

## JURASSIC ORGANIC-WALLED MARINE MICROPLANKTON FROM THE NEUQUÉN BASIN. DISTRIBUTION, BIOSTRATIGRAPHY AND PALEOBIOGEOGRAPHY. A REVIEW

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# JURASSIC ORGANIC-WALLED MARINE MICROPLANKTON FROM THE NEUQUÉN BASIN. DISTRIBUTION, BIOSTRATIGRAPHY AND PALEOBIOGEOGRAPHY. A REVIEW

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**Abstract.** The Mesozoic Era is crucial for analyzing the replacement of microplanktonic lineages resulting from the beginning of the break-up of Pangea. The paleogeography of South America, and hence of Argentina, underwent successive changes since this time. The opening of different seaways, mainly during the Jurassic, affected the global circulation pattern of the oceans which determined the composition of the organic-walled marine microplankton associations of the Neuquén Basin. These Jurassic marine palynofloras are summarized here, based on the information from outcrop samples of 12 units, which were analyzed from a paleobiogeographic point of view. The configuration of the basin during the Early Jurassic was characterized mainly by partially interconnected depocenters, with restricted marine circulation that favored the development of associations dominated by components of the green lineage (acritarchs and prasinophytes). The Cuyo and Lotena groups (Middle Jurassic) were accumulated during two important flooding episodes which generated the paleoecological conditions for an increase in the diversity of the red lineage (dinocysts). Since the late Callovian the Hispanic Corridor connected the Neuquén Basin with the Tethyan realm allowing the free interchange of species. The Late Jurassic marine palynofloras are best characterized in the Vaca Muerta and Picún Leufú formations. The anoxic condition that prevailed during the accumulation of the Vaca Muerta Formation marked the return to the dominance of the green lineage. Conversely, the Picún Leufú Formation represents neritic more oxygenated bottom waters that favored a relative increase in the abundance and diversity of dinoflagellate cysts.

**Key words.** Jurassic. Marine palynofloras. Paleobiogeography. Neuquén Basin. Argentina.

**Resumen.** MICROPLANKTON MARINO DE PARED ORGÁNICA, JURÁSICO DE LA CUENCA NEUQUINA. DISTRIBUCIÓN, BIOESTRATIGRAFÍA Y PALEOBIOGEOGRAFÍA. UNA REVISIÓN. El Mesozoico constituye un momento crucial para analizar el recambio de los distintos linajes microplancónicos producto del inicio de la ruptura de Pangea. La paleogeografía de Sudamérica y por lo tanto la de Argentina, experimentó sucesivos cambios durante este lapso de tiempo. La apertura de diferentes corredores oceánicos, principalmente durante el Jurásico, afectó los patrones de circulación global de los océanos, evidenciado en la Cuenca Neuquina en la variabilidad de composición de las asociaciones microplancónicas de pared orgánica. Se reúne la información proveniente de muestras de afloramiento de 12 unidades jurásicas, cuyas palinofloras marinas fueron analizadas desde un punto de vista paleobiogeográfico. La configuración de la cuenca durante el Jurásico Temprano se caracterizó principalmente por la presencia de una serie de depocentros parcialmente interconectados con circulación marina restringida. Este contexto favoreció el desarrollo del linaje verde (acritarcos y prasinofíceas). Dos grandes episodios de inundación marina provocaron la acumulación de los grupos Cuyo y Lotena (Jurásico Medio) generando las condiciones paleoecológicas para un incremento en la diversidad del linaje rojo (dinoquistes). A partir del Caloviano tardío la apertura del Corredor Hispánico permitió la conexión de la Cuenca Neuquina con el Dominio Tethiano y con ello, el libre intercambio de especies. El Jurásico Tardío es aquí caracterizado por las palinofloras marinas de las formaciones Vaca Muerta y Picún Leufú. Las condiciones anóxicas que prevalecieron durante la acumulación de la Formación Vaca Muerta constituyen un retorno al predominio del linaje verde. Por el contrario, la Formación Picún Leufú caracterizada por ambientes de plataforma con aguas relativamente más oxigenadas, favorecieron el incremento en la abundancia y diversidad de dinoflagelados.

**Palabras clave.** Jurásico. Palinofloras marinas. Paleobiogeografía. Cuenca Neuquina. Argentina.

THE FOSSIL record of the Paleozoic–Mesozoic boundary documents one of the most dramatic changes in Phanerozoic marine primary production. It is generally agreed that acritarchs and prasinophytes essentially represent the ma-

rine phytoplankton of the Paleozoic Era (Riegel, 2008 and references therein). These groups were included by several authors (Falkowski *et al.*, 2005; Riegel, 2008 and references therein) in the “green lineage”. Highly stratified anoxic bottom

water overlain by low-salinity, warm surface waters were advantageous conditions for green algae (van de Schootbrugge *et al.*, 2005).

During the Middle–Late Triassic new groups of photosynthetic eukaryotic phytoplankton taxa, including cyst-forming dinoflagellates and calcareous nannoplankton (coccolithophorids), appeared (Riegel, 2008 and references therein), which represent the “red lineage” (Falkowski *et al.*, 2005 *in* van de Schootbrugge *et al.*, 2005). The radiation of cyst-forming dinoflagellates began in the Late Triassic showing a rapid increase during the Early Jurassic (Fensome *et al.*, 1996). This time was decisive for dinoflagellate evolution and during the late Pliensbachian they replaced green algae as primary producers. The break-up of Pangea played a crucial role in the spread of the red lineage (Katz *et al.*, 2004 *in* Riegel, 2008). The radiation of cyst-forming dinoflagellates during the late Sinemurian and late Pliensbachian coincided with significant changes in paleoceanography and paleoclimate, possibly related to the opening and flooding of the Hispanic Corridor (van de Schootbrugge *et al.*, 2005). Hydrographic instabilities and well-oxygenated bottom waters appear to have facilitated cyst-forming dinoflagellate diversity (Bucefalo Palliani *et al.*, 2002; van de Schootbrugge *et al.*, 2005; Sluijs *et al.*, 2005).

The main goal of this contribution is to describe the way these worldwide paleoceanographic changes affected the distribution and diversity patterns of organic-walled marine microplankton in the Neuquén Basin, Argentina, during the Jurassic.

## GEOLOGICAL SETTING OF THE NEUQUÉN BASIN

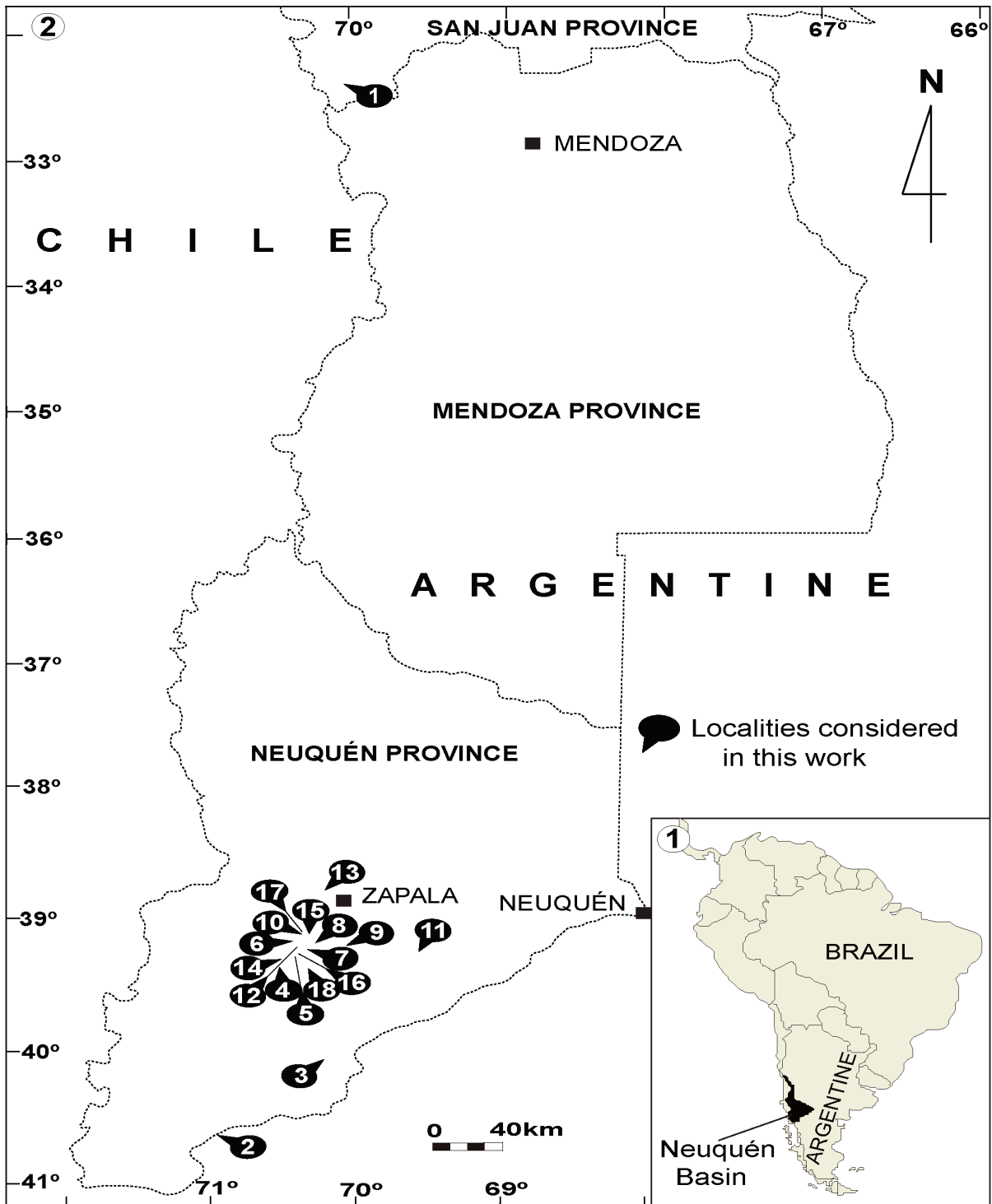
The Neuquén Basin is situated in west-central Argentina and eastern Chile between 34° and 41°S (Fig. 1). This basin, originated during the latest Triassic, was an important region of sedimentation during the Jurassic and Early Cretaceous (Mpodozis and Ramos, 1989). It has been interpreted as a back-arc basin related to the thermal-tectonic collapse of the continental crust behind a stationary magmatic arc during the Late Triassic (Mpodozis and Ramos, 1989; Vergani *et al.*, 1995).

