The Jurassic dinoflagellate cyst *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov.: An index species for the Late Callovian to earliest Oxfordian of the northern hemisphere

James B. Riding*

British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham NG12 5GG, UK

* Corresponding author. Tel.: +44(0)115 9363447

E-mail address: jbri@bgs.ac.uk (J.B. Riding).

ABSTRACT

Gonyaulacysta dentata is a very large and morphologically distinctive dinoflagellate cyst species which was first described from the Callovian (Middle Jurassic) strata of the Isle of Skye, northwest Scotland. The diagnosis and description of this species are emended herein in order to document the characteristic elongate pentagonal outline, the apicular structure, the bicavate cyst organisation, the prominent dorsal and lateral sutural crests which are typically denticulate, the discontinuous, low-relief midventral sutural ridges and the lack of a periarchaeopyle. *Gonyaulacysta dentata* is a reliable index taxon for the Late Callovian to earliest Oxfordian (Peltoceras athleta to Quenstedtoceras mariae zones) of the Boreal Realm and the Subboreal Province in the northern hemisphere. It is especially prominent in the Boreal Realm and the northern part of the Subboreal Province, and has been recorded from the Barents Sea region, arctic Canada, offshore Norway, the central and northern North Sea and northern Scotland. Typically this species represents a relatively low proportion of the overall dinoflagellate cyst assemblages. There are also reports of very rare specimens of *Gonyaulacysta dentata* from further south in the Northwest European Subprovince, i.e. France, Germany and Poland. It therefore appears to be a characteristic Boreal taxon, but low numbers migrated southwards into the Northwest European Subprovince due to a fall in palaeotemperatures during the Callovian-Oxfordian transition. The southwards expansion of this short-lived species parallels the southward migration of the Boreal ammonite family Cardioceratidae. There is a virtually mutually exclusive relationship between the Arctic species *Gonyaulacysta dentata* and the apparently warm-loving taxon *Scriniodinium crystallinum* during the Late Callovian to Early Oxfordian interval. This is consistent with the interpretation of *Gonyaulacysta dentata* as a cold water taxon.

Keywords: *Gonyaulacysta dentata*; dinoflagellate cysts; biostratigraphy; palaeobiology; provincialism; Mid-Late Jurassic; northern hemisphere

1. Introduction

In a major paper on the Mid and Late Jurassic dinoflagellate cyst biostratigraphy of the UK, Raynaud (1978, p. 395) described the large and distinctive species *Tubotuberella dentata* from the Callovian strata of the Isle of Skye, northwest Scotland. This species was subsequently transferred to *Gonyaulacysta* by Lentin and Vozzhennikova (1990, p. 116) due to its morphological similarity to *Gonyaulacysta eisenackii* (Deflandre 1938) Górka 1965. This attribution to *Gonyaulacysta* was endorsed by Helenes and Lucas-Clarke (1997, p. 179) in a major review of this genus. *Gonyaulacysta dentata* has been recorded throughout Europe, however it is especially prominent in the high northerly latitudes, and has been reported from the Barents Sea region, arctic Canada and offshore Norway. It is a reliable stratigraphical marker species for the Late Callovian-earliest Oxfordian interval. The purpose of this contribution is to emend the species diagnosis and description in order to stress the extremely characteristic morphology of *Gonyaulacysta dentata,* to document the previously reported occurrences of this species and to emphasise its palaeobiological, palaeogeographical and stratigraphical significance. The ammonite zones and subzones quoted are used herein in the sense of biozones, hence the index species are written in Roman font and the initial letters of zones and subzones are capitalised. Therefore the index species of the Quenstedtoceras lamberti Zone is the ammonite *Quenstedtoceras lamberti* (J. Sowerby).

2. Materials and methods

The specimens of *Gonyaulacysta dentata* examined as part of this study are from two samples of Upper Jurassic mudstone collected from foreshore outcrops at Dunans, Isle of Skye, western Scotland, United Kingdom (NG 472 708) (Fig. 1). The samples are from Bed 8 of Sykes and Callomon (1979) from the Lower Oxfordian part of the Dunans Clay Member of the Staffin Shale Formation, and assigned to the Cardioceras scarburgense Subzone of the Quenstedtoceras mariae Zone (Riding and Thomas, 1997, fig. 2). The samples are DUN 41 and DUN 42, at 30.17 m and 32.12 m from the base of the succession at Dunans respectively. The British Geological Survey (BGS) registration numbers of these samples are MPA 14066 and MPA 14067 respectively. The Dunans Clay Member is known to be extremely rich in well-preserved dinoflagellate cysts, pollen and spores. The dinoflagellate cyst associations are overwhelmingly dominated by *Mendicodinium groenlandicum* (Pocock & Sarjeant 1972) Davey 1979, with common to abundant *Chytroeisphaeridia chytroeides* (Sarjeant 1962) Downie & Sarjeant 1965, *Downiesphaeridium polytrichum* (Valensi 1947) Masure in Fauconnier & Masure 2004, *Gonyaulacysta jurassica* (Deflandre 1938) Norris & Sarjeant 1965 subsp. *adecta* Sarjeant 1982, the *Meiourogonyaulax caytonensis* (Sarjeant 1959) Sarjeant 1969 group, *Nannoceratopsis pellucida* Deflandre 1939, *Rhynchodiniopsis cladophora* (Deflandre 1939) Below 1981, *Rigaudella aemula* (Deflandre 1939) Below 1982, the *Sentusidinium rioultii* (Sarjeant 1968) Sarjeant & Stover 1978 group, *Surculosphaeridium*? *vestitum* (Deflandre 1939) Davey et al. 1966, *Trichodinium scarburghense* (Sarjeant 1964) Williams et al. 1993 and *Wanaea acollaris* Dodekova 1975. The presence of *Gonyaulacysta centriconnata* Riding 1983, *Gonyaulacysta jurassica* subsp. *jurassica* (autonym), *Rigaudella aemula* and *Trichodinium scarburghense* is characteristic of the Early Oxfordian interval, and the association is assigned to the earliest Oxfordian DSJ20 Zone of Poulsen and Riding (2003). The most common pollen grains are bisaccate pollen, *Callialasporites* spp. and *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967, and *Cyathidites* spp. dominates the spores. These assemblages have been fully described by Riding and Thomas (1997) and Riding and Kyffin-Hughes (2011). Selected photomicrographs of *Gonyaulacysta dentata* are presented in Plates I and II. All sample materials, i.e. unprocessed rock, organic residues, microscope slides, primary data and illustrated specimens are lodged in the collections of the British Geological Survey, Keyworth, Nottingham NG12 5GG, UK.

3. Systematic palaeontology

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. Helenes & Lucas-Clark 1997

Type: *Gonyaulacysta jurassica* (Deflandre 1938) Norris & Sarjeant 1965 emend. Sarjeant 1982

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov.

Plate I, 1-9; Plate II, 1-2; Fig. 2.

