

1 Mid Jurassic (Late Callovian) dinoflagellate cysts from the Lotena Formation of the  
2 Neuquén Basin, Argentina and their palaeogeographical significance

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17

18 **ABSTRACT**

19

20 The Lotena Formation from two localities, Picún Leufú and Portada Covunco, in the  
21 Neuquén Basin of west-central Argentina was studied palynologically. The material  
22 examined produced moderately diverse Late Callovian dinoflagellate cyst assemblages.

23 This age assignment is consistent with ammonite evidence. The dinoflagellate cyst  
24 floras are reminiscent of the Middle Jurassic associations of northwest Europe and  
25 surrounding areas. Marine palynomorphs typical of Australasia and the Arctic are

26 absent. The similarity with Europe is strongly suggestive of an open marine connection  
27 between western Tethys and the Neuquén Basin during the Late Callovian. This is  
28 interpreted as being via the Hispanic Corridor, with the palynofloras being passively  
29 dispersed to the southwest by the circum-Tropical Marine Current. Earlier studies  
30 indicate that this trans-Pangean equatorial seaway first began to allow biotic interchange  
31 during the Mid Jurassic and this study proves that this open marine connection was  
32 established by the Late Callovian. The similarities between the dinoflagellate cyst  
33 assemblages of Europe and the Neuquén Basin are consistent with the distribution of  
34 other marine fossils and the existence of geographically-continuous marine facies belts.

35

36 Keywords: Lotena Formation; Mid Jurassic; dinoflagellate cysts; biostratigraphy;  
37 palaeogeography; Argentina

38

## 39 **1. Introduction**

40

41 The palynofloras of the Lotena Formation of the Lotena Group from the  
42 Neuquén Basin, Argentina have previously been studied by Volkheimer and  
43 Quattrocchio, (1981), Quattrocchio and Sarjeant (1992), Martínez and Quattrocchio  
44 (2003; 2004) and Zavala et al. (2003). The Lotena Formation is of Mid-Late Jurassic  
45 age; more specifically Callovian-Oxfordian (Howell et al., 2005, fig. 3; Fig. 1). This  
46 contribution represents a restudy of some of the material of Quattrocchio and Sarjeant  
47 (1992) and Martínez and Quattrocchio (2004) (Fig. 2), and an interpretation of the  
48 dinoflagellate cyst assemblages in terms of their detailed biostratigraphy and  
49 palaeogeographical significance. Quattrocchio and Sarjeant (1992) is largely on  
50 systematics and Martínez and Quattrocchio (2004) is mainly focused on palynofacies.

51 Global palaeogeographical aspects were not considered in detail by either Quattrocchio  
52 and Sarjeant (1992) or Martínez and Quattrocchio (2004). The aims of this study are to  
53 refine the biostratigraphy, and to compare the dinoflagellate cysts of the Lotena  
54 Formation with coeval associations from other regions. Specifically, the latter goal  
55 seeks to determine whether these marine palynofloras have closer affinities with the  
56 western Tethys including the Subboreal Realm or with eastern Tethys/Australasia.

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58

## 59 **2. Geological Background**

60

61 The geological evolution of the Neuquén Basin was largely controlled by  
62 tectonic events on the western margin of Gondwana. Following initial extensional  
63 rifting during the Late Triassic, back-arc subsidence was initiated during the Early  
64 Jurassic due to the development of a subduction zone (and an associated magmatic arc)  
65 in western Gondwana. Thus, in western South America, subduction of Pacific oceanic  
66 crust along the north-south trending continental margin of Chile and Argentina  
67 accelerated significantly during the breakup of West and East Gondwana during the  
68 Early Cretaceous. Andean subduction therefore took place under extensional conditions,  
69 and was probably associated with negative trench roll-back. This led to the formation  
70 of a magmatic arc along the Coast Ranges from southern Peru to central Chile and, to  
71 the east, the Arequipa, Tarapacá and Neuquén extensional back arc basins (Mpodzis  
72 and Ramos, 2008).

73 The Neuquén Basin is located immediately to the east of the Andes Mountains in  
74 central western Argentina and eastern Chile between 31°S and 41°S (Figs. 1-3). It lies  
75 within the Argentine provinces of La Pampa, Mendoza, Neuquén (from which it takes

76 its name) and Río Negro. The depocentre represents the southern end of the more  
77 extensive Chilean Basin, is broadly triangular in outline, up to 700 km in a north-south  
78 direction and covers over 150,000 km<sup>2</sup>. The tectonic history of the Neuquén Basin  
79 consists of synrift (Late Triassic-Early Jurassic), postrift/back-arc (Early Jurassic-Early  
80 Cretaceous) and foreland stages (Howell et al., 2005, fig. 3). The basin fill is of Late  
81 Triassic to Palaeocene age, and is between 4,000 and 7,000 m of heterolithic marine and  
82 continental strata (Ramos, 1998; Howell et al., 2005). The majority of the Neuquén  
83 Basin fill was deposited during the postrift phase; this comprises the Cuyo, Lotena and  
84 Mendoza groups of Pliensbachian to Barremian age (Vergani et al., 1995; Howell et al.,  
85 2005, fig. 3).