Permo-Triassic volcanoclastics, constituting the Choiyoi Group (Groeber, 1946; Stipanovic *et al.*, 1968) are regarded as basement. Deposits are mainly marine in origin and

present well-defined records of cyclic sea-level changes at different scales (Howell *et al.*, 2005). The first major depositional episode after the basin was configured, the Cuyo Group (Groeber, 1946), comprises marine and continental deposits more than 2500 m thick, accumulated during a transgressive-regressive cycle which developed during the Hettangian–Middle Callovian (Zavala, 1996a). Although a Hettangian–Sinemurian marine transgression with ammonite fauna is recorded at the Río Atuel, Mendoza Province (Riccardi *et al.*, 1988), it did not reach the central and southern Neuquén Basin until the Pliensbachian. This group is composed of deposits consisting of a prograding clastic section with offshore fine-grained deposits of the Los Molles Formation (Weaver, 1931) (Fig. 2), isolated turbidite intervals and hyperpycnal flows (Zavala *et al.*, 2011, 2014; Martínez *et al.*, 2016). This formation is progressively overlain by sandstones and conglomerates reflecting shallow marine to continental environments belonging to the Lajas Formation (Weaver, 1931).

During the Early–Middle Jurassic the presence of a tectonic structure controlled the accumulation in the basin. This extensive and complex east-west oriented Mesozoic structure named Huincul Arch, located in the southern part of the Neuquén Basin, acted as a physical barrier isolating this part of the basin as a sub-basin named Picún Leufú (Hogg, 1993; Zavala and Freije, 2002). In this sub-basin the deposition of the Cuyo Group culminates with the continental deposits, red mudstones interbedded with sandstones and conglomerates, of the Challacó Formation (de Ferraris, 1947; Zavala and González, 2001).

The Lotena Group (*sensu* Zavala and González, 2001) represents the second marine incursion after the first broad disconnection (Zavala, 2005). It is a clastic-evaporitic unit deposited during the middle Callovian until the latest Oxfordian–Early Kimmeridgian (Zavala 2005; Olivera *et al.*, 2010). This group starts with evaporites of the Tábanos Formation (Stipanovic, 1966; Dellapé *et al.*, 1979) followed by the Lotena Formation (*sensu* Gulisano *et al.*, 1984) (Fig. 2), which is dominated by mudstone with subordinate evaporites, limestones and sandstones. This unit is overlain by the mainly carbonate succession of the La Manga Formation (Stipanovic, 1966; Stipanovic *et al.*, 1975). The partial isolation of the Picún Leufú sub-basin continued during the be-



**Figure 1.** 1, Location map of the Neuquén Basin, Argentina, South America. 2, Localities mentioned in the text; 1, Arroyo de los Patos Sur (Los Patillos Fm.); 2, Alicurá Dam (Nestares Fm.); 3, Cañadón La Pintada (Piedra Pintada Fm.); 4, Valle del Arroyo Lapa (Sierra Chacaico Fm.) and Arroyo Lapa-Estancia Charahuilla (Los Molles Fm.); 5, Charahuilla (Los Molles and Lajas formations); 6, Puesto Bascuñán (Lajas Fm.); 7, Puesto Policía (Los Molles Fm.); 8, Los Molles (Los Molles and Lajas formations); 9, Puente Picún Leufú (Los Molles, Lajas, Lotena, Vaca Muerta and Picún Leufú formations); 10, Lohan Mahuida (Los Molles, Cura Niyeu and Lajas formations); 11, Cerro Lotena (Los Molles Fm.); 12, Cerro Chacaico (Los Molles and Lajas formations); 13, Portada Covunco (Lajas, Lotena and Auquilco formations); 14, Sierra Chacaico: Peregrina, Rhea Gorge, Quilmez and Dagna (Lajas Fm.); 15, Quebrada del Sapo (Bosque Petrificado Fm.); 16, Cura Niyeu (Cura Niyeu Fm.); 17, Barda Norte (Lotena Fm.); 18, Caichigüe (Vaca Muerta Fm.).

ginning of the accumulation of the Lotena Group. These deposits represent fluvial-lacustrine to estuarine environments and are known as the Bosque Petrificado Formation (Zavala and Freije, 2002), which is chronologically, but not genetically, related to the Tábanos Formation (Zavala and González, 2001; Zavala and Freije, 2002).

Marine sequences developed throughout the basin during the Late Jurassic–Early Cretaceous are included in the Mendoza Group (Stipanovic, 1969). This group comprises several units, the Auquilco (Weaver, 1931), Tordillo (Groeber, 1946; Stipanovic, 1966), Quebrada del Sapo (Digregorio, 1972), Vaca Muerta (Leanza and Hugo, 1978; Legarreta *et al.*, 1981; Veiga and Orchueta, 1988), Picún Leufú (Leanza 1973), Quintuco (Digregorio, 1972), Mulichinco (Digregorio, 1972) and Agrio (Weaver, 1931) formations widely extending from southern Neuquén to Mendoza provinces. The Auquilco Formation comprises an evaporitic succession of up to 400 m thick related to a marginal hypersaline marine environment (Legarreta and Uliana 1999; Volkheimer and Moroni 1981). The continental deposits of the Tordillo and Quebrada del Sapo formations represent a temporal isolation of the Neuquén Basin from the Pacific Ocean. During the Tithonian, catastrophic flooding represents the return to a depositional context of a marine basin with anoxic bottom water (Legarreta and Uliana, 1999), which corresponds to the deposits of the Vaca Muerta Formation. The top of this unit is diachronous and progradational. It includes younger stages when passing from the southern (middle Tithonian) to the central sector of the basin (Berriasian–Valanginian) (Doyle *et al.*, 2005). Near the southern border of the basin, the Vaca Muerta Formation is replaced laterally by the whitish and greenish calcareous sandstones, and massive whitish limestones of the Picún Leufú Formation.

All the units mentioned in this contribution are summarized in a correlation chart between two geological provinces, Principal Cordillera and Neuquén Embayment (Fig. 2).

## PALEOGEOGRAPHIC FRAMEWORK

The paleogeography of the beginning of the Jurassic was similar to the one of the end of the Paleozoic (Fig. 3). The supercontinent Pangea, surrounded by the superocean Panthalassa, represented a large barrier to the free movement of marine biotas along the paleo-equator. However, a system of rift valleys started to form within west-central Pangea since the latest Triassic (Iturralde-Vinent, 2006). In this area, Damborenea and Manceñido (1979) proposed the existence of a shallow intermittent marine connection between western Tethys and the eastern Pacific, based on bivalve data. This seaway, known as the Hispanic Corridor (Smith, 1983) acted as a filter which only allowed the interchange of on-shore benthonic species since the Sinemurian (Damborenea, 2000). The effective opening of this marine passage was installed during the Middle Jurassic. The stratigraphic record indicates that this connection was fully functional and the Circum-Tropical marine current was probably active since the Bathonian and certainly since the Oxfordian (Iturralde-Vinent, 2004, 2006).

By the late Pliensbachian another seaway, called the Viking Corridor by Westermann (1993), was opened between Greenland and Norway connecting the Arctic and Tethys oceans (Aberhan, 2001).

Another migration route was established during the Middle Jurassic (Bathonian and Callovian) with the opening of the Mozambique Corridor (Heinze, 1996; Abdelhady and Fürsich, 2015), which communicated Madagascar and

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**Figure 2.** Correlation chart of selected Jurassic units from two geological provinces of Argentina. They are organized in integrated columns; only the main depocenters of these regions are taken into account, and they do not represent the entire units of each basin. The age range of each formation is mainly based on paleontological works (palynomorphs and ammonoids fossil-genera): La Ramada Basin: Volkheimer *et al.* (1977), Álvarez *et al.* (1994), Álvarez (1996); Río Atuel: Dimieri *et al.* (2005); Northward of Huinca Arch: Volkheimer and Moroni (1981), Zavala (1996 a,b), Martínez (2002), Martínez *et al.* (2005); Picún Leufú Sub-basin: Volkheimer (1973), Arguijo *et al.* (1982), González-Amicón and Volkheimer (1982a,b), Zavala and Freije (2002), Zavala *et al.* (2005), Armella *et al.* (2007), Zavattieri *et al.* (2008), Olivera *et al.* (2010). Abbreviations in the graphic: **CN**, Cura Niyeu Formation; **BP**, Bosque Petrificado Formation; **FM**, Fortín Primero de Mayo Formation; **QS**, Quebrada del Sapo Formation; **T**, Tordillo Formation; **VM (part.)**, Vaca Muerta Formation (partially); **PL (part.)**, Picún Leufú Formation (partially).

Era	Period	Epoch	Age	Ma	Principal Cordillera	Neuquén Embayment				
Mesozoic	Jurassic	Late	Titthonian	145	La Ramada Basin	Northward Huincul Arch	Picún Leufú Sub-basin			
				Quintuco Fm. (part.)	Rio Atuel		North area	South area		
				Vaca Muerta Fm.	Vaca Muerta Fm. (part.)		PL (part.)			
		Kimmeridgian	Oxfordian	152.1	Tordillo Fm.	Tordillo Fm.	Vaca Muerta Fm. (part.)	VM(part.)		
					Auquileo Fm.	Tordillo Fm.	T	QS		
					La Manga Fm.	Auquileo Fm.	FM			
		Callovian	163.5	166.1	Lotena Fm.	Lotena Fm.	Lotena Fm.	Lotena Fm.		
					Tábanos Fm.	Tábanos Fm.	BP			
					Calabozo Fm.	Lajas Fm.	Challacó Fm.			
		Bathonian	168.3	170.3	Lajas Fm.	Lajas Fm.	Lajas Fm.	Lajas Fm.		
					Tres Esquinas Fm.					
		Aalenian	174.1	182.7	Los Patillos Fm.	Puesto Araya Fm.	Los Molles Fm.	Los Molles Fm.		
Toarcian	182.7	Pliensbachian	"Vulcanias Jurásicas"	El Freno Fm.	Los Molles Fm.	Sierra Cha-Piedra Pincaico Fm.				
Early	Sinemurian	190.8	Rancho de Lata Fm. (part.)	El Freno Fm.	Los Molles Fm.	Sierra Cha-Piedra Pincaico Fm.				
Hettangian	201.3				Los Molles Fm.	Nestares Fm.				

