1   **The temporal and spatial distribution of Triassic dinoflagellate cysts**

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8   **Abstract**

9

10   The records of dinoflagellate cysts from the Late Triassic, the time during which they first

11   appear abundantly in the geological record, are reviewed. Most of the Triassic palynological

12   literature pertains to terrestrial palynomorphs, thus it is challenging to establish a global

13   picture of the temporal and spatial distribution of Late Triassic dinoflagellate cyst around the

14   supercontinent of Pangea. Moreover, data on Late Triassic dinoflagellate cysts are dispersed,

15   and there are currently no records of dinoflagellate cysts from many marine successions. With

16   the exception of an Australian record of the dinoflagellate cyst *Sahulidinium ottii* from the

17   late Mid Triassic, and a possible early Carnian occurrence of, among others, *Rhaetogonyaulax*

18   in the Swiss Alps, cyst-forming dinoflagellates first appeared relatively synchronously around

19   Pangea from the late Carnian. There are three to six species of pre-Norian species globally,

20   whereas species richness exceeded 25 by the end of the Norian. During the Rhaetian, marine

21   seaways had gradually opened due to sustained continental breakup, allowing the expansion

22   of dinoflagellates into many European basins. New species are present, some known only

23   from restricted areas, whereas others like *Dapcodinium* appear to have a global distribution.

24   The majority of Triassic dinoflagellate cyst taxa do not extend into the Jurassic.

28

1.   Introduction

1.1.   Background

Knowledge of the origination of cyst-forming dinoflagellates and their geographical and stratigraphical distribution around Pangea during the Late Triassic is relatively poor. These widely separated data, many from studies not principally focussed on dinoflagellate cysts, makes it difficult to obtain a comprehensive overview of their spatial and temporal distributions. Knowledge of the composition of the various Late Triassic assemblages varies due to a lack of quantitative data, and is therefore in part poorly known. Another complicating factor regarding their evolution includes the fact that the Late Triassic spans ~36 my (Lucas, 2010; Gradstein et al., 2012, Ogg et al. 2016) and the stratigraphical resolution is relatively poor, with a lack of macrofossil data and geochronological dating in most areas. In addition, many relevant publications are relatively old and have applied chrono- and lithostratigraphical nomenclature, which now is outdated, thereby hampering reliable age assignments and correlation. Determining exact stratigraphical occurrences and establishing correlations are therefore difficult, and age assignments of the dinoflagellate cyst records have, as a result, varying levels of uncertainty. Most of the ages given below are those from published studies and many of these have relatively large uncertainties in the ranges quoted. The relationships between the dinoflagellate cysts that evolved in northern Pangea and their counterparts from the southern margins of Neotethys are therefore unclear. To date, there are no records of Late

49 Triassic dinoflagellate cysts from intermediate regions such as the western or eastern margins

50 of Pangea.

51 As dinoflagellate cysts are important for relative age dating and correlation, as well as

52 proxies for some paleoenvironmental aspects, understanding their occurrence in time and

53 space is valuable (Stover et al., 1996). The nature of the data, as outlined below, makes it

54 challenging to establish an overview of Late Triassic dinoflagellate cyst distribution. A better

55 understanding of their occurrences in time and space is therefore required. This overview and

56 synopsis cannot provide comprehensive answers to all these questions. However, by

57 providing a global overview and presenting the state of the art on dinoflagellate cyst

58 distributions in space and time during the Late Triassic Epoch, we hope to provide a

59 significantly improved understanding. This paper therefore seeks to review existing

60 knowledge of the occurrences of Late Triassic dinoflagellate cysts along the coastlines of

61 Pangea. Following a summary of the known dinoflagellate cyst records from the various

62 geographical areas, their records and occurrences along the margins of Pangea are discussed,

63 in a stratigraphical context with reference to the various geographical records. A short note on

64 their paleoenvironmental significance is included. However to make further advances in this

65 regard, more work is needed in areas with marine Upper Triassic successions.

66

67 *1.2.   Triassic dinoflagellate cysts, state-of-the-art*

68 During the Late Triassic, landmasses were relatively symmetrically situated around the

69 equator, forming Pangea (Figure 1). Along the margins of this supercontinent, marine

70 deposition occurred. However, most Upper Triassic successions are terrestrial, having been

71 deposited in various continental, siliciclastic depositional systems produced by continental

72 rifting. During the Late Triassic, rifting increased, eventually leading to seafloor spreading

73 and the breakup of Pangea (Ziegler et al., 1983, 2003; Golonka, 2004, 2007; Golonka et al.,

74   2018). Consequently, marine deposition took place in some of these rifts, and the areal extent

75   of marine borderlands increased.

76   Surrounding the Late Triassic continents, the first abundant cyst-forming

77   dinoflagellates evolved, developed and spread into these relatively shallow marine

78   environments. According to MacRae et al. (1996), about 24 species of dinoflagellate cysts had

79   developed globally by the Norian. Dinoflagellate cysts continued to expand throughout the

80   Jurassic to peak in diversity in the Cretaceous (MacRae et al., 1996). Dinoflagellates represent

81   a substantial part of the phytoplankton population in the oceans today, and are one of the

82   major primary producers (Wiggan et al., 2018). In the fossil record, dinoflagellate cysts

83   represent valuable tools for biostratigraphy, palaeoclimatology and palaeoecology. This is

84   despite the fact that only about 15 % of extant dinoflagellate species produce fossilisable cysts

85   (Head, 1996).

86

87   Figure 1. The palaeogeography of the Late Triassic illustrating the locations of the first

88   occurrences of dinoflagellate cyst records (adapted from Golonka et al. 2018).

89

90   The first appearance of fossil dinoflagellate cysts in the geological record has been

91   extensively debated (Bujak and Williams, 1981; Fensome et al., 1999). Le Herisse et al.

92   (2012) ruled out the presence of body fossils of dinoflagellate cysts older than the Triassic,

93   but they are cytologically primitive and their phylogenetic lineages may be as old as the

94   Precambrian (Evitt, 1985; Fensome et al., 1999). This is also indicated by biogeochemistry

95   studies on dinosteranes (Moldowan et al. 1996, Moldowan & Talyzina 1998). The Australian

96   peridiniphycidaen species *Sahulidinium ottii* is however the oldest known fossil dinoflagellate

97   cyst (Harland et al., 1975; Stover and Helby, 1987). The reasons and circumstances leading to

98   their appearance at this time is unclear. Falkowski et al. (2004a, b) suggested that changes in

99   the ocean chemistry was a major factor. *Sahulidinium ottii* was described from the upper

100   Middle Triassic (Ladinian) to lowermost Carnian of Australia (Helby et al. 1987a; Riding et

101   al. 2010), however independent dating is lacking. Despite this isolated, probably uppermost

102   Middle Triassic occurrence, on a global scale, dinoflagellate cysts first appeared and evolved

103   with relatively low diversities during the Late Triassic (MacRae et al., 1996). Whether these

104   represent the first significant evolutionary development of dinoflagellates, or cyst-forming

105   dinoflagellates, or whether the longest lineages have developed over time is still not fully

106   understood. Following *S. ottii* stratigraphically, the peridiniphycidaen genus *Rhaetogonyaulax*

107   appears to be the first to emerge around the shores of Pangea during the Carnian (e.g. Riding

108   et al., 2010, Vigran et al., 2014; Paterson and Mangerud, 2015).

109   On a global scale, Late Triassic palynological data are relatively extensive but mainly

110   comprises records of terrestrially-derived palynomorphs. Several useful reviews on these

111   terrestrial floras have been produced, including Helby et al. (1987a), Cirilli (2010), Kürschner

112   and Herngreen (2010), Césari and Colombi (2013) and Li et al. (2016). In addition, papers on

113   the Triassic-Jurassic (Tr–J) boundary provide important contributions on dinoflagellate cyst

114   occurrences (see e.g. Lindström 2016). Despite the early pioneer work on Late Triassic

115   palynology, including dinoflagellate cysts from the present high Arctic (Wiggins, 1973;

116   Fisher and Bujak, 1975; Bujak and Fisher, 1976), relatively little work has been undertaken

117   on this region since. Recent work on Late Triassic palynology in the Barents Sea area has,

118   however, revealed several records of dinoflagellate cysts (Vigran et al., 2014).

