Jan du Chêne et al.: pl. 37, 1–3.

(A more comprehensive synonymy list was given by Sarjeant, 1982, p. 29–30).

Original description (in part). ‘The cell is elongate, generally polygonal in front view, and the transverse, helical groove separates it into two unequal parts. The epitheca, always larger than the hypotheca, is nearly conical, and terminates in a substantially cylindrical hollow horn. The flanks of this epitheca are straight, or slightly concave, or even convex. The same is true of the hypotheca, the flanks of which are, however, more rarely convex. This hypotheca is trapezoidal, sometimes at the pole a little rounded......' (Deflandre, 1938, p. 168–170; translated by the present authors; see Appendix 1 of the Supplementary material for the complete translation).

Emended diagnosis. A species of *Gonyaulacysta* that is subpentagonal in outline, bicavate, intermediate in size, and has a moderately large apical horn that is variable in shape. Most of the sutural features are prominent denticulate crests. Both the periphragm and endophragm are smooth.

Emended description. A species of *Gonyaulacysta*, subpentagonal in outline, with bicavate cyst organisation and intermediate in size. Some plate boundaries may exhibit suturocavation, especially in the precingular series. The moderately well-developed apical horn is formed by the periphragm; it may be relatively slender (delphicavate) and is always truncate distally. The endocyst may be ovoidal and may exhibit a small rounded apical protuberance. The tabulation is reflected by prominent sutural ridges or crests that vary in height and are distally denticulate. Gonal spines may be present on crests bounding the 1'''' plate; where present, they are 2–7 μm in height. The ellipsoidal opisthopyle on the ps plate is normally evident. The periphragm and endophragm are both smooth.

Holotype. Specimen AO 55 of Deflandre (1938, pl. 6, 2, 3; figs. 1, 2). The sample is from the lowermost Oxfordian Marnes de Villers Formation (*Quenstedtoceras mariae* ammonite zone, Villers sur Mer, Calvados, northern France. Curated in the Institut de Paléontologie, Musée Nationale d'Historie Naturelle, Paris, France.

Comments. *Gonyaulacysta jurassica*, the type of the genus, was established by Deflandre (1938). It is easy to recognize, being bicavate, having an apical horn of moderate size, and bearing denticulate crests. However, prior to the work of Sarjeant (1982), palynologists did not distinguish the epicavate specimens characteristic of the Callovian from the bicavate forms so distinctive of the Oxfordian and Kimmeridgian. Sarjeant (1982) established *Gonyaulacysta jurassica* subsp. *adecta* for the former group, the subspecies *Gonyaulacysta jurassica* subsp. *jurassica* being automatically established for the latter group because it includes the type of the species. This was a genuine breakthrough, because the earliest Oxfordian range base of *Gonyaulacysta jurassica* subsp. *jurassica* is an extremely useful biostratigraphical marker (Fig. 3). We propose below that *Gonyaulacysta jurassica* subsp. *adecta* should have species status. Thus, *Gonyaulacysta jurassica* subsp. *adecta* is raised to species rank, thereby making *Gonyaulacysta jurassica* subsp. *jurassica* redundant.

Gonyaulacysta jurassica (*sensu stricto*) is emended here to focus on the detailed overall morphology, for example the suturocavation, the shape of the epicyst and the hypocystal cavation. The cavation in the epicyst of *Gonyaulacysta jurassica* is highly variable (Sarjeant, 1982, fig. 1). When describing the holotype of *Gonyaulacysta jurassica*, Sarjeant (1982, p. 14) noted that the periphragm and endophragm of the hypocyst were separated laterally, but still in contact at the antapex. He included this feature in his description of *Gonyaulacysta jurassica* subsp. *jurassica*, stating that this subspecies exhibits a partial or complete development of the hypopericoel (Sarjeant, 1982, p. 30). Poulsen (1991, p. 213) restudied the holotype and demonstrated the complete separation of the two wall layers in the antapical region and therefore, *Gonyaulacysta jurassica* subsp. *jurassica* is clearly bicavate. Poulsen (1991, p. 213) stated that the opisthopyle is in the 1'''' plate. The present emendation revises this to the ps plate. The emendation of *Gonyaulacysta jurassica* subsp. *jurassica* (equating with our concept of *Gonyaualacysta jurassica*) by Sarjeant (1982,

p. 30) lacks key details. *Gonyaulacysta jurassica* is significantly variable in size, an aspect fully discussed below.

Comparison. The most similar species to *Gonyaulacysta jurassica* is *Gonyaulacysta adecta,* but the latter is consistently epicavate. *Gonyaulacysta desmos*, like *Gonyaulacysta jurassica,* has pericoels but is only partially antapically cavate (Fig. 2).

Dimensions. We have observed that the size of *Gonyaulacysta jurassica* significantly increased throughout its range. In order to investigate this phenomenon, material from Staffin Bay, Isle of Skye in northwestern Scotland and Lincolnshire in eastern England has been examined (Fig. 4, Table 2, Supplementary material Appendix 3, table 1). Measurements were carried out on 120 specimens from each locality, collectively covering the entire Oxfordian to lower Kimmeridgian succession. From the lower to middle Oxfordian the average length varies only slightly, decreasing from 69 μm to 67 μm for the Scottish material and from 67 μm to 66 μm for the English material (Fig. 4). However, in the upper Oxfordian and Kimmeridgian, specimens of *Gonyaulacysta jurassica* are significantly larger. The major increase is recorded in the upper Oxfordian, where the average length increases by 12 μm and 11 μm in Scotland and England respectively (Fig. 4). This was followed by a slight decrease in the lower Kimmeridgian at both localities. The results from both areas are clearly consistent with one another, suggesting that the overall trend is not arbitrary or controlled, for example, sedimentologically.

The dimensions of *Gonyaulacysta jurassica* studied herein, based on 120 specimens from the lower and middle Oxfordian, are: length of pericyst, 53 (67) 84; length of apical horn, 7 (12) 18; length of epipericyst, 33 (42) 58; length of hypopericyst, 13 (20) 31; length of endocyst, 33 (47) 62; width at cingulum, 36 (45) 60. The dimensions of material from the upper Oxfordian and lower Kimmeridgian, again based on 120 specimens, are: length of pericyst, 60 (77) 100; length of apical horn, 9 (14) 20; length of epipericyst, 33 (45) 60; length of hypopericyst, 13 (26) 40; length of endocyst, 40 (54) 71; width at cingulum, 33 (50) 69 (Supplementary material Appendix 3, table 1). The average length and width from the upper Oxfordian and lower Kimmeridgian compare well with the original material of Deflandre (1938, p.169–170); i.e. length of pericyst, 79; width at cingulum, 55. Deflandre (1938) also stated that the largest specimens reached 100 µm in length, whereas the smallest ones were 65 µm long. However, the original material of Deflandre (1938) is early Oxfordian in age.

Geographical and stratigraphical distribution. *Gonyaulacysta jurassica* occurs worldwide and is a prominent Late Jurassic species. In Europe and surrounding regions in the Northern Hemisphere, including the Arctic region, it is confined to the Oxfordian and Kimmeridgian (*Quenstedtoceras mariae* to *Aulacostephanus autissiodorensis* ammonite zones; Fig. 3), and its range base and top are very reliable stratigraphical markers (e.g. Feist-Burkhardt and Wille, 1992; Riding and Thomas, 1992; Poulsen and Riding, 2003). Throughout the Oxfordian to Kimmeridgian range in Europe, *Gonyaulacysta jurassica* is normally relatively common (e.g. Brenner, 1988; Kunz, 1990; Riding and Thomas, 1997; Riding et al., 1999; Riding, 2005b), especially so in the Oxfordian.

The species is also present in the Southern Hemisphere. In Australasia, *Gonyaulacysta jurassica* has a range of middle Bathonian to middle Kimmeridgian. It is only consistently present between the latest Bathonian and middle Oxfordian (Riding et al., 2010, fig. 12). The species does not occur in the late Bajocian to early Bathonian *Wanaea verrucosa* dinoflagellate cyst zone (Mantle and Riding, 2012). There are reports of sporadic specimens of *Gonyaulacysta jurassica* from the late Kimmeridgian to earliest Cretaceous in

Australasia (Helby et al., 1987; Davey, 1988); however, these occurrences are believed to represent reworking.

(Plates I and II and Fig. 4 near here)

Gonyaulacysta adecta (Sarjeant, 1982) stat. nov., emend. nov.

Fig. 2B; Plate III, 1–8; Plate IV, 1–9

Selected synonymy list:

1982 *Gonyaulacysta jurassica* Deflandre; subsp. *adecta* Sarjeant: p. 30–31, pls 1–3; pl. 4, 1–4, 9; pl. 6, 4–5, 9.

Original diagnosis. 'A subspecies of *Gonyaulacysta jurassica* in which no hypotractal cavation is developed, nor is an opisthopyle present.' (Sarjeant, 1982, p. 30).

Emended diagnosis. A subpentagonal, epicavate species of *Gonyaulacysta*, intermediate in size, with a short to moderately long apical horn. Most of the sutural features are denticulate/echinate sutural crests and ridges. The periphragm and endophragm are normally smooth.

Emended description. A subpentagonal species of *Gonyaulacysta*, intermediate in size, with epicavate or rarely cornucavate cyst organisation. The boundaries/sutures between the precingular and postcingular plates may be suturocavate. It has a short to relatively prominent apical horn made of periphragm, and which is distally truncate. The endocyst may exhibit a small rounded apical protuberance, or it may be ovoidal. The tabulation is indicated by denticulate/echinate sutural ridges or crests which are variable in height. The denticles/echinae are longest at the top of the precingular plates, around the cingulum and the 1'''' plate. The 1'''' plate may have small gonal spines up to 4 µm in length. The periphragm and endophragm are both smooth, but low-relief, nontabular ornamentation may be present. The periphragm is significantly thinner than the endophragm.

Holotype. Specimen SWS 2459/1/6, slide GMUS Pd 249 (Sarjeant, 1982, pl. 1, 2). Sample from the Dunans Shale Member of the Staffin Shale Formation (*Kosmoceras jason* ammonite zone), Trotternish, Isle of Skye, northwestern Scotland (NGR NG 472 708). Curated in the Department of Geological Sciences, University of Saskatoon, Saskatchewan, Canada.

Comments. Sarjeant (1982) noted that *Gonyaulacysta jurassica*, as the species was originally conceived, can either be bicavate or epicavate. Furthermore, Sarjeant (1982) perceptively reported that the earliest representatives of *Gonyaulacysta jurassica,* largely from the Callovian, are exclusively epicavate and have relatively short horns, whereas the bicavate morphotypes are confined to the Oxfordian and Kimmeridgian. The holotype of *Gonyaulacysta jurassica* is earliest Oxfordian in age, and is bicavate. Therefore, the largely Callovian epicavate forms can be consistently and easily separated from *Gonyaulacysta jurassica sensu stricto*. They were assigned to *Gonyaulacysta jurassica* subsp. *adecta* by Sarjeant (1982, p. 30–31). The subspecies name was derived from the Greek *adektos*, meaning unbitten or unmolested. Given the present authors' principal aim to simplify the taxonomy of the genus *Gonyaulacysta,* we here elevate *Gonyaulacysta jurassica* subsp. *adecta* to species status.

Gonyaulacysta adecta is a distinctly subpentangular, non-elongate species with an epicavate or cornucavate structure that is virtually always distinguishable from the bicavate

Gonyaulacysta jurassica. However, *Gonyaulacysta adecta* and *Gonyaulacysta jurassica* overlap in size and so, if the antapical area is damaged or obscured, the differentiation of these species may be problematical. All specimens of *Gonyaulacysta adecta* have an apical horn of moderate size. Because the cyst-wall layers are in contact in the antapical region, the opisthopyle on the ps plate is presumed to be present but is never visible. Many specimens are apparently not suturocavate, but some individuals demonstrably exhibit this feature in the precingular and postcingular plate series (Plate III, 8). Riding (1983, pl. 2, 9) illustrated a specimen which clearly exhibits suturocavation in the 1'' plate. In *Gonyaulacysta adecta,* both cyst wall layers are normally smooth, however low-relief, nontabular ornamentation such as granules may occasionally be present. The endophragm is markedly thick and robust. The sutural crests posterior to the apical series are often relatively high (up to 9 µm) and are distally echinate or denticulate. *Gonyaulacysta adecta* is emended here to expand the somewhat brief diagnosis of Sarjeant (1982, p. 30), who did not document the morphology in detail. This species is appreciably variable in size, as discussed below.

Comparison. *Gonyaulacysta jurassica* is the most similar species to *Gonyaulacysta adecta,* but the former is consistently bicavate (Fig. 2).

Dimensions. Sarjeant (1982, p. 30) identified two paratypes of *Gonyaulacysta jurassica* subsp. *adecta*, which he labelled A and B; the two are markedly different in size. The overall lengths of paratypes A and B are 57 µm and 79 µm respectively according to Sarjeant (1982). In order to investigate the size range of *Gonyaulacysta adecta*, the length and width of 303 specimens were measured and plotted (Fig. 5, Supplementary material Appendix 3, table 2). These data show that this species is strikingly variable in size, ranging from 44 µm to 93 µm in length. However, *Gonyaulacysta adecta* displays a continuum in size variability, and it is not possible to consistently identify the two paratypes documented by Sarjeant (1982).