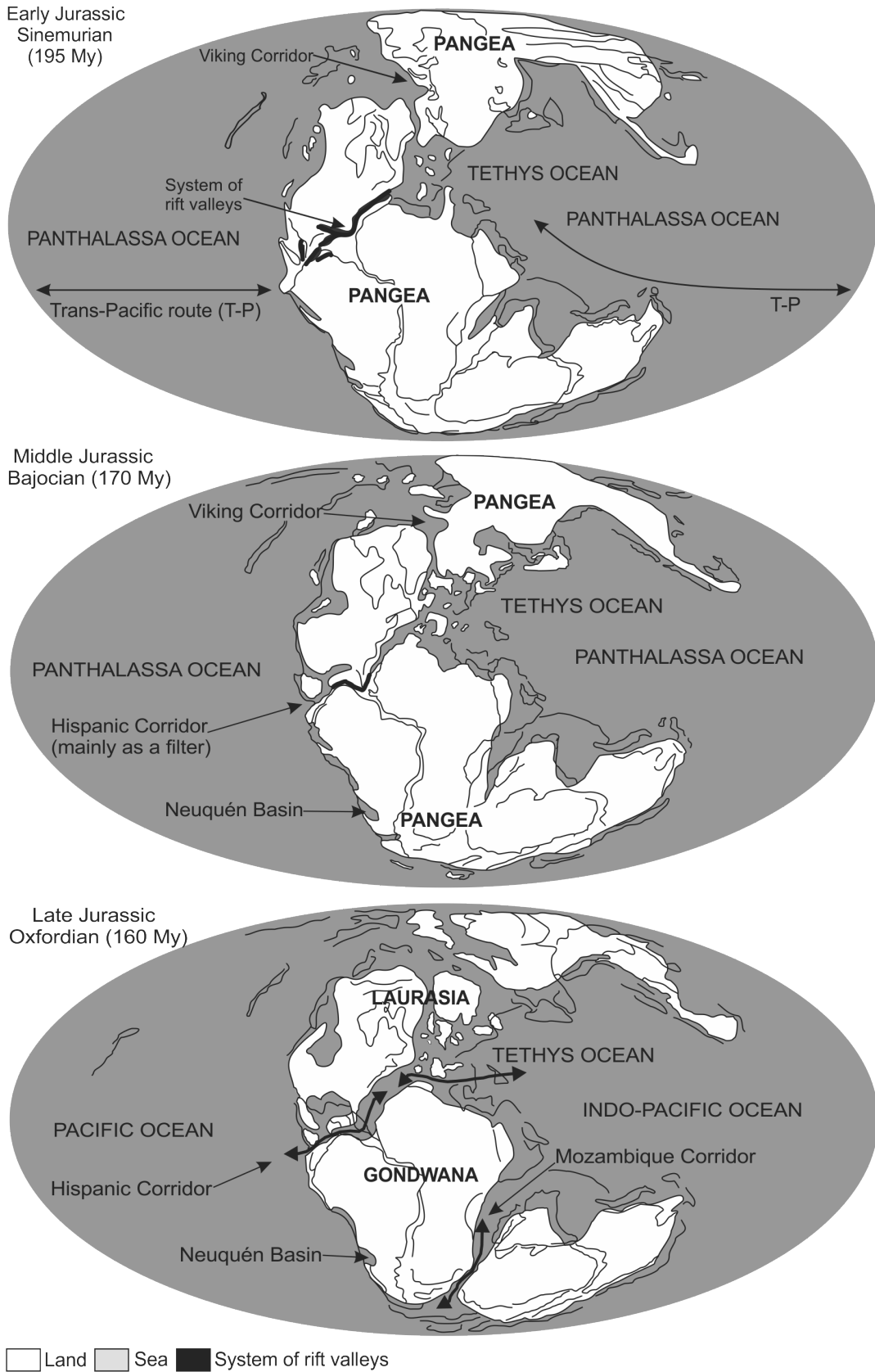


Figure 3. Paleogeographic maps of the Jurassic world (modified from Iturralde-Vinent, 2006).

southern Africa with the South Pacific. This seaway became wider towards the Oxfordian, allowing the incoming of the high-latitude bivalve taxa into the East African (Damborenea *et al.*, 2013).

## DISTRIBUTION OF ORGANIC-WALLED MARINE MICROPLANKTON FROM THE NEUQUÉN BASIN

The deposits of the Neuquén Basin are characterized by alternating transgressive marine and regressive non-marine phases. Thus, the stratigraphical record of marine organic-walled microplankton (dinoflagellates, prasinophytes, acritarchs and other algae) is discontinuous (Tab. 1). However, the distribution of mainly dinoflagellate cysts enabled an outline of general paleobiogeographic patterns. The Neuquén Basin has a significantly refined biozonation in terms of resolution based on abundant, diverse and very well preserved ammonite faunas. In this paper, the word "diversity" is used in its original sense to denote the number of species (Rosenzweig, 1995). Riccardi (2008) presented an update of these zonations.

### Early Jurassic

Currently, only five Liassic formations of the Neuquén Basin have provided palynological assemblages: Los Patillos (Álvarez *et al.*, 1994), Piedra Pintada (Stipanovic *et al.*, 1968; Gulisano and Pando, 1981), Sierra Chacaico (Volkheimer, 1973), Los Molles (Weaver, 1931) and Nestares (González Díaz, in Arrondo and Petriella, 1980) (Figs. 1, 2; Tabs. 1, 2).

Volkheimer *et al.* (1978) studied the lower (continental) and upper (marine) Member of the Los Patos Formation in the northern part of the Neuquén Basin (western slope of Espinacito Range, High Cordillera of San Juan). The upper Member contains ammonites of the *Fanninoceras* Assemblage Zone (see Riccardi *et al.*, 1990, 2000) (late Pliensbachian) and *Tenuicostatum* Standard Zone and *Dactylioceras hoelderi* Assemblage Zone (see Riccardi, 2008) (early Toarcian). The marine elements are represented only by acritarchs (*Schizocystia rara* Playford and Dettman 1965, *Leiosphaeridia* sp.) and prasinophytes (*Pleurozonaria* sp., *Cymatiosphaera* sp.). After Álvarez *et al.* (1994) the original Los Patos Formation should be considered a *nomen nudum*. They proposed that Los Patos should be divided in two units: Rancho de Lata and Los Patillos formations. The

levels studied by Volkheimer *et al.*, (1978), under the name upper Member, should now be considered as belonging to the lower section of Los Patillos Formation (Fig. 2).

A marine sequence, belonging to the Piedra Pintada Formation, crops out near Piedra del Aguila (southern border of the Neuquén Basin), which was assigned to the Pliensbachian due to the presence of *Austromorphites behrendseni* Jaworski (Arguijo *et al.*, 1982; Arguijo and Volkheimer, 1985). The marine components of the recovered palynological association are represented by cf. *Granodiscus staplinii* (Pocock) Jiabo 1978, *Tasmanites suevicus* (Eisenack) Wall 1965 and proximate indeterminate dinocysts. The Sierra Chacaico and Los Molles formations from the Sierra de Chacaico area yielded guide ammonites of the *Austromorphites behrendseni* Assemblage Zone (Hillebrandt, 1987, 2006) (late early Pliensbachian) and *Dactylioceras hoelderi* Assemblage Zone (see Hillebrandt, 1987; Riccardi *et al.*, 1990, 2000; Hillebrandt *et al.*, 1992) (early Toarcian), respectively (Volkheimer, 1973). The recovered marine palynological assemblages from these units are characterized by acritarchs (*Solisphaeridium* cf. *debilispinum* (Wall and Downie) Sarjeant 1973 and *Micrhystridium* sp.) and prasinophytes (*Campenia austroamericana* Volkheimer 1974, *Lancettopsis* sp., *Pterospermopsis* sp. A, *Pterospermopsis* sp. B and *Tasmanites suevicus*) (Volkheimer, 1974).

An Early Jurassic siliciclastic sequence crops out at Alicurá (Limay River) in the southern part of the Neuquén Basin. The marine assemblage recovered from the Las Coloradas Formation (Quartino *et al.*, 1981) was studied by Volkheimer *et al.* (1981), and assigned to the Pliensbachian–early Toarcian age. This unit is characterized by acritarchs, *Hyalinsphaeridia* cf. *hyalina* (Deflandre) Bernier and Courtinat 1979, *G. staplinii*), *Deunffia* and *Leiofusa*. Zavattieri *et al.* (2008) discussed the stratigraphic position of this unit, which for priority reasons is called the Nestares Formation (Fig. 2). These authors presented an interesting assemblage characterized by marine components, such as the *Parvocysta* suite, *Phallocysta*, *Nannoceratopsis* and *Suessiaceae* (Figs. 5.15–16) and *Callialasporites trilobatus* (Balme) Dev 1961 pollen grains, among others, based on a new sampling at the Alicurá Dam. This palynoflora suggests a late Toarcian age; therefore they relocated this unit to the basal part of the Cuyo Group.



TABLE 1 - Distribution of Jurassic organic-walled marine microplankton species from Neuquén Basin.