86         The strata of the Neuquén Basin are mostly shallow marine, related to a  
87 prolonged connection with the palaeo-Pacific. However, marine influence was  
88 periodically interrupted due to falls in sea-level (Mutti et al., 1994). These short-lived  
89 periods of terrestrial deposition are normally indicated by regional-scale angular  
90 unconformities which are indicative of tectonic overprints on eustatic changes.  
91 Transgressive successions were deposited above these unconformities, indicating  
92 progressive increases of accommodation space. The Lotena Group (Fig. 1) represents  
93 the second oceanic incursion into the Neuquén Basin. The basal hiatus significantly  
94 affected the overlying units (Zavala, 2002). This group largely comprises Middle  
95 Callovian and Oxfordian siliciclastic units with subordinate carbonates and evaporites  
96 (Fig. 3). The thickness of the Lotena Group is highly variable, ranging from as little as  
97 several metres to 650 m in the Sierra de la Vaca Muerta (Zavala, 2005). It  
98 unconformably overlies the continental and marine deposits of the Cuyo Group, and is  
99 in turn overlain by the Mendoza Group (Fig. 1).

100           The Lotena Group in the Sierra de la Vaca Muerta and Covunco areas in the  
101 southwest of the Neuquén Basin consists of six unconformity-bounded sequences. The  
102 oldest of these, Sequence 1, comprises the red beds and evaporites of the Tábanos  
103 Formation, and unconformably overlies the Cuyo Group with transgressive onlap. The  
104 Lotena Formation is dominated by mudstone with subordinate evaporites, limestones  
105 and sandstones: it comprises sequences 2 to 5. These are broadly similar and exhibit a  
106 basal unit of confined shelfal sandstone lobes, which grade upwards into unconfined  
107 shelfal sandstone lobes and carbonates. The basal confined shelfal sandstone lobes are  
108 restricted to areas where the successions are thickest. The youngest Sequence (6) is  
109 equivalent to the La Manga Formation and exhibits an irregular facies architecture  
110 which truncates the underlying deposits. It is almost entirely composed of massive  
111 carbonates that were deposited by turbidity currents. Facies analysis and mapping  
112 indicate the reworking of older units. The Lotena Group in the Sierra de la Vaca Muerta  
113 and adjacent areas probably accumulated in a tectonically unstable region. Sequences 4-  
114 6 show a northward shift of their depocentres and widespread truncation along the  
115 southern margins. The truncation may be related to intermittent uplift associated with  
116 the syndepositional development of the Covunco anticline (Zavala, 2005).

117

### 118 **3. Material studied**

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120           The three samples from the Lotena Formation analysed in this study are from the  
121 southern part of the Neuquén Basin (Fig. 2). The slides are housed in the Laboratory of  
122 Palynology, Universidad Nacional del Sur, Bahía Blanca, Argentina.

123

124 3.1. *Samples 2971 and 2970 from Puente del Arroyo Picún Leufú of Quattrocchio*  
125 *and Sarjeant (1992)*

126

127 Samples 2971 and 2970 were collected by Dr. Wolfgang Volkheimer from a  
128 prominent outcrop at the Puente del Arroyo Picún Leufú, where Nacional Route N40  
129 crosses the Arroyo Picún Leufú, around 40 km south of Zapala (Fig. 2). At this locality,  
130 the lower part of the Lotena Formation comprises 59 m of dark green mudstones with a  
131 basal conglomerate (Quattrocchio and Sarjeant, 1992, fig. 4). The samples 2971 and  
132 2970 are from 12 m and 34 m from the base of the lower conglomerate unit respectively  
133 (Quattrocchio and Sarjeant, 1992, fig. 4). This mudstone-dominated unit has yielded the  
134 ammonite *Rehmannia (Loczyceras) patagoniensis*, foraminifera and ostracods (Dellapé  
135 et al., 1979). *Rehmannia (L.) patagoniensis* is present at the base of the succession and  
136 is considered to be Mid to Late Callovian in age (Groeber et al., 1953, Stipanovic, 1969;  
137 Riccardi et al., 1990). Riccardi (2008) stated that *R. (L.) patagoniensis* is indicative of  
138 the Mid Callovian Jason and Coronatum chronozones.

