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

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ABSTRACT

The Lotena Formation from two localities, Picún Leufú and Portada Covunco, in the Neuquén Basin of west-central Argentina was studied palynologically. The material examined produced moderately diverse Late Callovian dinoflagellate cyst assemblages. This age assignment is consistent with ammonite evidence. The dinoflagellate cyst floras are reminiscent of the Middle Jurassic associations of northwest Europe and surrounding areas. Marine palynomorphs typical of Australasia and the Arctic are absent. The similarity with Europe is strongly suggestive of an open marine connection between western Tethys and the Neuquén Basin during the Late Callovian. This is interpreted as being via the Hispanic Corridor, with the palynofloras being passively dispersed to the southwest by the circum-Tropical Marine Current. Earlier studies indicate that this trans-Pangean equatorial seaway first began to allow biotic interchange during the Mid Jurassic and this study proves that this open marine connection was established by the Late Callovian. The similarities between the dinoflagellate cyst assemblages of Europe and the Neuquén Basin are consistent with the distribution of other marine fossils and the existence of geographically-continuous marine facies belts.

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

1. Introduction

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

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

2. Geological Background

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

The Neuquén Basin is located immediately to the east of the Andes Mountains in central western Argentina and eastern Chile between 31°S and 41°S (Figs. 1-3). It lies within the Argentine provinces of La Pampa, Mendoza, Neuquén (from which it takes its name) and Río Negro. The depocentre represents the southern end of the more extensive Chilean Basin, is broadly triangular in outline, up to 700 km in a north-south direction and covers over 150,000 km^2. The tectonic history of the Neuquén Basin consists of synrift (Late Triassic-Early Jurassic), postrift/back-arc (Early Jurassic-Early Cretaceous) and foreland stages (Howell et al., 2005, fig. 3). The basin fill is of Late Triassic to Palaeocene age, and is between 4,000 and 7,000 m of heterolithic marine and continental strata (Ramos, 1998; Howell et al., 2005). The majority of the Neuquén Basin fill was deposited during the postrift phase; this comprises the Cuyo, Lotena and Mendoza groups of Pliensbachian to Barremian age (Vergani et al., 1995; Howell et al., 2005, fig. 3).

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

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

3. Material studied

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

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

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

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

Sample 1525 of Martínez and Quattrocchio (2004) is by far the most palynologically productive of the three horizons studied by Martínez and Quattrocchio (2004) from the Lotena Formation of the Portada Covunco section, around 20 km from Zapala (Fig. 2). Here the formation is approximately 220 m thick and corresponds to units 2 and 3 of Zavala et al. (2002). The sample is a massive dark grey mudstone from Unit 2. No ammonites have been recorded from the Lotena Formation of the Portada Covunco section. However, the underlying Lajas Formation of the Cuyo Group has yielded the ammonite *Eurycephalites* cf. *vergarensis*, which is characteristic of the Vergarensis Chronozone, which is of Early Callovian age (Riccardi et al., 1989; 1990; Riccardi, 2008).

4. Description of the palynomorph assemblages

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

5. Biostratigraphy

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

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

A single specimen of *Protobatioladinium* cf. *P. lindiensis* Schrank 2005 was recorded in sample 2971. *Protobatioladinium lindiensis* was originally described from the Tithonian of Tanzania, and similar forms are present in the Bathonian-Ryazanian interval of Europe and Israel (Schrank, 2005). *Dissiliodinium volkheimeri* is confined to the Southern Hemisphere. It was recorded from the Bathonian and Callovian of offshore northwestern Australia by Mantle (2009a). Quattrocchio and Sarjeant (1992, p. 70) stated that *Dissiliodinium volkheimeri* is conspecific with *Dissiliodinium* sp. (no antapical node) of Helby et al. (1987), from the Bajocian-Bathonian of Australia. However, this contention is not supported here because *Dissiliodinium volkheimeri* has a thin autophragm and has extremely low-relief ornamentation. By contrast, *Dissiliodinium* sp. (no antapical node) of Helby et al. (1987) has an irregular reticulate ornamentation and is smaller. *Endoscrinium* cf. *E. galeritum* 1967 subsp. *reticulatum* is apparently endemic to the Neuquén Basin.

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

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

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

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

6. The provincialism of Jurassic dinoflagellate cysts

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

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

7. Palaeogeographical significance of the dinoflagellate cyst assemblages

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

Significantly, no taxa of exclusively Australasian affinity were observed in this study. In the Callovian of Australasia, several characteristic and endemic species are present including *Endoscrinium kempiae, Meiourogonyaulax penitabulata,* *Nannoceratopsis reticulata*, *Paragonyaulacysta helbyi*, *Ternia balmei*, *Voodooia tabulata*, *Wanaea digitata*, *Woodinia pedis* and others (Davey, 1987; Helby et al., 1987; 1988; Riding and Helby, 2001b; Mantle, 2005; 2009a,b). None of these taxa, and other endemic Austral forms, have been recorded from the Lotena Formation of the Neuquén Basin. Hence, due to the lack of Australasian elements, this assemblage is consistent with a strong marine connection with the Euro-Atlantic province to the north. This strongly implies that the Neuquén Basin was isolated from eastern Gondwana in terms of biotal exchange during the Callovian. Australasian dinoflagellate cysts could not have been passively dispersed westwards across the middle latitudes into the Neuquén Basin via trans-Pacific routes due to the wide geographical extent of this deep ocean basin, and the active subduction zone immediately to the west of the Americas (Fig. 4). Similarly, latitudinal and palaeotemperature barriers would probably have prevented dispersal from Australasia to South America around the southern margin of Gondwana (i.e. Australia and Antarctica) via the Southern Gondwanan Seaway (Hallam, 1983; Fig. 4).