		Taxa												
		Formations												
		Los Patillos	Piedra Pintada	Sierra Chacaico	Nestares	Los Molles	Cura Niyeu	Lajas	Bosque Petrificado	Lotena	Auquileo	Vaca Muerta	Picún Leufú	
Prasinophytes	<i>Cymatiosphaera</i> spp.	X			X	X	X	X	X			X		
	<i>Pleurozonaria</i> spp.	X				X	X							
	<i>Tasmanites suevicus</i> (Eisenack) Wall 1965		X			X								
	<i>Campenia austroamericana</i> Volkheimer 1974			X		X								
	<i>Lancettopsis</i> sp. (in Volkheimer 1974)			X		X	X							
	<i>Pterospermopsis</i> sp. A (in Volkheimer 1974)			X										
	<i>Pterospermopsis</i> sp. B (in Volkheimer 1974)			X										
	<i>Cymatiosphaera eupeplos</i> (Valensi) Deflandre 1954						X	X		X			X	
	<i>Cymatiosphaera</i> cf. <i>C. eupeplos</i> (in Martínez et al. 2005)						X							
	<i>Cymatiosphaera</i> cf. <i>C. volkheimerii</i> (in Martínez et al. 2005)						X							
	<i>Cymatiosphaera</i> sp. 1 (in Martínez et al. 2005)						X							
	<i>Cymatiosphaera</i> sp. 2 (in Martínez et al. 2005)						X							
	<i>Cymatiosphaera</i> sp. 3 (in Martínez et al. 2005)						X							
	<i>Pleurozonaria</i> cf. <i>P. picunensis</i> (in Martínez et al. 2005)						X							
	<i>Tasmanites</i> spp.						X	X						
	<i>Campenia</i> sp.							X						
	<i>Pleurozonaria picunensis</i> Quattrocchio 1980								X				X	X
	<i>Pterosphaeridia</i> spp.								X	X				
	<i>Cymatiosphaera volkheimerii</i> (Quattrocchio) Martínez et al. 2005												X	X
	<i>Pterospermella hartii</i> (Sarjeant) Eisenack et al. 1973												X	
Green lineage	<i>Schizocystia</i> sp. cf. <i>S. rara</i> (in Volkheimer et al. 1978)	X												
	<i>Leiosphaeridia</i> spp.	X			X		X	X		X			X	
	<i>Solisphaeridium</i> cf. <i>debilispinum</i> (in Volkheimer et al. 1974)			X			X							
	<i>Deunffia</i> sp.				X									
	<i>Leiofusa</i> sp.				X									
	<i>Hyalinsphaeridia</i> sp. cf. <i>H. hyalina</i> (in Quattrocchio 1980)				X	X		X		X	X			
	<i>Granodiscus staplinii</i> (Pocock) Jiabo 1978				X									
	<i>Micrhystridium</i> spp.				X	X	X	X	X	X			X	
	<i>Schizocystia</i> sp.				X									
	<i>Veryhachium</i> spp.				X		X			X				
	<i>Baltisphaeridium</i> spp.					X				X				
	<i>Comasphaeridium</i> cf. <i>debilispinum</i>					X								
	<i>Filisphaeridium balmei</i> (Sarjeant) Sarjeant and Stancliffe 1994					X				X				
	<i>Filisphaeridium</i> cf. <i>F. balmei</i> (in Martínez et al. 2005)					X								
	<i>Filisphaeridium castaninum</i> (Valensi) Sarjeant and Stancliffe 1994					X								
	<i>Filisphaeridium densispinum</i> (Valensi) Sarjeant and Stancliffe 1994					X								
	<i>Leiosphaeridia</i> sp. B (in Volkheimer et al. 1977)					X				X				
	<i>Leiosphaeridia</i> sp. E (in Prámparo 1989)					X								
<i>Leiosphaeridia</i> cf. <i>L. sp. F</i> (in Martínez et al. 2005)					X									

TABLE 1 - Continuation.

		Taxa	Formations												
			Los Patillos	Piedra Pintada	Sierra Chacaico	Nestares	Los Molles	Cura Niyeu	Lajas	Bosque Petrificado	Lotena	Auquico	Vaca Muerta	Picún Leufú	
Green lineage	Acritarchs	<i>Micrhystridium fragile</i> Deflandre 1947					X		X		X				
		<i>M. echinoides</i> cf. <i>forma minor</i> (in Martínez et al. 2005)					X								
		<i>M. brevispinosum</i> (Valensi) Sarjeant and Stancliffe 1994					X		X		X				
		<i>Micrhystridium</i> cf. <i>M. gregarium</i> (in Martínez et al. 2005)					X								
		<i>M. inconspicuum</i> (Deflandre) emend. Deflandre and Sarjeant 1970					X		X		X		X		
		<i>Micrhystridium</i> cf. <i>M. inconspicuum</i> (in Martínez et al. 2005)					X								
		<i>Micrhystridium nannacanthum</i> Deflandre 1945					X		X	X					
		<i>Micrhystridium recurvatum</i> Valensi 1953					X		X		X		X		
		<i>Polygonium</i> sp. cf. <i>P. jurassicum</i> (in Martínez et al. 2005)					X								
		<i>Polygonium</i> spp.					X		X		X				
		<i>Veryhachium valensii</i> (Valensi) Downie and Sarjeant 1965					X								
		<i>Hyalinsphaeridia hyalina</i> (Deflandre) Bernier and Courtinat 1979							X		X		X		
		<i>Granodiscus</i> sp. cf. <i>G. staplinii</i> (in Quattrocchio 1984a)							X		X		X	X	
		<i>Deunffia monospinosa</i> Downie 1960								X					
		<i>Leiosphaeridia</i> sp. C (in Quattrocchio and Volkheimer 1983)								X	X				
		<i>Leiosphaeridia</i> cf. L. sp. B (in Volkheimer et al. 1977)								X	X				
		<i>Micrhystridium echinoides</i> Valensi 1953								X	X				
		<i>Micrhystridium placophorum</i> Valensi 1948								X					
		<i>M. recurvatum</i> forma <i>recurvatum</i> Valensi 1953								X	X				
		<i>Micrhystridium stellatum</i> Deflandre 1945								X					
		<i>Solisphaericium stimulierum</i> (Deflandre) Pocock 1972									X				X
		<i>Hyalinsphaeridia acorpuscula</i> Bernier and Courtinat 1979										X			
		<i>G.</i> sp. cf. <i>G. granulatus</i> (in Volkheimer and Quattrocchio 1981)										X			
		<i>Micrhystridium rarispinum</i> Sarjeant 1960										X			
		<i>Granodiscus granulatus</i> Mädler 1963											X		
		<i>Leiosphaeridia</i> sp. cf. L. <i>variabilis</i>											X		
		<i>Comasphaeridium</i> sp.												X	
		<i>Filisphaeridium</i> sp.												X	
		<i>Hyalosphaera</i> sp.												X	
		<i>Leiosphaeridia</i> sp. A (in Volkheimer and Quattrocchio 1977)												X	
<i>Lecithodinium</i> sp.													X		
<i>Micrhystridium lymensis</i> var. <i>gliscum</i> Wall 1965													X		
Red lineage	Dinoflagellate cysts	<i>Batiacasphaera</i> sp.				X									
		<i>Mancodinium</i> sp.				X									
		<i>Mendicodinium</i> sp.				X									
		<i>Nannoceratopsis</i> spp.				X		X	X						
		<i>Phallocysta</i> spp.				X									
		<i>Parvocysta</i> sp.				X									
		<i>Sentusidinium</i> sp.				X									

TABLE 1 - Continuation.

		Formations												
		Los Patillos	Piedra Pintada	Sierra Chacaico	Nestares	Los Molles	Cura Niyeu	Lajas	Bosque Petrificado	Lotena	Auquico	Vaca Muerta	Picún Leufú	
Red lineage	Dinoflagellate cysts	<i>Parvocysta</i> sp.				X								
		<i>Sentusidinium</i> sp.				X								
		<i>Cleistosphaeridium</i> sp.					X							
		<i>Escharisphaeridia pocockii</i> (Sarjeant) Erkmén and Sarjeant 1980					X		X	X			X	X
		<i>Gonyaulacysta</i> spp.						X			X			X
		<i>Pareodinia</i> sp. A (in Quattrocchio 1984a)						X						
		<i>Rhaetogonyaulacaceae</i> Tipo 1 (in Quattrocchio 1984a)						X						
		<i>Rhaetogonyaulacaceae</i> Tipo 2 (in Quattrocchio 1984a)						X						
		<i>Rhaetogonyaulax</i> sp.						X						
		<i>Acanthaulax</i> sp.							X					
		<i>Ctenidodinium</i> spp.							X		X			X
		<i>Dissiliodinium psilatium</i> Prauss 1989							X					
		<i>Dissiliodinium</i> cf. <i>baileyi</i> (in Stukins et al. 2013)							X					
		<i>Dissiliodinium</i> spp.							X					
		<i>Endoscrinium</i> spp.							X		X			
		<i>Escharisphaeridia</i> spp.							X					
		<i>Jansonia psilata</i> Martínez et al. 1999							X				X	
		<i>Kallosphaeridium granulatum</i> (Norvick) Stover and Evitt 1978							X					
		<i>Kallosphaeridium</i> spp.							X					
		<i>Korystocysta kettonensis</i> (Sarjeant) Woollam 1983							X					
		<i>Korystocysta</i> sp.							X					
		<i>Mendicodinium groenlandicum</i> (Pocock and Sarjeant) Davey 1979							X		X			
		<i>Nannoceratopsis pellucida</i> Deflandre emend. Evitt 1961							X		X			
		<i>Rhynchodiniopsis cladophora</i> (Deflandre) Below 1981							X		X			
		<i>Acanthaulax downiei</i> (Sarjeant) Sarjeant 1976									X		X	
		<i>Ambonosphaera? Staffinensis</i> (Gitmez) Poulsen and Riding 1992									X			
		<i>Barbatacysta</i> cf. <i>brevispinosa</i> (in Courtinat and Gaillard 1980)									X			
		<i>Chytroisphaeridia chytrooides</i> (Sarjeant) Downie and Sarjeant 1965									X			
		<i>Cleistosphaeridium lumectum</i> (Sarjeant) Davey et al. 1969									X			
		<i>Diacanthum argentinum</i> Quattrocchio and Sarjeant 1992									X			X
		<i>Dissiliodinium volkheimeri</i> Quattrocchio and Sarjeant 1992									X			
		<i>Durotrigia</i> sp.									X			
		<i>Ellipsoidictyum gochtii</i> Fensome 1979									X			
		<i>Endoscrinium galeritum</i> subsp. <i>reticulatum</i> Klement 1960									X			
		<i>E.</i> cf. <i>E. g.</i> subsp. <i>reticulatum</i> (in Riding et al. 2011)									X			
<i>Gonyaulacysta jurassica</i> (Deflandre) Norris and Sarjeant 1965									X		X			
<i>Gonyaulacysta jurassica</i> subsp. <i>adecta</i> (Deflandre) Sarjeant 1982									X					
<i>Hystrichosphaeridium</i> sp. A (in Volkheimer and Quattrocchio 1981)									X					
<i>Liesbergia liesbergensis</i> Berger 1986									X					

TABLE 1 - Continuation.