Synonymy list (note that an asterisk indicates that the material was illustrated):

*Gonyaulacysta sp. Johnson and Hills (1973, p. 206, fig. 7, pl. 2/2, 3) (Mid-Late Callovian, Axel Heiberg Island, arctic Canada).

**Tubotuberella dentata* Raynaud 1978. Raynaud (1978, p. 395, fig. 5, pl. 2/13) (Mid-Late Callovian, Isle of Skye, northwest Scotland).

**Endoscrinium eisenackii* (Deflandre 1938) Gocht 1970 subsp. *oligodentatum* (Cookson & Eisenack 1958) Gocht 1970 (auct. non.). Thusu (1978, chart 2, pl. 9/1, 3 [not pl. 9/2]) (Late Callovian, Kong Karls Land, Svalbard).

**Tubotuberella dentata* Raynaud 1978. Jan du Chêne et al. (1986, pl. 123/14; pl. 126/1-3) (Mid-Late Callovian, Isle of Skye, northwest Scotland).

**Tubotuberella eisenackii* (Deflandre 1938) Stover & Evitt 1978 (auct. non.). Smelror (1988a, pl. VI/1) (Late Callovian, Kong Karls Land, Svalbard).

*Gonyaulacysta jurassica (Deflandre 1938) Norris & Sarjeant 1965 (auct. non.). Smelror (1988a, pl. VI/9) (Late Callovian, Kong Karls Land, Svalbard).

Tubotuberella dentata Raynaud 1978. Stancliffe and Sarjeant (1988, p. 775, table 5d) (Oxfordian-Kimmeridgian, undifferentiated Boreal Realm [compilation]).

Tubotuberella dentata Raynaud 1978. Århus et al. (1989, fig. 8) (Early Oxfordian, west of Vega Island, offshore Norway).

**Tubotuberella dentata* Raynaud 1978. Prauss (1989, fig. 49, pl. 14/10) (Late Callovian, south of Hannover, northwest Germany).

Tubotuberella dentata Raynaud 1978. Dimter and Smelror (1990, fig. 4) (latest Callovian, Kandern, southwest Germany).

**Tubotuberella dentata* Raynaud 1978. Kunz (1990, p. 25-26, fig. 13, pl. 5/15) (earliest Oxfordian, Hannoversches Bergland, northwest Germany).

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990. Lentin and Vozzhennikova (1990, p. 116) (new combination).

**Tubotuberella eisenackii* (Deflandre 1938) Stover & Evitt 1978 (auct. non.). Smelror and Below (1992, fig. 3, pl. III/1) (?Mid/Late Callovian-Early Oxfordian and younger, Barents Sea region).

Tubotuberella dentata Raynaud 1978. Riding et al. (1993, p. A2) (Early Oxfordian, central and northern North Sea [compilation]).

Tubotuberella dentata Raynaud 1978. Smelror (1993, tables 4, 5) (Late Callovian-Early Oxfordian, Barents Sea region, northwest Europe, east Greenland, offshore central Norway, Svalbard [compilation]).

**Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990. Fensome et al. (1996, pl. 1/20) (earliest Oxfordian, Isle of Skye, northwest Scotland).

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990. Iosifova (1996, table 2) (Ryazanian [= Berriasian], central Russian Platform, western Russia) (presumed reworked).

**Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990. Riding and Thomas (1997, figs. 2, 4e) (earliest Oxfordian, Isle of Skye, northwest Scotland).

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990. Huault (1999, fig. 10, table 4) (Late Callovian, Paris Basin, northeast France).

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990. Riding (2005, figs. 3, 7) (latest Callovian, Brora, northeast Scotland).

Tubotuberella dentata Raynaud 1978. Birkenmajer and Gedl (2007, table 2) (?Early Oxfordian, Pieniny Klippen Belt, southern Poland).

**Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990. Gedl (2008a, p. 225, figs. 4, 22O-Q [not figs. 22K, L]) (Late Callovian, Łukow, eastern Poland).

Tubotuberella dentata Raynaud 1978. Gedl (2008b, p. 219, fig. 91) (?Early Oxfordian, Pieniny Klippen Belt, southern Poland).

Gonyaulacysta dentata (Raynaud 1978) Lentin & Vozzhennikova 1990. Harding et al. (2011, online supplementary material tables 1, 2) (Mid-Late Tithonian/Early Barremian, central Russian Platform, western Russia) (presumed reworked).

**Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990. Riding and Kyffin-Hughes (2011, tables 1, 2, pl. I/3) (earliest Oxfordian, Isle of Skye, northwest Scotland).

The synonymy listing above gives all records of unequivocal *Gonyaulacysta dentata* known to the author as of October 2011. However, there have been several instances where *Gonyaulacysta dentata* has been misidentified. Smelror et al. (1991, pl. I/14) figured a relatively spinose specimen of *Tubotuberella dangeardii* (Sarjeant 1968) Stover & Evitt 1978 from the earliest Callovian of the Lusitanian Basin, western Portugal as *Tubotuberella dentata*. Smith (1999) worked on the Jurassic/Cretaceous transition of the Volga Basin, western Russia and figured a specimen as *Tubotuberella dentata* which appears to be an intermediate between *Gonyaulacysta eisenackii* and *Tubotuberella dangeardii* from the Middle and Upper Tithonian strata of Gorodische (Smith, 1999, pl. 14/21). This specimen is clearly not *Gonyaulacysta dentata* on both morphological and size grounds. The principal findings of Smith (1999) were subsequently published by Harding et al. (2011), and this misidentification of *Gonyaulacysta dentata* has unfortunately been perpetuated in the latter paper. Harding et al. (2011) stated that the specimens of *Gonyaulacysta dentata* from the Middle-Upper Tithonian to Lower Berriasian sedimentary rocks of the Volga Basin were probably reworked from the Callovian-Oxfordian. *Gonyaulacysta dentata* was also recorded by Iosifova (1996) from the Berriasian of the Moscow Basin, western Russia. This author did not illustrate her material, and these records are also assumed to represent Callovian/Oxfordian reworking. In a major paper on the Callovian-Berriasian palynostratigraphy of the Dutch sector of the North Sea, Herngreen et al. (2000) studied some comparative material from the Dorset coast, southern England. These authors figured a specimen of *Tubotuberella* sp. cf. *T. dangeardii* (see Herngreen et al., 2000, pl.12/5) from the latest Callovian (Quenstedtoceras lamberti Zone) of Dorset as *Tubotuberella dentata*. Herngreen et al. (2000, annexes 1-13) did not record *Gonyaulacysta dentata* from the North Sea. A specimen from the Upper Callovian of Poland figured by Gedl (2008a, figs. 22K, L) appears to be too small to be unequivocal *Gonyaulacysta dentata.*

Original diagnosis of Raynaud (1978, p. 395): A large species. Endophragm ovoid, smooth. Periphragm smooth to finely granulate. Apical horn sharply pointed. Apical and antapical pericoels present. The antapical pericoel is shorter than that of *Tubotuberella apatela*. Tabulation marked by high crests surmounted by regularly inserted denticles. A precingular archaeopyle and an antapical opening are present (translated by J.B. Riding, June 2011).