Further investigations were carried out to study the size variability of this species throughout the Callovian. One continuous and well-preserved Callovian succession from the Denver Sluice Borehole in Norfolk, eastern England, and a composite section with components from England and Scotland were studied. The latter section comprises material from the Nettleton Bottom, Warboys and Warlingham boreholes in central and southern England, as well as outcrop material from Bletchley Brick Pit, Buckinghamshire, southern England, and Staffin Bay, Isle of Skye, northwest Scotland (Woollam and Riding, 1983, appendix 1; Riding, 1987; Riding and Thomas, 1997). The dimensions of *Gonyaulacysta adecta* from each ammonite zone in these successions were measured, and we compared the two sections (Fig. 6). Note that the *Proplanulites koenigi/Sigaloceras calloviense* ammonite zones and *Kosmoceras jason/Erymnoceras coronatum* ammonite zones could not be differentiated in the English succession. The trends recorded during each zone in the Denver Sluice Borehole and the composite section are based on data in Supplementary material, Appendix 3, tables 3, 4. The Bathonian and lower Callovian are characterized by relatively small specimens that only occasionally approach 70 µm in length. Large specimens, exceeding 70 µm in length, first appear in the *Kosmoceras jason* ammonite zone, and became more common throughout the middle and upper Callovian, resulting in constant co-existence of small and large specimens. In the uppermost Callovian (*Quenstedtoceras lamberti* ammonite zone), the minimum length apparently increased (Fig. 6). The size patterns recorded in both succssions are extremely similar, suggesting that this trend of increasing size with time is consistent.

Size data based on four specimens of *Gonyaulacysta adecta* from the uppermost Bathonian (*Clydoniceras discus* ammonite zone) of southwest England are as follows: length of pericyst, 49 (57) 62; length of apical horn, 9 (9.5) 11; length of epipericyst, 29 (38) 44; length of hypopericyst, 7 (15) 20; length of endocyst, 40 (45) 51; and width at cingulum, 38 (44) 51 (Supplementary material, Appendix 3, table 5).

The dimensions of 60 specimens examined herein from the lower Callovian are: length of pericyst, 49 (58) 67; length of apical horn, 6 (9) 16; length of epipericyst, 29 (37) 49; length of hypopericyst, 9 (16) 27; length of endocyst, 33 (42) 58; and width at cingulum, 31 (43) 62 (Supplementary material, Appendix 3, table 6). These results compare well with the dimensions of paratype A of Sarjeant (1982), i.e. length of pericyst, 57; length of epipericoel, 12; length of endocyst, 45; width of endocyst, 31; width at cingulum, 37 (Sarjeant, 1982, p. 30).

The dimensions of 30 specimens from the upper Callovian are: length of pericyst, 53 (67) 84; length of apical horn, 7 (13) 20; length of epipericyst, 33 (45) 55; length of hypopericyst, 9 (19) 27; length of endocyst, 38 (50) 64; and width at cingulum, 40 (46) 64 (Supplementary material, Appendix 3, table 7). The average size increased in the upper Callovian due to the first occurrences of larger forms in the middle Callovian, as discussed above.

Geographical and stratigraphical distribution. *Gonyaulacysta adecta* is the oldest species of the genus. It is confined to the earliest Bathonian (*Zigzagiceras zigzag* ammonite zone) to the middle Oxfordian (*Cardioceras tenuiserratum* ammonite zone) of the Northern Hemisphere (Fig. 3; Sarjeant, 1972; Fenton et al., 1980; Feist Burkhardt and Wille, 1992; Poulsen, 1996; Riding and Thomas, 1997; Riding et al., 1999; Riding, 2005b; Wiggan et al., 2017; Wiggan et al., 2018). Occasional reports of *Gonyaulacysta adecta* from the late Oxfordian are known; these may represent reworking. For example, Riding (1987, fig. 5) noted an isolated occurrence from the lowermost upper Oxfordian (*Amoeboceras glosense* ammonite zone) of Eastern England. Also, the species was encountered in the upper Oxfordian (*Amoeboceras serratum* and *Amoeboceras regulare* ammonite zones) by Thomas and Cox (1988, fig. 3). The latter record appears to be substantially inconsistent with all other investigations. *Gonyaulacysta adecta* is extremely rare in the Bathonian and its consistent range is early Callovian (*Macrocephalites herveyi* ammonite zone) to middle Oxfordian (*Cardioceras tenuiserratum* ammonite zone). It is normally common throughout the Callovian (Fig. 3; Riding and Thomas, 1997; Riding, 2005b).

Gonyaulacysta adecta has never been reported from Australasia. However, it occurs in the upper Callovian Lotena Formation of the Neuquén Basin in west-central Argentina (Martinez and Quattrocchio, 2004; Quattrocchio et al., 2007; Riding et al., 2011). The Argentinian late Callovian dinoflagellate cyst assemblages are more similar to their counterparts in Europe than in Australia. This may be due to a marine connection between South America and Europe in the Hispanic Corridor, and driven by the circum-Tropical Marine Current (Riding et al., 2011). *Gonyaulacysta adecta* was also reported from the Callovian–Oxfordian Maguazo Unit of Ecuador (Litherland et al. 1994).

Gonyaulacysta sp. cf. *G. adecta* (Sarjeant, 1982) stat. nov., emend. nov.

Plate III, 9

Comments. A single specimen of an unusual morphotype of *Gonyaulacysta* from the Bathonian of England is illustrated herein (Plate III, 9). This form has small, markedly bifurcate spines surmounting the sutural crests, and has a distinctly sigmoidal sulcus. It most closely resembles *Gonyaulacysta adecta* because it is epicavate, thus it is assigned as *Gonyaulacysta* sp. cf. *G. adecta.* No other specimen of *Gonyaulacysta* has been reported with bifurcate sutural ornaments. As only a single specimen has been encountered it is not, at this stage, formally described.

(Plates III and IV and Figs 5 and 6 near here)

Gonyaulacysta australica (Cookson and Eisenack, 1982) comb. nov., emend. nov.

Fig. 2C; Plate V, 1–3

Synonymy list:

1982 *Psaligonyaulax australica* Cookson and Eisenack: p. 37–38, pl. 2, 13–15.

Original diagnosis. ‘A *Psaligonyaulax*, very similar to *Ps. apatela,* but which differs from the latter in that the antapical appendix, which is formed in *Ps. apatela* as a four-sided area, is either merely indicated or entirely absent in *Ps. australica*, so that *Ps. australica* then terminates antapically. The periphragm is thin, the surface smooth. A paneling [tabulation] is not perceptible. The endophragm is also thin-walled and delicate and often difficult to establish. The apical prominence, which is usually clear in *Ps. apatela*, is also present, but not always clear. The apical horn is well developed as in *Ps. apatela*; it is cylindrical to weakly conical and truncated at the end. The archaeopyle is horseshoe-shaped and sometimes very elongated; it extends from the belt [cingulum] region almost to the apical horn.’ (from Cookson and Eisenack 1982, p. 37, translation by the present authors. See Appendix 1 of the Supplementary material for original dimensions and discussion).

Emended diagnosis. A large, bicavate, smooth-walled species of *Gonyaulacysta* with a relatively short apical horn formed of periphragm. The cyst outline is subovoidal to subquadrangular, with a rounded, almost semicircular, hypocyst. The sutural features are low, smooth crests or ridges, which may be perforate and/or bear tiny denticles.

Emended description. A large, subovoidal/subquadrangular species of *Gonyaulacysta* with bicavate wall structure. The antapical region is markedly rounded and approaches a semicircle in outline. Its shape varies from noticeably elongate to somewhat squat. The epipericoel and hypopericoel are not extensive. The species has a relatively short, subtriangular apical horn comprised of periphragm, which is truncate distally. The endocyst may or may not exhibit a rounded apical protuberance. The tabulation is marked by sutural crests or ridges that are distally smooth or may bear tiny denticles. The crests or ridges are usually low and can be perforate. A small opisthopyle may be observable. Both the endophragm and periphragm are smooth.

Holotype. Specimen P. 47281 of Cookson and Eisenack (1982, pl. 2, 14). Sample from sample C.R.A., C.R. 69 from the upper part of the Dingo Claystone (Oxfordian to lower Kimmeridgian) between 1217 m and 1210 m in the Cape Range No. 2 Borehole, Exmouth Gulf, Carnarvon Basin, Western Australia. Curated in Museum Victoria, Melbourne, Australia.

Comments. *Gonyaulacysta australica* has not been documented since its initial description, and hence it appears not be a significant index fossil in Australasia. It is bicavate and characterized by a small apical horn, dominantly smooth sutural crests or ridges, and a rounded, virtually semicircular, hypocyst. This species was considered a taxonomic junior synonym of *Gonyaulacysta dualis* by Brenner (1988) and of *Scriniodinium*? (now *Gonyaulacysta*) *ceratophorum* by Jan du Chêne et al. (1986). It is close in morphology to

Gonyaulacysta ceratophora, however, we choose to retain both as separate species. This is because *Gonyaulacysta australica*, unlike *Gonyaulacysta ceratophora*, has a well-rounded ambitus and a moderately large apical horn; it also entirely lacks any sutural ornamentation.

Comparison. The most similar species to *Gonyaulacysta australica* is *Gonyaulacysta dualis*. However, the latter is subpentagonal in overall shape, has a prominent apical horn, and both the epipericoel and hypopericoel are very well developed.

Dimensions. According to Cookson and Eisenack (1982, p. 37), the size of the holotype of *Gonyaulacysta australica* is 140 x 76 µm. The dimensions of other specimens are 128 x 76 µm, 114 x 78 µm and 109 x 60 µm.

Geographical and stratigraphical distribution. *Gonyaulacysta australica* was reported from the Oxfordian and Kimmeridgian of Western Australia by Cookson and Eisenack (1982).

(Plate V near here)

Gonyaulacysta ceratophora (Cookson and Eisenack, 1960) Riding, 2005a

Fig. 2D; Plate VI, 1–9

Selected synonymy list:

1960 *Scriniodinium ceratophorum* Cookson and Eisenack: p. 249, pl. 37, 7.

1978 *Scriniodinium*? *ceratophorum* Cookson and Eisenack; Stover and Evitt: p. 187.

1988 *Scriniodinium* sp. cf. *S. ceratophorum* Cookson and Eisenack; Helby et al.: fig. 9S.

1992 *Scriniodinium*? cf. *ceratophorum* Cookson and Eisenack *sensu* Helby et al.; Keating et al.: figs 6i, j.

2005a *Gonyaulacysta ceratophora* Cookson and Eisenack; emend. Riding: p. 14–20, pl. 1, 1–9, figs 1C, 1D, 2.

Diagnosis. 'A partially tabulate to non-tabulate species of *Gonyaulacysta.* The midventral and middorsal areas normally lack any indications of tabulation. Where developed, low sutural ridges or crests are generally restricted to the antapical-lateral and apical areas. A poorly developed hypopericoel is usually developed.' (from Riding, 2005a, p. 14).

Description. Riding (2005a, p. 14–18); see Appendix 1 of the Supplementary material.

Holotype. Specimen P17769 of Cookson and Eisenack (1960, pl. 37, 7). Sample from the Jarlemai Siltstone (Oxfordian to lower Kimmeridgian) of the Broome No. 3 Borehole, Western Australia between 434.98 m and 428.24 m. Curated in Museum Victoria, Melbourne, Australia.

Comments. The species *Scriniodinium ceratophorum* was described from the Upper Jurassic of Western Australia by Cookson and Eisenack (1960), with only the holotype illustrated. This species is a bicavate, elongate, subpentagonal, largely non-tabulate, smooth form with a precingular archaeopyle, a prominent apical horn and a large epicyst. The species was comprehensively emended and transferred to *Gonyaulacysta* by Riding (2005a). The holotype is highly atypical in that the tabulation is only demonstrated by the archaeopyle and the cingulum. Most specimens have a partial tabulation that, together with the overall morphology, unequivocally demonstrates affinity with *Gonyaulacysta*. The plates are delineated by low crests and/or ridges in the polar regions, but the cingulum and the archaeopyle are the only features which are indicative of tabulation in the equatorial area (Riding, 2005a, figs 1C, D; pl. 1). Relatively high (13 µm) spines may occur at gonal points in the antapical regions and around the cingulum (Plate VI, 8).

Comparison. *Gonyaulacysta ceratophora* is most similar to *Gonyaulacysta dualis* in morphology, size and stratigraphical range. However, in *Gonyaulacysta dualis* the tabulation is entirely developed (Fig. 2F).

Dimensions. See Riding (2005a, table 1).

Geographical and stratigraphical distribution. *Gonyaulacysta ceratophora* is confined to Australasia, where it is a reliable stratigraphical marker for the early Oxfordian to the early Tithonian interval in Australia, New Zealand and Papua New Guinea (Wilson, 1984; Davey, 1988; Helby et al., 1988; Riding et al., 2010). Its range spans the *Wanaea spectabilis* Interval Zone to the *Omatia montgomeryi* Range Zone (Helby et al., 1987). The species is typically abundant in the middle and upper Oxfordian part of the *Wanaea spectabilis* Interval Zone; elsewhere within its overall range it is relatively inconsistent in occurrence (Riding, 2005a). Occasional specimens of *Gonyaulacysta ceratophora* have been recorded between the early Tithonian (latest *Omatia montgomeryi* Range Zone) and the early Cretaceous of Antarctica, Australia and New Zealand. These are interpreted as reworked (Wilson, 1982; Dettmann and Thomson, 1987; Wilson and Helby, 1987; Riding et al., 1992; Riding and Crame, 2002; Riding, 2005a).