		Taxa												
		Formations												
		Los Patillos	Piedra Pintada	Sierra Chacaico	Nestares	Los Molles	Cura Niyeu	Lajas	Bosque Petrificado	Lotena	Auquico	Vaca Muerta	Picún Leufú	
Red lineage	Dinoflagellate cysts	<i>Limbodinium absidatum</i> (Drugg) Riding 1987								X				
		<i>Lithodinia deflandrei</i> Sarjeant 1968									X			
		<i>Lithodinia jurassica</i> subsp. <i>reburrosa</i> (Eisenack emend. Gocht 1975) Quattrocchio and Sarjeant 1992									X			
		<i>Lithodinia</i> spp.									X			
		<i>Mancodinium semitabulatum</i> Morgenroth 1970									X			
		<i>Rhynchodiniopsis</i> spp.									X			
		<i>Sentusidinium villersense</i> (Sarjeant) Sarjeant and Stover 1978									X			X
		<i>Scriniocassis weberi</i> Gocht 1962									X			
		<i>Scriniodinium crystallinum</i> (Deflandre) Klement 1960									X			
		<i>Trichodinium scarburghensis</i> (Sarjeant) Williams et al. 1993									X			
		<i>Tubotuberella dangeardii</i> (Sarjeant) Stover and Evitt 1978									X			
		<i>Pareodinia</i> sp.									X			X
		<i>Pareodinia ceratophora</i> var. <i>pachyceras</i> Sarjeant 1959									X		X	
		<i>Pareodinia ceratophora</i> Deflandre 1947									X		X	
		<i>Protobatioladinium</i> cf. <i>P. lindiensis</i> (in Riding et al. 2011)									X			
		<i>Wanaea acollaris</i> Dodekova 1975									X			
		<i>Acanthaulax</i> aff. <i>Paliuros</i> (Sarjeant) Sarjeant 1968												X
		<i>Apteodinium bucculiatum</i> Davies 1983												X
		<i>Dichadogonyaulax</i> cf. <i>schizoblata</i> (in Quattrocchio and Sarjeant 1992)												X
		<i>Hystrichosphaerina neuquina</i> (Quattrocchio and Volkheimer) emend. Quattrocchio and Sarjeant 1992												X
		<i>Kalyptea diceras</i> Cookson and Eisenack 1960												X
		<i>Microdinium</i> sp. A (in Volkheimer and Quattrocchio 1977)												X
		<i>Paraevansia</i> sp.												X
		<i>Aptea notialis</i> Quattrocchio and Sarjeant 1992												X
		<i>Cribroperidinium</i> sp.												X
		<i>Ctenodinium tenellum</i> Deflandre 1938												X
		<i>Diacanthum</i> cf. <i>hollisteri</i> (in Quattrocchio and Sarjeant 1992)												X
		<i>Dichadogonyaulax culmula</i> subsp. <i>curtospina</i> (Norris) Quattrocchio and Sarjeant 1992												X
		<i>Dingodinium</i> sp.												X
		<i>Millioudodinium nuciforme</i> (Deflandre) Sarjeant 1982												X
		<i>Paraevansia mammillata</i> Quattrocchio and Sarjeant 1992												X
		<i>Pilosidinium cactosum</i> Quattrocchio and Sarjeant 1992												X
		<i>Rhynchodiniopsis setcheyensis</i> (Sarjeant) Sarjeant 1982												X
		<i>Rhynchodiniopsis</i> cf. <i>setcheyensis</i> (in Quattrocchio and Sarjeant 1992)												X
<i>Systematophora penicillata</i> (Ehrenberg) emend. Sarjeant 1980												X		

**TABLE 2 - Middle Jurassic localities considered in this study (the age of the units is based on paleontological contributions, main ammonoids and palynomorphs data, carried out by different authors and it does not represent the entire age range of each unit).**

Formation	Age	Localities	Contributions
Picún Leufú	late middle Tithonian–early Berriasian	Picún Leufú Creek	17
Vaca Muerta (partially)	early–middle Tithonian early Tithonian	PPL Caichigüe	14, 17, 18, 26, 27
Auquílco	late Oxfordian	PC	25
Lotena	late Callovian middle–late Callovian	Portada Covunco (PC) Puente Picún Leufú (PPL)	9, 19 17, 19, 28
Bosque Petrificado	Callovian	Quebrada del Sapo	12
Lajas	Middle Jurassic late Aalenian/early Bajocian–early Callovian	M, Ch Sierra de Chacaico LM, PPL, PC, Puesto Bascañán, CC	5, 20 21, 22, 23 3, 4, 8, 10, 11
Cura Niyeu	early–middle Bajocian	LM Cura Niyeu	15, 16 6, 7
Los Molles	early Bajocian late Aalenian–early Bajocian early Toarcian	Charahuilla (Ch) Lohan Mahuida (LM), Los Molles (M), Co. Lotena, PPL, Puesto Policía, Co. Chacaico (CC) Sierra de Chacaico	5 3, 8, 12, 13 24
Nestares	late Toarcian	Alicurá Dam	30, 31
Sierra Chacaico	late Early Pliensbachian	Sierra de Chacaico	24
Piedra Pintada	Pliensbachian	Piedra del Aguila	1, 2
Los Patillos	late Pliensbachian–early Toarcian	Arroyo de Los Patillos	29

1, Arguijo and Volkheimer, (1985); 2, Arguijo et al. (1982); 3, García, (1998); 4, García et al. (1994); 5, García et al. (2006); 6, González-Amicón and Volkheimer, (1982a); 7, González-Amicón and Volkheimer, (1982b); 8, Martínez, (1999); 9, Martínez and Quattrocchio, (2004); 10, Martínez et al. (1999); 11, Martínez et al. (2001); 12, Martínez et al. (2005); 13, Martínez et al. (2008); 14, Quattrocchio, (1980); 15, Quattrocchio, (1984a); 16, Quattrocchio, (1984b); 17, Quattrocchio and Sarjeant, (1992); 18, Quattrocchio and Volkheimer, (1990); 19, Riding et al. (2011); 20, Scafati and Morbelli, (1984); 21, Stukins, (2011); 22, Stukins et al. (2013a); 23, Stukins et al. (2013b); 24, Volkheimer, (1973); 25, Volkheimer and Moroni, (1981); 26, Volkheimer and Quattrocchio, (1975); 27, Volkheimer and Quattrocchio, (1977); 28, Volkheimer and Quattrocchio, (1981); 29, Volkheimer et al. (1978); 30, Volkheimer et al. (1981); 31, Zavattieri et al. (2008).

As pointed out above, during Early Jurassic times the organic-walled marine microplankton assemblages were very scarce and of low diversity in the Neuquén Basin. Mainly acritarchs and prasinophytes have been identified. The first diversified dinoflagellate cyst recorded in the South American late Early Jurassic was found in the late Toarcian Nestares Formation (Zavattieri *et al.*, 2008).

### Middle Jurassic

The palynology of Middle Jurassic deposits of the Neuquén Basin has been widely studied during the last five decades. Several formations have provided well preserved

continental and marine palynofloras (Figs. 1, 2; Tabs. 1–2). The Middle Jurassic units of the Cuyo Group represent the first effective oceanic incursion into the Neuquén Embayment. These paleoenvironmental conditions led to more relatively abundant and diversified microplanktonic marine assemblages than the Liassic associations. The majority of the analyzed formations represent marginal marine environments, yielding marine assemblages mainly dominated by acritarchs (*Micrhystridium* and *Verhachium* complexes) and prasinophytes (e.g., *Cymatiosphaera*, *Pleurozonaria* and *Tasmanites*).

The Los Molles Formation, in west-central Argentina,

was carefully calibrated through the ammonite zonation. Zavala (1996b) reported the presence of ammonite fauna belonging to the *Malarguensis* Standard Zone, *Singularis* Standard Zone, and *Giebeli* Standard Zone, which suggests a late Aalenian–early Bajocian age. The marine components of the palynoflora from this formation are characterized by acritarchs (mainly Acanthomorphae) and prasinophytes; dinocysts are scarce, *Escharisphaeridia pocockii* (Sarjeant) Erkmen and Sarjeant, 1980 (Fig. 5.19) and *Cleistosphaeridium* sp. These assemblages are in agreement with a marginal-marine environment with sub-normal salinity (Martínez *et al.*, 2008).

The stratigraphic position of the Lajas Formation is given by ammonite data. The presence of *Singularis* Standard Zone, *Giebeli* Standard Zone, *Humphriesianum* Standard Chronozone, *Rotundum* Standard Chronozone, and *Vergarensis* Standard Zone suggests an early Bajocian–early Callovian age (Zavala, 1996b, Quattrocchio *et al.*, 2007). This coincides with the age proposed by Stukins *et al.* (2013a), based on dinoflagellate cyst assemblages. The Lajas dinocyst assemblages are scarce, predominating proximate forms (*Escharisphaeridia pocockii*), species indicative of euhyaline conditions (*Nannoceratopsis pellucida* Deflandre *emend.* Evitt, 1961) and opportunistic taxa, *Jansonina psilata* Martínez *et al.*, 1999 (Figs. 5.17–18), (Martínez *et al.*, 1999; Martínez and Quattrocchio, 2005). Stukins (2011) and Stukins *et al.* (2013a,b) reported an early Bajocian assemblage containing *Dissiliodinium psilatium* Prauss 1989 and *Korystocysta kettonensis* (Sarjeant) Woollam 1983 at Sierra de Chacaico. In the uppermost part of the Lajas Formation, in Portada Covunco, these authors mentioned the presence of *Rhynchodiniopsis cladophora* (Deflandre) Below 1981 in association with *Mendicodinium groenlandicum* (Pocock and Sarjeant) Davey 1979 suggesting an early Callovian age.