Emended diagnosis: A large, highly dorsoventrally-compressed, elongate, bicavate species of *Gonyaulacysta* which has an angular pentagonal dorsoventral outline and normally bears a prominent apical horn often with a prominent apicular structure. The cingulum is subequatorial. The dorsal and lateral paratabulation is indicated by prominent variably denticulate to occasionally smooth sutural crests which dramatically reduce to discontinuous low, distally smooth ridges on the midventral surface and in the apical region. A periarchaeopyle is not developed, and a circular claustrum is present in the antapical plate.

Emended description: A large, elongate species of *Gonyaulacysta* which is significantly dorsoventrally compressed. The pericyst has an angular pentagonal outline normally with a prominent, largely hollow, distally pointed apical horn and a consistently truncated antapex. The distal part of the apical horn is frequently surmounted by a short (2 to 5 μm), solid apicular structure. The epicyst and hypocyst are broadly similar in overall length. The epicyst is subtriangular with straight sides. The hypocyst is quadrangular with straight to slightly convex sides; the antapical side is by far the shortest. The endocyst is elongate ovoidal to rounded subpentagonal to subhexangular in outline with no apical or antapical horns or protuberances. The species exhibits a bicavate cyst organisation, and the epipericoel and hypopericoel are both extremely well-developed. The epipericoel is subtriangular and the hypopericoel is subquadrate; both frequently extend equatorially towards the paracingulum. However the periphragm and endophragm normally become closely appressed in the central areas of the epicyst and hypocyst, thus a circumcavate or camocavate cyst organisation is never fully developed. There is typically more wall separation in the hypocyst than in the epicyst. A standard gonyaulacacean tabulation (?2pr, 4’, ?1a, 6’’, ?6c, 6’’’, 1p, 1’’’’, ?5s) is fully indicated by prominent sutural crests (normally 4-5 μm high) on the lateral and dorsal areas of the periphragm and discontinuous low, distally smooth sutural ridges on the midventral side and the apical region of the periphragm. The dorsal and lateral sutural crests are frequently surmounted by small (2-4 μm long) thorn-like gonal and intergonal denticles with pointed, truncate or bifurcate distal terminations, or they may be distally smooth. The denticles are normally densest and most prominent around the cingulum, on the hypocyst and especially around the antapex. The denticles may be absent or significantly reduced and this phenomenon, where developed, is typical of the epicyst. The plate boundaries of the antapical (1’’’’) plate are frequently marked by extremely prominent gonal denticles up to 12 μm long. The prominent dorsal and lateral parasutural crests reduce sharply to low, distally smooth ridges on and around the apical horn. The apical edges of the sutural crests on the epicyst are distinctly concave in an apical direction. This marked change in morphology imparts a highly distinctive outline to the apical part of the epicyst, close to the apical part of the endocyst, which frequently has the superficial appearance of having two small horns on either side of the main apical horn in dorsoventral view. A prominent laevorotatory equatorial cingulum 3-5 μm in height is present, and the dorsal cingular crests are relatively prominent. The cingulum is apparently undivided. The laevorotatory nature of the cingulum is often difficult to discern due to the reduced and discontinuous nature of the sutural ornamentation on the midventral surface. Similarly, the sulcus is not prominent because the midventral sutural ridges are low and may be locally suppressed. The sulcus is apparently undivided. The periphragm is relatively thin, and is smooth to shagreenate. The endophragm is relatively thick, smooth to shagreenate, occasionally locally microscabrate. The single-plate (3’’) precingular endoarchaeopyle is prominent and the free endoperculum is frequently displaced within the endocyst. A periarchaeopyle is not developed. The antapical (1’’’’) plate is virtually entirely represented by a subcircular claustrum.

Dimensions: The specimens measured here are all from sample DUN 42 (BGS registration number MPA 14067) which was collected from the lowermost Oxfordian succession of the Dunans Clay Member of the Staffin Shale Formation at Dunans, north of Staffin Bay, Isle of Skye, northwest Scotland (Fig. 1). The 10 parameters below are quoted in micrometres (μm) from 38 specimens. The three figures represent the minimum, mean (in parentheses) and maximum respectively. All these size data are presented in Table 1. Note that preservational factors and additional dorsoventral compression may have slightly distorted some of these measurements. *Gonyaulacysta dentata* is a particularly large Jurassic dinoflagellate cyst. It is ‘large’ (i.e. >100 μm) as defined by Stover and Evitt (1978, p. 5), hence is easy to identify using relatively low magnifications. Helenes and Lucas-Clark (1997, p. 176) commented that the total length of *Gonyaulacysta* is between 70 to 100 μm, hence *Gonyaulacysta dentata* is unusually large for this genus.

Length of pericyst including apical horn and denticles:	89 (110) 133
Length of apical horn including apicular structure:	4 (10) 16

Length of epipericoel including apical horn:	11 (19) 24
Length of epipericyst including apical horn, excluding cingulum:	38 (49) 69
Length of hypopericyst including denticles, excluding cingulum:	42 (59) 73
Length of hypopericoel including antapical denticles:	9 (18) 27
Equatorial width of pericyst including cingular denticles:	56 (72) 89
Dorsoventral antapical width of pericyst:	13 (26) 36
Length of endocyst:	53 (72) 84
Equatorial width of endocyst:	42 (60) 73

Raynaud (1978, p. 395) reported that the holotype of *Gonyaulacysta dentata* is 140 µm long and 92 µm wide, and further noted that the size variation in the type material is 136 to 170 µm by 90 to 96 µm. This compares to 89 to 133 µm by 56 to 89 µm herein (see above). Clearly this is a major disparity; this may be due to microscope calibration issues with the type material and/or swelling effects caused during the laboratory preparation of the sample material of Raynaud (1978). Glycerine jelly and alkali solutions are known to cause palynomorphs to increase in size (e.g. Andersen, 1960; Bruch and Pross, 1999 respectively), and pressure between the microscope slide and coverslip can have similar effects (Cushing, 1961) The measurements by Raynaud (1978) are deemed to be anomalously large because the dimensions quoted by other authors such as Johnson and Hills (1973, p. 206), Kunz (1990, p. 25) and Gedl (2008a, p. 225) are closely comparable to those herein.