(Plate VI near here)

Gonyaulacysta desmos (Poulsen, 1991) stat. nov., emend. nov.

Fig. 2E; Plate VII, 1–4

Synonymy list:

1982 *Gonyaulacysta jurassica* Deflandre; subsp. *jurassica* Sarjeant: fig. 2a, pl. 4, 8, pl. 5, 1.

1991 *Gonyaulacysta jurassica* Deflandre; subsp. *desmos* Poulsen: p. 213–214, pl. 1, 3, 6.

Original diagnosis. 'A subspecies of *Gonyaulacysta jurassica* which exhibits only partial development of the hypopericoel, i.e. there is a marginal separation of the hypoperiphragm and hypoendophragm, whereas the two wall layers are in contact at the mid-antapical region.' (Poulsen, 1991, p. 214).

Emended diagnosis. A subpentagonal, cornucavate species of *Gonyaulacysta* with a prominent apical horn and a partially developed hypopericoel. Most of the sutural features are echinate crests. The periphragm is smooth to microscabrate and the endophragm is smooth.

Emended description. A subpentagonal species of *Gonyaulacysta* that is intermediate in size and may be somewhat squat or elongate. The epicyst is cornucavate, and a hypopericoel is partially developed: in the antapical area, the endophragm and periphragm are in contact centrally, but separated laterally by up to 7 µm. This partial cavation in the hypocyst makes the antapical margin markedly concave. The species has a well-developed apical horn, composed of periphragm, that is usually relatively slender and consistently truncate distally. The endocyst is ovoidal and lacks an apical protuberance. The tabulation is reflected by distally echinate sutural ridges or crests that vary in height. The 1'''' plate may bear relatively small gonal spines 3–9 μm high. The periphragm is smooth or sometimes microscabrate; the endophragm is smooth.

Holotype. Specimen DGU catalogue number 1989-NEP-1 (Poulsen, 1991, figs 1, 2; pl. 1, 3). Sample from the Oxford Clay Formation (lower Oxfordian, *Quenstedtoceras mariae* ammonite zone) from a horizon 1 m below the base of the Lower Calcareous Grit Formation, at Cayton Bay, North Yorkshire, UK. Curated in the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark.

Comments. *Gonyaulacysta desmos* was originally described by Poulsen (1991) as a subspecies of *Gonyaulacysta jurassica*. The epithet *desmos* derives from the Greek for link, and is in reference to the transitional morphology of this taxon. Poulsen (1991, fig. 3) envisaged his *Gonyaulacysta jurassica* subsp. *desmos* as an intermediate morphotype between *Gonyaulacysta jurassica* subsp. *adecta* and *Gonyaulacysta jurassica* subsp. *jurassica*. The partially developed hypopericoel (Sarjeant, 1982, fig. 2a) is transitional between *Gonyaulacysta jurassica* subsp. *adecta* (cornucavate or epicavate), and *Gonyaulacysta jurassica* subsp. *jurassica* (bicavate or delphicavate), i.e. between *Gonyaulacysta adecta* and *Gonyaulacysta jurassica* as defined herein. This interpretation is supported, in a strictly phylogenetic sense, by the stratigraphical position of *Gonyaulacysta desmos* near the inception of *Gonyaulacysta jurassica* subsp. *jurassica* (Poulsen, 1991, fig. 3). This taxon is emended herein to note the cornucavate epicyst, echinate sutural crests, occasionally microscabrate periphragm, prominent apical horn, shape and size.

Comparison. *Gonyaulacysta desmos* is most similar to *Gonyaulacysta adecta* and *Gonyaulacysta jurassica*; it is morphologically transitional between these two species due to its partially developed hypopericoel.

Dimensions. *Gonyaulacysta desmos* is a relatively rare species, only sporadically encountered within its stratigraphical range. In this study, seven specimens were analysed. The dimensions are: length of pericyst, 64 (74) 84; length of apical horn, 11 (14) 16; length of epipericyst, 31 (38) 44; length of hypopericyst, 27 (31) 40; length of endocyst, 44 (51) 64; width at cingulum, 42 (51) 69 (Supplementary material Appendix 3, table 8). The overall length of the holotype and the paratype are 93 µm and 74 µm respectively (Poulsen, 1991). The size of the paratype is similar to the dimensions of the material studied herein.

Geographical and stratigraphical distribution. *Gonyaulacysta desmos* has only been recorded from the early Oxfordian of northwestern Europe, East Greenland and the USA. In England, this species is confined to the *Cardioceras praecordatum, Cardioceras bukowskii* and *Cardioceras costicardia* ammonite subzones (*Quenstedtoceras mariae* and *Caradioceras cordatum* ammonite zones) of the early Oxfordian according to Poulsen (1991). *Gonyaulacysta desmos* has also been recorded from the early Oxfordian of East Greenland (Poulsen, 1991), and Colorado and Utah, USA (Riding, 2016).

(Plate VII near here)

Gonyaulacysta dualis (Brideaux and Fisher, 1976) Stover and Evitt, 1978, emend. nov.

Fig. 2F; Plate VIII, 1–9

Full synonymy list:

1976 *Psaligonyaulax dualis* Brideaux and Fisher: p. 18–20, pl. 1, 4–6, 8–12; pl. 2, 1–2.

1978 *Psaligonyaulax dualis* Brideaux and Fisher; Tan and Hills: p. 67, pl. 12.2, 7, 8.

1978 *Gonyaulacysta dualis* Brideaux and Fisher; Stover and Evitt: p. 158.

1982 *Gonyaulacysta jurassica* subsp. *jurassica* var. *longicornuta* Sarjeant: p. 31–32, pl. 5, 5, 6.

1983 *Gonyaulacysta dualis* Brideaux and Fisher; Davies: pl. 4, 10.

1986 *Gonyaulacysta dualis* Brideaux and Fisher; Helenes: pl. 4, 1–7, 11.

1986 *Gonyaulacysta dualis* Brideaux and Fisher; Jan du Chêne et al.: pl. 37, 9–14.

1996 *Gonyaulacysta dualis* Brideaux and Fisher; Poulsen: pl. 21, 1.

1997 *Gonyaulacysta dualis* Brideaux and Fisher; Helenes and Lucas-Clark: pl. 1, 3, 4, 7, 10, 13.

2016 *Gonyaulacysta dualis* Brideaux and Fisher; Riding and Lucas-Clark: pl. 2, 2, pl. 16, 4–6.

Original diagnosis. ‘Periblast elongate, typically twice as long as broad, with slightly tapering apical horn; endoblast rhomboid with a short apical prominence and rounded antapex. Anterior breach typically present in the periblast, rarely closed by a moderately bulging antapical prominence. Periblast and endoblast in close contact only at latitude of cingulum, resulting in formation of distinct apical and antapical pericoels. Surface of periphragm and endophragm smooth or, rarely, scabrate. Archeopyle in each layer formed by loss of third reflected precingular plate; opercula separate and detached, elongate. Periblast forms sutural crests which outline a reflected tabulation of 1pr, 4’, 6’’, 6c, 5’’’–?6’’’, 1p, 1’’’’: crests variable, entire to denticulate, rarely spiny. Cingulum displaced up to two cingular widths, distinct: reflected sulcal tabulation absent but sulcal region distinct.' (Brideaux and Fisher, 1976, p. 18).

Original description. See Brideaux and Fisher 1976, p. 18–19 (reproduced in Appendix 1 of the Supplementary material).

Emended diagnosis. A large, elongate, bicavate species of *Gonyaulacysta* with a prominent apical horn formed of periphragm and a marked apical protuberance on the endocyst. Most of the sutural features are smooth ridges, but sporadically denticulate sutural crests and ridges may be developed.

Emended description. A large, elongate species of *Gonyaulacysta* with a bicavate cyst. Some of the precingular and postcingular plate boundaries may exhibit suturocavation. The epipericoel and hypopericoel are both large. It has a long, slender, distally truncate apical horn composed of periphragm. The endocyst exhibits a prominent rounded apical protuberance. The tabulation comprises sutural ridges or crests that are usually low and distally smooth. However, these sutural features may bear small, pointed denticles. Denticulate sutural crests/ridges typically occur around the cingulum, in the lateral regions and rarely surrounding the 1'''' plate. The 1'''' plate may bear relatively prominent gonal spines up to 5 μm in length. The opisthopyle is usually evident; it is subcircular to ellipsoidal and varies greatly in size. The periphragm may be smooth to markedly scabrate; the thicker endophragm is consistently smooth. The periarchaeopyle is large and may extend above the top of the endocyst.

Holotype. Brideaux and Fisher (1976, pl. 1, 4–5). Geological Survey of Canada (GSC) type number 34154; GSC location number C-12532, slide P810-13B. Ditch cuttings sample from the Gilmore Lake Member of the Langton Bay Formation, (upper Oxfordian–middle Kimmeridgian) between 552 m and 549 m in the Elf Horton River G-02 well, District of Mackenzie (now Northwest Territories), Canada. Specimen curated in the National Collection of Type Invertebrate and Plant Fossils, GSC, Ottawa, Ontario, Canada. At the time of writing, the specimen is on long-term loan to GSC Calgary.

Comments. This species was established by Brideaux and Fisher (1976) as *Psaligonyaulax dualis,* and transferred to *Gonyaulacysta* by Stover and Evitt (1978, p. 158). *Psaligonyaulax* has an equatorial cingulum and does not exhibit an opisthopyle (Sarjeant, 1966, fig. 35). Sarjeant (1982, p. 29) considered *Psaligonyaulax dualis* to be a taxonomic junior synonym of *Gonyaulacysta jurassica*, but Jan du Chêne et al. (1986, p. 131) retained *Gonyaulacysta dualis* as a separate species.

Gonyaulacysta dualis is emended herein to stress its large size, slender and elongate outline, bicavate cyst organisation, prominent apical horn, and largely distally smooth sutures. Also highly distinctive is the long, thin apical horn, which has the form of an elongate and distally truncated cone. This feature is mirrored by a prominent apical protuberance on the endocyst. *Gonyaulacysta dualis* is bicavate, with large polar pericoels. Sutural features are usually low, distally smooth ridges, but low, occasionally denticulate crests may be developed (Brideaux and Fisher 1976, pl. 1, 9–11). Other features that may be present are gonal spines around the 1'''' plate, and a scabrate periphragm (Plate VIII).

Sarjeant (1982, p. 31–32; pl. 5, 5, 6) established *Gonyaulacysta jurassica* subsp. *jurassica* var. *longicornuta.* The single specimen figured by Sarjeant (1982) is virtually identical in all respects to the holotype of *Gonyaulacysta dualis*. Hence it is clear that

Gonyaulacysta jurassica subsp. *jurassica* var. *longicornuta* is a taxonomic junior synonym of *Gonyaulacysta dualis.* We consider that the specimen illustrated as *Gonyaulacysta dualis* by Burger (1996, pl. 6W) is a misidentification.

Comparison. The most similar species to *Gonyaulacysta dualis* is *Gonyaulacysta longicornis* (not to be confused with *Gonyaulacysta jurassica* subsp. *jurassica* var. *longicornuta*). However *Gonyaulacysta longicornis* is epicavate and has highly denticulate sutural crests (Fig. 2).

Dimensions. *Gonyaulacysta dualis* is a large species; the dimensions of the material from Alaska studied herein based on 30 specimens are: length of pericyst, 93 (109) 122; length of apical horn, 20 (28) 38; length of epipericyst, 53 (66) 75; length of hypopericyst, 22 (36) 49; length of endocyst, 62 (73) 91; width at cingulum, 55 (70) 80 (Supplementary material Appendix 3, table 9). This compares well with measurements of the type material by Brideaux and Fisher (1976, p. 19): length of pericyst, 93–135; length of apical horn, 20–33; length of endocyst, 63–100; length of protuberance on the endocyst, 3–9; width at cingulum, 40–83.

Geographical and stratigraphical distribution. *Gonyaulacysta dualis* is largely confined to the Oxfordian and Kimmeridgian (Late Jurassic) of the high palaeolatitudes of North America. The stratigraphical extent of the original material from Arctic Canada is upper Oxfordian to middle Kimmeridgian (Brideaux and Fisher 1976, p. 19–20, fig. 13). These authors stated that the species is sporadic in the upper Kimmeridgian. Riding and Lucas-Clark (2016, pl. 2, 2; pl. 16, 4–6) figured specimens of *Gonyaulacysta dualis* from the Oxfordian of southwestern Alaska. This species was also recorded from the upper Oxfordian to upper Kimmeridgian, and the Oxfordian to middle Kimmeridgian of the Sverdrup Basin, Arctic Canada by Tan and Hills (1978) and Davies (1983) respectively. It was also recorded by Sarjeant (1982) from the lower to middle Kimmeridgian of northern Canada.