119   Late Triassic dinoflagellate cysts have been extensively recorded, but many papers in

120   which reports are present are principally focussed on the biostratigraphy of terrestrial

121   palynomorphs (e.g. Morbey and Neves, 1974; Smith, 1974; Warrington, 1974; Felix, 1975;

122   Bjærke and Manum, 1977; Warrington, 1978; Suneby and Hills, 1988; Aghanabati et al.,

123   2002, 2004; Warrington, 2005; Paterson and Mangerud, 2015, Vigran et al., 2014). In

124   addition, papers on the Triassic–Jurassic boundary (e.g. Warrington, 1983; Mettraux and

125   Mohr, 1989; Embry and Suneby, 1994; Warrington et al., 1995; Lindström and Erlström,

126   2006; Kürschner et al., 2007; Bonis et al., 2009; Ruckwied and Götz, 2009) and papers on

127   sequence stratigraphy (e.g. Paterson et al., 2016; Lindström et al., 2017b) have recorded Late

128   Triassic dinoflagellate cysts. The recorded genera include the suessiaceans *Beaumontella,*

129   *Lunnomidinium, Noricysta, Suessia* and *Wanneria,* together with the peridiniphycidaen forms

130   *Dapcodinium, Hebecysta*, *Heibergella, Rhaetogonyaulax*, *Sahulidinium, Sverdrupiella* and

131   *Valvaeodinium* (Table 1). The composition of these Late Triassic assemblages varies, and is

132   often poorly known in part due to a lack of quantitative data. Another complicating factor

133   regarding their evolution includes the fact that the Late Triassic spans ~36 myr (Lucas, 2010;

134   Gradstein et al., 2012, Ogg et al. 2016), and the stratigraphical resolution is relatively poor,

135   with a lack of macrofossil data and geochronological dating in many areas. Determining exact

136   stratigraphical occurrences and establishing correlations are therefore difficult, and age

137   assignments of the dinoflagellate cyst records have, as a result, varying levels of uncertainty.

138

139   TABLE 1. List of dinoflagellate cyst taxa appearing in Upper Triassic successions.

140   References to the author citations can be found in Williams et al. (2017).

141

142   Most of the ages given in section 3 below, are taken from published studies, and as

143   few independent age controls are available, there are relatively large uncertainties in the

144   ranges quoted (Figure 2). This paper summarises all published Late Triassic dinoflagellate

145   cyst occurrences, followed by a review of their stratigraphical importance and geographical

146   extent along the margins of Pangea.

147

148   **2.   Records of Late Triassic dinoflagellate cysts from various regions**

149

2.1.   The present Arctic

During the Late Triassic, large volumes of siliciclastic sediment were deposited along

the northern margins of Pangea. These now comprises the offshore and onshore successions

of the North Slope of Alaska, the Sverdrup Basin in the Canadian Arctic, Svalbard in the

Norwegian Arctic, the Barents Sea spanning the Norwegian-Russian sector and various basins

along the northern margins of Russia. Transgressive–regressive cycles have been confidently

correlated throughout this vast area (Mørk et al., 1989; Embry, 1997; Egorov and Mørk, 2000;

Mørk and Smelror, 2001), partially well dated by ammonites (e.g. Dagys et al. 1993).

Terrestrially derived material, mainly pollen and spores, dominate palynofloras from

the Upper Triassic successions of the present Arctic (e.g. Suneby and Hills, 1988; Hochuli et

al., 1989; Ilyina and Egorov, 2008; Vigran et al., 2014). However, marine palynomorphs are

relatively common in parts of these successions (e.g. Felix and Burbridge, 1978; Hochuli et

al., 1989; Vigran et al., 2014) and provide valuable information, for example on

palaeoecology. These marine assemblages mainly comprise acritarchs, largely the spine-

bearing genera *Micrhystridium* and *Veryhachium*, but also include levels dominated by

dinoflagellate cysts.

2.1.1.   The Norwegian Arctic (the Barents Sea area including Svalbard)

During the Triassic, the Barents Sea (including Svalbard) was an intracratonic basin,

situated within a large embayment that had developed during the Late Palaeozoic (Worsley,

2008). During the Late Triassic, most of this embayment was filled by vast quantities of

sediment sourced from the eastern and south-western margins of the basin. Triassic rocks

extensively outcrop in the Svalbard Archipelago, and thick deposits are widely distributed in

the subsurface of the Barents Sea (Mørk et al., 1982; Rønnevik et al., 1982; Faleide et al.,

174   1984; Mørk et al., 1993; van Veen et al., 1993; Riis et al., 2008). Palynological studies of the

175   Late Triassic which reported dinoflagellate cysts include Smith et al. (1975), Bjærke (1977),

176   Bjærke and Dypvik (1977), Bjærke and Manum (1977), Hochuli et al. (1989), Nagy et al.

177   (2011), Mueller et al. (2014), Vigran et al. (2014), Paterson and Mangerud (2015, 2017) and

178   Paterson et al. (2016, 2018. No records of dinoflagellate cysts below the Kapp Toscana Group

179   have been observed, with the exception of questionable *Sentusidinium*-like cysts recovered

180   from the Botneheia Formation at one locality in Spitsbergen (Vigran et al., 2014, pl. 5).

181   Records of dinoflagellate cysts from the Island of Hopen (Smith et al., 1975; Bjærke

182   and Manum, 1977; Vigran et al., 2014; Paterson and Mangerud, 2015; Paterson et al., 2016)

183   are based on material from the lower and middle Flatsalen Formation, which is assigned an

184   early Norian age based on ammonites (Korčinskaya, 1980; Smith, 1982). A dinoflagellate cyst

185   assemblage, which is dominated by *Rhaetogonyaulax rhaetica,* is recorded in this unit

186   (Paterson and Mangerud, 2015). *Rhaetogonyaulax rhaetica* is also recorded from the

187   underlying De Geerdalen Formation (Middle to Upper Carnian) in very low proportions.

188   Although devoid of age diagnostic macrofossil, the age of the Geerdalen Formation is well

189   constrained (Paterson & Mangerud 2015, page 103–104).

190   On Spitsbergen, the oldest records of dinoflagellate cysts are from the Isfjorden

191   Member of the De Geerdalen Formation (Upper Carnian) and in the Knorringfjellet/Flatsalen

192   formations (Norian). Occurences from the De Geerdalen Formation are largely sporadic and

193   rare, and are mainly confined to the upper part. However, at one locality (Festningen), they

194   sporadically occur in high abundances. At the same locality in the Knorringfjellet Formation

195   (Norian), the dominant species is still *Rhaetogonyaulax rhaetica*, but often *Heibergella* and

196   *Sverdrupiella* are also present (Vigran et al., 2014). This association was also observed at

197   Wilhelmøya Island in eastern Svalbard (Vigran et al., 2014). A rich assemblage of

198   *Rhaetogonyaulax*, including *Rhaetogonyaulax rhaetica,* together with *Sverdrupiella,* was also

recorded from the Flatsalen Formation of a Sentralbanken core (7533/2-U-2) in the central

Barents Sea (Vigran et al., 2014; Paterson et al., 2018). The latter study concluded that the

records of dinoflagellate cysts in the overlying Norian–Rhaetian Svenskøya Formation

observed in core 7532/2-U-1 by Vigran et al. (2014) are not *in situ*, as they are in an interval

with extensive rip-up clasts and are interpreted as reworking.

In the southern Barents Sea, Vigran et al. (2014) and Paterson and Mangerud (2017)

recorded low numbers of *Rhaetogonyaulax rhaetica* in Norian strata from exploration wells,

coeval with the Hopen successions. A few species of *Noricysta* and *Sverdrupiella* were also

found in an offshore well in strata of presumed Norian age by Vigran et al. (2014). In the few

Upper Triassic successions dominated by acritarchs from exploration wells in the southern

Barents Sea area, dinoflagellate cysts are however rare. This probably indicates a proximal,

paralic environment with minor marine incursions, where the early Norian transgression

barely reached the southern margins of the basin (Bugge et al., 2002; Glørstad-Clark et al.,

2010; Klausen et al., 2015).

2.1.2. The Sverdrup Basin, Canadian Arctic

Further west in the huge embayment which includes the Barents Sea area, the Sverdrup Basin

was an active depocentre between the Early Carboniferous (Mississippian) and the Neogene.

During the Late Triassic, this large rift/sag basin gradually subsided and was mainly filled by

deltaic deposits from the south and southwest. During the Norian, it also received sediments

from "Crockerland" to the north (Embry, 2009, 2011).