Cura Niyeu (at Lohan Mahuida) and Lotena formations yielded diversified and abundant dinocyst assemblages. The Cura Niyeu Formation contains ammonite faunas including lower Bajocian *Sonninia* cf. *zitteli* and *S. espinazitensis* and middle Bajocian *Chondroceras submicrostomum* and *Otoites* sp. (Quattrocchio, 1984a). The marine assemblage is mainly composed of acavate forms, such as rhaetogonyaulacoid cysts and *Nannoceratopsis* species (Quattrocchio and Volkheimer, 1990) (Tab. 1).

Lotena palynological marine associations have been recovered from Puente Picún Leufú and Portada Covunco (Quattrocchio and Sarjeant, 1992; Martínez and Quattrocchio, 2004). These sediments are considered as mid–late Callovian in age (Groeber *et al.*, 1953; Stipanovic, 1969; Riccardi *et al.*, 1990; Riccardi 2008) on account of the ammonite identified in the former locality, *Rehmannia (Loczyceras) patagoniensis* (Dellapé *et al.*, 1979). The Lotena Formation at the Portada Covunco section lacks ammonite faunas, however the underlying Lajas Formation yielded *Eurycephalites* cf. *vergarensis*, which is characteristic of the *Vergarensis* Chronozone, and suggests an early Callovian age (Riccardi *et al.*, 1989, 1990; Riccardi, 2008). The organic-walled marine microplankton of this unit is characterized by the appearance of chorate cysts (Quattrocchio and Volkheimer, 1990; Quattrocchio and Sarjeant, 1992). Riding *et al.* (2011) restudied the palynological samples of the localities mentioned above, and refined the biostratigraphy based on the dinocyst assemblages. These authors suggested a late Callovian age taking into account the first appearance of *Limbodinium absidatum* (Drugg) Riding 1987, *Wanaea a-collaris* Dodekova 1975, and *Scriniodinium crystallinum* (Deflandre) Klement 1960.

The Bosque Petrificado Formation (Zavala and Freije, 2002= “Challacó” Formation of Zavala and González, 2001) lacks ammonite control; however, it has been correlated with the basal part of the Lotena Formation. Thus, a Callovian age was suggested for these strata (Zavala and Freije, 2002), which was later confirmed by palynological studies (Martínez *et al.*, 2005). At the Quebrada del Sapo section this unit yielded a marginal marine assemblage characterized by *Escharisphaeridia pocockii* and *Micrhystridium* complex (Martínez *et al.*, 2005).

### Late Jurassic

Four units provided well preserved continental and marine palynofloras: Lotena, Auquilco, Vaca Muerta and Picún Leufú formations. However, the most diversified dinocyst assemblages were found in the Vaca Muerta and Picún Leufú formations (Figs. 1, 2; Tabs. 1–2).

Olivera *et al.* (2010) suggested marginal marine conditions at least until the latest Oxfordian–early Kimmeridgian for the Lotena Formation at Picún Leufú sub-basin (Barda

Norte locality), based on the presence of organic-walled marine microplankton and foraminifers.

The Auquilco Formation at Portada Covunco, late Oxfordian in age (Volkheimer and Moroni, 1981) bears a well preserved palynoflora deposited in a near shore marine environment. The microplankton is scarce and of low diversity, exclusively represented by acritarchs Sphaeromorphytae (*G. granulatus*, *Leiosphaeridia* sp. cf. *L. variabilis*, *Hyalinsphaeridia* cf. *hyalina*) and Acanthomorphytae (cf. *Baltisphaeridium* sp.).

The Vaca Muerta Formation has already been studied palynologically at Caichigüe and Puente Picún Leufú (Volkheimer and Quattrocchio, 1975, 1977; Quattrocchio, 1980; Quattrocchio and Volkheimer, 1990; Quattrocchio and Sarjeant, 1992). Fragmentary ammonites assigned to *Virgatosphinctes* sp. found in the Caichigüe area, together with correlation with the fossiliferous beds of the near locality of Charahuilla, suggest an early Tithonian age (Volkheimer and Quattrocchio, 1975). The marine association recovered from these sediments is widely dominated by acritarchs and prasinophytes, whereas dinocysts are very scarce (Volkheimer and Quattrocchio, 1977).

The lower part of the Vaca Muerta Formation sequence at Puente Picún Leufú yielded ammonites, including *Choicensiphinctes choicensis* (Burckhardt) and *Torquatisphinctes* sp. belonging to the *Virgatosphinctes mendozanus* Zone (Burckhardt 1900) of the latest early to middle Tithonian (Riccardi, 2008). This formation includes younger strata towards the centre of the Neuquén Basin (Leanza in Quattrocchio and Sarjeant, 1992). The organic-walled marine microplankton from the middle part of the Vaca Muerta Formation at the Puente Picún Leufú section shows similar proportions of dinocysts and acritarchs/prasinophytes suggesting a shallow marine environment (Quattrocchio and Sarjeant, 1992).

At the southeastern margin of the basin, the Vaca Muerta Formation is overlain by the shallow marine carbonates and siliciclastic sediments of the Picún Leufú Formation. A few ammonite levels yielding *Subdichotomoceras*, *Lytohoplites*, *Corongoceras* and *Substeueroeras* in the type locality, Picún Leufú Creek, suggest these sediments range between late middle Tithonian and early Berriasian in age (Armella *et al.*, 2007). The Picún Leufú Formation shows an increase in dinocyst diversity when compared with the

Vaca Muerta Formation. Moreover, several endemic taxa, such as *Aptea notialis*, *Diacanthum argentinum*, *Paraevansia mammillata* and *Pilosidinium cactosum*, were defined in this formation by Quattrocchio and Sarjeant (1992).

## DISCUSSION

At the global scale several authors have recognized the presence of two realms (Boreal and Tethyan) during the Early Jurassic, based on different ammonite, foraminiferal, brachiopod and calcareous nannofossil assemblages (in Bucefallo Palliani and Riding, 1999). From a palynological point of view, many diversified Early Jurassic dinocyst assemblages have been reported from these faunal provinces, mainly from the Northern Hemisphere. Some of these citations include *Dapcodinium* from the Hettangian stage and *Liasidinium* from the late Sinemurian in southwestern Germany (in Zavattieri *et al.*, 2008), *Luehndea*, *Mancodinium*, *Mendicodinium*, *Nannoceratopsis*, *Scrinocassis*, among others, from the Pliensbachian and Toarcian of many European localities (in Bucefallo Palliani and Riding, 1999), and the *Parvocysta* suite, including *Phallocysta*, throughout the late Toarcian of northern East Siberia (Riding *et al.*, 1999). These authors postulated that a mutual exchange of taxa occurred between the Boreal and Tethyan realms since the Pliensbachian. These migrations were possible due to the opening of an epicontinental passageway between Greenland and Norway named Viking Corridor (Fig. 3). Even though it is true that the dinocyst assemblage from the Nestares Formation shares more components, at a genus level, with northern East Siberian than with north-western Australian (Riding and Helby, 2001) assemblages, it is quite different from both assemblages. The reason the southern Neuquén Basin (Alicurá Dam) assemblages are unlike any other late Toarcian dinocyst associations may probably be due to the paralic bay depositional setting of the Nestares Formation.

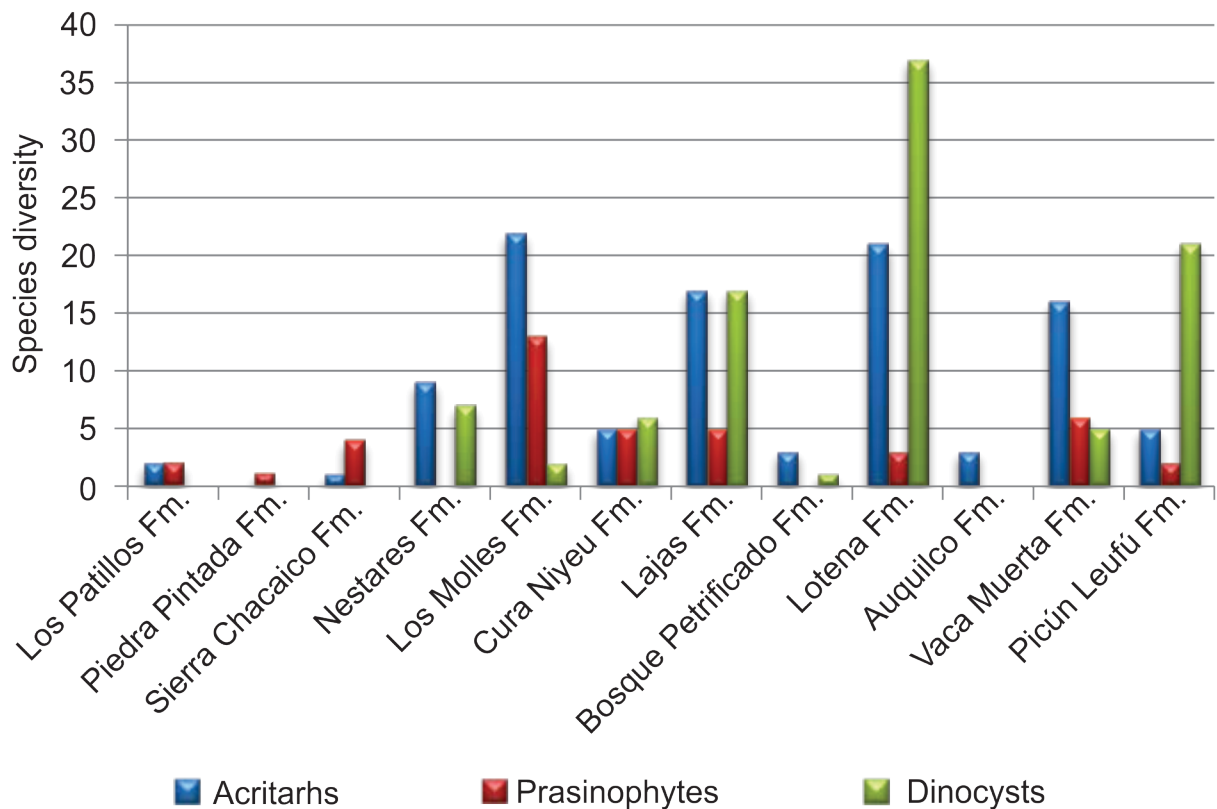
A plausible migration route of this marine biota might have been the Trans-Pacific route of Aberhan (2001) because the Hispanic Corridor mainly acted as a filter at this time; a latitudinal exchange surrounding Pangea would not be expected due to the presence of the Jurassic climatic zones proposed by Parrish (1992). Moreover, the absence of an active subduction zone immediately to the west of South America at this time would have allowed the trans-

pacific interchange (Howell *et al.*, 2005) (Fig. 3).