Brideaux and Fisher (1976, p. 19) stated that some specimens of *Gonyualacysta longicornis* from Europe closely resemble *Gonyaulacysta dualis.* However, in our view, the specimens figured by Klement (1960, pl. 2, 6–8), Sarjeant (1962, pl.1, 3) and Gitmez (1970, pl. 5, 11) have prominent denticulate sutural crests and are epicavate, and hence do not belong to *Gonyaulacysta dualis.* Likewise, we believe that the specimens of *Gonyaulacysta dualis* figured by Brenner (1988, pl. 8, 2, 5), with their high, denticulate sutural crests, relatively short apical horns, and lack of apical protuberances on the endocyst, belong to *Gonyaulacysta jurassica*. Riding et al. (1999, pl. RP8, 5; pl. RP9, 2, 3, 6) figured specimens assigned to *Gonyaulacysta dualis* from the middle and upper Oxfordian of the Russian Platform. However, these specimens are epicavate, lack a well-developed apical protuberance on the endocyst, and the specimens on plate RP9 lack obvious tabulation in the equatorial area; hence they do not belong to *Gonyaulacysta dualis*. The only positive identification of *Gonyaulacysta dualis* from Europe is a specimen illustrated from the lowermost Kimmeridgian of Denmark by Poulsen (1996, pl. 4, 1).

Cookson and Eisenack (1982, p. 37–38) described *Psaligonyaulax australica* from the upper part of the Dingo Claystone of the Carnarvon Basin of Western Australia (Oxfordian to lower Kimmeridgian). Brenner (1988, p. 54) stated that *Psaligonyaulax australica* is a junior synonym of *Gonyaulacysta dualis.* The holotype of *Psaligonyaulax australica* is large, elongate, and has largely smooth sutural ridges, and so is somewhat similar in morphology to *Gonyaulacysta dualis* and has a similar stratigraphical range. However, the apical horn of *Psaligonyaulax australica* is smaller than is normal for *Gonyaulacysta dualis,* and the former has a semicircular hypocyst. Thus, we do not follow the synonymy proposed by Brenner (1988). *Psaligonyaulax australica* is herein transferred to *Gonyaulacysta* (see above).

(Plate VIII near here)

Gonyaulacysta fenestrata Riding and Helby, 2001a, emend. nov.

Fig. 2G; Plate IX, 1–5

Selected synonymy list:

1980 *Gonyaulacysta jurassica* (Deflandre, 1938); Wiseman, pl. 2, 49.

1986 *Gonyaulacysta jurassica* (Deflandre, 1938); subsp. *jurassica* var. *quadrata* Kumar: pl. 1, 6; pl. 3, 1; fig. 4.

1987 *Gonyaulacysta jurassica* (Deflandre, 1938); Stevens, fig. 5K.

2001a *Gonyaulacysta fenestrata* Riding and Helby: p. 150, figs 7A–F.

Original description. 'A large, elongate species of *Gonyaulacysta* with a long, distally-blunt, slender apical horn. The cyst is primarily dorsoventrally flattened. The pericyst, excluding the apical horn, is elongate subellipsoidal to subpolygonal and is antapically truncate. The endocyst is elongate ellipsoidal, normally with a prominent apical protuberance. Bicavate cyst organisation; the epicyst may be epicavate or cornucavate. Paratabulation partially indicated by parasutural crests which are generally smooth distally and fenestrate. The fenestrae are subcircular, ellipsoidal or rectangular; normally they are best developed in the midlateral and antapical areas and inserted close to the distal margin of the crest. Occasionally, the parasutural crests may be distally irregular or undulose. Parasutural features are generally entirely lacking, or profoundly reduced, midventrally in the parasulcal area and the middorsal hypocystal area. A prominent subcircular claustrum is present in the antapical parasulcal paraplate. Periphragm is smooth to microscabrate and may be irregularly microreticulate. The endophragm is markedly thicker than the periphragm and smooth. The perioperculum is absent; the large endoperculum is frequently displaced and visible. Both the periarchaeopyle and the endoarchaeopyle is occasionally slightly enlarged posteriorly, at the 3''/3c-4c paraplate boundary.' (from Riding and Helby, 2001a, p. 150).

Emended diagnosis. A large, elongate, bicavate or delphicavate species of *Gonyaulacysta* with a prominent apical horn formed of periphragm and with or without an apical protuberance on the endocyst. The sutures are marked by distally smooth crests or ridges; the crests are fenestrate, and are best developed in the mid-lateral and antapical areas. The opisthopyle is normally prominent, and can be somewhat variable in shape.

Holotype. Riding and Helby (2001a, fig. 5D).

Comments. Kumar (1986, p. 386–388) established *Gonyaulacysta jurassica* subsp. *jurassica* var. *quadrata* and provided the following diagnosis: 'A delphicavate variety of *G. jurassica* subsp. *jurassica* Sarjeant (1982) whose hypopericoel has a broad, rounded quadrangular opisthopyle with either concave or straight basal margins'. Only two specimens were illustrated, and the photomicrographs do not clearly demonstrate the key feature of this species: the small fenestrae on the sutural crests. Kumar (1986, fig. 4) focussed on the somewhat quadrangular outline of the opisthopyle in his description. With careful observation, small fenestrae are clearly visible on the precingular sutural crests of a paratype (Kumar, 1986, pl. 3, 1). Subsequently, Riding and Helby (2001a) described and comprehensively illustrated *Gonyaulacysta fenestrata* from the Kimmeridgian to Tithonian of the Northwest Shelf of Australia. The most diagnostic feature of the latter species is fenestrate sutural crests. These authors were unaware of the fenestrate sutural crests in *Gonyaulacysta jurassica* subsp. *jurassica* var. *quadrata* of Kumar (1986).

Given that both *Gonyaulacysta jurassica* subsp. *jurassica* var. *quadrata* and *Gonyaulacysta fenestrata* are identical in age, geographical extent (eastern Gondwana), morphology and size, they are synonymized herein, with *Gonyaulacysta fenestrata* being the senior name at specific rank. In our emended diagnosis for *Gonyaulacysta fenestrata* above, we clarify that the species is bicavate or delphicavate (Sarjeant, 1982, figs 4c, f). Riding and Helby (2001a) stated that the cyst organisation is bicavate, and that the epicyst may be epicavate or cornucavate. This is clearly incorrect because a dinoflagellate cyst cannot be both bicavate and epicavate.

Comparison. The species which is most similar to *Gonyaulacysta fenestrata* is *Gonyaulacysta dualis.* However, the former species is the only one in the genus which exhibits fenestrate sutural crests (Fig. 2G).

Dimensions. Based on 35 specimens measured by Riding and Helby (2001a, p. 150), the dimensions of *Gonyaulacysta fenestrata* are: length of pericyst, 113 (133) 158; length of apical horn, 14 (24) 31; length of epipericyst (excluding cingulum), 69 (82) 100; length (height) of cingulum, 3 (5) 8; length of hypopericyst (excluding cingulum), 34 (45) 55; length of endocyst, 71 (86) 103; width of pericyst at cingulum, 55 (70) 86; width of endocyst at cingulum, 48 (62) 79; height of sutural crests, 1 (3) 7; diameter of fenestrae, 1 (1.5) 3. These dimensions are similar to those measured on ten specimens by Kumar (1986, p. 388), i.e. length of pericyst, 113–137; width at cingulum, 55–77; length of apical horn, 22–30; length of archaeopyle, 38.5–49.5; width of archaeopyle, 20–30; maximum diameter of opisthopyle, 33–38.5.

Geographical and stratigraphical distribution. *Gonyaulacysta fenestrata* has been reported only from eastern Gondwana; there are no reports from the Northern Hemisphere. In the Timor Sea region of Australia, *Gonyaulacysta fenestrata* ranges from the middle Kimmeridgian (*Dingodinium swanense* Interval Zone) to the early Tithonian (*Cribroperidinium perforans* Oppel Zone) according to Helby et al. (1987), Riding and Helby (2001a, p. 153) and Riding et al. (2010, fig. 12). The report from the Berriasian of Australia by Stevens (1987) is assumed to represent reworking. In the Indian subcontinent, *Gonyaulacysta fenestrata* apparently has an identical stratigraphical range to the specimens from the Timor Sea (Beju, 1979, 1980; Kumar, 1986; Riding and Helby 2001a).

Gonyaulacysta sp. cf. *G. fenestrata* Riding and Helby, 2001a, emend. nov.

Plate IX, 6

Comments. This form is virtually morphologically identical to *Gonyaulacysta fenestrata,* however the distal extremities of the sutural crests are entirely or partially surmounted by short (*c.* 1 μm) denticles. The two entities are also similar in size and stratigraphical range. Riding and Helby (2001a) did not find sufficient specimens in order to formalise *Gonyaulacysta* sp. cf. *G. fenestrata* as a new taxon.

(Plate IX near here)

Gonyaulacysta longicornis (Deflandre, 1938) stat. nov., emend. nov.

Fig. 2H; Plate X, 1–9; Plate XI, 1–9

Selected synonymy list (a more comprehensive synonymy list was given by Sarjeant, 1982, p. 31):

1938 *Gonyaulax jurassica* var. *longicornis* Deflandre: p. 171, pl. 6, 6.

1965 *Gonyaulacysta jurassica* var. *longicornis* Deflandre; Downie and Sarjeant: p. 115.

1973 *Gonyaulacysta jurassica* var. *brevis* Johnson and Hills: p. 206, pl. 1, 10, 14.

1973 *Gonyaulacysta jurassica* subsp. *longicornis* Deflandre; Lentin and Williams: p. 62.

1982 *Gonyaulacysta jurassica* subsp. *adecta* var. *longicornis* Deflandre; Sarjeant: p. 31.

Original description. 'This variety differs from the type only in its general form, the tabulation remaining the same as far as I have been able to ascertain. The epitheca has an elongated conical shape and extends into a long horn, nearly twice as long as the type. This elongation is mainly due to the development of the apical plates, but the preequatorial plates also appear to take part in the more slender look of the epitheca. The sutural crests, in the few individuals observed, and especially in that drawn as type, are less developed and less thorny, especially compared to the highly convex specimen of *G. jurassica*. The type of the *longicornis* variety is 88 μm long, 54 μm wide and the horn reaches 30 μm.' **(**Deflandre, 1938, p. 171, translated by the present authors).

Emended diagnosis. A large, usually elongate, epicavate species of *Gonyaulacysta* with a very prominent apical horn (*c*. 30% of the entire cyst length) formed of periphragm. The tabulation is reflected by denticulate sutural crests and ridges.

Emended description. A large species of *Gonyaulacysta* which is normally markedly elongate. The cyst is epicavate, and has a distinctly angular, three-sided hypocyst. The epipericoel is large, and the precingular and postcingular plate boundaries may exhibit suturocavation. This species has a very long, slender, distally truncate apical horn composed only of periphragm. The apical horn length comprises about 30% of the overall length of the entire cyst. The endocyst normally exhibits a small, rounded apical protuberance. The tabulation is complete, and is reflected by sutural crests and ridges that are distally denticulate. The cingulum and the sutures surrounding the 1'''' plate may have evident gonal spines (up to *c*. 5 µm). The opisthopyle is not observable because the endophragm and periphragm are in contact in the antapical region. The periphragm is generally smooth, but occasionally may bear low-relief ornamentation such as scabrae. The endophragm is thicker than the periphragm and consistently smooth. The periarchaeopyle is large, and may extend substantially above the top of the endocyst.

Holotype. Specimen AM 60 of Deflandre (1938, pl. 6, 6). Sample from the lower Oxfordian Marnes de Villers Formation (*Quenstedtoceras mariae* ammonite zone), Villers sur Mer, Calvados, northern France. Curated in the Institut de Paléontologie, Musée Nationale d'Historie Naturelle, Paris, France.

Comments. *Gonyaulacysta longicornis* was originally described from the lowermost Oxfordian of northern France by Deflandre (1938) as a variety of *Gonyaulax jurassica* in order to accommodate specimens with long apical horns. This taxon was transferred to *Gonyaulacysta* as a variety of *Gonyaulacysta jurassica* by Downie and Sarjeant (1965, p. 115), then elevated to subspecies level by Lentin and Williams (1973, p. 62). Sarjeant (1982, p. 31) re-assigned this taxon as a variety of *Gonyaulacysta jurassica* subspecies *adecta*. He deemed *Gonyaulacysta jurassica* var. *brevis* (Johnson and Hills, 1973) to be a taxonomic junior synonym of *longicornis*. Riding (2005b) and Riding et al. (2010) used the terms ‘elongate morphotype’ and ‘large morphotype’ respectively as suffixes following *Gonyaulacysta jurassica* subsp. *adecta* var. *longicornis* simply to emphasize the unusually elongate ambitus of this taxon. In our view, this taxon fully justifies species status. It has an extremely distinctive morphology and a restricted stratigraphical range (see below). Our present emendation emphasizes that *Gonyaulacysta longicornis* is large, epicavate and has a very long, slender, distally blunt apical horn.

Comparison. The species most similar to *Gonyaulacysta longicornis* are *Gonyaulacysta ceratophora* and *Gonyaulacysta dualis.* However, these species are bicavate and typically exhibit low sutural ornamentation. Tabulation in *Gonyaulacysta ceratophora* is absent except in the polar areas and the sutures in *Gonyaulacysta dualis* are typically distally smooth. In overall morphology, *Gonyaulacysta longicornis* also resembles *Gonyaulacysta adecta,* but the latter species is significantly smaller, has a relatively short apical horn, and is less elongate (Fig. 2B).

Dimensions. Based on 30 specimens measured herein, the dimensions of *Gonyaulacysta longicornis* are as follows: length of pericyst, 73 (91) 118; length of apical horn, 20 (25) 33; length of epipericyst, 40 (64) 78; length of hypopericyst, 13 (22) 29; length of endocyst, 47 (57) 73; width at cingulum, 44 (57) 84 (Supplementary material Appendix 3, table 10). This is consistent with the measurements of the type material by Deflandre (1938, p. 171): length of pericyst, 88; length of apical horn, 30; width at cingulum, 54.