Remarks: The large size, characteristic elongate subpentagonal outline and the prominent variably denticulate dorsal and lateral sutural crests of *Gonyaulacysta dentata* make this species very easy to identify (Fig. 2). One of the most characteristic morphological features of *Gonyaulacysta dentata* is the disparate heights of the dorsal and lateral sutural crests and the lower, partially discontinuous midventral and apical sutural ridges. This phenomenon has also been observed in *Gonyaulacysta jurassica* (see Stover and Evitt, 1978, p. 277), but otherwise is highly unusual. The tabulation pattern apparently conforms to that described by

Helenes and Lucas-Clark (1997) for *Gonyaulacysta,* although the second preapical plate (2pr) and the single anterior intercalary plate (1a) have not been unequivocally observed. This species is one of the largest Jurassic dinoflagellate cysts and was originally placed into the genus *Tubotuberella* Vozzhennikova 1967 by Raynaud (1978). It was subsequently transferred into *Gonyaulacysta* by Lentin and Vozzhennikova (1990, p. 116), where it is retained herein. Some authors such as Smelror (1993), Birkenmajer and Gedl (2007) and Gedl (2008b) have continued to use the name *Tubotuberella dentata.* Both *Gonyaulacysta* and *Tubotuberella* are elongate, subpentagonal, cavate gonyaulacacean genera which are prominent in the Jurassic. However *Tubotuberella* is consistently bicavate, with a prominent hypopericoel, and always exhibits an antapical claustrum. It also lacks the strongly denticulate sutural crests which are typical of *Gonyaulacysta* (see Lentin and Vozzhennikova, 1990, p. 116). The species of *Tubotuberella* which is most similar to *Gonyaulacysta* is *Tubotuberella dangeardii* because the sutural ridges frequently are surmounted by widely spaced short denticles (e.g. Riding and Thomas, 1992, pl. 2.11/3). Similarly, one of the species of *Gonyaulacysta* which is most similar to *Tubotuberella* is *Gonyaulacysta eisenackii* because of the antapical claustrum and the bicavate cyst organisation. Due to these morphological considerations, *Gonyaulacysta eisenackii* and *Tubotuberella dangeardii* may be considered to be intermediate species between *Gonyaulacysta* and *Tubotuberella*. For example, the presence of denticulate sutural crests in *Gonyaulacysta* is not exclusive; the species *Gonyaulacysta dualis* (Brideaux & Fisher 1976) Stover & Evitt 1978 typically has distally smooth sutural crests which only rarely bear low-relief denticles (Brideaux and Fisher, 1976, p. 18-19). However these two closely related, typically Jurassic, genera are maintained herein despite the strong morphological similarities between them. It is noted, however, that some species of *Gonyaulacysta* are characterised by unusually large epicysts, where the cingulum is significantly closer to the antapex than the apex (Stover and Evitt, 1978, p. 275-279). These comprise *Gonyaulacysta ceratophora* (Cookson & Eisenack 1960) Riding 2005, *Gonyaulacysta dualis, Gonyaulacysta fenestrata* Riding & Helby 2001 and *Gonyaulacysta jurassica*. These differ from other species such as *Gonyaulacysta centriconnata*, *Gonyaulacysta dentata* and *Gonyaulacysta eisenackii*, which all have equatorial cingulums.

Gonyaulacysta dentata exhibits some intraspecific variability. The apical horn is highly variable in length (Table 1), and the apicular structure may be prominent or very small. The antapical breadth of the hypopericoel also varies significantly (Table 1). The overall width also differs, with relatively broad forms (Plate I, 1-3 and Plate II, 1, 2) and elongate, slender morphotypes (Plate I, 4-6) observed. The majority of specimens are relatively broad, and the holotype one of these wide morphotypes (Raynaud, 1978, pl. 2/13; Fig. 2, Plate II). The density, length and morphology of the sutural denticles are all somewhat variable, particularly on the epicyst. In some individuals, many of the sutural crests can be relatively smooth distally. Furthermore, the size of the endocyst is relatively inconstant. In some specimens it occupies a greater part of the pericyst than others.

A description of *Gonyaulacysta dentata* was given by Gedl (2008a, p. 225) but this did not constitute a formal emendation. *Gonyaulacysta dentata* is emended herein to note several important features which were not mentioned by Raynaud (1978). These include the elongate pentagonal outline in dorsoventral view, the apicular structure, the bicavate cyst organisation, the morphological variability of the sutural denticles, the disparate nature of the dorsal and lateral, and midventral sutural ornamentation and the lack of a periarchaeopyle. Furthermore, the emended diagnosis and description note that the prominent denticulate dorsal sutural crests sharply reduce in height to low, distally smooth sutural ridges on and around the apical horn. The apically concave anterior edges of the sutural crests below the apical horn on the epicyst are extremely distinctive. This phenomenon is also developed in *Gonyaulacysta eisenackii* (see e.g. Beju, 1971, pl. 1/4-6; Riding, 1987, fig. 9.14) and other gonyaulacacean taxa.

Comparison: The most similar species to *Gonyaulacysta dentata* is *Gonyaulacysta eisenackii* in that this taxon has prominent denticulate sutural crests which do not extend to the apical horn. However, *Gonyaulacysta eisenackii* is significantly smaller (typically around 80 µm in length) than *Gonyaulacysta dentata.* Furthermore, the former is not as elongate as the latter, and has relatively small pericoels and a small apical horn which lacks an apicular structure (Deflandre, 1938, pl. VI/7-10). The cingulum of *Gonyaulacysta dentata* is equatorial, which contrasts markedly with the antapically offset cingulums of *Gonyaulacysta ceratophora*, *Gonyaulacysta dualis*, *Gonyaulacysta fenestrata* and *Gonyaulacysta jurassica*. *Gonyaulacysta dentata* is also larger and more denticulate than *Tubotuberella dangeardii* and other species of this genus (Jan du Chene et al, 1986, pl. 123).

Derivation of name: The specific name derives from the denticulate sutural crests which indicate the tabulation (Raynaud, 1978, p. 395).

Holotype and type locality: Raynaud (1978. pl. 2/13), preparation 14859, sample 22183/45; from the Callovian (Middle Jurassic) part of the Staffin Shale Formation from Staffin Bay, Trotternish, Isle of Skye, northwest Scotland.

4. The stratigraphical distribution of *Gonyaulacysta dentata*

The published statigraphical ranges of *Gonyaulacysta dentata* have been compiled herein as Table 2. The overall range of unequivocal, in situ *Gonyaulacysta dentata* is Late Callovian to earliest Oxfordian. The majority of the reports which are tied to ammonite biozones indicate that the reliable stratigraphical extent of this important marker species spans the Peltoceras athleta Zone to the Quenstedtoceras mariae Zone (Table 2). Raynaud (1978, fig. 5) reported this species from the Mid Callovian Erymnoceras coronatum Zone of Skye. However the Erymnoceras coronatum Zone is not developed at Trotternish, northeast Skye (Sykes, 1975, fig. 5; Riding and Thomas, 1997, fig. 2), and this occurrence has never been replicated.

Stancliffe and Sarjeant (1988, table 5d) depicted the range of *Tubotuberella dentata* as Oxfordian to Kimmeridgian in the Boreal Realm as part of a compilation of the ranges of Oxfordian dinoflagellate cysts. However, there are no published reports of this species from the Mid Oxfordian and Kimmeridgian, hence the sources of this compiled range are not known. In a major review of the biogeography of Bathonian to Oxfordian dinoflagellate cysts of the northwest hemisphere, Smelror (1993, tables 4, 5) stated that this species is present in the Late Callovian of northwest Europe and Svalbard, and the Early Oxfordian of east Greenland/Norway and Svalbard. However, *Gonyaulacysta dentata* has not been consistently identified (e.g. Smelror, 1988a, pl. VI/1, 9; Smelror and Below, 1992, pl. III/1) hence the compiled ranges in Smelror (1993, tables 4, 5) may not be entirely reliable.