139

140 3.2. *Sample 1525 from Portada Covunco of Martínez and Quattrocchio (2004)*

141

142 Sample 1525 of Martínez and Quattrocchio (2004) is by far the most  
143 palynologically productive of the three horizons studied by Martínez and Quattrocchio  
144 (2004) from the Lotena Formation of the Portada Covunco section, around 20 km from  
145 Zapala (Fig. 2). Here the formation is approximately 220 m thick and corresponds to  
146 units 2 and 3 of Zavala et al. (2002). The sample is a massive dark grey mudstone from  
147 Unit 2. No ammonites have been recorded from the Lotena Formation of the Portada  
148 Covunco section. However, the underlying Lajas Formation of the Cuyo Group has

149 yielded the ammonite *Eurycephalites cf. vergarensis*, which is characteristic of the  
150 Vergarensis Chronozone, which is of Early Callovian age (Riccardi et al., 1989; 1990;  
151 Riccardi, 2008).

152

#### 153 **4. Description of the palynomorph assemblages**

154

155 The three samples restudied here yielded moderately abundant palynomorph  
156 associations. The species recorded, and others discussed herein, are listed in Appendix  
157 1; their distribution and abundances are recorded in Table 1. A selection of  
158 dinoflagellate cysts are illustrated in Plate I. The assemblages are dominated by pollen  
159 grains with lesser proportions of dinoflagellate cysts. The pollen genus *Classopollis* is  
160 prominent; other pollen taxa recorded include the saccate forms *Alisporites* spp.,  
161 *Araucariacites* spp. and *Callialasporites* spp. (Table 1). The dominance of *Classopollis*  
162 is indicative of arid conditions. This is especially the case for samples 2971 and 2970  
163 from Puente del Arroyo Picún Leufú, which is more proximal than Portada Covunco  
164 (Martinez and Quattrocchio, 2004; Table 1). *Classopollis* was produced by  
165 representatives of the Cheirolepidaceae, and the parent plants were thermophylic and  
166 xerophytic. They preferred dry coastal regions (Pocock and Jansonius, 1961; Srivastava,  
167 1976), which is consistent with the palaeolatitudinal position of the Neuquén Basin  
168 during the Jurassic (Smith et al., 1994). Miscellaneous microplankton, including  
169 acritarchs and prasinophytes, and pteridophyte spores are also present in relatively  
170 minor proportions. This palynomorph spectrum is indicative of an offshore shelfal  
171 depositional setting.

172

#### 173 **5. Biostratigraphy**

174

175 5.1. Samples 2971 and 2970 from Puente del Arroyo Picún Leufú of Quattrocchio and  
176 Sarjeant (1992)

177

178 The dinoflagellate cyst assemblages in samples 2971 and 2970 (see Table 1) are  
179 entirely consistent with a Callovian age when compared to European assemblages. The  
180 prominence of *Nannoceratopsis pellucida* in 2971, together with the presence of forms  
181 such as *Chytroisphaeridia chytroeides*, *Ellipsoidictyum gochtii*, *Gonyaulacysta*  
182 *jurassica* subsp. *adecta*, *Meiourogonyaux* sp., *Mendicodinium groenlandicum*,  
183 *Pareodinia ceratophora*, *Sentusidinium* spp. and *Tubotuberella dangeardii* is typical of  
184 the Callovian of northwest Europe and adjacent areas (e.g. Riding, 1982; 1987a; 2005;  
185 Berger, 1986; Smelror, 1988a;b; Prauss, 1989; Feist-Burkhardt and Wille, 1992;  
186 Smelror and Below, 1992; Poulsen, 1996; Riding and Thomas, 1997). The presence of  
187 *Limbodinium absidatum* and *Wanaea acollaris* in sample 2971 refines this assessment  
188 to the Late Callovian. *Limbodinium absidatum* is confined to the Late Callovian-Early  
189 Oxfordian interval (Athleta to Coronatum chronozones) (Riding 1987b; Riding and  
190 Thomas, 1992). The range top of *Wanaea acollaris* is within the Late Callovian  
191 (Riding, 1984); the few, sporadic reports of this species in the Early Oxfordian are  
192 thought to represent contamination (Riding and Thomas, 1997). No exclusively  
193 Oxfordian markers such as *Leptodinium* spp. and *Systematophora* spp. were observed.  
194 The presence of *Ambonosphaera? staffinensis* in the Callovian is unusual; the range of  
195 this species is Mid Oxfordian to Early Cretaceous (Poulsen and Riding, 1992, fig. 2).