Geographical and stratigraphical distribution. *Gonyaulacysta longicornis* has only been reported from Laurasia. It has been recorded from England, Greenland, Norway, Russia, Scotland and Svalbard. Records with ammonite control indicate that this species is a reliable marker for the late Callovian (*Peltoceras athleta* ammonite zone) to the middle Oxfordian (*Cardioceras tenuiserratum* ammonite zone) interval. It is usually sporadic and relatively rare in the late Callovian, but is consistently common in the early and middle Oxfordian (Riding and Thomas, 1997, figs 2, 3; Riding et al., 1999, fig. 25; Riding, 2005b, figs 3, 4; Ilyina et al. 2005, figs 3, 7). The records of *Gonyaulacysta longicornis* in the latest Bathonian and early Callovian of eastern England by Riding (1987, fig. 4) are misidentifications of *Gonyaulacysta adecta.*

Smelror and Below (1992, fig. 3) recorded *Gonyaulacysta longicornis* from the upper Callovian and lower Oxfordian of the Barents Sea. This species has also been observed in the upper Callovian and Oxfordian of Arctic Russia, Greenland, Arctic Norway and Svalbard by, for example, Bjærke (1977), Thusu (1978), Lund and Pedersen (1985), Smelror (1986; 1988a; 1988b) and Århus et al. (1989). In view of the many reports of *Gonyaulacysta longicornis* from the high northerly latitudes, this species was probably a coldwater form (Riding and Michoux, 2013).

(Plates X and XI, and Table 2 near here)

3. Reassignment of species not considered attributable to *Gonyaulacysta*

According to the current Lentin and Williams Index of dinoflagellate cysts (Fensome et al., 2019, p. 357–376), 151 species, some of which have infraspecific taxa, have historically been placed in *Gonyaulacysta.* Of these species, 126 have been reassigned to more appropriate genera, some questionably (Appendix 4 of the Supplementary material). Hence, Fensome et al. (2019) listed 25 valid species of this genus; of these 15 were accepted as being legitimate, and 10 were deemed questionable. As described herein, *Gonyaulacysta* has an extremely characteristic morphology, and we only recognize eight species (section 2). This has meant that 11 further species need to be transferred from *Gonyaulacysta* into more suitable genera, and these recombinations are effected below.

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

Suborder GONYAULACINEAE (autonym)

Family GONYAULACACEAE Lindemann, 1928

Subfamily GONYAULACOIDEAE (autonym)

Genus ***Tubotuberella*** Vozzhennikova, 1967

Type. *Tubotuberella rhombiformis* Vozzhennikova, 1967

Comments. *Tubotuberella* differs from *Gonyaulacysta* in having an equatorial cingulum and an opisthopyle on plate 1'''' rather than on the ps plate.

Tubotuberella dentata Raynaud, 1978

Comments. The transfer of this highly distinctive species to *Gonyaulacysta* by Riding (2012) is not supported herein. The species is maintained in *Tubotuberella* because it has an equatorial cingulum and an opisthopyle which penetrates the 1’’’’ plate.

Tubotuberella eisenackii (Deflandre, 1938) Stover and Evitt, 1978

Fig. 7

Comments. The species *Gonyaulax eisenackii* Deflandre, 1938 was transferred to *Gonyaulacysta* by Górka (1965). This combination is inappropriate because this species has a small apical horn, an opisthopyle in the 1’’’’ plate and an equatorial cingulum (Fig. 7). The transfer to *Tubotuberella* by Stover and Evitt (1978, p. 197) is followed herein.

Genus ***Wrevittia*** Helenes and Lucas-Clark, 1997

Type. *Wrevittia helicoidea* (Cookson and Eisenack, 1960) Helenes and Lucas-Clark, 1997.

Comments. *Wrevittia* differs from *Gonyaulacysta* in having consistent S-type ventral tabulation, an equatorial cingulum and in displaying suturocavation in the hypocyst (Helenes and Lucas-Clark, 1997, p. 186).

Wrevittia axicerastes (Sarjeant, 1966) comb. nov.

Basionym. *Gonyaulacysta axicerastes* Sarjeant, 1966, p. 114–116; pl. 13, 11–12; fig. 25.

Comments. *Gonyaulacysta axicerastes* was described from the Lower Cretaceous (Barremian) of northern England by Sarjeant (1966). It clearly lacks the diagnostic features of *Gonyaulacysta* as redefined herein. The most appropriate genus is *Wrevittia*, on gross morphological grounds. For example, the venter is of S-type with a subtriangular 6’’ plate, the large plates on the hypocyst are suturocavate and it is apically cornucavate.

Wrevittia? *polythyris* (Davey, 1979) comb. nov.

Basionym. *Gonyaulacysta polythyris* Davey, 1979, p. 556; pl. 3, 1–3.

Comments. The species originally described as *Gonyaulacysta polythyris* by Davey (1979) has an equatorial cingulum and is clearly more appropriately placed in *Wrevittia*. However, the hypocyst may not be suturocavate, so it is questionably assigned to *Wrevittia.*

Wrevittia? *teichos* (Davey, 1974) comb. nov.

Basionym. *Gonyaulacysta teichos* Davey, 1974, p. 53–54; pl. 4, 5.

Comments. Davey (1974) described *Gonyaulacysta teichos.* On the basis of its overall morphology it is more appropriately placed in *Wrevittia.* However, this assignation is questionable as it is not clear whether the hypocyst exhibits suturocavation.

Subfamily LEPTODINIOIDEAE Fensome et al., 1993

Genus ***Endoscrinium*** (Klement, 1960) Vozzhennikova, 1967

Type. *Endoscrinium galeritum* (Deflandre, 1938) Vozzhennikova, 1967.

Comments. *Endoscrinium* differs from *Gonyaulacysta* in being circumcavate rather than bicavate or epicavate.

Endoscrinium? *centriconnatum* (Riding, 1983) comb. nov.

Basionym. *Gonyaulacysta centriconnata* Riding, 1983, p. 197–202; pl. 1, 1–3.

Comments. *Gonyaulacysta centriconnata* is a Middle–Late Jurassic (Callovian–Oxfordian) species which is prominently suturocavate (Riding, 1983). It does not exhibit the key diagnostic features of *Gonyaulacysta* and is hence transferred to the cavate genus *Endoscrinium*, albeit questionably because it is suturocavate rather than circumcavate.

Genus ***Rhynchodiniopsis*** Deflandre, 1935

Type. *Rhynchodiniopsis aptiana* (Deflandre, 1935) Sarjeant, 1982

Comments. *Rhynchodiniopsis* differs from *Gonyaulacysta* in having an equatorial cingulum and in being usually acavate, sometimes cornucavate.

Rhynchodiniopsis pectinigera (Gocht, 1970) comb. nov.

Basionym. *Leptodinium subtile* subsp. *pectinigerum* Gocht, 1970, p. 138–139; pl. 33, 1.

Comments. *Leptodinium subtile* subsp. *pectinigerum* was transferred to *Gonyaulacysta* by Fensome (1979), and elevated to species status. This species is acavate to slightly cornucavate, and has an equatorial cingulum. Therefore it is herein transferred to *Rhynchodiniopsis.*

Rhynchodiniopsis? *vesicula* (Dodekova, 1994) comb. nov.

Basionym. *Gonyaulacysta vesicula* Dodekova, 1994, p. 38–39; pl. 10, 15–16.

Comments. *Gonyaulacysta vesicula* does not belong in *Gonyaulacysta* becasue the former displays an equatorial cingulum. It most closely resembles *Rhynchodiniopsis*, to which it is transferred here, albeit questionably because it appears to be cornucavate to weakly epicavate.

Order PERIDINIALES Haeckel, 1894

Suborder PERIDINIINEAE (autonym)

Family PERIDINIACEAE Ehrenberg, 1831

Subfamily PALAEOPERIDINIOIDEAE (Vozzhennikova, 1961) Bujak and Davies, 1983

Genus ***Diconodinium*** Eisenack and Cookson, 1960

Type. *Diconodinium multispinum* (Deflandre and Cookson, 1955) Eisenack and Cookson, 1960

Diconodinium? *piriformum* (Conrad, 1941) comb. nov.

Basionym. *Gonyaulacysta piriformis* Conrad, 1941, p. 9; pl. 1, G ex Sarjeant, 1967, p. 255.

Comments. This latest Cretaceous species was initially named as *Palaeoperidinium piriforme* by Conrad (1941). However, this name was not validly published by the latter author because the genus *Palaeoperidinium* was not validly erected by Deflandre (1934), see Fensome et al. (2019, p. 373; 626). Sarjeant (1967, p. 255) questionably placed this taxon in *Gonyaulacysta*. However, it is clear from the type material that this species does not belong in either *Gonyaulacysta* or *Palaeoperidinium*. The single specimen illustrated is acavate and is densely covered by short denticles or spines. Plate sutures are visible, but the configuration is not immediately recognizable. It is possible that the specimen is in apical or ventral view. Consequently the most appropriate genus is not clear. Because of its vague biconical/rounded subquadrangular outline, cover of dense short spines and plate sutures it is questionably attributed to *Diconodinium*. We concur with the contention of Jan du Chêne et al. (1986, p. 132), who recommended that this name be restricted to the type.

Genus ***Subtilisphaera*** Jain and Millepied, 1973

Type. *Subtilisphaera senegalensis* Jain and Millepied, 1973

Subtilisphaera? *tianjianensis* (Liu Zhili and Zheng Yuefang in Liu Zhili et al., 1992) comb. nov.

Basionym. *Gonyaulacysta tianjianense* Liu Zhili and Zheng Yuefang in Liu Zhili et al., 1992, p. 68–69, pl. 1, 1–2.

Comments. Liu Zhili and Zheng Yuefang in Liu Zhili et al. (1992) established *Gonyaulacysta tianjianense* from the Paleogene of the Xialiaohe Basin, Liaoning Province, northeast China. This species is a relatively small, biconical form with a prominent cingulum, otherwise vague tabulation and low-relief, nontabular ornamentation of granules and/or verrucae. The holotype is apparently bicavate and the archaeopyle style is not clear. Due to the cavate cyst organisation and the lack of a clear archaeopyle, this species is questionable assigned to the peridiniacean genus *Subtilisphaera*.

Family PROTOPERIDINIACEAE Balech 1988 nom cons

Subfamily PROTOPERIDINIODEAE (autonym)

Genus ***Lejeunecysta*** Artzner and Dörhöfer, 1978

Type. *Lejeunecysta hyalina* (Gerlach, 1961) Artzner and Dörhöfer, 1978

Lejeunecysta? *diamanta* (Churchill and Sarjeant, 1962) comb. nov.

Basionym. *Peridinium*? *diamantum* Churchill and Sarjeant, 1962, p. 34–36; pl. 1, 19; fig. 3.

Comments. The species originally described as *Peridinium*? *diamantum* by Churchill and Sarjeant (1962, p. 34–36) was transferred to *Gonyaulacysta* by Lentin and Williams (1976, p. 76). It is clear that this species is peridinialean, for example the archaeopyle is clearly of anterior intercalary type. However, we questionably place the species into *Lejeunecysta* because it does not apparently have two antapical horns.

4. The variability of the ventral tabulation of *Gonyaulacysta* and related taxa

4.1 Gonyaulacacean tabulation

In his groundbreaking book on dinoflagellate cyst morphology, Evitt (1985, p. 89–117) eloquently described, in typically forensic detail, the relatively conservative tabulation patterns of the gonyaulacacean dinoflagellates and their cysts. This incorporated a new so-called Taylorian tabulation scheme for designating plates derived from a hypothetical precursor form (or model) that aimed at a more effective and consistent recognition of plate homologies in gonyaulacalean taxa than the traditional Kofoidian scheme. The basic Kofoidian tabulation pattern for the gonyaulacaceans is 0–2pr, 4', 0–2a, 6'', 6c, 6''', 1p, 1'''', 5s (Evitt, 1985, fig. 5.8). Note that the numbers of the preapical and anterior intercalary plates are variable. Evitt (1985, p. 97) stated that some relatively minor variations in gonyaulacacean tabulation occur at the apex, the right half of the epitheca/epicyst and the sulcal region.

With regard to the sulcal region, Evitt (1985, p. 97–102; figs 3.1C, 5.8A–B) described two distinct styles of ventral tabulation in gonyaulacacean cysts. These styles he termed L-type or longitudinal and S-type or sigmoidal, the initials also conveniently being the first letters of the names of two prominent genera bearing each of the styles—*Leptodinium* and *Spiniferites* respectively (Fig. 8; Fensome et al., 1996a, fig. 39). Gonyaulacacean dinoflagellate cysts with an L-type sulcus have a broadly longitudinal mid-ventral area with moderately offset extremities of the laevorotatory cingulum. By contrast, forms with an S-type sulcus display a laevorotatory cingulum whose proximal (right) end commonly markedly overhangs its distal (left) end, giving the ventral sulcal area a characteristic sigmoidal shape. Helenes and Lucas-Clark (1997, fig. 1) described two styles of S-type sulcus based on the genera *Stanfordella* and *Wrevittia*. The differences between these three configurations, and six important variations in tabulation, are documented in Table 3. The differerences in plate configurations are centred around the top right of the sulcus and the apex, and they largely involve the 1'–4', 5'', 6'' and as plates. Specifically the two ventral styles are produced by different configurations (i.e. the proximity and switching) of key plate triple junctions such as 4'/5''/6'', 4'/6''/1' and 6''/1'/as. The tabulation, or its visibility, within the sulcal area is frequently strongly suppressed in S-type venters (Figs 7, 8).