Gonyaulacysta dentata has been recorded extensively from the Arctic region. The species was first reported from arctic Canada by Johnson and Hills (1973) as *Gonyaulacysta* sp. These authors recorded *Gonyaulacysta* sp. in low proportions from the uppermost Lower Savik Member of the Savik Formation (samples 62-65) at Vantage Point, central west Axel Heiberg Island. The two specimens figured (Johnson and Hills, 1973, pl. 2/2, 3) are relatively poorly-preserved. They are badly obscured by pyrite and palynodebris, and have unusually poorly-developed epipericoels and narrow apical horns. Furthermore, the sutural denticles appear to be relatively sparse. Despite this, this material is considered to be conspecific with *Gonyaulacysta dentata*; the dimensions quoted by Johnson and Hills (1973, p. 206) are comparable to those recorded herein. Somewhat surprisingly, *Gonyaulacysta dentata* has not been recorded from Jameson Land and Milne Land, east Greenland (Fensome, 1979; Piasecki, 1980; Smelror, 1988b; Piasecki and Stemmerik, 2004; Piasecki et al., 2004a,b; S. Piasecki, personal communication July 2011).

The Callovian and Oxfordian strata of Kong Karls Land (Kongsøya Island), a small island east of Spitsbergen which is part of the Svalbard archipelago in the Barents Sea, have yielded *Gonyaulacysta dentata*. The first report was that of Thusu (1978) from the Callovian and Oxfordian, as *Endoscrinium eisenackii* subsp. *oligodentatum.* This author figured two very well-preserved specimens from the lower (Callovian) part of the Retziusfjellet Member (Janusfjellet Formation) on Hårfagrehaugen Mountain (Thusu, 1978, pl. 9/1, 3). The presence of the ammonite *Quenstedtoceras* and the diverse dinoflagellate cyst flora, which includes *Rigaudella aemula* (Deflandre 1938) Below 1982, is consistent with the Late Callovian (Arkell et al., 1957; Thusu, 1978, table 1.13; Riding and Thomas, 1997, fig. 2). The material from Kong Karls Land studied by Thusu (1978), and other samples, was restudied by Smelror (1988a). The latter author figured a beautiful specimen of *Gonyaulacysta dentata* as *Tubotuberella eisenackii* (see Smelror, 1988a, pl. VI/1). A somewhat less spectacular specimen of *Gonyaulacysta dentata* was figured as *Gonyaulacysta jurassica* (see Smelror, 1988a, pl. VI/9). These two specimens are from the same sample (S-14-46) as the unequivocal material figured by Thusu (1978). Smelror (1988a, fig. 6) stated that sample S-14-46 is of Late Callovian (Peltoceras athleta Zone) age. A specimen of *Gonyaulacysta dentata* from the ?Mid/Late Callovian to Early Oxfordian of the Barents Sea region was illustrated, as *Tubotuberella eisenackii,* by Smelror and Below (1992, pl. III/1). Detailed locality and sample data were not given by these authors. Århus et al. (1989, fig. 8) reported *Tubotuberella dentata* in relatively low numbers from the Lower Oxfordian (?Cardioceras cordatum Zone) from offshore shallow core 5 which was drilled west of Vega Island, offshore Norway.

In northwest Europe, *Gonyaulacysta dentata* has been documented only from northern France, Germany and northern Scotland. The first European record was that of Raynaud (1978, fig. 5), who reported the type material of *Tubotuberella dentata* in low proportions (‘uncommon’) from the Middle and Upper Callovian part of the Staffin Shale Formation from Staffin Bay on the Isle of Skye, northwest Scotland. This author stated that the species is present in the Erymnoceras coronatum, Peltoceras athleta and Quenstedtoceras lamberti zones. Jan du Chêne et al (1986, pl. 126/1-3) refigured the holotype. Riding and Thomas (1997) is an account of the Early Callovian to Early Kimmeridgian dinoflagellate cyst biostratigraphy of the Staffin Bay and Staffin Shale formations of the Isle of Skye. These authors reported *Gonyaulacysta dentata* in three samples (DUN 41, 42 and 43) from the lowermost Oxfordian part of the Dunans Clay Member of the Staffin Shale Formation at the type section at Dunans, immediately north of Staffin Bay (Fig. 1). These three samples are all from the Cardioceras scarburgense Subzone of the Quenstedtoceras mariae Zone (Riding and Thomas, 1997, fig. 2). *Gonyaulacysta dentata* is present in relatively sparse proportions in Skye; this species comprises 0.8%, 1.3% and 0.8% of the dinoflagellate cyst assemblage in samples DUN 41, 42 and 43 respectively. One of these specimens was also illustrated by Fensome et al. (1996, pl. 1/20). More recently, Riding and Kyffin-Hughes (2011, table 1) recorded 0.3% and 1.6% of *Gonyaulacysta dentata* as a percentage of the dinoflagellate cyst assemblage from DUN 42 using two different palynological preparation techniques. *Gonyaulacysta dentata* was recorded in relatively small proportions (2% of the dinoflagellate cyst assemblage) from samples B29 and B32, within the uppermost Callovian Fascally Siltstone and Fascally Sandstone members respectively, at Brora, northeast Scotland by Riding (2005). These samples were collected from the Quenstedtoceras henrici and Quenstedtoceras lamberti subzones respectively of the Quenstedtoceras lamberti Zone (Riding, 2005, figs. 3, 7). Riding et al. (1993, p. A2) reported that the range top of *Tubotuberella dentata* in the central and northern North Sea is of Early Oxfordian (Cardioceras cordatum Zone) age.

The first documented occurrence of *Gonyaulacysta dentata* from continental Europe is from Germany. Prauss (1989) recorded the species, as *Tubotuberella dentata,* from the Late Callovian (Peltoceras athleta and Quenstedtoceras lamberti zones) of south of Hannover, northwest Germany. A single specimen with a well-developed claustrum was illustrated from the Quenstedtoceras lamberti Zone (Prauss, 1989, pl. 14/10). Subsequently *Tubotuberella dentata* was noted, but not illustrated, from the latest Callovian (Quenstedtoceras lamberti Zone) of Kandern in southwest Germany by Dimter and Smelror (1990, fig. 4). Kunz (1990, fig. 13) reported sparse (<1%) *Tubotuberella dentata* from the lower part of the Oxford-Tonstein of the Hannoversches Bergland, northwest Germany. This is of earliest Oxfordian (Quenstedtoceras mariae Zone) age. This species is apparently extremely rare in northwest Germany; only one specimen was measured by Kunz (1990, pl. 5/15). The extreme sparsity of this taxon in Germany is emphasised by the fact that it was not mentioned in the major data compilation of Feist-Burkhardt and Wille (1992, fig. 2). Huault (1999) documented low numbers of *Gonyaulacysta dentata* from the Late Callovian of the Paris Basin, northeast France, but did not illustrate this species.