In summary, the scarcity of dinoflagellate cysts during the Early Jurassic in the Neuquén Basin was probably related to the paleogeographic configuration of the basin. During the earlier Jurassic Pre-Cuyo Group the paleogeography showed the dominance of isolated rift depocenters (Vergani *et al.*, 1995; Howell *et al.*, 2005). This context partially remained for the lower Cuyo Group deposits. The interconnection among the different depocenters would have been scarce with the development of relatively small basins with variable salinity and low oxygenated water conditions. This environment was highly unsuitable for the proliferation of cyst-forming dinoflagellates (van de Schootbrugge *et al.*, 2005 and references therein). Thus, these eco-

logical niches were colonized by green algae, including prasinophytes and acritarchs (Figs. 4, 5.1–14).

Since the late Toarcian, the isolated rift depocenters of earlier Jurassic times were gradually amalgamated into a single, broad basin. These paleoenvironmental conditions continued until the Early Cretaceous (Vergani *et al.*, 1995). The presence of this single basin allowed the development of relatively more diversified organic-walled marine microplankton assemblages (*i.e.*, acritarchs, prasinophytes and dinocysts) during the Middle Jurassic. The marine paly-nofloras were mainly dominated by acritarchs and prasinophytes during the Aalenian–early Callovian (Cuyo Group) when the marginal condition prevailed in the marine environment. The most diversified Jurassic dinocyst assem-



**Figure 4.** Histogram showing the distribution of the organic-walled marine microplankton (acritarchs, prasinophytes and dinocysts) from the units considered in this study.



blages have been reported from the late Callovian Lotena Formation which suggests the predominance of non-restricted open marine conditions in the Neuquén Basin at that time (Figs. 4, 5.20–26, 6.1–9; Tab. 1). A similar increase in dinoflagellate cyst diversity was reported for the late Callovian sequences of Europe (Riding *et al.*, 2010). The main affinity of the Lotena dinocyst association was inferred as European, suggesting a free movement via the Hispanic seaway (Riding *et al.*, 2011) which is reinforced by the presence of some cosmopolitan forms, such as *Gonyaulacysta jurassica* (Deflandre) Norris and Sarjeant 1965 and *Scriniodinium crystallinum*, in this palynoflora (Martínez and Quattrocchio, 2004). However, the presence of *Dissiliodinium volkheimeri* Quattrocchio and Sarjeant 1992 (Fig. 5. 26) a taxon confined to the Southern Hemisphere (Riding *et al.*, 2011) is worth noting. Mantle (2009) reported its first worldwide occurrence from the northern Bonaparte Basin, Timor Sea (Australia), from the *Wanaea indotata* Interval Zone (middle Bathonian–early Callovian) through the *Voodooia tabulata* Interval Zone (late Callovian). Thus, a connection from northern Australasia to the Neuquén Basin via the Mozambique Corridor cannot be entirely ruled out.

The next widespread Paleopacific marine transgression in the Neuquén Basin consists of bituminous shales, marls and limestones of the Vaca Muerta Formation (Legarreta and Uliana, 1991, 1996). There is a decrease in dinocyst diversity and an increase in the acritarchs and prasinophyte content in the Vaca Muerta Formation compared with the Lotena Formation (Quattrocchio, 1980; Quattrocchio and

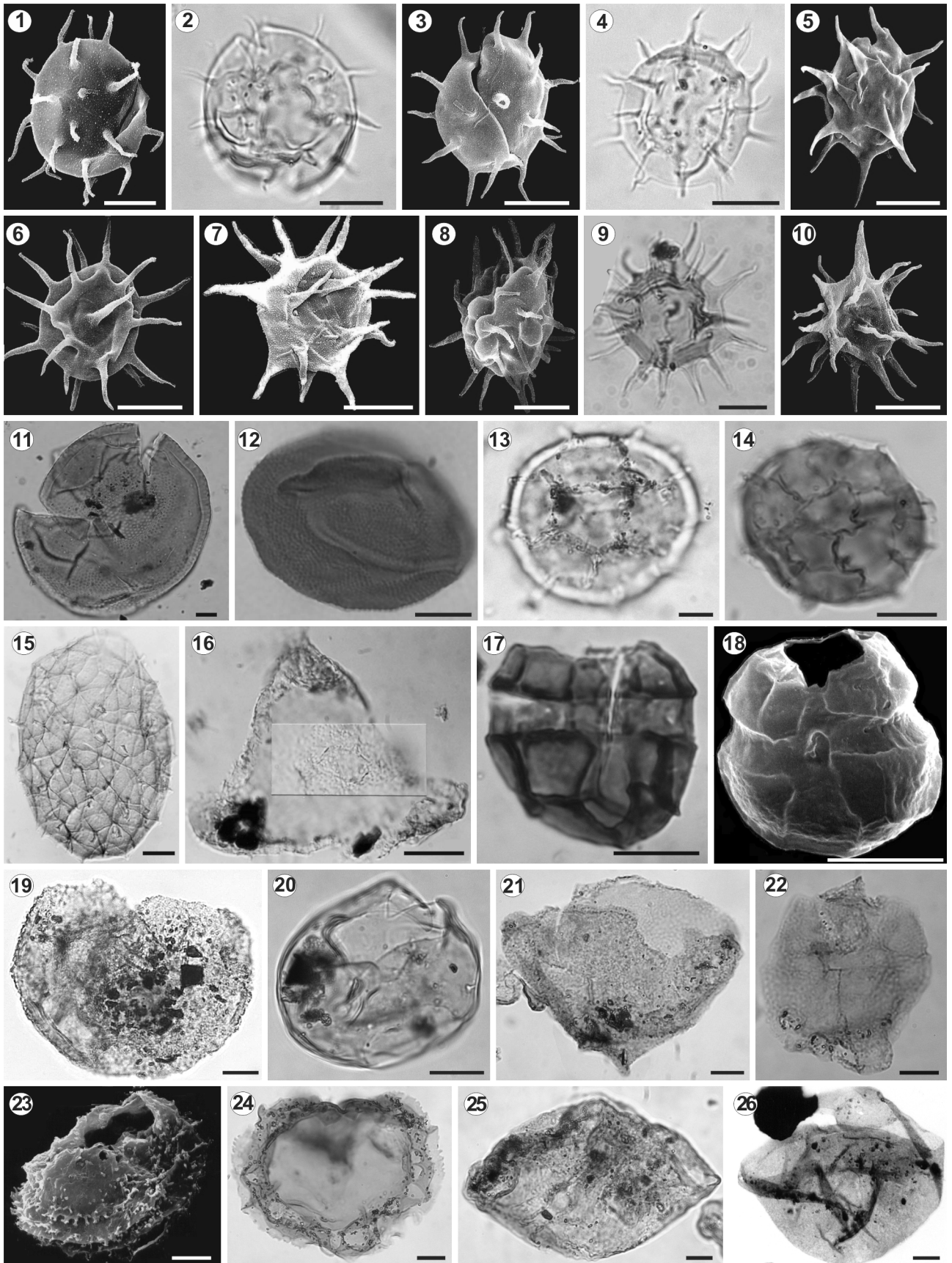
Volkheimer, 1990; Quattrocchio and Sarjeant, 1992), which may be related to the anoxic to dysoxic environmental condition that prevailed during the deposition of the Vaca Muerta Formation (Figs. 4, 6.15–16.18 Tab. 1). Studies on modern dinoflagellates have shown that oxygen availability exerts a strong control on cyst germination, with anaerobic conditions completely inhibiting the excystment of most taxa (Candel *et al.*, 2013 and references therein).

It may be argued that oxygen availability is one of the most important factors in controlling the diversity and abundance of benthic biota. The relative increase in dinocyst diversity in the Picún Leufú assemblages might be correlated with a more oxygenated condition of the water column at that time, compared with the underlying formation (Figs. 4, 6.10–14.17; Tab. 1).

The distribution of the cosmopolitan and endemic taxa is influenced by the ecology of the environment (Valentine, 1973). The Picún Leufú Formation was deposited during a highstand system tract and comprises a wide range of sub-environments within the whole marginal marine system (Armella *et al.*, 2007). As mentioned by Götz *et al.* (2005) during the highstand phase, the environmental conditions stabilize and the biota becomes more diverse, therefore the main mechanism of this enrichment is speciation of endemic taxa. This context highly correlates with the presence of several endemic species recorded in the Picún Leufú strata.