The palynology of early exploration wells in the Sverdrup Basin, where Upper

Triassic rocks are extensively exposed, has been investigated. This pioneering work on Late

Triassic dinoflagellate cysts from the Triassic part of the Heiberg Formation proved highly

significant. Macrofossil data are present but scarce, indicating a Norian age (Suneby and Hills

224 1988, p. 348). The dinoflagellate cyst assemblages were described to various degrees in a

225 number of papers including Brideaux (1975), Felix (1975), Fisher and Bujak (1975), Bujak

226 and Fisher (1976), Souaya (1976), Felix and Burbridge (1978), Staplin 1978 and Fisher and

227 van Helden (1979). Suneby and Hills 1988 established the first palynological zonation for this

228 unit based on a quantitative palynological approach for the Heiberg Formation. Embry and

229 Suneby (1994) later focused primarily on the palynology of the Triassic–Jurassic boundary.

230 Fisher and Bujak (1975) and Bujak and Fisher (1976) worked on material from eight

231 wells from the western Queen Elizabeth Islands in the western Sverdrup Basin. Bujak and

232 Fisher (1976) described four new genera from the lower Heiberg Formation: *Sverdrupiella*,

233 with eleven new species (nine of which are still valid); *Heibergella* and *Noricysta*, with three

234 new species each; and *Hebecysta*, as a monotypic genus (*Hebecysta brevicornuta*). The

235 samples were rich in the species *Sverdrupiella mutabilis*, *Sverdrupiella sabinensis,*

236 *Sverdrupiella septentrionalis* (including *Sverdrupiella cristata* and *Sverdrupiella downeii)*

237 and *Sverdrupiella usitata. Heibergella* was also relatively common, with *Heibergella*

238 *asymmetrica* being the most common species of this genus. The other species were sporadic

239 and rarer. *Noricysta fimbriata*, *Noricysta pannucea* and *Noricysta varivallata* were largely

240 recorded only from one sample in the Sandy Point L-46 well. Several of the new species of

241 *Sverdrupiella,* including *Sverdrupiella baccata*, *Sverdrupiella manicata*, *Sverdrupiella*

242 *ornaticingulata, Sverdrupiella raiaformis* and *Sverdrupiella spinosa,* have never been

243 reported from elsewhere. *Rhaetogonyaulax* was reported as being extremely rare and was only

244 present in two cuttings samples (Bujak and Fisher 1976). However, according to Fisher and

245 Bujak (1975), it is persistently present. Fisher and van Helden (1979) later stated, of

246 *Rhaetogonyaulax:* "Representatives of the genus are often abundant in Late Triassic

247 sediments from the Arctic Islands". They noted the resemblance to *Rhaetogonyaulax rhaetica*

248 from the Rhaetian of England. Their three new species (*Rhaetogonyaulax testacea,*

249 *Rhaetogonyaulax tortuosa* and *Rhaetogonyaulax uncinata*) were later reclassified as a junior

250 synonym of *Rhaetogonyaulax rhaetica* (Below, 1987a,b).

251   Felix and Burbridge (1977, 1978) reported abundant *Sverdrupiella usitata* from

252 offshore exploration wells, but not from equivalent successions onshore. They also recorded

253 *Hebecysta brevicornuta*, *Heibergella asymmetrica*, *Noricysta fimbriata*, *Rhaetogonyaulax*

254 *arctica* (as *Shublikodinium arcticum*) and *Rhaetogonyaulax rhaetica.* Felix and Burbridge

255 (1977, 1978) also noted that *Rhaetogonyaulax arctica* is present abundantly in the Schei Point

256 Group, underlying the Heiberg Formation. The upper part of their Schei Point Group is now

257 the Barrow Member of the Heiberg Formation. Those authors implied a Norian age for these

258 assemblages based on palynological correlation, but did not exclude the possibility that they

259 range down into the Carnian. The only record of dinoflagellate cysts below the Barrow

260 Member is *Rhaetogonyaulax arctica*. In contrast to the species listed above, Felix (1975)

261 reported common *Rhaetogonyaulax rhaetica* in the Heiberg Formation from nearby Ellef

262 Ringnes Island, however, no quantitative data were provided.

263   Suneby and Hills (1988) erected the first palynological zonation of the Heiberg

264 Formation and the uppermost Barrow Formation based on outcrop samples. They reported

265 rich assemblages of terrestrial palynomorphs and dinoflagellate cysts from outcrops on

266 Ellesmere Island from the eastern Sverdrup Basin. Four palynozones were established, three

267 of which are Late Triassic. The oldest one (the *Triancoraesporites ancorae–*

268 *Camarozonosporites laevigatus* Biozone) was subdivided into two subzones. The youngest of

269 these was characterised by the first appearance of the dinoflagellate cysts *Hebecysta*

270 *brevicornuta, Heibergella aculeata, Heibergella asymmetrica, Noricysta fimbriata, Noricysta*

271 *pannucea, Sverdrupiella mutabilis, Sverdrupiella sabinensis* and *Sverdrupiella usitata*. The

272 subzones were assigned a Norian age based on an ammonite and bivalves (Norford et al.,

273 1973; Embry, 1982). At McKinley Bay, near the basin margin, this subzone was only

274 recognised in two closely spaced samples, indicating facies control of these assemblages. A

275 few dinoflagellate cysts were also recorded from two localities in a narrow interval within the

276 underlying subzone; including *Valvaeodinium* (as *Comparodinium*), *Rhaetogonyaulax* sp. cf.

277 *R. dilatata* and *Suessia* sp. cf. *S. swabiana.* This subzone was tentatively assigned to the early

278 to late middle Norian.

279

280 *2.1.3. Alaska*

281   During the Late Triassic, Alaska was situated on the northern shores of Pangea,

282 probably facing the open Panthalassa Ocean (Figure 1). Triassic marine, sedimentary rocks of

283 the Shublik Formation were deposited on a shallow shelf that was believed to be an upwelling

284 zone, but this interpretation is not universally accepted (Parrish et al., 2001; Embry et al.,

285 2002). The Shublik Formation outcrops across most of the northern front of the Brooks

286 Range, extending into the North Slope subsurface and gradually pinching out into its distal

287 equivalent, the Otuk Formation (Kelly et al., 2007). Independent evidence for the Shublik and

288 Otuk formations being Late Triassic in age is the occurrence of the bivalve genus *Monotis*

289 (Helby et al. 1987b). Despite extensive exploration of these units, very few palynological data

290 on the Shublik and Otuk formations have been published.

291   The first published Late Triassic dinoflagellate record from this region was the

292 pioneering work of Wiggins (1973) on core material from an exploration well in the Shublik

293 Formation on the Alaskan North Slope. This work focused on taxonomy, describing 10 new

294 species of *Shublikodinium*; this genus was reclassified and included in *Rhaetogonyaulax* (see

295 Stover and Evitt, 1978; Lentin and Williams, 1989). *Shublikodinium* was split too broadly at

296 the species level by Wiggins (1973), and Stover and Evitt (1978) simplified the 10 species

297 into two, *Rhaetogonyaulax arctica* and *Rhaetogonyaulax dilatata.* Wiggins (1973) also briefly

298 mentioned the occurrence of undescribed dinoflagellate cysts in his material. Later, Helby et

299 al. (1987b) referred to *Sverdrupiella* occurrences from the middle to late Norian of the

300 Shublik Formation in Alaska. The dinoflagellate cysts were recorded from layers with two

301 different species of the bivalve *Monotis.*

302   In an open file report, Witmer et al. (1981) mentioned three Upper Triassic

303 dinoflagellate zones and the occurrence of foraminifera. These authors listed dinoflagellate

304 cysts including *Hebecysta* spp., *Noricysta* spp., *Suessia swabiana* and *Sverdrupiella* spp. Most

305 of the studied wells were barren or had only rare dinoflagellate cyst occurrences; and the few

306 specimens recorded were very poorly preserved.

307

308 Figure 2. A composite range chart of Late Triassic dinoflagellate cysts from various

309 geographical areas (Time Scale from Gradstein et al. 2016).