Gonyaulacysta dentata has also been recorded from the Late Callovian and ?Early Oxfordian of eastern and southern Poland by Birkenmajer and Gedl (2007) and Gedl (2008a,b). Birkenmajer and Gedl (2007) recorded this species as two single occurrences from the Sokolica Radiolarite Formation of Mt Hulina in the Pieniny Klippen Belt of southern Poland, and attributed this unit to the Oxfordian-?Kimmeridgian. The age of this material (samples Hln 6 and Hln 7) was subsequently revised to ?Early Oxfordian by Gedl (2008b, p. 195). Gedl (2008a) recorded *Gonyaulacysta dentata* from three samples of the Upper Callovian succession from near Łukow in eastern Poland.

Gonyaulacysta dentata was recorded by Iosifova (1996) from the Berriasian of the central Russian Platform, western Russia. No illustrations were provided by this author, and these records are presumed to have been reworked from the Callovian/Oxfordian.

5. The provincialism of dinoflagellate cysts at the Callovian-Oxfordian transition with emphasis on *Gonyaulacysta dentata*

Raynaud (1978) and Smelror (1993) stated that the Late Callovian to Early Oxfordian interval yields abundant and diverse dinoflagellate cyst associations which are remarkably stable throughout the Arctic, northwest Europe and the circum-Mediterranean region. This situation is unequivocally the case, with essentially similar Late Callovian to Early Oxfordian marine palynofloras present throughout much of the northern hemisphere including North America, the Middle East and Russia (e.g. Johnson and Hills, 1973; Beju, 1982; Thusu et al., 1988; Riding et al., 1999). Furthermore, the Late Callovian dinoflagellate cyst associations of South America are very similar to coeval floras from the northern hemisphere (Riding et al., 2011). These floras are similar, with very few discernibly latitudinally-controlled taxa present. These include the typically high latitude genus *Paragonyaulacysta* (see Riding, 2005). The dinoflagellates, like the ammonites, were cosmopolitan during this interval with a mixing of Boreal and Tethyan taxa (Poulsen and Riding, 2003; Cecca et al., 2005). By contrast, Prauss (1989) interpreted the uniformity in dinoflagellate cysts during the Late Callovian as a dominance of Tethyan taxa.

Gonyaulacysta dentata has been recorded from the Late Callovian to the earliest Oxfordian of the Boreal Realm and the Subboreal Province, i.e. the high northerly latitudes and northwest Europe south of Greenland respectively. Specifically this species has been reported from the Barents Sea region, arctic Canada, France, Germany, the central and northern North Sea, offshore Norway, Poland and northern Scotland (Figs. 3, 4; Table 2). It is especially prominent in the Boreal Realm and the northern part of the Subboreal Province (Stancliffe and Sarjeant, 1988, table 3a; Riding, 1990; 2005), despite *Gonyaulacysta dentata* never being particularly common. The reports from the Northwest European Subprovince are widely scattered, and represent extremely sparse relative proportions of this taxon (Fig. 4, Table 2). It has never been recorded from the Tethyan Realm (i.e. the mid palaeolatitudes), or the Southern Hemisphere (Smelror, 1993, p. 149; Riding et al., 2010; 2011). This disparity (or provincialism) can be elegantly demonstrated within the United Kingdom. *Gonyaulacysta dentata* is consistently present in the Late Callovian to earliest Oxfordian of northwest and northeast Scotland, but has never been reported from England despite many studies on this interval (e.g. Woollam, 1980; Riding, 1982; 1987; Woollam and Riding, 1983) (Fig. 4). The presence of *Gonyaulacysta dentata* in France, Germany, Poland and northeast Scotland, and the absence of the species in England may be related to the fact that England was at the margin of Tethys in the Jurassic (Figs. 3,4).

6. Palaeotemperature as a control on the palaeogeographical distribution of *Gonyaulacysta dentata* and other dinoflagellate cyst taxa at the Callovian/Oxfordian transition

6.1. Gonyaulacysta dentata

It is considered that the palaeogeographical distribution of *Gonyaulacysta dentata* was primarily controlled by palaeotemperature. This species is clearly most prominent and consistently present in the Arctic region and northern Scotland with only sporadic, extremely rare occurrences in continental Europe (Fig. 4). It appears that *Gonyaulacysta dentata* had its inception during the Late Callovian (Peltoceras athleta Zone) in the high northerly palaeolatitudes of the Boreal Realm (Thusu, 1978; Smelror, 1988a; Table 2), with the southernmost limit of the consistent occurrences being northern Scotland. The Callovian-Oxfordian transition was a time of significantly lowered palaeotemperatures, although estimates vary on the magnitude of this cooling event (Abbink et al., 2001; Jenkyns et al., 2002; Dromart et al., 2003; Poulsen and Riding, 2003; Cecca et al., 2005; Wierzbowski et al., 2009). This cooling event is considered to have allowed the migration of some individuals of the Arctic species *Gonyaulacysta dentata* southwards into France, Germany and Poland (Fig. 4). Hydrodynamic factors (i.e. ocean currents) may also have influenced the distribution of this species.

The sparsity of *Gonyaulacysta dentata* in continental Europe is demonstrated by the fact that out of an extremely extensive literature, only seven papers record this species (Prauss, 1989; Dimter and Smelror, 1991; Kunz, 1990; Huault, 1999; Birkenmajer and Gedl, 2007; Gedl, 2008a;b). Boreal ammonites were also migrating southwards at this time (Cariou, 1973). The Boreal ammonite family Cardioceratidae had also migrated southwards well into continental Europe during the Early Oxfordian, and Tethyan ammonites had migrated northwards at this time (Cecca et al., 2005, fig. 5). Hence it is suggested that the lowered palaeotemperatures at the Callovian-Oxfordian transition caused the motile dinoflagellates that produced *Gonyaulacysta dentata* to migrate southwards from the cool temperate Boreal Realm into the warm temperate palaeoclimatic belt which included continental Europe at that time (Sellwood and Valdes, 2008, fig. 2; Fig. 4). This means that the sparse, rare occurrences of *Gonyaulacysta dentata* in continental Europe are in the Boreal-Tethyan ammonite zone of mixing (Fig. 4). Other typically Arctic Callovian dinoflagellate cyst species such as

Ctenidodinium? *thulium* (Davies 1983) Jan du Chêne et al. 1986, *Evansia barentsensis* (Smelror 1988) Below 1990, *Evansia dalei* (Smelror & Århus 1989) Below 1990, *Evansia zabra* (Davies 1983) Jansonius 1986 and *Valvaeodinium groenlandicum* (Smelror 1988) Smelror 1988, however, have never been recorded in continental Europe. These taxa are confined to the high northerly latitudes and appear to have been less able to migrate southwards in response to relatively short-lived reductions in palaeotemperature than *Gonyaulacysta dentata*.