196 A single specimen of *Protobatioladinium* cf. *P. lindiensis* Schrank 2005 was  
197 recorded in sample 2971. *Protobatioladinium lindiensis* was originally described from  
198 the Tithonian of Tanzania, and similar forms are present in the Bathonian-Ryazanian



199 interval of Europe and Israel (Schrack, 2005). *Dissiliodinium volkheimeri* is confined to  
200 the Southern Hemisphere. It was recorded from the Bathonian and Callovian of offshore  
201 northwestern Australia by Mantle (2009a). Quattrocchio and Sarjeant (1992, p. 70)  
202 stated that *Dissiliodinium volkheimeri* is conspecific with *Dissiliodinium* sp. (no  
203 antapical node) of Helby et al. (1987), from the Bajocian-Bathonian of Australia.  
204 However, this contention is not supported here because *Dissiliodinium volkheimeri* has  
205 a thin autophragm and has extremely low-relief ornamentation. By contrast,  
206 *Dissiliodinium* sp. (no antapical node) of Helby et al. (1987) has an irregular reticulate  
207 ornamentation and is smaller. *Endoscrinium* cf. *E. galeritum* 1967 subsp. *reticulatum* is  
208 apparently endemic to the Neuquén Basin.

209         The Late Callovian age of sample 2971, 12 m from the base of the succession,  
210 inferred from the presence of *Limbodinium absidatum* and *Wanaea acollaris* is  
211 consistent with the occurrence of the Mid to Late Callovian ammonite *Rehmannia*  
212 (*Loczyceras*) *patagoniensis* in the lowermost bed. This suggests that the majority of the  
213 succession at Puente del Arroyo, Picún Leufú is of Late Callovian age.

214

#### 215 5.2. Sample 1525 from Portada Covunco of Martínez and Quattrocchio (2004)

216

217         The relatively low diversity dinoflagellate cyst assemblage in sample 1525 is  
218 also consistent with the Callovian Stage. *Gonyaulacysta jurassica* subsp. *adecta* is  
219 prominent, and *Chytroeisphaeridia chytroeides*, ?*Meiourogonyaulax* sp.,  
220 *Mendicodinium groenlandicum* and *Rynchodiniopsis cladophora* are also present. This  
221 association is typical of the Callovian of the Northern Hemisphere (e.g. Riding and  
222 Thomas, 1992; 1997; Riding et al., 1999; Riding, 2005). The presence of *Scriniodinium*  
223 *crystallinum* refines this assessment to no older than Late Callovian. The range of

224 *Scriniodinium crystallinum* in the Northern Hemisphere is Late Callovian to earliest  
225 Kimmeridgian (Riding, 1987a; Riding and Fensome, 2002). The questionable  
226 specimens of *Liesbergia liesbergensis*, *Trichodinium scarburghensis* and *Wanaea* sp.  
227 also support a Late Callovian age assessment. *Liesbergia liesbergensis* is indicative of  
228 the Mid Callovian to earliest Oxfordian interval of Europe (Berger, 1986; Riding,  
229 2005). *Trichodinium scarburghensis* is characteristic of the Late Callovian to Mid  
230 Oxfordian (Riding and Thomas 1992). ?*Wanaea* sp. has a spinose paracingular crest,  
231 hence is similar to forms such as the Late Callovian to Early Oxfordian marker *Wanaea*  
232 *thysanota* (see Riding and Helby, 2001a). No marker species with range bases within  
233 the Oxfordian such as *Endoscrinium luridum*, *Glossodinium dimorphum*,  
234 *Gonyaulacysta jurassica* subsp. *jurassica* and *Wanaea fimbriata* were recorded.

235

## 236 **6. The provincialism of Jurassic dinoflagellate cysts**

237

238         Because dinoflagellates are planktonic, their cysts can potentially have wide  
239 biogeographical distributions. In the Jurassic several prominent Mid-Late Jurassic  
240 species, such as *Gonyaulacysta jurassica*, *Nannoceratopsis pellucida* and  
241 *Scriniodinium crystallinum*, are known to be distributed globally. However, many other  
242 taxa appear to be restricted to northwest Europe/western Tethys, eastern  
243 Tethys/Australasia and the Arctic region (Norris, 1975). The Australasian biotic  
244 province is especially well-differentiated, having many endemic taxa (Helby et al.,  
245 1987; Riding and Ioannides, 1996). Typically in the Arctic/Boreal region, there is a  
246 mixture of widely-distributed Northern Hemisphere forms and endemic high latitude  
247 taxa (Brideaux and Fisher, 1976; Davies, 1983; Smelror and Below, 1992. Riding et al.,  
248 1999).