310

311 *2.1.4. Arctic Russia*

312   Interestingly, despite the existence of ammonite-dated, fossiliferous marine

313 successions from East Siberia (Russian Arctic) (Dagys et al., 1993, Egorov and Mørk, 1998;

314 Konstantinov et al., 2003; Ilyina and Egorov, 2008), there are no published records of Late

315 Triassic dinoflagellate cysts. However, *Rhaetogonyaulax* is present in Upper Triassic

316 successions in the Anabar region, Northern Siberia (personal communication, Vera Pospelova

317 2018). We attribute the lack of published records of Late Triassic dinoflagellate cysts from

318 this region to previous studies focussing exclusively on terrestrial palynomorphs.

319

320 *2.2. Europe*

321   The breakup of Pangea began during the Norian in the Late Triassic, and included the

322 opening of parts of the western Tethys (Hauser et al., 2002). However, in southern Europe,

the first rifting phases started in the Early Triassic, and carbonate platforms developed in the Calcareous Alps and the Inner Carpathians (Ciarapica, 2007; Golonka, 2007; Golonka et al., 2018). Many of the classic European Upper Triassic (Keuper) successions were non-marine. By contrast, during the Rhaetian, the incursion of intercontinental seaways into central Pangea caused the marine inundation of central Europe (Manspeizer, 1994, Hesselbo, 2012). Consequently, dinoflagellate cysts are absent in most pre-Rhaetian strata, although marine deposition took place earlier for example along the Neotethyan margins. The fact that there are very few records pre-dating the Rhaetian could be due to the poor preservation potential of the Neotethyan carbonate platforms and subsequent Alpine metamorphism may have also been influential.

Records of pre-Rhaetian dinoflagellate cysts in Europe include Hochuli and Frank (2000) from the Lower Carnian (Julian) marine dolomites of the Lower Raibl Group successions in eastern Switzerland in the Swiss Alps. These authors recorded indeterminate dinoflagellate cysts, cf. *Noricysta fimbriata,* cf. *Noricysta pannucea* and *Rhaetogonyaulax* cf. *wigginsii*. Hochuli and Frank (2000, 2006) made a correlation based on pollen and spores to the Lower Carnian (Julian) Stuttgart Formation of Germany; these are the oldest low latitude pre-Rhaetian dinoflagellate cysts. Heunisch (1986), however, reported acritarchs, but no dinoflagellate cysts, from the Carnian of Germany. A recent PhD thesis reported *Heibergella* sp. and indeterminate dinoflagellate cysts from boreholes in the Carnian Veszprém Marl Formation in the Transdanubian Range in Hungary (Baranyi 2018). By contrast, Götz et al. (2009) found that apparently marine Triassic–Jurassic boundary successions in Hungary are devoid of dinoflagellate cysts. Mettraux and Mohr (1989) reported *Rhaetogonyaulax rhaetica* from the Rhaetian of western Switzerland; *Dapcodinium priscum* was also observed in the uppermost strata close to the Triassic–Jurassic boundary. Similarly, Schneebeli-Hermann et

347   al. (2018) recorded *Dapcodinium priscum*, *Rhaetogonyaulax rhaetica* and *Valvaeodinium* spp.

348   from the Rhaetian of northern Switzerland.

349   Several authors have reported dinoflagellate cysts from Upper Triassic and Lower

350   Jurassic Tethyan marginal shelf facies in Austria. Karle (1984) reported common

351   *Rhaetogonyaulax rhaetica* from the upper Rhaetian mergel-facies in the Calcareous Austrian

352   Alps. From the Kendelbachgraben in Austria, Morbey and Neves (1974) reported

353   *Rhaetogonyaulax rhaetica* from the lowermost Rhaetian, and *Dapcodinium* and *Heibergella*

354   (as *Rhombodella*) in overlying Rhaetian strata. Morbey (1975) published a major, pioneering

355   biostratigraphical and taxonomic study. He described *Beaumontella caminuspina* (as

356   *Cleistosphaeridium mojsisovicsii*), *Heibergella kendelbachia* (as *Rhombodella kendelbachia)*,

357   *Suessia swabiana* and *Valvaeodinium koessenium* (as *Comparodinium koessenium*). Morbey

358   (1975) also reported *Dapcodinium priscum* and *R. rhaetica* from the Rhaetian. Hoelstein

359   (2004) recorded *Beamontella langii, Rhaetogonyaulax rhaetica*, *Suessia swabiana*,

360   *Valvaeodinium koessenium* and *Wanneria listeri* from the Kössen beds of Austria. He

361   demonstrated that the dinoflagellate cyst assemblages varied markedly in abundance

362   throughout the successions. Important multidisciplinary contributions from this region include

363   Krystin et al. (2007), Kürschner et al. (2007) and Bonis et al. (2009). Kürschner et al. (2007)

364   integrated quantitative palynological data from the Tiefengraben with independent dating

365   methods and clearly demonstrated the change from abundant *Rhaetogonyaulax rhaetica* to

366   *Dapcodinium priscum* immediately below the Triassic–Jurassic boundary. Note the

367   assemblage composition changed within the acme of *Dapcodinium priscum*, including the

368   inception of *Beaumontella caminuspina* (as *Cleistosphaeridium mojsisovicsii*), *Beaumontella*

369   *langii* and *Valvaeodinium koessenium*.

370   From the Tatra Mountains of Slovakia, Ruckwied and Götz (2009) reported rare to

371   common occurrences of *Rhaetogonyaulax rhaetica* in a Triassic–Jurassic boundary section

which is dominated by pollen and spores and calibrated by conodonts and foraminifera. This

region was situated in an embayment of the Tethyan shelf at this time (Golonka, 2004), and

Rhaetogonyaulax rhaetica was also recorded, although less frequently, in the lowermost

Hettangian. Ruckwied and Götz (2009) observed rare *Dapcodinium priscum* from the Upper

Rhaetian, with a more continuous record in the Hettangian. Michalík et al. (2010) also

reported *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* from this area but stressed that

marine palynomorphs are rare, attesting to shallow marine conditions. From the nearby

Pieniny Klippen Belt in the West Carpathian of Poland, reworked *Rhaetogonyaulax rhaetica*

was recorded and illustrated from Middle Jurassic successions by Gedl (2008) and Barski et

al. (2012).

Upper Triassic strata from a borehole in Western Ciscaucasia, southern Russia, in the

eastern Paleotethys, was studied by Yaroshenko (2007). *Dapcodinium priscum* and

Rhaetogonyaulax were recorded, together with pollen and spores that are believed to be

Rhaetian. However, this correlation is somewhat uncertain and the palynomorph assemblages

could be as old as Norian.

The records of Late Triassic dinoflagellate cysts from the UK are all confined to the

Rhaetian, and were eustatically controlled. The first record of Late Triassic dinoflagellate

cysts was from Gloucestershire, southwest England (Sarjeant, 1963). Subsequently, Rhaetian

dinoflagellate cyst assemblages from onshore and offshore UK, have been extensively

reported by, for example, Warrington (1974, 1977a, 1977b, 1978, 1983, 1997, 2005),

Warrington et al. (1986, 1995) and Bucefalo Palliani and Buratti (2006). Although the

primary focus was on the rich terrestrially derived floras, Warrington (1974) first recognised

the stratigraphical importance of *Dapcodinium priscum* and *Rhaetogonyaulax* in the Rhaetian

of Lancashire, northwest England. Later, Warrington (1997, 2005) reported other

396   dinoflagellate cysts, such as *Beaumontella caminuspina*, *Beaumontella langii* and

397   *Valvaeodinium koessenium* from England.

398   Bucefalo Palliani and Buratti (2006) studied the Rhaetian of St Audrie's Bay and

399   Manor Farm in southwest England. They recorded rich dinoflagellate cyst assemblages

400   dominated by *Rhaetogonyaulax rhaetica* from the uppermost Mercia Mudstone and the

401   Penarth groups. In addition, frequent *Suessia* sp. A from the Blue Anchor Formation and

402   common *Dapcodinum priscum* from the uppermost Cotham Member (Lilstock Formation)

403   were observed. Rare records of other species, including some not previously recorded in the

404   UK, included *Heibergella asymmetrica*, *Heibergella* sp. cf. *H. salebrosacea, Noricysta*

405   *pannucea, Suessia swabiana* and *Sverdrupiella mutabilis*. Bucefalo Palliani and Buratti

406   (2006) presented semi-quantitative data, related their dinoflagellate cyst record to the

407   palaeogeography and postulated migration events. These authors proved that dinoflagellate

408   cysts were relatively diverse and rich by the Late Rhaetian in the UK.