The overall tabulation pattern of *Gonyaulacysta* is, unsurprisingly, classically gonyaulacacean (Figs 1, 2). In terms of the nomenclature of Evitt (1985) and Fensome et al. (1993), it involves a sexiform gonyaulacacean antapical style with neutral torsion of the hypocyst. *Gonyaulacysta* was informally classified in the *Leptodinium* complex of Gs-cysts (Evitt, 1985, p. 222–223). However, the tabulation of the mid-ventral area of certain forms of *Gonyaulacysta* is somewhat variable and includes both L-type and S-type aspects.

Observations in the present study and those by Helenes and Lucas-Clark (1997, p. 176; figs 2, 3), clearly demonstrates that most specimens of *Gonyaulacysta* have an L-type sulcus using the criteria outlined in Table 3. We disagree with Evitt (1985, fig. 10.9B), the caption of which indicated that *Gonyaulacysta jurassica* has an S-type organisation; and similarly with Fensome et al. (1993, p. 91), who placed *Gonyaulacysta* in the subfamily Gonyaulacoideae, which is characterized by an S-type sulcus.

Nevertheless, the sulcuses in some specimens of *Gonyaulacysta adecta* are somewhat sigmoidal, despite their tabulation being demonstrably L-type (e.g. Plate III, 2; Plate IV, 2). Also, extremely rare specimens of *Gonyaulacysta* appear to exhibit S-type mid-ventral regions. For example, a specimen of *Gonyaulacysta* sp. cf. *G. adecta* figured here apparently exhibits an S-type venter (Plate III, 9). Consequently the emendation of *Gonyaulacysta* herein allows for both ventral morphologies.

Aside from *Gonyaulacysta*, several examples of gonyaulacacean dinoflagellate cysts exist that are inconsistent with the subfamily always having an L-type sulcus. The best example is perhaps the mainly Jurassic gonyaulacacean genus *Tubotuberella*. The species *Tubotuberella eisenackii* clearly has an S-type venter (Fig. 7; Deflandre, 1938, fig. 3; Sarjeant, 1982, fig. 4; Riding and Michoux, 2013, pl. 1, 7). However, most other species of *Tubotuberella* exhibit L-type sulcuses (Jan du Chene et al., 1986, pl. 123). For example, *Tubotuberella dangeardii* and *Tubotuberella dentata* have longitudinal venters (Sarjeant, 1968, fig. 3; Sarjeant, 1982, fig. 5; Riding and Michoux, 2013, fig. 2A).

Another example of this situation is the species *Rhynchodiniopsis pectinigera*. The holotype clearly has an L-type sulcus (Gocht, 1970, fig. 11; pl. 33, 1). However, subsequent records of specimens assigned to *Rhynchodiniopsis pectinigera* unequivocally exhibit sigmoidal venters, assuming they have been correctly identified. These include, for example, Fensome (1979, fig. 15A, pl. 6, 2 and 4), Helenes (1986, pl. 4, 10) and Helenes and Lucas-Clark (1997, pl. 1, 6). This has implications for the identification of this species. For example, practitioners may be understandably reluctant to assign a specimen to *Rhynchodiniopsis pectinigera* if the ventral tabulation is obviously S-type because this does not conform to the holotype. In addition, tracking these variations would be worthwhile because they may have stratigraphical significance.

(Figs 7 and 8, and Table 3 near here)

4.2. Implications for evolution and taxonomy

Observations on the tabulation of *Gonyaulacysta* and its variation merit some reflection of how dinoflagellates, with a focus on fossil cysts, are classified. Variation in the details of gonyaulacacean tabulation are generally agreed to be taxon-specific, for example L-type ventral configurations essentially defining the subfamily Leptodinioideae and S-type configurations denoting the subfamily Gonyaulacoideae. However, while there needs to be consistency in how we subdivide taxa, notably with agreement on the hierarchy of features to be used at different taxonomic levels, it is also critical that some flexibility be permitted, in the spirit of both understanding and interpreting evolution and recognising the subjective nature of taxonomy. For example, dinophysioid and gonyaulacoid–peridinioid tabulation types were recognized by Fensome et al. (1993) as fundamentally different entities, represented by separate groups of extant dinoflagellates (subclasses Dinophysiphycidae and Peridiniphycidae respectively) clearly distinguished today on morphological and molecular phylogenetic grounds. However, the tabulation of the exclusively Jurassic fossil genus *Nannoceratopsis* uniquely combines features of both the dinophysioid and gonyaulacoid-peridinioid tabulation types (Piel and Evitt, 1980). It has been generally assumed that *Nannoceratopsis* represents the common ancestor of dinoflagellates bearing the other two tabulation types, and fossil and other evidence generally support this (Fensome et al. 1996b). Also in the Jurassic, Riding et al. (1985) and Wiggan et al. (2017, 2018) demonstrated that, during the early evolution of the family Gonyaulacaceae in the early Middle Jurassic (Aalenian–Bathonian), many forms experimented with multiplate precingular and epicystal archaeopyles, before stabilisation to either single plate precingular or apical excystment apertures from the Callovian onwards. A third example involves the peridiniacean archaeopyles. By the Late Cretaceous and into the Paleogene, by far the two most common peridiniacean archaeopyle types among organic walled dinoflagellate cysts involved a single mid-dorsal anterior intercalary plate (e.g. *Chatangiella*, *Deflandrea*) or the loss of the entire anterior dorsal surface of the cysts as a single operculum (e.g. *Palaeoperidinium*). However, in the Early and middle Cretaceous, a plethora of genera have been defined based on different combinations of plates involved in archaeopyle formation (e.g. *Chichaoudinium*, *Luxadinium*; see Bujak and Davies, 1983). These three examples illustrate how, in the early evolution of a group, some degree of morphological experimentation led to later more stable morphological traits. It is perhaps in this light that the variation in the tabulation of *Gonyaulacysta* can be best viewed.

The earliest gonyaulacaceans had L-type ventral configurations, and this style was dominant over the S-type until the middle Cretaceous. Subsequent to this, the S-type arrangement gradually became predominant. Among Neogene and modern dinoflagellates, taxa with an L-type venter are not diverse and mostly belong to the Criroperidinioideae rather than the Leptodinioideae (i.e. they exhibit dextral hypocystal torsion). Perhaps what we are observing in *Gonyaulacysta* and its related contemporaries is experimentation with different ventral tabulation styles, which eventually led to the separation of distinct clades distinguished by these two different configurations. Clearly the strikingly distinctive morphology of *Gonyaulacysta*, with much larger epicyst than hypocyst and otherwise consistent tabulation traits, indicates that the genus is a biologically coherent entity; it would make no sense to split it according to S-type and L-type forms.

5. The biostratigraphy of *Gonyaulacysta*

5.1. Overview

Globally, the ranges of the eight species of *Gonyaulacysta* span the Bathonian to Tithonian interval across two broad phytogeoprovinces (Figs 3, 9; Table 1). The earliest species of the genus are *Gonyaulacysta adecta* and *Gonyaulacysta jurassica* in Laurasia and western Gondwana, and in eastern Gondwana respectively and the species spectrum changed markedly close to the Callovian–Oxfordian transition worldwide. Consequently

Gonyaulacysta is most diverse and prominent in the Oxfordian, and during this stage there are several key bioevents globally. *Gonyaulacysta* apparently became extinct at the Kimmeridgian–Tithonian transition in Laurasia and western Gondwana, but *Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* persisted into the Tithonian in eastern Gondwana (Fig. 3; Table 1). This pattern of Jurassic dinoflagellate cyst genera having younger apparent extinctions in eastern Gondwana than in Laurasia and western Gondwana is a familiar one. Both *Endoscrinium* and *Wanaea* also exhibit this phenomenon (Riding and Helby, 2001b, fig. 12; Riding and Fensome, 2002, fig. 2).

Gonyaulacysta jurassica is the only cosmopolitan species. Records of this taxon are present from the Bathonian to Kimmeridgian, with the most abundant, age-constrained and consistent occurrences being in the Oxfordian and Kimmeridgian. It appears very likely that pre-Oxfordian records such as those by Davey (1988, fig. 6), Thusu et al. (1988, fig. 7) and Riding et al. (2010, fig. 12) represent misidentifications of *Gonyaulacysta adecta*. *Gonyaulacysta jurassica* has been reported from Africa, the Americas, the Arctic, Australasia, China, India, the Middle East and Russia (Johnson and Hills, 1973; Wilson, 1982, 1984; Habib and Drugg, 1987; Helby et al., 1987, 1988; Davey, 1988; Thusu et al., 1988; Conway, 1990; Jiang et al., 1992; Sun and He, 1992; Olmstead et al., 1996; Riding et al., 1999, 2010, 2011, 2017; Piasecki et al., 2004; He et al., 2005; Ilyina et al., 2005; Msaky, 2011; Hssaida et al., 2014, 2017). The reliable range of *Gonyaulacysta jurassica* appears to be broadly globally isochronous as Oxfordian to Kimmeridgian (Fig. 3). Sparse post-Kimmeridgian occurrences in Australasia were interpreted as representing reworking by Helby et al. (1987), Stevens (1987) and Davey (1988). Occasional post-Kimmeridgian records are known in Laurasia and western Gondwana: these are also probably allochthonous and include the range top of *Gonyaulacysta jurassica* in the early Tithonian (early Volgian) *Subdichotomoceras subcrassum* ammonite zone of western Siberia (Ilyina et al., 2005, fig. 9).

Gonyaulacysta dualis is the most geographically constrained species; it is confined to the Oxfordian and Kimmeridgian of the Boreal Realm (Fig. 3; Table 1).

5.2. Europe

This subsection is centred on Europe, within the Laurasia and western Gondwanan phytogeoprovince, because it is here that there are the most records with independent age control. *Gonyaulacysta adecta* is present rarely and sporadically throughout the Bathonian of Europe (Woollam, 1982; Woollam and Riding, 1983; Riding et al., 1985, 1999). The occurrences from the earliest Bathonian (*Zigzagiceras zigzag* ammonite zone) of southern England and southwestern Germany by Fenton et al. (1980, table 1) and Wiggan et al. (2017, table 2b) respectively represent the oldest records of the entire genus. However, the inception of consistent records of *Gonyaulacysta* was within the earliest Callovian. Four species, *Gonyaulacysta adecta, Gonyaulacysta desmos, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis,* represent a prominent element of earliest Callovian (*Macrocephalites herveyi* ammonite zone) through latest Kimmeridgian (*Aulacostephanus autissiodorensis* ammonite zone) dinoflagellate cyst associations throughout Europe and surrounding regions (Fig. 3; Raynaud, 1978; Prauss, 1989; Kunz, 1990; Feist-Burkhardt and Wille, 1992; Riding and Thomas, 1988, 1992, 1997; Poulsen, 1996; Huault, 1999; Riding et al., 1999; Poulsen and Riding, 2003; Riding, 2005b).

Gonyaulacysta longicornis is present, but not in significant proportions, throughout the late Callovian. However, it becomes markedly more common at the base of the Oxfordian and this highly distinctive species is an excellent marker for the early and middle Oxfordian. *Gonyaulacysta adecta* and *Gonyaulacysta longicornis* both have their range tops at the middle–late Oxfordian boundary (Fig. 3). *Gonyaulacysta desmos* is a relatively rare species and is confined to the early Oxfordian in Europe. It may be an intermediate form between *Gonyaulacysta adecta* and *Gonyaulacysta jurassica* (see Poulsen, 1991). The range base of the latter species is a superb index for the base of the Late Jurassic of Europe (e.g. Riding and Thomas, 1997, fig. 2).

5.3. Eastern Gondwana

In contrast to the cosmopolitan *Gonyaulacysta jurassica,* the species *Gonyaulacysta australica, Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* are present from the early Oxfordian to the early Tithonian of eastern Gondwana. Most records are from Australasia. We have reproduced herein the only available data on the range of *Gonyaulacysta australica*, which is Oxfordian and Kimmeridgian. This stratigraphical extent is very similar to that of *Gonyaulacysta ceratophora* (Fig. 3). The temporal span of *Gonyaulacysta fenestrata*, middle Kimmeridgian to early Tithonian, is substantially shorter and may indicate that this species was an evolutionary offshoot of *Gonyaulacysta australica* and/or *Gonyaulacysta ceratophora.*

6. The palaeobiology of *Gonyaulacysta*

The single cosmopolitan species *Gonyaulacysta jurassica*, which is the type, appears to be descended from *Gonyaulacysta adecta* in Laurasia and western Gondwana. *Gonyaulacysta jurassica* is prominent throughout the Oxfordian and Kimmeridgian of Laurasia and northwestern Gondwana (e.g. Thusu et al., 1988; Hssaida et al., 2014, 2017).

Apparently, it has a much older range base in eastern Gondwana, where the inception is middle Bathonian (Riding et al., 2010, fig. 12). In this case, it is eminently possible that *Gonyaulacysta adecta* is present in eastern Gondwana, but has not been differentiated from *Gonyaulacysta jurassica*. *Gonyaulacysta dualis* is essentially confined to the Oxfordian and Kimmeridgian of the Boreal Realm, specifically Alaska and Arctic Canada where it is a useful index species (Johnson and Hills, 1973; Davies, 1983). This species may have been descended from *Gonyaulacysta jurassica*.