249           At certain times during the Jurassic, such as the Bathonian and the  
250   Kimmeridgian/Tithonian, it is possible to distinguish distinct Boreal (Arctic) and  
251   western Tethyan (Euro-Atlantic) provinces within the Northern Hemisphere (Riding et  
252   al., 1985; 1999; Riding and Ioannides, 1996). This marked provincialism was most  
253   likely due to a number of factors including lithofacies control, nutrient levels, ocean  
254   currents, salinity, seasonality (i.e. winter darkness) and temperature. One of the most  
255   important factors, however, was likely to have been the presence or absence of open  
256   marine connections. Organic cyst-producing dinoflagellates prefer shelfal environments  
257   (Wall et al., 1977). Therefore during periods of high sea levels, when extensive areas of  
258   continental shelf are flooded, dinoflagellates are passively dispersed over very wide  
259   areas. The Callovian and Oxfordian interval was a time of rising and relatively high sea  
260   levels (Ager, 1981; Haq et al., 1987). Consequently, dinoflagellate cyst associations are  
261   extremely similar in taxonomic spectrum and relative proportions in this interval  
262   throughout the equatorial, middle and high latitudes throughout the Americas, the Arctic  
263   and western Tethys (Johnson and Hills, 1973; Jain et al. 1986; Garg et al., 1987;  
264   Smelror, 1988a,b; Thusu et al., 1988; Conway, 1990; Poulsen, 1996; Riding et al., 1999;  
265   Ibrahim et al., 2002). This situation suggests significant levels of ocean current activity  
266   at this time. Such is the relative uniformity of Callovian-Oxfordian dinoflagellate cyst  
267   assemblages throughout much of the Northern Hemisphere, the Australasian  
268   phytoplankton province represents a major biotal contrast (Riding and Helby, 2001b;  
269   Mantle, 2005; 2009a,b).

270

## 271 **7. Palaeogeographical significance of the dinoflagellate cyst assemblages**

272

273           The dinoflagellate cyst associations from samples 2971, 2970 and 1525 are of  
274 moderate to low diversity, and are strongly reminiscent of the Late Callovian floras of  
275 the Northern Hemisphere. For example, the previous reports of *Ambonosphaera?*  
276 *staffinensis*, *Ellipsoidictyum gochti*, *Limbodinium absidatum*, *Rynchodiniopsis*  
277 *cladophora* and *Wanaea acollaris* are all from Europe, North America and adjacent  
278 regions (e.g. Johnson and Hills, 1973; Feist-Burkhardt and Wille, 1992; Riding and  
279 Thomas, 1992; Riding et al., 1999). By contrast, *Chytroeisphaeridia chytroeides*,  
280 *Mendicodinium groenlandicum*, *Nannoceratopsis pellucida*, *Pareodinia ceratophora*,  
281 *Scriniodinium crystallinum* and *Tubotuberella dangeardii* are global in distribution  
282 (Davey, 1987; Helby et al., 1987, Mantle, 2009a,b). The only species apparently  
283 confined to the Southern Hemisphere is *Dissiliodinium volkheimeri*. This form has been  
284 recorded from the Neuquén Basin and offshore northwestern Australia (Quattrocchio  
285 and Sarjeant, 1992; Mantle, 2009a). *Dissiliodinium* is a relatively morphologically  
286 simple genus and the majority of the species were described from the Northern  
287 Hemisphere. This implies that *Dissiliodinium volkheimeri* may not be confined to the  
288 Southern Hemisphere. A single specimen of *Protobatioladinium* cf. *P. lindiensis* was  
289 recorded from sample 2971 (Plate I, fig. 8). *Protobatioladinium lindiensis* was  
290 described from the Tithonian of Tanzania, East Africa by Schrank (2005). This species  
291 apparently has a wide distribution; similar forms have been recorded from the  
292 Bathonian to Ryazanian of Europe (Schrank, 2005, p. 72). *Endoscrinium* cf. *E.*  
293 *galeritum* subsp. *reticulatum* (Plate I, fig. 14) is prominent in sample 2971 (Table 1);  
294 this morphotype appears to be confined to the Neuquén Basin.

295           Significantly, no taxa of exclusively Australasian affinity were observed in this  
296 study. In the Callovian of Australasia, several characteristic and endemic species are  
297 present including *Endoscrinium kempiae*, *Meiourogonyaulax penitabulata*,

298 *Nannoceratopsis reticulata*, *Paragonyaulacysta helbyi*, *Ternia balmei*, *Voodooia*  
299 *tabulata*, *Wanaea digitata*, *Woodinia pedis* and others (Davey, 1987; Helby et al., 1987;  
300 1988; Riding and Helby, 2001b; Mantle, 2005; 2009a,b). None of these taxa, and other  
301 endemic Austral forms, have been recorded from the Lotena Formation of the Neuquén  
302 Basin. Hence, due to the lack of Australasian elements, this assemblage is consistent  
303 with a strong marine connection with the Euro-Atlantic province to the north. This  
304 strongly implies that the Neuquén Basin was isolated from eastern Gondwana in terms  
305 of biotal exchange during the Callovian. Australasian dinoflagellate cysts could not  
306 have been passively dispersed westwards across the middle latitudes into the Neuquén  
307 Basin via trans-Pacific routes due to the wide geographical extent of this deep ocean  
308 basin, and the active subduction zone immediately to the west of the Americas (Fig. 4).  
309 Similarly, latitudinal and palaeotemperature barriers would probably have prevented  
310 dispersal from Australasia to South America around the southern margin of Gondwana  
311 (i.e. Australia and Antarctica) via the Southern Gondwanan Seaway (Hallam, 1983; Fig.  
312 4).