6.2. Scriniodinium crystallinum

The large and distinctive cosmopolitan dinoflagellate cyst species *Scriniodinium crystallinum* (Deflandre 1938) Klement 1960 appears to have a mutually exclusive relationship with *Gonyaulacysta dentata* in the UK, and this appears to have been primarily influenced by palaeotemperature. The range base of *Scriniodinium crystallinum* is Late Callovian in England and continental Europe (Riding, 1982; 1987; Prauss, 1989). This bioevent in northern Scotland is intra Early Oxfordian, i.e. significantly younger than further south (Table 3). This difference was attributed to facies control by Hesketh and Underhill (2002), but this seems unlikely because both these areas were within extensive open marine depositional settings. Furthermore, in northern Scotland, the ranges of *Scriniodinium crystallinum* and *Gonyaulacysta dentata* do not overlap (Riding and Thomas, 1997; Riding, 2005; Tables 3, 4). These geographical and temporal distributions suggest that *Scriniodinium crystallinum* was probably produced by a warm-loving dinoflagellate. Hence, in the UK, the climatic cooling which commenced at the Callovian/Oxfordian transition allowed the migration of *Gonyaulacysta dentata* south from the Arctic into northern Scotland and, in very small numbers, parts of continental Europe (Fig. 4; Tables 2, 4). The palaeoenvironment was warmer in England during the Late Callovian than further north, which allowed *Scriniodinium crystallinum* to thrive. As the palaeoclimate ameliorated within the Early Oxfordian (Poulsen and Riding, 2003, fig. 6; Wierzbowski et al., 2009, fig. 6), this species then migrated northwards into northern Scotland (Table 3). This contention is supported by the co-occurrence of *Evansia perireticulata* (Århus et al. 1989) Lentin & Williams 1993 with

Gonyaulacysta dentata in northwest Scotland (unpublished data; Table 4). *Evansia perireticulata* is known to be a cold water species which ranges from the Early Callovian to Mid Oxfordian (Riding and Hubbard, 1999; Riding et al., 1999; Piasecki et al., 2004a). The occurrences of *Evansia perireticulata, Gonyaulacysta dentata* and *Scriniodinium crystallinum* in the northern hemisphere are summarised in Tables 3 and 4.

The range base of *Scriniodinium crystallinum* in Greenland is, like in northern Scotland, intra Early Oxfordian (Cardioceras cordatum Zone) (Piasecki, 1980; Smelror, 1988b; Table 3). It was also reported by Fensome (1979) (as *Endoscrinium oxfordianum* (Sarjeant 1962) Vozzhennikova 1967), Lund and Pedersen (1985), Piasecki and Stemmerik (2004) and Piasecki et al. (2004b) from the Oxfordian of east Greenland. The range of *Scriniodinium crystallinum* in Spitsbergen is Oxfordian-Kimmeridgian (Thusu, 1978; Table 3). However, Davies (1983), Poulsen (1985) and Århus et al. 1989 reported this species from the Callovian of the Arctic. These authors though did not figure this material, which may represent misidentifications. *Scriniodinium crystallinum* is relatively sparse in the high northerly latitudes (Stefan Piasecki, personal communication October 2011) and Smelror (1988a) and Smelror and Below (1992) did not record this species. Further south in continental Europe and Tethys, *Scriniodinium crystallinum* is abundant in the Oxfordian (Riding and Fensome, 2002, fig. 2), which is consistent with the putative warm-loving nature of this species.

The virtually mutually exclusive relationship of *Gonyaulacysta dentata* and *Scriniodinium crystallinum* at the Callovian/Oxfordian transition is therefore further good evidence of the cold-loving nature of the former species (Tables 3, 4).

7. Conclusions

Gonyaulacysta dentata is a large and morphologically distinctive dinoflagellate cyst species with an elongate pentagonal outline, an apicular structure, bicavate cyst organisation, prominent dorsal and lateral sutural crests which are normally denticulate and discontinuous low-relief midventral sutural ridges; furthermore, it lacks a periarchaeopyle. This taxon has been misidentified as *Gonyaulacysta eisenackii* and *Gonyaulacysta jurassica,* hence the diagnosis and description of *Gonyaulacysta dentata* are emended and expanded. It is an extremely reliable index taxon for the Late Callovian to earliest Oxfordian interval of the northern hemisphere. It has never been recorded in large proportions, and typically represents approximately 1% of the dinoflagellate cyst assemblage. Despite its sparsity, the species can be easily recognised at relatively low magnifications due to its large size. *Gonyaulacysta dentata* is confined to the Arctic region and continental Europe. It is consistently present, and is significantly more common, in the Arctic region and northern Scotland. The Callovian-Oxfordian transition was a time of significantly lowered palaeotemperatures, and this allowed low numbers of specimens of *Gonyaulacysta dentata* to migrate southwards into continental Europe. This short-lived dinoflagellate cyst species is interpreted as a primarily Arctic taxon which was able to expand southwards, hence exhibiting a migration pattern similar to the Boreal ammonite family Cardioceratidae. The virtually mutually exclusive relationship of *Gonyaulacysta dentata* and the warm-loving taxon *Scriniodinium crystallinum* in the Late Callovian-Early Oxfordian emphasises the preference of the former species for relatively cool marine waters. This type of detailed study allows the palaeoecological preferences of Mesozoic dinoflagellate cyst taxa to be determined and should enhance the use of these palynomorphs as palaeotemperature proxies.

Acknowlegements

James M. White (Geological Survey of Canada, Calgary) and John E. Williams (Natural History Museum, London) are thanked for assistance in compiling the previous reports of this species. Henry W. Holbrook and Keith J. Henderson drafted Figures 1 and 2 respectively. Sev Kender kindly drew Figures 3 and 4 and reviewed an early draft of the manuscript. The positive input of two anonymous referees is gratefully acknowledged. Caroline F. Adkin and Jayne E. Kmieciak assisted with the production of the Plates. This study was completed under the RCUK Individual Merit project entitled *Global Jurassic dinoflagellate cyst palaeobiology and its applications* awarded to James B. Riding, who publishes with the approval of the Executive Director, British Geological Survey (NERC).

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Fig. 1. The location of the two samples containing *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. which were studied herein. These were collected from the foreshore at Dunans, Staffin Bay, northwest Skye, western Scotland. A – a sketch map of the Staffin Bay area illustrating the foreshore at Dunans where samples DUN 41 and DUN 42 were collected. B, C – the broader geographical context of the Staffin Bay area. Adapted from Riding and Thomas (1997) and Riding and Kyffin-Hughes (2011).

Fig. 2. A line drawing of a dorsal view of an idealised specimen of the relatively broad morphotype of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. with relatively highly denticulate dorsal and lateral sutural crests. The drawing is very loosely based on the holotype of Raynaud (1978, pl. 2/13). Note the elongate subpentagonal outline, the subovoidal endocyst (in the intermediate ornament), the prominent apical horn with a solid, distal apicular structure, the prominent denticulate dorsal and lateral sutural crests, the bicavate cyst organisation (the two polar pericoels are in the lightest ornament), the displaced endoperculum (e – in the dark ornament) and the antapical opisthopyle (o). The plates are labelled using the traditional Kofoidian shorthand nomenclature. The 2pr, 1a and cingular plates are inferred.