409   Records of Rhaetian dinoflagellate cysts from Denmark and southern Sweden include

410   Dybkjær (1988, 1991), Batten et al. (1994), Lindström (2002), Nielsen (2003), Lindström and

411   Erlström (2006, 2007), Petersen et al. (2013) and Lindström et al. (2017a). An inverse

412   quantitative relationship between *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* was

413   noted by Batten et al. (1994), suggesting a relationship between brackish and marine

414   environments.

415   Lindström (2002) described *Lunnomidinium scaniense* from the Rhaetian Höganäs

416   Formation of southern Sweden from a succession dominated by pollen and spores.

417   ?*Beaumontella caminuspina, Dapcodinium priscum, Rhaetogonyaulax rhaetica* and

418   *Rhaetogonyaulax* sp. were also present sporadically. The evolution of *Lunnomidinium*

419   *scaniense* and *Suessia* sp. A and their affinities to the Suessiaceae was discussed by

420   Lindström (2006); these two forms may reflect different salinity levels. Only one occurrence

of *Lunnomidinium scaniense* from Schandelach, Germany has been reported outside Sweden (Lindström et al., 2017b). Lindström and Erlström (2006b) related the occurrences of dinoflagellate cysts to a regional model and demonstrated that the acme of *R. rhaetica* corresponds to a Late Rhaetian maximum flooding event in the Danish Basin. Recently, Lindström et al. (2017a) researched the correlation of Triassic–Jurassic boundary successions with focus on the terrestrial ecosystems, but reported the dinoflagellate cysts ?*Beaumontella caminuspina, Lunnomidinium scaniense*, *Rhaetogonyaulax rhaetica, Suessia swabiana* and *Suessia* sp. A. They confirmed that *Rhaetogonyaulax rhaetica* is a regional marker for maximum flooding surfaces. Lindström et al. (2017b) also correlated Triassic–Jurassic boundary sections from northwest Europe, Nevada and Peru and demonstrated how various abundance events of *Rhaetogonyaulax rhaetica* can be applied in correlation.

In western Tethys, large areas of clay-rich sediments deposited in low dysoxic–anoxic basins have yielded dinoflagellate cysts from marine Rhaetian successions. This includes Sicily and southern Italy, where Cirilli et al. (2015) reported *Dapcodinium priscum* from the Rhaetian part of the Streppenosa Formation.

Several studies recorded Rhaetian dinoflagellate cysts from south-eastern France (Doubinger and Adloff, 1977; Adloff and Doubinger, 1982; Fauconnier et al., 1996; Courtinat et al., 1998; 2002; Courtinat and Piriou, 2002). Courtinat et al. (1998) reported rich assemblages from the Rhaetian near Lyon, including dominant *Rhaetogonyaulax rhaetica*, representing up to 95% of the palynomorphs. However, some horizons lack *Rhaetogonyaulax rhaetica*; in addition *Beaumontella caminuspina*, *Beaumontella delicata*, *Beaumontella langii*, *Dapcodinium priscum* and *Suessia swabiana* were observed. These authors interpreted the succession as representing a marginal marine setting, becoming fully marine up-section. *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* were observed in the largely paralic Rhaetian of the Massif-Central, south of Lyon by Courtinat et al. (2002) in a study otherwise

446 focused on palynofacies from these paralic successions. From the same successions, Courtinat

447 and Piriou (2002) discussed the changing quantitative occurrences in twelve Rhaetian sections

448 of *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* and concluded that *Dapcodinium*

449 *priscum* seemed to be an opportunistic species occupying specific ecological niches, whereas

450 *Rhaetogonyaulax rhaetica* was a more open marine species.

451

452 *2.3.   Iran*

453   Several publications have documented dinoflagellate cysts from the Upper Triassic of

454 Iran including Aghanabati et al. (2002, 2004). The latter reported a relatively diverse

455 assemblage including *Heibergella aculeata*, *Heibergella asymmetrica, Hebecysta balmei* and

456 *Rhaetogonyaulax rhaetica*; this was divided into four assemblage zones, all of which are of

457 inferred Norian age.

458   Ghasemi-Nejad et al. (2004) published on the Alborz Mountains, immediately south of

459 the Caspian Sea. The dinoflagellate cysts were placed into the *R. wigginsii* and *R. rhaetica*

460 zones of the *Rhaetogonyaulax* Superzone of the well-established Australian zonation.

461 Independent ammonite dating suggests an early–middle Norian age for the *R. wigginsii* zone,

462 which comprises abundant *R. wigginsii* and intervals of abundant *Heibergella aculeata,*

463 *Heibergella asymmetrica* and *Heibergella salebrosacea*. By contrast, the *Rhaetogonyaulax*

464 *rhaetica* zone is characterised by a monospecific assemblage of the index taxon.

465   From northeastern Iran, in a region which faced the Paleotethys, Ghasemi-Nejad et al.

466 (2008) recorded diverse, poorly preserved Norian dinoflagellate cyst assemblages from the

467 Miankuhi Formation. These included various species of *Hebecysta*, *Heibergella*,

468 *Rhaetogonyaulax* and *Sverdrupiella* in addition to two indeterminate genera. Notably,

469 *Rhaetogonyaulax rhaetica* was not recorded. Their age determination is based on correlation

470 to the Upper Norian *H. balmei* zone of Australia.

471   Recent work in east-central Iran (Sabbaghiyan et al., 2015) described a rich

472   dinoflagellate cyst assemblage from the Nayband Formation. This unit is Rhaetian in age

473   based on plant macrofossils. *Rhaetogonyaulax rhaetica* is present throughout the interval

474   studied however; *Dapcodinium priscum, Hebecysta brevicornuta Heibergella asymmetrica,*

475   *Heibergella kendelbachia, Heibergella salebrosacea, Noricysta pannucea* and *Sverdrupiella*

476   cf. *mutabilis* are also present.

477

478   *2.4.   Oceania*

479   Upper Triassic successions mainly comprising deltaic, estuarine and marginal marine

480   successions have been extensively studied throughout the North West Shelf of Australia and

481   many wells have provided an extensive palynomorph database (Figure 2). Palynology, and in

482   rare cases conodonts, are the only biostratigraphical tools used, and the palynomorph

483   assemblages are largely dominated by pollen and spores. However, some contributions

484   include reports of dinoflagellate cysts (Helby et al., 1987a; Brenner, 1992; Nicoll and Foster,

485   1994; Backhouse and Balme, 2002; Backhouse et al., 2002).

486   The first Mesozoic palynomorph biozonation of the North West Shelf of Australia was

487   by Helby et al. (1987a), and was based on both marine and terrestrially derived forms. These

488   authors defined the *Shublikodinium* (now *Rhaetogonyaulax*) middle Triassic to lower Jurassic

489   Superzone which is of Anisian–Pliensbachian age. This unit includes six dinoflagellate cyst

490   zones, the oldest is based on the occurrence of *Sahulidinium ottii* in the Sahul Shoals-1 well.

491   In ascending order, their zones were based on the lowest occurrence of *Rhaetogonyaulax*

492   *wigginsii, Suessia listeria* (now *Wanneria listeri*), *Hebecysta balmei* and *Rhaetogonyaulax*

493   *rhaetica*. The youngest zone (within the Superzone) is the *Dapcodinium priscum* zone (as the

494   *Dapcodinium priscus* Zone) which has a base in the uppermost Rhaetian is defined by the

495   total range of *Dapcodinium priscum*.

496   Riding et al. (2010) critically reviewed the chronostratigraphical ages of the zones of

497   the *Rhaetogonyaulax* Superzone of Australia. The age of the base of this unit was revised to

498   Late Ladinian, probably Carnian, as opposed to Anisian. Furthermore, the base of the

499   *Rhaetogonyaulax wigginsii* zone was considered to be latest Carnian, and the uppermost

500   occurrence of *Rhaetogonyaulax rhaetica* is in the latest Triassic. According to Riding et al.

501   (2010) there is then a hiatus spanning most of the Carnian placing the base of the overlying

502   *Rhaetogonyaulax wigginsii* Interval Zone in the latest Carnian ranging up to the Middle

503   Norian. This is in contrast to Helby et al. (1987) who placed the base of the *Rhaetogonyaulax*

504   *wigginsii* zone near the base of the upper Carnian and its top at the base of the Norian (Riding

505   et al. 2010, fig. 3). At present most Australian palynologists align with Helby et al. (1987)

506   (personal communication, Daniel Mantle 2018).