In Laurasia, a possible evolutionary trajectory was that *Gonyaulacysta adecta* gave rise to *Gonyaulacysta desmos, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis* close to the Callovian–Oxfordian transition. *Gonyaulacysta jurassica* emerged abruptly during the earliest Oxfordian. It is possible that *Gonyaulacysta desmos* was a short-lived (early Oxfordian) and a rare evolutionary transitional form between *Gonyaulacysta adecta* and *Gonyaulacysta jurassica* (see Poulsen, 1991).

It has been established that the Jurassic dinoflagellate cyst floras of Laurasia and western Gondwana (i.e. Africa and South America), and eastern Gondwana (i.e. Antarctica, Australasia, India and Madagascar) exhibit significant differences (Fig. 9). There are substantial global similarities in dinoflagellate cyst genera during the Triassic and the early Middle Jurassic (e.g. Mantle and Riding 2012; Mantle et al., 2020). However, when assemblages diversified from the Callovian onwards, the numbers of endemic taxa significantly increased (Riding, 2002, 2003; Riding et al., 2010; Mantle and Riding, 2012). Hence, unsurprisingly, the most profound provincialism within *Gonyaulacysta* is between Laurasia and western Gondwana, and eastern Gondwana (Fig. 9). In Australia, the oldest species is *Gonyaulacysta jurassica,* which is apparently consistently present in the latest Bathonian to middle Oxfordian. In the early Oxfordian and middle Kimmeridgian, *Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* emerged (Riding and Helby, 2001a; Riding, 2005a). Thus, there appears to be an evolutionary trajectory from *Gonyaulacysta jurassica* to *Gonyaulacysta fenestrata* (middle Kimmeridgian–early Tithonian) via *Gonyaulacysta ceratophora* (early Oxfordian–early Tithonian). *Gonyaulacysta australica* was described from the Oxfordian–Kimmeridgian of Western Australia by Cookson and Eisenack (1982), and has never been recorded since.

The two principal Middle and Upper Jurassic geophytoprovinces based upon the geographical distribution of the species of *Gonyaulacysta* are illustrated in Fig. 9. The Laurasian and western Gondwanan province comprises *Gonyaulacysta adecta, Gonyaulacysta desmos, Gonyaulacysta dualis, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis* (Fig. 3). However, note that data from western Gondwana is relatively sparse and only *Gonyaulacysta adecta* has been recorded from this region. The inception of *Gonyaulacysta* in the high northerly latitudes (i.e. the Boreal Realm) is close to the Bathonian–Callovian transition according to Sarjeant (1972) and Davies (1983). The one species in this group which is confined to the Boreal Realm is *Gonyaulacysta dualis.* By contrast, in eastern Gondwana, four species have been recorded. These are *Gonyaulacysta australica, Gonyaulacysta ceratophora, Gonyaulacysta fenestrata* and *Gonyaulacysta jurassica* (Fig. 3). All of these except *Gonyaulacysta australica* are widespread throughout eastern Gondwana.

There are certain key trends observable in the fossil record of *Gonyaulacysta*. Firstly, the majority of the species (five) are bicavate, including all eastern Gondwanan species (Figs 2, 3; Table 1). *Gonyaulacysta adecta* and *Gonyaulacysta longicornis* are the only species that lack a hypopericoel and they are confined to the Bathonian–middle Oxfordian of Laurasia and western Gondwana. This means that no epicavate forms occur after the middle Oxfordian. *Gonyaulacysta desmos* is an intermediate form which has a partially developed hypopericoel.

The majority of species of *Gonyaulacysta,* and all the Laurasian forms, have sutural crests or ridges which are denticulate and/or echinate. Species with largely smooth and fenestrate sutural ridges are exclusively eastern Gondwanan (i.e. *Gonyaulacysta australica, Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata*) and Boreal (*Gonyaulacysta dualis*). The most noticeable morphological trend in *Gonyaulacysta* is overall size. The exclusively eastern Gondwanan and Boreal forms are large (>100 μm in length), whereas European species never exceed 100 μm in length. The oldest species in Laurasia, *Gonyaulacysta adecta*, is by far the smallest. However, the three species which have inceptions in the earliest Oxfordian (*Gonyaulacysta desmos, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis*) are overwhelmingly larger than *Gonyaulacysta adecta.* For example, *Gonyaulacysta longicornis* is on average 91 μm in length, which is 30% larger that early Callovian specimens of *Gonyaulacysta adecta* (Table 1).

(Fig. 9 near here)

7. Conclusions

Gonyaulacysta is one of the most distinctive genera in the entire dinoflagellate fossil record. It is a tabulate gonyaulacacean genus which is characterized by a prominent apical horn, variable cavation, a cingulum which is markedly offset antapically, an ovoidal endocyst and an opisthopyle in the posterior sulcal (ps) plate (Figs 1, 2, Table 1). Intruiguingly, *Gonyaulacysta* lacks a perioperculum (Eaton, 1984), and it includes individuals with both L-type and S-type ventral tabulation. Specimens with S-type sulcuses are, however, comparatively rare and tend to be among the earliest representatives of the genus. This phenomenon indicates that the tabulation style around the sulcus is not exclusively taxon specific, and that the individuals exhibiting S-type venters may represent morphological experimentation during the early evolutionary history of this genus. *Gonyaulacysta* and its relatives have been the subject of much morphological and taxonomic study. Many species have been erroneously attributed to *Gonyaulacysta*, and the present contribution provides a more coherent systematic treatment of the eight accepted species of this unique genus.

Gonyaulacysta is cosmopolitan and restricted to the Middle and Late Jurassic; it is sometimes abundant in the Callovian to Tithonian interval. *Gonyaulacysta jurassica*, the type, has a worldwide geographical range and is a reliable index for the Oxfordian–Kimmeridgian in Laurasia and western Gondwana. However, the remaining seven species exhibit provincialism, for example *Gonyaulacysta dualis* is confined to Oxfordian–Kimmeridgian of the Boreal Realm. Three species, *Gonyaulacysta adecta, Gonyaulacysta desmos* and *Gonyaulacysta longicornis,* are present in the Bathonian–Oxfordian of Laurasia and western Gondwana. *Gonyaulacysta australica, Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* are restricted to eastern Gondwana, and range from the Oxfordian to Tithonian. This Boreal/Laurasian and western Gondwanan/eastern Gondwanan provincialism is typical of Middle and Late Jurassic dinoflagellate cyst floras (Riding et al., 2010, 2011).

The earliest records of *Gonyaulacysta* are sporadic rare specimens of *Gonyaulacysta adecta* from the lowermost Bathonian of Europe. The genus is also rare in the Bathonian of Australia. *Gonyaulacysta* became significantly more consistent and prominent in the Callovian worldwide. In Laurasia and western Gondwana, *Gonyaulacysta adecta* is common throughout the Callovian, and there was a diversification around the Callovian–Oxfordian transition where *Gonyaulacysta desmos, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis* had their inceptions. *Gonyaulacysta desmos* is relatively rare and appears to be an intermediate form between *Gonyaulacysta adecta* and *Gonyaulacysta jurassica.* The distinctive large species *Gonyaulacysta longicornis* is confined to the late Callovian to middle Oxfordian of Laurasia and western Gondwana, and is especially characteristic of the early and middle Oxfordian. Throughout the Callovian of eastern Gondwana *Gonyaulacysta adecta* has not been reported, but is present in western Gondwana (Riding et al., 2011). In eastern Gondwana, the species composition of *Gonyaulacysta* is extremely distinctive. There appears to be a coherent evolutionary succession from *Gonyaulacysta jurassica* to *Gonyaulacysta fenestrata* via *Gonyaulacysta ceratophora* during the Oxfordian–Tithonian (Fig. 3).

Gonyaulacysta adecta and *Gonyaulacysta jurassica* exhibit coherent size trends throughout the majority of their respective stratigraphical ranges during the Bathonian–Kimmeridgian interval in Europe. The average sizes of these species increased relatively steadily throughout the Bathonian–Callovian and the Oxfordian–Kimmeridgian respectively. These phenomena do not coincide with palaeotemperature trends and may be the result of other palaeoenvironmental factors, or perhaps were genetically-driven.

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Fig. 1. Two schematic line drawings of *Gonyaulacysta jurassica* in ventral view (A) and dorsal view (B) illustrating the gross morphology and the tabulation. Note the small porichnion at the 2pr/1'/4' plate triple junction on the ventral side of the apical region, indicated by an open ovoid in A. The denticulate/echinate sutural crests have been omitted for clarity, and the plates are labelled using traditional Kofoidian nomenclature. Note the very large epicyst and the relatively small hypocyst. Adapted with permission from Riding (2005a, fig. 1).

Fig. 2. Schematic line drawings of ventral views of the eight species of *Gonyaulacysta* recognized herein in order to illustrate the key differences between them. Note that the apical horn, the extremely large epicyst, the ovoidal endocyst and the characteristic tabulation pattern are the principal characteristics of this genus. The denticulate/echinate sutural crests in *Gonyaulacysta jurassica, Gonyaulacysta adecta, Gonyaulacysta desmos* and *Gonyaulacysta longicornis* have been omitted from their respective drawings in the interests of clarity. A - *Gonyaulacysta jurassica* (bicavate); B - *Gonyaulacysta adecta* (epicavate); C - *Gonyaulacysta australica* (bicavate with a small apical horn and a semicircular hypocyst); D - *Gonyaulacysta ceratophora* (epicavate to bicavate, with incomplete tabulation); E - *Gonyaulacysta desmos* (cornucavate with a partially developed hypopericoel); F - *Gonyaulacysta dualis* (bicavate with a prominent apical horn and largely smooth sutural

features); G - *Gonyaulacysta fenestrata* (bicavate with fenestrate sutural crests); H - *Gonyaulacysta longicornis* (epicavate with a very large apical horn).

Fig. 3. The stratigraphical ranges of the eight species of *Gonyaulacysta* recognized herein from the Middle and Late Jurassic (Bathonian to Tithonian) of Laurasia and western Gondwana, and eastern Gondwana using the timescale of Gradstein et al. (2020). In Laurasia and western Gondwana, *Gonyaulacysta adecta, Gonyaulacysta desmos, Gonyaulacysta jurassica* and *Gonyaulacysta longicornis* are geographically extensive, however *Gonyaulacysta dualis* is largely confined to the Boreal Realm (i.e. Arctic North America). Note that *Gonyaulacysta jurassica* is cosmopolitan. These data are drawn from a wide literature base, which is referred to in the text. Abbreviations: Bath = Bathonian, E = Early, M = Middle, L/Lt = Late.

Fig. 4. Two graphs illustrating the changes in the average length of the pericyst of *Gonyaulacysta jurassica* throughout the Oxfordian and Lower Kimmeridgian of the UK. The solid black dots joined by a black line represent the raw data, and the dashed red line represents a five-point moving average. The average length values for each of the four substages are indicated by the numbers in red font. A - a composite section from Dunans and Flodigarry, Isle of Skye, northwest Scotland (Riding and Thomas, 1997); B - succession from the Nettleton Bottom Borehole, Lincolnshire, England (Riding, 1987). Note the consistent, and similar, increases in length with time in both successions during the late Oxfordian. The dataset used here is in the Supplementary material, Appendix 3, table 1.

Fig. 5. A graph illustrating the length (x axis) and width (y axis) of 303 specimens of *Gonyaulacysta adecta* from the Callovian and lower Oxfordian strata of England and

Scotland (Woollam and Riding, 1983 appendix 1; Riding and Thomas, 1997). The graph shows a broad continuity in size, and two distinct paratypes of Sarjeant (1982) cannot be distinguished. The data used are those in Supplementary material Appendix 3, table 2.

Fig. 6. The size range of *Gonyaulacysta adecta* throughout the Callovian strata of the UK (*Macrocephalites herveyi* to *Quenstedtoceras lamberti* ammonite zones). Two sections, the Denver Sluice Borehole, Norfolk (left) and a composite succession from England and northwest Scotland (right), are compared. The data used here are those in Supplementary material Appendix 3, tables 3, 4.

Fig. 7. Line drawings of *Tubotuberella eisenackii* illustrating the S-type sulcal area (adapted from Sarjeant, 1982, fig. 4). A – ventral view; B – dorsal view. This species is discussed in sections 3 and 4, and is typically around 75 μm long and 45 μm wide.

Fig. 8. The two different plate configurations of the sulcal region (shaded) exhibited by gonyaulacacean dinoflagellate cysts as documented by Evitt (1985, p. 97–102; figs 5.8–5.13). A, longitudinal (L-type) sulcus; B, sigmoidal (S-type) sulcus (adapted from Evitt, 1985, figs 5.8A, B). The plates are labelled using Kofoidian notation. The small 1''' plate forms part of the sulcus and consequently has been coloured grey.

Fig. 9. A palaeogeographical map for the middle Oxfordian (~160 Ma) depicting the two phytogeoprovinces occupied by *Gonyaulacysta* and described in the text (mainly section 6), i.e. Laurasia and western Gondwana, and eastern Gondwana (Fig. 3). The boundary between these provinces is the solid black line. Note that *Gonyaulacysta jurassica* is cosmopolitan. *Gonyaulacysta adecta, Gonyaulacysta desmos, Gonyaulacysta dualis, Gonyaulacysta*

jurassica and *Gonyaulacysta longicornis* are all present throughout Laurasia including the Boreal Realm. However note that *Gonyaulacysta desmos* and *Gonyaulacysta longicornis* have not been reported from western Gondwana, and that *Gonyaulacysta dualis* is confined to the Boreal Realm (indicated by the broken line). By contrast, *Gonyaulacysta australica, Gonyaulacysta ceratophora* and *Gonyaulacysta fenestrata* are confined to eastern Gondwana. The baseline palaeogeography was kindly provided by Ron Blakey (Deep Time Maps).