313         Similarly, characteristically Arctic/Boreal Callovian dinoflagellate cyst taxa  
314 such as *Evansia dalei*, *Evansia perireticulata*, *Paragonyaulacysta calloviensis* and  
315 *Paragonyaulacysta retiphragmata* have not been observed in the Neuquén Basin. These  
316 species were cold-adapted Arctic forms (e.g. Johnson and Hills 1973; Dörhöfer and  
317 Davies 1980; Smelror and Below, 1992). The absence of these forms indicates that  
318 potential southerly dispersal routes via the high northerly palaeolatitudes into the  
319 Hispanic Corridor were not viable for cyst-forming dinoflagellates.

320         In the western Tethys (i.e. eastern North America and North Africa) Jurassic  
321 biotas, including dinoflagellate cysts, were markedly different from their counterparts  
322 from southeastern Tethys (Australasia, eastern Asia and northeast India). Central

323 southern Tethys (i.e. East Africa, India and Madagascar) appears to have supported a  
324 mixed assemblage, with both European and Austral dinoflagellate cysts being present  
325 (e.g. Jiang et al. 1992, Garg et al. 2003, Msaky, 2007). During the Triassic and Jurassic,  
326 the Tethys circumglobal current (TCC) flowed westwards in the tropics and north-south  
327 currents during such greenhouse intervals tended to be relatively weak (Bush, 1997).  
328 Thus, the westward flow of the TCC would have potentially been responsible for the  
329 dispersal of planktonic organisms from eastern to western Tethys during the Mesozoic.  
330 Despite this, endemic Australasian dinoflagellate cyst taxa have not been observed west  
331 of East Africa. Interruptions in shelfal seas, water stratification and/or other constraints  
332 apparently prevented the westward dispersal of Austral dinoflagellate cysts during the  
333 Jurassic. Aberhan (2001) discussed bidirectional (seasonal) biotic exchange across the  
334 Hispanic Corridor during the Mid Jurassic driven by the establishment of a  
335 megamonsoonal ocean circulation.

336         The characteristically European affinity of the Callovian dinoflagellate cysts  
337 from the Lotena Formation of the Neuquén Basin is entirely consistent with the  
338 palaeogeography inferred from other fossil groups. The Hispanic Corridor or Caribbean  
339 Seaway represented a relatively narrow open marine connection from western Tethys  
340 southwestwards across Central America into western South America in the Mid and  
341 Late Jurassic (e.g. Hallam, 1983, fig. 1; Irurralde-Vinent, 2003, fig. 1; 2006, fig. 1; Fig.  
342 4). This seaway first opened during the Early Jurassic (Aberhan, 2001), and would have  
343 allowed the free interchange of marine biotas between the western Tethys and the  
344 Neuquén Basin from the Mid and Late Jurassic (Bathonian to Oxfordian). Contiguous  
345 shallow marine siliciclastic facies were present throughout the Hispanic Corridor during  
346 the Oxfordian (Irurralde-Vinent, 2003). This study strongly indicates that this open  
347 seaway was present during the Late Callovian (Fig. 4). Some studies have stated that

348 this connection was not fully established until the Late Jurassic (e.g. Irurralde-Vinent,  
349 2006, fig. 2). Previously, Pangea represented a major barrier to free movement of  
350 marine waters and biotas in the equatorial region. Van de Schootbrugge et al. (2005)  
351 postulated that the possible opening of the Hispanic Corridor may have caused the  
352 radiation in cyst-forming dinoflagellates during the Early Jurassic (Late Sinemurian and  
353 Late Pliensbachian). The passive dispersal facilitated by the opening of this seaway  
354 were probably driven westwards through the Hispanic Corridor on the circum-Tropical  
355 Marine Current (Parrish, 1992; Irurralde-Vinent, 2006), and interchanged with the  
356 Neuquén Basin via the western margin of South America. However, it is also possible  
357 that some marine connections were present between South America and Africa via the  
358 Mozambique Corridor (Longshaw and Griffiths, 1983, fig. 4).

359 Musacchio (1979; 1981) reported diverse associations of benthonic foraminifera  
360 and ostracods from the Lotena Formation. The foraminifera are cosmopolitan, and are  
361 similar to coeval faunas from northern Europe. This is consistent with a marine  
362 connection via the Hispanic Corridor. Boomer and Ballent (1996) concluded that the  
363 similarities between Early to Mid Jurassic marine ostracod faunas from southwest  
364 Britain, North Africa and the Neuquén Basin indicate westward migration into the  
365 eastern part of the Tethys along the Hispanic Corridor as opposed to via the  
366 Tethyan/Pacific seaway. This biotic evidence for a marine connection between further  
367 north in the Chilean Basin and into North America, and the Neuquén Basin is consistent  
368 with the configuration of shallow marine facies belts. In the Neuquén Basin, the area of  
369 Callovian marine deposition is surrounded by coastal and continental deposits, with  
370 definite closure towards the south (Zavala, 2005, fig. 1; Fig. 3).