507   Riding et al. (2010) also commented that of the 11 Triassic dinoflagellate cyst taxa in

508   the *Rhaetogonyaulax* Superzone, six are known from Europe, whereas the other five

509   (*Hebecysta balmei*, *Rhaetogonyaulax wigginsii*, *Sahulidinium ottii*, *Suessia* sp. A and

510   *Wanneria listeri*) are only known from Australia. However, *Wanneria listeri* had been

511   recorded from Austria by Feist-Burkhardt et al. (2002).

512   The work of Brenner (1992) was from Ocean Drilling Program material drilled on the

513   Wombat Plateau off northwest Australia and includes records of *Hebecysta balmei* (as

514   *Heibergella balmei)*, *Wanneria listeri* (as *Suessia listeria*), *Suessia swabiana* and

515   *Rhaetogonyaulax rhaetica*. He also provided plates of various unidentified and undescribed

516   forms, including species of *Noricysta*?, *Suessia* and *Rhaetogonyaulax*.

517   The first report of Late Triassic dinoflagellate cysts from New Zealand was a study of

518   the upper Norian by Wilson and Helby (1986) from the southern island. Subsequently, Helby

519   and Wilson (1988) described *Sverdrupiella warepaensis* from the type section of the Warepan

520   Stage, Otago. They reported *Sverdrupiella* to be the predominant dinoflagellate genus

521 occurring in association with only one single specimen of *Rhaetogonyaulax.* The assemblage

522 is recorded in beds with *Monotis* shellbeds which correlates to the Cordillaranus Zone of late

523 Norian age.

524 Martini et al. (2004) reported a well-preserved dinoflagellate cyst assemblage from the

525 Manusela Limestone (previously the Asinepe Limestone) from Indonesia. This area was an

526 island situated between Tethys and Panthalassa during the Late Triassic (Golonka, 2007).

527 Together with abundant terrestrially derived palynofloras, Martini et al. (2004) recorded

528 *Beaumontella caminuspina, Beaumontella delicata*, *Heibergella aculeata, Heibergella*

529 *asymmetrica* and *Rhaetogonyaulax rhaetica*. They correlated this assemblage to the middle–

530 upper Norian *Heibergella* (now *Hebecysta*) *balmei* Interval Zone (Helby et al., 1987a). This is

531 supported by evidence from corals and foraminifera with a clear Tethyan affinity (Charlton

532 and van Gorsel, 2014). From Seram, Helby et al (1987) reported rare *Sverdrupiella* in

533 association with *Heibergella* in the shallow water Kanikeh Formation. A short paper from the

534 Andaman Islands, India (Sharma and Sarjeant, 1987), reported *Heibergella* spp. and

535 *Rhaetogonyaulax rhaetica,* and linked these observations to Indonesia.

536 There is only one record of Triassic dinoflagellate cysts from Antarctica. Foster et al.

537 (1994) reported and illustrated one specimen of *Rhaetogonyaulax* from the Flagstone Bench

538 Formation of East Antarctica. This co-occurs with a well-preserved terrestrial Onslow

539 Microflora of Norian age. No other independent dating was available.

540

541 *2.5. Africa*

542 From the Upper Triassic Mbuo Formation in southern Tanzania, Hudson and Nicholas

543 (2014) reported *Dapcodinium priscum, Sverdrupiella* sp. and *Sahulidinium ottii* from

544 explorations wells. However, they based their observations on unpublished industry reports

545 and their only general age assignment is correlation of the terrestrial and marine palynomorph

546 assemblages.

547

548 *2.6.   South America*

549 No records of Late Triassic dinoflagellate cysts from South America have been reported thus

550 far. Most of the known successions are non-marine, for example the Ischigualasto Formation

551 of Argentina. Nonetheless, Upper Triassic marine successions are known, for example, in

552 Mendoza Province of central western Argentina, where Norian–Rhaetian bivalves and

553 brachiopods were reported by Damborenea and Manceñido (2012) and Damborenea et al.

554 (2017). Furthermore, Sansom (2000) documented Rhaetian conodonts and ichthyoliths from

555 Chile, and Ferrari (2015) reported Rhaetian marine gastropods from Peru, but relatively little

556 palynological research has been done on the fragmentary and sparse Upper Triassic strata

557 along this margin.

558

559 **3.   The stratigraphic records of Triassic dinoflagellate cysts**

560 *3.1.   Upper Ladinian? to Lower Carnian*

561   To date, the first known fossil dinoflagellate cysts recorded are *Sahulidinium ottii*

562 from the upper middle Triassic/lowermost Carnian of Australia, however the dating is

563 uncertain and is based on indirect evidence (Riding et al., 2010). Following substantial

564 hiatuses representing a time interval with no records of about 10 my, the next published

565 occurrences from this area are those from the upper Carnian. However, small

566 *Rhaetogonyaulax* have been recently recorded in lower Carnian successions from Australia

567 (personal communication, Daniel Mantle 2018), indicating this the apparent gap may actually

568 represent a continuous record. Stratigraphically, the next published occurrences on a global

569 scale are those from the northern shores of the Neotethys. These includes the lower Carnian

570   occurrences of Switzerland (Stover and Helby, 1987; Hochuli and Frank, 2000) and Hungary

571   (Baryani 2018). The two latter records are geographically separated and stratigraphically

572   isolated, but were connected to the Neotethys, an area with carbonate platforms and reefs. The

573   reported species includes *Rhaetogonyaulax* cf. *wigginsii*, an "Australian" species, cf.

574   *Noricysta* (Switzerland) and *Heibergella* sp. (Hungary). Interestingly none of these taxa have

575   so far been recorded in the Carnian from the northern shores of Pangea.

576

577   *3.2.   Upper Carnian*

578   Although records of Late Triassic dinoflagellate cysts from Pangea are fragmentary

579   and sporadic, and they are likely under-reported, dinoflagellate cysts seem to appear relatively

580   synchronously and consistently around Pangea from near the base of the upper Carnian

581   (Figure 2). In all areas, *Rhaetogonyaulax* seems to have been the pioneer genus.

582   In Australia, *Rhaetogonyaulax wigginsii* has been recorded from the upper Carnian

583   (Stover and Helby, 1987; Riding et al., 2010) and, with the exception of *Suessia swabiana,* no

584   other pre-Norian taxa are apparently present in this area. There are no confirmed records of

585   *Suessia swabiana* until the Rhaetian in other areas, but *Suessia* sp. cf. *Suessia swabiana* was

586   reported by Suneby and Hills (1988) from the Norian in the Sverdrup Basin.

587   Along the northern shores of Pangea, *Rhaetogonyaulax arctica* was the first species to

588   appear. So far, records include those from the embayment comprising the Norwegian Arctic

589   (Vigran et al., 2014; Paterson and Mangerud, 2015), the Sverdrup Basin (Fisher and Bujak,

590   1975; Bujak and Fisher, 1976, Felix and Burbridge 1978) and Alaska (Wiggins, 1973), an

591   area facing the open Panthalassa Ocean.

592   There is still some uncertainty related to the occurrences of other species in the upper

593   Carnian, as there are published records of other taxa from the upper Carnian in the Sverdrup

594   Basin. However, these richer Carnian records are from ditch cuttings samples (e.g. Bujak and

595 Fisher 1976, table 1 for the Skybattle Bay-15 well below 7594 feet) and it is therefore

596 possible that these occurrences represent caving from the overlying Norian shales. In the

597 Barents Sea, the only record of possible pre-Norian taxa other than *Rhaetogonyaulax* species

598 are those of Hochuli et al. (1989). These authors reported *Heibergella asymmetrica,*

599 *Heibergella salebrosacea* and *Sverdrupiella mutabilis,* co-occurring with *Rhaetogonyaulax*

600 *arctica,* in their Assemblage C which they assigned an early Norian age. Paterson and

601 Mangerud (2015) however, did not record these species on Hopen. Vigran et al. (2014),

602 recorded similar assemblages from the Knorringfjellet Formation of Norian age in the

603 Festningen section. Only species of *Rhaetogonyaulax* were recorded below the base of the

604 Norian at this locality. As Hochuli et al. (1989) do not provide range charts from the various

605 localities, there is still uncertainty as to the first appearance of these species. Neither can we

606 rule out that the appearance of *Rhaetogonyaulax* is diachronous across the region due to the

607 flooding from the Northwest. Nonetheless, it seems clear that *Rhaetogonyaulax* was the

608 pioneer genus, but that different species of this genus appeared approximately simultaneously

609 on the northern and southern flanks of Pangea. If this hypothesis is correct, it implies that the

610 number of pre-Norian forms globally were probably between three and five species. No

611 earlier records have so far been published from these localities, despite the fact that Middle

612 Triassic successions in these regions are dominantly marine, and have yielded many

613 acritarchs.