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

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

The characteristically European affinity of the Callovian dinoflagellate cysts from the Lotena Formation of the Neuquén Basin is entirely consistent with the palaeogeography inferred from other fossil groups. The Hispanic Corridor or Caribbean Seaway represented a relatively narrow open marine connection from western Tethys southwestwards across Central America into western South America in the Mid and Late Jurassic (e.g. Hallam, 1983, fig. 1; Iturralde-Vinent, 2003, fig. 1; 2006, fig. 1; Fig. 4). This seaway first opened during the Early Jurassic (Aberhan, 2001), and would have allowed the free interchange of marine biotas between the western Tethys and the Neuquén Basin from the Mid and Late Jurassic (Bathonian to Oxfordian). Contiguous shallow marine siliciclastic facies were present throughout the Hispanic Corridor during the Oxfordian (Iturralde-Vinent, 2003). This study strongly indicates that this open seaway was present during the Late Callovian (Fig. 4). Some studies have stated that this connection was not fully established until the Late Jurassic (e.g. Irurralde-Vinent, 2006, fig. 2). Previously, Pangea represented a major barrier to free movement of marine waters and biotas in the equatorial region. Van de Schootbruge et al. (2005) postulated that the possible opening of the Hispanic Corridor may have caused the radiation in cyst-forming dinoflagellates during the Early Jurassic (Late Sinemurian and Late Pliensbachian). The passive dispersal facilitated by the opening of this seaway were probably driven westwards through the Hispanic Corridor on the circum-Tropical Marine Current (Parrish, 1992; Irurralde-Vinent, 2006), and interchanged with the Neuquén Basin via the western margin of South America. However, it is also possible that some marine connections were present between South America and Africa via the Mozambique Corridor (Longshaw and Griffiths, 1983, fig. 4).

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

8. Conclusions

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

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

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Appendix 1.

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

Pollen

Araucariacites australis Cookson 1947

Microcachryidites castellanosii Menendez 1968

Vitreisporites pallidus (Reissinger 1938) Nilsson 1958

Spore

Retitriletes austroclavatidites (Cookson 1953) Döring et al. 1963

Dinoflagellate cysts

Ambonosphaera? *staffinensis* (Gitmez 1970) Poulsen & Riding 1992

Chytroeisphaeridia chytroeides (Sarjeant 1962) Downie & Sarjeant 1965

Dissiliodinium volkheimeri Quattrocchio & Sarjeant 1992

Ellipsoidictyum gochtii Fensome 1979

Endoscrinium cf. *E. galeritum* (Deflandre 1939) Vozzhennikova 1967 subsp. *reticulatum* (Klement 1960) Górka 1970

**Endoscrinium kempiae* (Stover & Helby 1987) Lentin & Williams 1989

**Endoscrinium luridum* (Deflandre 1939) Gocht 1970

**Evansia dalei* (Smelror & Århus 1989) Below 1990

**Evansia perireticulata* (Århus et al. 1989) Lentin & Williams 1993

**Glossodinium dimorphum* Ioannides et al. 1977

Gonyaulacysta jurassica (Deflandre 1939) Norris & Sarjeant 1965 subsp. *adecta* Sarjeant 1982

**Gonyaulacysta jurassica* (Deflandre 1939) Norris & Sarjeant 1965 subsp. *jurassica* (autonym)

Liesbergia liesbergensis Berger 1986

Limbodinium absidatum (Drugg 1978) Riding 1987

**Meiourogonyaulax penitabulata* Riding & Helby 2001

Mendicodinium groenlandicum (Pocock & Sarjeant 1972) Davey 1979

Nannoceratopsis pellucida Deflandre 1939

**Nannoceratopsis reticulata* Mantle 2005

**Paragonyaulacysta calloviensis* Johnson & Hills 1973

**Paragonyaulacysta helbyi* Mantle 2009

**Paragonyaulacysta retiphragmata* Dörhöfer & Davies 1980

Pareodinia ceratophora Deflandre 1947

Protobatioladinium cf. *P. lindiensis* Schrank 2005

Rynchodiniopsis cladophora (Deflandre 1939) Below 1981

Scriniodinium crystallinum (Deflandre 1939) Klement 1960

**Ternia balmei* Helby & Stover 1987

Trichodinium scarburghensis (Sarjeant 1964) Williams et al. 1993

Tubotuberella dangeardii (Sarjeant 1968) Stover & Evitt 1978

**Voodooia tabulata* Riding & Helby 2001

Wanaea acollaris Dodekova 1975

**Wanaea fimbriata* Sarjeant 1961

**Wanaea digitata* Cookson & Eisenack 1958

**Woodinia pedis* Riding & Helby 2001

Display material captions:

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

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

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

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

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

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

Plate I

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

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

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

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

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

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

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

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

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

12. *Rynchodiniopsis cladophora* (Deflandre 1939) Below 1981. Sample/slide UNSP PC 1525/d, EF H18/2.

13. *Chytroeisphaeridia chytroeides* (Sarjeant 1962) Downie & Sarjeant 1965. Sample/slide UNSP PC 1525/b, EF R66/2.

14. *Endoscrinium* cf. *E. galeritum* (Deflandre 1939) Vozzhennikova 1967 subsp. *reticulatum* (Klement 1960) Górka 1970. Sample/slide UNSP PL 2971/7, EF T44/2.