371

## 372 **8. Conclusions**

373

374           The Lotena Formation of the Neuquén Basin, Argentina yields low-moderate  
375 diversity dinoflagellate cyst assemblages indicative of a Late Callovian age by  
376 comparison with northwest Europe. No Australasian or Boreal forms were observed,  
377 and the floras of the Lotena Formation are extremely reminiscent of coeval Eurasian  
378 assemblages. This means that there must have been an open marine connection between  
379 Europe (and adjacent areas) and the Neuquén Basin via the circum-Tropical Marine  
380 Current through the Hispanic Corridor during the Late Callovian. Prior to the Mid  
381 Jurassic, there was no permanent ‘trans-Pangean’ equatorial seaway which allowed  
382 biotal interchange. This conclusion is consistent with evidence from shallow marine  
383 facies belts and other fossil groups including foraminifera and ostracods.

384           A more comprehensive study of the Lotena Formation at localities such as  
385 Puente del Arroyo Picún Leufú and Portada Covunco should be undertaken. This should  
386 allow a significant refinement of Callovian/Oxfordian biostratigraphy and  
387 palaeogeographical interpretations.

388

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390

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399

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630

631

632 Appendix 1.

633 An alphabetical list of palynomorphs identified below generic level in the  
634 Lotena Formation of the Neuquén Basin, and discussed in the text and/or Table 1, with  
635 author citations arranged in three groups. The taxa not recorded in this study, but  
636 mentioned in the text are asterisked. References to the dinoflagellate cyst author  
637 citations can be found in Fensome and Williams (2004).

638

639 **Pollen**

- 640 *Araucariacites australis* Cookson 1947
- 641 *Microcachryidites castellanosii* Menendez 1968
- 642 *Vitreisporites pallidus* (Reissinger 1938) Nilsson 1958
- 643
- 644 **Spore**
- 645 *Retitriletes austroclavatidites* (Cookson 1953) Döring et al. 1963
- 646
- 647 **Dinoflagellate cysts**
- 648 *Ambonosphaera? staffinensis* (Gitmez 1970) Poulsen & Riding 1992
- 649 *Chytroeisphaeridia chytrooides* (Sarjeant 1962) Downie & Sarjeant 1965
- 650 *Dissiliodinium volkheimeri* Quattrocchio & Sarjeant 1992
- 651 *Ellipsoidictyum gochtii* Fensome 1979
- 652 *Endoscrinium* cf. *E. galeritum* (Deflandre 1939) Vozzhennikova 1967 subsp.
- 653 *reticulatum* (Klement 1960) Górká 1970
- 654 \**Endoscrinium kempiae* (Stover & Helby 1987) Lentin & Williams 1989
- 655 \**Endoscrinium luridum* (Deflandre 1939) Gocht 1970
- 656 \**Evansia dalei* (Smelror & Århus 1989) Below 1990
- 657 \**Evansia perireticulata* (Århus et al. 1989) Lentin & Williams 1993
- 658 \**Glossodinium dimorphum* Ioannides et al. 1977
- 659 *Gonyaulacysta jurassica* (Deflandre 1939) Norris & Sarjeant 1965 subsp. *adecta*
- 660 Sarjeant 1982
- 661 \**Gonyaulacysta jurassica* (Deflandre 1939) Norris & Sarjeant 1965 subsp. *jurassica*
- 662 (autonym)
- 663 *Liesbergia liesbergensis* Berger 1986
- 664 *Limbodinium absidatum* (Drugg 1978) Riding 1987

- 665 \**Meiourogonyaulax penitabulata* Riding & Helby 2001
- 666 *Mendicodinium groenlandicum* (Pocock & Sarjeant 1972) Davey 1979
- 667 *Nannoceratopsis pellucida* Deflandre 1939
- 668 \**Nannoceratopsis reticulata* Mantle 2005
- 669 \**Paragonyaulacysta calloviensis* Johnson & Hills 1973
- 670 \**Paragonyaulacysta helbyi* Mantle 2009
- 671 \**Paragonyaulacysta retiphragmata* Dörhöfer & Davies 1980
- 672 *Pareodinia ceratophora* Deflandre 1947
- 673 *Protobatioladinium* cf. *P. lindiensis* Schrank 2005
- 674 *Rynchodiniopsis cladophora* (Deflandre 1939) Below 1981
- 675 *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960
- 676 \**Ternia balmei* Helby & Stover 1987
- 677 *Trichodinium scarburghensis* (Sarjeant 1964) Williams et al. 1993
- 678 *Tubotuberella dangeardii* (Sarjeant 1968) Stover & Evitt 1978
- 679 \**Voodooia tabulata* Riding & Helby 2001
- 680 *Wanaea acollaris* Dodekova 1975
- 681 \**Wanaea fimbriata* Sarjeant 1961
- 682 \**Wanaea digitata* Cookson & Eisenack 1958
- 683 \**Woodinia pedis* Riding & Helby 2001