614

615 *3.3.   Norian*

616   Although relatively few marine Norian successions which have produced

617 dinoflagellate cysts have been observed on a global scale, several of them comprise relatively

618 diverse and rich assemblages. This Norian "explosion" appears to be a genuine evolutionary

619 event and its inception in the northern areas coincided with a major transgression where

620   ammonoids provide independent dating for some of the palynological records. However, the

621   general scarcity of independent age control, later changes in lithostratigraphical successions,

622   uncertainties as to stage boundaries and stage durations, and thereby ties to the time scale,

623   makes it difficult to distinguish early and late Norian dinoflagellate cyst assemblages.

624   However, it seems clear that early Norian records include those from northern Pangea

625   (Alaska, the Barents Sea and the Sverdrup Basin) and from Australia, which was located on

626   the southern shores facing the Neotethys. Additionally, there are reports from Iran, which was

627   located in the northern parts of the Neotethys (Figure 2). The age constraints for these are

628   relatively good; several of these sections have independent ammonite control.

629   The dinoflagellate cyst assemblages reported as of early Norian age from the Sverdrup

630   Basin in the Canadian Arctic, included *Valvaeodinium* (as *Comparodinium*) and *Suessia* sp.

631   cf. *S. swabiana* (see Suneby and Hills 1988). Theses authors also reported upper Norian

632   assemblages comprising *Noricysta pannucea* and *Heibergella asymmetrica*. Other records

633   were given a general Norian age including those of *Hebecysta brevicornuta*, *Heibergella*

634   *aculeata*, *Noricysta fimbriata*, *Noricysta varivallata*, *Sverdrupiella mutabilis*, *Sverdrupiella*

635   *sabinensis* and *Sverdrupiella septentrionalis*. Suneby and Hills (1988) also reported

636   undifferentiated forms of *Rhaetogonyaulax* and Fisher and Bujak (1975) and Bujak and Fisher

637   (1976) recorded various species of *Hebecysta, Heibergella, Noricysta* and *Sverdrupiella* from

638   the western Queen Elisabeth Islands.

639   In contrast to the diverse associations from the Sverdrup Basin, mainly

640   *Rhaetogonyaulax arctica* and *Rhaetogonyaulax rhaetica* are present in the lower Norian of

641   the Norwegian Arctic, although *Heibergella*, *Noricysta* and *Sverdrupiella* occur rarely

642   (Vigran et al., 2014; Paterson & Mangerud, 2015). This could be due to the fact that the

643   Barents Sea was situated in the inner part of a huge embayment which received massive levels

644   of clastic input from the eroding Uralides mountains resulting in a dominantly paralic basin

645 fill, with occasional marine incursions. The largest of these was the early Norian

646 transgression. The upper Norian in the Norwegian Arctic is devoid of marine palynomorphs.

647   In the Neotethys area, Norian dinoflagellate cyst records are so far restricted to Iran

648 (Aghanabati et al. 2002; Aghanabati et al. 2004; Ghasemi-Nejad et al., 2004). From northern

649 Iran the lower middle Norian dinoflagellate assemblages are relatively rich comprising

650 abundant *Rhaetogonyaulax wigginsii*, *Heibergella asymmetrica*, *Heibergella salebrosacea*

651 and *Heibergella aculeata* (see Ghasemi-Nejad et al. 2004), resembling the assemblages from

652 Australia. Above in the Iranian successions, Ghasemi-Nejad et al. (2004) only recorded

653 species of *Rhaetogonyaulax* including *Rhaetogonyaulax rhaetica,* which they assigned a

654 younger late Norian to Rhaetian age. Also in Indonesia *Rhaetogonyaulax rhaetica* was

655 reported as of middle–late Norian age. It therefore seems that *Rhaetogonyaulax rhaetica*

656 appeared later in the Neotethys area compared to the northern flanks of Pangea, where it

657 appears in the early Norian. In northeastern Iran, Ghasemi-Nejad et al. (2008) also recorded

658 *Sverdrupiella* in assemblages of early Late Norian age. As no independent age control is

659 available here, it is, however, difficult to correlate this more exactly to other areas than

660 anticipating a general Norian age.

661   From Indonesia, situated latitudinally between Iran and Australia, Martini et al. (2004)

662 recorded similar Norian assemblages; however, they also reported *Beaumontella*

663 *caminuspina,* and *Beaumontella delicata*. This is interesting as *Beaumontella* was previously

664 considered to have its first global appearance in the Rhaetian, for example *Beaumontella*

665 *langii* from the Rhaetian of England and in the uppermost Rhaetian in Australia (Bucefalo

666 Palliani and Buratti, 2006; Riding et al., 2010). Interestingly *Beaumontella langii* has, recently

667 also been recorded from the late Norian in Australia (personal communication Daniel Mantle,

668 2018) showing that *Beaumontella* most likely appeared in the Neotethyan area and migrated

669 when the rifting increased.

In Australia, *Rhaetogonyaulax wigginsii* appeared around the Carnian–Norian transition (see above). In addition to *Rhaetogonyaulax wigginsii*, *Wanneria listeri* has a first appearance in the lowermost Norian. These first occurrences are therefore distinctly different from the those on the northern flank of Pangea. In Australia, these species are followed by *Hebecysta balmei, Noricysta* spp. and *Sverdrupiella* spp., resembling the assemblages in the Sverdrup Basin at the generic level. Also from the Carnarvon Basin, Backhouse et al. (2002) reported upper Norian dinoflagellate cyst assemblages dominated by *Hebecysta balmei* occurring in relatively thin intervals linked to flooding events.

The *Sverdrupiella* suite had a circum-Pacific distribution during the Norian, according to Helby et al. (1987b). The species in the high northerly latitudes are, however, different from those from Australia (Helby and Wilson, 1988) where *Sverdrupiella* appear to be rare. *Sverdrupiella* sp. cf. *S. septentrionalis* and *Sverdrupiella* cf. *S. mutabilis* are recorded from Iran, and rare *Sverdrupiella usitata* from Australia (Backhouse et al., 2002). Helby and Wilson (1988) described *Sverdrupiella warepaensis* from New Zealand. Other Australian records have reported undifferentiated *Sverdrupiella* spp. (Riding et al., 2010). With the exception of *Sverdrupiella warepaensis,* species of *Sverdrupiella* are few in Australia. The rich *Sverdrupiella* suite is mainly confined to the high northerly latitudes; in the Canadian Arctic nine species were recorded. The majority of the Arctic records outside the Sverdrup Basin include sparse occurrences from Alaska and the Barents Sea, most are only identified at the generic level. One of us (JBR) has observed the entire *Sverdrupiella* suite from the Northern Slope of Alaska (unpublished data), but there are large regions of this state where this flora is apparently absent (personal communication, Robert Ravn). *Sverdrupiella usitata* is typically the most common species of this assemblage, and has been observed reworked into younger strata (unpublished data). Based on the published records reviewed in the present

694 account the number of dinoflagellate species had globally exceeded 25 by the end of the

695 Norian–Rhaetian transition.

696

697 *3.4.   Rhaetian*

698 During the Rhaetian, marine inundation of the gradually opening rift system led to the

699 expansion of habitats for dinoflagellates. The Rhaetian transgression resulted in dinoflagellate

700 cyst migration into formerly land-locked regions of northern Pangea, including Austria,

701 Denmark, England, France, Italy, Slovakia, Sweden and Switzerland. In addition, there are a

702 number of Rhaetian records from other Neotethyan localities including Australia, Ciscaucasia

703 and east central Iran. In contrast to the Tethyan occurrences, the localities from the northern

704 shores of Pangea are characterised by paralic facies resulting in mainly non-marine Rhaetian

705 successions in the Barents Sea area and the Sverdrup Basin.

706   The Rhaetian assemblages are somewhat different to their Carnian and Norian

707 counterparts, with *Dapcodinium priscum* having its lowermost occurrence over a wide area.