Plate I. Five specimens of the small morphotype of *Gonyaulacysta jurassica* from the Middle Oxfordian strata of England and Scotland (Riding, 1987; Riding and Thomas, 1997; Riding and Head, 2018). All the photographs were taken using differential interference contrast. Note the moderately large apical horn, bicavate cyst organisation, subpentagonal ambitus and prominent sutural crests. 1 – British Geological Survey (BGS) specimen MPK 14593 in mid-dorsal view; full focus stack; length 67 µm, width 47 µm. 2 – BGS specimen MPK 14595 in oblique dorsal/right lateral view; full focus stack; length 73 µm, width 49 µm. 3 – BGS specimen MPK 4368 in mid-ventral view; full focus stack; length 67 µm, width 47 µm. 4–6 – BGS specimen MPK 14594 in mid-dorsal view; ventral focus, full focus stack and dorsal focus respectively; length 73 µm, width 53 µm. 7–9 – BGS specimen MPK 14597 in mid-ventral view; ventral focus, full focus stack and dorsal focus respectively; length 71 µm, width 44 µm. Note the displaced endoperculum. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate II. Five specimens of the large morphotype of *Gonyaulacysta jurassica* from the Upper Oxfordian and Lower Kimmeridgian strata of England and Scotland (Riding, 1987; Riding and Thomas, 1997). Photographs 1–6 were taken using plain transmitted light, and images 7–9 were taken using differential interference contrast. 1 – BGS specimen MPK 14726 in mid-dorsal view, full focus stack; length 78 µm, width, 62 µm. 2 – BGS specimen MPK 14596 in slightly oblique dorsal/left lateral view, full focus stack; length 75 µm, width 58 µm. 3 - BGS specimen MPK 3806 in mid-dorsal view, full focus stack; length 78 µm, width 62 µm. 4–6 - BGS specimen MPK 3806 in mid-ventral view; ventral, full focus stack and dorsal focus respectively; length 78 µm, width 60 µm. 7–9 – BGS specimen MPK 14598 in mid-ventral view; ventral focus, full focus stack and dorsal focus respectively; length 89 µm, width 60 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate III. Six specimens of the small morphotype of *Gonyaulacysta adecta* from the Upper Bathonian and Upper Callovian strata of England and Scotland, and a Lower Oxfordian succession from the USA (1–8), plus one specimen of *Gonyaulacysta* sp. cf. *G. adecta* from the Upper Bathonian sedimentary rocks of England (9) (Riding et al., 1985; Riding, 1987; Riding and Thomas, 1997; Riding, 2016). Photographs 4–6 were taken using plain transmitted light; the remainder (1–3 and 7–9) were taken using differential interference contrast. Note the relatively squat ambitus, the short apical horn and the epicavate cyst organisation. 1–3 – BGS specimen MPK 14727 in slightly oblique dorsal/left lateral view; ventral, full focus stack and dorsal focus respectively; length 60 µm, width 44 µm. A slightly globose specimen. 4 - BGS specimen MPK 4439 in mid-ventral view, full focus stack; length 60 µm, width 51 µm. 5 - BGS specimen MPK 14728 in mid-ventral view, full focus stack; length 62 µm, width 49 µm. 6 - BGS specimen MPK 14729 in mid-ventral view, full focus stack; length 60 µm, width 42 µm. 7 - BGS specimen MPK 14730 in oblique apical/right lateral/ventral view, full focus stack; length 53 µm, width 38 µm. 8 - BGS specimen MPK 4167 in slightly oblique ventral/right lateral view, full focus stack; length 64 µm, width 53 µm. 9 - BGS specimen MPK 14731 in slightly oblique ventral/left lateral view, full focus stack; length 51 µm, width 38 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate IV. Seven specimens of the large morphotype of *Gonyaulacysta adecta* from the Upper Callovian strata of England (Gallois, 1979; Woollam and Riding, 1983; Riding, 1987). All the photographs were taken using plain transmitted light. Note the angular subpentagonal ambitus and the thick endocyst wall. 1–3 - BGS specimen MPK 3863 in mid-ventral view; ventral, full focus stack and dorsal focus respectively; length 84 µm, width 58 µm. 4 - BGS specimen MPK 14732 in slightly oblique dorsal/left lateral view, full focus stack; length 73 µm, width 58 µm. 5 - BGS specimen MPK 14733 in mid-dorsal view, full focus stack; length 78 µm, width 51 µm. 6 - BGS specimen MPK 14734 in oblique left lateral/dorsal view, full focus stack; length 78 µm, width 55µm. 7 - BGS specimen MPK 14735 in mid-ventral view, full focus stack; length 87 µm, width 71 µm. 8 - BGS specimen MPK 14736 in mid-dorsal view, full focus stack; length 84 µm, width 67 µm. 9 - BGS specimen MPK 14737 in right lateral view, full focus stack; length 75 µm, width 49 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate V. Three specimens of *Gonyaulacysta australica* reproduced from Cookson and Eisenack (1982, pl. 2, 13–15 respectively) with the permission of Schweizerbart and Borntraeger science publishers, Germany. This material is from the Oxfordian to Kimmeridgian strata of offshore Western Australia (Cookson and Eisenack, 1982). All the specimens are curated at Museum Victoria, Melbourne, Australia. The photographs were all taken using plain transmitted light. Note the bicavate cyst organisation, smooth, subovoidal/subquadrangular ambitus and relatively short apical horn. 1 - A topotype specimen; length 128 µm, width 76 µm. 2 – The holotype, Museum Victoria specimen P.

47281; length 140 µm, width 76 µm. 3 - A topotype specimen; length 128 µm, width 76 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate VI. Seven specimens of *Gonyaulacysta ceratophora* from the Middle Oxfordian strata of offshore Western Australia (Riding, 2005a). All the photographs were taken using differential interference contrast. Note the distinctive subpentagonal ambitus and the bicavate cyst organisation. 1–3 - Geoscience Australia (GA) specimen CPC (Commonwealth Palaeontological Collection) 38837 in oblique dorsal/left lateral view; ventral, full focus stack and dorsal focus respectively; length 111 µm, width 73 µm. 4 – GA specimen CPC 38836 in mid-dorsal view, full focus stack; length 120 µm, width 75 µm. 5 – GA specimen CPC 38835 in dorsal view, full focus stack; length 113 µm, width 78 µm. 6 – BGS specimen MPK 14740 in mid-dorsal view, full focus stack; length 124 µm, width 75 µm. 7 – BGS specimen MPK 14741 in mid-ventral view, full focus stack; length 140 µm, width 84 µm. 8 - BGS specimen MPK 14742 in mid-ventral view, full focus stack; length 120 µm, width 80 µm. 9 – GA specimen CPC 38833 in mid-ventral view, full focus stack; length 102 µm, width 78 µm. Note the oblique 2’’’/1p plate suture at the bottom right. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate VII. Four specimens of *Gonyaulacysta desmos* from the Lower Oxfordian strata of Colorado and Utah, USA (Riding, 2016). Specimens 1–3 were taken using differential interference contrast, and 4 was photographed in plain transmitted light. Note the subpentagonal ambitus, the cornucavation and the partially developed hypopericoel. 1 – BGS specimen MPK 14743 in mid-dorsal view, full focus stack; length 84 µm, width 69 µm. 2 - BGS specimen MPK 14744 in mid-dorsal view, full focus stack; length 69 µm, width 51 µm.

3 - BGS specimen MPK 14745 in slightly oblique dorsal/left lateral view, full focus stack; length 78 µm, width 51 µm. 4 - BGS specimen MPK 14746 in mid-ventral view, full focus stack; length 73 µm, width, 49 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate VIII. Three very well-preserved specimens of *Gonyaulacysta dualis* from the Naknek Formation (Oxfordian) of Amber Bay, southwest Alaska, USA (Riding and Lucas-Clark, 2016). All the photographs were taken using differential interference contrast. Note the angular polygonal ambitus, bicavation, prominent apical horn and distally smooth to denticulate sutural crests. 1–3 - BGS specimen MPK 14747 in mid-dorsal view; ventral focus, full focus stack and dorsal focus respectively; length 120 µm, width 73 µm. 4–6 – BGS specimen MPK 14748 in mid-dorsal view; ventral focus, full focus stack and dorsal focus respectively; length 118 µm, width 67 µm. 7–9 - BGS specimen MPK 14562 in mid-ventral view; ventral focus, full focus stack and dorsal focus respectively; length 118 µm, width 73 µm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate IX. Four specimens of *Gonyaulacysta fenestrata* (1–5) and one specimen of *Gonyaulacysta* sp. cf. *G. fenestrata* (6) from the Kimmeridgian to Tithonian strata of offshore Western Australia. All the photographs were taken using plain transmitted light and are from Riding and Helby (2001a). Note the elongate outline, bicavate cyst organisation, prominent apical horn, opisthopyle and fenestrate, distally-smooth sutural crests. 1 – GA specimen CPC 35680 in dorsal view and focus; length 134 µm, width 77 µm. 2 - GA specimen CPC 35677 in slightly oblique dorsal/left lateral view and focus; length 148 µm, width 61 µm. 3 - GA specimen CPC 35679 in mid-ventral view, medium focus; length 158 µm, width 70 µm. 4, 5 -

GA specimen CPC 35676 (the holotype) in ventral view; dorsal and ventral focus respectively; length 127 μm, width 76 μm. 6 - GA specimen CPC 35683 in dorsal view and focus; length 128 μm, width 77 μm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate X. Five specimens of *Gonyaulacysta longicornis* from the Lower Oxfordian strata of Colorado and Utah, USA (Riding, 2016). All the photographs were taken using differential interference contrast. Note the elongate subpentagonal outline, epicavation, prominent apical horn formed of periphragm and displaced opercula. 1–3 – BGS specimen MPK 14749 in mid-ventral view; ventral focus, medium focus and dorsal focus respectively; length 82 μm, width 60 μm. 4–6 – BGS specimen MPK 14750 in oblique dorsal/left lateral view; dorsal/left lateral focus, medium focus and ventral/right lateral focus respectively; length 80 μm, width 60 μm. Note that this specimen has a relatively short apical horn. 7 – BGS specimen MPK 14751 in mid-ventral view, ventral/medium focus; length 80 μm, width 51 μm. 8 - BGS specimen MPK 14752 in mid-ventral view, ventral/medium focus; length 82 μm, width 58 μm. 9 - BGS specimen MPK 14753 in mid-dorsal view, dorsal focus; length 73 μm, width 53 μm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Plate XI. Five specimens of *Gonyaulacysta longicornis* from the Middle Oxfordian strata of Dunans, Isle of Skye, northwest Scotland (Riding and Thomas, 1997). The specimens have been relatively heavily stained using Safranin O (Riding, 2021). All the photographs were taken using differential interference contrast. 1–3 – BGS specimen MPK 14754 in mid-dorsal view; ventral focus, full focus stack and dorsal focus respectively; length 87 μm, width 51 μm. 4–6 – BGS specimen MPK 14755 in oblique ventral/right lateral view; ventral focus, full focus stack and dorsal focus respectively; length 84 μm, width 58 μm. 7 – BGS specimen MPK 14756 in oblique dorsal/left lateral view, full focus stack; length 75 μm, width 51 μm. 8 - BGS specimen MPK 14757 in right lateral view, full focus stack; length 91 μm, width 56 μm. 9 - BGS specimen MPK 14758 in oblique dorsal/left lateral view, full focus stack; length 102 μm, width 56 μm. More sample and specimen data on this material can be found in Table 2 and Appendix 2 of the Supplementary material.

Table 1. A tabulated summary of the morphology, stratigraphical range, size, holotype locality and phytogeoprovince of the eight species of *Gonyaulacysta* recognized herein. The species are arranged alphabetically within their two phytogeoprovinces. The species *adecta, dualis, longicornis* and *desmos* are confined to Laurasia and western Gondwana, and *Gonyaulacysta australica, ceratophora* and *fenestrata* are endemic to eastern Gondwana (Fig. 9). *Gonyaulacysta jurassica* is cosmopolitan. Note that several of the species may be suturocavate. The size categories used are those of Stover and Evitt (1978).

Table 2. Key data pertaining to the figured specimens in Plates I to XI and their respective samples in tabular form. In the 'geographical coordinates' column, these data are either in latitude/longitude form or, in the case of the UK, Ordnance Survey National Grid References are given. In the 'depth' column, a single asterisk (*) following the depth indicates the distance from the surface; two asterisks (**) following the depth indicates the distance measured up from the base of the respective section. In the 'museum number' column, the respective museum is indicated, i.e. BGS = British Geological Survey, MV = Museum Victoria and GA = Geoscience Australia. Abbreviations: NGR = National Grid Reference; EF = England Finder. These data, and more information, are provided in Appendix 2 of the Supplementary material.

Table 3. A tabulated summary of the eight principal differences between the L-type and S-type mid-ventral plate configurations of Evitt (1985) and Helenes and Lucas-Clark (1997). The latter authors defined the *Stanfordella* and *Wrevittia* styles of the S-type pattern. This was a formalisation of the differences originally noted by Evitt (1985, figs 5.12L; M).