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Figure 5. 1–2, *Michrystidium brevispinosum*; 1, UNSP LM 1312 (from Martínez *et al.*, 2001); 2, UNSP BN 1957c (from Olivera *et al.*, 2010); 3–4, *Michrystidium recurvatum* forma *recurvatum*; 3, UNSP LM 1312 (from Martínez *et al.*, 2001); 4, UNSP BN 1957c (from Olivera *et al.*, 2010); 5, *Michrystidium fragile*, UNSP LM 1312; 6, *Michrystidium inconspicuum*, UNSP LM 1312; 7, *Michrystidium placophorum* UNSP LM 1312; 8, *Michrystidium echinoides* UNSP LM 1312 (5–8, from Martínez *et al.*, 2001); 9, *Baltisphaeridium* sp., UNSP LM 1312f, EFco: R43/4; 10, *Polygonium* sp., UNSP LM 1312 (from Martínez *et al.*, 2001); 11, *Tasmanites* sp., UNSP PL 1429a; 12, *Pleurozonaria* cf. *P. picunensis*, UNSP PL 1429CAN; 13, *Cymatiosphaera* sp. 2, UNSP PL 1466a; 14, *Cymatiosphaera* cf. *C. volkheimerii*, UNSP PL 1429CAN (11–14, from Martínez *et al.*, 2005); 15, ?Suessiaceae indet. MPLP 7235E; 16, *Parvocysta* sp. MPLP 7187A (15–16, from Zavattieri *et al.*, 2008); 17–18, *Jansonis psilata*, UNSP LM 1312 (from Martínez *et al.*, 1999); 19, *Escharisphaeridia pocockii*, UNSP PL 1429c (from Martínez *et al.*, 2005); 20, *Chytroisphaeridia chytroides*, UNSP PC 1525d, EFco: O22/1; 21, *Wanaea acollaris*, UNSP PL 2971/2 (from Riding *et al.*, 2011); 22, *Ambonosphaera? staffinensis* UNSP PL 2970/8, EFco: H39; 23, *Lithodinia jurassica* subsp. *reburrosa* UNSP PL 2970 (from Quattrocchio and Sarjeant, 1992); 24, *Limbodinium absidatum*, UNSP PL 2971/7 (from Riding *et al.*, 2011); 25, *Mendicodinium groenlandicum*, UNSP PL 2971/7, EFco: E39/1; 26, *Dissiliodinium volkheimeri* UNSP PL 2970 (from Quattrocchio and Sarjeant, 1992). Scale bar = 10µm. Acronyms: UNSP (Universidad Nacional del Sur, Palinología); MPLP (Mendoza-Paleopalintoteca-Laboratorio de Palinología).



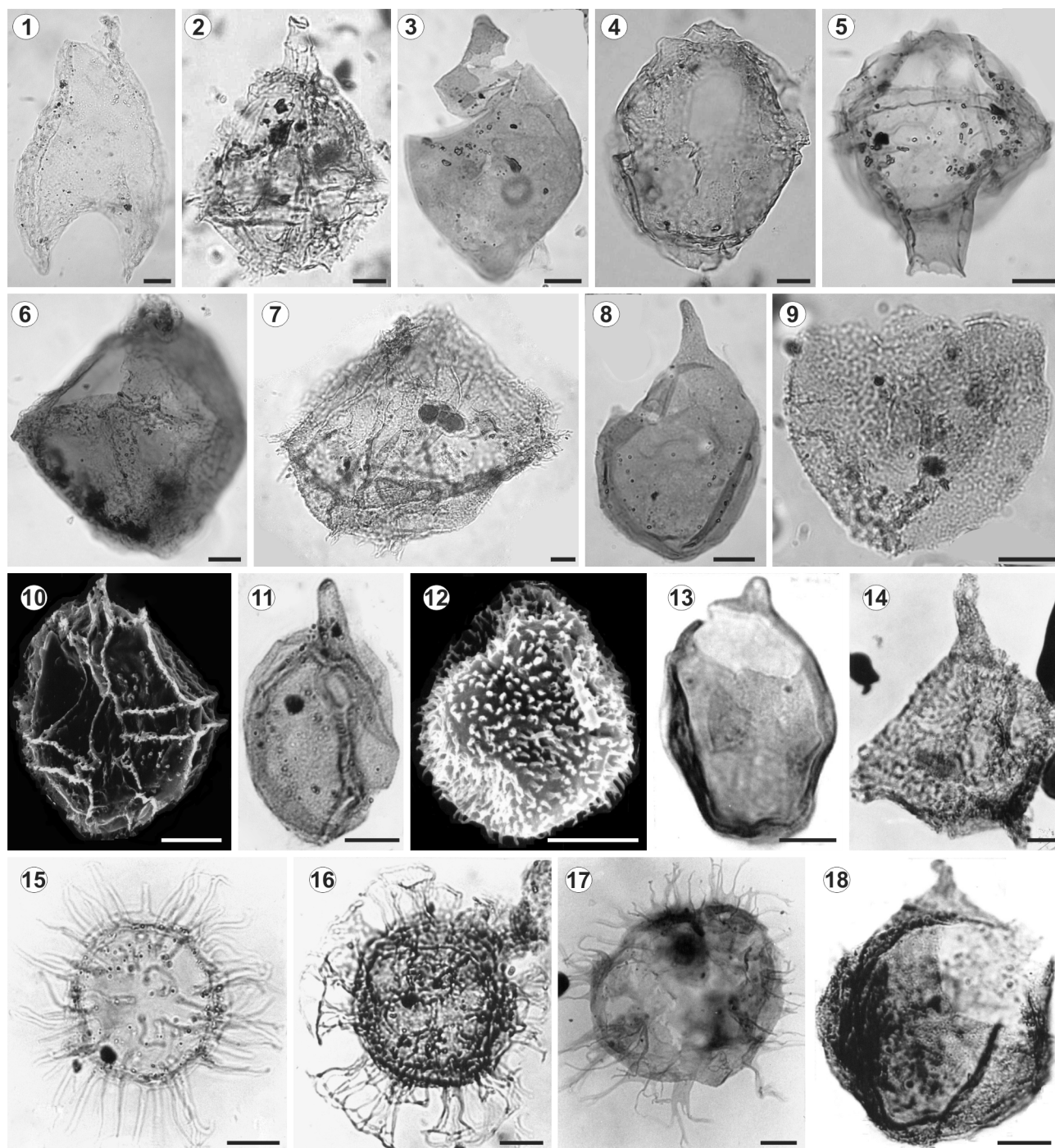


Figure 6. 1, *Nannoceratopsis pellucida*, UNSP PL 2971/3 (from Riding *et al.*, 2011); 2, *Gonyaulacysta jurassica* subsp. *adecta*, UNSP PC 1525b (from Martínez and Quattrocchio, 2004); 3, *Protobatioladinium* cf. *P. lindiensis*, UNSP PL 2971/3 (from Riding *et al.*, 2011); 4, *Scriniadinium crystallinum*, UNSP PC 1525c (from Martínez and Quattrocchio, 2004); 5, *Tubotuberella dangeardii*, UNSP PL 2971/7; 6, *Endoscrinium* cf. *E. galeritum* subsp. *reticulatum*, UNSP PL 2971/7; 7, *Rynchodiniopsis cladophora*, UNSP PC 1525d; 8, *Pareodinia ceratophora*, UNSP PL 2971/4 (5–8, from Riding *et al.*, 2011); 9, *Lithodinia deflandrei*, UNSP BN 1959c (from Olivera *et al.*, 2010); 10, *Rynchodiniopsis* cf. *setcheyensis*, UNSP PL 2966; 11, *Pareodinia ceratophora* var. *pachyceras*, UNSP PL 2965/1; 12, *Pilosidinium cactosum*, UNSP PL 2966; 13, *Paraevansia mammillata*, UNSP PL 2967/2; 14, *Aptea notialis*, UNSP PL 2966/2; 15, *Cleistosphaeridium lumectum*, UNSP PL 2970/4; 16, *Hystrichosphaerina neuquina*, UNSP PL 2965/6A; 17, *Systematophora pinicillata*, UNSP PL 2966/1; 18, *Milloudodinium nuciforme* UNSP PL 2969/4 (10–18, from Quattrocchio and Sarjeant, 1992). Scale bar= 10µm.

## CONCLUSIONS

This paper summarizes all available marine palynological information from the Jurassic units of the Neuquén Basin and constitutes our state of the art view of this topic.

The distribution of the Jurassic organic-walled marine microplankton of the Neuquén Basin is closely related to the paleoenvironmental conditions and the configuration of the basin, as well as to the global and local ocean circulation patterns.

The Early Jurassic units are highly dominated by green algae, including prasinophytes and acritarchs, with very scarce dinoflagellate cysts. This kind of marine palynoflora could correspond to the configuration of the basin which was characterized by different depocenters with scarce interconnections. The Nestares Formation is the only exception with a relatively diversified dinocyst assemblage. A possible migration route of the cosmopolitan marine biota recovered from this unit might have been the Trans-Pacific route, due to the Hispanic Corridor which mainly acted as a filter at that time.

The diversification of the organic-walled marine microplankton recorded in Middle Jurassic units could be the result of the fusion of the Early Jurassic rift depocenters into a single late Toarcian basin, increasing the number of niches available for colonization.

During the Middle Jurassic, two main pulses of marine microplankton diversification can be recognized. In the first one (Aalenian–early Callovian), the assemblages were mainly dominated by acritarchs and prasinophytes. These palynofloras were recovered from the marginal-marine Cuyo Group deposits. The second great episode of flooding in the basin marks the beginning of the second pulse, when more open-marine conditions were established. In this context, the late Callovian Lotena assemblages exhibit the highest dinoflagellate cyst diversity of all the Jurassic units. Two possible migration routes can be recognized for the main biota interchange: the Hispanic Corridor seaway, due to the European affinity of the associations, and the Mozambique Corridor, due to the record of *Dissiliodinium volkheimeri* that was only recognized in both the Bonaparte (Australia) and Neuquén (Argentina) basins, suggesting a possible Australian connection.

The diversity of the Late Jurassic dinocyst assemblages

shows a decrease in regard to the older Lotena assemblages. The anoxic to dysoxic environmental conditions that prevailed during the deposition of the Vaca Muerta Formation controlled the composition of the organic-walled marine microplankton assemblages, dominated by acritarchs and prasinophytes. On the other hand, the relative increase in dinocyst diversity of the Picún Leufú assemblages could be related to well-oxygenated and well-mixed bottom waters.

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