708 The other dinoflagellate cyst genus expanding in the Rhaetian is *Wanneria*, which first

709 appears in Australia and seems to have migrated northwards. *Wanneria misolensis* has a short

710 range in the early Rhaetian in Australia and is a useful marker. The cosmopolitan species

711 *Rhaetogonyaulax rhaetica,* which first appeared in the late Carnian, expanded both in

712 numbers and spatial extent during the Rhaetian and apparently became extinct close to the

713 Triassic–Jurassic boundary. Most other Triassic genera also extended into the Rhaetian and

714 had range tops close to the Triassic -Jurassic boundary. An exception to this is *Sverdrupiella*,

715 which is extremely rare in the Rhaetian. This genus was reported from the Rhaetian in Europe

716 by Morbey and Dunay (1978) and Powell (1992); however, these authors did not document

717 where *Sverdrupiella* was recorded or provided illustrations. The latter report is of a single

718 specimen of *Sverdrupiella* sp. from the Rhaetian of the Blyborough Borehole, Lincolnshire,

719 central England (JBR unpublished information).

720   A global regression caused an extremely widespread hiatus near the end of the

721 Triassic; however, a late Rhaetian transgression has been recognised in several areas. This

722 frequently resulted in an influx of dinoflagellate cysts. In southern Sweden, Lindström and

723 Erlström (2006) recorded the suessiacean species *Lunnomidinium scaniense*, together with

724 *Rhaetogonyaulax rhaetica,* below an influx of *Rhaetogonyaulax rhaetica*, with *Dapcodinium*

725 *priscum* just below the Triassic–Jurassic boundary. This represents the maximum extent of the

726 Rhaetian sea in this area.

727 A detailed analysis of the Triassic–Jurassic boundary is beyond the scope of this paper.

728 However, we note that there are uncertainties due to condensed sections and hiatuses in the

729 Global Stratotype Section and Point (GSSP) for the Hettangian at Kuhjoch, Austria (Morton,

730 2012; Hillebrandt et al., 2013). Important studies on the palynology of the Triassic–Jurassic

731 boundary include Kuhjoch (Kürschner et al., 2007; Bonis et al., 2009), St. Audrie's Bay, UK

732 (Bonis et al. 2010), and the Danish/Swedish basins (Lindström and Erlström, 2006; Lindström

733 et al., 2017a,b). Of the main Triassic dinoflagellate cyst taxa, only *Beaumontella langii,*

734 *Dapcodinium priscum* and *Heibergella*? *kendelbachia* extended into the Jurassic (Figure 2).

735

736 **4.   The paleoenvironmental preferences of Triassic dinoflagellate cysts**

737   At present, knowledge concerning the paleoenvironmental preferences of Late Triassic

738 dinoflagellates is very limited, and no focussed studies on this topic have been performed. In

739 most cases, their use as marine indicators have been their most important input. There are

740 occasional observations on their link to depositional environments for example, Helby et al

741 (1987) noted that *Sverdrupiella* on the Alaskan shelf was recorded in clastic sediments with

742 high nutrient contents and restricted circulation. However, there are at present insufficient

743 data to draw conclusions on this point.

744   One of the few attempts to link upper Triassic dinoflagellate cysts to

745 paleoenvironmental conditions include Courtinat and Piriou (2002) who recorded

746 *Dapcodinium* and *Rhaetogonyaulax* from the Rhaetian of the Tethyan region, frequently in an

747 inverse quantitative relationship. Batten et al. (1994) and Poulsen (1996) have also noted this

748 configuration. Courtinat and Piriou (2002) related this phenomenon to a mainly restricted

749 nearshore marine versus a deeper marine environment. They noted that *Rhaetogonyaulax*

750 *rhaetica* seemed to occur in more marine settings, compared to *Dapcodinium priscum* which

751 was recorded in more restricted depositional settings. They postulated that *Dapcodinium* is

752 therefore probably a more opportunistic euryhaline species. By contrast, Batten et al. (1994)

753 suggested that *Rhaetogonyaulax rhaetica* may have been more tolerant of brackish water

754 conditions, as it occurs in marine mudstones close to an intra-basinal high in the Danish

755 Basin. In their study *Dapcodinium priscum* was recorded with well-preserved plant material.

756 Ghasemi-Nejad et al. (2004) in more general terms related their dinoflagellate records to a

757 shallow sea with fluvial deposition, leading to rich nutrient conditions as a cause for

758 dinoflagellate cysts to flourish.

759   *Rhaetogonyaulax rhaetica* has been recorded in the terrestrially-dominated, shallow

760 marine successions for example of Slovakia (Ruckwied and Götz, 2009) in relatively low

761 proportions. Most records of *Rhaetogonyaulax* appear however to represent relatively deeper

762 water environments such as outer shelf. Paterson et al. (2016) demonstrated that

763 *Rhaetogonyaulax rhaetica* had abundance peaks which correlate to maximum flooding

764 surfaces. From the same study, *Rhaetogonyaulax arctica* seemed to occur during the early

765 stages of transgression (Paterson & Mangerud 2014, Paterson et al. 2016). The

766 palaeoenvironmental significance of this genus is therefore not fully understood. As more

767 dinoflagellate cyst data become available from the Upper Triassic, there should be potential to

768 link them to depositional settings and potentially use them as paleoenvironmental proxies.

769

770 **5.   Conclusions**

771 Based on present knowledge from published records, this review has shown that the global

772 appearance of dinoflagellate cysts around the shores of Pangea took place near the base of the

773 Upper Triassic, maybe as early as in the latest Middle Triassic in Australia. This marks the

774 first appearance of a new group of marine plankton in the oceans. The peridiniphycidaen

775 genus *Rhaetogonyaulax* seems to be the pioneer in all areas, and the cosmopolitan species

776 *Rhaetogonyaulax rhaetica,* which first occurred in the late Carnian, expanded in both

777 numbers and spatial extent during the Rhaetian. Four peridiniphycidaen genera (*Hebecysta,*

778 *Heibergella, Rhaetogonyaulax* and *Sverdrupiella*), and one suessiaceaen genus (*Noricysta*)

779 had already developed globally by the middle Norian on the northern side of Pangea, whereas

780 another two suessiaceaen genera (*Suessia* and *Wanneria*) had developed in the southern

781 shores of Neotethys in Australia. Following these genera, *Valvaeodinium* appeared within the

782 middle part of the Norian, followed by *Beaumontella*. The latter genus was previously thought

783 to be confined to the Rhaetian, but is recorded in upper Norian successions in Australia and

784 Indonesia. Near the base of the Rhaetian, *Dapcodinium* appears for the first time. Many

785 dinoflagellate cyst species are endemic, being confined to the northern or southern realms,

786 and the lack of independent dating makes precise correlation of the various assemblages

787 difficult.

788   It is clear that most Triassic genera extended into the Rhaetian, but *Sverdrupiella*

789 seems to be an exception, as it is extremely rare in the Rhaetian. The majority of Triassic

790 dinoflagellate cyst taxa became extinct at the Triassic–Jurassic boundary. The exceptions are

791 *Beaumontella langii* and *Dapcodinium priscum,* which range up into the lower Jurassic.

32

792 Knowledge on the paleoenvironmental significance of Late Triassic dinoflagellate cysts is so

793 far extremely limited.

794   Outstanding problems in understanding the spatial and temporal occurrences of Late

795 Triassic dinoflagellate cysts include the lack of records from Russia. Here, the potential for

796 future studies appears high because well-known ammonite dated marine successions are

797 present, and dinoflagellate cysts have been observed (see above). In addition, lack of records

798 from South America and other areas along the eastern side of Pangea hampers for example the

799 understanding of potential migration routes. In order to improve our knowledge on the oldest

800 occurrences of dinoflagellate cysts, studies of frontier areas, combined with more detailed

801 studies from the areas where they are already known to occur, offer rich potential for future

802 studies.

803

815 providing facilities to undertake this work. James B. Riding publishes with the approval of the

816 Executive Director, British Geological Survey (NERC).

817

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1296   **FIGURES**

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1298   Figure 1. The palaeogeography of the Late Triassic illustrating the locations of first

1299   occurrences of dinoflagellate cyst records (adapted from Golonka et al. 2018).

1300

1301   Figure 2. A composite range chart of Late Triassic dinoflagellate cysts from various

1302   geographical areas (time scale from Gradstein et al. 2016).

1303

1304   TABLE 1

1305

1306   List of dinoflagellate cyst taxa appearing in Upper Triassic successions. References to the

1307   author citations can be found in Williams et al. (2017).