684

685 **Display material captions:**

686

687 Fig. 1. A generalised lithological log of the succession in the Neuquén Basin (right hand  
 688 side), modified from Zavala (2005). The Lotena Group, which includes the Lotena  
 689 Formation, is highlighted. The upper left inset map illustrates the location of the

690 Neuquén Basin. The lower left inset map illustrates the detailed extent of the Neuquén  
691 Basin.

692

693 Fig. 2. The locations of the Portada Covunco and Picún Leufú sections from where the  
694 samples of the Lotena Formation studied herein were collected.

695

696 Fig. 3. The location of the Neuquén Basin, in central western Argentina and eastern  
697 Chile with a palaeogeographical reconstruction of this depocentre during the Late  
698 Callovian and Early Oxfordian (modified from Legarreta and Uliana, 1999).

699

700 Fig. 4. A palaeogeographical map of the world for the Oxfordian (161.2-155.7 Ma),  
701 immediately following the Callovian (164.7-161.2 Ma), modified after Iturralde-Vinent  
702 (2003). The continuously open nature of the Hispanic Corridor indicates the potential  
703 for biotal exchange between the western Tethys and the eastern Pacific oceans.  
704 Specifically, it is postulated that dinoflagellate cysts could have dispersed through the  
705 Hispanic Corridor during the Callovian. Note that shallow marine siliciclastic facies  
706 belts adjacent to continental areas extended from the western Tethys, through the  
707 Hispanic Corridor, to the Neuquén Basin.

708

709 Table 1. The numbers of palynomorphs counted in the three samples studied. An 'X'  
710 denotes a form which was recorded outside of the main count. Biostratigraphically-  
711 significant dinoflagellate cysts are in bold font. A question mark (?) indicates equivocal  
712 material.

713

714 Plate I

715 A selection of dinoflagellate cysts from the Upper Callovian part of the Lotena  
716 Formation of Puente del Arroyo Picún Leufú and Portada Covunco, in the Neuquén  
717 Basin, west-central Argentina. The sample number, slide number and England Finder  
718 (EF) coordinate are given for each specimen. All samples, slides and figured specimens  
719 are housed in the collections of the Laboratory of Palynology, Universidad Nacional del  
720 Sur, Bahía Blanca, Argentina. The scale bars all represent 10 µm. UNSP = Universidad  
721 Nacional del Sur- Palynology. PC = Portada Covunco. PL = Picún Leufú.

722

723 1, 5. *Gonyaulacysta jurassica* (Deflandre 1939) Norris & Sarjeant 1965 subsp. *adecta*  
724 Sarjeant 1982. 1 – sample/slide UNSP PC 1525/b, EF Y54/2. 5 – sample/slide UNSP  
725 PC 1525/b, EF T68/3.

726 2. *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960. Sample/slide UNSP PC  
727 1525/c, EF M9/2.

728 3, 4. *Nannoceratopsis pellucida* Deflandre 1939. 3 – sample/slide UNSP PL 2971/7, EF  
729 N50. 4 – sample/slide UNSP PL 2971/3, EF R50/1.

730 6. *Pareodinia ceratophora* Deflandre 1947. Sample/slide UNSP PL 2971/4, EF V32/4.

731 7. *Tubotuberella dangeardii* (Sarjeant 1968) Stover & Evitt 1978. Sample/slide UNSP  
732 PL 2971/7, EF J39/1.

733 8. *Protobatioladinium* cf. *P. lindiensis* Schrank 2005. Sample/slide UNSP PL 2971/3,  
734 EF Q47/3.

735 9. *Limbodinium absidatum* (Drugg 1978) Riding 1987. Sample/slide UNSP PL 2971/7,  
736 EF B48/1.

737 10, 11. *Wanaea acollaris* Dodekova 1975. 10 – sample/slide UNSP PL 2971/2, EF  
738 Q43/1. 11 – sample/slide UNSP PL 2971/7, EF S50/4.

- 739 12. *Rynchodiniopsis cladophora* (Deflandre 1939) Below 1981. Sample/slide UNSP PC  
740 1525/d, EF H18/2.
- 741 13. *Chytroeisphaeridia chytroeides* (Sarjeant 1962) Downie & Sarjeant 1965.  
742 Sample/slide UNSP PC 1525/b, EF R66/2.
- 743 14. *Endoscrinium* cf. *E. galeritum* (Deflandre 1939) Vozzhennikova 1967 subsp.  
744 *reticulatum* (Klement 1960) Górka 1970. Sample/slide UNSP PL 2971/7, EF T44/2.  
745