Fig. 3. A palaeogeographical map of western Eurasia and adjacent areas for the Late Callovian to Early Oxfordian interval (adapted from Smith et al., 1994 and Cecca et al., 2005) with the locations of primary, in situ records of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. indicated by the 11 black dots. The land areas are indicated in grey and the black lines depict selected modern coastlines.

Fig. 4. A palaeogeographical map of central Laurasia comprising present day Europe and adjacent areas for the Late Callovian to Early Oxfordian (adapted from Smith et al., 1994 and Cecca et al., 2005) with the locations of primary, in situ records of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. indicated by the five solid and the five open circles. The land areas are indicated in grey, and the black lines depict selected modern coastlines. The five solid circles represent occurrences of *Gonyaulacysta dentata* from Scotland (Raynaud, 1978; Riding and Thomas, 1997; Riding, 2005), the central and northern North Sea (Riding et al., 1993) and offshore western Norway (Århus et al., 1989). This region is considered to be within the palaeogeographical range of consistent and relatively common occurrences of this species. The five open circles represent occurrences of *Gonyaulacysta dentata* from France (Huault, 1999), Germany (Prauss, 1989; Dimter and Smelror, 1990; Kunz, 1990) and Poland (Birkenmajer and Gedl, 2007; Gedl, 2008a,b). On the basis of the highly sporadic and rare nature of these occurrences in continental Europe, this region is considered to be an area into which low numbers of *Gonyaulacysta dentata* migrated into as a result of a significant fall in palaeotemperature (see section 6). The direction of this putative migration is indicated by the arrow between Greenland and Norway. The ammonites exhibited similar trends; the most northerly of the west-east lines (alternate dots and dashes, labelled 'T') represents the northern limit of Tethyan forms (Oppeliidae and *Peltoceratoides*) and the most southerly of the west-east lines (solid/hatched, labelled 'C') indicates the southern limit of the Boreal ammonite family Cardioceratidae at the Callovian-Oxfordian transition. The sparse/rare continental European occurrences of *Gonyaulacysta dentata* that lie within this Boreal/Tethyan zone of ammonite mixing support the hypothesis of a southerly migration of this species from the Boreal Realm.

Table. 1. A compilation of the dimensions of 38 specimens of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. from sample DUN 42.

Table 2. A compilation of the documented occurrences of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. from the Callovian and Oxfordian of the northern hemisphere. These records all refer to primary data except the four studies which are asterisked; these are compilations of pre-existing data. The nine contributions in bold font include illustrations of unequivocal material. A triangle (▲ or ▼) indicates that the study extends stratigraphically beyond the interval depicted. Records with squares (■) indicate that the material studied has been positively correlated to ammonite zones. The circles (●) indicate that the samples examined have no ammonite control. Equivocal material is indicated by a question mark.

Table 3. A summary of the occurrences (■) of *Scriniodinium crystallinum* in the Late Callovian to Mid Oxfordian interval of Europe and the Arctic. Note the older, Late Callovian, range base in England and continental Europe (France, Germany etc.) than Scotland and areas to the north, where this bioevent is at the Callovian/Oxfordian transition. There are no unequivocal reports of *Scriniodinium crystallinum* from Arctic Canada and the Barents Sea region (e.g. Smelror and Below, 1992, fig. 3). A triangle (▲) indicates that the range extends stratigraphically higher than the interval depicted. Three dots (...) denote the absence of *Scriniodinium crystallinum.*

Table 4. A summary of the occurrences of *Evansia perireticulata* (EP) and *Gonyaulacysta dentata* (GD) in the Early Callovian to Early Oxfordian interval of continental Europe, Scotland, Norway, Greenland, Russia and the Arctic. The reports of *Gonyaulacysta dentata* from France, Germany and Poland represent extremely rare occurrences. Both these species have never been reported from England. Not all these occurrences are correlated to the ammonite zonation, see Table 2. A triangle (▲) indicates that the range extends stratigraphically higher than the interval depicted. Three dots (...) denote the absence of *Evansia perireticulata* and *Gonyaulacysta dentata.*

Plate I. Three well-preserved specimens of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. from the Lower Oxfordian part of the Dunans Clay Member of the Staffin Shale Formation at Dunans, Isle of Skye, western Scotland. All specimens are housed in the collections of the British Geological Survey, Nottingham, UK. The sample number and figured specimen number (prefixed MPK), slide number (prefixed MPA) and England Finder coordinates are provided. Note the apical horn which is variable in length and shape, the bicavate cyst organisation which may approach circumcavate, the sharply angular subpentagonal outline of the pericyst, the large, subovoidal endocyst, the displaced endoperculum (1-6), the highly variably denticulate dorsal and lateral sutural crests, the low, discontinuous smooth midventral sutural ridges and the antapical opisthopyle (1-6).

1-3. Specimen MPK 14210. Sample DUN 42, slide MPA 14067/12, England Finder coordinate Q55/1. A relatively broad specimen in dorsal view; a high to low focus sequence. Note the large denticle on the left of the hypocyst; this marks the 2’’’/3’’’/1p plate triple junction. The specimen is 104 µm long and 67 µm wide; the scale bar in 1 represents 50 µm.

4-6. Specimen MPK 6651. Sample DUN 41, slide MPA 14066/1, England Finder coordinate R53/3. An elongate specimen in ventral view; a high to low focus sequence. The diagonal low sutural ridge between plates 2’’’ and 1p is clearly visible on the hypocyst in 4. The specimen is 122 µm long and 64 µm wide; the scale bar in 4 represents 50 µm.

7-9 Specimen MPK 14211. Sample DUN 41, slide MPA 14066/1, England Finder coordinate K48/3. A relatively large specimen which is intermediate in width in oblique dorsal view; a high to low focus sequence. Note the extremely prominent denticle on the left of the hypocyst which marks the 2’’’/3’’’/1p plate triple junction and the low midventral sutural ridges in 9. The specimen is 129 µm long and 69 µm wide; the scale bar in 7 represents 50 µm.

Plate II. 1, 2 - A large, very well-preserved specimen in ventral view of the relatively broad morphotype of *Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emend. nov. from sample DUN 42, collected from the Lower Oxfordian part of the Dunans Clay Member of the Staffin Shale Formation at Dunans, Isle of Skye, western Scotland. 1 – low focus; 2 – high focus. The BGS specimen number is MPK 6650 and it is housed in the collections of the British Geological Survey, Nottingham, UK. The slide number and England Finder coordinate are MPA 14067/2 and G47/2 respectively. Note the prominent apical horn, the bicavate cyst organisation, the angular subpentagonal outline of the pericyst, the prominent subovoidal endocyst, the displaced endoperculum, the denticulate dorsal and lateral sutural crests which change to low ridges at the anterior part of the periarchaeopyle and the antapical opisthopyle. The prominent, highly denticulate lateral sutural crest on the right of the hypocyst which appears to be attenuated is the 2’’’/3’’’ plate boundary. The scale bar represents 50 μm.